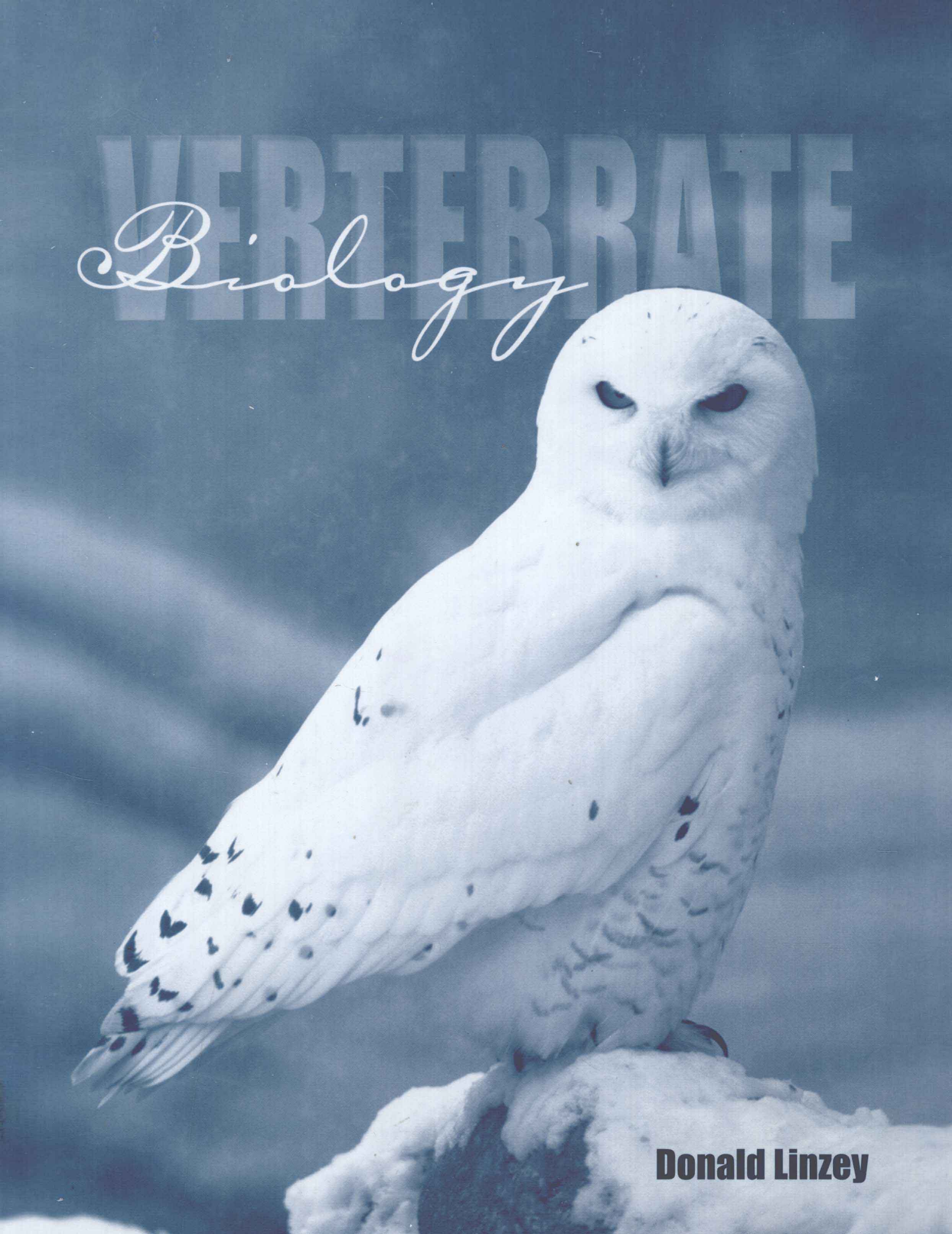
VERTEBRATE Biology



Donald Linzey

VERTEBRATE Biology

Donald Linzey

Wytheville Community College

With editorial contributions by

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VERTEBRATE BIOLOGY

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Cover image: The snowy owl (*Nyctea scandiaca*) is a diurnal arctic owl that winters as far south as the northern United States but which may occasionally winter as far south as South Carolina, Georgia, Louisiana, Texas, and California. Most adult birds are almost pure white. The large size (length to 27 inches; wingspan to 66 inches), pale plumage, and lack of ear tufts are diagnostic. Snowy owls prefer rolling to flat tundra and spend much of their time on such lookouts as banks, boulders, or knolls. When they visit the United States in winter, they are found in marshes, in dune areas, and in open farmland, where they perch on haystacks and buildings, seldom on trees. They feed on lemmings and other rodents and rabbits. Populations are cyclic, with population peaks occurring about every 4 years.

