Estelle Levetin • Karen McMahon

Eighth Edition

Plants & Society

McGraw Hill Education

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In loving memory of our mothers

Pauline Levetin

& *Dorothy Sink McMahon*

Contents in Brief

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Preface

In the twenty-first century, plant science is once again assuming a prominent role in research. Renewed emphasis on developing medicinal products from native plants has encouraged ethnobotanical endeavors. The destruction of the rain forests has made the timing for this research imperative and has spurred efforts to catalog the plant biodiversity in these environments. Efforts to feed the growing populations in developing nations have also positioned plant scientists at the cutting edge of genetic engineering with the creation of transgenic crops. However, in recent decades botany courses have seen a decline in enrollment, and some courses have even disappeared from the curriculum in many universities. We have written *Plants and Society* in an effort to offset this trend. By taking a multidisciplinary approach to studying the relationship between plants and people, we hope to stimulate interest in plant science and encourage students to further study. Also, by exposing students to society's historical connection to plants, we hope to instill a greater appreciation for the botanical world.

AUDIENCE

Recently, general botany courses have emphasized the impact of plants on society. In addition, many institutions have developed plants and society courses devoted exclusively to this topic. This emphasis has transformed the traditional economic botany from a dry statistical treatment of "bushels per acre" to an exciting discussion of "botanical marvels" that have influenced our past and will change our future. *Plants and Society* is intended for use in this type of course, which is usually one semester or one quarter in length. There are no prerequisites because it is an introductory course. The course covers basic principles of botany and places a strong emphasis on the economic aspects and social implications of plants and fungi.

Students usually take a course of this nature in their freshman or sophomore year to satisfy a science requirement in the general education curriculum. Typically, they are not biology majors. Although most students enroll to satisfy the science requirement, many become enthusiastic about the subject matter. Students, even those with a limited science background, should not encounter any problems with the level of scientific detail in this text.

As indicated, the primary market for this text is a plants and society course; however, it would certainly be suitable for an introductory general botany course as well.

ORGANIZATION

We feel that *Plants and Society* is a textbook with a great deal of flexibility for course design. It offers a unique balanced approach between basic botany and the applied or economic aspects of plant science. Other texts emphasize either the basic or applied material, making it difficult for instructors who wish to provide better balance in an introductory course. Another distinctive feature is the unit on algae and fungi. While other texts cover certain aspects of this topic, we have an expanded coverage of algae and fungi and their impact on society.

Plants and Society is organized into 26 chapters that are grouped into seven units. The first nine chapters cover the basic botany found in an introductory course. However, even in these chapters we have included many applied topics, some in the boxed essays but others directly in the chapter text.

UNIT I Plants and Society: The Botanical Connections to Our Lives. Chapter 1 stresses the overall importance of plants in everyday life. The properties of life, molecules of life, flowering and non flowering plants, algae, and fungi are introduced. The scientific method is explained as the process used by scientists to study and expand our knowledge of the natural world. The diversity and applications of phytochemicals are also presented.

UNIT II Introduction to Plant Life: Botanical Principles. This unit addresses basic botany. Chapters cover plant structure from the cellular level to the mature plant. Reproduction, including mitosis and meiosis and the life cycle of flowering plants, is discussed in two chapters. Other chapters cover genetics, evolution, plant physiology, plant systematics, and plant diversity. Some of the economic aspects of plants discussed in this unit are the importance of vegetables and fruits, the connection between sugar and slavery, plant essential oils and perfumes, phytoremediation, the applications of palynology, and species conservation.

UNIT III Plants as a Source of Food. This unit describes the major food crops. It begins with a chapter on the requirements for human nutrition and continues with a chapter on the origins of agriculture. Other chapters cover the grasses, the legumes, and starchy staples. The unit ends with a chapter on the Green Revolution, the loss of genetic diversity, the search for alternative crops, and the controversial development of transgenic crops.

UNIT IV Commercial Products Derived from Plants. This unit covers other crops that provide us with consumable products, such as beverages, herbs and spices, and materials such as cloth, wood, and paper. The historical origin and societal impact of these crops are explored.

UNIT V Plants and Human Health. This unit introduces students to the historical foundations of Western medicine, the practice of herbal medicine, and the chemistry of secondary plant products. Descriptions of the plants that provide us with medicinal products and psychoactive drugs are discussed. The unit also covers the common poisonous and allergy plants that are found in the environment.

UNIT VI Algae and Fungi: The Impact of Algae and Fungi on Human Affairs. This unit describes the economic importance of the algae and fungi, including their biology and crucial roles in the environment. The algae are recognized as key producers in aquatic environments and as sources of human food, devastating blooms, and industrial products. Fermented beverages and foods from fungi are discussed, as is the medical importance of fungi as sources of antibiotics, toxins, and diseases affecting crops and people.

UNIT VII Plants and the Environment. Chapter 26 is an introduction to the principles of ecology: the ecosystem, niches, food chains, biogeochemical cycles, and ecological succession. The major biomes of the world are discussed, with an emphasis on the economic value of certain desert plants and the strategy of extractive reserves in the rain forest. The problems associated with rising levels of the greenhouse gas CO_2 and the environmental consequences of global warming are addressed.

APPROACH

This textbook is written at the introductory level suitable for students with little or no background in biology. Like any introductory book, this book uses a broad-brush treatment. The nature of the course dictates an applied approach, with the impact of plants on society as the integrating theme, but the theoretical aspects of basic botany are thoroughly covered.

LEARNING AIDS

In addition to the textual material, each chapter begins with a chapter outline and key concepts. Important terms are in boldface type throughout the text, and each chapter ends with a summary and review questions. Thinking Critically questions are inserted in the text to draw the attention of the students as they read the chapter. The questions begin with either a summary of the preceding text or an introduction to new information that is complementary to the chapter. The questions that follow are designed not only to test comprehension but also, in many instances, to promote critical thinking by asking students to apply their knowledge to real-life situations. Thinking Critically questions may also be assigned by instructors or used to initiate in-class discussions. Three appendices and a glossary conclude the text. The classification of plants and other organisms discussed in the text and a review of metric units are located for quick access on the inside front and back covers, respectively.

NEW TO THE EIGHTH EDITION

The eighth edition of *Plants and Society* been updated to spotlight exciting discoveries and update major advancements in the science of plants, algae, and fungi, with special emphasis on how these organisms impact humanity. These include:

- Expanded information on the regulation of cell division (Chapter 2)
- Subsidiary cells in grasses enable the greater inflation of guard cells to bring in more carbon dioxide for photosynthesis as well as facilitating guard cells to respond rapidly to changing environmental conditions (Chapter 3).
- Sun pitchers (*Heliamphora*), carnivorous pitcher plants native to South America, exhibit remarkable adaptations: a nectar spoon to lure prey and a drainage pipe to siphon off excess water from the pitcher (Chapter 3).
- The section on orchids has been updated to include significantly more detail on the unique modifications of orchid flowers (Chapter 5).
- There are updates on the latest research surrounding colony collapse disorder and the search for alternative pollinators (Chapter 5).
- There is additional coverage of the ways in which researchers are using genomic analysis to discover how to enhance the flavors of mass-market tomatoes to better resemble heirloom varieties (Chapter 6).
- Information on CRISPR, a powerful technique in the gene editing of organisms, is presented (Chapters 7 and 15).
- Fiber in the diet may promote health as the food to support microbiota beneficial to the digestive tract (Chapter 10).
- The paleo diet, the so-called original diet of ancient humans, is evaluated (Chapter 11).
- A new update on the International Wheat Genome Sequencing Consortium's work to sequence the bread wheat genome is featured (Chapter 12).
- A Closer Look 13.1 has been updated to include new information on biofertilizers and A Closer Look 13.2 on Harvesting Oil also has data updates (Chapter 13).
- A Closer Look 14.1 features new information on the recent resurgence of Panama disease and its effect on bananas (Chapter 14).
- New evidence on the disjunct distribution of sweet potatoes is detailed (Chapter 14).
- A section on the effects of global warming on crops has been included (Chapter 15).

- Information on genetically modified rice and corn has been added (Chapter 15).
- A new Closer Look on Climate Change and the Future of Coffee has been added (Chapter 16).
- Update on the legal status of hemp cultivation (Chapter 18).
- There is a new content on the increased use of plant biomass (such as wood pellets) to supplement or replace coal (Chapter 18).
- A new section highlights the remarkable history of French lilac in the development of the medicine Metformin, which is used to treat both diabetes and polycystic ovarian syndrome (Chapter 19).
- Updated content is included on the antimalarial properties of certain plants used in Chinese medicine (Chapter 19).
- Updates on the legal status of marijuana has been included (Chapter 20).
- Giant Hogweed, an oversized invasive weed from Asia, produces a toxic sap that causes debilitating blisters and burns to the skin upon exposure to sunlight (Chapter 21).
- There are updates to gluten and nonceliac gluten sensitivity (Chapter 21).
- There is information on new research suggesting a potential connection between algae blooms and global warming (Chapter 22).
- A 2018 research on *Batrachochytrium dendrobatidis* fungus highlights how the pathogen traveled from the Korean peninsula and has been responsible for the extinction or decline of frog and salamander populations around the world (Chapter 23).
- A new section covers the history and cultivation of apple ciders, the alcoholic beverages made by fermenting apple juice (Chapter 24).
- With the rise of MRSA infections worldwide, there has been renewed interest in the therapeutic use of fusidic acid, covered now in additional detail (Chapter 25).
- The global, indelible impact of human activity on Earth has initiated a demand for the creation of a new geologic epoch, the Anthropocene (Chapter 26).
- The Paris Climate Agreement has revised its long-term goal of limiting global warming from an increase of 2.0°C above preindustrial temperatures down to 1.5°C (Chapter 26).
- Over 50 new photographs and several new or revised figures and tables have been added to the eighth edition.

ACKNOWLEDGMENTS

From our first introduction to botany as college students, we became irrevocably fixated on the lives of plants. We can remember the fascination we felt when we read about the plant explorers who discovered *extinct* ginkgo trees alive in China and how a trichome of the stinging nettle was the inspiration for the invention of the hypodermic needle. It is our hope that *Plants and Society* will present the world of plants and how they sustain humanity in a way that will inspire students to have a lifelong appreciation of plants.

We wish to thank the editorial staff at McGraw-Hill Higher Education for their editorial expertise and their endless patience during the publication of the eighth edition of *Plants and Society.* We especially want to acknowledge our Portfolio Manager, Michael Ivanov; Senior Product Developer, Chipper Scheid; Freelance Product Developer, Jen Thomas; and Content Project Manager, Becca Gill.

REVIEWERS

We are indebted to our colleagues who have taken time from demanding schedules to meticulously review *Plants and Society* for errors, inconsistencies, or omissions and to offer constructive feedback and suggestions. We thank you for making the eighth edition of *Plants and Society* the best edition.

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List of Boxed Readings

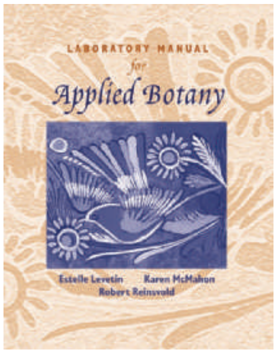
Supplements

PLANTS AND SOCIETY COMPANION WEBSITE

The companion website to accompany *Plants and Society* offers a variety of additional resources for instructors and students. Instructors will appreciate full-color PowerPoint image slides that contain illustrations and photos from the text, along with suggested activities. A comprehensive bank of test questions, aligned with each chapter of the text, is also available along with access to TestGen. TestGen. allows instructors to create paper and online tests or quizzes in one easy-to-use program. Students will find multiple-choice quizzes, short-answer concepts, and further resources to aid in their study. Also included is a listing of useful and poisonous plants, as well as tips for growing houseplants and home gardening.
www.mhhe.com/levetin8e

Craft your teaching resources to match the way you teach! With McGraw-Hill Create™, www.mcgrawhillcreate.com, you can easily rearrange chapters, combine material from other content sources, and quickly upload content you have written like your course syllabus or teaching notes. Find the content you need in Create by searching through thousands of leading McGraw-Hill textbooks. Arrange your book to fit your teaching style. Create even allows you to personalize your book's appearance by selecting the cover and adding your name, school, and course information. Order a Create book, and you'll receive a complimentary print review copy in 3–5 business days or a complimentary electronic review copy (eComp) via email in minutes. Go to www.mcgrawhillcreate.com today and register to experience how McGraw-Hill Create™ empowers you to teach your students your way.

THE *LABORATORY MANUAL FOR APPLIED BOTANY* BY LEVETIN, MCMAHON, AND REINSVOLD



The lab manual features 18 exercises that focus on examining plants and plant products that have sustained or affected human society. Although the manual includes standard information on plant cells and tissues, there is a practical approach to the investigations. Students extract plant dyes, make paper from plant fibers, and study starch grains used in archeology. Several laboratory topics are devoted exclusively to economically important crops—grasses, legumes, starchy staples, and spices. Four additional appendixes—titled Science as a Process, A Field Trip to a Health Food Store, A Taster's Sampler of Caffeine Beverages and Foods, and Notes for Instructors—provide additional information for each of the labs.

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UNIT I

CHAPTER

1

Plants in Our Lives

The botanical connections to our lives are many: food, medicines, materials, and beverages are just a few of the ways plants serve humanity.

KEY CONCEPTS

1. Green plants, especially flowering plants, are more than just landscaping for the planet, since they supply humanity with all the essentials of life: food and oxygen as well as other products that have shaped modern society.
2. The algae are an extremely diverse group of photosynthetic organisms that are key producers in aquatic food chains, a valuable source of human food, and the base for a number of commercial and industrial products.
3. Fungi are also an economically and ecologically important group of organisms that impact society in numerous ways, from fermentation in the brewing process to the use of antibiotics in medicine to their role as decomposers in the environment and as the cause of many plant and animal diseases.
4. All living organisms share certain characteristics: growth and reproduction, ability to respond, ability to evolve and adapt, metabolism, organized structure, and organic composition.
5. The processes of life are based on the chemical nature and interactions of carbohydrates, lipids, proteins, and nucleic acids.

CHAPTER OUTLINE

Much of modern society is estranged from the natural world; people living in large cities often spend over 90% of their time indoors and have little contact with nature. Urbanized society is far removed from the source of many of the products that make civilization possible: most food is purchased in large supermarkets, most medicines are purchased at pharmacies, and most building supplies are purchased at lumber yards. Society's dependence on nature, especially plants, is forgotten (table 1.1).

In less urbanized environments, lifestyles are more attuned to nature. The farmer's existence is dependent on crop survival, and the farmer's work cycle is timed to the growing season of the crops. The few hunter-gatherer cultures that remain in isolated areas of the world are even more dependent on nature as they forage for wild plants and hunt wild animals. These foragers know that without grains there would be no flour or bread; without plant fibers there would be no cloth, baskets, or rope; without medicinal herbs there would be no relief from pain; without wood there would be no shelter; without firewood there would be no fuel for cooking or heat; and without vegetation there would be no wild game.

PLANTS AND HUMAN SOCIETY

Whether forager, farmer, or city dweller, humans have four great necessities in life: food, clothing, shelter, and fuel. Of the four, an adequate food supply is the most pressing need, and, directly or indirectly, plants and algae are the source of virtually all food through the process of **photosynthesis.** Through photosynthesis, plants and algae use solar energy to convert carbon dioxide and water into sugars and, as such, are the **producers** in the **food chain.** They are the base of most food chains, whether eaten by humans directly as **primary consumers** or indirectly as **secondary consumers** when eating beef (which comes from grain-fed or pasture-fed cattle). In addition to the food produced by photosynthesis, the oxygen given off as a by-product is Earth's only continuous supply of oxygen. As sources of food, oxygen, lumber, fuel, paper, rope, fabrics, beverages, medicines, and spices, plants support and enhance life on the planet.

Thinking Critically

Plants are crucial to the existence of many organisms, including human beings.

Could life on Earth exist without plants? Explain.

The Flowering Plants

The word *plant* means different things to different people: to an ecologist, a plant is a producer; to a forester, it is a tree; to a home gardener, a vegetable; and to an apartment dweller, a houseplant. Although there are many different types of plants, the most abundant and diverse plants in the environment are the flowering plants, or **angiosperms.** These are also the most economically important members of the Plant Kingdom and are the primary focus of this book. From the more than 350,000 known **species*** of angiosperms, an overwhelming diversity of products has been obtained and utilized by society. The food staples of civilization—wheat, rice, and corn—are all angiosperms; in fact,

*Each kind of organism, or species, has a two-part scientific name consisting of a genus name and a specific epithet; for example, white oak is known scientifically as *Quercus alba*. After the first mention of a scientific name, the genus name can be abbreviated, *Q. alba*. When referring to oaks in general, it is acceptable to use the genus name, *Quercus*, alone. Sometimes an abbreviation for species, "sp." or plural "spp.," stands in for the specific epithet—for example, *Quercus* sp. or *Quercus* spp. Both common and scientific names are used throughout this book; details on this topic are found in Chapter 8.

Table 1.1
How Much Do Plants Affect Society?

__________	1.	True or False—Plants provide most of the calories and protein for the human diet.
__________	2.	True or False—Today plant extracts are widely used in herbal remedies and alternative medicine, but they are no longer important in prescription drugs.
__________	3.	True or False—The search for cinnamon led to the discovery of North America.
__________	4.	True or False—New varieties of plants are being created through genetic engineering; these provide enormous profits for large agrotechnology companies but have no practical value.
__________	5.	True or False—The introduction of the potato to Europe in the sixteenth century initiated events that led to a devastating famine in Ireland.
__________	6.	True or False—Trees are the only source of pulp for papermaking.
__________	7.	True or False—The estimated number of genes in *Arabidopsis thaliana,* the first plant genome sequenced, has about one-fourth the number of genes estimated for the human genome.
__________	8.	True or False—The Salem witchcraft trials in the 1690s might have resulted from a case of fungal poisoning.
__________	9.	True or False—Tomatoes were once considered to be an aphrodisiac.
__________	10.	True or False—A poisonous plant is one of the most important dietary staples in the tropics.

(*continued*)

Table 1.1
continued

Answers	
1. True	In nations such as the United States and those in Western Europe, approximately 65% of the total caloric intake and 35% of the protein are obtained directly from plants, while in developing nations close to 90% of the calories and over 80% of the protein are from plants (Chapters 10, 15).
2. False	Approximately 25% of all prescription drugs in Western society contain ingredients derived from plants; however, 80% of the world's population does not use prescription drugs but relies exclusively on herbal medicine (Chapter 19).
3. True	Columbus was one of many explorers trying to find a sea route to the rich spicelands of the Orient. Cinnamon and other spices were so valued in the fifteenth century that a new, faster route to the East would bring untold wealth to the explorer and his country (Chapter 17).
4. False	Transgenic crops, containing one or more genes from another organism, are being planted throughout the world. Some of these crops have been engineered to be more nutritious, disease resistant, or insect resistant and have been found to be beneficial to people and the environment (Chapter 15).
5. True	The potato, native to South America, became a staple food for the poor in many European countries, especially Ireland. The widespread dependence on a single crop led to massive starvation when a fungal disease, late blight of potato, destroyed potato fields in the 1840s. Over 1 million Irish died from starvation or subsequent diseases; another 1.5 million emigrated (Chapter 14).
6. False	While trees provide a sizeable percentage of pulp for the world's paper, many types of plant material can be used. Historically, cotton, hemp, linen, rice straw, and bamboo have been used as sources of pulp. Also, recycling paper helps decrease our dependence on trees for pulp. Recycling a 1.2-meter (4-foot) stack of newspapers would save a 12-meter (40-foot) tree (Chapter 18).
7. False	*Arabidopsis* is estimated to have over 27,000 genes, more than that of the fruit fly and even more than the estimate of 20,500 genes for the human genome (Chapter 7).
8. True	Searching for the cause of the hysteria that led to the accusations of witchcraft in Salem, Massachusetts, some historians have suggested ergot poisoning. Caused by a fungal disease of rye plants, an ergot forms in place of a normal grain and produces hallucinogenic toxins. Consumption of contaminated rye flour can lead to hallucinations, neurological symptoms, or even death (Chapter 25).
9. True	When tomato plants were first introduced to Europe, they were viewed with suspicion by many people, since poisonous relatives of the tomato were known. It took centuries for the tomato, neither poisonous nor an aphrodisiac, to fully overcome its undeserved reputation (Chapters 6, 20).
10. True	Bitter varieties of cassava (*Manihot esculenta*) contain deadly quantities of hydrocyanic acid (HCN), which can cause death by cyanide poisoning. Cultures in South America, Africa, and Indonesia have developed various processing methods to remove HCN and render the cassava edible (Chapter 14).

with minor exceptions, all food crops are angiosperms. The list of other products from angiosperms is considerable and includes cloth, hardwood, herbs and spices, beverages, many drugs, perfumes, vegetable oils, gums, and rubber.

All angiosperms are characterized by flowers and fruits. A typical angiosperm flower consists of four whorls of parts: **sepals, petals, stamens**, and one or more **carpels** (fig. 1.1). The stamens and carpels are the sexual reproductive structures. It is from the carpels that the fruit and its seeds will develop. The angiosperms traditionally have been divided into two groups, the **monocots** and the **dicots**, on the basis of structural and anatomical differences. Among the most familiar monocots are lilies, grasses, palms, and orchids. A few common dicots are geraniums, roses, tomatoes, dandelions, and most broad-leaved trees. The structure and reproduction of the angiosperms will be described in detail in later chapters.

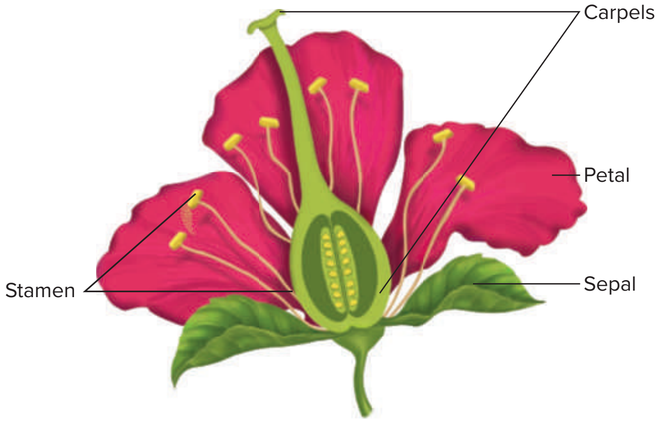


Figure 1.1 A flower, one of the defining characteristics of angiosperms.

The Non-Flowering Plants

In the Plant Kingdom, several distinct groups of non-flowering plants can be found; these range from green algae (fig. 1.2a) to mosses and ferns to giant redwood trees, which are the largest organisms on Earth. Redwoods belong to a group of plants called gymnosperms. Like angiosperms, gymnosperms are seed-bearing plants, but the seeds are not formed in fruits. Gymnosperm seeds are generally produced in cones. One group of gymnosperms consists of conifers, such as pines, cedars, and redwoods. Among the non-flowering plants, the conifers have the greatest impact on society as a source of wood for construction, fuel, and paper. Non-flowering land plants are presented in Chapter 9, and additional material on conifer wood is presented in Chapter 18.

