

## Taxonomy and Phylogeny of Animals



Molluscan shells from the collection of Jean Baptiste de Lamarck (1744 to 1829).

### Order in Diversity

Evolution has produced a great diversity of species in the animal kingdom. Zoologists have named more than 1.5 million species of animals, and thousands more are described each year. Some zoologists estimate that species named so far constitute less than 20% of all living animals and less than 1% of all those that have existed.

Despite its magnitude, the diversity of animals is not without limits. Many conceivable forms do not exist in nature, as our myths of minotaurs and winged horses show. Animal diversity is not random but has definite order. Characteristic features of humans and cattle never occur together in a single organism as they do in the mythical minotaurs; nor do characteristic wings of birds and bodies of horses occur together naturally as they do in the mythical horse, Pegasus. Humans, cattle, birds, and horses are distinct groups of animals, yet they do share some important features,

including vertebrae and homeothermy, that separate them from even more dissimilar forms such as insects and flatworms.

All human cultures classify familiar animals according to patterns in animal diversity. These classifications have many purposes. Some societies classify animals according to their usefulness or destructiveness to human endeavors; others may group animals according to their roles in mythology. Biologists organize animal diversity in a nested hierarchy of groups within groups according to evolutionary relationships as revealed by ordered patterns in their sharing of homologous features. This ordering is called a “natural system” because it reflects relationships that exist among animals in nature, outside the context of human activity. A systematic zoologist has three major goals: to discover all species of animals, to reconstruct their evolutionary relationships, and to communicate those relationships by constructing an informative taxonomic system.

**D**arwin's theory of common descent (Chapters 1 and 6) is the underlying principle that guides our search for order in the diversity of animal life. Our science of **taxonomy** ("arrangement law") produces a formal system for naming and grouping species to communicate this order. Animals that have very recent common ancestry share many features in common and are grouped most closely in our taxonomic system.

Taxonomy is part of the broader science of **systematics**, or comparative biology, in which studies of variation among animal populations are used to reveal their evolutionary relationships. The study of taxonomy predates evolutionary biology, however, and many taxonomic practices are remnants of a pre-evolutionary world view. Adjusting our taxonomic system to accommodate evolution has produced many problems and controversies. Taxonomy has reached an unusually active and controversial point in its development in which several alternative taxonomic systems are competing for use. To explain this controversy, one must first review the history of animal taxonomy.

## LINNAEUS AND TAXONOMY

The Greek philosopher and biologist Aristotle (384 to 332 BC) was the first to classify organisms according to their structural similarities. A unified taxonomic system for all animals and plants appeared for the first time more than two millennia later, in the work of Carolus Linnaeus (Figure 10.1).

Linnaeus was a Swedish botanist at the University of Uppsala. He had a great talent for collecting and classifying organisms, especially flowers. Linnaeus produced an extensive system of classification for both plants and animals. This scheme, published in his great work, *Systema Naturae*, used morphology (the comparative study of organismal form) for arranging specimens in collections. He divided the animal kingdom into species and gave each one a distinctive name. He grouped species into genera, genera into orders, and orders into



**Figure 10.1** Carolus Linnaeus (1707 to 1778). This portrait was made of Linnaeus at age 68, three years before his death.

"classes" (we use quotation marks or a capital letter to distinguish "class" as a formal taxonomic rank from its broader meaning as a group of organisms that share a common essential property). Because his knowledge of animals was limited, his lower categories, such as genera, often were very broad and included animals that are only distantly related. Much of his classification is now drastically altered, but the basic principle of his scheme is still in use.

Linnaeus's scheme of arranging organisms into an ascending series of groups of ever-increasing inclusiveness is a **hierarchical system** of classification. Major groupings of organisms called **taxa** (sing., **taxon**) took one of several standard **taxonomic ranks** to indicate the general degree of inclusiveness of the group. The hierarchy of taxonomic ranks has been expanded considerably since Linnaeus's time (Table 10.1). It now includes seven mandatory ranks for the animal kingdom, in descending series: kingdom, phylum, "class," order, family, genus, and species. All organisms must be placed into at least seven taxa, one at each of the mandatory ranks. Taxonomists have the option of subdividing these seven ranks further to recognize more than seven taxa (superfamily, subfamily, superorder, suborder, etc.) for any particular group of organisms. In all, more than 30 taxonomic ranks are recognized. For very large and complex groups, such as fishes and insects, these additional ranks are needed to express different degrees of evolutionary divergence.

A taxonomist's choice of a group of species for recognition as a formally ranked taxon always has some arbitrariness. For example, should the taxonomic family Hominidae be restricted to genus *Homo* (humans) and all fossil genera that are closer to *Homo* than to genus *Pan* (bonobos and chimpanzees), or should it comprise the more inclusive grouping of genera *Homo*, *Pan*, *Gorilla*, and *Pongo* (orangutans) plus fossils closer to these genera than to gibbons? Within the last few decades, anthropologists have shifted Hominidae from the former usage primarily to the latter one (p. 207). Does the confusing arbitrariness of ranking taxa outweigh the usefulness of ranks for reminding us which taxa are more inclusive than others? Could we devise a rank-free taxonomy that encodes the positions of species on an evolutionary tree of common descent? As we write, taxonomists are actively trying to answer these questions. Meanwhile, both ranked and rank-free taxonomies of animals are in use. Rank-free taxonomies often use indentations to specify levels of inclusiveness of each taxon as illustrated by the rank-free taxonomic ordering of bilaterally symmetrical animals shown in the last section of this chapter.

## Systematization versus Classification

Introduction of evolutionary theory into animal taxonomy has changed the taxonomist's role from one of classification to one of **systematization**. Classification denotes the construction of classes, groupings of organisms that possess a common feature, called an essence, used to define the class. Organisms that possess the essential feature are members of the class by definition, and those that lack it are excluded. Because evolving species are subject always to change, the static nature of classes makes them a poor basis for a taxonomy of living systems. The activity of a taxonomist whose groupings of species represent units of common evolutionary descent is systematization, not classification. Species placed into a taxonomic group include the most recent common ancestor of the group and its descendants and

TABLE 10.1

## Examples of Taxonomic Categories to Which Representative Animals Belong

Linnaean Rank	Human	Gorilla	Southern Leopard Frog	Fork-Tailed Bush Katydid
<b>Kingdom</b>	Animalia	Animalia	Animalia	Animalia
<b>Phylum</b>	Chordata	Chordata	Chordata	Arthropoda
<b>Subphylum</b>	Vertebrata	Vertebrata	Vertebrata	Uniramia
<b>Class</b>	Mammalia	Mammalia	Amphibia	Insecta
<b>Subclass</b>	Eutheria	Eutheria	—	Pterygota
<b>Order</b>	Primates	Primates	Anura	Orthoptera
<b>Suborder</b>	Anthropoidea	Anthropoidea	—	Ensifera
<b>Family</b>	Hominidae	Hominidae	Ranidae	Tettigoniidae
<b>Subfamily</b>	—	—	Raninae	Phaneropterinae
<b>Genus</b>	<i>Homo</i>	<i>Gorilla</i>	<i>Lithobates</i>	<i>Scudderia</i>
<b>Species</b>	<i>Homo sapiens</i>	<i>Gorilla gorilla</i>	<i>Lithobates sphenoccephala</i>	<i>Scudderia furcata</i>
<b>Subspecies</b>	—	—	—	<i>Scudderia furcata furcata</i>

The hierarchical taxonomy of four species (human, gorilla, Southern leopard frog, and fork-tailed bush katydid). Higher taxa generally are more inclusive than lower-level taxa, although taxa at two different levels may be equivalent in content. Closely related species are united at a lower point in the hierarchy than are distantly related species. For example, humans and gorillas are united at the level of the family (Hominidae) and above; they are united with the Southern leopard frog at the subphylum level (Vertebrata) and with the katydid at the kingdom level (Animalia).

thus form a branch of the phylogenetic tree of life. The species of a group thus formed constitute a system of common descent, not a class defined by possession of an essential characteristic. It remains common, although technically erroneous, for systematists to call their taxonomic systems classifications.

Because organismal characteristics are inherited from ancestral to descendant species, character variation is used to diagnose systems of common descent, but there is no requirement that an essential character be maintained throughout the system for its recognition as a taxon. The role of morphological or other features in systematization is therefore fundamentally different from the role of such characters in classification. In classification, a taxonomist asks whether a species being classified contains the defining feature(s) of a particular taxonomic class; in systematization, a taxonomist asks whether the characteristics of a species confirm or reject the hypothesis that it descends from the most recent common ancestor of a particular taxon. For example, tetrapod vertebrates descend from a common ancestor that had four limbs, a condition retained in most but not all of its descendants. Although they lack limbs, caecilians (p. 542) and snakes (p. 567) are tetrapods because they are parts of this system of common descent; other morphological and molecular characters group them respectively with living amphibians and lizards.

Although the hierarchical structure of Linnaean classification is retained in current taxonomy, the taxa are groupings of species related by evolutionary descent with modification, as diagnosed by sharing of homologous characters. As one moves up the taxonomic hierarchy from a species toward more inclusive groups, each taxon represents the descendants of an earlier ancestor, a larger branch of the tree of life.

## Binomial Species Nomenclature

Linnaeus's system for naming species is called **binomial nomenclature**. Each species has a latinized name composed of two words (hence binomial) printed in italics (or underlined if handwritten or typed). The first word names the **genus**, which is capitalized; the second word is

the **species epithet**, which identifies the species within the genus and is written in lowercase (Table 10.1). The great communicative value of Latin species names is that they are used consistently by scientists in all countries and languages; they are much more precise than are “common names,” which vary culturally and geographically.

The genus name is always a noun, and the species epithet is usually an adjective that must agree in gender with the genus. For instance, the scientific name of the common robin is *Turdus migratorius* (*L. turdus*, thrush; *migratorius*, of migratory habit). The species epithet never stands alone; the complete binomial must be used to name a species. Names of genera must refer only to single groups of organisms; the same name cannot be given to two different genera of animals. The same species epithet may be used in different genera, however, to denote different species. For example, the scientific name of the white-breasted nuthatch is *Sitta carolinensis*. The species epithet “*carolinensis*” is used in other genera for the species *Poecile carolinensis* (Carolina chickadee) and *Anolis carolinensis* (green anole, a lizard) to mean “of Carolina.” All ranks above the species are designated using uninomial nouns, written with a capital initial letter.

Sometimes a species is divided into subspecies using a trinomial nomenclature (see katydid example, Table 10.1, and salamander example, Figure 10.2); such species are called **polytypic**. The generic, specific, and subspecific names are printed in italics (underlined if handwritten or typed). A polytypic species contains one subspecies whose subspecific name is a repetition of the species epithet and one or more additional subspecies whose names differ. Thus, to distinguish geographic variants of *Ensatina eschscholtzii*, one subspecies is named *Ensatina eschscholtzii eschscholtzii*, and different subspecies names are used for each of six other subspecies (Figure 10.2). Both the genus name and the species epithet may be abbreviated as shown in Figure 10.2. Formal recognition of subspecies has lost popularity among taxonomists because subspecies are often based on minor



differences in appearance that do not necessarily diagnose evolutionarily distinct units. When further study reveals that named subspecies are distinct evolutionary lineages, the subspecies are then often recognized as full species; indeed, many authors argue that the subspecies of *Ensatina eschscholtzii* are in fact separate species. Subspecies designations, therefore, should be viewed as tentative statements indicating that the species status of the populations needs further investigation.

