PREFACE

Vertebrate evolution is one of the most extraordinary stories of life on Earth. It is all the more engaging because we ourselves emerge within that vast and rich history. Therefore, when students first meet the subject, they already have some vested interest in the subject of vertebrates. We can take advantage of this built-in interest about the history of vertebrate life to showcase how science unravels the associated mysteries.

Today, biology has emerged as the central science at the intersection of the natural sciences, with implications for the humanities and social sciences. And vertebrate morphology, in particular, is well-placed within a modern biology curriculum to advance student appreciation of science and to gain personal insights through its study. Students usually enter the course after some background in science, but at a point in their academic training when they should move beyond memorizing facts as an end in itself. Instead they should be challenged to evaluate and understand larger concepts and themes. In particular, vertebrate morphology can be studied to better understand the process of science as it applies to vertebrate form and function. The organization of this book supports and encourages students to do so.

This textbook was written from the ground up. From the first edition to this third edition, the organization of the book is intended to support and encourage students to be actively engaged in the material.

Pedagogy—The Art and Science of Teaching and Learning

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.
- Important literature is cited at the end of each chapter, and **Web links** connect them to further references and resources on the book's website at www.mhhe.com/zoology (click on this book's cover).
- Boxed essays are included in most chapters 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 engaged directly 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, 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. Students often expect that today we have the final answers. Students implore, "Just tell me what the answer is." 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 to be settled. But we know that science is a process of refinement, challenge, and sometimes revolutionary change. One boxed essay sets forth the case for dinosaur endothermy. That debate spawned further investigation that now returns to challenge such a view. Another boxed essay presents this newer and contraire 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 and 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, that 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 the axial skeleton, and the type of locomotion—flight, cursorial, or burrowing. The cardiovascular system, especially in organisms that exploit water and air, illustrates the close relationship between vascular morphology and the physiological flexibility it 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.

Coherence

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 that embryonic processes play in vertebrate evolutionary events.

The remaining chapters, chapters 6 through 18, develop each major system. Besides carrying overall themes, each chapter follows a consistent organization internally. 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 throughout.

New to the Third Edition

I am again indebted to colleagues who shared their thoughtful and critical comments on the second edition. It was a particular delight to hear from so many students who volunteered their enthusiasm and suggestions. When revising, I kept in mind the features and basic organization that won praise and helped present the delights of comparative vertebrate morphology to a new audience. In particular, I retained the emphasis on function and evolution of vertebrates that grows out of the anatomical detail. In addition, I retained the basic organization of the richly illustrated text. New developments and careful editing have also been incorporated or enhanced in this edition.

Phylogenetic Approach

Vertebrate groups are placed within a phylogenetic framework. This vertebrate phylogeny is established in chapter 3, and the evolution of organ systems refers to this phylogeny in subsequent chapters.

New Fossils and Phylogenies

Within the last few years, remarkable fossils have been discovered, some from the very dawn of vertebrate evolution. Others mark the evolution of dinosaurs and the birds that emerged within them. Analyzed by cladistic means, these fossils, together with larger databases of features, provide a clarifying picture of vertebrate evolution. These new phylogenies have been incorporated, especially as they revise our understanding of early vertebrate evolution, the early evolution of tetrapods, and the taxonomic relationships of reptiles.

Form and Function

Vertebrate morphology continues to benefit from new and advanced technologies that permit evaluation of performance: how form and function meet demands of the environment. These new views on function have been incorporated, especially on flight, terrestrial locomotion, respiratory mechanisms, cardiovascular performance, and the nervous system.

Chapter Overviews

An overview has been added at the end of most chapters. To claim the material as their own, students may compose, under their own efforts, a summary of the factual information within chapters. This engages them in the material, focuses their reading, and makes them active learners. To aid this effort, I have provided overviews, a general review of the material, drawing attention to the major conceptual points and their implications developed within the chapter.

