Chapter 29

Plant Diversity I: How Plants Colonized Land

Key Concepts

29.1 Land plants evolved from green algae

29.2 Land plants possess a set of derived terrestrial adaptations

29.3 The life cycles of mosses and other bryophytes are dominated by the gametophyte stage

29.4 Ferns and other seedless vascular plants formed the first forests

Framework

The evolution of plants involved adaptations to terrestrial habitats. The kingdom Plantae includes multicellular, photoautotrophic eukaryotes that develop from embryos nourished by the parent plant. Plants exhibit an alternation of generations in which the diploid sporophyte is the more conspicuous stage in all groups except the bryophytes. This chapter outlines the major periods of plant evolution in which bryophytes and seedless vascular plants appeared and radiated.

Chapter Review

For more than the first 3 billion years of Earth's history, life was confined to aquatic environments. Plants began to move onto land about 500 million years ago, and have now diversified into 290,000 species.

29.1 Land plants evolved from green algae

Several lines of evidence indicate that a few lineages of green algae, called charophyceans, are the closet relatives of land plants.

Morphological and Biochemical Evidence Land plants have chloroplasts containing chlorophylls *a* and *b* and cell walls of cellulose. These characteristics, however, are shared with several algal groups and cannot be used to distinguish plants from algae. Two features that do link plants to the charophyceans are **rosette cellulose-synthesizing complexes,** which produce the cellulose microfibrils of their cell walls, and enzymes within peroxisomes that help minimize photorespiration losses. Other derived homologies in charophyceans and land plants include similarities in sperm cells (in those land plants that have flagellated sperm) and the formation of a **phragmoplast** in mitosis. This alignment of cytoskeletal elements and vesicles in the synthesis of a cell plate is found only in plants and certain charophyceans, such as *Chara* and *Coleochaete.*

Genetic Evidence Results from the analysis of nuclear and chloroplast genes done during the international initiative called "Deep Green" confirm that charophyceans species such as *Chara* and *Coleochaete* are the closest living relatives of land plants.

Adaptations Enabling the Move to Land The tough polymer **sporopollenin** protects charophycean zygotes during fluctuations in water levels. With the accumulation of traits such as sporopollenin, ancient charophyceans living along the edges of ponds and lakes may have given rise to the first plants to colonize land.

■ INTERACTIVE QUESTION 29.1

List some of the lines of evidence that indicate that charophyceans and land plants shared a common ancestor.

29.2 Land plants possess a set of derived terrestrial adaptations

Defining the Plant Kingdom Systematists are debating three different ways in which to establish the boundaries of the plant kingdom: the traditional kingdom Plantae containing only embryophytes (plants with embryos); the kingdom Streptophyta, which includes the charophyceans; or the kingdom Viridiplantae, which includes the chlorophytes as well as the charophyceans with the embryophytes. This textbook uses the traditional embryophyte definition of kingdom Plantae.

Derived Traits of Plants The following derived traits distinguish land plants as a clade: apical meristems, alternations of generations, walled spores produced in sporangia, multicellular gametangia, and multicellular dependent embryos.

Regions of cell division at the tips of roots and shoots, called **apical meristems,** produce linear growth and cells that differentiate into a protective epidermis and internal plant tissues. The elongation of roots and shoots provides increasing access to environmental resources.

Alternation of generations is the life cycle found in all land plants. Whereas this type of reproductive cycle did evolve in various groups of algae, it does not occur in the charophyceans and appears to be a derived character of land plants. In this life cycle, the multicellular haploid **gametophyte** alternates with the multicellular diploid **sporophyte.** The sporophyte produces **spores,** which are reproductive cells that directly develop into new organisms. Review the alternation of generations in Interactive Question 29.2.

■ INTERACTIVE QUESTION 29.2

The gametophyte produces a. __________ by b. __________. Following fertilization, the c. __________ divides by d. __________ to develop into the e. __________. The sporophyte produces f. __________ by g. __________. The spores germinate and develop into the h. __________.

