Bark Structure of the Southern Pines

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ABSTRACT. The living inner bark is composed of thin-walled elements — sieve cells, albuminous cells, longitudinal and ray parenchyma, and epithelial cells. The rhytidome or outer bark is dead and has alternating areas of distorted phloem enclosed by periderm layers. Periderms consist of phellogen and its derivative cells — phelloderm and phellem. Phelloderm cells, to the inside of the phellogen, may be thickened or expanded. Radially elongated innermost phelloderm cells may be confused with expanded parenchyma. Phellem, to the outside of the phellogen, is comprised of bands of thin-walled suberized cork cells alternating with bands of thick-walled, unsuberized, spiculate stone cells. The proportions of each tissue may vary widely within a single sample. Only the innermost periderm is alive; each periderm subsequently dies when a new periderm forms closer to the vascular cambium. Periderms do not appear to be correlated with annual growth. In the transformation from inner bark to rhytidome, sieve cells collapse and parenchyma enlarge greatly. After this obliteration process, sieve cells probably form less than 30 percent of rhytidome volume. Sieve cells are comparable to wood tracheids in length; all other cells are much smaller. Stone cells and the outermost, thickened phelloderm cells are the only heavily lignified elements. Stone cells comprise about 10 percent or less of rhytidome, but they greatly influence density and hardness. In transverse view, longitudinal parenchyma are in discontinuous tangential rows or scattered. Elongated styloid crystals occur in lumina of many sieve cells and parenchyma. Longitudinal resin canals usually are not present; horizontal ducts occur in fusiform rays. Periderm shape and spacing varied greatly within species. Periderm color was dark in pond and loblolly pines, light in Virginia pine, and variable in all other species. Bark obliteration and thickness decreased with height in tree; no other variation with height was noted. Barks of Virginia, sand, and spruce pines were harder, more fibrous, and less obliterated than barks of the other seven species. Stone cell bands form the outer margins of spruce pine periderms; thin-walled cork cells comprise the outer portion of periderms in longleaf, Virginia, slash, and sand pines. Structural factors such as periderm shape and spacing, amount of stone cells, tangential zones of weakness, and degree of obliteration and expansion may explain most variation in physical and mechanical properties of southern pine barks.

BARK COMPRISES APPROXIMATELY 10 percent of the weight of merchantable southern pine stems. In general, industrial firms utilizing pine derive little return from this fraction of the tree, while they incur costs for transport, removal from the stem, and disposal. It seems timely, therefore, to analyze bark structure as a basis for developing possible future uses.

This paper reports a detailed anatomical study of the bark of the 10 southern pines. A companion paper has described southern pine stemwood; the reader is referred to it for structural comparisons (Howard and Manwiller 1969). In both studies sampling included the two races of sand pine and the South Florida

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At some distance from the cambium, a new tissue — the phellogen or cork cambium — appears within the older phloem. The phellogen (a single layer of dividing cells) produces a tangentially oriented periderm, which protects the delicate phloem tissue from harmful external influences. Portions of older phloem are sealed off from interior supplies of moisture and nutrients by the outward-curving and impervious periderm layers (Fig. 1); the cells of these isolated areas undergo striking changes and die. Each periderm and the phloem it isolates are in turn pushed outward; a new periderm arises further inward and the older periderm dies. Since outer layers are not sloughed off as rapidly as interior ones are formed, the thick scaly bark typical of southern pines is eventually accumulated.

A cross-sectional or radial cut through mature southern pine bark shows two distinct zones. The narrow light-colored region next to the vascular cambium is the inner bark; it contains the living food-conducting and storage cells. The thick outer bark (rhytidome) consists of areas of dark porous tissue (dead phloem) subdivided by relatively conspicuous, merging lines of periderm. The innermost periderm separates inner bark from rhytidome.

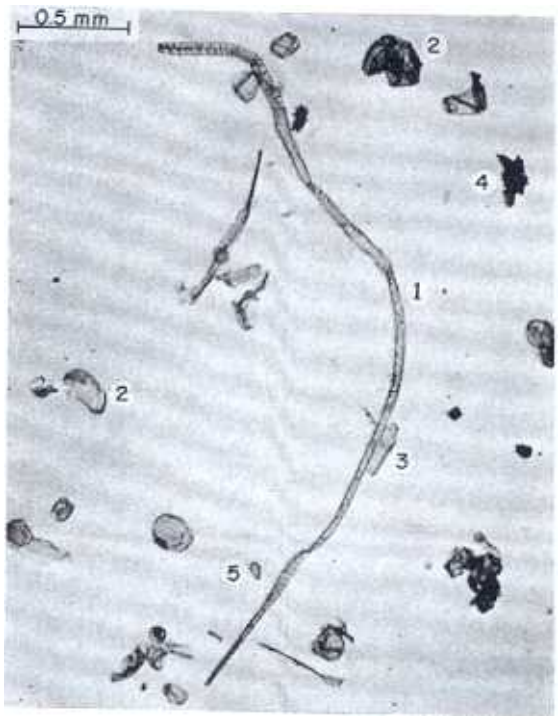


Figure 3. — Macerated bark from longleaf pine. All other cells are quite small in relation to sieve cells. (1) sieve cell, showing sieve areas (a portion of another sieve cell still adhering at upper left). (2) expanded parenchyma, (3) unexpanded parenchyma, (4) phellem stone cells, (5) phelloderm cell.

Inner Bark

Inner bark encompasses all the tissues from the vascular cambium outward to the innermost periderm. It includes the phloem produced during a number of years. In southern pines inner bark is relatively narrow; in trees observed in this study it ranged from 0.5 mm. to slightly over 2 mm. in width, and averaged about 1.5 mm. According to Huber (1958), only a very narrow band next to the cambium — perhaps 200 to 300 μm in width — is active in conducting photosynthates downward from the leaves to the various areas of use or storage.