The snowy owl breeds from the Bering Sea to Greenland as well as in northern Russia and Siberia. The nest is a depression in the soil or is located on a rocky shelf and is thinly lined with moss and feathers. It is located on the higher, drier spots in rolling tundra. A normal clutch consists of 5 to 8 white eggs.

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VERTEBRATE *Biology*

To my wife, Nita, whose love and enduring patience have made this work possible.

Preface to the Instructor

Vertebrate Biology is designed to provide a firm foundation for students interested in the natural history of vertebrates. While this may be the only course that some students will take dealing with the biology of vertebrates, othes will subsequently enroll in more specialized courses such as ichthyology, herpetology, ornithology, and mammology.

In writing *Vertebrate Biology,* I have tried to keep the needs and wishes of both instructors and students in mind. As an instructor for more than 35 years, I know how challenging it is to teach a dynamic, balanced, up-to-date course that is both relevant and interesting to students. I'm sure you feel the same way. A book that draws the reader's attention facilitates learning and an interested student is an avid learner. As instructors, our job is to guide students in their learning process.

As this text was taking shape, I pondered its length. If I wrote a short textbook, many topics would have to be omitted, and it would not meet the needs of many instructors. If I wrote a larger book, I could include more topics, discuss certain ones in more detail, and even include some supplemental information that would be interesting but not absolutely essential. I chose the latter course.

In order to keep the book to a reasonable length, most concepts are illustrated by one or two good examples for each group to which the concept applies rather than a catalog of many possible ones. It is my hope that you will utilize these examples to stimulate discussion of these concepts with your students. The structure of the text allows for flexibility in presenting the material and permits it to be adapted to a wide range of teaching styles. Chapters need not be taught in order but can be adapted to any sequence that best meets your curriculum.

Vertebrate biology is a broad field: there is no reason to ignore parts that may be currently unpopular or that do not engage us personally. Therefore, I have tried to achieve balance in terms of the whole field of vertebrate biology: systematics, paleontology, physiology, ecology, etc. I have also tried to achieve balance both taxonomically and geographically.

Following each chapter are several questions designed to encourage your students to apply what they have learned. You can use these in various ways: for discussion, for out-of-class assignment, or as potential short essay questions on tests.

Also at the end of each chapter is a list of supplemental readings and a listing of World Wide Web sites relevant to the material in that particular chapter that you (as well as your students) might find of interest. These can be used as a guide to the literature for student papers or used as a source of additional information on a topic of particular interest. All web addresses listed are up-to-date as of press time, and are, for the most part, maintained by universities, governmental agencies, institutions, museums, etc. Thus, the information they contain should be accurate and the web site should be more-or-less permanent. These addresses can be found as "hot links" by visiting the publisher's web page at www.mhhe.com/zoology.

I have tried to keep the vocabulary as plain as possible for the sake of clarity. I see no reason to use extensive technical terminology when simpler words will suffice. The use of technical terms is unavoidable in some cases, but when overdone, it makes the learning process more difficult for the student. Lucidity has been one of the two major goals of my writing. Interest for the reader has been the second goal.

Almost any textbook is certain to have some typographical and other errors. Although all errors are my sole responsibility, I would like to request your help in improving future editions of this book. Please send any errors you find, and your comments and suggestions for improvements, to Marge Kemp, Sponsoring Editor, Life Sciences, c/o McGraw-Hill Publishers, 2460 Kerper Blvd., Dubuque, Iowa 52001. She will send them to me. Please be assured that all comments and suggestions will be given serious consideration. As time allows, I will respond personally.

Thomas Jefferson once said that, "...difference of opinion leads to inquiry, and inquiry to truth." It is my hope that *Vertebrate Biology* will stimulate inquiry among our students and will enable them to become better informed future biologists.

Donald W. Linzey

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Finally, I thank my wife, Nita, for putting up with the piles of books, correspondence, and manuscript sections that cluttered several rooms of our home for varying periods of time. Her understanding and patience made possible the completion of this book. Her greatest joy came when the manuscript was completed and she was able to once again see the surface of our dining room table and to resume using our dining room for its intended purpose!

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complete glossaries for all life science disciplines, a section describing the classification system, an overview of word construction, and more than 500 vivid illustrations and animations of key processes.