The Algae

Algae are a diverse group of photosynthetic organisms that are found in marine and freshwater habitats where they serve as the base of food chains. They range from microscopic organisms to large seaweeds such as those found in the intertidal zone (fig 1.2a) and giant kelp that form extensive underwater forests. All algae were once considered the most primitive members of the Plant Kingdom, but today most types of algae are classified in separate kingdoms along with other simple organisms. Only the green algae are considered part of the Plant Kingdom. Many species of algae are recognized as important and nutritious food for people throughout the world; however, the widespread uses of algal extracts for industrial applications and as food additives generally go unrecognized.

A negative aspect of the algae is related to environmental damage caused by algal blooms, which are sudden population explosions of certain algal species. In recent years, the occurrence of algal blooms has increased throughout the world. Although these blooms sometimes occur naturally, the increase is believed to be related to nutrient pollution, especially from agricultural runoff, human sewage, and animal wastes. Blooms are particularly dangerous when the algae are capable of producing toxins that can cause massive fish kills or human poisoning. The algae and their connections to society will be examined in Chapter 22.

(a)

(b)

Figure 1.2 (a) Close-up view of *Fucus* (sometimes called rockweed or bladder wrack), a genus of brown algae commonly found in the intertidal zones of rocky shorelines in most parts of the world. (b) Cluster of deer mushrooms, *Pluteus cervinus,* growing on mulch in an Oklahoma garden.

The Fungi

One other group of organisms that has had a significant impact on society is the fungi, including the molds, mildews, yeast, and mushrooms (fig. 1.2b). Although biologists once considered the fungi a type of simple plant, today they classify them as neither plants nor animals but put them in other kingdoms. The fungi are of major economic importance as they provide many beneficial items, such as penicillin, edible mushrooms, and, through the process of fermentation, beer, wine, cheese, and leavened bread. A negative aspect of their economic importance is the impact of fungal disease and spoilage. The most serious diseases of our crop plants are caused by fungi, resulting in billions of dollars in crop losses each year.

Fungi generally have a threadlike body, the **mycelium,** and propagate by reproductive structures called **spores.** Fungi are nonphotosynthetic organisms, obtaining their nourishment from decaying organic matter as **saprobes** or as **parasites** of living hosts. Ecologically, the fungi play an essential role as **decomposers,** recycling nutrients in the environment. Many fungi are also involved in symbiotic relationships with other organisms. The best known of these relationships are lichens, which are composite organisms formed by a fungus and an alga living together. Because of their traditional ties to botany (the study of plants), the fungi and their impact on humanity will be considered in this book and are presented in Chapters 23–25.

Plant Sciences

When humans began investigating the uses of plants for food, bedding, medicines, and fuel, the beginnings of plant science were evident. Early peoples were skilled regional botanists and passed on their knowledge to succeeding generations. This

Table 1.2
Subdisciplines of Botany

Bryology	Study of mosses and liverworts
Economic botany	Study of the utilization of plants by humans
Ethnobotany	Study of the use of plants by indigenous peoples
Forestry	Study of forest management and utilization of forest products
Horticulture	Study of ornamental plants, vegetables, and fruit trees
Mycology	Study of fungi
Paleobotany	Study of fossil plants
Palynology	Study of pollen and spores
Phycology	Study of algae
Plant anatomy	Study of plant cells and tissues
Plant ecology	Study of the role of plants in the environment
Plant biotechnology	Study and manipulation of genes between and within species
Plant genetics	Study of inheritance in plants
Plant morphology	Study of plant form and life cycles
Plant pathology	Study of plant disease
Plant physiology	Study of plant function and development
Plant systematics	Study of the classification and naming of plants

folk botany gradually amassed a great body of knowledge, laying the foundation for scientific botany, which began in ancient Greece. As the body of knowledge expanded over the centuries, areas of specialization developed within botany, and today many of them are recognized as disciplines in their own right (table 1.2).

Scientific Method

Like other biologists, botanists make advances through a process called the scientific method. This process is the tool that scientists use to study nature and develop an understanding of the natural world. Although the exact steps vary depending on the scientific discipline, generally the scientific method includes careful observation of some natural phenomenon, the development of a hypothesis (tentative explanation for the observation), the use of the hypothesis to make predictions, and experimentation to test the hypothesis. It is often necessary to modify the hypothesis based on the results of the experiments. This, too, is part of the scientific method.

Observation

Scientific study often begins with an observation. It may be something seen repeatedly, such as the blooming of tulips only in the spring. Another type of observation might be the realization that you and others in your family have allergy problems only in September and early October. Observations lead to speculations and questions. You might wonder what causes your September hay fever. With some research on the subject, you might learn that ragweed pollen in the air is the leading cause of fall hay fever. A visit to an allergist confirms the fact that you are allergic to ragweed pollen; however, you cannot find any ragweed plants in your neighborhood. This may lead you to ask the following questions: “Is there ragweed pollen in the air even though there are no plants near my home? Could this be causing my hay fever symptoms?”

Hypothesis

A hypothesis is a possible explanation or working assumption for the original observations. It comes directly from your observations and questions. In the example given here, you might form the following hypothesis: “Airborne ragweed pollen causes my hay fever symptoms every September and October.” You may even make some predictions that your symptoms will increase when the airborne pollen level is high.

Hypothesis Testing

Once you have stated your hypothesis, you can find ways to test the hypothesis through experimentation. First, you must decide the type of evidence you will need. You find out information about air sampling and pollen identification and decide to conduct air sampling from July to October during the coming year and determine the types of pollen in the air. You also decide to keep a daily diary of hay fever symptoms during this time and to search for ragweed plants in other locations. Your field work shows that ragweed plants are abundant in an abandoned field about 1 mile south of your neighborhood and along the banks of the river running through your town. Your air sampling data show that ragweed pollen first appeared in the air in late August and increased during the first 2 weeks of September, with the peak on September 12. The pollen levels then began decreasing and were gone from the air by late October. Your symptom chart showed a similar pattern, and, with the help of a friend who is studying statistics, you find a significant correlation between the pollen level and symptoms. The occurrence of ragweed pollen in the air, your symptom diary, and the presence of ragweed plants in town allow you to accept the hypothesis as correct.

Through the use of the scientific method, the body of knowledge increases, allowing scientists to expand their understanding of the workings of the natural world and leading to the development of scientific theories. In science, a theory is an accepted explanation for natural phenomena that is supported by extensive and varied experimental evidence. This definition is very different from the common usage of the word *theory*, which often means a guess. The scientific meaning of theory will always be used

A CLOSER LOOK 1.1

Biological Mimics

The architecture of nature far surpasses any design developed by modern technology. In fact, engineers and inventors often appropriate their best ideas directly from the natural world. Both Velcro™ and barbed wire duplicate the designs found in certain plants.

Today, Velcro™ has hundreds of uses in diapers, running shoes, and space suits, even in sealing the chambers of artificial hearts. But it started from observations during the tedious task of removing cockleburs from clothing. In 1948, a Swiss hiker, George de Mestral, observed the manner in which cockleburs clung to clothing and thought that a fastener could be designed using the pattern. Cockleburs (box fig. 1.1a) have up to several hundred curved prickles that function in seed dispersal. These tiny prickles tenaciously hook onto clothing or the fur of animals and are thus transported to new areas. De Mestral envisioned a fastener with thousands of tiny hooks, mimicking the cocklebur prickles on one side and thousands of tiny eyes for the hooks to lock onto on the other side (box fig. 1.1b). It took 10 years to perfect the original concept of the "locking tape" that has become Velcro™, so common in modern life.

Osage orange (*Maclura pomifera*) is a tree in the mulberry family native to the south-central region of the United States in the area common to Oklahoma, Missouri, Texas, and Arkansas. It has several notable features. Female trees bear large, yellow-green fruits, nicknamed hedge apples (see fig. 8.5a). Hedge apples apparently contain chemicals that repel many insects, and they have been collected for that purpose. The bark is brown with a definite orange tint and becomes more furrowed and shaggier with age. The wood, which is bright orange, very dense, and resistant to rot and termites, was used by several Native American tribes to make war clubs and bows. This usage prompted the French to call the tree *bois d'arc,* meaning wood of the bow. But this story concentrates on the thorns. They are quite formidable. About an inch (2.54 centimeters) long, they alternate in spiral fashion along the length of the branch (box fig. 1.1c). It is these thorny branches that made the osage orange so valuable in the settling of the western plains in North America.

Osage orange was in great demand for its use as a living fence in the vast, treeless plains of the West. The trees were planted close and pruned aggressively to promote a bushy and thorny hedge. Because osage orange is a quick-growing tree, a fence of osage orange took only 4 or 5 years to fill out and could survive for more than a hundred years. Cuttings and seeds of osage orange were collected and sent to farmers throughout America to establish a thorny hedgerow to corral livestock and protect crops. In 1850, a single bushel of osage orange seed cost $50—a fantastic sum in those days. In 1860 alone, 10,000 bushels of seeds were sold, enough to produce 60,000 miles of hedge. In abandoned fields, you can still come across some of these old osage orange hedges or their descendants.

The osage orange hedge did have some drawbacks. A living fence could house insects and other vermin, rob the soil of nutrients and water, and produce shade that could interfere with crop growth. Also, they were not readily movable. What was needed was a new and improved hedgerow, and Michael Kelly was the first, in 1868, to patent a thorny fence made of wire that mimicked the branches of osage orange. It consisted of a single strand of wire with fitted, diamond-shaped sheet metal "barbs" at 6-inch intervals. Kelly established the

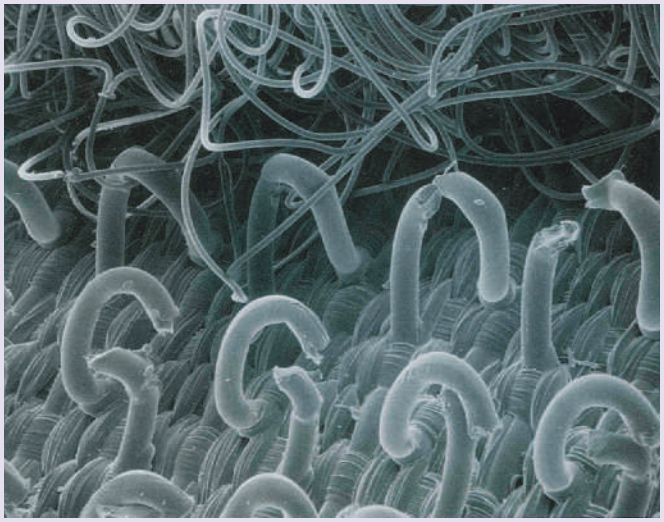
in this book. The Cell Theory and Darwin's theory of evolution through natural selection are two of the theories that will be described.

FUNDAMENTAL PROPERTIES OF LIFE

Although living organisms can be as different as oak trees, elephants, and bacteria, they share certain fundamental properties. These properties include the following:

1. **Growth and Reproduction** Living organisms have the capacity to grow and reproduce. *Growth* is defined as an irreversible increase in size and should not be confused with simple expansion. Although balloons and crystals can enlarge, this enlargement is not true growth. The ability to reproduce, or produce new individuals, is common to all life. Reproduction can be **sexual,** involving the fusion of **sperm** and **egg** to form a **zygote,** or **asexual,** in which the offspring are genetic clones of a single parent.
2. **Ability to Respond** The environment is never static; it is always changing, and living organisms have the capabilities to respond to these changes. These responses can be obvious, such as a stem turning toward the light (fig. 1.3) or an animal hibernating for the winter. Sometimes, however, the responses are subtle, such as

(a)



(b)

(c)

Box Figure 1.1 Biological mimicry. (a) The prickles on cocklebur. (b) Hooks on Velcro™. (c) Barbed wire is a design based on the thorny branches of osage orange.

Thorn Wire Hedge Company in 1876 to manufacture his invention. Ultimately, he was bested by his competitors, who had similar ideas and a more successful design. Soon, the vast, open plains of the West were crisscrossed with fences of barbed wire (box fig. 1.1c). In a real sense, the Wild West was tamed by the thorny branches of osage orange.

Figure 1.3 A field of sunflowers with their heads all facing the sun.

changes in the chemical composition of leaves in trees under attack by insects. The chemical composition of intact leaves is altered, making the leaves unpalatable to the insects.

3. **Ability to Evolve and Adapt** All life constantly changes, or evolves. This process has been going on for billions of years, as evidenced by the fossil record. Sometimes changes promote survival because the altered species is better adapted to its environment. Many desert plants have evolved water-storing tissue, an adaptation that helps them survive in their arid environment.
4. **Metabolism** Metabolism is the sum total of all chemical reactions occurring in living organisms. Two of the most important metabolic reactions are **cellular respiration** and

photosynthesis. Respiration is a metabolic process in which food is chemically broken down to release energy. All life requires energy to run chemical reactions, and respiration occurs in all living organisms. Photosynthesis occurs in green plants, algae, and some bacteria. It is the process that links the energy of the sun with life on Earth. In this process, photosynthetic organisms utilize solar energy to manufacture sugars.

5. **Organized Structure** All living organisms are composed of one or more cells; the cell is the basic structure of life. The unique structures encountered in living organisms are often the inspiration for manufactured items, as seen in A Closer Look 1.1: Biological Mimics. From the smallest unicellular organism to the largest multicellular organism, all show a high degree of organization and coordination. The simplest level of organization is seen in bacteria, which are **prokaryotic cells** (fig. 1.4a). These are the most primitive types of cells known. All other organisms are composed of **eukaryotic cells.** In a eukaryotic cell, the **nucleus,** containing the hereditary material, is clearly visible (fig. 1.4b), and different metabolic activities are compartmentalized into specialized membrane-bound structures called **organelles.** Prokaryotic cells lack a discernible internal organization. Prokaryotes have no organized nucleus or other obvious membrane-bound structures, but they have hereditary material and carry out all the activities of life.
6. **Organic Composition** All living organisms are composed mainly of four types of compounds: **carbohydrates, proteins, lipids,** and **nucleic acids.** These are the molecules of life.

MOLECULES OF LIFE

The chemical composition of life is based on the element carbon and the classes of carbon compounds known as carbohydrates, lipids, proteins, and nucleic acids. Carbon is covalently bonded to other carbon atoms to create carbon chains that form the skeletons of these molecules. These four classes of compounds are the most important molecules in living organisms and often exist as large, complex **macromolecules;** however, other compounds also occur (see A Closer Look 1.2: Perfumes to Poisons). Carbohydrates, lipids, and proteins also constitute the major nutrients in the human diet and are discussed in detail in Chapter 10.

Carbohydrates

Carbohydrates, which include **sugars** and **starches** as well as **cellulose,** are composed of carbon, hydrogen, and oxygen (fig. 1.5). Many carbohydrates, especially **glucose,** are sources of energy for cells, while other carbohydrates, such as cellulose, are structural materials. The smallest carbohydrates are the **monosaccharides,** or the simple sugars. These contain only one sugar molecule; the most familiar examples of monosaccharides are glucose and **fructose.** The general formula for monosaccharides is $C_nH_{2n}O_n$, with n equal to 3, 4, 5, 6, or 7. Glucose and fructose have the same general formula, $C_6H_{12}O_6$, but they have different arrangements of the atoms and react differently.

Two sugar molecules chemically bonded together are known as a **disaccharide.** Common table sugar, **sucrose,** is a disaccharide composed of one glucose molecule and one

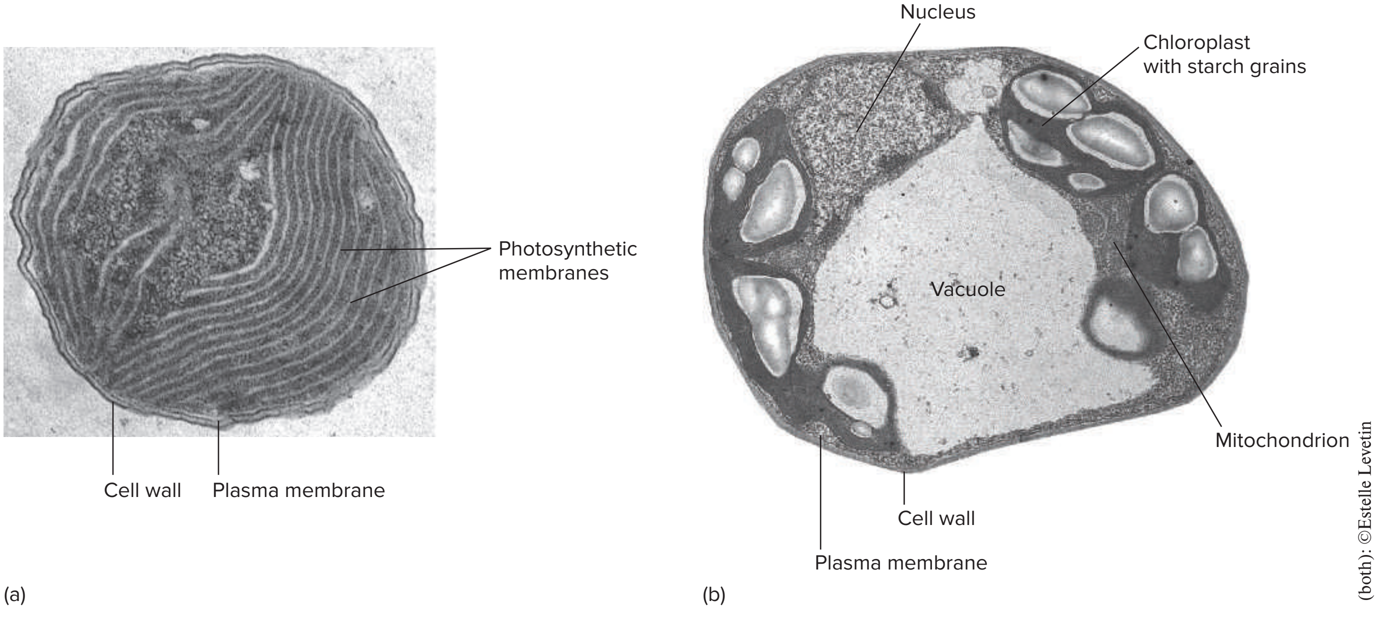


Figure 1.4 Cellular organization. (a) Prokaryotic cell. Although this cyanobacterial cell does contain internal photosynthetic membranes, there are no membrane-bound organelles or nucleus. (b) Eukaryotic cell. This *Elodea* leaf cell shows a nucleus and such membrane-bound organelles as chloroplasts, mitochondria, and a vacuole.

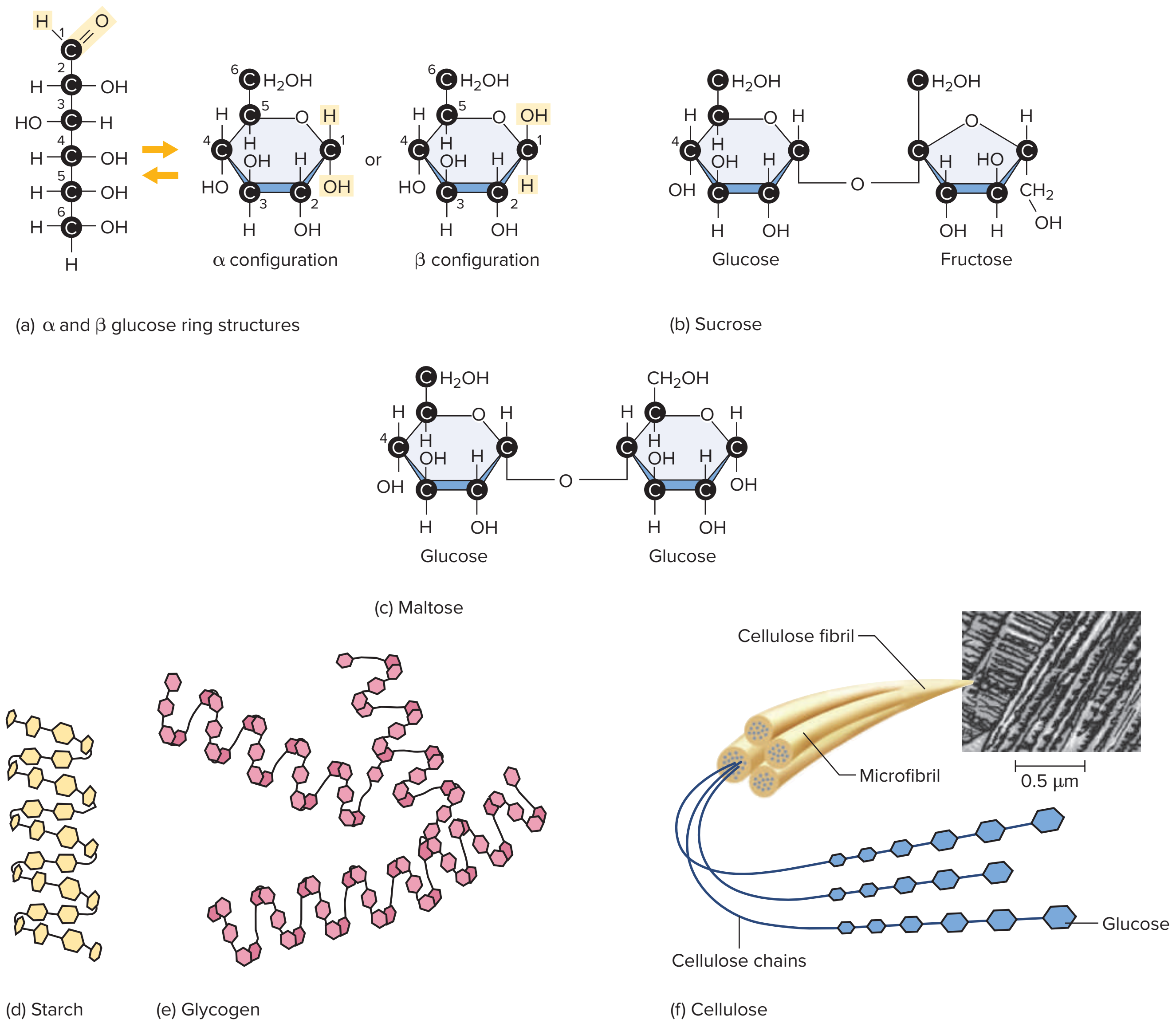


Figure 1.5 Carbohydrates. (a) Monosaccharides are known as simple sugars. Glucose, the most abundant monosaccharide, can exist in a straight chain or ring configuration. (b) Sucrose, a disaccharide, is composed of a molecule of glucose and a molecule of fructose bonded together. (c) Maltose, another disaccharide, forms from two glucose molecules. (d)–(f) Polysaccharides. All three molecules are made from thousands of glucose molecules, but they have different bonding arrangements. (d) Starch found as a storage molecule in green plants. (e) Glycogen found as a storage molecule in animals, bacteria, and fungi. (f) Cellulose, a structural component of plant cell walls, scanning electron micrograph.

fructose molecule. Although most plants transport carbohydrates from one part of the plant to another in the form of sucrose, only a few plants actually store this molecule (see A Closer Look 4.2: Sugar and Slavery). Most sucrose for table use comes from either sugarcane or sugar beet (fig. 1.5). Maltose, another disaccharide, contains two glucose molecules. This sugar is seldom found free in plants but is a breakdown product of starch and an important ingredient in the brewing of beer.

