

32

How We Classify Organisms

Concept Outline

32.1 Biologists name organisms in a systematic way.

The Classification of Organisms. Biologists name organisms using a binomial system.

Species Names. Every kind of organism is assigned a unique name.

The Taxonomic Hierarchy. The higher groups into which an organism is placed reveal a great deal about the organism.

What Is a Species? Species are groups of similar organisms that tend not to interbreed with individuals of other groups.

32.2 Scientists construct phylogenies to understand the evolutionary relationships among organisms.

Evolutionary Classifications. Traditional and cladistic interpretations of evolution differ in the emphasis they place on particular traits.

32.3 All living organisms are grouped into one of a few major categories.

The Kingdoms of Life. Living organisms are grouped into three great groups called domains, and within domains into kingdoms.

Domain Archaea (Archaeobacteria). The oldest domain consists of primitive bacteria that often live in extreme environments.

Domain Bacteria (Eubacteria). Too small to see with the unaided eye, eubacteria are more numerous than any other organism.

Domain Eukarya (Eukaryotes). There are four kingdoms of eukaryotes, three of them entirely or predominantly multicellular. Two of the most important characteristics to have evolved among the eukaryotes are multicellularity and sexuality.

Viruses: A Special Case. Viruses are not organisms, and thus do not belong to any kingdom.



FIGURE 32.1

Biological diversity. All living things are assigned to particular classifications based on characteristics such as their anatomy, development, mode of nutrition, level of organization, and biochemical composition. Coral reefs, like the one seen here, are home to a variety of living things.

All organisms share many biological characteristics. They are composed of one or more cells, carry out metabolism and transfer energy with ATP, and encode hereditary information in DNA. All species have evolved from simpler forms and continue to evolve. Individuals live in populations. These populations make up communities and ecosystems, which provide the overall structure of life on earth. So far, we have stressed these common themes, considering the general principles that apply to all organisms. Now we will consider the diversity of the biological world and focus on the differences among groups of organisms (figure 32.1). For the rest of the text, we will examine the different kinds of life on earth, from bacteria and amoebas to blue whales and sequoia trees.

32.1 Biologists name organisms in a systematic way.

The Classification of Organisms

Organisms were first classified more than 2000 years ago by the Greek philosopher Aristotle, who categorized living things as either plants or animals. He classified animals as either land, water, or air dwellers, and he divided plants into three kinds based on stem differences. This simple classification system was expanded by the Greeks and Romans, who grouped animals and plants into basic units such as cats, horses, and oaks. Eventually, these units began to be called **genera** (singular, **genus**), the Latin word for “groups.” Starting in the Middle Ages, these names began to be systematically written down, using Latin, the language used by scholars at that time. Thus, cats were assigned to the genus *Felis*, horses to *Equus*, and oaks to *Quercus*—names that the Romans had applied to these groups. For genera that were not known to the Romans, new names were invented.

The classification system of the Middle Ages, called the *polynomial system*, was used virtually unchanged for hundreds of years.

The Polynomial System

Until the mid-1700s, biologists usually added a series of descriptive terms to the name of the genus when they wanted to refer to a particular kind of organism, which they called a **species**. These phrases, starting with the name of the genus, came to be known as polynomials (*poly*, “many”; *nomial*, “name”), strings of Latin words and phrases consisting of up to 12 or more words. One name for the European honeybee, for example, was *Apis pubescens, thorace subgriseo, abdomine fusco, pedibus posticis glabris utrinque margine ciliatis*. As you can imagine, these polynomial names were cumbersome. Even more worrisome, the names were altered at will by later authors, so that a given organism really did not have a single name that was its alone.

The Binomial System

A much simpler system of naming animals, plants, and other organisms stems from the work of the Swedish biologist Carolus Linnaeus (1707–1778). Linnaeus devoted his life to a challenge that had defeated many biologists before him—cataloging all the different kinds of organisms. In the 1750s he produced several major works that, like his earlier

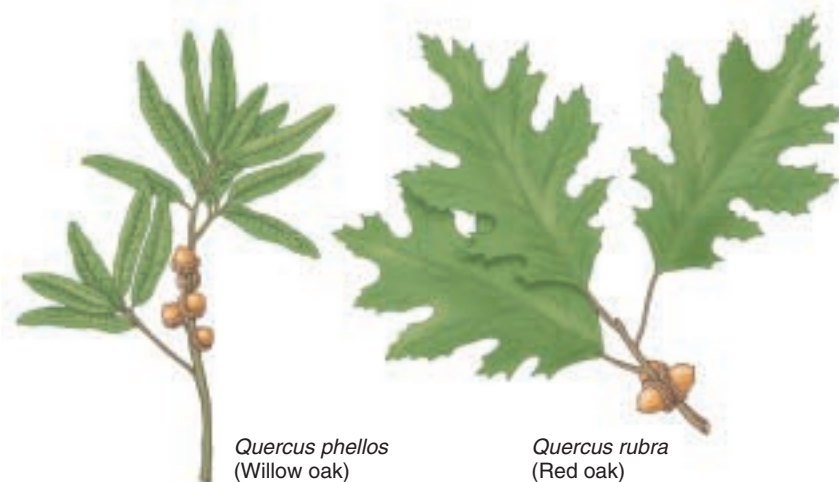


FIGURE 32.2

Two species of oaks. (a) Willow oak, *Quercus phellos*. (b) Red oak, *Quercus rubra*. Although they are both oaks (*Quercus*), these two species differ sharply in leaf shape and size and in many other features, including geographical range.

books, employed the polynomial system. But as a kind of shorthand, Linnaeus also included in these books a two-part name for each species. For example, the honeybee became *Apis mellifera*. These two-part names, or **binomials** (*bi*, “two”) have become our standard way of designating species.

A Closer Look at Linnaeus

To illustrate Linnaeus’s work further, let’s consider how he treated two species of oaks from North America, which by 1753 had been described by scientists. He grouped all oaks in the genus *Quercus*, as had been the practice since Roman times. Linnaeus named the willow oak of the southeastern United States (figure 32.2a) *Quercus foliis lanceolatis integerrimis glabris* (“oak with spear-shaped, smooth leaves with absolutely no teeth along the margins”). For the common red oak of eastern temperate North America (figure 32.2b), Linnaeus devised a new name, *Quercus foliis obtuse-sinuatis setaceo-mucronatis* (“oak with leaves with deep blunt lobes bearing hairlike bristles”). For each of these species, he also presented a shorthand designation, the binomial names *Quercus phellos* and *Quercus rubra*. These have remained the official names for these species since 1753, even though Linnaeus did not intend this when he first used them in his book. He considered the polynomials the true names of the species.

Two-part (“binomial”) Latin names, first utilized by Linnaeus, are now universally employed by biologists to name particular organisms.

Species Names

Taxonomy is the science of classifying living things, and a group of organisms at a particular level in a classification system is called a **taxon** (plural, **taxa**). By agreement among taxonomists throughout the world, no two organisms can have the same name. So that no one country is favored, a language spoken by no country—Latin—is used for the names. Because the scientific name of an organism is the same anywhere in the world, this system provides a standard and precise way of communicating, whether the language of a particular biologist is Chinese, Arabic, Spanish, or English. This is a great improvement over the use of common names, which often vary from one place to the next. As you can see in figure 32.3, corn in Europe refers to the plant Americans call wheat; a bear is a large placental omnivore in the United States but a koala (a vegetarian marsupial) in Australia; and a robin is a very different bird in Europe and North America.

Also by agreement, the first word of the binomial name is the genus to which the organism belongs. This word is always capitalized. The second word refers to the particular species and is not capitalized. The two words together are called the **scientific name** and are written in italics or distinctive print: for example, *Homo sapiens*. Once a genus has been used in the body of a text, it is often abbreviated in later uses. For example, the dinosaur *Tyrannosaurus rex* becomes *T. rex*, and the potentially dangerous bacterium *Escherichia coli* is known as *E. coli*. The system of naming animals, plants, and other organisms established by Linnaeus has served the science of biology well for nearly 230 years.

By convention, the first part of a binomial species name identifies the genus to which the species belongs, and the second part distinguishes that particular species from other species in the genus.



(a)



(b)



(c)



FIGURE 32.3

Common names make poor labels. The common names corn (a), bear (b), and robin (c) bring clear images to our minds (photos on left), but the images are very different to someone living in Europe or Australia (photos on right). There, the same common names are used to label very different species.

