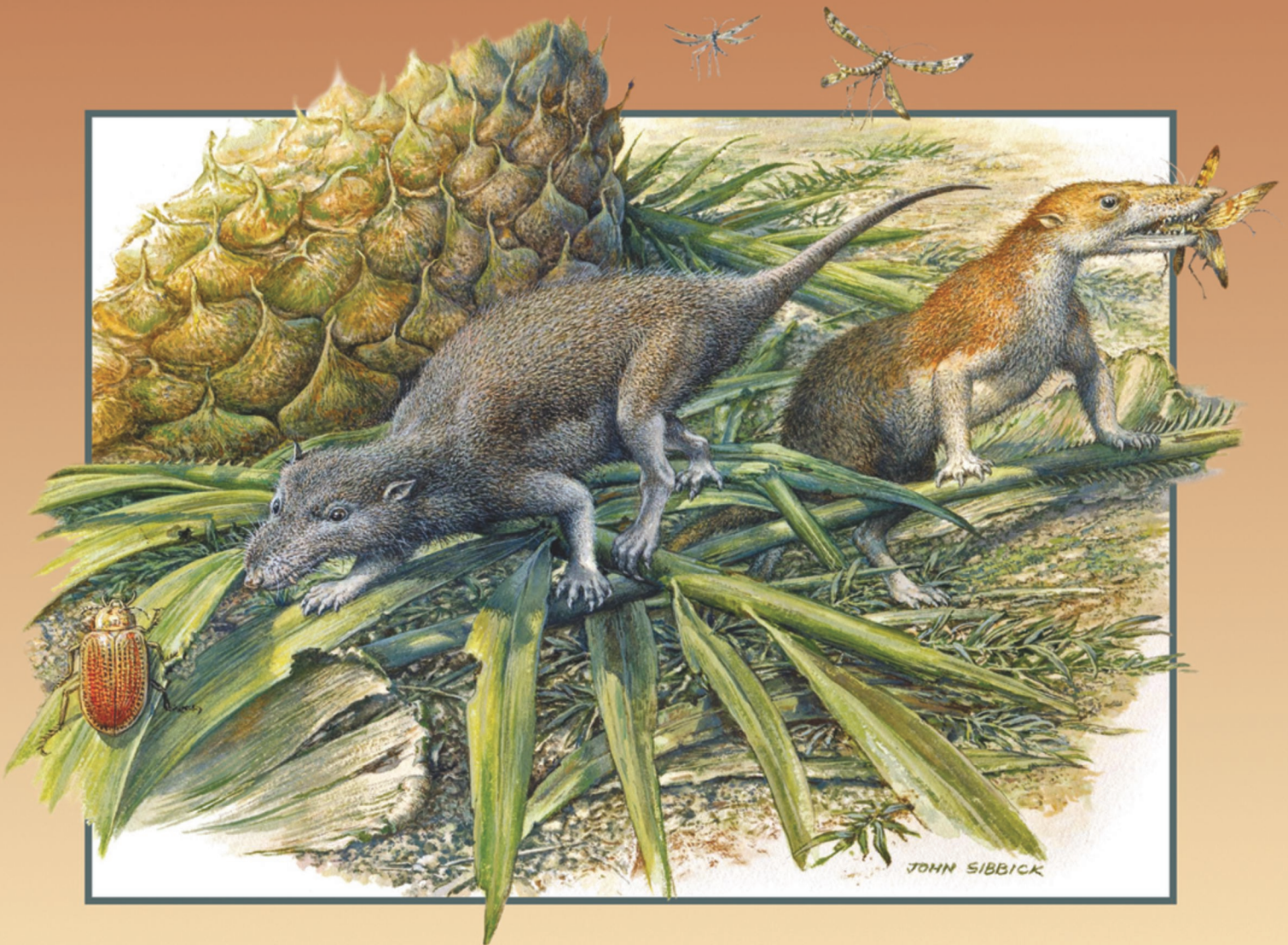


# Vertebrate Life

TENTH EDITION



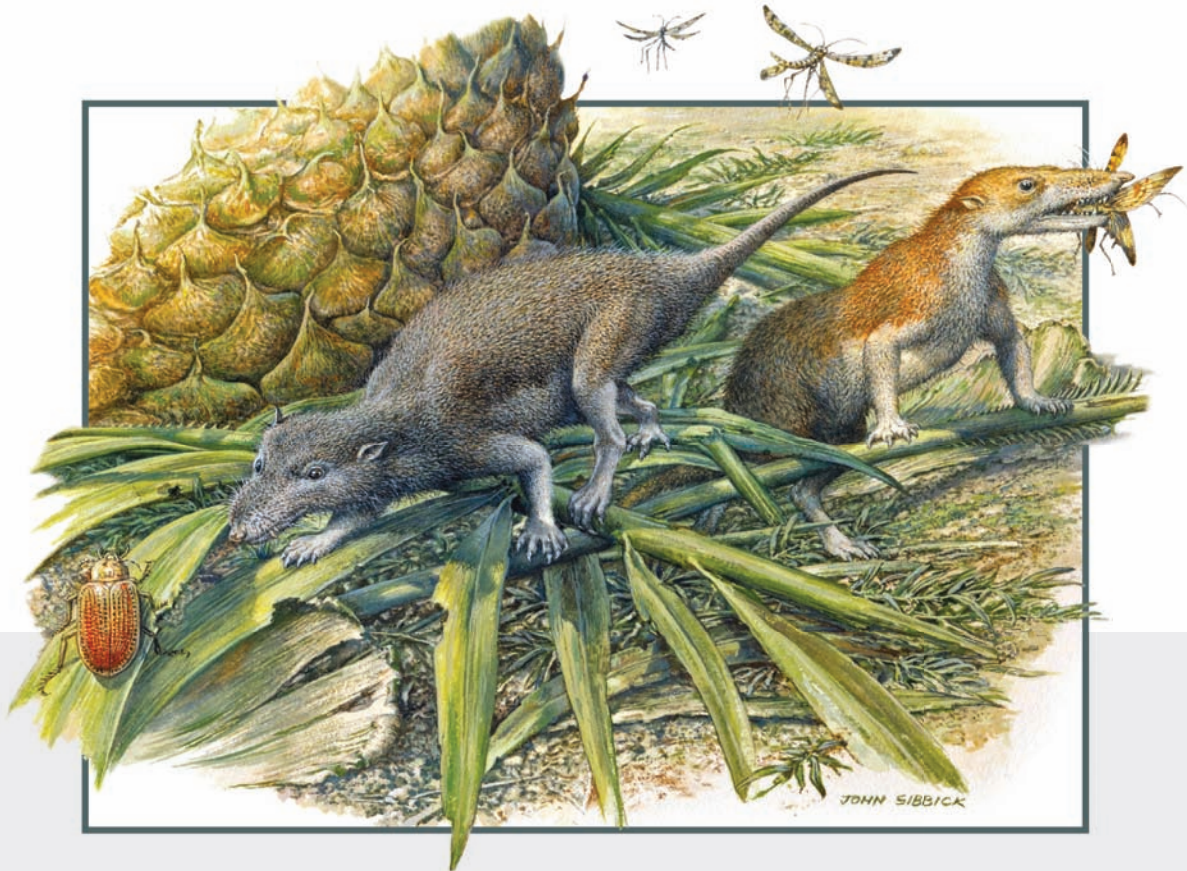
F. Harvey Pough • Christine M. Janis

**Vertebrate Life**  
TENTH EDITION



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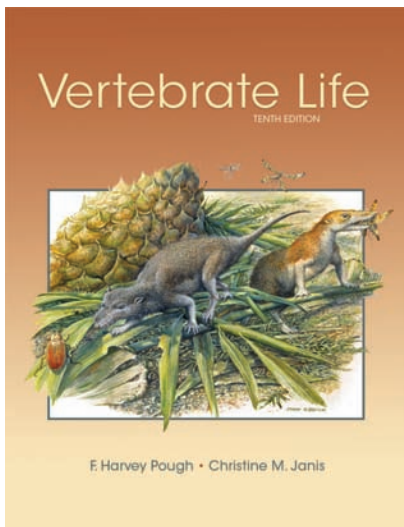
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**Chapter 26 "Primate Evolution and the Emergence of Humans"**

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Artist's reconstruction of two of the earliest mammals, *Morganucodon* (left) and *Kuehneotherium* (right). Both of these Early Jurassic mammals were insectivores about the size of extant shrews. (Painting by John Sibbick, 2013, © Pamela Gill.)

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# Preface

The sustainability of populations, and even the continued existence of some species of vertebrates, is becoming ever more problematic. In addition to overarching events that affect all living organisms—such as global climate change and acidification of the seas—each lineage of vertebrates faces threats that are intimately entwined with the biological characteristics of that lineage.

Thus, as we have prepared this tenth edition of *Vertebrate Life*, the study of vertebrates has taken on new urgency. Many areas of vertebrate biology have seen enormous advances since the previous edition:

- Phylogenies based on molecular data increasingly supplement, reinforce, and in some cases contradict phylogenies based on morphology. We have incorporated this information, including some of the cases where the two approaches have generated different hypotheses about the timing or sequence of evolutionary change.
- Our understanding of the genetic and epigenetic control of development has advanced greatly, and this evo-devo perspective provides a mechanistic understanding of evolutionary changes in phenotype.
- Newly discovered fossil sites, fossils, and even fossils that preserve soft tissue structures have added enormous detail (and often greater complexity) to our understanding of evolutionary lineages, especially early tetrapods, feathered nonavian dinosaurs, and humans.

This edition reflects these changes. What has not changed is the authors' view of vertebrates as complex and fascinating organisms that can best be understood by considering the interactions at multiple levels of biological organization that shape the biology of a species. This book presents vertebrates in a way that integrates all facets of their biology—from anatomy and physiology to ecology and behavior—in an evolutionary context

## Authors

Two changes of authorship have occurred in this edition. Ill health has compelled John B. Heiser to withdraw from active participation. John has been an author since the first edition of *Vertebrate Life*, enriching the chapters on fishes

with the experience gained from his field work in nearly every ocean. We thank him for his contributions, and wish him well.

