

26.1 | Evolution of Seed Plants

By the end of this section, you will be able to do the following:

- Describe the two major innovations that allowed seed plants to reproduce in the absence of water
- Explain when seed plants first appeared and when gymnosperms became the dominant plant group
- Discuss the purpose of pollen grains and seeds
- Describe the significance of angiosperms bearing both flowers and fruit

The first plants to colonize land were most likely related to the ancestors of modern day mosses (bryophytes), which are thought to have appeared about 500 million years ago. They were followed by liverworts (also bryophytes) and primitive vascular plants—the pterophytes—from which modern ferns are descended. The life cycle of bryophytes and pterophytes is characterized by the *alternation of generations*, which is also exhibited in the gymnosperms and angiosperms. However, what sets bryophytes and pterophytes apart from gymnosperms and angiosperms is their reproductive requirement for water. The completion of the bryophyte and pterophyte life cycle requires water because the male gametophyte releases *flagellated sperm*, which must swim to reach and fertilize the female gamete or egg. After fertilization, the zygote undergoes cellular division and grows into a *diploid sporophyte*, which in turn will form sporangia or "spore vessels." In the sporangia, mother cells undergo meiosis and produce the haploid spores. Release of spores in a suitable environment will lead to germination and a new generation of gametophytes.

In seed plants, the evolutionary trend led to a dominant sporophyte generation accompanied by a corresponding reduction in the size of the gametophyte from a conspicuous structure to a microscopic cluster of cells enclosed in the tissues of the sporophyte. Whereas lower vascular plants, such as club mosses and ferns, are mostly *homosporous* (producing only one type of spore), all seed plants, or spermatophytes, are *heterosporous*, producing two types of spores: megaspores (female) and microspores (male). Megaspores develop into female gametophytes that produce eggs, and microspores mature into male gametophytes that generate sperm. Because the gametophytes mature within the spores, they are not free-living, as are the gametophytes of other seedless vascular plants.

Ancestral heterosporous seedless plants, represented by modern-day plants such as the spike moss *Selaginella*, are seen as the evolutionary forerunners of seed plants. In the life cycle of *Selaginella*, both male and female sporangia develop within the same stem-like **strobilus**. In each male sporangium, multiple microspores are produced by meiosis. Each microspore produces a small *antheridium* contained within a spore case. As it develops it is released from the strobilus, and a number of flagellated sperm are produced that then leave the spore case. In the female sporangium, a single megaspore mother cell undergoes meiosis to produce four megaspores. Gametophytes develop within each megaspore, consisting of a mass of tissue that will later nourish the embryo and a few archegonia. The female gametophyte may remain within remnants of the spore wall in the megasporangium until after fertilization has occurred and the embryo begins to develop. This combination of an embryo and nutritional cells is a little different from the organization of a seed, since the nutritive *endosperm* in a seed is formed from a single cell rather than multiple cells.

Both seeds and pollen distinguish seed plants from seedless vascular plants. These innovative structures allowed seed plants to reduce or eliminate their dependence on water for gamete fertilization and development of the embryo, and to conquer dry land. Pollen grains are male gametophytes, which contain the sperm (gametes) of the plant. The small haploid ($1n$) cells are encased in a protective coat that prevents desiccation (drying out) and mechanical damage. Pollen grains can travel far from their original sporophyte, spreading the plant's genes. Seeds offer the embryo protection, nourishment, and a mechanism to maintain dormancy for tens or even thousands of years, ensuring that germination can occur when growth conditions are optimal. Seeds therefore allow plants to disperse the next generation through both space and time. With such evolutionary advantages, seed plants have become the most successful and familiar group of plants.

Both adaptations expanded the colonization of land begun by the bryophytes and their ancestors. Fossils place the earliest distinct seed plants at about 350 million years ago. The first reliable record of gymnosperms dates their appearance to the Pennsylvanian period, about 319 million years ago (**Figure 26.2**). Gymnosperms were preceded by progymnosperms, the first naked seed plants, which arose about 380 million years ago. *Progymnosperms* were a transitional group of plants that superficially resembled conifers (cone bearers)

because they produced wood from the secondary growth of the vascular tissues; however, they still reproduced like ferns, releasing spores into the environment. At least some species were heterosporous. Progymnosperms, like the extinct *Archaeopteris* (not to be confused with the ancient bird *Archaeopteryx*), dominated the forests of the late Devonian period. However, by the early (Triassic, c. 240 MYA) and middle (Jurassic, c. 205 MYA) Mesozoic era, the landscape was dominated by the true gymnosperms. Angiosperms surpassed gymnosperms by the middle of the Cretaceous (c. 100 MYA) in the late Mesozoic era, and today are the most abundant and biologically diverse plant group in most terrestrial biomes.

