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Parenchyma, Collenchyma, and Sclerenchyma

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6

Introduction

Regardless of the organ or tissue, all plant cells belong to one of three cell types: parenchyma, collenchyma, or sclerenchyma. Unlike animals, in which an organ, tissue, and cell type may have all the same name, the nomenclature of plant structures is more specific and detailed. For instance, we may speak of an organ called the liver, which is made of both liver tissue and liver cells. In this instance, the organ, tissue, and cell type all have the same name.

Plants are arranged differently. The plant body has four basic organs: roots, stems, leaves, and flowers/fruit (► Sect. 1.11), which in turn, are composed of tissues. Tissues are cell complexes, which are similar in origin and structure, and are designed to carry out specific functions. Tissues may be simple (consisting of one cell type only), as in the case of **aerenchyma** or **chlorenchyma**, or complex (consisting of two or more cell types) as in the case of xylem (► Chap. 7) or phloem (► Chap. 8). Thus, an organ such as a leaf is made of three different tissues (epidermis, mesophyll/chlorenchyma, and vasculature), with each tissue composed of up to three general cell types (parenchyma, sclerenchyma, or collenchyma). The three general cell types may be further divided based on function.

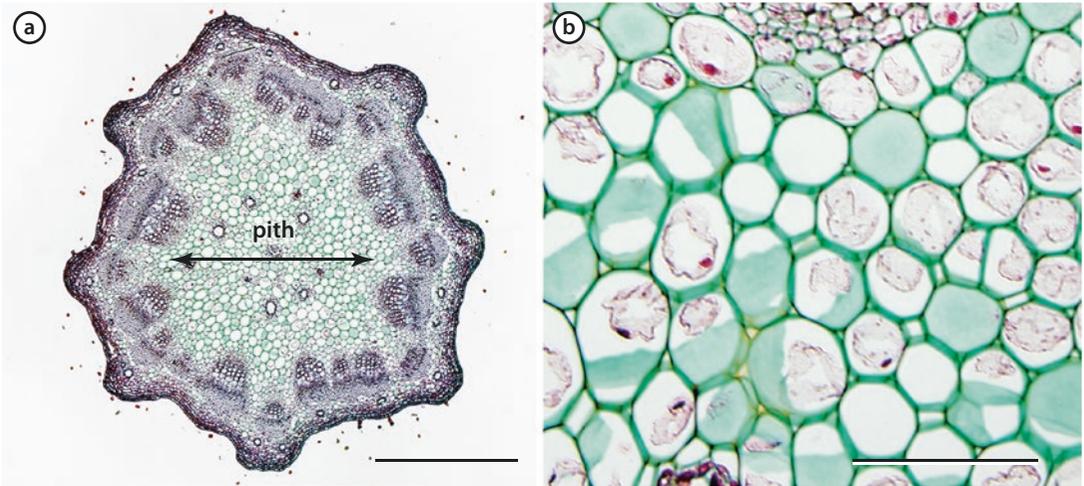## 6.1 Parenchyma Cells Are the Most Common Plant Cell Type

◘ Table 6.1 give examples of different forms and functions of the three basic plant cell types — parenchyma, collenchyma and sclerenchyma. **Parenchyma** cells are simple cells—alive, metabolically active, capable of dividing, and bounded by a primary cell wall. Altogether, parenchyma represents about 90% of the cells found in a typical herbaceous seed plant. Some of the most important activities of the plant, such as photosynthesis, nutrient assimilation, respiration, storage, and secretion are primarily based in parenchymatous tissues. While many parenchyma cells may be simple or unspecialized, they also possess the highest degree of developmental plasticity. This enables them in specialized circumstances to become transformed into all other cell types, a feature important for wound repair and a key characteristic of meristematic tissues (► Chap. 4). It is also noteworthy to point out that more primitive multicellular non-tracheophytes (► Sect. 1.14) tend to consist of parenchyma only. Lacking the support and water conduction made possible by collenchyma and sclerenchyma, bryophytes are mostly of small stature and typically only occupy moist habitats.

Parenchyma cells are found in ground tissues. Examples of such tissues are the pith of stems (◘ Fig. 6.1a, b) and the cortex of stems and roots (◘ Fig. 6.1c, d). Here, the cells serve primarily as basic filler tissue but may also be involved in apoplastic and symplastic transport and/or storage. Parenchyma cells may be highly specialized when they are parts of a complex tissue like the

Table 6.1 Characteristics, functions, and examples of parenchyma, collenchyma, and sclerenchyma cells (RR Wise)

Parenchyma	Collenchyma	Sclerenchyma
Characteristics	*Characteristics*	*Characteristics*
1° cell wall only*	1° cell wall only	mostly 2° cell wall
connected via	unevenly thickened cell	various patterns of wall
plasmodesmata	walls	thickenings
living at maturity	connected via	if connected, by pits
may be toti-/pleuropotent	plasmodesmata	usually dead at maturity*
	living at maturity	
Functions	*Functions*	*Functions*
serve as ground tissues	support of annual or young	protection
photosynthesis	stems and leaves	support
(chloroenchyma)		conduction (transpiration, via
protection (epidermis)		xylem)
storage		
meristematic		
conduction (translocation,		
via phloem)		
secretion		
wound repair		
Examples	*Examples*	*Examples*
pith parenchyma	angular collenchyma	xylem and phloem fibers
cortical parenchyma	annular collenchyma	sclereids*
leaf mesophyll	lamellar collenchyma	brachysclerids
(chloroenchyma)	lacunar collenchyma	astrosclerids
epidermis		macrosclerids
pavement cells		osteosclereids
subsidiary cells		xylem tracheary elements
guard cells	*"enchyma" is from the Greek éy (in) and χεῖν (to pour) and means to "pour in", "fill" or "occupy". Originally, the term was used to describe the primitive formative juice of animal and plant bodies. That "juice" was later found to be made of individual cells, but the root word persists.*	imperforate
trichomes		(andiosperms and
glandular/nonglandular		gymnosperms)
uniseriate/multiseriate		perforate (angiosperms)
1° meristems		
protoderm		
procambium		
ground meristem		
calyptrogen		*Some sclerids maintain a living protoplasm at maturity, but they are metabolically very quiet.*
2° meristems	*"par(e)" is from the Greek παρα (para) meaning "beside"*	
fasicular		
interfascicular		
lateral		
phelloderm		
pericycle	*"scler" is from the Greek σκληρός (scleros), meaning "hard"*	
phloem		
sieve tube elements		
(angiosperms)		
sieve cells	*"coll" is from the Greek κολλα (kolla), meaning "glue", which refers to the thick, glistening appearance of the walls in fresh tissues*	
(gymnosperms)		
companion cells		
(angiosperms)		
albuminous cells		
(gymnosperms)		
phloem parenchyma		
sclerified xylem		
parenchyma*		
secretion		
idioblasts		
hydathodes		
resin duct epithelia		
lithocysts		
glandular trichomes		
nectaries		
collaters		

6

◙ **Fig. 6.1**   **a** Pith parenchyma in a mugwort (*Artemisia* sp.) stem. **b** The pith tissue is composed of tightly packed parenchyma cells. Scale bars = 500 μm in **a**, and 50 μm in **b**. (**a**, **b** RR Wise)
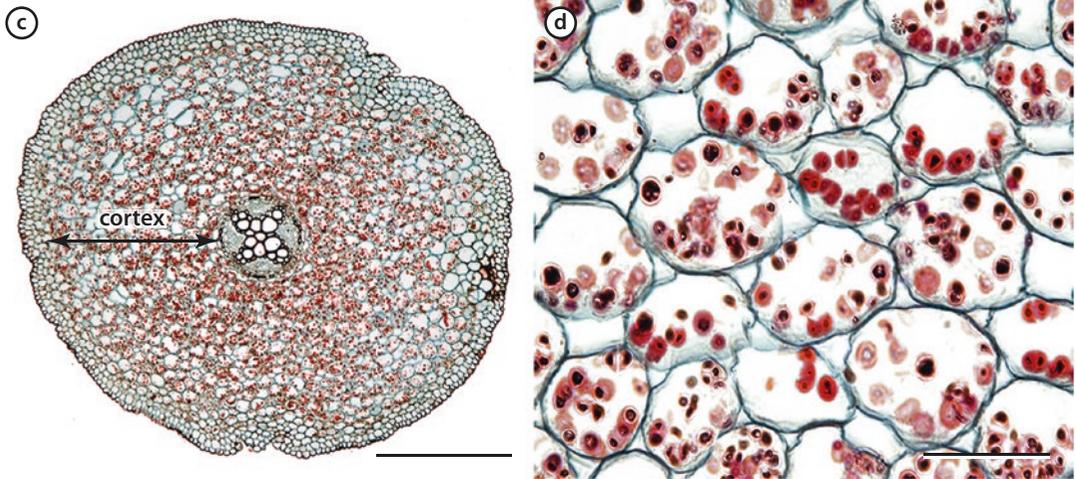
◙ **Fig. 6.1**   **d** Cortical parenchyma in a buttercup (*Ranunculus* sp.) root. The vascular system is in the center of the root, and the epidermis lies to the outside. **d** Note the presence of numerous starch grains (stained as red dots); thus, this cortical parenchyma is also storage parenchyma. Scale bars = 500 μm in **c**, and 50 μm in **d**. (**c**, **d** RR Wise)

chlorenchyma (chloroplast-containing parenchyma) of leaves that carry on abundant photosynthesis (◙ Fig. 6.1e). Parenchyma cells are well suited for photosynthetic activity because their thin primary cell walls allow more efficient diffusion of light, water, gases, and metabolites.

The plant epidermis is made of parenchyma cells and may include **pavement cells** (a.k.a. **ground epidermis**), guard cells of the stomata (◙ Fig. 6.1f, g), and glandular or non-glandular trichomes (▶ Chap. 9). Guard cells are the only epidermal cells to contain chloroplasts, which play a key role in stomatal opening and closing.
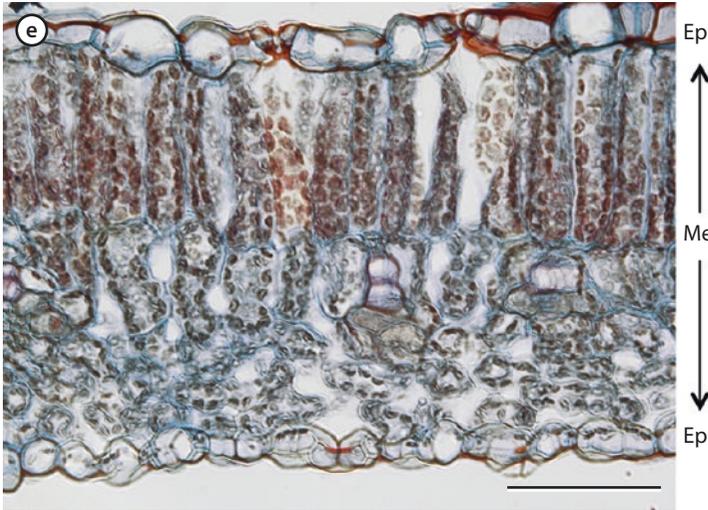
■ **Fig. 6.1** **e** Cross-section of a cucumber (*Cucumis sativus*) leaf showing chlorenchyma (with red-stained chloroplasts) in the center of the leaf (mesophyll, Me) with epidermal parenchyma (Ep) on the top (**adaxial**) and bottom (**abaxial**) surfaces. Scale bar = 50 μm. (RR Wise)
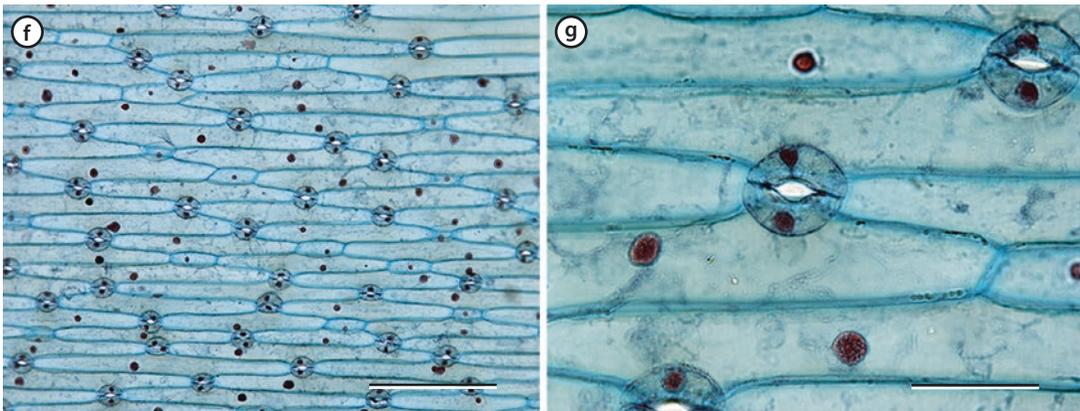

