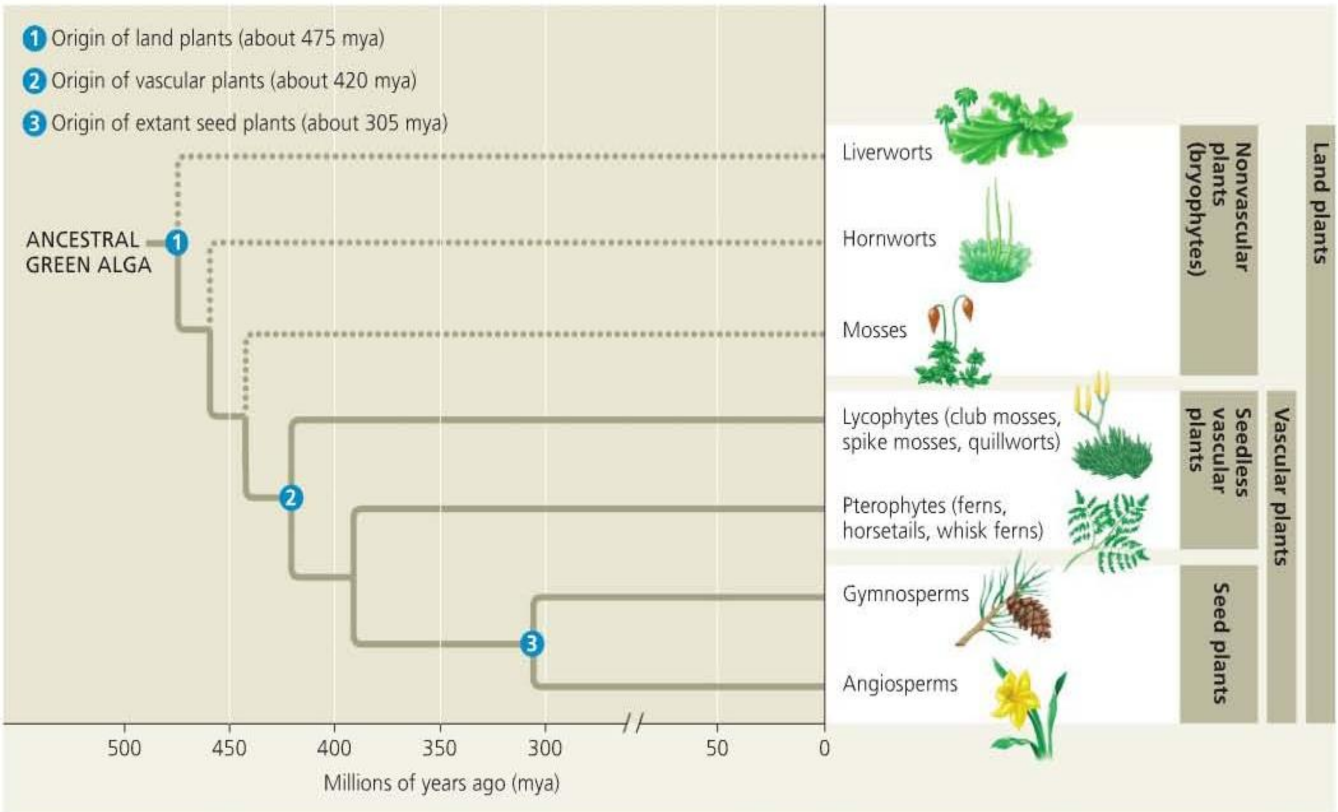
Table 29.1 Ten Phyla of Extant Plants

	Common Name	Estimated Number of Species
Nonvascular Plants (Bryophytes)		
Phylum Hepatophyta	Liverworts	9,000
Phylum Anthocerophyta	Hornworts	100
Phylum Bryophyta	Mosses	15,000
Vascular Plants		
Seedless Vascular Plants		
Phylum Lycophyta	Lycophytes	1,200
Phylum Pterophyta	Pterophytes	12,000
Seed Plants		
Gymnosperms		
Phylum Ginkgophyta	Ginkgo	1
Phylum Cycadophyta	Cycads	130
Phylum Gnetophyta	Gnetophytes	75
Phylum Coniferophyta	Conifers	600
Angiosperms		
Phylum Anthophyta	Flowering plants	250,000

some mosses do have simple vascular tissue. Nonvascular plants are often informally called **bryophytes** (from the Greek *bryon*, moss, and *phyton*, plant).

