ESAU'S PLANT ANATOMY

Meristems, Cells, and Tissues of the Plant Body: Their Structure, Function, and Development

Third Edition

RAY F. EVERT
Katherine Esau Professor of Botany and Plant Pathology, Emeritus
University of Wisconsin, Madison

With the assistance of
Susan E. Eichhorn
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WILEY-INTERSCIENCE
A John Wiley & Sons, Inc., Publication

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Dedicated to the late Katherine Esau, mentor and close friend

"In recognition of her distinguished service to the American community of plant biologists, and for the excellence of her pioneering research, both basic and applied, on plant structure and development, which has spanned more than six decades; for her superlative performance as an educator, in the classroom and through her books; for the encouragement and inspiration she has given a legion of young, aspiring plant biologists; for providing a special role model for women in science."

Citation, National Medal of Science, 1989

Katherine Esau

Contents

Preface

It has been over 40 years since the second edition of Esau's *Plant Anatomy* was completed. The enormous expansion of biological knowledge that has taken place during this period is unprecedented. In 1965, electron microscopy was just beginning to have an impact on plant research at the cellular level. Since then, new approaches and techniques, particularly those used in molecular-genetic research, have resulted in emphasis and direction toward the molecular realm of life. Old concepts and principles are being challenged at virtually every level, often, however, without a clear understanding of the bases upon which those concepts and principles were established.

A biologist, regardless of his or her line of specialization, cannot afford to lose sight of the whole organism, if his or her goal is an understanding of the organic world. Knowledge of the grosser aspects of structure is basic for effective research and teaching at every level of specialization. The ever-increasing trend toward a reduction of emphasis on factual information in contemporary teaching and the apparent diminution of plant anatomy and plant morphology courses at many colleges and universities make a readily accessible source of basic information on plant structure more important than ever. One consequence of these phenomena is a less precise use of terminology and an inappropriate adoption of animal terms for plant structures.

Research in plant structure has benefited greatly from the new approaches and techniques now available. Many plant anatomists are participating effectively in the interdisciplinary search for integrated concepts of growth and morphology. At the same time comparative plant anatomists continue to create new concepts on the relationships and evolution of plants and plant tissues with the aid of molecular data and cladistic analyses. The integration of ecological and systematic plant anatomy—ecophyletic anatomy—is bringing about a clearer understanding of the driving forces behind evolutionary diversifications of wood and of leaf attributes.

A thorough knowledge of the structure and development of cells and tissues is essential for a realistic interpretation of plant function, whether the function concerned is photosynthesis, the movement of water, the transport of food, or the absorption of water and minerals by roots. A full understanding of the effects of pathogenetic organisms on the plant body can only be achieved if one knows the normal structure of the plant concerned. Such horticultural practices as grafting, pruning, vegetative propagation, and the associated phenomena of callus formation, wound healing, regeneration, and development of adventitious roots and buds are more meaningful if the structural features underlying these phenomena are properly understood.

A common belief among students and many researchers alike is that we know virtually all there is to know about the anatomy of plants. Nothing could be further from the truth. Although the study of plant anatomy dates back to the last part of the 1600s, most of our knowledge of plant structure is based on temperate, often agronomic, plants. The structural features of plants growing in subtropical and tropical environments are frequently characterized as exceptions or anomalies rather than as adaptations to different environments. With the great diversity of plant species in the tropics, there is a wealth of information to be discovered on the structure and development of such plants. In addition, as noted by Dr. Esau in the preface of the first edition of *Anatomy of Seed Plants* (John Wiley & Sons, 1960) " . . . plant anatomy is interesting for its own sake. It is a gratifying experience to follow the ontogenetic and evolutionary development of structural features and gain the realization of the high degree of complexity and the remarkable orderliness in the organization of the plant."

A major goal of this book is to provide a firm foundation in the meristems, cells, and tissues of the plant body, while at the same time nothing some of the many advances being made in our understanding of their function and development through molecular research. For example, in the chapter on apical meristems, which have been the object of considerable molecular-genetic research, a historical review of the concept of apical organization is presented to provide the reader with an understanding of how that concept has evolved with the availability of more sophisticated methodology. Throughout the book, greater emphasis is made on structure-function relationships than in the previous two editions. As in the previous editions, angiosperms are emphasized, but some features of the vegetative parts of gymnosperms and seedless vascular plants are also considered.

These are exciting times for plant biologists. This is reflected, in part, in the enormity of literature output. The references cited in this book represent but a fraction of the total number of articles read in preparation of the third edition. This is particularly true of the molecular-genetic literature, which is cited most selectively. It was important not to lose focus on the anatomy. A great many of the references cited in the second edition were read anew, in part to insure continuity between the second and third editions. A large number of selected references are listed to support descriptions and interpretations and to direct the interested person toward wider reading. Undoubtedly, some pertinent papers were inadvertently overlooked. A number of review articles, books, and chapters in books with helpful reference lists are included. Additional pertinent references are listed in the addendum.

