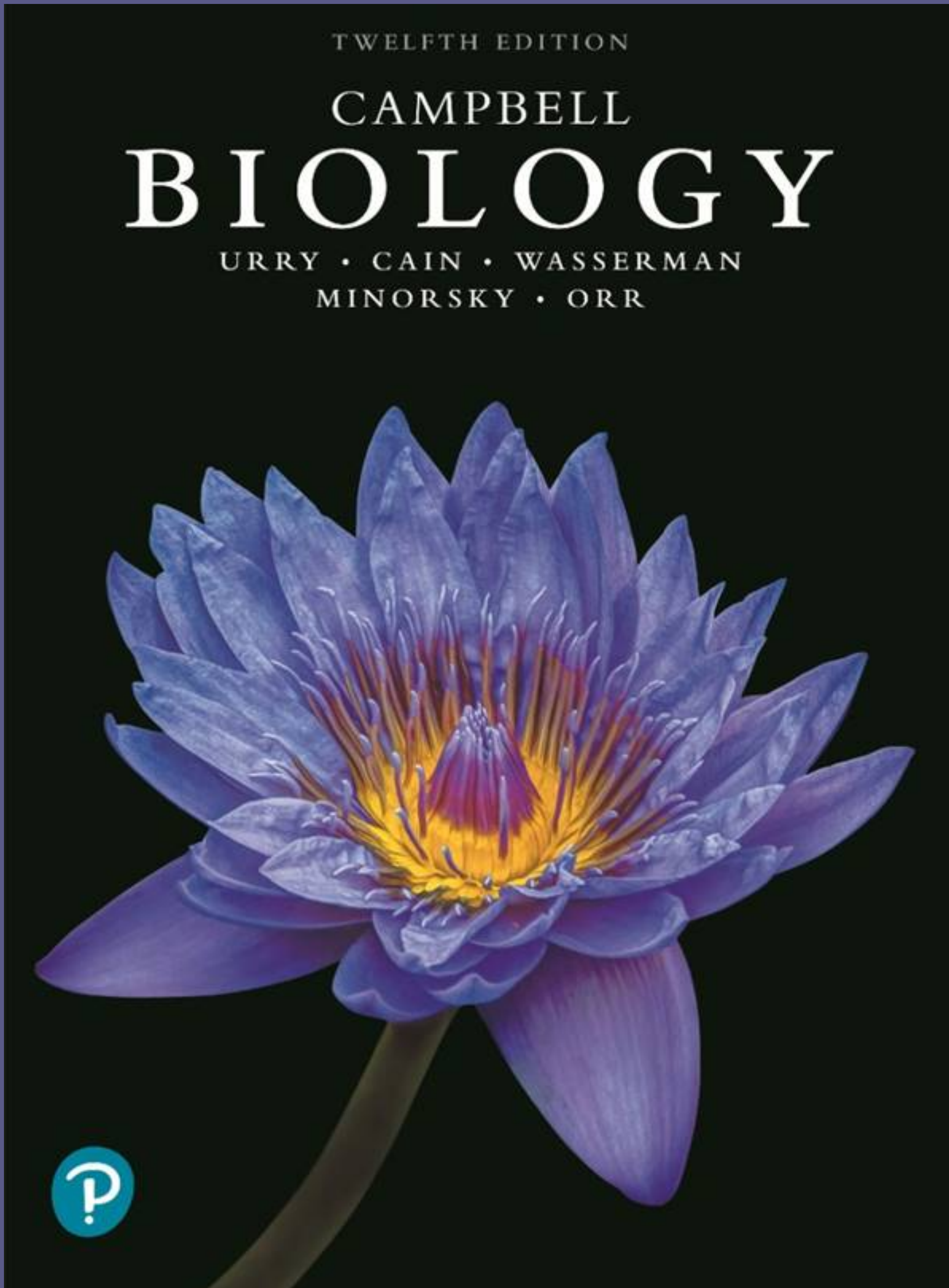


Chapter 35

Vascular Plant Structure, Growth, and Development

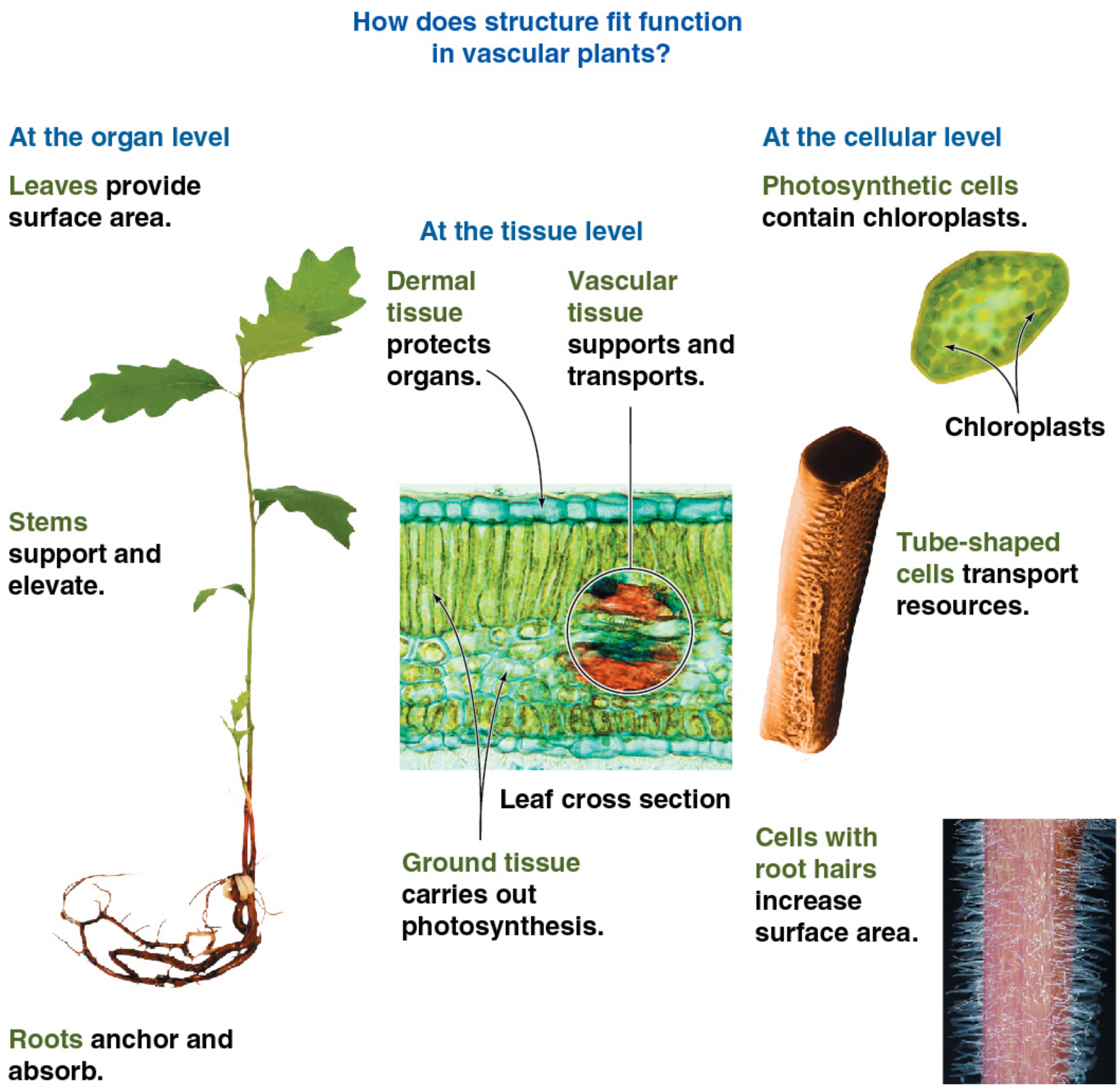
Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

How does structure fit function in vascular plants?

- Natural selection has molded plant structure to support function at the organ, tissue, and cellular levels

Figure 35.1

Figure 35.1


How does structure fit function in vascular plants?
At the organ level
Leaves provide surface area.
Stems support and elevate.
Roots anchor and absorb.
At the tissue level
Dermal tissue protects organs.
Vascular tissue supports and transports.
Leaf cross section
Ground tissue carries out photosynthesis.
At the cellular level
Photosynthetic cells contain chloroplasts.
Chloroplasts
Tube-shaped cells transport resources.
Cells with root hairs increase surface area.

CONCEPT 35.1: Plants have a hierarchical organization consisting of organs, tissues, and cells

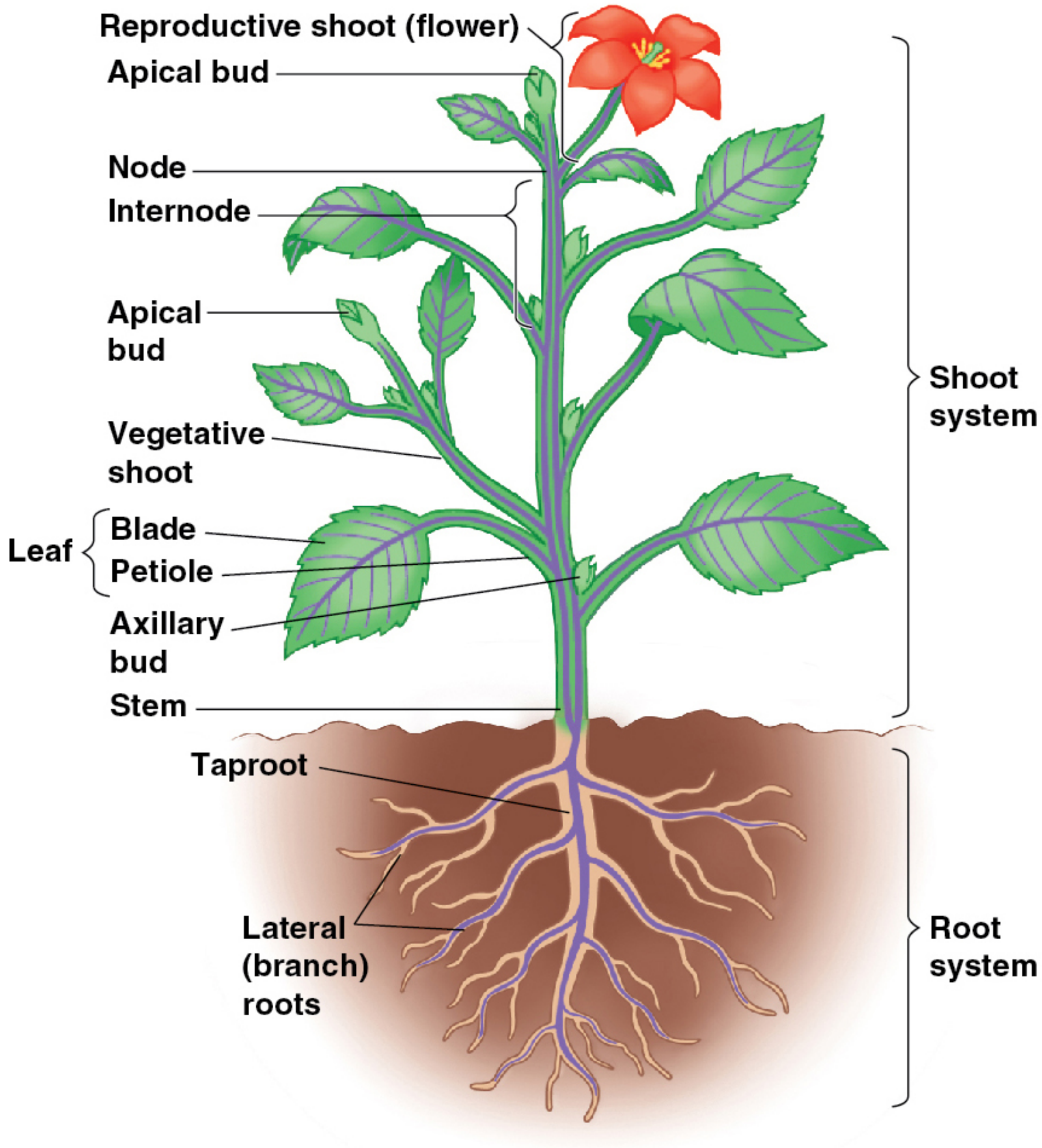
- Plant organs are composed of tissues, which in turn are composed of cells
- A **cell** is the fundamental unit of life
- A **tissue** is a group of cells consisting of one or more cell types that together perform a specialized function
- An **organ** consists of several types of tissues that together carry out particular functions

Vascular Plant Organs: Roots, Stems, and Leaves

- The basic morphology of vascular plants reflects adaptations to draw nutrients from above and below the ground
- Plants take up water and minerals from below ground
- Plants take up CO_2 and light from above ground

- Three basic organs evolved to facilitate efficient resource acquisition: roots, stems, and leaves
- They are organized into a **root system** and a **shoot system**
- The shoot system includes stems and leaves

Figure 35.2



Reproductive shoot (flower)
Apical bud
Node
Internode
Apical bud
Vegetative shoot
Leaf
Blade
Petiole
Axillary bud
Stem
Taproot
Lateral (branch) roots
Shoot system
Root system

- Roots rely on sugar produced by photosynthesis in the shoot system
- Shoots rely on water and minerals absorbed by the root system

Roots

- A **root** is an organ with important functions:
  - Anchoring the plant
  - Absorbing minerals and water
  - Storing carbohydrates
- The primary root is the first to emerge from the seed
- **Lateral roots** branch off from the primary root improving anchorage and water absorption

- Tall plants with large shoot masses generally have a taproot system
- The **taproot** usually develops from the primary root and functions in anchoring the plant in the soil
- Absorption primarily occurs in the tips of the lateral roots

- Small or trailing vascular plants generally have a fibrous root system that spreads out like a thick mat below the soil surface
- The primary root dies without forming a taproot
- Adventitious roots arise from the stem and give rise to many branching lateral roots
- Fibrous root systems prevent soil erosion by holding topsoil in place

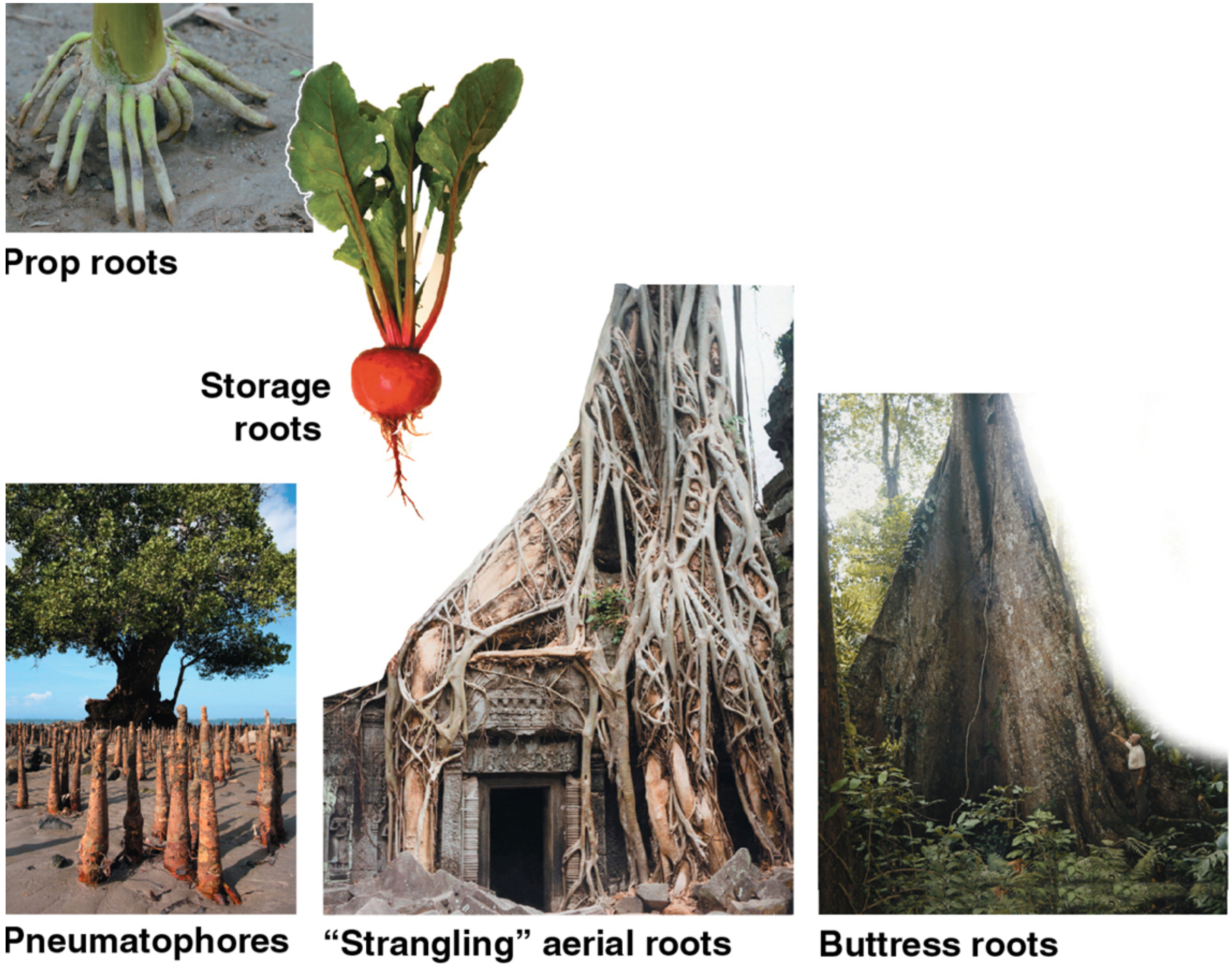
- Absorption of water and minerals typically occurs through the root hairs that grow near the root tips
- **Root hairs**, finger-like extensions of epidermal cells, increase the absorptive surface of the root
- Mycorrhizal associations, symbiotic interactions with soil fungi, increase mineral absorption in most plants

Figure 35.3

Video: Root Growth in a Radish Seedling

- Many plants have root adaptations with specialized functions

Figure 35.4


Prop roots
Storage roots
Pneumatophores
“Strangling” aerial roots
Buttress roots

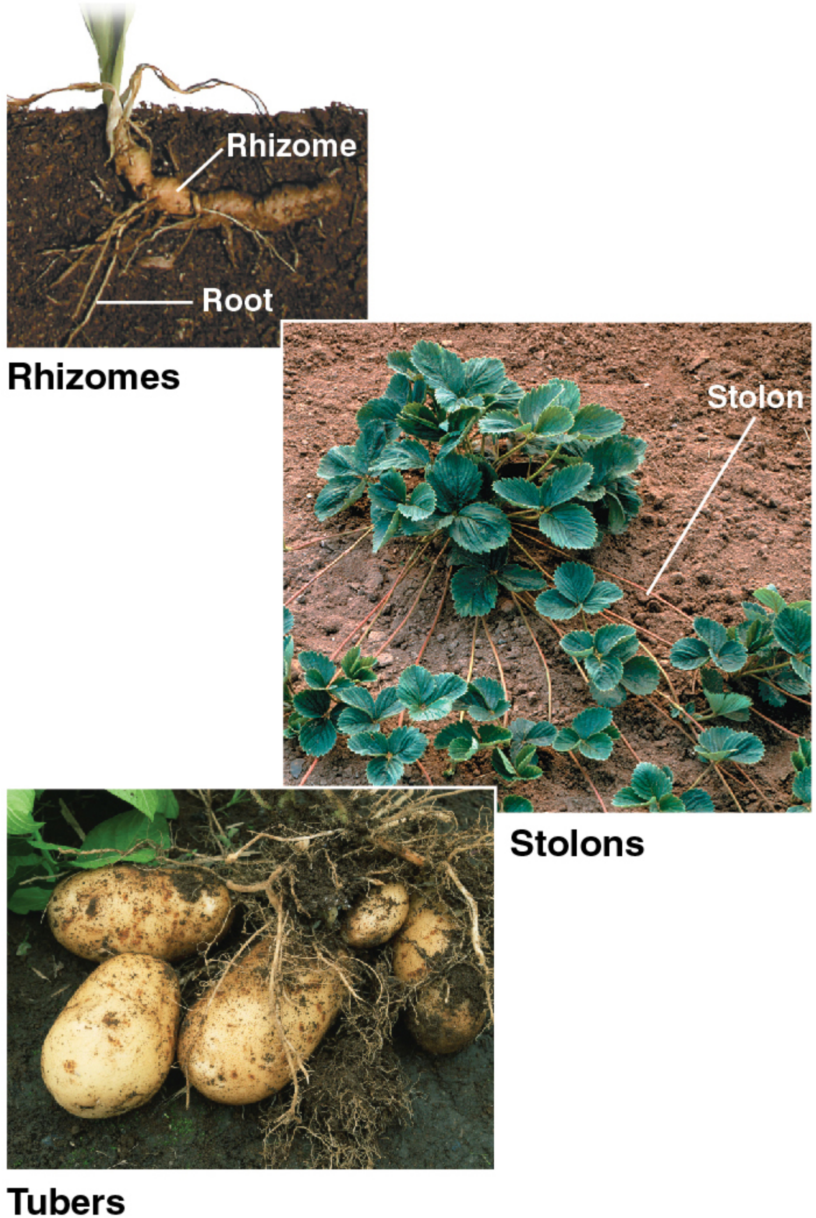
Stems

- A **stem** is a plant organ bearing leaves and buds
- Stems consist of an alternating system of nodes and internodes
- **Nodes** are the points at which leaves are attached
- **Internodes** are the stem segments between nodes

- The growing shoot tip, or **apical bud**, causes elongation of a young shoot
- An **axillary bud** is a structure that has the potential to form a lateral branch, thorn, or flower

- The primary function of the stem is to elongate and orient the shoot to maximize photosynthesis
- Many plants have modified stems that perform alternate functions

