

Introduction to Seed Plants: Gymnosperms

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OVERVIEW

The chapter begins by exploring the differences between ferns and seed plants and then gives a brief geological history of gymnosperms. The leaves, roots, and stems of pine trees are discussed, and the life cycle of a typical gymnosperm (pine) is given. Other conifers, such as yews, podocarps, junipers, and redwoods, are mentioned, and a brief discussion of *Ginkgo*, cycads, *Ephedra*, *Gnetum*, and *Welwitschia* follows. The chapter concludes with a digest of the human relevance of gymnosperms, with particular emphasis on the conifers.

Some Learning Goals

1. Learn the features common to typical conifer pollen and seed strobili and explain how they differ.
2. Understand what distinguishes the phyla of living gymnosperms from one another.
3. Know the significance of seeds and their evolutionary importance.
4. Learn the pine leaf modifications that adapt them to a harsh environment.
5. Indicate where the following structures occur in the life cycle of a pine tree: archegonia, eggs, sperms with flagella, male and female gametophytes, the sporophyte, integument, vessels, sporocytes, embryo, and pollen grains.
6. Explain the function of each of the following: resin canals, mycorrhizal fungi, nucellus, generative cell, megaspore, microsporocyte.
7. Identify and learn a use for each of at least 10 different gymnosperms.

Some of the giant tree ferns have large, graceful leaves held above an unbranched trunk (see Fig. 21.25) and superficially resemble coconut palms. Anyone who has sat at the base of a coconut palm when a coconut has fallen, however, has been reminded of a basic difference between ferns and coconut palms. The palms are flowering plants that produce seeds such as those of pine trees and other cone-bearing plants, whereas the ferns produce no seeds at all.

The oldest known seeds were produced by plants that appeared late in the Devonian period, more than 350 million years ago. Seeds provided a significant adaptation for plants that had invaded the land. Unlike spores, seeds have a protective seed coat and a supply of food (usually endosperm) for the embryo. The embryo may be capable of lying dormant through long periods of freezing weather, drought, and may, in some instances, even survive fire. This survival value of seeds undoubtedly played a major role in seed plants becoming the dominant vegetation on earth today.

The first seed plants were so fernlike in appearance that they were originally classified as ferns. When fossils with obvious seeds on the fronds were discovered, however, these *pteridosperms* (“seed ferns”) were reclassified as *gymnosperms*.

The name **gymnosperm** is derived from two Greek words: *gymnos*, meaning naked, and *sperma*, a seed. The name refers to the exposed nature of the seeds, which are produced on the surface of sporophylls or similar structures instead of being enclosed within a fruit as they generally are in the flowering plants (see the photograph of a cycad cone at the beginning of this chapter as well as Fig. 22.1). The seed-bearing sporophylls of the sporophyte are often spirally arranged in strobili (seed cones) that develop at the same time as smaller pollen-bearing strobili (pollen cones). The pollen cones produce *pollen grains*.

The female gametophyte is produced inside an **ovule** that contains a fleshy, nutritive diploid tissue called the **nucellus** (see Fig. 22.7). The nucellus is itself enclosed within one or more outer layers of diploid tissue. These outer layers of tissue constitute an **integument** that becomes a **seed coat** after the fertilization and development of an embryo takes place (see Fig. 22.8).

The sporophytes of gymnosperms are mostly trees and shrubs, with a few species being vines. The gametophytes are proportionately even more reduced in extent than they are in ferns and their relatives. Unlike the gametophytes discussed so far, they don't grow independently but develop within sporophyte structures.

Four phyla of living gymnosperms are recognized. Phylum Pinophyta includes about 575 species of pines, firs, spruces, hemlocks, cedars, redwoods, and other coniferous woody plants. Fossils of some conifers extend back 290 million years to the late Carboniferous period. Phylum Ginkgophyta has a single living representative, *Ginkgo*, which has fan-shaped leaves and seeds enclosed in a fleshy covering. The superficially palmlike cycads are assigned to Phylum Cycadophyta. Phylum Gnetophyta includes three genera of gnetophytes that have wood with vessels—a structural element unknown in other gymnosperms.

PHYLUM PINOPHYTA— THE CONIFERS

Pines

The largest genus of conifers, *Pinus* (pines) has over 100 living species. They are the dominant trees in the vast -coniferous forests of the Northern Hemisphere. They have also been planted extensively in the Southern Hemisphere, but only the Merkue pine occurs there naturally, and its distribution barely extends south of the equator. They include the world's oldest known living organisms, the bristlecone pines, native to the White Mountains of eastern central California and in the Snake range on the central Nevada-Utah border. Some trees still standing are about 4,600 years old, and one that was, unfortunately, cut down in 1964 was found to have been about 4,900 years old.

Structure and Form

Pine leaves are needlelike and are arranged in clusters or bundles of two to five leaves each (a handful of species have as many as eight or as few as one to a cluster). Regardless of the number of leaves, each cluster (*fascicle*) forms a cylindrical rod if the leaves are held together (Fig. 22.2). The fascicles are short shoots with restricted growth, a feature of some gymnosperms not found in flowering plants. Pines often live in areas where the topsoil is frozen for a part of the year, making it difficult for the roots to obtain water. In addition, the leaves may be exposed to high winds and bitterly cold temperatures. Accordingly, they have several modifications that enable them to survive in harsh environments.

Just beneath the epidermis there is a **hypodermis**, consisting of one to several layers of thick-walled cells. The epidermis itself is coated with a thick cuticle. The stomata, instead of being at the surface, are recessed or sunken in small cavities. The veins and their associated tissues are surrounded by an endodermis, and the mesophyll cells do not have the obvious air spaces typical of the spongy mesophyll of the leaves of flowering plants (see Figs. 7.6 and 7.11).

Conspicuous **resin canals** develop in the mesophyll. These resin canals, which are found throughout other parts of the plant as well, consist of tubes lined with special cells that secrete *resin*. Resin is aromatic and antiseptic and -prevents the development of fungi; it also deters insect attacks. Other conifers apparently produce resin canals in response to injury. Pine fascicles usually *absciss* (i.e., fall off—see Chapter 7) within 2 to 5 years of their maturing, but those of bristlecone pines persist for up to 30 years. The fascicles are lost a few at a time so that some functional leaves are always present on a healthy tree.

