20 | PHYLOGENIES AND THE HISTORY OF LIFE

Figure 20.1 The life of a bee is very different from the life of a flower, but the two organisms are related. Both are members of the domain Eukarya and have cells containing many similar organelles, genes, and proteins. (credit: modification of work by John Beetham)

Chapter Outline

- **20.1: Organizing Life on Earth**
- **20.2: Determining Evolutionary Relationships**
- **20.3: Perspectives on the Phylogenetic Tree**

Introduction

This bee and *Echinacea* flower (Figure 20.1) could not look more different, yet they are related, as are all living organisms on Earth. By following pathways of similarities and changes—both visible and genetic—scientists seek to map the evolutionary past of how life developed from single-celled organisms to the tremendous collection of creatures that have germinated, crawled, floated, swam, flown, and walked on this planet.

20.1 | Organizing Life on Earth

By the end of this section, you will be able to:

- Discuss the need for a comprehensive classification system
- List the different levels of the taxonomic classification system
- Describe how systematics and taxonomy relate to phylogeny
- Discuss the components and purpose of a phylogenetic tree

In scientific terms, the evolutionary history and relationship of an organism or group of organisms is called its **phylogeny**. A phylogeny describes the relationships of an organism, such as from which organisms it is thought to have evolved, to
which species it is most closely related, and so forth. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different.

**Phylogenetic Trees**

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A phylogenetic tree is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a “tree of life” can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms (Figure 20.2).

Unlike a taxonomic classification diagram, a phylogenetic tree can be read like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees rooted, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains—Bacteria, Archaea, and Eukarya—diverge from a single point and branch off. The small branch that plants and animals (including humans) occupy in this diagram shows how recent and miniscule these groups are compared with other organisms. Unrooted trees don’t show a common ancestor but do show relationships among species.

![Figure 20.2](credit a: modification of work by Eric Gaba)

In a rooted tree, the branching indicates evolutionary relationships (Figure 20.3). The point where a split occurs, called a branch point, represents where a single lineage evolved into a distinct new one. A lineage that evolved early from the root and remains unbranched is called basal taxon. When two lineages stem from the same branch point, they are called sister taxa. A branch with more than two lineages is called a polytomy and serves to illustrate where scientists have not definitively determined all of the relationships. It is important to note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split apart at a specific branch point, but neither taxa gave rise to the other.

![Figure 20.3](Credit: (credit a: modification of work by Eric Gaba))
The diagrams above can serve as a pathway to understanding evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing back towards the "trunk" of the tree, one can discover that species' ancestors, as well as where lineages share a common ancestry. In addition, the tree can be used to study entire groups of organisms.

Another point to mention on phylogenetic tree structure is that rotation at branch points does not change the information. For example, if a branch point was rotated and the taxon order changed, this would not alter the information because the evolution of each taxon from the branch point was independent of the other.

Many disciplines within the study of biology contribute to understanding how past and present life evolved over time; these disciplines together contribute to building, updating, and maintaining the “tree of life.” Information is used to organize and classify organisms based on evolutionary relationships in a scientific field called **systematics**. Data may be collected from fossils, from studying the structure of body parts or molecules used by an organism, and by DNA analysis. By combining data from many sources, scientists can put together the phylogeny of an organism; since phylogenetic trees are hypotheses, they will continue to change as new types of life are discovered and new information is learned.

### Limitations of Phylogenetic Trees

It may be easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly varied surroundings or after the evolution of a major new adaptation, it is possible for the two groups to appear more different than other groups that are not as closely related. For example, the phylogenetic tree in Figure 20.4 shows that lizards and rabbits both have amniotic eggs, whereas frogs do not; yet lizards and frogs appear more similar than lizards and rabbits.

![Figure 20.4](image)

*Figure 20.4* This ladder-like phylogenetic tree of vertebrates is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups based on the characteristics they share.

Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not account for length of time, only the evolutionary order. In other words, the length of a branch does not typically mean more time passed, nor does a short branch mean less time passed— unless specified on the diagram. For example, in Figure 20.4, the tree does not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the order in which things took place. Again using Figure 20.4, the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and like a real tree, it does not grow in only one direction after a new branch develops. So, for the organisms in Figure 20.4, just because a vertebral column evolved does not mean that invertebrate evolution ceased, it only means that a new branch formed. Also, groups that are not closely related, but evolve under similar conditions, may appear more phenotypically similar to each other than to a close relative.
Head to this website (http://openstaxcollege.org/l/tree_of_life) to see interactive exercises that allow you to explore the evolutionary relationships among species.

