Stems

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Introduction

Stems are typically aboveground organs that grow toward light (positive phototropism) and away from the ground (negative gravitropism). They provide support for the aerial portions of plants and serve multiple other functions in a plant. Stems play an important role as the conduits of the vascular tissues (xylem and phloem) needed for long-distance transport of water, minerals, photosynthetically derived sugars, and hormones. Indeed, the evolution of vasculature was one of the major advancements needed for plants to colonize the land. Accordingly, the evolution and design of the stem vascular system (a.k.a. **stele**) is of great interest to plant anatomists. This chapter will take an in-depth look at stem diversity and structure and introduce the basics of the plant vascular system.

11.1 Stems Have a Variety of Forms and Functions

One of the primary functions of a stem is the production of leaves and the proper arrangement of those leaves in space. Stems are also the organ from which flowers are generated and are held in the proper position for pollinators. Stems have tissues that provide a means to increase length (apical meristems), girth (lateral meristems), and additional branching (axillary buds). Roots can develop directly from a stem; such roots are called adventitious. By generating xylem and phloem, stems are a conduit for the long-distance transport of water, nutrients, and photosynthate and allow the leaves and the roots to engage in whole-plant communication (▣ Fig. 11.1a–c).

The stem is typically thought of as a long, thin projection from which leaves or flowers emerge. Indeed, that form is found on many extant plants and is the form to have evolved first. However, over time, natural selection produced several other forms and functions (▣ Fig. 11.1d–g). Flattened stems that lack leaves and perform photosynthesis are called **cladodes**; cactus "pads" are a common form. Cladodes that resemble leaves, such as those found on *Acacia* (Dong and He 2017), are also referred to as **cladophylls phyllodes** and **phylloclades**. **Rhizomes** are underground stems that can play the role of a root (anchorage and water uptake), allow for asexual reproduction, or serve as a storage organ as seen in the common potato tuber. **Stolons** differ from rhizomes in that rhizomes grow beneath the soil surface, while stolons grow across the soil surface. Stolons allow for plant dispersal and asexual reproduction. Stems may also serve as perennating organs. **Tendrils** may be modified leaves or stems that aid in attachment of viney plants. Stems may also serve as perennating organs. **Perennation** is the process of survival from one growing season to another as a perennial species. Rhizomes (or tubers) and **corms** (or bulbs) may also serve as perennating organs.

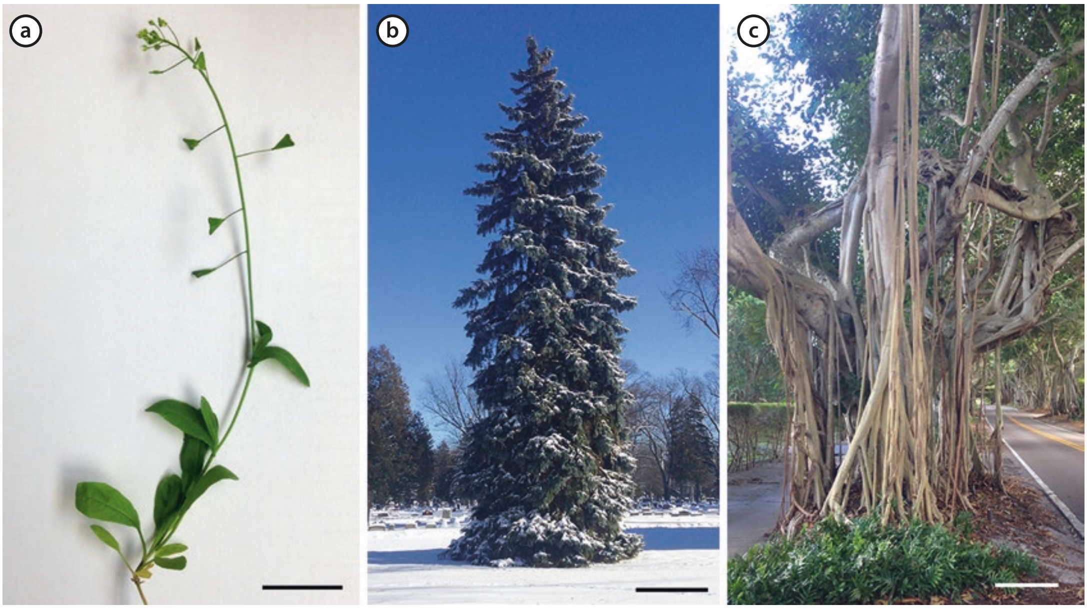


Fig. 11.1 **a**–**c** Stems may serve multiple functions. **a** Shepard's purse (*Capsella bursa*) stems give rise to the leaves, flowers, and the fruit that develop from flowers. **b** Tree stems provide the mechanisms for increase in girth as a tree develops over the course of time and provide the means to produce additional branching stem growth, as in white spruce (*Picea glauca*). **c** The banyan tree (*Ficus benghalensis*) starts as an epiphyte when an animal deposits a sticky seed on the limb of another tree. The plant develops roots that eventually reach the ground and send shoots up the host trunk. Subsequently, roots are initiated from the limbs, and growth extends outward from the original trunk. Scale bars = 2 cm in **a**, 2 m in **b**, and 1 m in **c**. (**a**–**c** RR Wise)

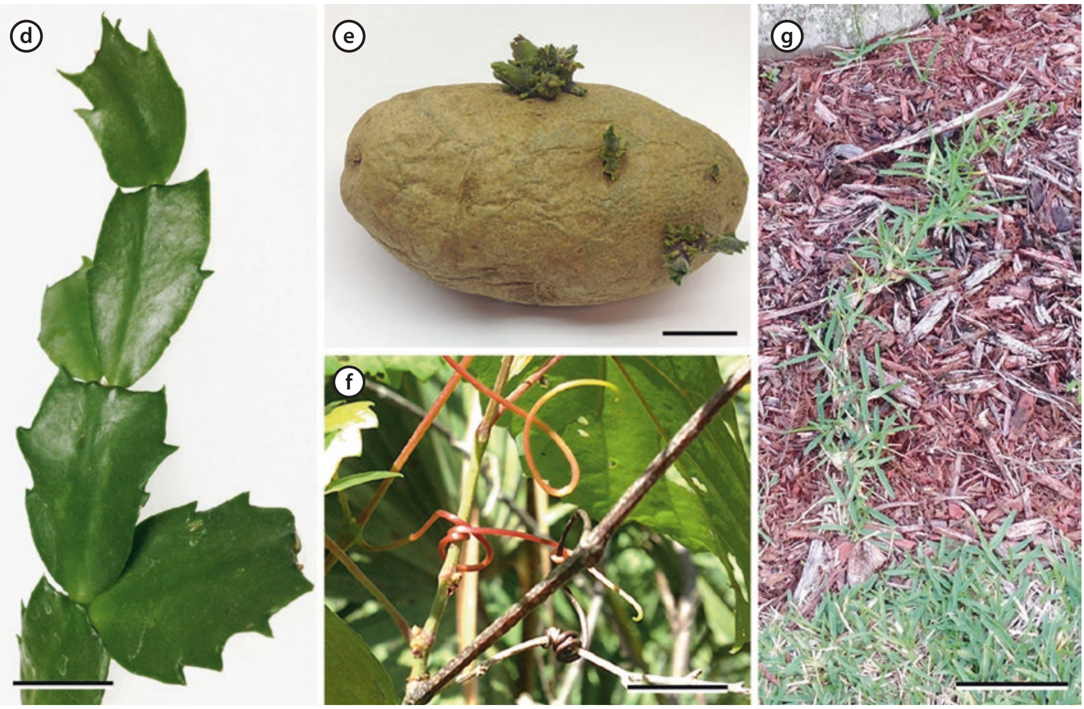
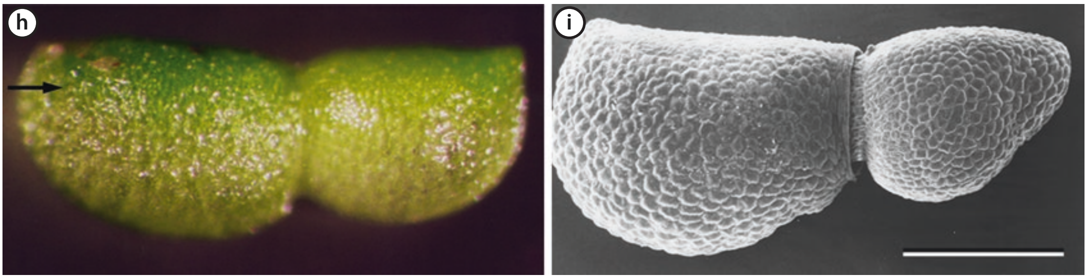


Fig. 11.1 **d** Cladodes of a Christmas cactus (*Schlumbergera* sp.) are clearly photosynthetic. **e** Rhizomes, such as potato (*Solanum tuberosum*) tubers, are underground stems that often function in starch storage. **f** Tendrils are modified stems that help passionflower (*Passiflora* sp.) vines climb up and cling to surfaces. **g** Stolons of St. Augustine grass (*Stenotaphrum secundatum*) grow across the soil surface and are a form of both plant dispersal and asexual reproduction. Scale bars = 2 cm in **d**, **e**, and **f** and 10 cm in **g**. (**d**–**g** RR Wise)

Not all plants possess a stem. For instance, the much-reduced members of the duckweed family (Lemnaceae) are monocots that have adapted an aquatic habitat. The true duckweeds (*Lemna* sp.) are composed of small leaf-like fronds and one to a few roots. Watermeal plants (*Wolffia* sp.) are even more reduced and consist of two connected individuals—a mother frond that asexually produces multiple daughter fronds from a pouch at one end (◘ Fig. 11.1h, i).

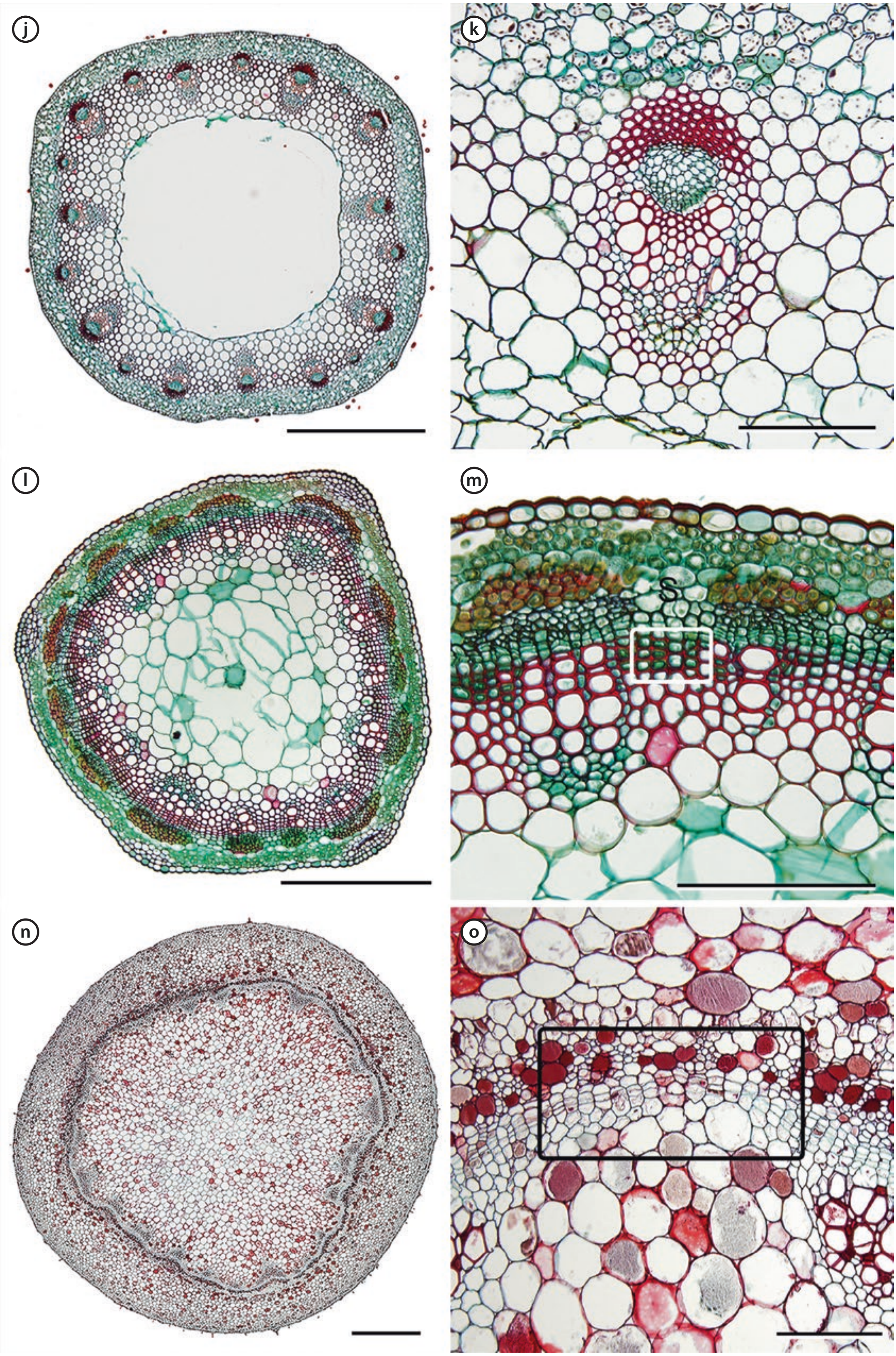
Several basic stem types are apparent based on (a) the presence or absence of secondary growth and (b) on the plant group. Stems with only primary growth are said to be herbaceous, a characteristic found in most annuals (one-year life cycle) and biennials (two-year life cycle). Stems with true secondary growth are commonly called woody stems. The secondary growth arises from a vascular cambium which, in some plants, may remain active for decades, centuries, or even millennia (refer to ◘ Fig. 11.8a), leading to accumulations of xylem and a very large stem diameter.

Eudicot stems may be either herbaceous or woody although a range of intermediate types may be identified (◘ Fig. 11.1j–o) and anomalous versions abound (► Sect. 14.5). Monocot stems lack true secondary growth. However, a primary thickening meristem and diffuse secondary growth (► Sect. 11.9) combined with heavy sclerification can produce large, perennial monocots (refer to the palm tree in ► Fig. 1.19). Woody eudicots will be discussed in more detail in ► Chap. 15—Wood.



◘ **Fig. 11.1** Northern watermeal (*Wolffia borealis*) imaged with light microscopy **h** and scanning electron microscopy **i**. Watermeal plants float on the water surface. These two specimens are laying on their sides, and the waterline is indicated by the arrow in **h**. The mother frond is to the left and the daughter frond to the right in both images. Watermeal is a monocot in the family Lemnaceae. Scale bar in **i** = 250 µm and applies to both panels. (**h, i** RR Wise)

◘ **Fig. 11.1** Examples of herbaceous stems. **j** The buttercup (*Ranunculus* sp.) stem is completely herbaceous with the xylem conducting elements and phloem fibers being the only sclerified tissues. The *Ranunculus* vascular bundles are in a ring and stay separated due to the absence of an **interfascicular cambium**. **k** No vascular cambium is present within the *Ranunculus* bundles, meaning the bundles are closed. **l** Alfalfa (*Medicago sativa*) vascular bundles are separated. **m** An interfascicular cambium is present in alfalfa, but it produces mostly sclerenchyma (cells in boxed area), not xylem conducting elements so the vasculature does not form a ring. **n** In the geranium (*Pelargonium* sp.) stem, the vascular bundles are close together. **o** An active interfascicular cambium (cells in boxed area) produces a cylinder of vasculature. Scale bars = 500 µm in **j** and **n**, 250 µm in **l**, and 100 µm in **k**, **m,** and **o**. (**j–o** RR Wise)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Box 11.1 Commercial Value of Edible Stems

From an economic standpoint, stems are very important plant parts. We use many plants stems as a food source. Here is a partial list of plants with edible stems or where the stems are important to obtain an edible product:

- Asparagus (*Asparagus officinalis*): entire stem consumed.
- Broccoli (*Brassica oleracea* var. *italica*): the stem and floral tissue are consumed in this species. Often uneaten in favor of broccoli florets, stalks are a good source of antioxidants including ascorbic acid, carotene, and phenols.
- Ginger (*Zingiber officinale*): the rhizome is a modified stem that is typically used to season foods.
- Kohlrabi (*Brassica oleracea* var. *gongylodes*): the same species as cabbage, broccoli, and cauliflower, in kohlrabi, the swollen stem is consumed.
- Maple trees (*Acer* sp.): tree trunks tapped for xylem sap from several tree species including sugar maple (*Acer saccharum*), red maple (*A. rubrum*), silver maple (*A. saccharinum*), and black maple (*A. nigrum*).
- Potato (*Solanum tuberosum*): stem tuber, which is an underground stem is consumed.
- Sugarcane (*Saccharum* sp.): sap of stem used to produce cane sugar.
- Taro (*Colocasia esculenta*): the corm, an underground stem, is made into flour and used in such products as bread and pancake mix.

