CHAPTER 21

The Seedless Vascular Plants: Ferns and Their Relatives

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OVERVIEW

This chapter opens with a brief review of the features that distinguish the major groups of vascular plants without seeds from one another and from the bryophytes and then discusses representatives of each phylum. Included in the discussion are whisk ferns (*Psilotum*), club mosses (*Lycopodium, Selaginella*), quillworts (*Isoetes*), horsetails (*Equisetum*), and ferns. A digest of the human and ecological relevance of each group is given, and life cycles of representatives are illustrated. The chapter concludes with an examination of fossils, and each type is briefly described. A table showing the geologic time scale is provided.

Some Learning Goals

1. Describe the basic structural differences between bryophytes and vascular plants.
2. Distinguish from one another the four phyla of seedless vascular plants.
3. Contrast the differences in the life cycles of ground pines (*Lycopodium*) and spike mosses (*Selaginella*).
4. Summarize the structural features of horsetail (*Equisetum*) sporophytes.
5. Know how to recognize and explain the functions of all the structures involved in Alternation of Generations in a fern.
6. Identify and list 10 important uses of vascular plants that do not produce seeds.
7. Explain what a fossil is and distinguish among the various types of fossils.

hus far, our survey of all organisms traditionally regarded as plants has taken us from simple, one-celled prokaryotic organisms, through more specialized eukaryotic protists and fungi, and on to the bryophytes. We now take up several phyla of plants whose members have internal conducting tissues but do not produce seeds.

In the introduction to the Plant Kingdom in Chapter 20, we mentioned that the ancestors of the bryophytes and the vascular plants probably were multicellular green algae that became established on the land over 400 million years ago. As green organisms moved ashore, they developed several new features, including sterile jackets of cells around gametangia, embryos within protective tissues, stomata for gas exchange, and a cuticle. Most of these features at least partly protected vital parts from drying out. Bryophytes have no significant internal tissues for conducting water, and most water used internally is absorbed directly through the aboveground parts. External water is required for -fertilization.

During the early stages of vascular plant evolution, internal conducting tissues (xylem and phloem) began to develop, true leaves appeared, and roots that function in absorption as well as anchorage developed. At the same time, gametophytes became progressively smaller and more dependent on sporophytes that became progressively larger. Initially the sporophyte also afforded gametophyte -protection.

Unlike conifers and flowering plants, the primitive vascular plants discussed in this chapter do not produce seeds. They include the ferns and a number of their relatives often referred to as "fern allies." Four phyla of seedless vascular plants are recognized:

1. **Phylum Psilotophyta** (*whisk ferns*). Features unique to members of this phylum of vascular plants include sporophytes that have neither true leaves nor roots, and stems and rhizomes that fork evenly.
2. **Phylum Lycophyta** (*club mosses* and *quillworts*). The stems of these plants are covered with **microphylls** (leaves with a single vein whose trace is not associated with a leaf gap—see Chapter 6). Most microphylls are photosynthetic.
3. **Phylum Equisetophyta** (*horsetails* and *scouring rushes*). The sporophytes of these plants have ribbed stems containing silica deposits and whorled, scalelike microphylls that lack chlorophyll.
4. **Phylum Polypodiophyta** (*ferns*). The sporophytes of ferns have **megaphylls** (leaves with more than one vein and a leaf trace that is associated with a leaf gap—see Chapter 6) that are often large and much divided.

Fossils, discussed at the end of the chapter, give us clues to the ancestry of some of these plants and also to the origins of seed plants discussed in the chapters to follow.

PHYLUM PSILOTOPHYTA-—THE WHISK FERNS

There is nothing very fernlike in the appearance of *whisk ferns*, commonly referred to by their scientific name of *Psilotum*, but they do loosely resemble small, green whisk brooms. Exactly where these plants fit in the Plant Kingdom is not clear. Traditionally, they have been associated with a number of extinct plants called *psilophytes* that flourished perhaps 400 million years ago, but there is not much fossil evidence to substantiate the link. Because whisk fern and true fern gametophytes share several features, some botanists classify them with the true ferns. They will be discussed first because, by most present criteria, they are among the simplest of all living seedless vascular plants.

Structure and Form

Psilotum sporophytes consist almost entirely of dichotomously forking (evenly forking) aerial stems and are unique among living vascular plants in having neither leaves nor roots. They usually grow up to 30 centimeters (1 foot) tall but occasionally grow as much as 1 meter (3 feet) or more tall (Fig. 21.1). The visible stems arise from short, branching rhizomes just beneath the surface of the ground.

Enations, which are tiny, green, superficially leaflike, veinless, photosynthetic flaps of tissue, are spirally arranged along the stems. Photosynthesis takes place in the outer cells of the stem (epidermis and cortex). A central cylinder of xylem is surrounded by phloem. The xylem is star-shaped in cross section. Short roots, aided by mycorrhizal fungi, are scattered along the surfaces of the rhizomes. Some of the mycorrhizal fungi become established in cortical cells just beneath the epidermis.

Reproduction

Small *sporangia* that are fused together in threes and resemble miniature yellow pumpkins are produced at the tips of very short, stubby branches in the upper parts of the angular stems. Spores released from the sporangia germinate slowly in the soil, in tree bark or tree fern "bark" crevices, or in other similar habitats. In Hawaii, they also grow in old lava flows.

The gametophytes, which lack pigmentation, develop from the spores beneath the soil surface and are easily overlooked. Sometimes they resemble tiny, transparent dog bones that are only about 2 millimeters (0.08 inch) wide and seldom more than 6 millimeters (0.25 inch) long. They are cylindrical and, like the aerial stems, may branch dichotomously. They have no chlorophyll and absorb their nutrients via one-celled, rootlike *rhizoids* aided by mycorrhizal fungi. Archegonia and antheridia develop randomly over the surface of the same gametophyte. After a sperm unites with an egg in an archegonium, the zygote develops a foot and a rhizome. As soon as the rhizome becomes established, upright stems are produced, and the rhizome separates from the foot (Fig. 21.2).

Whisk ferns are native to tropical and subtropical regions. In the United States, they are found in Florida, Louisiana, Texas, Arizona, and Hawaii. They are extensively cultivated in Japan and sometimes become a weed in greenhouses around the world. *Tmesipteris*, a close relative, has leaflike appendages; it is native to Australia and the South Pacific.