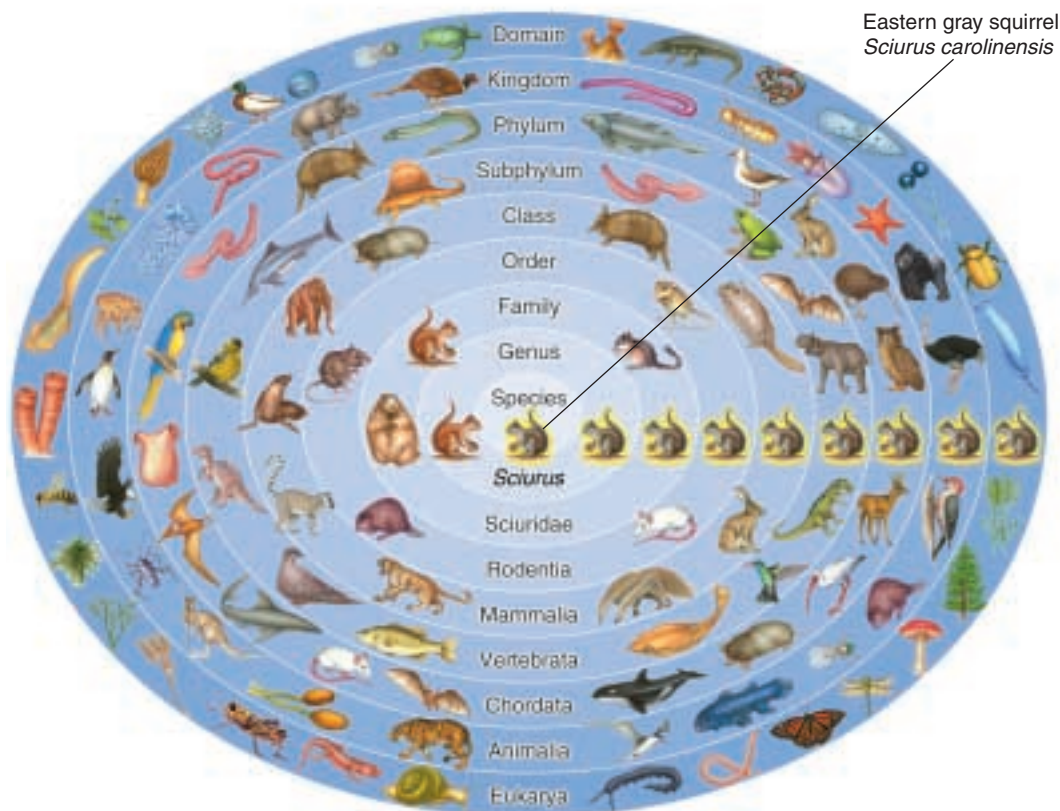
The Taxonomic Hierarchy

In the decades following Linnaeus, taxonomists began to group organisms into larger, more inclusive categories. Genera with similar properties were grouped into a cluster called a **family**, and similar families were placed into the same **order** (figure 32.4). Orders with common properties were placed into the same **class**, and classes with similar characteristics into the same **phylum** (plural, **phyla**). For historical reasons, phyla may also be called *divisions* among plants, fungi, and algae. Finally, the phyla were assigned to one of several great groups, the **kingdoms**. Biologists currently recognize six kingdoms: two kinds of bacteria (Archaea and Eubacteria), a largely unicellular group of eukaryotes (Protista), and three multicellular groups (Fungi, Plantae, and Animalia). In order to remember the seven categories of the taxonomic hierarchy in their proper order, it may prove useful to memorize a phrase such as “**kindly pay cash or furnish good security**” (**kingdom–phylum–class–order–family–genus–species**).

In addition, an eighth level of classification, called *domains*, is sometimes used. Biologists recognize three domains, which will be discussed later in this chapter. The scientific names of the taxonomic units higher than the genus level are capitalized but not printed distinctively, italicized, or underlined.

The categories at the different levels may include many, a few, or only one taxon. For example, there is only one living genus of the family Hominidae, but several living genera of Fagaceae. To someone familiar with classification or with access to the appropriate reference books, each taxon implies both a set of characteristics and a group of organisms belonging to the taxon. For example, a honeybee has the species (level 1) name *Apis mellifera*. Its genus name (level 2) *Apis* is a member of the family Apidae (level 3). All members of this family are bees, some solitary, others living in hives as *A. mellifera* does. Knowledge of its order (level 4), Hymenoptera, tells you that *A. mellifera* is likely able to sting and may live in colonies. Its class (level 5) Insecta indicates that *A. mellifera* has three major body segments, with wings and three pairs of legs attached to the middle segment. Its phylum (level 6), Arthropoda, tells us that the honeybee has a hard cuticle of chitin and jointed appendages. Its kingdom (level 7), Animalia, tells us that *A. mellifera* is a multicellular heterotroph whose cells lack cell walls.

Species are grouped into genera, genera into families, families into orders, orders into classes, and classes into phyla. Phyla are the basic units within kingdoms; such a system is hierarchical.



Eastern gray squirrel
Sciurus carolinensis

FIGURE 32.4
The hierarchical system used in classifying an organism. The organism is first recognized as a eukaryote (domain: Eukarya). Second, within this domain, it is an animal (kingdom: Animalia). Among the different phyla of animals, it is a vertebrate (phylum: Chordata, subphylum: Vertebrata). The organism’s fur characterizes it as a mammal (class: Mammalia). Within this class, it is distinguished by its gnawing teeth (order: Rodentia). Next, because it has four front toes and five back toes, it is a squirrel (family: Sciuridae). Within this family, it is a tree squirrel (genus: *Sciurus*), with gray fur and white-tipped hairs on the tail (species: *Sciurus carolinensis*, the eastern gray squirrel).

What Is a Species?

In the previous section we discussed how species are named and grouped, but how do biologists decide when one organism is distinct enough from another to be called its own species? In chapter 22, we reviewed the nature of species and saw there are no absolute criteria for the definition of this category. Looking different, for example, is not a useful criterion: different individuals that belong to the same species (for example, dogs) may look very unlike one another, as different as a Chihuahua and a St. Bernard. These very different-appearing individuals are fully capable of hybridizing with one another.

The **biological species concept** (figure 32.5) essentially says that two organisms that cannot interbreed and produce fertile offspring are different species. This definition of a species can be useful in describing sexually reproducing species that regularly **outcross**—interbreed with individuals other than themselves. However, in many groups of organisms, including bacteria, fungi, and many plants and animals, **asexual reproduction**—reproduction without sex—predominates. Among them, hybridization cannot be used as a criterion for species recognition.

Defining Species

Despite such difficulties, biologists generally agree on the organisms they classify as species based on the similarity of morphological features and ecology. As a practical definition, we can say that species are groups of organisms that remain relatively constant in their characteristics, can be distinguished from other species, and do not normally interbreed with other species in nature.

Evolutionary Species Concept

This simple definition of species leaves many problems unsolved. How, for instance, are we to compare living species with seemingly similar ones now extinct? Much of the disagreement among alternative species concepts relates to solving this problem. When do we assign fossil specimens a unique species name, and when do we assign them to species living today? If we trace the lineage of two sister species backwards through time, how far must we go before the two species converge on their common ancestor? It is often very hard to know where to draw a sharp line between two closely related species.

To address this problem, biologists have added an evolutionary time dimension to the biological species concept. A current definition of an evolutionary species is *a single lineage of populations that maintains its distinctive identity from other such lineages*. Unlike the biological species concept, the evolutionary species concept applies to both asexual and sexually reproducing forms. Abrupt changes in diagnostic features mark the boundaries of different species in evolutionary time.



(a)



(b)



(c)

FIGURE 32.5
The biological species concept. Horses (a) and donkeys (b) are not the same species, because the offspring they produce when they interbreed, mules (c), are sterile.

How Many Species Are There?

Scientists have described and named a total of 1.5 million species, but doubtless many more actually exist. Some groups of organisms, such as flowering plants, vertebrate animals, and butterflies, are relatively well known with an estimated 90% of the total number of species that actually exist in these groups having already been described. Many other groups, however, are very poorly known. It is generally accepted that only about 5% of all species have been recognized for bacteria, nematodes (roundworms), fungi, and mites (a group of organisms related to spiders).

By taking representative samples of organisms from different environments, such as the upper branches of tropical trees or the deep ocean, scientists have estimated the total numbers of species that may actually exist to be about 10 million, about 15% of them marine organisms.

Most Species Live in the Tropics

Most species, perhaps 6 or 7 million, are tropical. Presently only 400,000 species have been named in tropical Asia, Africa, and Latin America combined, well under 10% of all species that occur in the tropics. This is an incredible gap in our knowledge concerning biological diversity in a world that depends on biodiversity for its sustainability.

These estimates apply to the number of eukaryotic organisms only. There is no functional way of estimating the numbers of species of prokaryotic organisms, although it is clear that only a very small fraction of all species have been discovered and characterized so far.

