30

Plant Diversity II: The Evolution of Seed Plants

▲ **Figure 30.1 What human reproductive organ is functionally similar to this seed?**

EVOLUTION

KEY CONCEPTS

30.1 Seeds and pollen grains are key adaptations for life on land

30.2 Gymnosperms bear "naked" seeds, typically on cones

30.3 The reproductive adaptations of angiosperms include flowers and fruits

30.4 Human welfare depends greatly on seed plants

OVERVIEW

Transforming the World

Continuing the saga of how plants have transformed Earth, this chapter follows the emergence and diversification of seed plants. Fossils and comparative studies of living plants offer clues about the origin of seed plants some 360 million years ago. As this new group of plants became established, they dramatically altered the course of plant evolution. We'll begin our exploration of how this occurred by looking at the innovation for which seed plants are named: seeds (**Figure 30.1**).

A **seed** consists of an embryo and its food supply, surrounded by a protective coat. When mature, seeds are dispersed from their parent by wind or other means. Because it nourishes and protects the embryo, yet can move away from the mother plant, a seed is analogous to a detachable and mobile version of a pregnant woman's uterus. As we'll see, seeds are a key adaptation that helped seed plants to become the dominant producers on land and to make up the vast majority of plant biodiversity today.

Seed plants have also had an enormous impact on human society. Starting about 12,000 years ago, humans began to cultivate wheat, figs, maize (commonly called corn in the United States), rice, and other wild seed plants. This practice emerged independently in various parts of the world, including the Near East, East Asia, Africa, and the Americas. One piece of evidence, the well-preserved squash seed in Figure 30.1, was found in a cave in Mexico and dates from between 8,000 and 10,000 years ago. This seed differs from wild squash seeds, suggesting that squash was being domesticated by that time. The domestication of seed plants, particularly angiosperms, produced the most important cultural change in human history, transforming most human societies from roving bands of hunter-gatherers to permanent settlements anchored by agriculture.

In this chapter, we will first examine the general characteristics of seed plants. Then we will look at the distinguishing features and evolution of gymnosperms and angiosperms.

CONCEPT **30.1**

Seeds and pollen grains are key adaptations for life on land

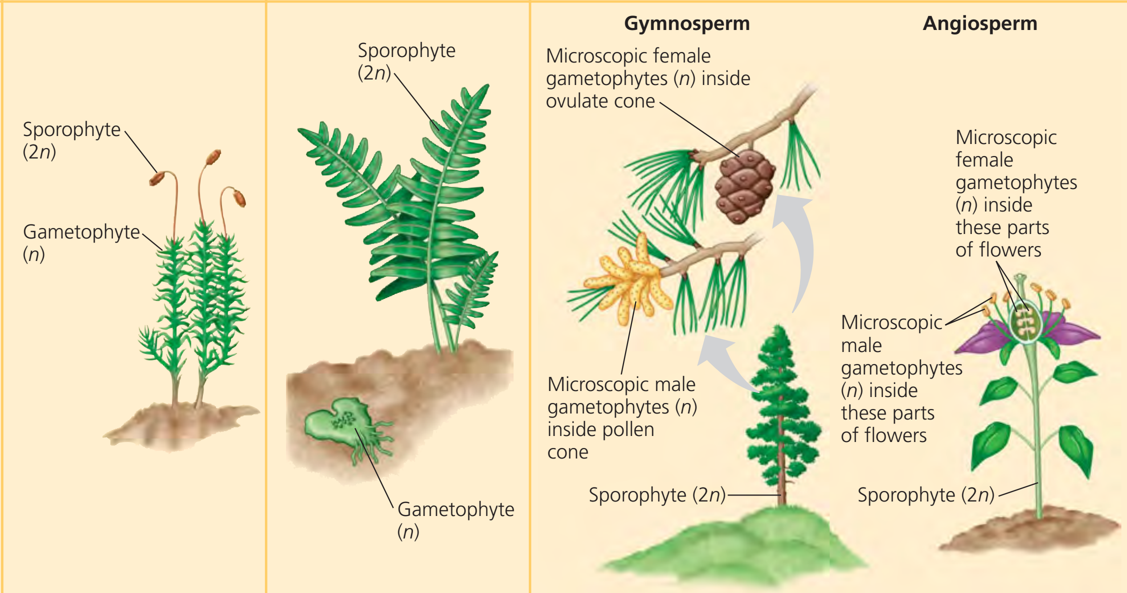
We begin with an overview of terrestrial adaptations that seed plants added to those already present in nonvascular plants (bryophytes) and seedless vascular plants (see Chapter 29). In addition to seeds, the following are common to all seed plants: reduced gametophytes, heterospory, ovules, and pollen. As you'll read, these adaptations provided new ways for seed plants to cope with terrestrial conditions such as drought and exposure to the ultraviolet (UV) radiation in sunlight. Novel adaptations also freed seed plants from requiring water for fertilization, enabling reproduction to occur under a broader range of conditions than in seedless plants.

Advantages of Reduced Gametophytes

Mosses and other bryophytes have life cycles dominated by gametophytes, whereas ferns and other seedless vascular plants have sporophyte-dominated life cycles. The evolutionary trend of gametophyte reduction continued further in the vascular plant lineage that led to seed plants. While the gametophytes

	PLANT GROUP		
	Mosses and other nonvascular plants	Ferns and other seedless vascular plants	Seed plants (gymnosperms and angiosperms)
Gametophyte	Dominant	Reduced, independent (photosynthetic and free-living)	Reduced (usually microscopic), dependent on surrounding sporophyte tissue for nutrition
Sporophyte	Reduced, dependent on gametophyte for nutrition	Dominant	Dominant

Example



▲ **Figure 30.2 Gametophyte-sporophyte relationships in different plant groups.**

MAKE CONNECTIONS *In seed plants, how does retaining the gametophyte within the sporophyte likely affect embryo fitness? (See pp. 346, 472, and 480 in Chapters 17 and 23 to review mutagens, mutations, and fitness.)*

of seedless vascular plants are visible to the naked eye, the gametophytes of seed plants are mostly microscopic.

This miniaturization allowed for an important evolutionary innovation in seed plants: Their tiny gametophytes can develop from spores retained within the sporangia of the parental sporophyte. This arrangement protects the gametophytes from environmental stresses. The moist reproductive tissues of the sporophyte shield the gametophytes from UV radiation and protect them from drying out. This relationship also enables the dependent gametophytes to obtain nutrients from the sporophyte. In contrast, the free-living gametophytes of seedless plants must fend for themselves. **Figure 30.2** contrasts the gametophyte-sporophyte relationships in nonvascular plants, seedless vascular plants, and seed plants.

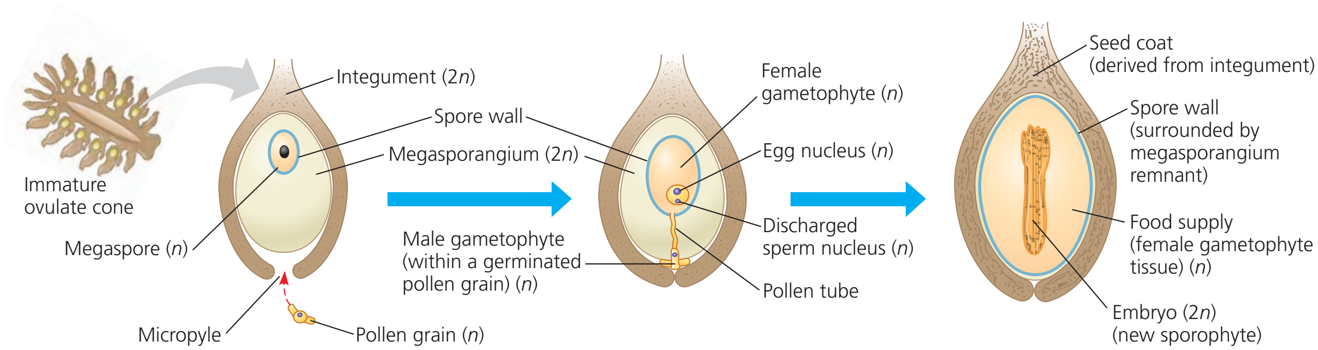
Heterospory: The Rule Among Seed Plants

You read in Chapter 29 that most seedless plants are *homosporous*—they produce one kind of spore, which usually gives rise to a bisexual gametophyte. Ferns and other close relatives of seed plants are homosporous, suggesting that seed plants had homosporous ancestors. At some point, seed plants or their ancestors became *heterosporous*, producing two kinds of spores: Megasporangia produce *megaspores* that give rise to female gametophytes, and microsporangia produce *microspores* that give rise to male gametophytes. Each megasporangium has a single functional megaspore, whereas each microsporangium contains vast numbers of microspores.

As we noted previously, the miniaturization of seed plant gametophytes likely contributed to the great success of this clade. Next we will look at the development of the female gametophyte within an ovule and the development of the male gametophyte in a pollen grain. Then we will follow the transformation of a fertilized ovule into a seed.

Ovules and Production of Eggs

Although a few species of seedless plants are heterosporous, seed plants are unique in retaining the megasporangium within the parent sporophyte. A layer of sporophyte tissue



(a) Unfertilized ovule. In this longitudinal section through the ovule of a pine (a gymnosperm), a fleshy megasporangium is surrounded by a protective layer of tissue called an integument. The micropyle, the only opening through the integument, allows entry of a pollen grain.

(b) Fertilized ovule. A megaspore develops into a female gametophyte, which produces an egg. The pollen grain, which had entered through the micropyle, contains a male gametophyte. The male gametophyte develops a pollen tube that discharges sperm, thereby fertilizing the egg.