Fossil Whisk Fern Look-Alikes

Fossil plants that somewhat resemble whisk ferns have been found in Silurian geological formations (Table 21.1). These formations are estimated to be as much as 400 million years old. One group of these fossil plants, of which *Cooksonia* and *Rhynia* are examples (see Fig. 21.22), had naked stems and terminal sporangia. *Cooksonia* is the oldest plant known to have had xylem. A second group of fossils, represented by *Zosterophyllum*, had somewhat rounded sporangia produced along the upper parts of naked stems. *Zosterophyllum* and its relatives first appeared during the Devonian period (Table 21.1). They are thought to be ancestral to the club mosses, discussed in the next section, "Phylum Lycophyta—The Ground Pines, Spike Mosses, and Quillworts."

Whisk ferns are of little economic importance. Their spores have a slightly oily feel and were once used by Hawaiian men to reduce loincloth irritations of the skin. Hawaiians also made a laxative liquid by boiling whisk ferns in water.

PHYLUM LYCOPHYTA—THE GROUND PINES, SPIKE MOSSES, AND QUILLWORTS

When I was in high school, my father was interviewed by a newspaper reporter in a hotel room of a large South American city. At the end of the interview, which took place with the rest of the family present, the reporter set up a press camera and said he wanted to take a picture of the family. After posing us, he took a vial from his pocket and poured a little powder along a metal bar attached to one end of a T-shaped device that otherwise looked like a flashlight. He then told us to smile, and a moment later, there was a flash of light followed by a large billow of smoke. I learned later that the *flash powder* (forerunner of flashbulbs and strobe lights) he had used contained millions of spores of primitive vascular plants collectively called **club mosses.**

The 950 or so known species of club mosses (referred to in this text as *ground pines* and *spike mosses*) mostly look enough like large true mosses that the Swedish naturalist Linnaeus lumped both together in a single class. Once details of the structure and the form of club mosses were known, however, it became obvious that they are quite unrelated to true mosses.

Today, there are living representatives of two major genera and two minor genera of club mosses. Several others became extinct about 270 million years ago. The sporophytes of all species have microphylls (leaves with a single unbranched vein that is not associated with a leaf gap—see Chapter 6) that are usually quite small; they also have true stems and true roots.

The two major genera of club mosses with living members are *Lycopodium,* with about 50 species, and *Selaginella,* with over 700 species. They are distributed throughout the world, but they are more abundant in the tropics and wetter temperate areas.

Lycopodium—Ground Pines

Structure and Form

Lycopodium plants often grow on forest floors. They are sometimes called *ground pines,* partly because they resemble little Christmas trees, complete with "cones" that are usually upright or, in a few species, hang down (Fig. 21.3). The stems of ground pine sporophytes are either simple or branched. The plants are mostly less than 30 centimeters (1 foot) tall, although some tropical species grow to heights of 1.5 meters (5 feet) or more. The upright, or sometimes pendent, stems develop from branching rhizomes. The leaves may be whorled or in a tight spiral and are rarely more than 1 centimeter (0.4 inch) long. Adventitious roots, whose epidermal cells often produce root hairs, develop along the rhizomes.

Reproduction

At maturity, some species of ground pines produce kidney-bean-shaped sporangia on short stalks in the axils of specialized leaves. Such sporangium-bearing leaves are called **sporophylls.** In other species, the sporophylls have no chlorophyll, are smaller than the other leaves, and are in terminal conelike clusters called **strobili** (singular: **strobilus**). In the sporangia, *sporocytes* undergo meiosis, producing spores that are released and carried away by air currents. The spores of some species germinate in a few days if they land in a suitable location, but spores of other species may not germinate for up to several years.

After germination, independent gametophytes develop from the spores. The gametophytes vary in shape, some resembling tiny carrots. The gametophyte body usually develops in the ground in association with mycorrhizal fungi. Some gametophytes, however, develop primarily on the surface where the exposed parts turn green. All types produce both antheridia and archegonia on the same gametophyte that, in some species, may live for several years. Since the sperm are flagellated, water is essential for fertilization to occur.

Zygotes first become embryos with a foot, stem, and leaves and then develop into mature sporophytes (Fig. 21.4). If the gametophyte is underground, chlorophyll does not develop in the young sporophyte until it emerges into the light. Several sporophytes may be produced from a single gametophyte. A number of ground pines also reproduce asexually by means of small bulbils (bulbs produced in the axils of leaves), each of which is capable of developing into a new sporophyte.

Selaginella—Spike Mosses

Structure and Form

The sporophytes of *Selaginella*, the larger of the two major genera of living club mosses, are sometimes called *spike mosses* (Fig. 21.5). The approximately 700 species are widely scattered around the world in wetter areas, but they are especially abundant in the tropics. A few are common weeds in greenhouses. They tend to branch more freely than ground pines, from which they differ in several respects. The two most obvious differences are (1) their leaves each have a tiny extra appendage, or tongue, called a **ligule,** on the upper surface near the base and (2) they produce two different kinds of spores and gametophytes—an advanced feature referred to as **heterospory.** The seed-bearing coniferous and flowering plants discussed in chapters to follow are all heterosporous.

Reproduction

Sexual reproduction of spike mosses and ground pines both involve the production of sporangia, but spike moss sporangia develop on either *microsporophylls* or *megasporophylls* (Fig. 21.6). **Microsporophylls** bear *microsporangia* containing numerous **microsporocytes** that undergo meiosis, producing tiny **microspores.** The *megasporangia* of **megasporophylls** usually contain a **megasporocyte** that, after meiosis, becomes four comparatively large **megaspores.**

Each microspore may become a male gametophyte consisting simply of a somewhat spherical antheridium surrounded by a sterile jacket of cells within the microspore wall. Either 128 or 256 sperm cells with flagella are produced in each antheridium. A megaspore develops into a female gametophyte that is also relatively simple in structure. By the time this gametophyte is mature, however, it consists of many cells that have been produced inside the megaspore. As it increases in size, it eventually ruptures its thickened spore wall and produces -several -archegonia in the exposed seams. The development of both male and female gametophytes often begins before the spores are released from their sporangia. Fertilization and development of new sporophytes are similar to those of ground pines.

