Chapter 20

Introduction to the Plant Kingdom: Bryophytes

OVERVIEW

This chapter opens with a discussion of the features of the Plant Kingdom and its members and then introduces bryophytes with a note about their past use as bandages. Liverworts are explored after the habitats and general life history of bryophytes are discussed. Next, the chapter examines hornworts and their life cycles and then goes over mosses in greater detail. The chapter concludes with observations on the human and ecological relevance of bryophytes.

Some Learning Goals

1. Know the features that distinguish the Plant Kingdom from other kingdoms.
2. Understand how bryophytes as a group differ from other plants.
3. Learn the basic differences between thalloid liverworts and "leafy" liverworts.
4. Explain how a liverwort thallus can be distinguished from that of a hornwort.
5. Know the structures involved in the life cycle of a moss and in which structures meiosis and fertilization occur.
6. Learn which features liverworts, hornworts, and mosses have in common and understand how their sporophytes differ.
7. Learn five uses of bryophytes by humans.

lder botany texts tended to apply the term **plants** to many of the simpler organisms mentioned in previous chapters. Today, however, the majority of botanists confine this term to bryophytes, ferns, cone-bearing plants, flowering plants, and various relatives of each of these groups. These groups are the subjects of the next several chapters.

Plants and green algae, discussed in Chapter 18, share several major pigments (e.g., chlorophyll *a*, chlorophyll *b*, carotenoids). Plants and green algae also have starch in common as the primary food reserve and cellulose in their cell walls. When plant and some algal cells divide, they develop *phragmoplasts* and *cell plates*, both of which are unknown in other organisms. These shared features suggest plants and green algae were derived from a common ancestor.

Fossils reveal that land plants first appeared about 400 million years ago, so any hypothetical ancestor probably progressed from an aquatic to a land habitat even earlier. By the time plants became established on land, they had developed several features that kept them from drying out. (1) A fatty cuticle that retards water loss developed on plant surfaces. (2) The **gametangia** (gamete-producing structures) and **sporangia** (spore-producing structures) of plants became multicellular and surrounded by a sterile cell jacket. (3) Plant zygotes developed into multicellular **embryos** (immature plantlets) within parental tissues that originally surrounded the egg.

Most members of the Plant Kingdom are more complex and varied in form than those of the kingdoms examined in the preceding chapters, and their tissues are correspondingly more specialized for photosynthesis, conduction, support, anchorage, and protection. The sporophyte phases of the life cycles are predominant in the more advanced members, and reproduction is primarily sexual.

The multicellular embryos of plants are unknown in the kingdoms discussed in the preceding chapters. This was recognized in past classifications when all organisms were placed in either the Plant Kingdom or the Animal Kingdom. The Plant Kingdom was then divided into two subkingdoms. The bacteria, protists, and fungi were put in the Subkingdom Thallophyta ("thallus plants"), and all other organisms except animals were put in the Subkingdom Embryophyta ("embryo plants").

In this text, three phyla of essentially nonvascular plants, the *bryophytes,* and several phyla of **vascular plants** (plants with xylem and phloem) are included in the Plant Kingdom. The bryophytes are discussed in this chapter, and the vascular plants are examined throughout the remaining chapters of the book.

INTRODUCTION TO THE BRYOPHYTES

In the midst of heavy battles in France during World War I, nurses, at what is now referred to as a M.A.S.H. unit, on one occasion ran out of bandages for the wounded soldiers. In desperation, they substituted some soft green plant material they found growing in the water at the edge of a nearby lake. To their surprise, the material turned out to be a great substitute for the bandages; there were fewer infections in the wounds with the plant bandages than in those with the cotton bandages.

The material the nurses used was a species of *Sphagnum* moss (bog or peat moss), which has since been experimentally demonstrated to have antiseptic properties. This moss has specialized water-absorbing "leaves" (see Fig. 20.10) and has been used as a packing material in the past. It is still widely used as a soil conditioner. The "bandage" *Sphagnum* is one of about 23,000 species of **bryophytes** that include *mosses,liverworts,*and *hornworts,* many of which frequently make a soft and cool-looking green covering on damp banks, trees, and logs that are shaded for at least a part of the day (Fig. 20.1).

In contrast, some bryophytes can withstand long periods of desiccation and are also found on bare rocks in the scorching sun (Fig. 20.2), while others occur on frozen alpine slopes. The habitats of bryophytes range in elevation from sea level near ocean beaches up to 5,500 or more meters (18,000 or more feet) in mountains.

Some bryophytes are restricted to very specific habitats. For example, a few species are found only on the antlers and bones of dead reindeer. Others are confined to the dung of herbivorous animals, while still others grow only on the dung of carnivores. A few tropical bryophytes thrive only on large insect wing covers. The pygmy mosses, which appear annually on bare soil after rains, are only 1 to 2 millimeters (0.04 to 0.08 inch) tall and can complete their whole life cycle in a few weeks.