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TITLES OF RELATED INTEREST

Comparative Anatomy Laboratory Dissection Guide, Second Edition ©1998, by Kardong/Zalisko (ISBN: 0-697-37879-9) is a complete dissection guide that is organized systematically to present basic animal architecture and anatomy. The exercises can be customized to suit most vertebrate course needs.

Mammalogy: Adaptation, Diversity and Ecology, ©1999, by Feldhamer, Drickamer, Vessey, and Merritt (ISBN: 0-697-16733-X) is an introductory mammalogy text for use in upper level undergraduate or graduate level courses, and assumes students have a basic background in zoology of the vertebrates.

Zoology, Fourth Edition ©1999, by Miller/Harley (ISBN: 0-697-34555-6) is a comprehensive, principles-oriented full-color text with an unmatched pedagogical system, Internet references, and a comprehensive web page.

Integrated Principles in Zoology, Eleventh Edition ©2001, by Hickman/Roberts/Larson (ISBN: 0-072-90961-7) remains the leading text in zoology. With outstanding artwork and a continued comprehensive and straightforward approach, the new edition includes current issues such as biotechnology, immunity, and conservation, and provides chapter web links for further study. This text is also supported by a comprehensive web page.

Biology of Animals, Seventh Edition ©1998, by Hickman/Roberts/Larson (ISBN: 0-697-28933-8) is an introductory zoology text which features a variety of pedagogical aids and a supporting web page.

Animal Diversity, Second Edition ©2000, by Hickman/Roberts/Larson (ISBN: 0-070-12200-8) covers the animal kingdom in sixteen survey chapters and is prefaced by evolution, animal architecture, and classification. Internet references are included in the text for further research, and the text is supported by a web site that includes additional student aids.

Laboratory Studies in Integrated Principles of Zoology, Tenth Edition ©2001, by Hickman/Kats (ISBN: 0-072-90966-8) uses a comprehensive, phylogenetic approach in emphasizing basic biological principles, animal form and function, and evolutionary concepts. This introductory lab manual is ideal for a one- or two-semester course. The new edition incorporates more interactivity for students throughout the laboratory exercises, and also has new molecular exercises. This text may be customized to include only the exercises that best suit your course needs.

General Zoology Laboratory Guide, Thirteenth Edition ©2000, by Lytle (ISBN: 0-07-012220-2) emphasizes the dissection and microscopic study of live and preserved specimens. This laboratory guide is also customizable to contain only the exercises that best fit your course.

Understanding Evolution, Sixth Edition ©2000, by Volpe/Rosenbaum (ISBN: 0-697-05137-4) is an introduction to principles of evolution text that is ideally suited as a main text for general evolution or as a supplement for General Biology, Genetics, Zoology, Botany, Anthropology, or any life science course that utilizes evolution as the underlying theme of all life.

Foundations of Parasitology, Sixth Edition ©2000, by Roberts/Janovy (ISBN: 0-697-42430-8) is written for biological/zoological students at the undergraduate level and emphasizes principles with related information on the biology, physiology, morphology, and ecology of the major parasites of humans and domestic animals.

Biology of the Invertebrates, Fourth Edition ©2000, by Pechenik (ISBN: 0-070-12204-0) is the most concise and readable invertebrates book in terms of detail and pedagogy. All phyla of invertebrates covered (comprehensive) with an emphasis on unifying characteristics of each group.

Animal Behavior: Mechanisms, Ecology, Evolution, Fifth Edition ©2001, by Drickamer/Vessey/Jakob (ISBN: 0-070-12199-0) is a unique balance of the necessary elements of mechanisms, ecology, and evolution that support a comprehensive study of behavior. This one-semester text is suitable for upper-level courses.

Marine Biology, Third Edition ©2000, by Castro/Huber (ISBN: 0-07-012197-4) is appropriate for introductory courses and features a global approach, using examples from numerous regions and ecosystems. This edition also includes Internet references for further study, and is supported by a complete web site with additional student study aids.

Preface to the Student

The field of vertebrate biology is changing constantly. As discoveries are made, old concepts fade away and new ones emerge. We are now at a point in time where acceptable solutions must be found to major environmental problems such as global warming, fragmentation of habitats, isolation of populations, and the decline in biodiversity—all of which play a role in the distribution and abundance of vertebrate populations. Trying to discover the knowledge that is really worth knowing is an exciting and never-ending process.