Wood varies considerably in hardness. Most gymnosperm wood, including that of pines, consists primarily of tracheids and differs from the wood of dicots in having no vessel members or fibers. Conifer wood, because of the absence of thick-walled cells, is said to be *soft*, while the wood of broadleaf trees is described as *hard*.

In many conifers, the annual rings of the xylem are often fairly wide as a result of a comparatively rapid growth rate during the growing season. Resin canals are formed both vertically and horizontally throughout various tissues (Fig. 22.3). The bark includes the secondary phloem and may be relatively thick. It often becomes 7.5 centimeters (3 inches) or more wide, and in the giant redwood, it may become as much as 60 centimeters (2 feet) wide. Companion cells are absent from the phloem, but similar *albuminous cells* apparently perform the same function.

Mycorrhizal fungi are associated with the roots of most conifers. In fact, pine seedlings that germinate in sterilized soil do not grow well at all until the fungi are introduced or allowed to develop. The roots of adjacent pines often interweave. New England pioneers made use of this characteristic in eastern white pines when clearing land. After trees were felled, they would tip over the stumps with the roots still attached and use them for fences. The fences survived for many years.

Reproduction

Pines, like spike mosses, quillworts, and a few of the ferns, produce two kinds of spores (see Fig. 22.8). **Pollen cones** (male strobili) consist of papery or membranous scales arranged in a spiral or in whorls around an axis; they are usually produced in the spring. The pollen cones usually develop toward the tips of the lower branches in clusters of up to 50 or more (Fig. 22.4) and are mostly less than 4 centimeters (about 1.5 inches) long. **Microsporangia** develop in pairs toward the bases of the

scales.

Each of the **microsporocytes** in the microsporangia undergoes meiosis, producing four haploid **microspores**. These then develop into **pollen grains**; each grain consists of four cells and a pair of external air sacs. The air sacs look something like tiny water wings (Fig. 22.5) and give the pollen grains added buoyancy that may result in the grains being carried great distances by the wind.

Pines produce pollen grains in astronomical numbers. For example, it has been estimated that each of the 50 or more pollen cones commonly found in a single cluster may produce more than 1 million grains, and there may be hundreds of such clusters on one tree. The grains accumulate as a fine yellow dust on cars, shrubbery, or anything else in the vicinity, and they often form an obvious scum on pools and puddles. Within a few weeks after the pollen has been released, the now shriveled pollen cones fall from the trees.

Megaspores are produced in **megasporangia** located within ovules at the bases of the seed cone scales. The **seed cones** (female strobili) are much larger than the pollen cones, becoming as much as 60 centimeters (2 feet) long in sugar pines and weighing as much as 2.3 kilograms (5 pounds) in Coulter pines. When mature, they have woody scales, with inconspicuous bracts between them, arranged in a spiral around an axis. They are mostly produced on the upper branches of the same tree on which the pollen cones appear (Fig. 22.6).

The ovules (Fig. 22.7) occur in pairs toward the base of each scale of the immature seed cones and are larger and more complex than the microsporangia of pollen cones. Each ovule has within it a *megasporangium* containing the **nucellus** and a single **megasporocyte**. This, in turn, is surrounded and enclosed by a thick, layered **integument**. The integument has a somewhat tubular channel or pore called a **micropyle** that is pointed toward the cone's central axis. One of the integument layers later becomes the **seed coat** of the seed.

A single megasporocyte within the megasporangium of each ovule undergoes meiosis, producing a row of four relatively large megaspores. Three of the megaspores soon degenerate. Over a period of months, the remaining one slowly develops into a *female gametophyte* that ultimately may consist of several thousand cells. The nucellus is used as the food source for the growing gametophyte.

As gametophyte development nears completion, two to six *archegonia* differentiate at the end facing the micropyle. Each archegonium contains a single large egg. When a stained, thin, lengthwise section of a pine ovule is examined with a microscope, only one archegonium or egg may be seen, or the micropyle may appear to be missing. This is due to the section not having been sliced precisely through the middle of all the structures.

Seed cones are at first usually reddish or purplish in color and commonly take two seasons to mature into the green and finally the brownish woody structures with which we are all familiar (Fig. 22.8). During the first spring, the immature cone scales spread apart, and pollen grains carried by the wind sift down between the scales. There they catch in sticky drops of fluid (*pollen drops*) oozing out of the micropyles. As the fluid evaporates, the pollen is drawn down through the micropyle to the top of the nucellus.

After pollination, the scales grow together and close, protecting the developing ovule. Meiosis and megaspore development don't occur until about a month after pollination. After a functional megaspore is produced, the female gametophyte and its archegonia don't mature until more than a year later.

Meanwhile, the pollen grain (immature *male gametophyte*) produces a **pollen tube** that slowly grows and digests its way through the nucellus to the area where the archegonia develop. While the pollen tube is growing, two of the original four cells in the pollen grain enter it. One of these, called the **generative cell**, divides and forms two more cells, called the sterile cell and the **spermatogenous cell**. The spermatogenous cell divides again, producing two male gametes, or **sperms**. The sperms have no flagella (unlike the sperms of other organisms discussed in the preceding chapters) and are confined to the pollen tube until just before fertilization occurs. The germinated pollen grain, with its pollen tube and two sperms, constitutes the mature *male gametophyte*. Notice that no antheridium has been formed.

About 15 months after pollination, the tip of the pollen tube arrives at an archegonium, unites with it, and discharges the contents. One sperm unites with the egg, forming a zygote. The other sperm and remaining cells of the pollen grain degenerate. The sperms of other pollen grains present may unite with the eggs of other archegonia, and each zygote begins to develop into an **embryo** that is nourished by the female gametophyte. This is similar to the development of fraternal twins or triplets in animals. At a later stage, an embryo may divide in such a way as to produce the equivalent of identical twins or quadruplets in animals. Normally, however, only one embryo completes development. While this development is occurring, one of the layers of the integument hardens, becoming a *seed coat*. A thin membranous layer of the cone scale becomes a "wing" on each seed. The wing may aid in the seed's dispersal. Squirrels and other animals may also help dispersal by breaking open the cones.

