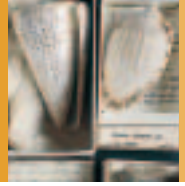


chapter four

Classification and Phylogeny of Animals

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, diversity of animals is not without limits. There are many conceivable forms that do not exist in nature, as our myths of minotaurs and winged horses show. Animal diversity is not random but has a definite order. Characteristic features of humans and cattle never occur together in a single organism as they do in mythical minotaurs. Nor do the 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. Animals may be classified in some societies according to their usefulness or destructiveness to human endeavors. Others may group animals according to their roles in mythology. Biologists group animals according to their evolutionary relationships as revealed by ordered patterns in their sharing of homologous features. This classification 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 classify them accordingly.

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

Darwin's theory of common descent (see Chapter 1) is the underlying principle that guides our search for order in diversity of animal life. Our science of taxonomy ("arrangement law") produces a formal system for naming and classifying species that reflects this order. Animals that have very recent common ancestry share many features in common and are grouped most closely in our taxonomic classification; dissimilar animals that share only very ancient common ancestry are placed in different taxonomic groups except at the "highest" or most inclusive levels of taxonomy. Taxonomy is part of a broader science of **systematics,** which uses everything known about animals to understand their evolutionary relationships. Taxonomy predates evolutionary biology, however, and many taxonomic practices are relics of pre-evolutionary world views. 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 with several alternative taxonomic systems competing for use. To understand this controversy, we need to review the history of animal taxonomy.

figure 4.1
Carolus Linnaeus (1707–1778). This portrait was made of Linnaeus at age 68, three years before his death.

Linnaeus and the Development of Classification

The Greek philosopher and biologist Aristotle was the first to classify organisms based on their structural similarities. Following the Renaissance in Europe, the English naturalist John Ray (1627–1705) introduced a more comprehensive system of classification and a new concept of species. Rapid growth of systematics in the eighteenth century culminated in the work of Carolus Linnaeus (1707–1778; figure 4.1), who produced our current scheme of classification.

Linnaeus was a Swedish botanist at the University of Uppsala. He had a great talent for collecting and classifying objects, 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 classes. Because his knowledge of animals was limited, his lower categories, such as genera, were very broad and included animals that are only distantly related. Much of his classification has been drastically altered, but his basic principles are still followed.

Linnaeus's scheme of arranging organisms into an ascending series of groups of increasing inclusiveness is a **hierarchical system** of classification. The major categories, or **taxa** (sing., **taxon**), into which organisms are grouped are given one of several standard taxonomic ranks to indicate the general inclusiveness of each group. The hierarchy of taxonomic ranks has been expanded considerably since Linnaeus's time (table 4.1). It now includes seven mandatory ranks for the animal kingdom, in descending series: kingdom, phylum, class, order, family, genus, and species. All organisms being classified must be placed into at least seven taxa, one at each of these mandatory ranks. Taxonomists have the option of subdividing these seven ranks even further to recognize more than seven taxa (superclass, subclass, infraclass, superorder, suborder, and others) for any particular group of organisms. More than 30 taxonomic ranks now 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. Unfortunately, they also make taxonomy more complex.

Linnaeus's system for naming species is known as **binomial nomenclature.** Each species has a Latinized name composed of two words (hence binomial) written in italics (underlined if handwritten or typed). The first word is the name of the **genus,** written with a capital initial letter; the second word is the **species epithet** which is peculiar to the species within the genus and is written with a small initial letter (table 4.1). The name of a genus 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 a common robin is *Turdus migratorius* (L. *turdus,* thrush; *migratorius,* of the migratory habit). A 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; a single name cannot be given to two different genera of animals. The same species epithet may be used in different genera, however, to denote different and unrelated species. For example, the scientific name of a white-breasted nuthatch is *Sitta carolinensis.* The species epithet *"carolinensis"* is used in other genera, including *Parus carolinensis* (Carolina chickadee) and *Anolis carolinensis* (green anole, a lizard) to mean "of Carolina." All ranks above species are designated using uninomial nouns, written with a capital initial letter.

table 4.1 Examples of Taxonomic Categories to Which Representative Animals Belong

	Human	Gorilla	Southern Leopard Frog	Bush Katydid
Kingdom	Animalia	Animalia	Animalia	Animalia
Phylum	Chordata	Chordata	Chordata	Arthropoda
Subphylum	Vertebrata	Vertebrata	Vertebrata	Uniramia
Class	Mammalia	Mammalia	Amphibia	Insecta
Subclass	Eutheria	Eutheria	—	Pterygota
Order	Primates	Primates	Anura	Orthoptera
Suborder	Anthropoidea	Anthropoidea	—	Ensifera
Family	Hominidae	Pongidae	Ranidae	Tettigoniidae
Subfamily	—	—	Raninae	Phaneropterinae
Genus	*Homo*	*Gorilla*	*Rana*	*Scudderia*
Species	*Homo sapiens*	*Gorilla gorilla*	*Rana sphenocephala*	*Scudderia furcata*
Subspecies	—	—	—	*Scudderia furcata furcata*

Hierarchical classification applied to four species (human, gorilla, Southern leopard frog, and bush katydid). Higher taxa generally are more inclusive than lower-level taxa, although taxa at two different levels may be equivalent in content (for example, family Hominidae contains only the genus Homo, *making these taxa equivalent in content, whereas the family Pongidae contains genera* Gorilla, Pan, *and* Pongo, *making it more inclusive than any of these genera). 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 suborder (Anthropoidea) and above; they are united with Southern leopard frogs at the subphylum level (Vertebrata) and with bush katydids at the kingdom (Animalia) level.*

Taxonomic Characters and Reconstruction of Phylogeny

A major goal of systematics is to reconstruct an evolutionary tree or **phylogeny** that relates all extant and extinct species. This tree is constructed by studying organismal features, formally called **characters,** that vary among species. A character is any feature that a taxonomist uses to study variation within or among species. We find potentially useful taxonomic characters in morphological, chromosomal, and molecular features. Taxonomists find characters by observing patterns of similarity among organisms. If two organisms possess similar features, they may have inherited these features from an equivalent one in a common ancestor. Character similarity that results from common ancestry is called **homology** (see p. 15). Similarity does not always reflect common ancestry, however. Independent evolutionary origins of similar features on different lineages produce patterns of similarity among organisms that do not reflect common descent; this occurrence complicates the work of taxonomists. Character similarity that misrepresents common descent is called nonhomologous similarity or **homoplasy.**

Some species are divided into subspecies, in which case a trinomial nomenclature is employed (see katydid example, table 4.1). Thus to distinguish the southern form of the robin from the eastern robin, the scientific term *Turdus migratorius achrustera* (duller color) is employed for the southern type. Generic, specific, and subspecific names are printed in italics (underlined if handwritten or typed). A subspecies name may be a repetition of the species epithet. Formal recognition of subspecies has lost popularity among taxonomists because boundaries between subspecies rarely are distinct. Recognition of subspecies usually is based on one or a few superficial characters that do not diagnose an evolutionarily distinct unit. Subspecies, therefore, should not be taken too seriously.

