Anatomical Characteristics of Southern Pine Stemwood

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ABSTRACT. To obtain a definitive description of the wood anatomy of all 10 species of southern pine, juvenile, intermediate, and mature wood was sampled at three heights in one tree of each species and examined under a light microscope. Photographs and three-dimensional drawings were made to illustrate the morphology. No significant anatomical differences were found which would separate individual species.

In all species, latewood tracheids occasionally contained short segments of spiral thickening. Callitroid-like thickenings were found at some latewood pits and sometimes appeared to be associated with the spiral thickenings. Tangential pits of the same size as adjacent radial pits were scattered throughout the annual ring. Only uniseriate radial pitting was found in early-wood tracheids of Virginia pine, but this is of little diagnostic value, as individual samples from other species may lack two- and three-row pitting.

Ray tracheids of spruce pine generally appeared less dentate than those of the other species; all except spruce pine contained sporadic thick-walled ray parenchyma. Longitudinal parenchyma partially surrounds most vertical resin canals.

As part of its program to characterize the southern pines as an industrial raw material, the Southern Forest Experiment Station's forest utilization laboratory at Alexandria, La., conducted a study of the anatomy of the species comprising this group of the hard pines.

Since the aim was to achieve a definitive description, sampling was intensive and was extended to all 10 species, including both races of sand pine and the South Florida variety of slash pine. In addition, special effort was devoted to making drawings[1] and photos illustrating important characteristics. The species were:

Loblolly (*Pinus taeda* L.)
Longleaf (*P. palustris* Mill.)
Pitch (*P. rigida* Mill.)
Pond (*P. serotina* Michx.)
Sand (*P. clausa* Vasey) — the Ocala race and the Choctawhatchee race[2]
Shortleaf (*P. echinata* Mill.)
Slash (*P. elliottii* var. *elliottii* Engelm.)
South Florida slash (*P. elliottii* var. *densa* Little and Dorman)
Spruce (*P. glabra* Walt.)
Table-mountain (*P. pungens* Lamb.)
Virginia (*P. virginiana* Mill.)

The study was designed in the knowledge that most U.S. authorities consider the southern pines anatomically indistinguishable. It was felt, however, that this point should not be regarded as settled, especially for the minor species. Budkevich (3) has published a key that subdivides the species and individually separates pond, sand, and Virginia pines. In Greguss's (6) descriptions there are differences from which a key could be devised, and Panshin *et al.* (11, p. 429) present a supplemental key for the four major species. Jacquiot's (8) key separates four species by

[1] The drawings were made by Irmgard Knoth under the supervision of the authors.

[2] Ward (14) proposes that the open-coned Choctawhatchee sand pine is a variety rather than a race; he gives the name *P. clausa* var. *immuginata* var. nov.

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resin-canal diameters and crossfield pitting. The research therefore had the additional aim, pursued resolutely but with varying hope, of finding a reasonably simple and practicable method of identification.

So that the description, as well as any identification points that might be developed, would not rest on characteristics that may vary randomly within the stem, we decided to examine systematically and in considerable detail a single tree of each species, variety, and race. (A few features were checked in additional trees.) We were looking for the presence or absence of individual structures and any obvious variation in size, frequency, distribution, and form of structures. There was no attempt to make morphological counts and measurements for computation of statistical differences among species. If such differences could be shown to exist, variation between samples would still defeat efforts to apply them in identifying any one piece of wood.

Procedure

Sample trees were felled, and cross-sectional disks were cut from the stems at three heights — 1 foot above ground, one-third of tree height, and two-thirds of tree height. From each disk, samples were taken of juvenile (0-5 years), intermediate (13-18 years), and mature wood (25-30 years). Conventional microtechnique was used to prepare permanent sections for four views — transverse, radial, tangential earlywood, and tangential latewood. Two blocks were cut for each view and two sections were mounted per block. Thus there were 144 sections per tree: three heights × three ages × four views × two blocks × two replications/block.

