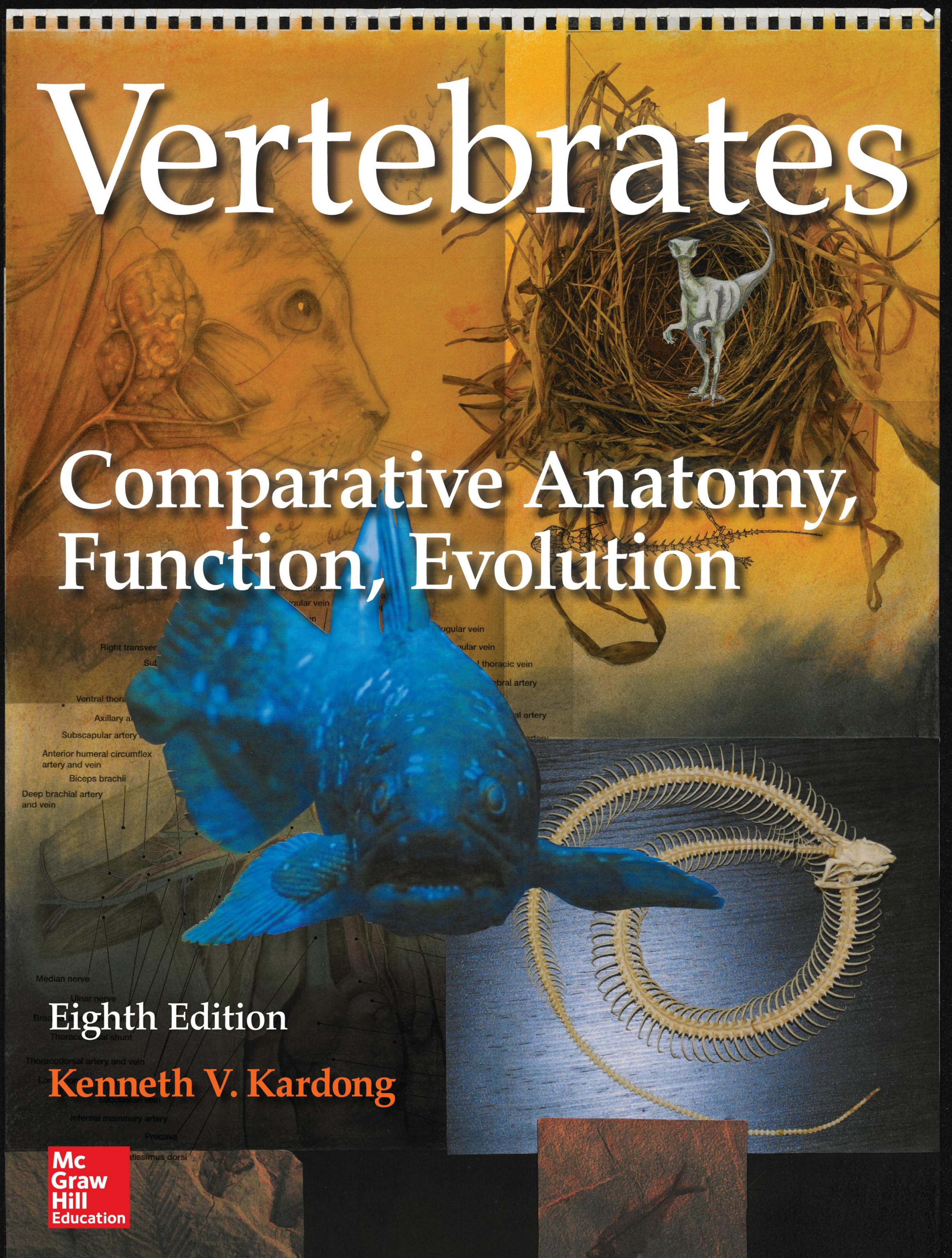
Vertebrates

Comparative Anatomy, Function, Evolution

Eighth Edition

Kenneth V. Kardong



McGraw Hill Education

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Kenneth V. Kardong, Ph.D.
Washington State University

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Dedicated with pleasure, good memories, and gratitude to
T. H. Frazzetta and
Richard C. Snyder

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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/nature2 1700) 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 rending 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 their point of view, at least their influence within this edition and accept my sincere thanks for their thoughtful suggestions and criticisms. For their special help in this edition and earlier editions, I recognize:

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It has been a special pleasure for me to work previously with several especially supportive and helpful colleagues. I also want to note especially the help from Ira F. Greenbaum, Texas A & M University, for engaging in a pleasurable and productive exchange on all things vertebrate. The sharp, critical eye, and thorough reading of parts of the textbook and laboratory manual by Jon Mallatt, Washington State University, are gratefully acknowledged.

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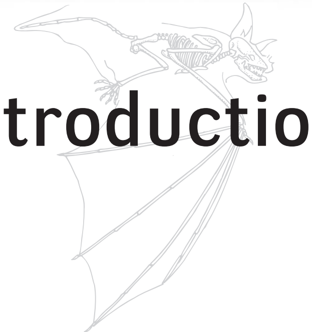
To friends and family, I remain grateful and thank them for their support during various editions of this textbook.

CHAPTER 1



Introduction

Comparative Vertebrate Morphology

Comparative morphology deals with anatomy and its significance. We focus on animals, in particular vertebrate animals, and the significance these organisms and their structure may hold. The use of comparison in comparative morphology is not just a convenience. It is a tool. Comparison of structures throws similarities and differences into better relief. Comparison emphasizes the functional and evolutionary themes vertebrates carry within their structures. Comparison also helps formulate the questions we might ask of structure.

For example, different fishes have different tail shapes. In the **homocercal** tail, both lobes are equal in size, making the tail symmetrical (figure 1.1a). In the **heterocercal** tail, found in sharks and a few other groups, the upper lobe is elongated (figure 1.1b). Why this difference? The homocercal tail is found in teleost fishes—salmon, tuna, trout, and the like. These fishes have a swim bladder, an air-filled sac that gives their dense bodies neutral buoyancy. They neither sink to the bottom nor bob to the surface, so they need not struggle to keep their vertical

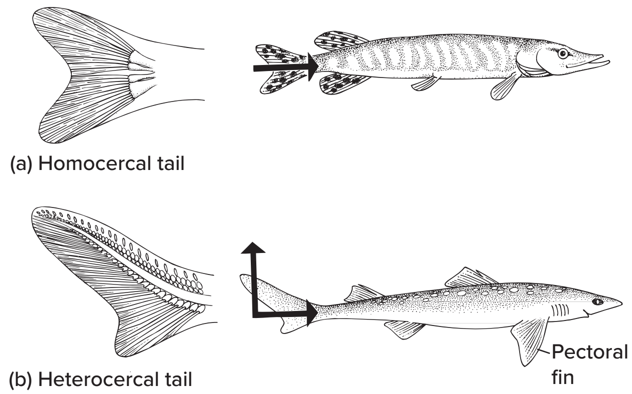


FIGURE 1.1 **Homocercal and heterocercal fish tails.** Form differs because function differs. (a) Sweeping, side-to-side movements of the homocercal tail, common in fishes with neutral buoyancy, drive the body forward. (b) Swimming strokes of the heterocercal tail propel the fish forward, and motion of the long extended upper lobe imparts an upward lift to the posterior end of the fish. Sharks, which are a good deal denser than water, need the upward forces provided by the extended lobe of the tail to counteract a tendency to sink.

position in the water. Sharks, however, lack swim bladders and so tend to sink. The extended lobe of their heterocercal tail provides lift during swimming to help counteract this sinking tendency. So, the differences in structure, homocercal versus heterocercal, are related to differences in function. Why an animal is constructed in a particular way is related to the functional requirements the part serves. Form and function are coupled. Comparison of parts highlights these differences and helps us pose a question. Functional analysis helps answer our question and gives us a better understanding of animal design. **Functional morphology** is the discipline that relates a structure to its function.

Comparative analysis thus deploys various methods to address different biological questions. Generally, comparative analysis is used either in a historical or a nonhistorical context. When we address historical questions, we examine evolutionary events to work out the history of life. For example, on the basis of the comparison of characters, we may attempt to construct classifications of organisms and the evolutionary phylogeny of the group. Often such historical comparisons are not restricted to classification alone but center on the process of evolution behind morphological units, such as jaws, limbs, or eyes.

When we make nonhistorical comparisons, as is frequently the case, we look outside an evolutionary context, with no intention of concluding with a classification or elucidation of an evolutionary process. Nonhistorical comparisons are usually extrapolative. For example, by testing a few vertebrate muscles, we may demonstrate that they produce a force of 15 N (newtons) per square centimeter of muscle fiber cross section. Rather than testing all vertebrate muscles, a time-consuming process, we usually assume that other muscles of similar cross section produce a similar force (other things being equal). The discovery of force production in some muscles is extrapolated to others. In medicine, the comparative effects of drugs on rabbits or mice are extrapolated to tentative use in humans. Of course, the assumed similarities upon which an extrapolation is based often do not hold in our analysis. Insight into the human female reproductive cycle is best obtained if we compare the human cycle with those in higher primates because primate reproductive cycles, including the human one, differ significantly from those of other mammals.

Extrapolation allows us to make testable predictions. Where tests do not support an extrapolation, science is well served because this forces us to reflect on the assumptions behind the comparison, perhaps to re-examine the initial analysis of structures and to return with improved hypotheses about the animals or systems of interest. Comparison itself is not just a quick and easy device. The point to emphasize is this: Comparison is a tool of insight that guides our analysis and helps us set up hypotheses about the basis of animal design.

Designs of Students

Such philosophical niceties, however, usually do not entice students into their first course in morphology. Most students first venture into a course in vertebrate morphology on their way into some other profession. Customarily, morphology courses prepare students headed into technical fields such as human medicine, dentistry, or veterinary medicine. Vertebrate form and function will be the foundation for these medical fields. As will, for example, diagnostic medicine that benefits from the development of anatomically and functionally correct prosthetic devices to replace injured body parts lost to disease and trauma.

In addition, morphology is important to taxonomists who use the structure of animals to define characters. In turn, these characters are used as the basis for establishing relationships between species.

Morphology is central to evolutionary biology as well. Many scientists, in fact, would like to see a discipline devoted to the combined subject, namely, **evolutionary morphology.** Evidence of past evolutionary changes is inscribed in animal structure. Within the amphibian limb are the structural reminders of its fish-fin ancestry; within the wing of a bird are the evidences of its derivation from the reptilian forelimb. Each modern group living today carries forward mementos of the evolutionary course traveled by its ancestors. For many biologists, a study of the morphological products of the past gives insight into the processes that produced them, insight into the natural forces that drove evolutionary changes, and insight into the limitations of evolutionary change.

Vertebrate Design—Form and Function

Morphology offers more than charitable assistance to other disciplines. The study of morphology provides its own pleasure.

BOX ESSAY 1.1

The Scientific Method—What They Tell You and What They Don't

Formally, the scientific method includes formulation of a hypothesis, design of a test, carrying out of an experiment, analysis of results, corroboration or falsification of the hypothesis, and formulation of a new hypothesis. In practice, science does not follow such a stately and linear sequence. Broken equipment, uncooperative animals, paperwork, and committee meetings all conspire against the well-laid plans of mice, men, and women. It is more than the "expected unexpected" that affects experiments and tests one's blood pressure. The intellectual questions themselves do not always find satisfying answers. Accidents, chance, and even dreams are part of the creative process.

Otto Loewi shared the 1936 Nobel Prize in medicine with Henry Dale for demonstrating that nerve impulses pass from one nerve cell to the next in series across the space between them, the synapse, by a chemical transmitter. Early in the twentieth century, opinion had been divided between those physiologists who felt that this neuron-to-neuron transmission was chemical and those who felt that it was electrical. A definitive experiment settling the issue was needed. One night, when he was deep in sleep, the definitive experiment came to Loewi and woke him. Relieved and satisfied, he went back to sleep looking forward to the next day. When awaking the next morning, he remembered dreaming the experiment but had forgotten what it was. Several frustrating weeks passed until, once again deep in sleep, Loewi dreamt the same dream, and the experimental design came back. Leaving nothing to chance this time, he got up, dressed, and in the middle of the night went to his laboratory to begin the experiment that would settle the issue of transmission and years later win him a share of the Nobel Prize.

Loewi's experiment was as simple as it was elegant. He removed the heart and associated vagus nerve from the body of a frog and isolated them in a beaker of saline. Next he stimulated the free vagus nerve, causing the heart rate to slow. Loewi then took this saline and poured it over another isolated frog heart from which the vagus had been removed. The rate of this heart also slowed, providing clear evidence that a chemical produced by the stimulated vagus nerve controlled heart rate. Transmission between nerve (vagus) and organ (heart) was brought about by chemical agents, not by electrical currents.

As a young cell biologist, Herbert Eastlick began a series of experiments to pursue his interest in embryonic development of young muscle. He transplanted the still formative hindlimbs of a chick to the side of a host chick while the host was still developing in its egg. The transplanted hindlimbs were usually received and grew well enough on the side of the host chick to allow study. One day, when a local supplier was temporarily out of the white leghorn eggs Eastlick had used, he substituted brown leghorns, a breed with brown feathers. After three days of incubation, one egg was opened and both leg-forming areas of a brown leghorn were transplanted to a white leghorn host. Results were puzzling. The right transplanted leg from the brown leghorn developed brown feathers, the left transplanted leg from the same brown leghorn developed white feathers. What caused these contrary results?

Eastlick checked his notes, repeated his experiments, and used great care in performing more transplants. Still some transplanted legs were brown and some were white. It then dawned on him that the stump of the transplanted limb might in some instances include nearby neural crest cells, but not in all instances. Neural crest cells form first on top of the nerve tube and then normally disperse about the embryo. He tried limbs with and without accompanying neural crest cells. That was it. Those brown leghorn limbs with neural crest cells produced brown feathers. Those without lacked pigment cells and were white. Eastlick, who started out working on muscles, confirmed what a few had guessed at the time, namely, that one derivative of neural crest cells is pigment cells that give feathers their color.

Alexander Fleming (1881–1955), while studying bacteria, noticed that when molds occasionally contaminated cultures, the bacteria next to the molds failed to grow. Hundreds of students and fellow bacteriologists before Fleming had seen molds and likely noticed the stunted growth of bacteria. But it was Fleming's curiosity that precipitated the serious question, "What causes this reaction?" In answering it, he discovered that molds produced penicillin, a bacterial inhibitor. Fleming's question opened the way for development of a new branch of pharmacology and a new industry. His answer established the basis of disease control through antibiotics.

Testing of a well-crafted hypothesis forms the center of the scientific method. But where the next hypothesis comes from cannot always be predicted. A thought in the middle of the night, an experiment gone wrong, a close observation of the ordinary, these too may inspire a new scientific hypothesis and are part of the method of science.

It raises unique questions about structure and offers a method to address these questions. In brief, vertebrate morphology seeks to explain vertebrate design by elucidating the reasons for and processes that produce the basic structural plan of an organism. For most scientists today, evolutionary processes explain form and function. We might hear it said that the wings of birds, tails of fishes, or hair of mammals arose for the adaptive advantages each structure provided, and so they were favored by natural selection. Certainly this is true, but it is only a partial explanation for the presence of these respective features in bird, fish, and mammal designs. The external environment in which an animal design must serve certainly brings to bear evolutionary pressures on its survival and thus on those anatomical features of its design that convey adaptive benefits.

Internal structure itself also affects the kinds of designs that do or do not appear in animals. No terrestrial vertebrate rolls along on wheels. No aerial vertebrate flies through the air powered by a rotary propeller. Natural selection alone cannot explain the absence of wheels in vertebrates. It is quite possible to imagine that wheels, were they to appear in certain terrestrial vertebrates, would provide considerable adaptive advantages and be strongly favored by natural selection. In part, the explanation lies in the internal limitations of the structure itself. Rotating wheels could not be nourished through blood vessels nor innervated with nerves without quickly twisting these cords into knots. Wheels and propellers fall outside the range of structural possibility in vertebrates. Structure itself contributes to design by the possibilities it creates; evolution contributes to design by the favored structures it preserves. We must consult both structure and evolution to understand overall design. That is why we turn to the discipline of morphology. It is one of the few modern sciences that addresses the natural unity of both structure (form and function) and evolution (adaptation and natural selection). By wrapping these together in an integrated approach, morphology contributes a holistic analysis of the larger issues before contemporary biology. Morphology is concerned centrally with the emergent properties of organisms that make them much more than the reduced molecules of their parts.

Grand Design

Vertebrate design is complex, often elegant, and sometimes remarkably precise. To many early-day morphologists, this complexity, this elegance, and this precision implied the direct intervention of a divine hand in guiding the production of such sophisticated designs. However, not everyone was convinced. Spectacular mountain ranges do not require recourse to divine intervention to explain them. Plate tectonics offers a natural explanation. Under pressure from colliding tectonic plates, the Earth's crust crumples to produce these ranges. With knowledge, scientific explanations uncover the mysteries that shroud geological events.

Similarly, biology has found satisfying natural explanations to replace what were once assumed to be direct divine causes. Modern principles of evolution and structural biology offer a fresh approach to vertebrate design and an insight into the processes responsible for producing that design. Just as processes of plate tectonics help geologists understand the origin of the Earth's surface features, structural and evolutionary processes help biologists understand the origin of plant and animal life. Life on Earth is a product of these natural processes. Humans are not exempt, nor are we given special dispensation from these processes. Like our fellow vertebrates, humans too are products of our evolutionary past and basic structural plan. The study of morphology, therefore, brings us an understanding of the integrated processes that forged us. To understand the processes behind our design is to understand the product, namely, humans themselves, both what we are and what we can become.

But I am getting ahead of the story. We have not had an easy intellectual journey in reaching the clarity of morphological concepts we seem to enjoy at the moment. The principles were not always so obvious, the evidence not always so clear. In fact, some issues prevalent over 100 years ago remain unresolved. The significance of underlying structure to the evolution of design, central to much of biology early in the nineteenth century, is only recently being re-examined for its potential contribution to modern morphology. Morphology has often been internally beset by unhappy contentions between those scientists centered on structure and those centered on evolution. To some extent, the fundamental principles of both structure and evolution have grown from different intellectual sources and different intellectual outlooks. To understand this, we need to examine the historical development of morphology. Later in this chapter, we examine the intellectual roots of theories about structure. But first, let's look to the intellectual roots of theories about evolution.

Historical Predecessors—Evolution

The concept of evolution is tied to the name Charles Darwin (figure 1.2). Yet most persons are surprised to learn that Darwin was not first, nor was he ever foremost, in proposing that organisms evolve. In fact, the idea of change through time in animals and plants dates back to ancient schools of Greek philosophy. Over 2,500 years ago, Anaximander developed ideas about the course of change from fishlike and scaly animals to land forms. Empedocles saw original creatures come together in oddly assembled ways—humans with heads of cattle, animals with branches like trees. He argued that

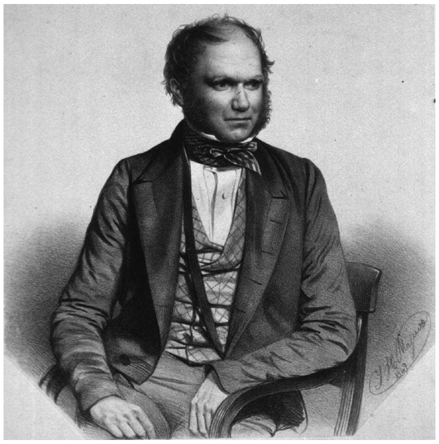


FIGURE 1.2 **Charles Darwin** (1809–1882), about 30 years old and three years back from his voyage aboard H.M.S. *Beagle*. Although *On the Origin of Species* was still just a few notebooks in length and several decades away from publication, Darwin had several accomplishments behind him, including his account of *The Voyage of the Beagle*, a collection of scientific observations. At this time, he was also engaged to his cousin Emma Wedgwood, with whom he would live a happy married life.

Source: Courtesy of the National Library of Medicine most perished, but only those creatures who came together in practical ways survived. Even at their best, these armchair views are more poetic than scientific, so it would be an exaggeration to characterize this Greek philosophical thought as a practical predecessor of modern evolutionary science. Nevertheless, the idea of evolution existed long before Darwin, thanks to these Greek philosophers.

The Process behind the Change

What the Englishman Charles Darwin contributed was not the idea that species evolve. Rather, Darwin proposed the conditions for and mechanism of this evolutionary change. He proposed three conditions:

First, if left unchecked, members of any species increase naturally in number because all possess a *high reproductive potential.* Even slow-breeding elephants, Darwin pointed out, could increase from a pair to many millions in a few hundred years. We are not up to our rooftops in elephants, however, because as numbers increase, resources are consumed at an accelerating rate and become scarce. This brings about condition two, *competition* for the declining resources. In turn, competition leads to condition three, *survival of the few.* Darwin termed the mechanism now determining which organisms survive and which do not **natural selection,** nature's way of weeding out the less fit. In this struggle for existence, those with superior adaptations would, on average, fare better and survive to pass on their successful adaptations. Thus, descent with modification resulted from the preservation by natural selection of favorable characteristics.