Although the term *bryophyte* is commonly used to refer to all nonvascular plants, debate continues over the relationships of liverworts, hornworts, and mosses to each other and to vascular plants. Whereas some molecular studies have concluded that bryophytes do not form a monophyletic group (a clade; see Figure 26.10), several recent analyses of amino acid sequences in chloroplasts assert that bryophytes do form a clade. Whether or not bryophytes are monophyletic, they share some derived traits with vascular plants, such as multicellular embryos and apical meristems, while lacking many innovations of vascular plants, such as roots and true leaves.

Vascular plants, which form a clade that comprises about 93% of all plant species, can be categorized further into smaller clades. Two of these clades are the **lycophytes** (club mosses and their relatives) and the **pterophytes** (ferns and their relatives). The plants in each of these clades lack seeds, which is why collectively the two clades are often informally called **seedless vascular plants**. However, notice in Figure 29.7 that seedless vascular plants are paraphyletic, not monophyletic. Groups such as the seedless vascular plants are sometimes referred to as a **grade**, a collection of organisms that share a common level of biological organization or adaptation.



▲ **Figure 29.7 Highlights of plant evolution.** Several hypotheses about relationships between plant groups are actively under debate, including one proposing that bryophytes are a monophyletic group. The dotted lines indicate groups whose evolutionary relationships are unclear.

DRAW IT *Redraw this phylogeny assuming that bryophytes are a monophyletic group in which liverworts diverged first.*

Although grades can be informative by grouping organisms according to key biological features (such as lack of seeds), they can be misleading in other ways. Pterophytes, for example, share a more recent common ancestor with seed plants than with lycophytes. As a result, we would expect pterophytes and seed plants to share key traits not found in lycophytes—and they do, as you'll read.

A third clade of vascular plants consists of seed plants, which represent the vast majority of living plant species. A **seed** is an embryo packaged with a supply of nutrients inside a protective coat. Seed plants can be divided into two groups, gymnosperms and angiosperms, based on the absence or presence of enclosed chambers in which seeds mature. **Gymnosperms** (from the Greek *gymnos*, naked, and *sperm*, seed) are grouped together as "naked seed" plants because their seeds are not enclosed in chambers. Living gymnosperm species, the most familiar of which are the conifers, probably form a clade. **Angiosperms** (from the Greek *angion*, container) are a huge clade consisting of all flowering plants. Angiosperm seeds develop inside chambers called ovaries, which originate within flowers and mature into fruits. Nearly 90% of living plant species are angiosperms.

Note that the phylogeny depicted in Figure 29.7 focuses only on the relationships between extant plant lineages. Paleobotanists have also discovered fossils belonging to extinct plant lineages. Many of these fossils reveal intermediate steps in the emergence of the distinctive plant groups found on Earth today.

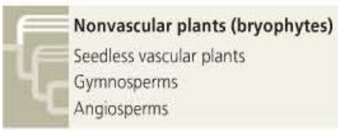
CONCEPT CHECK 29.1

1. Why do researchers identify charophytes rather than another group as the closest relatives of land plants?
2. Identify three derived traits that distinguish plants from charophytes *and* facilitate life on land. Explain.
3. **WHAT IF?** What would the human life cycle be like if we had alternation of generations? Assume that the multicellular diploid stage is similar in form to an adult human.

For suggested answers, see Appendix A.

