

Chapter 29

Plant Diversity I: How Plants Colonized Land

Overview: The Greening of Earth

- For more than the first 3 billion years of Earth's history, the terrestrial surface was lifeless
 - About 1.2 billion years ago, the 1st signs of life on land were thin coatings of cyanobacteria
 - It was only within the last 500 million years that small plants, along with fungi and animals, appeared ashore
 - About 370 million years ago, some plants appeared that could grow much taller, leading to the formation of the first forests
 - Since colonizing land, plants have diversified into roughly 290,000 living species
- The presence of land plants has allowed the existence of other life-forms, including animals, to survive on land
 - Plants supply oxygen and are the ultimate source of most food eaten by land animals



Concept 29.1: Land plants evolved from green algae

- Green algae called charophytes are the closest relatives of land plants
 - Many key characteristics of land plants also appear in a variety of algal clades, mainly algae
 - Multicellularity
 - Eukaryotic
 - Photosynthetic autotrophs
 - Cell walls made of cellulose
 - Chloroplasts containing chlorophylls *a* and *b*

Concept 29.1: Land plants evolved from green algae

- However, land plants share four key traits only with charophytes, strongly suggesting that they are the closest relatives of plants:

- 1) Rose-shaped complexes for cellulose synthesis

- Cells of both land plants and charophytes have circular, petal-shaped arrays of proteins in their plasma membranes

- These proteins synthesize the cellulose that makes up the cell wall

- In contrast, other types of algae have linear arrays of these same proteins



- 2) Peroxisome enzymes

- The peroxisome enzymes of both land plants and charophytes contain enzymes that help minimize the loss of organic products as a result of photorespiration

- The peroxisomes of other algae lack these enzymes

Concept 29.1: Land plants evolved from green algae

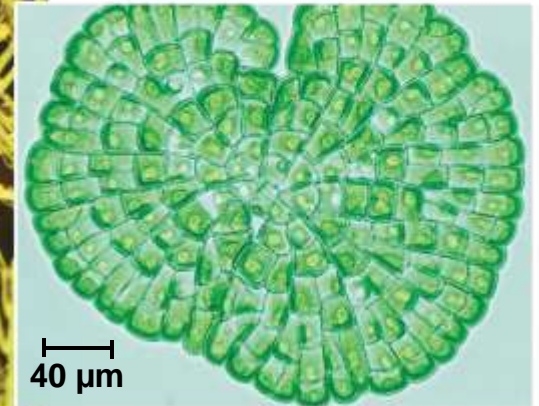
- 3) Structure of flagellated sperm
 - In those species of land plants that have flagellated sperm, the structure of this sperm closely resembles that of charophyte sperm
- 4) Formation of a **phragmoplast**
 - Certain details of cell division occur only in land plants and certain charophytes
 - A group of microtubules known as the phragmoplast forms between the daughter nuclei of a dividing cell
 - A cell plate then develops in the middle of the phragmoplast at the midline of the dividing cell
 - This cell plate then gives rise to a new cross wall that separates the daughter cells

- There is also genetic evidence for the close relationship between land plants and charophytes
 - Comparisons of both nuclear and chloroplast genes point to charophytes, particularly *Chara* and *Coleochaete*, as the closest living relatives of land plants
- Note that land plants are not descended from modern charophytes, but share a common ancestor with modern charophytes



◀ *Chara* species, a pond organism

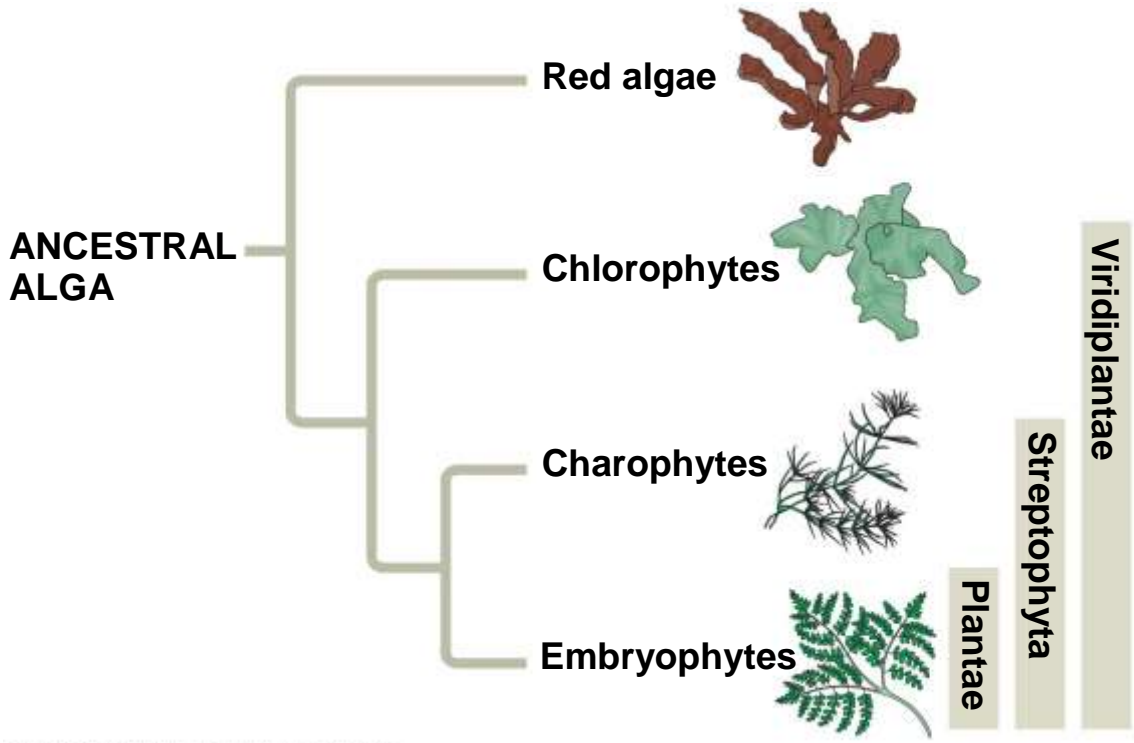
▼ *Coleochaete orbicularis*, a disk-shaped charophyte that also lives in ponds (LM)



Adaptations Enabling the Move to Land

- Many species of charophyte algae live in shallow water around the edges of lakes and ponds
 - In these environments, natural selection favors algae that can survive periods when they are not submerged in water
 - In charophytes, a layer of a durable polymer called **sporopollenin** prevents exposed zygotes from drying out
 - A similar chemical adaptation is found in the sporopollenin walls that encase plant spores
 - The accumulation of such traits by charophyte ancestors probably allowed their descendants to live permanently above the waterline
 - The movement onto land carried many benefits, including unfiltered sun, more plentiful CO₂, nutrient-rich soil, and few herbivores or pathogens
 - These benefits were also accompanied by challenges, including a scarcity of water and lack of structural support against gravity
- Land plants diversified as they evolved adaptations that meet these demands

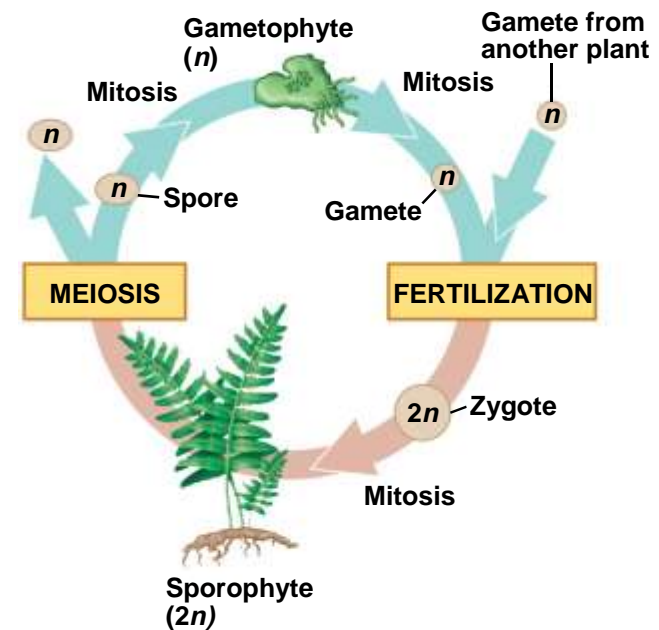
- Systematists are currently debating the boundaries of the plant kingdom
 - Many biologists include only embryophytes (plants with embryos) in kingdom Plantae
 - Some biologists think the plant kingdom should be expanded to include some or all green algae
- Until this debate is resolved, we will retain the embryophyte definition of kingdom Plantae



Derived Traits of Plants

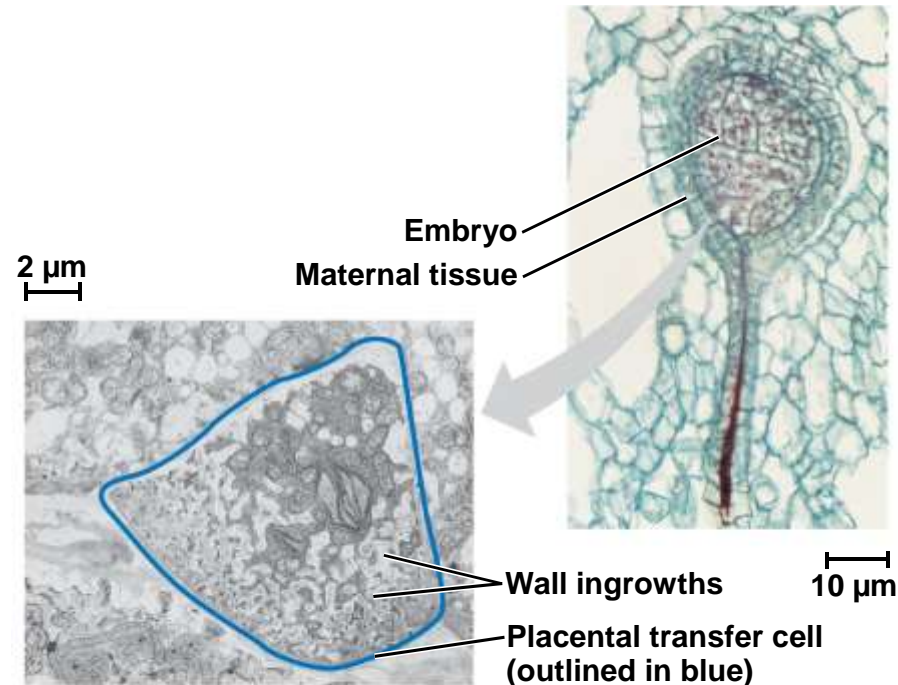
- Many adaptations facilitating survival and reproduction on dry land also emerged after land plants diverged from algae
 - Four key traits appear in nearly all land plants but are absent in the charophytes:
 - Alternation of generations (with multicellular, dependent embryos)
 - Walled spores produced in sporangia
 - Multicellular gametangia
 - Apical meristems
 - These characteristics are called derived traits since they were absent in the ancestor common to land plants and charophytes

- Plants alternate between two multicellular stages, a reproductive cycle called **alternation of generations**
 - The **gametophyte** (“**gamete-producing plant**”) is haploid and produces haploid gametes (egg and sperm) by mitosis
 - Fusion of these gametes gives rise to the diploid **sporophyte** (“**spore-producing plant**”), which produces haploid **spores** by meiosis
 - Spores are reproductive cells that can develop into a new haploid organism without fusing with another cell
 - Mitotic division of the spore cell produces a new multicellular gametophyte, and the cycle begins again
- In many seedless plants (ferns), the gametophyte and sporophyte look like different types of plants even though they are different forms of the same species
 - In seed plants, the gametophytes are microscopic, while the familiar plants we see are sporophytes