We are delighted to have gained the assistance of Sergi López-Torres who authored the chapter on primates and the evolution of humans. Primate evolution is an extraordinarily active field of research, and Sergi brings the depth and breadth of knowledge of human evolution needed for an overview of this increasingly complex field.

## Organization

The scope of vertebrate biology and of evolutionary time is vast, and encapsulating this multiplicity of themes and mountains of data into a book or a semester course is a continuing challenge. Following suggestions from users, the text has been extensively reorganized to improve the flow of information. Topics have been split or merged, and some have been deleted, resulting in presentation of information in more manageable segments. Each chapter includes a list of sources that will be useful to students, and all of the sources that we consulted in preparing this edition, as well as many sources from earlier editions, are available on the book's web page, [oup.com/us/vertebratelife10e](http://oup.com/us/vertebratelife10e).

## Sources

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

- 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://mammal-diversity.org/>
- IUCN Red List of threatened species: <http://www.iucnredlist.org/>



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to accompany **Vertebrate Life**, TENTH EDITION

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# Evolution, Diversity, and Classification of Vertebrates



Luiti Konovall/23RF

Evolution is central to vertebrate biology because it provides a principle that organizes the diversity we see among living vertebrates and helps fit extinct forms into the context of extant (currently living) species. In this chapter, we present an overview of the environments, the participants, and the events that have shaped the evolution and biology of vertebrates.

## 1.1 The Vertebrate Story

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—the more than 67,000 extant species of vertebrates range in size from fishes weighing as little as 0.1 gram to whales weighing over 100,000 kilograms. 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 the fishes, migrating birds fly over the peaks of the Himalayas.

The behaviors of vertebrates are as diverse and complex as their body forms and habitats. Life as a vertebrate is energetically expensive, and vertebrates obtain the energy they need from the food they eat. Carnivores eat the flesh of other animals and show a wide range of methods of capturing prey. Some predators actively search the environment to find prey, whereas others remain stationary and wait for prey to come to them. Some carnivores pursue their prey at high speeds, and others pull prey into their mouths by suction. Many vertebrates swallow their prey intact, sometimes while it is alive and struggling, and other vertebrates have specific methods of dispatching prey. Venomous snakes, for example, inject complex mixtures of toxins, and cats (of all sizes, from house cats to tigers) kill their prey with a distinctive bite on the neck.