CONCEPT **29.2**

Mosses and other nonvascular plants have life cycles dominated by gametophytes



The nonvascular plants (bryophytes) are represented today by three phyla of small herbaceous (nonwoody) plants: **liverworts** (phylum Hepatophyta), **hornworts** (phylum Anthocerophyta), and **mosses** (phylum Bryophyta). Liverworts and hornworts are named for their shapes, plus the suffix *wort* (from the Anglo-Saxon for "herb"). Mosses are familiar to many people, although some plants commonly called "mosses" are not really mosses at all. These include Irish moss (a red seaweed), reindeer moss (a lichen), club mosses (seedless vascular plants), and Spanish mosses (lichens in some regions and flowering plants in others).

Note that the terms *Bryophyta* and *bryophyte* are not synonymous. Bryophyta is the formal taxonomic name for the phylum that consists solely of mosses. As mentioned earlier, the term *bryophyte* is used informally to refer to *all* nonvascular plants—liverworts, hornworts, and mosses. Systematists continue to debate the sequence in which the three phyla of bryophytes evolved.

Liverworts, hornworts, and mosses acquired many unique adaptations over the long course of their evolution. Nevertheless, living bryophytes likely reflect some traits of the earliest plants. The oldest known fossils of plant fragments, for example, include tissues very similar to those inside liverworts. Researchers hope to discover more parts of these ancient plants to see if this resemblance is reflected more broadly.

