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9. XYLEM: VARIATIONS IN WOOD STRUCTURE

WOODS ARE USUALLY CLASSIFIED IN TWO MAIN GROUPS, THE SOFTwoods and the hardwoods. The term softwood is applied to gymnosperm wood, that of hardwood to the dicotyledon wood. The two kinds of woods show basic structural differences, but they are not necessarily distinct in degree of density and hardness. The gymnosperm wood is homogeneous in structure—with long straight elements predominating—and, therefore, easily workable. It is highly suitable for papermaking. Many commercially important dicotyledon woods are especially strong, dense, and heavy because of high proportion of fiber tracheids and libriform fibers (e.g., *Quercus, Carya, Eucalyptus, Acacia*), but some are light and soft (the lightest and softest is balsa, *Ochroma*). Among the gymnosperms only the conifers are an important source of commercial timber, and among the angiosperms only the dicotyledons. The monocotyledons that have secondary growth do not produce a commercially important homogeneous body of secondary xylem.

CONIFER WOOD

The secondary xylem of the conifers is relatively simple in structure (figs. 9.1 and 9.2; Greguss, 1955), simpler than that of most of the dicotyledons. One of its outstanding features is the lack of vessels. The tracheary elements are imperforate and are mainly tracheids.

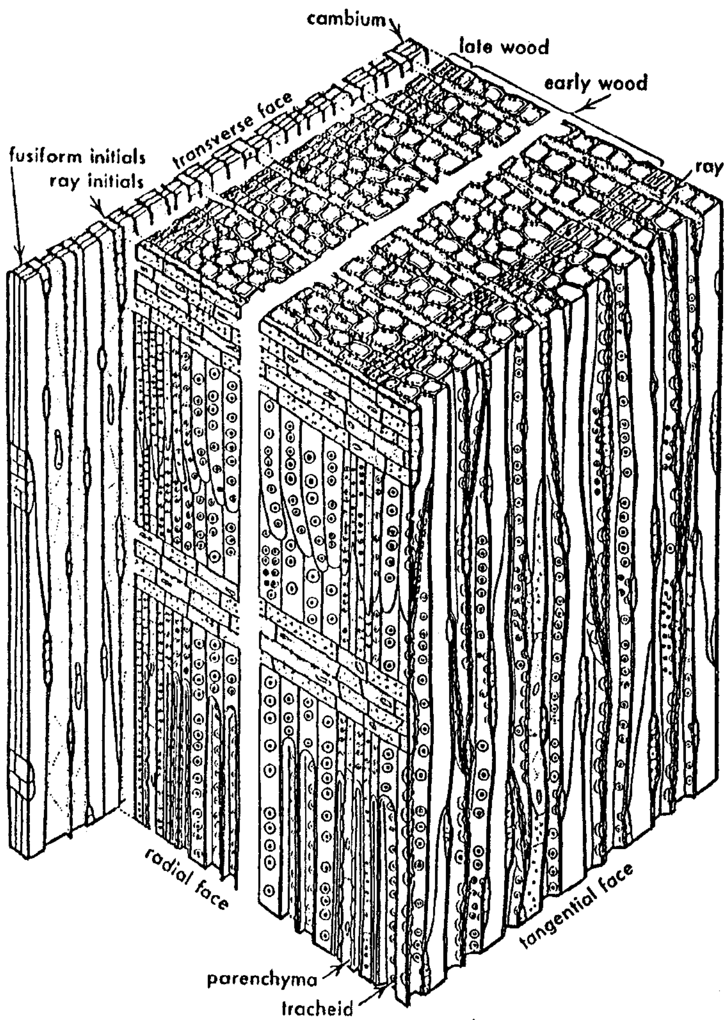


Fig. 9.1. Block diagram of vascular cambium and wood of *Thuja occidentalis* (white cedar), a conifer. The axial system is composed of tracheids and some parenchyma cells. The rays contain only parenchyma cells. (From Esau, *Plant Anatomy*, John Wiley and Sons, 1953. Courtesy of I. W. Bailey. Drawn by Mrs. J. P. Rogerson under the supervision of L. G. Livingston. Redrawn.)

