Chapter 24

Gymnosperms

KEY CONCEPTS

1. The evolution of seeds, pollen, and wood freed plants from the need for water during reproduction, allowed for more effective dispersal of sperm, increased parental investment in the next generation and allowed for greater size and strength.

2. Seed plants originated in the Devonian period from a group called the progymnosperms, which possessed wood and heterospory, but reproduced by releasing spores. Currently, five lineages of seed plants survive--the flowering plants plus four groups of gymnosperms: cycads, Ginkgo, conifers, and gnetophytes. Conifers are the best known and most economically important group, including pines, firs, spruces, hemlocks, redwoods, cedars, cypress, yews, and several Southern Hemisphere genera.

3. The pine life cycle is heterosporous. Pollen strobili are small and seasonal. Each sporophyll has two microsporangia, in which microspores are formed and divide into immature male gametophytes while still retained in the microsporangia. The gametophytes are released to the wind as pollen grains. Ovulate cones are large and require 2 years to mature. Each cone scale has two magasporangia, in which megaspores are formed. The megaspores divide into mature female gametophytes while still retained in the megasporatgia.

4. Pollen grains sift down into ovulate cones and germinate, producing a pollen tube, which grows through the megasporangium toward a megagametophyte. Both male and female gametophytes are small, simple structures and depend on the sporophyte for nutrition.

5. Fertilization of one egg is sufficient to trigger the development of a seed. Pine seeds contain an embryo sporophyte, stored food (in the form of megagametophyte tissue), and a seed coat. The function of the seed is to protect and disperse the next generation away from the parent plant, in both space and time.

24.1 GYMNOSPERMS: SEEDS, POLLEN, AND WOOD

In the long evolutionary history of plants, few developments have had more profound consequences than the evolution of seeds and pollen. Seed-bearing plants have been prominent in nearly all terrestrial ecosystems from the Paleozoic era to today. Their success in undoubtedly due, in large part, to the evolution of seeds and pollen, which freed them from the films of water needed by other tracheophytes for sperm to swim to the archegonia. The advent of seeds and pollen also provided other benefits to plants. Megagametophytes are retained in the megasporangium, where they receive nutrition and protection. Microgametophytes (pollen) have a brief period of independence that ends when they land on a megasporangium. If they succeed in entering the megasporangium, they receive nutrition and protection and complete their development inside of it. Seeds and pollen thus allow significant parental investment in the next generation.

A prominent characteristic of the seed-bearing plants is extensive secondary growth and the production of wood. Other groups, such as the lepidodendrids and sphenophytes, independently evolved lateral cambia and secondary growth. However, the ancestors of seed plants evolved a different sort of secondary growth that led to the ability to produce exceptionally large and strong plants, something the secondary growth mechanisms of seedless plants never achieved.

The earliest **seed plants** produced seeds that sat unprotected on the surface of leaves or modified stems. Although many of the descendants of these first seed plants hid their seeds beneath cone scales or other specialized structures, they are collectively called **gymnosperms** (derived from the Greek *gymnos* meaning "naked" and *sperma* meaning "seed"). This characteristic distinguishes them from another lineage, the flowering plants, which embed their seeds inside a fruit (Fig. 24.1). The nonflowering seed plants persist today as a diverse group of about 900 species of trees, shrubs, or vines. They are present throughout the world, in most ecosystems, and are particularly prominent in cool-temperate forests.

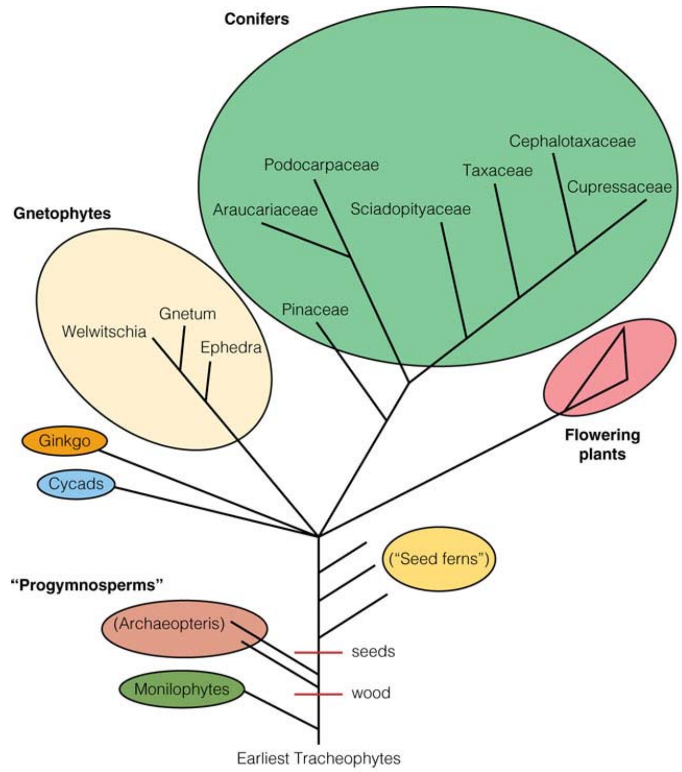

Figure 24.1. Cladogram of the relationships among seed plants. All five lineages of seed plants are shown as emerging from a single point, because there is uncertainly about the actual order of branching. Some studies suggest that gnetophytes are in the conifer sub-clade or a sister to it. Many analyses show cycads as the basal-most gymnosperm group.

Common examples of living gymnosperms include cycads (*Cycas, Dioon, Zamia*), maidenhair tree (*Ginkgo*), cedar (*Cedrus*), fir (*Abies*), juniper (*Juniperus*), pine (*Pinus*; Fig. 24.2), redwood (*Sequoia, Metasequoia, Sequoiadendron*), spruce (*Picea*), and Mormon tea or joint fir (*Ephedra*). Some of these plants have great economic and ecological importance. This chapter considers the origin and evolution of the key innovations of seed plants and surveys the diversity of living gymnosperms.

The Origin of Seeds, Pollen, and Wood

A variety of intriguing fossils from the Devonian and early Carboniferous periods give us a picture of how seed plants originated. Fossils belonging to an extinct group called **progymnosperms** are particularly important in shaping out understanding of this phase of plant evolution. The progymnosperms represent an intermediate

Figure 24.2. Gymnosperms include the pines, which have needlelike leaves borne in clusers and seeds borne naked in woody cones. This species is ponderosa pine (*Pinus ponderosa*).

Figure 23.3. A reconstruction of Archaeopteris, a Devonian tree about 25 m in height.

form, or "missing link," revealing the transition from a spore-releasing vascular plant to a seed plant. In the middle to late Devonian period, progymnosperms existed that were small (shrub-sized at most) and homosporous and added wood to their stems from a solid central core of vascular tissue. Beginning in the late Devonian period, another group of progymnosperms appeared that were quite different. One spectacular example was *Archaeopteris*, a tree that may have reached 25 m in height (Fig. 24.3). Fossils show that this plant had a vascular system with a ring of separate bundles around a pith of parenchyma cells and that it produced abundant secondary xylem. The wood and the growth form of these trees were similar to familiar modern trees such as pines and redwoods. However, these gymnosperm-like trunks bore small leaves arranged in flattened sprays reminiscent of fern fronds, and, like ferns, they reproduced by releasing spores into the air.

Plants with true seeds also appeared in the Devonian period. Unattached seeds were found in fossil bed from this period, but for a long time the plants that produced them were unknown (Fig. 24.4a). Small trees with fernlike foliage were found in these beds, too, and were thought to be a sort of tree fern. Paleobotanists eventually found fossils of the seeds attached to the fronds of these small trees and realized that they were not ferns but seed plants. The name seed fern was created to describe them. Several lineages of Paleozoic seed ferns are now known.

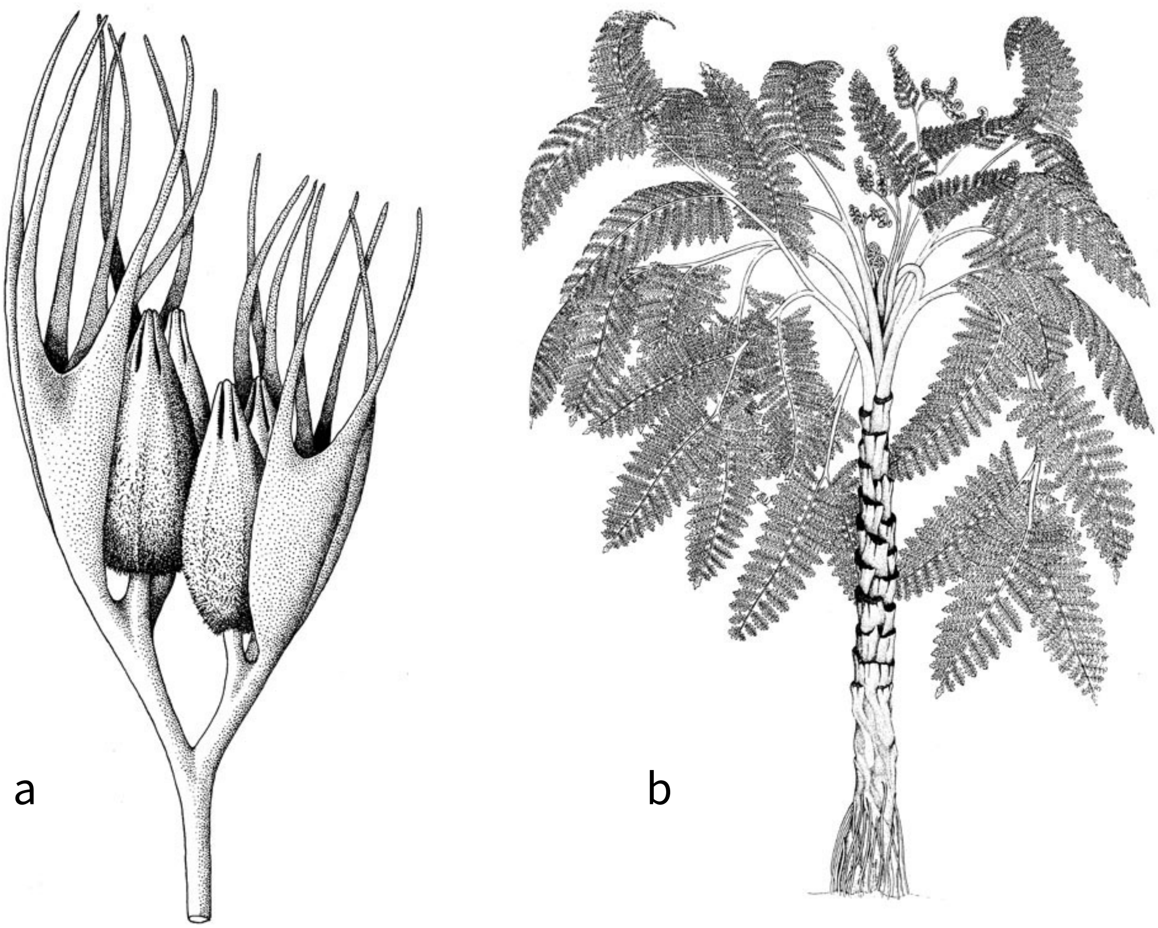

Figure 24.4. Reconstructions of Paleozoic seed ferns. (a) A precursor of the seed surrounded by leaflike structures produced by *Archeosperma arnoldii*, from the Devonian period. (b) *Medullosa noei*, a small seed fern (about 1 m tall) from the Carboniferous.