The Levels of Classification

**Taxonomy** (which literally means “arrangement law”) is the science of classifying organisms to construct internationally shared classification systems with each organism placed into more and more inclusive groupings. Think about how a grocery store is organized. One large space is divided into departments, such as produce, dairy, and meats. Then each department further divides into aisles, then each aisle into categories and brands, and then finally a single product. This organization from larger to smaller, more specific categories is called a hierarchical system.

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. For example, after the common beginning of all life, scientists divide organisms into three large categories called a domain: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a **kingdom**. After kingdoms, the subsequent categories of increasing specificity are: **phylum, class, order, family, genus,** and **species** (Figure 20.5).
The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, *Canis lupus familiaris*, is a subspecies of *Canis lupus*, which also includes the wolf and dingo. (credit “dog”: modification of work by Janneke Vreugdenhil)

The kingdom Animalia stems from the Eukarya domain. For the common dog, the classification levels would be as shown in Figure 20.5. Therefore, the full name of an organism technically has eight terms. For the dog, it is: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis*, and *lupus*. Notice that each name is capitalized except for species, and the genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, in what is called binomial nomenclature. Therefore, the scientific name of the dog is *Canis lupus*. The name at each level is also called a taxon. In other words, dogs are in order Carnivora. Carnivora is the name of the taxon at the order level; Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, in this case, dog. Note that the dog is additionally a subspecies: the “*familiaris*” in *Canis lupus familiaris*. Subspecies are members of the same species that are capable of mating and reproducing viable offspring, but they are considered separate subspecies due to geographic or behavioral isolation or other factors.

Figure 20.6 shows how the levels move toward specificity with other organisms. Notice how the dog shares a domain with the widest diversity of organisms, including plants and butterflies. At each sublevel, the organisms become more
similar because they are more closely related. Historically, scientists classified organisms using characteristics, but as DNA technology developed, more precise phylogenies have been determined.

**Figure 20.6** At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of work by “berduchwal”/Flickr; credit “insect”: modification of work by Jon Sullivan; credit “fish”: modification of work by Christian Mehlführer; credit “rabbit”: modification of work by Aidan Wojtas; credit “cat”: modification of work by Jonathan Lidbeck; credit “fox”: modification of work by Kevin Bacher, NPS; credit “jackal”: modification of work by Thomas A. Hermann, NBII, USGS; credit “wolf”: modification of work by Robert Dewar; credit “dog”: modification of work by “digital_image_fan”/Flickr)

At what levels are cats and dogs considered to be part of the same group?
Visit this website (http://openstaxcollege.org/l/classify_life) to classify three organisms—bear, orchid, and sea cucumber—from kingdom to species. To launch the game, under Classifying Life, click the picture of the bear or the Launch Interactive button.

Recent genetic analysis and other advancements have found that some earlier phylogenetic classifications do not align with the evolutionary past; therefore, changes and updates must be made as new discoveries occur. Recall that phylogenetic trees are hypotheses and are modified as data becomes available. In addition, classification historically has focused on grouping organisms mainly by shared characteristics and does not necessarily illustrate how the various groups relate to each other from an evolutionary perspective. For example, despite the fact that a hippopotamus resembles a pig more than a whale, the hippopotamus may be the closest living relative of the whale.

20.2 | Determining Evolutionary Relationships

By the end of this section, you will be able to:
- Compare homologous and analogous traits
- Discuss the purpose of cladistics
- Describe maximum parsimony

Scientists must collect accurate information that allows them to make evolutionary connections among organisms. Similar to detective work, scientists must use evidence to uncover the facts. In the case of phylogeny, evolutionary investigations focus on two types of evidence: morphologic (form and function) and genetic.

Two Options for Similarities

In general, organisms that share similar physical features and genomes tend to be more closely related than those that do not. Such features that overlap both morphologically (in form) and genetically are referred to as homologous structures; they stem from developmental similarities that are based on evolution. For example, the bones in the wings of bats and birds have homologous structures (Figure 20.7).

Figure 20.7 Bat and bird wings are homologous structures, indicating that bats and birds share a common evolutionary past. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM)
Notice it is not simply a single bone, but rather a grouping of several bones arranged in a similar way. The more complex the feature, the more likely any kind of overlap is due to a common evolutionary past. Imagine two people from different countries both inventing a car with all the same parts and in exactly the same arrangement without any previous or shared knowledge. That outcome would be highly improbable. However, if two people both invented a hammer, it would be reasonable to conclude that both could have have the original idea without the help of the other. The same relationship between complexity and shared evolutionary history is true for homologous structures in organisms.

**Misleading Appearances**

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. Similarly, unrelated organisms may be distantly related, but appear very much alike. This usually happens because both organisms were in common adaptations that evolved within similar environmental conditions. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is called an analogy or homoplasy. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different. These are called analogous structures (Figure 20.8).