Polysaccharides consist of many thousands of sugar molecules bonded together. The three most common polysaccharides are starch, glycogen, and cellulose. These three are all composed of repeating glucose molecules, but they have different chemical bonding and arrangements (fig. 1.5). Both starch and glycogen are storage molecules; starch occurs in green plants, while glycogen is found in fungi, bacteria, and animals. Starch stored in plant stems, roots, seeds, and fruit is a major source of food for the human population (Chapters 6, 12, and 14). Cellulose is a structural component of plant cell walls, while chitin, a more complex molecule, is the major structural component in fungal cell walls.

Proteins

Proteins are large, complex macromolecules composed of smaller molecules known as **amino acids.** Carbon, hydrogen, oxygen, nitrogen, and sulfur are the elements found in

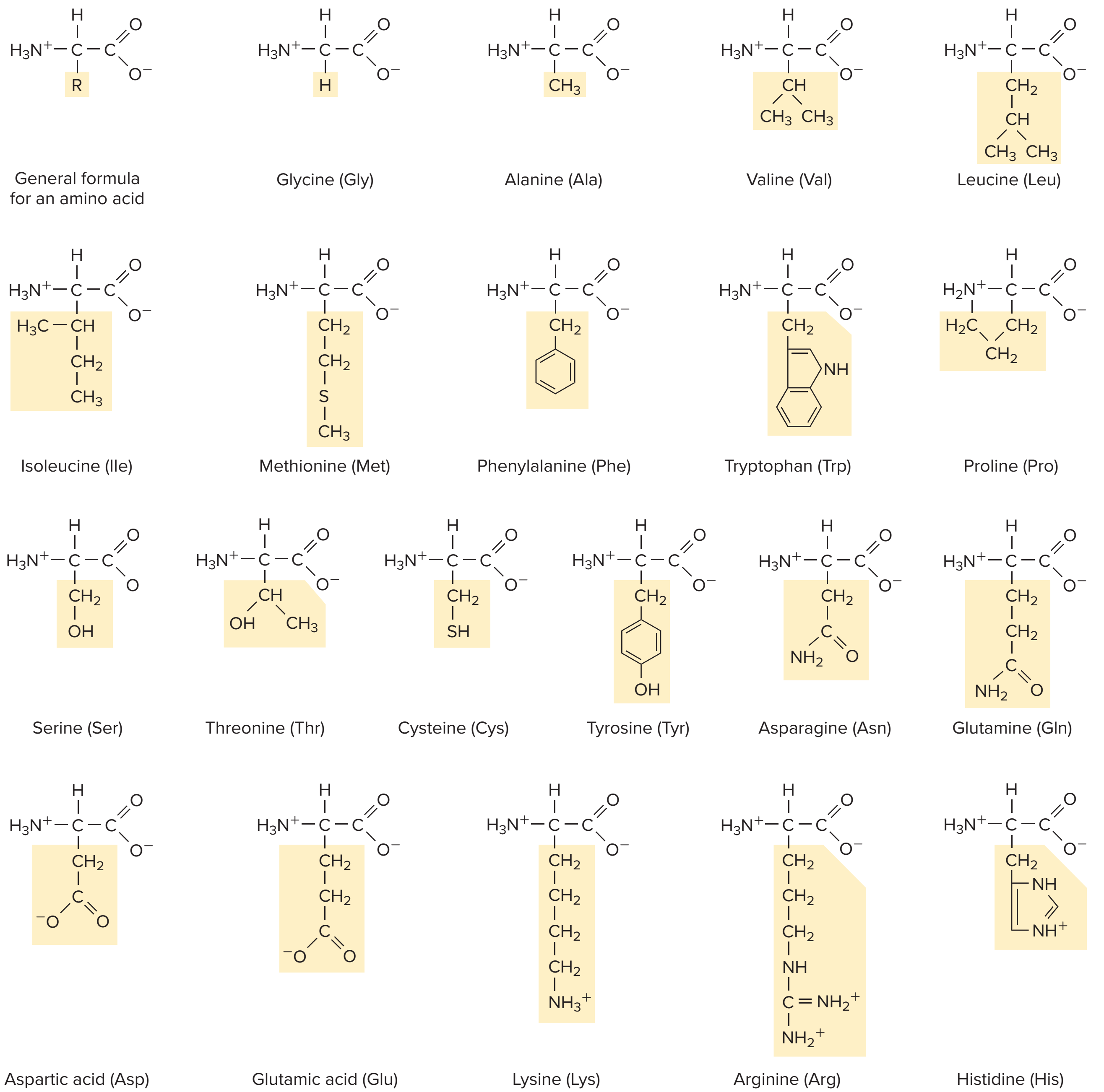


Figure 1.6 Amino acids. General formula for an amino acid and the 20 naturally occurring amino acids. All have the same backbone (N-C-C) and differ only in the side group (R-group) attached to the center carbon.

proteins. There are 20 different amino acids that are common to all life forms. All amino acids have a common backbone with a nitrogen atom and two carbon atoms (N-C-C) and differ only in the side group, called an R-group, attached to the central carbon atom (fig. 1.6). The number and arrangement of these 20 amino acids result in an infinite variety of proteins. Amino acids are attached to each other by a special covalent bond called a peptide bond, and long chains of amino acids are called **polypeptide** chains. In the complete protein structure, the polypeptide chain is twisted and folded into a specific, three-dimensional shape (fig. 1.7). Proteins have many functions; they can serve as enzymes (biological catalysts), structural materials, regulatory molecules, or transport molecules, to name a few of their many roles. Proteins produced by plants, especially legumes, are an important source of nutrients for the human diet (Chapter 13).

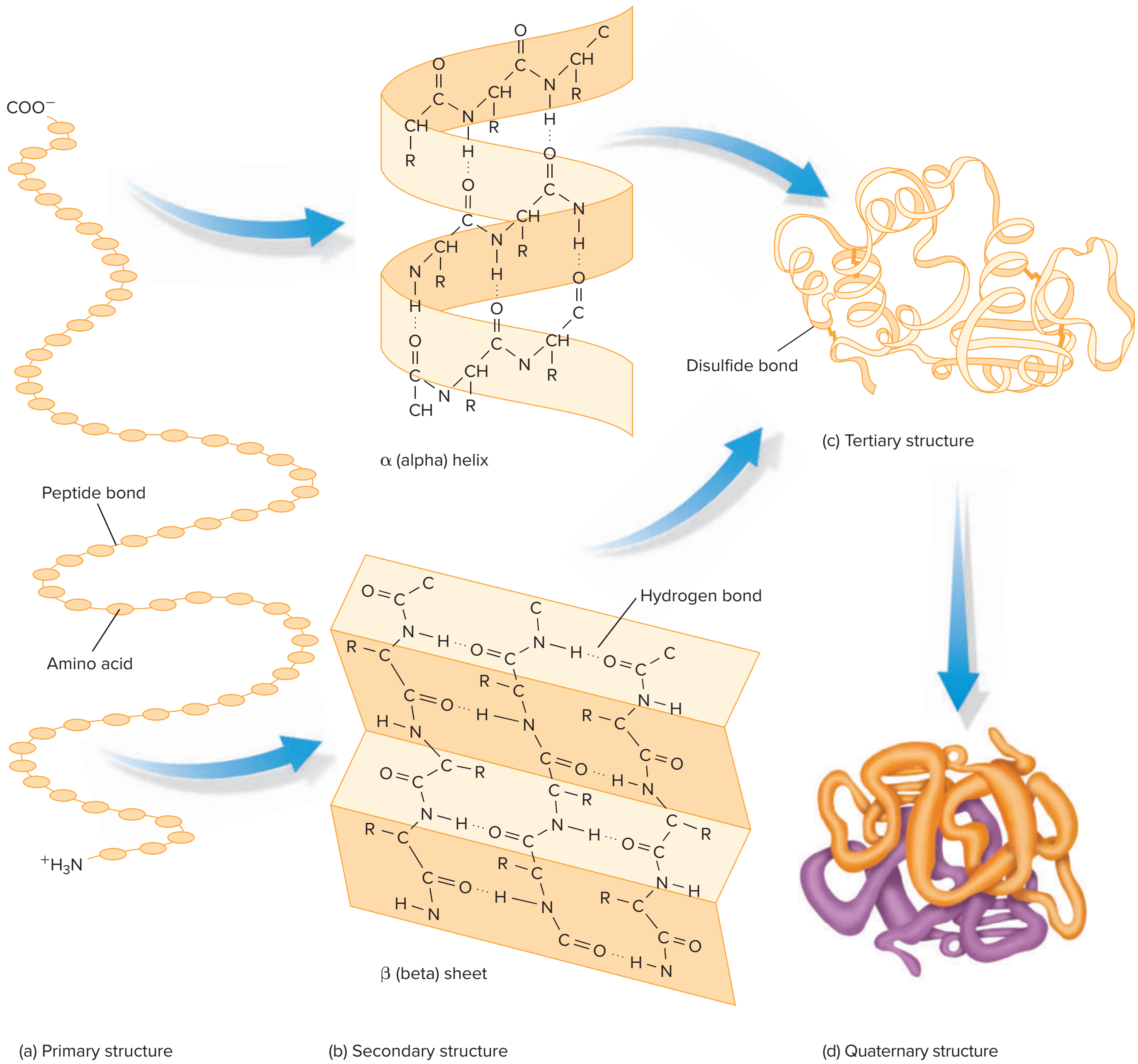


Figure 1.7 Protein structure. (a) Primary protein structure consists of the sequence of amino acids bonded together by peptide bonds to make a polypeptide chain. (b) Secondary protein structure consists of a helix, or pleated sheet, that spirals or folds the polypeptide chain. This is stabilized by hydrogen bonds. (c) Tertiary structure is a twisting and folding of the molecule. (d) Quaternary structure contains more than one polypeptide chain, each with its own tertiary structure.

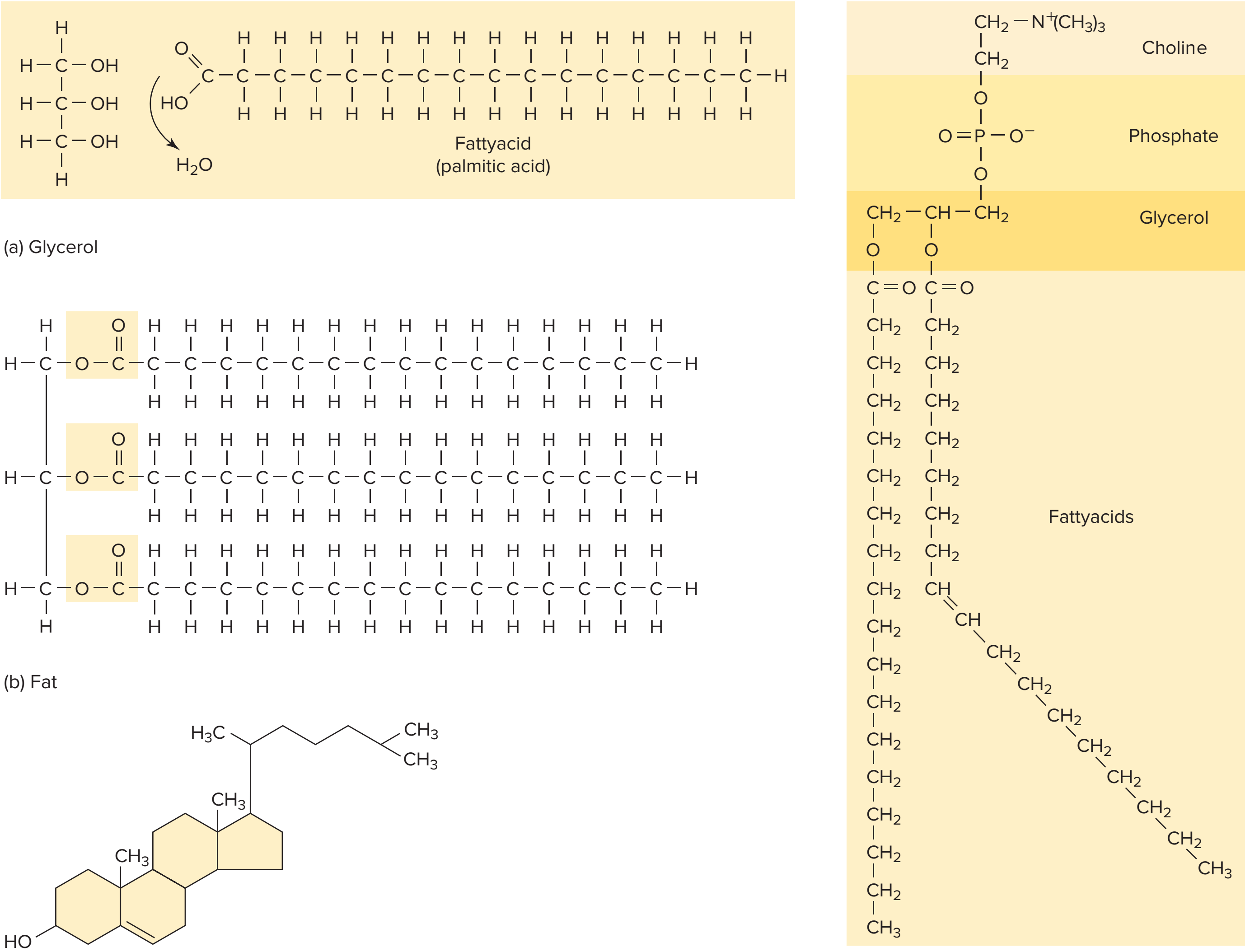
Thinking Critically

The four major groups of macromolecules in living organisms are carbohydrates, proteins, lipids, and nucleic acids.

What are the primary roles of each of the molecules?

Lipids

Lipids are a diverse group of substances largely composed of only carbon and hydrogen. Small amounts of oxygen may occur in some lipids. There are many different types of lipids; what they have in common is that they are insoluble in water. Lipids include such compounds as **triglcerides, phospholipids, steroids** (fig. 1.8), and waxes. Different types of lipids have different functions. They can be important as sources of energy



(d) Cholesterol

(c) Phospholipid

Figure 1.8 Lipids. (a) The building blocks of fats and oils consist of glycerol and fatty acids. (b) A fat, or triglyceride, formed from glycerol and three fatty acids. (c) A phospholipid is formed from glycerol, two fatty acids, a phosphate group, and choline. (d) Cholesterol, one of many steroids, is a more complex lipid. The four-ring steroid backbone is shaded.

(triglycerides), as structural components of cell membranes (phospholipids and cholesterol), or as hormones (steroids). Triglycerides, better known as fats and oils, function as food reserves in many organisms. Fats are the usual energy reserves in animals, while seeds and fruits of certain plants store appreciable amounts of oil, which has been used by humans for thousands of years (Chapter 13).

Nucleic Acids

Nucleic acids contain carbon, hydrogen, oxygen, nitrogen, and phosphorus. They are composed of repeating units called **nucleotides,** which consist of a sugar (either **ribose** or **deoxyribose**), a phosphate group $(PO_4)^{-3}$, and a nitrogenous base (either a **purine** or a **pyrimidine** base) (fig. 1.9). Five different types of nucleotides occur, depending on the type of base. There are two purine bases, **adenine** and **guanine,** and three pyrimidine bases, **thymine, cytosine,** and **uracil. Deoxyribonucleic acid (DNA)** and **ribonucleic acid (RNA)** are the two types of nucleic acids. Nucleotides containing adenine, guanine, and cytosine occur in both DNA and RNA. Thymine nucleotides occur only in DNA; uracil replaces thymine in RNA. Thus, both DNA and RNA contain four types of nucleotides, two purines and two pyrimidines.

It is the sequence of these nucleotide bases in the DNA molecule that is the essence of the genetic code. DNA is the hereditary material of life, unique in its ability to replicate itself and thus pass on the genetic code from one generation to the next. DNA, often called the **double helix** (fig. 1.9), exists as a double-stranded molecule that is twisted into a helix.

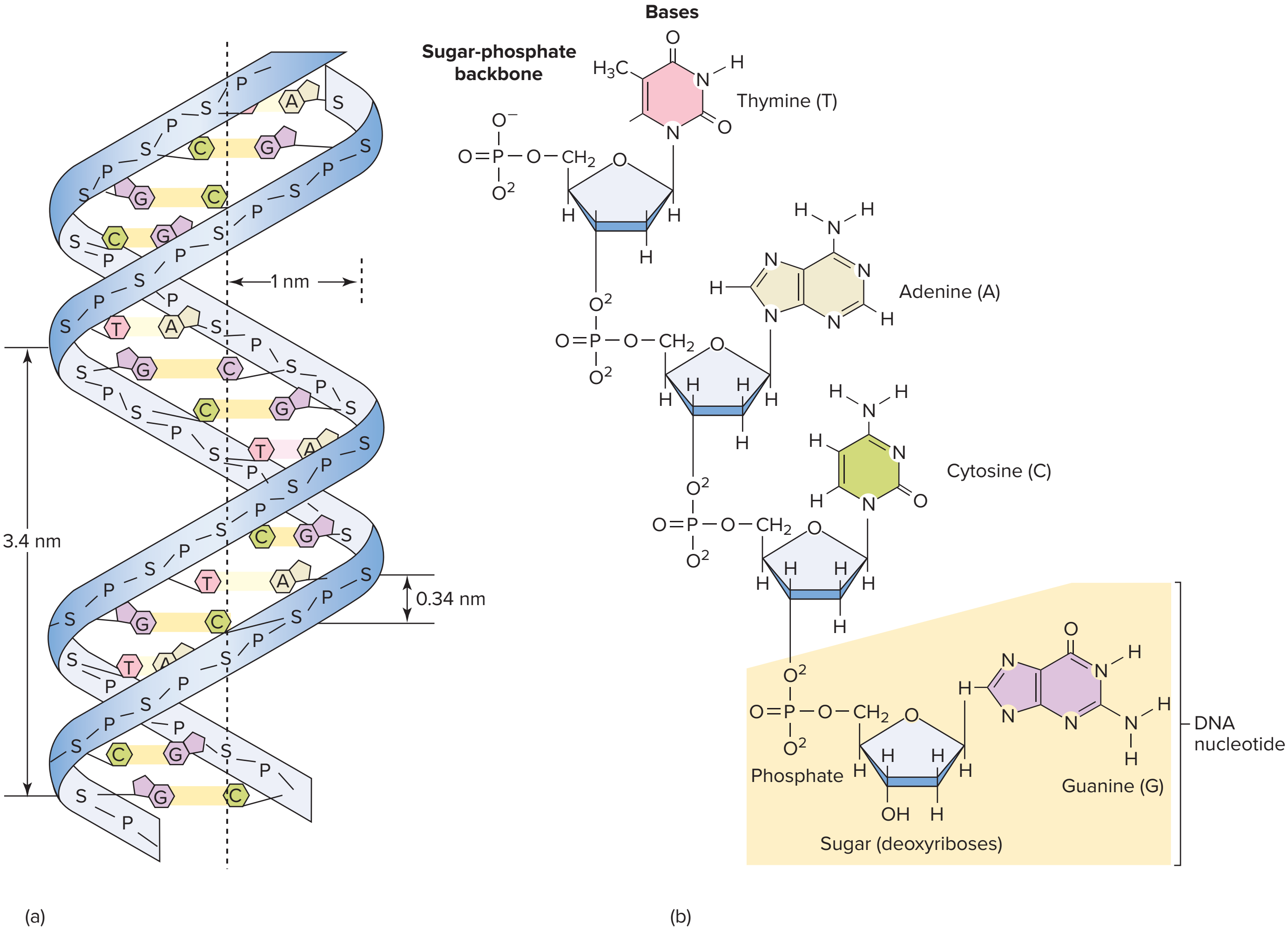


Figure 1.9 DNA molecule. (a) The double helix with the sugar-phosphate backbone making up the sides and the paired nitrogenous bases the interior. (b) Structures of the nucleotides (sugar, phosphate, and base) that make up the DNA molecule.

The sides of the helix are made of alternating sugar (deoxyribose) and phosphate groups, and the nitrogenous bases are found as purine-pyrimidine pairs (adenine always pairs with thymine and guanine with cytosine) in the interior of the helix.

Unlike DNA, RNA usually consists of a single strand, with ribose as part of the sugar-phosphate backbone. RNA is involved in the manufacture of proteins, using the instructions coded on the DNA molecule. The sequence of bases in DNA makes up a **gene,** and each gene codes for the formation of a specific product (see Chapter 7).

CHAPTER SUMMARY

1. Angiosperms, also called flowering plants, supply humanity with the essentials of life. The food staples of civilization—wheat, rice, and corn—are all angiosperms, as are almost all other food crops. Other angiosperm products that have shaped modern society include cloth, hardwood, herbs and spices, beverages, drugs, perfumes, vegetable oils, gums, and rubber.
2. The algae are aquatic, photosynthetic organisms that show a great diversity of form, ranging in size from the microscopic unicellular algae to gigantic seaweeds. They are important as components of aquatic food chains, contributors to the global photosynthetic rate, and sources of a number of economically important products. However, in the case of algal blooms, they can be detrimental to both the environment and the economy.
3. Fungi are also an economically important group of organisms. They include molds, mildews, yeast, and mushrooms. Fungi provide many beneficial items, such as penicillin, beer, wine, edible mushrooms, and leavened bread. A negative aspect of their economic importance is the impact of fungal disease and spoilage.

A CLOSER LOOK 1.2

Perfumes to Poisons: Plants as Chemical Factories

Carbohydrates, lipids, proteins, and nucleic acids are essential to life and are termed *primary metabolites* because they occur in the major, or primary, metabolic pathways. Many plants and fungi also produce other chemical compounds that are produced along secondary pathways and are referred to as secondary compounds (or secondary metabolites). They include four large classes of chemicals: terpenes, phenolics, glycosides, and alkaloids. Many secondary compounds are actually derived from primary metabolites, such as lipids, carbohydrates, or amino acids, and may even be combinations of these. At one time, it was thought that these compounds were by-products of metabolism; however, it is now known that these compounds have diverse functions in plants. They may attract pollinators, inhibit bacterial and fungal pathogens, deter grazing animals, deter insects, or inhibit the growth of competing plants. Humans have discovered that many of these compounds have other applications, and this discovery has made certain plants of tremendous value to society. Some are medicinal; some impart interesting flavors to food; some produce useful products; and some are highly toxic.