Figure 35.5

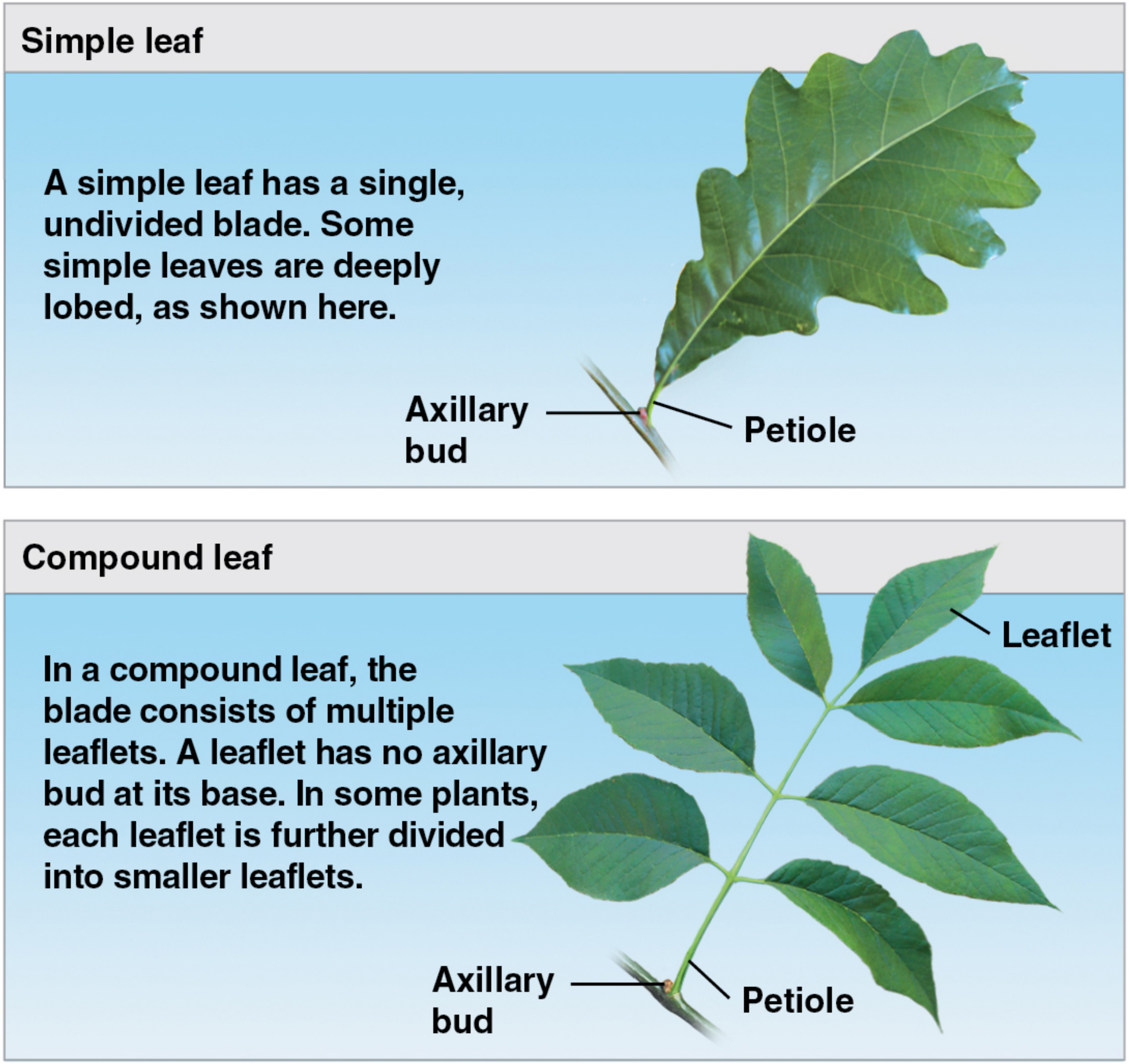


Leaves

- The **leaf** is the main photosynthetic organ of most vascular plants
- Leaves intercept light, exchange gases, dissipate heat, and defend against herbivores and pathogens
- A leaf generally consists of a flattened **blade** and a stalk, the **petiole**, which joins the leaf to the stem

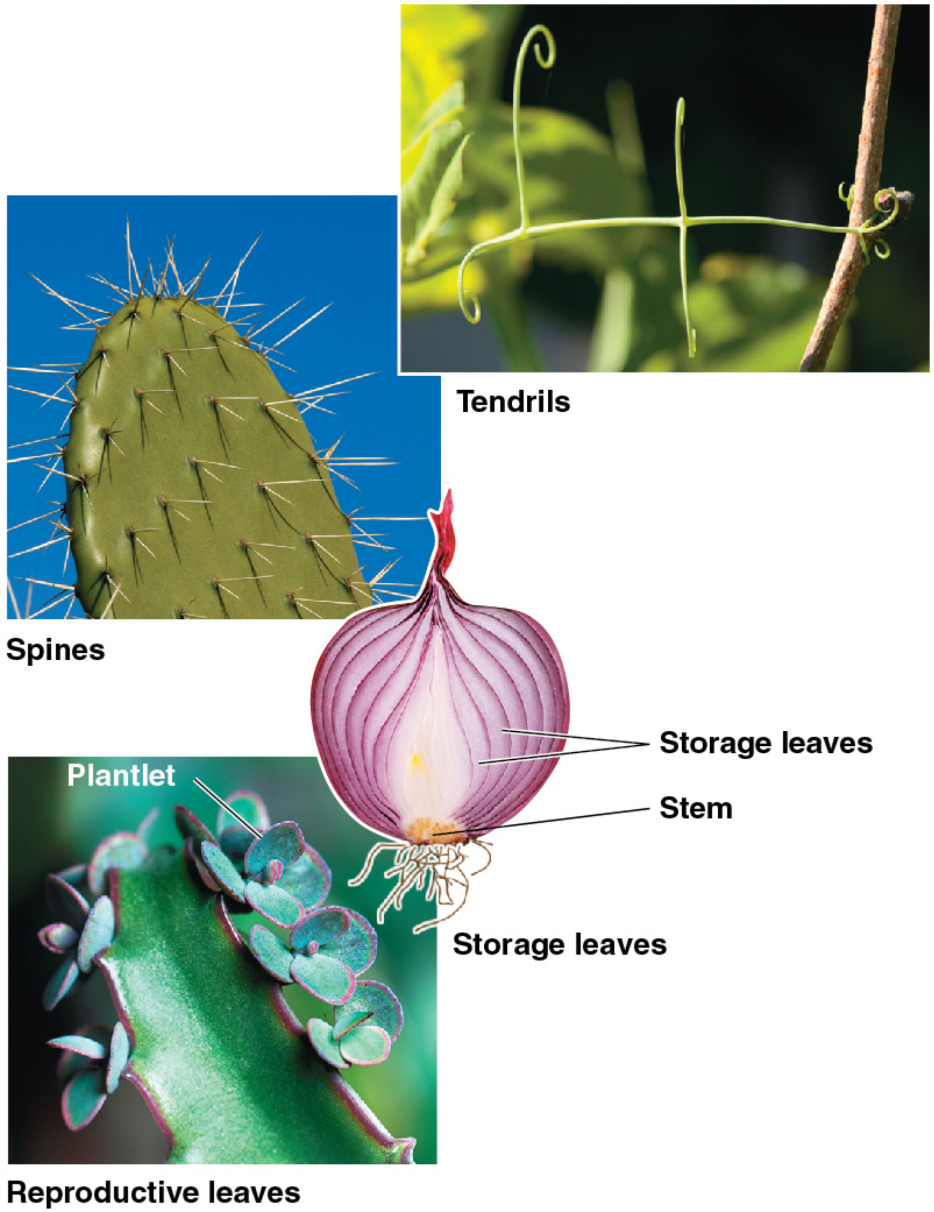
- Monocots and eudicots differ in the arrangement of **veins**, the vascular tissue of leaves
  - Most monocots have parallel veins
  - Most eudicots have branching veins
- Leaf shape, arrangement of veins, and spatial pattern of leaves can help with plant identification
- Leaf shape may be simple or compound

Figure 35.6


Simple leaf
A simple leaf has a single, undivided blade. Some simple leaves are deeply lobed, as shown here.
Axillary bud
Petiole
Compound leaf
In a compound leaf, the blade consists of multiple leaflets. A leaflet has no axillary bud at its base. In some plants, each leaflet is further divided into smaller leaflets.
Leaflet
Axillary bud
Petiole

- Most leaves are specialized for photosynthesis
- Some plant species have evolved modified leaves that serve additional functions

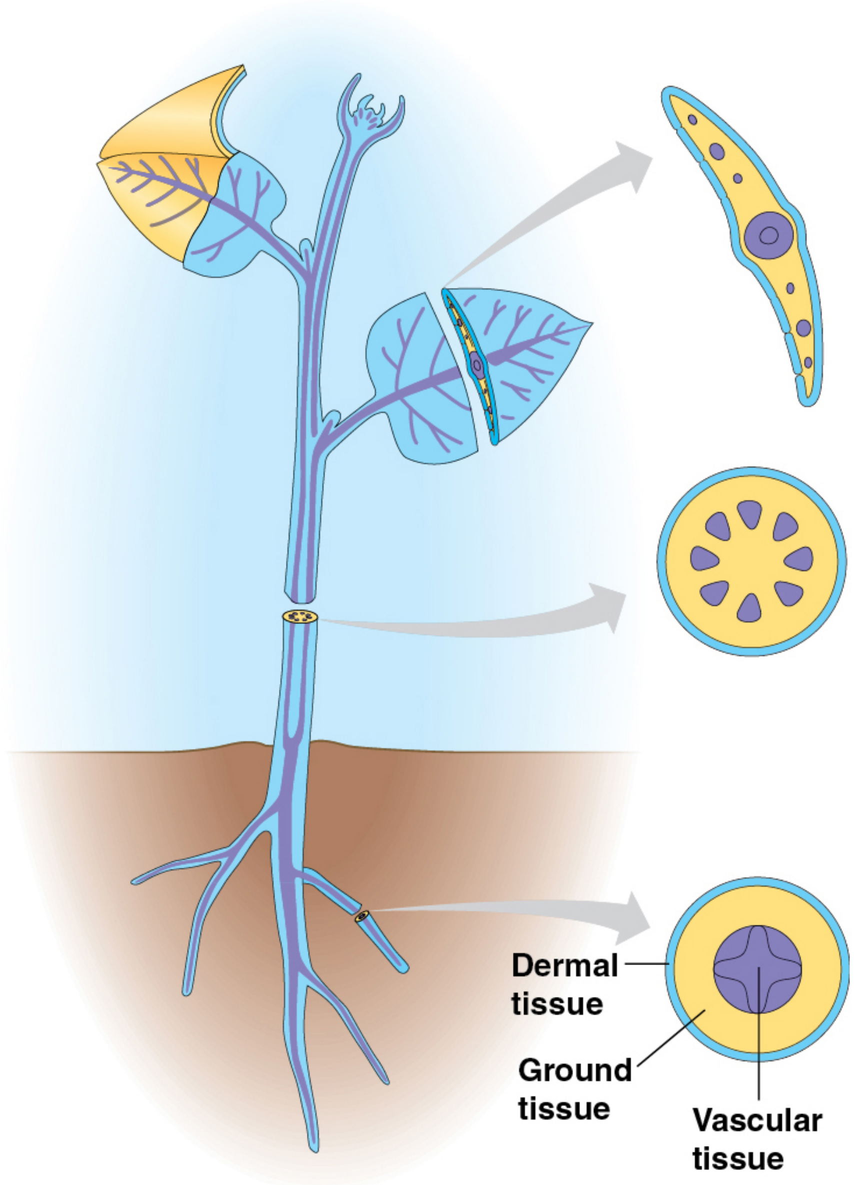
Figure 35.7


Tendrils
Spines
Storage leaves
Stem
Plantlet
Storage leaves
Reproductive leaves

Dermal, Vascular, and Ground Tissues

- Roots, stems, and leaves are composed of three tissue types: dermal, vascular, and ground tissues
- Each of these tissue types forms a **tissue system** that is continuous throughout the plant
- The characteristics of the tissues and their spatial relationships vary in different organs

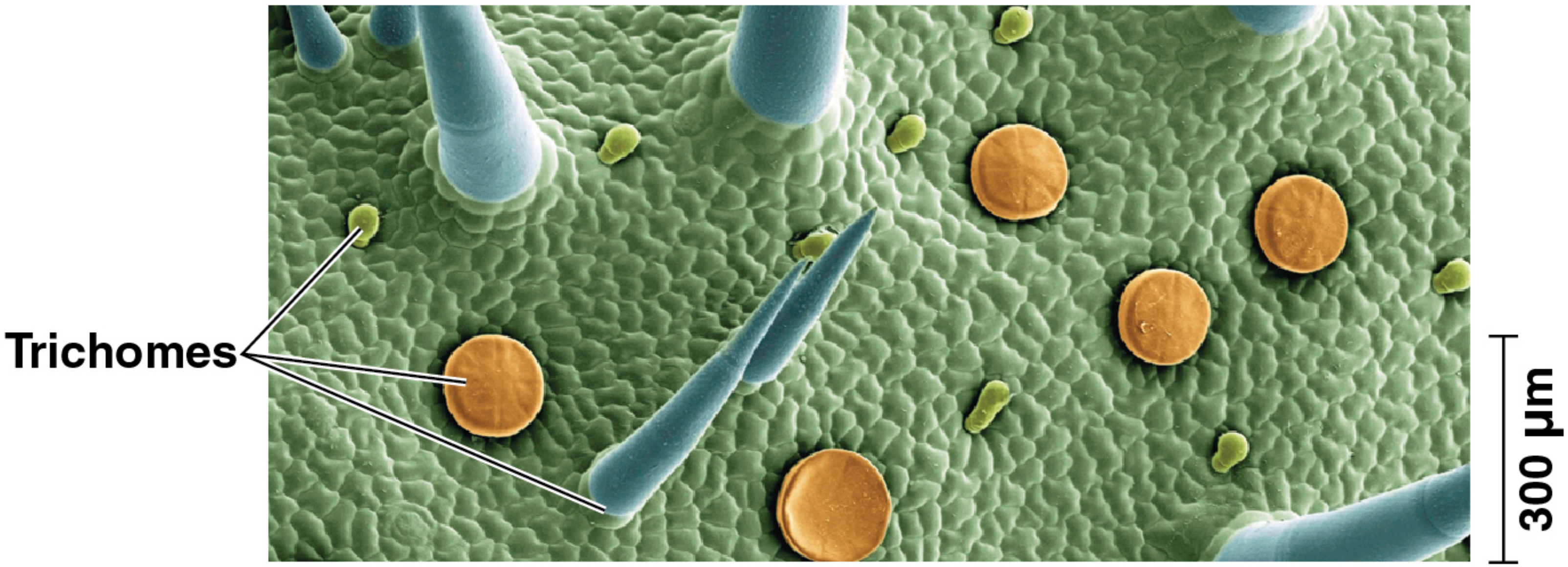
Figure 35.8



- **Dermal tissue** serves as a protective outer coating
- In nonwoody plants, it is usually a single tissue layer called the **epidermis**
- A waxy **cuticle** covers the epidermis and protects leaves and most stems from water loss
- A protective layer called the **periderm** replaces the epidermis in older regions of woody stems and roots

- **Guard cells** are specialized dermal cells that facilitate gas exchange in shoots
- **Trichomes** are hairlike outgrowths of epidermal cells that help reduce water loss, reflect light, and defend against insects

Figure 35.9



- **Vascular tissue** facilitates the transport of materials through the plant and provides mechanical support
- Vascular tissue includes xylem and phloem
  - **Xylem** conducts water and dissolved minerals upward from roots into the shoots
  - **Phloem** transports sugars from where they are made (primarily leaves) to actively growing parts of the plant or storage structures

- The vascular tissue of a root or stem is collectively called the **stele**
- Arrangement of the stele varies by species and organ
- In angiosperms, the stele of the root is a solid central vascular cylinder of xylem and phloem
- The stele of angiosperm stems and leaves is divided into vascular bundles, which are separate strands of xylem and phloem

- Tissue that are neither dermal nor vascular is **ground tissue**
- Ground tissue internal to the vascular tissue is **pith**; ground tissue outside the vascular tissue is **cortex**
- Ground tissue includes cells specialized for storage, photosynthesis, support, and short-distance transport

Common Types of Plant Cells

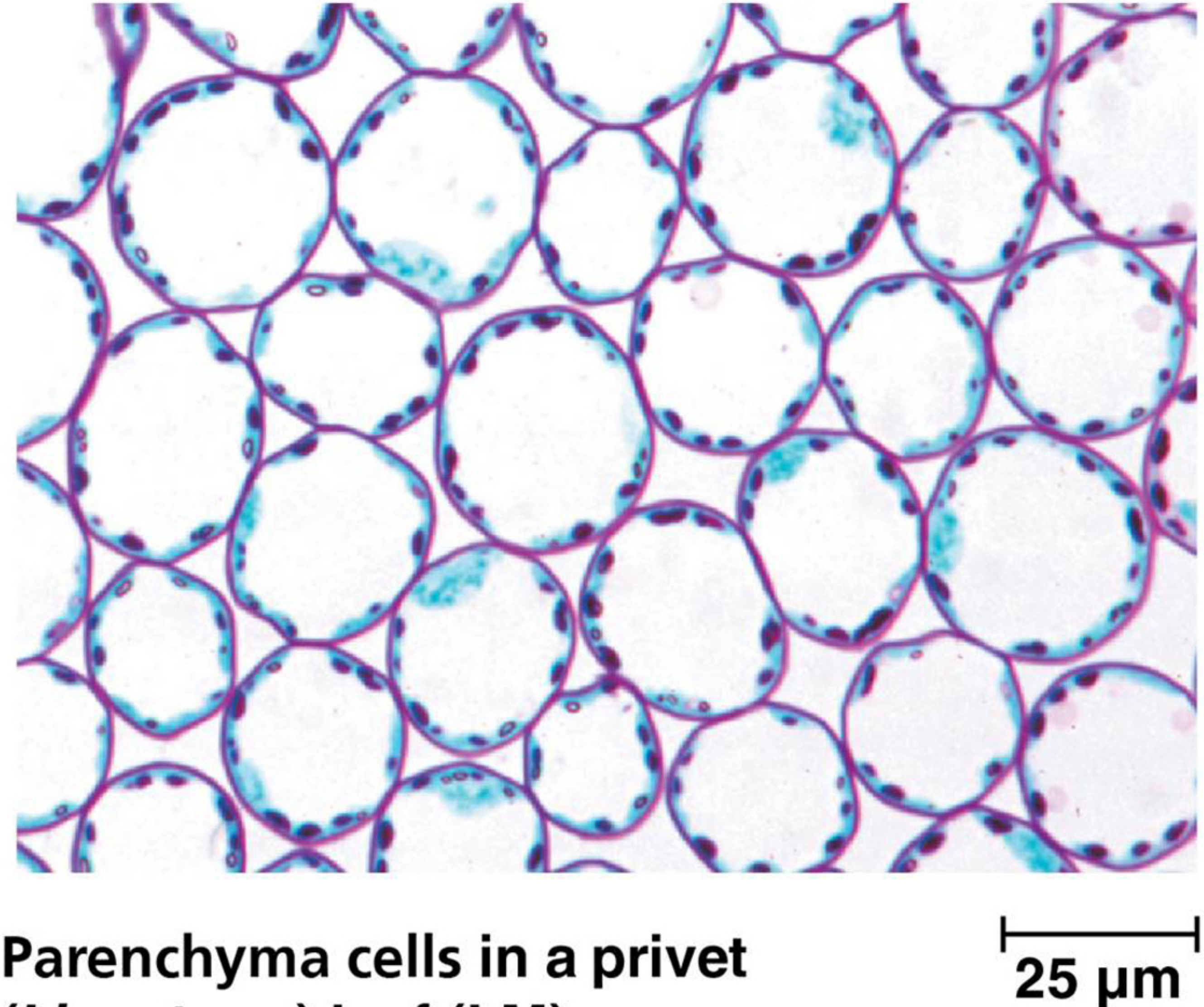
- Plant cells undergo cell differentiation; that is, specialization in structure and function, during development
- The structural adaptations of various types of plant cells make their specific functions possible

- The major types of plant cells are
  - Parenchyma
  - Collenchyma
  - Sclerenchyma
  - Water-conducting cells of the xylem
  - Sugar-conducting cells of the phloem

Parenchyma Cells

- Mature **parenchyma cells**
  - Have thin and flexible primary walls
  - Generally lack secondary walls
  - Have a large central vacuole
  - Perform most of the metabolic functions
  - Retain the ability to divide and differentiate

