ELEMENTS OF BARK STRUCTURE AND TERMINOLOGY

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ABSTRACT
Bark structure varies considerably from that of wood, although analogies may be drawn between specific elements and overall structure and function. The terminology of bark structure is discussed and various cellular elements are described. Several bark structures are illustrated with light and electron micrographs pointing out differences between species and species groups.

INTRODUCTION

Bark is an important physiological and protective component of our woody plants and comprises a considerable volume of the logs removed from a forest. Improved utilization of this material will be enhanced not only by research on its structure and properties, but also by better understanding of its structure and technical terminology. Our intent in this paper is twofold. First, we wish to present the latest information available on bark structure and its component cells. Second, we wish to have in the literature a recent, generally available, reference point on the structure of both softwood (gymnosperm) and hardwood (angiosperm) barks. In order to approach these objectives, we will discuss the terminology of barks with descriptions of the cells involved. We will illustrate structure at a wide range of magnification in micrographs and drawings, and compare bark elements to wood elements to aid the wood technologist. For more extensive descriptions of bark structure and formation, we refer the reader to Chang (1954a, b) and Esau (1959).

SYMBOLS

The following symbols are used in identifying features in the figures:

A	Albuminous cell
C	Cambium
CO	Companion cell
Cr	Crystal
F	Fiber
P	Phloem
Pa	Parenchyma
Pd	Phelloderm
Pe	Periderm
Po	Pore or pit canal
Pg	Phellogen
Ph	Phellem
R	Rhytidome
Ra	Ray
Re	Resin canal
S	Sieve element
Sa	Sieve area
Sc	Sclereid
Sp	Sieve plate
X	Xylem

TERMINOLOGY

We might best begin our discussion of bark by using the definition given by the Society of American Foresters (1958) as "the tissues of the stem, branch, and root outside the cambium layer." They further define inner bark as the physiologically active tissues between the cambium and the last-formed periderm or protective layer, and outer bark as the layer of dead tissue of a dry, corky nature outside the last-formed periderm. Anatomists would refer to the inner bark as *phloem* and the outer bark as *rhytidome.* The phloem is generally light or creamy in color, while the rhytidome is generally tan or brown in the interior and often discolored to various shades of light gray to black on its surface.

Periderm

Periderm is an important layer in the protection of stems from desiccation and probably also biological organisms. It consists of three layers of cells. Within the phloem of mature stems, some parenchyma become meristematic and are termed *phellogen*, which produce *phellem* or cork cells to the outside and *phelloderm* cells to the inside. The phellem cells are generally highly suberized and are the important cell in protecting the life functions of the stem. The phelloderm are thin- or thick-walled; they blend into the phloem parenchyma, and probably function in providing thermal protection. The thick-walled phelloderm may provide some protection from pathogens and desiccation.

With the exception of the cells of the periderm, no cells appear in the rhytidome that are not present in the phloem. Their shape, composition, and functions are different, however.

Sieve cells and sieve tube elements

Sieve elements function in conduction mainly of foodstuffs in a stem or root. Sieve cells occur in the softwoods, are similar in size and shape to the tracheid of the wood, and have sieve areas through which translocation occurs from one sieve cell to the next. Sieve tube elements are found in hardwood and resemble small-diameter and relatively long vessel elements. Translocation occurs through sieve areas and sieve plates. Both *sieve cells* and sieve tube elements are usually thin-walled and usually collapse by the time they are incorporated into the rhytidome. As opposed to wood, where the tracheids and vessels function in conduction after dying, the sieve components conduct materials in the live condition, the cytoplasm being without a nucleus at the time. The sieve components remain alive through much of the phloem region, but only a small fraction of them, those most immediately adjacent to the vascular cambium, are active in translocation.

Albuminous and companion cells

Albuminous cells are the regulatory cells for the functions of sieve cells in conifers, whereas *companion cells* regulate the seive tube elements of the angiosperms. The albuminous cells are generally located on the margins of rays, much as the ray tracheids of the wood are located. Companion cells of the angiosperms are a special longitudinal parenchyma lying immediately adjacent to and paralleling a sieve tube. The precise mechanism of their regulatory functions is not known, but undoubtedly they operate through plasmodesmata connecting the cytoplasm of the two cells. Albuminous and companion cells are nucleate, thus giving them a regulatory center to control the functions of the anucleate sieve elements.