Bryophytes of all phyla often have mycorrhizal fungi associated with their rhizoids. In some instances, the fungi apparently are at least partially parasitic. One species of completely colorless liverwort that lives underneath mosses is totally dependent nutritionally on its fungal associate. The gametophytes of more advanced plants are completely dependent on their sporophytes for their nutrition.

The widespread peat mosses are ecologically very important in bogs and in the transformation of bogs to dry land. Peat mosses sometimes form floating mats over water and keep conditions acid enough to inhibit the growth of bacteria and fungi. Organisms that die in such waters or bogs are often preserved for hundreds or even thousands of years.

The luminous mosses are found in caves near the entrances and in other dark, damp places. They are called luminous because they glow an eerie golden-green in reflected light. The upper surfaces of their cells are slightly curved, and each cell functions as a tiny magnifying glass, concentrating the dim light on the chloroplasts at the base. This allows photosynthesis to take place in light otherwise too faint for it to occur (Fig. 20.3).

None of the bryophytes have true xylem or phloem, and to be able to reproduce, all bryophytes must have external water, usually in the form of dew or rain. Many mosses do have special water-conducting cells called *hydroids* in the centers of their stems, and a few have food-conducting cells called *leptoids* surrounding the hydroids. Neither type of cell, however, conducts as efficiently as vessel elements or tracheids of xylem and sieve tube members of phloem, and most water is absorbed directly through the surface. The absence of xylem and phloem makes most bryophytes soft and pliable, and it is not surprising, therefore, that birds often use them to line their nests. In one study in the Appalachian Mountains of Virginia in 1975, for example, David Breil and Susan Moyle found birds native to the area used at least 65 species of bryophytes in the construction of their nests.

Alternation of Generations is more conspicuous in bryophytes and ferns than in most other organisms. In mosses, the "leafy" plant is a major part of the *gametophyte* generation that produces the *gametes*. The *sporophyte* generation, which grows from a "leafy" gametophyte, produces the *spores*. It usually resembles a tiny can with a rimmed lid at the tip of a slender, upright stalk.

All bryophytes have similar life cycles, chromosomes, and habitats. However, based on their structure and reproduction, they are separated into three distinct phyla. None of the bryophytes appear closely related to other living plants, and fossils provide little evidence that members of each phylum are related to those of the other phyla. Botanists speculate that the three lines of bryophytes may have arisen independently from ancestral green algae.

PHYLUM HEPATICOPHYTA—LIVERWORTS

The word *wort* simply means plant or herb. In medieval times, when the *Doctrine of Signatures*[1] held sway, the -herbalists of the day thought some of the bryophytes—specifically those with flattened bodies and liver-shaped lobes (Fig. 20.4)—were useful for treating liver diseases. This belief proved to be without merit, but the name *liverwort* is still universally used today.

Structure and Form

There are about 8,000 known species of liverworts. The most common and widespread liverworts have flattened, lobed, somewhat leaflike bodies called **thalli** (singular: **thallus**). The *thalloid liverworts,* however, constitute only about 20% of the species. The other 80% are "leafy" and superficially resemble mosses.

Liverworts differ from mosses in several details and are considered less complex. Their thalli or "leafy" stages (gametophytes) develop from spores. When the spores -germinate, they may produce a *protonema,* which is an immature -gametophyte consisting of a short filament of cells. Typically, the protonema develops further into a more extensive gametophyte, or in some instances, the protonemal stage may be absent, the mature gametophyte then developing directly from the spore. Thalloid liverworts have smooth upper surfaces with various markings and pores, and the corners of cell walls of most liverworts are specially thickened. The lower surfaces have many one-celled *rhizoids*. Growth is prostrate instead of upright, and the rhizoids, which look like tiny roots, anchor the plants.

Thalloid Liverworts

The best-known species of thalloid liverworts are in the genus *Marchantia* (named in honor of French botanist N. Marchant) (see Fig. 20.4). The most widespread *Marchantia* species is often found on damp soil after a fire. The thallus, which is about 30 cells thick in the center and 10 cells thick at the margin, forks dichotomously as it grows. Each branch has a notch at the apex and a central groove that extends back lengthwise behind the notch. The thalli grow in size as the meri-stematic cells at the notches continue to divide. Older tissues at the rear decay as the new growth is added. The upper surface of the thallus is divided into diamond-shaped or polygonal segments, the segment lines marking the limits of chambers below. Each segment has a small bordered pore opening into the interior.