■ **Fig. 6.1** **f** Epidermal parenchyma on the surface of an onion (*Allium* sp.) leaf. Multiple pairs of guard cells can be seen. All other cells in the images are subsidiary (or pavement) cells. Trichomes (not shown here) are also parenchyma cells. **g** The dark red dots are nuclei. Scale bars = 100 μm in **f**, and 25 μm in **g**. (**f, g** RR Wise)

Aerenchyma tissue is composed of parenchyma cells and is quite common in the leaves, stems, and roots of aquatic plants (■ Figs. 6.1h–j) (Takahashi et al. 2014). In these plants, the air in the spaces serves not only for aeration, but (when they occur in floating leaves or stems) also to give the plants buoyancy and support. The air spaces form an elaborate system that is continuous from the leaf to the root, thereby allowing oxygen to diffuse from its point of highest concentration in the leaves, to places of scarcity in the tissues that are lacking chlorophyll. The buoyancy of many water plants further enables them to capture light at the surface of the water for effective photosynthesis.
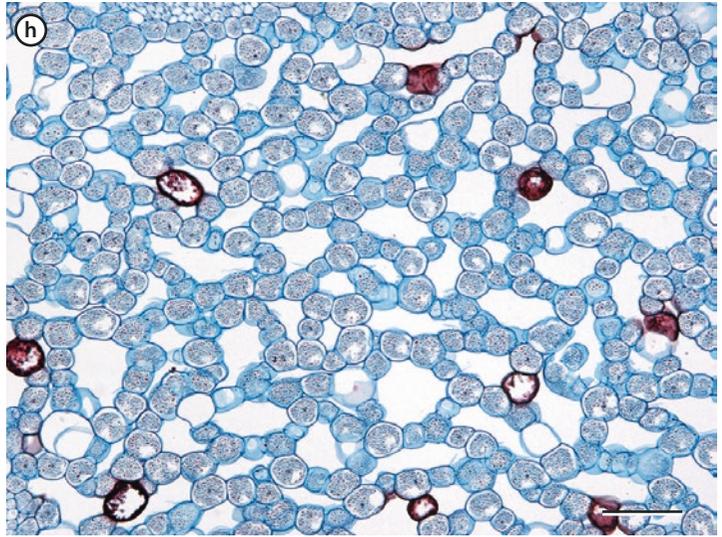
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◼ **Fig. 6.1   h** A section through the underground stem of sweet flag (*Acorus* sp.) showing large separation of the parenchyma tissues along the middle lamella. The intercellular spaces enable the movement of large amounts of water, dissolved gasses, and minerals to travel throughout much of the plant. The red cells are sclerified and serve as support tissue. Scale bar = 100 μm. (RR Wise)
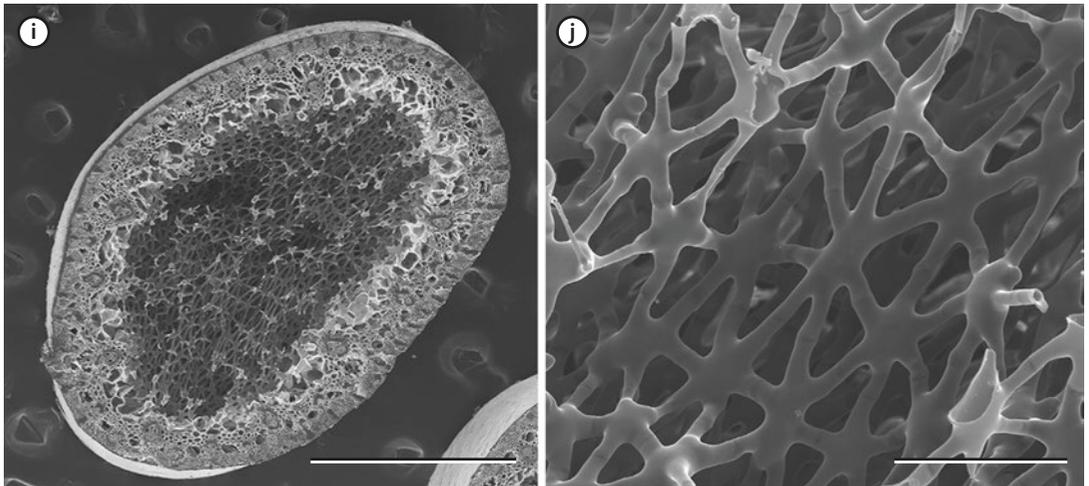

◼ **Fig. 6.1   i** Aerenchyma tissue occupying the center of a bullrush (*Juncus* sp.) stem. **j** The individual parenchyma cells form a network of aerenchyma tissue. Scale bars = 1 μm in **i** and 100 μm in **j**. (**i**, **j** RR Wise)

Storage parenchyma of seeds and tubers contains large quantities of carbohydrates, mostly in the form of starch, or oils (◼ Fig. 6.1k, l). In seeds such as *Asparagus*, *Coffea*, *Diospyros*, and *Iris*, the carbohydrates may be in the form of thickened walls and are represented by hemicelluloses. Oils are typically in the form of triglycerides in seeds, but in tubers and roots, there are many complex oils that vary by species as well as climatic and environmental conditions.

While parenchyma cells are generally thought of as being thin-walled, they sometimes have very thick primary walls as in the case of seed endosperm cells of lily (*Lilium* sp., ◼ Fig. 6.1m), date palm
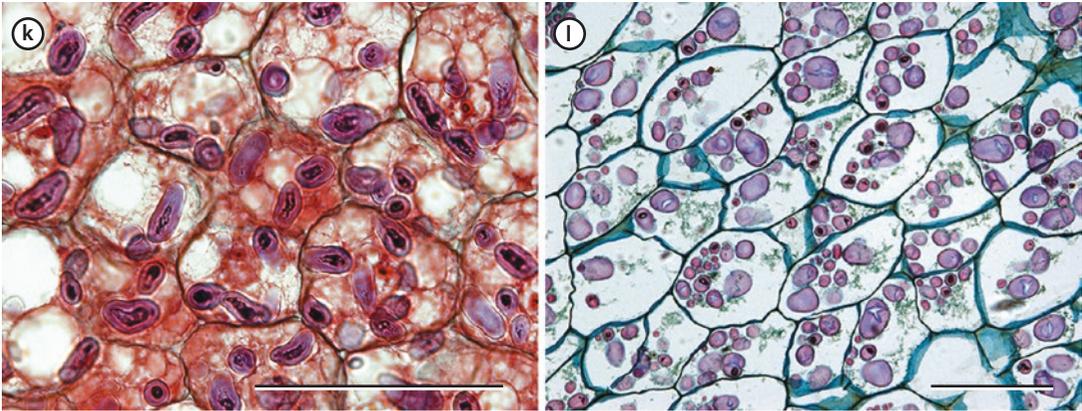
◪ Fig. 6.1   k Storage parenchyma of bean seed (*Phaseolus vulgaris*) and **l** potato tuber (*Solanum tuberosum*, right). Both tissues were stained with I$_2$KI to enhance internal starch deposits, which appear as purple grains. The cells are compressed into a multifaceted form by contact pressure, with little intercellular air space in these storage tissues. Scale bars = 50 μm in both panels. (**k, l** RR Wise)
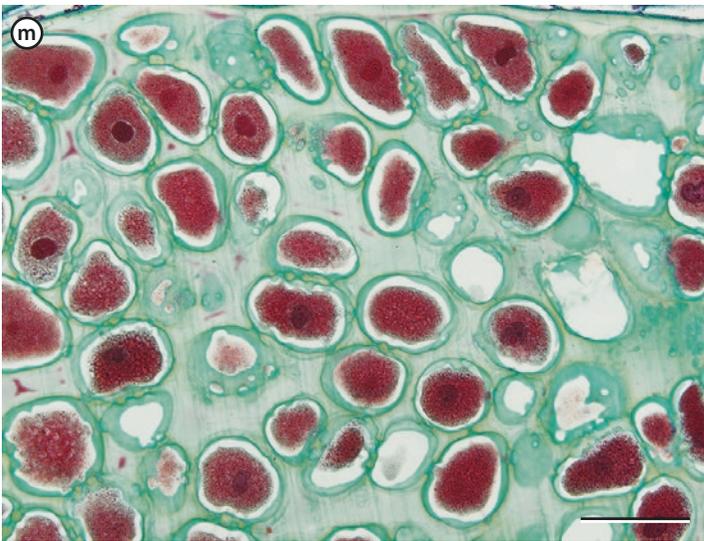
◪ Fig. 6.1   m Lily (*Lilium* sp.) seed endosperm showing thick primary walls, stained green. The cell protoplasm has stained red, with the nucleus slightly darker. Scale bar = 100 μm. (RR Wise)

(*Phoenix dactylifera*), asparagus (*Asparagus* sp.), and coffee (*Coffea arabica*). This is often due to the large deposition of hemicelluloses.

The three-dimensional shape of parenchyma cells has been a matter of considerable study (◪ Fig. 6.1n). A number of studies have shown that parenchyma cells consist of a variety of three-dimensional polyhedra that have an average of 14 faces. A geometrically perfect, 14-sided polyhedron with 8 hexagonal and 6 quadrilateral faces has been named an **orthic tetrakaidecahedron**. This ideal figure is compromised in plants that may have a range of facets, but usually averaging 14. Pressure and surface tension both appear to play a major role in determining the number of facets for a particular parenchyma cell.

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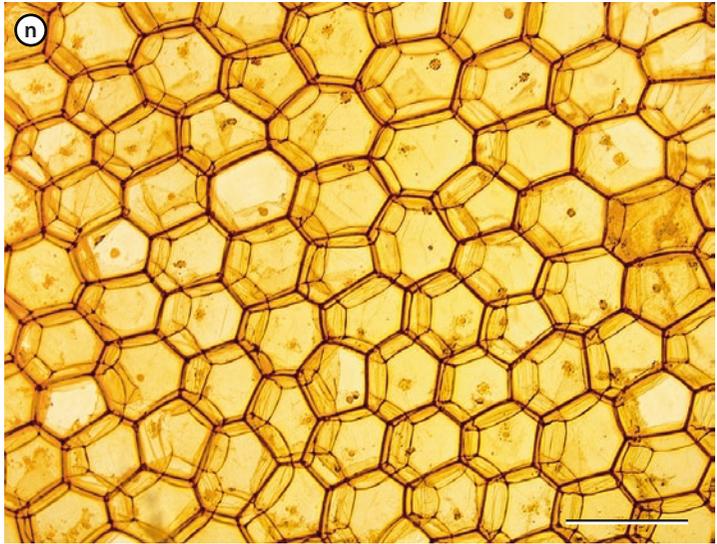
☐ **Fig. 6.1** **n** LM of Wandering Jew (*Tradescantia zebrina*) adaxial epidermis showing its angular appearance. Scale bar = 100 µm. (RR Wise)

6.2 Parenchyma Cells May Exhibit Totipotency

Parenchyma is the only one of the three cell types that can engage in mitotic divisions, and they can retain that ability for years. In animals, only stem cells, which are quite rare, retain the ability to carry out mitosis. Consequently, parenchyma cells are the types found in primary and secondary meristems (refer to ► Chap. 4) and the cells that are used for wound repair. The retention of the ability to divide and then continue to differentiate into any of the other cell types is called totipotency, and it enables some parenchyma cells (under the right environmental conditions) to develop into other specialized tissues, including an entirely new viable plant (White 1939).