Isoetes—Quillworts

Structure and Form

There are about 60 species of *quillworts* (all in the genus *Isoetes*) (Fig. 21.7). Most are found in areas where they are at least partially submerged in water for part of the year. Their leaves (microphylls) are slightly spoon-shaped at the base and look like green porcupine quills, although they are not stiff and rigid. They are arranged in a tight spiral on a stubby stem, which resembles the corm of a gladiola or a crocus. *Ligules* occur toward the leaf bases. The corms have a vascular cambium and may live for many years. Wading birds and muskrats often eat the corms. The plants are generally less than 10 centimeters (4 inches) tall, but the leaves of one species become 0.6 meter (2 feet) long.

Reproduction

Reproduction is similar to that of spike mosses, except that no strobili are formed. Both types of sporangia are produced at the bases of the leaves (Fig. 21.8). Up to 1 million microspores may occur in a single microsporangium.

Ancient Relatives of Club Mosses and Quillworts

Some of the ancient and extinct relatives of the club mosses were large and treelike and grew up to 30 meters (100 feet) tall; their trunks were up to 1 meter (3 feet 3 inches) in diameter. They were dominant members of the forests and swamps of the Carboniferous period that reached its peak some 325 million years ago (see Table 21.1). Quillworts first appeared in the Cretaceous period, about 130 million years ago. Their fossils reveal that even the oldest were remarkably similar to their present-day relatives (Fig. 21.9). A knowledge of the life histories and ancestry of various members of this phylum enhances our understanding of the development and diversity of the Plant Kingdom as a whole.

Human and Ecological Relevance of Club Mosses and Quillworts

Like the whisk ferns, club mosses and quillworts are of little economic importance today. As mentioned earlier, large numbers of club moss spores produce a flash of light when ignited. This characteristic was exploited at one time in the manufacture of theatrical explosives and photographic flashlight powders. In the past, druggists mixed spore powder with pills and tablets to prevent them from sticking to one another. The spore powder itself has been used for centuries in folk medicine, particularly for the treatment of urinary disorders and stomach upsets. Some Native Americans used it as a talcum powder for babies, snuffed it to arrest nosebleeds, and applied it following childbirth to staunch hemorrhaging. It was also sometimes used to stop bleeding from wounds.

Club moss extracts have been used in several countries in the past to reduce fevers, but partly because of undesirable side effects, medicinal use of club mosses has now largely been abandoned. Native Americans of Washington, Oregon, and British Columbia became mildly intoxicated after chewing parts of one local species of club moss. It is reported that they became unconscious if they chewed too much.

Novelty stores sometimes sell a species of spike moss native to Mexico and to the southwestern United States. Known as the *resurrection plant,* it shrivels and rolls up in a ball when dry, appearing to be completely dead, but quickly unfolds and turns green when sprinkled with water. Other spike mosses have been placed on shelves indoors without water for nearly 3 years and then have resumed growth when given water. Ground pines and spike mosses have been used ornamentally indoors and outdoors as ground covers. Some ground pines are spray painted and used as Christmas ornaments or in floral wreaths. Several species of *Lycopodium* have been exploited to the extent that they are now on rare and endangered or threatened species lists; they should no longer be collected.

Quillwort corms have been eaten by domestic and wild animals, waterfowl, and humans.

PHYLUM EQUISETOPHYTA—THE HORSETAILS AND SCOURING RUSHES

Many backpackers and campers have become aware of a unique use of a relatively common and widespread genus of plants (*Equisetum*) known as *horsetails* or *scouring rushes.* Significant deposits of silica accumulate on the inner walls of the epidermal cells of the stems, which make excellent scouring material for dirty metal pots and pans. Native Americans were aware of this scouring property of the plants and used them extensively.

Structure and Form

About 25 species of horsetails (the name usually applied to branching forms that look a little like a horse's tail) and scouring rushes (unbranched forms) (Fig. 21.10) are scattered throughout all continents, including Australia, where they are weeds. They usually grow less than 1.3 meters (4 feet) tall, but some in the tropics and coastal redwood forests of California exceed 4.6 meters (15 feet) in height. Where branches occur, they are normally in whorls at regular intervals along the jointed stems. Both branched and unbranched species have tiny, scalelike leaves (microphylls) in whorls at the nodes. These leaves are fused together at their bases, forming a collar. They are green when they first appear, but they soon wither and bleach, and virtually all photosynthesis occurs in the stems.

The stems are distinctly ribbed and have obvious nodes and internodes; there are numerous stomata in the grooves between the ribs. A cross section of a stem (Fig. 21.11) reveals that the pith breaks down at maturity, leaving a hollow central canal. There are two cylinders of smaller canals outside of the pith. The inner cylinder consists of water--conducting *carinal canals* that are aligned opposite the ribs of the stem. Each canal has a patch of xylem and phloem to the outside. The canals of the outer cylinder, called *vallecular canals,* contain air. They are larger than the carinal canals and are aligned opposite the "valleys" between the ribs.

The aerial stems develop from horizontal rhizomes, which also have regular nodes, internodes, and ribs. In some species, the rhizomes have adventitious roots and may form extensive branching systems as much as 2 meters (6.5 feet) below the surface. Both internal stem structure and external features help distinguish the various species of horsetails from one another.

Reproduction

If stems or rhizomes are broken up by a disturbance, such as a storm or foraging animals, the fragments can grow into new sporophyte plants. In most species, however, reproduction usually involves a sexual process. In the spring, some species produce special cream- to buff-colored non-photosynthetic stems from rhizomes (Fig. 21.12). Small, conelike **strobili** develop at the tips of these special stems or, in other species, at the tips of regular photosynthetic stems.

The strobili are usually about 2 to 4 centimeters (0.75 to 1.5 inches) long. Hexagonal, dovetailing plates at the surface of the strobilus give it the appearance of an ellipsoidal honeycomb. Each hexagon marks the top of a *sporangiophore* that has 5 to 10 elongate sporangia connected to the rim. The stalks of the sporangiophores are attached to the central axis of the strobilus. The sporangia surround the sporangiophore stalks and point inward. These hidden sporangia are not visible until maturity when the sporangiophores separate slightly. The spores are then released.