Terpenes are hydrocarbons, which are compounds containing only carbon and hydrogen atoms; they range greatly in size and structure and include essential oils, resins, and polyterpenes. Essential oils provide the flavor and aroma of many herbs and spices as well as the scents used in perfumes and incense. Resins are used in the production of pharmaceuticals, dental adhesives, varnishes, insecticides, chewing gum, turpentine, rosin, perfumes, and oil-based paints. Polyterpenes include the elastic compounds found in latex, which is a milky sap produced by many plants. The most important of these compounds is natural rubber from *Hevea brasiliensis*, the rubber tree. Other terpenes include the carotenoid pigments, which are the red, orange, and yellow pigments found in plants; however, these are usually classified as primary metabolites. Taxol is a terpene from the bark of Pacific yew trees that is important in chemotherapy for treating ovarian and breast cancer.

Phenolics are a large and diverse category of compounds, which all contain one or more aromatic benzene rings (a ring of six carbon atoms with six hydrogen atoms attached) with one or more hydroxyl (OH) groups. They range from small molecules to large, complex macromolecules and include flavonoids, tannins, and lignin. The natural browning in cut surfaces of apples and potatoes is caused by the interaction of phenolics with oxygen in the air. Although many essential oils are terpenes, others are phenolic compounds; examples are clove oil and bergamot oil, which is used to flavor Earl Grey tea. Flavonoids include water-soluble plant pigments known as anthocyanins, which are found in red cabbage and in many flower petals. These pigments, along with other phenolics, are important sources of natural dyes. Tannins occur in many plants and have been traditionally used to tan animal skins to form leather. Also, tannins in tea, red wine, and some fruits are important components of the flavors. The flavonoids and possibly the tannins found in red grapes (and red wine) are believed to reduce the risk of heart disease. Urushiol is the phenolic compound in poison ivy and poison oak that causes the blistering, itchy rash that comes from contact with the plants. Tetrahydrocannabinol (THC), a phenolic resin, is the active ingredient in marijuana plants. Finally, mention should be made of lignin, a primary metabolite composed of thousands of phenolic molecules. Lignin is found in the cell wall of certain plants and is the substance that gives wood its hardness and strength.

Glycosides are compounds containing glucose (or a different sugar) combined with another, nonsugar molecule. Typically, these are combinations of glucose and a terpene, a steroid, or a phenolic compound. Three common categories of glycosides are saponins, cardioactive glycosides, and cyanogenic glycosides. Saponins, which form a soapy lather when vigorously mixed with water, consist of a combination of a sugar and a steroid. Saponins are bitter tasting and can cause gastric upsets. Plants rich in saponins have

4. All living organisms have the capacity to grow and reproduce, the ability to respond, the ability to evolve and adapt, a metabolism, an organized structure, and an organic composition.
5. The chemical nature of living matter is based on the element carbon and its ability to covalently bond to other carbon atoms to form the skeletons of carbohydrates, lipids, proteins, and nucleic acids—the molecules of life. Monosaccharides, especially glucose molecules, serve as sources of energy for cells; polysaccharides have storage and structural functions. Proteins, composed of long chains of amino acids, have many functions as enzymes, structural molecules, regulatory molecules, and transport molecules. Lipids are a diverse group of compounds that are insoluble in water. Some serve as energy reserves, others as structural materials or hormones. DNA serves as the hereditary material of life by encoding information in the sequences of bases. RNA functions in the manufacture of proteins using information encoded in the DNA molecule.

been used in detergents, shampoos, and other products. Saponins from yams are the source of steroids that have been used in the manufacture of human sex hormones and cortisone. Cardioactive glycosides are similar in structure to the saponins; however, the steroid portion of the molecule is modified. As the name implies, these compounds affect the heart; in fact, they are fatal if consumed in enough quantity. However, at the proper dosage, digitoxin, a cardiac glycoside from foxglove, is one of the most important treatments for congestive heart failure. Cyanogenic glycosides release hydrogen cyanide (HCN) when metabolized. HCN is a deadly compound, yet cassava, which contains cyanogenic glycosides, is a dietary staple in many tropical countries. Proper processing of cassava removes these toxic metabolites. Another category of glycosides are glucosinolates, which are mainly found in the Brassicaceae (the mustard and cabbage family). Glucosinolates constitute a large group of important flavor molecules in broccoli, cabbage, and other vegetables and also impart the sharp biting taste of mustard and horseradish. Research suggests that the glucosinolates in broccoli and similar vegetables have anticancer properties and help protect people from colon and rectal cancer.

Alkaloids are a large group of nitrogen-containing secondary metabolites that are synthesized from various amino acids and found in many plants and fungi. These compounds are well known for their effects on mammalian physiology, especially on the central nervous system. Many alkaloids are structurally similar to neurotransmitters found in the brain, and most are considered psychoactive. Some alkaloids, such as caffeine and cocaine, are stimulants; others, such as morphine and codeine, are depressants. Still others—such as mescaline, the tropane alkaloids, and the ergot alkaloids—are hallucinogenic. In high doses, some alkaloids are deadly poisons; these include nicotine, the alkaloid in tobacco. Many have important medicinal applications, but the addictive properties of other alkaloids have caused widespread problems throughout the world.

Throughout this book are numerous examples of how terpenes, phenolics, glycosides, and alkaloids have been used by people and even examples of how they have altered the course of civilization (table 1.A).

Table 1.A Commonly Occurring Secondary Products

Class of Compound	Examples	Use by Humans	Chapter
Terpenes	Essential oils	Herbs and spices/flavor	Chapter 17
	Essential oils	Perfumes and incense	Chapter 5
	Taxol	Chemotherapy	Chapter 19
Phenolics	THC	Hallucinogen/glaucoma treatment	Chapter 20
	Urushiol	Allergen	Chapter 21
Glycosides	Cassava—cyanogenic glycosides	Starchy staple	Chapter 14
	Yam—saponin	Starchy staple/source of steroids	Chapter 14
	Digitoxin	Heart medication	Chapter 19
Alkaloids	Caffeine	Stimulant	Chapter 16
	Ephedrine	Stimulant/decongestant	Chapter 19
	Quinine	Treatment for malaria	Chapter 19
	Morphine	Pain relief, psychoactive	Chapter 20
	Cocaine	Anesthetic/psychoactive	Chapter 20
	Mescaline	Hallucinogen	Chapter 20

REVIEW QUESTIONS

1. What are the characteristics of angiosperms? of fungi? of algae?
2. Crystals can increase in size and seemingly grow. Would you consider crystals to be living? Why or why not?
3. Describe the levels of protein structure.
4. What are the differences between monosaccharides, disaccharides, and polysaccharides?
5. How do triglycerides and phospholipids differ in structure and function?
6. Define the following terms: *simple sugar, starch, amino acid,* and *polypeptide.*
7. Investigate the similarity of design between the hairs of the stinging nettle and the hypodermic syringe (Chapter 21).

UNIT II

CHAPTER

2

The Plant Cell

©Steven P. Lynch

Bulblets often replace flowers in the wild onion; the bulblets drop off to the ground and vegetatively produce clones of the parent plant. Mitosis is the underlying cell division for vegetative, or asexual, reproduction.

KEY CONCEPTS

1. The Cell Theory establishes that the cell is the basic unit of life, that all living organisms are composed of cells, and that cells arise from preexisting cells.
2. Plant cells are eukaryotic, having an organized nucleus and membrane-bound organelles.
3. Substances can move into and out of cells by diffusion and osmosis.
4. Mitosis, followed by cytokinesis, results in two genetically identical daughter cells. Growth, replacement of cells, and asexual reproduction all depend on the process of cell division.

CHAPTER OUTLINE

All plants (and every other living organism) are composed of cells. In some algae and fungi, the whole organism consists of a single cell, but angiosperms are complex, multicellular organisms composed of many different types of cells. Plant cells are microscopic and typically range from 10 to 100 µm in length. This means that there would be between 254 and 2,540 of these cells to an inch (fig. 2.1). In Chapter 3, we will be looking at the variety of cells, but in this chapter we will focus on a composite angiosperm plant cell.

EARLY STUDIES OF CELLS

The first person to describe cells was the Englishman Robert Hooke in 1665. Hooke was examining the structure of cork with a primitive microscope (fig. 2.2) and noticed that it was organized into small units that resembled the cubicles in monasteries where monks slept. These rooms were called "cells." He gave that name to each of the little compartments in cork, and the term was eventually applied to mean the basic unit of life. Although the cork was not living, Hooke later looked at living plants and identified cells there also.

Other scientists in the late seventeenth and eighteenth centuries continued the microscopic examination and study of a variety of organisms. It was not until the mid-nineteenth century, however, that Matthias Schleiden and Theodor Schwann, and later Rudolf Virchow, firmly established the **Cell Theory,** which recognizes the cell as the basic unit of life. The Cell Theory further states that all organisms are composed of cells and all cells arise from preexisting cells. This theory is one of the major principles in biology.

Although these early scientists were unable to identify many structures within a cell, today it is possible to magnify extremely small details of the cell using an electron microscope. Use of the electron microscope has greatly expanded our knowledge of cellular structure and function. The structures in a eukaryotic plant cell that are visible with an electron microscope are illustrated in Figure 2.3.

National Museum of Health and Medicine, Armed Forces Institute of Pathology

Figure 2.2 Robert Hooke's microscope.

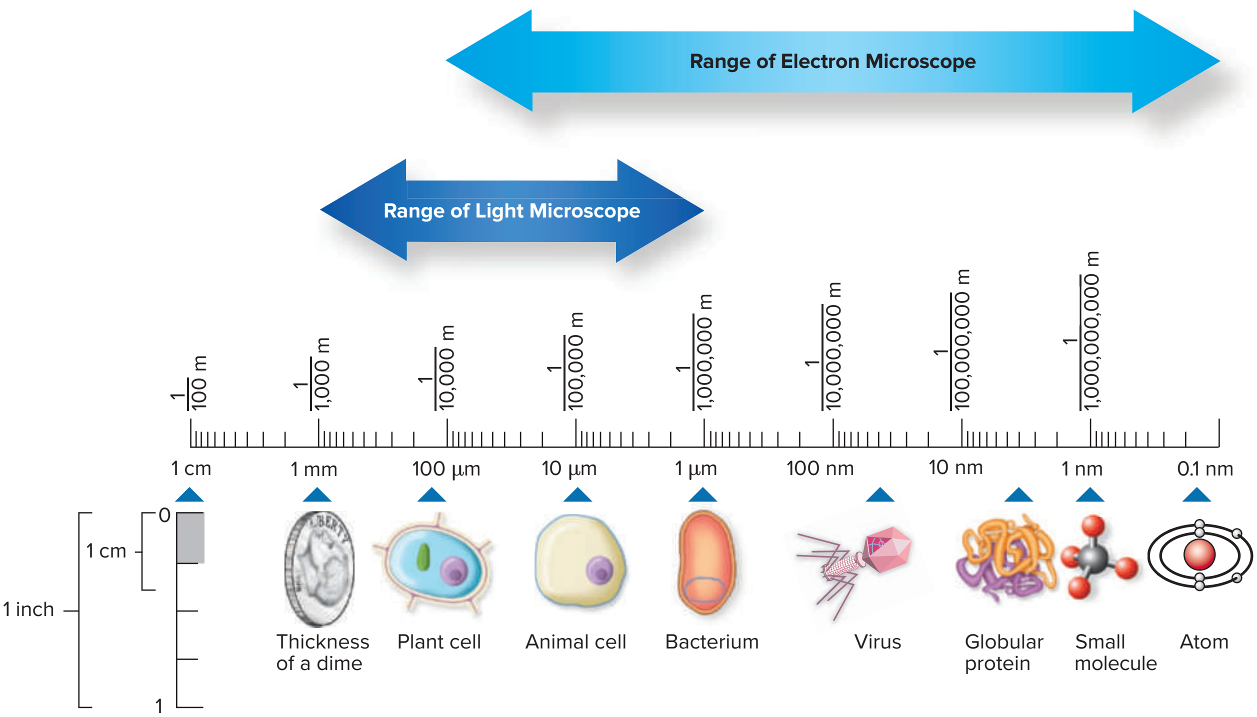


Figure 2.1 Biological measurements. The scale ranges from 1 centimeter (0.01 meter) down to 0.1 nanometer (0.0000000001 meter).

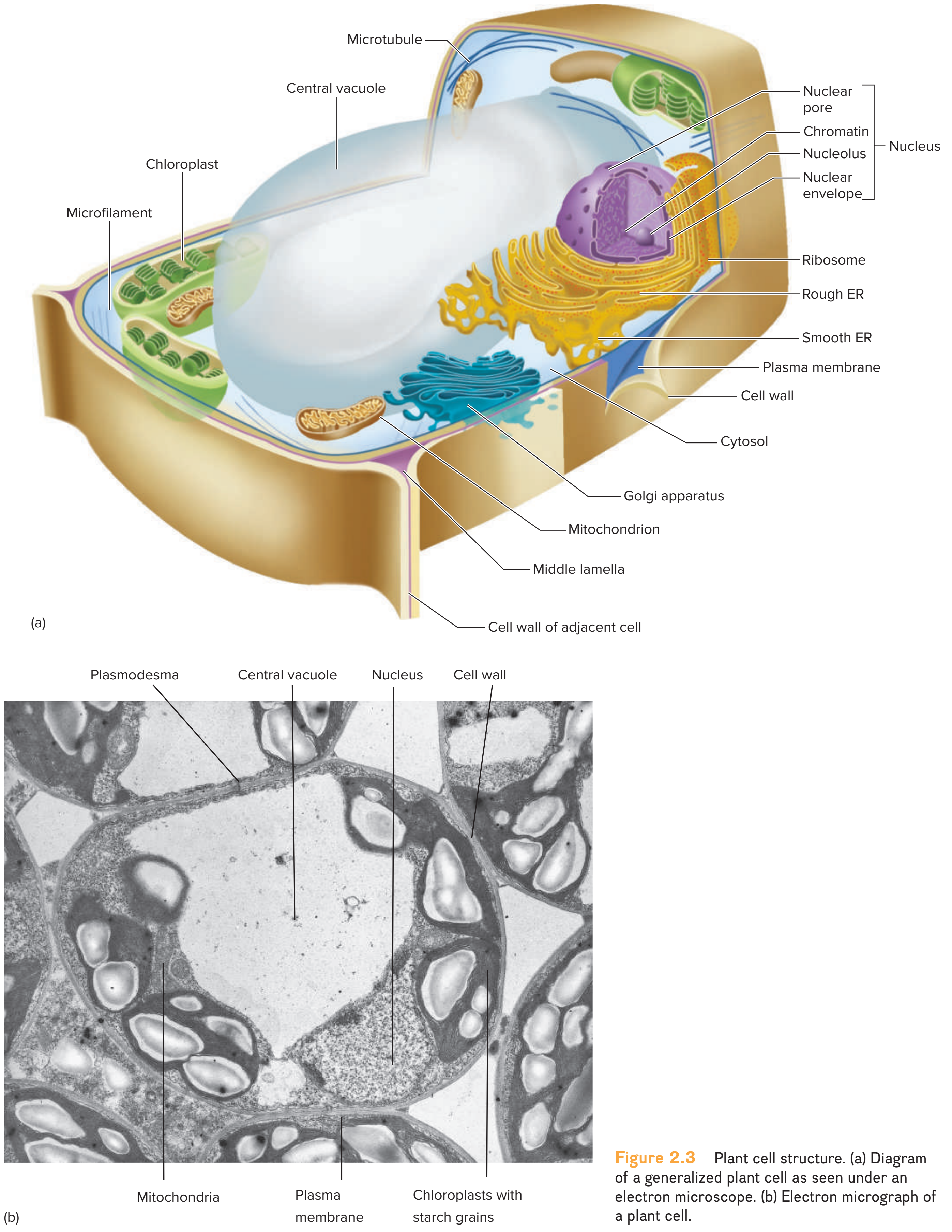


Figure 2.3 Plant cell structure. (a) Diagram of a generalized plant cell as seen under an electron microscope. (b) Electron micrograph of a plant cell.

THE CELL WALL

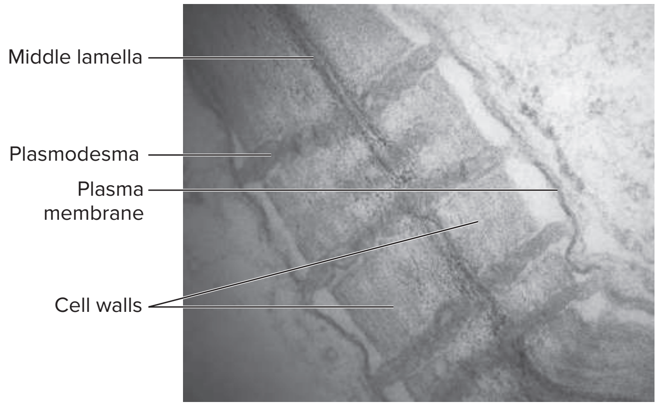
The **cell wall** encloses all other parts of the plant cell, collectively called the **protoplast.** The cell wall material is formed by the protoplast. Plant cell walls may consist of one or two layers. The first layer, or the **primary wall,** is formed early in the life of a plant cell. It is composed of a number of polysaccharides, principally cellulose. The cellulose is in the form of fibrils, extremely fine fibers (see fig. 1.5f). These fibrils are embedded in a matrix of other polysaccharides.

The **secondary wall** is laid down internal to the primary wall. In cells with secondary walls, **lignin,** a very complex organic molecule, is a major component of the walls, in addition to the cellulose and other polysaccharides. Considering all the plant material on Earth, it is not surprising that cellulose is the most abundant organic compound, with lignin not far behind.

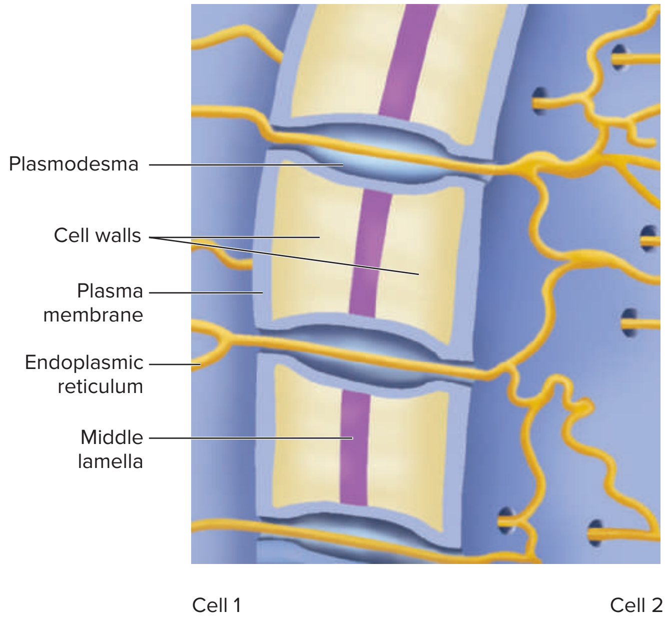
Only certain types of plant cells have secondary walls, usually just those specialized for support, protection, or water conduction. Lignin is known for its toughness; it gives wood its characteristic strength and provides protection against attack by **pathogens** (disease-causing agents) and consumption by herbivores (although certain species of wood-rotting fungi have the ability to break down lignin—see A Closer Look 23.2: Dry Rot and Other Wood Decay Fungi). To compare the characteristics of primary and secondary walls, imagine a chair made of lettuce leaves instead of wood!

Although the cell wall is one or two layers thick, it is not a solid structure. Minute pores, or **pits,** exist; most of these are large enough to be seen with a light microscope. Pits allow for the transfer of materials through cell walls. Cytoplasmic connections between adjacent plant cells often occur. These are called **plasmodesmata** and pass through the pits in the cell wall. These allow for the movement of materials from cell to cell (fig. 2.4).

A sticky layer called the **middle lamella** (fig. 2.3) can be found between the walls of adjacent plant cells. This acts as a cellular cement, gluing cells together. It is composed of **pectins,** the additive often used in making fruit jellies.



(a)



(b)

Figure 2.4 Plasmodesmata permit the passage of materials from cell to cell. (a) Electron micrograph. (b) Drawing.

THE PROTOPLAST

The protoplast is defined as all of the plant cell enclosed by the cell wall. It is composed of the nucleus plus the **cytoplasm.** The cytoplasm consists of various **organelles** (cellular structures) distributed in the **cytosol,** a matrix consisting of large amounts of water (in some cells, up to 90%), proteins, other organic molecules, and ions. Also found in the cytoplasm is a network of proteinaceous **microtubules** and **microfilaments** that make up the **cytoskeleton,** a cellular scaffolding that helps support and shape the cell and is involved in all aspects of cell movement (fig. 2.3).

Membranes

The outermost layer of the protoplast is the plasma membrane, which is composed of phospholipids and proteins. The **fluid mosaic model,** the currently accepted idea of membrane structure, is shown in Figure 2.5. This model consists of a double layer of phospholipids with scattered proteins. Some of the proteins go through the lipid bilayer **(integral proteins),** while others are on either the inner or the outer surface **(peripheral proteins).** Some of the membrane proteins and lipids have carbohydrates attached; they are called **glycoproteins** and **glycolipids,** respectively. The carbohydrates are usually short chains of about five to seven monosaccharides. Some have described this membrane model as "protein icebergs in a sea of lipids." The plasma membrane serves as a permeability barrier, allowing some molecules (such as water), but not others, to pass through.

