The Greening of Earth

- For much of Earth's history, the terrestrial surface was lifeless
- Cyanobacteria and protists likely existed on land 1.2 billion years ago
- Around 500 million years ago, small plants, fungi, and animals emerged on land

- Since colonizing land, plants have diversified into roughly 290,000 living species
- Land plants are defined as having terrestrial ancestors, even though some are now aquatic
- Land plants do not include photosynthetic protists (algae)
- Plants supply oxygen and are the ultimate source of most food eaten by land animals

Figure 29.1

Figure 29.1a

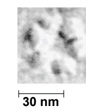
Concept 29.1: Land plants evolved from green algae

- Green algae called charophytes are the closest relatives of land plants

Morphological and Molecular Evidence

- Many characteristics of land plants also appear in some algae
- However, land plants share the following traits with only charophytes
  - **Rings of cellulose-synthesizing proteins**
  - **Structure of flagellated sperm**
  - **Formation of a phragmoplast**

Figure 29.UN01



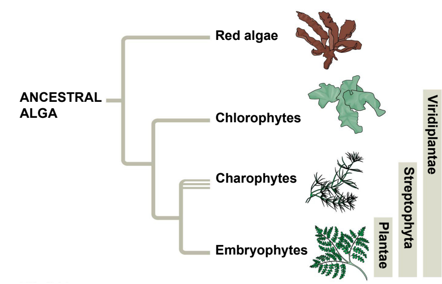
- Comparisons of both nuclear and chloroplast genes point to charophytes as the closest living relatives of land plants
- Note that land plants are not descended from modern charophytes, but share a common ancestor with modern charophytes

Adaptations Enabling the Move to Land

- In charophytes a layer of a durable polymer called **sporopollenin** prevents exposed zygotes from drying out
- Sporopollenin is also found in plant spore walls
- The movement onto land by charophyte ancestors provided unfiltered sun, more plentiful CO_2, and nutrient-rich soil
- Land presented challenges: a scarcity of water and lack of structural support

- Land plants diversified as adaptations evolved that enabled them to thrive despite challenges
- The placement of the boundary dividing land plants from algae is the subject of ongoing debate
- Until this debate is resolved, we define plants as embryophytes, plants with embryos

Figure 29.2



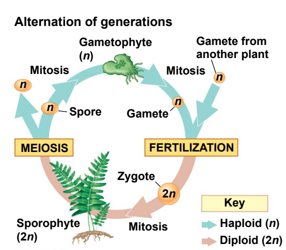
Derived Traits of Plants

- Five key traits appear in nearly all land plants but are absent in the charophytes
  - Alternation of generations
  - Multicellular, dependent embryos
  - Walled spores produced in sporangia
  - Multicellular gametangia
  - Apical meristems

Alternation of Generations

- Plants alternate between two multicellular stages, a reproductive cycle called **alternation of generations**
- The **gametophyte** is haploid and produces haploid gametes by mitosis
- Fusion of the gametes gives rise to the **diploid sporophyte**, which produces haploid **spores** by meiosis

Figure 29.3a



Multicellular, Dependent Embryos

- The diploid embryo is retained within the tissue of the female gametophyte
- Nutrients are transferred from parent to embryo through placental transfer cells
- Land plants are called **embryophytes** because of the dependency of the embryo on the parent

Figure 29.3b

Multicellular, dependent embryos

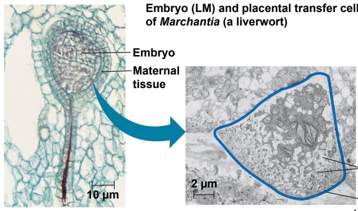
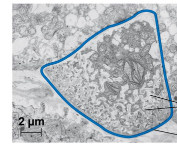


Figure 29.3ba

Figure 29.3bb

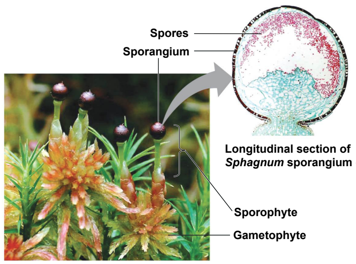


Walled Spores Produced in Sporangia

- The sporophyte produces spores in organs called **sporangia**
- Diploid cells called **sporocytes** undergo meiosis to generate haploid spores
- Spore walls contain sporopollenin, which makes them resistant to harsh environments