Using Character Variation to Reconstruct Phylogeny

To reconstruct phylogeny of a group using characters that vary among its members, the first step is to determine which variant form of each character was present in the most recent common ancestor of the entire group. This form is called the

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 often appear after a species name. Thus, *Didelphis marsupialis* Linnaeus, 1758, tells us that Linnaeus was the first person to publish the species name of opossums. The authority citation is not part of the scientific name but rather is an abbreviated bibliographical reference. Sometimes, generic status of a species is revised following its initial description. In this case, the authority's name is presented in parentheses.

ancestral character state for the group as a whole. We presume that all other variant forms of the character arose later within the group, and these forms are called evolutionarily **derived character states. Polarity** of a character refers to ancestral/descendant relationships among its different states. For example, if we consider as a character dentition of amniotic vertebrates (reptiles, birds, and mammals), presence versus absence of teeth constitute two different character states. Teeth are absent from birds but present in other amniotes. To evaluate 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 polarity of a variable character is called **outgroup comparison.** We begin by selecting an additional group of organisms, called an **outgroup,** that is phylogenetically close but not within the group being studied. Amphibians and different groups of bony fishes constitute appropriate outgroups to amniotes for polarizing variation in dentition of amniotes. Next, we infer that any character state found both within the group being studied and in an outgroup is ancestral for the study group. 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. Polarity of this character indicates that teeth were lost in an ancestral lineage of all modern birds. Polarity of characters is evaluated most effectively when several different outgroups are used. All character states found in a study group that are absent from appropriate outgroups are considered derived (see figure 4.2 for additional examples).

Organisms or species that share derived character states form subsets within the study group; these subsets are called **clades** (Gr. *klados,* branch). A derived character shared by 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 organisms forms a clade. Within amniotes, absence of teeth and presence of feathers are synapomorphies that identify birds as a clade. A clade corresponds to a unit of evolutionary common descent; it includes the most recent common ancestor of a group and all of that ancestor's descendants. The pattern formed by derived states of all characters within our study group will take the form of a **nested hierarchy** of clades within clades. The goal is to identify all clades nested within the study group, which would reveal patterns of common descent among all species in the group.

A nested hierarchy of clades is presented as a branching diagram called a **cladogram** (figure 4.2; see also figure 1.17). Taxonomists often make a technical distinction between a cladogram and a **phylogenetic tree.** The branches on a cladogram are only a formal device for indicating a nested hierarchy of clades within clades. A 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 a cladogram information concerning ancestors, durations of evolutionary lineages, or amounts of evolutionary change that occurred on lineages. Because the branching order of a cladogram matches that of the corresponding phylogenetic tree, however, a cladogram often serves as a first approximation of the structure of the corresponding phylogenetic tree.

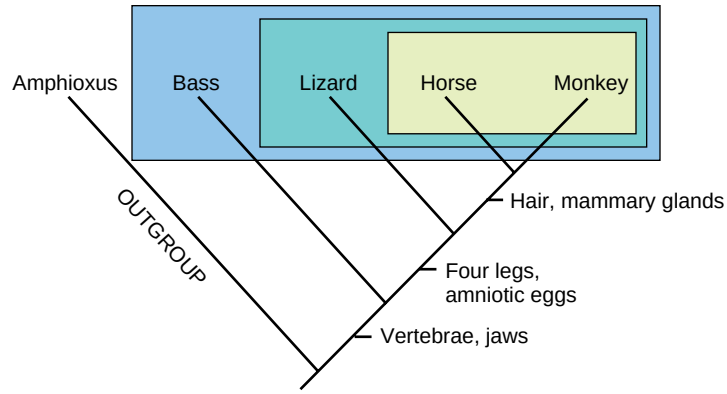


figure 4.2

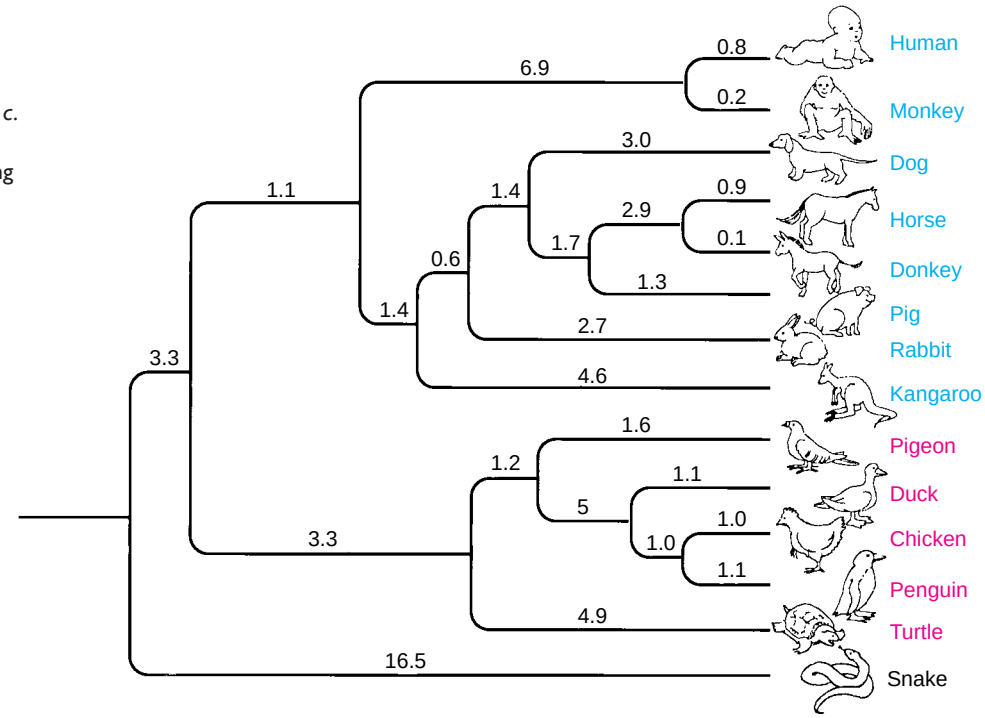
A cladogram as a nested hierarchy of taxa. *Amphioxus* (p. 292) is the outgroup, and the study group comprises four vertebrates (bass, lizard, horse, and monkey). Four characters that vary among vertebrates are used to generate a simple cladogram: presence versus absence of four legs, amniotic eggs, hair, and mammary glands. For all four characters, absence is considered the ancestral state in vertebrates because this condition occurs in the outgroup, *Amphioxus;* for each character, presence is derived within vertebrates. Because they share presence of four legs and amniotic eggs as synapomorphies, lizards, horses, and monkeys form a clade relative to bass. This clade is subdivided further by two synapomorphies (presence of hair and mammary glands) that unite horses and monkeys relative to lizards. We know from comparisons involving even more distantly related animals that presence of vertebrae and jaws constitute synapomorphies of vertebrates and that *Amphioxus,* which lacks these features, falls outside the vertebrate clade.