Species are groups of organisms that differ from one another in recognizable ways and generally do not interbreed with one another in nature.

32.2 Scientists construct phylogenies to understand the evolutionary relationships among organisms.

Evolutionary Classifications

After naming and classifying some 1.5 million organisms, what have biologists learned? One very important advantage of being able to classify particular species of plants, animals, and other organisms is that individuals of species that are useful to humans as sources of food and medicine can be identified. For example, if you cannot tell the fungus *Penicillium* from *Aspergillus*, you have little chance of producing the antibiotic penicillin. In a thousand ways, just having names for organisms is of immense importance in our modern world.

Taxonomy also enables us to glimpse the evolutionary history of life on earth. The more similar two taxa are, the more closely related they are likely to be. By looking at the differences and similarities between organisms, biologists can construct an evolutionary tree, or **phylogeny**, inferring which organisms evolved from which other ones, in what order, and when. The reconstruction and study of phylogenies is called **systematics**. Within a phylogeny, a grouping can be either monophyletic, paraphyletic, or polyphyletic. A **monophyletic** group includes the most recent common ancestor of the group and all of its descendants. A **paraphyletic** group includes the most recent common ancestor of the group but not all of its descendants. And, a **polyphyletic** group does not include the most recent common ancestor of all the members of the group. Monophyletic groups are commonly assigned names, but systematists will not assign a taxonomic classification to a polyphyletic group. Paraphyletic groups may be considered taxa by some scientists, although they do not accurately represent the evolutionary relationships among the members of the group (figure 32.6).

Cladistics

A simple and objective way to construct a phylogenetic tree is to focus on key characters that a group of organisms share because they have inherited them from a common ancestor. A **clade** is a group of organisms related by descent, and this approach to constructing a phylogeny is called **cladistics**. Cladistics infers phylogeny (that is, builds family trees) according to similarities derived from a common ancestor, so-called derived characters. A derived character that is unique to a particular clade is sometimes called a **synapomorphy**. The key to the approach is being able to identify morphological, physiological, or behavioral traits that differ among the organisms being studied and can be attributed to a common ancestor. By examining the distribution of these traits among the organisms, it is possible to construct a **clado-**

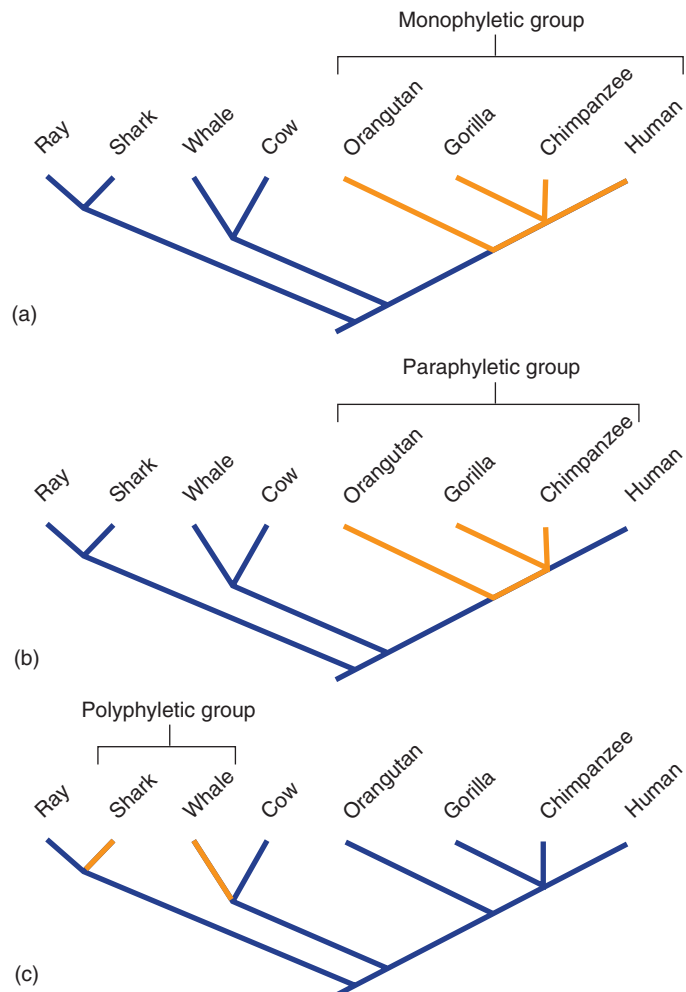


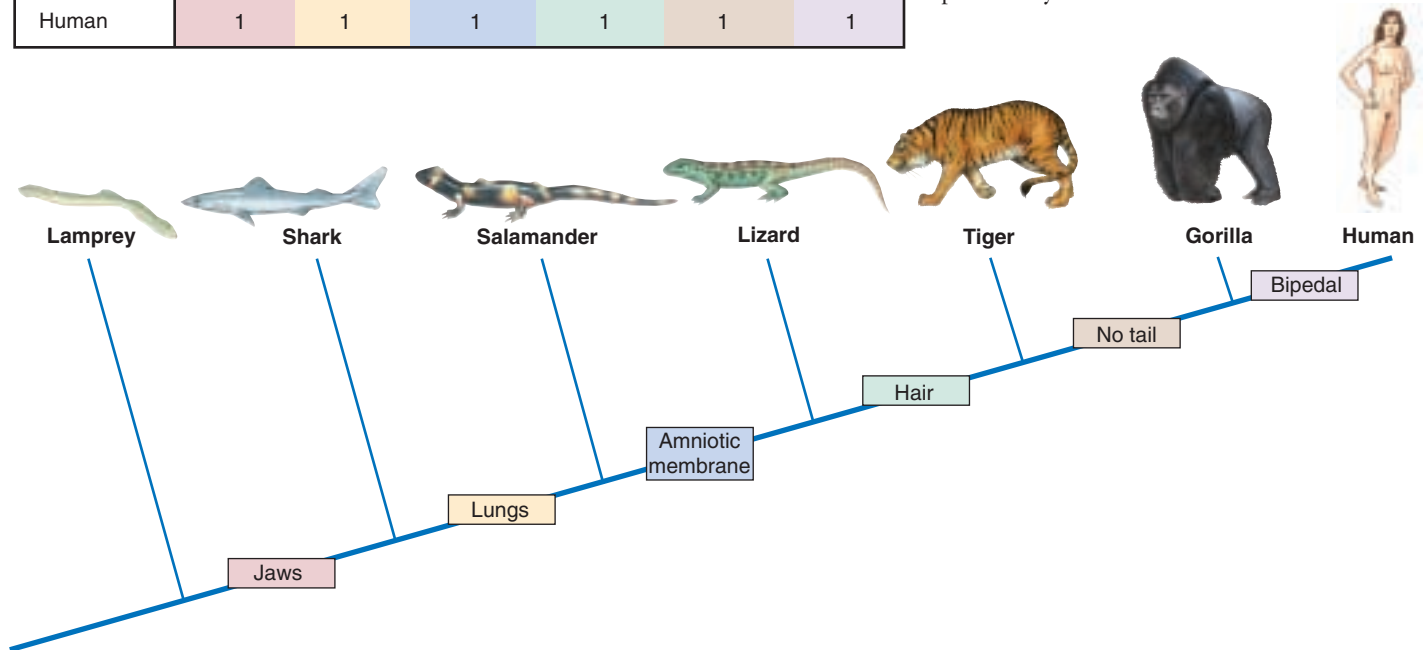
FIGURE 32.6

(a) A monophyletic group consists of the most recent common ancestor and all of its descendants. All taxonomists accept monophyletic groups in their classifications and in the above example would give the name “Apes” to the orangutans, gorillas, chimpanzees, and humans. (b) A paraphyletic group consists of the most recent common ancestor and some of its descendants. Taxonomists differ in their acceptance of paraphyletic groups. For example, some taxonomists arbitrarily group orangutans, gorillas, and chimpanzees into the paraphyletic family Pongidae, separate from humans. Other taxonomists do not use the family Pongidae in their classifications because gorillas and chimpanzees are more closely related to humans than to orangutans. (c) A polyphyletic group does not contain the most recent common ancestor of the group, and taxonomists do not assign taxa to polyphyletic groups. For example, sharks and whales could be classified in the same group because they have similar shapes, anatomical features, and habitats. However, their similarities reflect convergent evolution, not common ancestry.