This book has been planned primarily for advanced students in various branches of plant science, for researchers (from molecular to whole plant), and for teachers of plant anatomy. At the same time, an effort has been made to attract the less-advanced student by presenting the subject in an inviting style, with numerous illustrations, and by explaining and analyzing terms and concepts as they appear in the text. It is my hope that this book will enlighten many and inspire numerous others to study plant structure and development.

R. F. E.
Madison, *Wisconsin*
July, *2006*

Acknowledgments

Illustrations form an important part of a book in plant anatomy. I am indebted to various persons who kindly provided illustrations of one kind or another for inclusion in the book and to others, along with publishers and scientific journals, for permission to reproduce in one form or another their published illustrations. Illustrations whose source(s) are not indicated in the figure captions are original. Numerous figures are from research articles by me or coauthored with colleagues, including my students. A great many of the illustrations are the superb work—line art and micrographs—of Dr. Esau. Some figures are expertly rendered electronic illustrations by Kandis Elliot.

Sincere thanks are extended to Laura Evert and Mary Evert for their able assistance with the process of obtaining permissions.

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CHAPTER ONE

Structure and Development of the Plant Body—An Overview

The complex multicellular body of a vascular plant is a result of evolutionary specialization of long duration—specialization that followed the transition of multicellular organisms from an aquatic habitat to a terrestrial one (Niklas, 1997). The requirements of the new and harsher environments led to the establishment of morphological and physiological differences among the parts of the plant body so that they became more or less strongly specialized with reference to certain functions. The recognition of these specializations by botanists became embodied in the concept of **plant organs** (Troll, 1937; Arber, 1950). At first, botanists visualized the existence of many organs, but later as the interrelationships among the plant parts came to be better understood, the number of vegetative organs was reduced to three: **stem**, **leaf**, and **root** (Eames, 1936). In this scheme, stem and leaf are commonly treated together as a morphological and functional unit, the **shoot**.

Researchers in evolution postulate that the organization of the oldest vascular plants was extremely simple, perhaps resembling that of the leafless and rootless Devonian plant *Rhynia* (Gifford and Foster, 1989; Kenrick and Crane, 1997). If the seed plants have evolved from rhyniaceous types of plants, which consisted of dichotomously branched axes without appendages, the leaf, the stem, and the root would be closely interrelated through phylogenetic origin (Stewart and Rothwell, 1993; Taylor and Taylor, 1993; Raven, J. A. and Edwards, 2001). The common origin of these three organs is even more obvious in their ontogeny (development of an individual entity), for they are initiated together in the embryo as the latter develops from the unicellular zygote into a multicellular organism. At the apex of the shoot the leaf and stem increments are formed as a unit. At maturity, too, the leaf and stem imperceptibly merge with one another both externally and internally. In addition, the root and the stem constitute a continuum—a continuous structure—and have many common features in form, anatomy, function, and method of growth.

As the embryo grows and becomes a seedling, stem and root increasingly deviate from one another in their organization (Fig. 1.1). The root grows as a more or less branched cylindrical organ; the stem is composed of nodes and internodes, with leaves and branches attached at the nodes. Eventually the plant enters the reproductive stage when the shoot forms inflorescences and flowers (Fig. 1.2). The flower is sometimes called