In other species, such as the lodgepole, jack, and knobcone pines, the cones remain on the tree with the scales closed until they are seared by fire or open with old age. Sometimes, these cones are slowly buried as the cambium adds tissues that increase the girth of the branch. Seeds of such engulfed cones have been reported to germinate after they have been dug out of the stem.

Other Conifers

Some conifers don't produce woody seed cones with conspicuous scales, nor do all produce both pollen and seed cones on

the same plant. For example, yew (*Taxus*) and California nutmeg (*Torreya*) produce ovules singly at the tips of short axillary shoots. Each ovule is at least partially surrounded by a fleshy, cuplike covering called an **aril**. In yews, this is bright red and open at one end, giving the fleshy seed the appearance of a small, red hors d'oeuvre olive with its stuffing removed (Fig. 22.9). The seeds with their fleshy arils are produced only on female plants, while the pollen cones are produced only on male plants.

Podocarps are conifers of the Southern Hemisphere and are widely planted as ornamentals in regions with milder climates. Their fleshy-coated seeds are produced singly and are similar to those of yews. They are not, however, open at one end and have an additional larger appendage at the base (Fig. 22.10). The origin of these fleshy seeds is not clear and has led to speculation that yews and podocarps may have diverged from other conifers very early in the evolution of gymnosperms.

The scales of the seed cones of junipers tend to be fleshy at maturity, and they look more like berries than cones. Juniper pollen grains, as well as those of a number of other conifers, do not have air sacs. Cypress and redwood seed cone scales are flattened at the tips and narrow at the base, where they do not overlap one another as do pine cone scales.

The two California species of redwoods are both renowned for their size, height, and longevity. Coastal redwoods occasionally grow to a height of 90 meters (295 feet), and one tree in Humboldt County, California, is 111.6 meters (366.2 feet) tall; it is believed to be the tallest conifer in the world. The other species, usually referred to as *Big Tree* or *Giant Redwood*, is confined to the western slopes of California's Sierra Nevada range. It does not grow quite as tall as the coastal redwood but exceeds it in total mass. The General Sherman tree in Sequoia National Park, for example, is 31 meters (101.5 feet) in circumference at the base and over 24 meters (79 feet) in circumference 1.5 meters (5 feet) above the ground. It weighs an estimated 5,594 metric tons (6,167 tons). There are 600,000 board feet of timber in this single tree—enough to build more than 75 five-room houses (although the wood is generally not suitable for construction purposes) or to make 20 billion toothpicks. It is over 3,500 years old.

OTHER GYMNOSPERMS

Living representatives of other gymnosperms are not as numerous or as well-known as the conifers and outwardly don't resemble them at all. In fact, some of them look more like leftover props from a science-fiction movie set. They include the **ginkgos**, the **cycads**, and the **gnetophytes** (pronounced née-toe-fytes).

Phylum Ginkgophyta—*Ginkgo*

There is only one living species of *Ginkgo* (Fig. 22.11), whose name is derived from Chinese words meaning “silver apricot.” The fossil record indicates *Ginkgo* and other members of its family (Ginkgoaceae) were once widely distributed, especially in the Northern Hemisphere. Despite isolated reports to the contrary, there are doubts that ginkgos now exist anywhere they have not been cultivated, and the plant has often been called a living fossil.

Ginkgos are often referred to as *maidenhair trees* because their notched, broad, fan-shaped leaves look like larger versions of the individual pinnae of maidenhair ferns. They are widely cultivated in the United States and are popular street trees in some areas. The leaves are mostly produced in a spiral on short, slow-growing spurs and have no midrib or prominent veins. Instead, hairlike veins branch *dichotomously* (fork evenly) and are relatively uniform in their width. They are deciduous and turn a bright golden yellow before abscission in the fall.

Ginkgo is dioecious, with a life cycle similar to that of pines. The sperms, however, have flagella, and being dioecious, the male and female reproductive structures are produced on separate trees. The mature seeds resemble small plums and are enclosed in fleshy seed coats. The flesh is, however, unrelated to that of true fruits. In North America, male trees (propagated from cuttings) are preferred for ornamental purposes because the seed flesh has a nauseating odor and is irritating to the skin of some individuals. In China and Korea, however, the seeds are considered a delicacy, and female trees predominate; a minimal number of males are propagated to ensure pollination.

Phylum Cycadophyta—The Cycads

Cycads have the appearance of a cross between a tree fern and a palm but are related to neither. These slow-growing plants of the tropics and subtropics have unbranched trunks that grow more than 15 meters (50 feet) tall in a few species and have a crown of large, pinnately divided leaves. Several of the approximately 100 known living species of cycads are presently facing extinction. During the Mesozoic era, now extinct gymnosperms known as *cycadeoids* were abundant. Cycadeoids bore a superficial resemblance to cycads but had very different reproductive structures and are not related.

Cycad life cycles are similar to those of conifers, except that pollination of cycads is generally brought about by beetles instead of wind. In addition, each sperm of cycads has from 10,000 to 20,000 spirally arranged flagella. Cycads are dioecious, and both the pollen strobili and seed strobili of some species are huge (e.g., more than a meter [3 feet 3 inches] long with a weight of over 220 kilograms [100 pounds]) (Fig. 22.12). The scales of seed strobili of some species are covered with feltlike or woolly hairs.

Phylum Gnetophyta— The Gnetophytes

The 70 known species of *gnetophytes* are distributed among three distinctive genera. They are unique among the gymnosperms in having vessels in the xylem. More than half of the gnetophytes are species of *joint firs* in the genus *Ephedra*. These shrubby plants inhabit drier regions of southwestern North America. Their tiny leaves are produced in twos and threes at a node and turn brown soon after they appear. The stems and branches, which are often whorled, are slightly ribbed; they are photosynthetic when they are young (Fig. 22.13).