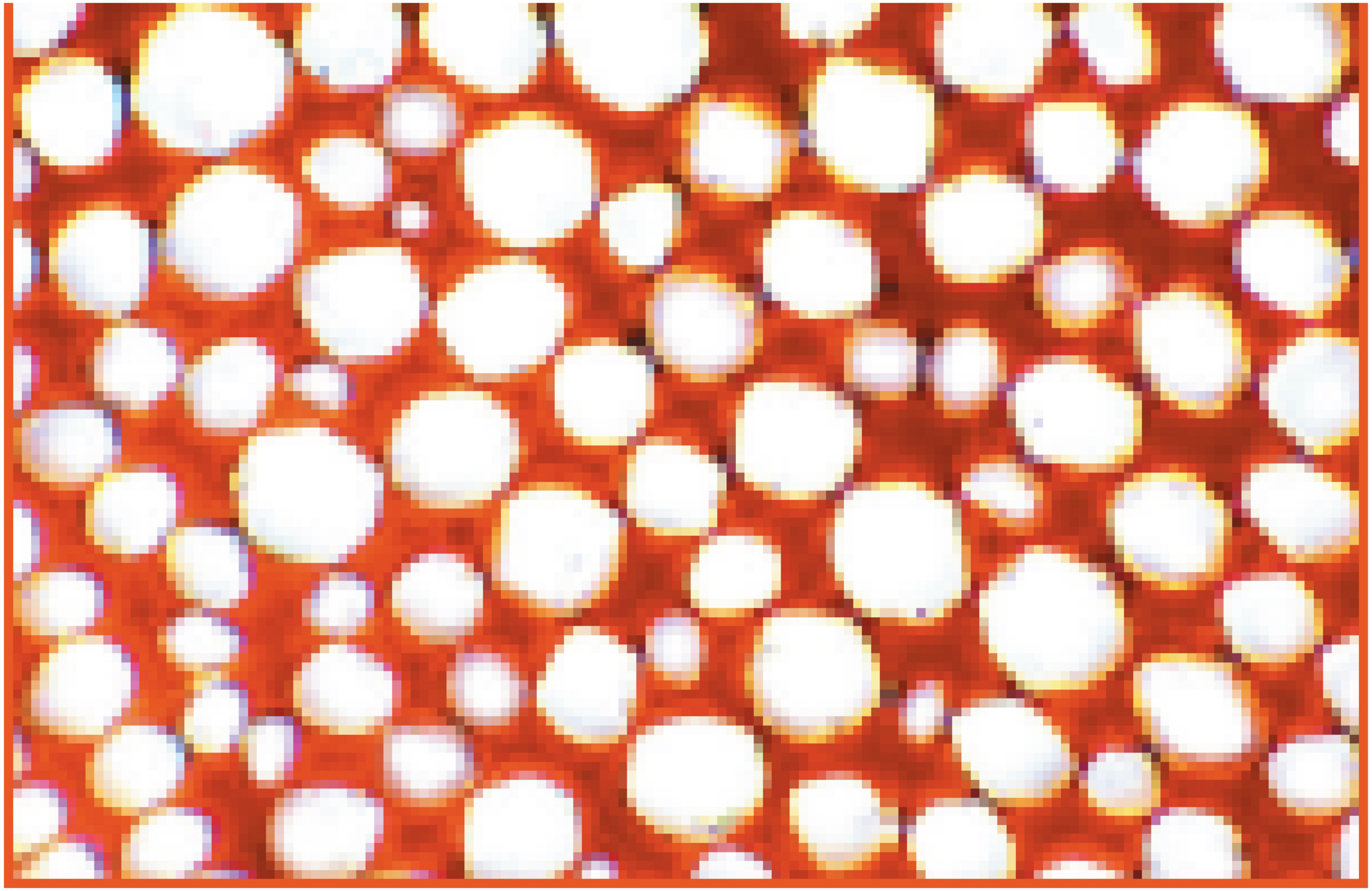
Figure 35.10a



Parenchyma cells in a privet (*Ligustrum*) leaf (LM)

Collenchyma Cells

- **Collenchyma cells** are grouped in strands and help support young parts of the plant shoot
- They have unevenly thickened primary cell walls
- They are living at maturity
- These cells provide flexible support without restraining growth



Collenchyma cells in a common nettle (*Urtica dioica*) stem (LM)

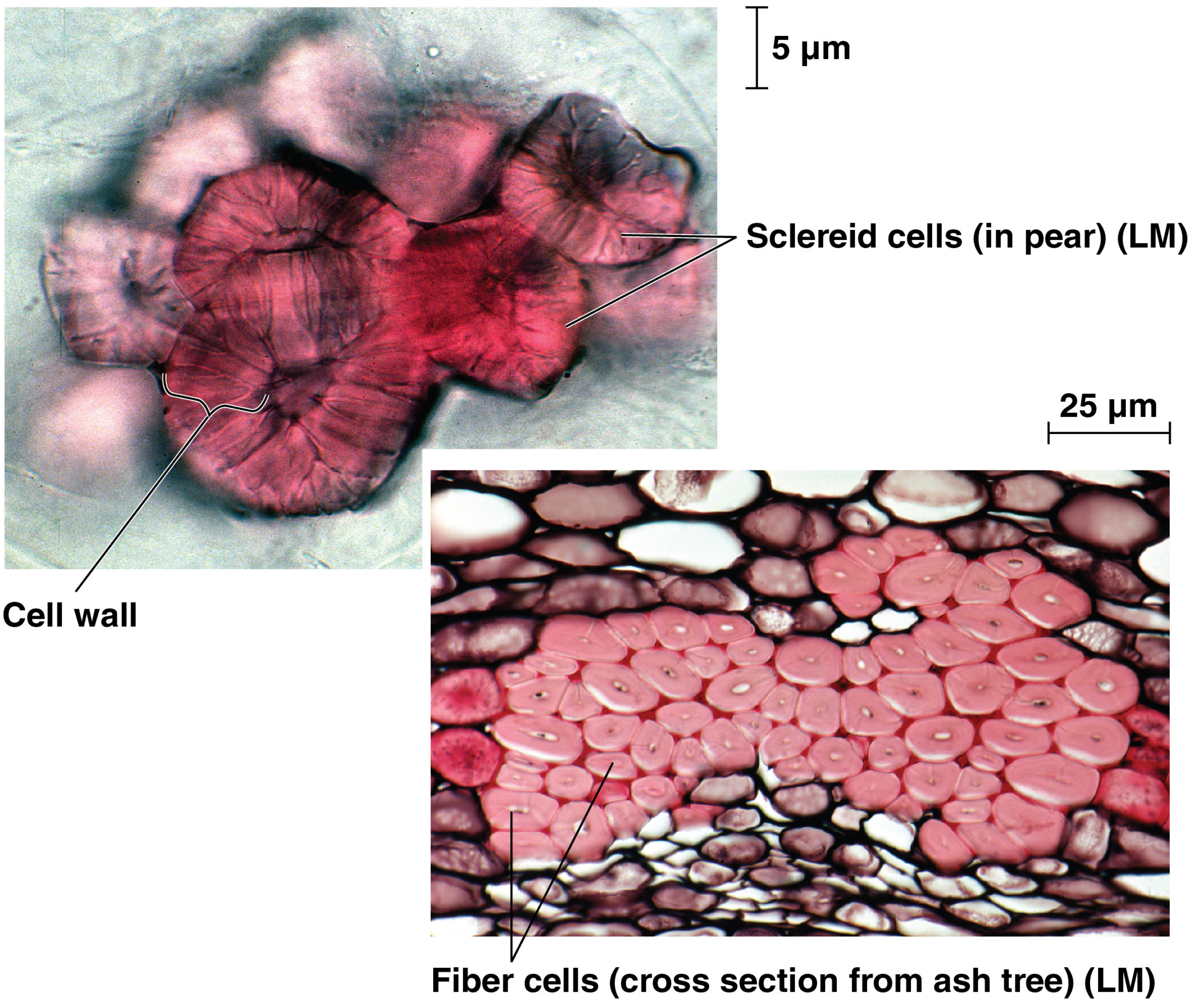
5 µm

Sclerenchyma Cells

- **Sclerenchyma cells** are rigid cells with secondary cell walls containing **lignin**, a strengthening polymer, for support
- Many are dead at maturity; the rigid cell walls remain to support the plant

- Two types of sclerenchyma cells are specialized entirely for support and strengthening
  - Sclereids are boxy and irregular in shape and have very thick, lignified secondary walls
  - Long, slender fibers are tapered and grouped in strands

Sclerenchyma Cells



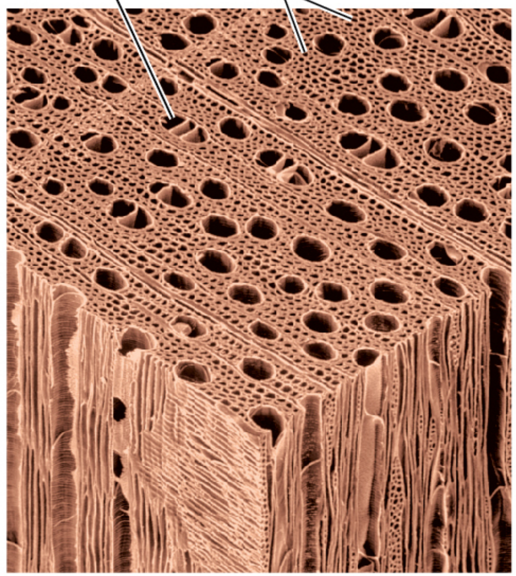
Water-Conducting Cells of the Xylem

- Water-conducting cells that are dead at maturity have lignified secondary cell walls for plant support
- **Tracheids** are long, thin, tapered cells found in the xylem of all vascular plants
- Water moves between tracheids through pits, thin regions lacking secondary cell wall

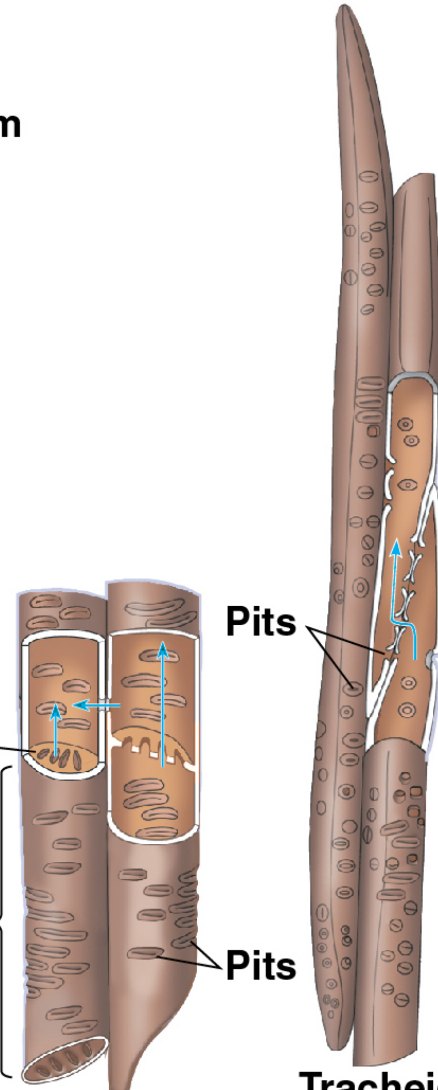
- **Vessel elements**, wider, shorter, and thinner than tracheids, align end to end to form long pipes called **vessels**
- The end walls have perforation plates that allow water to flow freely through the vessels
- Most angiosperms, and a few gymnosperms and seedless vascular plants have vessel elements

Figure 35.10d

Water-Conducting Cells of the Xylem



Tracheids and vessels (colorized SEM)



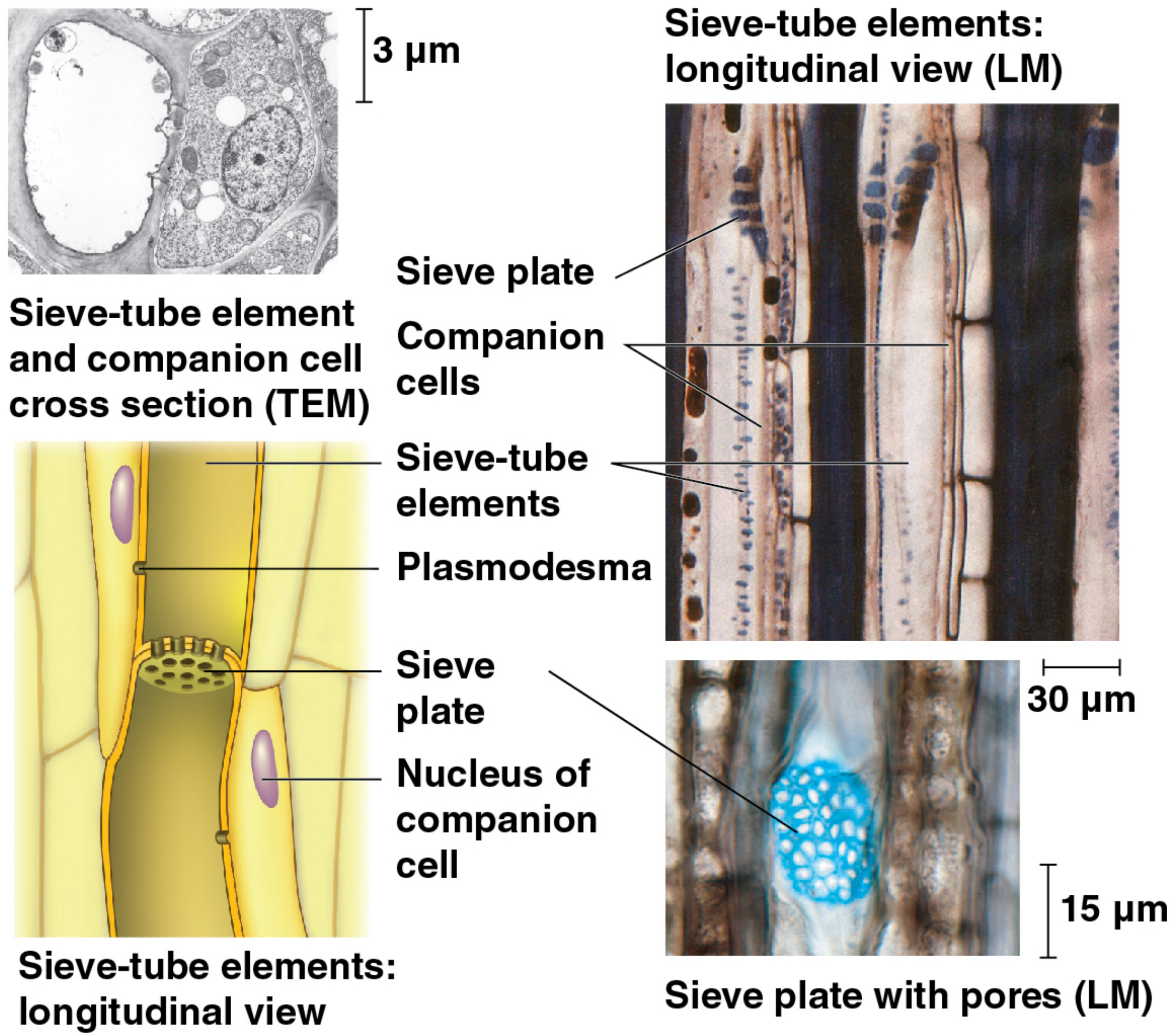
Sugar-Conducting Cells of the Phloem

- Sugar-conducting cells of the phloem are alive at maturity, but lack a nucleus, ribosomes, vacuole, and elements of the cytoskeleton
- In seedless vascular plants and gymnosperms, sugars are transported through sieve cells
- In angiosperms, sugars are transported in sieve tubes, chains of cells called **sieve-tube elements**

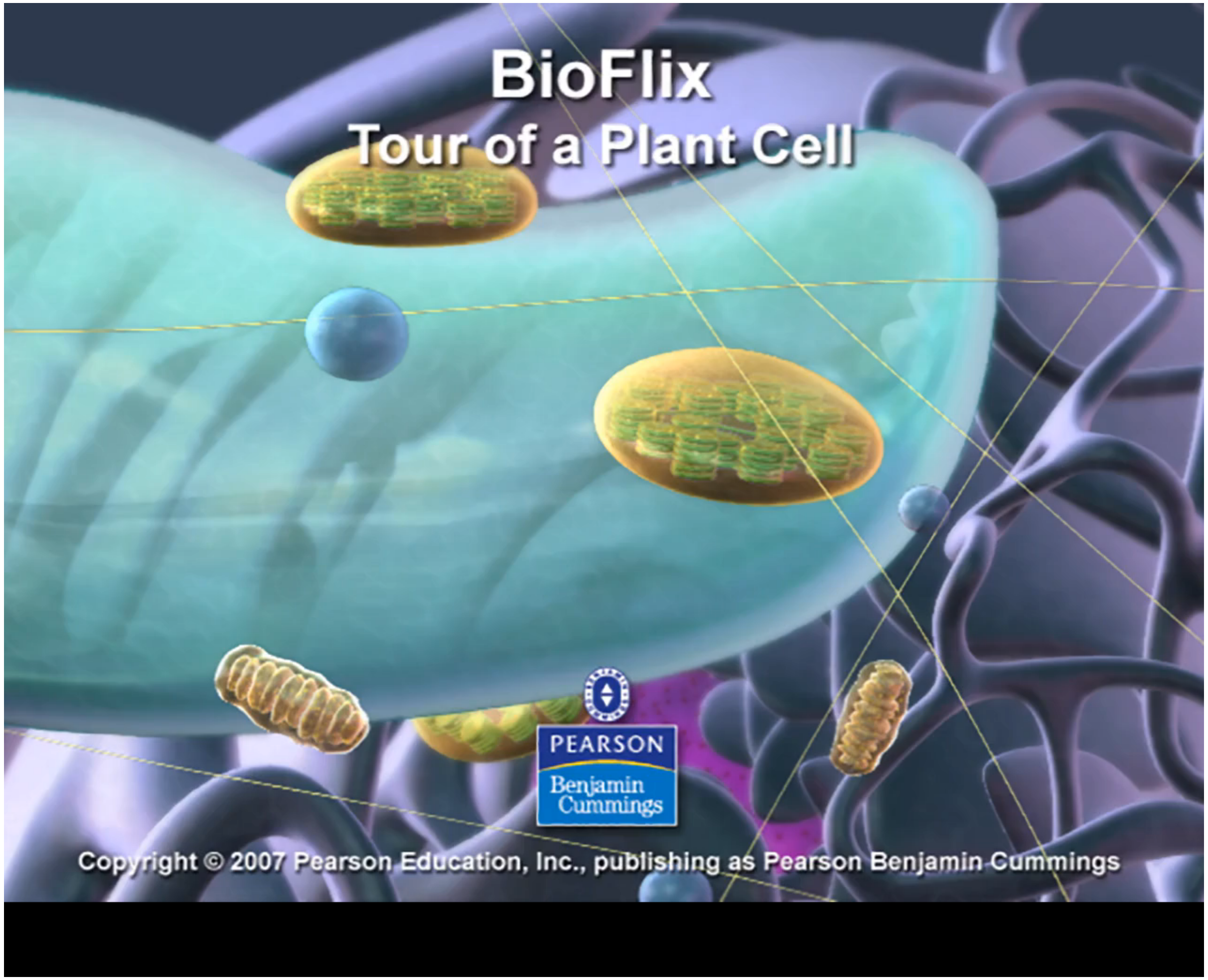
- **Sieve plates** are porous end walls between sieve-tube elements that allow fluid to flow between cells
- Each sieve-tube element is connected to a **companion cell** by numerous plasmodesmata
- The nucleus and ribosomes of the companion cell also serve the sieve-tube element

Figure 35.10e

Sugar-Conducting Cells of the Phloem



BioFlix® Animation: Tour of a Plant Cell



CONCEPT 35.2: Different meristems generate new cells for primary and secondary growth

- A plant can grow throughout its life; this is called **indeterminate growth**
- Continuous growth is possible due to the activity of **meristems**, undifferentiated tissues composed of dividing cells
- Most animals and some plant organs cease to grow at a certain size; this is called **determinate growth**

Figure 35.11a

Primary Growth (growth in length)

Primary growth is made possible by apical meristems at the tips of shoots and roots.

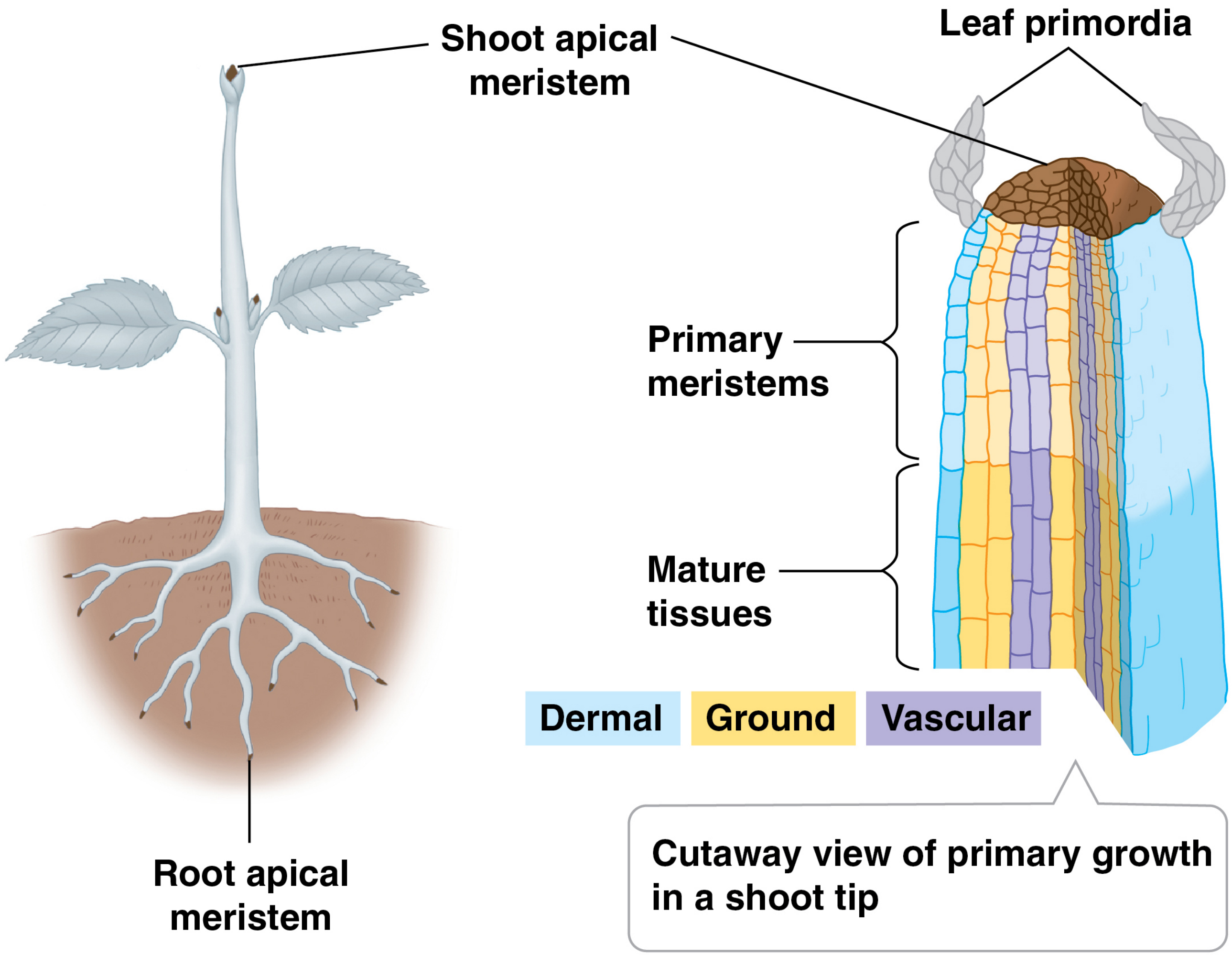
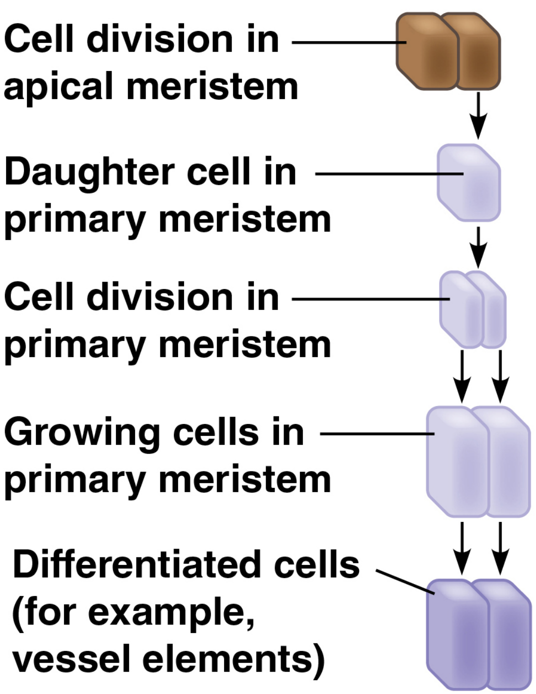
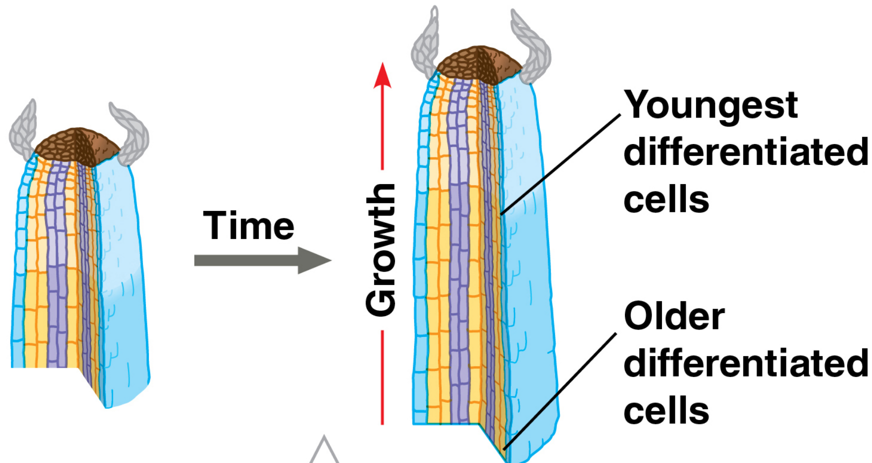


