VERTEBRATE LIFE

ELEVENTH EDITION

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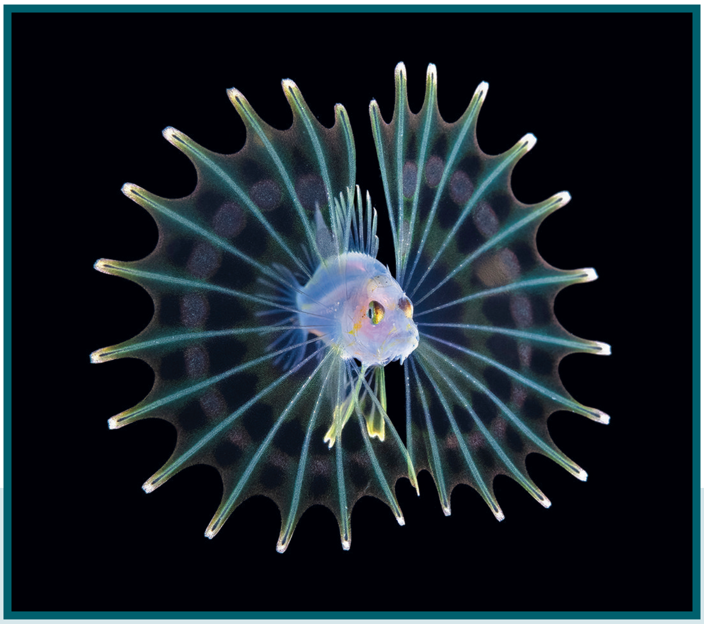

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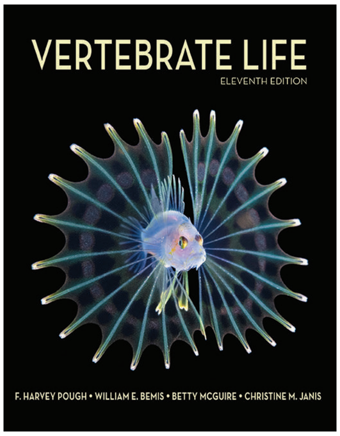

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Lionfish larva, *Pterois* sp., photographed during blackwater drift dive in open ocean at 20–40 feet with bottom at 700 plus feet below, Palm Beach, Florida, USA, Atlantic Ocean.

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Preface

In the fall of 1972, I started my college career with a course that changed my life. That course was called "The Vertebrates" and the professor who taught it was Dr. F. Harvey Pough, the lead author of this book. I learned so much in that class and became so fascinated with vertebrates that I have studied, written, and taught about them ever since. Today I teach The Vertebrates in the same classroom where I took the course as a student 50 years ago.

When Harvey invited my wife, Betty McGuire, and me to join the author team for the eleventh edition of *Vertebrate Life*, the book that Harvey and his original coauthors first published in 1979, we were thrilled.

The approach of this eleventh edition traces back to the course that I took so long ago. Then, as now, the goal was to integrate morphology, physiology, ecology, and behavior in a phylogenetic context to provide an organism-level understanding of vertebrates and their evolution. Back then, it was a little easier to contemplate such an undertaking, for only about half as many vertebrate species were known in 1972. As of this writing there are more than 70,000 species of vertebrates, and scientists describe several hundred new species each year.

When the first edition of *Vertebrate Life* was published in 1979, the types of phylogenetic rigor and methods of organizing phylogenetic information that we use today were in their infancy and no one had access to the molecular tools that we now take for granted. The many subsequent editions of *Vertebrate Life* progressively incorporated modern phylogenetics, more behavior, and more ecology, as well as new insights from paleontology and Earth history, and more recently from evolutionary developmental biology, or evo-devo. Especially and always, *Vertebrate Life* reflects a deep appreciation and respect for vertebrate diversity and conservation.

For this new edition, we focused first on phylogenetic content. We oriented the trees horizontally to improve readability, providing bracketed phylogenetic classifications to the right. We incorporated the dagger symbol (†) to indicate extinct taxa, a helpful convention in a field that requires constant comparisons between extinct and extant taxa. For most groups, we provide anatomical synapomorphies that students can see in the specimens that they study in course laboratories. We also discuss and incorporate molecular phylogenetic interpretations.

We worked to eliminate nonmonophyletic groups in the text and figures with the goal of encouraging clear thinking about phylogenetic trees and classifications. I always emphasize to my students that all trees are hypotheses, many are wrong, and all are subject to revision. But I also tell them that trees and phylogenetic classifications are the most useful and concise way to organize what we know about organisms and that their challenge as biologists is to think critically about the information that supports or falsifies a particular branching pattern. This prepares students to take the next step of using trees to explore anatomy, behavior, ecology, and other aspects of vertebrate life.

We are delighted by the return of Sergi López-Torres who authored the chapter on primates and the evolution of humans in the previous edition, and we welcome Emanuel Tschopp, the author of two chapters on dinosaurs in this edition. These are extraordinarily active fields of research and Sergi and Emanuel bring the depth and breadth of knowledge needed to describe these increasingly complex topics.

The eleventh edition includes more than 475 figures composed of nearly 2,000 individual photographs and illustrations, of which more than 1,100 are new. We critically evaluated every existing figure, redrew many, replaced others, and worked to find the best photographs to highlight vertebrate diversity. We developed new and informative part labels that appear directly on the figures, providing "instant captions" to orient students and serve instructors who depend on illustrations for teaching. Graphic balloons call attention to key points in many figures. Our goal has been to develop fun and informative visual interpretations to help students think about vertebrate evolution. We are indebted to Elizabeth Morales, Will Sillin, Sabrina Shih, as well as hundreds of amazing photographers and illustrators from around the world who graciously shared their work through Creative Commons licensing. All uncredited color illustrations of vertebrates are based on images by William E. Bemis and William B. Sillin, rendered by Sabrina Shih.

New to this edition are Learning Objectives presented at the start of each section within a chapter to highlight key take-away concepts for the section. Other specific improvements include:

- Development of background materials for the study of vertebrate evolution, exemplified by Figure 1.2, and the many new time trees and cladograms throughout the book
- Many updated examples using key fossil vertebrates to explore new phylogenetic interpretations and explain how particular anatomical features, such as the mammalian middle ear, evolved (see Figure 22.11)
- Reorganization of key topics within chapters to improve continuity and connections among chapters along with new cross-referencing to link topics between chapters
- Enhanced coverage and reorganization of chapters on sharks (Chapter 6), ray-finned fishes (Chapter 7), sarcopterygians (Chapter 8), early tetrapods, lissamphibians, and amniotes (Chapter 9), dinosaurs (Chapters 18 and 19), synapsids (Chapter 22), therians (Chapter 23), and primates (Chapter 24)
- Consolidation and reorganization of chapters to better highlight the role of thermoregulation and comparative physiology in vertebrate evolution (Chapter 14)
- Incorporation of new behavioral and ecological information to showcase vertebrate lives;
- Updated Discussion Questions at the end of each chapter
- A list of the sources that we consulted in preparing this edition, as well as many sources from earlier editions, that are available on the book's web page: https://learninglink.oup.com/access/content/pough-11e

We hope that you will find the eleventh edition of *Vertebrate Life* an inspiring introduction to the biology of these remarkable and enduringly fascinating animals.

William E. Bemis
Freeville, NY
January 2022

Sources for extant species diversity and common and scientific names

We relied upon these sources for the numbers of extant species and their common and scientific names.

- Eschmeyer's Catalog of Fishes: https://www.calacademy.org/scientists/projects/eschmeyers-catalog-of-fishes
- FishBase: http://www.fishbase.se/search.php
- AmphibiaWeb: https://amphibiaweb.org/
- The Reptile Database: http://www.reptile-database.org/
- IOC World Birds list: http://www.worldbirdnames.org/
- Avibase: http://avibase.bsc-eoc.org/checklist.jsp
- Mammal Species of the World: https://www.departments.bucknell.edu/biology/resources/msw3/
- ASM Mammal Diversity Database: https://mammaldiversity.org/
- IUCN Red List of threatened species: http://www.iucnredlist.org/
- Time Tree of Life: http://www.timetree.org

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The Natural History Museum
United States Fish and Wildlife Service
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The authors are only the visible tip of the iceberg that is a textbook

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Digital Resources for Vertebrate Life, Eleventh Edition

For the instructor

(Available at learninglink.oup.com/access/pough11e) Instructors using *Vertebrate Life*, Eleventh Edition, have access to a wide variety of resources to aid in course planning, lecture development, and student engagement. Content includes:

- *News Links:* A continually-updated collection of vertebrate biology news links.
- *Video Guide:* A curated collection of video links for further exploration of specific key topics within each chapter.
- *Image PowerPoints*: The complete set of figures from each chapter.
- *Layered Figures:* Selected key figures throughout the textbook are prepared as step-by-step and animated presentations that build the figure one piece at a time.
- *Active Learning Exercises:* Engaging exercises for each chapter are provided as Word documents.
- *Answers to End-of-Chapter Discussion Questions:* Answers to all the end-of-chapter Discussion Questions are provided as Word documents.
- *Complete References:* The complete citations for the literature referenced through the textbook.

For the student

Enhanced e-book

(ISBN 9780197564899)

Ideal for self-study, the *Vertebrate Life*, Eleventh Edition, enhanced e-book delivers extensive digital resources in a format independent from any courseware or learning management system platform. The enhanced e-book is available through leading higher-education e-book vendors and includes the following student resources:

- *Learning Objectives* outline the important take-aways of every major section
- *Layered Figures* let students work through complex figures step-by-step
- *Discussion Questions* following each chapter to help foster engagement with the material
- *Flashcards* help students learn and review the many new terms introduced in the textbook
- *Complete References* to the research literature cited in the textbook

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A student curator cares for vertebrate specimens

1

Diversity, Classification, and Evolution of Vertebrates

Evolution is central to biology. It is the overarching principle that helps us understand how living organisms work and allows us to organize their diversity. Evolutionary organization is at the core of the field of phylogenetic systematics, an approach that uses both morphological and molecular data to interpret the evolutionary history of extant (living) and extinct species. This book is specifically about the evolution of vertebrates, from their early forms to their current diversity, habitats, interactions, and means of survival.

This chapter reviews the extant vertebrate groups, summarizes phylogenetic systematics, and discusses genetic mechanisms and environmental events that shaped the evolution and biology of the vertebrates.

1.1 The Vertebrate Story

LEARNING OBJECTIVES

1.1.1 Summarize the diversity of living species in different vertebrate groups and understand how they are classified based on their phylogeny.

1.1.2 Explain the historical origin of binominal nomenclature and why we still rely on it.

1.1.3 Understand terms used to describe the organization of phylogenetic trees.

1.1.4 Differentiate the concepts of basal versus derived taxa.

Say the word "animal" and most people picture a vertebrate. Vertebrates are abundant and conspicuous parts of people's experience of the natural world. They are also remarkably diverse—more than 70,000 extant species ranging in size from fishes weighing as little as 0.1 gram to whales weighing over 100,000 kilograms (**Figure 1.1**). Vertebrates live in virtually all of Earth's habitats. Bizarre fishes, some with mouths so large they can swallow prey bigger than their own bodies, live in the depths of the sea, sometimes luring prey with glowing lights. Some 15 kilometers above these fishes, migrating birds fly over the peaks of the Himalayas.

But extant species are only a small proportion of the species of vertebrates that have existed. For each of the more than 70,000 extant species, there may be hundreds of extinct species, and some of these have no counterparts among extant forms. For example, the non-avian dinosaurs that dominated Earth for 180 million years are so entirely different from extant animals that it is hard to reconstruct the lives they led. Even mammals were once more diverse than they are now. The Pleistocene saw giants of many kinds, such as ground sloths as big as modern rhinoceroses and raccoons as large as bears. The number of species of terrestrial vertebrates probably reached its maximum in the middle Miocene, between 14 and 12 million years ago, and has been declining since then.

The diversity of extant and extinct vertebrates makes organizing them into a coherent system of classification that takes their evolutionary history into account an extraordinarily difficult task. Initially, classifying species was treated like an office filing system: Each species was placed in a pigeonhole marked with its name, and when all species were in their pigeonholes, the diversity of vertebrates would have been encompassed. This approach to classification was satisfactory as long as species were regarded as static and immutable; once a species was placed in the filing system, it was there to stay. Acceptance of the fact that species evolve made that kind of classification inadequate.

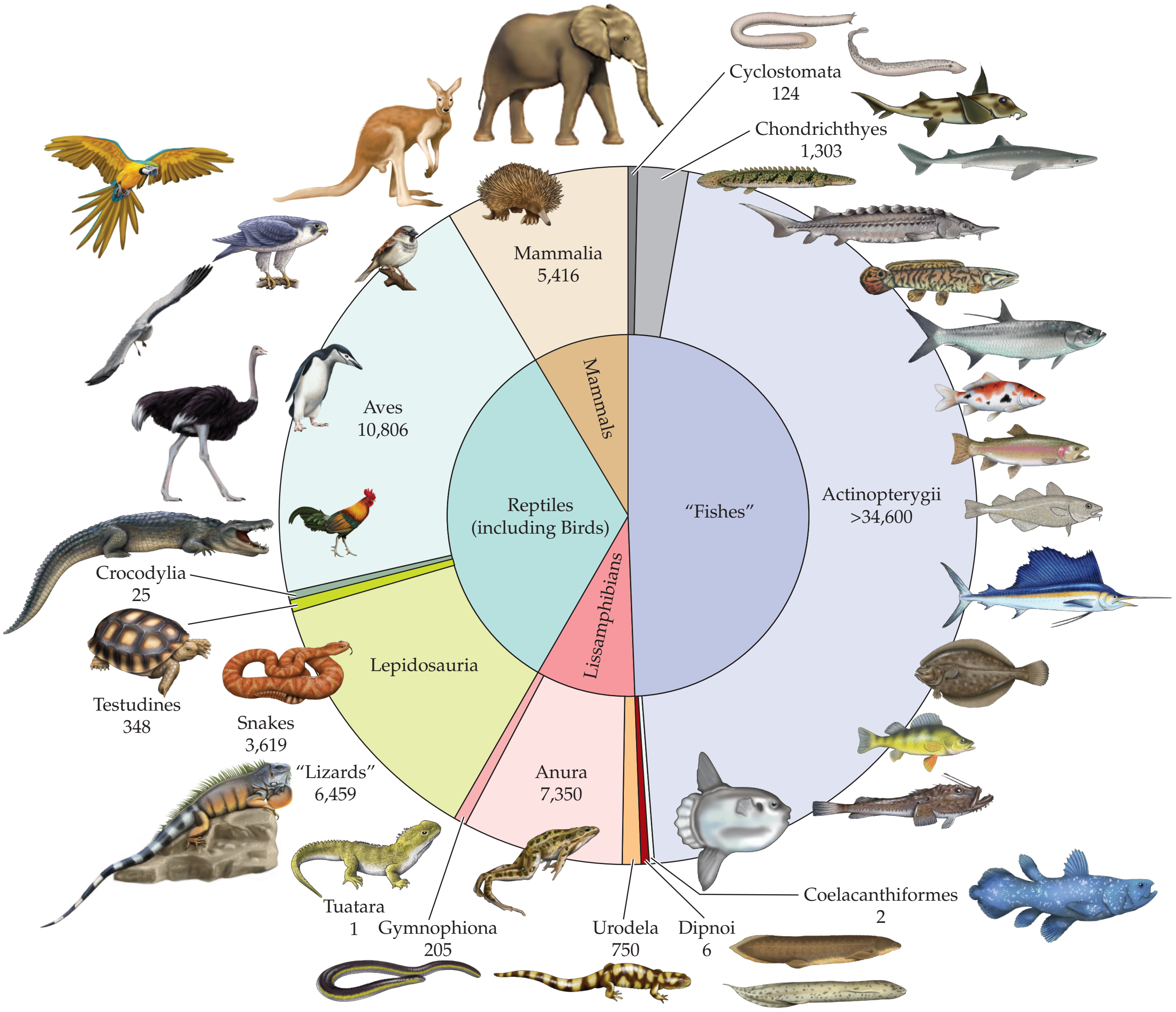


Figure 1.1 Diversity of extant vertebrates. Areas in the pie chart correspond to approximate numbers of extant species in each group as of 2021; numbers change as new species are described or existing species become extinct. Common names are in the center circle, with formal names for the groups shown in the outer circle. The two major extant lineages of vertebrates are Actinopterygii (ray-finned fishes) and Sarcopterygii (see the classification brackets in Figure 1.2), each of which includes about 35,000 extant species. (Some illustrations after K. Liem et al. 2001. *Functional Anatomy of the Vertebrates*, 3rd ed. Cengage/Harcourt College: Belmont, CA.)

Today's phylogenies are expected to express evolutionary relationships among species. Ideally, a classification system should not only attach a label to each species but also encode information about evolutionary relationships between that species and other species. Modern phylogenetic systematics—the naming and evolutionary classification of organisms—generates testable hypotheses about evolution, as we will describe in the next three sections. The first step, however, remains attaching a label—a unique name—to every species.

Binominal nomenclature

Our system of naming species is pre-Darwinian. It traces back to methods established by the naturalists of the 17th and 18th centuries, especially those of Carl von Linné, the Swedish naturalist better known by his Latin pen name, Carolus Linnaeus. The Linnaean system names species using **binomial nomenclature**: two names, a genus name and a species epithet. Species are grouped in hierarchical categories (family, order, class, and so on). These categories are called **taxa** (singular *taxon*), and the discipline of naming organisms is **taxonomy** (Greek *taxo*, "to arrange"; *nomos*, "order"). Goals for scientific names are threefold: uniqueness (i.e., no two species can share the same name); universality (i.e., everyone agrees to use the same name); and stability (i.e., a species name cannot be changed once it is properly named).

The scientific naming of species became standardized with the publication of the 10th edition of Linnaeus's monumental work *Systema Naturae* (*The System of Nature*) in 1758. The work was published in 12 editions between 1735 and 1766, each edition improving—and expanding on—the previous ones. The names that Linnaeus used in the 10th edition represent the formal start of biological nomenclature; any names published before 1758 are not accepted as scientific names (i.e., they are invalid). Linnaeus attempted to give an identifying binomial name to every known species of plant and animal. Familiar examples include *Homo sapiens* for human beings (Latin *homo*, "human" and *sapiens*, "wise"), *Passer domesticus* for the house sparrow (Latin *passer*, "sparrow" and *domesticus*, "belonging to the house"), and *Canis familiaris* for the domestic dog (Latin *canis*, "dog" and *familiaris*, "domestic").

Why use Latin? Latin was the early universal language of European scholars and scientists. It provided a uniform usage that scientists, regardless of their native language, continue to recognize worldwide. The same species may have different colloquial names, even in the same language. For example, *Felis concolor* (Latin, "uniformly colored cat") is known in various parts of North America as the cougar, puma, mountain lion, American panther, painter, and catamount. In Central and South America it is called león Colorado, león de montaña, pantera, onça vermelha, onça parda, yagua pytá, and suçuarana. But biologists of all nationalities recognize the name *Felis concolor* as referring to this specific kind of cat.

If stability of names is a goal of nomenclature, then why do species names seem to change so often? There are several reasons. First, upon further study, a systematist may decide that what was thought to be one species turns out to be two or more species. In other cases, a species thought to be distinct is found to be the same as another species; or that a species originally placed in one genus belongs in another genus; or that the species name was already in use for another organism (often an insect).

Another reason for instability of names is the principal of priority, which means that the first person who recognizes and names a species in an appropriate publication is credited as the author of that species name; any other names that someone else subsequently applies to that species are invalid. This happens less frequently now than it did 200 years ago, because methods of communication and dissemination of scientific names are much faster today, but it still happens as systematists study and revise taxa. Even though changes in the names of familiar species may seem inconvenient, they represent important scientific progress, which is why we work to keep scientific names used in this book up to date.

Extant vertebrate groups

Figure 1.2 shows extant vertebrate groups arranged in a **phylogeny**, or **phylogenetic tree** (or just "tree," for convenience). It is important to understand this figure because we use this design to organize the trees throughout this book. The **root** (sometimes called the **base**) is at the upper left in our design (it could have been placed at the bottom or top, which would change the tree's appearance but not the information it contains). From its root, the tree branches—splits in two—at a **node**. Splits at subsequent nodes, in an earliest-to-most-recent time progression, lead to all the branches in the tree. Each branch ends in a **terminal taxon,** the group named at the tip of the branch. The first branch split leads to two terminal taxa, hagfishes (Myxiniformes) and lampreys (Petromyzontiformes). Together, hagfishes and lampreys are within the **classification bracket** labeled Cyclostomata. All groups in Figure 1.2 are nested within the classification bracket Vertebrata ("nested" in this case means that all of the smaller classification brackets are included within the large bracket labeled Vertebrata).

The second node of Figure 1.2 branches out to eventually encompass all extant vertebrates that are *not* cyclostomes; these comprise the classification bracket Gnathostomata, or jawed vertebrates. Morphological characters indicated at each node along the "trunk" of the tree give some of the major evidence that supports this particular phylogeny. For example, the character "Four limbs with digits" characterizes the classification bracket Tetrapoda; the character "Amniotic egg" characterizes Amniota; and so forth. We often use the term **basal** when referring to taxa such as Cyclostomata that branch closer to the root of a particular tree. Taxa that branch after Cyclostomata, from cartilaginous fishes to placental mammals at the bottom of the figure, are said to be **derived** relative to hagfishes.

The arrangement of branches and taxa in a tree are collectively termed the tree's **topology**. Note that simply *rotating* a branch does not change the tree's topology. For example, if you swap the positions of hagfishes and lampreys with each other, then they will still be connected to the same branch, and will still be enclosed in the classification bracket Cyclostomata. However, branch *rearrangement*—changing the positions of nodes—changes the tree's topology and the resulting phylogenetic classification. For example, if you found convincing evidence that the branch leading to lampreys should connect not with hagfishes but with the branch that leads to chimaeras, that would yield a new topology and change the classification—and you could probably count on publishing your results in an extremely prestigious journal, because such a dramatic rearrangement would be extremely noteworthy.

You can consider the relationships in Figure 1.2 as you study the overview of extant vertebrates on pages 5–6.