Similar traits can be either homologous or analogous. Homologous structures share a similar embryonic origin; analogous organs have a similar function. For example, the bones in the front flipper of a whale are homologous to the bones in the human arm. These structures are not analogous. The wings of a butterfly and the wings of a bird are analogous but not homologous. Some structures are both analogous and homologous: the wings of a bird and the wings of a bat are both homologous and analogous. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.

![Figure 20.8](image_url)

*Figure 20.8* The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, the honeybee wing is not composed of bones and has a distinctly different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate an analogy—similar structures that do not share an evolutionary history. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM; credit c: modification of work by Jon Sullivan)
This website (http://openstaxcollege.org/l/relationships) has several examples to show how appearances can be misleading in understanding the phylogenetic relationships of organisms.

**Molecular Comparisons**

With the advancement of DNA technology, the area of molecular systematics, which describes the use of information on the molecular level including DNA analysis, has blossomed. New computer programs not only confirm many earlier classified organisms, but also uncover previously made errors. As with physical characteristics, even the DNA sequence can be tricky to read in some cases. For some situations, two very closely related organisms can appear unrelated if a mutation occurred that caused a shift in the genetic code. An insertion or deletion mutation would move each nucleotide base over one place, causing two similar codes to appear unrelated.

Sometimes two segments of DNA code in distantly related organisms randomly share a high percentage of bases in the same locations, causing these organisms to appear closely related when they are not. For both of these situations, computer technologies have been developed to help identify the actual relationships, and, ultimately, the coupled use of both morphologic and molecular information is more effective in determining phylogeny.
Why Does Phylogeny Matter?

Evolutionary biologists could list many reasons why understanding phylogeny is important to everyday life in human society. For botanists, phylogeny acts as a guide to discovering new plants that can be used to benefit people. Think of all the ways humans use plants—food, medicine, and clothing are a few examples. If a plant contains a compound that is effective in treating cancer, scientists might want to examine all of the relatives of that plant for other useful drugs.

A research team in China identified a segment of DNA thought to be common to some medicinal plants in the family Fabaceae (the legume family) and worked to identify which species had this segment (Figure 20.9). After testing plant species in this family, the team found a DNA marker (a known location on a chromosome that enabled them to identify the species) present. Then, using the DNA to uncover phylogenetic relationships, the team could identify whether a newly discovered plant was in this family and assess its potential medicinal properties.

Building Phylogenetic Trees

How do scientists construct phylogenetic trees? After the homologous and analogous traits are sorted, scientists often organize the homologous traits using a system called **cladistics**. This system sorts organisms into clades: groups of organisms that descended from a single ancestor. For example, in Figure 20.10, all of the organisms in the orange region
evolved from a single ancestor that had amniotic eggs. Consequently, all of these organisms also have amniotic eggs and make a single clade, also called a **monophyletic group**. Clades must include all of the descendants from a branch point.

![Art Connection](image)

**Figure 20.10** Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

Which animals in this figure belong to a clade that includes animals with hair? Which evolved first, hair or the amniotic egg?

Clades can vary in size depending on which branch point is being referenced. The important factor is that all of the organisms in the clade or monophyletic group stem from a single point on the tree. This can be remembered because monophyletic breaks down into “mono,” meaning one, and “phyletic,” meaning evolutionary relationship. **Figure 20.11** shows various examples of clades. Notice how each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.
All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades.

What is the largest clade in this diagram?

**Shared Characteristics**

Organisms evolve from common ancestors and then diversify. Scientists use the phrase “descent with modification” because even though related organisms have many of the same characteristics and genetic codes, changes occur. This pattern repeats over and over as one goes through the phylogenetic tree of life:

1. A change in the genetic makeup of an organism leads to a new trait which becomes prevalent in the group.
2. Many organisms descend from this point and have this trait.
3. New variations continue to arise: some are adaptive and persist, leading to new traits.
4. With new traits, a new branch point is determined (go back to step 1 and repeat).

If a characteristic is found in the ancestor of a group, it is considered a **shared ancestral character** because all of the organisms in the taxon or clade have that trait. The vertebrate in Figure 20.10 is a shared ancestral character. Now consider the amniotic egg characteristic in the same figure. Only some of the organisms in Figure 20.10 have this trait, and to those that do, it is called a **shared derived character** because this trait derived at some point but does not include all of the ancestors in the tree.