## SPECIES

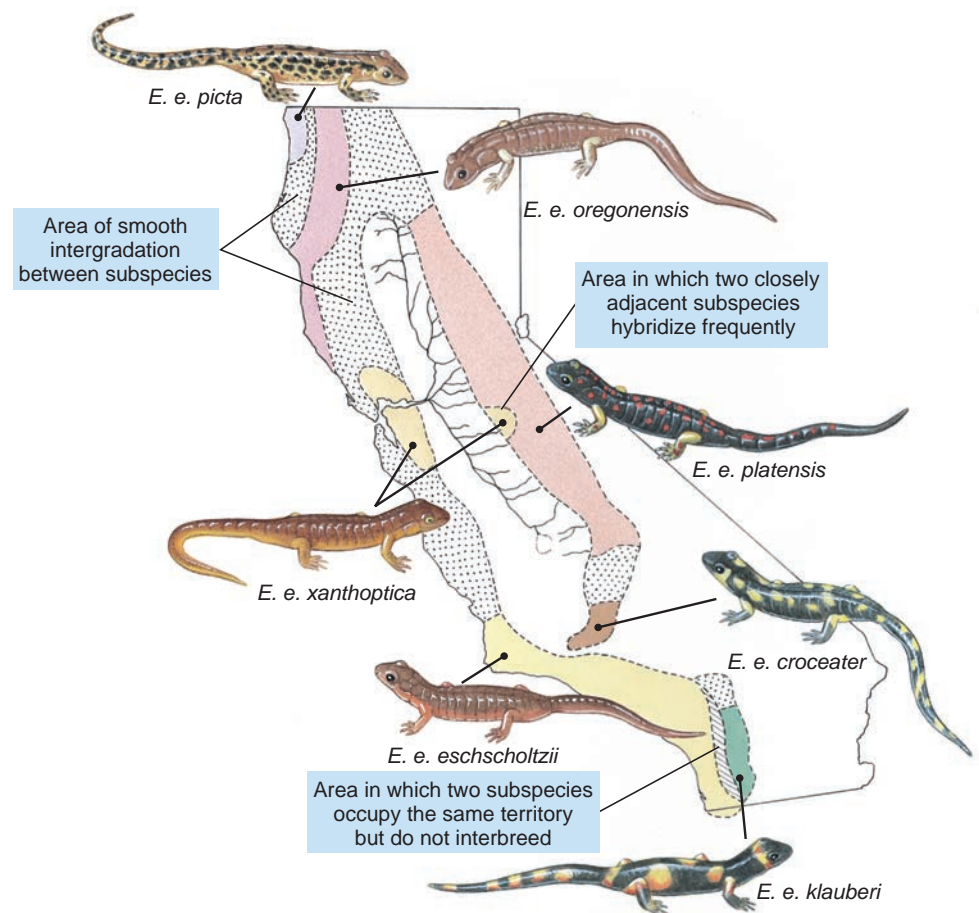
While discussing Darwin's book, *On the Origin of Species*, in 1859, Thomas Henry Huxley asked, "In the first place, what is a species? The question is a simple one, but the right answer to it is hard to find, even if we appeal to those who should know most about it." We have used the term "species" so far as if it had a simple and unambiguous meaning. Actually, Huxley's commentary is as valid today as it was in 1859. Our concepts of species have become more sophisticated, but the diversity of different concepts and disagreements surrounding their use are as evident now as in Darwin's time.

Despite widespread disagreement about the nature of species, biologists have repeatedly used certain criteria for identifying species. First, **common descent** is central to nearly all modern concepts of species. Members of a species must trace their ancestry to a common ancestral population, although not necessarily to a single pair of parents. Species are thus historical entities. A second criterion is that species must be the **smallest distinct groupings** of organisms sharing patterns of ancestry and descent; otherwise, it would be difficult to separate species from higher taxa, whose members also share common descent. Morphological characters traditionally have been important in identifying such groupings, but chromosomal and molecular characters now are used extensively for this purpose. A third important criterion is that of **reproductive community**. Members of a species must form a reproductive community that excludes members of other species. For sexually reproducing populations, interbreeding is critical for maintaining a reproductive community. For organisms whose reproduction is strictly asexual, reproductive community entails occupation of a particular ecological habitat in a particular place so that a reproducing population responds as a unit to evolutionary forces such as natural selection and genetic drift (p. 123).

Any species has a distribution through space, its **geographic range**, and a distribution through time, its **evolutionary duration**. Species differ greatly from each other in both dimensions. Species having very large geographic ranges or worldwide distributions are

called **cosmopolitan**, whereas those with very restricted geographic distributions are called **endemic**. If a species were restricted to a single point in space and time, we would have little difficulty recognizing it, and nearly every species concept would lead us to the same decision. We have little difficulty distinguishing from each other the different species of animals that we can find living in our local park or woods. However, when we compare a local population to similar but not identical populations located hundreds of miles away, it may be hard to determine whether these populations represent a single species or multiple species (Figure 10.2).

Throughout the evolutionary duration of a species, its geographic range can change many times. A geographic range may be either continuous or disjunct, the latter having breaks within it where the species is absent. Suppose that we find two similar but not identical populations living 300 miles apart with no related populations between them. Are we observing a single species with a disjunct distribution or two different but closely related species? Suppose that these populations have been separated historically for 50,000 years. Is this enough time for them to have evolved separate reproductive communities, or can we still view them as parts of the same reproductive



**Figure 10.2** Geographic variation of color patterns in the salamander genus *Ensatina*. The species status of these populations has puzzled taxonomists for generations and continues to do so. Current taxonomy recognizes only a single species (*Ensatina eschscholtzii*) divided into subspecies as shown. Hybridization is evident between most adjacent populations, but studies of variation in proteins and DNA show large amounts of genetic divergence among populations. Furthermore, populations of the subspecies *E. e. eschscholtzii* and *E. e. klauberi* can overlap geographically without interbreeding.

community? Clear answers to such questions are very hard to find. Differences among species concepts pertain to solving these problems.

## Typological Species Concept

Before Darwin, a species was considered a distinct and immutable entity. Species were defined by fixed, essential features (usually morphological) considered a divinely created pattern or archetype. This practice constitutes the **typological** (or **morphological**) **species concept**. Scientists recognized species formally by designating a **type specimen** that was labeled and deposited in a museum to represent the ideal form or morphology for the species (Figure 10.3). When scientists obtained additional specimens and wanted to assign them to a species, the type specimens of described species were consulted. The new specimens were assigned to a previously described species if they possessed the essential features of its type specimen. Small differences from the type specimen were considered accidental imperfections. Large differences from existing type specimens would lead a scientist to describe a new species with its own type specimen. In this manner, the living world was categorized into species.

Evolutionists discarded the typological species concept, but some of its traditions remain. Scientists still name species by describing type specimens deposited in museums, and the type specimen formally bears the name of the species. Organismal morphology is likewise still important in recognizing species; however, species are no longer viewed as classes of organisms defined by possession of certain morphological features. The basis of the evolutionary world view is that species are historical entities whose properties are subject always to change. Variation that we observe among organisms within a species is not an imperfect manifestation of an eternal “type”; the type itself is only an abstraction taken from the very real and important variation present within the species. A type is at best an average form that changes as organismal variation is sorted through time by natural selection. A type specimen serves only as a guide to the general morphological features that one might expect to find in a particular species as we observe it today.

The person who first describes a type specimen and publishes the name of a species is called the authority. This person's name and date of publication are often written after the species name. Thus, *Didelphis marsupialis* Linnaeus, 1758, tells us that Linnaeus was the first person to publish the species name of the opossum. Sometimes, the generic status of a species is revised following its initial description. In this case, the name of the authority is presented in parentheses. The Nile monitor lizard is denoted *Varanus niloticus* (Linnaeus, 1766) because the species originally was named by Linnaeus as *Lacerta nilotica*, and subsequently placed into a different genus.

## Biological Species Concept

The most influential concept of species inspired by Darwinian evolutionary theory is the **biological species concept** formulated by Theodosius Dobzhansky and Ernst Mayr. This concept emerged during the evolutionary synthesis of the 1930s and 1940s from earlier ideas, and it has been refined and reworded several times since then. In 1982, Mayr stated the biological species concept as follows: “A species



**Figure 10.3** Specimens of birds from the Smithsonian Institution (Washington, D.C.), including birds originally collected by John J. Audubon, Theodore Roosevelt, John Gould, and Charles Darwin.

is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature.” Note that a species is identified here according to reproductive properties of populations, not according to possession of any specific organismal characteristics. A species is an **interbreeding population** of individuals having common descent and sharing intergrading characteristics. Studies of populational variation in organismal morphology, chromosomal structure, and molecular genetic features are very useful for evaluating the geographical boundaries of interbreeding populations in nature. The criterion of the “niche” (see Chapter 38) recognizes that members of a reproductive community are expected also to have common ecological properties.

Because a reproductive community should maintain genetic cohesiveness, we expect organismal variation to be relatively smooth and continuous within species and discontinuous between them. Although the biological species is based on reproductive properties of populations rather than organismal morphology, morphology nonetheless can help us to diagnose biological species. Sometimes species status can be evaluated directly by conducting breeding experiments. Controlled breeding is practical only in a minority of cases, however, and our decisions regarding species membership usually are made by studying character variation. Variation in molecular characters is very useful for identifying geographical boundaries of reproductive communities. Molecular studies have revealed the occurrence of cryptic or **sibling species** (p. 115), which are too similar in morphology to be diagnosed as separate species by morphological characters alone.

Criticism of the biological species concept reveals several perceived problems. First, the concept lacks an explicit temporal dimension. It provides a means for diagnosing species status of contemporary populations but little guidance for tracing the temporal duration of a species lineage through its past history. Proponents of the biological species concept often disagree on the degree of reproductive isolation necessary for considering two populations separate species, thereby revealing some ambiguity in the concept. For example, should occurrence of limited hybridization between populations in a small geographic area cause them to be considered a single species despite evolutionary differences between them? Another

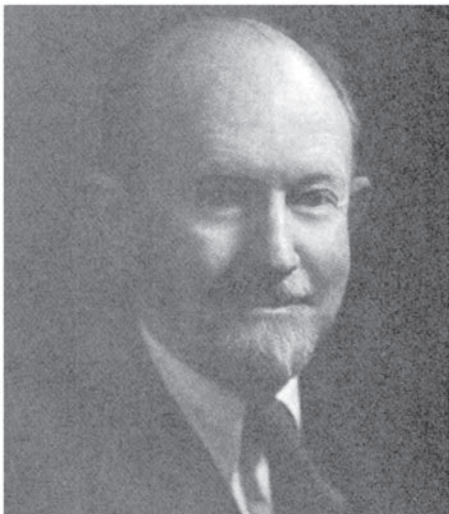


problem is that because the biological species concept emphasizes interbreeding as the criterion of reproductive community, it denies the existence of species in groups of organisms that reproduce only asexually. It is common systematic practice, however, to describe species in all groups of organisms, regardless of whether reproduction is sexual or asexual.

## Evolutionary and Cohesion Species Concepts

The time dimension creates obvious problems for the biological species concept. How do we assign fossil specimens to biological species that are recognized today? If we trace a lineage backward through time, how far must we go before we have crossed a species boundary? If we could follow the unbroken genealogical chain of populations backward through time to the point where two sister species converge on their common ancestor, we would need to cross at least one species boundary somewhere. It would be very hard to decide, however, where to draw a sharp line between the two species.

To address this problem, mammalian palaeontologist George Gaylord Simpson (Figure 10.4) proposed the **evolutionary species concept** to add an evolutionary time dimension to the biological species concept. This concept persists in a modified form today. A current definition of the evolutionary species is *a single lineage of ancestor-descendant populations that maintains its identity from other such lineages and that has its own evolutionary tendencies and historical fate*. Note that the criterion of common descent is retained here in the need for a lineage to have a distinct historical identity. Reproductive cohesion is the means by which a species maintains its identity from other such lineages and keeps its evolutionary fate separate from other species. The same kinds of diagnostic features discussed for the biological species concept are relevant for identifying evolutionary species, although in most cases only morphological features are available from fossils. Unlike the biological species concept, the evolutionary species concept applies to both sexually and asexually reproducing forms. As long as continuity of diagnostic features is maintained by the evolving



**Figure 10.4** George Gaylord Simpson (1902 to 1984) formulated the principles of evolutionary taxonomy.

lineage, it is recognized as a species. Abrupt changes in diagnostic features mark the boundaries of different species in evolutionary time.

