squirrels). A changing world presented new environmental habitats and new food sources also. Insects fed on flowering plants and, in turn, became food for mammals. Primates lived in trees where fruits were available.

Sympatric Speciation

Speciation without the presence of a geographic barrier is termed **sympatric speciation** [Gk. *sym*, together, and *patri*, fatherland]. Sympatric speciation has been difficult to substantiate in animals. For example, two populations of the Meadow Brown butterfly, *Maniola jurtina*, have different distributions of wing spots. The two populations are both in Cornwall, England, and they maintain the difference in wing spots, even though there is no geographic boundary between them. But, as yet, no reproductive isolating mechanism has been found.

In contrast, sympatric speciation involving **polyploidy** (a chromosome number beyond the diploid [2n] number) is well documented in plants. A polyploid plant can reproduce with itself, but cannot reproduce with the 2n population because not all the chromosomes would be able to pair during meiosis. Two types of polyploidy are known: autoploidy and alloploidy.

Autoploidy occurs when a diploid plant produces diploid gametes due to nondisjunction during meiosis (see Fig. 10.10). If this diploid gamete fuses with a haploid gamete, a triploid plant results. A triploid (3n) plant is sterile and cannot produce offspring because the chromosomes cannot pair during meiosis. Humans have found a use for sterile plants because they produce fruits without seeds. Figure 17.11 contrasts a diploid banana with seeds to today's polyploid banana that produces no seeds. If two diploid gametes fuse, the plant is a tetraploid (4n) and the plant is fertile, so long as it reproduces with another of its own kind. The fruits of polyploid plants are much larger than those of diploid plants. The huge strawberries of today are produced by octaploid (8n) plants.

Alloploidy [Gk. *allo*, other, and *ploidy*, uncountable] requires a more complicated process than autoploidy because it requires that two different but related species of plants hybridize (Fig. 17.12). Hybridization is followed by doubling of the chromosomes. For example, the Western wildflower, *Clarkia concinna*, is a diploid plant with fourteen chromosomes (seven pairs). The related species, *C. virgata*, is a diploid plant with ten chromosomes (five pairs). A hybrid of these two species is not fertile because seven chromosomes from one plant cannot pair evenly with five chromosomes from the other plant. However, meiosis occurs normally in the hybrid, *C. pulchella*, due to doubling of the chromosome number, which allows the chromosomes to pair during meiosis.

Alloploidy also occurred during the evolution of the wheat plant, which is commonly used today to produce bread. The parents of our present-day bread wheat had 28 and 14 chromosomes, respectively. The hybrid with 21 chromosomes is sterile, but bread wheat with 42 chromosomes is fertile because the chromosomes can pair during meiosis. Recent molecular data tell us that polyploidy is common in plants and makes a significant contribution to the evolution of new plants.

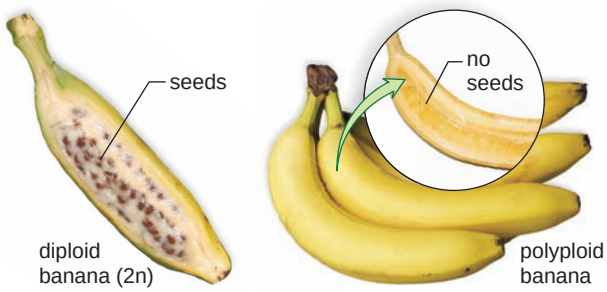

FIGURE 17.11 Autoploidy produces a new species.

The small, diploid-seeded banana is contrasted with the large, polyploid banana that produces no seeds.

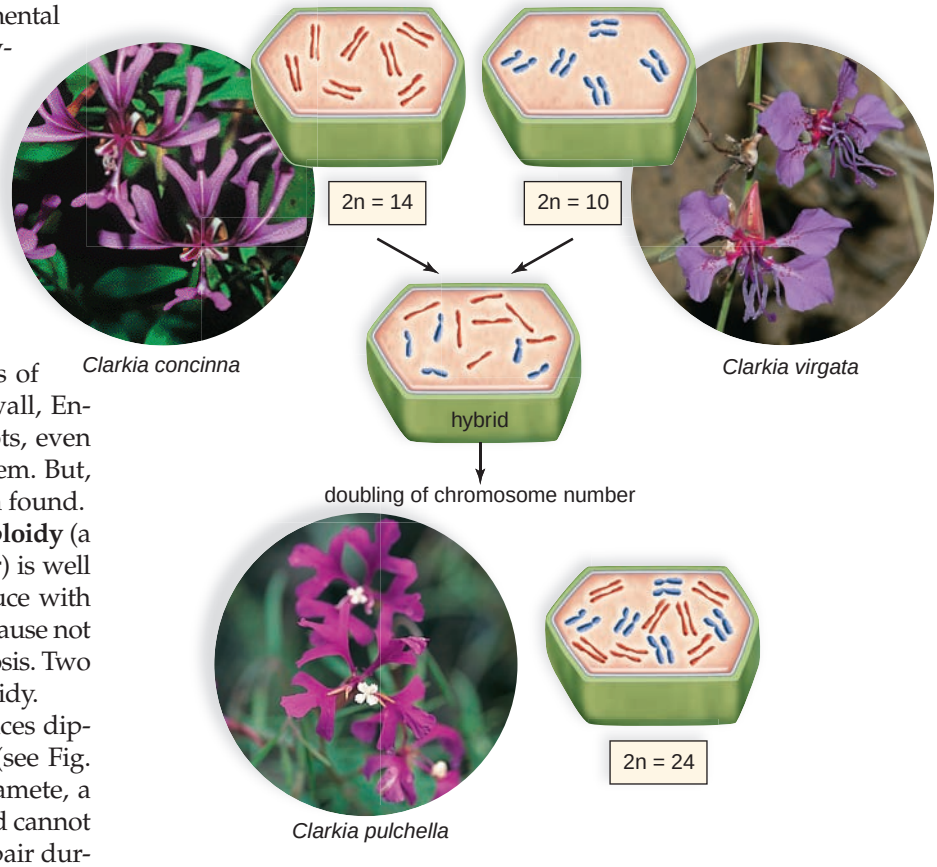

FIGURE 17.12 Alloploidy produces a new species.

Reproduction between two species of *Clarkia* is a sterile hybrid. Doubling of the chromosome number results in a fertile third *Clarkia* species that can reproduce with itself only.

Check Your Progress 17.2

1. Five species of big cats are classified in a single genus: *Panthera leo* (lion), *P. tigris* (tiger), *P. pardus* (leopard), *P. onca* (jaguar), and *P. uncia* (snow leopard). What evidence would you need to show that this is a case of adaptive radiation?
2. What fossil evidence might support the hypothesis that the different species of cats arose sympatrically?

science focus

The Burgess Shale Hosts a Diversity of Life

Finding the Burgess Shale, a rock outcropping in Yoho National Park, British Columbia, was a chance happening. In 1909, Charles Doolittle Walcott of the Smithsonian Institution was out riding when his horse stopped in front of a rock made of shale. He cracked the rock open and saw the now-famous fossils of the animals depicted in Figure 17A. Walcott and his team began working the site and continued on their own for quite a few years. Around 1960, other paleontologists became interested in studying the Burgess Shale fossils.

As a result of uplifting and erosion, the intriguing fossils of the Burgess Shale are relatively common in that particular area. However, the highly delicate impressions and films found in the rocks are very difficult to remove from their matrix. Early attempts to remove the fossils involved splitting the rocks along their sedimentary plane and using rock saws. Unfortunately, these methods were literally "shots in the dark," and many valuable fossils were destroyed in the process. New methods, involving ultraviolet light to see the fossils and diluted acetic acid solutions to remove the matrix, have been more successful in freeing the fossils.

The fossils tell a remarkable story of marine life some 540 MYA (million years ago), during the Precambrian era. In addition to fossils of organisms that had external skeletons, many of the fossils are remains of soft-bodied invertebrates; these are a great find because soft-bodied animals rarely fossilize. During this time, all organisms lived in the sea, and it is believed the barren land was subject to mudslides, which entered the ocean and buried the animals, killing them. Later, the mud turned into shale, and later still, an upheaval raised the shale. Be-

FIGURE 17A Burgess Shale.

Burgess Shale quarry (*above*), where many ancient fossils (shown in Fig. 17B) have been found.

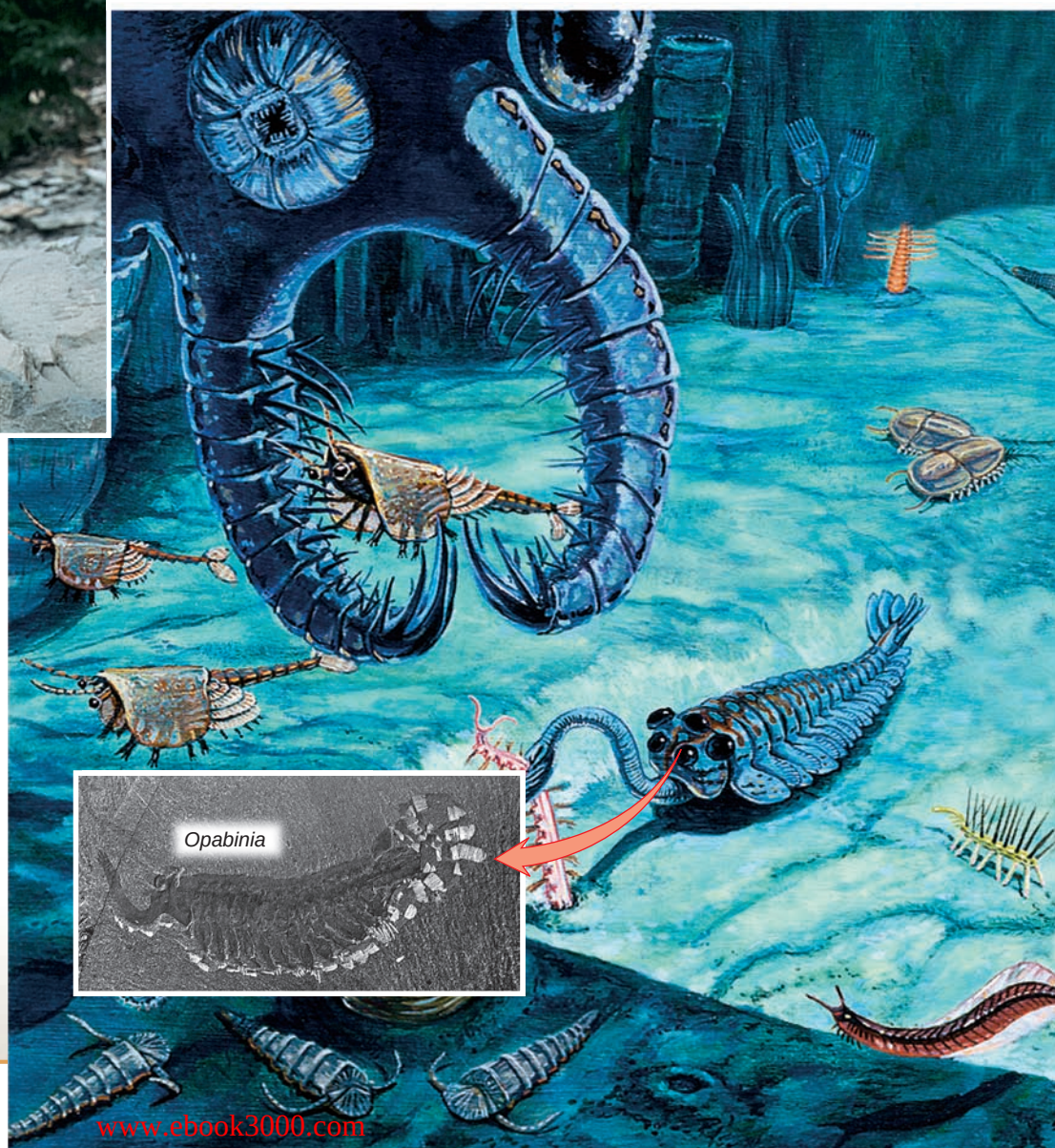

FIGURE 17B Fossils found at the Burgess Shale.

Variety of fossils alongside drawings of the animals based on their fossilized remains.

