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BARK STRUCTURE OF NORTH AMERICAN CONIFERS

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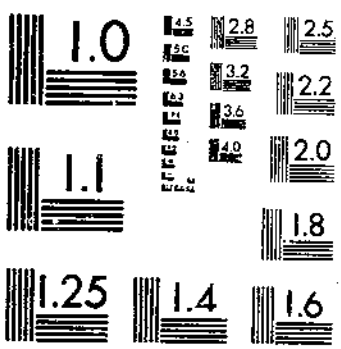

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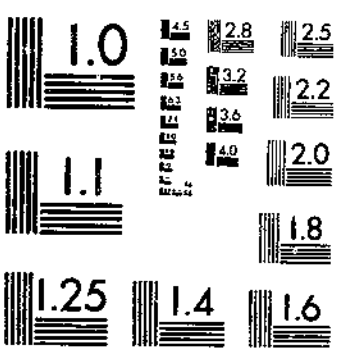

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Bark Structure of North American Conifers[1]

By YING-PE CHANG,[2] *collaborator, Forest Products Laboratory,*[3] *Forest Service*

INTRODUCTION

An anatomical description of bark cells was first recorded in the 17th century, when Robert Hooke observed "cells" in cork and other tissues under the "magnifying lens" and published his discovery in 1665 in his Micrographia. Founders of plant anatomy, such as Malpighi and Grew and their successors up to the late 19th century, were interested in studying stems as a whole rather than parts of them, but the material they used was mostly from young branches. During that period, Chauveaud, De Bary, Hartig, Hill, Moeller, Mohl, Rossow, Strasburger, Van Tieghem, and many others contributed knowledge directly or indirectly related to the anatomy of coniferous barks, although their results sometimes confuse modern research workers. Important contributions in this field, especially in relation to the development and structure of phloem tissue, have been intensively reviewed by Esau (*11, 12*)[4] in publications reporting her own findings.

In recent years, miscellaneous studies relating to the structure of coniferous barks have been published. Citations are made in the appropriate parts of this report, but those by the American authors, such as Abbe and Crafts (*1*) and Isenberg (*27*), and the European authors, such as Holdheide (*21, 22*), Huber (*23, 27, 26*), and Lehmann and Wilke (*33*), deserve particular mention. In general, the contributions emphasized either certain tissues or random species.

In comparison with the development of wood anatomy, research n bark is far behind. The usual neglect of this important part of the oody stem (except in pharmacognosy) may be due in part to overaphasis of the structure of the secondary xylem by the wood anatoists and in part to the influence of the wood industry, which has not own much interest in bark in the past, on the trend of studies in wood chnology. Now, however, the possibilities of bark utilization appeal many wood enthusiasts and conservationists. For a better underanding of this part of our natural resources, a fundamental study of ne structure of bark should be one of the first steps taken toward its tilization.

In order to obtain a full picture of the native barks, a comparative udy of a natural systematic group seems indispensable. For this eason, the study reported here covered all the North American genera nd included the commercially important species of conifers. The roject was approached with the following objectives:

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[1] Submitted for publication April 12, 1954.

[2] This study was performed under the Economic Cooperation Administration f the U. S. Department of State and sponsored by the Forest Products Laboratory. The author wishes to express his gratitude to the Department of State for nancing this research, and to the Forest Products Laboratory, especially to the Division of Silvicultural Relations, for the facilities made available for this ork; and to Dr. B. F. Kukachka, Wood Technologist, for his suggestions.

[3] Maintained at Madison, Wis., in cooperation with the University of Wisconsin.

[4] Italic numbers in parentheses refer to Literature Cited, p. 84.

(1) *To determine the basic anatomical structure of coniferous barks.*—The bark structure of conifers has its own anatomical category among other vegetative organs in living woody plants. Following the modern conceptions of plant anatomy, cell types and arrangement of all tissues outside the cambium of mature barks were examined.

(2) *To evaluate the bark features of diagnostic value and other related findings as means for bark identification.*—Patterns of bark structure are rather constant within a genus and sometimes have unique characteristics for certain species. The bark structure alone or combined with the wood structure may help a great deal in identification of species. For this purpose, the characteristics of bark with diagnostic value were particularly noted and will be enumerated in this report. Chemical methods for bark diagnosis were considered as a supplementary means for bark identification.

(3) *To induce the viewpoints that would correlate bark structure to closely related research.*—This part briefly compares the bark structure of conifers with their wood structure and considers the essential features of bark structure in relation to research associated with bark and forest products. It is a general review and discussion of the trends of "bark technology."

An attempt was made to select as representative North American coniferous barks as possible. Technical problems were solved to a certain extent, so that better observations were obtained from both sections and macerated material.

Although definite conclusions were reached as far as this 1-year project is concerned, the work should be considered as a starting point for further extensive investigations of bark structure.

MATERIAL AND METHODS

Material

The selection of species was based upon two categories: (1) Those species of commercial importance for timber or of other special economic value; (2) those species whose anatomical characteristics should be learned in order to establish reliable criteria for recognizing their bark by structure. Accordingly, this study covered all the North American coniferous genera and most of the important species. The material used included dry specimens, which were collected by the U. S. Forest Products Laboratory a long time ago and were well preserved, and fresh barks from the main trunk and young branches of the same trees, which were collected and sent to the Laboratory by various experiment stations of the U. S. Forest Service.

The following list shows the species and specimen numbers used for this investigation. Common names given are the official tree names of the U. S. Forest Service. The dagger and asterisk marks († and *) following an item indicate that permanent slides for the species were prepared from sections and from macerated materials, respectively. Those species not marked were studied from temporary slides of freehand sections. The numbers following each species name refer to the wood collection numbers of the U. S. Forest Products Laboratory. The structural descriptions given later for the genera studied follow the order of the following list.

List of Species and Specimen Numbers

Taxaceae

(1) *Taxus brevifolia* Nutt. (Pacific yew), 651, 15568.†*
(2) *Torreya californica* Torr. (California torreya), 658.†*

Pinaceae

Subfamily Abietoideae.

(3) *Abies amabilis* (Dougl.) Forb. (Pacific silver fir), 441, 448.*
(4) *Abies balsamea* (L.) Mill. (balsam fir), 456, 507, 15547.*
(5) *Abies concolor* (Gord. & Glend.) Lindl. (white fir), 424, 15522.*
(6) *Abies grandis* (Dougl.) Lindl. (grand fir), 477, 15530.†*
(7) *Abies lasiocarpa* var. *arizonica* (Merriam) Lemm. (corkbark fir), 6241, 8418c.†*
(8) *Larix laricina* (Du Roi) K. Koch (tamarack), 6658, 15542, 15555.†*
(9) *Larix lyallii* Parl. (subalpine larch), 409, 410.*
(10) *Larix occidentalis* Nutt. (western larch), 402.*
(11) *Picea engelmannii* Parry (Engelmann spruce), 308, 15540.*
(12) *Picea glauca* (Moench) Voss (white spruce), 320, 15545, 15562.†*
(13) *Picea mariana* (Mill.) B. S. P. (black spruce), 311.*
(14) *Picea sitchensis* (Bong.) Carr. (Sitka spruce), 325–88, 339.†

Pinus

Subgenus I. Haploxylon

(15) *Pinus albicaulis* Engelm. (whitebark pine), 34, 35, 6339a, 15548.†*
(16) *Pinus aristata* Engelm. (bristlecone pine), 67, 6221, 15521.*
(17) *Pinus balfouriana* Grev. & Balf. (foxtail pine), 72, 6321.
(18) *Pinus cembroides* Zucc. (Mexican pinyon), 31, 15553.*
(19) *Pinus edulis* Engelm. (pinyon), 112, 6257, 15554.†*
(20) *Pinus flexilis* James (limber pine), 63, 6223, 6410, 15567.†*
(21) *Pinus lambertiana* Dougl. (sugar pine), 22, 6309, 15533, 15668.†*
(22) *Pinus monticola* Dougl. (western white pine), 6, 17, 6317a, 6318, 6334a, 15538, 15551.†*
(23) *Pinus strobus* L. (eastern white pine), 5, 12, 19, 5946, 15544, 15557.†*

Subgenus II. Diploxylon

(24) *Pinus banksiana* Lamb. (jack pine), 98, 105, 15572.*
(25) *Pinus contorta* Dougl. (lodgepole pine), 13645, 15552, 6312.*
(26) *Pinus echinata* Mill. (shortleaf pine), 234, 245, 1107, 15526, 15559.†*
(27) *Pinus elliottii* Engelm. (slash pine), 28, 15563, 15565.*
(28) *Pinus glabra* Walt. (spruce pine), 15528.
(29) *Pinus jeffreyi* Grev. & Balf. (Jeffrey pine), 127, 135.*
(30) *Pinus muricata* D. Don (bishop pine), 203, 6288, 15670.
(31) *Pinus palustris* Mill. (longleaf pine), 264, 273, 15525, 15566.*
(32) *Pinus ponderosa* Laws. (ponderosa pine), 6201a, 6289a, 15539, 15669.†*
(33) *Pinus radiata* D. Don (Monterey pine), 6268a, 15564.†*
(34) *Pinus resinosa* Ait. (red pine) 86, 94, 5889, 15531, 15543, 15569.†*
(35) *Pinus rigida* Mill. (pitch pine), 5916, 5918, 15527, 15561.*
(35a) *Pinus serotina* Michx. (pond pine), 5934, 5988, 15535.†*
(36) *Pinus sylvestris* L. (Scotch pine) (naturalized species), 13444.*
(37) *Pinus taeda* L. (loblolly pine), 147, 161, 6490d, 15534, 15560.*
(38) *Pinus virginiana* Mill. (Virginia pine), 210, 212.*
(39) *Pinus coulteri* D. Don (Coulter pine), 196, 201.*
(40) *Pinus sabiniana* Dougl. (Digger pine), 190, 194.*
(41) *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), 15550, 15541.†*
(42) *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), 357, 362, 15537, 15540.†*
(43) *Tsuga canadensis* (L.) Carr. (eastern hemlock), 341.