As simple as this sounds today, Darwin's insight was profound. He performed no decisive experiment, mixed no chemicals in test tubes, ground no tissue in a blender. Rather, Darwin's insight arose from observation and reflection. The controversy over evolutionary processes emerges at one of three levels—fact, course, mechanism—and asks a different question at each level. The first level addresses the *fact of evolution* and asks if organisms change through time. Did evolution occur? The fact that evolution has occurred is today well established by many lines of evidence, from gene changes to the fossil record. But this does not mean that all controversies over evolution are comfortably settled. At the next level, we might ask: What *course* did evolution then take? For example, anthropologists who study human evolution usually agree on the fact that humans did evolve, but they often disagree, sometimes violently, over the course of that evolution. Finally we can ask: What *mechanism* produced this evolution? At this third level in the evolutionary debate, Darwin made his major contribution. For Darwin, natural selection was the mechanism of evolutionary change.

Verbal scuffles over the fact, course, and mechanism of evolution often become prolonged and steamy because opponents ask questions at different levels and end up arguing at cross-purposes. Each of these questions had to be settled historically as well to bring us to an understanding of the evolutionary process. Historians have taken much notice of the violent public reaction to Darwin's ideas on evolution, a reaction spurred by their challenge to religious convention. But what of the scientific climate at that time? Even in scientific circles, opinion was strongly divided on the issue of "transmutation" of species, as evolution was termed then. The issue initially centered around the fact of evolution. Do species change?

Linnaeus

Foremost among the scientists who felt that species were fixed and unchangeable was Carl von Linné (1707–1778), a Swedish biologist who followed the custom of the day by latinizing his name to Carolus Linnaeus, by which he is most recognized today (figure 1.3). Linnaeus devised a system for naming plants and animals, which is still the basis of modern taxonomy. Philosophically, he argued that species were unchangeable, created originally as we find them today. For several thousand years, Western thought had kept company with the biblical view, namely, that all species resulted from a single and special act of divine creation, as described in Genesis, and thereafter species remained unchanged.

Although most scientists during the 1700s sought to avoid strictly religious explanations, the biblical view of creation was a strong presence in Western intellectual circles because it was conveniently at hand and meshed comfortably

FIGURE 1.3 **Carolus Linnaeus** (1707–1778). This Swedish biologist devised a system still used today for naming organisms. He also firmly abided by and promoted the view that species do not change.

Source: ©Pixtal/age Fotostock

with the philosophical arguments put forth by Linnaeus and those who argued that species were immutable (unchanging). However, it was more than just the compatibility of Genesis with secular philosophy that made the idea of immutable species so appealing. At the time, evidence for evolution was not assembled easily, and the evidence available was ambiguous in that it could be interpreted both ways, for or against evolution.

Naturalists

Today, we understand the perfected adaptations of animals—the trunks of elephants, the long necks of giraffes, the wings of birds—as natural products of evolutionary change. Diversity of species results. To scientists of an earlier time, however, species adaptations reflected the care exercised by the Creator. Diversity of plant and animal species was proof of God's almighty power. Animated by this conviction, many sought to learn about the Creator by turning to the study of what He had created. One of the earliest to do so was the Reverend John Ray (1627–1705), who summed up his beliefs along with his natural history in a book entitled *The Wisdom of God Manifested in the Works of the Creation* (1691). He tackled the tricky question of why the Divine made obnoxious creatures. To paraphrase Ray, consider lice: They harbor and breed in clothes, "an effect of divine providence, designed to deter men and women from sluttishness and sordidness, and to provoke them to cleanliness and neatness." William Paley (1743–1805), archdeacon of Carlisle, also articulated the common belief of his day in his book *Natural Theology; or Evidences of the Existence and Attributes of the Deity Collected from the Appearances of Nature* (1802). Louis Agassiz (1807–1873), curator of the Museum of Comparative Zoology at Harvard University, found much public support for his successful work to build and stock a museum that collected the remarkable creatures that were this world's manifestations of the divine mind (figure 1.4). For most scientists, philosophers, and laypeople, there was, in the biological world of species, no change, thus no evolution. Even in secular circles of the mid-nineteenth century, intellectual obstacles to the idea of evolution were formidable.

J-B. de Lamarck

Among those taking the side of evolution, few were as uneven in their reputation as Jean-Baptiste de Lamarck (figure 1.5a). Most of his life, Lamarck lived on the border of poverty. He did not even hold the equivalent of a professorship at the Jardin du Roi in Paris (later the Muséum National d'Histoire Naturelle; figure 1.5b). Abrupt speech, inclination to argument, and strong views did little to endear Lamarck to his colleagues. Yet his *Philosophie Zoologique,* generally dismissed when published in 1809 as the amusing ruminations of a "poet," eventually established the theory of evolutionary descent as a respectable scientific generalization.

Lamarck's ideas spoke to the three issues of evolution—fact, course, and mechanism. As to the fact of evolution, Lamarck argued that species changed through time. Curiously, he thought that the simplest forms of life arose by spontaneous generation; that is, they sprang ready-made in muck from inanimate matter but thereafter evolved onward and upward into higher forms. As to the course of evolution, he proposed a progressive change in species along an ascending scale, from the lowest on one end to the most complex and "perfect" (meaning humans) on the other. As to the mechanism of evolution, Lamarck proposed that need itself produced heritable evolutionary change. When environments or behaviors changed, an animal developed new needs to meet the demands the environment placed upon it. Needs altered metabolism, changed the internal physiology of the organism, and triggered the appearance of a new part to address these needs. Continued use of a part tended to develop that part further; disuse led to its withering. As environments changed, a need arose, metabolism adjusted, and new organs were created. Once acquired, these new characteristics were passed on to offspring. This, in summary, was Lamarck's view. It has been called evolution by means of the *inheritance of acquired characteristics.* Characters were "acquired" to meet new needs and then "inherited" by future generations.

FIGURE 1.4 **Louis Agassiz** (1807–1873) was born in Switzerland but came to his second and permanent home in the United States when he was 39. He studied fossil fishes and was first to recognize evidence of the worldwide ice ages, episodes of glaciation in Earth's history. He founded the Museum of Comparative Zoology at Harvard University. Although brilliant and entertaining in public and in anatomical research, Agassiz remained unconvinced of Darwinian evolution to the end of his life.

Source: ©Archive Farms Inc/Alamy Stock Photo

While a debt is owed Lamarck for championing evolutionary change and so easing the route to Darwin, he also created obstacles. Central to his philosophy was an inadvertent confusion between physiology and evolution. Any person who begins and stays with a weight-lifting program on a regular basis can expect to see strength increase and muscles enlarge. With added weight, use (need) increases; therefore,

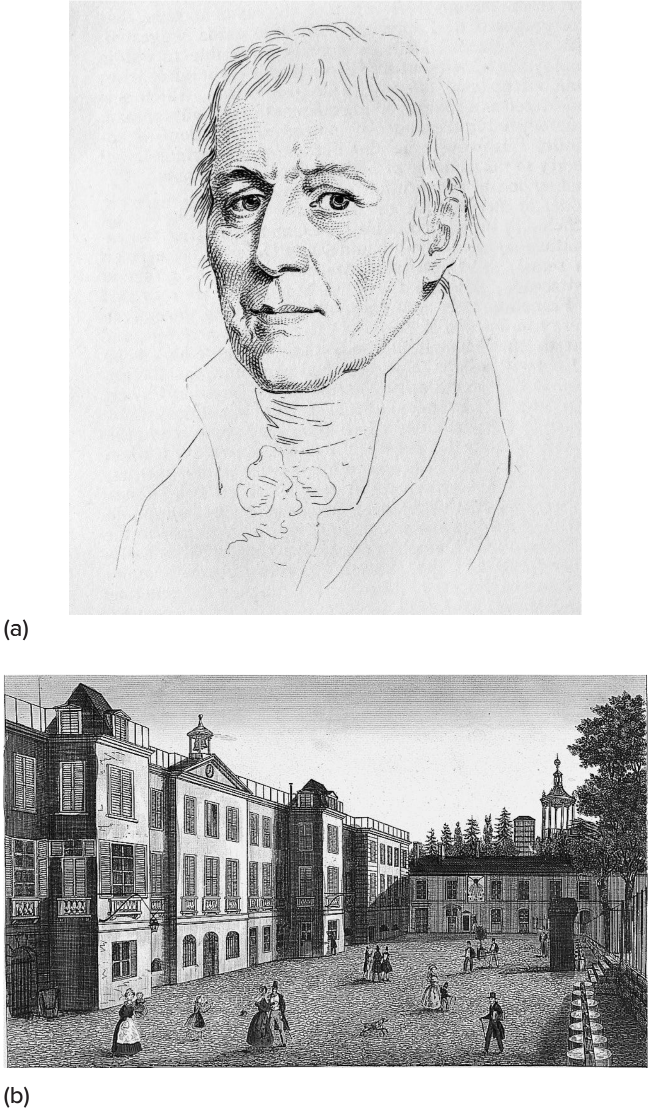


FIGURE 1.5 **(a) J-B. de Lamarck** (1744–1829) worked most of his scientific life at the Muséum National d'Histoire Naturelle (b). His academic position gave him a chance to promote the idea that species change.

Source: (a) ©Paul D. Stewart/Nature Picture Library; (b) ©RMN-Grand Palais/Art Resource, NY

big muscles appear. This physiological response is limited to the exercising individual because big muscles are not passed genetically to offspring. Charles Atlas, Arnold Schwarzenegger, and other bodybuilders do not pass newly acquired muscle tissue to their children. If their children seek large muscles, they too must start from scratch with their own training program. Somatic characteristics acquired through use cannot be inherited. Lamarck, however, would have thought otherwise.

Unlike such physiological responses, evolutionary responses involve changes in an organism that are inherited from one generation to the next. We know today that such characteristics are genetically based. They arise from gene mutation, not from somatic alterations due to exercise or metabolic need.

Acquired Characteristics

Lamarck's proposed mechanism of inheritance of acquired characteristics failed because it confused immediate physiological response with long-term evolutionary change. Yet most laypeople today still inadvertently think in Lamarckian terms. They mistakenly view somatic parts arising to meet immediate needs. Recently, a moderator of a nature program on giraffes unknowingly resorted to a Lamarckian explanation when he informed us that the origin of the long neck helped giraffes meet the "needs" of reaching treetop vegetation. But, environmental demands do not reach into genetic material and directly produce appropriate heritable improvements to address new needs or new opportunities. Bodybuilding changes muscles, not DNA. That route of inheritable modification does not exist in any organism's physiology.

The other side of the Lamarckian coin is disuse, loss of a part following loss of a need. Some fishes and salamanders live in deep caves not reached by daylight. These species lack eyes. Even if they return to the light, eyes do not form. Evolutionarily, the eyes are lost. It is tempting to attribute this evolutionary loss of eyes to disuse in a dark environment. That, of course, would be invoking a Lamarckian mechanism. Contrary to Lamarck's theory, somatic traits are not inherited.

Because it comes easily, it is difficult to purge a Lamarckian explanation from our own reasoning. We fall automatically and too comfortably into the convenient habit of thinking of parts as rising to meet "needs," one creating the other. For Darwin, and for students coming to evolution fresh today, Lamarck's theory of acquired characteristics impedes clear reasoning. Unfortunately, Lamarck helped popularize an erroneous outlook that current culture perpetuates.

Upward to Perfection

The proposed course of evolution championed by Lamarck also remains an intellectual distraction. The concept of the "scale of nature" (Latin, *scala naturae*) goes back to Aristotle and is stated in various ways by various philosophers. Its central theme holds that evolving life has a direction beginning with the lowest organisms and evolving to the highest, progressively upward toward perfection. Evolutionists, like Lamarck, viewed life metaphorically as ascending a ladder one rung at a time, up toward the complex and the perfected. After a spontaneous origin, organisms progressed up this metaphorical ladder or scale of nature through the course of many generations.

The concept of a ladder of progress was misleading because it viewed animal evolution as internally driven in a particular direction from the early, imperfect, soft-bodied forms up toward perfected humans. As water runs naturally downhill, descent of animals was expected to run naturally to the perfected. Simple animals were not seen as adapted in their own right but rather as springboards to a better future. The scale of nature concept encouraged scientists to view animals as progressive improvements driven by anticipation of a better tomorrow. Unfortunately, remnants of this idea still linger in modern society. Certainly humans are perfected in the sense of being designed to meet demands, but no more so than any other organism. Moles and mosquitoes, bats and birds, earthworms and anteaters all achieve an equally perfect match of parts-to-performance-to-environmental demands. It is not the benefits of a distant future that drive evolutionary change. Instead, the immediate demands of the current environment shape animal design.

The idea of perfection rooted in Western culture is perpetuated by continued technological improvements. We bring it unnoticed, like excess intellectual baggage, into biology where it clutters our interpretation of evolutionary change. When we use the terms *lower* and *higher,* we risk perpetuating this discredited idea of perfection. Lower animals and higher animals are not poorly designed and better designed, respectively. *Lower* and *higher* refer only to order of evolutionary appearance. Lower animals evolved first; higher animals arose after them. Thus, to avoid any suggestion of increasing perfection, many scientists prefer to replace the terms *lower* and *higher* with the terms **primitive** and **derived** to emphasize only evolutionary sequence of appearance, early and later, respectively.

To Lamarck and other evolutionists of his day, nature got better and animals improved as they evolved "up" the evolutionary scale. Thus, Lamarck's historical contribution to evolutionary concepts was double sided. On the one hand, his ideas presented intellectual obstacles. His proposed mechanism of change—inheritance of acquired characteristics—confused physiological response with evolutionary adaptation. By championing a flawed scale of nature, he diverted attention to what supposedly drove animals to a better future rather than to what actually shaped them in their present environment. On the other hand, Lamarck vigorously defended the view that animals evolved. For many years, textbooks have been harsh in their treatment of Lamarck, probably to ensure that his mistakes are not acquired by modern students. However, it is also important to give him his place in the history of evolutionary ideas. By arguing for change in species, Lamarck helped blunt the sharp antievolutionary dissent of contemporaries such as Linnaeus, gave respectability to the idea of evolution, and helped prepare the intellectual environment for those who would solve the question of the origin of species.

Natural Selection

The mechanism of evolution by means of natural selection was unveiled publically by two persons in 1858, although it was conceived independently by both. One was Charles Darwin; the other was Alfred Wallace. Both were part of the respected naturalist tradition in Victorian England that encouraged physicians, clergymen, and persons of leisure to devote time to observations of plants and animals in the countryside. Such interests were not seen as a way to pass idle time in harmless pursuits. On the contrary, observation of nature was respectable because it encouraged intercourse with the Creator's handiwork. Despite the reason, the result was thoughtful attention to the natural world.

A. R. Wallace

Alfred Russel Wallace, born in 1823, was 14 years younger than Darwin (figure 1.6). Although following the life of a naturalist, Wallace lacked the comfortable economic circumstances of most gentlemen of his day; therefore, he turned to a trade for a livelihood. First he surveyed land for railroads in his native England, and eventually, following his interest in nature, he took up the collection of biological specimens in foreign lands to sell to museums back home. His search for rare plants and animals in exotic lands took him to the Amazon jungles and later to the Malay Archipelago in the Far East. We know from his diaries that he was impressed by the great variety and number of species to which his travels introduced him. In early 1858, Wallace fell ill while on one of the Spice Islands (Moluccas) between New Guinea and Borneo. During a fitful night of fever, his mind recalled a book he had read earlier by the Reverend Thomas Malthus entitled *An Essay on the Principle of Population, as It Affects the Future Improvement of Society.* Malthus, writing of human populations, observed that unchecked breeding causes populations to grow geometrically, whereas the supply of food grows more slowly. The simple, if cruel, result is that people increase faster than food. If there is not enough food to go around, some people survive but most die. The idea flashed to Wallace that the same principle applied to all species. In his own words written some years later:

> It occurred to me to ask the question, Why do some die and some live? And the answer was clearly, that on the whole the best fitted lived. From the effects of disease the most healthy escaped; from enemies, the strongest, the swiftest, or the most cunning; from famine, the best hunters or those with the best digestion; and so on.

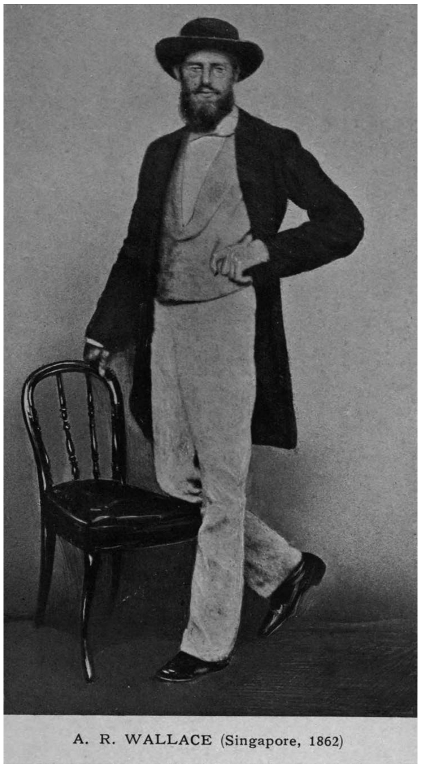


FIGURE 1.6 **Alfred Russel Wallace** (1823–1913) in his thirties.

Source: ©LLP Collection/Alamy Stock Photo

> Then I at once saw, that the ever present variability of all living things would furnish the material from which, by the mere weeding out of those less adapted to the actual conditions, the fittest alone would continue the race.
>
> There suddenly flashed upon me the idea of the survival of the fittest.
>
> The more I thought over it, the more I became convinced that I had at length found the long-sought-for law of nature that solved the problem of the Origin of Species.
>
> (Wallace, 1905)

Wallace began writing that same evening and within two days had his idea sketched out in a paper. Knowing that Darwin was interested in the subject but unaware of how far Darwin's own thinking had progressed, he mailed the manuscript to Darwin for an opinion. The post was slow, so the journey took four months. When Wallace's paper arrived out of the blue with its stunning coincidence to his own ideas, Darwin was taken by complete surprise.

Charles Darwin

Unlike Wallace, Charles Darwin (1809–1882) was born into economic security. His father was a successful physician, and his mother part of the Wedgwood (pottery) fortune. He tried medicine at Edinburgh but became squeamish during operations. Fearing creeping idleness, Darwin's father redirected him to Cambridge and a career in the church, but Darwin proved uninterested. At formal education, he seemed a mediocre student. While at Cambridge, however, his long-standing interest in natural history was encouraged by John Henslow, a professor of botany. Darwin was invited on geological excursions and collected biological specimens. Upon graduation, he joined as *de facto* naturalist of the government's H.M.S. *Beagle* over the objections of his father, who wished him to get on with a more conventional career in the ministry.

He spent nearly five years on the ship and explored the coastal lands it visited. The experience intellectually transformed him. Darwin's belief in the special creation of species, with which he began the voyage, was shaken by the vast array of species and adaptations the voyage introduced to him. The issue came especially to focus on the Galápagos Islands off the west coast of South America. Each island contained its own assortment of species, some found only on that particular island. Local experts could tell at sight from which of the several islands a particular tortoise came. The same was true of many of the bird and plant species that Darwin collected.

Darwin arrived back in England in October 1836 and set to work sorting his collection, obviously impressed by the diversity he had seen but still wedded to misconceptions about the Galápagos collection in particular. He had, for instance, thought that the Galápagos tortoise was introduced from other areas by mariners stashing reptilian livestock on islands to harvest during a later visit. Apparently Darwin dismissed reports of differences among the tortoises of each island, attributing these differences to changes that attended the animals' recent introductions to new and dissimilar habitats. However, in March of 1837, almost a year and a half after departing the Galápagos, Darwin met in London with John Gould, respected specialist in ornithology. Gould insisted that the mockingbirds Darwin had collected on the three different Galápagos Islands were actually distinct species. In fact, Gould emphasized that the birds were endemic to the Galápagos—distinct species, not just varieties—although clearly each was related to species on the South American mainland. It seemed to have suddenly dawned on Darwin that not only birds but plant and tortoise varieties were distinct as well. These tortoises geographically isolated on the Galápagos were not only derivatives of ancestral stocks but now distinct island species.

Here then was the issue. Was each of these species of tortoise or bird or plant an act of special creation? Although distinct, each species also was clearly related to those on the other islands and to those on the nearby South American mainland. To account for these species, Darwin had two serious choices. Either they were products of a special creation, one act for each species, or they were the natural result of evolutionary adaptation to the different islands. If these related species were acts of special divine creation, then each of the many hundreds of species would represent a distinct act of creation. But if this were so, it seemed odd that they would all be similar to each other, the tortoises to other tortoises, the birds to other birds, and the plants to other plants on the various islands, almost as if the Creator ran out of new ideas. If, however, these species were the natural result of evolutionary processes, then similarity and diversity would be expected. The first animal or plant washed or blown to these oceanic islands would constitute the common stock from which similar but eventually distinct species evolved. Darwin sided with a natural evolution.

