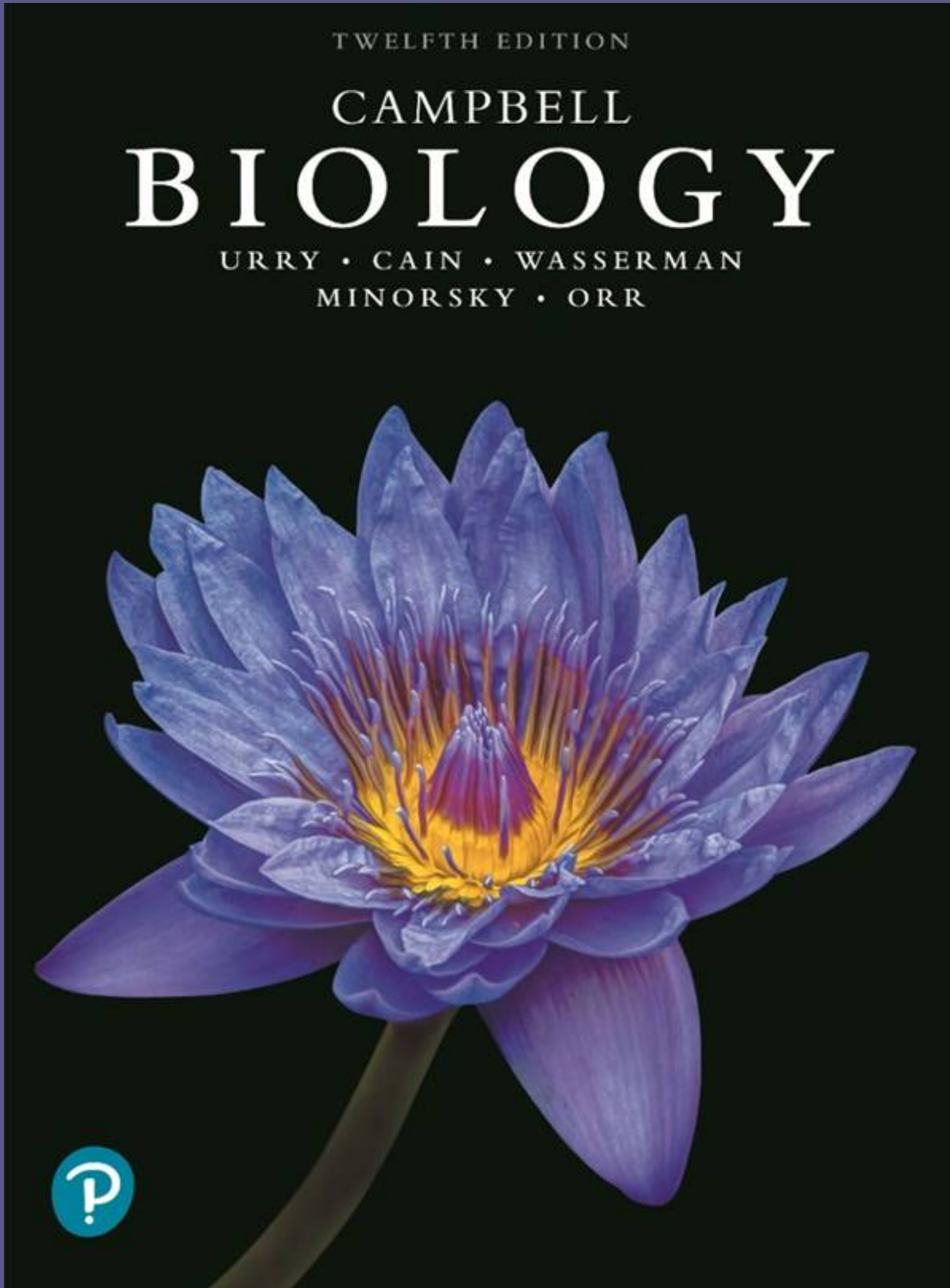


Chapter 29

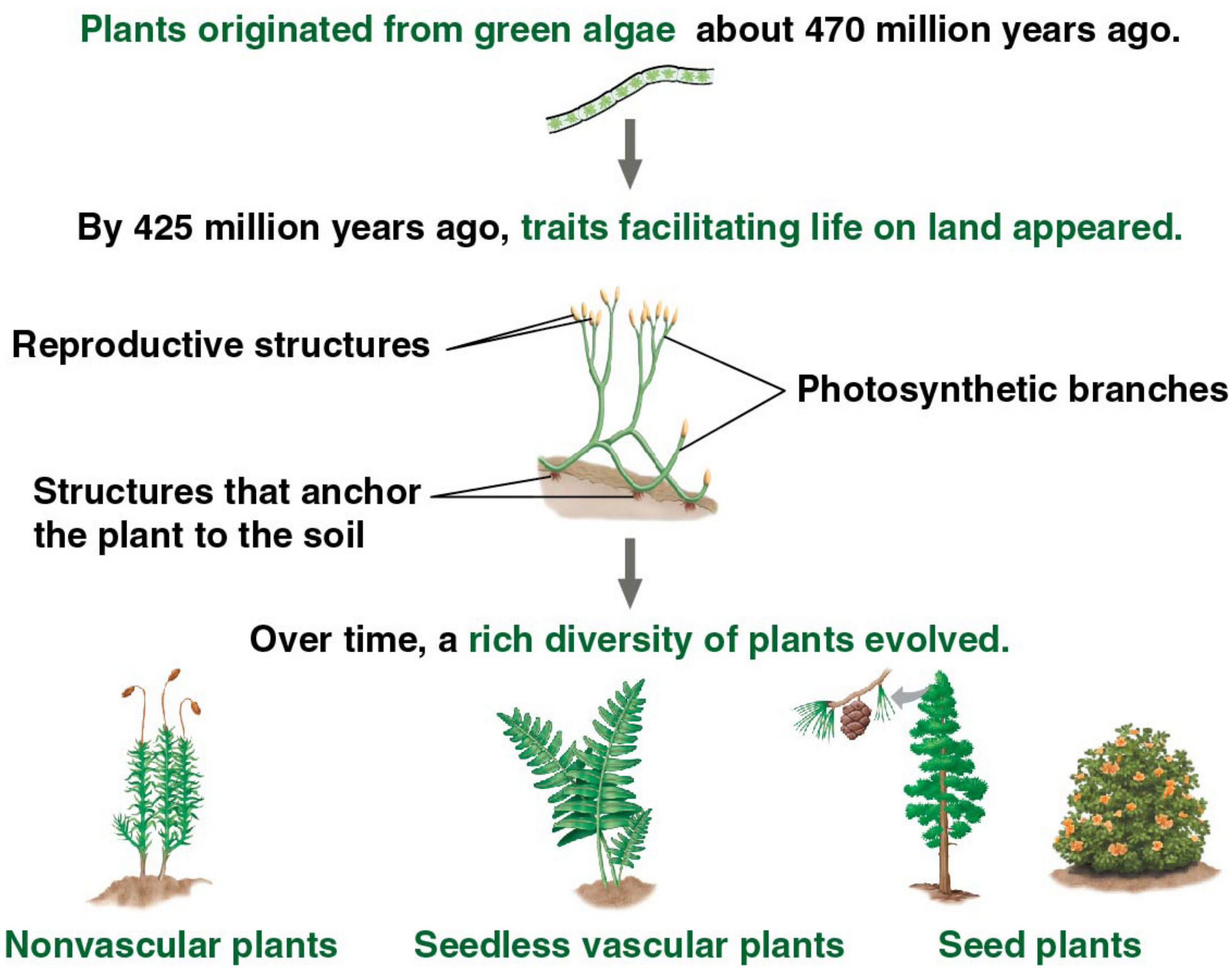
Plant Diversity I: How Plants Colonized Land

Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

Figure 29.1a

Figure 29.1b

What were the major developments in the evolution of plants?



CONCEPT 29.1: Plants evolved from green algae

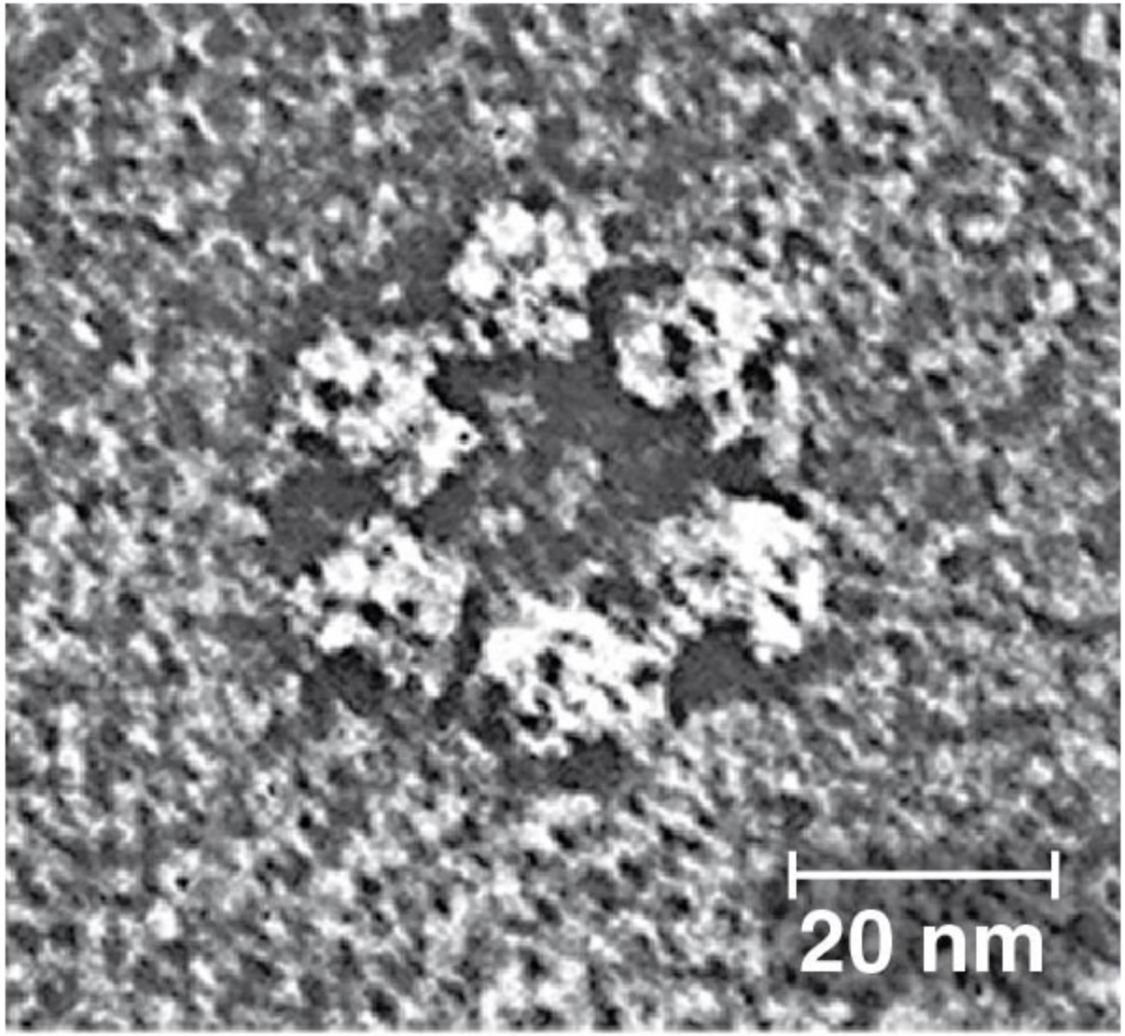
- There are more than 325,000 known plant species today; most live on land
- Plants supply oxygen, food sources, and habitat for many other terrestrial organisms
- Green algae (photosynthetic protists) called charophytes are the closest relatives of plants

Evidence of Algal Ancestry

- Many key traits of plants also appear in some algae
  - For example, plants and some algae are multicellular, eukaryotic, photosynthetic autotrophs
  - Some algae, like plants, have cellulose in their cell walls and chloroplasts containing chlorophyll *a* and *b*