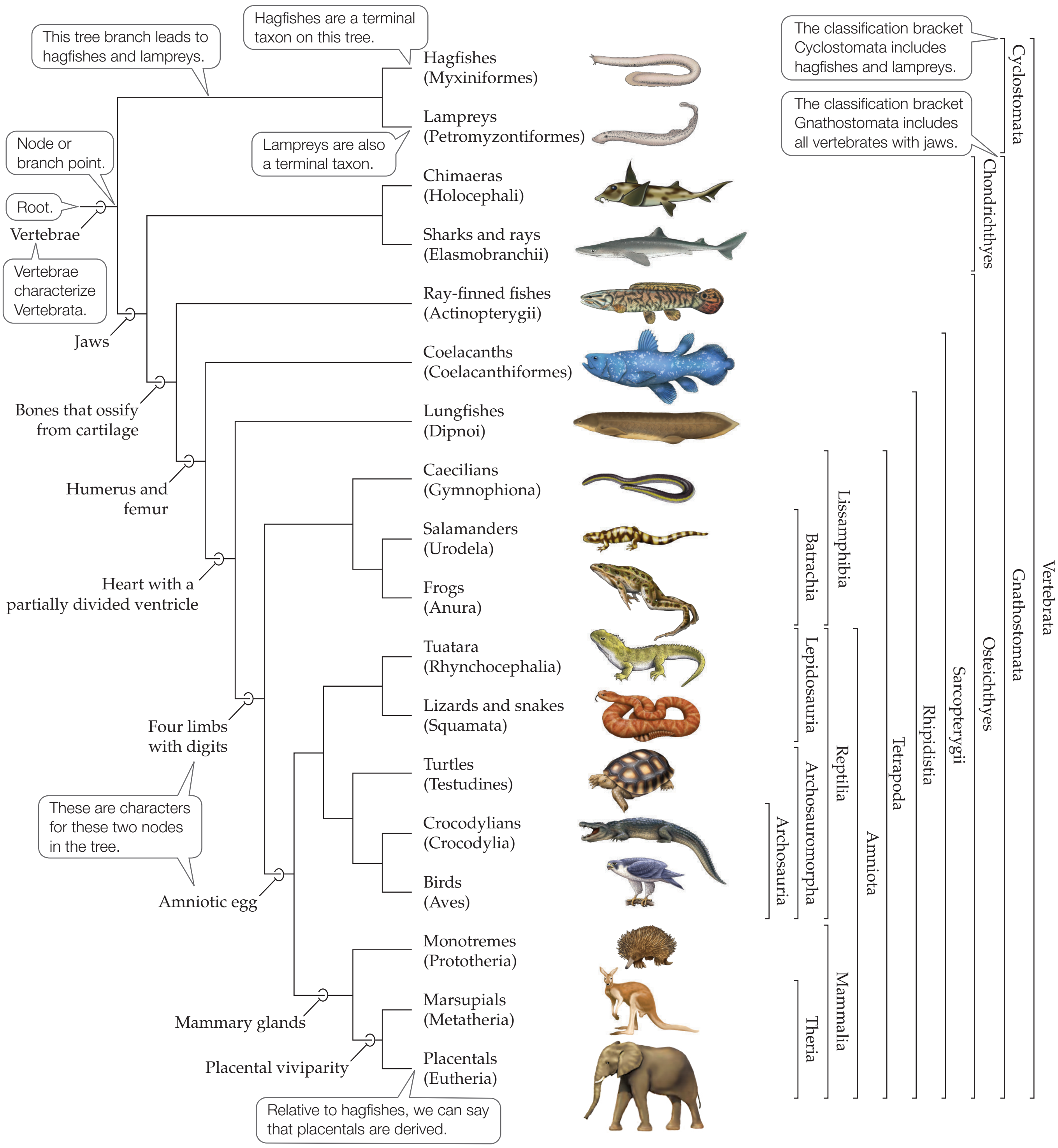


Figure 1.2 Phylogenetic relationships of extant vertebrate groups. Tree of extant vertebrate groups summarizing the phylogeny and classification used in this book. Branches of the tree lead to 18 terminal taxa, all of which are covered in this book. Nodes on the left indicate major characters that distinguish clades. Classification brackets are shown on the right. (Some illustrations after K. Liem et al. 2001. *Functional Anatomy of the Vertebrates*, 3rd ed. Cengage/Harcourt College: Belmont, CA.)

1.2 Phylogenetic Systematics

LEARNING OBJECTIVES

1.2.1 Understand the significance of monophyly.

1.2.2 Define the terms used in phylogenetic systematics and understand their significance in evolution.

Once we've given species their names, how do we decide where each one fits on our tree? All methods of classifying organisms are based on similarities shared by the included species, but some similarities are more significant than others. For example, nearly all terrestrial vertebrates have paired limbs with digits, but only a few vertebrate groups have mammary glands. Consequently, knowing that two species have mammary glands tells you more about the closeness of their relationship than does knowing they have paired limbs. A way to assess the relative importance of different characteristics was

Extant Vertebrate Groups

The topology of the tree in Figure 1.2 is well supported by modern morphological, molecular, and genomic research. Names for the nested classification brackets follow the most currently accepted concepts for these taxa. Here we briefly treat all terminal taxa in Figure 1.2 and their higher classification with the goal of familiarizing you with names used throughout this book.

All animals on the tree belong to **Vertebrata**, the vertebrates, and are distinguished by the presence of vertebral elements or vertebrae: serially arranged structures that form a spinal column.

Hagfishes and lampreys: Cyclostomata Named for their round mouth openings (Greek *cyclos*, "round"; *stoma*, "mouth"), hagfishes and lampreys lack jaws; members of both groups are elongate, limbless, scaleless, and lack bone. Hagfishes (Myxiniformes) are highly specialized for life as marine scavengers. They live burrowed in deep-water muddy seafloors. Typical adult lampreys (Petromyzontiformes) feed parasitically on blood and tissue fluids; they hatch from eggs laid in rivers or creeks, spend several years as filter-feeding larvae, migrate to sea to mature, and return to freshwater to spawn.

All extant vertebrates more derived than Cyclostomata belong to **Gnathostomata** (Greek *gnathos*, "jaw"), a group united by the presence of jaws.

Sharks, rays, and chimaeras: Chondrichthyes Chondrichthyes (Greek *chondros*, "gristle"; *ichthys*, "fish") refers to the cartilaginous skeletons of these fishes. Sharks have captured human imagination since antiquity, and have a reputation for ferocity that all but a few shark species would have difficulty living up to. Some are small (< 25 cm), while the largest species, the whale shark (*Rhincodon typus*), grows to 17 m and filter feeds on plankton. Most rays are dorsoventrally flattened bottom feeders that swim using undulations of their broad pectoral fins. Chimaeras, also known as ratfishes or rabbit fishes, are a small but ancient group of marine fishes that forage on the seafloor and feed on hard-shelled prey such as crustaceans and mollusks.

All extant gnathostomes more derived than Chondrichthyes belong to **Osteichthyes** (Greek *osteon*, "bone"), a group united by presence of bones that ossify from cartilages (endochondral bone; see Section 2.5).

Ray-finned fishes: Actinopterygii Most of the animals we think of as fishes belong to Actinopterygii (Greek *aktin* "ray"; *pteryg* "fin"), a group with nearly 35,000 extant species living in nearly every imaginable aquatic habitat, from rivers, ponds, and lakes to coral reefs and deep ocean trenches, to subzero waters of the Antarctic Ocean. Some survive temperatures in desert pools that would kill any other vertebrate. Most actinopterygians are higher bony fishes, or teleosts (Greek, *teleios* "complete"; *osteon*, "bone"), a group that spans tarpons, herrings, carps, catfishes, and trout to perches, swordfishes, tunas, flatfishes, and giant ocean sunfishes. Our understanding of teleost diversity continues to expand: on average, about 400 new species are described annually, and many thousands of new species await discovery.

All extant osteichthyans more derived than Actinopterygii belong to **Sarcopterygii**, a group united by presence of a single bone, the humerus or femur, as the only skeletal element at the base of the paired fins or limbs. Muscles associated with these bones are the source of the name Sarcopterygii (Greek *sarcos*, "flesh"; *pteron* "fin"). From a phylogenetic standpoint, Sarcopterygii includes all extant groups of terrestrial vertebrates—lissamphibians, reptiles (including birds), and mammals, which together are about 35,000 species. In a broadly comparative sense, about half of the living vertebrates are actinopterygians; most of the rest are sarcopterygians.

Coelacanths: Coelacanthiformes The two extant species of Coelacanthiformes (Greek *koilos*, "hollow"; akantha "spine") occur in moderately deep waters (~200 m) off the east coast of Africa and Indonesia. They are relicts of a small group that has persisted since the Devonian Era.

All extant sarcopterygians more derived than Coelacanthiformes belong to **Rhipidistia**. This group is characterized by a heart with a partially divided ventricle, which helps to separate oxygenated from deoxygenated blood flowing through the heart.

Lungfishes: Dipnoi Six extant species of lungfishes or Dipnoi (Greek *di*, "double"; *pnoe*, "breath") live in South America, Africa, and Australia. They can extract oxygen from water with gills and from air with lungs. Well represented in the Devonian, lungfishes are the closest living relatives of land vertebrates.

All extant rhipidistians more derived than Dipnoi are terrestrial vertebrates belonging to **Tetrapoda**, a group characterized by the presence of four limbs with digits. An extensive series of fossils allows us to trace the transformation of characters in fish-like sarcopterygians to those of tetrapods.

Caecilians, salamanders, and frogs: Lissamphibia Popularly known as amphibians (Greek *amphis*, "double"; *bios*, "life"), most species of lissamphibians have biphasic life histories, which typically include an aquatic larval form (larva for caecilians and salamanders; tadpole for frogs) and a terrestrial adult. We infer that such an amphibious life history also characterized the earliest Devonian tetrapods, and that it was retained in the branch of tetrapods leading to lissamphibians. Although we often think of lissamphibians as tied to water for reproduction, many species lack aquatic larvae and spend their entire lives on land.

Lissamphibians are characterized by smooth skin without scales (Greek *lissos*, "smooth") that is important in the exchange of water, ions, and gases with their environment. Caecilians (Gymnophiona) are legless aquatic or burrowing animals; salamanders (Urodela) are elongate, mostly terrestrial, and usually have four legs; frogs (Anura) are short-bodied, with large heads and large hindlegs used for walking, jumping, and climbing. Much evidence shows that salamanders and frogs are more closely related to each other than they are to caecilians, and they are placed together in **Batrachia**.

All extant tetrapods more derived than Lissamphibia belong to **Amniota**, a group characterized by the presence of an amniotic egg with an amnion, chorion, and allantois. These three new membranes develop from the embryo's body and are not made by the reproductive tract of the

(*Continued*)

Extant Vertebrate Groups *(continued)*

mother (this contrasts with egg membranes, egg cases, or eggshells, which are secreted by the mother's oviduct). The innermost extraembryonic membrane, the amnion, encloses the embryo in fluid. The other two membranes serve roles in gas exchange and protection. Most amniotes are terrestrial, but there are secondarily aquatic species such as sea turtles and whales.

Amniota has two extant clades: **Reptilia** and **Mammalia**. Reptilia includes the lepidosaurs, turtles, crocodylians, and birds.

Tuatara, lizards, and snakes: Lepidosauria Lepidosaurs (Greek *lepsis*, "scale"; *sauros*, "lizard") have scaly skins and share many skeletal characters. The tuatara (*Sphenodon punctatus*, a stocky lizardlike animal found only on some offshore islands of New Zealand) is the sole living remnant of a more diverse Mesozoic lineage. In contrast, **Squamata** (lizards and snakes) is now at its peak diversity.

Remaining groups of extant reptiles belong to **Archosauromorpha**, represented today by turtles, crocodylians, and birds.

Turtles: Testudines The ~350 species of Testudines (Latin *testudo*, "turtle") belong to a distinctive and immediately recognizable group. The shell that encloses the body of a turtle does not occur in other vertebrates, and unique morphological modifications associated with the shell make turtles extremely peculiar animals. They are, for example, the only vertebrates with the shoulders (pectoral girdle) and hips (pelvic girdle) enclosed by the ribs. Their distinctiveness makes them something of an evolutionary enigma, and over the years systematists have placed turtles in several different locations on the tree. Our placement in Figure 1.2 is based chiefly on molecular phylogenetic interpretation.

All extant archosauromorphs more derived than Testudines belong to **Archosauria**, represented today by crocodylians and birds.

Alligators and crocodiles: Crocodylia These impressive animals draw their name from the Latin word for them (*crocodilus*). Extant crocodylians are semiaquatic predators with long snouts with large pointed teeth. They range from dwarf crocodiles and caimans (1.5 m long) to the saltwater crocodile (*Crocodylus porosus*), which can grow to 6 m. The skin contains many bones (osteoderms; Greek *osteon*, "bone"; *derma*, "skin") that form in their scales and provide a kind of armor plating. Crocodylians provide parental care for eggs and young.

Birds: Aves Birds (Latin *avis*, "bird") are dinosaurs that evolved flight in the Mesozoic. Discoveries of fossil archosaurs that lack wings but have feathers ("feathered dinosaurs") show that feathers evolved long before flight. The first feathers were almost certainly used in courtship displays and for insulation, and their modifications in birds (as airfoils and for streamlining) were secondary events. This disparity illustrates an important principle: The function of a trait in an extant species is not necessarily the same as that trait's function when it first appeared. In other words, current utility is not the same as evolutionary origin.

The last amniote group on the tree is Mammalia, all of which feed their young with milk produced by female mammary glands.

Mammals: Mammalia Extant mammals (Latin *mamma*, "teat") include about 5,400 species in three groups: monotremes (**Prototheria**), marsupials (**Metatheria**), and placentals (**Eutheria**). Monotremes—platypus and echidnas—occur today in Australia, and one species of echidna reaches New Guinea. Monotreme young hatch from eggs. Today, marsupials dominate the mammalian fauna only in Australia, although more than 100 species occur in South and Central America, and one, the Virginia opossum (*Didelphis virginiana*), lives in North America. Placentals are by far the largest extant group of mammals in terms of species (most are rodents or bats), but the name "placentals" is misleading, because both marsupials and placentals have placentas, which are structures that transfer nutrients from the mother to the embryo and remove waste products of an embryo's metabolism. Because of the shared presence of a placenta, we group Metatheria and Eutheria together as **Theria**.

developed in the mid-20th century by Willi Hennig, who introduced a method of hypothesizing evolutionary relationships called **phylogenetic systematics** (Greek *phylon*, "tribe"; *genesis*, "origin").

A core concept of phylogenetic systematics is the recognition of groups of organisms at different hierarchical levels within an **evolutionary lineage**, or **clade**. Clades must have a single evolutionary origin—that is, they must be **monophyletic** (Greek *mono*, "one" or "single"), and include all the descendants of a **common ancestor**. Members within monophyletic groups are linked by nested sets of characters that trace the evolutionary history of the group. These principles—monophyly and the inclusion of all descendants—underpin the discipline of **cladistics**.

Hennig's approach embodied the concept that monophyletic groups can be identified only on the basis of **shared derived characters**—that is, characters that have the same evolutionary origin (i.e., are homologous) and that differ from an ancestral condition (are derived). A derived character is called an **apomorphy** (Greek *apo*, "away from"; *morphe*, "form"; thus, "away from the ancestral condition"). A shared derived character is a **synapomorphy** (Greek *syn*, "together"). In our example from the previous paragraph, mammary glands are a synapomorphy for Mammalia (note that this is shown as a character for Mammalia in Figure 1.2).

Of course, organisms within a clade can also share characters that they have inherited unchanged from their ancestors. These are called **plesiomorphies** (Greek *plesios*, "near," in the sense of "similar to the ancestor"). The vertebral column of terrestrial vertebrates, for example, was inherited from sarcopterygian fishes, and, by itself, the mere presence of a vertebral column cannot tell us anything about evolutionary relationships within tetrapods. The same character can be either plesiomorphic or apomorphic, depending on the level within the phylogeny. A vertebral column is a plesiomorphic character of vertebrates, so it provides no information about evolutionary relationships of vertebrates to one another, but it is a synapomorphy of vertebrates when compared with nonvertebrate chordates.

1.3 Applying Phylogenetic Criteria

LEARNING OBJECTIVES

1.3.1 Explain what an outgroup is and understand the use of outgroups in proposing a phylogeny.
1.3.2 Apply principles of phylogenetic systematics to interpret phylogenetic trees.
1.3.3 Explain how morphological and molecular characters are used to propose phylogenies.
1.3.4 Explain what the dagger (†) symbol means and why it is important to use it.

Although the conceptual basis of phylogenetic systematics is straightforward, applying the criteria can become complicated. Scientists analyze character states and apply phylogenetic criteria to propose hypotheses about evolutionary relationships among organisms. To proceed, however, we need to address a central issue of phylogenetic systematics: How do scientists know which character state is ancestral (plesiomorphic) and which is derived (apomorphic)? That is, how can we determine the direction (polarity) of evolutionary transformation of the characters? The basic method is to compare characters in the group of interest, the **ingroup**, to those of an **outgroup**, a reference group or groups that, although known to be related to the organisms we are studying, is less closely related to any member of the ingroup than the ingroup members are to each other. For example, sarcopterygian fishes such as coelacanths and lungfishes are appropriate outgroups for studying characters of terrestrial vertebrates.

Evaluating possible phylogenies

To illustrate tree thinking and phylogenetic classifications, consider **Figure 1.3**, which shows the possible phylogenies of three taxa identified as 1, 2, and 3. Note that when we are comparing information about three taxa, there are always three possible resolved phylogenies. Each of the resolutions specifies that two of the taxa are more closely related to each other than they are to the third taxon.

To make this hypothetical example more concrete, we'll consider three characters: the number of toes on the front feet, the skin covering (scales or no scales), and the presence or absence of a tail. In the ancestral character state—based on the outgroup—there are five toes on the front feet, and in the derived state there are four toes; the tail is present in the ancestral state and absent in the derived state; the ancestral state is scaly skin, and the derived state is a lack of scales (Figure 1.3A). This information can be presented as a data matrix in which the ancestral state in indicated by 0, the derived state by 1:

	Five front toes	Tail	Scales
Outgroup	0	0	0
Taxon 1	0	0	1
Taxon 2	0	1	0
Taxon 3	1	1	0

How can we use the information in this data matrix to decipher the evolutionary relationships of the three groups of animals? Notice that the derived number of four toes occurs only in taxon 3, the derived tail condition (absent) is found in taxa 2 and 3, and the derived loss of scales occurs only in taxon 1. *Any change in a structure is an unlikely event, so the most plausible phylogeny is the one requiring the fewest changes.* The **most parsimonious phylogeny** (i.e., the branching sequence requiring the fewest number of changes) is represented by Figure 1.3B, where only three changes are needed to produce the current distribution of character states. In the evolution of taxon 1, scales are lost; in the evolution of the lineage that includes taxa 2 and 3, the tail is lost; and in the evolution of taxon 3, a toe is lost. The phylogenies in Figures 1.3C and D are possible, but they require tail loss to occur independently twice (i.e., four evolutionary changes rather than three), so they are less parsimonious than the first phylogeny.

Like any scientific hypothesis, a phylogeny is constantly tested as new character data or taxa are discovered. If it fails the test, it is falsified; that is, it is rejected, and a different hypothesis (a different branching sequence) is proposed. The process of testing phylogenetic hypotheses and replacing those that are falsified is a continuous one, and changes in the phylogenies in successive editions of this book show where new information has generated new hypotheses.

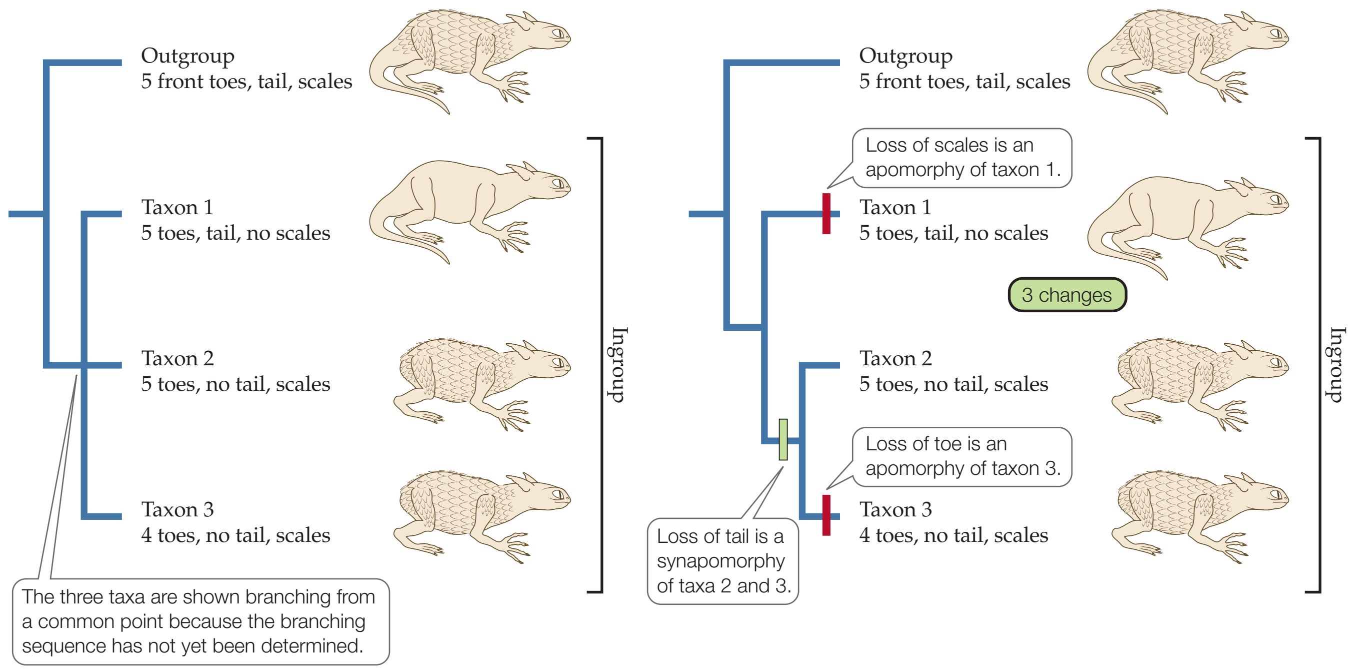
Molecules and morphology

Initially, scientists classified organisms according to their morphology, and morphology is still paramount in taxonomy. We will cover characters that define all vertebrates in Chapter 2, and subsequent chapters will describe the various and sometimes unique ways these characters have become adapted among members of the different groups. In the last half-century, however, we have also gained access to a vast amount of molecular and genetic data. Such data have become an important source of information and have led to many revisions in phylogenies.