The oldest known seed plant, *Elkinsia polymorpha,* was a small tree with the typical fernlike foliage of seed ferns and a ring of separate vascular bundles that gave rise to cambia and secondary growth. Fossils of this plant have been found in West Virginia and Belgium. Another example of an early seed fern is *Medullosa,* a common Coal Age tree (Fig. 24.4b).

Seeds and Pollen Are Key Reproductive Innovations for Life on Land

Seeds are distinctive structures consisting of a protective outer covering (the seed coat), an embryo, and stored food. A seed develops from a megasporangium. Before the megasporangium matures into a seed, it is called an **ovule**. An ovule does not yet have an embryo, and it is composed of megasporangium tissue inside a protective covering called the **integument** that is equipped with a tiny hole at one end, the **micropyle**, which allows for the entrance of pollen. The megasporangium tissue, called the **nucellus** in seed plants, functions both to give rise to the megaspore by meiosis and to provide nutrition to the developing megagametophyte.

As the ovule develops, the retained megaspore gives rise to a megagametophyte, which ultimately produces egg cells. The ovule becomes a seed when the egg cell is fertilized and an embryo develops, the integument hardens into a seed coat, and the micropyle closes. In the mature seed, the megagametophyte tissue provides nutrition for the embryo and seedling.

How did such a complex structure evolve? A series of small steps can account for the evolution of seeds. The first step must have been the appearance of heterospory. The earliest tracheophytes were homosporous, but heterospory arose independently in many later lineages, including progymnosperms, the ancestors of seed plants. Heterospory is a crucial first step because it creates a division of labor, enhancing the sedentary nature of one type of gametophyte (*mega-*) and the mobility of the other (*micro-*).

Once heterospory was established, a key innovation was the retention of the megaspore inside the megasporangium. However, this innovation creates a potential problem. When the retained megaspores germinate, the resulting megagametophytes must complete their development within the sporangium. In seedless vascular plants, such as *Selaginella*, four megaspores, products of meiosis, typically are produced per megasporangium. In seed plants, the number of functional megaspores must be reduced to one to avoid competition for space and food; therefore, in seed plants, three of the four megaspores resulting from meiosis typically disintegrate.

A single functional megaspore, giving rise to a megagametophyte while still inside the sporangium, is nearly an ovule. The only missing piece is the integument. How the integument originated has caused much debate. Paleobotanists have shown that some of the early Paleozoic seed ferns from the late Devonian and Carboniferous periods had a series of separate lobes of tissue around their megasporangia. These progressively fused to form more complete coverings. In later plants, they covered the entire megasporangium, except for a region near the tip.

If the megagametophyte remains inside the megasporangium, surrounded by an integument and attached to the parent sporophyte, then another problem arises. How does the sperm get from the microgametophyte to the egg? The sperm cannot swim to the megagametophyte, but rather must be delivered directly. The solution to this problem is **pollen**.

A pollen grain is an immature microgametophyte. In seedless vascular plants with heterospory, the microspore leaves the microsporangium, germinates, and undergoes a series of mitotic divisions to create a microgametophyte within the spore wall. This microgametophyte consists of a layer of antheridial jacket cells and a mass of sperm-producing cells. In contrast, pollen begins its development inside the microsporangium, goes through fewer mitotic divisions, and does not produce the antheridial jacket layer. When a pollen grain is ready to leave the microsporangium, it consists of between two and five haploid nuclei. If it reaches an ovule, it goes through several more rounds of mitosis and produces two sperm cells and an elongated structure called a pollen tube, which in most seeds conveys the sperm to the egg.

Seed Plants have Distinctive Vegetative Features

In addition to seeds and pollen, gymnosperms are characterized by a number of vegetative features, including megaphylls, originally fernlike, but later typically reduced to simple leaves, needles, or scales; a primary stem vascular system composed of a ring of separate bundles with phloem toward the outside and xylem toward the center; secondary growth from lateral cambia, producing abundant secondary xylem to the inside and secondary phloem to the outside; and a main stem that has lateral branching, with nodes made up of leaves and axillary buds.

All but a few gymnosperms are woody. Most are trees, some of which have great bulk, such as the coast and Sierran redwoods.

Relationships among Gymnosperms

Based on cladistic studies using morphology in fossil groups and molecules and morphology in living groups, botanists believe that seeds arose only once. The appearance of seeds coincided with a great adaptive radiation of new plant groups. All these early seed plants (the seed ferns) became extinct, but they gave rise to a number of lineages that persisted. Currently, five major lines of seed plants remain, which form a clade (Fig. 24.1). One lineage, the flowering plants, has been particularly successful and dominates the world's flora. The four other surviving lineages are the gymnosperms.

Large-sale molecular analyses have indicated, to the surprise of many systematists, that flowering plants did not evolve from one of the living gymnosperm groups, as had long been assumed. Instead, the living gymnosperms form a clade that is a sister group to flowering plants (Fig. 24.1).

These four gymnosperm groups traditionally have been classified as divisions. Studies indicate that each of the four lineages is monophyletic (with the possible exception of the conifers), but the exact relationships among them have proven to be a stubborn problem. Because of uncertainly concerning the phylogeny of gymnosperms, Figure 24.1 shows them all as originating from the same point.

Despite the uncertainty about relationships, most analyses place cycads at the base of the gymnosperm tree because they possess a series of ancestral features. Ginkgo also retains a number of ancestral traits, but it shares many similarities with conifers. Conifers make up the bulk of gymnosperm species. A distinctive and puzzling group, the gnetophytes, has created a great deal of debate among botanists. They possess certain vegetative and reproductive traits that are amazingly similar to flowering plants, but recent molecular analyses have classified them in the gymnosperm lineage.

THE MESOZOIC: ERA OF GYMNOSPERM DOMINANCE

The Mezozoic era (245 million to 65 million years ago) was the age of gymnosperms, dinosaurs, and moving continents. During the Permian period, which marked the end of the Paleozoic era, climates became cooler and drier. Dominance of the world's vegetation by seedless vascular plants came to an end. Gymnosperm groups evolved increasingly effective adaptations to arid conditions and spread into many habitats. Our best geologic reconstruction of the world at the start of the Mesozoic era is that all the continents were joined into a single landmass near the equator. Beginning in the Triassic period, this primeval supercontinent, called **Pangaea**, began to break apart, North and South America split from Europe and Africa, and the Atlantic Ocean formed. Prominent Mesozoic gymnosperms included a great variety of cycads, *Ginkgo* relatives, and gnetophytes (Fig 24.5). Conifers similar to those in our modern flora, including forms of cypress, juniper, monkey puzzle tree, pine, and redwood, first appeared in the early Triassic period.

Several other groups of gymnosperms that are completely extinct today were also important elements of many Mesozoic floras. These include a diverse assemblage of Mesozoic seed ferns and the curious Cycadeoids, which had large compound leaves and short, unbranched stems like cycads. Despite their similarity to cycads, cycadeoids had a different life history, including flower-like structures that contained both megasporangia and microsporangia (Fig. 24.5b). Because of this characteristic, they have been proposed as possible relatives or ancestors of the flowering plants. Currently, it has not been determined where they fit into the phylogeny of plants, but they were probably not closely related to cycads.

Figure 24.5. Reconstructions of two extinct gymnosperms. (a) *Cordaites*, 9 to 30 m in height, from the Carboniferous period. (b) *Williamsonia*, 5 m in height, a cycadeoid, an extinct group superficially similar to cycads.

As the Mesozoic era drew to a close, climates and continents continued to change. A southern continent called Gondwanaland split apart, and India became an island. Mountain building created cool weather at high elevations and arid regions in their lee. The climatic gradient from tropics to poles became steeper. Many gymnosperms, including all seed ferns, became extinct, and the first flowering plants came to dominate the flora. Dinosaur populations declined, whereas social insects and mammals multiplied and diversified. Today, gymnosperms have fewer species and growth forms, and they occupy fewer habitats than during the Mesozoic era.

24.3 THE VASCULAR SYSTEM OF GYMNOSPERMS

Gymnosperms are anatomically and morphologically more complex and longer lived than any group discussed so far in our survey of plants. They all share a primary stem vascular system composed of a ring of bundles defining a distinct pith and cortex region. Each vascular bundle contains primary phloem to the outside and primary xylem toward the center. As gymnosperms grow, they form a vascular cambium, which produces the secondary tissues. The process is the same for all gymnosperms, but there are some differences in their secondary growth patterns. For example, cycads produce a light wood, containing abundant living parenchyma cells, whereas *Ginkgo* and conifers produce dense wood, composed primarily of cells that are dead at maturity.

All gymnosperm trunks have secondary xylem and phloem, rays, and bark. The anatomy of most gymnosperm wood is extremely regular (Fig. 24.6). Part of the reason for this regularity is the absence of vessels. In many gymnosperms, including a majority of conifers and *Ginkgo*, tracheids produced in the spring are largest in diameter; as the season progresses, new tracheids are smaller in diameter and have thicker walls. Some tracheids are so thick that they resemble fibers and are called fiber-tracheids. The seasonal variation in tracheid size results in annual rings in the wood. Xylem rays are thin and are composed of brick-shaped parenchyma cells and, in some cases, special ray tracheids. Other parenchyma cells are stacked in vertical columns; these are called axial parenchyma. Gnetophytes differ from all other conifers in that they may have vessels in their wood.

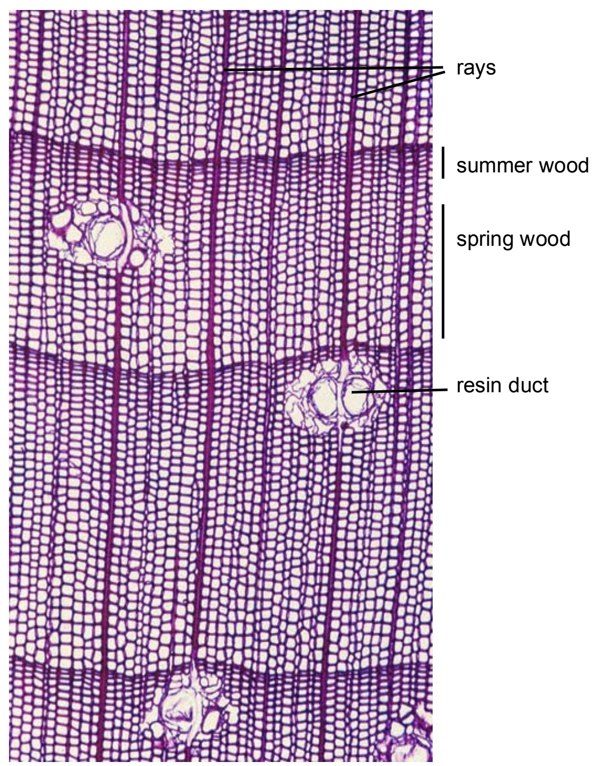

Figure 24.6. Three growth rings of pine, as seen in cross section. Several resin ducts are visible, but not all conifers have resin ducts in their xylem.