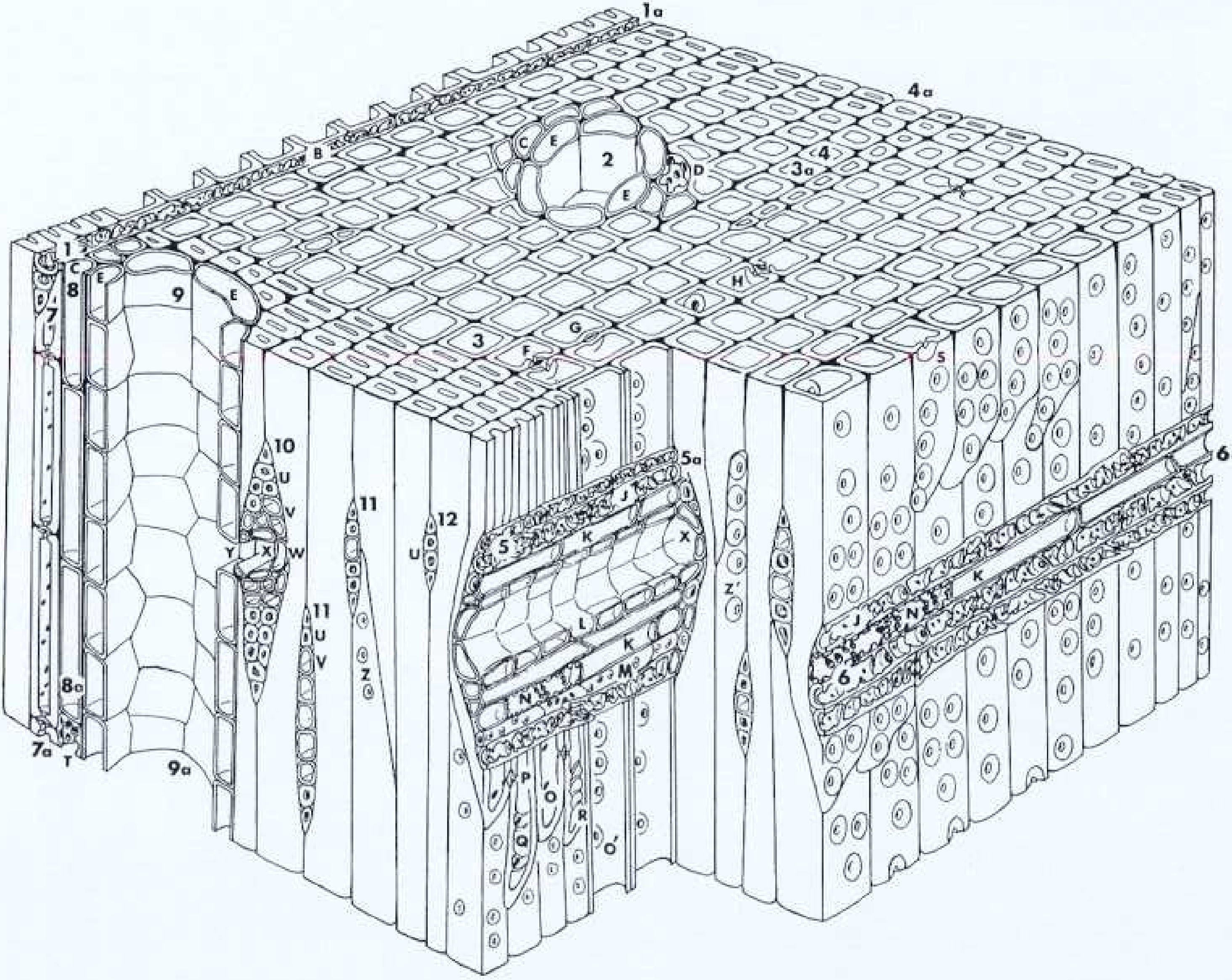
Results

By our nonstatistical anatomical approach the southern pines in general could not be individually separated. Therefore, the following description and drawings apply to all southern pines. The tissues and cell types of a block of typical wood are illustrated in Figure 1.

Longitudinal Elements

Tracheids. — The longitudinal tracheids (Figs. 1 and 2) are typical of conifers. They

Figure 1. — Schematic drawing of typical southern pine wood.
Transverse view. *1-1a*, ray; *B*, dentate ray tracheid; *2*, resin canal; *C*, thin-walled longitudinal parenchyma; *D*, thick-walled longitudinal parenchyma; *E*, epithelial cells; *3-3a*, earlywood tracheids *F*, radial bordered pit pair cut through torus and pit apertures; G, pit pair cut below pit apertures; *H*, tangential pit pair; *4-4a*, latewood.
Radial view. *5-5a*, sectioned fusiform ray; *J*, dentate ray tracheid; *K*, thin-walled parenchyma; *L*, epithelial cells; *M*, unsectioned ray tracheid; *N*, thick-walled parenchyma; *O*, latewood radial pit (inner aperture); *O'*, earlywood radial (inner aperture); *P*, tangential bordered pit; *Q*, callitroid-like thickenings; *R*, spiral thickening; *S*, radial bordered pits (the compound middle lamella has been stripped away, removing crassulae and tori); *6-6a*, sectioned uniseriate heterogeneous ray.
Tangential view. *7-7a*, strand tracheids; *8-8a*, longitudinal parenchyma (thin-walled); *T*, thick-walled parenchyma; *9-9a*, longitudinal resin canal; *10*, fusiform ray; *U*, ray tracheids; *V*, ray parenchyma; *W*, horizontal epithelial cells; *X*, horizontal resin canal *Y*, opening between horizontal and vertical resin canals *11*, uniseriate heterogeneo *12*, uni- omogeneous ray; *Z*, small tial pits in *Z'*, large tangential p in earlywood.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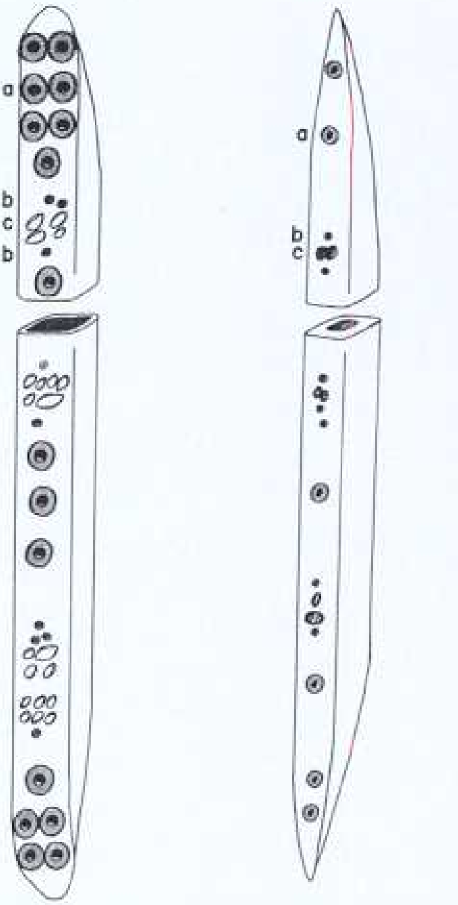