Subfamily Taxodioideae

(44) *Sequoia gigantea* (Lindl.) Decne. (giant sequoia), 15667.†
(45) *Sequoia sempervirens* (D. Don) Endl. (redwood), 15666, 15671.*
(46) *Taxodium distichum* (L.) Rich. (baldcypress), 554, 555, 15523, 15536.†*

Subfamily Cupressoideae

(47) *Chamaecyparis lawsoniana* (A. Murr.) Parl. (Port-Orford-cedar), 594.*
(48) *Chamaecyparis nootkatensis* (D. Don) Spach. (Alaska-cedar), 5861.*
(49) *Chamaecyparis thyoides* (L.) B. S. P. (Atlantic white-cedar), 589.*
(50) *Cupressus arizonica* Greene (Arizona cypress), 580.
(51) *Cupressus macrocarpa* Hartw. (Monterey cypress), 576.†*
(52) *Juniperus monosperma* (Englm.) Sarg. (one-seed juniper), 609, 610.
(53) *Juniperus scopulorum* Sarg. (Rocky Mountain juniper), 632.*
(54) *Juniperus virginiana* L. (eastern redcedar), 15558, 15570.†*
(55) *Libocedrus decurrens* Torr. (incense-cedar), 585, 15524.†*
(56) *Thuja occidentalis* L. (northern white-cedar), 518, 15546, 15550.†*
(57) *Thuja plicata* Donn (western redcedar), 15529, 15582.†*

METHODS

Microtechnique

The fresh bark was cut to the desired sizes from the selected parts of specimens and fixed immediately in formaldehyde-acetic acid-alcohol solution. For preparing suitable sections from the mature barks, the following steps were necessary.

(1) *Bleaching.*—This is especially useful for those specimens with abundant "resinous" and "tanniferous" substances. A solution containing 20 cubic centimeters of 15-percent hydrogen peroxide and 4 drops of ammonium hydroxide usually bleaches 10 blocks, ½ by ¼ inch, within 4 hours. Bleaching not only reduces the deep colors but increases the penetrability in step (2).

(2) *Softening.*—Commercial hydrofluoric acid diluted to one-half strength is recommended for softening bark. This step, however, is necessary only for those barks composed of fibers or sclereids.

(3) *Washing and dehydration.*—Washing should be very thorough during the course of changing from one solution to another. Dehydration with either ethyl alcohol or a mixture of butyl and ethyl alcohol should be done by increasing the percentage of alcohol very gradually.

(4) *Embedding.*—Bark from young branches can be embedded in paraffin alone. For mature barks, celloidin, up to 4 to 6 percent, followed by paraffin has been recommended. Chloroform is the most satisfactory hardening agent for celloidin-embedded material. After the hardening, the bark is put into benzene or xylene, and this step is then repeated twice with fresh liquid. Next it is transferred into ordinary paraffin, followed by a high-melting-point paraffin for final embedding.

To eliminate the expensive procedure of double embedding, a simple paraffin-embedding method was used. The preceding schedule was followed through the stage of low-melting-point paraffin, and the specimens were then transferred to a mixture of a paraffin with a melting point of 60° to 62° C. and a paraffin with a melting point of 56° to 58° C. The sections cut from bark embedded by this process were quite satisfactory.

(5) *Cutting.*—A rotary microtome was used to cut sections from 8 to 16 microns thick, depending on the nature of the bark. For the

tangential sections, series sections or sections cut at reasonable intervals from the desired parts were obtained.

(6) *Mounting.*—For mounting the paraffin sections on slides, Haupt's adhesive was used. A thin coat of dilute celloidin was applied to hold the sections from slipping away into the subsequent stages.

(7) *Staining.*—Safranin and fast green FCF (FD and C No. 3) were used for staining. The time required was shortened from 12 hours to 15 minutes by accelerating the penetration of stain at a temperature of approximately 53° C.

(8) *Final mounting.*—A synthetic resin medium was used for the final mounting.

Besides the method just outlined, a simple method was developed by which thin layers of bark tissue suitable for general microscopic examination could be prepared by splitting softened material that was previously boiled in water or in dilute solutions used for maceration. This process takes advantage of the high tenacity of bark tissues, especially of their cellulose cell walls. Applying a little mechanical force to the partially softened barks may help split the intercellular substances without damage to the cell walls. Although the exact dimensions and thickness cannot be controlled, thin layers about one cell thick that are good enough for certain purposes can be prepared within a short time.

In addition to the foregoing methods, which were primarily for making thin series sections, freehand sections cut from random fresh material were often prepared. These sections were observed mostly without any artificial treatment and sometimes by applying aqueous stains that are used for detecting specific cell structures or contents. (Such well-known stains as iodine-potassium iodide, ferric chloride, aniline blue, methyl blue, and lacmoid are commonly used for this purpose.) Good sections of this kind were preserved by aqueous mounting media.

To obtain well-macerated tissue elements from bark, the "inner bark" and the "outer bark" should be treated separately or under a fractional procedure. Among the various solutions used for wood maceration, the popular Jeffrey solution, equal parts of 10-percent chromic acid and 10-percent nitric acid, is not so satisfactory for bark as it is for wood. The best approach for securing a better solution for macerating barks would be to find out the real nature of the intercellular substances in bark tissues, especially those in sieve cells; most authorities agree that polyuronides are the main substance. Care should be taken to avoid damage to the delicate cell walls of bark tissues. Chlorination followed by boiling in 3-percent sodium sulfite usually gives well-macerated tissue elements from inner bark.

The macerated delicate tissue elements became easily deformed after several changes of solutions or after having undergone the dehydration procedure for preparing permanent slides. This difficulty was reduced somewhat in the coniferous bark study by keeping the macerated material in a swelling agent. Aman's lactophenol, which is used for handling algae, was used for preserving the macerated material, and glycerin jelly or diaphane was used as the mounting medium.

Description and Illustration

The general methods used for describing wood structure will be followed in reporting the study on coniferous barks. A considerable number of terms with confused meanings should be explained, however. The following definitions of important terms are based upon the consensus of contemporary investigators in this field, especially Eames and MacDaniels (*10*) and Esau (*11, 12*). The terms are used in this report in the sense indicated. Some terms for the general appearance of bark recently suggested by Wood (*56*) were also considered.

(1) *Bark.*—All tissues outside the cambium; a nontechnical usage already long established.

(2) *Inner bark.*—That region of bark nearest the wood, composed mainly of secondary phloem and extending from the cambium to the innermost or last-formed layer of periderm. It usually comprises several seasons' growth. It is often called "active bark," although some tissues at the outer region of inner bark are functionless.

(3) *Outer bark.*—All the bark region from the last-formed periderm to the attached outermost part of the bark. It includes alternate layers of periderm and secondary phloem, or the cortical region in some hardwoods. Both inner bark and outer bark are rather conventional terms.

(4) *Rhytidome.*—The alternate layers of periderm and dead cortical or phloem tissues. Theoretically, it is equivalent to the "outer bark" as previously defined.

(5) *Periderm.*—A secondary tissue in gymnosperms and woody dicotyledons that is derived from *phellogen*, or cork cambium. Structurally, periderm is applied to the phellogen and its two derivative tissues, cork, or *phellem*, and *phelloderm*, which is adjacent to the cortex or secondary phloem.

(6) *Cortex.*—A term used strictly for the primary tissue contiguous to the epidermis and sometimes to the periderm. Other primary tissues, such as primary phloem, do not persist in the old bark; the "pericycle" was not observed in the coniferous bark study.

(7) *Secondary phloem.*—All tissues formed by the cambium toward the outside of the normal stele. Tissues and cell types of this region are as follows.

(a) *Sieve cells.*—The conducting elements in the secondary phloem of gymnosperms and some lower vascular plants. They are elongated, tapering in shape, and lack sieve plates. The *sieve areas* of all cell walls are of the same degree of specialization. The terms *sieve cells* in gymnosperms and *sieve tubes*, with the individual *sieve tube elements*, in angiosperms, parallel those which are used for the two types of tracheary elements in xylem: the tracheids and the vessels with their individual vessel elements, respectively. *Sieve areas* on the walls are comparable to pits. A wall or

part of a wall, bearing one or more highly specialized sieve areas, is referred to as a *sieve plate*, which is a parallel term to perforation for a vessel element. The connecting protoplasmic strands in sieve areas are visible at those cells close to the cambial region. They are simply called *connecting strands*. In later stages of bark formation, the *definitive callus* develops. After the disappearance of definitive callus, the minute pores in the sieve areas become very distinctly surrounded by the reticulate cellulose walls.

(b) *Albuminous cells.*—Primarily, the erect phloem ray marginal cells, which are physiologically associated with sieve cells. The term is comparable to the *companion cells* in angiosperms. Some albuminous cells or their equivalent are in a longitudinal system, but have a function similar to those albuminous cells at the phloem ray margins.

(c) *Phloem parenchyma.*—The vertical parenchyma cells in the secondary phloem, except albuminous and companion cells. A single vertical unit of these cells is called a parenchyma strand.

(d) *Phloem ray.*—The horizontal parenchyma in the secondary phloem. It corresponds exactly to the xylem ray, and the terms used for describing xylem rays are adopted.

(e) *Sclerenchyma.*—The sclerenchyma cells are of two types, *sclereids* and *fibers*. "Extraxylary fibers" is used in the general sense of "libriform fibers," indicating the much-elongated sclerenchyma cells characteristic of the phloem. "Sclereids" is used in a general sense to indicate short, ramified, and sclerified cells. Since the polymorphism and transitions of sclerenchyma cells are still not clearly understood, none of the special terms used for those cells by many authors is adopted in this report.

(8) *The alternate layers of secondary phloem tissues.*—Phloem fibers, sieve cells, and parenchyma in the secondary phloem of Taxodiaceae and Cupressaceae are differentiated in regular sequence. Along a radial axis they would occur in the order of fiber, sieve cell, parenchyma, sieve cell, and fiber again (without special reference as to which one was developed first). In other words, a tangential layer of sieve cells is always adjacent to a tangential layer of phloem fibers on one side and a tangential layer of phloem parenchyma on the other; a tangential layer of fibers or of parenchyma is always between two layers of sieve cells. A complete cycle of these three kinds of cells is called a *unit*, and the units appear in regular *alternate layers*. Some local variations are considered as irregularities.