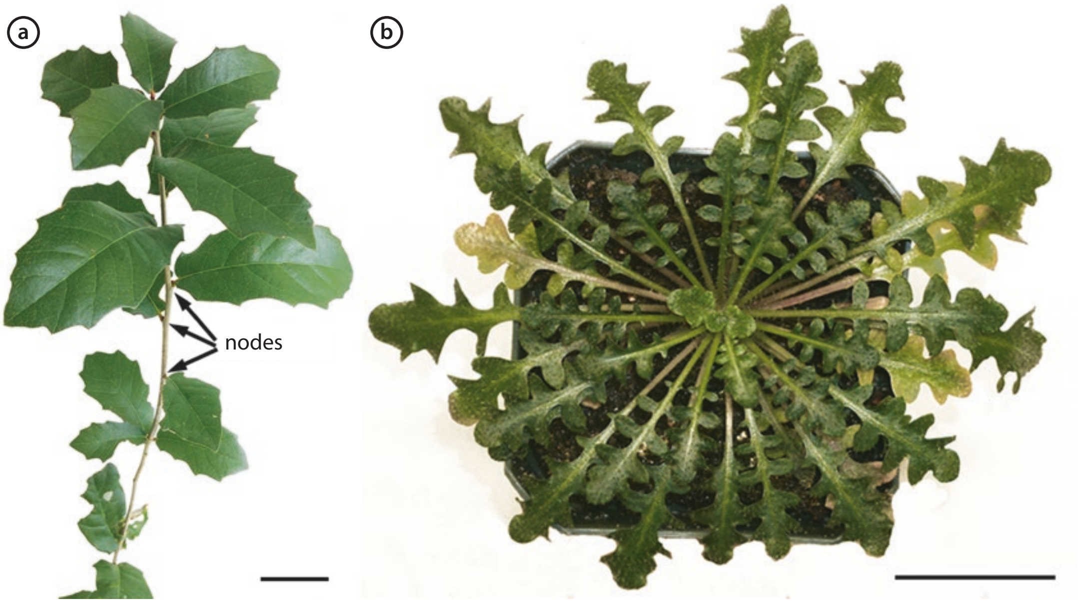
Reference Wolf (1989)

11.2 External Stem Morphology Varies Among Monocots and Herbaceous Eudicots

Stems are divided along their length into nodes and internodes (◘ Fig. 11.2a). Nodes are the points along a stem where lateral organs originate—leaves, flowers, and branches. Internodes are the portions of the stem between nodes, and they develop by intercalary growth. **Intercalary growth** means there is no organized meristem, and the mitotic activity (cell division) occurs between nodes. Internodes vary greatly in length. In rosette plants and bulbs, the internodes are so short that these plants are said to lack internodes entirely (◘ Fig. 11.2b).

Eudicot stems that show secondary growth retain marks of the previous year's growth (◘ Fig. 11.2c–g). The terminal bud represents a separate node at the tip of a short internode that separates it from a pair of subtending lateral (or **axillary**) buds. In the overwintering stage, the terminal bud is covered by several layers of bud scales, which are modified leaves. Leaf scars remain from abscised leaves and show the pattern of leaf traces in the vascular node as indicated by the site(s) of such scars that encircle the stem, with internodes in between the sets of bud scale scars.

Monocot stems may have obvious nodes, such as those seen in bamboo (◘ Fig. 11.2h). The nodes along much of the bamboo stem lack leaves, and an intercalary meristem at each node is responsible for



◘ **Fig. 11.2** **a**, **b** Eudicot stems. **a** Photograph of a stem with node labeled. **b** Picture of a rosette plant (*Arabidopsis lyrata*) showing no stem. Scale bars = 2 cm in both panels. (**a**, **b** RR Wise)

the increase in the length of the stem. A secondary thickening meristem also contributes to the stem growth (refer to ► Sect. 11.9). Many grasses have a stem in which most of the supportive tissue is actually a combination of multiple **leaf sheaths** arranged in concentric rings around a small pith. The leaf is initiated at a node (which is concealed by the subtending leaf sheath) and elongates for some distance as a leaf sheath before the leaf blade extends away from the stem (◘ Fig. 11.2i).

Phyllotaxis is the pattern of leaf distribution on the stem. It is an easily identifiable and genetically controlled trait and thus of considerable value to plant systematics in the characterization and identification of plant species. There are three common patterns with numerous variations on the theme: alternate, opposite, and whorled (◘ Fig. 11.2j–l). In an alternate pattern, a node produces a single leaf, while the nodes above and below produce leaves on the opposite side of the stem. An opposite phyllotaxis produces two leaves on the same node that are directly opposite each other. In a whorled pattern, multiple leaves arise from a single node.

If successive leaf pairs in an opposite pattern are at right angles to each other, the pattern is called **decussate** (◘ Fig. 11.2m). Leaves in a **distichous** phyllotaxis pattern may be either opposite or alternate and lie in vertical rows to either side of the stem, resulting in a fan-shaped plant (◘ Fig. 11.2n). Many cacti and succulent plants have a spiral pattern that produces a striking plant form (◘ Fig. 11.2o).

Box 11.2 Colonization of Land and the Monocot/Eudicot Split

As the stem evolved, it became important for adaptation to land dwelling as well as aquatic. Aquatic plants did not need the type of support that stems give to aerial portions of the plant. Some of the developmental changes involved the generation of lignin for support, cuticular waxes that prevented water loss, and vascular tissue for long-distance transport of a variety of internal substances in the course of evolution. For larger plants (i.e., those capable of experiencing secondary growth), the tissues that give rise to the vasculature (vascular cambium) do double duty as the tissues that give rise to the supportive tissues (wood). Air (and the more directional light that an atmosphere provides) was a new three-dimensional resource to access, leading to stems and phyllotaxy.

Monocotyledonous plants (monocots) and eudicotyledonous plants (eudicots) have shoot systems with very different architectures. Using molecular and genomic data sets, it has been estimated that the monocots diverged from the established eudicots some 140 million years ago (mya; in the late Jurassic period) and that core eudicots diverged approximately 110 mya. Keep in mind that conifers are not flowering plants and that only monocots and eudicots are descended from flower-producing plants.
Reference Wolf (1989)

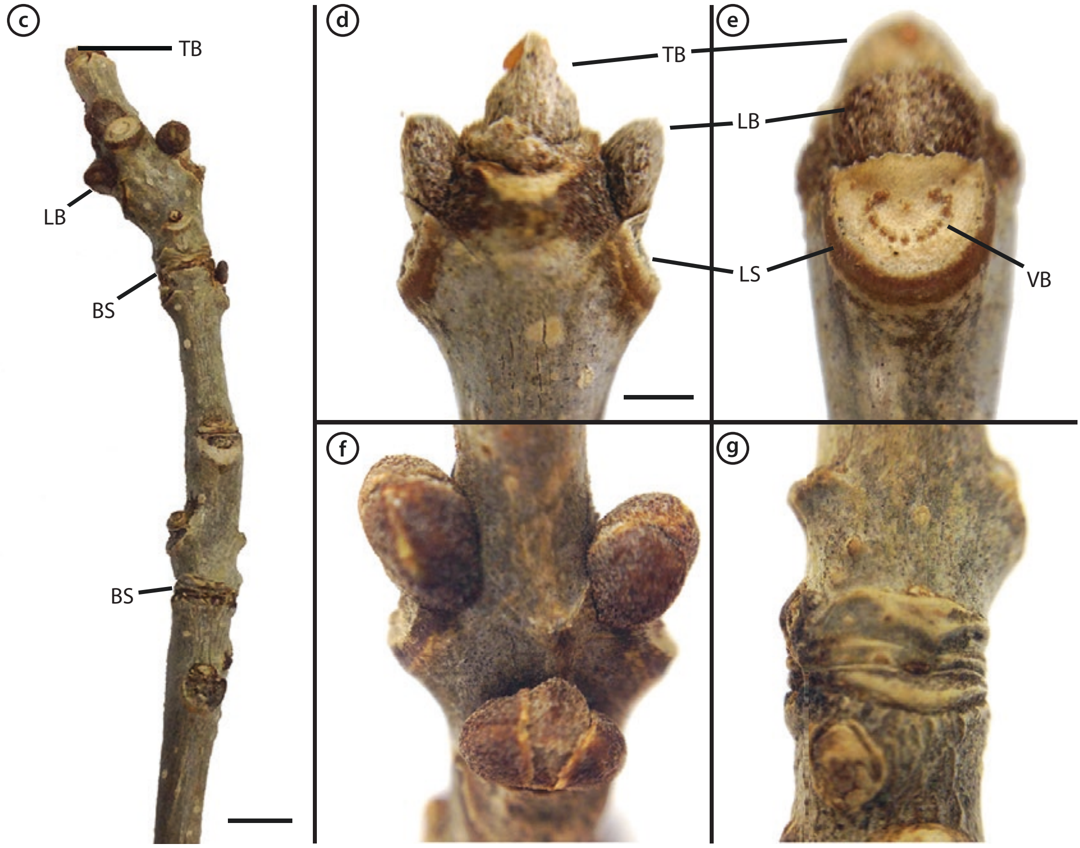


Fig. 11.2 **c** Stem tip of an overwintering green ash (*Fraxinus pennsylvanica*) showing a single terminal bud (TB), multiple lateral buds (LB), and two sets of bud scale scars (BS). The bud scale scars mark the nodes. The other four panels are higher magnification views of **d** a terminal bud with a pair of subtending lateral buds and a pair of leaf scars (LS), **e** a leaf scar seen face-on with a semicircle pattern of vascular bundle (VB) scars, **f** three lateral buds near the stem tip (two above and one below a short internode), and **g** bud scale scars from a previous year's terminal bud. Scale bars = 1 cm in **c** and 5 mm in **d**. The scale bar in **d** also applies to panels **e**, **f**, and **g**. (**c**–**g** RR Wise)

Fig. 11.2 Monocot stems. **h** A forest of moso bamboo (*Phyllostachys edulis*) stems in the Arashiyama Bamboo Grove, Japan, clearly showing nodes and internodes. **i** Zebra grass (*Miscanthus sinensis*) stem with multiple leaf sheaths visible. Scale bars = 1 m in **h** and 5 cm in **i**. (Image **h** courtesy of N.E. Wise; **i** RR Wise)

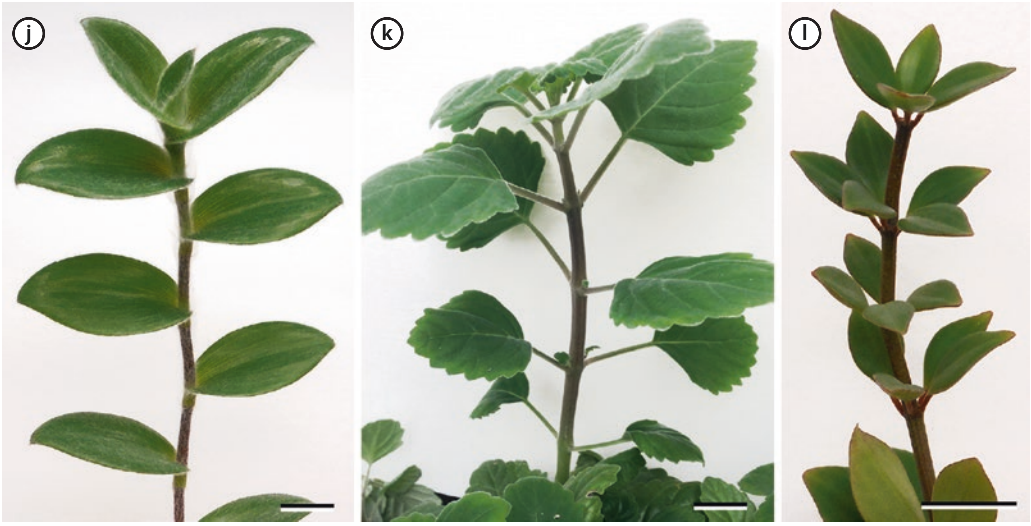
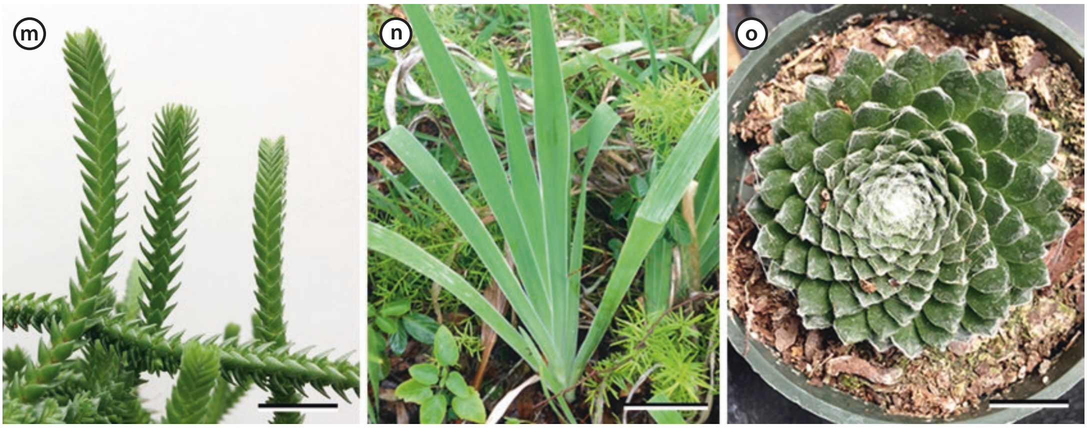


Fig. 11.2 **j** Common phyllotaxis patterns of alternate (*Tradescantia sillamontana*), **k** opposite (*Plectranthus ernstii*), and **l** whorled (*Peperomia pereskiifolia*) leaf arrangements. Scales bars = 2 cm in all three panels. (**j**–**l** RR Wise)



■ **Fig. 11.2** Patterns of leaf initiation. **m** Decussate pattern in rattail crassula (*Crassula muscosa*). **n** Distichous pattern in blackberry lily (*Iris domestica*). **o** Spiral pattern in a cobweb houseleek (*Sempervivum arachnoideum*). Scale bars = 1 cm in **m**, 5 cm in **n,** and 1 cm in **o**. (**m**–**o** RR Wise)

11.3 The Stem Is Composed of Three Tissues: Dermal, Ground, and Vascular

Stem dermal, ground, and vascular tissues are so categorized based on their developmental origins and their final function. **Dermal tissues** originate at the shoot apex, are derived from the protoderm, and function largely in protection. The ground meristem produces the ground tissues of cortex, pith, and conjunctive tissues that provide bulk to the stem as well as possible organic storage. The procambium gives rise to the vascular tissues of xylem and phloem.

Monocot and eudicot stems in the primary state of growth differ slightly in their arrangement of dermal tissue, ground tissue, and vascular tissue (■ Figs. 11.3a–c and 11.3d–f). Both have an outer epidermis and inner vascular bundles. However, the circular arrangement of the eudicot vascular bundles divides the ground tissue into two zones. The region between the epidermis and the vasculature is called the **cortex**, while the ground tissue in the center of the stem is termed **pith** (a.k.a. **medulla**). The vascular bundles of the monocot stem are intermixed with the ground tissues and termed **medullary bundles**. In case of monocots, all of the ground tissue, regardless of where found in the stem, is called **conjunctive tissue** because there is no clear delimitation between the cortex and the pith as in the eudicot stem.