Moving Into and Out of Cells

Cells constantly exchange materials with their environment. One way this exchange occurs is by **diffusion.** Diffusion is the spontaneous movement of particles or molecules from areas of higher concentration to areas of lower concentration. Examples of diffusion occur everywhere. Open a bottle of perfume; soon the scent spreads throughout the room. Try the same thing with a bottle of ammonia. In both cases, the

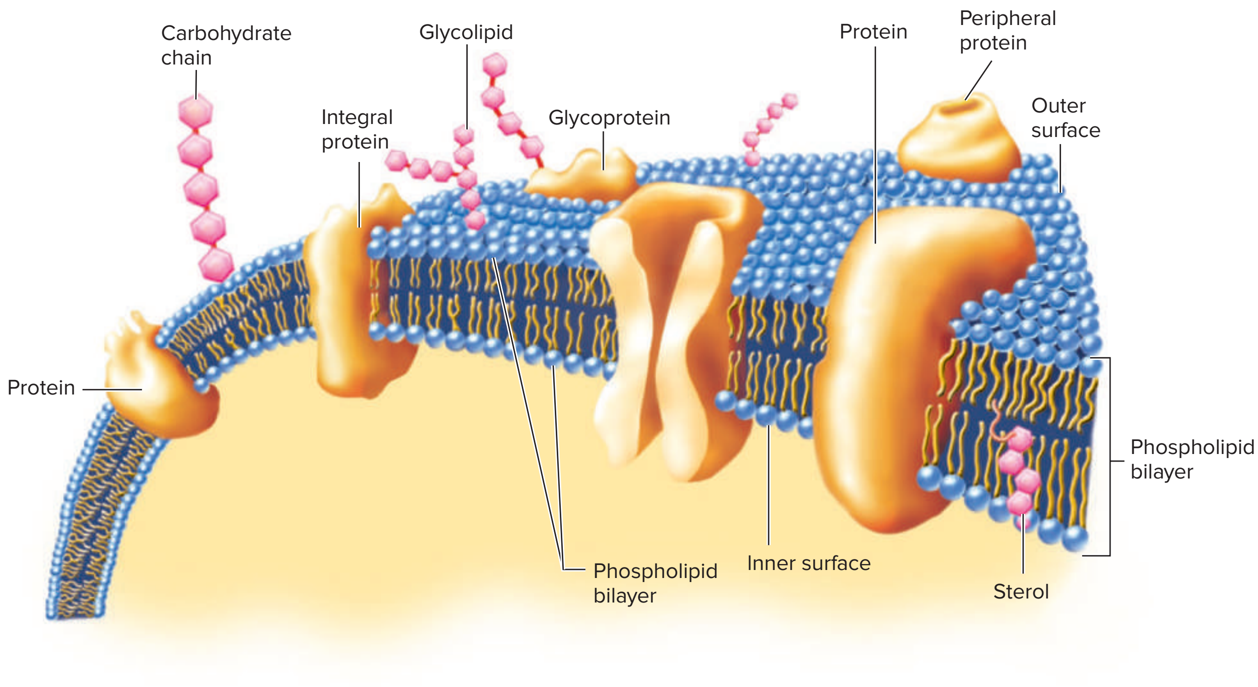


Figure 2.5 Fluid mosaic model of the plasma membrane. The plasma membrane is composed of a phospholipid bilayer with embedded proteins.

molecules diffuse from where they were most concentrated. Diffusion can also be easily demonstrated in liquids. Place a sugar cube in a cup of hot tea; eventually, the sugar will diffuse and be distributed, even without stirring.

Diffusion also occurs within living organisms, but the membranes present barriers to this movement of molecules. Membranes such as the plasma membrane can be described as **differentially permeable.** They permit the diffusion of some molecules but present a barrier to the passage of other molecules. Many molecules are simply too large to diffuse through membranes.

The diffusion of water across cell membranes is called **osmosis.** Water can move freely through membranes. The direction the water molecules move is dependent on the relative concentrations of substances on either side of the membrane. If you place a cell in a highly concentrated solution of salt or sugar, water will leave the cell. The water is attracted to the solute molecules and associates with them. More water will remain on the side of the differentially permeable member that has the higher solute concentration. On the other hand, if you place a cell in distilled (pure) water, water will enter the cell where the concentration of solutes is higher (fig. 2.6).

If a plant cell is left in a highly concentrated, or **hypertonic,** solution for any length of time, so much water will leave that the protoplast actually shrinks away from the cell wall. When this happens the cell is said to be **plasmolyzed.** In a wilted leaf, many of the cells are plasmolyzed (fig. 2.6).

When a plant cell is in pure water or a very weak, **hypotonic,** solution, water will enter until the vacuole is fully extended, pushing the cytoplasm up against the cell wall. Such cells look plump, or **turgid.** This is the normal appearance of cells in a well-watered plant. The crispness and crunch of fresh celery are due to its turgid cells. When the cell is placed in a solution of the same concentration, **isotonic,** there is no net movement of water, and the cell is not turgid (fig. 2.6).

Diffusion and osmosis take place when molecules move along a **concentration gradient,** from higher to lower concentrations. However, cells can also move substances against a concentration gradient; sometimes sugars are accumulated this way. This type of movement is called **active transport** and requires the expenditure of energy by the cell. Membrane proteins are involved in transporting these substances across the membrane.

Organelles

A variety of organelles can be found in the plant cell (fig. 2.3). Most of these are membrane-bound, with the membrane being similar in structure and function to the plasma membrane. In leaf cells, the most distinctive organelles are the disk-shaped **chloroplasts,** which, in fact, are double membrane-bound. These organelles contain several pigments; the most abundant pigments are the chlorophylls, making leaves green. Carotenes and xanthophylls are other pigments present; these orange and yellow pigments are normally masked by the more abundant chlorophylls but become visible in autumn when the chlorophylls break down before the leaves are shed. The pigments are located within **thylakoids,** the internal membranes of the chloroplasts, and are most concentrated in membranous stacks called **grana** (sing., **granum**). The individual grana are interconnected and embedded in the **stroma,** a protein-rich environment. Although chloroplasts are easily seen with a light microscope, the internal organization, or ultrastructure, is visible only with an electron microscope. Photosynthesis occurs in the chloroplasts; this process allows plants to manufacture

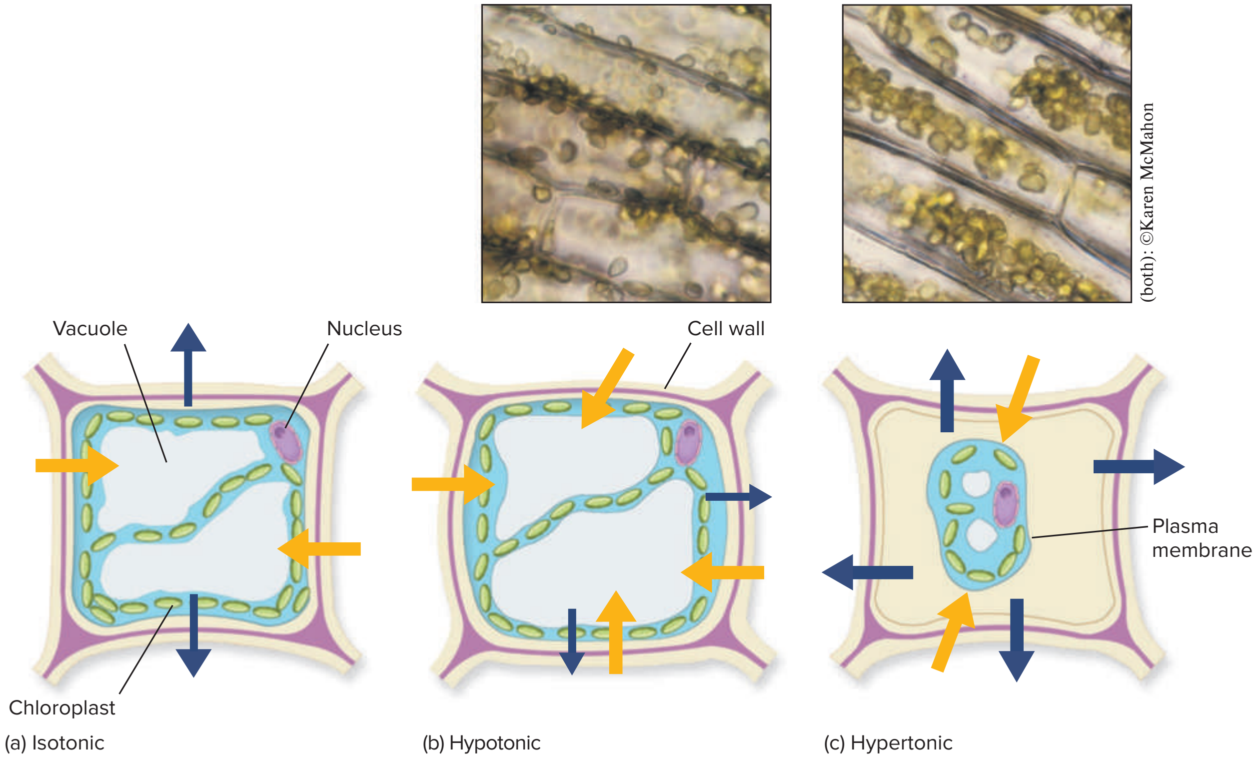


Figure 2.6 Osmosis in plant cells. The direction of the arrows indicates the direction of the water movement; the size of the arrow indicates the relative amount of water moving into or out of the cell. (a) In an isotonic solution, the cell neither gains nor loses water; water flows equally both into and out of the cell. (b) In a hypotonic solution, the cell gains water because more water enters the cell than leaves. (c) In a hypertonic solution, the cell loses water because more water leaves the cell than enters.

food from carbon dioxide and water using the energy of sunlight. More details on the ultrastructure of chloroplasts and the photosynthetic process are covered in Chapter 4.

Two other organelles that may be found in plant cells are **leucoplasts** and **chromoplasts.** Chloroplasts, leucoplasts, and chromoplasts are collectively called **plastids.** Leucoplasts are colorless organelles that can store various materials, especially starch. The starch grains filling the cells of a potato are found in a type of leucoplast called an **amyloplast** (fig. 2.7). Chromoplasts contain orange, red, or yellow pigments and are abundant in colored plant parts, such as petals and fruits. The orange of carrots, the red of tomatoes, and the yellow of marigolds result from pigments stored in chromoplasts.

These pigments are called carotenoids; although they can be part of the color in animals—the yellow in egg yolks or the pink in the feather of a flamingo—it was thought that animals received these carotenoids directly from the plants, algae, or fungi in their diet, but animals did not possess the genes to produce carotenoids themselves. However, it was discovered that the pea aphid (*Acyrthosiphon pisum*), which lives off the sugary sap in phloem and can come in green, yellow, and red forms, actually manufactures its own carotenoids. Some time ago, the gene coding for the synthesis of carotenoids was transferred from a fungus to an aphid and has been passed down from aphid to aphid over the generations. Apparently, the yellow aphids have one copy of the carotenoid gene and the red aphids two copies, while the green pea aphids lack the carotenoid gene altogether.

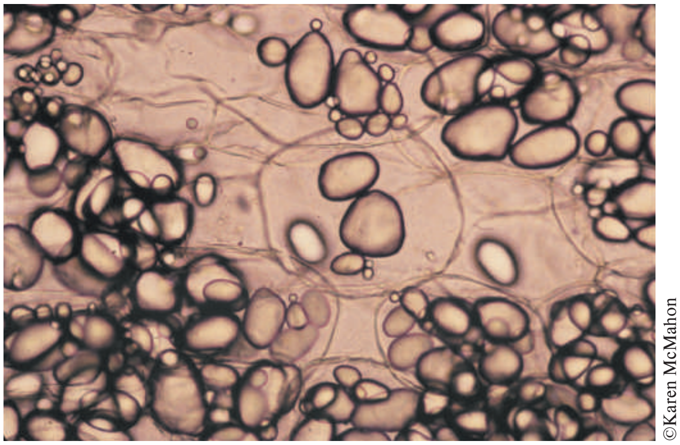


Figure 2.7 Amyloplasts in white potato.

Another organelle bound by a double membrane is the **mitochondrion** (pl., **mitochondria**), which is the site of many of the reactions of cellular respiration in all eukaryotic cells (fig. 2.3). Recall that cellular respiration is the metabolic process in which glucose is chemically broken down to release energy in a usable form, ATP. Mitochondria are not easily studied with a light microscope; the electron microscope has made the study of their ultrastructure possible. The size, shape, and numbers of mitochondria vary among different types of cells, but all mitochondria have a smooth outer membrane and an inner membrane with numerous infoldings called **cristae.** The compartment

A CLOSER LOOK 2.1

Origin of Chloroplasts and Mitochondria

As stated in Chapter 1, prokaryotes were the first organisms on Earth. Evidence indicates that prokaryotes first appeared approximately 3.5 billion years ago, while eukaryotes appeared only around 1.5 billion years ago. One question that has intrigued biologists for many years is, How did the eukaryotic cell evolve? The Endosymbiont Theory attempts to answer how eukaryotic cells evolved from prokaryotic cells. This theory states that the organelles of eukaryotic cells are the descendants of once free-living prokaryotes that took up residence in a larger cell, establishing a symbiotic relationship (symbiosis: two or more organisms living together). This association evolved into the well-studied eukaryotic cell.

Chloroplasts and mitochondria provide the best examples of this theory. Both organelles resemble free-living prokaryotes. In fact, as long ago as the 1880s, some biologists observed that chloroplasts of eukaryotic cells resembled cyanobacteria (then called blue-green algae). Both chloroplasts and mitochondria have structures that are associated with free-living cells. For example, they contain both DNA and ribosomes, which are bacterial in size and nature, allowing them to synthesize some of their own proteins. Both chloroplasts and mitochondria can divide to produce new chloroplasts and mitochondria in a manner very similar to prokaryotic cell division. The inner membranes of both organelles closely resemble the plasma membrane of prokaryotes. These features, as well as additional biochemical similarities, provide support for the validity of the Endosymbiont Theory.

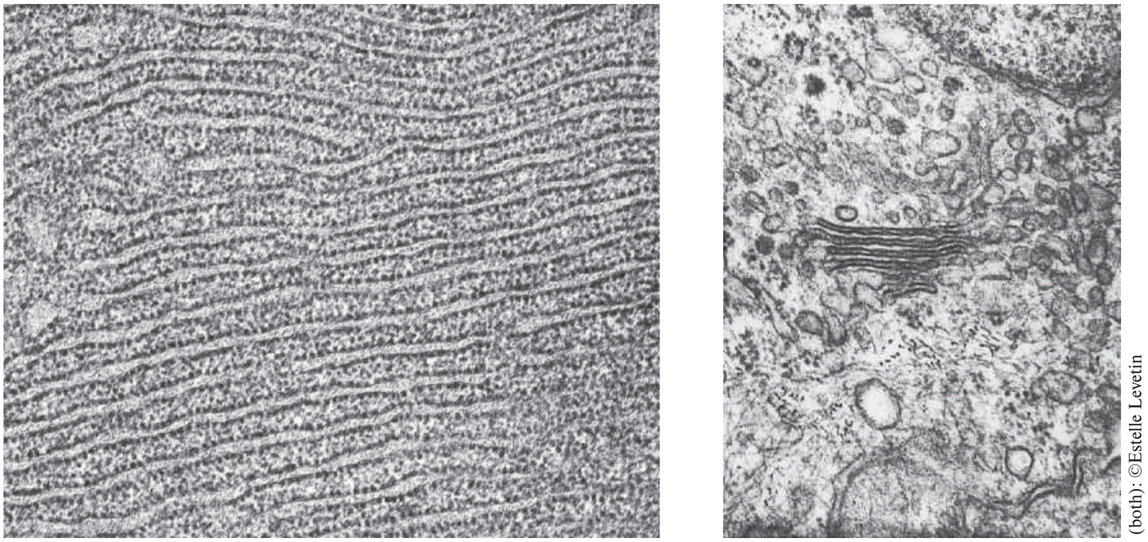
Recent research has discovered certain bacteria that appear to be in the process of evolving into organelles as predicted by the Endosymbiont Theory. Approximately 10% of insect species house bacterial endosymbionts. Some of the best studied are bacteria that live inside specialized gut cells of sap-sucking pests. The sugary sap of plants is deficient in amino acids, and apparently the bacterial endosymbionts produce needed amino acids and other essential nutrients for their insect hosts. In return, bacterial endosymbionts have been passed from generation to generation in insect hosts for over hundreds of millions of years. During this time, the bacterial endosymbionts have lost most of the genes that are necessary for bacteria to be self-sufficient. They no longer possess the genes to make the outer plasma membrane, to metabolize lipids and nucleotides, to transport materials into a cell, or for cell division. There is evidence that some of these bacterial genes may have been transferred to the nucleus of the host cell that now supports the endosymbiont.

Carsonella ruddii, an endosymbiont found in the gut cells of psyllids, a type of agricultural pest also known as jumping plant lice, has the smallest genome known for any bacterium, with only 160,000 base pairs of DNA. Its genome size is similar to that of the mitochondria (<600,000 base pairs) and chloroplasts (220,000 base pairs) found in terrestrial plants. Perhaps this endosymbiont will one day evolve into an organelle.

enclosed by the inner membrane is called the **matrix;** the matrix contains enzymes that are used in cellular respiration, while the cristae are the sites of ATP formation. Chapter 4 contains additional information on the role of mitochondria in cellular respiration, and A Closer Look 2.1: Origin of Chloroplasts and Mitochondria details how these organelles may have evolved.

Most mature plant cells (fig. 2.3) are characterized by a large **central vacuole** that is separated from the rest of the cytoplasm by its own membrane. In some cells, the vacuole takes up 90% of the cell volume, pushing the cytoplasm into a thin layer against the plasma membrane. The vacuole contains the cell sap, a watery solution of sugars, salts, amino acids, proteins, and crystals, all separated from the cytoplasm by the vacuolar membrane. The cell sap is often acidic; the tartness of lemons and limes is due to their very acidic cell sap. Some of the substances in the vacuole are waste products; others can be drawn upon when needed by the cell. The concentrations of these materials in the vacuole may become so great that they precipitate out as crystals. The leaves of the common houseplant dumb cane (*Dieffenbachia* spp.) are poisonous because of the presence of large amounts of calcium oxalate crystals (see Chapter 21). If consumed, the crystals can injure the tissues of the mouth and throat, causing a temporary inability to speak—hence the common name dumb cane. Pigments can also be found in the vacuole; these are called **anthocyanin** and are responsible for the deep red, blue, and purple colors of many plant organs, such as red onions and red cabbage. Unlike the pigments of the chloroplasts and chromoplasts, the anthocyanins are water soluble and are distributed uniformly in the cell sap. Anthocyanins have also been utilized for millenia as dyes for fabrics as discussed in A Closer Look 18.2: Herbs to Dye For.

An internal membrane system also occurs in plant cells (figs. 2.3 and 2.8). This consists of the **endoplasmic reticulum (ER),** Golgi apparatus, and microbodies. These structures are all involved in the synthesizing, packaging, and transporting of materials within the cell. The ER is a network of membranous channels throughout the cytoplasm. In some places the cytoplasmic side of the ER is studded with minute bodies called **ribosomes.** Ribosomes, composed of RNA and protein, are not membrane-bound and are the sites of protein synthesis. Portions of the ER with ribosomes attached are referred to as **rough ER.** Owing to the presence of ribosomes, rough ER



(a) (b)

Figure 2.8 The internal membrane system of plant cells. (a) Rough endoplasmic reticulum. (b) Golgi apparatus.

is active in protein synthesis. Ribosomes are also found free in the cytoplasm. Portions of the ER without ribosomes are called **smooth ER,** which functions in the transport and packaging of proteins and the synthesis of lipids.

The **Golgi apparatus** is a stack of flattened, hollow sacs with distended edges; small vesicles are pinched off the edges of these sacs (figs. 2.3 and 2.8). The Golgi apparatus functions in the storage, modification, and packaging of proteins that are produced by the ER. Once the proteins are transported to the Golgi sacs, they are modified in various ways to form complex biological molecules. Often, carbohydrates are added to proteins to form glycoproteins. The vesicles that are pinched off contain products that will be secreted from the cell. Some of the polysaccharides (not cellulose) found in the cell wall are also secreted by these Golgi vesicles.

Microbodies are small, spherical organelles in which various enzymatic reactions occur. Plant cells can contain two types of microbodies: **peroxisomes,** which are found in leaves and play a limited role in photosynthesis under certain conditions, and **glyoxysomes,** which are involved in the conversion of stored fats to sugars in some seeds.

Proteasomes are tunnel-shaped complexes of proteases, protein-degrading enzymes. There can be as many as 30,000 proteasomes in a cell. Proteasomes disassemble proteins tagged by an identifier called ubiquitin for destruction. Proteins targeted for destruction may be misfolded or otherwise abnormal and would not be able to function properly. The activity of proteasomes is critical to regulating metabolism, controlling cell reproduction, and understanding the mechanism for certain diseases. For example, destruction of a regulatory protein that is an enzyme in a biochemical pathway will stop the reaction, while destroying a regulator that inhibits cell division will promote reproduction. Diseases such as Parkinson's or Alzheimer's accumulate anomalous proteins in nerve cells; a drug that could stimulate proteasome activity might alleviate symptoms. Drugs that inhibit proteasome activity could be used to destroy mutated cells like those in cancer.

The **tannosome** is a newly discovered organelle unique to plants. As the name implies, these plastids contain **tannins,** compounds produced by a wide variety of plants, especially woody plants, to ward off herbivory by insects and other animals. Tannins also afford plants protection from UV radiation. Naturally dark brown in color, tannins have a tart taste and contribute to the flavor and color of black tea and red wine (Chapters 16 and 24). Tannins from oaks have also been used in the processing (accordingly called *tanning*) of animal skins into leather. Leather is more durable because tannins deactivate proteins, making the skins less subject to microbial decomposition. Tannins have also been used in the dyeing of fabrics from natural sources (Chapter 18).

Tannosomes arise from the thylakoids, the internal membrane system in chloroplasts, which are arranged in stacks called grana. At first, the thylakoid membranes become loose and swell. Next, small sections of the membrane bud off and form tiny spheres. The newly constructed tannosomes are then collected into larger membrane-bound transport structures called shuttles. Shuttles convey the tannosomes out of the chloroplasts through the cytoplasm to be released into the large central vacuole. Along this journey, tannins are constructed from subunits in the tannosomes. As the concentration of tannins rises, the tannosomes change color from chlorophyll green to the characteristic brown hue. Eventually the vacuole will completely fill up with tannosomes.

The Nucleus

One of the most important and conspicuous structures in the cell is the **nucleus,** the center of control and hereditary information (fig. 2.3). The nucleus is surrounded by a double membrane with small openings called **nuclear pores,** which lead to the cytoplasm. In places, the nuclear membrane is connected to the ER. Contained within the nucleus is granular-appearing **chromatin,** which consists of DNA (the hereditary material), RNA, and proteins. Another structure within the nucleus is the **nucleolus;** one or more dark-staining nucleoli are always

Table 2.1
Plant Cell Structures and Their Functions

Structure	Description	Function
Cell wall	Cellulose fibrils	Support and protection
Plasma membrane	Lipid bilayer with embedded proteins	Regulates passage of materials into and out of cell
Central vacuole	Fluid-filled sac	Storage of various substances
Nucleus	Bounded by **nuclear envelope**; contains chromatin	Control center of cell; directs protein synthesis and cell reproduction
Nucleolus	Concentrated area of RNA and protein within the nucleus	Ribosome formation
Ribosomes	Assembly of protein and RNA	Protein synthesis
Endoplasmic reticulum	Membranous channels	Transport and protein synthesis (rough ER)
Golgi apparatus	Stack of flattened, membranous sacs	Processing and packaging of proteins; secretion
Chloroplast	Double membrane-bound; contains chlorophyll	Photosynthesis
Leucoplast	Colorless plastid	Storage of various materials, especially starch
Chromoplast	Pigmented plastid	Imparts color
Mitochondrion	Double membrane-bound	Cellular respiration
Microbodies	Vesicles	Various metabolic reactions
Cytoskeleton	Microtubules and microfilaments	Cell support and shape
Plasmodesmata	Cytoplasmic bridges	Movement of materials between cells
Proteasome	Tunnel containing proteases	Disassembly of proteins targeted for destruction
Tannosome	Membrane-bound sphere	Production of tannins

present. The nucleolus is not membrane-bound and is roughly spherical; it is involved in the formation of ribosomes. Table 2.1 is a summary of the functions of the cellular components.

