



An Introduction to
**Plant Structure
and Development**

Plant Anatomy for the Twenty-First Century

SECOND EDITION

CHARLES B. BECK

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An Introduction to Plant Structure and Development

Plant Anatomy for the Twenty-First Century
Second Edition

This is a plant anatomy textbook unlike any other on the market today. As suggested by the subtitle, it is plant anatomy for the twenty-first century. Whereas traditional plant anatomy texts include primarily descriptive aspects of structure with some emphasis on patterns of development, this book not only provides a comprehensive coverage of plant structure, but also introduces, in some detail, aspects of the mechanisms of development, especially the genetic and hormonal controls, and the roles of the cytoskeleton. The evolution of plant structure and the relationship between structure and function are also discussed throughout the book. Consequently, it provides students and, perhaps, some teachers as well, with an introduction to many of the exciting, contemporary areas at the forefront of research, especially those areas concerning development of plant structure. Those who wish to delve more deeply into areas of plant development will find the extensive bibliographies at the end of each chapter indispensable. If this book stimulates a few students to become leaders in teaching and research in plant anatomy of the future, the goal of the author will have been accomplished.

CHARLES B. BECK, Professor Emeritus of Botany at the University of Michigan, received his PhD degree from Cornell University where he developed an intense interest in the structure of fossil and living plants under the influence of Professor Harlan Banks and Professor Arthur Eames. Following post-doctoral study with Professor John Walton at Glasgow University in Scotland, he joined the faculty of the University of Michigan. At Michigan he served one term each as Chairman of the Department of Botany and Director of the Museum of Paleontology. His graduate students pursued research in either plant structure and development or paleobotany. He taught courses in plant anatomy, plant morphology and paleobotany over a period of 35 years.

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Charles B. Beck
University of Michigan



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To
My wife, Janice,
and our daughters, Ann and Sara
for their love, encouragement,
and enduring support,

and

to my students,

David Benzing

Robert Chau

Crispin Devadas

Margaret Knaus

G. Kadambari Kumari

Rudolf Schmid

William Stein

Garland Upchurch

Richard White

David Wight

who are a continuing inspiration and
from whom I have learned much.

It is important that students bring
a certain ragamuffin barefoot
irreverence to their studies; they
are not here to worship what is
known but to question it.

Jacob Bronowski
The Ascent of Man (1975)

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Preface to the second edition

Although it has been only five years since this book was first published, research activity during this period in many areas of plant development has resulted in much new and important information. The basic information on plant structure is quite stable. As a result, inclusion of new information about various aspects of development comprise the major changes in this 2nd edition. In addition, a new section on the evolution of tracheary elements has been added.

The areas expanded and/or upgraded include the structure and function of the cytoskeleton, and its roles in cell wall formation and pollen tube tip growth; the role of auxin and other hormones in development, especially in the development of tracheary elements, as well as in cambial activity and tissue patterning, and the role of PIN proteins in the movement of auxin from cell to cell by auxin efflux transporters. The discussion on the mechanism of movement of stomatal guard cells has been expanded and improved. Sections on long-distance transport in the secondary xylem and phloem have been modified to emphasize widely accepted mechanisms of transport, and the discussion of bidirectional transport in the phloem has been expanded. The discussion of gravitropism has been brought up to date. Finally, throughout the book, discussions of the role of genetics in plant development have been expanded.

I believe the changes listed above have made the book more useful to advanced students and researchers without adversely affecting its usefulness as an introductory plant anatomy textbook. It is not designed to be used as the only source of information in a course in plant anatomy, i.e., to take the place of the teacher, but rather, to be a supplement to the teacher's lectures and a means for the student to reinforce information from the teacher and the laboratory exercises. The book can, of course, also be an original source of information for students beyond that provided by the teacher. When used in a course that emphasizes development, the student will have the opportunity to expand his or her knowledge of plant structure, and in a course that emphasizes plant structure, the student can expand his or her knowledge of plant development. Ideally, however, a twenty-first century course in plant anatomy should consist of an integration of structure and development. It is this ideal that I have tried to promote in the design and preparation of this book.

For granting me permission to use photographs in this 2nd edition of the book, I express my appreciation to university and commercial publishers and all other copyright holders. I am especially grateful to Professor Philip Gingerich for allowing me to use the facilities and services of the University of Michigan Museum of Paleontology, and to three very talented persons in this unit, Bonnie Miljour, senior scientific

illustrator, Cindy Stauch, business administrator, and Christina Minor, research secretary who were so helpful in many ways.

I express my gratitude to Dominic Lewis, commissioning editor, life sciences, Rachel Eley, assistant editor, life sciences, Caroline Brown, production editor, and Lesley Bennun, copy-editor, and acknowledge their important roles in the preparation and production of this book.

Finally, I owe a special debt of gratitude to my wife, Janice, whose patience and encouragement have contributed so importantly to the completion of this project.

Charles B. Beck
Ann Arbor, 2009

Preface

Since my introduction to plant anatomy by William Strickland at the University of Richmond and my interaction with Arthur Eames and Harlan Banks at Cornell University during graduate study, I have been entranced by the elegant beauty of plant structure. At the University of Michigan I taught both paleobotany and plant anatomy for many years, and served as committee chair for graduate students, some of whom studied fossil plants and others of whom worked on the structure and development of extant taxa. During the past several decades during which the introduction of new techniques of study at the subcellular and molecular levels has resulted in a resurgence of research throughout the world, my interest in the development of plant structure has grown steadily.

Many books on plant structure, some highly technical, have appeared since the publication of the seminal textbooks of Katherine Esau during the 1950s and 1960s, but no single book that, in my opinion, incorporates both the basic knowledge of plant anatomy and contemporary information and ideas about the development of structure and form that could be used as an effective introductory textbook. Consequently, I have tried to meet the challenge of preparing such a book. In each chapter I have presented what I consider to be the fundamental knowledge essential for an understanding of basic plant structure and development and have integrated with this the results of some of the most significant recent research on plant development. Whereas emphasis throughout the book is on structure and development, I have also included sections on evolution and function where it seemed essential and appropriate to do so. The application of cellular and molecular biological approaches and techniques in the study of plant development has revolutionized the field. Understanding of the integrative significance of plasmodesmata and the concept of the symplast have led to an appreciation and widespread acceptance of the organismal theory of plant multicellularity which in turn has influenced research on plant development. Exciting and significant areas of research such as the role of the cytoskeleton in development, signal transduction, genetic control of development, among others have greatly advanced our understanding. I have not treated the very important subject of the genetic control of development in any depth because it requires a much deeper knowledge of genetics than the undergraduate for which this book is written is likely to have attained. I have, however, included references to important genetic studies in the bibliographies of several chapters. Other subjects may not be as fully covered as some teachers and researchers would desire, but they are very likely to find pertinent references to literature on those subjects in the extensive bibliographies to which they can direct their students who have the necessary backgrounds.

Diverging from the approach in many textbooks, I have included in this book tentative conclusions that are essentially still hypotheses, and discussions of research that is controversial, often providing opposing viewpoints. I believe that, in addition to providing well-established information on a subject, a textbook should also provide the student with an understanding of the nature of ongoing scientific research.

In order to make this book more readable for the undergraduate, I have omitted most literature citations in sections of the text in which the basic, widely accepted knowledge in the field is presented, but have included some references of historical importance in the references at the end of each chapter. On the other hand, when presenting new information, ideas, and conclusions that are not yet widely accepted, I have cited in the text and included in the references the sources of this information. Thus, students as well as researchers who wish to consult the original papers may find the reference sections useful.

My objective has been to prepare a new plant anatomy textbook for a new century, incorporating the best research in the most active and significant areas with the widely accepted common knowledge that provides the foundation of the field. Only you the readers can decide whether or not I have succeeded.

Charles B. Beck
Ann Arbor, 2004

Acknowledgements

One's knowledge comes from many sources. Not least are the research and writings of many predecessors in the field. Men and women such as Nägeli, De Bary, Strasburger, Haberlandt, Van Tieghem, Solereder, Jeffrey, Eames, Bailey, Metcalfe and Chalk, Esau and countless others have provided the foundation upon which current-day researchers are building. To these, whom sometimes we forget, we owe a debt of gratitude. I acknowledge a profound debt to my college and university teachers, William Strickland and Robert Smart who introduced me to plant structure in the first place, Arthur Eames and Harlan Banks who widened my horizons and reinforced my understanding of the fundamentals of plant anatomy, and to John Walton who encouraged me to take risks and taught me how to write. I acknowledge, as well, the significant contributions to my knowledge of the many researchers who are currently active in the field.

Direct assistance during the preparation of this book has come from many sources. I feel particularly indebted to colleagues who have critically read chapters in manuscript and made important suggestions for change and improvement. These are Professor William Stein of the State University of New York, Binghamton who read several chapters, Professor Shirley Tucker of the University of California at Santa Barbara, Professor Nancy Dengler of the University of Toronto, and Professor Darleen DeMason of the University of California, Riverside. Other colleagues have provided information on special topics. Professor Peter Ray of Stanford University provided information on the functional significance of the optical qualities of epidermal cells in leaves, Professor Judy Jernstedt of the University of California at Davis provided information on contractile roots, Professor Larry Nooden of the University of Michigan was a source of important information on several aspects of plant physiology, Professor Robert Fogel of the University of Michigan provided information on mycorrhizae, and Professor Edward Voss and Dr. Christiane Anderson of the University of Michigan were valuable sources of information on plant taxonomy. To all of these I express my sincere appreciation.

Professor Philip Gingerich, Director of the Museum of Paleontology at the University of Michigan, made available to me the resources and services of the Museum. Preparation of this book would not have been possible without this assistance, and to Phil I express my sincere gratitude. The illustrations are nearly as important as the text in a plant anatomy book. In this book all original line drawings were finished by Bonnie Miljour, artist *par excellence* of the Museum of Paleontology. Ms. Miljour also grouped and placed all illustrations in electronic files. The importance to this project of her great expertise cannot be overemphasized. Thank you, Bonnie, for the beauty of your work and for your very important contribution to this book. Two members of the Museums

office staff, Cindy Stauch and Meegan Novara, were also of inestimable assistance in many ways. I express my sincere appreciation to them.