Sources of Phylogenetic Information

We find characters used to construct cladograms in comparative morphology (including embryology), comparative cytology, and comparative biochemistry. **Comparative morphology** examines varying shapes and sizes of organismal structures, including their developmental origins. As we discuss in later chapters, 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 the sequences of amino acids in proteins and the sequences of nucleotides in nucleic acids to identify variable characters for constructing a cladogram or phylogenetic tree (figure 4.3). Recent work has shown that some fossils retain enough DNA for comparative biochemical studies. **Comparative cytology** uses variation in numbers, shapes, and sizes of chromosomes and their parts to obtain variable characters for constructing

figure 4.3

A phylogenetic tree of representative amniotes based on inferred base substitutions in the gene that encodes the respiratory protein, cytochrome *c*. Numbers on branches are estimated numbers of mutational changes that occurred in this gene along different evolutionary lineages.



cladograms. Comparative cytology is used almost exclusively on living rather than fossilized organisms because chromosomal structure is not well preserved in fossils.

To add the evolutionary timescale needed for producing a phylogenetic tree, we must consult the fossil record. We look for the earliest appearance of derived morphological characters in fossils to estimate ages of clades distinguished by those characters. The ages of fossils showing derived characters of a particular clade are determined by radioactive dating (p. 13) to estimate the age of the clade. A lineage representing the most recent common ancestor of all species in the clade is then added to the phylogenetic tree.

Theories of Taxonomy

A theory of taxonomy establishes principles that we use to recognize and to rank taxonomic groups. There are two currently popular theories of taxonomy: (1) traditional evolutionary taxonomy and (2) phylogenetic systematics (cladistics). Both are based on evolutionary principles. We will see, however, that these two theories differ on how evolutionary principles are used. These differences have important implications for how we use a taxonomy to study evolutionary processes.

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 4.4). A taxon is monophyletic if it includes the most recent common ancestor of all members of a group and all descendants of that ancestor (figure 4.4A). 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 4.4B). A taxon is polyphyletic if it does not include the most recent common ancestor of all members of a group; this situation requires the group to have had at least two separate evolutionary origins, usually requiring independent evolutionary acquisition of a diagnostic feature (figure 4.4C). For example, if birds and mammals were grouped in a taxon called Homeothermia, we would have a polyphyletic taxon because birds and mammals descend from two quite separate amniotic lineages that have evolved homeothermy independently. The most recent common ancestor of birds and mammals is not homeothermic and does not occur in the polyphyletic Homeothermia just described. Both evolutionary and cladistic taxonomy accept monophyletic groups and reject polyphyletic groups in their classifications. They differ regarding acceptance of paraphyletic groups.

Traditional Evolutionary Taxonomy

Traditional **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.

The mammalian paleontologist George Gaylord Simpson (figure 4.5) was highly influential in developing and formalizing principles of evolutionary taxonomy. According to Simpson, a particular branch on an evolutionary tree is given the status of 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

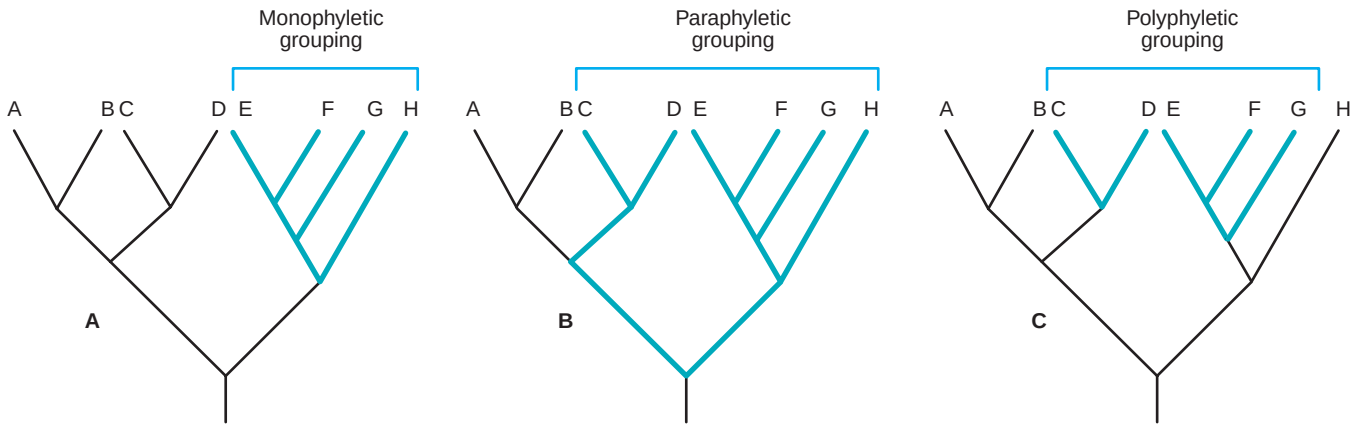


figure 4.4
Relationships between phylogeny and taxonomic groups illustrated for a hypothetical phylogeny of eight species (A through H). **A,** *Monophyly*—a monophyletic group contains the most recent common ancestor of all members of the group and all of its descendants. **B,** *Paraphyly*—a paraphyletic 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 does not contain the most recent common ancestor of all members of the group, thereby requiring the group to have at least two separate phylogenetic origins.

figure 4.5
George Gaylord Simpson (1902–1984) formulated principles of evolutionary taxonomy.

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 completely new way.

A taxon forming 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 form of the body and wings to permit a switch from aerial to aquatic locomotion (figure 4.6). Aquatic birds that can fly both in air and underwater are somewhat intermediate in habitat, morphology, and behavior between aerial and aquatic adaptive zones. Nonetheless, obvious modifications of a penguin's wings and body for swimming represent a new grade of organization. Penguins are therefore recognized as a distinct taxon within birds, family Spheniscidae. The Linnean rank of a taxon depends upon breadth of its adaptive zone: the broader the adaptive zone when fully occupied by a group of organisms, the higher the rank that the corresponding taxon is given.