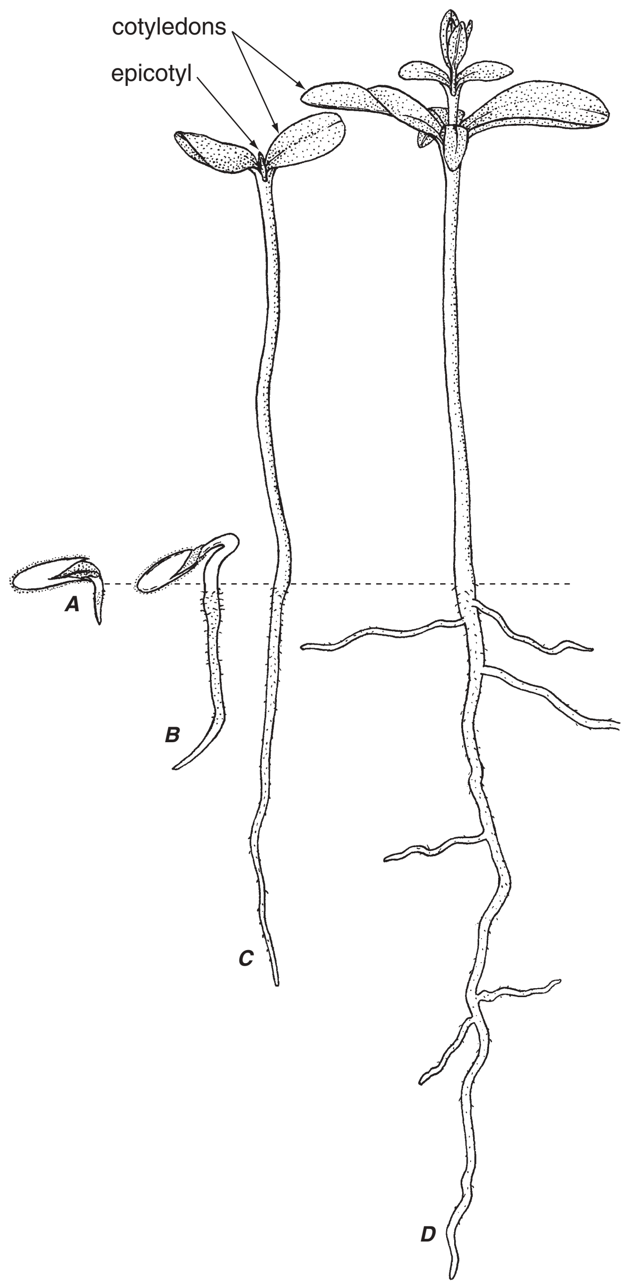

FIGURE 1.1

Some stages in development of the flax (*Linum usitatissimum*) seedling. **A**, germinating seed. The taproot (below interrupted line) is the first structure to penetrate the seed coat. **B**, the elongating hypocotyl (above interrupted line) has formed a hook, which subsequently will straighten out, pulling the cotyledons and shoot apex above ground. **C**, after emergence above ground, the cotyledons, which in flax persist for about 30 days, enlarge and thicken. The developing epicotyl—the stem-like axis or shoot above the cotyledons—is now apparent between the cotyledons. **D**, the developing epicotyl has given rise to several foliage leaves, and the taproot to several branch roots. (From Esau, 1977; drawn by Alva D. Grant.)

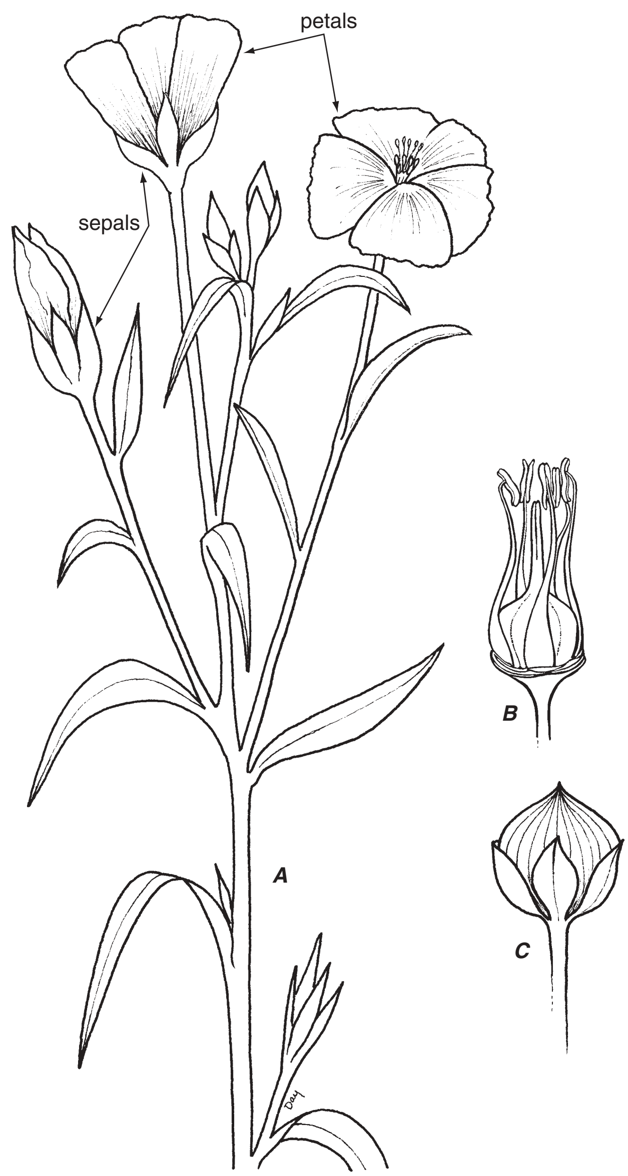

FIGURE 1.2

Inflorescence and flowers of flax (*Linum usitatissimum*). **A**, inflorescence, a panicle, with intact flowers showing sepals and petals. **B**, flower, from which the sepals and petals have been removed, to show the stamens and gynoecium. Flax flowers usually have five fertile stamens. The gynoecium consists of five united carpels, with five distinct styles and stigmas. **C**, mature fruit (capsule) and persistent sepals. (Drawn by Alva D. Grant.)

an organ, but the classical concept treats the flower as an assemblage of organs homologous with the shoot. This concept also implies that the floral parts—some of which are fertile (stamens and carpels) and others sterile (sepals and petals)—are homologous with the leaves. Both the leaves and the floral parts are thought to have originated from the kind of branch systems that characterized the early, leafless and rootless vascular plants (Gifford and Foster, 1989).

Despite the overlapping and intergrading of characters between plant parts, the division of the plant body into morphological categories of stem, leaf, root, and flower (where present) is commonly resorted to because it brings into focus the structural and the functional specialization of parts, the stem for support and conduction, the leaf for photosynthesis, and the root for anchorage and absorption. Such division must not be emphasized to the degree that it might obscure the essential unity of the plant body. This unity is clearly perceived if the plant is studied developmentally, an approach that reveals the gradual emergence of organs and tissues from a relatively undifferentiated body of the young embryo.

