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CHAPTER 2

Structure of Wood

2.1 Introduction

The identification of wood species presupposes a basic knowledge of wood anatomy. In the following review on the structure of wood, main attention has been paid to the features which are of interest to the fiber microscopist, that is, to the kinds of wood cells, and the pits which are the most important diagnostic feature in the identification of wood species in pulp. The Structure of Wood is largely based on a paper published by the author in 1977.

2.2 Planes of Wood

In the description of wood structure, three reference planes are used: the cross-section or transverse surface, the radial surface, and the tangential surface. The following parts can be distinguished in the transverse surface of a stem (Figs. 2.1 and 2.2):

- In the center of the stem is the *pith*, which usually differs from the surroundings by its darker color.
- The pith is surrounded by the xylem, the inner part of which is heartwood, and the outer part sapwood. In many trees the heartwood is darker in color than the sapwood.
- Around the sapwood is a layer of living cells, the *cambium*.
- Outside the cambium is the bark, which is composed of the living inner bark (phloem) and the dead outer bark (rhytidome).

The transverse surface also shows concentric growth rings and rays; vertical resin canals are present in many softwoods.

Wood is composed of elongated cells which are oriented either axially or radially. Most cells are axial. Only the cells of rays which transport liquids in the transverse direction are radial.

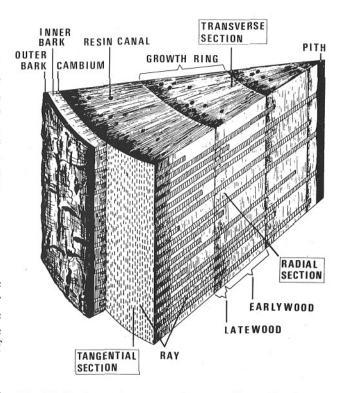


Fig. 2.1. Sections of a young pine stem. (According to Strasburger)

2.3 Formation of Wood

Wood tissue is formed through the division of the cells. Longitudinal growth proceeds at the tips of the stem, branches, and roots. Radial growth takes place in the vascular cambium.

Cambium is between the xylem and the bark, and is composed of a one-cell-wide layer of initials (Fig. 2.2). It surrounds the xylem of the stem, branches, and roots as a uniform mantle. At the beginning of the growing season, cambium cells are divided, producing new wood cells on the inside (secondary xylem) and new bark cells on the outside (secondary phloem). Xylem cells are formed more often than bark cells. The daughter cells are divided once or more before they are differentiated to the new

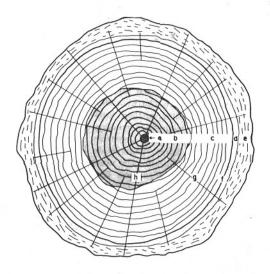


Fig. 2.2. Transverse section of a mature pine stem.

 $a = pith & e = outer bark \\ b = heartwood & f = cambium \\ c = sapwood & g = secondary ray \\ d = inner bark & h = primary ray$

xylem or bark cells. The one-cell-wide layer of cambium and the layers of the dividing daughter cells are called the cambial zone (Fig. 2.3). In temperate climates, cambial activity is restricted to spring and summer months.

In the temperate zones, the seasonal growth is reflected in the formation of growth rings or growth increments (Fig. 2.1) that are produced one per year, and are referred to as annual rings. They are visible in the cross-section of

the stem as concentric rings. The inner part of the ring is formed as a result of rapid growth in spring, it is of lower-density wood, and is called *earlywood* or springwood. The outer part, which is formed later in the growing season, is denser wood, and is called *latewood* or summerwood. Growth rings are clearly visible in softwoods (Figs. 2.4 and 2.5), and in ring-porous hardwoods, which produce larger vessels in spring than in summer (Fig. 2.7). The total age of the tree can be calculated from the number of the annual rings at the base near the ground.

The boundary between growth rings reflects the period of dormancy, and it is always sharp. The transition from earlywood to latewood can be abrupt or gradual according to species. It is abrupt, for instance, in larch (Fig. 2.5) and in the southern pines of North America (Pinus taeda, etc.), gradual in spruce, Scots pine (Fig. 2.4), and sugar pine. It is indistinct in birch (Fig. 2.6), but well defined in ring-porous hardwoods, as in oak (Fig. 2.7).

In the *tropical regions*, regular annual rings are lacking as a rule. However, tropical woods may exhibit growth rings, which reflect the alteration of wet and dry seasons. Several growth rings may occur during one year. In regions with seasonality in rainfall or flooding, tropical trees may form annual rings.

The width of growth rings varies greatly, depending on the species, age of tree, and growth conditions. Certain trees, such as aspen and

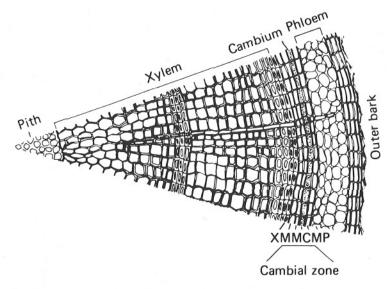


Fig. 2.3. Cross-section of a young pine stem. Cambial zone consists of four tiers of cells: cambial initals (C), xylem and phloem mother cells (M), mature xylem (X) and phloem (P) cells. (Brown 1970)

Structure of Wood

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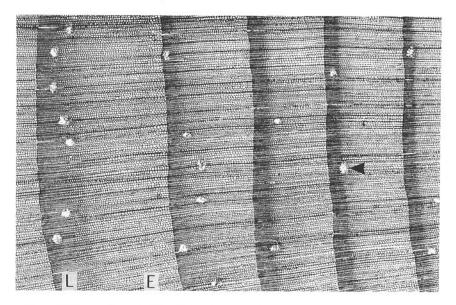


Fig. 2.4. Cross-section of *Pinus sylvestris*. Transition from earlywood (E) to latewood (L) is gradual. Arrowhead indicates a vertical resin canal. 15x

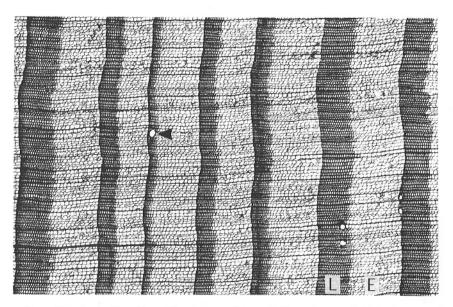


Fig. 2.5. Cross-section of *Larix decidua*. Transition from earlywood (E) to latewood (L) is abrupt. The vertical resin canals (arrowhead) are smaller and fewer than those of pine (Fig. 2.4). 15x

some pines (e.g., *Pinus radiata*), are fast-growing and develop wide rings, while slow-growing trees, such as maple and juniper, develop narrow rings under the same conditions. The rings near the pith (juvenile wood) are in general the widest, whereas the rings of the sapwood, which are formed at the older age of the tree, are the most narrow ones.

The percentage of latewood varies for reasons similar to those governing the width of

growth rings. In Scandinavia the percentage of latewood for pine (*Pinus sylvestris*) is about 25% (15–50%) and for spruce (*Picea abies*) about 15% (10–40%) (Jalava 1952 p. 40).

Trees grow continuously, although the growth becomes slower in the course of time. Giant sequoias on the west coast of North America can reach an age of 4000 years, a height of 100 m, and a diameter of 12 m at the base.

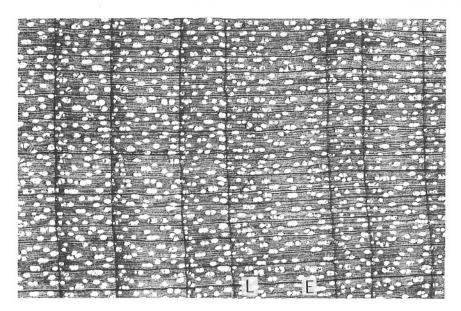


Fig. 2.6. Cross-section of *Betula verrucosa* (diffuse-porous wood). Transition from earlywood (E) to latewood (L) is indistinct. The vessels (white dots) are fairly uniform in size throughout the growth ring. 15x

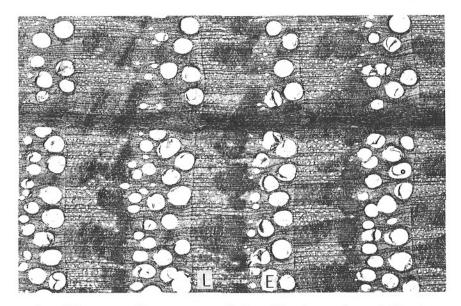


Fig. 2.7. Cross-section of *Quercus* sp. (ring-porous wood). Transition from earlywood (E) to latewood (L) is well defined. The earlywood vessels (white holes) are much larger than those of latewood (white dots). 15x

2.4 Wood Cells

All wood cells have specific functions to perform. On the basis of functions, the cells can be divided into three groups: conducting cells, supporting cells, and storage cells.

Conducting and supporting cells are elongated, axial cells. In hardwoods, the conducting cells consist of vessel elements, and the

supporting cells consist of fibers. In softwoods, tracheids perform both these functions. Conducting and supporting cells are dead cells whose cell cavities are filled with water and air.

Storage cells consist of short, thin-walled parenchyma cells with living cell contents. They are concerned with storage and distribution of food, and remain living as long as they belong to sapwood.

2.5 Pits

2.5.1 Simple and Bordered Pits

A pit is a recess in the cell wall through which liquids pass laterally from one cell to the next. All cells of wood are in contact with neighboring cells through pits.

Pits have two essential parts, the pit *cavity* and the pit *membrane* (Fig. 2.8A). The cavity is open internally to the lumen of the cell, and it is closed by the pit membrane. Pits are of many shapes and sizes. They are, in general, reduced to two basic types on the basis of the shape of the cavity, the simple pits and the bordered pits.

- 1. In the *simple pit*, the cavity is nearly straight-walled, or perhaps only gradually widens or narrows toward the cell lumen (Fig. 2.8A). The lumen end of the cavity is known as the pit *aperture*.
- 2. In the *bordered pit*, the cavity constricts toward the lumen, forming a dome-shaped chamber, which is overarched by the pit *border* (Fig. 2.8B).

Bordered pits are elaborate and variable in structure. If the pit border is thin, as is the case in the thin-walled cells, the pit opening is known as the aperture (Fig. 2.8B). If the border is thick, an elongated, often widening canal is

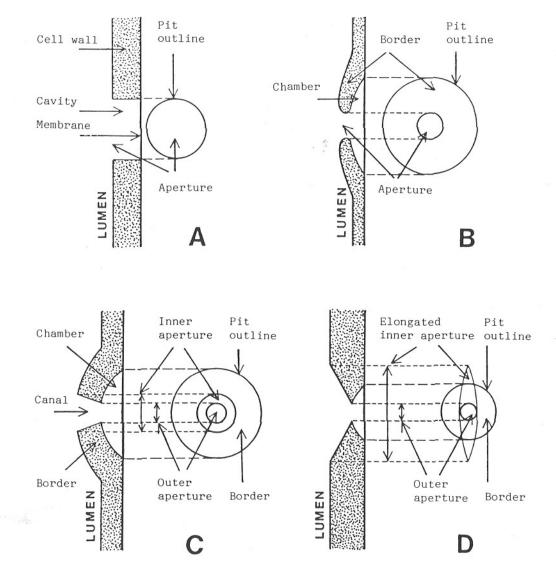


Fig. 2.8. Diagrammatic pictures of simple and bordered pits in sectional (left) and face (right) views. A Simple pit. B Bordered pit with thin border. C Bordered pit with

thick border and elongated pit canal. **D** Bordered pit with thick border showing a narrow, elongated inner aperture and a small, circular outer aperture

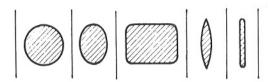


Fig. 2.9. Different shapes of pit apertures in face view: circular, oval, angular, lenticular, and slitlike. (Wagenführ 1980)

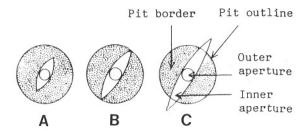


Fig. 2.10. Bordered pit with lenticular inner aperture in face view. The inner aperture is inside the pit outline in A (included aperture), touches the outline in B, and extends beyond the outline in C (extended aperture)

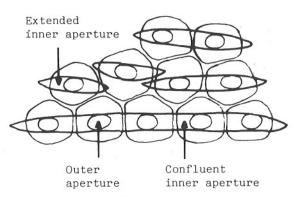


Fig. 2.11. Pits with extended and confluent inner apertures in face view. (Drawn from the micrograph in Fig. 2.16I)

formed between the chamber and the lumen (Fig. 2.8C). In this case, two apertures are distinguished: the chamber end of the canal is known as the outer aperture, and the lumen end as the inner aperture. The pit apertures may be circular, oval, angular, lenticular, or slitlike in face view (Fig. 2.9). The inner and the outer apertures are commonly unlike in size and shape: the inner is rather large lenticular or slitlike, the outer small and circular (Esau 1953 p. 43, Wagenführ 1980 p. 138). The outer aperture is rarely visible in the pits of pulp fibers.

The elongated pit canal may appear in a variety of forms. For instance, if the inner aperture is narrow and elongated, and the outer aperture is small and circular, the canal has the shape of a flattened funnel (Fig. 2.8D) (Esau 1953 p. 44, Fahn 1982 p. 41). If this kind of pit is inspected in face view, the inner aperture may be included or extended. When the inner aperture is within the pit outline, it is said to be included (Fig. 2.10A); if it extends beyond the outline, then it is said to be extended (Fig. 2.10C) (Panshin and de Zeeuw 1980 pp. 110, 115). Pits with extended inner aperture may occur in both softwoods and hardwoods (Figs. 2.15G and 2.16I); in softwoods they occur most commonly in the piceoid pit type. In the extreme case, narrow elongated inner apertures of adjacent pits may be united to form grooves in the inner surface of the cell wall (Fig. 2.11). These are called confluent (or coalescent) inner apertures (confluent pitting). They are characteristic of birch, but can also be found in other hardwoods (Fig. 2.16H, I) (Barefoot and Hankins 1982 p. 83, Carlquist 1988 p. 93).

The type of pitting is characteristic of various cell types. Simple pits occur in living parenchyma cells, but may also occur in the vessel elements of hardwoods. Bordered pits are confined to dead water-conducting and supporting cells, that is, to tracheids and ray tracheids in softwoods, and to vessel elements and fibers in hardwoods.

2.5.2 Pit Pairs

In wood the pits of adjacent cells are usually paired, thereby forming three types of pit pairs (Fig. 2.12):

- 1. The *simple pit pair* is composed of two simple pits. It occurs between parenchyma cells, in hardwoods also between vessel elements and parenchyma cells.
- 2. The bordered pit pair is composed of two bordered pits. It occurs between tracheids in softwoods, and between vessel elements in hardwoods.
- 3. The half-bordered pit pair is composed of a bordered pit and a simple pit. It is found between a tracheid and a parenchyma cell in softwoods, and between a vessel element and a parenchyma cell in hardwoods. The simple pit is in the parenchyma cell wall.

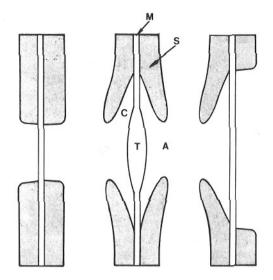


Fig. 2.12. Simple (left), bordered (middle), and half-bordered (right) pit pairs. A = aperture, C = chamber, M = middle lamella-primary wall, S = secondary wall, T = torus. (Siau 1984)

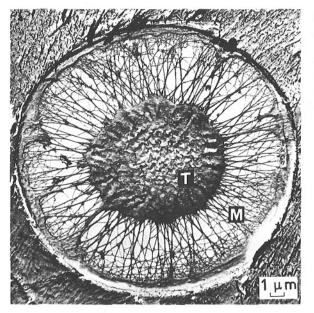


Fig. 2.13. Membrane of a bordered pit. The torus (T) is surrounded by the margo (M) through which liquids pass from one cell into the next. *Tsuga canadensis*. (Comstock and Côté 1968)

In the pit pairs, the pit membrane is common to both pits (Fig. 2.12). It consists of a middle lamella which is sandwiched between two primary walls. In the bordered pit pairs of most softwoods, the membrane has a disk-

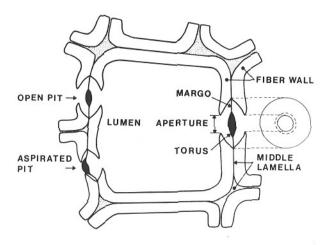


Fig. 2.14. Cross-section of a tracheid showing open and aspirated bordered pits. (Modified from Knuchel 1954)

shaped central portion, called the *torus*, which is somewhat larger in diameter than the aperture. The membrane around the torus, the *margo*, is porous (Fig. 2.13). When the membrane is in the middle of the pit pair, water passes through the margo from one tracheid to another (Fig. 2.14). When the torus is pressed against one of the apertures (aspirated pit), the passage of water is prevented. This occurs when the sapwood is transformed into heartwood, or when wood dries. There is no torus in the bordered pit pairs of hardwoods, nor in simple or half-bordered pit pairs.

Pit membranes are generally destroyed in pulping. However, some intact membranes are always present in unbleached pulp fibers. In unbleached softwood sulfite fibers the torus can be seen when stained with alkaline stains (eye formation).

2.5.3 Pits in Pulp Cells

In pulping, wood cells are separated from one another, and hence the pits appear as single pits in pulp fibers and other pulp cells.