Figure 29.3c

Walled spores produced in sporangia

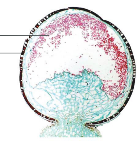


Sporophytes and sporangia of *Sphagnum* (a moss)

Figure 29.3ca

Sporophytes and sporangia of *Sphagnum* (a moss)

Figure 29.3cb



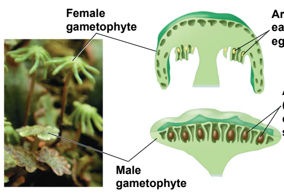
Longitudinal section of *Sphagnum* sporangium (LM)

Multicellular Gametangia

- Gametes are produced within organs called **gametangia**
- Female gametangia, called **archegonia**, produce eggs and are the site of fertilization
- Male gametangia, called **antheridia**, produce and release sperm

Figure 29.3d

Multicellular gametangia



Archegonia and antheridia of *Marchantia* (a liverwort)

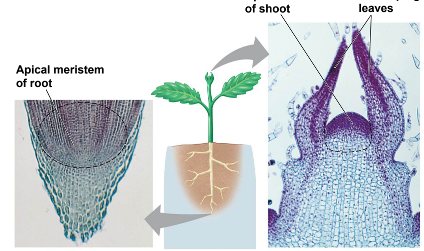
Figure 29.3da

Apical Meristems

- Plants sustain continual growth in their **apical meristems**
- Cells from the apical meristems differentiate into various tissues

Figure 29.3e

Apical meristems



Apical meristems of plant roots and shoots

Figure 29.3ea

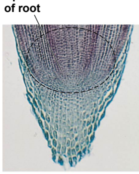
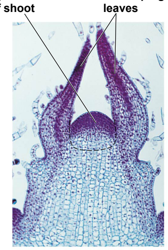


Figure 29.3eb



- Additional derived traits include
  - **Cuticle**, a waxy covering of the epidermis
  - **Stomata** are specialized cells that allow for gas exchange between the outside air and the plant
  - Mycorrhizae, symbiotic associations between fungi and land plants that may have helped plants without true roots to obtain nutrients

The Origin and Diversification of Plants

- Fossil evidence indicates that plants were on land at least 470 million years ago
- Fossilized spores and tissues have been extracted from 450-million-year-old rocks

Figure 29.4

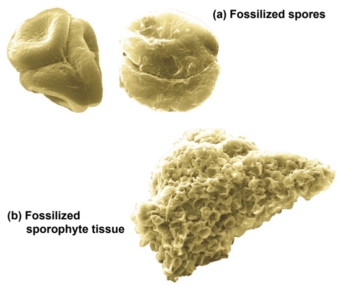
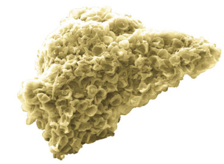


Figure 29.4a

(a) Fossilized spores

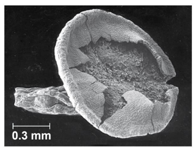
Figure 29.4b



(b) Fossilized sporophyte tissue

- Fossils of larger structures, such as sporangium, date to 425 million years ago

Figure 29.UN02



Cooksonia sporangium fossil

- Ancestral species gave rise to a vast diversity of modern plants

Table 29.1

Table 29.1 Ten Phyla of Extant Plants

	Common Name	Number of Known Species
Nonvascular Plants (Bryophytes)		
Phylum Hepatophyta	Liverworts	9,000
Phylum Bryophyta	Mosses	15,000
Phylum Anthocerophyta	Hornworts	100
Vascular Plants		
Seedless Vascular Plants		
Phylum Lycophyta	Lycophytes	1,200
Phylum Monilophyta	Monilophytes	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