Descriptions of bark structure given in this bulletin are confined to their generic characteristics and the differences among species within a genus; some particularly interesting species are specially mentioned. By so doing, repetition of all the similarities of closely allied species is reduced as much as possible. Important structures and patterns of cell arrangement are illustrated by photomicrographs.

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DESCRIPTION OF BARK STRUCTURE AND SPECIFIC AND GENERIC CHARACTERISTICS

TAXACEAE

Taxus brevifolia Nutt.

GENERAL FEATURES

Bark of all available specimens less than one-eighth inch thick. Outer bark smooth and exfoliating into large, thin flakes; brownish red to rose red on outer surface. Inner bark usually about one-sixteenth inch thick; light yellowish brown with pinkish tinge. Lines of secondary phloem tissues visible under lens, rather lustrous.

MICROSCOPIC STRUCTURE

Periderm thin, usually composed of 5 to 12 layers of phellem, a layer of phellogen, and 2 to 5 layers of phelloderm. Phellem cells rectangular in cross section of bark, about 10 to 20 microns radially and 15 to 30 microns tangentially; vertically about 20 to 40 microns high as shown in radial section; mostly hexagonal as shown in tangential section. Phelloderm cells slightly broader than phellem cells and often mingled with phloem parenchyma cells; simple pits rather distinct in cell walls; more or less "lignified" cell walls appear on these cells at outer rhytidomes. Both phellem and phelloderm cells often contain "resinous" substances.

Sieve cells mostly differentiated rather regularly in alternating sequence with phloem parenchyma and fibers, but sometimes 2 to 3 or even 5 sieve cells in a continuous radial row without occurrence of parenchyma and fiber in that region; rectangular in cross section, about 15 microns and 30 microns in radial and tangential dimensions, respectively, and varying from 1.5 to 2.8 millimeters long, mostly about 2 millimeters. Sieve areas rather evenly distributed and in a widely spaced vertical row on radial surface of sieve cells; oval to orbicular, about 8 to 10 microns in diameter. Connecting strands and definitive callus distinct in those seive cells close to cambium. Pores and pore groups in sieve areas rather sparse. Network of cellulose cell walls retained within a sieve area distinct, with walls usually broader in central portion of area than at marginal parts.

Fibers differentiated rather regularly in alternating sequence with sieve cells and parenchyma, sometimes not developed at certain alternate units; maturation of fibers rather late, appearing mostly at outer part of inner bark and in discontinuous tangential lines, as shown in cross section. Majority of fibers in inner bark underdeveloped or not much "lignified"; about same size and shape as sieve cells in cross section; mature or strongly "lignified" fibers tend to be square or slightly elongated radially, mostly about 2 millimeters long. Numerous small crystals embedded in cell walls; walls distinct in both mature and immature fibers; simple pits sometimes distinct on walls of immature thin-walled fibers.

Parenchyma forming tangential lines between 2 tangential lines of sieve cells, occasionally 1 or a few cells not in regular place. Individual cells of parenchyma strands about same shape and size as sieve

cells and "unlignified" fibers in cross section; somewhat elongated radially and tending to be oval in radial section; about 80 to 220 microns, mostly about 160 microns high. Simple pits distinct, in 1 or 2 rows, on radial walls, occasionally 2 or 3 pits grouped together to give the appearance of a small sieve area. Cells contain starch grains and "resinous" substance. No definite distinction between regular phloem parenchyma and those supposed to be longitudinal systems of albuminous cells could be determined from material in this investigation.

Phloem rays mainly uniseriate and about 10 cells or 150 microns but sometimes up to 25 cells or 300 microns high; individual cells in radial section about 50 microns in radial dimension and 20 microns high. Erect marginal cells or albuminous cells rare, occasionally 1 or 2 such cells observed on rays close to cambial region; slightly higher than ordinary ray cells and about half as wide in radial dimension. Ray cells contain starch grains and "resinous" substance.

The bark structure of *Taxus brevifolia* is characterized by its rosy rhytidomes, which are usually exfoliated into large, papery flakes; crystalliferous fibers, which are comparatively fine and short, and often remain in the immature or "unlignified" stage; and the sometimes irregular differentiation of secondary phloem tissues into short radial multiples of sieve cells. The presence of crystals in phloem fibers in *Taxus* was reported by Moeller (*40*) many years ago.

Torreya californica Torr.

General features

Bark thin, that of available specimens measuring about one-eighth inch thick (bark of old trees reported as up to one-fourth inch thick). Outer bark with grayish-brown surface, broken into shallow strips with short horizontal scales, fibrous; inner bark light yellow. Irregular tangential lines of fibers, often lustrous, visible in cross section under lens; phloem rays barely visible under lens; other secondary phloem tissues and periderm indistinct under lens.

Microscopic structure

Periderm not well developed, composed of 2 to 5 layers of phellem, a layer of phellogen, and about 2 to 5 layers of pelloderm. Phellem cells thin walled, uniform in thickness; rectangular in both cross and radial sections, about 50 microns in tangential direction and 15 to 30 microns in radial direction; about 30 to 60 microns high in radial section. Pelloderm slightly variable in size; cell walls comparatively thicker as compared with phellem cell walls; simple pits distinct on those cells at outer rhytidomes. Both phellem and pelloderm cells often contain "resinous" substances. Cells in last-formed and early-formed periderm layers very similar.

Sieve cells mostly differentiated regularly in alternating sequence with fibers and parenchyma cells as in barks of Cupressaceae and Taxodiaceae but often simply alternating with parenchyma cells or 3 to 4 sieve cells in a radial row; rectangular in cross section, about 20 to 30 microns and 30 to 50 microns in radial and tangential directions, respectively; variable in length from 1.0 to 3.0 millimeters, mostly about 2.6 millimeters.

Sieve areas rather abundant but not crowded and more or less evenly spaced; oval to nearly orbicular, about 10 microns in diameter. Number and size of pores in a sieve area variable according to size of sieve area and, in turn, to size of sieve cells; usually about 2 to 5 pores in a small group and about 5 to 10 pore groups in a sieve area. Network of cellulose walls among pore groups distinct; border of sieve areas rather broad and distinct. Figure 1 shows the general features of sieve cells of this species.

Fibers differentiated very early, some appearing only about 5 cells away from last-formed xylem cells. Newly formed fibers more or less square in cross section; comparatively thin walled and with a large lumen; about 20 to 30 microns in diameter; radially elongated. Cell walls becoming thickened with a trace of lumen left as fibers mature

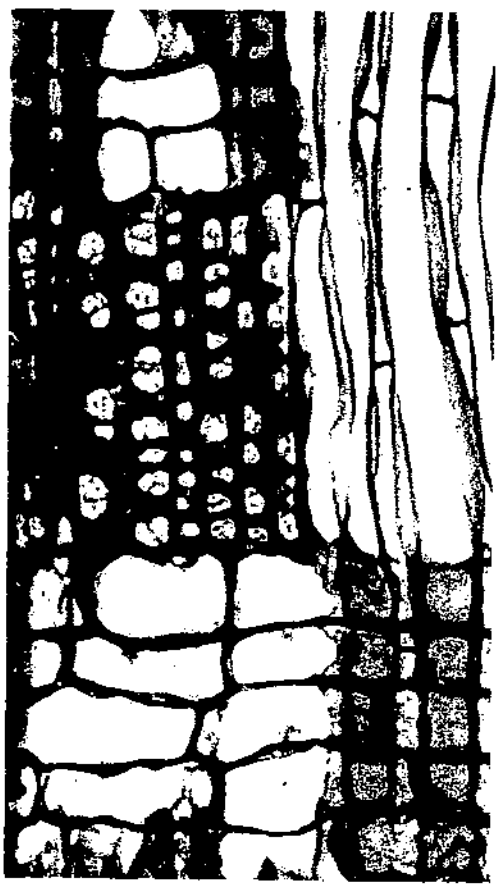

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FIGURE 1.—*Torreya californica.* Radial section of inner bark showing phloem ray without albuminous cell. Sieve cells alternate mainly with parenchyma strands. Parenchyma cells comparatively narrow and with distinct pits in region passing through ray cells.

at outer part of inner bark; abundant small crystals embedded in cell walls. Fibers in inner bark variable in length from 1.5 to 3.0 millimeters, mostly about 2.6 millimeters, those in outer bark tending to be shorter and more uniform in length, mostly around 2.3 millimeters long. Pits on cell walls indistinct.

Immature fibers usually differentiated regularly in alternate layers with parenchyma and sieve cells but sometimes lacking and replaced by parenchyma or sieve cells. Matured fibers appear rather sporadically, forming discontinuous tangential lines in cross section; surrounding cells often squeezed into irregular position by enlarged, mature fibers, so that general appearance is like a cavity or sheath surrounding large fibers. The general appearance of the fibers is shown in figure 2.