Simple pits show a single ring (Fig. 2.8A), which may be circular, oval, angular, or elongated in shape (Figs. 2.15A–C and 2.16A, B, F).

Bordered pits show two concentric rings, the inner one arising from the pit aperture, and the outer from the outline of the chamber (Fig. 2.8B). The rings are visible in the bordered pits of softwood tracheids (Fig. 2.15E). A third incomplete ring, which is sometimes

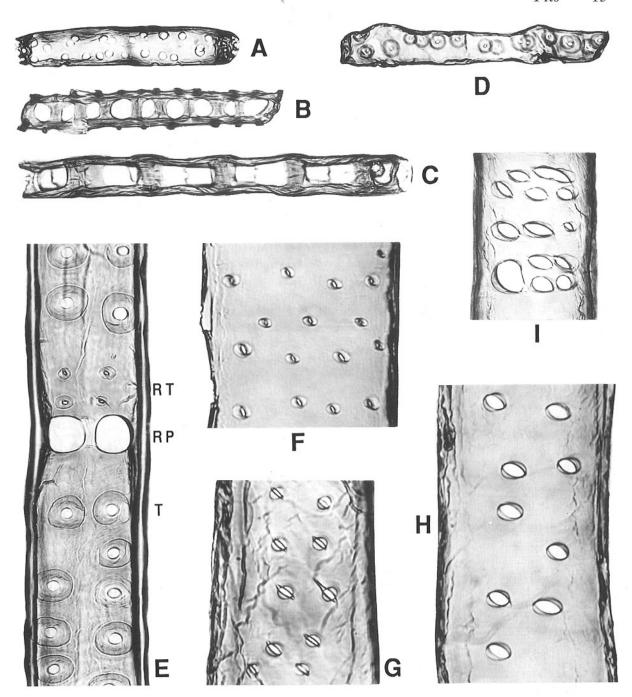


Fig. 2.15. Different types of pits in softwood cells.

- A Small simple pits in the ray parenchyma cell of Larix decidua (cell end walls are nodular). 450x
- B, C Simple pits in the ray parenchyma cells of *Pinus strobus* (B latewood) and *Pinus sylvestris* (C earlywood). 450x
- D Small bordered pits in the ray tracheid of *Pinus strobus*. 450x
- E Large (T) and small (RT) bordered pits, and windowlike pits (RP) in the tracheid of *Pinus monticola* (T = intertracheid pits, RT = pits to ray tracheids, RP = pits to ray parenchyma). 450x
- F Pits with narrow apertures and broad borders in the tracheid of *Larix occidentalis* (piceoid pits to ray parenchyma). 750x
- G Pits with extended apertures in the tracheid of *Tsuga heterophylla* (cupressoid to piceoid pits leading to ray parenchyma). 750x
- H Pits with wide apertures and narrow borders in the tracheid of *Cryptomeria japonica* (taxodioid pits to ray parenchyma). 750x
- I Pits of different size and shape in the tracheid of *Pinus echinata* (pinoid pits to ray parenchyma). 450x

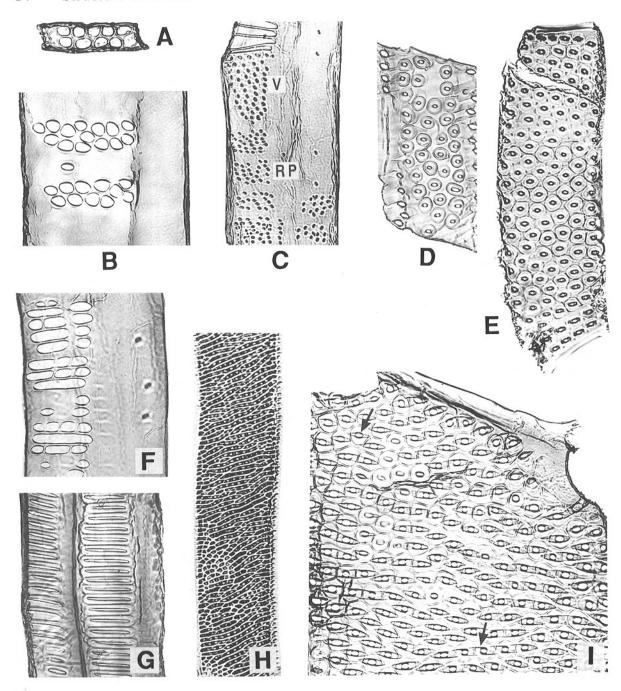


Fig. 2.16. Different types of pits in hardwood cells. 400x

- A Simple pits in the ray parenchyma cell of *Populus* tremula
- **B** Oval, nearly simple pits in the vessel element of *Populus tremuloides* (pits to ray parenchyma)
- C Small bordered pits in the vessel element of *Alnus glutinosa*. V = intervessel pits, RP = pits to ray parenchyma
- D, E Bordered pits with oval apertures and round-oval
 (D) to hexagonal (E) outlines in the vessel elements of *Ulmus americana* (intervessel pits)
- F Oval to elongated, nearly simple pits in the vessel
- element of Liriodendron tulipifera (pits to ray parenchyma)
- G Linear bordered pits in the vessel element of Magnolia acuminata (intervessel pits)
- H Very small bordered pits with confluent inner apertures in the vessel element of *Betula verrucosa*. Small, white dots are outer apertures (intervessel pits)
- I Bordered pits with extended (upper arrow) or confluent (lower arrow) inner apertures in the vessel element of *Musanga smithii*. Outer apertures are small-oval (intervessel pits)

visible in unbleached pulp fibers, arises from the boundary of the torus (Fig. 2.14). Bordered pits may exhibit considerable variation in size and shape (Figs. 2.15D–I and 2.16C–E, G–I).

The diagnostic features of softwood pits are discussed in Chapters 3.2.2 and 3.2.3, those of hardwoods in Chapter 3.3.5.

2.6 Softwood Cells

2.6.1 Cell Types

Softwoods are simple and regular in their structure. Their wood substance is composed mainly of two kinds of cells: longitudinal tracheids and ray parenchyma. Approximately 90–95% of the wood volume is occupied by the longitudinal tracheids (Table 2.1). These two types of cells are present in all softwoods. Besides these, longitudinal and epithelial parenchyma, and short tracheids (ray tracheids, strand tracheids) may be present according to species. The types of softwood cells are:

Ce	ll type	Function
	Longitudinal tracheids Parenchyma	Support, conduction
	- Ray parenchyma	Storage
	 Longitudinal parenchyma 	Storage
	 Epithelial parenchyma 	Excretion of resin
3.	Short tracheids	
	 Ray tracheids 	Conduction
	 Strand tracheids 	Conduction

2.6.2 Longitudinal Tracheids

Longitudinal (or vertical) tracheids, commonly called tracheids or fibers, are long, narrow cells with closed ends and bordered pits (Fig. 2.17). The average length of tracheids varies from about 2 to 6 mm (Table 2.2). Among the papermaking softwoods, average lengths over 6 mm occur only in *Taxodium*, *Sequoia*, and *Araucaria*. The tangential width of tracheids is about 1/100 of the length. The length and width of tracheids vary within and between species, and within individual stems (Ilvessalo-Pfäffli 1977 p. 68, Panshin and de Zeeuw 1980 p. 251).

Table 2.1. Proportions of cells in softwoods

Species	Percent of to		Reference		
	Tracheids		Longitudinal parenchyma	Resin canals	
Abies alba	90.4	9.6	Trace	· · ·	2
A. balsamea	94.3	5.7			1
Araucaria angustifolia	94.5	5.5	Trace		2
Larix decidua	91.2	8.8	0.9		2
L. laricina	89.0	10.0	0.9	0.1	1
Picea abies	95.3	4.7	1.4 ^a		2
P. mariana	94.8	5.0		0.2	1
P. sitchensis	92.5	7.2		0.3	1
Pinus lambertiana	94.0	5.5		0.5	1
P. palustris	90.8	8.4		0.8	1
P. ponderosa	93.0	6.7		0.3	1
P. radiata	88.6	11.2			2
P. strobus	94.0	5.3		0.7	1
P. sylvestris	93.1	5.5			2
Podocarpus salignus	89.0	9.0	2.0		2
Pseudotsuga menziesii	92.5	7.3		0.2	1
Sequoia sempervirens	91.2	7.8	1.0		1
Thuja plicata	93.1	6.9	Trace		1
Tsuga heterophylla	91.2	8.8			1

¹ Isenberg 1963.

a Including epithelial cells.

² Wagenführ and Scheiber 1974.

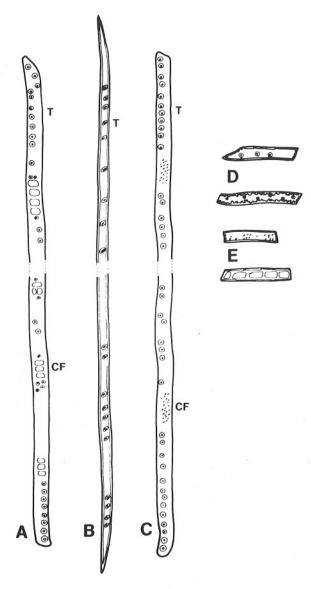


Fig. 2.17. Main types of softwood cells. T = intertracheid pits, CF = cross-field pits.

- A Earlywood tracheid of pine
- B Latewood tracheid of pine
- C Earlywood tracheid of spruce
- D Ray tracheids of spruce (above) and pine (below)
- E Ray parenchyma cells of spruce (above) and pine (below)

The main functions of the softwood tracheids are support of the tree (latewood tracheids) and conduction of water (earlywood tracheids). The tracheids of earlywood and latewood differ structurally from one another due to their different functions:

- The *earlywood tracheids* are thin-walled, squarish in cross-section, and have large cell

cavities (lumina) (Fig. 2.18). Fiber ends are wedge-shaped, blunt in radial (Fig. 2.17A), pointed in tangential view.

 The latewood tracheids are thick-walled, rectangular in cross-section, with narrow cell cavities (Fig. 2.18) and pointed ends (Fig. 2.17B).

In addition to the typical earlywood and latewood tracheids, there are smaller or larger amounts of *transitional forms* (Fig. 2.18).

In certain softwoods, such as *Pseudotsuga* and *Taxus*, the tracheids exhibit *spiral thickenings* (Fig. 2.19A, B). They are deposits on the inner face of the cell wall (Butterfield and Meylan 1980 p. 16, Panshin and de Zeeuw 1980 pp. 116, 137). Spiral thickenings are visible in pulp fibers, and are of great diagnostic value (Chap. 3.2.4).

Tracheids may show special structures, such as *trabeculae*. These are rodlike structures that occasionally traverse the lumina of several cells in a radial row. They are visible in pulp fibers (Fig. 2.19C), but are of no diagnostic value, as they may occur in any of the conifers. Trabeculae can also occur in hardwoods, where they may traverse many different cell types in a radial file, including vessel elements, longitudinal parenchyma cells, and fibers. There are also solitary trabeculae traversing the lumina of single cells (Core et al. 1979 p. 119, Butterfield and Meylan 1980 p. 20, Panshin and de Zeeuw 1980 p. 138).

Water conduction between tracheids, in both lateral and vertical directions, takes place through bordered pits, termed *intertracheid pits* (Fig. 2.17). Most of these are located on the radial walls, and are in 1–3 (4) vertical rows in earlywood tracheids. The pits of earlywood tracheids are large, circular, averaging about 200 pits per tracheid, that is about 100 pits per radial wall. Latewood tracheids show rather small, slitlike pits, 10 to 50 per tracheid (Trendelenburg and Mayer-Wegelin 1955 p. 132).

Liquids also move from the tracheids to the cells of rays. Each tracheid is in contact with one or many rays. The pits in the crossings of the tracheids and the ray cells are called *cross-field pits* (Fig. 2.17). Their size, shape, and arrangement vary according to species. Cross-field pitting is the most important feature in the identification of softwood species in pulp (Figs. 2.20 and 2.21) (Chap. 3.2.2).

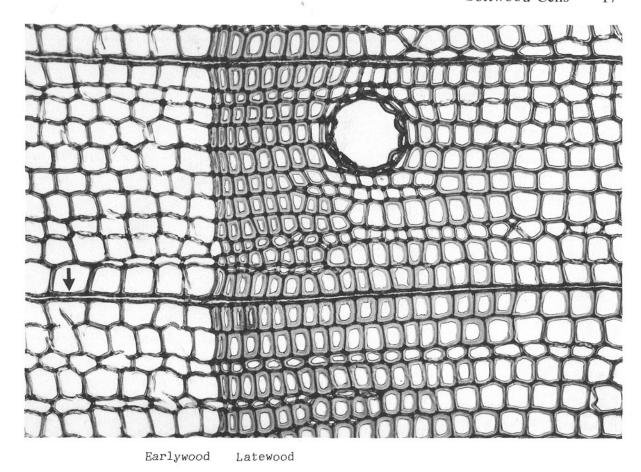


Fig. 2.18. Cross-section of *Picea abies* at earlywood-latewood boundary. Wide, thin-walled earlywood tracheids are gradually changed into narrow, thick-walled latewood tracheids. Vertical resin canal at the margin of the latewood. Arrow indicates a ray. 200x

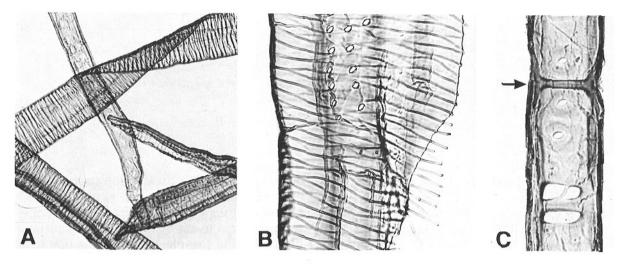


Fig. 2.19. A Spiral thickenings in the pulp fibers of *Pseudotsuga menziesii*, 150x. B Spiral thickenings as seen from the lumen side of a tracheid of *Pseudotsuga menziesii*, 450x. C Trabecula (arrow) in the tracheid of *Pinus nigra*, 270x

Table 2.2. Length and width of softwood tracheids

Species	Fiber length, mm		Fiber width, µm		Reference
	Average	Range	Average	Range	
Abies alba	3.7	1.6-5.7	38	18-58	1
A. balsamea	3.5	1.9-5.6	30-40		9
A. sibirica	3.4				10
Araucaria angustifolia	7.2	5.6-9.0	47	19-60	6
Chamaecyparis nootkatensis	3.2		27		11
Cryptomeria japonica	2.0 - 2.8		29-41		2
Larix decidua	3.5	1.4 - 6.2	38	24 - 52	1
L. occidentalis	5.0		40-50		9
Picea abies	3.4	1.1 - 6.0	31	21-40	1
P. glauca	3.5		25-30		9
P. sitchensis	5.6	3.6 - 7.3	35-45		9
Pinus banksiana	3.5	1.5-5.7	28-40		9
P. caribaea	4.6		41-52		11, 8
P. contorta	3.1		35-45		9
P. echinata	4.0		39		5
P. elliottii	4.0		43		5
P. halepensis	2.6	0.7 - 4.3	35	16-51	4
P. kesiya	2.5-3.7	0.7 1.5	50-62	10 01	7, 8
P. lambertiana	5.9	1.6 - 7.9	40-50		3
P. merkusii	3.0-4.0	1.0 7.5	44		8
P. monticola	2.9		35-45		9
P. nigra	3.2	0.5 - 4.9	39	16-60	4
P. palustris	4.0	0.5 4.5	41	10 00	4 5
P. patula	2.0-4.9		49-55		7, 8
P. pinaster	2.7	6	41		11
P. ponderosa	3.6	. \$	35-45		9
P. radiata	3.0		44		11
P. resinosa	3.4	1,2-5.2	30-40		9
P. rigida	3.5	1,2-3.2	32		5
P. strobus	3.0	1.6 - 5.0	25-35		9
P. sylvestris	3.1	1.8-4.5	35	14-46	1
P. taeda	4.0	1.0-4.5	45	14-40	5
Podocarpus salignus	2.4	1,4-3.2	23	14-31	6
Pseudotsuga menziesii	3.9	1.7 - 7.0	35-45	14-31	9
Sequoisuga menziesii Sequoia sempervirens	7.0	2.9-9.3	50-65		9
Sequoia sempervirens Taxodium distichum	6.2	2.9-9.3	45-60		9
Taxoatum aisticnum Thuja plicata	3.5	1.4-5.9	30-40		9
Tsuga canadensis	3.0	1.4-3.7	28-40		9
	4.2	1.8-6.0	30-40		9
T. heterophylla	4.2	1.8-6.0	30-40	Ç.	9

¹ Trendelenburg and Mayer-Wegelin 1955.

2.6.3 Strand Tracheids

Some softwoods, as for instance *Larix* and *Pseudotsuga*, have short longitudinal tracheids, called strand tracheids. They are rectangular cells, and are placed endwise in longitudinal strands (see Fig. 4-8 in Panshin

and de Zeeuw 1980). Strand tracheids are dead cells with bordered pits, and appear to function in conduction. They differ from the longitudinal parenchyma by their thicker walls and bordered pits (simple in longitudinal parenchyma) (Butterfield and Meylan 1980 p. 42, Panshin and de Zeeuw 1980 p. 141).

² Doat and Tissot 1988.

³ Isenberg 1963.

⁴ Sierra and Simon 1969.

⁵ Koch 1972.

⁶ Wagenführ and Scheiber 1974.

⁷ FAO 1980a.

⁸ FAO 1980b.

⁹ Isenberg 1980.