Most of the phloem cells are oriented longitudinally. Fusiform initials of the cambium produce the vertical phloem elements: sieve cells, longitudinal parenchyma, and some albuminous cells. There are no typical phloem fibers. Ray initials give rise to the horizontal system of ray cells: ray parenchyma, albuminous cells and, in fusiform rays, epithelial cells. Elements of southern pine phloem are illustrated in Figure 2. Their xylem counterparts are as follows:

Xylem

- Tracheids
- Rays
  - Ray tracheids
  - Ray parenchyma
  - Epithelial cells (only at resin canals of fusiform rays)
- Longitudinal parenchyma (at longitudinal resin canals only)

Phloem

- Sieve cells
- Rays
  - Albuminous cells
  - Ray parenchyma
  - Epithelial cells (only at resin canals of fusiform rays)
- Dispersed longitudinal parenchyma (longitudinal resin canals normally absent)

Sieve cells. — The only distinctly elongated elements of southern pine bark are the sieve cells (Figs. 2A, 3, 4). They are the main food-conducting cells and are vertically oriented. Sieve cells are comparable to xylem tracheids in size, shape, and arrangement. They are long and slender with overlapping ends. The thin, non-lignified, cellulosic walls have numerous circular to oval sieve areas (specialized pit fields); they correspond to tracheid pitting and are mainly confined to the radial walls. Walls in the sieve areas are thinner than in the rest of the cell and contain a variable number of pores which are often clustered into several groups. In living tissue, protoplasmic connecting strands pass through the pores to sieve areas of other sieve cells and to ray albuminous cells.

Sieve areas were observed to be of only one structural type, but they varied in size according to cell dimensions and position. In a single sample they ranged from 5 μm to 30 μm in diameter.

The functioning life of sieve cells in southern pines is not precisely known, although for most trees it is presumed to be only 1 year, or possibly 2 years, after formation (Esau 1965, p. 302; Srivastava 1964). A carbohydrate deposit called callose lines the pores of sieve areas (Esau 1965, p. 277). With reduced activity of the cell, callose grows to become the massive accumulation known as definitive callose. This marks the end of the functioning life of the sieve cell. Definitive callose gradually disappears (leaving minute open perforations) after death of the cell; only rarely, therefore, are remnants found in outer bark. With the loss of turgidity, the sieve cells collapse and their original radial alignment becomes distorted while they are still in inner bark.

Chang (1954a, p. 224) reported that in *P. elliottii* sieve cells make up 54.2 percent and parenchyma 37.5 percent of inner bark. The volume that sieve cells occupy in rhytidome is substantially reduced (probably to less than 30 percent) because of further sieve cell collapse, parenchyma enlargement, and introduction of periderm tissue.

Longitudinal parenchyma. — In southern pine wood, longitudinal parenchyma is found only in association with the vertical resin canals (Howard and Manwiller 1969). In phloem, however, vertical resin canals usually are lacking and the longitudinal parenchyma is dispersed among the sieve cells. Phloem parenchyma cells, like those of wood, have thin primary walls, are somewhat cylindrical, and occur in vertical strands (Figs. 2 and 4).

While in some specimens tangential alignment of parenchyma was discernible in undistorted phloem, it was usually only one cell wide and somewhat discontinuous. In transverse views of some samples parenchyma appeared scattered. It has been suggested that parenchyma arrangement may indicate seasonal growth increments, but this has not been confirmed by growth studies. Tangential arrangement, where present, is soon distorted and eventually obscured; consequently, it is not observed in rhytidome of most specimens.

Starch, tannins, resins, oil globules, crystals, and other substances are stored in phloem parenchyma. Walls of parenchyma cells have primary pit fields (areas of the primary wall with submicroscopic pores) through which they communicate with other parenchyma and with ray cells. Parenchyma cells usually do not appear to be associated with sieve cells (Srivastava 1963; den Outer 1967). Some parenchyma cells become meristematic and give rise to phellogen.

Rays. — Phloem rays are continuous with xylem rays and perform similar conductive functions. As in southern pine xylem, rays in phloem are mostly uniseriate, but some fusiform rays containing horizontal resin canals are present (Figs. 2B and 4). All ray cells in phloem have

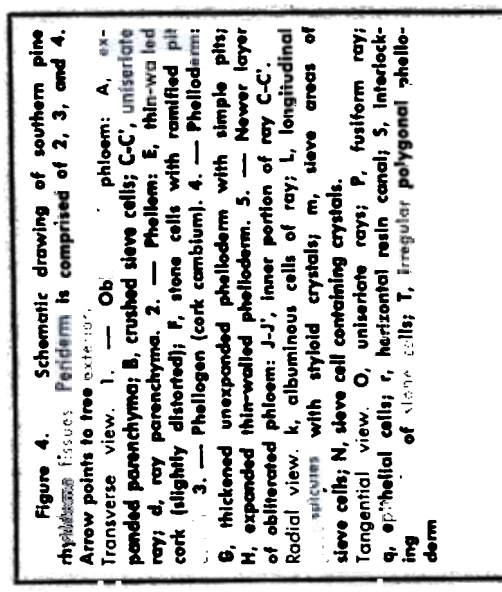
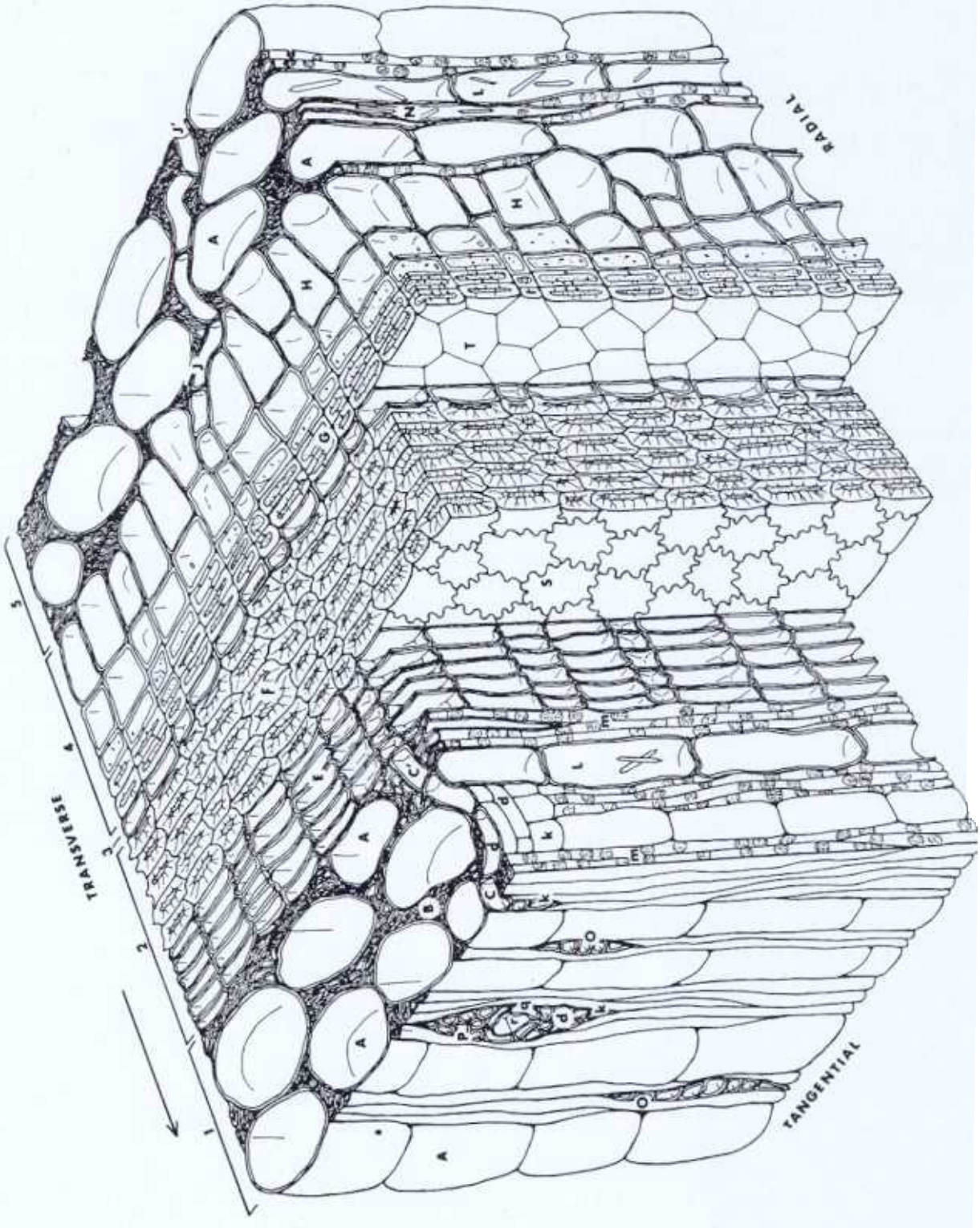