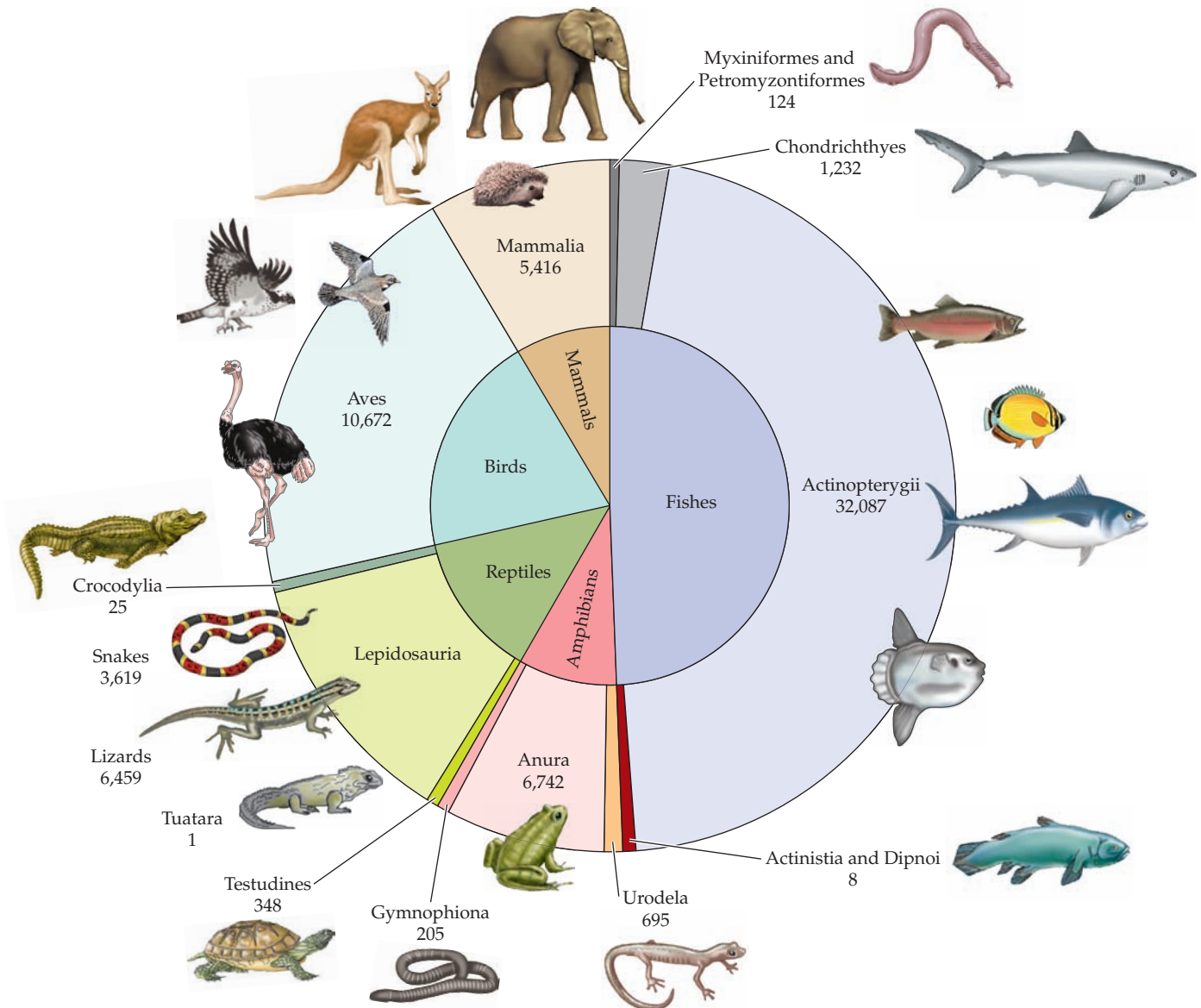
Herbivores eat plants. Plants cannot run away when an animal approaches, so they are easy to catch, but they are hard to chew and digest and frequently contain toxic compounds. Herbivorous vertebrates show an array

of specializations to deal with the difficulties of eating plants. Elaborately sculptured teeth tear apart tough leaves and expose the surfaces of cells, but the cell walls of plants contain cellulose, which no vertebrate can digest directly. Herbivorous vertebrates rely on microorganisms living in their digestive tracts to digest cellulose and to detoxify the chemical substances that plants use to protect themselves.

Reproduction is a critical factor in the evolutionary success of an organism, and vertebrates show an astonishing range of behaviors associated with mating and reproduction. In general, males court females and females care for the young, but many species of vertebrates reverse those roles. At the time of birth or hatching, some vertebrates are entirely self-sufficient and never see their parents, whereas other vertebrates (including humans) have extended periods of obligatory parental care. Extensive parental care is found in seemingly unlikely groups of vertebrates—fishes that incubate eggs in their mouths, frogs that carry their tadpoles to water and then return to feed them, and birds that feed their nestlings a fluid called crop milk that is similar in composition to mammalian milk.

The diversity of living vertebrates is enormous, but the extant species are only a small proportion of the species of vertebrates that have existed. For each extant species, there may be hundreds of extinct species, and some of these have no counterparts among extant forms. For example, the 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.

Where and when the vertebrates originated, how they evolved, what they do, and how they work provide endless intriguing details. In preparing to tell this story, we first introduce some basic information, including what the different kinds of vertebrates are called, how they are classified, and what the world was like as their story unfolded.



**Figure 1.1 Diversity of extant vertebrates.** Areas in the pie chart correspond to the approximate numbers of extant species in each group as of 2017; the 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 lineages of extant vertebrates are Actinopterygii (ray-finned fishes; lavender) and Sarcopterygii (all other colors except gray), each of which includes more than 33,000 extant species. In its formal sense, Sarcopterygii includes the lineages Actinistia, Dipnoi, Urodela, Anura, Gymnophiona, Testudines, Lepidosauria, Crocodylia, Aves, and Mammalia (i.e. the lobe-finned fishes and all their descendants, including all amphibians, reptiles, birds, and mammals.)

### Major extant groups of vertebrates

Two major groups of vertebrates are distinguished on the basis of an innovation in embryonic development: the appearance of three membranes formed by tissues that are generated by the embryo itself. The innermost of these membranes, the amnion, surrounds and cushions the embryo, and animals with this structure (the reptiles, birds, and mammals) are called **amniotes**. The split between non-amniotes and amniotes corresponds roughly to the division between aquatic and terrestrial vertebrates, although many amphibians and a few fishes lay non-amniotic eggs in nests on land. Among the amniotes, we can distinguish two major evolutionary lineages: the **sauropsids** (reptiles, including birds) and the **synapsids** (mammals). These lineages separated from each other in the mid-Carboniferous, before vertebrates had developed many of the characters we see in extant species. As a result, synapsids and sauropsids represent parallel but independent origins of basic characters such as lung ventilation, kidney function, insulation, and

temperature regulation. **Figure 1.1** shows the major groups of vertebrates and the approximate number of extant species in each. Next we briefly describe these vertebrate groups.