Seen through a microscope, a sectioned liverwort thallus looks like groups of short, erect, branching rows of cells with chloroplasts, sitting on a wall of colorless "bricks" (Fig. 20.5). The "brick wall," which may comprise most of the thallus, consists of parenchyma cells that have few, if any, chloroplasts. The tissue apparently stores substances produced in other cells. The bottom layer of cells is an epidermis from which rhizoids and scales arise. The individual groups of upright chlorenchyma cells are enclosed by vertical walls that are covered by a slightly dome-shaped layer of epidermal cells. A conspicuous pore is located in the center of each "roof" and remains open at all times. It resembles a tiny, short, suspended, open-ended barrel.

Marchantia—*Asexual Reproduction*

Marchantia reproduces asexually by means of **gemmae** (singular: **gemma**). Gemmae are tiny, lens-shaped pieces of tissue that become detached from the thallus. They are produced in small gemmae cups scattered over the upper surface of the liverwort gametophyte (Fig. 20.6). Raindrops may splash the gemmae as much as 1 meter (3 feet) away. While gemmae are in the cup, lunularic acid inhibits their further development, but each is capable of growing into a new thallus as soon as it leaves the cup. In addition, parts of an older thallus may die, isolating patches of active tissue, which may then continue to grow independently.

Marchantia—*Sexual Reproduction*

The gametangia of *Marchantia* are produced on separate male and female gametophytes and are more specialized than those of other liverworts. Both types of gametangia are formed on **gametophores** (umbrellalike structures borne on slender stalks rising from the central grooves of the thallus) (see Fig. 20.6). The top of the male gametophore, or **antheridiophore,** is disclike with a scalloped margin, while that of the female gametophore, or **archegoniophore,** looks like the hub and spokes of a wagon wheel.

Club-shaped male gametangia (**antheridia**) containing numerous *sperms* are produced in rows just beneath the upper surface of the antheridiophore. **Archegonia** are flasklike female gametangia, each containing a single *egg;* they are also produced in rows and hang neck downward beneath the spokes of the archegoniophore. Raindrops sometimes splash the released sperms, which have numerous flagella, more than 0.5 meter (1.5 feet) away. Fertilization may occur before the stalks of the archegoniophores have finished growing.

After fertilization, the zygote develops into a multicellular **embryo** (an immature *sporophyte*) that is totally dependent on the gametophyte for sustenance. A knoblike **foot** anchors the sporophyte (the diploid, spore-producing phase) in the tissues of the archegoniophore. The sporophyte hangs suspended by a short, thick stalk called the **seta.** The main part of the sporophyte, in which different types of tissues develop, is called a **capsule**. Liverwort sporophytes typically have no stomata.

Sporocytes in the capsule undergo meiosis, producing haploid *spores*. Other capsule cells do not undergo meiosis but remain diploid and develop instead into long, pointed **elaters** with spiral thickenings. They are sensitive to changes in humidity (Fig. 20.7). Spore dispersal in *Marchantia* takes place as the elaters twist and untwist rapidly. In the sporophytes of other liverworts, the elaters may aid spore dispersal with a snapping action or by suddenly expanding.

Until the young sporophyte is mature, it is protected by the **calyptra,** a caplike tissue that grows out from the gametophyte, and by other membranes covering the capsule. The capsule splits at maturity, and air currents carry the spores away.

Under favorable conditions, the spores germinate, producing new gametophytes.

Other thalloid forms, such as the floating or amphibious liverworts, do not produce gametophores. Instead, the archegonia and antheridia develop within the thallus beneath the central grooves, where the sporophytes also are formed. The spores are liberated from the submerged sporophytes as the thallus decays.

“Leafy” Liverworts

“Leafy” liverworts (Fig. 20.8) are often abundant in tropical forests and in fog belts. They always have two rows of partially overlapping “leaves” whose cells contain distinctive oil bodies. The “leaves” have no midribs, and unlike the “leaves” of mosses, they often have folds and lobes. In the tropics, the lobes form little water pockets in which tiny animals are nearly always present. It has been suggested these water -pockets may function like the pitchers of pitcher plants (discussed in Chapter 7). A third row of “underleaves” is often present on the underside of “leafy” liverworts. The “underleaves” are smaller than the other “leaves” and not visible from the top. A few rhizoids that anchor the plants develop from the stemlike axis at the base of the “underleaves.”

The archegonia and antheridia of the “leafy” liverworts are produced in cuplike structures composed of a few modified “leaves,” either in the axils of “leaves” or on separate branches. At maturity, the sporophyte capsule may be pushed out from among the “leaves” as the seta elongates. When a spore germinates, it produces a **protonema** consisting of a short filament of photosynthetic cells. The protonema soon develops into a mature gametophyte plant.