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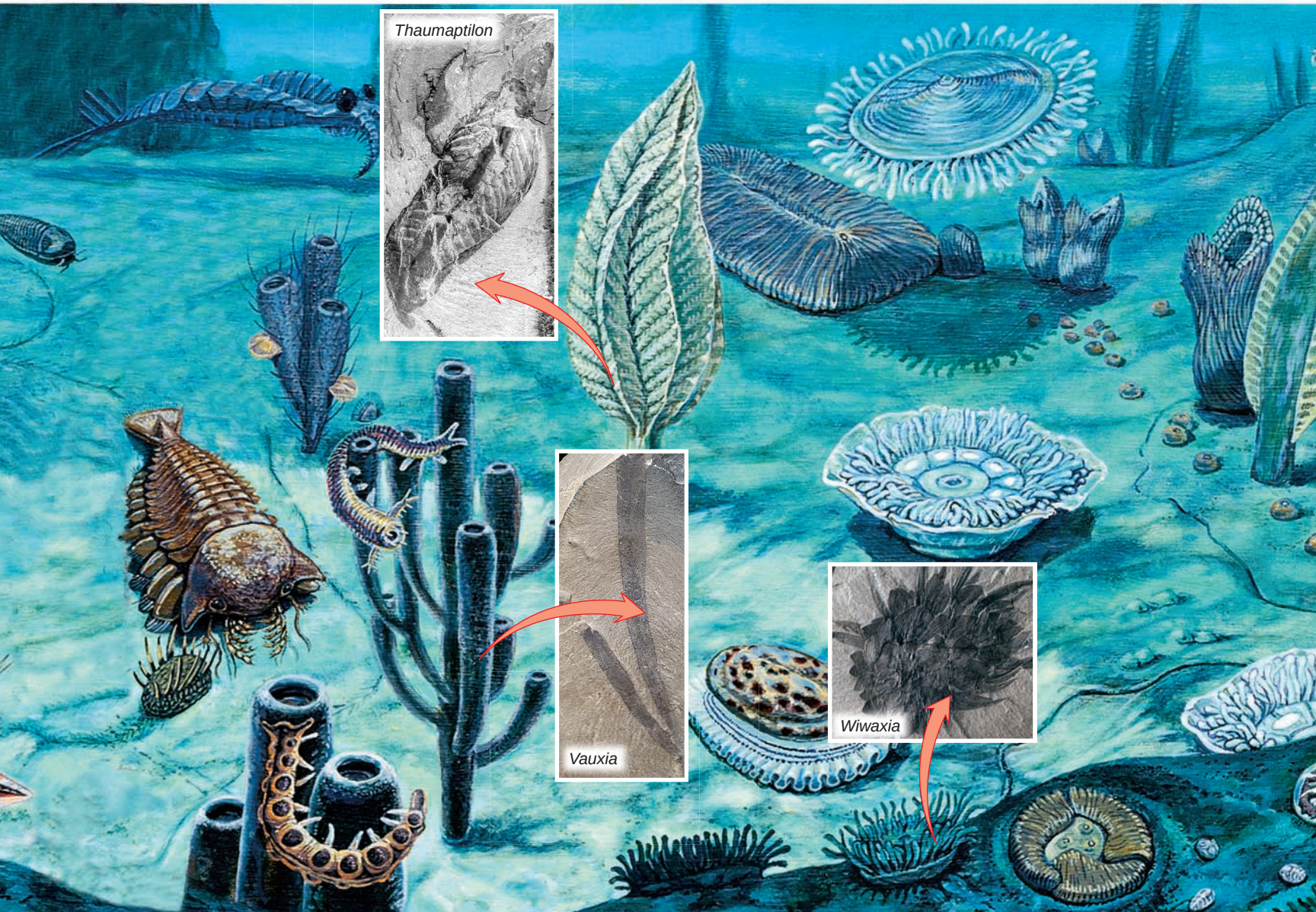
fore the shale formed, fine mud particles filled the spaces in and around the organisms so that the soft tissues were preserved and the fossils became somewhat three-dimensional.

The fossils tell us that the ancient seas were teaming with weird-looking, mostly invertebrate animals (Fig. 17B). All of today's groups of animals can trace their ancestry to one of these strange-looking forms, which include sponges, arthropods, worms, and trilobites, as well as spiked creatures and oversized predators. The vertebrates, like ourselves, are descended from *Pikaia,* the only one of the fossils that has a supporting rod called a notochord. (In vertebrates, the notochord is replaced by the vertebral column during development.)

Unicellular organisms have also been preserved at the Burgess Shale site. They appear to be bacteria, cyanobacteria, dinoflagellates, and other protists. Fragments of algae are preserved in thin, shiny carbon films. A technique has been perfected that allows the films to be peeled off the rocks.

Anyone can travel to Yoho National Park, look at the fossils, and get an idea of the types of animals that dominated the world's oceans for nearly 300 million years. Some of the animals had external skeletons, but many were soft-bodied. Interpretations of the fossils vary. Some authorities hypothesize that the great variety of animals in the Burgess Shale evolved within 20–50 million years, and therefore the site supports the hypothesis of punctuated equilibrium. Others believe that the animals started evolving much earlier and that we are looking at the end result of an adaptive radiation requiring many more millions of years to accomplish. Some investigators present evidence that all the animals are related to today's animals and should be classified as such. Others believe that several of them are unique creatures unrelated to the animals of today. Regardless of the controversies, the fossils tell us that speciation, diversification, and eventual extinction are part of the history of life.



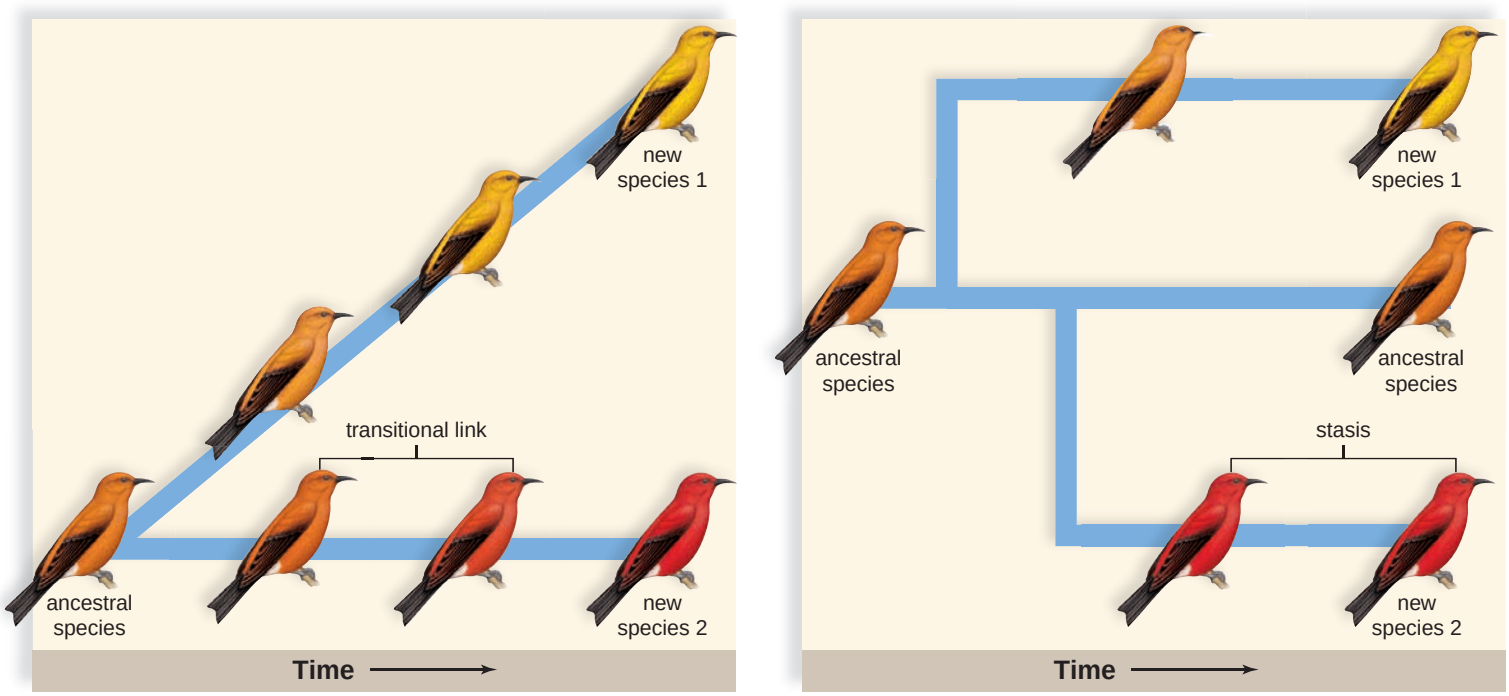
17.3 Principles of Macroevolution

Many evolutionists hypothesize, as Darwin did, that **macroevolution,** which is evolution at the species or higher level of classification, occurs gradually. After all, natural selection can only do so much to bring about change in each generation. Therefore, these evolutionists support a *gradualistic model*, which proposes that speciation occurs after populations become isolated, with each group continuing slowly on its own evolutionary pathway. These evolutionists often show the history of groups of organisms by drawing the type of diagram shown in Figure 17.13*a*. Note that in this diagram, an ancestral species has given rise to two separate species, represented by a slow change in plumage color. The gradualistic model suggests that it is difficult to indicate when speciation occurred because there would be so many transitional links (see Fig. 15.12).

After studying the fossil record, some paleontologists tell us that species can appear quite suddenly, and then they remain essentially unchanged phenotypically during a period of stasis (sameness) until they undergo extinction. Based on these findings, they developed a *punctuated equilibrium model* to explain the pace of evolution. This model says that periods of equilibrium (no change) are punctuated (interrupted) by speciation. Figure 17.13*b* shows this way of representing the history of evolution over time. This model suggests that transitional links are less likely to become fossils and less likely to be found. Moreover, speciation is more likely to involve only an isolated population at one locale, because a favorable genotype could spread more rapidly within such a population. Only when this population expands and replaces other species is it apt to show up in the fossil record.

A strong argument can be made that it is not necessary to choose between these two models of evolution and that both could very well assist us in interpreting the fossil record. In other words, some fossil species may fit one model, and some may fit the other model. In a stable environment, a species may be kept in equilibrium by stabilizing selection for a long period. On the other hand, if the environment changes slowly, a species may be able to adapt gradually. If environmental change is rapid, a new species may arise suddenly before the parent species goes on to extinction. The differences between all possible patterns of evolutionary change are rather subtle, especially when we consider that, because geologic time is measured in millions of years, the "sudden" appearance of a new species in the fossil record could actually represent many thousands of years. Using only a small rate of change (.0008/year), two investigators calculated that the brain size in the human lineage could have increased from 900 cm^3 to 1,400 cm^3 in only 135,000 years. This would appear to be a very rapid change in the fossil record, and it actually took much longer (about 500,000 years), indicating that the real pace was slower than it might have been.

The difficulty of deciding the tempo of evolution from examining the fossil record is exemplified by a review of the forms of life fossilized in the Burgess Shale (see the Science Focus on pages 308–9). It is difficult to tell how rapidly these animals evolved.



a. Gradualistic model

b. Punctuated equilibrium

FIGURE 17.13 Gradualistic and punctuated equilibrium models.

a. Speciation occurs gradually and many transitional links occur. Therefore, apparent stasis (sameness) is not real. **b.** Speciation occurs rapidly, transitional links do not occur, and stasis is real.

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Developmental Genes and Macroevolution

Investigators have discovered genes that can bring about radical changes in body shapes and organs. For example, it is now known that the *Pax6* gene is involved in eye formation in all animals, and that homeotic (*Hox*) genes determine the location of repeated structures in all vertebrates

Gene Expression Can Influence Development

Whether slow or fast, how could evolution have produced the myriad of animals in the Burgess Shale and, indeed, in the history of life? Or, to ask the question in a genetic context, how can genetic changes bring about such major differences in form? It has been suggested since the time of Darwin that the answer must involve development processes. In 1917, D'Arcy Thompson asked us to imagine an ancestor in which all parts are developing at a particular rate. A change in gene expression could stop a developmental process or continue it beyond its normal time. For instance, if the growth of limb bones were stopped early, the result would be shorter limbs, and if it were extended, the result would be longer limbs compared to those of an ancestor. Or, if the whole period of growth were extended, a larger animal would result, accounting for why some species of horses are so large today.

Using new kinds of microscopes and the modern techniques of cloning and manipulating genes, investigators have indeed discovered genes whose differential expression can bring about changes in body shapes and organs. This result suggests that these genes must date back to a common ancestor that lived more than 600 MYA (before the Burgess Shale animals), and that despite millions of years of divergent evolution, all animals share the same control switches for development.

Development of the Eye

The animal kingdom contains many different types of eyes, and it was long thought that each type would require its own set of genes. Flies, crabs, and other arthropods have compound eyes that have hundreds of individual visual units. Humans and all other vertebrates have a camera-type eye with a single lens. So do squids and octopuses. Humans are not closely related to either flies or squids, so wouldn't it seem as if all three types of animals evolved "eye" genes separately? Not so. In 1994, Walter Gehring and his colleagues at the University of Basel, Switzerland, discovered that a gene called *Pax6* is required for eye formation in all animals tested (Fig. 17.14). Mutations in the *Pax6* gene lead to failure of eye development in both people and mice, and remarkably, the mouse *Pax6* gene can cause an eye to develop on the leg of a fruit fly (Fig. 17.15).

Development of Limbs

Wings and arms are very different, but both humans and birds express the *Tbx5* gene in developing limb buds. *Tbx5* codes for a transcription factor that turns on the genes needed to make a limb. What seems to have changed as birds and humans evolved are the genes that *Tbx5* turns on. Perhaps in an ancestral tetrapod, the *Tbx5* protein triggered the transcription of only one gene. In humans and birds, a few genes are expressed in response to *Tbx5* protein, but the particular genes are different. There is also the question of timing. Changing the timing of gene expression, as well as which genes are expressed, can result in dramatic changes in shape.

Development of Overall Shape

Vertebrates have repeating segments, as exemplified by the vertebral column. Changes in the number of segments can lead to changes in overall shape. In general, *Hox* genes control the number and appearance of repeated structures along the main body axes of vertebrates. Shifts in when *Hox* genes are expressed in embryos are responsible for why a snake has hundreds of rib-bearing vertebrae and essentially no neck in contrast to other vertebrates, such as a

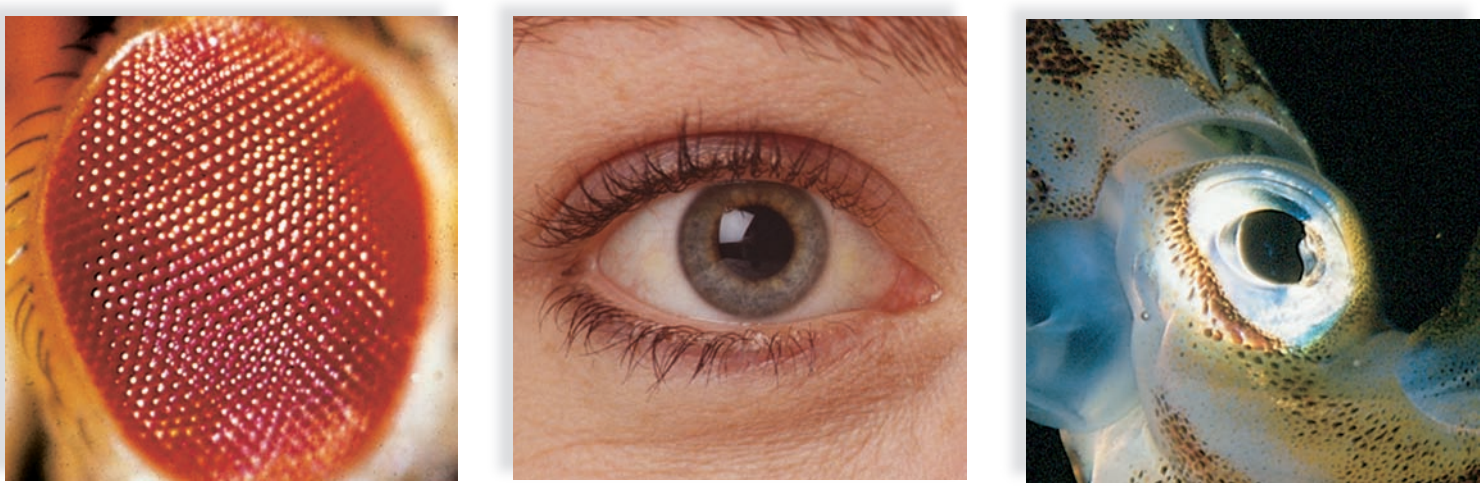

FIGURE 17.14 ***Pax6* gene and eye development.**

Pax6 is involved in eye development in a fly, a human, and a squid.