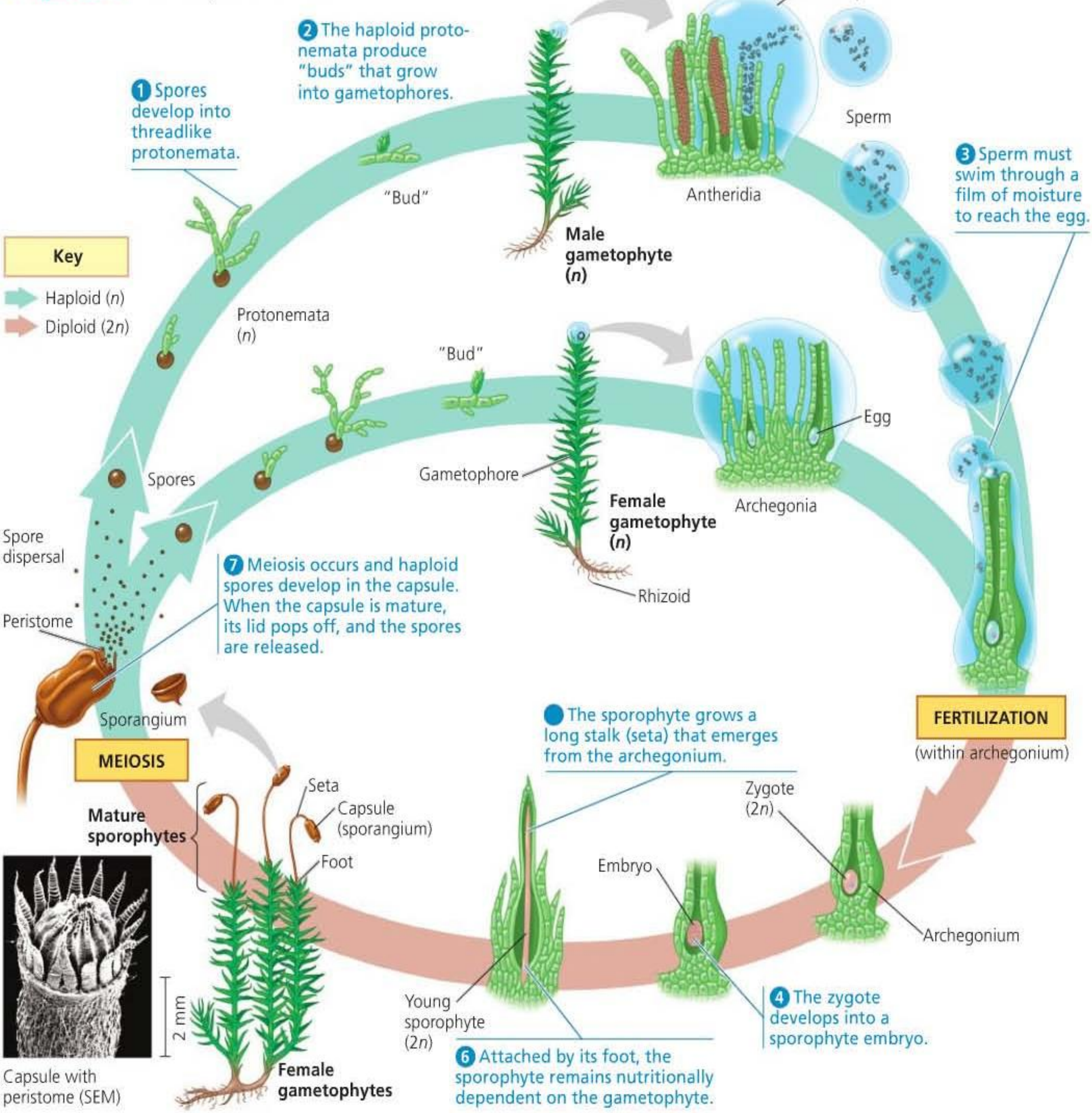
Bryophyte Gametophytes

Unlike vascular plants, in all three bryophyte phyla the gametophytes are the dominant stage of the life cycle: They are larger and longer-living than the sporophytes, as shown in the moss life cycle in **Figure 29.8**. Sporophytes are typically present only part of the time.

When bryophyte spores are dispersed to a favorable habitat, such as moist soil or tree bark, they may germinate and grow into gametophytes. Germinating moss spores, for example, characteristically produce a mass of green, branched, one-cell-thick filaments known as a **protonema** (plural, *protonemata*; from the Greek *proto*, first, and *nema*, threads). A protonema has a large surface area that enhances absorption of water and minerals. In favorable conditions, a protonema produces one or more "buds." (Note that when referring to nonvascular plants, we typically use quotation marks for structures similar to the buds, stems, and leaves of vascular plants because the definitions of these terms are based on vascular plant organs.) Each of these bud-like growths has an apical meristem that generates a gamete-producing structure known as a **gametophore** ("gamete bearer"). Together, a protonema and one or more gametophores make up the body of a moss gametophyte.

Bryophyte gametophytes generally form ground-hugging carpets, partly because their body parts are too thin to support a tall plant. A second constraint on the height of many bryophytes is the absence of vascular tissue, which would enable long-distance transport of water and nutrients. The thin structure of bryophyte organs makes it possible to distribute materials without specialized vascular tissue. Some mosses, however, such as the genus *Polytrichum*, have conducting tissues in the center of their "stems." A few of these mosses can grow as tall as 2 m as a result.

▼ Figure 29.8 The life cycle of a moss.



Phylogenetic analyses suggest that in these and some other bryophytes, conducting tissues similar to those of vascular plants arose independently by convergent evolution.

The gametophytes are anchored by delicate **rhizoids**, which are long, tubular single cells (in liverworts and hornworts) or filaments of cells (in mosses). Unlike roots, which are characteristic of vascular plants, rhizoids are not composed of tissues. Bryophyte rhizoids also lack specialized conducting cells and do not play a primary role in water and mineral absorption.

Mature gametophytes form gametangia that produce gametes and are covered by protective tissue. A gametophyte may have multiple gametangia. Eggs are produced singly in pear-shaped archegonia, whereas each antheridium produces many sperm. Some bryophyte gametophytes are bisexual, but in mosses the archegonia and antheridia are typically carried on separate female and male gametophytes. Flagellated sperm swim through a film of water toward eggs, entering the archegonia in response to chemical attractants. Eggs are not released but instead remain within the bases of archegonia. After fertilization, embryos are retained within the archegonia. Layers of placental transfer cells help transport nutrients to the embryos as they develop into sporophytes.

