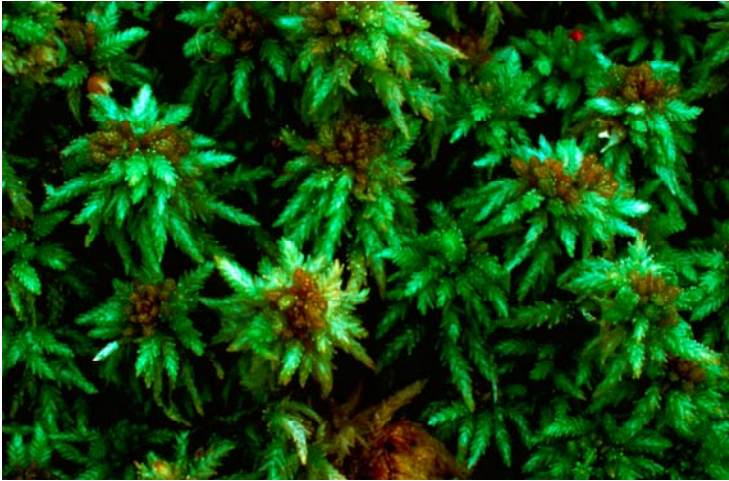


# *Bryophytes*



## THE LEAP ONTO LAND

*Bryophytes Faced Many Problems When They Moved onto the Land  
Key Innovations in Land Plants First Appear in the Bryophytes*

## BRYOPHYTES ARE NOT A NATURAL GROUP

*Bryophyte Relationships Remain Uncertain*

## HORNWORTS

## LIVERWORTS

*Some Liverworts Have Thalloid Bodies  
Most Liverworts Have Leafy Bodies*

## MOSSES

*Gametophytes Have Protonemal, Bud, and Leafy Phases  
Mosses Have Several Forms of Asexual Reproduction  
Sexual Reproduction Typically Occurs at the Ends of Stems  
Moss Sporophytes Have Complex Capsules  
Mosses Have Significant Economic and Ecological Value*

## SUMMARY

**PLANTS, PEOPLE, AND THE ENVIRONMENT:** *The Ultimate Shade Plants*

**ECONOMIC BOTANY:** *Mining Moss: Peat for Profit*

## KEY CONCEPTS

1. Bryophytes are land plants that differ from all other plants lacking lignified vascular tissue by having the gametophyte generation dominant and having unbranched sporophytes that produce a single sporangium.
2. Modern bryophytes almost certainly evolved from a single common ancestor, and they likely represent several lineages along the evolutionary path to vascular plants. Recent fossil discoveries push back the earliest appearance of bryophytes to 475 million years ago. Existing bryophytes preserve a suite of ancestral characteristics that give us insight into the origin of land plants. Bryophyte relationships remain uncertain; however, existing bryophytes fall into three lineages: liverworts (Marchantiophyta), hornworts (Anthocerotophyta), and mosses (Bryophyta). Traditionally, liverworts have been considered the earliest evolving lineage of bryophytes, but recent evidence suggests that hornworts may be the earliest. Mosses are likely the closest sister group to vascular plants.
3. Key innovations of the bryophyte radiation, not present in their algal ancestors, include multicellular gametangia (antheridia and archegonia) that protect and insulate gametes from the environment; a multicellular sporophyte that develops from an embryo embedded within and nutritionally dependent on the gametophyte; and the presence of a waxy coating on the shoots (cuticle) and the spores (sporopollenin). The most complex bryophyte sporophytes also contain novel structures such as stomata and water- and sugar-conducting tissue (unlignified vascular tissue). Bryophyte gametophytes are not able to control their water balance, and they dry out rapidly in the absence of free water. The desiccated plants are still alive and can become active within minutes of being rewetted.
4. Mosses are important in many ecosystems. They provide most of the biomass in boreal vegetation such as tundra, they dominate the understory of cool-temperate forests, and they are common in damp microenvironments. Some species are aquatic and most require humid conditions, but some can colonize dry, exposed habitats such as rock outcrops and desert soil surfaces.

### 22.1 THE LEAP ONTO LAND

Despite being common almost everywhere, **bryophytes** often are ignored because of their small stature, lack of familiar features, and the fact that in many environments they are dormant for much of the year. Yet bryophytes are exceptionally diverse, with nearly 25,000 named species. Among land plants, only flowering plants and ferns have more species. Bryophytes also are extremely widespread, being present on all continents, including Antarctica. They have a long evolutionary history, and some bryophytes are a sister group to vascular plants (Fig. 22.1).

The great diversity of bryophyte species reflects a stunning diversity of habitats, from barren arctic and alpine ground to hot deserts, from the bottom of lakes to the canopy of tropical rain forests. Peat mosses grow submerged in the acidic waters of bogs, whereas various liverworts grow as epiphytes on the leaves of trees. Some mosses grow on rocks exposed to ocean salt spray or intense heat and sunlight. Others tolerate very dim light and grow in the understory of dense forests or inside caves and burrows (Fig. 22.2). These adaptable plants can be found nearly everywhere that plant life is possible. But despite being so adaptable, all bryophytes have one major limitation. They require free water, not just soil moisture, in their environment. Without it, they cannot reproduce sexually.

As you might expect from the diverse environments inhabited by bryophytes, they have a corresponding diversity of body forms, from the giant moss *Dawsonia superba*, which can reach a height of 70 cm and resembles a pine tree seedling, to *Ptychomnion aciculare*, in which "dwarf" male plants grow attached to the leaves of the female plants.

These relatively inconspicuous and overlooked plants warrant more careful study for a number of reasons. Bryophytes can be important ecologically, by altering pH, absorbing carbon, regulating nutrient cycling, colonizing barren surfaces, creating soils, and reducing erosion. They often are important elements in the local water cycle, absorbing and holding moisture so that other plants benefit. They are also useful to environmental scientists because the majority of bryophytes, despite their amazing resilience, are intolerant of pollution and often disappear from contaminated areas. This sensitivity makes them good indicators of air and water quality. Bryophytes also possess many physiological adaptations that interest scientists. For example, some bryophytes can survive extended periods (more than

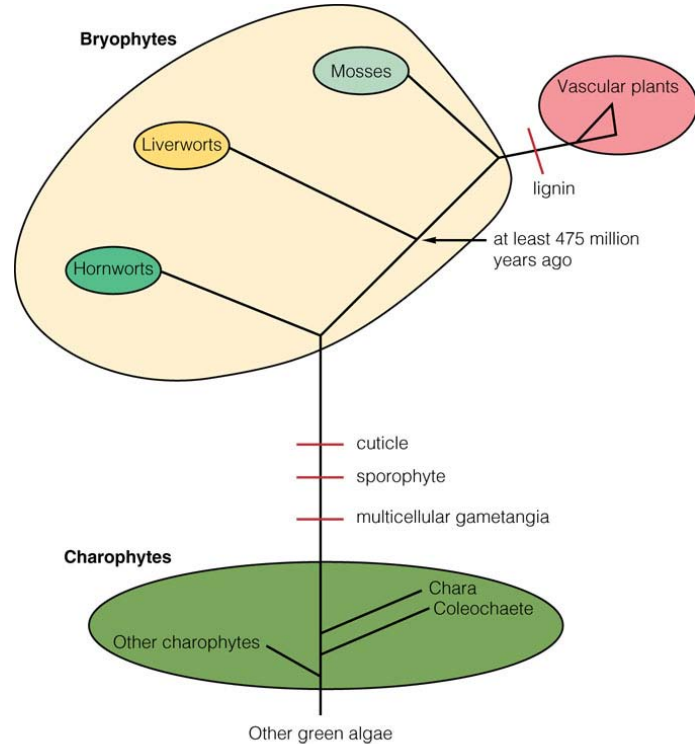


Figure 22.1. A cladogram of relationships between the bryophytes and vascular plants. Hornworts are the basal-most lineage of land plants, although other hypotheses place liverworts in that position. Mosses are almost certainly the sister group to vascular plants.

20 years) of desiccation and then when rewetted revive in a matter of minutes to resume normal growth.