Alternation of generations

- As part of a life cycle with alternation of generations, the diploid multicellular embryo develops from zygotes that are retained within the tissue of the female parent (gametophyte)
 - This parental tissue provides the developing embryo with nutrients (sugars, amino acids)
 - Nutrients are transferred from parent to embryo through elaborate ingrowths of the cell wall and plasma membrane of **placental transfer cells**
 - These specialized cells are found in the embryo and are also sometimes present in adjacent maternal tissue
- Land plants are called **embryophytes** because of the dependency of the embryo on the parent



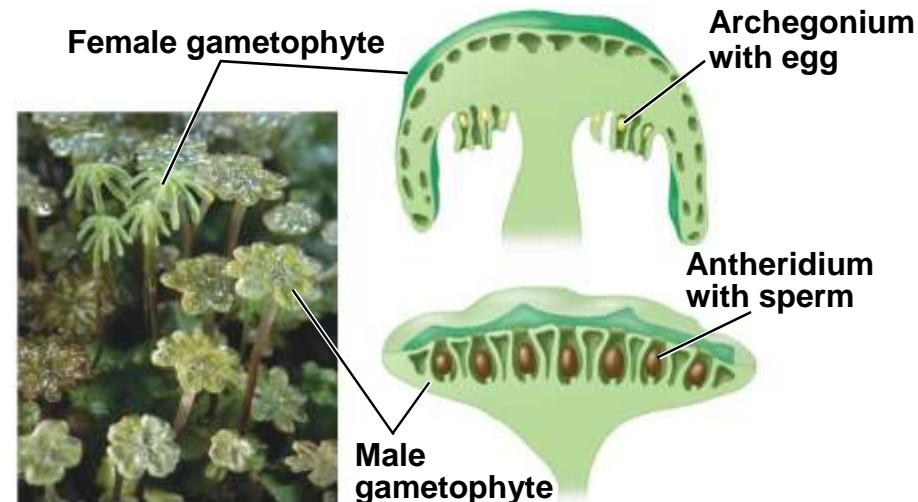
Embryo (LM) and placental transfer cell (TEM) of *Marchantia* (a liverwort)

- Multicellular sporangia that produce spores with sporopollenin-enriched walls are other key terrestrial adaptations of land plants
 - The polymer sporopollenin makes the walls of plant spores tough and resistant to harsh environments
 - This allows spores to be dispersed through dry air without harm
 - The spores of charophytes, which are flagellated and water-dispersed, lack sporopollenin
 - The sporophyte of land plants produces spores in organs called **sporangia**
 - Within the sporangium, diploid cells called **sporocytes** (spore mother cells) undergo meiosis to generate haploid spores
 - The outer tissues of the sporangium protect the developing spores until they are released into the air
 - Charophytes lack these multicellular sporangia



Sporophytes and sporangia of *Sphagnum* (a moss)

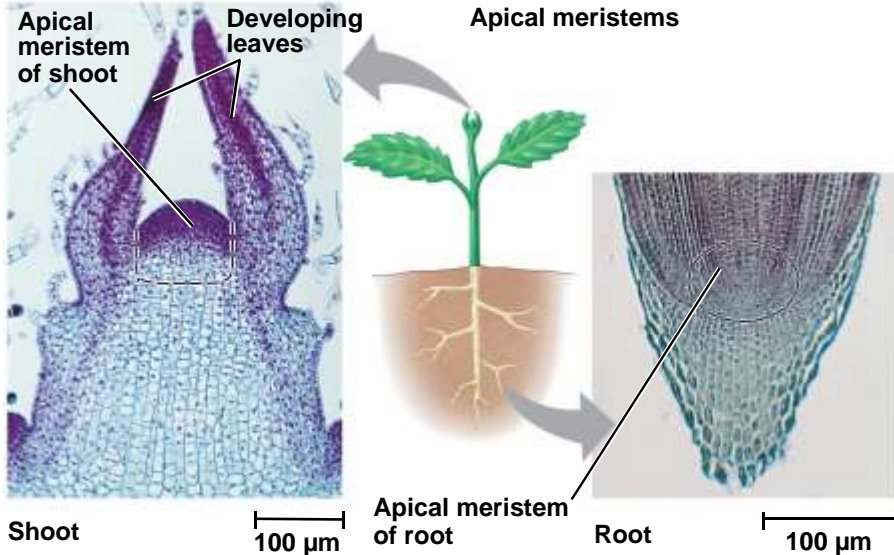
- Another distinguishing feature of early land plants is the production of gametes within multicellular organs called **gametangia**
 - Female gametangia, called **archegonia**, produce eggs and are the site of fertilization
 - This pear-shaped organ produces a single nonmotile egg that is retained within the bulbous part of the organ
 - After fertilization, the zygote develops into an embryo at this same location
 - Male gametangia, called **antheridia**, are the site of sperm production and release
 - In many modern plants, the sperm have flagella that allow them to swim to the eggs through water droplets or a film of water
- The gametophytes of seed plants have become so reduced in some lineages that the archegonia and antheridia have been lost



Archegonia and antheridia of *Marchantia* (a liverwort)

- Another derived trait of land plants is the evolution of the apical meristem, which helps plants sustain continual growth
 - Apical meristems are localized regions of cell division at the tips of roots and shoots
 - Elongation of these roots and shoots through cell division is important because this allows increased exposure to environmental resources
 - Ex) Light and CO₂ above ground; water and mineral nutrients in the soil

- Cells from the apical meristems differentiate into various tissues
 - Some differentiate into the outer epidermis and various types of internal tissues
 - Shoot apical meristems also generate leaves in most plants

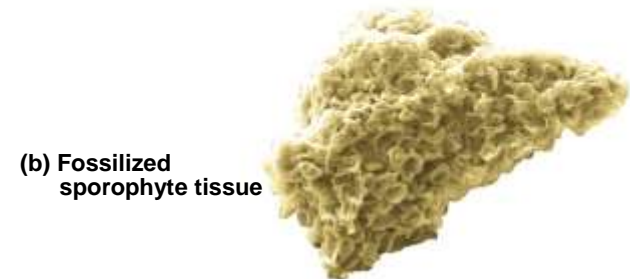
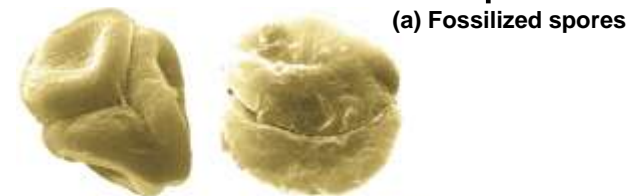


- Additional derived traits such as a **cuticle** evolved in many plant species
 - The cuticle consists of polyester and wax polymers and covers the epidermis of many species
 - It acts as waterproofing by helping prevent excessive water loss from the above-ground plant organs
 - In addition, the cuticle also provides some protection against microbial attack
- Another adaptation of early land plants was the formation of symbiotic associations with fungi that may have helped plants without true roots to obtain nutrients
 - These associations are called ***mycorrhizae***
 - Mycorrhizal fungi form extensive networks of filaments through the soil, allowing them to absorb nutrients more effectively than a plant can on its own
 - These fungi then transfer nutrients to their symbiotic plant partner

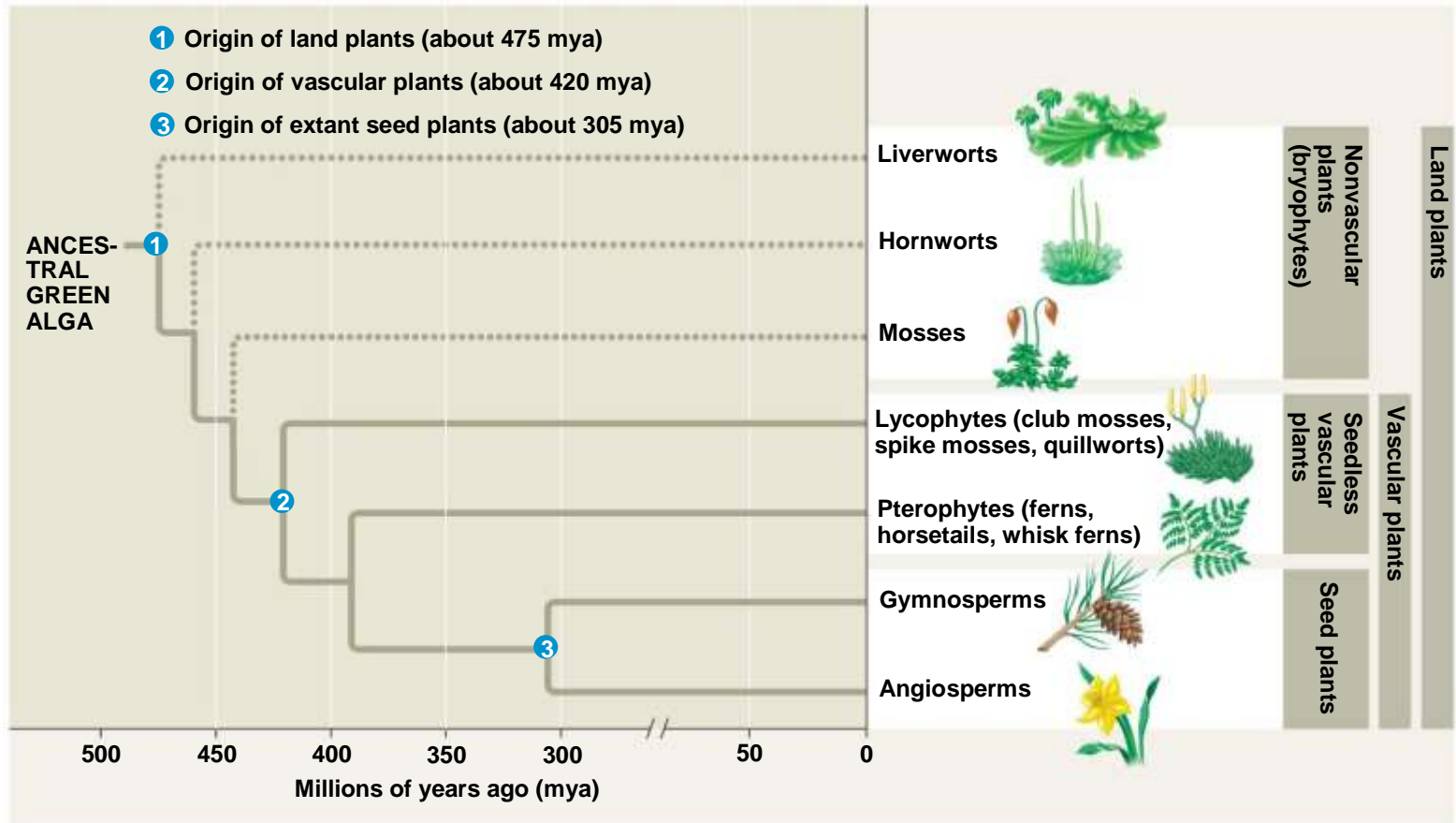
- A final derived trait of many land plants is their ability to produce molecules called ***secondary compounds***
 - Secondary compounds are the products of secondary metabolic pathways that branch off from the primary pathways used to produce the major groups of organic compounds (ex: lipids)
 - Secondary compounds include alkaloids, terpenes, tannins, and phenolics such as flavonoids
 - Terpenes, tannins, and alkaloids have a bitter taste, strong odor, or toxic effect that helps defend against herbivores and parasites
 - In addition, flavonoids absorb harmful UV radiation
 - Other phenolics help deter attack by pathogens
 - Humans have also benefited from these secondary compounds
 - Many of these substances are used in spices, medicines, and other products