Figure 2. — Earlywood (left) and latewood (right) tracheids: *a*, inter-tracheid bordered pits; *b*, bordered pits to ray tracheids; *c*, pinoid pits to ray parenchyma.

are aligned radially, have overlapping ends, and taper to a point in tangential view but are blunt and rounded radially. The transition between earlywood and latewood generally is abrupt. Frequently, the last rows of latewood cells are flattened radially.

Tracheid walls have three kinds of pits: (a) large bordered pits connecting neighboring tracheids; (b) smaller bordered pits communicating with ray tracheids; and (c) half-bordered pinoid pits leading to ray parenchyma cells (Fig. 2). Pits between tracheids are chiefly on the radial walls and tend to be concentrated near the ends. Radial pitting may be uniseriate (pits in a single row), biseriate, or rarely triseriate. In earlywood, pits are large and have round apertures; in late-

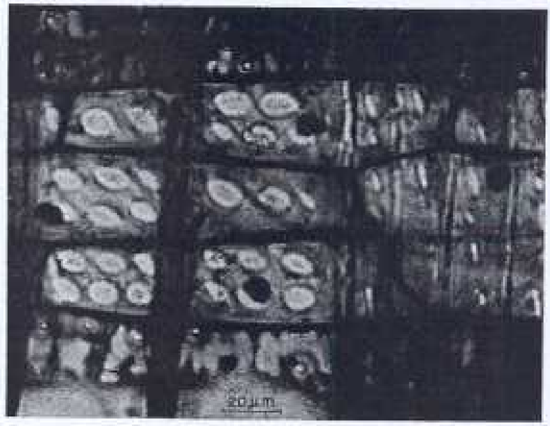

Figure 3. — Crossfield pinoid pitting, earlywood and latewood. Radial section.

wood they are smaller and have elliptical or slit-like apertures. Crassulae frequently bound the upper and lower edges of radial pits in earlywood.

Narrow borders are usually visible on the pinoid pits occurring between longitudinal tracheids and ray parenchyma (Figs. 3 and 4). These pits are of various shapes and sizes

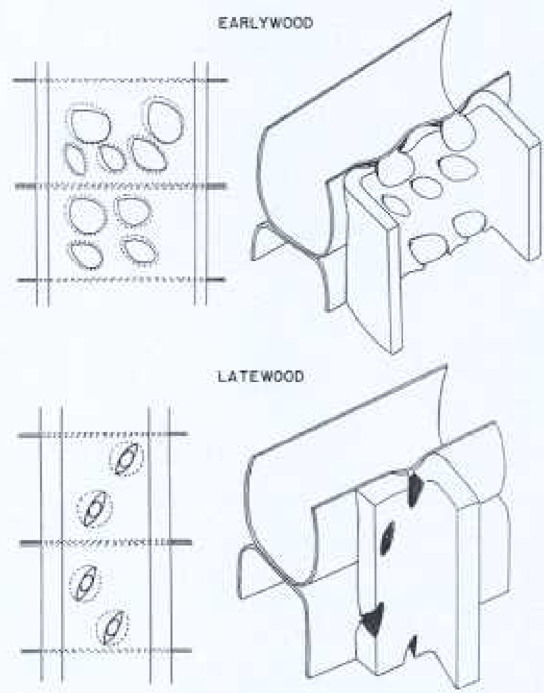

Figure 4. — Pinoid pits between tracheids and ray parenchyma. Left, microscopic views. Right, three-dimensional, opaque drawings.

and are arranged in clusters of two to seven (rarely eight) in earlywood and one to two (occasionally three) in latewood.

Tangential pits connecting tracheids, though not so frequent as radial pits, are fairly common in the southern pines. Contrary to most statements in the literature, they are not confined to the last-formed latewood and first-formed earlywood. Rather, they are found throughout the growing ring, more frequently in earlywood than in latewood. Most earlywood sections contain several examples. The pits are grouped near the ends of the cells. No instances were found in which tangential pits were smaller than the adjacent radial pits — in all cases both radial and tangential pits were about equal in size (Fig. 5). The frequent statements that tangential pits are always smaller probably stem from comparisons of latewood tangential pits with earlywood radial pits — see, for example, the illustration on p. 101 of Panshin *et al.* (11).