PHYLUM ANTHOCEROPHYTA—HORNWORTS

Structure and Form

Hornworts, whose mature sporophytes look like miniature, greenish to blackish rods that may curve slightly, have gametophytes that resemble filmy versions of thalloid liverworts. They are usually less than 2 centimeters (0.8 inch) in diameter and thrive mostly on moist earth in shaded areas, although some occur on trees. There are only about 100 species worldwide; they are uncommon in arctic regions. They differ from liverworts and mosses in several respects and appear to be only distantly related to them. Hornworts usually have only one large chloroplast in each cell (a few species have up to eight). Each chloroplast has pyrenoids similar to those of green algae. The thalli have pores and cavities filled with mucilage, in contrast to the air-filled pores and cavities of thalloid liverworts. Nitrogen-fixing cyanobacteria often grow in the mucilage. Rhizoids anchor the plants.

Asexual Reproduction

Hornworts reproduce asexually primarily by fragmentation or as lobes separate from the main part of the thallus. A few hornworts form tiny tubers that are capable of becoming new gametophytes.

Sexual Reproduction

In sexual reproduction, archegonia and antheridia are produced in rows just beneath the upper surfaces of the gametophytes. Like both mosses and liverworts, some species of hornworts have *unisexual* plants, whereas other species are *bisexual*.

The distinctive sporophytes of hornworts have numerous stomata. They have no setae (stalks) and look like tiny, green broom handles or horns rising through a basal sheath from a foot beneath the surface of the thallus (Fig. 20.9). A meristem above the foot continually increases the length of the sporophyte from the base when conditions are favorable. As growth occurs, sporocytes surrounding a central rodlike axis in the sporophyte undergo meiosis, producing spores. Diploid elaters similar to those of liverworts are intermingled with the spores. The tip of the sporophyte horn splits into two or three ribbonlike segments, releasing the spores, and the segments continue to peel back as long as the meristem is producing new tissue at the base.

PHYLUM BRYOPHYTA—MOSSES

Structure, Form, and Classes

Many different organisms have been called *mosses*. In fact, almost any greenish covering or growth on tree trunks and forest floors has probably been called “moss” at one time or another. Examples include lichens (e.g., reindeer moss), red algae (e.g., Irish moss), flowering plants (e.g., Spanish moss), and club mosses. Club mosses look somewhat like large true mosses but are vascular plants with xylem and phloem. About 15,000 species of mosses are currently known. These are divided into three different classes, commonly called *peat mosses, true mosses,* and *rock mosses*. Mosses are distinct, both in form and reproduction, and possibly in origin, from any other group of organisms.

The "leaves" of moss gametophytes have no mesophyll tissue, stomata, or veins such as those of the leaves of more complex plants. The blades are nearly always only one cell thick, except at the *midrib,* which runs lengthwise down the middle, and they are never lobed or divided, nor do they have a *petiole* (leaf stalk). The midrib (absent in some genera) occasionally projects beyond the tip in the form of a hair or spine. The "leaf" cells usually contain numerous lens-shaped chloroplasts, except at the midrib. The "leaves" of peat mosses, however, have large, transparent cells (without chloroplasts) that absorb and store water. Small, green photosynthetic cells are sandwiched between the large cells (Fig. 20.10). The "leaves" are intially formed in three ranks and usually end up appearing to be arranged in a spiral or alternately on an axis that twists as it grows.

The axis is somewhat stemlike but has no xylem or phloem, although there is often a distinctive central strand of hydroids. At the base, there are rootlike rhizoids consisting of several rows of colorless cells that anchor the plant. Some water absorbed by rhizoids rises up the central strand, but most water used by the plant apparently travels up the outside of the plant by means of capillarity. The closely packed habit of many mosses, and the fact that they rarely extend more than a few centimeters (2 to 3 inches) into the air, favor such outside movements of water. Water is absorbed directly through the plant surfaces.

Sexual Reproduction

Sexual reproduction in mosses begins with the formation of multicellular gametangia, usually at the apices of the "leafy" shoots of gametophytes (see Fig. 20.13), although they frequently form on special separate branches. Both male and female gametangia are often produced on the same plant, but in some species, they occur on separate plants. The archegonia (female gametangia) are somewhat cylindrical and project upward from the base of the expanded gametophyte tip (Fig. 20.11). A single *egg* cell is produced in a cavity that develops when certain cells break down in the swollen base of the archegonium. The part of the archegonium above the cavity (known as the **venter**) is called the *neck*. The neck may taper toward the tip and contains a narrow *canal*. The canal is at first plugged with cells, but these break down as the archegonium matures, leaving an opening to the outside at the top. Several archegonia usually are produced at the same time, with sterile hairlike, multicellular filaments called *paraphyses* (singular: *paraphysis*) scattered among them.