(c) Gymnosperm seed. Fertilization initiates the transformation of the ovule into a seed, which consists of a sporophyte embryo, a food supply, and a protective seed coat derived from the integument. The megasporangium dries out and collapses.

▲ **Figure 30.3 From ovule to seed in a gymnosperm.**

? *A gymnosperm seed contains cells from how many different plant generations? Identify the cells and whether each is haploid or diploid.*

called **integument** envelops and protects the megasporangium. Gymnosperm megasporangia are surrounded by one integument, whereas those in angiosperms usually have two integuments. The whole structure—megasporangium, megaspore, and their integument(s)—is called an **ovule** **(Figure 30.3a)**. Inside each ovule (from the Latin *ovulum*, little egg), a female gametophyte develops from a megaspore and produces one or more eggs.

Pollen and Production of Sperm

A microspore develops into a **pollen grain** that consists of a male gametophyte enclosed within the pollen wall. (The outer layer of the pollen wall is composed of molecules secreted by sporophyte cells; hence, we refer to the male gametophyte as being *in* the pollen grain, not *equivalent to* the pollen grain.) The tough pollen wall, which contains the polymer sporopollenin, protects a pollen grain as it is transported from the parent plant by wind, for example, or by hitchhiking on the body of an animal. The transfer of pollen to the part of a seed plant that contains the ovules is called **pollination**. If a pollen grain germinates (begins growing), it gives rise to a pollen tube that discharges sperm into the female gametophyte within the ovule, as shown in **Figure 30.3b**.

Recall that in nonvascular plants and seedless vascular plants such as ferns, free-living gametophytes release flagellated sperm that swim through a film of water to reach eggs. The distance for this sperm transport rarely exceeds a few centimeters. By contrast, in seed plants a sperm-producing male gametophyte inside a pollen grain can be carried long distances by wind or by animals, eliminating the dependence on water for sperm transport. The sperm of seed plants also do not require motility because sperm are carried directly to the eggs by pollen tubes. Living gymnosperms provide evidence of the evolutionary transition to nonmotile sperm. The sperm of some gymnosperm species (such as ginkgos and cycads, shown a little later in Figure 30.5) retain the ancient flagellated condition, but flagella have been lost in the sperm of most gymnosperms and all angiosperms.

The Evolutionary Advantage of Seeds

If a sperm fertilizes an egg of a seed plant, the zygote grows into a sporophyte embryo. As shown in **Figure 30.3c**, the whole ovule develops into a seed: the embryo, along with a food supply, packaged within a protective coat derived from the integument(s).

Until the advent of seeds, the spore was the only protective stage in any plant life cycle. Moss spores, for example, may survive even if the local environment becomes too cold, too hot, or too dry for the mosses themselves to live. Their tiny size enables the spores to be dispersed in a dormant state to a new area, where they can germinate and give rise to new moss gametophytes if and when conditions are favorable enough for them to break dormancy. Spores were the main way that mosses, ferns, and other seedless plants spread over Earth for the first 100 million years of plant life on land.

Although mosses and other seedless plants continue to be very successful today, seeds represent a major evolutionary innovation that contributed to the opening of new ways of life for seed plants. What advantages do seeds provide over spores? Spores are usually single-celled, whereas seeds are multicellular, consisting of an embryo protected by a layer of tissue, the seed coat. A seed can remain dormant for days, months, or even years after being released from the parent plant, whereas most spores have shorter lifetimes. Also, unlike spores, seeds have a supply of stored food. Under favorable conditions, the seed can emerge from dormancy and germinate, with its stored food providing critical support for growth as the sporophyte embryo emerges as a seedling. Most seeds land close to their parent sporophyte plant, but some are carried long distances (up to hundreds of kilometers) by wind or animals.

CONCEPT CHECK 30.1

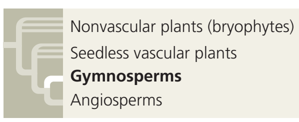
1. Contrast sperm delivery in seedless plants with sperm delivery in seed plants.
2. What features not present in seedless plants have contributed to the enormous success of seed plants on land?
3. **WHAT IF?** If a seed could not enter dormancy, how might that affect the embryo's transport or survival?

For suggested answers, see Appendix A.

◀ **Figure 30.4 A progymnosperm.** *Archaeopteris,* which lived 380 million years ago, produced wood and was heterosporous, but it did not produce seeds. Growing up to 20 m tall, it had fernlike leaves.

CONCEPT 30.2

Gymnosperms bear "naked" seeds, typically on cones



As shown in this phylogeny, extant seed plants form two sister clades: gymnosperms and angiosperms. Recall from Chapter 29 that gymnosperms have "naked" seeds that are not enclosed in ovaries. Their seeds are exposed on modified leaves (sporophylls) that usually form cones (strobili). (Angiosperm seeds are enclosed in fruits, which are mature ovaries.) We turn now to the origin of gymnosperms and other early seed plants.

Gymnosperm Evolution

Fossils reveal that by the late Devonian period (about 380 million years ago), some plants had acquired adaptations characteristic of seed plants. For example, *Archaeopteris* was a heterosporous tree with a woody stem **(Figure 30.4)**. But it did not bear seeds. Such transitional species of seedless vascular plants are sometimes called **progymnosperms**.

The first seed plants to appear in the fossil record date from around 360 million years ago, 55 million years before the first gymnosperm fossils and more than 200 million years before the first angiosperm fossils. These early seed plants became extinct, as did several later lineages. It remains uncertain which of these extinct seed plant lineages ultimately gave rise to the gymnosperms.

The earliest fossils of gymnosperms are about 305 million years old. These early gymnosperms lived in Carboniferous ecosystems still dominated by lycophytes, horsetails, ferns, and other seedless vascular plants. As the Carboniferous period gave way to the Permian, markedly drier climatic conditions favored the spread of gymnosperms. The flora and fauna changed dramatically, as many groups of organisms disappeared and others became prominent (see Chapter 25). Though most pronounced in the seas, the changeover also affected terrestrial life. For example, in the animal kingdom, amphibians decreased in diversity and were replaced by reptiles, which were especially well adapted to the arid conditions. Similarly, the lycophytes, horsetails, and ferns that dominated the Carboniferous swamps were largely replaced by gymnosperms, which were more suited to the drier climate. Gymnosperms have the key terrestrial adaptations found in all seed plants, such as seeds and pollen. In addition, some gymnosperms were particularly well suited to arid conditions because of the thick cuticles and relatively small surface areas of their needle-shaped leaves.

Geologists consider the end of the Permian period, about 251 million years ago, to be the boundary between the Paleozoic ("old life") and Mesozoic ("middle life") eras. Life changed profoundly as gymnosperms dominated terrestrial ecosystems throughout much of the Mesozoic, serving as the food supply for giant herbivorous dinosaurs. Toward the end of the Mesozoic, angiosperms began to replace gymnosperms in some ecosystems. The Mesozoic era ended 65 million years ago with mass extinctions of dinosaurs and many other animal groups, and further increases in the biodiversity and importance of angiosperms. Although angiosperms now dominate most terrestrial ecosystems, many gymnosperms remain an important part of Earth's flora. For example, vast regions in northern latitudes are covered by forests of cone-bearing gymnosperms called **conifers**, which include spruce, pine, fir, and redwood (see Figure 52.12, p. 1155).

Of the ten plant phyla in the taxonomic scheme adopted by this textbook (see Table 29.1), four are gymnosperms: Cycadophyta, Ginkgophyta, Gnetophyta, and Coniferophyta. The relationships of these four phyla to each other are uncertain. **Figure 30.5**, on the next two pages, surveys the diversity of extant gymnosperms.

▼ **Figure 30.5**

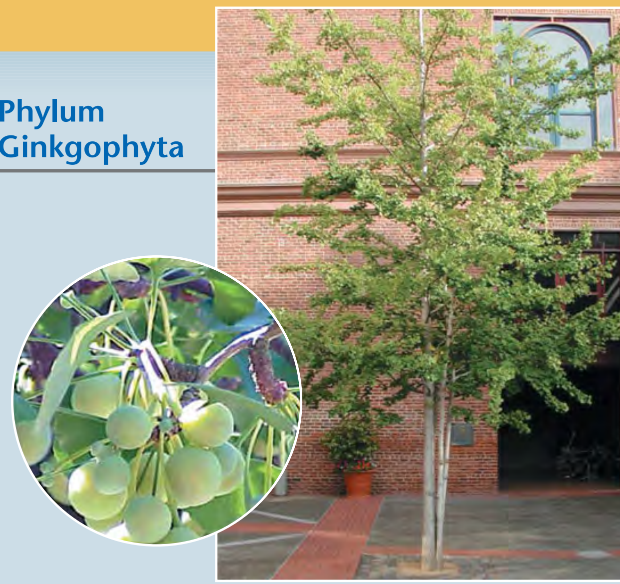
Exploring Gymnosperm Diversity

Phylum Cycadophyta

Cycads are the next largest group of gymnosperms after the conifers. They have large cones and palmlike leaves (true palm species are angiosperms). Only about 130 species survive today, but cycads thrived during the Mesozoic era, known as the age of cycads as well as the age of dinosaurs.