¹⁰ Laamanen 1981, unpublished results.

¹¹ Aitken et al. 1988.

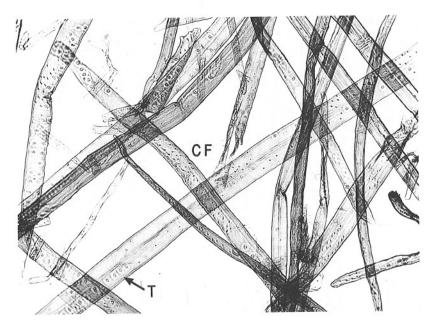


Fig. 2.20. Spruce (Picea abies) sulfite fibers showing intertracheid pits (T) and small, oval cross-field pits (CF). 100x

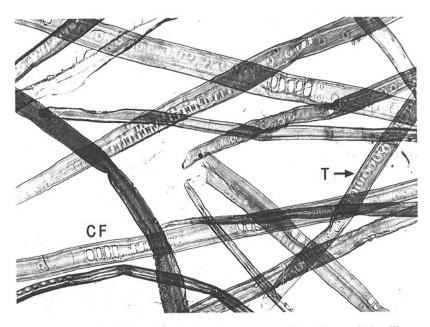


Fig. 2.21. Pine (*Pinus sylvestris*) sulfate fibers showing intertracheid pits (T) and large windowlike cross-field pits (CF). 100x

2.6.4 Longitudinal Parenchyma

Longitudinal parenchyma, also known as axial, strand, or wood parenchyma, is present in certain softwood genera. The cells occur in strands, which in some woods consist in part of strand tracheids. They have simple pits, and

are often conspicuous because of the presence of dark-colored inclusions (see Fig. 4-9 in Panshin and de Zeeuw 1980). Their end walls may appear nodular (Table 1 in TAPPI St. 1988 T 263). Longitudinal parenchyma is never abundant in softwoods (Table 2.1). It is absent from pines (Butterfield and Meylan 1980 p. 40).

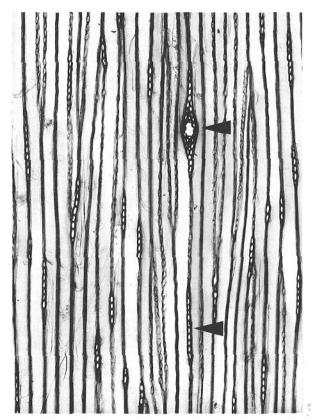


Fig. 2.22. Tangential section of *Picea abies* showing uniseriate rays (lower arrowhead) and a fusiform ray with a horizontal resin canal (upper arrowhead). 100x

2.6.5 Rays

Rays are ribbonlike structures of short cells extending radially in the stem (Figs. 2.1 and 2.2). Their function is to store and distribute horizontally the food of the tree. The first-formed rays extend from the pith to the outer bark (primary rays), the others extend from some later-formed annual ring to the corresponding ring in the bark (secondary rays). The rays of softwoods are mostly one cell wide in the tangential direction (uniseriate rays) (Fig. 2.22), and 1 to 20, sometimes up to 60 cells high (Esau 1953 p. 249, Butterfield and Meylan 1980 p. 38). Only rays that have a horizontal resin canal in their center are several cells wide (fusiform rays). Rays occupy about 5–11% of the softwood volume (Table 2.1).

The rays of softwoods are composed either of parenchyma cells alone or of parenchyma cells and ray tracheids. The ray tracheids may occur in one or several rows at the margins of the ray (Figs. 2.23 and 2.24) or they may be in

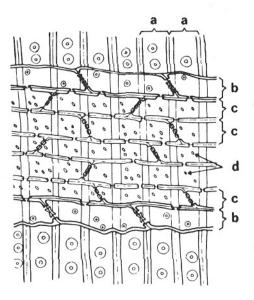


Fig. 2.23. Radial section of a ray of spruce (Picea abies).

- a = vertical tracheids with large bordered pits
- b = ray tracheids with small bordered pits and nondentate inner walls
- c = ray parenchyma cells
- d = small, oval pits between a ray parenchyma cell and a vertical tracheid

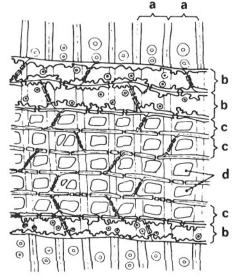


Fig. 2.24. Radial section of a ray of pine (Pinus sylvestris).

- a = vertical tracheids with large bordered pits
- b = ray tracheids with small bordered pits and dentate inner walls
- c = ray parenchyma cells
- d = large windowlike pits between a ray parenchyma cell and a vertical tracheid

the interior of the ray. They are regularly present in the rays of *Pinus*, *Picea*, *Larix*, *Pseudotsuga*, and *Tsuga*, but are absent or extremely rare in *Abies*, *Cryptomeria*, *Thuja*, *Taxodium*, and *Sequoia*. Ray tracheids may sometimes constitute the entire ray.

Ray parenchyma cells are rather bricklike, thin-walled, living cells. They have simple pits, which provide liquid transport to the other ray cells and the longitudinal tracheids (Figs. 2.23 and 2.24). The pits on their radial walls vary from small-oval (spruce, larch) to large windowlike (some pines) matching the cross-field pits of the adjacent longitudinal tracheids (Fig. 2.15A–C). Their end walls are nodular in some species (Abies, Larix, Picea, Tsuga, the soft pines, Fig. 2.15A) (Butterfield and Meylan 1980 p. 40, Panshin and de Zeeuw 1980 p. 151, Barefoot and Hankins 1982 p. 47). This diagnostic feature is, however, very rarely of use in the identification of wood species in pulp.

Ray tracheids are about the same size as the ray parenchyma cells. They are dead cells with small bordered pits (difference from ray parenchyma) leading to the other ray cells and the longitudinal tracheids (Fig. 2.15D). The structure of their inner wall varies according to species from smooth to dentate (Figs. 2.23 and 2.24). The presence of the ray tracheids in pulp and the structure of their inner wall are important diagnostic features (Chap. 3.2.6).

2.6.6 Resin Canals

Resin canals (or resin ducts) are tubelike intercellular spaces which transport resin in both the vertical and horizontal directions. The vertical and horizontal resin canals are interconnected, and form a uniform network in the tree. The horizontal canals are located inside the rays (Fig. 2.22), and are more numerous than the vertical ones. The canals are lined with resin-producing epithelial parenchyma (Fig. 2.18). Resin canals are present in *Pinus*, *Picea*, *Larix*, and *Pseudotsuga*. *Abies*, *Tsuga*, *Thuja*, *Taxodium*, and *Sequoia* do not contain normal resin canals, but they may contain traumatic resin canals resulting from injury to the tree.

The size and frequency of resin canals vary according to species. Pine contains more, and larger canals than do spruce and other softwoods (Figs. 2.4 and 2.5). In spruce, the resin is

evenly distributed throughout the stem, whereas in pine, it tends to concentrate in the heartwood and root. The cells of resin canals are of no value in fiber identification.

2.7 Hardwood Cells

2.7.1 Cell Types

Hardwoods are more advanced and more complex in their structure than softwoods. In softwoods the functions of conduction and support are performed by one cell type, the tracheid. During evolution, hardwoods have developed special types of cells from the tracheid: vessel elements for conduction and fibers for support.

In the beginning of the *development of plants*, water conduction and mechanical support were closely linked, and this is still the case in many present-day plants that have no vessels, such as conifers. Tracheids appear to have been the only highly specialized water-conducting elements in existence for some 300 million years. At the end of this time, when flowering plants arose, xylem became more specialized by a separation of water conduction from mechanical support. Sediments of the lower Cretaceous (ca. 125 million years ago) contain fossil wood that looks quite like modern dicotyledonous wood. It is not known how long such vessel-containing wood had been in existence prior to that time (Zimmermann 1983 p. 4).

The cell types of hardwoods are:

Cell type	Function
Vessel elements	Conduction
2. Fibers	Support
 Libriform fibers 	
 Fiber tracheids 	
3. Tracheids	Conduction
 Vascular tracheids 	
 Vasicentric tracheids 	
4. Parenchyma	Storage
 Ray parenchyma 	
 Longitudinal parenchyma 	

Vessel elements, fibers, and parenchyma compose the main part of hardwoods, and are present in all species.

Tracheids, in hardwoods, are not the constant feature they are in softwoods. *Vascular* and *vasicentric tracheids* occur in only a few species and are present in small amounts (Sect. 2.7.4). *Fiber tracheids* occur in most

22 Structure of Wood

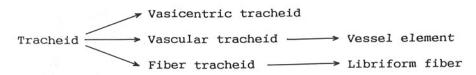


Fig. 2.25. Development of vessel elements and libriform fibers from the tracheid through intermediate forms. (According to Bosshard 1974)

Table 2.3. Proportions of cells in hardwoods

Species	Percent of total volume				Reference	
	Fibers	Vessels	Rays	Longitudinal parenchyma		
Acer pseudoplatanus	75.9	6.9	17.2	Trace	1	
A. rubrum	68.0	18.0	13.3	0.1	2 2	
A. saccharum	61.0	21.0	17.9	0.1	2	
Alnus glutinosa	58	29	12	Trace	1	
Betula papyrifera	75.7	10.6	11.7	2.0	2	
B. verrucosa	64.8	24.7	8.5	2.0	1	
Carpinus betulus	66	10	22	2	1	
Carya ovata	66.5	6.5	20.0	8.0	2	
Castanea sativa	56.5	26.3	17.2	Trace	1	
Eucalyptus globulus	49	21	14	16	1	
Fagus grandifolia	56.7	21.4	20.4	_	2	
F. sylvatica	37.4	31.0	27.0	4.6	1	
Fraxinus excelsior	62.4	12.1	14.9	10.6	1	
Juglans nigra	48.7	21.0	16.8	13.5	2	
J. regia	63.8	12.0	16.2	8.0	1	
Liquidambar styraciflua	26.6	54.9	18.3	0.2	2	
Liriodendron tulipifera	49.0	36.6	14.2	0.2	2	
Magnolia acuminata	47.3	38.6	13.9	0.2	2	
Musanga smithii	70.2	6.1	19.7	4.0	1	
Nyssa sylvatica	45.0	38.4	17.6	_	2	
Populus deltoides	53.1	33.0	13.7	0.2	2	
P. tremula	60.9	26.4	12.7	_	1	
Quercus alba	47.8	16.1	28.0	8.0	2	
Q. robur (narrow-ringed)	44.3	39.5	16.2	_	1	
Q. robur (wide-ringed)	58.1	7.7	29.3	4.9	1	
Salix alba	31	52	17	Trace	1	
S. nigra	54.4	38.1	7.4	0.1	2	
Shorea polysperma	45	26	18	11	1	
Tilia cordata	72	17	9	2	1	
Ulmus americana	34.7	48.0	11.3	6.0	2	
U. glabra	51	29	14	6	1	

¹ Wagenführ and Scheiber 1974.

hardwoods and may be abundant in some species (Sect. 2.7.5). The vascular tracheid and the fiber tracheid are considered to be intermediate evolutionary forms, the former between the tracheid and the vessel element, and the latter between the tracheid and the libriform fiber (Fig. 2.25). The vasicentric tracheid is regarded as a degenerate form (Bosshard

1974 p. 22, Wagenführ 1980 pp. 96, 112). Other trends of evolution have also been suggested (Carlquist 1988 p. 109).

The proportions of vessels, fibers, and parenchyma vary with species (Table 2.3). In most species, fibers contribute about 50% or more of the total wood volume and are the main constituents of the hardwood pulps.

² Panshin and de Zeeuw 1980.

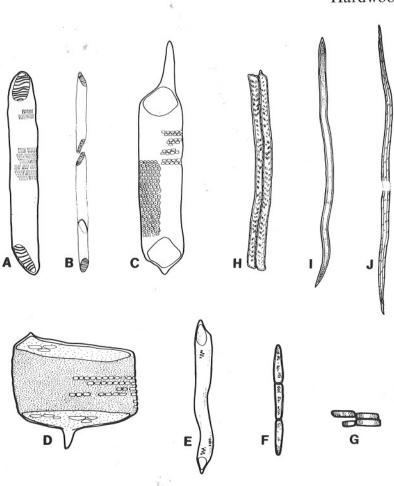


Fig. 2.26. Hardwood cells.

- A Vessel element of birch
- B Vessel of birch
- C Vessel element of aspen
- D Earlywood vessel element of oak
- E Latewood vessel element of oak

- F Longitudinal parenchyma cells
- G Ray parenchyma cells
- H Tracheid of oak
- I Tracheid of birch
- J Libriform fiber of oak

2.7.2 Vessels and Vessel Elements

Vessels are composed of single cells, the vessel elements. These, joining end to end in wood, form longitudinal tubes, which can be several meters long (Fig. 2.26A, B). In the course of evolution, the end walls of the component vessel elements have wholly or partially disappeared. Wide vessels without end walls, such as those of the earlywood of oak (Fig. 2.26D), are best suited for water conduction, and are considered to be an advanced form of the vessels. In birch and alder, the end walls have ladderlike bars (Fig. 2.26A), in aspen they have wholly disappeared (Fig. 2.26C). Because of the vessels, water transport is easier in hardwoods than in softwoods. Vessel elements are,

like the softwood tracheids, dead cells containing water and air. Their walls are pitted, and they may contain spiral thickenings.

Vessels appear in the cross-section of wood as pores or holes (Fig. 2.27), and hence hardwoods are referred to as porous woods in contrast to nonporous softwoods. The size and distribution of the vessels (pores) within the growth rings vary with species. Temperate zone hardwoods can be divided into three groups: diffuse-porous, ring-porous, and semi-ring-porous (Fig. 2.28) (Grosser 1977 p. 30, Parham and Gray 1990 pp. 14, 21).

1. In *diffuse-porous* woods the vessels are fairly uniform in size and quite evenly distributed

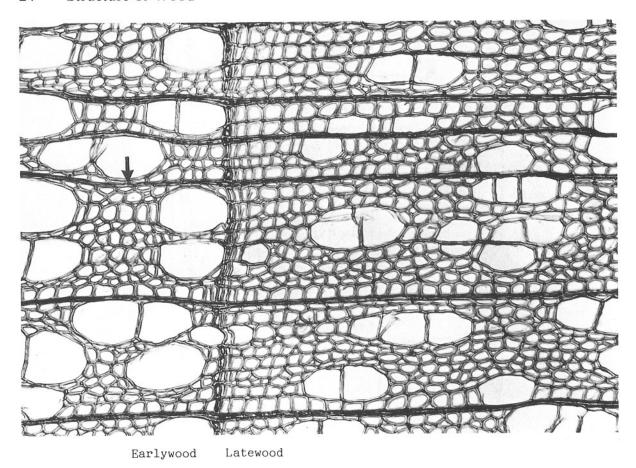


Fig. 2.27. Cross-section of *Populus tremula* (diffuse-porous wood) at earlywood-latewood boundary showing vessels (large holes) and rays (arrow). 200x

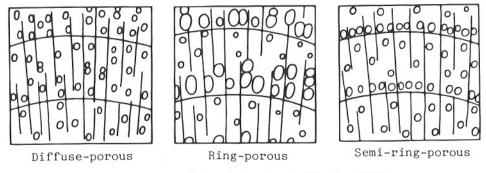


Fig. 2.28. Arrangement of vessels within growth rings in hardwoods. (Bosshard 1974)

- throughout the ring (Acer, Alnus, Betula, Carpinus, Fagus, Liquidambar, Liriodendron, Magnolia, Nyssa, Populus tremula, Salix, Tilia).
- 2. In ring-porous woods the earlywood vessels are much larger than those formed later in the season (Carya ovata, Castanea, Fraxinus, Quercus, Ulmus).
- 3. In *semi-ring-porous* (or semi-diffuse-porous) woods the vessels of earlywood are somewhat larger or more abundant than those of latewood (*Juglans*, *Populus deltoides*, *Populus tremuloides*).

The diffuse-porous group is the most common among the papermaking hardwoods.

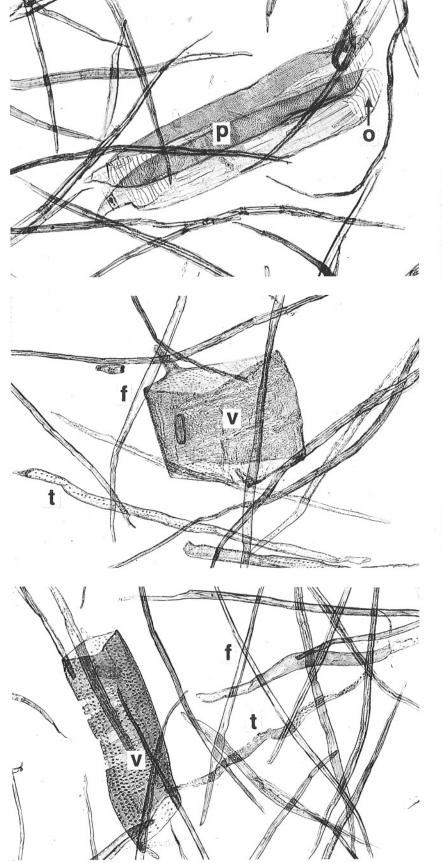


Fig. 2.29. Birch (Betula verrucosa) pulp showing vessel elements and fibers.
o = opening with ladderlike bars between two vessel elements, p = pitted surface between two vessel elements.
100x

Fig. 2.30. Oak (*Quercus* sp.) pulp showing a wide earlywood vessel element (v), libriform fibers (f), and fiber tracheids (t). 100x

Fig. 2.31. Eucalyptus (Eucalyptus sp.) pulp showing a vessel element (v), libriform fibers (f), and vasicentric tracheids (t). 100x

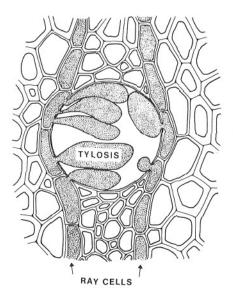


Fig. 2.32. Development of tyloses from ray cells. Cross-section of oak. (Modified from Chattaway 1949)

During pulping, the single cells comprising the vessels are separated and appear in pulp as vessel elements, also known as vessel members or vessel segments (Figs. 2.29–2.31). The presence of vessel elements is the most distinctive difference between softwood and hardwood

pulps. The identification of hardwood species in pulp is performed mainly by the pitting and other features of the vessel elements (Chap. 3.3.2–3.3.6).