Phloem parenchyma

Phloem parenchyma occur in both conifers and angiosperms, and the term is generally used to exclude the albuminous and companion cells because of their special functions. Parenchyma occur in both longitudinal and transverse positions and are generally quite short longitudinally. They are quite thin-walled, but often exhibit considerable radial expansion as the old phloem passes in to the rhytidome, thus often accounting for a lowering of the density of the rhytidome.

Sclerenchyma

Sclerenchyma are the thickest walled cells of bark, and are of two types—*fibers* and *sclereids*. Fibers are long and quite straight, and they are comparable to the libriform fibers of hardwoods or thick-walled summerwood tracheids of softwoods. Sclereids are often short ramified cells, and have often been called stone cells. Some sclereids, such as those of Douglas-fir, become quite elongated and resemble a fiber in many respects. In general, the sclereids will be shorter than the fusiform initials in the cambium and the fibers of either wood or bark. Both fibers and sclereids are highly lignified.

In order to clarify the structure and functions of bark cells and tissues, we might illustrate (Table 1) the most closely analogous cells of the wood or xylem. One should keep in mind that the analogies may not be too accurate, but yet may be helpful in orienting those familiar with wood. It

TABLE 1. *Analogous elements of bark and wood in angiosperms and gymnosperms*

ANGIOSPERMS Hardwoods		GYMNOSPERMS Softwoods	
	Longitudinal		
Phloem element	Xylem element	Phloem element	Xylem element
Sclerenchyma		Sclerenchyma	
Sclereids (stone cells)	None	Sclereids	None
		Fibers	
Fibers	Tracheids and fibers		Tracheids
Seive tube elements	Vessels	Seive cells	
Companion cells	(Parenchyma)		
Parenchyma	Parenchyma	Parenchyma Epithelial cells	Parenchyma Epithelial cells
	Transverse		
Ray parenchyma	Ray parenchyma	Ray parenchyma Albuminous cells Epithelial cells	Ray parenchyma Ray tracheids Epithelial cells
	Periderm		
Phellem (cork)	None	Phellem (cork)	None
Phellogen (cork cambium)	None	Phellogen (cork cambium)	None
Phelloderm	None	Phelloderm	None

should be noted particularly that there are no xylem cells comparable to those of the periderm or to the short sclereids.

Differences in internal structure of cells are partially illustrated by considering the substantial variation in chemical composition between different cell types (Fig. 1).

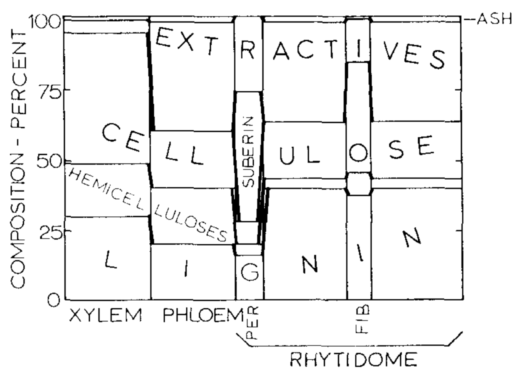

Fig. 1. The various cellular components of bark exhibit great differences in chemical composition, a fact that may be quite significant in understanding and using it.

The concentration of some chemicals in one type of cell may make it worth while to remove a given chemical component from a specific cell type as opposed to extraction from ground whole bark as is often done. The information contained in the figure represents no single tree species, but was compiled from data available in the literature. Bark would be a poor source for cellulose, for instance, except for the fibrous components. Further examination of extractives available might indicate particular cellular components to be high in a given chemical.

STRUCTURE

Equipped with the basic terminology of bark structure, let's proceed to observations of bark structure. We might begin by considering the view of bark and wood as one would ordinarily encounter them (Figs. 2 and 3). The xylem (X) is to the bottom, separated from the living phloem (P) by

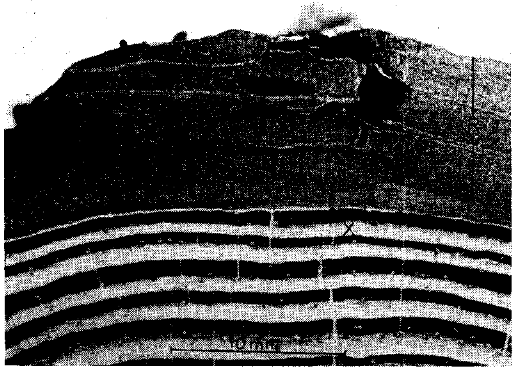

Fig. 2. The phloem of softwoods is generally quite narrow, pond pine (*Pinus serotina* Michx.) in this case, in comparison to hardwoods. The periderm layers are quite flat, and the rhytidome gives a soft, low-density appearance in comparison to the xylem (light photograph, transverse section).