When the sporocytes in the sporangia undergo meiosis, distinctive-appearing green spores are produced. At one pole, the spores have four ribbonlike appendages that are slightly expanded at the tips (Fig. 21.13). The appendages are called **elaters** (not structurally or otherwise related to the elaters of liverworts and hornworts). The elaters are very sensitive to changes in humidity and aid spores in their dispersal. While spores are being carried by an air current, the elaters are more or less extended like wings. If a spore enters a humid air pocket above a damp area below, the elaters coil, causing the spore to drop in an area that is more likely to support germination and growth.

Germination of spores usually occurs within a week of their release. Lobed, cushionlike, green gametophytes develop and seldom grow to more than 8 millimeters (0.36 inch) in diameter. Rhizoids anchor them to the surface. At first, about half of the gametophytes are male with antheridia, and the other half are female with archegonia. After a month or two, however, the female gametophytes of most species become bisexual, producing only antheridia from then on. When water contacts mature antheridia, sudden changes in water pressure cause the sperms produced within to be explosively ejected. Several eggs on a female or bisexual gametophyte may be fertilized, and the development of more than one sporophyte is common.

Ancient Relatives of Horsetails

Horsetails and scouring rushes belong to the single remaining genus (*Equisetum*) of a phylum of several different orders that flourished in the Carboniferous period about 300 million years ago. At that time, some members of this phylum, like the ancient club mosses, were treelike (Fig. 21.14) and grew over 15 meters (50 feet) tall, while others were vinelike. Some were similar to present-day horsetails in having leaves in whorls (Fig. 21.15), jointed stems with internal canals, and sporangiophores with sporangia hanging down from the rims.

Human and Ecological Relevance of Horsetails and Scouring Rushes

The 7th-century Romans ate the boiled young strobili of field horsetails or fried them after mixing them with flour. Native Americans peeled off the tough epidermis of young stems and ate the inner parts either raw or boiled, while others cooked the rhizomes of the giant horsetail for food. Cows, goats, muskrats, bears, and geese also have been known to eat horsetails. Hopi Indians ground dried horsetail stems to flour, which they mixed with cornmeal to make bread or mush. Horsetails have, however, occasionally been reported to be poisonous to horses, and they are not recommended for human consumption.

Native Americans and Asians had several other uses for these plants. One tribe drank the water from the carinal canals of the stem, and another thought the shoots were “good for the blood.” It is not known if there was any basis for this latter idea, but there is an old unconfirmed report that field horsetail consumption “produces a decided increase in blood corpuscles.” At least one or two species are known to have a mild diuretic effect (a *diuretic* is a substance that increases the flow of urine), and they have been used in the past in folk medicinal treatment of urinary and bladder disorders. Some have also been used as an antacid or an astringent (an *astringent* is a substance that arrests discharges, particularly of blood). One species was used in the treatment of gonorrhea, and others were used for tuberculosis.

At least two Native American tribes burned the stems and used the ashes to alleviate sore mouths or applied the ashes to severe burns. Members of another tribe ate the strobili of a widespread scouring rush to cure diarrhea, and still others boiled stems in water to make a hair wash for the control of lice, fleas, and mites.

During pioneer times when the covered wagons moved westward, the use of scouring rush stems for scouring and sharpening was widespread. They were used not only for cleaning pots and pans but also for polishing brass, hardwood furniture and flooring, and for honing mussel shells to a fine edge. Scouring rushes are still in limited use for these purposes today. Some species of horsetails accumulate certain minerals in addition to silica. Veins of such minerals have been located beneath populations of horsetails by analyzing the plants’ mineral contents. This process of analysis involves a chemical treatment of the tissues followed by the use of X-ray equipment.

In the geological past, the giant horsetails and club mosses were a significant part of the vegetation growing in vast swampy areas. In some instances, the swamps were stagnant and slowly sinking, permitting the gradual accumulation of plant remains, which, because of the lack of oxygen in the water, were not readily attacked by decay bacteria. Such circumstances, over aeons of time, were ideal for the formation of coal. Today, if you section a lump of coal thinly enough and examine it under the microscope, you can still see bits of tissue and spores of plants that were living hundreds of millions of years ago. One soft coal known as *cannel* consists primarily of the spores of giant horsetails and club mosses that, through the ages, were reduced to carbon.

For the scientific names of species discussed, see Appendix 1.

PHYLUM POLYPODIOPHYTA—THE FERNS

When I was a small child, my family had a large potted fern on each side of a fireplace. I became quite attached to the plants, and believing I was removing a “disease,” I carefully scraped off the little brownish patches that appeared from time to time on the lower surfaces of the leaves. It wasn’t until I got to college I learned that instead of controlling a disease, I had inadvertently been frustrating the sex life of my favorite plants!

If we could take a worldwide opinion poll about ornamental plants, ferns undoubtedly would rank high in popularity. In fact, in some parts of the world, it is difficult to find a household without at least one fern either inside or out in the garden. Their leaves are so infinitely varied in form and aesthetically pleasing that Thoreau was once moved to state, “God made ferns to show what He could do with leaves."

Structure and Form

The approximately 11,000 known species of ferns vary in size from tiny floating forms less than 1 centimeter (0.4 inch) in diameter to giant tropical tree ferns up to 25 meters (82 feet) tall. Fern leaves are *megaphylls* (leaves associated with leaf gaps and having branching veins—see Chapter 6) that are commonly referred to as **fronds.** They are typically divided into smaller segments and are feathery in appearance (Fig. 21.16), but some are undivided, pleated, or tonguelike, and others resemble a four-leaf clover or grow in such a way as to form "nests." In the tropics, the "nest" ferns often accumulate enough humus to provide food and shelter for huge earthworms that are up to 0.6 meter (2 feet) long. Since ferns require external water for their sexual reproduction, they are most abundant in wetter tropical and temperate habitats, but a few are adapted to drier areas.

Reproduction

The sporophyte is the conspicuous phase of the life cycle in all the plants discussed in this chapter (Fig. 21.17). A fern sporophyte consists of the fronds, a stem in the form of a rhizome, and adventitious roots that arise along the rhizome. The fronds, regardless of their ultimate form, usually first appear tightly coiled at their tips. These *croziers* (unrelated to the croziers of sac fungi), or "fiddleheads" (Fig. 21.18), then unroll and expand, revealing the blades. At maturity, the blades are often divided into segments called **pinnae** (singular: **pinna**) that are attached to a midrib, or rachis. A stalk, or petiole, is usually present at the base.