But Darwin needed a mechanism by which such evolutionary diversification might proceed, and at first he had none to suggest. Not until his return to England did Darwin's experiences from the Galápagos Islands and throughout his voyage crystallize. Two years after his return, and while in the midst of writing up his results of other studies from the *Beagle,* Darwin read for amusement the essay on population by Malthus, the same essay Wallace would discover years later. The significance struck Darwin immediately. If animals, like humans, outstripped food resources, then competition for scarce resources would result. Those with favorable adaptations would fare best, and new species incorporating these favored adaptations would arise. "Here then I had at last got a theory by which to work" wrote Darwin. In a moment of insight, he had solved the species problem. That was 1838, and you would think the excitement would have set him to work on papers and lecturing. Nothing of the sort happened. In fact, four years lapsed before he wrote a first draft, which consisted of 35 pages in pencil. Two years later, he expanded the draft to over 200 pages in ink, but he shoved it quietly into a drawer with a sum of money and a sealed letter instructing his wife to have it published if he met an untimely death. A few close friends knew what he had proposed, but most did not, including his wife with whom he otherwise enjoyed a close and loving marriage. This was Victorian England. Science and religion fit hand and glove.

Darwin's delay testifies to how profoundly he understood the larger significance of what he had discovered. He wanted more time to gather evidence and write the volumes he thought it would take to make a compelling case. Then in June 1858, 20 years after he had first come upon the mechanism of evolution, Wallace's manuscript arrived. Darwin was dumbfounded. By coincidence, Wallace had even hit upon some of the same terminology, specifically, natural selection. Mutual friends intervened, and much to the credit of both Wallace and Darwin, a joint paper was read in the absence of both before the Linnaean Society in London the following month, July 1858. Wallace was, as Darwin described him, "generous and noble." Wallace, in "deep admiration," later dedicated his book on the Malay Archipelago to Darwin as a token of "personal esteem and friendship." Oddly, this joint paper made no stir. But Darwin's hand was now forced.

Critics and Controversy

Darwin still intended a thick discourse on the subject of natural selection but agreed to a shorter version of "only" 500 pages. This was *On the Origin of Species,* published at the end of 1859. By then word was out, and the first edition sold out as soon as it appeared.

Largely because he produced the expanded case for evolution in *On the Origin of Species* and because of a continued series of related work, Darwin is remembered more than Wallace for formulating the basic concept. Darwin brought a scientific consistency and cohesiveness to the concept of evolution, and that is why it bears the name Darwinism.

Science and religion, especially in England, had been tightly coupled. For centuries, a ready answer was at hand for the question of life's origin, a divine explanation, as described in Genesis. Darwinism challenged with a natural explanation. Controversy was immediate, and in some remnant backwaters, it still lingers today. Darwin himself retired from the fray, leaving to others the task of public defense of the ideas of evolution.

Sides quickly formed. Speaking before the English Parliament, the future Prime Minister Benjamin Disraeli safely chose his friends: "The question is this—Is man an ape or an angel? My lord, I am on the side of the angels."

Despite the sometimes misguided reactions, two criticisms stuck, and Darwin knew it. One was the question of variation, the other the question of time. As to time, there seemed not to be enough. If the evolutionary events Darwin envisioned were to unfold, then the Earth must be very old to allow time for life to diversify. In the seventeenth century, James Ussher, Archbishop of Armagh and Primate of All Ireland, made an honorable effort to calculate the age of the Earth. From his biblical studies of who begot whom and from historical dates available at the time, Ussher determined that the first day of Creation began in 4004 B.C. on Saturday, October 22, at nightfall. A contemporary, Dr. John Lightfoot, vice-chancellor at Cambridge University, estimated further that humans were created five days later, at 9:00 in the morning, presumably Greenwich mean time. Many took this date as literally accurate, or at least as indicative of the recent origin of humans, leaving no time for evolution from apes or angels. A more scientific effort to age the Earth was made by Lord Kelvin, who used temperatures taken in deep mine shafts. Reasoning that the Earth would cool from its primitive molten state to present temperatures at a constant rate, Kelvin extrapolated backward to calculate that the Earth was no more than 24 million years old. He did not know that natural radioactivity in the Earth's crust keeps the surface hot. This fact deceptively makes it seem close in temperature and thus in age to its molten temperature at first formation. The true age of the Earth is actually several billion years, but unfortunately for Darwin, this was not known until long after his death.

Critics also pointed to inheritance of variation as a weak spot in his theory of evolution. The basis of heredity was unknown in Darwin's day. The popular view held that inheritance was blending. Like mixing two paints, offspring received a blend of characteristics from both parents. This view, although mistaken, was taken seriously by many. It created two problems for Darwin. From where did variation come? How was it passed from generation to generation? If natural selection favored individuals with superior characteristics, what ensured that these superior characteristics were not blended and diluted out of existence in the offspring? If favored characters were blended, they would effectively be lost from view and natural selection would not work. Darwin could see this criticism coming and devoted much space in *On the Origin of Species* to discussing sources of variation.

Today, we know the answers to this paradox. Mutations in genes produce new variations. Genes carry characteristics unaltered and without dilution from generation to generation. This mechanism of inheritance was unknown and unavailable to Darwin and Wallace when they first sought answers to the origin of species. It was probably no coincidence that the intellectual breakthroughs of both were fostered by voyages of separation from the conventional scientific climate of their day. Certainly, study of nature was encouraged, but a ready interpretation of the diversity and order they observed awaited such naturalists. Although the biblical story of creation in Genesis was conveniently at hand and taken literally by some to supply explanations for the presence of species, there were scientific obstacles as well. Confusion between physiological and evolutionary adaptation (Lamarck), the notion of a scale of nature, the idea of fixity of species (Linnaeus and others), the young age of Earth (Kelvin), and the mistaken views of variation and heredity (blending inheritance) all differed from predictions of evolutionary events or confused the picture. It is testimony to their intellectual insight that Darwin and Wallace could see through the obstacles that defeated others.

Historical Predecessors—Morphology

We might expect that the study of structure and the study of evolution historically shared a cozy relationship, each supporting the other. After all, the story of evolution is written in the anatomy of its products, in the plants and animals that tangibly represent the unfolding of successive changes through time. For the most part, direct evidence of past life and its history can be read in the morphology of fossils. By degrees, living animals preserve evidence of their phylogenetic background. It might seem then that animal anatomy would have fostered early evolutionary concepts. For some nineteenth-century anatomists, this was true. T. H. Huxley (1825–1895), remembered for many scientific contributions including monographs on comparative anatomy, remarked upon first hearing Darwin's ideas of natural selection words to the effect, "How truthfully simple. I should have thought of it." Huxley was won over (figure 1.7). Although Darwin retired from public controversy following the publication of *On the Origin of Species,* Huxley pitched in with great vigor, becoming "Darwin's Bulldog" to friend and foe alike.

Not all anatomists joined the evolutionary bandwagon so easily, however. Some simply misread morphology as giving evidence of only stasis, not change. On the other hand, many raised solid objections to Darwinian evolution, some of which still have not been addressed even today by evolutionary biologists. To understand the contribution of morphology to intellectual thought, we need to backtrack a bit to the anatomists who preceded Darwin. Foremost among these was the French comparative anatomist, Georges Cuvier.

FIGURE 1.7 **Thomas H. Huxley** (1825–1895) at age 32.

Source: ©Pictorial Press Ltd/Alamy Stock Photo

Georges Cuvier

Georges Cuvier (1769–1832) brought attention to the function that parts performed (figure 1.8). Because parts and the function they served were tightly coupled, Cuvier argued that organisms must be understood as functional wholes. Parts had dominant and subordinate ranking as well as compatibility with each other. Certain parts necessarily went together, but others were mutually exclusive. Possible combinations were thus limited to parts that meshed harmoniously and met necessary conditions for existence; therefore, the number of ways parts could be assembled into a workable organism was predictable. Given one part of an organism, Cuvier once boasted, he could deduce the rest of the organism. Parts of organisms, like parts of a machine, serve some purpose. Consequently, for the entire organism (or machine) to perform properly, the parts must harmonize. Sharp carnivore teeth would be necessarily set in jaws suited for biting, into a skull that buttressed the jaw, on a body with claws for snaring prey, with a digestive tract for digesting meat, and so forth (figure 1.9). Alter one part, and the structurally and functionally integrated machinery of the organism would fail. If one part is altered, function of connected parts is disrupted, and performance fails. Evolution could not happen. If an animal were altered, harmony among the parts would be destroyed, and the animal would no longer be viable. Change (evolution) would cease before it began. Cuvier's functional morphology put him in intellectual company with Linnaeus but in opposition to Lamarck's evolutionary ideas.

Cuvier took comfort as well from the known fossil record of his day. Gaps existed between major groups, as would be

FIGURE 1.8 **Georges Cuvier** (1769–1832). His life spanned the French Revolution, which at first won his sympathies, but as lawlessness and bloodshed became more of its character, he grew increasingly dismayed by its excesses. His life also overlapped with Napoleon's rule. Cuvier came to Paris in 1795 to take a post at the Muséum National d'Histoire Naturelle, where he pursued administrative duties and studies in paleontology, geology, and morphology for most of his remaining life.

Source: ©traveler1116/Getty Images

expected if species were immutable and evolution did not occur. During his time, ancient Egyptian mummies of humans and animals were being pilfered by Napoleon's armies and sent to European museums. Dissection proved that these ancient animal mummies were structurally identical to modern species. Again, this was evidence of no change, at least to Cuvier. Today, with a more complete fossil record at our disposal and a realization that evolution occurred over millions of years, not just within the few millennia since the time of the pharoahs, we could enlighten Cuvier. In his day, however, the mummies were for Cuvier sweet pieces of evidence confirming what his view of morphology required. Parts were adapted to perform specific functions. If a part was changed, function failed and an animal perished. Thus, there was no change and no evolution of species.

Richard Owen

English anatomist Richard Owen (1804–1892) believed like Cuvier that species were immutable, but unlike Cuvier, he felt that the correspondence between parts (homologies) could not be left without explanation (figure 1.10a). Virtually the same bones and pattern are present in the flipper of a dugong, the forelimb of a mole, and the wing of a bat (figure 1.10b). Each possesses the same bones. Why?

From our twentieth-century perspective, the answer is clear. Out of a common ancestry, evolution passes along similar structures to perform new adaptive functions. But Owen, opposed to evolutionary ideas, was determined to find an alternative explanation. His answer centered around **archetypes.** An archetype was a kind of biological blueprint, a supposed underlying plan upon which an organism was built. All parts arose from it. Members of each major animal group were constructed from the same essential, basic plan. All vertebrates, for instance, were thought to share the same archetype, which explained why all possessed the same fundamental parts. Specific differences were forced on this underlying plan by particular functional needs. Owen was fuzzy about why he ruled out an evolutionary explanation, but he was vigorous in promoting his idea of archetypes.

He even carried this idea to repeated parts within the same individual (figure 1.11a). For example, he envisioned that the vertebrate skeleton consisted of a series of idealized segments he termed vertebrae (figure 1.11b). Not all available parts of these serially repeated vertebrae were expressed at each segment, but all were available if demanded. Taken together, this idealized series of vertebrae constituted the archetype of the vertebrate skeleton. Johann Wolfgang von

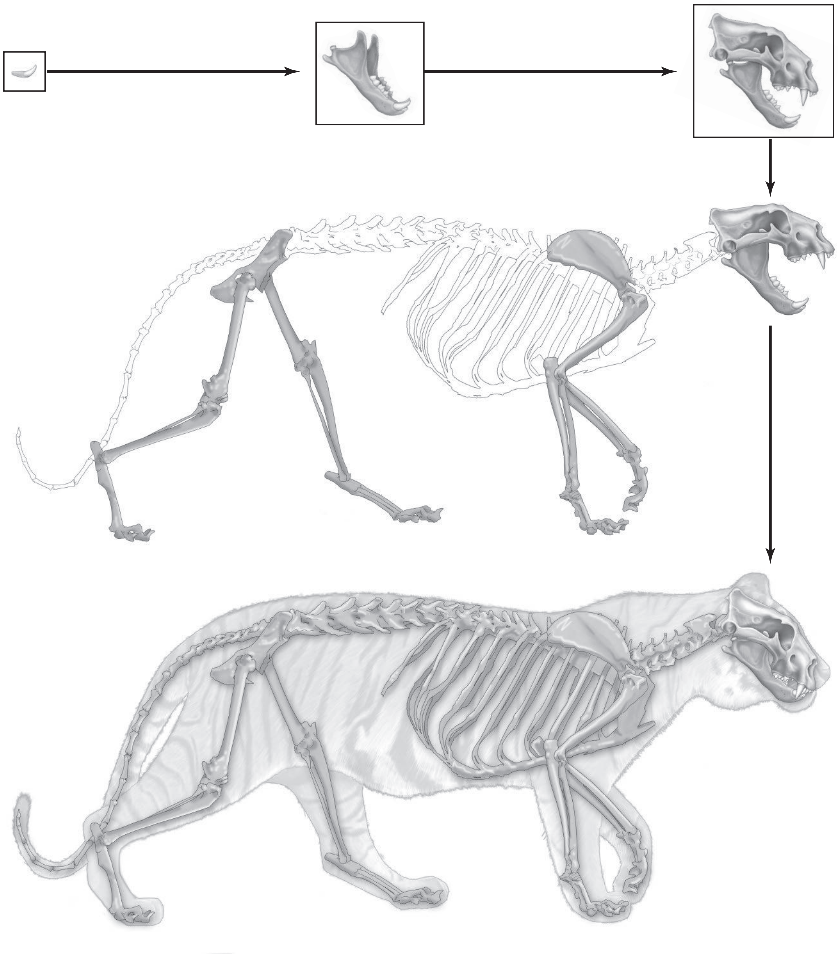


FIGURE 1.9 Irreducible design. Cuvier recognized that organisms were complex functional wholes. Certain parts necessarily fit together. Remove a part and the whole organism fails. Consequently, Cuvier boasted that given one part, he could deduce the rest. Start with a carnivore's tooth and it necessarily fit into a strong jaw, part of a robust skull, aided by clawed limbs to snare prey, set into a predator's body, and so forth.

Goethe (1749–1832), although perhaps best remembered as a German poet, also dabbled in morphology and was the first to suggest that the vertebrate skull was created from modified and fused vertebrae. His idea was expanded by others, such as Lorenz Oken (1779–1851), so by Owen's time, the concept was well known. Owen considered the skull to be formed of vertebrae extended forward into the head. He held that all four vertebrae contributed and even went so far as to derive human hands and arms from parts of the fourth contributing vertebra, "the occipital segment of the skull."

T. H. Huxley, in a public lecture (published in 1857–1859), took to task the "vertebral theory of the skull," as it had become known. Bone by bone, he traced homologies and developmental appearances of each skull component. He reached two major conclusions. First, all vertebrate skulls are constructed on the same plan. Second, this developmental plan is *not* identical to the developmental pattern of the vertebrae that follow. The skull is not an extension of vertebrae, at least according to Huxley. Ostensibly, the subject of Huxley's public lecture was the skull, but his target was Owen and the archetype. The archetype is, wrote Huxley, "fundamentally opposed to the spirit of modern science."

Certainly Owen was the leader of those morphologists who idealized structure and pushed the vertebral theory of the skull too far and too literally. On the other hand, Huxley succeeded too well in discrediting the concept of archetypes. The two men clashed over archetypes and came down on opposite sides of evolution as well (Huxley for, Owen against). With the eventual triumph of Darwinian evolution in the twentieth century, the issues raised by morphologists such as Owen and Cuvier also tended to be forgotten. In a sense, the baby got thrown out with the bath water; that is, serious morphological issues were forgotten as evolutionary concepts triumphed.

The rise of molecular biology in recent times has further contributed to the displacement of morphology. Molecular biology has won a deserved place in modern science, with its successes in medicine and insights into the molecular machinery of the cell. Unfortunately, in some circles, all significant biological issues that humans face have been reduced to the chemical laws that govern molecules. In its extreme, such a reductionist view sees an organism as nothing more than the simple sum of its parts—know the molecules to know the person.

Certainly this is naive. A long distance separates the molecules of DNA from the final product we recognize as a fish or a bird or a human. Furthermore, as obvious as it might sound, the action of DNA does not reach upward to affect the agency of natural selection, but rather natural selection acts downward on DNA to affect the genetic structure of populations. A great deal of what we need to understand about ourselves comes from the world around us, not just from the DNA within.

Practitioners of morphology have begun to take these issues that occupied Cuvier and Owen a century and a half ago and bring them forward in a modern context. Cuvier's emphasis on adaptation has been given new life because of the clarity it brings to our appreciation of biological design.

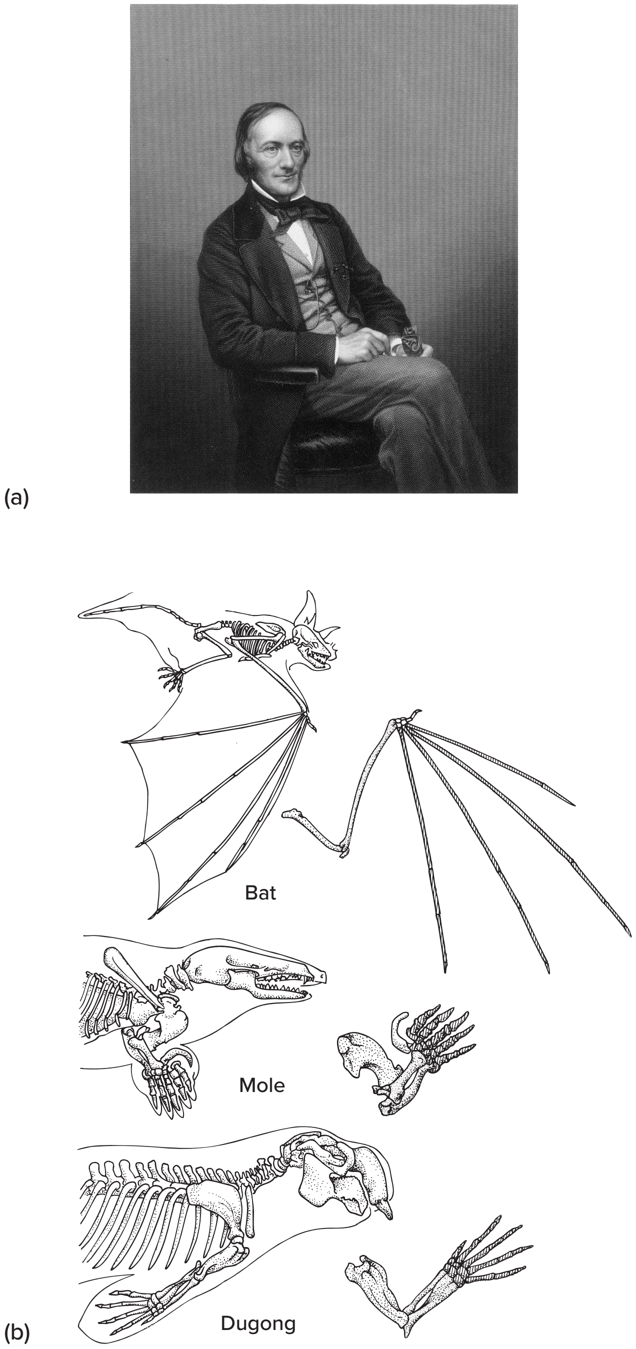


FIGURE 1.10 **Richard Owen** (1804–1892). (a) Although admired for his anatomical research, Owen was a difficult man from the accounts of those who worked or tangled with him. He agreed with Cuvier's emphasis on adaptation; however, he felt some explanation for homologies was required and, therefore, introduced the idea of archetypes. (b) Forelimbs of bat, mole, and dugong. Owen noted that each limb performs a different function—flight, digging, and swimming, respectively—and each is superficially different, but he could trace all three to an underlying common plan he called the archetype. Today, we recognize that common ancestry accounts for these underlying similarities, although we would join Owen in crediting adaptation for the superficial differences among these homologous parts.

Source: (a) ©World History Archive/Alamy Stock Photo; (b) From R. Owen.