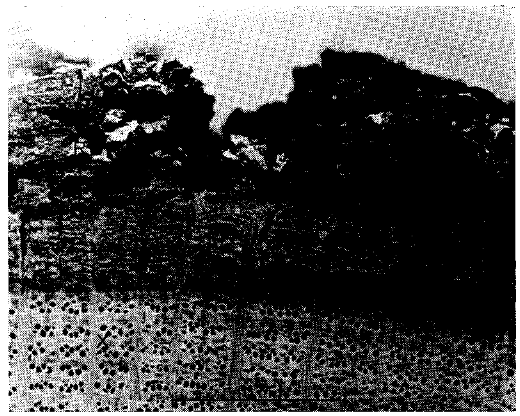

Fig. 3. Black oak illustrates the relatively wide phloem of many hardwoods with the roughly fissured rhytidome. The inner phloem is darker in the illustration, primarily because of a higher moisture content, and the contrast with the pores of the xylem is quite distinct. Periderm layers are not pronounced (light photograph, transverse section).

the narrow cambial region (C), essentially invisible to the naked eye. To the outside of the phloem is the last-formed periderm (Pe), which marks the beginning of the rhytidome (R), or outer dead bark. The rhytidome consists of alternating layers of old periderm layers and dead phloem, much of which has been distorted by the obliteration of cells that takes place in both the outer phloem region and the rhytidome.

In the hard or yellow pines (*Pinus* spp.), as in Fig. 2, the tendency is for the periderms to lie flat in a nearly tangential plane. In the soft pines, and many other trees, periderm layers are often more rounded or irregular. In the Black oak (*Quercus velutina* Lam.) of Fig. 3, dilation of the rays occurs near the outer regions of the phloem, a condition that occurs in many hardwood barks. Some gradation in color occurs within the phloem region of Fig. 3, perhaps because of moisture gradients occurring within the region.

General bark structure can be illustrated best, perhaps, by an illustration devoid of the many extraneous elements appearing in a photograph (Fig. 4). This illustration most nearly represents the structure of eastern white pine (*Pinus strobus* L.), but the

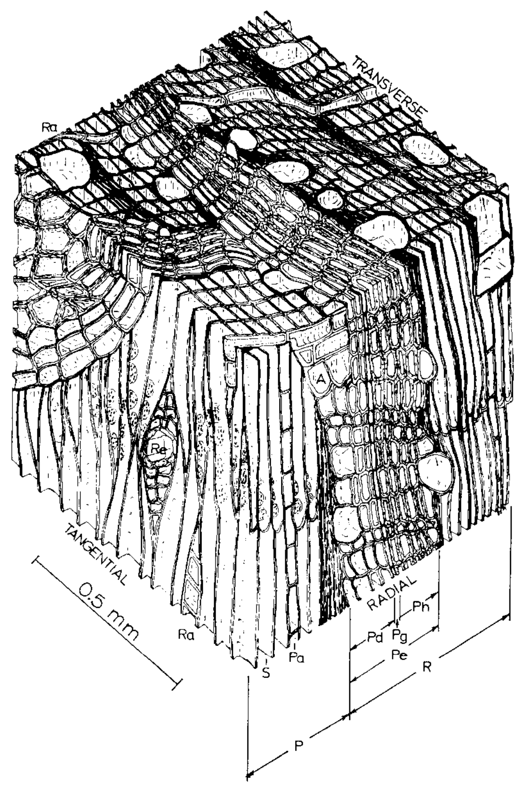

Fig. 4. Diagrammatic illustration of bark structure. The figure most nearly represents bark of eastern white pine.

