Wood: Economics, Structure, and Composition

The original version of this chapter was revised. The correction to this chapter can be found at https://doi.org/10.1007/978-3-319-77315-5_20

R. Crang et al., *Plant Anatomy*, https://doi.org/10.1007/978-3-319-77315-5_15

Introduction
Wood and the trees that produce it are all around us. Humans (and other animals) have used wood for thousands of years and in thousands of applications. Wood provides shelter, tools, furniture, heat, food additives, medicines, and drugs, to name just a few of the many applications. About 20%, or 66,065, of all plant species are trees (Beech et al. 2017), the wood of which provides a wealth of possibilities. Unfortunately, many tree species are endangered due to overharvesting, habitat destruction, and global climate change. The future will see if humans can continue to exploit wood as a valuable resource and not put up too many parking lots.

15.1 Wood Has Significant Worldwide Economic Value

Wood is the multiyear accumulation of xylem growth (refer to ► Chap. 7). It functions to provide support to the plant and acts as a conduit for the transport of water from the soil to the leaves. Wood is the most widely used plant product in the world (FAO 2017) with items ranging from toothpicks to massive beams. The wide range of wood properties—strength, color, grain, and workability—make it an extremely versatile material for all manner of human uses (◘ Fig. 15.1a–u).

Wood is the product of secondary growth as revealed in annual growth rings. As is well known, wood is used in furniture making, as a fuel, in electrical generation, and even as a food supplement. In India, the export of various raw timbers, as well as finished furniture and other home products, is a major industry largely comprised of darker woods such as teak (*Tectona grandis*), meranti (*Shorea* sp.), and mahogany (*Toona* sp.). In China, the export of unfinished wood was once a growing industry, but has leveled off since 2005 in which furniture and plywood are now the primary products produced and sold on the open market. The lack of growth in the China wood industry can largely be attributed to the reduction in the amount of wood that is being harvested. The timber products from China are mostly made into furniture and plywood that are exported and shipped to other nearby Asian countries, the USA, and Europe—primarily the UK. The majority of Chinese-exported woods are from pines, fir, eucalyptus, and some birch.

The USA is also a contributor to the export of woods, but primarily as logs and lumber, mostly softwoods, which are usually assembled as already made products (e.g., casks, door frames, and prefabricated wood buildings) and fuel (e.g., wood chips). Many individuals might find it surprising that Canada is the world's leader as an exporter of softwood lumber, wood pulp, and newsprint. It is also the leading seasonal producer of Christmas trees—largely pine, spruce, and fir.

Fig. 15.1 Some examples of different types of North American hardwoods used in furniture and finished flooring applications. **a** Red maple (*Acer rubrum*), **b** sugar maple (*Acer saccharum*), **c** chestnut (*Castanea dentata*), **d** green ash (*Fraxinus pennsylvanica*), **e** butternut (*Juglans cinerea*), **f** black walnut (*Juglans nigra*), **g** sweet gum (*Liquidambar styraciflua*), **h** tulip poplar (*Liriodendron tulipifera*), **i** apple (*Malus pumila*), **j** black cherry (*Prunus serotina*), **k** white oak (*Quercus alba*), and **l** red oak (*Quercus rubra*). Scale bar in **l** = 2 cm and applies to all panels (**a**–**l** RR Wise)

◘ **Fig. 15.1** Nine New World and Old World tropical hardwoods, selected to emphasize the range of natural variation in color and figure: **m** Bahia rosewood (*Dalbergia nigra*), **n** eucalyptus (*Eucalyptus* sp.), **o** zebrawood (*Microberlinia brazzavillensis*), **p** wenge (*Millettia laurentii*), **q** purpleheart (*Peltogyne paniculata*), **r** padauk (*Pterocarpus* sp.), **s** Honduras mahogany (*Swietenia macrophylla*), **t** tamarind (*Tamarindus indica*), and **u** teak (*Tectona grandis*). Scale bar in **u** = 2 cm and applies to all panels (**m**–**u** RR Wise)

Brazil is another major exporter of wood products. The Brazilian wood largely comes from the forests in the Amazon region and includes pine and eucalyptus which are either processed or exported as pulp, wood chips, plywood, paper, flooring, and furniture. Like China, these products are exported to countries all over the world. However, in Brazil due to vast deforestation, certain woods are governmentally prohibited to be harvested. These woods include rosewood, nut trees, and the native brazilwood (*Caesalpinia echinata*).

15.2 A Wide Variety of Products Are Made from Wood Fibers and Wood Extracts

Various paper products may be made from wood fibers. Smooth and soft paper products like napkins, tissue paper, and absorbent towels are typically produced from debarked hardwood trees after lengthy cooking and digesting in sodium hydroxide and sodium sulfide. The pulp product is then filtered for particle size, and chalk, clay, starch, or titanium oxide may be added to meet the color and absorbency nature of the pulp. The treated pulp is then run through metal rollers, dried and cut to size. Less processed pulp (i.e., shorter digestion, larger filter size, and less chemical treatment) will result in heavier products such as boxes or pressed wood. In addition to paper products from wood, some technically non-woody materials are flax, which can be used for cigarette paper, and cotton and linens, which are used in the form of rope and textiles. Bamboo, straw, and even sugarcane, as well as linens, are used as additives to wood pulp to produce specialty paper products such as bank checks, résumé paper, and paper money.

Some wood products are exclusively composed of cellulose fibers to make artificial sponges, chewing gum from chicle sap, various types of dyes from bark, and rubber from latex derived from the phloem of the rubber tree (*Hevea brasiliensis*). Cellulose derived from wood is also used as a food thickener and is often employed in the production of ice cream. Finally, sugar, such as in maple syrup, and spices, such as cinnamon, are food products produced from woods.

A long history exists in the medical field involving the production of medical products, called **silvichemicals**, which are extracted from certain types of woods and are used in the healing or prevention of illness. Quinine, used to treat malaria, is also derived from the bark of the *Cinchona* sp. (family Rubiaceae) tree. Other medicinal extracts such as betulin from birch bark are known to have antibacterial properties, and pine compounds include sterols which may be used as additives in margarines and yogurt products and reduce cholesterol when consumed regularly. Additional drug items from trees include the ones found in cough syrup, laxatives, pain relievers, tranquilizers, and worm repellents. Many cosmetics contain a cellulose derivative called carboxymethyl cellulose (also known as cellulose gum) to help stabilized and thicken makeup creams.

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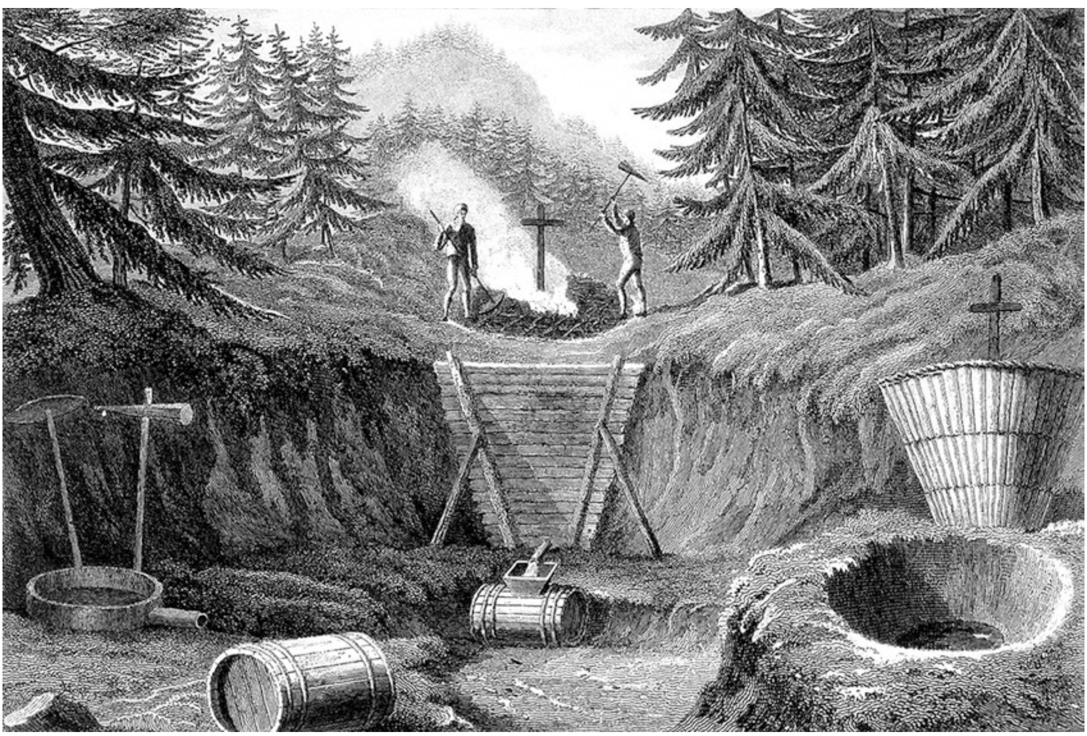
Box 15.1 Natural Wood Fibers Meet Modern-Day Plastics
Research at the University of Southern Mississippi's School of Polymers and High Performance Materials uses natural wood fibers to reinforce plastic products. The renewable wood fiber composites could revolutionize building construction, automobiles, and aircraft. It could also be a boon for the paper industry by providing new uses for fibers that can strengthen plastics. It further enables products to be shaped without having to melt them in the preparation. Other products, such as permanent

bonded magnets which are used in computers and cars, can develop higher energy without the use of rare earth metal alloys by designing magnetic powders with polymer matrices from wood fibers and do so at needed higher temperatures. Nanostructured hybrid organic-inorganic thermoplastic materials containing wood products can demonstrate many benefits in plastic composites without the disadvantages, giving improved energy efficiency in laser fusion systems, biomaterials, storage materials for nuclear wastes, and in load-bearing hybrid composites. Furthermore, the organic-inorganic hybrid materials make products more moisture resistant, thereby providing greater control over biodegradation processes.
Reference: Otaigbe and Naim (2014)

During the eighteenth and nineteenth centuries and the first half of the twentieth century, pine trees mostly from Finland and Sweden were extensively harvested and baked under moss or canvass in order to extract resin by heat, which was then collected in barrels as tar (◘ Fig. 15.2). The pine tar was exported throughout



◘ **Fig. 15.2** Representation of the process of making tar in the forests of Sweden. A pine tar pit is excavated in a hillside, and then piles of pine logs and branches are arranged at the lower in the pit, with the lower end covered by planks. The pile is ignited and then covered with layers of moss, earth, or a tarpaulin to eliminate air. The pine sweats tar during the burning process and drips out of the bottom of the pile, and it is collected in barrels. The wood is oxidized to charcoal. (Image from Clarke (1816), public domain) the world, especially to New York City, for use in roofing and in the construction of roads. Some was used as a sealant for wooden ship hulls, and by-products included turpentine and pine oil. Pine tar also has a long history as a topical treatment for skin conditions (Barnes and Greive 2017). The vast deforestation of this European forest resulted in a major loss of a large part of that country's native trees, such that today there are only rare sites in Finland that have native forestation.

15.3 Wood Development and Composition Show Annual Cycles

Wood develops from the secondary growth of cambium in gymnosperms and woody eudicots. ◘ Figure 15.3a–d shows the progressive changes that take place during early secondary growth of a perennial eudicot stem. The cells of the vascular cambium involved in secondary growth are termed fusiform initials. They are characterized by being elongated with tapered ends and give rise to the cellular elements of the axial system in secondary woods. The manufacture of wood (secondary xylem) takes place in major steps, starting with cell division, cell expansion (elongation and radial enlargement), cell wall thickening (involving cellulose, hemicellulose, cell wall proteins, and lignin biosynthesis and deposition), and ending with programmed cell death.

Each successive year of vascular cambial activity leaves a layer of xylem to the interior and phloem to the exterior. The xylem persists and accumulates with each growing season producing one tree ring (see below), while the phloem (► Chap. 8) becomes crushed and incorporated into the periderm (► Chap. 16).

In most temperate woody species, vessel element and tracheid diameters respond to the seasonal growth conditions that reflect rapid growth in the spring, slowing of growth over the summer, and the cessation of growth in the fall (◘ Fig. 15.3e, g). This causes annual growth rings and the related wood characters called "figure" or "grain." Most conifers and temperate eudicot trees have prominent growth rings (◘ Fig. 15.3f, h). Many tropical ecosystems have little annual variation in temperature or rainfall. Therefore, tropical hardwood species such as eucalyptus and mahogany (◘ Fig. 15.1n, s) have less prominent annual growth rings and have an appearance called "smooth grained."

The science of **dendrochronology** relies on the generation of a new growth ring every year, but that is not always the case. If growth conditions are unfavorable, a tree may not lay down a continuous ring of xylem every season. A period of inactivity, followed by a resumption of activity, will result a missing ring. A false ring forms when there is a growth interruption, such as a severe spring drought, from which the tree recovers and starts a new ring later in the growing season. There will be the appearance of two rings.

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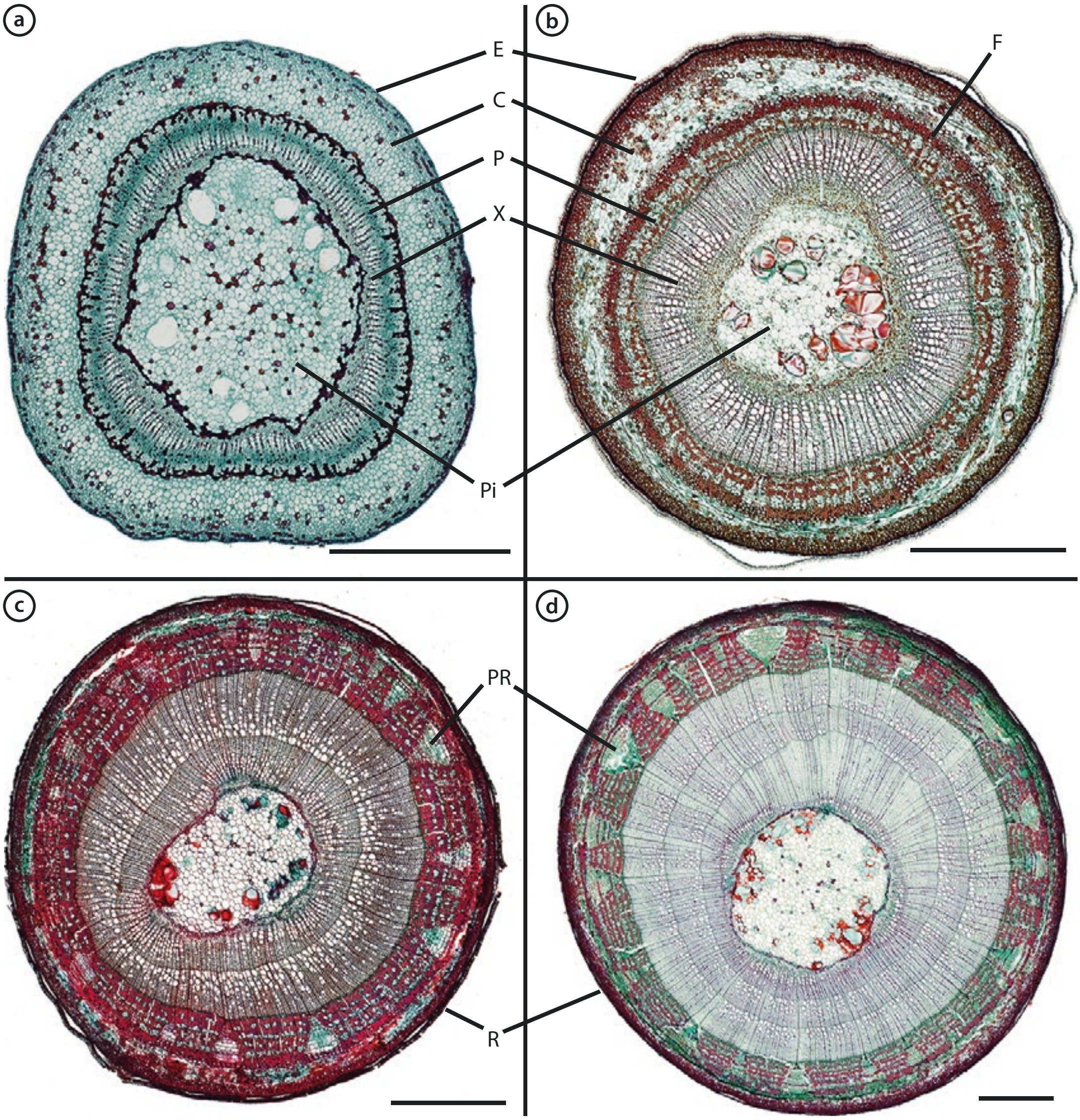

◘ Fig. 15.3 **a**–**d** Cross-sections of American basswood (*Tilia americana*) stems. **a** Stem at the beginning of the first year of growth with a continuous ring of developing xylem and phloem. Pith is seen at the center of all four stems. A cortex has developed at this early stage and the epidermis is thin. **b** Stem at the end of year one. The epidermis has sclerified and a ring of phloem fibers (F) has developed. A large ring of xylem indicates the first year's woody growth. **c** Stem at the end of year two. The phloem has become progressively more sclerified, and a second growth ring surrounding the first year's woody growth is apparent. Phloem rays have expanded to accommodate the increase in stem circumference. A third layer of xylem has been produced and phloem rays have expanded. The epidermis has transformed to a rhytidome. C cortex, E epidermis, P phloem, Pi pith, PR phloem ray, R rhytidome, X xylem. Scale bar = 500 µm in all panels (**a**–**d** RR Wise)

Discontinuous rings, also called locally absent rings, form when a portion of the vascular cambium goes quiescent (but does not die) for a year or more, while other regions continue to generate xylem derivatives. The area of the spruce stem shown in ◘ Fig. 15.3i, j was quiescent for 6 years before resuming growth.