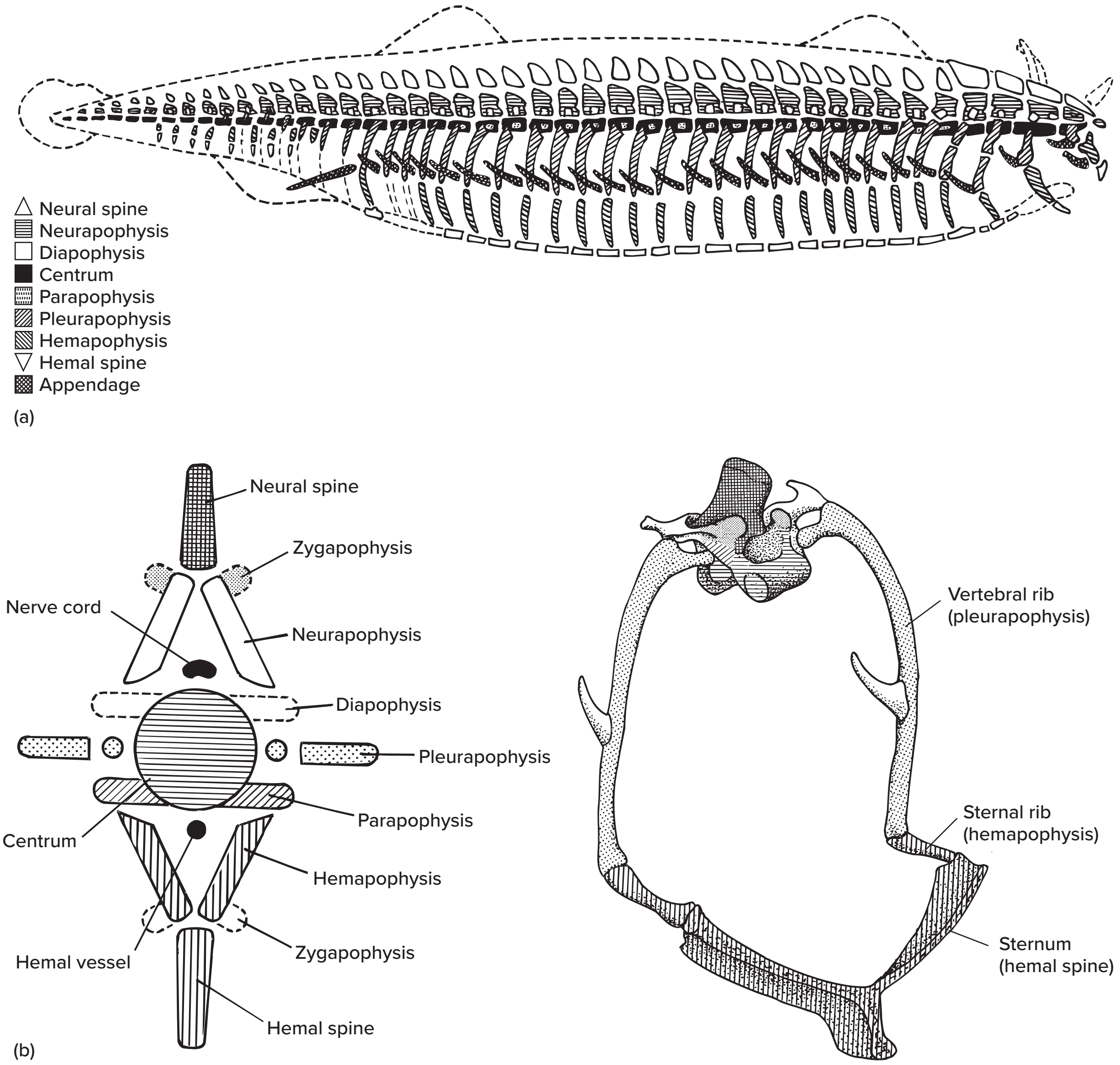


FIGURE 1.11 Vertebrate archetype. Richard Owen saw the underlying pattern of the vertebrate body as a repeating series of vertebral units, collectively the vertebrate archetype (a). Owen supported the view that these vertebral units, carried forward into the head, even produced the basic elements of the skull. (b) Ideal vertebra. Each vertebra potentially included numerous elements, although not all were expressed in each segment. An actual section from a bird's skeleton indicates how this underlying plan might be realized.

Source: From R. Owen.

The idea of a pattern underlying the process of design has also been revisited. The result of this has been quite surprising. To explain biological design, we need more than Darwinism. Morphology, too, must be seen as a cause of design.

Why Are There No Flying Elephants?

Not all animal designs are equally likely. Some imaginable animal concoctions simply do not work mechanically, so they never arise. Their bulk is too great or their design unwieldy. An elephant with wings would literally never fly; that is obvious. Yet many modern evolutionary biologists tend to forget about physical limitations when discussing animal design. Most resort solely to evolutionary explanations. It is tempting to be satisfied with such comfortable explanations of animal design—the long necks of giraffes give them reach to treetop vegetation, the hair of mammals insulates their warm-blooded bodies, the fins of fishes control their swimming, the venom of vipers improves their hunting success.

These and other examples of animal design were favored by natural selection, presumably for the adaptive advantages each conferred. This is reasonable, as far as it goes, but it is only half an explanation. Figuratively, natural selection is an external architect that chooses designs to fit current purposes. But the raw materials or morphology of each animal is itself a factor in design. To build a house with doors, walls, and roof, the architect lays out a scheme, but the materials available affect the character of the house. Use of brick, wood, or straw will place limits or constraints on the design of the house. Straw cannot bear several stories of weight as can bricks, but it can be bent into rounded shapes. Wood makes for economical construction but is susceptible to rot. Opportunities and limitations for design lie in each material.

To explain form and design, we must certainly consider the environment in which an animal resides. Among bird groups, there are no truly burrowing species that are counterparts to mammalian moles. So-called burrowing owls exist, but these are hardly equal to moles in exploiting a subterranean existence. Most modern amphibians occur near water because of their moisture requirements. Gliding fishes exist, but truly flying forms with strong wings do not. Elephants are large and ponderous in construction, which precludes a flying form on the elephant plan no matter how strongly natural selection favors it.

To understand form and to explain design, we must evaluate both external and internal factors. The external environment assaults an organism with a wrath of predators, challenges of climate, and competition from others. Natural selection is a manifestation of these factors. Internal factors play a part as well. Parts are integrated into a functionally whole individual. If design changes, it must do so without serious disruption of the organism. Because parts are interlocked into a coherent whole, there exist limits to change before the organism's machinery will fail. The internal construction of an organism sets boundaries to allowable change. It establishes possibilities engendered by natural selection. As new species appear, further possibilities open. But natural selection does not initiate evolutionary changes in design. Like a jury, natural selection acts only on the possibilities brought before it. If natural selection is strong and possibilities are few, then extinction occurs or diversification along that particular evolutionary course is curtailed. As a result, the avian design for delicacy of flight offers few possibilities for evolution of robust design and powerful forelimbs for digging. On the other hand, the avian design allows for the further evolution of airborne vertebrate species. Not all evolutionary changes are equally probable, in large part because not all morphologies (combinations of parts) are equally available to natural selection.

Morphology embraces the study of form and function, of how a structure and its function become an integrated part of an interconnected design (the organism), and of how this design itself becomes a factor in the evolution of new forms. The term **morphology** is not just a synonym for the word **anatomy.** It has always meant much more; for Cuvier, it meant the study of structure with function; for Owen, it meant the study of archetypes behind the structure; and for Huxley, it meant a study of structural change over time (evolution). Today, diverse schools of morphology in North America, Europe, and Asia all generally share an interest in the structural integration of parts, the significance of this for the functioning of the organism, and the resulting limitations and possibilities for evolutionary processes. Morphology does not reduce explanations of biological design to molecules alone. Morphological analysis focuses on higher levels of biological organization—at the level of the organism, its parts, and its position within the ecological community.

Morphological Concepts

To analyze design, concepts of form, function, and evolution have developed. Some of the most useful of these address similarity, symmetry, and segmentation.

Similarities

In different organisms, corresponding parts may be considered similar to each other by three criteria—ancestry, function, and appearance. The term **homology** applies to two or more features that share a common ancestry, the term **analogy** to features with a similar function, and the term **homoplasy** to features that simply look alike (figure 1.12). These terms date back to the nineteenth century but gained their current meanings after Darwin established the theory of common descent.

More formally, features in two or more species are homologous when they can be traced back in time to the same feature in a common ancestor. The bird's wing and the mole's arm are homologous forelimbs, tracing their common ancestry to reptiles. Homology recognizes similarity based upon common origin. A special case of homology is **serial homology,** which means similarity between successively repeated parts in the *same* organism. The chain of vertebrae in the backbone, the several gill arches, or the successive muscle segments along the body are examples.

Analogous structures perform similar functions, but they may or may not have similar ancestry. Wings of bats and

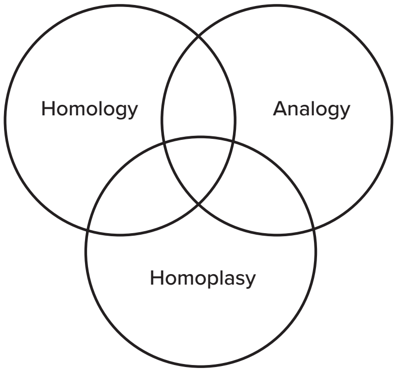


FIGURE 1.12 **Similarities.** Parts may be similar in ancestry, function, and/or appearance. Respectively, these are defined as homology, analogy, or homoplasy. None of these types of similarities is mutually exclusive. Parts may simultaneously be homologous and analogous and homoplastic.

bees function in flight, but neither structure can be traced to a similar part in a common ancestor. On the other hand, turtle and dolphin forelimbs function as paddles (analogy) and can be traced historically back to a common source (homology). Analogy recognizes similarity based upon similar function.

Homoplastic structures look alike and may or may not be homologous or analogous. In addition to sharing a common origin (homology) and function (analogy), turtle and dolphin flippers also look superficially similar; they are homoplastic. The most obvious examples of homoplasy come from mimicry or camouflage, where an organism is in part designed to conceal its presence by resembling something unattractive. Some insects have wings shaped and sculptured like leaves. Such wings function in flight, not in photosynthesis (they are not analogous to leaves), and certainly such parts share no common ancestor (they are not homologous to leaves), but outwardly they have a similar appearance to leaves; they are homoplastic.

Keep in mind that the similarities are not exact, point by point, but represent overall similarities in appearance. Such simple definitions of similarities have not been won easily. Historically, morphology has struggled to clarify the basis of structural similarities. Before Darwin, biology was under the influence of idealistic morphology, the view that each organism and each part of an organism outwardly expressed an underlying plan. Morphologists looked for the essence or ideal type behind the structure. The explanation offered for this ideal was the unity of plan. Owen proposed that archetypes were the underlying source for an animal's features. Homology for Owen meant comparison to the archetype, not to other adjacent body parts and not to common ancestors. Serial homology meant something different too, based again on this invisible archetype. But Darwinian evolution changed this by bringing an explanation for similarities, namely common descent.

Analogy, homology, and homoplasy are each separate contributors to biological design. Dolphins and bats live quite different lives, yet within their designs we can find fundamental likenesses—hair (at least some), mammary glands, similarities of teeth and skeleton. These features are shared by both because both are mammals with a distinct but common ancestry. Dolphins and ichthyosaurs belong to quite different vertebrate ancestries, yet they share certain likenesses—flippers in place of arms and legs and streamlined bodies. These features appear in both because both are designed to meet the common hydrodynamic demands of life in open marine waters. In this example, convergence of design to meet common environmental demands helps account for likenesses of some locomotor features (figure 1.13). On the other hand, the webbed hindfeet of gliding frogs and penguins have little to do with common ancestry (they are not closely related) or with common environmental demands (the frog glides in air, the penguin swims in water). Thus, structural similarity can arise in several ways. Similar function in similar habitats can produce convergence of form (analogy); common historical ancestry can carry forward shared and similar structure to descendants (homology); occasionally, accidents or incidental events can lead to parts that simply look alike (homoplasy). In explaining design, we can invoke one, two, or all three factors in combination. To understand design, we need to recognize the possible contribution of each factor separately.

Symmetry

Symmetry describes the way in which an animal's body meets the surrounding environment. **Radial symmetry** refers to a body that is laid out equally from a central axis, so that any of several planes passing through the center divides the animal into equal or mirrored halves (figure 1.14a). Invertebrates such as jellyfishes, sea urchins, and sea anemones provide examples. With **bilateral symmetry,** only the **midsagittal plane** divides the body into two mirrored images, left and right (figure 1.14b).

Body regions are described by several terms (figure 1.14c). **Anterior** refers to the head end **(cranial), posterior** to the tail **(caudal), dorsal** to the back, and **ventral** to the belly or front. The midline of the body is **medial;** the sides are **lateral.** An attached appendage has a region **distal** (farthest) and **proximal** (closest) to the body. The **pectoral region** or chest supports the forelimbs; the **pelvic region** refers to hips supporting the hindlimbs. A **frontal plane (cononal plane)** divides a bilateral body into dorsal and ventral sections, a **sagittal plane** splits it into left and right portions, and a **transverse plane** separates it into anterior and posterior portions.

Because humans carry the body upright and walk with the belly forward, the terms **superior** and **inferior** generally replace the terms *anterior* and *posterior,* respectively, in medical anatomy. Like many terms used only in the descriptive anatomy of humans, *superior* and *inferior* are poor ones to employ in general comparative research because few animals other than humans walk upright. If you venture into the study of human anatomy, you can expect to meet such specialized terms.

Segmentation

A body or structure built of repeating or duplicated sections is segmented. Each repeated section is referred to as a **segment** (or **metamere**), and the process that divides a body into duplicated sections is called **segmentation** (or **metamerism**). The backbone, composed of repeating vertebrae, is a segmental structure; so is the lateral body musculature of fish that is built from repeating sections of muscle.

Not all body segmentation is the same. To understand design based upon segmentation, we need to turn our attention to invertebrates. Among some invertebrates, segmentation is the basis for amplifying reproductive output. In tapeworms, for example, the body begins with a head (the scolex), followed by duplicated sections called proglottids (figure 1.15). Each section is a self-contained reproductive "factory" housing complete male and female reproductive organs. The more sections, the more factories, and the more eggs and sperm produced. Some overall body unity is established by simple but continuous nerve cords and excretory canals that run from segment to segment. Other than this, each segment is semiautonomous, a way to

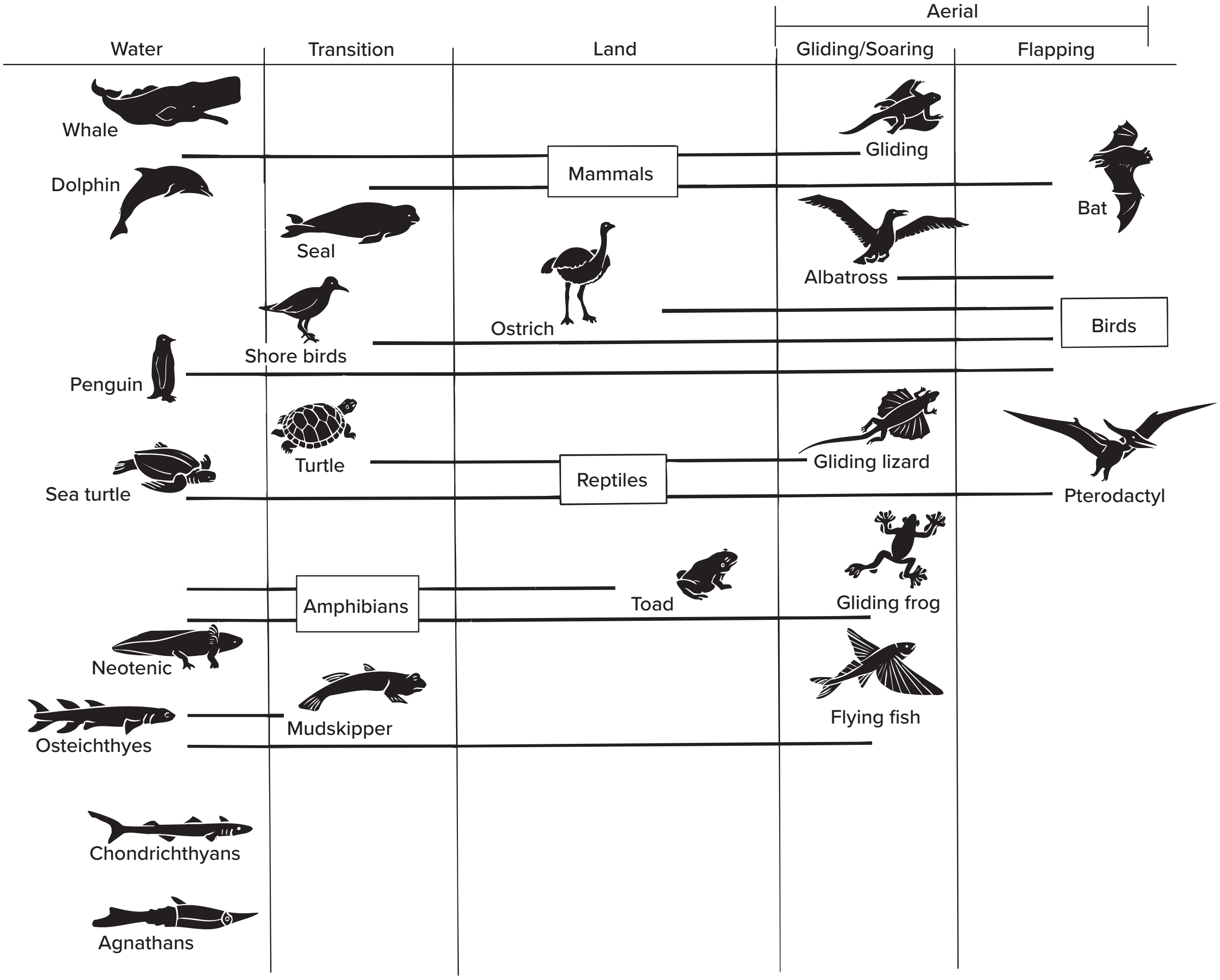


FIGURE 1.13 **Convergence of design.** Groups of animals often evolve in habitats that differ from those of most other members of their group. Most birds fly, but some, such as ostriches, cannot and live exclusively on land; others, such as penguins, live much of their lives in water. Many, perhaps most, mammals are terrestrial, but some fly (bats), and others live exclusively in water (whales, dolphins). "Flying" fishes take to the air. As species from different groups enter similar habitats, they experience similar biological demands. Convergence to similar habitats in part accounts for the sleek bodies and fins or flippers of tuna and dolphins because similar functions (analogy) are served by similar parts under similar conditions. Yet tuna and dolphins come from different ancestries and are still fish and mammal, respectively. Common function alone is insufficient to explain all aspects of design. Each design carries historical differences that persist despite similar habitat.

replicate sex organs and boost overall reproductive output, which is quite unlike segmentation found in other animals.

Annelids, such as earthworms and leeches, have segmented bodies that provide support and locomotion rather than reproduction. Annelid segmentation differs from that of tapeworms because the annelid body coelom is fluid filled and forms a hydrostatic skeleton. The hydrostatic skeleton is one of two basic types of supportive systems found in animals.

The other supportive system we see in animals is a rigid skeleton. We are familiar with a rigid skeleton because our bones and cartilage constitute such a system. Another example is the chitinous outer skeletons of arthropods, such as crabs, lobsters, and insects. Rigid skeletons are efficient systems of levers that allow selective muscle use to produce movement.

Although hydrostatic skeletons are perhaps less familiar to you, they are common among animals. As the term *hydro* suggests, this supportive system includes a fluid-filled cavity enclosed within a membrane. A hydrostatic skeleton usually is further encased within a muscular coat. At its simplest, the muscular coat is composed of circular and longitudinal bands of muscle fibers (figure 1.16). Movement is accomplished by controlled muscle deformation of the hydrostatic skeleton.

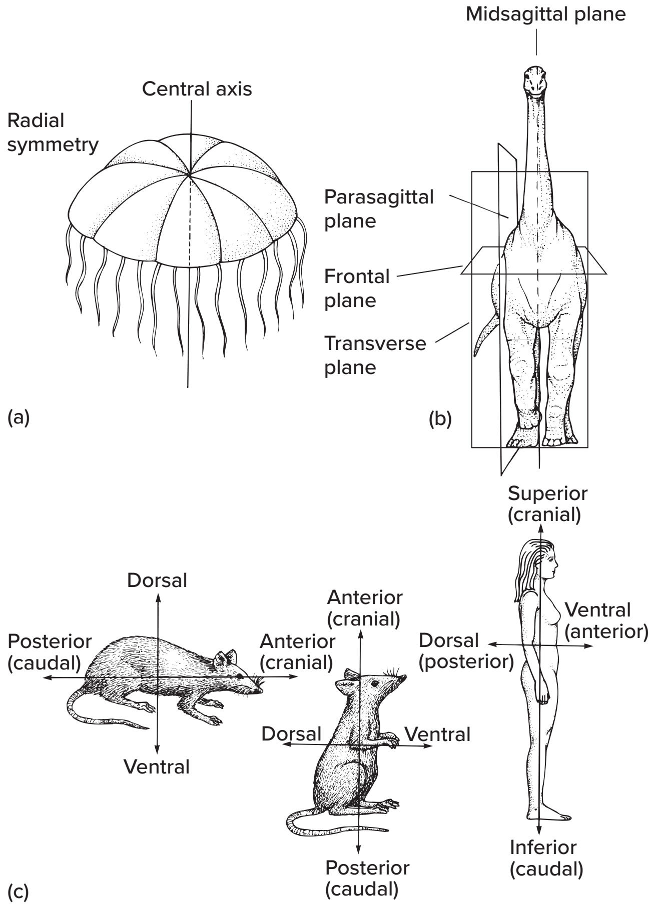


FIGURE 1.14 **Body symmetry.** Radial and bilateral are the two most common body symmetries. (a) Radially symmetrical bodies are laid out regularly around a central axis. (b) Bilaterally symmetrical bodies can be divided into mirror images only through the midsagittal plane. (c) Dorsal and ventral refer to back and belly, respectively, and anterior and posterior to cranial and caudal ends, respectively. In animals that move in an upright position (e.g., humans), superior and inferior apply to cranial and caudal ends, and ventral and dorsal apply to anterior and posterior sides, respectively.