### Non-amniotes

The embryos of non-amniotes are enclosed and protected by membranes that are produced by the reproductive tract of the female. This is the condition seen among the

invertebrate relatives of vertebrates, and it is retained in the non-amniotes (fishes and amphibians).

**Hagfishes and lampreys: Myxiniiformes and Petro-myzontiformes** Lampreys and hagfishes are elongate, limbless, scaleless, and slimy and have no internal bony tissues. They are scavengers and parasites and are specialized for those roles. Hagfishes are marine, living on the seabed at depths of 100 meters or more. In contrast, many species of lampreys are migratory, living in oceans and spawning in rivers. Hagfishes and lampreys are unique among extant vertebrates because they lack jaws.

**Sharks, rays, and ratfishes: Chondrichthyes** The name Chondrichthyes (Greek *chondros*, “gristle”; *ichthys*, “fish”) refers to the cartilaginous skeletons of these fishes. Extant sharks and rays form a group called Neoselachii (Greek *neos*, “new”; *selachos*, “shark”), but the two kinds of fishes differ in body form and habits. Sharks have a reputation for ferocity that most species would have difficulty living up to. Some sharks are small (25 cm or less), while the largest species, the whale shark (*Rhincodon typus*), grows to 17 m long and is a filter feeder that subsists on plankton it strains from the water. Rays are mostly bottom feeders; they are dorsoventrally flattened and swim with undulations of their extremely broad pectoral fins.

The second group of chondrichthyans, the ratfishes or chimaeras, gets its name, Holocephali (Greek *holos*, “whole”; *kephale*, “head”), from the single gill cover that extends over all four gill openings. These are bizarre marine animals with long, slender tails. Some species have a bucktoothed face that looks rather like a rabbit. They forage on the seafloor and feed on hard-shelled prey, such as crustaceans and mollusks.

**Bony fishes: Osteichthyes** Osteichthyes (Greek *osteon*, “bone”) are so diverse that any attempt to characterize them briefly is doomed to failure. Two broad categories can be recognized: the ray-finned fishes (Actinopterygii; Greek *aktis*, “ray”; *pteron*, “wing” or “fin”) and the lobe-finned or fleshy-finned fishes (Sarcopterygii; Greek *sarco*, “flesh”).

Actinopterygians have radiated extensively in both fresh and salt water, and more than 32,000 species have been named. Nearly 400 species have been described annually since 1997, and several thousand additional species may await discovery. A single project, the Census of Marine Life, is describing 150–200 previously unknown species of ray-finned fishes annually.

Actinopterygians can be divided into three groups: (1) the monophyletic and derived Neopterygii (almost all extant ray-finned fishes); (2) the more basal Chondrostei (sturgeons and paddlefish); and (3) Cladistia (polypterids, including bichirs and reedfish, which are swamp- and river-dwellers from Africa). Sturgeons are large fishes with protrusible, toothless mouths that suck food items from the bottom. Sturgeon eggs are the source of caviar, and many species have been driven close to extinction by overharvesting of females for

their eggs. Paddlefishes (two species, one in the Mississippi system of North America and another nearly extinct species in China’s Yangtze River) have a paddlelike snout with organs that locate prey by sensing electrical fields.

Neopterygii, the modern radiation of ray-finned fishes, can be divided into two lineages. One these—Holostei, the gars and bowfins—is a relict of an earlier radiation. These fishes have cylindrical bodies, thick scales, and jaws armed with sharp teeth. They seize prey in their mouths with a sudden gulp, and lack the specializations of the jaw apparatus that allow the bony fishes to use more complex feeding modes. The second neopterygian lineage, Teleostei, includes 95% of actinopterygians, embracing every imaginable combination of body form, ecology, and behavior. Most of the fishes that people are familiar with are teleosts, from sport fishes like trout and swordfishes, to food staples like tuna and salmon, to the “goldfish” and exotic tropical fishes in home aquaria. Modifications of the body and jaw apparatus have allowed many teleost species to be highly specialized in their swimming and feeding habits.

The third neopterygian lineage, Teleostei, includes 95% of actinopterygians, embracing every imaginable combination of body form, ecology, and behavior. Most of the fishes that people are familiar with are teleosts—the trout, bass, and panfishes that anglers seek; the sole (a kind of flounder) and swordfishes featured by seafood restaurants; and the salmon and tuna that find their way into both sushi and cat food. Modifications of the body and jaw apparatus have allowed many teleosts to be highly specialized in their swimming and feeding habits.

In one sense, only eight species of sarcopterygian fishes survive: the six species of lungfishes (Dipnoi) found in South America, Africa, and Australia; and two species of coelacanth (Actinistia), one from deep waters off the east coast of Africa and a second species discovered near Indonesia. These are the extant fishes most closely related to terrestrial vertebrates, however, and from an evolutionary standpoint the diversity of sarcopterygians includes all of their terrestrial descendants—amphibians, turtles, lepidosaurs (the tuatara [*Sphenodon punctatus*], lizards, and snakes), crocodylians, birds, and mammals. From this perspective, bony fishes include two major evolutionary radiations—one in the water and the other on land—each containing more than 33,000 species.

**Salamanders, frogs, and caecilians: Urodela, Anura, and Gymnophiona** These three groups of vertebrates are popularly known as amphibians (Greek *amphis*, “double”; *bios*, “life”) in recognition of their complex life histories, which often include an aquatic larval form (the larva of a salamander or caecilian and the tadpole of a frog) and a terrestrial adult. All amphibians have bare skins (i.e., lacking scales, hair, or feathers) that are important in the exchange of water, ions, and gases with their environment. Salamanders are elongate animals, mostly terrestrial, and usually with four legs; anurans (frogs) are short-bodied, with large heads



and large hindlegs used for walking, jumping, and climbing; and caecilians are legless aquatic or burrowing animals.