The ability of geographic populations to evolve collectively as a single, genetically cohesive unit through evolutionary time is critical to the evolutionary species concept. Population geneticist Alan Templeton updated this concept in 1989 to make explicit the expectation that populations of a species evolve as a genetically cohesive unit by natural selection and genetic drift. Templeton defined his **cohesion species concept** as follows: *the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms*. The cohesion mechanisms include gene flow across the geographic expanse of the species, shared loss of alleles through genetic drift, and shared genetic changes caused by natural selection. Another way of stating the cohesion criterion is that any individual in a species is a possible common ancestor of the entire species at some future time. For example, a new allele that arises by mutation in a single person could spread throughout the human population over many generations, ultimately to become shared by all members of the species at some future time. New mutations arising in other species, even in our closest relatives of the genus *Pan*, could not enter the human gene pool.

## Phylogenetic Species Concept

Ornithologist Joel Cracraft defined the last concept that we present: the **phylogenetic species concept**. The phylogenetic species concept is an *irreducible (basal) grouping of organisms diagnosably distinct from other such groupings and within which there is a parental pattern of ancestry and descent*. This concept emphasizes most strongly the criterion of common descent. Both asexual and sexual groups are covered.

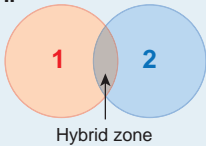

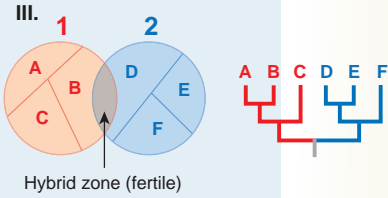
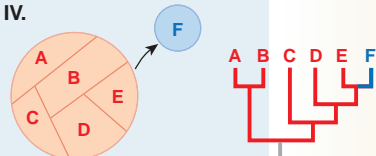

A phylogenetic species is a single population lineage with no detectable branching. The main difference in practice between the evolutionary/cohesion and phylogenetic species concepts is that the latter emphasizes recognizing as separate species the smallest groupings of organisms that have undergone independent evolutionary change. The evolutionary and cohesion species concepts place greater emphasis on whether historically separated populations have the biological potential to merge into a single lineage in the future. The evolutionary or cohesion species concepts would group into a single species geographically disjunct populations that demonstrate some phylogenetic divergence but are judged similar in their “evolutionary tendencies,” thus permitting future gene exchange and possible merging, whereas the phylogenetic species concept would treat them as separate species. In general, a greater number of species would be described using the phylogenetic species concept than by any other species concept, and many taxonomists consider it impractical for this reason. For strict adherence to cladistic systematics (p. 207), the phylogenetic species concept is ideal because only this concept guarantees strictly monophyletic units at the species level.

The phylogenetic species concept intentionally disregards details of evolutionary process and gives us a criterion that allows us to describe species without first needing to conduct detailed studies on evolutionary processes. Advocates of the phylogenetic species concept do not necessarily disregard the importance of studying evolutionary process. They argue, however, that the first step in studying evolutionary process is to have a clear picture of life’s history. To accomplish this task, the pattern of common descent must be reconstructed in

## Species Concepts in Practice

These hypothetical examples illustrate conditions that challenge taxonomists in judging the numbers of species represented by a group of populations being studied. I. Two geographic populations of sexually reproducing forms make geographic contact along a borderline at which hybrids (offspring whose parents come from different geographic populations) occur (I. A. natural hybrids are fertile; I. B. natural hybrids are infertile). II. Two geographically allopatric populations of sexually reproducing forms appear morphologically and ecologically equivalent (I. A. artificial crosses produce fertile hybrids; I. B. artificial crosses produce infertile hybrids). III. Six genetically divergent populations of sexually reproducing forms have geographic and phylogenetic relationships as shown with hybrids produced between populations B and D. Populations A–C (group 1) are morphologically indistinguishable from each other but differ from populations D–F (group 2), which are morphologically indistinguishable from each other (III. A. groups 1

and 2 are ecologically equivalent; III. B. groups 1 and 2 are ecologically distinct). IV. Sexually reproducing populations A–E are genetically divergent but similar in ecology and morphology; population F was derived from population E by a founder event and is reproductively isolated from the others. V. Two allopatric populations of animals that reproduce only asexually are ecologically and morphologically distinct from each other. Each box indicates the number of different species that a taxonomist would recognize using the species concept(s) at the head of the column. Some concepts have inherent ambiguities permitting some room for individual judgment separating taxonomic “lumpers” from “splitters”; such cases are indicated by “1-2” in the appropriate column with the source of ambiguity indicated in column 5. Assume that the individual populations discussed are internally genetically homogeneous based on molecular genetic data, but that they are diagnosably distinct from others using those same data.

Geography / Phylogeny		Biological Species	Evolutionary and Cohesion Species	Phylogenetic Species	Source of Ambiguity
<b>I.</b> 	A. hybrids fertile	1 - 2	1 - 2	2	Will 1 & 2 eventually merge or remain distinct with a small hybrid zone?
	B. hybrids infertile	2	2	2	None
<b>II. Artificial cross</b> 	A. hybrids fertile	1	1	2	None
	B. hybrids infertile	2	2	2	None
<b>III.</b> 	A. 1 & 2 are ecologically similar	1 - 2	1 - 2	6	Will 1 & 2 eventually merge or remain distinct with a small hybrid zone?
	B. 1 & 2 are ecologically distinct	1 - 2	2	6	Is ecological isolation sufficient for separate species status without reproductive isolation?
<b>IV.</b> 		2	2	6	None
<b>V.</b> 		0	2	2	None

the greatest detail possible by starting with the smallest taxonomic units that have a history of common descent distinct from other such units.

## Dynamism of Species Concepts

Herpetologist Kevin de Queiroz argues that the various competing concepts of species have a common underlying principle despite their differences. In each case, a species constitutes a segment of a population-level lineage, what de Queiroz calls the **general lineage concept** of species. For the biological species concept, the segment is a temporally short one with reproductive community among sexually reproducing populations being the critical secondary attribute that separates the biological species concept from alternatives. For the phylogenetic species concept, a population lineage diagnosable as having evolved independently since its evolutionary separation from another such lineage provides the secondary attribute that distinguishes this concept from others. The general lineage concept of species has gained popularity among systematists because it emphasizes the common goal of identifying the phylogenetic history of population-level lineages in detail. It does not solve the problem, however, that taxonomists using contrasting species concepts may differ greatly in how many species they judge worthy of a Linnaean Latin binomial (see boxed essay Species Concepts in Practice).

Taxonomists agree that historically distinct population lineages, the species of the phylogenetic species concept, are real entities in nature. Such entities exist as the indivisible units of evolutionary process and change independent of our knowledge of them. Advocates of the other species concepts do not deny these claims, but they consider such lineages too numerous and too ephemeral for each one to deserve recognition with a Latin species binomial, especially when the biological differences among lineages are judged superficial. Given the power of molecular genetic data to diagnose species lineages, it is perhaps impractical to expect each one to be given formal species status. A taxonomic system must be practical to serve us well, but when we defer to practicality we risk making our recognized species arbitrary constructs that lose their integrity as natural individuals.

Current disagreements concerning concepts of species should not be considered discouraging. Whenever a field of scientific investigation enters a phase of dynamic growth, old concepts are reevaluated and either refined or replaced with newer, more progressive ones. The active debate occurring within systematics shows that this field has acquired unprecedented activity and importance in biology. Just as Thomas Henry Huxley's time was one of enormous advances in biology, so is the present time. Both times are marked by fundamental reconsiderations of the meaning of species. Researchers whose main interests are branching of evolutionary lineages, evolution of reproductive barriers among populations (p. 113), or ecological properties of species may favor different species concepts. The conflicts among the current concepts lead us into the future. In many cases, different concepts agree on the locations of species boundaries, and disagreements identify particularly interesting cases of evolution in action. Understanding the conflicting perspectives, rather than learning a single species concept, is therefore of greatest importance for people now entering the study of zoology.

## DNA Barcoding of Species

**DNA barcoding** is a technique for identifying organisms to species using sequence information from a standard gene present in all animals. The mitochondrial gene encoding cytochrome *c* oxidase subunit 1 (*COI*), which contains about 650 nucleotide base pairs, is a standard "barcode" region for animals. DNA sequences of *COI* usually vary among individuals of the same species but not extensively, so that variation within a species is much smaller than differences among species. DNA barcoding is applied to specimens in nature by taking a small DNA sample from blood or another expendable tissue. The method is useful also for specimens in natural-history museums, zoos, aquaria, and frozen-tissue collections. DNA sequences from such sources are checked against a public reference library of species identifiers to assign unknown specimens to known species. DNA barcoding does not solve the controversies regarding use of different species concepts, but it often permits the origin of a specimen to be identified to a particular local population, which is valuable information regardless of the species status that a taxonomist assigns to that population.

## TAXONOMIC CHARACTERS AND PHYLOGENETIC RECONSTRUCTION

A major goal of systematics is to infer the evolutionary tree or **phylogeny** that relates all extant and extinct species. This task is accomplished by identifying organismal features, formally called **characters**, that vary among species. A character is any feature that a taxonomist uses to study variation within and among species. Taxonomists find characters by observing patterns of similarity among organisms in morphological, chromosomal, and molecular features (see p. 204), and less frequently in behavioral and ecological ones. Phylogenetic analysis depends upon finding among organisms shared features that are inherited from a common ancestor. Character similarity that results from common ancestry is called **homology** (see Chapter 6). Similarity does not always reflect common ancestry, however. Independent evolutionary origin of similar features on different lineages produces patterns of similarity among organisms that misrepresent common descent; this occurrence complicates the work of taxonomists. Character similarity that misrepresents common descent is called nonhomologous similarity or **homoplasy**. Endothermy of birds and mammals illustrates homoplasy; this condition arose separately in ancestral lineages of birds and mammals. Variation in other characters shows that birds and mammals are not each other's closest relatives (p. 558). For an example of molecular homoplasy, see the interpretation of character 41 (p. 210) in the boxed essay, Phylogenies from DNA Sequences.

## Using Character Variation to Reconstruct Phylogeny

To infer the phylogeny of a taxon using characters that vary among its species, the first step is to determine which variant form of each character was present in the common ancestor of the entire taxon of interest. This character state is called **ancestral** for the taxon as a whole. We presume that all other variant forms of the character arose later within

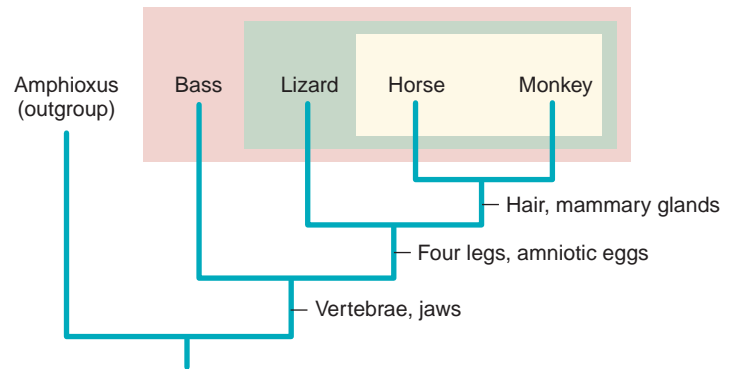


the group, and these are called evolutionarily **derived character states**. Determining the **polarity** of a character refers to identifying which one of its contrasting states is ancestral and which one(s) derived. For example, if we consider as a character the dentition of amniotic vertebrates (reptiles, birds, and mammals), presence versus absence of teeth in the jaws constitute alternative character states. Teeth are absent from modern birds but present in most other amniotes. To evaluate the polarity of this character, we must determine which character state, presence or absence of teeth, characterized the most recent common ancestor of amniotes and which state was derived subsequently within amniotes.