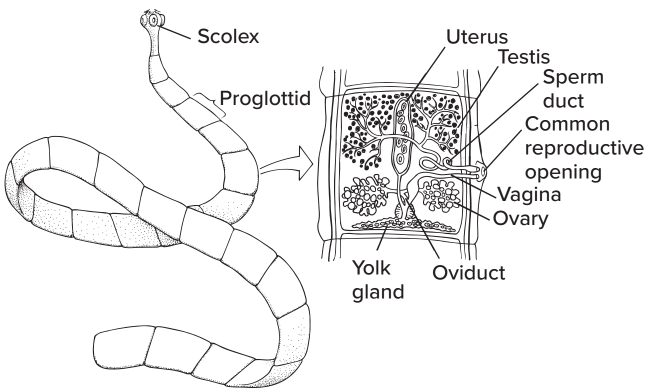


FIGURE 1.15 **Segmented tapeworm.** Each section, or proglottid, is a reproductive factory producing eggs and sperm.

In burrowing or crawling animals, movement is usually based on peristaltic waves produced in the body wall. Swimming motions are based on sinusoidal waves of the body.

The advantage of a hydrostatic skeleton is the relatively simple coordination. Only two sets of muscles, circular and longitudinal, are required. Consequently, the nervous system of animals with hydrostatic systems is usually simple as well. The disadvantage is that any local movement necessarily involves the entire body. Because the fluid-filled cavity extends through the entire body, muscle forces developed in one region are transmitted through the fluid to the entire animal. Thus, even when movement is localized, muscles throughout the body must be deployed to control the hydrostatic skeleton.

In truly segmented animals, **septa** sequentially subdivide the hydrostatic skeleton into a series of internal compartments. As a consequence of compartmentalization, the body musculature is also segmented, and in turn the nerve and blood supply to the musculature are segmentally arranged as well. The locomotor advantage is that such segmentation allows for more localized muscle control and localized changes in shape (figure 1.17). For instance, the segmented body of an earthworm is capable of localized movement.

Segmentation among vertebrates is less extensive than segmentation among invertebrates. Lateral body musculature is laid out in segmental blocks, and nerves and blood vessels supplying it follow this segmental pattern. But segmentation goes no deeper. The viscera are not repeated units, and the body cavity is not serially compartmentalized. Locomotion is provided by a rigid skeleton, and the vertebral column (or notochord) is served by segmental body musculature; however, segmentation of the outer body musculature does not extend inward to the coelom and viscera.

Although the vertebrate body is not composed of a hydrostatic skeleton, selected organs are based on the principle of hydrostatic support. The notochord, for instance,

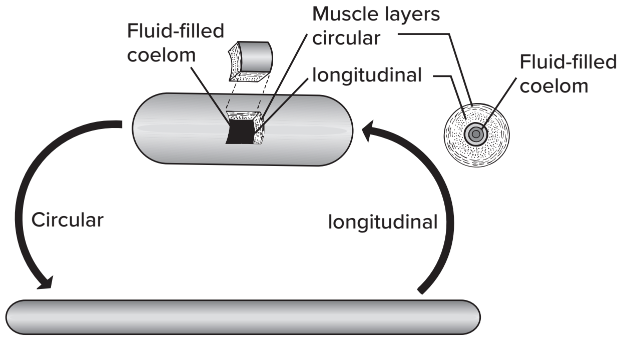


FIGURE 1.16 **Hydrostatic skeleton.** At its simplest, changes in shape and movement involve two mechanical units, the muscle layers of the body wall (longitudinal and circular) and the fluid-filled body coelom within. Contraction of the circular muscles lengthens the shape; contraction of longitudinal muscles shortens the body. The fluid within is incompressible so that muscular forces are spread throughout the body to bring about changes in shape.

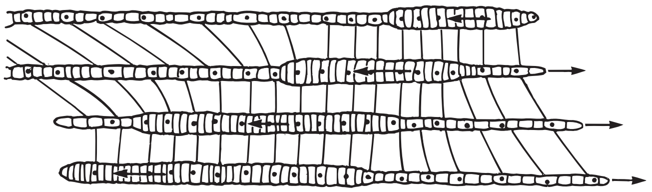


FIGURE 1.17 Locomotion of a segmented worm. Fluid within the body cavity flows into selected compartments, filling and expanding each. This ballooning of the body is controlled selectively by each body segment and coordinated overall by the worm's nervous system. As the fluid passes backward from one compartment to the next, each expanded segment pushes against the surrounding soil in turn and establishes a firm hold on the walls of the worm's tunnel-shaped body. Extension of the anterior body pushes the head forward in order for the worm to make progress through the soil.

Source: After Gray and Lissmann.

contains a core of fluid-engorged cells tightly wrapped in a sheath of fibrous connective tissue. This incompressible but flexible rod is a hydrostatic organ that functions to keep the body at a constant length. The penis is another example of a hydrostatic organ. When properly stimulated, cavities within it fill firmly with fluid, in this case with blood, to give the penis an erect rigidity of some functional significance.

Evolutionary Morphology

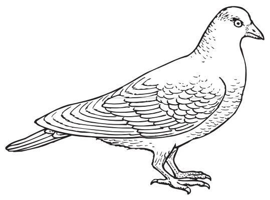
As mentioned previously, evolution and morphology have not always been happy companions. On the brighter side, the more recent cooperation between scientists in both disciplines has clarified our understanding of animal design. With this cooperation, concepts of design and change in design have come into better relief.

Function and Biological Role

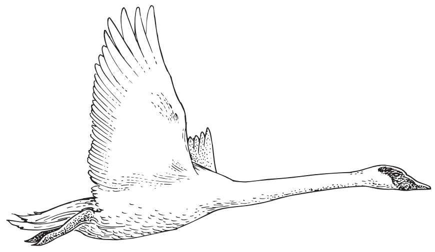
For most of us, the concept of function is rather broad and used loosely to cover both how a part works in an organism and how it serves adaptively in the environment. The cheek muscles in some small mice act to close their jaws and chew food. In so doing, these muscles perform the adaptive role of processing food. The same structure works both within an organism (chewing) and in the role of meeting environmental demands (resource processing). To recognize both services, two terms are employed. The term **function** is restricted to mean the action or property of a part as it works *in an organism.* The term **biological role** (or just **role**) refers to how the part is used *in the environment* during the course of the organism's life history.

In this context, the cheek muscles of mice function to close the jaws and serve the biological role of food processing. Notice that a part may have several biological roles. Not only do jaws serve a role in food processing, but they might also serve the biological role of protection or defense if used to bite an attacking predator. One part may also serve several functions. The quadrate bone in reptiles functions to attach the lower jaw to the skull. It also functions to transmit sound waves to the ear. This means that the quadrate participates in at least two biological roles: feeding (food procurement) and hearing (detection of enemies or prey). Body feathers in birds provide another example (figure 1.18a–c). In most birds, feathers function to cover the body. In the environment, the biological roles of feathers include insulation (thermoregulation), aerodynamic contouring of body shape (flight), and in some, display during courtship (reproduction).

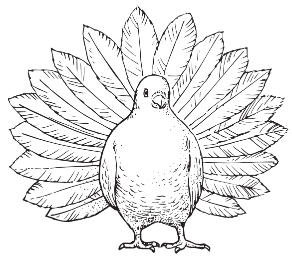
Functions of a part are determined largely in laboratory studies; biological roles are observed in field studies. Inferring biological roles only from laboratory studies can be misleading. For example, some harmless snakes produce oral secretions in which laboratory biologists discovered toxic properties. Many leaped to the conclusion that the biological role of such toxic oral secretions must be to kill prey rapidly, but field studies proved that this was not the case. Humans also produce a saliva that is mildly toxic (function), but certainly we do not use it to envenomate prey (biological role).



(a) Thermoregulation



(b) Contour



(c) Courtship

FIGURE 1.18 Biological roles. The same structure may serve several biological roles. For example, in addition to producing lift for flight, feathers play a part in (a) thermoregulation (insulation), to prevent heat loss to a cold environment; (b) aerodynamic contouring (flight), to streamline the body; and (c) reproduction (courtship), to display colors to rivals or mates. Redrawn from W. J. Bock, "The Role of Adaptive Mechanisms in the Origin of Higher Levels of Organization," *Systematic Zoology*, 14: 272–287, 165. Reprinted with permission.

Saliva serves the biological role of processing food by initiating digestion and lubrication of food. Toxicity is an inadvertent by-product of human saliva, without any adaptive role in the environment.

Preadaptation

For many scientists, the word **preadaptation** is chilling because it seems to invite a misunderstanding. Alternative terms have been proposed (protoadaptation, exaptation), but these really do not help and only congest the literature with redundant jargon. If we keep in mind what preadaptation does not mean as well as what it signifies, then the term should present no special difficulty. Preadaptation means that a structure or behavior possesses the necessary form and function *before* (hence *pre-*) the biological role arises that it eventually serves. In other words, a preadapted part can do the job before the job arrives. The concept of preadaptation does not imply that a trait arises in anticipation of filling a biological role sometime in the future. Adaptive traits serve roles of the moment. If there is no immediate role, selection eliminates the trait.

For example, feathers likely evolved initially in birds (or in their immediate ancestors) as insulation to conserve body heat. Like hair in mammals, feathers formed a surface barrier to retard the loss of body heat. For warm-blooded birds, feathers were an indispensable energy-conserving feature. Today, feathers still play a role in thermoregulation; however, for modern birds, flight is the most conspicuous role of feathers. Flight came later in avian evolution. Immediate ancestors to birds were ground- or tree-dwelling, reptilelike animals. As flight became a more important lifestyle in this evolving group, feathers already present for insulation became adapted into aerodynamic surfaces in order to serve flight. In this example, we can say that insulating feathers were a preadaptation for flight. They were ready to serve as aerodynamic surfaces before that biological role actually arose.

Similarly, the wings of diving birds are preadapted as paddles. In pelicans and auks, they are used to swim while the bird is submerged. If, as now seems likely, primitive lungs for respiration arose early in fishes, then they were preadapted to become swim bladders, buoyancy devices of later fishes. Fish fins were preadapted to become tetrapod limbs.

One hypothetical scheme of preadaptation traces the origin of birds from reptiles through a series of five preflight stages (figure 1.19). Beginning with reptiles that lived in or frequented trees, the sequence shows that some leaped from branch to branch in order to escape pursuing predators or get to adjacent trees without making a long journey down one tree and back up the other. Such behavior established the animal's practice of taking to the air temporarily. Next came parachuting, in which the animal spread its limbs and flattened its body to increase resistance and slow descent during the vertical drop, softening the impact on landing. Gliding was next. The animal deflected from the line of fall, so horizontal travel increased. Flailing, an early stage of active flight, further increased the horizontal distance. Flapping flight gave access to habitats unavailable to terrestrial species. In fact, a new mode of life was achieved, and modern birds are the result.

Such a view, although hypothetical, presents a plausible sequence by which flight in birds might have arisen. It helps address several criticisms leveled at morphological processes of evolutionary change. One long-standing complaint against the concept of evolutionary change is that many structures, such as large, complicated wings and feathers, could not possibly have had any selective value when they first appeared. Such **incipient structures** would be small and formative when they first made their evolutionary debut. The argument goes like this: Incipient structures would not enjoy selective favor until they were large and elaborate enough to perform the role that brought an adaptive advantage, such as flapping flight. However, this example shows that large, complicated structures need not have evolved all at once in one large evolutionary binge. In the hypothesized five-stage evolution of bird flight, no preceding stage anticipated the next. There was no drive in the stages themselves propelling them necessarily to the next stage. Each stage was adaptive in its own right, for the immediate advantages enjoyed. If conditions changed, organisms may have evolved further, but there were no guarantees.

Some mammals, such as "flying" squirrels, are still gliders. They are well adapted to conifer forests. Others, such as bats, are full-fledged, powered fliers. In an evolutionary sense, gliding squirrels are not necessarily "on their way" to becoming powered fliers like bats. Gliding is sufficient to meet demands the squirrels face when moving through the canopy of northern conifer forests. Gliding in these squirrels serves the environmental demands of the present. It does not anticipate powered flight in the distant future.

The example of bird flight also reminds us that a new biological role usually precedes the emergence of a new structure. With a shift in roles, the organism experiences new selective

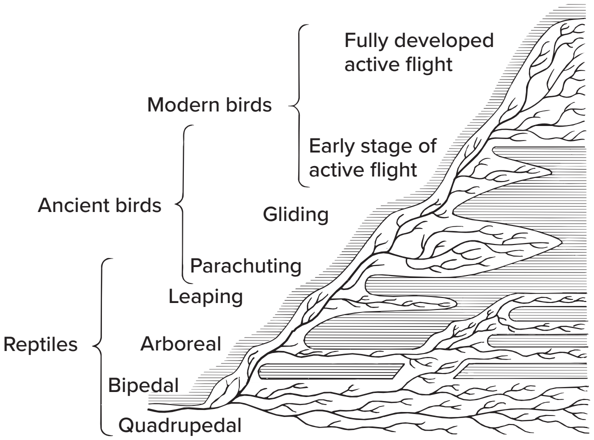


FIGURE 1.19 **Evolution of bird flight** modeled as a series of successive steps, each preadapted to the next, that trace the evolution of birds from reptiles. Each step is adaptive in its own right, but after having been achieved, each sets the stage for the next.

Source: After Bock.

pressures in a slightly new niche. The shift from leaping to parachuting, or from parachuting to gliding, or from gliding to early flailing flight initially placed old structures in the service of new biological roles. This initial shift in roles exposed the structure to new selection pressures favoring those mutations that solidify a structure in its new role. First comes the new behavior, and then the new biological role follows. Finally, a change in structure becomes established to serve the new activity.

Evolution as Remodeling

The scheme that traces the evolution of bird flight also tells us that evolutionary change usually involves renovation, not new construction. Old parts are altered, but seldom are brand new parts added. Almost always, a new structure is just an old part made over for present purposes. In fact, if a complete novelty made a sudden appearance, it would probably disrupt the organism's smooth, functional harmony and would be selected against.

Because evolution proceeds largely through the process of remodeling, descendant organisms bear the traces of ancestral structures. Preadaptation does not cause change but is only an interpretation of evolutionary outcomes after they occur. Preadaptation is hindsight, a look backward to see out of what ancestral parts present structures arose. In hindsight, we might see that leaping preceded parachuting, parachuting preceded gliding, and gliding preceded flailing. Each preceding step preadapted to the next. The conceptual mistake would be to interpret these steps as internally driven inevitably from grounded reptiles to flying birds. Nothing of the sort is intended. We do not know ahead of time the future course of evolution, so we cannot tell which structures are preadapted until after they have evolved into new roles.

Phylogeny

The course of evolution, known as **phylogeny,** can be summarized in graphic schemes, or **dendrograms,** that depict treelike, branched connections between groups. Ideally, the representation is a faithful expression of the relationships between groups. But the choice of dendrogram is based on intellectual bent and practical outcome. Dendrograms summarize evolution's course. This brevity gives them their attractiveness. All have risks, all flirt with oversimplification, and all take shortcuts to make a point. Let us look at the advantages and disadvantages of several types of dendrograms.

Of Bean Stalks and Bushes

In 1896, Ernst Haeckel wrote *The Evolution of Man,* in which he depicted the human pedigree or human phylogeny (figure 1.20). The book is a useful summary of his thoughts on the subject. Some today might wish to correct points in Haeckel's explicit phylogeny, but what does not stick out so readily is the assumption behind his dendrogram, namely, that humans are the pinnacle of evolution. Neither then (nineteenth century) nor now (twenty-first century) was Haeckel alone in assuming that nature climbed from one species to the next like rungs on a ladder, from primitive to perfected, from lower forms to humans at the top of the scale of nature. What such a dendrogram subtly promotes is the mistaken view that humans stand alone as the sole possessor of the top rung of the evolutionary ladder.

In reality, the human species is just one of thousands of recent evolutionary products. Evolution does not proceed up a single ladder but bushes outward along several simultaneous courses. Although mammals continued to prosper largely on land, birds evolved concurrently and teleost fishes diversified in all waters of the world. Birds, mammals, fishes, and all species surviving today represent the current, and still evolving, species within their groups. No single species is

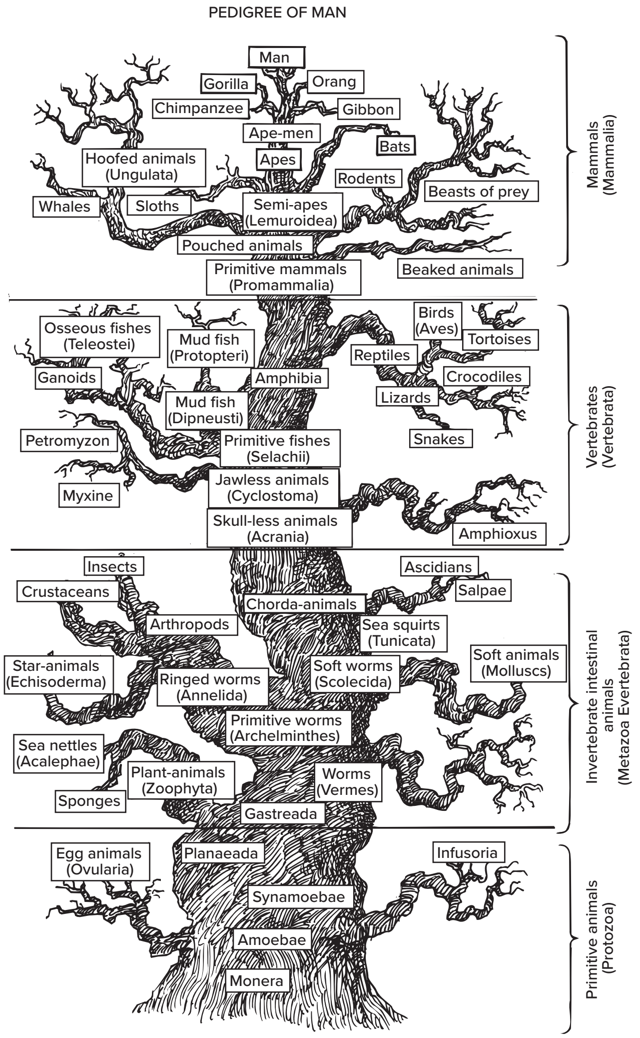


FIGURE 1.20 **Haeckel's phylogeny.** Like a tree, this phylogeny displays the proposed branching of species. Although many lines of evolution are shown, Haeckel chose to call it the "Pedigree of Man," subtle evidence of the common view that humans represent the culmination of evolution's efforts.

Source: From Ernst Haeckel.

a Mount Everest among the rest. Humans share the current evolutionary moment with millions of other species, all with long histories of their own. All adapted in their own ways to their own environments.

To reflect this diverse pattern of evolution faithfully, dendrograms should look like bushes, not like bean stalks or ladders (figure 1.21a, b). After birds evolved from reptiles, reptiles not only persisted but actually diversified and continued to evolve and prosper. The same holds for amphibian ancestors that gave rise to reptiles and for fishes that gave rise to these amphibian ancestors. Certainly modern amphibians have carried forward primitive features from their early ancestors; however, they have also continued to evolve independently of reptiles since the two lineages parted company over 300 million years ago. Frogs are structurally quite different, for instance, from the earliest amphibian ancestors.

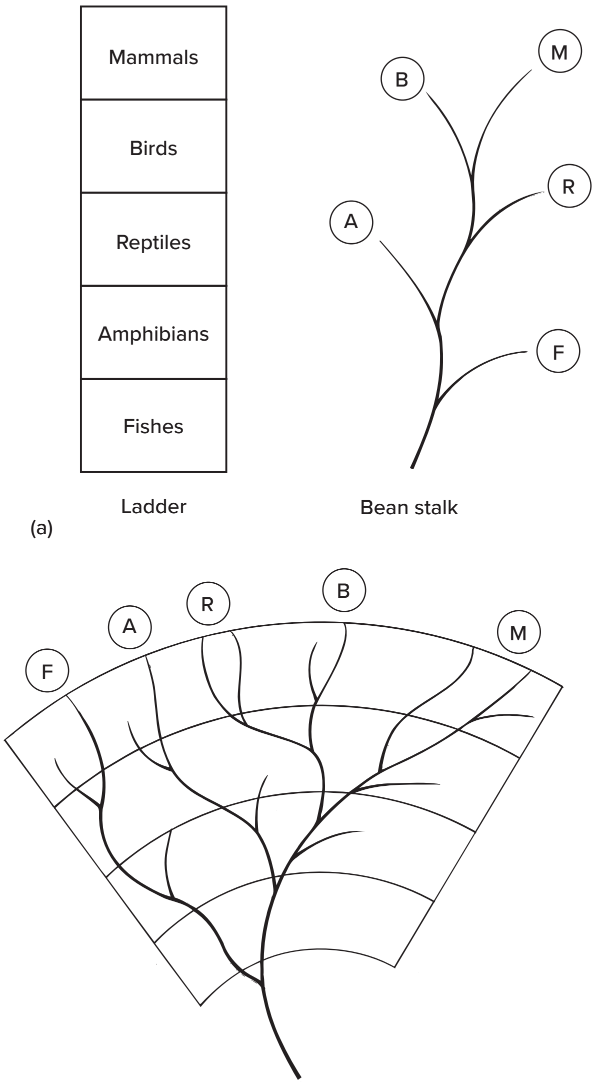


FIGURE 1.21 **Bean stalks and bushes.** (a) The "ladder of creation" is a misleading metaphor. Evolution proceeds not in a stately fashion up a ladder of species, one to the next, but along parallel lines that branch outward. Dendrograms shaped like bean stalks illustrate the order in which a group appeared but nurture the misleading view that species evolved in linear sequence up to the present time. (b) The diversity of unfolding evolution is better represented by a dendrogram shaped like a bush.