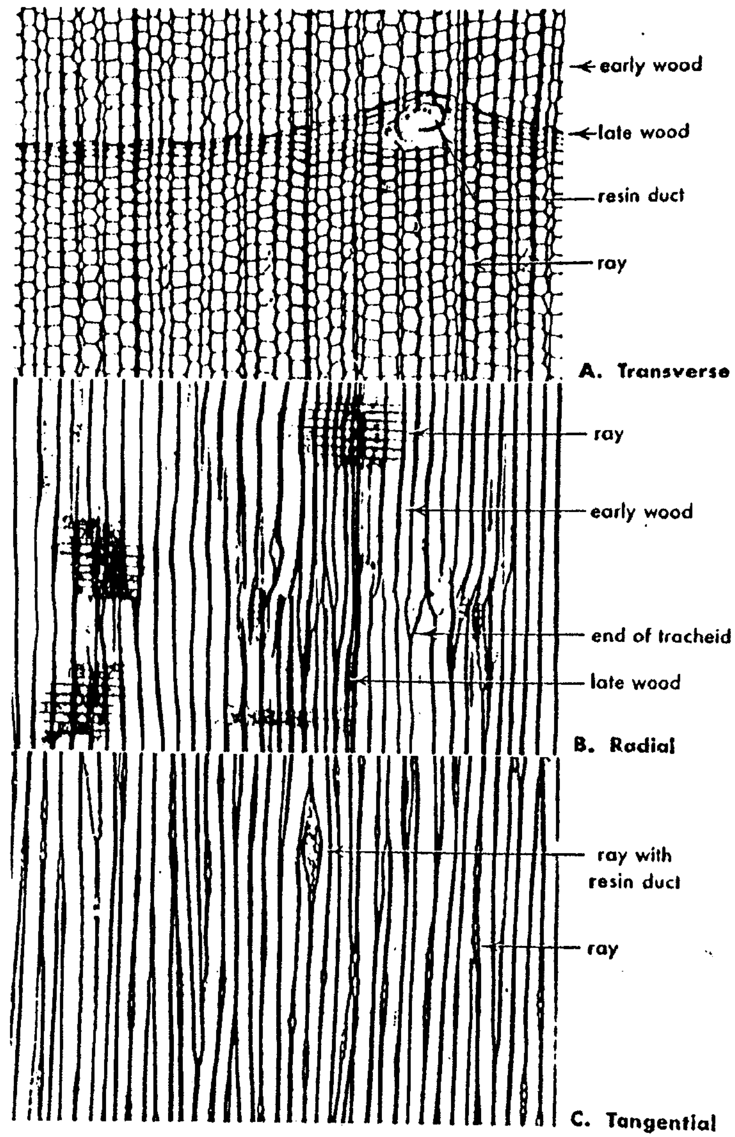


Fig. 9.2. Wood of pine (*Pinus strobus*), a conifer in three sections. (All, ×53.)

Fiber-tracheids may occur in the late wood, but libriform fibers are absent. The tracheids are narrow elongated cells averaging 2 to 5 millimeters in length (fig. 8.3, *A;* Trendelenburg, 1955). Their overlapping ends may be curved and branched because of intrusive growth. Basically the ends are wedge shaped, with the truncated end of the wedge exposed in the radial section (fig. 9.1).

The early-wood tracheids have circular bordered pits with circular inner apertures (fig. 9.3, *D*). The late-wood tracheids (or fiber-tracheids) have somewhat reduced borders with oval inner apertures. This difference in pit structure is a concomitant of the increase in wall thickness in the late-wood cells. The pit-pairs between tracheids are usually with tori (fig. 9.3, *D, F*). Throughout most of a growth layer the pits are restricted to the radial walls (fig. 9.1); only in the late wood may the tangential walls bear pits. The pit-pairs are abundant on the overlapping ends including the parts that were added by intrusive growth. The pits are typically in one row. In the Taxodiaceae and Pinaceae some wide early-wood tracheids may have two or more rows of pits in opposite arrangement, and in the Araucariaceae pits occur in alternate arrangement (Phillips, 1948). In addition to the pitted secondary wall layers, conifer tracheids may have helical thickenings (fig. 9.3, *B*).