The original photographs were taken primarily by two University of Michigan photographers, Louis Martonyi, now deceased, who was photographer for the Department of Biology during the 1980s, and David Bay, current photographer for the Department of Ecology and Evolutionary Biology. Thank you, David, for your excellent work. A few photographs were taken by the author in the facilities of the Microscopy and Image-analysis Laboratory of the University of Michigan Medical School. This was made possible by the kindness of the Laboratory Manager, Chris Edwards and with the technical assistance of Shelley Almburg, to both of whom I express my appreciation. I express my sincere gratitude to colleagues who provided photographs: Professor Pedro J. Casero of Universidad de Extremadura, Badajoz, Spain; Professor P. Dayanandan of Madras Christian College, India; Dr. Elisabeth de Fayë of Université Henri Poincaré, Nancy, France; Professor Nancy Dengler of the University of Toronto, Canada; Dr. Katrin Ehlers of the Justus-Liebig-Universität, Giessen, Germany; Dr. Irene Lichtscheidl of Universität Wien, Austria; Dr. E. Panteris of the University of Athens, Greece; and Dr. Koichi Uehara of Chiba University, Japan. Professor P. Maheshwari of the University of New Delhi sent me many excellent slides during his lifetime, many of which have been photographed for use in this book. I have also used many illustrations from published sources, and I express my gratitude to the individuals, commercial publishers, university presses, and professional societies that have granted permission for the use of their copyrighted materials.

Although every effort has been made to secure necessary permissions to reproduce copyrighted material in this work, it has proved impossible in two cases to trace the copyright holders. The copyright holder of the original illustration from Lehninger (1961), which I have used as my Fig. 3.7a, is Dr. A. E. Vatter. The copyright holder of the original illustrations from Eames and MacDaniels (1925), which I have used as my Figs 13.3, 13.4, 14.5, 16.15c, and 16.21 is David Eames. Appropriate acknowledgements will be included in any reprinting or in any subsequent edition of this book if the copyright holders are located.

In order to understand copyright law, which varies somewhat throughout the world, I called on my friend, Professor John Reed of the University of Michigan Law School, for advice. He directed me to Professor Molley Van Houweling, a specialist in copyright law, who gave me valuable information. I am grateful to these colleagues.

Without the resources of the University of Michigan Library this book could not have been written, and the excellent assistance of the reference librarians in the Shapiro Science Library is acknowledged with gratitude.

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Finally, I must acknowledge friends and family who through their interest and support have made a contribution to this project greater than they can imagine. Every morning for many years past and during the several years of this project I have joined friends for coffee. We call the group the Coffee Klatch. Members have included Robert Lowry, cytogeneticist and microscopist, Erich Steiner, plant geneticist, Norman Kemp, animal morphologist, Ralph Loomis, teacher of English literature, Harry Douthit, microbiologist, James Cather, developmental biologist, Michael Wynne, phycologist, Barbara Brown, university bus driver, and me. Conversation has ranged over a broad spectrum of interests and activities, but almost never on “the book.” Interaction with this wonderful group of university colleagues has provided me with a daily means of relaxation and a time to forget about cells, tissues, microtubules, and actin microfilaments. On the other hand, I have felt the subtle but genuine support for me and this project by members of the group. So I express my sincere appreciation to my friends of the Coffee Klatch.

One person, however, stands out above all others in importance. My wife, Janice, has supported me with remarkable patience and understanding during work on this book. She has added to her busy schedule many activities for which I would ordinarily have taken responsibility and has been a constant source of support and encouragement. Thank you, Sweetheart, for being the wonderful person you are, and for your most important contributions to this project.

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Problems of adaptation to a terrestrial environment

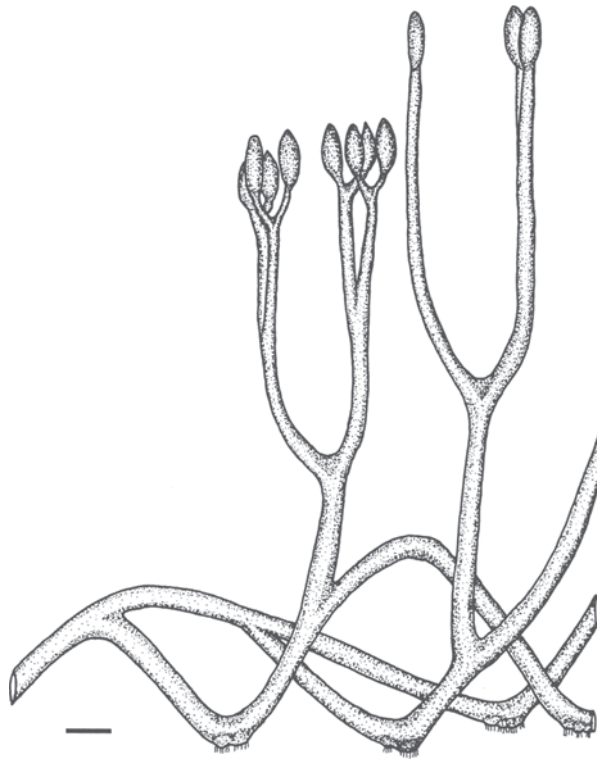
Perspective: the origin of vascular plants

Land plants, plants that complete their life cycle entirely in a terrestrial environment, are represented largely by bryophytes and vascular plants. In all taxa except seed plants, however, at least a thin film of water is required for fertilization; and even in two primitive groups of seed plants, the cycads and *Ginkgo*, fertilization is by free-swimming spermatozoids released into a liquid medium in the archegonial chamber. A few angiosperms, although terrestrial in origin, have reverted to an aquatic existence.

Vascular plants are by far the dominant groups on the Earth comprising over 255 000 species in contrast to about 22 000 species of bryophytes and approximately 20 000 species of algae. The first vascular plants appear in the fossil record in the late Silurian, about 420 million years ago, but their green algal ancestors are thought to have appeared nearly 400 million years earlier! Shared features comprise the major evidence that vascular plants, possibly also bryophytes, evolved from green algae: both synthesize chlorophylls a and b, both store true starch in plastids; both have motile cells with whiplash flagella, and both (but only a few green algae) are characterized by phragmoplast and cell plate formation following mitosis. A green alga, with these and other significant characteristics, that may provide a model of an algal ancestor of vascular plants is *Coleochaete*, a member of the Charophyceae. Features in addition to those listed above that lead to this conclusion are the development in *Coleochaete* of a zygote in which cell division begins while embedded in the gametophyte thallus, the presence of sporopollenin in the wall of the zygote, and the presence of lignin in the gametophyte. It is widely believed that the Embryophyta (bryophytes and vascular plants) and the Charophyceae evolved from a common aquatic ancestor. Detailed presentations of the evidence for this viewpoint and the nature of the presumed common ancestor can be found in major works by Graham (1993) and Niklas (1997, 2000).

The first, indisputable vascular plants were characterized by a conducting system containing xylem and phloem, a waxy cuticle,

Figure 1.1 Reconstruction of *Aglaophyton major*. Bar = 10 mm. From Edwards (1986). Used by permission of The Linnean Society of London.



epidermal stomata, and a reproductive system that produced **trilete spores** (spores with a triradiate scar resulting from their development in spherical tetrads) and probably containing sporopollenin in the walls. Such plants appear first in the late Silurian, but *Aglaophyton major* (see Edwards, 1986) from the Lower Devonian, which has morphologic and structural features of both some bryophytes and primitive vascular plants, provides perhaps the best available model of a vascular plant precursor. *Aglaophyton* was a small plant, probably no more than 180 mm (about 7 inches) high, composed of dichotomous, upright axes that branched from rhizomes on the surface of the substrate (Fig. 1.1). The epidermis of all axes was covered by a cuticle and contained stomata. Some upright axes were terminated in pairs of sporangia, containing small spores of one size only. Edwards suggested that the plant probably formed extensive mats, consisting largely of vegetative axes, but produced fertile axes, bearing sporangia, “at irregular intervals.” The rhizomes were probably vegetative axes that formed clusters of **rhizoids** (absorbing structures) where some axes arched over and contacted the substrate. One of the most interesting structural features of the axes of *Aglaophyton* was the central conducting strand. Although appearing superficially as a vascular strand consisting of xylem and phloem, and described that way by earlier workers, Edwards was unable to detect characteristic structural features of tracheary elements (that is, cells with secondary wall material deposited in the form of rings, helices, or a reticulum) or of sieve elements. Instead, he found three

regions of cells, an inner column of thin-walled cells surrounded by thick-walled cells, the walls of both of which were dark in color. These were enclosed by an outer zone of thin-walled cells with light-colored walls. He concluded that the two inner regions of cells with dark cell walls were probably analogous to tracheids but most similar to the **hydroids** (water-conducting cells) of some mosses and that the outermost cells with light-colored walls were analogous to sieve elements and very similar to the **leptoids** (photosynthate-conducting cells) of mosses. *Aglaophyton* was, therefore, a non-vascular plant sporophyte in which the sporophyte was the dominant phase in a system of pteridophytic (free-sporing) reproduction. In gross morphology and branching pattern, and the presence of an epidermis covered by a cuticle and containing stomata, it was very similar to primitive vascular plants that lived during Upper Silurian and Lower Devonian times. In its water- and photosynthate-conducting cells closely resembling, respectively, hydroids and leptoids, as well as in its small size and free-sporing reproduction, it closely resembled mosses. It is reasonable, therefore, to hypothesize that vascular plants evolved from this or plants of similar morphology and anatomy. (For detailed information on the earliest vascular plants, see Stewart and Rothwell (1993) and Taylor and Taylor (1993).)