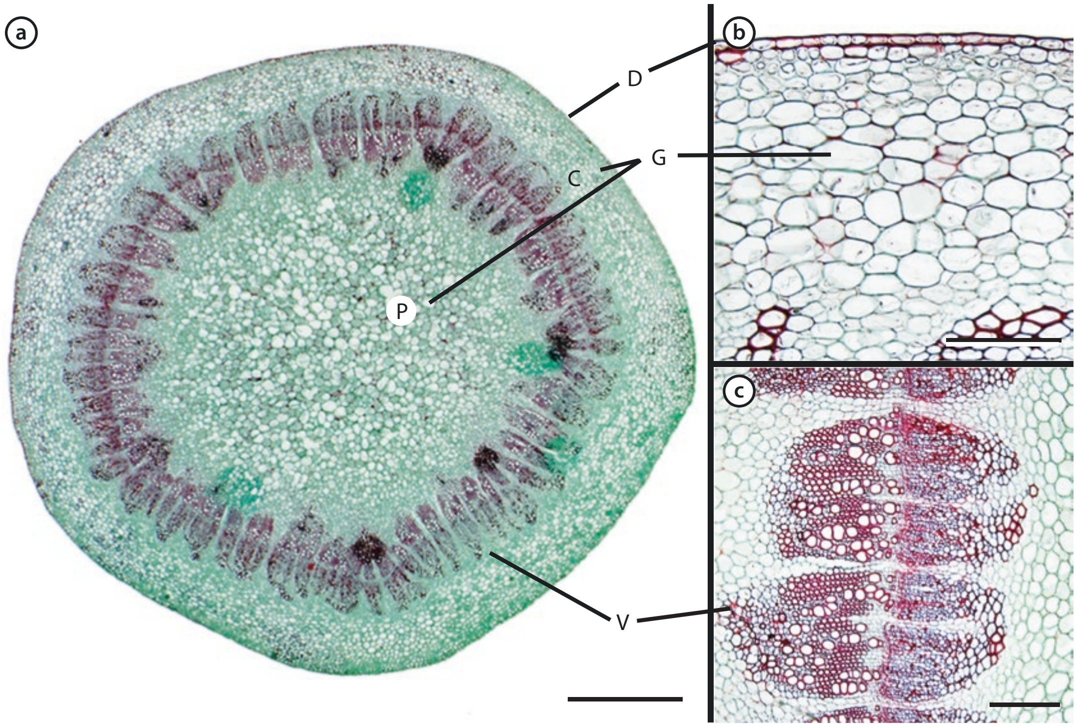


Fig. 11.3 **a**–**c** Cross-section of a eudicot stem (wild cabbage, *Brassica oleracea*) showing dermal tissue (D), ground tissues (G) consisting of cortex (C) and pith (P), and a ring of vascular tissue (V). Scale bars = 500 μm in **a** and 100 μm in **b** and **c**. (**a**–**c** RR Wise)

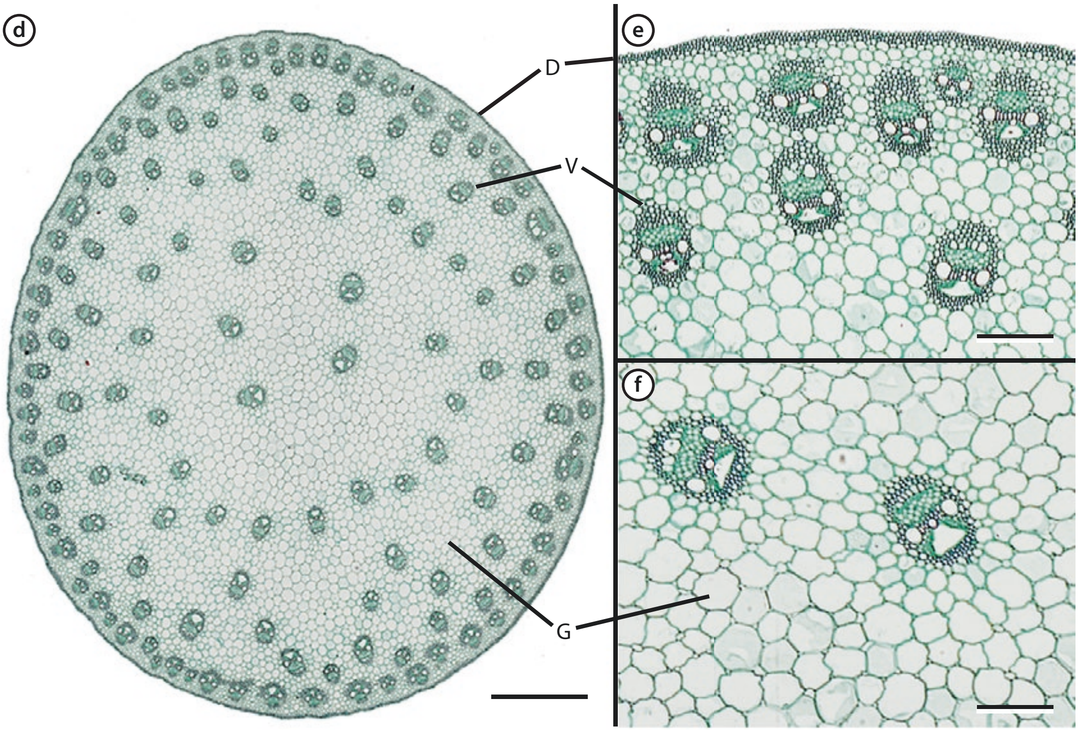
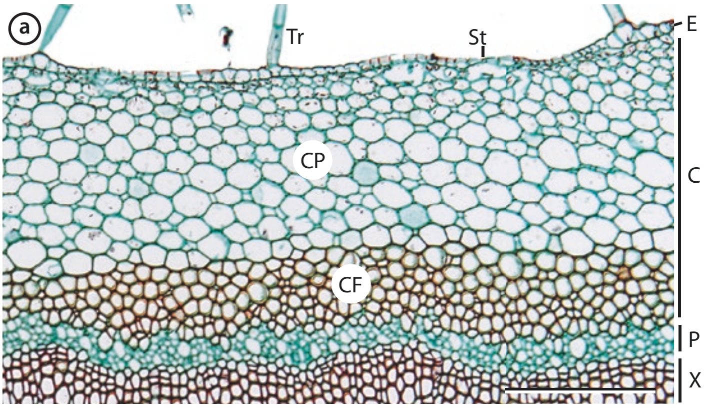


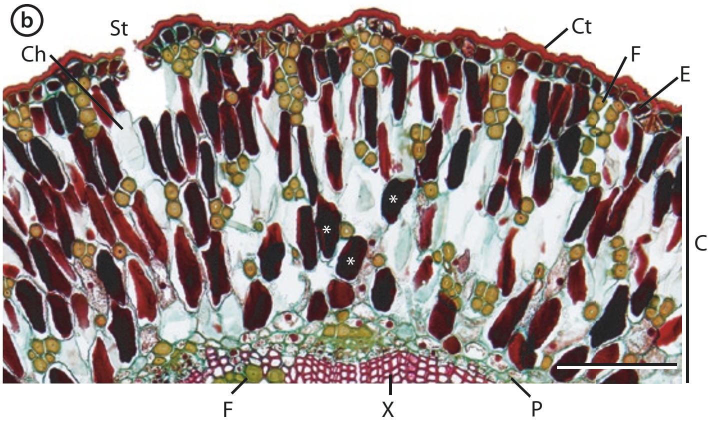
Fig. 11.3 **d**–**f** Cross-section of a monocot stem (maize, *Zea mays*) showing dermal tissue (D), ground tissue (G, a.k.a. conjunctive tissue), and vascular bundles (V). Scale bars = 500 μm in **d** and 100 μm in **e** and **f**. (**d**–**f** RR Wise)

11.4 Dermal Tissues Cover the Stem Exterior

In young stems or those experiencing primary growth, the dermal layer consists in most instances of a single-layered epidermis covered with a waxy cuticle (■ Fig. 11.4a, b). Epidermal cells are frequently smaller than the underlying cortical parenchyma, and the cuticle varies in thickness depending on age of stem and habitat. Note that the mesophytic *Digitalis* stem and the hydrophytic *Myriophyllum* stem shown in ■ Fig. 11.5a have a thin cuticle (too thin to be seen in the image), while the xerophytic *Ephedra* stem has a thick cuticle (■ Fig. 11.4b). The stem epidermis may also have trichomes and stomata, common features of most plant epidermises (refer to ▶ Chap. 9). In plants with prolonged secondary growth, the epidermis is replaced by a complex tissue called the periderm (▶ Chap. 16).



■ **Fig. 11.4** **a** A portion of purple foxglove (*Digitalis purpurea*) stem epidermis and cortex showing trichomes (Tr), one stoma (St), the single-cell epidermal layer (E), and a thick cortex (C) containing cortical parenchyma (CP) and cortical fibers (CF). Phloem (P) and xylem (X) lie to the interior. Scale bar = 50 µm. (RR Wise)



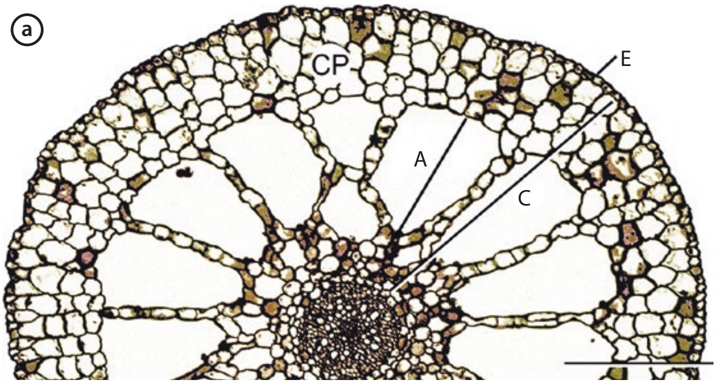
■ **Fig. 11.4** **b** California jointfir (*Ephedra californica*) stem in cross-section showing a thick, red-stained cuticle (Ct), a single layer of tannin-filled epidermal cells (E), one stoma (St), and a cortex (C) containing a mixture of light-blue chlorenchyma (Ch) and tannin-filled cortical parenchyma (three in the middle of the image are marked with *). Fibers (F), stained tan, are seen scattered throughout the cortex, phloem (P), and xylem (X). Scale bar = 50 µm. (RR Wise)

11.5 Ground Tissues Compose the Cortex, Pith, and Conjunctive Tissue

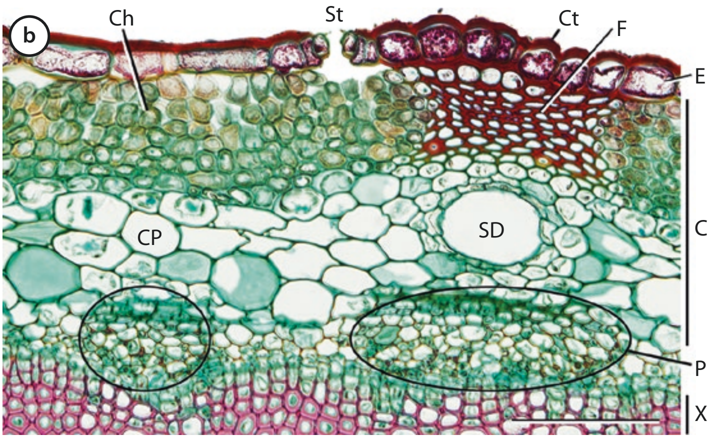
Ground tissues include the cortex and pith in eudicots and conjunctive tissue in monocots. For example, conjunctive tissue in monocots is often represented as parenchyma surrounding the vascular bundles, or it may consist of fibers whose walls can become very thick. Such is the case with corn stem, gingers, lilies, and bulbs like onion. Those fibers surrounding, but not derived from, the vascular bundle are called **perivascular fibers**.

The eudicot stem cortex can be quite varied in thickness, components, and function. The *Digitalis* cortex shown in ◘ Fig. 11.4a consists of parenchyma cells surrounding a ring of cortical fibers for stem support. *Digitalis* is a mesophytic, annual plant with limited secondary growth. *Ephedra* is a desert perennial with a photosynthetic stem, as is evidenced by the stoma and chlorenchyma seen in ◘ Fig. 11.4b. Fibers and tannin-filled cells in the cortex aid in herbivory deterrence. The cortex in milfoil, an aquatic eudicot, consists exclusively of a non-photosynthetic parenchyma and aerenchyma (◘ Fig. 11.5a). The gas-filled aerenchyma tissue provides buoyancy for support and a diffusional pathway for the exchange of carbon dioxide and oxygen between the roots and leaves. Stem aerenchyma often forms as an adaptive response in plants such as sedges (Cyperaceae) that are exposed to transient water logging events (Nawaz et al. 2014). Some stems engage in significant levels of photosynthesis and contain multiple layers of cortical chlorenchyma, as shown in the *Daucus* stem in ◘ Fig. 11.5b. That stem also has a cortical secretory duct, a common feature in other plant stems as well. The cortex may also contain crystals or other idioblasts (◘ Fig. 11.5c, d).

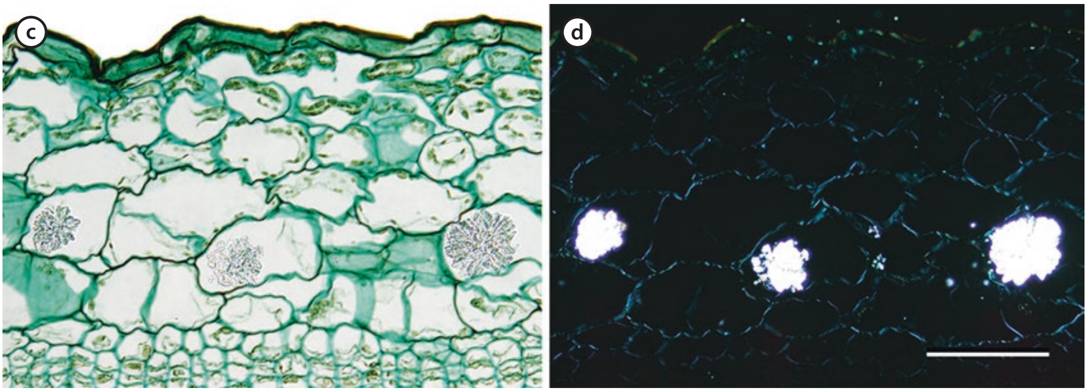
The hypodermis is a region of the cortex consisting of one or more layers of cells lying under the epidermis of some stems. It is



◘ **Fig. 11.5** **a** Water milfoil (*Myriophyllum* sp.) is an aquatic eudicot. Its stem has a single layer of epidermal cells (E) and a wide cortex consisting of an outer layer of parenchyma cells (CP) and an inner zone of aerenchyma (A). The cortical zone (C) extends from inside the epidermis to the inner vascular tissues. Milfoil gains its support from the water and thus has no cortical fibers. Phloem and xylem occupy the center of the stem, and there is no pith. Scale bar = 250 µm. (RR Wise)



◘ **Fig. 11.5** **b** This wild carrot (*Daucus carota*) stem cross-section shows one stoma (St), a thick cuticle (Ct), a single layer of epidermal cells (E), and a thick cortex (C). The cortex has multiple layers of chlorenchyma (Ch), a region of cortical parenchyma (CP), a dense patch of fibers (F), and a secretory duct (SD). Phloem (P) exists in discrete patches (circled), and xylem (X) is to the interior. Note the crushed protophloem to the exterior of the phloem patches. Scale bar = 50 µm. (RR Wise)

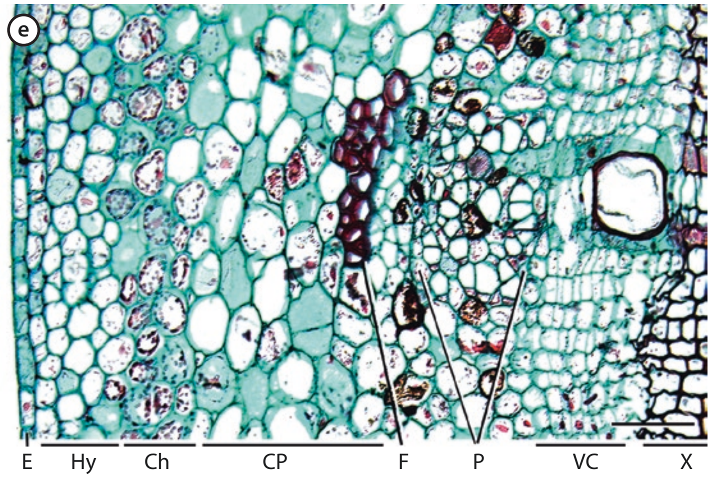


◘ **Fig. 11.5** **c**, **d** Two views of the stem of sowbane (*Chenopodium murale*) in **c** brightfield, and **d** polarized light showing calcium oxalate crystals in cortex. Scale bar = 50 µm. (**c**, **d** RR Wise)

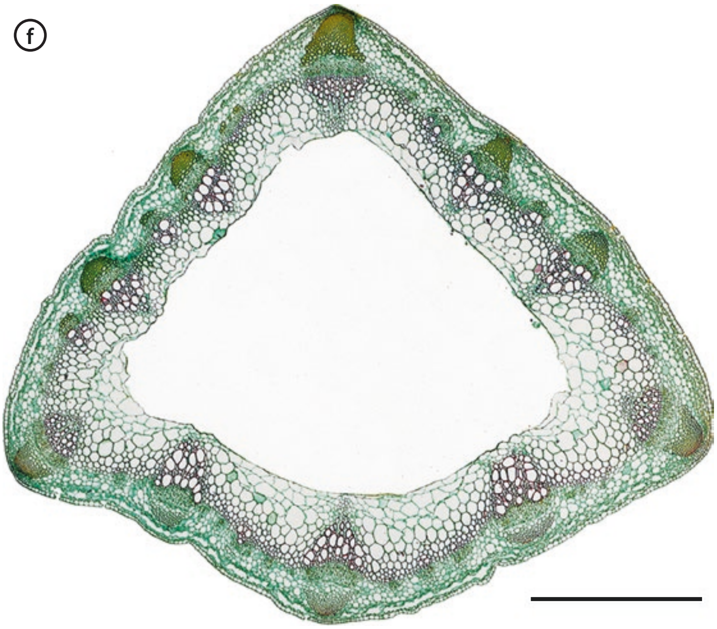
more common in roots than in stems. In xerophytes and succulents (◘ Fig. 11.5e), the hypodermis serves as a water storage tissue. In other stems, hypodermal cells often have thickened walls and may serve as a supportive tissue.