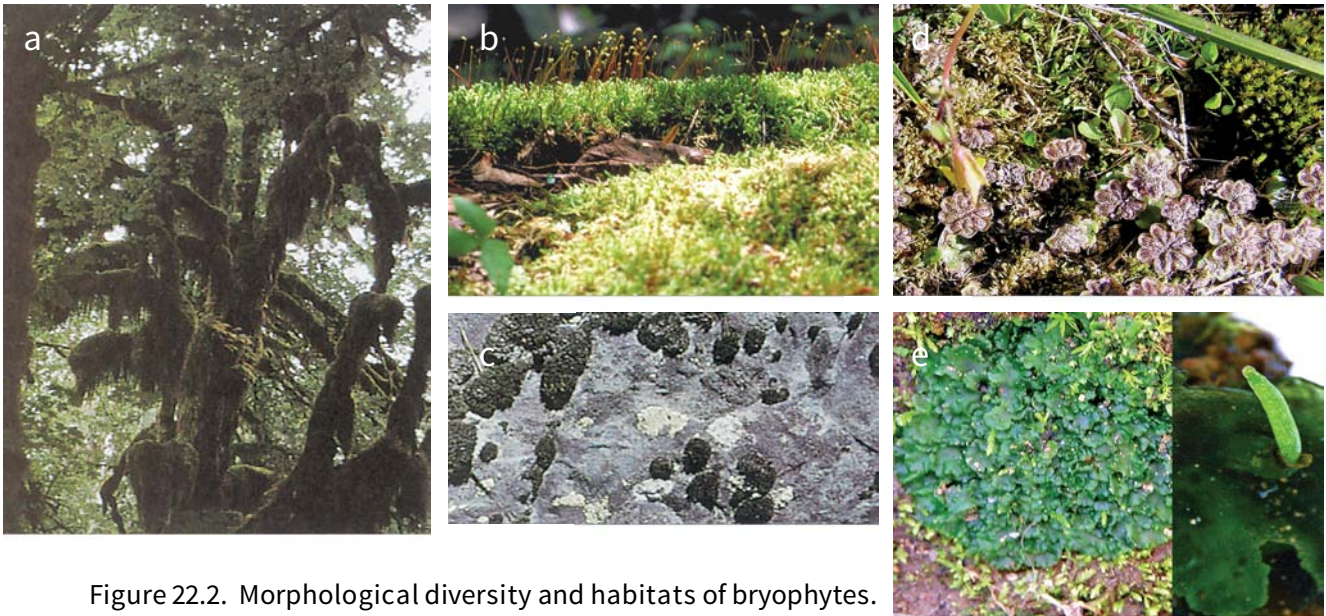


Figure 22.2. Morphological diversity and habitats of bryophytes.

(a) Epiphytic mosses on trees in Olympic National Park, WA.

(b) Moss. (c) Granite moss *Grimmea* growing on bare rock outcrop in the Appalachian Mountains. (d) Liverwort. (e) Hornwort.

### **Bryophytes Faced Many Problems When They Moved onto the Land**

Bryophytes retain many of the characteristics of their algal ancestors, including a nutritionally independent (photosynthetic) and complex gametophyte; the photosynthetic pigments chlorophyll *a* and *b*, carotenoids, and xanthophylls; sperm that swim by means of two asymmetrically attached flagella; chloroplasts with conspicuous grana, which store food as starch; and cell walls composed primarily of cellulose and pectin. Bryophytes also engage in a particular type of cell division that is present in charophytes but absent in other green algae: the nuclear envelope breaks down and microtubules oriented perpendicular to the plane of division form a cell plate that grows from the center to the outer portion of the cell.

Faced with the great difficulties of a terrestrial life, bryophytes also evolved many new and highly successful adaptations. The primary problems of life on land were preventing death by drying out, dispersing spores through the air, and avoiding damage from weather and intense solar radiation. The responses to these problems, which bryophytes pioneered, were subsequently passed on to all their descendents and have become the fundamental innovations that define land plants.

### **Key Innovations in Land Plants First Appear in the Bryophytes**

Bryophytes evolved important advances in both phases of the land plant life cycle. These key innovations allowed plants to colonize the land, setting off a series of spectacular adaptive radiations, first among bryophytes and later in vascular plants.

**SPOROPHYTE EVOLUTION** One of the most important innovations of early bryophytes was a multicellular **sporophyte** (Fig. 22.3). Two simple steps can account for the evolution of this new structure. First, meiosis must be delayed in the zygote, which, as you recall, is retained on the parent gametophyte in land plant ancestors. Second, the zygote must undergo mitotic cell divisions to create a multicellular body.

Bryophytes nurture their sporophytes initially by embedding the young sporophyte in the tissues of the gametophyte and providing nutrients, water, and hormones for development. This **embryo** phase of the sporophyte has been retained in all extant land plants, and it is so characteristic of them that **embryophyte** is used as a name for the whole land plant group. In all bryophyte groups, the sporophyte remains dependent on the gametophyte for its entire life. The sporophytes of the earliest land plants were probably nothing more than a "jacket" of cells surrounding a mass of **sporocytes** (the cells that undergo meiosis to produce spores).

The value of these first sporophytes must have been enormous because they would have protected the developing spores from desiccation. They also allowed bryophytes to produce many more spores than their algal ancestors. By using mitosis to multiply the number of diploid cells that can divide by meiosis, bryophytes greatly increased their spore production potential. In the hostile terrestrial environment, where most spores would probably land in unsuitable locations, there would have been great selective pressure to increase the number of spores released. The spores themselves also adapted to the new environment. They lost their flagella, which would have been useless on land, and became coated with a weather-resistant wall.

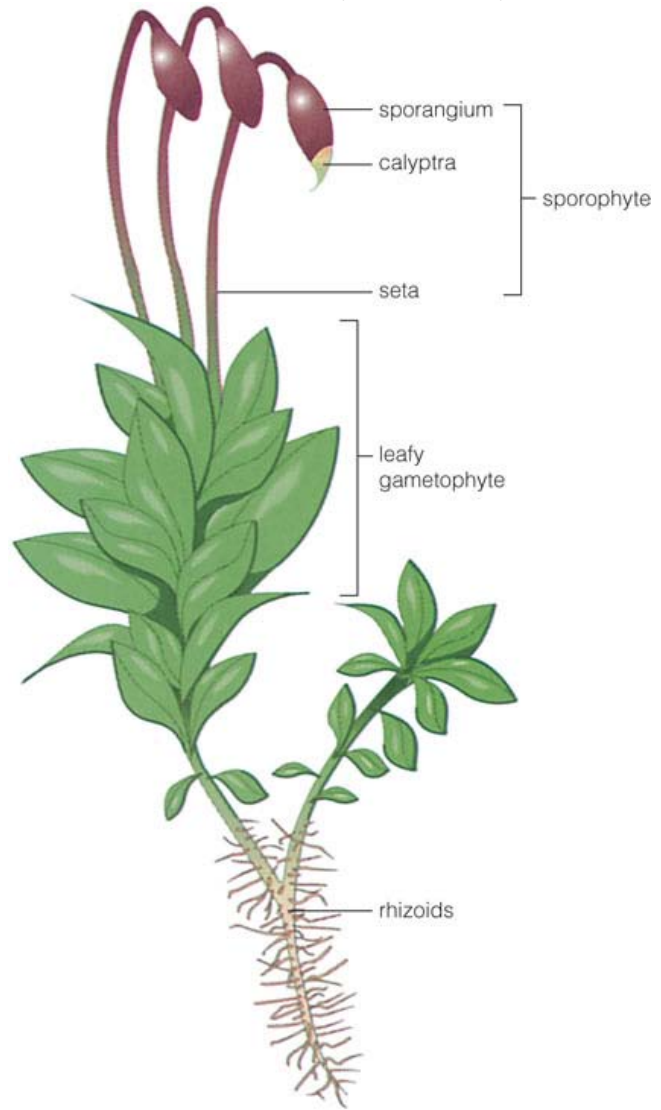


Figure 22.3. The moss *Mnium*, showing both sporophyte and gametophyte generations.

Bryophyte sporophytes remain today the leafless, unbranched structures they have been since their first appearance nearly 500 million years ago. However, each of the lineages of bryophytes and the vascular plants have evolved different sporophyte structures and spore dispersal mechanisms, which suggests that these lineages were separate from each other, no longer exchanging genes, before the sporophyte had undergone much evolution. The great differences among them seem to represent four independent ways of elaborating the simple sporophytes of the first land plants.

**GAMETOPHYTE EVOLUTION** Bryophytes have the largest, most elaborate gametophytes of any living land plant group, some possessing conducting tissue similar to the xylem and phloem in stems and leaves of vascular plants. Bryophyte gametophytes are not only complex structurally, but they often produce a vast array of secondary chemicals to protect against weather, bright light, and herbivory.

Another important innovation of the bryophytes was the multicellular structures surrounding the gametes, called **gametangia**. In these structures, sperm cells are made in globular or club-shaped sacs called **antheridia**; eggs are produced singly in vase-shaped structures called **archegonia** (Fig. 22.4). Gametangia protect gametes during development.

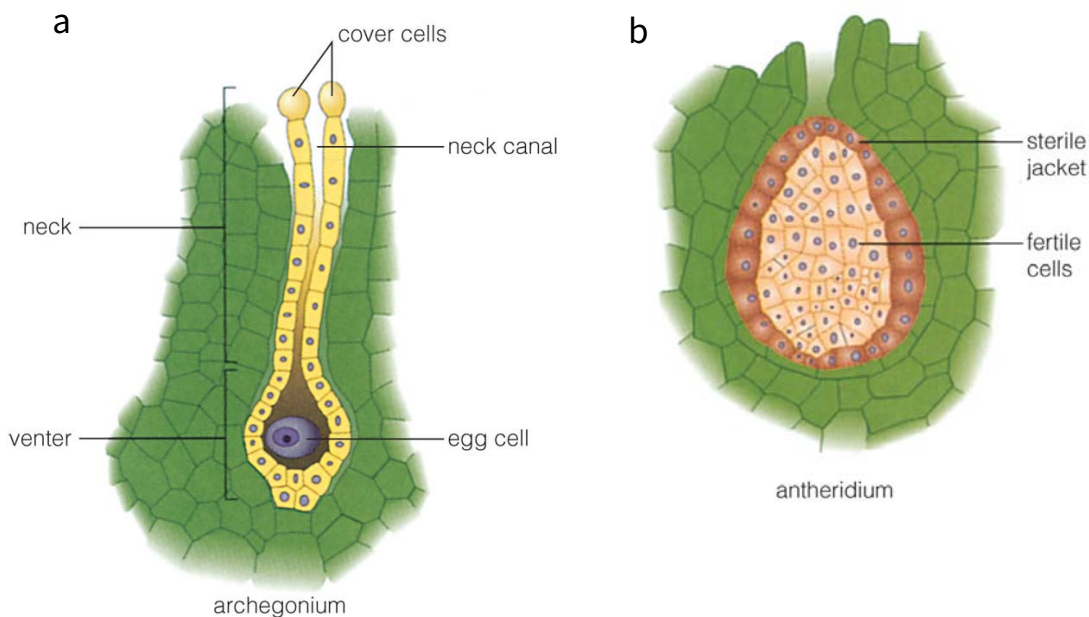


Figure 22.4. Gametangia and gametes can be embedded in the gametophyte tissue as shown here, or attached at the surface of the gametophyte. (a) A long neck extends beyond the venter, capped at the tip with cover cells. (b) An antheridium with an outer row of sterile (nonsperm-forming) cells enclosing inner fertile cells, each of which becomes a sperm.