Figure 29.5

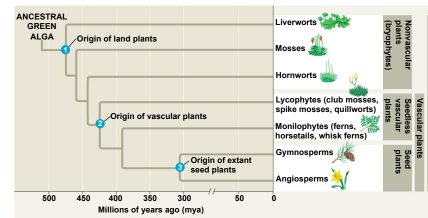


Figure 29.5a

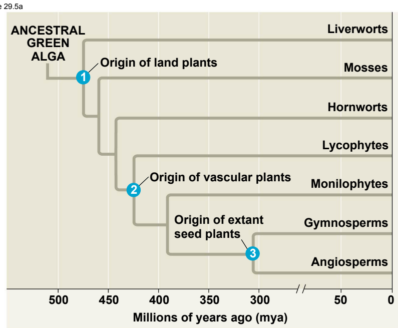
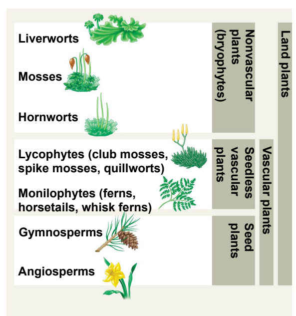


Figure 29.5b



- Land plants can be informally grouped based on the presence or absence of **vascular tissue**
- Most plants have vascular tissue; these constitute the **vascular plants**
- Nonvascular plants are commonly called **bryophytes**
- Bryophytes are not a monophyletic group

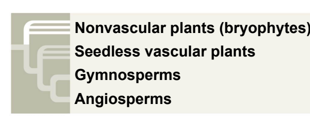
- **Seedless vascular plants** can be divided into clades
  - **Lycophytes** (club mosses and their relatives)
  - **Monilophytes** (ferns and their relatives)
- Seedless vascular plants do not form a clade
- Organisms that are grouped based on shared key biological features, rather than shared ancestry, can be referred to as a grade

- A **seed** is an embryo and nutrients surrounded by a protective coat
- Seed plants form a clade and can be divided into further clades
  - **Gymnosperms**, the “naked seed” plants, including the conifers
  - **Angiosperms**, the flowering plants

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
  - **Mosses**, phylum Bryophyta
  - **Hornworts**, phylum Anthocerophyta
- These groups are thought to represent the earliest lineages to diverge from the common ancestor of land plants

Figure 29.UN03



Bryophyte Gametophytes

- In all three bryophyte phyla, gametophytes are larger and longer-living than sporophytes
- Sporophytes are typically present only part of the time

Figure 29.6

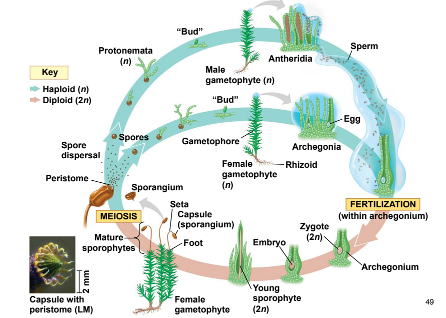
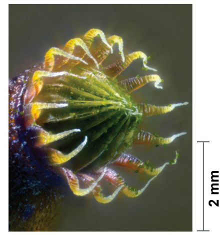


Figure 29.6a



Capsule with peristome (LM)