### Amniotes

A novel set of membranes associated with the embryo appeared during the evolution of vertebrates. These are called **fetal membranes** because they are derived from the embryo itself rather than from the reproductive tract of the mother. As mentioned at the start of this chapter, the amnion is the innermost of these membranes, and vertebrates with an amnion are called amniotes. In general, amniotes are more terrestrial than non-amniotes; but there are also secondarily aquatic species of amniotes (such as sea turtles and whales) as well as many species of salamanders and frogs that spend their entire lives on land despite being non-amniotes. However, many features distinguish non-amniotes (fishes and amphibians) from amniotes (mammals and reptiles, including birds), and we will use the terms to identify which of the two groups is being discussed.

By the Permian, amniotes were well established on land. They ranged in size from lizardlike animals a few centimeters long through cat- and dog-size species to the cow-size pareiasaurs. Some were herbivores; others were carnivores. In terms of their physiology, we can infer that they retained ancestral characters. They had scale-covered skins without an insulating layer of hair or feathers, a simple kidney that could not produce highly concentrated urine, simple lungs, and a heart in which the ventricle was not divided by a septum. Early in their evolutionary history, terrestrial vertebrates split into two lineages—synapsids (today represented by mammals) and sauropsids (modern reptiles, including birds).

Terrestrial life requires lungs to extract oxygen from air, a heart that can separate oxygen-rich arterial blood from oxygen-poor venous blood, kidneys that can eliminate waste products while retaining water, and insulation and behaviors to keep body temperature stable as the external temperature changes. These features evolved in both lineages, but because synapsids and sauropsids evolved terrestrial specializations independently, their lungs, hearts, kidneys, and body coverings are different.

**Sauropsid amniotes** Extant sauropsids are the animals we call reptiles: turtles, the scaly reptiles (tuatara, lizards, and snakes), crocodylians, and birds. Extinct sauropsids include the forms that dominated the world during the Mesozoic—dinosaurs and pterosaurs (flying reptiles) on land and a variety of marine forms, including ichthyosaurs and plesiosaurs, in the oceans.

- **Turtles: Testudines** Turtles (Latin *testudo*, “turtle”) are probably the most immediately recognizable of all vertebrates. The shell that encloses a turtle has no exact duplicate among other vertebrates, and the 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) inside the ribs.

- **Tuatara, lizards, and snakes: Lepidosauria** These three kinds of vertebrates can be recognized by their scale-covered skin (Greek *lepisma*, “scale”; *sauros*, “lizard”) as well as by characters of the skull. The tuatara, a stocky-bodied animal found only on some offshore islands of New Zealand, is the sole living remnant of an evolutionary lineage of animals called Rhynchocephalia, which was more diverse in the Mesozoic. In contrast, lizards and snakes (which are highly specialized lizards) are now at the peak of their diversity.
- **Alligators and crocodiles: Crocodylia** These impressive animals, which draw their name from the ancient Latin word for them (*crocodilus*) are in the same evolutionary lineage (Archosauria) as dinosaurs and birds. The extant crocodylians are semiaquatic predators with long snouts armed with numerous teeth. They range in size from the saltwater crocodile (*Crocodylus porosus*), which can grow to 6 m, to dwarf crocodiles and caimans that are 1.5 m long. Crocodylian skin contains many bones (osteoderms; Greek *osteon*, “bone”; *derma*, “skin”) that lie beneath their scales and provide a kind of armor plating. Crocodylians are noted for the parental care they provide for their eggs and young.
- **Birds: Aves** Birds (Latin *avis*, “bird”) are a lineage of dinosaurs that evolved flight in the Mesozoic. Feathers are characteristic of extant birds, and feathered wings are the structures that power a bird’s flight. Discoveries of dinosaur fossils with feathers show that feathers evolved long before flight. This disparity between the time feathers are first seen and the time flight appeared 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 original feathers were almost certainly structures used in courtship displays, and their modifications as airfoils, for streamlining, and as insulation in birds were secondary events.

**Synapsid amniotes: Mammalia** The synapsid lineage contains the three kinds of extant mammals: the **monotremes** (prototheria; platypus and echidnas), **marsupials** (metatherians), and **placentals** (eutherians). Extinct synapsids include forms that diversified in the Paleozoic—pelycosaurs and therapsids—and the rodentlike multituberculates of the late Mesozoic.

The mammals (Latin *mamma*, “teat”) originated in the Late Triassic. Extant mammals include about 5,400 species in three groups: placentals (by far the largest group), marsupials, and monotremes. The name “placentals” is misleading, because both placentals and marsupials have a placenta, a structure that transfers nutrients from the mother to the embryo and removes the waste products of the embryo’s metabolism. Placentals have a long gestation period and have largely completed development at birth, whereas marsupials have a short gestation period and give

birth to very immature young that continue their development attached to a nipple, often within a pouch on the mother's abdomen. Marsupials dominate the mammalian fauna only in Australia, although some 100 species are found in South and Central America, and one species, the Virginia opossum (*Didelphis virginiana*), has migrated from South America to North America. Kangaroos, koalas, and wombats are familiar Australian marsupials. Finally, the monotremes—platypus and echidnas—are unusual mammals whose young hatch from eggs. All mammals, including monotremes, feed their young with milk.

## 1.2 Classification of Vertebrates

The diversity of vertebrates (more than 67,000 extant species and perhaps 100 times that number of extinct species) makes organizing them into a coherent system of classification extraordinarily difficult. Yet classification has long been at the heart of evolutionary biology. Initially, classification of species was seen as a way of managing the diversity of organisms, much as an office filing system manages the paperwork of the office. Each species could be placed in a pigeonhole marked with its name; 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 has made that kind of classification inadequate. Now biologists must express evolutionary relationships among species by incorporating evolutionary information in the system of classification. Ideally, a classification system should not only attach a label to each species but also encode the evolutionary relationships between that species and other species. Modern techniques of **systematics** (the evolutionary classification of organisms) have become methods for generating testable hypotheses about evolution.

### Binominal nomenclature

Our system of naming species is pre-Darwinian. It traces back to methods established by the naturalists of the seventeenth and eighteenth centuries, especially those of Carl von Linné, the Swedish naturalist better known by his Latin pen name, Carolus Linnaeus. The Linnaean system identifies a species using two names—a genus name and a species name; hence, this convention is called **binomial nomenclature**. Species are arranged in hierarchical categories (family, order, and so on). These categories are called **taxa** (singular *taxon*), and the discipline of naming organisms is called **taxonomy** (Greek *taxo*, “to arrange”; *nomos*, “order”).

The scientific naming of species became standardized when Linnaeus's monumental work *Systema Naturae* (*The System of Nature*) was published in sections between 1735 and 1758. Linnaeus attempted to give an identifying 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 suçarana. But biologists of all nationalities recognize the name *Felis concolor* as referring to this specific kind of cat.