Cycas revoluta

Phylum Ginkgophyta

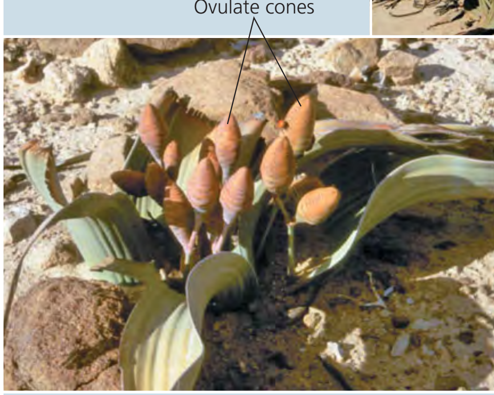


Ginkgo biloba is the only surviving species of this phylum. Also known as the maidenhair tree, it has deciduous fanlike leaves that turn gold in autumn. It is a popular ornamental tree in cities because it tolerates air pollution well. Landscapers often plant only pollen-producing trees because the fleshy seeds smell rancid as they decay.

Phylum Gnetophyta

Plants in the phylum Gnetophyta, called gnetophytes, consist of three genera: *Gnetum*, *Ephedra*, and *Welwitschia*. Some species are tropical, whereas others live in deserts. Although very different in appearance, the genera are grouped together based on molecular data.

▶ ***Welwitschia.*** This genus consists of one species, *Welwitschia mirabilis*, a plant that lives only in the deserts of southwestern Africa. Its straplike leaves are among the largest leaves known.



◀ ***Gnetum.*** This genus includes about 35 species of tropical trees, shrubs, and vines, mainly native to Africa and Asia. Their leaves look similar to those of flowering plants, and their seeds look somewhat like fruits.

▶ ***Ephedra.*** This genus includes about 40 species that inhabit arid regions worldwide. These desert shrubs, commonly called "Mormon tea," produce the compound ephedrine, which is used medicinally as a decongestant.

Phylum Coniferophyta

Phylum Coniferophyta is by far the largest of the gymnosperm phyla, consisting of about 600 species of conifers (from the Latin *conus*, cone, and *ferre*, to carry). Many are large trees, such as cypresses and redwoods. A few conifer species dominate vast forested regions of the Northern Hemisphere, where the growing season is relatively short because of latitude or altitude.

Most conifers are evergreens; they retain their leaves throughout the year. Even during winter, a limited amount of photosynthesis occurs on sunny days. When spring comes, conifers already have fully developed leaves that can take advantage of the sunnier, warmer days. Some conifers, such as the dawn redwood, tamarack, and larch, are deciduous trees that lose leaves each autumn.

▶ **Douglas fir.** This evergreen tree (*Pseudotsuga menziesii*) provides more timber than any other North American tree species. Some uses include house framing, plywood, pulpwood for paper, railroad ties, and boxes and crates.

▶ **Common juniper.** The "berries" of the common juniper (*Juniperus communis*) are actually ovule-producing cones consisting of fleshy sporophylls.

◀ **European larch.** The needle-like leaves of this deciduous conifer (*Larix decidua*) turn yellow before they are shed in autumn. Native to the mountains of central Europe, including Switzerland's Matterhorn, depicted here, this species is extremely cold-tolerant, able to survive winter temperatures that plunge to –50°C.

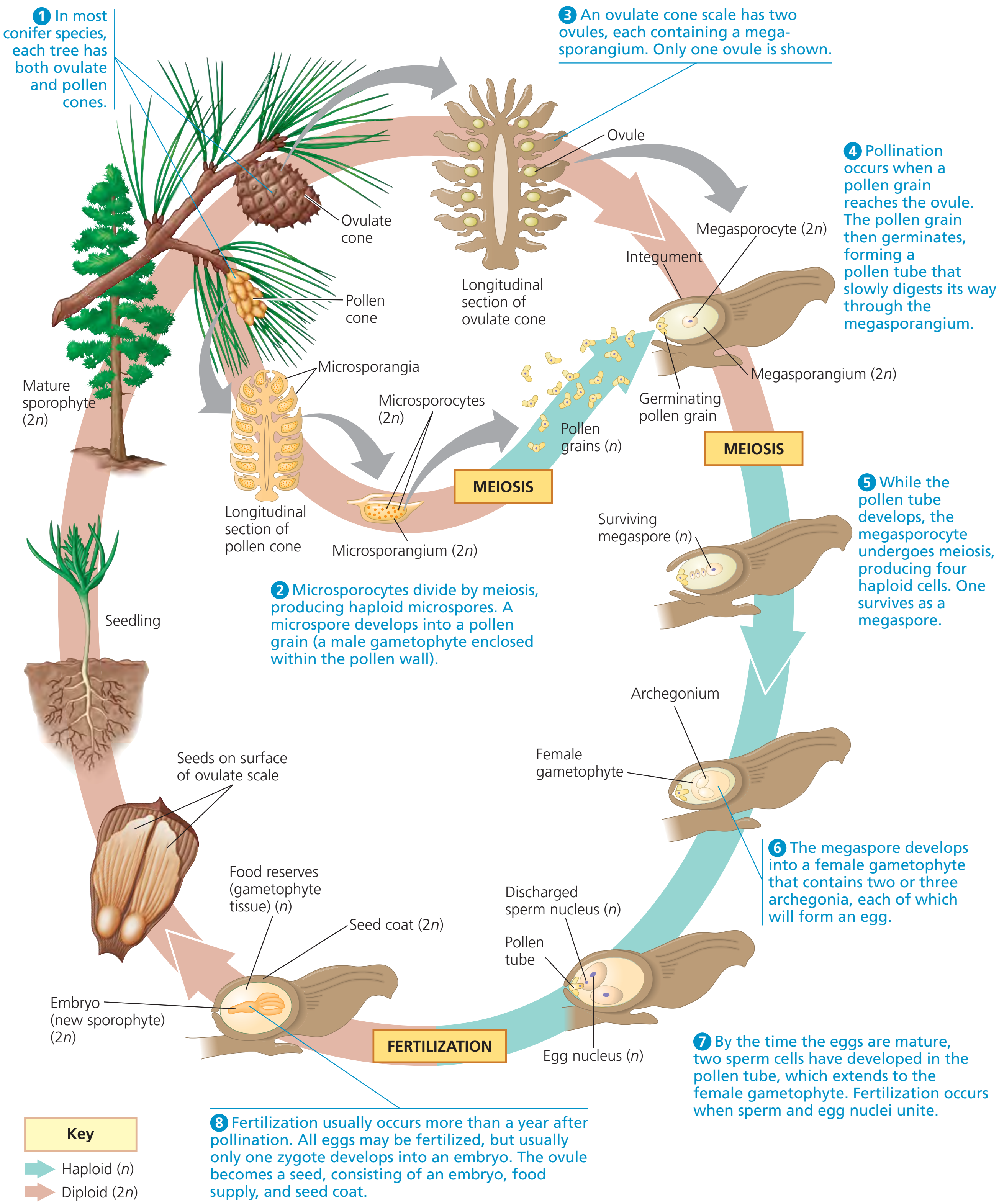
◀ **Wollemi pine.** Survivors of a conifer group once known only from fossils, living Wollemi pines (*Wollemia nobilis*) were discovered in 1994 in a national park only 150 km from Sydney, Australia. The species consists of just 40 known individuals in two small groves. The inset photo compares the leaves of this "living fossil" with actual fossils.

▶ **Sequoia.** This giant sequoia (*Sequoiadendron giganteum*) in California's Sequoia National Park weighs about 2,500 metric tons, equivalent to about 24 blue whales (the largest animals) or 40,000 people. The giant sequoia is one of the largest living organisms and also among the most ancient, with some individuals estimated to be between 1,800 and 2,700 years old. Their cousins, the coast redwoods (*Sequoia sempervirens*), grow to heights of more than 110 m (taller than the Statue of Liberty) and are found only in a narrow coastal strip of northern California and southern Oregon.

▶ **Bristlecone pine.** This species (*Pinus longaeva*), which is found in the White Mountains of California, includes some of the oldest living organisms, reaching ages of more than 4,600 years. One tree (not shown here) is called Methuselah because it may be the world's oldest living tree. To protect the tree, scientists keep its location a secret.

▼ **Figure 30.6 The life cycle of a pine.**

MAKE CONNECTIONS *What type of cell division occurs as a megaspore becomes a female gametophyte? (See Figure 13.9, p. 256.)*



The Life Cycle of a Pine: *A Closer Look*

As you read earlier, seed plant evolution has included three key reproductive adaptations: the increasing dominance of the sporophyte; the advent of the seed as a resistant, dispersible stage in the life cycle; and the appearance of pollen as an airborne agent that brings gametes together. **Figure 30.6**, on the facing page, shows how these adaptations come into play during the life cycle of a pine, a familiar conifer.

The pine tree is the sporophyte; its sporangia are located on scalelike structures packed densely in cones. Like all seed plants, conifers are heterosporous. In conifers, the two types of spores are produced by separate cones: small pollen cones and large ovulate cones. In most pine species, each tree has both types of cones. In pollen cones, microsporocytes (microspore mother cells) undergo meiosis, producing haploid microspores. Each microspore develops into a pollen grain containing a male gametophyte. In pines and other conifers, the yellow pollen is released in large amounts and carried by the wind, dusting everything in its path. Meanwhile, in ovulate cones, megasporocytes (megaspore mother cells) undergo meiosis and produce haploid megaspores inside the ovule. Surviving megaspores develop into multicellular female gametophytes, which are retained within the sporangia.

From the time young pollen and ovulate cones appear on the tree, it takes nearly three years for the male and female gametophytes to be produced and brought together and for mature seeds to form from the fertilized ovules. The scales of each ovulate cone then separate, and the seeds are dispersed by the wind. A seed that lands in a suitable environment then germinates, its embryo emerging as a pine seedling.