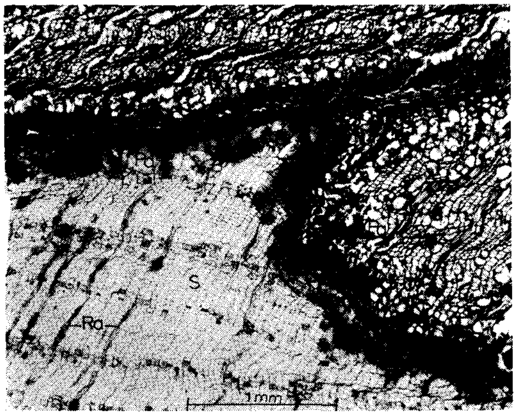

Fig. 5. The soft pines tend to have broad, gently curving periderms, as does this transverse section of eastern white pine. Obliteration of old phloem is not extensive (light micrograph).

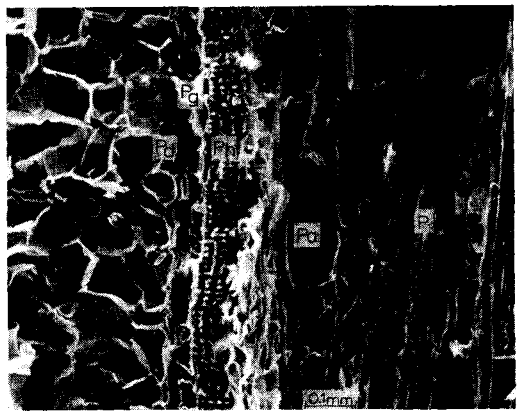

Fig. 6. The rhytidome of hard pines exhibit extensive obliteration of old phloem due to expansion of parenchyma and phelloderm. Phellem in this radial face of longleaf pine are predominantly of a cog-wheel shape (scanning electron micrograph).

structural features are appropriate to many hardwood and softwood barks. On the radial face the phloem (P) is to the front, and would ordinarily be light in color in the living tree. Most of the living phloem is not visible here, but would lie farther to the left toward the center of the tree. The rhytidome (R) begins with the last-formed periderm (Pe), and outward from this the bark is generally dark-colored and its cellular components are dead.

Returning to the phloem region, the long cellular components are sieve cells (S), whose walls are modified by almost circular sieve areas. In the sieve areas of living cells, plasmodesmatal strands connect the cytoplasm of one cell with the next and furnish the connecting link for translocation of foods down the stem. Other longitudinal cells are the strand parenchyma (Pa). Rays can be seen to traverse the phloem, and the albuminous cells (A), which control the functions of the sieve cells, lie on the ray margins. A transverse resin canal (Re) appears on the tangential face in a fusiform phloem ray. In contrast with the wood, longitudinal resin canals ordinarily occur only in the primary phloem and in secondary phloem of the Cupressaceae (2).

As a portion of the phloem becomes old, meristematic phellogen cells (Pg) arise from parenchyma and form a new periderm. The phellogen produces phelloderm (Pd) cells to the inside and phellem or cork (Ph) cells to the outside.

Formation of a periderm generally signifies not only the death but also the obliteration of phloem cells located to its exterior. Obliteration is not as extensive in white pine as in many trees, as the diametral expansion of parenchyma and phelloderm is not as extensive. In white pine, pronounced tangential bands of collapsed sieve cells occur both in the outer living phloem and the old, dead phloem of the rhytidome. Because of cell collapse and obliteration, the phloem rays often pursue an irregular path through the phloem and rhytidome, and they are interrupted at the periderm.

The cells of the periderm—phelloderm, phellogen, and phellem— are flattened radially and isodiametric longitudinally and tangentially, although generally of four to six sides, as can be seen on the tangential face of Fig. 4. One exception to these cells being flattened radially is the large, expanded, and thin-walled phelloderm on the inside edge of the periderm. In the center of the transverse face, a more recently formed periderm curves outward toward an older periderm, isolating more old phloem.

Fig. 7. The periderms of sugar maple are multilayered. Large fiber bundles, separated by obliterated phloem, abound in the rhytidome (light micrograph, transverse section).

Bark structure varies around the general pattern of a phloem from which regions are periodically isolated by a newly formed periderm, thus forming another layer of rhytidome. The variations are almost endless, and bark can be used for identification only between species groups.

In the eastern white pine of Fig. 5, one curving periderm can be seen to join an older periderm. In both the phloem and rhytidome, much of the phloem remains intact, although tangential bands of parenchyma and obliterated phloem are apparent. A greater degree of obliteration of old phloem occurs in hard pines than in soft pines (Figs. 5 and 6). In the hard pine of Fig. 6, many parenchyma cells have expanded greatly in diameter, as have phelloderm cells originating on the inner side of the periderm. The pines in general contain no sclerenchyma, although most of the softwood barks do contain fibers of sclereids, or both.