Parenchyma cells rather abundant and often replacing fibers in alternate layers with sieve cells; in cross section about same size as sieve cells and alined in radial rows, sometimes smaller and out of radial line,

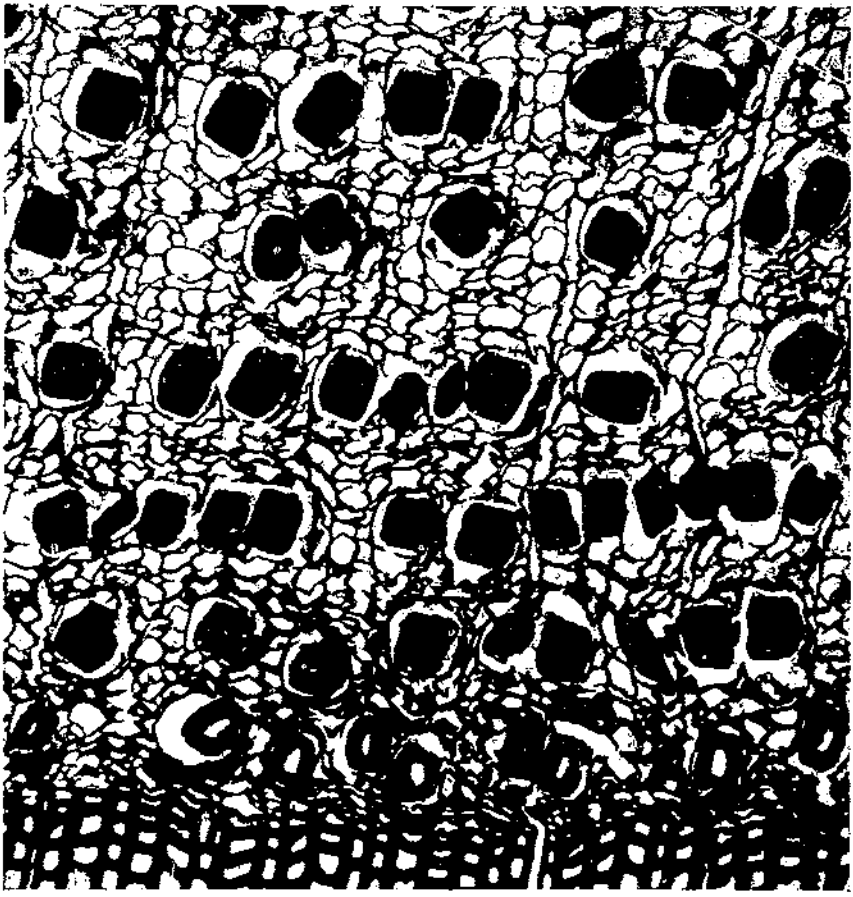

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FIGURE 2.—*Torreya californica*. Cross section of inner bark showing discontinuous tangential rows of matured crystalliferous fibers.

especially those cells close to enlarged mature fibers. Individual cells varying from 50 to 200 microns high, mostly about 100 to 150 microns; radial dimension usually narrower than that of adjacent sieve cells. Simple pits distinct on radial surface of cells, especially in region passing through ray cells; usually in single rows and rather evenly spaced, sometimes 2 or 3 close together, somewhat like small sieve areas but much smaller. Cells contain starch grains and "resinous" substance. No definite distinction between regular phloem parenchyma and parenchyma cells supposed to be in longitudinal systems of albuminous cells.

Phloem rays similar to corresponding xylem rays; not much dilated in outer part of inner bark or even in outer bark; uniseriate and rarely partly biseriate; mostly about 6 cells or 70 microns high, but sometimes up to 12 cells or 100 microns. Individual cells 20 to 50 microns, mostly about 35 microns in radial dimension; rather uniform in height, mostly about 15 microns. Erect marginal cells or albuminous cells rarely observed in sections prepared for this investigation; occasionally a few cells slightly higher than ordinary ray cells but doubtful if typical albuminous cells.

Transformation from inner to outer bark very gradual, the major changes being maturation of fibers, slight expansion of parenchyma cells, obliteration of sieve cells, and increase in cell contents; same changes also occurring at outer part of inner bark.

The significant characteristics of the bark of *Torreya californica* are its thinness, strong yellowish hue, large crystalliferous fibers, and irregularity of development and maturation of the secondary phloem tissues. It differs from the bark structure of *Taxus* by its conspicuously low phloem rays and more mature and larger fibers.

PINACEAE

ABIETOIDEAE

Abies grandis (Dougl.) Lindl.

GENERAL FEATURES

Bark rather thick, that of available specimens measuring up to 1 inch thick; exfoliating into deep fissures with rough but rather firm small scales; grayish brown on outer surface, secondary phloem with reddish hue; inner bark about three-sixteenths to three-eighths inch thick, light yellowish brown. Periderm rather broad and often with layered appearance, distinct to naked eye; light-colored sclereids diffused and alined more or less in tangential lines at outer part of inner bark, distinct to naked eye; phloem rays and parenchyma lines barely visible under lens in region very close to cambium.

MICROSCOPIC STRUCTURE

Periderm composed of well-developed phellem, a layer of phellogen, and conspicuous phelloderm. Phellem often remains up to 40 layers in a periderm layer, occasionally with a layer of slightly thicker walled cells suggesting a growth differentiation; cells like ordinary cork cells, thin walled, uniform in thickness, rectangular in cross section, sometimes radially elongated. Phelloderm varying from 2 to 6 layers in each periderm layer; cells about same size and shape as phellem cells, cell walls slightly thicker; simple pits rather distinct in all walls;

sometimes phelloderm cells merged with phloem parenchyma cells. Both phellem and phelloderm cells contain "resinous" substances; occasionally, small crystals observed in phellem cells.

Sieve cells in radial rows of about 5 cells, interspersed by 1 or 2 parenchyma cells; cells alined rather regularly at region close to cambium; rectangular in cross section, about 15 to 25 microns in radial dimension and 20 to 55 microns in tangential dimension; rather short, mostly about 2.5 millimeters long; ends chisellike, sometimes blunt. Sieve areas occurring mainly on radial surface of sieve cells, occasionally observed on tangential surface at outer bark region due to obliteration of sieve cells; mostly in a single vertical row but occasionally in partial pairs, not evenly spaced, sometimes 2 or 3 very close together; oval to elliptic, about 10 to 15 microns in diameter; often smaller and crowded at end of seive cells. Connecting strands and definitive callus distinct on those sieve cells close to cambial region. Pores distinct after disappearance of definitive callus; usually 2 to 12 pores forming a small group and about 2 to 5 pore groups occurring in a sieve area. Cell walls retained among pores and pore groups forming a distinct network; border from pore groups to margin of sieve area distinct.

Phloem parenchyma well developed in region close to cambium; usually 1 or 2 cells appearing at an interval of about every 5 sieve cells; alined more or less in tangential lines; obliterated and indistinct in cross section because of expanded sclereids but sometimes conspicuously expanded at spaces among sclereid groups; strands about same length as adjacent sieve cells. Individual cells about 100 microns high and 30 to 40 microns in tangential dimension, variable in radial dimension according to position of cells from cambium; conspicuously expanded, with cell walls becoming thicker and "lignified" at outer portion of inner bark; containing abundant starch and "resinous" substance and single crystals of calcium oxalate, mostly isodiametric as shown in both cross and longitudinal views.

Sclereid formation beginning rather early, appearing about 5 or 10 cells from first-formed phloem tissues. Individual cells mostly much branched and twisted, outline in cross section irregular and more or less oval; walls very thick and uneven in thickness, lamellate layers of secondary walls very distinct; simple pits distinct in cell walls, similar to those on stone cells. Cell size variable, mostly about 600 microns long; diameter of main body mostly about 60 microns, but sometimes about 20 microns depending on part of specimen cut. Usually about 10 to 15 cells form a group; sclereid groups elliptic, often locally alined more or less in tangential rows, mostly diffused but rather crowded at outer part of inner bark. Some nonbranching, untwisted sclereids and a few long, fiberlike sclerenchyma cells observed at cambial region (figs. 3 and 4).

Phloem rays at newly developed inner bark similar to corresponding xylem rays; not much dilated at outer part of inner bark but often squeezed by expansion of sclereids and rather wavy in outline; mainly uniseriate or partially biseriate, sometimes 3 pairs close together; mostly 10 to 20 cells but sometimes up to 40 cells or 800 microns high. Individual cells about 50 to 100 microns in radial dimension and usually less than 50 microns high; walls smooth and end walls often rounded; rather uniform in shape and size.

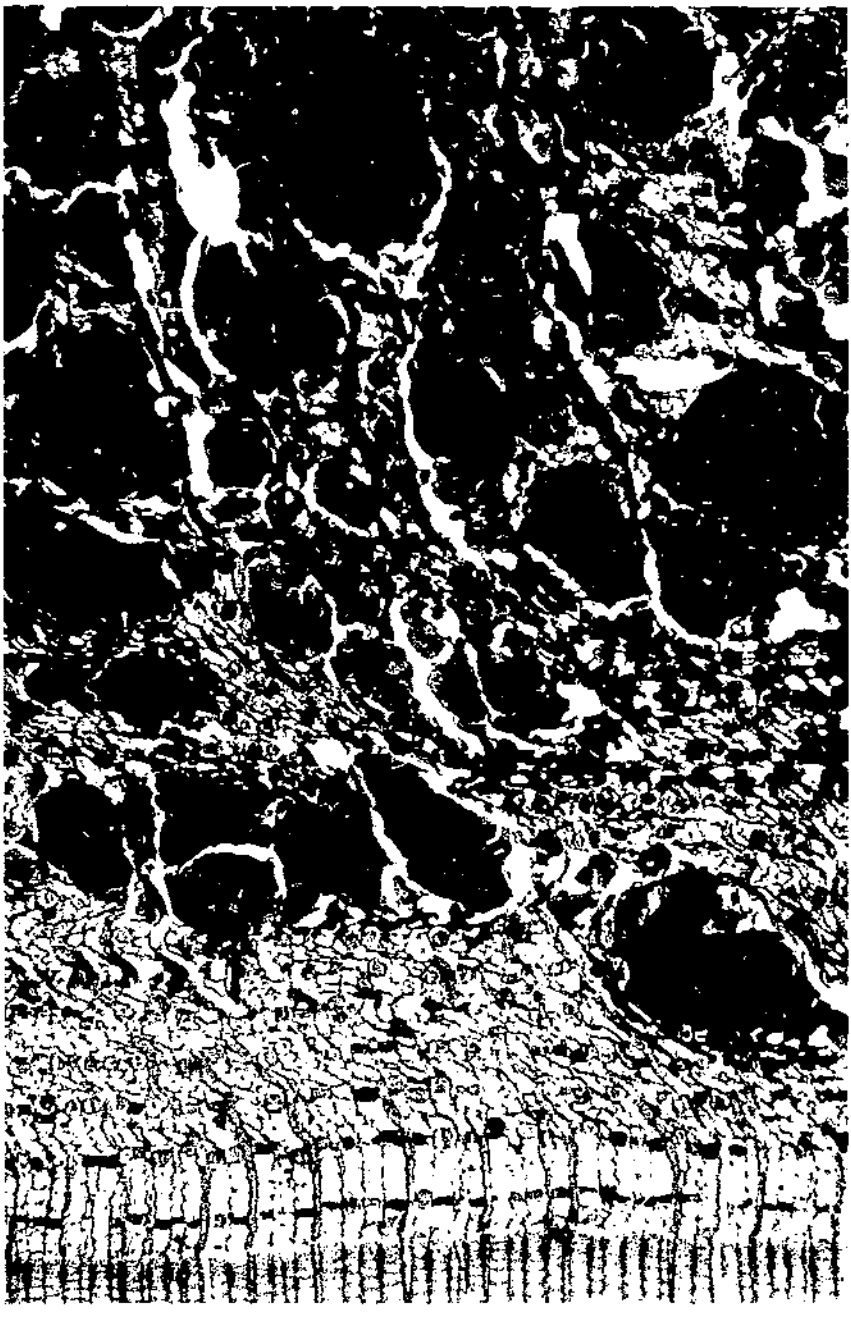

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FIGURE 5.—*Abies grandis.* Cross section of inner bark showing arrangement of tissues close to cambial region to be very different from that at outer part. Sclereid groups occupy most spaces; sieve cells and parenchyma tissues are mostly crushed.