In the 1960s, American anthropologist Vincent Sarich pioneered the use of molecular character information by using immunological comparison of blood serum

(A) Starting point for resolving relationships among three taxa

(B) Distribution of characters on first tree



(C) Distribution of characters on second tree

(D) Distribution of characters on third tree

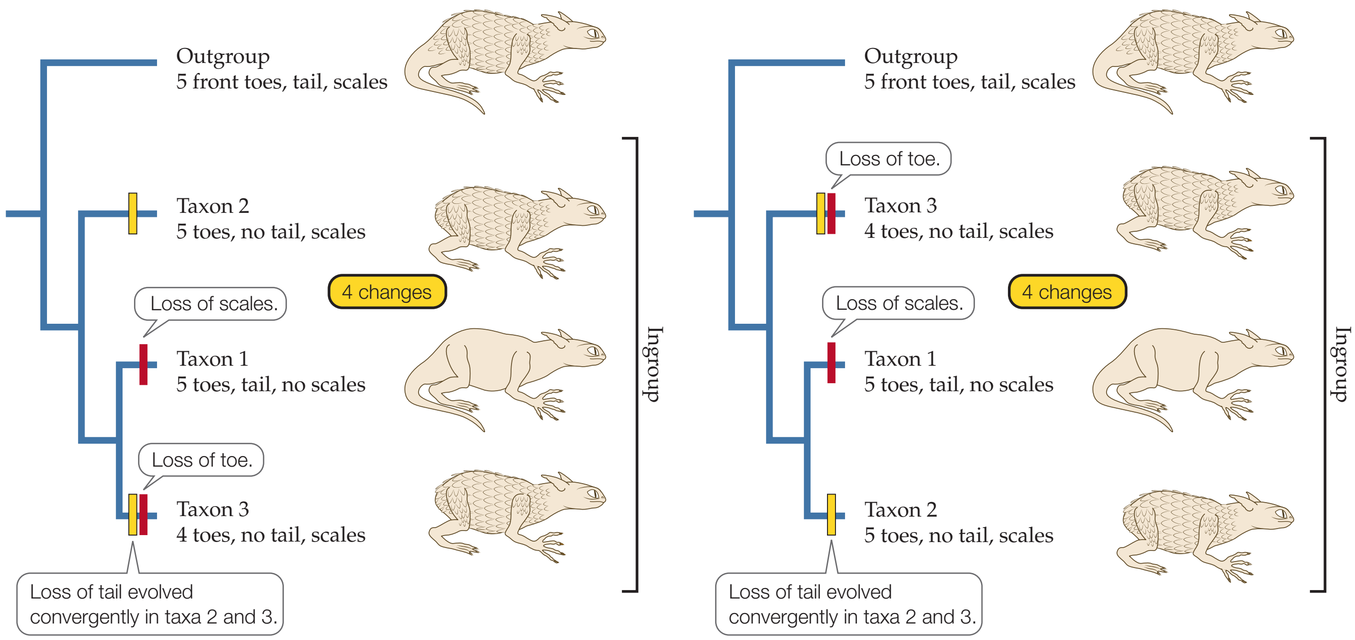


Figure 1.3 Resolving phylogenetic relationships. (A) An outgroup is used to determine the best branching sequence for the evolution of the ingroup (taxa 1, 2, 3). The outgroup has the ancestral (plesiomorphic) character states, which are five toes on the front feet, a tail, and a scaly body covering. (B–D) Three possible evolutionary trees with different arrangements of the ingroup taxa. Bars identify derived evolutionary changes, or apomorphies. The green bar in (B) indicates a shared derived character, or synapomorphy, of the lineage that includes taxa 2 and 3. Orange bars in (C) and (D) indicate two independent evolutionary losses of the tail; we say that tail loss in the taxa on these two trees occurred convergently. Because phylogeny (B) requires only three changes in characters, we say it is more parsimonious than either (C) or (D) and thus is most likely to reflect evolutionary history.

albumins to determine that chimpanzees are the apes most closely related to humans. In the 1970s, amino acid sequences of proteins and base sequences of mitochondrial and nuclear DNA were added to the repertoire of molecular phylogeny. That same decade saw the development of computer algorithms that can rapidly sort and arrange large numbers of characters in a phylogeny. More recently, we have entered the era of genomic-level comparisons, which may help to confirm or refute earlier phylogenetic hypotheses. It is still early days, however, and it will be fascinating to see what happens as we learn more.

Any set of characters can produce multiple possible phylogenies, and the number of possible trees grows exponentially as the number of taxa and characters increase, putting it beyond one person's ability to interpret all possible trees. Algorithms developed since the 1960s use various methods (e.g., parsimony, maximum likelihood, Bayesian inference) to discover and identify the most plausible sequences of changes. Ever more powerful computers made it possible for anybody to use these algorithms. With the establishment of public-access repositories such as GenBank in 1982, MorphoBank in 2005, and MorphoSource in 2012, vast quantities of both genetic and morphological data became available on the Internet. As a result, phylogenetic systematics moved from humans analyzing a few characters to computer-based analyses of huge data sets (although analyses of the largest phylogenetic data sets can require weeks of processing time).

Molecular characters came to be regarded as superior to morphological characters for evaluating phylogenies. The ease with which large quantities of molecular data can be obtained contributed to this perception, as did the assumption that molecular data would be free from some of the problems of interpretation associated with morphological data. More recently, however, molecular phylogenies have lost some of their luster. The assumptions that all types of molecular data are equally useful for phylogenetics and that more data always produce better results are being questioned. Some molecular characters are appropriate for looking at recent divergences, while others are better at resolving older splits; mixing the two can produce conflicting results.

Differences of that sort are usually easy to see in morphological data, but harder to see in molecular data. For example, coat color of mammals can be useful for distinguishing among different species within a genus, but it is not useful at higher taxonomic levels. Different patterns of striping distinguish different species of zebras, but stripes cannot be used as a character to ally zebras with tigers. Molecular characters are more difficult to assess in this fashion, because the functional significance of differences in base sequences or amino acids is rarely known—most molecular and even genomic characters remain black boxes as far as function is concerned. Furthermore, fossils seldom yield molecules, and when they do the molecules are often degraded, so molecular characters can rarely be used to determine the relationships of fossil organisms to one another or to extant species. This is a critical shortcoming. A morphology-based phylogeny can be drastically rearranged by the addition of a single fossil that alters the polarity of morphological characters, but molecular phylogenies cannot be tested in this manner.

The problem of dating

Dating the time that lineages separated is another weakness of molecular phylogenies, because dates are based on assumptions about the rates at which mutations occur and must be anchored by reference to an estimated age of a group based on its fossil record. The age of a fossil can almost always be determined—provided that you have a fossil. One difficulty with fossils is the incompleteness of the fossil record. There are gaps, sometimes millions of years long, in the record of many taxa. For example, we have fossil lampreys from the Late Devonian (~360 Ma[1]), the Late Carboniferous (~300 Ma), and the Early Cretaceous (~145 Ma), but nothing between those dates.

Considering the difficulties with both molecular and morphological phylogenies, it's remarkable that they mostly agree about branching patterns. Disagreements often center on dates of divergence. For example, molecular phylogenies indicate that the extant lineages of lissamphibians diverged in the Late Carboniferous (~315–300 Ma), whereas the earliest fossils indicate that the divergence occurred in the Late Permian (~260–255 Ma). However, molecular and morphological methods sometimes agree; molecular evidence indicates that humans separated from their common ancestor with chimpanzees about 6.6 Ma, and this date fits well with the earliest fossil in the human lineage, †*Ardipithecus* (5.8 Ma). There are, of course, some particularly stubborn groups, in the sense that they have been difficult to place whether you study molecules or morphology. Turtles are a good example of this, and their placement on the tree in Figure 1.2 as the sister taxon of archosaurs is just one of many possible arrangements proposed in recent decades.

The best information sometimes comes from combining molecular and morphological data. Studies that include extant and extinct organisms often employ the technique of **molecular scaffolding**: the extant taxa are placed in their phylogenetic position by the relationships established by the molecular data, and then morphological data are used to integrate the fossil taxa with the extant taxa.

Dagger (†) convention adopted in this book

Fossil vertebrates offer information about morphology, evolutionary relationships, and paleoenvironments, but it is not always easy to integrate fossils into phylogenetic analyses. Fossils are usually incomplete. Even so-called whole-body fossils that preserve the skeleton in a lifelike position and sometimes include evidence of soft tissues can never allow us to see and evaluate all the types of characters that we can study in a living vertebrate. Thus, we will always know less about vertebrates known only from fossils. This is important to remember, because it colors our ideas about the quality of the information

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[1] Ma is the abbreviation for mega-anna, "millions of years" or, when referring to a specific date range, "million years ago."
Analogously, ka = kilo-anna (thousand years, thousand years ago), and Ga = giga-anna (billion years, billion years ago).

available for our evaluation. In this book, then, we indicate wholly extinct taxa with a dagger symbol (†) before the taxon name. The dagger symbol helps to distinguish extinct from extant taxa and reminds us about the lack of information for extinct taxa. This convention is particularly important for extinct higher taxa (higher taxa are genera and any group names, such as family names, that include genera), which often prove difficult to place with confidence on trees of extant vertebrates.

1.4 Using Phylogenetic Trees

LEARNING OBJECTIVES

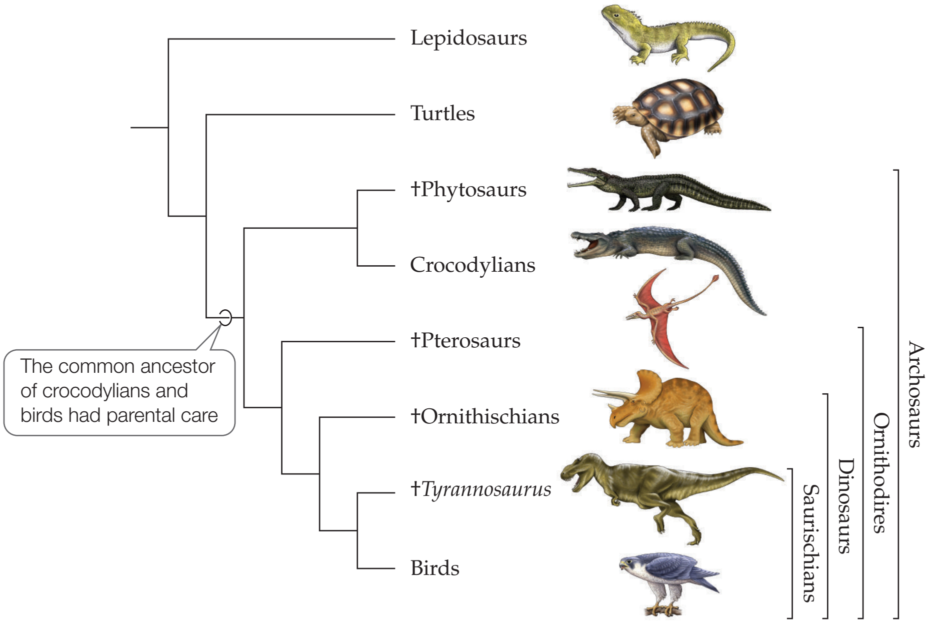
- 1.4.1 Use the concept of an extant phylogenetic bracket to make inferences about extinct taxa.
- 1.4.2 Understand why paraphyly is problematic.
- 1.4.3 Explain the difference between crown groups and stem groups.

Phylogenetic systematics is based on the assumption that organisms in a lineage share a common heritage that accounts for their similarities. Because of that common heritage, we can use phylogenetic trees to ask questions about evolution. By examining the origin and significance of characters of extant animals, we can make inferences about the biology of extinct species. For example, some fossilized dinosaur nests contain remains of partly grown baby dinosaurs, suggesting that at least some extinct dinosaurs cared for their young. Is that a plausible inference? Obviously there is no direct way to determine what sort of care extinct dinosaurs provided to their eggs and young. The tree in **Figure 1.4** provides an indirect way to approach the question by examining the closest living relatives of extinct dinosaurs, which are crocodylians and birds.

Extant phylogenetic brackets

Take a look at the phylogenetic relationship of crocodylians, non-avian dinosaurs, and birds in Figure 1.4. The intermediate lineages in the phylogenetic tree (†pterosaurs and non-avian dinosaurs) are extinct, so we cannot observe their reproductive behavior. But crocodylians are the extant sister taxon of birds, and together, crocodylians and birds form what is called an **extant phylogenetic bracket**. We know that both crocodylians and birds provide parental care. Looking at extant representatives of more distantly related lineages (outgroups), we see that parental care is not universal among lepidosaurs, or turtles. The most parsimonious explanation of the occurrence of parental care in both crocodylians and birds is that it evolved after archosaurs separated from turtles but before the lineages leading to crocodylians and birds separated from each other. We cannot "prove" that parental care did not evolve independently in crocodylians and birds, but a single origin of parental care is more likely than two separate origins. Thus, the most parsimonious hypothesis is that parental care is a derived character of the evolutionary lineage containing crocodylians + birds. That means we are probably correct when we interpret fossil evidence as showing that non-avian dinosaurs did indeed exhibit parental care.

Figure 1.4 also provides an example of the important term **sister group** (or **sister taxon**), which refers to the monophyletic lineage most closely related to the monophyletic lineage being discussed. Here the lineage that includes crocodylians + †phytosaurs is the sister group of ornithodires. Similarly, †pterosaurs are the sister group of dinosaurs, †ornithischians are the sister group of saurischians (including birds), and †*Tyrannosaurus rex* on this tree is the sister group of birds.



The common ancestor of crocodylians and birds had parental care

Figure 1.4 Using a phylogenetic tree to make inferences about behavior. Did extinct dinosaurs provide parental care? The tree shows currently accepted relationships among Archosauria, a group that includes several extinct lineages as well as extant crocodylians and birds. Crocodylians and birds (together, the extant phylogenetic bracket labelled archosaurs) display extensive parental care of eggs and young, but turtles do not. The most parsimonious explanation is that parental care evolved in the archosaur lineage after its separation from turtles but before the separation of crocodylians from ornithodires. (†Phytosaur by Jeff Martz; all others after K. Liem et al. 2001. *Functional Anatomy of the Vertebrates*, 3rd ed. Cengage/Harcourt College: Belmont, CA.)

Paraphyly

Figure 1.4 also reveals how phylogenetics has made talking about certain groups of animals more complicated than it used to be. Suppose you wanted to refer to just the two branches in this tree that are popularly known as “dinosaurs”—†ornithischians and extinct saurischians, such as †*Tyrannosaurus rex*. What do you call them? If you call them “dinosaurs,” you’re not being phylogenetically correct, because Dinosauria as a lineage includes birds. So when you say “dinosaurs,” you are including †ornithischians + all saurischians, which in a phylogenetic sense includes birds, even though any 7-year-old would understand that you mean to restrict the conversation to extinct Mesozoic animals.

In fact, there is no technically correct name in phylogenetic systematics for just those animals popularly known as “dinosaurs.” That’s because cladists recognize only monophyletic groups (see Section 1.2), and a monophyletic group includes an ancestral form and all of its descendants. If birds are omitted from Dinosauria, then the group no longer includes all the descendants of the common ancestor. The lineage †ornithischians + saurischians *minus* birds is **paraphyletic** (Greek *para*, “beside” or “near,” meaning a taxon that includes the common ancestor and some, but not all, of its descendants).

The only technically correct way of referring to the animals popularly known as dinosaurs is to call them “non-avian dinosaurs,” and you will find that term and other examples of paraphyletic groups in this book. Sometimes even this construction does not work because there is no appropriate name for the part of the lineage you want to distinguish. In that situation, we use quotation marks (e.g., "†ostracoderms”) to indicate that the group is paraphyletic, or we refer to individual taxa (usually genera) when we are talking about fossil vertebrates.

We try to avoid naming or referring to paraphyletic groups in this book, but sometimes it is convenient to do so, particularly when the name is in common usage. For example, “Fishes” in Figure 1.1 is not monophyletic because it does not include all of the descendants of a single common ancestor. Still, the term “fishes” no doubt calls to mind the image of an aquatic animal that uses gills to breathe water. Sometimes such a mental picture is worth a thousand words, and we use quotation marks as the standard convention for referring to such groups.

Crown and stem groups

Even though phylogenetic methods allow us to decipher evolutionary pathways and construct phylogenetic classifications for extant groups, difficulties arise when we try to find names for groups that include fossils. The derived characters found in extant groups did not all evolve at the same time. On the contrary, derived characters typically evolve in a stepwise or mosaic fashion. Extant members of a group have all of the derived characters of that group because that is how we define the group today, but as we move backward through time to fossils that represent outgroups to the extant species, we encounter forms that have a mosaic of ancestral and derived characters.

The farther back in time we go, the fewer derived characters the fossils may have. What can we call the parts of a lineage that contain these fossils? They cannot have the same name as the extant group because they lack some of the derived characters that we use to define the group. The solution lies in recognizing crown groups and stem groups. **Crown groups** have all of the derived character states found in extant species. Not all members of a crown group have to be extant; an extinct species with all of the derived characters is a member of the crown group. **Stem groups** are those extinct forms that lack some of the derived characters. Put another way, stem groups are fossils with some derived characters, and crown groups contain extant species plus fossils that have all the derived characters of the extant group. Stem groups are paraphyletic because they do not contain all the descendants of the ancestor of the stem group.

1.5 Genetic Mechanisms of Evolutionary Change

LEARNING OBJECTIVES

1.5.1 Describe the various lines of research that converged to become the Modern Synthesis.
1.5.2 Understand the significance of developmental biology in current evolutionary studies.
1.5.3 Explain the difference between “survival of the fittest” and “arrival of the fittest.”
1.5.4 Describe an example of developmental gene regulation and its effect on a phenotypic character.
1.5.5 Define heterochrony, heterotopy, and heterometry and explain how each can produce phenotypic change.

“Descent with modification” is the phrase that Charles Darwin used to describe evolution. He drew his evidence from the animals and plants he encountered during his voyage aboard the HMS *Beagle* (1831–1836) and from his familiarity with selective breeding of domestic animals. Darwin emphasized the roles of natural selection and sexual selection as the mechanisms of evolution, although the basis of the traits he described was a mystery at the time. Gregor Mendel’s meticulous and remarkable work documenting evidence of particulate inheritance (i.e., separate inheritance of specific traits, such as yellow versus green and smooth versus wrinkled peas) was published in 1866, but was not widely read at the time and was largely forgotten for more than 40 years. The rediscovery of Mendel’s work in the early 20th century resulted in its extension and application to Darwin’s ideas and led to the firm establishment of genes as the basis of heritable traits.

The 1930s, 40s, and early 50s saw the blending of Darwin’s ideas on natural selection, Mendelian genetics, paleontology, and quantitative population biology into a comprehensive view of evolution known as the **Modern Synthesis**. Molecular research in the 1950s and

60s established DNA as the gene's self-replicating repository of the information that produces life's essential proteins, followed by the elucidation of the genetic code, and eliminated any doubt that evolution is the force that drives diversity.

The last three decades of the 20th century saw exponential increases in our knowledge of molecular biology, and in the 1980s and 90s this vast new understanding transformed the study of embryos into the modern field of developmental biology. Embryological studies were not a significant element of the Modern Synthesis, but the ever expanding findings of developmental biology were quickly seen to be integral to evolution, giving rise to the important field of **evolutionary developmental biology** (colloquially known as **evo-devo**). Current evolutionary approaches blend the insights and methods of all data sources and methods, and the new science of genome editing using CRISPR/Cas9 promises even more insights into the links between genotypes and phenotypes.

Phenotypes and fitness

Among many other findings, the Modern Synthesis established that most genes are polymorphic; that is, they have two or more **alleles** (forms of a gene that differ in their DNA base sequence). The phenotype, or physical form, of an organism is determined by its genotype—that is, by its particular combinations of alleles—and natural selection acts on phenotypes via differential survival and reproduction. Genetic mutations that result in new alleles occur randomly, and heritable allelic variation produced by mutation is the raw material of evolution.

An axiom of evolution is that *it is populations, not individuals, that evolve*. Although the phrase "survival of the fittest" may conjure images of individual combat, in fact evolutionary success is measured in terms of reproductive success: some phenotypes leave more descendants than others. The Modern Synthesis quantified this concept, showing that the frequency of the alleles that produce those phenotypes increases from one generation to the next. **Darwinian fitness** is a shorthand term that refers to the genetic contribution of a specific genotype to succeeding generations relative to the average contribution of all the genotypes in that generation. **Positive selection** is revealed by an increase in the frequency of a genetic trait in successive generations. Among humans, for example, we know that positive selection has increased the frequencies of genotypes associated with traits that are controlled by hundreds of genes, including adult height (there is positive selection for taller individuals in most human populations), adult female hip size, and infant head circumference (both of which affect maternal and infant mortality).

Developmental regulatory genes

Natural selection is a series of compromises because it is possible only to tinker with what is already present, not to redesign structures from scratch. The Modern Synthesis in combination with natural selection sought to explain the *survival* of the fittest, but it did not account for the *arrival* of the fittest—that is, the origin of the phenotypic variation on which natural selection acts. For this, we need to consider genetic mechanisms of changes in embryonic development and the effects of these changes on phenotype. Evolutionary developmental biology emphasizes interactions of developmental regulatory genes that are arranged in hierarchical networks.

Groups of cells can release molecules (paracrine factors) that diffuse to neighboring cells and tissues, where they trigger **signal cascades** that result in transcription factors (proteins) that bind to DNA and can activate or repress (silence) gene expression. Changing gene expression in one group of cells can in turn produce factors that change gene expression in their neighboring cells, sometimes feeding back to influence genes in the cells that produced the first set of paracrine factors.

Genes are often grouped in **gene families** that produce multiple structurally related forms of the same protein, and regulatory genes from a relatively small number of families control a host of developmental processes. These **developmental regulatory genes** can be expressed in different parts of the body, affect diverse aspects of the phenotype, and can interact. For example, there are at least 23 bone morphogenetic proteins (BMPs). Originally identified by their ability to induce bone formation, BMPs also regulate cell division, differentiation, cell migration, and apoptosis (programmed cell death). Sonic hedgehog (Shh), a member of the Hedgehog family, participates in determining the left–right body axis, the proximal–distal axis of limbs, and the formation of feathers, among other processes. Gremlin, a member of the deadenylating nuclease (DAN) family, blocks the action of BMP and works with Shh to regulate limb growth.

The *Runx2* gene encodes a factor that regulates the transcription of genes associated with the formation of bone, including expression of BMPs. Acting through BMPs, Runx2 stimulates development of bone by inducing the formation of osteoblasts (bone-forming cells) and by delaying the conversion of osteoblasts to mature bone cells (osteocytes) that no longer form new bone. Changes in the timing and extent of expression of Runx2 and BMPs have profound effects on the phenotype of a developing embryo because early formation of osteoblasts or delayed conversion to osteocytes allows more bone to develop.

Alleles of *Runx2* differ in the relative number of glutamine and alanine residues they contain; alleles with higher glutamine/alanine ratios are expressed more strongly, resulting in more active synthesis of bone. The effect of this variation in the glutamine/alanine ratio can be seen in changes in the heads of bull terriers that were produced by selective breeding between 1931 and 2004 (**Figure 1.5**). Human cleidocranial dysplasia (*kleis*, "clavicle"; *kranion*, "skull"; *dysplasia*, "abnormal form") is also the result of *Runx2* alleles that differ in glutamine/alanine ratio. Analysis of the glutamine/alanine ratio of *Runx2* alleles in 30 species of carnivores showed that the glutamine/alanine ratio of the *Runx2* alleles characteristic of each species correlates with the snout length of that species (**Figure 1.6**).