Like the cortex, the pith is part of the ground tissue. It occupies the central region of the typical eudicot stem and is usually pure parenchyma (◘ Fig. 11.3a). Pith develops early in the life of a stem and may play a role in the development of the other tissues that it surrounds, such as the maturing vasculature. Because it is laid down early, and made of weak parenchyma cells, the pith may be destroyed during stem elongation and expansion as shown in the pea stem in ◘ Fig. 11.5f.

The pith can function for storage in a variety of species. Potato tubers, which are rhizomes (◘ Fig. 11.1e), are almost completely



■ **Fig. 11.5** **e** Cross-section of the outer portion of a euphorbia (*Euphorbia* sp.) stem. The epidermis (E) is a single layer of cells. The cortex consists of a hypodermis (Hy), two to three cell layers of chlorenchyma (Ch), cortical parenchyma (CP), and cortical fibers (F). Phloem (P), a wide vascular cambial zone (VC), and xylem (X) lie to the interior. Scale bar = 50 µm. (RR Wise)



■ **Fig. 11.5** **f** LM of a torn pith in a pea (*Pisum sativum*) stem. Even at this low magnification, the thin cortex, the ring of individual vascular bundles at the periphery of the stem, and the minor pith remnants are apparent. Scale bar = 500 µm. (RR Wise)

filled with pith which functions entirely in starch storage. There is no free starch in a plant cell. All starch is manufactured in plastids and specifically amyloplasts in the case of storage organs. The pith of woody stems, as well, can be a site of starch storage (■ Fig. 11.5g).

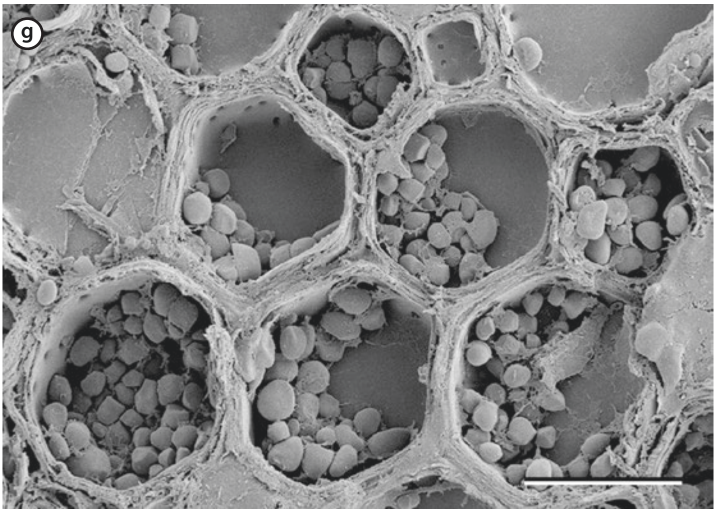


Fig. 11.5 **g** Pith cells observed with SEM of an overwintering Katsura (*Cercidiphyllum japonicum*) stem containing numerous amyloplasts, as seen in the scanning electron microscope. Scale bar = 25 µm. (RR Wise)

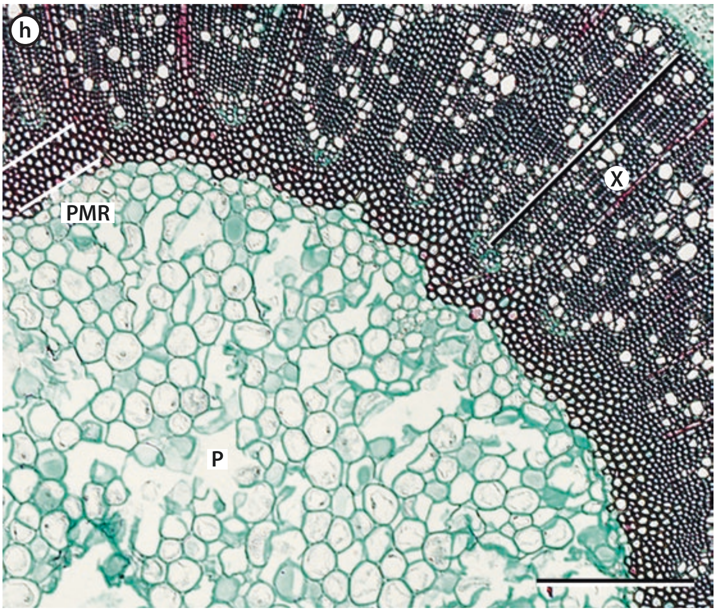
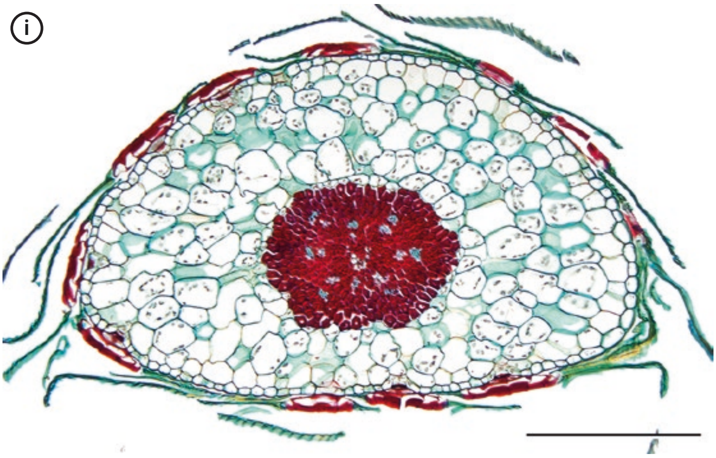


Fig. 11.5 **h** The perimedullary region (PMR, between the two white lines) in this English ivy (*Hedera helix*) stem is a zone of sclerified cells that lies between the xylem (X) to the exterior and pith (P) to the interior. Scale bar = 100 µm. (RR Wise)

In some viney stems, portions of the pith may sclerify to provide support. In *Hedera helix*, the outer cells of the pith sclerify and develop into a zone of supportive tissue called the **perimedullary region** (Fig. 11.5h). The cells of the perimedullary region are derived from pith cells and are therefore part of the ground tissues, not the vascular tissues, in spite of their close association

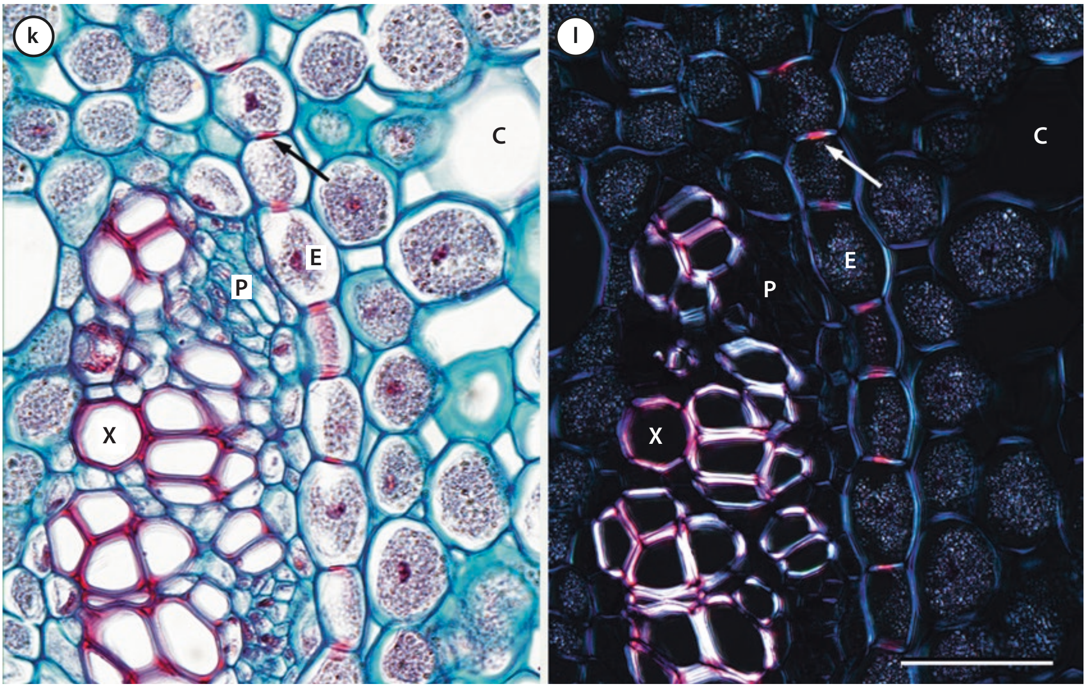


◘ **Fig. 11.5** **i** Cross-section of a Spanish moss (*Tillandsia usneoides*) stem with a cortex of chlorenchyma cells and a central core of sclerenchyma. The small, blue-stained regions in the sclerenchyma core are isolated vascular bundles. Note the peltate trichomes on the stem surface and compare to ◘ Fig. 9.6r, s. Scale bar = 100 µm. (RR Wise)

◘ **Fig. 11.5** **j** Chambered pith of black walnut (*Juglans nigra*). The pith is made at the onset of the first year's primary growth and is soon surrounded by woody xylem of secondary growth origin. Scale bar = 1 cm. (RR Wise)

with the vasculature. In contrast, in Spanish moss stems, it is the inner pith cells that sclerify and are the main supporting tissue of the stem (◘ Fig. 11.5i). Spanish moss is an epiphyte in the bromeliad family that hangs in large masses from tree limbs and requires a small and very flexible stem. In this plant, the stem cortex is composed of chlorenchyma, and the pith contains a dense collection of fibers that provide support. In other plants, tannins, crystals, or laticifers may occupy the pith. The chambered pith of walnut (◘ Fig. 11.5j) is an important taxonomic trait in that taxon. In some stems, medullary rays connect pith parenchyma with cortical parenchyma. The *Aristolochia* stem in ◘ Fig. 14.5b is a good example.

Like the epidermis (refer to ► Chap. 9), the endodermis is a layer of cells that provides a barrier between two regions or zones (Geldner 2013). Such tissues are sometimes called "limiting layers." The epidermis is the limiting layer between the atmosphere (or water in the case of an aquatic plant) and the interior of the organ,

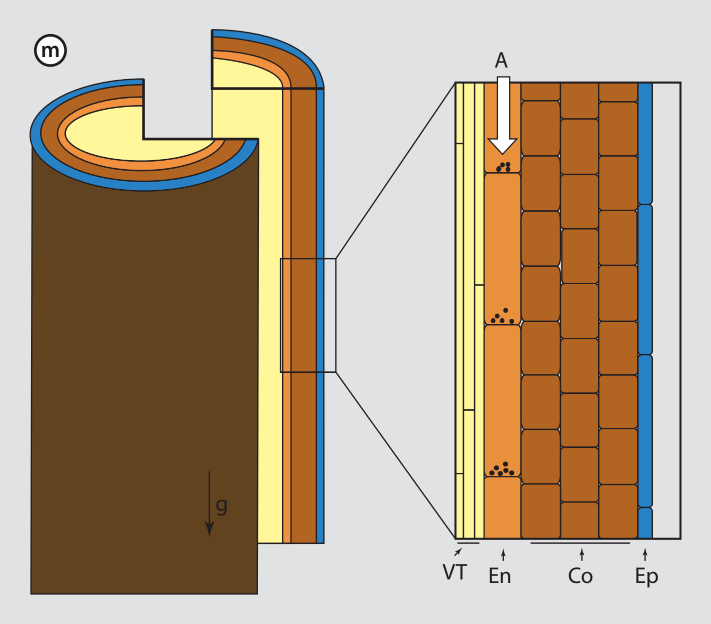


■ **Fig. 11.5** **k**, **l** The endodermis (E) in a sweet flag (*Acorus* sp.) rhizome as seen in (k) brightfield and (l) polarized microscopies. Cortex (C) is to the right, and xylem (X) and phloem (P) are to the left in both images. The Casparian strips (*arrows*) appear red under LM brightfield illumination **k** and show birefringence when viewed through cross-polarizers **l**. Scale bar = 25 µm. (**k**, **l** RR Wise)

whereas the endodermis is a limiting layer between the cortex and the stele or **vascular cylinder** (■ Fig. 11.5k, l). In terms of origin, the endodermis is considered to be the inner layer of the cortex.

The degree of separation provided by an endodermis varies between and among plant habitat, species, and organ. A prominent endodermis is relatively rare in aerial stems (Lersten 1997) probably because the pattern of vascular bundles in a eustele (refer to ► Sect. 11.8) is too large to be bound by a single-layer endodermis. However, in roots (► Chap. 10), and some rhizomes, the endodermis is anatomically distinct with thick cell walls and a conspicuous Casparian strip (or band). The Casparian strip (named after Robert Caspary, a nineteenth century German botanist) is a band of cell wall material impregnated with suberin, and sometimes lignin, in the radial and transverse walls of the endodermal cells. It presents an apoplastic barrier to water and solute flow.

The function of the stem endodermis appears to be associated with those organs that might develop a positive pressure in the stele. Under most conditions, the water in the stele is under tension, not pressure, because transpiration from the leaves “pulls” water up the stem. However, the lower part of aerial stems and rhizomes (■ Fig. 11.5k, l) are subject to the development of root pressure, a process seen when the water potential of the xylem water is higher than that of the soil. Root pressure would force water out of the stele and waterlog the cortex were it not for the barrier to water flow presented by the endodermis. In another



◘ **Fig. 11.5** **m** Schematic of the role of endodermal amyloplasts in gravisensing. The endodermis (En) lies between the vascular tissue (VT) to the inside and the cortex (Co) and epidermis (Ep) to the outside. In the presence of a gravitational vector (g), the amyloplasts (A) sediment to the bottom of the endodermal cells. (Redrawn from Palmieri and Kiss 2006)

example, some **halophytes** (plants growing in saline water) such as pickleweed (*Salicornia* sp.) possess an endodermis, presumably to allow salt exchange between the cortex and surrounding water while restricting the loss of water from the stele to the cortex via osmosis.

In addition to the role that the shoot endodermis plays in the water relations of some stems and rhizomes, it may also function in gravisensing, much like the columella of the root cap (► Sect. 10.4). Shoots are negatively gravitropic (grow away from the gravitational field), while roots are positively gravitropic (growing downward). Amyloplasts, which are heavy, starch-containing plastids, are concentrated in the stem endodermal cells (◘ Fig. 11.5m). They settle to the bottom of the endodermal cells and signal directionality via the mechanism described in ► Sect. 3.5.4. The stem tissues respond by redistributing auxin, a plant hormone that induces cell wall loosening and cell elongation, to the lower side of the stem. Those cells elongate, and the stem points upward and away from the gravitational vector.

11.6 Stem Vascular Tissues Are Arranged in Bundles

The vascular system runs throughout the plant—from the roots, through the stem, and out to the leaves and flowers. Many of the concepts and structural motifs discussed in this section on the vasculature of the stem also apply to the xylem and phloem in the other plant organs. In particular, the developmental transitions from protophloem to metaphloem and protoxylem to metaxylem, as described for stems, are similar in other organs as well.

