The Plant Kingdom

- A plant is a photosynthetic eukaryote that uses chlorophylls *a* and *b*, stores carbohydrates, and develops from an embryo protected by tissues of the parent plant.
- The kingdom Plantae is monophyletic, forming a single branch of the evolutionary tree.
- Because of their development from embryos, plants are sometimes referred to as embryophytes.
- This textbook defines the kingdom Plantae as comprising only the embryophytes. (See Figure 29.1.)

There are ten surviving phyla of plants

- The surviving members of the kingdom Plantae fall naturally into ten phyla. (Table 29.1 shows the classification of plant phyla.)
- The seven plant phyla whose members possess well-developed vascular systems that transport materials throughout the plant body are called the tracheophytes.
- The remaining three phyla (liverworts, hornworts, and mosses) lack tracheids and are collectively referred to as the nontracheophytes.

Life cycles of plants feature alternation of generations

- The alternation of generations is a universal feature of the life cycles of plants. (See Figure 29.2.)
  - This life cycle includes both multicellular diploid individuals and multicellular haploid individuals.
  - Gametes are produced by mitosis, not meiosis. Meiosis produces spores that develop into multicellular haploid individuals.
- The multicellular, diploid plant is called the sporophyte.
  - Cells contained in the sporangia on the sporophyte produce haploid, unicellular spores through meiosis.
- The multicellular, haploid plant formed by mitosis and cytokinesis of a spore is called the gametophyte.
  - The gametophyte produces haploid gametes.
- The fusion of two gametes results in the formation of a diploid cell, the zygote, and the cycle repeats.
- The sporophyte generation extends from the zygote through the adult, multicellular, diploid plant; the gametophyte generation extends from the spore through the adult, multicellular, haploid plant to the gamete.
- Some protist life cycles also feature alternation of generations, suggesting that the plants arose from one of these protist groups.

The Plantae arose from a green algal clade

- Evidence indicates that the closest living relatives of the plants are a group of green algae called charophytes. (See Figure 29.1.)
  - We don't yet know, however, which charophyte clade is the sister group to the plants.
- The ancestral green algae lived at the margins of ponds or marshes. From these marginal habitats, early plants made the move onto land.
- (See Videos 29.1 and 29.2.)

The Conquest of the Land

- Plants or their immediate ancestors pioneered and modified the terrestrial environment, first invading 400–500 mya.
- The availability of water that was essential for life was a key difference between the aquatic and terrestrial environments. Water can be difficult to find and retain in the terrestrial environment.
- The land plants had to adapt to the new challenges that faced them in the terrestrial environment.

Adaptations to life on land distinguish plants from green algae

- Most of the characteristics that distinguish plants from the green algae are evolutionary adaptations to life on land. (See Figure 29.4.)
- Many of the following characteristics proved adaptive to land plants. A plant ancestral to today's plants probably shared all of the following characteristics:
  - The cuticle, a waxy covering that prevents drying
  - Gametangia, cases that enclose plant gametes and prevent drying
  - Embryos, young sporophytes contained within a protective structure
  - Pigments that afford protection against the mutagenic ultraviolet radiation that bathes the terrestrial environment
  - Thick spore walls to prevent drying and resist decay
  - A mutualistic association with a fungus that promotes nutrient uptake from the soil

Most present-day plants have vascular tissues

- The first plants lacked both water-conducting and food-conducting cells.
- The nontracheophytes utilize the following behaviors and structures to obtain water and minerals in the absence of a vascular system:
  - Many grow in dense masses through which water can move by capillary action. (See Figure 29.9*a*.)
  - They have leaflike structures that catch and hold water that splashes onto them.
  - They are small enough that minerals can be distributed evenly by diffusion.
- The tracheophytes differ from the nontracheophytes in many ways, one of which is the possession of a well-developed vascular system.
  - This vascular system consists of two specialized tissues used in the transport of materials from one part of the plant to another.
    - The phloem is used to conduct products of photosynthesis from sites where they are produced or released to sites where they are used or stored.
    - The xylem conducts water and minerals from the soil to the aerial parts of the plants.
    - The xylem, stiffened by a substance called lignin, also provides support in the terrestrial environment.
- The nontracheophyte plants evolved tens of millions of years before the tracheophyte plants, even though tracheophytes appear earlier in the fossil record. Because of their structure and chemical makeup, tracheophytes form fossils more readily.