Figure 35.11b

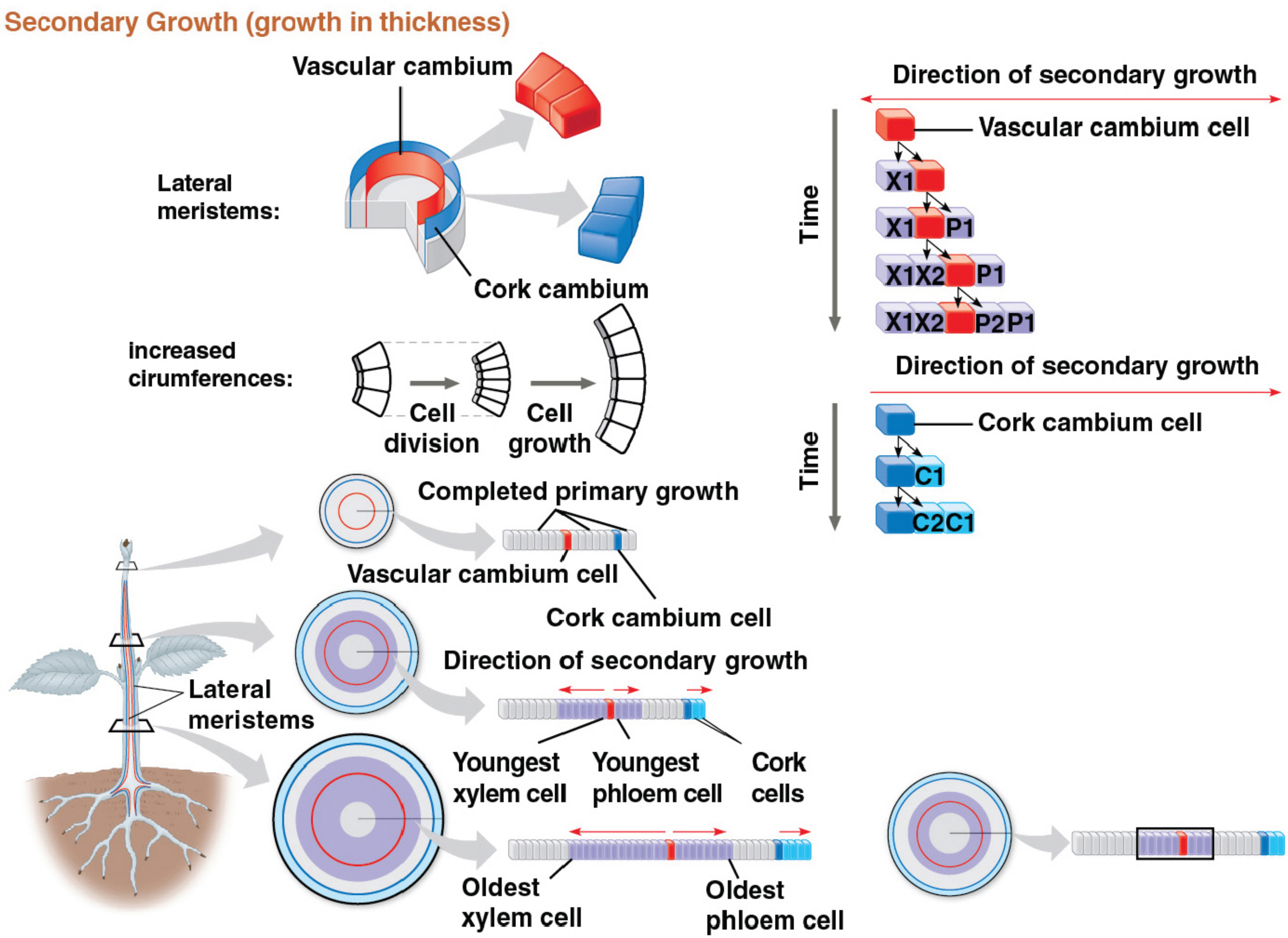
Apical meristem cells are undifferentiated. When they divide, some daughter cells remain in the apical meristem, ensuring a continuing population of undifferentiated cells. Other daughter cells become partly differentiated as primary meristem cells. After dividing and growing in length, they become fully differentiated cells in the mature tissues.





The addition of elongated, differentiated cells lengthens a stem (as shown here) or root.

Figure 35.11c



Animation: Primary and Secondary Growth

- There are two main types of meristems: apical meristems and lateral meristems
- **Apical meristems** are located at the tips of roots and shoots
- Cells of the apical meristems allow for elongation of shoots and roots, a process called **primary growth**

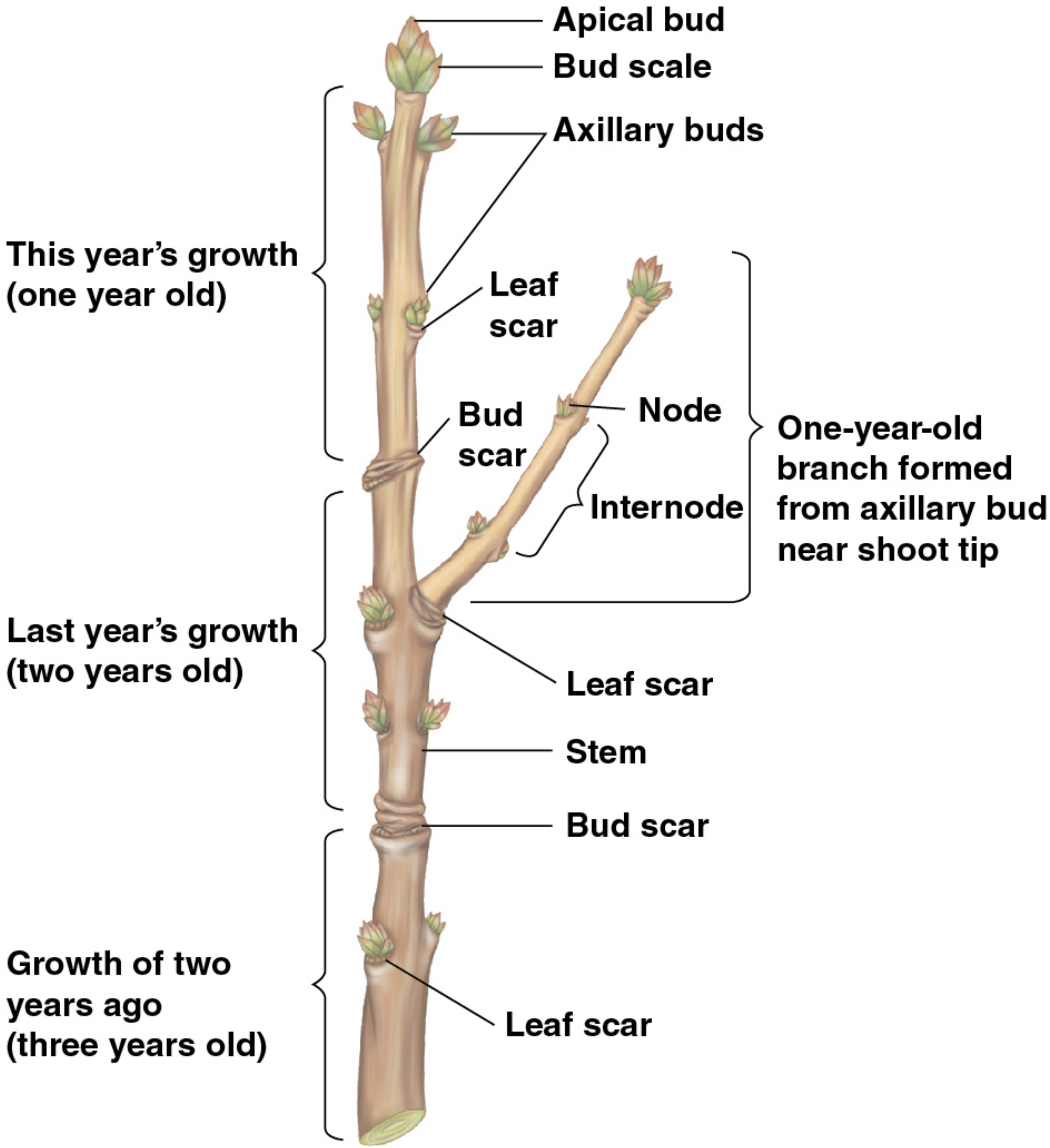
- **Lateral meristems** allow the stems and roots of woody plants to grow in circumference, a process called **secondary growth**
- There are two lateral meristems
  - **Vascular cambium** adds vascular tissue called secondary xylem (wood) and secondary phloem
  - **Cork cambium** replaces the epidermis with thicker, tougher periderm

- Cells in the apical and lateral meristems divide frequently during the growing season
- Initials, also called stem cells, are new cells that remain in the meristem and produce more cells
- Other new cells differentiate and are incorporated into tissues and organs

- Cells displaced from the meristem give rise to three tissues called **primary meristems** that will produce mature tissues
  - The protoderm produces dermal tissue
  - The ground meristem produces ground tissue
  - The procambium produces vascular tissue

- Lateral meristems in woody plants also have stem cells, which give rise to secondary growth
- Each year, primary growth extends woody shoots, and secondary growth increases the diameter of parts formed in the previous years

Figure 35.12



Apical bud
Bud scale
Axillary buds
This year's growth (one year old)
Leaf scar
Bud scar
Node
Internode
One-year-old branch formed from axillary bud near shoot tip
Last year's growth (two years old)
Leaf scar
Stem
Bud scar
Growth of two years ago (three years old)
Leaf scar

- Flowering plants can be categorized based on the length of their life cycle
  - Annuals complete their life cycle in a year or less
  - Biennials require two growing seasons
  - Perennials live for many years

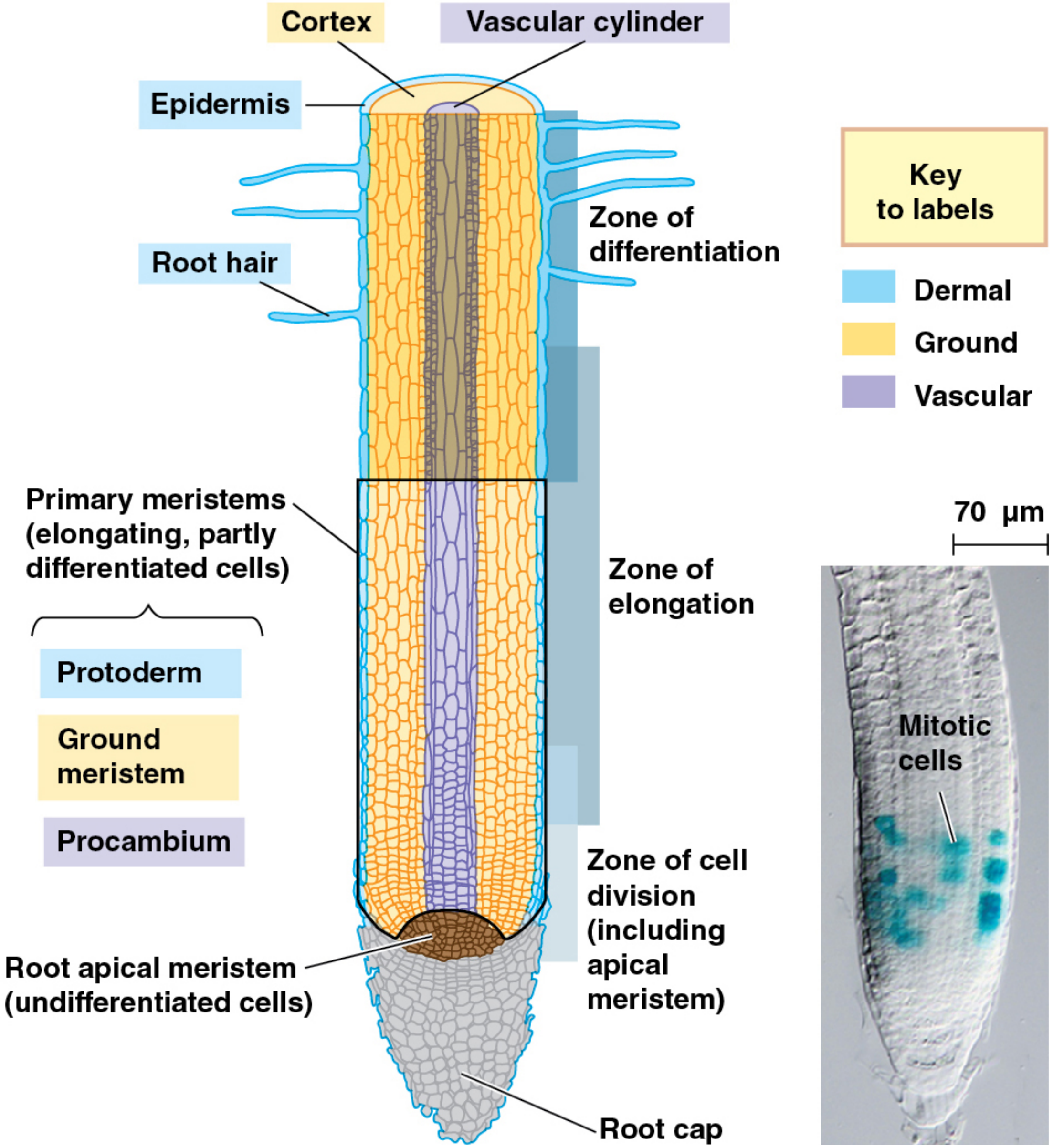
CONCEPT 35.3: Primary growth lengthens roots and shoots

- Primary growth arises from cells produced by apical meristems and elongates roots and shoots
- In herbaceous plants, most of the plant consists of primary growth; in woody plants only new, non-woody parts represent primary growth

Primary Growth of Roots

- A **root cap** covers the root tip to protect the apical meristem and polysaccharide slime lubricates the passage as the root pushes through soil
- Growth occurs just behind the tip, in three zones:
  - Zone of cell division
  - Zone of elongation
  - Zone of differentiation, or maturation

Figure 35.13



Cortex
Vascular cylinder
Epidermis
Root hair
Zone of differentiation
Key to labels
Dermal
Ground
Vascular
Primary meristems (elongating, partly differentiated cells)
Protoderm
Ground meristem
Procambium
Zone of elongation
Zone of cell division (including apical meristem)
Root apical meristem (undifferentiated cells)
Root cap
70 μm
Mitotic cells

Video: Root Growth in a Radish Seedling

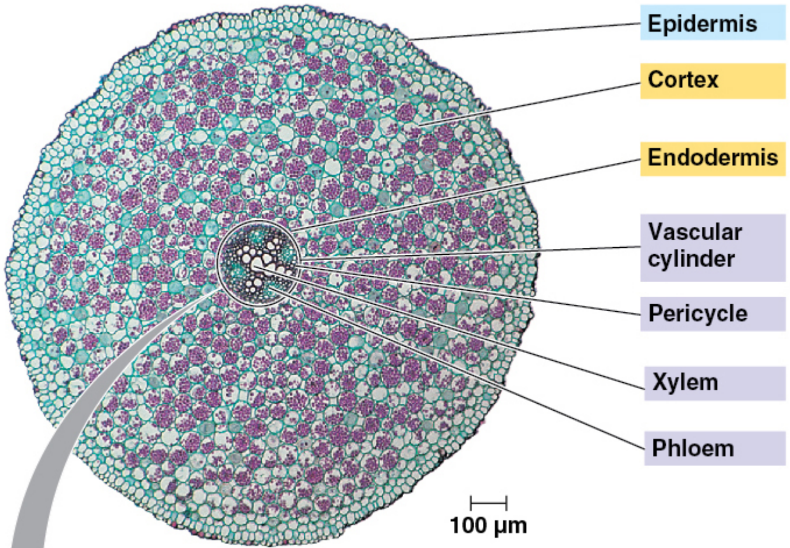
- The primary growth of roots produces the epidermis, ground tissue, and vascular tissue
- The protoderm is the outermost primary meristem; it gives rise to the epidermis
- Root hairs, epidermal cells modified for absorption, make up 70–90% of the total root surface area

- Between the protoderm and procambium is the ground meristem, which produces the ground tissue
- Ground tissue, mostly parenchyma cells, makes up the region between the vascular tissue and the epidermis called the cortex
- The innermost layer of the cortex is called the **endodermis**; it regulates passage into and out of the vascular cylinder

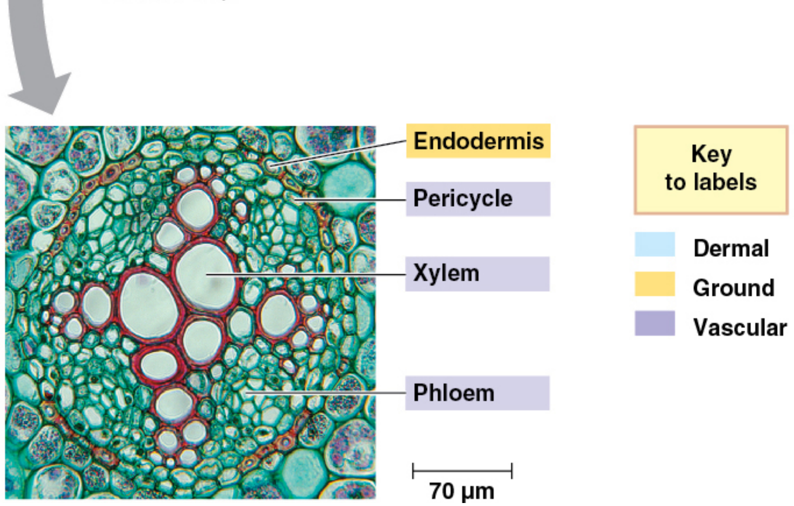
- The innermost primary meristem is the procambium; it gives rise to the central vascular cylinder
- The vascular cylinder has a solid core of xylem and phloem surrounded by a cell layer called the **pericycle**

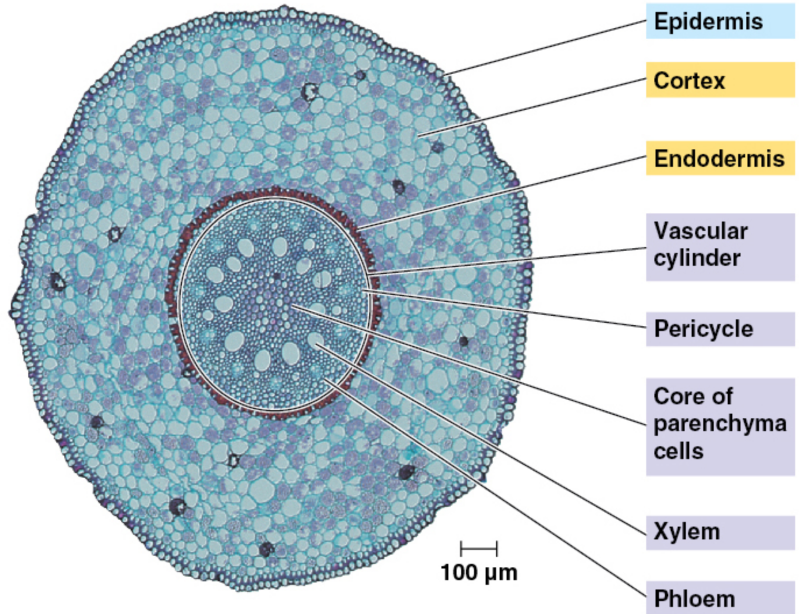
- In most eudicots, the xylem has a starlike appearance in cross section with phloem between the “arms”
- In many monocots, a core of parenchyma cells is surrounded by alternating rings of xylem and phloem

Figure 35.14



(a) Root with xylem and phloem in the center (typical of eudicots).