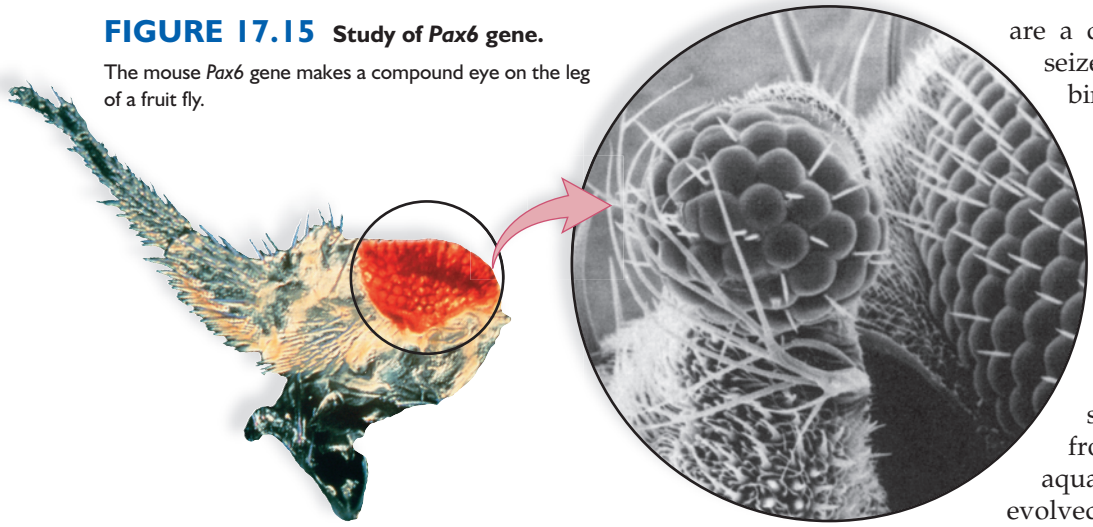

FIGURE 17.15 Study of *Pax6* gene.

The mouse *Pax6* gene makes a compound eye on the leg of a fruit fly.

chick (Fig. 17.16). *Hox* genes have been found in all animals, and other shifts in the expression of these genes can explain why insects have just six legs and other arthropods, such as crayfish, have ten legs. In general, the study of *Hox* genes has shown how animal diversity is due to variations in the expression of ancient genes rather than to wholly new and different genes.

Pelvic-Fin Genes

The three-spined stickleback fish occurs in two forms in North American lakes. In the open waters of a lake, long pelvic spines help protect the stickleback from being eaten by large predators. But on the lake bottom, long pelvic spines are a disadvantage because dragonfly larvae seize and feed on young sticklebacks by grabbing them by their spines.

The presence of short spines in bottom-dwelling fish can be traced to a reduction in the development of the pelvic-fin bud in the embryo, and this reduction is due to the altered expression of a particular gene. Hindlimb reduction has occurred during the evolution of other vertebrates. The hindlimbs became greatly reduced in size as whales and manatees evolved from land-dwelling ancestors into fully aquatic forms. Similarly, legless lizards have evolved many times. The stickleback study has shown how natural selection can lead to major skeletal changes in a relatively short time.

Human Evolution

The sequencing of genomes has shown us that our DNA base sequence is very similar to that of chimpanzees, mice, and, indeed, all vertebrates. Based on this knowledge and the work just described, investigators no longer expect to find new genes to account for the evolution of humans. Instead, they predict that differential gene expression and/or new functions for "old" genes will explain how humans evolved.

Mutations of developmental genes occur by chance, and in the next section, we observe that evolution is not directed toward any particular end.

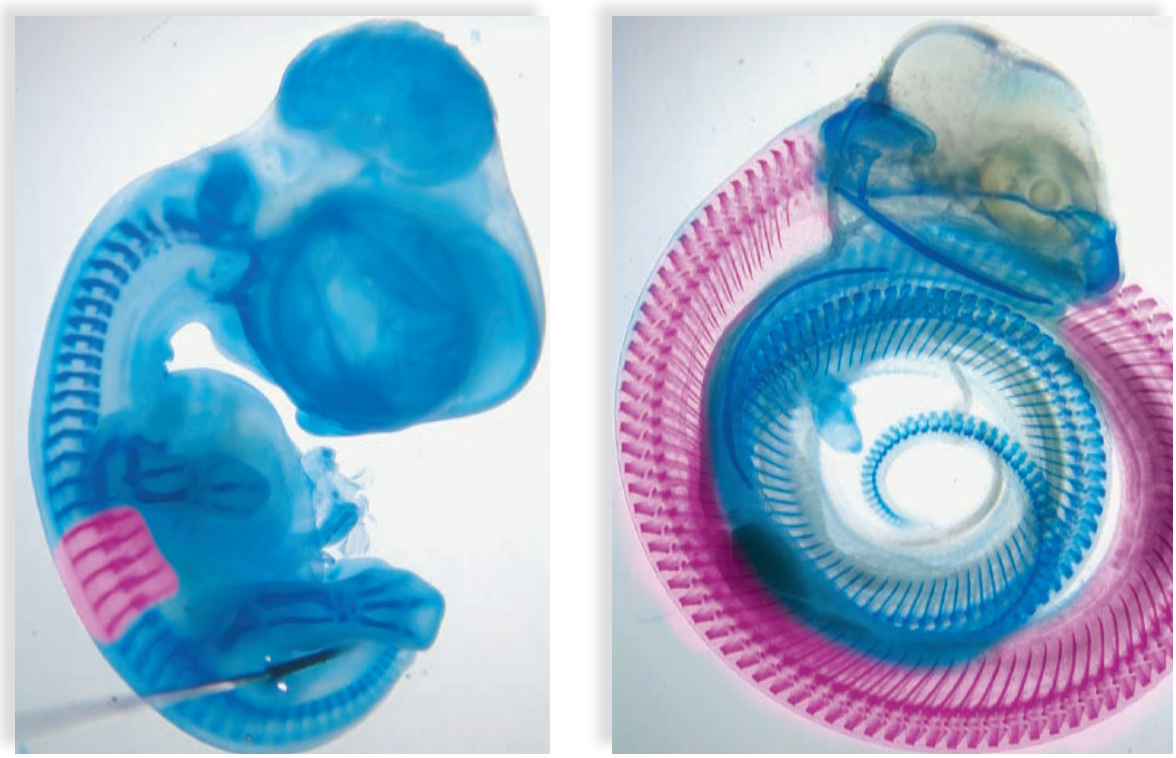

FIGURE 17.16
***Hox6* genes.**

Differential expression of *Hox6* genes causes a chick to have seven vertebrae (*purple*) and a snake to have many more vertebrae (*purple*).

Burke, A. C. 2000, *Hox* genes and the global patterning of the somitic mesoderm. In Somitogenesis. C. Ordahl (ed.), *Current Topics in Developmental Biology*, Vol. 47. Academic Press.

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Macroevolution Is Not Goal-Oriented

The evolution of the horse, *Equus*, has been studied since the 1870s, and at first the ancestry of this genus seemed to represent a model for gradual, straight-line evolution until its goal, the modern horse, had been achieved. Three trends were particularly evident during the evolution of the horse: increase in overall size, toe reduction, and change in tooth size and shape.

By now, however, many more fossils have been found, making it easier to tell that the lineage of a horse is complicated by the presence of many ancestors with varied traits. Which fossils represent the direct ancestors to *Equus* is not known. After all, humans, not nature, drew the oversimplified tree in Figure 17.17. The tree is an oversimplification because each of the names is a genus that contains several species, and not all past genera in the horse family are included. It is apparent, then, that the ancestors of *Equus* form a thick bush of many equine species and that straight-line evolution did not occur. Because *Equus* alone remains and the other genera have become extinct, it might seem as if evolution was directed toward producing *Equus*, but this is not the case. Instead, each of these ancestral species was adapted to its environment. Adaptation occurs only because the members of a population with an advantage are able to have more offspring than other members. Natural selection is opportunistic, not goal-directed.

Fossils named *Hyracotherium* have been designated as the first probable members of the horse family, living about 57 MYA. These animals had a wooded habitat, ate leaves and fruit, and were about the size of a dog. Their short legs and broad feet with several toes would have allowed them to scamper from thicket to thicket to avoid predators. *Hyracotherium* was obviously well adapted to its environment because this genus survived for 20 million years.

The family tree of *Equus* does tell us once more that speciation, diversification, and extinction are common occurrences in the fossil record. The first adaptive radiation of horses occurred about 35 MYA. The weather was becoming drier, and grasses were evolving. Eating grass requires tougher teeth, and an increase in size and longer legs would have permitted greater speed to escape enemies. The second adaptive radiation of horses occurred about 15 MYA and included *Merychippus* as a representative of those groups that were speedy grazers who lived on the open plain. By 10 MYA, the horse family was quite diversified. Some species were large forest browsers, some were small forest browsers, and others

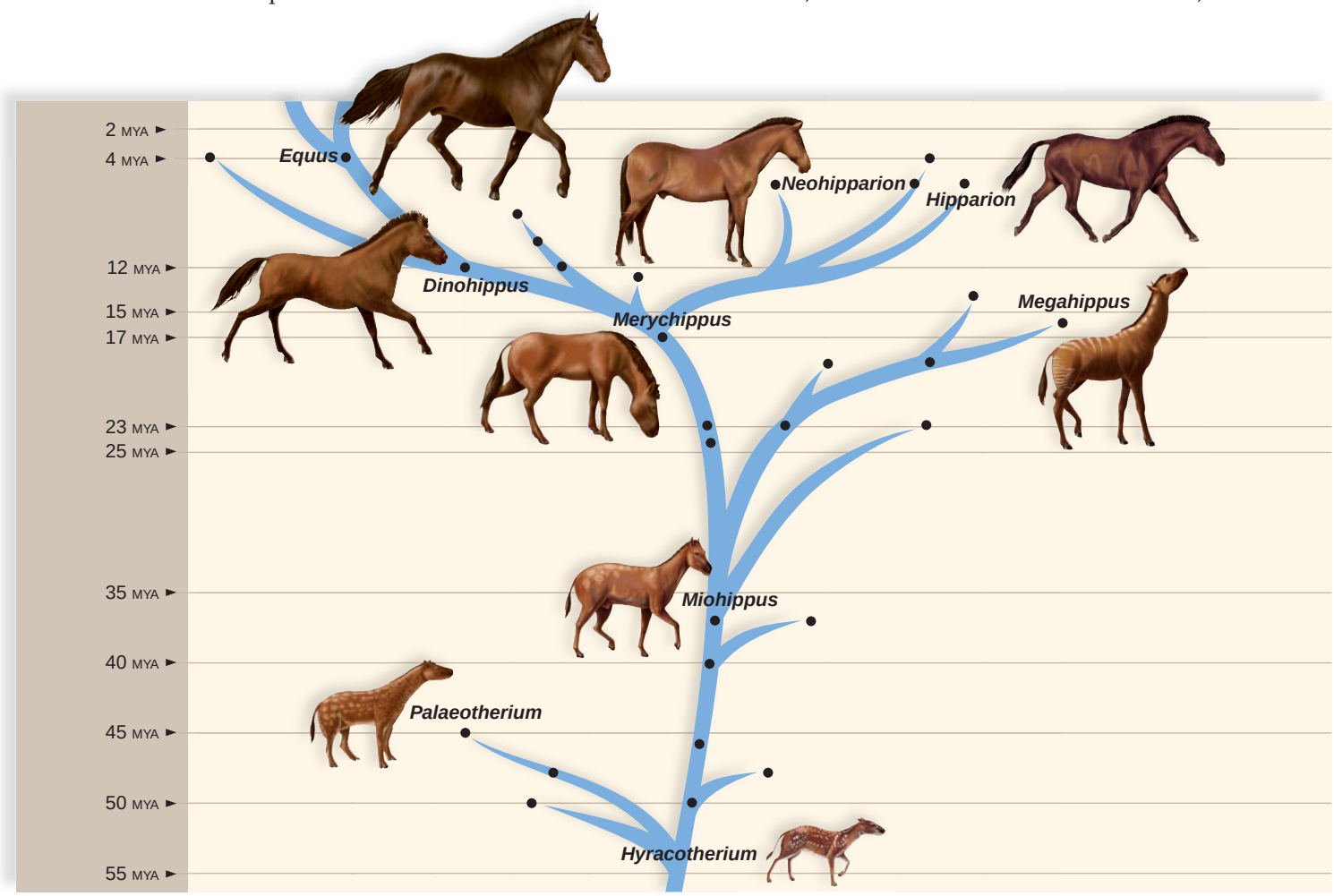

FIGURE 17.17 **Simplified family tree of *Equus*.**

Every dot represents a genus.

were large plains grazers. Many species had three toes, but some had one strong toe. (The hoof of the modern horse includes only one toe.)

Modern horses evolved about 4 MYA from ancestors who had features that are adaptive for living on an open plain, such as large size, long legs, hoofed feet, and strong teeth. The other groups of horses prevalent at the time became extinct no doubt for complex reasons. Humans have corralled modern horses for various purposes, and this makes it difficult to realize that the traits of a modern horse are adaptive for living in a grassland environment.