The Origin and Diversification of Plants

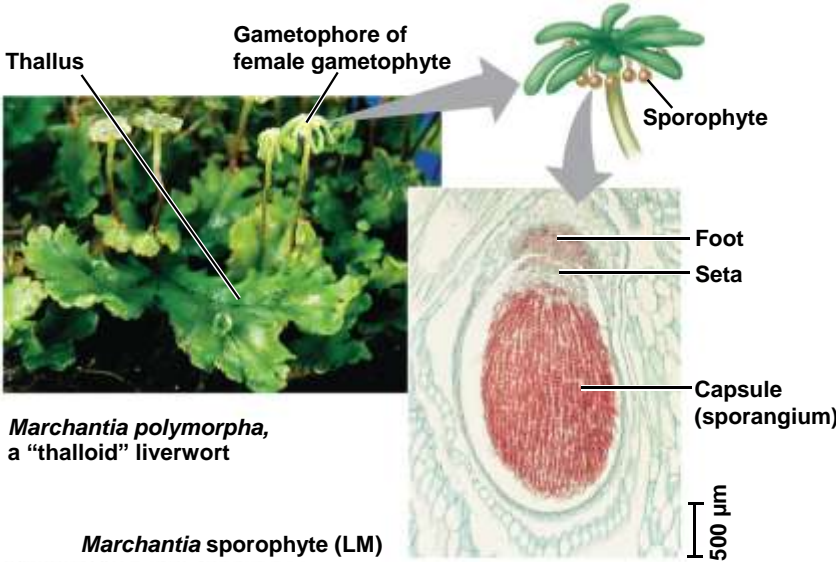
- Fossil evidence indicates that plants were on land at least 475 million years ago
 - Fossilized spores and tissues have been extracted from 475-million-year-old rocks
 - Although these fossil spores resemble those of living plants, they also have some striking differences
 - Whereas spores of modern plants are usually dispersed as single grains, fossil spores are fused together in groups of two or four
 - This difference raises the possibility that these fossil spores were not produced by plants but by some extinct algal relative
 - In 2003, however, scientists discovered some of these fossilized spores that were embedded in plant cuticle material similar to the spore-bearing tissue of living plants
 - After uncovering other small fragments of tissue that clearly belonged to plants, scientists concluded that these spores represent fossil plants rather than algae



- Those ancestral species of land plants gave rise to a vast diversity of modern plants
 - Modern plants can be informally grouped based on the presence or absence of **vascular tissue**
 - Most plants have vascular tissue and are therefore called **vascular plants**
 - Nonvascular plants, or those with very simple vascular tissue are commonly called **bryophytes**
 - Ex) Liverworts, hornworts, and mosses



- Liverworts belong to phylum Hepatophyta
 - This phylum’s common and scientific name (*hepaticus*=liver) refer to the liver-shaped gametophytes of its members
 - In medieval times, their shape was thought to be a sign that these plants could help treat liver diseases
 - Some liverworts (*Marchantia*) are described as “thalloid” because of the flattened shape of their gametophytes
 - Other liverworts (*Plagiochila*) are called “leafy” because their stemlike gametophytes have many leaflike appendages



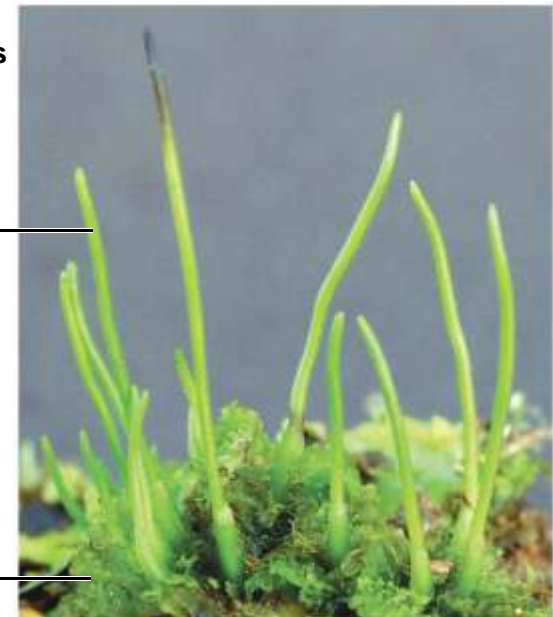
Plagiochila deltoidea, a “leafy” liverwort

- Hornworts belong to phylum Anthoceroophyta
 - This phylum’s scientific and common names (*keras*=horn) refer to the long, tapered shape of the sporophyte, which can grow to be ~5 cm high
 - Unlike liverwort and moss sporophytes, the hornwort sporophyte lack a seta and consists only of a sporangium
 - This sporangium releases mature spores by splitting open, starting at the tip of the horn
 - The gametophytes, which usually have multiple sporophytes attached, are ~1-2 cm in diameter and grow mostly horizontally
 - Hornworts have a symbiotic relationship with nitrogen-fixing cyanobacteria that allows them to colonize open areas with moist soils, where nitrogen is often in short supply