2.7.3 Tyloses

In some hardwoods, vessels may be partly or completely filled with bubblelike inclusions, called tyloses. Tylosis (or tylose) is an outgrowth from an adjacent ray (or longitudinal) parenchyma cell through a pit-pair into the vessel lumen (Fig. 2.32). It is apparently formed as a response to loss of water in the vessel (Zimmermann 1983 p. 103). However, it is not known how the absence of water on the vessel's side stimulates the living parenchyma to grow into the vessel. Formation of tyloses is related to the size of the pits between the vessel and the parenchyma cell. According to Chattaway (1949), tyloses can be formed only when the pit apertures are at least 10 µm wide.

Tyloses are formed in the inner sapwood, just prior to its transformation into heartwood, but also in the outer sapwood, particularly in regions where, for some reason, the water content falls below normal. They are also formed pathologically, as a result of

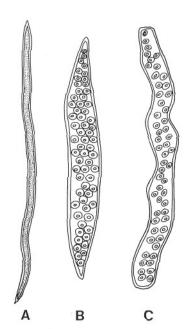
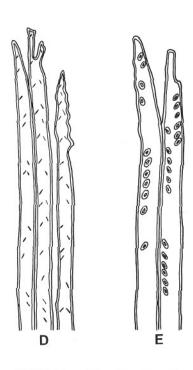


Fig. 2.33. Tracheids and fibers of hardwoods,
A, B Vascular tracheids (bordered pits abundant)
C Vasicentric tracheid (bordered pits abundant)



D Libriform fibers (small scattered pits)E Fiber tracheids (bordered pits in vertical lines)

mechanical injury or infection with diseases (Panshin and de Zeeuw 1980 p. 177). Tyloses tend to be present in the wider vessels, but are rare in the narrow ones. They are especially common in the wide earlywood vessels of some ring-porous woods. Wood with tyloses is impermeable to liquids and an excellent material for barrels. Presence of tyloses can be a useful guide to the fiber analyst (Chap. 3.3.6).

2.7.4 Vascular and Vasicentric Tracheids

Vascular and vasicentric tracheids are smaller fibrous cells, which occur in some hardwoods in association with vessels, and function mainly as conducting cells (Sect. 2.7.1). They are imperforate, and their walls are usually densely covered with bordered pits (Figs. 2.33A–C and 3.32F–I, L–P).

Vascular tracheids occur in wood in longitudinal series, like the small latewood vessel elements with which they are associated. A given series may consist entirely of vascular tracheids, or of a mixture of these and vessel elements (Panshin and de Zeeuw 1980 p. 180). Vascular tracheids are formed at the end of a growth ring, and their function is to provide the last-formed and safest conductive tissue (Carlquist 1988 p. 134).

Vasicentric tracheids abound in wood in the proximity of the large earlywood vessel elements, and are not in longitudinal series (Panshin and de Zeeuw 1980 p. 181). Their function is also to increase conductive safety. They are especially abundant in *Quercus* and *Castanea*. In the former, the vessels may be sheathed by many layers of vasicentric tracheids (Carlquist 1988 p. 136).

Vascular and vasicentric tracheids often occur in woods in which fiber tracheids (Sect. 2.7.5) are also present. *Intermediate forms* occur between vascular and vasicentric tracheids, as well as between these and fiber tracheids (Grosser 1977 p. 46).

The diagnostic features of vascular and vasicentric tracheids are discussed in Chapter 3.3.7.

2.7.5 Fibers

Fibers are classified into *libriform fibers* and *fiber tracheids* (Sect. 2.7.1). Their primary function is to provide mechanical support to the

tree; fiber tracheids can also participate in conduction.

Fibers contribute 30–75% of the wood volume (Table 2.3). Usually both libriform fibers and fiber tracheids are present in the same species. The amount of fiber tracheids varies with species. They may be abundant, forming the bulk of the fibers, or they may be few, or absent. There is no clear distinction between these two fiber types, and they often intergrade, sometimes even in the same growth ring (Parham and Gray 1990 p. 17).

Fibers are long, narrow, and thick-walled, but not invariably. The ends are pointed, sometimes forked, or equipped with dentations (Fig. 2.33D). The average length ranges from 0.7 to 2.0 mm, the average width from 10 to 60 μm (Table 2.4). Fiber tracheids are, in general, somewhat shorter and thinner-walled than the libriform fibers (Grosser 1977 pp. 45, 46), and they may have rounded ends (Fig. 2.33E). The difference between libriform fibers and fiber tracheids is based on the nature of the pitting (Panshin and de Zeeuw 1980 p. 182):

- Libriform fibers have small, slitlike, or dotlike pits. The pits are simple or with inconspicuous borders; they are sparse, and occur commonly scattered over the fiber wall (Figs. 2.33D and 3.32A, B).
- Fiber tracheids exhibit conspicuous bordered pits, which are larger and more numerous than those of the libriform fibers, and tend to be in vertical lines (Figs. 2.33E and 3.32D).

In the macerated samples examined during the preparation of this book, fiber tracheids were abundant in Castanea, Quercus, Fagus, Liquidambar, Eucalyptus, and Anthocephalus. They were absent or sparse in Populus, Salix, Fraxinus, and Ulmus. In Castanea sativa, libriform fibers are sparse, the main part of fibers being composed of fiber tracheids and vasicentric tracheids (Sect. 2.7.4). The fiber tracheids of Castanea are exceptionally wide, and resemble the vasicentric tracheids. In Anthocephalus chinensis, fibers are composed entirely of fiber tracheids (Table 1 in Donaldson 1984).

The presence of fiber tracheids, where they are abundant, can be a guide to the fiber analyst.

28 Structure of Wood

Fibers exhibit modifications. Spiral thickenings are present in some species, such as Ilex and Arbutus (Parham and Gray 1990 pp. 146, 152). Sometimes thin transverse walls are formed in the fibers, resulting in septate libriform fibers or fiber tracheids (Fig. 2.34A). Septate fibers remain living for a longer period, and

then function as storage cells; they can deposit crystals of calcium oxalate (Fig. 2.34B) (von Wolkinger 1969).

Septate fibers may be confused with a strand of longitudinal parenchyma (Fig. 2.34C). They can be separated by the thinner transverse walls of the former: a septum consists of a middle lamella and primary walls and lacks

Table 2.4. Length and width of hardwood fibers

Species	Fiber lengtl	n, mm	Fiber width, µm		Reference
	Average	Range	Average	Range	_
Acacia auriculiformis	0.8		14		5
Acer pseudoplatanus	0.7 - 1.1		10 - 20		3
A. rubrum	0.8	0.3 - 1.1	16 - 30		8
A. saccharum	0.8	0.3 - 1.3	16 - 30		8
Albizzia falcataria	1.0 - 1.1		24 - 42		5, 6
Alnus glutinosa	1.2	0.4 - 1.8	28	15 - 46	1
A. rubra	1.2		16 - 40		8
Anthocephalus chinensis	1.2 - 1.5		33 - 38		5, 6
Betula papyrifera	1.3		25		10
B. verrucosa	1.3	0.8 - 1.8	25	18 - 36	1
Carpinus betulus	1.2	0.6 - 1.7	21	14 - 28	2
Carya ovata	1.3	· ·	17		10
Castanea sativa	0.9	0.3 - 1.4	23	14 - 35	1
Eucalyptus globulus	1.1	0.3 - 1.5	20	10 - 28	1
E. regnans	1.0				6
E. saligna	0.8 - 0.9		16 - 21		5
Fagus grandifolia	1.2	0.6 - 1.9	16 - 22		8
F. sylvatica	1.2	0.5 - 1.7	21	14-30	1
Fraxinus excelsior	0.9	0.4 - 1.5	22	12 - 32	1
Gmelina arborea	1.0		28 - 38		5
Juglans nigra	1.2				7
J. regia	1.3	1.0 - 2.0	22	12 - 31	4
Liquidambar styraciflua	1.7	1.0 - 2.5	20-40		8
Liriodendron tulipifera	1.9	0.8 - 2.7	24-40		8
Magnolia acuminata	1.6	0.8 - 2.3	28 - 40		8, 10
M. grandiflora	1.7	0.9 - 2.6	30		8
Musanga smithii	1.7	0.9-2.5	59	38-40	2
Nyssa sylvatica	1.8	0.8-2.7	20-32		8
Populus deltoides	1.0	,	25-40		8
P. tremula	0.9	0.2-1.6	19	13-30	4
P. tremuloides	1.0	0.4-1.9	10-27		8
Quercus alba	1.4		14-22		8
Q. robur	1.1	0.5-1.6	23	14 - 30	1
Salix alba	1.1		22	1970/19	6
S. nigra	1.1	0.5-2.3	16-32		8
Shorea polysperma	1.3	0.9-1.7	27	17 - 39	4
Tilia americana	1.1	0.4-1.9	24-36		8
T. cordata	0.9	0.5-1.4	18	11-24	4
Ulmus americana	1.5	010 11-1	14-26		9
U. glabra	1.2	0.9 - 2.4	11 20		4

¹ Ezpeleta and Simon 1970.

² Ezpeleta and Simon 1971.

³ Bosshard 1974.

⁴ Wagenführ and Scheiber 1974.

⁵ FAO 1980a.

⁶ FAO 1980b.

⁷ Panshin and de Zeeuw 1980.

⁸ Isenberg 1981.

⁹ Isenberg 1951.

¹⁰ Aitken et al. 1988.

both secondary walls; therefore, it is obviously thinner than the transverse cell walls in a strand of longitudinal parenchyma (von Wolkinger 1969, 1970, Barefoot and Hankins 1982 p. 84, Carlquist 1988 pp. 123, 129).

Septate fibers are common in tropical hard-woods. In the temperate zone woods they occur in some species only (Grosser 1977 p. 47).

2.7.6 Longitudinal Parenchyma

Longitudinal parenchyma, also known as axial, strand, or wood parenchyma, consists of short, bricklike, or isodiametric cells provided with simple (more commonly) or bordered pits. The nature of the pits is affected by the type of pitting of the adjoining cells (Figs. 3.27) and 3.28). Parenchyma cells are involved in storage, and remain living as long as they are a part of the sapwood. The arrangement of longitudinal parenchyma in wood varies from scattered strands (Figs. 2.34C and 2.36) to aggregations in definite patterns. According to its position to the vessels, it may be paratracheal (located adjacent to vessels) or apotracheal (not in contact with vessels) (Panshin and de Zeeuw 1980 p. 186, Wagenführ 1980 p. 122).

Longitudinal parenchyma is more abundant in hardwoods than in softwoods, and is present in most species (Table 2.3). It is especially abundant in tropical hardwoods, and can constitute over half of the wood volume.

Pits leading from vessel elements to longitudinal parenchyma are often useful in identification (Chap. 3.3.5.3).

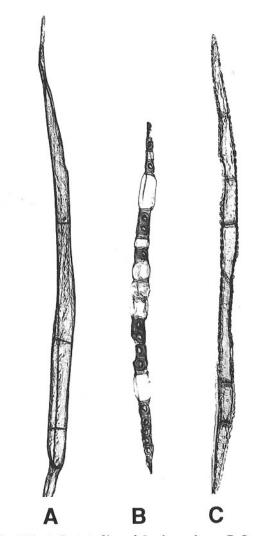


Fig. 2.34. A Septate fiber of *Gmelina arborea*. **B** Septate fiber with crystals, *Albizzia falcataria*. **C** Strand of longitudinal parenchyma, *Betula maximowicziana*. 150x

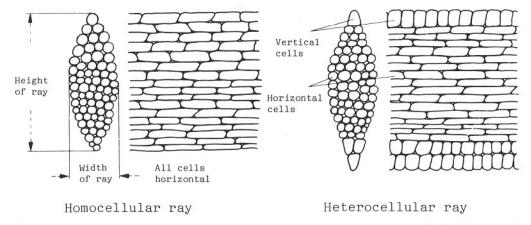


Fig. 2.35. Homocellular and heterocellular rays of hardwoods in tangential (left) and radial (right) views. (Bosshard 1974)

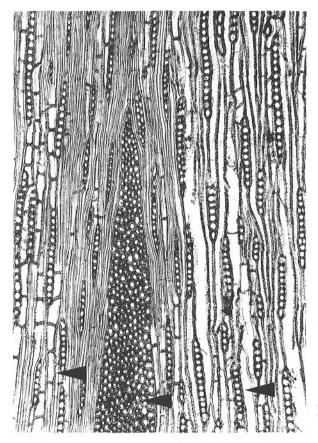


Fig. 2.36. Tangential section of oak (*Quercus* sp.) showing a multiseriate ray (middle arrowhead), uniseriate rays (right arrowhead), and strands of longitudinal parenchyma (left arrowhead). 100x

2.7.7 Rays

Rays of hardwoods consist entirely of parenchyma cells. They are of two structural types, homocellular or heterocellular (Fig. 2.35).

- 1. A homocellular (or homogeneous) ray is composed of one cell type, that is, of horizontal (procumbent), vertical (upright), or square cells (Acer, Alnus, Betula, Populus).
- 2. A heterocellular (or heterogeneous) ray is composed of two or three types of cells. Usually the horizontal cells are in the middle of the ray, the vertical and/or square cells are on the margins (Nyssa, Salix, Anthocephalus).

The homocellular ray is the more common type in the papermaking woods.

The rays of hardwoods vary greatly in width and height. The rays of aspen are uniseriate, that is one cell wide in the tangential direction, those of birch are 1–3 seriate, and those of oak 1–30 seriate (Fig. 2.36). Multiseriate rays are spindel-shaped. The height of rays varies from one to several hundred cells. The rays of oak are up to 5 cm high, and are visible with the naked eye on the tangential and radial surfaces of wood. In hardwoods, average ray volumes range from about 7% to about 30% (Table 2.3).

Ray cells vary in size and shape, and have simple (more commonly) or bordered pits. The nature of the pits is influenced by the complementary pits of the adjacent cells. Ray cells facing vessel elements have larger and densely placed pits (Fig. 3.25), while cells facing fibers, tracheids, or each other have small and sparse pits (Carlquist 1988 p. 211). It is often difficult to distinguish between longitudinal parenchyma and ray parenchyma cells in pulp (compare Figs. 3.25 and 3.28).

Some woods (Carpinus, Alnus) may have broad aggregate rays. They are composed of several small rays separated by rows of fibers (Wagenführ 1980 p. 127, Carlquist 1988 p. 199).

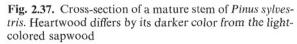
Pits leading from vessel elements to ray parenchyma are of important diagnostic value in the identification of hardwood species in pulp (Chap. 3.3.5.2).

2.8 Sapwood and Heartwood

In young stems, all cells participate in the life functions of the tree. As the diameter of the stem grows, the water conduction and living processes are transferred to the most newly formed peripheral region, called sapwood. The central core of the stem begins to change to a dead heartwood which serves as a support only. In many trees (Pinus, Larix, Castanea, Quercus), heartwood differs by its darker color from the light-colored sapwood (Fig. 2.37). In certain trees (Picea, Abies, Betula, Populus) no color difference is discernible.

The main functional change between sapwood and heartwood is the death of the living parenchyma cells and the diminishing of the water conduction. This is associated with many secondary changes. In softwoods the bordered pits are closed, and in some





hardwoods the vessels are blocked with tyloses (Sect. 2.7.3). In many trees various chemical compounds, known collectively as extractives, are deposited; these may cause the heartwood to darken in color, become less permeable to liquids, or be resistant to decay (Panshin and de Zeeuw 1980 p. 24).

The age when the formation of heartwood begins and its proportion in wood vary ac-

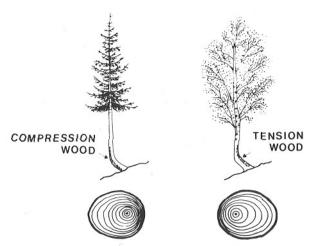
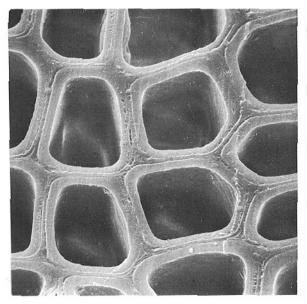


Fig. 2.38. Formation of reaction wood in leaning stems

cording to species, environmental factors, etc. In old conifers, the sapwood layer may be 1-2 cm wide. Heartwood is present in all trees after a certain age, also in those trees that show no color differentiation. There is no generally accepted theory on the formation of heartwood.