Check Your Progress 17.3

1. Would the presence of ligers in the fossil record be used as evidence for a gradualistic or a punctuated equilibrium model of evolution? Explain.
2. How does a study of developmental genes support the possibility of rapid speciation in the fossil record? Explain.
3. Why does it seem that differential expression must occur during the development of ligers?
4. There are only five species of cats in the genus *Panthera*. Does this represent a goal of evolution?

Connecting the Concepts

Macroevolution, the study of the origin and history of the species on Earth, is the subject of this chapter and the next. The biological species concept states that the members of a species have an isolated gene pool and can only reproduce with one another.

This chapter concerns speciation. Speciation usually occurs after two populations have been separated geographically. If two populations of salamanders were suddenly separated by a barrier, each population would become adapted to its particular environment over time. Eventually, the two populations might become so genetically different that even if members of each population came in contact, they would not be able to produce fertile offspring. Because gene flow between the two populations would no longer be possible, the salamanders would be considered separate species. Aided by geographic separation, multiple species can repeatedly arise from an ancestral species, as when a common ancestor from the mainland led to 13 species of Galápagos finches, each adapted to its own particular environment.

Does speciation occur gradually, as Darwin supposed, or rapidly (in geologic time), as described by the punctuated equilibrium model? The fossils of the Burgess Shale support the punctuated equilibrium model. How can genetic changes bring about such major changes in form, whether fast or slow? Investigators have now discovered ancient genes whose differential expression can bring about changes in body shapes and organs.

Evolution is not directed toward any particular end, and the traits of the species alive today arose through common descent with adaptations to a local environment. The subject of Chapter 18 is the origin and history of life.

summary

17.1 Separation of the Species

The evolutionary species concept recognizes that every species has its own evolutionary history and can be recognized by certain diagnostic morphological traits. The biological species concept recognizes that a species is reproductively isolated from other species and, therefore, the members of a species breed only among themselves. The use of DNA sequence data can also be used today to distinguish one species from another.

Prezygotic isolating mechanisms (habitat, temporal, behavior, mechanical, and gamete isolation) prevent mating from being attempted or prevent fertilization from being successful if mating is attempted. Postzygotic isolating mechanisms (zygote mortality, hybrid sterility, and F_2 fitness) prevent hybrid offspring from surviving and/or reproducing.

17.2 Modes of Speciation

During allopatric speciation, geographic separation precedes reproductive isolation. Geographic isolation allows genetic changes to occur so that the ancestral species and the new species can no longer breed with one another. A series of salamander subspecies on either side of the Central Valley of California has resulted in two species that are unable to successfully reproduce when they come in contact. During sympatric speciation, a geographic barrier is not required, and speciation is simply a change in genotype that prevents successful reproduction. The best example of sympatric speciation is occurrence of polyploidy in plants.

Adaptive radiation is multiple speciation from an ancestral population because varied habitats permit varied adaptations to occur. Adaptive radiation, as exemplified by the Hawaiian honeycreepers, is a form of allopatric speciation.

During sympatric speciation, no geographic separation precedes reproductive isolation. In plants, the occurrence of polyploidy (chromosome number above 2n) reproductively isolates an offspring from the former generation. Autoploidy occurs within the same species. For example, if—due to nondisjunction—a diploid gamete fuses with a haploid gamete, a triploid plant results that cannot reproduce with 2n plants because some of the chromosomes would not pair during meiosis. Alloploidy occurs when two species hybridize. If an odd number of chromosomes results, the hybrid is sterile unless a doubling of the chromosomes occur and the chromosomes can pair during meiosis. The sex chromosomes in animals makes speciation by polyploidy highly unlikely.

17.3 Principles of Macroevolution

Macroevolution is evolution of new species and higher levels of classification. The fossil record, such as is found in the Burgess Shale, gives us a view of life many millions of years ago. The hypothesis that species evolve gradually is now being challenged by the hypothesis that speciation can occur rapidly. In that case, the fossil record could show periods of stasis interrupted by spurts of change, for example, a punctuated equilibrium. Transitional fossils would be expected with gradual change but not with punctuated equilibrium.

It could be that both models are seen in the fossil record, but rapid change can occur by differential expression of regulatory

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genes. The same regulatory gene (*Pax6*) controls the development of both the camera-type and the compound-type eye. *Tbx5* gene controls development of limbs, whether the wing of a bird or the leg of a tetrapod. *Hox* genes control the number and appearance of a repeated structure along the main body axes of vertebrates. The same pelvic-fin genes control the development of a pelvic girdle. Changing the timing of gene expression, as well as which genes are expressed, can result in dramatic changes in shape.

Speciation, diversification, and extinction are seen during the evolution of *Equus*. These three processes are commonplace in the fossil record and illustrate that macroevolution is not goal-directed. The life we see about us represents adaptations to particular environments. Such adaptations have changed in the past and will change in the future.

understanding the terms

adaptive radiation 306
allopatric speciation 304
alloploidy 307
autoploidy 307
biological species concept 300
evolutionary species concept 300
macroevolution 310
polyploidy 307
postzygotic isolating mechanism 303
prezygotic isolating mechanism 302
speciation 304
sympatric speciation 307

Match the terms to these definitions:

a. _____ Anatomic or physiological difference between two species that prevents successful reproduction after mating has taken place.
b. _____ Evolution of a large number of species from a common ancestor.
c. _____ Origin of new species due to the evolutionary process of descent with modification.
d. _____ Origin of new species after populations have been separated geographically.

reviewing this chapter

1. Give the pros and cons of the evolutionary species concept and the biological species concept. Give an example to show that DNA sequence data can distinguish species. 300–301
2. List and discuss five prezygotic isolating mechanisms and three postzygotic isolating mechanisms. 302–3
3. Use the *Ensatina* salamander example to explain allopatric speciation. 304
4. Use the honeycreepers of Hawaii and the Galápagos finches to explain adaptive radiation. 306
5. How does sympatric speciation differ from allopatric speciation, and why is sympatric speciation common in plants but rare in animals. 307
6. Does the Burgess Shale help us determine whether speciation occurs quickly or slowly? Explain. 308–9
7. With regard to the speed of speciation, how do the gradualistic model and the punctuated equilibrium model differ? Which model predicts the occurrence of many transitional fossils? Explain. 310
8. What types of genes are pertinent to the discussion of the speed of speciation? Explain. 311–12
9. Use the evolution of the horse to show that speciation is not goal-oriented. 313–14

testing yourself

Choose the best answer for each question.

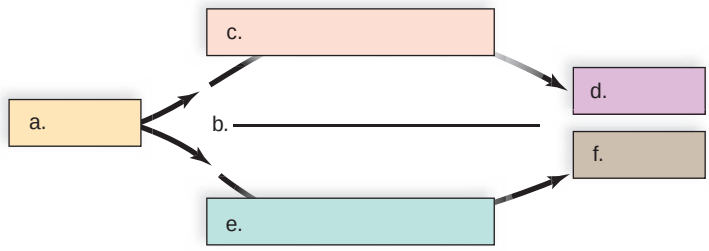
1. A biological species
   a. always looks different from other species.
   b. always has a different chromosome number from that of other species.
   c. is reproductively isolated from other species.
   d. never occupies the same niche as other species.

For questions 2–7, indicate the type of isolating mechanism described in each scenario.

KEY:

a. habitat isolation
b. temporal isolation
c. behavioral isolation
d. mechanical isolation
e gamete isolation
f. zygote mortality
g. hybrid sterility
h. low F_2 fitness

2. Males of one species do not recognize the courtship behaviors of females of another species.
3. One species reproduces at a different time than another species.
4. A cross between two species produces a zygote that always dies.
5. Two species do not interbreed because they occupy different areas.
6. The sperm of one species cannot survive in the reproductive tract of another species.
7. The offspring of two hybrid individuals exhibit poor vigor.
8. Which of these is a prezygotic isolating mechanism?
   a. habitat isolation
   b. temporal isolation
   c. hybrid sterility
   d. zygote mortality
   e. Both a and b are correct.
9. Male moths recognize females of their species by sensing chemical signals called pheromones. This is an example of
   a. gamete isolation.
   b. habitat isolation.
   c. behavorial isolation.
   d. mechanical isolation.
   e. temporal isolation.
10. Which of these is mechanical isolation?
    a. Sperm cannot reach or fertilize an egg.
    b. Courtship pattern differs.
    c. The organisms live in different locales.
    d. The organisms reproduce at different times of the year.
    e. Genitalia are unsuitable to each other.
11. Complete the following diagram illustrating allopatric speciation by using these phrases: genetic changes (used twice), geographic barrier, species 1, species 2, species 3.



12. The creation of new species due to geographic barriers is called
    a. isolation speciation.
    b. allopatric speciation.
    c. allelomorphic speciation.
    d. sympatric speciation.
    e. symbiotic speciation.
13. The many species of Galápagos finches are each adapted to eating different foods. This is the result of
    a. gene flow.
    b. adaptive radiation.
    c. sympatric speciation.
    d. genetic drift.
    e. All of these are correct.
14. Allopatric, but not sympatric, speciation requires
    a. reproductive isolation.
    b. geographic isolation.
    c. spontaneous differences in males and females.
    d. prior hybridization.
    e. rapid rate of mutation.
15. Which of the following is not a characteristic of plant alloploidy?
    a. hybridization
    b. chromosome doubling
    c. related species mating
    d. All of these are characteristics of plant alloploidy.
16. Corn is an allotetraploid, which means that its
    a. chromosome number is 4n.
    b. occurrence resulted from hybridization.
    c. occurrence required a geographic barrier.
    d. Both a and b are correct.
17. Transitional links are least likely to be found if evolution proceeds according to the
    a. gradualistic model.
    b. punctuated equilibrium model.
18. Adaptive radiation is only possible if evolution is punctuated.
    a. true
    b. false
19. Why are there no fish fossils in the Burgess Shale?
    a. The habitat was not aquatic.
    b. Fish do not fossilize easily because they do not have shells.
    c. The fossils of the Burgess Shale predate vertebrate animals.
    d. There are fish fossils in the Burgess Shale.
20. Which of the following can influence the rapid development of new types of animals?
    a. The influence of molecular clocks.
    b. A change in the expression of regulating genes.
    c. The sequential expression of genes.
    d. All of these are correct.
21. Which gene is incorrectly matched to its function?
    a. *Hox*—body shape
    b. *Pax6*—body segmentation
    c. *Tbx5*—limb development
    d. All of these choices are correctly matched.
22. In the evolution of the modern horse, which was the goal of the evolutionary process?
    a. large size
    b. single toe
    c. Both a and b are correct.
    d. Neither a nor b is correct.
23. Which of the following was not a characteristic of *Hyracotherium*, an ancestral horse genus?
    a. small size
    b. single toe
    c. wooded habitat
    d. All of these are characteristics of *Hyracotherium*.
24. Which statement about speciation is not true?
    a. Speciation can occur rapidly or slowly.
    b. Developmental genes can account for rapid speciation.
    c. The fossil record gives no evidence that speciation can occur rapidly.
    d. Speciation always requires genetic changes, such as mutations, genetic drift, and natural selection.
25. Which statement concerning allopatric speciation would come first?
    a. Genetic and phenotypic changes occur.
    b. Subspecies have a three-part name.
    c. Two subpopulations are separated by a barrier.

thinking scientifically

1. You want to decide what definition of a species to use in your study. What are the advantages and disadvantages of one based on DNA sequences as opposed to the evolutionary and biological species concept?
2. You decide to create a hybrid by crossing two species of plants. If the hybrid is a fertile plant that produces normal size fruit, what conclusion is possible?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

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18

Origin and History of Life

Today, paleontologists are setting the record straight about dinosaurs. It now appears that dinosaurs nested in the same manner as birds! Bowl-shaped nests containing dinosaur eggs have been found in Mongolia, Argentina, and Montana. The nests contain fossilized eggs and bones along with eggshell fragments. From this evidence, it seems that baby dinosaurs stayed in the nest after hatching until they were big enough to walk around and fragment the eggshells. The spacing between the nests suggests that this dinosaur, Maisaura *(meaning good mother lizard in Greek), fed its young. The remains of an enormous herd of about 10,000 found in Montana is further evidence that* Maisaura *was indeed social in their behavior.*

Maisaura *and* Microraptor, *the winged gliding dinosaur featured below, provide us with structural and behavioral evidence of the link between dinosaurs and birds. In this chapter, we trace the origin of life before considering the history of life.*

Many transitional forms, such as *Microraptor* shown here in reconstruction, indicate a link between dinosaurs and birds.

concepts

18.1 ORIGIN OF LIFE

- A chemical evolution proceeded from monomers to polymers to protocells. 318–20
- The first cell was a heterotroph bounded by a membrane and containing a replication system—that is, DNA, RNA, and proteins. 320–22

18.2 HISTORY OF LIFE

- The fossil record allows us to trace the history of life, which has evolved during the Precambrian time, the Paleozoic era, the Mesozoic era, and the Cenozoic era. 322–24
- The first fossils are of prokaryotes dated about 3.5 BYA (billion years ago). Prokaryotes diversified for about 1.5 billion years before the eukaryotic cell, followed by multicellular forms, evolved during the Precambrian time. 324–27
- The Paleozoic includes the Cambrian period, when diverse animals appear, and the Carboniferous period, when swamp forests on land contained seedless vascular plants, insects, and amphibians. 327–29
- The Mesozoic era is best known for dinosaurs, cycads, and the origins of mammals and birds. 330
- The Cenozoic era is known for the development of modern flowering plants and an adaptive radiation of mammals. 331

18.3 FACTORS THAT INFLUENCE EVOLUTION

- The position of the continents changes over time because the Earth's crust consists of moving plates. 332
- Continental drift and meteorite impacts have contributed to several episodes of mass extinction during the history of life. 333

18.1 Origin of Life

We have no data that suggests life arises spontaneously from nonlife, and we say that "life comes only from life." But if this is so, how did the first form of life come about? Since it was the very first living thing, it had to come from nonliving chemicals. Could there have been an increase in the complexity of the chemicals—could a **chemical evolution** have produced the first cell(s) on early Earth?