Updated Information and Figures

Chapter 1 (Introduction)

The popular historical overview has been retained to survey the parallel development of evolutionary and morphological theory. However, the geological time scales have been updated. "Tools of the Trade" preserves a discussion of technology that serves morphological studies, including the basic methodology of cladistics.

Chapter 2 (Origin of Chordates)

Evidence derived from anatomical and molecular (DNA, proteins) clues provides new insight into chordate origins and relationships. These are included along with new figures and text.

Chapter 3 (The Vertebrate Story)

Science is a process of ongoing research. Nowhere, perhaps, is that more evident than in phylogenetics, the analysis of vertebrate relationships. Construction of phylogenetic hypotheses, via cladistics, is one of the major additions to functional and evolutionary morphology. Thus, the basics are included. However, as with other subjects, I leave it to instructors to decide what to emphasize in their courses.

Challenges to existing phylogenies arrive almost every Monday morning with the publication of new journals carrying new phylogenies. For example, as I wrote (rewrote) the phylogenies of early vertebrates, I had half a dozen phylogenies, many contradictory, from which to choose. This is as it should be within such a vigorous area, newly armed with the important techniques of phylogenetics. Here competing phylogenies, techniques, and databases (morphological, molecular) are rivals to insight into animal evolution. Students need to be prepared for new phylogenies (they arrive almost daily) rather than committing one to memory forever. They also need to remember that rigorous and careful taxonomists produce phylogenies that are no better than the tricky molecular or morphological databases from which they are built.

This chapter includes these newer phylogenies, and introduces students to the major taxonomic groups that express the radiation within vertebrate historical lineages.

Chapter 4 (Biological Design)

Biomechanics and biophysics, even simple principles, provide remarkable insights into animal design. This chapter provides some simple principles, illustrates them, and then returns to these in later chapters where they can be applied. This also represents one of the important changes in the study of animal (and plant) architecture and functional morphology. As in other disciplines, quantitative analyses have become a larger part in the biological treatment of organisms.

Chapter 5 (Life History)

This chapter has been edited, material added, and new illustrations prepared. In particular, amphioxus embryology is re-illustrated, heterochrony has been rewritten and re-illustrated, and the historical significance of the "biogenetic law" revisited.

Chapter 6 (Integument)

A section on horse hooves has been added, accompanied by new art, and a revision of the horns and antler illustrations have been revised.

Chapter 7 (Skull)

The text in this chapter has received extensive revision, incorporating new information, and bringing the discussion of the skull within a current phylogenetic context.

Many of the figures have been relabeled and revised, and new art has been included on the evolution of the synapsid skull. This further supports the extraordinary story of the evolutionary transformation of bones of the skull from feeding to hearing functions.

Chapter 8 (Axial Skeleton) and Chapter 9 (Appendicular Skeleton)

These chapters maintain the successful integration of anatomy and function. The transition from water to land is followed, and the recent theories of the intermediate stages are discussed. Many of the figures have been revised to improve their presentation and accuracy. A new section with accompanying art is included on flight aerodynamics, correcting the widely misunderstood views attributed to Bernoulli.

The human skeleton is especially considered for the unique engineering problems presented by the upright carriage of our own axial and appendicular skeletons.

Chapter 10 (Muscular System)

Figures have been rearranged and relabeled to better present special aspects of the muscular system. The text has been revised to clarify the explanations and more accurately represent current views.

Chapter 11 (Respiratory System)

Along with updating revisions of the text, the figures have been revised to better illustrate functional and evolutionary aspects of the respiratory system. A revised discussion of gill and lung ventilation clarifies the basic methods of respiration, especially in vertebrates that are transitional between water and air.

Chapter 12 (Circulatory System)

To improve presentation, many figures have been revised and rearranged. New art is included that shows the evolution of the major aortic arch system. The text has been edited and updated throughout.

Chapter 13 (Digestion), Chapter 14 (Urogenital System), and Chapter 15 (Endocrine System)

These chapters have been updated, with many figures modified and special attention paid to the revision of ruminant digestion. Castration not only produces better horses and roosters, but also better opera singers, as we are told in a chapter 15 boxed essay.