**STOMATA AND CUTICLE** Stomata and cuticle first appear in the bryophytes. These new features became crucial adaptations to life on land, and virtually all vascular plants possess them. Several lineages of bryophytes have stomata on their

sporophytes. Whether bryophytes have stomata on their gametophytes currently is controversial. Some produce pores that initially develop in a manner similar to stomata on the sporophyte. These may be homologous, or they may represent convergent evolution.

Cuticle may function as it does in most plants today--to reduce the risk of desiccation. However, in many bryophytes, only part of the plant is covered, so the role of the cuticle may be to protect against ultraviolet radiation or fungal infection as well as to reduce dehydration. Many bryophytes could not afford to completely cover themselves with cuticle because they absorb much of their water and minerals directly through their dermal layer.

## 22.2 BRYOPHYTES ARE NOT A NATURAL GROUP

Bryophyte is a common name applied to three distinct lineages of plants that lack lignified vascular tissue.

Bryophytes do not form a monophyletic group, because vascular plants are descended from them. This chapter considers them as three lineages (Table 22.1).

Mosses are familiar to everyone as a green mat in shady, moist places or lining the cracks in rocks and walls (Fig. 22.2b). Although less familiar, the liverworts also are quite common and can be found in many places if you know what to look for (Fig. 22.2d). The hornworts are the least familiar, because they often are rare and inconspicuous (Fig. 22.2e). Because they lack lignified stiffening and vascular tissues, bryophytes remain small. Mosses and liverworts, however, seldom grow alone. Colonies can cover large areas of ground and represent substantial biomass in certain communities.

Some bryophytes have flat, ribbon-like bodies called **thalli** (singular, *thallus*) that often bifurcate as they grow, whereas others have a more familiar upright form with tiny leaves born on short stems.

Table 22.1 Bryophyte Taxonomy	
Common Name	Traditional Taxonomic Name
Hornworts	Anthocerotophyta (=Anthocerophyta)
Liverworts	Marchantiophyta (=Hepaticophyta or Hepatophyta)
Leafy liverworts	Jungermanniopsida Jungermanniidae Porellales <i>Porella</i> Radulales Pleuroziales Lepicoleales Jungermanniales
Simple thalloids	Metzgeriidae Metzgeriales Haplomitriales Blasiales Trebiales Fossombroniales
Complex thalloids	Marchantiopsida Marchantiales <i>Marchantia</i> Sphaerocarpaceae Monocleales Ricciales <i>Riccia</i>
Mosses	Bryophyta
Granite mosses	Andreaeopsida
Peat mosses	Sphagnopsida <i>Sphagnum</i>
True mosses	Bryopsida <i>Dawsonia</i> , <i>Ptychomnion</i> , <i>Bryum</i> Takak Jungermanniidae iopsida

Bryophytes frequently also possess minute projections composed of single or multiple cells that anchor the plants to the soil and thus resemble roots. In some species, they may even serve to conduct water and minerals from the substrate. However, because these structures are quite different from true roots in development, form, and function, they are called **rhizoids** (Fig. 22.3).

All of the traits discussed in this section are ancestral in the land plant lineage--that is, they were inherited from a common ancestor. Because only derived traits can reveal the exact path of evolution, we must examine differences among bryophyte lineages to determine how their body forms and life histories changed over time in their great leap onto the land.

### **Bryophyte Relationships Remain Uncertain**

It is currently unclear how the three lineages of bryophytes are related to each other and to the vascular plants. A great number of distinct lines of evidence support the idea that they share a common ancestor among the ancient charophyte algae. Systematists have long suspected that the genus *Coleochaete* is the closest living algal relative of the land plants, but a recent analysis of relationships based on DNA comparisons found that another green alga, *Chara*, is one branch point (node) closer to land plants on a cladogram.

One area of great interest is the identity of the first lineage of land plants. Traditionally, on the basis of their relative simplicity of organization and lack of features present in other groups, liverworts have been considered the earliest diverging lineage. However, some recent molecular reappraisals using nucleic acid sequences from each of the three genome compartments (the nucleus, the chloroplast, and the mitochondrion) have revealed that hornworts may represent the earliest lineage. Reassessments of morphological characteristics using more complete data sets support this conclusion. Evidence from studies of morphology, development, and DNA suggests, moreover, that mosses and liverworts are closely related.

Another important question in bryophyte evolution concerns the timing of their first appearance and subsequent radiations. **Megafossils**, fossils that can be seen without a microscope, of bryophytes are rare (Fig. 22.5). Until recently, the earliest known megafossils of a bryophyte were liverwort fossils from 425 million years ago (late Silurian period). Curiously, vascular plants, which descended from bryophytes, appear in the fossil record 5 to 45 million years earlier. However, spores of land plants that could be bryophyte in origin can be found as early as 475 million years ago (Ordovician period). Some recent finds from Oman confirm these are, in fact, bryophyte spores and explain the 50-million-year gap between the spore and the plants that produced them. Sifting through organic remains dissolved out of Ordovician period rocks, paleontologists found masses of early spores preserved inside tiny sporangia. The sporangia were associated with fragmentary fossils of bryophyte plants. These plants had previously escaped discovery because they are extremely small and lack certain features usually associated with bryophytes. Future research undoubtedly will yield even more evidence of the first plants to colonize the



land. The fossil record now agrees with the results of phylogenetic analyses: the first land plants were bryophytes.

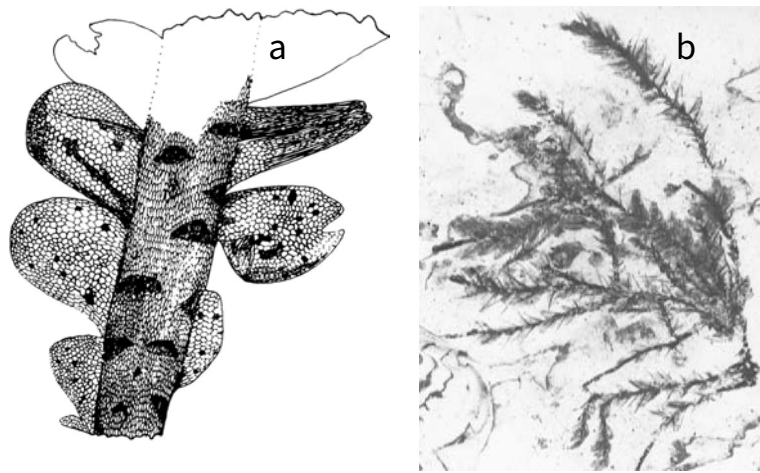


Figure 22.5. Fossil bryophytes. (a) A fragment of a Devonian hepatic. (b) *Aulocumnium heterostichoides*, an Eocene moss.

Studies of bryophytes have provided a great deal of support for the following hypotheses: (1) land plants evolved only once from a single algal ancestor, specifically a charophyte; (2) the first land plants were bryophytes and appeared no later than the Ordovician period, about 475 million years ago; (3) the bryophytes form a non-monophyletic group (that is, the bryophytes gave rise to vascular plants); and (4) each of the three living bryophyte lineages--the hornworts, liverworts, and mosses--is monophyletic.

### 22.3 HORNWORTS

The **hornworts** have relatively simple gametophytes, consisting of a flat thallus, roughly circular in outline or, especially in epiphytic varieties, long and ribbon-shaped with a prominent midrib (Fig 22.6). The gametophytes of hornworts produce copious mucilage inside their thalli, and the ventral portion of the thallus has pores. These may be homologous to the stomata present on the sporophytes. Cyanobacteria (genus *Nostoc*) enter the thallus through these clefts and form symbiotic colonies, which can be seen as blue-green dots when the thallus is held up to the light. *Nostoc* fixes atmospheric nitrogen to ammonia, which the hornworts require; in return, *Nostoc* lives protected in the hornwort gametophyte.

The photosynthetic cells of hornworts are unique among land plants but strikingly similar to algae in that they each typically contain one giant chloroplast with distinct visible pyrenoids. Archegonia and antheridia develop embedded in the thallus: the antheridia are clustered in groups of up to 25 in roofed chambers in the upper portion of the thallus, and the archegonia are sunken into the thallus, with only the neck protruding. Sperm are released from the antheridia. They swim toward an archegonium, where they are caught in the mucilage that covers it and are drawn down into the neck canal. Once inside the archegonium, a single sperm fertilizes the egg, creating a zygote.