The tricky aspect to shared ancestral and shared derived characters is the fact that these terms are relative. The same trait can be considered one or the other depending on the particular diagram being used. Returning to Figure 20.10, note that the amniotic egg is a shared ancestral character for the Amniota clade, while having hair is a shared derived character for some organisms in this group. These terms help scientists distinguish between clades in the building of phylogenetic trees.
Choosing the Right Relationships

Imagine being the person responsible for organizing all of the items in a department store properly—an overwhelming task. Organizing the evolutionary relationships of all life on Earth proves much more difficult: scientists must span enormous blocks of time and work with information from long-extinct organisms. Trying to decipher the proper connections, especially given the presence of homologies and analogies, makes the task of building an accurate tree of life extraordinarily difficult. Add to that the advancement of DNA technology, which now provides large quantities of genetic sequences to be used and analyzed. Taxonomy is a subjective discipline: many organisms have more than one connection to each other, so each taxonomist will decide the order of connections.

To aid in the tremendous task of describing phylogenies accurately, scientists often use a concept called maximum parsimony, which means that events occurred in the simplest, most obvious way. For example, if a group of people entered a forest preserve to go hiking, based on the principle of maximum parsimony, one could predict that most of the people would hike on established trails rather than forge new ones.

For scientists deciphering evolutionary pathways, the same idea is used: the pathway of evolution probably includes the fewest major events that coincide with the evidence at hand. Starting with all of the homologous traits in a group of organisms, scientists look for the most obvious and simple order of evolutionary events that led to the occurrence of those traits.

Head to this website (http://openstaxcollege.org/l/using_parsimony) to learn how maximum parsimony is used to create phylogenetic trees.

These tools and concepts are only a few of the strategies scientists use to tackle the task of revealing the evolutionary history of life on Earth. Recently, newer technologies have uncovered surprising discoveries with unexpected relationships, such as the fact that people seem to be more closely related to fungi than fungi are to plants. Sound unbelievable? As the information about DNA sequences grows, scientists will become closer to mapping the evolutionary history of all life on Earth.

20.3 Perspectives on the Phylogenetic Tree

By the end of this section, you will be able to:

• Describe horizontal gene transfer

• Illustrate how prokaryotes and eukaryotes transfer genes horizontally

• Identify the web and ring models of phylogenetic relationships and describe how they differ from the original phylogenetic tree concept

The concepts of phylogenetic modeling are constantly changing. It is one of the most dynamic fields of study in all of biology. Over the last several decades, new research has challenged scientists’ ideas about how organisms are related. New models of these relationships have been proposed for consideration by the scientific community.

Many phylogenetic trees have been shown as models of the evolutionary relationship among species. Phylogenetic trees originated with Charles Darwin, who sketched the first phylogenetic tree in 1837 (Figure 20.12a), which served as a pattern for subsequent studies for more than a century. The concept of a phylogenetic tree with a single trunk representing a common ancestor, with the branches representing the divergence of species from this ancestor, fits well with the structure of many common trees, such as the oak (Figure 20.12b). However, evidence from modern DNA sequence analysis and
newly developed computer algorithms has caused skepticism about the validity of the standard tree model in the scientific community.

Figure 20.12 The (a) concept of the “tree of life” goes back to an 1837 sketch by Charles Darwin. Like an (b) oak tree, the “tree of life” has a single trunk and many branches. (credit b: modification of work by “Amada44”/Wikimedia Commons)

Limitations to the Classic Model

Classical thinking about prokaryotic evolution, included in the classic tree model, is that species evolve clonally. That is, they produce offspring themselves with only random mutations causing the descent into the variety of modern-day and extinct species known to science. This view is somewhat complicated in eukaryotes that reproduce sexually, but the laws of Mendelian genetics explain the variation in offspring, again, to be a result of a mutation within the species. The concept of genes being transferred between unrelated species was not considered as a possibility until relatively recently. Horizontal gene transfer (HGT), also known as lateral gene transfer, is the transfer of genes between unrelated species. HGT has been shown to be an ever-present phenomenon, with many evolutionists postulating a major role for this process in evolution, thus complicating the simple tree model. Genes have been shown to be passed between species which are only distantly related using standard phylogeny, thus adding a layer of complexity to the understanding of phylogenetic relationships.

The various ways that HGT occurs in prokaryotes is important to understanding phylogenies. Although at present HGT is not viewed as important to eukaryotic evolution, HGT does occur in this domain as well. Finally, as an example of the ultimate gene transfer, theories of genome fusion between symbiotic or endosymbiotic organisms have been proposed to explain an event of great importance—the evolution of the first eukaryotic cell, without which humans could not have come into existence.