Axial parenchyma may or may not be present in conifer wood (I͡atsenko-Khmelevskiĭ, 1954; Phillips, 1948). In Podocarpaceae, Taxodiaceae, and Cupressaceae parenchyma is prominent in the wood (figs. 9.1 and 9.3, *C*). It is scantily developed or absent in Araucariaceae, Pinaceae, and Taxaceae. In some genera axial parenchyma is restricted to that associated with resin ducts (*Pinus, Picea, Larix, Pseudotsuga*). Resin ducts (figs. 9.2 and 9.3, *A*) appear as a constant feature of some woods (Pinaceae), but they also develop as a result of injury (traumatic resin ducts). They occur in the axial and in the radial systems.

The rays of conifers are mostly one cell wide (figs. 9.1 and 9.2), occasionally biseriate (fig. 9.3, *C*), and from one to twenty or even to fifty cells high. Presence of resin ducts makes the normally uniseriate rays appear multiseriate (fig. 9.2, *C*). The rays consist of parenchyma cells or may also contain ray tracheids. These tracheids resemble parenchyma cells in shape but are devoid of protoplasts at maturity and have secondary walls with bordered pits (fig. 9.3, *E*). Ray tracheids are normally present in most Pinaceae, occasionally in *Sequoia* and the Cupressaceae (Phillips, 1948). The ray tracheids commonly occur along the margins of rays, one or more cells in depth.

Each axial tracheid is in contact with one or more rays (fig. 9.1). The pit-pairs between the axial tracheids and ray parenchyma cells are