2.9 Reaction Wood and Opposite Wood

The term reaction wood is applied to the special wood that is produced in leaning stems and branches, or in general in those parts of a tree that are displaced from their normal position



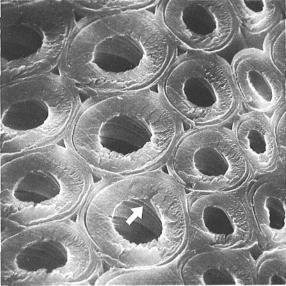


Fig. 2.39. Cross-sectional views of normal wood (left) and compression wood (right) of *Pinus sylvestris*. Note the helical checks (arrow), rounded fibers, and intercellular spaces in the compression wood. SEM 1300x. (Photo H. Eklund)

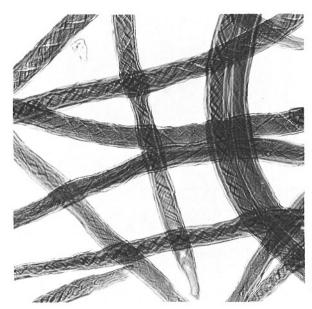


Fig. 2.40. Pulp fibers of the compression wood of *Picea* abies showing criss-cross patterns. 100x

(Fig. 2.38). The function of the reaction wood is to restore the displaced stem to its normal vertical orientation or to maintain a preferred angle in branches. The reaction wood in softwoods is formed on the lower side (compression side) of leaning stems and branches, and is called *compression wood*, whereas in hardwoods it is formed on the upper side, and is known as *tension wood*. As a rule, reaction wood is associated with eccentric growth, and it is contained on the wider side of the growth rings. Compression wood is common in all *conifers*. Tension wood, in contrast, is restricted to certain hardwood species (Timell 1969).

Compression wood differs from normal wood in that the tracheids tend to be rounded in cross-section, and consequently there are intercellular spaces between them (Fig. 2.39). Compression wood tracheids are characterized by helical checks that form an angle of about 40°-60° with the cell axis (Tsoumis 1968 p. 160). The tracheids are shorter and thickerwalled than those of normal wood, and their ends are frequently distorted (Panshin and de Zeeuw 1980 p. 306). Pulp fibers from compression wood can usually be recognized by the

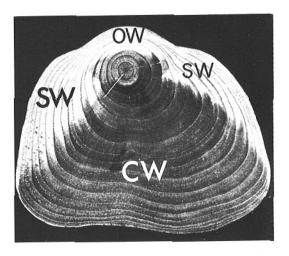


Fig. 2.41. Cross-section of a stem of *Pinus resinosa* showing the location of compression wood (CW), opposite wood (OW), and side wood (SW). (Timell 1973a)

criss-cross patterns (Fig. 2.40), which are due to the helical checks in the cell wall (difference from spiral thickenings, see Chap. 3.2.4). Since compression wood is common in all softwoods, it is of no diagnostic value.

Tension wood differs from normal wood mainly with respect to the fibers, which have a thick gelatinous layer on the lumen side of the cell wall (see Fig. 8-12 in Panshin and de Zeeuw 1980). The gelatinous layer is almost pure cellulose. Fibers from tension wood cannot be recognized in pulp.

The wood which is formed opposite to reaction wood in leaning stems and branches is called *opposite wood* (Fig. 2.41). The wood between the reaction wood and opposite wood is generally referred to as *sidewood*. Opposite wood differs anatomically from normal wood in both softwoods and hardwoods (Panshin and de Zeeuw 1980 pp. 306, 316).

In softwoods, the growth rings of opposite wood are often extremely narrow, and the tracheids tend to be slightly longer than those of normal wood. Timell (1973b) has established the presence of spiral thickenings on the latewood tracheids in the opposite wood of *Larix laricina*, *Picea rubens*, and *Pinus resinosa*. The spirals are oriented transversely or in a very flat helix, and are attached to the inner surface of the cell wall.

CHAPTER 3

Identification of Wood Species in Pulp

3.1 Introduction

The identification of wood species in pulp is based on the structural features of individual cells, in softwoods mostly on the cross-field pitting of the tracheids, and in hardwoods mostly on the pitting and other features of the vessel elements.

The degree of success in identification depends on the number of components in the fiber mixture, the species present, etc. The result is also greatly influenced by the pulping process, bleaching, and beating. In highly beaten pulps, for example, it is often difficult to find intact cross-field pits (Fig. 3.1) or vessel elements.

The identification of different wood genera is usually possible, but the identification of individual species is often difficult and in many cases impossible, because species of the same genus are closely related in anatomical structure.

An inevitable qualification for identification is sufficient knowledge on the structure of wood and the diagnostic features of wood cells. Authentic fiber samples and photomicrographs with descriptions are of great help to the fiber analyst. It is also an advantage to know the origin of the sample as well as the geographic distribution of the common papermaking woods. It must be remembered, however, that many trees are cultivated outside

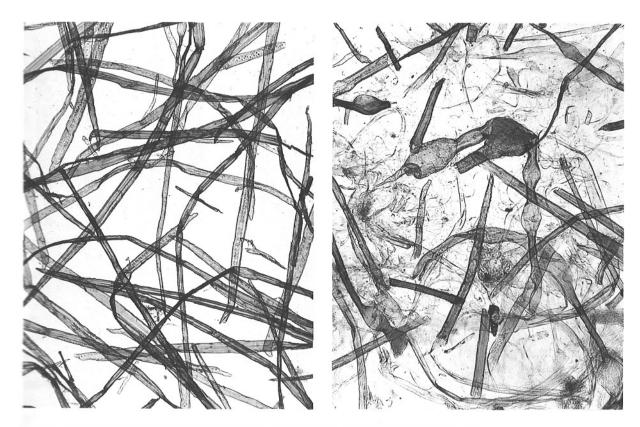


Fig. 3.1. Unbeaten (left) and highly beaten (right) sulfite pulp of spruce (Picea abies). 50x

their natural habitats and that imported pulpwoods are used in many countries.

3.2 Identification Features of Softwoods

3.2.1 Introduction

As previously mentioned, the identification of softwoods is performed mainly by the cross-field pitting of the tracheids. Besides the main diagnostic features, tracheids exhibit several minor structural features that are of auxiliary value. In the identification of pine species, the structure of the inner wall of ray tracheids is diagnostically important. Some softwoods (*Pseudotsuga*, *Araucaria*) possess special features that allow ready and precise identification. The features available for the identification of softwoods are (Figs. 3.2 and 3.3):

- 1. Cross-field pitting of tracheids.
 - Pits to ray parenchyma (pit type, number of pits per cross-field, arrangement of pits).
 - Pits to ray tracheids (presence or absence).
 - Height of cross-field areas.
- Intertracheid pitting (number of vertical rows).
- 3. Spiral thickenings (presence).
- 4. Width of earlywood tracheids.
- 5. Structure of the inner wall of ray tracheids (identification of pine species).

The identification is performed on *early-wood tracheids*, which appear in pulp in collapsed state, and have large pits. Latewood tracheids do not usually collapse during pulping, they have smaller and fewer pits, and cannot be used for identification.

3.2.2 Cross-Field Pitting

Cross-field pitting occurs as one or several prominent groups on the radial walls of tracheids (Fig. 3.2).

The contact area between a ray and a vertical tracheid is known as the *cross-field area* or ray contact area (Fig. 3.3).

The contact area between a single ray cell and a vertical tracheid is known as the *cross-field*.

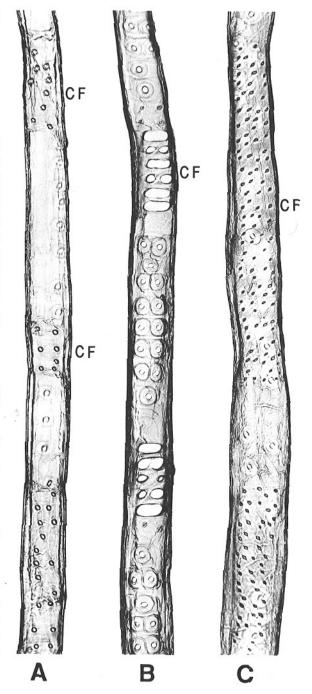


Fig. 3.2. Cross-field areas of different height (CF). A Cryptomeria japonica. B Pinus kesiya. C Larix sibirica. 200x

In many woods (see Sect. 3.2.2.2) cross-field pitting is composed of two kinds of pits:

- 1. Pits leading to ray parenchyma, often called ray parenchyma pits, or cross-field pits for brevity.
- 2. Pits leading to ray tracheids, often called ray tracheid pits.

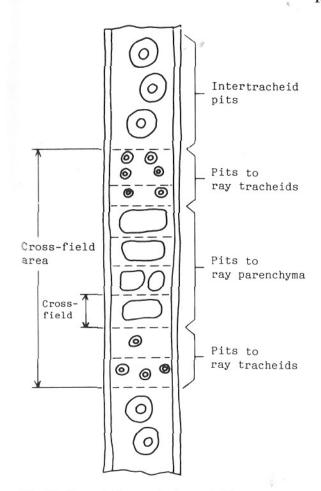


Fig. 3.3. Cross-field area of pine tracheid

3.2.2.1 Pits to Ray Parenchyma

Pits leading from the tracheids to ray parenchyma (Fig. 3.3) are classified by their structure into five main types: windowlike, pinoid, piceoid, cupressoid, and taxodioid. The names, except for the first one, are derived from the corresponding generic names: Pinus, Picea, Cupressus, and Taxodium. Windowlike and pinoid pits occur in pines; piceoid, cupressoid, and taxodioid pits in other conifers. In addition to these main types, some authors (Greguss 1955 p. 25, Barefoot and Hankins 1982 p. 58) have presented araucaroid, podocarpoid, and dacrydioid pit types, which occur in the genera of Araucaria, Podocarpus, and Dacrydium.

Ray parenchyma pits are bordered. In the windowlike and pinoid pits, the borders are sometimes so narrow that they are hard to distinguish.

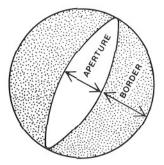


Fig. 3.4. Diagrammatic picture of a piceoid cross-field pit in face view. The aperture is narrower than the border

When defining the pit type, attention has to be paid to the following features:

- 1. Size and shape of the pit. The pits vary in size from the large windowlike pits that occupy most of the cross-field, as in the case of many pines (Fig. 3.5), to the very small piceoid pits of spruce and larch that occupy only a small portion of the cross-field (Fig. 3.7). The pits can be round, oval, angular, or somewhat irregular in shape.
- 2. Width and orientation of the pit aperture. The width of the aperture can be equal to, less, or greater than the width of the border on both sides of it (Fig. 3.4). The border is often poorly visible in chemical pulp fibers. The long axis of the aperture can vary from vertical to horizontal with respect to the fiber axis.
- 3. Number and arrangement of the pits in the cross-field. The number of the pits per cross-field varies from 1 to about 8, or more, as in Araucaria. The pits may occur in horizontal (or diagonal) rows or groups, or they may be irregularly arranged. The number and the arrangement of the pits vary according to pit type and genus. Piceoid and cupressoid pits are commonly less regularly arranged, and it is often difficult to see their number per cross-field in pulp fibers (Figs. 3.7 and 3.8). Taxodioid pits tend to be in horizontal rows (Fig. 3.9), pinoid pits in horizontal rows or groups (Fig. 3.6 Pinus taeda).

Identification and occurrence of the main types of ray parenchyma pits:

1. Windowlike (or fenestriform) pits (Fig. 3.5). 1–2 large, rectangular pits or 2–3 (4) oval pits

per cross-field. The border is narrow, sometimes barely discernible. Occurrence: *Pinus strobus*, *P. monticola*, *P. lambertiana*, *P. sylvestris*, *P. resinosa*, *P. kesiya*, etc.

- 2. Pinoid pits (Fig. 3.6). Smaller than windowlike pits, variable in size and shape, 1–7 pits per cross-field. The border is mostly narrow, sometimes barely discernible, and often wider on one side of the aperture than on the other. The pits tend to be in horizontal rows, groups, or clusters (crowded group); in some pine species they are diagonally arranged (Fig. 3.6 Pinus radiata). The pinoid type is the most common type of pitting in pines. Occurrence: Pinus halepensis, P. ponderosa, P. contorta, P. radiata, P. pinaster, P. taeda, P. caribaea, P. banksiana, etc.
- 3. **Piceoid pits** (Fig. 3.7). Very small, oval to round, bordered pits of fairly uniform size, 2–4 (1–6) pits per cross-field in *Picea*, 4–6 (1–8) in *Larix*. The aperture is narrow (narrower than the border), often slitlike, and frequently extended beyond the pit outline (Fig. 2.10C). The long axis of the aperture varies in position from about 30° (to the fiber axis) to vertical. In *Picea* the pits are commonly irregularly arranged; in *Larix* they tend to be in an irregular horizontal row or less frequently in two rows per cross-field. Occurrence: *Picea*, *Larix*, and *Pseudotsuga*.
- 4. Cupressoid pits (Fig. 3.8). Small, oval to round, bordered pits of fairly uniform size, 1–4 (6) pits per cross-field, somewhat larger than the piceoid type. The aperture is oval and about as wide as the border. The long axis of the aperture is about 45° to the fiber axis. The pits may resemble the piceoid type. Occurrence: *Tsuga*, *Chamaecyparis*, and *Taxodium*.
- 5. Taxodioid pits (Fig. 3.9). Oval to nearly round, bordered pits of fairly uniform size, larger than the piceoid or cupressoid types, 2–4 (1–6) pits per cross-field. The aperture is large and wide, the border is narrow. The long axis of the aperture is slightly canted or nearly horizontal. The pits tend to be in horizontal rows. Occurrence: Abies, Cryptomeria, Thuja, Taxodium, and Sequoia.

Intermediate forms of the piceoid, cupressoid, and taxodioid pit types are rather common. Some woods may display two types of

pits, for instance baldcypress (Taxodium distichum) exhibits both taxodioid and cupressoid types, the intermediate form dominates (Fig. 3.10). The cupressoid pits of hemlock (Tsuga) may show piceoid or taxodioid features (see Tsuga heterophylla Fig. 4.25F and T. canadensis Fig. 4.23F). The piceoid pits of spruces (Picea spp.) and larches (Larix spp.) often show cupressoid or taxodioid features.

Much experience is needed in order to determine the pit type. It is advisable to study the pits with careful focusing and at different magnifications.

Ray parenchyma pitting provides the most important feature by which to distinguish between the softwood species in pulp.

3.2.2.2 Pits to Ray Tracheids

Pits leading to ray tracheids (Fig. 3.3) occur in one or several rows on the margins of the cross-field areas and are sometimes interspersed among the ray parenchyma pits (Figs. 3.6 and 3.7). Pits to ray tracheids are bordered, and can be distinguished from the intertracheid bordered pits by their smaller size.

Pits to ray tracheids occur in certain softwood genera. They are regularly present in Pinus, Picea, Larix, Pseudotsuga, and Tsuga, absent or very rare in Abies, Cryptomeria, Thuja, Taxodium, and Sequoia. They are absent in Chamaecyparis obtusa, but usually present in C. nootkatensis.

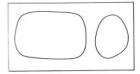
Low cross-field areas may sometimes be composed exclusively of pits to ray tracheids (Fig. 3.11). This feature is occasionally present in pines, but may also be found in other softwoods.

Pits to ray tracheids are easily rendered inconspicuous by chemical treatment and beating, but can usually be detected when several margins of cross-field areas are examined with careful focusing.

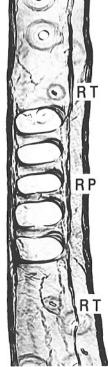
The presence or absence of ray tracheid pits is of great diagnostic value in the identification of softwood species in pulp.

3.2.2.3 Height of Cross-Field Areas

The height of cross-field areas (=height of rays) varies according to species (Fig. 3.2), although appreciable variations may occur within species. The height of cross-field areas can



Windowlike



。 RT RP

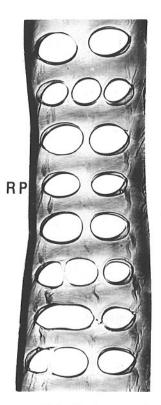
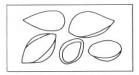


Fig. 3.5. Windowlike pits to ray parenchyma (RP) and pits to ray tracheids (RT). 450x

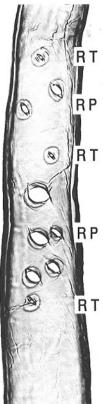
Pinus resinosa

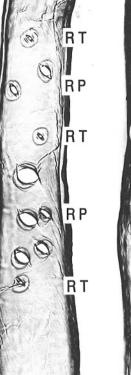
P. kesiya

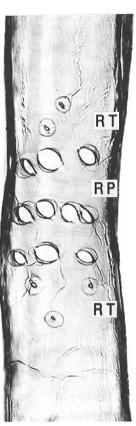
P. lambertiana



Pinoid







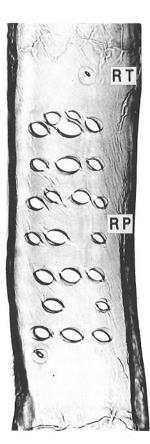


Fig. 3.6. Pinoid pits to ray parenchyma (RP) and pits to ray tracheids (RT). 450x

Pinus radiata

P. pinaster

P. taeda



Piceoid

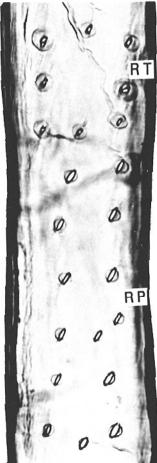
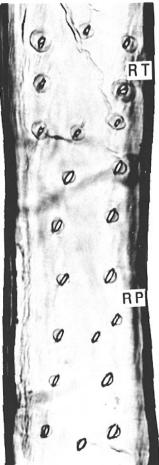
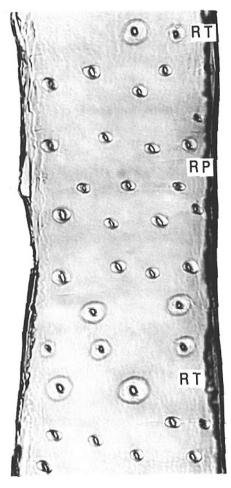


Fig. 3.7. Piceoid pits to ray parenchyma (RP) and pits to ray tracheids (RT). 750x



Picea abies



Larix occidentalis

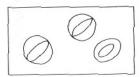
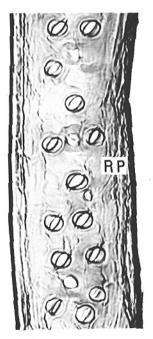
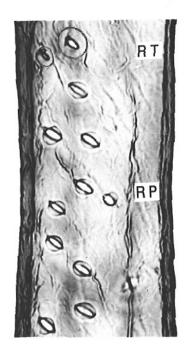


Fig. 3.8. Cuperssoid pits to ray parenchyma (RP) and pits to ray tracheids (RT). 750x.