INTERNAL ORGANIZATION OF THE PLANT BODY

The plant body consists of many different types of cell, each enclosed in its own cell wall and united with other cells by means of a cementing intercellular substance. Within this united mass certain groupings of cells are distinct from others structurally or functionally or both. These groupings are referred to as **tissues**. The structural variations of tissues are based on differences in the component cells and their type of attachment to each other. Some tissues are structurally relatively **simple** in that they consist of one cell type; others, containing more than one cell type, are **complex**.

The arrangement of tissues in the plant as a whole and in its major organs reveals a definite structural and functional organization. Tissues concerned with conduction of food and water—the **vascular tissues**—form a coherent system extending continuously through each organ and the entire plant. These tissues connect places of water intake and food synthesis with regions of growth, development, and storage. The **nonvascular tissues** are similarly continuous, and their arrangements are indicative of specific interrelations (e.g., between storage and vascular tissues) and of specialized functions (e.g., support or storage). To emphasize the organization of tissues into large entities showing topographic continuity, and revealing the basic unity of the plant body, the expression **tissue system** has been adopted (Sachs, 1875; Haberlandt, 1914; Foster, 1949).

Although the classification of cells and tissues is a somewhat arbitrary matter, for purposes of orderly description of plant structure the establishment of categories is necessary. Moreover, if the classifications issue from broad comparative studies, in which the variability and the intergrading of characters are clearly revealed and properly interpreted, they not only are descriptively useful but also reflect the natural relation of the entities classified.

The Body of a Vascular Plant Is Composed of Three Tissue Systems

According to Sachs's (1875) convenient classification based on topographic continuity of tissues, the body of a vascular plant is composed of three tissue systems, the dermal, the vascular, and the fundamental (or ground). The **dermal tissue system** comprises the **epidermis**, that is, the primary outer protective covering of the plant body, and the **periderm**, the protective tissue that supplants the epidermis, mainly in plants that undergo a secondary increase in thickness. The **vascular tissue system** contains two kinds of conducting tissues, the **phloem** (food conduction) and the **xylem** (water conduction). The epidermis, periderm, phloem, and xylem are complex tissues.

The **fundamental tissue system** (or **ground tissue system**) includes the simple tissues that, in a sense, form the ground substance of the plant but at the same time show various degrees of specialization. **Parenchyma** is the most common of ground tissues. Parenchyma cells are characteristically living cells, capable of growth and division. Modifications of parenchyma cells are found in the various secretory structures, which may occur in the ground tissue as individual cells or as smaller or larger cell complexes. **Collenchyma** is a living thick-walled tissue closely related to parenchyma; in fact, it is commonly regarded as a form of parenchyma specialized as supporting tissue of young organs. The fundamental tissue system often contains highly specialized mechanical elements—with thick, hard, often lignified walls—combined into coherent masses as **sclerenchyma** tissue or dispersed as individual or as small groups of sclerenchyma cells.

Structurally Stem, Leaf, and Root Differ Primarily in the Relative Distribution of the Vascular and Ground Tissues

Within the plant body the various tissues are distributed in characteristic patterns depending on plant part or plant taxon or both. Basically the patterns are alike in that the vascular tissue is embedded in ground tissue and the dermal tissue forms the outer covering. The principal differences in the structure of stem, leaf, and root lie in the relative distribution of the vascular and ground tissues (Fig. 1.3). In the stems of eudicotyledons