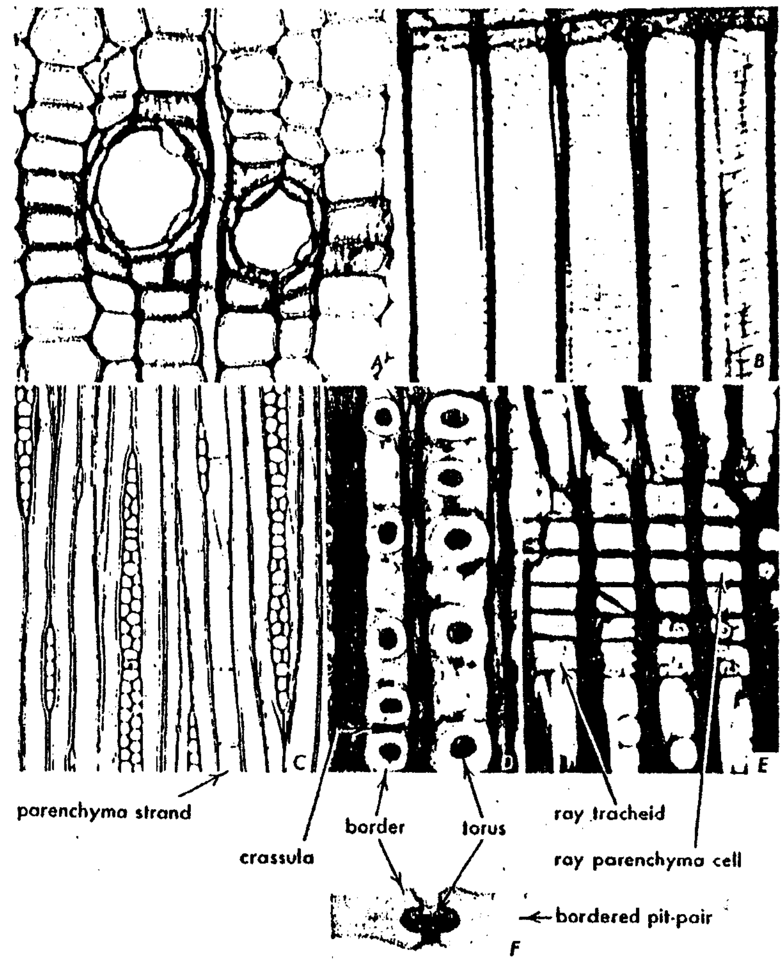


Fig. 9.3. Details of conifer wood. *A, B, Pseudotsuga taxifolia,* Douglas fir. *A,* resin ducts with thick-walled epithelial cells, in cross section. *B,* tracheids with spiral innermost layer of secondary wall in radial section. *C, Sequoia sempervirens* wood in tangential section: tracheids, axial parenchyma, uniseriate and biseriate rays. *D, E, F,* pine wood in radial (*D, E*) and tangential (*F*) sections. Only axial tracheids in *D, F;* ray with ray tracheids and parenchyma cells in *E.* (*A, B, E,* ×200; *C,* ×70; *D,* ×280; *F,* ×850.)

half-bordered, with the border on the side of the tracheid (chapter 8); those between the axial and the ray tracheids are fully bordered. The pitting between the ray parenchyma cells and the axial tracheids form such characteristic patterns in radial sections that the cross-field, or the rectangle formed by the radial wall of a ray cell against an axial tracheid (fig. 9.2, *B*), is utilized in classification and in phylogenetic studies of conifer woods.

DICOTYLEDON WOOD

The wood of the dicotyledons is more varied than that of the gymnosperms. The wood of the primitively vesselless dicotyledons is relatively simple, but that of the vessel-containing species is usually complex. Wood of the latter species may have both vessels and tracheids, one or more categories of fibers (chapter 8), axial parenchyma, and rays of one or more kinds (figs. 9.4, 9.5, and 9.6).

Storied and nonstoried wood

In transverse sections the secondary xylem shows more or less orderly radial seriation of cells—a result of the origin of cells from tangentially dividing cambial cells. In the homogeneous conifer wood this seriation is pronounced (fig. 9.2); in vessel-containing dicotyledons it may be somewhat obscured by the ontogenetic enlargement of the vessel members and the consequent displacement of adjacent cells (figs. 9.5 and 9.6). Radial sections also reveal the radial seriation; moreover, these sections show that the radial series of the axial system are superimposed one upon the other in horizontal strata (figs. 9.4 and 9.6). The tangential sections, however, are more varied in their appearance in different woods. In some, the cells of one stratum unevenly overlap those of another; in others the horizontal strata are as regular in tangential sections as they are in the radial sections. Thus, some woods are nonstratified, or nonstoried, in tangential sections (e.g., fig. 9.7, *A*; *Castanea, Fraxinus, Juglans, Quercus*), others stratified, or storied (e.g., fig. 9.7, *B*; *Aesculus, Cryptocarya, Ficus, Tilia,* and numerous Leguminosae). The storied condition is especially pronounced when the height of the ray matches that of a horizontal stratum of the axial system. From the evolutionary aspect the storied woods are more highly specialized than the nonstoried. They are derived from vascular cambia with short fusiform initials. Many intermediate patterns are found between the strictly stratified woods and the