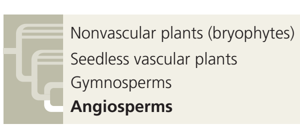
CONCEPT CHECK 30.2

1. Use examples from Figure 30.5 to describe how various gymnosperms are similar yet distinctive.
2. Explain how the pine life cycle in Figure 30.6 reflects the five adaptations common to all seed plants (see p. 618).
3. **MAKE CONNECTIONS** Does the hypothesis that gymnosperms and angiosperms are sister clades imply that they originated at the same time? (See pp. 538–539.)

For suggested answers, see Appendix A.

CONCEPT 30.3

The reproductive adaptations of angiosperms include flowers and fruits



Commonly known as flowering plants, angiosperms are seed plants that produce the reproductive structures called flowers and fruits. The name *angiosperm* (from the Greek *angion*, container) refers to seeds contained in fruits, the mature ovaries. Today, angiosperms are the most diverse and widespread of all plants, with more than 250,000 species (about 90% of all plant species).

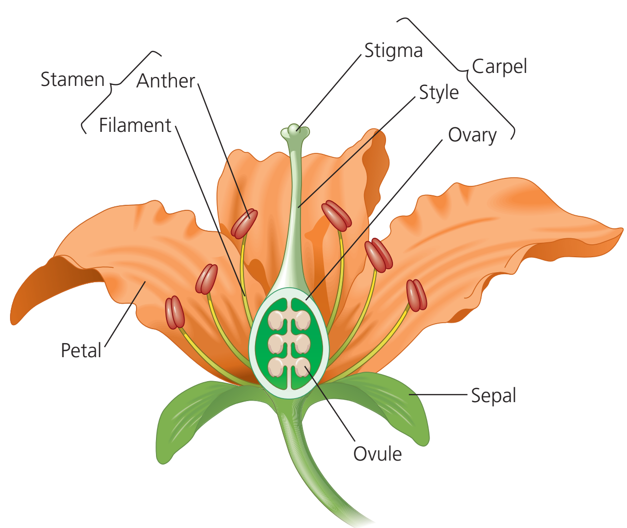
Characteristics of Angiosperms

All angiosperms are classified in a single phylum, Anthophyta (from the Greek *anthos*, flower). Before considering the evolution of angiosperms, we will examine their key adaptations—flowers and fruits—and the roles of these structures in the angiosperm life cycle.

Flowers

The **flower** is an angiosperm structure specialized for sexual reproduction. In many angiosperm species, insects or other animals transfer pollen from one flower to the sex organs on another flower, which makes pollination more directed than the wind-dependent pollination of most gymnosperms. However, some angiosperms *are* wind-pollinated, particularly those species that occur in dense populations, such as grasses and tree species in temperate forests.

A flower is a specialized shoot that can have up to four rings of modified leaves (sporophylls) called floral organs: sepals, petals, stamens, and carpels (**Figure 30.7**). Starting at the base of the flower are the **sepals**, which are usually green and enclose the flower before it opens (think of a rosebud). Interior to the sepals are the **petals**, which are brightly colored in most flowers and aid in attracting pollinators. Flowers that are wind-pollinated, however, generally lack brightly colored parts. In all angiosperms, the sepals and petals are sterile floral organs, meaning that they do not produce sperm or eggs. Within the petals are two whorls of fertile floral organs that produce spores,



▲ **Figure 30.7 The structure of an idealized flower.**

the stamens and carpels. **Stamens** produce microspores that develop into pollen grains containing male gametophytes. A stamen consists of a stalk called the **filament** and a terminal sac, the **anther**, where pollen is produced. **Carpels** make megaspores and their products, female gametophytes. Some flowers have a single carpel, whereas others have multiple carpels, which are either separate or fused together. At the tip of the carpel is a sticky **stigma** that receives pollen. A **style** leads from the stigma to the **ovary** at the base of the carpel; the ovary contains one or more ovules. If fertilized, an ovule develops into a seed.

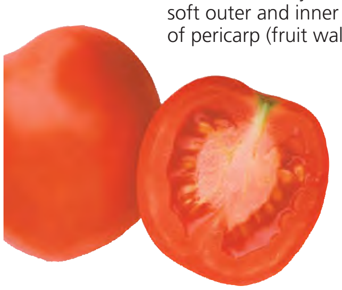
Fruits

A **fruit** typically consists of a mature ovary but can also include other flower parts. As seeds develop from ovules after fertilization, the ovary wall thickens. A pea pod is an example of a fruit, with seeds (mature ovules, the peas) encased in the ripened ovary (the pod). (We'll examine the developmental origin of fruits in Figure 38.10.)

Fruits protect dormant seeds and aid in their dispersal. Mature fruits can be either fleshy or dry **(Figure 30.8)**.

▼ Figure 30.8 Some variations in fruit structure.

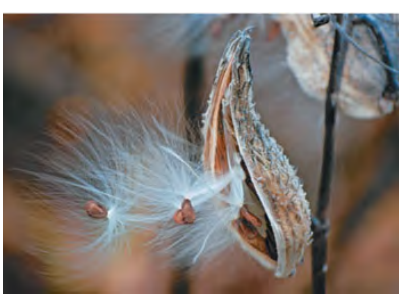
▼ Tomato, a fleshy fruit with soft outer and inner layers of pericarp (fruit wall)



▼ Ruby grapefruit, a fleshy fruit with a firm outer layer and soft inner layer of pericarp

▶ Nectarine, a fleshy fruit with a soft outer layer and hard inner layer (pit) of pericarp

▼ Hazelnut, a dry fruit that remains closed at maturity



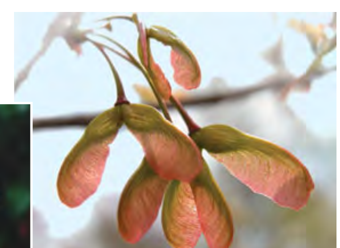
◀ Milkweed, a dry fruit that splits open at maturity

Tomatoes, plums, and grapes are examples of fleshy fruits, in which the wall (pericarp) of the ovary becomes soft during ripening. Dry fruits include beans, nuts, and grains. Some dry fruits split open at maturity to release seeds, whereas others remain closed. The dry, wind-dispersed fruits of grasses, harvested while on the plant, are major staple foods for humans. The cereal grains of maize, rice, wheat, and other grasses, though easily mistaken for seeds, are each actually a fruit with a dry outer covering (the former wall of the ovary) that adheres to the seed coat of the seed within.

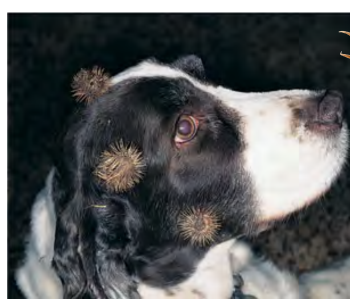
As shown in **Figure 30.9**, various adaptations of fruits and seeds help to disperse seeds. The seeds of some flowering plants, such as dandelions and maples, are contained within fruits that function like parachutes or propellers, adaptations that enhance dispersal by wind. Some fruits, such as coconuts, are adapted to dispersal by water (see Figure 38.11). And many angiosperms rely on animals to carry seeds. Some of these plants have fruits modified as burrs that cling to animal fur (or the clothes of humans). Other angiosperms produce edible fruits, which are usually nutritious, sweet tasting, and vividly colored, advertising their ripeness. When an animal eats the fruit, it digests the fruit's fleshy part, but the tough seeds usually pass unharmed through the animal's digestive tract. Animals may deposit the seeds, along with a supply of natural fertilizer, many kilometers from where the fruit was eaten.

▼ Figure 30.9 Fruit adaptations that enhance seed dispersal.

▶ Wings enable maple fruits to be carried by the wind.



◀ Seeds within berries and other edible fruits are often dispersed in animal feces.



