8.5 Macroevolution

The history of life on Earth has been one of continual evolutionary change. From simple beginnings, life on Earth has become more diverse and more complex over time. The original single-celled ancestors of all living things have given rise to the millions of species that are alive today, as well as to the many millions that have become extinct. In this section you will explore factors that influence these large-scale processes of **macroevolution** in more detail and learn how biologists use evidence to infer the evolutionary relationships between different species and groups.

macroevolution large-scale evolutionary changes including the formation of new species and new taxa

The Tree of Life

The simplified tree of life in **Figure 1** depicts the evolution pathways of some of the major branches of living organisms. The diagram raises an obvious question: how did life begin? Or, alternatively, how did the first cell originate? The study of **abiogenesis**, the formation of life from non-living matter, is being actively researched. There are many fascinating and competing theories. It is known, for instance, that many of the key building blocks of life, such as amino acids, hydrocarbon chains, and other simple organic molecules, can form under natural conditions. Some even occur in space and are compounds within comets. It is also known that some RNA molecules are capable of replicating themselves, independent of any other cell components. RNA molecules are strong candidates for the first self-replicating precursors to living cells. The challenge to scientists who study abiogenesis is to conceive of all the physical and chemical situations that may have existed on Earth billions of years ago.

abiogenesis the origin of life from non-living matter

WEB LINK

To learn more about the current theories and evidence regarding abiogenesis,

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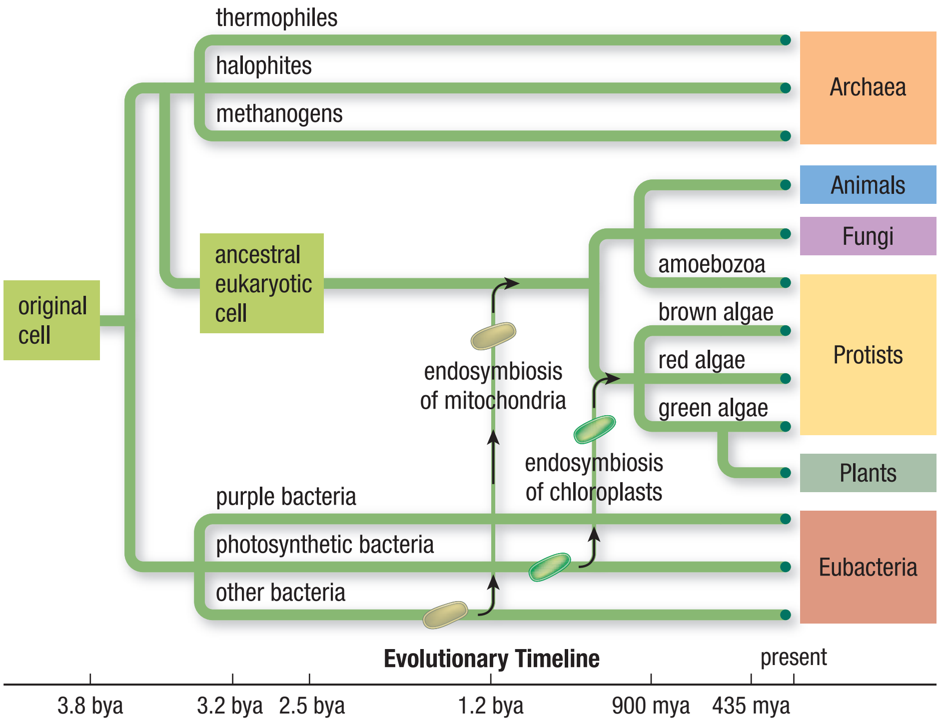

Figure 1 Simple single-celled life has existed on Earth since at least 3.5 billion years ago (bya). Eukaryote evolution occurred much later and involved a number of endosymbiosis events (two are shown here). By 500 million years ago (mya), eukaryote evolution had given rise to the great diversity of complex multicellular organisms.

There are many competing theories about the origin of the very first cells. Scientists, however, are now convinced that life has existed on Earth for more than 3.5 billion years and has been evolving ever since. It took more than 2 billion years for eukaryotic organisms to evolve and another several hundred million years for multicellular life forms to evolve. While single-celled organisms are very small and simple, multicellular organisms evolved into a great diversity of forms.

