chambers at the center of a flower; the walls of the chamber later develop into a fruit.

visual CONNECTION

STREPTOPHYTES: THE GREEN PLANTS							
Charophytes	**Embryophytes: The Land Plants**						
	Non-vascular			Vascular			
	Seedless Plants Bryophytes			**Seedless Plants**		**Seed Plants** Spermatophytes	
				Lycophytes	**Pterophytes**		
	Liver-worts	Horn-worts	Mosses	Club Mosses	Whisk Ferns	**Gymno-sperms**	**Angio-sperms**
				Quillworts	Horsetails		
				Spike Mosses	Ferns		

Figure 25.6 Streptophytes. This table shows the major divisions of green plants.

Which of the following statements about plant divisions is false?

a. Lycophytes and pterophytes are seedless vascular plants.
b. All vascular plants produce seeds.
c. All non-vascular embryophytes are bryophytes.
d. Seed plants include angiosperms and gymnosperms.

25.2 | Green Algae: Precursors of Land Plants

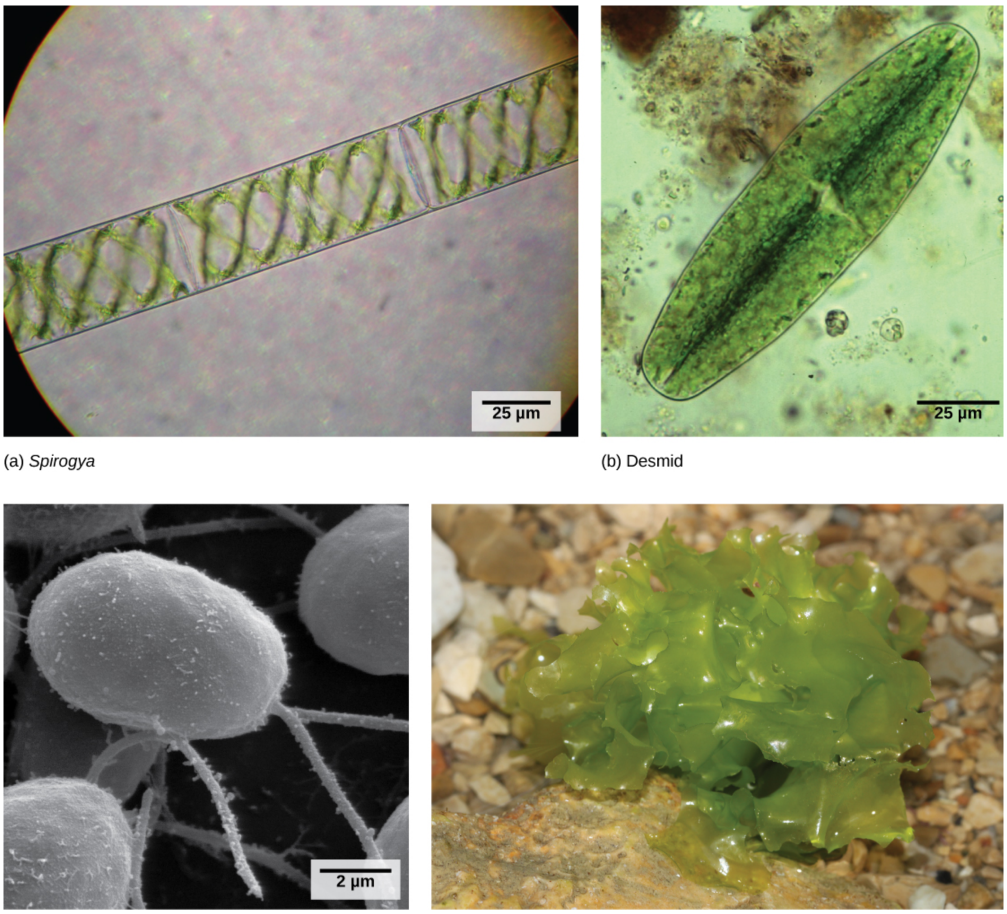
By the end of this section, you will be able to do the following:

- Describe the traits shared by green algae and land plants
- Explain why charophytes are considered the closest algal relative to land plants
- Explain how current phylogenetic relationships are reshaped by comparative analysis of DNA sequences

Streptophytes

Until recently, all photosynthetic eukaryotes were classified as members of the kingdom Plantae. The brown and golden algae, however, are now reassigned to the protist supergroup Chromalveolata. This is because apart from their ability to capture light energy and fix CO_2, they lack many structural and biochemical traits that are characteristic of plants. The plants are now classified, along with the red and green algae, in the protist supergroup Archaeplastida. Green algae contain the same carotenoids and chlorophyll a and b as land plants, whereas other algae have different accessory pigments and types of chlorophyll molecules in addition to chlorophyll a. Both green algae and land plants also store carbohydrates as starch. Their cells contain chloroplasts that display a dizzying variety of shapes, and their cell walls contain cellulose, as do land plants. Which of the green algae to include among the plants has not been phylogenetically resolved.