Thinking Critically

Researchers synthesized a bacterial chromosome and transplanted it into another bacterial cell. The artificial chromosome replaced the native DNA, and the cell soon began replicating and making proteins according to the instructions from the synthetic genes.

Have these scientists created a living cell? Why or why not?

CELL DIVISION

The cell, with its organelles just described, is not a static structure but dynamic, continually growing, metabolizing, and reproducing. Inherent in all cells are the instructions for cell reproduction or **cell division**, the process by which one cell divides into two.

The Cell Cycle

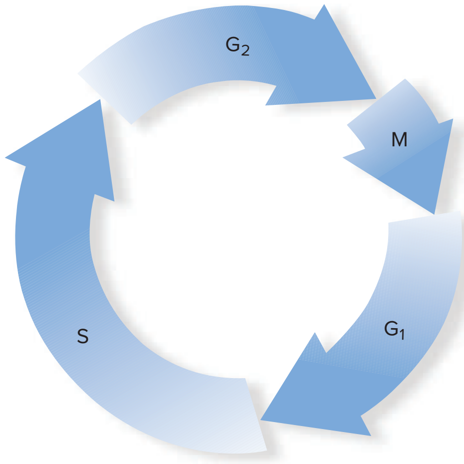
The life of an actively dividing cell can be described in terms of a cycle, which is the time from the beginning of one division to the beginning of the next (fig. 2.9). Most of the cycle is spent in the nondividing, or **interphase,** stage. This metabolically active stage consists of three phases: G_1, S, and G_2. The G_1 (first gap) phase is a period of intense biochemical activity; the cell is actively growing; enzymes and other proteins are rapidly synthesized; and organelles are increasing in size and number. The S, or synthesis, phase is crucial to cell division, for this is the time when DNA is duplicated; other chromosomal components such as proteins are also synthesized in this phase. After the S phase, the cell enters the G_2, or second gap, phase, during which protein synthesis increases and the final preparations for cell division take place. The G_2 phase ends as the cell begins division. Regulatory proteins, called **kinases** and **cyclins,** signal when a cell is to begin a phase of the cell cycle (**G_1**, **S**, **G_2** or mitosis). Cyclins are proteins whose concentrations fluctuate during the cell cycle. **Cyclin–dependent kinases (CdK)** are enzymes activated when attached to a particular cyclin to initiate a specific stage in the cell cycle. Conversely if the kinase is dissociated from the cyclin, the stage is arrested.

During cell division, two exact copies of the nucleus result from a process known as **mitosis. Cytokinesis,** the division of the cytoplasm, usually occurs during the later stages of mitosis.

Chromatin, consisting of DNA and protein, is prominent in the nucleus of a nondividing, or interphase, cell. Although the chromatin appears granular when viewed through a microscope, it is actually somewhat threadlike (fig. 2.10). The chromatin has already been duplicated during the S phase prior to mitosis. The events of mitosis are described as four intergrading stages: **prophase, metaphase, anaphase,** and **telophase** (fig. 2.10).

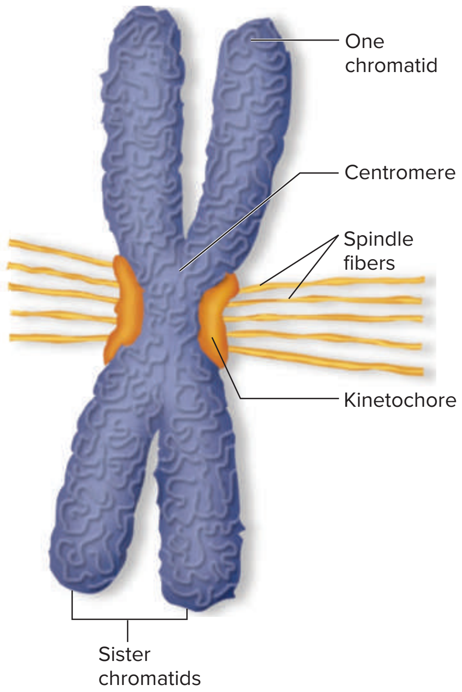
Prophase

During prophase, the appearance of the nucleus changes dramatically. The chromatin begins to condense and thicken,



	Phase	Main Events	*Vicia faba* (hr)
Interphase	G_1	Cells are metabolically active; organelles begin to increase in number	4
	S	Replication of DNA	7.5
	G_2	Synthesis of proteins Final preparations for cell division	4.9
	M	Mitosis	2.0
		Total	19.3

(a)



(b)

Figure 2.9 (a) The cell cycle consists of four stages (G_1, S, G_2, and M [mitosis]). The events that occur in each stage and the length of each stage, using the broad bean (*Vicia faba*) as an example, are depicted. (b) A duplicated chromosome consists of two sister chromatids held together at the centromere.

coiling up into bodies referred to as chromosomes. Each **chromosome** is double, composed of two identical **chromatids**, which represent the condensed duplicated strands of chromatin. The chromatids are joined at a constriction known as the **centromere** (fig. 2.9). By the end of prophase, the chromosomes are fully formed. Also during prophase, the nuclear membrane and the nucleoli disperse into the cytoplasm and are no longer visible. This leaves the chromosomes free in the cytoplasm.

Telomeres are repeated sequences of DNA that are found at the ends of chromosomes. Telomeres work like caps at the end of shoelaces, protecting the chromosomes from being shortened or otherwise damaged during cell divisions. Shortening of the telomeres happens each time cells divide and, consequently, the genetic content becomes more susceptible to damage. In 2009, three scientists from the United States (Elizabeth Blackburn, Jack Szostak, and Carol Greider) who worked on identifying and elucidating the role of telomeres received the Nobel Prize in Physiology or Medicine.

Factors in the environment can be either protective or destructive of telomere length. One study compared the length of telomeres between women who took multiple vitamin supplements and those who did not. Women who took multivitamins had telomeres that were an average of 5% longer, with approximately an extra 273 DNA base pairs. Women who had been taking multivitamin supplements for 5 years or more had telomeres that were 8% longer. The women who did not take multivitamins had telomeres that appeared to be about 10 years older because telomeres shorten by approximately 28 base pairs each year as a person ages. Not all supplements are equal in protecting telomeres. Taking an iron supplement alone results in telomeres that are an average of 9% shorter. Iron is associated with oxidation reactions in the cell, which are known to be linked to cell stress and damage. On the other hand, supplements rich in the antioxidant vitamins (C, D, and E) result in even longer telomeres.

Metaphase

The chromosomes arrange themselves across the center of the cell during metaphase, the second stage of mitosis. The **spindle,** which begins forming in prophase, is evident during this stage. Spindle fibers, composed of microtubules, stretch from each end, or pole, of the cell to the **kinetochore** of each chromatid. Kinetochores are formed during late prophase; they are specialized regions on the centromere that attach each chromatid to the spindle. Other spindle fibers stretch from each pole to the equator (fig. 2.10).

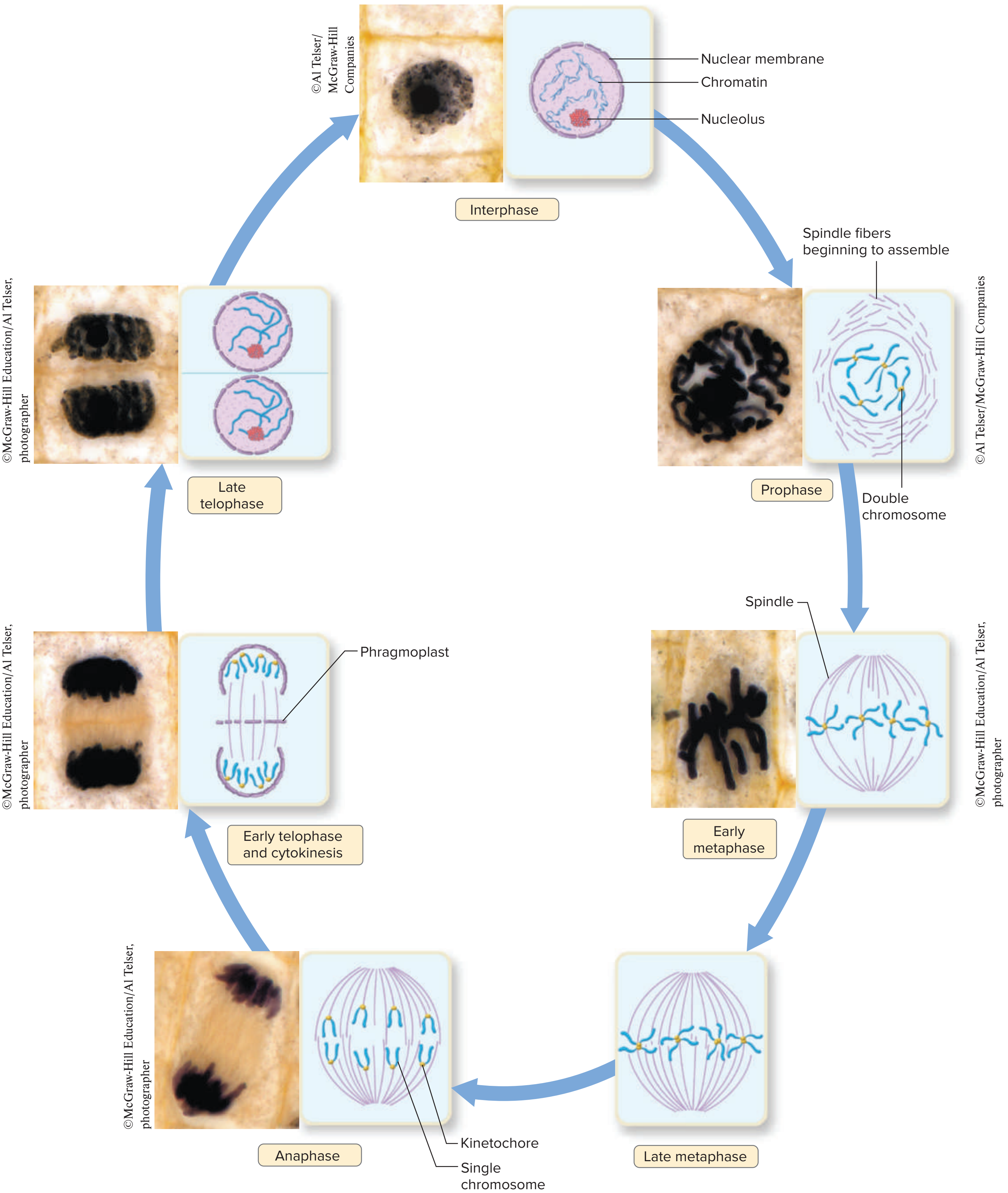


Figure 2.10 Mitosis in a plant cell.

Anaphase

In anaphase, chromatids of each chromosome separate, pulled by the spindle fibers to opposite ends of the cell. This step effectively divides the genetic material into two identical sets, each with the same number of single chromosomes. At the end of anaphase, the spindle is less apparent (fig. 2.10).

Telophase

During telophase, the chromatin appears again as the chromatids, at each end of the cell, begin to unwind and lengthen. At each pole, a nuclear membrane reappears around the chromatin. Now two distinct nuclei are evident. Within each nucleus, nucleoli become visible (fig. 2.10).

Cytokinesis

Cytokinesis, the division of the cytoplasm, separates the two identical daughter nuclei into two cells. Cytokinesis begins during the latter part of anaphase and is completed by the end of telophase. The **phragmoplast,** which consists of vesicles, microtubules, and portions of ER, accumulates across the center of the dividing cell. These coalesce to form the **cell plate,** which becomes the cell wall separating the newly formed daughter cells (fig. 2.10).

The production of new cells through cell division enables plants to grow, repair wounds, and regenerate lost cells. Cell division can even lead to the production of new, genetically identical individuals, or **clones**. This type of reproduction is known as asexual, or vegetative. When you make a leaf cutting of an African violet and a whole new plant develops from the cutting, you are facilitating asexual reproduction and seeing the results of cell division on a large scale. Many of our crops are actually propagated through asexual methods that will be discussed in detail in future chapters. Also, in Chapter 5, you will learn of another type of cell division called meiosis, which is involved in sexual reproduction.

Thinking Critically

Cloning based on cell division has become a major issue for discussion since researchers have cloned sheep, cattle, pigs, goats, cats, dogs, horses, primates, and other animals.

Is there a biological difference between cloning plants and cloning animals? an ethical difference?

CHAPTER SUMMARY

1. All life on Earth, including plant life, has a cellular organization. The plant cell shares many characteristics with other eukaryotic cells. The plant protoplast includes the cytoplasm with the embedded organelles and nucleus. Within the nucleus is DNA, the genetic blueprint of all cells.
2. The plasma membrane, composed of phospholipids and proteins according to the fluid mosaic model, regulates the passage of materials into and out of the cell. Numerous mitochondria can be found within the cytoplasm; they are the sites of cellular respiration. The endoplasmic reticulum, Golgi apparatus, and microbodies make up an internal membrane system that functions in the synthesizing, packaging, and transporting of materials.
3. Some features of a plant cell are unique. The primary cell wall containing cellulose surrounds a plant protoplast, providing protection and support. In certain specialized plant cells, a secondary cell wall, impregnated with the toughening agent lignin, imparts extra strength. Chloroplasts are the site for photosynthesis; they are one of several types of plastids. Other plastids are the food-storing leucoplasts and the pigment-containing chromoplasts. Tannosomes store tannins responsible for the dark brown color and tartness of many plant products. A large central vacuole may take up approximately 90% of the mature plant cell and act as a storage site for many substances.
4. The life of a cell can be described in terms of a cycle. Most cells spend the majority of the time in interphase, a nondividing stage. But at certain times in its life a cell may undergo division whereby one cell divides into two. Mitosis is the duplication of the nucleus into two exact copies. There are four intergrading stages in mitosis: prophase, metaphase, anaphase, and telophase. The division process is complete when, in the process of cytokinesis, the cytoplasm is split and two identical daughter cells are formed.

REVIEW QUESTIONS

1. What is the significance of the Cell Theory to biology?
2. List the parts of a plant cell, and for each part describe its structure and function.
3. Describe the events occurring during the G_1, S, and G_2 stages of interphase.
4. Describe the stages of mitosis.
5. Describe the similarities and differences between chloroplasts and mitochondria.
6. Differentiate between osmosis and diffusion.
7. Cancer cells are abnormal cells undergoing repeated cell divisions. Vincristine is a drug obtained from the Madagascar periwinkle that has been highly effective in treating certain cancers. Vincristine disrupts microtubules, preventing spindle formation. Explain the success of vincristine on the cellular level.
8. Plant cells are compartmentalized into organelles, each with a specialized function. Which organelles would be abundant in the following: leaf cells of a spinach plant, cells of a potato tuber, yellow petals of a tulip?

CHAPTER

3

The Plant Body

©Karen McMahon

The cytoskeleton of a leaf reveals the extensive network of the xylem vascular tissue supplying water and minerals to plant cells.

KEY CONCEPTS

1. Tissues are groups of cells that perform a common function and have a common origin and structure.
2. Flowering plants are made up of three basic tissue types: dermal, ground, and vascular.
3. These tissues make up the vegetative organs of higher plants: roots, stems, and leaves.

CHAPTER OUTLINE

The earliest life forms were unicellular, and that single cell was capable of carrying out all the necessary functions of life. When multicellular organisms evolved, certain cells became specialized in structure and function, leading to a division of labor. Groups of specialized cells performing specific functions are usually referred to as **tissues**. In flowering plants, various tissues compose the familiar organs: roots, stems, and leaves.

PLANT TISSUES

Meristems

All flowering plants are multicellular, with the cells all originating from regions of active cell division. These regions are known as **meristems** (fig. 3.1). Plant growth is localized in meristems. The cells originating from meristems give rise to the various tissue types that make up a plant, such as the cells of the epidermis that form the protective layer in a plant. The three basic tissue types in higher plants are **dermal, ground,** and **vascular** (fig. 3.2).

Apical meristems are located at the tips of all roots and stems and contribute to the increase in length of the plant. Tissues that develop from these apical meristems are part of the **primary growth** of the plant and give rise to the leaves and nonwoody stems and roots. Some plants have additional meristematic tissues that contribute to increases in diameter. These are the **vascular cambium** and **cork cambium**. Tissues developing from them are considered part of the plant's **secondary growth** (fig. 3.2).

Dermal Tissue

Dermal tissues are the outermost layers in a plant. In young plants and nonwoody plant parts, the outermost surface is the **epidermis** (fig. 3.3a). It is usually a single layer of flattened cells. Epidermal cells in leaves and stems secrete **cutin,** a waxlike

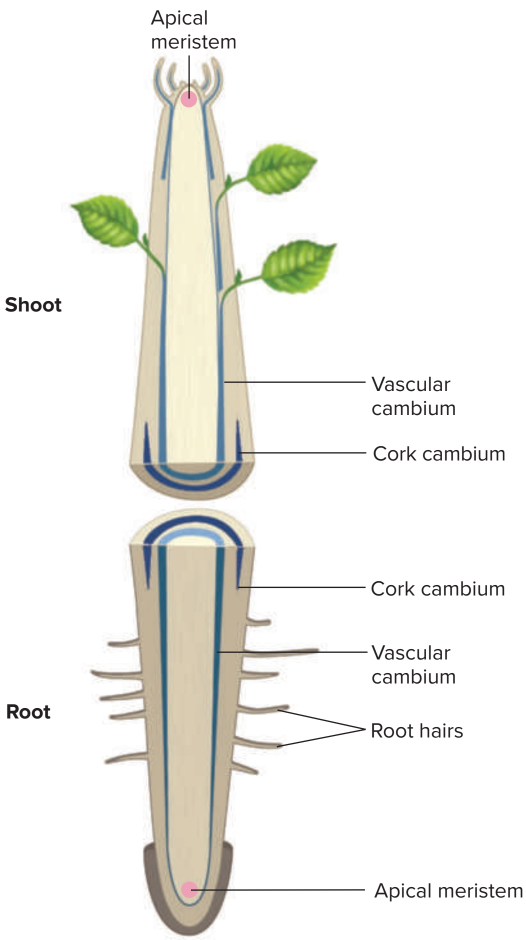
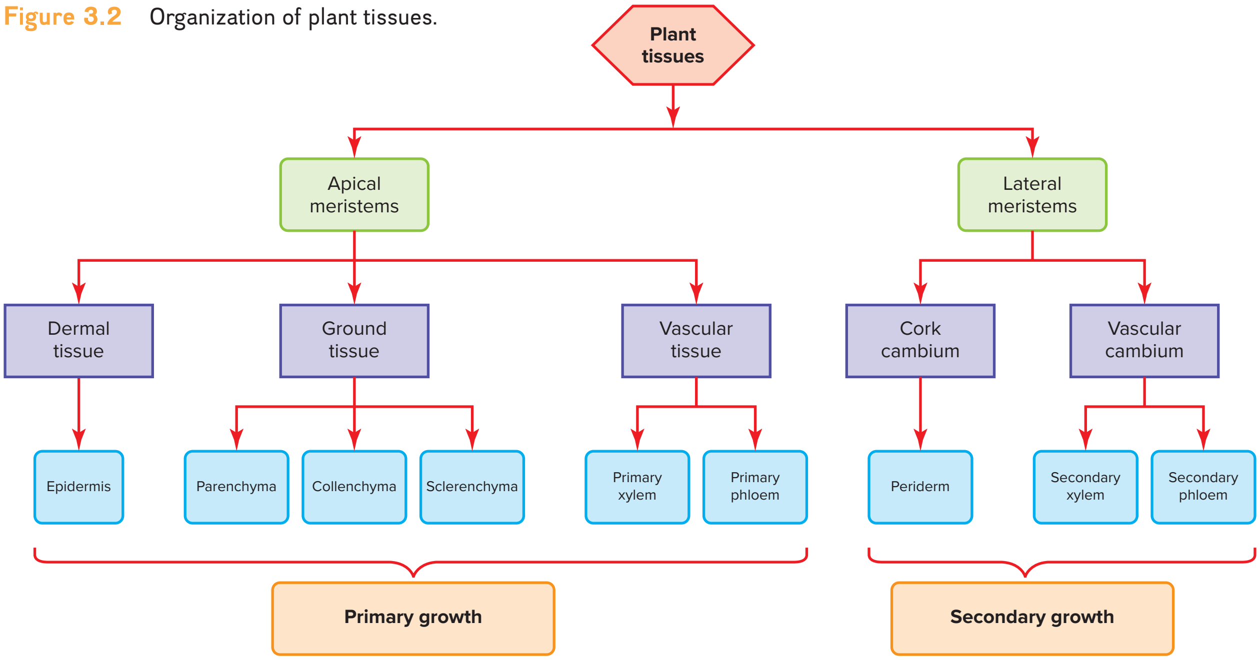


Figure 3.1 Plant meristematic tissues in a diagram of a shoot tip and root tip. Apical meristems contribute to increases in the length of the plant, or primary growth. Vascular cambium and cork cambium are present in plants that have secondary growth, an increase in the girth of the plant body.

Figure 3.2 Organization of plant tissues.