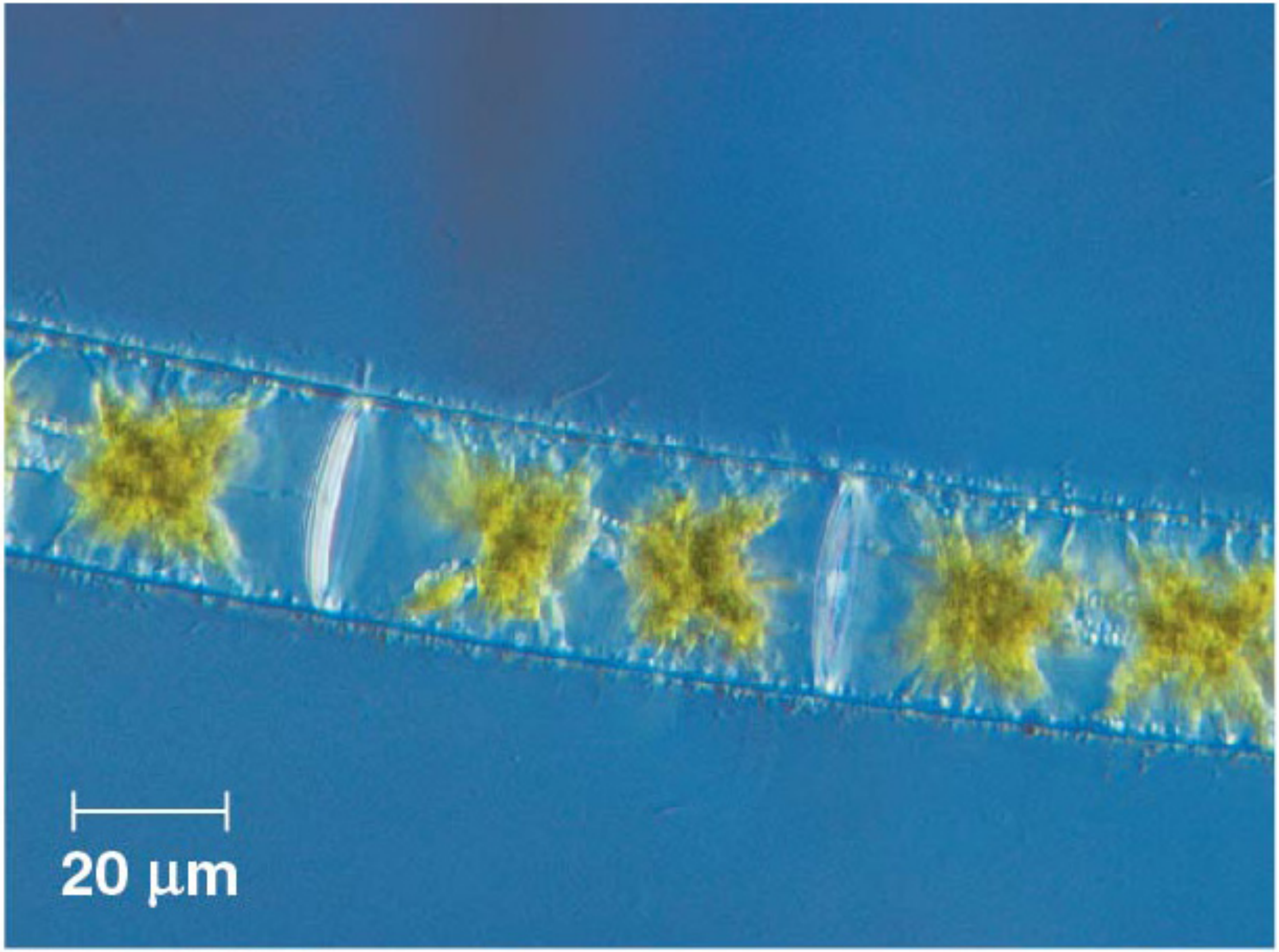
- Plants share the following traits only with their closest algal relatives, the charophytes:
  - Cellulose-synthesizing membrane proteins are arranged in rings, rather than linear sets
  - Structure of flagellated sperm
  - Sequence similarities in nuclear, chloroplast, and mitochondrial DNA

Figure 29.2



- Recent genetic analysis indicates charophytes in the clade Zygnematophyceae are the closest living relatives of plants
- Plants are not descended from modern charophytes, but share a common ancestor with them

Figure 29.3



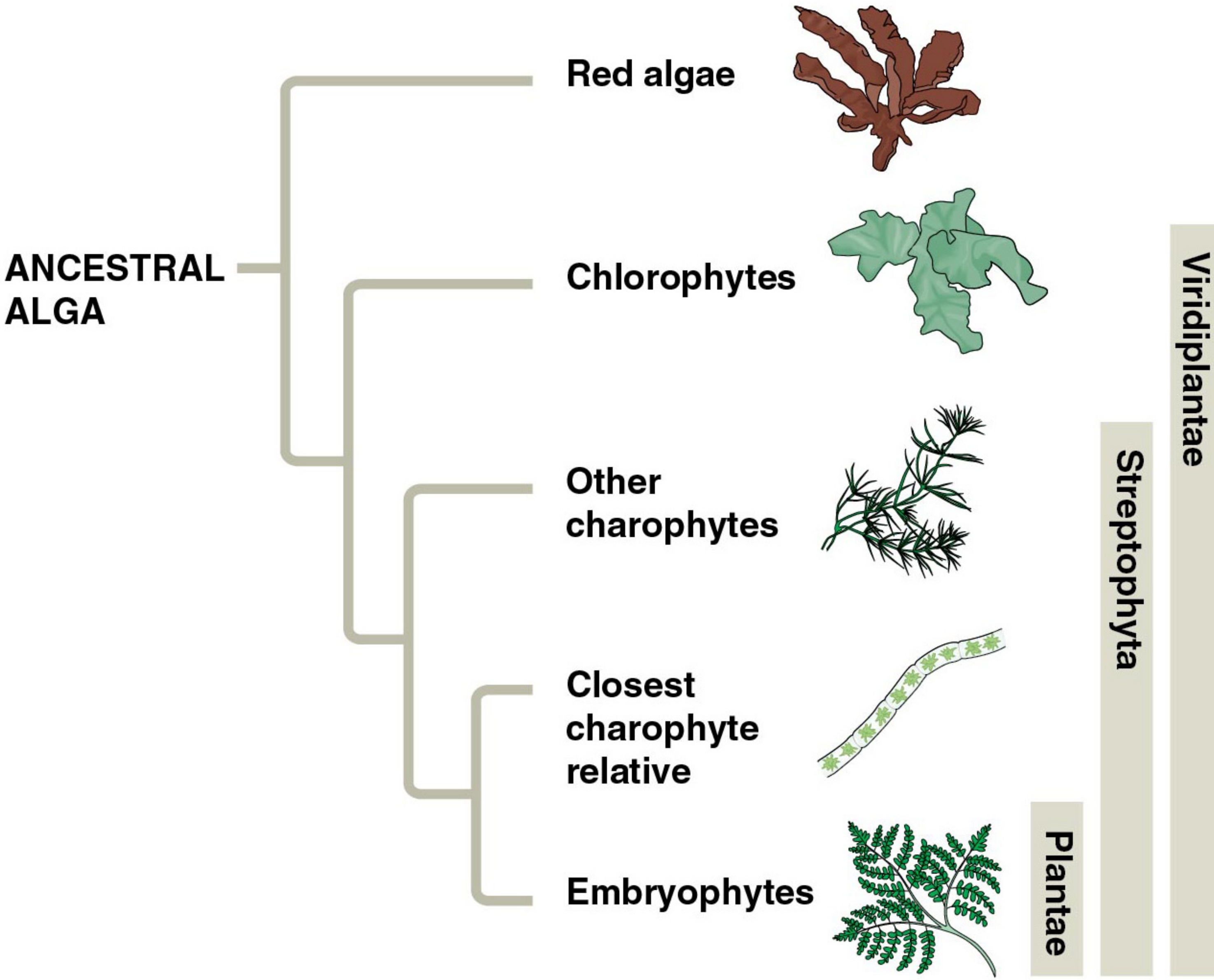
Adaptations Enabling the Move to Land

- Charophytes have a coating of **sporopollenin**, a polymer that prevents zygotes from drying out
- Sporopollenin is also found in plant spore walls

- The move to land provided benefits: unfiltered sunlight, more plentiful CO_2, and nutrient-rich soil
- Land also presented challenges: a scarcity of water and lack of structural support against gravity
- Plants diversified as adaptations evolved that enabled them to thrive on land despite challenges

- The placement of the boundary dividing plants from algae is the subject of ongoing debate
- The traditional definition equates the kingdom Plantae with embryophytes (plants with embryos)

Figure 29.4



ANCESTRAL ALGA
Red algae
Chlorophytes
Other charophytes
Closest charophyte relative
Embryophytes
Plantae
Streptophyta
Viridiplantae

Derived Traits of Plants

- Four key traits appear in nearly all plants but are absent in the charophytes
  - Alternation of generations
  - Walled spores produced in sporangia
  - Apical meristems

Alternation of generations

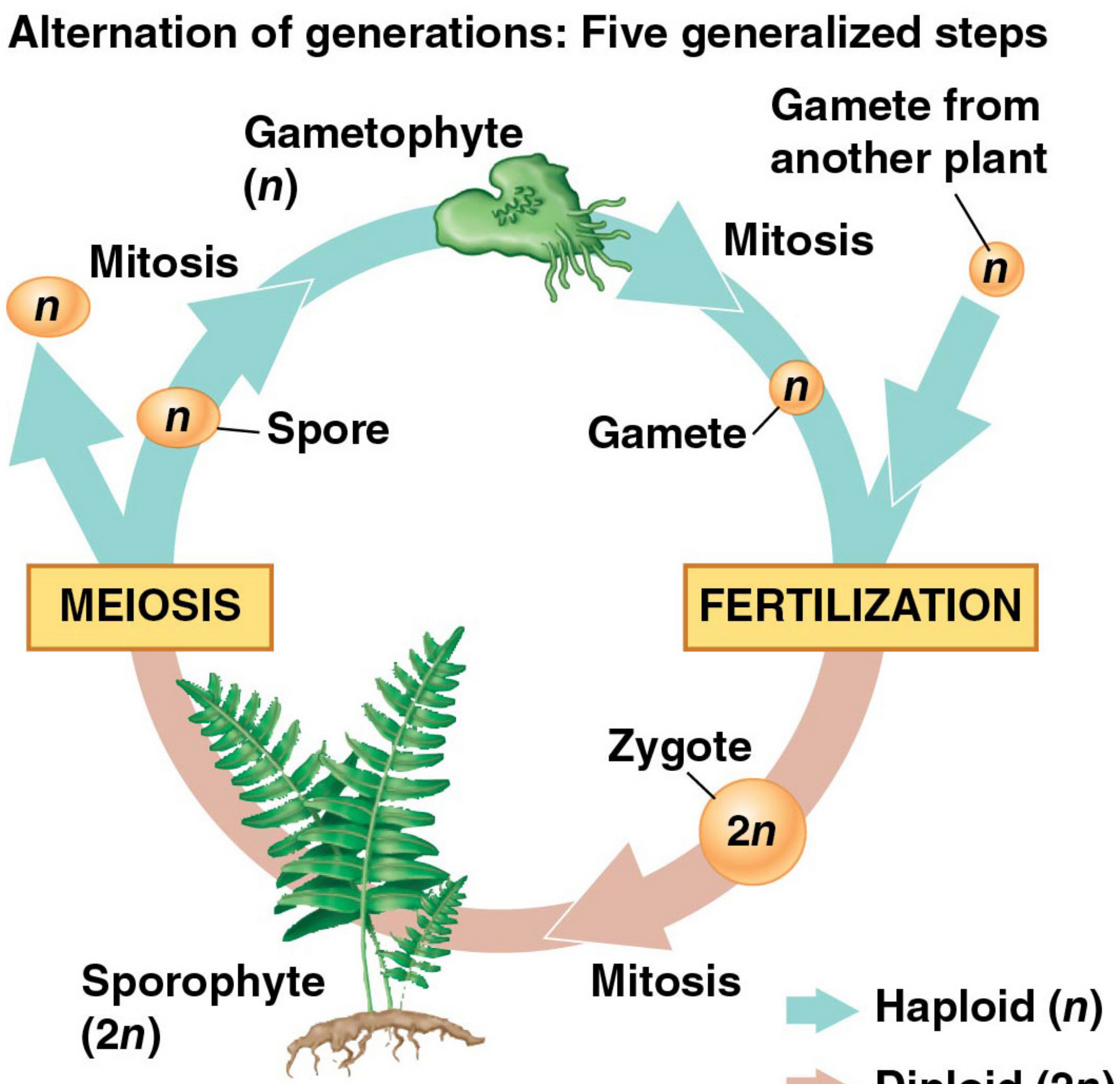
- Type of plant life cycle consisting of multicellular forms that gives rise to each other in turn.

Figure 29.5 Exploring Alternation of Generations

Alternation of Generations

- **Alternation of generations** is the process by which the life cycles of plants alternate between two generations of multicellular organisms: gametophytes and sporophytes
- The multicellular haploid **gametophyte** produces haploid gametes (sperm and eggs) by mitosis
- The multicellular diploid **sporophyte** produces haploid **spores** by meiosis
- Spores develop into gametophytes and fertilized eggs (zygotes) develop into sporophytes

Figure 29.5a



Alternation of generations: Five generalized steps
Gametophyte
(n)
Gamete from
another plant
Mitosis
Mitosis
n
n
n
Spore
Gamete
n
MEIOSIS
FERTILIZATION
Zygote
2n
Sporophyte
(2n)
Mitosis
Haploid (n)
Diploid (2n)