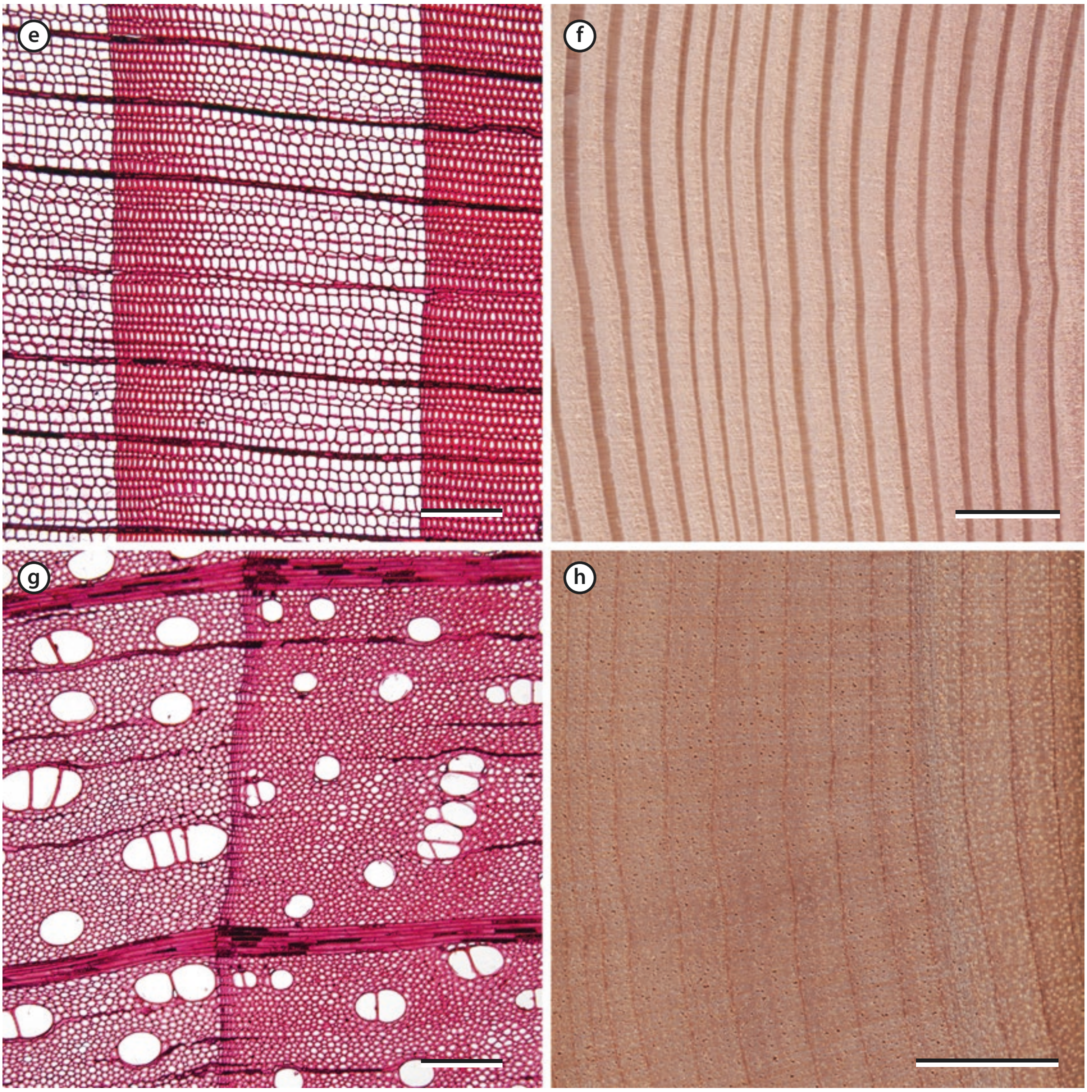

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Fig. 15.3 Annual growth rings in a conifer and eudicot. **e** Annual rings of Douglas fir (*Pseudotsuga menziesii*), a coniferous softwood species, showing the springwood as the light portion and summerwood as the dark part of the rings. **f** Higher-magnification view on one growth ring. The summerwood tracheids (on the left edge of each ring) are smaller with thicker cell walls than the springwood tracheids. **g** Annual rings in sugar maple (*Acer saccharum*) accompanied with **h** an LM of the rings. Scale bars = 100 µm for **e** and **g** and 0.5 cm for **f** and **h** (**e**–**h** RR Wise)

15.4 Wood Varies in Its Architecture and Composition

15.4.1 Cross, Radial, and Tangential Planes of Section

Wood is a complex three-dimensional tissue that is best viewed in three different planes of section (Fig. 15.4a) (Meylan and Butterfield 1972). A **cross-section** is perpendicular to the long axis of the stem (or limb or trunk). It is the best section for revealing annual growth rings. A **radial section** (also called longitudinal

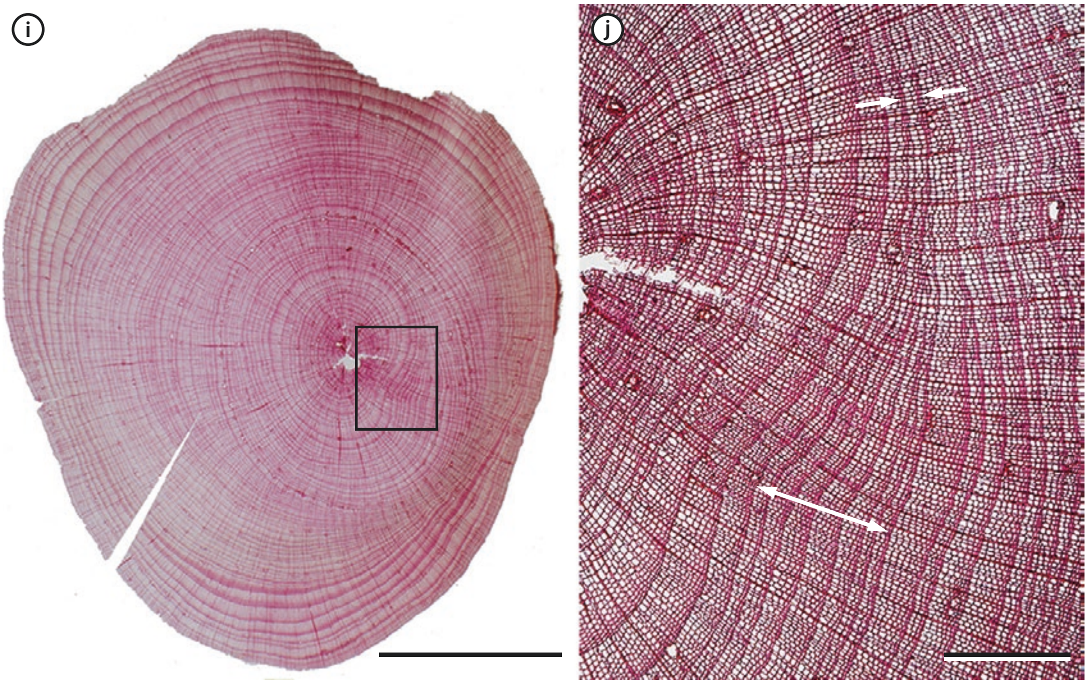


Fig. 15.3 **i** A spruce (*Picea* sp.) stem showing discontinuous tree rings. **j** A higher-magnification view of the boxed area in 15.3i. The single growth ring at the top of the image (*between arrows*) connects with seven growth rings at the bottom of the image (*arrow*). This particular stem has several areas of discontinuous growth rings; only one is highlighted. Scale bars = 0.5 cm in **i** and 250 µm in **j** (**i**, **j** Specimen prepared by JF Reed, Dartmouth College RR Wise)

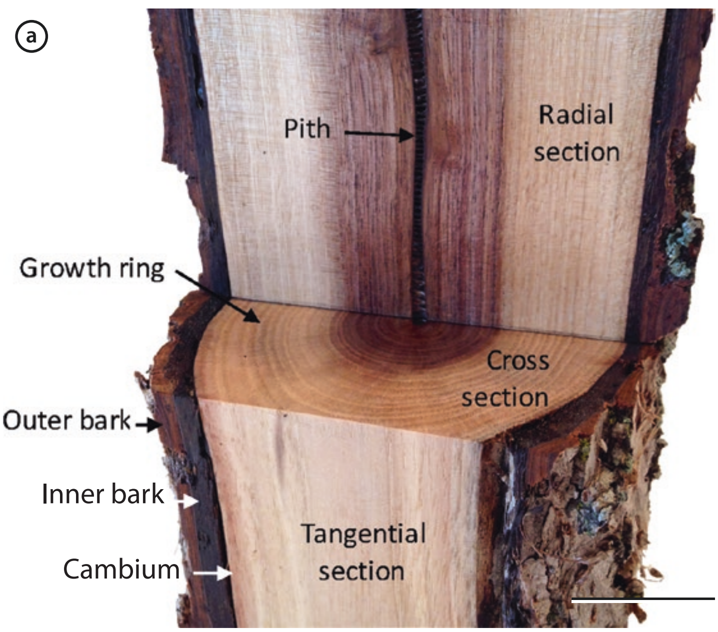
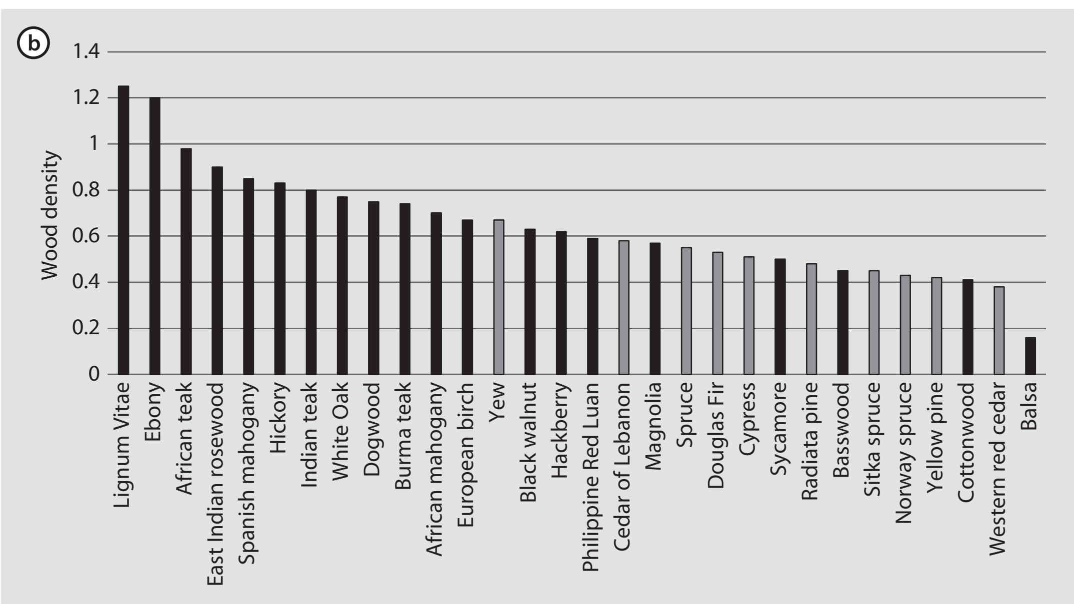


Fig. 15.4 **a** A 28-year-old black walnut (*Juglans nigra*) stem cut to expose the three planes of section—cross-section, radial section, and tangential section. Dark heartwood is at the center and lighter sapwood to the periphery. The location of growth rings, **outer bark**, **inner bark**, cambium, and pith are indicated. The age of the stem was determined by counting the annual **growth rings**. Scale bar = 2 cm (RR Wise)

section) is parallel to the longitudinal axis and runs through the center of the stem. The surface exposed by a radial section is therefore side view of the rays that extend from the center of the stem to the exterior. A **tangential section** is also parallel to the longitudinal axis, but is off-center. This plane of section allows for a visualization of ends of the rays as they run from the center to the exterior. The different planes of section reveal different information. For instance, because pits connect tracheids via the anticlinal walls, they are best viewed in a radial (c.f. ◘ Fig. 15.5g) or tangential section (c.f. ◘ Fig. 15.5l, m).

15.4.2 Softwood vs. Hardwood

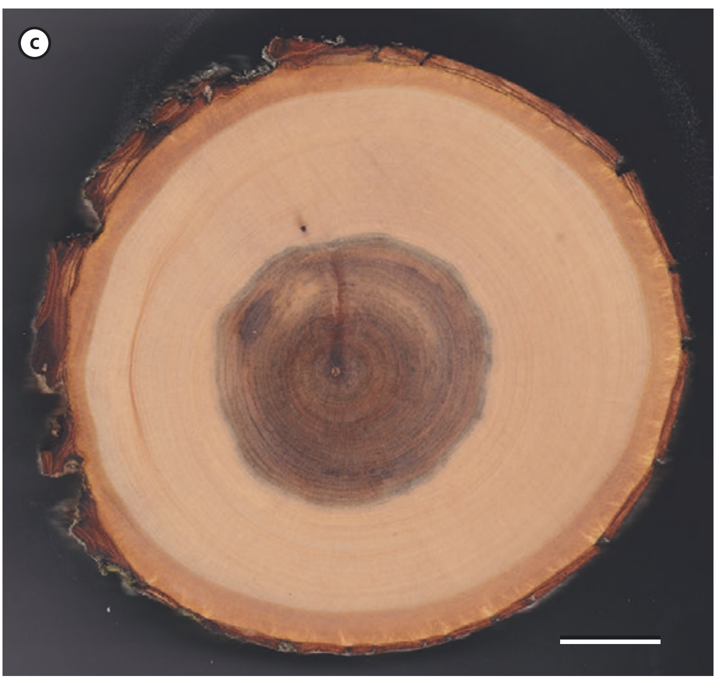
It should be evident that not all woods are the same. Of course, the taxonomic nature of the species has much to do with the overall internal structure of wood, but other factors such as environmental conditions (e.g., temperature, humidity, and elevation) along with age and nutrition also play key roles. To begin with, most individuals have heard the terms "**softwood**" and "**hardwood**." While there is often a true difference in the physical hardness of woods, the term softwood is used in both the common and commercial senses to mean gymnosperm, while the hardwoods are angiosperm eudicots. Density is a common measure of wood hardness, and most hardwoods have a higher density than softwoods, but that is not always the case (◘ Fig. 15.4b). The primary difference is not necessarily the physical hardness of the wood but rather the presence of vessel elements (aka pores) and fibers in hardwoods vs. the lack of such cell types in softwoods. In addition, softwoods typically have a



◘ **Fig. 15.4** **b** Specific gravities of selected eudicot (black bars) wood and gymnosperm (gray bars) wood. Note that not all hardwoods are high in density and not all softwoods are low in density. Units of wood density are 103 kg m^{-3}. (Figure compiled from publicly available data) (RR Wise) faster rate of growth than hardwoods, which is related to their lower density. Some common examples of softwoods are pine, spruce, Douglas fir, and juniper. Typical hardwoods are eudicots such as oak, maple, beech, ash, walnut, and hickory. There are exceptions to the eudicot = hardwood definition; balsa tree (*Ochroma pyramidale*) is a eudicot in the Malvaceae family with extremely soft- and low-density wood.