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FIGURE 4.—*Abies grandis*. Radial section showing sclereid groups; irregular size and shape of these cells are characteristic of this kind of sclereid. Judging from position of mature and newly transformed sclereids on radial sections and observations of cross and tangential sections, the sclereids are transformed and "lignified" parenchyma strands and some adjacent ray cells.

Marginal erect cells or albuminous cells distinct only in region very close to cambium, usually slightly higher than ordinary ray cells and about one-third as wide, outer marginal walls rounded; no distinct erect marginal ray cells show at a distance about 20 cells away from cambium. No fusiform rays nor distinct resin pocket formed from enlarged marginal ray cell; occasionally some large-sized marginal ray

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cells containing rather abundant "resinous" substance distributed sporadically. Starch grains and "resinous" substances rather abundant in ordinary ray cells; occasionally small crystals observed in those ray cells merged in parenchyma cells close to peridermal region.

The presence of rather regularly arranged secondary phloem tissues in the cambial region seems to be the main difference between the inner bark and the outer bark of *Abies grandis*. Since the formation of sclereid groups starts early in the inner bark and most of the sieve cells become obliterated with the expansion of sclereids, there is no conspicuous difference between the outer bark and the outer part of inner bark, except the degree of modification of those cells.

In general, the bark structure of the species of *Abies* investigated has many characteristics in common. They are: The broad band of thin-walled phellem cells; abundant sclereid groups usually alined more or less in discontinuous tangential lines; sieve cells arranged in short radial rows and shorter than those of most of the other genera; abundant isodiametric crystals in the parenchyma; and the lack of fusiform rays.

Among the species investigated in this genus, the bark structure of *A. lasiocarpa* var. *arizonica* is very distinguishable from others by its well-developed cork, which often continuously grows without formation of rhytidome. It is reported that the first-formed band of periderm of this bark often grows continuously up to 100 years. The abundant pocketlike resin passages are also characteristic (fig. 5). *A. balsamea* has comparatively much thinner bark, abundant large-sized resin pockets, and fewer sclereids. The gross features of *A. grandis* and *A. concolor* are very similar with respect to the comparatively rough, thick bark as well as abundant sclereid groups. The periderm in *A. concolor*, however, has a yellowish hue and is much lighter in color than that of *A. grandis*, which has a reddish hue.

Larix laricina (Du Roi) K. Koch

General features

Bark comparatively thin, often about one-fourth to one-half inch thick in ordinary-sized trees, sometimes up to ¾ inch thick. Outer bark exfoliating into shallow furrows with thin scales; reddish brown, with purplish red hue in periderm; periderm often compact and with fine lines. Inner bark often wider than last-formed rhytidome layer; scattered sclerenchyma dots distinct under lens; parenchyma lines and phloem rays visible; resin canals rather abundant.

Microscopic structure

Periderm comparatively thin, usually composed of about 5 or more layers of phellem, a layer of phellogen, and 2 to 5 layers of last-formed phelloderm. Phellem cells entirely thin walled or alternating with a few layers of thick-walled cells which were probably transformed from phelloderm; thin-walled cells rather uniform in thickness and like ordinary cork cells; thick-walled cells rather irregular in shape, with very narrow lumen and distinct simple pits: cells of both types variable from 10 to 30 microns tangentially and 10 to 15 microns ra-

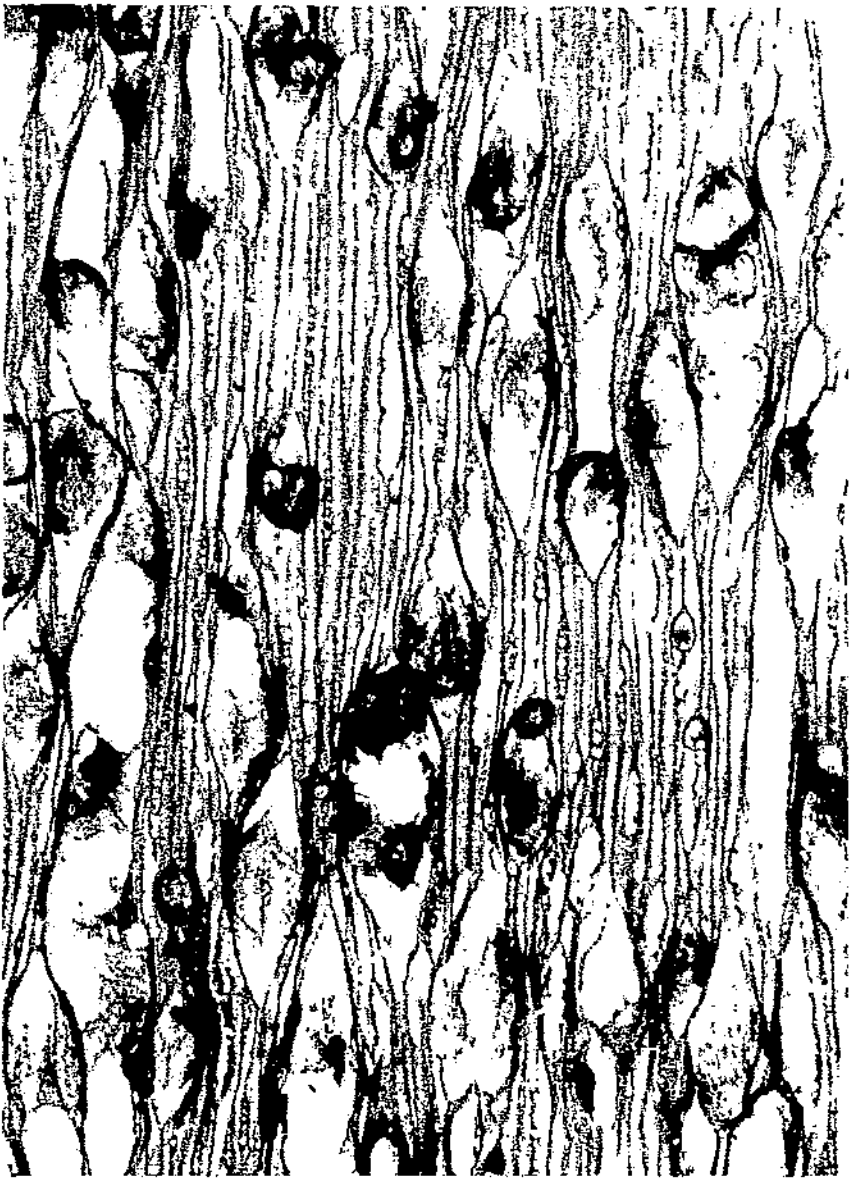

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FIGURE 5. *Abies lasiocarpa* var. *arizonica*. Tangential section showing well-developed pocketlike resin passage differentiated from ray cells, without definite border surrounding passage.

dially in cross section and about 20 to 30 microns high. The last-formed phellodern cells about same size and shape as phellem cells; rather uniform in size at layers close to phellogen, becoming slightly elongated radially and merged into secondary phloem parenchyma cells.

Sieve cells in radial rows of 5 to 10 cells interspersed by a layer of parenchyma or fibers, mostly about 5 cells in a radial row interspersed by a layer of parenchyma; about 30 to 50 microns in tangential dimension and 15 to 30 microns in radial dimension; varying from 2.0 to 4.6 millimeters long, mostly about 3 millimeters; ends usually gradually pointed but often blunt.

Sieve areas oval to elliptic; mostly in a single vertical row on radial walls of sieve cells, unevenly spaced and occasionally partially crowded; variable in size according to size of sieve cells, generally about 10 microns in diameter. Connecting strands and definitive callus distinct in those sieve cells close to cambial region. Pores in sieve areas distinct in those cells at outer part of inner bark; often 3 to 6 pores in a group and about 2 to 5 groups in an area. Borderline of sieve areas distinct; cellulose cell walls retained within a sieve area branchlike without definite pattern.

Fibers very sporadic, about 2 to 8 mature fibers in a square millimeter, mainly solitary; rather short, varying in length from 0.7 to 1.5 millimeters, mostly about 1 millimeter; outline in cross section oval to irregularly rounded; diameter variable according to position being cut, mostly about 40 to 60 microns. Individual cells mostly straight but occasionally slightly branched, ends gradually pointed or abrupt; cell walls very thick with lamellate layers, narrow lumen, visible simple pits.

Parenchyma cells often occur singly or 2 to 4 in a short radial row, tangentially more or less continuously alined; parenchyma strands about same height as adjacent sieve cells. Individual cells about same size and shape in cross section as sieve cells, usually radially elongated at outer part of inner bark, about 100 microns high; simple pits similar to small sieve areas on walls of cells at outer bark; end walls more or less rounded. Cells contain abundant "resinous" substance and isodiametric crystals.