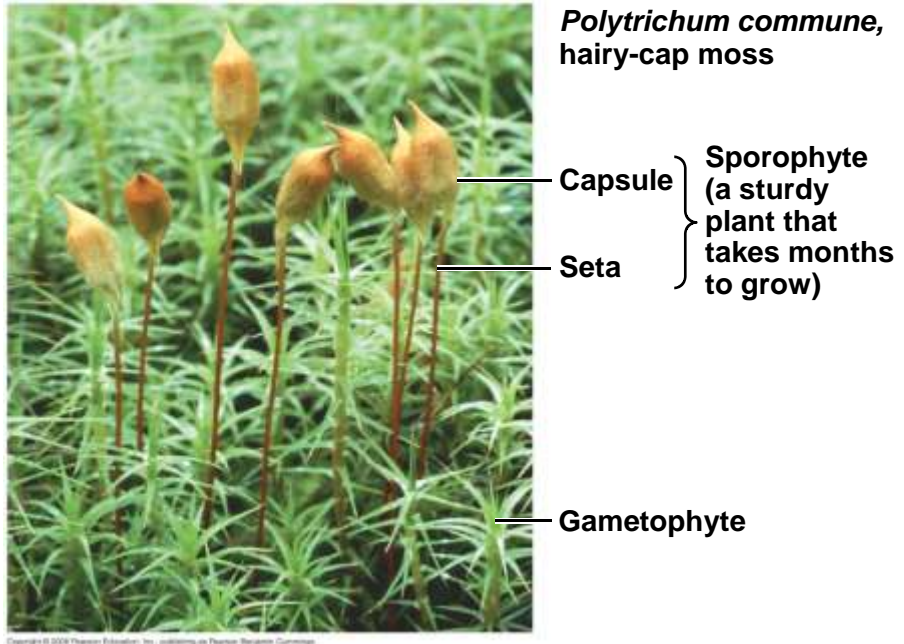
An *Anthoceros*
hornwort species

Sporophyte

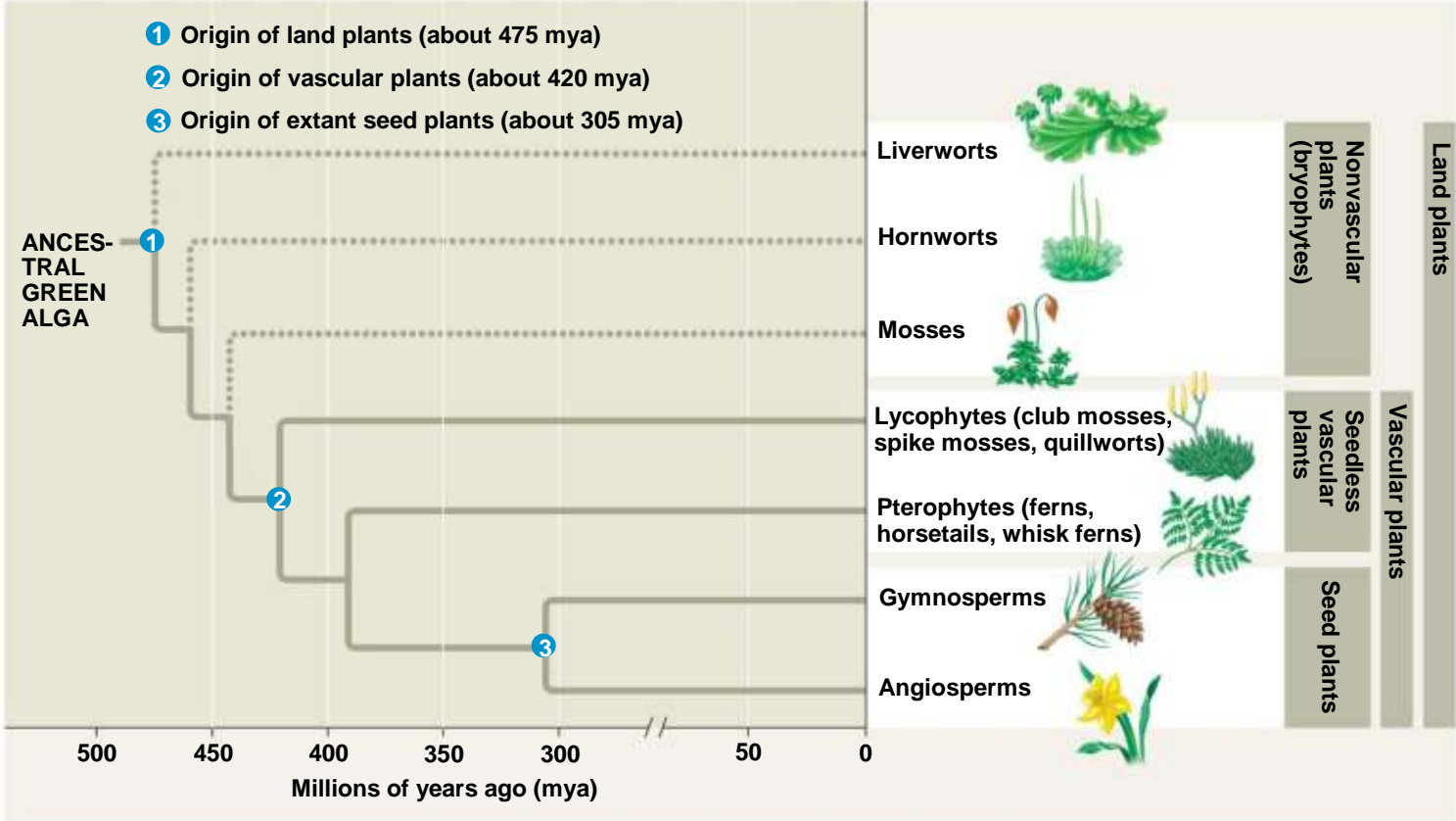
Gametophyte



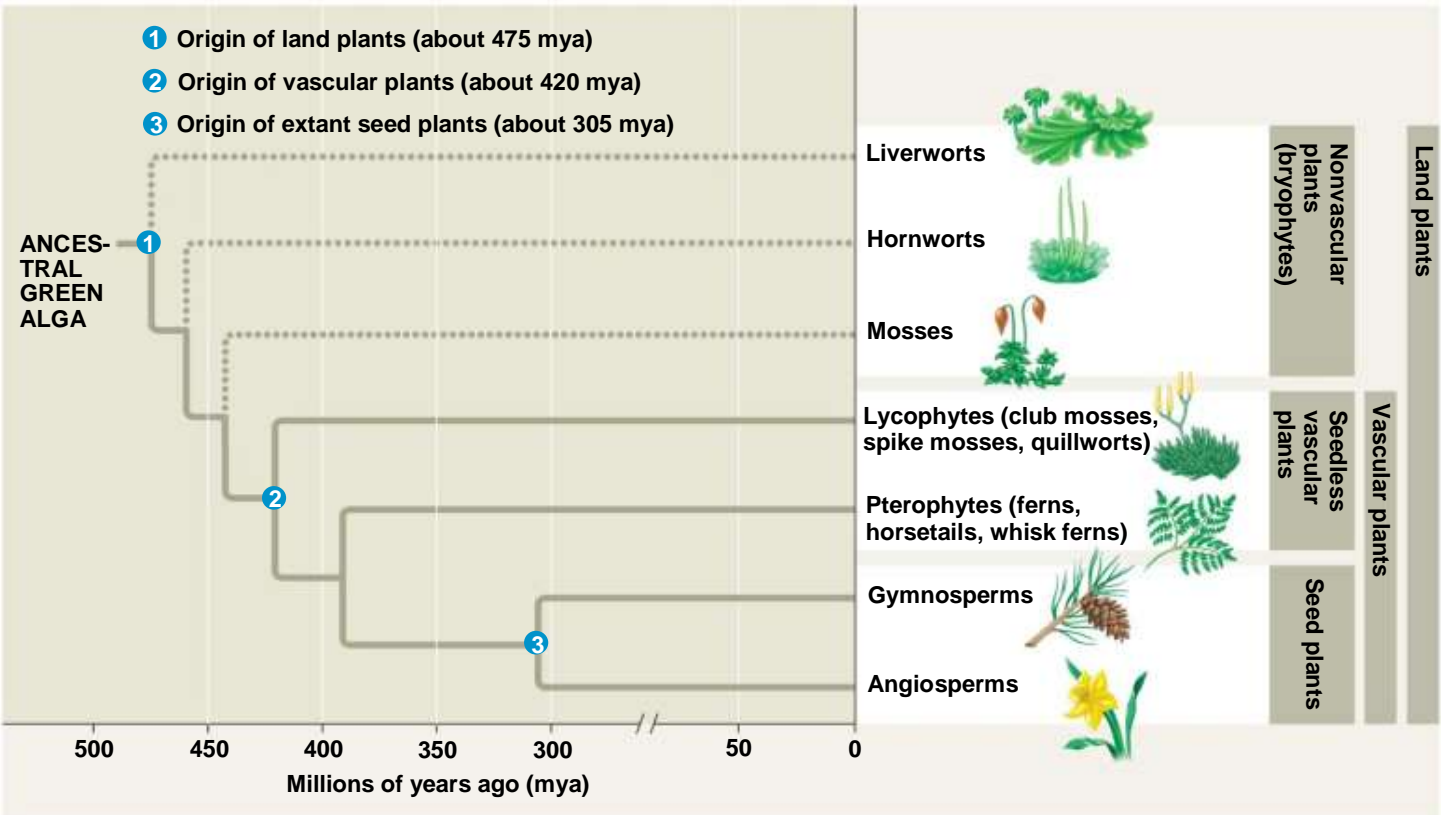
- Mosses belong to phylum Bryophyta
 - Moss gametophytes range in height from less than 1 millimeter to about 2 meters, with an average of less than 15 cm in most species
 - The familiar “carpet” of moss you observe consists mainly of gametophytes
 - Moss sporophytes are usually elongated and visible to the naked eye, with heights ranging to up to ~20 cm
 - These sporophytes are green and photosynthetic when young
 - As they prepare to release spores, however, these sporophytes turn tan or brownish red



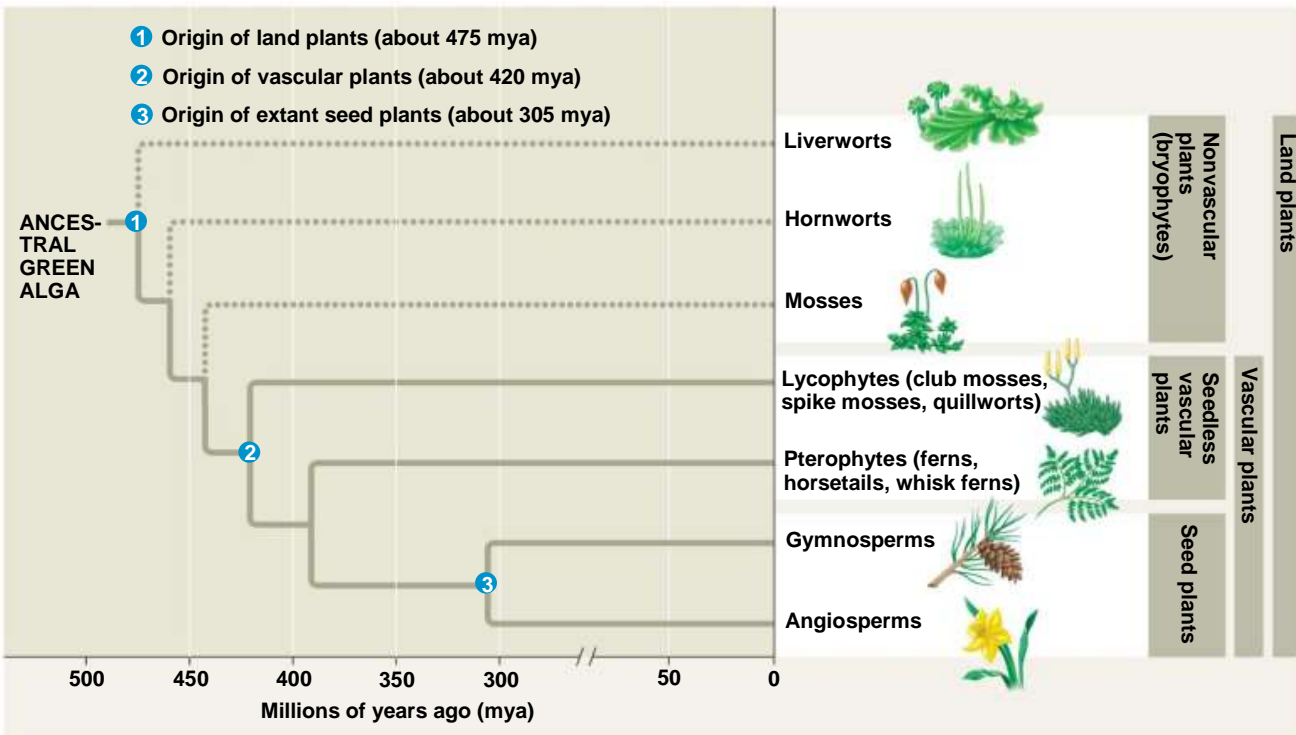
- Although debate remains as to whether bryophytes form a monophyletic group, they do share some derived traits with vascular plants
 - Ex) Multicellular embryos and apical meristems
- Bryophytes nonetheless lack many innovations of vascular plants
 - Ex) Roots and true leaves



- Vascular plants, which form a clade that includes ~93% of all plant species, can be further categorized:
 - Two of these clades include plants that lack seeds, which are known as **seedless vascular plants**
 - **Lycophytes** (club mosses and their relatives)
 - **Pterophytes** (ferns and their relatives)

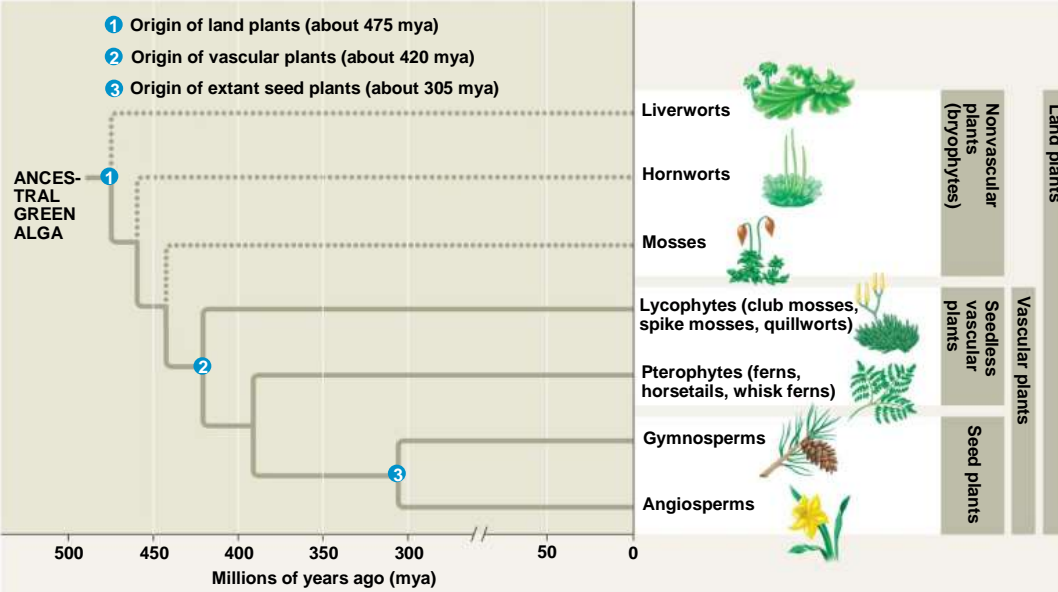


- Seedless vascular plants are paraphyletic and are therefore sometimes referred to as a **grade**
 - A grade is a collection of organisms that share a common level of biological organization or adaptation (lack of seeds)
 - Although grades can be informative by grouping organisms according to key biological features, they can also be misleading
- Ex) Pterophytes share a more recent common ancestor with seed plants than with lycophytes, meaning they have derived traits not found in lycophytes



- A third clade of vascular plants, representing the majority of living plant species, consists of seed plants
 - A **seed** is an embryo and nutrients surrounded by a protective coat
- Seed plants form a clade and can be divided into further clades based on the presence or absence of enclosed chambers in which seeds mature:
 - **Gymnosperms** (“naked seed” plants, including the conifers) contain seeds that are not enclosed in chambers
 - **Angiosperms** (flowering plants) have seeds that develop inside chambers called ovaries that originate inside flowers and mature into fruit

- Nearly 90% of all living plant species are angiosperms



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Table 29.1 Ten Phyla of Extant Plants

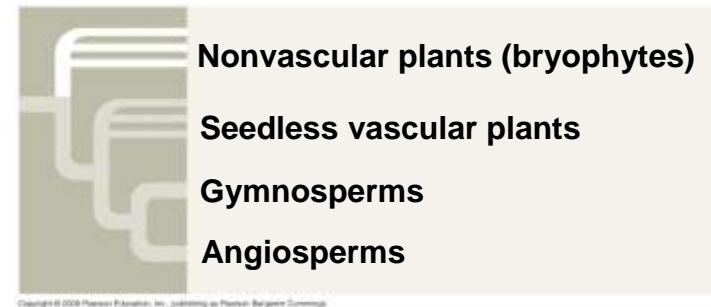
	Common Name	Estimated Number of Species
Nonvascular Plants (Bryophytes)		
Phylum Hepatophyta	Liverworts	9,000
Phylum Anthoceroophyta	Hornworts	100
Phylum Bryophyta	Mosses	15,000
Vascular Plants		
Seedless Vascular Plants		
Phylum Lycophyta	Lycophytes	1,200
Phylum Pterophyta	Pterophytes	12,000
Seed Plants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

Concept Check 29.1

- 1) Why do researchers identify charophytes rather than another group as the closest relatives of land plants?
- 2) Identify 3 derived traits that distinguish plants from charophytes *and* facilitate life on land. Explain.
- 3) 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.