Diversification and Mass Extinction

At one time dinosaurs dominated Earth's terrestrial ecosystems. These reptiles, some of which were enormous, first evolved some 250 million years ago and began to diversify and flourish about 200 million years ago. For more that 100 million years, dinosaurs were the dominant vertebrate herbivores and carnivores on land. Despite all their success, however, the dinosaurs' reign ended abruptly with a now famous mass extinction event 65 million years ago (**Figure 2**). The only surviving descendants of the dinosaurs are birds.

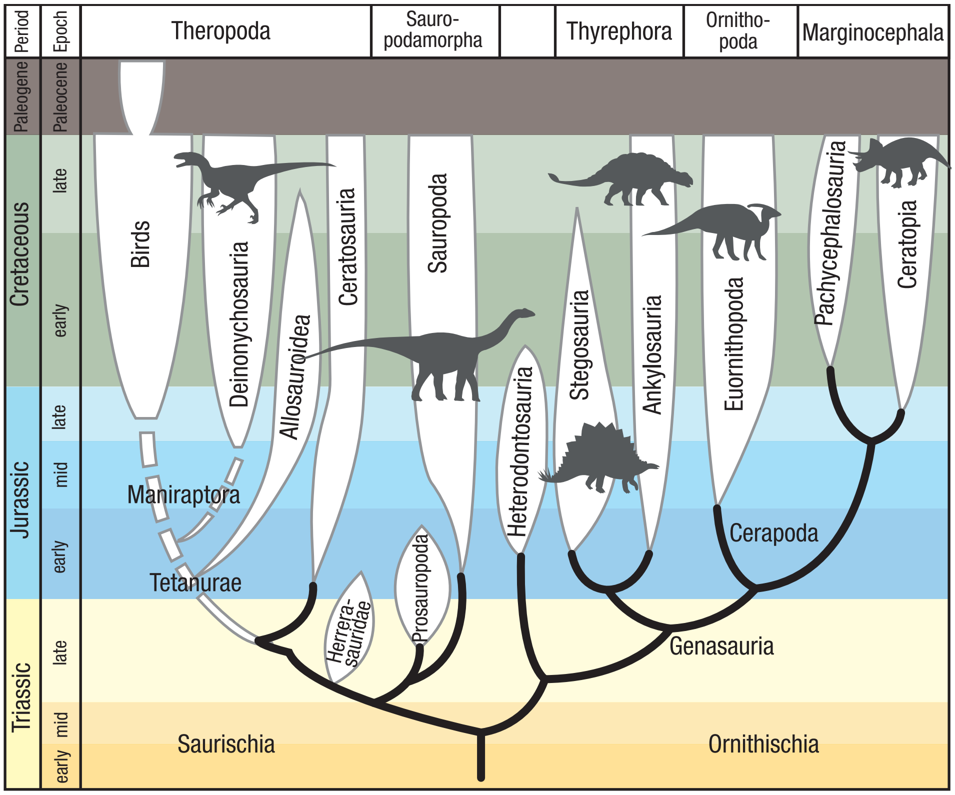

Figure 2 The early dinosaurs branched into two major clades—the Ornithischia and the Saurischia. The Ornithischia include the stegosaurs, triceratops, and duck-billed dinosaurs, while the Saurischia include the massive sauropods, the famous *Tyrannosaurus rex,* and the birds.

While the dinosaurs themselves were a truly remarkable group of animals, their evolutionary history of successful diversification followed by mass extinction is by no means unique. As you learned in Section 8.3, groups of organisms often undergo a period of divergent evolution as they evolve to fill ecological niches. In the case of the dinosaurs, this led to the evolution of more than 300 known species and perhaps many more.

Although individual species may become extinct for a variety of reasons, what could cause the sudden disappearance of so many otherwise successful species? The strongest evidence for the cause of this mass extinction 65 million years ago is the asteroid crater located on the edge of the Yucatan peninsula (**Figure 3**). The crater is almost 10 km deep and 200 km in diameter. Some theorize that the asteroid would have been moving at about 160 000 km/h and would have blasted 200 000 km^3 of vaporized debris and dust into Earth's atmosphere. The energy released by the impact would have produced a wave of super-heated air capable of killing all life on land for thousands of kilometres. Tsunamis 120 m high would have inundated coastlines around the world, and smoke and dust would have blocked most sunlight for months. The resulting cold temperatures would have had devastating consequences for countless species. Recent findings suggest multiple large impacts may have occurred over a period of several thousand years.