Structural adaptations

During the past 350–400 million years many structural and physiological changes occurred as vascular plants evolved. Evolution on land posed many problems for plants such as *Aglaophyton* and its descendants not shared with their marine algal ancestors. In an aquatic environment, conditions are equable, and problems of water loss, support, absorption of water and minerals, and transport of water and minerals, photosynthate, and hormones, are either minimal or non-existent. This is true also, in large part, for very small plants such as most mosses. For example, the absence of efficient water-conducting cells in mosses apparently does not pose a problem for them since in many taxa water and minerals are absorbed through the external surfaces of the sporophytes and gametophytes. This is not unlike the situation in aquatic plants in which water and minerals are absorbed by all parts of the plant directly through the epidermis, which lacks a cuticle. Consequently, there is no need for a highly efficient system of transport of water and minerals. Likewise, with few exceptions, the transport of hormones and photosynthate is also not a problem since these substances are produced in all cells. On land, however, solar radiation, wind, and temperature extremes result in a much harsher environment. As *Aglaophyton* and its descendants evolved on land, structural features evolved as adaptations to both this harsher environment and to their increase in size.

Adaptations reducing water loss were the evolution of a three-dimensional, rod-like plant body which decreased the surface/volume

ratio, and an epidermis covered by a waxy cuticle largely impermeable to the passage of water. Although the evolution of a rod-like form was advantageous in restricting the surface area from which water could be lost, an optimal surface area in relation to volume was required through which transpiration as well as gaseous exchange could occur. The evolution of stomata in the epidermis allowed the exchange of O₂ and CO₂, essential in respiration and photosynthesis, and by their ability to control the size of pores through which water vapor diffused, stomata also contributed to a restriction of water loss from the plant. Adequate surface area was also required, however, through which the plant could receive signals from the environment – signals such as light, temperature, or the presence of other organisms such as pathogens or symbionts as well as chemical signals from the atmosphere or from other organisms. We now know that chemicals produced by plants living today are also released through the surface and may elicit responses from other organisms such as moths and hummingbirds that function as pollinators. The response of plants to environmental signals, referred to as **signal transduction**, is a new and active area of research in plant biology.

Protection of spores and gametes, so very important in a terrestrial environment, was accomplished through the evolution of sporangia and gametangia enclosed in sterile jackets of cells. The spores themselves became encased in walls containing **sporopollenin**, a substance which restricts water loss and is highly resistant to decay.

Absorption of water and minerals from the soil was facilitated by the evolution of rhizoids and roots, the latter often containing symbiotic fungi forming mycorrhizae which, as we shall see in detail later, enhanced their absorptive function. Roots, in particular, also served to anchor the plant in its substrate and to prevent its displacement by wind and flowing water.

The effective transport of water and minerals as well as hormones, photosynthate, and other substances became increasingly important with increase in size of the descendants of *Aglaophyton* or other vascular plant precursors. This was accomplished by the evolution of complex vascular tissues containing tracheids and vessel members in the xylem and sieve cells and sieve tube members in the phloem, conducting cells especially adapted structurally for the transport of these materials. Associated with the evolution of cellular transport systems, specialized mechanisms evolved which facilitated the efficient transport of water and minerals from the roots to and out of the leaves of tall trees. Concurrently, mechanisms for the translocation of photosynthate and other assimilates throughout the plant evolved.

The problem of support of the plant body also became increasingly severe with increase in size and was solved by structural adaptations. In plants, or parts of plants, consisting largely of living tissues, support was provided by their enclosure by an epidermis as well as by turgor pressure within the cells. Ultimately, some of the functions of the epidermis were taken over by **periderm** (a major component of bark) consisting

largely of non-living cells, the walls of which are impregnated with **suberin** that restricted the passage of water through them. Support was also provided by the production of tissues consisting largely of non-living, longitudinally elongate cells with thick, lignified, cellulose walls. The major supporting tissue in large plants is the xylem, consisting in pteridophytes and their ancestors as well as in gymnosperms primarily of tracheids, and in angiosperms of fibers and vessel members. **Lignin** in the cell walls increased the tensile strength of elongate cells comprising the xylem, thus endowing vascular plants with both strength and flexibility, so very important in conditions of high wind velocity.

The above-ground parts of the plant bodies of primitive vascular plants consisted primarily of radially symmetrical branching axes, all of which were photosynthetic. With the evolution of larger vascular plants consisting of stems and branches covered with bark, an adaptation that facilitated the process of photosynthesis was necessary. This was accomplished by the evolution of leaves which increased the surface/volume ratio of photosynthetic tissues in the plant. Structural adaptations in the leaves, such as the orientation of thin-walled elongate cells at right angles to the upper surface which channeled light at relatively high intensity into the leaves, and the complex system of intercellular channels which provided extensive wet surface area for the absorption of CO₂ facilitated efficient photosynthesis. For further information on adaptations by early plants to a terrestrial environment, and the evolution of plant body plans, please see Niklas (2000).

Preview of subsequent chapters

As we proceed through this book we shall encounter progressively detailed information on the structure and development as well as some aspects of evolution and function of the descendants of primitive plants such as *Aglaophyton*. We shall consider many members of the Embryophyta, including the Lycopphyta (lycophytes and their relatives), Sphenophyta (sphenophytes), and Pterophyta (ferns), but the major emphasis will be on the seed plants (gymnosperms and angiosperms). In order to provide an orientation to all who have had little or no training in plant anatomy, and to introduce some important concepts, the following chapter will be an overview of plant structure and development. If you have had a good course in introductory botany or biology, you may wish to proceed to later chapters. [Chapters 3 and 4](#) present, respectively, basic information on the cell protoplast and the cell wall. The cell protoplast is usually covered in some detail in introductory courses, but the cell wall is often neglected. Consequently this book provides a fairly comprehensive discussion of its structure and development.

[Chapter 5](#) presents very important information on apical meristems of the shoot, apical regions from which other cells and tissues in the

shoot system are derived, and which provide to vascular plants their distinctive characteristic of indeterminate growth. Appendages such as leaves and lateral branches also are ultimately derived from the apical meristems. In [Chapters 6, 7, and 8](#) we consider the structure and development of the various tissues and tissue systems that result from the activity of apical meristems. These chapters include, in sequence, discussions of the primary vascular tissues (xylem and phloem) that are embedded in the parenchyma of the pith and cortex; the architecture of the primary vascular system and its relationship to the arrangement of leaves; and the epidermis, the single layer of tissue that bounds all of these other primary tissues and tissue systems, and which forms an outer protective and supportive layer of the plant prior to the development of secondary tissues.

The second part of the book, [Chapters 9 through 12](#), consists of discussions of the vascular cambium, a lateral meristem, the activity of which results in the formation of secondary vascular tissues, and the effects of their formation on the tissues and tissue systems produced by the apical meristems early in the development of the plant body. It also includes detailed presentations of the structure, development, and to a lesser extent evolution and function of the secondary xylem and the secondary phloem.

[Chapters 13 through 18](#) deal with secretory structures and functions; anomalous stem and root structure; the outer protective tissues and tissue regions of stems that produce secondary tissues (the periderm and rhytidome) that comprise the bark; the structure, development, and function of leaves as well as a brief discussion of their evolution; a presentation of the structure, development, and function of roots, with some comments on their evolution; and finally, a chapter on reproduction which includes some basic life cycles, discussions of the structure and morphology of flowers, the structure and development of fruits and seeds, and some aspects of the ecology of reproduction in angiosperms.

The author hopes that you will enjoy this book and that by the end of your course in plant anatomy you will be as enthusiastic about this exciting field as he is.

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An overview of plant structure and development

Perspective: origin of multicellularity

Since early in the study of plants botanists have been interested in the structure, function, development, and evolution of cells, tissues, and organs. Because some green plants are very small and unicellular, but others are large and multicellular, the origin of multicellularity in plants also has been of great interest to botanists. Among the green algae from which higher plants are thought to have evolved, some colonial taxa such as *Pandorina*, *Volvox*, and relatives consist of aggregations of motile cells that individually appear identical to apparently related unicellular forms (Fig. 2.1). Consequently, it was concluded early in the history of botany, and widely accepted, that multicellular plants evolved by the aggregation of unicellular organisms. This viewpoint led to the establishment of the **cell theory of multicellularity** in plants which proposes that cells are the building blocks of multicellular plants (Fig. 2.2). As early as 1867, however, Hoffmeister proposed that cells are simply subdivisions within an organism. This viewpoint, supported and expanded upon in 1906 by Lester Sharp at Cornell University, has been elucidated and clarified more recently by Hagemann (1982), Kaplan (1992), and Wojtaszek (2000) among others. These workers conclude on the basis of abundant evidence that a unicellular alga and a large vascular plant are organisms that differ primarily in size and in the degree to which they have been *subdivided* by cells (Fig. 2.2). This **organismal theory of multicellularity** has gained many adherents within the past several decades (see Kaplan, 1992), and is of great importance because of ways in which it has influenced the thinking of botanists about the processes of development.

A primary and convincing basis for the organismal theory is the nature and result of cell division in plants. Following mitosis and cell plate formation, the protoplasts of the two resulting daughter cells maintain continuity through highly specialized cytoplasmic strands called **plasmodesmata** (Fig. 2.3) (see Chapter 4 for a detailed discussion of plasmodesmata). Thus, although the plant is blocked off in regions called cells, the plasmodesmata provide for an interconnected system

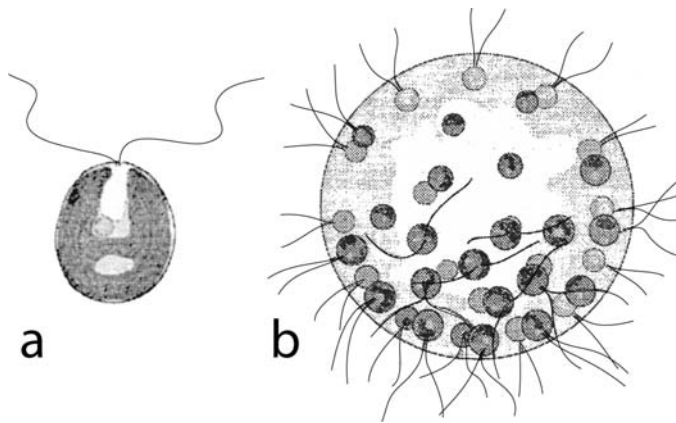


Figure 2.1 Unicellular and colonial body plans among green algae. (a) *Chlamydomonas* sp. (b) *Pandorina morum*. From Niklas (2000). Used by permission of Oxford University Press.