Cupressoid



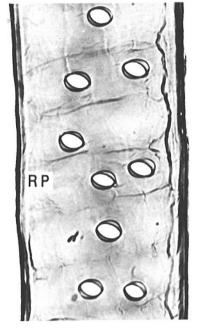
Chamaecyparis obtusa



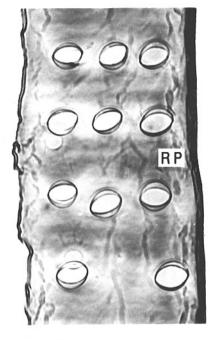
Tsuga heterophylla



Taxodioid



Cryptomeria japonica



Sequoia sempervirens

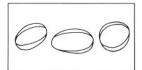
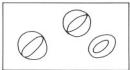


Fig. 3.9. Taxodioid pits to ray parenchyma (RP). 750x



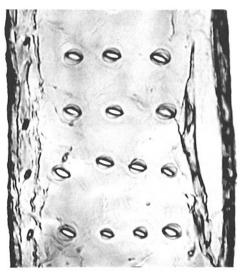
Taxodioid

Cupressoid

Fig. 3.10. Pits to ray parenchyma showing both taxodioid and cupressoid features.

Taxodioid features: the pits are nearly horizontal, and are in horizontal rows.

Cupressoid features: the pits are relatively small (smaller than the taxodioid type); the aperture is oval and about as wide as the border. 750x



Taxodium distichum

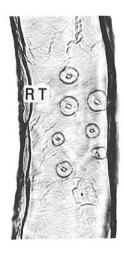


Fig. 3.11. Low cross-field area composed of pits to ray tracheids (RT), *Pinus taeda*. 450x

be used as an auxiliary diagnostic feature for species exhibiting either very high or very low cross-field areas (Phillips 1948 p. 12).

High cross-field areas (rays frequently more than 30 cells high) are present in:

Abies alba Larix occidentalis, L. sibirica (not invariably) Sequoia sempervirens Taxodium distichum Podocarpus spicatus

Low cross-field areas (rays rarely more than 15 cells high) are found in:

Abies balsamea, A. firma, and some other Abies species.

Chamaecyparis (all species) (Greguss 1955 p. 101).

Cryptomeria japonica.

It should be noted that the height of cross-field areas may vary considerably between the species of a single genus; for instance, *Abies* species exhibit both very high (*A. alba, A. lasiocarpa, A. procera*) and very low (*A. balsamea, A. firma, A. concolor*) cross-field areas (Greguss 1955 p. 122).

In the genus *Pinus*, high cross-field areas are rare (Greguss 1955 Table VIII). Among the common papermaking pines, rays up to 25–30 cells high may occur in *Pinus halepensis* (Jacquiot 1955 p. 80), *P. patula*, and *P. ponderosa* (Greguss and Varga 1950 pp. 49, 100).

3.2.3 Intertracheid Pitting

Intertracheid pitting occurs in one or several (1–4) vertical rows along the *radial walls* of earlywood tracheids. The number of pit rows is related to the width of the tracheids. Woods with relatively narrow fibers (*Picea*) exhibit pits in a single row (uniseriate pitting, Fig. 3.12A, B). Woods with wider fibers (*Larix*, *Abies*) have two rows fairly constantly (biseriate pitting, Fig. 3.12C). Very wide fibers (*Taxodium*, *Sequoia*, *Pinus lambertiana*) show 2–3 (4) pit rows (multiseriate pitting, Fig. 3.12D).

In biseriate and multiseriate pitting, the arrangement of the pits may be opposite or alternate (Fig. 3.12C–F). In the *opposite* arrangement the pits are in horizontal pairs or rows across the cell wall; in the *alternate* arrangement the rows are diagonal. Multiseriate pitting is opposite in all common conifers except for *Araucaria* and *Agathis*. In these two

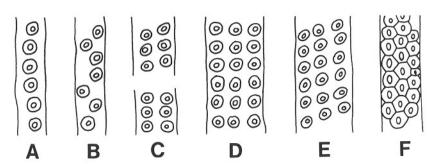


Fig. 3.12. Arrangement of intertracheid pitting. A Uniseriate with a storied row. B Uniseriate with a staggered row. C Biseriate alternate (above) and biseriate opposite (below). D Multiseriate opposite. E Multiseriate alternate. F Crowded alternate

genera the alternate bordered pits are often so crowded that the normally circular pit outline assumes a hexagonal shape (Fig. 3.12F).

The vertical pit rows are not, in general, regular throughout the whole length of the tracheids, e.g., spruces with uniseriate pitting often show staggered rows (Fig. 3.12B), scattered pits, or occasional pit pairs. The pits are usually more numerous and the pit pairs more common toward the ends of tracheids, where the tracheids overlap each other in wood. Accordingly, attention has to be paid to the common occurrence of the pits throughout the tracheids and not to occasional groups that may occur on fiber ends.

Because of the many variations, intertracheid pitting is not of definite diagnostic value except for some species (*Araucaria*, *Agathis*), but it can be used as an auxiliary feature for distinguishing certain wood genera. Intertracheid pitting may also occur on the tangential walls of the tracheids. Where present, it is confined mainly to the tracheids of the last rows of latewood and the first rows of earlywood (Koran 1977, Panshin and de Zeeuw 1980 p. 137). The pits on the tangential walls are smaller than those on the radial walls (Fig. 3.13). According to Phillips (1948 pp. 11, 34), tangential pitting occurs in all conifers showing well-defined growth rings except for certain pine species. It can be of diagnostic value in some differentiations.

The presence of intertracheid pitting is one of the main distinguishing features between softwoods and hardwoods in pulp.

3.2.4 Spiral Thickenings

Spiral (or helical) thickenings are present as a constant feature in the tracheids of only one

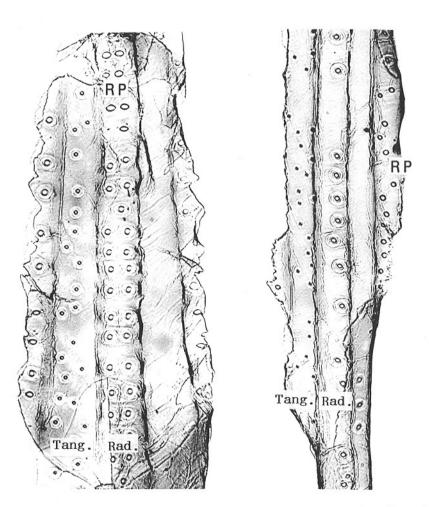


Fig. 3.13. Intertracheid pitting on the radial and tangential walls as seen from the lumen side of a tracheid. RP = pits to ray parenchyma on the radial wall. Sequoia sempervirens (left), Abies alba (right). 200x

commercial coniferous pulpwood, viz. *Pseudotsuga*, and it can be readily distinguished by this feature. Spiral thickenings are regularly present in the earlywood tracheids of *Pseudotsuga*, frequently present in the ray tracheids, and absent or poorly developed in the latewood tracheids (Fig. 2.19A).

Spiral thickenings are also regularly present in *Taxus*, a small tree of limited commercial importance, and in *Picea smithiana* (Himalayan spruce), a timber of some commercial importance in India (Greguss 1955).

Spiral thickenings are found occasionally in some spruce, larch, and pine species as follows:

- 1. In the latewood of *Larix laricina*, juvenile wood of spruce, and the latewood of some hard pines (Parham and Gray 1990 p. 14).
- 2. In the latewood tracheids of the opposite wood of Larix laricina, Picea rubens, and Pinus resinosa (Timell 1973b) (Chap. 2.9).
- 3. In the knot wood of Picea abies (Boutelje 1966).

The spiral thickenings mentioned above are not of diagnostic value except for those of point 3, which may be useful in differentiating between the Scandinavian spruce (*Picea abies*) and pine (*Pinus sylvestris*) in knotter pulp.

Spiral thickenings should not be confused with compression wood striations (helical checks) (Chap. 2.9), which are steeper and do not encircle the cell (compare Figs. 2.19A and 2.40) (Barefoot and Hankins 1982 p. 12).

3.2.5 Width of Tracheids

Because of the great variations, fiber width is of restricted diagnostic value. It can provide clues as to the wood species only when very wide or very narrow tracheids are present in the sample. In the descriptions of the softwood species, the width of the tracheids has been characterized by the maximum width values as follows:

Class	Max. width of macerated tracheids, μm	Genus or species
Very wide	>100	Taxodium, Sequoia, Pinus lambertiana
Wide	80–100	Larix spp., Pinus monticola, P. taeda and other southern pines, P. caribaea, P. kesiya, P. merkusii, etc.
Narrow or very narrow	< 60	Picea abies, P. glauca, Chamaecyparis obtusa, Pinus strobus, P. sylvestris, P. rigida (very narrow), etc.

Note that the width values measured on the macerated, collapsed tracheids are larger than those measured on the stem cross-sections.

3.2.6 Inner Wall of Ray Tracheids

The inner wall of ray tracheids may be non-dentate (smooth) or dentate (toothed) in appearance.

The inner wall is nondentate in *Picea*, *Larix*, *Tsuga*, and some pine species (*Pinus strobus*, *P. monticola*, *P. lambertiana*) (Fig. 3.14A, B). Minute dentations can be present in *Picea*, and sporadically in *Larix* (TAPPI St. 1988 T 263).

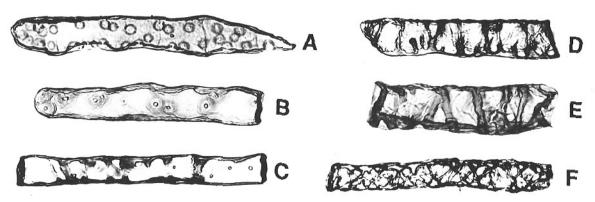


Fig. 3.14. Ray tracheids showing nondentate and dentate inner walls. A Nondentate with minute dentations (*Picea glauca*). B Nondentate (*Pinus lambertiana*). C Dentate with local bridgelike thickenings (*Pinus*)

sylvestris). **D** Prominently dentate (*Pinus ponderosa*). **E** Bridgelike (*Pinus elliottii*). **F** Reticulate (*Pinus echinata*). 450x

In most pine species the inner wall of the ray tracheids is dentate, that is, it exhibits irregular toothlike thickenings. In the radial view under the microscope, low thickenings are seen as teeth or ridges, and high thickenings as bridgelike or reticulate patterns (Fig. 3.14C–F). The structure of the inner wall varies according to species, so it is of diagnostic value. The inner wall is nondentate in the pines of the Strobus group, dentate in the Sylvestris and Ponderosa groups, and strongly dentate to reticulate in the Taeda group (see Sect. 3.2.7). For example, the presence of a reticulate ray tracheid (Fig. 3.14F) in a pulp sample shows the presence of some pine of the Taeda group. Owing to their small size, the ray tracheids are easily lost in processing, and are therefore usually sparse in chemical pulp.

The dentation varies somewhat within a species (Howard and Manwiller 1969). Local variations may occur even within a single cell; for instance, a ray tracheid with a moderate dentate inner wall may show local bridgelike patterns (Fig. 3.14C).

3.2.7 Identification Groups of Pines

This book presents the identification of 42 softwood species. Of these, 22 are pines. To assist the identification and differentiation, the pines have been divided into six groups. The grouping has been done on the basis of the cross-field pitting and the structure of the inner wall of the ray tracheids, and is based on the classification by Rol (Phillips 1948 p. 34) with some modifications. Pines are, as a rule, readily distinguished from the other softwoods by the cross-field pitting. Species identification is in many cases difficult, unless the geographic origin of the sample is known, but it is often possible to classify the pines under one of the following groups:

- 1. **Strobus group.** Cross-field pits windowlike, generally 1–3 (4) pits per cross-field (Fig. 4.4). Ray tracheids nondentate (*Pinus strobus*, *P. monticola*, *P. lambertiana*).
- 2. Sylvestris group. Cross-field pits window-like, generally 1 (2) pits per cross-field (Fig. 4.4). Ray tracheids dentate (*Pinus sylvestris*, *P. resinosa*).

- 3. **Halepensis group.** Cross-field pits pinoid, generally 2–3 (1–4) pits per cross-field (Fig. 4.5). Ray tracheids nondentate to dentate (*Pinus halepensis*).
- 4. **Ponderosa group.** Cross-field pits pinoid, generally 2-5 (1-6) pits per cross-field (Fig. 4.5). Ray tracheids prominently dentate, often with local bridgelike or reticulate thickenings (*Pinus ponderosa*, *P. contorta*, *P. patula*, *P. radiata*, *P. pinaster*).
- 5. **Taeda group.** Cross-field pits pinoid, generally 2–5 (1–7) pits per cross-field (Fig. 4.6). Ray tracheids strongly dentate to reticulate (*Pinus taeda*, *P. echinata*, *P. elliottii*, *P. palustris*, *P. rigida*, *P. caribaea*, *P. banksiana*).
- 6. **Kesiya group.** Cross-field pits both windowlike and pinoid, generally 1–2 (3, rarely 4) pits per cross-field (Fig. 4.7). Ray tracheids mostly dentate (*Pinus kesiya*, *P. merkusii*, *P. densiflora*, *P. nigra*).

The identification groups are treated in more detail in Tables 4.3–4.7.

Note. In the American literature, the pines are often separated into two groups, namely, the soft pines and the hard pines (Harlow et al. 1979 p. 60). In the former group the wood is relatively soft (not invariably), in the latter group it is fairly hard. The North American soft pines include Pinus strobus, P. monticola, and P. lambertiana; the hard pines include P. resinosa, P. ponderosa, P. contorta, P. banksiana, and the southern pines. The groups of the soft and hard pines correspond with the botanical subgenera Haploxylon and Diploxylon.

3.3 Identification Features of Hardwoods

3.3.1 Introduction

There is a much greater range of morphological characteristics for hardwoods than for softwoods. Consequently, the identification of hardwoods is less difficult in general.

Hardwoods have several types of cells. Vessel elements are, however, the only cell type showing constant structural variation between the different genera. Because of this, the identification of hardwoods is based mainly on the features of vessel elements. In addition, the presence of vascular or vasicentric tracheids is

diagnostically important. Fibers are rarely of diagnostic value. The main features available for the identification of hardwoods are:

- 1. Vessel elements.
 - Size and shape.
 - Type of perforations (simple or scalariform).
 - Spiral or reticulate thickenings (presence).
- 2. Pitting on vessel elements.
 - Intervessel pitting (alternate, opposite, or scalariform).
 - Pits to ray parenchyma (size, shape, and arrangement).
 - Pits to longitudinal parenchyma (sometimes useful).
 - Pits to vascular or vasicentric tracheids (presence).
- 3. Tyloses (presence).
- 4. Vascular or vasicentric tracheids (presence).

3.3.2 Size and Shape of Vessel Elements

The size and shape of vessel elements vary from drum- and barrel-shaped to oblong and linear, with or without broadly tapering or tail-like extensions at one or both ends (Fig. 3.15). The size and shape of vessel elements are peculiar to each genus, although there may be a lot of variation within a genus and species, and in different parts of a single trunk.

The vessel elements of most of the north temperate zone hardwoods are *linear*, often several times longer than broad (Fig. 3.15A–D). Their size varies according to species, and is of diagnostic value. In the descriptions of the hardwood species, the *size of the linear vessel elements* is characterized by the terms "short, medium-long to long, and very long" as follows:

Class	Length of vessel elements, mm	Genus or species
Short	< 0.5	Acer, Tilia
Medium- long to lon	2.0	Alnus, Betula, Liriodendron, Magnolia acuminata, Carpinus, Populus, Salix, Fagus
Very long	>1.0	Betula maximowicziana, Nyssa, Liquidambar, Magnolia grandiflora

The vessel elements of ring-porous woods (Chap. 2.7.2) are of two size classes; the earlywood vessel elements are large and wide, often drum- or barrel-shaped, those of the latewood are small and narrow (Fig. 3.15G). There are only a few ring-porous species among papermaking hardwoods (Fraxinus, Ulmus, Carya ovata, Castanea, Quercus), and hence the presence of ring-porosity is of diagnostic value.

