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KEY CONCEPTS

1. Living organisms are classified into three domains: Archaea, Bacteria, and Eukarya.
2. Land plants occur in the kingdom Plantae of the domain Eukarya and include a diverse group of organisms that impacts our lives in many economically and ecologically important ways.
3. All plants have an alternation of diploid and haploid generations although the structure of each generation differs in the various divisions.



CHAPTER

9

Diversity of Plant Life

With the overwhelming diversity of life on Earth, scientists have long sought to categorize these organisms into a meaningful system. For many years, organisms were classified as either plants or animals. As our knowledge increased, it became evident that many organisms could not be conveniently classified as either. Other kingdoms have been suggested to solve the problems with the two-kingdom system. One system proposed by Robert Whittaker in 1969 classified organisms into five kingdoms: Animalia, Plantae, Fungi, Protista, and Monera. In this system, the kingdom Monera contained organisms with prokaryotic cells while the other four kingdoms had eukaryotic cells. Recall that a prokaryotic cell lacks a nucleus and membrane-bound organelles that occur in eukaryotes. Research during the 1970s and 1980s changed the scientific understanding about relationships among prokaryotic organisms; two distinctly different types of prokaryotic organisms were recognized. This research led to the current classification of living organisms into three domains. A domain is a taxonomic category above the rank of kingdom.

THE THREE-DOMAIN SYSTEM

In 1990 microbiologist Carl Woese proposed the reorganization of life into the domains **Eukarya**, **Archaea**, and **Bacteria** (Eubacteria). The domain Eukarya includes all the eukaryotic kingdoms while Archaea and Bacteria are prokaryotic domains. Although archaea look like bacteria, they represent a distinct evolutionary line.

The majority of prokaryotic organisms are in the domain Bacteria. The Archaea include methane producers as well as organisms that live in hot springs and environments with high salt content. It has been suggested that these extreme environments may be similar to conditions that existed during early Earth history. The two domains of prokaryotic organisms have differences in ribosomal RNA as well as several other molecular and biochemical characteristics. In fact for some of the molecular characteristics, archaea are similar to eukaryotic cells.

The domain Eukarya includes the kingdoms Protista, Plantae, Fungi, and Animalia although some researchers have suggested splitting the kingdom Protista into several smaller kingdoms. Organisms in the **kingdom Protista** consist of unicellular and simple multicellular organisms that can be plant-like, fungus-like, or animal-like. The remaining three kingdoms are all multicellular in organization and can be distinguished by their modes of nutrition. Members of the **kingdom Plantae** are land plants that are **autotrophic**, capable of manufacturing their own food through photosynthesis. The organisms in the **kingdoms Animalia** and **Fungi** cannot make their own food and rely on external sources of nutrition. They are, therefore, considered **heterotrophic**. Animals, from primitive sponges to highly evolved mammals, are **ingestive heterotrophs**, engulfing their food and digesting it internally. The fungi, from molds to mushrooms, are **absorptive heterotrophs**, secreting into their surroundings

enzymes that break down food, which is then absorbed. Although historically fungi were considered members of the plant kingdom, recent molecular evidence suggests a closer evolutionary relationship between fungi and animals.

Organisms that were once regarded as plants in the old two-kingdom system now are included in three eukaryotic kingdoms and the domain Bacteria. In particular, the algae and fungi are not included in the kingdom Plantae. The algae consist of a diverse grouping of photosynthetic organisms that have been classified according to pigment types, storage products, and ultrastructural features. They range from prokaryotic microscopic forms to giant kelps and can be found in marine and freshwater habitats where they form the base of the food chains. The cyanobacteria, which were previously known as bluegreen algae, are in the domain Bacteria, and all the other groups of algae are in the kingdom Protista of the Eukarya. The algae will be discussed in detail in Chapter 22. Organisms traditionally called fungi are also included in two kingdoms. In the kingdom Protista are several groups of funguslike organisms that evolved along separate evolutionary pathways. The majority of fungi are classified in the kingdom Fungi. The fungi will be covered in Chapters 23–25.

SURVEY OF THE PLANT KINGDOM

The kingdom Plantae includes a diverse group of complex photosynthetic organisms ranging from mosses to flowering plants. Recall from Chapter 8 that large groupings of similar organisms are called divisions (or phyla). This kingdom includes 12 divisions of plants with living representatives; however, other groups are extinct and known only from the fossil record. These 12 divisions are often referred to as land plants to distinguish them from the algae. One of the features of all land plants is the retention of the embryo. After fertilization, the zygote develops into a multicellular embryo while still enclosed in the female gametangium (reproductive structure). Land plants are often called **embrophytes** to reflect this trait although some algae are found on land (damp soil), none retain an embryo; therefore, the term *land plants* will be used only to refer to plants that retain an embryo.

The fossil record indicates that land plants first evolved about 400 million years ago. Evidence from biochemistry, ultrastructure, and molecular biology indicates that these plants evolved from freshwater green algae along a common evolutionary path (fig. 9.1). The 12 divisions of land plants can be easily distinguished from each other by various traits. Plants in the divisions Bryophyta, Hepatophyta, and Anthoceroophyta lack vascular tissue while the other nine divisions contain both xylem and phloem (table 9.1). Although all land plants produce spores and gametes at different stages of their life cycles, five divisions of plants also produce seeds. Recall from Chapter 6 that seeds *contain an embryo* and a food supply enclosed by a seed coat. Lastly, members of one division of seed plants, the Magnoliophyta, produce flowers. The life cycles of organisms in several of these divisions are described in A Closer Look 9.1—Alternation of Generations.