Male gametangia also have paraphyses among them and are sausage-shaped to roundish, with walls that are one cell thick. These *antheridia* (Fig. 20.12) are borne on short stalks. A mass of tissue inside each antheridium develops into numerous coiled or comma-shaped *sperm* cells. This mass of sperms is forced out of the top of the antheridium when it absorbs water and swells. After release, the sperm mass breaks up into individual cells, each with a pair of flagella. It is believed the breakup of the sperm mass is aided, in some cases, by fats produced by the moss, while in other instances, rain splash is responsible.

Archegonia release sugars, proteins, acids, or other substances that attract the sperm, and eventually a sperm, after swimming down the neck of an archegonium, unites with the egg, forming a diploid *zygote* (Fig. 20.13). The zygote usually grows rapidly into a spindle-shaped *embryo*. The embryo breaks down the cells at the base of the archegonium and becomes firmly established in the tissues of the stem by means of a swollen knob called a *foot*. As the embryo grows, cells around the venter divide, thereby accommodating its increasing size. The length of the embryo soon exceeds the length of the cavity in the venter. The top of the venter is split off and is left sitting like a pixie cap on top of the embryo. By this time, the embryo is a developing *sporophyte*. The pixie cap, called a *calyptra,* remains until the sporophyte is mature. In one genus with the common name of "extinguisher mosses," the calyptra looks just like a little candlesnuffer, and in the hairy cap mosses, it resembles a miniature, pointed, goatskin cap such as might be worn by a Shakespearean actor.

The cells of the sporophyte become photosynthetic as it develops, remaining so until maturity. The sporophyte, however, depends to varying degrees on the gametophyte for some of its carbohydrate needs as well as for at least a part of its water and minerals, which are absorbed through the foot.

The mature sporophyte is at first green and photosynthetic; it consists of a *capsule* located at the tip of a slender stalk called the *seta*. Depending on the species, the seta may be less than 1 millimeter (0.04 inch) long, or it may be up to 15 centimeters (6 inches) long. Most, however, are less than 5 centimeters (2 inches) long. The capsule may resemble a tiny apple, a pear, an urn, a box, or a wingtip fuel tank of an airplane and usually has from 3 or 4 to over 200 stomata at or near its surface. Unless extremely dry conditions prevail, the stomata normally remain open until the capsule begins to age, and then they close permanently. The free end of the capsule is usually protected by a little rimmed lid, the **operculum,** which falls off at maturity.

As the capsule matures, *sporocytes* inside it undergo meiosis, producing haploid *spores*. These spores, often numbering in the millions, are released from the capsule, usually through a structure called a **peristome,** after the operculum falls off. Most peristomes consist of a circular row or two of narrowly triangular and membranous teeth arranged around the rim of the capsule, each row having 16 teeth. The teeth are frequently colored orange or red and are often beautifully sculptured with bars and fringes. They open or close in response to changes in humidity. In a few species of mosses, the peristome is a cone-shaped structure with pores through which the spores are released.

Some rock mosses have neither a peristome nor an operculum. The spores in these mosses are released when the capsule splits lengthwise along four lines. In the dung mosses, a putrid odor is given off when the spores are ready for release. Some of the spores adhere to the legs and bodies of flies, which are attracted by the odor, and are disseminated as the insects clean themselves. Most moss spores are, however, simply blown away by the wind, and if they fall in a suitable damp location, they usually germinate relatively quickly.

In most mosses, fine, green tubular threads, consisting of single rows of cells with chloroplasts, first emerge from the spores. These soon branch and grow, forming an algalike *protonema*. The protonema can be distinguished from a filamentous green alga by the oblique crosswalls of its cells and by the lens-shaped chloroplasts. If light and other conditions are favorable, tiny "leafy" *buds* appear at intervals along the protonemal filaments after about 2 to 4 weeks of growth. These "leafy" buds develop rhizoids at the base and grow into new "leafy" gametophytes, completing the cycle.

Asexual Reproduction

Some reproduction in mosses does not depend on such a sexual cycle and its Alternation of Generations. It has been demonstrated under laboratory conditions that cells of archegonia and antheridia, paraphyses, "leaves," stems, and rhizoids all can develop protonemata. Two American biologists once -collected bryophyte gametophyte fragments from a snowbed in the Canadian high arctic and found that 12% of their samples resumed growth in various ways when cultured in the laboratory. They calculated that for each cubic meter (1.3 cubic yards) of snow at their study site, there were over 4,000 bryophyte fragments capable of becoming new plants. They suggested that wind dispersal of fragments may be routine in arctic regions. Such dispersal and vegetative reproduction also occur widely in more temperate areas.

HUMAN AND ECOLOGICAL RELEVANCE OF BRYOPHYTES

Some bryophytes and lichens are pioneers on bare rock after volcanic eruptions or other geological upheavals and after the retreat of glaciers. They slowly accumulate mineral and organic matter that can then be inhabited or utilized by other organisms. This process, called *succession,* is discussed in Chapter 25. Mosses, in particular, retain moisture, slowly releasing it into the soil. They reduce flooding and erosion and contribute to humus formation. Some mosses grow only in soils that are rich in calcium; the presence of others indicates higher than usual soil salinity or acidity.