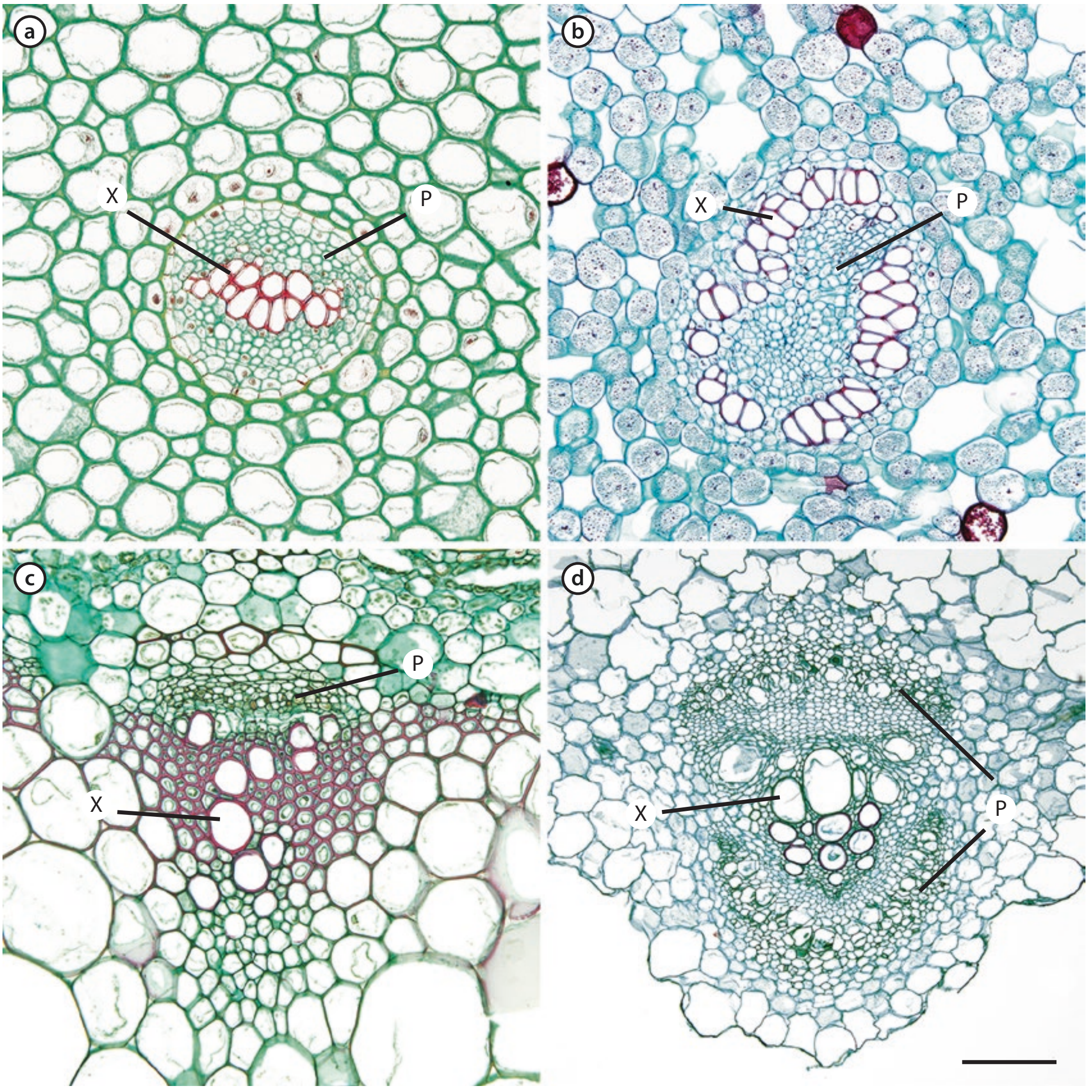
11.6.1 Relationship of Xylem to Phloem in Vascular Bundles

The relationship of xylem to phloem in an individual vascular bundle varies. In an **amphivasal bundle**, the phloem is surrounded by xylem as seen in the stem of *Acorus*, a primitive monocot (◘ Fig. 11.6a). An **amphicribral bundle** has the opposite arrangement, with phloem surrounding the xylem (◘ Fig. 11.6b). Amphicribral and amphivasal bundles are more common in ferns and primitive monocots than gymnosperms and advanced angiosperms. In a **collateral bundle**, the most common type found in angiosperms, phloem is to the outside (abaxial to) the xylem (◘ Fig. 11.6c). However, in some eudicots only, the primary phloem may be found on both the inner and outer sides of the xylem, and this arrangement is called **bicollateral** (◘ Fig. 11.6d). In this case, one area of phloem is adjacent to the cortex, and the other is adjacent to the pith.

Vascular bundles that have a vascular cambium are said to be open because the cambium can continue to generate new xylem and phloem tissues for the life of the bundle. Those that lack a vascular cambium are called closed, meaning all the cells of the vascular bundle fully differentiate to xylem or phloem tissues and none remain in the meristematic state. Beet (◘ Fig. 11.6c) and squash (◘ Fig. 11.6d) are examples of stems with open vascular bundles. Examples of closed vascular bundles are found in *Ranunculus* (◘ Fig. 11.1k) and *Zea* (◘ Fig. 11.6f). Stems with primary growth may have either open or closed vascular bundles.

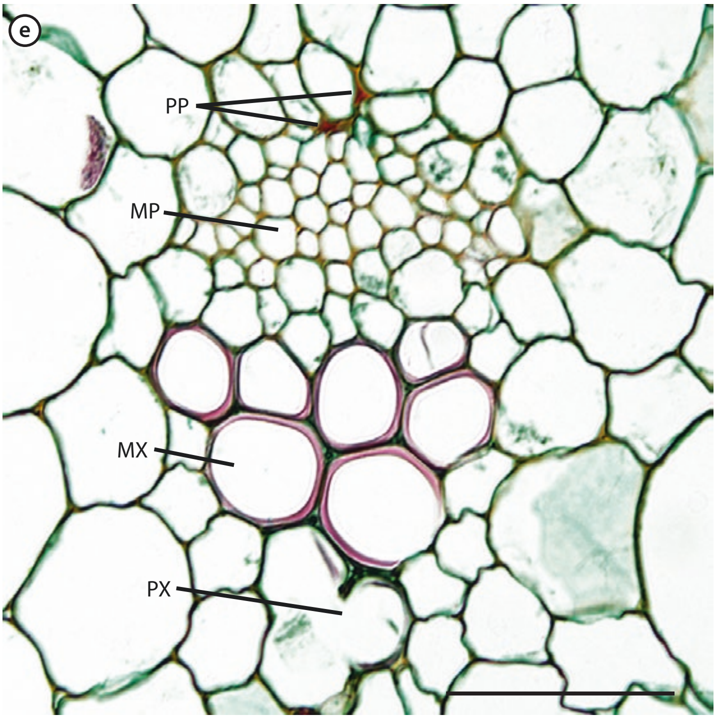
Differentiation of primary vascular tissues from the procambium is asynchronous. Protoxylem and protophloem are first to mature, followed by metaxylem and metaphloem. Protoxylem and protophloem originate at the stem apical meristem as a consequence of divisions of the procambium. Protoxylem tracheary elements are dead at maturity and may continue to serve as conduits for water flow for some time. They typically are small in diameter and have annular or spiral wall thickenings (◘ Fig. 11.6e), a characteristic that is of advantage in a tissue undergoing elongation. However, protophloem sieve tube elements are often small in both length and diameter and may lack sieve plates and companion cells. They are easily stretched and typically destroyed by stem elongation. Protoxylem, as well, may be torn during stem expansion. The result is a protoxylem lacuna or hole (◘ Fig. 11.6f).

After internode elongation has ceased, parenchyma cells further down the stem and, adjacent to the protoxylem and



◘ **Fig. 11.6** **a**-**d** Examples of vascular bundle types with different xylem (X)-phloem (P) arrangements: **a** amphicribral bundle from a fern (*Polypodium* sp.) rhizome, **b** amphivasal from a sweet flag (*Acorus* sp.) rhizome, **c** a collateral bundle from a beet (*Beta vulgaris*) stem, and **d** a bicollateral bundle from a squash (*Cucurbita pepo* sp.) stem. Beet and squash have open vascular bundles. Scale bar in **d** = 50 µm and applies to the other panels. (**a**–**d** RR Wise)

protophloem, differentiate into the second type of primary vasculature, **metaxylem** and metaphloem. Note that protoxylem, protophloem, metaxylem, and metaphloem are all primary tissues (◘ Fig. 11.6g). There is no sharp demarcation between protoxylem and metaxylem, and the two forms grade from one to the other during development. However, the latter are usually larger in length and diameter than the former. In plants with true secondary growth, **secondary xylem** and secondary phloem later develop from the vascular cambium (► Chap. 14). In those plants lacking secondary growth, the metaxylem and metaphloem are the functional vascular tissues for the life of the plant.



■ **Fig. 11.6** **e** In this cross-section of a young castor bean (*Ricinus communis*) stem, protophloem (PP) and protoxylem (PX) developed first. The protophloem was crushed by expansion and elongation of the stem, while the protoxylem was ripped. Metaxylem (MX) and metaphloem (MT) subsequently developed in an exarch pattern. The stem surface (the adaxial direction) is to the top of the image. This bundle will develop a vascular cambium and, ultimately, be connected in a ring with adjacent bundles via the activity of an interfascicular cambium. The result of that secondary growth will be similar to the example shown in Fig. 11.1n. Scale bar = 50 µm. (RR Wise)

11.6.2 Patterns of Xylem Development in the Stem

With their thick secondary wells, which are not easily ripped or torn, the development of metaxylem vessel elements within vascular bundles is easier to visualize and study than metaphloem development. As a result, four patterns of metaxylem maturation are recognized (■ Fig. 11.6h–k). Plants with a **centrarch** pattern of maturation possess a single vascular cylinder with protoxylem in the center, surrounded by metaxylem. A **mesarch** stem is similar to centrarch with protoxylem surrounded by metaxylem, but mesarch stems have multiple vascular strands with this maturation pattern. Centrarch and mesarch developmental patterns are characteristic of extinct and living fern taxa. In the **endarch** developmental pattern, metaxylem development is to the exterior (adaxial) of protoxylem. This is the most common form found in the stems of angiosperms. An **exarch** pattern is one in which metaxylem development is to the interior (abaxial) of the protoxylem, as is seen in most angiosperm roots (► Chap. 10—Roots).

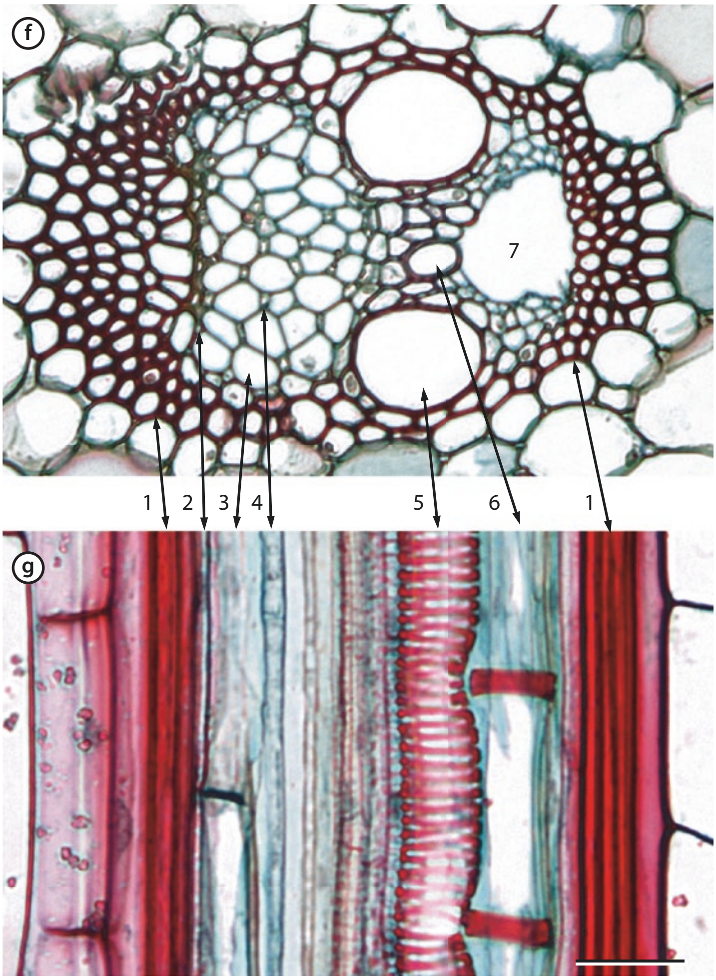
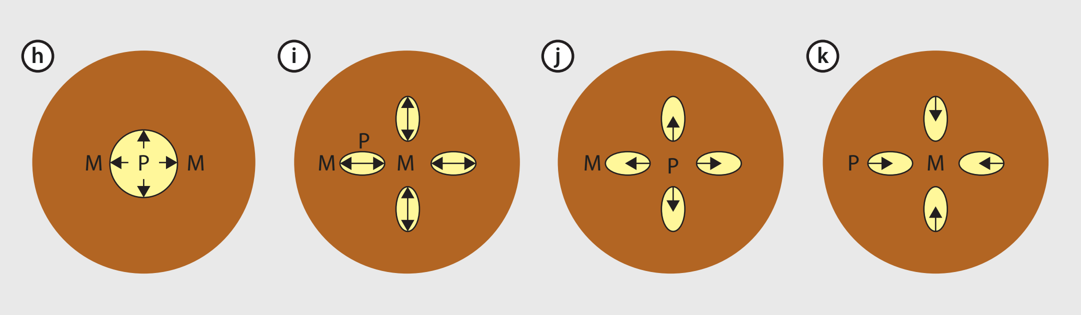


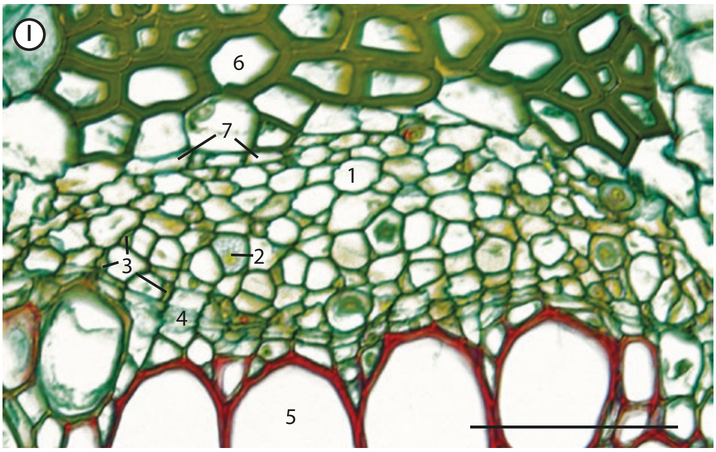
Fig. 11.6 **f**, **g** Closed vascular bundles from a mature maize *(Zea mays)* stem. **f** A bundle seen in cross-section is composed of xylem and phloem. A bundle sheath of sclerenchyma fibers (stained dark red due to lignification) surrounds the vascular bundle and separates it from the ground parenchyma or conjunctive tissues. **g** A corresponding longitudinal section shows cell types labeled as 1 = perivascular fibers of the bundle sheath; 2 = crushed protophloem; 3 = metaphloem sieve tube element; 4 = metaphloem companion cell; 5 = metaxylem vessel element; 6 = protoxylem vessel element; 7 = protoxylem lacuna. Given that xylem vessel elements are dead at maturity, water can move through the protoxylem lacuna during transpiration. The metaxylem vessel elements and the internal fibers serve to keep the lacuna from collapsing. Scale bar in **g** = 50 μm and applies to both panels. (**f**, **g** RR Wise)

11.6.3 Patterns of Phloem Development in the Stem

As with xylem, two sequential states of phloem development are identified in gymnosperms and eudicots: primary phloem and secondary phloem (refer to Sect. 1.19.2). The primary phloem develops from the procambium, whereas secondary phloem is produced



◘ **Fig. 11.6** **h–k** Patterns of metaxylem development. The locations of protoxylem (P) and metaxylem (M) are indicated. Phloem development is not considered. (Drawing modified from Wikipedia)



◘ **Fig. 11.6** **l** Cross-section of an open vascular bundle in a pea (*Pisum sativum*) stem. All functional phloem shown here is secondary, i.e., produced by the vascular cambium (#4). The primary phloem (7) is being crushed by growth and expansion of the secondary phloem. Phloem parenchyma cells are present but difficult to identify except in longitudinal section. Examples of the various cell types are labeled as 1 = sieve tube element, 2 = sieve plate, 3 = companion cells, 4 = vascular cambium, 5 = secondary xylem, 6 = phloem fibers. Scale bar = 50 µm. (RR Wise)

by vascular cambium. In stems and roots of plants with secondary growth, primary phloem is very short-lived, and, except in leaves, it is replaced by secondary phloem.

Monocots lack true secondary growth and thus, only have primary phloem. Primary phloem is axial only; there is no radial primary vasculature in gymnosperms, monocots, or eudicots. Developing roots, stems, and leaves may all possess protophloem. It is different from metaphloem in that it has sieve tube cells only—there are no companion cells in protophloem and rarely phloem parenchyma or fibers. The sieve tube elements (STEs) are typically short-lived and are crushed at an early stage by expansion of the organ and subsequent metaphloem development. ◘ Figure 11.6f shows a thin layer of crushed protophloem STEs between the sclerenchymatous bundle sheath and the metaphloem in maize.