Evolutionary taxa may be either monophyletic or paraphyletic. Recognition of paraphyletic taxa requires, however, that taxonomies distort patterns of common descent. An evolutionary taxonomy of anthropoid primates provides a good example (figure 4.7). This taxonomy places humans (genus *Homo*) and their immediate fossil ancestors in family Hominidae and places chimpanzees (genus *Pan*), gorillas (genus *Gorilla*), and orangutans (genus *Pongo*) in family Pongidae. However, pongid genera *Pan* and *Gorilla* share more recent common ancestry with *Hominidae* than they do with the remaining pongid genus, *Pongo.* Family Pongidae is therefore paraphyletic because it does not include humans, who also descend from its most recent common ancestor (figure 4.7). Evolutionary taxonomists nonetheless recognize pongid genera as a single, family-level grade of arboreal, herbivorous primates having limited mental capacity; in other words, they show a family-level adaptive zone. Humans are terrestrial, omnivorous primates who possess greatly expanded mental and cultural attributes, thereby comprising a distinct adaptive zone at the taxonomic level of a family. Unfortunately, if we want our taxa to constitute adaptive zones, we compromise our ability to present common descent in a straightforward taxonomic manner.

Traditional 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, overall similarity of organisms evaluated without regard to phylogeny. This

Phylogenies from DNA Sequences

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 the 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 Madagascaran 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:

```
                10        20        30        40        50
                 |         |         |         |         |
Uromastyx   AAACCTTAAAAGACACCACAACCATATGAACAACAACACCAACAATCAGCACACTAC
B. theili   AAACACTACAAAATATAACAACTGCATGAACAACATCAACCACAGCAAACATTTTAC
B. brygooi  AAACACTACAAGACATAACAACAGCATGAACTACTTCAACAACAGCAAATATTACAC
C. feae     AAACCCTACGAGACGCAACAACAATATGATCCACTTCCCCCACAACAAACACAATTT
```

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 the 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
                 |         |         |         |         |
Uromastyx   AAACCTTAAAAGACACCACAACCATATGAACAACAACACCAACAATCAGCACACTAC
B. theili   AAACACTACAAAATATAACAACTGCATGAACAACATCAACCACAGCAAACATTTTAC
B. brygooi  AAACACTACAAGACATAACAACAGCATGAACTACTTCAACAACAGCAAATATTACAC
C. feae     AAACCCTACGAGACGCAACAACAATATGATCCACTTCCCCCACAACAAACACAATTT
```

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 here in blue:

```
                10        20        30        40        50
                 |         |         |         |         |
Uromastyx   AAACCTTAAAAGACACCACAACCATATGAACAACAACACCAACAATCAGCACACTAC
B. theili   AAACACTACAAAATATAACAACTGCATGAACAACATCAACCACAGCAAACATTTTAC
B. brygooi  AAACACTACAAGACATAACAACAGCATGAACTACTTCAACAACAGCAAATATTACAC
C. feae     AAACCCTACGAGACGCAACAACAATATGATCCACTTCCCCCACAACAAACACAATTT
```

principle is known as **phenetic taxonomy.** Phenetic taxonomy did not have a strong impact on animal classification, and scientific interest in this approach is in decline.

Despite 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 simplicity.

Phylogenetic Systematics/Cladistics

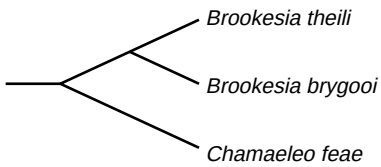
A second and stronger challenge to evolutionary taxonomy is one known as **phylogenetic systematics** or **cladistics.** As the first name implies, this approach emphasizes the criterion of common descent and, as the second name implies, it is based on the cladogram of a group being classified. This approach to

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 in the appropriate column.

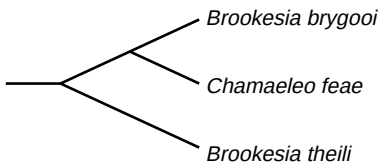
```
                    10        20        30        40        50
                     |         |         |         |         |
Uromastyx   AAACCTTAAAAGACACCACAACCATATGAACAACAACACCAACAATCAGCACACTAC
B. theili   AAACACTACAAAATATAACAACTGCATGAACAACATCAACCACAGCAAACATTTTAC
B. brygooi  AAACACTACAAGACATAACAACAGCATGAACTACTTCAACAACAGCAAATATTACAC
C. feae     AAACCCTACGAGACGCAACAACAATATGATCCACTTCCCCCACAACAAACACAATTT
                1          1        11         2    1 3    1       11
```

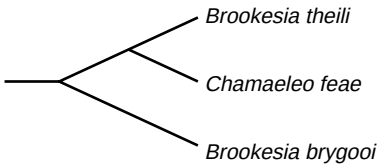
The eight characters marked "1" show synapomorphies grouping the two Madagascaran species (*Brookesia theili* and *B. brygooi*) to the exclusion of the Equatorial Guinean species, *Chamaeleo feae.* We can represent these relationships as a cladogram.



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 changes of these characters.

Characters marked "2" and "3" disagree with our cladogram and favor alternative relationships:





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 cladogram 2 or 3, we need at least two changes for each of these characters.

Systematists often use a principle called **parsimony** to resolve conflicts among taxonomic characters, as seen here. We choose as our best working hypothesis the cladogram that requires the smallest total amount of character change. In our example, cladogram 1 is favored by parsimony. 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 shown. 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.

taxonomy was first proposed in 1950 by German entomologist Willi Hennig (figure 4.8) and therefore is sometimes called "Hennigian systematics." All taxa recognized by Hennig's cladistic system must be monophyletic. We saw previously how evolutionary taxonomists' recognition of 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 family Hominidae, recognition of Pongidae is incompatible with cladistic taxonomy.

The disagreement regarding 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

figure 4.6

A, Penguin. **B,** Diving petrel. Penguins (avian family Spheniscidae) were considered by George G. Simpson 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 families within a common order (Ciconiiformes).

A

B

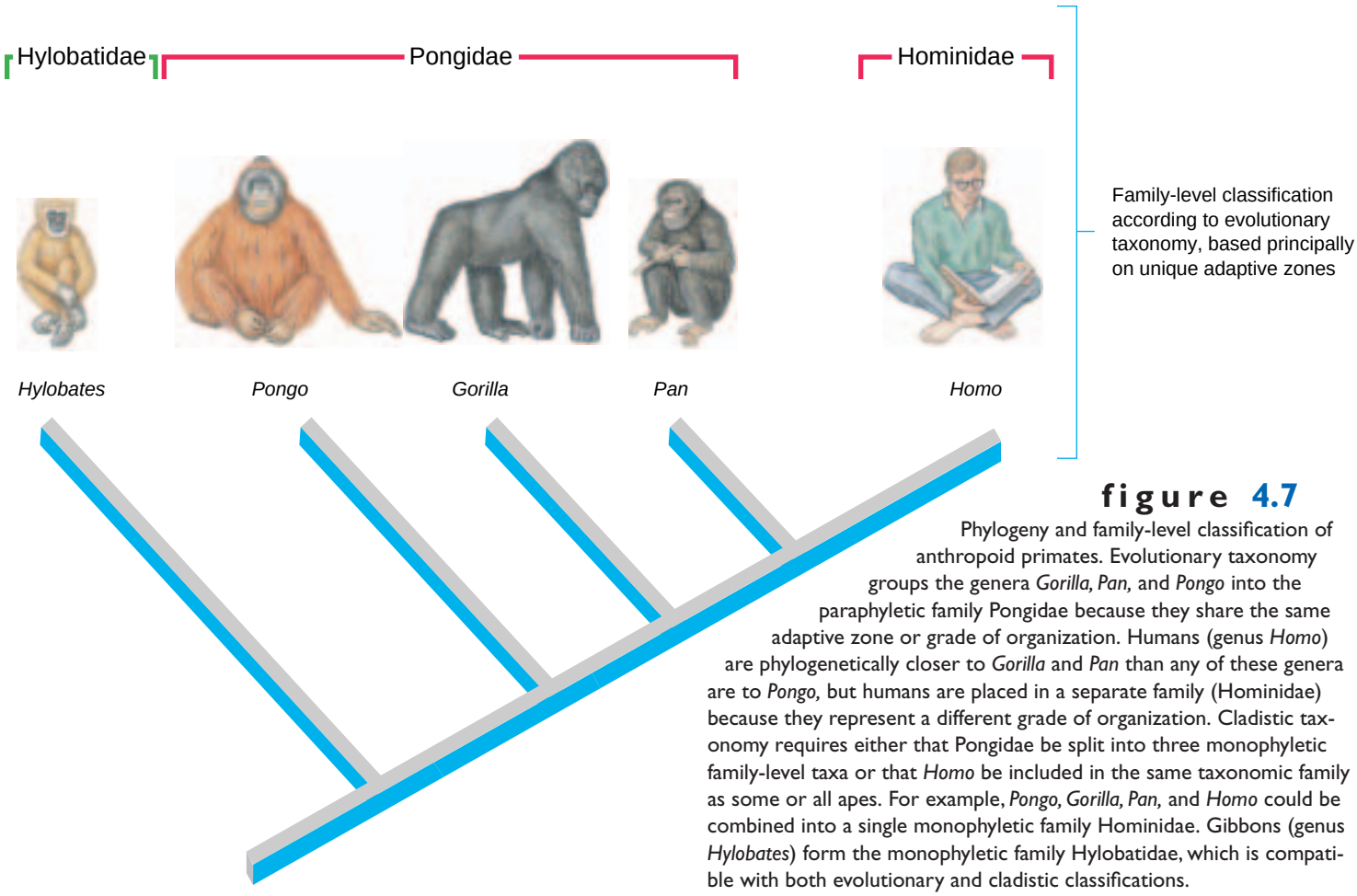


figure 4.7

Phylogeny and family-level classification of anthropoid primates. Evolutionary taxonomy groups the genera *Gorilla, Pan,* and *Pongo* into the 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 different grade of organization. Cladistic taxonomy requires either that Pongidae be split into three monophyletic family-level taxa or that *Homo* be included in the same taxonomic family as some or all apes. For example, *Pongo, Gorilla, Pan,* and *Homo* could be combined into a single monophyletic family Hominidae. Gibbons (genus *Hylobates*) form the monophyletic family Hylobatidae, which is compatible with both evolutionary and cladistic classifications.

from reptiles, or that humans evolved from apes may 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 that are not shared by a descendant group?

Paraphyletic groups are usually defined in a negative manner. They are distinguished only by absence of features found in a particular descendant group, because any traits

figure 4.8
Willi Hennig (1913–1976), German entomologist who formulated the principles of phylogenetic systematics/cladistics.

shared from their common ancestry are 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, tailless organisms of large brain capacity evolved from arboreal, tailed organisms of smaller brain capacity. To a cladist, however, the statement that humans evolved from apes says essentially that humans evolved from something that they are not, a trivial statement that contains no useful information. An extinct ancestral group is always paraphyletic because it excludes a descendant that shares its most recent common ancestor. Although many such groups have been recognized by evolutionary taxonomists, none are recognized by cladists.

Cladists denote the common descent of different taxa by identifying **sister taxa.** Sister taxa share more recent common ancestry with each other than either one does with any other taxon. The sister group of humans appears to be chimpanzees, with gorillas forming a sister group to humans and chimpanzees combined. Orangutans are the sister group of the clade that contains humans, chimpanzees, and gorillas; gibbons form the sister group of the clade that contains orangutans, chimpanzees, gorillas, and humans (see figure 4.7).

Current State of Animal Taxonomy

The formal taxonomy of animals that we use today was established using principles of evolutionary systematics and has been revised recently in part using principles of cladistics. Introduction of cladistic principles initially has the effect of replacing paraphyletic groups with monophyletic subgroups while leaving the remaining taxonomy mostly unchanged. A thorough revision of taxonomy along cladistic principles, however, will require profound changes, one of which almost certainly will be abandonment of Linnean ranks. In our coverage of animal taxonomy, we try as much as possible to use taxa that are monophyletic and therefore consistent with criteria of both evolutionary and cladistic taxonomy. We continue, however, to use Linnean ranks. In some cases in which familiar taxa 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 referring to groups of organisms as being 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.