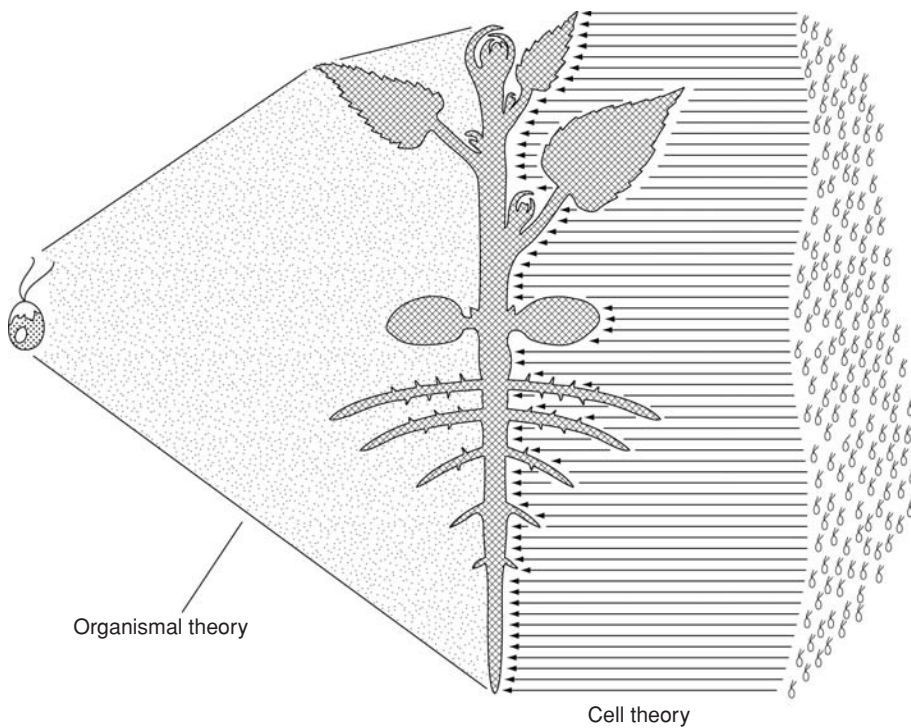
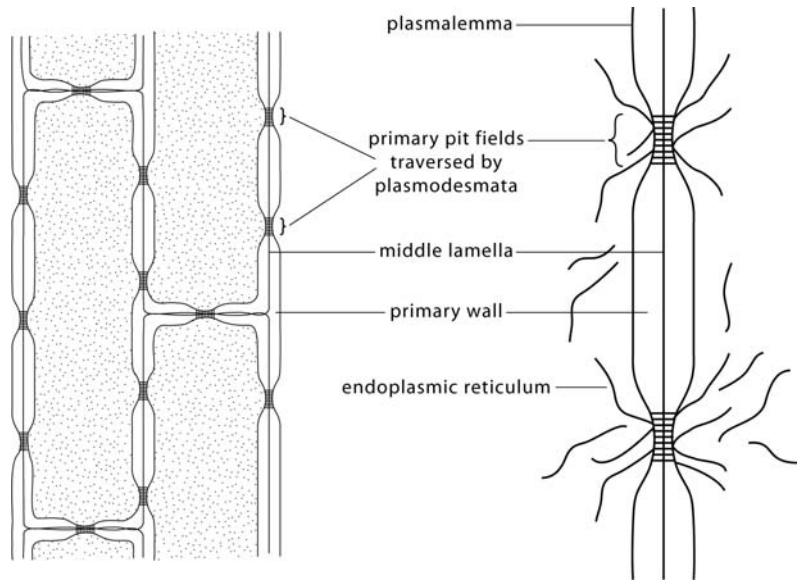


Figure 2.2 Diagram showing the relationship between a unicellular and a multicellular organism according to the organismal theory of multicellularity and the cell theory. From Kaplan (1992). Used by permission of the University of Chicago Press. © 1992 The University of Chicago. All rights reserved.

of protoplasts called the **symplast**. The plasmodesmata function as passageways for communication between living cells, that is, for the transmission between cells of molecules of varying size including even large molecules such as proteins and nucleic acids (e.g., Lucas *et al.*, 1993; Kragler *et al.*, 1998; Ehlers and Kollmann, 2001). It has become

Figure 2.3 Diagrams of primary pit fields traversed by plasmodesmata in primary cell walls. The plasmodesmata connect the protoplasts of adjacent parenchyma cells.



clear in recent years that this communication between cells has a profound influence in plant development (e.g., Verbeke, 1992). These and other workers believe that plasmodesmata may exert a “controlling influence” on cell differentiation, tissue formation, organogenesis, and specialized physiological functions.

For more detailed discussions of evidence in support of the organismal theory of multicellularity in plants and the significance of this theory in understanding plant development, see Kaplan and Hagemann (1991), Niklas and Kaplan (1991), Kaplan (1992), and Wojtaszek (2000).

Let us now look at the vascular plant body in general terms and obtain an overview of its structure and development. In subsequent chapters we shall consider in more detail many aspects of plant structure and development as well as of function and evolution.

Some aspects of the shoot system of the vascular plant

The vascular plant consists of an aerial shoot system and, typically, a subterranean root system (Fig. 2.4). The **shoot system** consists of a main axis that bears lateral branches. Leaves may be borne on both the main axis and lateral branches in plants that complete their life cycle in one growing season, but in those that live for several to many years, leaves are usually found only on the parts of lateral branches that have developed in the past year or the last several years. For example, in deciduous plants (e.g., many woody angiosperms), leaves develop only on the most distal segments of the laterals, i.e., the parts produced during the most recent growing season (Fig. 2.5) and will fall from the plant at the end of the same growing season. In most conifers and other

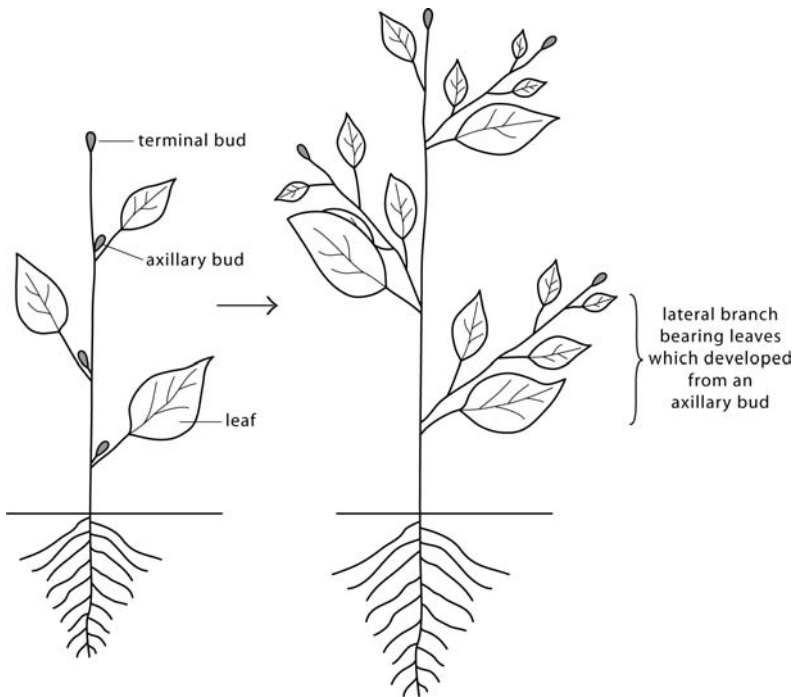


Figure 2.4 Diagrams of two stages in the development of an annual vascular plant.

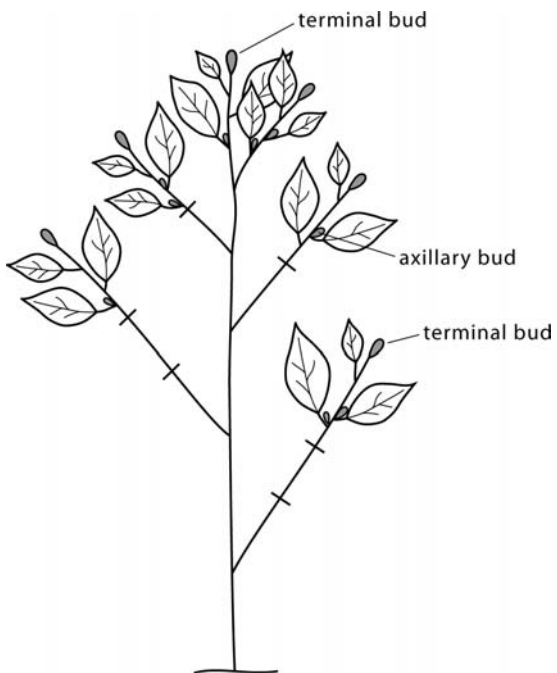
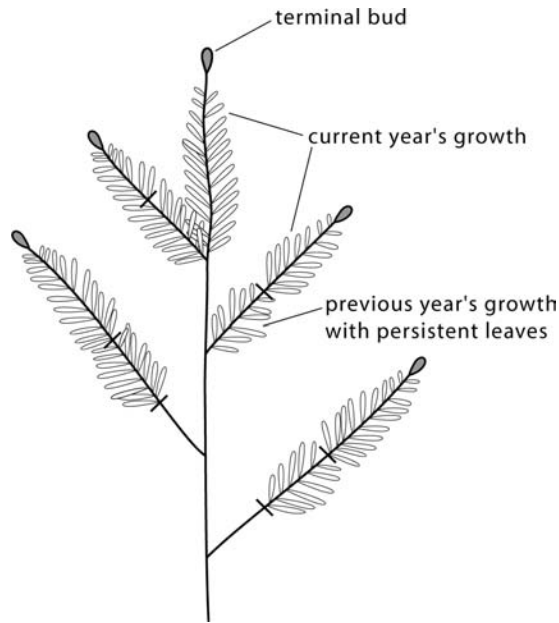


Figure 2.5 Diagram of the shoot of a deciduous, woody perennial with leaves and axillary buds, on terminal twigs only, produced during the current growing season. Each bar (at right angles to a lateral branch) indicates the previous site of a terminal bud.