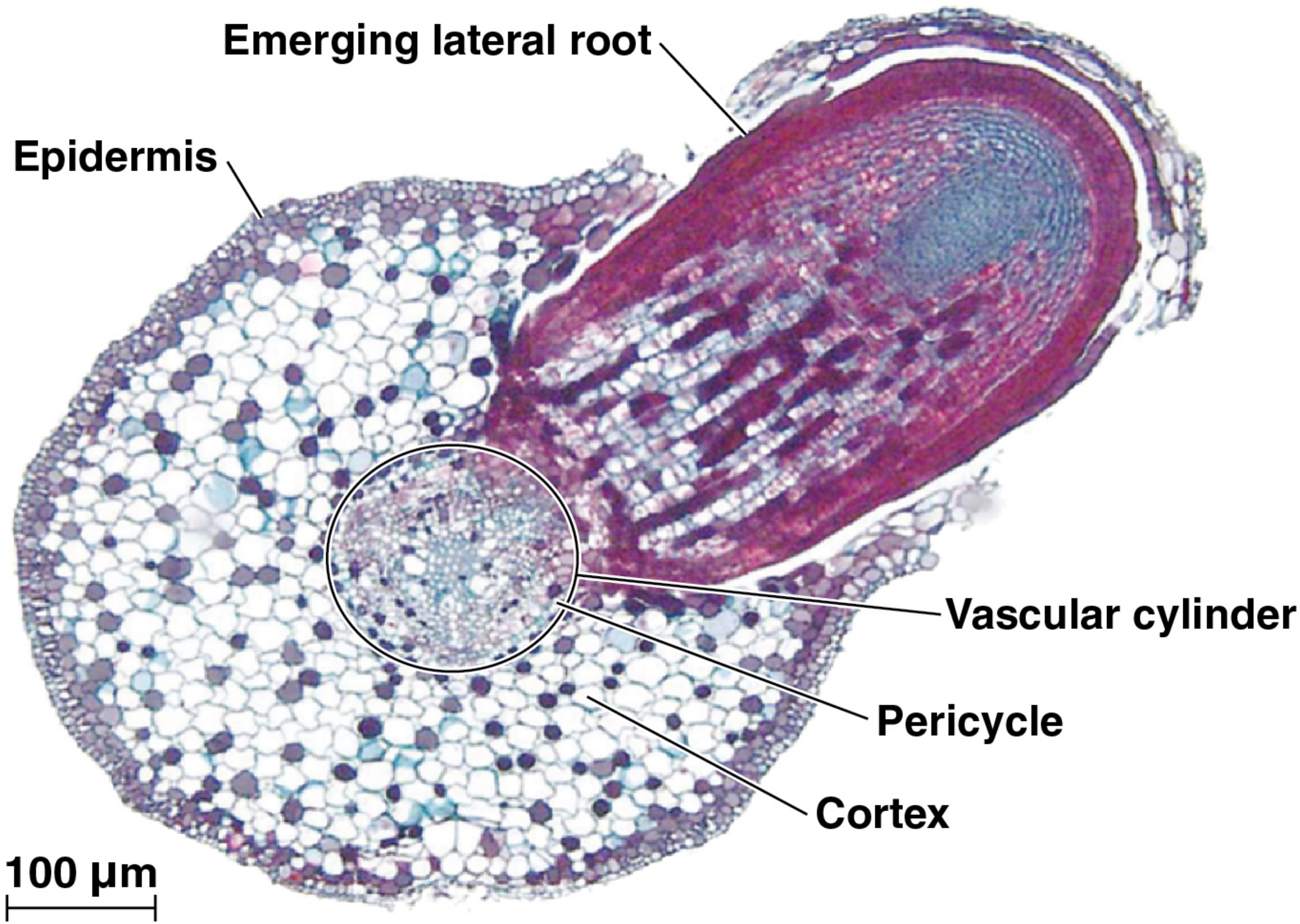
(b) Root with parenchyma in the center (typical of monocots).

Animation: Root Cross Sections

[redacted]

- Lateral (branch) roots arise from the pericycle and destructively push through the outer tissues
- Branching is a form of primary growth

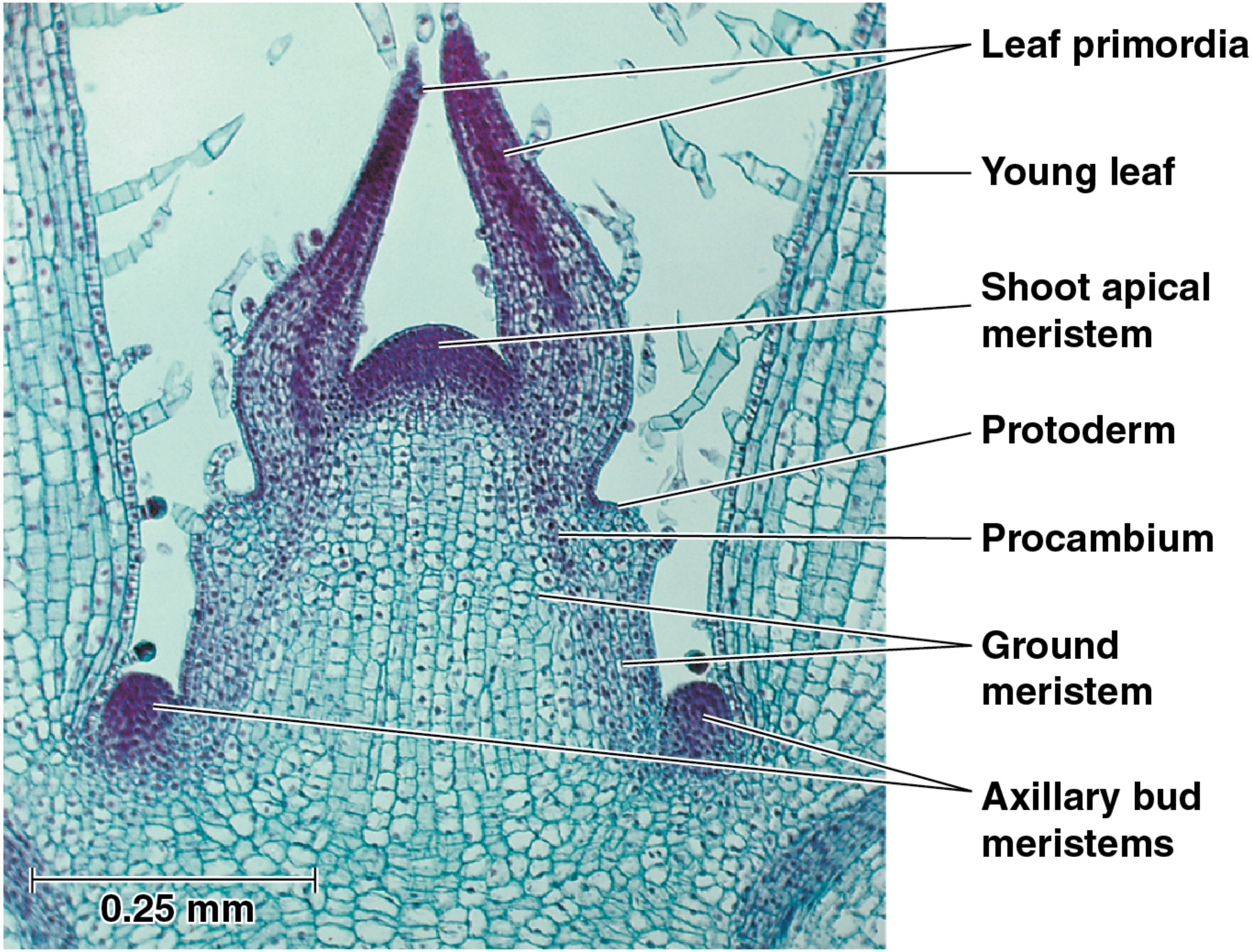
Figure 35.15


Emerging lateral root
Epidermis
Vascular cylinder
Pericycle
Cortex
100 µm

Primary Growth of Shoots

- A shoot apical meristem is a dome-shaped mass of dividing cells at the shoot tip
- The leaves of the apical bud protect the meristem
- Axillary buds develop from meristematic cells left at the bases of leaf primordia
- The shoot apical meristem gives rise to three primary meristems—the protoderm, ground meristem and procambium

Figure 35.16


Leaf primordia
Young leaf
Shoot apical meristem
Protoderm
Procambium
Ground meristem
Axillary bud meristems
0.25 mm

- Axillary buds are kept dormant by chemical communication from the apical bud
- The closer an axillary bud is to the active apical bud, the more inhibited it is
- Axillary buds are released from this **apical dominance** if the shoot tip is removed or shaded
- Lateral shoots emerge from axillary buds that have been released from dormancy

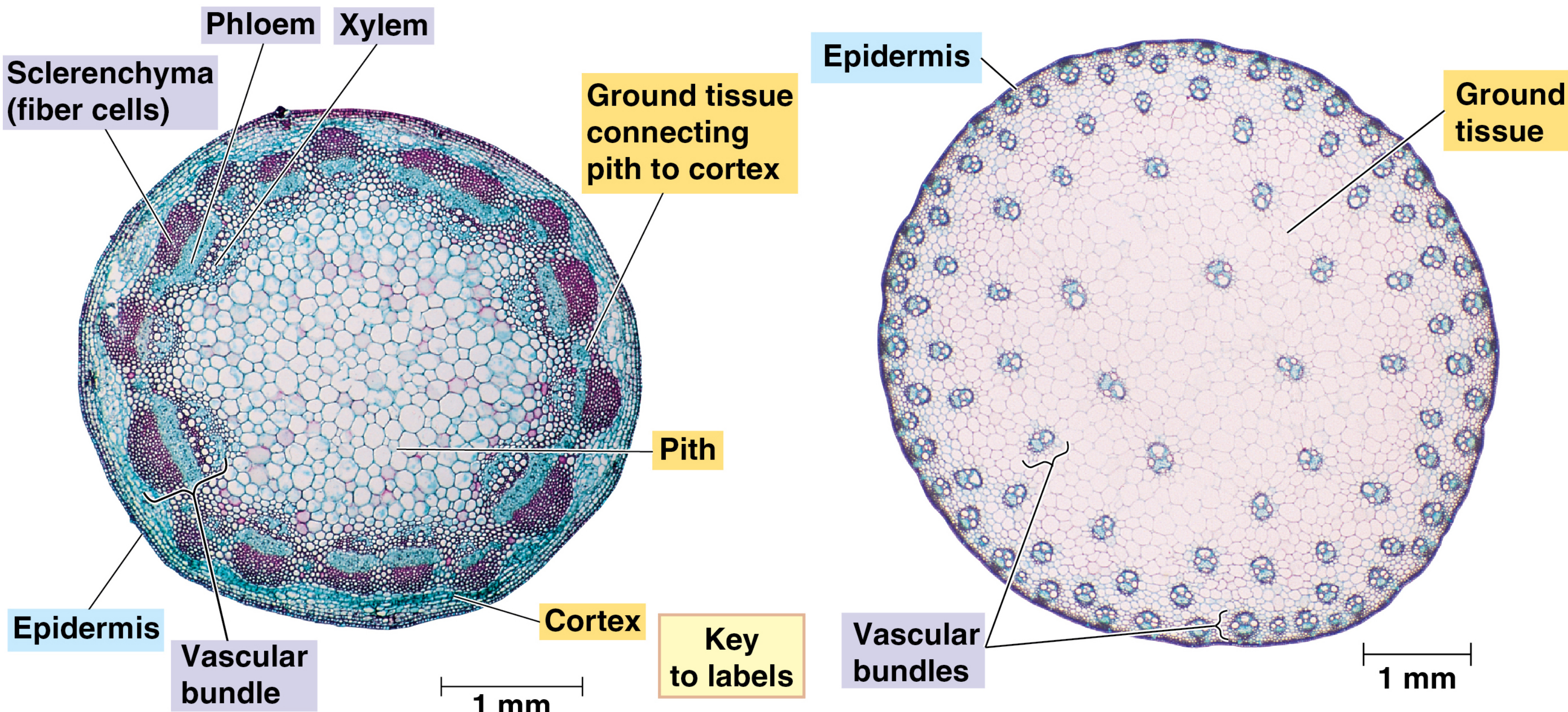
Stem Growth and Anatomy

- The stem is covered by the epidermis and a waxy cuticle
- The ground tissue is composed primarily of parenchyma cells
- Collenchyma and sclerenchyma cells strengthen and support the stem

- Unlike lateral roots, emerging shoots do not damage stem tissues
- Lateral shoots arise from axillary bud meristems on the stem surface

- In most eudicots, the vascular tissue consists of vascular bundles arranged in a ring
- In most monocot stems, the vascular bundles are scattered throughout the ground tissue

Figure 35.17



(a) Cross section of stem with vascular bundles forming a ring (typical of eudicots).

(b) Cross section of stem with scattered vascular bundles (typical of monocots).

Animation: Stem Cross Sections

Leaf Growth and Anatomy

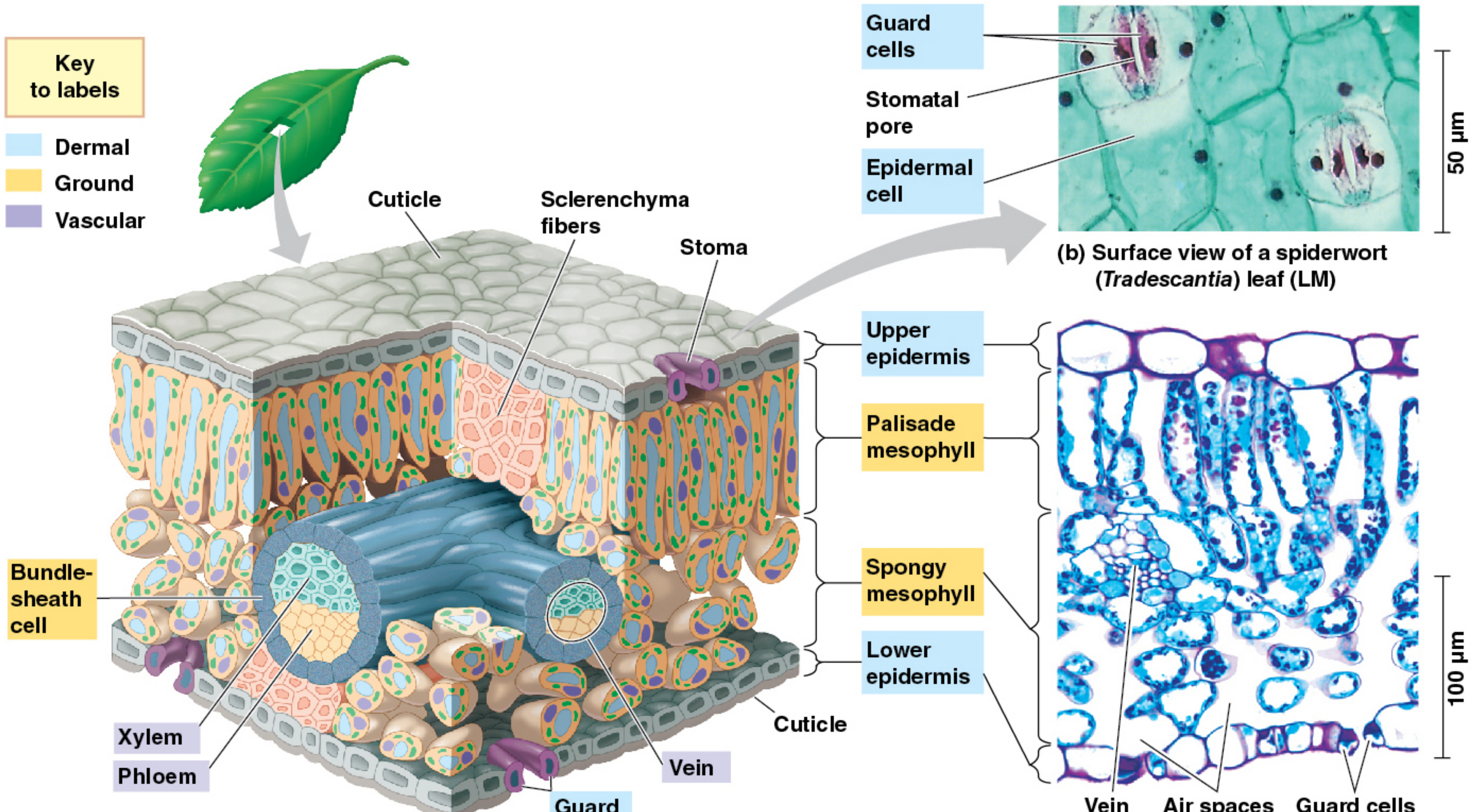
- Leaves develop from **leaf primordia** along the sides of the shoot apical meristem
- Unlike roots and stems, secondary growth in leaves is minor or nonexistent

- The waxy cuticle coating the leaf epidermis reduces water loss except where interrupted by stomata
- **Stomata**, pores in the epidermis, allow exchange of CO_2 and O_2 between the surrounding air and photosynthetic cells inside the leaf
- Each stoma is flanked by two guard cells, which regulate its opening and closing to reduce water loss

- The ground tissue in a leaf, called **mesophyll**, is sandwiched between the upper and lower epidermis
- The mesophyll of eudicots has two layers:
  - Cells of the palisade mesophyll (upper layer) are rich in chloroplasts to maximize light capture
  - Cells of the spongy mesophyll (lower layer) are loosely packed to create air spaces for gas exchange

- The vascular tissue of each leaf is continuous with the vascular tissue of the stem
- Veins are the leaf's vascular bundles and they also provide structural support for the leaf
- Leaf veins are enclosed by a protective bundle sheath that regulates movement of substances between the vascular tissue and the mesophyll

Figure 35.18



(a) Cutaway drawing of leaf tissues

(b) Surface view of a spiderwort (*Tradescantia*) leaf (LM)

(c) Cross section of a lilac (*Syringa*) leaf (LM)

Animation: Leaf Anatomy

[redacted]

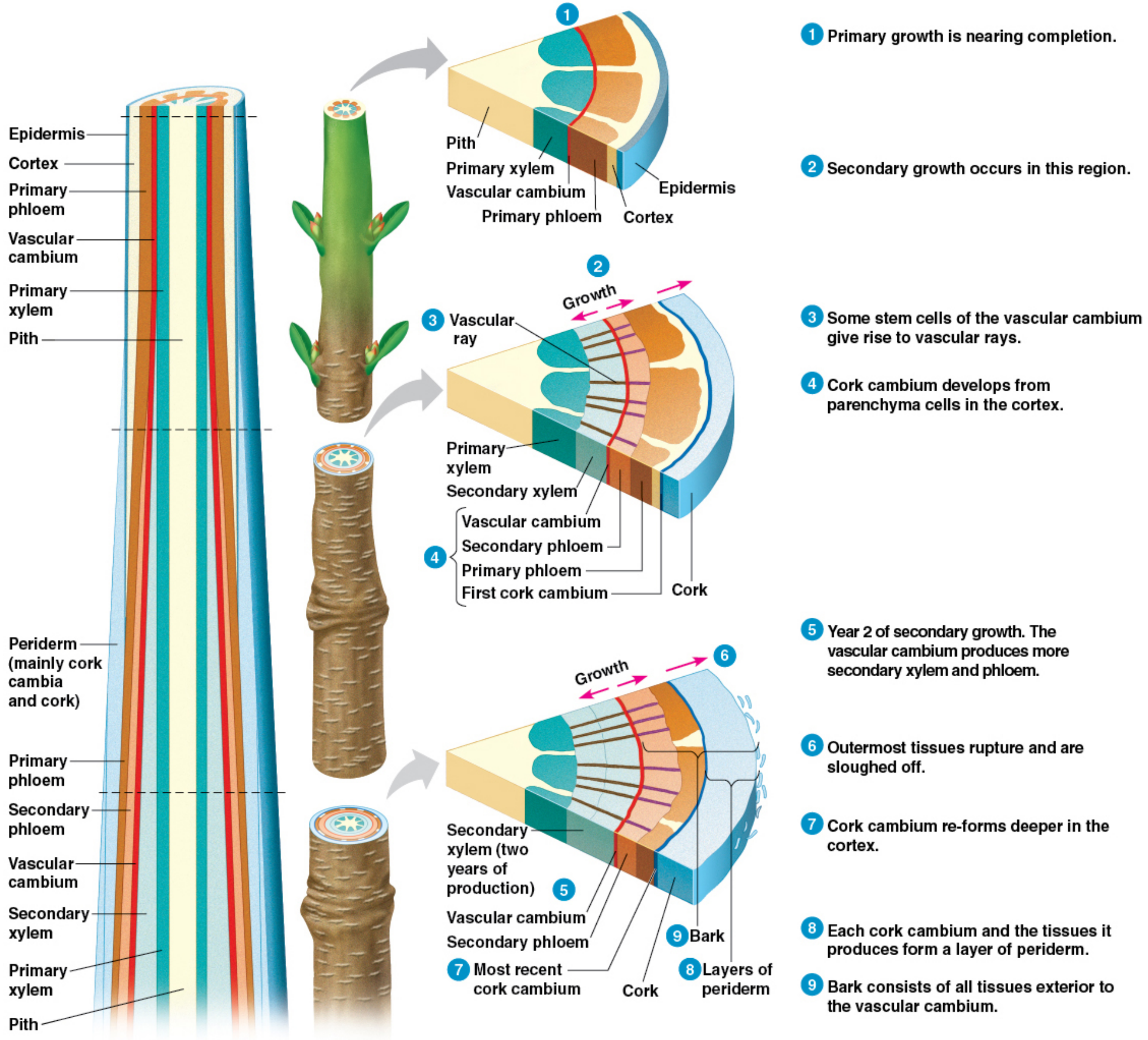
CONCEPT 35.4: Secondary growth increases the diameter of stems and roots in woody plants

- Many land plants display secondary growth, the growth in thickness produced by lateral meristems
- Secondary growth occurs in gymnosperms and many eudicots, but is rare in monocots

- Secondary growth consists of the tissues produced by the vascular cambium and cork cambium
- The vascular cambium adds secondary xylem (wood) toward the interior and secondary phloem toward the exterior of the stem
- The cork cambium produces a tough covering to protect the stem from water loss and pathogen invasion