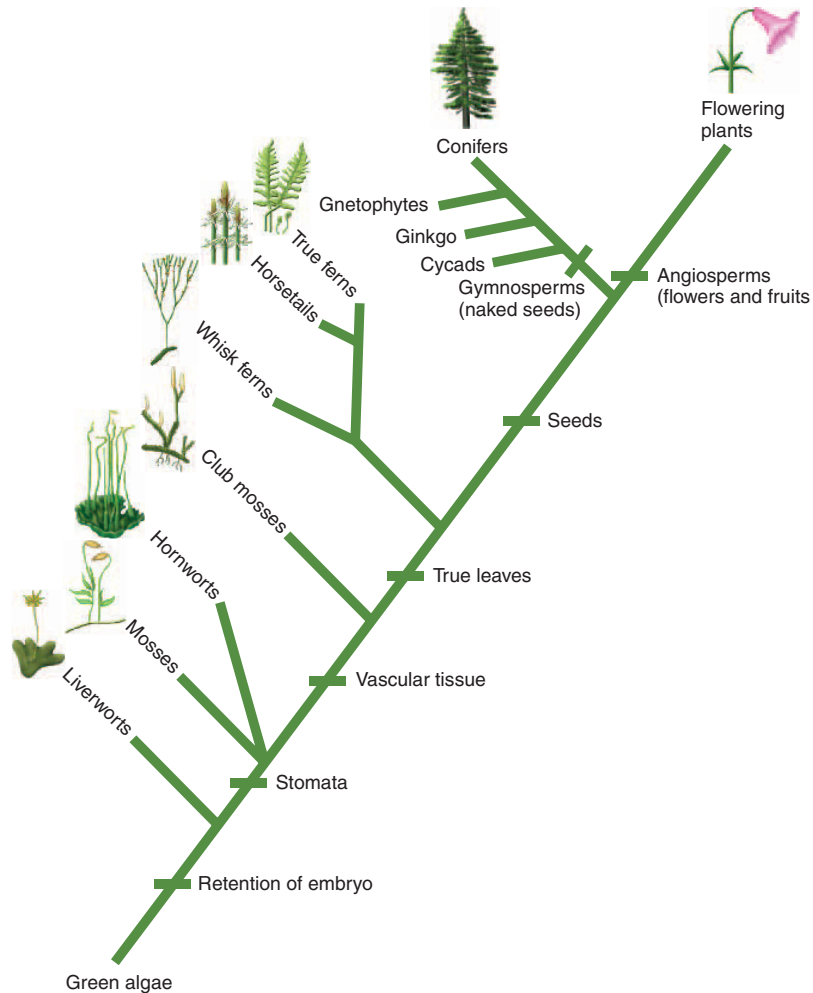


Figure 9.1 Phylogenetic diagram showing the possible relationships among the major groups in the Plant Kingdom. The groups can be distinguished from each other by various traits.



Table 9.1
Divisions in the Plant Kingdom

Division	Common Name	Vascular Tissue	Reproduction
Bryophyta	Mosses	Absent	No seeds
Hepatophyta	Liverworts	Absent	No seeds
Anthocerophyta	Hornworts	Absent	No seeds
Lycophyta	Club mosses	Present	No seeds
Psilophyta	Whisk ferns	Present	No seeds
Sphenophyta	Horsetails	Present	No seeds
Pterophyta	Ferns	Present	No seeds
Cycadophyta	Cycads	Present	Naked seeds
Ginkgophyta	Ginkgo	Present	Naked seeds
Coniferophyta	Conifers	Present	Naked seeds
Gnetophyta	Gnetophytes	Present	Naked seeds
Magnoliophyta	Flowering plants	Present	Seeds in a fruit

A CLOSER LOOK 9.1

Alternation of Generations

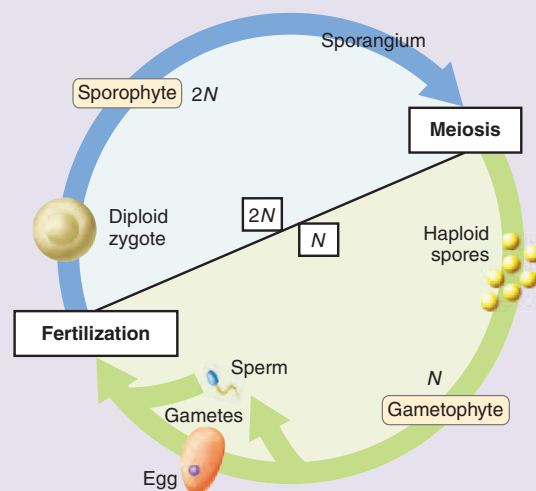
One characteristic of plants is a life cycle with an alternation of haploid and diploid generations. Each cell in the diploid generation has two sets of chromosomes while the cells in the haploid generation have only one set. The haploid generation is called the gametophyte because it gives rise to gametes; the sporophyte, which produces spores, is the diploid generation. The links between the two generations are the processes of fertilization and meiosis. During fertilization, haploid gametes fuse to form a diploid zygote, which develops into the sporophyte. In time, the diploid sporophyte undergoes meiosis to produce haploid spores, which begin the gametophyte generation (box fig. 9.1a). The prominence of each generation is variable among the different divisions. For example, the gametophyte is highly reduced and dependent on the sporophyte in angiosperms, but in some nonflowering plants the gametophyte generation may be prominent and often independent.

One division in which the gametophyte is conspicuous is the Bryophyta, the mosses. In fact, in this group the gametophyte is the dominant form; the mossy carpet often seen growing on a rock or tree trunk consists of gametophytes. At certain times of the year the moss undergoes sexual reproduction, resulting in a sporophyte that is attached to and dependent on the gametophyte. The gametophytes of mosses are usually either male or female. The male gametophyte develops structures known as **antheridia** (sing., **antheridium**) where the sperm form. The female gametophyte produces flask-shaped **archegonia** (sing., **archegonium**); each contains a single egg cell. When mature, the flagellated sperm will leave the antheridium and, if sufficient moisture is present, will swim to the archegonium of a female gametophyte. The sperm will fertilize the egg, forming a zygote, which establishes the diploid sporophyte. The sporophyte consists of a stalk and a **capsule**; the stalk is embedded in the female gametophyte and receives both water and nutrients from it (box fig. 9.1b.2). Within the capsule meiosis occurs, generating haploid spores. If the spores released from the capsule land on a suitable environment, each will germinate into a threadlike structure called a protonema. From the protonema the mature moss gametophyte develops. The moss life cycle is shown in Box Figure 9.1b.1; similar life cycles exist for liverworts and hornworts.

The lower vascular plants in the divisions Lycopphyta, Sphenophyta, Psilophyta, and Pterophyta all share a similar life cycle, with a dominant sporophyte and a small but free-living gametophyte. The ferns will be used as a model for this group (box fig. 9.1c). Unlike the mosses, it is the sporophyte stage of ferns that is the dominant form. In the fern sporophyte, sporangia generally form on the underside