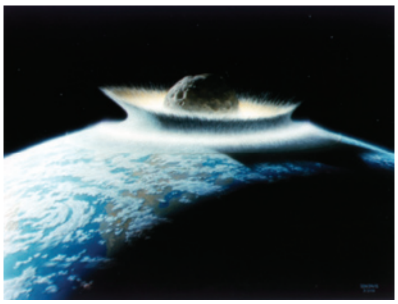

Figure 3 The extinction of most species of dinosaurs 65 million years ago is thought to have been caused by a large meteorite impact.

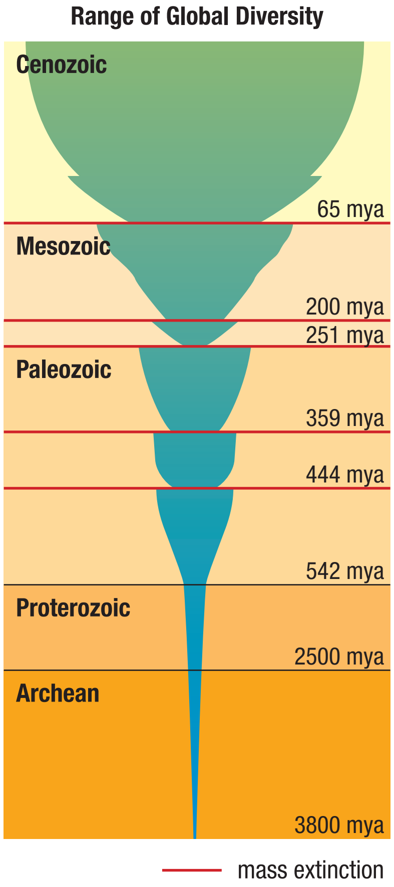

Figure 4 The history of life on Earth is characterized by increasing diversity interrupted by a number of sudden mass extinction events, five of which were particularly dramatic.

Cambrian explosion the rapid evolution of most major animal phyla that took place over approximately 40 million years during the Cambrian period

Earth's history is divided into five eras based on dramatic changes in the fossil record. Notice the trend of ever-increasing diversity interrupted by sudden extinction events (**Figure 4**). The Palaeozoic era, for instance, begins with the Cambrian explosion about 542 mya and ends with the most massive extinction event in Earth's history. The **Cambrian explosion** is so called because it was the time during which most major groups of animals first evolved and underwent rapid diversification. Around 251 million years ago, a series of cataclysmic events eradicated more than 90 % of known marine species. Although uncertainty remains about the cause of the extinction event, many scientists suspect that massive tectonic movements accompanied by volcanoes and rapid climate change played a primary role.

A cataclysmic event is not needed to cause an extinction. Perhaps surprisingly, even the five major mass extinction events since the Cambrian explosion account for only about 4 % of all extinctions that took place during this time.

As you are aware, the current rate of species extinction, due almost entirely to the actions of humans, is very high.

Cladistics and Phylogeny

Cladograms are used to illustrate the evolutionary relationships, or phylogeny, of different groups of species of organisms. The cladogram in **Figure 5**, for example, shows the phylogeny of some major groups of vertebrates. By examining a cladogram, one can infer which groups are more closely related and the general sequence of events that gave rise to each group. In this example, Species A is the most recent common ancestor shared by all groups, while Species B is a common ancestor to all groups except the ray-finned fish. Species C gives rise to the mammals and to a clade that includes all living and extinct reptiles. The cladogram also indicates that birds and crocodiles are closely related, sharing the most recent common ancestor of any two groups (Species E).