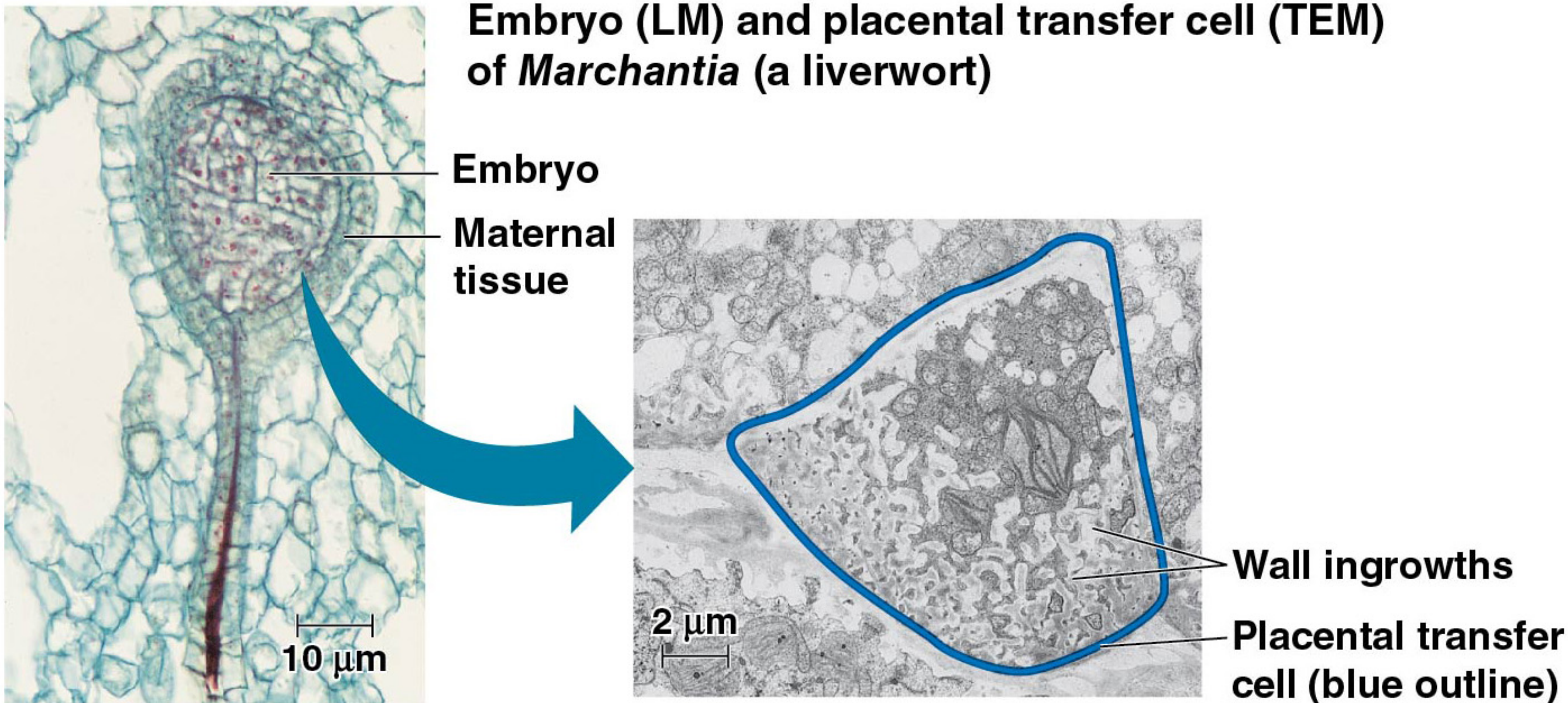
Multicellular, Dependent Embryos

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

Figure 29.5b

Multicellular, Dependent Embryos

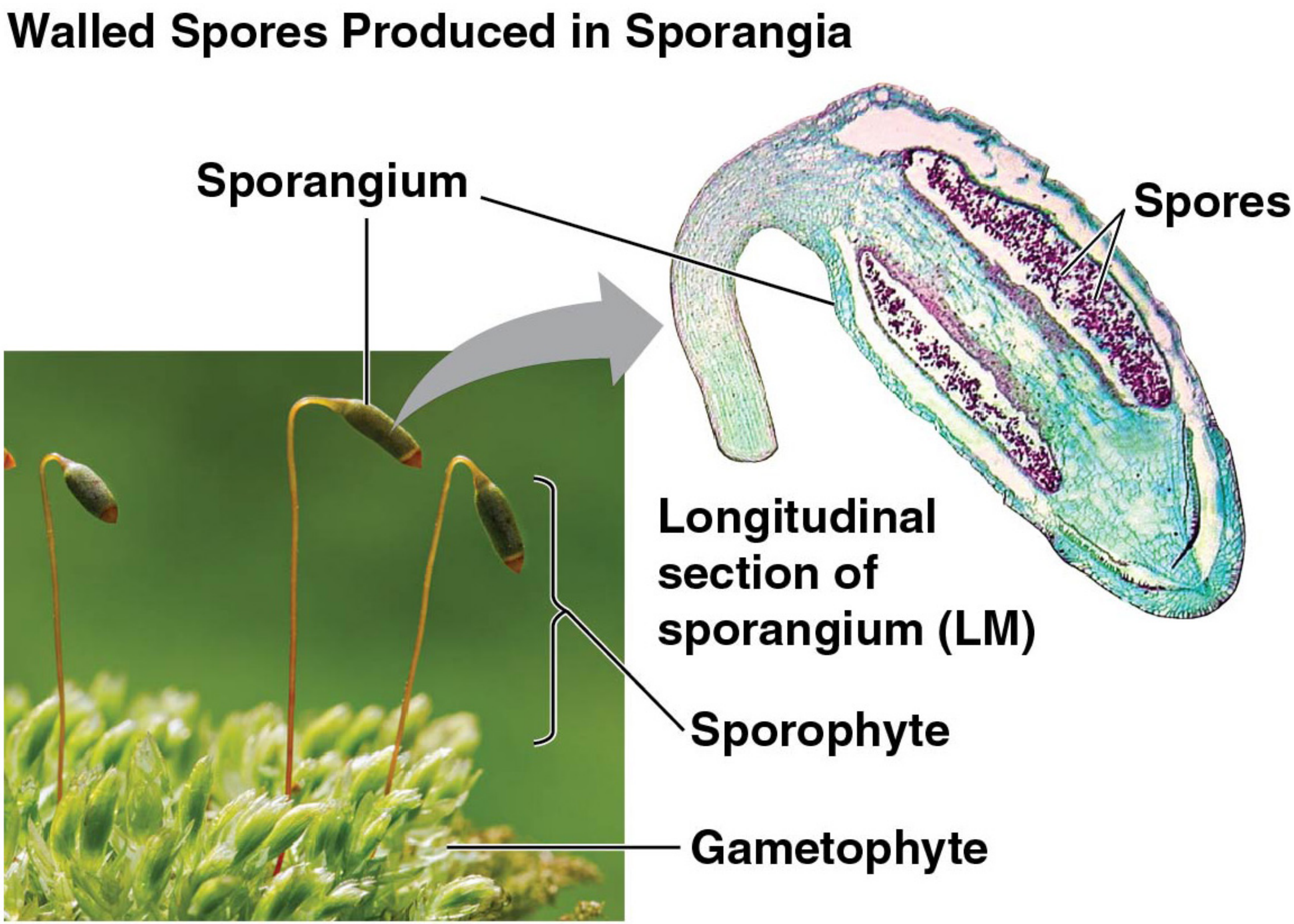
Embryo (LM) and placental transfer cell (TEM) of *Marchantia* (a liverwort)



Walled Spores Produced in Sporangia

- The sporophyte produces spores in multicellular organs called **sporangia**
- Spore walls contain sporopollenin, which makes them resistant to harsh environments

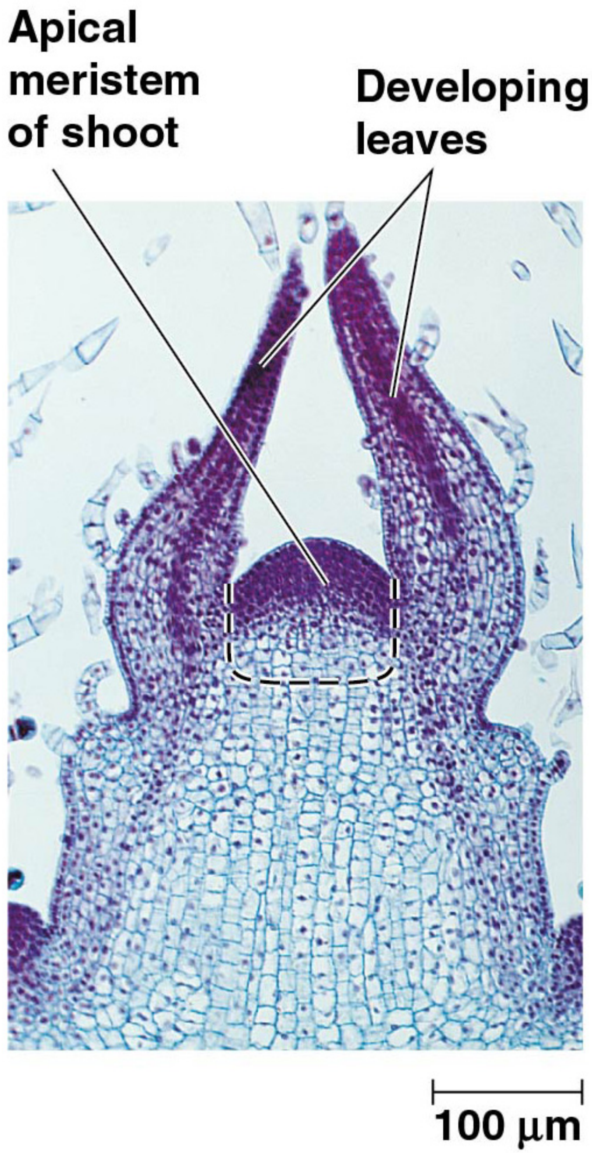
Figure 29.6


Walled Spores Produced in Sporangia
Sporangium
Spores
Longitudinal section of sporangium (LM)
Sporophyte
Gametophyte

Apical Meristems

- Localized regions of cell division at the tips of roots and shoots are called **apical meristems**
- These cells divide continuously, enabling elongation of roots and shoots for better resource acquisition

Figure 29.7



- Additional derived traits of plants include
  - The **cuticle**, a waxy covering of the epidermis that reduces water loss
  - The **stomata**, pores that facilitate gas exchange between the outside air and internal plant tissues

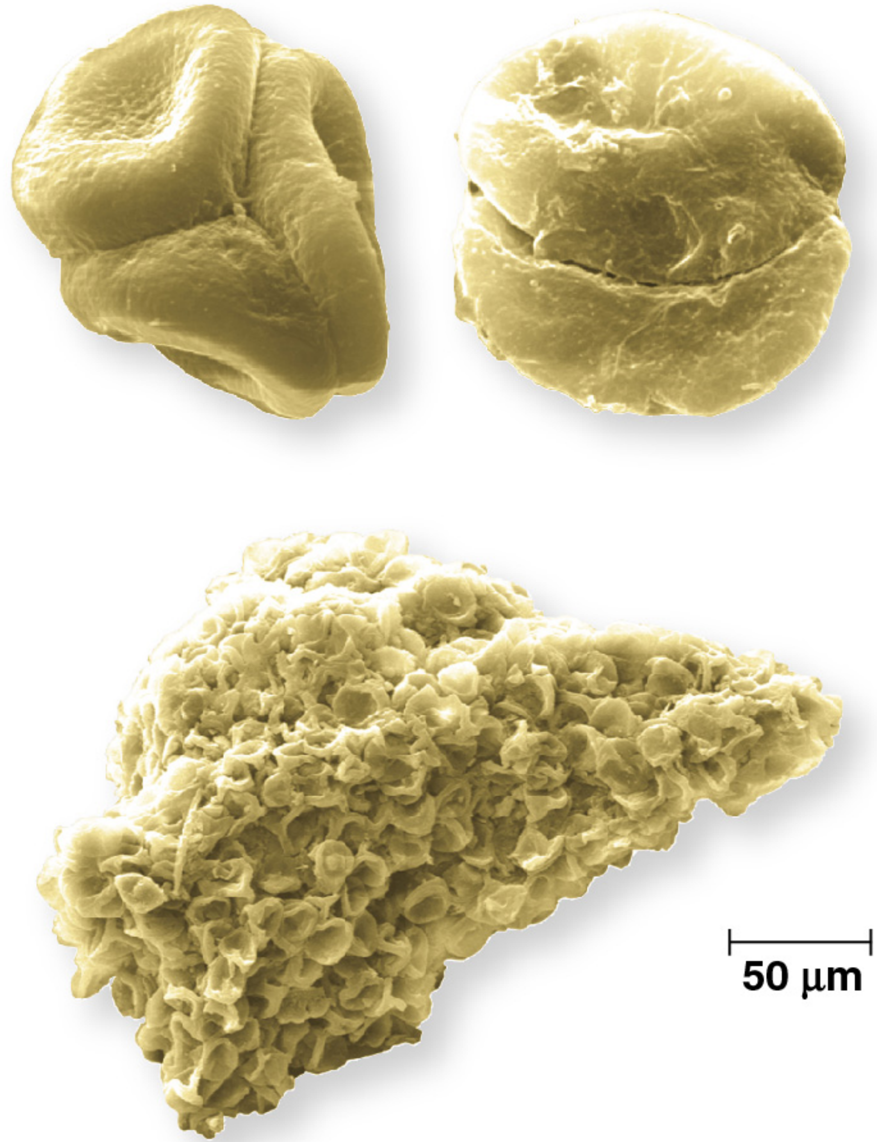
- Early plants lacked true roots (and leaves) making absorption of nutrients from the soil challenging
- 420 million-year-old fossils suggest that symbiotic associations with fungi (mycorrhizae), may have helped plants without roots to colonize land

The Origin and Diversification of Plants

- Microorganisms colonized land 3.2 billion years ago
- Plant spores first appear in the fossil record from about 470 million years ago
- Fossilized spores embedded in sporophyte tissue have been extracted from 450-million-year-old rocks