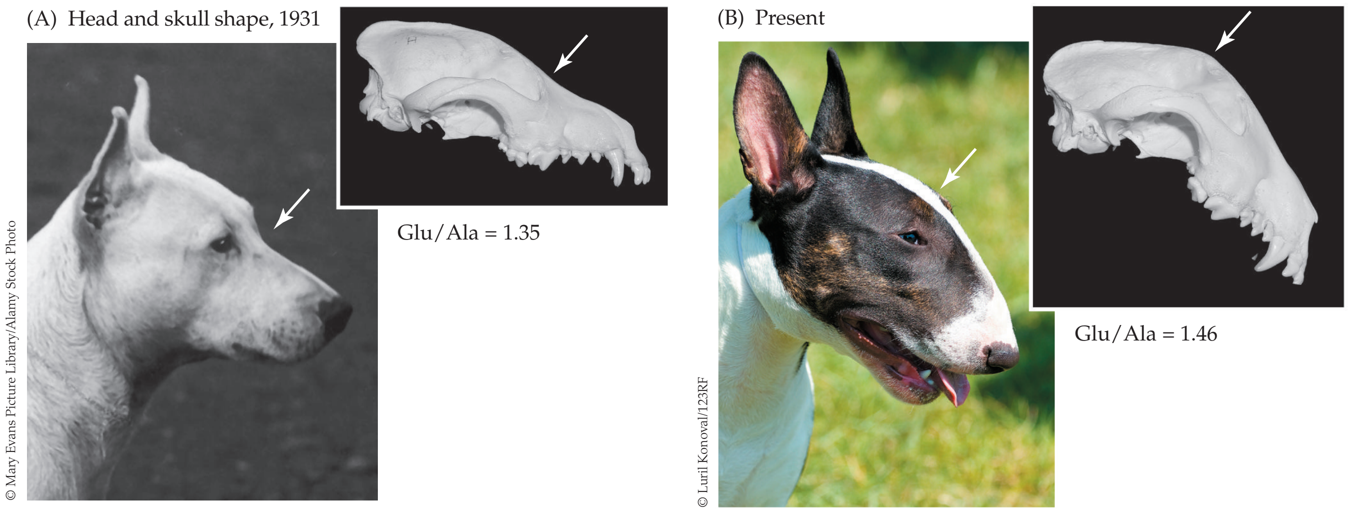


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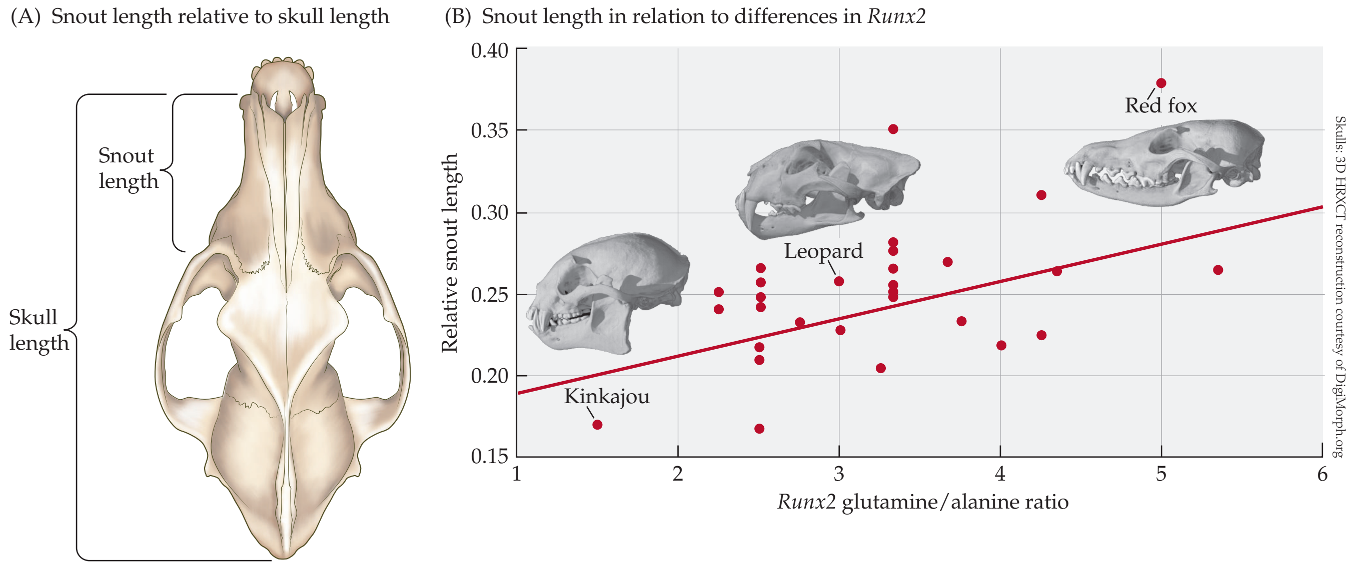
Figure 1.5 Rapid evolution of skull shape in bull terriers. Selective breeding changed the head shape of bull terriers. (A) In the early 20th century, the inflection point between the snout and the cranium (arrow) was at the level of the eyes, and the snout was horizontal. (B) In modern bull terriers, the inflection point has shifted behind the eyes, and the snout slopes downward. Selective breeding favored alleles of *Runx2* with high glutamine/alanine ratios that cause strong expression of *Bmp*. Stronger expression of *Bmp* is associated with accelerated bone growth leading to the sharply angled snout. (Skull images from J.W. Fondon et al. 2004. *PNAS* 101: 18058–18063, © National Academy of Sciences USA.)

Three kinds of change in the expression of developmental genes can produce phenotypic variation that is subject to natural selection: the *time* during development that a gene is expressed, the *place* it is expressed, and *how strongly* it is expressed (i.e., the amount of protein synthesized).

Heterochrony **Heterochrony** (Greek *heteros*, "different"; *chronos*, "time") refers to changes in the timing of gene expression during development. Heterochrony can involve the length of time during which a gene is expressed during development, as in the case of expression of the *Runx2* gene in bull terriers, or the time at which one gene is expressed relative to expression of other genes. Heterochrony can occur at any stage of development, and can produce phenotypic changes in morphology, physiology, or behavior.

Body proportions of most vertebrates change substantially between infancy and maturity. For example, the head of a human infant is about 25% of its total body length, whereas the head of an adult is only about 13% of total body length. The cranium of an infant is large in proportion to its trunk, its snout is short, and its eyes are large in proportion to its head. The body proportions of infants explain why the rounded heads, big eyes, and short snouts



Skulls: 3D HRXCT reconstruction courtesy of DigiMorph.org

Figure 1.6 Changes in the snouts of carnivores. Increased glutamine/alanine ratios in *Runx2* among 30 species of Carnivora are associated with lengthening of the snout. (A) Relative snout length is expressed as the ratio of the snout length to the skull length. (B) Relative snout length is proportional to the glutamine/alanine ratio of each species' *Runx2* gene. (After K.E. Sears et al. 2007. *Evol. Dev.* 9: 555–565.)

of puppies and kittens are so appealing to humans. Larval and juvenile fishes also have proportionally larger heads and eyes than adult fish.

Because body proportions change during development, stopping development early produces an adult that retains body proportions that are characteristic of juveniles of its species, a phenomenon called **paedomorphosis** (Greek *pais*, “child”; *morph*, “form”). Paedomorphosis is a widespread form of phenotypic change among vertebrates, and the paedomorphic nature of the heads of birds compared with those of non-avian dinosaurs clearly reveals the role of heterochrony in the evolution of birds.

Once again, comparisons of the two extant groups of archosaurs—crocodylians and birds—provides evidence of developmental changes. Juvenile alligators may not be as cute as puppies, but they do have rounded heads, big eyes, and short snouts (**Figure 1.7A**). Differential growth of the cranium, eyes, and snout during maturation leads to a very different morphology in adult alligators, which have flat heads, small eyes, and long snouts (**Figure 1.7B**). In contrast, the heads of juvenile and adult ostriches are much more alike (**Figure 1.7C,D**). Heterochrony—in this case early truncation of head development—has left adult ostriches with head proportions much like those of juveniles.

Heterotopy A change in the physical location of a gene’s expression is called **heterotopy** (“different place”) and can lead to dramatic phenotypic changes. During embryonic development, the fingers and toes of vertebrates are initially connected by a web of skin (remnants of this interdigital webbing are visible at the bases of your fingers and toes). Most of the webbing is lost before birth by apoptosis—except in web-footed aquatic vertebrates such as ducks, which retain interdigital webbing as adults. Embryonic ducks and chickens both have interdigital webbing, but chickens lose the webbing before hatching while ducks retain it. Apoptosis is initiated when *Bmp2*, *Bmp4*, and *Bmp7* are expressed in the webbing of both chickens and ducks. This BMP-induced apoptosis removes the webbing between the toes of chickens, but the feet of ducks also express the Gremlin protein, a BMP inhibitor that prevents apoptosis, thus leaving the webbing in place.

Webbing between the digits in the wings of bats is also preserved by inhibition of BMP. In this case, both Gremlin and a second inhibitor of BMP, fibroblast growth factor 8 (Fgf8), are expressed in the interdigital webbing, leaving the webbing intact to form the bat’s wings. Additional examples of heterotopic changes include the reduction of limbs seen in many lepidosaurs.

Heterometry **Heterometry** (“different measure”) refers to a change in the *amount* of a gene product. A heterometric change in the production of BMP4 is responsible for one of the classic examples in evolution, beak evolution in Darwin’s finches. Found in the Galápagos and Cocos islands, this radiation of about 15 species of ground-finches (genus *Geospiza*), descended from a single ancestral species from South America, provides one of the best-studied examples of adaptive radiation and natural selection.

These birds forage for seeds on the ground, and their beak morphology is correlated with the kinds of seeds each species selects (**Figure 1.8**). The large ground-finch (*G. magnirostris*) uses its massive beak to crack hard-shelled seeds but the small ground-finch (*G. fuliginosa*)

(A) Juvenile alligator (C) Juvenile ostrich

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(B) Adult alligator (D) Adult ostrich

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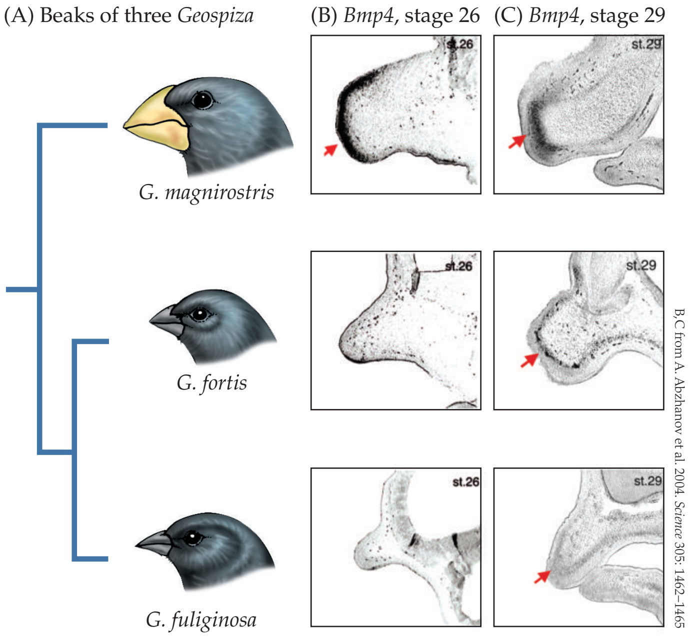
Figure 1.7 Heterochrony results in paedomorphosis in birds. Paedomorphosis (retention of juvenile traits) in extant birds can be seen by comparing alligators and ostriches. (A) A juvenile alligator has a short snout, rounded cranium, and large eyes relative to the rest of the head. (B) The head of an adult alligator has quite different proportions: the snout is long, the cranium is flat, and the eyes are small in proportion to the size of the head. (C) A juvenile ostrich also has a short snout, rounded cranium, and large eyes. (D) These proportions are little changed in the adult ostrich as a result of heterochrony—specifically, the early truncation of head development.



B,C from A. Abzhanov et al. 2004. *Science* 305: 1462–1465

Figure 1.8 Heterometry, heterochrony, and heterotopy affect beak shape. (A) Three species of Galápagos ground-finches (*Geospiza*) show different beak phenotypes. (B,C) Dark areas (arrows) in the histological sections of developing beaks indicate the location and intensity of *Bmp4* expression. (B) At developmental stage 26, *Bmp4* is strongly expressed in *G. magnirostris*, somewhat expressed in *G. fortis*, and not expressed in *G. fuliginosa*. (C) At developmental stage 29, *Bmp4* expression is intense in *G. magnirostris*. It is also expressed, but limited to smaller areas, in *G. fortis* and *G. fuliginosa*.

picks up small, soft seeds with its pointed beak. The medium ground-finch (*G. fortis*) has a beak intermediate between those of the other two species and feeds on a broader range of seeds but is less effective than either specialist at opening soft-shelled or hard-shelled seeds. The different beak phenotypes of these three species result from differences in the expression of *Bmp4* during development of the upper beak. Early onset and a high level of expression of the *Bmp4* gene produces the heavy beak of *G. magnirostris*, whereas progressively later and weaker expression leads to the smaller beaks of *G. fortis* and *G. fuliginosa*.

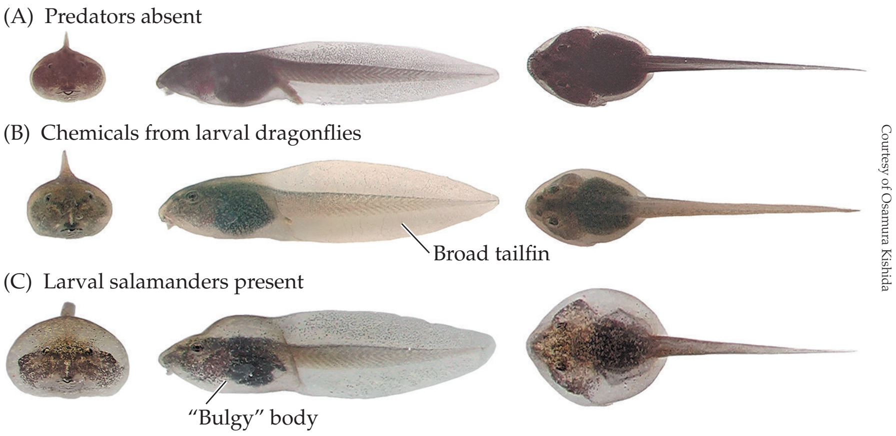
1.6 Epigenetic Effects

LEARNING OBJECTIVES

- **1.6.1** Know how an epigenetic effect differs from a genetic effect.
- **1.6.2** Explain what is meant by an “intragenerational epigenetic effect,” an “intergenerational epigenetic effect,” and a “transgenerational epigenetic effect.”

Some phenotypic variation results from modification of gene expression via **epigenetic effects** (Greek *epi*, “above, outside of, around”). Epigenetic mechanisms modify the expression of genes without changing the DNA sequence of the gene. A wide variety of factors, including diet, stress, temperature, and chemicals in the environment, can modify the behavior, physiology, or morphology of a developing organism, a phenomenon called **phenotypic plasticity**.

For example, chemicals released into the water by predators of tadpoles lead to epigenetic changes in the tadpoles’ body form and behavior that improve their chances of escaping predation (**Figure 1.9**). This is an example of an **intragenerational epigenetic effect** ($F_0 \rightarrow F_0$). That is, the phenotypic changes are limited to those individuals exposed to the stimulus; their offspring do not inherit the modified



Courtesy of Osamura Kishida

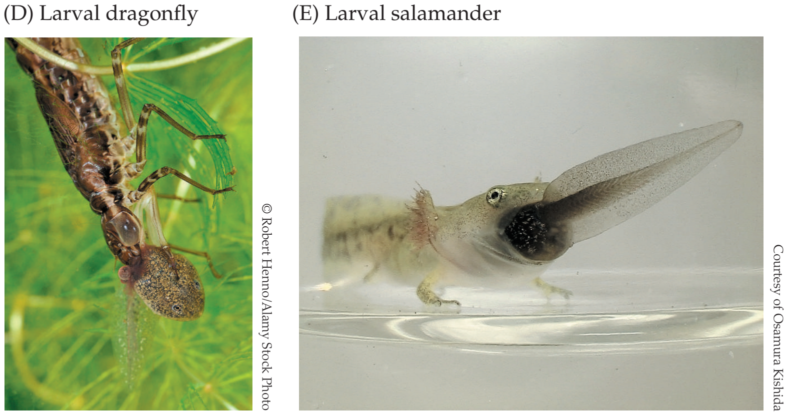


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Figure 1.9 Phenotypic plasticity of tadpoles. (A–C) Head-on, lateral, and dorsal views of tadpoles of the Hokaido brown frog (*Rana pirica*) show epigenetic changes produced by exposure to predators. (A) Tadpoles raised in the absence of predators have streamlined bodies with low tailfins. (B) Tadpoles exposed to chemicals released by dragonfly larvae have streamlined bodies and broad tailfins. (C) Tadpoles living in aquaria with larval salamanders develop bulgy bodies and broad tailfins. (D) Dragonfly larvae seize and dismember resting tadpoles. Broad tails (photo B) may increase acceleration during swimming, allowing tadpoles to evade these predators. (E) Salamander larvae swallow tadpoles whole, and thus may be unable to swallow a tadpole with a bulgy body (photo C).

phenotypes. Many examples of intragenerational epigenetic effects have been described, including development of a cannibal morph of lissamphibian larvae and the role of incubation temperature in determining the sex of a variety of reptiles, topics that are discussed in later chapters.

Intergenerational ($F_0 \rightarrow F_1$) and **transgenerational** ($F_0 \rightarrow F_n$) epigenetic effects have been difficult to document in free-living animals, but laboratory studies have shown that epigenetic effects can extend across generations. For example, exposing adult stickleback fishes to predators modified the behavioral responses of the sticklebacks' offspring to predators. Moreover, the behavioral change seems to depend on whether it was the mother or the father that was exposed to predators, and on the sex of the offspring. Sons, but not daughters, of predator-exposed fathers were *less* cautious than sons of control fathers, whereas both sons and daughters of predator-exposed mothers were *more* cautious than offspring of control mothers. Studies of laboratory mice have documented behavioral changes resulting from postnatal stress in the mother that extend to the F_2 generation (grandchildren).

1.7 Earth History and Vertebrate Evolution

LEARNING OBJECTIVES

- 1.7.1 Know the difference between eons, eras, periods, and epochs.
- 1.7.2 Describe the pattern of continental movements from the Cambrian to the present.
- 1.7.3 Explain three components of continental drift that have influenced the evolution of vertebrates.

Since their origin in the early Paleozoic, vertebrates have been evolving in a world that has changed enormously and repeatedly. These changes have affected vertebrate evolution both directly and indirectly. Understanding the sequence of changes in the locations of continents and the significance of those locations for climates and interchange of faunas is central to understanding the vertebrate story. The history of Earth spans three geological **eons**: the Archean, Proterozoic, and Phanerozoic. Only the Phanerozoic, the eon of visible life (Greek *phanero*, "visible"; *zoon*, "animal") that began about 541 Ma, contains vertebrate life. The Phanerozoic is divided into three geological **eras**: Paleozoic (Greek *palaios*, "ancient"), Mesozoic (Greek *mesos*, "middle"), and Cenozoic (Greek *kainos*, "recent"), which we describe in Chapters 5, 10, and 20, respectively. These eras are divided into **periods**, which can be further subdivided in a variety of ways, such as the **epochs** within the Cenozoic era (see Appendix).

Movements of landmasses—**continental drift**—have been a feature of Earth's history at least since the Proterozoic, and the course of vertebrate evolution has been shaped by continental movements. The rate of continental drift remains low (movement of only about 1 millimeter a year) for tens of millennia. Then, as the strain begins to exceed the force holding a continent together, the rate of drift can increase to 20 mm/year (about the rate at which fingernails grow), causing rifts to develop and widen in a geologically brief period. For example, westward movement of North America relative to northern Africa remained at ~1 mm/year from 240 to 200 Ma, increased to ~12 mm/year from 200 to 190 Ma, increased again to ~20 mm/year from 190 to 180 Ma, then fell back to ~10 mm/year. A still greater acceleration, reaching 40 mm/year, accompanied the separation of southern Africa from South America between 128 and 120 Ma.

The continents are still drifting. Indeed, Australia is moving north so rapidly that land-based latitudinal coordinates established in 1994 are now 1.5 m out of register with global coordinates determined by GPS satellites. Because the movements are so complex, the sequence, the varied directions, and the precise timing of the changes are difficult to summarize. When the movements are viewed broadly, however, a simple pattern unfolds during vertebrate history: continental fragmentation during the Cambrian, coalescence by the Devonian, and a return to fragmentation by the Late Cretaceous.

During that coalescence some 300 Ma, the continents combined to form a single landmass known as Pangaea, which was the birthplace of terrestrial vertebrates. Persisting and drifting northward as an entity, this huge continent began to break apart about 150 Ma. Its separation occurred in two stages: first into Laurasia in the north and Gondwana in the south, and then into a series of units that have drifted to become the continents we know today.

The complex movements of the continents through time had major effects on the evolution of vertebrates. Most obvious is the relationship between the location of landmasses and their climates. At the end of the Paleozoic, much of Pangaea was located on the Equator, a situation that persisted through the middle of the Mesozoic; thus, throughout this time frame large areas of land enjoyed tropical conditions. Terrestrial vertebrates evolved and spread in these tropical regions. By the end of the Mesozoic, much of Earth's landmass had moved out of equatorial regions, and by the middle of the Cenozoic most terrestrial climates in the higher latitudes of the Northern and Southern hemispheres were temperate rather than tropical.

A less obvious effect of the position of continents on terrestrial climates comes from changes in patterns of oceanic circulation. For example, the Arctic Ocean is now largely isolated from the other oceans and does not receive warm water via currents flowing from more equatorial regions. High latitudes are cold because they receive less solar radiation than do areas closer to the Equator, and the Arctic basin does not receive enough warm water to offset the lack of solar radiation. As a result, the Arctic Ocean has an extensive covering of ice, and cold climates extend well southward across the continents.

The Atlantic Meridional Overturning Circulation (AMOC) drives the Gulf Stream as it brings warm water north and east near the surface of the Atlantic Ocean and transports cold water south at greater depth, eventually to warm, rise to the surface, and move north again in the Gulf Stream. Heat transported by the AMOC is responsible for the relatively warm climates of northern North America and northern Europe. Sudden, drastic weakenings of the AMOC during the middle of the last ice age (~35 ka) were associated with abrupt cooling events at intervals of about 1.5 ka. Icebergs released from the ice sheet covering Canada melted and diluted seawater in the North Atlantic, making it less dense so that it did not sink to form the southward flow of deep, cold water that drives the AMOC.

Another factor that influences climates is the relative levels of the continents and the seas. At some periods in Earth's history, most recently in the late Mesozoic and again in the first part of the Cenozoic, shallow seas flooded large parts of the continents. These **epicontinental seas** extended across the middle of North America and the middle of Eurasia during the Cretaceous and early Cenozoic, forming barriers between the eastern and western portions of those landmasses.

Water absorbs heat as air temperature rises, then releases that heat as air temperature falls. Thus, areas of land bordering large bodies of water have maritime climates—they do not get very hot in summer or very cold in winter, and they are usually moist because water that evaporates from the sea falls as rain on the land. Continental climates, which characterize areas far from the sea, are usually dry with cold winters and hot summers. The draining of the epicontinental seas at the end of the Cretaceous probably contributed to the demise of the non-avian dinosaurs as climates in the Northern Hemisphere became more continental.

On a continental scale, advances and retreats of glaciers throughout the Pleistocene caused homogeneous habitats to split and merge repeatedly, isolating populations of widespread species and leading to the evolution of new species. For example, during glacial maxima, when much of the world's water was trapped in ice, much of the continental shelf of North America was exposed as land and the ranges of many terrestrial and freshwater vertebrates were forced southward into glacial refugia. As the ice retreated, recolonization of more northern environments provided many opportunities for diversification.

In addition to changing climates, continental drift has formed and broken land connections between the continents. Isolation of different lineages on different landmasses has produced dramatic examples of the independent evolution of similar types of organisms, an evolutionary phenomenon known as **convergent evolution**. Many groups of mammals on separate continents independently evolved superficially similar forms during the mid-Cenozoic, a time when Earth's continents reached their greatest separation during the history of vertebrates. For example, jerboas are small, desert-dwelling saltatorial (ricocheting, which means bipedal jumping) rodents from Africa and the Middle East that strongly resemble kangaroo rats living in southwestern deserts of North America (**Figure 1.10**).