The phloem of gymnosperms contains **sieve cells** (conducting cells similar to sieve-tube members but not associated with companion cells), fibers, ray parenchyma, and axial parenchyma.

Many gymnosperms, particularly conifers, produce **resin**, a mix of complex organic compounds. Typically, resin accumulates and flows in long **resin ducts**, chambers enclosed by parenchyma cells (Fig. 24.6). Resin inhibits wood-boring insects. If insects penetrate the trunk and break through any resin duct, they are encased in a flow of resin and immobilized. Trees that are stressed by drought or disease produce less resin, making them susceptible to insect infestation.

Many gymnosperms, both fossil and living, are supremely adapted to survive drought. Pine needles (leaves), for example, show many anatomical adaptations to aridity. They have a thick cuticle, sunken stomata, a fibrous epidermis, closely packed mesophyll cells without intercellular air spaces, and veins (vascular bundles) only in the center of the leaf (Fig. 24.7). Leaves are thick, rather than thin, yielding a low surface-to-volume ratio. These traits reduce the loss of water vapor. Needles have a life span that ranges from 3 to 30 years, depending on the species. Although the leaves do not continue growing during that life span, their vascular bundles do undergo secondary growth, producing a limited amount of secondary phloem but no secondary xylem.

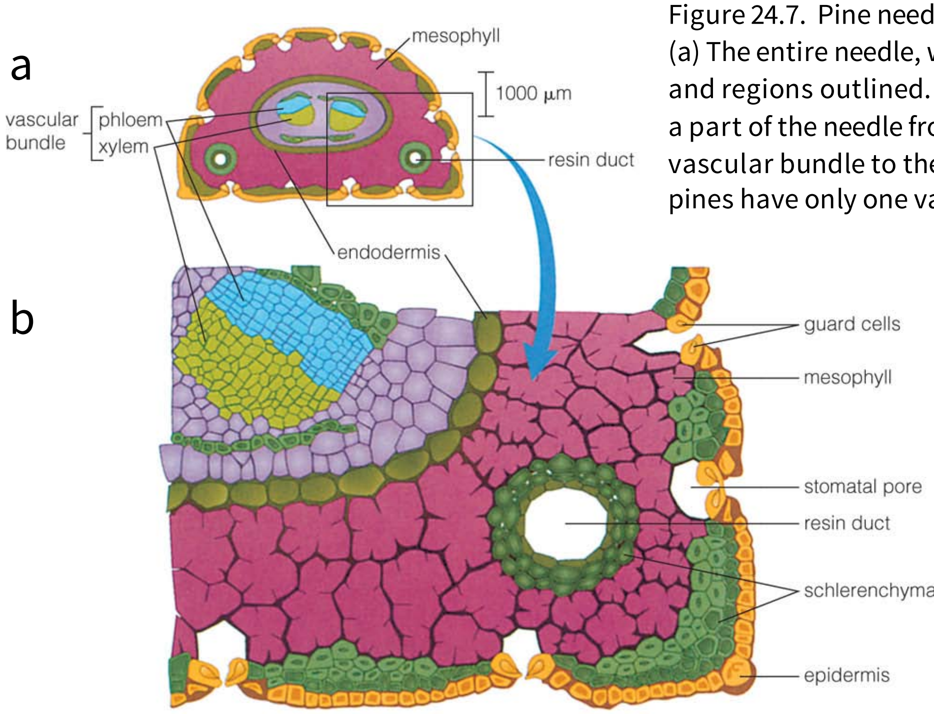

Figure 24.7. Pine needles in cross-section. (a) The entire needle, with major tissues and regions outlined. (b) Cellular details of a part of the needle from one of two vascular bundle to the epidermis. Some pines have only one vascular bundle.

24.4 CYCADS

Some 200 million years ago, during the early Mesozoic era, cycads made up a large part of the earth's vegetation and were probably food for herbivorous dinosaurs. Today, the once-diverse group contains only 11 genera and about 125 species, which grow in widely separated areas, largely in the tropics. Only one species, *Zamia integrifolia*, occurs naturally in the United States, in Florida and southern Georgia.

Cycads contain potent toxins, but they can be eaten in prepared correctly. There is archeological evidence for extensive consumption of cycad seeds in Australia up to 13,000 years ago. The stem pith also can yield edible starch, and a commercial starch extraction industry existed in south Florida between 1845 and 1925. The genera *Cycas*, *Dioon*, and *Zamia* are widely propagated as ornamental plants, either outdoors or in greenhouses (Fig. 24.8).

Figure 24.8. Cycads. (a) *Cycas revoluta* (sago palm). (b) *Zamia furfuracea* with ovulate cones.

Many cycads are palmlike in appearance, and some of their common names reflect this nature (*Cycas revoluta* is sago palm, for example). Others, such as *Zamia*, have largely subterranean stems. Cycads are slow-growing: a specimen 2 m in height might be as old as 1,000 years.

Cycads have a number of distinctive features. They are the only gymnosperms to produce large compound leaves. They branch rarely, if at all, and although they have secondary growth, the wood is different from the wood of conifers because it has a lot of parenchyma in the xylem.

All cycads are dioecious. The seed-producing cone (ovulate strobilus or ovulate cone) is large and often protected by sharp prickles or woody plates. The pollen strobili also are large and upright; pollen is transported to the ovules by beetles in some species, or by wind. The microgametophytes grow a pollen tube that infiltrates the tissues of the ovule. Eventually, the microgametophyte produces two large multiflagellated sperm that swim to an enormous egg cell. The seeds of many cycads are covered with a fleshy, brightly colored seed coat to attract animal dispersers.

24.5 GINKGO

A single living representative remains of the ancient ginkgophytes, the maidenhair tree (*Ginkgo biloba*; Fig. 24.9). It grows wild today only in warm-temperate forests of

China, but it has been grown for centuries on Chinese and Japanese temple grounds as a traditional decorative tree. It also is widely planted throughout the world as an urban street tree, because it is tolerant of pollution.

Chinese herbalists prescribe infusions of the leaves as a medicine for many ailments, and the tree is a symbol of longevity. *Ginkgo* leaf is currently one of the most widely used herbal supplements, taken for brain dysfunction and cardiovascular fitness. The seeds have been as important food in Asia for more than 2,000 years, despite being mildly toxic. They were consumed in Japan in great quantities during World War II because of food shortages, and cases of poisoning were common. Although today poisoning is rare, it still occurs, especially in children.

Figure 24.9. A branch and leaves of *Ginkgo biloba* (maidenhair tree). The leaves have turned yellow and are about to fall off as winter begins.

Like conifers, *Ginkgo* is a large, diffusely branching tree; some trees have trunks more than 3 m in diameter. The dense wood of *Ginkgo* is similar to conifer wood and lacks the abundant parenchyma of cycads. The leaves of *Ginkgo* are unique. They are fan-shaped and often are divided into two lobes. In fall, they turn a brilliant golden color and drop.

Like cycads, *Ginkgo* is strictly dioecious. The pollen is produced in small strobili and transported by wind to ovulate trees. The microgametophytes are similar to those of cycads, and they produce large, flagellated sperm. The ovules are borne in pairs on stalks rather than in a strobilus. Pollen-producing trees are preferred as ornamentals because the seeds are covered with a foul-smelling, fleshy seed coat.

24.6 CONIFERS

The most widely known and economically important gymnosperms are the **conifers**, with approximately 650 species. Woody seed cones are unique and so conspicuous a feature that this group is named for them: *conifer* means "cone-bearer." Conifers that lack woody cones include junipers, podocarps, yews, and plum yews; in these plants, a berry-like tissue surrounds the seeds, making them resemble the fruits of flowering plants. Botanists, however, interpret the fleshy coverings as either modified cone scales or as an elaboration of the integument.

Traditionally, the conifers have been divided into eight taxonomic families. Cladistic analyses using ribosomal RNA genes have revealed that, with one exception, the families are all monophyletic (Fig. 24.10). To solve the remaining problem, one family (Taxodiaceae) has been nullified, and all of its members placed in another family (Cupressaceae). This section uses the traditional names for the groups because they are familiar. However, these names are used in a phylogenetic context, to designate clades and not taxonomic ranks. Pinaceae is the basal lineage. The remaining conifers fall into two big clades; one is composed on the largely Southern Hemisphere groups Araucariaceae and Podocarpaceae; the other clade includes the Taxaceae, Cupressaceae, and two groups unfamiliar in the United States, Sciadopityaceae and Cephalotaxaceae.

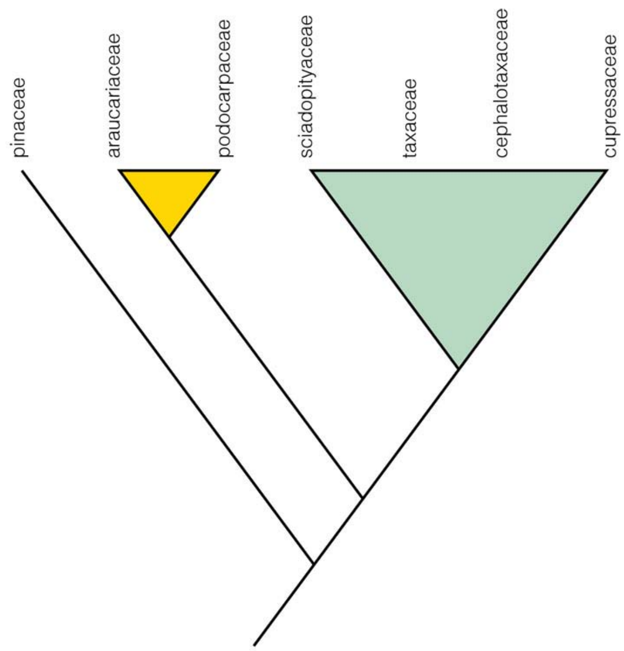

Figure 24.10. A cladogram of relationships among conifer families.

Figure 24.11. Fascicles of needles borne on short pine shoots.

Pinaceae Include the Pine, Firs, and Spruces

Pinaceae are important economically for wood, pulp, turpentine, and resin, as well as for ornamentals. Found primarily in the Northern Hemisphere, this group constitutes the bulk of conifer forests. Leaves are needlelike and are borne singly or in clusters called **fascicles** on special short shoots (Fig. 24.11). Most species are monoecious. The seed cone scales have two seeds each, and the seeds usually are provided with a wing made of a thin layer of cone scale tissue. The bract beneath each cone scale is free of (not fused to) the cone scale, at least initially. There are 10 genera in the family.