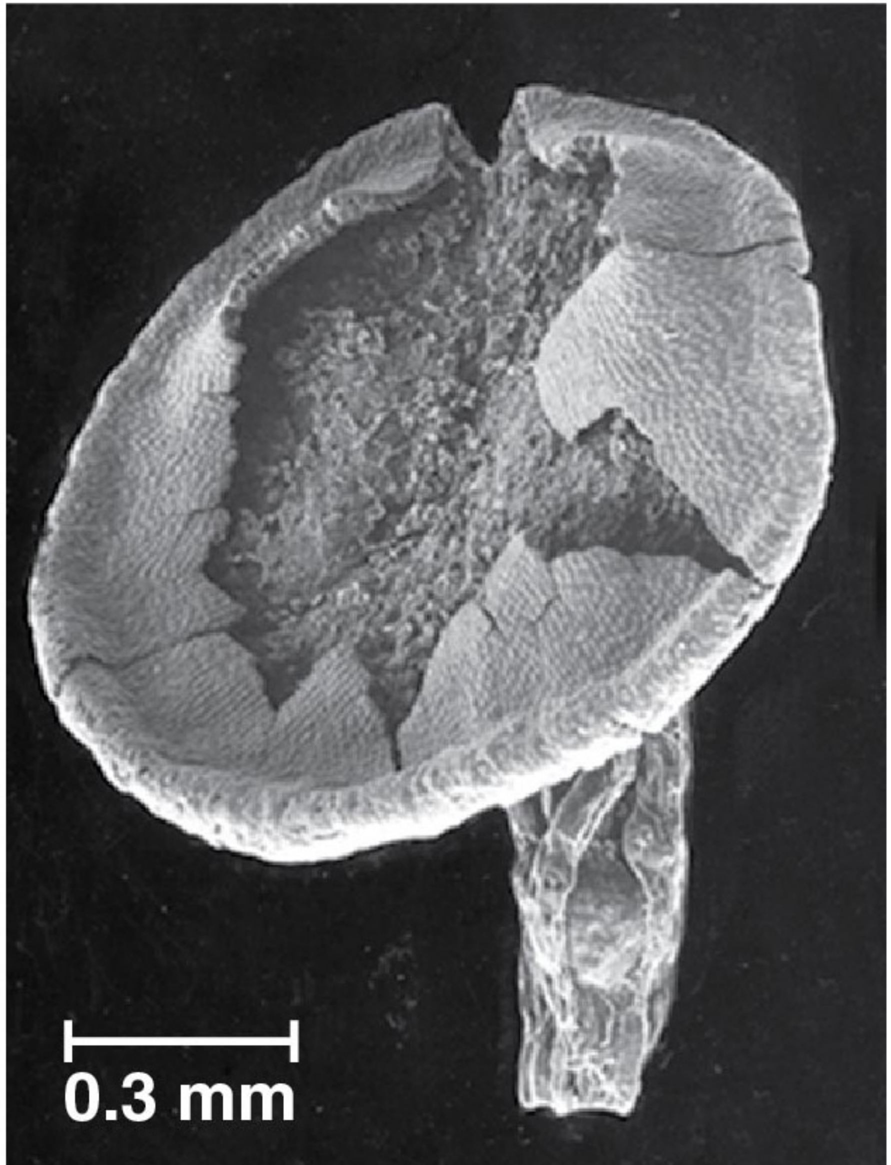
(a) Fossilized spores.

(b) Fossilized sporophyte tissue.



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

Figure 29.9

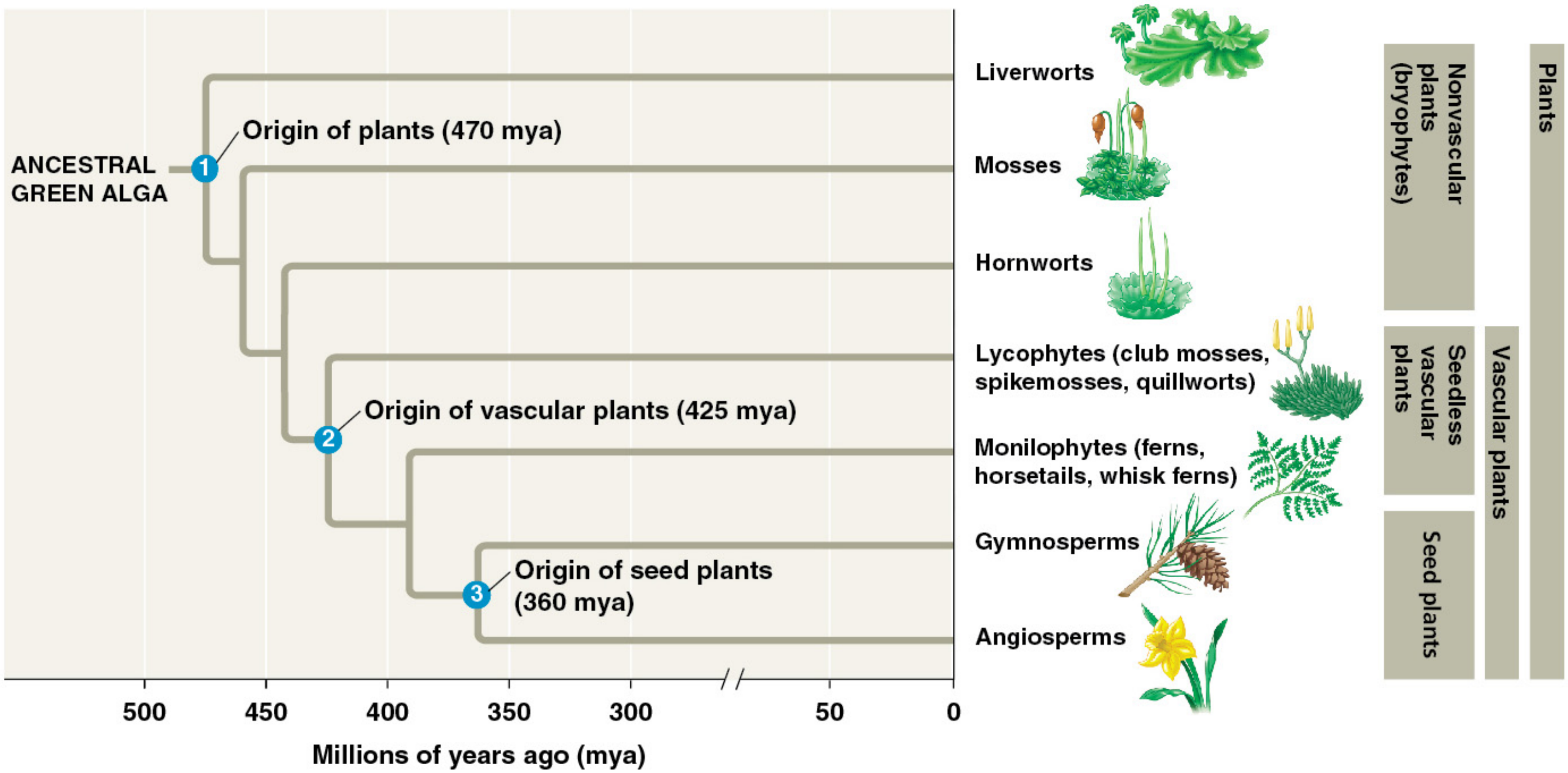


- Ancestral species evolved to produce the vast diversity of plants present on Earth today

Table 29.1

	Common Name	Number of Known Species
Nonvascular Plants (Bryophytes)		
Phylum Hepatophyta	Liverworts	9,000
Phylum Bryophyta	Mosses	13,000
Phylum Anthocerophyta	Hornworts	225
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	350
Phylum Gnetophyta	Gnetophytes	75
Phylum Coniferophyta	Conifers	600
Angiosperms		
Phylum Anthophyta	Flowering plants	290,000

Figure 29.10



ANCESTRAL GREEN ALGA
Origin of plants (470 mya)
Origin of vascular plants (425 mya)
Origin of seed plants (360 mya)
Liverworts
Mosses
Hornworts
Lycophytes (club mosses, spikemosses, quillworts)
Monilophytes (ferns, horsetails, whisk ferns)
Gymnosperms
Angiosperms
Nonvascular plants (bryophytes)
Seedless vascular plants
Seed plants
Vascular plants
Plants
500
450
400
350
300
50
0
Millions of years ago (mya)

- Most plants have **vascular tissue**, cells joined into tubes for the transport of water and nutrients
- Plants that have a complex vascular tissue system are called **vascular plants**

- “Nonvascular” plants lack an extensive transport system
- All nonvascular plants—liverworts, mosses, and hornworts—are informally called **bryophytes**
- Bryophytes are not a monophyletic group (clade)

- **Seedless vascular plants** have an extensive vascular transport system, but do not produce seeds
- They are divided into two clades:
  - **Lycophytes** are club mosses and their relatives
  - **Monilophytes** are ferns and their relatives
- The seedless vascular plants do not form a clade

- It is sometimes informative to group organisms based on shared key biological features
- In some cases, these shared features do not reflect shared ancestry

- The majority of living plants are seed plants—vascular plants that produce seeds
- A **seed** is an embryo packaged with a supply of nutrients inside a protective coat

- Seed plants can be divided into two groups
  - **Gymnosperms** form a clade that produce seeds that are not enclosed in chambers (“naked seeds”)
  - **Angiosperms** form a clade that produce seeds that develop inside chambers that originate within flowers
- Nearly 90% of living plant species are angiosperms

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 diverged from other plant lineages early in the history of plant evolution

Figure 29.UN01

Nonvascular plants (bryophytes)