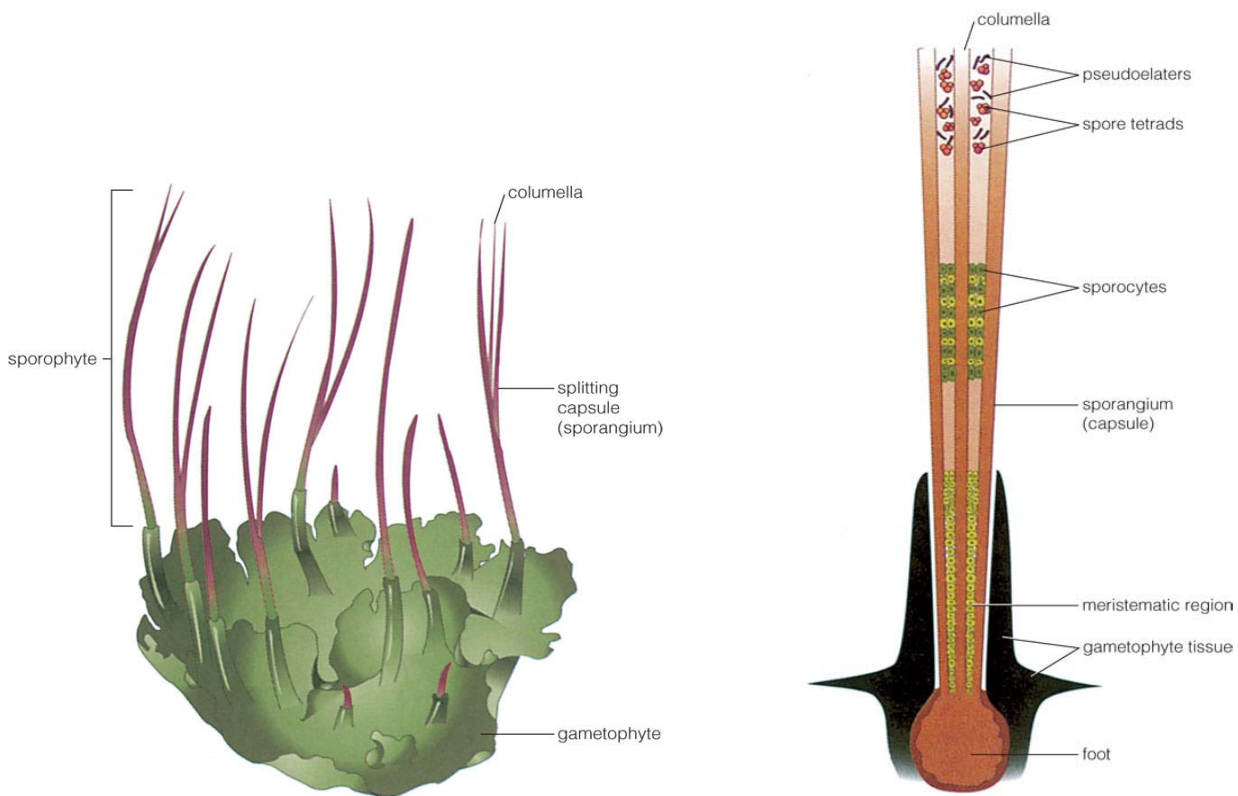


Figure 22.6 (left). The hornwort *Phaeoceros*, showing gametophyte and sporophyte stages. Mature hornwort sporangia split into longitudinal strips, beginning at the tip and opening downward. Rhizoids, which anchor gametophytes to the ground, are not shown. Figure 22.7 (right). A longitudinal section through a hornwort (*Anthoceros*) sporophyte. Only the mid-portion of the sporophyte is shown, omitting the tip of the sporangium and rhizoids at the base. The tubular sporophyte is mainly an elongated sporangium. Sporophyte cells within the sporangium undergo meiosis to produce haploid spores. Other cells produce twisted pseudoelaters, which assist in the ejection of spores from the sporangium.

The sporophyte of hornworts is unique among plants in that it grows continually from a meristem at its base. It is long and pointed, creating the appearance of horns protruding from the thallus (hence, the name of the division). It consists of a foot embedded in the gametophyte thallus and an upright sporangium or **capsule** (Fig. 22.7). The epidermis of some hornwort sporophytes contains stomata but generally lacks chloroplasts; beneath the epidermis there is a layer of chlorenchyma tissue, and beneath this there is a mass of sporocytes, which undergo meiosis to produce haploid spores. The spores are intermingled with pseudoelaters, which help separate and disperse the spores. In the center of the sporangium is a central cylinder of sterile tissue, the **columella**.

When mature, the tip of the capsule splits into two **valves** (sections), and spores are released (Fig. 22.7). A meristematic region just above the foot adds new cells to the base of the sporangium so that more sporocytes are continually created. The sporangium thus grows upward from the base much like a blade of grass and continues to release spores over a long period. Its total height may reach several

centimeters. If the spores land in a suitable environment, they undergo mitosis and produce new gametophytes.

## 22.4 LIVERWORTS

Approximately 9,000 species of plants comprise the group known as **liverworts**, or *hepatics* (derived from the Greek word meaning "liver"). The name is old, having been recorded in medieval manuscripts as early as the ninth century A.D. It was probably applied to these plants because of their fancied resemblance to the liver and the belief that plants could cure diseases of the organs that they resembled. A prescription for a liver complaint in the sixteenth century called for "liverworts soaked in wine."

As is the case with all bryophytes, the liverwort gametophyte is the more prominent phase of the life cycle. Most grow in moist, shady habitats. Those in temperate regions usually grow as a green ribbon or heart-shaped band of tissue (Fig. 22.8a). These thalli can resemble hornworts. The thallus is held to the surface of the damp soil by single-celled rhizoids. Individual plants are small, ranging in size from one to several centimeters across. However, colonies of liverworts can occupy large areas.

Some liverworts are more elaborate, with distinct leaves and stems. The leaves are blunt-tipped or lobed and are attached to the stems in two or three overlapping rows (Fig. 22.8b). The gametophytes of liverworts produce an enormous variety of volatile oils, which are stored in a unique single membrane-enclosed organelle called an oil body. These oils give many liverworts a distinctive aroma, and they may serve to prevent herbivory. Some of these compounds are promising as antibiotics and anti-tumor agents.

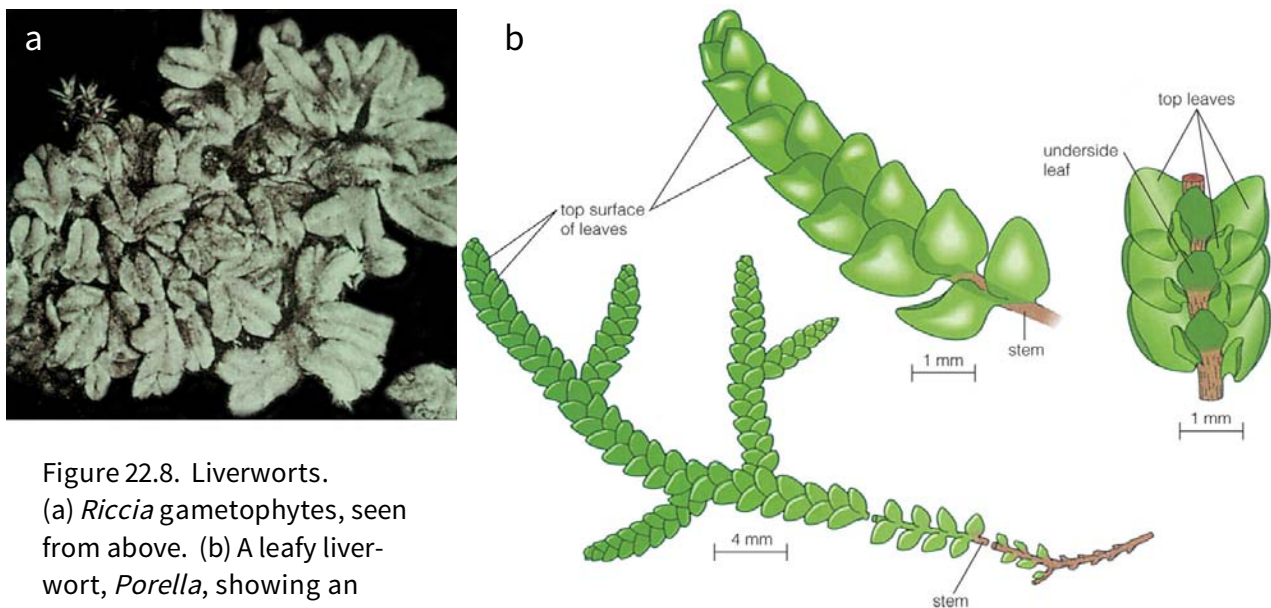


Figure 22.8. Liverworts.  
(a) *Riccia* gametophytes, seen from above. (b) A leafy liverwort, *Porella*, showing an entire plant and details of the stem and leaves.