The method used to examine the polarity of a variable character is **outgroup comparison**. We consult an additional group of organisms, called an **outgroup**, that is phylogenetically close but not within the taxon being studied. We infer that any character state found both within the taxon being studied and in the outgroup is ancestral for the study taxon. Amphibians and different groups of bony fishes constitute appropriate outgroups to the amniotes for polarizing variation in dentition of amniotes. Teeth are usually present in amphibians and bony fishes; therefore, we infer that presence of teeth is ancestral for amniotes and absence of teeth is derived. The observation of abundant teeth in crocodylians, the closest living relatives of birds, strengthens this inference. The polarity of this character indicates that teeth were lost in the ancestral lineage of all modern birds. Polarity of characters is evaluated most effectively when several different outgroups are used. All character states found in the study group that are absent from appropriate outgroups are considered derived.

Species that share derived character states form subsets within the study group called **clades** (Gr. *klados*, branch). A derived character shared by the members of a clade is formally called a **synapomorphy** (Gr. *synapsis*, joining together, + *morphē*, form) of that clade. Taxonomists use synapomorphies as evidence of homology to infer that a particular group of species forms a clade. Among extant amniotes, absence of teeth and presence of feathers are synapomorphies that identify the birds as a clade. A clade corresponds to a unit of evolutionary common descent; it includes an ancestral lineage and all descendants of that lineage. The pattern formed by the derived states of all characters within our study taxon reveals a **nested hierarchy** of clades within clades. The goal is to identify all of the different clades nested within the study taxon, which would give a complete account of the structure of common descent among species in the taxon.

Character states ancestral for a taxon are often called **plesiomorphic** for that taxon, and the sharing of ancestral states among species is termed **symplesiomorphy**. Unlike synapomorphies, however, symplesiomorphies do not provide useful information on nesting of clades within clades. In the example just given, we found that presence of teeth in jaws was plesiomorphic for amniotes. If we grouped together mammalian and reptilian groups, which possess teeth, to the exclusion of modern birds, we would not obtain a valid clade. Birds also descend from all common ancestors of reptiles and mammals and therefore lie within any clade that includes all reptiles and mammals. Errors in determining polarity of characters therefore clearly can produce errors in inference of phylogeny. It is important to note, however, that character states that are plesiomorphic at one taxonomic level can be synapomorphies at a more inclusive level. For example, the presence of jaws bearing teeth is a synapomorphy of gnathostome vertebrates (p. 506), a group that includes amniotes plus amphibians, bony fishes,



**Figure 10.5** A cladogram as a nested hierarchy of taxa among five sampled chordate groups (Amphioxus, bass, lizard, horse, monkey). Amphioxus is the outgroup, and the study group comprises the four vertebrates. We generate a simple cladogram from four characters that vary among vertebrates: presence versus absence of four legs, amniotic eggs, hair, and mammary glands. For all four characters, absence is the ancestral state in vertebrates because this is the condition found in the outgroup, Amphioxus; for each character, presence is the derived state in vertebrates. Because they share presence of four legs and amniotic eggs as synapomorphies, the lizard, horse, and monkey form a clade relative to the bass. This clade is subdivided further by two synapomorphies (presence of hair and mammary glands) that unite the horse and monkey relative to the lizard. We know from comparisons involving even more distantly related animals that vertebrae and jaws constitute synapomorphies of vertebrates and that Amphioxus, which lacks these features, falls outside the vertebrate clade.

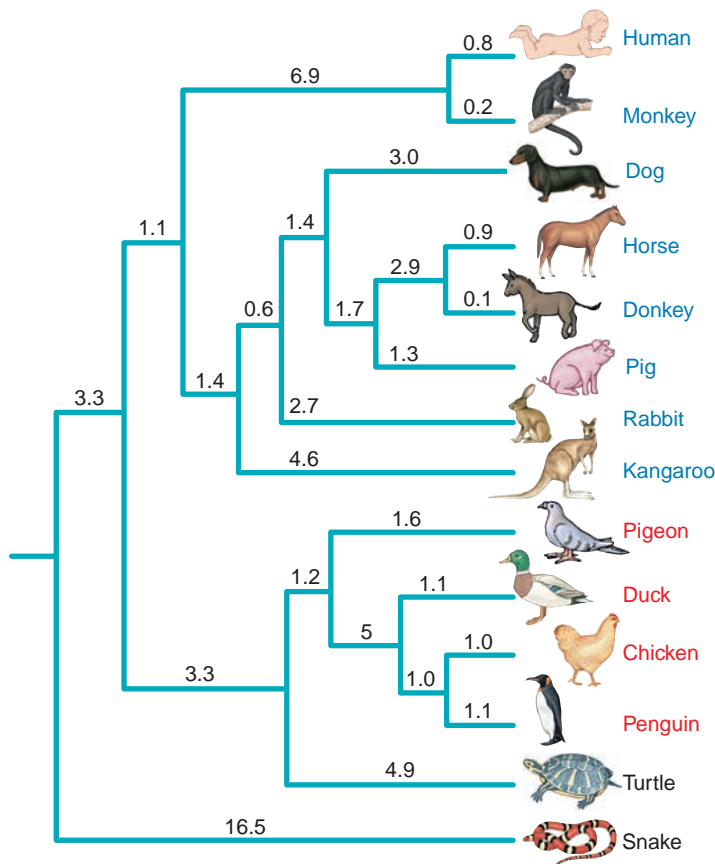
and cartilaginous fishes, although teeth have been lost in birds and some other gnathostomes. The goal of phylogenetic analysis therefore can be restated as one of finding the appropriate taxonomic level at which any given character state is a synapomorphy. The character state is then used at that level to identify a clade.

A nested hierarchy of clades is presented as a branching diagram called a **cladogram** (Figure 10.5; see also Figure 6.16, and try to reconstruct this cladogram using only the sharing of numbered synapomorphies among the bird species). Taxonomists often make a technical distinction between a cladogram and a **phylogenetic tree**. The branches of a cladogram are only a formal device for indicating the nested hierarchy of clades within clades. The cladogram is not strictly equivalent to a phylogenetic tree, whose branches represent real lineages that occurred in the evolutionary past. To obtain a phylogenetic tree, we must add to the cladogram important additional interpretations concerning ancestors, the durations of evolutionary lineages, or the amounts of evolutionary change that occurred on the lineages. A cladogram is often used, however, as a first approximation of the branching structure of the corresponding phylogenetic tree.

## Sources of Phylogenetic Information

We find characters used to construct cladograms in comparative morphology (including embryology), comparative cytology, and comparative biochemistry. **Comparative morphology** examines the varying shapes and sizes of organismal structures, including their developmental origins. Both macroscopic and microscopic characters are used, including details of cellular structure revealed by histology. As seen in

Chapters 23 through 28, the variable structures of skull bones, limb bones, and integument (scales, hair, feathers) are particularly important for reconstructing the phylogeny of vertebrates. Comparative morphology uses specimens obtained from both living organisms and fossilized remains. **Comparative biochemistry** uses sequences of amino acids in proteins and the sequences of nucleotides in nucleic acids (see Chapter 5) to identify variable characters for constructing a cladogram (Figure 10.6). Direct sequencing of DNA is regularly applied to phylogenetic studies; however, comparisons of protein sequences are usually indirect, involving immunological or allozymic (see Figure 6.32) methods, or inferences from DNA sequences of protein-coding genes. Recent studies show that comparative biochemistry can be applied to some fossils in addition to living organisms. **Comparative cytology** (also called karyology) uses variation in the numbers, shapes, and sizes of chromosomes and their parts (see Chapter 3 and p. 109) to obtain variable characters for constructing cladograms. Comparative cytology is used almost exclusively on living rather than fossilized organisms.



**Figure 10.6** An early phylogenetic tree of representative amniotes based on inferred base substitutions in the gene that encodes the respiratory protein, cytochrome *c*. Numbers on the branches are the expected minimum numbers of mutational changes needed to explain amino acid substitutions along the different evolutionary lineages. Publication of this tree by Fitch and Margoliash in 1967 was influential in convincing systematists that molecular sequences contain phylogenetic information. Subsequent work confirms some hypotheses, including the hypotheses that mammals (blue) and birds (red) form nonoverlapping clades, while rejecting others; kangaroo, for example, should be outside a branch containing all other mammals sampled.

To add an evolutionary timescale necessary for producing a phylogenetic tree, we must consult the fossil record. We can look for the earliest appearance in fossils of derived morphological characters to estimate the ages of clades distinguished by those characters. The age of a fossil showing the derived characters of a particular clade is determined by radioactive dating (p. 106). An example of a phylogenetic tree constructed using these methods is Figure 25.1, page 539.

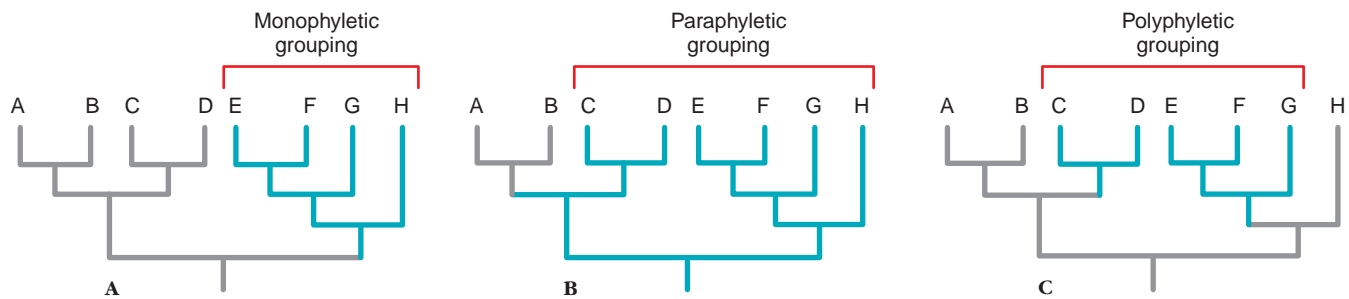
We can use comparative biochemical data to estimate the ages of different lineages on a phylogenetic tree. Some protein and DNA sequences undergo approximately linear rates of divergence through evolutionary time. The age of the most recent common ancestor of two species is therefore proportional to the differences measured between their proteins and DNA sequences. We calibrate evolution of proteins and DNA sequences by measuring their divergence between species whose most recent common ancestor has been dated using fossils. We then use the molecular evolutionary calibration to estimate ages of other branches on the phylogenetic tree.

## THEORIES OF TAXONOMY

A theory of taxonomy establishes the principles that we use to recognize and to rank taxonomic groups. There are two currently popular theories of taxonomy: (1) evolutionary taxonomy and (2) phylogenetic systematics (cladistics). Both are based on evolutionary principles. These two theories differ, however, on how evolutionary principles are used. These differences have important implications for how we use a taxonomy to study evolutionary processes. Evolutionary taxonomy predates phylogenetic systematics and retains many aspects of Linnaean taxonomy; for this reason, it is sometimes called “traditional evolutionary taxonomy.” Evolutionary taxonomy was well established by the 1940s; phylogenetic systematics arose in the 1960s as a replacement for evolutionary taxonomy, which some systematists considered arbitrary and misleading.