Figure 4. Schematic drawing of southern pine rhytidome tissues. Periderm is comprised of 2, 3, and 4. Arrow points to tree exterior. Transverse view. 1. — Ob phloem: A, expanded parenchyma; B, crushed sieve cells; C-C', uniseriate ray; d, ray parenchyma. 2. — Phellem: E, thin-walled cork (slightly distorted); F, stone cells with ramified pit 3. — Phellogen (cork cambium). 4. — Phelloderm: G, thickened unexpanded phelloderm with simple pits; H, expanded thin-walled phelloderm. 5. — Never layer of obliterated phloem: J-J', inner portion of ray C-C'. Radial view. k, albuminous cells of ray; L, longitudinal with styloid crystals; m, sieve areas of sieve cells; N, sieve cell containing crystals. Tangential view. O, uniseriate rays; P, fusiform ray; q, epithelial cells; r, horizontal resin canal; S, interlocking of sieve cells; T, irregular polygonal phelloderm


RADIAL
TRANSVERSE
TANGENTIAL

thin, primary, unlignified walls. No ray tracheids are present; instead, erect structures called albuminous cells form the margins of most rays (Fig. 4k). Their presence is a characteristic of conifer phloem. They may occasionally occur in the middle of a ray and have been reported distributed among the other phloem tissues (Chang 1954a; Srivastava 1963; Esau 1965, p. 288). Albuminous cells are physiologically associated with sieve cells and communicate with them through one-sided sieve areas on the sieve cell wall only. They are thought to regulate sieve cell activities and serve in translocation between sieve cells and ray parenchyma. Albuminous cells die and collapse simultaneously with their associated sieve cells.

Ray parenchyma in phloem is much like that in xylem. Since the sieve cells normally do not have sieve-area contact with ray parenchyma, southern pine phloem has no visible features analogous to crossfield pits.

Epithelial cells line the horizontal resin ducts of fusiform rays and are similar to those of xylem. In older phloem, epithelial cells may sometimes overproliferate and clog resin ducts with tylosoids.

Radial alignment of rays becomes distorted at a short distance from the cambium. Long before they enter the rhytidome (Fig. 5), rays assume an undulating pattern in cross section; consequently, in radial section only discontinuous portions are visible. Slightly enlarged rays were occasionally observed in older