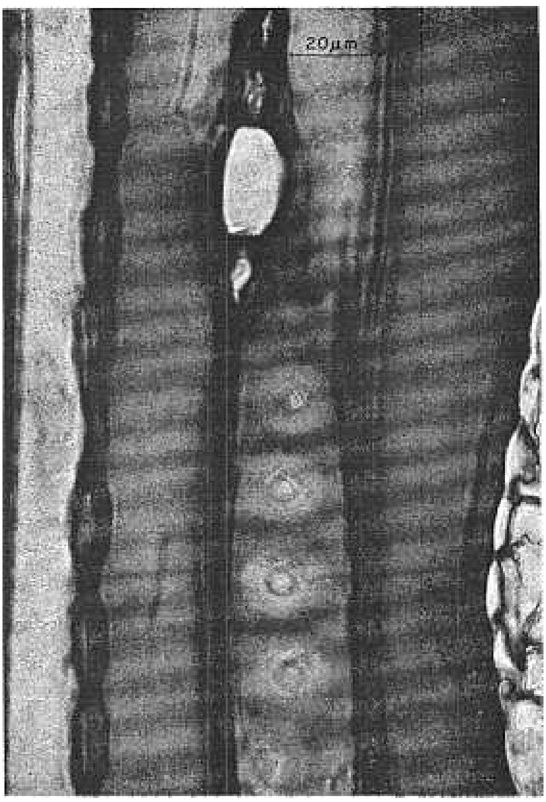

Figure 5. — Tangential pits in earlywood, tangential section. Compare with radial pits on left.

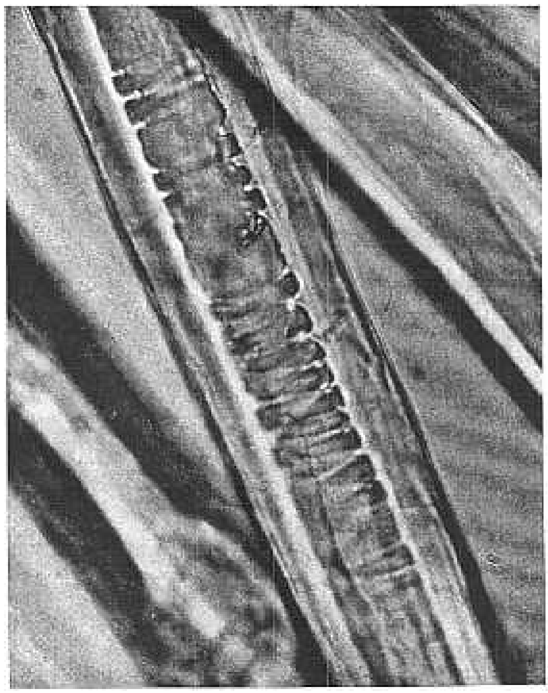

Figure 6. — Spiral thickening in macerated tracheid of mature latewood.

Spiral thickenings are not a constant feature of southern pine but were found sporadically in all trees examined, usually in latewood. The thickenings usually occur for short distances along the tracheid length (Fig. 6), sometimes with several groupings per tracheid.

Observations of latewood tracheids in both radial and tangential views reveal that some bordered pit apertures are bounded by transverse thickenings (Figs. 7 and 8). The ridges closely resemble the callitroid thickenings described in some *Callitris* species (4, 12, 13). They appear to extend across the aperture edges on the radial wall, flattening and disappearing on the tangential wall. Spiral thickenings sometimes appear to be associated with them. These callitroid-like thickenings occasionally appear on tangential pits and pits connecting longitudinal tracheids with rays.

The thickenings were most pronounced and frequent in pond pine but also were well developed in pitch, shortleaf, slash, and loblolly pines. They were less pronounced and less frequent in longleaf, table-mountain, and spruce pines. In Virginia, South Florida slash

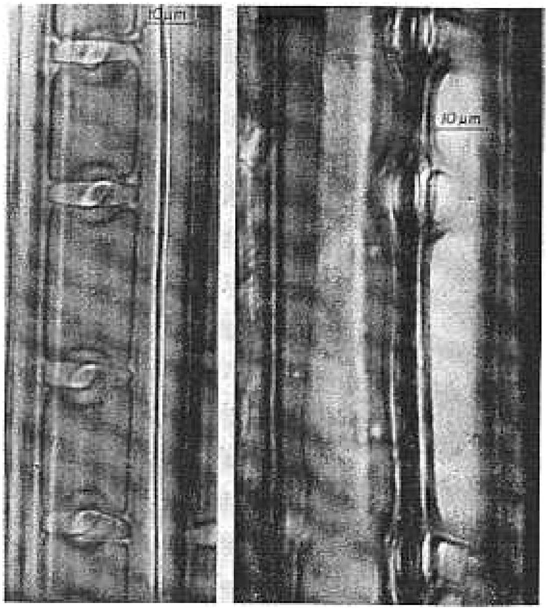

Figure 7. — Callitroid-like thickenings of latewood. Left, radial section. Right, tangential section.