Horizontal Gene Transfer

Horizontal gene transfer (HGT) is the introduction of genetic material from one species to another species by mechanisms other than the vertical transmission from parent(s) to offspring. These transfers allow even distantly related species to share genes, influencing their phenotypes. It is thought that HGT is more prevalent in prokaryotes, but that only about 2% of the prokaryotic genome may be transferred by this process. Some researchers believe such estimates are premature: the actual importance of HGT to evolutionary processes must be viewed as a work in progress. As the phenomenon is investigated more thoroughly, it may be revealed to be more common. Many scientists believe that HGT and mutation appear to be (especially in prokaryotes) a significant source of genetic variation, which is the raw material for the process of natural selection. These transfers may occur between any two species that share an intimate relationship (Table 20.1).

| Summary of Mechanisms of Prokaryotic and Eukaryotic HGT |
|----------------|----------------|----------------|
| Mechanism    | Mode of Transmission | Example       |
| Prokaryotes  | transformation     | DNA uptake    | many prokaryotes |

Table 20.1
**Summary of Mechanisms of Prokaryotic and Eukaryotic HGT**

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<th>Mode of Transmission</th>
<th>Example</th>
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<td>from viral infections</td>
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**Table 20.1**

**HGT in Prokaryotes**

The mechanism of HGT has been shown to be quite common in the prokaryotic domains of Bacteria and Archaea, significantly changing the way their evolution is viewed. The majority of evolutionary models, such as in the Endosymbiont Theory, propose that eukaryotes descended from multiple prokaryotes, which makes HGT all the more important to understanding the phylogenetic relationships of all extant and extinct species.

The fact that genes are transferred among common bacteria is well known to microbiology students. These gene transfers between species are the major mechanism whereby bacteria acquire resistance to antibiotics. Classically, this type of transfer has been thought to occur by three different mechanisms:

1. Transformation: naked DNA is taken up by a bacteria
2. Transduction: genes are transferred using a virus
3. Conjugation: the use a hollow tube called a pilus to transfer genes between organisms

More recently, a fourth mechanism of gene transfer between prokaryotes has been discovered. Small, virus-like particles called gene transfer agents (GTAs) transfer random genomic segments from one species of prokaryote to another. GTAs have been shown to be responsible for genetic changes, sometimes at a very high frequency compared to other evolutionary processes. The first GTA was characterized in 1974 using purple, non-sulfur bacteria. These GTAs, which are thought to be bacteriophages that lost the ability to reproduce on their own, carry random pieces of DNA from one organism to another. The ability of GTAs to act with high frequency has been demonstrated in controlled studies using marine bacteria. Gene transfer events in marine prokaryotes, either by GTAs or by viruses, have been estimated to be as high as $10^{13}$ per year in the Mediterranean Sea alone. GTAs and viruses are thought to be efficient HGT vehicles with a major impact on prokaryotic evolution.

As a consequence of this modern DNA analysis, the idea that eukaryotes evolved directly from Archaea has fallen out of favor. While eukaryotes share many features that are absent in bacteria, such as the TATA box (found in the promoter region of many genes), the discovery that some eukaryotic genes were more homologous with bacterial DNA than Archaea DNA made this idea less tenable. Furthermore, the fusion of genomes from Archaea and Bacteria by endosymbiosis has been proposed as the ultimate event in eukaryotic evolution.

**HGT in Eukaryotes**

Although it is easy to see how prokaryotes exchange genetic material by HGT, it was initially thought that this process was absent in eukaryotes. After all, prokaryotes are but single cells exposed directly to their environment, whereas the sex cells of multicellular organisms are usually sequestered in protected parts of the body. It follows from this idea that the gene transfers between multicellular eukaryotes should be more difficult. Indeed, it is thought that this process is rarer in eukaryotes and has a much smaller evolutionary impact than in prokaryotes. In spite of this fact, HGT between distantly related organisms has been demonstrated in several eukaryotic species, and it is possible that more examples will be discovered in the future.

In plants, gene transfer has been observed in species that cannot cross-pollinate by normal means. Transposons or “jumping genes” have been shown to transfer between rice and millet plant species. Furthermore, fungal species feeding on yew trees, from which the anti-cancer drug TAXOL® is derived from the bark, have acquired the ability to make taxol themselves, a clear example of gene transfer.
In animals, a particularly interesting example of HGT occurs within the aphid species (Figure 20.13). Aphids are insects that vary in color based on carotenoid content. Carotenoids are pigments made by a variety of plants, fungi, and microbes, and they serve a variety of functions in animals, who obtain these chemicals from their food. Humans require carotenoids to synthesize vitamin A, and we obtain them by eating orange fruits and vegetables: carrots, apricots, mangoes, and sweet potatoes. On the other hand, aphids have acquired the ability to make the carotenoids on their own. According to DNA analysis, this ability is due to the transfer of fungal genes into the insect by HGT, presumably as the insect consumed fungi for food. A carotenoid enzyme called a desaturase is responsible for the red coloration seen in certain aphids, and it has been further shown that when this gene is inactivated by mutation, the aphids revert back to their more common green color (Figure 20.13).