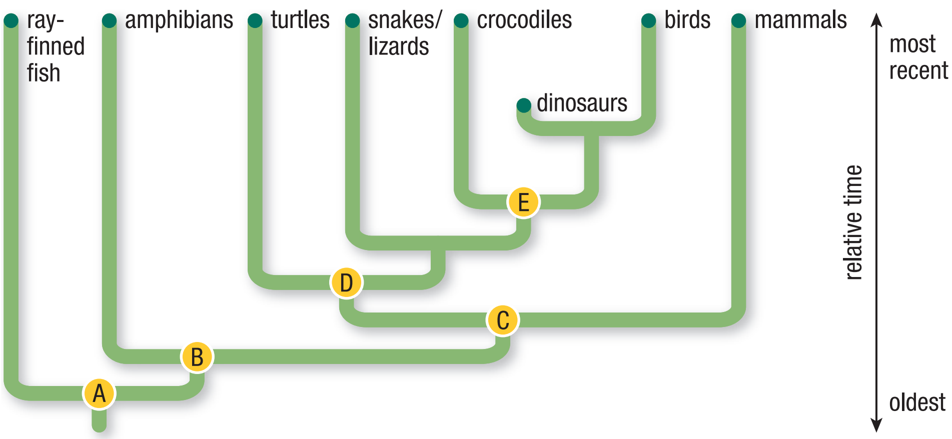

Figure 5 Cladograms show the evolutionary relationships between groups of organisms. Letters at branching points represent the most recent common ancestor of groups that arise beyond that point.

Phylogenies are based on a careful evaluation of a wide range of evidence, including the fossil record, morphology, and genetics. The most widely accepted method of applying this evidence is called cladistics. **Cladistics** uses the presence or absence of recently evolved traits, or **derived traits**, as the key to determining how closely two groups are related. Two groups that share a recently evolved trait, a **synapomorphy**, are thought to be more closely related to each other than to groups that do not share the trait. For example, all birds have feathers and are more closely related to each other than to reptiles without feathers. Only the recently evolved form of a trait is useful for grouping. Consider, for example, the presence or absence of a tail as a feature for grouping vertebrates. Salamanders and howler monkeys have long tails, but apes, such as chimpanzees and gorillas, do not. It would be an error to think that because howler monkeys have tails they are more closely related to salamanders than to apes. Instead, the evolutionary loss of a tail is the more recently derived trait and therefore can be used as evidence that chimpanzees and gorillas are more closely related to each other than to monkeys or salamanders.

cladistics a method of determining evolutionary relationships based on the presence or absence of recently evolved traits

derived trait a trait that has evolved relatively recently with respect to the species or groups being discussed

synapomorphy a derived trait shared by two or more species or groups

The key to cladistic analysis is to make inferences based on synapomorphies. Unfortunately, evolutionary changes can make this challenging. Some suspected synapomorphies may be lost, while others may turn out to be false. All mammals, for example, have evolved from ancestors with hair, but whales have lost their hair. So the presence of hair is an ideal synapomorphy for distinguishing most but not all mammals from other vertebrates. Humans and birds both walk on two legs, but this trait evolved independently, among both our ancestors and those of birds. In this case we must consider these two instances of bipedalism as separate traits.

Biologists are able to apply the science of cladistics to large numbers of related organisms and determine their phylogenetic relationships, based on synapomorphies. They use advanced software programs and large data sets from many sources that include a wealth of genetic information. This science is extremely valuable in understanding the evolution of new strains of disease-causing viruses and micro-organisms. Cladistic analysis of human immunodeficiency viruses (HIV), for example, reveals that closely related but distinct strains have evolved from an original SIV (simian immunodeficiency virus) and have jumped from chimpanzees and monkeys to humans on five separate occasions.

Tutorial 1 Constructing Cladograms

Sample Problem 1: Creating a Cladogram

Use the morphological evidence presented in **Table 1** to construct a cladogram. Based on the cladogram, describe the phylogeny of the organisms.

Table 1 Morphological Data

Animal	Characteristics			
	Digits	**Skin surface**	**Forelimbs**	**Tail**
lemur	five digits	hair	grasping hands	present
deer	two digits	hair	non-grasping	present
cow	two digits	hair	non-grasping	present
chimpanzee	five digits	hair	grasping hands	absent
human	five digits	hair	grasping hands	absent
lizard*	five digits	scales	non-grasping	present

*One group must be included as an “outgroup.” An outgroup is a group that is not closely related to the groups of interest and therefore unlikely to share any recent traits with other groups. In this case a lizard was chosen as a distantly related vertebrate.

Solution:

Step 1. Consider each characteristic and judge which trait is the more recently derived trait. This can usually be done by comparing the traits with the outgroup.

In this case we make the following inferences:

- Two digits on each foot is a derived trait (having five digits is the primitive condition).
- Having hair is a derived trait (having scales like reptiles and fish is a primitive condition).
- Having grasping hands is a derived trait (having four non-grasping “feet” is the primitive condition).
- The lack of a tail is a derived trait (having a tail is the primitive condition).