This is why vertebrate biology is so important: it is not just another college course to be passed for credit. It is an opportunity for you to learn about the other organisms most closely related to us with whom we share this ever-more-crowded planet. During this course we will use information from physical sciences such as chemistry and geology as well as from a wide variety of biological specializations such as botany, genetics, cell biology, physiology, anatomy, and ecology.

While many biologists become more specialized and restrict their reading and research to a narrow area of interest, a general textbook author is forced to be a generalist, who understands (in my case) the whole field of vertebrate biology: to this end the author must illustrate the interrelationships and synthesize available information into some kind of coherent whole. My objective has been to write a general text that reflects the broad diversity of subjects that make vertebrate biology such an exciting field. The need for a readable, user-friendly book covering the biology of vertebrates has been recognized for many years. *Vertebrate Biology* is designed to provide a broad and basic background of vertebrate biology: to explain how vertebrates function, evolve, and interact with each other and their nonliving surroundings.

A second objective of writing *Vertebrate Biology* is to provide a balanced overview of the various areas of vertebrate biology—origin, phylogeny, fossil history, adaptations, distribution, and population dynamics; to explore these areas in some detail; to provide a basic reference source; and to produce a readable, user-friendly text. All sources are documented in order to assist you in your search for more detailed information than this text provides.

I could have written a short textbook that omitted many topics, but that strategy would not meet the needs of many instructors. On the other hand, I could have written a larger book and designed it to be flexible enough to be used in many different ways. I chose the latter. This text has been designed to be used in courses with different lengths and emphases. As a result, your instructor has great flexibility in designing the course you are taking according to the time available.

Numerous features enable this textbook to stand out above all others. Among these are review questions at the end of each chapter, supplemental sources of information including relevant journals, a glossary of well over 300 terms, an extensive bibliography, an appendix of endangered species, and a directory of World Wide Web sites dealing with various aspects of vertebrate biology. This latter feature is unique because if you become interested in a particular topic, you can access relevant web sites throughout the world. The World Wide Web is an excellent resource for vertebrate biology and contains a wide array of information. The web addresses listed are up-to-date as of press time, and are, for the most part, maintained by universities, governmental agencies, institutions, museums, etc. The information they contain should be factual and these sites will be kept up-to-date by the publisher. You can access these weblinks at www.mhhe.com/zoology.

Vertebrate Biology begins with an introductory chapter relating vertebrates to other chordates. This chapter also gives a broad overview and comparison of major vertebrate characters, introduces relevant terminology, discusses the significance of vertebrates, and highlights future research topics. Chapter 2 traces the development of systematics as it relates to vertebrates and discusses evolutionary concepts including natural selection, speciation, and geographic variation. Zoogeography is covered in Chapter 3. Chapters 4 through 9 discuss the evolution and biology of each vertebrate group—jawless fishes, fishes, amphibians, reptiles, and mammals. The remaining chapters draw out common themes across all of the vertebrates: population dynamics (10); movements (11); intraspecific behavior (12); interspecific interactions (13); techniques for ecological and behavioral studies (14); extinction and extirpation (15); and conservation and management (16). Subsection headings are included where appropriate to make it easier for you to retrieve specific pieces of information. Thus, I have attempted to blend the two approaches (taxonomic and concept). At the end of each chapter is a set of discussion questions designed to help you develop your critical thinking skills and apply what you have learned.

My goal is to communicate with you, not confuse you. I have tried to write in a clear, interesting, and informal style. I keep sentences and paragraphs fairly short. I try not to use

long words and excessive technical terms when short words and nontechnical terms can express an idea just as clearly. Information is presented in a very straightforward, readable manner. It is not weighed down with excessive terminology.

Writing and publishing a textbook is an extremely complex process. Even though the manuscript has been reviewed, copy edited, checked, and rechecked by a large number of teachers and experts, almost any textbook is certain to have some errors. Although all errors are my sole responsibility, I need your help in improving future editions of this book. Please send any errors you find and your comments and suggestions for improvement to Marge Kemp, Sponsoring Editor, Life Sciences, c/o McGraw-Hill Publishers, 2460 Kerper Blvd., Dubuque, Iowa 52001. She will send them to me. Please be assured that all comments and suggestions will be seriously evaluated and considered. As time allows, I will respond personally to your suggestions.

It is my hope that this text will give you a deeper understanding of the biology of a unique group of animals—including ourselves—and an appreciation of the complexity of issues such as the problems of speciation and phylogeny, the thermal physiology of dinosaurs, and the origin of flight in birds, to name but a few.