Before pollination, the ovules of *Ephedra* produce a small tubular extension resembling the neck of a miniature bottle extending into the air. Sticky fluid oozes out of this extension, which constitutes the micropyle, and airborne pollen catches in the fluid. Male and female strobili may be produced on the same plant or on different ones, depending on the species.

Most of the remaining species in this division are in the genus *Gnetum* (Fig. 22.14), which has not been given an English common name. Its members occur in the tropics of South America, Africa, and Southeast Asia. Most are vinelike, with broad leaves similar to those of flowering plants. The best-known species of *Gnetum*, however, is a tree that grows up to 10 meters (33 feet) tall.

The third genus, *Welwitschia*, has only one species, which is confined to the temperate Namib and Mossamedes deserts of southwestern Africa. Here the average annual rainfall is only 2.5 centimeters (1 inch), and in some years, it does not rain at all. The plants carry on CAM photosynthesis, and their stomata are open at night. The plants apparently survive much of the time on dew and condensate from fog that rolls in off the ocean at night.

Welwitschia plants are also truly extraordinary in appearance. The stem rises only a short distance above the ground's surface and is in the form of a large shallow cup that tapers at the base into a long taproot. The plants may live to be 100 years old and at maturity have a crusty, barklike covering on the surface of the stem cup. The stems may be more than 1 meter (3 feet 3 inches) in diameter (Fig. 22.15).

Throughout their life span, *Welwitschia* plants usually produce only two leaves. The leaves are wide and straplike, each with a meristem at the base. The meristems constantly add to the length of the leaves, but as the leaves flap about in the wind, they become tattered and split, wearing off at the tips so that they are seldom more than 2 meters (6.5 feet) long. *Welwitschia* is dioecious, with both male and female strobili being produced on axes that emerge from the axils of the leaves. This makes the strobili appear to be growing around the rim of the stem cup.

HUMAN RELEVANCE OF GYMNOSPERMS

What do we plant when we plant the tree?
We plant the ship, which will cross the sea.
We plant the mast to carry the sails;
We plant the planks to withstand the gales—
The keel, the keelson, the beam, the knee;
We plant the ship when we plant the tree.

What do we plant when we plant the tree?
We plant the houses for you and me.
We plant the rafters, the shingles, the floors,
We plant the studding, the lath, the doors,
The beams, the siding, all parts that be;
We plant the house when we plant the tree.

What do we plant when we plant the tree?
A thousand things that we daily see;
We plant the spire that out-towers the crag,
We plant the staff for our country's flag,
We plant the shade, from the hot sun free;
We plant all these when we plant the tree.

Henry Abbey

As a group, the gymnosperms are second only to the flowering plants in their impact on our daily lives. Space does not permit a detailed account of all they contribute, but the following sections provide an overview of some of their uses, past and present.

Conifers

In the early 1970s, the late author-naturalist Euell Gibbons filmed a series of television commercials in which he mentioned uses of several wild plants for food. In one of the commercials, he rhetorically inquired if his audience had ever eaten a pine tree and added, “many parts are edible.”

The edibility of parts of many conifers was known to Native Americans long before Europeans set foot on the North American continent. In fact, early explorers found large numbers of pines stripped of their bark. For centuries, these inner parts (phloem, cambium) had been used for emergency food. The Adirondack Mountains of New York are believed to have received their name from a Mohawk Indian word meaning “tree eater,” in reference to Native American use of the inner bark of eastern white pines. This material (specifically the phloem) contains sugars that make it taste sweet. Some tribes ate the material raw, some dried it and ground it to flour, and others boiled it or stored dried strips for winter food. Early settlers in New England candied strips of eastern white pine inner bark. To prevent scurvy, both they and local Native Americans drank a tea made of the needles, which are rich in vitamin C.

The seeds of nearly all pines are edible, but those of western North America include the larger and better-tasting species. The protein content of those analyzed generally ranges between 15% and 30%, with much of the remainder consisting of oils.

California Native Americans relished gray pine seeds in particular, but even the small seeds of ponderosa pine were eaten raw or made into a meal for soups and bread. Cones of pinyons were collected by tribes of the Southwest and thrown on a fire to loosen the seeds. These were then pounded and made into cakes or soup. The soup was often fed to infants. In Siberia, local residents crush the seeds of Siberian white pine to obtain a nutritious oil, but its use has declined since corn and cottonseed oils became available.

Italians and other Europeans cook “pignolias,” the seeds of the stone pine, in stews and soups. The seeds are also used in cakes and cookies, and some are exported to the United States for this purpose. Many of the so-called nuts used by commercial American bakers in cakes and confectionery, however, are really seeds from the east Himalayan chilgoza pine. Other sources include the Mexican stone pine and a few pinyons.

Eastern white pines were often used as masts in sailing vessels. In colonial days, the royal surveyors marked certain trees for the use of the Crown, and severe penalties were imposed on colonists who ignored the ban on the use of any white pine not growing on private land. It was, however, legal for colonists to use white pines that had blown down, which gave rise to the term *windfall*. Eastern white pine wood contains less resin than that of other species and was extensively used for crates, boxes, matchsticks, furniture, flooring, and paneling. By the end of the 19th century, eastern white pines, which originally occurred over vast tracts of the northeastern United States and Canada, had been decimated by wholesale logging done with no thought to conservation. Bald cypress trees in the southeastern United States met a similar fate. White pine blister rust also took its toll. Although new growth is now being promoted, most white pine lumber used today comes from large stands of western white pine in the Pacific Northwest.

The trunks of lodgepole pines are used in both the United States and Canada for telephone poles; the straight-grained wood is also used for railroad ties, mine timbers, and pulp.

Smog has severely damaged ponderosa and other native pines in California. For a number of years, the U.S. Forest Service has experimented with Afghanistan pine, a smog- and drought-resistant pine from Russia and adjacent areas, as a replacement for native trees. Growth rates in tests have been very rapid. Rapid growth is a desirable commercial feature, since considerably more timber can be produced in the same time needed to obtain it from slower-growing species, but the wisdom of introducing non-native plants into natural communities is in question, since there are many examples of such activities thoroughly disrupting delicate ecological balances.