### Phylogenetic systematics

All methods of classifying organisms, even Linnaean systems, 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, but only a few kinds of vertebrates 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 developed in the mid-20th century by Willi Hennig, who introduced a method of determining evolutionary relationships called **phylogenetic systematics** (Greek *phylon*, “tribe”; *genesis*, “origin”).

The groups of organisms recognized by phylogenetic systematics are called natural groups, and the members of these groups are linked by a nested series of characters that trace the evolutionary history of the lineage. Hennig's contribution was to insist that these groups can be identified only on the basis of homologous **derived characters**—that is, characters that have the same evolutionary origin (i.e., are homologous) and that differ from the ancestral condition (are derived). A derived character is called an **apomorphy** (Greek *apo*, “away from” and *morphe*, “form,” which is interpreted as “away from the ancestral condition”).

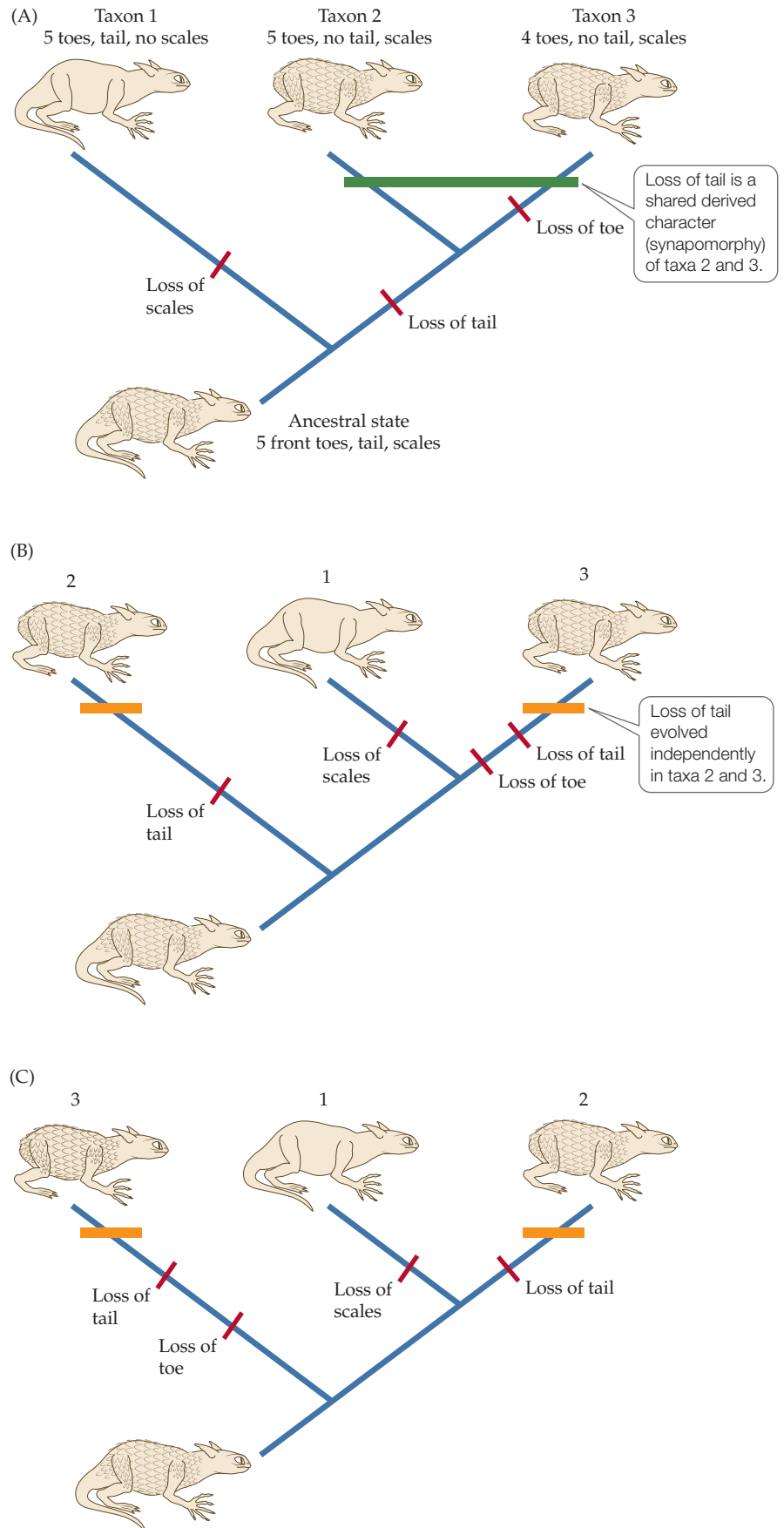
For example, the feet of terrestrial vertebrates have distinctive bones—the carpals, tarsals, and digits. This arrangement of foot bones is different from the ancestral pattern seen in lobe-finned fishes, and all lineages of terrestrial vertebrates either have that derived pattern of foot bones or had it at some stage in their evolution. Many groups of terrestrial vertebrates—horses, for example—have subsequently modified the foot, and some, such as snakes, have lost the limbs entirely. The significant point is that those evolutionary lineages include ancestral species that had the derived terrestrial pattern. Thus, the terrestrial pattern of foot bones is a **shared derived character** of terrestrial vertebrates. Shared derived characters

are called **synapomorphies** (Greek *syn*, “together,” so synapomorphy can be interpreted as “together away from the ancestral condition”).

Of course, organisms also share ancestral characters—that is, 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 lobe-finned fishes. Hennig called such shared ancestral characters **symplelesiomorphies** (*sym*, like *syn*, is a Greek root that means “together”). A character can be either plesiomorphic or apomorphic, depending on the level at which the distinction is applied. A vertebral column is a symplelesiomorphy of vertebrates, so it provides no information about evolutionary relationships of vertebrates to one another, but it is an apomorphy when vertebrates are compared with nonvertebrate chordates.