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 reptilian groups, birds, and mammals) in addition to the finned, aquatic animals that evolutionary taxonomists normally group under the term "fish." Cladistic use of "reptiles" includes birds in addition to snakes, lizards, turtles, and crocodilians; however, it excludes some fossil forms, such as synapsids, that evolutionary taxonomists traditionally place in Reptilia (see Chapter 18). Taxonomists must be very careful to specify when using these seemingly familiar terms whether traditional evolutionary taxa or newer cladistic taxa are being discussed.

Species

While discussing Darwin's book, *On the Origin of Species,* in 1859, Thomas Henry Huxley (p. 10) 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 140 years ago. 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.

Criteria for Recognition of Species

Despite widespread disagreement about the nature of species, biologists repeatedly have designated certain criteria as being important to their identification of 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 increasingly are used for this purpose. A third important criterion is that of reproductive community, which applies only to sexually reproducing organisms; members of a species must form a reproductive community that excludes members of other species. This criterion is very important to many modern concepts of species.

Concepts of Species

Before Darwin, a species was considered a distinct and immutable entity. The concept that species were defined by fixed, essential features (usually morphological) is called the **typological species concept.** This concept was discarded following establishment of Darwinian evolutionary theory.

The most influential concept of species inspired by Darwinian evolutionary theory is the **biological species concept** formulated by Theodosius Dobzhansky and Ernst Mayr. In 1983, Mayr stated the biological species concept as follows: *"A species 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 morphology. A species is an *interbreeding* population of individuals having *common descent.* By adding the criterion of **niche,** an ecological concept denoting an organism's role in its ecological community, we recognize that members of a reproductive community constitute an ecological entity in nature. Because reproductive community should maintain genetic cohesiveness, organismal variation should be relatively smooth and continuous within species and discontinuous between them. Although a biological species is based on reproductive properties of populations rather than organismal morphology, morphology nonetheless can help us to diagnose biological species.

The biological species concept has been strongly criticized. To understand why, we must keep in mind several important facts about species. First, a species has dimensions in space and time, which often creates problems for locating discrete boundaries between species. Second, we view species both as a unit of evolution and as a rank in a taxonomic hierarchy; these roles sometimes conflict. A third problem is that according to the biological species concept, species do not exist in groups of organisms that reproduce only asexually. It is common taxonomic practice, however, to describe species in all groups of organisms.

The **evolutionary species concept** was proposed by Simpson (see figure 4.5) in the 1940s 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 species to have a distinct historical identity. Unlike the biological species concept, the evolutionary species concept applies both to sexually and asexually reproducing forms. As long as continuity of diagnostic features is maintained by an evolving lineage, it will be recognized as a single species. Abrupt changes in diagnostic features will mark a boundary between different species in evolutionary time.

The last concept that we present is the **phylogenetic species concept.** The phylogenetic species concept is defined as 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 also emphasizes common descent, and both asexual and sexual groups are covered. The phylogenetic species is a strictly monophyletic unit, making it ideal for cladistic systematics. Any population that has become separated from others and has undergone character evolution that distinguishes it will be recognized as a species. The criterion of irreducibility requires that no more than one such population can be placed in a single species. The main difference in practice between the evolutionary and phylogenetic species concepts is that the latter emphasizes recognizing as species the smallest groupings of organisms that have undergone independent evolutionary change. The evolutionary species concept would group into a single species geographically disjunct populations that demonstrate some genetic divergence but are judged similar in their major "evolutionary tendencies," whereas the phylogenetic species concept would treat them as separate species. In general, a larger number of species would be described using the phylogenetic species concept than any other concept. The phylogenetic species concept is intended to encourage us to reconstruct patterns of evolutionary common descent on the finest scale possible.

Current disagreements concerning concepts of species should not be considered trivial or discouraging. Whenever a field of scientific investigation enters a phase of dynamic growth, old concepts will be reevaluated and either refined or replaced with newer, more progressive ones. Active debate among systematists 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. We cannot predict yet which, if any, of these concepts of species will prevail. Understanding conflicting perspectives, rather than learning a single concept of species, is therefore of greatest importance for people now studying zoology.