Sugar maple (*Acer saccharum* Marsh.) has multilayered periderms of thin- and thick-walled phellem (Fig. 7). Much of the older phloem is obliterated, and large bundles of fibers are present.

The bigtooth aspen (*Populus grandidentata* Michx.) from which the bark in Fig. 8 was obtained had developed a rough bark. The outer bark can be seen to contain very

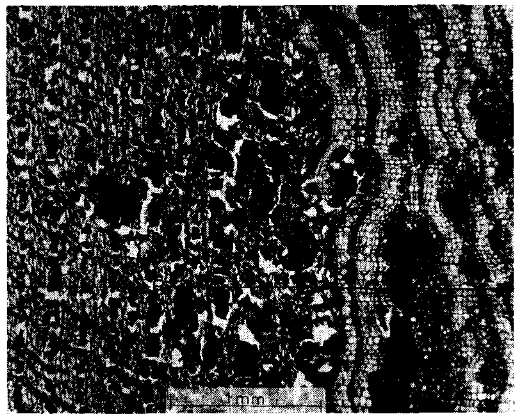

Fig. 8. Bigtooth aspen bark displays tangential rows of fiber bundles throughout the phloem region to the left. As we near the periderm, bundles of sclereids become abundant and are frequent among the alternating thin- and thick-walled phellem (light micrograph, transverse section).

few remnants of old phloem among the alternating layers of thick- and thin-walled phellem cells. A few sclereids and fibers are present, but even in radial section it is difficult to find evidence of the fibers that are so prevalent in tangential bands of the phloem.

American elm (*Ulmus americana* L.) tends to have periderms with two or more alternations of thin- and thick-walled cells (Fig. 9). The periderms are generally quite

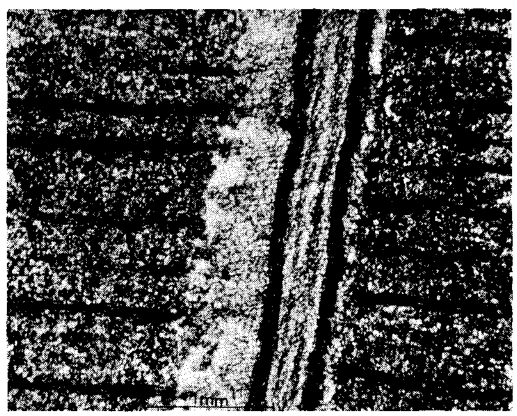

Fig. 9. The curving periderms of American elm generally exhibit two or more alternating layers of thin- and thick-walled phellem (light micrograph, transverse section).

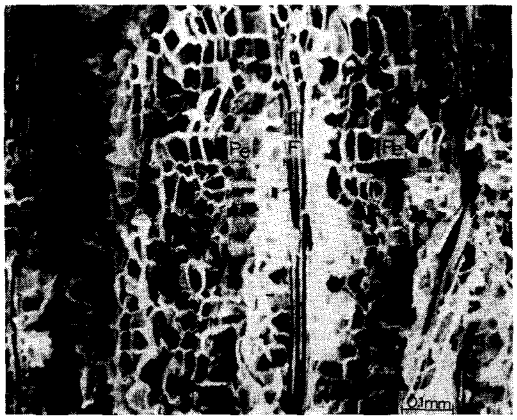

Fig. 10. Ray dilation is extensive among some rays of yellow poplar, leaving the fiber bundles suspended among thin-walled isodiametric cells (scanning electron micrograph).

rounded in nature, and clearly can be seen to intercept rays. Obliteration of old phloem is not extensive.

In the outer regions of yellow poplar (*Liriodendron tulipifera* L.) phloem, ray dilation is quite prevalent. Much of the rhytidome, therefore, exhibits fiber bundles apparently suspended in the ray tissue (Fig. 10). The periderm appears to consist mostly of one layer of thick-walled phellem.

Red Oak (*Quercus rubra* L.) periderm also contains a single layer of each type of periderm cell (Fig. 11). Most of the phellem and phelloderm are relatively thin-walled, although exceptions occur as near the bottom of the figure. To the outside of the periderm are many thick-walled, small-lumened fibers, among which occur crystal-bearing parenchyma.