When certain mosses are present in a dry area, it is a good indication that running water occurs there some time during the year. A few mosses are occasionally a problem in water reservoirs, where they may plug entrances to pipes. A few bryophytes are reported to be grazed, along with lichens, by foraging mammals in arctic regions, but bryo-phytes are not generally edible. Some mosses have been used for packing dishes and stuffing furniture, and Native Americans are reported to have used mosses for diapers and under splints when setting broken limbs.

By far, the most important bryophytes to humans are the peat mosses. When allowed to absorb water, 1 kilogram (2.2 pounds) of dry peat moss will take up 25 kilograms (55 pounds) of water. Its extraordinary absorptive capacity has made it very useful as a soil conditioner in nurseries and as a component of potting mixtures. Live shellfish and other organisms are shipped in it. The natural acidity produced inhibits bacterial and fungal growth and gives it antiseptic properties. The absorbency, which is greater than that of cotton, combined with the antiseptic properties, has made it a useful poultice material for application to wounds. It was used for this purpose during the Crimean War of 1854 to 1856 and, as indicated in the chapter introduction, on an emergency basis during World War I. Extensive peat deposits have been formed from the remains of peat mosses that flourished in past eras. Peat, like the undecomposed peat mosses, is used around the world as a soil conditioner and as a fuel. In the manufacture of Scotch whiskey, sprouted barley is dried on a screen over a peat fire. The peat smoke permeates the barley and imparts a smoky flavor to the beverage. See Appendix 1 for the scientific names of all the bryophytes discussed.

Summary

1. Members of the Plant Kingdom have a cuticle and produce their gametes and spores in multicellular organs surrounded by a sterile jacket of protective cells. Their zygotes develop into embryos; and tissues specialized for photosynthesis, conduction, support, anchorage, protection, and reproduction are produced.
2. Cell plates and phragmoplasts appear when plant cells divide. Outside of the Plant Kingdom, these occur only in certain green algae. The similarity in pigments, food reserve (starch), and occurrence of cell plates suggests a common ancestor for the green algae and plants. The Plant Kingdom includes three phyla of bryophytes and several phyla of vascular plants.
3. Bryophytes (liverworts, hornworts, mosses) occur in highly varied and also very specific habitats.
4. Water is essential to bryophyte reproduction. Most water is absorbed directly through the plant surfaces.
5. Liverwort gametophytes with flattened, dichotomously forking thalli are common, but about 80% of the liverwort species are "leafy." Liverworts have distinct upper and lower surfaces, with one-celled rhizoids that function in anchorage on the lower surface.
6. A *Marchantia* thallus has a central lengthwise groove along its upper surface and is chambered, each chamber containing

chlorenchyma cells and having a surface pore. Rhizoids and scales arise from the thallus base.

7. *Marchantia* reproduces asexually by means of gemmae produced in surface cups and by thallus fragmentation.
8. *Marchantia* reproduces sexually by means of eggs and sperms produced in archegonia and antheridia on archegoniophores and antheridiophores that arise from the thallus.
9. The zygote develops into a sporophyte that is anchored to the archegoniophore by a foot, from which is suspended a capsule connected to the foot by a seta. Sporocytes in the capsule undergo meiosis, producing spores. Diploid elaters that aid in spore dispersal do not undergo meiosis.
10. The calyptra and other membranes protect the spores until they are released as the capsule splits; the spores may then develop into new gametophytes.
11. "Leafy" liverworts have two rows of overlapping "leaves" and frequently a third row of "underleaves" not visible from above. The "leaves" often have lobes that retain rain water.
12. Hornworts have one chloroplast with pyrenoids in each cell, and they resemble liverworts in their gametophytes. Their sporophytes are hornlike and have a meristem above the foot. Hornwort thalli have pores and cavities filled with mucilage, where cyanobacteria often grow.
13. Asexual reproduction in hornworts is by fragmentation. Sexual reproduction involves archegonia and antheridia produced in rows beneath the upper surface of a thallus. The tip of the hornlike sporophyte splits vertically, releasing the spores.
14. A moss gametophyte consists of an axis to which "leaves" are attached, with rhizoids at the base. The "leaves" are haploid and have no mesophyll, stomata, or veins. Water is absorbed primarily directly through the plant surfaces.
15. Multicellular archegonia and antheridia are produced at the tips of "leafy" shoots. Each archegonium has a cavity, the venter, containing a single egg and a neck through which a sperm gains access to the egg. Sperms are produced in antheridia.
16. After fertilization, the zygote grows into an embryo that is attached to the gametophyte by an embedded foot. The sporophyte developing from the embryo consists of a capsule and a seta. A calyptra derived from the gametophyte partially covers the capsule. Sporocytes in the capsule undergo meiosis, producing spores that are released through the teeth of the peristome, a structure at the tip of the capsule.
17. An operculum that falls off when the spores mature initially covers the peristome and protects sporocytes and spores. When moss spores germinate, protonemata with "leafy" buds develop. The buds grow into new gametophytes.
18. Mosses may be pioneers, along with lichens, on bare rocks. They are indicators of soil calcium, salinity, and acidity. Mosses are not generally edible, although a few are grazed in arctic regions. Some mosses are used for packing material, but the most significant use is that of peat mosses for soil conditioners. Peat mosses can absorb and retain large amounts of water, and their natural acidity gives them antiseptic properties. Peat deposits, from peat mosses that flourished in past eras, are used for fuel and also as a soil -conditioner.