Much of evolutionary history appears to depend on whether a particular lineage was in the right place at the right time. This random element of evolution is assuming increasing prominence as more detailed information about the times of extinction of old groups and radiation of new groups suggests that competitive replacement of one group by another is not the usual mechanism of large-scale evolutionary change. As a result, movements of continents and their effects on climates and the isolation or dispersal of animals are taking an increasingly central role in our understanding of vertebrate evolution.

(A) Hairy-footed jerboa, *Dipus sagitta*

(B) Merriam's kangaroo rat, *Dipodomys merriami*

Svyatoslav Knyazev CC BY-SA 4.0

Nick Bonzey CC BY-SA 4.0

Figure 1.10 Convergent evolution of ricocheting rodents. (A) Jerboas (family Dipodidae) are found in deserts from North Africa through the Middle East into Asia. (B) Kangaroo rats (family Heteromyidae) inhabit the deserts in southwestern North America. Although the lineages separated in the Late Cretaceous (~75 Ma), jerboas and kangaroo rats are similar in appearance, ecology, and behavior.

Summary

1.1 The Vertebrate Story

There are more than 70,000 extant species of vertebrates. Vertebrates live in virtually all of Earth's habitats and range in size from 0.1 g to more than 100,000 kg.

Some key events and characters in vertebrate history include the evolution of jaws (Gnathostomata), bones that ossify from cartilage (Osteichthyes), the humerus and femur (Sarcopterygii), a heart with a partially divided ventricle (Rhipidistia), four limbs with digits (Tetrapoda), the amniotic egg (Amniota), mammary glands (Mammalia), and placental viviparity (Theria).

Scientists name species using a system from the 18th century developed by Linnaeus for his great work, *Systema Naturae*. Every named species has a Latinized binomial consisting of a genus name that can encompass closely related species and a second identifier known as the species epithet that is unique to that species (e.g., humans = *Homo sapiens*).

1.2 Phylogenetic Systematics

Phylogenetic systematics produces branching evolutionary diagrams or phylogenetic trees showing changes in characters. New monophyletic groups at each branch point can be named, producing a nested series of named lineages.

Phylogenetic systematics groups organisms in evolutionary lineages on the basis of synapomorphies, which are homologous characters shared by the organisms in a group that differ from those of an ancestor.

1.3 Applying Phylogenetic Criteria

Parsimony is one basis for identifying the most likely sequence of evolutionary changes; any change is an unlikely event, so the phylogeny that requires the fewest changes to account for the observed distribution of characters is favored.

Today many phylogenies combine molecular and morphological characters. The branching patterns generally agree. When they disagree, the discrepancy often lies in estimated dates of divergence of lineages.

1.4 Using Phylogenetic Trees

An extant phylogenetic bracket allows us to draw inferences about characters of the enclosed extinct lineages when direct evidence is lacking.

It is sometimes convenient to refer to groups that are not phylogenetically correct in that they do not include an ancestral group and all of its descendants. Such a group is referred to as paraphyletic.

Crown groups are composed of extant or extinct species that have all of the derived characters of the lineage. Stem groups include extinct taxa that lack some derived characters of other taxa in the lineage but are nonetheless more closely related to the taxa in the crown group than they are to taxa in other lineages.

1.5 Genetic Mechanisms of Evolutionary Change

In the 19th century, Charles Darwin characterized evolution as "descent with modification" and invoked natural selection and sexual selection. Gregor Mendel described and documented the particulate nature of genetic inheritance.

During the first half of the 20th century, the Modern Synthesis combined the perspectives of Darwinian selection, Mendelian genetics, and quantitative population biology to explain "survival of the fittest" as the result of differential reproduction of phenotypes and consequent changes in allele frequencies within populations.

In the late 20th century, molecular genetics and embryology came together in the field of evolutionary developmental biology ("evo-devo") to show how genes acting early in embryonic development can produce profound phenotypic changes and provide novel raw material for the action of selection (the "arrival of the fittest").

1.6 Epigenetic Effects

Epigenetic mechanisms modify the expression of genes without changing the DNA sequence of the gene.

Intragenerational epigenetic effects result from changes in gene expression initiated by external factors such as diet, temperature, or the presence of predators. Intragenerational changes are limited to the individuals exposed to the stimulus and are not transmitted to their offspring ($F_0 \rightarrow F_0$).

Intergenerational (parent to children, $F_0 \rightarrow F_1$) and transgenerational (parent to grandchildren, $F_0 \rightarrow F_2$) epigenetic effects have been demonstrated in laboratory studies.

1.7 Earth History and Vertebrate Evolution

At the time vertebrates first evolved, the continental landmasses were scattered across the globe. They coalesced into one enormous continent, Pangaea, about 300 Ma, which began to fragment again about 150 Ma.

This pattern of fragmentation, coalescence, and fragmentation has isolated and renewed contacts of major groups of vertebrates, producing the biogeographic distributions of vertebrates today.

Discussion Questions

1.1 Why is the nested set of names in Figure 1.2 referred to as a phylogenetic classification? What would happen to the classification if new data changed the arrangement of the branches on the tree?

1.2 Why doesn't phylogenetic systematics have a fixed number of hierarchical categories like the Linnaean system?

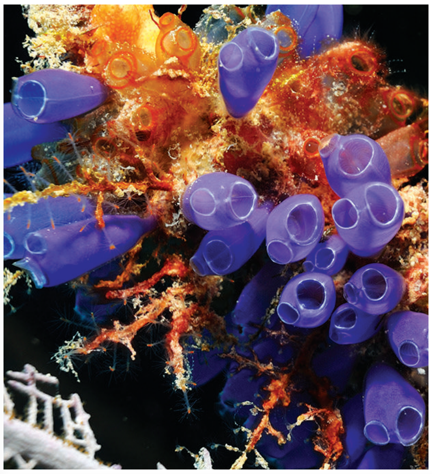
1.3 Why does phylogenetic systematics represent evolution more clearly than pre-cladistic methods?

1.4 What inference can you draw from Figure 1.4 about parental care by †pterosaurs? What about †phytosaurs?

1.5 Suppose that you have firm evidence that †phytosaurs did not exhibit parental care. What would be the most parsimonious hypothesis about the appearance or disappearance of parental care in the archosaur lineage?

1.6 What problems might the types of convergent evolution seen between jerboas and kangaroo rats pose for phylogenetic analyses?

1.7 Today, molecular, genomic, and developmental data play crucial roles in examining evolutionary relationships among species and lineages. What difficulties arise when we try to apply these tools to the phylogenetic analysis of fossil vertebrates?



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2

What Is a Vertebrate?

Bluebell tunicate, *Clavelina puertosecensis*

- 2.1 Vertebrates in Relation to Other Animals
- 2.2 Characteristics of Chordates
- 2.3 What Distinguishes a Vertebrate?
- 2.4 Vertebrate Embryonic Development
- 2.5 Vertebrate Tissues
- 2.6 Vertebrate Organ Systems

Vertebrates are a diverse and fascinating group of animals. Because we are vertebrates ourselves, that statement may seem chauvinistic, but vertebrates are remarkable in comparison with most other animal groups. Vertebrates are **chordates**, members of phylum **Chordata**. Only arthropods (Arthropoda, which includes insects, crustaceans, and spiders) rival vertebrates in diversity of forms and habitats. And it is only among mollusks (Mollusca) that we find animals such as octopuses and squids that approach the large sizes of some vertebrates and that have a capacity for complex learning.

The relationship of chordates to other animal phyla is revealed by anatomical, physiological, biochemical, and developmental characters. In this chapter, we first discuss evolutionary relationships among vertebrates and other members of the animal kingdom. We then describe some characteristic structures of vertebrates and present an overview of the organ systems that make vertebrates functional animals. These fundamentals will help you appreciate changes that occurred during vertebrate evolution and will allow you to trace homologies between basal and more derived vertebrates.

2.1 Vertebrates in Relation to Other Animals

LEARNING OBJECTIVES

- 2.1.1 Differentiate between diploblasty and triploblasty and describe the features that distinguish bilaterian animals.
- 2.1.2 Compare Protostomia and Deuterostomia with respect to their diversity.
- 2.1.3 Specify the developmental feature that is synapomorphic for Deuterostomia.
- 2.1.4 Describe phylogenetic relationships among the major clades of Ambulacraria.

The animal kingdom, or **Metazoa**, contains more than 30 phyla, of which Chordata is one (**Figure 2.1**). All metazoans are multicellular heterotrophs (feeding on other organisms). They are also motile (capable of movement) for at least part of their life cycle (many are motile as larvae but sessile as adults). Sponges, the most basal metazoans, differentiate from a single layer of cells. Cnidarians are **diploblastic**, having two embryonic germ layers (Latin *germen*, "bud"): ectoderm that becomes the cells of the outer body, and endoderm that differentiates and lines the gut. All other phyla in Figure 2.1 have a third germ layer, mesoderm, that contributes to many organ systems and makes these organisms **triploblastic** (see Section 2.4). The triploblastic phyla comprise **Bilateria** (Latin, "two sides"). At some point in their life cycle, whether as larvae or adults or both, all bilaterians have a body plan with two sides that are mirror images of each other (i.e., they are bilateral).

Current molecular data place the origin of Bilateria late in the Proterozoic, probably between 688 and 596 Ma. Fossils of undisputed bilaterians first occur ~553 Ma, at the end of the Proterozoic. Most bilaterian phyla first appear in the geological record during the early Cambrian (~541 Ma), and the term "Cambrian Explosion" has been used to describe this phenomenon. The apparent suddenness of this diversification probably relates to two artifacts of the fossil record: (1) the frequency with which hard parts, such as shells, are preserved; and (2) a few fossil localities with exceptional preservation that record soft-bodied animals, which are usually absent from the fossil record.

There are two major divisions within Bilateria: **Protostomia** (Greek *pro*, "earlier"; *stoma*, "mouth") and **Deuterostomia** (Greek *deuteros*, "second"). This division was originally based on embryonic features, including development of the mouth and anus during **gastrulation.**

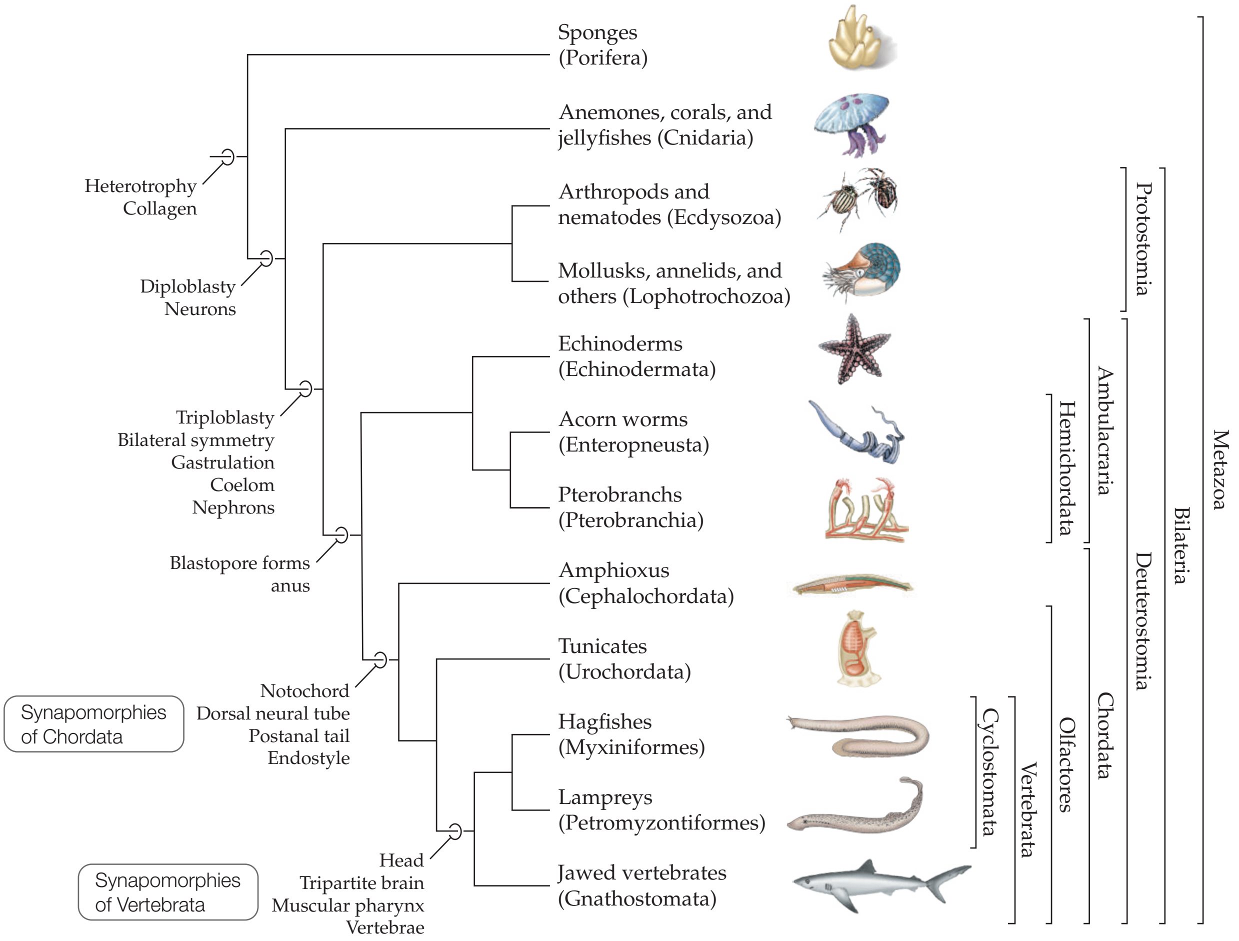


Figure 2.1 Simplified phylogeny of Metazoa. This tree emphasizes Deuterostomia, the clade that includes Vertebrata.

During gastrulation, undifferentiated cells of the early embryo move into three germ layers and the body axes are defined. The original embryonic gut opening is the **blastopore** (Greek *poros*, "small opening"), and a second opening develops before gastrulation concludes. The classic view is that the blastopore becomes the mouth of protostomes and the second opening becomes the anus, whereas in deuterostomes the second opening becomes the mouth and the blastopore becomes the anus.

Protostomia comprises more than 90% of bilaterian phyla and is divided into two main groups: Ecdysozoa, including arthropods and nematodes, and Lophotrochozoa, including mollusks and annelids, such as earthworms.

Deuterostomia is a much smaller grouping, but it is our focus here, since it includes Chordata (and thus Vertebrata). In addition to Chordata, there are two other deuterostome phyla: Echinodermata (starfishes, sea urchins, and similar animals) and Hemichordata (acorn worms and pterobranchs, which uniquely share a three-part body plan consisting of a proboscis, collar, and trunk). Fossils and molecular data indicate that the common ancestor of extant deuterostomes was probably a small, marine, wormlike, free-swimming filter-feeder.

Adult echinoderms lack a distinct head and have pentaradial (fivefold and circular) symmetry. Based on appearance alone, it seems unlikely that echinoderms would be related to vertebrates, which have distinct head (anterior) and tail (posterior) ends, bilateral limbs, and bilateral (left–right) symmetry as adults. However, echinoderm *larvae* are bilaterally symmetrical, and a relationship between echinoderms and vertebrates is firmly established by developmental and molecular information. Diversity of extinct echinoderms was greater than that of extant forms, and some Paleozoic echinoderms were bilaterally symmetrical, meaning that the fivefold symmetry of adult echinoderms is a derived character.

Molecular characters unite echinoderms and hemichordates as **Ambulacraria** (Latin *ambulacrum*, "alley," in reference to the ambulacral grooves for the tube-feet of echinoderms). Hemichordates were long considered to be the sister group of chordates because both groups have a **pharynx** (Latin *pharynx*, "throat") with **pharyngeal slits** that open to the outside. However, a pharynx with slits now is considered to be a feature of the common ancestor of all deuterostomes, a view supported by a shared cluster of genes that are present in all deuterostomes and are expressed during pharyngeal development. Thus, a pharynx with slits is not a shared derived character uniting chordates and hemichordates.

2.2 Characteristics of Chordates

LEARNING OBJECTIVES

2.2.1 Name the shared derived features for chordates and explain their significance.

2.2.2 List the shared derived features for cephalochordates and for urochordates.

2.2.3 Explain why ascidean tunicates, despite their dramatic metamorphosis from larva to adult, are chordates.

2.2.4 Categorize the evidence (morphological, developmental, molecular, or behavioral) indicating urochordates are the sister group of vertebrates.

Chordates are united by four synapomorphies—shared derived features—that occur in all members of the group at some point in their life cycle:

- A *notochord*, a dorsal (Latin *dorsum*, "back") stiffening rod that gives phylum Chordata its name
- A dorsal *neural tube*
- A muscular *postanal tail* (i.e., a tail that extends beyond the anus)
- An *endostyle*, a ciliated, glandular groove on the floor of the pharynx

The first three of these features allow larvae to swim using a muscular tail. The **notochord** (Greek *notos*, "back"; *chorde*, "string") serves not only as a stiffening rod but also as an attachment site for segmental muscles that power swimming. In most vertebrates, the notochord is transient, replaced during development by the vertebral column and remaining in adults only as a portion of the intervertebral discs. The neural tube coordinates muscle activity needed for swimming and, in vertebrates, develops into the spinal cord and brain, collectively known as the central nervous system. Muscles of the **postanal tail** provide more power for swimming than other mechanisms, such as cilia. In addition to secreting mucus to trap food particles during filter feeding, the **endostyle** takes up iodine like the vertebrate thyroid gland.

Other features have been debated as chordate characters. For example, all chordates pump blood, but not all chordates have a definitive heart. Cephalochordates pump blood using a simple enlargement of the main ventral blood vessel consisting of a single layer of contractile myocardial cells. Gene expression as this enlargement develops is similar to that in the development of the heart in vertebrates.

Chordate origins and evolution

Compared with other metazoans, the internal organization of chordates appears to be "upside down." Annelids such as earthworms, for example, have a nerve cord on the ventral (Latin *venter*, "belly") side and heart and primary blood vessel on the dorsal side; in chordates, these positions are reversed. In the early 19th century, the French naturalist Étienne Geoffroy Saint-Hilaire proposed an "inversion hypothesis" to explain this observation. His idea fell into disrepute but has been revitalized in recent years by evolutionary developmental biology. We have learned that the early embryos of chordates express genes on the dorsal side that are expressed on the ventral side in nonchordates. This heterotopic event (see Section 1.5) seems to have happened at the evolutionary origin of chordates.

Although the notochord is unique to chordates, gene expression patterns suggest similarities with the annelid axochord. Likewise, genomic studies identify a possible homolog of the endostyle in the epibranchial ridge of hemichordates.

As mentioned at the end of Section 2.1, gene expression patterns during development show that pharyngeal slits are homologous across deuterostomes to the extent that they represent outpocketings of the pharynx that perforate to the exterior. Although pharyngeal slits are not found in extant echinoderms, they may have been present in some Paleozoic echinoderms and are present in their living sister group, the hemichordates.

Vertebrates have pharyngeal arches between pharyngeal pouches containing neural, muscular, circulatory, and skeletal tissues derived from neural crest cells. Neural crest is unique to vertebrates, but the skeletal supports of the pharynx of other deuterostomes are cartilages based on fibrillar collagen as in vertebrates. Neural crest and pharyngeal arches will be described in more detail in Section 2.4.

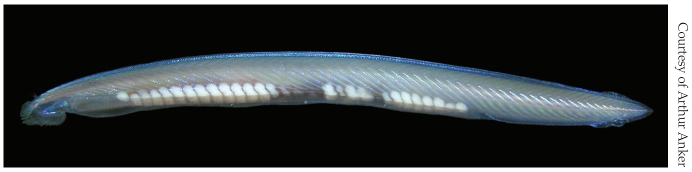
Extant nonvertebrate chordates

Extant nonvertebrate chordates are small marine animals in two clades: lancelets (**Cephalochordata**) and tunicates (**Urochordata**). Cephalochordata refers to the notochord's extension to the anterior tip of the body (Greek *kephale*, "head"). Urochordata refers to the position of the notochord in the larval tail (Greek *oura*, "tail"). The anterior tip of the vertebrate notochord ends midway through the head region and extends posteriorly to the tip of the tail. Other nonvertebrate chordate groups existed in the past, but such soft-bodied animals are rarely preserved as fossils.

Cephalochordates The 29 species of lancelets, also known as amphioxus (Greek *amphis*, "double"; *oxys*, "sharp"), are superficially fishlike marine animals usually less than 5 cm long (**Figure 2.2A**). Lancelets share with vertebrates some anatomical features that are absent from tunicates. However, molecular analyses place tunicates as the sister group of vertebrates. Structures such as segmental muscles along the body and a tail fin might be basal chordate characters that have been lost in tunicates. In addition to their unique notochord, lancelets have a ring of oral cirri that prevents coarse particles from entering the mouth (**Figure 2.2B**).

Lancelets swim using **myomeres** (Greek *mys* "muscle"; *mere* "segment"). Myomeres are segmental blocks of skeletal muscle fibers arranged along both sides of the body and separated by sheets of connective tissue termed myosepta. Sequential contraction of myomeres bends the

(A) A lancelet, *Branchiostoma lanceolatum*



Courtesy of Arthur Anker

(B) Anatomical features of lancelets

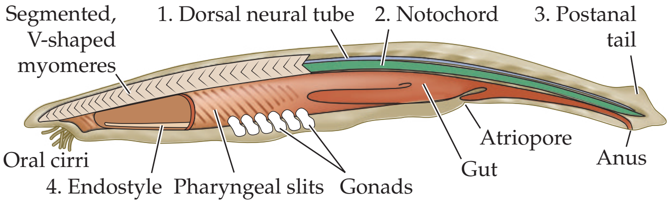


Figure 2.2 Cephalochordates. (A) Adult lancelets are burrowing, sedentary animals that are widely distributed in shallow marine waters of the continental shelves. (B) The four synapomorphies lancelets share with all chordates are numbered in this schematic view of a generalized lancelet.