The Early Earth

The sun and the planets, including Earth, probably formed over a 10-billion-year period from aggregates of dust particles and debris. At 4.6 billion years ago (BYA), the solar system was in place. Intense heat produced by gravitational energy and radioactivity produced several stratified layers. Heavier atoms of iron and nickel became the molten liquid core, and dense silicate minerals became the semiliquid mantle. Upwellings of volcanic lava produced the first crust.

The Earth's mass is such that the gravitational field is strong enough to have an atmosphere. Less mass and atmospheric gases would escape into outer space. The early Earth's atmosphere was not the same as today's atmosphere; it was produced primarily by outgassing from the interior, exemplified by volcanic eruptions. The early atmosphere most likely consisted mainly of these inorganic chemicals: water vapor (H_2O), nitrogen (N_2), and carbon dioxide (CO_2), with only small amounts of hydrogen (H_2), methane (CH_4), ammonia (NH_3), hydrogen sulfide (H_2S), and carbon monoxide (CO). The early atmosphere may have been a reducing atmosphere, with little free oxygen. If so, that would have been fortuitous because oxygen (O_2) attaches to organic molecules, preventing them from joining to form larger molecules.

At first it was so hot that water was present only as a vapor that formed dense, thick clouds. Then, as the early Earth cooled, water vapor condensed to liquid water, and rain began to fall. It rained in such enormous quantity over hundreds of millions of years that the oceans of the world were produced. Our planet is an appropriate distance from the sun: any closer, water would have evaporated; any farther away, water would have frozen.

It is also possible that the oceans were fed by celestial comets that entered the Earth's gravitational field. In 1999, physicist Louis Frank presented images taken by cameras on NASA's *Polar* satellite to substantiate his claim that the Earth is bombarded with 5–30 icy comets the size of a house every minute. The ice becomes water vapor that later comes down as rain, enough rain, says Frank, to raise the oceans' level by an inch in just 10,000 years.

Monomers Evolve

Several hypotheses suggest how organic monomers could have evolved, and these are that (1) monomers came from outer space, (2) monomers came from reactions in the atmosphere, or (3) monomers came from reactions at hydrothermal vents.

Alternative Hypotheses

In support of monomers coming from outer space, we know that comets and meteorites have constantly pelted the Earth throughout history. In recent years, scientists have confirmed the presence of organic molecules in some meteorites. Many scientists, championed by Chandra Wickramsinghe, feel that these organic molecules could have seeded the chemical origin of life on early Earth. Others even hypothesize that bacterium-like cells evolved first on another planet and then were carried to Earth. A meteorite from Mars labeled ALH84001 landed on Earth some 13,000 years ago. When examined, experts found tiny rods similar in shape to fossilized bacteria. Therefore this hypothesis is being investigated.

In support of monomers coming from reactions in the atmosphere, Stanley Miller performed a famous experiment in 1953 (Fig. 18.1). He was following up on the suggestion made by A. I. Oparin (a Russian biochemist) and J. B. S. Haldane (a Scottish physiologist and geneticist) who independently suggested in the early 1900s that monomers could have been produced from early atmospheric gases in the presence of strong energy sources. The energy sources on early Earth included heat from volcanoes and meteorites, radioactivity from isotopes, powerful electric discharges in lightning, and solar radiation, especially ultraviolet radiation. Oparin's idea is called abiotic synthesis, the formation of simple monomers (sugars, amino acids, nucleotide bases) from inorganic molecules.

For his experiment, Miller placed a mixture resembling a strongly reducing atmosphere—methane (CH_4), ammonia

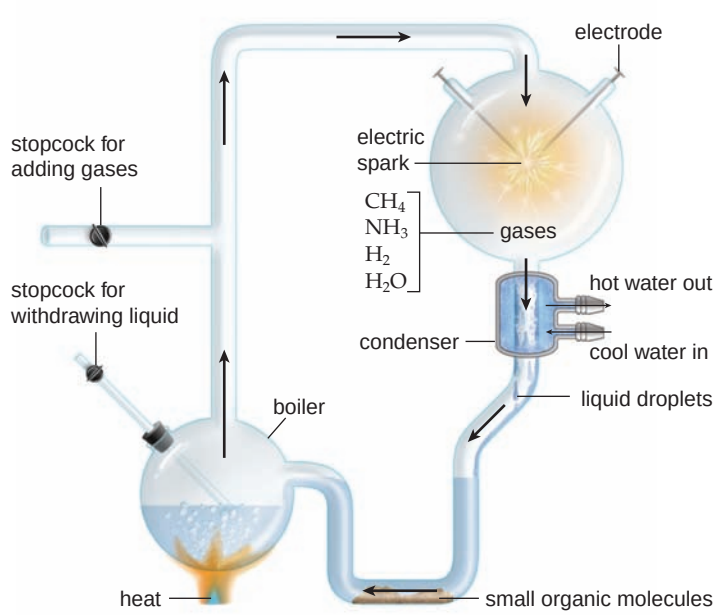

FIGURE 18.1 Stanley Miller's apparatus and experiment.

Gases that were thought to be present in the early Earth's atmosphere were admitted to the apparatus, circulated past an energy source (electric spark), and cooled to produce a liquid that could be withdrawn. Upon chemical analysis, the liquid was found to contain various small organic molecules, which could serve as monomers for large cellular polymers.

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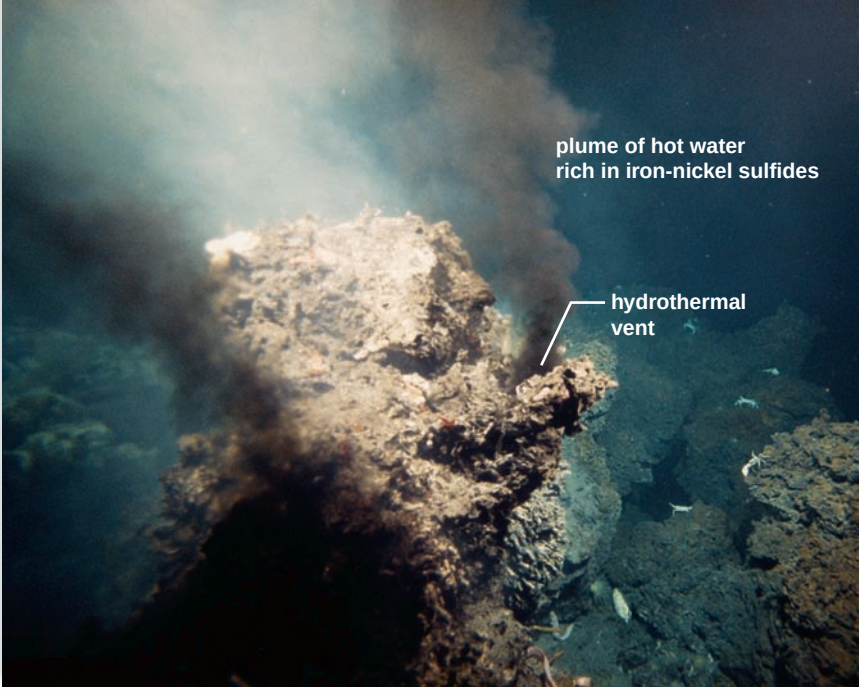


FIGURE 18.2 Chemical evolution at hydrothermal vents.

Minerals that form at deep-sea hydrothermal vents like this one can catalyze the formation of ammonia and even monomers of larger organic molecules in cells.

(NH_3), hydrogen (H_2), and water (H_2O)—in a closed system, heated the mixture, and circulated it past an electric spark (simulating lightning). After a week's run, Miller discovered that a variety of amino acids and organic acids had been produced. Since that time, other investigators have achieved similar results by using other, less-reducing combinations of gases dissolved in water.

If atmospheric gases did react with one another to produce small organic compounds, neither oxidation (there was no free oxygen) nor decay (there were no bacteria) would have destroyed these molecules, and rainfall would have washed them into the ocean, where they accumulated for hundreds of millions of years. Therefore, the oceans would have been a thick, warm organic soup.

In support of monomers coming from reactions at hydrothermal vents, a team of investigators at the Carnegie Institution in Washington, D.C. first point out that Miller used ammonia as one of the atmospheric gases. Whereas inert nitrogen gas (N_2) would have been abundant in the primitive atmosphere, ammonia (NH_3) would have been scarce. However, ammonia would have been plentiful at hydrothermal vents on the ocean floor. These vents line huge **ocean ridges,** where molten magma wells up and adds crust to the ocean floor in each direction. Cool water seeping through the vents is heated to a temperature as high as 350°C, and when it spews back out, it contains various mixed iron-nickel sulfides that can act as catalysts to change N_2 to NH_3 (Fig. 18.2). A laboratory test of this hypothesis worked perfectly. Under ventlike conditions, 70% of various nitrogen sources were converted to ammonia within 15 minutes. German organic chemists Gunter Wachtershaüser and Claudia Huber have gone one more step. They have shown that organic molecules will react and amino acids will form peptides in the presence of iron-nickel sulfides under ventlike conditions.

Polymers Evolve

In cells, organic monomers join to form polymers in the presence of enzymes, which of course are proteins. How did the first organic polymers form if there were no proteins yet? As just mentioned, Wachtershaüser and Huber have managed to achieve the formation of peptides using iron-nickel sulfides as inorganic catalysts under ventlike conditions of high temperature and pressure. These minerals have a charged surface that attracts amino acids and provides electrons so they can bond together.

Alternative Hypotheses

Sidney Fox has shown that amino acids polymerize abiotically when exposed to dry heat. He suggests that once amino acids were present in the oceans, they could have collected in shallow puddles along the rocky shore. Then the heat of the sun could have caused them to form **proteinoids,** small polypeptides that have some catalytic properties. When he simulates this scenario in the lab and returns proteinoids to water, they form **microspheres** [Gk. *mikros,* small, little, and *sphaera,* ball], structures composed only of protein that have many properties of a cell (Fig. 18.3*a*). It's possible that even newly formed polypeptides had enzymatic properties, and some proved to be more capable than others. Those that led to the first cell or cells had a selective advantage. Fox's **protein-first hypothesis** assumes that DNA genes came after protein enzymes arose. After all, it is protein enzymes that are needed for DNA replication.

Another hypothesis is put forth by Graham Cairns-Smith. He hypothesizes that clay was especially helpful in causing polymerization of monomers to produce both proteins and nucleic acids at the same time. Clay also attracts small organic molecules and contains iron and zinc, which may have served as inorganic catalysts for polypeptide formation. In addition, clay has a tendency to collect energy from radioactive decay and to discharge it when the temperature and/or humidity changes. This could have been a source of energy for polymerization to take place. Cairns-Smith suggests that RNA nucleotides and amino acids became associated in such a way that polypeptides were ordered by and helped synthesize RNA. This hypothesis suggests that both polypeptides and RNA arose at the same time.

There is still another hypothesis concerning this stage in the origin of life. The **RNA-first hypothesis** suggests that only the macromolecule RNA (ribonucleic acid) was needed to progress toward formation of the first cell or cells. Thomas Cech and Sidney Altman shared a Nobel Prize in 1989 because they discovered that RNA can be both a substrate and an enzyme. Some viruses today have RNA genes; therefore, the first genes could have been RNA. It would seem, then, that RNA could have carried out the processes of life commonly associated today with DNA (deoxyribonucleic acid, the genetic material) and proteins (enzymes). Those who support this hypothesis say that it was an "RNA world" some 4 BYA.

A Protocell Evolves

Before the first true cell arose, there would have been a **protocell** or **protobiont** [Gk. *protos,* first], a structure that first and foremost has an outer membrane. After all, life requires chemical reactions that take place within a boundary.

The Plasma Membrane

The plasma membrane separates the living interior from the nonliving exterior. There are several hypotheses about the origin of the first membrane. Sidney Fox has shown that if lipids are made available to microspheres, lipids tend to become associated with microspheres (Fig. 18.3*a*), producing a lipid-protein membrane. Microspheres have many interesting properties: They resemble bacteria, they have an electrical potential difference, and they divide and perhaps are subject to selection. Although Fox believes they are a cell, others disagree.

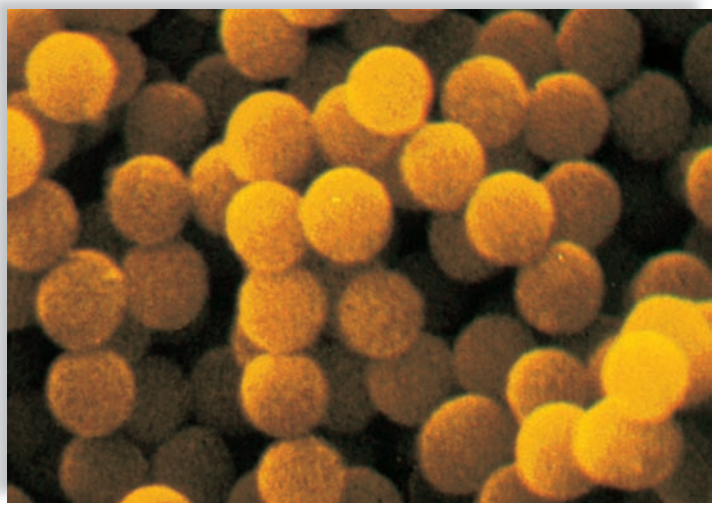
Oparin, who was mentioned previously, showed that under appropriate conditions of temperature, ionic composition, and pH, concentrated mixtures of macromolecules tend to give rise to complex units called **coacervate droplets.** Coacervate droplets have a tendency to absorb and incorporate various substances from the surrounding solution. Eventually, a semipermeable-type boundary may form about the droplet.

In the early 1960s, biophysicist Alec Bangham of the Animal Physiology Institute in Cambridge, England, discovered that when he extracted lipids from egg yolks and placed them in water, the lipids would naturally organize themselves into double-layered bubbles roughly the size of a cell. Bangham's bubbles soon became known as **liposomes** [Gk. *lipos,* fat, and *soma,* body] (Fig. 18.3*b*). Later, biophysicist David Deamer of the University of California and Bangham realized that liposomes might have provided life's first boundary. Perhaps liposomes with a phospholipid membrane engulfed early molecules that had enzymatic, even replicative abilities. The liposomes would have protected the molecules from their surroundings and concentrated them so they could react (and evolve) quickly and efficiently. These investigators called this the "membrane-first" hypothesis, meaning that the first cell had to have a plasma membrane before any of its other parts. Perhaps the first membrane formed in this manner, and the protocell contained only RNA, which functioned as both genetic material and enzymes.