15.4.3 Sapwood vs. Heartwood

Another common distinction that is made in wood is age-related and often revealed by a difference in pigmentation (◘ Fig. 15.4c). For trees of several years of age, and then throughout the rest of their standing existence, an outer portion of wood, the **sapwood**, may appear lighter in color, has a relative high level of moisture due to the active transport of water by some living cells, and stores some energy reserves. Transpirational water moves through the open cells of the sapwood. Such wood is also often designated as living wood. Alternatively, the innermost region of wood, which is often darker in color, has less water and mineral reserves and is no longer active in translocation (i.e., dead tissue) and is designated as the **heartwood**. The darker color of heartwood is due to the buildup of resins, terpenes, and polyphenolic compounds as the wood ages.



◘ **Fig. 15.4** **c** Cross-section of a Norway maple (*Acer platanoides*) stem showing a central, dark heartwood core surrounded by lighter sapwood. The sample has 58 annual growth rings, which are too small to be seen here. The first 28–30 years of growth have been converted to heartwood, while the subsequent ~30 years of growth remain as sapwood. Scale bar = 2 cm (RR Wise)

The center of the heartwood may be a small central region of soft, spongy-like material, which represents pith from the first year's primary growth that eventually becomes obscured in most species by being crushed. In a few cases, such as black walnut (*Juglans nigra*), it remains as a chambered pith (refer to ◘ Fig. 11.5j) but has no true function. Over the course of time, the heartwood becomes the dominant portion of a tree trunk. Because of its color, density, and strength, heartwood is usually the preferred type of wood for the purposes of furniture fabrication. The strength is largely due to the very low water content, since sapwood warps and shrinks somewhat when dried. Sapwood is also prone to decay and staining due to fungal infections. Those trees that have more rapid growth typically have more sapwood than heartwood, whereas the opposite is usually the case with slower growing species or in individuals where environmental conditions favor slow growth.

15.5 Conifer Wood Has Tracheids, Parenchyma, and Rays

Xylem vessel elements (perforate tracheary elements; refer to ► Chap. 7) are a common feature of most angiosperm species but are only rarely found in gymnosperms. The gnetophytes (phylum Gnetophyta) which include three genera—*Ephedra*, *Gnetum*, and *Welwitschia*—are the only gymnosperm taxa that contain vessels (◘ Fig. 15.5a, b) (Carlquist 2001); all other gymnosperms only have tracheids (imperforate tracheary elements) as water-conducting cells.

Tracheids in the axial system of a gymnosperm stem act as conduits for the movement of transpirational water from the roots to the leaves. Their structure has been detailed in ► Chap. 7 (Xylem) and will be briefly reviewed here.

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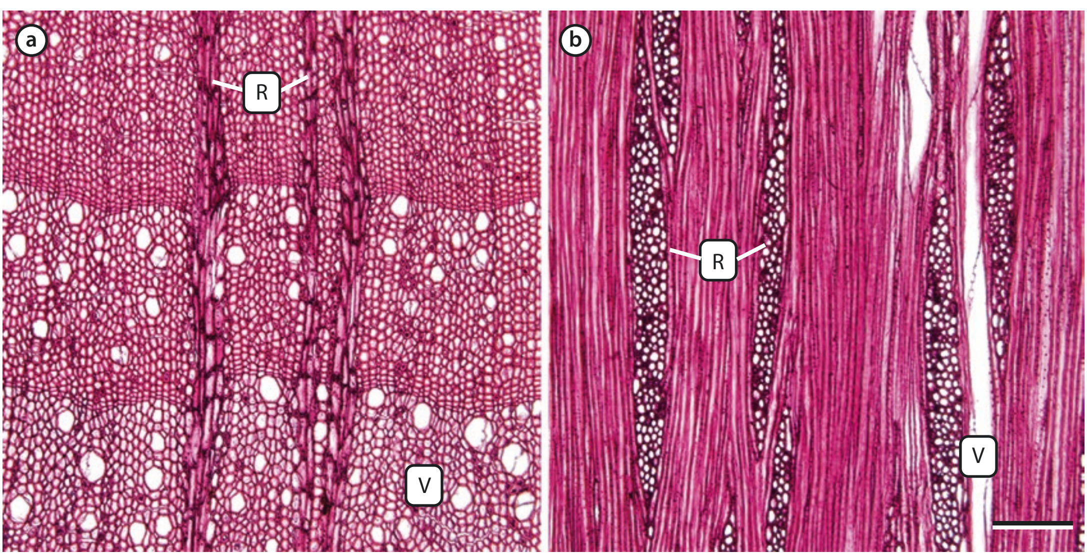
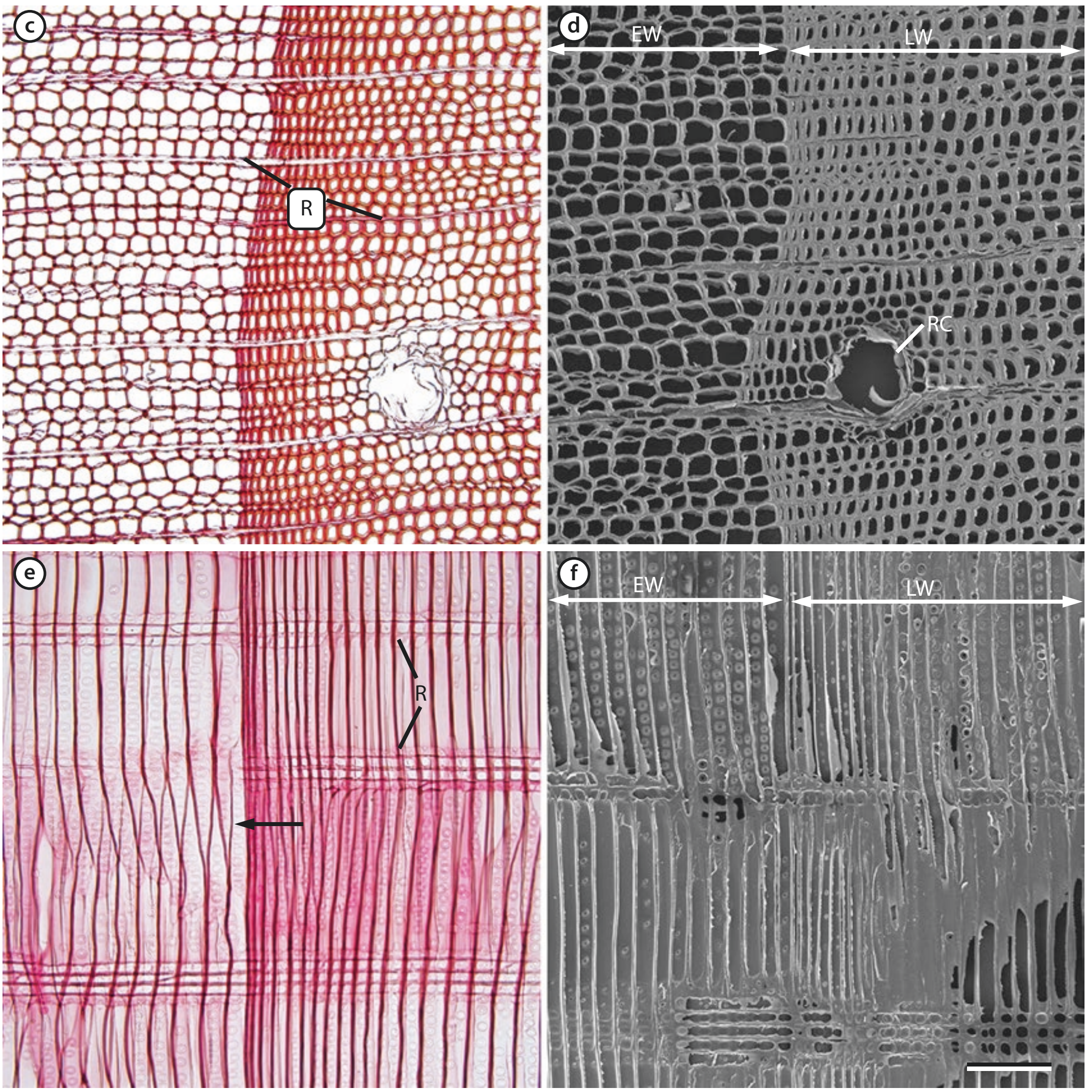
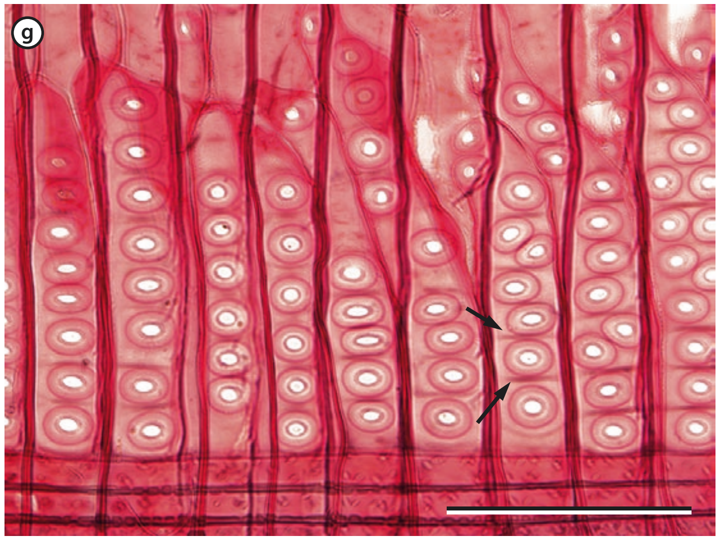


◘ **Fig. 15.5** **a**, **b** Joint fir (*Ephedra trifurca*, Gnetophyta) wood in **a** cross-section and **b** tangential section showing presence of vessel elements (V). Rays (R) are also apparent in both images. Scale bar in **b** = 100 µm and applies to both panels (**a**, **b** RR Wise)

The basic features of gymnosperm wood are shown in ◘ Fig. 15.5c–f. Tracheids have the typical long and narrow shape with tapered ends. Abundant water at the beginning of the growing season allows for larger tracheids with thinner walls, so-called earlywood. As the growing season progresses and water becomes more limiting, smaller tracheids develop with thicker walls, latewood. This growth pattern produces the **annual rings** seen in ◘ Fig. 15.3e, f. The tapered ends overlap with those of tracheids both above and below in the stem of the tree. Lateral movement of water from one tracheid to the next is via **circular bordered pits** in the anticlinal walls (◘ Fig. 15.5g). ◘ Figure 15.5g also shows **crassulae** (also called bars of Sanio for the seminal work of Sanio, 1872) which are cellulose thickenings found between individual pits.



◘ **Fig. 15.5** **c**–**f** Gymnosperm (*Pinus* sp.) wood seen in cross-section **c**, **d** and radial section **e**, **f**. **c**, **d** The cross-sectional views cover a boundary between annual growth rings with thinner-walled tracheids in the earlywood (EW) and thicker-walled tracheids in the latewood (LW). Axial resin canals (RC) are lined with secretory parenchyma. **e**, **f** *Pinus* rays are a mixture of parenchyma and tracheids. Refer to ◘ Fig. 15.5g, h for a higher-magnification view of a single ray. Note the tapered and overlapping tracheids in **e** (*arrow*). Scale bar in **f** = 100 μm and applies to all panels (**c**–**f** RR Wise)

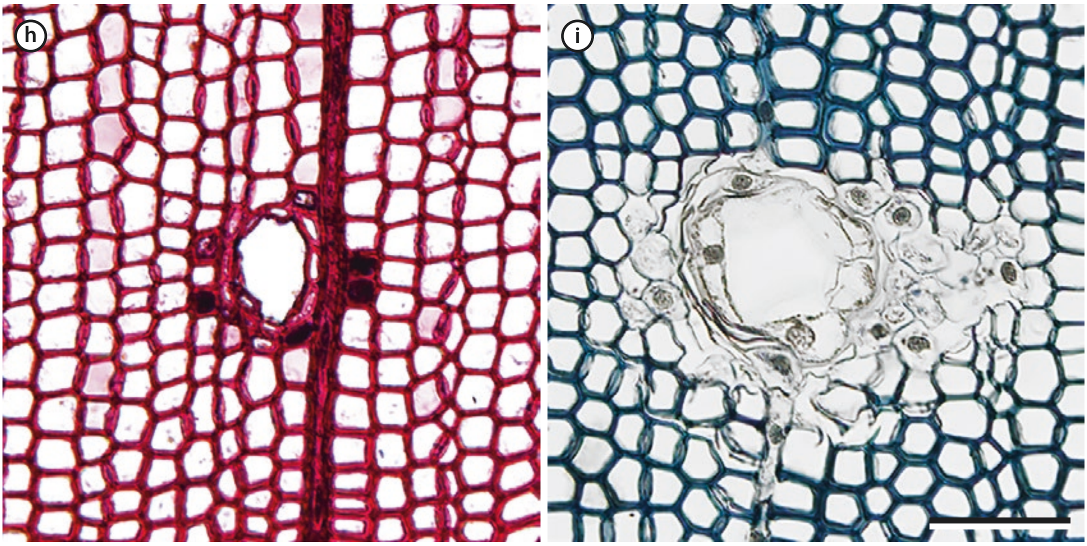


■ **Fig. 15.5** **g** Circular bordered pits and crassulae (*arrows*) in a radial section of Norway spruce (*Picea abies*) wood. Note the tapered ends of the tracheids and that a ray traverses the bottom of the figure. Arrows indicate crassulae. Scale bar = 50 µm (RR Wise)

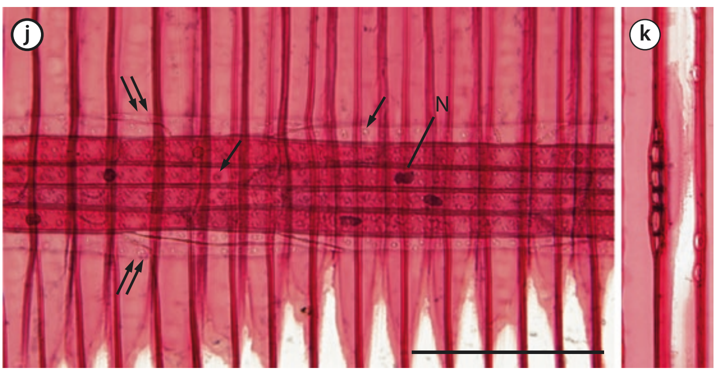
Tracheids lack the perforation plate found in angiosperm vessel elements, so axial water movement between cells occurs through pits in the long overlapping areas at the tapered ends (■ Fig. 15.5e). Xylem **resin canals** (■ Fig. 15.5c, d) are an evolutionary advancement not found in the earliest fossil gymnosperm wood or in extant species such as the true firs (*Abies* sp.) that are considered to have primitive features (Carlquist 2001). Lacking the ability to produce resin in the xylem, balsam fir wood has poor resistance to insect damage and rot and therefore not well suited for outdoor construction.

Gymnosperm axial resin canals may be simple, with a single layer of **epithelium** or more complex with two or more layers of epithelial cells (■ Fig. 15.5h, i). The presence of resin imparts insect and rot resistant, two characteristics that are important in determining the commercial and practical uses of the woods.

Tracheids in the ray system of a gymnosperm stem act as conduits for the movement of water in a radial direction from the stem out to the vascular cambium and periderm. Most of the rays in gymnosperm wood are uniseriate; only those rays with resin canals are multiseriate. Uniseriate rays are clearly seen in a radial section (■ Fig. 15.5j, k). They may be composed exclusively of parenchyma cells, or may be a mixture of parenchyma and ray tracheids, depending on species. Both ray parenchyma and ray tracheids are said to be procumbent (i.e., with their long axis in a horizontal plane) and share circular bordered pits with adjacent **axial tracheids**. Rays are the source of water and minerals for the living tissues that lie to the exterior of the vascular cambium, i.e., the phelloderm and phellogen of the periderm (▶ Chap. 16).