The Nontracheophytes: Liverworts, Hornworts, and Mosses

- The nontracheophytes usually grow in dense mats in moist habitats. (See Figure 29.9*a*.)
- The nontracheophytes are generally small, most likely because they lack an efficient system for conducting water and minerals from the soil to distant parts of the plant body.
- Layers of maternal tissue prevent loss of water from the embryo.
- The nontracheophytes have a thin cuticle, though it is not highly effective in retarding water loss.
- The nontracheophytes are widespread across six continents and exist locally on the coast of Antarctica.

Nontracheophyte sporophytes are dependent on gametophytes

- In nontracheophytes, the familiar green structure visible to the naked eye is the gametophyte. (See Figure 29.5.)
- A nontracheophyte sporophyte produces unicellular, haploid spores as products of meiosis within a sporangium or capsule. The spore germinates and gives rise to a multicellular, haploid gametophyte whose cells contain chloroplasts and thus are photosynthetic.
- Gametangia are specialized sex organs in which gametes are formed.
  - The archegonium is a multicellular, flask-shaped female sex organ with a long neck and a swollen base that contains a single egg. (See Figure 29.6*a*.)
  - The antheridium is a male sex organ in which sperm are produced in large numbers. (See Figure 29.6*b*.)
- The sporophyte produces a sporangium, or capsule, within which meiotic divisions produce spores and thus the next gametophyte generation.
- (See Video 29.3.)

Liverworts may be the most ancient surviving plant clade

- The common name for members of the phylum Hepatophyta is liverworts. (See Figure 29.7.)
- Rhizoids are water-absorbing filaments that are found on the lower surfaces of the simplest liverwort gametophytes.
- Liverwort sporophytes have a stalk that connects the capsule and the foot. The stalk can elongate to raise the capsule above ground level, aiding in the dispersal of spores when they are released.
- Other liverworts utilize springlike structures to disseminate their spores.
  - In dry conditions, these structures shrink and cause a spring-like compression of a helical structure present in their cell walls.
  - With sufficient stress, this compressed structure snaps back into its original position, throwing spores in all directions.
- Species of the genus *Marchantia* are among the most familiar of the liverworts.
  - *Marchantia* and some other liverworts reproduce sexually and asexually.
  - Lens-shaped clumps of cells called gemmae are the means by which vegetative reproduction takes place.
- (See Video 29.4.)

Hornworts evolved stomata as an adaptation to terrestrial life

- The hornworts are the common name for the phylum Anthocerophyta.
- The hornworts, along with the mosses and the tracheophytes, all have an adaptation to life on land not found in the liverworts.
  - These groups all possess stomata that allow the uptake of CO_2 and the release of O_2, and can close to prevent excessive water loss.
- There are two characteristics that distinguish hornworts from liverworts and mosses.
  - The cells of hornworts contain a single large, platelike chloroplast, whereas the other nontracheophytes contain numerous small, lens-shaped chloroplasts.
  - Of all of the nontracheophyte sporophytes, the hornworts come closest to being capable of indeterminate growth.
    - Unlike the moss or liverwort sporophyte, whose stalk stops growing as the capsule matures, the hornwort sporophyte has no stalk.
    - The basal region of the hornwort sporophyte capsule remains capable of indefinite cell division that continuously produces new spore-bearing tissue.
- Cyanobacteria often populate internal, mucilage-filled cavities within hornworts. These cyanobacteria are able to fix atmospheric nitrogen gas into a nutrient form that can be used by the hornwort.
- The exact evolutionary status of hornworts is still unresolved.