Major Divisions of Life

From Aristotle's time, people have tried to assign every living organism to one of two kingdoms: plant or animal. Unicellular forms were arbitrarily assigned to one of these kingdoms, whose recognition was based primarily on properties of multicellular organisms. This system has outlived its usefulness. It does not represent common descent among organisms accurately. Under the traditional, two-kingdom system, neither animals nor plants constitute monophyletic groups.

Several alternative systems have been proposed to solve the problem of classifying unicellular forms. In 1866 Haeckel proposed a 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. Finally, important differences between the anucleate bacteria and cyanobacteria (prokaryotes) and all other organisms that have membrane-bound nuclei (eukaryotes) were recognized. In 1969 R. H. Whittaker proposed a five-kingdom system that incorporated a basic prokaryote-eukaryote distinction. Kingdom Monera contained prokaryotes. Kingdom Protista contained unicellular eukaryotic organisms (protozoa and unicellular eukaryotic algae). Multicellular organisms were split into three kingdoms on the basis of mode of nutrition and other fundamental differences in organization. Kingdom Plantae included multicellular photosynthesizing organisms (higher plants and multicellular algae). Kingdom Fungi contained molds, yeasts, and fungi, which obtain their food by absorption. Invertebrates (except the protozoa) and vertebrates form the kingdom Animalia. Most of these forms ingest their food and digest it internally, although some parasitic forms are absorptive.

All of these different systems were proposed without regard to phylogenetic relationships needed to construct evolutionary or cladistic taxonomies. The oldest phylogenetic events in the history of life have been obscure, because different forms of life share very few characters that can be compared among these higher taxa to reconstruct their phylogeny. 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 ribosomal RNA, figure 4.9). According to this tree, Carl Woese, Otto Kandler, and Mark Wheelis recognized three monophyletic domains above the kingdom level: Eucarya (all eukaryotes), Bacteria (the true bacteria), and Archaea (prokaryotes differing from bacteria in structure of membranes and in ribosomal RNA sequences). They did not divide Eucarya into kingdoms, although if we retain Whittaker's kingdoms Plantae, Animalia, and Fungi, Protista is paraphyletic because this group does not contain all descendants of its most recent common ancestor (figure 4.10). To maintain a cladistic classification, Protista must be discontinued by recognizing as separate kingdoms Ciliata, Flagellata, and Microsporidia as shown in figure 4.9, and phylogenetic information must be gathered for additional protistan groups, including amebas. This taxonomic revision has not been made; however, if the phylogenetic tree in figure 4.9 is supported by further evidence, revision of taxonomic kingdoms will be necessary.

Until recently, animal-like protistans were traditionally studied in zoology courses as the animal phylum Protozoa. Given current knowledge and principles of phylogenetic systematics, this practice commits two taxonomic errors; "protozoa" are neither animals nor are they a valid monophyletic taxon at any level. Kingdom Protista is likewise invalid because it is not monophyletic. Animal-like protistans, now arrayed in

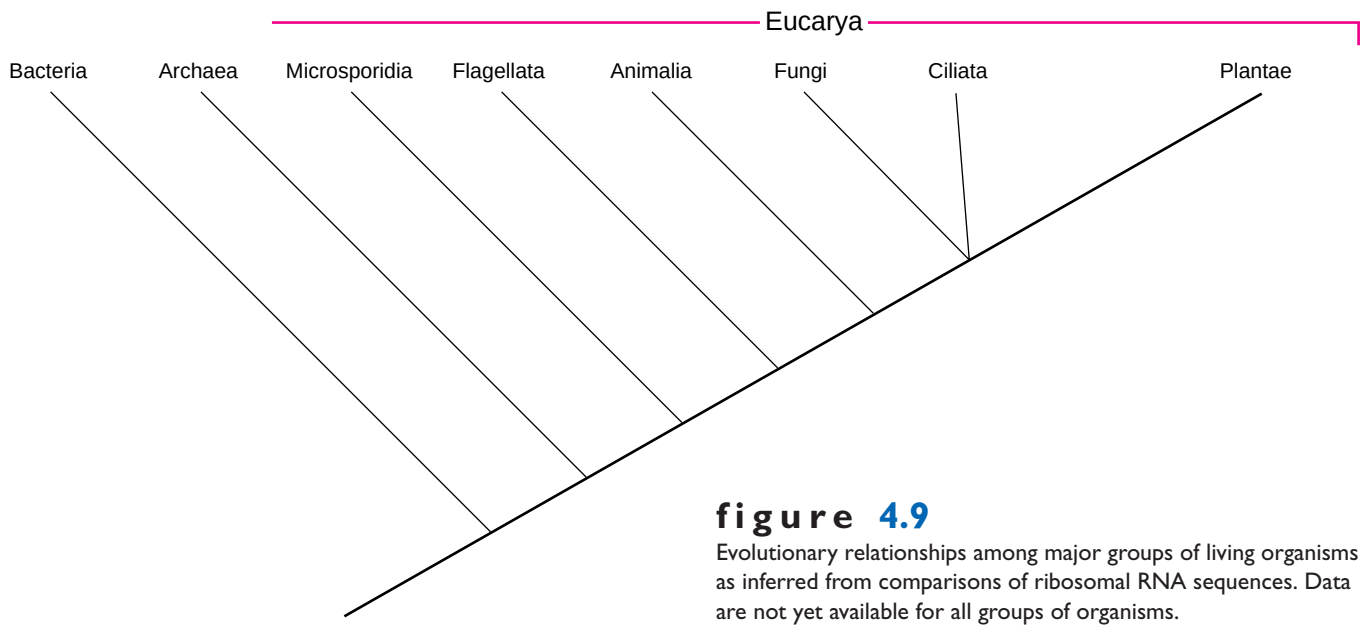
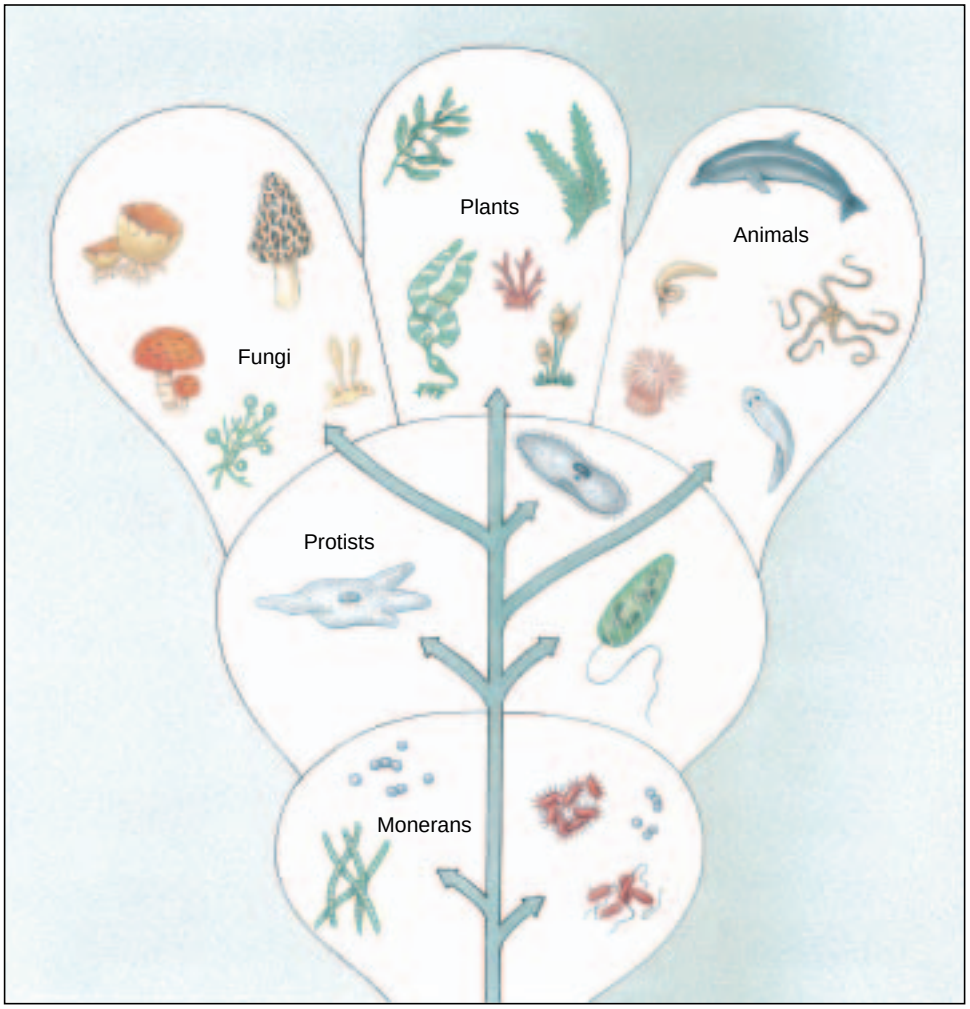


figure 4.9
Evolutionary relationships among major groups of living organisms as inferred from comparisons of ribosomal RNA sequences. Data are not yet available for all groups of organisms.

figure 4.10
Whittaker's five-kingdom classification superimposed on a phylogenetic tree showing living representatives of these kingdoms. Note that kingdoms Monera and Protista constitute paraphyletic groups (because they do not include all of their descendants) and are therefore unacceptable to cladistic systematics.



seven separate phyla, are nonetheless of interest to students of zoology because of their animal-like properties. We therefore cover them in this book.

Major Subdivisions of the Animal Kingdom

The phylum is the largest category in Linnean classification of the animal kingdom. Animal phyla are often grouped together to produce additional, informal taxa intermediate between phylum and kingdom. These taxa are based on embryological and anatomical characters that reveal phylogenetic affinities of different animal phyla. Zoologists once recognized subkingdom Protozoa, which contained primarily unicellular phyla, and subkingdom Metazoa, which contained multicellular phyla. As noted previously, however, "protozoa" do not form a valid taxonomic group and do not belong within the animal kingdom, which is synonymous with Metazoa. The traditional higher-level groupings of true animal phyla are:

- Branch A (Mesozoa): phylum Mesozoa, the mesozoa
- Branch B (Parazoa): phylum Porifera, the sponges, and phylum Placozoa
- Branch C (Eumetazoa): all other phyla
  - Grade I (Radiata): phyla Cnidaria, Ctenophora
  - Grade II (Bilateria): all other phyla
    - Division A (Protostomia): characteristics in figure 4.11
      - Acoelomates: phyla Platyhelminthes, Gnathostomulida, Nemertea
      - Pseudocoelomates: phyla Rotifera, Gastrotricha, Kinorhyncha, Nematoda, Nematomorpha, Acanthocephala, Entoprocta, Priapulida, Loricifera
      - Eucoelomates: phyla Mollusca, Annelida, Arthropoda, Echiurida, Sipunculida, Tardigrada, Pentastomida, Onychophora, Pogonophora
    - Division B (Deuterostomia): characteristics in figure 4.11; phyla Phoronida, Ectoprocta, Chaetognatha, Brachiopoda, Echinodermata, Hemichordata, Chordata

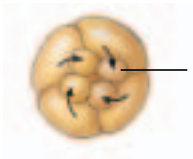
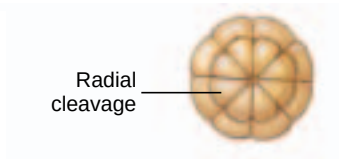
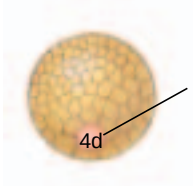
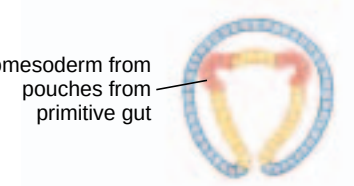
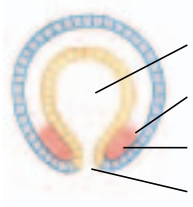
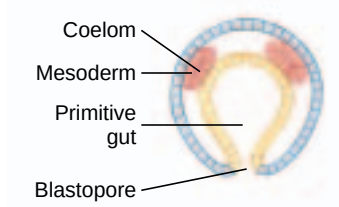
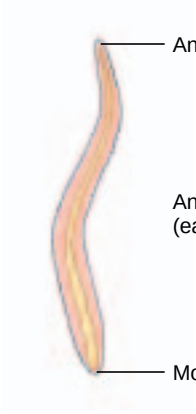
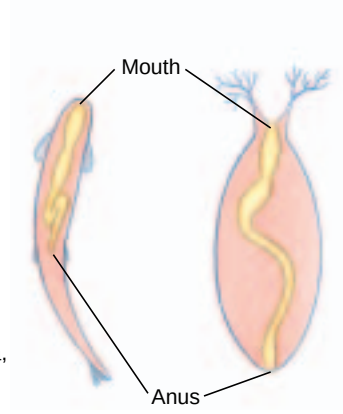