Seedless vascular plants

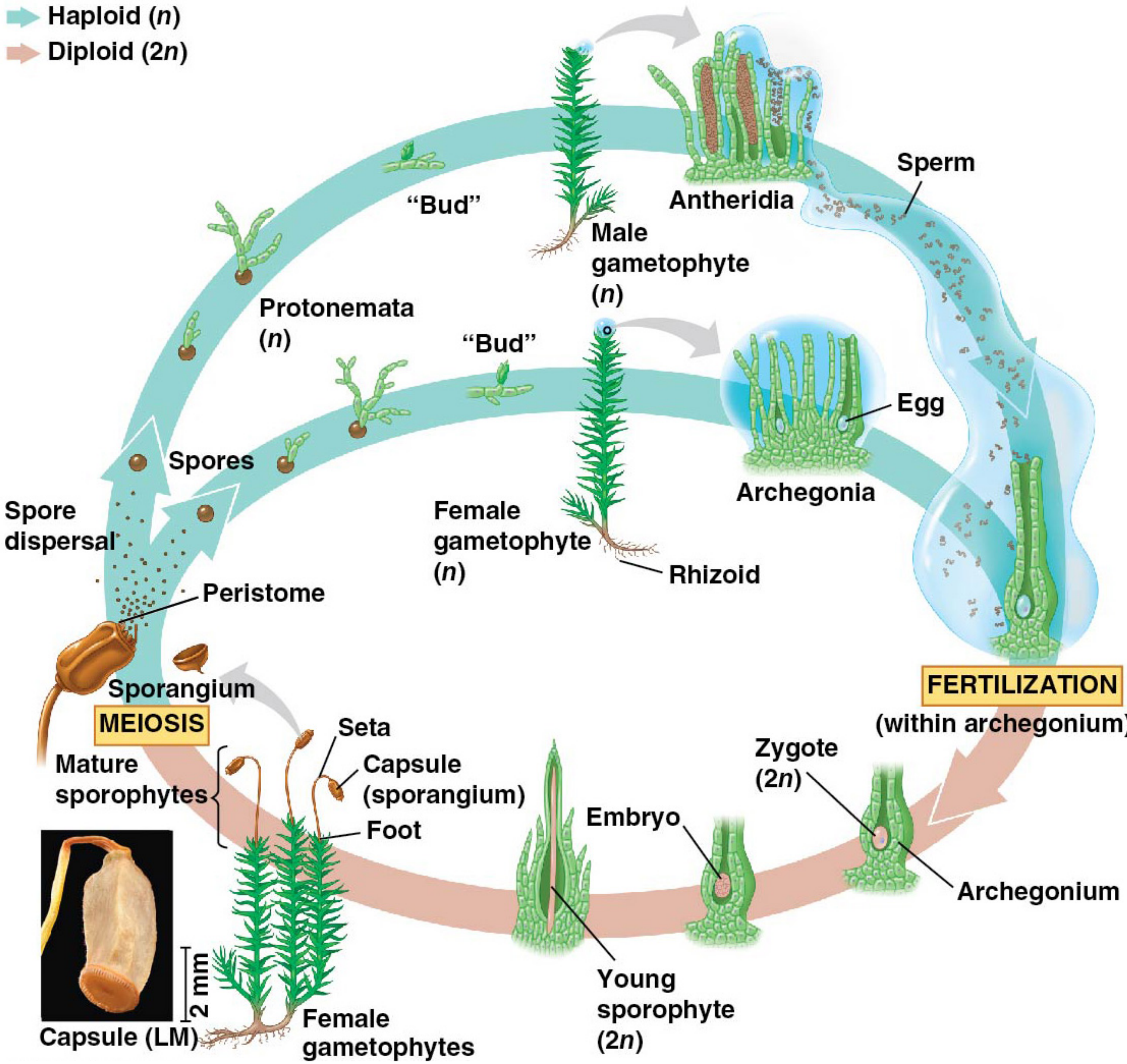
Gymnosperms

Angiosperms

Bryophyte Gametophytes

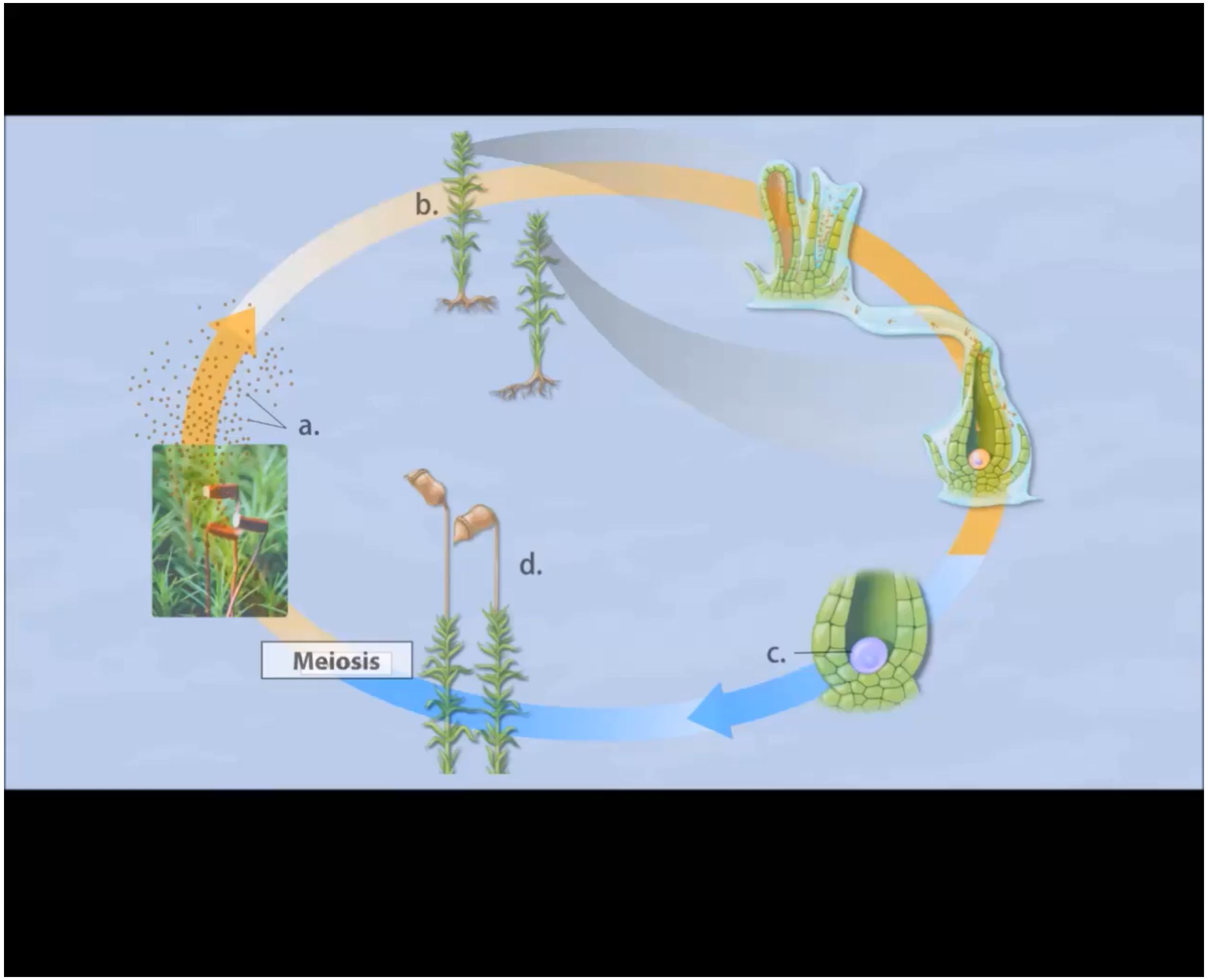
- Haploid gametophytes are dominant (larger and longer-living than sporophytes) in all bryophytes
- Sporophytes are usually present for only part of the life cycle

Figure 29.11



Haploid (n)
Diploid (2n)
"Bud"
Male gametophyte (n)
Antheridia
Sperm
Protonemata (n)
"Bud"
Egg
Archegonia
Spores
Spore dispersal
Female gametophyte (n)
Rhizoid
Peristome
Sporangium
MEIOSIS
FERTILIZATION
(within archegonium)
Seta
Capsule (sporangium)
Mature sporophytes
Foot
Zygote (2n)
Embryo
Archegonium
2 mm
Capsule (LM)
Female gametophytes
Young sporophyte (2n)

Animation: Moss Life Cycle



- When dispersed to a favorable habitat, bryophyte spores germinate and develop into gametophytes
- Moss spores produce a mass of green, branched, one-cell-thick filaments called a **protonema**
- The protonema absorbs water and nutrients and forms “buds” that develop into gametophytes

- Most bryophytes are constrained in height by
  - Lack of rigid support tissues
  - Lack of vascular tissue for long distance transport
- Some moss species have conducting tissues that enable growth up to 60 cm (2 feet) tall

- **Rhizoids** are root-like structures that anchor gametophytes to the substrate
- They lack specialized conducting cells and do not participate in water or mineral absorption

- Gametophytes can produce multiple **gametangia**, structures that produce gametes
- **Archegonia**, female gametangia, produce a single nonmotile egg
- **Antheridia**, male gametangia, produce many motile sperm

- Flagellated sperm swim to the egg through a film of water in response to chemical attractants
- The fertilized egg and resulting embryo are retained within the archegonium

- Sexual reproduction is limited by water availability and the proximity of male and female gametophytes
- Many bryophytes also reproduce asexually
  - For example, some mosses produce brood bodies, small plantlets that detach and form new plants

Figure 29.12

Bryophyte Sporophytes

- Bryophyte sporophytes are attached to and dependent on the gametophyte throughout their lives
- The gametophyte supplies sugars, amino acids, minerals, and water to the sporophyte
- These are the smallest sporophytes of all extant plant groups

- A typical bryophyte sporophyte consists of three major parts
  - The **foot** absorbs nutrients from the gametophyte
  - The **seta** (stalk) conducts nutrients to the sporangium
  - The sporangium, also called a **capsule**, produces spores by meiosis
- A **peristome** at the top of the capsule disperses spores when conditions are dry

- Moss and hornwort sporophytes are larger and more complex than liverworts
- They also have stomata, which liverworts lack

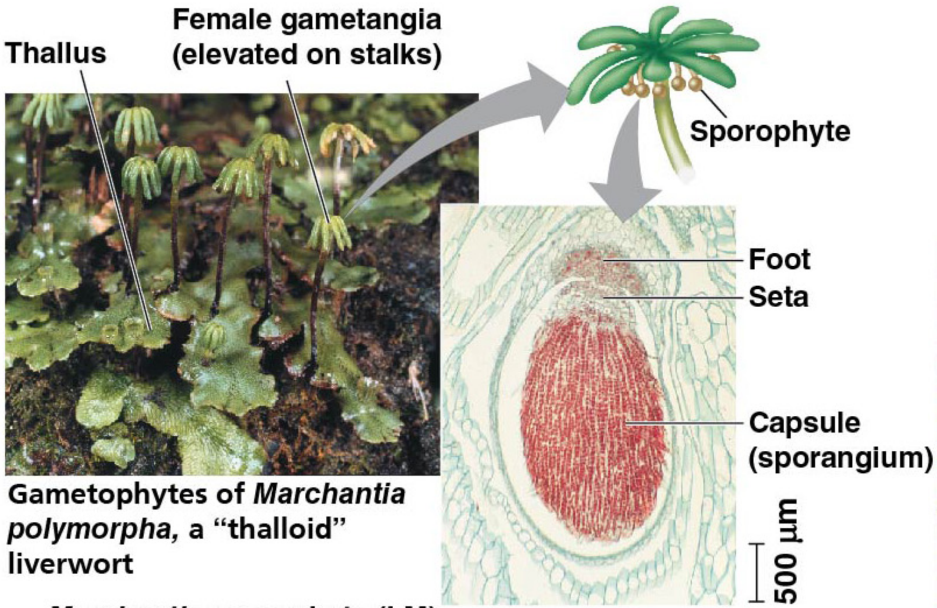
Figure 29.13 Exploring bryophyte diversity

Liverworts (Phylum Hepatophyta)

- Liverworts are named for their liver-shaped gametophytes
- Some species have gametangia elevated on stalks; others have stemlike gametophytes with many leaflike appendages

Figure 29.13a

Liverworts (Phylum Hepatophyta)



Gametophytes of *Marchantia polymorpha,* a “thalloid” liverwort

Marchantia sporophyte (LM)

Plagiochila deltoidea, a “leafy” liverwort

Hornworts (Phylum Anthocerophyta)

- Sporophytes are long and tapered horn-shaped structures, growing up to 5 cm tall
- Spores are released when the horn splits open
- Gametophytes are usually 1-2 cm diameter, grow horizontally, and have multiple sporophytes attached
- They form symbioses with nitrogen-fixing bacteria

Hornworts (Phylum Anthocerophyta)

An *Anthoceros* hornwort species

Mosses (Phylum Bryophyta)

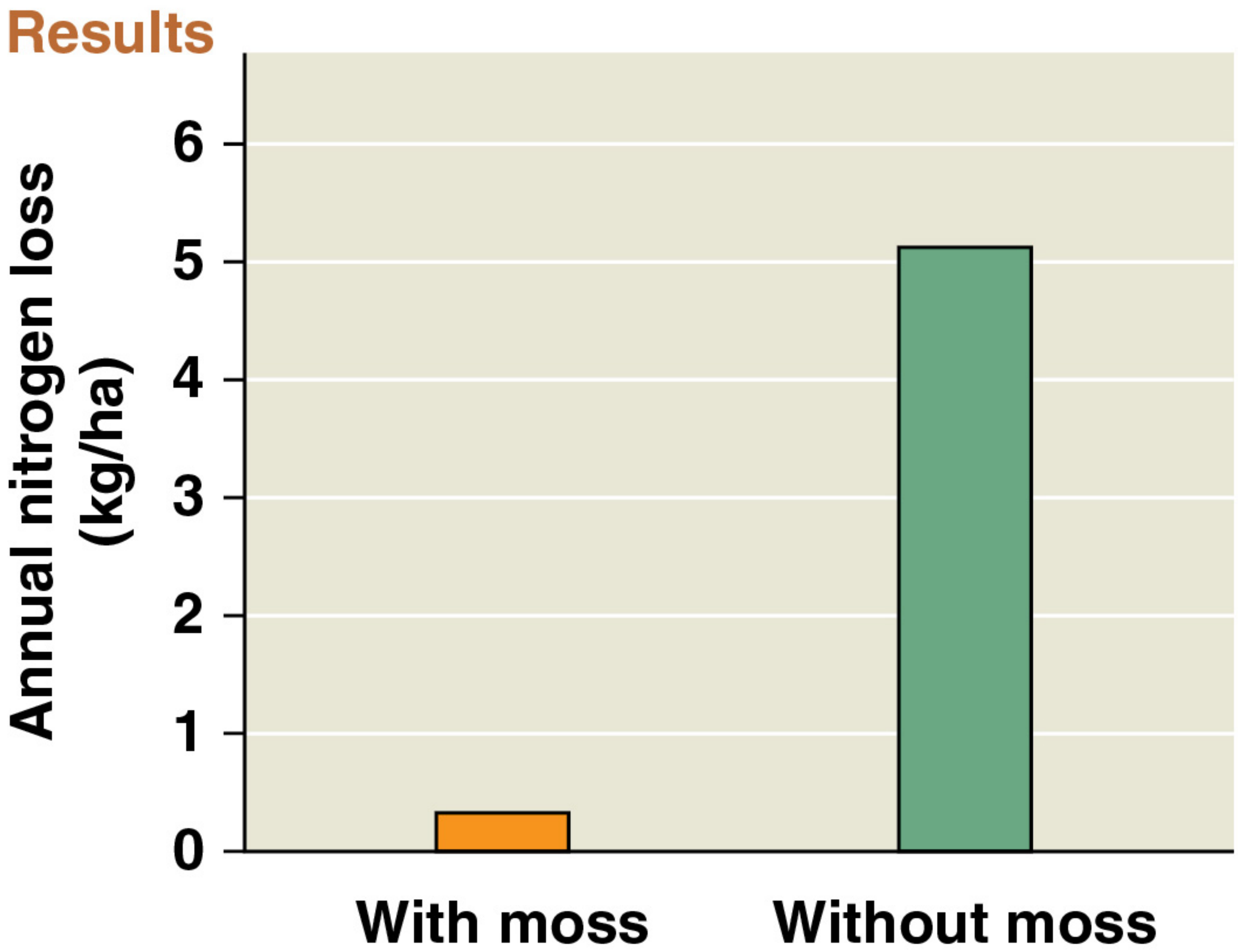
- Gametophytes are usually less than 15 cm tall, but range from 1 mm to 60 cm
- Sporophytes are usually visible to the naked eye
- They are green and photosynthetic when young, and turn brown before releasing spores

Mosses (Phylum Bryophyta)

The Ecological and Economic Importance of Mosses

- Mosses are common in moist forests and wetlands
- They also inhabit extremely cold, hot, and dry environments, rehydrating after complete desiccation
- Some colonize and help retain nitrogen in bare, sandy soils

Figure 29.14


Results
Annual nitrogen loss (kg/ha)
6
5
4
3
2
1
0
With moss
Without moss

- *Sphagnum*, or “peat moss,” forms extensive deposits of partially decayed organic material known as **peat**
- Peat can be used as a source of fuel
- The low temperature, pH, and oxygen level of peatlands inhibit decay of moss and other organisms
- Some peatlands have preserved corpses for thousands of years

(a) Peat being harvested from a peatland

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

- Peatlands cover 3% of Earth's land surface but contain one-third of the world's soil carbon
- Overharvesting of *Sphagnum* contributes to global warming by releasing stored CO_2
- Decomposition will start releasing even more CO_2 if water levels drop with warming temperatures

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

- Bryophytes were the prominent vegetation for the first 100 million years of plant evolution
- The earliest vascular plant fossils are 425 million years old
- Vascular tissue allowed plants to grow much taller
- Seedless vascular plants are still restricted to moist habitats where the sperm can swim to the egg

Figure 29.UN02

Nonvascular plants (bryophytes)