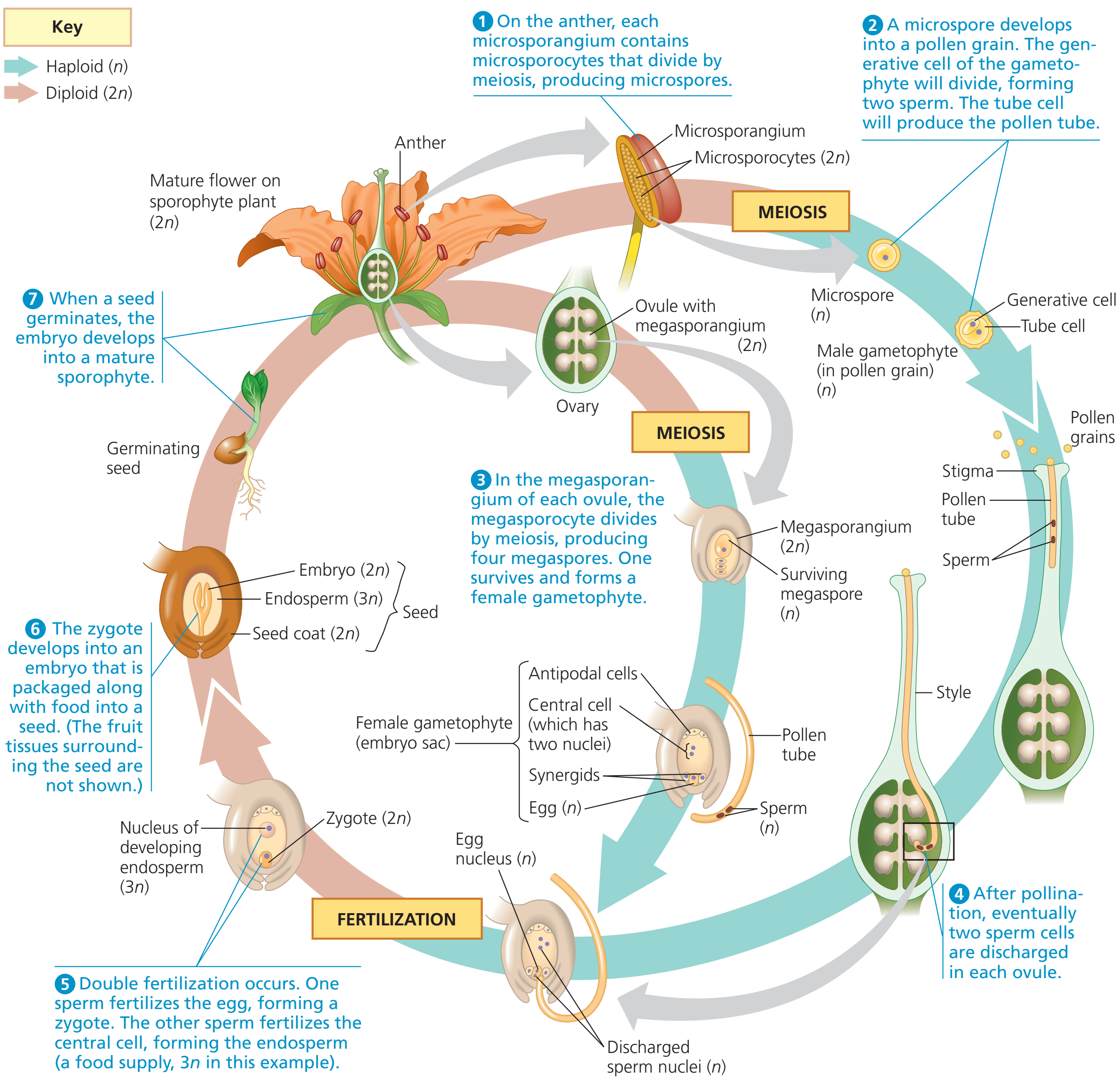
◀ The barbs of cockleburs facilitate seed dispersal by allowing the fruits to "hitchhike" on animals.

The Angiosperm Life Cycle

You can follow a typical angiosperm life cycle in **Figure 30.10**. The flower of the sporophyte produces microspores that form male gametophytes and megaspores that form female gametophytes. The male gametophytes are in the pollen grains, which develop within microsporangia in the anthers. Each male gametophyte has two haploid cells: a *generative cell* that divides, forming two sperm, and a *tube cell* that produces a pollen tube. Each ovule, which develops in the ovary, contains a female gametophyte, also known as an **embryo sac**. The embryo sac consists of only a few cells, one of which is the egg. (We will discuss gametophyte development in more detail in Chapter 38.)

After its release from the anther, the pollen is carried to the sticky stigma at the tip of a carpel. Although some flowers self-pollinate, most have mechanisms that ensure **cross-pollination**, which in angiosperms is the transfer of pollen from an anther of a flower on one plant to the stigma of a flower on another plant of the same species. Cross-pollination enhances genetic

▼ **Figure 30.10 The life cycle of an angiosperm.**



variability. In some species, stamens and carpels of a single flower may mature at different times, or they may be so arranged that self-pollination is unlikely.

The pollen grain absorbs water and germinates after it adheres to the stigma of a carpel. The tube cell produces a pollen tube that grows down within the style of the carpel. After reaching the ovary, the pollen tube penetrates through the **micropyle**, a pore in the integuments of the ovule, and discharges two sperm cells into the female gametophyte (embryo sac). One sperm fertilizes the egg, forming a diploid zygote. The other sperm fuses with the two nuclei in the large central cell of the female gametophyte, producing a triploid cell. This type of **double fertilization**, in which one fertilization event produces a zygote and the other produces a triploid cell, is unique to angiosperms.

After double fertilization, the ovule matures into a seed. The zygote develops into a sporophyte embryo with a rudimentary root and one or two seed leaves called **cotyledons**. The triploid central cell of the female gametophyte develops into **endosperm**, tissue rich in starch and other food reserves that nourish the developing embryo.

What is the function of double fertilization in angiosperms? One hypothesis is that double fertilization synchronizes the development of food storage in the seed with the development of the embryo. If a particular flower is not pollinated or sperm cells are not discharged into the embryo sac, fertilization does not occur, and neither endosperm nor embryo forms. So perhaps double fertilization is an adaptation that prevents flowering plants from squandering nutrients on infertile ovules.

Another type of double fertilization occurs in some gymnosperm species belonging to the phylum Gnetophyta. However, double fertilization in these species gives rise to two embryos rather than to an embryo and endosperm.

As you read earlier, the seed consists of the embryo, the endosperm, and a seed coat derived from the integuments. An ovary develops into a fruit as its ovules become seeds. After being dispersed, a seed may germinate if environmental conditions are favorable. The coat ruptures and the embryo emerges as a seedling, using food stored in the endosperm and cotyledons until it can produce its own food by photosynthesis.

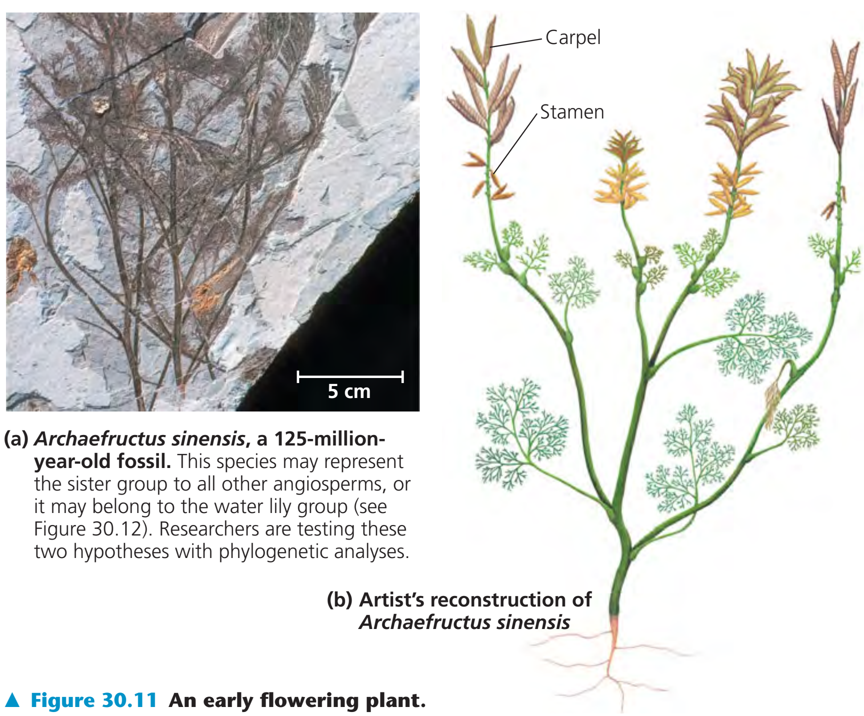
Angiosperm Evolution

Clarifying the origin of angiosperms—what Charles Darwin once called an "abominable mystery"—poses fascinating challenges to evolutionary biologists. Angiosperms originated at least 140 million years ago, and during the late Mesozoic, the major branches of the clade diverged from their common ancestor. By the mid-Cretaceous period (100 million years ago), angiosperms began to dominate many terrestrial ecosystems. Landscapes changed dramatically as conifers, cycads, and other gymnosperms gave way to flowering plants in many parts of the world.

The flowers and fruits of angiosperms distinguish them markedly from living gymnosperms, which makes the origins of angiosperms puzzling. To understand how the angiosperm body plan emerged, scientists are studying fossils, refining angiosperm phylogeny, and elucidating developmental patterns that underlie flowers and other angiosperm innovations. As we'll see, much progress has been made toward solving Darwin's mystery—but we still do not fully understand how angiosperms originated from earlier seed plants.

Fossil Angiosperms

In the late 1990s, scientists in China discovered several intriguing fossils of 125-million-year-old angiosperms. These fossils, now named *Archaefructus liaoningensis* and *Archaefructus sinensis* **(Figure 30.11)**, share some traits with living angiosperms but lack others. *Archaefructus sinensis*, for example, has anthers and also has seeds inside closed carpels but lacks petals and sepals. In 2002, scientists completed a phylogenetic comparison of *Archaefructus* with 173 living plant species. The researchers concluded that *Archaefructus* may belong to the earliest-diverging group of angiosperms known.



(a) *Archaefructus sinensis*, a 125-million-year-old fossil. This species may represent the sister group to all other angiosperms, or it may belong to the water lily group (see Figure 30.12). Researchers are testing these two hypotheses with phylogenetic analyses.

(b) Artist's reconstruction of *Archaefructus sinensis*

▲ **Figure 30.11 An early flowering plant.**

Based on *Archaefructus* fossils, can we infer traits of the common ancestor of *Archaefructus* and living angiosperms? The fossils indicate that *Archaefructus* had simple flowers and was herbaceous with bulbous structures that may have served as floats, suggesting it was aquatic. But investigating whether the angiosperm common ancestor had simple flowers and was herbaceous and aquatic also requires examining fossils of other seed plants thought to have been closely related to angiosperms. All of those plants were woody, indicating that the common ancestor was probably woody. Furthermore, paleobotanists have found angiosperm fossils from later-diverging lineages that became aquatic and have flowers resembling those of *Archaefructus*. This suggests that simple flowers and an aquatic growth form may have been derived traits of *Archaefructus* rather than traits of the common ancestor. Overall, while most researchers agree that the angiosperm common ancestor was woody, debate continues about many of its other features.