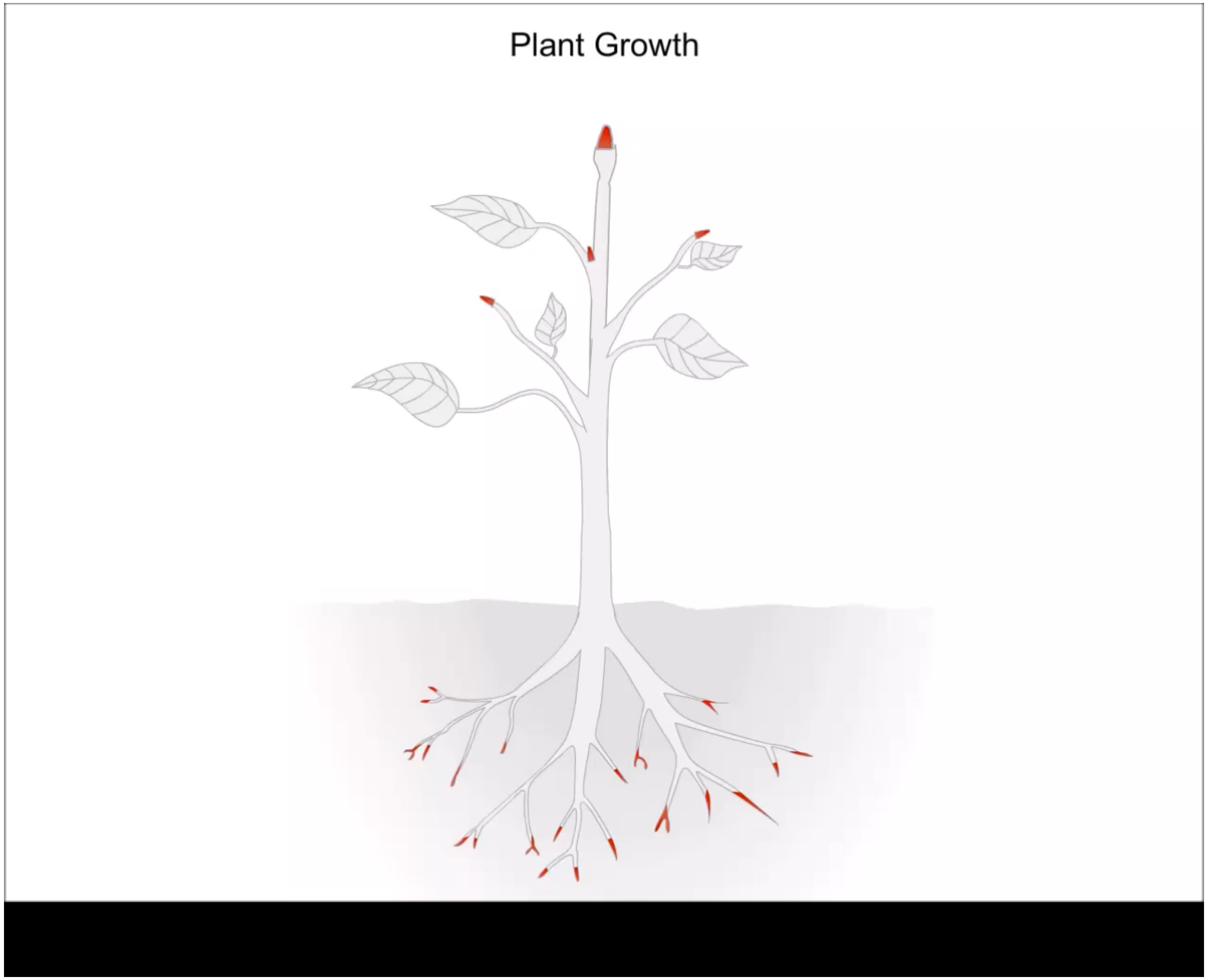
- In woody plants, primary and secondary growth occur simultaneously

Figure 35.19



Epidermis
Cortex
Primary phloem
Vascular cambium
Primary xylem
Pith
Periderm (mainly cork cambia and cork)
Primary phloem
Secondary phloem
Vascular cambium
Secondary xylem
Primary xylem
Pith
1
Pith
Primary xylem
Vascular cambium
Primary phloem
Epidermis
Cortex
2
Growth
3 Vascular ray
Primary xylem
Secondary xylem
4
Vascular cambium
Secondary phloem
Primary phloem
First cork cambium
Cork
Growth
6
Secondary xylem (two years of production) 5
Vascular cambium
Secondary phloem
7 Most recent cork cambium
Cork
9 Bark
8 Layers of periderm
1 Primary growth is nearing completion.
2 Secondary growth occurs in this region.
3 Some stem cells of the vascular cambium give rise to vascular rays.
4 Cork cambium develops from parenchyma cells in the cortex.
5 Year 2 of secondary growth. The vascular cambium produces more secondary xylem and phloem.
6 Outermost tissues rupture and are sloughed off.
7 Cork cambium re-forms deeper in the cortex.
8 Each cork cambium and the tissues it produces form a layer of periderm.
9 Bark consists of all tissues exterior to the vascular cambium.

Animation: Secondary Growth



The Vascular Cambium and Secondary Vascular Tissue

- The vascular cambium is wholly responsible for the production of secondary vascular tissue
- In a typical woody stem, the vascular cambium is located outside the pith and primary xylem and to the inside of the primary phloem and the cortex
- In a typical woody root, the vascular cambium forms exterior to the primary xylem and interior to the primary phloem and pericycle

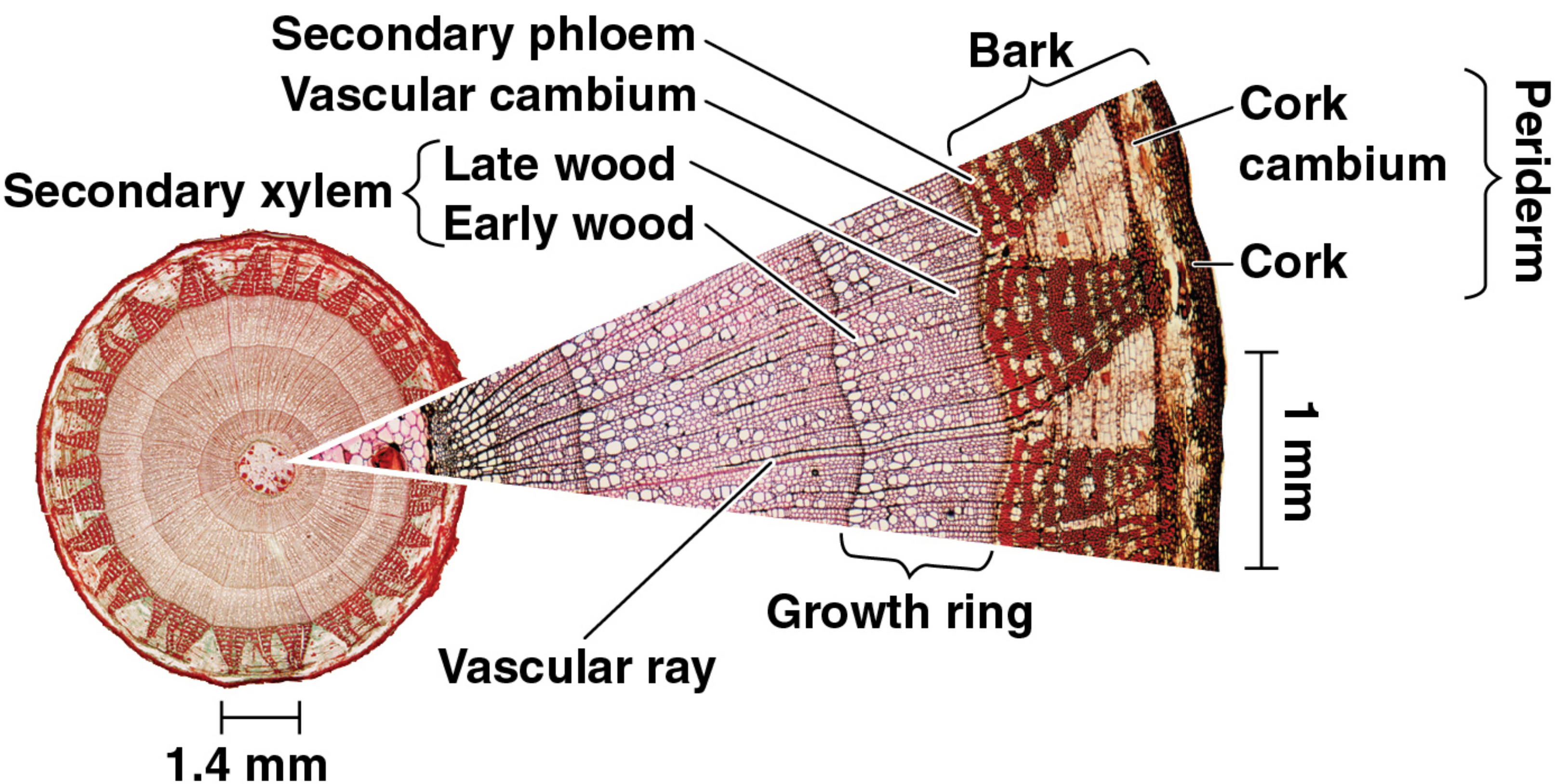
- In cross section, the vascular cambium appears as a ring of meristematic cells
- Cell division increases the vascular cambium’s circumference and adds secondary xylem to the inside and secondary phloem to the outside

- Elongated stem cells are oriented parallel to the axis of the stem or root
- They give rise to tracheids, vessel elements, fibers of xylem, sieve-tube elements, companion cells, axially oriented parenchyma, and fibers of the phloem

- Shorter stem cells are oriented perpendicular to the axis of the stem or root
- They produce vascular rays—radial files of parenchyma cells that connect secondary xylem and phloem

- Secondary xylem accumulates as wood and consists mainly of tracheids, vessel elements, and fibers
- Early wood, formed in the spring in temperate regions, has thin cell walls to maximize water delivery
- Late wood, formed in the summer, has thick-walled cells and contributes more to stem support

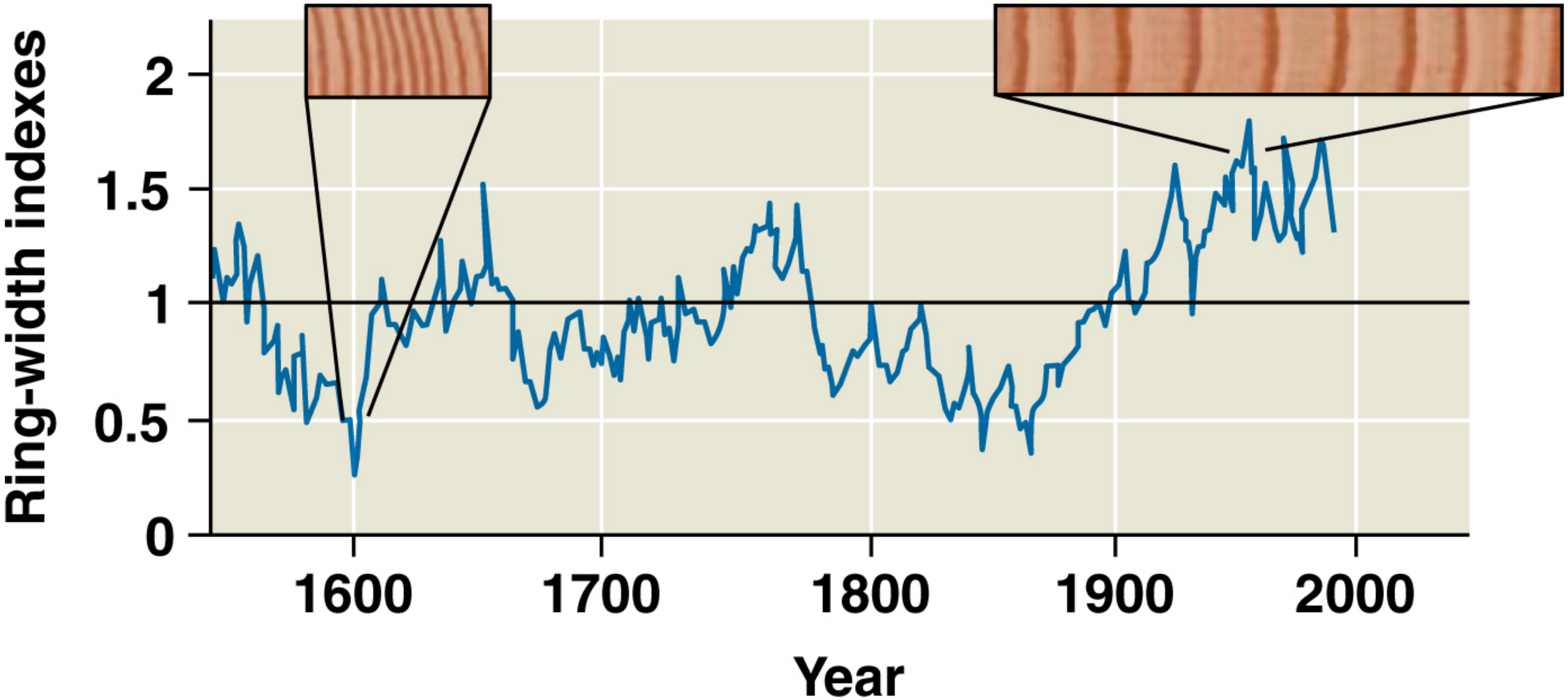
Figure 35.20



Secondary phloem
Vascular cambium
Secondary xylem
Late wood
Early wood
Bark
Cork
cambium
Cork
Periderm
1 mm
Growth ring
Vascular ray
1.4 mm

- Tree rings are visible where late and early wood meet and can be used to estimate a tree’s age
- Dendrochronology, the analysis of tree ring growth patterns, can be used to study past climate change
- Thick rings indicate a year with warm or wet growing conditions; thin rings indicate a cold or dry year

Figure 35.21



Data from G. C. Jacoby et al., Mongolian tree rings and 20th-century warming, *Science* 273:771–773 (1996).

- As a tree or woody shrub ages, the older layers of secondary xylem, the heartwood, no longer transport water and minerals
- The outer layers, known as sapwood, still transport materials through the xylem
- Older secondary phloem sloughs off and does not accumulate

Figure 35.22

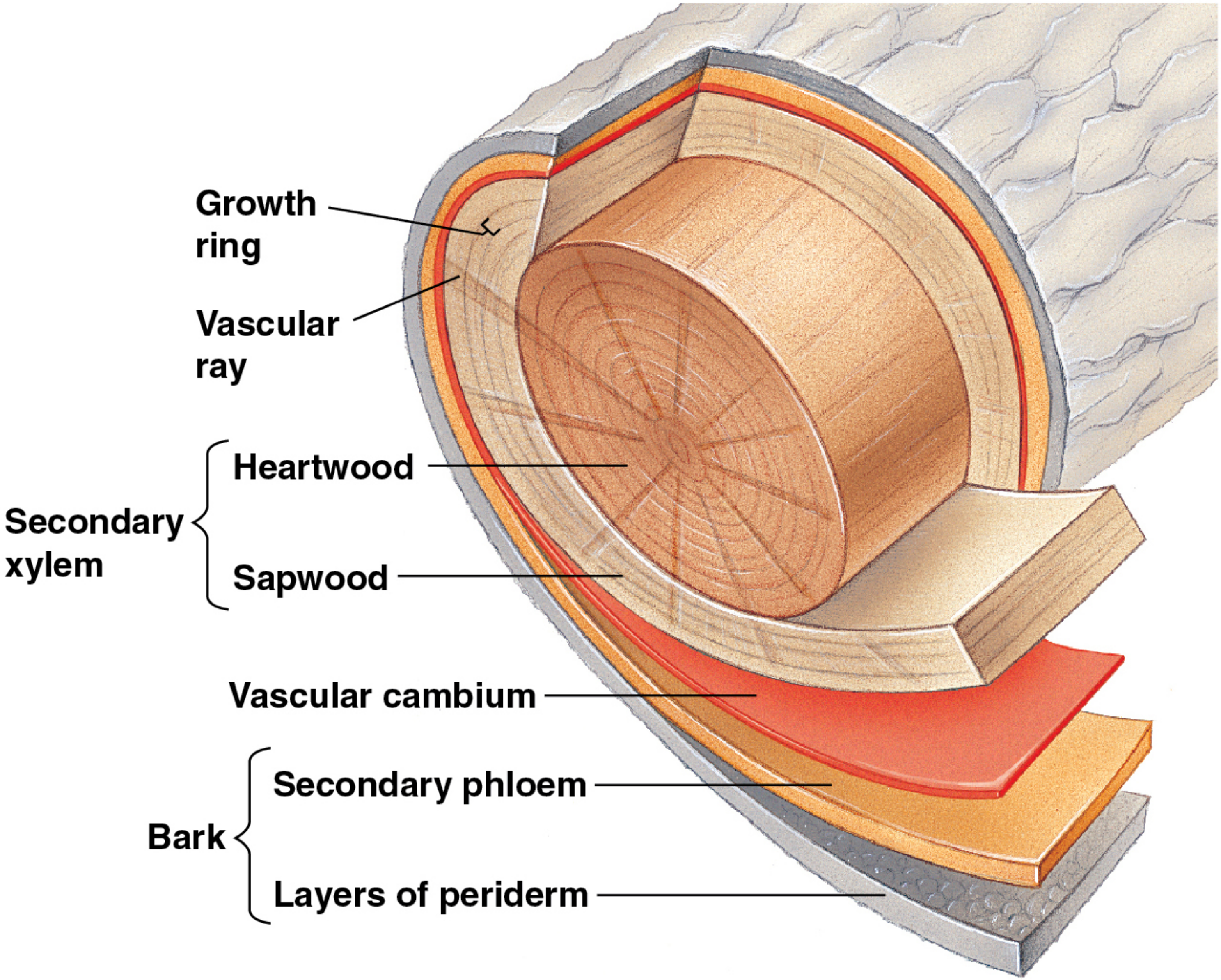
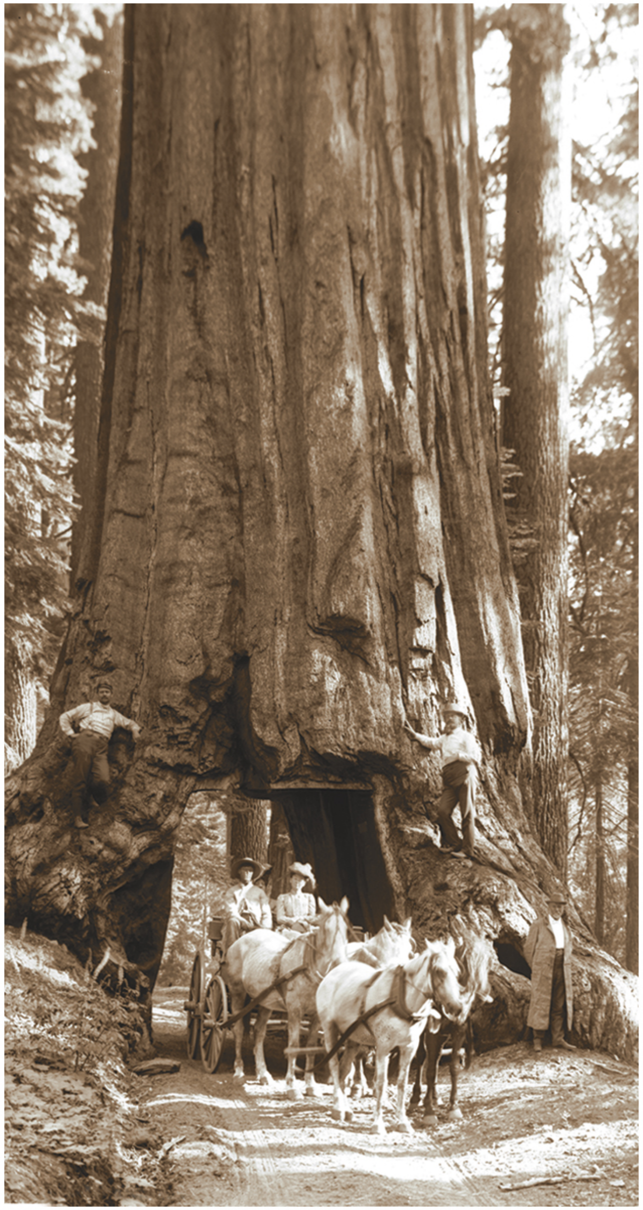

Growth ring
Vascular ray
Secondary xylem
Heartwood
Sapwood
Vascular cambium
Bark
Secondary phloem
Layers of periderm

Figure 35.23

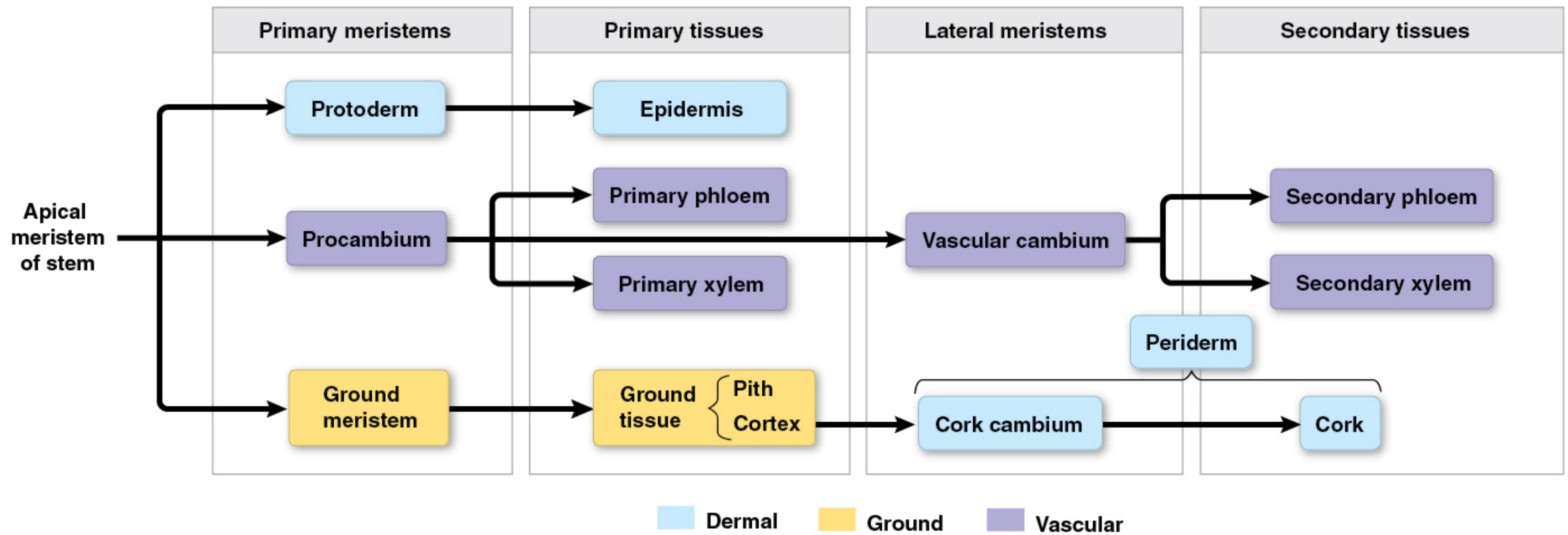


The Cork Cambium and the Production of Periderm

- Cork cambium gives rise to cork cells that accumulate to the exterior of the cork cambium
- Before dying, cork cells deposit waxy suberin in their walls, creating a water and gas impermeable barrier
- The cork cambium and the tissues it produces form a layer of periderm that replaces the epidermis