The pines (*Pinus*) are the largest genus in the family, with 93 species. Pines usually are large, long-lived trees with an asymmetrical shape. Bristlecone pines (*Pinus longaeva*) are the oldest living organisms, some individuals reaching more than 5,000 years of age. Pine needles are clustered, two to five per fascicle, except for the single-leaf pinyon (*Pinus monophylla*). They are oval to triangular in cross section. Cones are pendant (hanging) and vary greatly in size. Usually, cones are shed once the seeds have matured and spilled out. Some closed-cone pines, however, keep their scales closed until heated by fire, which may not occur for many years. The ecological advantage of this behavior is that a rain of seeds falls onto the mineral-rich ashes immediately after a fire have removed all competing vegetation. Although the parent generation of pines is killed by the fire, the species retains its dominance because the site is reoccupied by the next generation.

Firs (*Abies*) have a symmetrical, cylindrical, or pyramidal shape. Firs are neither as long-lived nor as large as pines. Each year's growth is marked by a symmetrical whorl of branches, and it is possible to determine the age of young trees by counting the number of branch whorls from tip to base. Needles are borne singly. Seed cones are carried erect on the branches (Fig. 24.12), and they shatter at maturity rather than falling as a unit. There are about 40 species of firs, all restricted to cooler parts of the Northern Hemisphere.

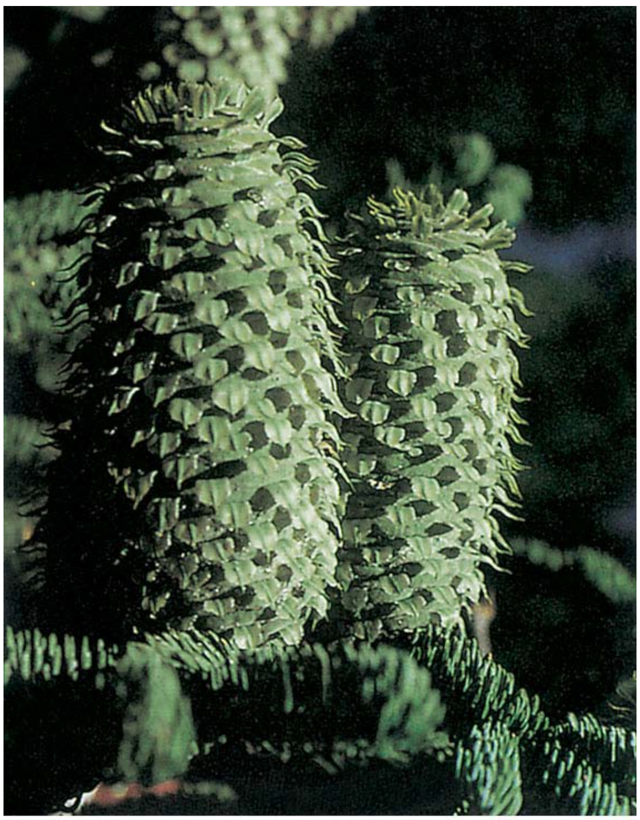

Figure 24.12. (left) Mature ovulate cones of Shasta red fir, *Abies magnifica* var. *shastensis*. Cones in this genus are borne upright. Note the long bracts projecting beyond the cone scales.

Figure 24.13. *Picea abies* (Norway spruce) cones. Although light, they are pendant (hang down).

Spruces (*Picea*) closely resemble the firs, but the needles are angular in cross section and often are sharply pointed (Fig. 24.13), rather than flat and blunt as are fir needles. Tree crowns often are narrowly columnar. Seed cones are pendant and fall as a unit when mature, except for those of black spruce (*Picea mariana*), a closed-cone conifer and an important species all across Canada. Large-scale wildfires periodically sweep through the Canadian forest, and the closed cones of black spruce allow the species to quickly reestablish itself.

There are about 40 species of spruce, all in the Northern Hemisphere. They tend to require wetter sites than firs, which explains why spruces are absent from places like the Sierra Nevada where firs are common.

Spruces were formerly important for another reason. The Native Americans and later the European immigrants collected the resin from spruce and chewed it. In 1848, John B. Curtis and his brother began to produce what they called State of Maine Pure Spruce Gum. The new gum was slow to catch on, but eventually it became quite popular. Two pieces of spruce gum cost one cent. Gum manufacturers eventually shifted to paraffin and then to chicle latex from an angiosperm tree.

Hemlocks (*Tsuga*) are pyramidal with slender, horizontal branches and drooping tops. The needles are somewhat flat with a short petiole. They resemble the leaves of firs but are much shorter. Cones are small and pendant. There are 10 species of hemlock in North America and Asia.

Douglas firs (*Pseudotsuga*) comprise a genus of only five species, two in North America and three in Asia. One of these species (*Pseudotsuga menziesii*) is the most heavily cut timber tree in the United States. It dominates much of the Pacific Northwest, Cascade, and Rocky Mountain regions. It may grow to a height of 60 m and have a trunk diameter of 3 m. Its smaller branches hang down, and the singly borne needles resemble those of spruce but are much softer. Douglas fir seed cones are pendant and easily recognized by the three-pointed bracts, which are longer than the cone scales and stick out from between them (Fig. 24.14).

Figure 24.14. A *Pseudotuga menziesii* (Douglas fir) branch with needles and cones. The cones are about 8 cm long, and bracts stick out beyond the cone scales. Foliage is soft, in contrast to that of spruce and fir.

Larches and tamaracks (*Larix*) are unusual among conifers in being deciduous. (Some members of the Cupressaceae, such as bald cypress and dawn redwood, are the only others.) They lose all their needles in the fall. Older larch branches have needles grouped into crowded clusters on short shoots. One-year-old shoots, in contrast, have needles arranged singly and spirally. The American larch, or tamarack (*Larix laricina*), frequently is found at the edge of bogs.

Cedars (*Cedrus* sp.) are native to North Africa and Asia. They are widely planted as ornamentals in North America. They vary from asymmetrical to pyramidal in shape, and the needles are borne singly or in fascicles of 10 or more. The cones are thin-scaled and erect on the branches. They usually disintegrate when mature. The cedars have been important timber trees since biblical times.

Cupressaceae Include the Junipers, Cypresses, and Redwoods

Cupressaceae are shrubs or trees, often with small, scalelike or awl-shaped leaves and open branching patterns. Plants can be monoecious or dioecious. Cone scales may be woody, as in cypress (*Cupressus*), or fleshy, as in juniper (*Juniperus*; Fig. 24.15). In either case, the bracts are fused to the cone scales. As in the Pinaceae, there are two seeds per cone scale. The family contains more than 130 species, with a world-wide distribution. Some cypresses are closed-cone conifers. The fleshy cones of junipers are eaten and used to flavor gin.

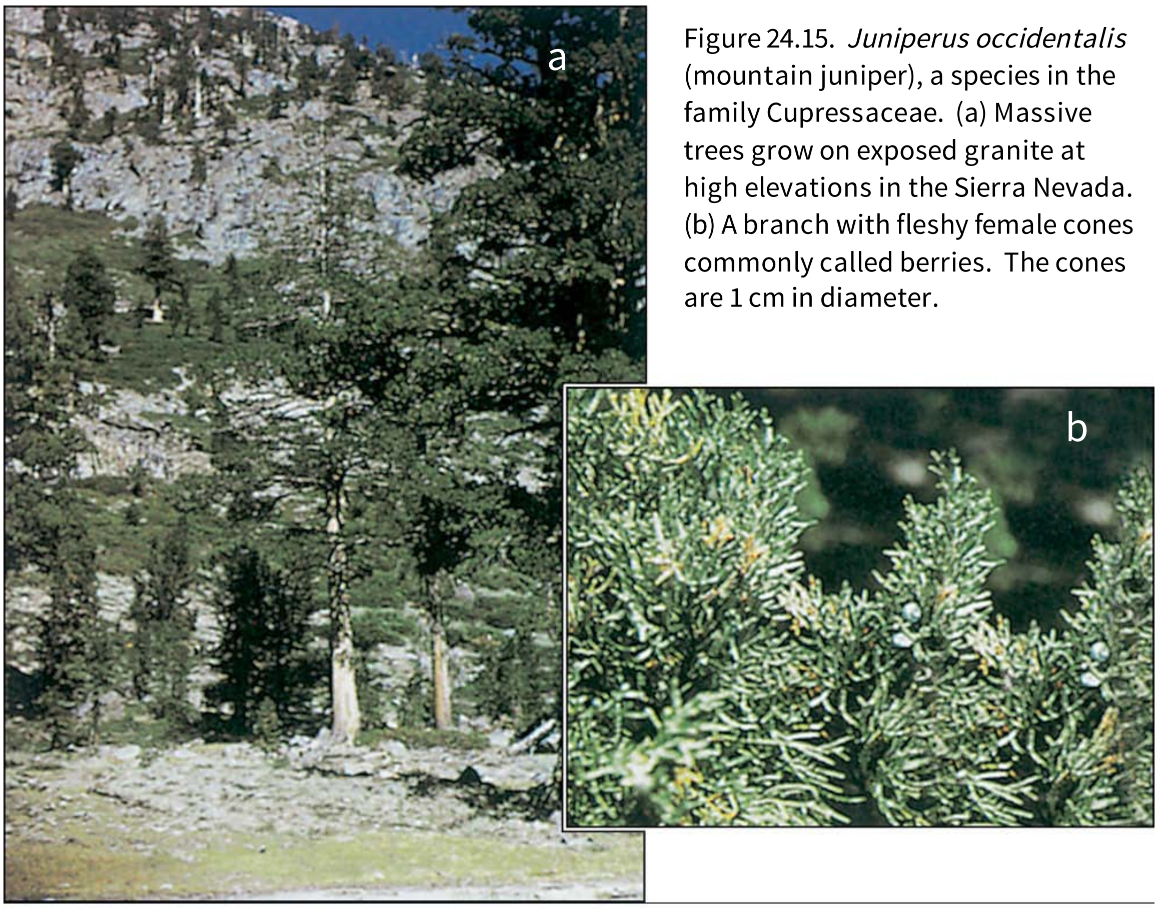

Figure 24.15. *Juniperus occidentalis* (mountain juniper), a species in the family Cupressaceae. (a) Massive trees grow on exposed granite at high elevations in the Sierra Nevada. (b) A branch with fleshy female cones commonly called berries. The cones are 1 cm in diameter.

A number of the members of this group were previously placed in another traditional taxonomic family, Taxodiaceae, but research has shown that these two families are a single lineage. Species formerly in Taxodiaceae are the dawn redwood of China (*Metasequoia gyptostroboides*), the California coast redwood (*Sequoia sempervirens*), the Sierra redwood (*Sequoiadendron giganteum*), the bald cypress of the eastern United States (*Taxodium distichum*), and several other genera from eastern Asia. The dawn redwood and the bald cypress are deciduous. The coast redwood is possibly the tallest tree in the world; individual trees more than 60 m in height are common, and the greatest recorded height is 112 m (see "PLANTS, PEOPLE, AND THE ENVIRONMENT: The California Coast Redwood Forest" end note). Redwood has outstanding lumber qualities, not the least of which is its resistance to decay, conferred by natural byproducts that accumulate in the wood. Sierra redwood is the most massive tree in the world; trunks at breast height reach nearly 10 m in diameter. The trunk alone of the largest living tree, the General Sherman tree in Sequoia-Kings Canyon National Park, is estimated to weigh 1120 metric tons.