(var. *densa*), and both races of sand pine they were very rare and poorly defined.

During heartwood formation, resin is sometimes secreted from the rays into adjacent tracheids. There it forms amorphous deposits, reddish brown to black, that partially or completely fill the cell as viewed in cross-section. In longitudinal section the deposits appear as transverse plates across the cell or as lumps on the tracheid wall (11, p. 103). Occurrence of resinous tracheids is sporadic in the southern pines.

Strand Tracheids. — Strand tracheids occasionally occur along vertical resin canals outside the parenchymatous tissue. They are shorter than the longitudinal tracheids and are characterized by pitted transverse ends and tiny bordered pits along the vertical walls (Fig. 1, 7-7a).

Epithelial Cells. — Of all the conifers, the pines have the largest and most numerous resin canals. Horizontal and vertical ducts interconnect to form a continuous system (Fig. 1, 9-9a, X, Y).

The resin canals are lined with the thin-walled epithelial cells that secrete oleoresin into them. In longitudinal section these secretory cells vary in shape from more or less square to somewhat hexagonal (Fig. 9). Resin canals in heartwood frequently are obstructed by tylosoids resulting from proliferation of epithelial cells.

Parenchyma. — The literature generally states that trees of the genus *Pinus* do not contain longitudinal parenchyma. However, Bannan (2), Phillips (13), Esau (5, p. 248), and Nyren and Back (10) recognize its occurrence in conjunction with resin canals.

In southern pines longitudinal parenchyma partially surrounds most longitudinal resin canals. The parenchyma lies in strands just outside the sheath of epithelial cells, and in vertical section is distinguishable from them by the longer, narrow dimensions and more rectangular shape (Fig. 1, 8-8a, C; Fig. 9). When more than one layer is present, cells of the innermost strand are slightly longer than the epithelial cells, whereas units of the outermost layer are one-and-one-half to three times as long.

Most longitudinal parenchyma cells are thin-walled; thick-walled specimens are occasionally found. These have conspicuous simple pits that give a nodular appearance to all walls (Fig. 1, D, T).

Horizontal Elements

The rays contain all the horizontal elements of the xylem: ray tracheids, ray parenchyma, and epithelial cells (Figs. 1 and 10). A southern pine ray may be either homogeneous

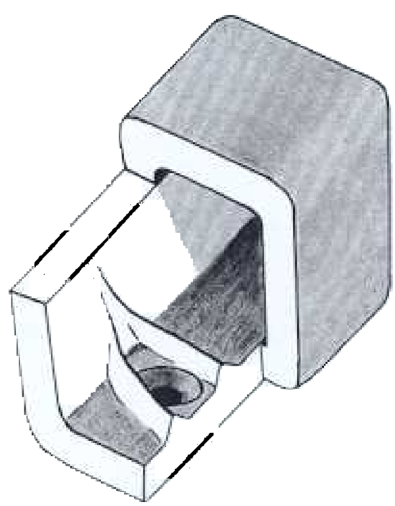

Figure 8. — Callitroid-like thickenings at radial pit in latewood.

(composed of only one cell type), or heterogeneous (containing both ray tracheids and parenchyma). Most rays are uniseriate, *i.e.*, one cell wide. Multiseriation is found only in the central portion of fusiform rays, which contain horizontal resin canals.

Ray Tracheids. — The ray tracheids are distinctive in possessing prominent and complicated wall thickenings (Fig. 11). In radial

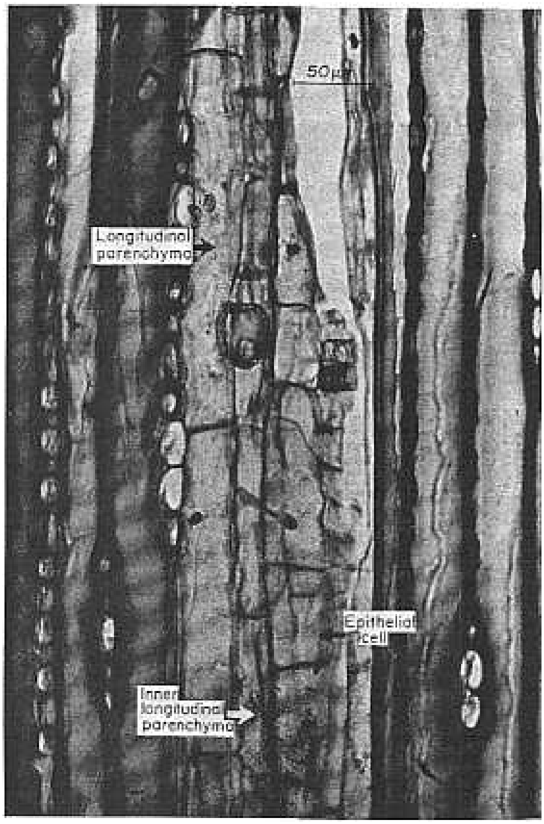

Figure 9. — Longitudinal parenchyma and epithelial cells of resin canal. Longitudinal section.