The relationship between a taxonomic group and a phylogenetic tree or cladogram is important for both theories. This relationship can take one of three forms: **monophyly**, **paraphyly**, or **polyphyly** (Figure 10.7). A taxon is monophyletic if it includes the most recent common ancestor of the group and all descendants of that ancestor (Figure 10.7A). The terms “monophyletic group” and “clade” are synonymous. A taxon is paraphyletic if it includes the most recent common ancestor of all members of a group and some but not all descendants of that ancestor (Figure 10.7B). A taxon is polyphyletic if it does not include the most recent common ancestor of all members of a group; this condition requires that the group has had at least two separate evolutionary origins, usually requiring independent evolutionary acquisition of similar features (Figure 10.7C).

Monophyletic and paraphyletic groups share the property of **convexity**, which distinguishes them from polyphyletic groups. A group is convex if you can trace a path between any two members of the group on a cladogram or phylogenetic tree without leaving the group. For example, on Figure 10.7 you could trace a connection between any pair of points in the blue areas of parts A or B without leaving the blue area. For the polyphyletic grouping in part C of Figure 10.7, one cannot trace the path between species C and E without leaving the group designated by blue shading. In Figure 10.7C, if a systematist added the full path connecting species C and E



**Figure 10.7** Relationships between phylogeny and taxonomic groups illustrated for a hypothetical phylogeny of eight species (A through H). **A, Monophyly**—a monophyletic group contains the most recent common ancestor of all members of the group and all of its descendants. **B, Paraphyly**—a paraphyletic group contains the most recent common ancestor of all members of the group and some but not all of its descendants. **C, Polyphyly**—a polyphyletic group typically does not contain the most recent common ancestor of all members of the group, thereby requiring that the group have at least two separate phylogenetic origins. Monophyletic and paraphyletic groups are *convex*, meaning that one can trace a path from any member of the group to any other member without leaving the group; any group that fails the convexity criterion is considered polyphyletic.

to the group shown but continued to omit the paths leading to species A, B, and H, then the new grouping thus formed would be convex and paraphyletic rather than polyphyletic. Demonstration that a group is not convex is the formal criterion for considering the group polyphyletic.

Both evolutionary and cladistic taxonomy accept monophyletic groups and reject polyphyletic groups. They differ on acceptance of paraphyletic groups, however, and this difference has important evolutionary implications.



A



B

**Figure 10.8** **A, Penguin.** **B, Diving petrel.** Penguins (avian order Sphenisciformes) were recognized by George G. Simpson as a distinct adaptive zone within birds because of their adaptations for submarine flight. Simpson believed that the adaptive zone ancestral to penguins resembled that of diving petrels, which display adaptations for combined aerial and aquatic flight. Adaptive zones of penguins and diving petrels are distinct enough to be recognized taxonomically as different orders.

## Evolutionary Taxonomy

**Evolutionary taxonomy** incorporates two different evolutionary principles for recognizing and ranking higher taxa: (1) common descent and (2) amount of adaptive evolutionary change, as shown on a phylogenetic tree. Evolutionary taxa must have a single evolutionary origin, and must show unique adaptive features.

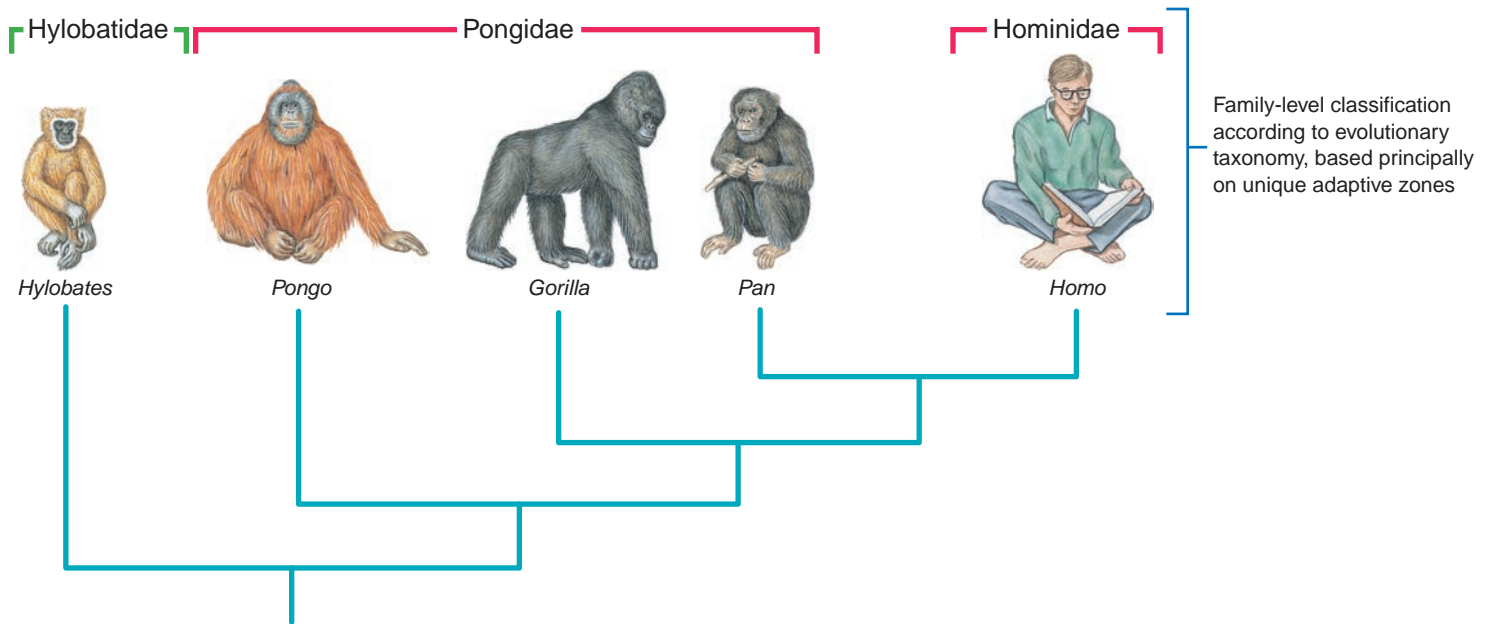
George Gaylord Simpson (Figure 10.4) and Ernst Mayr (see Figure 6.19) were highly influential in developing and formalizing the procedures of evolutionary taxonomy. According to Simpson and Mayr, a particular branch on an evolutionary tree is considered a higher taxon if it represents a distinct **adaptive zone**. Simpson describes an adaptive zone as “a characteristic reaction and mutual relationship between environment and organism, a way of life and not a place where life is led.” By entering a new adaptive zone through a fundamental change in organismal structure and behavior, an evolving population can use environmental resources in a new way.

A taxon that constitutes a distinct adaptive zone is termed a **grade**. Simpson gives the example of penguins as a distinct adaptive zone within birds. The lineage immediately ancestral to all penguins

underwent fundamental changes in the form of the body and wings to switch from aerial to aquatic locomotion (Figure 10.8). Aquatic birds that use their flight apparatus to propel themselves through air and water are somewhat intermediate in habitat, morphology, and behavior between aerial and aquatic adaptive zones. Nonetheless, the obvious modifications of the wings and body of penguins for swimming represent a new grade of organization. Penguins are therefore recognized as a distinct taxon within birds, the order Sphenisciformes. The broader the adaptive zone when fully occupied by a group of organisms, the higher the rank given to the corresponding taxon.

Evolutionary taxa may be either monophyletic or paraphyletic. Recognition of paraphyletic taxa requires, however, that our taxonomies distort patterns of common descent. An evolutionary taxonomy of the anthropoid primates provides a good example (Figure 10.9). This taxonomy places humans (genus *Homo*) and their immediate





**Figure 10.9** Phylogeny and family-level classification of anthropoid primates. Evolutionary taxonomy groups the genera *Gorilla*, *Pan*, and *Pongo* into a paraphyletic family Pongidae because they share the same adaptive zone or grade of organization. Humans (genus *Homo*) are phylogenetically closer to *Gorilla* and *Pan* than any of these genera are to *Pongo*, but humans are placed in a separate family (Hominidae) because they represent a new grade of organization. Cladistic taxonomy discontinues recognition of paraphyletic family Pongidae, consolidating *Pongo*, *Gorilla*, *Pan*, and *Homo* in family Hominidae.

fossil ancestors in the family Hominidae, and it places the chimpanzees (genus *Pan*), gorillas (genus *Gorilla*), and orangutans (genus *Pongo*) in the family Pongidae. However, the pongid genera *Pan* and *Gorilla* share more recent common ancestry with the Hominidae than they do with the remaining pongid genus, *Pongo*. This arrangement makes the family Pongidae paraphyletic because it does not include humans, who also descend from the most recent common ancestor of all pongids (Figure 10.9). Evolutionary taxonomists nonetheless recognize the pongid genera as a single, family-level grade of arboreal, herbivorous primates having limited mental capacity; in other words, they show the same family-level adaptive zone. Humans are terrestrial, omnivorous primates who have greatly expanded mental and cultural attributes, thereby forming a distinct adaptive zone at the taxonomic level of the family. Unfortunately, if we want our taxa to constitute adaptive zones, we compromise our ability to present common descent effectively.

Evolutionary taxonomy has been challenged from two opposite directions. One challenge states that because phylogenetic trees can be very difficult to obtain, it is impractical to base our taxonomic system on common descent and adaptive evolution. We are told that our taxonomy should represent a more easily measured feature, the overall similarity of organisms evaluated without regard to phylogeny. This principle is called **phenetic taxonomy**. Phenetic taxonomy contributed some useful analytical methods but did not have a strong impact on animal taxonomy, and scientific interest in this approach has declined. Despite the difficulties of reconstructing phylogeny, zoologists still consider this endeavor a central goal of their systematic work, and they are unwilling to compromise this goal for methodological purposes.

## Phylogenetic Systematics/Cladistics

A second and stronger challenge to evolutionary taxonomy is one called **phylogenetic systematics** or **cladistics**. As the first name implies, this approach emphasizes the criterion of common descent and, as the second name implies, it is based on the cladogram of the group being classified. This approach to taxonomy was first proposed in 1950 by the German entomologist Willi Hennig (Figure 10.10), and therefore is sometimes called “Hennigian systematics.” All taxa



**Figure 10.10** Willi Hennig (1913 to 1976), German entomologist who formulated the principles of phylogenetic systematics/cladistics.

recognized by Hennig's cladistic system must be monophyletic. We saw in Figure 10.9 how evolutionary taxonomists' recognition of the primate families Hominidae and Pongidae distorts genealogical relationships to emphasize adaptive uniqueness of the Hominidae. Because the most recent common ancestor of the paraphyletic family Pongidae is also an ancestor of the Hominidae, recognition of the Pongidae is incompatible with cladistic taxonomy. To avoid paraphyly, cladistic taxonomists have discontinued use of the traditional family Pongidae, placing chimpanzees, gorillas, and orangutans with humans in the family Hominidae. We adopt the cladistic classification in this book.

Disagreement on the validity of paraphyletic groups may seem trivial at first, but its important consequences become clear when we discuss evolution. For example, claims that amphibians evolved from bony fish, that birds evolved from reptiles, or that humans evolved from apes might be made by an evolutionary taxonomist but are meaningless to a cladist. We imply by these statements that a descendant group (amphibians, birds, or humans) evolved from part of an ancestral group (bony fish, reptiles, and apes, respectively) to which the descendant does not belong. This usage automatically makes the ancestral group paraphyletic, and indeed bony fish, reptiles, and apes as traditionally recognized are paraphyletic groups. How are such paraphyletic groups recognized? Do they share distinguishing features not shared by the descendant group?