Relax and enjoy yourself as you learn more about one of the exciting groups of animals with whom we share this planet.

Donald W. Linzey

SUPPLEMENTARY MATERIALS

For the Student

A variety of print and media products are available from McGraw-Hill to supplement your learning, in addition to the titles listed below. Visit www.mhhe.com or contact your bookstore to order these products:

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About the Author

Dr. Donald W. Linzey, a native of Baltimore, Maryland, is a biologist living and working in southwestern Virginia. He has received degrees from Western Maryland College in Westminster, Maryland (B.A., 1961), and Cornell University in Ithaca, New York (M.S., 1963, PhD., 1966). Since the early 1960s, he has been studying mammals and other vertebrates in the eastern United States. In the early 1960s, he worked as a park ranger and naturalist in the Great Smoky Mountains National Park, and he has taught biological and environmental sciences at Cornell University, The University of South Alabama, Virginia Tech, and, since 1986, Wytheville Community College in Wytheville, Virginia. In addition to authoring nine texts and over 50 articles for scientific journals, Dr. Linzey is presently coordinating a long-term multidisciplinary study of the decline of amphibians in Bermuda and coordinating all mammal investigations for the All Taxa Biological Inventory in the Great Smoky Mountains National Park.

For the past 10 years, Dr. Linzey has served as Director of the Blue Ridge Highlands Regional Science Fair and has recently completed a three-year term on the Science Service Advisory Board, which oversees the annual Intel International Science and Engineering Fair. Dr. Linzey's recent awards include Outstanding Faculty Award from the Virginia State Council of Higher Education (1996), Distinguished Service Award for Wytheville Community College (1998), the Chancellor's Professorship Award from the Virginia Community College System (1998), and the 1999 Virginia Professor of the Year Award from the Carnegie Foundation for the Advancement of Teaching.

Dr. Linzey resides in Blacksburg, Virginia with his wife, Juanita. They have four sons.

Brief Table of Contents

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CHAPTER 1

The Vertebrate Story: An Overview

INTRODUCTION

Life on Earth began some 3.5 billion years ago when a series of reactions culminated in a molecule that could reproduce itself. Although life forms may exist elsewhere in our universe or even beyond, life as we know it occurs only on the planet Earth. From this beginning have arisen all of the vast variety of living organisms—viruses, bacteria, fungi, protozoans, plants, and multicellular animals—that inhabit all parts of our planet. The diversity of life and the ability of life forms to adapt to seemingly harsh environments is astounding. Bacteria live in the hot thermal springs in Yellowstone National Park and in the deepest parts of the Pacific Ocean. Plants inhabit the oceans to the lower limit of light penetration and also cover land areas from the tropics to the icepacks in both the Northern and Southern Hemispheres. Unicellular and multicellular animals are found worldwide. Life on Earth is truly amazing!

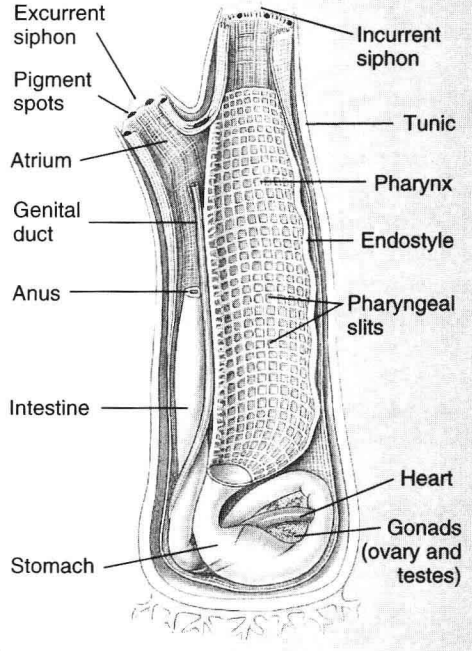
Our knowledge of the processes that create and sustain life has grown over the years and continues to grow steadily as new discoveries are announced by scientists. But much remains to be discovered—new species, new drugs, improved understanding of basic processes, and much more.

All forms of life are classified into five major groups known as **kingdoms**. The generally recognized kingdoms are Monera (bacteria), Fungi (fungi), Protista (single-celled organisms), Plant (plants), and Animal (multicellular animals). Within each kingdom, each group of organisms with similar characteristics is classified into a category known as a **phylum**.