The tough polymer sporopollenin protects spores as they disperse on land. Spores develop and are protected within multicellular **sporangia** on the sporophyte plant. Diploid cells called **sporocytes,** or spore mother cells, undergo meiosis and produce haploid spores in sporangia.

Gametes are produced within multicellular **gametangia.** Sperm are produced in gametangia called **antheridia.** A single egg cell is produced and fertilized within an **archegonium,** where the zygote develops into an embryo. In the reduced gametophytes of seed plants, the antheridia and archegonia have been lost in most lineages.

Plant embryos, which are retained in the female plant, have **placental transfer cells** that facilitate the transfer of nutrients from parental tissues. This derived trait is the basis for referring to land plants as **embryophytes.**

Many land plants have a waxy **cuticle** coating their leaves and stems, which protects from water loss and microbial attack. Many plants produce secondary compounds through side branches of their main metabolic pathways. These compounds, which include alkaloids, terpenes, tannins, and phenolics, may discourage herbivory or microbial attack, protect from UV radiation, or serve as signals.

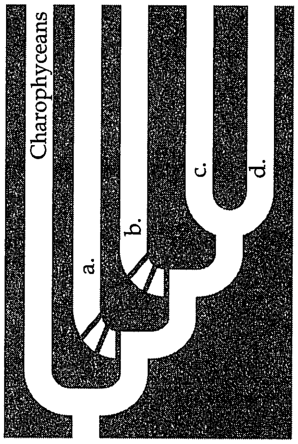
The Origin and Diversification of Plants Fossil spores have been found that date back 475 million years. In 2003 a "molecular clock" study estimated that the common ancestor of living plants lived 490 to 425 million years ago.

Most plants have **vascular tissue,** a transport system composed of cells joined into tubes, and are called **vascular plants.** Liverworts, hornworts, and mosses do not have an extensive transport system and are referred to as nonvascular plants and informally called **bryophytes.** Whether or not these groups form a clade is still debated.

Vascular plants, about 93% of plant species, do form a clade, and are divided into three smaller clades. The **lycophytes** (club mosses and their relatives) and the **pterophytes** (ferns and their relatives) are two clades informally called **seedless vascular plants.** A **seed** is an embryo enclosed with a supply of nutrients in a protective coat. The third clade, the seed plants, contains two groups: The **gymnosperms** are called "naked seed" plants because their seeds are not enclosed; **angiosperms** are the flowering plants, in which seeds develop inside chambers called ovaries in a flower. Taxonomists recognize ten phyla of extant plants.

■ **INTERACTIVE QUESTION 29.3**

Fill in this overview diagram of the major plant groupings. (Note that the plants in b. do not constitute a clade—they are not monophyletic. The plants in a. may or may not form a clade.)



29.3 The life cycles of mosses and other bryophytes are dominated by the gametophyte stage

The three separate phyla of nonvascular plants are **liverworts** (phylum Hepatophyta), **hornworts** (phylum Anthocerophyta), and **mosses** (phylum Bryophyta). The evolutionary relationships of these groups continue to be debated.

Bryophyte Gametophytes In the bryophytes, the gametophyte is the prevalent generation; sporophytes are present only part of the time. Liverwort and hornwort gametophytes grow more horizontally than do moss gametophyte. When moss spores germinate in a moist habitat, they grow into a mass of green filaments called a **protonema.** Meristem-containing buds grow into gamete-producing upright "stems" called **gametophores.** Bryophyte gametophytes are generally only a few cells thick and low growing. They are anchored by **rhizoids.**

Some mosses, such as *Polytrichum,* have leaf ridges coated with cuticle and conducting tissues in their "stems." Plant biologists have yet to determine whether these tissues are homologous or analogous with vascular tissue.

Gametangia are enclosed in jackets of protective tissue. Sperm are produced in antheridia, from which they swim to eggs retained in archegonia. Zygotes develop into embryos, which rely on nutrients transported by placental transfer cells to develop into sporophytes.