Review Questions

1. What basic features distinguish members of the Plant Kingdom from those of other kingdoms?
2. What features distinguish the bryophytes discussed in this chapter from other plants?
3. How could you tell a hornwort thallus from that of a thalloid liverwort?
4. Contrast the sporophytes of mosses, liverworts, and hornworts.
5. What is a protonema? Do all bryophytes have them? How would you tell a protonema from a green alga?
6. What adaptations do bryophytes have for their particular habitats?
7. Which parts of the life cycles of bryophytes have haploid (n) cells? Which parts have diploid ($2n$) cells?
8. Why is a bryophyte "leaf" technically not the same as a flowering plant leaf?
9. Define calyptra, operculum, capsule, peristome, paraphysis, foot, seta, archegoniophore, thallus, underleaves, and elaters.
10. If you were to single out one bryophyte as being the most important member of its phylum from a human viewpoint, which would you choose? Why?

Discussion Questions

1. Very few fossils of bryophytes have been found. Suggest reasons for this.

2. Do the multicellular sex structures of plants give them any advantages over other organisms with unicellular sex structures?
3. After reading about the characteristics and uses of peat mosses, can you suggest some possible new uses for these plants?
4. Some bryophytes produce unisexual gametophytes, while others produce bisexual gametophytes. Should one type have any survival or adaptive advantage over the other? Explain.

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CHAPTER

Moss-covered rocks in a small stream bed. *(© Digital Vision/Getty Images)*

Figure 20.1 Mosses and ferns growing on a tree trunk.

Figure 20.2 *Grimmia,* a rock moss that survives on bare rocks, often in scorching sun.

Figure 20.3 Lenslike cell of the protonema of the luminous moss. The cell concentrates light on the chloroplasts at the base. *(After D. von Denffer, W. Schumacher, K. Magdefrau, and F. Ehrendorfer. 1976. Strasburger's* Textbook of Botany, *30th German ed., translated by P. Bell and D. Coombe. 1976. Redrawn by permission of Gustav Fischer Verlag, Stuttgart, and Longman Group, London and New York.)*

While most bryophytes are confined to moist, shaded areas, some can withstand long periods of desiccation on bare rocks in the scorching sun or survive in frozen alpine and arctic environments. Many bryophytes that are found in highly restricted environments play significant roles in the early stages of community succession. The peat mosses are very important in the successional processes that transform bogs into dry land, a transformation that stored vast amounts of atmospheric carbon in the peat bogs of northern environments. One reason that biomass accumulates in peat bogs rather than decomposing is that peat mosses, by establishing an acid pH, inhibit the growth of decomposer microbes. The antibiotic and absorbent properties of peat mosses have also been put to practical use in the past, when peat mosses have been used as bandages. Bryophytes are useful to other organisms in the community as well: Many birds use soft, pliable bryophytes for nesting materials, and many mycorrhizal fungi are associated with the rhizoids of bryophytes.

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1. The *Doctrine of Signatures* held that any plant part that resembled a human body part would be helpful in healing that body part if it was diseased or hurting.

Figure 20.4 *Marchantia* (a thalloid liverwort). *A.* Thalli with male gametophores. *B.* Thalli with female gametophores.

Figure 20.5 A longitudinal section through a portion of a *Marchantia* thallus.

Figure 20.6 Life cycle of the thalloid liverwort *Marchantia.*

Figure 20.7 A longitudinal section through a sporophyte of *Marchantia.*

Figure 20.8 *Frullania,* a "leafy" liverwort.

Figure 20.9 *A.* Hornwort sporophytes. *B.* Detail of a hornwort sporophyte.

A.

Figure 20.10 An enlargement of a portion of a peat moss (*Sphagnum*) leaf. *A.* Surface view. *B.* A further-enlarged cross section of living and dead cells.