☐ Figure 6.2 shows plantlets derived from plant tissue culture techniques. As an example, carrot tissue is easily cultured with the following procedure. A carrot root can be sliced into several sections, and the parenchyma storage tissue (cortex) is pulverized with a blender that separates individual cells. Some of these may be cultured in a nutrient medium and will undergo mitosis. Placing these young developing cells into a semisolid nutrient medium will allow them to start growing into new young plantlets due to their totipotency (ability to differentiate into any number of cell types). These, in turn, can be transferred to an enriched soil where full development occurs into a mature carrot plant. Plant tissue culture has many uses in horticulture, plant propagation, and biotechnology.

Fig. 6.2 Plant tissue cultures being grown at a USDA facility (USDA, public domain)

6.3 Collenchyma Cells Are Used for Support and Are the Least Common Cell Type

Collenchyma, together with sclerenchyma, belongs to a group of plant tissues often designated as supporting or mechanical and is primarily found in angiosperms. They essentially have only primary walls (Fig. 6.3a), but in some cases, it is believed that secondary deposition may occur resulting in a gradient of development (Leroux 2012). The designation, collenchyma, is derived from the Greek word, κόλλα, meaning glue, which is a reference to the thick, glistening appearance of unstained collenchyma cell walls (refer to Leroux 2012 for the etymology). Of the three types of fundamental tissue found in plants, only about 1% can be considered to be collenchyma.

Given the lack of a secondary cell wall, collenchyma cells can be thought of as being relatively "inexpensive" to produce and reasonably stretchable. Therefore, they are typically in one of two places in herbaceous plant organs. First, collenchyma cells are found in short-lived and rapidly expanding tissues such as large leaf petioles where there is not the time or need to invest in sclerenchyma for support. Second, they may be found in elongating stems, which could not continue to expand in the presence of rigid sclerenchyma. While there have been a few cases in which collenchyma tissues have appeared in roots, most of those have been aerial roots. In leaves, collenchyma appears as axially elongated strands, often located above and below major veins, as well as in petioles and sometimes

■ **Fig. 6.3   a** A transmission electron micrograph of angular collenchyma from the petiole of celery (*Apium* sp.) revealing detail of walls and cytoplasmic structure. Note the irregular primary cell wall thickenings in the corners of the cell. Scale bar = 1 µm. (Image from: Ledbetter and Porter 1970, Introduction to the Fine Structure of Plant Cells, Springer-Verlag, with permission)

leaf blade margins. In stems, it appears as a hollow cylinder around vascular tissues, or as peripheral longitudinal strands even though the cells have various amounts of living protoplasm. Chloroplasts are rarely found.

The walls of collenchyma are largely hydrated cellulose, but small amounts of hemicelluloses and pectins have also been reported (Leroux 2012). Lignin does not appear to be a normal component of collenchyma cell walls. Collenchyma cells have unequally thickened primary walls, especially when observed in cross-sectional view. The different thickness patterns of the wall are a characteristic feature formed during elongation. There are four primary types of collenchyma based on the arrangement of the wall thickenings: **angular** (■ Fig. 6.3b, c), **lamellar** (or plate, ■ Fig. 6.3d), **lacunar** (■ Fig. 6.3e), and **annular** (■ Fig. 6.3f).

Collenchyma is a living tissue composed of elongated cells with thick non-lignified primary walls. Such cells are most closely aligned physiologically with parenchyma cells. Where collenchyma and parenchyma cells are found adjacent to each other, they frequently intergrade through transitional cells. The resemblance to parenchyma is further stressed by the ability of this tissue to undergo reversible changes in wall thickness and to engage in meristematic activities. Thus, it is entirely appropriate to consider these two cell types in the same chapter of study.

The thickened walls of collenchyma cells consist mainly of cellulose and hemicelluloses and contain considerable water (as much as 67% based on fresh weight). Thickening of the walls occurs during elongation growth of the cells, with successive layers of wall material
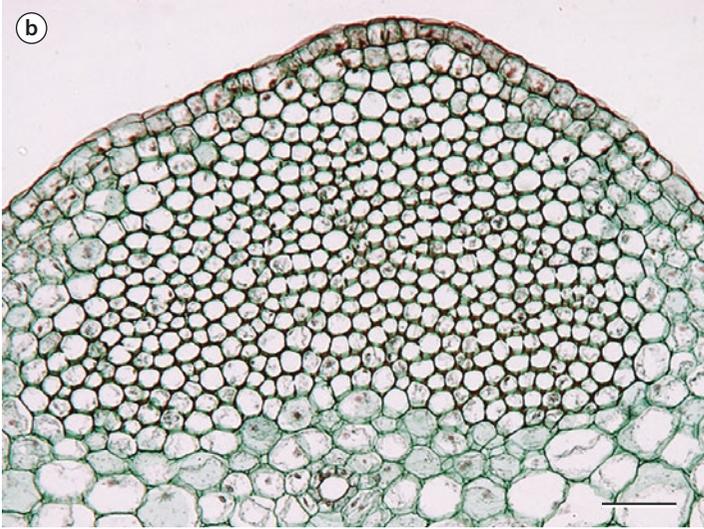
◩ Fig. 6.3   b Angular collenchyma from celery (*Apium* sp.) petiole. Angular collenchyma has greatest wall thickenings where cells meet in corners. The thickened portion of cell walls in contiguous collenchyma cells merges, forming three to four angles. Scale bar = 100 μm. (RR Wise)
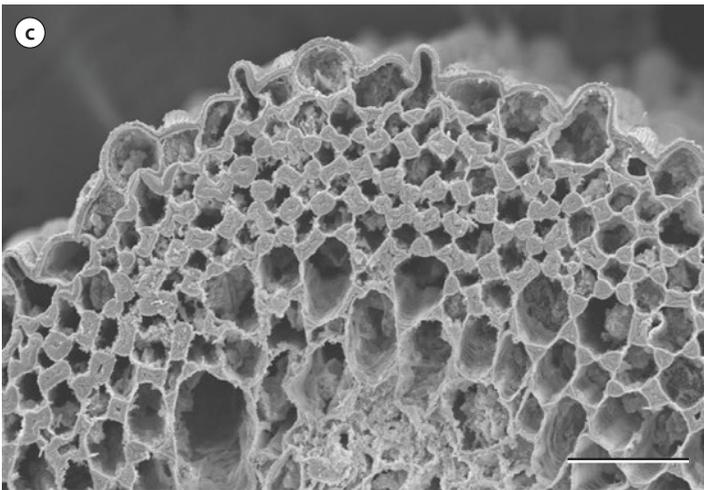
◩ Fig. 6.3   c Angular collenchyma from rhubarb (*Rheum rhabarbarum*) leaf petiole showing the extensive amount of angular collenchyma, as viewed with scanning electron microscopy. Scale bar = 100 μm. (RR Wise)

formed around the entire cell, but they are wider in the places of thickenings. Cellulose microfibrils have a helicoidal texture in collenchyma cell walls that largely sets them apart from parenchyma cells (◩ Fig. 6.3g).

In some cases, it has been reported that the degree of wall thickening in collenchyma is increased if, during development, the plants are exposed to motion by wind or other mechanical forces. On the other hand, wall thickenings may be removed in response
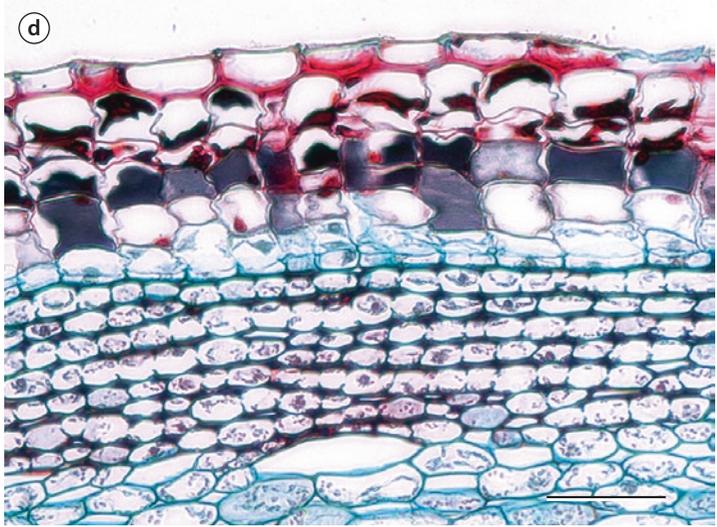
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☐ **Fig. 6.3   d** Lamellar (a.k.a. plate) collenchyma from a black elderberry (*Sambucus canadensis*) stem is characterized by thickened portions of cell walls that are present only on tangential cell walls, i.e., those parallel to the surface. There are no substantial thickenings on the radial cell walls, and thus they often tear during sectioning. Scale bar = 100 μm. (RR Wise)
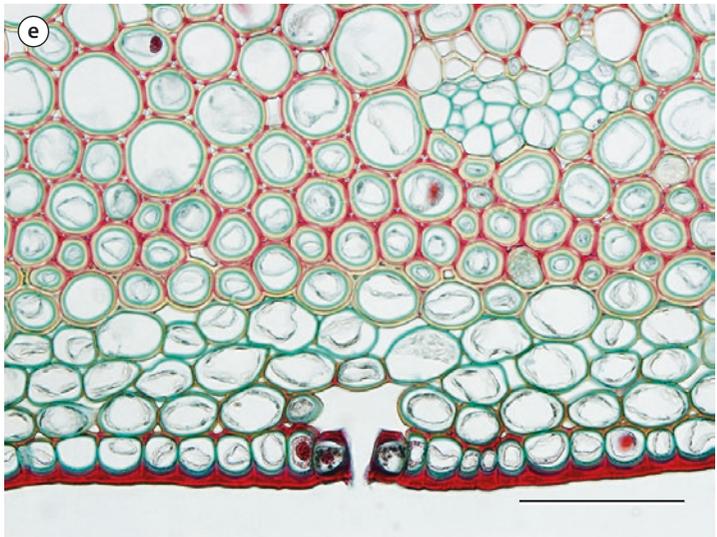

☐ **Fig. 6.3   e** Lacunar collenchyma in the outer cortex of a young stem of lily (*Lilium* sp.). The presence of intercellular spaces is a characteristic feature of a less common type of collenchyma called lacunar. It is somewhat similar to angular collenchyma but contains an intercellular space in the center of "angles." Note the guard cell pair and thick wax coating of the stem epidermis. Scale bar = 50 μm. (RR Wise)

to injuries and wound-healing reactions. Collenchyma that differentiates early in a given organ becomes more highly specialized, whereas that which is formed later is often more like parenchyma (Leroux 2012).
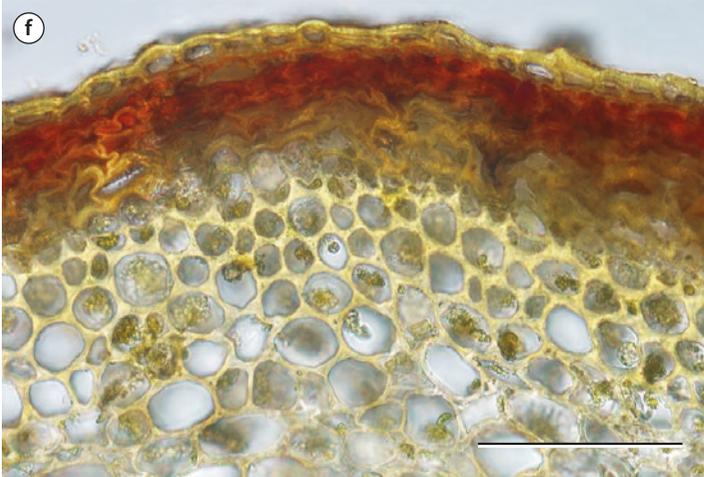
☐ **Fig. 6.3   f** Annular collenchyma in the stem of paper flower (*Bougainvillea glabra*) is the least common type of collenchyma. It is characterized by evenly deposited primary wall thickenings and little or no intercellular spaces. The cell lumen acquires a rounded outline in cross-section, and the cells become similar to fibers, but with unlignified walls. Fresh section and stained with phloroglucinol. Scale bar = 50 μm. (RR Wise)

6.4 Birefringence Is a Common Phenomenon in Collenchyma Walls

A phenomenon called **birefringence** occurs when crystalline materials or specimens with highly ordered molecules are being observed with the polarized light. When a polarizing filter is used to order light into a single plane through the specimen, some of the light is retarded and rotated by the specimen so that when the light encounters a second polarizing filter above the objective lens of the light microscope, some light has rotated to a new plane and may have experienced interference to produce new colors. Light leaving the filter is said to be plane polarized and consists of light waves essentially in a single plane (all parallel to one another). That light not changed by the specimen will be blocked and will not appear. The birefringence seen in collenchyma cell walls (☐ Fig. 6.4a, b) is a direct consequence of their layered structure.