Metaphloem development initiates after the organ ceases growth in length, and this tissue must last for the life of the organ because, by definition, there is no vascular cambium to produce additional secondary phloem. Metaphloem sieve tube elements are larger than those found in protophloem, no doubt in keeping with the increased demand for translocation as the growing plant increases in size. Companion cells are present, and in maize, metaphloem sieve tube elements alternate with narrow companion cells in an orderly fashion resulting in a "checkerboard" pattern when seen in cross-section (refer to ◘ Fig. 11.6f). Metaphloem in woody dicots (which display secondary growth) is crushed by growth of secondary phloem (◘ Fig. 11.6l), much like protophloem is crushed by metaphloem in monocots. Herbaceous eudicots, which lack secondary growth, have a metaphloem that is somewhat similar to that found in monocots in terms of cell sizes.

11.7 Evolutionary Advances Led to Variations in Stem Architecture

Plants colonized the land approximately 480 million years ago. The first land plants were small and leafless and lacked a vascular system, similar to their aquatic ancestors. Life on land required the development of a number of unique structures, mainly lignin to provide support, a cuticle to limit water loss, stomata to allow for gas exchange, leaves to increase the photosynthetic surface area, and vasculature to move water, minerals, and photosynthate throughout the plant.

Stems evolved first, and the first stem vascular systems, like the first land plants, were simple. As plants increased in size and complexity, so did the vasculature of their stems. The subsequent evolution of the leaf, in particular, had a large impact on stem vasculature because the leaf vasculature has to be directly connected to the stem vasculature via a strand of xylem and phloem called a **leaf trace**. The various patterns of stem vasculature are discussed below.

The stele is the cylinder of vascular tissue in the center of a root or stem, and there is significant variation in the arrangement of xylem and phloem in the tracheophyte stele. A number of classification systems have been proposed to define and categorize the different arrangements. The treatment used herein describes two basic types of steles: **protosteles** (no central pith) and **siphonosteles** (central pith) with several variants of each (◘ Table 11.1).

Protosteles (*proto* = first, *stele* = column) have xylem located as a solid mass in the center with no pith. Phloem surrounds the xylem with an endodermis to the exterior of the phloem. Protosteles occur before the siphonostele in the fossil record and are currently found in the seedless vascular plants (ferns and fern allies). Because the types of plants that have protosteles typically have no leaves or, at the most, microphylls, protosteles lack **leaf gaps**, i.e., gaps in the stele where leaf vasculature branches off. In fact, the definition of a microphyll is an appendage that emerges from the protostele without leaving a leaf gap (refer to ► Chap. 12—Leaves).

◘ **Table 11.1** Organization of stele types

Protosteles	Haplostele	Cylindrical core of xylem surrounded by phloem	
	Actinostele	Lobed core of xylem surrounded by phloem	
	Plectostele	Interconnected plate-like regions of xylem surrounded by and immersed in phloem tissue	
Siphonosteles	Solenostele	Ectophloic	Phloem to the exterior of xylem
		Amphiphloic	Phloem to both sides of xylem
	Dictyostele	Multiple leaf gaps result in a net-like arrangement	
	Eustele	Discrete vascular bundles are arranged in a field of pith; eudicots have a eustele with a ring of bundles	
		An atactostele is subtype of eustele in which vascular bundles are apparently scattered throughout the pith; found in monocots	

There are three types of protosteles—haplostele, actinostele, and plectostele. The **haplostele** (*haplo* = simple) is the most basic of protosteles, with a cylindrical core of xylem surrounded by phloem and then an endodermis. This type of stele is the most common in roots and, as is shown in ◘ Fig. 11.7a, b, the rhizome of *Lygodium* (fern). An **actinostele** (*actino* = star) is a protostele in which the core of xylem is lobed but the entire stele is surrounded by an endodermis. This type of stele is found in stems of the whisk fern, *Psilotum* sp. (◘ Fig. 11.7c, d) and is common in the roots of seed plants. A **plectostele** (*plecto* = folded or pleated, sometimes called a polystele) is a protostele in which interconnected plate-like regions of xylem are surrounded and immersed in phloem tissue, all in turn surrounded by an endodermis. Many modern club mosses (Lycopodiopsida) have this type of stele within their stems (◘ Fig. 11.7e, f). Given that protosteles are defined as having a central core of xylem, it follows that all protosteles are **ectophloic**, meaning the phloem is to the exterior (*ecto*) of the xylem.

The evolution of the leaf drove advancements in stele design producing more complex patterns resulting in the siphonostele (*siphono* = tube or pipe). Siphonosteles have a pith in the center of their stems, surrounded by a cylinder of various designs containing the vascular tissue. There are two types of siphonosteles, solenostele (amphiphloic or ectophloic), and dictyostele. The **solenostele** (*soleno* = cylinder) is the most basic of siphonosteles, with a central core of pith enclosed in a cylinder of vascular tissue. The cylinder

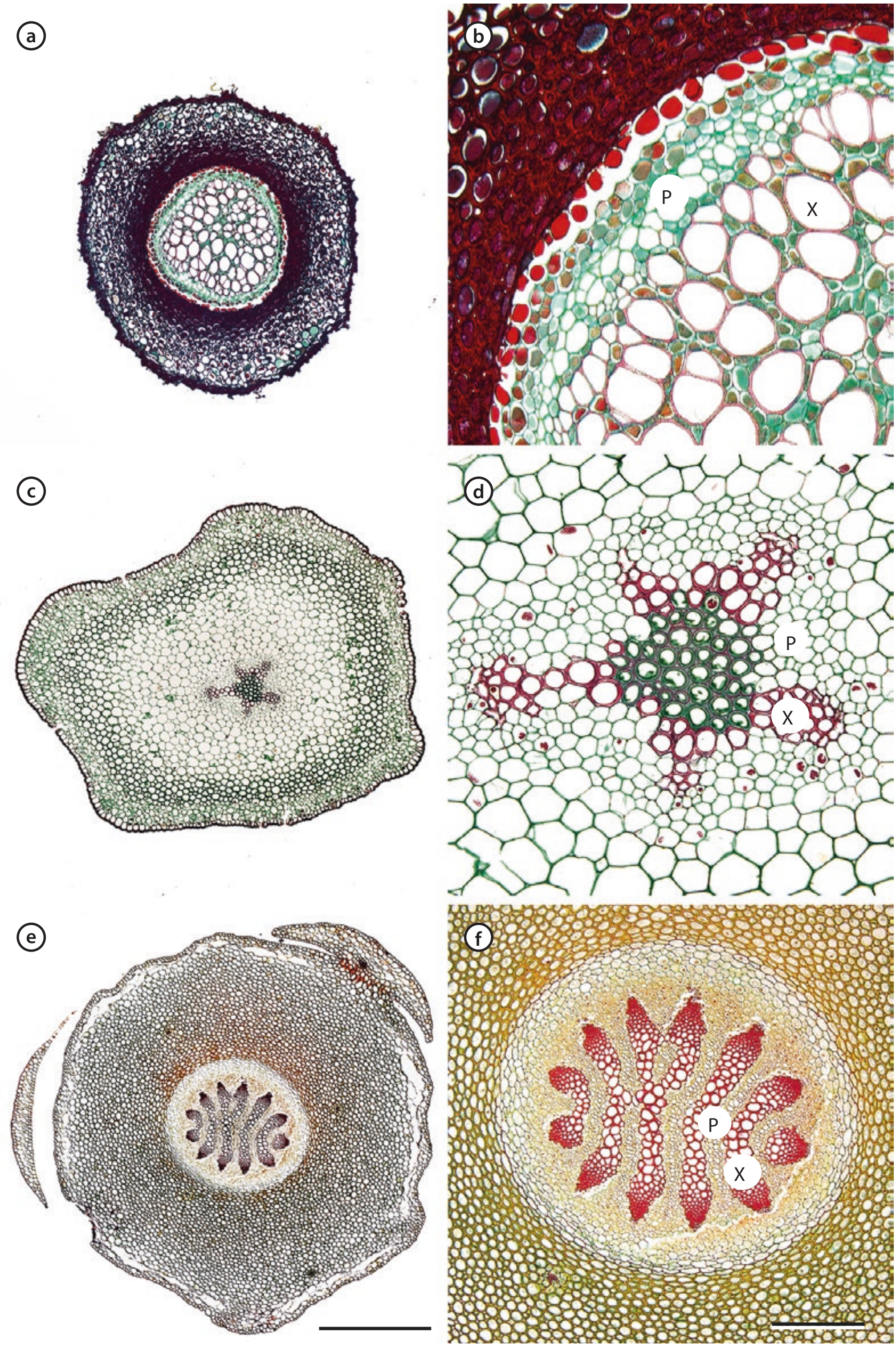
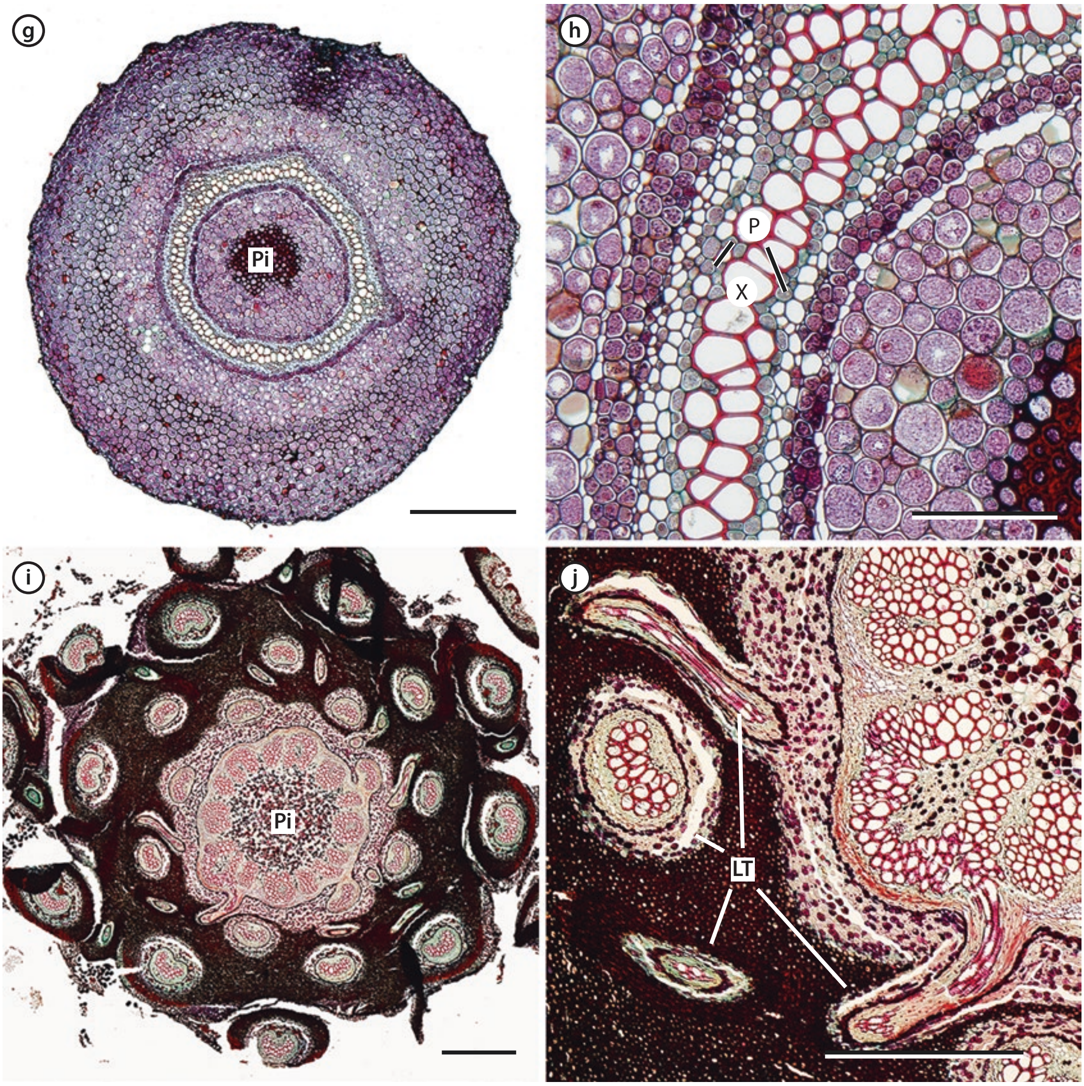


Fig. 11.7 **a**–**f** Examples of the three types of protosteles: **a** and **b**, haplostele from a climbing fern (*Lygodium* sp.) rhizome; **c** and **d**, actinostele from a whisk fern (*Psilotum* sp.) rhizome. **e** and **f**, Plectostele from a ground pine (*Lycopodium* sp.) rhizome. Scale bars = 250 µm for **a**, **c**, and **e** and 100 µm for **b**, **d**, and **f**. (**a**–**f** RR Wise)



◘ **Fig. 11.7** **g**–**j** Examples of the two types of solenosteles. **g** and **h**, Ectophloic solenostele from a royal fern (*Osmunda* sp.) rhizome. **i** and **j**, Amphiphloic solenostele from a maidenhair fern (*Adiantum pedatum*) rhizome. Leaf traces (LT) are indicated. Scale bars = 500 µm in **g** and **i** and 100 µm in **h** and **j**. (**g**–**j** RR Wise)

only shows breaks at the leaf gaps. This type of stele is found only in fern stems today. An **amphiphloic** solenostele (*amphi* = both) has phloem both interior and exterior to the xylem (◘ Fig. 11.7g, h), while an ectophloic solenostele only has phloem to the exterior (◘ Fig. 11.7i, j). [Note: an amphiphloic stele has a continuous layer of phloem to both sides of the xylem in the siphonostele (◘ Fig. 11.7g), an amphicribral vascular bundle has phloem completely surrounding the xylem in a single bundle (◘ Fig. 11.7l), and a bicollateral vascular bundle has a patch of phloem to both sides of the xylem in a single bundle (◘ Fig. 11.6d)].