(A) An appendicularian tunicate, *Oikopleura dioica*

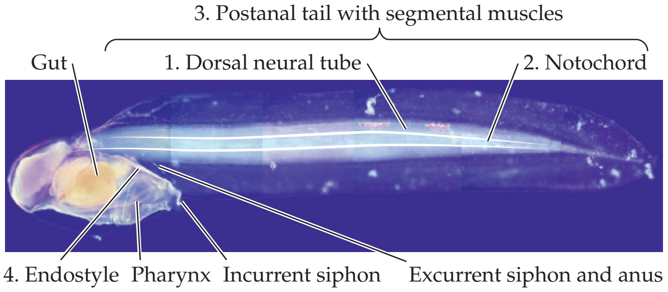
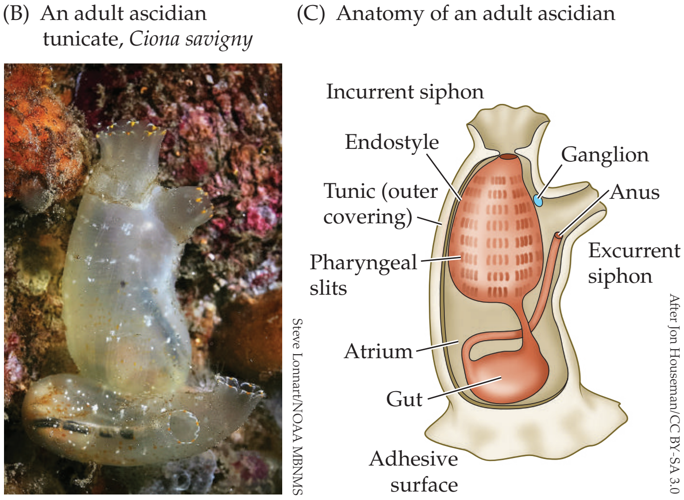


Photo by R. Rudolph

(B) An adult ascidian tunicate, *Ciona savigny*

(C) Anatomy of an adult ascidian



Steve Lonhart/NOAA MBNMS

After Jon Houseman/CC BY-SA 3.0

Figure 2.3 Urochordates. (A) Appendicularian tunicates are free-swimming throughout their lives and retain all four chordate synapomorphies (numbered). (B) The larvae of ascidian tunicates metamorphose into sedentary adults attached to the substrate. These adult tunicates do not retain the structural similarity to cephalochordates or vertebrates seen in their larval stages. (C) Schematic view of a generalized adult ascidian. (A from N.H. Patel. 2004. *Nature* 431: 28–29.)

body from side to side, resulting in forward or backward swimming. The notochord acts as an incompressible elastic rod that prevents the body from shortening when the myomeres contract.

Lancelets have a cerebral vesicle, a thickening at the anterior end of the neural tube that expresses genes also expressed in portions of the vertebrate brain. These studies reinforce the growing understanding that differences in how, when, and where genes are expressed (see Section 1.5) are as important as differences in which genes are present.

Urochordates Tunicate synapomorphies include a tadpole larva, an outer covering known as a tunic, and heartbeat reversal. Appendicularian tunicates, also known as larvaceans, are motile, filter-feeding animals of the marine pelagic realm that retain all four chordate characters throughout life (**Figure 2.3A**). The more commonly studied ascidian tunicates have motile but nonfeeding larvae that metamorphose to become sessile adults (**Figure 2.3B**), in the process losing the postanal tail and notochord and reducing the neural tube to a ganglion (bundle of nerve cells). The tunic is made primarily from cellulose, a structural carbohydrate otherwise seen only in plants. Tunicates appear to have acquired the ability to synthesize cellulose by horizontal gene transfer from bacteria. They filter food particles from the water with a basketlike perforated pharynx and capture them in secretions from the endostyle (**Figure 2.3C**). Blood is pumped toward the pharynx and, after a short pause, in the reverse direction, toward the intestine. The function of this reversal is unknown.

Molecular analyses place tunicates and vertebrates as sister taxa (see Figure 2.1), in a group that was given the unfortunate name of **olfactores** based on the mistaken interpretation that tunicates, certain fossil echinoderms, and vertebrates share characters of the olfactory system. In addition to a heart, tunicates share some derived features with vertebrates, such as cells that may be homologous with vertebrate neural crest cells (see Section 2.4). The simple morphology of adult tunicates is considered to be highly derived rather than primitive, and tunicates have a greatly reduced genome in comparison with other chordates. This phylogenetic interpretation implies that tunicates lost features such as myomeres.

2.3 What Distinguishes a Vertebrate?

LEARNING OBJECTIVES

2.3.1 Describe how the head and brain of vertebrates differ from those of nonvertebrate chordates.

2.3.2 Explain how differences in structure of the respiratory and digestive tracts of nonvertebrate chordates and vertebrates allowed the evolution of active, large-bodied vertebrates.

2.3.3 Identify the key embryonic tissue of vertebrates that is responsible for many of the differences between nonvertebrate chordates and vertebrates.

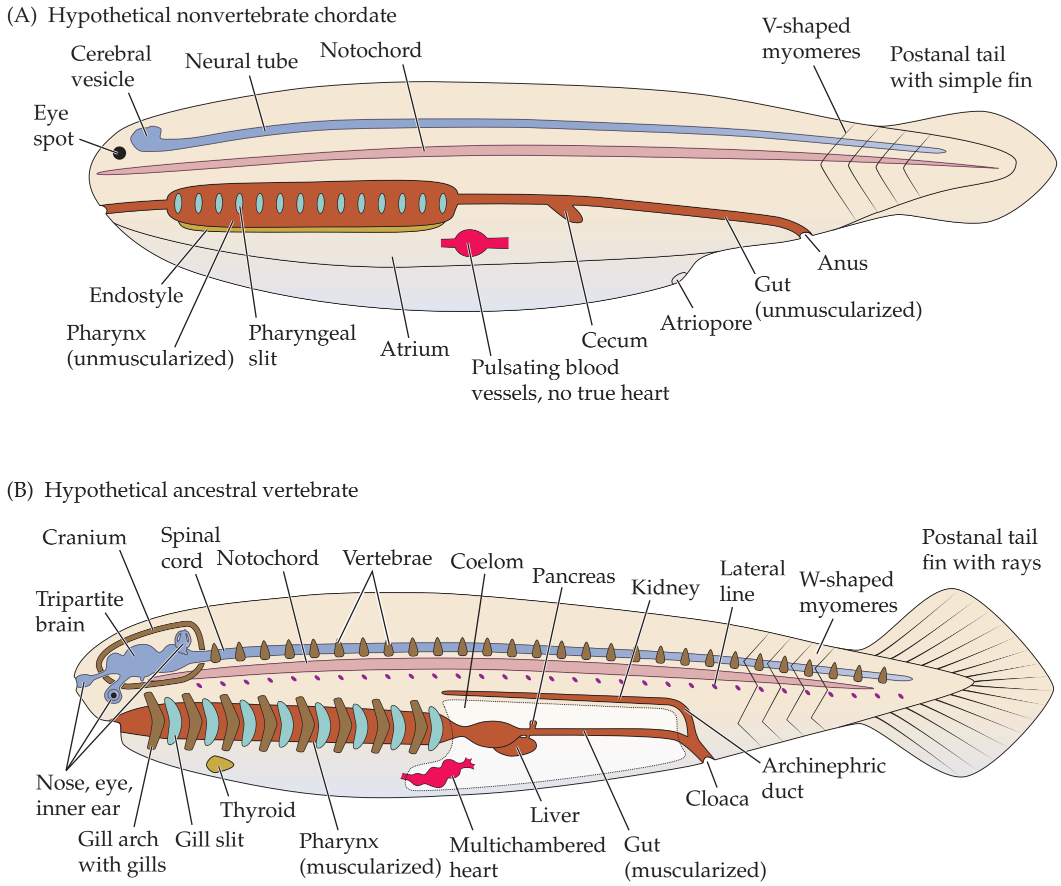


Figure 2.4 Comparing structures of nonvertebrates and vertebrates. A hypothetical nonvertebrate chordate (A) is shown in comparison with a hypothetical vertebrate (B). The neural tube of vertebrates expands in the head to form the tripartite brain; posteriorly, it is the spinal cord. Vertebrae are segmental skeletal elements flanking the spinal cord. The pharyngeal region of vertebrates is muscularized and has gill arches that support gills. Other differences include presence in vertebrates of organs such as the liver and pancreas, kidneys and associated ducts, and a multichambered heart. Myomeres, segmental blocks of muscle used for locomotion, are W-shaped in vertebrates. The cloaca of vertebrates is the common exit for the digestive, urinary, and reproductive systems.

Vertebrates take their name from **vertebrae**, serially arranged bones that make up the **vertebral column**, or backbone. The earliest known vertebrates, from Cambrian sediments, have segmented dorsal structures interpreted as vertebrae. **Figure 2.4** compares a generalized, hypothetical nonvertebrate chordate with a hypothetical ancestral vertebrate; **Table 2.1** compares features of extant nonvertebrate chordates and vertebrates.

Vertebral structure varies, but all vertebrates have segmentally organized elements composed of cartilage or bone that protect the spinal cord (see Figure 2.4B). In **gnathostomes**, the jawed vertebrates, vertebral elements known as **centra** (singular centrum) typically form in close association with the embryonic notochord, which is largely replaced by centra in most adult vertebrates.

Vertebrates have additional unique characters, including:

- *Cranium.* The cranium, or braincase, is a bony, cartilaginous, or fibrous structure surrounding the brain.
- *Head, sense organs, and brain.* Although many animals have heads, the vertebrate head is notable for its prominence and its array of complex sense organs, including the nose, eyes, and ears. The embryonic vertebrate brain is tripartite, having a forebrain, midbrain, and hindbrain to integrate sensory information.
- *Complex endocrine organs.* Endocrine glands, such as the thyroid, produce hormones that regulate many body functions.
- *Muscularized gut tube.* Vertebrates have muscles in the wall of the gut tube for efficient processing of large amounts of food.
- *Multichambered heart.* Vertebrate circulation is powered by a multichambered heart that distributes respiratory gases and nutrients to all cells of the body.
- *Mineralized tissues.* Vertebrates deposit minerals (primarily calcium compounds) in tissues, creating rigid structures such as calcified cartilage and bone and exposed surfaces with different degrees of resistance to abrasion including enamel, enameloid, dentine, and cementum.
- *Gills derived from endoderm.* Vertebrates have gills derived from the embryonic germ layer endoderm (see Section 2.4) for efficient respiration.

Table 2.1 Comparison of features of nonvertebrate chordates and vertebrates

Nonvertebrate chordates	Vertebrates
Head and brain	
No cranium	Cranium surrounds and protects brain
Head poorly distinguished from trunk	Head distinct from trunk
Notochord extends to anterior end of head (lancelets) or is restricted to the tail of larvae (tunicates)	Notochord starts midway through the head region and extends to tip of embryonic tail
Simple "brain"	Tripartite brain for sensory integration: Forebrain (olfaction); midbrain (vision); hindbrain (hearing and balance)
Simple sense organs and no cranial nerves	Specialized sense organs concentrated in the head served by cranial nerves
Neural tube gives rise to neurons	Neural tube, neural crest, and neurogenic placodes give rise to neurons
Endocrine control	
Limited endocrine integration of body functions	Complex endocrine system with many glands to integrate body functions
Pharynx and respiration	
Pharynx is not muscularized; water moved by ciliary action	Muscular pharynx moves water by pumping for feeding and respiration
No gills	Gills derived from endoderm
Feeding and digestion	
No teeth	Teeth composed of keratin in cyclostomes and dentine and enamel in gnathostomes
Gut not muscularized; food moved by ciliary action	Muscular contractions (peristalsis) move food
Limited differentiation of gut tube	Differentiated digestive organs and regionalized gut tube
Intracellular digestion: Food particles are taken into cells lining the gut and digested	Extracellular digestion: Food particles are digested in the gut and breakdown products are absorbed across gut wall
Heart and circulation	
Few capillaries	Extensive capillary networks
Blood moved by vessel contractions (lancelets); single-chambered heart with heartbeat reversal (tunicates)	Multichambered heart pumps blood
No neural control of the heart	Neural control of rate and force of cardiac contractions
No respiratory pigment or red blood cells; O_2 and CO_2 transported in solution	Red blood cells contain hemoglobin, which binds O_2 and CO_2 and aids their transport and delivery to tissues
Osmoregulation	
Body fluid osmolal concentration and ion composition same as external environment	Body fluid osmolal concentration and ion composition differ from external environment (except hagfishes)
Support and locomotion	
Mineralized tissues absent	Mineralized tissues present in osteognathostomes, including calcified cartilage, bone, dentine, enamel, enameloid
Acellular cartilage	Cellular cartilage
Vertebral elements absent	Vertebral elements present
V-shaped myomeres	W-shaped myomeres
True fins absent	Median fins in cyclostomes + gnathostomes; paired fins or limbs in gnathostomes

Together, these features give vertebrates far more powerful and efficient feeding, respiration, and locomotion than nonvertebrate chordates. Vertebrates are large, active animals. The evolution of almost all of the organ systems that support their large body sizes and activity is linked to embryonic development, and notably to the neural crest, a unique embryonic tissue that contributes to the formation of many vertebrate organ systems.

2.4 Vertebrate Embryonic Development

LEARNING OBJECTIVES

- 2.4.1 Describe the three embryonic germ layers and their fates.
- 2.4.2 Explain how compartments of the coelom differ in number and location among adult sharks, salamanders, and cats.
- 2.4.3 Explain the functions of neural crest and its significance in vertebrate evolution.
- 2.4.4 Summarize similarities and differences between neural crest and neurogenic placodes.

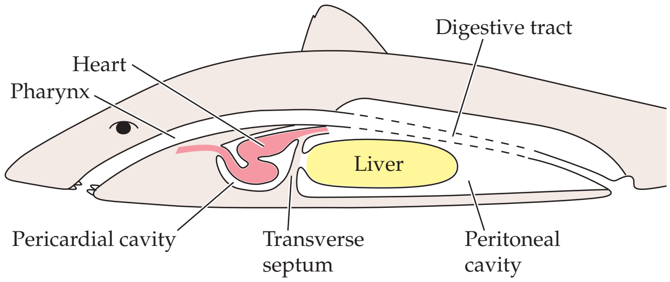
Studies of embryonic development and its physical, functional, and evolutionary constraints and opportunities provide clues about ancestral conditions and homologies between structures in different groups.

Development of the body

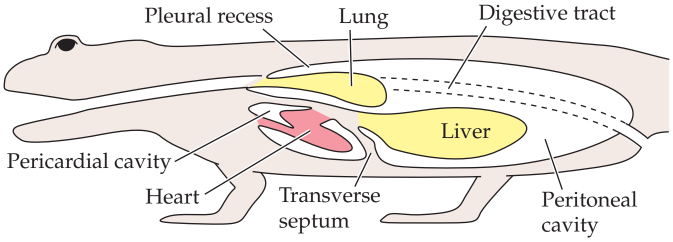
Bodies of all bilaterians form from three embryonic germ layers. The fates of these germ layers are largely conserved throughout vertebrate evolution.

- **Ectoderm**, the outermost layer, forms the superficial layers of skin (epidermis), linings of the most anterior and most posterior parts of the digestive tract, and most of the nervous system (Greek *ectos*, "outside"; *derm*, "skin").
- **Endoderm**, the innermost layer, forms the rest of the digestive tract lining, as well as glands associated with the gut, including the liver and pancreas (Greek *endos*, "within"). It also lines portions of the urinary system and forms respiratory surfaces of gills and lungs. Taste buds and the thyroid, parathyroid, and thymus glands develop from endoderm. Germ cells, which give rise to gametes, migrate from the endoderm into the progenitors of the gonads.
- **Mesoderm**, the middle layer, forms muscles, skeleton (including the notochord, vertebrae, skull, limb girdles, and limb bones), deeper layers of the skin (dermis), connective tissues, and the circulatory and urogenital systems (including the heart, kidneys, portions of the gonads and urogenital ducts; Greek *mesos*, "middle").

(A) Coelom and its two subdivisions in a shark



(B) Coelom and its two subdivisions in a salamander



(C) Coelom and its four subdivisions in a cat

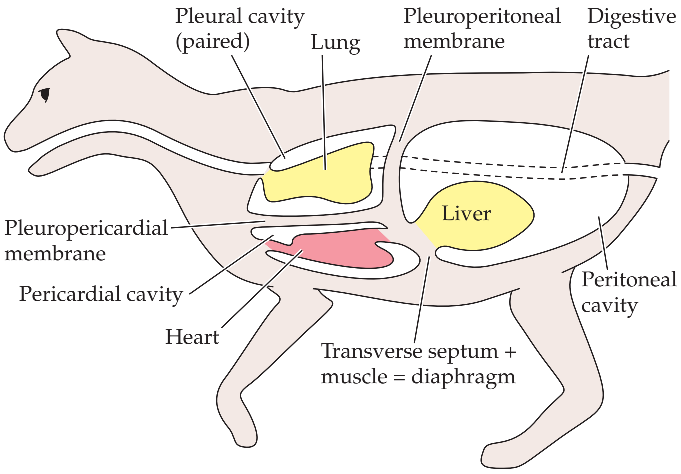
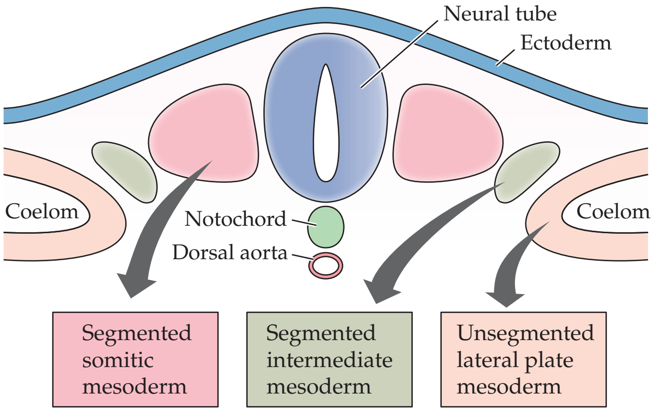


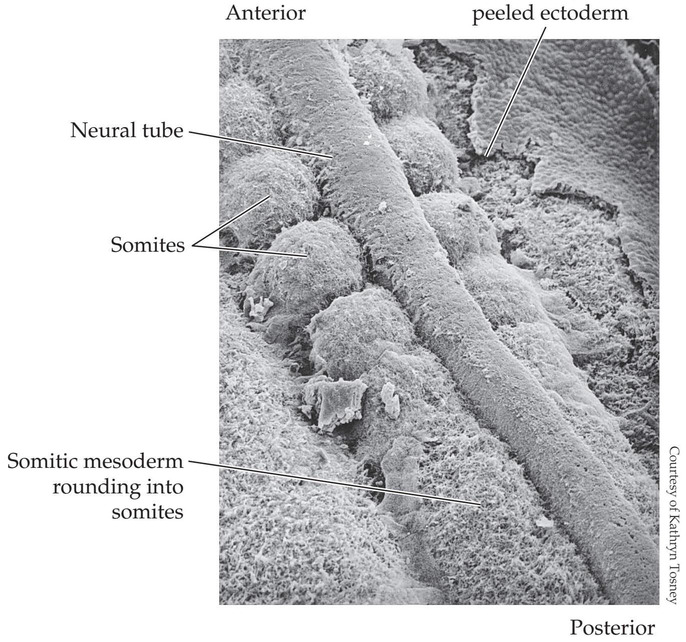
Figure 2.5 Divisions in the vertebrate coelom. (A) A shark's coelom has a pericardial cavity containing the heart and a peritoneal cavity containing abdominal organs. (B) Like the shark, a salamander has a pericardial cavity and a peritoneal cavity. However, the salamander heart is located more caudally than the shark's, and portions of the peritoneal cavity containing the lungs (pleural recesses) lie directly above the pericardial cavity. (C) A cat has a pericardial cavity, paired pleural cavities containing the lungs, and a peritoneal cavity. (After K. Liem et al. 2001. *Functional Anatomy of the Vertebrates*, 3rd ed. Cengage/Harcourt College: Belmont, CA.)

Within the mesoderm is the body cavity or **coelom** (Greek *koilia*, "cavity") that contains the internal organs of the body, such as the heart and gut tube (see Figure 2.4B). The coelom becomes subdivided in vertebrates and differs across them, being relatively simple in sharks and more complicated in mammals (**Figure 2.5**). In sharks, it is divisible into the **pericardial cavity**, which contains the heart, and the **peritoneal cavity**, which contains the viscera (gastrointestinal tract, liver, pancreas, and gallbladder). The two cavities are separated by the transverse septum, a partition between the heart and liver, as shown in the adult shark in Figure 2.5A. Note that the heart and surrounding pericardial cavity are located beneath the pharynx in the anterior portion of the body and the peritoneal cavity lies posteriorly. The same arrangement characterizes embryonic tetrapods, but during development the heart moves caudally to a position beneath the lungs; this condition can be seen in the adult salamander (Figure 2.5B). In the adult salamander, the anterior portion of the peritoneal cavity lies above the pericardial cavity and the areas around the lungs are called pleural recesses. In derived tetrapods such as mammals, the paired pleural recesses develop into cavities separate from the rest of the peritoneal cavity (Figure 2.5C). Thus, in adulthood, mammals have a pericardial cavity, paired pleural cavities, and a peritoneal cavity (i.e., four separate compartments rather than the two compartments of sharks and salamanders). The separate pleural cavities allow the lungs to expand and contract without interfering with other organs. Also, the muscular diaphragm of mammals develops to help separate the pericardial and paired pleural cavities from the peritoneal cavity; it functions in respiration. Coelomic cavities are lined by thin sheets of mesoderm referred to as **peritoneum** (in the peritoneal and pleural cavities) and **pericardium** (on the surface of the heart and lining the pericardial cavity). The gut is suspended in the peritoneal cavity by folds of peritoneum called **mesenteries**.

(A) Cross section through trunk of a developing amniote



(B) Dorsal view of developing somites



Courtesy of Kathryn Tosney

Figure 2.6 Major divisions of mesoderm. (A) Segmented somitic mesoderm forms somites that contribute to segmented structures such as vertebrae and unsegmented structures such as endothelial cells that line the vessels of the circulatory system. Segmented intermediate mesoderm gives rise to segmented structures such as kidney tubules as well as kidney and reproductive ducts and portions of the gonads. Unsegmented lateral plate mesoderm contributes to smooth muscle layers of the gut and muscles of the ventral body wall. (B) When surface ectoderm is peeled away, scanning electron microscopy reveals somites forming adjacent to the neural tube. Development proceeds from the anterior end of the embryo toward the posterior, where somites are just beginning to form. (A, after S.F. Gilbert and M.J.F. Barresi. 2016. *Developmental Biology*, 11th ed. Oxford University Press/Sinauer: Sunderland, MA)

Postcranial portions of the vertebrate body develop in a segmented fashion from anterior to posterior, with each segment having an initial component of spinal nerves, major blood vessels, progenitors of bone and muscles, and other internal structures. This segmentation can be seen in the arrangement of human vertebrae and ribs. **Figure 2.6A** shows how the developing mesoderm is divided into somitic, intermediate, and lateral plate mesoderm.

- **Somites** are segmented blocks of mesoderm that form on either side of the neural tube (**Figure 2.6B**). Derivatives of **somitic mesoderm** include the segmentally arranged vertebrae, dermis, and skeletal muscles. Dorsally forming skeletal muscles and dermis later grow ventrally and are innervated by the voluntary nervous system.
- Derivatives of **intermediate mesoderm** are the kidney tubules and ducts, gonads (except for the cells that give rise to gametes, which come from endoderm), and gonadal ducts.
- Derivatives of the **lateral plate mesoderm** are principally the viscera, smooth muscle lining the gut, and cardiac muscle of the heart, which are innervated by the autonomic, or involuntary, nervous system.

Development of the pharyngeal region

The term **pharyngeal arch** encompasses the segmental structures of the vertebrate pharynx that include internal skeletal components, associated muscles, nerves, and blood vessels best seen in a **pharyngula,** an early developmental stage common to vertebrate embryos. Pharyngeal arches are delimited on the outside by grooves called pharyngeal clefts (**Figure 2.7**). On the inside of the pharynx, a series of outpocketings known as pharyngeal pouches separate the arches from each other. Derivatives of the pharyngeal arches are strongly conserved throughout vertebrate history (**Table 2.2**).