PROTOSTOMES		DEUTEROSTOMES	
 Spiral cleavage	Cleavage mostly spiral	Cleavage mostly radial	 Radial cleavage
 Cell from which mesoderm will derive (4d)	Endomesoderm usually from a particular blastomere designated 4d	Endomesoderm from enterocoelous pouching (except chordates)	 Endomesoderm from pouches from primitive gut
 Primitive gut; Mesoderm; Coelom; Blastopore	In coelomate protostomes the coelom forms as a split in mesodermal bands (schizocoelous)	All coelomate, coelom from fusion of enterocoelous pouches (except chordates, which are schizocoelous)	 Coelom; Mesoderm; Primitive gut; Blastopore
 Anus; Annelid (earthworm); Mouth	Mouth from, at, or near blastopore; anus a new formation Embryology mostly determinate (mosaic) Includes phyla Platyhelminthes, Nemertea, Annelida, Mollusca, Arthropoda, minor phyla	Anus from, at, or near blastopore, mouth a new formation Embryology usually indeterminate (regulative) Includes phyla Echinodermata, Hemichordata and Chordata, and formerly Chaetognatha, Phoronida, Ectoprocta, Brachiopoda	 Mouth; Anus

figure 4.11
Basis for distinctions between divisions of bilateral animals.

As in the outline, bilateral animals are customarily divided into **Protostomia** and **Deuterostomia** based on their embryological development (figure 4.11). Note, however, that the individual characters listed in figure 4.11 are not completely diagnostic in separating protostomes from deuterostomes. Some phyla are difficult to place into one of these two categories because they possess characteristics of each group.

Recent molecular phylogenetic studies have challenged traditional classification of Bilateria. Molecular phylogentic results place four phyla traditionally classified as deuterostomes (Brachiopoda, Chaetognatha, Ectoprocta, and Phoronida) in Protostomia. Furthermore, the traditional major groupings of protostome phyla (acoelomates, pseudocoelomates, and eucoelomates) appear not to be monophyletic. Instead, protostomes are divided into two major monophyletic groups called Lophotrochozoa and Ecdysozoa. Reclassification of Bilateria is:

Grade II: Bilateria
- Division A (Protostomia):
  - Lophotrochozoa: phyla Platyhelminthes, Nemertea, Rotifera, Gastrotricha, Acanthocephala, Mollusca, Annelida, Echiurida, Sipunculida, Pogonophora, Phoronida, Ectoprocta, Chaetognatha, Brachiopoda
  - Ecdysozoa: phyla Kinorhyncha, Nematoda, Nematomorpha, Priapulida, Arthropoda, Tardigrada, Onychophora
- Division B (Deuterostomia): phyla Chordata, Hemichordata, Echinodermata

Further study is needed to confirm these new groupings, and to add to the classification four phyla (Entoprocta, Gnathostomulida, Loricifera, and Pentastomida) whose relationships have not been determined. We organize our survey of animal diversity using the traditional classification, but discuss implications of the new one.

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 hierarchically in taxonomic groups (taxa) that convey 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. The names of species are binomial, with the first name designating the genus to which the species belongs (first letter capitalized) followed by a species epithet (lowercase), both written in italics. Taxa at all other ranks are given single nonitalicized names.

Two major schools of taxonomy are currently active. Traditional evolutionary taxonomy groups species into higher taxa according to joint criteria of common descent and adaptive evolution; such taxa have a single evolutionary origin and occupy a distinctive adaptive zone. A second approach, known as 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 common descent among species be assessed before higher taxa are recognized. Comparative morphology (including development), cytology, and biochemistry are used to reconstruct the nested hierarchical relationships among taxa that reflect the branching of evolutionary lineages through time. The fossil record provides estimates of ages of evolutionary lineages. Comparative studies and the fossil record jointly permit us to reconstruct a phylogenetic tree representing the evolutionary history of the animal kingdom.

The biological species concept has guided 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 its 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 and the phylogenetic species concept. No single concept of species is universally accepted by all zoologists.

Traditionally, all living forms were placed into two kingdoms (animal and plant) but more recently, a five-kingdom system (animals, plants, fungi, protistans, and monerans) has been followed. Neither system conforms to principles of evolutionary or cladistic taxonomy because both 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, which comprises multicellular forms (metazoa).

review questions

1. List in order, from most inclusive to least inclusive, the principal categories (ranks of taxa) in Carolus Linnaeus's system of classification.
2. Explain why the system for naming species that originated with Linnaeus is "binomial."
3. How do monophyletic, paraphyletic, and polyphyletic taxa differ? How do these differences affect validity of such taxa for both evolutionary and cladistic taxonomies?
4. How are taxonomic characters recognized? How are such characters used to construct a cladogram?
5. What is the difference between a cladogram and a phylogenetic tree? Given a cladogram for a group of species, what additional information is needed to obtain a phylogenetic tree?
6. How would cladists and evolutionary taxonomists differ in their interpretations of the statement that humans evolved from apes, which evolved from monkeys?
7. How does the biological species concept differ from earlier typological concepts of species? Why do evolutionary biologists prefer it to typological species concepts?
8. What problems have been identified with the biological species concept? How do other concepts of species attempt to overcome these problems?
9. What are the five kingdoms distinguished by Whittaker? How does their recognition conflict with principles of cladistic taxonomy?

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See also general references on page 406.

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