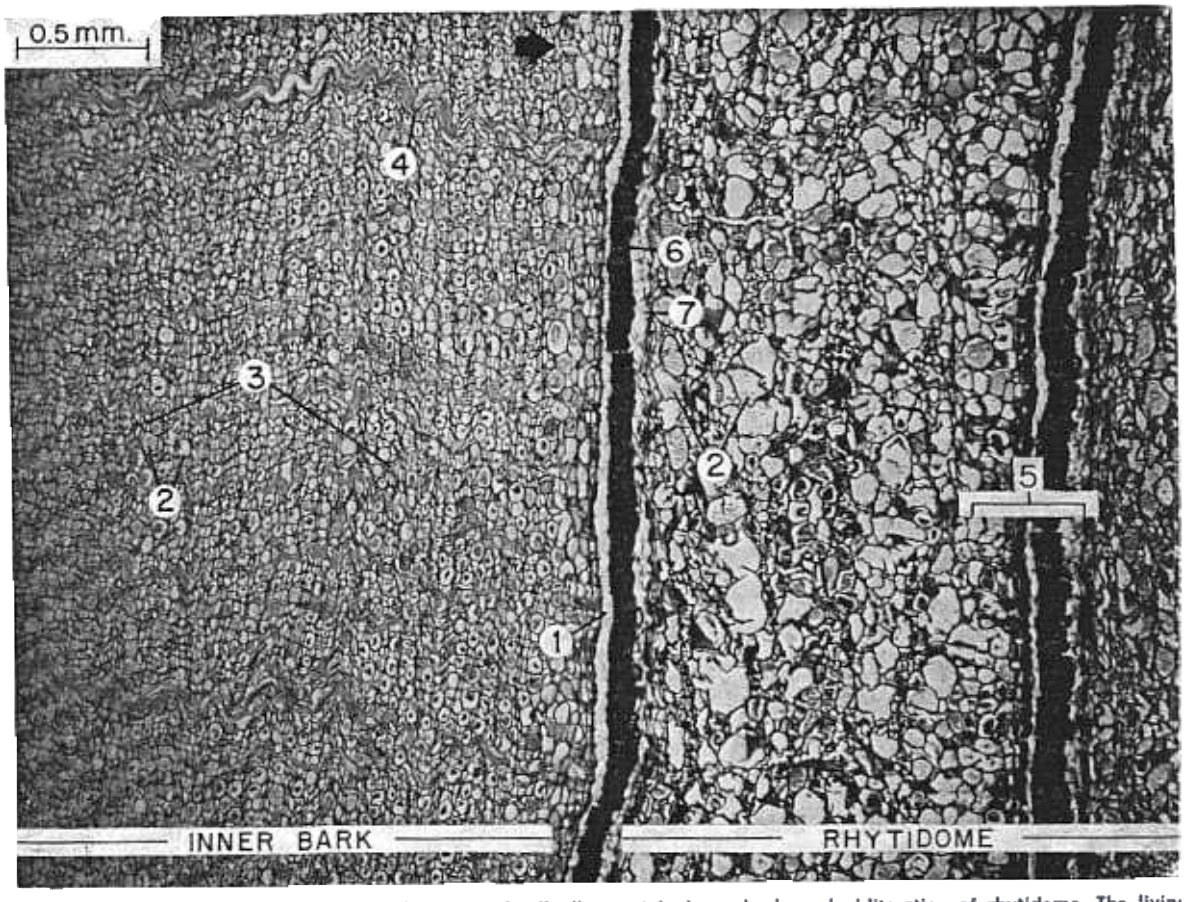


Figure 5. — Cross section showing distortion of cell alignment in inner bark and obliteration of rhytidome. The livin periderm, with the active phellogen (1) in its center, separates the two zones. Large arrow indicates outward growth Vascular cambium is just outside the left edge of the photo. (1) active phellogen, (2) parenchyma, (3) sieve cells, (4 undulating ray, (5) dead older periderm, (6) phellem stone cells, (7) thin-walled cork.

phloem; the rays of southern pines do not, however, undergo the extreme dilation found in many other species.

Except for the albuminous cells, rays remain alive throughout inner bark and transport nutrients from the actively conducting zone to living longitudinal parenchyma and the innermost phellogen. The outermost portions of rays die when ultimately sealed off by formation of a new and deeper phellogen.

Crystals. — Abundant crystals were observed throughout southern pine inner bark and rhytidome (Fig. 2A). They are composed of calcium oxalate, and are deposited as a by-product of metabolism (Srivastava 1964; Esau 1965, p. 29; Kennedy *et al.* 1968). Therefore, the quantity of crystals in a particular sample may be somewhat dependent on nutrient availability and tree vigor (Great Britain Forestry Commission 1932). Crystals were found in the lumina of both sieve cells and longitudinal parenchyma. In contrast with those reported in other species, the crystal-bearing cells in southern pines do not appear specially modified for this function. The southern pines, and other hard pines, have crystals that are characteristically elongated prisms with chisel-like ends (Fig. 6), whereas soft pines have crystals with square rhomboidal ends (Chang 1954b; Srivastava 1963) Crystals of all southern pines were similar in shape but varied greatly in size (from 15 to 105 μm in length), even within the same cell.

Figure 6. — Typical styloid crystal found in sieve cells and longitudinal parenchyma of southern pine bark.

Rhytidome Formation

In southern pines the transformation from inner bark to rhytidome involves drastic

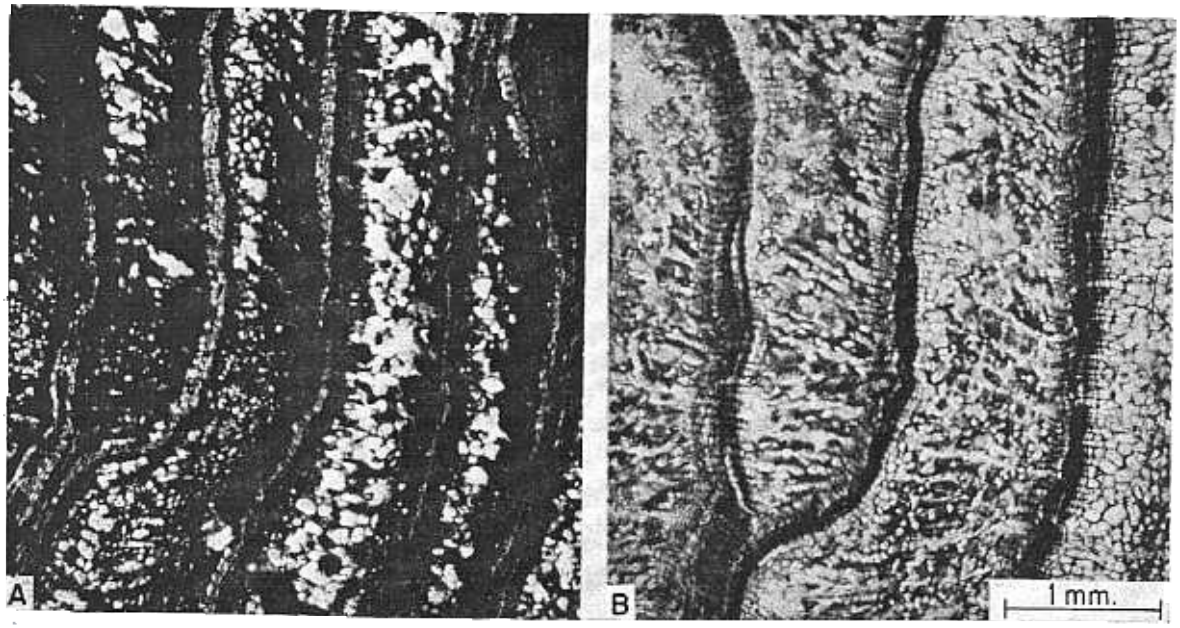


Figure 7. — Deposits in rhytidome of Ocala sand pine. A. — Untreated section. B. — Same section after bleaching. Both are at the same magnification: the section expanded during treatment. Radial alignment of periderm cells is easily seen in bleached section.

Figure 8. — Interior tangential view of periderms, looking outward from the stem. Inner bark has delaminated, revealing highly irregular periderm shapes, mostly elongated in direction of tree axis. (Table-Mountain pine.)

changes: 1) formation of a new tissue system — the periderm, 2) extreme alteration of cell structures and arrangements, and 3) abundant deposition of substances in the cells.