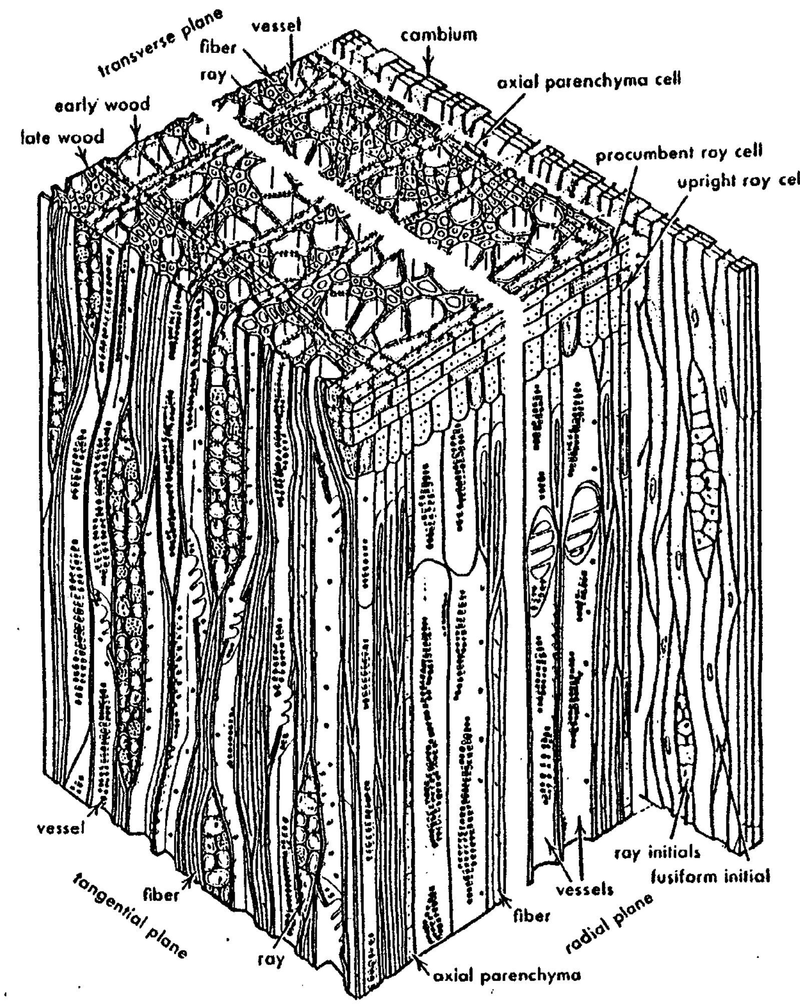


Fig. 9.4. Block diagram of vascular cambium and wood of *Liriodendron tulipifera* (tulip tree), a dicotyledon. The axial system consists of vessel members with scalariform perforation plates, fiber-tracheids, and axial xylem parenchyma strands in terminal arrangement. (Courtesy of I. W. Bailey. Drawn by Mrs. J. P. Rogerson under the supervision of L. G. Livingston. Redrawn.)

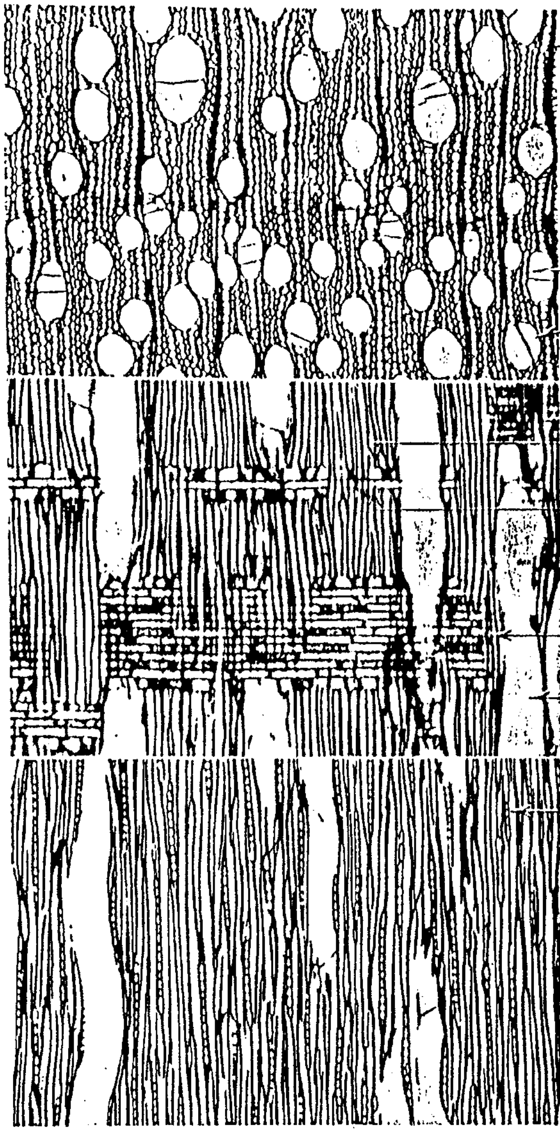


Fig. 9.5. Wood of willow (*Salix nigra*), a dicotyledon, in three sections. Diffuse-porous nonstoried wood with uniseriate heterocellular rays. (All, ×53.)