Figure 20.11 A longitudinal section through the tip of a female gametophyte of the moss *Mnium.*

Figure 20.12 A longitudinal section through the tip of a male gametophyte of the moss *Mnium.*

Figure 20.13 Life cycle of a moss.

Hibernating Mosses

Mosses are the "amphibians" of the plant world, so-called because they are at home in either semiaquatic environments, such as moist stream banks, or drier habitats, such as rock surfaces or the arctic tundra. Unlike their towering cousins, the flowering plants, mosses are dependent on a watery landscape to reproduce. Because moss sperms are flagellated, a film of water is needed for the sperm to swim to the egg. But life on land is not easy, especially when water becomes limited or nonexistent for months. The genetic diversity of mosses is exceptional, and they inhabit some of the most inhospitable habitats on earth. Dry heaths, rock faces, tree trunks, and even deserts are home to these remarkable plants. Distinctive adaptations allow moss species this wide range of habitats, including the ability to tolerate drying out, a process known as **desiccation.**

Vascular plants have structural mechanisms that maintain an adequate water supply within plant tissues. These include an impermeable waxy cuticle on leaf surfaces, an internal water transport system (xylem), water-absorbing organs (roots), and leaf pores (stomata) that can close, conserving water. Parts of the life cycle, such as seeds, are especially tolerant of desiccation. Mosses do not possess these adaptations to living in a dry land environment. This means the internal water balance in mosses is in equilibrium with the atmosphere. When the air is dry, mosses are dry. When it rains, mosses quickly absorb water and become rehydrated. They are "opportunists" in this regard.

Some species of mosses are incapable of withstanding this desiccation-rehydration cycle, but those that have this capacity can "return from the dead" with each cycle. It is as if they have been hibernating. There are several mechanisms that slow water loss from mosses that make the cycle less drastic. Many mosses form dense mats or tufts that create a moist microatmosphere within the tufts and over the plants. *Polytrichum commune* is a common moss that has moderate desiccation tolerance. It lives in habitats such as bogs or temperate, moist forests and can grow up to 40 centimeters tall. It grows luxuriantly during rainy periods but then twists into rusty red mats upon drying in the sun. These mosses have a thin, waxy cuticle covering their tiny "leaves" (8 to 10 millimeters in length) that retards water loss. They also have primitive water-conducting cells (*hydroids*) that move water through the plant when water is lost to the atmosphere by evaporation. Instead of root hairs, they have a rhizoid system that absorbs water from the soil. However, if dry conditions persist, all available water is lost to the atmosphere.

Additional mechanisms by which mosses are capable of surviving these desiccation-rehydration cycles are being discovered. *Tortula ruralis* is one of the most desiccation--tolerant mosses known, and research has centered on its ability to recover after prolonged or repeated desiccation events. Hydrated *T. ruralis* cells are similar to mesophyll cells in the leaves of vascular plants. There are chloroplasts with stacks of grana and a prominent nucleus. Mitochondria are numerous and similar in size and shape to those of higher plants, with internal membranes folded into cristae.

During desiccation, *T. ruralis* dries out, and its "leaves" fold up around the stem. Cells of desiccated plants are damaged. There is extensive plasmolysis as water is lost from the protoplast. Chloroplasts become smaller and more spherical, and starch is not present. Internal thylakoid membranes are collapsed and disorganized. Mitochondria in the hydrated cell are elongated with numerous cristae membranes. In the desiccated state, mitochondria are smaller and rounded, with few internal cristae membranes. The nucleoplasm of nuclei becomes dense, and chromatin is condensed. Compact-appearing nucleoli are prominent. The plasma membrane is damaged, and electrolytes leak out. In all desiccated mosses, photosynthesis stops, and respiration slows or ceases.

When the plants are rehydrated, dried "leaves" unfold and return to the normal hydrated state within 2 minutes. Most of the internal damage is repaired within a few more minutes. Activity of a drought-repair gene increases in the minutes after rehydration, and repair proteins are quickly manufactured and mobilized for action. Respiration resumes after a few minutes. Photosynthesis resumes up to 24 hours later.

Scientists at the USDA's Agricultural Research Service are attempting to locate the genes responsible for drought repair in *Tortula* species in the hope of transferring them to crop plants. With crops having more drought tolerance, rain shortage would be less of a problem than it is now. Arid lands currently unsuited for agriculture could blossom with crop plants genetically engineered with drought-tolerant genes. World population increases of 1.6% yearly means that an additional 78,000 metric tons of grain per day are required just to maintain current consumption levels. A lowly moss might someday be responsible for a revolution in food production.

D.C. Scheirer

Box Figure 20.1 *Polytrichum commune* (hairy cap moss) growing in a deciduous forest of the northeastern United States. *(Photo by Daniel Scheirer)*

A.
B.