Figure 29.6b-1

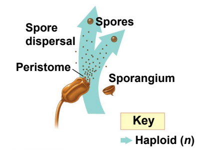


Figure 29.6b-2

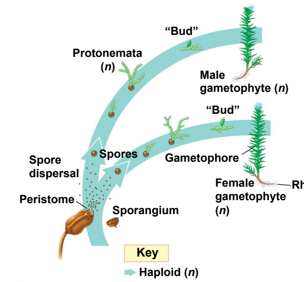


Figure 29.6b-3

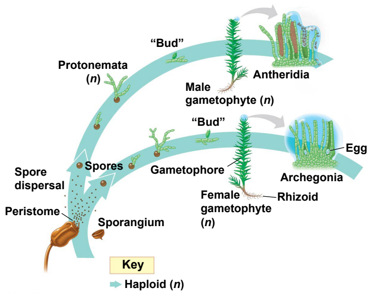


Figure 29.6b-4

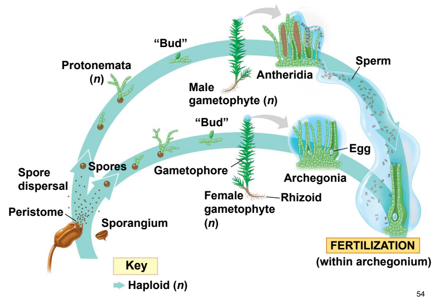


Figure 29.6c-1

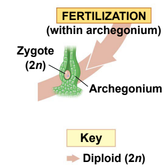


Figure 29.6c-2

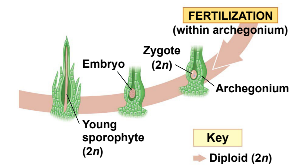
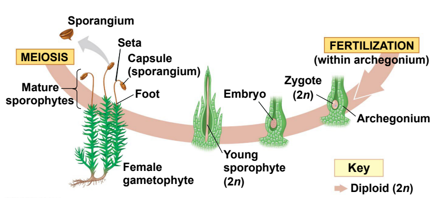
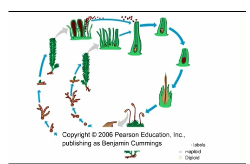


Figure 29.6c-3



Animation: Moss Life Cycle



- A spore germinates into a gametophyte composed of a **protonema** and gamete-producing **gametophore**
- The height of gametophytes is constrained by lack of vascular tissues
- **Rhizoids** anchor gametophytes to substrate
- Mature gametophytes produce flagellated sperm in antheridia and an egg in each archegonium
- Sperm swim through a film of water to reach and fertilize the egg

Figure 29.UN04

Bryophyte Sporophytes

- Bryophyte sporophytes grow out of archegonia, and are the smallest and simplest sporophytes of all extant plant groups
- A sporophyte consists of a **foot**, a **seta** (stalk), and a sporangium, also called a **capsule**, which discharges spores through a **peristome**
- Hornwort and moss sporophytes have stomata; liverworts do not

Figure 29.7a

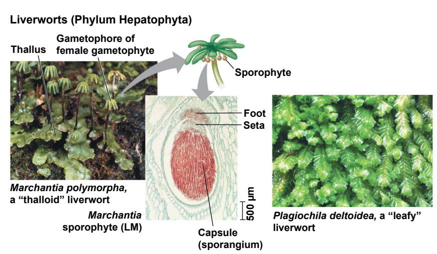
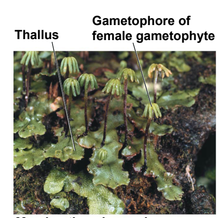
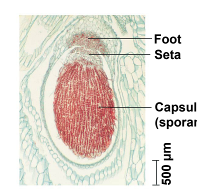


Figure 29.7aa



Marchantia polymorpha, a "thalloid" liverwort

Figure 29.7ab



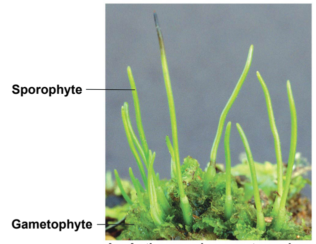
Marchantia sporophyte (LM)

Figure 29.7ac

Plagiochila deltoidea, a “leafy” liverwort

Figure 29.7b

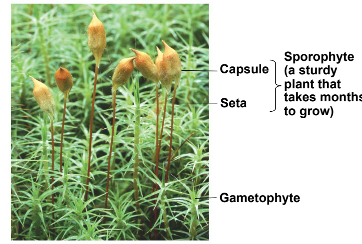
Hornworts (Phylum Anthocerophyta)



An *Anthoceros* hornwort species

Figure 29.7c

Mosses (Phylum Bryophyta)



Polytrichum commune, hairy-cap moss

The Ecological and Economic Importance of Mosses

- Mosses are capable of inhabiting diverse and sometimes extreme environments, but are especially common in moist forests and wetlands
- Some mosses might help retain nitrogen in the soil

Figure 29.8

- *Sphagnum*, or “peat moss,” forms extensive deposits of partially decayed organic material known as **peat**
- Peat can be used as a source of fuel
- Low temperature, pH, and oxygen level of peatlands inhibits decay of moss and other organisms

Figure 29.9

(a) Peat being harvested from a peatland

(b) “Tollund Man,” a bog mummy dating from 405–100 B.C.E.