As sieve cells cease to conduct and begin to collapse, the vertical parenchyma cells enlarge. This process is called obliteration. Resultant cell changes are easily visible in older portions of inner bark and are strikingly evident to the outside of the newest periderm (Fig. 5). Here the longitudinal parenchyma cells are many times their original diameters and the sieve cells are crushed. In inner bark, longitudinal parenchyma cells are greatly outnumbered by sieve cells and occupy little volume; in rhytidome, however, the enormously enlarged parenchyma cells occupy most of the volume of old phloem tissue. Rhytidome therefore has a very porous structure.

Collapse of sieve cells, parenchyma expansion, and the resultant displacement of old phloem cells alters original radial or tangential alignment and obscures any possible evidence of growth rings in outer bark.

In the trees studied, obliteration was most evident in the lower samples and least pronounced in bark from the uppermost height. No consistent radial variation was noted. Although some degradation may occur in older rhytidome layers, only where the protective periderms have been ruptured (as in the extreme outer layers or near furrows) is there any noticeable variation from the inner rhytidome layers.

Rhytidome contains an abundance of deposited materials (Fig. 7). These amorphous deposits — mainly tannins, phlobaphenes, and other phenolic substances — may be found in all cell types and are responsible for the dark reddish-brown color. Although the physiological function of these phenolic compounds is not clear, it has been suggested that they resist fungal attack and act as antioxidants (Kurth 1944). A limited degree of lignification is sometimes observed in dead phloem tissues of rhytidome, but in stained sections the coloration of

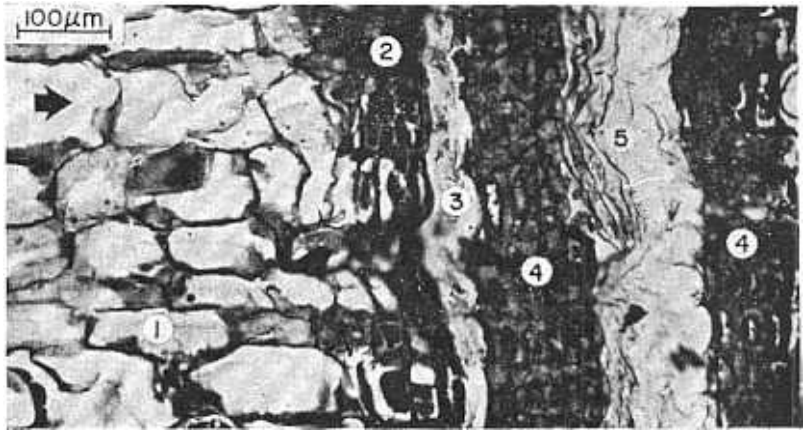


Figure 9. — Radial section of shortleaf pine periderm. (1) radially elongated phelloderm, (2) thickened unexpanded phelloderm, with dark deposits in lumens, (3) phellogen, (4) stone cells, (5) thin-walled cork (distorted here). Periderm cells appear the same in both radial and transverse sections. Arrow points to exterior of tree. Phelloderm develops toward the interior of the phellogen and phellem toward the exterior.

deposits adhering to the inner walls may be mistaken for lignin.

Periderm

The inner bark is protected from desiccation by the periderms, of which only the innermost is alive. Periderms form in discontinuous irregularly shaped layers (Fig. 8) with the edges curving outward to merge with older periderms (Fig. 1). A periderm is composed of three types of cells — phellogen, phelloderm, and phellem. Phellogen is a layer of meristematic cells which differentiate from unspecialized longitudinal and ray parenchyma cells in older phloem. Phellogen cells divide tangentially to produce radially aligned cells toward both the inside (phelloderm) and the outside (phellem or cork). Usually more phellem cells are produced than phelloderm (Figs. 4, 5, and 9).

Phellogen. — Phellogen may be recognized as the thin-walled row of cells in the midst of the periderm, just to the outside of a 2- or 3-cell band of thick-walled phelloderm cells (Figs. 4, 5, and 9). Like the vascular cambium, it is considered one cell wide, but may appear slightly wider if undifferentiated daughter cells are present. Unlike vascular cambium, phellogen has only one type of initial. The cells are flattened radially and are narrowly rectangular in cross and radial sections, but they are irregularly polygonal in tangential view (Srivastava 1964). Except for those which enlarge or become stone cells, most derivative cells (phelloderm and phellem) retain the original phellogen arrangement and have 5 to 7 sides when viewed tangentially (Figs. 4, and 10A).

Derivative cells are aligned in radial files but not tangentially or longitudinally (Figs. 4 and 11).

Phelloderm. — The function of phelloderm is not entirely understood. In the innermost, or living, periderm these cells are relatively uniform, unenlarged, and unlignified. In all older periderms, cell morphology changes across the width of the phelloderm (Figs. 9 and 11).

The 2 or 3 rows of cells nearest the phellogen are similar in shape and size to the mother phellogen but have thickened lignified walls and numerous simple pits (Figs. 4, 10A, 11A).