Figure 2.6 Diagram of an “evergreen” conifer shoot with leaves on the current and previous year’s growth. The bars at right angles to the lateral branches indicate previous positions of terminal buds.



evergreens, however, leaves may stay on the plant for several years, but the youngest, i.e., the most recently developed leaves, are borne on twigs produced in the current or most recent past growing season (Fig. 2.6).

A unique feature of vascular plants is the presence of buds which occur at the tips of the main and lateral branches and, in gymnosperms and angiosperms, commonly (but not always in gymnosperms) in the **axils of leaves** (the angle between leaves and the stem to which they are attached) (Fig. 2.5). A **bud** consists of an apical meristem encloded by protective bud scales (modified leaves) (Fig. 2.7). A **meristem** is a localized region of cells that is characterized by active cell division, the ultimate result of which is the addition of new cells, tissues, and organs (such as leaves) to the plant body. It is, thus, the structural feature that imparts to plants their distinctive serial mode of development – so different from that of animals.

In contrast to animals whose development can be characterized as determinate, plant development, by virtue of the presence of apical meristems, is **indeterminate**. That is, plants have the ability to add new cells and tissues to the plant body during each growing season as long as the plant lives. This makes possible the enormous size of very old trees such as the redwoods of California or the very large deciduous trees of virgin hardwood forests of northeastern USA. The development of some parts of plants such as leaves and components of flowers, however, is **determinate** in that their form, and to some extent, size are genetically predetermined. Once these plant parts have completed their development, they do not grow further no matter how long they remain on the plant as functional entities.

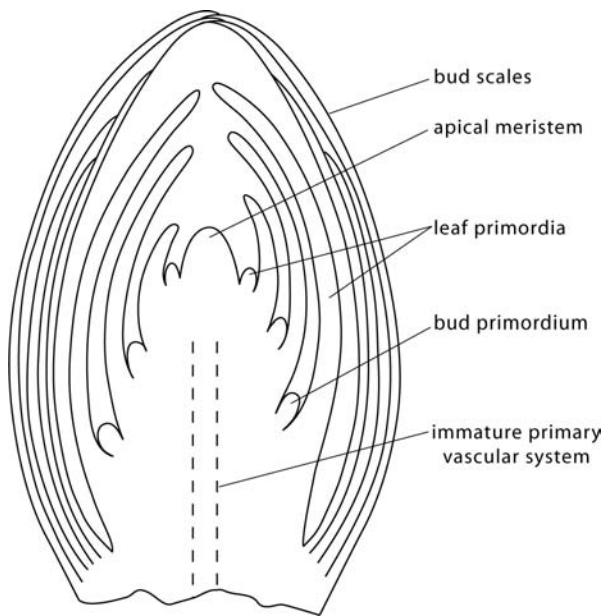
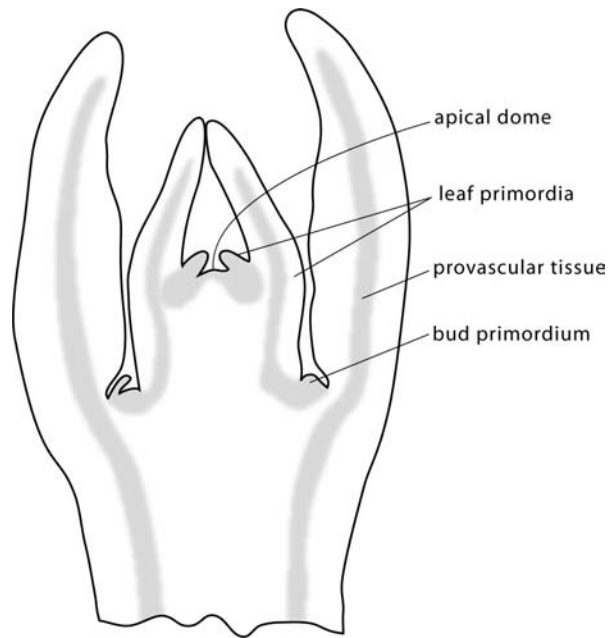


Figure 2.7 Diagram of a terminal bud as viewed in a median longitudinal section. Space is left between foliar components for clarity.

Apical meristems

We shall now look at the gross internal structure of buds and, in particular, consider the activity of apical meristems and some aspects of the differentiation of cells and tissues resulting from this activity. The apical meristem of the shoot is a dome-shaped structure that comprises the apical-most region of the main and lateral axes. In the root, the apical meristem is covered by the root cap. In this chapter we shall consider only the apical meristem of the shoot, deferring discussion of the apical meristem of the root to [Chapter 16](#). In the shoot, small protuberances, the **leaf primordia**, from which leaves will develop, form around the base on the periphery of the apical meristem ([Fig. 2.8](#)). **Bud primordia** develop in the axils of older leaf primordia. Because of its permanently apical position, cells, tissues, and structures such as leaf and bud primordia close to the apical meristem are younger, and consequently, less mature than those farther away. It is apparent, therefore, that the direction in which differentiation proceeds is **acropetal**, that is, from the more mature, proximal part of the shoot toward the less mature, distal region near the apical meristem. In other words, cells, tissues, and lateral appendages (e.g., leaves) become progressively more mature in the direction of the apical meristem which is actively producing new cells that are added on to those produced earlier. If this concept of acropetal development is difficult for you, consider this analogy. In building a wall a bricklayer starts at the base, adding layer after layer of bricks until the wall is completed. The mortar between the first two layers of bricks at the base of the wall sets (i.e., hardens or “differentiates”) first. That between subsequent layers sets later and later until finally that between the last two layers at the top of the walls has set.

Figure 2.8 Diagram of a shoot apex as viewed in a median longitudinal section.



In other words, the mortar in the wall can be thought of as having differentiated sequentially from bottom to top, that is, acropetally.

Cell derivatives of the apical meristem, as well as of other meristems, initially resemble closely cells of the meristem. Plant tissues are composed of many different types of cells, and the cells produced by meristems must, therefore, grow and differentiate during development, ultimately attaining the specific characteristics of particular, mature, functional cells (Fig. 2.9).

Before proceeding further, we must distinguish between the processes of development and differentiation. **Development** consists of the integrated processes of growth, differentiation, and morphogenesis. Growth results in increase in size, and during growth, differentiation occurs. **Differentiation** is the process whereby cells, tissues, or organs achieve their distinctive, mature morphological and physiological characteristics during gradual change from their state as single or groups of meristematic derivatives. **Morphogenesis** is the achievement of form during development. Although commonly applied to the whole plant it, like differentiation, can also be applied to the various components of the plant body. Morphogenesis and differentiation are highly integrated processes, but they do not necessarily have a controlling influence on each other. They are probably controlled separately by different genes or gene complexes.

Now in order to more fully understand the process of differentiation, let us consider the differentiation through time of a single cell derivative of an apical meristem. From the time it is first produced it begins to grow, to some degree in diameter, but primarily in length, with its long axis paralleling the long axis of the stem, root, or branch in which it resides. In other words, the derivative grows longitudinally.

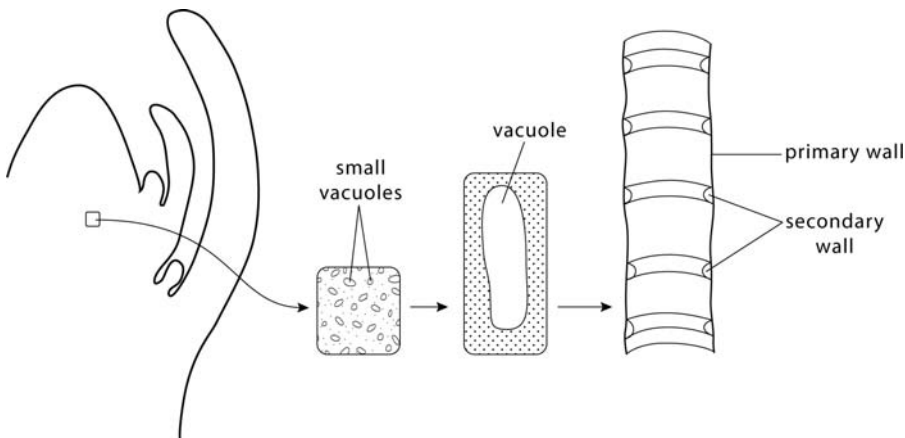
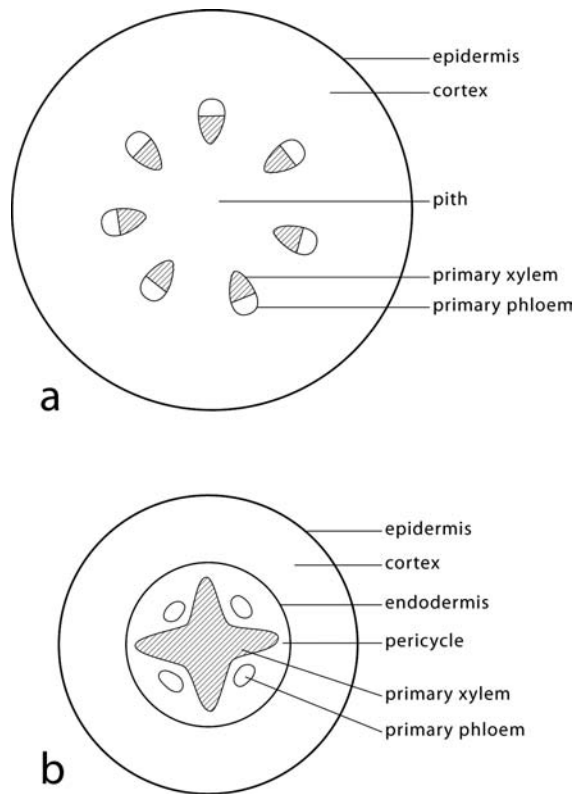


Figure 2.9 Diagrammatic representation of growth and differentiation of a type of water-conducting cell produced by the apical meristem. Note that growth consists primarily of increase in length. Very small vacuoles fuse to form a large central vacuole resulting in the peripheral location of the cytoplasm. Prior to death of the protoplast, secondary wall is deposited in the form of rings.