Figure 11. — Sectioned dentate ray tracheids.

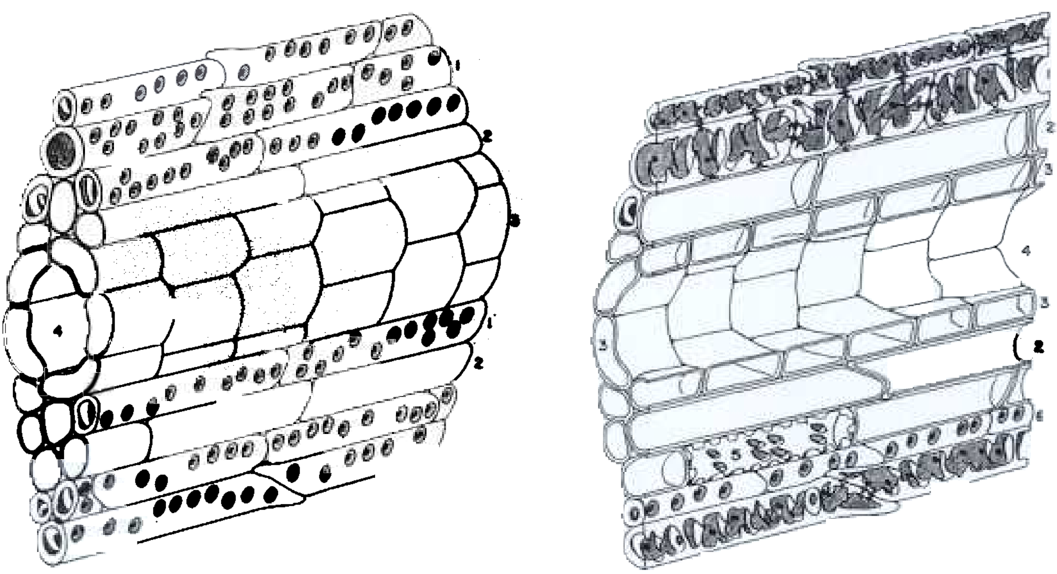

Figure 10. — Fusiform ray. Left, unsectioned. Right, sectioned longitudinally. *1*, ray tracheids; *2*, ray parenchyma; *3*, epithelial cells; *4*, resin canal; *5*, thick-walled parenchyma with simple pits; *6*, unsectioned ray tracheids with bordered pits.

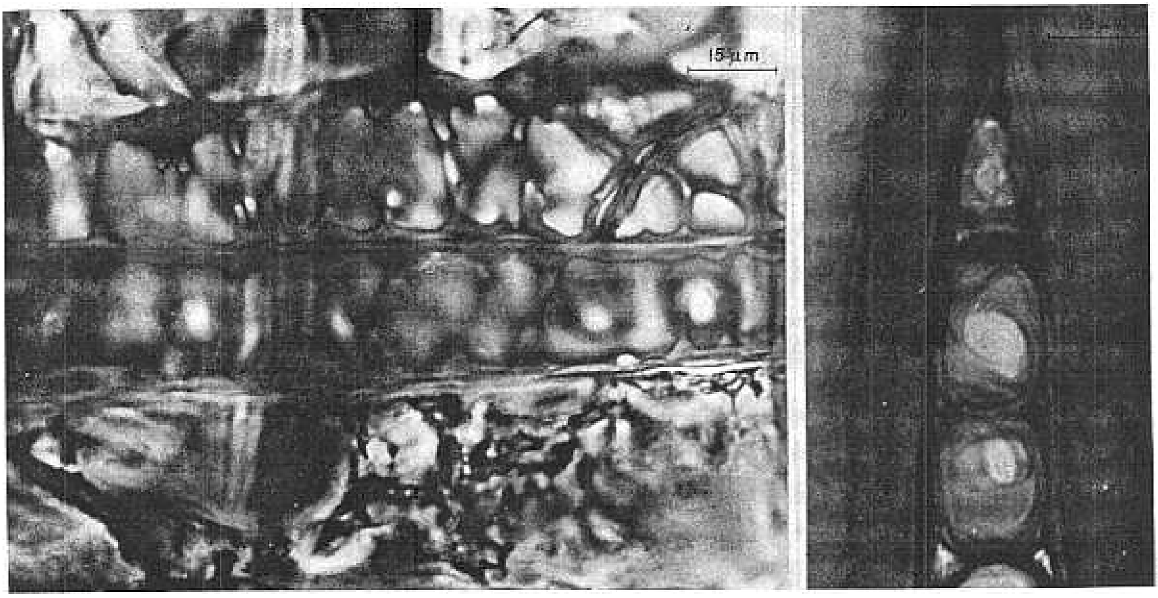

Figure 12. — Dentate ray tracheids. Left, radial section. Living parenchyma at bottom. Right, tangential section.