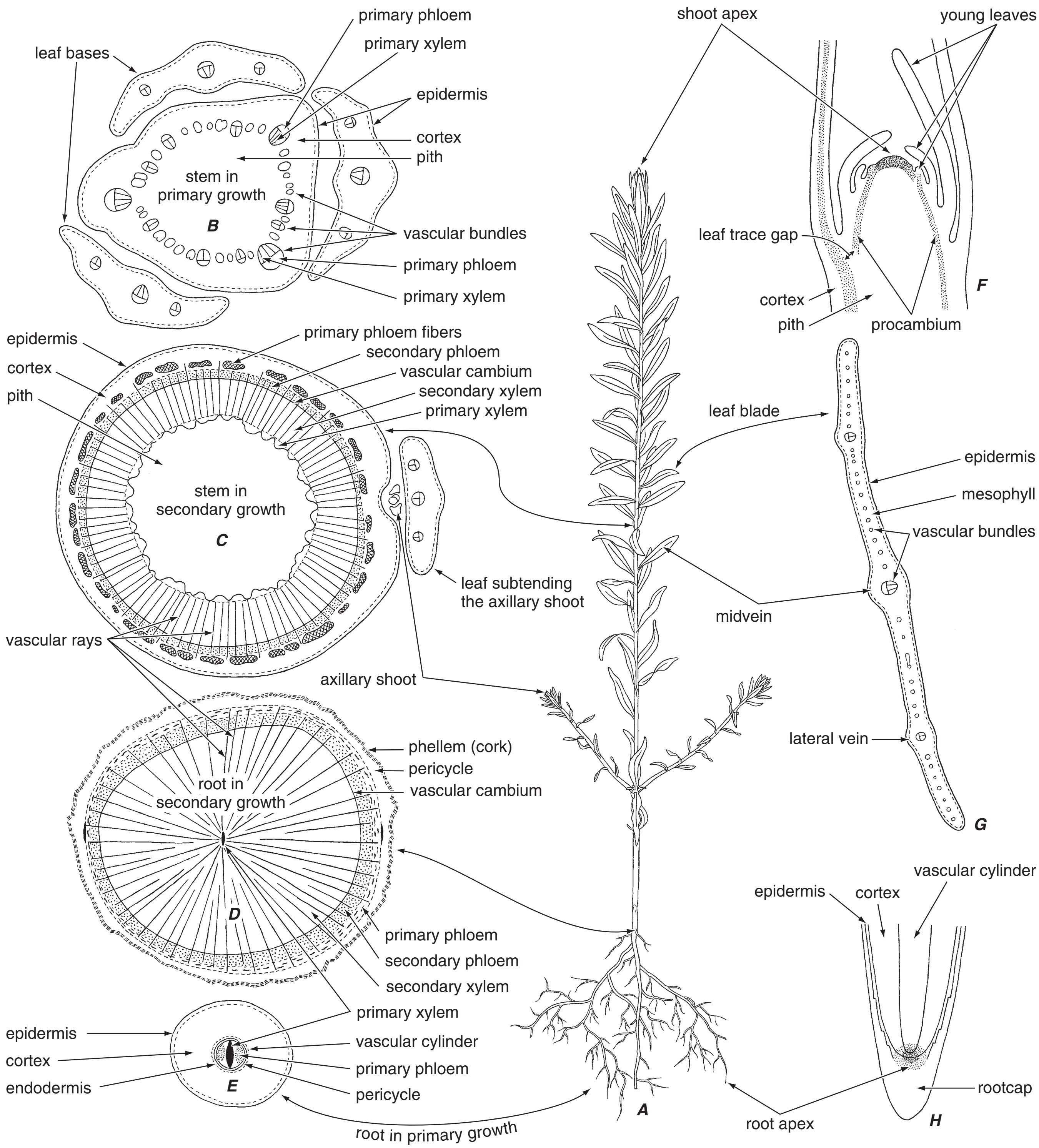

FIGURE 1.3

Organization of a vascular plant. **A**, habit sketch of flax (*Linum usitatissimum*) in vegetative state. Transverse sections of stem at **B**, **C**, and of root at **D**, **E**. **F**, longitudinal section of terminal part of shoot with shoot apex and developing leaves. **G**, transverse section of leaf blade. **H**, longitudinal section of terminal part of root with root apex (covered by rootcap) and subjacent root regions. (A, ×2/5; B, E, F, H, ×50; C, ×32; D, ×7; G, ×19. **A**, drawn by R. H. Miller.)

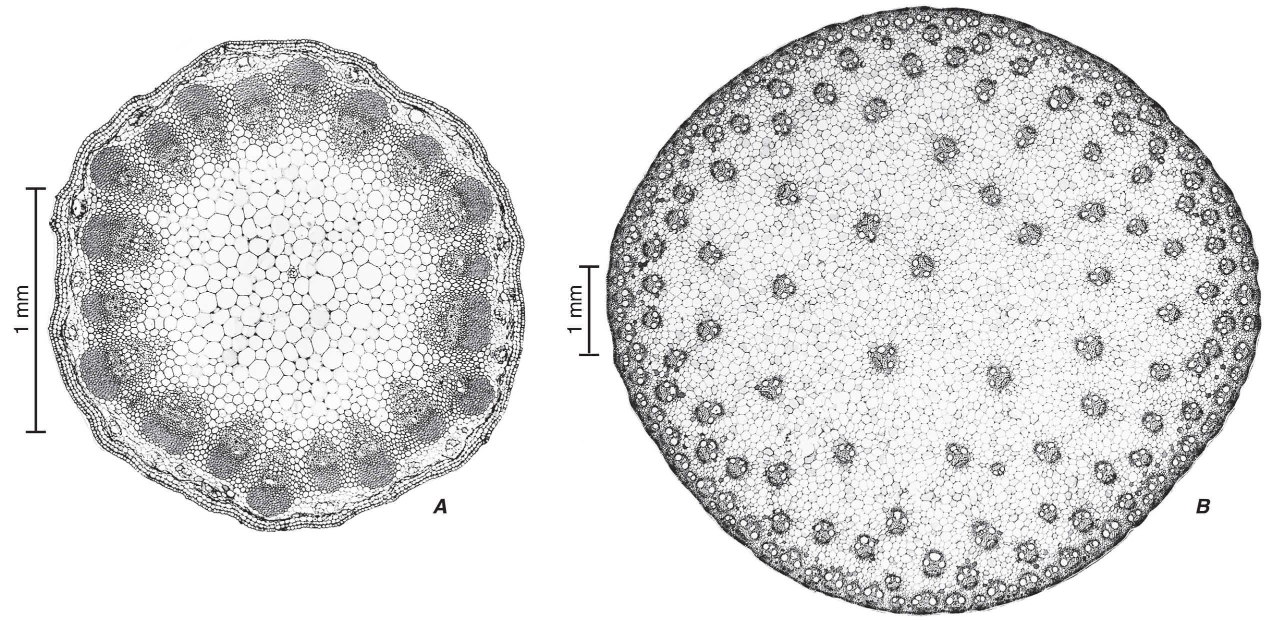

FIGURE 1.4

Types of stem anatomy in angiosperms. **A**, transverse section of stem of *Helianthus*, a eudicot, with discrete vascular bundles forming a single ring around a pith. **B**, transverse section of stem of *Zea*, a monocot, with the vascular bundles scattered throughout the ground tissue. The bundles are more numerous near the periphery. (From Esau, 1977.)