Redwoods currently are restricted in their range, but they were once more numerous and widely distributed. Early in the Cenozoic era, 20 to 60 million years ago, they were part of a rich forest that covered the cool-temperate zone of the Northern Hemisphere. This forest had a unique mix of gymnosperm and flowering trees--a mix not found anywhere today. Fossil deposits of this forest have been recovered from Asia, North America, Greenland, and Europe. Climatic change and continental drift fragmented the forest and forced redwoods into a continually shrinking habitat. Dawn redwood, in fact, is so rare and narrowly distributed that it was known only from the fossil record until living trees were discovered in China's Szechwan Province in the 1940s. Seeds have since been distributed all over the world. Dawn redwoods now grow in many botanical gardens and are used as ornamental plants.

Taxaceae Include the Yews, But Plum Yews Belong to Cephalotaxaceae

Taxaceae are shrubs or trees with dark-colored, broadly linear, sharp-pointed leaves. Plants are dioecious. The seeds are borne singly and are covered with a fleshy aril (Fig. 24.16). These are the only conifers to lack cones. One of the family's more than 20 species is the English yew (*Taxus baccata*), famous for excellent bows made of its wood and its connection to English medieval history and folklore. The quality of the wood results from extra spiral thickenings of secondary wall material in tracheids. More recently, the Pacific yew of the western United States (*Taxus brevifolia*) was found to contain an important anticancer compound, taxol (paclitaxel; Bristol-Meyers Squibb, New York, NY). Taxol is present in such small amounts in the bark of Pacific yew (a 100-year-old tree contains only 300 mg) that environmentalists were concerned that deforestation would be justified in the name of medicine. However, chemists synthesized the taxol molecule in the laboratory in 1994, thereby making it unnecessary to fell trees.

Figure 24.16. A branch of Taxus baccata (English yew), a species in the family Taxaceae. The seed is enclosed in an edible, fleshy red aril, attractive to birds, which disperse the seeds.

Cephalotaxaceae consist of fewer than 10 species of Chinese shrubs and trees. Leaves are yew-like. Seeds are borne in pairs and are covered with an aril; they are 2 to 3 cm in length and resemble oval plums. Minute cone scales are associated with the seeds. Plants are dioecious.

Podocarpaceae and Araucariaceae Are Largely Southern Hemisphere Conifers

The Podocarpaceae and Araucariaceae lineages form a clade of predominantly Southern Hemisphere conifers, distinguished by a reduction to a single ovule (and seed) per cone scale. Podocarps are shrubs or trees (Fig. 24.17). Leaves vary, depending on the species, from short needles to long and broadly oblong blades. Plants may be monoecious, but most are dioecious. The seeds are borne singly and enclosed in a fleshy cone scale. The bracts also are sometimes fleshy. As is also true for juniper berries, the cones of podocarps are attractive to birds that digest the fleshy part but defecate the seed.

Many excellent lumber trees of Australasia, Africa, and South America are in this group. *Podocarpus dacrydioides* and *Podocarpus totara* of New Zealand, for example, reach 60 m in height. This is a large lineage, with about 140 species. Most are restricted to the southern Hemisphere, but some occur in Japan, Central America, and the West Indies. A number of species are widely planted as ornamentals.

Araucariaceae are relative large trees in the genera *Araucaria* (monkey puzzle, southern pine), *Agathis* (kauri), and the recently discovered *Wollemia* (wollemi pine). The tallest trees in the tropics, reaching up to 89 m, are species of *Araucaria*; and *Agathis australis* of New Zealand has trunks rivaling those of redwood in girth. Leaves vary from needle-like to flat and broad. Cones tend to be large and globose, and--like fir cones--they disintegrate when ripe. The more than 30 species are exclusively native to the southern Hemisphere, but some, such as the strikingly symmetrical Norfolk Island pine, *Araucaria heterophylla* (Fig. 24.18), are widely planted as ornamentals throughout the world.

Figure 24.17. *Phyllocladus*, a genus of New Zealand shrubs in the podocarp family. Most podocarps are southern hemisphere shrubs or trees. They lack woody cones and instead have fleshy cones often mistaken for berries, like those of junipers.

Figure 24.18. The genus *Araucaria* (southern pines) includes trees among the tallest and most massive in the world. the trees shown here are *Araucaria heterophylla*.

24.7 THE LIFE CYCLE OF *PINUS*, A REPRESENTATIVE GYMNOSPERM

We use pine (*Pinus*) to repesent the typical life cycle of gymnosperms (Fig. 24.19). Pine is a convenient plant to use as a model for several reasons: each tree has both megasporangia and microsporangia, seeds do not have fleshy coverings, and a great deal is known about the life cycle. However, keep in mind that other groups of gymnosperms differ from pine in many ways.

Pollen and Ovules Are Produced in Different Kinds of Structures

All pine sporophytes, like all seed plants, are heterosporous. Pollen is produced in small papery strobili; a **strobilus** is a series of densely aggregated sporophylls that are spirally attached to a stem axis. Female gametophytes in conifers typically are produced in larger, woody structures that are called ovulate or seed cones. In conifers, pollen strobili and ovulate cones differ in size, architecture, longevity, and location on the tree.

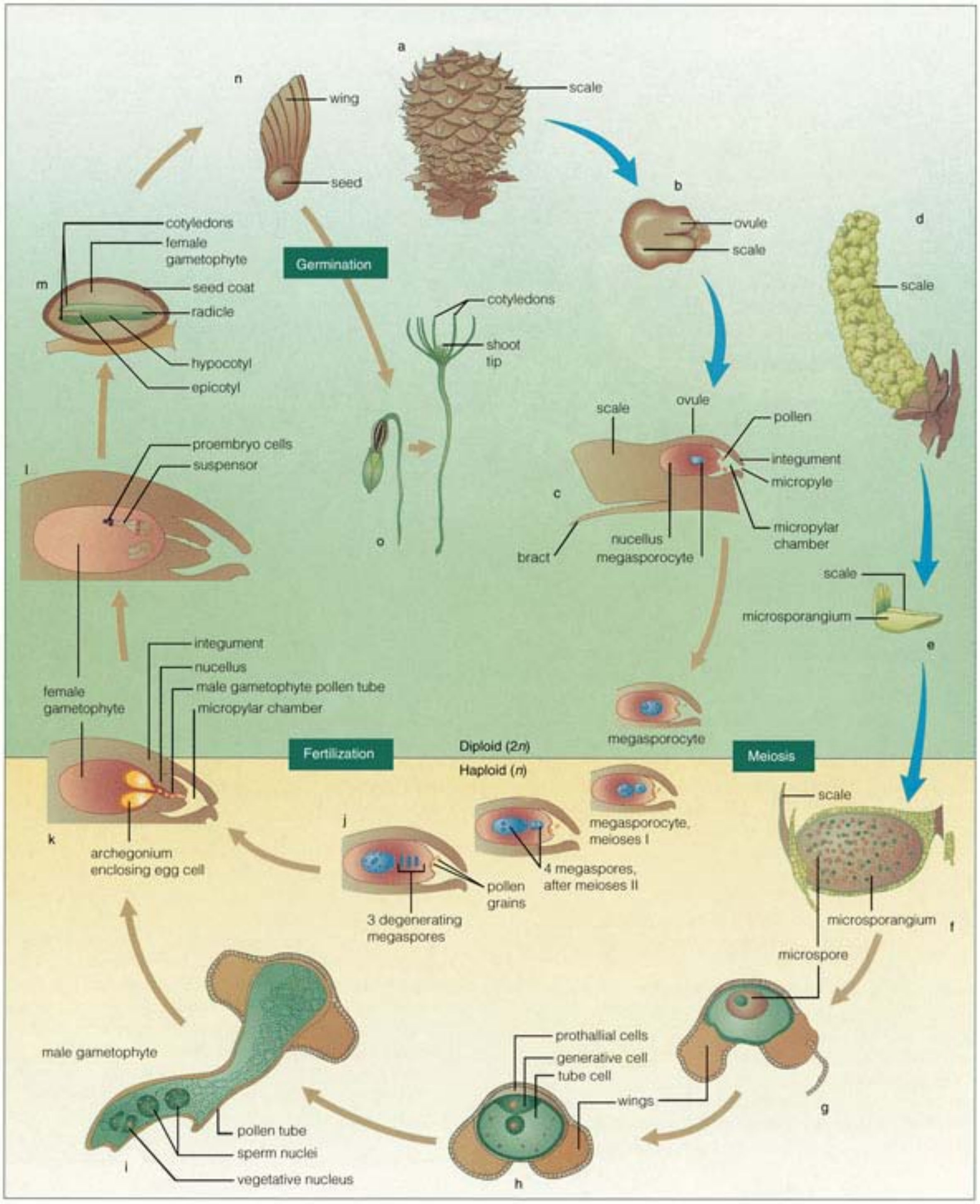

Figure 24.19. Stages in the life cycle of a pine. (a) A young ovulate (seed) cone. (b) A scale from an ovulate cone with two ovules on its upper surface. (c) Longitudinal section of an ovulate cone at the time of pollination. (d) A pollen strobilus. (e) One scale from a pollen strobilus. (f) A section of a microsporangium with mature pollen grains inside. (g-i) A developing make gametophyte. (c,j,k) A developing female gametophyte. (j-n) A developing seed. (o) Germination of the seed.

Pine pollen strobili average 1 cm in length and 5 mm in diameter (Fig. 24.20a). they are borne in groups, usually on the lower branches of trees. Each strobilus is composed of a large number of small microsporophylls attached spirally to an axis. Two microsporangia (more in some conifers) develop on the underside of each sporophyll (Fig. 24.20b). The microsporangium is lined with a layer of nutritive cells called the **tapetum**. Inside are microsporocytes that undergo meiosis and produce haploid microspores. The nucleus within each microspore divides several times by mitosis within the spore wall. The resulting pollen grain contains two nuclei that will undergo further divisions and several squashed vegetative cells (Fig. 24.19g). A pollen grain is an immature male gametophyte (Fig. 24.20c).

a

b

c

Figure 24.20. Pollen strobili. (a) A cluster of strobili at the time of pollen release. (b) Longitudinal section of one strobilus, showing microsporangia attached to the underside of each scale. (c) A pollen grain consists of two cells, each with its own nucleus.

Enormous numbers of **pollen grains** eventually are shed from the microsporangia of a single tree. The pollen grains are yellow and light in weight for dispersal by wind. Windrows of pollen are visible on the ground during the period of release, which is generally in spring. Pine pollen grains have two inflated wings that are outgrowths of the wall; these help orient the pollen grain on the pollination droplet of the ovule. The pollen grains of many other gymnosperm species lack such wings or have a different number.