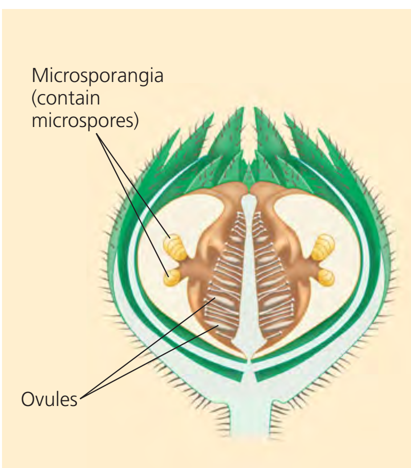
Angiosperm Phylogeny

To shed light on the body plan of early angiosperms, scientists have long sought to identify which seed plants, including fossil species, are most closely related to angiosperms. Molecular and morphological evidence suggests that living gymnosperms are a monophyletic group whose earliest lineages diverged from the ancestors of angiosperms about 305 million years ago. Note that this does not necessarily imply that angiosperms originated 305 million years ago, but that the most recent common ancestor of gymnosperms and angiosperms lived at that time. Angiosperms may in fact be most closely related to extinct seed plants such as the Bennettitales, a group with flowerlike structures that may have been pollinated by insects **(Figure 30.12a)**. Systematists hope to resolve this issue through phylogenetic studies that combine data from fossil and living species of a wide range of seed plants.

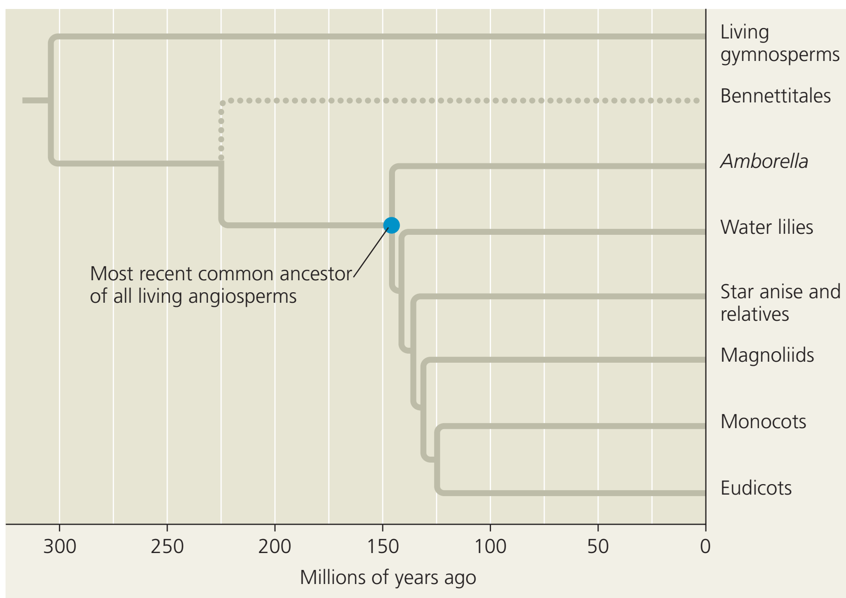
Making sense of the origin of angiosperms also depends on working out the order in which angiosperm clades diverged from one another. Here, dramatic progress has been made in recent years. Molecular and morphological evidence suggests that a small South Pacific shrub called *Amborella trichopoda* and water lilies are living representatives of two of the most ancient angiosperm lineages **(Figure 30.12b)**.

Developmental Patterns in Angiosperms

Additional clues about the origin of flowering plants are emerging from studies of plant development. For example, a 2006 study demonstrated that in *Amborella*, eggs form from precursor cells that differ from the egg precursor cells of most other living angiosperms. Intriguingly, the way in which eggs form in *Amborella* has similarities to how eggs



(a) A possible ancestor of the angiosperms? This reconstruction shows a cross section through the flowerlike structures found in the Bennettitales, an extinct group of seed plants hypothesized to be more closely related to angiosperms than to gymnosperms.



(b) Angiosperm phylogeny. This tree represents one current hypothesis of angiosperm evolutionary relationships, based on morphological and molecular evidence. Angiosperms originated at least 140 million years ago. The dotted line indicates the uncertain position of the Bennettitales, a possible sister group to the angiosperms.

▲ **Figure 30.12 Angiosperm evolutionary history.**

? *Would the branching order of the phylogeny in (b) necessarily have to be redrawn if a 150-million-year-old fossil monocot were discovered? Explain.*

form in gymnosperms—a possible link to the ancient common ancestor of gymnosperms and angiosperms. Other studies suggest that in a variety of early angiosperms (as well as in *Amborella*), the outer of the two protective integuments appears to be a modified leaf that originates separately from the inner integument. Because gymnosperms have only one integument, scientists are curious about exactly how the second integument originated in angiosperms. Researchers are also studying key developmental genes in gymnosperms and angiosperms, including genes that control flower development in angiosperms. Early results have uncovered developmental pathways shared by gymnosperms and angiosperms. These shared pathways may reveal clues about steps leading to the origin of flowering plants.

Angiosperm Diversity

From their humble beginnings in the Mesozoic, angiosperms have diversified into more than 250,000 living species. Until the late 1990s, most systematists divided flowering plants into two groups, based partly on the number of cotyledons, or seed leaves, in the embryo. Species with one cotyledon were called **monocots**, and those with two were called **dicots**. Other features, such as flower and leaf structure, were also used to define the two groups. For example, monocots typically have parallel leaf veins (think of a grass blade), whereas the veins of most dicots have a netlike pattern (think of an oak leaf). Some examples of monocots are orchids, palms, and grain crops such as maize, wheat, and rice. Some examples of dicots are roses, peas, sunflowers, and maples.

Recent DNA studies, however, indicate that the monocot-dicot distinction does not completely reflect evolutionary relationships. Current research supports the hypothesis that monocots form a clade but reveals that the species traditionally called dicots are polyphyletic. The vast majority of species once categorized as dicots form a large clade, now known as **eudicots** ("true" dicots). The rest of the former dicots are now grouped into several small lineages. Three of these lineages are informally called **basal angiosperms** because they appear to include the flowering plants belonging to the oldest lineages. A fourth lineage, called the **magnoliids**, evolved later. **Figure 30.13** provides an overview of angiosperm diversity.

▼ **Figure 30.13**

Exploring Angiosperm Diversity

Basal Angiosperms

Surviving basal angiosperms are currently thought to consist of three lineages comprising only about 100 species. The oldest lineage seems to be represented by a single species, *Amborella trichopoda* (right). The other surviving lineages diverged later: a clade that includes water lilies and a clade consisting of the star anise and its relatives.

Water lily (*Nymphaea "Rene Gerard"*). Water lilies are living members of a clade that may be predated only by the *Amborella* lineage.

Star anise (*Illicium*). This genus belongs to a third surviving lineage of basal angiosperms.

***Amborella trichopoda*.** This small shrub, found only on the South Pacific island of New Caledonia, may be the sole survivor of a branch at the base of the angiosperm tree. *Amborella* lacks vessels, which are present in angiosperms in later-developing lineages. Consisting of xylem cells arranged in continuous tubes, vessels transport water more efficiently than tracheids. Their absence in *Amborella* indicates they may have evolved after the lineage that gave rise to *Amborella* diverged.

Magnoliids

Magnoliids consist of about 8,000 species, most notably magnolias, laurels, and black pepper plants. They include both woody and herbaceous species. Although they share some traits with basal angiosperms, such as a typically spiral rather than whorled arrangement of floral organs, magnoliids are more closely related to eudicots and monocots.

Southern magnolia (*Magnolia grandiflora*). This member of the magnolia family is a woody magnoliid. The variety of southern magnolia shown here, called "Goliath," has flowers that measure up to about a foot across.

Monocots

About one-quarter of angiosperm species are monocots—about 70,000 species. These examples represent some of the largest families.

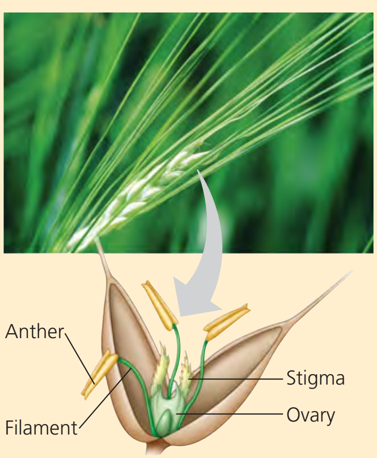
Eudicots

More than two-thirds of angiosperm species are eudicots—roughly 170,000 species. Below is a sampling of eudicot floral diversity.