Traits: Organism	Jaws	Lungs	Amniotic membrane	Hair	No tail	Bipedal
Lamprey	0	0	0	0	0	0
Shark	1	0	0	0	0	0
Salamander	1	1	0	0	0	0
Lizard	1	1	1	0	0	0
Tiger	1	1	1	1	0	0
Gorilla	1	1	1	1	1	0
Human	1	1	1	1	1	1

FIGURE 32.7

A cladogram. Morphological data for a group of seven vertebrates is tabulated. A “1” indicates the presence of a trait, or derived character, and a “0” indicates the absence of the trait. A tree, or cladogram, diagrams the proposed evolutionary relationships among the organisms based on the presence of derived characters. The derived characters between the cladogram branch points are shared by all organisms above the branch point and are not present in any below it. The outgroup, in this case the lamprey, does not possess any of the derived characters.



gram (figure 32.7), a branching diagram that represents the phylogeny.

In traditional phylogenies, proposed ancestors will often be indicated at the nodes between branches, and the lengths of branches correspond to evolutionary time, with extinct groups having shorter branches. In contrast, cladograms are not true family trees in that they do not identify ancestors, and the branch lengths do not reflect evolutionary time (see figure 32.6). Instead, they convey comparative information about relative relationships. Organisms that are closer together on a cladogram simply share a more recent common ancestor than those that are farther apart. Because the analysis is comparative, it is necessary to have something to anchor the comparison to, some solid ground against which the comparisons can be made. To achieve this, each cladogram must contain an **outgroup**, a rather different organism (but not too different) to serve as a baseline for comparisons among the other organisms being evaluated, the **ingroup**. For example, in figure 32.7, the lamprey is the outgroup to the clade of animals that have jaws.

Cladistics is a relatively new approach in biology and has become popular among students of evolution. This is because it does a very good job of portraying the order in which a series of evolutionary events have occurred. The great strength of a cladogram is that it can be completely objective. In fact, most cladistic analyses involve many characters, and computers are required to make the comparisons.

Sometime it is necessary to “weight” characters, or take into account the variation in the “strength” of a character, such as the size or location of a fin or the effectiveness of a lung. To reduce a systematist’s bias even more, many analyses will be run through the computer with the traits weighted differently each time. Under this procedure, several different cladograms will be constructed, the goal being to choose the one that is the most **parsimonious**, or simplest and thus most likely. Reflecting the importance of evolutionary processes to all fields of biology, most taxonomy today includes at least some element of cladistic analysis.

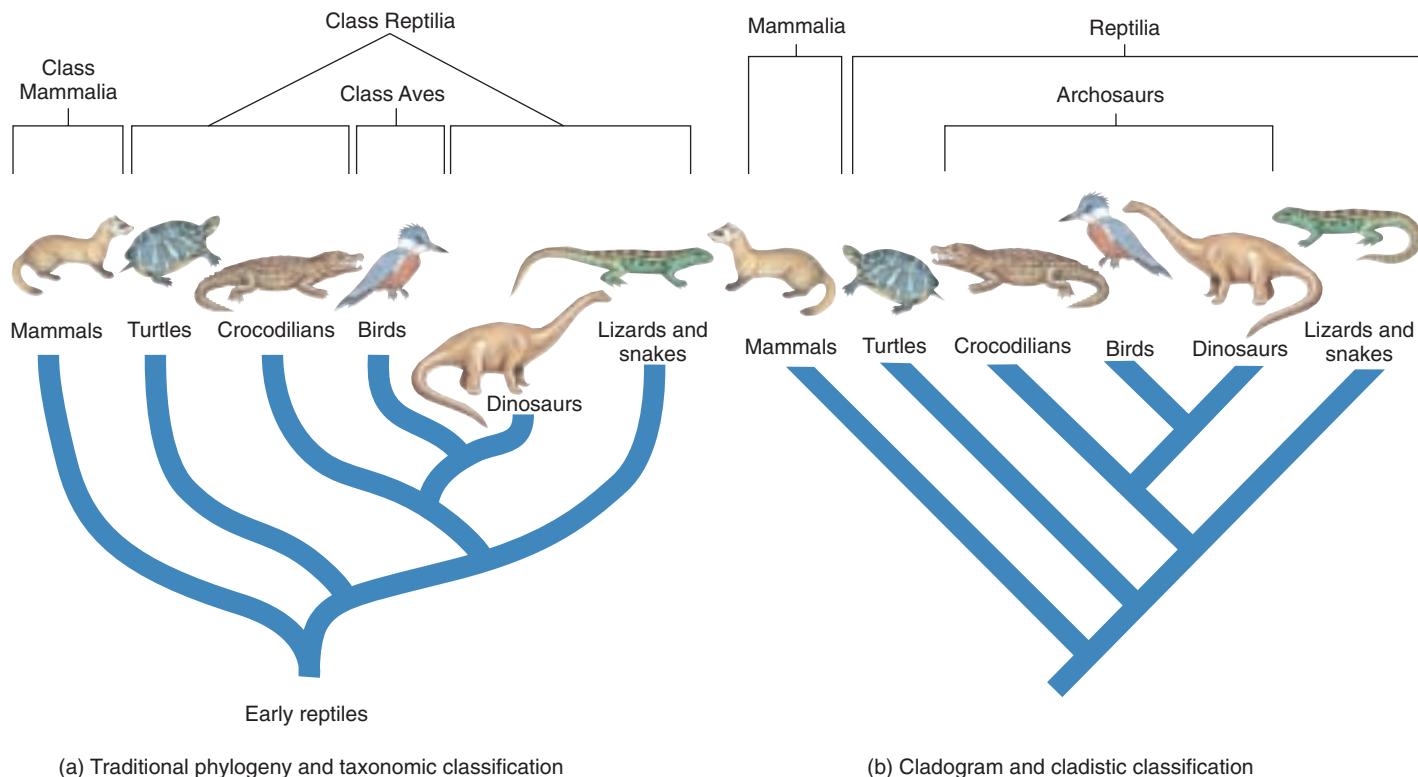


FIGURE 32.8

Traditional and cladistic interpretations of vertebrate classification. Traditional and cladistic taxonomic analyses of the same set of data often produce different results: in these two classifications of vertebrates, notice particularly the placement of the birds. (a) In the traditional analysis, key characteristics such as feathers and hollow bones are weighted more heavily than others, placing the birds in their own group and the reptiles in a paraphyletic group. (b) Cladistic analysis gives equal weight to these and many other characters and places birds in the same grouping with crocodiles, reflecting the close evolutionary relationship between the two. Also, in the traditional phylogeny, the branch leading to the dinosaurs is shorter because the length corresponds to evolutionary time. In cladograms, branch lengths do not correspond to evolutionary time.

Traditional Taxonomy

Weighting characters lies at the core of **traditional taxonomy**. In this approach, taxa are assigned based on a vast amount of information about the morphology and biology of the organism gathered over a long period of time. Traditional taxonomists consider both the common descent and amount of adaptive evolutionary change when grouping organisms. The large amount of information used by traditional taxonomists permits a knowledgeable weighting of characters according to their biological significance. In traditional taxonomy, the full observational power and judgment of the biologist is brought to bear—and also any biases he or she may have. For example, in classifying the terrestrial vertebrates, traditional taxonomists place birds in their own class (*Aves*), giving great weight to the characters that made powered flight possible, such as feathers. However, cladists (figure 32.8) lumps birds in among the reptiles with crocodiles. This accurately reflects their true an-

cestry but ignores the immense evolutionary impact of a derived character such as feathers.

Overall, classifications based on traditional taxonomy are information-rich, while classifications based on cladograms need not be. Traditional taxonomy is often used when a great deal of information is available to guide character weighting, while cladistics is a good approach when little information is available about how the character affects the life of the organism. DNA sequence comparisons, for example, lend themselves well to cladistics—you have a great many derived characters (DNA sequence differences) but little or no idea of what impact the sequence differences have on the organism.

A phylogeny may be represented as a cladogram based on the order in which groups evolved. Traditional taxonomists weight characters according to assumed importance.

32.3 All living organisms are grouped into one of a few major categories.

The Kingdoms of Life

The earliest classification systems recognized only two kingdoms of living things: animals and plants (figure 32.9a). But as biologists discovered microorganisms and learned more about other organisms, they added kingdoms in recognition of fundamental differences discovered among organisms (figure 32.9b). Most biologists now use a six-kingdom system first proposed by Carl Woese of the University of Illinois (figure 32.9c).

In this system, four kingdoms consist of eukaryotic organisms. The two most familiar kingdoms, **Animalia** and **Plantae**, contain only organisms that are multicellular during most of their life cycle. The kingdom **Fungi** contains multicellular forms and single-celled yeasts, which are thought to have multicellular ancestors. Fundamental differences divide these three kingdoms. Plants are mainly stationary, but some have motile sperm; fungi have no motile cells; animals are mainly motile. Animals ingest their food, plants manufacture it, and fungi digest it by means of secreted extracellular enzymes. Each of these kingdoms probably evolved from a different single-celled ancestor.