(Fig. 12, left) and transverse section these give a jagged appearance and have commonly been described as "toothlike projections." In tangential view (Fig. 12, right) the sculpturings are seen as irregular, circular, or semicircular ridges extending partially around the interior but not completely closing the lumen. An illustration by Jacquiot (8) points toward a similar concept of these dentations and reticulations.

In heterogeneous rays, ray tracheids form the margins and may be interspersed among the central parenchyma rows. Small bordered pits connect the ray tracheids with each other and with longitudinal tracheids. Walls adjacent to ray parenchyma have half-bordered pits.

The degree of dentation varies between individual rows of ray tracheids; those nearer the center of the ray are more dentate. Hudson (7) points out that the greatest degree of variation between specimens is found in the outermost marginal row. The maximum dentation occurs in the latewood and first-formed rows of earlywood.

Occasionally enlarged marginal ray tracheids of highly irregular shape are found; they extend vertically into the longitudinal tissues and may join with cells of other rays. Such "erect" structures are considered abnormal and are not of diagnostic value.

Ray Parenchyma. — Ray parenchyma cells are located in the central portion of heterogeneous rays. Two forms may be found. The majority are thin-walled and unpitted, but thick-walled, heavily pitted cells occur (Figs. 10, 13, and 14). The latter have a nodular appearance in section and appear lignified. Balatinecz and Kennedy (1) observed that in the hard pines having pinoid pits (which includes the southern pines), the number of thick-walled cells increases as the sapwood-heartwood boundary is approached. Wall-thickening was associated with maturation as defined by lignification. Both thick- and thin-walled forms may be found in the same ray. Where both are present, the thick-walled cells are nearer the ray margins, usually adjacent to ray tracheids. Pitting is simple. Rays of all trees except spruce pine contained occasional thick-walled parenchyma.

Pinoid pits occur where longitudinal tracheids and ray parenchyma are in contact (Figs. 3 and 4). These pits are bordered on the tracheid side. The corresponding area in thick-walled parenchyma contains a simple pit, but in thin-walled parenchyma there is no apparent decrease in wall thickness. There-

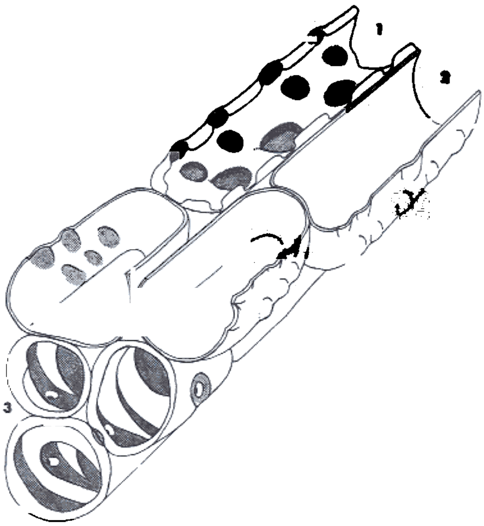

Figure 13. — Sectioned ray parenchyma. 1, thick-walled parenchyma with simple pitting; 2, thin-walled parenchyma. Note bulges where wall conforms to tracheid bordered pit chamber at crossfield. 3, dentate ray tracheids.

fore, the crossfield pitting seen in radial section actually exists on the tracheid wall only and is visible through the transparent parenchyma (Fig. 4). The thin parenchyma wall may sometimes (particularly in the larger pits) bulge outward slightly to conform with the tracheid pit chamber. Number, shape, and size of crossfield pits vary considerably within a single ray and from ray to ray.

Epithelial Cells. — Horizontal epithelial cells are found only in rays containing resin canals (fusiform rays) (Figs. 1, L, W, and 10). They are similar to, but smaller than, epithelial cells of the vertical resin canals.

Discussion

Our investigation, like that of Hudson (7), disclosed no anatomical features that would permit positive identification of the wood of any species of southern pine. As Phillips (13) points out, it is difficult to apply keys dealing with a limited number of species, *e.g.*, Jacquiot (8) and Panshin *et al.* (11, p. 429), unless it is known that the specimen to be identified is one of those in the key. We found that the differences reported by Budkevich (3) and implied by Greguss (6) were not valid. Their descriptions apparently were based on sample sizes insufficient to recognize natural variation. In the sections we examined there was more variation within trees than between species.

Virginia pine tracheids typically have uniseriate radial pitting in earlywood. Care