**Box 6.1   Chemical Composition of Collenchyma Cell Walls (Finally) Revealed**
Collenchyma, as a distinct cell type, has been described for over 100 years. Collenchyma cell shape, location, mechanical properties, and wall appearance are very well known. Surprisingly, however, the chemical composition of the collenchyma cell wall was only recently revealed. Chen et al. (2017) reported the first detailed investigation of the cell wall composition of collenchyma from any plant. The authors isolated collenchyma strands from celery petioles, a classic study system for collenchyma. Using a vast array of modern

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❏ **Fig. 6.3   g** Transmission electron micrograph of angular collenchyma from burdock (*Arctium* sp.) petiole. The thickenings of the collenchyma cell wall have a helicoidal arrangement of the cellulose microfibrils that may make the walls more flexible. In cross-section, the wall appears to be multilayered because the microfibrils gradually change their orientation from longitudinal to transverse and back again to longitudinal during cell elongation. In the thin layers of the wall, the microfibrils are cut longitudinally, and in the thicker regions, there are many layers of microfibrils. Note the very thin layer of cytoplasm at the inner surface of the wall (arrow). Scale bar = 100 nm. (Crang and Vassilyev 2003)

chemical analytical techniques, they determined that the collenchyma cell wall contained many of the same polysaccharide components as found in the extensively studied parenchyma cell wall. However, the proportions and chemical species were distinctly different. Pectin is the major polysaccharide in the *Apium* collenchyma cell wall, followed by cellulose, xyloglucans, heteroxylans, and heteromannans. This long overdue study on collenchyma will serve as a good comparison to the large amount of data available for the structure and chemical composition of cell walls of parenchyma tissues.

Reference: Chen et al. (2017).
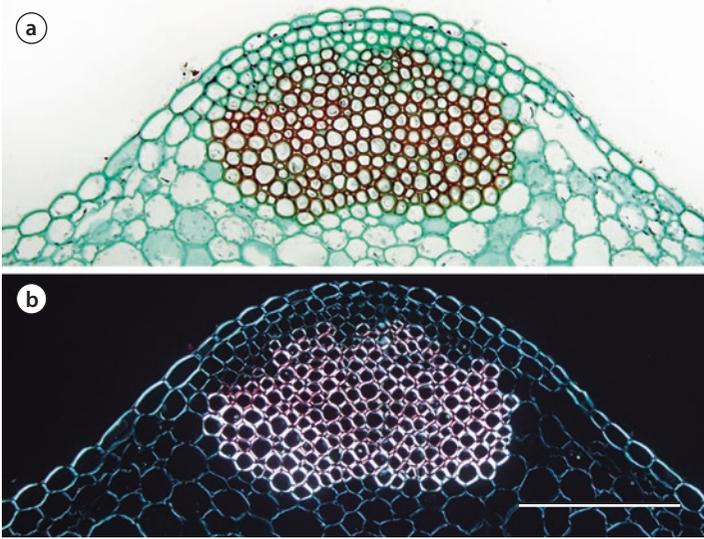
◼ **Fig. 6.4**   **a**, **b** Collenchyma in a carrot (*Daucus carota*) petiole. **a** Brightfield microscopy. **b** Polarized light microscopy. Scale bar = 100 μm. (**a**, **b** RR Wise)
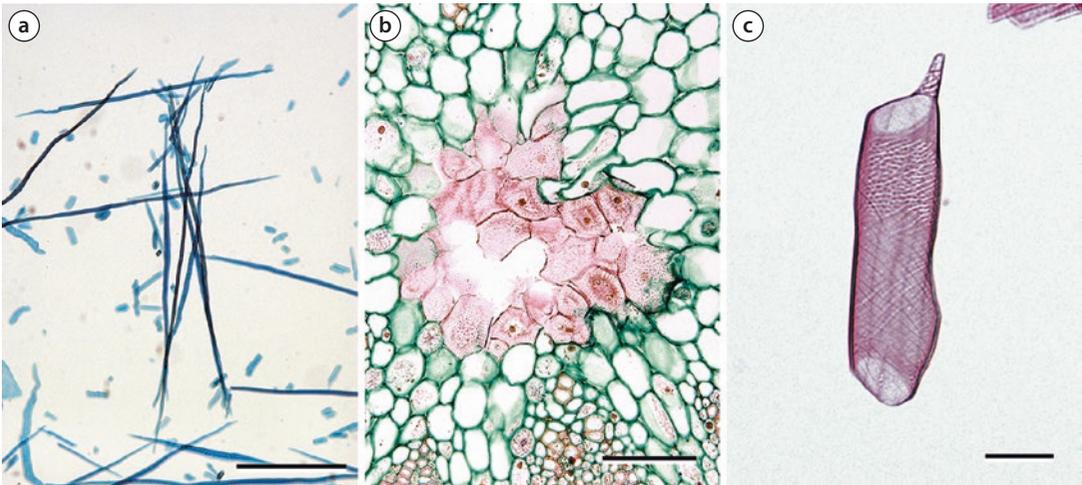
◼ **Fig. 6.5**   **a**–**c** Three basic sclerenchyma cell types. **a** Fibers from macerated red oak (*Quercus rubra*) wood. Scale bar = 500 μm. **b** Sclereids in the central pith of a mistletoe (*Viscum* sp.) stem. Scale bar = 100 μm. **c** A water-conducting xylem vessel element from macerated basswood (*Tilia americana*) wood. Scale bar = 50 μm. (**a**–**c** RR Wise)

6.5 Sclerenchyma Cells Provide Support, Protection, and Long-Distance Water Transport

Sclerenchyma cells vary greatly in regard to their origin, distribution, shape, and structure. However, they may be classified into three categories, namely, fibers, sclereids, and water-conducting sclerenchyma (◼ Fig. 6.5a–c). Along with parenchyma and collenchyma, they constitute the third group of fundamental tissues but in total represent only less than 10% of all the cells in living (i.e., non-woody) tissues. Sclerenchymas are structural support cells that

do not depend on turgor to remain rigid, but rather on the presence of a rigid secondary wall, and are usually dead at maturity.

Water-conducting sclerenchymas, such as vessel elements, are a major cell type in xylem tissue and will be presented in detail in ► Chap. 7. Fibers and sclereids will be discussed below in ► Sects. 6.6, 6.7, and 6.8.

6.6 Fibers Impart Support and Protection

Fibers are long (up to 2 mm), narrow (typically 20 μm), thick-walled cells that are dead at maturity. Generally, fibers are not associated with water conduction, although one type of fiber—the fiber tracheid—has sidewall pits (► Chap. 7). Fibers are found in various parts of plants, often in association with vascular tissues, particularly phloem in primary growth (◘ Fig. 6.6a, b) and secondary xylem/ wood (► Chap. 15). Fibers differentiate early into elongated cells with few simple pits in their cell walls and always appear in clusters.

◘ Figure 6.6a shows fibers to the adaxial (at the top in the figure) and abaxial (at the bottom) sides of a vascular bundle in a maize stem. In young maize stems, the fibers serve primarily to protect the fragile
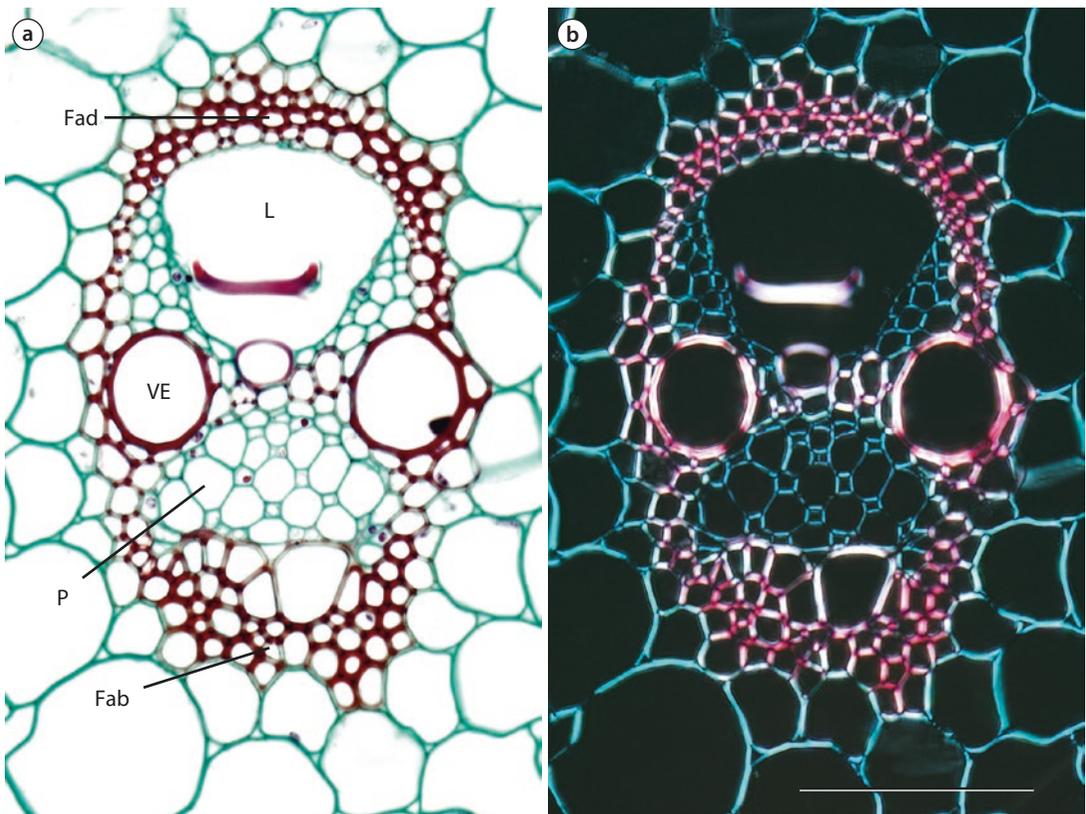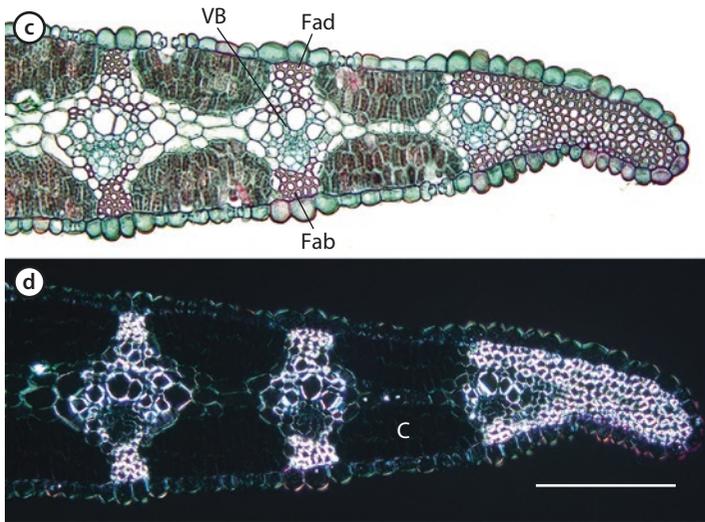

◘ **Fig. 6.6**   **a** Caps of fibers adaxial (Fad) and abaxial (Fab) to a vascular bundle in a young maize (*Zea mays*) stem. The two large cells to either side are xylem vessel elements (VE), and a patch of phloem (P) is visible in the center. The empty space in the top-middle is a lacuna (L), or hole, caused by tearing of the tissue during growth. **b** Same specimen viewed in polarized light to show lignification of fibers and vessel elements. Scale bar = 50 μm. (**a**, **b** RR Wise)

phloem tissues with structural support being a secondary function. The lignified cell walls of the fibers and the two large vessel elements show red birefringence when viewed in polarized light (◧ Fig. 6.6b).