Figure 29.9a

(a) Peat being harvested from a peatland

Figure 29.9b

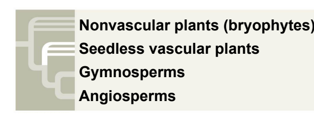
(b) “Tollund Man,” a bog mummy dating from 405–100 B.C.E.

- *Sphagnum* is an important global reservoir of organic carbon
- Overharvesting of *Sphagnum* and/or a drop in water level in peatlands could release stored CO_2 to the atmosphere

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

- Bryophytes were prominent types of vegetation during the first 100 million years of plant evolution
- The earliest fossils of vascular plants date to 425 million years ago
- Vascular tissue allowed these plants to grow tall
- Seedless vascular plants have flagellated sperm and are usually restricted to moist environments

Figure 29.UN05



Origins and Traits of Vascular Plants

- Early vascular plants had independent, branching sporophytes
- Living vascular plants are characterized by
  - Life cycles with dominant sporophytes
  - Vascular tissues called xylem and phloem
  - Well-developed roots and leaves

Figure 29.10

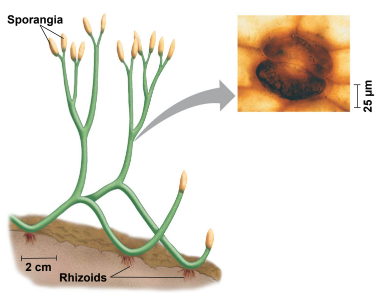
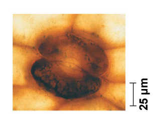


Figure 29.10a



Life Cycles with Dominant Sporophytes

- In contrast with bryophytes, sporophytes of seedless vascular plants are the larger generation, as in familiar ferns
- The gametophytes are tiny plants that grow on or below the soil surface