We have attempted to illustrate bark structure through a limited series of photographs. We can (in general) summarize structure by stating that most often we have a phloem, the older, outer regions of which are periodically isolated by formation of new periderms. The alternating layers of old phloem and periderm constitute the rhytidome. Within the rhytidome, the old phloem is obliterated to varying degrees, because of diametral expansion of parenchyma and some cells of the periderm, and

Fig. 11. A transverse section of red oak (*Quercus rubra* L.) rhytidome exhibits relatively thin-walled phellem in the center of the photograph, with fiber bundles and crystal-bearing parenchyma immediately to the right. To the left of the phellem are the very thin-walled phellogen and the phelloderm (light micrograph).

because of dilation of rays. In the obliteration process, the sieve elements are generally crushed, while the sclerenchyma remain intact.

CELLULAR COMPONENTS

Let us turn our attention to various cellular components of bark. We might begin by first examining those elements of the phloem with their analogous xylem components. We can then examine those cells of the periderm, for which there are no xylary analogs.

Sieve elements comprise a large portion of the living phloem of a tree, and Chang (1954a) recorded them to occupy from 54 to 80% of the inner bark of gymnosperms. Their cell walls are generally thin, with little secondary thickening. The overall size of the gymnosperm sieve cell is comparable to springwood tracheids, but the wall is modified by sieve areas rather than the pits of tracheids, and sieve areas of eastern hemlock (*Tsuga canadensis* L.) are shown in Fig. 12. The sieve plates and sieve areas located on the sieve tube elements of angiosperms often display more detail (Fig. 13). The yellow poplar sieve areas displayed here on the walls of old

Fig. 12. Sieve areas of connifers occur much as the pitting of their tracheids, but the internal formation of the structure is different (Eastern hemlock, scanning electron micrograph, radial face).

Fig. 14. Long narrow spiculate crystals are common in phloem parenchyma of many conifers, as illustrated by this crystal in loblolly pine (*Pinus taeda* L.) (scanning electron micrograph, radial face).

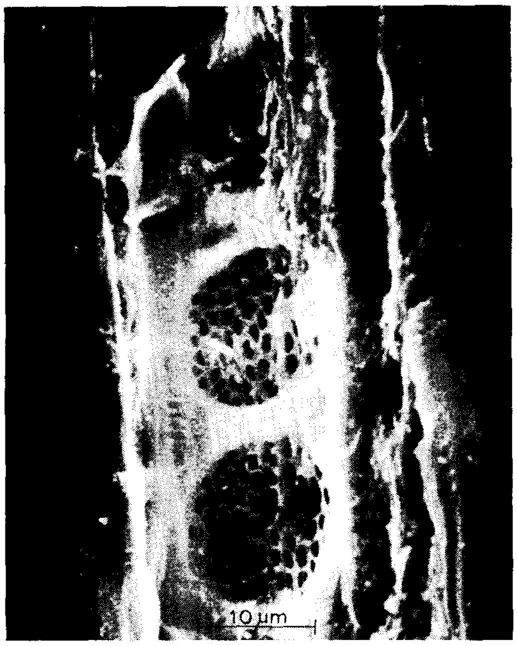

Fig. 13. Sieve areas on the lateral faces of a yellow poplar sieve tube element lack development of a characteristic definitive callous (scanning electron micrograph, radial face).

sieve tube elements lack the formation of the characteristic definitive callous that generally builds up as sieve elements age. The shape of the sieve tube element is quite comparable to small diameter vessel elements. Sieve areas are located laterally on the elements and sieve plates on the end walls, much as the perforation plates are located on the end walls of vessel segments.

Phloem parenchyma constitutes from 12 to 38% of the inner bark volume of North American tree species, according to Chang (1954a). The parenchyma may be strand or fusiform in shape and contain many of the crystals formed in bark (Figs. 14, 15, and 16). The crystals take various shapes, and may be variable within any species.

Fibers and sclereids exhibit multilayered, birefringent walls. In most species, both types of sclerenchyma tend to be in groups surrounded by mechanically weaker tissue, a fact that has enhanced separation of fibrous components of many barks. Chang

Fig. 15. Crystals of various shapes occur in the bark of trees (Red oak, *Quercus rubra* L., scanning electron micrograph, radial face).