(Although this is a common pattern of cell growth in plants, some cells grow almost equally in diameter and length.) It is generally agreed that the motive force for cell growth is turgor pressure within the cell. In order for the protoplast to grow, the cell wall must also grow, concurrently, by increasing in surface area. (Growth of the cell wall, which includes synthesis of the chemical and structural components of which it is composed, is an area of great interest and active research, and will be considered in detail later.) Changes that occur in the cell protoplast during growth and differentiation include the fusion of small vacuoles to form larger vacuoles, and increase in the volume of cytoplasm within which develop various cell organelles such as mitochondria, plastids, and Golgi bodies as well as endoplasmic reticulum, microtubules, and microfilaments. Eventually, the total complement of originally small vacuoles will have fused into a single central vacuole forcing the cytoplasm with its organelles, filamentous structures and nucleus into a peripheral position (Fig. 2.9). Other dramatic changes in cells during differentiation are exemplified by conducting cells in the phloem and xylem. In the phloem the organelles and even the nucleus of a differentiating conducting cell become modified or may even degenerate prior to achievement of functional maturity by the cell. Concurrently, the end walls become highly perforate, which facilitates the transport of photosynthate, hormones, and other chemical substances from cell to cell. The protoplasts in conducting cells of the xylem actually die, but prior to death the cell walls become highly modified. The walls increase in thickness, often differentially, resulting in structural features that strengthen the cells, and the walls may become pitted. They may also become heavily impregnated with lignin, a compound that increases their tensile strength. The absence of a protoplast and the

Figure 2.10 (a) Primary tissue regions of a dicotyledon stem shown in transverse section. (b) Primary tissue regions of a seed plant root. Note the ribbed primary xylem column, and the separate bundles of primary phloem.



modifications of the cell walls facilitate the transport of water and dissolved mineral nutrients. In later chapters we shall consider in detail the structural changes of conducting cells in the phloem and xylem and the relationship of these to the processes of transport.

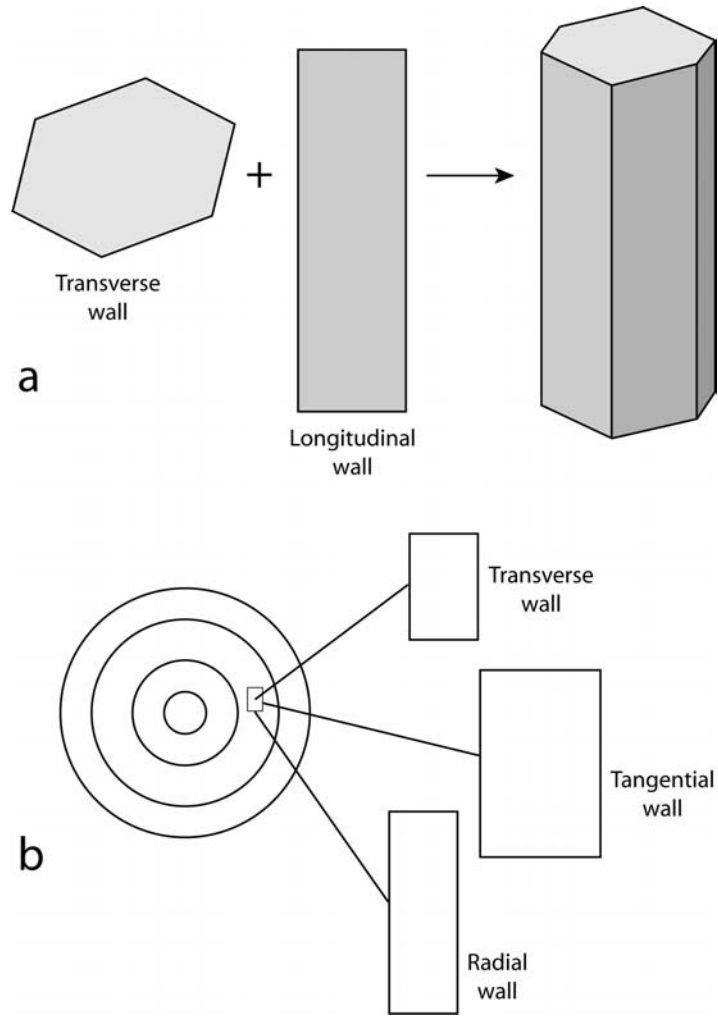
A major activity of apical meristems is the production of **primary tissues** in stems and roots, resulting in an increase in the length and, to a lesser extent, an increase in thickness (diameter) of these axes. Among the primary tissues produced are the primary phloem and primary xylem which, in seed plants, comprise vascular bundles, and the parenchyma, collenchyma, and sclerenchyma of which the pith and cortex are composed (Fig. 2.10). Meristematic activity in shoot systems also results in the production of leaf primordia that define **nodes**, sites of attachments of leaves, and **internodes**, segments of the stem between nodes. Close to the apical meristem, internodes are very short, but increase in length with distance from it. In most vascular plants internodal elongation results primarily from the growth of cells produced earlier by the apical meristem and subjacent tissues. As meristematic activity continues, the internodal tissues differentiate largely acropetally. In some plants, e.g., *Equisetum* (horsetail) and grasses, however, differentiation in internodes is primarily **basipetal** (i.e., tissues differentiate progressively toward the base). We shall consider development in these plants in some detail in Chapter 5.

Primary tissue regions of the stem and root

As a result of the activity of apical meristems, and subsequent differentiation of cells and tissues, axes of the shoot and root systems are composed of several distinct **tissue regions** (Fig. 2.10). In the stem and the root there may be a central pith surrounded by vascular tissue (xylem and phloem) variously arranged. The vascular tissue may be continuous, or comprised of vascular bundles that may or may not be interconnected. The central region in some stems and most roots is a solid column of vascular tissue and, thus, there is no pith (Fig. 2.10b). To the exterior of the region of vascular tissue are the cortex and epidermis. In some stems a single-layered region called the endodermis comprises the innermost layer of the cortex. It bounds the pericycle, a tissue region between itself and the vascular tissue. The pericycle is usually recognized only in axes that also have an endodermis which defines its outer limit. The pericycle and endodermis are common in roots (Fig. 2.10b) as well as in the stems of plants that live in aquatic environments.

Each tissue region may be composed of several **simple tissues**, containing a single type of cell, or a **complex tissue**, comprising several types of cells. As we now know, tissues derived from the apical meristems are **primary tissues**, whereas those derived from lateral meristems are **secondary tissues**. In order to better understand the nature of these tissues we must be able to visualize their component cells in three dimensions. Different types of cells have evolved as adaptations to the terrestrial environment in which most vascular plants live and have become specialized for the performance of one or more functions. Some cells function largely in the synthesis of important compounds or in other metabolic processes such as respiration, digestion, etc. Others function solely or largely in transport (or conduction) of substances whereas some function mainly in providing mechanical support. Thus there are many different types of cells with different morphologies that we must understand. Since all of these types often occur together in complex tissues this poses a difficult, but not insoluble problem. There are two ways in which we can comprehend the morphology of a particular cell in three dimensions. For example, we can macerate a piece of tissue by immersing it in an acid solution that dissolves the intercellular cementing material which holds cells together in tissues. Thus separated, we can observe the individual cells. We may, however, wish to comprehend the three-dimensional form of cells in intact tissues such as sections. To do this we must learn to think in three dimensions on the basis of sections of cells in two dimensions. If we observe the cell in question in both transverse and longitudinal views, we can then combine these, mentally, to obtain a three-dimensional conception of the cell (Fig. 2.11a). To understand the detailed morphology of a cell type we will usually have to observe the cell in transverse view as well as in two longitudinal views: radial and tangential (Fig. 2.11b). Transverse, radial, and tangential views of cells can be

Figure 2.11 (a) With knowledge of the shape of a transverse wall and a longitudinal wall of a cell, one can envision its three-dimensional form. (b) If a wall of a cell is parallel to a transverse plane it is called a transverse wall; if parallel to a radial plane it is called a radial wall; if parallel to a tangential plane, it is called a tangential wall.



observed in transverse, radial, and tangential sections (Fig. 2.12). A **transverse section** is a thin sheet of tissue cut at right angles to the long axis of a stem or root, a **radial section** is one cut along a radius of the circle formed by the exterior boundary of the axis, whereas a **tangential section** is one cut on a tangent perpendicular to the radius (Fig. 2.12). One can refer to the walls of cells that lie in the same plane as radial or tangential sections as radial or tangential walls. Likewise, end walls of cells may be called transverse walls when they occur in a plane parallel to a transverse section.