The resin produced in the resin canals of conifers is a combination of a liquid solvent called *turpentine* and a waxy substance called *rosin*. When a conifer tree is wounded or damaged by insects, resin usually covers the area, sometimes trapping the insects. Out in the air, the turpentine evaporates quickly, leaving a protective layer of rosin, which deters water loss and fungal attacks. Both turpentine and rosin are very useful products, and a large industry centered in the southern United States and in the south of France is devoted to their extraction and refinement. They are often referred to as *naval stores*, a term that originated when the British Royal Navy used large quantities for caulking and sealing their sailing ships. Today, most naval stores and a third or more of the lumber used in the United States come from a group of southern yellow pines, particularly slash pine.

Pitch pine, also a source of naval stores before slash and other yellow pines became more profitable, was used in the past for the waterwheels of mills. Pitch pine wood was also used as fuel for steam engines, as it produces considerable heat when it burns. Turpentine is considered a premier paint and varnish solvent; rosin is used by musicians on violin bows and by baseball pitchers to improve their grip on the ball. Batters apply pine tar to the handles of bats to minimize slippage.

In the past, pine pitch was used by Native Americans for patching canoes, and it has been suggested that Noah’s ark was sealed with pitch from aleppo pine. Pine resin was used for purifying wine in the 1st century A.D., and today, Greeks still add it to certain wines. *Colofonia* is the Spanish word for a type of resin Monterey pines produced abundantly around the old Spanish capital of Monterey. The early California priest Padre Arroyo suggested during the first half of the 19th century that California received its name from this Spanish word. California was, however, the name of a mythical paradise in a Spanish novel published in the early 16th century, and no more than an interesting similarity between two Spanish words may be in-

volved.

The huge kauri pines (*Agathis*) of New Zealand are in a family separate from that of true pines. They are the source of a mixture of resins called *dammar*, which is used in high-quality, colorless varnishes. Dammar was also the resin originally used in the manufacture of linoleum.

In New Zealand, dammar, also called *amber*, is obtained primarily in fossil form from former or present kauri pine forest areas. Most amber, however, has come from extinct conifers that flourished 60 to 70 million years ago in the Baltic area of the former Soviet Union and from other extinct conifers in what is now the Dominican Republic. It occurs as lumps of translucent material with a deep orange-yellow tint. According to Greek mythology, amber was the congealed tears of Phaëthon's sisters who, while weeping over his death, were turned into trees. Some of the lumps weigh up to 45 kilograms (100 pounds). The supply was at its peak at the beginning of the 20th century but is now nearing exhaustion. Remarkably lifelike preservations of prehistoric insects millions of years old have occurred in amber (Fig. 22.16).

Other products refined from resin are used in the manufacture of menthol for cigarettes (menthol also occurs naturally in members of the Mint Family), floor waxes, printer's ink, paper coatings, varnishes, and perfumes.

White spruce is the chief source of pulpwood for newsprint (Fig. 22.17) and other paper in North America. Enormous quantities of paper are used every day. A single midweek issue of a large metropolitan newspaper may use an entire year's growth of 50 hectares (123 acres) of these trees, and that amount may double for weekend editions. A large American publishing company, in an attempt to find ways of reducing paper consumption in the United States, tried trimming 2.5 centimeters (1 inch) from the width of all rolls of toilet paper in their building facilities. They found that the employees still used the same number of rolls per month as they had previously. From this, it was calculated that if all rolls of toilet paper were similarly trimmed in width, 1 million trees would be saved each year in the United States alone.

Split roots of the white spruce are quite pliable and were used by Native Americans for lashing canoes and for basketry. Spruce beer, brewed from young twigs and leaves with an added sugar source, such as honey or molasses, was once used as a remedy for scurvy. Resin of white, red, black, and Sitka spruces was used as a type of chewing gum by Native Americans, who sometimes hardened it slightly in cold water. Europeans who have tried it report that it has to be of the right consistency to be enjoyable, since it behaves like unhardened taffy if it is too soft and is bitter if it is too hard. In southeast Alaska, Sitka spruce buds are boiled in sugar water to make spruce bud syrup.

The tracheids of spruces have spiral thickenings on the inner walls. These apparently are responsible for giving the wood a resonance that makes it ideal for use as soundboards for musical instruments (Fig. 22.18). Sitka spruce of the Pacific Northwest produces a strong, resilient wood that is a favorite material of manufacturers of light aircraft.

Larches, which along with the dawn redwood and bald cypress are exceptions to the rule that conifers are evergreens, have some of the most durable of all conifer woods. Fence posts of larch are known to last 20 years. In the southern and southwestern United States, posts of juniper wood and bald cypress last even longer, some remaining usable for 40 to 50 years or more. The resin of the western larch has been used in the manufacture of baking powder, and the European larch is the source of a special type of turpentine.

There are about 40 species of true firs that are widely used in the construction, plastic, and paper industries, as ornaments, and as Christmas trees. The balsam fir produces on its bark blisters containing a clear resin. This resin, known as *Canada balsam*, was used in the past for cementing optical lenses and is still occasionally used for making permanent mounts on microscope slides. It has medicinal properties, too, and was used by New England colonists in sore throat medications.

Douglas fir, found in the mountains of the West, is not a true fir. In the Pacific Northwest, it grows into giant trees that are second only to the redwoods in size. It is probably the most desired timber tree in the world today. The wood is strong and relatively free of knots as a result of rapid growth, with less branching than most other conifers. It is heavily used in plywoods and is a major source of large beams. A useful wax is extracted from the bark of Douglas firs. Exploitation has nearly eliminated old-growth stands, but large numbers of new trees are being grown in managed forests.

Coastal redwoods are also prized for their wood, which contains substances that inhibit the growth of fungi and bacteria. The wood is light in weight, strong, and soft, but it splits easily. It is used for some types of construction, furniture, posts, greenhouse benches, and for many other purposes. California wineries use it extensively for wine barrels. The Giant Redwoods (Big Trees) are so huge that a double bowling alley was built on the log of the first specimen cut down. They are no longer logged and now serve almost exclusively as tourist attractions in California. They are, however, being planted as timber trees in Romania and Yugoslavia.