The large number of unicellular eukaryotes are arbitrarily grouped into a single kingdom called **Protista** (see chapter 35). This kingdom includes the algae, all of which are unicellular during parts of their life cycle.

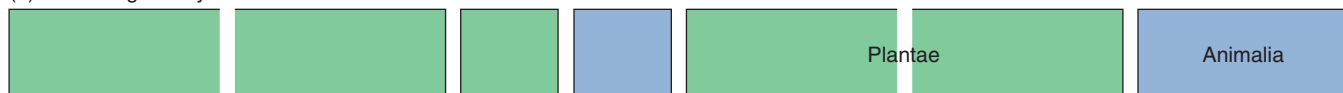
The remaining two kingdoms, **Archaeobacteria** and **Eubacteria**, consist of prokaryotic organisms, which are vastly different from all other living things (see chapter 34). Archaeobacteria are a diverse group including the methanogens and extreme thermophiles, and differ from the other bacteria, members of the kingdom Eubacteria.

Domains

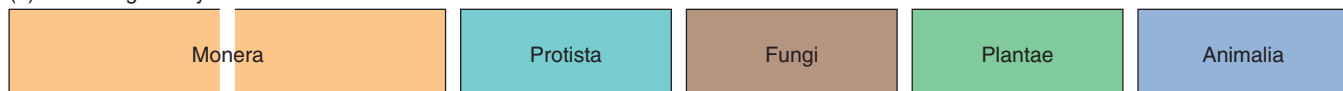
As biologists have learned more about the archaeobacteria, it has become increasingly clear that this ancient group is very different from all other organisms. When the full genomic DNA sequences of an archaeobacterium and a eubacterium were first compared in 1996, the differences proved striking. Archaeobacteria are as different from eubacteria as eubacteria are from eukaryotes. Recognizing this, biologists are increasingly adopting a classification of living organisms that recognizes three **domains**, a taxonomic level higher than kingdom (figure 32.9d). Archaeobacteria are in one domain, eubacteria in a second, and eukaryotes in the third.

Living organisms are grouped into three general categories called domains. One of the domains, the eukaryotes, is subdivided into four kingdoms: protists, fungi, plants, and animals.

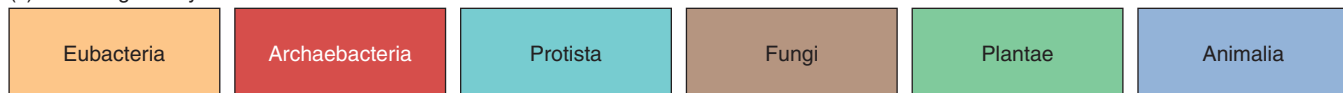
(a) A two-kingdom system—Linnaeus



(b) A five-kingdom system—Whittaker



(c) A six-kingdom system—Woese



(d) A three-domain system—Woese



FIGURE 32.9

Different approaches to classifying living organisms. (a) Linnaeus popularized a two-kingdom approach, in which the fungi and the photosynthetic protists were classified as plants, and the nonphotosynthetic protists as animals; when bacteria were described, they too were considered plants. (b) Whittaker in 1969 proposed a five-kingdom system that soon became widely accepted. (c) Woese has championed splitting the bacteria into two kingdoms for a total of six kingdoms, or even assigning them separate domains (d).

Domain Archaea (Archaeobacteria)

The term *archaeobacteria* (Greek, *archaios*, ancient) refers to the ancient origin of this group of bacteria, which seem to have diverged very early from the eubacteria (figure 32.10). This conclusion comes largely from comparisons of genes that encode ribosomal RNAs. The last several years have seen an explosion of DNA sequence information from microorganisms, information which paints a more complex picture. It had been thought that by sequencing numerous microbes we could eventually come up with an accurate picture of the phylogeny of the earliest organisms on earth. The new whole-genome DNA sequence data described in chapter 19 tells us that it will not be that simple. Comparing whole-genome sequences leads evolutionary biologists to a variety of trees, some of which contradict each other. It appears that during their early evolution microorganisms have swapped genetic information, making constructing phylogenetic trees very difficult.

As an example of the problem, we can look at *Thermotoga*, a thermophile found on Volcano Island off Italy. The sequence of one of its RNAs places it squarely within the eubacteria near an ancient microbe called *Aquifex*. Recent DNA sequencing, however, fails to support any consistent relationship between the two microbes. There is disagreement as to the serious effect of gene swapping on the ability of evolutionary biologists to provide accurate phylogenies from molecular data. For now, we will provisionally accept the tree presented in figure 32.10. Over the next few years we can expect to see considerable change in accepted viewpoints as more and more data is brought to bear.

Today, archaeobacteria inhabit some of the most extreme environments on earth. Though a diverse group, all archaeobacteria share certain key characteristics (table 32.1). Their cell walls lack peptidoglycan (an important component of the cell walls of eubacteria), the lipids in the cell membranes of archaeobacteria have a different structure than those in all other organisms, and archaeobacteria have distinctive ribosomal RNA sequences. Some of their genes possess introns, unlike those of other bacteria.

The archaeobacteria are grouped into three general categories, methanogens, extremophiles, and nonextreme archaeobacteria, based primarily on the environments in which they live or their specialized metabolic pathways.

Methanogens obtain their energy by using hydrogen gas (H_2) to reduce carbon dioxide (CO_2) to methane gas (CH_4). They are strict anaerobes, poisoned by even traces of oxygen. They live in swamps, marshes, and the intestines of mammals. Methanogens release about 2 billion tons of methane gas into the atmosphere each year.

Extremophiles are able to grow under conditions that seem extreme to us.

Thermophiles (“heat lovers”) live in very hot places, typically from 60° to 80°C. Many thermophiles are autotrophs and have metabolisms based on sulfur. Some

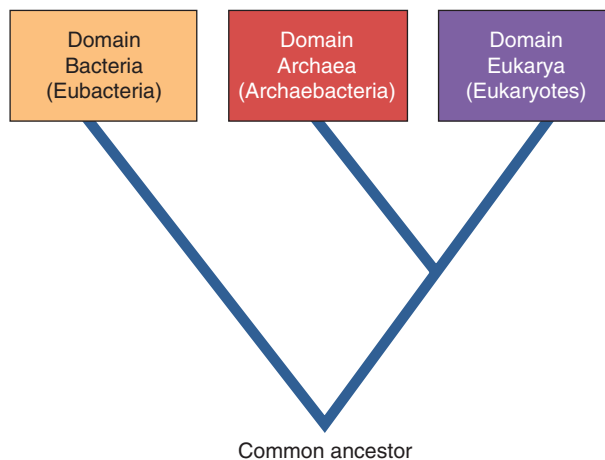


FIGURE 32.10
An evolutionary relationship among the three domains.
Eubacteria are thought to have diverged early from the evolutionary line that gave rise to the archaeobacteria and eukaryotes.

thermophilic archaeobacteria form the basis of food webs around deep-sea thermal vents where they must withstand extreme temperatures and pressures. Other types, like *Sulfolobus*, inhabit the hot sulfur springs of Yellowstone National Park at 70° to 75°C. The recently described *Pyrolobus fumarii* holds the current record for heat stability, with a 106°C temperature optimum and 113°C maximum—it is so heat tolerant that it is not killed by a one-hour treatment in an autoclave (121°C)!

Halophiles (“salt lovers”) live in very salty places like the Great Salt Lake in Utah, Mono Lake in California, and the Dead Sea in Israel. Whereas the salinity of seawater is around 3%, these bacteria thrive in, and indeed require, water with a salinity of 15 to 20%.

pH-tolerant archaeobacteria grow in highly acidic (pH = 0.7) and very basic (pH = 11) environments.

Pressure-tolerant archaeobacteria have been isolated from ocean depths that require at least 300 atmospheres of pressure to survive, and tolerate up to 800 atmospheres!

Nonextreme archaeobacteria grow in the same environments eubacteria do. As the genomes of archaeobacteria have become better known, microbiologists have been able to identify **signature sequences** of DNA present in all archaeobacteria and in no other organisms. When samples from soil or seawater are tested for genes matching these signal sequences, many of the bacteria living there prove to be archaeobacteria. Clearly, archaeobacteria are not restricted to extreme habitats, as microbiologists used to think.

Archaeobacteria are poorly understood bacteria that inhabit diverse environments, some of them extreme.