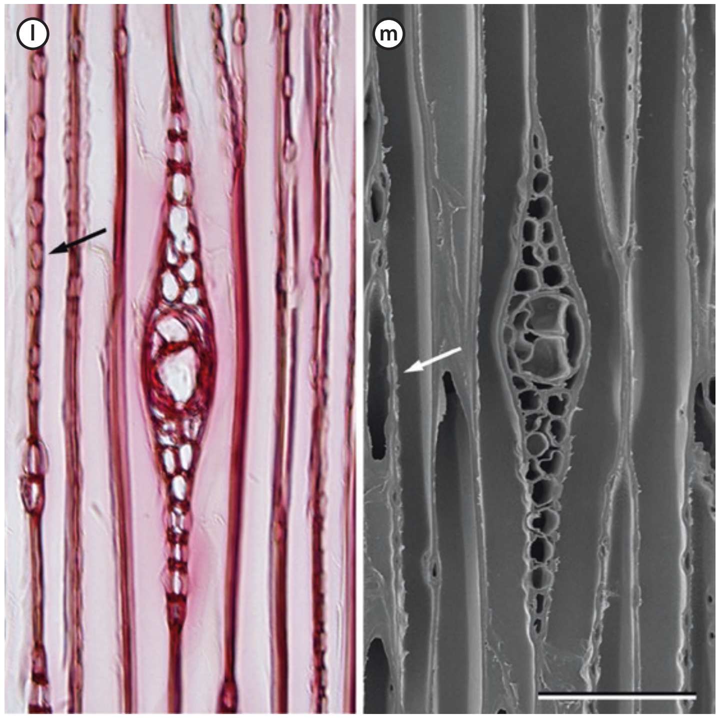


■ **Fig. 15.5** Cross-sectional views of resin canals. **h** The canals in Douglas fir (*Pseudotsuga menziesii*) have a thin layer of epithelial parenchyma cells. **i** Resin canals in white pine (*Pinus strobus*) are much larger with a thick epithelial layer. Scale bar in **i** = 50 µm and applies to both panels (**h**, **i** RR Wise)



■ **Fig. 15.5** **j**, **k** Radial **j** and tangential **k** views of xylem rays in the wood of Norway spruce (*Picea abies*). **j** Axial tracheids can be seen running in a vertical direction in the background, and a ray runs horizontally. The ray has three rows of ray parenchyma with conspicuous nuclei (N) bordered by a row of ray tracheids on the top and bottom (*double arrows*). Simple pits connecting the ray cells to the axial tracheids are indicated by single arrows. Note that the ray parenchyma cell ends are blunt and the ray tracheid end walls are tapered. **k** The uniseriate ray is viewed in tangential section and has the same number of rows of ray parenchyma and ray tracheids as in **j**. Scale bar in **j** = 100 µm and applies to both panels (**j**, **k** RR Wise)

Many gymnosperms, particularly the pines, have radial resin canals, in addition to the axial resin canals described above. Resin canals containing rays are multiseriate (■ Fig. 15.5l, m) due to the biosynthetic nature of the tissue. The axial and radial resin canals are the tissues that synthesize the compounds that are extracted as pine tar, discussed in ► Sect. 15.2.



■ **Fig. 15.5** **l**, **m** Two radial resin canals seen in tangential section in the wood of pine (*Pinus* sp.). Note the bordered pits on the tracheid anticlinal walls (*arrows*). Scale bar in **m** = 100 μm and applies to both panels (**l**, **m** RR Wise)

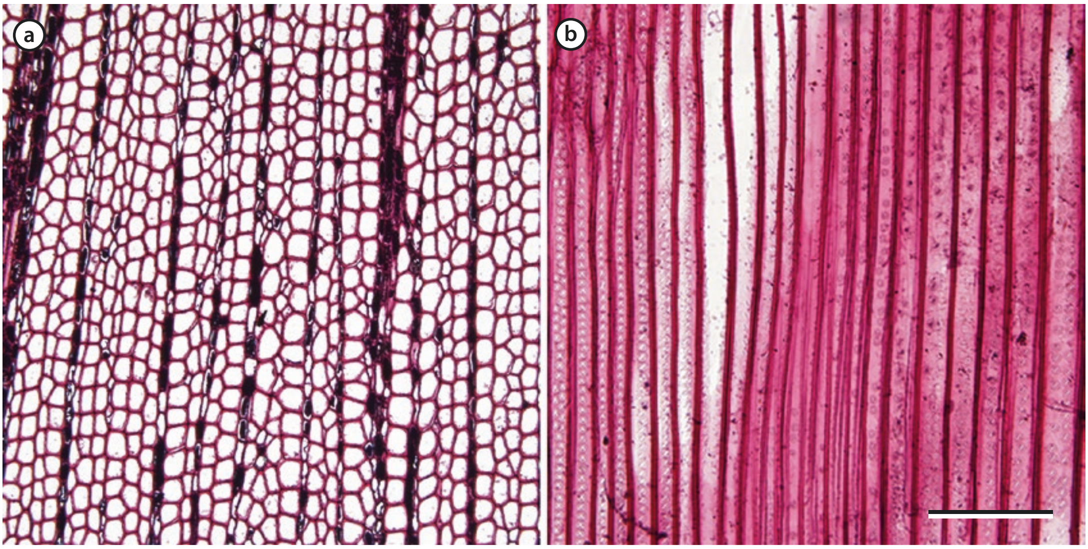
The presence, abundance, or absence of xylem axial resin canals, radial resin canals, ray parenchyma, ray tracheids, and crassulae are of value to the identification and systematics of both extant and extinct gymnosperm species.

15.6 Eudicot Wood Is Characterized by Vessel Elements, Tracheids, Parenchyma, and Rays

Eudicot wood identification is based on several characters that are visible with a simple 10x hand lens. Those characters include (1) the distribution of vessel elements (also called "pores" here and "perforate tracheary elements" in ► Chap. 7) within a single growth ring, (2) the arrangements of individual vessels as solitary or grouped regardless of where they are in the annual growth ring, (3) the pattern and distribution of xylem parenchyma, and (4) ray architecture. It should be noted that there are a number of angiosperm taxa that lack rays entirely, a characteristic called "raylessness," which has been related to the mechanical and functional needs of the stem (Carlquist 2015).

15.6.1 Patterns of Xylem Vessel Element Distribution

Just as not all gymnosperms are vessel-less, not all angiosperms possess vessel elements. Pepperbush is a shrubby, primitive, vessel-less



◘ **Fig. 15.6** **a**, **b** Purple pepperbush (*Tasmannia purpurascens*) wood seen in **a** cross-section and **b** longitudinal section. Note abundant tracheids and lack of vessel elements. Scale bar in **b** = 100 μm and applies to both panels (**a**, **b** RR Wise)

eudicot (◘ Fig. 15.6a, b) in the Winteraceae family. Both the vessel-containing gymnosperms, such as *Ephedra* (◘ Fig. 15.5a, b), and the vessel-less angiosperms have been studied extensively for clues to the evolution of xylem vessels.

◘ Figure 15.6c–f shows four basic patterns of vessel element distribution in growth rings when observed in cross-sections. Woods such as catalpa, ash, oak, and hickory have their largest pores develop in the early (spring) wood and microscopically appear to form a ring pattern at the juncture of the annual growth rings. Thus, such a pattern is termed "**ring-porous**" (◘ Fig. 15.6c). Alternatively, in other angiosperms, the pores are generated uniformly throughout the growing season, giving rise to their designation as "**diffuse-porous**" wood (◘ Fig. 15.6d). These include common species such as birch, cherry, maple, and poplar. In many hardwoods such as chestnut, black walnut, and magnolia, pores are less grouped together at the starting sites of the annular rings but rather trail off throughout the growth season, giving rise to a designation as "**semi-ring-porous**" (◘ Fig. 15.6e). A "**dendritic**" pattern (from the Greek *dendron*, meaning tree or branched) is one in which vessel elements branch out from the earlywood to the latewood. Intermediate patterns exist and species may share features of more than one pattern. White oak (◘ Fig. 15.6f), for instance, is a ring-porous wood with dendrites of vessel elements spread across the growth ring.

15.6.2 Vessel Grouping

Vessel elements may be solitary, as in beech (◘ Fig. 15.6g), found in small clusters of two to three cells which are common in the birches (◘ Fig. 15.6h), or arranged in radial files of three to ten or more cells as seen in hornbeam (◘ Fig. 15.6i). Elm is characterized as having large clusters of vessel elements (◘ Fig. 15.6j). A single species

Fig. 15.6 **c**–**f** Cross-sections of **c** ring-porous hardwood from northern catalpa (*Catalpa speciosa*), **d** diffuse-porous hardwood from paper birch (*Betula papyrifera*), **e** semi-ring-porous hardwood from horse chestnut (*Aesculus hippocastanum*), and **f** ring-porous with dendrites in white oak (*Quercus alba*). The central axis of the tree is toward the bottom in all four images. The tissues at the top of panel **f** are phloem and bark. Scale bar in **f** = 250 μm and applies to all panels (**c**–**f** RR Wise)

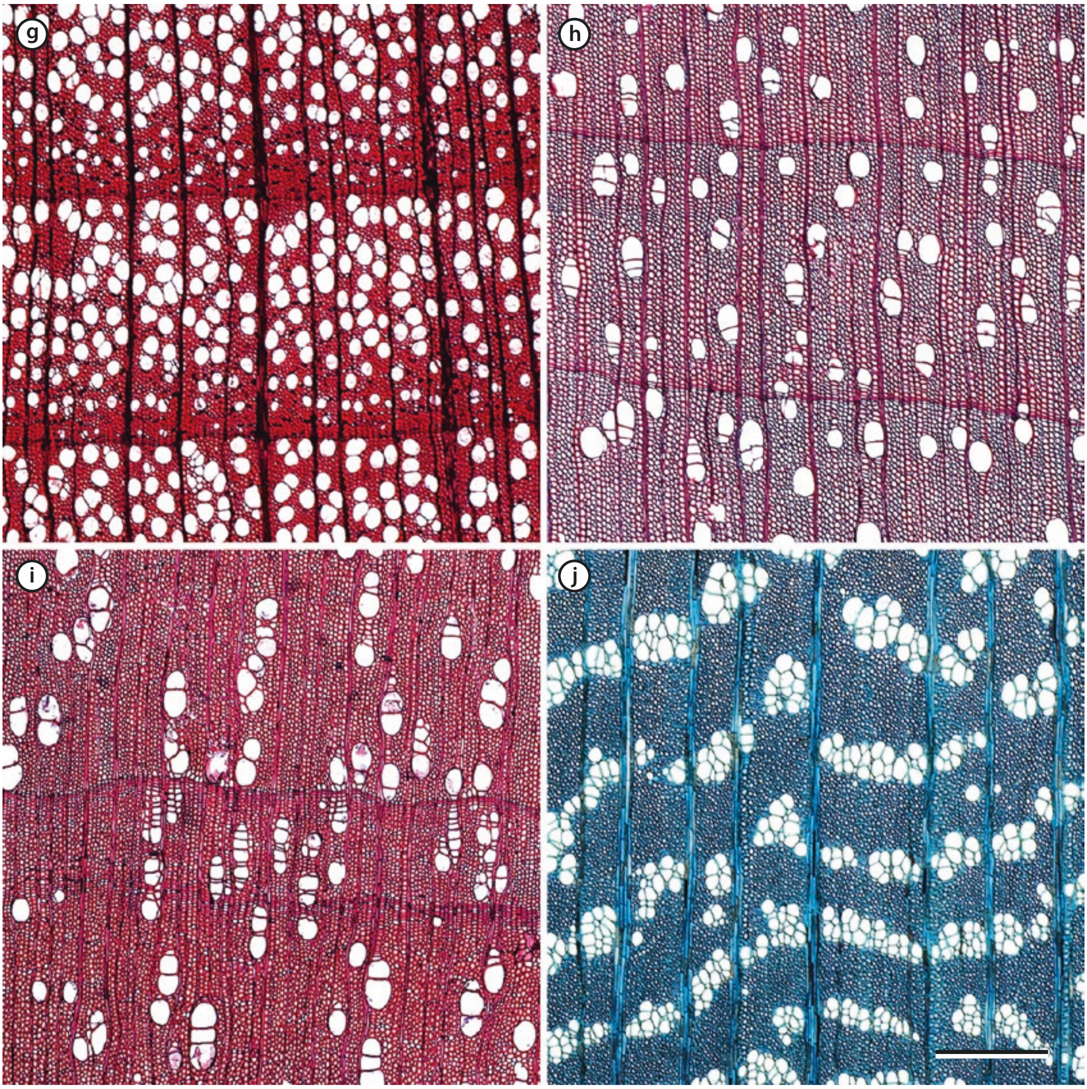
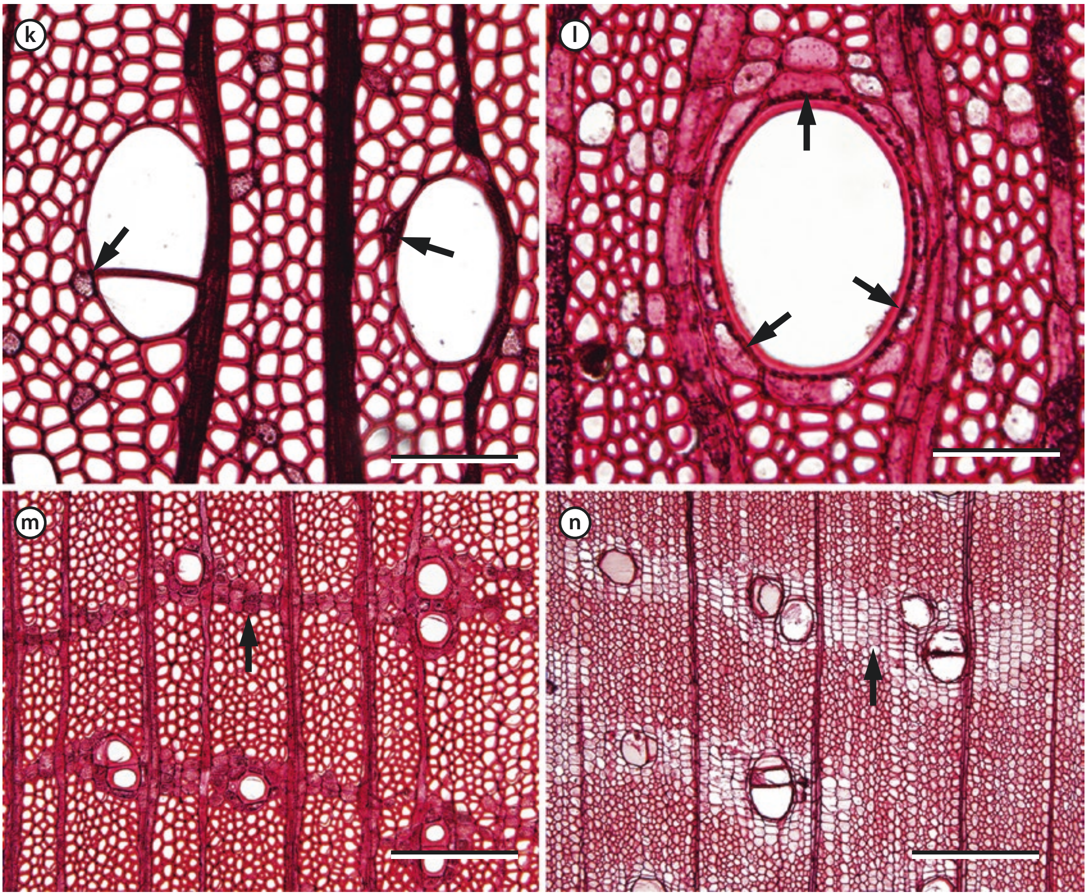


Fig. 15.6 **g**–**j** Groupings of vessel elements. **g** Solitary in American beech (*Fagus grandifolia*), **h** small clusters in silver birch (*Betula alba*), **i** radial files in American hop hornbeam (*Ostrya virginiana*), **j** large, multi-vessel clusters in American elm (*Ulmus americana*). Scale bar in **j** = 250 µm and applies to all panels (**g**–**j** RR Wise)

may exhibit one or more of the vessel element patterns shown. For instance, while most of the vessel elements in beech are solitary, a few exist as pairs (Fig. 15.6g).