Seedless vascular plants

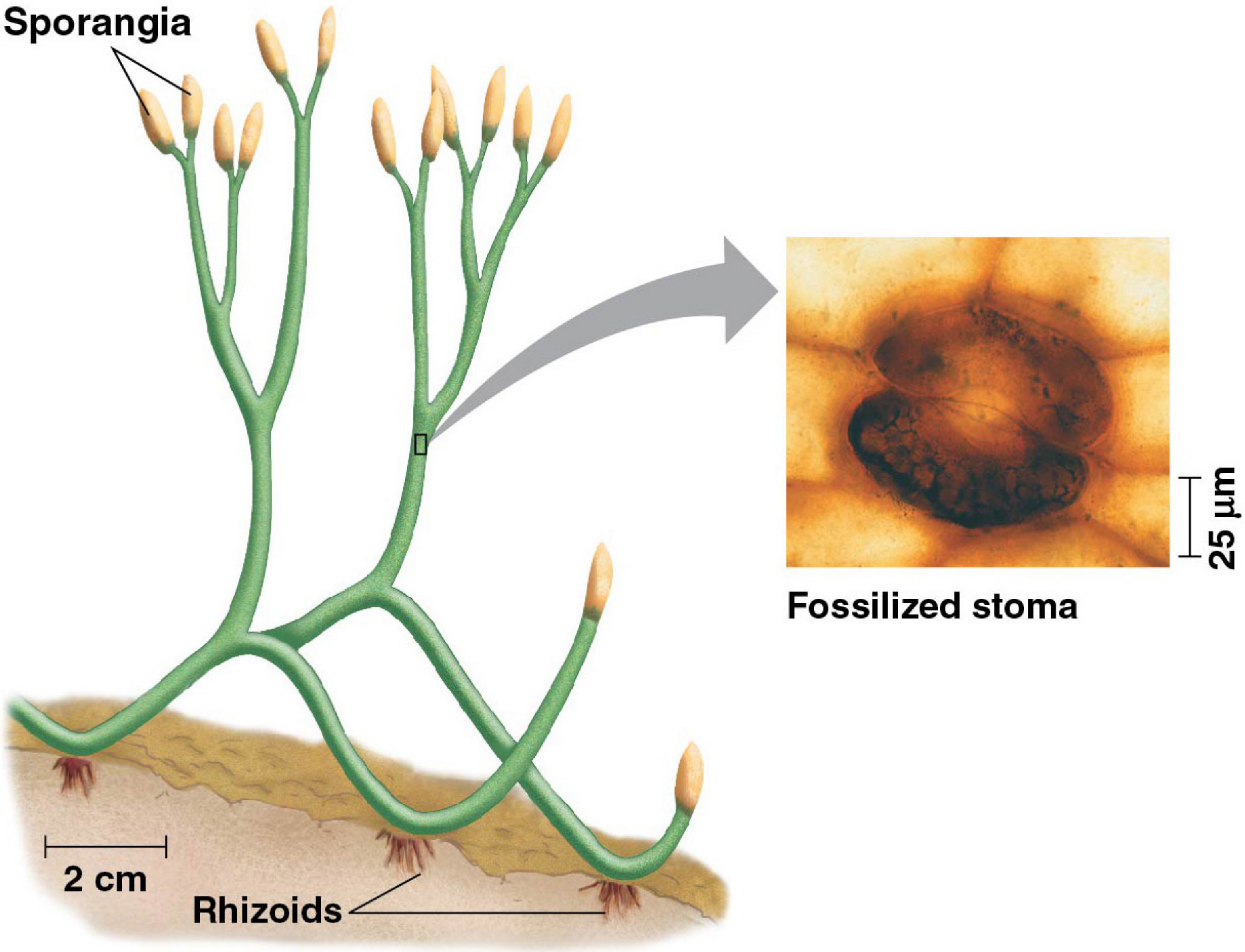
Gymnosperms

Angiosperms

Origins and Traits of Vascular Plants

- Early vascular plants had branching sporophytes that were less than 20 cm tall
- Unlike bryophytes, the vascular sporophyte lived relatively independent of the gametophyte
- Competition for space and sunlight likely stimulated further evolution within the vascular plants

Figure 29.16

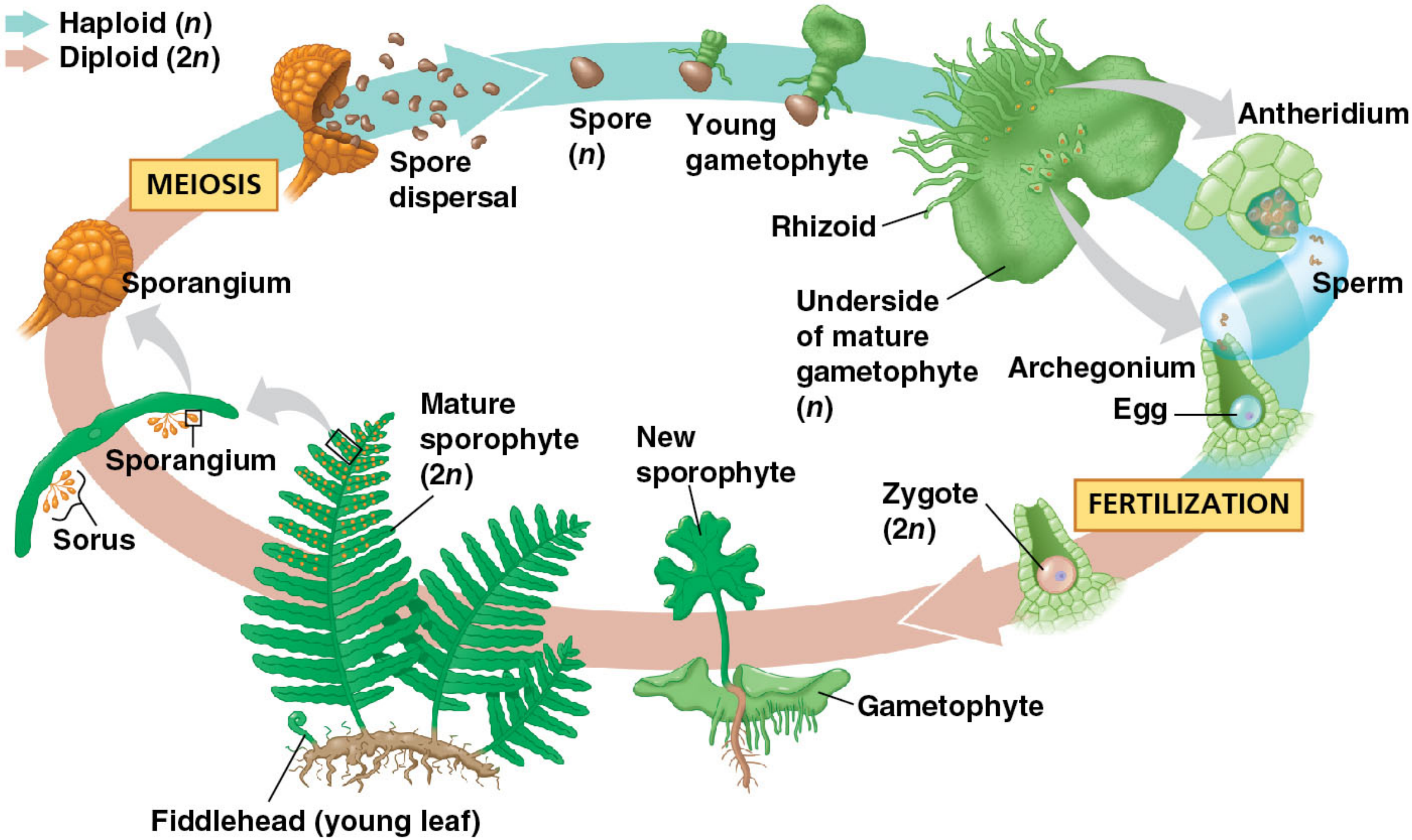


- Living vascular plants are characterized by
  - Life cycles with dominant sporophytes
  - Transport in vascular tissues called xylem and phloem
  - Well-developed roots and leaves
  - Spore-bearing leaves called sporophylls

Life Cycles with Dominant Sporophytes

- In seedless vascular plants the sporophytes are larger and more complex than the gametophytes
  - For example, in ferns, the familiar leafy plants are the sporophytes; gametophytes are tiny plants growing on or below the soil surface

Figure 29.17



Haploid (n)
Diploid (2n)
MEIOSIS
Spore dispersal
Spore (n)
Young gametophyte
Rhizoid
Underside of mature gametophyte (n)
Antheridium
Sperm
Archegonium
Egg
FERTILIZATION
Zygote (2n)
New sporophyte
Gametophyte
Mature sporophyte (2n)
Fiddlehead (young leaf)
Sporangium
Sporangium
Sorus

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**
- Xylem cells are dead at functional maturity and are lignified: strengthened by the polymer **lignin**

- The cells of the **phloem** tissue are arranged in tubes for transport of organic materials, such as sugar
- Phloem cells are alive at functional maturity

- Vascular tissue provided the structural support and long distance transport needed for plants to grow tall
- Taller plants were better able to compete for sunlight and could disperse spores further than shorter plants
- Selection for ever taller forms gave rise to the first forests 385 million years ago

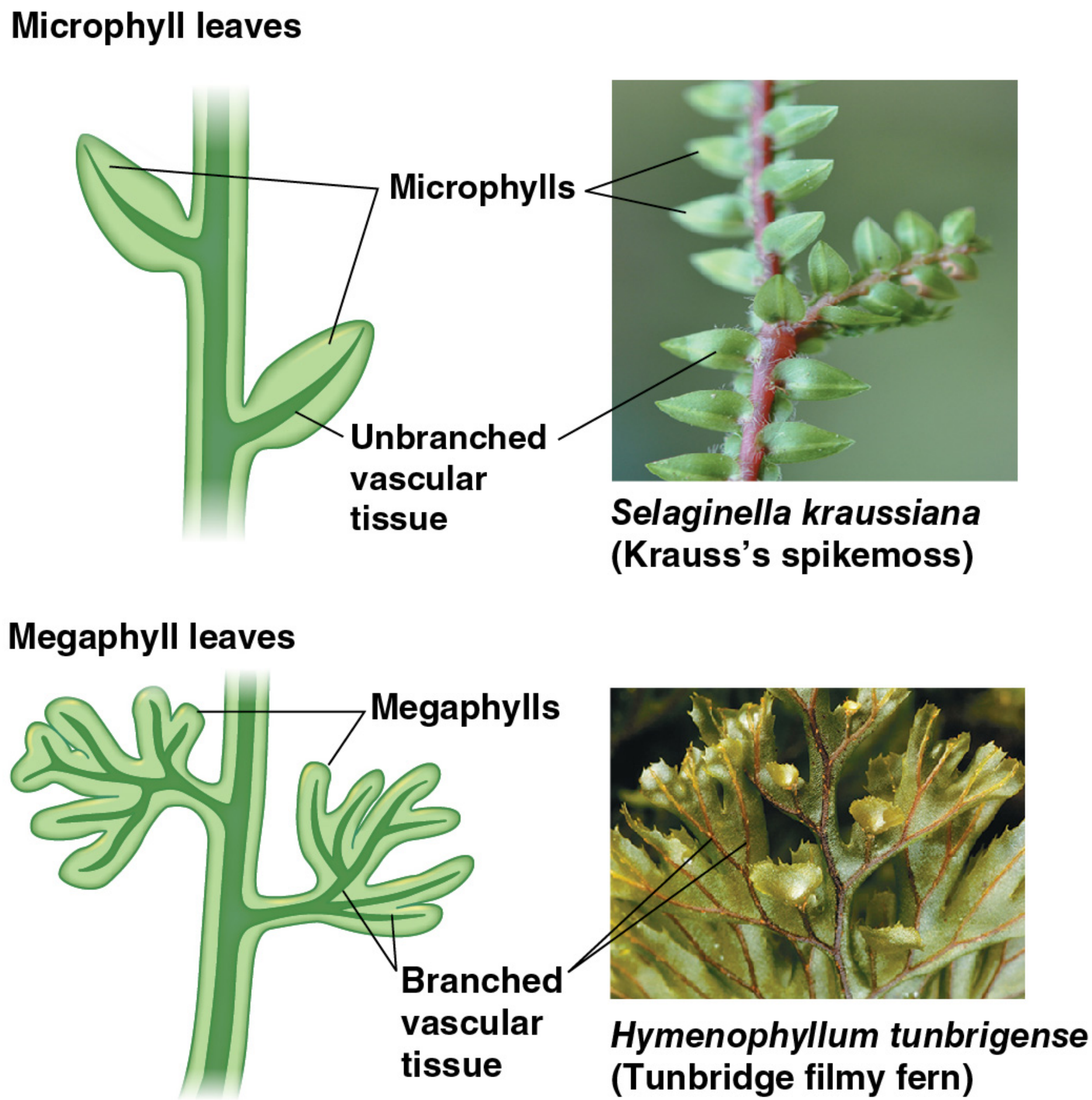
Evolution of Roots

- **Roots** are organs that anchor vascular plants into ground and absorb water and nutrients from the soil
- Root tissues closely resemble stem tissue of early vascular plants; roots may have evolved from belowground stems

Evolution of Leaves

- **Leaves** increase surface area for light capture and conduct most of the photosynthesis in plants
- They are categorized by two types:
  - **Microphylls**, small, often spine-shaped leaves with a single vein, are found only in lycophytes
  - **Megaphylls**, larger leaves with a highly branched vascular system, are found in all other plant groups

Figure 29.18


Microphyll leaves
Microphylls
Unbranched
vascular
tissue
Selaginella kraussiana
(Krauss's spikemoss)
Megaphyll leaves
Megaphylls
Branched
vascular
tissue
Hymenophyllum tunbrigense
(Tunbridge filmy fern)