Figure 20.13 (a) Red aphids get their color from red carotenoid pigment. Genes necessary to make this pigment are present in certain fungi, and scientists speculate that aphids acquired these genes through HGT after consuming fungi for food. If genes for making carotenoids are inactivated by mutation, the aphids revert back to (b) their green color. Red coloration makes the aphids a lot more conspicuous to predators, but evidence suggests that red aphids are more resistant to insecticides than green ones. Thus, red aphids may be more fit to survive in some environments than green ones. (credit a: modification of work by Benny Mazur; credit b: modification of work by Mick Talbot)

**Genome Fusion and the Evolution of Eukaryotes**

Scientists believe the ultimate in HGT occurs through genome fusion between different species of prokaryotes when two symbiotic organisms become endosymbiotic. This occurs when one species is taken inside the cytoplasm of another species, which ultimately results in a genome consisting of genes from both the endosymbiont and the host. This mechanism is an aspect of the Endosymbiont Theory, which is accepted by a majority of biologists as the mechanism whereby eukaryotic cells obtained their mitochondria and chloroplasts. However, the role of endosymbiosis in the development of the nucleus is more controversial. Nuclear and mitochondrial DNA are thought to be of different (separate) evolutionary origin, with the mitochondrial DNA being derived from the circular genomes of bacteria that were engulfed by ancient prokaryotic cells. Mitochondrial DNA can be regarded as the smallest chromosome. Interestingly enough, mitochondrial DNA is inherited only from the mother. The mitochondrial DNA degrades in sperm when the sperm degrades in the fertilized egg or in other instances when the mitochondria located in the flagellum of the sperm fails to enter the egg.

Within the past decade, the process of genome fusion by endosymbiosis has been proposed by James Lake of the UCLA/NASA Astrobiology Institute to be responsible for the evolution of the first eukaryotic cells (Figure 20.14a). Using DNA analysis and a new mathematical algorithm called conditioned reconstruction (CR), his laboratory proposed that eukaryotic cells developed from an endosymbiotic gene fusion between two species, one an Archaea and the other a Bacteria. As mentioned, some eukaryotic genes resemble those of Archaea, whereas others resemble those from Bacteria. An endosymbiotic fusion event, such as Lake has proposed, would clearly explain this observation. On the other hand, this work is new and the CR algorithm is relatively unsubstantiated, which causes many scientists to resist this hypothesis.

More recent work by Lake (Figure 20.14b) proposes that gram-negative bacteria, which are unique within their domain in that they contain two lipid bilayer membranes, indeed resulted from an endosymbiotic fusion of archaeal and bacterial species. The double membrane would be a direct result of the endosymbiosis, with the endosymbiont picking up the second membrane from the host as it was internalized. This mechanism has also been used to explain the double membranes found in mitochondria and chloroplasts. Lake’s work is not without skepticism, and the ideas are still debated within the biological science community. In addition to Lake’s hypothesis, there are several other competing theories as to the origin of eukaryotes. How did the eukaryotic nucleus evolve? One theory is that the prokaryotic cells produced an additional membrane that surrounded the bacterial chromosome. Some bacteria have the DNA enclosed by two membranes; however, there is no evidence of a nucleolus or nuclear pores. Other proteobacteria also have membrane-bound chromosomes. If the eukaryotic nucleus evolved this way, we would expect one of the two types of prokaryotes to be more closely related to eukaryotes.
The theory that mitochondria and chloroplasts are endosymbiotic in origin is now widely accepted. More controversial is the proposal that (a) the eukaryotic nucleus resulted from the fusion of archaeal and bacterial genomes, and that (b) Gram-negative bacteria, which have two membranes, resulted from the fusion of Archaea and Gram-positive bacteria, each of which has a single membrane.

The nucleus-first hypothesis proposes that the nucleus evolved in prokaryotes first (Figure 20.15a), followed by a later fusion of the new eukaryote with bacteria that became mitochondria. The mitochondria-first hypothesis proposes that mitochondria were first established in a prokaryotic host (Figure 20.15b), which subsequently acquired a nucleus, by fusion or other mechanisms, to become the first eukaryotic cell. Most interestingly, the eukaryote-first hypothesis proposes that prokaryotes actually evolved from eukaryotes by losing genes and complexity (Figure 20.15c). All of these hypotheses are testable. Only time and more experimentation will determine which hypothesis is best supported by data.
Web and Network Models

The recognition of the importance of HGT, especially in the evolution of prokaryotes, has caused some to propose abandoning the classic “tree of life” model. In 1999, W. Ford Doolittle proposed a phylogenetic model that resembles a web or a network more than a tree. The hypothesis is that eukaryotes evolved not from a single prokaryotic ancestor, but from a pool of many species that were sharing genes by HGT mechanisms. As shown in Figure 20.16a, some individual prokaryotes were responsible for transferring the bacteria that caused mitochondrial development to the new eukaryotes, whereas other species transferred the bacteria that gave rise to chloroplasts. This model is often called the “web of life.” In an effort to save the tree analogy, some have proposed using the *Ficus* tree (Figure 20.16b) with its multiple trunks as a phylogenetic to represent a diminished evolutionary role for HGT.