Let us now consider the tissues of the pith and cortex. Three simple tissues, parenchyma, collenchyma, and sclerenchyma, singly, in combinations of two, or all three, may comprise either or both of these tissue regions. **Parenchyma** is thought of as the ground tissue of an axis since it occurs in greatest abundance and is the tissue in which the vascular tissues are embedded. Parenchyma cells (Fig. 2.13a, b) may be variably isodiametric in both the pith and the cortex, but

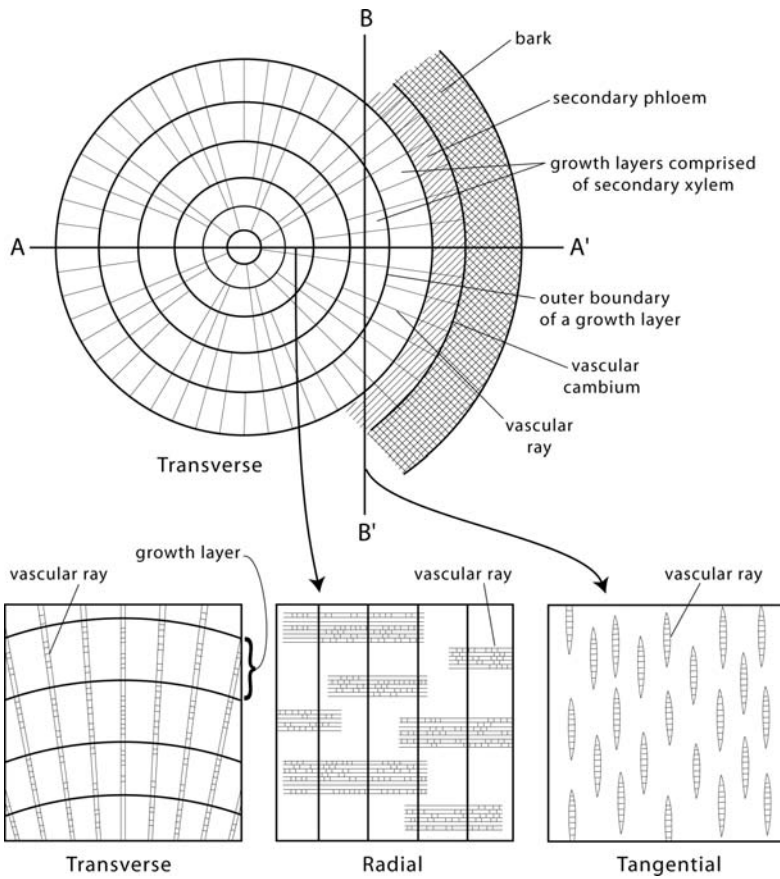


Figure 2.12 Planes of section through secondary xylem. Any section cut parallel to the plane of the page is a transverse section. Note that vascular rays cross growth layers at right angles. Any section cut parallel to a radius of the circle formed by any growth layer is a radial section as, for example, a section cut parallel to plane A–A'. In a radial section, rays appear in side view, crossing growth layers at right angles. Any section cut parallel to a tangent to any imaginary circle parallel to the boundary of a growth layer is a tangential section as, for example, a section cut parallel to plane B–B'. In a tangential section vascular rays appear in end view.

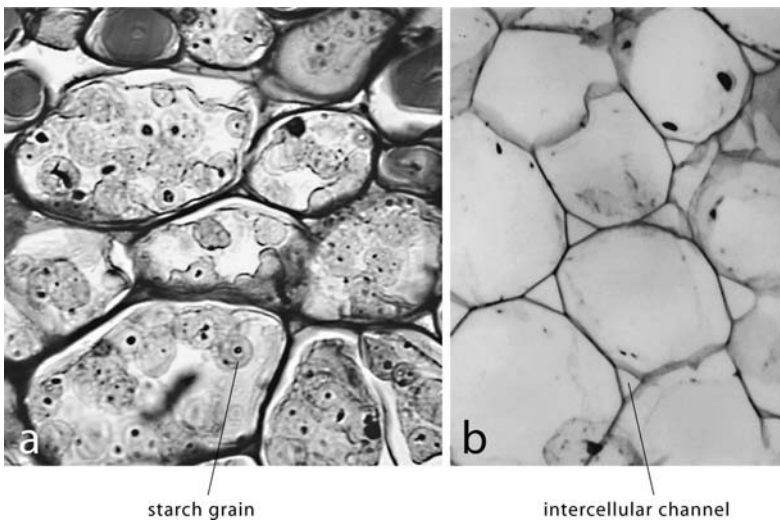
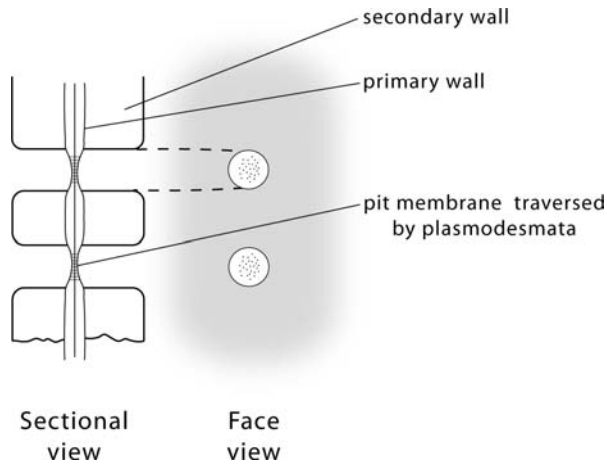


Figure 2.13 (a) Starch grains in parenchyma cells of the cortex. (b) Parenchyma tissue in the pith containing conspicuous intercellular channels. Magnification $\times 408$.

Figure 2.14 Simple pit-pairs in sectional and face views with plasmodesmata connecting the protoplasts of contiguous cells.



are more commonly longitudinally elongate in the cortex. They have relatively thin walls that almost always consist of both primary and secondary wall layers. Wall layers are continuous except in the regions of **simple pits**, circular to irregularly shaped regions lacking secondary wall material. These simple pits usually occur opposite each other, forming **pit-pairs** in the walls of contiguous cells (Fig. 2.14). Multiple **plasmodesmata** (specialized strands of endoplasmic reticulum) form interconnections with the protoplasts of adjacent living cells through the primary walls of simple pit-pairs. Plasmodesmata are not restricted to pit-pairs, however, and may traverse other regions of the wall as well. These interconnections make possible communication (i.e., the transport of chemical compounds) between cell protoplasts which, collectively, comprise the **symplast**. The transport of water and inorganic solvents can occur solely through the cell walls which, collectively, comprise the **apoplast**. Long-distance transport, however, occurs primarily through the **lumina** (the cavities enclosed by cell walls) of non-living cells such as tracheids and vessel members. Some workers include the lumina of these cells as components of the apoplast.

Various metabolic processes occur in parenchyma tissues including the synthesis of hormones, enzymes, pigments, essential oils, toxic substances, etc. One of the processes of synthesis most important to both the plant and to animals including humans, is photosynthesis which produces glucose, the basic food substance for all living beings. Another equally important metabolic process is respiration which provides the source of energy utilized by the plant in carrying out its various activities. Other important processes are the conversion of glucose to starch, the form in which it is stored in parenchyma tissues, and the reverse process of digestion of starch which makes glucose available for use by the plant. Another highly important compound composed of glucose molecules is **cellulose** which is the primary structural material of cell walls.

A system of **intercellular channels** (Figs 2.13b, 2.15), often referred to as gas spaces, characterizes the parenchyma tissue of plants. The intercellular channels, commonly connected to the outside atmosphere

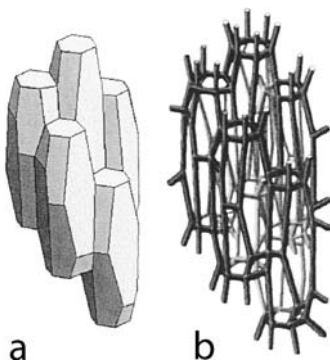


Figure 2.15 Diagram of the system of intercellular channels (b) between parenchyma cells (a).

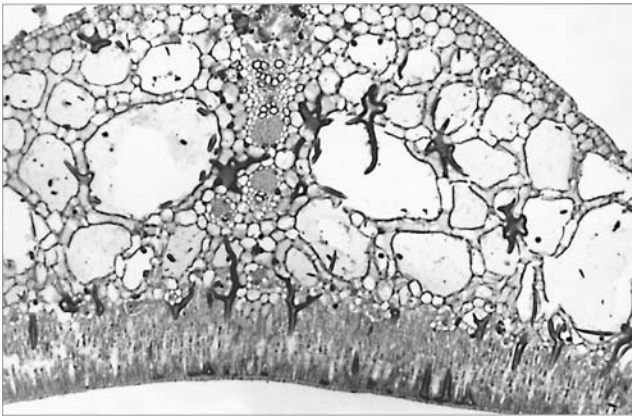


Figure 2.16 Large gas-filled spaces in the leaf of *Nymphaea* (water lily), an aquatic dicotyledon. Note, also, the large astroscleroids. Magnification $\times 65$.