Sporophylls and Spore Variations

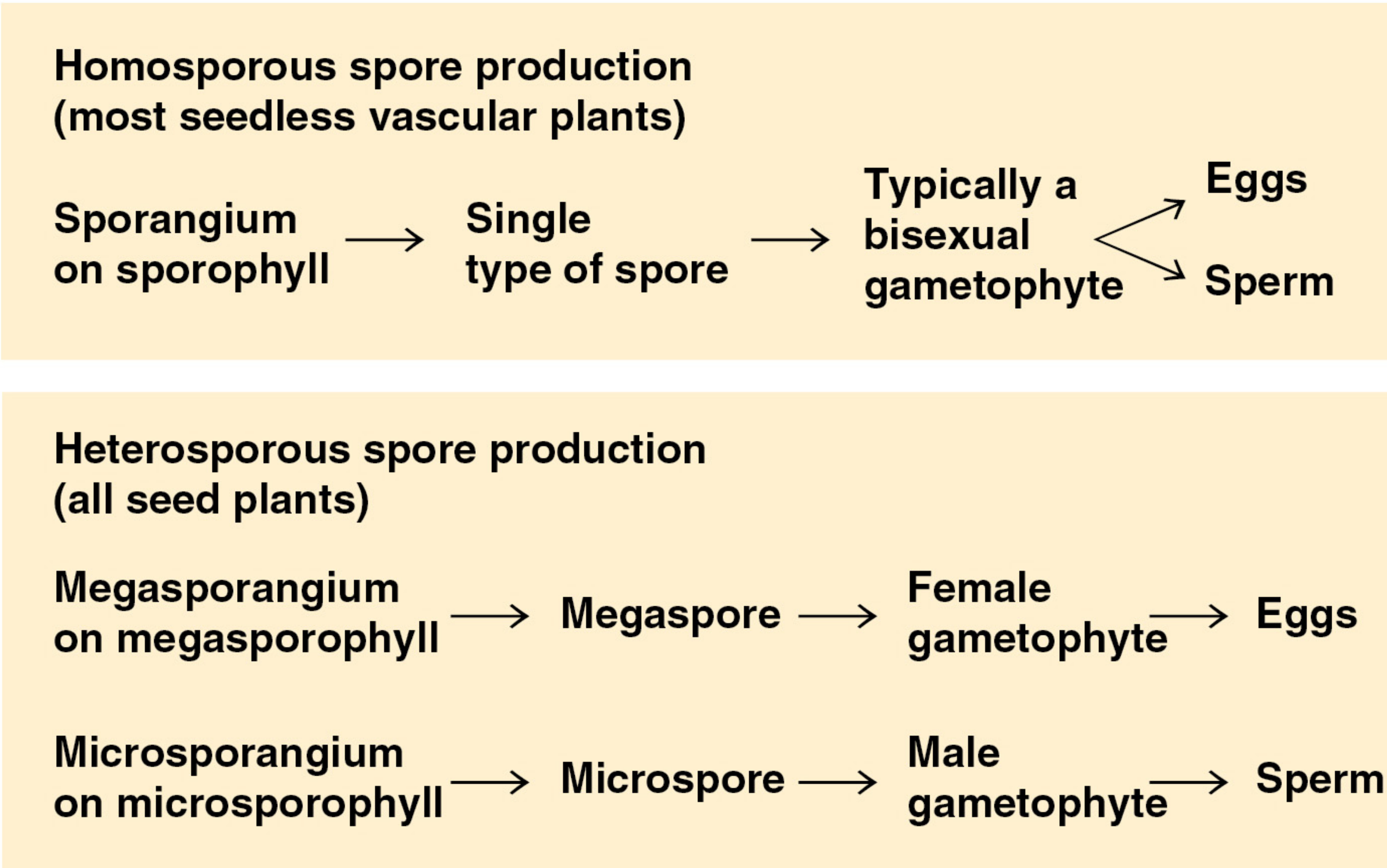
- **Sporophylls** are modified leaves with sporangia
- **Sori** are clusters of sporangia on the undersides of fern sporophylls
- Many lycophytes and most gymnosperms have **strobili**, clumps of sporophylls in cone-like structures
- The sporophylls of angiosperms are called carpels and stamens

- Most seedless vascular plants are **homosporous**
- They have one type of sporophyll and sporangium, which produces one type of spore
- The spores usually produce bisexual gametophytes

- All seed plants and some seedless vascular plants are **heterosporous**
- They have two types of sporophylls bearing different sporangia that produce different spore types
- The spores give rise to either male or female gametophytes

- Megasporophylls bear megasporangia, which produce relatively large megaspores
  - **Megaspores** develop into female gametophytes
- Microsporophylls bear microsporangia, which produce relatively small microspores
  - **Microspores** develop into male gametophytes

Figure 29.UN03



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

Figure 29.19 Exploring seedless vascular plant diversity

Lycophytes (Phylum Lycophyta)

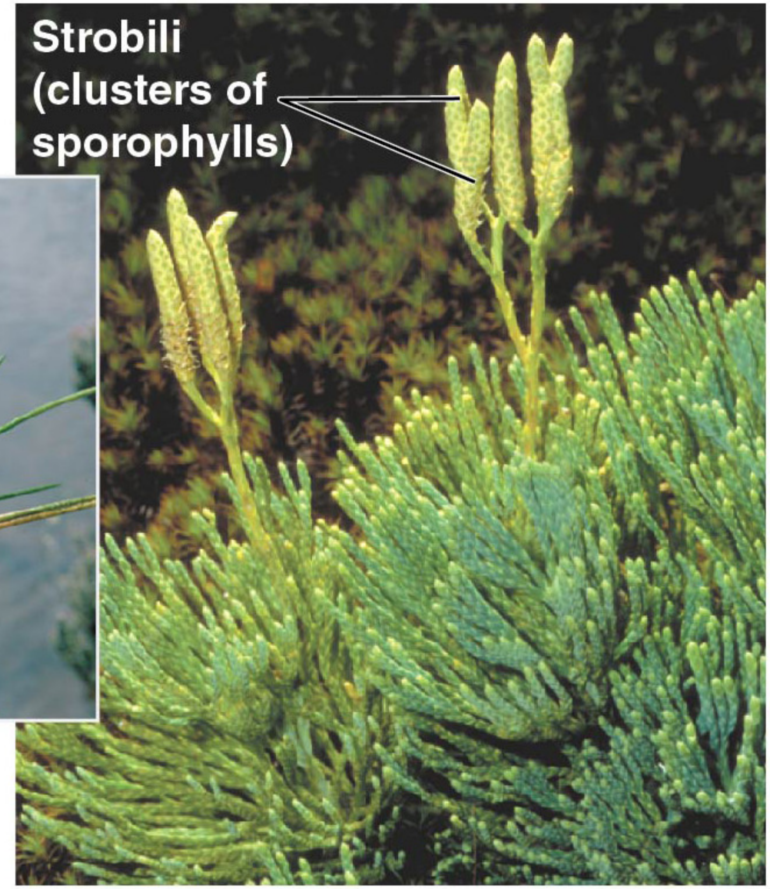
- Lycophytes grow in diverse habitats
- Some gametophytes are photosynthetic; others form below ground symbioses with fungi
- Sporophytes have both leaf-forming upright stems, and ground-hugging root-forming stems

- Spikemosses and quillworts are all heterosporous; clubmosses are homosporous
- Many spikemosses and clubmosses have strobili, sporophylls clustered into club-shaped cones

Lycophytes (Phylum Lycophyta)

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

***Isoetes gunnii*, a quillwort**



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

Monilophytes (Phylum Monilophyta)

- Monilophytes include ferns, horsetails, and whisk ferns and relatives

Monilophytes (Phylum Monilophyta)

Matteuccia struthiopteris **(ostrich fern)**

2.5 cm

Ferns

***Equisetum telmateia*, giant horsetail**

Strobilus on fertile stem

Vegetative stem

3 cm

Horsetails

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

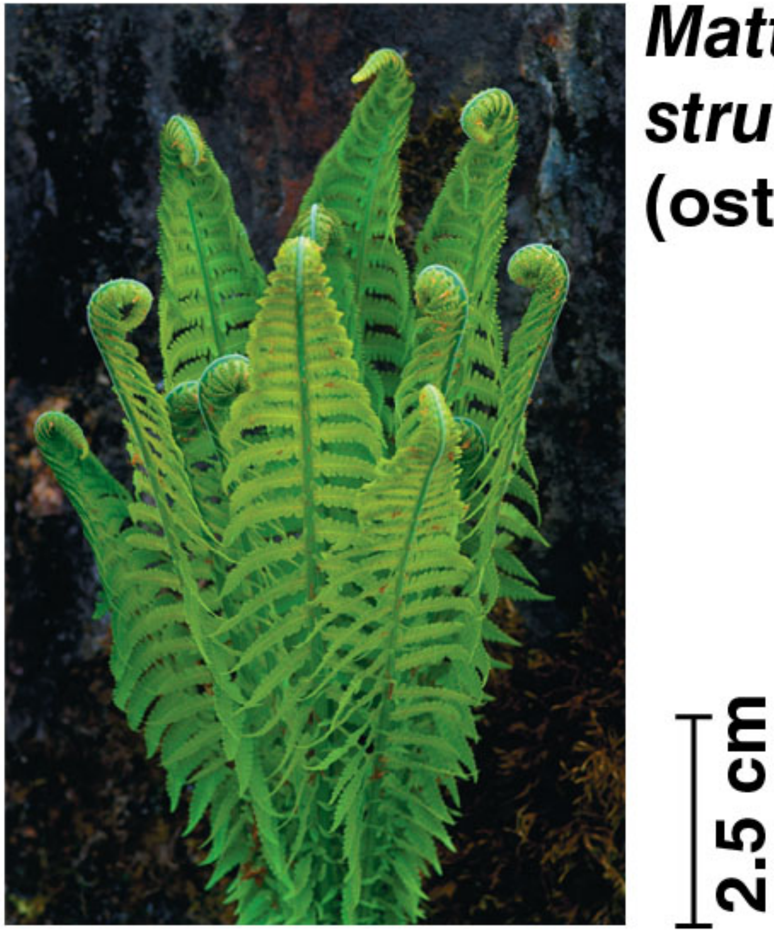
4 cm

Whisk Ferns and Relatives

Ferns

- Fern sporophytes have large megasporophylls (fronds) that are divided into leaflets
- A frond is coiled at the tip (the fiddlehead), which unfurls as the leaf grows
- Most species are homosporous, and have springlike devices for spore dispersal

Figure 29.19ba



***Matteuccia struthiopteris* (ostrich fern)**

Ferns

Horsetails

- Horsetail sporophytes have jointed stems with rings of small leaves or branches
- The gritty stems have historically been used for scouring pots and pans
- Some have separate fertile and vegetative stems
- Gametophytes are bisexual

Figure 29.19bb

Horsetails

Whisk Ferns and Relatives

- Whisk fern sporophytes have dichotomously branching stems but no roots
- Three fused sporangia form a yellow knob on the end of each stem
- All are homosporous with bisexual gametophytes
- *Tmesipteris*, closely related to whisk ferns, lack roots but have leaflike outgrowths of the stem

Psilotum nudum, **a whisk fern**

Whisk Ferns and Relatives

Phylum Lycophyta: Club Mosses, Spike Mosses, and Quillworts

- Lycophytes diversified into small herbaceous plants and giant trees by the Carboniferous period
- Trees survived for millions of years in moist swamps, but were lost to climate drying during the Permian period

- About 1,200 species of small lycophytes remain now
- Though commonly called club mosses and spike mosses, they are not true mosses
- They are vascular plants; true mosses are nonvascular

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; some live in arid habitats

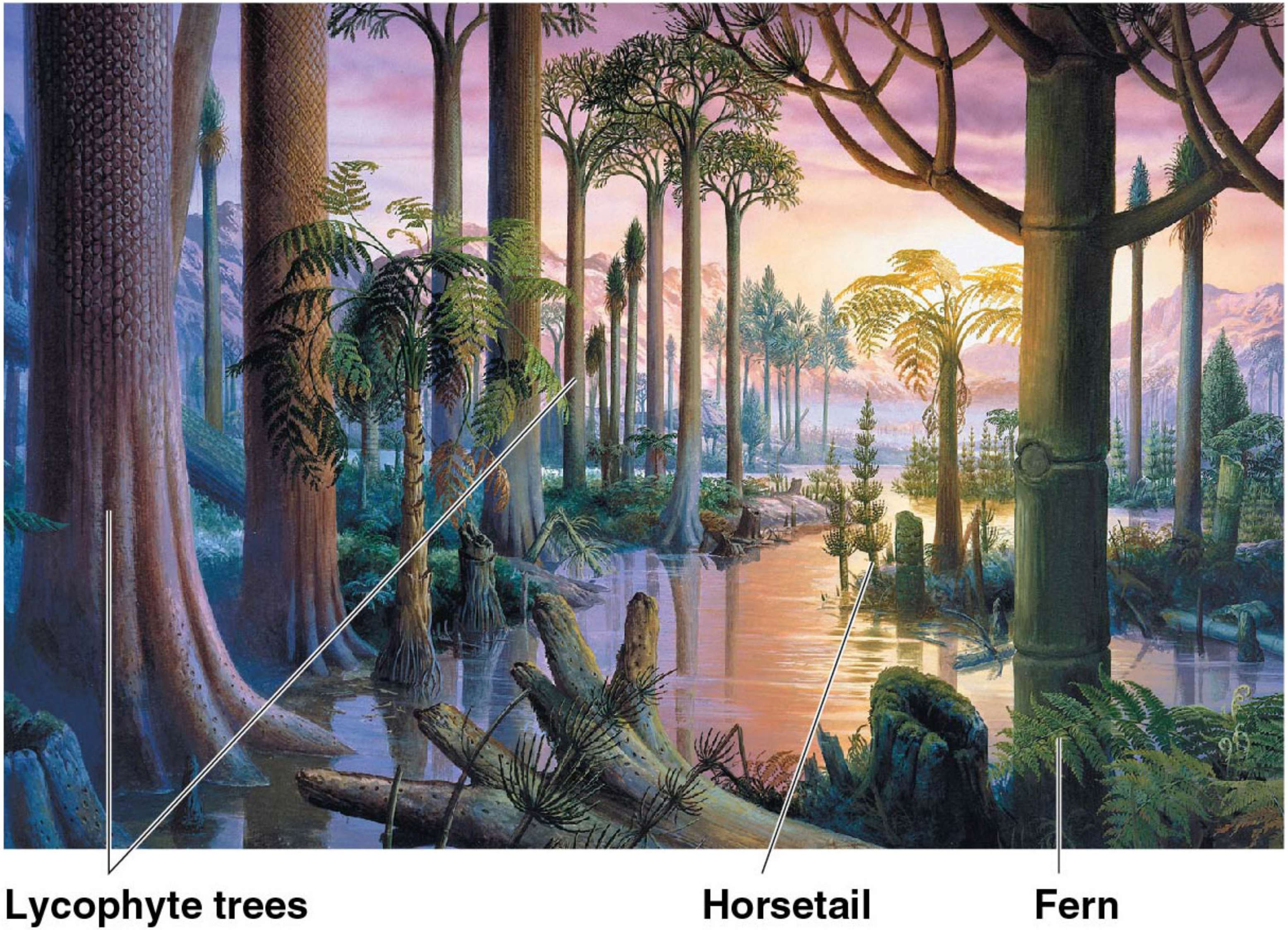
- Monilophytes are more closely related to seed plants than lycophytes
- Monilophytes and seed plants have megaphylls and roots that branch at variable points