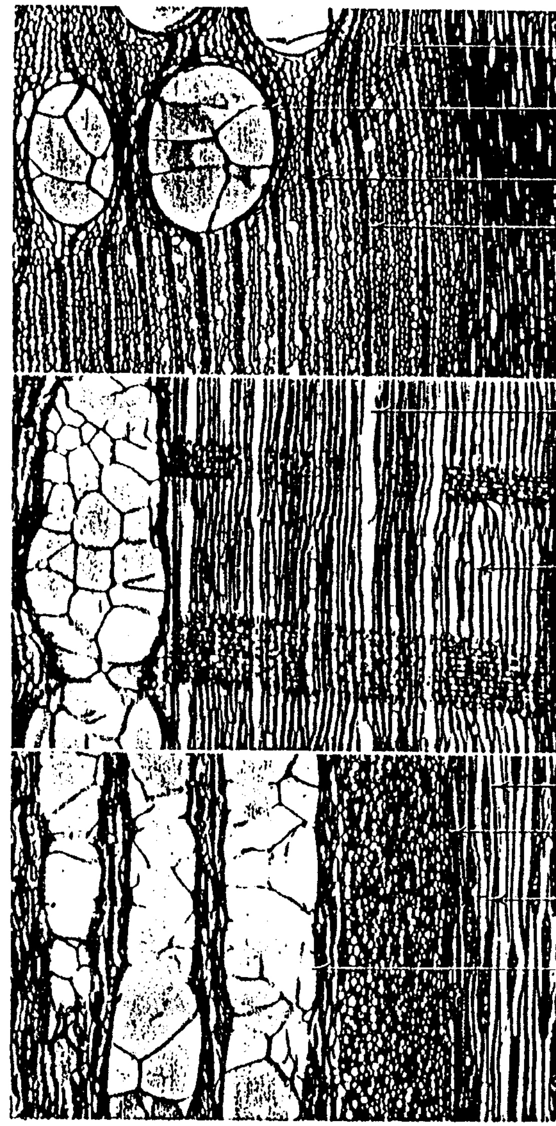
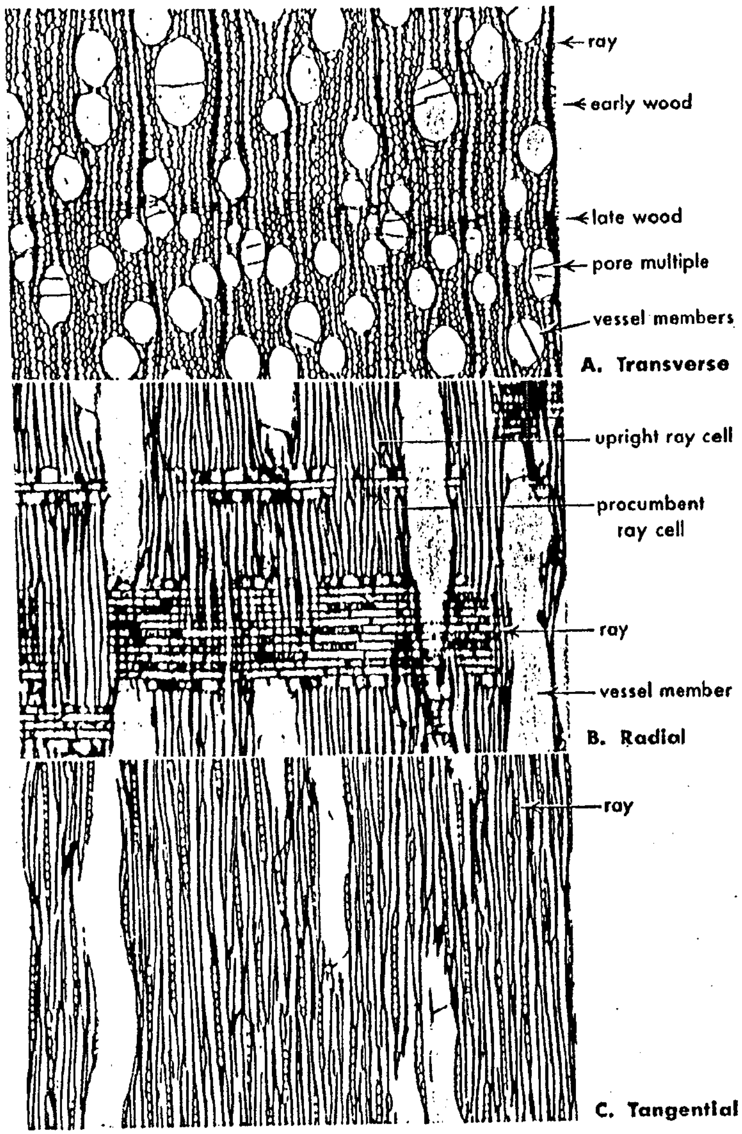