Nutrition

The protocell would have had to carry on nutrition so that it could grow. If organic molecules formed in the atmosphere and were carried by rain into the ocean, nutrition would have been no problem because simple organic molecules could have served as food. This hypothesis suggests that the protocell was a heterotroph [Gk. *hetero,* different, and *trophe,* food], an organism that takes in preformed food. On the other hand, if the protocell evolved at hydrothermal vents, it may have carried out chemosynthesis. Chemoautotrophic bacteria obtain energy for synthesizing organic molecules by oxidizing inorganic compounds, such as hydrogen sulfide (H_2S), a molecule that is abundant at the vents. When hydrothermal vents were first discovered in the 1970s, investigators were surprised to discover complex vent ecosystems supported by organic molecules formed by chemosynthesis, a process that does not require the energy of the sun.

At first, the protocell may have used preformed ATP (adenosine triphosphate), but as this supply dwindled,



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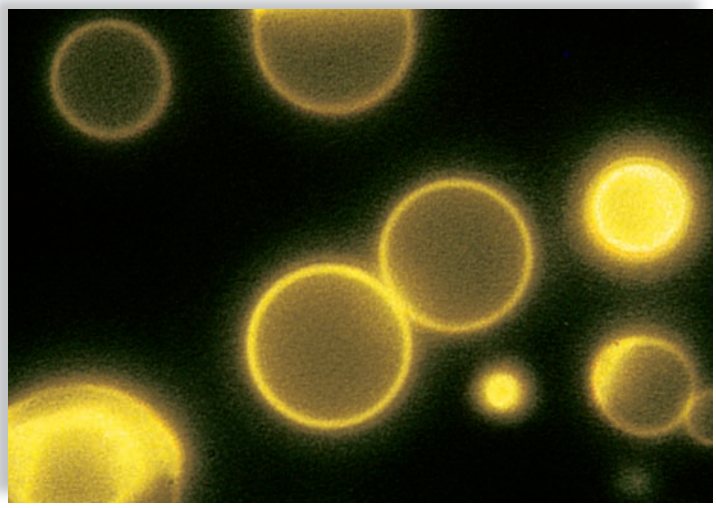

b.

FIGURE 18.3 Origin of plasma membrane.

a. Microspheres have a number of cellular characteristics and could have evolved into the protocell. For example, microspheres are composed only of protein, but if lipids are added, the proteins combine with them. Perhaps this was the step that led to the first plasma membrane. **b.** Liposomes form automatically when lipids are put into water. Phospholipids also have a tendency to form a circle. Perhaps the first plasma membrane was simply a phospholipid bilayer without any proteins being present.

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natural selection favored any cells that could extract energy from carbohydrates in order to transform ADP (adenosine diphosphate) to ATP. Glycolysis is a common metabolic pathway in living things, and this testifies to its early evolution in the history of life. Since there was no free oxygen, we can assume that the protocell carried on a form of fermentation. At first the protocell must have had limited ability to break down organic molecules, and scientists speculate that it took millions of years for glycolysis to evolve completely. Interestingly, Fox has shown that microspheres from which protocells may have evolved have some catalytic ability, and Oparin found that coacervates do incorporate enzymes if they are available in the medium.

A Self-Replication System Evolves

Today's cell is able to carry on protein synthesis in order to produce the enzymes that allow DNA to replicate. The central dogma of genetics states that DNA directs protein synthesis and that information flows from DNA to RNA to protein. It is possible that this sequence developed in stages.

Alternative Hypotheses

According to the RNA-first hypothesis, RNA would have been the first to evolve, and the first true cell would have had RNA genes. These genes would have directed and enzymatically carried out protein synthesis. Today, ribozymes are enzymatic RNA molecules. Also, today we know there are viruses that have RNA genes. These viruses have a protein enzyme called reverse transcriptase that uses RNA as a template to form DNA. Perhaps with time, reverse transcription occurred within the protocell, and this is how DNA genes arose. If so, RNA was responsible for both DNA and protein formation. Once there were DNA genes, protein synthesis would have been carried out in the manner dictated by the central dogma of genetics.

According to the protein-first hypothesis, proteins, or at least polypeptides, were the first of the three (i.e., DNA, RNA, and protein) to arise. Only after the protocell developed a plasma membrane and sophisticated enzymes did it have the ability to synthesize DNA and RNA from small molecules provided by the ocean. Because a nucleic acid is a complicated molecule, the likelihood RNA arose *de novo* (on its own) is minimal. It seems more likely that enzymes were needed to guide the synthesis of nucleotides and then nucleic acids. Again, once there were DNA genes, protein synthesis would have been carried out in the manner dictated by the central dogma of genetics.

Cairns-Smith proposes that polypeptides and RNA evolved simultaneously. Therefore, the first true cell would have contained RNA genes that could have replicated because of the presence of proteins. This eliminates the baffling chicken-and-egg paradox: Assuming a plasma membrane, which came first, proteins or RNA? It means, however, that two unlikely events would have had to happen at the same time.

After DNA formed, the genetic code had to evolve before DNA could store genetic information. The present genetic code is subject to fewer errors than a million other possible codes. Also, the present code is among the best at minimizing the effect of mutations. A single-base change in a present codon is likely to result in the substitution of a chemically similar amino acid and, therefore, minimal changes in the final protein. This evidence suggests that the genetic code did undergo a natural selection process before finalizing into today's code.

A Recap of the Steps

Figure 18.4 reviews how most biologists hypothesize that life evolved on early Earth.

1. An abiotic synthesis process created small organic molecules such as amino acids and nucleotides, perhaps in the atmosphere or at hydrothermal vents.
2. These monomers joined together to form polymers along the shoreline (warm seaside rocks or clay) or at the vents. The first polymers could have been proteins or RNA, or they could have evolved together.

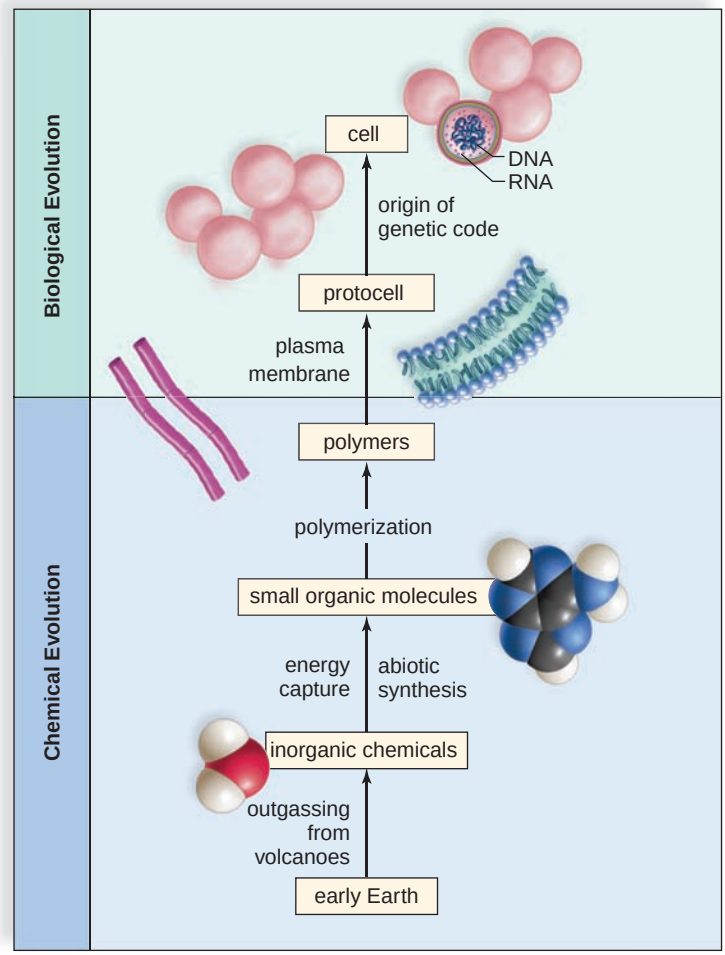

FIGURE 18.4 Origin of the first cell(s).

There was an increase in the complexity of macromolecules, leading to a self-replicating system (DNA ⟶ RNA ⟶ protein) enclosed by a plasma membrane. The protocell, a heterotrophic fermenter, underwent biological evolution, becoming a true cell, which then diversified.

3. The aggregation of polymers inside a plasma membrane produced a protocell, which had enzymatic properties such that it could grow. If the protocell developed in the ocean, it was a heterotroph; if it developed at hydrothermal vents, it was a chemoautotroph.
4. Once the protocell contained DNA genes, a true cell had evolved. The first genes may have been RNA molecules, but later DNA became the information storage molecule of heredity. Biological evolution—and the history of life—had begun!

Check Your Progress 18.1

1. What function can RNA perform that a protein cannot perform in cells?
2. Without mitochondria, what metabolic pathway would have allowed the first cell or cells to produce ATP molecules?

18.2 History of Life

Macroevolution includes large-scale patterns of change taking place over very long periods of time. The fossil record records such changes.

Fossils Tell a Story

Fossils [L. *fossilis,* dug up] are the remains and traces of past life or any other direct evidence of past life. Traces include trails, footprints, burrows, worm casts, or even preserved droppings. Usually when an organism dies, the soft parts are either consumed by scavengers or decomposed by bacteria. Occasionally, the organism is buried quickly and in such a way that decomposition is never completed or is completed so slowly that the soft parts leave an imprint of their structure. Most fossils, however, consist only of hard parts such as shells, bones, or teeth, because these are usually not consumed or destroyed. **Paleontology** [Gk. *palaios,* ancient, old, and *ontos,* having existed; *-logy,* study of, from *logikos,* rational, sensible] is the science of discovering and studying the fossil record and, from it, making decisions about the history of life, ancient climates, and environments.

The great majority of fossils are found embedded in or recently eroded from sedimentary rock. **Sedimentation** [L. *sedimentum,* a settling], a process that has been going on since the Earth was formed, can take place on land or in bodies of water. Weathering and erosion of rocks produce an accumulation of particles that vary in size and nature and are called sediment. Sediment becomes a **stratum** (pl., strata), a recognizable layer in a stratigraphic sequence (Fig. 18.5*a*). Any given stratum is older than the one above it and younger than the one immediately below it. Figure 18.5*b* shows the history of the Earth as if it had occurred during a 24-hour time span that starts at midnight. (The actual years are shown on an inner ring of the diagram.) This figure illustrates dramatically that only unicellular organisms were present during most (about 80%) of the history of the Earth.

If the Earth formed at midnight, prokaryotes do not appear until about 5 A.M., eukaryotes are present at approximately 4 P.M., and multicellular forms do not appear until around 8 P.M. Invasion of the land doesn't occur until about 10 P.M., and humans don't appear until 30 seconds before the end of the day. This timetable has been worked out by studying the fossil record. In addition to sedimentary fossils, more recent fossils can be found in tar, ice, bogs, and amber. Petrified wood, shells, and bones are also relatively common (Fig. 18.6).

Relative Dating of Fossils

In the early nineteenth century, even before the theory of evolution was formulated, geologists sought to correlate the strata worldwide. The problem was that strata change their character over great distances, and therefore a stratum in England might contain different sediments than one of the same age in Russia. Geologists discovered that each stratum of the same age contained certain **index fossils** that serve to identify deposits made at apparently the same time in different parts of the world. These index fossils are used in **relative dating** methods. For example, a particular species of fossil ammonite (an animal related to the chambered nautilus) has been found over a wide range and for a limited time period. Therefore, all strata around the world that contain this fossil must be of the same age.

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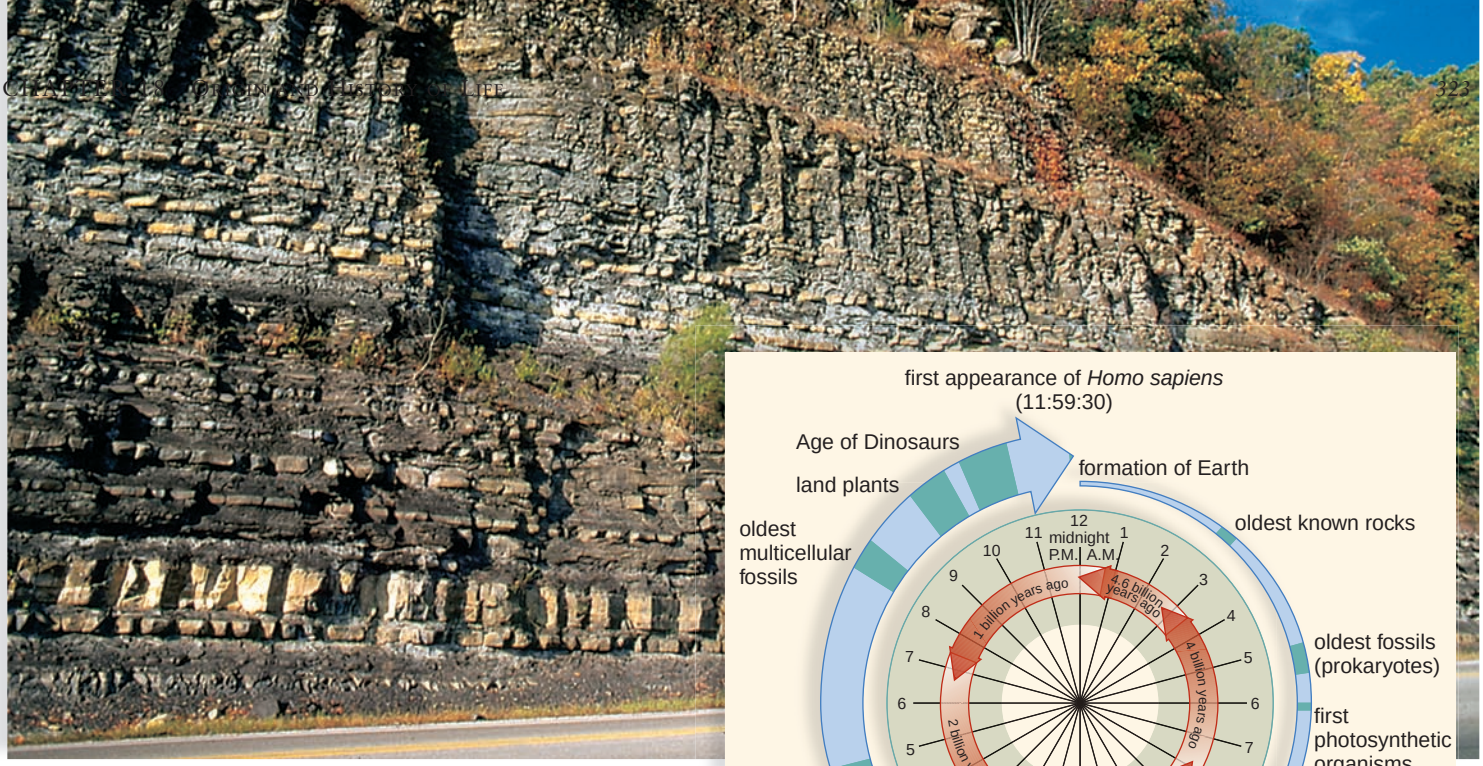