The mature ovulate cone is the familiar pinecone that is commonly associated with pines and other conifers. It is composed of many woody scales attached to an axis in a spiral arrangement. Each scale has a bract attached to the axis beneath it. This bract is relative small and obscure in pines, but is quite large and even longer than the cone scale in some genera such as Shasta red fir (*Abies magnifica* var. *shastensis*; see Fig. 24.12)

When the ovulate cone is young, it often is reddish and is softer and smaller than the male strobilus. Cones develop singly in early spring at the tips of young branches in the upper part of the tree (Fig. 24.21a). Two ovules develop on the upper surface of each scale (Fig. 24.21b). The pine ovule, consisting of a megasporangium and its integument layer, first appear as small protuberances close to the axis of the cone. The integument, which forms the outermost protective layer of the ovule, possesses an open pore facing the axis of the cone. This pore is the micropyle, through which pollen grains later enter. In pine, only one of the many cells filling the young ovule is a megasporocyte (Fig. 24.21c). The rest of the megasporangium forms the nucellus, a nutritive tissue. When the megasporocyte divides by meiosis, the result is four megaspores arranged in single file. Only one of the megaspores develops into a megagametophyte; the other three degenerate.

The megaspore grows slowly into a female gametophyte. Most conifers require several months, and pine takes just over a year. The development of the gametophyte takes place entirely within the ovule. Two or more archegonia differentiate at the micropylar end of the growing gametophyte, using energy from digestion of the nearby nucellus. Thus, the gametophyte is completely dependent on sporophyte tissue..

At maturity, the ovule consists of an integument, a thin layer of remaining nucellus, and an ovoid female gametophyte that is undifferentiated except for several archegonia at one end, each with an enclosed egg (Fig. 24.22). There is a space between the micropyle and the nucellus; this is the **micropylar chamber**, where pollen grains begin to grow pollen tubes.

Pollination Replaces the Need for Free Water

In flowers, pollination is the transfer of pollen from anther to stigma. In conifers, it is the transfer of pollen from male strobilus to ovulate cone. Wind is the vector that carries conifer pollen. In pine, the placement of ovulate cones above pollen strobili makes it more likely that pollen will be carried to another tree rather than settling on a cone of the same tree. Thus, cross-pollination is usual. For those conifer groups that are dioecious--the Cephalotaxaceae, Cupressaceae, Podocarpaceae, and Taxaceae--self-pollination is impossible; cross-pollination always occurs. Cross-pollination is valuable because it creates more genetic variation in the next generation, increasing the capacity of a species to take advantage of diversity in the environment.

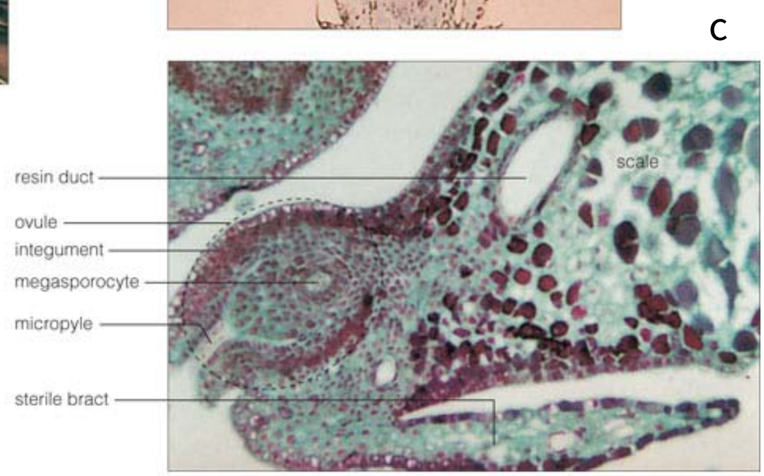

Figure 24.21. Ovulate cones at the time of pollination. (a) two-month-old cones at the tip of a young branch. (b) Longitudinal section through a 2-month-old cone. (c) A closer view of one ovule (dashed area). Note the large megasporocyte inside the nucellus. Meiosis has not yet occurred.

Studies of the aerodynamics of pollen near cones have demonstrated that the shape of the young ovulate cone can create unique air currents and eddies that bring pollen grains of the appropriate species close to the open scales, increasing the probability that pollen will land in the cone. Thus, wind pollination is not entirely random.

Pollination occurs when the ovulate cone is about nine months old (Table 24.1). Female cone buds are initiated in the late summer preceding the spring of pollination. The cone is fully formed in the bud and merely enlarges when the bud breaks in spring. Cone scales at this stage turn slightly away from the cone axis, providing space for pollen grains to drift down to the ovules. A sticky **pollination drop** exudes from the micropyle. The drop is chemically similar to the nectar of flowers, containing about 8% sugar (glucose and fructose) and traces of amino acids. It does not seem to attract animals, but it passively traps pollen grains that touch it.

A chemical signal diffuses from the trapped pollen to the ovule, triggering rapid absorption of the liquid. This draws pollen grains through the micropyle and into the micropylar chamber, where they come to lie on the surface of the nucellus.

The pollen grain germinates, slowly developing an elongating pollen tube that grows through the nucellus toward an egg (Fig. 24.22). Several nuclear divisions occur in the tube, but no cell walls are formed. The final division produces two sperm nuclei. The pollen tube, containing two sperm nuclei and several vegetative nuclei, is the mature microgametophyte.

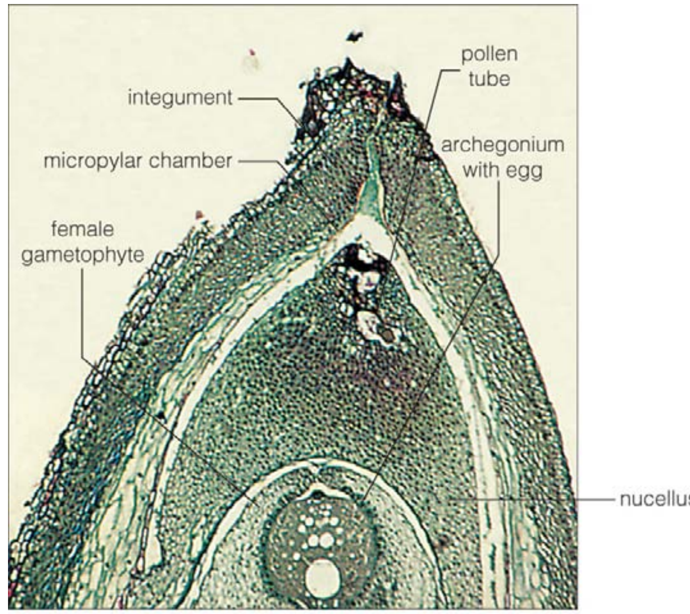

Figure 24.22. An older ovulate cone at the time of fertilization. Only half of the ovule is shown, but the closed micropyle, a pollen tube growing through the nucellus, and a differentiated archegonium with a large egg cell are visible.

Fertilization leads to Seed Formation

At the time of pollination, the megasporocyte is undergoing meiosis (Table 24.1). As the pollen tube grows, the female gametophyte forms. The small reddish cone grows larger and turns green, and the scales become tightly closed. Timing of male and female gamete formation is coordinated so that the egg is ready for fertilization by the time the pollen tube with its sperm nuclei has reached the archegonium. In pine, this development takes about 12 months.

The sperm nuclei, together with the cytoplasmic contents of the pollen tube, are discharged directly around the egg cell. Sperm nuclei do not possess flagella; therefore, they are not motile. One sperm nucleus comes in contact with the egg and enters it. This is not the end of its journey; it must pass through the egg cytoplasm to reach the egg nucleus and fuse with it. Pine egg cells have hundreds of times the volume of a sperm nucleus. How a sperm nucleus finds its way through that huge space to an egg nucleus is unknown.

The fertilized egg becomes a diploid zygote, and it begins to divide immediately into a relatively elaborate **proembryo**, the apical cells of which develop into an embryo (Fig. 24.19m).

Sometimes more than one embryo will form. The multiple embryos can originate in two ways. Each female gametophyte has more than one archegonium, and all can be fertilized if there are enough pollen grains. Furthermore, each proembryo is capable of forming as many as four embryos. In the first case, fraternal siblings would be formed; in the second, identical siblings. Generally, however, only a single embryo survives to maturity.

Table 24.1 The Timing of Development in the Life History of Pine

Event	Structure			Season, Year
Cone development		Pine tree (sporophyte)		
	Male cone		Female cone	
Meiosis	Microsporocyte		Megasporocyte	Summer, 0
	Microspore		Megaspore	Spring, 1
Pollination and pollen germination	Pollen grain (immature male gametophyte)			Early summer, 1
	Pollen tube (mature male gametophyte)		Female gametophyte	
Fertilization	Sperm nuclei		Egg	Late spring, 2
		Zygote		
		Proembryo		
Dispersal		Mature embryo within a modified ovule (a seed)		Summer, 2
		Cone opens		Fall, 2
Stratification				
		Seed outside the cone		Winter, 3
Germination		Seedling		Spring, 4

While the embryo develops, the female gametophyte also continues to grow by digesting the remaining nucellus, and its cells become packed with food. The integument hardens and becomes a seed coat. The micropyle has closed. The ovulate cone enlarges still more, becomes woody, and loses its green color.

When the seeds are mature, the cone scales open and the seeds fall out. Pine seeds usually have a wing, which catches the wind and aids in the dispersal of seeds from the parent tree (Fig. 24.19n). The wing is formed from the cone scale. Seeds are usually shed immediately on ripening, in late summer or early fall. The mature, open cone is two years old when seeds are dispersed (Table 24.1).

Seeds are dispersal packages containing a dormant embryo, stored food, and a protective outer coat. Their richness in carbohydrates has made pine seeds an important food source for human and animal populations. Native Americans ground the seeds into a meal and used the flour, much as other cultures have used grains. Many birds and mammals eat and cache pine seeds.

Seeds that escape predation by herbivores usually lie dormant until the next spring. The dormant embryos have a low metabolic rate, and their water content is low. They are able to tolerate aridity, anaerobic conditions, and temperature extremes while in this state. Their dormancy is broken by exposure to cold, wet winter conditions. Dormancy can be artificially broken by storing seeds in wet cheesecloth at temperatures a few degrees greater than freezing for 4 to 6 weeks, a process known as *stratification*. Dormancy prevents pines from germinating on warm fall days, when seedlings would have to endure inhospitable winter growing conditions.

When the seed does germinate, the radicle emerges first. Then the hypocotyl elongates, taking the cotyledons and epicotyl above the surface while still enclosed in the seed coat. The cotyledons absorb nutrients stored in the female gametophyte and then enlarge, pulling themselves out of the seed coat (Fig. 24.19o). When light strikes the cotyledons, they turn green and become photosynthetic. The young pine grows slowly in the first year, and most growth occurs below ground in the root system. The cotyledons may remain attached into the second year; until then, the true leaves are few in number and are relatively small. In such cases, the cotyledons continue to grow and elongate until they are shed.