Paraphyletic groups are usually defined in a negative manner. They are distinguished only by lacking features found in a particular descendant group, because any traits that they share from their common ancestry are symplesiomorphies present also in the excluded descendants (unless secondarily lost). For example, apes are those "higher" primates that are not humans. Likewise, fish are those vertebrates that lack the distinguishing characteristics of tetrapods (amphibians and amniotes). What does it mean then to say that humans evolved from apes? To an evolutionary taxonomist, apes and humans are different adaptive zones or grades of organization; to say that humans evolved from apes states that bipedal organisms of large brain capacity evolved from arboreal organisms of smaller brain capacity. To a cladist, however, the statement that humans evolved from apes says essentially that humans evolved from an arbitrary grouping of species that lack the distinctive characteristics of humans, a trivial statement that conveys no useful information. To a cladist, any statement that a particular monophyletic group descends from a paraphyletic one is nothing more than a claim that the descendant group evolved from something that it is not. Extinct ancestral groups are always paraphyletic because they exclude a descendant that shares their most recent common ancestor. Although many such groups have been recognized by evolutionary taxonomists, none are recognized by cladists.

Zoologists often construct paraphyletic groups because they are interested in a terminal, monophyletic group (such as humans), and they want to ask questions about its ancestry. It is often convenient to lump together species whose features are considered approximately equally distant from the group of interest and to ignore the unique features of those species. It is significant in this regard that humans have never been placed in a paraphyletic group, whereas most other organisms have been. Apes, reptiles, fishes, and invertebrates are all terms that traditionally designate paraphyletic groups formed by combining various "side branches" found when human ancestry is traced backward

through the tree of life. Such a taxonomy can give the erroneous impression that all of evolution is a progressive march toward humanity or, within other groups, a progressive march toward whatever species humans designate most "advanced." Such thinking is a relic of pre-Darwinian views that there is a linear scale of nature having "primitive" creatures at the bottom and humans near the top just below angels. Darwin's theory of common descent states, however, that evolution is a branching process with no linear scale of increasing perfection along a single branch. Nearly every branch contains its own combination of ancestral and derived features. In cladistics, this perspective is emphasized by recognizing taxa only by their own unique properties and not grouping organisms only because they lack the unique properties found in related groups.

Fortunately, there is a convenient way to express the common descent of groups without constructing paraphyletic taxa. It is done by finding what is called the **sister group** of the taxon of interest to us. Two different monophyletic taxa are each other's sister group if they share common ancestry with each other more recently than either one does with any other taxa. The sister group of humans appears to be genus *Pan* (bonobos and chimpanzees), with gorillas forming the sister group to humans, bonobos, and chimpanzees combined. Orangutans are the sister group of a clade that comprises humans, bonobos, chimpanzees, and gorillas; gibbons form the sister group of the clade that comprises orangutans, bonobos, chimpanzees, gorillas, and humans (Figure 10.9).

## Current State of Animal Taxonomy

The formal taxonomy of animals that we use today was established using the principles of evolutionary systematics and has been revised recently in part using the principles of cladistics. Introduction of cladistic principles initially replaces paraphyletic groups with monophyletic subgroups while leaving the remaining taxonomy mostly unchanged. A thorough revision of taxonomy along cladistic principles, however, would require profound changes, one of which almost certainly would be abandonment of Linnaean ranks. A new taxonomic system called PhyloCode is being developed as an alternative to Linnaean taxonomy; this system replaces Linnaean ranks with codes that denote the nested hierarchy of monophyletic groups conveyed by a cladogram. In our coverage of animal taxonomy, we try to use taxa that are monophyletic and therefore consistent with criteria of both evolutionary and cladistic taxonomy. We continue, however, to use Linnaean ranks. For familiar taxa that are clearly paraphyletic grades, we note this fact and suggest alternative taxonomic schemes that contain only monophyletic taxa.

When discussing patterns of descent, we avoid statements such as "mammals evolved from reptiles" that imply paraphyly and instead specify appropriate sister-group relationships. We avoid calling groups of living organisms primitive, advanced, specialized, or generalized because all groups of animals contain combinations of primitive, advanced, specialized, and generalized features; these terms are best restricted to describing specific characteristics and not an entire group. We likewise avoid calling a living species or group of living species "basal," because no species or group is more basal than its sister taxon. The term "basal" is best reserved for describing branch points or "nodes" on a phylogenetic tree; the most basal node is the one closest to the root of the tree.

## Phylogenies from DNA Sequences

Most phylogenetic reconstruction currently underway comes from collecting genomic DNA sequences for the species of interest and analyzing those data using statistical approaches, especially maximum-likelihood and Bayesian methods. Such analysis requires sophisticated computer algorithms and cannot be done by hand. Nonetheless, statistical inference of phylogenies is designed to separate patterns of homology from homoplasy in the data, and to use the former to trace common descent of the species being studied. To explain statistical phylogenetics, we first must examine the basic phylogenetic principles of character analysis that underlie statistical phylogenetics.

A simple example illustrates cladistic analysis of DNA sequence data to examine phylogenetic relationships among species. The study group in this

example contains three species of chameleons, two from the island of Madagascar (*Brookesia theili* and *B. brygooi*) and one from Equatorial Guinea (*Chamaeleo feae*). The outgroup is a lizard of genus *Uromastyx*, which is a distant relative of chameleons. Do the molecular data in this example confirm or reject the prior taxonomic hypothesis that the two Madagascan chameleons are more closely related to each other than either one is to the Equatorial Guinean species?

The molecular information in this example comes from a piece of the mitochondrial DNA sequence (57 bases) for each species. Each sequence encodes amino acids 221–239 of a protein called “NADH dehydrogenase subunit 2” in the species from which it was obtained. These DNA base sequences are aligned and numbered as follows:

	10	20	30	40	50
<i>Uromastyx</i>	AAACCTTAAAAGACACCACAACCATATGAACAACAACACCAACAATCAGC	CACACTAC			
<i>B. theili</i>	AAACACTACAAAATATAACAACCTGCATGAACAACATCAACCACAGCAAACATTTTAC				
<i>B. brygooi</i>	AAACACTACAAGACATAACAACAGCATGAACTACTTCAACAACAGCAAATATTACAC				
<i>C. feae</i>	AAACCCTACGAGACGCAACAACAATATGATCCACTTCCCCCACAACAACACAATTT				

Each column in the aligned sequences constitutes a character that takes one of four states: A, C, G, or T (a fifth possible state, absence of a base, is not observed in this example). Only characters that vary among the three

chameleon species potentially contain information on which pair of species is most closely related. Twenty-three of the 57 aligned bases show variation among chameleons, as shown here in bold letters:

	10	20	30	40	50
<i>Uromastyx</i>	AAACCTTAAA <b>AGACACCACAACCATATGAACAACAACACCAACAATCAGC</b>	<b>CACACTAC</b>			
<i>B. theili</i>	AAACACTAC <b>AAAATATAACAACCTGCATGAACAACATCAACCACAGCAAACATTTTAC</b>				
<i>B. brygooi</i>	AAACACTACA <b>AGACATAACAACAGCATGAACTACTTCAACAACAGCAAATATTACAC</b>				
<i>C. feae</i>	AAACCCTAC <b>GAGACGCAACAACAATATGATCCACTTCCCCCACAACAACACAATTT</b>				

To be useful for constructing a cladogram, a character must demonstrate sharing of derived states (=synapomorphy). Which of these 23 characters demonstrate synapomorphies for chameleons? For each of the 23 variable characters, we must ask whether one of the states observed in chameleons

is shared with the outgroup, *Uromastyx*. If so, this state is judged ancestral for chameleons and the alternative state(s) derived. Derived states are identified for 21 of the 23 characters just identified; derived states are shown in blue:

	10	20	30	40	50
<i>Uromastyx</i>	AAACCTTAAA <b>AGACACCACAACCATATGAACAACAACACCAACAATCAGC</b>	<b>CACACTAC</b>			
<i>B. theili</i>	AAAC <b>ACTACAAAATATAACAACCTGCATGAACAACATCAACCACAGCAAACATTTTAC</b>				
<i>B. brygooi</i>	AAAC <b>ACTACAAGACATAACAACAGCATGAACTACTTCAACAACAGCAAATATTACAC</b>				
<i>C. feae</i>	AAACCCTAC <b>GAGACGCAACAACAATATGATCCACTTCCCCCACAACAACACAATTT</b>				

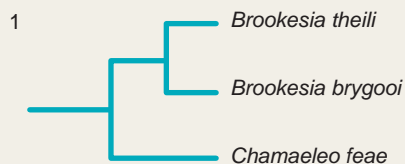
Note that polarity is ambiguous for two variable characters (at positions 23 and 54) whose alternative states in chameleons are not observed in the outgroup.

Of the characters showing derived states, 10 of them show synapomorphies among chameleons. These characters are marked here with numbers 1, 2, or 3 below the appropriate column.

	10	20	30	40	50
<i>Uromastyx</i>	AAACCTTAAA <b>AGACACCACAACCATATGAACAACAACACCAACAATCAGC</b>	<b>CACACTAC</b>			
<i>B. theili</i>	AAAC <b>ACTACAAAATATAACAACCTGCATGAACAACATCAACCACAGCAAACATTTTAC</b>				
<i>B. brygooi</i>	AAAC <b>ACTACAAGACATAACAACAGCATGAACTACTTCAACAACAGCAAATATTACAC</b>				
<i>C. feae</i>	AAACCCTAC <b>GAGACGCAACAACAATATGATCCACTTCCCCCACAACAACACAATTT</b>				
	1	1	11	2 1 3	1 11

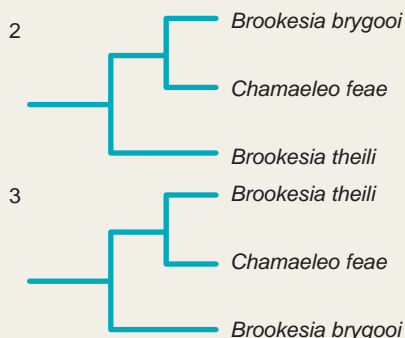


The eight characters marked 1 show synapomorphies grouping the two Madagascar species (*Brookesia theili* and *B. brygooi*) to the exclusion of the Equatorial Guinean species, *Chamaeleo feae*. We can represent these relationships as a cladogram:

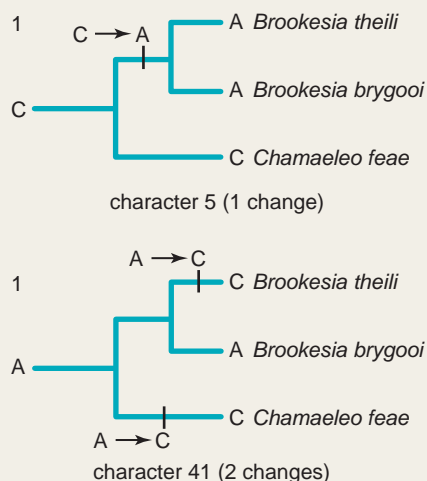


We can explain evolution of all characters favoring this cladogram by placing a single mutational change on the branch ancestral to the two *Brookesia* species. This is the simplest explanation for evolutionary change of these characters.

Characters marked 2 and 3 disagree with our cladogram and favor alternative relationships as shown here:



To explain evolutionary changes in characters favoring cladograms 2 or 3 using cladogram 1, we need at least two changes per character. Likewise, if we try to explain evolution of characters favoring cladogram 1 on cladograms 2 or 3, we need at least two changes for each of these characters. These two diagrams show the minimum numbers of changes required for character 5 (which favors cladogram 1) and character 41 (which favors cladogram 3) on cladogram 1; the ancestral state of each character is shown at the root of the tree and the states observed in each species at the tips of the branches:



A principle called **parsimony** can be used to resolve conflicts among taxonomic characters, as seen here. Parsimony represents the simplest limiting case of the maximum-likelihood and Bayesian methods for statistical

inference of phylogeny, so we present it first and then show how the statistical methods build on this framework. We choose as our best working hypothesis the cladogram that requires the smallest total amount of character change. In our example, parsimony favors cladogram 1. For all 10 phylogenetically informative characters, cladogram 1 requires a total of 12 changes of character state (one for each of the 8 characters favoring it and two for each of the other 2 characters). Cladograms 2 and 3 each require at least 19 character-state changes, 7 steps longer than cladogram 1. By choosing cladogram 1, we claim that characters favoring cladograms 2 and 3 show homoplasy in their evolution.