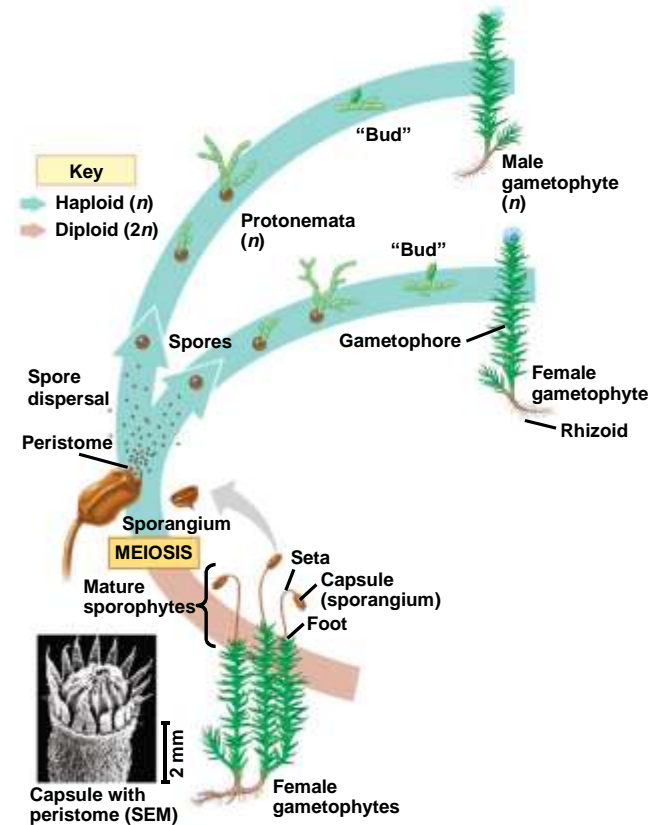
Concept 29.2: Mosses and other nonvascular plants have life cycles dominated by gametophytes

- Bryophytes are represented today by three phyla of small herbaceous (nonwoody) plants:
 - **Liverworts**, phylum Hepatophyta
 - **Hornworts**, phylum Anthoceroophyta
 - Liverworts and hornworts are named for their shapes, plus the suffix *wort* meaning “herb”
 - **Mosses**, phylum Bryophyta
 - Mosses are most closely related to vascular plants
- Note that the terms *bryophyte* and *Bryophyta* are not synonymous
 - Bryophyta is the formal taxonomic name for the phylum consisting only of mosses
 - The term bryophyte is used informally to refer to all nonvascular plants, including liverworts, hornworts, and mosses



Bryophyte Gametophytes

- Unlike in vascular plants, gametophytes are larger and longer-living than sporophytes in all three bryophyte phyla
 - Sporophytes are typically present only part of the time
- When dispersed to a favorable habitat, bryophyte spores germinate and grow into gametophytes
 - Germinating moss spores produce a mass of green, branched, one-cell-thick filaments called **protonemata**
 - A protonema has a large surface area that enhances absorption of water and minerals
 - In favorable conditions, this protonema produces one or more bud-like growths with apical meristems
 - These apical meristems generate a gamete-producing structure known as a gametophore (“gamete-bearer”)
 - Together, a protonema and one or more of its gametophores make up the body of a moss gametophyte

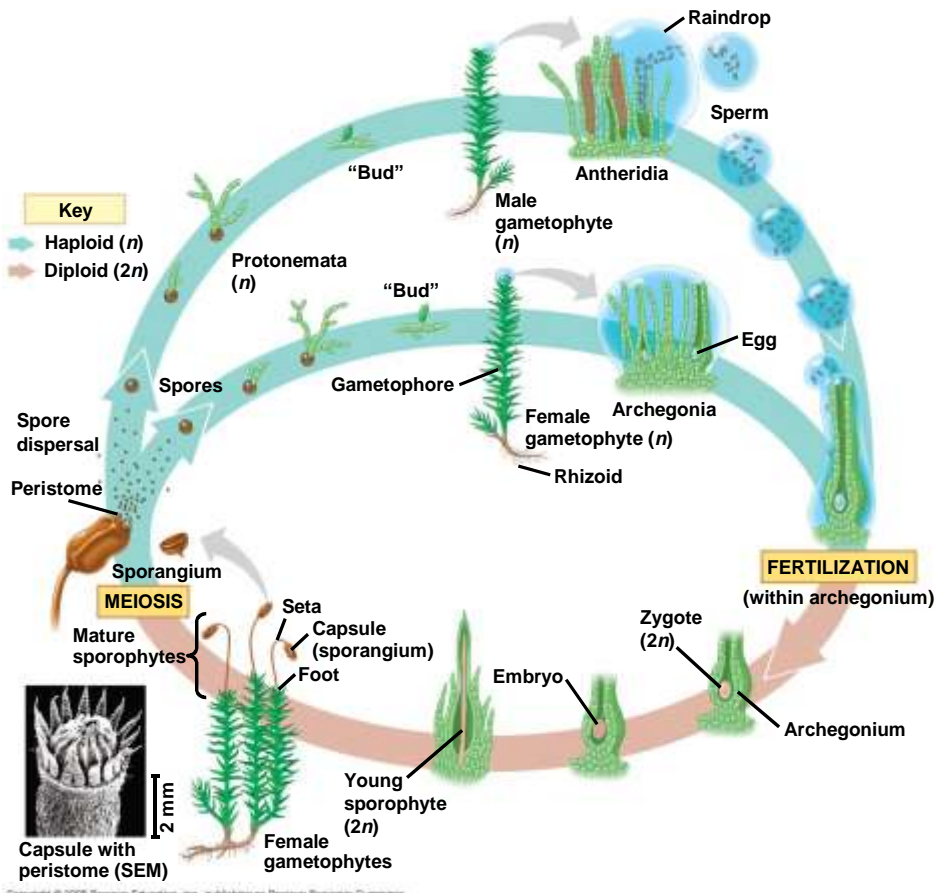


- Bryophyte gametophytes usually take the form of ground-hugging carpets because their body parts are too thin to support a tall plant
 - A second constraint on the height of many bryophytes is the absence of vascular tissue which would normally enable long-distance transport of water and nutrients
 - The thin structure of bryophyte organs makes it possible to instead distribute materials without specialized vascular tissue
 - Some mosses, however, have conducting tissue in the center of their “stems,” allowing them to grow as tall as 2 meters
 - Phylogenetic analyses indicate that these conducting tissues, though similar to those of vascular plants, arose independently by convergent evolution

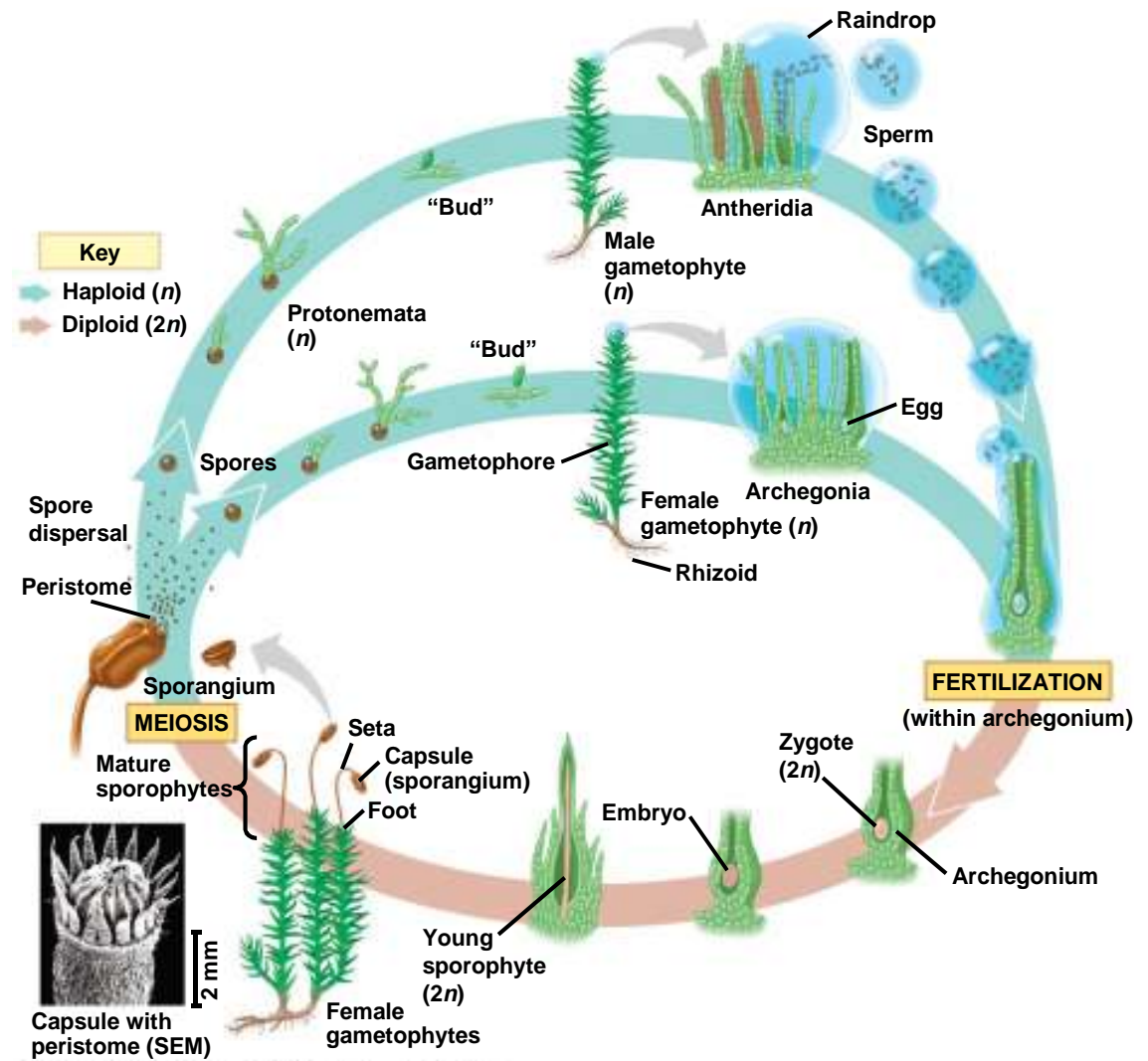
- Bryophyte gametophytes are anchored by delicate structures called **rhizoids**
 - Rhizoids, unlike roots, that lack specialized conducting cells and thus do not play a major role in water and mineral absorption
- Mature gametophytes form one or more gametangia that produce gametes and are covered by protective tissue

- Nonmotile eggs are produced singly in the pear-shaped archegonia, whereas each antheridium produces many flagellated sperm

- Some bryophyte gametophytes are bisexual, but in mosses, the male and female gametangia are typically carried on separate gametophytes



- Sperm swim through a film of water to reach and fertilize the egg within the base of the archegonia
 - Because sperm require water to reach the egg, many bryophyte species are found in moist habitats
- The resulting embryo is retained within the archegonia
- As it develops into a sporophyte, layers of placental transfer cells help transport nutrients to the embryo