When the fronds have expanded, small, often circular, rust-colored patches of powdery--looking material may appear on the lower surfaces of some or all of the blades. Because these patches appear similar to fungal rusts, some fern owners have thought their plants were diseased and have turned to sprays to deal with the "problem" or have even carefully scraped the patches off. The development of the patches is normal and healthy, however, and examination with a hand lens or dissecting microscope will reveal that they are actually clusters of *sporangia* (Fig. 21.19). The sporangia may be scattered evenly over the lower surfaces of the fronds, but they are often confined to the margins. The sporangia are mostly found in numerous discrete clusters called **sori** (singular: **sorus**). In many ferns, the sori, while they are developing, are protected by thin, individual flaps of colorless tissue called **indusia** (singular: **indusium**). As the sporangia mature, the indusium, which often resembles a tiny, semi-transparent umbrella attached by its base to the frond surface, shrivels and exposes the sporangia beneath.

Most of the sporangia are microscopic and stalked and look something like tiny, transparent baby rattles with a conspicuous row of heavy-walled, brownish cells along the edge. This row of cells, which looks like a tiny millipede, is called an **annulus.** It functions in catapulting spores out of the sporangium with a distinct snapping action influenced by moisture changes in the cells (Fig. 21.20).

Sporocytes undergo meiosis in the sporangia, usually producing either 48 or 64 spores per sporangium. Sporangia of some of the primitive adder's tongue ferns may have up to 15,000 spores, however, and the number of sporangia is often so great that it has been estimated that a single beech fern plant will produce a total of 50 million spores.

Two kinds of spores are produced in certain aquatic or amphibious ferns such as the clover fern (*Marsilea*) and *Salvinia*. Single, large *megaspores* are produced in some sporangia, while numerous, tiny *microspores* are produced in others. The vast majority of fern species, however, produce only one kind of spore.

After the spores have been flung out of their sporangia, they are dispersed by wind; relatively few end up in habitats suitable for their survival. Such habitats include shady, wet ledges and rock crevices or moist soil. The spores can also easily be germinated on damp clay flowerpots in the home or greenhouse. Those that germinate in favorable locations produce little "Irish valentines," or **prothalli** (singular: **prothallus**), as the green, heart-shaped gametophytes of these and other seedless vascular plants are more properly called (Fig. 21.21). These structures often curl slightly at their edges and may be 5 to 6 millimeters (0.25 inch) in diameter; they are visible without a microscope.

Prothalli are only one cell thick, except toward the middle where they are slightly thicker. Antheridia are interspersed among the rhizoids produced on the lower surface of the central area of most prothalli, with archegonia also being produced, usually closer to the notch of the heart-shaped gametophyte. The archegonia are somewhat flask-shaped, with curving necks that protrude slightly above the surface, whereas the antheridia are more spherical and often elevated above the surface on short stalks. In a few species, antheridia and archegonia are produced on separate prothalli.

A single antheridium may produce from 32 to several hundred sperms, each with few to many flagella. Fertilization of an egg takes place within an archegonium and is chemically influenced so that it usually occurs with a sperm from a different prothallus. Only one zygote develops into a young sporophyte on any prothallus, regardless of the number of eggs that may be fertilized. This sporophyte usually has smaller, simpler fronds during its first season of growth, but typical full-sized fronds grow from the persisting rhizomes in succeeding years.

Fossil Relatives of Ferns

Fossil remains of ferns and plants thought to be ancestors of ferns abound in ancient deposits. Possible ancestors of ferns (Fig. 21.22) are found in Devonian formations (see Table 21.1) estimated to be 375 million years old. Most resemble ferns in habit, but they have no broad fronds and otherwise are more like whisk ferns than true ferns. Well-preserved fossils of tree ferns related to large, tropical ferns of the present day are found in geological strata dating back to between 250 and 320 million years ago (Fig. 21.23).

Ferns (especially tree ferns) became so abundant during the latter part of the Carboniferous period that this era in the past was referred to as the *Age of Ferns*. The discovery of seeds on some of them, however, raised questions about relationships, and the term *Age of Ferns* was dropped.

Human and Ecological Relevance of Ferns

In some parts of North America, it is unusual to find a house without at least a Boston fern growing within. Ferns make ideal house plants because many of them are adapted to growing in low light, and most are not as susceptible as other plants to aphids, mites, mealybugs, and similar pests. Outdoors, ferns are equally popular as ornamentals. Some eventually become subjects for an artist's brush or a natural history photographer's camera.

Apart from the pleasing aesthetic aspects of ferns, they function well as air filters. For example, during a single hour, one average-sized Boston fern can remove about 1,800 micrograms of formaldehyde (a common pollutant from carpets) from the air in a typical room measuring 3 meters by 3 meters (10 feet by 10 feet). According to the Environmental Protection Agency, if properly maintained, the fern can almost completely rid the air of pollutants on a daily basis.

Ferns also have other practical value. Commercial growers of the brilliantly colored anthuriums in Hawaii and elsewhere have found that native tree ferns provide the ideal amount of shade and other environmental conditions needed for bringing their flowers to perfection. Tree fern rhizome or root bark[1] and rhizome bark of certain other species, such as the royal fern (which produces osmunda bark), are a favorite medium of orchid, bromeliad, and staghorn fern growers. Its texture is well suited to the growth of the orchids' aerial roots, and as the bark slowly decomposes, rain water trickling over its surface picks up nutrients that are particularly appropriate for these plants. The demand for fern bark for orchids has exceeded the supply for a number of years, and it has become very expensive on the market (Fig. 21.24).

As the young "fiddleheads" of many species of ferns unroll, a dense covering of hairs is visible on the petiole and rachis. In the past, the silky hairs of some of the larger tropical tree ferns (Fig. 21.25) were stripped and used for upholstery, pillow, and mattress stuffing. During the late 1800s, over 1,900 metric tons (2,094 tons) of this material were shipped from Hawaii to the mainland, and if it were not for the eventual substitution of alternative materials, these magnificent plants might have been totally destroyed. Some tropical hummingbirds use these hairs along with scales of other ferns to line their nests, and at one time, Polynesians used them in a form of embalming for their dead. The trunks of tree ferns have been used in the construction of small houses in the tropics. Parts of one Hawaiian species of small tree fern and the fronds of an Asian fern yield red pigments used for dyeing cloth.