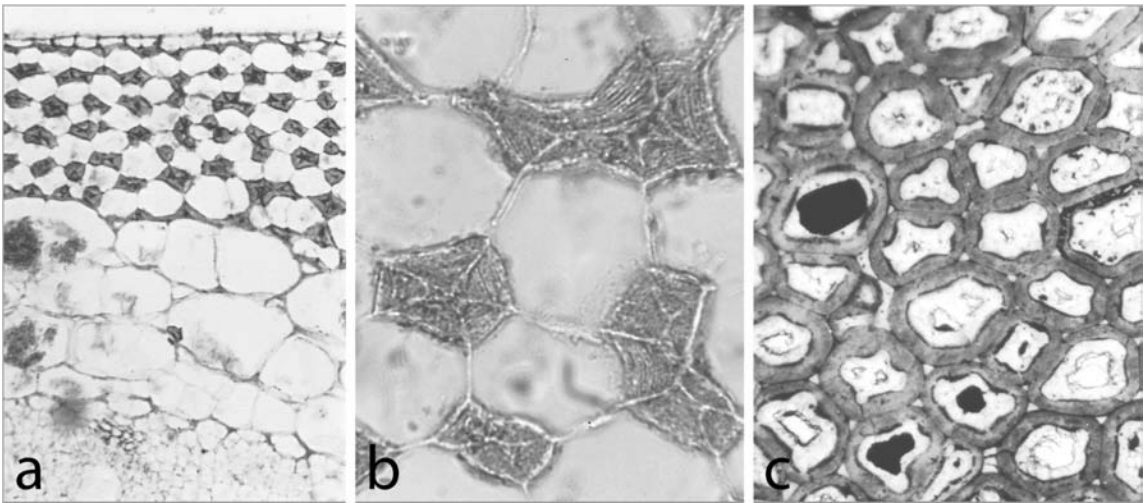


Figure 2.17 Collenchyma. (a) Angular collenchyma in the outer cortex just beneath the epidermis with thickened walls in the corners of the cells. Magnification $\times 18$. (b) Enlargement of a part of (a) showing the lamellate nature of the thickened regions of the cell walls. Magnification $\times 1150$. (c) Lamellar collenchyma with regions of thickened walls between cell corners. Magnification $\times 220$.

through stomata (or lenticels in older stems), comprise an extensive system in the pith and cortex in stems, roots, and some rhizomes as well as in leaves and some fruits. They are especially well developed in roots and rhizomes in aquatic plants or plants that live in wet soils. The gas-filled spaces vary from the narrow channels between cells to the large, irregular spaces in the mesophyll of leaves and in the aerenchyma of aquatic plants (Fig. 2.16) (Raven, 1996; Prat *et al.*, 1997). Intercellular channels are significant in providing aeration, i.e., facilitating an interchange of O_2 and CO_2 in this tissue which is the site of both photosynthesis (which utilizes CO_2 and produces O_2) and respiration (which utilizes O_2 and produces CO_2). In aquatic plants the system of gas-filled intercellular channels is also important in providing buoyancy.

Collenchyma, like parenchyma, is a tissue in which the various metabolic processes mentioned above also occur. Unlike parenchyma, however, collenchyma forms only a small part of the pith or cortex. In fact, it is only rarely found in the pith, but occurs commonly in the cortex, especially in the outer cortex of herbaceous stems (Fig. 2.17). It is also an important component of leaves and some flower parts. In the stem it often occurs as a continuous layer or as longitudinal ribs in

Figure 2.18 Sclereids of diverse forms. (a, b) Brachysclereids (stone cells) from the fruit of *Pyrus* (pear). (c, d) Sclereids from the stem cortex of *Hoya* (wax plant), in sectional (c) and surface (d) views. (e, f) Macrosclereids from the endocarp of *Malus* (apple). (g) Columnar sclereid with branched ends from the palisade mesophyll of *Hakea*. (h, i) Sclereids of variable form from the petiole of *Camellia*. (j) An astrosclereid from the stem cortex of *Trochodendron*. (k) An extensive layer of macrosclereids from the epidermis of a clove scale of *Allium sativum* (garlic). From Esau (1977). Used by permission of John Wiley and Sons, Inc.

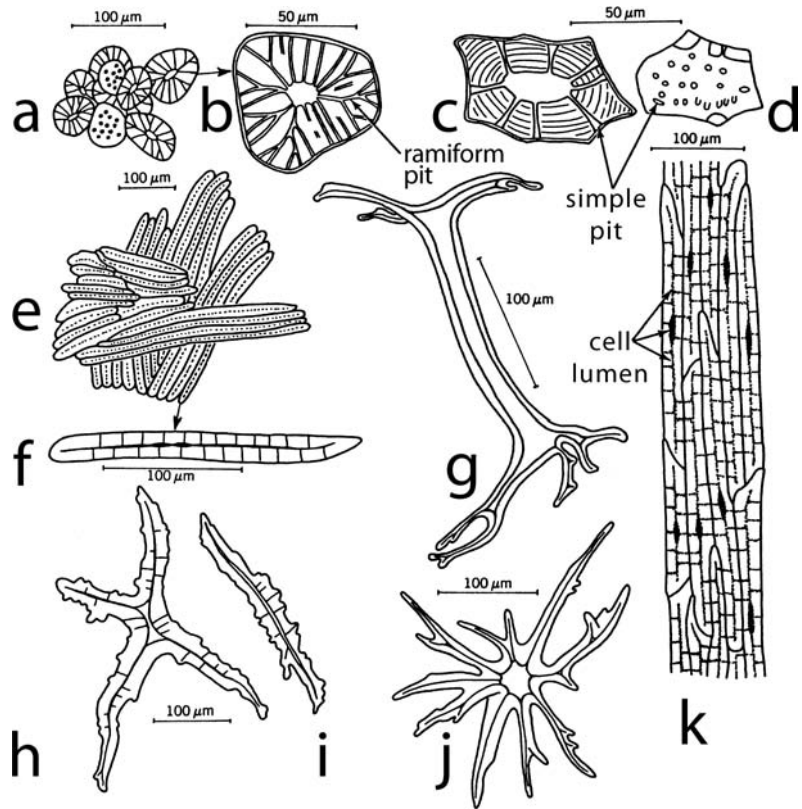


Figure 2.19 A large sclereid from the leaf of *Nymphaea*. Note the thin cell wall containing numerous simple pits. Sclereids of this type often retain a living protoplast. Magnification $\times 370$.

the outermost cortex. In leaves and flower parts it often accompanies major vascular bundles. Wherever it occurs it provides a supporting function.

Collenchyma cells are characterized by relatively thick, but unevenly thickened and un lignified primary walls. The walls are usually highly hydrated, and often conspicuously lamellate (Fig. 2.17b). In the most common type of collenchyma the greatest wall thickening occurs in the corners of the longitudinally elongate cells which are polygonal in transverse shape. Collenchyma of this type is called **angular collenchyma** (Fig. 2.17a, b) if there are no, or only very small, intercellular channels in the tissue, or **lacunar collenchyma** if the tissue contains conspicuous intercellular channels. In a third type of collenchyma, however, the regions of greatest wall thickening occur between the corners. This type is called **lamellar collenchyma** (Fig. 2.17c).

Sclerenchyma is the major supporting tissue in primary tissue regions and consists of either fibers or sclereids. **Sclereids** are more or less isodiametric, but of highly variable form (Fig. 2.18), and have relatively thin to very thick lignified walls containing, in very thick walls, simple pits that are canal-like and often branched (ramiform). Many sclereids, especially those with relatively thin walls, have living protoplasts (Fig. 2.19). Sclereids with different shapes are given different

names (Fig. 2.18). **Brachysclereids**, a common type of ovoid to somewhat irregular shape, and often called “stone cells,” are common in the flesh of fruits occurring singly or in clusters, as in pear. In fruits with stony endocarps, e.g., peaches, almonds, cherries, etc., they may be the sole cell type comprising the stony layer. They also occur singly or clustered in the pith and/or cortex of some stems. **Macrosclereids** are columnar or rod-shaped and are common components of the epidermis of seeds and the endocarp of fruits. **Osteosclereids** are bone-shaped and are common in leaves and seed coats. **Astrosclereids** are irregularly star-shaped with elongate, relatively thin-walled processes extending from a central region. They are common in the leaves of many tropical dicotyledons and in the stems and leaves of some aquatic plants (Fig. 2.16). **Trichosclereids** are very slender, hair-like, and sparsely branched. They may reach lengths of several millimeters and are common in the stems and roots of aquatic plants.

Fibers that occur in primary tissues of roots and stems are commonly very elongate cells with relatively thick, lignified walls containing simple pits (Fig. 2.20). They may comprise separate bundles or bands, often in the peripheral regions of stems, sometimes in the inner cortex (Fig. 2.21a) or, very commonly, may be associated with vascular bundles as bundle sheaths or bundle caps (Fig. 2.21b, c). Fibers serve a largely supporting function in the plant. They tend to be flexible and have great tensile strength and, thus, allow bending without breaking of plant axes. Fibers in primary tissue regions, especially those obtained from some monocots (Fig. 2.21c), are utilized commercially in the production of twine, rope, doormats, burlap, etc. Somewhat similar fibers occur in the secondary phloem, and fibers that are shorter, narrower and often thinner-walled are very common in the secondary xylem. In this book we shall restrict the term sclerenchyma fibers to those that occur in primary tissues.

We shall defer a discussion of the pericycle and endodermis until a later chapter on the root (Chapter 16). The very important single-layered tissue region, the epidermis, which comprises the outer boundary of stems, roots, and other plant organs in regions in which periderm has not formed will receive detailed treatment in Chapter 8, devoted solely to it. All other important tissues and tissue regions will also be discussed in detail in later chapters.

Vascular bundle types

Primary xylem and primary phloem, are complex tissues, comprising several distinctive cell types. In later chapters we shall consider in detail the composition, development, and functions of these tissues, but shall now consider the morphology of the different types of vascular bundles in which they occur in seed plants.

Vascular bundles vary in morphology largely on the basis of the topographic arrangement of their constituent primary xylem and primary phloem. The vascular tissues are, typically, though not always,

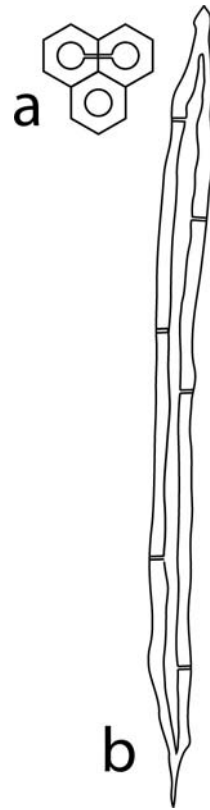


Figure 2.20 (a) Sclerenchyma fibers in transverse view, showing a simple pit-pair. (b) Sclerenchyma fiber in longitudinal view.