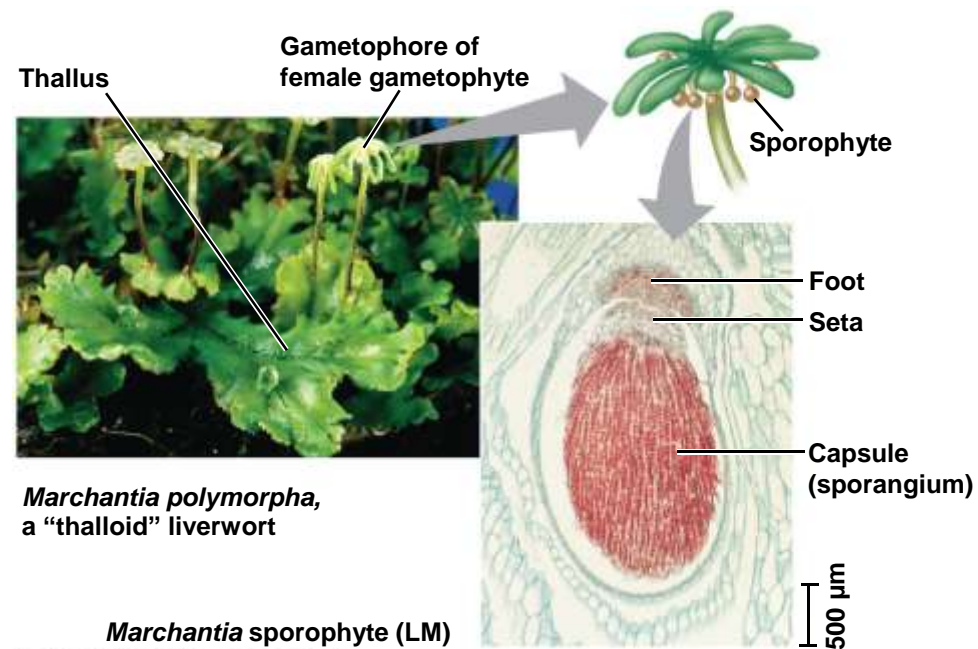


Animation: Moss Life Cycle



Bryophyte Sporophytes

- Although bryophyte sporophytes are usually green and photosynthetic when young, they cannot live independently of their parental gametophytes, which supply them with sugars, amino acids, minerals, and water
 - Bryophyte sporophytes are the smallest and simplest sporophytes of all extant plant groups
- A typical bryophyte sporophyte consists of:
 - A **foot** embedded in the archegonium that absorbs nutrients from the gametophyte
 - A **seta** (stalk) that conducts these materials to the sporangium
 - The seta of most mosses becomes elongated to enhance spore dispersal by elevating the sporangium
 - A sporangium, also called a **capsule**, which uses the nutrients to produce spores by meiosis



Bryophyte Sporophytes

- Newly-produced spores are discharged through a ring of interlocking, tooth-like structures on the upper part of the capsule called **peristomes**
 - These “teeth” open under dry conditions and close again when it is moist, allowing spores to be discharged gradually via periodic gusts of wind
- Hornwort and moss sporophytes are larger and more complex than those of liverworts
 - Both have specialized pores called **stomata** for gas (O_2 and CO_2) exchange between the outside air and the sporophyte interior
 - Stomata are also found in vascular plants

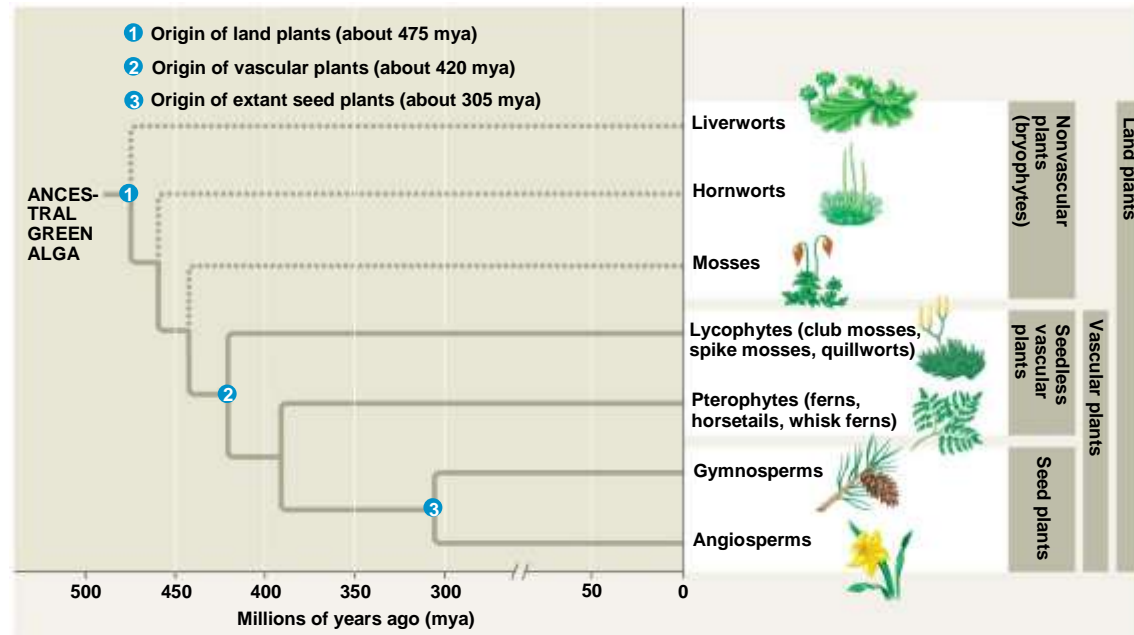
g. 20.100
An *Anthoceros*
hornwort species

Sporophyte

Gametophyte



- The presence of these stomata suggests 3 possible hypotheses for their evolution:
 - If liverworts are the deepest-branching lineage of land plants:
 - Then stomata may have evolved only once, in the common ancestor of hornworts, mosses, and vascular plants
 - If hornworts and mosses are the deepest-braching lineage or if bryophytes are monophyletic:
 - Then stomata may have evolved once in a common ancestor to all nonvascular plants and then been lost in the liverwort lineage
 - If hornworts are the deepest-branching lineage and mosses are the closest relatives of vascular plants:
 - Then hornworts may have acquired stomata independently of mosses and vascular plants



The Ecological and Economic Importance of Mosses

- Wind dispersal of lightweight spores has distributed mosses throughout the world
 - These plants are most common and diverse in moist forests and wetlands
 - Some mosses are capable of colonizing bare, sandy soil, where they help retain nitrogen in the soil
 - Still other mosses are capable of inhabiting extreme environments
 - Ex) Mountaintops, tundra, desert

- One wetland moss genus, *Sphagnum*, or “peat moss,” is especially widespread, forming extensive deposits of partially decayed organic material known as **peat**
 - The boggy regions dominated by this moss, called peatlands, inhibit decay of moss and other organisms due to their low temperature, pH, and oxygen levels
 - Peat has also been used as a fuel source and as a soil conditioner for packing plant roots during shipment
 - Peat moss has large dead cells that can absorb ~20X the moss’s weight in water
 - *Sphagnum* is also an important global reservoir of organic carbon and may help stabilize atmospheric CO₂ concentrations



(a) Peat being harvested



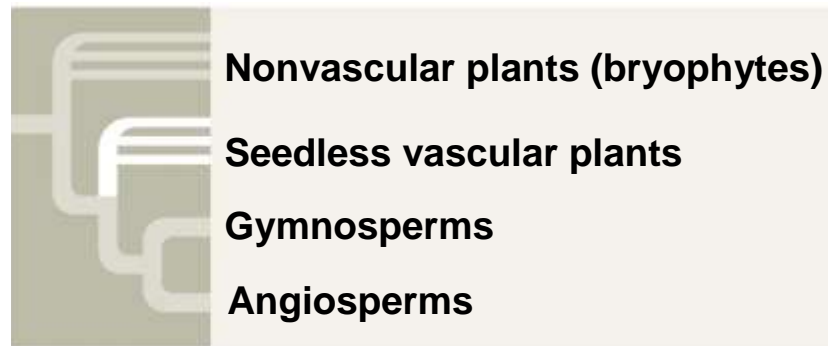
(b) “Tollund Man,” a bog mummy

Concept Check 29.2

- 1) How do bryophytes differ from other plants?
- 2) Give 3 examples of how structure fits function in bryophytes.
- 3) For each hypothesis of stomatal evolution, label each gain and loss of stomata on the phylogenetic tree in Figure 29.7 (pp. 605).

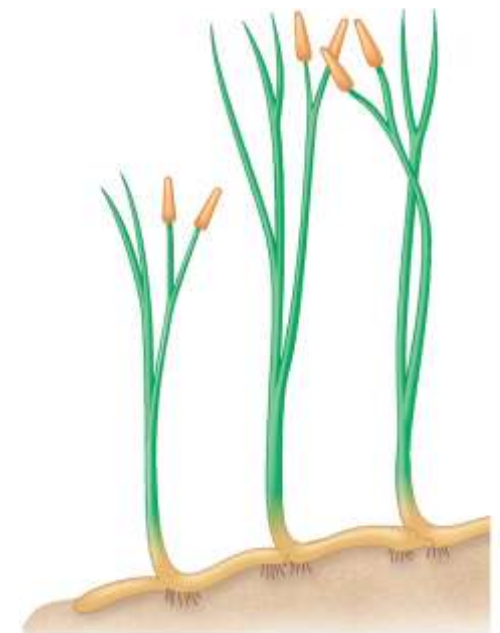
Concept 29.3: Ferns and other seedless vascular plants were the first plants to grow tall

- Bryophytes and bryophyte-like plants were the prevalent vegetation during the first 100 million years of plant evolution
 - Vascular plants began to diversify during the Devonian and Carboniferous periods
 - Fossils show that lycophytes, ferns, and other seedless vascular plants had well-developed vascular systems by the Devonian
 - Vascular tissue allowed these plants to grow taller than their bryophyte counterparts
- As is the case with nonvascular plants, however, seedless vascular plants also have flagellated sperm and are usually restricted to moist environments



Origins and Traits of Vascular Plants

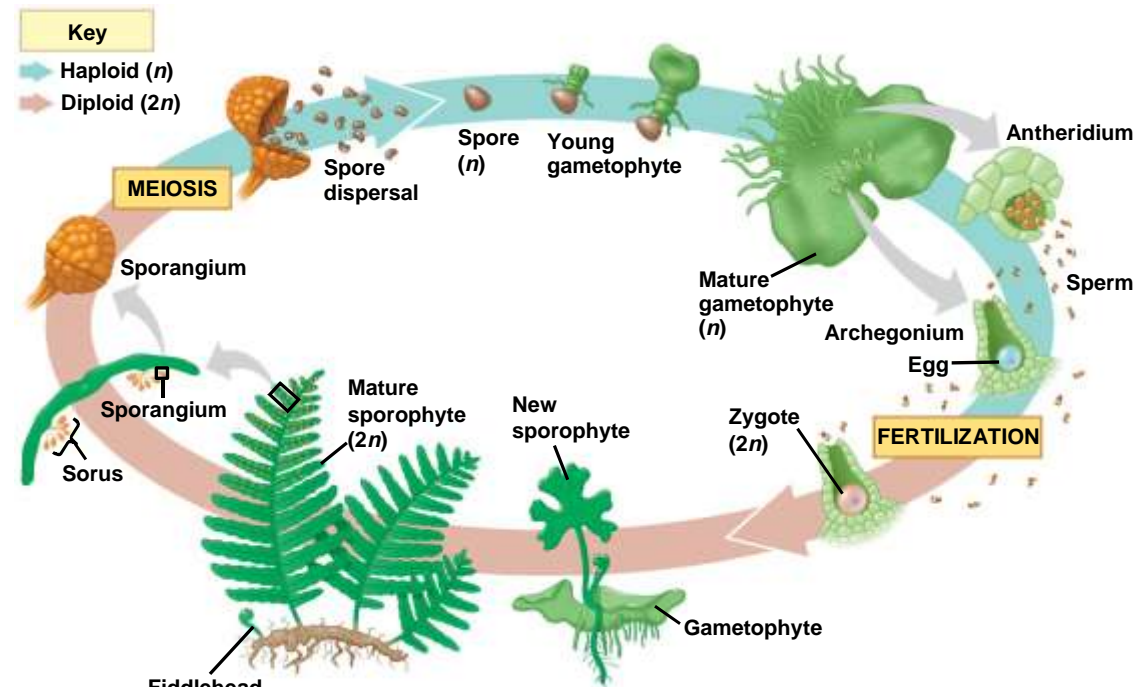
- Fossils of the vascular plants date back about 420 million years
 - Unlike nonvascular plants, these early tiny plants had branching sporophytes that were not dependent on the gametophyte for nutrition
 - This branching made possible more complex bodies with multiple sporangia
 - As their bodies became increasingly complex, competition for space and sunlight probably increased, stimulating even more evolution in vascular plants
- Living vascular plants have certain key derived traits:
 - Life cycles with dominant sporophytes
 - Vascular tissues called xylem and phloem
 - Well-developed roots and leaves