The molecular sequences shown in this example therefore confirm predictions of the prior hypothesis, based on appearance and geography of these chameleons, that the *Brookesia* species shared a common ancestor with each other more recently than either one did with *Chamaeleo feae*.

As a further exercise, you should convince yourself that the 12 characters that vary among chameleons but which do not demonstrate unambiguous sharing of derived states are equally compatible with each of the three possible cladograms. For each character, find the minimum total number of changes that must occur to explain its evolution on each cladogram. You will see, if you do this exercise correctly, that the three cladograms do not differ in minimum numbers of changes required for each of these characters. For this reason, the characters are phylogenetically uninformative by the parsimony criterion.

The parsimony method just illustrated makes some assumptions: that base substitutions are equally likely to occur at any of the 57 sites, that all 3 possible substitutions are equally likely at any site (for example, at site 5 one assumes that C would be equally likely to change to A, G, or T given that a substitution occurs), and that the expected amount of molecular evolution on any branch is proportional to its temporal duration. Suppose that site 16 is unusually subject to mutational change, that a change from C to T is ten times more likely than one from C to A or G, and that the internal branch on the tree is very short compared to the tip branches (those that terminate in a living species whose DNA sequence was determined). The likelihood of getting the observed data for that site by parallel changes C to T in the tip branches of the two *Brookesia* species might equal or exceed the likelihood of a single change C to T in the internal branch of hypothesis 1. The data at site 16 then would not necessarily favor hypothesis 1 over the alternatives. If we can obtain detailed knowledge of the evolutionary properties of the sites in this DNA sequence (for example, by studying its evolution in a large number of lizards), we might favor a phylogenetic method that incorporates a detailed model of DNA-sequence evolution.

Maximum-likelihood and Bayesian approaches to phylogenetic inference are efficient means for using detailed models of molecular evolution to test phylogenetic hypotheses from aligned DNA sequences. First, we analyze the aligned sequences to estimate an evolutionary model: how much do sites differ from each other in their tendencies to vary, and which kinds of substitutions (C to A, C to G, C to T, etc.) are most likely to occur? Second, we evaluate each site with respect to each of the alternative possible trees to determine which tree has the highest likelihood of producing the observed data (such as the CTTC pattern shown for site 16). In this second step, branches of the tree can vary in length, relaxing the assumption that expected amounts of substitution are proportional to the temporal duration of the branch. For our data, the maximum-likelihood method would evaluate the probability of observing the results in each of the 57 columns considering all possible trees, and measure the likelihood of the entire data set for each contrasting tree. The tree with the highest likelihood of producing the observed data is the favored phylogenetic hypothesis. We can reject contrasting trees whose likelihoods are judged much lower than would be expected by chance alone. The Bayesian approaches operate in a similar

manner, but they permit an investigator to evaluate the contributions of a new data set relative to prior results. For example, we could evaluate the probability that the data favor hypothesis 1 after incorporating phylogenetic results for these same species obtained from another data set. Calculating likelihoods for contrasting trees is part of the Bayesian operation, and in most phylogenetic applications this is the critical factor in favoring one tree over alternatives. For this reason, results of maximum-likelihood and Bayesian analyses are usually the same, with Bayesian analyses currently more popular because of computational efficiency.

Note that the maximum-likelihood and Bayesian approaches use more of the data set than our parsimony analysis did. To estimate branch lengths (numbers of substitutions occurring on them), sites whose derived states arose on a single terminal branch contribute useful information. Given hypothesis 1, the terminal branch connecting *C. feae* to the tree is longer than the terminal branches connecting the *Brookesia* species to their most recent common ancestor with each other. Using sites for which we identified derived states in the preceding exercise but which were not parsimony informative, we see that the terminal branch leading to *C. feae* requires 7 substitutions (sites 10, 15, 30, 32, 38, 56, 57), whereas the terminal branch leading to *B. brygooi* requires only 3 changes (sites 32, 50, 55), and the terminal branch leading to *B. theili* requires only two changes (sites 12, 14). Using the maximum-likelihood method, these sites collectively would favor hypothesis 1 even though none of the sites is parsimony informative.

We thus expect parallel substitutions to occur more frequently in the *C. feae* lineage and one of the two *Brookesia* lineages (as probably occurred at sites 35 and 41) than in both *Brookesia* lineages (a pair of parallel changes on the *Brookesia* lineages would produce a parsimony-informative site favoring hypothesis 1, indistinguishable in our data from sites undergoing one change in the lineage immediately ancestral to the two *Brookesia* species).

The previous two paragraphs should make clear why inferring phylogenies using maximum-likelihood and Bayesian approaches would be very hard to do by hand, even for the data in our example. Finding the optimal tree topologies, branch lengths, relative probabilities of substitution at different sites, and relative probabilities of different kinds of substitution requires testing many alternative conditions and comparing their likelihoods. Computer algorithms can explore this parameter space in an efficient manner, but it would be prohibitively tedious to do by hand. Nonetheless, sharing of derived states at a site as predicted by hypotheses of homology remains the primary reason why the tree that requires only a single evolutionary change to explain the observed variation has a higher likelihood than do trees that require two or more parallel substitutions. Statistical inference of phylogeny using maximum-likelihood and Bayesian methods thus remains grounded in the basic cladistic principles. When parameters of the maximum-likelihood and Bayesian analyses are set to the simple conditions used for parsimony analysis, their results correspond to those that we obtained using parsimony.

---

Data from Townsend, T., and A. Larson. 2002. Molecular phylogenetics and mitochondrial genomic evolution in the Chamaeleonidae (Reptilia, Squamata). *Molecular Phylogenetics and Evolution* 23:22–36.

Revision of taxonomy according to cladistic principles can cause confusion. In addition to new taxonomic names, we see old ones used in unfamiliar ways. For example, cladistic use of “bony fishes” includes amphibians and amniotes (including non-avian reptilian groups, birds, and mammals) in addition to finned, aquatic animals that we normally term “fish.” Cladistic use of “reptiles” includes birds in addition to snakes, lizards, turtles, and crocodylians; however, it excludes some fossil forms, such as synapsids, that were traditionally placed in Reptilia (see Chapters 26 through 28). Taxonomists must be very careful to specify when using these seemingly familiar terms whether the traditional evolutionary taxa or newer cladistic taxa are being referenced.

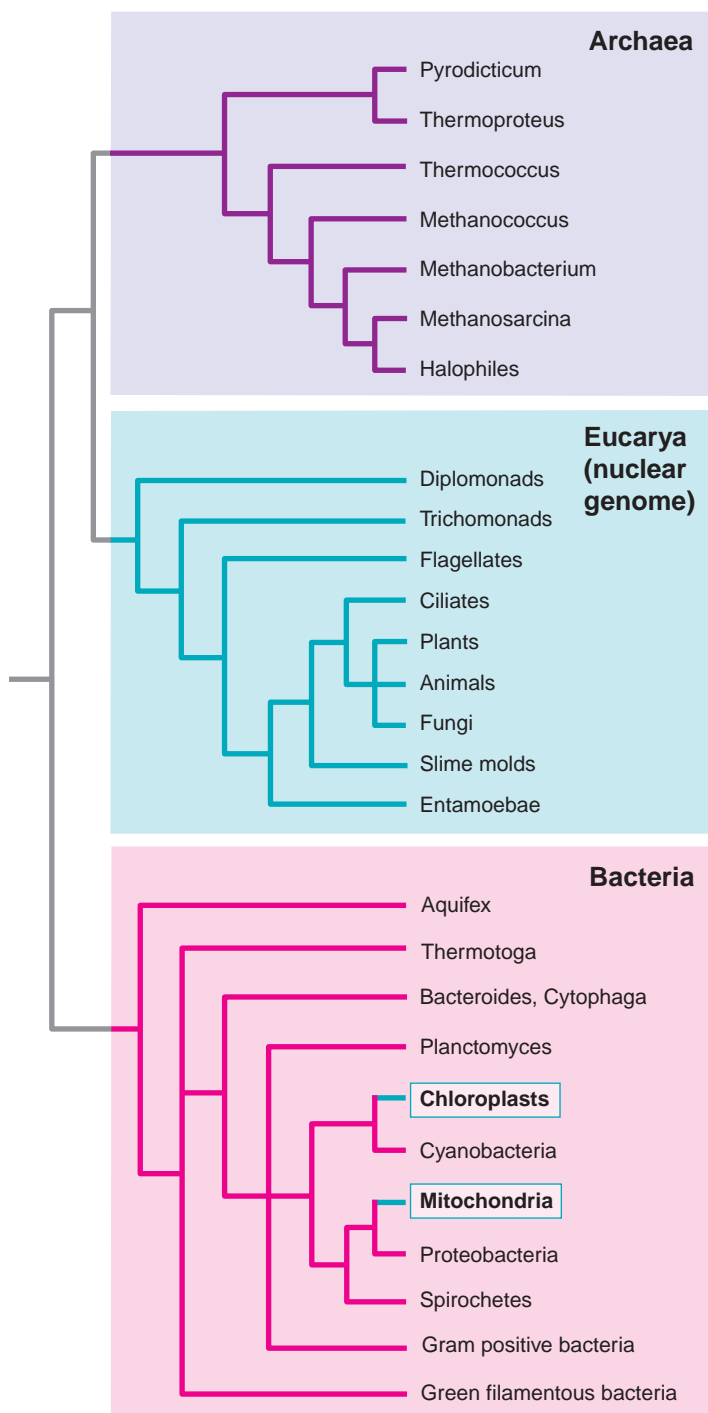
## MAJOR DIVISIONS OF LIFE

From Aristotle’s time to the late 1800s, every living organism was assigned to one of two kingdoms: plant or animal. However, the two-kingdom system had serious problems. Fungi and unicellular organisms presented difficulties (see Chapter 11). Some forms were claimed both for the plant kingdom by botanists and for the animal kingdom by zoologists. An example is *Euglena* (p. 223), which is motile, like animals, but has chlorophyll and photosynthesis, like plants. Other groups, such as bacteria, were assigned rather arbitrarily to the plant kingdom.

Several alternative systems have been proposed to solve the problem of classifying unicellular forms. In 1866 Haeckel proposed the new kingdom Protista to include all single-celled organisms.

At first bacteria and cyanobacteria (blue-green algae), forms that lack nuclei bounded by a membrane, were included with nucleated unicellular organisms. Eventually, important differences were recognized between the anucleate bacteria and cyanobacteria (prokaryotes) and all other organisms that have membrane-bound nuclei (eukaryotes). In 1969 R. H. Whittaker proposed a five-kingdom system that incorporated the basic prokaryote-eukaryote distinction. The kingdom Monera contained the prokaryotes. The kingdom Protista contained the unicellular eukaryotic organisms (protozoa and unicellular eukaryotic algae). Multicellular organisms were split into three kingdoms by mode of nutrition and other fundamental differences in organization. The kingdom Plantae included multicellular photosynthesizing organisms, higher plants, and multicellular algae. Kingdom Fungi contained molds, yeasts, and fungi that obtain their food by absorption. Invertebrates (except the protozoa) and vertebrates compose the kingdom Animalia. Most of these forms ingest their food and digest it internally, although some parasitic forms are absorptive.