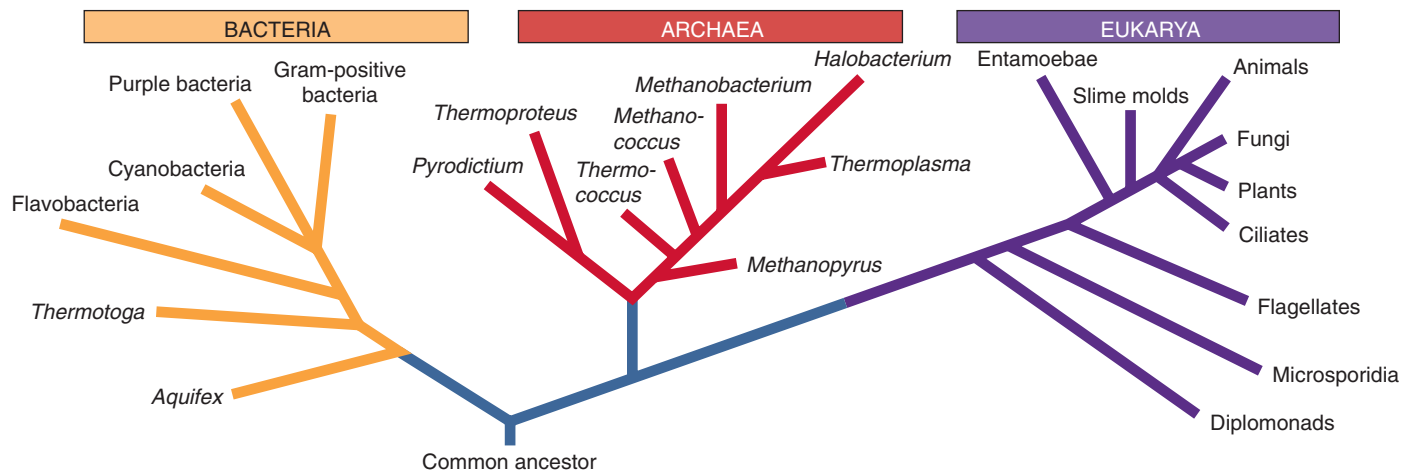


FIGURE 32.11

A tree of life. This phylogeny, prepared from rRNA analyses, shows the evolutionary relationships among the three domains. The base of the tree was determined by examining genes that are duplicated in all three domains, the duplication presumably having occurred in the common ancestor. When one of the duplicates is used to construct the tree, the other can be used to root it. This approach clearly indicates that the root of the tree is within the eubacterial domain. Archaeobacteria and eukaryotes diverged later and are more closely related to each other than either is to eubacteria.

Domain Bacteria (Eubacteria)

The eubacteria are the most abundant organisms on earth. There are more living eubacteria in your mouth than there are mammals living on earth. Although too tiny to see with the unaided eye, eubacteria play critical roles throughout the biosphere. They extract from the air all the nitrogen used by organisms, and play key roles in cycling carbon and sulfur. Much of the world's photosynthesis is carried out by eubacteria. However, certain groups of eubacteria are also responsible for many forms of disease. Understanding their metabolism and genetics is a critical part of modern medicine.

There are many different kinds of eubacteria, and the evolutionary links between them are not well understood. While there is considerable disagreement among taxonomists about the details of bacterial classification, most recognize 12 to 15 major groups of eubacteria. Comparisons of the nucleotide sequences of ribosomal RNA (rRNA) molecules are beginning to reveal how these groups are related to one another and to the other two domains. One view of our current understanding of the "Tree of Life" is presented in figure 32.11. The oldest divergences represent the deepest rooted branches in the tree. The root of the tree is within the eubacterial domain. The archaeobacteria and eukaryotes are more closely related to each other than to eubacteria and are on a separate evolutionary branch of the tree, even though archaeobacteria and eubacteria are both prokaryotes.

Eubacteria are as different from archaeobacteria as from eukaryotes.

Table 32.1 Features of the Domains of Life

Feature	Domain		
	Archaea	Bacteria	Eukarya
Amino acid that initiates protein synthesis	Methionine	Formyl-methionine	Methionine
Introns	Present in some genes	Absent	Present
Membrane-bounded organelles	Absent	Absent	Present
Membrane lipid structure	Branched	Unbranched	Unbranched
Nuclear envelope	Absent	Absent	Present
Number of different RNA polymerases	Several	One	Several
Peptidoglycan in cell wall	Absent	Present	Absent
Response to the antibiotics streptomycin and chloramphenicol	Growth not inhibited	Growth inhibited	Growth not inhibited

Domain Eukarya (Eukaryotes)

For at least 2 billion years, bacteria ruled the earth. No other organisms existed to eat them or compete with them, and their tiny cells formed the world's oldest fossils. The third great domain of life, the eukaryotes, appear in the fossil record much later, only about 1.5 billion years ago. Metabolically, eukaryotes are more uniform than bacteria. Each of the two domains of prokaryotic organisms has far more metabolic diversity than all eukaryotic organisms taken together. However, despite the metabolic similarity of eukaryotic cells, their structure and function allowed larger cell sizes and, eventually, multicellular life to evolve.

Four Kingdoms of Eukaryotes

The first eukaryotes were unicellular organisms. A wide variety of unicellular eukaryotes exist today, grouped together in the kingdom Protista on the basis that they do not fit into any of the other three kingdoms of eukaryotes. Protists are a fascinating group containing many organisms of intense interest and great biological significance. They vary from the relatively simple, single-celled amoeba to multicellular organisms like kelp that can be 20 meters long.

Fungi, plants, and animals are largely multicellular kingdoms, each a distinct evolutionary line from a single-celled ancestor that would be classified in the kingdom Protista.

Because of the size and ecological dominance of plants, animals, and fungi, and because they are predominantly multicellular, we recognize them as kingdoms distinct from Protista, even though the amount of diversity among the protists is much greater than that within or between the fungi, plants, and animals.

Symbiosis and the Origin of Eukaryotes

The hallmark of eukaryotes is complex cellular organization, highlighted by an extensive endomembrane system that subdivides the eukaryotic cell into functional compartments. Not all of these compartments, however, are derived from the endomembrane system. With few exceptions, all modern eukaryotic cells possess energy-producing organelles, the mitochondria, and some eukaryotic cells possess chloroplasts, which are energy-harvesting organelles. Mitochondria and chloroplasts are both believed to have entered early eukaryotic cells by a process called **endosymbiosis** (*endo*, inside). We discussed the theory of the endosymbiotic origin of mitochondria and chloroplasts in chapter 5; also see figure 32.12. Both organelles contain their own ribosomes, which are more similar to bacterial ribosomes than to eukaryotic cytoplasmic ribosomes. They manufacture their own inner membranes. They divide independently of the cell and contain chromosomes similar to those in bacteria. Mitochondria are about the size of bacteria and contain DNA. Comparison of the nucleotide sequence of this DNA with that of a variety of organisms

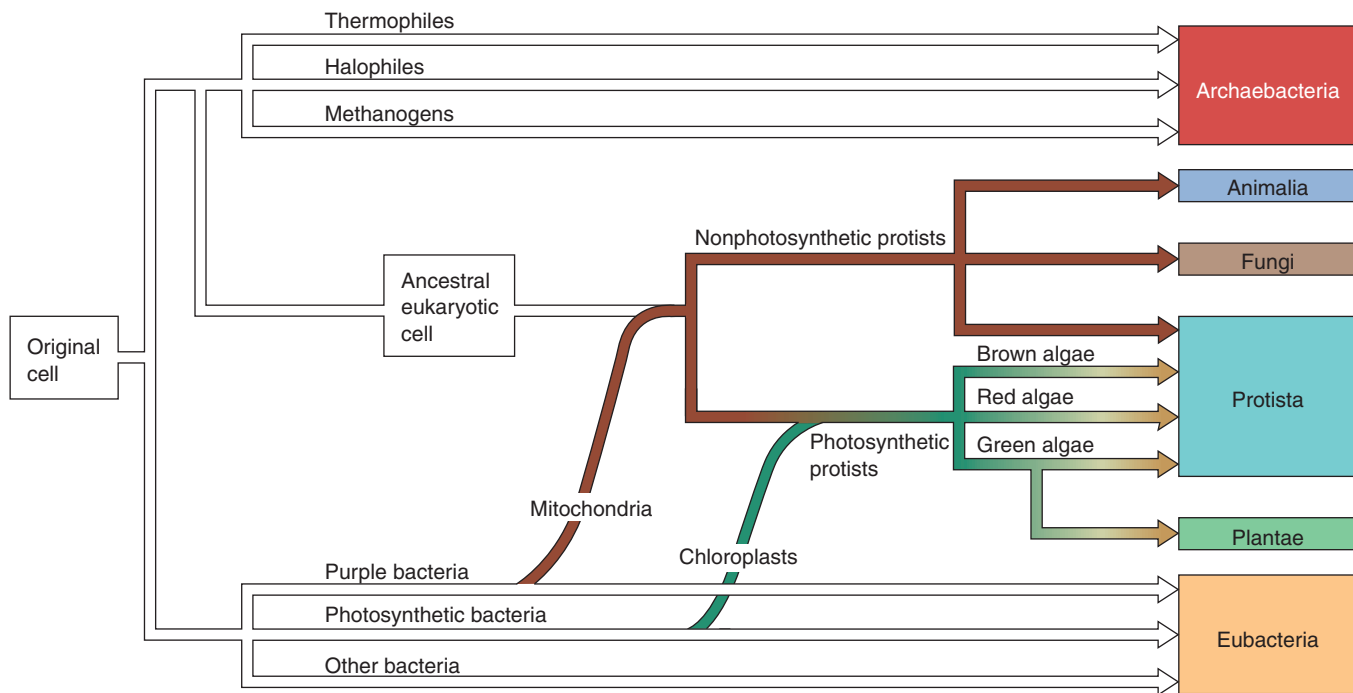


FIGURE 32.12 Diagram of the evolutionary relationships among the six kingdoms of organisms. The colored lines indicate symbiotic events.