Fig. 17. Eastern hemlock (*Tsuga canadensis* L.) bark contains a large number of short sclereids. This sclereid, isolated by maceration, has a rough, irregular exterior contour (scanning electron micrograph).

(1954a) has indicated that over 40% of the inner bark of red oak (*Quercus rubra* L.) may be sclereids (31.6%) and fibers (12.4%). All hardwood barks he investigated contained sclereids or fibers, or both. Among North American conifers, the genus *Pinus* appears to be the only genus containing no sclerenchyma. Other genera contain sclereids of varying forms from the roughly isodiametric "stone" cell (Figs. 17 and 18)

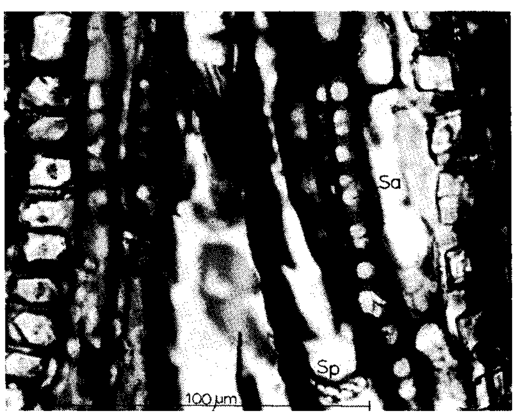

Fig. 16. Lateral sieve areas and the end wall sieve plate make the sieve tube elements of bigtooth aspen quite distinctive. Crystals abound in longitudinal parenchyma (light micrograph, radial section).

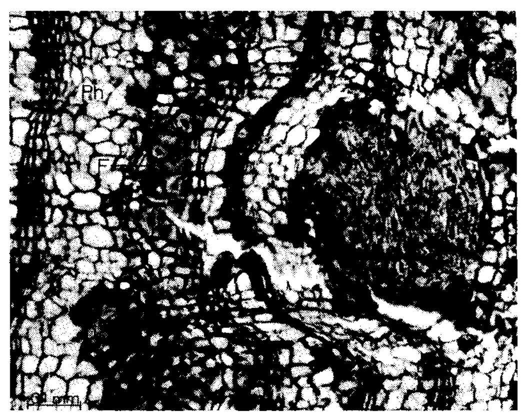

Fig. 18. Thick walls and narrow lumens characterize the sclerenchyma of most hardwood barks (in this case bigtooth aspen). The sclereids are typical of the "stone" cells common to many barks (light micrograph, transverse face).

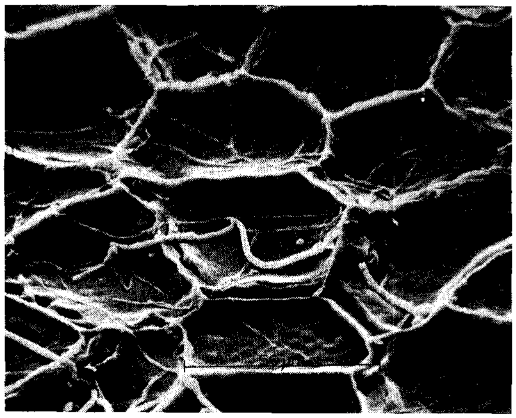

Fig. 19. The phellogen of all trees investigated is thin-walled and flattened radially. Fungal hyphae may have hastened rupture at this characteristically weak layer (scanning electron micrograph).

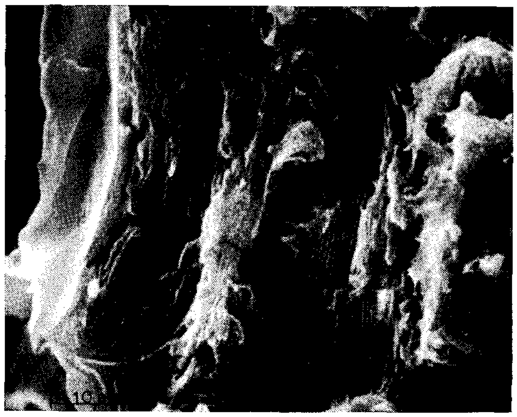

Fig. 21. The thick-walled cogwheel phellem of longleaf pine display multilayered cell walls traversed by pore or pit canals, and a lumen often containing extractive material (scanning electron micrograph, radial face).

to a short fibrous form, or may contain fibers of approximately the same length as wood fibers and tracheids.