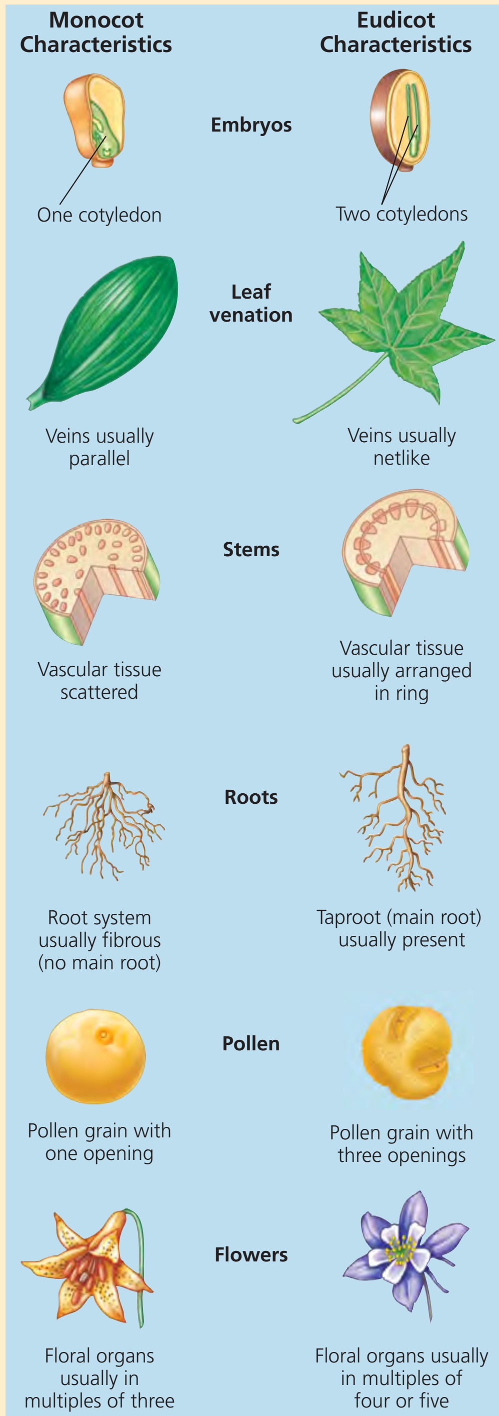
Orchid (*Lemboglossum rossii*)

Pygmy date palm (*Phoenix roebelenii*)

Lily (*Lilium "Enchantment"*)



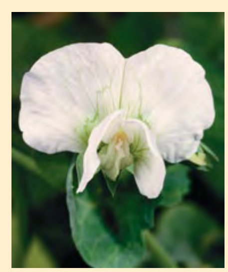
Barley (*Hordeum vulgare*), a grass



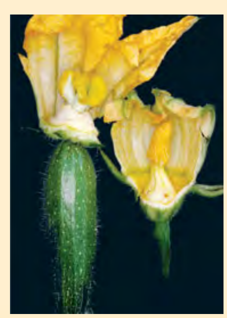
California poppy (*Eschscholzia californica*)

Pyrenean oak (*Quercus pyrenaica*)

Dog rose (*Rosa canina*), a wild rose



Snow pea (*Pisum sativum*), a legume



Zucchini (*Cucurbita pepo*) flowers

◀ **Figure 30.14 A plant pollinated by flies.** *Rafflesia arnoldii*, the "monster flower" of Indonesia, is the size of an automobile tire. It attracts fly pollinators with an odor like that of a decaying corpse.

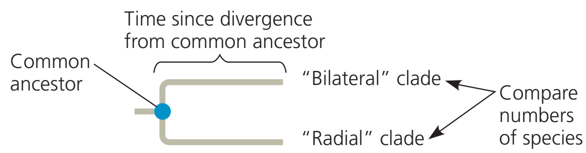
Evolutionary Links Between Angiosperms and Animals

Ever since they colonized land, animals have influenced the evolution of terrestrial plants, and vice versa. For example, herbivores can reduce a plant's reproductive success by eating its roots, leaves, or seeds. As a result, if a novel and effective defense against herbivores originates in a group of plants, those plants may be favored by natural selection—as will any herbivores that can overcome this new defense. Plant-pollinator and other mutually beneficial interactions can have similar evolutionary effects, as seen in **Figure 30.14**.

In the examples we just discussed, interactions between plants and animals led to reciprocal evolution in the particular pairs of species involved. However, interactions between plants and animals also may have affected broader patterns in the history of life, such as rates at which new species form. Consider the evolutionary impact of how flower petals are arranged. Flower petals can be symmetrical in one direction only (*bilateral symmetry*, as in the pea blossom in Figure 30.13), or they can be symmetrical in all directions (*radial symmetry*, as in the dog rose in Figure 30.13). On a flower with bilateral symmetry, an insect pollinator may be able to obtain nectar only when it approaches the flower from a certain direction **(Figure 30.15)**. This constraint can make it more likely that as an insect moves from flower to flower, pollen is placed on a part of the insect's body that will come into contact with the stigma of a flower of the same species. Such specificity of pollen transfer tends to reduce gene flow between diverging populations and hence could lead to increased rates of plant speciation.

◀ **Figure 30.15 Pollinating a bilaterally symmetrical flower.** To harvest nectar (a sugary solution secreted by flower glands) from this bilaterally symmetrical Scottish broom flower, a honeybee must land as shown. This releases a tripping mechanism that arches the flower's stamens over the bee and dusts it with pollen. Later, some of this pollen will rub off onto the stigma of the next flower of this species that the bee visits.

How can this hypothesis be tested? One approach is illustrated in this diagram:



A key step is to identify cases in which a clade with bilaterally symmetrical flowers shares an immediate common ancestor with a clade whose members have radially symmetrical flowers. One recent study identified 19 such pairs of closely related "bilateral" and "radial" clades. On average, the clade with bilaterally symmetrical flowers had nearly 2,400 more species than did its closely related clade with radially symmetrical flowers. This result suggests that flower shape can affect the rate at which new species form, with speciation occurring more rapidly in clades with bilateral symmetry. Overall, the effects of plant-pollinator interactions are thought to have contributed to the increasing dominance of flowering plants in the Cretaceous period, helping to make angiosperms of central importance in ecological communites.

CONCEPT CHECK 30.3

1. It has been said that an oak is an acorn's way of making more acorns. Write an explanation that includes these terms: sporophyte, gametophyte, ovule, seed, ovary, and fruit.
2. Compare and contrast a pine cone and a flower in terms of structure and function.
3. **WHAT IF?** Do speciation rates in closely related clades of flowering plants show that flower shape is *correlated with* the rate at which new species form, or that flower shape is *responsible for* this rate? Explain.

For suggested answers, see Appendix A.

CONCEPT 30.4

Human welfare depends greatly on seed plants

Throughout Unit Five, we are highlighting the ways in which humans depend on various organisms. In forests and on farms, seed plants are key sources of food, fuel, wood products, and medicine. Our reliance on them makes the preservation of plant diversity critical.

Products from Seed Plants

Most of our food comes from angiosperms. Just six crops—maize, rice, wheat, potatoes, cassava, and sweet potatoes—yield 80% of all the calories consumed by humans. We also depend on angiosperms to feed livestock: It takes 5–7 kg of grain to produce 1 kg of grain-fed beef.

Today's crops are the products of artificial selection—the result of plant domestication that began about 12,000 years ago. To appreciate the scale of this transformation, note how the number and size of seeds in domesticated plants are greater than those of their wild relatives, as in the case of maize and the grass teosinte (see Figure 38.16). Scientists can glean information about domestication by comparing the genes of crops with those of wild relatives. With maize, dramatic changes such as increased cob size and loss of the hard coating around teosinte kernels may have been initiated by as few as five mutations.

Flowering plants also provide other edible products. Two popular beverages come from tea leaves and coffee beans, and you can thank the tropical cacao tree for cocoa and chocolate. Spices are derived from various plant parts, such as flowers (cloves, saffron), fruits and seeds (vanilla, black pepper, mustard), leaves (basil, mint, sage), and even bark (cinnamon).

Many seed plants are sources of wood, which is absent in all living seedless plants. Wood consists of tough-walled xylem cells (see Figure 35.22). It is the primary source of fuel for much of the world, and wood pulp, typically derived from conifers such as fir and pine, is used to make paper. Wood also remains the most widely used construction material.

For centuries, humans have also depended on seed plants for medicines. Many cultures use herbal remedies, and scientists have extracted and identified the relevant secondary compounds (see p. 604) from many of these plants, and later synthesized them. Willow leaves and bark, for instance, have long been used in pain-relieving remedies, including prescriptions by the Greek physician Hippocrates. In the 1800s, scientists traced the willow's medicinal property to the chemical salicin. A synthesized derivative, acetylsalicylic acid, is what we call aspirin. Plants also remain a direct source of medicinal compounds. In the United States, about 25% of prescription drugs contain an active ingredient from plants, typically seed plants. Other ingredients were discovered in seed plants and then synthesized artificially. **Table 30.1** lists some medicinal uses of secondary compounds found in seed plants.

Table 30.1 Examples of Plant-Derived Medicines

Compound	Source	Use
Atropine	Belladonna plant	Eye pupil dilator
Digitalin	Foxglove	Heart medication
Menthol	Eucalyptus tree	Throat soother
Quinine	Cinchona tree	Malaria preventive
Taxol	Pacific yew	Ovarian cancer drug
Tubocurarine	Curare tree	Muscle relaxant
Vinblastine	Periwinkle	Leukemia drug

Threats to Plant Diversity

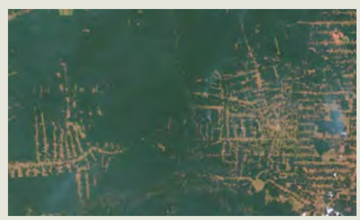
Although plants may be a renewable resource, plant diversity is not. The exploding human population and its demand for space and resources are extinguishing plant species at a high rate. The problem is especially severe in the tropics, where more than two-thirds of the human population live and where population growth is fastest. About 55,000 km^2 (14 million acres) of tropical rain forest are cleared each year (**Figure 30.16**), a rate that would completely eliminate the remaining 11 million km^2

▼ **Figure 30.16**

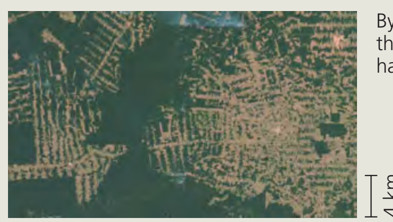
IMPACT

Clear-Cutting of Tropical Forests

Over the past several hundred years, nearly half of Earth's tropical forests have been cut down and converted to farmland and other uses. Satellite images, such as those below, show that together these regions cover an area roughly the size of Canada. Living trees release large quantities of water to the atmosphere, cooling the local environment (much as evaporation of sweat cools your body) and putting moisture into the air that is recycled as rain. When trees are cut down, less moisture is released to the atmosphere, causing increased temperatures and decreased rainfall. Tree removal also reduces the absorption of atmospheric carbon dioxide (CO_2) that occurs during photosynthesis.