Bryophyte Sporophytes Although they are usually photosynthetic when young, bryophyte sporophytes remain attached to and dependent on their parental gametophytes. A sporophyte has a **foot** that obtains nutrients from the gametophyte, a stalk **(seta)** that elongates for spore dispersal, and a sporangium or **capsule** in which millions of spores are produced by meiosis. The protective **calyptra** covers the immature capsule. The specialized "toothed" **peristome** gradually releases spores to be dispersed by wind currents.

Liverworts have tiny, simple sporophytes. The sporophytes of hornworts and mosses have **stomata,** pores through which gases are exchanged and water evaporates. There are three possible evolutionary origins of stomata: in the ancestor of all three groups and later lost in the liverwort lineage; in the ancestor of the branch leading to hornworts, mosses, and vascular plants; or in the ancestor of mosses and vascular plants, with an independent origin in hornworts.

■ **INTERACTIVE QUESTION 29.4**

Review the life cycle of a typical moss plant by filling in the following blanks.

The dominant generation is the a. __________. Female gametophytes produce eggs in b. __________. Male gametophytes produce sperm in c. __________. Sperm d. __________ through the damp environment to fertilize the egg. The zygote remains in the archegonium and grows into the e. __________ still attached to the female gametophyte. Spores are formed by the process of f. __________ in the g. __________. When shed, spores develop into the h. __________.

Ecological and Economic Importance of Mosses Bryophytes are widely distributed and common in moist habitats. Some are adapted to very cold or dry habitats due to their ability to dehydrate and rehydrate without dying. Phenolic compounds absorb damaging radiation in harsh environments. *Sphagnum,* or peat moss, is an abundant wetland moss that forms undecayed organic deposits known as **peat.** The decay-resistant compounds in peat bogs can preserve organisms for thousands of years. Peat serves as huge stores of organic carbon and helps to stabilize atmospheric carbon dioxide concentrations. Peat is harvested for use as fuel, a soil conditioner, and plant packing material.

29.4 Ferns and other seedless vascular plants formed the first forests

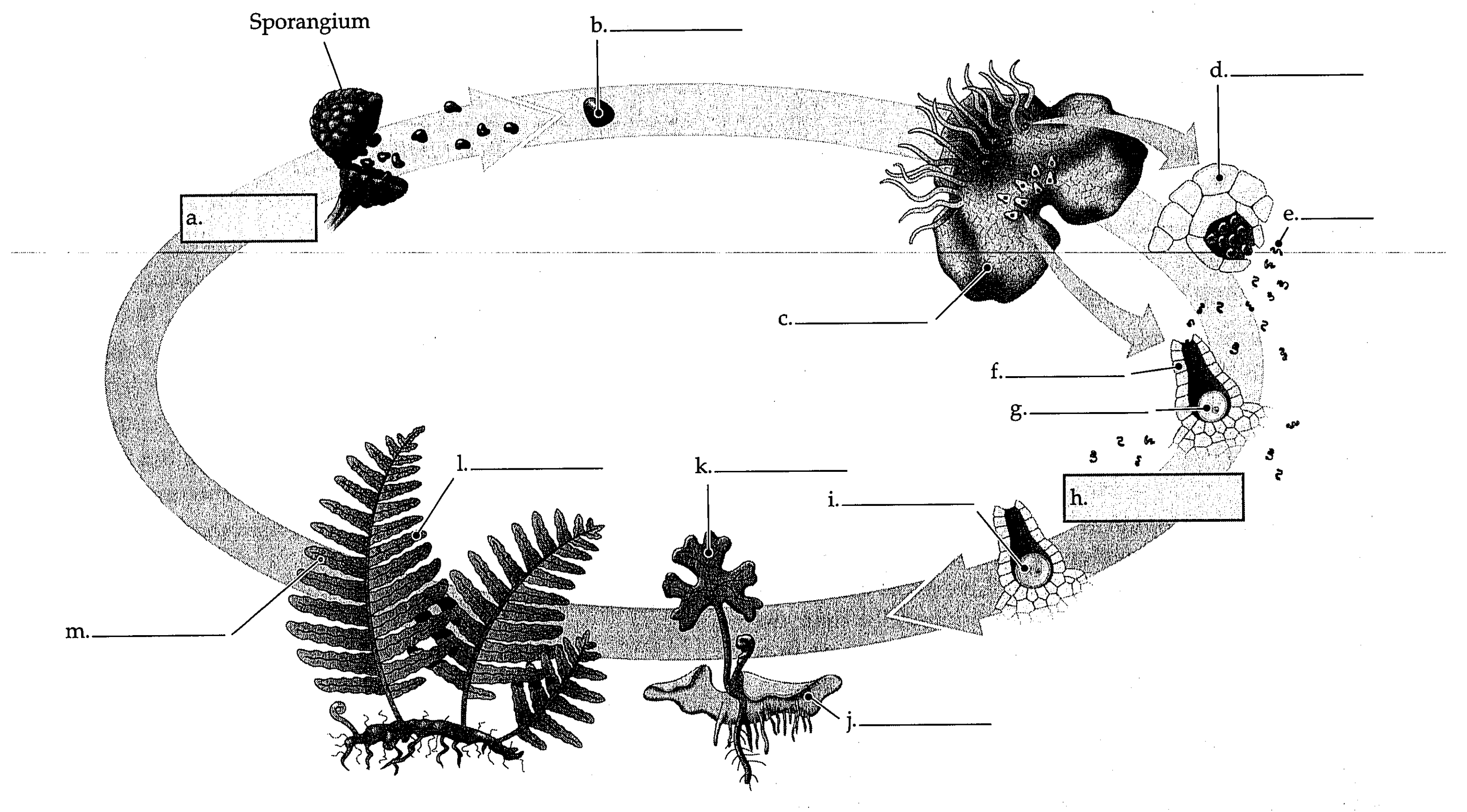
Bryophytes were the dominant plants in the first 100 million years of plant evolution. Seedless vascular plants began to spread during the Carboniferous period, but remained limited to damp habitats because of their swimming sperm and fragile gametophytes.