15.6.3 Patterns of Xylem Parenchyma

Like xylem vessel element distribution, the pattern or xylem parenchyma is a species-specific trait very useful in wood identification. Xylem parenchyma cells, which function as storage sites as well as aiding in the transport of water and dissolved substances, are scattered throughout the sapwood in several recognizable patterns. The parenchyma cells may be found individually or in aggregate



■ **Fig. 15.6** **k**–**n** Various forms of paratracheal parenchyma, e.g., parenchyma associated with a vessel element. **k** Scanty paratracheal parenchyma in paper birch (*Betula papyrifera*); note also the apotracheal parenchyma in the field of view. **l** Pecan (*Carya illinoinensis*) wood has vasicentric paratracheal parenchyma completely surrounding a vessel element. **m** Ash (*Fraxinus* sp.) is characterized as having narrow bands of confluent paratracheal parenchyma that appear darker than the surrounding tracheids. **n** The broad bands of confluent paratracheal parenchyma in the foxglove tree (*Paulownia tomentosa*) are lighter than the surrounding tracheids. Arrows indicate the location of the parenchyma. Scale bars = 50 µm in **k** and **l**, 100 µm in **m**, and 200 µm in **n** (**k**–**n** RR Wise)

clusters throughout the wood. They may also be found oriented in the longitudinal axis along the length of the tree trunk or in rays that appear along the radial axis. Parenchyma cells that are associated with xylem vessels are called **paratracheal** parenchyma (■ Fig. 15.6k–n). They may be scanty (only one or two per vessel element, ■ Fig. 15.6k), **vasicentric** (completely surrounding a vessel element, ■ Fig. 15.6l), or **confluent** (extending from one vessel to another). Confluent xylem parenchyma may be in narrow (■ Fig. 15.6m) or broad bands (■ Fig. 15.6n), depending on the species. Paratracheal parenchyma may be further classified as **aliform** (winged) if it forms, as seen in cross-sections, tapered extensions on the sides of a vessel element (not shown) or as **scalariform** parenchyma if it forms narrow bands between rays (■ Fig. 15.6m). Multiple types of xylem parenchyma may be seen in one image. Indeed, ■ Fig. 15.6m shows confluent, scalariform, and paratracheal parenchyma.

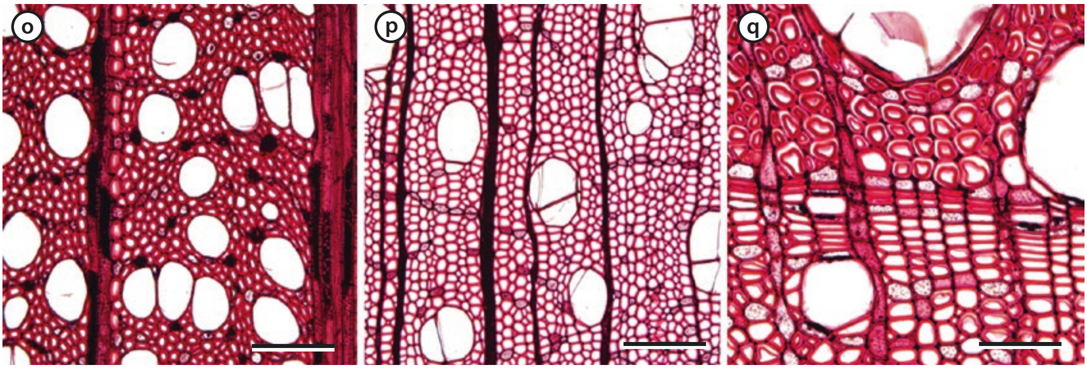


Fig. 15.6 **o** Diffuse apotracheal parenchyma in sycamore (*Platanus occidentalis*), **p** banded apotracheal parenchyma in paper birch (*Betula papyrifera*), **q** terminal apotracheal parenchyma in black walnut (*Juglans nigra*). Scale bars = 100 μm in **o** and **p** and 50 μm in **q** (**o**–**q** RR Wise)

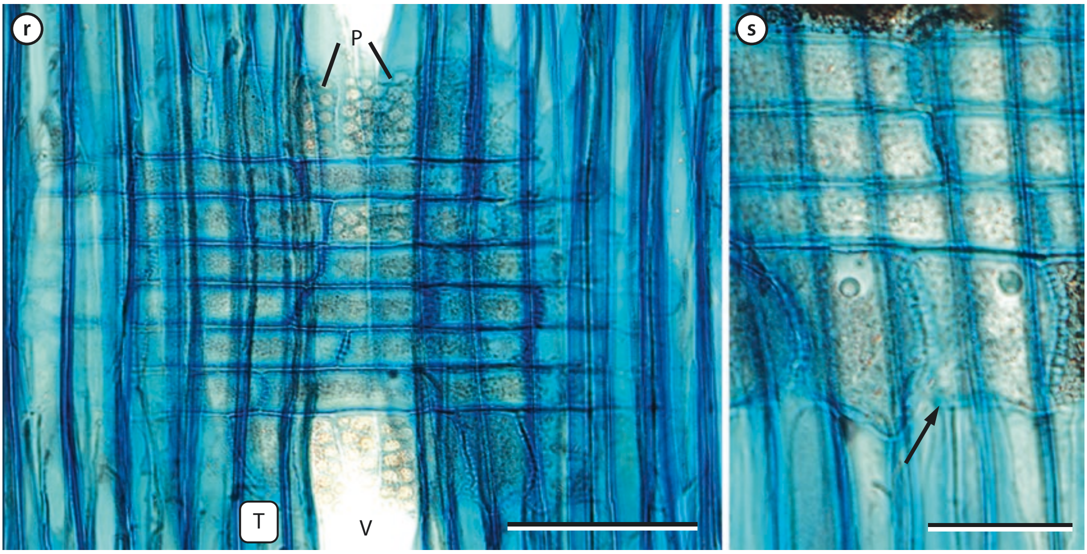
Those parenchyma cells not associated with a vessel element are called diffuse or **apotracheal** parenchyma, meaning not associated with vessel elements (Fig. 15.6o–p). They may be **diffuse** (Fig. 15.6o), **banded** (extending between rays, Fig. 15.6p), or **terminal** (found at the boundary of an annual growth ring, Fig. 15.6q). Regardless of its specific pattern—paratracheal or apotracheal—parenchyma cells constitute approximately the same relative volume (~10%) in both softwoods and hardwoods. Wood is a tissue whose primary functions are support and long-distance water conduction. Parenchyma contributes to neither of those functions, thereby placing a limit on their abundance.

15.6.4 Ray Architecture

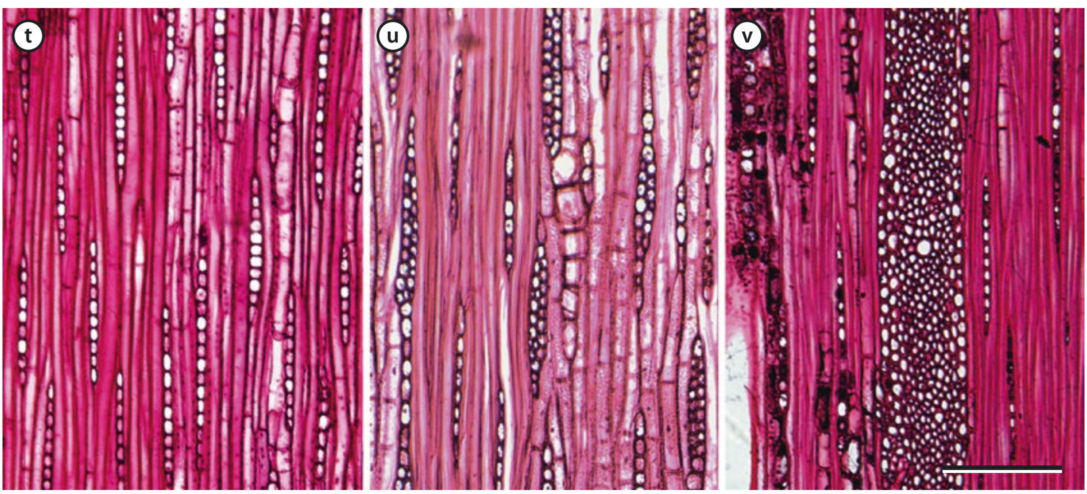
Rays are groups of xylem cells generated by the vascular cambium (specifically, **ray initials**) that transport xylem sap (water and minerals, but not photosynthate) through wood in a radial direction. Similar to gymnosperm rays, eudicot rays are joined to the axial xylem system via numerous interconnecting pits (Fig. 15.6r). The main direction of the sap flux is from the axial system, through pits, to the ray system and interior toward the exterior. Rays may be composed of living (parenchyma) and dead (tracheids) cells and function for a number of years. Most of the living cells in wood are those found in rays, the exception being the paratracheal or apotracheal parenchyma of the axial system.

Homocellular rays have a single-cell type, either parenchyma or tracheid. Rays in maple, sycamore, and alder are homocellular and composed of only procumbent ray parenchyma cells. **Heterocellular rays** have a mixture of parenchyma (upright or procumbent) and/or tracheids, such as found in walnut, oaks, and willow (Fig. 15.6r, s).

Rays can vary considerably in height and width due to the number of cells comprising the ray; tangential sections offer the best view of ray size (Fig. 15.6t–v). Ray height is designated as short



■ **Fig. 15.6** **r** Heterogeneous willow (*Salix nigra*) ray with six rows of procumbent parenchyma cells in the middle and top and bottom rows of upright (square) marginal cells. Numerous pits (P) connect the marginal cells with a vessel element (V). Tracheids (T) are to either side of the vessel element. **s** Higher magnification of a similar specimen showing upright cells (*arrow*) in the margin of ray. Scale bars = 50 μm in **r** and 25 μm in **s** (**r**, **s** RR Wise)



■ **Fig. 15.6** Tangential sections showing wood rays. **t** American chestnut (*Castanea dentata*) wood has uniseriate rays. **u** Black walnut (*Juglans nigra*) has both uni- and biseriate rays. **v** Red oak (*Quercus rubra*) has numerous uniseriate rays as well as large aggregate rays. Scale bar in **v** = 100 μm and applies to all panels (**t**–**v** RR Wise)

or tall. Short rays have 2–10 cells in a vertical direction, and tall rays have ten to several hundreds. Narrow rays may have only one to three cells in width, whereas relatively wide rays can be more than ten cells in width. The width of rays as determined by the cell number is often referred to as the seriate number, as in **uniseriate**, **biseriate**, etc. In a number of species (e.g., oak, *Quercus*; hornbeam, *Carpinus*; alder, *Alnus*; etc.), rays may merge to form aggregate rays, some of which may not only be very wide, but extremely tall (■ Fig. 15.6v).

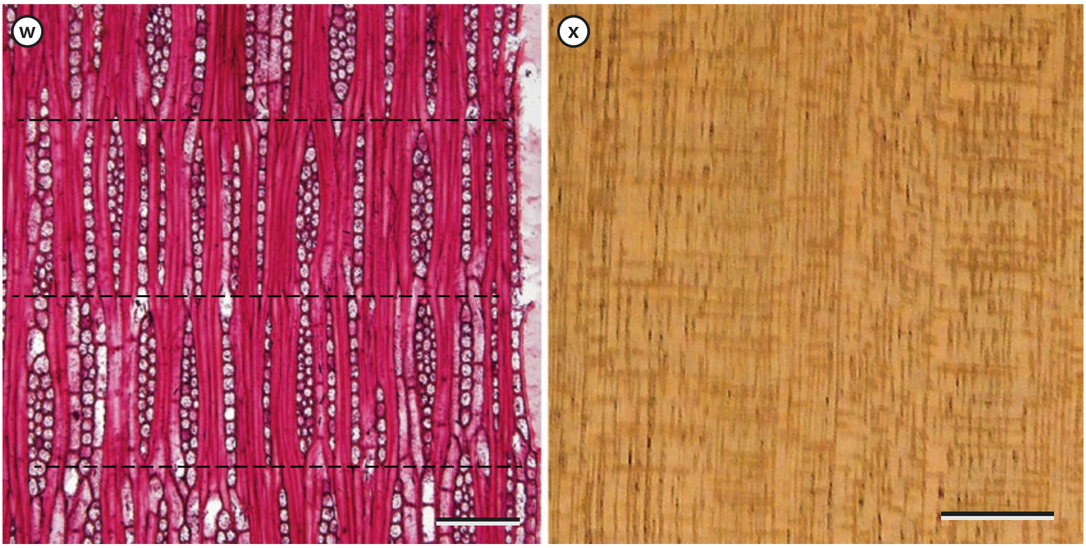


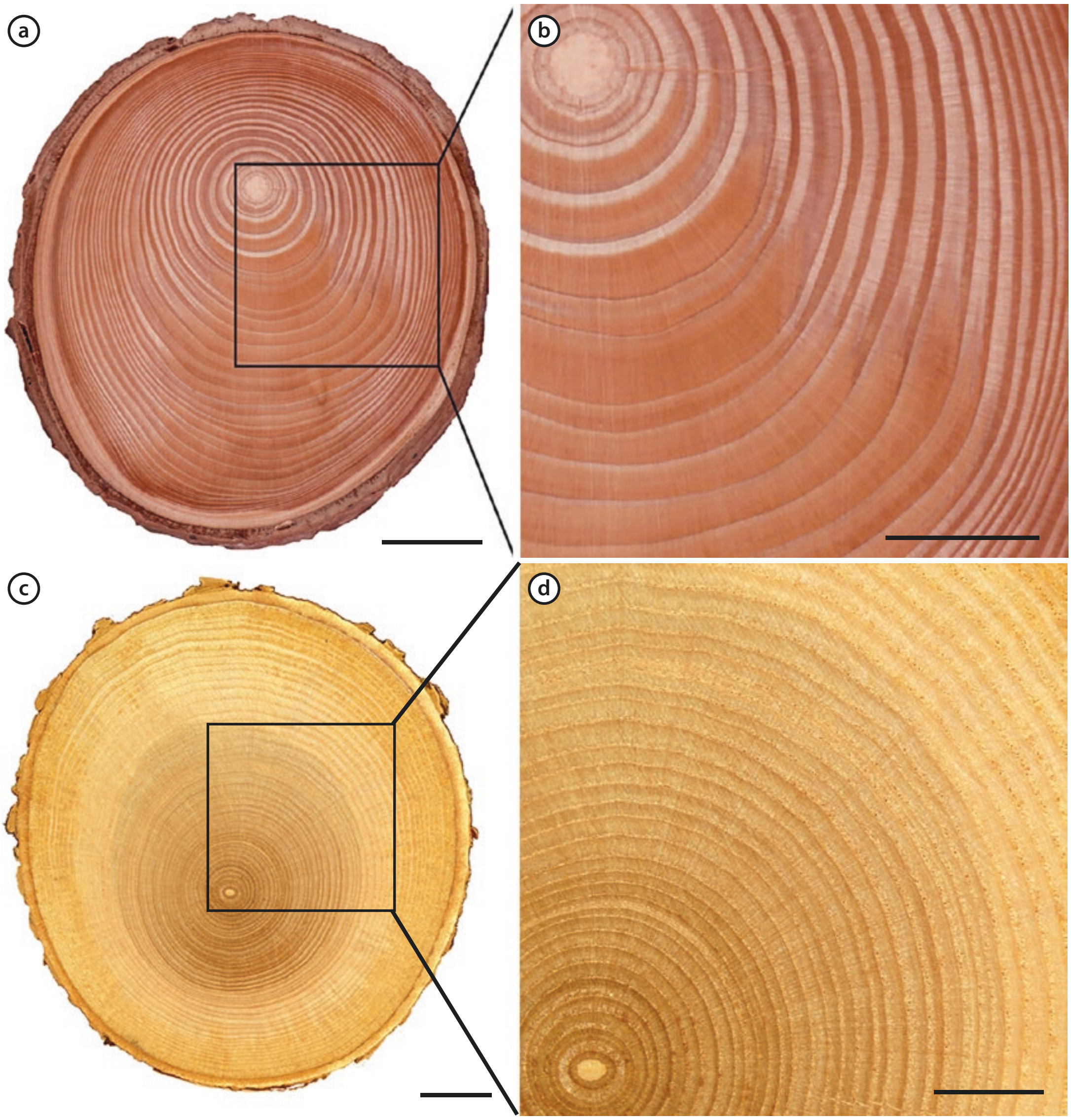
Fig. 15.6 **w** Tangential wood section of persimmon (*Diospyros virginiana*) revealing the storied nature of the rays, both uniseriate and multiseriate. Dashed horizontal lines highlight the stories of rays. **x** A flat-sawn (i.e., radial section) sample of sapele (*Entandrophragma cylindricum*), a hardwood tree native to tropical Africa, showing ripple marks caused by storied rays. Scale bars = 100 µm in **w** and 2 cm in **x** (**w**, **x** RR Wise)

Different planes of section, cross, radial, and tangential, can show strikingly different views of wood anatomy, even to the naked eye. Flat-sawn boards have the tangential surface exposed. In some hardwood species, such as a number of tropical trees, the rays are generally aligned in horizontal rows or tiers (Fig. 15.6w). These are called storied rays, and they impart stripes of alternating light and dark bands, called ripple marks (Fig. 15.6x). In other woods, ripple marks may also result from similar patterns of fibers or parenchyma cells.