### Applying phylogenetic criteria

The conceptual basis of phylogenetic systematics is straightforward, although applying the criteria to real organisms can become complicated. To illustrate phylogenetic classification, consider the examples presented in **Figure 1.2**. Each of the three hypothetical **phylogenies**—diagrams showing sequences of branching during evolution—illustrates a possible evolutionary relationship for the three



**Figure 1.2** Phylogenies showing the possible evolutionary relationships of hypothetical taxa 1, 2, and 3. In this hypothetical example, the red bars identify changes (evolution) from the ancestral (plesiomorphic) character states of tail, skin, and number of toes on the front feet to three different derived (apomorphic) conditions. The green bar shows a shared derived character (a synapomorphy) of the lineage that includes taxa 2 and 3. Orange bars represent two separate origins of the same derived character state (loss of tail) that in these cases must be assumed to have occurred independently, since the apomorphy is not found in the most recent common ancestor of taxa 2 and 3. Phylogeny (A) requires a total of three changes from the ancestral condition to explain the distribution of characters in the extant taxa, whereas phylogenies (B) and (C) both require four changes. Because phylogeny (A) is more parsimonious (i.e., requires the smallest number of changes), it is considered to be the most likely evolutionary sequence.

taxa identified as 1, 2, and 3. To make the example more concrete, we 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. For this example, in the ancestral character state there are five toes on the front feet, and in the derived state there are four toes. We'll say that the ancestral state is scaly skin, and the derived state is a lack of scales. As for the tail, it is present in the ancestral state and absent in the derived state.

How can we use the information in Figure 1.2 to decipher the evolutionary relationships of the three groups of animals? Notice that the derived number of four toes occurs only in taxon 3, and the derived tail condition (absent) is found in taxa 2 and 3. The **most parsimonious** phylogeny (i.e., the branching sequence requiring the fewest number of changes) is represented by Figure 1.2A. 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 including taxa 2 and 3, the tail is lost; and in the evolution of taxon 3, a toe is lost.

The other two phylogenies shown in Figure 1.2 are possible, but they require tail loss to occur independently in taxa 2 and 3. Any change in a structure is an unlikely event, so the most plausible phylogeny is the one requiring the fewest changes. The second and third phylogenies each require four evolutionary changes, so they are less parsimonious than the first phylogeny, which requires only three changes.

A phylogeny (also called a phylogenetic tree or simply a tree) is a hypothesis about the evolutionary relationships of the groups included. Like any scientific hypothesis, it can be tested when new data become available. If it fails that test, it is falsified; that is, it is rejected, and a different hypothesis (a different branching sequence) is proposed. The process of testing 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.

So far we have avoided 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? For that, we need additional information. Increasing the number of characters we are considering can help, but the preferred method is to compare the characters we are interested in with those of an **outgroup**, a reference group that, although related to the **ingroup**—the organisms we are studying—is less closely related to any member of the ingroup than those members are to each other. For example, lobe-finned fishes are an appropriate outgroup for terrestrial vertebrates.

### ***Morphology-based and molecular-based phylogenies***

Initially, anatomical traits were the only characters that could be used to determine the relationships among organisms, but advances in molecular biology and genetics in the latter

20th century made it possible to include proteins and DNA in phylogenies. The American anthropologist Vincent Sarich pioneered the use of molecular characters in the 1960s, using immunological comparison of blood serum 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. At the same time, computer algorithms were devised that could sort and arrange large numbers of characters in a phylogeny. Any set of characters can produce multiple possible phylogenies, and these algorithms use various methods (e.g., parsimony, maximum likelihood, Bayesian inference) to identify the most plausible sequences of changes.

The late 20th century was also when personal computers came into general use, so that anybody could use these algorithms. Additionally, with the establishment of public-access repositories such as GenBank in 1982 and MorphoBank in 2005, vast quantities of genetic and morphological data became available on the internet. As a result, phylogenetic systematics has moved from human-based analyses of small numbers of characters to computer-based analyses of huge data sets.

Molecular characters rapidly came to be regarded as superior to morphological characters for creating 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, molecular phylogenies have lost some of their luster. The assumptions that all types of molecular data are equal in creating a phylogeny and that more data produce better results are being questioned. Some characters are appropriate for looking at short-term changes and others at long-term processes; mixing the two can produce erroneous results.

Differences of that sort are 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 characters are black boxes. Furthermore, fossils seldom yield molecules, 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.

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. In

contrast, the age of a fossil can almost always be determined—provided that one has a fossil. The difficulty with fossils is the incompleteness of the fossil record. There are gaps, sometimes millions of years long, in the records of many taxa. For example, we have fossil lampreys from the Late Devonian (~360 million years ago, abbreviated Ma<sup>1</sup>), the Late Carboniferous (~300 Ma), and the Early Cretaceous (~145 Ma), but nothing between those dates.

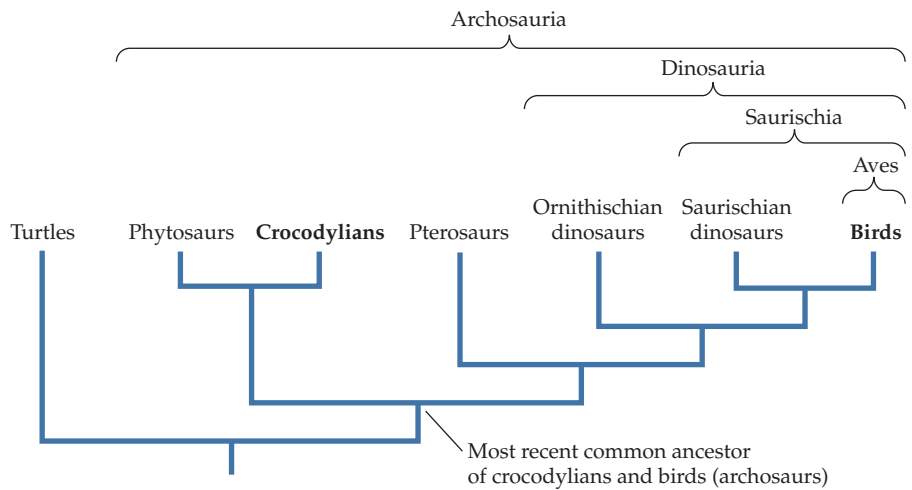
Considering the difficulties with both molecular and morphological phylogenies, it's remarkable that they mostly agree about branching patterns. Disagreements usually center on dates of divergence. For example, molecular phylogenies indicate that the extant lineages of amphibians diverged in the Late Carboniferous (~315–300 Ma), whereas fossil data indicate divergence in the Late Permian (~260–255 Ma). However, molecular and morphological methods can 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).

The best information 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.

### Using phylogenetic trees

Phylogenetic systematics is based on the assumption that organisms in a lineage share a common heritage, which 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, the phylogenetic relationship of crocodylians, dinosaurs, and birds is shown in **Figure 1.3**.