A satellite image from 2000 shows clear-cut areas in Brazil surrounded by dense tropical forest.



By 2009, much more of this same tropical forest had been cut down.

WHY IT MATTERS Higher temperatures and increased atmospheric CO_2 resulting from destruction of tropical forests contribute to global warming, making preservation of these forests a high priority. Moreover, changes in rainfall patterns are expected to reduce agricultural production in some of the poorest countries. Finally, tropical forests harbor 50% or more of all species on Earth. Hence, higher temperatures, reduced rainfall, and habitat loss caused by clear-cutting tropical forests may lead to extinction of many species.

FURTHER READING G. P. Asner, T. K. Rudel, T. M. Aide, R. Defries, and R. Emerson, A contemporary assessment of change in humid tropical forests, *Conservation Biology* 23:1386–1395 (2009).

WHAT IF? How would clear-cutting affect the temperature and moisture along the edges of a remaining forest fragment?

of tropical forests in 200 years. The most common cause of this destruction is slash-and-burn clearing of forests for agricultural use (see Chapter 56). As forests disappear, so do large numbers of plant species. Of course, once a species becomes extinct, it can never return.

The loss of plant species is often accompanied by the loss of insects and other rain forest animals. Researchers estimate that habitat destruction in rain forests and other ecosystems is pushing hundreds of species toward extinction each year. If current rates of loss in the tropics and elsewhere continue, scientists estimate that within the next few centuries, 50% or more of Earth's species will become extinct. Such losses would constitute a global mass extinction, rivaling the Permian and Cretaceous mass extinctions and forever changing the evolutionary history of land plants (and many other organisms).

Many people have ethical concerns about contributing to the extinction of living forms. In addition, there are practical reasons to be concerned about the loss of plant diversity. So far, we have explored the potential uses of only a tiny fraction of the more than 290,000 known plant species. For example, almost all our food is based on the cultivation of only about two dozen species of seed plants. And fewer than 5,000 plant species have been studied as potential sources of medicines. The tropical rain forest may be a medicine chest of healing plants that could be extinct before we even know they exist. If we begin to view rain forests and other ecosystems as living treasures that can regenerate only slowly, we may learn to harvest their products at sustainable rates. What else can we do to preserve plant diversity? Few questions are as important, as we'll explore more fully in Unit Eight (Ecology).

CONCEPT CHECK 30.4

1. Explain why plant diversity can be considered a nonrenewable resource.
2. **WHAT IF?** How could phylogenies be used to help researchers search more efficiently for novel medicines derived from seed plants?

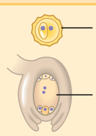
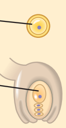
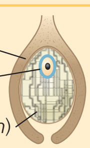
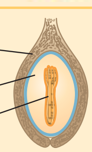
For suggested answers, see Appendix A.

30 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 30.1

Seeds and pollen grains are key adaptations for life on land (pp. 618–621)

Five Derived Traits of Seed Plants	
Reduced gametophytes	Microscopic male and female gametophytes (*n*) are nourished and protected by the sporophyte (2*n*)  Male gametophyte; Female gametophyte
Heterospory	Microspore (gives rise to a male gametophyte); Megaspore (gives rise to a female gametophyte) 
Ovules	Ovule (gymnosperm): Integument (2*n*), Megaspore (*n*), Megasporangium (2*n*) 
Pollen	Pollen grains make water unnecessary for fertilization 
Seeds	Seeds: survive better than unprotected spores, can be transported long distances: Seed coat, Food supply, Embryo 

? *Describe how the parts of an ovule (integument, megaspore, megasporangium) correspond to the parts of a seed.*

CONCEPT 30.2

Gymnosperms bear "naked" seeds, typically on cones (pp. 621–625)

- Gymnosperms appear early in the plant fossil record and dominated many Mesozoic terrestrial ecosystems. Living seed plants can be divided into two monophyletic groups: gymnosperms and angiosperms. Extant gymnosperms include cycads, *Ginkgo biloba*, gnetophytes, and conifers.
- Dominance of the sporophyte generation, the development of seeds from fertilized ovules, and the role of pollen in transferring sperm to ovules are key features of a typical gymnosperm life cycle.

? *Although there are fewer than 1,000 species of gymnosperms, the group is still very successful in terms of its evolutionary longevity, adaptations, and geographic distribution. Explain.*

CONCEPT 30.3

The reproductive adaptations of angiosperms include flowers and fruits (pp. 625–632)

- Flowers generally consist of four whorls of modified leaves: sepals, petals, stamens (which produce pollen), and carpels (which produce ovules). Ovaries ripen into fruits, which often carry seeds by wind, water, or animals to new locations.
- An adaptive radiation of angiosperms occurred during the Cretaceous period. Fossils, phylogenetic analyses, and developmental studies offer insights into the origin of flowers.
- Several groups of basal angiosperms have been identified. Other major clades of angiosperms include magnoliids, monocots, and eudicots.

- Pollination and other interactions between angiosperms and animals may have contributed to the success of flowering plants during the last 100 million years.

? *What makes the origin of angiosperms puzzling? Has Darwin's "abominable mystery" been solved? Explain.*

CONCEPT 30.4

Human welfare depends greatly on seed plants (pp. 632–634)

- Humans depend on seed plants for products such as food, wood, and many medicines.
- Destruction of habitat threatens the extinction of many plant species and the animal species they support.

? *Explain why destroying the remaining tropical forests might harm humans and lead to a mass extinction.*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Where in an angiosperm would you find a megasporangium?
- a. in the style of a flower
- b. inside the tip of a pollen tube
- c. enclosed in the stigma of a flower
- d. within an ovule contained within an ovary of a flower
- e. packed into pollen sacs within the anthers found on a stamen

2. A fruit is most commonly
- a. a mature ovary.
- b. a thickened style.
- c. an enlarged ovule.
- d. a modified root.
- e. a mature female gametophyte.

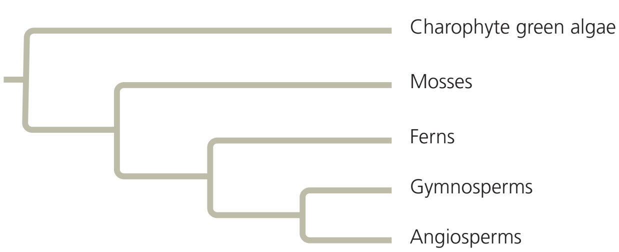
3. With respect to angiosperms, which of the following is *incorrectly* paired with its chromosome count?
- a. egg—n
- b. megaspore—$2n$
- c. microspore—n
- d. zygote—$2n$
- e. sperm—n

4. Which of the following is *not* a characteristic that distinguishes gymnosperms and angiosperms from other plants?
- a. alternation of generations
- b. ovules
- c. integuments
- d. pollen
- e. dependent gametophytes

5. Gymnosperms and angiosperms have the following in common *except*
- a. seeds.
- b. pollen.
- c. vascular tissue.
- d. ovaries.
- e. ovules.

LEVEL 2: APPLICATION/ANALYSIS

6. **DRAW IT** Use the letters a–d to label where on the phylogenetic tree each of the following derived characters appear.
- a. flowers
- b. embryos
- c. seeds
- d. vascular tissue



7. **EVOLUTION CONNECTION**
The history of life has been punctuated by several mass extinctions. For example, the impact of a meteorite may have wiped out most of the dinosaurs and many forms of marine life at the end of the Cretaceous period (see Chapter 25). Fossils indicate that plants were less severely affected by this and other mass extinctions. What adaptations may have enabled plants to withstand these disasters better than animals?

LEVEL 3: SYNTHESIS/EVALUATION

8. **SCIENTIFIC INQUIRY**
DRAW IT As will be described in detail in Chapter 38, the female gametophyte of angiosperms typically has seven cells, one of which, the central cell, contains two haploid nuclei. After double fertilization, the central cell develops into endosperm, which is triploid. Because magnoliids, monocots, and eudicots typically have female gametophytes with seven cells and triploid endosperm, scientists assumed that this was the ancestral state for angiosperms. Consider, however, the following recent discoveries:
- Our understanding of angiosperm phylogeny has changed to that shown in Figure 30.12b.
- *Amborella trichopoda* has eight-celled female gametophytes and triploid endosperm.
- Water lilies and star anise have four-celled female gametophytes and diploid endosperm.
  - a. Draw a phylogeny of the angiosperms (see Figure 30.12b), incorporating the data given above about the number of cells in female gametophytes and the ploidy of the endosperm. Assume that all of the star anise relatives have four-celled female gametophytes and diploid endosperm.
  - b. What does your labeled phylogeny suggest about the evolution of the female gametophyte and endosperm in angiosperms?

9. **WRITE ABOUT A THEME**
The Cellular Basis of Life Cells are the basic units of structure and function in all organisms. A key feature in the life cycle of plants is the alternation of multicellular haploid and diploid generations. Imagine a lineage of flowering plants in which mitotic cell division did not occur between the events of meiosis and fertilization (see Figure 30.10). In a short essay (100–150 words), describe how this change in the timing of cell division would affect the structure and life cycle of plants in this lineage.

For selected answers, see Appendix A.