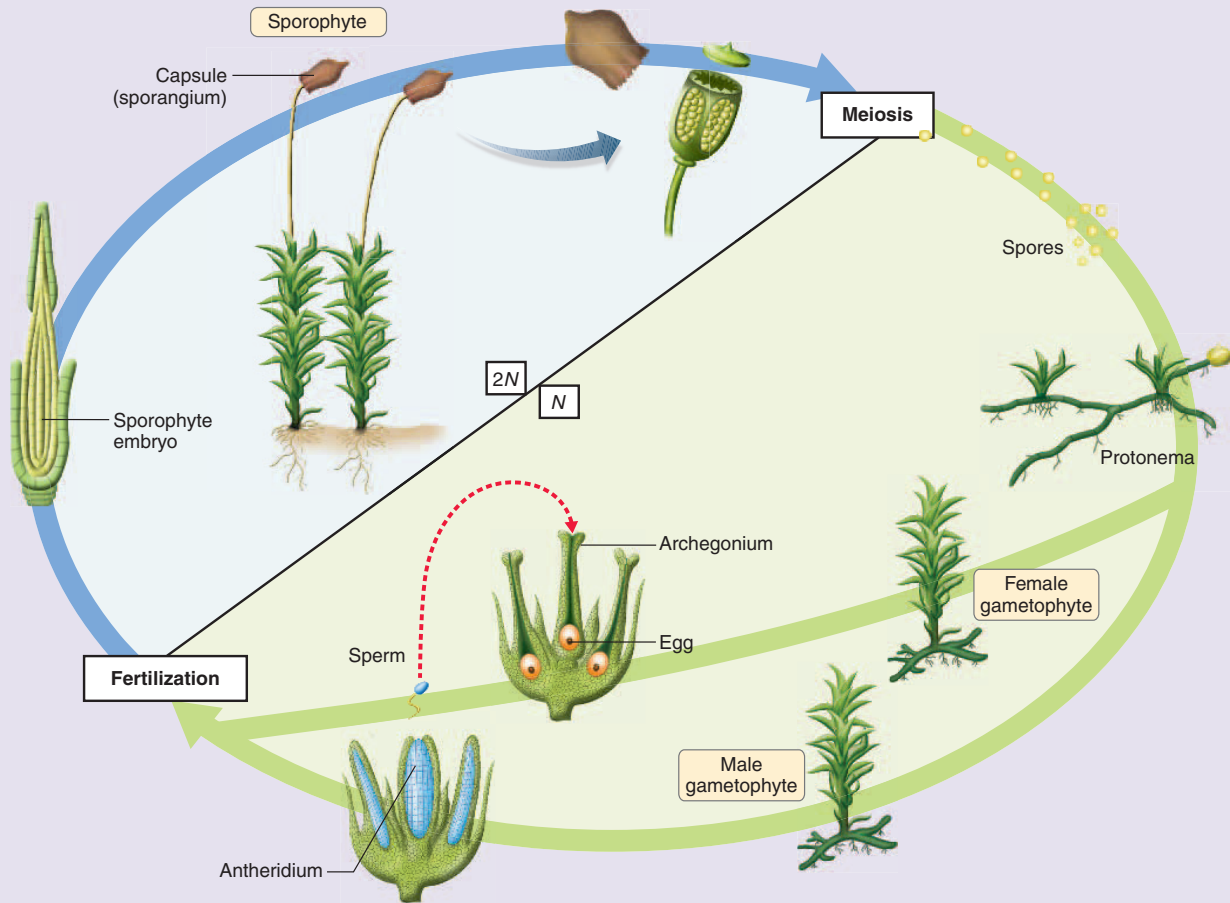
of the leafy frond. Sporangia are often clustered into **sori** (sing., **sorus**), which are visible with the naked eye; meiosis occurs in these sporangia, producing haploid spores. In a hospitable environment, spores give rise to small, flat, often heart-shaped gametophytes that bear both archegonia and antheridia. Flagellated sperm from the antheridia swim to the archegonia, fertilizing the eggs; however, only one sporophyte will emerge from each gametophyte. Although initially attached to the gametophyte, the sporophyte soon grows and becomes independent while the gametophyte dies.

Like the angiosperms (see Chapter 5), the gymnosperms have an extremely reduced, dependent gametophyte generation, with the sporophyte generation being the dominant and familiar form. A pine in the division Coniferophyta will be used as an example of the gymnosperm life cycle (box fig. 9.1d). The characteristic pollen and seed cones are the reproductive structures of a pine. The pollen cone consists of sporophylls, which are modified leaves that bear microsporangia; two occur on each sporophyll. Microspores are produced in these microsporangia. The microspore develops into the pollen grain that constitutes the male gametophyte generation. At the time the pollen grain is released from the cone, it consists of four cells: two body cells, one generative cell, and one tube cell. Pines are wind pollinated; air bladders in the walls of the pollen grain contribute to their buoyancy. The pollen grains are carried to the seed cone where they



(a)

Box Figure 9.1 (a) Alternation of generations. Plants display an alternation of haploid and diploid phases in their life cycles.



(b.1)



(b.2)

Box Figure 9.1 Continued (b.1) Moss life cycle; (b.2) Moss sporophytes;

are trapped by a sticky fluid. The pollen grain germinates with the tube cell, producing a pollen tube that will eventually carry nonflagellated sperm to the egg.

The seed cone is larger and more complex structurally than the pollen cone. Ovules develop on the upper surface of cone scales, which are arranged around a central axis. Normally, two ovules are borne on each cone scale. Recall from the life cycle of angiosperms that the ovule is a megasporangium surrounded by integuments, with an opening, the micropyle, facing the central axis. Meiosis produces four megaspores within each ovule, but three degenerate. The one surviving megaspore develops into the female gametophyte. At maturity the female gametophyte usually contains two archegonia, each with a single egg. While the female gametophyte is developing, the pollen tube is slowly growing through the surrounding tissues. During this time the generative cell within the pollen tube divides to form two sperm. Although both nonmotile sperm are carried to the archegonium, only one sperm fertilizes the egg, giving rise to the new sporophyte generation. Within the ovule only one embryo is produced, with the female gametophyte as its nutrient tissue. As the fertilized ovule develops into the seed,

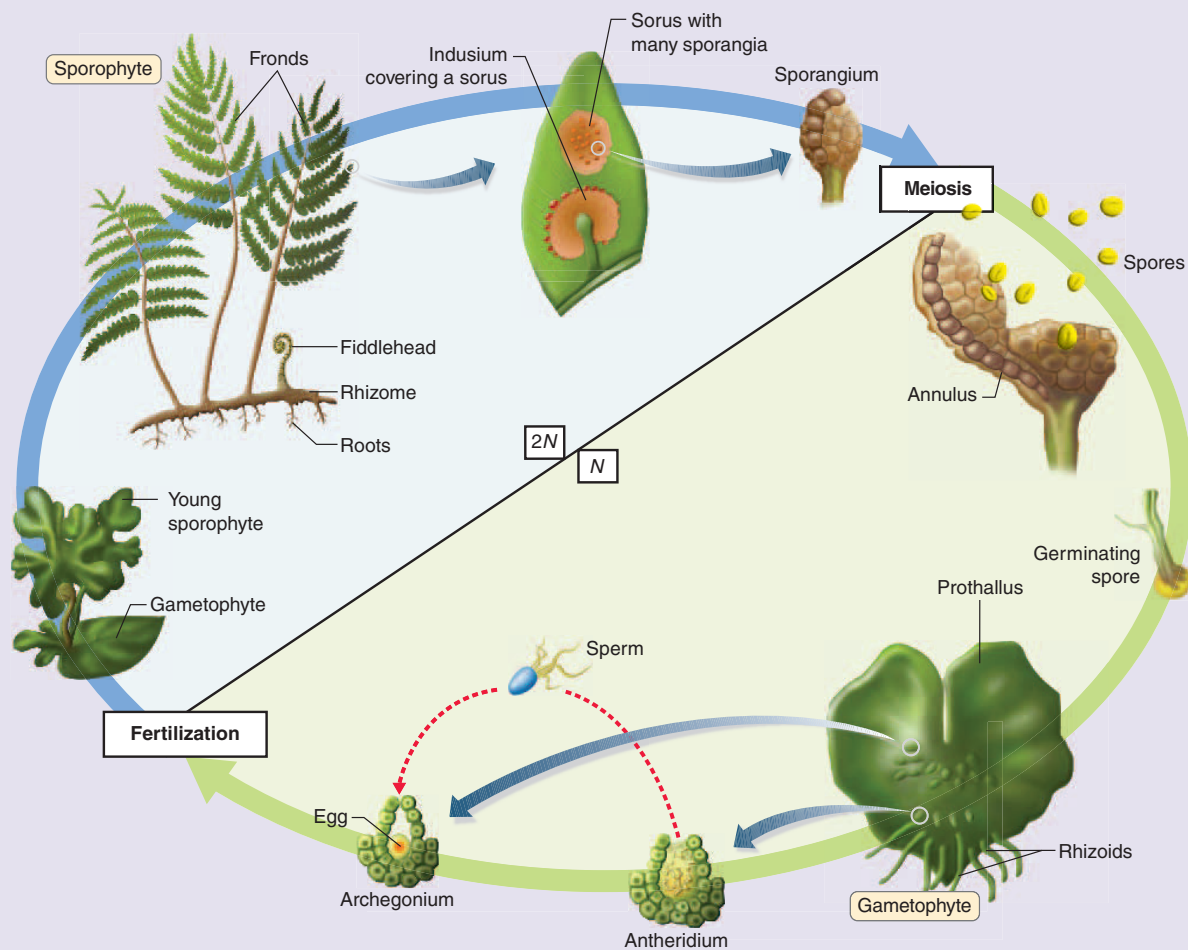
the integuments develop into the seed coat. When the seeds are mature, the seed cone opens and sheds the seeds, which are wind dispersed.