Wood of the bald cypress, found in southern swamps, is like that of the redwood in being very resistant to decay. In the past, it was used for railroad ties, coffins, general construction, guttering, and shingles. The trees are well known for their "knees," which rise above the water as tapering growths from the roots (Fig. 22.19). At one time, it was widely believed that these were a means of admitting oxygen to the roots, but this now appears doubtful. They are favored for making knickknacks, such as wall ornaments and lamp bases. The leaves of the bald cypress yield a red dye.

A dull red dye can be obtained from the younger bark of the eastern hemlock, which is also a source of tannins for shoe leather. The tanning industry so depleted the native eastern hemlocks that it now has had to use tropical substitutes. The wood of these small trees contains exceptionally hard knots that can chip an axe blade. It sputters and throws out sparks freely when placed on a fire. Native Americans made a poultice for scrapes and cuts by pounding the inner bark. British Columbia Indians used to scrape out the cambium and phloem of both the western and mountain hemlocks for food, killing the trees in the process.

Northern white cedar, also known as *arborvitae*, is a favorite ornamental in temperate areas. The wood is pliable, and several Native American tribes used it for canoes. The Atlantic or southern white cedar was the first tree to be used for the construction of pipes for pipe organs in North America. During World War II, old logs of this species found in a swamp in New Jersey were milled and used in the construction of patrol torpedo boats.

The fleshy red aril surrounding the seeds of yews is sweet and edible, but the seeds themselves and other parts of the plants are very poisonous. The wood is tough and resilient and is favored for making bows.

English yew, the wood of long bows, changed history in 1415 and brought an end to the Middle Ages at the Battle of Agincourt, when the English long bow proved its superiority over heavily armored cavalry. A red or purple dye can be obtained from the bark and roots of yew. Podocarps, two species of which are valuable timber trees in New Zealand, have edible seeds.

In 1989, researchers at the Johns Hopkins Oncology Center reported that 12 women with advanced ovarian cancers that had not responded to traditional therapies (-including, in some cases, surgery) had a decrease of 50% or more in the size of their tumors and one woman's tumor disappeared altogether after treatment with *taxol*, a drug obtained from the bark of the Pacific yew tree. Pacific yew trees are small and do not occur in extensive stands. They also grow so slowly it takes more than 70 years to attain their full size, and removal of their bark kills them. Despite the problems of the drug's availability, scientists are excited about the potential of the drug in the fight against ovarian cancer, and the trees are now being mass-produced in nurseries.

The wood of incense cedars has been used in the manufacture of venetian blinds and pencils. Red cedar wood is also used for pencils, as well as for cedar chests, closet lining, fence posts, and cigar boxes. It was used at one time in Germany for smoking hams. An aromatic oil used in floor-sweeping compounds is extracted from red cedar wood, and the "berries" of this and related junipers are widely eaten by birds. Many Native American tribes used the berries and inner bark as survival food during bleak winters. Some roasted the dried berries and brewed a beverage from them. Western red cedar was the most important single plant of Native Americans of the Northwest who used it for housing, clothing, nets, canoes, totem poles, medicines, and other purposes. Berries of the dwarf juniper are used to flavor gin. Some authorities indicate that the word *gin* may have been derived from *genievre*, the French word for juniper berry.

Other Gymnosperms

Despite the foul odor of the fleshy seed coat of seeds of *Ginkgo*, the starchy food reserves of the seeds themselves have a nutlike flavor punctuated with a hint of shrimp. In the Orient, *Ginkgo* seeds are widely used for food, either boiled or roasted, and are found imported in canned form in Chinese food stores of large metropolitan areas in the United States and Canada. Extracts of *Ginkgo* plants have been clinically demonstrated to improve blood circulation in humans, and in 1998, more than 25 million Europeans were routinely taking *Ginkgo* extracts to counteract the effects of aging. Clinical studies have shown that *Ginkgo* leaf extracts do, indeed, improve blood supply to the brain and lungs, thereby improving both short-term memory and breathing.

Florida arrowroot starch was once obtained from the extensive cortex and pith of a species of cycad whose northernmost distribution occurs in Florida. Before it could be used for human consumption, however, a poisonous substance had to be leached out. Since cycads grow too slowly to make continued preparation of the arrowroot starch profitable, the practice has been abandoned. Today, cycads seen outside of their natural habitats are being grown primarily for ornamental or educational purposes. In Louisiana and elsewhere, however, the large compound leaves are used in Palm Sunday religious services. Some species are nearing extinction in the wild and may soon be known only in botanical gardens and conservatories.

In the southwestern United States, joint firs (*Ephedra*) are grazed by livestock, and the stems are still brewed into "Mormon tea." To offset a slight bitterness, a teaspoon of sugar, honey, or jam is added to each cup of tea. Native Americans and pioneers used a concentrated version of the tea in the treatment of venereal diseases. They also ground the seeds into flour from which a bitter bread was made. The drug *ephedrine*, widely used in the treatment of asthma and other respiratory problems, still is extracted from a Chinese species, but most of the drug now in use is synthetically produced. The Chinese used ephedrine medicinally more than 4,700 years ago. Continued medicinal use of ephedrine is now questionable because of potentially serious side effects.

One species of *Gnetum* is cultivated in Java for the shoots, which are eaten after being cooked in coconut milk. Fibers from the bark are made into a rope.

See Appendix 1 for scientific names of species discussed in this chapter.

Summary

1. The exposed seeds of gymnosperms are produced on sporophylls, forming a strobilus, or cone. The seed (female) cones and smaller pollen (male) cones are produced on the sporophytes.
2. A female gametophyte develops within a nucellus that is enclosed in an integument inside an ovule. The integument becomes the seed coat of a seed after fertilization, and the female gametophyte nurtures the development of the embryo.
3. Four phyla of living gymnosperms are recognized. Phylum Pinophyta includes the conifers. *Ginkgo* is the sole living repre-

sentative of Phylum Ginkgophyta. The cycads are in Phylum Cycadophyta. Phylum Gnetophyta includes the gnetophytes *Ephedra*, *Gnetum*, and *Welwitschia*.