Whereas many members of the Animal kingdom possess skeletal, muscular, digestive, respiratory, nervous, and reproductive systems, there is only one group of multicellular animals that possess the following combination of structures: (1) a dorsal, hollow nerve cord; (2) a flexible supportive rod (notochord) running longitudinally through the dorsum just ventral to the nerve cord; (3) pharyngeal slits or pharyngeal pouches; and (4) a postanal tail. These morphological characteristics may be transitory and may be present only during a particular stage of development, or they may be present throughout the animal's life. This group of animals forms the phylum **Chordata**. This phylum is divided into three **subphyla**: Urochordata, Cephalochordata, and Vertebrata. The Urochordata and Cephalochordata consist of small, nonvertebrate marine animals and are often referred to collectively as protochordates. To clearly understand and compare their evolutionary significance in relation to the vertebrates, it is necessary to briefly discuss their characteristics.

Subphylum **Urochordata** (tunicates): Adult tunicates, also known as sea squirts, are mostly sessile, filter-feeding marine animals whose gill slits function in both gas exchange and feeding (Fig. 1.1). Water is taken in through

FIGURE 1.1



Structure of a tunicate, *Ciona* sp.

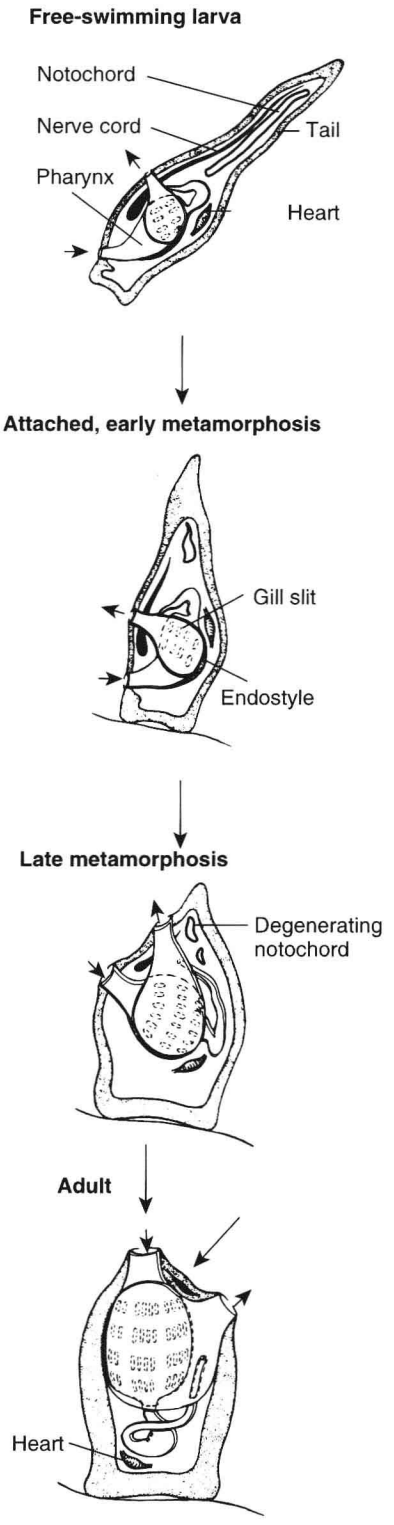
an incurrent siphon, goes into a chamber known as the pharynx, and then filters through slits into the surrounding atrium. Larval tunicates, which are free-swimming, possess a muscular larval tail that is used for propulsion. This tail contains a well-developed notochord and a dorsal hollow nerve cord. The name Urochordate is derived from the Greek *oura,* meaning tail, and the Latin *chorda,* meaning cord; thus, the "tail-chordates." When the larva transforms or metamorphoses into an adult, the tail, along with its accompanying notochord and most of the nerve cord, is reabsorbed (Fig. 1.2).

Subphylum **Cephalochordata** (lancelet; amphioxus): Cephalochordates are small (usually less than 5 cm long), fusiform (torpedo-shaped) marine organisms that spend most of their time buried in sand in shallow water. Their bodies are oriented vertically with the tail in the sand and the anterior end exposed. A well-developed notochord and long dorsal hollow nerve cord extend from the head (*cephalo* means head) to the tail and are retained throughout life. The numerous pharyngeal gill slits are used for both respiration and filter-feeding (Fig. 1.3). Cephalochordates have a superficial resemblance to the larvae of lampreys (ammocoete), which are true vertebrates (Fig. 1.3).