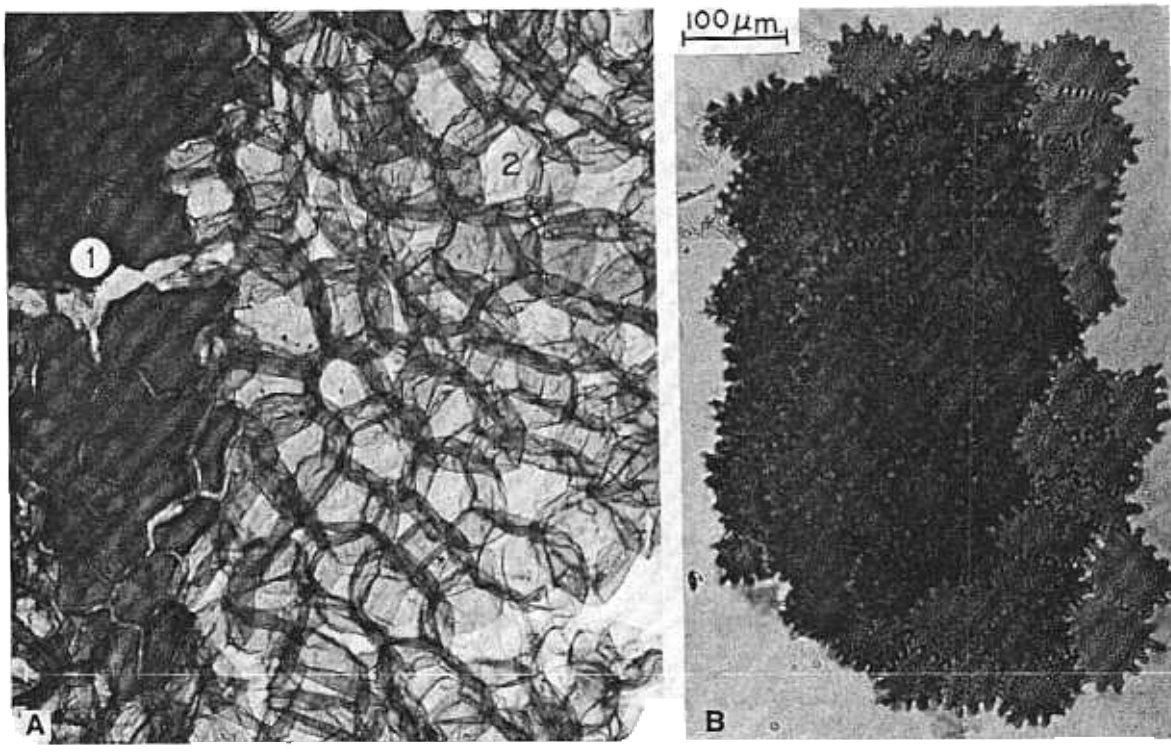


Figure 10. — Masses of periderm cells from partially macerated bark. A. — (1) thickened phelloderm cells, (2) thin-walled cork cells. Tangential view, slightly oblique. Note angular shape and configuration of cork cells (slash pine). B. — Phellem stone cells. Tangential view showing interlocked arrangement and profuse minute pits (longleaf pine).

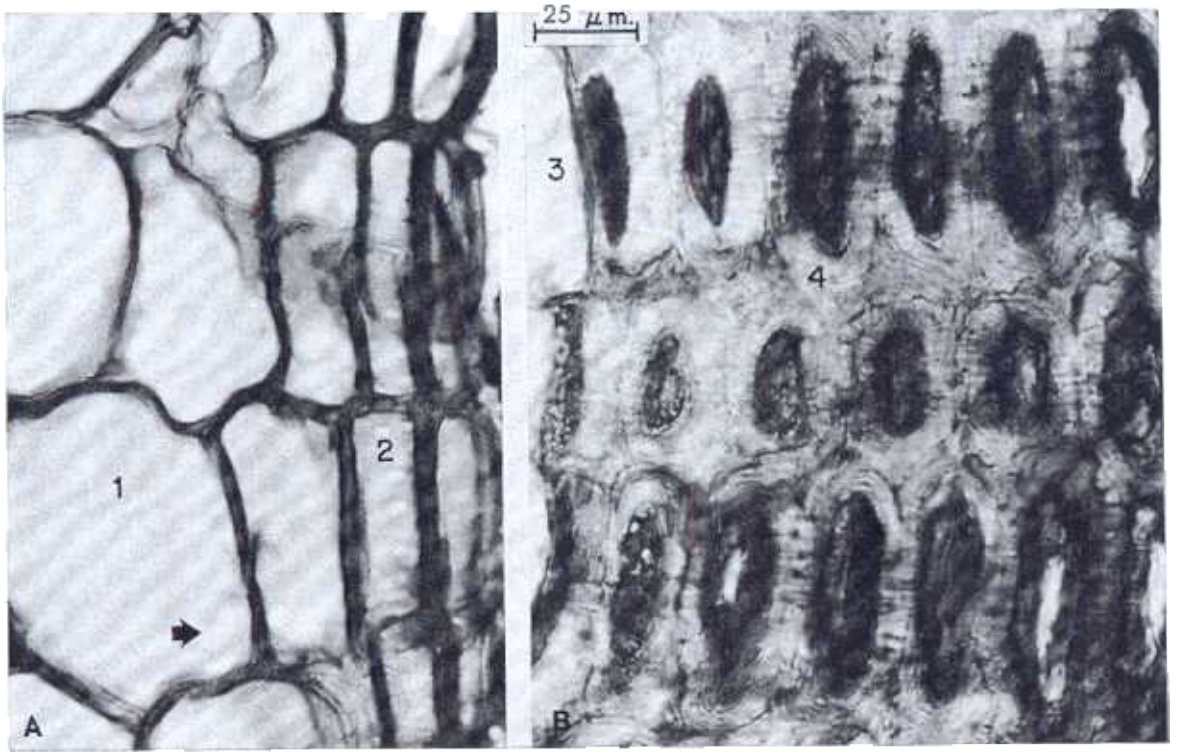


Figure 11. — Periderm, cross sectional views. Arrow points to exterior of tree. Files of cells are not in precise alignment either longitudinally or tangentially. (1) partially expanded phelloderm, (2) unexpanded phelloderm with simple pits of varying size, (3) phellogen, (4) phellem stone cells with distinct lamellae and numerous pit canals. Lumens are occluded with deposits. Cells which appear smaller were cut near their borders. A. — Pond pine. B. — Longleaf pine.

It was noted that with increasing distance inward (within each periderm) the older phelloderm cells are progressively more enlarged, with thinner, radially stretched walls and enlarged pits. The innermost — hence oldest — cells have very thin walls and usually are as large as expanded phloem parenchyma, with which they seem to merge (Fig. 5).

Radial alignment distinguishes these expanded phelloderm cells from the adjacent old phloem tissue. In addition, the older phelloderm usually is radially elongated, whereas the phloem parenchyma cells tend to be enlarged more in the tangential direction. The distinction between expanded phelloderm tissue and phloem parenchyma is best seen in radial section (Fig. 4A, H).

It is not known why the older phelloderm cells should enlarge radially (seemingly in direct contradiction to the tangential stresses and radial compression produced by stem growth) whereas the phloem parenchyma cells appear somewhat stretched by forces in the tangential direction.

In this study, more cell layers of phelloderm were observed than have been previously reported for southern pines. Because the innermost phelloderm layers are expanded and thin-walled, they are easily mistaken for a portion of the obliterated phloem. There are usually 2 or 3, but occasionally 4, layers of thick-walled phelloderm plus a variable number (commonly 3 to 4, but occasionally 9 or more) of phelloderm cells in varying stages of enlargement. In some specimens the expanded phelloderm occupied most of the volume between periderms; in these cases, periderms were very closely spaced. The usual descriptions — *i.e.*, that phelloderm is only 2-4 cells deep — probably stem from recognition of only the thick-walled unexpanded layers.