We know that both crocodylians and birds display extensive parental care of their eggs and young. Some fossilized dinosaur nests contain remains of partly grown baby dinosaurs, suggesting that at least some dinosaurs cared for their young. Is that a plausible inference? Obviously, there is no direct way to determine what sort of parental care dinosaurs provided to their eggs and young. The intermediate lineages in the phylogenetic tree (pterosaurs and



**Figure 1.3 Using a phylogenetic tree to make inferences about behavior.** The tree shows the relationships of the Archosauria, the evolutionary lineage that includes today's crocodylians and birds. (Phytosaurs were crocodile-like animals that disappeared at the end of the Triassic; pterosaurs were flying reptiles of the Jurassic and Cretaceous.) Both extant archosaur groups (i.e., crocodylians and birds) display extensive parental care of eggs and young, but turtles do not. The most parsimonious explanation of this situation assumes that parental care evolved in the archosaur lineage after the separation from turtles, but before the separation of phytosaurs + crocodylians from pterosaurs + dinosaurs.

dinosaurs) are extinct, so we cannot observe their reproductive behavior. However, the phylogenetic tree in Figure 1.3 provides an indirect way to approach the question by examining the lineage that includes the closest living relatives of dinosaurs, crocodylians, and birds.

Crocodylians are the basal taxon in this tree (the lineage closest to the ancestral form), and birds are the most derived (farthest from the ancestral form). Together, crocodylians and birds form what is called an **extant phylogenetic bracket**. 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 fishes, amphibians, or turtles. The most parsimonious explanation of the occurrence of parental care in both crocodylians and birds is that it evolved in that lineage after the lineage separated from turtles and before crocodylians separated from dinosaurs + birds. We cannot prove that parental care did not evolve independently in crocodylians and in birds, but a single change to parental care is more likely than two separate changes. Thus, the most parsimonious hypothesis is that parental care is a derived character of the evolutionary lineage containing crocodylians + pterosaurs + dinosaurs + birds. That means we are probably correct when we interpret fossil evidence as showing that dinosaurs did indeed exhibit parental care.

Figure 1.3 also shows how phylogenetics has made talking about restricted groups of animals more complicated than it used to be. Suppose you wanted to refer to just the two lineages of animals that are popularly known as

<sup>1</sup>Ma is the abbreviation for mega-annums, "million years." It is used to mean both "million years" and, when referring to a specific date range, "million years ago." Analogously, ka = kilo-annums (thousand years, thousand years ago).

dinosaurs—ornithischians and saurischians. What could you call them? If you call them “dinosaurs,” you’re not being phylogenetically correct, because the Dinosauria lineage includes birds. So if you say “dinosaurs,” you are including ornithischians + saurischians + birds, even though any 7-year-old would understand that you mean to restrict the conversation to the extinct Mesozoic animals.

In fact, there is no technically correct name in phylogenetic taxonomy for just those animals popularly known as dinosaurs. That’s because phylogenetics recognizes only monophyletic lineages (see Section 1.3), and a monophyletic lineage includes an ancestral form and all of its descendants. As you can see in Figure 1.3, the most recent common ancestor of ornithischians + saurischians + birds lies at the intersection of the lineage of ornithischians with saurischians + birds, so Dinosauria is a monophyletic lineage. If birds are omitted, however, the lineage no longer includes all the descendants of the common ancestor. The lineage ornithischians + saurischians *minus* birds does not fit the definition of a monophyletic lineage and would be called **paraphyletic** (Greek *para*, “beside” or “near,” meaning a taxon that includes the common ancestor and some, but not all, of its descendants).

Biologists who are interested in how organisms function often talk about paraphyletic groups. After all, dinosaurs (in the popular sense of the word) differ from birds in many ways. The only technically correct way of referring to the animals popularly known as dinosaurs is to call them “nonavian 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 will use quotation marks (e.g., “ostracoderms”) to indicate that the group is paraphyletic.

Another important term is **sister group**, which refers to the monophyletic lineage most closely related to the monophyletic lineage being discussed. In Figure 1.3, for example, the lineage that includes crocodylians + phytosaurs is the sister group of the lineage that includes pterosaurs + ornithischians + saurischians + birds. Similarly, pterosaurs are the sister group of ornithischians + saurischians + birds, ornithischians are the sister group of saurischians + birds, and saurischians are the sister group of birds.

### 1.3 Crown and Stem Groups

Evolutionary lineages must have a single evolutionary origin; that is, they must be **monophyletic** (Greek *mono*, “one” or “single”), and they must also include all the descendants of the ancestor. The phylogenetic tree in **Figure 1.4** shows the hypothesis of the evolutionary relationships of the major extant groups of vertebrates that we will follow throughout this book. A series of dichotomous branches extends from the origin of vertebrates to the groups of extant

vertebrates. Phylogenetic terminology assigns names to the lineages originating at each branch point.

This method of tracing ancestor–descendant relationships allows us to decipher evolutionary pathways that extend from fossils to extant groups, but a difficulty arises when we try to find names for groups that include fossils. The derived characters that define the extant groups of vertebrates did not all appear at the same time. On the contrary, derived characters appear in a stepwise fashion. The 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 are ancestral 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 have. What can we call the parts of a lineage that contain these fossils? They are not the same as the extant group because they lack some of the derived characters that define those groups, but the fossils in a lineage are more closely related to the animals in the extant group than they are to animals in other lineages. The solution to this problem lies in naming two types of groups: **crown groups** and **stem groups**. Crown groups have the character states of extant species. That is, members of the crown group have all the derived characters, but they don’t have to be extant. An extinct species with all of the derived characters is included in a crown group. Stem groups are the extinct forms in the lineage that lack some of the derived characters. Basically, stem groups contain fossils with some derived characters, and crown groups contain extant species plus fossils that have all of the derived characters of the extant species. Stem groups are paraphyletic because they do not contain all of the descendants of the ancestor of the stem group.

### 1.4 Genetic Mechanisms of Evolutionary 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. Selective breeding of plants and domestic animals was practiced in the 19th century, but the phenotype of the offspring was thought to be a blend of the phenotypes of the parents. Gregor Mendel did not publish evidence of particulate inheritance (i.e., separate inheritance of specific genetic traits, such as yellow versus green and smooth versus wrinkled peas) until 1866. The rediscovery and extension of Mendel’s work in the early 20th century firmly established genes as the basis of heritable traits, and the 1930s and 1940s saw