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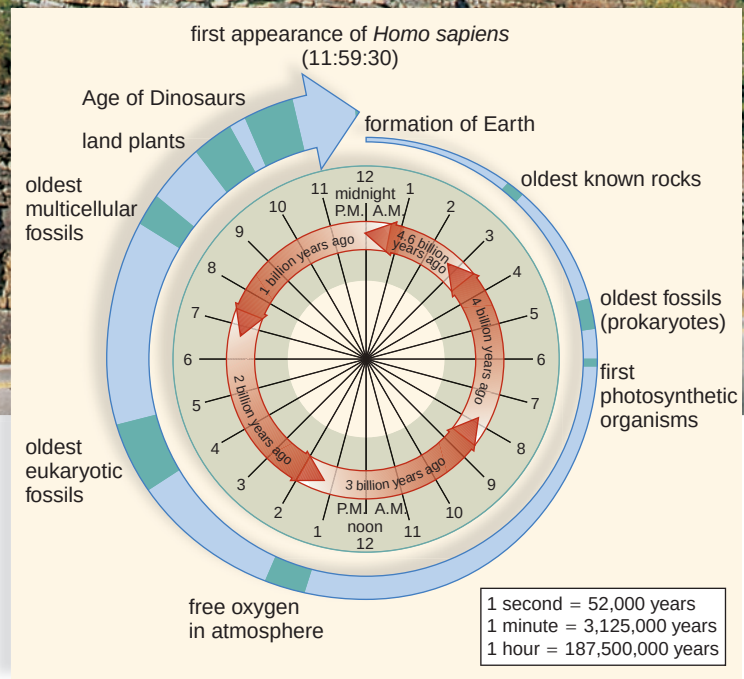

b.

FIGURE 18.5 The history of life.

a. Strata, layers seen in sedimentary rock as exposed by road cuts, are the source of fossils that tell us about the history of life. **b.** The blue ring of this diagram shows the history of life as it would be measured on a 24-hour timescale starting at midnight. (The red ring shows the actual years going back in time to 4.6 BYA.) The fossil record suggests that a very large portion of life's history was devoted to the evolution of unicellular organisms. The first multicellular organisms do not appear in the fossil record until just before 8 P.M., and humans are not on the scene until less than a minute before midnight. BYA = billion years ago

FIGURE 18.6 Fossils.

Fossils are the remains of past life. They can be impressions left in rocks, footprints, mineralized bones, shells, or any other evidences of life-forms that lived in the past.

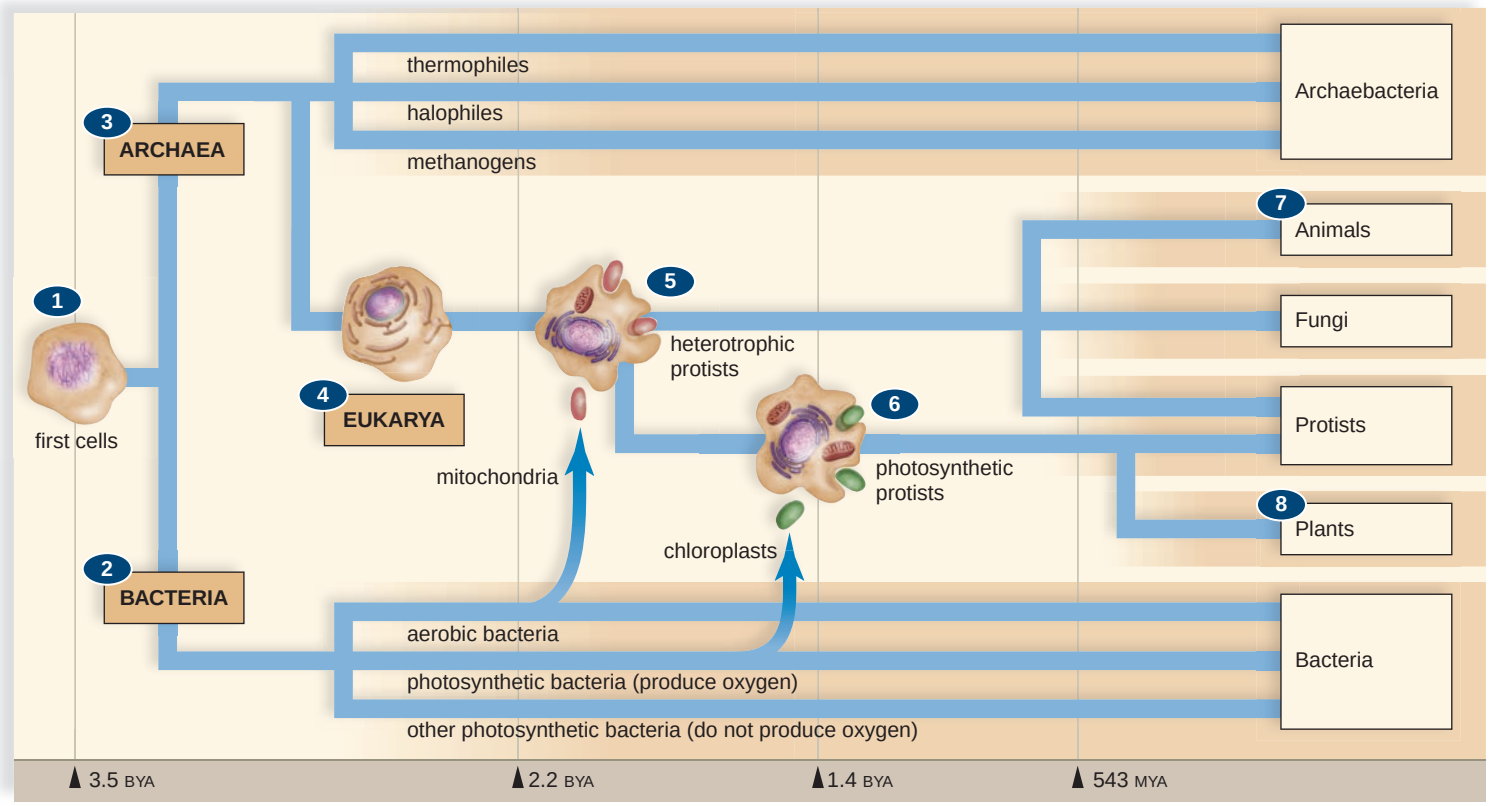

FIGURE 18.7 The tree of life.

During the Precambrian time, 1 the first cell or cells give rise to 2 bacteria and 3 archaea; 4 the first eukaryotic cell evolves from archaea. 5 Heterotrophic protists arise when eukaryotic cells gain mitochondria by engulfing aerobic bacteria, and 6 photosynthetic protists arise when these cells gain chloroplasts by engulfing photosynthetic bacteria. 7 Animals (and fungi) evolve from heterotrophic protists, and 8 plants evolve from photosynthetic protists. BYA = billion years ago

Absolute Dating of Fossils

An **absolute dating** method that relies on radioactive dating techniques assigns an actual date to a fossil. All radioactive isotopes have a particular half-life, the length of time it takes for half of the radioactive isotope to change into another stable element. If the fossil has organic matter, half of the carbon 14 (^{14}C) will have changed to nitrogen 14 (^{14}N) in 5,730 years. To know how much ^{14}C was in the organism to begin with, it is reasoned that organic matter always begins with the same amount of ^{14}C. (In reality, it is known that the ^{14}C levels in the air—and therefore the amount in organisms—can vary from time to time.) Now we need only compare the ^{14}C radioactivity of the fossil to that of a modern sample of organic matter. The amount of radiation left can be converted to the age of the fossil. After 50,000 years, however, the amount of ^{14}C radioactivity is so low that it cannot be used to measure the age of a fossil accurately.

^{14}C is the only radioactive isotope contained within organic matter, but it is possible to use others to date rocks, and from that to infer the age of a fossil contained in the rock. For instance, the ratio of potassium 40 (^{40}K) to argon 40 trapped in rock is often used to date rocks.

The Precambrian Time

As a result of their study of fossils in strata, geologists have devised the **geologic timescale,** which divides the history of the Earth into eras and then periods and epochs (Table 18.1). We will follow the biologist's tradition of first discussing Precambrian time. The Precambrian is a very long period of time, comprising about 87% of the geologic timescale. During this time, life arose and the first cells came into existence (Fig. 18.7). The first cells were probably prokaryotes. Prokaryotes do not have a nucleus or membrane-bounded organelles. Prokaryotes, the archaea and bacteria, can live in the most inhospitable of environments, such as hot springs, salty lakes, and airless swamps—all of which may typify habitats on early Earth. The cell wall, plasma membrane, RNA polymerase, and ribosomes of archaea are more like those of eukaryotes than those of bacteria.

The first identifiable fossils are those of complex prokaryotes. Chemical fingerprints of complex cells are found in sedimentary rocks from southwestern Greenland, dated at 3.8 BYA (billion years ago). But paleobiologist J. William Schopf found the oldest prokaryotic fossils in western Australia. These 3.46-billion-year-old microfossils resemble today's cyanobacteria, prokaryotes that carry on photosynthesis in the same manner as plants. At this time, only volcanic rocks jutted above the waves, and there were as yet no continents. Strange-looking boulders, called **stromatolites,** littered beaches and shallow waters (Fig. 18.8*a*). Living stromatolites can still be found today along Australia's western coast. The outer surface of a stromatolite is alive with cyanobacteria that secrete a mucus. Grains of sand get caught in the mucus and bind with calcium carbonate from the water to form rock. To gain access to sunlight, the photosynthetic organisms move outward

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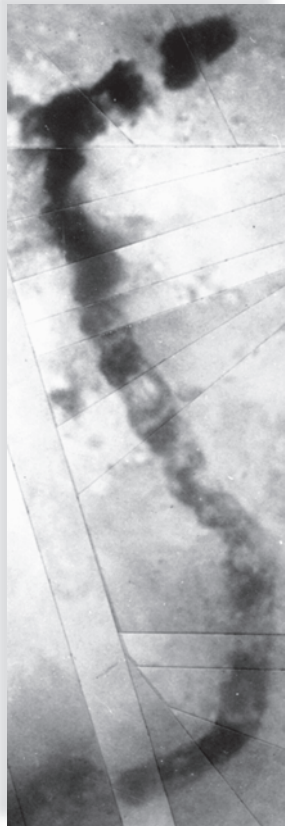
a. Stromatolites



b. *Primaevifilum*

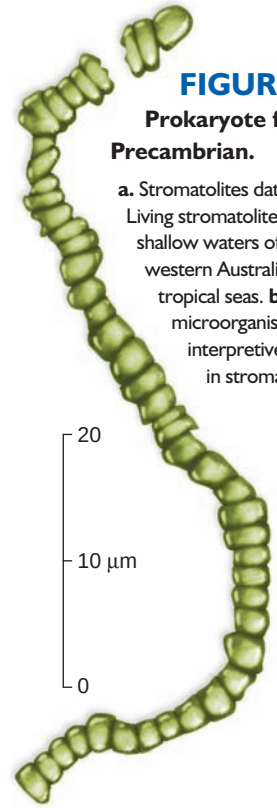


FIGURE 18.8

Prokaryote fossils of the Precambrian.

a. Stromatolites date back to 3.46 BYA. Living stromatolites are located in shallow waters off the shores of western Australia and also in other tropical seas. **b.** The prokaryotic microorganism *Primaevifilum* (with interpretive drawing) was found in stromatolites.

toward the surface before they are cemented in. They leave behind a menagerie of aerobic and then anaerobic bacteria caught in the layers of the rock.

The cyanobacteria in ancient stromatolites added oxygen to the atmosphere (Fig. 18.8*b*). By 2.0 BYA, the presence of oxygen was such that most environments were no longer suitable for anaerobic prokaryotes, and they began to decline in importance. Photosynthetic cyanobacteria and aerobic bacteria proliferated as new metabolic pathways evolved. Due to the presence of oxygen, the atmosphere became an oxidizing one instead of a reducing one. Oxygen in the upper atmosphere forms ozone (O_3), which filters out the ultraviolet (UV) rays of the sun. Before the formation of the **ozone shield,** the amount of ultraviolet radiation reaching the Earth could have helped create organic molecules, but it would have destroyed any land-dwelling organisms. Once the ozone shield was in place, living things were sufficiently protected and able to live on land (see page 880).

Eukaryotic Cells Arise

The eukaryotic cell, which originated around 2.1 BYA, is nearly always aerobic and contains a nucleus as well as other membranous organelles. Most likely, the eukaryotic cell acquired its organelles gradually. The nucleus may have developed by an invagination of the plasma membrane. The mitochondria of the eukaryotic cell were once free-living aerobic bacteria, and the chloroplasts were free-living photosynthetic prokaryotes. The **endosymbiotic theory** states that a nucleated cell engulfed these prokaryotes, which then became organelles (see Fig. 18.7). The evidence for the theory is the following:

1. The present-day mitochondria and chloroplasts have a size that lies within the range of that for bacteria.
2. Mitochondria and chloroplasts have their own DNA and make some of their own proteins. (The DNA of the nucleus also codes for some of the mitochondrial proteins.)
3. The mitochondria and chloroplasts divide by binary fission, the same as bacteria do.
4. The outer membrane of mitochondria and chloroplasts differ—the outer membrane resembles that of a eukaryotic cell and the inner membrane resembles that of a bacterial cell.