![Models for Evolution of the Three Domains](image.png)

Figure 20.15 Three alternate hypotheses of eukaryotic and prokaryotic evolution are (a) the nucleus-first hypothesis, (b) the mitochondrion-first hypothesis, and (c) the eukaryote-first hypothesis.
Figure 20.16 In the (a) phylogenetic model proposed by W. Ford Doolittle, the “tree of life” arose from a community of ancestral cells, has multiple trunks, and has connections between branches where horizontal gene transfer has occurred. Visually, this concept is better represented by (b) the multi-trunked Ficus than by the single trunk of the oak similar to the tree drawn by Darwin Figure 20.12. (credit b: modification of work by “psyberartist”/Flickr)

Ring of Life Models

Others have proposed abandoning any tree-like model of phylogeny in favor of a ring structure, the so-called “ring of life” (Figure 20.17); a phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes. Lake, again using the conditioned reconstruction algorithm, proposes a ring-like model in which species of all three domains—Archaea, Bacteria, and Eukarya—evolved from a single pool of gene-swapping prokaryotes. His laboratory proposes that this structure is the best fit for data from extensive DNA analyses performed in his laboratory, and that the ring model is the only one that adequately takes HGT and genomic fusion into account. However, other phylogeneticists remain highly skeptical of this model.

Figure 20.17 According to the “ring of life” phylogenetic model, the three domains of life evolved from a pool of primitive prokaryotes.

In summary, the “tree of life” model proposed by Darwin must be modified to include HGT. Does this mean abandoning the tree model completely? Even Lake argues that all attempts should be made to discover some modification of the tree model to allow it to accurately fit his data, and only the inability to do so will sway people toward his ring proposal.
This doesn’t mean a tree, web, or a ring will correlate completely to an accurate description of phylogenetic relationships of life. A consequence of the new thinking about phylogenetic models is the idea that Darwin’s original conception of the phylogenetic tree is too simple, but made sense based on what was known at the time. However, the search for a more useful model moves on: each model serving as hypotheses to be tested with the possibility of developing new models. This is how science advances. These models are used as visualizations to help construct hypothetical evolutionary relationships and understand the massive amount of data being analyzed.
KEY TERMS

**analogy** (also, homoplasy) characteristic that is similar between organisms by convergent evolution, not due to the same evolutionary path

**basal taxon** branch on a phylogenetic tree that has not diverged significantly from the root ancestor

**binomial nomenclature** system of two-part scientific names for an organism, which includes genus and species names

**branch point** node on a phylogenetic tree where a single lineage splits into distinct new ones

**cladistics** system used to organize homologous traits to describe phylogenies

**class** division of phylum in the taxonomic classification system

**eukaryote-first hypothesis** proposal that prokaryotes evolved from eukaryotes

**family** division of order in the taxonomic classification system

**gene transfer agent (GTA)** bacteriophage-like particle that transfers random genomic segments from one species of prokaryote to another

**genome fusion** fusion of two prokaryotic genomes, presumably by endosymbiosis

**genus** division of family in the taxonomic classification system; the first part of the binomial scientific name

**horizontal gene transfer (HGT)** (also, lateral gene transfer) transfer of genes between unrelated species

**kingdom** division of domain in the taxonomic classification system

**maximum parsimony** applying the simplest, most obvious way with the least number of steps

**mitochondria-first hypothesis** proposal that prokaryotes acquired a mitochondrion first, followed by nuclear development

**molecular systematics** technique using molecular evidence to identify phylogenetic relationships

**monophyletic group** (also, clade) organisms that share a single ancestor

**nucleus-first hypothesis** proposal that prokaryotes acquired a nucleus first, and then the mitochondrion

**order** division of class in the taxonomic classification system

**phylogenetic tree** diagram used to reflect the evolutionary relationships among organisms or groups of organisms

**phylogeny** evolutionary history and relationship of an organism or group of organisms

**phylum** (plural: phyla) division of kingdom in the taxonomic classification system

**polytomy** branch on a phylogenetic tree with more than two groups or taxa

**ring of life** phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes

**rooted** single ancestral lineage on a phylogenetic tree to which all organisms represented in the diagram relate

**shared ancestral character** describes a characteristic on a phylogenetic tree that is shared by all organisms on the tree

**shared derived character** describes a characteristic on a phylogenetic tree that is shared only by a certain clade of organisms