Liverworts produce relatively simple sporophytes that are hidden in folds in the gametophyte tissue. As spores develop, special cells near the base of the sporophyte elongate rapidly to form a stalk, called a **seta**, which pushes the sporangium, or capsule, above the surface of the thallus. The capsule then splits into four valves and releases all of its spores at one time. Special thickened cells inside the capsules, called **elaters**, separate the spores and aid in spore dispersal. If the spores land in a suitable environment, they undergo mitosis and produce one new gametophyte plant per spore.

Our discussion of this group focuses on the genera *Riccia* and *Marchantia*, two types of thalloid liverworts, and the genus *Porella*, a leafy liverwort. These three examples represent the morphological variation of hepatic plants.

### Some Liverworts Have Thalloid Bodies

Gametophytes of the **thalloid** (ribbon-shaped) liverworts usually grow Y-shaped branches by a simple forking at the growing tip. In some species, a rosette of branches is formed. About 15% of all liverwort species are thalloid, and of these about two-thirds have simple undifferentiated thalli. The remaining third have more complex thalli with distinct layers visible.

The gametophyte of *Marchantia* is a good example of a thalloid liverwort. It has a prominent midrib, and the tips of the branches are notched. A typical thallus is 1 to 2 cm across. The size and degree of branching depend on growing conditions. On the upper epidermis are polygonal areas, each with a conspicuous pore in the center (Fig. 22.9). These areas demarcate air chambers below the pore, which bathe chlorenchyma cells in air containing carbon dioxide. The pores perform the same function as stomata. The lower cells of the thallus are colorless parenchyma, modified for carbohydrate storage. Rhizoids and sheets of cells called scales project from the lower surface, increasing the surface area in contact with the substrate and anchoring the thallus.

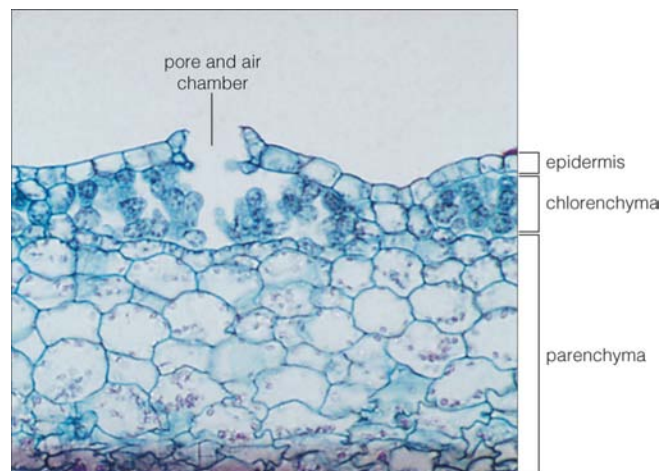


Figure 22.9. Cross section of a *Marchantia* thallus, showing the pore, air chamber, epidermis, chlorenchyma, and parenchyma storage tissue.

*Marchantia* reproduces asexually in two ways: by fragmentation when older parts of the thallus die, separating younger portions that then develop as separate individuals; and by small clumps of tissue called **gemmae** (singular, *gemma*). These clumps are produced in small *gemmae cups* that form on the upper surface of the thallus (Fig. 22.10). When the gemmae are mature, raindrops can break them free of

the cup and scatter them away from the thallus. If a gemma lands on a suitable substrate, it is capable of developing into a gametophyte plant by mitosis.



Figure 22.10. Gemmae cups, involved with asexual reproduction, as they appear on the upper surface of a *Marchantia* gametophyte thallus.

For sexual reproduction, *Marchantia* has stalked structures on which the gametangia are produced. The stalks of some gametophytes resemble tiny beach umbrellas and produce only antheridia. These are called **antheridiophores** (Fig. 22.11a). The stalks of other gametophytes resemble tiny palm trees and are called **archegoniophores**; these produce archegonia underneath their "fronds" (Fig. 22.11b). Both antheridiophores and archegoniophores serve to hold the gametangia well above the main body of the thallus. After fertilization, the sporophytes develop under the archegoniophores. Eventually, the sporangium capsule becomes visible hanging upside down from the archegoniophore on a short, thick seta. When mature, the sporangia split open and release the spores.



Antheridiophore



Archegoniophore

Figure 22.11. Gametangium-bearing structures of *Marchantia*. (a) Antheridiophores. (b) Archegoniophores.

## Most Liverworts Have Leafy Bodies

The largest group of liverworts, containing about 85% of all known species, has leafy gametophytes. Leafy liverworts are found from the arctic to the tropics and are especially common in humid climates, where they may be the most abundant bryophytes. Like mosses, which often are found growing with them, leafy liverworts thrive in shady moist areas, but they may also be found in full sunlight. Some leafy liverworts can tolerate extreme desiccation, whereas others grow underwater. Some are epiphytes on woody plants, and a few are even epiphytes on other bryophytes.

These plants can be distinguished from mosses by the leaf arrangement. Mosses have spirally arranged leaves, whereas leafy liverworts have two or three distinct rows. In addition, the leaves of leafy liverworts usually are lobed, unlike those of mosses.

*Porella*, a common, widespread genus (Fig. 22.8b), forms dense mats on rocks and trees. Young portions of stems are densely clothed with leaves arranged in three ranks. The leaves in the upper two ranks are large and lobed; the lower rank has much smaller, unlobed leaves. The leaves are one cell in thickness and lack a cuticle. Shaded, older portions of stems lack leaves, and new rhizoids arise along those naked segments. Some liverwort species, including *Porella*, have very few rhizoids.

Leafy liverworts reproduce asexually by gemmae, which often are found attached to leaves or stems. When sexual reproduction occurs, antheridia are produced in the axils of leaves, and archegonia grow on specialized short, leafy branches. The production of archegonia is the last series of cell divisions undertaken by the branches that produce archegonia; therefore, the archegonia are always terminal on the stems where they occur. The sporophytes, as with other liverworts, consist of a foot, a seta, and a sporangium. The sporangium splits into four valves when mature, and in some cases, elaters actively flick out the spores.

## 22.5 MOSSES

**Mosses** are the most conspicuous bryophytes because they are larger, have wider distributions, and have many more species than the liverworts and hornworts. They often cluster to form easily visible tufts or carpets of vegetation on the surface of rocks, soil, or bark. Taxonomists divide them into a number of groups. The most prominent are granite mosses, small, dark-colored plants that grow on rocks in cool climates; peat mosses, which are much larger and are confined mainly to acidic bogs; and the "true" or typical mosses, with the widest habitat range and the most species.

The life cycle of a typical moss, such as *Mnium*, is explored in the following section.

### Gametophytes Have Protonemal, Bud, and Leafy Phases

Moss gametophytes have three growth phases, starting when a spore germinates into a branching, filamentous structure called the **protonema** (Fig. 22.12a,b). The second phase begins when buds form on the protonema (Fig. 22.12c). In the third

phase, the buds grow into upright, branching axes, bearing small, spirally arranged leaves and rhizoids. Each protonema may produce a dense population of many genetically identical leafy gametophytes; a single spore thus can produce many separate gametophytes.

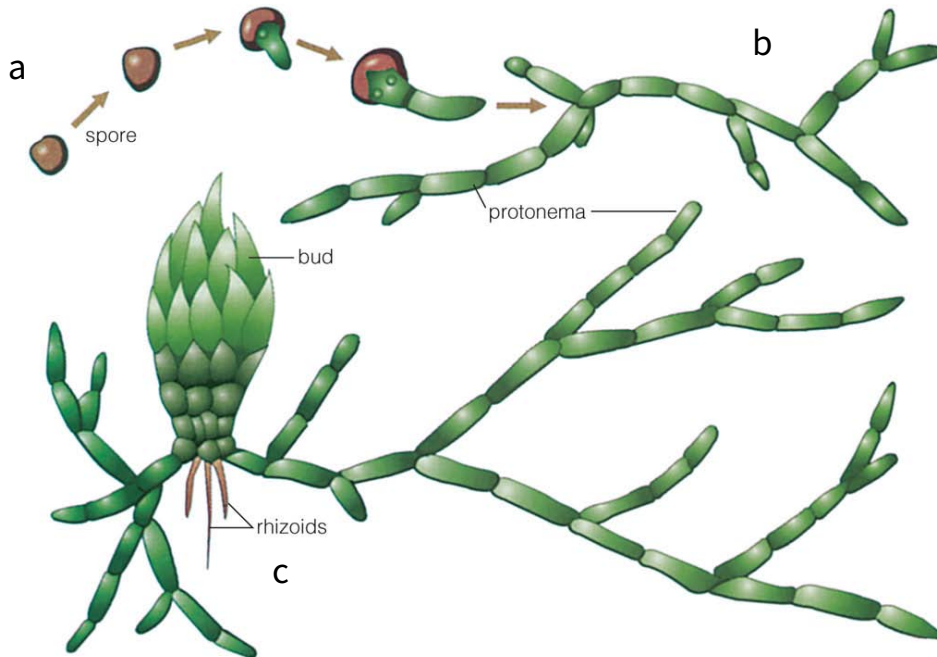


Figure 22.12. Early gametophyte development in the moss *Funaria*. (a) The germination of haploid spores. (b) A protonema. (c) An older protonema with one bud.

As the leafy gametophyte grows, cells in the stems differentiate and mature into specialized tissues. Mosses typically have an epidermal layer of small, thick-walled cells surrounding a homogeneous cortex of parenchyma tissue. Some species have a thin cuticle over the parts of the epidermis, but other lack a cuticle. Stomata are absent. The epidermis of *Sphagnum* is unique in containing large, empty, clear cells (Fig. 22.13). These cells can fill with water through a pore when moistened and serve as a reservoir of moisture for the moss plant.