Step 2. Create a table of synapomorphies (shared derived traits) (**Table 2**).

Table 2 Synapomorphies

Animal	Synapomorphies—shared derived traits			
	Two digits	**Hair**	**Hands**	**No tail**
lemur	−	+	+	−
deer	+	+	−	−
cow	+	+	−	−
chimpanzee	−	+	+	+
human	−	+	+	+
lizard	−	−	−	−

Step 3. Draw a “V,” with the outgroup at the upper left (**Figure 6(a)**). The base of the V represents the common ancestor to all animals.

Step 4. All the animals except the lizard share the feature of having hair. We can indicate the evolution of hair on the right branch leading away from the lizard (**Figure 6(b)**).

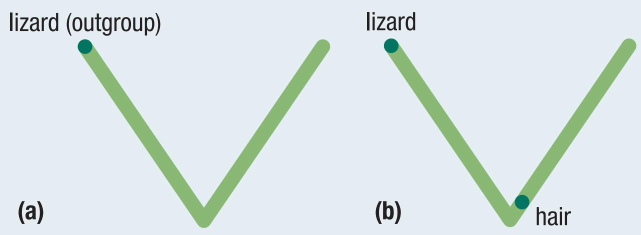

Figure 6

Step 5. The remaining animals fall into two groups—those with two digits and those with grasping hands. We therefore split the right branch into two and locate the evolution of these traits above the split (**Figure 7(a)**). We can divide the deer/cow branch in two and place the name of an animal at the end of each branch.

Notice that when you split a branch, the choice of left or right branch for positioning the groups is arbitrary. We could have chosen to place the deer/cow lineage on the left rather than on the right.

Step 6. The chimpanzee and human both lack a tail, so we create a new branch and locate this derived trait above the split. (**Figure 7(b)**). Label the ends of the remaining branches.

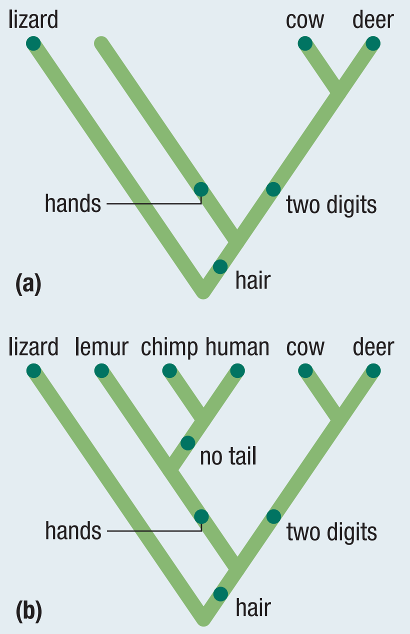

Figure 7

Conclusion:

Based on the completed phylogeny, we can infer that the cow and the deer are more closely related to each other than to other groups. Similarly, humans and chimpanzees are more closely related to each other than to other groups. We can also conclude that lemurs are more closely related to chimps and humans than to cows and deer.

Practice

1. Use the morphological evidence presented in **Table 3** to construct a cladogram. Based on the cladogram, describe the phylogeny of the organisms.

Table 3 Morphological Data

Animal	Characteristics			
	Mouth opening	**Skin surface**	**Respiratory organ**	**Bony limbs**
lungfish	jaw	scales	lungs	absent
turtle	jaw	scales	lungs	present
robin	jaw	feathers	lungs	present
pike	jaw	scales	gills	absent
lamprey*	no jaw	scales	gills	absent

*The lamprey has been chosen as the outgroup.

Investigation 8.5.1

Looking for SINEs of Evolution (page 367)

You can now complete Investigation 8.5.1. In this controlled experiment you will use genetic data to reveal the evolutionary relationships of whales.

Gradualism and Punctuated Equilibrium

Another topic of great interest to evolutionary biologists is the pace of evolution. How quickly do new species and entirely new groups evolve? How long, for example, did it take birds to evolve from their reptile ancestor? And how quickly can existing species adapt to changes in their environment? Answers to these questions have significant implications. Knowing the answers might allow us to judge how species will respond to climate change and other human-influenced impacts on the environment.

Biologists know that at the level of individual species, some evolutionary changes can be quite sudden. For example, a single mutation causing polyploidy can give rise to a new species. Alternatively, other changes, such as the evolution of the giraffe's long neck, have occurred gradually over a period of millions of years. Biologists have proposed two theories to explain the patterns of evolution that take place over very long periods of time.