The bracken fern, which is distributed worldwide and is a weed in parts of Europe, has been used and even cultivated for human food for many years, particularly in Japan and New Zealand. It has, however, also long been known to be mildly poisonous to livestock. Research in both Europe and Japan has shown conclusively that bracken fronds fed to experimental animals produce intestinal tumors, and because of this, the consumption of these fronds for food is now actively discouraged.

Indigenous peoples of many areas where ferns occur have eaten the cooked rhizomes and young fronds of various ferns. Native Americans often baked the rhizomes of sword ferns, lady ferns, and others in stone-lined pits, removed the outer layers, and ate the starchy inner material. Similarly, native Hawaiians ate the starchy core of their tree ferns as emergency food. In Asia, the oriental water fern is still sometimes grown for food in rice paddies and used as a raw or cooked vegetable. In Malaysia, a relative of the lady fern is frequently used as a vegetable.

Uses of ferns in folk medicine abound. They have been used in the treatment of diarrhea, dysentery, rickets, diabetes, fevers, eye diseases, burns, wounds, eczema and other skin problems, leprosy, coughs, stings and insect bites, as a poison antidote, for labor pains, constipation, dandruff, and a host of other maladies. The male fern, which is more common in Europe than in North America, contains a drug that is effective in expelling intestinal worms (e.g., tapeworms). Its use for this purpose dates back to ancient times, and it is still occasionally used, although synthetic medicines have now largely replaced it. The licorice fern was used in the past by Native Americans of the Pacific Northwest for the treatment of sore throats and coughs and was also used as a flavoring agent and sugar substitute. Members of a tribe in California chewed stalks of goldback ferns to quell toothaches and snuffed a liquid made from the fronds of the bird's-foot fern to arrest nosebleeds.

The fronds of bracken and other ferns have been used in the past for thatching houses. Anyone who has placed such fronds in compost piles knows they break down much more slowly than do the leaves of other plants. Bracken fronds are still occasionally used as an overnight bedding base by fishermen and hunters. A substance extracted from these fronds has been used in the preparation of chamois leather, and the rhizome is used in northern Europe in the brewing of ale.

The chain fern has large fronds up to 2 meters (6.5 feet) long that have two flexible, leathery strands in the petiole and rachis of each frond. Native Americans and others have gathered the fronds for many years to strip these strands for use in basketry and weaving. They do so by gently cracking the long axis with stones to expose the strands, which are then easily removed. The glossy, black petioles of the five-finger fern have also been used in intricate basketry patterns by Native Americans. In Southeast Asia, the climbing fern has fronds with a rachis that may grow up to 12 meters (40 feet) long; it is still a favorite material (when available) for the weaving of baskets.

The mosquito fern, which is a floating water fern in the genus *Azolla,* forms tiny plants little bigger than duckweeds. It is found over wide areas where the climate is relatively mild. It sometimes forms such dense floating mats that it is believed to suffocate mosquito larvae that periodically need to reach the surface for air. This same fern frequently has cyanobacteria living symbiotically in cavities between cells. The cyanobacteria fix nitrogen, and it has been shown experimentally that plants without these organisms do not grow as well as those with them. In some parts of the world, mosquito ferns are thrown into rice paddies so that the cyanobacteria associated with them will fix nitrogen and reduce the need for added fertilizers.

Many ferns are now commercially propagated through tissue culture (discussed in Chapter 14). The scientific names of ferns mentioned in this chapter are given in Appendix 1.

FOSSILS

Introduction

Several references to fossils have been made in this and preceding chapters, and other references occur in the chapters that follow. We have become increasingly aware of worldwide limitations of energy sources, and we now frequently hear references to fossil fuels as nonrenewable resources. Exactly what is a fossil, and how did it come into existence?

Originally, the word *fossil* was applied to anything unusual found in rocks, but its use is now more or less confined to any recognizable prehistoric organic object (or its impression) that has been preserved from past geological ages in the earth's crust (see Table 21.1). Such a definition includes teeth marks, borings, impressions of footprints and tracks, dung deposits, and deposits of chemicals that are evidence of the activities of algae and bacteria. Age itself does not make a fossil. Human remains thousands of years old that have been found in caves and tombs are not regarded as fossils, but it is conceivable that other remains of the same age could be preserved in rocks and regarded as fossils.

Fossils are formed in a number of different ways. The conditions for their formation almost always include the accumulation of sediments in an area where plants, animals, or other organisms are present or to which they have been transported. Such areas are found in swamps, oceans, lakes, or other bodies of water. Hard parts, such as wood or bones, are more likely to be preserved than soft parts. Other environmental factors, such as the presence of salt or antiseptic chemicals or stagnation resulting in low oxygen content of the water, all favor fossil formation.

Quick burial is another factor enhancing the chances of organic material becoming fossilized. Such burial might result if an organism was unable to avoid a rain of ash from a volcanic eruption or was trapped in a cave or sudden sandstorm. Other forms of quick burial occur when an organism falls into quicksand, a body of water, or asphalt. Descriptions of several common types of fossils follow.

Molds, Casts, Compressions, and Imprints

After silt or other sediment has buried an object and hardened into rock, the organic material may be slowly washed away by water percolating through the pores of the rock. This leaves a space, which may then be filled in with silica deposits. If only a space is left, it is called a *mold;* if it is filled in with silica, it is called a *cast.* Artificial casts of plaster or wax compounds may be made from molds of the original objects. When objects such as leaves are buried by layers of sediment, the sheer weight of the overlying material may compress them to as little as 5% of their original thickness. When this occurs, all that is left is a thin film of organic material and an outline showing some surface details. Virtually no preservation of cells or other internal structure takes place. Such fossils are very common and are called *compressions* (Fig. 21.26). The image of a compression, like the details of a foot or a hand pressed into wet cement, is called an *imprint*. Coal is a special type of compression, often involving different plant parts that are thought to have been subjected to enormous pressures after the fallen plants slowly accumulated in a swamp.