The three life cycles described here illustrate the variation of the basic alternation of a haploid generation with a diploid generation found in the plant kingdom. Other types of life cycles can be found in the algae (see Chapter 22) and the fungi (see Chapter 23).

Concept Quiz

In the majority of land plants, the sporophyte is the dominant stage while the gametophyte is reduced, becoming completely dependent upon the diploid phase in the most advanced divisions.

Suggest a reason why natural selection favored the dominance of the diploid sporophyte over the gametophyte.



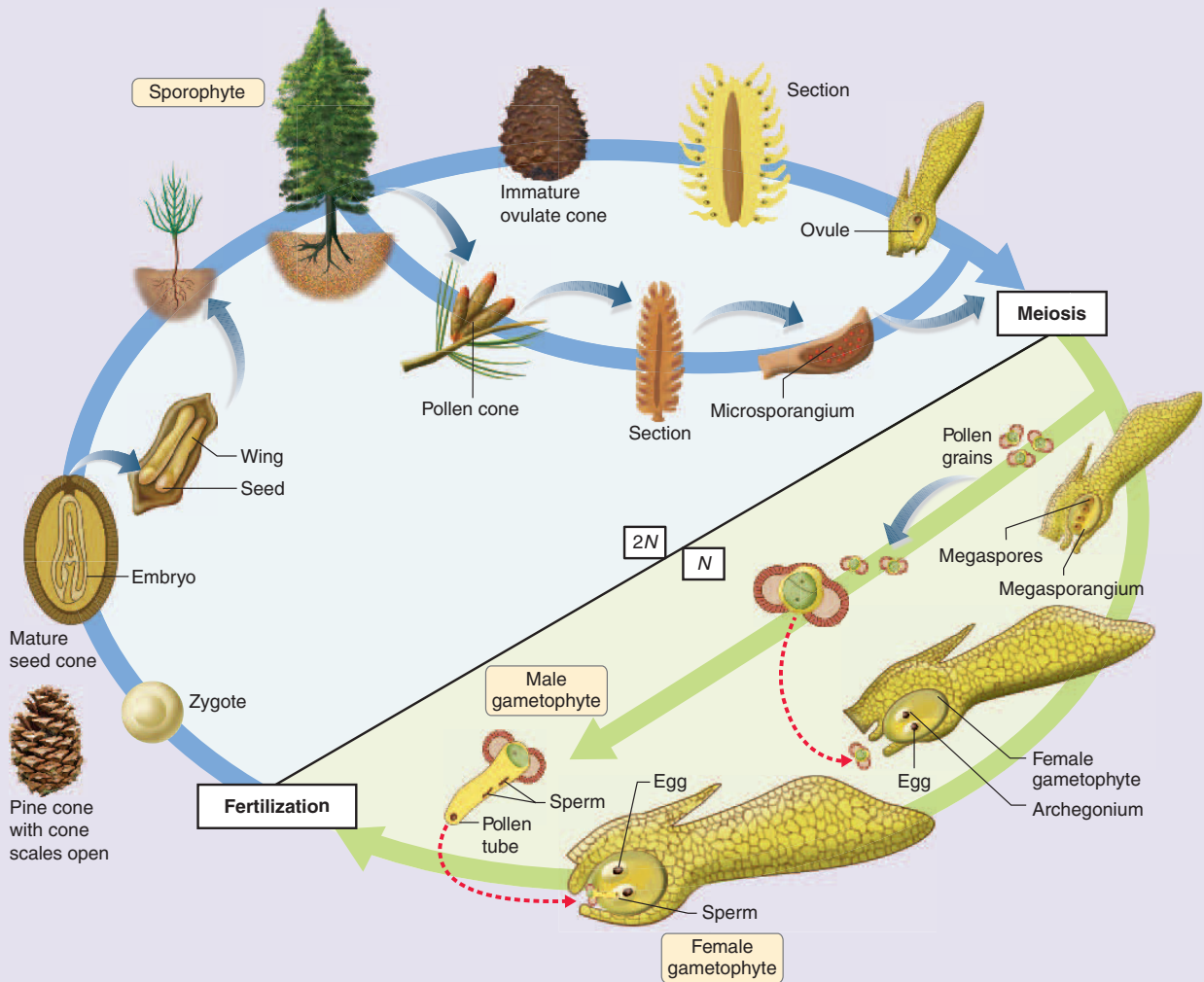
(c)

Box Figure 9.1 Continued (c) Fern life cycle;

Mosses, Liverworts, and Hornworts

The first land plants to be considered are the mosses, liverworts, and hornworts. Traditionally these plants had been grouped together in a single division. However, distinct differences in these three groups have led to their reclassification into three separate divisions: the **Bryophyta** (mosses), the **Hepatophyta** (liverworts), and the **Anthocerotophyta**

(hornworts). Today the term *bryophyte* is still used as a collective term to refer to plants in any or all of these divisions. Bryophytes are small plants generally restricted to moist environments although many bryophytes can withstand extended dry periods. It is estimated that there are about 25,000 species of bryophytes. The mosses have small appendages, appearing somewhat similar to leaves; the

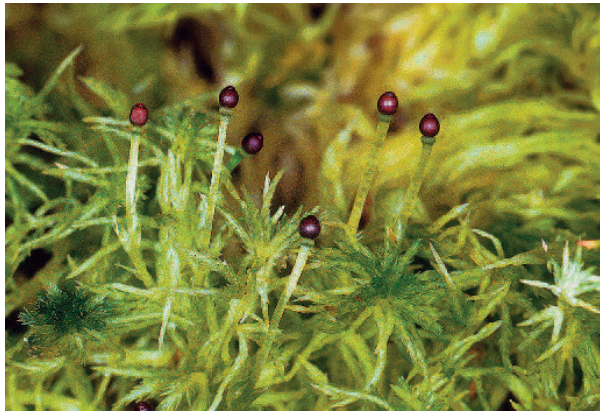


(d)

Box Figure 9.1 Continued (d) Pine life cycle.

liverworts are either leafy or flat and ribbonlike; and the hornworts have a flattened and somewhat lobed appearance (Fig. 9.2). The presence of stomata in the sporophyte distinguishes mosses and hornworts from liverworts. A distinctive feature found in hornworts is a meristem near the base of the sporophyte that permits continued growth of the sporophyte under favorable conditions.