Sporophytes of *Aglaophyton major*

Life Cycles with Dominant Sporophytes

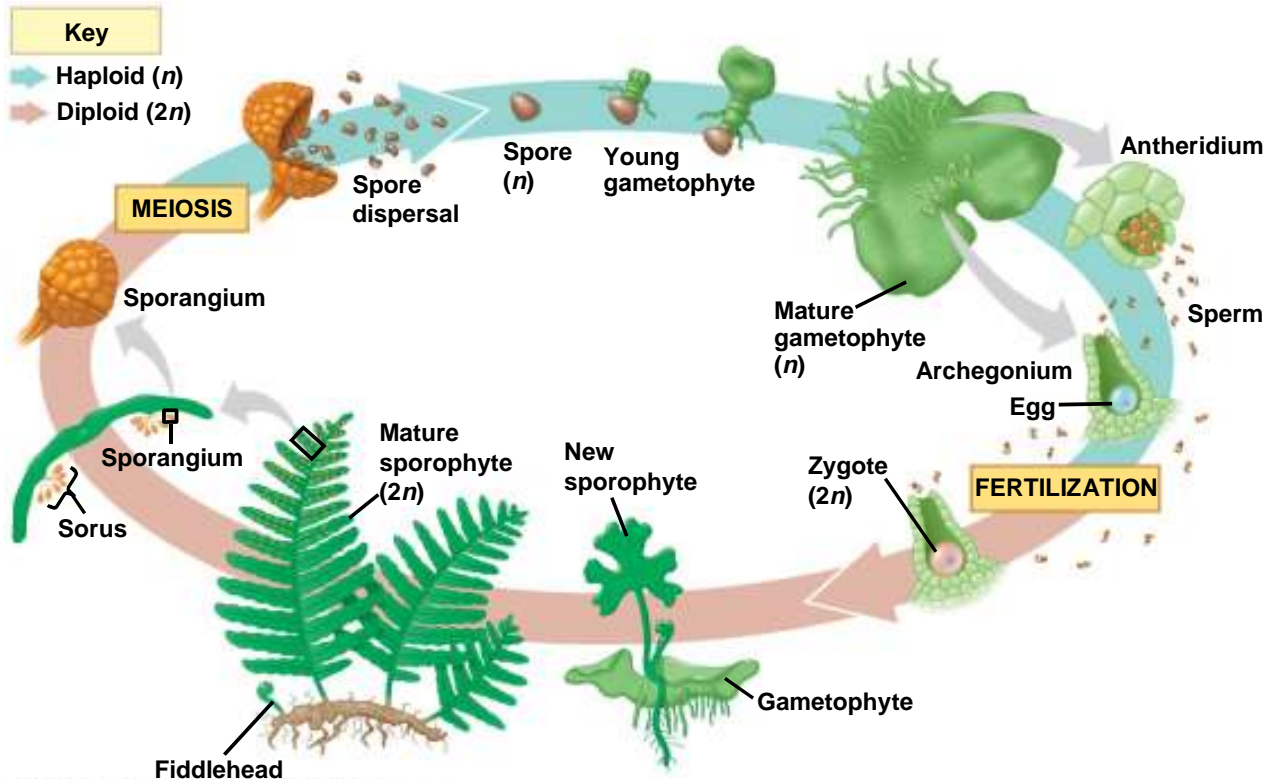
- Fossils suggest that the ancestors of vascular plants had gametophytes and sporophytes that were about equal in size
 - Among living vascular plants, however, the sporophyte (diploid) generation is the large and more complex plant in the alternation of generations
 - Ex) The familiar leafy plants in fern are sporophytes
- The gametophytes are tiny plants that grow on or below the soil surface



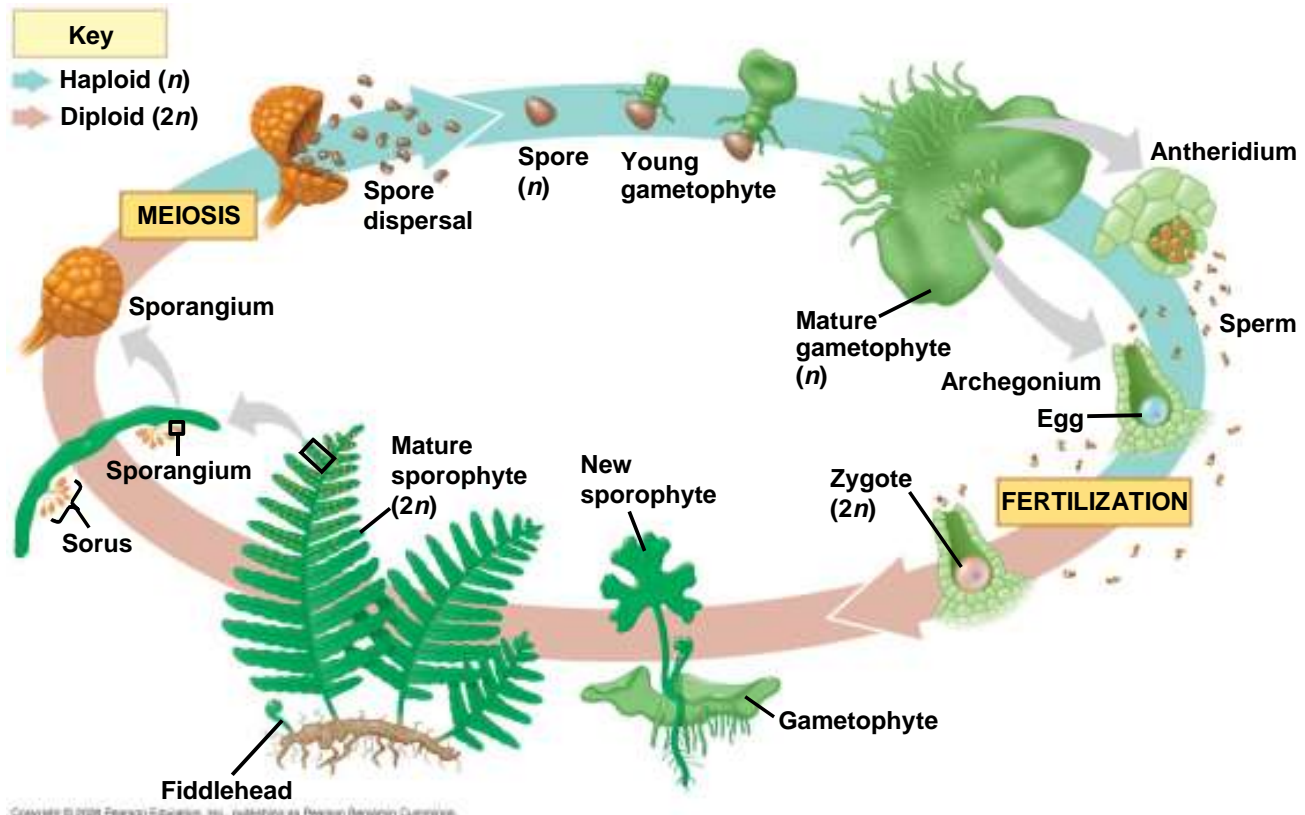
PLAY

Animation: Fern Life Cycle

- 1) Sporangia release spores
 - Most fern species produce a single type of spore that develops into a bisexual photosynthetic gametophyte
- 2) A variety of mechanisms promote cross-fertilization between gametophytes
- 3) Sperm use flagella to swim from the antheridia to eggs in the archegonia



- 4) A zygote develops into a new sporophyte
 - The young plant grows out from the archegonium of its parent (the gametophyte)
- 5) Spots called sori are located on the underside of the sporophyte's reproductive leaves
 - Each sorus is a cluster of sporangia



Transport in Xylem and Phloem

- Vascular plants have two types of vascular tissue: xylem and phloem
 - **Xylem** conducts most of the water and minerals and includes dead cells called **tracheids**
 - These tube-shaped cells carry water and minerals up from the roots
 - Because nonvascular plants lack these tracheids, vascular plants are sometimes referred to as tracheophytes
 - The water-conducting cells in vascular plants are *lignified*, meaning that their cell walls are strengthened by a phenolic polymer called **lignin**
 - The tissue called **phloem** consists of living cells arranged into tubes that distribute sugars, amino acids, and other organic products

- Lignified vascular tissue permitted vascular plants to grow tall
 - Their stems were strong enough to provide support against gravity,
 - They also had the ability to transport water and mineral nutrients high above ground
- Growing tall was a major evolutionary innovation in that tall plants could shade other plants
 - This reduced their access to sunlight needed for photosynthesis, giving vascular plants a competitive edge over nonvascular plants
 - Taller growth forms have thus been favored by natural selection, which led to the formation of treelike plants in the 1st forests ~370 mya

Evolution of Roots

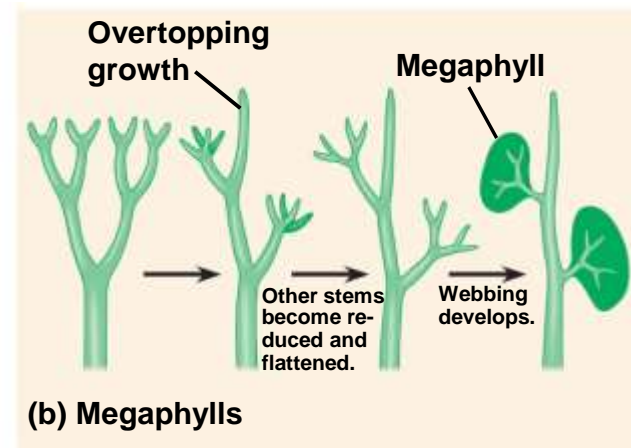
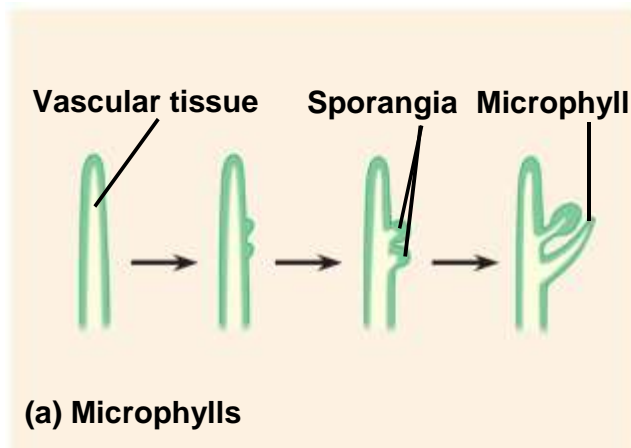
- Lignified vascular tissue also provided benefits below the ground
 - Instead of the rhizoids seen in bryophytes, roots evolved in almost all vascular plants
 - **Roots** are organs that absorb water and nutrients from the soil and anchor vascular plants
 - Root tissues of living plants closely resemble stem tissues of early vascular plant fossils
 - This suggests that roots may have evolved from the lowest belowground (subterranean) portion of stems in ancient vascular plants
- It remains unclear whether roots evolved only once in the common ancestor of all vascular plants or independently in different lineages
 - Fossil evidence hints at convergent evolution
 - Ex) The oldest lycophyte fossils already displayed simple roots 400 mya, during which time the ancestors of ferns and seed plants still had none