The **dictyostele** (*dictyo* = net) is actually a variation of the solenostele caused by multiple leaves and short internodes

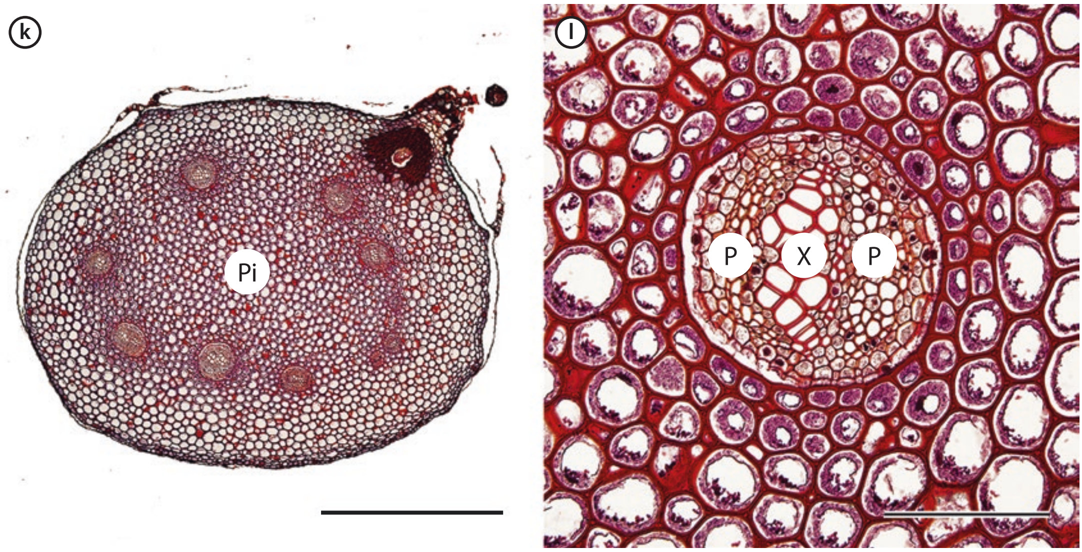


Fig. 11.7 **k** A dictyostele from a fern (*Polypodium* sp.) rhizome with a central core of pith (Pi) and several vascular bundles. The individual bundles interconnect either above or below the level of the section, which is characteristic of a highly dissected siphonostele, as opposed to a eustele. **l** The individual bundles have a central core of xylem (X) surrounded by phloem (P) making this an amphicribral bundle. Scale bars = 500 µm in (k) and 100 µm in **l**. (**k**, **l** RR Wise)

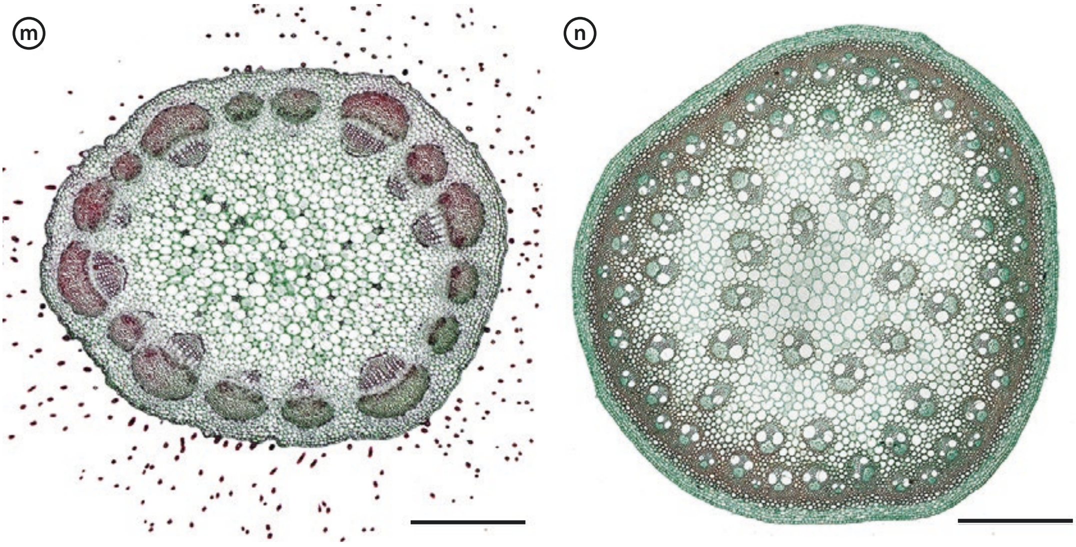


Fig. 11.7 **m** Cross-section of a red clover (*Trifolium pratense*) eustele stem showing a ring of vascular bundles at the periphery surrounding a central pith. The dots surrounding the stem are trichomes. **n** A greenbrier (*Smilax* sp.) stem in cross-section displaying the atactostele architecture that is characteristic of monocots. Scale bars = 500 µm in both panels. (**m**, **n** RR Wise)

(Fig. 11.7k, l). In portions of the stem, the vasculature is still in a tube-like arrangement (a true siphonostele), but the presence of closely arranged leaves along the stem axis creates multiple gaps in the stelar core creating the impression in a single cross-section of a network of vasculature, similar to a eustele, which it is not. Among living plants, dictyosteles are found only in the stems or rhizomes of ferns. They are sometimes called a **dissected siphonostele**, because that is an apt descriptor of their origin and structure.

The **eustele** is the most common stelar arrangement in stems of seed plants. Here, the vascular tissue is arranged in discrete vascular bundles, usually in one or two rings around the central pith, and the endodermis, in eudicot stems at least, is missing (◘ Fig. 11.7m). In addition to being found in stems, the eustele appears in the roots of monocots where an endodermis is present. Monocot stems have a variation on the eustele called an **atactostele** (*atacto* = scattered; Brebner 1902) in which numerous bundles are apparently scattered throughout the stem (◘ Fig. 11.7n). While that notion of "scattered vascular bundles" persists in the literature and texts, and is consistent with what one can see in a single stem cross-section, recent studies have been able to resolve a level of order to the arrangement of bundles (Korn 2016). If viewed in a three-dimensional organization, they are actually distributed in an ordered fashion and interconnected in a complex format as they approach a node. Typically, only two protoxylem and two metaxylem vessels are present in each vascular bundle.

This basic difference in stem architectures between eudicots and monocots arises from the pattern of vascular origination. In eudicots, the procambium arises near the **leaf buttresses**, which bud off the outside of the shoot apical meristem (► Sect. 4.7). Thus, the resulting vascular bundles are near the outer edge of the stem, and the interior of the stem is filled with pith parenchyma produced by the ground meristem. Conversely, in the monocot leaf and stem, procambium initiation is scattered within the intercalary meristem, resulting in the apparent scattered distribution of vascular bundles in the mature stem.

11.8 Secondary Growth in Eudicots Initiates in Three Basic Patterns

Secondary growth of the eustele vascular system in eudicot stems can be seen as following three different patterns. In the first, primary growth proceeds as described above with the formation of discrete vascular bundles. Subsequently, an interfascicular cambium forms, and the resulting secondary growth produces xylem and phloem which connect the bundles and form a continuous cylinder, as in elderberry stems (◘ Fig. 11.8a, d). In stems displaying a second form, primary growth produces a continuous ring of vasculature, which is then mirrored with the secondary growth. The tobacco stem is an example (◘ Fig. 11.8b, e). Eudicot stems displaying the second form of secondary growth develop an interfascicular cambium, but it produces only parenchyma, resulting in pith rays. This form is seen most often in vines that need to retain some flexibility such as moonseed (◘ Fig. 11.8c, f) as well as Dutchman's pipe (◘ Fig. 14.5b, c). Repeated annual cycles of secondary growth generates wood and will be discussed in ► Chap. 15—Wood.

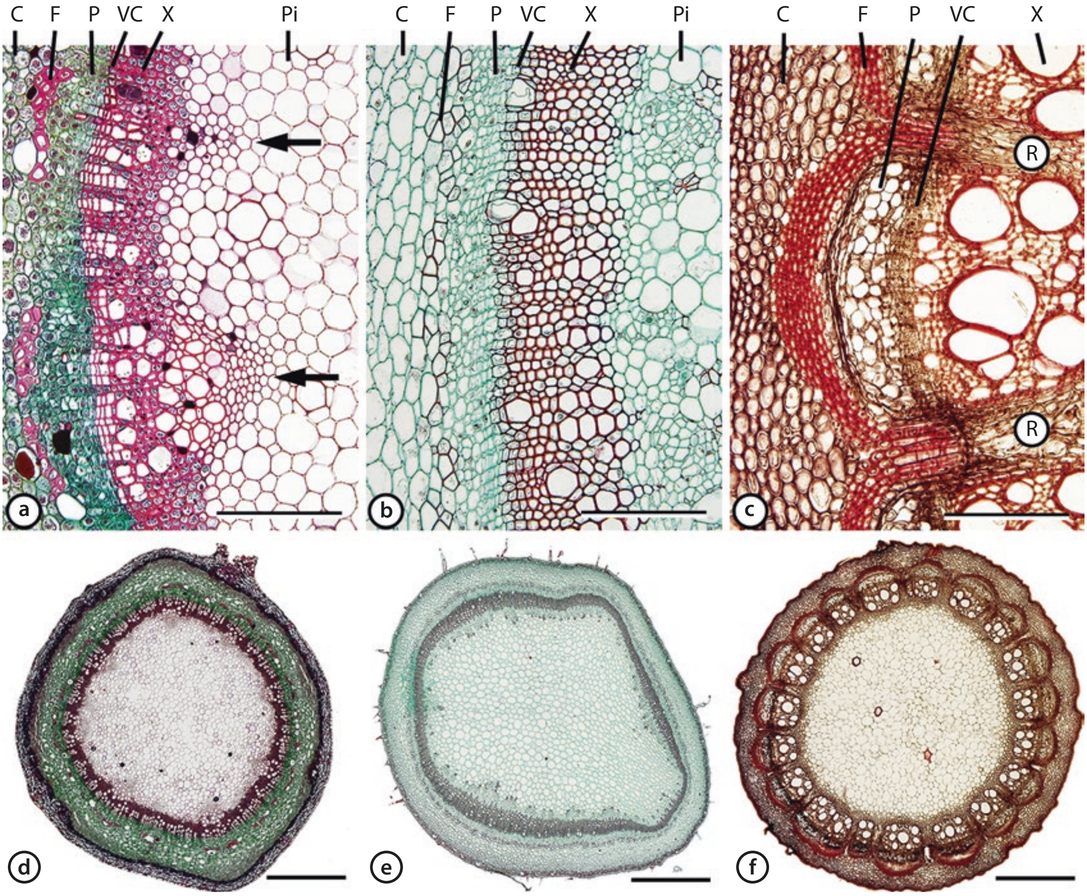
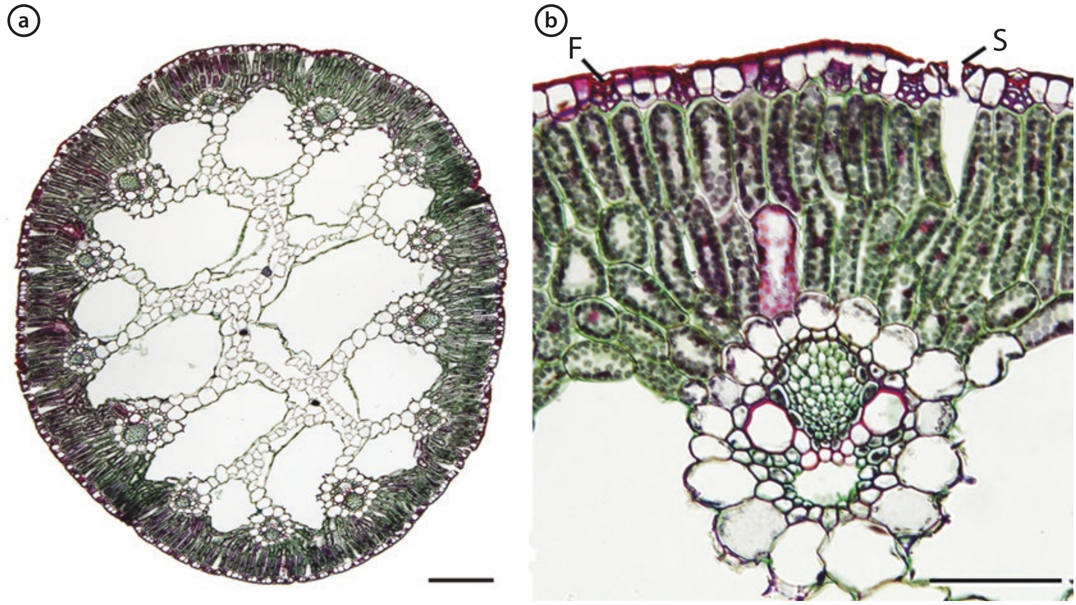


Fig. 11.8 **a**–**f** Stem cross-sections displaying different secondary growth patterns. **a**, **d** In elderberry (*Sambucus* sp.) the primary vascular system is in strands (*arrows*) which later connect into a ring by the action of an interfascicular cambium. **b**, **e** Both the primary and secondary vascular systems are ring shaped in a tobacco (*Nicotiana tabacum*) stem. **c**, **f**) In the moonseed (*Menispermum* sp.) stem, primary and secondary vascular systems form discrete bundles, and the interfascicular cambium forms parenchyma, resulting in pith rays (R). Cortex (C), fibers (F), phloem (P), vascular cambium (VC), xylem (X), and pith (Pi) are labeled. Scale bars = 100 μm in **a**, **b**, and **c** and 500 μm in **d**, **e**, and **f**. (**a**–**f** RR Wise)

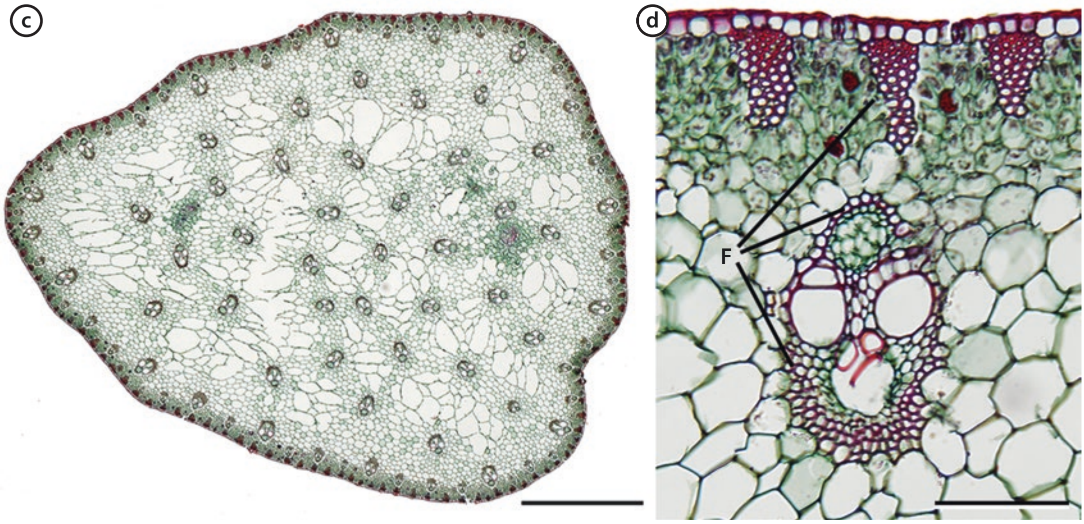
11.9 Monocot Stems Show a Different Form of Secondary Growth than Eudicots

One of the products of eudicot secondary growth is the accumulation of significant supportive tissue in the form of wood, a form of sclerenchyma. Although lacking wood, many monocots stems gain significant support from sclerenchyma tissues and fibrous strands. *Juncus* sp. (Fig. 11.9a, b) is a common wetland monocot with an aerenchyma-filled stem and small, peripheral fiber bundles for support. Its stems may reach a meter in length, but unlike other monocots, *Juncus* does not typically have sclerified bundle sheaths. The stem is photosynthetic, with a thick layer of cortical chlorenchyma.

The stem of the three-square bulrush (*Schoenoplectus americanus*) gains support from its angular shape and multiple, large bun-



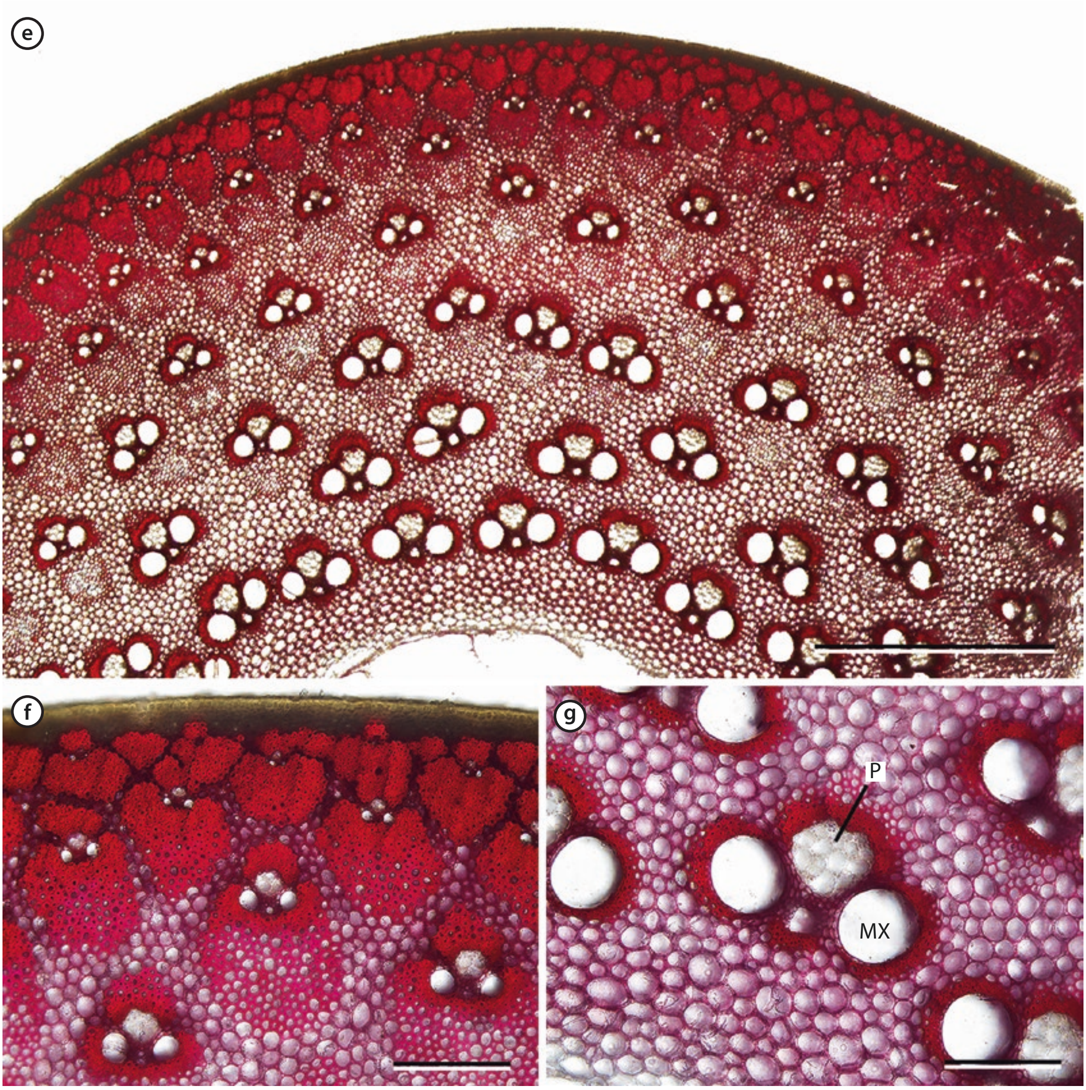
◘ **Fig. 11.9** **a**, **b** Cross-sections of a Baltic rush (*Juncus balticus*) stem. **a** Uncharacteristic of monocots, the vascular bundles in this stem are arranged in a ring because the center of the stem is filled with aerenchyma tissue that facilitates shoot to root gas exchange. The interior aerenchyma is often torn during growth, but not in this stem. **b** A higher magnification image reveals small bundles of fibers (F) adjacent to the epidermis and no fibers surrounding the vascular bundle (center of image). The cortical chlorenchyma cells assume a palisade-like appearance and are highly photosynthetic. Individual chloroplasts can be observed in the periphery of the cortical chlorenchyma cells. Note the stomatal complex (S). Scale bars = 100 μm in **a** and 50 μm in **b**. (**a**, **b** RR Wise)



◘ **Fig. 11.9** **c**, **d** Cross-section of a three-square bulrush (*Schoenoplectus americanus*) stem. **c** The stem interior is intact and filled with vascular bundles ordered throughout the conjunctive tissue in the stem. **d** A thick cuticle covers the stem surface, and large bundles of fibers (F) lie in the green chlorenchyma tissue, just inside the epidermis. Additional fibers are seen surrounding the vascular bundle in the middle of the image. Scale bars = 500 μm in **c** and 50 μm in **d**. (**c**, **d** RR Wise) dles of fibers at the stem periphery (◘ Fig. 11.9c). The vascular bundle sheaths are also heavily sclerified (◘ Fig. 11.9d). Like *Juncus*, *Schoenoplectus* is a wetland plant with a spongy, aerenchyma-filled stem interior well suited for gas exchange.