Phloem rays in two sizes, uniseriate rays and fusiform rays with horizontal resin canals. Uniseriate rays rather high, mostly about 15 cells or 300 microns, but sometimes up to 40 cells or 700 microns high; individual cells about 50 to 70 microns in radial dimension and about 20 microns high, usually containing "resinous" substance and starch grains. Albuminous cells conspicuous and appear in most ray sections close to cambial region; slightly higher than ordinary ray cells to twice as high, mostly about 20 to 30 microns in radial dimension. Fusiform rays variable in size at different stages of development and position in tangential sections; local expansion or vertical elongation through radial course often conspicuous; canals present with well-defined border of 2 to 3 layers of epithelial cells.

Specimens of *Larix occidentalis* and *L. lyallii* were also examined. The arrangement of tissues in secondary phloem and the size and shape of the individual cells generally are about the same as in *L. laricina*. Definite distinctions between these three species could not be established in this study. Phloem fibers in the bark of *L. occidentalis* are mostly about 1.6 millimeters long, comparatively longer than in the other two species, and comparatively abundant in the outer bark. The bark of *L. occidentalis* is thicker than that of the other two species.

The bark structure of *Larix* is characterized by the roughened, reddish brown, brittle scales of the outer bark; abundant resin canals; both thin- and thick-walled periderm cells; short, sporadic fibers; the presence of fusiform rays; and parenchyma with isodiametric crystals. Some of these structures are illustrated in figures 6, 7, and 8.

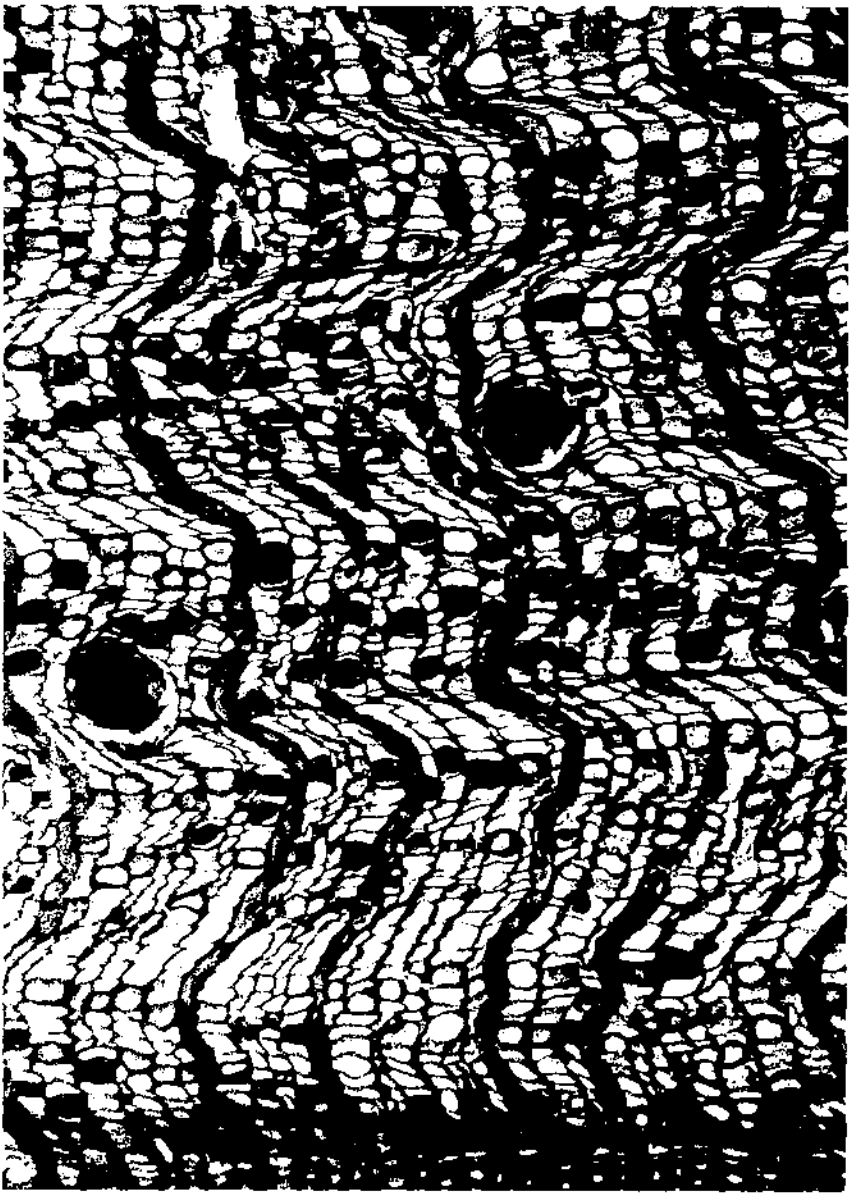

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FIGURE 6. *Larix laricina.* Cross section of inner bark showing arrangement of sieve cells, parenchyma, and sporadic fibers

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FIGURE 7.—*Larix laricina*. Radial section showing part of sieve cell with sieve areas, adjacent to parenchyma cell with isodiametric crystals. Distinct border in each sieve area and cell wall among pore groups are visible.

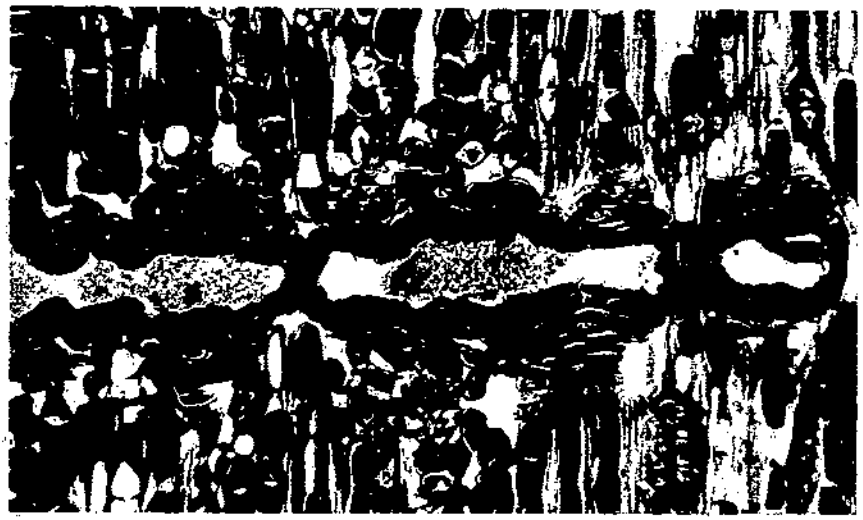

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FIGURE 8.—*Larix laricina*. Radial section showing a fusiform ray with horizontal resin canal. The radial disconnection and local expansion of the canal are explained in figure 16.

Picea glauca (Moench) Voss

General features

Bark thin, that of available specimens usually measuring not over one-half inch but sometimes up to three-eighths inch thick. Outer surface grayish brown with slightly pinkish hue, forming thin, small scales. Inner bark rather narrow, from one-sixteenth to one-eighth inch wide in the dried specimens studied; parenchyma lines and rays visible under lens; sporadic sclerenchyma groups visible in inner bark and rather distinct at outer bark. Periderm distinct, slightly deeper in color than secondary phloem tissues in rhytidome.

Microscopic structure

Periderm composed of 2 or 3 layers of the last-formed phelloderm, a layer of phellogen, and alternate layers of thin-walled phellem cells and thick-walled cells which were probably originated from phelloderm; total number of phellem cells in a periderm layer variable, often over 20 cells.

Phellem cells rectangular in cross section, about 10 to 20 microns and 20 to 30 microns in radial and tangential dimensions, respectively, and usually about 50 microns high in radial section: often 1 to 3 layers of thick-walled cells alternating with 1 to 3 layers of thin-walled cells; thick-walled cells with very narrow lumen and distinct simple pits, thin-walled cells rather uniform in thickness and with large lumen like ordinary corky cells: both types of cells often containing "resinous" substance and small isodiametric crystals. The last-formed phelloderm cells about same size as phellem cells but narrower radially, merged into parenchyma cells of secondary phloem tissues; cells occasionally "lignified" and containing "resinous" substance; simple pits distinct in those cells in outer bark region.

Sieve cells usually in radial rows of about 15 cells interspersed with parenchyma cells, rather regularly alined at region close to cambium; about 10 to 20 microns and 10 to 30 microns in radial and tangential dimensions, respectively, and 2 to 4.5 millimeters long, mostly about 3.8 millimeters: obliterated or crushed in outer part of inner bark and in most of outer bark.

Sieve areas usually in a vertical row on radial surface of sieve cell walls, not evenly spaced, sometimes crowded or 2 to 3 areas close together or small areas in tangential pairs; oval to elliptic and usually oblique, forming a small angle to vertical axis of cell walls; mostly about 10 microns in diameter but variable according to size of sieve cells. Connecting strands of definitive callus distinct in those sieve cells close to cambium. Pores distinct in inactive sieve cells, forming small groups and varying in number in different-sized sieve areas; network of cell walls among pores distinct and without definite pattern. (See fig. 9.)

Sclereids in groups or clusters usually of 10 or more cells; groups very sporadic at outer part of inner bark, oval to elliptic on cross section, about 150 microns in radial dimension and 200 to 400 microns in tangential dimension. Individual cells about 15 to 25 microns in diam-

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FIGURE 9.—*Picea mariana*. Macerated inner bark showing general appearance of sieve cells.

eter but variable according to position of cell cut, short, twisted, and branched; cell walls very thick, with a very narrow lumen, and distinct simple pits.