Development of the brain

Initially represented by a thickening on the dorsal surface of the embryo known as the **neural plate**, the nervous system undergoes early and dramatic development to form the **neural tube**. The neural tube is the primary

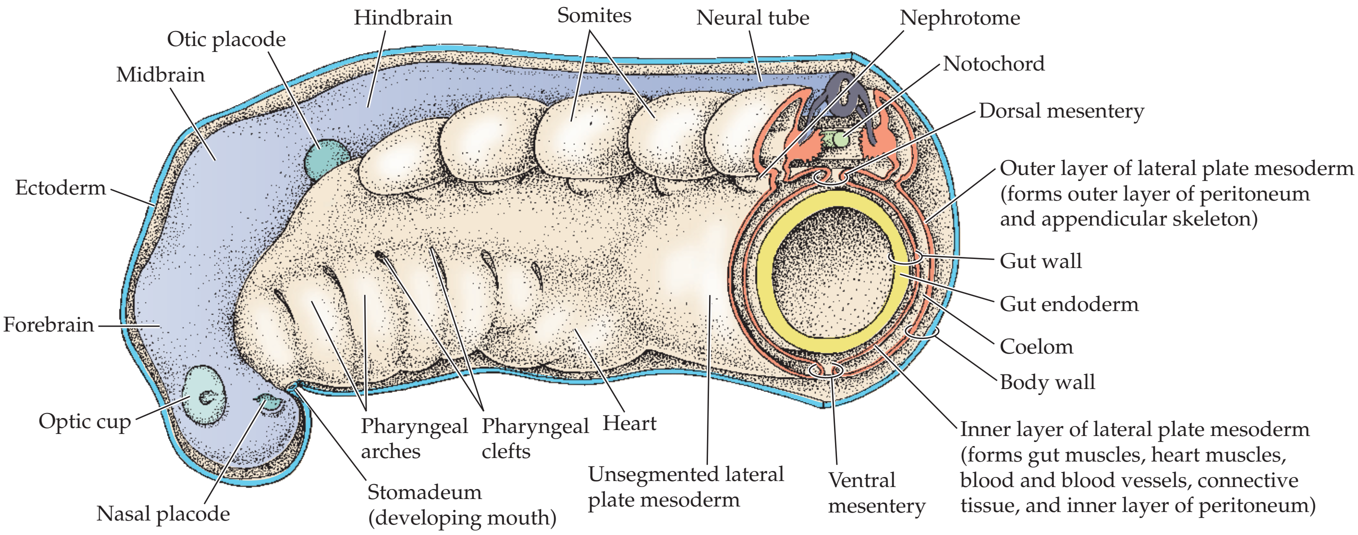


Figure 2.7 Development of the pharyngeal region. Three-dimensional view of a portion of a generalized vertebrate pharyngula, the embryonic stage when pharyngeal pouches appear. The ectoderm is stripped off the left side to show pharyngeal development and segmentation of the mesoderm in the trunk region. (After J.S. Kingsley. 1912. *Comparative Anatomy of Vertebrates*. Philadelphia, P. Blakiston's Son & Co.)

neurogenic (neuron-generating) tissue of vertebrates. By the early embryonic stage shown in Figure 2.7, the three primary brain regions have differentiated (Table 2.3). The **forebrain** is associated with the olfactory system and in most vertebrates becomes an integrative and associative area. Information from the eyes is projected to centers in the **midbrain**. The **hindbrain** receives input from many senses, including balance, hearing, taste, and touch. It also coordinates outgoing voluntary and involuntary motor activities, including respiration and circulation.

Other neurogenic tissues of vertebrates

Many differences between vertebrates and other chordates relate to the appearance of two new embryonic tissues, neural crest and neurogenic placodes, which contribute to formation of the nervous system and sense organs.

Table 2.2 Fates of the pharyngeal arches of gnathostomes

Arch number and name	Skeletal and muscle derivatives (sharks)	Cranial nerve (sharks and mammals)	Aortic arch (mammals)	Skeletal and muscle derivatives (mammals)[a]
Arch 1: Mandibular arch	Upper and lower jaws and jaw-closing muscles	V (trigeminal)	Remnant forms maxillary artery	Incus and malleus in middle ear and muscles of mastication
Arch 2: Hyoid arch	Hyomandibula, ceratohyal, and associated muscles	VII (facial)	Stapedial artery	Stapes, dorsal portions of hyoid, and muscles of facial expression
Arch 3: Carotid arch	1st gill arch and associated muscles	IX (glossopharyngeal)	Carotid artery	Ventral portions of hyoid and stylopharyngeus muscle
Arch 4	2nd gill arch and associated muscles	X (vagus)	Systemic aorta	Thyroid cartilage and extrinsic laryngeal muscles
Arch 5	3rd gill arch and associated muscles	X (vagus)	Lost in adults	None
Arch 6	4th gill arch and associated muscles	X (vagus)	Pulmonary artery	Arytenoid cartilages and intrinsic laryngeal muscles

[a] Only major muscles are included.

Table 2.3 Regions of the developing vertebrate brain and the resulting adult structures

Region	Structure	Characteristics
Forebrain	Telencephalon	Develops in association with the olfactory system and coordinates inputs from other sensory modalities. The area for olfaction is unique to vertebrates. In derived vertebrates the telencephalon becomes enlarged and is known as the cerebrum or cerebral hemispheres, the area responsible for associative processing of information
	Diencephalon	The pineal organ, a median dorsal outgrowth of the diencephalon, regulates circadian (daily) rhythms based on light The floor of the diencephalon (location of the hypothalamus) and the adenohypophysis (anterior pituitary gland, a ventral outgrowth of the diencephalon) form the primary center for neural-hormonal coordination and integration
Midbrain	Mesencephalon	The tectum (dorsal portion) receives sensory information (visual, auditory, and touch). The tegmentum (ventral portion) is the pathway for incoming sensory information and outgoing responses to and from the forebrain
Hindbrain	Metencephalon	The cerebellum, a dorsal outgrowth, receives sensory information from the vestibular system and coordinates and regulates motor activities (whether reflexive, such as maintenance of posture, or directed, such as escape movements)
	Myelencephalon	Controls involuntary (autonomic) functions such as respiration and circulation

Neural crest Key features of **neural crest** cells are their migratory ability and multipotency—they move to distant sites in the body where they differentiate into many different cell types, resulting in even more cell types than are formed by mesoderm (**Figure 2.8**). Neural crest occurs only in vertebrates and is perhaps the most important innovation in the evolutionary origin of the vertebrate body plan. Because of this, many scientists regard neural crest as a fourth germ layer, in addition to ectoderm, mesoderm, and endoderm.

Neural crest develops in both the head and trunk and contributes to many unique vertebrate structures, including cranial skeletal elements, cranial nerves and sense organs, cranial muscles, adrenal glands, pigment cells in the skin, secretory cells of the gut, and smooth muscle tissue of the blood vessels. Gnathostomes (jawed vertebrates) have even more features that form from neural crest, including the sympathetic nervous system and dentine found in teeth. Neural crest cells interact extensively with other tissues to form these structures.

Lancelet larvae express a gene during early development that may be homologous with a vertebrate gene active in neural crest formation, and similar genes are expressed in some tunicates. Cells resembling migratory neural crest cells occur in larvae of some tunicate species, where they differentiate into pigment cells. Thus, neural crest probably had antecedents among nonvertebrate chordates.

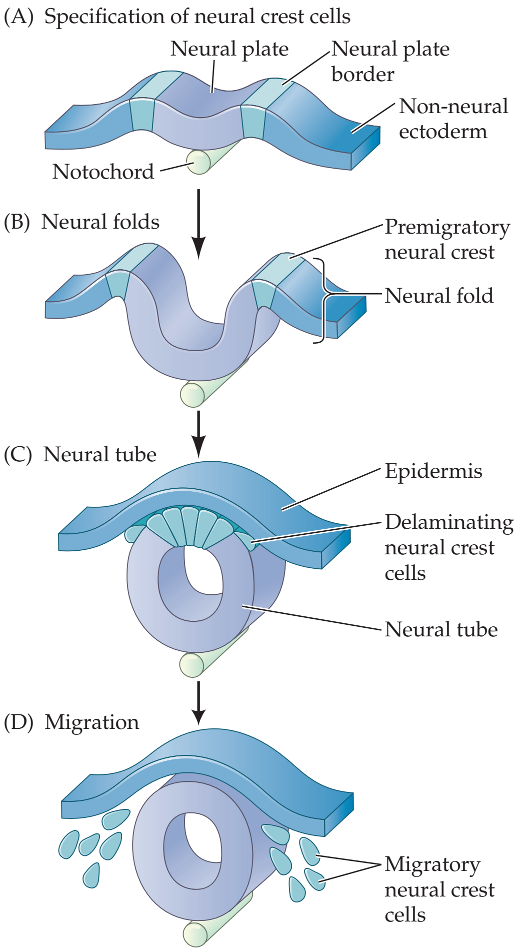


Figure 2.8 **Formation and migration of neural crest cells.** (A) Neural crest cells are specified at the border of the neural plate. (B) As the neural plate folds to form the neural tube, the premigratory neural crest cells are carried to the top of the fold. (C, D) As the neural tube closes, neural crest cells delaminate (separate from the epidermal sheet) and migrate. (After S.F. Gilbert and M.J.F. Barresi. 2016. *Developmental Biology*, 11th ed. Oxford University Press/Sinauer: Sunderland, MA.)

Neurogenic placodes Embryonic vertebrates uniquely have thickenings of the ectoderm in the anterior portion of the head, called **neurogenic placodes**, that give rise to nerves and sensory receptors of the nose, ear, and other sensory systems (see Figure 2.7). Like neural crest, cells of neurogenic placodes migrate. Some placodal cells migrate caudally to contribute to the trunk lateral lines of fishes and lissamphibians and to the cranial nerve that innervates them. Other placodal thickenings in the embryonic ectoderm are not neurogenic, giving rise to structures such as feathers and hair.

2.5 Vertebrate Tissues

LEARNING OBJECTIVES

2.5.1 Categorize the four types of tissues of vertebrates.

2.5.2 Differentiate dermal bone, endochondral bone, and perichondral bone.

At the whole-animal level, increased body size and increased activity levels distinguish vertebrates from nonvertebrate chordates. Because of their relatively larger sizes, vertebrates need efficient, specialized tissues and organ systems to carry out processes accomplished by diffusion or cilia in smaller animals. The origin of vertebrates probably was linked to changes from filter feeding to active predation. These changes, including a muscular pharynx, cranial nerves, and more complex sense organs, are largely based on tissues derived from neural crest. A muscularized, multichambered heart also supports higher levels of activity and oxygen transport in the circulatory system.

Here and in Section 2.6 we introduce general aspects of vertebrate anatomy and function. Evolutionary changes and further specializations of these structures in the different vertebrate taxa are described in later chapters.

Adult tissue types

Vertebrate bodies are made of four types of tissues:

1. *Epithelial tissues* consist of sheets of tightly connected cells that form boundaries between the inside and outside of the body, such as the skin, and between compartments within the body.
2. *Muscular tissues* are made of cells containing the filamentous proteins actin and myosin, which together cause muscle cell contraction to exert forces.
3. *Neural tissues* include neurons, which are the cells that transmit information via electrical and chemical signals; and glial cells, which support the neurons and perform many functions, including formation of myelin sheaths that enhance conduction speeds of neural impulses.
4. *Connective tissues* provide structural support, protection, and strength. Connective tissues include not only bone and cartilage that form the skeleton but also tendons, ligaments, adipose tissue, and blood.

Mineralized tissues

Mineralized connective tissues are typically composed of cells that secrete a proteinaceous tissue matrix, usually composed of collagen and crystals of calcium hydroxyapatite (**Table 2.4**). Hydroxyapatite crystals often align on the matrix of collagenous fibers in layers with alternating directions, much like the structure of plywood. This combination of cells, fibers, and minerals gives bone a latticework structure that combines strength with relative lightness. Mineralized tissues readily fossilize and supply most of the information we have about extinct vertebrates. Thus, we discuss mineralized tissues throughout this book as we trace vertebrate evolutionary history.

Bone Vertebrates have three main types of bone: dermal, endochondral, and perichondral.

- **Dermal bone** forms in the dermis of the skin by a process called **intramembranous ossification**; such bones lack a cartilaginous precursor. The precursor tissue in embryos is called mesenchyme, and it consists of cells surrounded by an extensive extracellular matrix. During intramembranous ossification, mesenchyme cells transform into osteocytes (bone cells) that secrete additional extracellular matrix specialized to bind with bone minerals.
- **Endochondral bone** is made up of osteocytes that form within a cartilaginous precursor deeper within the body. In bony fishes and tetrapods, endochondral bone forms the internal skeleton.
- **Perichondral bone** is like dermal bone in some respects and like endochondral bone in others. It forms deep within the body, like endochondral bone, but within the perichondral membrane surrounding an individual cartilage or bone, and thus has some aspects of dermal bone.

Genes expressed during development of endochondral bone are absent from cyclostomes and were secondarily lost in chondrichthyans (cartilaginous fishes), but the presence of bone in extinct jawless fishes indicates that bone is an ancestral character for gnathostomes.

Teeth Toothlike components called odontodes were part of the dermal armor of early fossil vertebrates, and recent studies indicate that odontodes were the primary elements from which the oral teeth of gnathostomes evolved. Gnathostome teeth are harder than bone and more resistant to wear because they are composed of

Table 2.4 Mineralized tissues of vertebrates

Tissue	Occurrence	Approximate mineral content
Enamel	Teeth, some fish scales, and armor of early vertebrates	96%
Enameloid	Teeth and scales of some extant and fossil fishes	96%
Dentine	Teeth, some fish scales, and armor of early vertebrates	90%
Bone	Internal skeleton and dermal skeleton of bony fishes and tetrapods, as well as external structures such as antlers	70%
Calcified cartilage	Internal skeleton of chondrichthyans; mineral typically organized as prisms and sometimes referred to as prismatic calcification	70%
Cementum	Mammalian teeth; helps fasten teeth into sockets	45%

dentine and enamel, both of which are more mineralized than bone (see Table 2.4).

An oral tooth of a gnathostome typically forms at the interface between ectoderm and a dental papilla derived from neural crest. Enamel-forming cells (ameloblasts) develop from ectoderm; the neural crest-derived dental papilla forms the dentine-forming cells (odontoblasts); and reciprocal developmental interaction leads to tooth formation.

2.6 Vertebrate Organ Systems

LEARNING OBJECTIVES

2.6.1 List and characterize the organ systems of vertebrates.
2.6.2 Describe the three components of the cranial skeleton.
2.6.3 Explain why it is important to think beyond the five sensory systems of mammals.

An animal is more than the sum of its parts, and a key level of organization lies in integrated combinations of tissues to form organs and organ systems. In this section, we briefly describe the general characteristics of the vertebrate organ systems listed in **Table 2.5**. Subsequent chapters will describe modifications in these systems that evolved in particular taxa as vertebrates reached their current extraordinary diversity.

Integumentary system

The integumentary system consists of skin and its derivatives, including dermal bone, teeth, glands (mucus, oil, sweat, wax-producing, and mammary), and so-called "appendages" of the skin (scales, feathers, hair, horns, antlers, and hooves). The main functions of skin and its derivatives are protection, regulation of body temperature, sensation, and communication.

Vertebrate skin consists of two layers, the **epidermis** (outer layer) and **dermis** (inner layer); the basement membrane between them consists of extracellular material secreted by both epidermal and dermal cells and serves as the foundation on which the epithelial cells of the epidermis are organized (**Figure 2.9**). The epidermis is relatively thin and derived from ectoderm. It is constantly renewed by cell division in its most basal layer, the stratum germinativum. The skin of non-amniotes typically has a layer of mucus secreted by goblet cells. The epidermal cells proper, especially those of terrestrial vertebrates, synthesize keratin (Greek *keras*, "horn"), an insoluble protein that ultimately fills the cells of the outermost layer of epidermis, the stratum corneum (Latin *cornu*, "horn"), before they are shed at the skin's surface.

The dermis is unique to vertebrates and is much thicker than the epidermis. Derived from mesoderm and neural crest, the dermis contains connective tissue, nerves, and blood vessels. Beneath the skin is the **hypodermis**, a loose connective tissue layer that anchors the skin to underlying muscles and organs. Derived from mesoderm and also unique to vertebrates, the hypodermis protects internal organs and serves as a site for fat storage in some vertebrates, including birds and mammals.

Skeletal system

Bones and joints make up the skeletal system. Functions of this organ system include protection of internal organs, movement, storage of fat and minerals, and production of formed elements of the blood (red blood cells, white blood cells, and platelets). Fat is stored in yellow bone marrow,

Table 2.5 Vertebrate organ systems

Integumentary system	Skin (epidermis and dermis) and its derivatives, including dermal bone, teeth, claws, scales, feathers, hair, and some exocrine glands (mucus, oil, sweat, wax-producing, and mammary)
Skeletal system	Bones and joints, organized as part of the axial skeleton (cranial skeleton, vertebrae, ribs, sternum, and median fins) or appendicular skeleton (pectoral and pelvic girdles and associated fin or limb bones)
Muscular system	Three types of muscles that control either voluntary movements (skeletal muscle) or involuntary movements (cardiac muscle and smooth muscle)
Nervous system	Cells and organs that regulate and integrate information from the internal and external environments. Includes the brain and spinal cord, as well as sensory organs that receive signals for chemosensation (taste and smell), mechanosensation (touch and pressure), vision, and hearing. Some aquatic vertebrates can perceive electrical impulses generated by muscle contractions of other organisms.
Endocrine system	Ductless glands that regulate and coordinate internal body functions by secreting hormones that interact with specific target cells
Respiratory system	Organs involved in ventilation, the movement of water or air across surfaces such as those of the gills, skin, or lungs, where respiratory gases are exchanged
Circulatory system	Heart pumps blood through a closed system of vessels that transports oxygen and nutrients to cells and removes carbon dioxide and other metabolic wastes
Digestive system	Organs (mouth, pharynx, esophagus, stomach, and small and large intestines) that take in complex food compounds and break them down into small molecules that are absorbed across the gut wall for transport to cells
Excretory system	Kidneys filter nitrogenous waste from the blood and regulate salt and water balance
Reproductive system	Gonads (testes in males and ovaries in females) and their ducts. Oviducts in some female vertebrates enlarge to form paired uteri or fuse to form a single uterus where fertilized eggs develop. Some male vertebrates have an intromittent organ used for internal fertilization

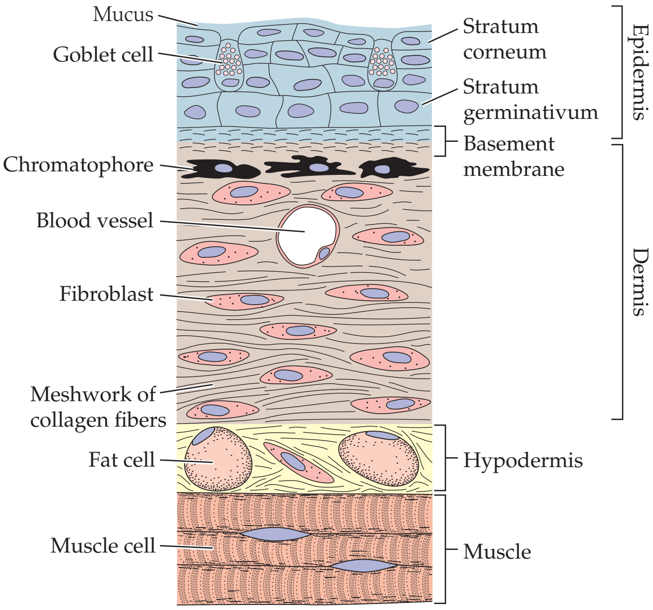


Figure 2.9 Simplified schematic of vertebrate skin. In the epidermis, cells of the stratum germinativum multiply mitotically, with some cells moving toward the surface where they are sloughed off (in terrestrial vertebrates these cells become filled with keratin as they move upward to the surface and die). Goblet cells in the epidermis produce mucus. Chromatophores are pigment cells derived from neural crest. Fibroblasts are connective tissue cells that produce fibers of the extracellular matrix of the dermis. (After K. Liem et al. 2001. *Functional Anatomy of the Vertebrates*, 3rd ed. Cengage/Harcourt College: Belmont, CA.)

and blood cells and platelets are formed from stem cells in red bone marrow.

Structures of the vertebrate internal skeleton include the vertebrae, chondrocranium, and gill arch skeleton (**Figure 2.10A**). We infer that both neural arches (which are components of the vertebrae) and elements that support the caudal and other median fins were present in early Paleozoic vertebrates. Subsequently, vertebrates evolved a dermal skeleton of external plates and scales that protected soft tissues of the body. Many dermal skeletal elements persisted throughout vertebrate history. For example, much of our skull is dermal bone.

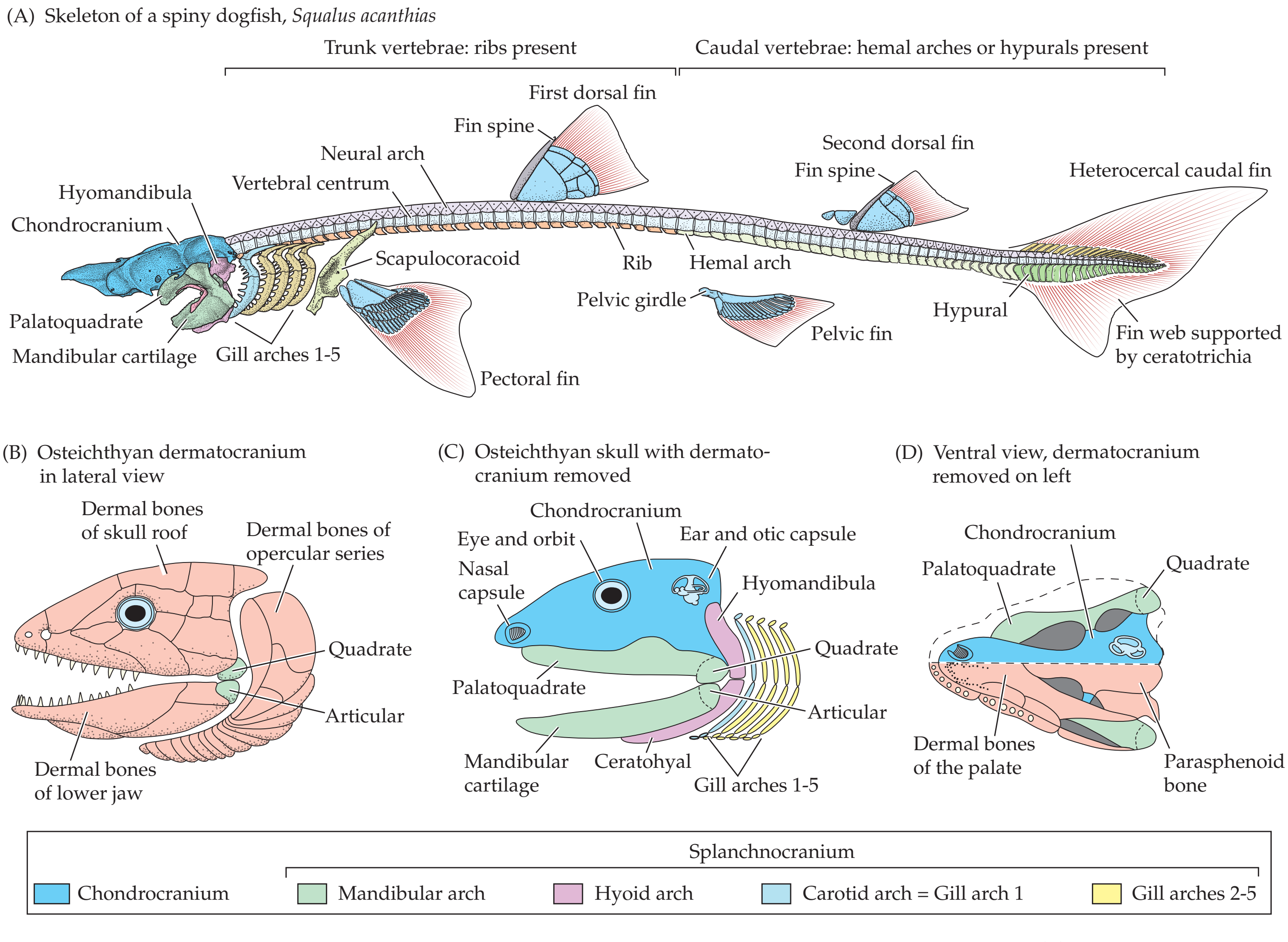


Figure 2.10 Components of the skeleton. (A) Skeleton of a shark. (B–D) Cranium of an idealized osteichthyan based on the bowfin, *Amia calva*. (B) Lateral view of dermatocranium showing dermal bones and jaw joint between quadrate and articular bones. (C) Lateral view with dermatocranium removed to show chondrocranium and splanchnocranium. (D) Ventral view with left side of dermatocranium removed. (A after S.G. Gilbert. 1973. *Pictorial Anatomy of the Dogfish*. U. Washington Press. B–D after K. Liem et al. 2001. *Functional Anatomy of the Vertebrates*, 3rd ed. Cengage/Harcourt College: Belmont, CA.)