Serially arranged blocks of muscle known as **myomeres** occur along both sides of the body of the lancelet. Because the notochord is flexible, alternate contraction and relaxation of the myomeres bend the body and propel it. Other similarities to vertebrates include a closed cardiovascular system with a two-chambered heart, similar muscle proteins, and the organization of cranial and spinal nerves. No other group of living animals shows closer structural and developmental affinities with vertebrates. However, even though cephalochordates now are believed to be the closest living relatives of vertebrates, there are some fundamental differences. For example, the functioning units of the excretory system in cephalochordates are known as protonephridia. They represent a primitive type of kidney design that removes wastes from the coelom. In contrast, the functional units of vertebrate kidneys, which are known as nephrons, are designed to remove wastes by filtering the blood. What long had been thought to be ventral roots of spinal nerves in cephalochordates have now been shown to be muscle fibers (Flood, 1966). Spinal nerves alternate on the two sides of the body in cephalochordates rather than lying in successive pairs as they do in vertebrates (Hildebrand, 1995).

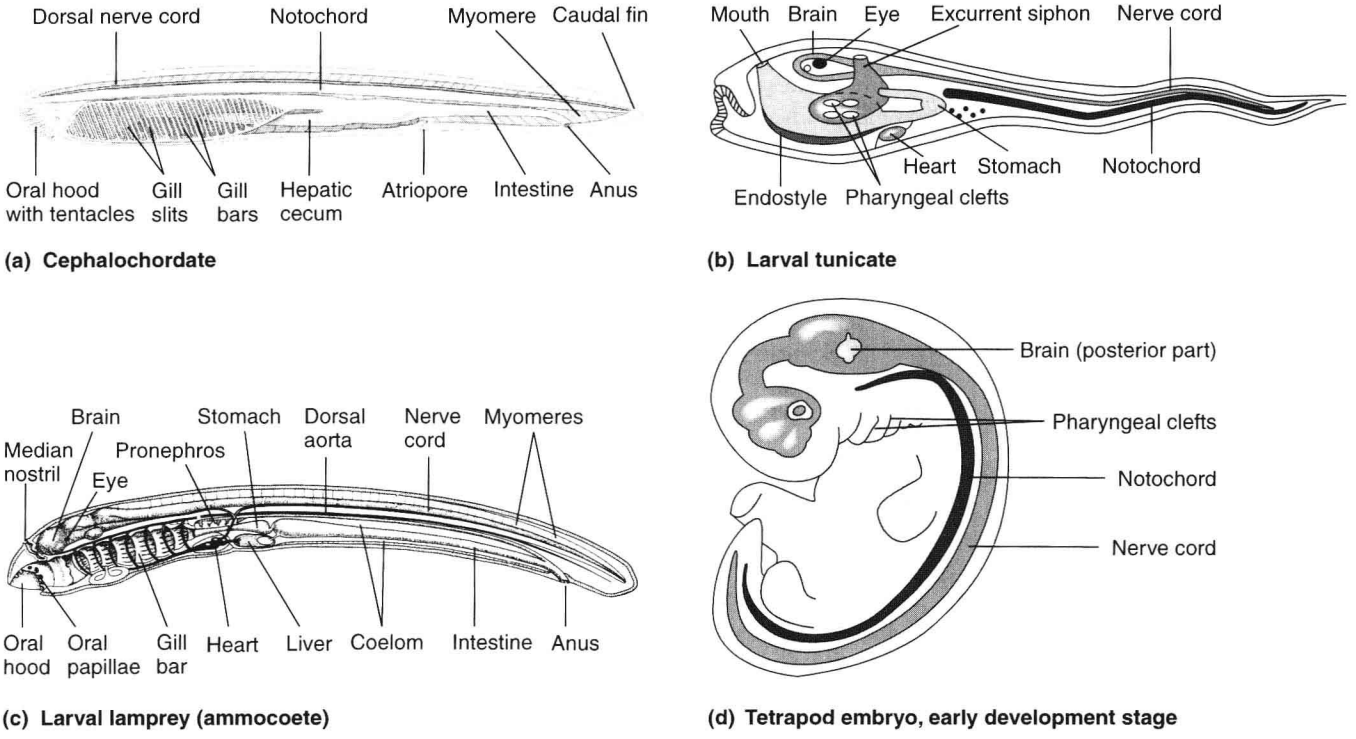
Subphylum **Vertebrata** (vertebrates): Vertebrates (Fig. 1.4) are chordates with a "backbone"—either a persistent notochord as in lampreys and hagfishes, or a vertebral column of cartilaginous or bony vertebrae that more or less replaces the notochord as the main support of the long axis of the body. All vertebrates possess a cranium, or braincase, of cartilage or bone, or both. The cranium supports and protects the brain and major special sense organs. Many authorities prefer the term Craniata instead of Vertebrata, because it recognizes that hagfish and lampreys have a cranium but no vertebrae. In addition, all vertebrate embryos pass through a stage when pharyngeal pouches