Parenchyma usually in layers of 1 to 3 cells in short radial multiples, alined more or less in a discontinuous tangential line in cross section:

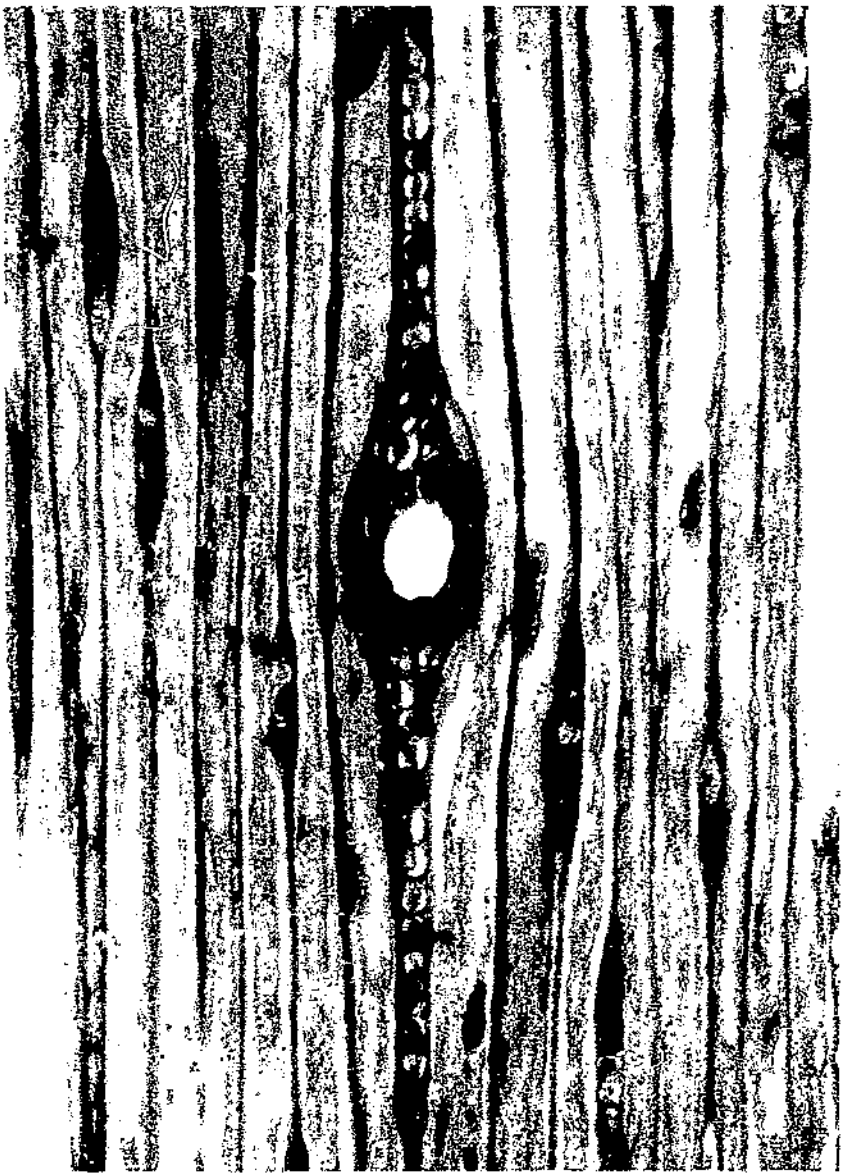

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FIGURE 10. *Picea engelmannii*. Tangential section of secondary phloem close to cambial region. Notice pattern of epithelial cells in horizontal resin canal and inclusions in sieve cells.

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parenchyma strands about same length as adjacent sieve cells. Individual cells about 50 to 150 microns high; distinct simple pits in cell walls, especially in those cells in outer bark or outer part of inner bark, with 2 or 3 pits close together somewhat like small sieve areas. Cells contain "resinous" substance and occasionally isodiametric crystals; starch grains distinct in fresh material.

Phloem rays of two sizes, uniseriate and fusiform. Uniseriate rays mostly about 10 to 15 cells or 200 to 300 microns high but sometimes up to 25 cells or 400 or more microns. Individual cells in radial section about 15 to 20 microns high and 40 to 100 microns in radial dimension; contain "resinous" substance and abundant starch grains. Marginal erect cells or albuminous cells present in almost every ray close to cambial region, usually in layer of single cells or 2 cells; about 20 to 30 microns wide and 40 to 60 microns high; with large nucleus; no distinct starch reaction.

Fusiform rays with horizontal resin canals common; usually 2 to 5 layers of thin-walled epithelial cells forming distinct border around canals; innermost epithelial cells usually over 6 in number, individual

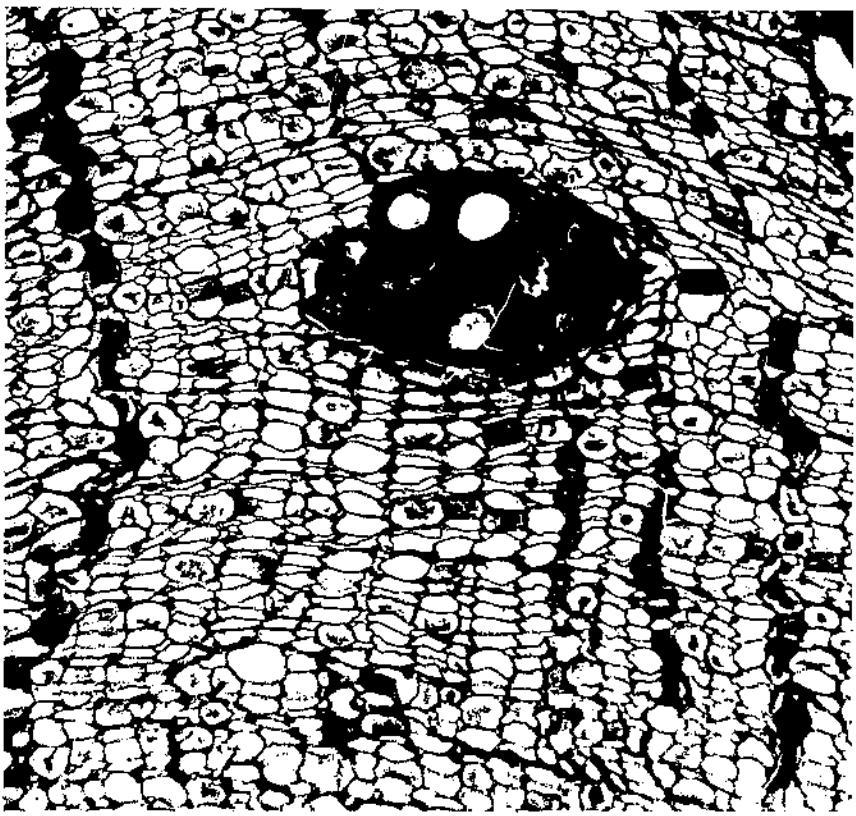

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FIGURE 11.—*Picea sitchensis.* Cross section of inner bark with a single sclereid group differentiated. Most tissues in this region were still in good condition

cells small and nearly circular in tangential section (fig. 10); size of canals variable depending on stage of development at position cut; local expansion occurring very often throughout entire radial passage; parts of many vertically elongated canals often present at outer border of inner bark.

Judging by the available specimens of the four species *Picea glauca*, *P. engelmannii*, *P. mariana*, and *P. sitchensis*, the microscopic structures of spruces have some features in common. Their barks are all comparatively thin and usually less than one-half inch thick. The periderm is composed of both very thick- and thin-walled cells. Sclereids occur in small groups (fig. 11), and the groups are rather sporadic and sometimes absent in the inner bark of comparatively young trees. Fusiform rays with horizontal resin canals are always present. The occurrence of parenchyma at certain intervals between two radial rows of sieve cells seems rather constant in the different species, on the basis of the specimens collected from several localities. *P. sitchensis* has more sclereid groups than any other species observed. Definite distinction of species was not established by this study, however.

Pinus monticola Dougl.

General features

Bark comparatively thin, up to three-fourths inch thick in available specimens (reported as up to 1½ inches thick in old trees). Outer surface grayish brown with cinnamon-brown secondary phloem; exfoliating into deep fissures and with small scales; scales of rhytidomes about one-eighth to one-fourth inch in tangential dimension, radial distance between scales about one-sixteenth to three-sixteenths inch in cross section, middle portion of scale lines often conspicuously radially convex, and scales often rounded in region of overlap. Inner bark rather narrow, usually about one-sixteenth inch wide but very uneven in width in bark from different sides or parts of trunk. Phloem rays and parenchyma lines visible under lens; parenchyma not much expanded at outer bark; ray lines often in good alinement throughout outer rhytidomes. Resin canals abundant, distinct to naked eye.

Microscopic structure

Periderm rather broad, composed of 2 to 8 layers of last-formed phelloderm, a layer of phellogen, and 10 or more layers of phellem; sometimes number of phellem layers variable in different portions of periderm. Phellem composed of thin-walled ordinary cork cells entirely or of thin-walled and thick-walled cells in alternate bands, the latter type probably originating from phelloderm; cells mostly square to rectangular and tangentially elongated in cross section, about 20 to 50 microns in radial dimension and 40 to 80 microns in tangential dimension, height in radial section about same as tangential dimension in cross section; thick-walled cells more variable in size; simple pits distinct in cell walls. The last-formed phelloderm cells thin walled; alined rather regularly and uniform in shape and size in those cells close to phellogen, becoming larger and tending to