Origins and Traits of Vascular Plants Fossils of ancient relatives of modern vascular plants date back 420 million years. These tiny plants had branched, independent sporophytes and terminal sporangia. The branching made possible more complex bodies and multiple sporangia. They lacked other derived traits of vascular plants.

In modern vascular plants, the diploid sporophyte is the larger and more complex plant. Gametophytes are tiny structures growing on or under the soil surface. Trace the life cycle of a fern in Interactive Question 29.5.

■ INTERACTIVE QUESTION 29.5

In the following diagram of the life cycle of a fern, label the processes (in the boxes) and structures (on the lines). Indicate which portion of the life cycle is haploid and which is diploid.



Water and minerals are conducted up from roots in **xylem.** The xylem of all vascular plants includes tube-shaped cells called **tracheids** with cell walls strengthened by **lignin.** Vascular plants are also called tracheophytes. **Phloem** transports sugars and other organic nutrients through living cells arranged into tubes.

Unlike the rhizoids of bryophytes, **roots** both anchor plants and absorb water and nutrients. Roots may have evolved from subterranean stems, either once in a common ancestor or independently in different lineages of vascular plants.

Leaves increase a plants photosynthetic surface area. The single-veined leaves of lycophytes, known as **microphylls,** are usually small and spine-shaped. The branching vascular systems of **megaphylls,** typical of most other vascular plants, support larger leaves with greater photosynthetic capacity. Megaphylls appear in the fossil record at the end of the Devonian period, 40 million years after the appearance of microphylls.

Microphylls may have originated as small outgrowths of stems, supported by single vascular tissue strands, whereas megaphylls may have evolved by the joining of closely lying branches.

Sporophylls are modified leaves bearing sporangia. In ferns, clusters of sporangia called **sori** are produced on the undersides of sporophylls. Cones, or strobili, are formed from groups of sporophylls in gymnosperms and many lycophytes. Most seedless vascular plants are **homosporous,** producing only one kind of spore, which develops into bisexual gametophytes. **Heterosporous** plants include all seed and some seedless vascular plants and produce two kinds of spores: **megaspores** that develop into female gametophytes and **microspores** that develop into male gametophytes.