In addition to considering the types of bone, ossification patterns, and position within the body, another way to think about organization of the vertebrate skeleton is to recognize its components: the **axial skeleton** (cranial skeleton, vertebrae, ribs, sternum, and median fins) and the **appendicular skeleton** (pectoral and pelvic girdles and associated fin or limb bones).

The cranial skeleton of most extant vertebrates forms from three components (**Figure 2.10B–D**):

1. **Dermatocranium** (Greek *derma*, “skin”; Latin *cranium*, “skull”), which forms by intramembranous ossification in the dermis of the skin and functions to protect the brain, anchor teeth, and provide attachment sites for muscles. Anterior regions of the dermatocranium form from neural crest and posterior regions form from mesoderm. Bones of the dermatocranium often cover cartilage or bones derived from the chondrocranium and splanchnocranium.
2. **Chondrocranium** (Greek *chondros*, "gristle"), which forms in part from neural crest and in part from mesoderm and functions to protect the brain, nose, and inner ear.
3. **Splanchnocranium** (Greek *splanchnon*, “viscera”), which forms from neural crest and contributes to the upper and lower jaws as well as the gill arch skeleton and functions in feeding and respiration.

Components of the splanchnocranium are known by many names: visceral arches, gill arches, pharyngeal arches, and branchial arches. In adult gnathostomes, the first two arches are the mandibular and hyoid, and they form jaws and jaw supports, respectively. In adult fishes, arches 3–7 bear gill tissue, and we call these **gill arches**.

Muscular system

Vertebrates have three types of muscle tissue: skeletal muscle (attached to the skeleton; voluntary control of contraction), cardiac muscle (in the walls of the heart; involuntary control), and smooth muscle (in walls of visceral organs and blood vessels; involuntary control). We focus here on skeletal muscles of the head and trunk**.**

Cranial muscles Vertebrates have two main groups of skeletal muscles in the head. The first are those associated with the pharyngeal arches, including the jaws. Muscles of the mandibular arch form the jaw-closing muscles of all gnathostomes. In fishes, muscles of the more posterior arches power gill ventilation, but in adult tetrapods, which have lost gill ventilation, these muscles evolved new functions (see Table 2.2). The second group of skeletal muscles in the head are the extrinsic eye muscles, which rotate the eyeball.

Axial muscles Axial musculature consists of segmental myomeres folded in three dimensions so that each extends anteriorly and posteriorly to span several body segments (**Figure 2.11**). The original function of myomeres was to produce lateral undulations of the body for swimming. Myomeres of nonvertebrate chordates are V-shaped whereas those of vertebrates are W-shaped (see Figure 2.4). The segmental pattern of axial muscles is clearly visible in fishes; you may have observed it when a piece of cooked fish flakes apart into zigzag blocks, each block representing a myomere. The segmental pattern is less obvious in tetrapods, but can be observed in the six-pack abdomen of a body builder, where each ridge represents a segment of the rectus abdominis muscle.

Nervous system and sense organs

The nervous system regulates and integrates information from both the external and internal environments to control motor, sensory, and automatic body functions (those not requiring conscious thought), as well as higher functions of the brain, such as cognition. It is a system for rapid communication that works via both electrical signals (action

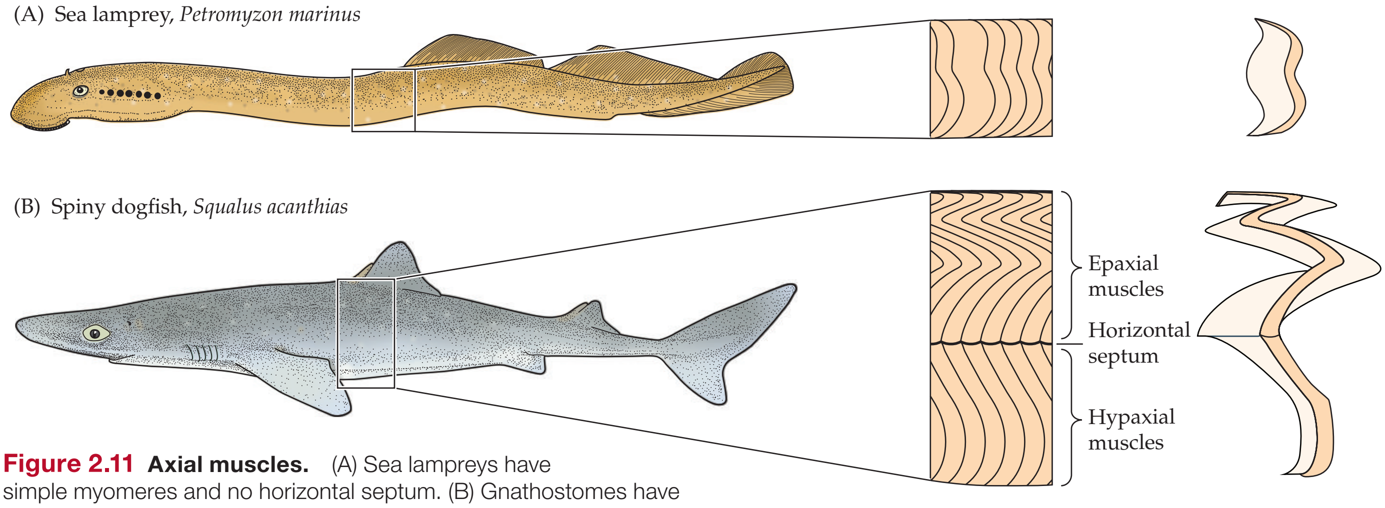


Figure 2.11 Axial muscles. (A) Sea lampreys have simple myomeres and no horizontal septum. (B) Gnathostomes have more complexly folded myomeres and a horizontal septum that divides trunk musculature into epaxial (dorsal) and hypaxial (ventral) portions. This division correlates with the evolution of paired fins, as will be described in Chapter 3.

potentials) and chemical signals (neurotransmitters). We focus on the sense organs of vertebrates because these organs often reveal much about the sensory world of an animal. Sense organs contain receptor cells that transduce environmental signals, such as light or sound, into action potentials that travel via sensory neurons to the brain.

Because we are mammals, we think of vertebrates as having five senses—taste, touch, sight, smell, and hearing—but this list does not include all senses of extant vertebrates. Many groups have complex, multicellular sense organs formed from neurogenic placodes tuned to the sensory stimuli important to those species.

Chemosensation The ability to perceive and react to chemical signals (molecules) in the external environment is the most universal of sensory abilities—plants, fungi, animals, and even bacteria all have this vital and often extraordinary ability (think of sharks that can detect small amounts of blood in the open ocean). Among vertebrates, taste (gustation) and smell (olfaction) involve detection of dissolved molecules by specialized receptors. We humans think of taste and smell as interlinked; for example, our sense of taste is poorer if our sense of smell is blocked when we have a cold. However, these two senses operate at different distances and have different pathways in the brain. Odorants are detected at a distance, and the sensations are received in the forebrain. Tastant molecules are perceived upon direct contact, and the sensations are received initially in the hindbrain.

Vision A vertebrate's eye consists of a cornea, lens, iris, and retina. The retina, which develops as an outgrowth of the brain, has three main layers: photoreceptors, which are the light-sensitive cells, interneurons, and output neurons. Rods are photoreceptors used to see in low light levels, such as dusk. Cones are color-sensitive photoreceptors that require higher light levels. Both rods and cones contain opsin photopigments. Color vision using different opsins appears to be a plesiomorphic feature of vertebrates.

Electroreception The capacity to perceive electrical impulses generated by muscle contractions of other organisms is a form of distance reception that works only in water. Electroreception was probably an important feature of early vertebrates, and it is widespread among extant fishes and aquatic lissamphibians but has been lost in amniotes. Electroreception secondarily evolved in monotreme mammals such as the platypus, but the mechanism and innervation of the system differ from those of fishes. Some fishes not only detect weak electric fields but also produce electrical discharges to sense their environment and communicate with other individuals. Still others, such as electric eels, produce strong electrical discharges that can subdue prey and deter predators.

Mechanoreception All vertebrates have sensory cells or organs that respond to mechanical forces; touch receptors in the skin are a familiar example. A more specialized class of mechanoreceptors are **hair cells**; found in all vertebrates, hair cells detect motion in fluids. The fluid can be outside the body, such as water surrounding a fish, or within the body, such as fluid within the inner ear. They are called hair cells because they have hairlike microscopic specializations on the cell surface. When these hairlike projections are deflected, the cell detects the direction of fluid motion. Hair cells function in many sensory systems, including the vestibular system and hearing (see below), and in the lateral line system of fishes and aquatic lissamphibians, which detects water movements (see Chapter 4).

Vestibular system The inner ear is enclosed within the braincase (**Figure 2.12A**). The **vestibular system** is the component of the inner ear that detects changes in an animal's position in space using hair cells and fluid (endolymph) contained within its chambers and semicircular canals (**Figure 2.12B**). Chambers of the inner ear, the utriculus and sacculus, house sensory patches called maculae that contain tiny crystals of calcium carbonate resting in a jellylike substance on hair cells. Macular sensations tell the animal which way is up and detect linear acceleration

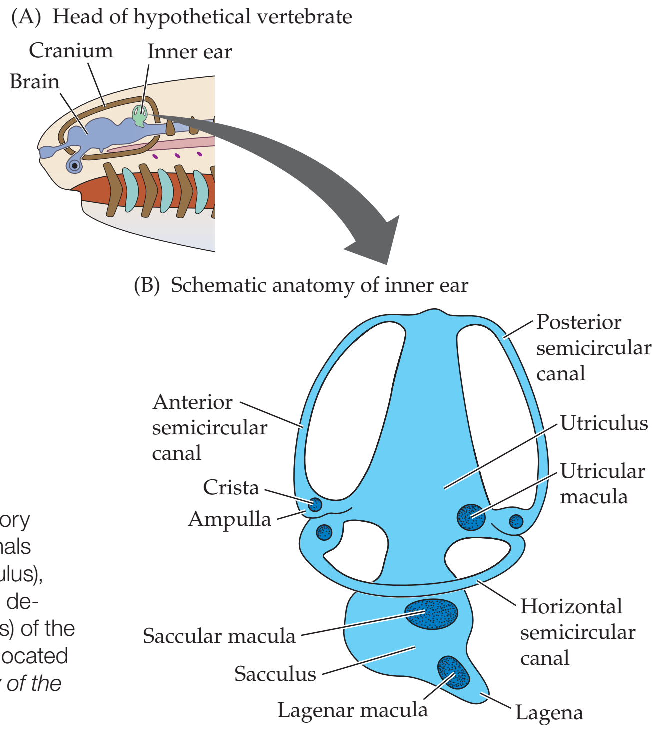


Figure 2.12 Schematic interpretation of the inner ear. The inner ear, located within the braincase (A), serves vestibular and auditory senses. An idealized gnathostome inner ear (B) has three semicircular canals (anterior, posterior, and horizontal) and two chambers (utriculus and sacculus), allowing the animal to detect motions in three dimensions. Sensations are detected by hair cells in small sensory patches (cristae) in ampullae (swellings) of the semicircular canals, and by hair cells in larger sensory patches (maculae) located within the chambers. (Modified from Liem et al. 2001. *Functional Anatomy of the Vertebrates*, 3rd ed. Cengage/Harcourt College: Belmont, CA.)

(movement in a straight line). At the base of each semicircular canal is a swelling (ampulla), which contains a smaller sensory patch called a crista. Cristae also have hair cells embedded in the same jellylike substance found in the sensory areas of the sacculus and utriculus. Cristae detect angular acceleration (such as head rotation) by monitoring the displacement of endolymph within the semicircular canals during motion.

Gnathostomes have three semicircular canals—anterior, posterior, and horizontal—that allow detection of motion in three dimensions (see Figure 2.12B). Cyclostomes differ, with hagfishes interpreted as having only one semicircular canal and lampreys two. Recent work suggests that the vestibular system of lampreys is more complicated than previously believed and that it functions as effectively as that of gnathostomes.

We often fail to realize the importance of our own vestibular sense because we usually depend on vision to determine our position. We can sometimes be fooled, however, as when sitting in a stationary train or car and thinking that we are moving, only to realize from the lack of input from our vestibular system that it is the vehicle next to us that is moving.

Hearing The inner ear of fishes and tetrapods is also used to detect sound waves. The lagena is an extension off the sacculus that is specialized for sound reception in different groups of vertebrates (see Figure 2.12B); in mammals, for example, the lagena evolved into an elongated, snail-shaped cochlea. Sound waves transmitted to the cochlea create waves of compression that pass through the endolymph, stimulating auditory hair cells.

The ways in which sound waves reach the inner ear differ across vertebrates. An elegant example in some fishes is the Weberian apparatus, a chain of small bones that connects the gas bladder (which is also important in regulating buoyancy) to the inner ear (see Chapter 7). Mammals have a large external ear, or pinna, and a chain of three small bones in the middle ear that transmit vibrations from the ear drum to the inner ear (see Chapter 22).

Associated with hearing is the evolution of sound production for communication. Perhaps half the living species of fishes produce sounds, and many fishes do this using the gas bladder. Tetrapods typically make sounds by expelling air through the larynx (frogs and mammals) or syrinx (birds). Neural control of sound production in fishes appears to be homologous with that in tetrapods.

Endocrine system

The endocrine system regulates and coordinates activities of the body, but the speed of information transfer is generally much slower than that of the nervous system. It consists of many separate **endocrine glands**, ductless glands that secrete hormones. Examples include the adenohypophysis (also known as the anterior pituitary) and the thyroid and adrenal glands. Organs that contain some endocrine tissue but have additional functions also are part of the endocrine system, including parts of the digestive system (stomach, small intestine, and pancreas), as well as reproductive organs (ovaries and testes).

Endocrine cells secrete hormones into the surrounding fluid where they typically diffuse into the bloodstream for transport throughout the body (some are transported in other fluids, such as cerebrospinal fluid or lymph). Although hormones contact virtually all cells, they influence only target cells that have receptors for specific hormones. Hormones can initiate relatively short-term changes in behavior and physiology (for example, the fight-or-flight response mediated by the adrenal glands) or longer-term changes, such as those associated with development and growth (mediated by the adenohypophysis and the thyroid gland).

Endocrine glands differ from **exocrine glands**, which secrete products such as mucus, oil, sweat, wax, milk, saliva, or digestive enzymes into ducts leading to the skin, mouth, or digestive tract. Mucus, oil, sweat, wax-producing, and mammary glands are part of the integumentary system mentioned earlier. Salivary glands, the liver, and exocrine glands of the stomach, intestines, and pancreas are part of the digestive system.

Respiratory system

Getting oxygen to cells requires both ventilation and circulation. **Ventilation** refers to movement of the respiratory medium (water or air) across a respiratory surface through which gases are exchanged via diffusion with the blood. Respiratory surfaces such as those of the gills, skin, or lungs are thin, moist, highly vascularized, and characterized by large surface areas. One or more pumps are needed to move the respiratory medium over the respiratory surface; examples of pumps used by vertebrates include the mouth and oral cavity, rib cage, and diaphragm. Fishes typically use movements of the oral cavity to draw water into the mouth and pump it out over the gills. Mammals use movements of the rib cage and diaphragm to move air in and out of the lungs.

Circulatory system

Circulation is movement of blood through vessels to the vicinity of cells where diffusion of gases again occurs. In all vertebrates, the pump that powers circulation is the heart.

Blood is a fluid connective tissue that is pumped through blood vessels. It is composed of liquid plasma, red blood cells (erythrocytes, which contain the iron-rich protein hemoglobin used to transport respiratory gases), several different types of white blood cells (leukocytes), and specialized cells (or cell-like structures) that promote clotting of blood (such as platelets in mammals). Blood transports oxygen and nutrients to cells, removes carbon dioxide and other metabolic waste products, and

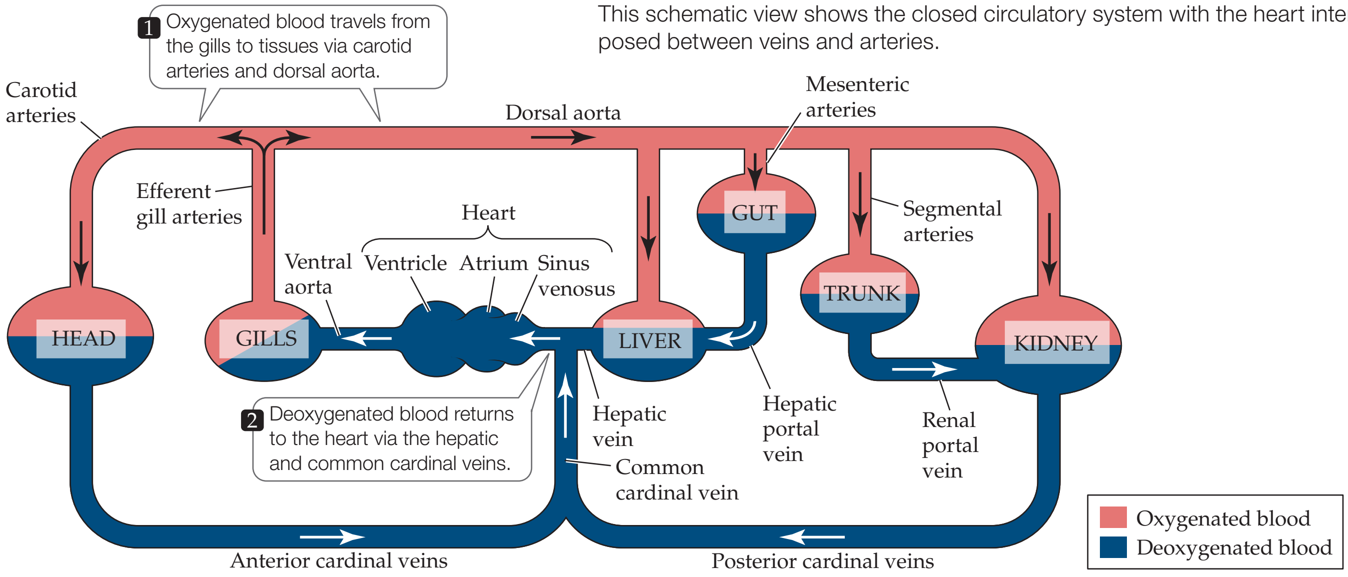


Figure 2.13 Circulatory system of a hypothetical vertebrate with gills. This schematic view shows the closed circulatory system with the heart interposed between veins and arteries.

1 Oxygenated blood travels from the gills to tissues via carotid arteries and dorsal aorta.

2 Deoxygenated blood returns to the heart via the hepatic and common cardinal veins.

stabilizes the internal environment. It also carries hormones from their sites of release to target tissues and plays essential roles in immunity.

The vertebrate circulatory system and the pump that powers it—the heart—offer an interesting look at some important and unique vertebrate synapomorphies and their evolution.

Closed circulation Vertebrates have **closed circulatory systems**—arteries and veins are connected by capillaries so that blood always stays within vessels. **Arteries** carry blood away from the heart, and **veins** return blood to the heart. Blood pressure is higher in arteries than in veins, and arterial walls have a layer of smooth muscle that is absent from veins.

The dorsal aorta is flanked by paired cardinal veins that return blood to the heart. Anterior cardinal veins (draining the head) and posterior cardinal veins (draining the body) unite on each side in common cardinal veins that enter a common chamber known as the sinus venosus before entering the atrium of the heart (**Figure 2.13**). In lungfishes and tetrapods, the posterior cardinal veins are functionally replaced by a single median vessel, the posterior vena cava.

Interposed between the smallest arteries (arterioles) and smallest veins (venules) are **capillaries**, which are sites of exchange between blood and tissues. Capillaries pass close to every cell and their walls are only one cell layer thick, facilitating diffusion. Collectively, capillaries provide an enormous surface area for exchange of gases, nutrients, and waste products. Arteriovenous anastomoses connect arterioles directly to venules, allowing blood to bypass a capillary bed, and normally only a fraction of the capillaries in a tissue have blood flowing through them.

Blood vessels that connect two capillary beds are called **portal vessels**. For example, the hepatic portal vein, present in all vertebrates, connects capillary beds of the gut and liver (see Figure 2.13). Substances absorbed from the gut are transported directly to the liver, where toxins are rendered harmless and some nutrients are processed or stored. Most vertebrates also have a renal portal system connecting veins returning from the tail and posterior region of the trunk to the kidneys. The renal portal system is not well developed in jawless vertebrates and has been lost in adult mammals.

The vertebrate heart The heart develops as a muscular tube that folds on itself and becomes constricted into sequential chambers: **sinus venosus**, **atrium**, and **ventricle** (see Figure 2.13). The **conus arteriosus** is added in gnathostomes. Therian mammals—marsupials and placentals—incorporate the sinus venosus into the wall of the right atrium as the **sinoatrial node**, which controls heartbeat; in these mammals the conus arteriosus is subsumed into the base of the aorta. The heart wall is composed of a thick layer of cardiac muscle—the myocardium—with a thin outer epicardium and inner endocardium.

In basal gnathostomes such as sharks, the sinus venosus is a thin-walled sac with few cardiac muscle fibers. Blood moves from the sinus venosus into the atrium, which has valves at each end to prevent backflow. The ventricle has thick muscular walls with an intrinsic pulsatile rhythm that can be speeded up or slowed down by the nervous system. Ventricular contraction forces blood into the ventral aorta. Researchers think that, originally, six pairs of aortic arches branched from the ventral aorta to supply the gills (**Figure 2.14**). Oxygenated blood flows from the gills to the paired dorsal aortae above the gills.