Water and sugar transport mechanisms emerged in the mosses

- Members of the phylum Bryophyta are commonly known as mosses.
- The mosses are sister to the tracheophytes.
- Hydroid cells, a type of cell found in many mosses, are a likely progenitor of the characteristic water-conducting cell of the tracheophytes.
  - When hydroid cells die, they leave a tiny channel through which water can flow.
- The sporophytes of the mosses and tracheophytes grow by apical cell division, whereby a region at the growing tip provides an organized pattern of cell division, elongation, and differentiation.
- The moss gametophyte that develops following spore germination is a branched, filamentous structure called a protonema. (See Figure 29.5 and Animated Tutorial 29.1.)
  - Some filaments in the protonema are photosynthetic, whereas others, called rhizoids, are nonphotosynthetic and anchor the protonema to the substrate.
  - The tips of the photosynthetic filament eventually form buds.
  - The buds differentiate into a distinct tip and produce a leafy moss shoot with leaflike structures arranged spirally.
  - These leafy shoots produce the antheridia and the archegonia.
- Moss sporophyte stalks grow at their apical end, as do tracheophyte sporophytes.
- Sporophyte development in most mosses results in the formation of an absorptive foot, a stalk, and a swollen capsule at the tip.
- After meiosis and spore development are complete, the top of the capsule is shed.
- A series of toothlike structures surrounds the opening of the capsule and digs into the mass of spores when the atmosphere is dry.
- When the atmosphere becomes moist, they are flung out. Thus the spores are dispersed when conditions favor germination.
- The mosses have simple systems of internal transport, but because they lack xylem and phloem, they are not tracheophytes.

Introducing the Tracheophytes

- Although the tracheophytes are a large and diverse group, their appearance can be attributed to a single evolutionary event that occurred sometime during the Paleozoic era.
  - The sporophyte generation of a now-extinct organism produced a new cell type, called the tracheid. (See Figure 29.10.)
  - The tracheid is the principal water-conducting element in the xylem in all tracheophytes except the angiosperms.
- The evolution of tissue composed of tracheids had two important consequences:
  - It provided a pathway for long-distance transport of water and minerals from a source of supply to a source of need.
  - It provided rigid structural support, something almost completely unnecessary in the aquatic green algae.

- The tracheid set the stage for the complete and permanent invasion of land by plants.
- The tracheophytes also feature a branching, independent sporophyte.
- There are seven distinct phyla that are present-day evolutionary descendants of the early tracheophytes. (See Figure 29.10.)
- These seven phyla can be sorted into two groups: those that produce seeds and those that do not.

Tracheophytes have been evolving for almost half a billion years

- The plant kingdom successfully invaded the terrestrial environment between 400 and 500 million years ago.
- During the Devonian period, 409 to 354 mya, some remarkable developments arose.
  - The appearance and proliferation of the club mosses (lycopods), horsetails, and ferns made the environment more hospitable to animals.
  - Trees of various kinds appeared during this period.
  - Forests of lycopods flourished during the Carboniferous period. (See Figure 29.11.)
- In the subsequent Permian period, the 200-million-year reign of the lycopod–fern forests came to an end as they were replaced by forests of seed plants.

The earliest tracheophytes lacked roots and leaves

- The first tracheophytes belonged to the now-extinct phylum Rhyniophyta. (See Figure 29.12.)
- The rhyniophytes, which appear to have been the only tracheophytes during the Silurian period, had early versions of the structural features found in all other tracheophyte phyla.
- In 1917, the British paleobotanists Kidston and Lang found well-preserved tracheophyte fossils embedded in Devonian rocks near Rhynie, Scotland.
  - The fossil plants had a simple vascular system of xylem and phloem.
  - They lacked leaves and roots and were apparently anchored to the soil by horizontal portions of stem called rhizomes.
  - The presence of xylem indicated that these plants were tracheophytes.
  - It was initially unknown whether the plants were sporophytes or gametophytes.
  - Inspection of fossil sporangia showed that the spores were in groups of four.
  - Most living nonseed tracheophytes show an arrangement of spores such as this only in the sporophyte.
  - Because a group of four closely packed spores is found only immediately after meiosis, and because the only plant that produces such a group of four must be a diploid sporophyte, it was concluded that the Rhynie fossils must be sporophytes.

Early tracheophytes added new features

- Two new phyla of tracheophytes evolved—one (the Lycophyta) during the Silurian, and another (the Pteridophyta) during Devonian.
- These new groups had true roots, true leaves, and a differentiation between two types of spores.
- The origin of roots:
  - Roots probably had their evolutionary origins as a branch, either of a rhizome or of the aboveground portion of a stem.
  - The branch presumably penetrated the soil and branched further, thus anchoring the plant firmly and possibly absorbing water and minerals.
  - The underground and aboveground branches were subjected to sharply different environments and thus very different selection during the succeeding millions of years.
  - Therefore, the shoot and root systems diverged in structure and evolved distinct internal and external anatomies.
- The origin of true leaves:
  - A leaf is a flattened photosynthetic structure emerging laterally from a main axis or stem and possessing true vascular tissue.
  - The first leaf type, the microphyll, has a single vascular strand that has departed from the stem without disturbing the stem’s vascular structure. Plants of the phylum Lycophyta (club mosses) have such simple leaves.
  - The megaphyll is a larger, more complex leaf found in ferns and seed plants. It is thought to have arisen from a branching stem system followed by the development of photosynthetic tissue between the members of overtopped branches (groups of branches in which one branch differentiates from the others).
  - Figure 29.13 shows the evolution of microphylls and megaphylls.
- Homospory and heterospory:
  - Plants that bear a single type of spore are said to be homosporous. (See Figure 29.14*a*.)
  - Plants that bear two distinct types of spores evolved later, and are said to be heterosporous. (See Figure 29.14*b*.)