(eudicots), for example, the vascular tissue forms a "hollow" cylinder, with some ground tissue enclosed by the cylinder (**pith**, or **medulla**) and some located between the vascular and dermal tissues (**cortex**) (Figs. 1.3B, C and 1.4A). The primary vascular tissues may appear as a more or less continuous cylinder within the ground tissue or as a cylinder of discrete strands, or bundles, separated from one another by ground tissue. In the stems of most monocotyledons (monocots) the vascular bundles occur in more than one ring or appear scattered throughout the ground tissue (Fig. 1.4B). In the latter instance the ground tissue often cannot be distinguished as cortex and pith. In the leaf the vascular tissue forms an anastomosing system of **veins**, which thoroughly permeate the **mesophyll**, the ground tissue of the leaf that is specialized for photosynthesis (Fig. 1.3G).

The pattern formed by the vascular bundles in the stem reflects the close structural and developmental relationship between the stem and its leaves. The term "shoot" serves not only as a collective term for these two vegetative organs but also as an expression of their intimate physical and developmental association. At each node one or more vascular bundles diverge from the strands in the stem and enter the leaf or leaves attached at that node in continuity with the vasculature of the leaf (Fig. 1.5). The extensions from the vascular system in the stem toward the leaves are called **leaf traces**, and the wide gaps or regions of ground tissue in the vascular cylinder located above the level where leaf traces diverge toward the leaves are called **leaf trace gaps** (Raven et al., 2005) or **interfascicular regions** (Beck et al., 1982). A leaf trace extends from its connection with a bundle in the stem (called a **stem bundle**, or an **axial bundle**), or with another leaf trace, to the level at which it enters the leaf (Beck et al., 1982).

Compared with the stem, the internal structure of the root is usually relatively simple and closer to that of the ancestral axis (Raven and Edwards, 2001). Its relatively simple structure is due in large part to the absence of leaves and the corresponding absence of nodes and internodes. The three tissue systems in the primary stage of root growth can be readily distinguished from one another. In most roots, the vascular tissues form a solid cylinder (Fig. 1.3E), but in some they form a hollow cylinder around a pith. The vascular cylinder comprises the vascular tissues and one or more layers of nonvascular cells, the **pericycle**, which in seed plants arises from the same part of the root apex as the vascular tissues. In most seed plants branch, or lateral, roots arise in the pericycle. A morphologically differentiated

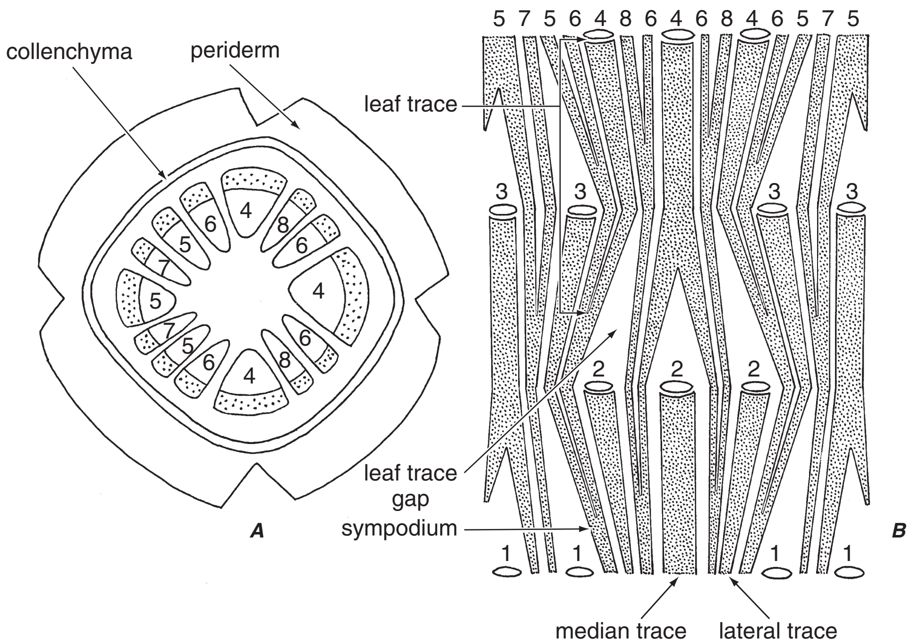

FIGURE 1.5

Diagrams illustrating primary vascular system in the stem of elm (*Ulmus*), a eudicot. **A**, transverse section of stem showing the discrete vascular bundles encircling the pith. **B**, longitudinal view showing the vascular cylinder as though cut through median leaf trace 5 and spread out in one plane. The transverse section (**A**) corresponds to the topmost view in **B**. The numbers in both views indicate leaf traces. Three leaf traces—a median and two lateral traces—connect the vascular system of the stem with that of the leaf. A stem bundle and its associated leaf traces are called a sympodium. (From Esau, 1977; after Smithson, 1954, with permission of the Council of the Leeds Philosophical and Literary Society.)