15.7 Reaction Woods Develop in Response to Gravity

Wood, despite its natural strength due to lignified secondary cell walls, is still subject to forces of nature including high winds, gravity, weight-bearing loads, leaning, and other environmental factors. Such situations, however, vary between wood from gymnosperms and that of angiosperms and result in changes in the structure and composition of cell walls, which is generically termed as **reaction wood**. Gymnosperms and angiosperms (woody eudicots) contain uniquely different types of reaction wood.

Reaction wood is a development response driven by directional transport of the hormone indoleacetic acid (IAA). Statocysts in the endodermis (refer to Fig. 11.5m) settle to the bottom of the stem, which causes the transport of IAA in the same direction. In gymnosperms, the relatively higher IAA concentration at the lower side of the stem induces the vascular cambium to produce thicker cell walls and increased deposition of lignin, which gives greater strength to



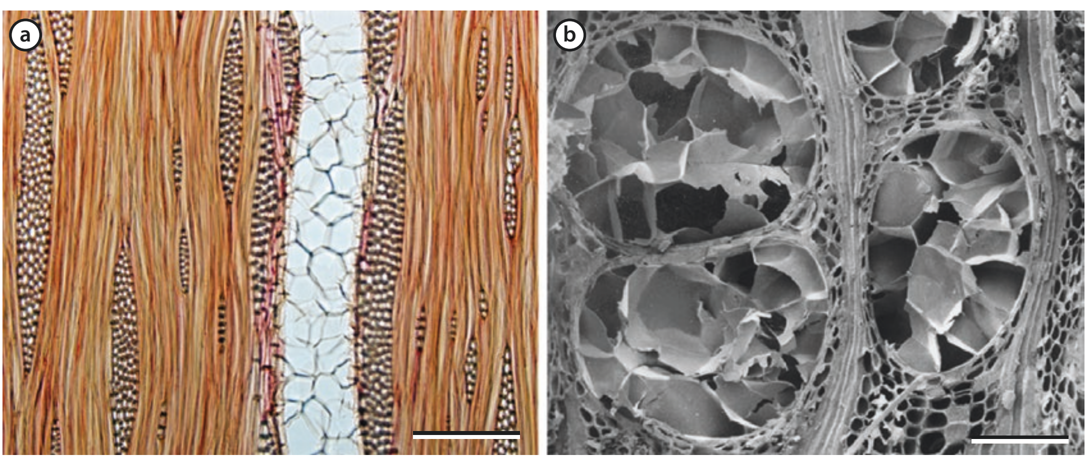
■ **Fig. 15.7** **a**–**d** Two forms of reaction wood. **a**, **b** Compression wood develops at the bottom of gymnosperm stems and limbs. Norway spruce (*Picea abies*) is shown. **c**, **d** Tension wood develops on the upper part of the stem of a horizontal or leaning woody eudicot stem, as shown in this cross-section of a green ash (*Fraxinus pennsylvanica*) limb. Scale bars = 2 cm in **a** and **c**, 1 cm in **b** and **d**. (Images **a** and **b** by Michael Rosenthal, Technische Universität Dresden – Rosenthal and Bäucker (2012), CC BY-SA 3.0, images **c** and **d** by RR Wise)

the site of stress. Specifically, the reaction wood of conifers is termed "**compression wood**." The compression wood may have the appearance of a dark stain (■ Fig. 15.7a, b). On the other hand, the reaction wood of eudicot angiosperms is designated as "**tension wood**" and develops on the upper side of branches (■ Fig. 15.7c, d) where it is found as **gelatinous fibers** (see also ■ Fig. 6.7g) (recall that gymnosperms lack fibers) and greater amounts of cellulose, but with reduced amounts of lignin. That condition exists when the concentration of indoleacetic acid is low.

The composition of reaction wood enables a branch to become more flexible and resist breaking in high winds or other forms of stress. The tension wood of eudicots, like the compression wood of gymnosperms, is also produced by stimulated cambial activity, but on the opposite side of a branch or affected tree trunk. Because of the unique patterns of darkened wood and cellular distributions, reaction woods are highly sought after for their use in furniture and wooden panels. The compression wood of gymnosperms, on the other hand, is considered to be of lower quality than normal wood due to uneven drying and warping of lumber. It can be dangerous to saw and machine. Reaction wood has also been reported in some roots for both gymnosperms and eudicots and most recently has been found in cycads (a primitive gymnosperm) indicating that reaction wood may have been formed at an early evolutionary period in seed plants.

15.8 Tyloses and Crystals May Be Found in Some Woods

A **tylosis** (pl: tyloses) is a vascular occlusion in a vessel element or tracheid caused by the protoplasm of an adjacent xylem parenchyma cell extending through a shared pit and filling the cell lumen (◘ Fig. 15.8a, b). In the formation of wood, paratracheal parenchyma cells are adjacent to vessel elements, where they largely function in food storage. However, as vessels age, or when an infection takes place, and when drought or mechanical damage may occur to the wood, the cell walls of the parenchyma may protrude through pit pairs in a matter of hours due to the production of enzymes that dissolve the pit membrane. The protrusion in a balloon-like manner extends throughout the lumen of the vessel element (and in a few cases into tracheids), thus blocking of the passage of water and dissolved substances, but also blocking the passage of any infectious materials.

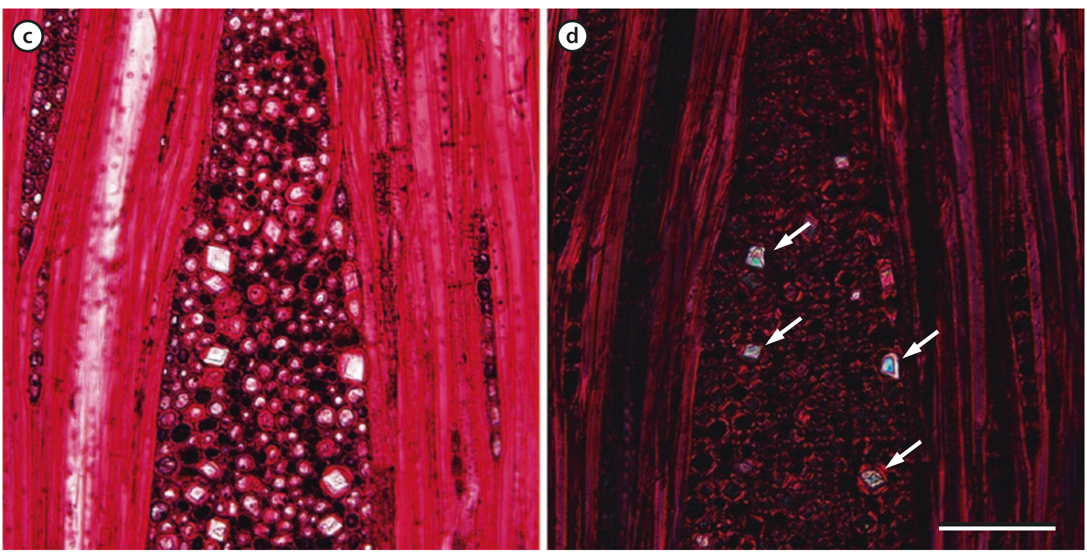


◘ **Fig. 15.8** **a**, **b** Black locust (*Robinia pseudoacacia*) wood with tyloses in **a** longitudinal section and **b** cross-section. The tyloses developed from parenchyma cells adjacent to the vessel elements. Scale bars = 100 µm in **a** and 50 µm in **b**. (**a** RR Wise; Image **b** courtesy of John Curtis)

While they often form in response to infection, some woods naturally form tyloses. For instance, white oak (*Quercus alba*) has abundant tyloses in the heartwood that are no longer participating in water conduction. Red oak (*Quercus rubra*), on the other hand, has few. Coopers (makers of wooden barrels, kegs, and casks) learned early on that a barrel made of red oak would leak, whereas a white oak barrel would not.

The bacterium *Xylella fastidiosa* is spread by biting insects and causes Pierce's disease, a deadly disease of peaches, grapes, citrus, and other plants (Baldi and La Porta 2017). The bacterium enters the xylem conducting tissue and multiplies. The plant's response is to produce tyloses in the infected tissues, which block transpiration and cause leaf and, ultimately, plant death. There is currently no treatment or cure for Pierce's disease, although some plants show significant resistance, meaning there could be a genetic basis for protection that could be transferred to susceptible varieties or species (Svyantek et al. 2016).

In addition to tyloses, mineral crystals may be found in the lumen of vessel elements such as red mulberry (*Morus rubra*) and teak (*Tectona grandis*) and have been observed in parenchyma cells of wood rays as in the American beech (◘ Fig. 15.8c, d) and numerous other species. The chemical composition of these crystals has been found to be calcium oxalate or magnesium oxalate. Other crystals may be composed of silicon dioxide (Carlquist 2001).



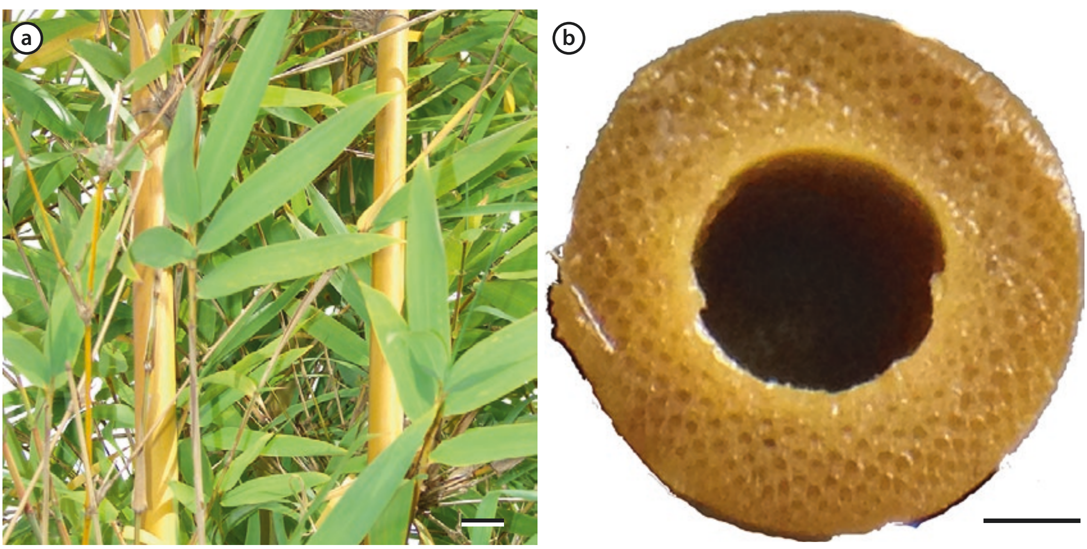
◘ **Fig. 15.8** **c**, **d** Tangential section of a ray in American beech (*Fagus grandifolia*) wood viewed under **c** bright-field and **d** polarized illumination. Arrows in **d** mark the birefringent crystals in the ray parenchyma cells. Scale bar = 50 µm (**c**, **d** RR Wise)

15.9 Monocot "Wood" Does Not Come from True Secondary Growth

As discussed in ▶ Chap. 11, stems of monocotyledonous plants are characterized by their disordered distribution of vascular bundles throughout the cross-sectional organization—a pattern that does not give rise to the annual layered secondary growth seen in woody eudicots. Thus, monocots cannot form true wood. However, some perennial monocots such as bamboo (Poaceae, subfamily Bambusoideae) and the palms (Arecaceae) can produce a very strong, long-lasting stem or trunk.

Monocots lack a vascular cambium encircling the stem (▶ Chap. 11), which is the source of true wood in eudicots. However, they do have a cambium in each of the many vascular bundles. Therefore, monocots increase stem strength by heavy sclerification of the fiber caps on each bundle, not by sclerifying the entire stem and steadily increasing stem diameter with each growing season, as woody eudicots do. The result is a mass of supportive tissues that, taken together, constitute monocot "wood."

Bamboo (*Bambusa* sp.), a common fast-growing monocot, has a hollow stem (referred to as a 'culm' in monocots) with thick walls (◘ Fig. 15.9a, b). It has numerous vascular bundles comprising xylem, phloem, and fiber caps embedded in parenchymatous tissues (refer to ◘ Fig. 11.5e–g). It is the fiber caps that provide mechanical



◘ **Fig. 15.9** **a**, **b** Photographs of weaver's bamboo (*Bambusa textilis*) culms. **a** Side view showing leaves arising from nodes. **b** End view showing end-wall thickness. Scale bars = 2 cm in **a** and 2 mm in **b** (**a** Forest and Kim Starr, CC BY 3.0; **b** RR Wise)