Dendrograms that look like bean stalks or ladders are quick, uncomplicated summaries of the course of evolution (figure 1.21a). This is their strength. But they can also mislead because they imply that the most significant achievement of an earlier group is to serve as the source for a derivative group—fish for amphibians, amphibians for reptiles, and so on. Dendrograms in the shape of ladders warp our view in that more recent groups are somehow depicted as better perfected than earlier groups. Dendrograms that look like bushes not only track the course of new groups but also show us that after one group gives rise to another, both may continue to evolve concurrently and adapt to their own environments (figure 1.21b). Once a new group is produced, evolution among ancestors does not stop, nor does a derived group necessarily replace its ancestors.

The evolution of life is a continuous and connected process from one moment to the next. New species may evolve gradually or suddenly, but there is no point of discontinuity, no break in the lineage. If a break occurs in the evolving lineage, the consequence is extinction, a finality not redeemed. When taxonomists study current living species, they examine an evolutionary cross section of time in that they view only the most recent but continuing species with a long diverging history behind them. The apparent discreteness of species or groups at the current moment is partly due to their previous divergence. When followed back into their past, the connectedness of species can be determined. A dendrogram showing lineages in three dimensions (figure 1.22) emphasizes this continuity. If reduced to a two-dimensional branching dendrogram, the relationships stand out better but imply an instant distinctiveness of species at branch points. The sudden branches are a taxonomic convention but may not faithfully represent the gradual separation and divergence of species and new groups.

Simplification

Most dendrograms intend to make a point and are simplified accordingly. For example, the evolution of vertebrates is depicted in figure 1.23a to make a point about steps along the way. Although this representation is considerably simplified, it is a convenient summary; but if taken literally, the dendrogram is quite implausible. The first four species are living, so they are unlikely direct ancestral species in the steps. A more plausible representation of their evolution is shown in figure 1.23b. Species at each division point lived millions of years ago and are certainly extinct by now. Only distantly

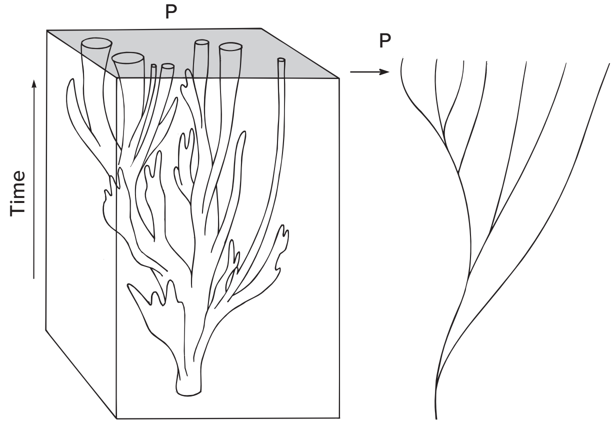


FIGURE 1.22 **Evolution of dendrograms.** The course of evolution, with some branches becoming extinct, is depicted by the left dendrogram. We stand at the time horizon plane (P) to observe the lineages that have persisted to the present. The illustration on the right is one possible two-dimensional dendrogram that represents only the major surviving lines of descent.

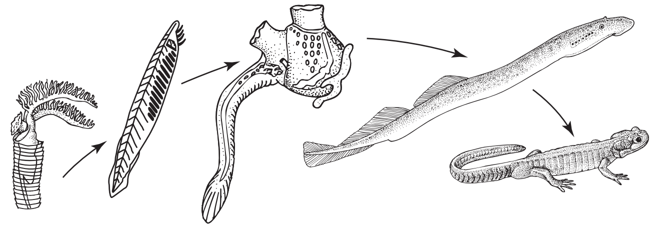
related derivative ancestors survive to the present and are used to represent steps in the origin of vertebrates.

A more complicated dendrogram of birds is shown in figure 1.24. Many groups are included, their likely evolution traced, and the relationships between them proposed. Thus, their phylogeny is more faithfully represented, although the complexity of the diagram makes major trends less apparent. Notice how the more complete detail makes the dendrogram hard to read and, hence, less useful in identifying major trends. In choosing a dendrogram, we should strike some compromise between simple (but perhaps misleading) and complex (but perhaps overwhelming).

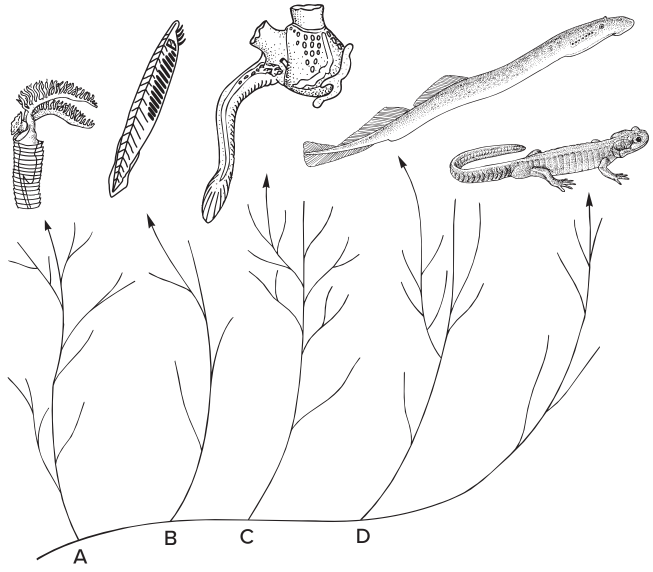
Patterns of Phylogeny

Dendrograms can be used to express relative abundance and diversity. The swollen and narrowed shapes of the "balloons" in figure 1.25 roughly represent the relative numbers of vertebrates that existed in each group during various geological times. The first mammals and birds arise within the Mesozoic but do not become abundant and prominent components in terrestrial faunas until much later—in fact, not until after the decline of the contemporaneous reptiles at the end of the Cretaceous. Shapes of branches within a dendrogram convey this additional information.

Rates at which new species appear can also be represented by the sharpness of branching within a dendrogram. One dendrogram is sharply angular, which implies rapid change and relatively sudden appearance of new species (figure 1.26a). The other shows smooth branches, implying the gradual appearance of new species (figure 1.26b). Behind these two types of dendrograms stand different sets of assumptions about the process of evolution. One sees evolution working gradually to produce new species. The other sees the process as an event in which species persist for long stretches with relatively little change followed by a rather abrupt appearance of a new species. In the 1940s, G. G. Simpson termed such long intervals of unchanged evolution occasionally interrupted by short bouts of rapid change as **quantum evolution.** Efforts to celebrate this in dendrograms have recently found favor again, termed **punctuated equilibrium** by those sharing Simpson's view.



(a)



(b)

FIGURE 1.23 **Steps in vertebrate evolution.** (a) Examples of a hemichordate, a cephalochordate, a urochordate larva, a lamprey, and a salamander (from left to right). All are living species, so they are not likely the immediate ancestors of each succeeding group, as this scheme mistakenly implies. (b) Their actual ancestors (from A to D, respectively) lived millions of years ago and are now extinct. Modified descendants that represent these species today carried forward some of the primitive traits of their extinct ancestors, but they also evolved additional modifications.

Grades and Clades

Living vertebrates derive from a succession of distant ancestors and differ considerably from them. Modern vertebrates carry forward the collective results of these changes upon

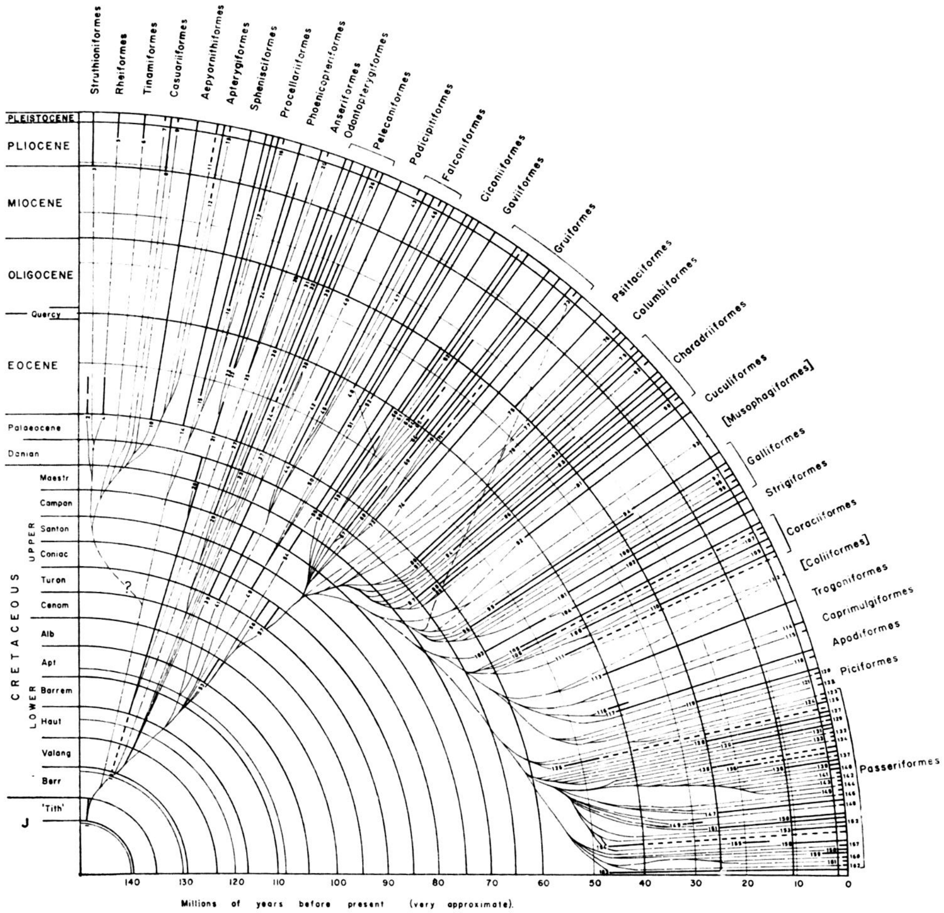


FIGURE 1.24 Phylogeny of birds. This dendrogram attempts to detail the relationships and the time of origin of each group of modern birds. Although it expresses the hypotheses of these relationships in detail, the diagram is too complex and difficult to view easily. General trends are less evident as well.

Source: © J. Fisher, *"Fossil Birds and Their Adaptive Radiation," in* The Fossil Record, *The Geological Society of London, 1967.* Reprinted with permission of the Geological Society of London.

changes—thousands of them. Taken together, these collective changes produce the modern groups as we meet them today. To reconstruct this history, we may examine particular characters, using them to track the history of these changes. Formally, the earlier (or ancestral) state of a character is its **primitive condition,** referred to as a **plesiomorphic trait;** its later (or descendant) state after transformation is its **derived condition,** referred to as a **synaphomorphic trait.** A **taxon** is simply a named group of organisms. A taxon may be a **natural taxon,** one that accurately depicts a group that exists in nature resulting from evolutionary events. Or, a taxon may be an **artificial taxon,** one that does not correspond to an actual unit of evolution. A **sister group** is the taxon most closely related to the group we are studying. Using transformed characters as our guide, we inspect the pattern of vertebrate evolution and assign names for taxa accordingly, but we may do so with different goals in mind.

If a group of organisms carries a large number of distinctive derived characteristics, we might wish to recognize this by suggesting that the group has reached a new stage, step, or grade in its organization. In a traditional sense, a **grade** was meant to be an expression of the degree of change or level of adaptation reached by an evolving group. Treating groups as grades has been used in the past in some taxonomic schemes. For example, the fused and distinctive shell of turtles might be seen as a drastic reorganization of the skeleton requiring taxonomic recognition. This could be done by elevating turtles to a distinctive taxonomic rank co-equal with birds. In this sense of grade, evolving groups collect such a large number of derived characteristics that they pass an imagined threshold that earns them a high taxonomic rank. By such a view, mammals could be considered a taxonomic grade; so could birds. Although sometimes useful as a way of recognizing the degree of anatomical divergence between groups, grades can be misleading. The group Reptilia traditionally includes members with scales and a shelled egg (cleidoic egg). But such a grade does not represent a single evolving group. Instead, the reptilian grade has been reached independently, once within the line to modern reptiles and once early within the line to mammals. Conversely, current groups may not seem to look alike—crocodiles and birds, for example. But these are survivors of a common lineage that places them more closely related to each other than either is to modern reptiles. Therefore, we may prefer to recognize groups based on their genealogy rather than on a subjective judgment of the degree of change alone.

If members of a group of organisms share a unique common ancestor, we can recognize this by naming the lineage itself. A **clade** is a lineage—all organisms in a lineage plus the ancestor they have in common. **Traditional systematics** places

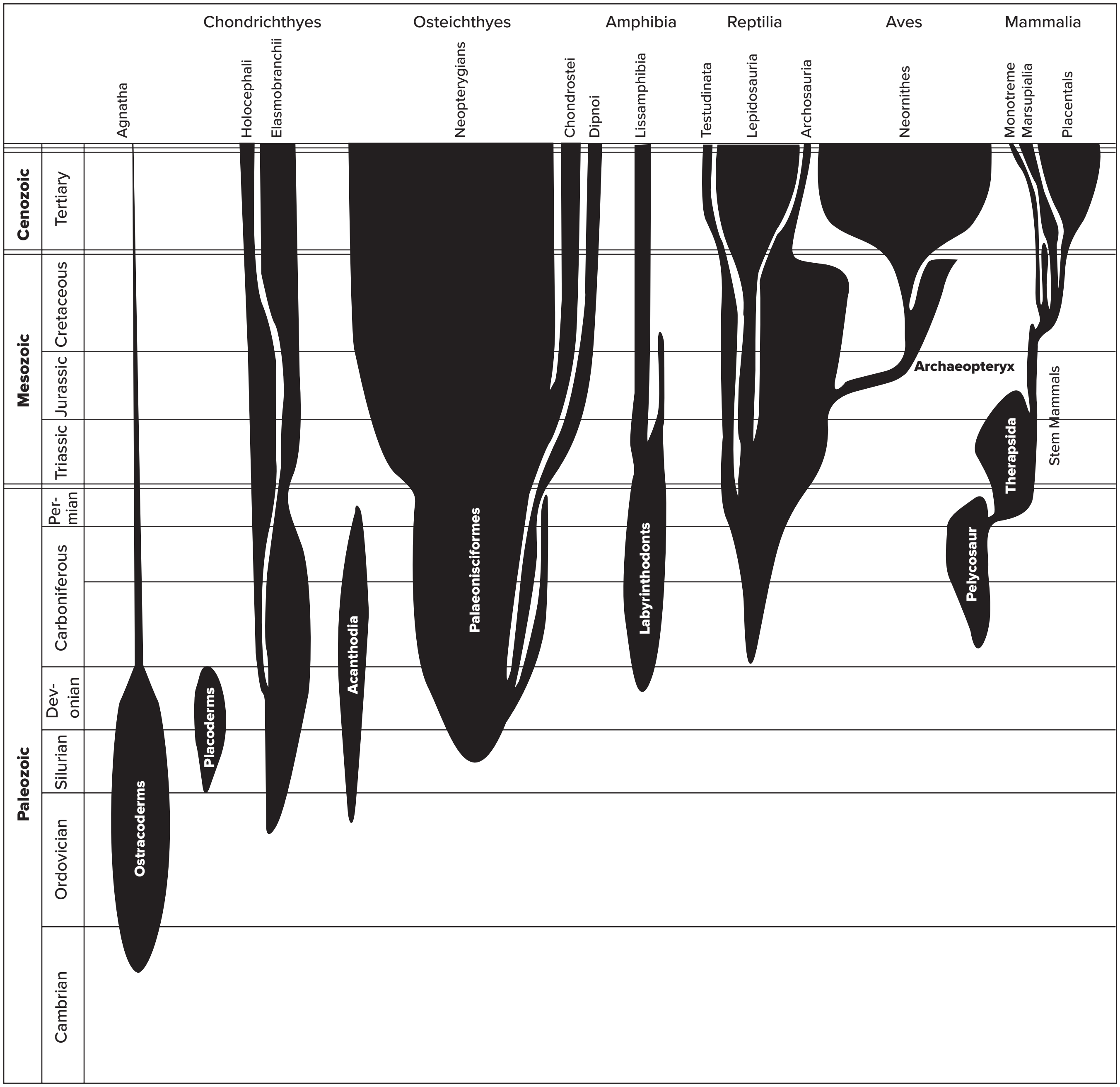


FIGURE 1.25 Abundance phylogeny. This dendrogram attempts to represent the first time each vertebrate group appeared and the relative abundance of each group (depicted by the size of each balloon).

together organisms with similar or homologous characteristics. The newer **phylogenetic systematics** places together organisms belonging to the same clade and hence is also called **cladistics.** Within cladistics, the taxon name refers to the clade—to the genealogy itself—not necessarily to characters per se. Clades are recognized without concern for the amount of anatomical variation within the taxon. Consequently, some clades might include members very homogeneous in their basic morphology (e.g., birds, snakes, frogs) or quite heterogeneous (e.g., actinopterygian fishes). Genealogy, not within-group variation, is the basis for recognizing a clade. The dendrogram depicting this genealogy is a **cladogram,** a hypothesis about the lineages and their evolutionary relationships. The advantage of such cladograms is the clarity and ease with which they may be critiqued. A practical disadvantage is the swiftness by which a cladogram may be replaced with a newer cladogram, leaving us with abandoned taxon names replaced with newer names for more recent hypotheses of relationship. Character transformations play a central part in producing cladograms. In particular, derived characteristics are most important.

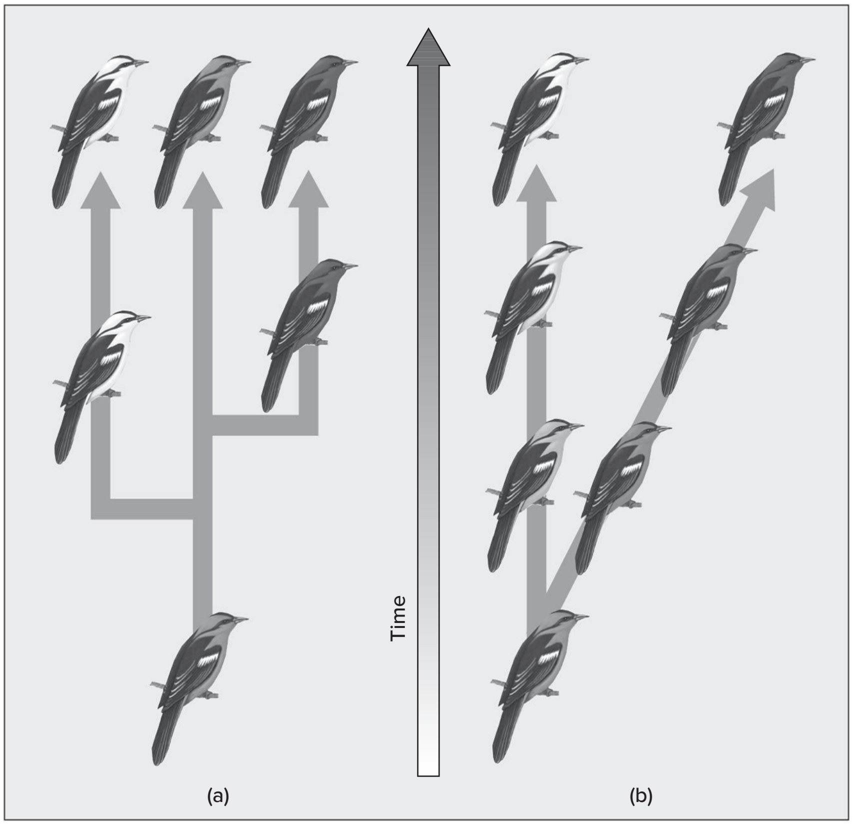


FIGURE 1.26 **Patterns of evolution.** A dendrogram may be intended to represent the abrupt (a) or gradual (b) appearance of new species represented by a new branch. Although the two dendrograms agree on the relationships of species, they depict two different processes behind their evolution, namely, a rapid evolutionary process (a) or a gradual process of evolution (b).

Relationships between groups are recognized on the basis of derived characteristics. The more derived characteristics shared by two groups, the more likely it is they are closely related. The assortment of taxa we are interested in examining is our **ingroup;** the **outgroup** is close to but not part of this assortment and is used as a reference. In particular, the outgroup helps us make decisions about which character state represents the derived condition. The sister group is the first outgroup we might consult because it is the most closely related. But we might also successively make comparisons to more distantly related second or third outgroups. Often, at this point, fossils may play an important reference role so that we can better decide primitive and derived states of a character. Once the degree of shared, derived characteristics is determined, we can represent associations in a Venn diagram (figure 1.27a). Because evolution proceeds by descent with modification, as Darwin helped establish, we expect those groups most closely related to be part of a common lineage. Therefore, from this diagram, we produce our hypothesis of genealogy, the cladogram (figure 1.27b), based on the characters we have examined. The layers of brackets above the cladogram represent the levels of inclusiveness of our groups within clades. As we name each clade, we would be producing our classification of this ingroup. In our cladogram, we could mark the sites at which particular character transformations occur. We could thereby use the cladogram to summarize important points of character transformation in the evolution of the groups and identify the distinctive derived characters that are associated with each clade.