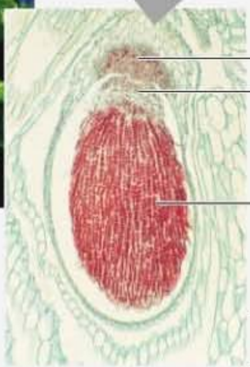
Figure 29.9

Exploring Bryophyte Diversity

Liverworts (Phylum Hepatophyta)

This phylum's common and scientific names (from the Latin *hepaticus*, liver) refer to the liver-shaped gametophytes of its members, such as *Marchantia*, shown below. In medieval times, their shape was thought to be a sign that the plants could help treat liver diseases. Some liverworts, including *Marchantia*, are described as "thalloid" because of the flattened shape of their gametophytes. (Recall from Chapter 28 that the body of a multicellular alga is called a thallus.) *Marchantia* gametangia are elevated on gametophores that look like miniature trees. You would need a magnifying glass to see the sporophytes, which have a short seta (stalk) with an oval or round capsule. Other liverworts, such as *Plagiochila*, below, are called "leafy" because their stemlike gametophytes have many leaflike appendages. There are many more species of leafy liverworts than thalloid liverworts.

Marchantia polymorpha, a "thalloid" liverwort



***Marchantia* sporophyte (LM)**

Plagiochila deltoidea, a "leafy" liverwort

Hornworts (Phylum Anthocerophyta)

This phylum's common and scientific names (from the Greek *keras*, horn) refer to the long, tapered shape of the sporophyte. A typical sporophyte can grow to about 5 cm high. Unlike a liverwort or moss sporophyte, a hornwort sporophyte lacks a seta and consists only of a sporangium. The sporangium releases mature spores by splitting open, starting at the tip of the horn. The gametophytes, which are usually 1–2 cm in diameter, grow mostly horizontally and often have multiple sporophytes attached. Hornworts are frequently among the first species to colonize open areas with moist soils; a symbiotic relationship with nitrogen-fixing cyanobacteria contributes to their ability to do this (nitrogen is often in short supply in such areas).

An *Anthoceros* hornwort species

Mosses (Phylum Bryophyta)

Moss gametophytes, which range in height from less than 1 mm to up to 2 m, are less than 15 cm in most species. The familiar carpet of moss you observe consists mainly of gametophytes. The blades of their "leaves" are usually only one cell thick, but more complex "leaves" that have ridges coated with cuticle can be found on the common hairy-cap moss (*Polytrichum*, below) and its close relatives. Moss sporophytes are typically elongated and visible to the naked eye, with heights ranging up to about 20 cm. Though green and photosynthetic when young, they turn tan or brownish red when ready to release spores.

***Polytrichum commune*, hairy-cap moss**

Bryophyte sperm require a film of water to reach the eggs. Given this requirement, it is not surprising that many bryophyte species are found in moist habitats. The fact that sperm must swim through water to reach the egg also means that in species with separate male and female gametophytes (most mosses), sexual reproduction is likely to be more successful when individuals are located close to one another. Many bryophyte species can increase the number of individuals in a local area through various methods of asexual reproduction. For example, some mosses reproduce asexually by forming *brood bodies*, small plantlets that detach from the parent plant and grow into a new, genetically identical copy of their parent.

Bryophyte Sporophytes

Although bryophyte sporophytes are usually green and photosynthetic when young, they cannot live independently. They remain attached to their parental gametophytes, from which they absorb sugars, amino acids, minerals, and water.

Bryophytes have the smallest sporophytes of all extant plant groups, consistent with the hypothesis that larger sporophytes evolved only later, in the vascular plants. A typical bryophyte sporophyte consists of a foot, a seta, and a sporangium. Embedded in the archegonium, the **foot** absorbs nutrients from the gametophyte. The **seta** (plural, *setae*), or stalk, conducts these materials to the sporangium, also called a **capsule**, which uses them to produce spores by meiosis. One capsule can generate up to 50 million spores.