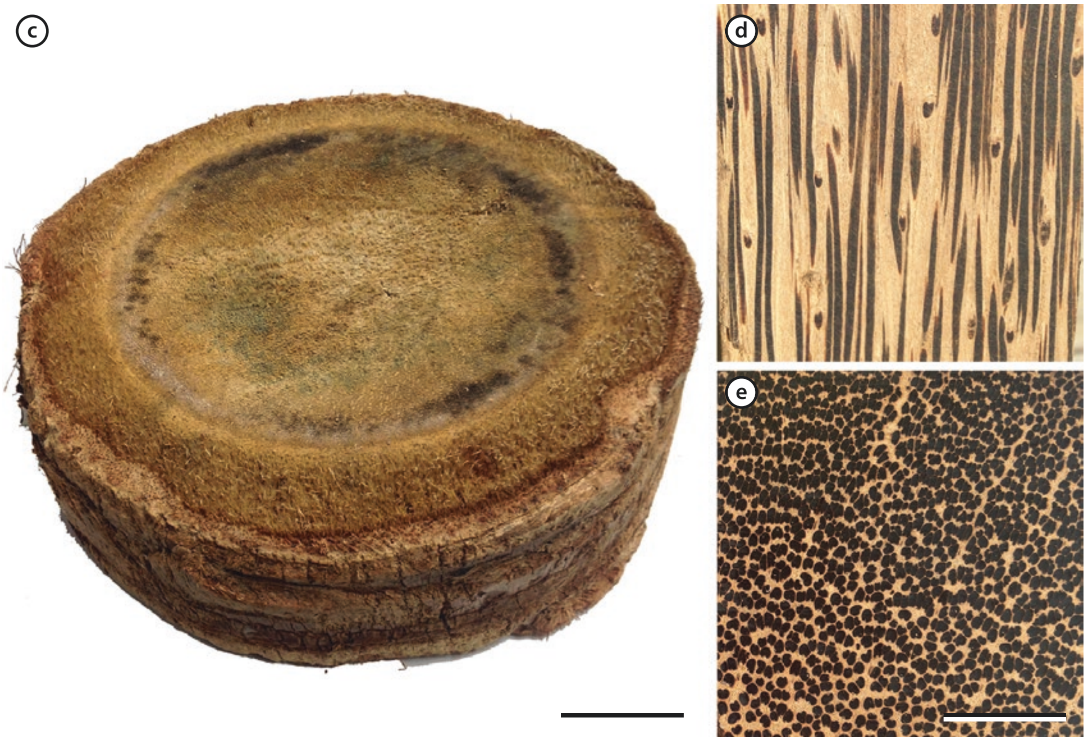
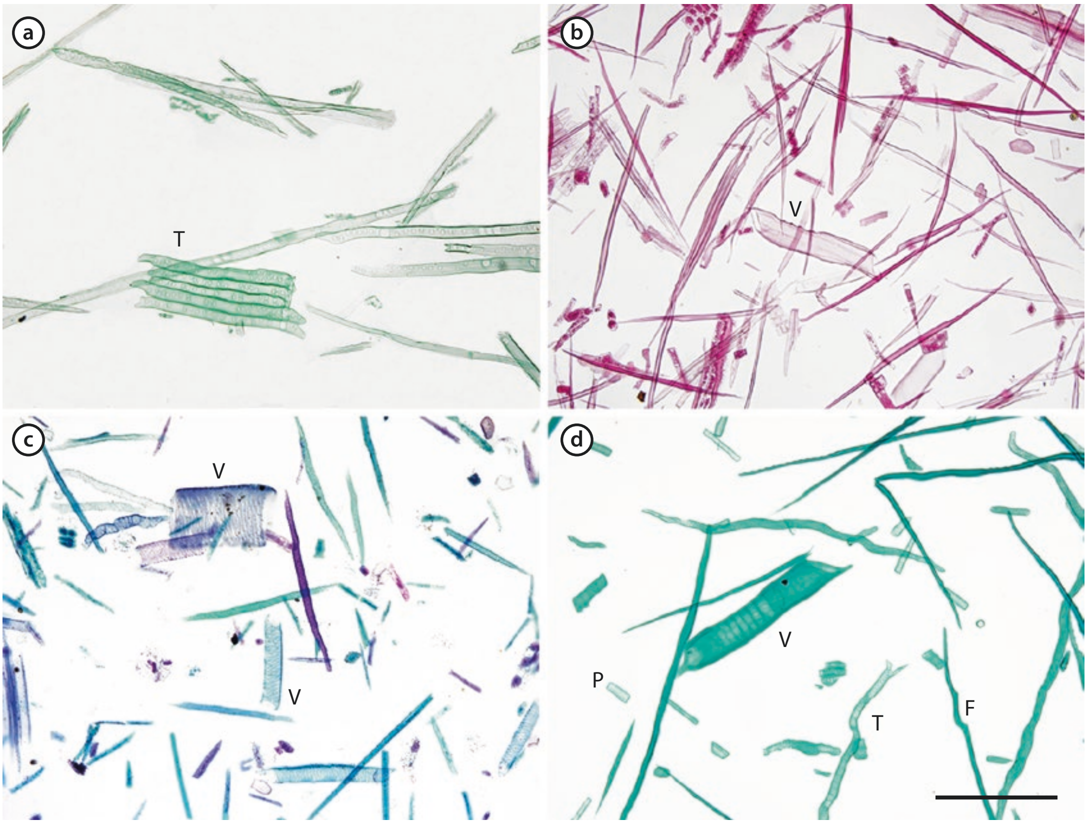


Fig. 15.9 **c** Cross-section of a cabbage-palm (*Sabal palmetto*) "tree trunk." The stem is solid with several radial zones that represent different ratios of fiber to parenchyma. **d** Longitudinal and **e** cross sections of black palm (*Borassus flabellifer*) "wood." The dark brown streaks in **d** and spots in **e** are sclerified vascular bundle fiber caps. The intervening tan tissue is parenchyma. Scale bars = 5 cm in **c** and 1 cm in **d** and **e** (**c**–**e** RR Wise)

support for the stem, particularly where they are concentrated at the periphery and where bending stress is typically the greatest. As the plant ages, new cell wall material is deposited to the fibers with increasing amounts of lignin in alternating layers that contributes additional strength. The abundance of heavily sclerified vascular bundles makes for an extremely strong stem. It is worth noting that many of the vascular bundles converge in the internodal regions to form a complex, intertwined arrangement that adds strength to the stem. In Asia, bamboo scaffolding is often used in building construction, frequently in high-rise buildings more than 20 stories high, attesting to its considerable strength (Lo et al. 2008) and its availability as an inexpensive, lightweight, and easily assembled material.

Palm "trees" have a solid stem which, like bamboo, is composed of heavily sclerified vascular bundles embedded in a matrix of parenchyma cells (Fig. 15.9c). Palm trees may reach considerable size (refer to Fig. 1.19). For some species, the percent fiber is so high that the lumber, when cured and dried, can be made into flooring and siding in building construction. Black palm (Fig. 15.9d, e) is one example. The almost 3000 species of palms have numerous other uses. Palm leaves can be used for thatched roofs, oil, wax, and many types of straw hats. The tree trunks can also provide sap for sugars and for fermented drinks. Due to their rapid growth, palms



◘ **Fig. 15.10** **a**–**d** Macerations of **a** pine (*Pinus* sp.) wood, **b** ephedra (*Ephedra* sp.) wood, **c** Dutchman's pipe (*Aristolochia* sp.) stem, and **d** red oak (*Quercus rubra*) wood showing isolated parenchyma (P), tracheids (t), and vessel elements (V). Scale bar in **d** = 100 µm and applies to all panels (**a**–**d** RR Wise)

have been used for the production of biodiesel fuel. Palms are major food sources with coconut (liquid and hardened endosperm) and date (fleshy fruit) being the primary examples.

15.10 Wood Macerations Are Useful for Species Identification, Product Identification, and Forensics

In order to visualize the individual cells of wood from virtually all directions, a process of cellular separation is often employed that chemically and/or enzymatically dissolves the middle lamella and then allows for the individual cells to be viewed. This process is termed maceration. ◘ Figure 15.10a–d reveals such structures from a variety of woods. The maceration process typically involves treating small pieces of wood with 10% nitric and/or chromic acid or potassium chlorate, which breaks down the middle lamella but does not damage the primary and secondary walls. After up to 24 h in that solution, the cells are washed in distilled water and can be examined by light (or laser confocal) microscopy. If greater contrast is required, staining with safranin (red) or methyl green solutions can be employed.

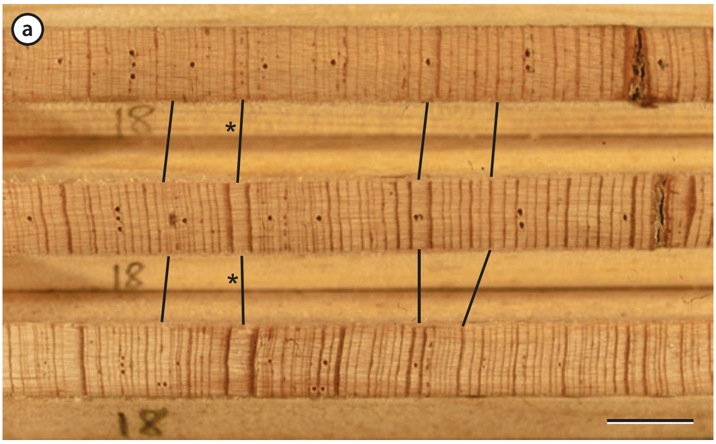
In addition to wood, other plant tissues can be treated by maceration such as stem or leaf materials that contain a large number of sclereids of different nature. It has also proven useful to combine maceration with polarizing microscopy to show birefringence and, therefore, the orientation of cell wall layers. It is common in the paper industry to test competitors' paper products to determine the amount and ratios of wood fibers used in production. Knowing the physical nature of fibers in wood from paper has also been utilized in forensic studies to document papers that may, or may not, share a common origin.

15.11 The Study of Tree Rings Is Important in Archeology, Climatology, and Forensics

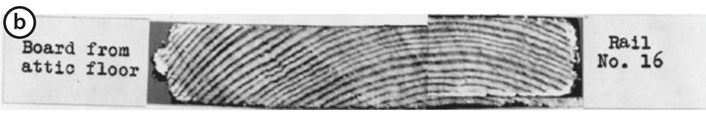
Dendrochronology is the science that studies annual tree rings in the secondary growth of gymnosperms and eudicots in order to reveal past climate and environmental changes year by year. When there are good years with plentiful water and a favorable, long growing season, the annular growth rings in the secondary xylem will be wider. However, if the conditions are not favorable, the width of the growth rings will be considerably narrower. Thus, the cross-sectional view of the secondary xylem can be used to trace the overall environmental conditions over the life of a tree, regardless of whether it is a gymnosperm or a woody eudicot. In most cases, it is not necessary to cut an entire cross-section of a trunk in order to count and examine the growth rings. Instead, an increment borer can be used to drill into the living tree to obtain the same information, but without killing the tree. Of course, the missing rings, false rings, and discontinuous rings discussed in ► Sect. 15.3 will complicate such studies.

Data from growth rings coupled with studies of entrapped carbon dioxide specimens from ice sheets and the bleaching of corals have shown that temperatures in the tropical oceans, and in the air above the northern hemisphere, began to rise in the 1830s, much earlier than first thought (Jacoby and D'Arrigo 1997).

Using dendrochronology, which was first employed in the early twentieth century by A. E. Douglass, a process termed archeological dating has developed; that is a precise means of using the information to determine archeological conditions over the course of long periods of time (e.g., approximately 10,000 years being the longest dating time recorded). The tree growth rings can also be used in conjunction with radiocarbon (^{14}C) dating due to the natural carbon content present in the rings. Since most trees only live for 100–200 years, the longer time spans of information are obtained by visually matching rings from living trees with older samples of preserved specimens by examining the parts that show overlapping growth ring patterns (◘ Fig. 15.11a). In a similar manner, those can also be matched with even older ones, and so on as far back as ancient



■ **Fig. 15.11** **a** Increment cores taken from three Douglas fir (*Pseudotsuga menziesii*) trees growing at El Malpais National Monument, New Mexico, USA. The "18" indicates the location of the year 1800, marked by three dots in all three cores. The vertical lines connect corresponding narrow and wide rings, demonstrating cross dating between the trees. The thickest ring on all three cores (indicated with an asterisk) is the year 1816, the "Year Without a Summer." The Mount Tambora volcano in Indonesia erupted on April 10, 1815, causing widespread global cooling. In the USA Southwest, cooler atmospheric temperatures led to increased soil moisture and increased growth in the year after the eruption. Scale bar = 0.5 cm. (Image courtesy of Henri D. Grissino-Mayer, The University of Tennessee, Knoxville)



■ **Fig. 15.11** **b** Wood cross-section from attic floor of presumed Lindbergh kidnapper on the left and the matching wood from the home-made ladder rail used by the kidnapper on the right (Forest History Society, Durham, NC)

specimens of the same species can be obtained. Dendrochronology has been used to assign dates to buildings, ships, musical instruments, and artworks, in some cases verifying or refuting the authenticity of the piece.

The pattern of growth rings as seen in cross-sectional view can also be used in forensic investigations, perhaps the most famous of which was in the kidnapping and murder trial of the Charles Lindbergh baby in 1932. The suspected kidnapper used a home-made ladder to reach the upstairs bedroom window of the young child and left it at the site. A part of the ladder was not made from the same wood as the rest, and, when analyzed via matching tree rings, it was found to be from wood of the kidnapper's attic—ponderosa pine (*Pinus ponderosa*) (■ Fig. 15.11b). On that basis, and additional forensic analysis of the wood samples, the kidnapper was sentenced and later executed.

Box 15.2 Advances in Forensic Wood Identification

When plant material is confiscated and inspected for illegal trade, law enforcement officials use traditional anatomical, morphological, and/or fluorescent techniques to identify wood samples. However, distinguishing closely related species that may be endangered and banned from trade may be impossible to accomplish unless more sophisticated techniques are used, especially when the origin of the wood is unknown. This presents an important problem in some areas of the world, particularly in the Amazon, where 80% of the total harvest was estimated to be illegal.

Direct Analysis in Real Time Time-of-Flight Mass Spectrometry (DART-TOFMS) may provide a means to identify unknown wood samples in the field by ionizing samples using a DART ion source followed by mass spectrometry using the TOFMS. Unknown specimens can be identified to species by comparing the DART-TOFMS output with specific chemical signatures of reference samples. In the Amazon and other areas, wood products from protected trees can easily be confused with trees that are unprotected due to similarity in appearance. To test this technique, Lancaster and Espinoza (2012) identified chemical signatures of 13 tree species, tested unknowns using DART-TOFMS, and analyzed differences in species using linear discriminant analysis. The techniques were highly reproducible for correctly identifying species 91 to 100% of the time. Thus, DART-TOFMS may provide a means of rapidly identifying protected plants to solve problems in forensic botany.

Reference: Lancaster and Espinoza (2012)

15.12 Chapter Review

Concept Review

15.1 *Wood has significant worldwide economic value.* Wood is extremely versatile and the most heavily used plant product in the world. It is used in energy production, building construction, furniture, plywood, flooring, paper, and many other applications.

15.2 *A variety of products can be made from wood fibers and wood extracts.* Wood can be digested to produce wood fibers. The resulting fibers are used in many different types of paper and in food products as thickeners and extenders or to affect the food texture, clumping, and consistency. The extraction of chemicals from wood yields tars, resins, pharmaceuticals, dyes, syrup, and spices.

15.3 *Wood development and composition show annual cycles.* The growth of wood reflects the annual cycle of growing seasons, especially in temperate climatic zones. Each season of growth leaves behind a layer of xylem to the interior and generates a new layer of phloem to the exterior. Wood "grain" is a result of seasonal variation in the size of vessels and tracheids. Dendrochronology is the science of using tree rings to reconstruction climate history.

15.4 *Wood varies in its architecture and composition.* Wood is best studied by examination of cross, radial, and tangential sections. Woody eudicots produce "hardwood," while conifers produce "softwood." Waste products and tannins are deposited in the older, inner layers, resulting in "heartwood." Transpiration takes place in the younger, outer layers called "sapwood."

15.5 *Conifer wood has tracheids, parenchyma, and rays.* Tracheids serve for water conduction and support in gymnosperms. They are long and narrow and tapered at the ends, tapered to the extent that they lack end walls. Tracheids have numerous pits in the side walls through which water moves from one tracheid to the next. Resin canals secrete and store rot- and insect-deterring resins; they may be axial or radial. Gymnosperm xylem rays are composed of a mixture of tracheids and parenchyma.

15.6 *Eudicot wood is characterized by vessel elements, tracheids, parenchyma, and rays.* Woody eudicots contain vessel elements, which may also be called "pores." The size and arrangement of pores is both genetically and environmentally control and very useful in taxonomy and in determining the structural, mechanical, and functional properties of the wood. Pore arrangement may be ring-porous, diffuse-porous, semi-porous, or dendritic. Vessels may be grouped in recognizable patterns or scattered randomly throughout the wood, depending on the species. Likewise, xylem parenchyma distribution shows species-specific distribution patterns. Xylem rays are composed of tracheids and parenchyma and serve to transport water and nutrients to the periderm.

15.7 *Reaction woods develop in response to gravity.* Reaction wood develops in response to sustained gravitational pull. Gymnosperms develop compression wood on the lower side of a horizontal trunk branch, while angiosperms develop tension wood on the upper side. The S2 layer of the secondary cell wall is the main area to see thickening in reaction woods.

15.8 *Tyloses and crystals may be found in some woods.* Tyloses occur when the protoplasm of a paratracheal parenchyma cell extends through a pit into the lumen of an adjacent vessel element. They form naturally in some species and in response to infection in other species. Calcium oxalate, Mg oxalate, or SiO_2 crystals may be found in the vessels or parenchyma of some species.

15.9 *Monocot "wood" does not come from true secondary growth.* Wood is generated by the vascular cambium during secondary growth. Even though monocots lack true secondary growth, some such as palm trees and bamboo develop thick layers of fibers around each of the dozens or hundreds of individual vascular bundles scattered throughout the stem. The end result is a structurally strong and tough stem that can be used in many of the same ways that true eudicot wood is used.

15.10 *Wood macerations are useful for species identification, product identification, and forensics.* Maceration is the process of dissolving out the lignin that holds together the tracheids, fibers, and vessel elements of wood. This is a simple and easy way to study the individual cells of the wood and is valuable in species identification and in determining the composition of paper products.