24.8 GNETOPHYTES

Gnetophytes are represented by three living genera: *Ephedra*, *Gnetum*, and *Welwitschia* (Fig. 24.23). This enigmatic group has a number of traits in common with flowering plants, and botanists have speculated that gnetophytes are closely related or even ancestral to them. Some of these traits include vessel elements in the xylem, ovules surrounded by a fleshy layer, pollen-producing structures resembling stamens, and reduced gametophytes. However, a closer look at the similarities suggests that these features are convergences and not evidence of relationships. For example, the vessel elements of gnetophytes have a different developmental origin than the vessel elements of flowering plants, and the fleshy layers around gnetophyte seeds are not at all similar to fruits.

Despite great dissimilarity in their appearances, the three genera of gnetophytes share a series of morphological features strongly supporting the idea that they form a monophyletic group. In addition to the traits mentioned earlier, gnetophytes share opposite (or whorled) leaves, extension of the micropyle into a long tube, and a series of sterile bracts (bracts that are not directly associated with sporangia) making up the strobili. One shared feature of gnetophytes that represents an amazing example of convergence with flowering plants is that both have sperm from a microgametophyte fuse with a cell in the megagametophyte. In *Gnetum* and *Welwitschia*, the gametophytes are highly reduced and, like flowering plants, lack archegonia.

The basic units of a gnetophyte pollen strobilus are similar in all three genera and bear a striking resemblance to flowers. Each unit consists of several opposite or whorled bracts surrounding stamen-like structures. Several microsporangia dangle from these structures, appearing like anthers. Pollen is carried by wind or sometimes by insects (typically moths) from the microsporangia to the ovules.

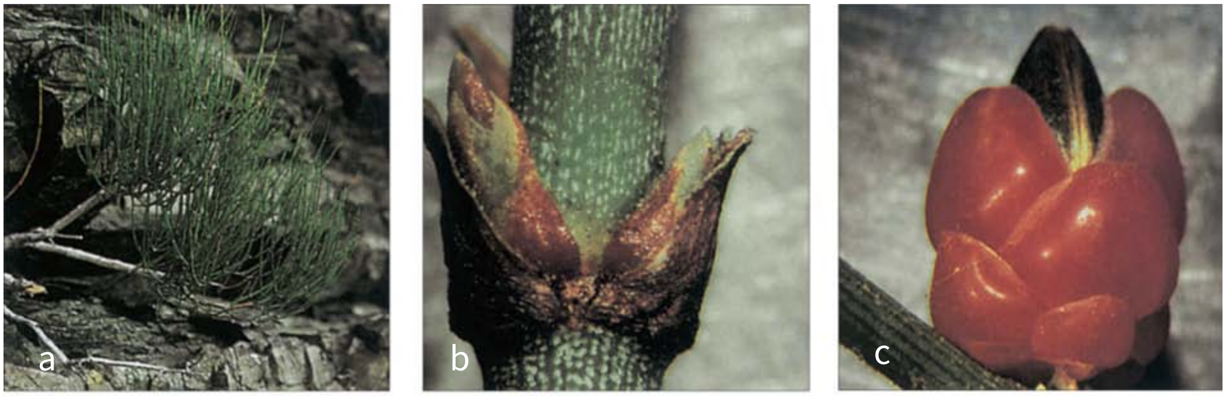

Figure 24.23 Two examples of gnetophytes. (a) Branches of the shrub *Ephedra viridis* (Mormon tea), about 1 m high, growing in the White Mountains of California. (b) A stem node and small, scale-like leaves of *E. viridis*. (c) *E. viridis* eed surrounded by a red aril. (d) *Gnetum leyboldii*, a tropical vine

Ovulate strobili also consist of a series of opposite or whorled bracts. A single ovule forms in each strobilus surrounded by a pair of fused bracts. In some species, these bracts can be fleshy and colored to attract birds, whereas in other species, the bracts form collars or wings around the seed. The integuments are extended into a distinctive long papery, micropylar tube.

Ephedra (also called joint fir or Mormon tea) is the only gnetophyte found in North America. Its 40 species are distributed through the Mediterranean rim, India, China, the southwestern deserts of the united States, and mountainous parts of South America. It is a vine or shrub with opposite or whorled leaves and prominent joints (Fig. 24.23a,b). The leaves are little more than scales; therefore, most photosynthesis is conducted by the green stems.

Joint fir is the source of the drug ephedrine, an alkaloid that constricts swollen blood vessels and also is a mild stimulant. An overdose can be fatal. The Asian species contain significantly more ephedrine and are important in Chinese herbal medicine, where it is called *ma huang*. Some Native American groups used the tea to cure venereal diseases, and Europeans emigrating to the southwest adopted this remedy. Strong *Ephedra* tea was a once a common offering at brothels in Nevada and California.

Gnetum is a tropical genus of 30 species, which include lianas (climbing vines), shrubs, and trees. The leaves are nearly indistinguishable those of a broad-leafed flowering plant (Fig. 24.23c), and unless reproductive structures are present, *Gnetum* is difficult to identify.

Welwitschia is found in the Namib Desert, along the arid southwest coast of Africa. It has two (rarely four) long, leathery, straplike leaves that trail along the soil surface (Fig. 24.24). When Austrian naturalist Friedrich Welwitsch first saw this plant on a field trip in 1859 near the Angolan coast, he is said to have fallen to his knees in disbelief. Specimens taken to Europe caused Darwin to describe it as a platypus of the plant kingdom. Local Africans called it *otjitumbo* ("stump"), but the English taxonomist Joseph Hooker named it *Welwitschia mirabilis*--the genus honors its European discoverer and the species epithet is the Latin word for "wonderful."

The plants are slow-growing, with most photosynthate going into an exceptionally well-developed tap root. The aboveground portion consists of a thick

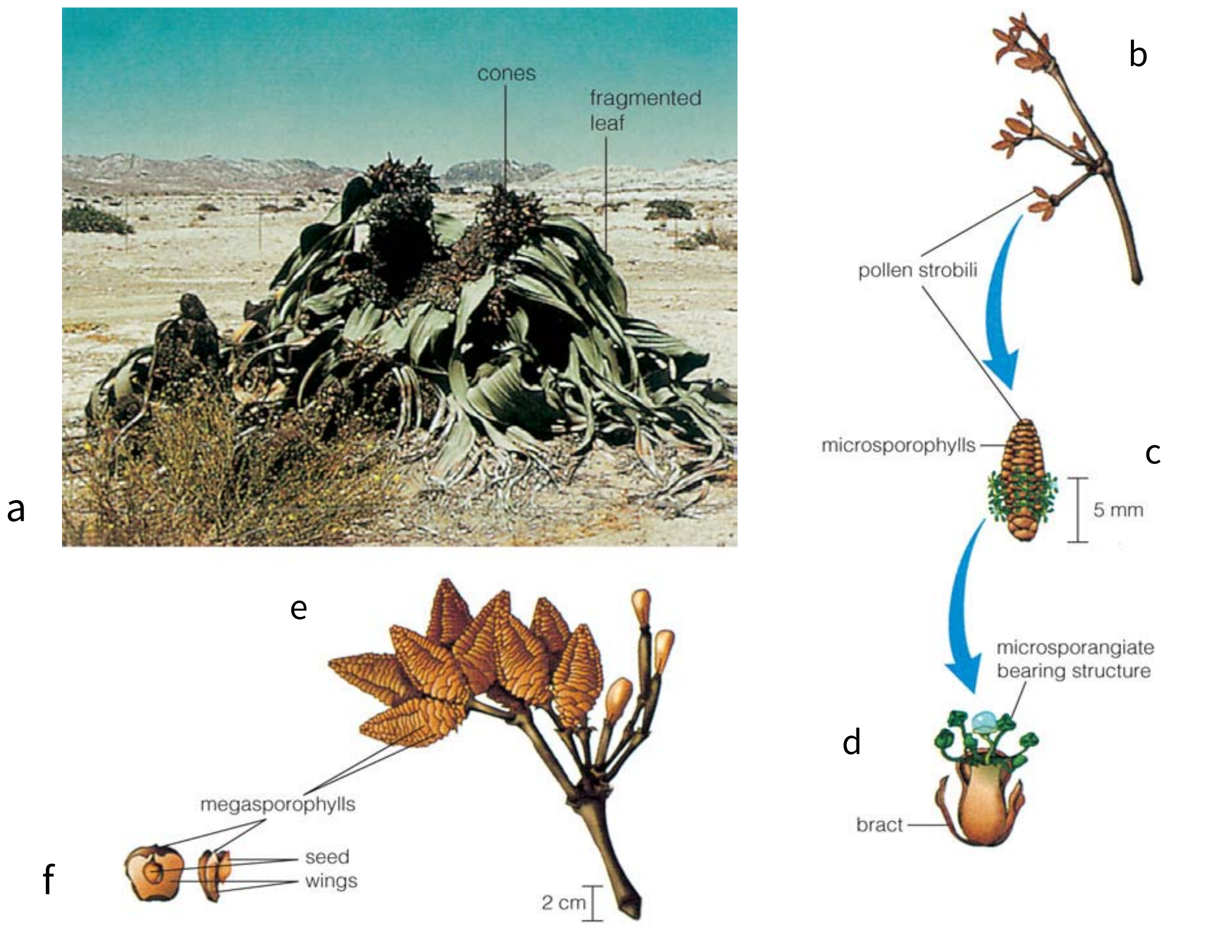

Figure 24.24. *Welwitschia mirabilis*, a plant of the Namib Desert in southwestern Africa. (a) The two old foliage leaves of this plant have become fragmented into ribbon-like strips. Strobili are visible at the juncture of the stem crown and leaves. A plant this size, about 1 m in height, is about 1,000 years old. (b) A cluster of microsporophylls resembling a conifer pollen strobilus. (c,d) The strobilus of microsporophylls at the time of pollen release. (e) A cluster of megaporangia strobili, which resemble ovulate strobili of conifers. (f) Each megasporophyll has a bract that encloses an ovule, and when the ovule has matured, outgrowths of the integument form wings.

woody crown and two broad leaves. These grow continuously from their base and fray at the ends, eventually becoming tangled into a large mound of what appears like many leaves. The leaf tissue has many sclereids, a considerable concentration of lignin, and numerous crystals of calcium oxalate--all combining to make them durable and inedible. Stomata are sunken, an adaptation to the arid habitat. Annual rainfall in its growing region is only 2 cm, although condensation from fog can add the equivalent of another 5 cm. Individual plants can attain ages of 1,000 to 2,000 years.

24.9 THE ECOLOGICAL AND ECONOMIC IMPORTANCE OF GYMNOSPERMS

Gymnosperms have great ecological importance. Although their habitats range from tropical forests to deserts, their centers of dominance are the cool-temperate zones of the Northern and Southern Hemispheres. In North America, they are part of low-elevation forests across Alaska, Canada, and New England and down the Pacific coast; in addition they are part of high-elevation forests in the Appalachian, Rocky, and Cascade-Sierra mountain chains. They also occur in more localized habitats within the southeastern coastal plain. The gymnosperm landscape covers more than one third of the North American landmass.