4. Pines are the most numerous conifers. The needle-like leaves are arranged in clusters of two to five and have modifications adapting them to harsh environments.
5. Resin canals, occurring throughout the plants, secrete resin that inhibits fungi and certain insect pests.
6. Pine xylem lacks vessel members and fibers and is relatively soft. The phloem lacks companion cells but has albuminous cells that apparently perform the same function. Pine roots are always associated with mycorrhizal fungi, which are essential to normal development of the plants.
7. Two kinds of spores are produced. Microspores are produced in papery pollen cones that, in turn, develop in clusters toward the tips of lower branches. The microsporangia develop in pairs toward the base of the pollen cone scales and give rise to four-celled pollen grains that occur in huge numbers.
8. Megaspores are formed in ovules at the bases of seed cone scales. The integument of the ovule has a pore called the micropyle. One megaspore develops into a female gametophyte. The mature female gametophyte contains archegonia.
9. Before the archegonia mature, pollen grains catch in sticky pollination drops between the cone scales. Each pollen grain produces a pollen tube that digests its way down to the developing archegonia, and two of the original four cells in the pollen grain migrate into the tube as it grows. The generative cell divides and produces a sterile cell and a spermatogenous cell that itself divides, producing two sperms.
10. After pollination, one sperm unites with the egg, forming a zygote. The zygote develops into an embryo of a seed that has a membranous wing formed from a layer of the cone scale.
11. Some conifers produce seeds enclosed in fleshy or berrylike coverings. Their evolutionary origin is not clear.
12. *Ginkgo* has small, fan-shaped leaves with evenly forking veins. The life cycle of *Ginkgo* also is similar to that of cycads. The edible seeds are enclosed in a fleshy covering that has a rank odor at maturity.
13. Cycads superficially resemble palm trees with unbranched trunks and crowns of large, pinnately divided leaves. They have strobili and life cycles similar to those of conifers, but their sperms, unlike those of pines, have numerous flagella.
14. Gnetophytes all have vessels in their xylem. Half the species are in the genus *Ephedra*, whose members have jointed stems and leaves reduced to scales. *Gnetum* species have broad leaves and occur in the tropics, primarily as vines. *Welwitschia* is confined to southwest African deserts. Its stem is in the form of a shallow cup with straplike leaves that extend from the rim; basal meristems on the leaves constantly add to their length.
15. The seeds and inner bark of pines are edible, and a tea has been made from the leaves. Eastern white pine stems were used as masts for sailing vessels and for crates, furniture, flooring, paneling, and matchsticks. Western white pine is the source of most such lumber today.
16. Resin from pines consists of turpentine and rosin. Turpentine is used as a solvent, and resin is used by musicians and by baseball players. Dammar from kauri pines is used in colorless varnishes. Amber is fossilized resin. Resin is also used in floor waxes, printer's ink, paper coatings, perfumes, and the manufacture of menthol.
17. White spruce is the chief source of newsprint. It was also used for basketry and canoe lashing by Native Americans, with molasses or honey for treating scurvy, and in brewing a beer. Spruce resin was used for a type of chewing gum. The wood is used as soundboards for musical instruments and in the construction of -aircraft.
18. Larch and juniper woods are used for fence posts. Firs are used in the construction, paper, ornament, and Christmas-tree industries. Douglas fir is probably the most desired timber tree in the world today.
19. Coastal redwoods are also prized for their wood, which is resistant to fungi and insects. Bald cypress wood, used in the past for coffins and shingles, is also resistant to decay.
20. A dye and tannins are obtained from the eastern hemlock. Native Americans used parts of hemlocks for poultices and for food.
21. Eastern white cedar's wood was used for canoes, and that of the Atlantic cedar was used for construction of pipes for pipe organs. Yew wood is used for making bows, and an extract has potential for the treatment of human ovarian cancer.
22. Podocarps of New Zealand have edible seeds. Incense cedar wood is used for cedar chests, cigar boxes, pencils, and fence posts. Juniper berries are used to flavor gin and were used by Native Americans for food and a beverage.
23. *Ginkgo* seeds are edible, and *Ginkgo* plant extracts are used to improve blood circulation. Arrowroot starch was once obtained from a cycad. Mormon tea is brewed from the leaves and stems of joint firs (*Ephedra*), which, in the past, were also a source of the drug ephedrine and a venereal disease treatment. One *Gnetum* species is cultivated in Java for food.

Review Questions

1. What is a gymnosperm? How is it distinguished from any other kind of organism?
2. What is the difference between a seed and a spore?
3. How are the leaves of pines different from those of broadleaf flowering plants?
4. What is a resin canal, and what is its function? Where are resin canals found?
5. How do pines differ in their reproduction from ground pines and ferns?
6. How do pollen grains differ from spores or sperms?
7. Which conifers discussed in this chapter do not have woody seed cones?
8. If you had samples of leaves of a pine, *Ginkgo*, a cycad, a joint fir, and *Welwitschia* all together, indicate how you could tell them apart by constructing a key.
9. What parts of a pine are considered edible?
10. What is resin? Discuss some of its uses, past and present.

Discussion Questions

1. *Ginkgo* and cycads have broad leaves, whereas those of pines are needle-like. Can you suggest any significance of this in terms of the climates and habitats involved?
2. If no distinction were made at the level of kingdom between plants and animals, what would be the equivalent, if any, of sporophyte and gametophyte in humans?
3. Both bristlecone pines and redwoods can live to be thousands of years old. What do you suppose makes this possible?
4. Most of the old-growth stands of conifers in North America are now gone, and others will be gone soon. Much of what has been harvested is being replaced with new growth, sometimes with hybrids and non-native plants. Our forests are essential to our economy as we know it. If you had the power to change the way we manage and exploit our natural forest resources, what would you do differently, assuming you did not want to damage the economy?
5. If money were no object and you wished to landscape your yard primarily with gymnosperms, realistically, what would you include, taking into account your particular geographical area? Why?