Petrifactions

Petrifactions (Fig. 21.27) are uncompressed, rocklike materials in which the original cell structure has been preserved. About 20 different mineral substances, including silica and the salts of several metals, are known to bring about petrifaction. At one time, it was believed the process occurred through the replacement of the plant parts by minerals in solution, one molecule at a time. It is now believed that chemicals in solution infiltrate the cells and cell walls, where they crystallize and harden, permanently preserving the original material.

Petrifactions can be studied by cutting thin sections with a diamond or carborundum saw and polishing the material with extremely fine grit powder until it is thin enough for light to pass through. Then it can be examined with a compound microscope. Another simpler method of studying petrifactions involves etching the cut surface with a dilute acid and then applying a plastic or similar film. As soon as the film hardens, it can be peeled off. Such peels display lifelike microscopic details of the surface with which they were in contact. They are commonly used by paleo-botanists (botanists who study fossil plant materials) in their research.

Coprolites

Coprolites are the fossilized dung of prehistoric animals and humans. They may contain pollen grains and other plant and animal parts that provide clues to the food and feeding habits of past organisms and cultures.

Unaltered Fossils

Some plants or animals fell into bodies of oil or water that, because of substances present or a nearly total lack of oxygen, did not permit decay to occur. Some animals died in snowfields, and their bodies were permanently frozen. In such instances, preservation in the unaltered state occurred. Unaltered fossils, particularly frozen ones, are very rare.

Summary

1. Four phyla of seedless vascular plants are recognized: Psilotophyta (whisk ferns); Lycophyta (club mosses and quillworts); Equisetophyta (horsetails and scouring rushes); and Polypodiophyta (ferns).
2. Whisk ferns (*Psilotum*) are the simplest of all living vascular plants, consisting of evenly forking, green stems that have small protuberances called enations, but no leaves; roots are also lacking. The stem contains a central cylinder of xylem and phloem.
3. Whisk fern spores germinate into tiny gametophytes, with antheridia and archegonia scattered over their surfaces. The zygote develops into a foot and a rhizome. Upright stems are produced when the rhizome separates from the foot.
4. *Tmesipteris*, an Australian relative of whisk ferns, has leaflike appendages. Fossil plants resembling whisk ferns have been found in Silurian geological formations.
5. There are two genera of club mosses with living members. Ground pines (*Lycopodium*) develop sporangia in the axils of sporophylls. Several sporophytes may be produced from one gametophyte. Spike mosses (*Selaginella*) are heterosporous and have a ligule on each microphyll; microspores develop into male gametophytes with antheridia, and the megaspores develop into female gametophytes with archegonia.
6. Quillworts (*Isoetes*) are heterosporous and have quill-like microphylls that arise from a cormlike base. The corms have a cambium that remains active for many years.
7. Some fossil relatives of club mosses were large, dominant members of the forests and swamps of the Carboniferous period.
8. Club moss spores have been used for flash powder, medicinal purposes, as talcum powder, and to staunch bleeding. The plants themselves have been used as ornamentals, novelty items, Christmas ornaments, and for intoxicating purposes.
9. Horsetails and scouring rushes (*Equisetum*) accumulate deposits of silica in their epidermal cells and have made good scouring material. They occur in both unbranched and branched forms. The stems are jointed and ribbed and have tiny, scale-like leaves in whorls at each joint.
10. The stems of *Equisetum* are centrally hollow and contain cylindrically arranged carinal and vallecular canals. The stems arise from rhizomes that branch extensively below the surface of the ground.
11. Some species of *Equisetum* produce non-photosynthetic stems. Conelike strobili are produced in the spring in all species. *Equisetum* spores have ribbonlike elaters that are sensitive to changes in humidity.
12. Equal numbers of male and female gametophytes are produced, but female gametophytes may become -bisexual. The development of more than one sporophyte from a gametophyte is common.
13. Ancient relatives of horsetails were the size of trees when they flourished in the Carboniferous period of 300 million years ago.
14. Horsetails have been used for food after the parts containing silica were removed, but they are not recommended for human consumption. They have also been used medicinally as a diuretic, as an astringent, and in the treatment of venereal disease and tuberculosis. Other uses include a hair wash, a mineral indicator, and a metal polish. Cannel coal consists primarily of spores of giant horsetails that were reduced to carbon.
15. Fern leaves (fronds) are typically divided and feathery in appearance but vary greatly in form. They usually first appear as croziers that unroll and expand.
16. Patches of sporangia appear on the lower surfaces of fern fronds. The sporangia commonly occur in sori, which may be

protected by indusia. Each sporangium has an annulus that functions in catapulting mature spores out of the sporangium.

17. Fern gametophytes (prothalli) develop after spores germinate. Most prothalli contain both archegonia and antheridia; only one zygote develops into a sporophyte.
18. Possible ancestors of ferns are found in Devonian deposits estimated to be 375 million years old.
19. Ferns are used as ornamentals, air filters, a source of “bark” for growing orchids and other plants, a source of stuffing materials for bedding, in tropical construction, as food, and in numerous folk medicinal applications. Other uses include basketry and weaving material, ingredient in brewing ale, and ingredient in the preparation of chamois leather. One floating fern forms dense mats and is believed to suffocate mosquito larvae.
20. Fossils are recognizable prehistoric organic objects that are formed in different ways. Molds, casts, compressions, and imprints are formed when material buried by silt or other sediment has hardened into rock and the organic material has slowly been washed away by water.
21. Petrifactions are uncompressed, rocklike materials in which the original cell structure has been preserved. Coprolites are fossilized dung that may contain pollen grains and other plant and animal parts. Unaltered fossils are those of plants or animals that may have fallen into bodies of oil or water or snowfields and were not subjected to decay.