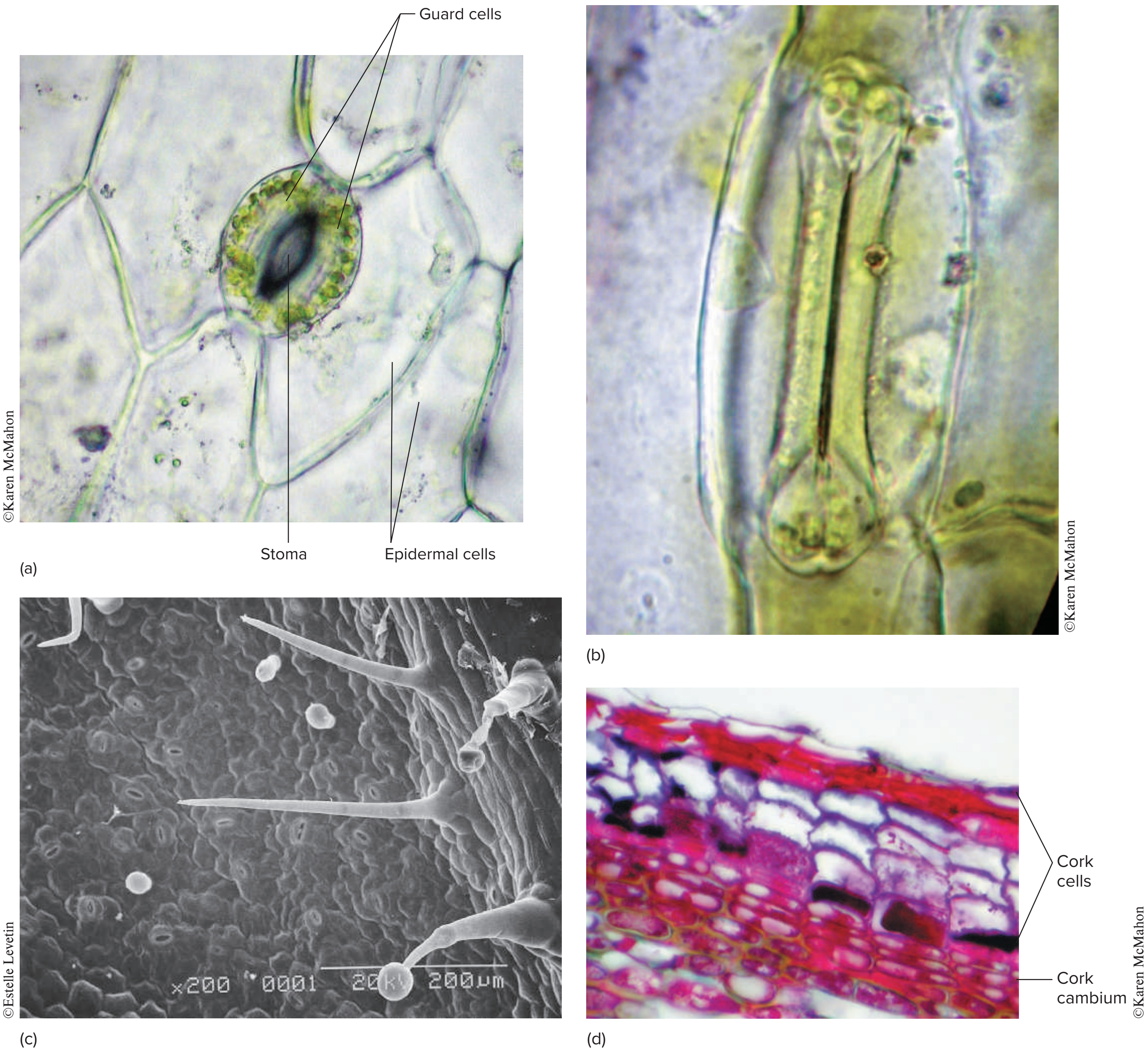


Figure 3.3 Dermal tissues. (a) Leaf epidermis contains stomata for gas exchange. (b) Dumbbell-shaped guard cells with subsidiary cells in a grass leaf. (c) Trichomes. (d) Periderm is a complex tissue consisting of a thick outer layer of cork cells that arise from the cork cambium.

substance that makes up the **cuticle** on the external surface. The cuticle prevents evaporative water loss from the plant by acting as a waterproof barrier. In many leaves, the cuticle is so thick that the leaf has a shiny surface; this is especially true in succulents, such as the jade plant, and tropical plants, such as philodendron.

In some plants, **trichomes** (hairs) may be present on the epidermis (fig. 3.3c). Although usually microscopic, they may be abundant enough to give a fuzzy appearance and texture to leaves or stems. Trichomes may also be glandular, often imparting an aroma when they are brushed, as you can experience by rubbing a geranium or tomato leaf.

Scattered through the leaf epidermis are pores known as **stomata** (sing., **stoma**). Gases, such as carbon dioxide, oxygen, and water vapor, are exchanged through these stomata. A pair of kidney bean shaped cells, **guard cells,** occur on each side of the pore and regulate the opening and closing of each stoma (fig. 3.3a). The guard cells are the only epidermal cells with chloroplasts. Stomata and guard cells can also be found in the epidermis of some stems.

Guard cells of grasses differ in that their shape resembles a pair of dumbbells. Additionally, grass guard cells are linked to two adjacent cells called **subsidiary cells** (fig 3.3b). Recently, research has shown that it is the flexibility of the subsidiary cells that enable guard cells in grasses to open the stomata wider to bring in more carbon dioxide for photosynthesis and to close down the stomata quickly when changing environmental conditions, such as the sudden onset of strong winds, accelerate water loss. As grass guard cells expand to open stomata, the subsidiary cells deflate providing room for the greater inflation of the guard cells and, consequently, the widening the stomata. The role of subsidiary cells in making grass stomata more responsive to environmental conditions may explain why grasses can be found in a variety of habitats and are one of the most widely distributed plant families.

In plant parts that become woody, the epidermis cracks and is replaced by a new surface layer, the **periderm,** which is continuously produced by the cork cambium as the tree increases in girth. The periderm, which consists of cork cells, the cork cambium, and sometimes other cells, makes up the outer bark seen on mature trees (fig. 3.3d). In fact, the cork in wine bottles is the periderm from *Quercus suber,* the cork oak tree native to the western Mediterranean. Cork is principally made up of dead cells whose walls contain **suberin,** another waterproofing fatty substance. It prevents water loss and protects underlying tissues (see Chapter 18).

Ground Tissue

Ground tissues make up the bulk of nonwoody plant organs and perform a variety of functions. The three categories of ground tissue are **parenchyma, collenchyma,** and **sclerenchyma.** The most versatile of these is parenchyma. Although often described as a thin-walled, 14-sided polygon, parenchyma cells can be almost any shape or size. Usually parenchyma tissue is loosely arranged, with many intercellular spaces. Parenchyma cells are capable of performing many different functions (fig. 3.4a). They are the photosynthetic cells in leaves and green stems and the storage cells in all plant organs. The starch in potato tubers, the water in cactus stems, and the sugar in sugar beet roots are all stored in parenchyma cells.

Collenchyma cells are the primary support tissue in young plant organs. They can be found in stems, leaves, and petals. Collenchyma cells are elongated cells with unevenly thickened primary cell walls, often with the walls thickest at the corners (fig. 3.4b). They are found tightly packed together just below the epidermis. The tough strings in celery are actually strands of collenchyma cells.

Sclerenchyma tissue has two cell types: **fibers** and **sclereids.** Like collenchyma cells, the fibers are elongated cells that function in support. Unlike collenchyma, they are nonliving at maturity and have thickened secondary walls (fig. 3.4c). For centuries, people have used leaf and stem fibers from many plants in the making of cloth and rope (see Chapter 18). Sclereids have many shapes but are seldom elongate like fibers. The major function of these cells is to provide mechanical support and protection. The extremely thick secondary walls of sclereids account for the hardness in walnut shells and the grit of pear fruit.

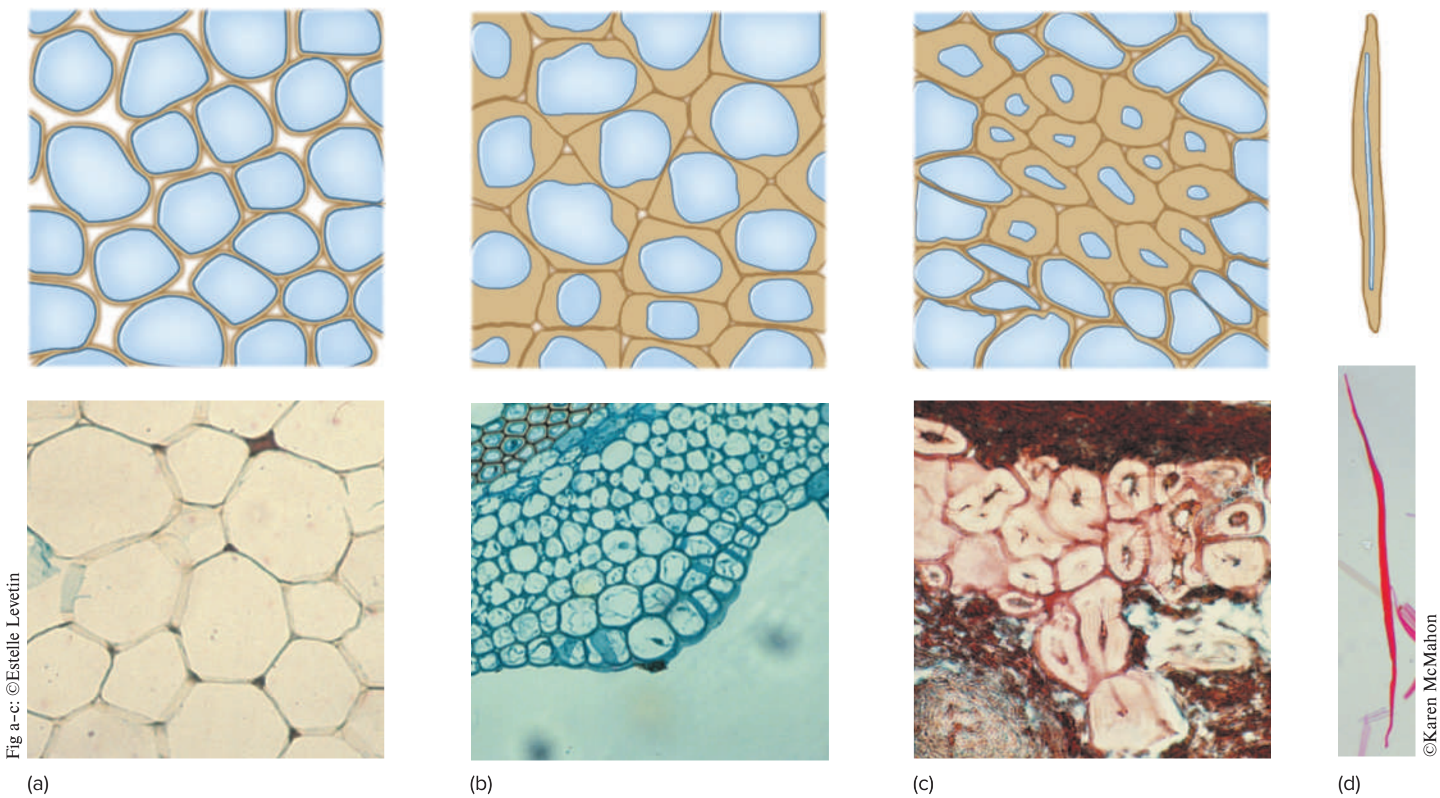


Figure 3.4 Ground tissues. (a) Parenchyma cells are the most abundant plant tissue type and have characteristically thin cell walls. (b) Collenchyma cells have primary cell walls that are thickest at the corners. (c) Sclerenchyma cells have very thick secondary cell walls and are nonliving. (d) Fiber is type of sclerenchyma cell that is elongated and narrow.

Vascular Tissue

Vascular tissues are the conducting tissues in plants. You can readily see the vascular tissues in a leaf; they are the **veins.** The vascular tissues form a continuum throughout the plant, allowing the unrestricted movement of materials. There are two types: **xylem,** which conducts water and minerals from the roots upward, and **phloem,** which transports organic materials synthesized by the plant. Both xylem and phloem are complex tissues composed of several cell types.

Tracheids and **vessel elements** are the water-conducting cells in the xylem. Both cell types have secondary walls, and at maturity these cells are dead and consist only of cell walls. Tracheids are long, thin cells with tapering ends and numerous pits in the walls; these cells also function in support. **Pits** are depressions in plant cell walls where the wall is thinner because the primary wall is not covered by secondary wall. Vessel elements are usually shorter and wider and often have horizontal end walls with large openings. Like the tracheids, the side walls have numerous pits. Vessel elements are attached end to end to form a long, pipelike **vessel** (fig. 3.5a).

Tracheids and vessel elements are found in angiosperms, but only tracheids occur in other plants with vascular tissue. Fibers are present in the xylem, where they provide

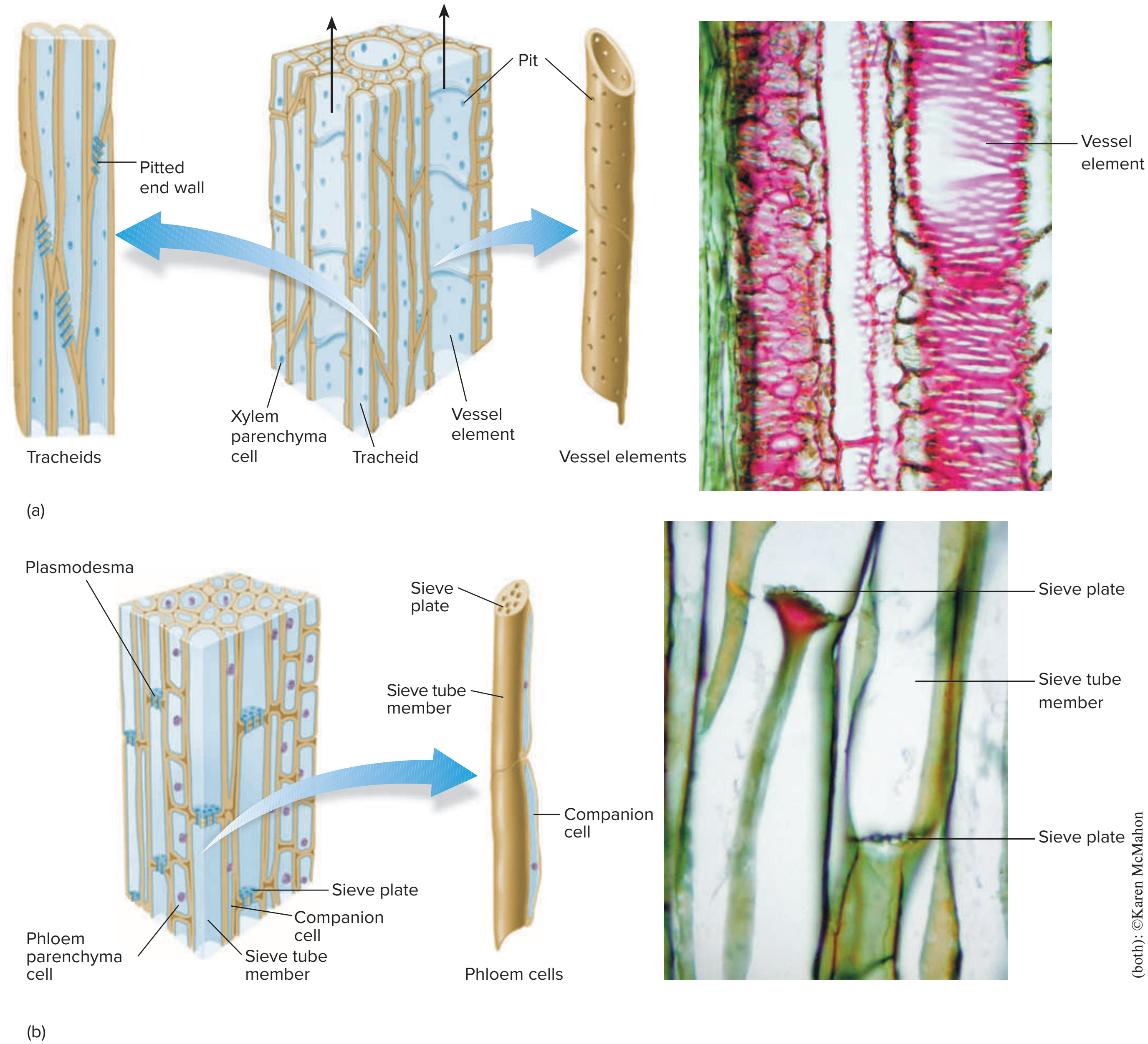


Figure 3.5 (a) Xylem. The conducting cells of xylem are tracheids and vessel elements. (b) Phloem. Sugars are loaded by companion cells into sieve tube members for transport.

additional support. Parenchyma cells, which also occur in the xylem, are the only living and metabolically active cells in this tissue.

Xylem can be either primary or secondary; primary xylem originates from the apical meristem, while secondary xylem comes from the vascular cambium. In trees, secondary xylem is very extensive; it is what we call **wood.**

The cells involved in the transport of organic materials in the phloem are the **sieve tube members.** Unlike the conducting cells in the xylem, the sieve tube members are living cells with only primary walls. But they are unusual living cells because the nucleus and some organelles degenerate as the sieve tube member matures. The end walls of these cells have several to many large pores and are called **sieve plates.** They allow plasmodesmata, cytoplasmic connections, to occur between adjacent sieve tube members and provide channels for conduction. The column of connected sieve tube members is referred to as a **sieve tube** (fig. 3.5b).

Adjoining each sieve tube member is a **companion cell,** which is physiologically and developmentally related to its sieve tube member. The smaller companion cell has a large nucleus that controls the adjacent sieve tube member through the numerous plasmodesmata that connect the two cells. The companion cells are involved in the loading and unloading of organic materials for transport. As in the xylem, both fibers and parenchyma cells are found in the phloem. Both primary and secondary phloem occur; again, the primary phloem is produced by the apical meristem and the secondary by the vascular cambium. Table 3.1 is a summary of these plant tissues.

Table 3.1
Plant Tissues

Tissue Type	Cell Types	Function
Dermal		
Epidermis	Epidermal cells	Protection
Periderm	Cork cells	Protection
Ground		
Parenchyma	Parenchyma cells	Storage, photosynthesis
Collenchyma	Collenchyma cells	Support
Sclerenchyma	Sclereids, fibers	Support, protection
Vascular		
Xylem	Tracheids, vessel elements, fibers, parenchyma	Water conduction, support
Phloem	Sieve tube members, companion cells, fibers, parenchyma	Food transport

Thinking Critically

Xylem and phloem are the vascular, or conducting, tissues in plants. Xylem conducts water and dissolved minerals, while phloem conducts organic materials.

How do the conducting cells of xylem (vessel elements and tracheids) differ from the sieve tube members and companion cells in phloem?

PLANT ORGANS

The principal vegetative organs of flowering plants are stems, roots, and leaves. Roots anchor the plant and absorb water and nutrients from the soil; stems support the plant and transport both water and organic materials; and leaves are the main photosynthetic structures.

Stems

Recall that angiosperms are divided into two classes of plants, the dicots and the monocots. Although the major differences between these classes are in the flower and seed, anatomical differences can also be seen in stems, roots, and leaves.

A monocot stem is best exemplified by examining a cross section of a corn stem. The outermost tissue is a single layer of epidermis. Beneath the epidermis are two to three layers of sclerenchyma for support. **Vascular bundles** are scattered throughout the stem. These vascular bundles are composed of both xylem and phloem and are usually surrounded by a **bundle sheath** of fibers. Parenchyma fills in the rest of the stem (figs. 3.6a and b).

Dicot stems can be either **herbaceous** (nonwoody) or **woody.** In herbaceous dicots, the vascular tissue occurs as a ring of separate vascular bundles. Again, each vascular bundle contains both xylem and phloem, with the xylem toward the center of the stem and the phloem toward the outside. This ring of vascular bundles surrounds the **pith,** a central area of ground tissue composed of parenchyma cells. On the other side of the ring of vascular bundles, toward the outside of the stem, is the **cortex,** another region of ground tissue. Although the cortex consists mainly of parenchyma cells, fibers often occur in this region. Between the vascular bundles, the ground tissue of the pith and cortex is continuous. The outermost layer of the stem is the epidermis. In some plants, support tissue, either sclerenchyma or collenchyma, can be found beneath the epidermis (figs. 3.6c and d).

In woody dicots, the vascular tissue, especially the xylem, is much more extensive and makes up the bulk of the stem. As it does in the herbaceous dicots, the pith occupies the center of the stem. Surrounding the pith are rings of secondary xylem. Each ring represents the xylem formed by the vascular cambium during one growing season and is called an

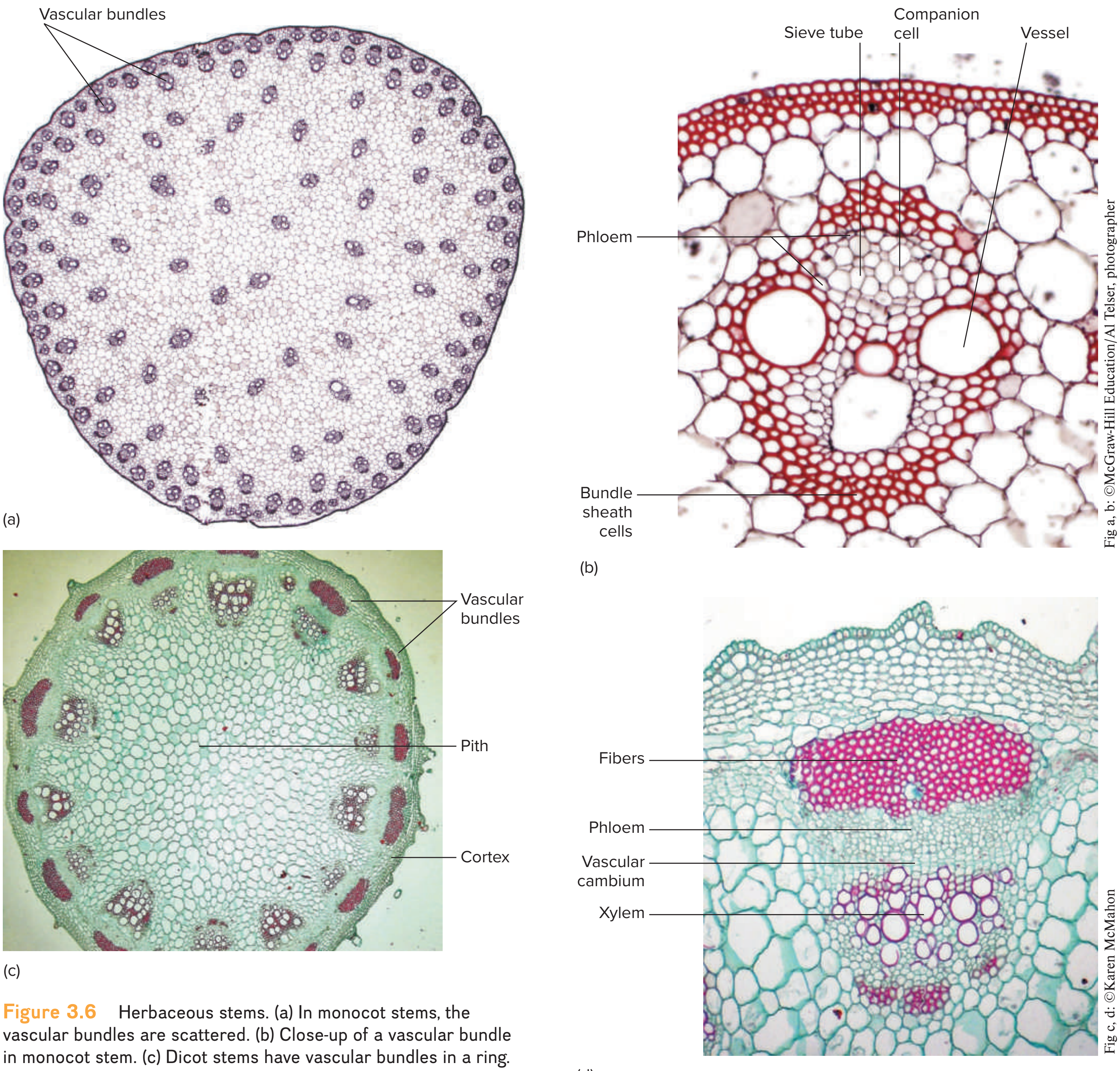


Figure 3.6 Herbaceous stems. (a) In monocot stems, the vascular bundles are scattered. (b) Close-up of a vascular bundle in monocot stem. (c) Dicot stems have vascular bundles in a ring. (d) Close-up of vascular bundles in a dicot stem.

annual ring. The rings, which are easily visible to the naked eye, are due to the different sizes of cells formed through the growing season. Wood produced in the spring, when water is more abundant, is called **springwood** or **early wood** and consists of cells noticeably larger than those found in **summerwood,** or **late wood** produced during the late summer. The portion of each ring with springwood appears lighter than the area with the smaller, densely packed cells of summerwood. Since each ring typically represents one growing season, in temperate regions the age of the tree can be determined by counting the annual rings (fig. 3.7 and see A Closer Look 3.1: Studying Ancient Tree Rings).