Perhaps the most strikingly different cells of the bark are those of the periderm. As discussed previously, phellogen produces phellem or cork to the outside, and phelloderm to the inside. All three cells are roughly isodiametric longitudinally and tangentially, generally with four to six sides. Phellogen remains thin-walled and often forms a plane of failure for natural sloughing of bark (Fig. 19). Invasion by fungi along this layer may hasten the sloughing process. Phellem and phelloderm may be thin- or thick-walled and especially phelloderm may exhibit radial expansion (Figs. 6 and 20).

Thick-walled phellem generally displays several alternating layers of material penetrated by long, narrow pit or pore canals (Fig. 21). Alternating layers of the walls are birefringent, and Sitte (1955) has stated the layers of cork oak phellem to be alternating wax and suberin. Some investigators

Fig. 20. Periderm of longleaf pine illustrates thick-walled phelloderm to the left, phellogen in the center, and thick-walled, cogwheel phellem to the right. Two phellem cells have broken, displaying multilayered cell walls (scanning electron micrograph, radial face).

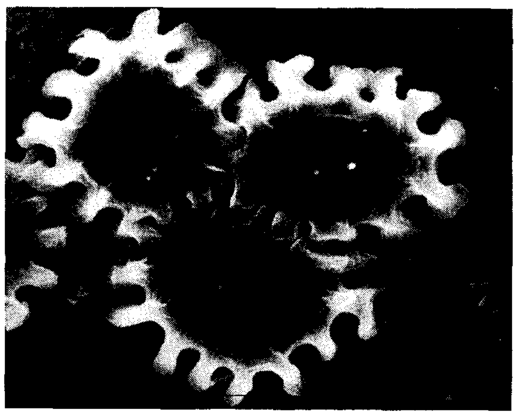

Fig. 22. The cogs of longleaf pine phellem interlock extensively and may contain intercellular fibrils (maceration, scanning electron micrograph, tangential view).

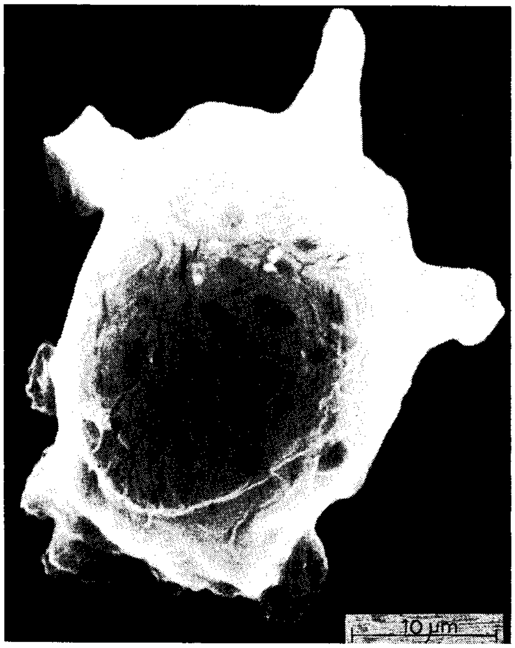

Fig. 23. The thick-walled phellem of some species, such as this cell from loblolly pine, may assume irregular shapes (maceration, scanning electron micrograph, tangential view).

Fig. 24. This phelloderm cell of longleaf pine displays three main layers, the outer two of which contain sublayers (scanning electron micrograph, radial face).

indicated the thick-walled phellem cells to be highly lignified but not suberized, and found suberin in thin-walled phellem by histological techniques (Chang 1954b; Esau 1959; Howard 1970). The southern yellow pines contain phellem with a cogwheel shape (Figs. 22 and 23), a fact that was largely overlooked until recently (Howard 1970), and the extent of their occurrence is still not known. Investigations now being carried out may shed more light on the subject.

Some phelloderm appears to contain three main layers of material, and the outer layers consist of sublayers (Fig. 24). The innermost layer appears amorphous and is most likely an extraneous deposit in the cell lumen.

SUMMARY

We have attempted to present a brief description of general bark structure in the hope of increasing understanding and improved utilization of the material. Most bark cells have an analog in the wood, the exceptions being the short sclereids or stone cells and the cells of the periderm. Comprehensive studies of the bark, particularly the outer bark or rhytidome, are lacking for most of our trees, and the composition and structure of some components are not clearly defined.

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