The vessel elements of tropical hardwoods are, in general short and wide (Fig. 3.15E, F), and they may resemble the earlywood vessel elements of the ring-porous woods.

The shape of vessel element ends is not of definite diagnostic value, except for eucalyptus, which can be identified by the long, threadlike tails (Fig. 3.15E).

3.3.3 Perforations

Vessel elements are open or scalariform at their ends. When the end wall consists of a single, large opening, it is termed a simple perforation (Fig. 3.16); when the end wall bears barlike structures, it is termed a scalariform perforation. There are also other types of perforations, reticulate and foraminate, which are found occasionally in the common pulpwoods (Esau 1953 p. 223, Panshin and de Zeeuw 1980 p. 173, Miller and Baas 1981 p. 117). Ordinarily, a given vessel element possesses two perforations, one at each end, but occasionally three perforations can be present.

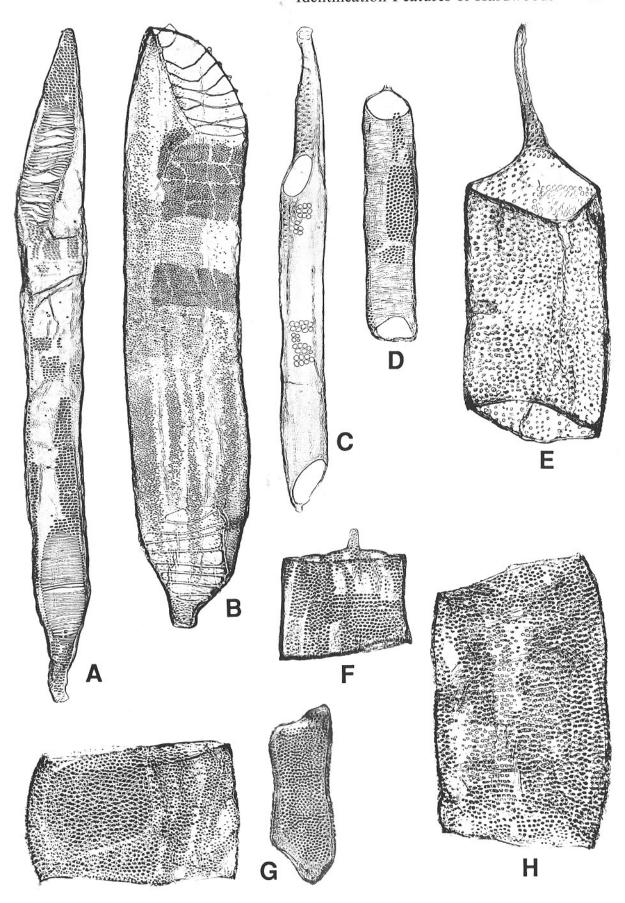
The number of bars in a scalariform perforation varies from 1 to 50 or more. In *Liriodendron* and *Magnolia grandiflora* the number of bars is generally less than 10, in *Betula*, *Alnus*, and *Liquidambar* 5–25, and in *Nyssa* 20–55 (Fig. 3.17). The bars may be thin or thick, and occasionally branched (Fig. 3.15B). Thin bars will easily become broken during pulping.

Fig. 3.15. Vessel elements of different size and shape. 150x

A-D Linear vessel elements of Nyssa sylvatica (**A**), Betula maximowicziana (**B**), Populus tremula (**C**), and Acer pseudoplatanus (**D**)

E Oblong vessel element with long tail, Eucalyptus globulus F Small, nearly drum-shaped vessel element of Acacia auriculiformis

G Drum-shaped earlywood vessel element (left) and narrow latewood vessel element (right) of *Fraxinus excelsior* H Barrel-shaped vessel element of *Carya ovata*



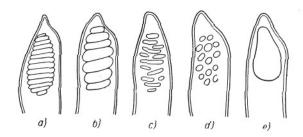


Fig. 3.16. Types of perforations: scalariform (a, b), reticulate (c), foraminate (d), and simple (e). (Wagenführ 1980)

Some woods that as a rule have a simple perforation may also show scalariform perforations (Fagus, Carpinus, Castanea), the scalariform type usually occurring in the latewood. In Magnolia acuminata, the scalariform type occurs in the wood near the pith (Parham and Gray 1990 p. 154).

The presence of scalariform perforations and the number of bars are important diagnostic features (Table 5.3 and Fig. 5.1). Table 5.2

lists the occurrence of scalariform perforations in the common hardwoods.

3.3.4 Thickenings

Spiral (or helical) thickenings are present in the vessel elements of certain hardwoods. They may be present in all vessel elements (Acer, Tilia, Carpinus, Magnolia grandiflora), in the smaller vessel elements or latewood elements only (Ulmus), or they may be restricted to the vessel element tails (Nyssa, Liquidambar). The spirals can be distinct or faint; they can be widely spaced, close, or swirled (Fig. 3.18). Spiral thickenings, their presence and nature, are important features in identification (Table 5.4 and Fig. 5.2). Table 5.2 lists their occurrence among the common hardwoods (see also Table 7 in Core et al. 1979). Tropical hardwoods rarely show spiral thickenings (Panshin and de Zeeuw 1980 p. 176).

Reticulate thickenings are present in Juglans nigra and in three less important Juglans

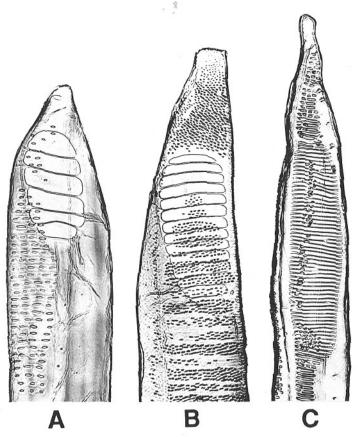


Fig. 3.17. Different types of scalariform perforations. The number of bars varies from 5 to about 55. A Liriodendron tulipifera. B Betula verrucosa. C Nyssa sylvatica. 220x

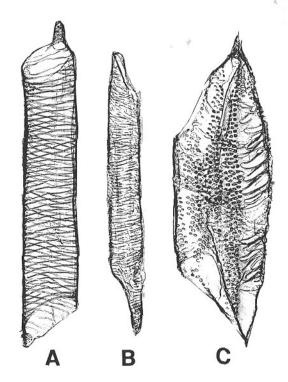


Fig. 3.18. Vessel elements showing spiral and reticulate thickenings. A Prominent, widely spaced spirals in *Tilia cordata*. B Close, swirled spirals in *Acer saccharum*. C Reticulate thickenings in *Juglans nigra* (on the right side of the vessel element). 150x

species. In these species the radial walls of the smaller vessel elements show an interlacing reticulum of thickenings (Fig. 3.18C). Reticulate thickenings furnish a reliable feature for the separation of *Juglans nigra* from all common hardwoods and some other *Juglans* species (Miller 1976a, b, Panshin and de Zeeuw 1980 p. 176). Faint reticulate thickenings occur occasionally on the walls of the vessel elements of *Liquidambar*.

3.3.5 Pitting on Vessel Elements

Pitting on the vessel elements varies depending on the cells that have been in contact with them in wood. The following kinds of pits can be present on the vessel walls (Fig. 3.19):

Pits to adjacent vessel elements (intervessel pits).

Pits to ray parenchyma.

Pits to longitudinal parenchyma.

Pits to fibers (libriform fibers, fiber tracheids). Pits to vascular or vasicentric tracheids.

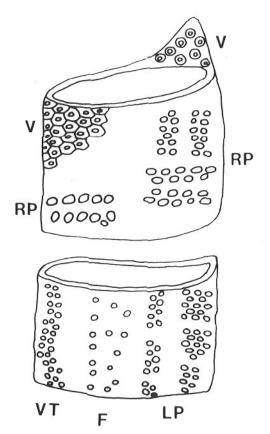


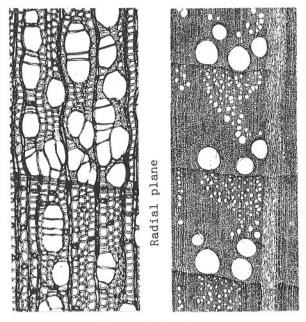
Fig. 3.19. Pitting on the vessel element.

- V Uncrowded (tail) and crowded (left) intervessel pits.
- RP Pits to ray parenchyma in horizontal or vertical groups (right) or horizontal rows (left)
- LP Pits to longitudinal parenchyma in longitudinal series (broken lines)
- VT Pits to a vasicentric tracheid in a longitudinal line (not broken, difference from LP pits)
- F Pits to fibers in a vertical line or scattered

The pits on a vessel element may occur in groups, rows, longitudinal lines or series (broken lines), or in larger areas, conforming to the configuration of the adjacent cells.

3.3.5.1 Intervessel Pitting

The pitting that occurs between adjacent vessel elements is termed intervessel (or intervascular) pitting. It may occur on the side walls or tails of the vessel elements. The occurrence of intervessel pitting is dependent on the arrangement of vessels in wood (Fig. 3.20). If the individual vessels, as seen in transverse section, occur in clusters or files (Alnus, Betula), they can have abundant intervessel pitting. Normally, it is most abundant on the tangential



Tangential plane

Fig. 3.20. Arrangement of vessels in the transverse section of wood. (Left) Vessels are in radial files or clusters, *Alnus glutinosa*. 75x. (Right) Vessels are solitary, *Quercus robur*. 25x

walls of the elements, since they are in contact most often in this plane. If the vessels are solitary (*Quercus*, *Castanea*, *Eucalyptus*), the intervessel pitting is scarce, and occurs solely on the areas of overlapping vessel element ends, above and below the perforations. Three arrangements of intervessel pitting are recognized: alternate, opposite, and scalariform (Fig. 3.21).

- 1. In the *alternate* arrangement the pits are in diagonal rows. If the pits are uncrowded, their outlines are circular to oval, if crowded the outlines become angular or frequently hexagonal.
- 2. In the *opposite* arrangement the pits are in horizontal rows. They are for the most part crowded and nearly rectangular in outline.
- 3. In the *scalariform* arrangement elongated or linear pits are in a vertical row.

The alternate, more or less crowded pitting, is the most common type of pitting in hardwoods (Fig. 3.22A, B). The opposite arrangement is rare, and therefore of great diagnostic value. It occurs in *Liquidambar*, *Liriodendron*

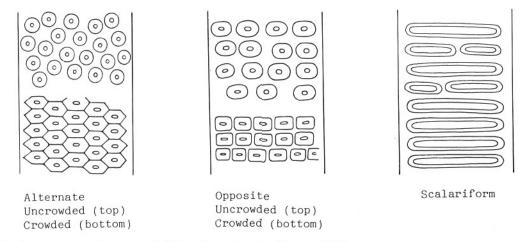


Fig. 3.21. Arrangement of intervessel pitting. (According to Grosser 1977)

Fig. 3.22. Types of intervessel pitting (V) as seen at low (150x, left) and higher (400x, right) magnification.

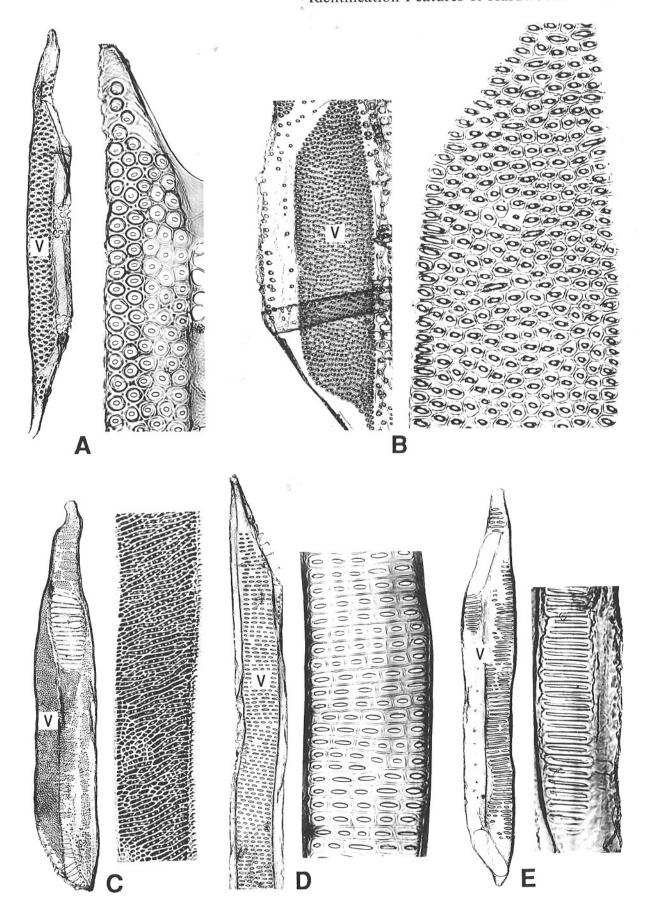
A Alternate, crowded pits with round-oval to hexagonal outlines in *Populus tremula*

B Alternate, crowded pits with nearly hexagonal outlines in *Shorea polysperma*

C Very small, crowded, alternately or spirally arranged pits with confluent inner apertures in *Betula* verrucosa

D Opposite, crowded pits with rectangular outlines in Liriodendron tulipifera

E Scalariform pits in Mangolia acuminata



(Fig. 3.22D), and *Nyssa*. The scalariform arrangement is even more rare than the opposite. It occurs constantly in *Magnolia* (Fig. 3.22E), frequently in *Liquidambar*, and occasionally in *Nyssa* (Table 5.2).

The intervessel pits are bordered, and the borders are mostly broad (Fig. 3.22). The pits vary in size and shape from the very small pits of Betula (Fig. 3.22C) to the exceptionally large linear pits of Magnolia (Fig. 3.22E). The pits of Populus (Fig. 3.22A) may be considered as the

average size. The intervessel pits of *Betula* are commonly confluent (Chap. 2.5.1).

3.3.5.2 Pits to Ray Parenchyma

Pits to ray parenchyma, also called ray parenchyma, vessel-ray, or cross-field pits, occur on the radial walls of the vessel elements, because they communicate between the vessels and the cells of rays. If the entire ray is in contact with the vessel element, as in *Betula*, the ray

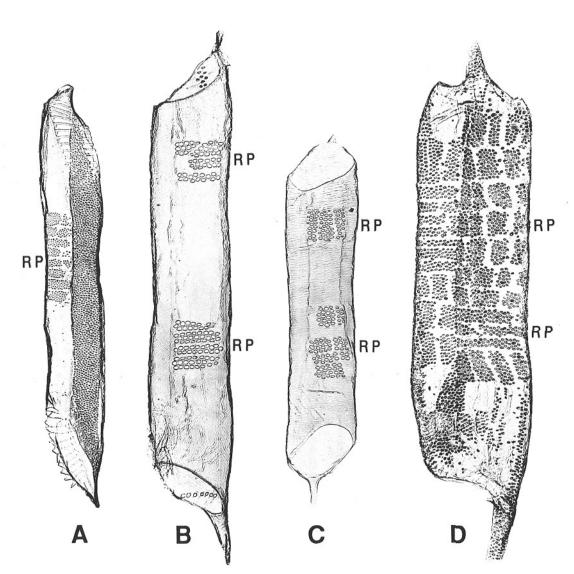


Fig. 3.23. Arrangement of ray parenchyma pitting (RP). 150x

A The pits are in horizontal groups (homocellular pitting), and are uniformly distributed on the vessel wall. Betula verrucosa

B The pits are in horizontal groups (homocellular pitting). The pitting areas appear widely spaced. *Populus deltoides*

C The pits are in vertical or horizontal to square groups (heterocellular pitting). The pitting areas appear widely spaced. Salix alba

D The pits are in vertical or horizontal groups (heterocellular pitting), and are uniformly distributed on the vessel wall. Anthocephalus chinensis

parenchyma pits are uniformly distributed on the vessel wall (Fig. 3.23A). If the ray contacts the vessel element only at the upper and lower margins, as in *Populus* and *Salix*, the pitting areas appear widely spaced (Fig. 3.23B, C).

Pits to ray parenchyma are in general *simple* or have narrow borders (see *Populus* and *Salix* in Fig. 3.24, bottom left) differing from the intervessel pits, which have broad borders. Ray parenchyma pits with broad borders are found only exceptionally in the common hardwoods, as e.g., in *Shorea* (Fig. 3.24, bottom right).

The size, shape, and arrangement of the ray parenchyma pits vary according to species. In some woods, such as *Alnus*, *Betula*, and *Fraxinus*, the pits are very small and similar to intervessel pits when seen at low magnification (diagnostic feature, Table 5.5 and Fig. 5.3). In most hardwoods, ray parenchyma pits and intervessel pits differ appreciably from one another.

Ray parenchyma pitting appears as horizontal, vertical, or square groups, or as horizontal rows (Fig. 3.19), reflecting the structure of the ray (Chap. 2.7.7). When

the pitting is composed of one group type (horizontal, vertical, or square), it is termed homocellular (Fig. 3.23B). If it is composed of two or three types of groups, it is said to be heterocellular (Fig. 3.23D). Table 5.2 lists the type of pitting present in the common hardwoods.

Heterocellular pitting is rare among the papermaking hardwoods, and consequently it is of diagnostic value (*Salix*, *Nyssa*, *Anthocephalus*) (Fig. 3.23C, D). Some woods show both homocellular and heterocellular arrangements of pits (*Liquidambar*, *Liriodendron*, *Magnolia*).