Figure 29.11

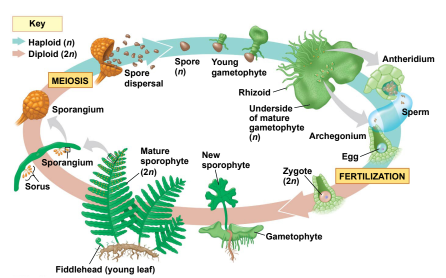


Figure 29.11a-1

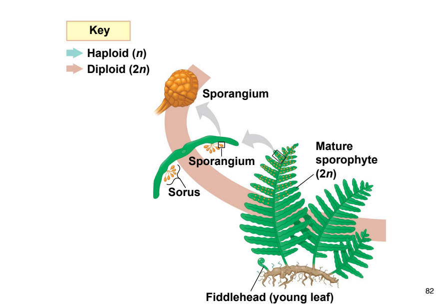


Figure 29.11a-2

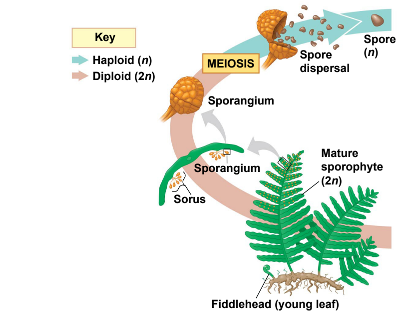


Figure 29.11b-1

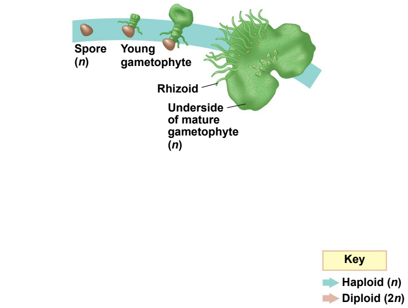


Figure 29.11b-2

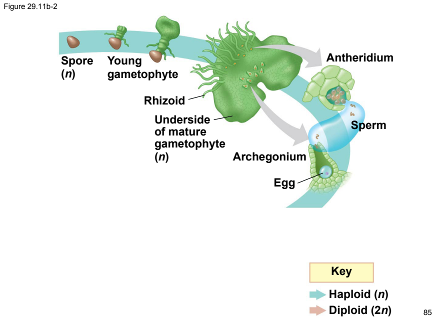
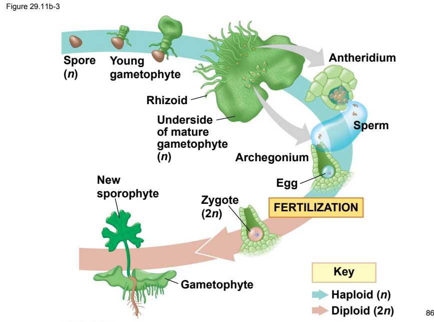
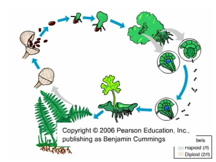


Figure 29.11b-3



Animation: Fern Life Cycle



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 tube-shaped cells called **tracheids**
- Water-conducting cells are strengthened by **lignin** and provide structural support
- **Phloem** has cells arranged into tubes that distribute sugars, amino acids, and other organic products
- Vascular tissue allowed for increased height, which provided an evolutionary advantage

Evolution of Roots

- **Roots** are organs that anchor vascular plants
- They enable vascular plants to absorb water and nutrients from the soil
- Roots may have evolved from subterranean stems

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 by two types
  - **Microphylls**, leaves with a single vein
  - **Megaphylls**, leaves with a highly branched vascular system

Figure 29.12

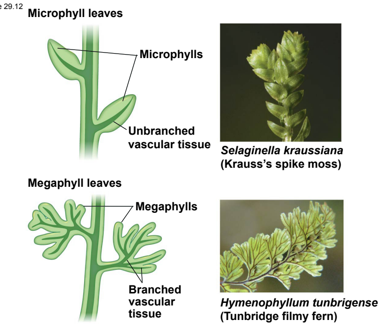
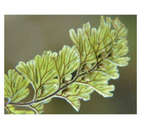


Figure 29.12a

Selaginella kraussiana (Krauss's spike moss)

Figure 29.12b



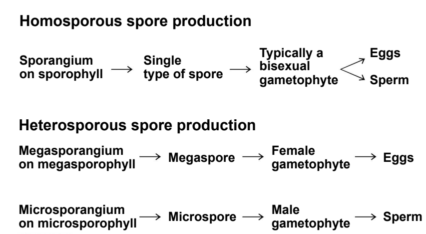
Hymenophyllum tunbrigense (Tunbridge filmy fern)

Sporophylls and Spore Variations

- **Sporophylls** are modified leaves with sporangia
- **Sori** are clusters of sporangia on the undersides of sporophylls
- **Strobili** are cone-like structures formed from groups of sporophylls

- Most seedless vascular plants are homosporous, producing one type of spore that develops into a bisexual gametophyte
- All seed plants and some seedless vascular plants are **heterosporous**
- Heterosporous species produce **megaspores**, which give rise to female gametophytes, and **microspores**, which give rise to male gametophytes

Figure 29.UN07



Classification of Seedless Vascular Plants

- There are two clades of seedless vascular plants
  - Phylum Lycophyta includes club mosses, spike mosses, and quillworts
  - Phylum Monilophyta includes ferns, horsetails, and whisk ferns and their relatives

Phylum Lycophyta: Club Mosses, Spike Mosses, and Quillworts

- Giant lycophyte trees thrived for millions of years in moist swamps
- Surviving species are small herbaceous plants
- Club mosses and spike mosses have vascular tissues and are not true mosses

Figure 29.13a

Lycophytes (Phylum Lycophyta)