In leaves such as those found in cattail (◧ Fig. 6.6c, d), fibers provide most of the leaf support, in addition to protecting the phloem. Large bundles of fibers to either side of the vascular bundles and at the leaf margin make for a stiff leaf that will support itself and be resistant to tearing in the wind.

Fibers may be commonly found in the cortex of developing or older stems. ◧ Figure 6.6e shows a large patch of fibers in a

◧ **Fig. 6.6** **c** Brightfield and **d** polarized images of fiber bundles (F) in a cattail (*Typha latifolia*) leaf. Fibers are adaxial and abaxial (Fad and Fab) to the three vascular bundles (VB) and strengthen the leaf margin (far right). Note the large patches of chlorenchyma (C) in the leaf mesophyll. Scale bar = 100 μm. (**c**, **d** RR Wise)
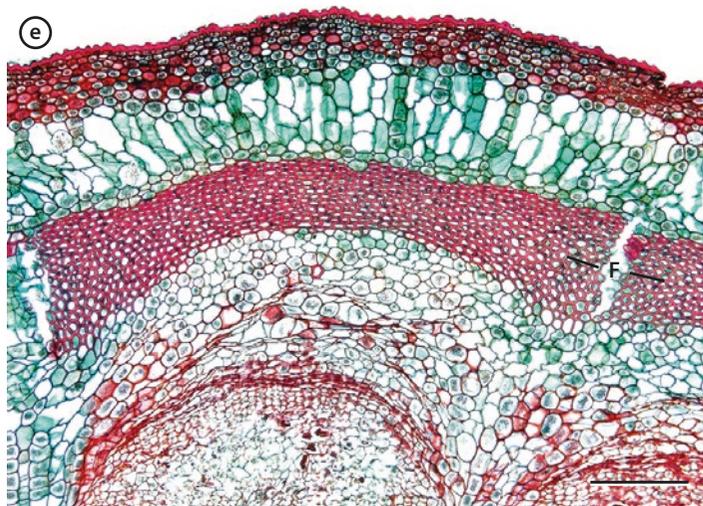

◧ **Fig. 6.6** **e** Large area of fibers (F) in a 2-year-old Dutchman's pipe (*Aristolochia* sp.) stem. Scale bar = 100 μm. (RR Wise)

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2-year-old *Aristolochia* stem. Because perennial stems grow for multiple years, large areas of fibers can accumulate. The fiber cells are initiated as cortical parenchyma, which subsequently differentiate into sclerenchyma and develop thick secondary walls.

Bundles of fibers are often found in the leaves of monocots where they provide support, particularly in large leaves of tropical plants. These heavily lignified bundles are often referred to as "hard" fibers. On the other hand, "soft" fibers may or may not be lignified and are usually quite flexible. The terms "soft" and "hard" are commercial designations referring to the texture of the raw materials used in making products and are not strict anatomical terms.

The walls of fibers are rather elastic, a feature which allows them to return to their original shape after bending or stretching, although the cells themselves are usually rigid. **Gelatinous fibers** are found in the tension wood (a type of reaction wood of dicots that shrink and pull, ▶ Chap. 15), and have a non-lignified cell wall, which is deposited over one or more layers of the secondary walls (◘ Fig. 6.6f, g).

Sclerenchyma fibers are subdivided according to their localization into xylary (or woody) fibers or extraxylary fibers. **Libriform**
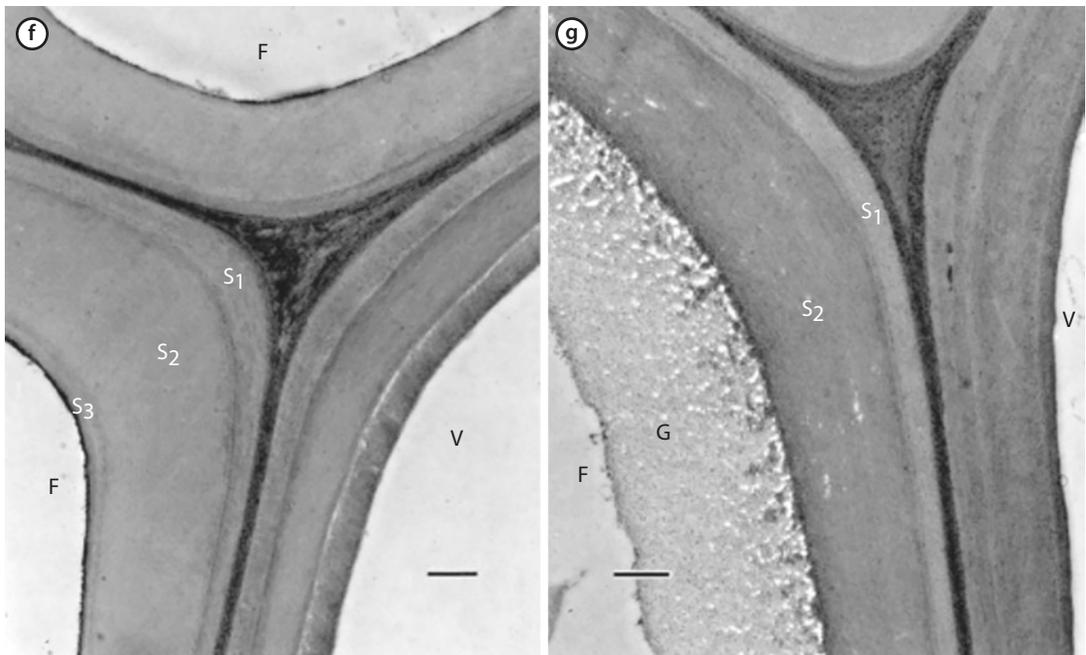
◘ **Fig. 6.6   f**, **g** Transmission electron micrograph of thin sections through *Populus deltoides* wood. Periodic acid-thiocarbohydrazide-silver proteinate (PATAg) staining. **g** Tension wood fiber has developed a gelatinous layer (G-layer) against an S_2 layer that is thinner than in **g** normal wood fiber. F = fiber; V = vessel; S_1, S_2, and S_3 = secondary wall sub-layers; G = gelatinous layer. Scale bars = 0.5 μm. (TA Tabet and FA Aziz, National University of Malaysia, CC BY 3.0)

fibers and **fiber tracheids** are part of the vascular bundle and are considered to be xylary fibers. They will be discussed further in ► Chap. 7—Xylem. Extraxylary fibers, on the other hand, are not located within a vascular bundle or xylem tissue meaning they may be mitotically derived from the phloem (phloem fibers), from cells immediately external to the phloem (perivascular fibers) or in the cortex (cortical fibers). All of the fibers discussed in this section have been extraxylary fibers. Wood fibers are discussed in ► Chap. 15.

Bast is a term used for over 150 years to refer to several different extraxylary fibers or tissues that could be stripped from a plant stem and used to tie or bind. As knowledge of plant anatomy developed, bast was first used to refer to phloem tissue (known then as the "inner bark" or "skin"), before the true nature of that tissue was known (► Chap. 8). Now, the term is used in a generic sense to refer to a variety of fibers of commercial importance, and its value as an anatomical term has diminished. The cell walls of most bast fibers, although thick and strong, are often not lignified and are therefore considered to be soft fibers. Some well-known examples of bast fibers are hemp for cordage (◘ Fig. 6.6h, i), jute for cordage and coarse textiles (◘ Fig. 6.6j), and flax for linen thread, textiles and fine papers, and ramie, which is used

◘ **Fig. 6.6   h** A hemp (*Cannabis* sp.) field in Brittany, France. **i** Cross-section of a hemp (*Cannabis sativus*) stem showing green, thick-walled, non-lignified bast fibers in the stem cortex. Scale bar = 100 μm. (**h** Barbetorte CC SA 3.0; **i** RR Wise)

◙ Fig. 6.6   j Jute (from *Corchorus* sp.) being placed out to dry. The hanging fibers are used for making textiles. (Image by La Roche Jagu-Chanvre, attribution ShareAlike 3.0)

for various textiles (Pari et al. 2015). Refer to ▶ Sect. 8.6 for more on phloem fibers. Leaves are also a good source of fibers, such as those found in New Zealand flax (*Phormium tenax*, Carr et al. 2005) and sisal (*Agave sisalana*).

6.7   Sclereids Are Reduced Sclerenchyma Cells That Occur Singly or in Clumps

Unlike the elongated fibers (▶ Sect. 6.6) and water-conducting sclerenchyma (▶ Chap. 7), **sclereids** are smaller in size and more varied in shape. Fibers and water-conducting sclerenchyma are characteristics of vascular tissues and may extend, in an overlapping fashion, the entire length of the root or shoot. Sclereids, on the other hand, occur singly or in clusters in various locations in the plant body such as stems, seed coats, fruit pulp, and leaves (especially in the mesophyll). They have thick secondary walls that are heavily lignified. Development of sclereids appears to be dependent, at least in part, on plant hormonal (auxin) levels. Elevated levels of auxin (as may occur in wounding) may elicit the development of greater numbers of sclereids. Sclereids are classified as brachysclereids, astrosclereids, osteosclereids, or macrosclereids. Examples of each type are discussed below.

   Brachysclereids (also termed **stone cells**) are the smallest form of sclereids (◙ Fig. 6.7a, b). Brachysclereids are complex cells that lend
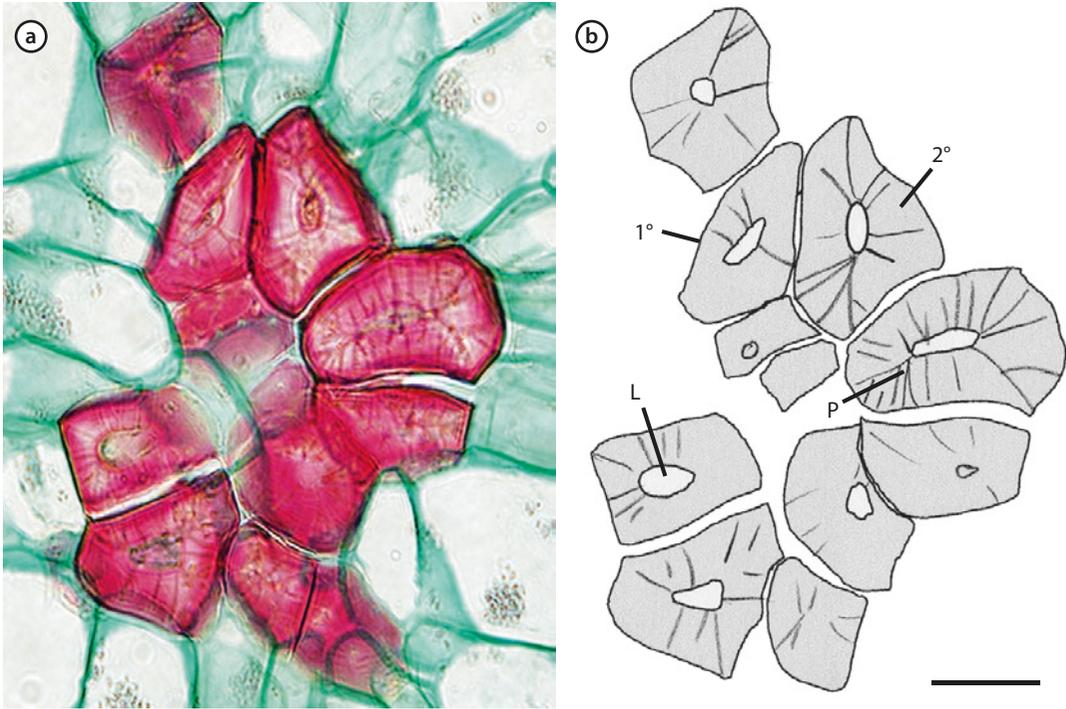
☐ **Fig. 6.7**   **a**, **b** Fresh brachysclereids are naturally yellow in pear (*Pyrus communis*), but in **a** are stained with phloroglucinol that gives them a reddish appearance due to the presence of lignin. They give support to the soft tissues of the fruit. **b** Interpretation of the pit details. Due to concentric cell divisions, clusters of sclereids typically develop as shown here. 1° = primary wall, 2° = secondary wall, P = ramified pit, L = cell lumen. Scale bar = 50 μm. (**a**, **b** RR Wise)

strength and support to tissues such as the **peduncle**, the stem by which an apple is attached to the tree (Horbens et al. 2015). They occur in many species and organs but are probably the most easily seen in the flesh of pear fruit, where they impart the gritty texture found when eating fresh pears. Brachysclereids occur in clumps of 10–50 cells, are **isodiametric**, and possess very thick lignified cell walls with numerous pits, many of which may be branched (thus are said to be **ramiform** in organization). Such ramiform pits develop by fusion of simple pits during the increase in thickness of the secondary wall.