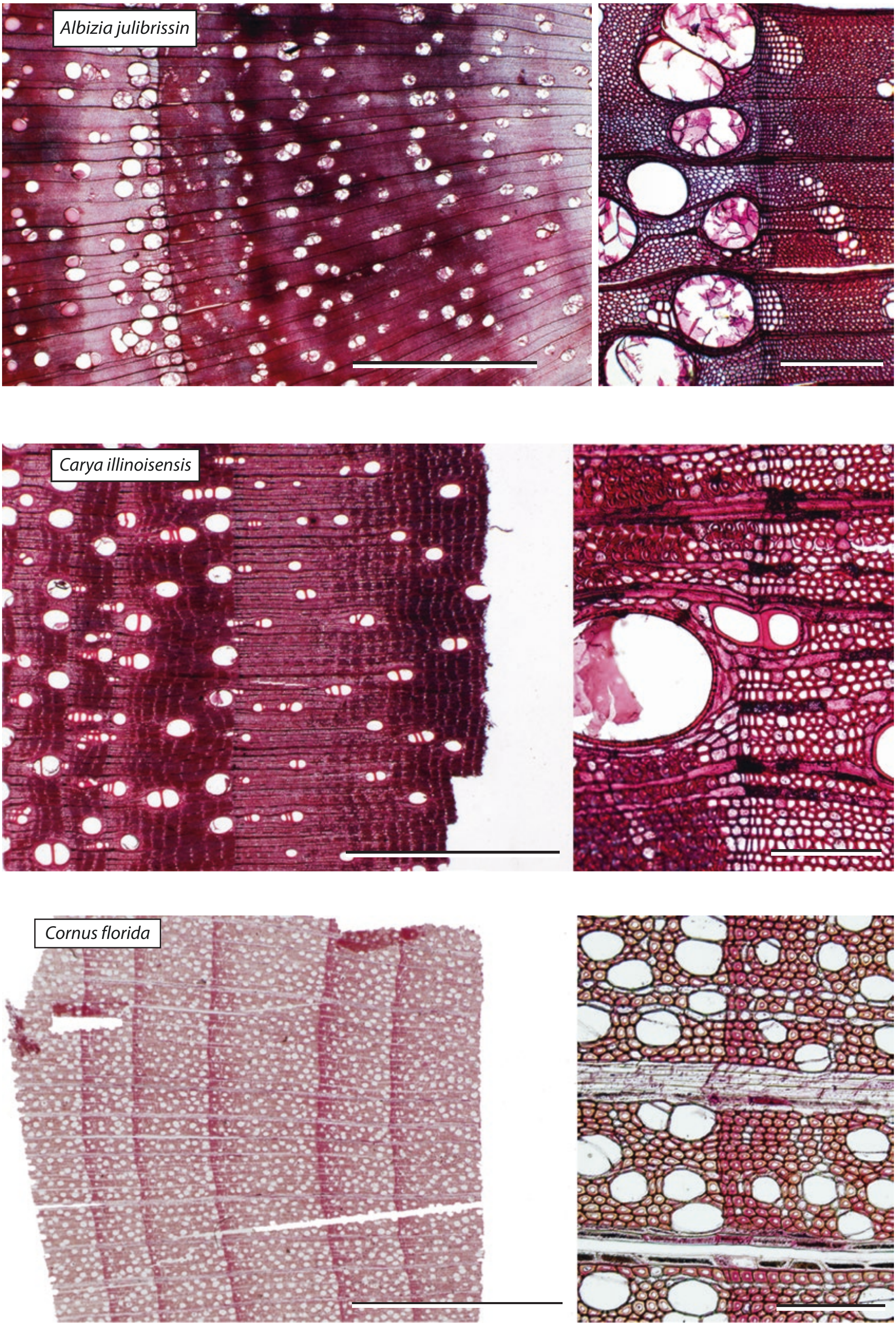
15.11 *The study of tree rings is important in archeology, climatology, and forensics.* Because growing conditions have a large effect on tree ring thickness, morphology, and composition, and tree rings accumulate on an annual basis, every tree contains a historical environmental record. The science of dendrochronology has been able to reconstruct thousands of years of continuous climatological record. It can also be used to date in buildings, ships, musical instruments, and artworks.

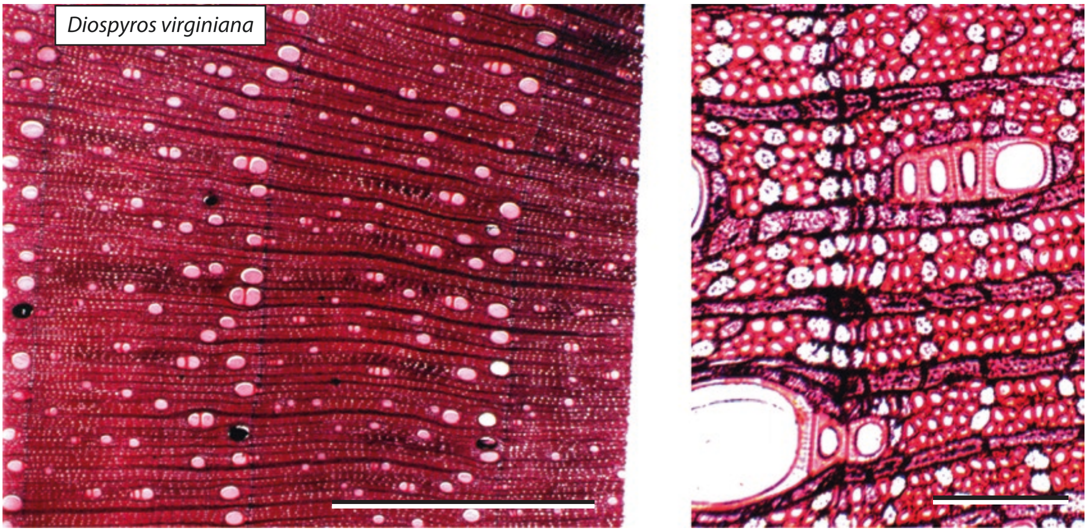
■ Concept Connections

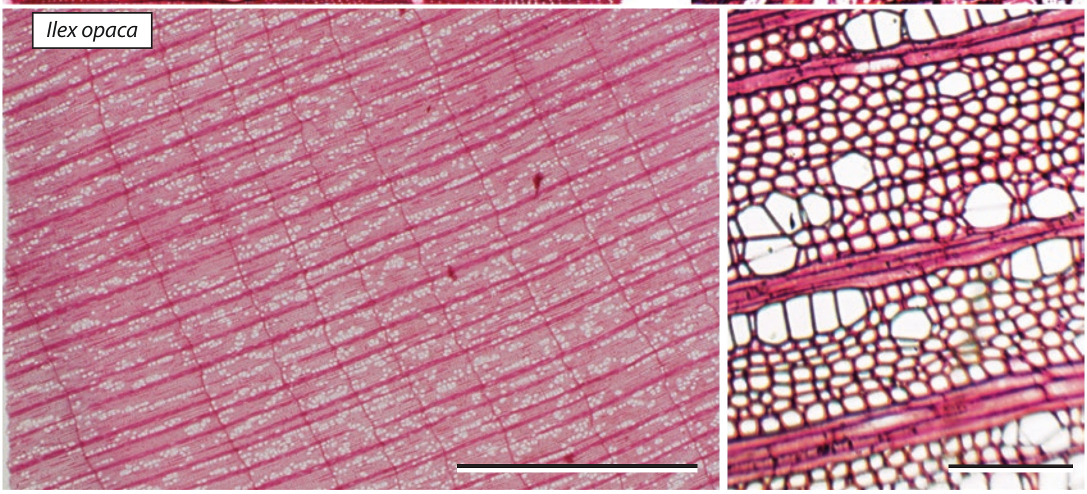
1. Match the description of the wood anatomy given in the table to the proper image that follows beneath (Descriptions from The Wood Database – ► www.wood-database.com)

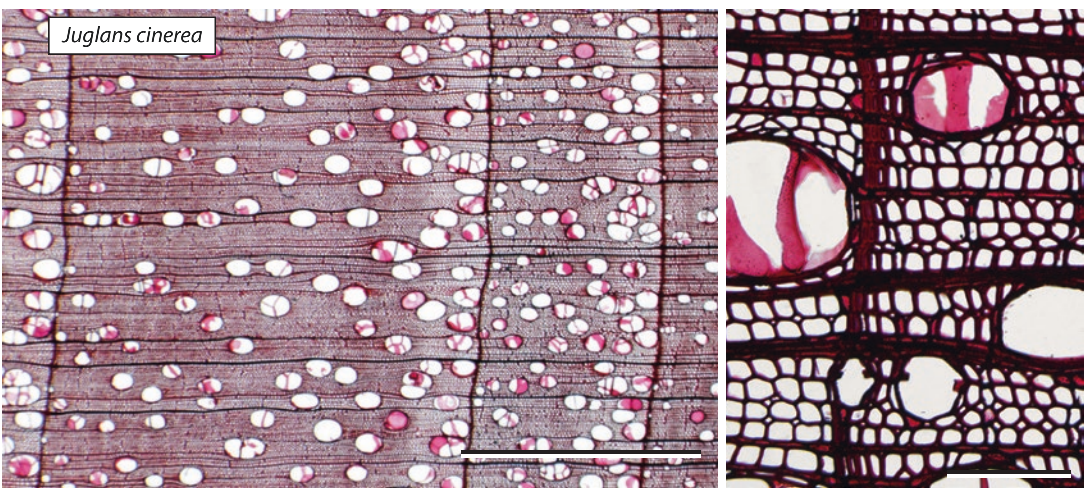
	Description
a	Ring-porous; large earlywood pores three to six rows wide, small latewood pores solitary and radial multiples of two to four; tyloses common; growth rings distinct; rays visible without lens; parenchyma around latewood pores vasicentric, aliform (winged), and confluent
b	Ring-porous; two to four rows of large, exclusively solitary earlywood pores, numerous small latewood pores in radial arrangement; tyloses absent; growth rings distinct; rays large and visible without lens; apotracheal parenchyma diffuse in aggregates (short lines between rays)
c	Ring-porous to semi-ring-porous; large to very large earlywood pores in a single intermittent row, medium to small latewood pores solitary and radial multiples of two to three, few; tyloses common; parenchyma reticulate (bands absent from earlywood row in true hickory group, but present in pecan hickory group); narrow rays, close spacing

	Description
d	Semi-ring-porous; medium to large earlywood pores sometimes form broken rows, latewood pores medium to small; solitary and radial multiples of two to three; growth rings usually distinct; rays not visible without lens; parenchyma diffuse in aggregates, vasicentric, and banded (reticulate and marginal).
e	Semi-ring-porous; medium to large earlywood pores gradually decreasing to small latewood pores; solitary and radial multiples of two to three; tyloses occasionally to abundantly present; growth rings distinct; rays barely visible without lens; parenchyma banded (marginal); apotracheal parenchyma diffuse in aggregates (sometimes very faint and barely visible even with lens)
f	Diffuse-porous or semi-ring-porous; small to medium pores predominantly in radial multiples of two to four, commonly arranged in radial rows, moderately numerous to numerous; growth rings may be distinct due to an intermittent row of earlywood pores; rays in variable sizes from narrow to very wide, normal to fairly close spacing; parenchyma not typically visible with lens
g	Diffuse-porous; small to very small pores tending to occur in increased frequency in earlywood zone; exclusively solitary; growth rings distinct; rays usually not visible without lens; parenchyma not typically visible with lens
h	Diffuse-porous; solitary and radial multiples; large to very large pores in no specific arrangement, very few; tyloses abundant; parenchyma vasicentric, lozenge, confluent, and marginal; narrow to medium rays, spacing normal
i	Diffuse-porous (growth rings generally distinct due to gradually decreasing pore density in latewood); small to medium pores in no specific arrangement, moderately numerous to numerous; exclusively solitary; tyloses occasionally present; parenchyma not visible; medium to wide rays, spacing normal
j	Diffuse-porous; small to medium pores in no specific arrangement, numerous; solitary and radial multiples of two to three; growth rings distinct; narrow rays visible without lens, normal spacing; parenchyma marginal
All scale bars = 1 mm for left panels and 100 μm for right panels	

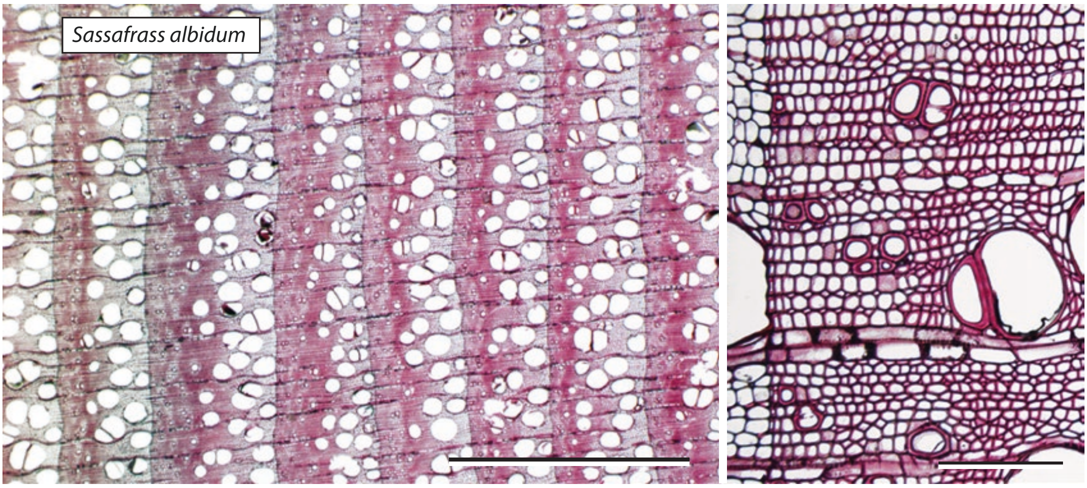

Albizia julibrissin
Carya illinoisensis
Cornus florida


Diospyros virginiana


Ilex opaca


Juglans cinerea


Magnolia virginiana
Malus pumila
Quercus rubra



Concept Assessment

2. Summerwood is
   a. the same as heartwood.
   b. found to the outside of each annular ring of xylem.
   c. found to the inside of each annular ring of xylem.
   d. formed throughout the growing season.
   e. only found in monocots.

3. Monocot "wood" is the result of
   a. secondary growth.
   b. heartwood.
   c. dedifferentiation of phloem fibers.
   d. massive fiber development of fiber caps.
   e. conversion of fibers to fiber tracheids.

4. All gymnosperms lack vessel elements
   a. true.
   b. false.

5. Paratracheal parenchyma may be found
   a. at the interface of spring and summerwood.
   b. around wood rays.
   c. in phloem.
   d. in conifers.
   e. around vessels.

6. Heterocellular rays contain
   a. vessels and tracheids.
   b. fibers and vessels.
   c. fibers and tracheids.
   d. vessels and parenchyma.
   e. tracheids and parenchyma.

7. An example of a diffuse-porous wood would be
   a. oak.
   b. sugar maple.
   c. elm.
   d. osage orange.
   e. ash.

8. Wood pulp may contain
   a. vessel members.
   b. libriform fibers.
   c. tracheids.
   d. fiber tracheids.
   e. all of the above.

9. Gymnosperm resin is produced by
   a. the vascular cambium.
   b. epithelial cells.
   c. tracheids.
   d. vessel elements.
   e. fibers.

10. Trees from tropical climates show less "figure" than trees from temperate climates because
    a. most tropical trees are monocots.
    b. temperate trees grow slower than tropical trees.
    c. the tropics have less seasonal variation in growth conditions.
    d. tropical trees grow faster than temperate trees.
    e. figure is a result of variations in phloem development.

11. Most transpiration is via the
    a. heartwood.
    b. summerwood.
    c. sapwood.
    d. reaction wood.
    e. hardwood.

Concept Applications

12. Imagine you have the ability to genetically engineer poplar trees (*Populus tremuloides*) to express any anatomical character you wish. Which anatomical traits would you select if you were to engineer poplar for the boat building industry, the furniture industry, or the paper industry?

13. Wood has been called the ultimate recycling material, but cutting down trees kills them and many trees are threatened or endangered. Use the Internet to research "sustainable lumber," and write a minute paper on those efforts (a minute paper is a brief summary of a specific topic).

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