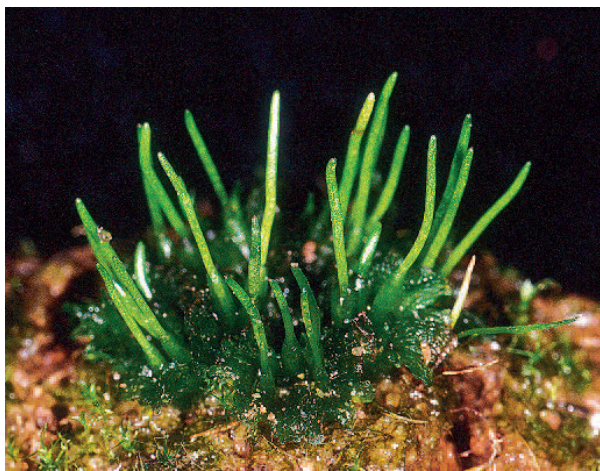
The well-known peat moss, *Sphagnum*, is unusual because it grows in acid water, making the water even more acidic and often converting the pond into a bog. The acidity restricts the growth of other plants and prevents the growth of microorganisms that cause decay. This creates a perfect environment for preservation. Important archeological finds have been made in peat bogs; several 2,000-year-old fully clothed



(a)



(b)



(c)



(d)

Figure 9.2 Bryophytes include mosses, liverworts, and hornworts: (a) *Sphagnum* moss with gametophytes. (b) *Marchantia*. Gametes are produced in the umbrella-like structures shown arising from the flattened liverwort. (c) Hornwort, *Anthoceros*. (d) *Sphagnum* moss. A peat bog being drained and peat harvested.

bodies have been found in bogs in Denmark. In addition, the 7,000-year-old skeletal remains of American Indians were recently found in Florida. Although most of the flesh was decayed, many of the brains were preserved. Scientists are hoping to examine the DNA from this tissue to see if major genetic changes have taken place over the past 7,000 years.

There are several economic uses for *Sphagnum* as well. Dried peat moss is commonly used as a potting and bedding material by gardeners, since it has a great water-holding capacity. For centuries, the peat bogs of northern Europe, especially those in Ireland, have been the source of a home heating fuel. The peat from these bogs, which is partially decomposed *Sphagnum*, is harvested, dried (fig. 9.2d), and burned in large quantities. As late as World War I, *Sphagnum* also was used as a dressing for wounds because of its anti-septic properties. In contrast, most other bryophytes are of limited economic importance.

Fern-Allies and Ferns

The remaining divisions in the plant kingdom are all **vascular plants**; i.e., they all contain **vascular tissues** that conduct both water and food throughout the plant body. The evolution of vascular tissue allowed the establishment of land plants in areas where freestanding water was limited. The first four divisions of vascular plants are nonseed plants and include the **ferns** and **fern-allies**.

The **club mosses** make up the division **Lycophyta**. Today these plants range from small prostrate forms commonly found on the forest floor to larger epiphytic forms in the tropics. (**Epiphytes** are plants hanging from other larger forms of vegetation.) Superficially these plants resemble mosses because their stems are covered with small overlapping scalelike leaves; however, they are not mosses, but vascular plants with conducting tissue occurring in the roots, stems, and leaves. Two to three hundred million years ago there were treelike species of

lycophods that formed extensive forests. These prehistoric forests are the basis for many of our coal deposits today (fig. 9.3).

In many species of *Lycopodium*, a member of the division Lycophyta, the sporangia are arranged in compact clusters at the ends of erect or hanging stems. The clusters of sporangia often have a clublike appearance (fig. 9.4a). Creeping jenny and ground pine are two well-known club mosses often used in Christmas wreaths. In the early days of photography, *Lycopodium* spores were the original flash powder. *Lycopodium* powder was also used in the past as a type of talcum powder, as a coating for pills, to stop bleeding from wounds, and for other medicinal purposes. Another common plant in this division is the resurrection plant, *Selaginella lepidophylla*, a native of arid regions, which appears as a dried brown clump when water is scarce yet quickly becomes green and photosynthetic when water is available. This plant is often sold as a novelty in shops.

Today the division **Sphenophyta** contains only one genus, *Equisetum*, the **horsetails**. These plants have ribbed, jointed, photosynthetic stems with whorls of tiny leaves that soon become brown and nonphotosynthetic. Sporangia are grouped into conelike structures at the tips of some stems. Although most horsetails are small, some species may be tall, 2 meters (6 feet) or more, but have very slender stems (fig. 9.4b). As in the division Lycophyta, tree-sized species existed 2 to 3 hundred million years ago and also contributed to coal deposits that are mined today. One interesting feature of the horsetails is the presence of silica in their cell walls. The silica in the walls makes the stems abrasive, and for this reason, pioneers in North America used these plants



Figure 9.3 *Lepidodendron* (left) and *Calamites* (right) fossils. These tree-sized plants were often important components of the Carboniferous Period (360 to 286 million years ago) forests. Modern descendants of *Lepidodendron* include the club mosses, and descendants of *Calamites* are horsetails. *Lepidodendron* fossils are characterized by diamond-shaped leaf scars while *Calamites* fossils are recognized by ribbed, jointed stems similar to modern horsetails.



(a)



(b)

Figure 9.4 Fern-allies. (a) *Lycopodium*, a club moss. (b) *Equisetum*, the only living genus in the Sphenophyta.

as a primitive scouring pad to clean pots and pans. People in developing nations still use them for this purpose. This feature explains another common name for these organisms—the scouring rushes. Musicians also use the scouring rushes to sand the reeds on wind instruments.

The whisk ferns in the division **Psilophyta** are a small group of primitive-looking vascular plants with only two genera. *Psilotum* consists of green branching stems with tiny scalelike appendages and globose yellow sporangia (sing., sporangium), structures in which spores develop (fig 9.5). Traditionally, many botanists considered these plants related to the earliest vascular land plants that existed over 400 million years ago; however, no fossil evidence supports this link. Other botanists believed that these plants were related to primitive ferns. Recent molecular evidence supports this latter view and shows that whisk ferns, horsetails, and ferns are a closely related group of organisms that evolved along a single evolutionary path, as shown in Figure 9.1. In addition, electron microscopy of *Psilotum* sperm cells shows that these plants are related to the ferns and horsetails.

The ferns, division **Pterophyta**, are the largest group of nonseed vascular plants (fig. 9.6). Ferns range from small aquatic types less than 1.25 cm (0.5 inch) in size to large tropical tree ferns that grow to 20 meters (60 feet) in height. The ferns that we are most familiar with, from temperate forests and as houseplants, have large divided leaves called fronds that arise from a horizontal underground stem, a **rhizome**, which also gives rise to roots. The sporangia of some ferns are borne on the underside of the fronds; the distribution of sporangia on the frond is a characteristic that can be used as an aid in identification. Young fern leaves first appear as tightly coiled fiddleheads, which gradually unroll as they grow. The fiddleheads of some ferns are considered a gourmet delicacy. Although there are about 12,000 species of ferns in the world today, the ferns were more abundant during past geological times and contributed to our coal deposits.



Figure 9.5 Branching stems of *Psilotum* showing numerous sporangia.