Within this landscape, ecosystems are created largely by conifers. Conifer foliage is rich in organic acid, so its decomposition, in turn, makes the soil acidic and relative low in nutrients. Only those shrub and herb species that can tolerate such soil conditions, and the low level of light beneath the dense conifer overstory, are able to grow here. The acidity also hinders bacteria but favors fungi, so the decomposer microflora is strongly affected. Conifer foliage and wood are high in secondary compounds that inhibit grazing; therefore, mammal and insect diversity is low, as is that of insectivorous birds.

Gymnosperms also have great economic importance. They are a major source of lumber, paper pulp, turpentine, and resins, and they are used as fuel for heat. More than one historian has pointed out that humans have always lived in a Wood Age, even if we talk about the Stone Age, Bronze Age, and Iron Age. Wood has provided energy for smelting, heating, and cooking, as well as raw building material for habitations and vehicles throughout human history. Minoan, Greek, and Roman civilizations rose and fell depending on their access to forests, often forests of grymnosperm trees. In North America, economic growth has depended particularly on lumber of ponderosa pine (*Pinus ponderosa*), eastern white pine (*Pinus strobus*), and Douglas fir (*Pseudotsuga menziesii*). A significant amount of raw or sawn logs is exported to countries that no longer have this natural resource.

The magnitude of forest exploitation on the North American continent rivals modern deforestation in the tropics. Enormous lowland forests of pine from the states bordering the Great Lakes and the Southeast United States, as well as equally extensive upland conifer forests in the West, have been clear-cut in the last 100 years--a cumulative area greater than 40 million hectares (100 million acres). The white pine forests of the Great Lakes area have never recovered from harvesting, and the second-growth forests of the West lack the biotic diversity and ecological stability the pristine forests had acquired over centuries of slow development.

Gymnosperms are widely used in landscaping because of their evergreen habit and the diversity of their growth forms. They can be pruned into low ground covers, hedges, and dramatically branched trees. Many have rapid growth rates. Some, such as the Norfolk Island pine (*Araucaria heterophylla*), cycads (*Cycas*), or the Monterey cypress (*Cupressus macrocarpa*), have unique canopy architectures; many people find these trees pleasing and therefore have brought them to countries far outside their original ranges.

KEY TERMS

conifer
cycad
fascicle
gnetophyte
gymnosperm
integument
micropylar chamber
micropyle
nucellus
ovule
Pangaea
pollen, pollen grain
pollination drop
proembryo
progymnosperm
resin
resin duct
seeds
seed plants
sieve cell
strobilus
tapetum

SUMMARY

1. Gymnosperms are tracheophytes whose life cycle have novel features. The new traits include the ovule, the seed, pollination, and wood, all of which are adaptations for survival on land. Gymnosperm means "*naked seed*."

2. Living gymnosperms number approximate 900 species and belong to four lineages: cycads, ginkgo, conifers, and gnetophytes. They have great economic and ecological importance, mainly in the temperate zones of the world.

3. Pine provides a typical example of a gymnosperm life cycle. Pine is monoecious; an individual pine tree will produce both pollen and ovules. Some other gymnosperms are dioecious.

4. Pollen strobili are small and seasonal. They consist of sporophylls attached to a central axis. Two microsporangia are attached to the underside of each sporophyll. Microspores develop into pollen grains within the microsporangium. The pollen grains (immature male gametophytes) are liberated from the microsporangium and carried passively on the wind to ovules, generally on another tree.

5. Ovulate cones are the cones commonly associated with conifers. When young, a cone is as small as a pollen strobilus, but it ultimately become larger. It consists of scales with a bract beneath each scale. Two integumented megasporangia (ovules) are attached to the upper surface of each scale. An ovule consists of an integument with a micropyle and micropylar chamber at one end and nucellus (megasporangium tissue) with a single megasporocyte. This is the stage of development at the time of pollination.

6. The megasporocyte divides by meiosis into four megaspores, but only one develops into a megagametophyte. At maturity, the megagametophyte is a relatively small mass of cells with several archegonia at the micropylar end. In the meantime, the pollen grain has been pulled through the micropyle by a shrinking pollination drop until it lies on the surface of the nucellus. It germinates into a pollen tube that grows slowly through the nucellus toward an archegonium and egg. Cell division in the tube produces two nonmotile sperm nuclei, one of which fertilizes an egg, forming a zygote.

7. The zygote divides to produce a proembryo, some of whose cells divide to produce an embryo with cotyledons and epicotyl, hypocotyl, and radicle regions. Surrounding the embryo is the megagametophyte, itself surrounded by a seed coat, which forms from the integument. Embryos are dormant when seeds are shed. Germination is possible after the seeds are exposed to cold, wet conditions for several weeks--a process called stratification. Thus, a seed is a dormant embryo with stored food and a protective outer coat; its function is to disperse the embryo away from the parent plant over time and space.

8. Cycads comprise 100 species of woody tropical plants that possess some ancestral features such as large, compound leaves and swimming sperm. Plants are dioecious. Strobili are large. Pollination involves beetles as vectors in some species.

9. *Ginkgo biloba* is the sole surviving species of its lineage, and although native to China, it is widely used as a street tree and ornamental. Its fan-shaped leaves are deciduous. Ginkgo is dioecious and has swimming sperm, like the cycads, but has wood similar to the conifers.

10. The conifers are the largest group of gymnosperms and consist of the familiar pines, spruces, firs, junipers, redwoods, yews, cedars, and cypresses. Other members of the group include the monkey puzzle tree, plum yew, and podocarps. They are all, except for the yews, distinguished by the presence of ovulate cones. Cones are typically woody structures composed of a branch system, but in some cases they are fleshy.

11. Gnetophytes consist of three dissimilar genera. All have a series of features that unite them, including vessels, fleshy coverings on the seeds, a micropylar tube, and fusion by both sperm. Only the genus *Ephedra* is found in North America. *Gnetum* is a tropical genus, and most species are lianas. *Welwitschia*, native to the arid coat of southwest Africa, is a bizarre plant with only two leaves.

Questions

1. How do the novel life cycle features of ovule, pollen, and seed adapt conifers to life on land?

2. In what ways does conifer wood play an important role in technological economies? Is it going too far to say that the human species has always lived in--and still does live in--a Wood Age?

3. What are the key differences between the megasporangium of a seed plant and the megasporangium of *Selaginella*? Compare the products of the megasporangia in both groups.

4. Why is a pollen grain an *immature* male gametophyte? When does it become completely developed?

5. Can you see any trends in gametophyte-sporophyte relationships in the moss-to-fern-to-conifer sequence?

6. In what ways are conifers different from cycads and ginkgos?

PLANTS, PEOPLE, AND THE ENVIRONMENT: ***The California Coast Redwood Forest***

Figure An old-growth coast redwood forest, showing an overstory dominated by tall, old trees and an understory covered with many species of perennial herbs.

Coast redwood, California redwood, and sequoia are names that bring to mind images of fog, looming trees, silent forests, and a sense of prehistoric time. Like other members of the Taxodiaceae family, *Sequoia sempervirens* grows in a humid climate with moderate winters. Over geologic time, its once wide range throughout the north temperate zone shrank to a 700-km-long strip of land hugging the California coast. The redwood belt is less than 55 km wide, and it occupies coast-facing slopes below an elevation of 800 m. The total area of its modern range amounts to less than 800,000 hectares--less than 1% of California's area and less than 0.003% of the earth's surface.

Yet the coast redwood is well known. It dominates a forest that has a remarkable growth rate, and its biomass (weight of organic matter) is greater than any forest in the world (Fig. 1). Overstory redwood trees commonly exceed 100 m in height and 3 m across at the base of their trunks and attain ages of 1,000 years. The above ground biomass is estimated to reach 3,600 metric tons per hectare. The tropical rain forests have only one-seventh as much biomass.

The redwood forest exists where it does because the nearby ocean keeps air temperatures buffered throughout the year. Winters do not have hard frosts, and summers are mild. In addition, cold, upwelling, offshore water creates fog banks that extend inland far enough to bathe the redwoods during most summer days. Fog reduces temperature and moisture stresses around the needles. Also, the tree canopies comb the fog as it passes through them, forming larger droplets that drip to the ground and add the equivalent of 20 cm of rain each year.

Redwood trees are uniquely tolerant of fires, which occur naturally during California's dry fall days when lightning strikes the ground. Redwood bark is thick and usually provides an effective insulation for the vascular cambium deep beneath. If the fire is hot enough to kill the tree's crown, however, the base of the tree and all the underground roots remain alive, because soil is an even better insulator than bark. At the junction of root and shoot lies a band of dormant buds. If the tree overstory is killed, the normal hormone balance is modified, and the buds break dormancy. Many fast-growing shoots emerge through the bark and above the soil. Over time, some of these will mature, producing a circle of trees, all genetically identical to the parent that previously occupied the space in their center. Few other conifers can reproduce vegetatively in this manner.

Fires often lead to floods during the following wet season, because ground cover has been removed, leaving nothing to slow the runoff of rainwater. Redwoods also are tolerant of floods, whereas most other species are killed by the layer of silt left behind by floodwaters, which suffocate the roots. Redwood has the capacity to generate adventitious roots from the buried trunk. New feeder roots than take on the function of the dying deeper roots. Redwood seedlings also survive best on bare mineral soil--either fresh silt or soil burned of its litter. Litter harbors damping-off fungi that otherwise infect and kill virtually every seedling.

In summary, the redwood maintains its hold because of episodic catastrophes, not despite them. Other species that compete with redwood for dominance are killed by fire and flood. Thus, park managers who try to protect the redwood forest by suppressing fires may instead be enabling the transition over time from a redwood forest to a fir-hardwood forest. Park managers in many other parts of the world are learning a similar lesson: disturbance is a natural part of the environment, and we cannot preserve some ecosystems without allowing that disturbance to continue.

There are few areas of mature redwood forest left to manage. Because of redwood's timber value, it has been intensively harvested for the last 150 years. Only 3% of the original acreage remains, almost all of it in state and federal parks. Although many young redwoods remain in the cutover areas, species composition and forest architecture are different. It takes more than 200 years for a redwood tree to attain mature size, and only mature trees are capable of supporting certain animals. Marbled murrelets, spotted owls, flying squirrels, and tree voles require large trees for nesting or roosting habitat. Certain insects, fungi, and wood-decaying microbes require a thick layer of litter on the forest floor, which is achieved only in old growth forests. Shade-loving herbs, mycorrhizal fungi, and small vertebrates do not grow and reproduce successfully until the overstory is deep and dense enough to create the required low-light humid environment.

A wise management scheme for this small remnant of a once-great forest must be a high priority if future generations of humans are to enjoy it. But how exactly does one manage enormous, long-lived organisms that maintain their dominance only with the help of episodic floods and fires that may recur only once a century: Redwood park management needs a long-term plan, extending 100 or more years into the future. The human species has a difficult time planning even a few years ahead. Can we create the will, the public agencies, and the policy to achieve century-long plans?

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