endodermis (the innermost, and compactly arranged, layer of cells of the cortex in seed plants) typically surrounds the pericycle. In the absorbing region of the root the endodermis is characterized by the presence of **Casparian strips** in its anticlinal walls (the radial and transverse walls, which are perpendicular to the surface of the root) (Fig. 1.6). In many roots the outermost layer of cortical cells is differentiated as an **exodermis**, which also exhibits Casparian strips. The Casparian strip is not merely a wall thickening but an integral band-like portion of the wall and intercellular substance that is impregnated with suberin and sometimes lignin. The presence of this hydrophobic region precludes the passage of water and solutes across the endodermis and exodermis via the anticlinal walls (Lehmann et al., 2000).

SUMMARY OF TYPES OF CELLS AND TISSUES

As implied earlier in this chapter, separation of cells and tissues into categories is, in a sense, contrary to the fact that structural features vary and intergrade with each other. Cells and tissues do, however, acquire differential properties in relation to their positions in the plant body. Some cells undergo more profound changes than others. That is, cells become specialized to varied degrees. Cells that are relatively little specialized retain living protoplasts and have the capacity to change in form and function during their lifetimes (various kinds of parenchyma cells). More highly specialized cells may develop thick, rigid cell walls, become devoid of living protoplasts, and cease to be capable of structural and functional changes (tracheary elements and various kinds of sclerenchyma cells). Between these two extremes are cells at varying levels of metabolic activity and degrees of structural and functional specialization. Classifications of cells and tissues serve to deal with the phenomena of differentiation—and the resultant diversification of plant parts—in a manner that allows making generalizations about common and divergent features among related and unrelated taxa. They make possible treating the phenomena of ontogenetic and phylogenetic specialization in a comparative and systematic way.

Table 1.1 summarizes information on the generally recognized categories of cells and tissues of seed plants without special regard to the problem of structural and functional intergrading of characteristics. The various

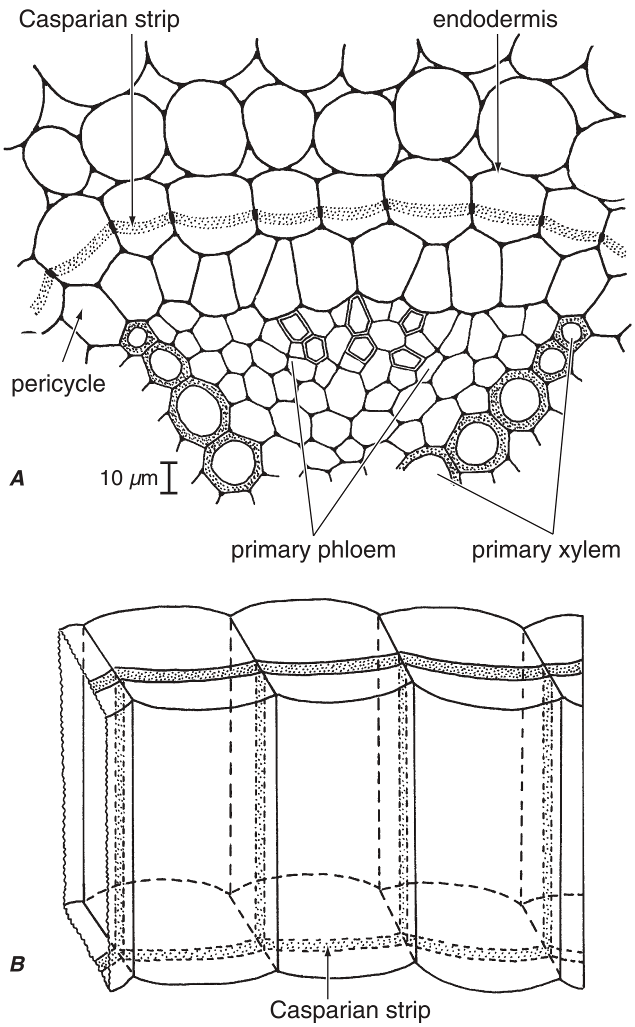

FIGURE 1.6

Structure of endodermis. **A**, transverse section of part of a morning glory (*Convolvulus arvensis*) root showing position of the endodermis in relation to vascular cylinder consisting of pericycle, primary xylem, and primary phloem. The endodermis is shown with transverse walls bearing Casparian strips in focus. **B**, diagram of three connected endodermal cells oriented as they are in **A**; Casparian strip occurs in transverse and radial walls (i.e., in all anticlinal walls) but is absent in tangential walls. (From Esau, 1977.)

types of cells and tissues summarized in the table are considered in detail in Chapters 7 through 15. Secretory cells—cells that produce a variety of secretions—do not form clearly delimited tissues and therefore are not included in the table. They are the topics of Chapters 16 and 17.