Bamboo stems (◘ Fig. 11.2h and 11.9e–g) are extremely strong and have numerous uses such as scaffolding and construction material, especially in Asia. Their strength comes from a tight packing of heavily sclerified vascular bundles (◘ Fig. 11.9e–g).

Even in the absence of true secondary growth (as defined for eudicots), monocot stems such as screw pines (Pandanaceae) and palms

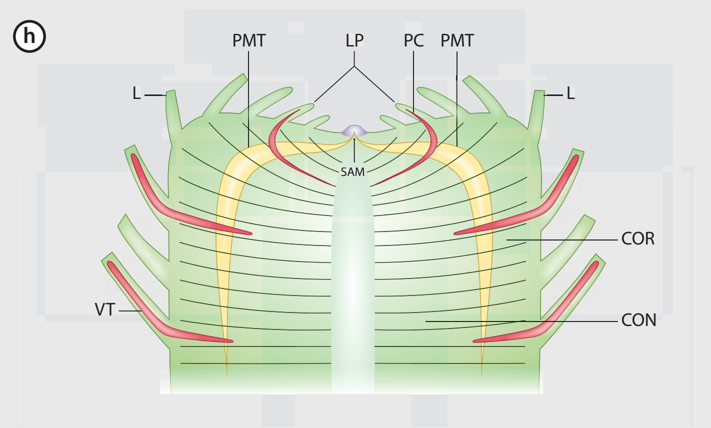


◘ **Fig. 11.9** **e**–**g** Sclerification of vascular bundles in a seabreeze bamboo (*Bambusa malingensis*) stem; phloroglucinol was used to stain the lignin red. **g** A low magnification view showing the heavy sclerification of the outer layers and sclerified bundles to the interior. **f** The outer vascular bundles are almost entirely sclerified. They serve mainly for support, with little role in water movement. **g** The inner vascular bundles provide support and also serve as conduits for transpiration via the metaxylem (MX) and translocation via the phloem (P). Compare the sizes of the metaxylem and phloem in **f** and **g**. The two micrographs are at the same magnification. Scale bars = 500 µm in **g** and 100 µm in **f** and **g**. (**e**–**g** RR Wise)

(Araceae) can be quite large. Monocots have three mechanisms to increase stem diameter and strength: primary thickening meristems, secondary thickening meristems, and intercalary meristems (intercalary meristems were described above).

The **primary thickening meristem** (PMT) is found at the stem apex, and its cells divide in a periclinal plane (parallel to the organ surface), generating anticlinal (perpendicular to the cell surface) files of derivatives (◘ Fig. 11.9h). At the apex, the PMT forms a disc of meristematic cells. The PMT generates a wide crown and contributes to the increase in stem thickness. In some species, PMT activity at the shoulders creates large bulges that extend beyond the shoot apex, leaving it in a recess at the stem tip. As the stem elongates and leaves behind the PMT, its orientation gradually changes to become parallel with the stem axis, while remaining parallel to the stem surface. The PMT also becomes thinner and less active further down the stem. Thus, in most plants with a PMT, the stem diameter is set by the PMT, and further increases in diameter are not possible.

Many monocots have the ability to thicken and strengthen the stem by the activity of a **secondary thickening meristem** (STM). *Cordyline* is a monocot genus of tropical plants that possesses a STM and several other unusual features (◘ Fig. 11.9i–l). First, primary growth produces the stem proper with a pith full of primary vascular bundles surrounded by parenchyma cells (the conjunctive tissue). These primary vascular bundles are collateral, with xylem to the interior and phloem to the exterior (◘ Fig. 11.9l). A primary cortex, sclerified hypodermis, and epidermis develop to



◘ **Fig. 11.9** **h** Diagrammatic representation of a monocot stem tip with a primary thickening meristem (PMT). The shoot apical meristem (SAM) generates leaf primordia (LP) in an exogenous manner, as in all stems. A procambium (PC) develops for each leaf primordium and eventually supplies each leaf (L) with a vascular trace (VT). The procambium also generates the axial vascular bundles. The activity of the PMT at the "shoulders" of the stem tilts the leaf bases outward so they point forward and become aligned parallel to the stem axis. PMT derivatives contribute to the cortex (COR) and conjunctive tissues (CON). (Figure modified from DeMason (1983)) (RR Wise)

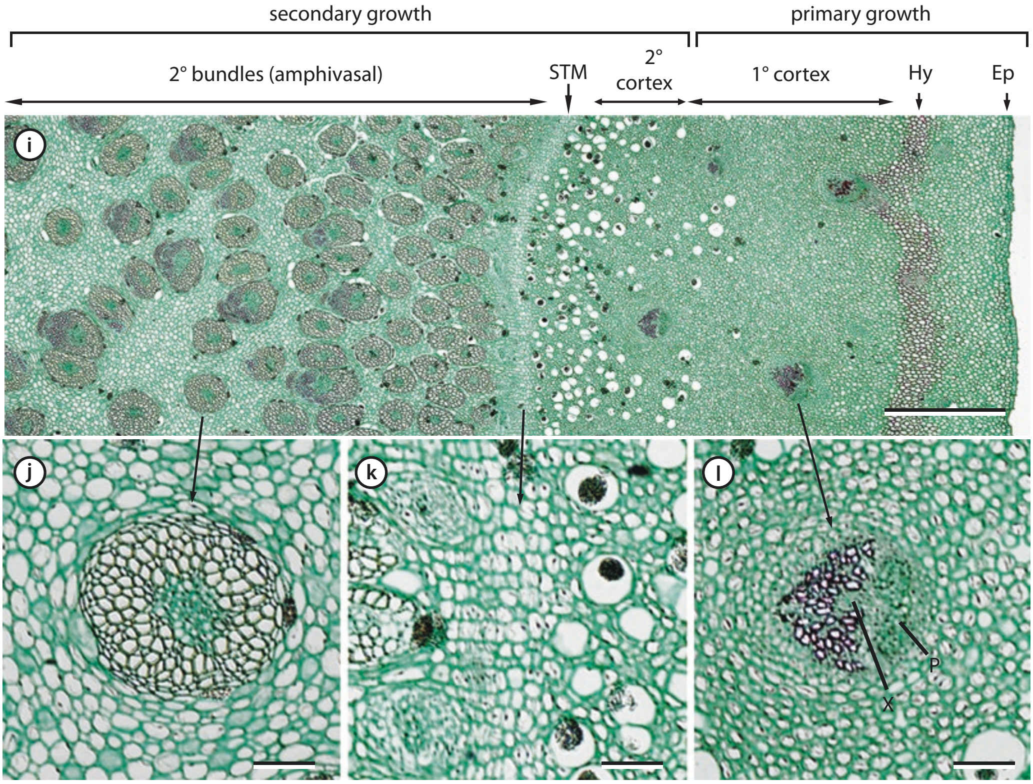


Fig. 11.9 **i** Cordyline (*Cordyline* sp.) stem in cross-section. The secondary thickening meristem (STM) is in the center of the image and shown enlarged in **k**. It has produced a small amount of secondary cortex to the right (exterior) that merges with the primary cortex. **j** The numerous secondary vascular bundles are amphivasal, while **l** the bundles produced by primary growth are collateral. Ep epidermis, Hy hypodermis, P phloem, STM secondary thickening meristem, X xylem. Scale bars = 250 µm in **i** and 25 µm in **j**–**l**. (**i**–**l** RR Wise)

the outside. Subsequently, parenchyma cells near to periphery of the stem become meristematic and generate a ring of vascular cambium called the secondary thickening meristem (STM, ◘ Fig. 11.9i, k).

Alternatively, in yucca, the STM has been shown to be a continuum of the PTM (DeMason and Diggle 1984). The STM generates secondary vascular bundles (not a ring but bundles) and additional parenchyma to the inside and a small amount of secondary cortex to the outside. The secondary bundles thus produced are in a pattern sometimes called **diffuse secondary growth** with isolated bundles in a field of ground parenchyma cells. In another unusual twist, the secondary vascular bundles are amphivasal, with a central core of phloem surrounded by xylem as seen in ◘ Fig. 11.9j for cordyline.

In a special case of monocot stem thickening, the increased stem thickness seen at the base of many palms (◘ Fig. 11.9m) is due to the development of adventitious roots. They are initiated in the stem interior, and, as they grow outward, they cause the stem to bulge.

Fig. 11.9 **m** Thickening at the base of a queen palm (*Syagrus romanzoffiana*) caused by the development of adventitious roots deep within the stem. Scale bar = 0.5 m. (RR Wise)

11.10 Chapter Review

Concept Review

11.1 *Stems have a variety of forms and functions.* The typical stem produces and supports leaves and flowers. Other stem functions include photosynthesis (cladodes), attachment (tendrils), underground storage (rhizomes), and asexual reproduction (rhizomes and stolons).

11.2 *External stem morphology varies among monocots and herbaceous eudicots.* Stems are divided into nodes, the region where leaves and flowers originate, and internodes, the regions between the nodes. Perennial eudicot stems show evidence of previous year's growth in the form of leaf and bud scale scars. Monocot stems may be quite substantial, as in bamboo, or made of overlapping leaf sheaths as in the grasses. Phyllotaxy is the arrangement of leaves on a stem.

11.3 *The stem is composed of three tissues—dermal, ground, and vascular.* The dermis covers the stem exterior, the vascular tissue contains xylem and phloem, and the ground tissue is represented by the cortex, pith, and conjunctive tissue. The basic arrangement of the three tissues differs between monocots and eudicots.

11.4 *Dermal tissues cover the stem exterior.* The dermal tissue that covers the exterior of the stem has an outer, waxy cuticle and may contain stomata and trichomes.

11.5 *Ground tissues fill the stem interior.* Ground tissue may contain parenchyma, fibers, tannins, starches, and secretory ducts. Ground tissue makes up the cortex, pith, and conjunctive tissue of the stem. An endodermis may separate the cortex from the vascular tissue (stele).

11.6 *Stem vascular tissues are arranged in bundles.* Vascular bundles are arranged in a ring in most eudicot stems and scattered throughout the monocot stem. Depending on the species, xylem may be positioned to the interior, exterior, surround by, or on both sides of the phloem. Protoxylem and protophloem are derived from the procambium; metaxylem and metaphloem are derived from the vascular cambium. Open vascular bundles have a vascular cambium (they possess metaxylem/phloem), closed vascular bundles do not (only have protoxylem/phloem).

11.7 *The stem vascular system shows several forms.* The stele is the vascular cylinder in a stem or root. Protosteles have a solid center of xylem; there are three types. The xylem is cylindrical in a haplostele, lobed in an actinostele, and plate-like in a plectostele. Siphonosteles have pith in the center; there are three types, with subtypes. Solenosteles have either phloem exterior to the xylem (ectophloic) or on both sides of the xylem (amphiphloic). A dictyostele has multiple leaf gaps. A eustele has discrete vascular bundles in a field of pith. Eudicots have a eustele with the bundles arranged in a ring. Monocots have an atactostele—a eustele with the appearance of scattered vascular bundles.

11.8 *Secondary growth in eudicots has three basic patterns.* The ring of vascular bundles in a eudicot eustele showing secondary growth may develop as a) individual vascular bundles that become connected via the activity of an interfascicular cambium, b) a single ring of vascular cambium that produces concentric rings of xylem and phloem, or c) individual bundles that stay separated because the interfascicular cambium produces parenchyma. In the latter case, the tissue between the bundles is called a pith ray.

11.9 *Monocot stems show a different form of secondary growth than eudicots.* Monocot stems lack true secondary growth but can become quite "woody" via the development of sclerified bundle sheaths, the activity of a primary thickening meristem, or the activity of a secondary thickening meristem.

Concept Connections

1. Match the structure in the left column to the function in the right column. Some structures may have more than one function.

a. Rhizome	i. Storage
b. Corm	ii. Attachment
c. Stolon	iii. Perennation
d. Cladode	iv. Asexual reproduction
e. Tendril	v. Photosynthesis

Concept Assessment

2. Primary and secondary thickening meristems are mostly found in
   a. ferns.
   b. gymnosperms.
   c. dicots.
   d. monocots.
   e. uniformly found in all of the above.

3. Herbaceous stems differ from woody stems in that
   a. herbaceous stems only show secondary growth.
   b. herbaceous stems are only found in monocots.
   c. herbaceous refers to monocots. woody refers to eudicots.
   d. herbaceous stems rarely show secondary growth.
   e. herbaceous stems are characteristic of a perennial growth habit.

4. Phyllotaxis is
   a. the generation of roots from a stem.
   b. the ability to undergo secondary growth.
   c. a leaf pattern in which successive leaves are at right angles to each other.
   d. a meristem that contributes to both primary and secondary growth.
   e. the pattern of leaf initiation on the stem.

5. The outer layer of the stem apical meristem is covered by the
   a. dermal layer.
   b. cortex.
   c. endodermis.
   d. ground tissues.
   e. aerenchyma.

6. Lateral organs of stems (leaves, branches, and floral organs) are produced in what manner?
   a. endogenous.
   b. exogenous.

c. intercalary.
d. from pericycle.
e. from endodermis.

7. The hypodermis is relatively rare in stems.
a. true.
b. false.

8. A leaf gap is found in the ______
a. vascular system of a leaf.
b. apical meristem of a shoot.
c. ground tissue of a leaf.
d. ground tissue of a stem.
e. vascular system of a stem.

9. Support is provided in Spanish moss (*Tillandsia usneoides*) stems by a
a. vascular cambium.
b. sclerified epidermis.
c. sclerified pith.
d. strands of collenchyma.
e. a cortex of chlorenchyma.

10. Protosteles have a simple anatomy with
a. a central core of xylem surrounded by phloem.
b. a central core of pith surrounded by xylem and phloem.
c. a hollow core surrounded by pith, xylem and phloem, in that order.
d. a solid core of sclereids surrounded by chlorenchyma.
e. a tube of xylem and phloem lying just underneath the epidermis.

11. The primary source of stem thickening in squash is
a. sub-epidermal collenchyma.
b. xylem.
c. internal phloem.
d. vascular cambium.
e. perivascular fibers.

■ Concept Applications

12. Monocot stems lack true vascular cambium, yet some monocots, like palm and bamboo, can make a very strong stem. How do monocots do this?

13. Explain how the monocot primary thickening meristem can contribute to both the length and girth of the stem.

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