Green algae fall into two major groups, the chlorophytes and the charophytes. The chlorophytes include the genera *Chlorella*, *Chlamydomonas*, the “sea lettuce” *Ulva*, and the colonial alga *Volvox*. The charophytes include desmids, as well as the genera *Spirogyra*, *Coleochaete*, and *Chara*. There are familiar green algae in both groups. Some green algae are single cells, such as *Chlamydomonas* and desmids, which adds to the ambiguity of green algae classification, because plants are multicellular. Other green algae, like *Volvox*, form colonies, and some, like *Ulva* are multicellular (**Figure 25.7**). *Spirogyra* is a long filament of colonial cells. Most members of this genus live in fresh water, brackish water, seawater, or even in snow patches. A few green algae can survive on soil, provided it is covered by a thin film of moisture within which they can live. Periodic dry spells provide a selective advantage to algae that can survive water stress.



(a) *Spirogya* (b) Desmid (c) *Chlamydomonas* (d) *Ulva*

Figure 25.7 Green algae. Charophyta include (a) *Spirogyra* and (b) desmids. Chlorophyta include (c) *Chlamydomonas*, and (d) *Ulva*. Desmids and *Chlamydomonas* are single-celled organisms, *Spirogyra* forms chains of cells, and *Ulva* forms multicellular structures resembling leaves, although the cells are not differentiated as they are in higher plants (credit b: modification of work by Derek Keats; credit c: modification of work by Dartmouth Electron Microscope Facility, Dartmouth College; credit d: modification of work by Holger Krisp; scale-bar data from Matt Russell)

The chlorophytes and the charophytes differ in a few respects that, in addition to molecular analysis, place the land plants as a sister group of the charophytes. First, cells in charophytes and the land plants divide along cell plates called phragmoplasts, in which microtubules parallel to the spindle serve as guides for the vesicles of the forming cell plate. In the chlorophytes, the cell plate is organized by a phycoplast, in which the microtubules are perpendicular to the spindle. Second, only the charophytes and the land plants have plasmodesmata, or intercellular channels that allow the transfer of materials from cell to cell. In the chlorophytes, intercellular connections do not persist in mature multicellular forms. Finally, both charophytes and the land plants show *apical growth*—growth from the tips of the plant rather than throughout the plant body. Consequently, land plants and the charophytes are now part of a new monophyletic group called Streptophyta.

Reproduction of Green Algae

Green algae reproduce both asexually, by fragmentation or dispersal of spores, or sexually, by producing gametes that fuse during fertilization. In a single-celled organism such as *Chlamydomonas*, there is no mitosis after fertilization. In the multicellular *Ulva*, a sporophyte grows by mitosis after fertilization (and thus exhibits alternation of generations). Both *Chlamydomonas* and *Ulva* produce flagellated gametes.

Charophytes

The charophytes include several different algal orders that have each been suggested to be the closest relatives of the land plants: the Charales, the Zygnematales, and the Coleochaetales. The Charales can be traced back 420 million years. They live in a range of freshwater habitats and vary in size from a few millimeters to a meter in length. The representative genus is *Chara* (**Figure 25.8**), often called muskgrass or skunkweed because of its unpleasant smell. Large cells form the *thallus*: the main stem of the alga. Branches arising from the nodes are made of smaller cells. Male and female reproductive structures are found on the nodes, and the sperm have flagella. Although *Chara* looks superficially like some land plants, a major difference is that the stem has no supportive tissue. However, the Charales exhibit a number of traits that are significant for adaptation to land life. They produce the compounds *lignin* and *sporopollenin*, and form plasmodesmata that connect the cytoplasm of adjacent cells. Although the life cycle of the Charales is haplontic (the main form is haploid, and diploid zygotes are formed but have a brief existence), the egg, and later, the zygote, form in a protected chamber on the haploid parent plant.

Figure 25.8 *Chara*. The representative alga, *Chara,* is a noxious weed in Florida, where it clogs waterways. (credit: South Florida Information Access, U.S. Geological Survey)

The Coleochaetes are branched or disclike multicellular forms. They can produce both sexually and asexually, but the life cycle is basically haplontic. Recent extensive DNA sequence analysis of charophytes indicates that the Zygnematales are more closely related to the embryophytes than the Charales or the Coleochaetales. The Zygnematales include the familiar genus *Spirogyra*, as well as the desmids. As techniques in DNA analysis improve and new information on comparative genomics arises, the phylogenetic connections between the charophytes and the land plants will continued to be examined to produce a satisfactory solution to the mystery of the origin of land plants.

25.3 | Bryophytes

By the end of this section, you will be able to do the following:

- Identify the main characteristics of bryophytes
- Describe the distinguishing traits of liverworts, hornworts, and mosses
- Chart the development of land adaptations in the bryophytes
- Describe the events in the bryophyte lifecycle

Bryophytes are the closest extant relatives of early terrestrial plants. The first bryophytes (liverworts) most likely appeared in the Ordovician period, about 450 million years ago. Because they lack lignin and other resistant structures, the likelihood of bryophytes forming fossils is rather small. Some spores protected by *sporopollenin* have survived and are attributed to early bryophytes. By the Silurian period (435 MYA), however, vascular plants