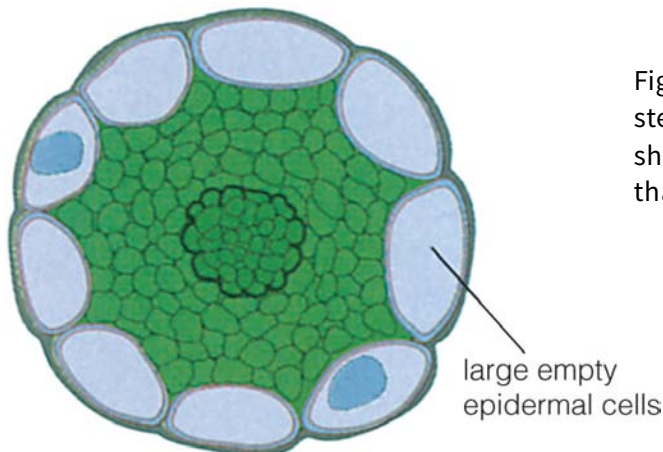


Figure 22.13. Cross section of the stem of the moss *sphagnum*, showing specialized epidermal cells that store water.

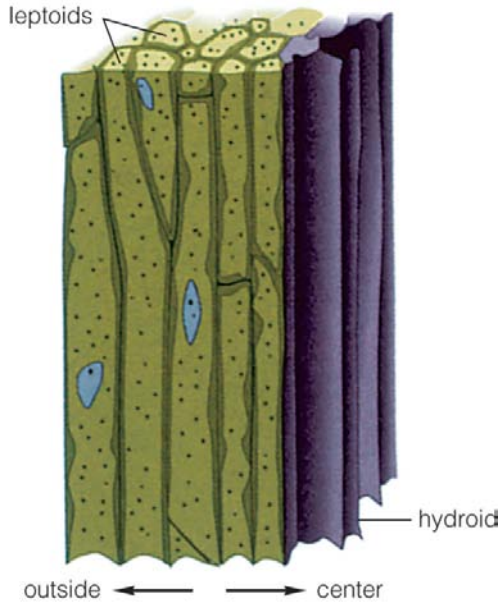


Figure 22.14. A longitudinal section showing details of conducting cells in the stem of the moss, *Polytrichum*.

Many mosses have a more complex stem anatomy, with a central strand of conducting tissue. One kind of conducting tissue is made up of **hydroids**--elongated, thin-walled, dead, empty cells that conduct water (Fig. 22.14). Their end walls are oblique, sometimes very thin, perforated with pores, or partly dissolved. Experiments with dyes show that the translocation of water can occur in this tissue. Some mosses have continuous hydroid tissue from the stems to the midribs of the leaves. Hydroids resemble vessels but lack their specialized pitting and lignified walls.

Some mosses also contain a layer of cells called **leptoids**, which resemble the sieve cells of vascular plants (Fig. 22.14). Leptoids surround the hydroids and are living, but their nuclei degenerate. Nearby

parenchyma cells may assist the leptoids, like companion cells assist sieve tubes in angiosperms. Tracer studies show that sugars may move through these cells at rates of up to 30 cm per hour.

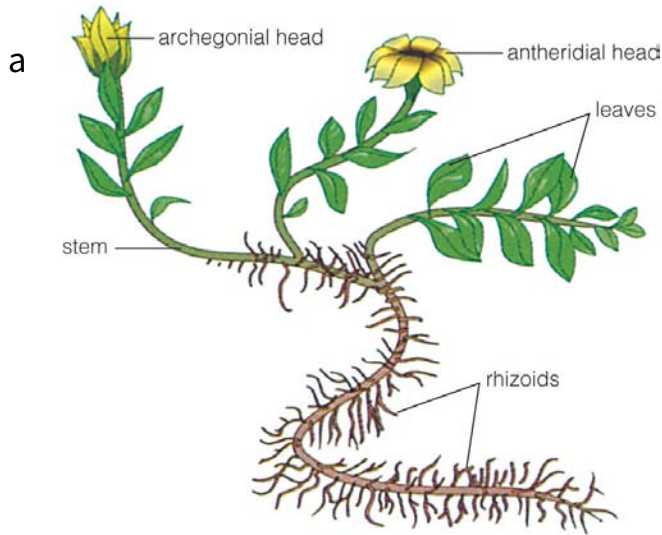
### Mosses Have Several Forms of Asexual Reproduction

Asexual reproduction is accomplished in several ways. First, the protonema may continue to produce new buds, so a miniature forest of moss plants may spread outward in all directions, mat-like, at the edges of the clone. In this respect, the protonema is analogous to a network of runners or rhizomes. Second, leaf tissue placed in wet soil may produce protonemal strands from which buds and new moss individuals develop. Third, rhizoids sometimes can produce buds. Fourth, lens-shaped gemmae may form on rhizoids, leaves, at the ends of special stalks, and even in specialized gemmae cups. Gemmae have the same function in mosses as they do in liverworts: if detached from the parent plant and dispersed to a suitable habitat, each can begin mitotic cell division and differentiate into a new gametophyte.

### Sexual Reproduction Typically Occurs at the Ends of Stems

When undergoing sexual reproduction, most mosses produce gametangia at the gametophyte stem tips (Fig. 22.15a). The gametangia often are separated and held upright by filaments called **paraphyses** (Fig. 22.15b). Some moss species produce antheridia and archegonia on separate plants. Other species have both on a single plant, either together or on separate parts of the plant.





c

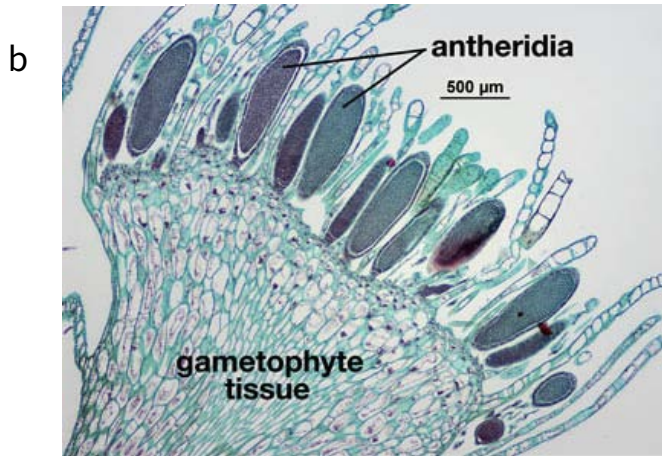


Figure 22.15. Gametangia of *Mnium*, a moss that produces antheridia and archegonia on different heads but on the same plant. (a) The general appearance of antheridial and archegonial heads. (b) An antheridial head, showing dark-stained antheridia and longate filaments of cells called paraphyses. (c) An archegonial head, showing elongate archegonia enclosing dark-stained eggs, surrounded by many paraphyses.

Antheridia release mature sperm when free water is present. Each sperm cell is propelled by two flagella. In some mosses, the leaves that surround antheridial heads spread out like the petals of a flower and function as a splash cup, using the force of raindrops to eject sperm some distance away. Sperm can remain mobile for a long as 6 hours and swim up to 50 cm. The sperm cells of some mosses, such as *Bryum capillare*, on rare occasions become attached to insects that have been attracted to the antheridial heads, either by the red and yellow colors or by secretions from the paraphyses.

Each archegonium has a long neck, a thickened **venter** region that surrounds a single egg, and a long stalk (Fig. 22.15c). When the egg is mature, the neck opens, creating a canal. Attracted by a gradient of chemical attractant emitted by the egg, sperm swim down the canal toward the egg. Water is necessary to carry sperm from an antheridium to an egg, and leaves arranged around archegonial and antheridial heads help retain a film of water over the gametangia. When a sperm cell reaches an egg, it fertilizes the egg, creating a diploid zygote cell.