- **Bark** consists of all the tissues external to the vascular cambium, including secondary phloem and periderm
- **Lenticels** are pores in the periderm that allow for gas exchange between living cells of the stem or root and the outside air

Figure 35.24



Primary meristems
Primary tissues
Lateral meristems
Secondary tissues
Apical meristem of stem
Protoderm
Procambium
Ground meristem
Epidermis
Primary phloem
Primary xylem
Ground tissue
Pith
Cortex
Vascular cambium
Cork cambium
Periderm
Secondary phloem
Secondary xylem
Cork
Dermal
Ground
Vascular

Evolution of Secondary Growth

- Adding weights to the herbaceous plant *Arabidopsis thaliana*, stimulates secondary growth in the stem
- This finding indicates that weight carried by the stem activates development leading to wood formation

- The processes of primary and secondary growth may have evolved more closely than previously thought
- Developmental genes that regulate shoot apical meristems in *Arabidopsis* also regulate vascular cambium activity in poplar (*Populus*) trees

CONCEPT 35.5: Growth, morphogenesis, and cell differentiation produce the plant body

- Cells form specialized tissues, organs, and organisms through the process of **development**
- Developmental plasticity describes the effect of environment on development
  - For example, in the aquatic plant *Cabomba aquatica*, different leaves are formed depending on whether the shoot apical meristem is submerged

Figure 35.25

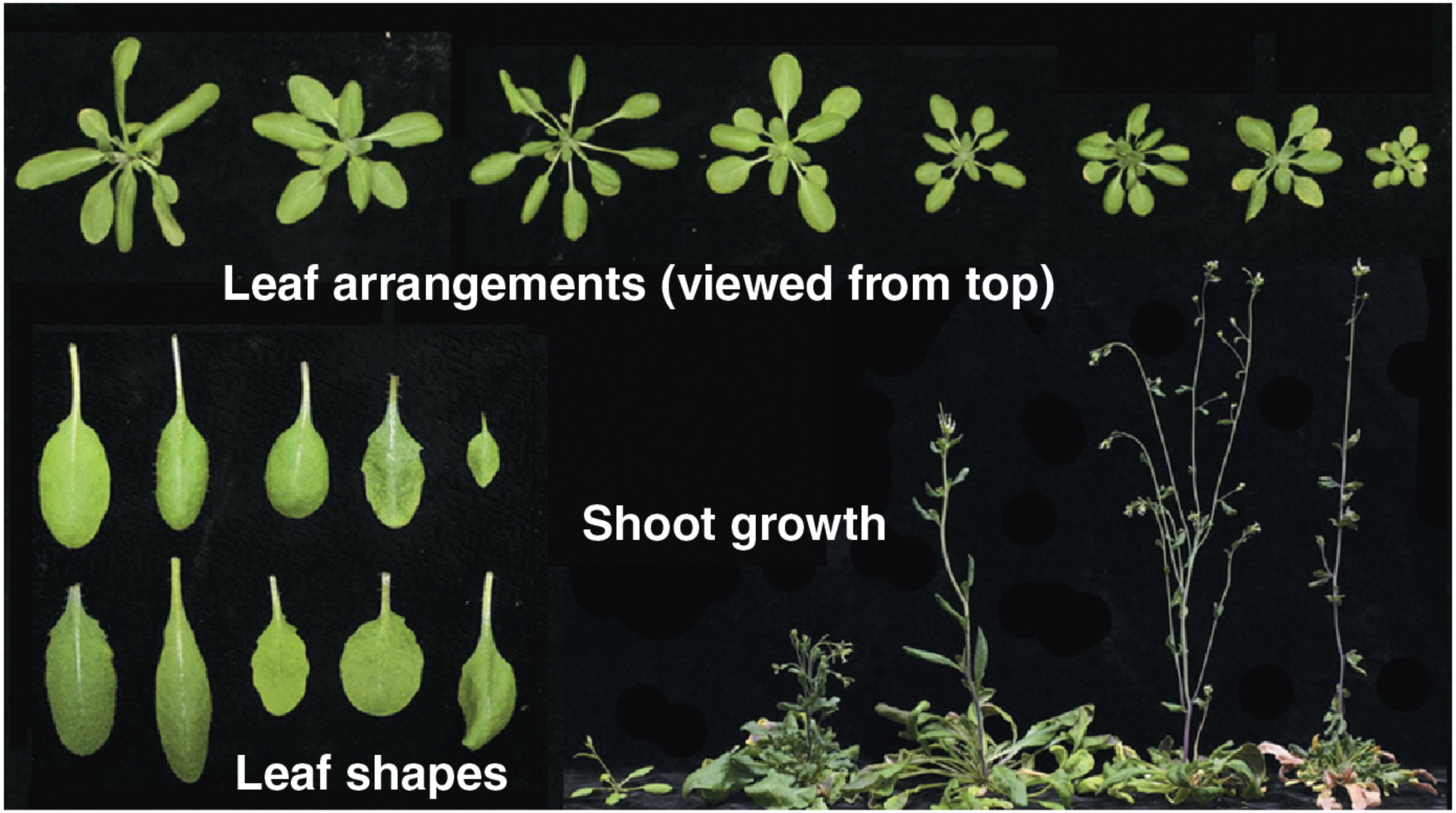
- Growth, morphogenesis, and cell differentiation are the processes involved in the development of multicellular organisms
  - Growth is an irreversible increase in size
  - Morphogenesis is the development of body form and cell organization
  - Cell differentiation is the process by which cells with the same genes become different from each other

Model Organisms: Revolutionizing the Study of Plants

- *Arabidopsis* is model organism for genetic analysis due to its small size, short generation time, prolific seed production, and small genome size
- *Arabidopsis* was the first plant to have its entire genome sequenced; it has 27,000 genes divided among five pairs of chromosomes

- The outward appearance of *Arabidopsis* varies markedly among populations from locations with different environmental conditions
- Genome sequencing will provide insight into the evolutionary adaptations that allowed *Arabidopsis* to occupy such varied environments

Figure 35.26



Leaf arrangements (viewed from top)
Shoot growth
Leaf shapes

- *Arabidopsis* is easily transformed with transgenes, genes from a different organism that are introduced into the genome of another
- CRISPR technology has also been used to “knock out” specific genes to learn about their functions
- Researchers aim to determine the blueprint for plant development by identifying the function and pathway for every gene in *Arabidopsis*

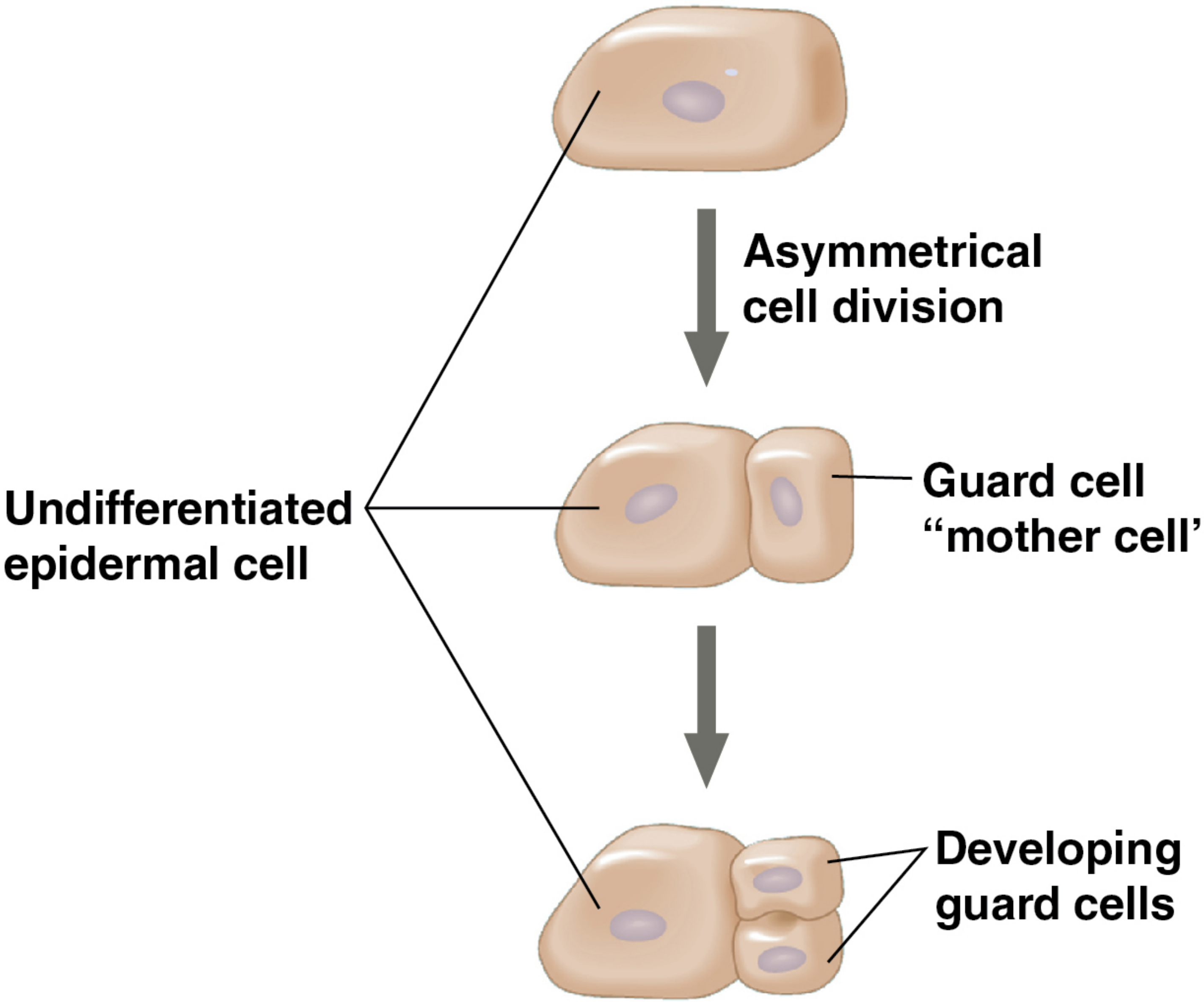
Growth: Cell Division and Cell Expansion

- Cell division in meristems increases the number of cells and, therefore, the potential for growth
- Cell elongation is the process directly responsible for increase in plant size

Cell Division

- New cell walls formed during cytokinesis develop from the cell plate that bisects the dividing cell
- The plane of division is typically the shortest path required to equally divide the cytoplasm
- Asymmetrical cell division signals a key event in development
  - For example, guard cell formation follows asymmetrical division and a change in the plane of cell division

Figure 35.27

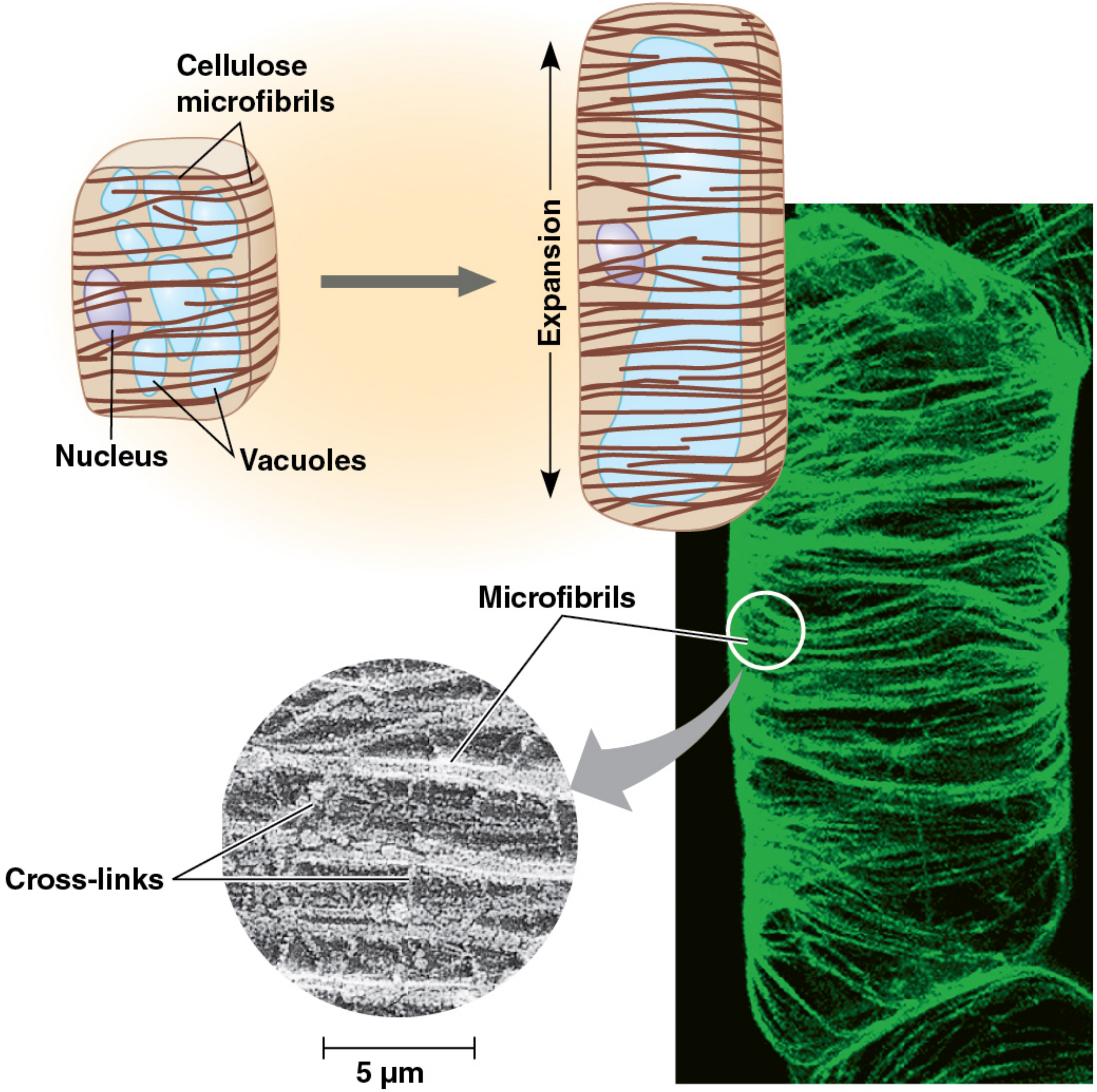

Asymmetrical cell division
Undifferentiated epidermal cell
Guard cell "mother cell"
Developing guard cells

Cell Expansion

- Animal cells grow by synthesizing protein-rich, energetically “expensive” cytoplasm
- About 90% of plant cell expansion is facilitated through intake and storage of water in vacuoles
- This allows plants to grow rapidly and economically
  - For example, bamboo shoots can grow more than 2 m per week

- The greatest expansion of plant cells is typically along the plant’s main axis
- Growth is restricted to the plane perpendicular to the orientation of cellulose microfibrils in the cell wall
  - For example, cells near the root tip may elongate more than 20 times their original length without increasing in width

Figure 35.28


Cellulose microfibrils
Nucleus
Vacuoles
Expansion
Microfibrils
Cross-links
5 µm

Morphogenesis and Pattern Formation

- **Pattern formation** is the development of specific structures in specific locations
- Two hypotheses explain the fate of plant cells during pattern formation
  - Lineage-based mechanisms propose that cell fate is determined early in development and passed to daughter cells
  - Position-based mechanisms propose that cell fate is determined by final position

- Plant cell fate has been experimentally demonstrated to be dependent on cell position
- In contrast, cell fate in animals is largely determined by lineage-dependent mechanisms
- Homeotic (*Hox*) genes in animals affect the number and placement of appendages in embryos

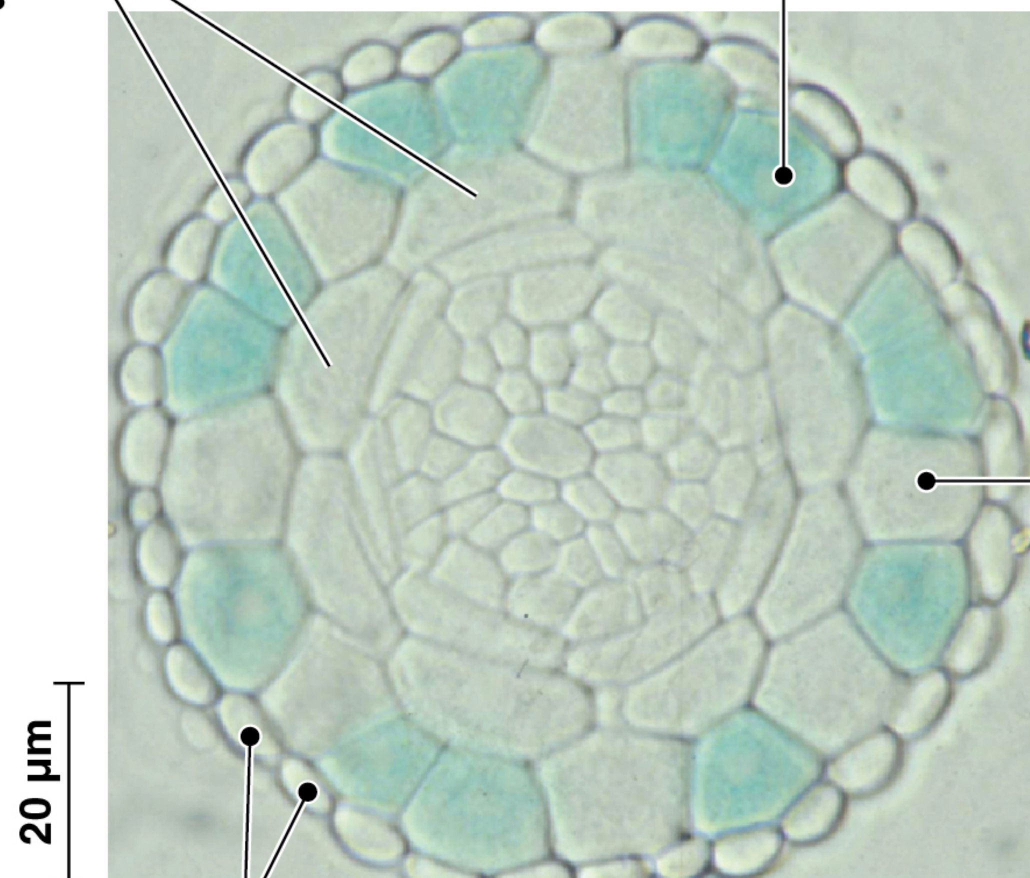
- A homolog of *Hox* genes in maize, *KNOTTED-1*, does not affect the number or placement of organs
- Unrelated transcription factors called *MADS-box* proteins fulfill this role in plants
- *KNOTTED-1* is important in the development of leaf shape
  - For example, overexpression of *KNOTTED-1* causes tomato leaves to become “super-compound”

Figure 35.29

Gene Expression and the Control of Cell Differentiation

- Despite having a common genome, cells can synthesize different proteins and diverge in structure and function
- Cellular differentiation depends on gene expression, but is determined by position
- Positional information is communicated through cell interactions

- Gene activation or inactivation depends on cell-to-cell communication
  - For example, *Arabidopsis* root epidermis forms root hairs or hairless cells depending on the number of cortical cells it is touching
  - Formation of root hairs is dependent on the differential expression of the *GLABRA-2* gene


When an epidermal cell borders a single cortical cell, the homeotic gene *GLABRA-2* is expressed, and the cell remains hairless.
Cortical cells
Here an epidermal cell borders two cortical cells. *GLABRA-2* is not expressed, and the cell will develop a root hair.
20 µm
The root cap cells external to the epidermal layer will be sloughed off before root hairs emerge.