In most mosses, the seta becomes elongated, enhancing spore dispersal by elevating the capsule. Typically, the upper part of the capsule features a ring of interlocking, tooth-like structures known as the **peristome** (see Figure 29.8). These "teeth" open under dry conditions and close again when it is moist. This allows spores to be discharged gradually, via periodic gusts of wind that can carry them long distances.

Hornwort and moss sporophytes are larger and more complex than those of liverworts. Both hornwort and moss sporophytes also have specialized pores called **stomata** (singular, *stoma*), which are also found in all vascular plants. These pores support photosynthesis by allowing the exchange of CO_2 and O_2 between the outside air and the sporophyte interior (see Figure 10.3). Stomata are also the main avenues by which water evaporates from the sporophyte. In hot, dry conditions, the stomata close, minimizing water loss.

The fact that stomata are present in mosses and hornworts but absent in liverworts suggests three possible hypotheses for their evolution. If liverworts are the deepest-branching lineage of land plants, as in Figure 29.7, then stomata may have evolved once in the ancestor of hornworts, mosses, and vascular plants. If hornworts or mosses are the deepest-branching lineage, or if bryophytes are monophyletic, stomata may have evolved once and then been lost in the liverwort lineage. Finally, if hornworts are the deepest-branching lineage and mosses are the closest relatives of vascular plants, it is also possible that hornworts acquired stomata independently of mosses and vascular plants. This question is important to understanding plant evolution because stomata play a crucial role in the success of vascular plants, as you will learn in Chapter 36.

Figure 29.9, on the facing page, shows some examples of gametophytes and sporophytes in the bryophyte phyla.

The Ecological and Economic Importance of Mosses

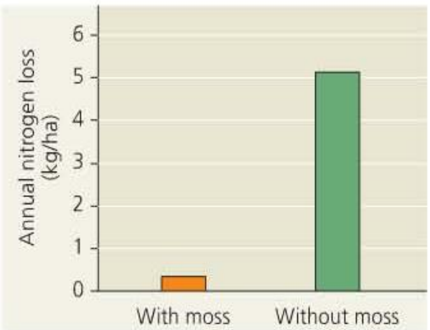
Wind dispersal of their lightweight spores has distributed mosses throughout the world. These plants are particularly common and diverse in moist forests and wetlands. Some mosses colonize bare, sandy soil, where researchers have found they help retain nitrogen in the soil **(Figure 29.10)**. Other

▼ **Figure 29.10 Inquiry**

Can bryophytes reduce the rate at which key nutrients are lost from soils?

EXPERIMENT Soils in terrestrial ecosystems are often low in nitrogen, a nutrient that is required for normal plant growth. Richard Bowden, of Allegheny College, measured annual inputs (gains) and outputs (losses) of nitrogen in a sandy-soil ecosystem dominated by the moss *Polytrichum*. Nitrogen inputs to the ecosystem were measured from rainfall (dissolved ions such as nitrate, NO_3^-), biological N_2 fixation, and wind deposition. Nitrogen losses were measured in leached water (dissolved ions, such as NO_3^-) and gaseous emissions (such as NO_2 emitted by some bacteria). Bowden measured nitrogen losses for soils with *Polytrichum* and for soils where the moss had been removed two months before the experiment began.

RESULTS A total of 10.5 kg of nitrogen per hectare (kg/ha) entered the ecosystem each year. Little nitrogen was lost by gaseous emissions (0.10 kg/ha per year). The results of comparing nitrogen losses by leaching are shown below.



CONCLUSION The moss *Polytrichum* greatly reduced the loss of nitrogen by leaching in this ecosystem. Each year, the moss ecosystem retained over 95% of the 10.5 kg/ha of total nitrogen inputs (only 0.1 kg/ha and 0.3 kg/ha were lost to gaseous emissions and leaching, respectively).

SOURCE R. D. Bowden, Inputs, outputs, and accumulation of nitrogen in an early successional moss (*Polytrichum*) ecosystem, *Ecological Monographs* 61:207–223 (1991).

WHAT IF? How might the presence of *Polytrichum* affect plant species that typically colonize the sandy soils *after* the moss?