Fig. 9.6. Wood of oak (*Quercus alba*), a dicotyledon, in three sections. Ring-porous nonstoried wood with high multiseriate and low uniseriate rays. The large vessels are occluded by tyloses. (All, ×53.)



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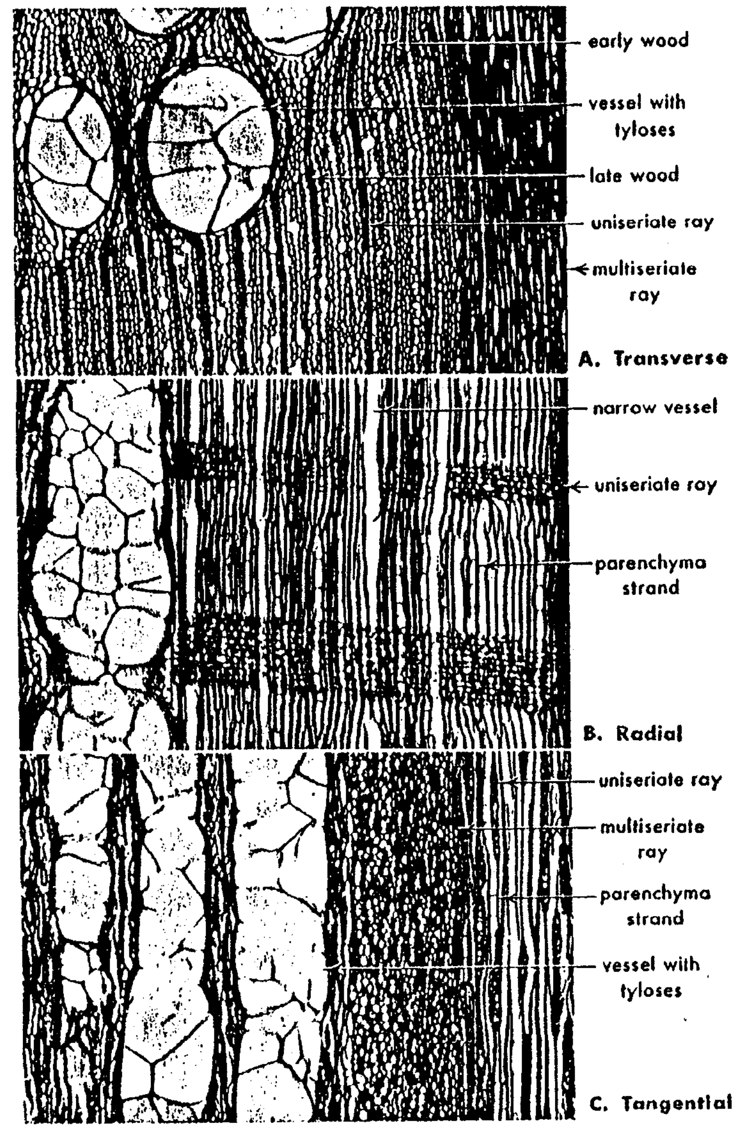

Fig. 9.6. Wood of oak (*Quercus alba*), a dicotyledon, in three sections. Ring-porous nonstoried wood with high multiseriate and low uniseriate rays. The large vessels are occluded by tyloses. (All, ×53.)