EON	ERA	PERIOD	MILLIONS OF YEARS AGO	
Phanerozoic	Cenozoic	Quaternary	1.6	Flowering Plants
		Tertiary	66	
		Cretaceous	138	
	Mesozoic	Jurassic	205	Gymnosperms
		Triassic	240	
		Permian	290	
	Paleozoic	Pennsylvanian	330	Pterophytes
		Mississippian	360	
		Devonian	410	Lycophytes
		Silurian	435	
		Ordovician	500	Liverworts and Mosses
		Cambrian	570	
Proterozoic	Late Proterozoic Middle Proterozoic Early Proterozoic		2500	
Archean	Late Archean Middle Archean Early Archean		3800?	
Pre-Archean				

Figure 26.2 Plant timeline. Various plant species evolved in different eras. (credit: United States Geological Survey) Figure modified from source.

Evolution of Gymnosperms

The fossil plant *Elkinsia polymorpha*, a "seed fern" from the Devonian period—about 400 million years ago—is considered the earliest seed plant known to date. Seed ferns (**Figure 26.3**) produced their seeds along their branches, in structures called cupules that enclosed and protected the ovule—the female gametophyte and associated tissues—which develops into a seed upon fertilization. Seed plants resembling modern tree ferns became more numerous and diverse in the coal swamps of the Carboniferous period.



Figure 26.3 Seed fern leaf. This fossilized leaf is from *Glossopteris*, a seed fern that thrived during the Permian age (290–240 million years ago). (credit: D.L. Schmidt, USGS)

Fossil records indicate the first gymnosperms (progymnosperms) most likely originated in the Paleozoic era, during the middle Devonian period: about 390 million years ago. The previous Mississippian and Pennsylvanian periods, were wet and dominated by giant fern trees. But the following Permian period was dry, which gave a reproductive edge to seed plants, which are better adapted to survive dry spells. The Ginkgoales, a group

of gymnosperms with only one surviving species—the *Ginkgo biloba*—were the first gymnosperms to appear during the lower Jurassic. Gymnosperms expanded in the Mesozoic era (about 240 million years ago), supplanting ferns in the landscape, and reaching their greatest diversity during this time. The Jurassic period was as much the age of the cycads (palm-tree-like gymnosperms) as the age of the dinosaurs. Ginkgoales and the more familiar conifers also dotted the landscape. Although angiosperms (flowering plants) are the major form of plant life in most biomes, gymnosperms still dominate some ecosystems, such as the taiga (boreal forests) and the alpine forests at higher mountain elevations (**Figure 26.4**) because of their adaptation to cold and dry growth conditions.



Figure 26.4 Conifers. This boreal forest (taiga) has low-lying plants and conifer trees. (credit: L.B. Brubaker, NOAA)

Seeds and Pollen as an Evolutionary Adaptation to Dry Land

Bryophyte and fern spores are haploid cells dependent on moisture for rapid development of multicellular gametophytes. In the seed plants, the female gametophyte consists of just a few cells: the egg and some supportive cells, including the endosperm-producing cell that will support the growth of the embryo. After fertilization of the egg, the diploid zygote produces an embryo that will grow into the sporophyte when the seed germinates. Storage tissue to sustain growth of the embryo and a protective coat give seeds their superior evolutionary advantage. Several layers of hardened tissue prevent desiccation, and free the embryo from the need for a constant supply of water. Furthermore, seeds remain in a state of dormancy—induced by desiccation and the hormone *abscisic acid*—until conditions for growth become favorable. Whether blown by the wind, floating on water, or carried away by animals, seeds are scattered in an expanding geographic range, thus avoiding competition with the parent plant.

Pollen grains (**Figure 26.5**) are male gametophytes containing just a few cells and are distributed by wind, water, or an animal pollinator. The whole structure is protected from desiccation and can reach the female organs without depending on water. After reaching a female gametophyte, the pollen grain grows a tube that will deliver a male nucleus to the egg cell. The sperm of modern gymnosperms and all angiosperms lack flagella, but in cycads, *Ginkgo*, and other primitive gymnosperms, the sperm are still motile, and use flagella to swim to the female gamete; however, they are delivered to the female gametophyte enclosed in a pollen grain. The pollen grows or is taken into a fertilization chamber, where the motile sperm are released and swim a short distance to an egg.