It's been suggested that flagella (and cilia) also arose by endosymbiosis. First, slender undulating prokaryotes could have attached themselves to a host cell to take advantage of food leaking from the host's plasma membrane. Eventually, these prokaryotes adhered to the host cell and became the flagella and cilia we know today. The first eukaryotes were unicellular, as are prokaryotes.

Multicellularity Arises

Fossils identified as multicellular protists and dated 1.4 BYA have been found in arctic Canada. It's possible that the first multicellular organisms practiced sexual reproduction. Among today's protists we find colonial forms in which some cells are specialized to produce gametes needed for sexual reproduction. Separation of germ cells, which produce gametes from somatic cells, may have been an important first step toward the development of the Ediacaran invertebrates discussed next, which appeared about 630 MYA (million years ago) and died out about 545 MYA.

TABLE 18.1

The Geologic Timescale: Major Divisions of Geologic Time and Some of the Major Evolutionary Events of Each Time Period

Era	*Period*	*Epoch*	*Million Years Ago (MYA)*	*Plant Life*	*Animal Life*
Cenozoic		Holocene	(0.01–0)	Human influence on plant life	Age of *Homo sapiens*
		Significant Mammalian Extinction			
	Quaternary	Pleistocene	(1.80–0.01)	Herbaceous plants spread and diversify.	Presence of Ice Age mammals. Modern humans appear.
	Tertiary	Pliocene	(5.33–1.80)	Herbaceous angiosperms flourish.	First hominids appear.
		Miocene	(23.03–5.33)	Grasslands spread as forests contract.	Apelike mammals and grazing mammals flourish; insects flourish.
		Oligocene	(33.9–23.03)	Many modern families of flowering plants evolve.	Browsing mammals and monkeylike primates appear.
		Eocene	(55.8–33.9)	Subtropical forests with heavy rainfall thrive.	All modern orders of mammals are represented.
		Paleocene	(65.5–55.8)	Flowering plants continue to diversify.	Primitive primates, herbivores, carnivores, and insectivores appear.
Mesozoic		**Mass Extinction: Dinosaurs and Most Reptiles**			
	Cretaceous		(145.5–65.5)	Flowering plants spread; conifers persist.	Placental mammals appear; modern insect groups appear.
	Jurassic		(199.6–145.5)	Flowering plants appear.	Dinosaurs flourish; birds appear.
		Mass Extinction			
	Triassic		(251–199.6)	Forests of conifers and cycads dominate.	First mammals appear; first dinosaurs appear; corals and molluscs dominate seas.
Paleozoic		**Mass Extinction**			
	Permian		(299–251)	Gymnosperms diversify.	Reptiles diversify; amphibians decline.
	Carboniferous		(359.2–299)	Age of great coal-forming forests; ferns, club mosses, and horsetails flourish.	Amphibians diversify; first reptiles appear; first great radiation of insects.
		Mass Extinction			
	Devonian		(416–359.2)	First seed plants appear. Seedless vascular plants diversify.	First insects and first amphibians appear on land.
	Silurian		(443.7–416)	Seedless vascular plants appear.	Jawed fishes diversify and dominate the seas.
		Mass Extinction			
	Ordovician		(488.3–443.7)	Nonvascular land plants appear on land.	First jawless and then jawed fishes appear.
	Cambrian		(542–488.3)	Marine algae flourish.	All invertebrate phyla present; first chordates appear.
Precambrian Time			630	Soft-bodied invertebrates	
			1,000	Protists diversify.	
			2,100	First eukaryotic cells	
			2,700	O_2 accumulates in atmosphere.	
			3,500	First prokaryotic cells	
			4,570	Earth forms.	

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a. b.

FIGURE 18.9 Ediacaran fossils.

The Ediacaran invertebrates lived from about 600–545 MYA. They were all flat, soft-bodied invertebrates. **a.** Classified as *Spriggina*, this bilateral organism had a crescent-shaped head and numerous segments tapering to a posterior end. **b.** Classified as *Dickinsonia*, these fossils are often interpreted to be segmented worms. However, in the opinion of some, they may be cnidarian polyps.

In 1946, R. C. Sprigg, a government geologist assessing abandoned lead mines in southern Australia, discovered the first remains of a remarkable biota that has taken its name from the region, the Ediacara Hills. Since then, similar fossils have been discovered on a number of other continents. Many of the fossils, dated 630–545 MYA, are thought to be of soft-bodied invertebrates (animals without a vertebral column) that most likely lived on mudflats in shallow marine waters. Some may have been mobile, but others were large, immobile, bizarre creatures resembling spoked wheels, corrugated ribbons, and lettucelike fronds. All were flat and probably had two tissue layers; few had any type of skeleton (Fig. 18.9). They apparently had no mouths; perhaps they absorbed nutrients from the sea or else had photosynthetic organisms living on their tissues. These soft-bodied animals could flourish because there were no predators to eat them. Their fossils are like footprints—impressions made in the sandy seafloor before their bodies decayed away. Whether the Ediacaran animals were simply a failed evolutionary experiment or whether they are related to animals of the Cambrian period is not known. With few exceptions they disappear from the fossil record at 545 MYA, but even so some may have given rise to modern cnidarians and related animals. What caused their demise is not known, but they very well could have been eaten by the myriad of animals with mouths that suddenly appear in the Cambrian.

Check Your Progress 18.2A

1. What sequence of events in Precambrian time led to heterotrophic protists and photosynthetic protists?
2. What additional event is needed before animals, fungi, and plants could arise?

The Paleozoic Era

The Paleozoic era lasted about 300 million years. Even though the era was quite short compared to the length of the Precambrian, many events occurred during this era, including three major mass extinctions (see Table 18.1). An **extinction** is the total disappearance of all the members of a species or higher taxonomic group. **Mass extinctions,** which are the disappearance of a large number of species or a higher taxonomic group within an interval of just a few million years, are discussed on page 333.

Cambrian Animals

The seas of the Cambrian period, which began at about 542 MYA, teemed with invertebrate life as illustrated in Figure 17B, pages 308–9. Life became so abundant that scientists refer to this period in Earth's history as the Cambrian explosion. All of today's groups of animals can trace their ancestry to this time, and perhaps earlier, according to new molecular clock data. A **molecular clock** is based on the principle that mutations in certain parts of the genome occur at a fixed rate and are not tied to natural selection. Therefore, the number of DNA base-pair differences tells how long two species have been evolving separately.

Even if certain of the animals in Figure 18.10 had evolved earlier, no fossil evidence of them occurs until the Cambrian period, perhaps because they lacked a skeleton. Animals that lived during the Cambrian possessed protective outer skeletons known as exoskeletons. These structures are capable of surviving the forces that are apt to destroy soft-bodied organisms. For example, Cambrian seafloors were dominated by now-extinct trilobites, which had thick, jointed armor covering them from head to tail. Trilobites are classified as arthropods, a major phylum of animals today. (Some Cambrian species, with most unusual eating and locomotion appendages, have been classified in phyla that no longer exist today.)

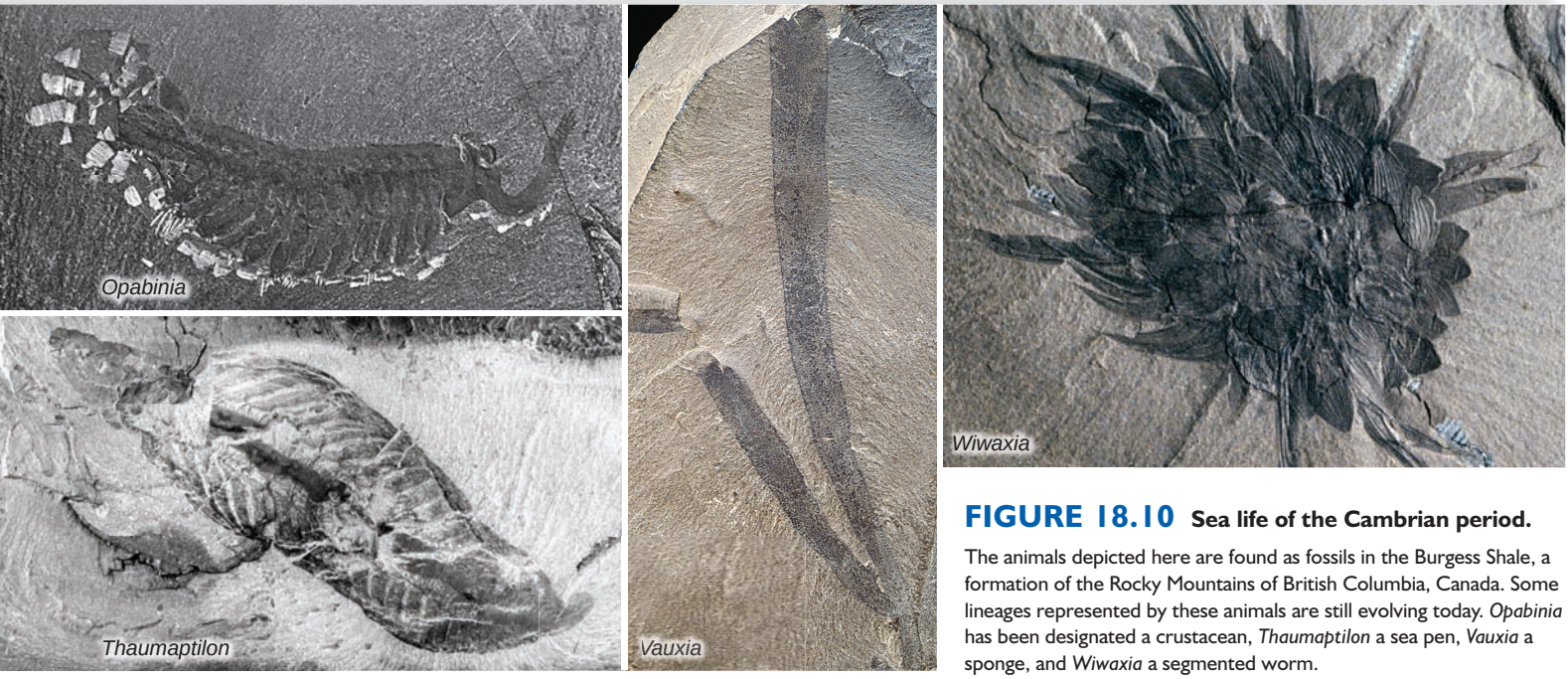

FIGURE 18.10 Sea life of the Cambrian period.

The animals depicted here are found as fossils in the Burgess Shale, a formation of the Rocky Mountains of British Columbia, Canada. Some lineages represented by these animals are still evolving today. *Opabinia* has been designated a crustacean, *Thaumaptilon* a sea pen, *Vauxia* a sponge, and *Wiwaxia* a segmented worm.

Paleontologists seek an explanation for why animals of the Cambrian period possessed exoskeletons and why this development did not occur during the Precambrian. By this time, not only cyanobacteria but also various algae, which are floating photosynthetic organisms, were pumping oxygen into the atmosphere at a rapid rate. Perhaps the oxygen supply became great enough to permit aquatic animals to acquire oxygen even though they had outer skeletons. The presence of a skeleton reduces possible access to oxygen in seawater. Steven Stanley of Johns Hopkins University suggests that predation may have played a role. Skeletons may have evolved during the Cambrian period because skeletons help protect animals from predators. If so, the evolutionary arms race came of age in the Cambrian seas.

Invasion of Land

Plants. During the Ordovician period, algae, which were abundant in the seas, most likely began to take up residence in bodies of fresh water. Eventually, algae invaded damp areas on land. The first land plants were nonvascular (did not possess water-conducting tissues) similar to the mosses and liverworts that survive today. The lack of water-conducting tissues limited the height of these plants to a few centimeters. Although the Ordovician evidence is scarce, spore fossils from this time support this hypothesis.

Fossils of seedless vascular plants (those having tissue for water and organic nutrient transport) date back to the Silurian period. They later flourished in the warm swamps of the Carboniferous period. Club mosses, horsetails, and seed ferns were the trees of that time, and they grew to enormous size. A wide variety of smaller ferns and fernlike plants formed an underbrush (Fig. 18.11).

Invertebrates. The jointed appendages and exoskeleton of arthropods are adaptive for living on land. Various arthropods—spiders, centipedes, mites, and millipedes—all preceded the appearance of insects on land. Insects enter the fossil record in the Carboniferous period. One fossil dragonfly from this period had a wingspan of nearly a meter. The evolution of wings provided advantages that allowed insects to radiate into the most diverse and abundant group of animals today. Flying provides a way to escape enemies, find food, and disperse to new territories.

Vertebrates. Vertebrates are animals with a vertebral column. The vertebrate line of descent began in the early Ordovician period with the evolution of jawless fishes. Jawed fishes appeared later in the Silurian period. Fishes are ectothermic (cold-blooded) aquatic vertebrates that have gills, scales, and fins. The cartilaginous and ray-finned fishes made their appearance in the Devonian period, which is called the Age of Fishes.

At this time, the seas were filled with giant predatory fish covered with protective armor made of external bone. Sharks cruised up deep, wide rivers, and smaller lobe-finned fishes lived at the river's edge in waters too shallow for large predators. Fleshy fins helped the small fishes push aside debris or hold their place in strong currents, and the fins may also have allowed these fishes to venture onto land and lay their eggs safely in inland pools. Much data tells us that lobe-finned fishes were ancestral to the amphibians and to modern-day lobe-finned fishes.

Amphibians are thin-skinned vertebrates that are not fully adapted to life on land, particularly because they must return to water to reproduce. The Carboniferous swamp forests provided the water they needed, and amphibians adaptively radiated into many different sizes and shapes. Some superficially resembled alligators and were covered with protective scales; others were small and snakelike; and a few were larger plant eaters. The largest measured 6 m

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