Cladistics demands that we staunchly follow the practice of naming clades that recognize genealogy (figure 1.28). A clade is **monophyletic** in that it includes an ancestor and *all* its descendants—but *only* its descendants. Groups formed on the basis of nonhomologous characters are **polyphyletic.** If we combined birds and mammals together because we mistook their endothermic physiology (warm-blooded) as the result of common descent, we would be forming an artificial, polyphyletic group. Groups that include a common ancestor and some, but not all, of its descendants are **paraphyletic.** This can happen with some traditional definitions of Reptilia. Modern reptiles and birds derive from a common ancestor. If birds were left out of the clade that represented this common lineage, then what remained would be a paraphyletic group. If paraphyletic groups are used for convenience, the names are usually placed in quotation marks to signal the unnatural composition of the group. Both polyphyletic and paraphyletic taxa are artificial taxa. They do not reflect the actual, complete course of evolution within a common lineage. Further, within cladistics we discover a second meaning for the term *grade.* Here, *grade* is a synonym for a paraphyletic group. When we visit specific vertebrate groups in chapter 3, we shall meet these issues directly.

By producing explicit and uncluttered hypotheses of relationship, cladograms have become part of the modern

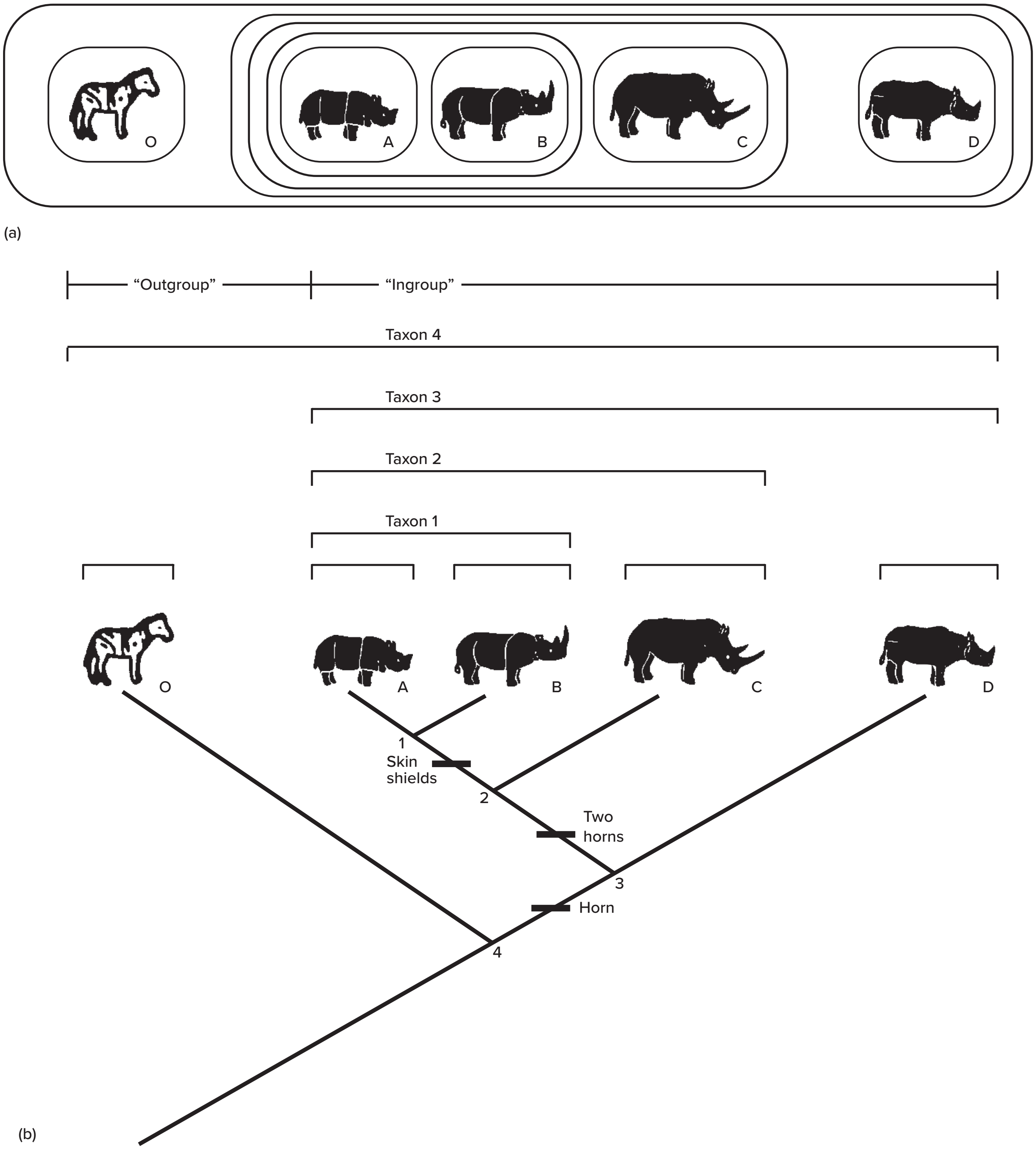


FIGURE 1.27 **Classification.** (a) Venn diagrams sort individuals into successive boxes of relatedness. Individuals of the same species are most closely related and put together in the smallest group—A, B, C, D, and O. If species A and B share more unique, derived features in common than with any others, then we would place them in a common group, and so on, expanding our diagram to include those more distantly related. (b) The genealogy of these species can be expressed in the branching diagram, with the brackets representing successive clades of common descent. The point of branching is the node, the distance between nodes the internode. Taxon 1 includes Species A and B, together with their common ancestor 1 at the node. Taxon 2 includes the clade of Species A, B, and C plus their common ancestor 2, represented at the node, and so on. To make the genealogy more familiar, each taxon would be named. For example, Taxon 3 might be named "Rhinocerotidae." To make the genealogy even more useful, we could identify at the internodes some of the many character transformations that occurred. For example, a horn first arises between nodes 4 and 3; a second horn between nodes 3 and 2; thick skin shields between nodes 2 and 1.

Source: (b) Modified from Classification, British Museum (Natural History).

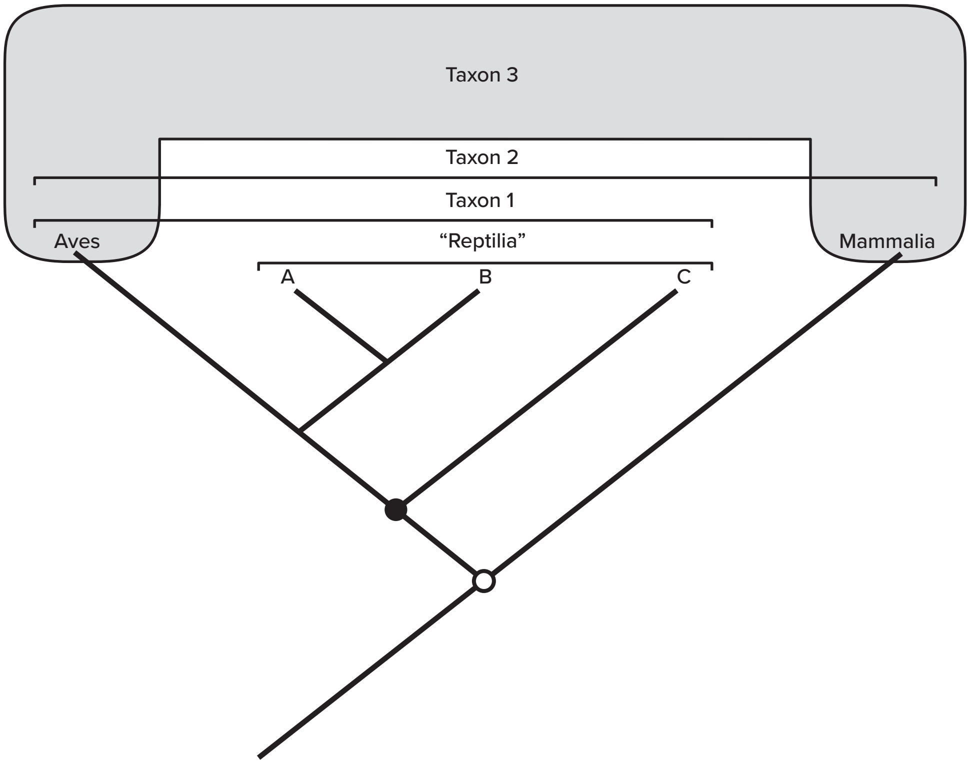


FIGURE 1.28 Cladistic concepts. Monophyletic groups include an ancestor and all of the descendant groups. Taxon 1 is monophyletic because it includes the common ancestor (solid circle at node) plus all descendants—groups A, B, C, and Aves. However, "Reptilia" is paraphyletic, an artificial grouping that deletes Aves, one of the descendants of the same ancestor groups A, B, and C share. Taxon 3 is polyphyletic, also an artificial group, because it places Aves (birds) and Mammalia together on the mistaken view that their endothermy is a homologous feature. Taxon 2 (Amniota) is also monophyletic because it unites all groups descended from the same common ancestor (open circle at the node).

language of evolutionary analysis. But the starkness of these straightened cladograms should not obscure the bushiness of the evolutionary pattern they represent. If for reasons of convenience or incompleteness fossils are excluded, then a cladogram based only on living taxa can be rather barren (figure 1.29a). This does not suggest that modern birds evolved from crocodiles (or crocodiles from birds), only that among recent taxa birds are more closely related to crocodiles than they are to any other living group. Adding only a few of the fossil taxa (figure 1.29b) should make it clear that the cladogram could be enlarged to better reflect the richness and actual diversity of evolution within these vertebrate groups. Adding fossil groups also helps us understand the transitional steps between living groups. In this phylogeny (figure 1.29a), only representatives of the living groups are represented. If we had only these living groups to reconstruct the steps in early vertebrate evolution, then a great deal of connecting information would be unavailable. However, a rich series of fossil groups provides concrete intermediate steps, giving us greater confidence in our interpretation of this phylogeny.

Formally, the **crown group** is the smallest clade that includes all living members of a group and any fossils nested within. The **stem group** is the set of extinct taxa that are not in the crown group but are more closely related to the crown group than to any other. Together, the crown and stem groups constitute the **total group** (figure 1.30). For example, in figure 1.29, the crown groups are the boxed groups; the stem groups are unboxed.

Students should recognize dendrograms as summaries of information about the course of vertebrate evolution. But you should realize that dendrograms also contain, even if inadvertently, hidden expressions of intellectual preference and personal bias. Dendrograms are practical devices designed to illustrate a point. Sometimes this requires complex sketches, and other times just a few simple branches on a phylogenetic tree serve our purposes.

Paleontology

The late paleontologist Alfred Romer once poetically referred to the grandeur and sweep of vertebrate evolution as the "vertebrate story." And in a sense it is exactly that, a story with twists and turns that could not have been known beforehand—the debut of new groups, the loss of old ones, the mysteries of sudden disappearances, the evolutionary tales told by the parade of characters. Like a good story, when we finish it, we will know the characters better, and because we ourselves are part of this story, we will come to know ourselves a little better as well. The vertebrate story unfolds over a span of half a billion years, a depth of time almost unimaginable (figure 1.31). To help us fathom this vastness of time, we consult paleontology, the discipline devoted to events of the distant past.

The vertebrate story is a narrative spoken partially from the grave, because of all species ever to exist most are now extinct. The evolutionary biologist and paleontologist G. G. Simpson once estimated that of all animal species ever to evolve, roughly 99.9% are extinct today. So in this story of life on Earth, most of the cast of characters are dead. What survives are their remnants, the fossils and the sketchy vignettes these fossils tell of the structure and early history of vertebrates.

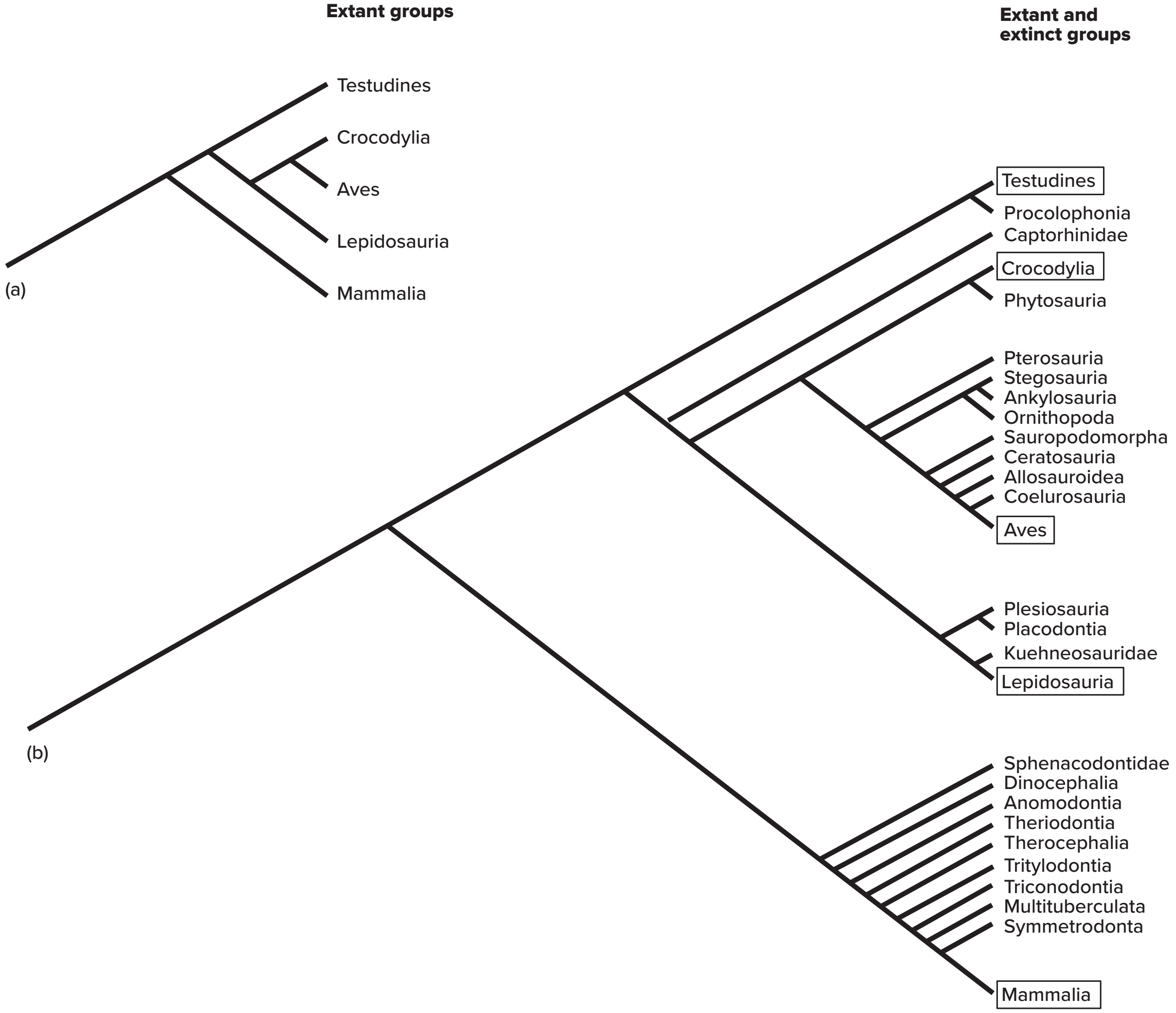


FIGURE 1.29 **Extant and extinct groups.** (a) The cladogram of living groups of amniotes clearly shows the close relationship between birds (Aves) and crocodiles (Crocodylia) but should not suggest that modern groups derive directly from each other. (b) Adding extinct groups illustrates the richness of the historical associations back through which modern groups (boxed) trace their evolution to a common ancestor. Fossils, when added to the analysis, also help to determine the primitive and derived states of characters, and thereby help improve our ability to sort groups on the basis of shared, derived features.

Source: Modified from A. B. Smith.

Fossilization and Fossils

When we think of fossil vertebrates, we probably picture bones and teeth, the hard parts of a body that more readily resist the destructive processes following death and burial. Certainly most fossil vertebrates are known from their skeletons and dentition. In fact, some extinct species of mammals are named on the basis of a few distinct teeth, the only remnants to survive. The calcium phosphate compound composing bones and teeth is a mineral usually preserved indefinitely, with little change in structure or composition. If groundwater seeps through bones lying in soil or rock, over time other minerals such as calcite or silica may soak into the tiny spaces of bone to add further minerals and harden it.

Fossils are more than bones and teeth, however. Occasionally, products of vertebrates, such as eggs, will fossilize. If tiny young bones are preserved inside, we can identify them and the group to which they belong (figure 1.32). This tells us more than just the structure of this species; it also tells us something about its reproductive biology. The discovery in Montana of fossilized clumps of eggs belonging to duck-billed dinosaurs testified to the reproductive style of this species, but there was accompanying circumstantial evidence to imply even more. The clumps or clutches of eggs were near each other, about two adult body lengths apart, suggesting that the area was a breeding colony. Analysis of the rock sediments in which they were found indicates that the colony was on

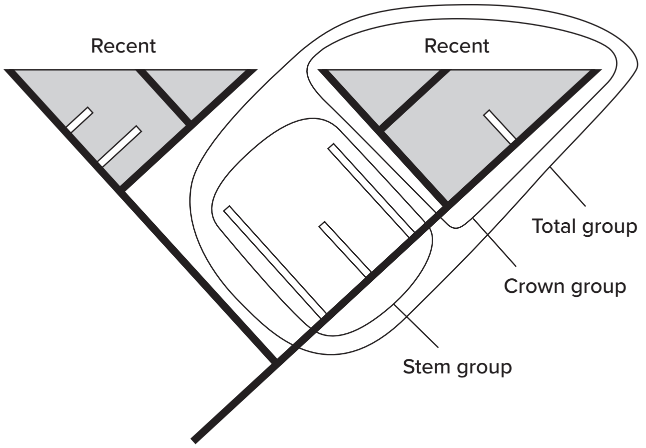


FIGURE 1.30 **Extant and extinct in phylogenies.** The cladogram shows the relationship between extant (black lines) and extinct (white lines) groups. The stem groups include all the intermediate but now extinct fossil groups. Together, crown plus stem groups constitute the total group, the monophyletic clade.

an island in the middle of a runoff stream from the nearby Rocky Mountains. At the same site, bones from duck-billed dinosaurs of different sizes, and thus different ages, were present. This could happen only if young stayed around the nest until they were fully grown. Perhaps the parents even gathered food and brought it back to nourish the newly hatched young. For this species of duck-billed dinosaurs, the emerging picture is not one of a dispassionate reptile that laid its eggs and departed. Instead, this reptile appears to have had sophisticated parental care and supportive social behavior. Gathering of food, protecting and teaching of young, and bonding of pairs are implied by the fossils.