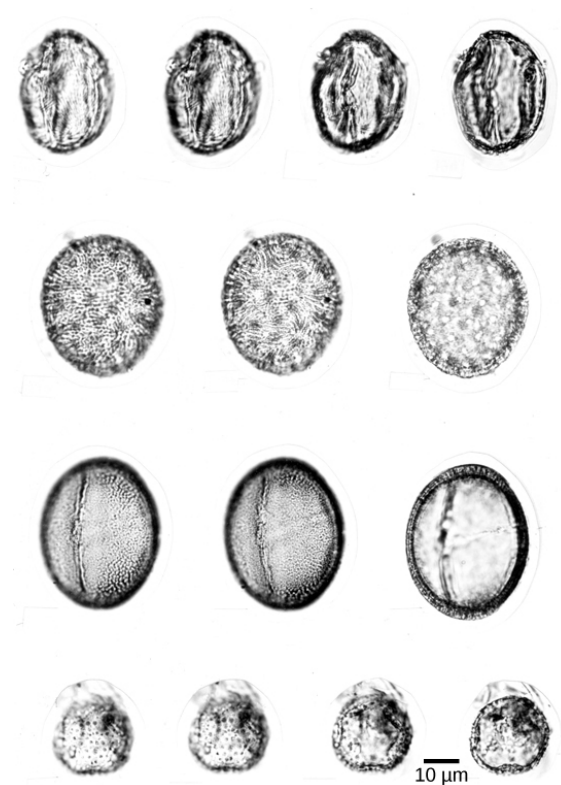


Figure 26.5 Pollen fossils. This fossilized pollen is from a Buckbean fen core found in Yellowstone National Park, Wyoming. The pollen is magnified 1,054 times. (credit: R.G. Baker, USGS; scale-bar data from Matt Russell)

Evolution of Angiosperms

The roughly 200 million years between the appearance of the gymnosperms and the flowering plants gives us some appreciation for the evolutionary experimentation that ultimately produced flowers and fruit. Angiosperms (“seed in a vessel”) produce a flower containing male and/or female reproductive structures. Fossil evidence (**Figure 26.6**) indicates that flowering plants first appeared about 125 million years ago in the Lower Cretaceous (late in the Mesozoic era), and were rapidly diversifying by about 100 million years ago in the Middle Cretaceous. Earlier traces of angiosperms are scarce. Fossilized pollen recovered from Jurassic geological material has been attributed to angiosperms. A few early Cretaceous rocks show clear imprints of leaves resembling angiosperm leaves. By the mid-Cretaceous, a staggering number of diverse flowering plants crowd the fossil record. The same geological period is also marked by the appearance of many modern groups of insects, suggesting that pollinating insects played a key role in the evolution of flowering plants.

New data in comparative genomics and paleobotany (the study of ancient plants) have shed some light on the evolution of angiosperms. Although the angiosperms appeared after the gymnosperms, they are probably not derived from gymnosperm ancestors. Instead, the angiosperms form a sister clade (a species and its descendants) that developed in parallel with the gymnosperms. The two innovative structures of flowers and fruit represent an improved reproductive strategy that served to protect the embryo, while increasing genetic variability and range. There is no current consensus on the origin of the angiosperms. Paleobotanists debate whether angiosperms evolved from small woody bushes, or were related to the ancestors of tropical grasses. Both views draw support from cladistics, and the so-called woody *magnoliid hypothesis*—which proposes that the early ancestors of angiosperms were shrubs like modern magnolia—also offers molecular biological evidence.

The most primitive living angiosperm is considered to be *Amborella trichopoda*, a small plant native to the rainforest of New Caledonia, an island in the South Pacific. Analysis of the genome of *A. trichopoda* has shown that it is related to all existing flowering plants and belongs to the oldest confirmed branch of the angiosperm family tree. The nuclear genome shows evidence of an ancient whole-genome duplication. The mitochondrial genome is large and multichromosomal, containing elements from the mitochondrial genomes of several other species, including algae and a moss. A few other angiosperm groups, called basal angiosperms, are viewed as having ancestral traits because they branched off early from the phylogenetic tree. Most modern angiosperms

are classified as either monocots or eudicots, based on the structure of their leaves and embryos. Basal angiosperms, such as water lilies, are considered more ancestral in nature because they share morphological traits with both monocots and eudicots.



Figure 26.6 *Ficus* imprint. This leaf imprint shows a *Ficus speciosissima*, an angiosperm that flourished during the Cretaceous period. (credit: W. T. Lee, USGS)

Flowers and Fruits as an Evolutionary Adaptation

Angiosperms produce their gametes in separate organs, which are usually housed in a flower. Both fertilization and embryo development take place inside an anatomical structure that provides a stable system of sexual reproduction largely sheltered from environmental fluctuations. With about 300,000 species, flowering plants are the most diverse phylum on Earth after insects, which number about 1,200,000 species. Flowers come in a bewildering array of sizes, shapes, colors, smells, and arrangements. Most flowers have a mutualistic pollinator, with the distinctive features of flowers reflecting the nature of the pollination agent. The relationship between pollinator and flower characteristics is one of the great examples of coevolution.