The brachysclereid secondary wall consists of many thin concentric layers, which are laid down to the interior of the cell. As a consequence, the living protoplasm of the cell continually shrinks as the cell wall thickens. ☐ Figure 6.7c shows how the cytoplasm has been reduced to less than 10% of the cell volume. Pits traverse the secondary wall and connect adjacent cells with living cytoplasm (☐ Fig. 6.7c, insert).

Plants respond to wounding caused by insect or other damage by sealing off the damaged area. Sclerification, which is the rapid production of a thick secondary cell wall, forms an effective seal,

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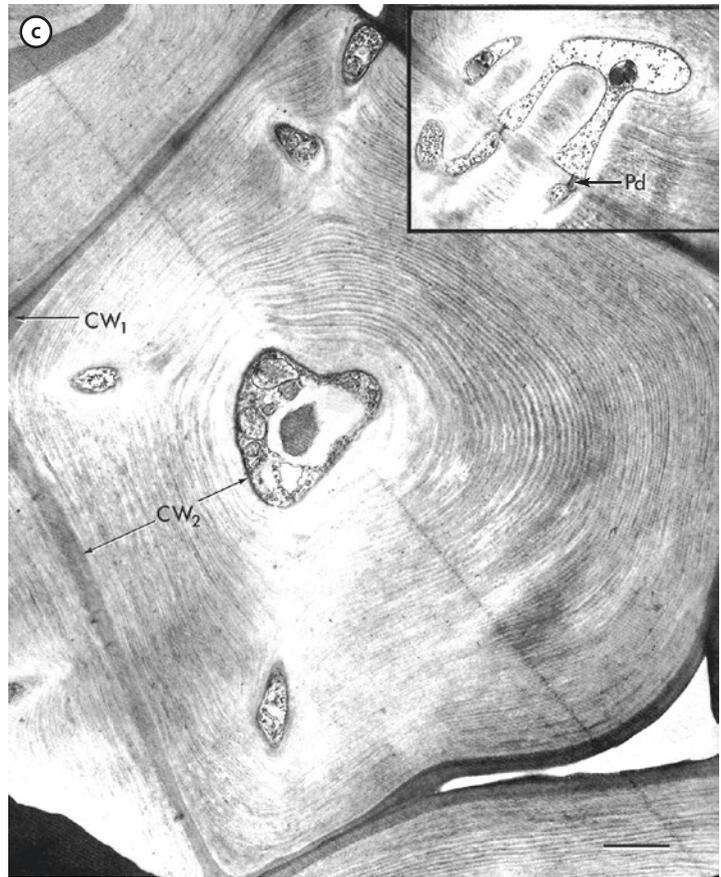
�integral **Fig. 6.7   c** Transmission electron micrograph of a single pear (*Pyrus communis*) brachysclereid. Note the dark primary cell wall (CW_1) and the extremely thick secondary cell wall (CW_2). Inset: two simple pits appear with plasmodesma (Pd) in the pit membrane. Scale bar = 1 μm. (Image from: Ledbetter and Porter 1970, Introduction to the Fine Structure of Plant Cells, Springer-Verlag, with permission)

and can convert living parenchyma cells into brachysclereids at the site of the wound (�integral Fig. 6.7d, e). The parenchyma cells at the site of the injury are mostly isodiametric; therefore, they differentiate into similarly shaped brachysclereids upon the deposition of a thick secondary cell wall.

Astrosclereids (star-shaped sclereids) appear as radiantly branched structures with numerous processes (�integral Fig. 6.7f) and are found in such disparate tissues as needles of the Douglas fir (*Pseudotsuga menziesii*), leaves and petioles of water lily (*Nymphaea odorata*, �integral Fig. 6.7g, h), and the leaves of monstera (*Monstera deliciosa*), a common houseplant. Their function is assumed to be one of support, although little experimental evidence supports this notion. Astrosclereids are often covered with calcium oxalate crystals, which are easily identified by their birefringence under polarized light (�integral Fig. 6.7i–k). Astrosclereids are
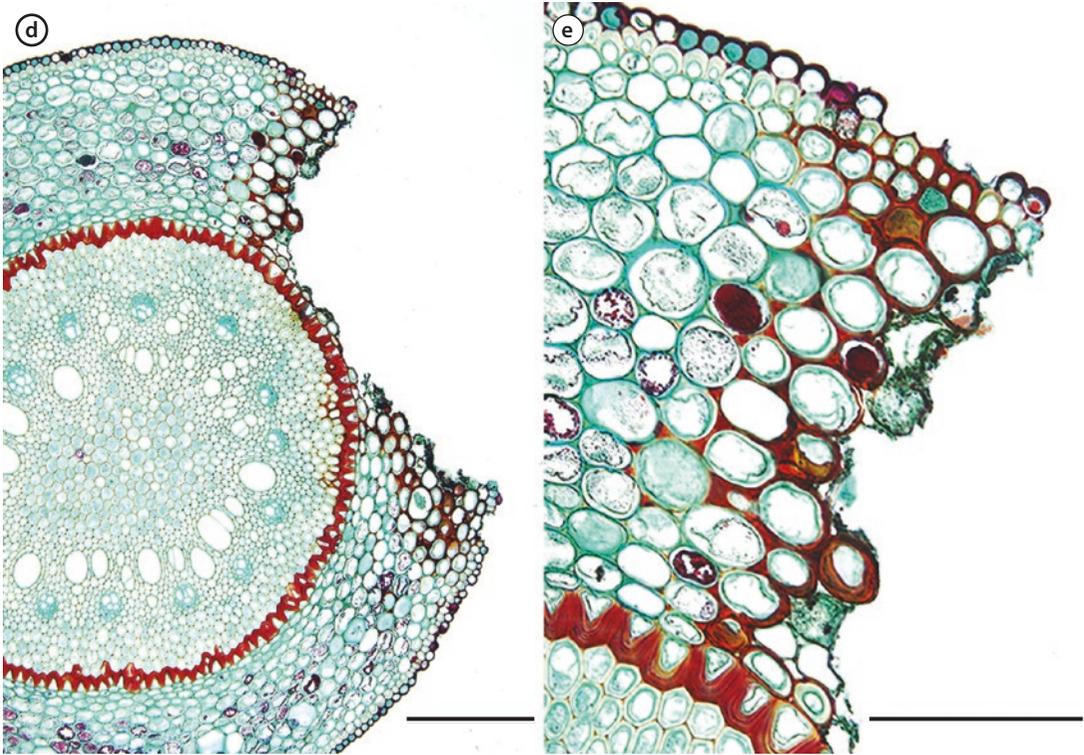
■ **Fig. 6.7   d** A large wound in a greenbrier (*Smilax* sp.) root. **e** Sclereids showing lignification have developed at the site of the damage. Scale bars = 200 μm in **d** and 100 μm in **e**. (**d**, **e** RR Wise)
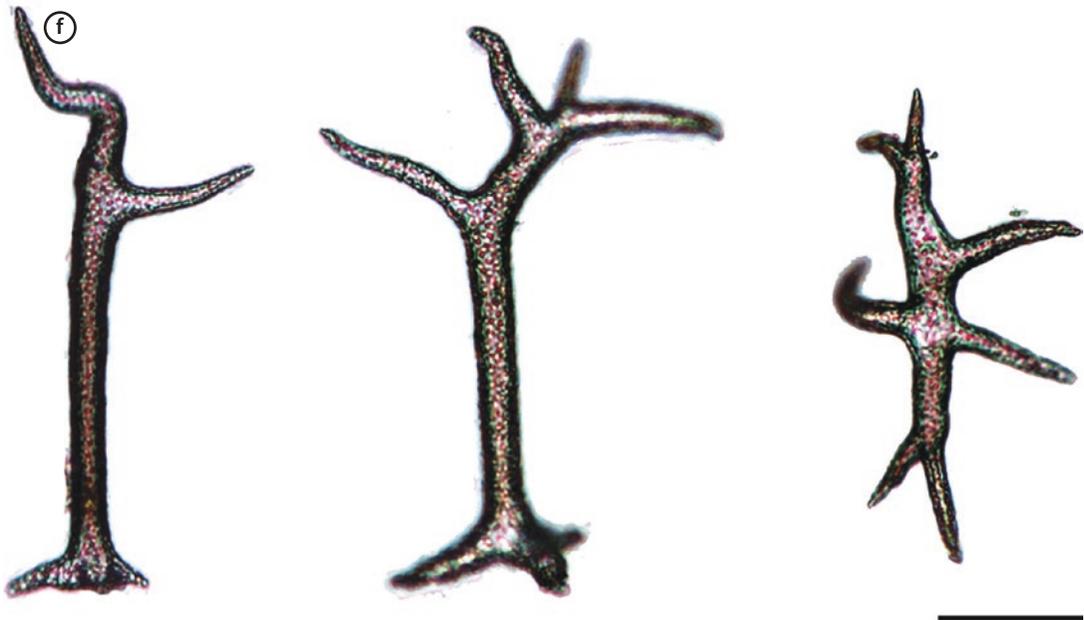
■ **Fig. 6.7   f** Representative astrosclereids isolated from an American white water lily (*Nymphaea odorata*) leaf. Scale bar = 50 μm. (RR Wise)
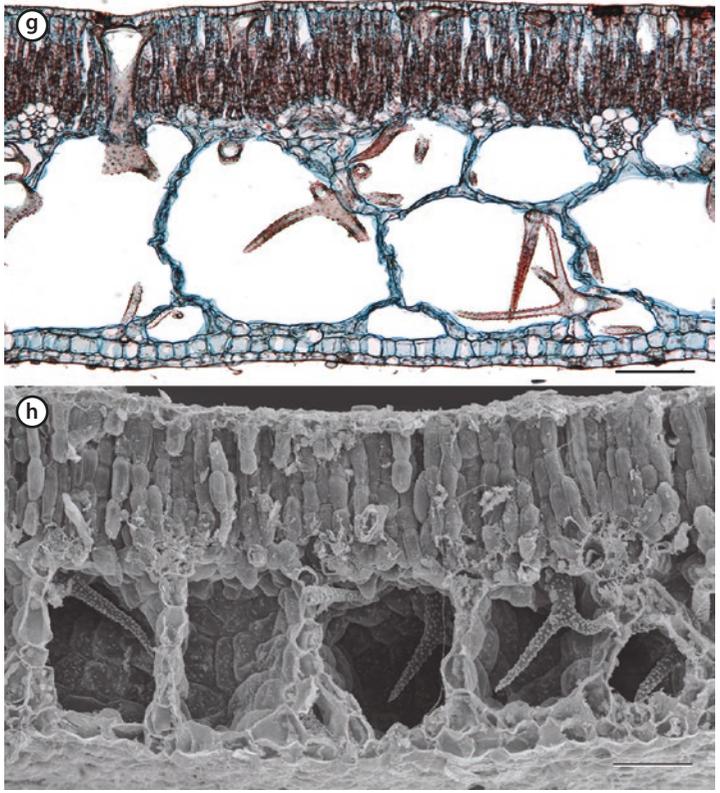
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☐ **Fig. 6.7   g**, **h** Cross-sectional views of a leaf blade of a water lily (*Nymphaea odorata*) with portions of several astrosclereids observed via light microscopy of **g** a stained section and **h** an SEM of a fresh section. Scale bars = 100 μm in both panels. (**g**, **h** RR Wise)
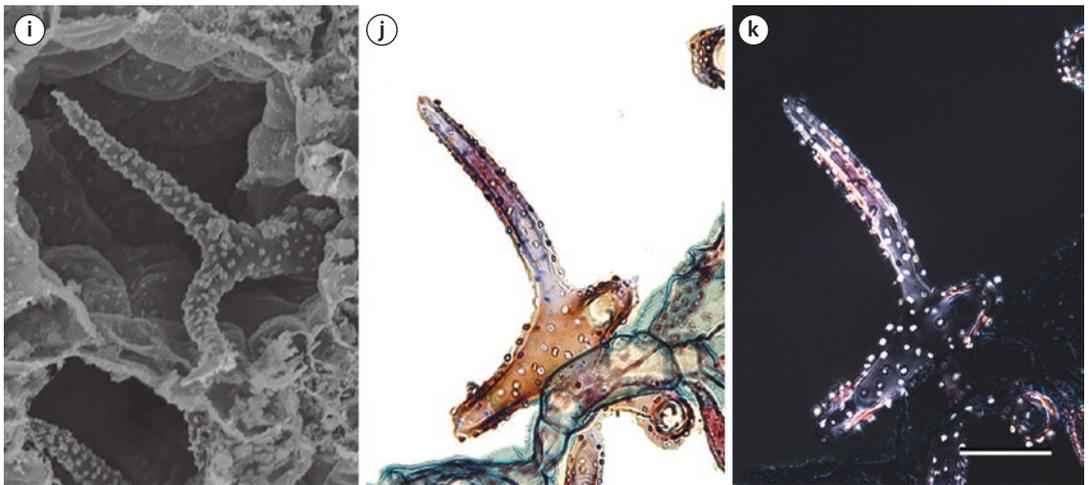