Classification of Seedless Vascular Plants The two clades of living seedless vascular plant are classified into two phyla: phylum Lycophyta and phylum Pterophyta. Some systematists still retain three separate phyla in the pterophyte clade: phylum Pterophyta (ferns), phylum Sphenophyta (horsetails), and phylum Psilophyta (whisk ferns).

Lycophytes were a major part of the landscape during the Carboniferous period. One evolutionary line, the giant lycophytes, became extinct when the climate became cooler and drier. The other line of small lycophytes is represented today by the club mosses, spike mosses, and quillworts. Many tropical species grow on trees as epiphytes—plants that anchor to other organisms but are not parasites. Sporophytes grow upright with many small leaves; horizontal stems grow along the surface and produce roots.

Ferns were also found in the great forests of the Carboniferous period and are the most numerous seedless vascular plants in the modern flora. The large fern leaves (megaphylls), or fronds, often grow from horizontal stems. Most fern species are homosporous; gametophytes are small.

Horsetails grew as tall plants during the Carboniferous period. A few species of the genus *Equisetum* are the only representatives found today. These small, upright plants grow in damp locations and many have cones at the tips of some of the green, jointed stems.

Because of their dichotomous branching and lack of true leaves and roots, plant biologists initially considered *Psilotum,* the whisk fern, to be "living fossils." Molecular analysis and sperm structure comparisons now indicate that whisk ferns are closely related to ferns, and the true roots and leaves of the ancestor of whisk ferns were lost during evolution.

The Significance of Seedless Vascular Plants The seedless vascular plants of the Carboniferous forests decreased CO_2 levels in the atmosphere, perhaps contributing to the global cooling at the end of the Carboniferous. Dead plant material did not completely decay in the stagnant swamp waters, and great accumulations of peat developed. When the sea later covered the swamps and marine sediments piled on top, heat and pressure converted the peat to coal.

Word Roots

-angio = vessel (*gametangia:* the reproductive organ of bryophytes, consisting of the male antheridium and female archegonium; a multichambered jacket of sterile cells in which gametes are formed)

-phore = bearer (*gametophore:* the mature gamete-producing structure of a gametophyte body of a moss)

bryo- = moss; **-phyte** = plant (*bryophytes:* the mosses, liverworts, and hornworts; a group of nonvascular plants that inhabit the land but lack many of the terrestrial adaptations of vascular plants)

gymno- = naked; **-sperm** = seed (*gymnosperm:* a vascular plant that bears naked seeds not enclosed in any specialized chambers)

hetero- = different; **-sporo** = a seed (*heterosporous:* referring to plants in which the sporophyte produces two kinds of spores that develop into unisexual gametophytes, either female or male)

homo- = like (*homosporous:* referring to plants in which a single type of spore develops into a bisexual gametophyte having both male and female sex organs)

mega- = large (*megaspores:* a spore from a heterosporous plant that develops into a female gametophyte bearing archegonia)

micro- = small; **-phyll** = leaf (*microphylls:* the small leaves of lycophytes that have only a single, unbranched vein)

peri- = around; **-stoma** = mouth (*peristome:* the upper part of the moss capsule often specialized for gradual spore discharge)

phragmo- = a partition; **-plast** = formed, molded (*phragmoplast:* an alignment of cytoskeletal elements and Golgi-derived vesicles across the midline of a dividing plant cell)

proto- = first; **-nema** = thread (*protonema:* a mass of green, branched, one-cell-thick filaments produced by germinating moss spores)