Phellem. — Phellem cells are primarily responsible for the protective characteristics of the periderm. All the southern pines have two distinct types of cells in the phellem region: thin-walled cork cells and thick-walled stone cells. Bands of both are usually found in the

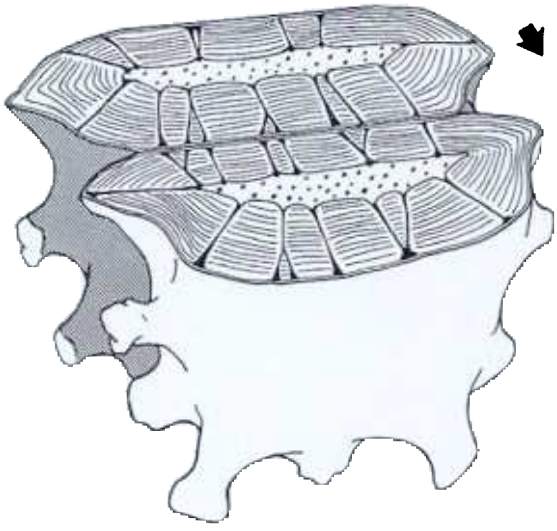


Figure 12. — Two phellem stone cells of a radial file. Cross-sectional cut reveals distinctly lamellate walls with numerous ramified pit canals. Arrow points toward exterior of tree.

same periderm (Figs. 4, 5); alternating bands occur frequently (Fig. 9).

Thin-walled cork cells have unpitted cellulose walls overlaid with a lamella of suberin and waxes, which renders them practically impervious to moisture and gases (Sitte 1957; Esau 1965, p. 340). Cell shapes, except for slight crushing, are approximately the same as those of the mother phellogen cells (Figs. 4 and 10A). The cork cells are compactly arranged, without intercellular spaces, and may be empty or filled with dark deposits.

Some phellem cells sclerify and become stone cells (Figs. 3, 4, 10B, 11B, 12).[2] They are arranged in tangential bands of variable width, commonly five to six cells, and form the only heavily lignified tissue of southern pine bark. The stone cells are about the same size as cork cells but have very thick secondary walls with profuse, tiny, ramified pit canals. The walls are composed of a number of concentric lamellae which are distinct in both ordinary and polarized light. The outer tangential wall is usually thicker than the side nearer the phellogen (Figs. 11B, and 12). The inner wall of the last-formed cell layer of a band is especially thin. Cell lumens are narrow and occluded with deposits.

The phellem stone cells are easily identified in tangential sections and macerated tissue (Figs. 3, 4, 10B). Distinct irregular projections form the cell margins and interlock with adjacent cells in a cog-like manner. Tangential walls are comparatively flat.

Unlike the thin-walled cork cells, which gave a positive reaction with Sudan IV (a stain for suberin), the thick-walled phellem cells did

[2]Chang (1954a, b) called these cells "transformed phelloderm," probably because a few somewhat similar, sclerified cells occasionally can be found in the outermost cell row of phelloderm.

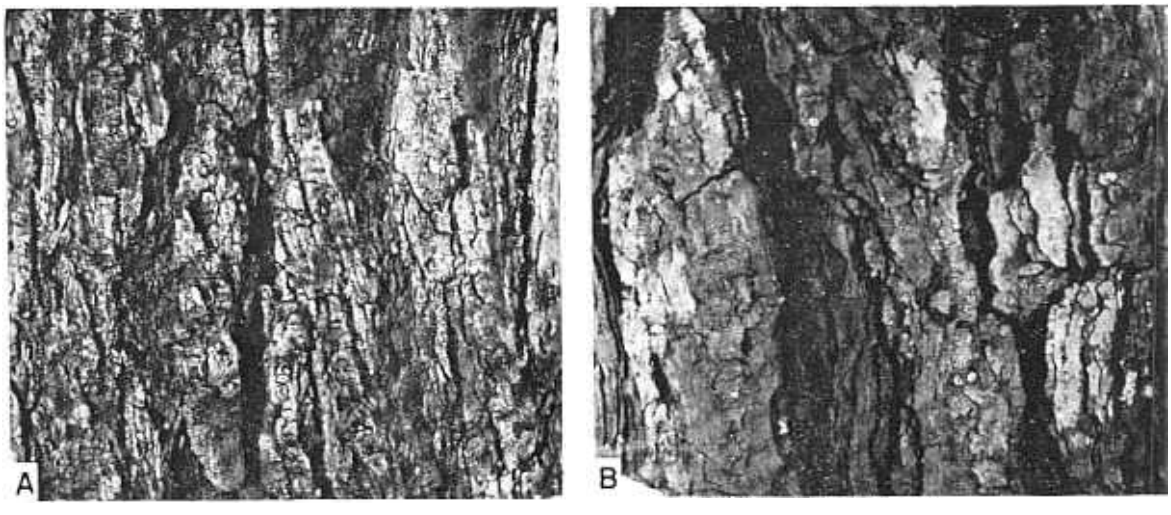


Figure 13. — Oak-like appearance and small transverse cracks distinguish mature spruce pine bark (A) from that of th other southern pine species, as typified by loblolly pine bark (B). Samples are from bolts of the same size.

not stain for suberin in any portion of their walls.

From visual estimates of bark examined in this study, stone cells appear to occupy about 10 percent, or less, of most rhytidome samples.

Species Comparison

External Characteristics

In external appearance, the bark of individual southern pines is highly variable within a species, while samples from trees of different species may be quite similar. Surface coloration varies with exposure conditions, and spacing and depth of fissures are known to be greatly affected by growth rate. Manner and ease of scale exfoliation are related to structure and may have some species significance, but the sampling was too limited to permit definite determination. The oak-like surface of spruce pine had numerous small, very shallow transverse cracks (Fig. 13); in thicker bark, especially where outer scales had been detached, ridges often curved outward at the edges to form concave longitudinal depressions (Fig. 14). Although occasional resin pockets were enclosed in rhytidome layers of several species, only in shortleaf pine did they appear as conspicuous and numerous surface craters or nodules (Fig. 15).