These different systems were proposed without regard to the phylogenetic relationships needed to construct evolutionary or cladistic taxonomies. The oldest phylogenetic events in the history of life have been obscure because the different forms of life share very few characters that can be compared among them to reconstruct phylogeny. More recently, however, a cladistic classification of all life-forms has been proposed based on phylogenetic information obtained from molecular data (the nucleotide base sequence of DNA encoding ribosomal RNA). According to this tree (Figure 10.11),



**Figure 10.11** Phylogenetic overview of the three domains of life, Archaea, Eucarya, and Bacteria, based on analysis of genes encoding ribosomal RNA. Because of their endosymbiotic origin (p. 31), organellar genomes of domain Eucarya (mitochondria, chloroplasts) are phylogenetically within the Bacteria rather than the clade that includes all eukaryotic nuclear genomes. Organisms of domain Eucarya therefore include cellular components of disparate evolutionary origins.

Woese, Kandler, and Wheelis (1990) recognized three monophyletic **domains** above the kingdom level: Eucarya (all eukaryotes), Bacteria (the true bacteria), and Archaea (prokaryotes differing from bacteria in membrane structure and ribosomal RNA sequences). They did not divide Eucarya into kingdoms, although if we retain Whittaker's kingdoms Plantae, Animalia, and Fungi, Protista becomes a paraphyletic group (Figure 10.11). To maintain a cladistic classification, Protista must be discontinued by recognizing as separate kingdoms all of the labeled branches of Eucarya as shown in Figure 10.11.

Until a few years ago, animal-like protists were traditionally studied in zoology courses as animal phylum Protozoa. Given current knowledge and the principles of phylogenetic systematics, this taxonomy commits two errors: "protozoa" are not animals; nor are they a valid monophyletic taxon at any level. Kingdom Protista is likewise invalid because it is not monophyletic. Animal-like protists, now divided into seven or more phyla, are nonetheless of interest to students of zoology because they provide an important phylogenetic context for the study of animal diversity.

## MAJOR SUBDIVISIONS OF THE ANIMAL KINGDOM

The phylum is the largest formal taxonomic category in the Linnaean classification of the animal kingdom. Animal phyla are often grouped together to produce additional, informal taxa intermediate between the phylum and the animal kingdom. Taxon Eumetazoa includes all animal phyla except Porifera and Placozoa, with the placement of phylum Mesozoa in Eumetazoa remaining controversial. Taxon Eumetazoa is divided into Radiata (phyla Cnidaria and Ctenophora) and Bilateria (all remaining eumetazoan phyla).

Bilateral animals are customarily divided into Protostomia and Deuterostomia based on their embryological development (p. 169), with further subdivision of taxon Protostomia into taxa Lophotrochozoa and Ecdysozoa (see Chapter 14 for details):

### Bilateria

#### Division A (Protostomia):

##### Phylum Chaetognatha

Lophotrochozoa: phyla Platyhelminthes, Nemertea, Rotifera, Gastrotricha, Acanthocephala, Mollusca, Annelida, Echiurida, Sipunculida, Phoronida, Ectoprocta, Entoprocta, Gnathostomulida, Micrognathozoa, Brachiopoda

Ecdysozoa: phyla Kinorhyncha, Nematoda, Nematomorpha, Priapulida, Arthropoda, Tardigrada, Onychophora, Loricifera

#### Division B (Deuterostomia): phyla Chordata, Hemichordata, Echinodermata

We present the details of animal taxonomy in Chapters 12–28.



## SUMMARY

Animal systematics has three major goals: (1) to identify all species of animals, (2) to evaluate evolutionary relationships among animal species, and (3) to group animal species in a hierarchy of taxonomic groups (taxa) that conveys evolutionary relationships. Taxa are ranked to denote increasing inclusiveness as follows: species, genus, family, order, “class,” phylum, and kingdom. All of these ranks can be subdivided to signify taxa that are intermediate between them. Names of species are binomial, with the first name designating the genus to which the species belongs (capitalized) followed by a species epithet (lowercase), both written in italics. Taxa at all other ranks are given single capitalized but nonitalicized names.

The biological species concept has guided the recognition of most animal species. A biological species is defined as a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature. A biological species is not immutable through time but changes during the course of evolution. Because the biological species concept may be difficult to apply in spatial and temporal dimensions, and because it excludes asexually reproducing forms, alternative concepts have been proposed. These alternatives include the evolutionary species concept, the cohesion species concept, and the phylogenetic species concept. No single concept of species is universally accepted by all zoologists, but zoologists agree that a species should constitute a population lineage with a history of evolutionary descent separate from other such lineages. Because species lineages are expected to differ from each other in the DNA sequence of the rapidly evolving mitochondrial gene *COI*, this gene sequence is used as a diagnostic “barcode” to assign specimens to species.

Two major schools of taxonomy are currently active. Evolutionary taxonomy groups species into higher taxa according to the joint criteria of common descent and adaptive evolution; such taxa have a single evolutionary origin and occupy a distinctive adaptive zone. A second approach, called phylogenetic systematics or cladistics, emphasizes common descent exclusively in grouping species into higher taxa. Only monophyletic taxa (those having a single evolutionary origin and containing all descendants of the group’s most recent common ancestor) are used in cladistics. In addition to monophyletic taxa, evolutionary taxonomy recognizes some taxa that are paraphyletic (having a single evolutionary origin but excluding some descendants of the most recent common ancestor of the group). Both schools of taxonomy exclude polyphyletic taxa (those having more than one evolutionary origin).

Both evolutionary taxonomy and cladistics require that patterns of common descent among species be assessed before higher taxa are recognized. Comparative morphology (including development), cytology, and biochemistry are used to reconstruct nested hierarchical relationships among taxa that reflect the branching of evolutionary lineages through time. The fossil record provides estimates of the ages of evolutionary lineages. We diagnose clades by identifying shared derived characters, formally called synapomorphies, that distinguish members of the clade from all other taxa. We hypothesize that such synapomorphies represent homologies that arose in the clade’s most recent common ancestor. Comparative studies of living species and the fossil record jointly permit us to reconstruct a phylogenetic tree representing the evolutionary history of the animal kingdom. Using a simple example, we illustrate how a systematist infers a phylogenetic tree from aligned DNA sequences using the principles of maximum-parsimony, maximum-likelihood, and Bayesian statistics.

Traditionally, all living forms were placed into two kingdoms (animal and plant) or more recently into a five-kingdom system (animals, plants, fungi, protists, and monerans). Neither of these systems conforms to the principles of evolutionary or cladistic taxonomy because they place single-celled organisms into either paraphyletic or polyphyletic groups. Based on our current knowledge of the phylogenetic tree of life, “protozoa” do not form a monophyletic group and they do not belong within the animal kingdom. The three most inclusive taxa of living organisms consistent with cladistic taxonomy are domains Archaea, Bacteria, and Eukarya, which includes animals. The most inclusive formal taxon within animals is the phylum, but zoologists commonly use some more inclusive but controversial informal taxa above the phylum level.

Phylogenetic relationships among animal phyla have been clarified by molecular phylogenetic studies, although many of these higher-level groupings remain tentative. Particularly controversial is the grouping of bilaterally symmetrical animals into clades Deuterostomia, Protostomia, Ecdysozoa, and Lophotrochozoa.

## REVIEW QUESTIONS

- List in order, from most inclusive to least inclusive, the principal categories (taxa) in Linnaean classification as currently applied to animals.
- Explain why the system for naming species that originated with Linnaeus is “binomial.”
- How does the biological species concept differ from earlier typological concepts of a species? Why do evolutionary biologists prefer it to typological species concepts?
- What problems have been identified with the biological species concept? How do other species concepts attempt to overcome these problems?
- How are taxonomic characters recognized? How are such characters used to construct a cladogram?
- How do monophyletic, paraphyletic, and polyphyletic taxa differ? How do these differences affect the validity of such taxa for both evolutionary and cladistic taxonomies?
- How many different clades of two or more species are possible for species A–H shown in Figure 10.7A?
- What is the difference between a cladogram and a phylogenetic tree? Given a cladogram for a group of species, what additional interpretation is needed to obtain a phylogenetic tree?
- How would cladists and evolutionary taxonomists differ in their interpretations of the statement that humans evolved from apes, which evolved from monkeys?
- What taxonomic practices based on the typological species concept are retained in systematics today? How has their interpretation changed?
- What are the five kingdoms distinguished by Whittaker? How does their recognition conflict with the principles of cladistic taxonomy?

**For Further Thought** If a taxonomist constructs a rooted phylogenetic tree for a group of living species, the structure of the tree alone can be used to distinguish hypotheses of monophyly versus nonmonophyly of a particular subgroup. If monophyly is rejected for a particular subgroup, tree topology alone cannot distinguish paraphyly from polyphyly. What additional information is needed to distinguish paraphyly from polyphyly?

## SELECTED REFERENCES

- Avice, J. C. 2006. Evolutionary pathways in nature: a phylogenetic approach. Cambridge, U.K., Cambridge University Press. *A synthetic treatment of phylogenetic knowledge.*
- Baum, D. A., and S. D. Smith. 2013. Tree thinking: an introduction to phylogenetic biology. Greenwood Village, CO, Roberts and Company Publishers. *A thorough coverage of phylogenetic principles for beginners.*
- de Queiroz, K. 1988. Systematics and the Darwinian revolution. *Philosophy of Science* **55**:238–259. *Criticism of evolutionary taxonomy by a phylogenetic systematist, including the contrast between classification and systematization.*
- Ereshefsky, M. (ed.). 1992. The units of evolution. Cambridge, Massachusetts, MIT Press. *A thorough coverage of concepts of species, including reprints of important papers on the subject.*
- Ereshefsky, M. 2001. The poverty of the Linnaean hierarchy. Cambridge, U.K., Cambridge University Press. *A philosophical critique of Linnaean taxonomy illustrating its problems with cladistic taxonomy.*
- Felsenstein, J. 2004. Inferring phylogenies. Sunderland, Massachusetts, Sinauer Associates, Inc. *A thorough coverage of phylogenetic methods.*
- Hall, B. K. 1994. Homology: the hierarchical basis of comparative biology. San Diego, Academic Press. *A collection of papers discussing the many dimensions of homology, the central concept of comparative biology, and systematics.*
- Hull, D. L. 1988. Science as a process. Chicago, University of Chicago Press. *A study of the working methods and interactions of systematists, containing a thorough review of the principles of evolutionary, phenetic, and cladistic taxonomy.*
- Maddison, W. P., and D. R. Maddison. 2008. MacClade version 4.08. Sunderland, Massachusetts, Sinauer Associates, Inc. *A computer program for the MacIntosh that conducts phylogenetic analyses of systematic characters. The instruction manual stands alone as an excellent introduction to phylogenetic procedures. The computer program is user-friendly and excellent for instruction in addition to serving as a tool for analyzing real data.*
- Swofford, D. 2002. Phylogenetic analysis using parsimony (and other methods) PAUP\* version 4. Sunderland, Massachusetts, Sinauer Associates, Inc. *A powerful computer package for constructing phylogenetic trees from data.*
- Valentine, J. W. 2004. On the origin of phyla. Chicago, University of Chicago Press. *Phylogenetic analysis of animal phyla in a paleontological perspective.*
- Wagner, G. P. (ed.). 2001. The character concept in evolutionary biology. San Diego, Academic Press. *A thorough coverage of evolutionary character concepts.*
- Woese, C. R., O. Kandler, and M. L. Wheelis. 1990. Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National Academy of Sciences, USA*, **87**:4576–4579. *Proposed cladistic classification for the major taxonomic divisions of life.*

Visit [www.mhhe.com/hickmanipz16e](http://www.mhhe.com/hickmanipz16e) for chapter quizzing, key term flash cards, web links, and more!