indicates clearly that mitochondria are the descendants of purple bacteria that were incorporated into eukaryotic cells early in the history of the group. Chloroplasts are derived from cyanobacteria that became symbiotic in several groups of protists early in their history.

Some biologists suggest that basal bodies, centrioles, flagella, and cilia may have arisen from endosymbiotic spirochaete-like bacteria. Even today, so many bacteria and unicellular protists form symbiotic alliances that the incorporation of smaller organisms with desirable features into eukaryotic cells appears to be a relatively common process.

Key Characteristics of Eukaryotes

Multicellularity. The unicellular body plan has been tremendously successful, with unicellular prokaryotes and eukaryotes constituting about half of the biomass on earth. Yet a single cell has limits. The evolution of multicellularity allowed organisms to deal with their environments in novel ways. Distinct types of cells, tissues, and organs can be differentiated within the complex bodies of multicellular organisms. With such a functional division within its body, a multicellular organism can do many things, like protect itself, resist drought efficiently, regulate its internal conditions, move about, seek mates and prey, and carry out other activities on a scale and with a complexity that would be impossible for its unicellular ancestors. With all these advantages, it is not surprising that multicellularity has arisen independently so many times.

True multicellularity, in which the activities of individual cells are coordinated and the cells themselves are in contact, occurs only in eukaryotes and is one of their major characteristics. The cell walls of bacteria occasionally adhere to one another, and bacterial cells may also be held together within a common sheath. Some bacteria form filaments, sheets, or three-dimensional aggregates (figure 32.13), but the individual cells remain independent of each other, reproducing and carrying on their metabolic functions and without coordinating with the other cells. Such bacteria are considered colonial, but none are truly multicellular. Many protists also form similar colonial aggregates of many cells with little differentiation or integration.

Other protists—the red, brown, and green algae, for example—have independently attained multicellularity. Cer-

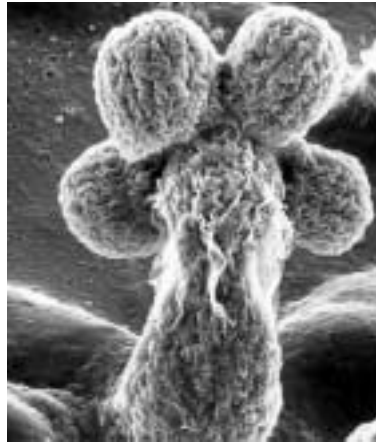


FIGURE 32.13
Colonial bacteria. No bacteria are truly multicellular. These gliding bacteria, *Stigmatella aurantiaca*, have aggregated into a structure called a fruiting body; within, some cells transform into spores.

tain forms of multicellular green algae were ancestors of the plants (see chapters 35 and 37), and, like the other photosynthetic protists, are considered plants in some classification schemes. In the system adopted here, the plant kingdom includes only multicellular land plants, a group that arose from a single ancestor in terrestrial habitats and that has a unique set of characteristics. Aquatic plants are recent derivatives.

Fungi and animals arose from unicellular protist ancestors with different characteristics. As we will see in subsequent chapters, the groups that seem to have given rise to each of these kingdoms are still in existence.

Sexuality. Another major characteristic of eukaryotic organisms as a group is sexuality. Although some interchange of genetic material occurs in bacteria (see chapter 34), it is certainly not a regular, predictable mechanism in the same sense that sex is in eukaryotes. The sexual

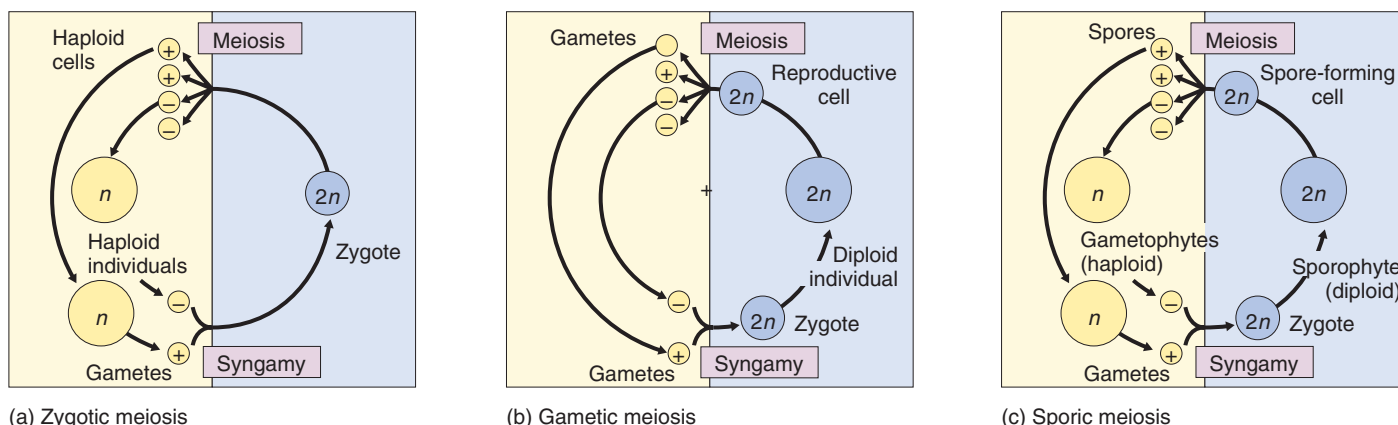
cycle characteristic of eukaryotes alternates between **syngamy**, the union of male and female gametes producing a cell with two sets of chromosomes, and meiosis, cell division producing daughter cells with one set of chromosomes. This cycle differs sharply from any exchange of genetic material found in bacteria.

Except for gametes, the cells of most animals and plants are diploid, containing two sets of chromosomes, during some part of their life cycle. A few eukaryotes complete their life cycle in the haploid condition, with only one set of chromosomes in each cell. As we have seen, in diploid cells, one set of chromosomes comes from the male parent and one from the female parent. These chromosomes segregate during meiosis. Because crossing over frequently occurs during meiosis (see chapter 12), no two products of a single meiotic event are ever identical. As a result, the offspring of sexual, eukaryotic organisms vary widely, thus providing the raw material for evolution.

Sexual reproduction, with its regular alternation between syngamy and meiosis, produces genetic variation. Sexual organisms can adapt to the demands of their environments because they produce a variety of progeny.

In many of the unicellular phyla of protists, sexual reproduction occurs only occasionally. Meiosis may have originally evolved as a means of repairing damage to DNA, producing an organism better adapted to survive changing environmental conditions. The first eukaryotes were probably haploid. Diploids seem to have arisen on a number of separate occasions by the fusion of haploid cells, which then eventually divided by meiosis.

Key: Haploid Diploid



(a) Zygotic meiosis

(b) Gametic meiosis

(c) Sporic meiosis

FIGURE 32.14

Diagrams of the three major kinds of life cycles in eukaryotes. (a) Zygotic meiosis, (b) gametic meiosis, and (c) sporic meiosis.

Eukaryotic Life Cycles

Eukaryotes are characterized by three major types of life cycles (figure 32.14):

1. In the simplest cycle, found in algae, the zygote is the only diploid cell. Such a life cycle is said to be characterized by **zygotic meiosis**, because the zygote immediately undergoes meiosis.
2. In most animals, the gametes are the only haploid cells. Animals exhibit **gametic meiosis**, meiosis producing gametes which fuse, giving rise to a zygote.
3. Plants show a regular *alternation of generations* between a multicellular haploid phase and a multicellular diploid phase. The diploid phase undergoes meiosis producing haploid spores that give rise to the haploid phase, and the haploid phase produces

gametes that fuse to form the zygote. The zygote is the first cell of the multicellular diploid phase. This kind of life cycle is characterized by **alternation of generations** and has **sporic meiosis**.