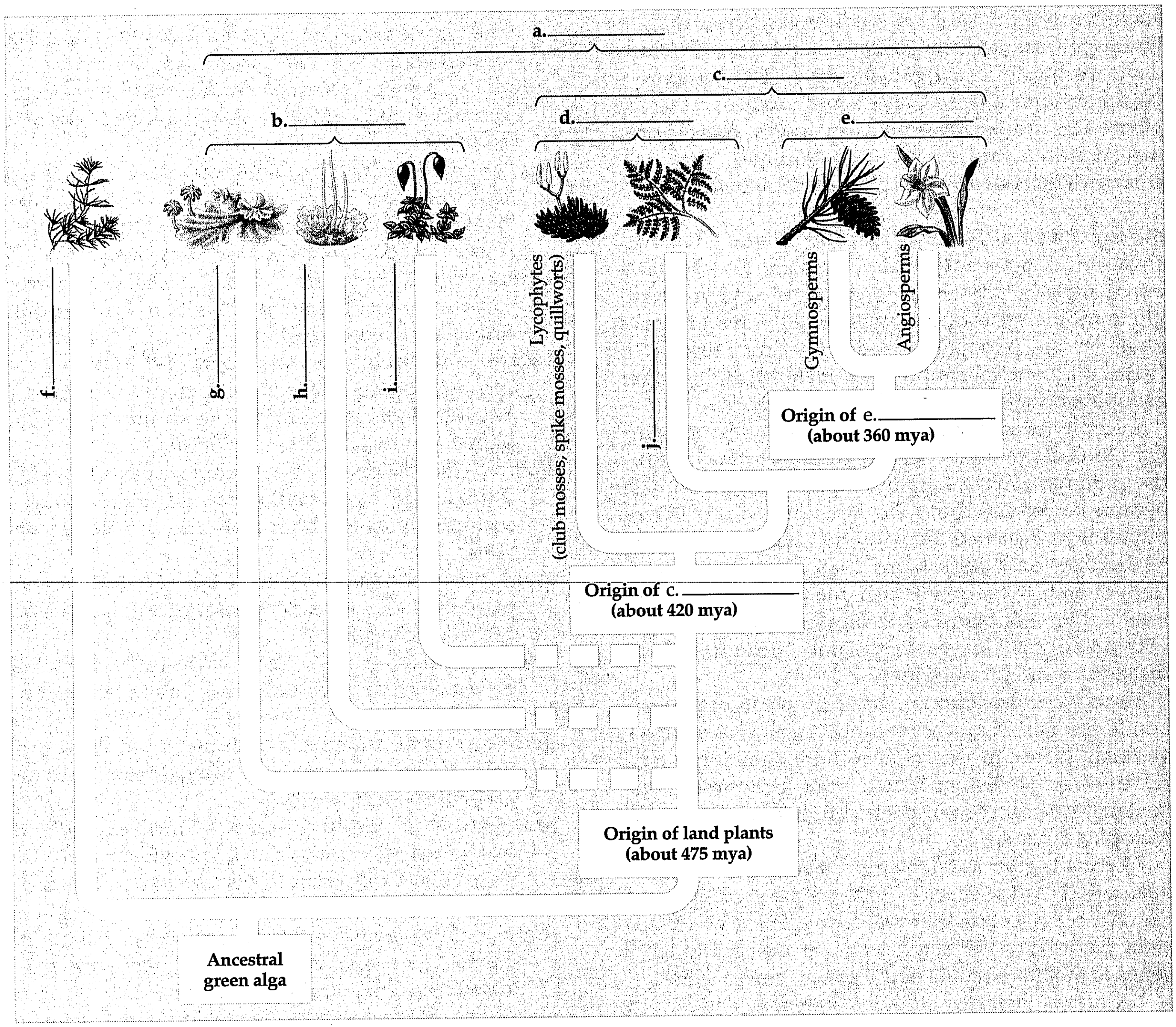
pter- = fern (*pterophytes:* seedless plants with true roots with lignified vascular tissue; the group includes ferns, whisk ferns, and horsetails)

rhizo- = root; **-oid** = like, form (*rhizoids:* long tubular single cells or filaments of cells that anchor bryophytes to the ground)

Structure Your Knowledge

1. The evolution of land plants involved adaptations to the terrestrial habitat. List some of these adaptations that evolved in the bryophytes and the seedless vascular plants.

2. The diagram below presents a widely held view of plant phylogeny. Fill in blanks a–e with the informal names for the major groups and blanks f–j with the common names for the modern plant groups (give the 3 groups included in clade j).



Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Adaptations for terrestrial life seen in all plants are
   a. chlorophylls *a* and *b*.
   b. cell walls of cellulose and lignin.
   c. sporopollenin, protection and nourishment of embryo by gametophyte.
   d. vascular tissue and stomata.
   e. alternation of generations.

2. Plants are thought to be most closely related to charophyceans based on
   a. peroxisome enzymes that minimize photorespiration.
   b. rosette cellulose-synthesizing complexes in their plasma membranes.
   c. phragmoplast formation of cell plates in mitosis.
   d. similarities in sperm cells (in those land plants with flagellated sperm).
   e. all of the above.

3. Megaphylls
   a. are large leaves.
   b. are gametophyte plants that develop from megaspores.
   c. are leaves specialized for reproduction.
   d. are leaves with branching vascular systems.
   e. were a dominant group of the great coal forests.

4. Bryophytes differ from all other land plant groups because
   a. their gametophyte generation is dominant.
   b. they are lacking gametangia.
   c. they have flagellated sperm.
   d. they are not embryophytes.
   e. of all of the above.

5. Which of the following plant groups is *incorrectly* paired with its gametophyte generation?
   a. charophycean—no alternation of generations
   b. lycophyte—either green or nonphotosynthetic underground plants
   c. moss—green matlike plant
   d. fern—frond growing from horizontal stem
   e. liverwort—flattened, low-growing green plant

6. Which of the following is most likely the closest relative of the vascular plants?
   a. charophyceans
   b. mosses
   c. liverworts
   d. pterophytes
   e. lycophytes

7. The evolution of sporopollenin was important to the movement of plants onto land because it
   a. provided a mechanism for the dispersal of spores and pollen.
   b. provided the structural support necessary to withstand gravity.
   c. enclosed developing gametes and embryos in maternal tissue and prevented desiccation.
   d. provided a tough coating for spores so they could disperse on land.
   e. initiated the alternation of generations that is characteristic of all plants.

8. If a plant's life cycle includes both a male and female gametophyte, the sporophyte plant must be
   a. heterosporous.
   b. homosporous.
   c. homologous.
   d. analogous.
   e. megasporous.

9. Xylem and phloem are found in
   a. all plants.
   b. bryophytes, ferns, conifers, and angiosperms.
   c. only the gametophytes of vascular plants.
   d. the vascular plants, which include ferns, conifers, and angiosperms.
   e. only the vascular plants with seeds.

10. Which of the following functions may secondary compounds serve?
    a. protect plant from ultraviolet radiation
    b. support plant cell walls (lignin)
    c. discourage herbivory or inhibit microbes
    d. function as signaling molecules
    e. all of the above

11. Which of the following is most likely the closet relative of the seed plants?
    a. bryophytes
    b. moss
    c. lycophytes
    d. pterophytes
    e. gymnosperms

12. Which of the following has been proposed by plant biologists as the clade that establishes the boundary of the plant kingdom?
    a. kingdom Plantae, which includes only the embryophyte clade
    b. kingdom Streptophyta, which also includes the charophyceans
    c. kingdom Viridiplantae, which also includes all green algae (chlorophytes)
    d. kingdom Vasculata, which includes only the vascular plants
    e. a, b, and c have all been proposed as the clade that defines the plant kingdom

13. Large stores of organic carbon that help to stabilize atmospheric carbon dioxide concentrations are found in
    a. huge tropical swamps dominated by mosses and ferns.
    b. peat.
    c. coal deposits left by Cambrian forests.
    d. the abundant epiphytic lycophytes found in tropical regions.
    e. large tracts of small seedless vascular plants found in boreal regions.

14. Which of the following is synonymous with tracheophytes?
  a. bryophytes
  b. pterophytes
  c. lycophytes
  d. vascular plants
  e. seed plants

15. If you could take a time machine back to the Carboniferous period, which of the following scenarios would you most likely encounter?
  a. creeping mats of low-growing bryophytes
  b. fields of tall grasses swaying in the wind
  c. swampy forests dominated by large lycophytes, horsetails, and ferns
  d. huge forests of naked-seed trees filling the air with pollen
  e. the dominance of flowering plants