Surrounding the outermost ring of xylem is the vascular cambium, the meristematic tissue that produces both secondary xylem toward the inside and secondary phloem toward the outside. The amount of secondary phloem produced each year is very small when compared with the xylem. No annual rings are evident in the phloem, although bands of fibers occur in some plants (fig. 3.7).

Vascular rays, resembling spokes of a wheel, are seen crossing both xylem and phloem. Composed of parenchyma cells, these rays are involved in radial transport of materials.

A small band of cortex can be found outside the phloem. In older trees, however, the cortex is completely replaced by

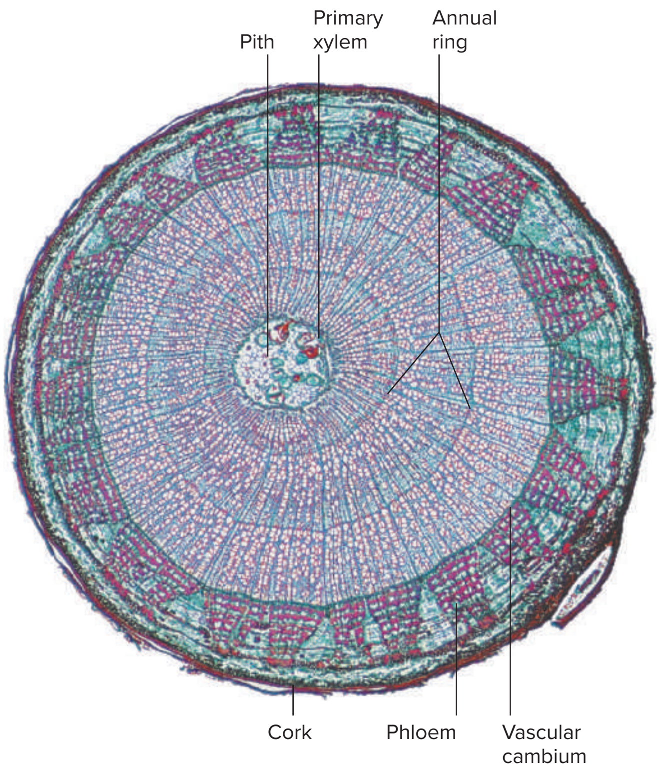


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Figure 3.7 Anatomy of a woody stem.

Figure 3.8 Root systems. (a) The fibrous root system of barley. (b) The taproot of a dandelion.

the periderm, or cork (fig. 3.7). In fact, even the older, outermost layers of phloem are replaced by the periderm. The thickness and texture of the periderm depend on the type of tree, and the periderm varies from thin and papery in cherry or paper birch to extremely thick in cork oak.

Roots

Two major types of root systems can be found in flowering plants: **taproots** and **fibrous roots.** Taproots have one large main root with small lateral, or branch, roots. Taproots can be enlarged for storage, as evident in carrots, turnips, and beets (see also A Closer Look 4.2: Sugar and Slavery). Fibrous roots are highly branched and lack a central main root, as in many grasses (fig. 3.8).

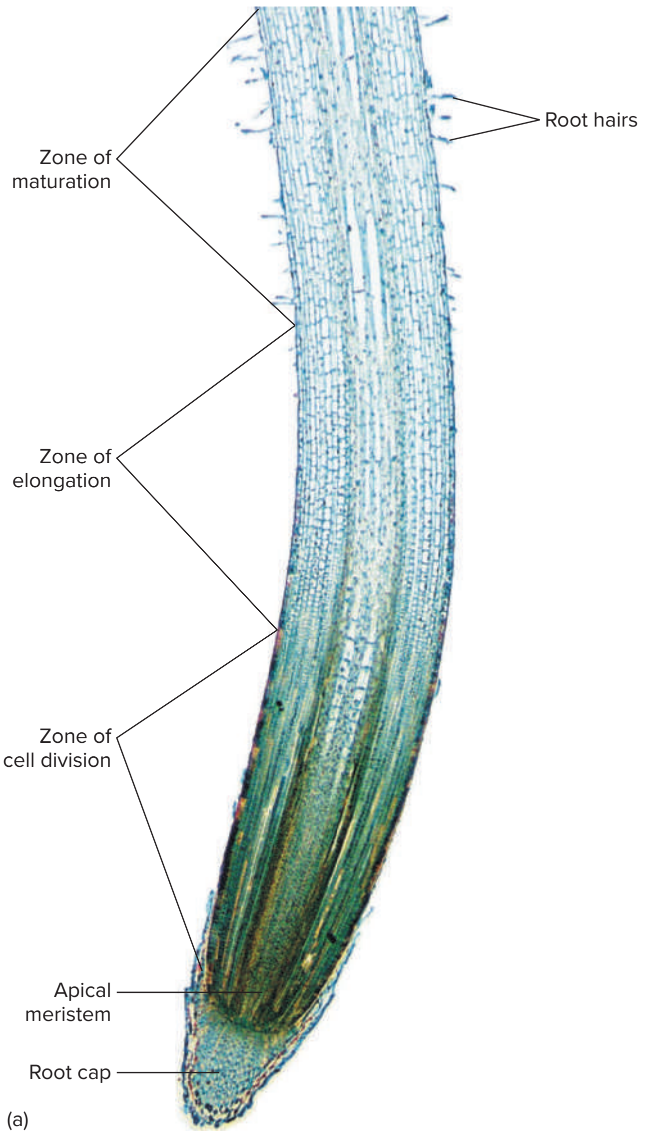
At the tips of all main roots or branch roots are thimble-shaped **root caps,** which protect the root meristems as the roots grow through the soil. The meristem **(zone of cell division)** accounts for primary growth in roots. Just behind the meristem the newly formed cells elongate **(zone of elongation)** considerably before they begin to differentiate into the various tissues that constitute the root (fig. 3.9a).

A cross section of a dicot root in the region where cells have differentiated **(zone of maturation)** is seen in Figure 3.9b. The vascular tissue is found in the center of the root, making up the **stele,** or **vascular cylinder.** In the very center of the stele is the xylem, usually in a star-shaped configuration. The number of arms of this star is variable, with bundles of phloem found between the arms of xylem. In monocot roots, a pith is present and is encircled by alternating bundles of xylem and phloem (fig. 3.10a). The outermost layer of cells in the stele is known as the **pericycle,** which is a meristematic layer that can give rise to branch roots (figs. 3.9 and 3.10).

Surrounding the stele is the cortex, composed of parenchyma cells, which are sites of storage. The innermost layer of the cortex (just outside the pericycle) is known as the **endodermis.** Endodermal cells are characterized by the presence of a **Casparian strip,** a waxy material ringing each endodermal cell. The faces of the cell wall next to the cortex and stele do not have a Casparian strip. Because of this strip, water and minerals must pass through the endodermal cells, not between them (see Chapter 4).

The cortex is usually quite large, making up the bulk of the root. The outermost layer of cells is the epidermis. Extensions of the epidermal cell are called **root hairs;** these greatly increase the surface area and are the sites of maximum water and mineral absorption.

Root structure can be further modified as a result of adaptations to the environment. Native to North America, the bald cypress tree (*Taxodium distichum*) is a conifer commonly found in freshwater swamps. Under these conditions, the tree produces aerial outgrowths, called cypress knees or **pneumatophores,** from its submerged root system. These conical roots project about the water surface and contain **aerenchyma** tissue (a type of parenchyma in which there are numerous intercellular spaces). Pneumatophores provide a passageway for oxygen to pass from the air to the submerged



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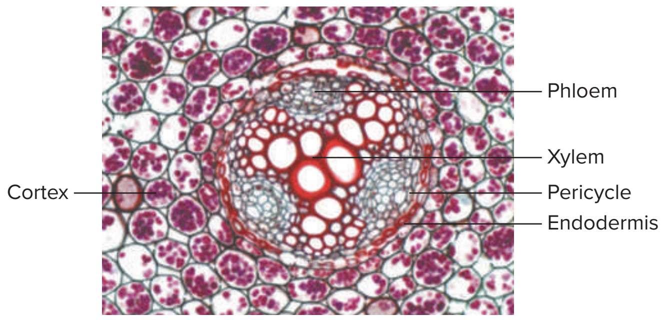

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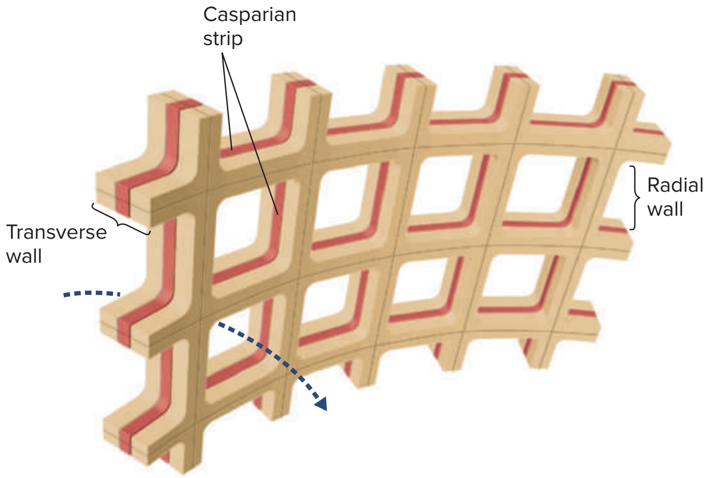
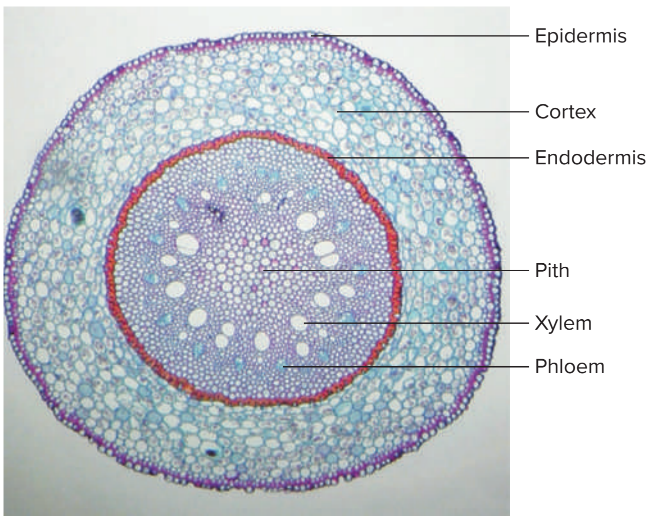
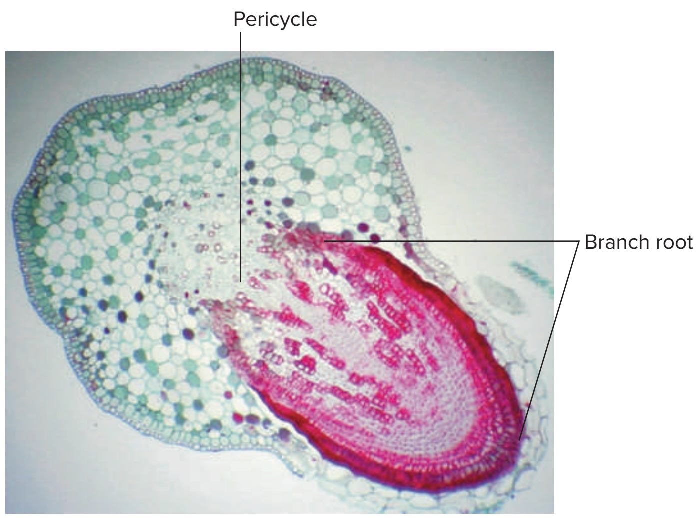


(c)

Figure 3.9 Root tip. (a) A root tip is divided into four zones. (b) The vascular cylinder, or stele, in a dicot root as seen in cross section typically shows the xylem in a star-shaped pattern. (c) The Casparian strip in the wall of the endodermis directs the passage of water and minerals into the xylem.



(a)



(b)

Figure 3.10 (a) The vascular cylinder of monocot roots typically contains a pith. (b) Branch roots originate from the pericycle.

A CLOSER LOOK 3.1

Studying Ancient Tree Rings

The study of tree rings is known as **dendrochronology** and is of value to fields as diverse as astronomy, ecology, and anthropology. The science began in the early twentieth century by Andrew Douglass in Arizona. Douglass, an astronomer, frequently visited logging camps to study the annual ring patterns on tree stumps. The size of a ring can indicate climatic conditions that existed when the ring was formed (box fig. 3.1). A very narrow ring may indicate a year of low rainfall or drought, while a wide ring may indicate abundant rainfall. Douglass wondered if the climatic changes brought about by the 11-year cycle of sunspots was evident in tree-ring patterns. Although Douglass did not find the answer to the sunspot question, he did see that tree-ring patterns from different areas throughout northern Arizona showed the same patterns of wide and narrow rings.

Douglass continued the study of tree rings for many years. By matching patterns from living trees, remains of fallen trees, and wood samples from Pueblo ruins, Douglass was able to date all the ancient pueblos throughout the Southwest. In 1937, Douglass founded the Laboratory of Tree Ring Research at the University of Arizona. Today, this laboratory is still a major world center for tree-ring study.

Conditions in Arizona are ideal for this type of study. Since rainfall is always limiting for tree growth, a small change in the weather has a great effect on the width of the tree ring. Also, the arid climate prevents the decay of dead trees and wooden artifacts. In fact, in the Southwest, scientists have been able to construct a chronology of tree rings going back approximately 9,000 years.

By contrast, in other areas of the United States and in Europe, tree-ring analysis is more difficult because more favorable growing conditions that are relatively consistent result in more uniform tree rings. Also, when trees die they decay in the moister environment.

Another aspect of tree-ring research is **dendroclimatology.** By studying the annual rings of very old trees, scientists have been able to reconstruct major climatic changes of the past. Tree-ring specialists are trying to determine if droughts occur in a cyclic pattern. Others are looking at the effects of pollution, pests, forest fires, volcanoes, and earthquakes on tree rings.

Recently, tree-ring data have provided insight into the high mortality of the first Jamestown colonists and the disappearance of the Lost Colony of Roanoke Island. Taking cores from 800-year-old bald cypress trees (*Taxodium distichum*) from Virginia, the Tree-Ring Laboratory at the University of Arkansas was able to reconstruct the precipitation and temperature patterns in the region from A.D. 1185 to 1984. They discovered that the last sighting of the settlers at Roanoke Island off the North Carolina coast in August 1587 coincided with the beginning of an extreme drought (1587–1589), the driest period in 800 years. Similarly, the Jamestown colonists had the misfortune to begin their settlement in April 1607 during the driest 7-year period (1606–1612) in over 770 years. These studies suggest that the disappearance of the Lost Colony at Roanoke Island and the 80% mortality of colonists during the establishment of Jamestown were in part due to the drought. Both colonies had planned to live off the land and barter for additional supplies from indigenous peoples. This strategy failed as the lack of rainfall caused crops and livestock to die, affecting the food supply not only of the colonists but also of the native peoples. The extreme

roots. Without pneumatophores, the bald cypress roots would not have the oxygen necessary for cellular respiration and would not survive under flood conditions.

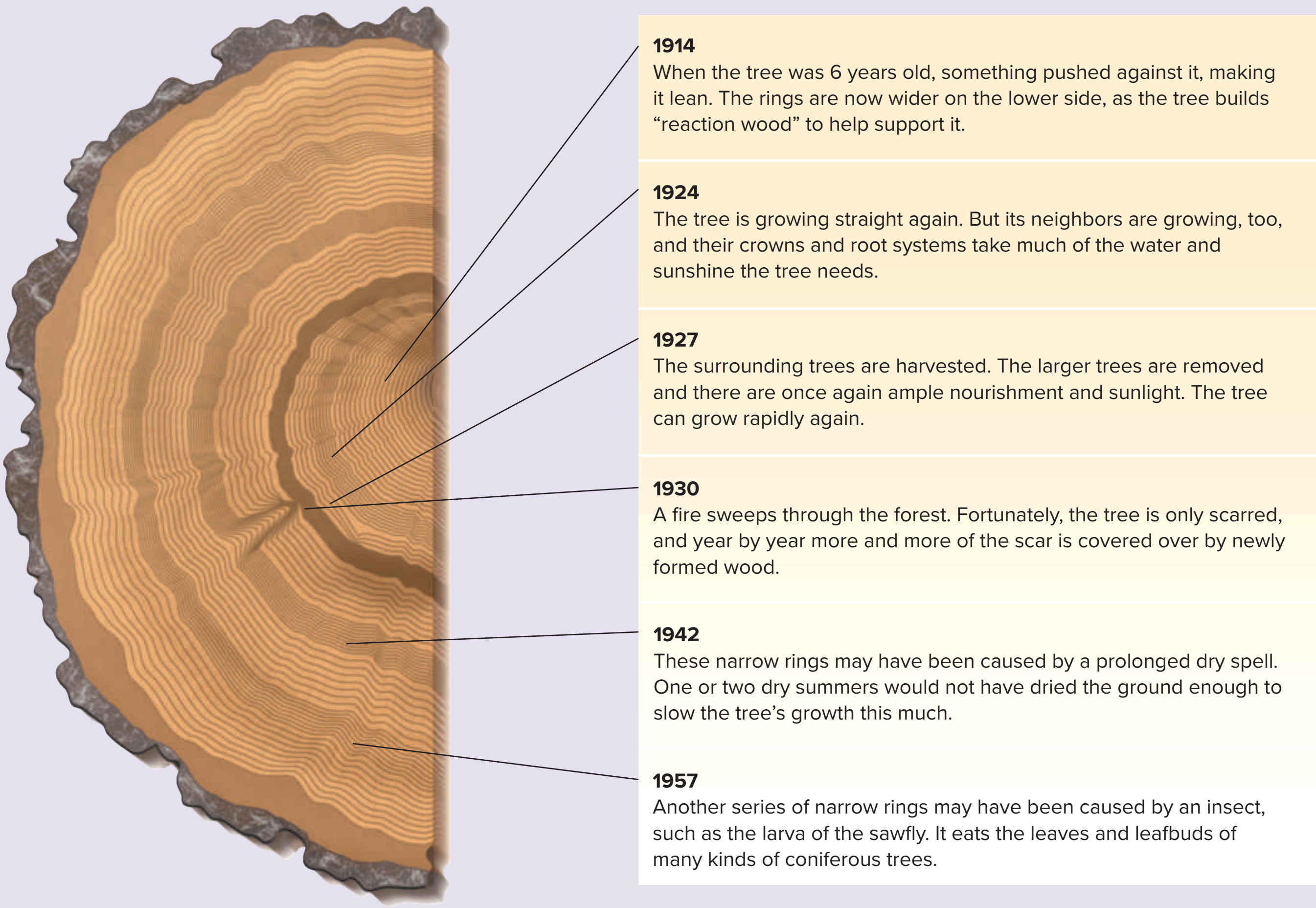
Many tropical rain forest orchids are **epiphytes,** plants that physically lodge on other plants. Tropical rain forest trees can be festooned with epiphytic orchids on their upper limbs in the full sunlight of the tree canopy. Epiphytic orchids have aerial roots, which are at first green and photosynthetic but later become covered with **velamen,** a white outgrowth of the epidermis, which waterproofs the aerial root against water loss. **Prop roots** sprout from the nodes of stems but then grow down into the soil. Prop roots provide aboveground support and belowground anchorage plus conduction of water and dissolved nutrients to the stem. Examples of plants with prop roots are corn (*Zea mays*) and the screw pine (*Pandanus* spp.).

Contractile roots can be found in the common dandelion (*Taraxacum officinale*) and other plants with short stems. Cells in the upper cortex of the root change shape, expanding in width but losing more than half their height. This shape change pulls the stem down, either keeping it at soil level or slightly below. Storage adaptations in roots are discussed in Chapter 14.

Plants that have woody stems have extensive secondary xylem and annual rings in roots as well as in stems. One major difference between a woody root and a woody stem is that the woody root has no pith.

Leaves

Leaves have often been called the photosynthetic factories of the plant, since photosynthesis is their major function. (Some plants have leaves that are modified for other functions, such as trapping insects. See A Closer Look 3.2: Plants That Trap Animals.) The flat, expanded **blade** of the leaf is ideally suited



Box Figure 3.1 The pattern of annual rings is correlated with events in the life of this tree.

Source: Adapted from St. Regis Paper Company, 1966.

climatic conditions of 1587–1589 and of 1606–1612, determined by the deciphering of tree-ring data, can explain the fate of the early colonists in Roanoke and Jamestown.

Overall, we know that trees are living histories. Contained within the tissues of the tree is the history of the environment for the year in which a ring was formed.

for the photosynthetic process. The **petiole,** or leaf stalk, connects the leaf blade to the stem and transports materials to and from the blade. Some leaves have no petiole; in those cases, the blade is attached directly to the stem. Small, paired appendages called **stipules** may be present at the base of the leaf (fig. 3.11a). Stipules are varied in form: in some plants, they are leaflike; in others, they are thornlike.

The place where the petiole is attached to the stem is called the **node.** The areas of the stem between adjacent nodes are **internodes.** There are three patterns of leaf arrangement on stems. If only one leaf is present at a node, the arrangement is known as **alternate.** If two leaves occur at a node, the arrangement is **opposite;** with three or more, the arrangement is **whorled** (fig. 3.11b).

There is a great variety of leaf forms and shapes, ranging from small, **simple leaves,** as in elm, whose blade is undivided, to large, **compound leaves,** as in pecan and buckeye, whose blades are divided into **leaflets.** When the leaflets occur in a featherlike pattern, it is called **pinnately compound,** whereas it is called **palmately compound** when the leaflets have a common attachment. It may be difficult to determine whether you are looking at a leaf or a leaflet. One reliable indicator is the position of the **axillary bud.** The upper angle that forms between the top surface of a leaf and the stem is called the **axil,** and it is here that a **bud** (embryonic shoot) is located. Axillary buds are found only at the base of leaves (fig. 3.11a), so if you see an axillary bud you are looking at a leaf. Figure 3.11a illustrates the varieties of simple and compound leaves.

The vascular tissues of leaves make up the venation patterns usually visible to the naked eye. Monocot leaves usually have **parallel venation** because the vascular bundles are arranged in parallel lines running the length of the blade. In contrast, dicots have **net,** or **reticulate, venation**, in which the vascular tissue is highly branched, forming a network