(a)



(b)



(c)

Figure 9.6 Ferns. (a) Fiddleheads unrolling in springtime. (b) *Dryopteris* sp., wood fern, growing in a cloister garden. (c) Sporangia are grouped into sori on the underside of this fern frond.

Gymnosperms

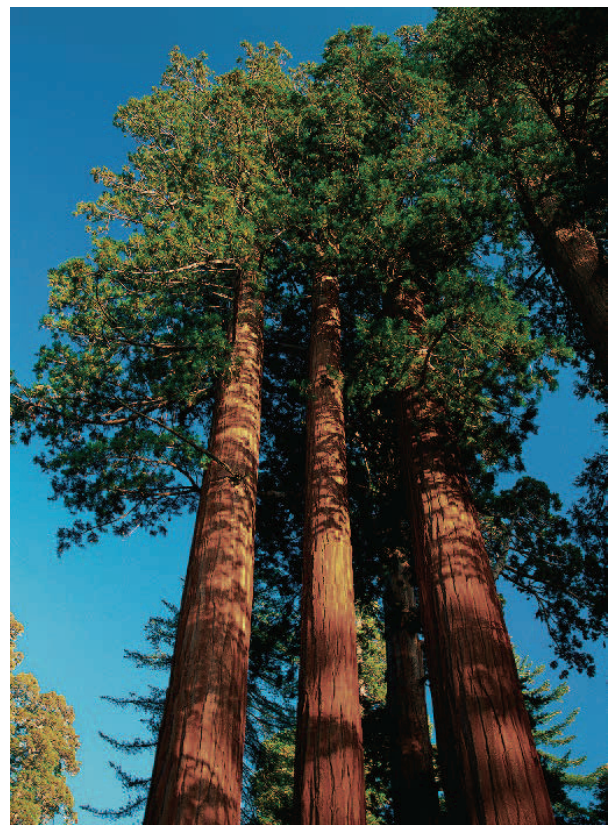
The remaining five divisions in the plant kingdom are all **seed plants**. The seed plants are the dominant vegetation in the world. Recall that a seed contains a small embryonic plant with a food supply encased in a tough protective coat. Seeds are found in either cones or fruits. In cones, the seeds are exposed at maturity and said to be “naked.” Plants with naked seeds are called **gymnosperms** while plants with seeds enclosed or hidden within fruits are called **angiosperms**.

There are four divisions of gymnosperms: **Coniferophyta**, **Cycadophyta**, **Ginkgophyta**, and **Gnetophyta**. **Conifers**, members of the Coniferophyta, are the most familiar gymnosperms and include pines, spruces, yews, firs, cedars, redwoods, and larches. The largest, tallest, and oldest trees in the world are all conifers (fig. 9.7). Conifers are cone bearers, typically producing both pollen and seed cones. The pollen cones are usually small and inconspicuous and produce pollen while the seed cones, which produce seeds, are larger and often take several years to mature (fig. 9.8). The pollen and seed cones may be on the same or different trees.

The conifers, like all gymnosperms, are an ancient group of plants that reached their greatest diversity during past geological periods. Periodically, scientists have discovered certain gymnosperm species alive that have previously been known only from the fossil record. The most recent discovery of a “living fossil” is the Wollemi pine (*Wollemia nobilis*). Forty specimens of this tree were discovered in August 1994 in a secluded rain forest gully of Wollemi National Park about 200 kilometers (125 miles) west of Sydney, Australia. Wollemi pines have been classified in the family Araucariaceae along with Norfolk Island pines, but their closest relatives are fossils from the Jurassic Period (200–136 million years ago) and the Cretaceous Period (136–65 million years ago). Although the oldest trees in the stand at Wollemi National Park are only about 150 years old, the survival of this species is considered remarkable and may be one of the most significant botanical discoveries of the twentieth century. It has been described as equivalent to finding a small dinosaur alive. Intense study of these trees is under way. The National Parks and Wildlife Service in Australia has been



(a)



(b)

Figure 9.7 (a) Bristlecone pine, *Pinus longaeva*. Individual trees of this species may live 3,000 to 5,000 years, making them the oldest living trees. (b) Giant sequoias, *Sequoiadendron giganteum*. As a group, the giant sequoias are considered the world’s largest (most massive) trees. The largest on record is the currently the General Sherman tree, which is reported to be 83.8 m (274.9 feet) tall with a circumference of 31.3 m (102.6 feet).

carefully protecting the grove of trees from tourists and is also working on efforts to propagate the species and establish other populations. Someday you may be able to plant a Wollemi pine in your yard.

The conifers are the dominant trees in the northernmost forests of the world. They are important sources of lumber, paper pulp, and products such as turpentine, rosin, and pitch (see Chapter 18 and A Closer Look 9.2—Amber: A Glimpse into the Past). Although conifers are not usually considered as food, pine nuts, seeds of the pinyon pine, are enjoyed by many. Also, some types of cedar, *Juniperus* spp., are essential in the production of gin, a popular alcoholic beverage. The seed cones of these cedars are unusual because they are small and fleshy, resembling waxy blue berries (fig. 9.8b). These “berries” impart the flavoring to gin. Next time you see a *Juniperus*, pick a few “berries,” crush them, and sniff the aroma of gin. *Taxus* species, commonly called yews, are noted as the source of taxol used in cancer chemotherapy (see Chapter 19) and also the source of poisonous alkaloids (see Chapter 21).

The **cycads** (Cycadophyta) are a small group of short shrubs to moderate-sized, long-lived trees native to tropical and subtropical regions. These trees are often mistaken for palms because the leaves are large and palmlike (fig. 9.9a). The sago palm, a cycad commonly used for landscaping in subtropical to tropical climates, is also a popular houseplant. Like the conifers, most cycads bear cones. The seed cones of certain species can be quite large; some weigh up to 100 pounds (45.36 kilograms)! Cycads are dioecious, with seed cones and pollen cones on separate individuals. Whereas the conifers are wind pollinated, recent research has shown that cycads are pollinated by weevils and beetles. Some botanists believe that cycads may be the earliest insect-pollinated plants.

Today the cycads are mere remnants of plants that were the dominant features of the Mesozoic landscape. Although the Mesozoic Era (240–65 million years ago) is usually known as the Age of Dinosaurs, botanists consider this time the Age of Cycads. A real Jurassic Park would have had cycad forests. Only about 250 species of cycads in 11 genera are found today, with the greatest number of species occurring in the Southern Hemisphere. Many species are threatened with extinction because they live in tropical forests, which are endangered habitats, while other species are threatened by extensive collecting. Cycad breeding programs are under way at botanical gardens in various parts of the world to preserve these primitive seed plants.

Cycads are rich in starch, which is found in the roots, stems, and seeds, and they have a long history as a food source as well as a medicinal plant. However, cycads contain toxic compounds, which must be removed by processing the starch before the flour is used. Cycasin and BMAA (beta-methylamino-alanine) are distinct toxins found in cycads. Cycasin is a carcinogenic and neurotoxic glycoside;



(a)



(b)

Figure 9.8 (a) Seed cone of *Pinus monticola*, western white pine. (b) Seed cones of *Juniperus ashei*, mountain cedar. The small, berrylike cones of *Juniperus* are a sharp contrast to the seed cones of *Pinus*.