Odor. — Freshly cut surfaces of some dry samples, notably from the two varieties of slash pine, emitted a strong spicy fragrance reminiscent of cinnamon and cedar. Occasionally samples of other species yielded a faint fragrance.

Periderm color. — When viewed with a hand lens, most periderms display two or more lines of varying color, arrangement, and width. These individual lines may be dark and dull, ivory white, or dark and shiny. In the samples investigated, wide bands of phellem stone cells resulted in white lines. Samples with dark lines had bands of cells (primarily thin-walled phellem) filled with very dark deposits. Lack of such dark inclusions apparently resulted also in light-colored periderm lines.

Observations of periderm color were made only on freshly cut surfaces, as coloration of older surfaces is often altered by exposure. Four loblolly and four pond pines were examined and found to have dark inconspicuous periderms, as reported by DeVall (1945). Of six Virginia pines, all had light-colored periderm lines, although lines in some samples were very narrow and inconspicuous. The other seven species were variable, some highly so even in adjacent periderms. Although periderm lines were predominantly light in slash pine

Figure 14. — Mature spruce pine bark with edges of some ridges curved outward, forming concave longitudinal depressions. Some outer scales have been detached.

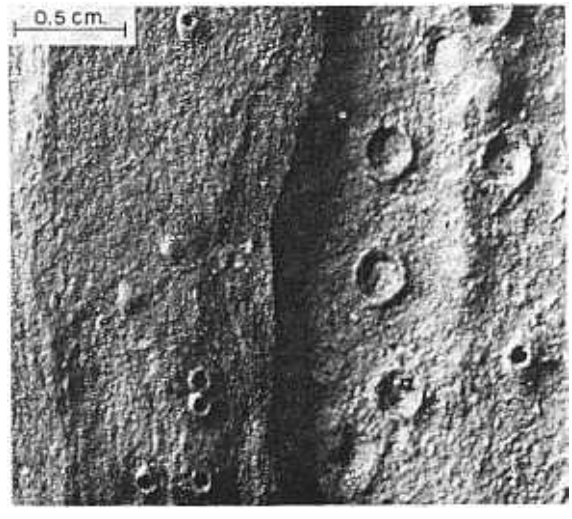


Figure 15. — Characteristic resin pockets on surface of shortleaf bark, in form of craters and nodules. Samples from two trees show varying size. Craters result when periderm diverges to form behind the resin deposit; periderm formation around the outer portion of the deposit produces a nodule.

Figure 16. — Radia
tion of Ocala sand
(1) old phloem (rela
unobliterated), (2) ra
elongated phelloderm
phellem of alternating
walled stone cells and
walled cork cells.
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and mostly dark in other species (*e.g.*, spruce and sand pines), the variation from stem to stem ruled out positive identification of individual trees by this feature alone.

Periderm shape. — Periderm shape, spacing, and length were found to vary greatly within a species. Chang (1954b) noted that barks of the soft pines have very short and sharply curved periderms; they may therefore be distinguished from barks of hard pines, which have longer, mostly parallel periderms that gradually overlap. In most sample trees of the present study, the periderms were generally parallel and straight, except where edges curved to join other periderms (Fig. 1). However, some specimens had very short, distinctly curved periderm patterns.

Microstructure. — All species contain the same periderm cell-types, but wide within-species variations occur in periderm arrangement. Several species, however, seem to be consistent in the type of cell forming the outermost band of each periderm.

Except for an occasional incompletely differentiated cell, stone cell bands consistently formed the outer margin of each spruce pine periderm. In longleaf, sand (both races), slash (both varieties), and Virginia pines, the outer margins were comprised of thin-walled cork cells. The other five species (loblolly, pitch, pond, shortleaf, and Table-Mountain pines) were variable. The value of this feature for separation of species requires further study.

Phloem obliteration was less pronounced in bark from the upper stem than in bark taken near the ground. In some species, particularly spruce pine, Virginia pine, and the two sand pines, old phloem of the rhytidome was much more intact than in other species (Fig. 16). Furthermore, bark of these species was more difficult to section, as it was fibrous, brittle, and noticeably harder. Bark from Virginia pine and the two sand pines was extremely thin at the upper height. Although it is not yet verified whether these are consistent species characteristics, it is interesting to note that bark samples from the three species outranked bark of other southern pines in several physical and mechanical properties measured by Martin and Crist (1968) and Martin (1969).

Physical Properties

The relationship between the anatomical features of southern pine bark and its physical and mechanical properties is relatively unexplored and poorly understood. A comparison of samples with obviously differing characteristics indicated that several structural features may influence properties of rhytidome.

Phellem stone cells, with their thick, heavily lignified walls and narrow lumens, are the densest and hardest cells in southern pine bark. Their interlocking arrangement adds cohesive strength. Variation in their proportion should account for much of the variation in density and hardness. Since the periderms are aligned

tangentially, stone cells are the primary obstacle to radial shear. Stone cell bands are less flexible than surrounding tissues and somewhat inhibit longitudinal and tangential shrinkage.[3] Barks with closely spaced periderms have a high proportion of periderm tissues, and therefore usually a high proportion of stone cells. Periderms with sharply curved edges, and with stone cells in these curves, should be relatively resistant to radial compression. Bark with periderms that are closely spaced and short in both longitudinal and tangential directions should be less permeable than bark with widely spaced long periderms.

Southern pine bark tends to separate along the periderms in scale exfoliation, under shear stress in the tangential plane, and in longitudinal and tangential compression. Three tissues form tangential zones of weakness; thin-walled phellem, phellogen, and, to a lesser extent, expanded inner phelloderm.

Bark with unexpanded parenchyma in rhytidome should be denser and less porous than bark of a well-obliterated specimen. Parenchyma in bark from the upper stem was less expanded than at lower levels; this observation probably accounts for the increase in bark density with height, as the amount of stone cells did not appear to be height-correlated. Samples with little expansion should rank high in density-related properties; it was observed that relatively unobliterated samples were hard and fibrous, and had little tendency to powder when sliced. It may be that lack of obliteration in some barks is due to special wall characteristics that enable sieve cells to resist collapse; if so, obliteration-resistant barks should have greater tensile strength than obliterated barks.

Expanded parenchyma in the phloem plus wide zones of both expanded phelloderm and thin-walled cork cells probably contribute to the thermal insulation value of barks.

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[3] Martin and Crist (1968) report that shrinkage in these directions is considerably less than radial shrinkage.