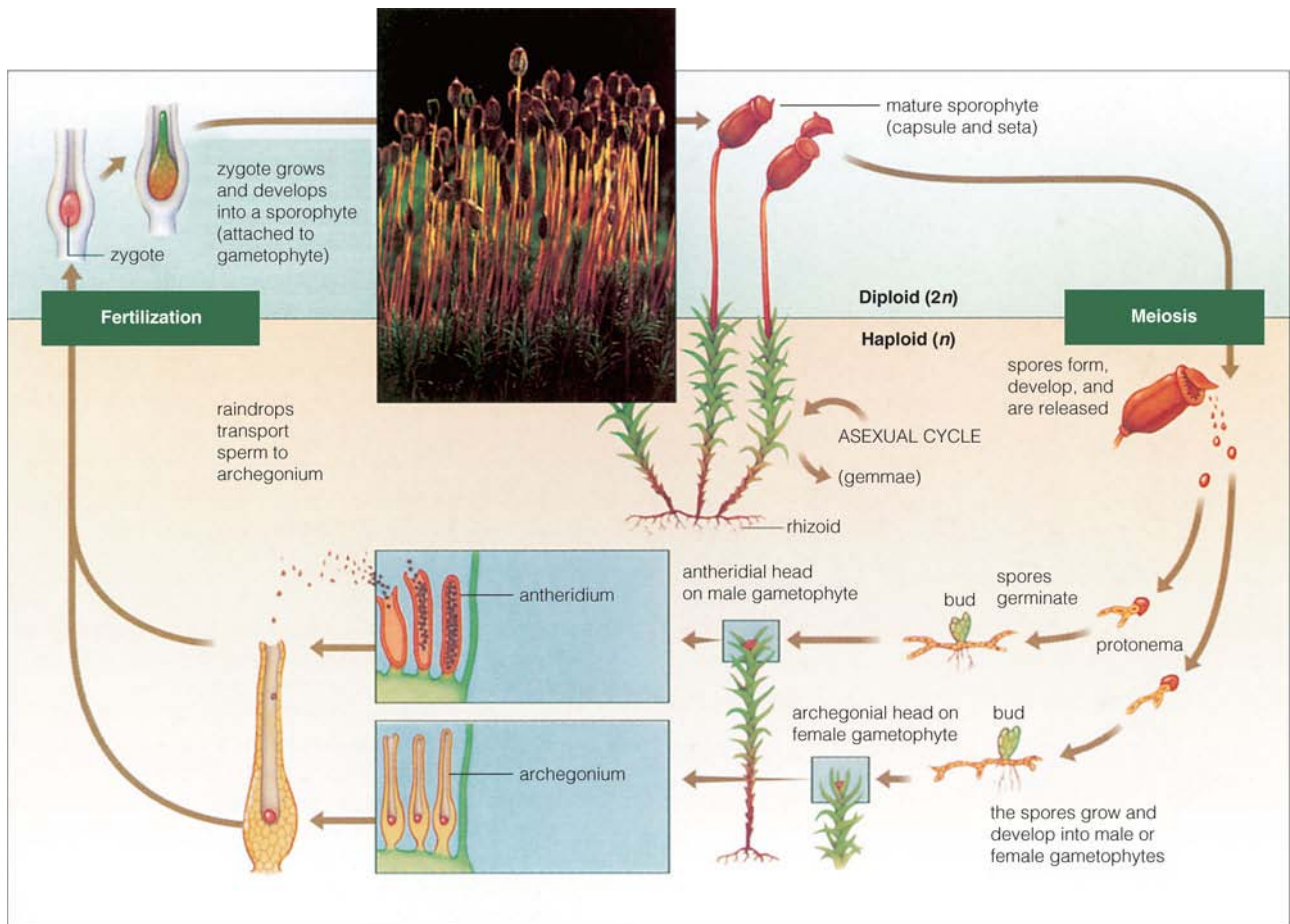


Figure 22.16. Life cycle of *Polytrichum*, a typical moss.

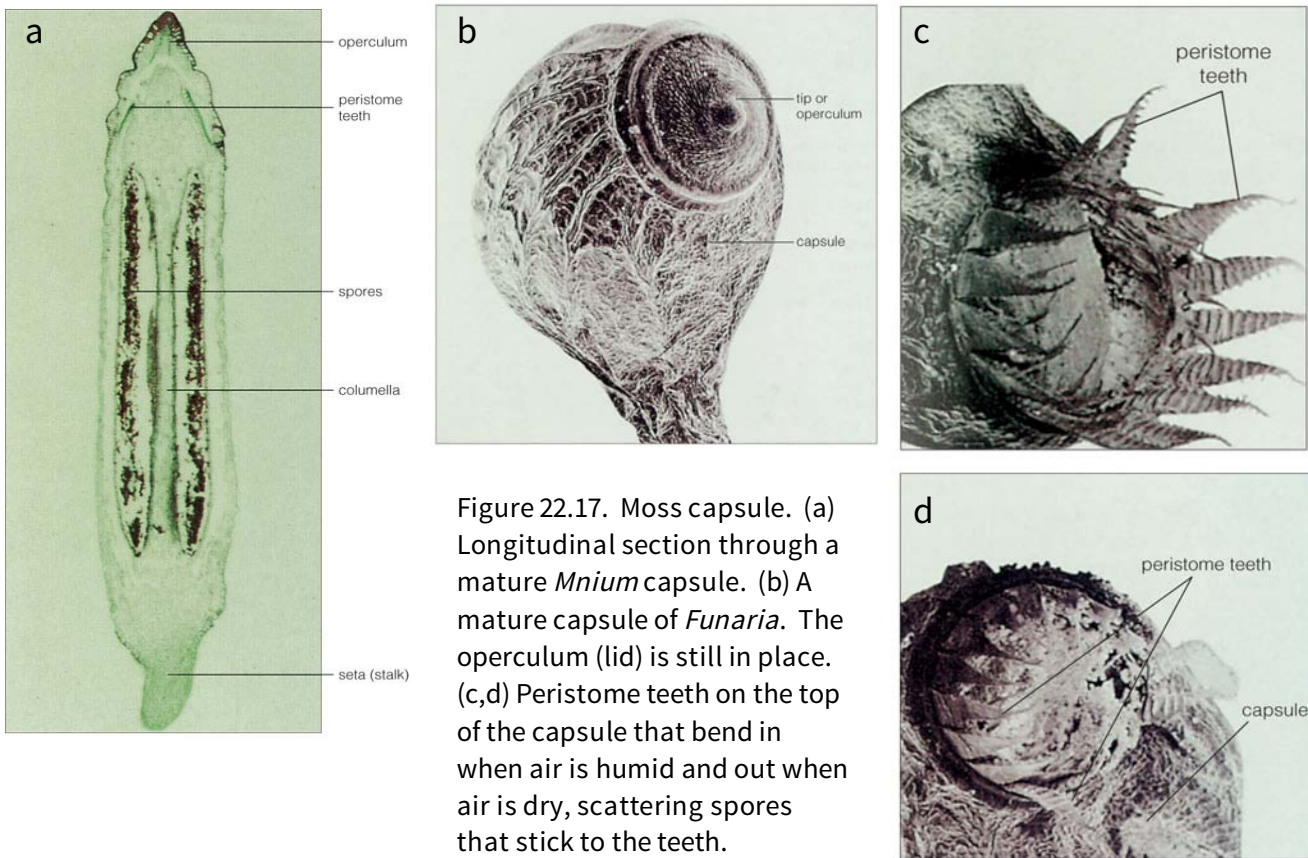
### Moss Sporophytes Have Complex Capsules

Soon after fertilization, the zygote develops into an embryo that differentiates into a foot, seta, and sporangium. The foot penetrates through the venter and into the gametophyte stem, where transfer cells move water and nutrients from the gametophyte to the dependent sporophyte. The seta elongates rapidly, raising the yet-to-be-formed sporangium above the top of the leafy gametophyte (Fig. 22.16). The archegonium increases in size as the sporophyte enlarges, and it is now called the **calyptra** (see Fig. 22.3). It remains for a time as a protective covering for the sporangium. Interestingly, the presence of the calyptra is necessary for normal growth and differentiation of the sporophyte. The mature sporangium (capsule) and seta can have a complex anatomy, with a thick-walled epidermis, a cuticle layer, and stomata; a cortex region; and a central strand of conducting tissue.

Most moss sporophytes contain chlorenchyma and stomata, allowing photosynthesis. The sporophyte can fix 10% to 50% of the carbohydrate needed for

growth and maintenance, the rest coming from the gametophyte. Mature sporophytes of the granite mosses, however, lack chlorophyll.

When mature, the seta may elevate the sporophyte capsule more than 10 mm above the gametophyte, allowing for better spore dispersal. Eventually cells inside the capsule undergo meiosis to form thousands of spores. Granite moss capsules open by slits to disperse the spores. Peat moss capsules have lids that blow off when the capsule dries, violently ejecting all the spores at once. In true mosses, the capsule has a central column of sterile tissue, the columella (Fig. 22.17a). When the capsule is mature, it dries and forms a lid, or **operculum** (Fig. 22.17b). Cells immediately below the operculum form a double row of triangular **peristome teeth**. Eventually, the operculum falls away, exposing the peristome teeth and the spores (Fig. 22.17c,d).



Peristome teeth of many mosses are sensitive to atmospheric humidity. When the air is humid, they bend into the capsule's cavity. When the air is dry, they straighten and lift out some of the spores, which are then disseminated by wind. Spores may travel thousands of kilometers, but typically they fall just a few meters from the parent plant. One family of mosses that grows on dung or carrion (the Splachnaceae) has spores dispersed by insects. These cling together in a sticky mass on the columella, which projects beyond the operculum at maturity. The capsule takes on purple, red, yellow, and white colors and resembles a small flower from a distance. The colors and mushroom-like odors attract flies, which carry the sticky

spores considerable distances away. Moss spores have a waxy covering and are resistant to aridity. They are capable of remaining dormant for decades.

### **Mosses Have Significant Economic and Ecological Value**

*Sphagnum*, a large genus of peat mosses, is by far the most economically important bryophyte. Because of their special epidermal cells, *Sphagnum* mosses are frequently added to potting soil to increase its water-holding capacity. Tons of *Sphagnum* are harvested throughout the world and then sold in the nursery industry in many countries. During World War I, *Sphagnum* was used on a large scale as a wound dressing because its acidic sterile tissue acts as both an antiseptic and an absorbent. In some cold-temperate areas, *Sphagnum* and other mosses accumulate as a thick, compacted, semi-decomposed layer atop the mineral soil. This deposit, called *peat*, can be cut out in blocks, dried, and burned as fuel for cooking and heating (see the endnote, "ECONOMIC BOTANY: Mining Moss: Peat for Profit"). On a much larger scale, the Rhode generating station in Ireland burns 2,000 metric tons of peat a day to produce electricity.