Review Questions

1. What basic features of the ferns and their relatives distinguish them from any organisms studied thus far?
2. How does the gametophyte of a whisk fern differ from that of a true fern?
3. Which of the fern relatives have significantly functional leaves? In those without conspicuous leaves, how are the carbohydrate needs of the plants met?
4. How does one distinguish among ground pines, spike mosses, and quillworts?
5. How did the ancient ground pines differ from those of the present day?
6. How do the spores and the female gametophytes of horsetails differ from those of any other plants studied thus far?
7. What is the location and function of carinal canals?
8. In your opinion, which have the most human relevance today: club mosses and horsetails of the present or those of the geological past? Why?
9. Define crozier, rachis, pinna, indusium, and prothallus.
10. Diagram the life cycle of a typical fern.
11. Summarize present and past human uses of ferns.
12. How are fossils formed, and what different types are recognized?

Discussion Questions

1. Would you assume there is any significance to the fact that both the sporophytes and the gametophytes of whisk ferns branch in the same manner?
2. Do spike mosses, which produce two kinds of spores and gametophytes, have any advantage over ground pines, which produce only one kind of spore and gametophyte?
3. Some gametophytes of fern relatives develop underground, while others develop at the surface. If you were to be a gametophyte, which would you prefer? Why?
4. After looking at the internal structure of a horsetail stem, can you suggest a function for the silica in the ribs?
5. How would we be affected if all ferns were to become extinct in a few years?

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’Ama’uma’u (*Sadleria cyatheoides*), a small Hawaiian tree fern.

Figure 21.1 *Psilotum* sporophytes. The small, yellowish objects are three-lobed sporangia.

Figure 21.2 Life cycle of *Psilotum*.

TABLE 21.1

Geologic Time Scale

ERA	PERIOD	AGE	EARLIEST EVIDENCE OF PLANTS	DURATION (MILLIONS OF YEARS)	MILLION YEARS BEFORE PRESENT
	Quaternary	Age of modern seed		63	
	Tertiary				65
	Cretaceous			65	
					130
	Jurassic		Grasses	45	
			Flowering		
					175
	Triassic	Age of ancient seed		45	
					220
	Permian		Ginkgoes	50	
			Conifers		
					270
	Carbonifero			80	
			Seed ferns		
					350
	Devonian	Age of spore-bearing	Lycopods	50	
			Horsetails		

			Bryophytes		
					400
	Silurian			40	
					440
	Ordovician	Age of bacteria and		60	
					500
	Cambrian		Marine algae	100	
					600
	Precambrian			1,700?	2,300?

Figure 21.3 *A. Lycopodium cernum,* a club moss native to the tropics. *B. Lycopodium obscurum,* native to northern and eastern North America.

A.
B.
Figure 21.4 Life cycle of the ground pine *Lycopodium,* a homosporous lycopod.

Figure 21.6 Life cycle of the spike moss *Selaginella,* a heterosporous lycopod.

Figure 21.7 Quillwort (*Isoetes*) sporophytes. *(Courtesy Robert A. Schlising)*

Figure 21.8 Life cycle of a quillwort (*Isoetes*), a heterosporous member of the phylum.

Figure 21.9 A small portion of the surface of the fossil lycopod, *Lepidodendron,* showing leaf (microphyll) bases similar to those seen in modern lycopods. *(Specimen courtesy University of Illinois Paleobotany Laboratory)*

Figure 21.10 Horsetails (*Equisetum*). *A.* An unbranched species. *B.* A branched species.

A.
B.
Figure 21.11 A horsetail (*Equisetum*) stem in cross section. ca. ×20.
Figure 21.12 Life cycle of a horsetail (*Equisetum*) that has separate vegetative and reproductive shoots.

Figure 21.13 Horsetail spores. *A.* With elaters coiled. *B.* With elaters spread.

Figure 21.14 Reconstruction of a coal age (Carboniferous) forest. *(Photo by Field Museum of Natural History, Chicago)*

Figure 21.15
Reconstruction of the fossil giant horsetail, *Calamites.*

A.
B.
D.
C.
Figure 21.16 Common ferns with typically dissected fronds. *A.* A maidenhair fern. *B.* Cinnamon fern. The cinnamon-colored fertile frond in the center is non-photosynthetic and produces large numbers of sporangia. *C.* Ostrich fern. *D.* ‘Ama’uma’u, a small Hawaiian tree fern.

Figure 21.18 A crozier (fiddlehead) of a tropical fern.

Figure 21.19 Pinnae of fern fronds, showing some types of arrangements of sporangia on undersides of leaves. *A. Cheilanthes. B. Polypodium. C. Cystopteris. D. Cibotium. E. Davallia. F. Cyathea.*

Figure 21.22 Possible ancestors of ancient ferns. *A. Aglao-phyton. B. Psilophyton* (?). The 19th-century origin of this drawing apparently was a composite of three distantly related genera.

A.
B.
Figure 21.23 A fossil fern.

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1. Ferns do not have a cork cambium and do not, therefore, produce bark that is typical of woody seed plants. The cells of the outer layers of fern roots and rhizomes, however, do become impregnated with suberin and consequently become bark-like in appearance and function.

The ferns and their relatives were the first land plants with significant internal tissues for conducting water and roots for absorbing water and nutrients, morphological innovations that increased the environments in which these ancient plants could live. In the ancient geologic period known as the Carboniferous, giant horsetails and club mosses grew in great abundance in swampy areas. The biomass produced by these plants accumulated in huge deposits. The lack of oxygen inhibited bacteria-mediated decay of the plant biomass, which was eventually transformed into coal. These coal deposits represent large quantities of carbon dioxide removed from the ancient atmosphere by ferns and their relatives. The reintroduction of this carbon dioxide into the atmosphere in modern times, as we burn coal, may produce rapid climate change.

Figure 21.17 Life cycle of a fern.

Figure 21.20 Release of spores from a fern sporangium. *A.* An intact sporangium. *B.* Spores being ejected as the sporangium splits; the annulus first draws back and then snaps forward.

A.
B.
C.
D.
Figure 21.21 Fern prothalli. *A.* Surface view. ×10. *B.* A prothallus as seen with the aid of a light microscope. ×20. *C.* Archegonia. ×100. *D.* Antheridia. ×100.

A.
B.
Figure 21.25 *A.* A Brazilian tree fern. *B.* The growing tip of a tree fern, showing the protective rust-colored hairs.

Figure 21.24 An orchid plant growing on fern bark.

Figure 21.26 A compression fossil.

Figure 21.27 Petrified wood. *(Courtesy Sharon Stern)*

Figure 21.5 *Selaginella,* a spike moss.