The **theory of gradualism** states that as new species evolve, they appear very similar to the original species and only gradually become more distinctive (**Figure 8(a)**). Over long periods of time small changes accumulate, resulting in dramatically different organisms. If this theory holds true for all or most species, we would expect to find this pattern in the fossil record, with many fossil species representing changing transitional forms. The fossil evidence of whale and horse evolution, for example, illustrates this pattern of gradual change over millions of years (**Figure 9**).

theory of gradualism a theory that attributes large evolutionary changes in species to the accumulation of many small and ongoing changes and processes

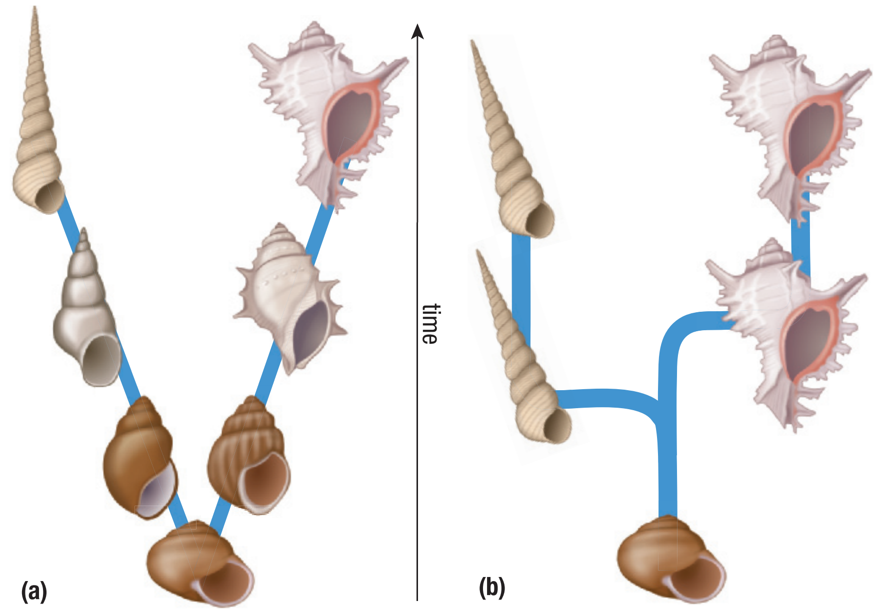

Figure 8 (a) The theory of gradualism suggests that most evolutionary changes are gradual. (b) The theory of punctuated equilibrium proposes that most evolutionary changes are abrupt.

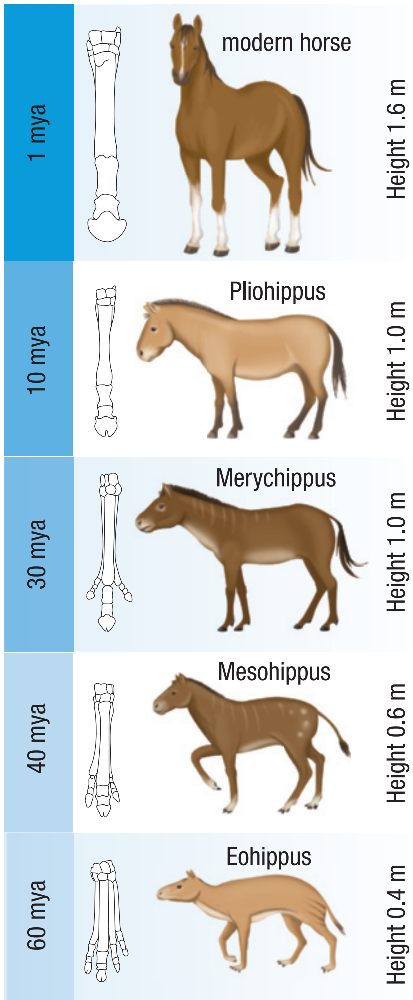

Figure 9 The ancestors of the horse include many intermediate forms between small four-toed mammals and the present-day single-toed horse. The complete fossil record also reveals a highly branched tree with many species.