Evolution of Leaves

- **Leaves** are organs that increase the surface area of vascular plants, thereby capturing more solar energy that is used for photosynthesis
 - Leaves are categorized in terms of size and complexity:
 - **Microphylls**: small, usually spine-shaped leaves with a single vein
 - Microphylls are found only in the oldest lineage of modern vascular plants – the lycophytes
 - **Megaphylls**: leaves with a highly branched vascular system
 - Megaphylls support greater photosynthetic productivity than microphylls as a result of the greater surface area served by their network of veins

Evolution of Leaves

- Microphylls first appear in the fossil record 410 mya, but megaphylls do not emerge until ~370 mya
 - According to one model of evolution, microphylls evolved first, as outgrowths of stems
 - Megaphylls, in contrast, may have evolved from a series of branches lying close together on a stem
 - As one of these branches grew above (overtop) the others, the lower branches became flattened and developed webbing that joined them together
 - These joined branches thus became a leaf attached to a branch that overtopped them

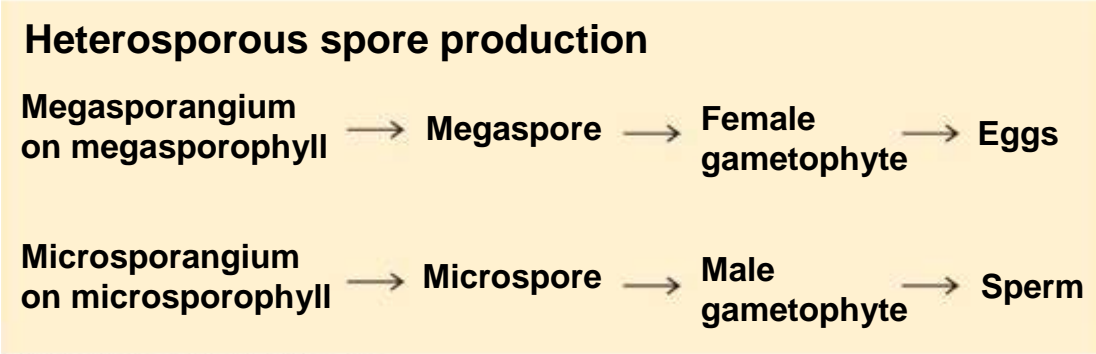
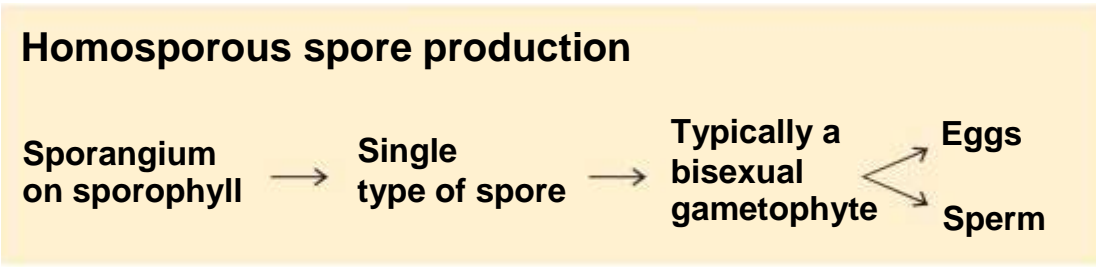


Sporophylls and Spore Variations

- One milestone in the evolution of plants was the emergence of sporophylls
 - **Sporophylls** are modified leaves containing sporangia
 - Sporophylls vary in structure:
 - Fern sporophylls produce clusters of sporangia known as **sori**, usually on the undersides of the sporophylls
 - In many lycophytes and most gymnosperms, groups of sporophylls form cone-like structures called **strobili**

- Most seedless vascular plants are **homosporous**, meaning they have one type of sporangium that produces one type of spore
 - This spore usually develops into a bisexual gametophyte
- In contrast, all seed plants and some seedless vascular plants are **heterosporous**
 - Heterosporous species have two types of sporangia and thus produce two kinds of spores
 - Megasporangia on megasporophylls produce **megaspores** that develop into female gametophytes

- Microsporangia on microsporophylls produce **microspores** that develop into male gametophytes

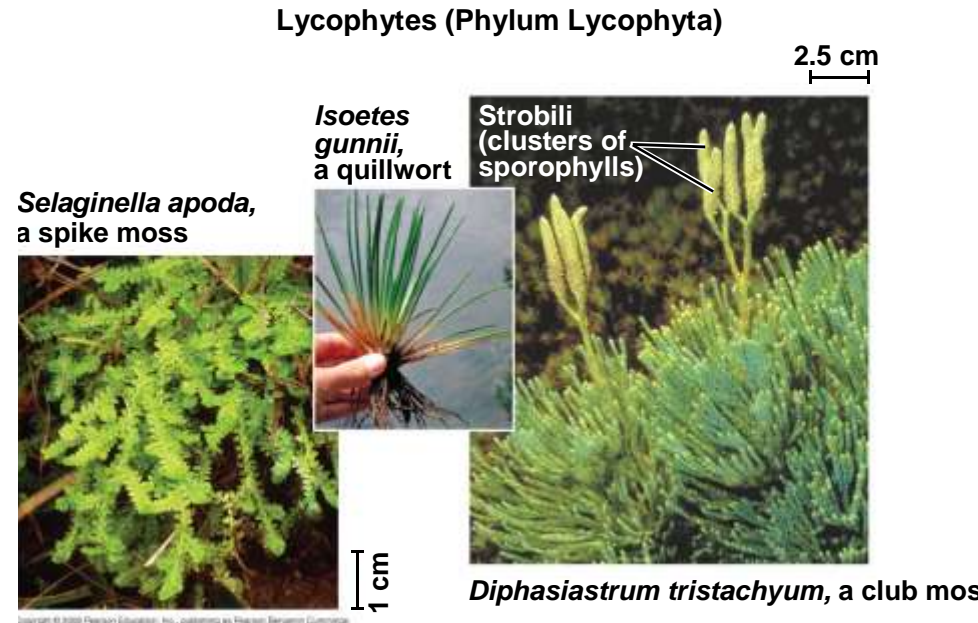


Classification of Seedless Vascular Plants

- There are two phyla of seedless vascular plants:
 - Phylum Lycophyta (lycophytes) includes club mosses, spike mosses, and quillworts
 - Phylum Pterophyta (pterophytes) includes ferns, horsetails, and whisk ferns and their relatives
 - Because the pterophytes differ greatly in appearance, they have long been considered separate phyla
 - Phylum Pterophyta: ferns
 - Phylum Sphenophyta: horse-tails
 - Phylum Psilophyta: whisk ferns
 - Recent molecular comparisons, however, provide convincing evidence that all 3 groups form a single clade

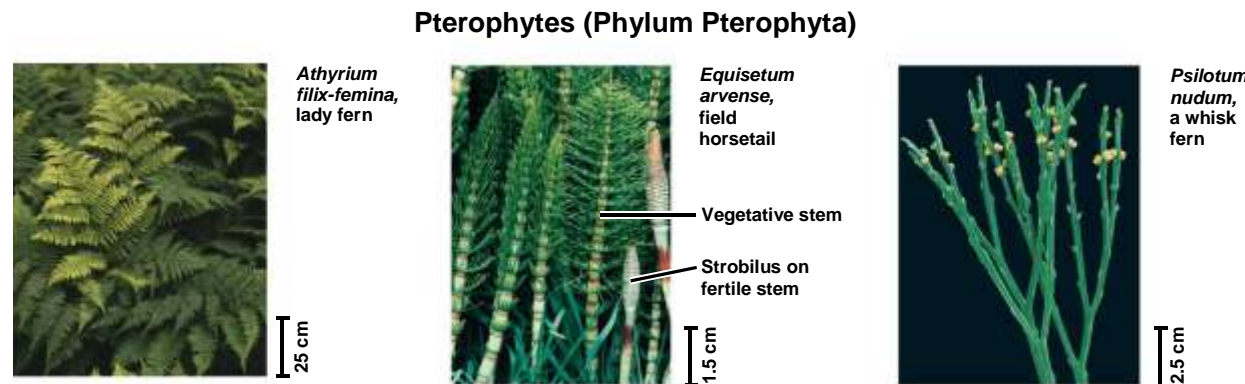
Phylum Lycophyta: Club Mosses, Spike Mosses, and Quillworts

- There were two lineages of lycophytes during the Carboniferous
 - One consisted of giant woody treelike plants with diameters of more than 2 meters and heights of more than 40 meters
 - These giant lycophytes thrived for millions of years in moist swamps but became extinct when the Earth's climate became drier at the end of the Carboniferous
 - The other consisted of small herbaceous plants
 - The small lycophytes survived and today represent 1,200 species
- Club mosses and spike mosses, even though they are called “mosses,” have vascular tissues and are therefore not true mosses



Phylum Pterophyta: Ferns, Horsetails, and Whisk Ferns and Relatives

- Ferns are the most diverse seedless vascular plants, with more than 12,000 species
 - They are most diverse in the tropics but also thrive in temperate forests
- Horsetails were diverse during the Carboniferous period, but are now restricted to the genus *Equisetum*
 - This genus contains only ~15 species, and its members are found widely distributed along streams and marshy places
- Whisk ferns resemble ancestral vascular plants but are closely related to modern ferns
 - These plants are the only vascular plants lacking true roots, which were probably lost in the course of evolution
 - Today, these plants absorb water and nutrients through numerous absorptive rhizoids



The Significance of Seedless Vascular Plants

- The ancestors of modern lycophytes, horsetails, and ferns grew to great heights during the Devonian and Carboniferous, forming the first forests
- With the evolution of vascular tissue, roots, and leaves, these plants increased their rate of photosynthesis, which removed large amounts of CO₂ from the atmosphere
 - This may have helped produce the global cooling at the end of the Carboniferous period that resulted in widespread glacier formation
- The decaying plants of these Carboniferous forests eventually became coal, which was crucial to the Industrial Revolution
 - Dead plants did not completely decay in the stagnant waters of the Carboniferous, turning the organic material into thick layers of peat
 - This peat was later covered by the sea, and a combination of marine sediment, heat, and pressure converted the peat to coal



Concept Check 29.3

- 1) List the key derived traits that are found in pterophytes and seed plants, but not in lycophytes.
- 2) How do the main similarities and differences between seedless vascular plants and nonvascular plants influence function in these plants?
- 3) If (contrary to current evidence) lycophytes and pterophytes formed a clade, what could you conclude about how members of this clade gained (or lost) traits shared by pterophytes and seed plants?

You should now be able to:

1. Describe four shared characteristics and four distinct characteristics between charophytes and land plants
2. Distinguish between the phylum Bryophyta and bryophytes
3. Diagram and label the life cycle of a bryophyte
4. Explain why most bryophytes grow close to the ground and are restricted to periodically moist environments

5. Describe three traits that characterize modern vascular plants and explain how these traits have contributed to success on land
6. Explain how vascular plants differ from bryophytes
7. Distinguish between the following pairs of terms: microphyll and megaphyll; homosporous and heterosporous
8. Diagram and label the life cycle of a seedless vascular plant