(a)



(b)



(c)

Figure 9.9 (a) *Dioon edule*, a cycad growing in the Fairchild Tropical Gardens in Florida. (b) *Ginkgo biloba*, the maidenhair tree, branch with leaves, seeds shown in inset. (c) *Ephedra viridis*, a desert shrub.

BMAA is an unusual amino acid that is also neurotoxic. BMAA is believed to block the function of receptors that enable nerve cells to communicate with each other in the brain. Most detoxification methods focus on soaking the crushed seeds in water; soaking slowly dissolves the toxins out of the plant material over several days to weeks. The resulting paste is baked into breads. Toxins also occur in the leaves of many cycads, and these have caused poisonings in cattle and sheep grazing on the leaves.

Although gastrointestinal and liver problems can also occur, cycad toxins have been implicated in a number of neurological conditions, including Guam disease. Following World War II, physicians found that ALS (amyotrophic lateral sclerosis, which is also known as Lou Gehrig's disease) was about 100 times greater among members of the Chamorro tribe, the native population in Guam, than the rest of the world. Later studies found that the incidence of Parkinson's disease and Alzheimer's-like dementia were also much higher among the Chamorros. Although many scientists believed that the neurotoxins in cycads were at least partly responsible, it was only in 2003 that the proposed connection between the toxins and the neurological conditions was explained. Initially it was believed that the direct consumption of a tortilla-like cycad bread led to these conditions, but the concentration of toxin is low in cycad flour and probably would not be sufficient to cause the symptoms. A team of researchers led by Paul Cox and Sandra Banack suggested that biological magnification of the toxin may be the answer. Biological magnification is the increase in concentration of toxins as they are passed along a food chain (see Chapter 26).

The consumption of a type of bat, called a flying fox, by the Chamorro people may be a key link in the toxicity. Cycad seeds are a major food source for flying foxes, and the Chamorro people traditionally ate these animals boiled in coconut milk at weddings and other festive events. Following World War II, firearms became more widely available, and it became easier to hunt bats. As a result, the consumption of bats greatly increased. In fact hunting led to the extinction of one species of flying fox and the near extinction of the second species native to Guam. Chemical analysis of tissues collected from museum specimens of flying foxes showed levels of the BMAA toxins that were 100 times higher than levels in the cycad seeds.

Although the concentration of BMAA is highest in cycad reproductive structures, it also occurs at low levels in other parts of the plant. Normal roots lack the toxin; however, Cox and Banack found BMAA present in modified roots called coralloid roots. These short, wide, lateral roots grow at the soil surface and form a symbiotic relationship with cyanobacteria present within small cavities of the root. (**Symbiosis** is the intimate association of two species living together in a relationship that can be beneficial to one or both organisms.) Investigating further, the researchers found that when cultured alone, the cyanobacteria synthesized BMAA.



A CLOSER LOOK 9.2

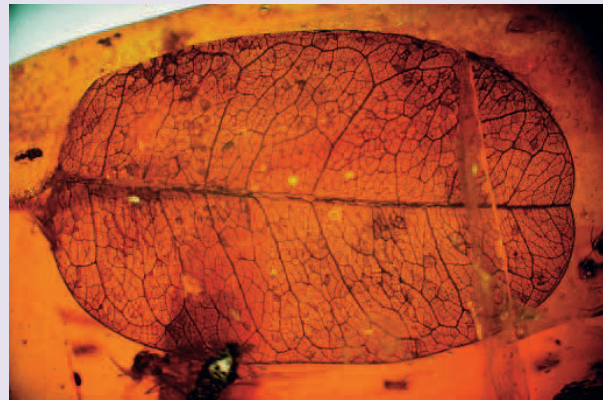
Amber: A Glimpse into the Past

Many economically useful products are derived from conifers; much of the lumber and paper industry is based on pine, spruce, and other coniferous species. Resin is another product that is usually obtained from conifers; it is the material often seen oozing from the trunk of a pine tree. Resins are sticky secretions that harden as they dry. Wounding a plant initiates the release of resins that promote healing by sealing off a wound against water loss, pathogens, and insects. Resins are best known as the source of turpentine and rosin (see Chapter 18).

If conditions are right and the resin is buried before it can oxidize, it fossilizes. Amber is fossilized tree resin. Translucent and typically golden-brown, amber has been valued as a semiprecious stone for millennia. Stone Age figurines of amber have been found in the Baltic area; they may have been talismans. Roman soldiers wore amber-studded armor for good luck, and the emperor Nero established trade routes with the Germanic tribes of the North to obtain it. The pinnacle of amber artistry was the famed Amber Room in the Catherine palace of Russia. A gift from the Prussian King Frederick Wilhelm I to the Russian Czar Peter the Great, the room was lined with intricately carved pieces of amber fitted together on wooden wall panels. The panels were disassembled and stolen by the Nazis during World War II. The reassembled panels were later put on display in Königsberg, Germany, but disappeared during the last days of the war. The fate of the panels remains a mystery.

Amber has been gathered for centuries on the shores of the Baltic Sea, an area well known for its rich deposits. As waves erode away the shoreline, amber is washed free

and can be found floating in the water. The largest amber-producing mines are located in the town of Palmnicken on the Baltic Sea. Approximately 30 million years ago, this area was subtropical in climate and had forests of conifers. The resins of these conifers are the source for the 700 tons of amber mined each year. Amber-rich beds are found 40 meters (120 feet) below the surface; as much as 4.05 kilograms per cubic meter (7.7 pounds per cubic yard) can be found. The earth is strip-mined to the amber beds; the sediments are then washed with water from huge pressurized hoses and the



Box Figure 9.2 Leaf of a tree in the legume family is preserved in amber from the Dominican Republic. An insect also trapped in the amber is visible near the bottom of the photo.

Putting all these pieces together, Cox and Banack suggest that the biological magnification of the BMAA starts with the toxin synthesis by cyanobacteria in the roots and continues with its accumulation in cycad seeds, its further accumulation in the tissues of the flying fox, and its final ingestion by the Chamorro people. The incidence of the neurological problems decreased following the population decline of the flying foxes on Guam. Today, different species of flying foxes are imported from other islands in the South Pacific for Chamorro consumption. Since cycads do not occur on these other islands, the toxin is no longer present in the Chamorro food chain.

Ginkgo biloba, the maidenhair tree, is the only living species of the Ginkgophyta. This species is another “living fossil” because it is the only remaining species of a larger group of plants that were abundant in the Mesozoic Era over much of the world. Examination of fossils indicates that

these plants have changed very little over millions of years. Although ginkgo became extinct over much of its range, it survived in China and has been cultivated for centuries, especially around Buddhist temple gardens and monasteries. It became known to Europeans in the eighteenth century and was first introduced into the United States in 1784. Today, ginkgo is a popular tree in city landscaping because it is air pollution tolerant and hardy. It is a moderate-sized tree with unique fan-shaped leaves that may or may not be notched in the middle (fig. 9.9b).

Ginkgo seeds are partially surrounded by a fleshy coat that smells like rancid butter when the seed is mature. Fortunately, ginkgo is dioecious, with separate male and female trees; therefore, efforts are made to screen for pollen-bearing trees before planting. However, the seed itself is considered a delicacy in China and other Asian countries. The seed, also called a ginkgo nut, is boiled or roasted and

amber is separated out. Only 13% of the amber is usable for jewelry; the rest is used in paint thinners, varnishes, and polishes.