In many other cases, however, this is not the case. Instead, the fossil record often shows new species appearing quite suddenly and then remaining little changed over long periods of time. A theory to account for this pattern was proposed by Niles Eldredge of the American Museum of Natural History and Stephen Jay Gould of Harvard University. Their alternative **theory of punctuated equilibrium** suggests that the process of evolution is slow, but is occasionally punctuated by periods of rapid change (**Figure 8(b)**). The theory of punctuated equilibrium consists of three main assertions:

- New species evolve rapidly in evolutionary time.
- Speciation usually occurs in small isolated populations and therefore leaves behind few transitional fossils.
- After the initial burst of evolution, additional changes are very slow.

theory of punctuated equilibrium a theory that attributes most evolutionary changes to relatively rapid spurts of change followed by long periods of little or no change

It is now widely accepted that both gradualism and punctuated equilibrium play a significant role in evolution. In situations where the environment changes slowly, evolutionary changes would likely be gradual. In contrast, when a species is exposed to new or rapidly changing environmental conditions, we can expect rapid evolution. After a mass extinction event, for example, species that do survive enter an environment with far fewer competitors.

Gaps and Missing Links?

Our scientific understanding of the world around us is incomplete. There are many significant gaps in our knowledge of biology, chemistry, and physics. If this were not the case, there would be no need for future scientific research. If we knew everything about chemistry, research chemists would be out of work. If we knew everything about disease, medical research would be unnecessary. But this is not the case. In fact, scientific research is more active than it has ever been in human history. As our scientific knowledge has grown, so has the number of research scientists looking for answers to new questions.

LEARNING TIP

Theories and Gaps

Missing information or a lack of understanding does not undermine knowledge and theories that are supported by other evidence. Historians, for example, will never know all of the events that took place leading up to and during the War of 1812, but they do know that the war took place and have great confidence in their knowledge of many of the details. The same is true in science.

transitional form a fossil or species intermediate in form between two other species in a direct line of descent

Figure 10 The fossil of *Archaeopteryx* shows features that are clearly transitional between those of a reptile and a bird.

A commonly held misconception is that a gap in our scientific understanding reflects scientific uncertainty over the underlying theory. The misconception is often expressed in this form: "if scientists cannot explain how X happened, or have still not discovered Y, then their theory must be weak or flawed." Such gaps, however, should not cause uncertainty in a scientific theory. Chemists had great confidence in the validity of the periodic table of the elements long before it was complete. Our understanding of atomic theory, evolution, and quantum theories are incomplete but are not in any scientific doubt. These theories account for much of what we do know, and they are in agreement with an extraordinary wealth of evidence.

In evolutionary biology, a key source of evidence is the fossil record. The fossil record, however, is not complete—there are many gaps. Species with delicate bodies do not fossilize readily, and many species do not live in environments where the conditions for fossilization occur. In Darwin's day, evolutionary biologists had a very limited fossil record. There were few fossils of **transitional forms**—organisms intermediate in form between their modern forms and their ancient relatives. These gaps in the fossil record were referred to as "missing links." For example, there were no fossils of early land animals to offer direct evidence of life invading the land. There were no fossils of early birds showing the beginnings of feathers and flight. Darwin knew that a lack of evidence was not evidence against his theory and that an understanding of evolution would enable biologists to make predictions about these transitional forms.

Today there is a wealth of fossil evidence, and many of the initial missing links between major groups of organisms have been filled. The first and most famous fossil of a transitional species was that of *Archaeopteryx* (**Figure 10**). This species had features of both birds and more primitive reptiles. It had a bony jaw with teeth and a long bony tail, but also feathered wings. Many more ancestral bird fossils are now being unearthed in China. With these fossils, we are learning about the evolution of flight.

Another gap has been filled with a series of fossils of early whales found in Pakistan (**Figure 11**). The discovery of the fossilized skull of *Aetiocetus* filled a missing link between the early ancestors of whales with nostrils on the end of their snout, and modern whales with nostrils on the top of their head. The nostrils of *Aetiocetus* are "halfway" between and provide an excellent example of a transitional fossil.

Figure 11 *Aetiocetus* is the transitional form between modern whales and their ancesters.

8.5 Summary

- The history of life on Earth follows a general trend toward increasing diversity marked by rare mass extinction events.
- Cladistics uses the occurrence of shared derived traits to infer evolutionary relationships.
- The theory of gradualism proposes that most evolutionary changes occur over long periods of time.
- The theory of punctuated equilibrium proposes that major evolutionary changes happen relatively rapidly and are then followed by long periods of little change.
- All scientific understandings are incomplete. Scientific investigations continue to fill these gaps.