Following fertilization of the egg, the ovule grows into a seed. The surrounding tissues of the ovary thicken, developing into a fruit that will protect the seed and often ensure its dispersal over a wide geographic range. Not all fruits develop completely from an ovary; such “false fruits” or *pseudocarps*, develop from tissues adjacent to the ovary. Like flowers, fruit can vary tremendously in appearance, size, smell, and taste. Tomatoes, green peppers, corn, and avocados are all examples of fruits. Along with pollen and seeds, fruits also act as agents of dispersal. Some may be carried away by the wind. Many attract animals that will eat the fruit and pass the seeds through their digestive systems, then deposit the seeds in another location. Cockleburs are covered with stiff, hooked spines that can hook into fur (or clothing) and hitch a ride on an animal for long distances. The cockleburs that clung to the velvet trousers of an enterprising Swiss hiker, George de Mestral, inspired his invention of the loop and hook fastener he named Velcro.

evolution CONNECTION

Building Phylogenetic Trees with Analysis of DNA Sequence Alignments

All living organisms display patterns of relationships derived from their evolutionary history. Phylogeny is the science that describes the relative connections between organisms, in terms of ancestral and descendant species. Phylogenetic trees, such as the plant evolutionary history shown in **Figure 26.7**, are tree-like branching diagrams that depict these relationships. Species are found at the tips of the branches. Each branching point, called a node, is the point at which a single taxonomic group (taxon), such as a species, separates into two or more species.

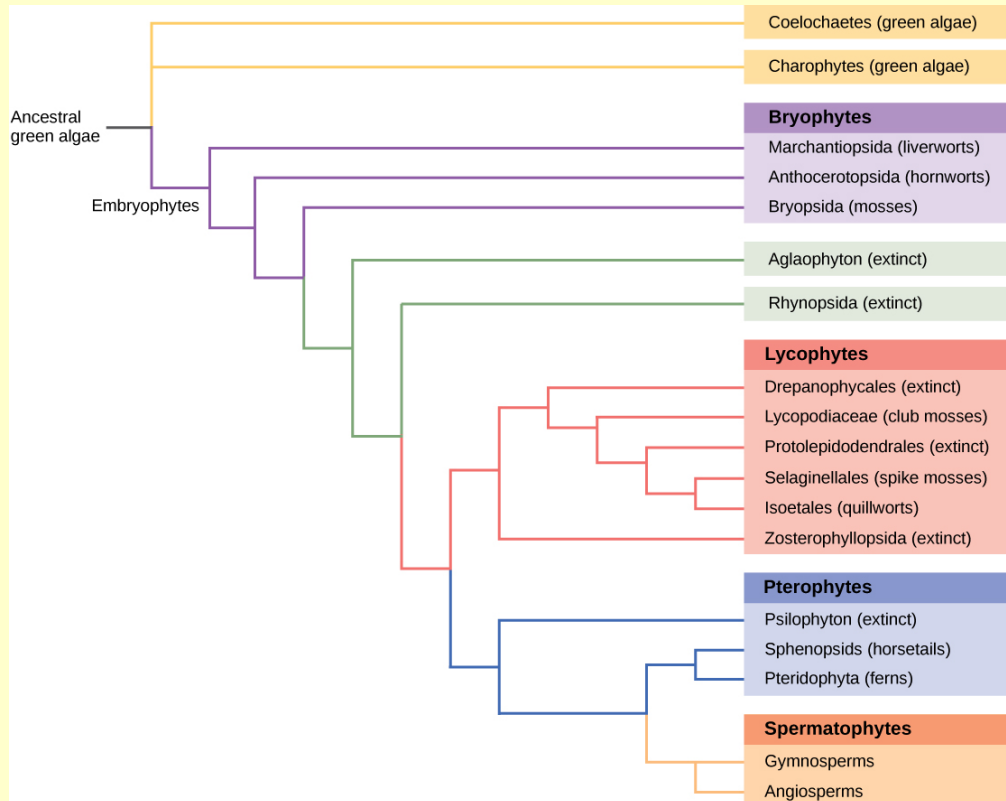


Figure 26.7 Plant phylogeny. This phylogenetic tree shows the evolutionary relationships of plants.