FIGURE 1.2



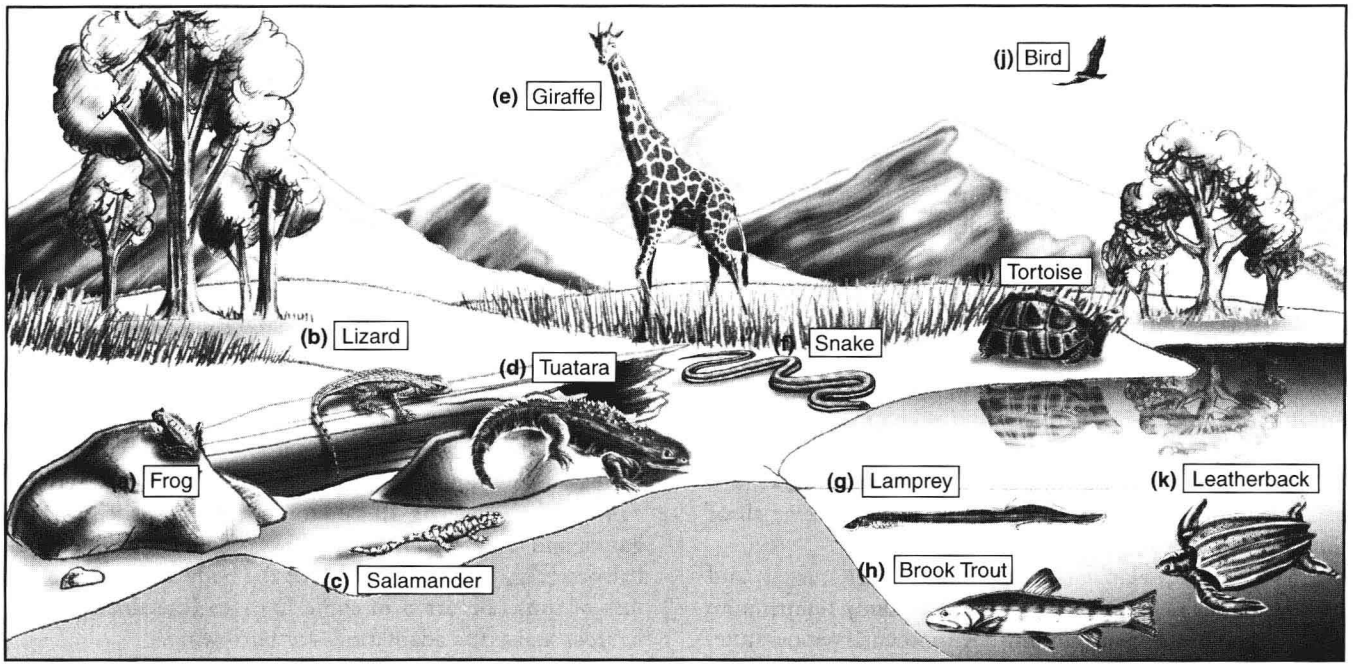
Metamorphosis of a free-swimming tunicate (class Ascidiacea) tadpole-like larva into a solitary, sessile adult. Note the dorsal nerve cord, notochord, and pharyngeal gills slits.

FIGURE 1.3



Three chordate characters (dorsal tubular nerve cord, notochord, and pharyngeal clefts) as seen in (*a*) a cephalochordate (amphioxus), (*b*) a larval tunicate, (*c*) a larval lamprey, and (*d*) a tetrapod embryo.

FIGURE 1.4



Representative vertebrates: (*a*) wood frog, class Amphibia; (*b*) fence lizard, class Reptilia; (*c*) spotted salamander, class Amphibia; (*d*) tuatara, class Reptilia; (*e*) giraffe, class Mammalia; (*f*) garter snake, class Reptilia; (*g*) lamprey, class Cephalaspidomorphi; (*h*) brook trout, class Osteichthyes; (*i*) gopher tortoise, class Reptilia; (*j*) red-tailed hawk, class Aves; and (*k*) leatherback sea turtle, class Reptilia.