- In heterosporous plants, the megaspore develops into a larger, specifically female gametophyte, whereas the microspore develops into the smaller, male gametophyte.
- The most ancient tracheophytes were all homosporous.
- Heterospory evolved independently and repeatedly, suggesting that it affords selective advantages.

The Surviving Nonseed Tracheophytes

- The nonseed Tracheophytes have a large, independent sporophyte and a small, independent, short-lived gametophyte.
- The single-celled spore is the most prominent resting stage of the life cycle, as in the fungi, the green algae, and the nontracheophytes (but not in the seed plants).
- Nonseed tracheophytes must have an aqueous environment for at least one stage of their life cycle because fertilization is accomplished by motile, flagellated sperm.
- Today, the ferns are the most abundant and diverse phylum of the nonseed tracheophytes, but club mosses and horsetails used to be the dominant elements of Earth's vegetation.

The club mosses are sister to the other tracheophytes

- The club mosses (phylum Lycophyta) diverged earlier than all other living tracheophytes.
- They bear microphylls, exhibit apical growth, and have roots that branch dichotomously.
- Sporangia in many club mosses are contained within conelike structures called strobili, clusters of spore-bearing leaves inserted between a specialized leaf and the stem. (See Figure 29.15.) Other club mosses bear their sporangia between a photosynthetic leaf and the stem.
- There are both homosporous and heterosporous species.
- The Lycophyta are one of the two phyla that appear to have been the dominant vegetation during the Carboniferous period.
- The fossilized spores of a tree lycopod called *Lepidodendron* form an abundant type of coal.

Horsetails, whisk ferns, and ferns constitute a clade

- The horsetails, whisk ferns, and ferns form a clade, the phylum Pteridophyta.
- Horsetails grow at the bases of stem segments.
  - The horsetails (phylum Pteridophyta) have true roots that branch irregularly, bear simple leaves that form circles around the stem, and exhibit basal growth. (See Figure 29.16.)
- Present-day whisk ferns resemble the most ancient tracheophytes.
  - The existence of two genera of rootless, spore-bearing plants, *Psilotum* and *Tmesipteris*, caused disagreement about whether the rhyniophytes were entirely extinct. (See Figure 29.17.)
  - DNA sequence data settled this disagreement in favor of a more modern origin from fernlike ancestors.
  - Whisk ferns are considered to be highly specialized plants that evolved fairly recently.

Ferns evolved large, complex leaves

- The sporophytes of the ferns typically have large leaves with branching vascular strands.
- The ferns first appeared during the Devonian period and today consist of about 12,000 species.
- About 97 percent of fern species belong to one clade, the leptasporangiate ferns. These ferns have sporangia with walls only one cell thick, borne on a stalk.
- Ferns are characterized by fronds (see Figure 29.18) and male gametes that require water for transportation to the female gametes.
- Sporangia are found on the undersurfaces of leaves; in most species, they are clustered in groups called sori. (See Figure 29.19.)

The sporophyte generation dominates the fern life cycle

- Figure 29.20 shows the life cycle of a fern.
- A spore germinates and forms a heart-shaped gametophyte, bearing antheridia or archegonia (or both) on its underside.
- Stimulated by water, the antheridia release sperm that swim to a nearby archegonium and fertilize an egg.
  - These spiral-shaped, flagellated sperm are guided by chemical attractants released from the archegonia (also, in response to water).
- The resulting diploid embryo forms roots and fronds, and grows into the familiar sporophyte life stage.
- Most ferns are homosporous, but there are two groups of aquatic ferns that are heterosporous: the Marsileales and Salviniales.

- (See Video 29.5.)