☐ **Fig. 6.7   i**–**k** Astrosclereids of water lily (*Nymphaea odorata*) leaf covered with numerous calcium oxalate crystals. **i** Viewed with SEM, **j** brightfield light microscopy, and **k** polarized light showing birefringence of the CaOx crystals. Scale bar in **k** = 50 μm and applies to all three panels. (**i**–**k** RR Wise)

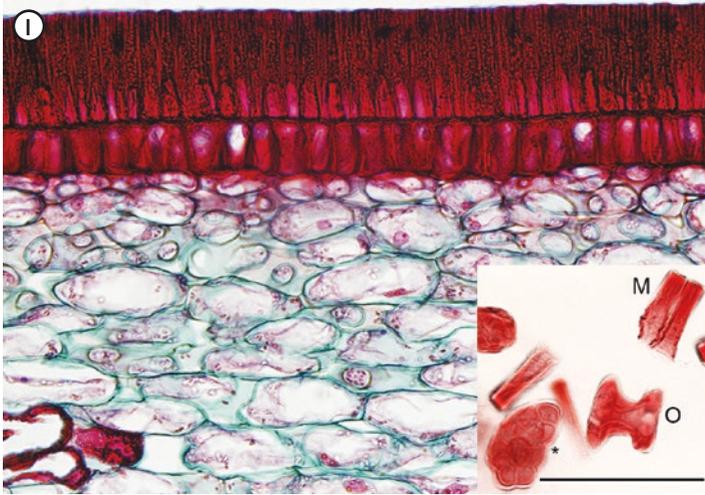▣ **Fig. 6.7** **I** Bean (*Phaseolus vulgaris*) seed coat with an outer layer of macrosclereids and an inner layer of osteosclereids. Starch-containing endosperm is to the bottom of the image. Inset: isolated macrosclereids (M) and ostosclereids (O) from a chemically macerated broad bean (*Vicia faba*). A small bundle of 10 macrosclereids seen end-on is in the lower left corner of the inset. Scale bar = 50 μm for both main image and inset. (RR Wise)

resistant to decay. Those from the yellow water lily (*Nuphar lutea*) can persist in lake sediments for millennia and have proven useful in reconstructing paleoenvironments (Lacourse and Davies 2015).

Osteosclereids and **macrosclereids** (▣ Fig. 6.7I) form the thick, waterproof layer of the **seed coats** of certain legumes. The cells are tightly adhered to each other and prevent desiccation, keep dormancy-promoting hormones from leaching out, and deter herbivory. When isolated (inset to figure), they often appear as "dog bones."

Box 6.2   Anatomical and Biochemical Changes in Legume Pod Wall Were Driven by Crop Domestication
The domestication of crop plants required the selection for many features such as reduced dormancy, reduced seed dispersal (which leads to a preharvest loss of valuable seeds), and increased cooking ability—three traits that are directly influenced by the anatomy of the seed coat. In legumes, domestication favored a thinning of the pod wall which increased the retention of seeds in the pod until they could be harvested (reduced pod shattering) and eased the steps involved in cooking and food preparation. Hradilová et al. (2017) performed an extensive study of seed coats from the wild, dehiscent species *Pisum elatius* (which releases seeds

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upon pod maturity, the seeds maintain dormancy) and the cultivated, indehiscent *Pisum sativum* (which does not release seeds upon pod maturity, the seeds lack dormancy). The *P. elatius* seed coat was found to have significantly larger macrosclereids and be much more structurally robust than the domesticated *P. sativum*, which would lead to increased shattering and loss of seeds upon harvest. This anatomical trait was also associated with higher amounts of dormancy-promoting chemicals such as proanthocyanidins, quercetin, myricetin rhamnosides, and hydroxylated fatty acids. Loss of dormancy allows for more even and predictable germination upon planting. Genetic analysis showed a downregulation of several genes associated with pod shattering in *P. sativum*, as compared to *P. elatius*. Together, these results show that domestication of the garden pea resulted in the selection of seed coat anatomical and biochemical characteristics that made for more dependable germination, higher yield, and ease of cooking ability.

   Reference: Hradilová et al. (2017).

6.8 Xylem Vessel Elements Are Water-Conducting Sclerenchyma

The third type of sclerenchyma, water-conducting sclerenchyma, are also called tracheary elements. They will only be mentioned here to complete the survey of sclerenchyma but will treated more fully in ► Chap. 7, Xylem. In brief, **tracheary elements** provide a conduit for the water of the transpirational stream to flow from the roots to the leaves. There are two basic types (with many variations) of tracheary elements: **tracheids**, which are long and narrow and **vessel elements**, which are shorter and much wider. Gymnosperms only possess tracheids, while angiosperms have both tracheids and vessel elements. Tracheid morphology does not vary significantly, but vessel elements range from relatively long and narrow to extremely wide and short (◘ Fig. 6.8a–d).
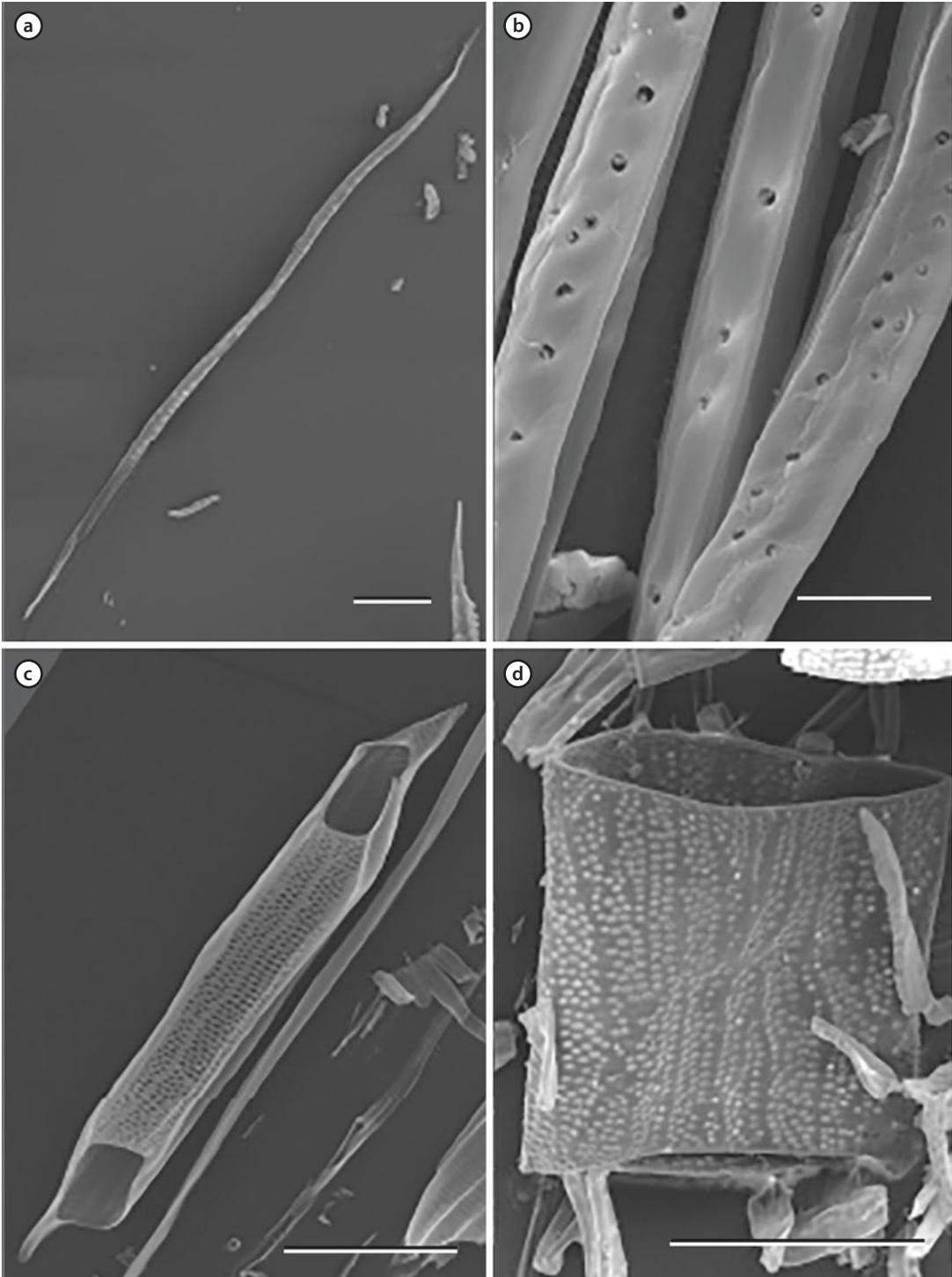
◻ **Fig. 6.8   a–d** Examples of tracheids and vessel elements from various woods. **a** Tracheid from grape (*Vitis riparia*) stem. Scale bar = 100 μm. **b** Tracheid from grape (*Vitus riparia*) stem. Scale bar = 20 μm. **c** Vessel element from red maple (*Acer rubrum*) wood. Scale bar = 100 μm. **d** Vessel element from honey locust (*Gleditsia triacanthos*) wood. Scale bars = 100 μm. (**a–d** RR Wise)

6.9 Chapter Review

■ Concept Review

6.1 *Parenchyma cells are the most common plant cell type.* Parenchyma cells are living, thin-walled cells that perform a wide variety of functions in the plant. They are generated at the meristem and are the precursors to all other cell types. Parenchyma cells make up the bulk of the stem pith and root cortex, the epidermis, and the aerenchyma tissue. Storage tissues in seeds and tubers are made of parenchyma cells.