Shifts in Development: Phase Changes

- Plants develop from a juvenile phase to an adult vegetative stage to an adult reproductive stage
- These developmental stages, **phase changes**, are restricted to the shoot apical meristem
- The most obvious morphological changes occur in leaf size and shape

Figure 35.31

Juvenile leaf

Mature leaf

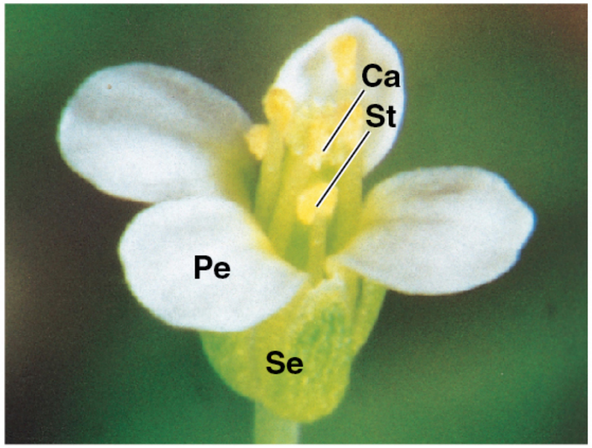
Genetic Control of Flowering

- Flower formation involves a phase change from vegetative growth to reproductive growth
- It is triggered by a combination of environmental cues and internal signals, such as hormones
- Flower production stops the primary growth of that shoot
- The transition to flowering is associated with the switching on of flower-inducing genes

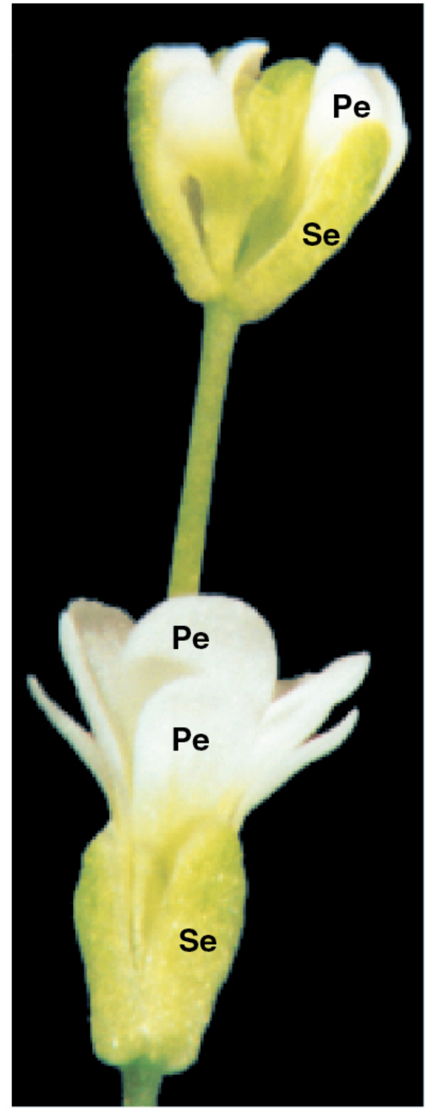
- The order of primordium emergence determines its development into a sepal, petal, stamen, or carpel
- Floral organs form four whorls in roughly concentric “circles” viewed from above
- Sepals are outermost and form first, followed by petals, stamens, and then the innermost carpels

- Several genes encode transcription factors that regulate development of floral pattern
- Positional information determines which genes are expressed in a particular floral organ primordium
- A mutation in a flower-inducing gene can cause abnormal floral development

Figure 35.32



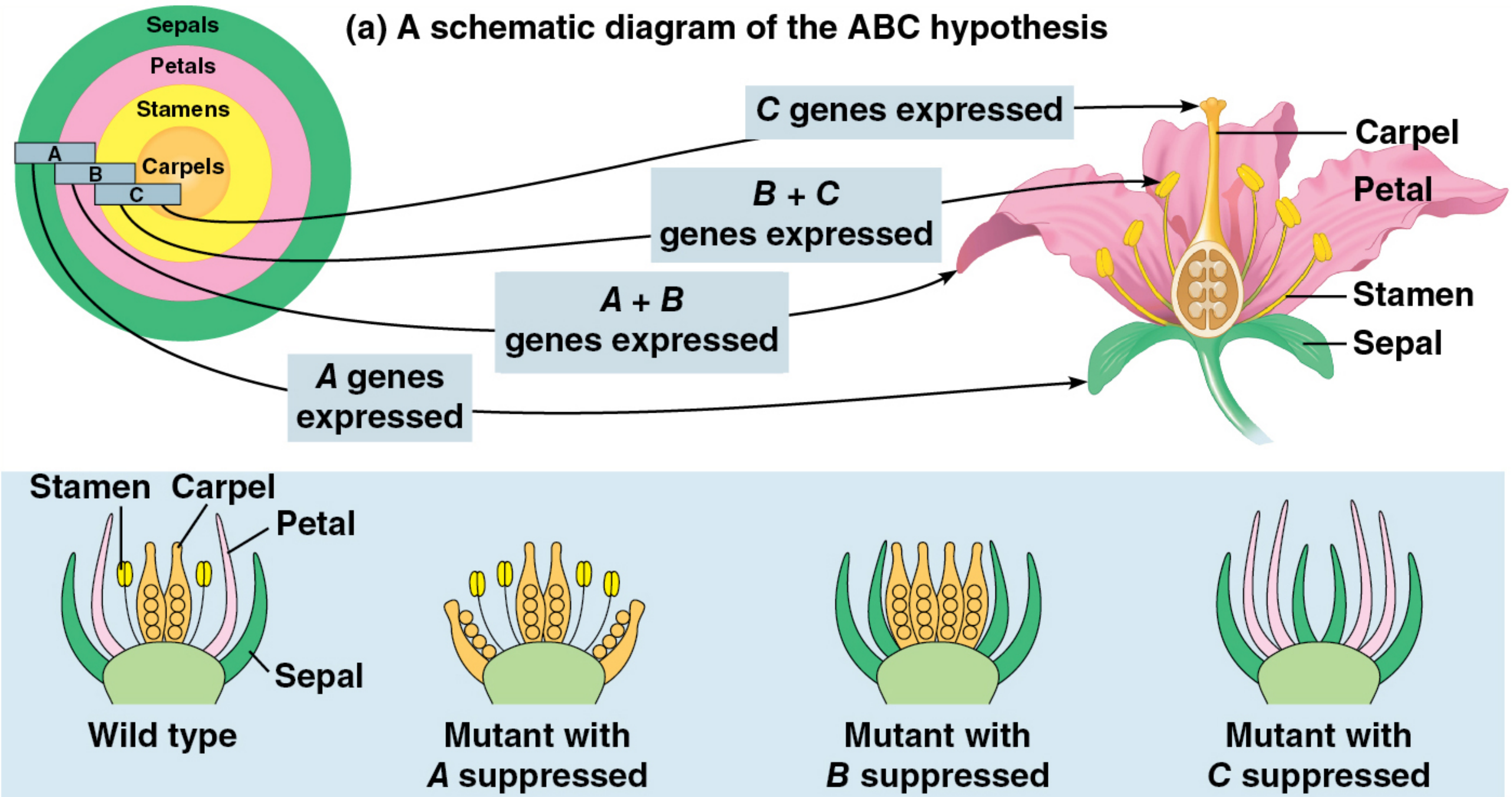
Normal *Arabidopsis* flower



Abnormal *Arabidopsis* flower

- The **ABC hypothesis** of flower formation proposes that three classes of genes direct the formation of the four types of floral organs
- Each class of genes is switched on in two specific whorls of the floral meristem

Figure 35.33



(b) Side view of wild-type flower and flowers with organ identity mutations.

Figure 35.UN01a

Figure 35.UN01b

Seed Collection Site	Average Area of a Single Tooth (cm^2)		Number of Teeth per cm^2 of Leaf Area	
	Grown in Rhode Island	Grown in Florida	Grown in Rhode Island	Grown in Florida
Ontario (43.32°N)	0.017	0.017	3.9	3.2
Pennsylvania (42.12°N)	0.020	0.014	3.0	3.5
South Carolina (33.45°N)	0.024	0.028	2.3	1.9
Florida (30.65°N)	0.027	0.047	2.1	0.9

Data from D. L. Royer et al., Phenotypic plasticity of leaf shape along a temperature gradient in *Acer rubrum, PLoS ONE* 4(10):e7653 (2009).

Figure 35.UN02

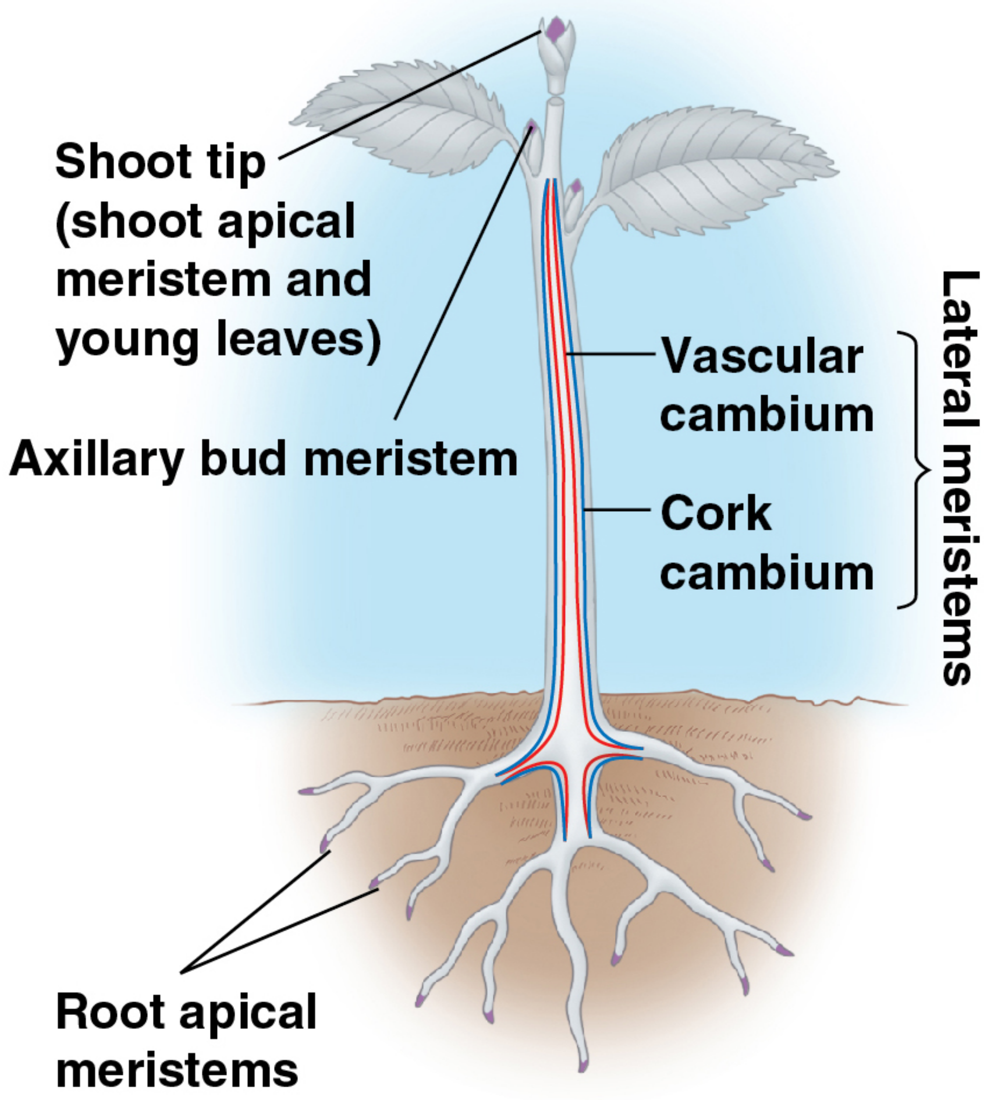


Figure 35.UN03

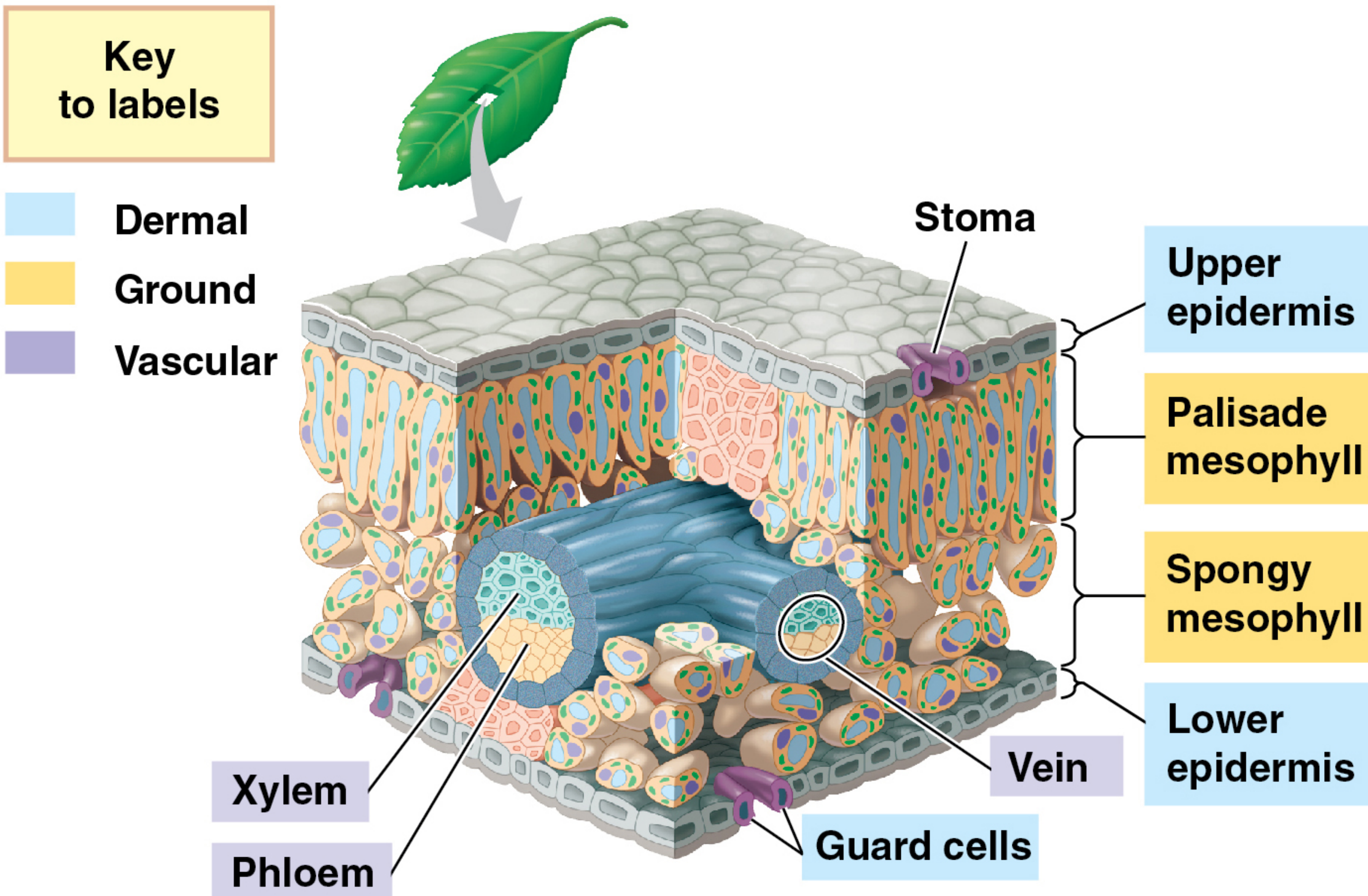


Figure 35.UN04

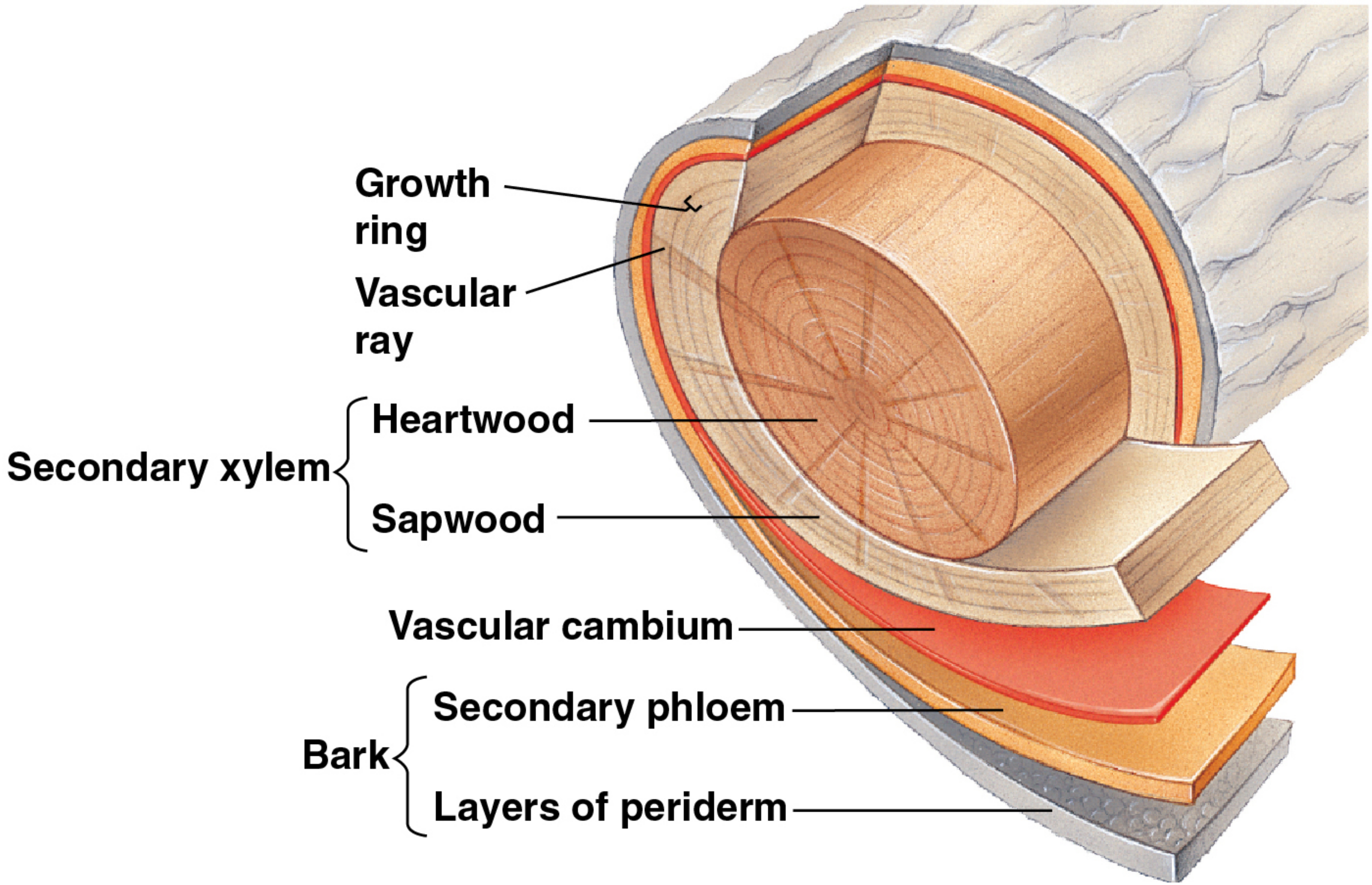


Figure 35.UN05

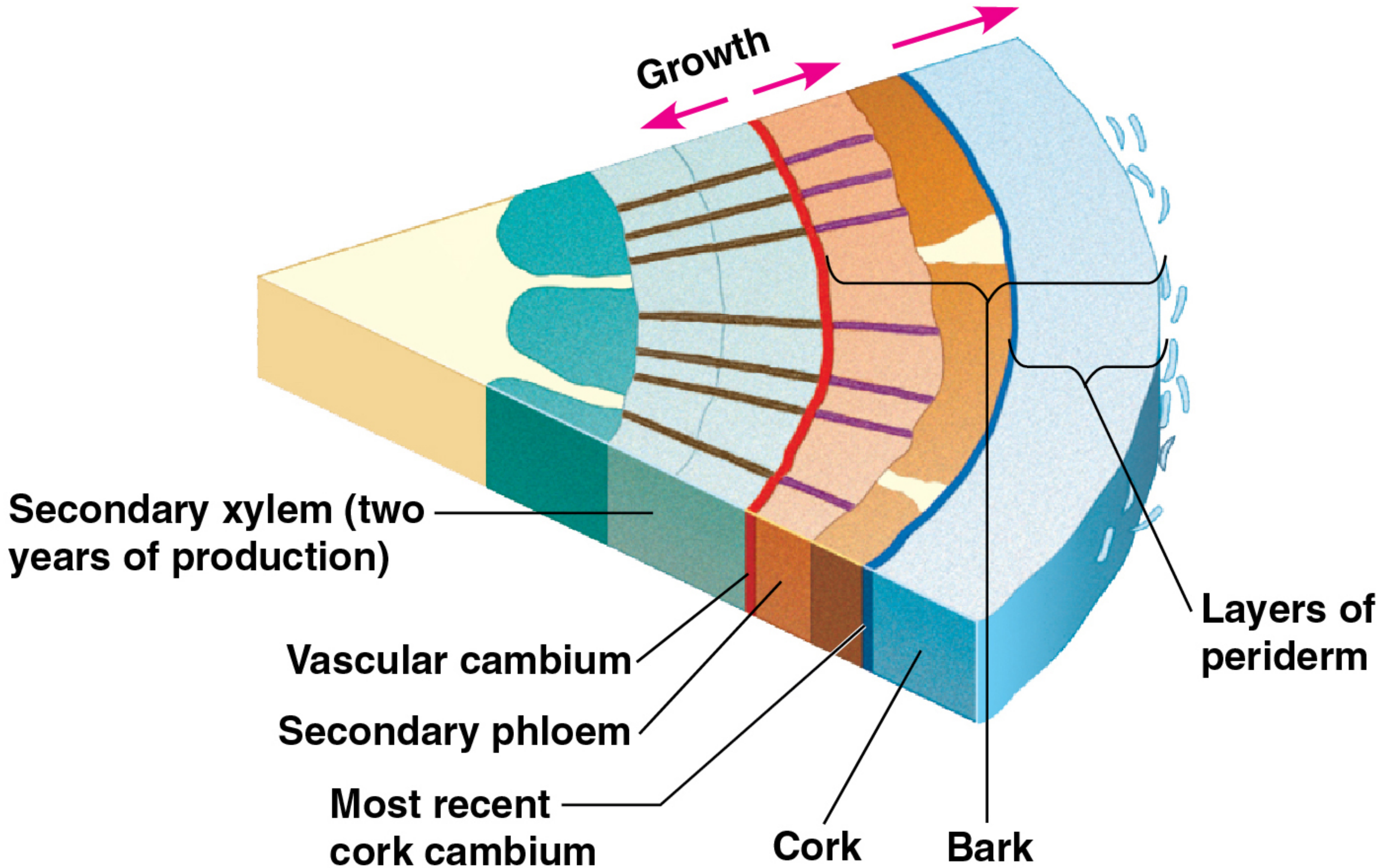


Figure 35.UN06