8.5 Questions

1. Many scientists believe that at one time conditions on Mars may have been suitable for the evolution of life. Use the Internet and other sources to learn about any evidence that supports the possibility of past or present life on Mars or other planets. K/U T/I A
   (a) Define abiogenesis.
   (b) Why is abiogenesis considered to be distinct from evolution?
   (c) Suggest ways in which the same principles of natural selection might have influenced the formation of chemicals and the very first cell-like structures.
   (d) What evidence suggests that life might have been possible on Mars in the distant past?
2. In what way was endosymbiosis critical for the evolution of animals, plants, and fungi? K/U
3. You hear a scientist describe the history of life on Earth as one of both increasing diversity and mass extinction. Explain this statement using a diagram to illustrate the relationship between these opposing processes. T/I A
4. Some scientists suggest that without the mass extinction of the dinosaurs, mammals would not have been able to undergo adaptive radiation. Use your understanding of competition for resources to support or refute this suggestion. T/I A
5. Birds are the only group of dinosaurs that survived the mass extinction of 65 million years ago. Speculate on how their ability to fly and endothermy (being warm-blooded) may have been keys to their survival. T/I A
6. Both salamanders and dogs have long tails, while bears do not. However, both bears and dogs have hair, while salamanders do not. Explain why having a long tail *is not* evidence that dogs are more closely related to salamanders than they are to bears. Explain why having hair *is* good evidence that dogs and bears are more closely related than dogs and salamanders. K/U T/I A
7. Many scientists consider the term "missing link" to be misleading. They suggest that it gives a false impression that evidence should have been found. Instead, they counter that newly discovered evidence simply adds to our understanding—and that it was never "missing." Do you think the term "missing link" is misleading? Why or why not? A C
8. Use the cladogram in **Figure 12** to answer the following questions. Assume that each number represents the evolution of a new feature and that each letter represents a species alive today. K/U T/I C

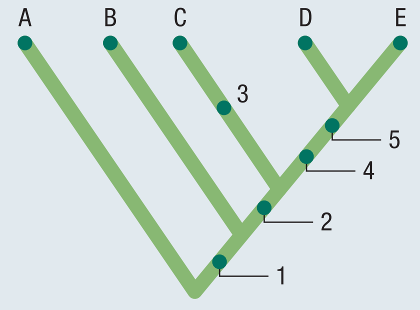

Figure 12

   (a) Construct a table of derived traits, using the relationships shown in Figure 10.
   (b) Which two species are most closely related?
   (c) List the synapomorphies shared by Species C and E.
   (d) To which species is Species C most closely related?
   (e) Is Species B more closely related to Species A or E? Explain your reasoning.
   (f) Do any numbers represent new features that were not needed to draw this cladogram? Which?
9. Examine the fossil hind limbs in **Figure 13**. Scientists believe this animal was a transitional species between land mammals and modern whales. Do you think this animal spent all, some, or none of its time on land? Explain your answer. T/I

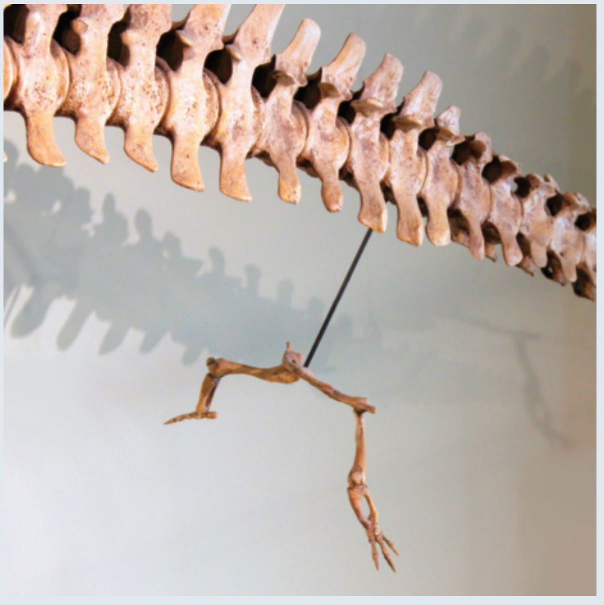

Figure 13

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