The characteristics of the six kingdoms are outlined in table 32.2.

Eukaryotic cells acquired mitochondria and chloroplasts by endosymbiosis, mitochondria being derived from purple bacteria and chloroplasts from cyanobacteria. The complex differentiation that we associate with advanced life-forms depends on multicellularity and sexuality, which must have been highly advantageous to have evolved independently so often.

Table 32.2 Characteristics of the Six Kingdoms

Kingdom	Cell Type	Nuclear Envelope	Mitochondria	Chloroplasts	Cell Wall
Archaeobacteria and Eubacteria	Prokaryotic	Absent	Absent	None (photosynthetic membranes in some types)	Noncellulose (polysaccharide plus amino acids)
Protista	Eukaryotic	Present	Present or absent	Present (some forms)	Present in some forms, various types
Fungi	Eukaryotic	Present	Present or absent	Absent	Chitin and other noncellulose polysaccharides
Plantae	Eukaryotic	Present	Present	Present	Cellulose and other polysaccharides
Animalia	Eukaryotic	Present	Present	Absent	Absent

Viruses: A Special Case

Viruses pose a challenge to biologists as they do not possess the fundamental characteristics of living organisms. Viruses appear to be fragments of nucleic acids originally derived from the genome of a living cell. Unlike all living organisms, viruses are acellular—that is, they are not cells and do not consist of cells. They do not have a metabolism; in other words, viruses do not carry out photosynthesis, cellular respiration, or fermentation. The one characteristic of life that they do display is reproduction, which they do by hijacking the metabolism of living cells.

Viruses thus present a special classification problem. Because they are not organisms, we cannot logically place them in any of the kingdoms. Viruses are really just complicated associations of molecules, bits of nucleic acids usually surrounded by a protein coat. But, despite their simplicity, viruses are able to invade cells and direct the genetic machinery of these cells to manufacture more of the molecules that make up the virus (figure 32.15). Viruses can infect organisms at all taxonomic levels.

Viruses are not organisms and are not classified in the kingdoms of life.

FIGURE 32.15

Viruses are cell parasites. In this micrograph, several T4 bacteriophages (viruses) are attacking an *Escherichia coli* bacterium. Some of the viruses have already entered the cell and are reproducing within it.

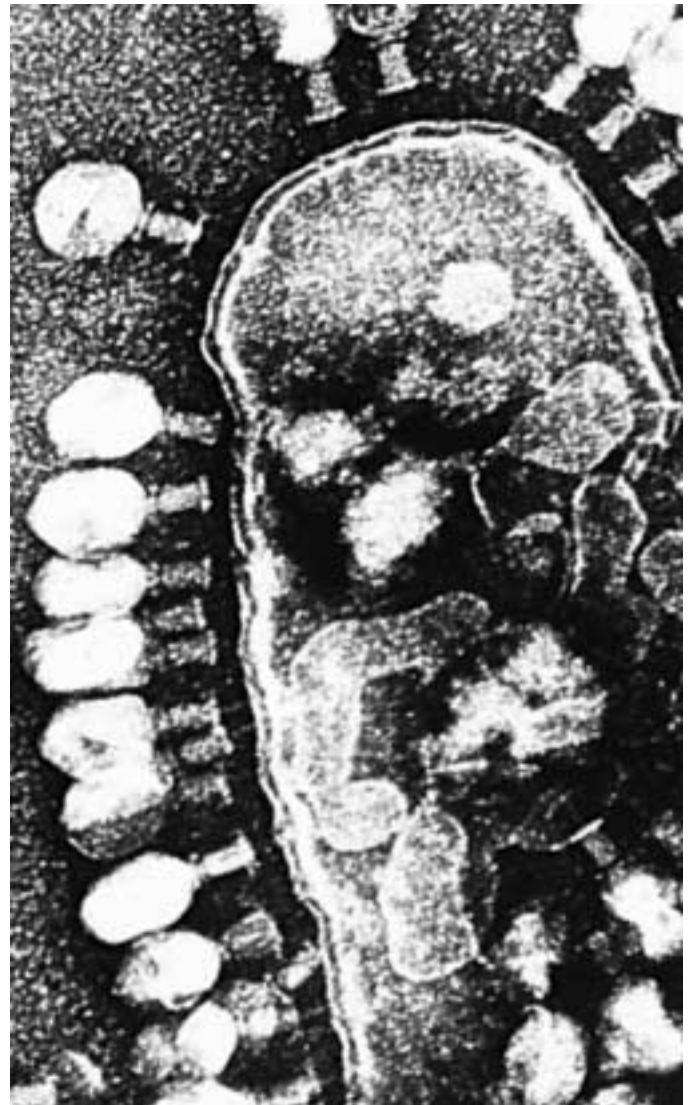


Table 32.2 Characteristics of the Six Kingdoms

Means of Genetic Recombination, if Present	Mode of Nutrition	Motility	Multicellularity	Nervous System
Conjugation, transduction, transformation	Autotrophic (chemosynthetic, photosynthetic) or heterotrophic	Bacterial flagella, gliding or nonmotile	Absent	None
Fertilization and meiosis	Photosynthetic or heterotrophic, or combination of both	9 + 2 cilia and flagella; amoeboid, contractile fibrils	Absent in most forms	Primitive mechanisms for conducting stimuli in some forms
Fertilization and meiosis	Absorption	Nonmotile	Present in most forms	None
Fertilization and meiosis	Photosynthetic chlorophylls <i>a</i> and <i>b</i>	None in most forms, 9 + 2 cilia and flagella in gametes of some forms	Present in all forms	None
Fertilization and meiosis	Digestion	9 + 2 cilia and flagella, contractile fibrils	Present in all forms	Present, often complex



Summary

Questions

Media Resources

32.1 Biologists name organisms in a systematic way.

- Biologists give every species a two-part (binomial) name that consists of the name of its genus plus a distinctive specific epithet.
- In the hierarchical system of classification used in biology, genera are grouped into families, families into orders, orders into classes, classes into phyla, and phyla into kingdoms.
- There are perhaps 10 million species of plants, animals, fungi, and eukaryotic microorganisms, but only about 1.5 million of them have been assigned names. About 15% of the total number of species are marine; the remainder are mostly terrestrial.

1. What was the polynomial system? Why didn't this system become the standard for naming particular species?
2. From the most specific to the most general, what are the names of the groups in the hierarchical taxonomic system? Which two are given special consideration in the way in which they are printed? What are these distinctions?



- Hierarchies



- Book Reviews:
Ship Fever by Barrett

32.2 Scientists construct phylogenies to understand the evolutionary relationships among organisms.

- Taxonomists may use different approaches to classify organisms.
- Cladistic systems of classification arrange organisms according to evolutionary relatedness based on the presence of shared, derived traits.
- Traditional taxonomy classifies organisms based on large amounts of information, giving due weight to the evolutionary significance of certain characters.

3. What types of features are emphasized in a cladistic classification system? What is the resulting relationship of organisms that are classified in this manner?
4. What does it mean when characters are weighted?

32.3 All living organisms are grouped into one of a few major categories.

- A fundamental division among organisms is between prokaryotes, which lack a true nucleus, and eukaryotes, which have a true nucleus and several membrane-bound organelles.
- Prokaryotes, or bacteria, are assigned to two quite different kingdoms, Archaeobacteria and Eubacteria.
- The eukaryotic kingdoms are more closely related than are the two kingdoms of prokaryotes. Many distinctive evolutionary lines of unicellular eukaryotes exist, most are in the Protista kingdom.
- Three of the major evolutionary lines of eukaryotic organisms that consist principally or entirely of multicellular organisms are recognized as separate kingdoms: Plantae, Animalia, and Fungi.
- True multicellularity and sexuality are found only among eukaryotes. Multicellularity confers the advantages of functional specialization. Sexuality permits genetic variation among descendants.
- Viruses are not organisms and are not included in the classification of organisms. They are self-replicating portions of the genomes of organisms.

5. Is there a greater fundamental difference between plants and animals or between prokaryotes and eukaryotes? Explain.
6. From which of the four eukaryotic kingdoms have the other three evolved?
7. What is the apparent origin of the organelles found in almost all eukaryotes?
8. What defines if a collection of cells is truly multicellular? Did multicellularity arise once or many times in the evolutionary process? What advantages do multicellular organisms have over unicellular ones?
9. What are the three major types of life cycles in eukaryotes? Describe the major events of each.



- Art Activity:
Organism
Classification



- Kingdoms
- Three Domains
- Phylogeny



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