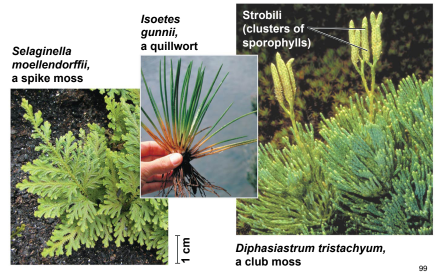


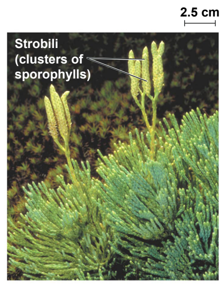
Figure 29.13aa

***Selaginella moellendorffii*, a spike moss**

Figure 29.13ab

***Isoetes gunnii*, a quillwort**

Figure 29.13ac



***Diphasiastrum tristachyum*, a club moss**

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

- Ferns are the most widespread 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*
- Whisk ferns resemble ancestral vascular plants but are closely related to modern ferns

Figure 29.13b

Monilophytes (Phylum Monilophyta)

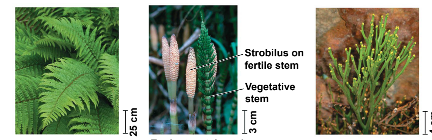
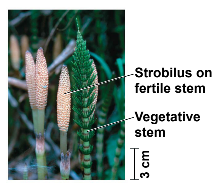


Figure 29.13ba

***Athyrium filix-femina*, lady fern**

Figure 29.13bb



***Equisetum telmateia*, giant horsetail**

Figure 29.13bc

***Psilotum nudum*, a whisk fern**

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
- Increased growth and photosynthesis removed CO_2 from the atmosphere and may have contributed to global cooling at the end of the Carboniferous period
- The decaying plants of these Carboniferous forests eventually became coal

Figure 29.14

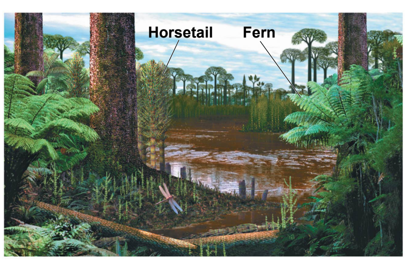
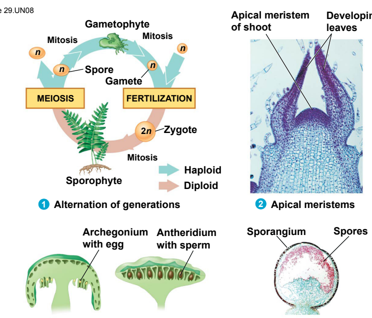


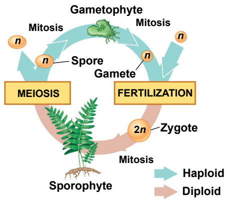
Figure 29.UN06a

	Ca^{2+} (μmol)		Mg^{2+} (μmol)		K^{+} (μmol)	
	Granite	Andesite	Granite	Andesite	Granite	Andesite
Mean weathered amount released in water in the control microcosms	1.68	1.54	0.42	0.13	0.68	0.60
Mean weathered amount released in water in the experimental microcosms	1.27	1.84	0.34	0.13	0.65	0.64
Mean weathered amount taken up by moss in the experimental microcosms	1.09	3.62	0.31	0.56	1.07	0.28

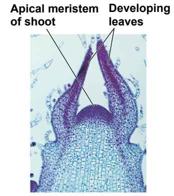
Figure 29.UN06b

Figure 29.UN08

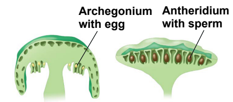




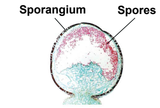
1 Alternation of generations



2 Apical meristems



3 Multicellular gametangia



4 Walled spores in sporangia

Age (years after fire)	N fixation rate (kg N per ha per yr)
35	0.001
41	0.005
78	0.08
101	0.3
124	0.9
170	2.0
220	1.3
244	2.1
270	1.6
300	3.0
355	2.3

Source: Data from O. Zackrisson et al., Nitrogen fixation increases with successional age in boreal forests, *Ecology* 85:3327–3334 (2006).