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A female cycad cone (*Cycas* sp.). Cycads are slow-growing, superficially palmlike gymnosperms. Gymnosperm means naked-seeded, and the developing seeds can be seen here out in the open at the edges of the cone scales.

The evolution of seeds by the seed plants, including the gymnosperms, facilitated their invasion of land. Encased in a seed, the embryo of seed plants can withstand the extremes of the terrestrial environment such as freezing weather, drought, and even fire. Other characteristics, such as a thick cuticle on the epidermis, sunken stomata, and a hypodermis, consisting of one to several layers of thick-walled cells, also enable gymnosperms to withstand harsh environmental conditions from the freezing winters of the far north to dry desert areas. Resins produced by gymnosperms provide defense against fungal and insect attacks, while mycorrhizal fungi increase availability of soil nutrients and water to gymnosperms. Mutualistic associations with squirrels and birds, such as nutcrackers, promote gymnosperm seed dispersal. Gymnosperms provide humans with a wealth of "nature's services," ranging from construction materials to cancer treatments.

Figure 22.1 A comparison between exposed gymnosperm seeds and enclosed angiosperm seeds. A. Exposed seeds on a woody seed cone of a pine tree. B. A single seed cone scale with two seeds. C. A section through an apple (angiosperm fruit), showing the enclosed seeds.

Figure 22.2 A cluster (fascicle) of pine needles in cross section, showing how the needles form a loose, cylindrical rod.

Figure 22.3 A portion of a cross section of a pine stem, showing annual rings.

Figure 22.4 A cluster of pine pollen cones.

Figure 22.5 Pollen grains of a pine, as seen with the aid of a light microscope. Each pollen grain has a pair of air sacs that provides added buoyancy. $\times 300$.

A.

B.

Figure 22.6 Seed cones of pines. A. Immature cones shortly after being produced. B. A mature cone.

Figure 22.7 A longitudinal section through a pine ovule. ca. $\times 40$.

Figure 22.8 Life cycle of a pine.

Figure 22.9 The seeds of yew (*Taxus*) are not produced in cones but are surrounded at maturity by a red, fleshy, cuplike structure called an *aril*.

Figure 22.10 Fleshy seeds of a podocarp (*Podocarpus*). Note the large appendage at the base of each seed.

Figure 22.11 Ginkgo. A. A mature tree in the fall. B. Seeds and leaves. C. Male strobili.

A.

B.

C.

A.

B.

Figure 22.12 A. A male cycad with a strobilus. B. A female cycad with a strobilus.

Figure 22.13 Joint fir (*Ephedra*). A. Part of a single plant. B. Male strobili. $\times 20$. C. A female strobilus. $\times 20$.

A.

B.

C.

Figure 22.14 A climbing *Gnetum*.

Figure 22.15 A female *Welwitschia* plant in the Namibian Desert. (Photo by Margaret Marker, in the collection of the National Botanical Institute, Kirstenbosch. Courtesy Fiona Getliffe Norris.)

Figure 22.16 A prehistoric red wolf spider preserved in Dominican Republic amber. The amber is estimated to be between 20 and 30 million years old. (Photograph by John Yellen)

Figure 22.17 A modern newsprint factory. (Courtesy International Paper Company)

Figure 22.18 A violin with a soundboard made from red spruce.

Figure 22.19 Bald cypress trees in a southern swamp. Note the "knees" protruding above the surface.

A Living Fossil?

Just imagine a real-life Jurassic Park, where prehistoric dinosaurs long-thought extinct actually are alive. Well, something close to this happened in Australia in 1994. David Noble, while hiking on his Christmas holiday in the Wollemi National Park near Sydney, stepped into a stand of trees that, until that moment, were thought to have been extinct for over 150 million years. Known only as fossils, there they stood—about 40 pine trees growing in an isolated, rugged, rain-forest gully that had protected them all these years. This is one of the most significant botanical finds of the 20th century—and the trees are among the rarest plants alive.

Now called the *Wollemi pine* (*Wollemia nobilis*), these conifer (cone-bearing) trees are so distinct they constitute a new genus. While most conifers have dark green leaves, Wollemi pine leaves are bright and lighter green, almost the color of green apples. The leaves are complex and unusual. The trees are bisexual, with bright green seed cones and brown cylindrical pollen cones on the tips of upper branches. Also distinctive is the corklike knobby bark, which is an unusual chocolate brown. The tallest tree is estimated to be 150 years old, towering 130 feet from the ground, with a trunk about 3 feet wide. The new trees belong to the plant family Araucariaceae, which, while found only in the Southern Hemisphere today (Norfolk Island pine is an example), had a worldwide distribution during the Jurassic and Cretaceous periods (208–66 million years ago). This suggests that the Wollemi pines' closest relatives lived when Australia, New Zealand, Africa, South America, and India were all parts of the supercontinent Gondwana. During this period, the eastern coast of Australia lay close to the South Pole, when worldwide climates were relatively warm to hot and wet.

Sydney's Royal Botanic Gardens and the New South Wales National Parks and Wildlife Service are jointly studying the Wollemi pine with methods ranging from scanning electron microscopy of the leaf and pollen, to DNA extraction and gene-sequencing studies. One priority is to study its propagation methods so the plant can be established in cultivation. Although the Wollemi site is within 200 kilometers of Sydney, Australia's largest city, the exact location remains a secret to protect the plant from seed collectors and poachers.

The Wollemi pines, protected in their sheltered spot, not only escaped when their closest relatives died some 50 million years ago, but remained hidden until this exciting, remarkable find. *Wollemi* is an aboriginal word meaning "look around you." What an appropriate name for this real living fossil—it reminds all of us that there remains much to understand and explore in our world.

D. C. Scheirer

Box Figure 22.1 Drawings of Wollemi pine. *Top*: Leaves and branch; *Middle*: Pollen cone (male) at end of branch; *Bottom*: Seed cone (female). Scale bar = 2 cm. (Illustration by David MacKay, Royal Botanic Gardens, Sydney.)