Chapter 16 (Nervous System)

The functional significance of parts of the nervous system has been revised extensively, especially of the higher brain centers. The tables and figures have been edited, and the evolution of the vertebrate cerebral hemispheres revised.

Chapter 17 (Sensory Organs)

Illustrations in this chapter have been revised to improve clarity and detail. Further, the evolution of the tympanic ear has been completely revised, bringing this up to date and giving notice to the multiple times such a vertebrae ear evolved.

Chapter 18 (Conclusions)

The concluding chapter again brings together the larger issues illustrated throughout the textbook and summarizes the modern themes of evolutionary and functional biology.

End Material

The appendices have been edited and the classifications updated.

Supplements

Newly and substantially revised, *Comparative Vertebrate Anatomy: A Laboratory Dissection Guide,* Thrid Edition, by Ken Kardong and Edward Zalisko, is now available. Almost half of the major labeled illustrations have been replaced with new art. These new figures appear throughout the dissection guide, but especially in the muscular, digestive, circulatory, respiratory and soft-tissue systems. At the end of this dissection guide, the authors added what we believe to be a novel, but effective supplement—a *Student Art Notebook*. In fact, this innovation was suggested by students who used the previous edition. 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/zoology (click on this book's title to access it.) 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 masters. The website also includes several functional labs, and will be updated regularly to post new information on vertebrate phylogenies, function, and evolution.

Digital Zoology is a new and 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.

BioCourse.com is an electronic meeting place for students and instructors. It provides a comprehensive set of resources that is up-to-date and easy to navigate. Visit BioCourse.com, and set up your account and password to access a variety of valuable tools. BioCourse.com sorts information into these main categories:

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Student Center—information for students, including: study aids; resume writing and information on jobs and internships; graduate school options; information for MCAT and other tests; and links to content websites by topic.

R & D Center features our newest simulations, animations, and other teaching and learning tools. This portion of our site allows faculty members and students to try out our materials as they are being developed.

BioLabs features materials for lab students and instructors. Tools for students include: dissection techniques, equipment tutorials, and safety and setup procedures. Tools for instructors include: lab preparations, lab support, and simulations.

Lifelong Learning Content Warehouse is a powerful indexing tool and hierarchical outline of content resources for searching by students and faculty. Users can search by topic through a "content warehouse" featuring text material, activities, visuals, and animations to learn more about a selected topic.

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During the preparation of this new edition, many colleagues kindly fielded my questions, shared their special knowledge, and volunteered their challenges to my interpretations of the functional and evolutionary significance of vertebrate morphology. This, the third edition, is the next installment of a work in progress. My hope is that these colleagues will see, if not their point of view, at least their influence within this edition, and accept my sincere thanks for their thoughtful suggestions and criticisms. In particular I recognize and am especially grateful to the following individuals: Warren Burggren (University of Nevada), T. H. Frazzetta (University of Illinois), James Hanken (Harvard University), Susan W. Herring (University of Washington), Linda Z. Holland (Scripps Institution of Oceanography), R. Glenn Northcutt (University of California, Scripps), John A. Ruben (Oregon State University), Anthony P. Russell (University of Calgary), Tamara L. Smith (Washington State University), Jeanette Wyneken (Florida Atlantic University), Edward J. Zalisko (Blackburn College), and G. A. Zweers (University of Leiden).

It is a special pleasure to work again with an artist as careful and creative as L. Laszlo Meszoly (Harvard University), who kindly contributed new illustrations to this edition.

I am indebted to the patient, able, and good-humored people at McGraw-Hill who were so important in seeing this edition through to the book you now hold in your hands. Among these, I wish to recognize especially Donna Nemmers and Marge Kemp. To friends and family I remain grateful, especially to Willemina J. Kardong, who helped, encouraged, tolerated, and supported during the various editions of this book.

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