A marine fossil of an ichthyosaur, a dolphinlike reptile, was recovered from limestone rocks dating to 175 million years ago (figure 1.33). This adult specimen appears to be a female fossilized in the act of giving birth. Several small (young) skeletons remain with her body, one apparently emerging through the birth canal and another already born

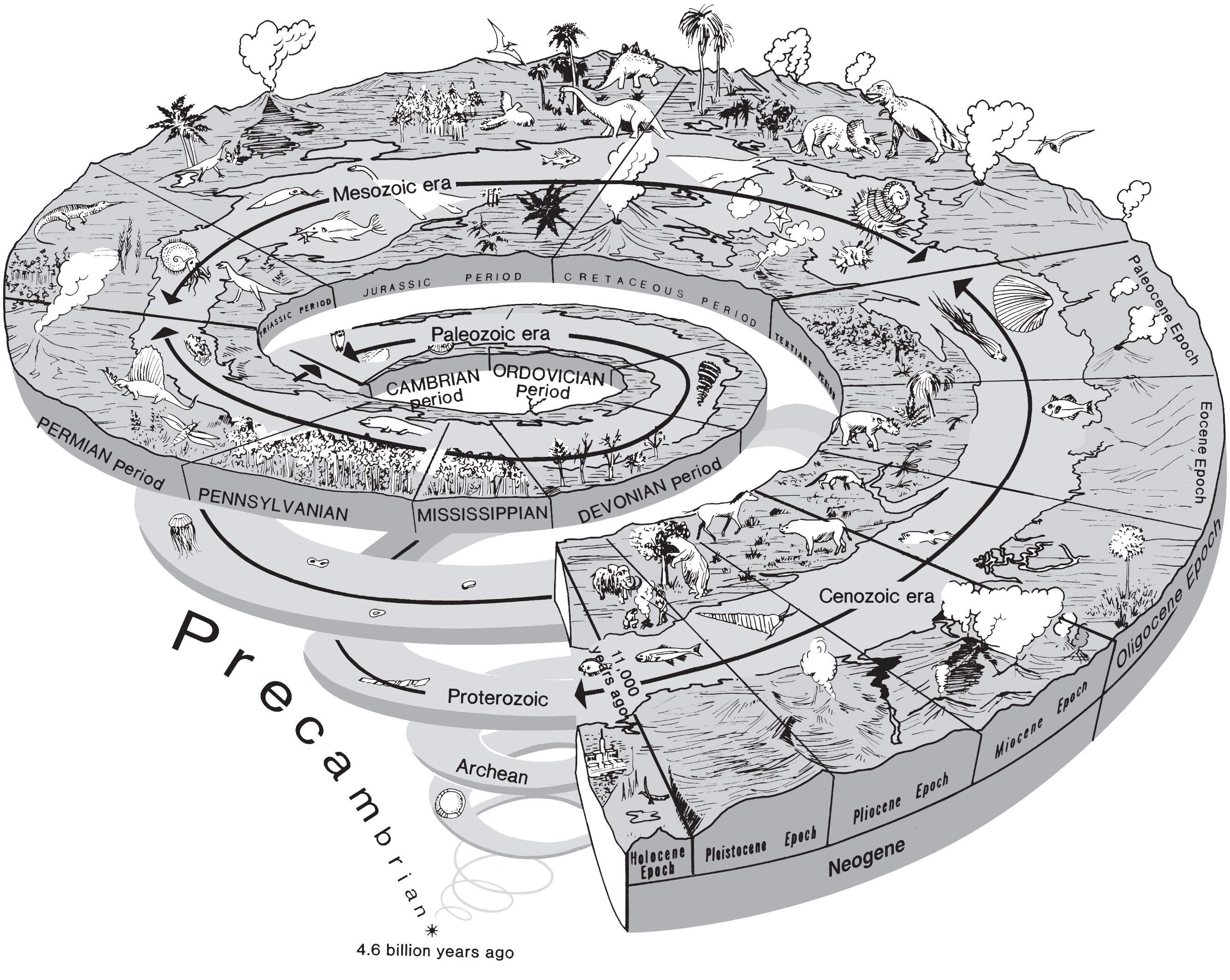


FIGURE 1.31 **Geologic time.** The gathering of cosmic gases under gravity's pull created Earth some 4.6 billion years ago. Yet life became neither abundant nor complicated until the Cambrian period, about 542 million years ago, when the first vertebrates appeared.

Source: After U.S. Geological Survey publication, Geologic Time.

BOX ESSAY 1.2 Missing Links

Thomas Jefferson, when vice president of the United States, reported before a scientific society and subsequently published in 1797 a paper on *Megalonyx*, a fossil ground sloth, whose bones had been discovered in Virginia (later named *Megalonyx jeffersonii*). He also knew of large bones of mastodons and other great fossil animals from the eastern United States. When president, he set up the Lewis and Clark expedition to lay a claim to the land, gather scientific information, and find a northwest passage. Part of their goal was to see if mastodons or any other animals discovered as fossils still existed alive in the vastness of the western continent. In 1806, the expedition found a giant leg bone near Billings, Montana, that was certainly a dinosaur. Unfortunately, no living mastodons were found. We now know they disappeared from North America at least 8,000 years earlier.

Prior to the American Revolution, the French naturalist George Louis LeClerc de Buffon proposed that compared to his rich European environment, the North American environment was impoverished, unable to support any animals robust in character. His patriotic pride stung, Jefferson countered using the mastodon as an example of such an animal that had thrived in the New World.

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lying beside her (figure 1.33). If this represents a "fossilized birth," then unlike most reptiles, ichthyosaurs bore live young who were fully functional, like young dolphins today.

Occasionally, fossils preserve more than just their hard parts. If a full animal skeleton is discovered, microscopic analysis of the region occupied in life by the stomach might reveal the types of foods eaten shortly before its death. Dung is sometimes fossilized. Although we might not know which animal dropped it, we can gain some notion about the types of foods eaten. Soft parts usually decay quickly after death and seldom fossilize. A dramatic exception to this has been the discovery of woolly mammoths, distant relatives to elephants, frozen whole and preserved in the Arctic deep freeze of Alaska and Siberia. When thawed, these mammoths yielded hair, muscles, viscera, and digested food, exceptional finds indeed. Rarely are paleontologists so lucky. Occasionally, soft parts leave an impression in the terrain in which they are buried. Impressions of feathers in the rock around the skeleton of *Archaeopteryx* demonstrate that this animal was a bird (figure 1.34). Similar impressions of skin tell us about the surface textures of other animals—scaly or smooth, plated or fine beaded (figure 1.35a, b).

FIGURE 1.32 **Fossil eggs.** Examination of the fetal bones within these eggs reveals that these are of *Protoceratops*, a Cretaceous dinosaur that lived in what is today Mongolia.

Source: Photo courtesy of Lowell Carhart

The past behavior of now extinct animals is sometimes implied by their fossilized skeletons. Nearly complete skeletons of fossilized snakes have been found in lifelike positions in rocks dating to 32 million years ago. These natural aggregations seem to represent, as in many modern species of temperate snakes, a social event to prepare for hibernation during the cold winter season. Other vertebrate behaviors, or at least their locomotor patterns, are implied in fossilized footprints (figure 1.36). Size and shape of footprints, together with our knowledge of animal assemblages of the time, give us a good idea of who made them. With dinosaur tracks, it has been possible to estimate the velocity of the animal at the time the tracks were made. Three-and-a-half-million-year-old volcanic ash, now hardened to stone, holds the footprints of ancestral

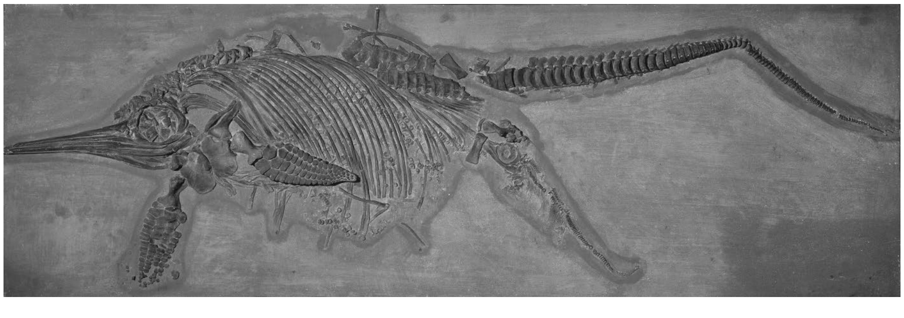


FIGURE 1.33 **Fossil ichthyosaur.** Small skeletons are seen within the adult's body and next to it. This may be a fossilized birth, with one young already born (outside), one in the birth canal, and several more still in the uterus. Such special preservations suggest the reproductive pattern and live birth process in this species.

Source: ©The Natural History Museum/Alamy Stock Photo

FIGURE 1.34 **Archaeopteryx. The original feathers have long since disintegrated, but their impressions left in the surrounding rock confirm that the associated bones are those of a bird.**

Source: ©gekaskr/123RF

humans. Discovered in present-day Tanzania by Mary Leakey, the sets of footprints are those of a large individual, a smaller individual, and a still smaller individual walking in the steps of the first. These human footprints confirm what had been deciphered from skeletons, namely, that our ancestors of over 3 million years ago walked upright on two hindlegs.

Recovery and Restoration

Paleontologist and artist combine talents to re-create the extinct animal as it might have looked in life. Remnants of long-dead animals provide source material from which basic anatomy is reassembled. After such a length of time in the ground, even mineral-impregnated bone becomes brittle. If the original silty sediments around bone have hardened to stone, they must be chipped or cut away to expose the fossilized bone encased within. Picks and chisels help to partially expose the upper surface and sides of the bone, which are wrapped in protective plaster and allowed to harden (figure 1.37). Following this procedure, the remainder of the bone is exposed and the plaster wrap extended to encase it completely. The brittle bones are shipped to laboratories within their plaster support. Once specimens reach the lab, the plaster, along with any further rock, is removed. Tiny needles were once used to pick away the rock. Today, a stream of fine sand from a pencil-sized nozzle is used to sandblast or carve away rock to free the fossil.

Confidence in a restored version of a fossil rests largely on direct fossil evidence and knowledge of modern, living counterparts, which indirectly supply the likely biology of the fossil (figure 1.38). Size and body proportions are readily determined from the skeleton. Muscle scars on bones help determine how muscles might have run. When added to the skeleton, these give us an idea of body shape. General feeding type—herbivore or carnivore—is implied by the type of teeth; and lifestyle—aquatic, terrestrial, or aerial—is determined by the presence of specialized features such as claws, hooves, wings, or fins. The type of rock from which the fossil was recovered—marine or terrestrial deposits, swamp or dryland—further testifies to its lifestyle. Comparison with related and similarly structured living vertebrates helps fill in locomotor style and environmental requirements (figure 1.38a–c).

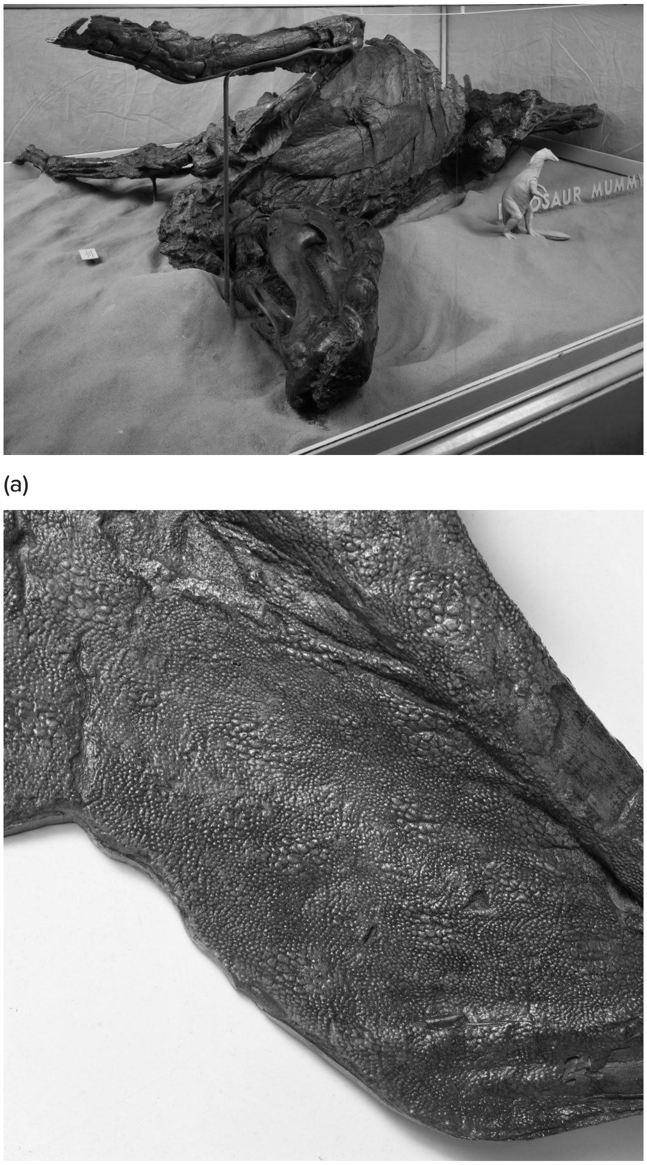
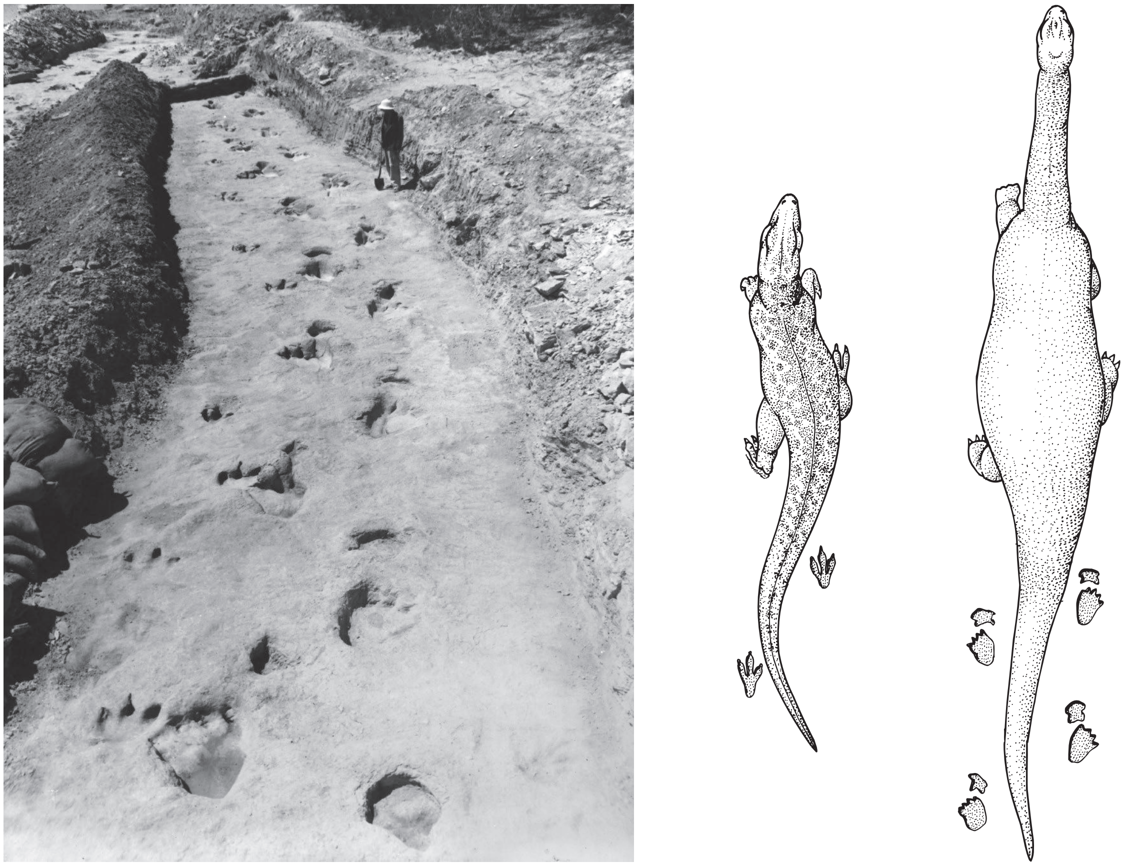


FIGURE 1.35 **Mummification.** (a) Fossil mummified carcass of the duck-billed dinosaur *Anatosaurus*. (b) Detail shows the surface texture of the skin.

Source: (a) ©Lynton Gardiner/Getty Images; (b) ©The Natural History Museum/ Alamy Stock Photo

The presence or absence of ears, proboscis (trunk), nose, hair, and other soft parts must be guessed at. Living relatives help in this process. For instance, all living rodents have vibrissae, long hairs on the snout, so these might be included in restorations of extinct rodents. Except for some burrowing or armored forms, most mammals have a coat of fur, so it is fair to cover a restored mammal with hair. All living birds have feathers, and reptiles have scales, both of which can logically be added to restored avian or reptilian fossils, although the length or



(a)

(b)

FIGURE 1.36 Dinosaur tracks. (a) Tracks from the Late Jurassic were made in soft sand that later hardened to form rock. Two sets are present: the large tracks of (b) a sauropod and the three-toed tracks of a smaller carnosaur, a bipedal carnivorous dinosaur.

Source: (a) Granger/Granger

(a)

(b)

FIGURE 1.37 Fossil dig in Wyoming. (a) Partially exposed dinosaur bones. The work crew prepares the site and notes the location of each excavated part. (b) This *Triceratops* femur is wrapped in a plaster jacket to prevent disintegration or damage during transport back to the museum.

Source: Photos courtesy of Dr. David Taylor, Executive Director, Northwest Museum of Natural History, Portland, Oregon.

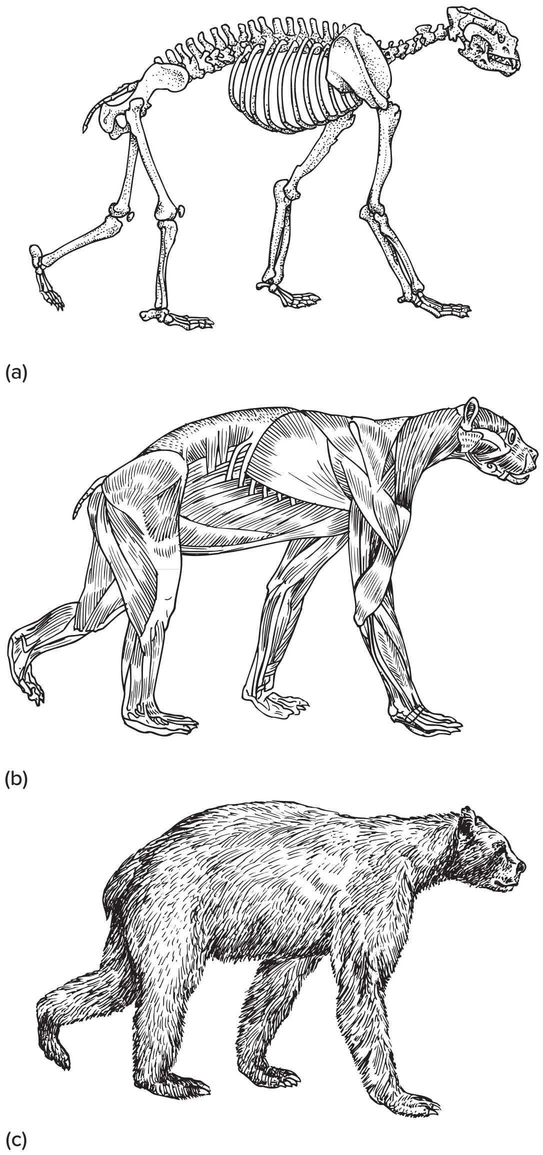


FIGURE 1.38 **Reconstruction of an extinct animal.** (a) The skeleton of the extinct short-faced bear, *Arctodus simus,* is positioned in its likely posture in life. (b) Scars on the bones from muscular attachments and knowledge of general muscle anatomy from living bears allow paleontologists to restore muscles and hence to create the basic body shape. (c) Hair added to the surface completes the picture and gives us an idea of what this bear might have looked like in its Alaskan habitat 20,000 years ago.

size must be guessed. Surface colors or patterns, such as stripes or spots, are never preserved directly in an extinct vertebrate. In living animals, colored patterns camouflage appearance or emphasize courtship and territorial behaviors. Reasonably, surface patterns had similar functions among extinct animals, but specific colors and patterns chosen for a restoration must usually be produced from the artist's imagination.

However, recovered genetic material can sometimes help. The dark and light hairy coats preserved with frozen woolly mammoths suggested color variations, but it was initially not known if this represented natural color variation or if it was an artifact of preservation. Now genetic material isolated from the leg bone of a 43,000-year-old mammoth includes a gene that in at least two living forms, mice and people, produces shades of light and dark hair. Restoring mammoths as blondes or brunettes is now more reasonable. In a nice piece of forensic paleontology, scientists have also extracted enough DNA from extinct Neanderthal skulls to isolate a gene for hair color. In modern humans, this same gene causes red hair. If it acted the same in Neanderthals, then at least some were redheads. Some dinosaurs and fossil birds retain melanosomes, packets of pigment granules in their feathers. The shapes of these melanosomes imply colors. In modern birds, oblong-shaped melanosomes make black-gray colors; spherical-shaped make brown to red tones. The presences of these shapes in dinosaurs argue that dinosaurs were covered, at least in part, by plumage from blacks, grays, and brown to red.

A dynamic museum mural showing dinosaurs at battle or Neanderthals on the hunt may satisfy our curiosity for what they might have looked like in life. However, in any such restorations, human interpretation stands between the actual bones and the fully colored reconstruction.

New fossil finds, especially of more complete skeletons, improve the evidence upon which we build a view of extinct vertebrates. Often, however, new insights into old bones arise from an inspired reassessment of the assumptions upon which original restorations were based. Such is largely the case with recent reassessment of dinosaurs. Their structures, size, and success now seem to make them warm-blooded, active vertebrates living a lifestyle less like reptilian lizards and turtles of today and more like mammals or birds. New fossil discoveries got us thinking, but the major change in the way artists and paleontologists restore dinosaurs today reflects new courage in interpreting them as predominantly active land vertebrates of the Mesozoic.

Reconstruction of human fossils has followed fashion as well as new discoveries. When first unearthed in the late nineteenth century, Neanderthal bones were thought to be those of a single individual, a Cossack soldier from the Napoleonic wars fought a few decades earlier. In the beginning of the twentieth century, this view gave way to a stoop-shouldered, beetle-browed, and dim-witted image. Neanderthals were reassessed to be a breed apart from modern *Homo sapiens,* and restoration reflected this demoted image. Today, Neanderthals are classified again as a human species, *Homo sapiens neanderthalensis*. Shaven and suited, the claim goes, a Neanderthal could walk the streets of New York without drawing a second glance or a raised eyebrow. In New York, perhaps, but this "new" elevation of Neanderthal to modern status has been inspired by current artists' restorations that make the species look human.

The point is not to smirk at those who err or follow fashion but to recognize that any restoration of a fossil is several steps of interpretation away from the direct evidence of