Ray parenchyma pitting is the most important feature in the identification of hardwoods in pulp. Figure 3.24 shows different types of ray parenchyma pits of papermaking hardwoods.

Note. Similar type of pitting occurs in the *ray* parenchyma cells that have been in contact with the vessels in wood (Fig. 3.25), and is of some diagnostic value; compare the pitting visible on the ray parenchyma cells (Fig. 3.25D) and the vessel element of Salix nigra (Fig. 3.24, bottom left).

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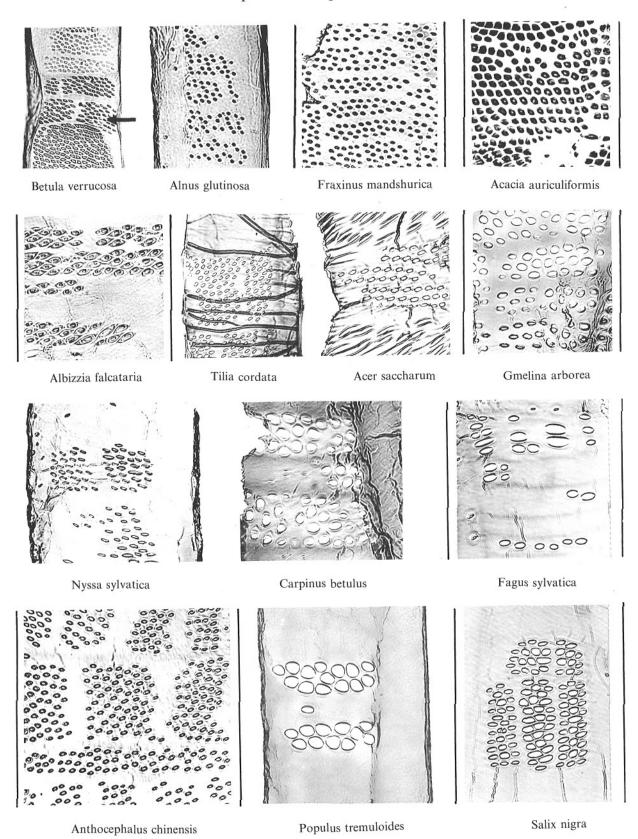


Fig. 3.24. Pits leading from vessel element to ray parenchyma. 400x

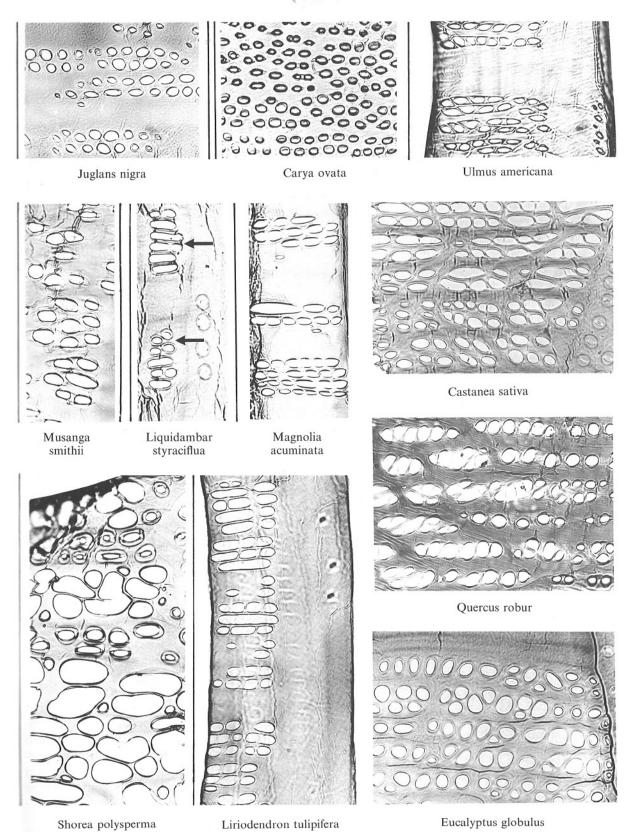


Fig. 3.24. Continued. 400x

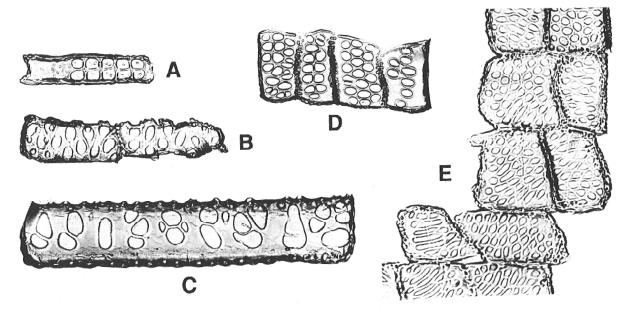


Fig. 3.25. Ray parenchyma cells showing different types of pits leading to vessel elements. A Populus tremula. B Eucalyptus saligna. C Shorea polysperma. D Salix nigra. E Anthocephalus chinensis. 400x

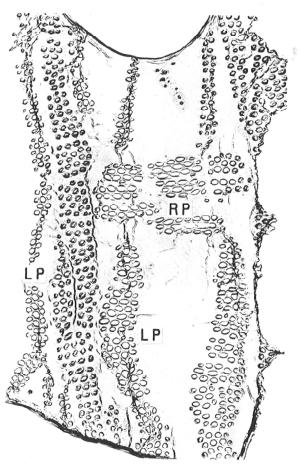


Fig. 3.26. Pits to longitudinal parenchyma (LP) in longitudinal series (broken lines) on the vessel wall of $Juglans\ nigra$. RP= pits to ray parenchyma. 220x

3.3.5.3 Pits to Longitudinal Parenchyma

Pits to longitudinal (or axial) parenchyma (Chap. 2.7.6) occur as longitudinal series (broken lines), which can be one to two, or several pits wide (Figs. 3.19 and 3.26). The pits are simple or have narrow borders. They are often similar in appearance to the ray parenchyma pits, and may be difficult to distinguish from these. Pits to longitudinal parenchyma are present in most hardwoods, and are abundant in *Carya*, *Fraxinus*, *Juglans*, and the tropical hardwoods. Their presence and grouping can be a useful guide in identification. The same type of pitting occurs in the adjacent longitudinal parenchyma cells (Figs. 3.27 and 3.28).

3.3.5.4 Pits to Fibers and Tracheids

Pits leading to fibers (libriform fibers and fiber tracheids, Fig. 3.32A–E), form uniseriate vertical lines or occur scattered on the vessel wall (Figs. 3.19 and 3.29). The pits are usually bordered (Panshin and de Zeeuw 1980 p. 175), but the detection of the border may sometimes be difficult.

Pits to libriform fibers (Chap. 2.7.5) are usually small, inconspicuous, and sparse. In some woods whose fibers are composed

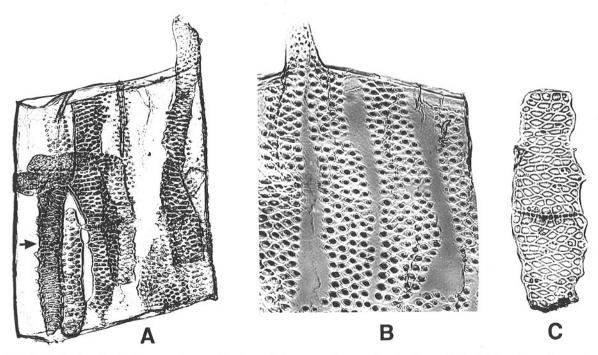


Fig. 3.27. A Longitudinal parenchyma cells (arrow) in contact with the vessel element, as in the wood. *Acacia auriculiformis* 200x. B Pits to longitudinal parenchyma

on the vessel wall. Same 400x C Complementary pits (leading to vessel element) on the longitudinal parenchyma cells. Same 400x

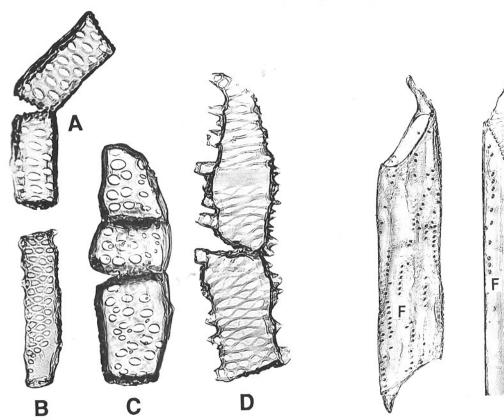


Fig. 3.28. Longitudinal parenchyma cells showing different types of pits leading to vessel elements. A *Juglans nigra*. B *Acacia auriculiformis*. C *Gmelina arborea*. D *Albizzia falcataria*. 400x

Fig. 3.29. Pits leading to fibers (F) (mostly to fiber tracheids) on the vessel elements of *Quercus robur* (left) and *Liquidambar styraciftua* (right). 150x

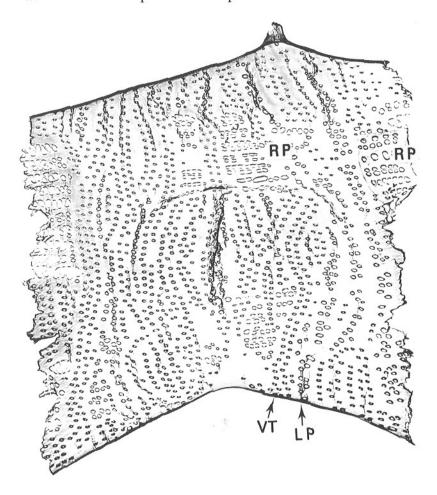


Fig. 3.30. Pits to vasicentric tracheids (VT, in longitudinal lines), and pits to longitudinal parenchyma (LP, in broken longitudinal lines) on the vessel wall of *Quercus alba*. RP = pits to ray parenchyma. 200x

entirely of libriform fibers, no fiber pitting is visible on the vessel elements (see *Populus* and *Salix* in Figs. 5.54B, C and 5.62A–C).

- Pits to fiber tracheids (Chap. 2.7.5) are well discernible, larger than the pits to libriform fibers, and tend to be in vertical lines (Fig. 3.29).

Pits leading to vascular or vasicentric tracheids (Fig. 3.32F–O) (Chap. 2.7.4) are bordered and well discernible. They occur in narrow longitudinal lines, conforming to the configuration of these cells (Figs. 3.19 and 3.30). In some woods, as in oak, the most obvious pitting on the vessel elements is often that to vasicentric tracheids. Pits to vascular and vasicentric tracheids may be a guide to the fiber analyst.

3.3.6 Tyloses

Tyloses (Chap. 2.7.3) occur in pulp either still in the vessel elements, or separated from these, appearing as balloonlike structures (Fig. 3.31). Most tyloses are thin-walled, but may be thick-walled in some species. They exhibit simple pits, which are inconspicuous in the thin-walled tyloses, but are prominent in the thick-walled ones (Panshin and de Zeeuw 1980 p. 122). Woods contain tyloses in varying amounts. They are common in Juglans, Carya, Castanea, and the white oaks. They do not normally occur in Acer, Alnus, Betula, Carpinus, Liquidambar, Nyssa, Salix, or Tilia. The presence of tyloses can be a helpful guide in identification. However, this feature should be used only in the positive sense.

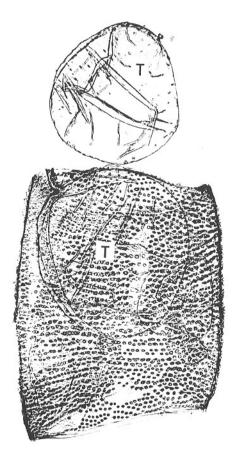


Fig. 3.31. Included and protruding tyloses (T) in the vessel element of *Carya ovata*. 150x

3.3.7 Vascular and Vasicentric Tracheids

Vascular and vasicentric tracheids (Chap. 2.7.4) may be present in some hardwood pulps. Within the same species, they are generally longer than the vessel elements, but shorter than the fibers. The pitting on the tracheids varies, depending on the cells that are in contact with these in wood. The main part of the pitting is usually composed of bordered pits leading to vessel elements.

Vascular tracheids may resemble small latewood vessel elements, but are closed at the ends (Fig. 3.32F–I). They have numerous bordered pits of the same type as the intervessel pits, and they may possess spiral thickenings (Fig. 3.32F). Vascular tracheids are rare. They occur sporadically in Alnus, Betula, Carpinus, Tilia, and Ulmus.

Vasicentric tracheids are irregularly shaped cells with rounded ends and numerous bordered pits (Fig. 3.32L-P). They are abundant

in Castanea and Quercus, common in Eucalyptus and Shorea, rare in Fagus. They differ from the vascular type in that they are generally longer, have rounded ends, and are irregular in shape (not always). Both types may occur in the same wood, and their differentiation may sometimes be difficult.

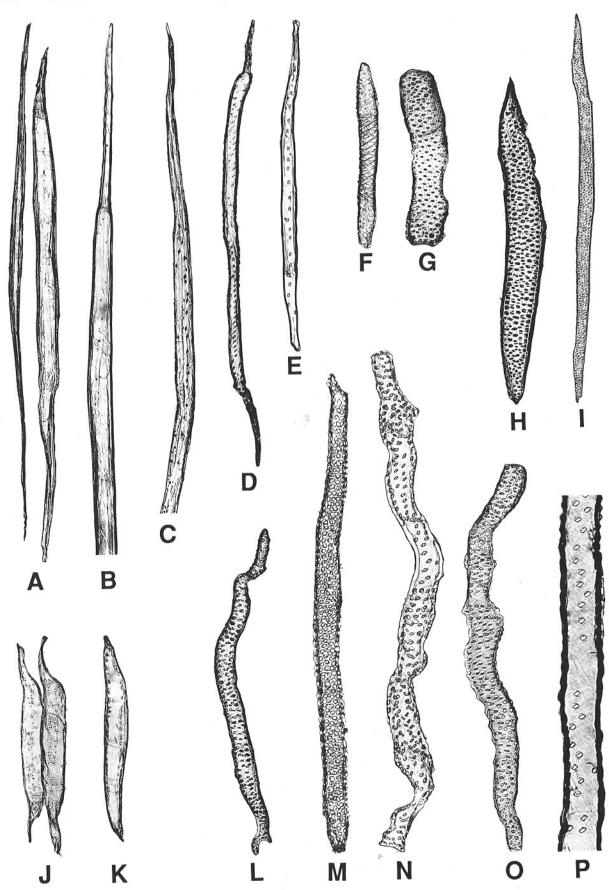
Another type of vasicentric tracheids is commonly present in *Fraxinus* (Fig. 3.32J, K). These are short, wide cells, with pointed or rounded ends and small bordered pits, and they may be somewhat irregular in shape (Panshin and de Zeeuw 1980 p. 623).

Since vascular and vasicentric tracheids occur in only a few species (Table 5.2), their presence is of diagnostic value.

3.3.8 Identification Groups of Hardwoods

This book presents the identification of 41 hardwood species. In order to help the identification and differentiation, the hardwoods have been divided into five groups, listed in the table below. The grouping is based on features that are usually easily recognized at a magnification of about $100 \times$. The groups include all hardwoods described in this text, except for *Populus*, *Salix*, *Fagus*, *Juglans*, and *Magnolia acuminata*. *Eucalyptus* has been included in the group of tropical hardwoods, although it is mainly a subtropical genus.

Identification group		Genera or species	
1.	Woods with scalariform perforations in all vessel elements (Fig. 5.1)	Alnus, Betula, Nyssa, Liquidambar, Liriodendron, Magnolia grandiflora	
2.	Woods with spiral thickenings in all vessel elements (Fig. 5.2)	Acer, Tilia, Carpinus, Magnolia grandiflora	
3.	Woods in which all pits on vessel elements are small to very small and similar in appearance at low magnification (Fig. 5.3)	Alnus, Betula, Fraxinus, Acacia, Albizzia, Anthocephalus	
4.	Ring-porous woods (Fig. 5.4)	Fraxinus, Ulmus, Carya, Castanea, Quercus	
5.	Tropical hardwoods (Fig. 5.5)	Gmelina, Acacia, Albizzia, Anthocephalus, Eucalyptus, Musanga, Shorea	



The *tropical hardwoods* show no distinct features common to them all; however, it is often possible to recognize their presence by the following features (Fig. 5.5):

- 1. Vessel elements are in general drum- to barrel-shaped or oblong, except for An-
- thocephalus, which also shows linear vessel elements.
- 2. Vessel elements are profusely pitted.
- 3. Parenchyma is abundant.
- 4. Vasicentric tracheids are present in *Eucalyptus* and *Shorea*.
- 5. Fibers of *Albizzia* and *Musanga* are wide and thin-walled.

Fig. 3.32. Fibers and tracheids of hardwoods. A-O 150x, P 400x

A, B Libriform fibers with inconspicuous pits. A Castanea sativa. B Albizzia falcataria

C-E Fiber tracheids with distinct bordered pits.
 C Anthocephalus chinensis (pits are scattered).
 D Quercus alba (pits tend to be in vertical lines).
 E Eucalyptus regnans

F-I Vascular tracheids with profuse bordered pits.

F Ulmus glabra. G Ulmus americana. H Carpinus betulus. I Alnus rubra

J, K Vasicentric tracheids with small bordered pits.
J Fraxinus excelsior. K Fraxinus mandshurica

L-O Vasicentric tracheids with profuse bordered pits.
L Quercus alba. M Shorea polysperma. N Eucalyptus regnans. O Castanea sativa

P Bordered pits in a vasicentric tracheid of Quercus robur