Secretory cells occur within other tissues as single cells or as groups or series of cells, and also in more or less definitely organized formations on the surface of the plant. The principal secretory structures on plant surfaces are glandular epidermal cells, hairs, and various glands, such as floral and extrafloral nectaries, certain hydathodes, and digestive glands. The glands are usually differentiated into secretory cells on the surfaces and nonsecretory cells support the secretory. Internal secretory structures are secretory cells, intercellular cavities or canals lined with secretory cells (resin ducts, oil ducts), and secretory cavities resulting from disintegration of secretory cells (oil cavities). Laticifers may be placed among the internal secretory structures. They are either single cells (nonarticulated laticifers) usually much branched, or series of cells united through partial dissolution of common walls (articulated laticifers). Laticifers contain a fluid called latex, which may be rich in rubber. Laticifer cells are commonly multinucleate.

DEVELOPMENT OF THE PLANT BODY

The Body Plan of the Plant Is Established during Embryogenesis

The highly organized body of a seed plant represents the sporophyte phase of the life cycle. It begins its existence with the product of gametic union, the unicellular **zygote**, which develops into an embryo by a process known as **embryogenesis** (Fig. 1.7). Embryogenesis establishes the body plan of the plant, consisting of two superimposed patterns: an **apical-basal pattern** along the main axis and a **radial pattern** of concentrically arranged tissue systems. Thus patterns are established in the distribution of cells, and the embryo as a whole assumes a specific, albeit relatively simple, form as contrasted with the adult sporophyte.

The initial stages of embryogenesis are essentially the same in eudicots and monocots. Formation of the embryo begins with division of the zygote within the embryo sac of the ovule. Typically the first division of the zygote is transverse and asymmetrical, with regard to the long axis of the cell, the division plane coinciding with the minimum dimension of the cell (Kaplan and Cooke, 1997). With this division the **polarity** of the embryo is established. The upper pole, consisting of a small **apical cell** (Fig. 1.7A), gives rise to most of the mature embryo. The lower pole, consisting of a larger **basal cell** (Fig. 1.7A), produces a stalk-like **suspensor** (Fig. 1.7B) that anchors the embryo at the micropyle, the opening in the ovule through which the pollen tube enters. Through a progression of divisions—in some species (e.g., *Arabidopsis*; West and Harada, 1993) quite orderly, in others (e.g., cotton and maize; Pollock and Jensen, 1964; Poethig et al., 1986) not obviously so—the embryo differentiates into a nearly spherical structure, the **embryo proper** and the suspensor. In some angiosperms polarity is already established in the egg cell and

TABLE 1.1 ■ Tissues and Cell Types

Tissues		Cell Type	Characteristics	Location	Function
Dermal	Epidermis		Unspecialized cells; guard cells and cells forming trichomes; sclerenchyma cells	Outermost layer of cells of the primary plant body	Mechanical protection; minimizes water loss (cuticle); aeration of internal tissue via stomata
	Periderm		Comprises cork tissue (phellem), cork cambium (phellogen), and phelloderm	Initial periderm generally beneath epidermis; subsequently formed periderms deeper in bark	Replaces epidermis as protective tissue in roots and stems; aeration of internal tissue via lenticels
Ground	Parenchyma	Parenchyma	Shape: commonly polyhedral (many-sided); variable Cell wall: primary, or primary and secondary; may be lignified, suberized, or cutinized Living at maturity	Throughout the plant body, as parenchyma tissue in cortex, pith, pith rays, and mesophyll; in xylem and phloem	Such metabolic processes as respiration, digestion, and photosynthesis; storage and conduction; wound healing and regeneration
	Collenchyma	Collenchyma	Shape: elongated Cell wall: unevenly thickened, primary only—nonlignified Living at maturity	On the periphery (beneath the epidermis) in young elongating stems; often as a cylinder of tissue or only in patches; in ribs along veins in some leaves	Support in primary plant body
	Sclerenchyma	Fiber	Shape: generally very long Cell wall: primary and thick secondary—often lignified Often (not always) dead at maturity	Sometimes in cortex of stems, most often associated with xylem and phloem; in leaves of monocots	Support; storage
		Sclereid	Shape: variable; generally shorter than fibers Cell wall: primary and thick secondary—generally lignified May be living or dead at maturity	Throughout the plant body	Mechanical; protective
Vascular	Xylem	Tracheid	Shape: elongated and tapering Cell wall: primary and secondary; lignified; contains pits but not perforations Dead at maturity	Xylem	Chief water-conducting element in gymnosperms and seedless vascular plants; also found in angiosperms
		Vessel element	Shape: elongated, generally not as long as tracheids; several vessel elements end-on-end constitute a vessel Cell wall: primary and secondary; lignified; contains pits and perforations Dead at maturity	Xylem	Chief water-conducting element in angiosperms