**sister taxa** two lineages that diverged from the same branch point

**systematics** field of organizing and classifying organisms based on evolutionary relationships
taxon (plural: taxa) single level in the taxonomic classification system

taxonomy science of classifying organisms

web of life phylogenetic model that attempts to incorporate the effects of horizontal gene transfer on evolution

CHAPTER SUMMARY

20.1 Organizing Life on Earth

Scientists continually gain new information that helps understand the evolutionary history of life on Earth. Each group of organisms went through its own evolutionary journey, called its phylogeny. Each organism shares relatedness with others, and based on morphologic and genetic evidence, scientists attempt to map the evolutionary pathways of all life on Earth. Historically, organisms were organized into a taxonomic classification system. However, today many scientists build phylogenetic trees to illustrate evolutionary relationships.

20.2 Determining Evolutionary Relationships

To build phylogenetic trees, scientists must collect accurate information that allows them to make evolutionary connections between organisms. Using morphologic and molecular data, scientists work to identify homologous characteristics and genes. Similarities between organisms can stem either from shared evolutionary history (homologies) or from separate evolutionary paths (analogies). Newer technologies can be used to help distinguish homologies from analogies. After homologous information is identified, scientists use cladistics to organize these events as a means to determine an evolutionary timeline. Scientists apply the concept of maximum parsimony, which states that the order of events probably occurred in the most obvious and simple way with the least amount of steps. For evolutionary events, this would be the path with the least number of major divergences that correlate with the evidence.

20.3 Perspectives on the Phylogenetic Tree

The phylogenetic tree, first used by Darwin, is the classic “tree of life” model describing phylogenetic relationships among species, and the most common model used today. New ideas about HGT and genome fusion have caused some to suggest revising the model to resemble webs or rings.

ART CONNECTION QUESTIONS

1. Figure 20.6 At what levels are cats and dogs considered to be part of the same group?

2. Figure 20.10 Which animals in this figure belong to a clade that includes animals with hair? Which evolved first, hair or the amniotic egg?

3. Figure 20.11 What is the largest clade in this diagram?

REVIEW QUESTIONS

4. What is used to determine phylogeny?
   a. mutations
   b. DNA
   c. evolutionary history
   d. organisms on earth

5. What do scientists in the field of systematics accomplish?
   a. discover new fossil sites
   b. organize and classify organisms
   c. name new species
   d. communicate among field biologists

6. Which statement about the taxonomic classification system is correct?
   a. There are more domains than kingdoms.
   b. Kingdoms are the top category of classification.
   c. Classes are divisions of orders.
   d. Subspecies are the most specific category of classification.

7. On a phylogenetic tree, which term refers to lineages that diverged from the same place?
   a. sister taxa
   b. basal taxa
   c. rooted taxa
   d. dichotomous taxa

8. Which statement about analogies is correct?
   a. They occur only as errors.
   b. They are synonymous with homologous traits.
   c. They are derived by similar environmental constraints.
   d. They are a form of mutation.

9. What do scientists use to apply cladistics?
   a. homologous traits
b. homoplasies

c. analogous traits

d. monophyletic groups

10. What is true about organisms that are a part of the same clade?
   a. They all share the same basic characteristics.
   b. They evolved from a shared ancestor.
   c. They usually fall into the same classification taxa.
   d. They have identical phylogenies.

11. Why do scientists apply the concept of maximum parsimony?
   a. to decipher accurate phylogenies
   b. to eliminate analogous traits
   c. to identify mutations in DNA codes
   d. to locate homoplasies

12. The transfer of genes by a mechanism not involving asexual reproduction is called:
   a. meiosis
   b. web of life
   c. horizontal gene transfer

13. Particles that transfer genetic material from one species to another, especially in marine prokaryotes:
   a. horizontal gene transfer
   b. lateral gene transfer
   c. genome fusion device
   d. gene transfer agents

14. What does the trunk of the classic phylogenetic tree represent?
   a. single common ancestor
   b. pool of ancestral organisms
   c. new species
   d. old species

15. Which phylogenetic model proposes that all three domains of life evolved from a pool of primitive prokaryotes?
   a. tree of life
   b. web of life
   c. ring of life
   d. network model

CRITICAL THINKING QUESTIONS

16. How does a phylogenetic tree relate to the passing of time?

17. Some organisms that appear very closely related on a phylogenetic tree may not actually be closely related. Why is this?

18. List the different levels of the taxonomic classification system.

19. Dolphins and fish have similar body shapes. Is this feature more likely a homologous or analogous trait?

20. Why is it so important for scientists to distinguish between homologous and analogous characteristics before building phylogenetic trees?


22. Compare three different ways that eukaryotic cells may have evolved.

23. Describe how aphids acquired the ability to change color.