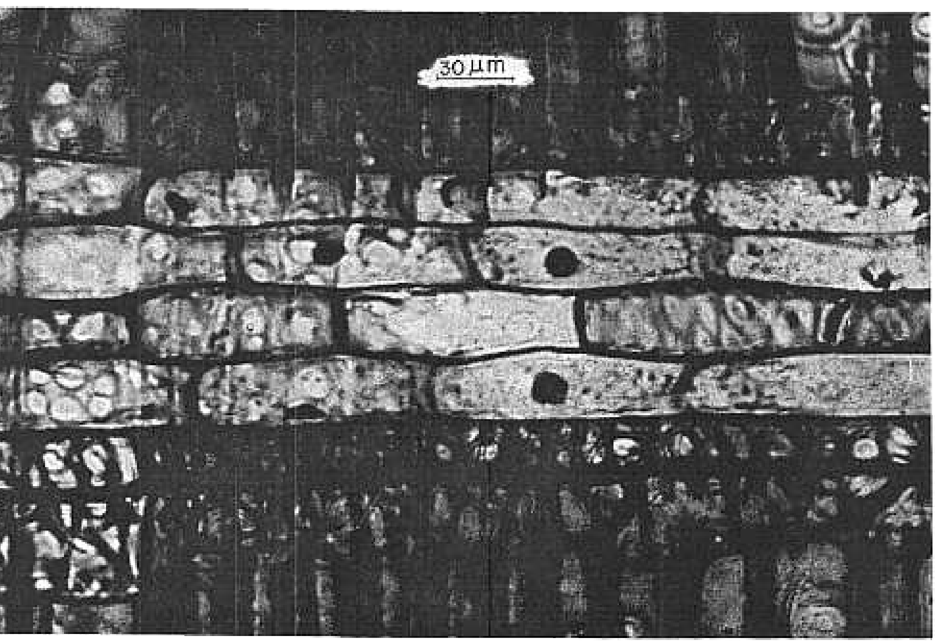

Figure 14. — Ray with both thin- and thick-walled parenchyma. Radial view.

should be taken, however, in identification by this feature alone, for table-mountain, spruce, Ocala sand, Choctawhatchee sand, and pitch pines also have one-row pitting with few biseriate pits. While ray tracheids are less dentate in spruce pine than in most other southern pines (7), the species cannot positively be separated on this basis alone, as trees of most other species also exhibit some instances of minor dentation. No thick-walled parenchyma was found in spruce pine; however, only three trees were observed. In any event, the scarcity of thick-walled parenchyma in other species would make this feature of minor diagnostic value.

Several notations of interest emerged from this study. Tangential pits are not confined to a particular portion of the growth ring, though they occur more frequently in earlywood and are usually in the tracheid ends. They are of the same size and shape as radial pits in the same area.

Callitroid-like thickenings are visible in radial and tangential sections of some latewood tracheids. Varying degrees of development and frequency were noted in the various species of the southern pines.

Ray tracheid dentations and reticulations are not in the form of "teeth," as the radial appearance might indicate. Rather, the inside wall is sculptured on all sides into highly irregular ridges or thickenings that partially encircle the interior.

Longitudinal parenchyma is present in strands adjacent to the epithelial cells of vertical resin canals. Its presence is, for the most part, overlooked in the literature. Small amounts of sporadic spiral thickening are present in all species. Longitudinal resinous tracheids occur occasionally. Most parenchyma and epithelial cells have thin walls, but thick-walled cells with simple pits may be found infrequently in all types of parenchymatous tissue, particularly in the rays.

Literature Cited

1. Balatinecz, J. J., and R. W. Kennedy. 1967. Maturation of ray parenchyma cells in pine. Forest Prod. J. 17(10):57-64.
2. Bannan, M. W. 1936. Vertical resin ducts in the secondary wood of the Abietineae. New Phytol. 35:11-46.
3. Budkevich, E. V. 1961. Wood of the Pines. Izd. Akad. Nauk SSR, Moscow-Leningr., pp. 85-96, 118-125, 136-139.
4. Cronshaw, J. 1961. The nature of callitroid thickenings. J. Inst. Wood Sci. 8:12-13.
5. Esau, K. 1953. Plant Anatomy. 735 pp. N.Y.: John Wiley & Sons, Inc.
6. Greguss, P. 1955. Identification of Living Gymnosperms on the Basis of Xylotomy. Akad. Kiado, Budapest, pp. 241-246.
7. Hudson, R. H. 1960. The anatomy of the genus Pinus in relation to its classification. J. Inst. Wood. Sci. 6:26-46.
8. Jacquiot, C. 1955. Atlas d'Anatomie des Bois des Conifères. Inst. Nat. du Bois, Paris, pp. 16-34, 84-93.
9. Jane, F. W. 1956. The Structure of Wood. 427 pp. London: A & C Black.
10. Nyren, V., and E. Back. 1959. Characteristics of parenchymatous cells and tracheidal ray cells of *Pinus sylvestris* pulpwood. The resin in parenchymatous cells and resin canals of conifers. III. Norsk Skogindustri 13(8):267-278.
11. Panshin, A. J., C. deZeeuw, and H. P. Brown. 1964. Textbook of Wood Technology. Vol. 1. Structure, identification, uses and properties of commercial woods of the United States. Ed. 2, 643 pp. N.Y.: McGraw-Hill Book Co., Inc.
12. Patton, R. T. 1927. Anatomy of Australian coniferous timbers. Proc. Roy. Soc. Victoria 40(1): 1-16.
13. Phillips, E. W. J. 1941. The identification of coniferous woods by their microscopic structure J. Linn. Soc. London—Bot. 52(343):259-320.
14. Ward, D. B. 1963. Contributions to the flora of Florida — 2 *Pinus* (Pinaceae). Castanea 28(1) 1-10.