There are other amber deposits in many parts of the world, dating from the late Carboniferous to the Pleistocene (300–1.5 million years ago). Some of the oldest amber hails from the central Appalachian region in the eastern United States. Amber from the Dominican Republic holds the record for the greatest number of inclusions, encasing insects, spiders, bits of wood, flowers, seeds and leaves (box fig. 9.2) and even feathers. For every 100 pieces of amber from the Dominican Republic, one piece contains an insect fossil; in Baltic amber, the ratio drops to a mere one in 1,000. Excavations in the 1990s of a large deposit of Cretaceous amber from New Jersey have been the source of several exciting finds. What was once an ancient marsh in coastal New Jersey and is now a sandy coastal pit is the site of charcoaled flowers so well preserved that petals, pollen grains, and even tiny ovules are discernible. More than 200 species of angiosperms have been identified, with many of the flowers related to modern-day hydrangeas, carnations, azaleas, pitcher plants, oaks, and the tropical mangosteen. The origin of flowering plants as well as many insect lineages dates back to the Cretaceous Period. In the New Jersey amber, 90-million-year-old flowers with scent glands and nectaries have been uncovered, which were obviously insect pollinated. The association between flowering plants and their insect pollinators extends further back in time than previously thought. This same Cretaceous amber field also yielded the oldest intact mushrooms ever found. An even older fossil of a coral fungus (related to mushrooms) was found in amber from Myanmar (Burma) in 2003. The reproductive structures were clearly visible in the amber, which is dated to the Cretaceous Period and is approximately 100 million years old. In 2006, scientists identified the oldest known bee preserved in amber also from Myanmar. This 100-million-year-old specimen is approximately 40 million years older than other bee fossils.

Recently, amber and the biological specimens trapped within have been the focus of much interest and controversy because of the possibility of extracting and deciphering the entrapped fossil DNA. Amber is especially good at preserving ancient DNA because the resin contains compounds that dry and fix living tissue and, at the same time, inhibit bacterial decomposition. Forty-million-year-old fungus gnats were so perfectly preserved in amber that organelles such as mitochondria, ribosomes, and cell membranes could be clearly seen in the abdominal cells. The first extraction of amber DNA was from a species of extinct bee. Since that first extraction, the genetic material of a 120-million-year-old weevil and that of a 30-million-year-old extinct species of termite have also been reported.

One problem with the technique is contamination with extant DNA. One research team thought they had isolated fossil DNA only to find out it was contaminated with the DNA from modern species. In fact, some scientists have questioned the authenticity of all of these fossil DNA finds. The method of extraction presents another problem. The amber is cracked and destroyed in order to scrape out the specimen's DNA. Less destructive methods are being investigated, such as drilling a tiny hole in which a small needle is inserted so that only a portion of the specimen is extracted and the amber is saved.

Once the DNA has been isolated, it can be sequenced to determine the base code. This information will be invaluable in tracing evolutionary lineages. It may even be possible to some day reconstruct long-extinct species from a deciphered genetic blueprint. The plot of the science fiction book and movie *Jurassic Park* is based on this possibility.

Right now reconstructing dinosaur DNA is only a remote possibility since the most successful isolation of amber-fossilized DNA has sequenced only 200 base pairs. Even a bacterium contains approximately 2 million base pairs, and humans have over 3 billion. Nevertheless, amber has opened the gateway to looking at fossil DNA and examining the evolutionary past of ancestral and fossil organisms.

included in both sweet and savory dishes. It is frequently included in meals served at Chinese weddings because it is a symbol of good luck. The seed has also been used medicinally to treat coughs, asthma, and other respiratory complaints. Today, extracts of ginkgo leaves are widely used as an herbal remedy to improve short-term memory and enhance concentration (Chapter 19).

The Gnetophyta is a very small group of gymnosperms with unusual morphological and anatomical features that have intrigued botanists for years. *Ephedra* is an economically important member of this group. This desert shrub produces the alkaloids ephedrine and pseudoephedrine, which are useful in the treatment of bronchial asthma, sinusitis, the common cold, and hay fever (fig. 9.9c). The medicinal uses of *Ephedra* are discussed in Chapter 19. Also the leaves of the tropical vine *Gnetum* are used as a vegetable in parts of central and west Africa. Traditionally the leaves were collected

from the wild, cut into strips, and cooked. Over exploitation of this resource has threatened the *Gnetum* populations in some tropical forests. Recently, the Limbe Botanical Garden in Cameroon has developed cultivation methods for two *Gnetum* species to insure future availability of this nutritious vegetable.

Concept Quiz

The discovery of the Wollemi pine emphasizes the value of national parks in the protection of natural habitats.

What are some of the other benefits of national parks?

Angiosperms

The last remaining division in the plant kingdom is the **Magnoliophyta**, the flowering plants, or angiosperms. The angiosperms constitute the most widespread vegetation on Earth today, ranging in form from small herbaceous plants to large trees. This division includes most of our familiar plants such as lawn grasses, crop plants, vegetables, weeds, and houseplants as well as oaks, elms, maples, and many other trees. Over 250,000 species of angiosperms have been described, and it has been suggested that as many as 1 million undescribed species may exist in tropical forests. In the previous eight chapters we focused on the anatomy, reproduction, and physiology of angiosperms. In the chapters that follow we shall see that most of our economically useful plants are, in fact, angiosperms.

CHAPTER SUMMARY

1. Currently biologists accept the three-domain system of classification. In this system, living organisms are classified as Archaea, Bacteria, and Eukarya.
2. The kingdom Plantae of the domain Eukarya contains land plants, which manufacture their own food through photosynthesis and retain a multicellular embryo within the female gametangium. All plants have an alternation of generations.
3. Some plants, such as mosses, hornworts, and liverworts, have a dominant gametophyte generation. These are small plants that are confined to moist environments since they have no vascular tissue.
4. All vascular plants have a dominant sporophyte. Four divisions of vascular plants do not form seeds. The ferns and fern-allies have a long fossil history, and in past geological ages they dominated the landscape.
5. The seed plants are currently the dominant vegetation in the world. Four divisions of seed plants are gymnosperms. Conifers are the most familiar gymnosperms and include the largest, tallest, and oldest trees in the world. Conifers are of great economic importance as the source of wood, pulp, and chemicals. The angiosperms constitute the most widespread and diverse vegetation today. They provide most of the food for life on the planet as well as economically useful products.

REVIEW QUESTIONS

1. How does the three-domain system compare to the two-kingdom and five-kingdom systems?
2. Organisms traditionally called plants are now assigned to other kingdoms. Describe which groups have been reassigned and why.

3. Describe the divisions of seed plants.
4. What are the basic features of the ferns and fern-allies? What is the economic impact of these groups, both living and fossil?
5. Describe the alternation of generations in vascular plants.
6. Define sporangium, archegonium, antheridium, sporophyte, and gametophyte.
7. Discuss the economic and ecological value of the gymnosperms.
8. Describe the uses of peat moss.
9. Compare the life cycle of a moss, a fern, a gymnosperm, and an angiosperm. What changes have taken place to the gametophyte generations in seed plants?

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