- Horsetails were diverse during the Carboniferous period; today only 15 species in a single genus, *Equisetum*, remain
- *Psilotum* (whisk ferns) and *Tmesipteris* superficially resemble ancestral vascular plants but are closely related to modern ferns

The Significance of Seedless Vascular Plants

- Forests of lycophytes, horsetails, and ferns formed during the Devonian and Carboniferous periods
- Tree roots broke down rocks, releasing chemicals that reacted with CO_2
- The resulting compounds were washed into oceans
- Global cooling and widespread glaciation resulted from the subsequent drop in atmospheric CO_2

Figure 29.20



- Decay was slow in Carboniferous swamps; undecayed organic material slowly turned into peat
- Oceans formed, piling up marine sediments, and exerting heat and pressure on the peat
- Over millions of years, peat converted to coal, which people have burned since the Industrial Revolution

- Primitive seed plants also grew in early forests
- They rose to prominence after the swamps began to dry at the end of the Carboniferous period

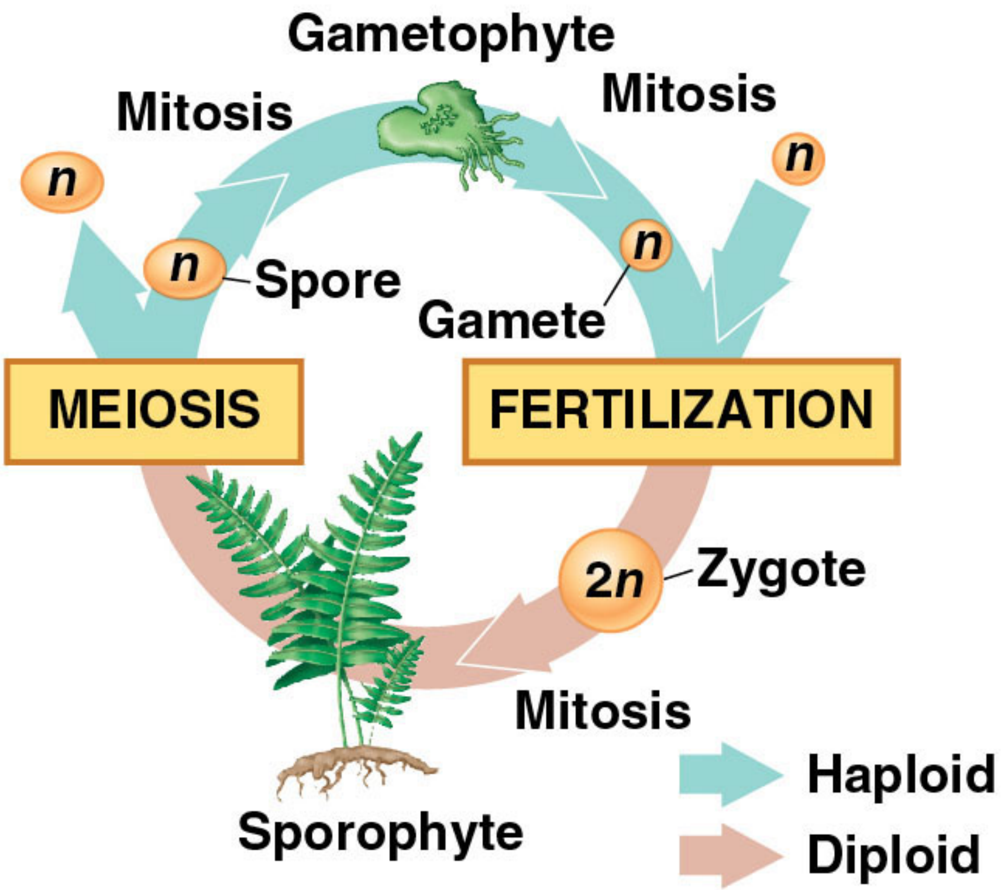
Figure 29.UN04a

	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

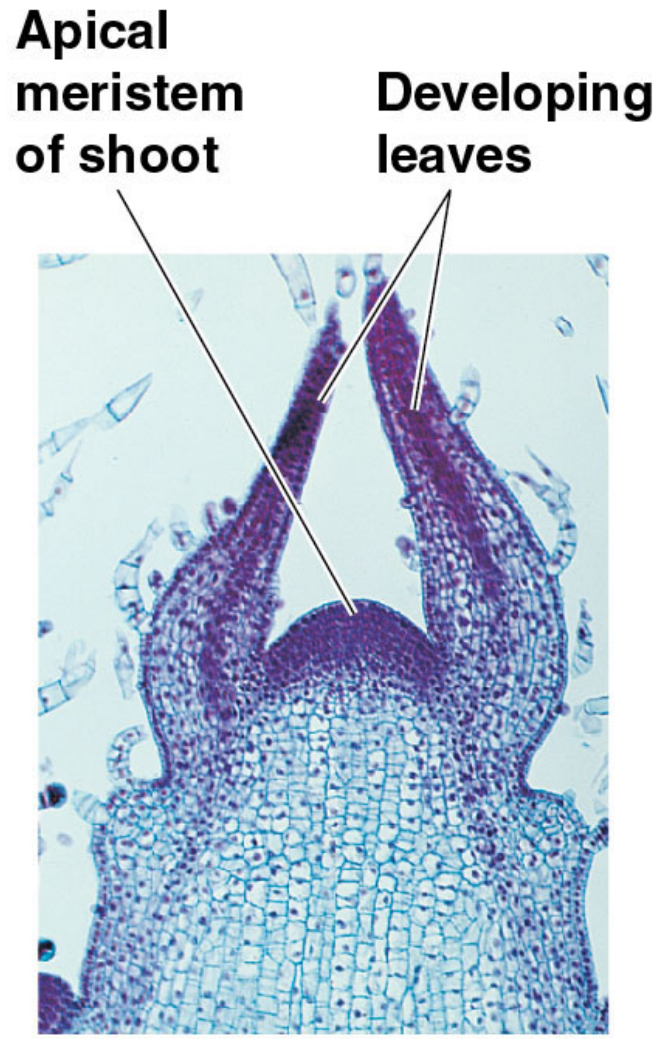
Data from O. Zackrisson et al., Nitrogen fixation increases with successional age in boreal forests, *Ecology* 85:3327–3334 (2006).

Figure 29.UN04b

Figure 29.UN05a

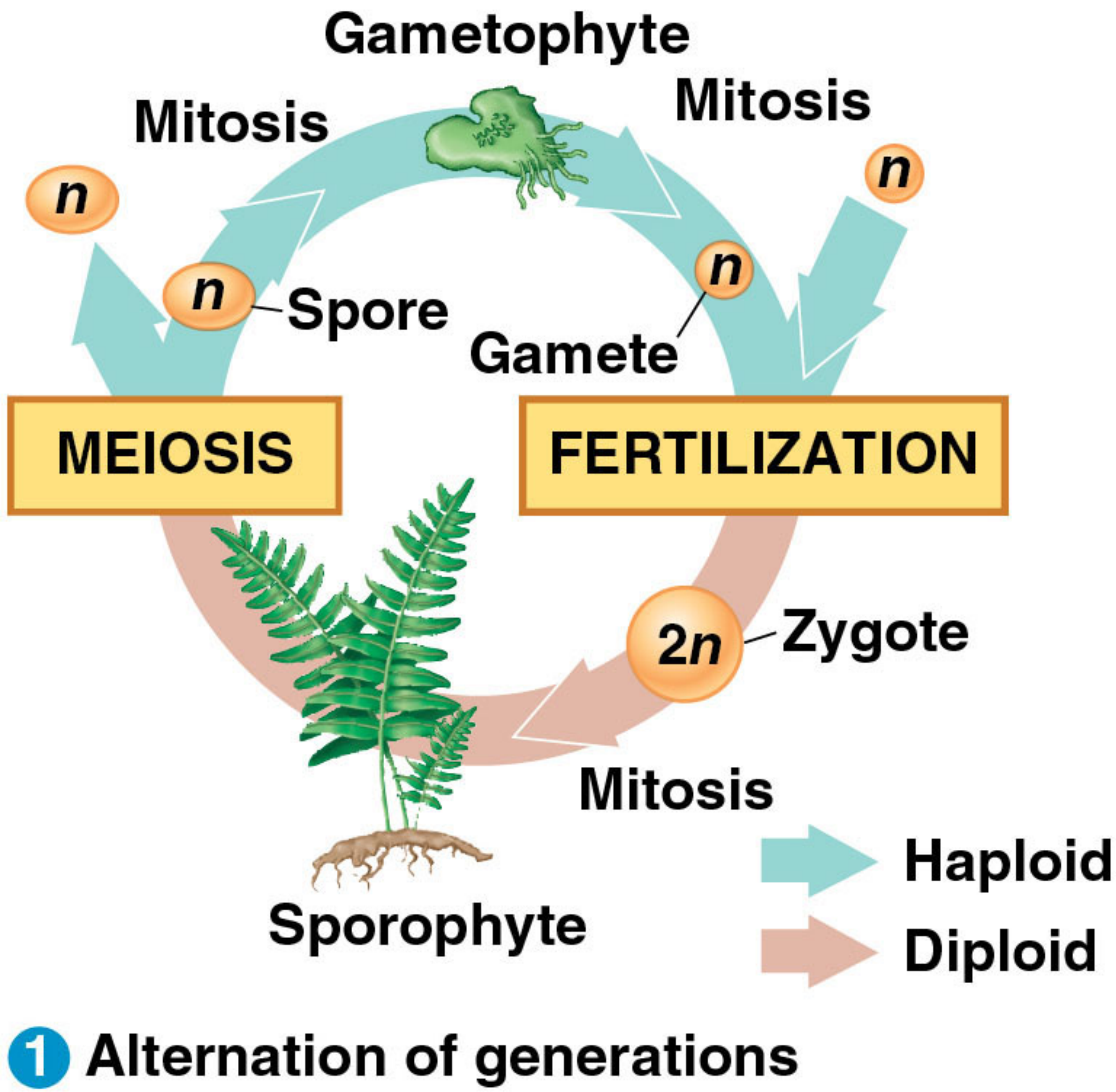


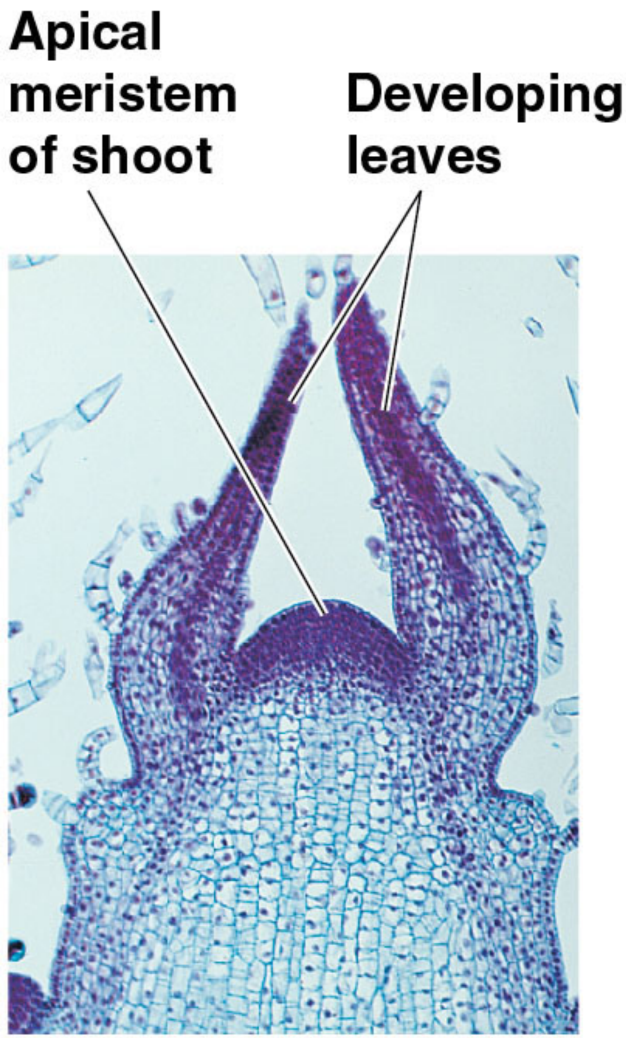
1 Alternation of generations



2 Apical meristems

Figure 29.UN05b





2 Apical meristems

Figure 29.UN06

Age (years after fire)	N fixation rate [Kg N/(ha · 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

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

Figure 29.UN07