6.2 *Parenchyma cells may exhibit totipotency.* Parenchyma cells are physiologically active and, under many circumstances, are capable of mitosis and differentiation into all other cell types. This is important for wound repair and has been exploited by plant scientists to regenerate entire plants from a single cell.

6.3 *Collenchyma cells are used for support and are the least common cell type.* Collenchymata are living cells with thick, unevenly deposited primary cell walls consisting mostly of cellulose. They are found in short-lived or expanding tissues where sclerenchyma would be too costly or too restrictive. Four types of collenchyma may be identified depending on the pattern and location of cell wall thickenings: angular, annular, lamellar, and lacunar.

6.4 *Birefringence is a common phenomenon in collenchyma walls.* The layered collenchyma cell wall shows birefringence using crossed polarizers for light microscopy due to the orientation of multiple cell wall layers of microfilaments.

6.5 *Sclerenchyma cells provide support, protection, and long-distance water transport.* Sclerenchyma cells have thick secondary walls and are usually dead or have little physiological activity at maturity. There are three general classifications: fibers, sclereids, and water-conducting sclerenchyma.

6.6 *Fibers are elongated with tapered ends.* The long, thin sclerenchyma fibers are almost exclusively structural and are found in a variety of tissues and organs, particularly alongside vascular bundles and in the cortex of stems and roots. Fibers are somewhat elastic, with gelatinous fibers being the most flexible. Fibers found in the wood are called xylary fibers (two types: libriform fibers and fiber tracheids), while those not associated with wood are extraxylary (or bast) fibers.

6.7 *Sclereids are compact sclerenchyma cells that occur singly or in clumps.* Sclereids have a variety of shapes (brachysclereids, astrosclereids, macrosclereids, and osteosclereids) and, like fibers, provide structural support and protection to stems, leaves, seeds, and fruit. Many are studded with calcium oxalate crystals.

6.8 *Xylem vessel elements are water-conducting sclerenchyma.* Water-conducting sclerenchyma, also known as xylem tracheary elements, functions in the movement of water from the roots to the leaves during the process of transpiration. Tracheids are long and narrow with tapered ends. Vessel elements are short and wide with various end-wall styles.

■ **Concept Connections**

❓ 1. Identify each of the cell types shown in the following images.

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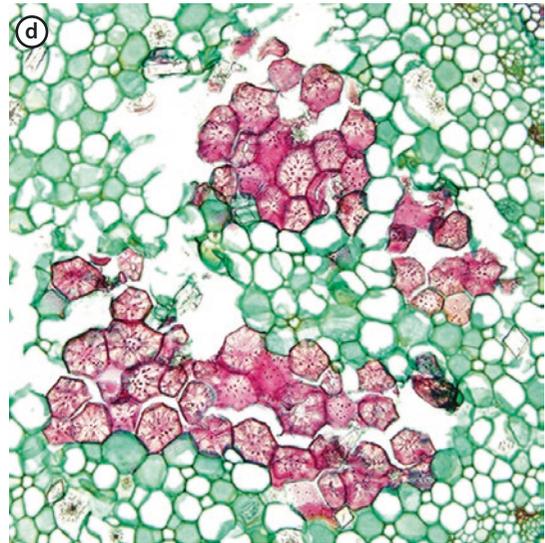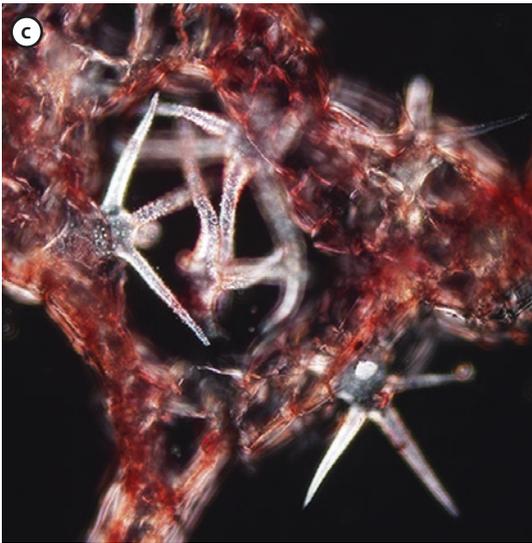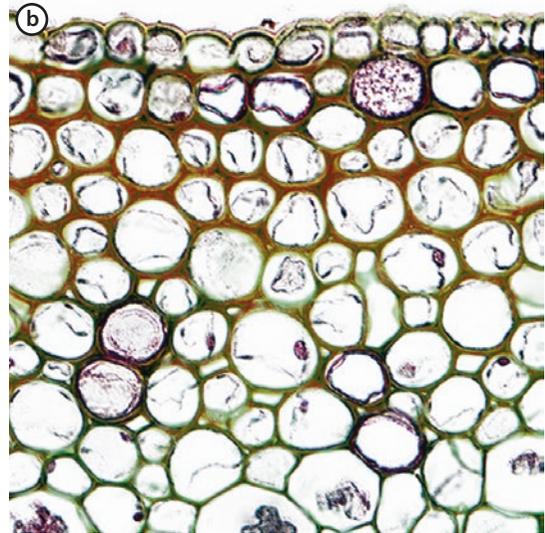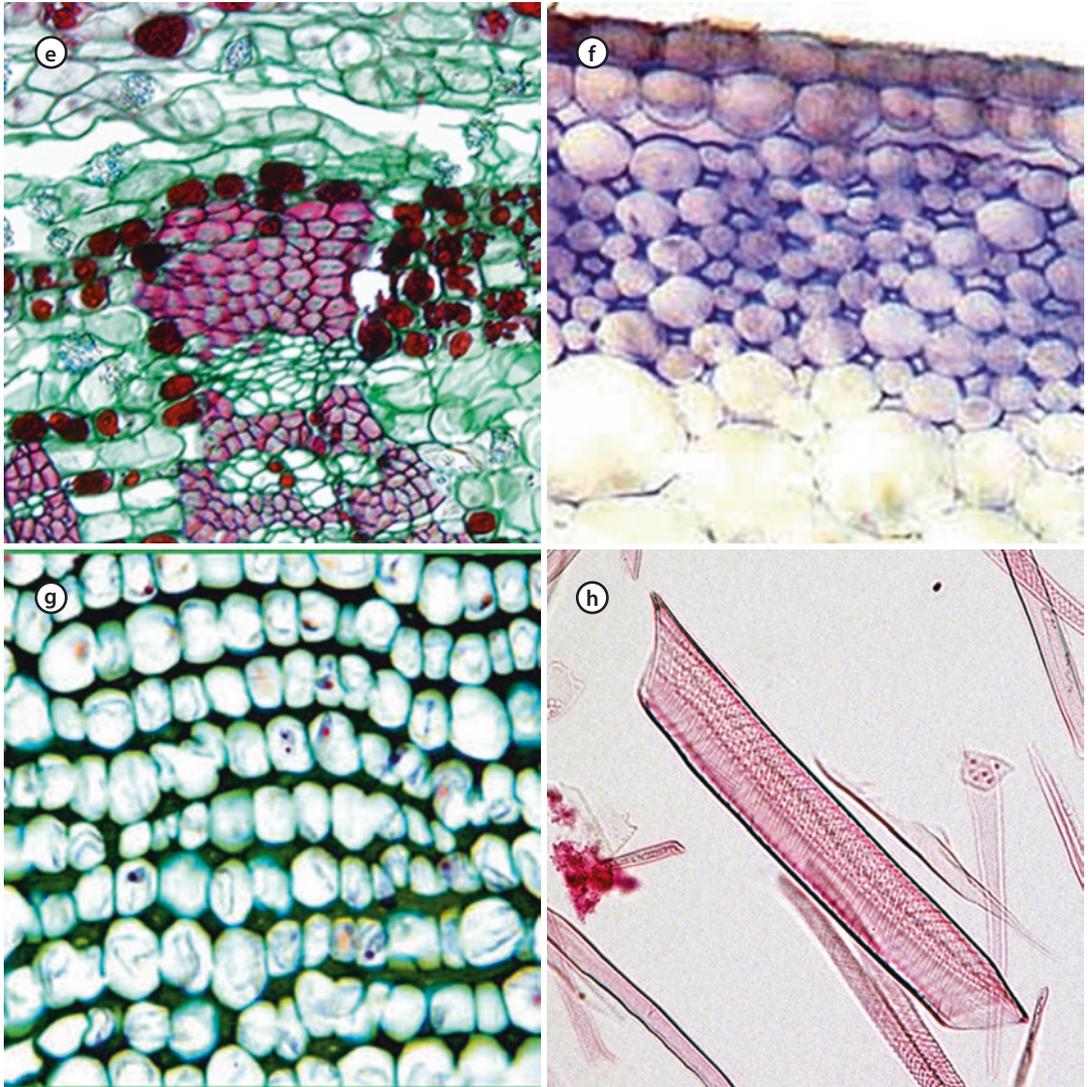
■   **Concept Assessment**

2. Cell walls of collenchyma cells are flexible due to
   a. a high lignin content.
   b. their elastic nature due to contractile proteins.
   c. irregular secondary thickenings.
   d. a helicoidal arrangement of cellulose microfibrils.
   e. layers that slide past one another.

3. Sclereids develop from
   a. fibers.
   b. parenchyma cells.
   c. collenchyma cells.
   d. apical meristems.
   e. cork cambium.

❓ 4. Libriform fibers are found in
    a. epidermis.
    b. cortex.
    c. phloem.
    d. xylem.
    e. pith.

❓ 5. Most parenchyma cells are capable of
    a. mitosis.
    b. metabolism.
    c. dedifferentiation.
    d. sclerification.
    e. all of the above.

❓ 6. Lamellar collenchyma shows thickenings
    a. on the tangential (periclinal) walls.
    b. on the radial (anticlinal) walls.
    c. uniformly around the cell.
    d. adjacent to intercellular spaces.
    e. at the ends of elongated cells.

❓ 7. Totipotency is the ability of a cell to
    a. undergo metabolism.
    b. undergo mitosis.
    c. differentiate into any cell type.
    d. die at maturity.
    e. secrete cell wall material.

❓ 8. Macrosclereids are most often found in
    a. leaves.
    b. seed coats.
    c. root tips.
    d. vascular bundles.
    e. ground (storage) tissues.

❓ 9. The three basic types of sclerenchyma are
    a. collenchyma, parenchyma, and stone cells.
    b. totipotent, monopotent, and dedifferentiated.
    c. astrosclereids, macrosclereids, and osteosclereids.
    d. fibers, sclereids, and water-conducting sclerenchyma.
    e. angular, lacunar, and lamellar.

❓ 10. Vascular tissues in herbaceous stems are frequently
    accompanied by bundles of extraxylary fibers. These fibers
    serve to
    a. deter herbivory.
    b. provide structural support to the stem.
    c. expand with the expansion of the stem.
    d. conduct water from the roots to the leaves.
    e. protect fragile phloem tissues from damage.

? 11. Collenchyma cells are most commonly found in
- a. stems that are still growing.
- b. leaves of aquatic plants.
- c. rapidly expanding leaf petioles.
- d. aerial roots.
- e. a and c.

■ **Concept Applications**

? 12. In animals, the word "liver," as an example, is used to describe an organ (liver), a tissue (liver tissue), and a cell type (liver cells). The same is true for the heart, muscle, bone, etc. Most animal organs, tissues, and cell types share a common name. However, in plants, organs (roots, stems, leaves), tissues (dermal, ground, vascular), and cell types (parenchyma, sclerenchyma, collenchyma) do not share common names. Explain this *fundamental* difference in animal versus plant organ/tissue/cell organization.

? 13. Define totipotency and explain how it differs between animal cells and plant cells.

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