Phylogenetic trees have been built to describe the relationships between species since the first sketch of a tree that appeared in Darwin's *Origin of Species*. Traditional methods involve comparison of homologous anatomical structures and embryonic development, assuming that closely related organisms share anatomical features that emerge during embryo development. Some traits that disappear in the adult are present in the embryo; for example, an early human embryo has a postanal tail, as do all members of the Phylum Chordata. The study of fossil records shows the intermediate stages that link an ancestral form to its descendants. However, many of the approaches to classification based on the fossil record alone are imprecise and lend themselves to multiple interpretations. As the tools of molecular biology and computational analysis have been developed and perfected in recent years, a new generation of tree-building methods has taken shape. The key assumption is that genes for essential proteins or RNA structures, such as the ribosomal RNAs, are inherently conserved because mutations (changes in the DNA sequence) could possibly compromise the survival of the organism. DNA from minute samples of living organisms or fossils can be amplified by *polymerase chain reaction* (PCR) and sequenced, targeting the regions of the genome that are most likely to be conserved between species. The genes encoding the 18S ribosomal RNA from the small subunit and plastid genes are frequently chosen for DNA alignment analysis. Once the sequences of interest are obtained, they are compared with existing sequences in databases

such as GenBank, which is maintained by The National Center for Biotechnology Information. A number of computational tools are available to align and analyze sequences. Sophisticated computer analysis programs determine the percentage of sequence identity or homology. Sequence homology can be used to estimate the evolutionary distance between two DNA sequences and reflect the time elapsed since the genes separated from a common ancestor. Molecular analysis has revolutionized phylogenetic trees. In some cases, prior results from morphological studies have been confirmed: for example, confirming *Amborella trichopoda* as the most primitive angiosperm known. However, some groups and relationships have been rearranged as a result of DNA analysis.

26.2 | Gymnosperms

By the end of this section, you will be able to do the following:

- Discuss the type of seeds produced by gymnosperms, as well as other characteristics of gymnosperms
- Identify the geological era dominated by the gymnosperms and describe the conditions to which they were adapted
- List the four groups of modern-day gymnosperms and provide examples of each
- Describe the life cycle of a typical gymnosperm

Gymnosperms, meaning “naked seeds,” are a diverse group of seed plants. According to the “anthophyte” hypothesis, the angiosperms are a sister group of one group of gymnosperms (the Gnetales), which makes the gymnosperms a paraphyletic group. Paraphyletic groups are those in which not all descendants of a single common ancestor are included in the group. However, the “netifer” hypothesis suggests that the gnetophytes are sister to the conifers, making the gymnosperms monophyletic and sister to the angiosperms. Further molecular and anatomical studies may clarify these relationships. Characteristics of the gymnosperms include naked seeds, separate female and male gametes, pollination by wind, and tracheids (which transport water and solutes in the vascular system).

Gymnosperm seeds are not enclosed in an ovary; rather, they are only partially sheltered by modified leaves called **sporophylls**. You may recall the term **strobilus** (plural = strobili) describes a tight arrangement of sporophylls around a central stalk, as seen in pine cones. Some seeds are enveloped by sporophyte tissues upon maturation. The layer of sporophyte tissue that surrounds the megasporangium, and later, the embryo, is called the **integument**.

Gymnosperms were the dominant phylum in the Mesozoic era. They are adapted to live where fresh water is scarce during part of the year, or in the nitrogen-poor soil of a bog. Therefore, they are still the prominent phylum in the coniferous biome or *taiga*, where the evergreen conifers have a selective advantage in cold and dry weather. Evergreen conifers continue low levels of photosynthesis during the cold months, and are ready to take advantage of the first sunny days of spring. One disadvantage is that conifers are more susceptible than deciduous trees to leaf infestations because most conifers do not lose their leaves all at once. They cannot, therefore, shed parasites and restart with a fresh supply of leaves in spring.

The life cycle of a gymnosperm involves alternation of generations, with a dominant sporophyte in which reduced male and female gametophytes reside. All gymnosperms are heterosporous. The male and female reproductive organs can form in cones or strobili. Male and female sporangia are produced either on the same plant, described as **monoecious** (“one home” or bisexual), or on separate plants, referred to as **dioecious** (“two homes” or unisexual) plants. The life cycle of a conifer will serve as our example of reproduction in gymnosperms.

Life Cycle of a Conifer

Pine trees are conifers (coniferous = cone bearing) and carry both male and female sporophylls on the same mature sporophyte. Therefore, they are monoecious plants. Like all gymnosperms, pines are heterosporous and generate two different types of spores (male microspores and female megaspores). Male and female spores develop in different strobili, with small male cones and larger female cones. In the male cones, or staminate cones, the **microsporocytes** undergo meiosis and the resultant haploid microspores give rise to male