Ecologically, bryophytes are important as colonizers of bare rock and sand. Their small bodies trap dust and wind-blown silt, building soil. Mosses create stabilizing soil crusts in such inhospitable places as coastal dunes and inland deserts. Some bryophytes harbor symbiotic nitrogen-fixing cyanobacteria and significantly increase the amount of nitrogen available to the biosphere. In tundra vegetation, bryophytes constitute as much as 50% of the aboveground biomass, and they are an important component of the food chain that supports animals within the ecosystem. Temperate and cold-temperate forests also have significant amounts of moss biomass.

Bryophytes also are important as tools to improve our basic understanding of fundamental biological processes. Scientists have come to recognize mosses in particular as excellent experimental plants. They are easy to propagate, to grow in small spaces, to clone into genetically identical replicates, and to observe for growth and developmental changes. Because gametophytes are haploid, mutations that would be recessive in diploid cells are expressed. Many discoveries about moss genetics, tissue development, and ecology in the past several decades have proved widely applicable to land plants in general.

## KEY TERMS

antheridia	gametangia	protonema
antheridiophore	gemma	rhizoid
archegonia	hornworts	seta
archegoniophore	hydroid	sporocyte
bryophytes	leptoid	sporophyte
calyptra	liverworts	thalli
capsule	megafossil	thalloid
columella	mosses	valve
elater	operculum	venter
embryo	paraphyses	
embryophytes	peristome teeth	

## SUMMARY

1. Bryophytes are small, herbaceous plants. They have in common an unusual life history in which the gametophytes live longer and are more prominent than the sporophytes, and they all possess unbranched sporophytes, each bearing a single sporangium. Their habitats range from aquatic, to humid or wet terrestrial, to epiphytic, to arid.
2. Bryophytes successfully moved into terrestrial habitats by evolving a series of traits that enabled them to resist desiccation, including a multicellular sporophyte phase with an initial embryo stage, specialized gametangia (antheridia and archegonia), and weather-resistant, sporopollenin-coated spores. Some members of the division have leaflike and stemlike organs. They also typically have rhizoids that anchor the plants to the substrate. At the same time, they resemble algae in that free water is essential for the movement of sperm to the egg, there is no lignified supportive tissue, and the gametophyte generation is most prominent.
3. Most plant biologists believe that bryophytes evolved from a single algal ancestor in the charophyta. In this textbook, the 25,000 living species of bryophytes are classified as three separate lineages: hornworts; liverworts or hepatics, which include thalloid liverworts and leafy liverworts; and mosses, represented by granite mosses, peat mosses, and true mosses.
4. Bryophytes are almost certainly not a monophyletic group because they gave rise to vascular plants. It is unclear which bryophyte lineage represents the first to diverge, but recent molecular and morphological analyses suggest it may have been the hornworts.
5. Hornworts have thalloid gametophytes. They form symbiotic relationships with nitrogen-fixing bacteria and produce pores that may be homologous to stomata.

Their sporophytes have an elongated sporangium with indeterminate growth, and sometimes stomata are present.

6. Liverworts include organisms with thalloid gametophytes (*Marchantia*) and others with leafy gametophytes (*Porella*). All liverworts have rhizoids that anchor the plants to their substrate.
7. Sexual reproduction within the liverworts involves archegonia, antheridia, embryos, and small sporophytes; but their morphology and placement depend on the species. *Marchantia* gametangia, for example, are on elevated organs called antheridiophores and archegoniophores.
8. The major points of the moss life cycle are as follows: the life cycle is sporic; the gametophyte generation is dominant; sperm are produced in multicellular antheridia and eggs in multicellular archegonia; water is essential as a medium to allow the sperm to swim from an antheridium to an archegonium; and an embryo stage is present.
9. Moss gametophytes begin growth as a filamentous, alga-like protonemal phase that produces buds, which then develop by mitosis into plants with leaflike appendages on stemlike axes.
10. Specialized tissue in some moss gametophytes includes chlorenchyma, parenchyma, epidermis, water-conducting hydroids, and sugar-conducting leptoids. Some moss gametophytes are capable of tolerating extreme dehydration and then resuming normal activity within minutes or being rewetted. However, despite the presence of conducting tissue in some genera, these organisms are considered to be nonvascular plants.

### Questions

1. The bryophytes have added several innovations to the algal life cycle, including multicellular gametangia and an embryo stage. How do these innovations contribute to the survival of bryophyte plants?
2. Draw a diagram of the basic life cycle of a bryophyte. Label all the steps and structures involved. Describe each of the structures for a typical liverwort and a typical moss.
3. In what ways is it possible to conclude that the gametophyte generation is dominant over the sporophyte generation in the bryophytes?
4. Describe the difference in morphological and anatomical complexity between the gametophytes of the liverwort *Marchantia* and that of a typical moss and also between the sporophyte of *Marchantia* and that of a moss.

5. Describe the conducting tissue of some of the most advanced mosses. Why is it not the same as the vascular tissue of higher plants?
  
6. Mosses cannot control their water balance, and yet they are important elements of the biotic crust of desert soils. How can mosses persist in a desert environment? When would they reproduce?

## PLANTS, PEOPLE, AND THE ENVIRONMENT: *The Ultimate Shade Plants*

It is common to find mosses growing in the dim light of shallow caves, under 30 cm of snow, or on the floor of a dense forest. In some places, the lush carpets of green they form may be the only vegetation present. This affinity for low light can even be life-saving: the famous tendency for mosses to grow thickest on the shadier north side of tree trunks enables wood-wise hikers to orient themselves. How can mosses not only survive, but thrive in these places where other plants cannot?



Some mosses are sensitive to light. The light compensation point for photosynthesis, where the rate of photosynthesis just equals the rate of respiration, is reached at 1% of full sun, and the saturation point, where the rate of photosynthesis is maximum, at only 4% to 20% of full sun. Some mosses have specialized cells capable of focusing any available light onto chloroplasts. These adaptations allow shade-tolerant mosses to inhabit many places where all other plants are completely excluded. In these extreme habitats, mosses are the dominant vegetation and the basis of food chains, a role they lost everywhere else more than 400 million year ago, when vascular plants appeared.



## ECONOMIC BOTANY: *Mining Moss: Peat for Profit*

Peat is any kind of plant matter that accumulates under water-soaked conditions and that does not completely decompose because the amount of oxygen is limited. Peat is a mixture of freshwater marsh plants such as reeds, sedges, and grasses, and it often include peat mosses belonging to the genus *Sphagnum*. If conditions are right--cold temperatures, abundant moisture, and water that is acidic and low in nutrients--peat can accumulate in layers, at rates as fast as 25 cm per century to a slower 25 cm per



Peat in Lewis, Scotland.

millennium. The oldest deposits are tens of meters in thickness. The thousands of square kilometers of peat lands in the cold temperate regions of the world, multiplied by depth, total more than 200 billion metric tons of dry biomass.

Peat has been put to a variety of human uses. It is, first of all, a fuel. During the Stone Age, Europeans found that it could be dug out in blocks, dried, and burned for heat. Currently, Russia, Ireland, Finland, Sweden, Germany, and Poland extensively harvest peat for fuel. An Irish home may use 15 metric tons of dry peat each year, an amount that can be harvested by one person in a month's time. Two-bladed shovels called *slanes* are used by individuals, but commercial operations use specialized tractors, millers, harrows, and harvesters. Such costly investment is needed to harvest the large volumes of peat burned in power plants in Russia and Ireland. The use of peat as a fuel in the United States is minimal, but the energy content is estimated to exceed all current, combined reserves of coal, petroleum, and natural gas.

Peat is also used in horticulture. When added to potting mixes, peat increases the soil's water-holding capacity and lightens the soil, allowing air and water to move more freely. Peat is used as a mulch for acid-loving ornamentals such as rhododendrons and heaths. Compressed peat can be formed into planting containers for seeds, seedlings, cuttings, and root balls. These containers can take up and retain moisture and also decompose over time, releasing the roots to the surrounding soil.

Peat lands also can be cultivated, if drained. Once the peat becomes drier and aerated, it decomposes, releasing nitrogen and other nutrients. Such cool-climate crops and carrots, beets, potatoes, onions, lettuce, cabbage, broccoli, mint, blueberries, and strawberries do well on peat. However, cultivation over the course of many years causes the soil surface to drop because the peat literally oxidizes and blows away. Within a century, several meters of depth can be lost. Agricultural peat lands in California's delta region have to be protected by levees because their surface elevations have dropped as much as 6 m below sea level.

The conservation of peat lands has become an ecological issue in several countries, including the United Kingdom and Ireland, where nearly all of the once-extensive bogs have been stripped. Peat bogs are unique ecosystems, with plant and animal components that have evolved over geologic time. The natural environmental processes that produce bogs proceed so slowly that it is not possible to restore them in a human lifetime once they have been modified. We certainly have the technology and will to convert bogs to other ecosystems, but could we have the ability and will to speed up their formation?

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Sidebar: "Mining Moss: Peat for Profit" <http://en.wikipedia.org/wiki/Peat>