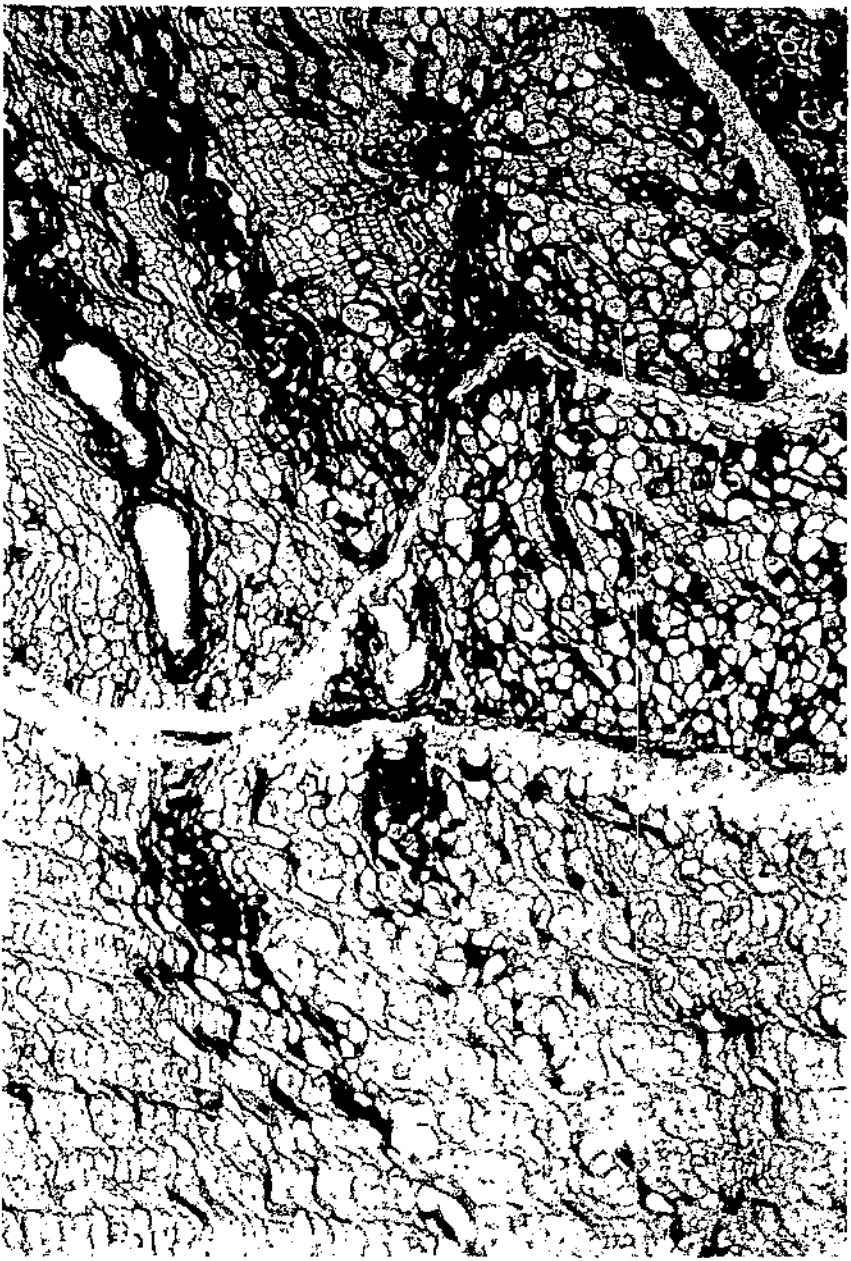

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FIGURE 12.—*Pinus monticola*. Cross section with inner bark at lower part and rhytidome formation at upper part; particularly illustrates only slightly expanded secondary phloem tissues in outer bark and most of sieve cells and parenchyma still in regular shape; outlines of periderm are mostly curved, especially at overlapping areas. These features are characteristic of soft pine barks.

be oval and merged into phloem parenchyma cells; simple pits distinct in cell walls. Both phellem and phelloderm cells often contain "resinous" substance.

Sieve cells alined in regular radial rows, often about 10 cells but sometimes only 5 cells continuously in a row, interspersed by 1 to 3 parenchyma cells. Individual cells rectangular in cross section, about 30 to 50 microns in tangential dimension and 20 to 30 microns in radial dimension; from 1.6 to 4.1 millimeters long but mostly about 2.6 to 3.5 millimeters; ends chisellike and gradually pointed.

Sieve areas in a single row on radial surface of sieve cells, not evenly spaced, and occasionally 2 or 3 close together or in local pairs; oval to elliptic; size variable according to size of sieve cells, mostly about 10

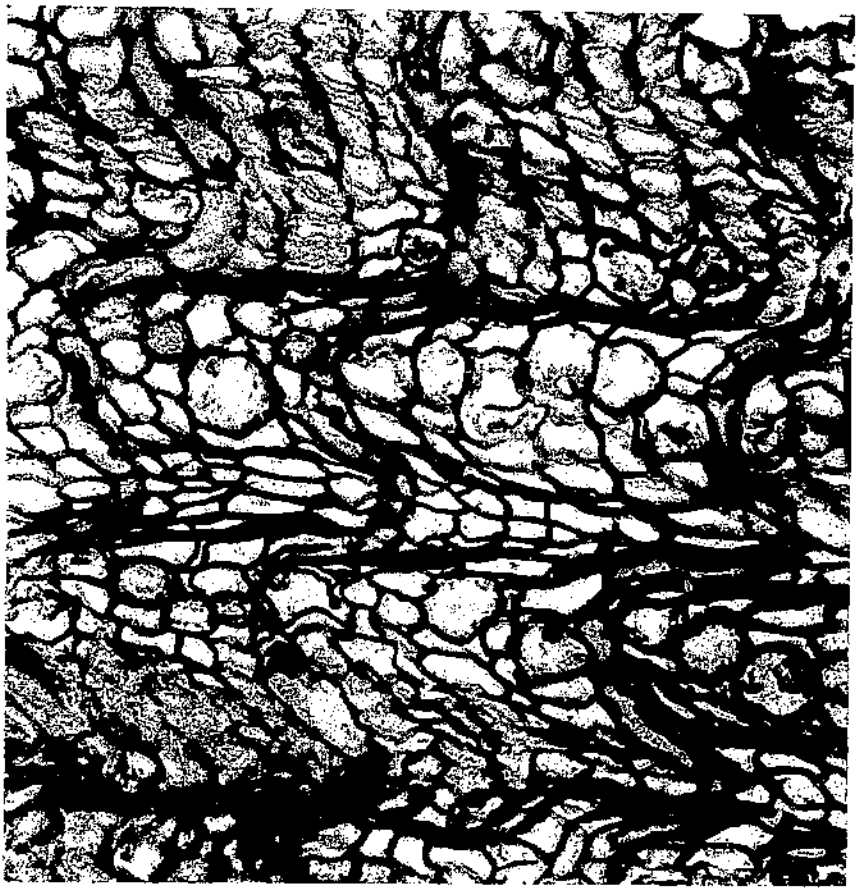

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FIGURE 13.—*Pinus strobus*. Cross section of outer part of inner bark showing general appearance of pine bark. Secondary phloem is characterized by no fibers nor sclereids, large-sized parenchyma forming more or less continuous tangential rows. Tissues between 2 tangential crushed lines probably are equivalent to 1 season's growth. Cells are alined in wavy, not straight radial rows. Section was prepared from dried specimen.

to 15 microns in diameter. Connecting strands and definitive callus distinct in those sieve cells close to cambium. Pores of sieve areas distinct after disappearance of definitive callus; often 5 to 10 pores form a small group with about 3 to 6 pore groups occurring in a sieve area; distinct network of cellulose walls retained among pore groups; narrow borderline formed between margin of sieve area and outline of pore groups. Cells not much obliterated at outer bark, but cell walls shrunk and "lignified."

Parenchyma strands often of single cells or up to 3 cells in radial rows alined more or less in discontinuous tangential lines in cross section; occasionally a few cells sporadically distributed between two regular lines; length of strands about same as that of sieve cells. Individual cells similar in shape and size in cross section to sieve cells close to the cambial region, becoming radially expanded and oval in outer part of inner bark, about 50 to 150 microns high; often containing "resinous" substance and crystals with rectangular lateral

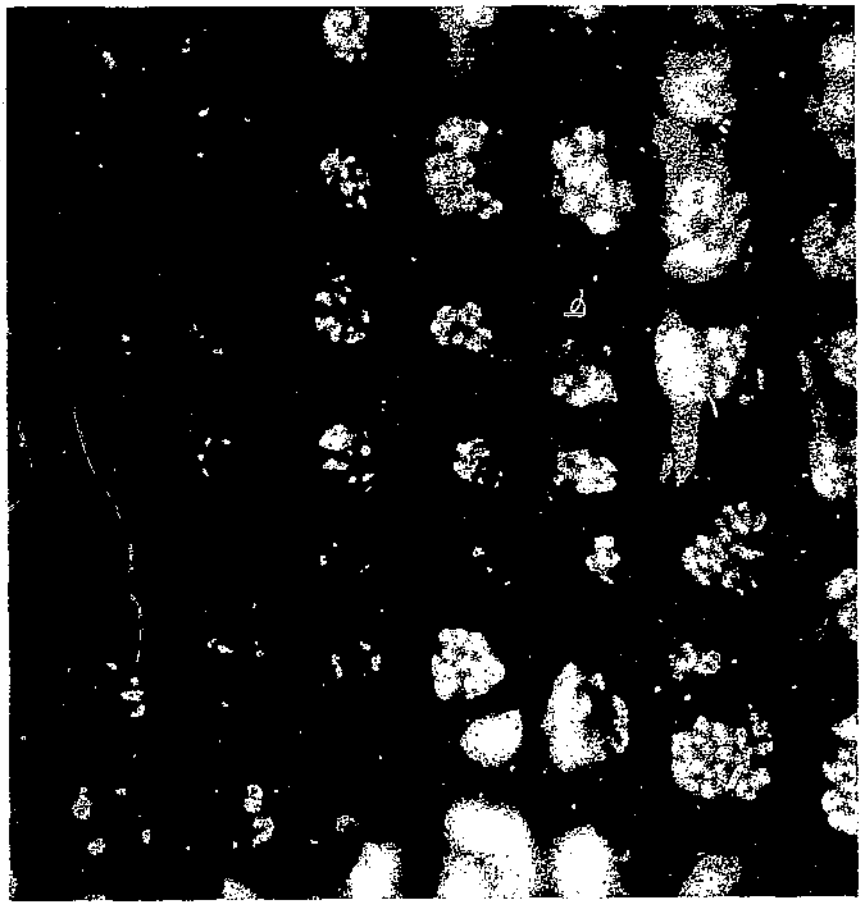

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FIGURE 14.—*Pinus strobus.* Radial section through a group of sieve cells; showing well-developed sieve areas with pore groups.

faces about 10 by 20 microns; simple pits distinct in those cells in outer part of inner bark or outer bark region. Radial expansion of parenchyma cells conspicuous only in remote outer bark.

Phloem rays of two sizes, uniseriate and fusiform with horizontal resin canals. Uniseriate rays often partially biseriate; mostly about

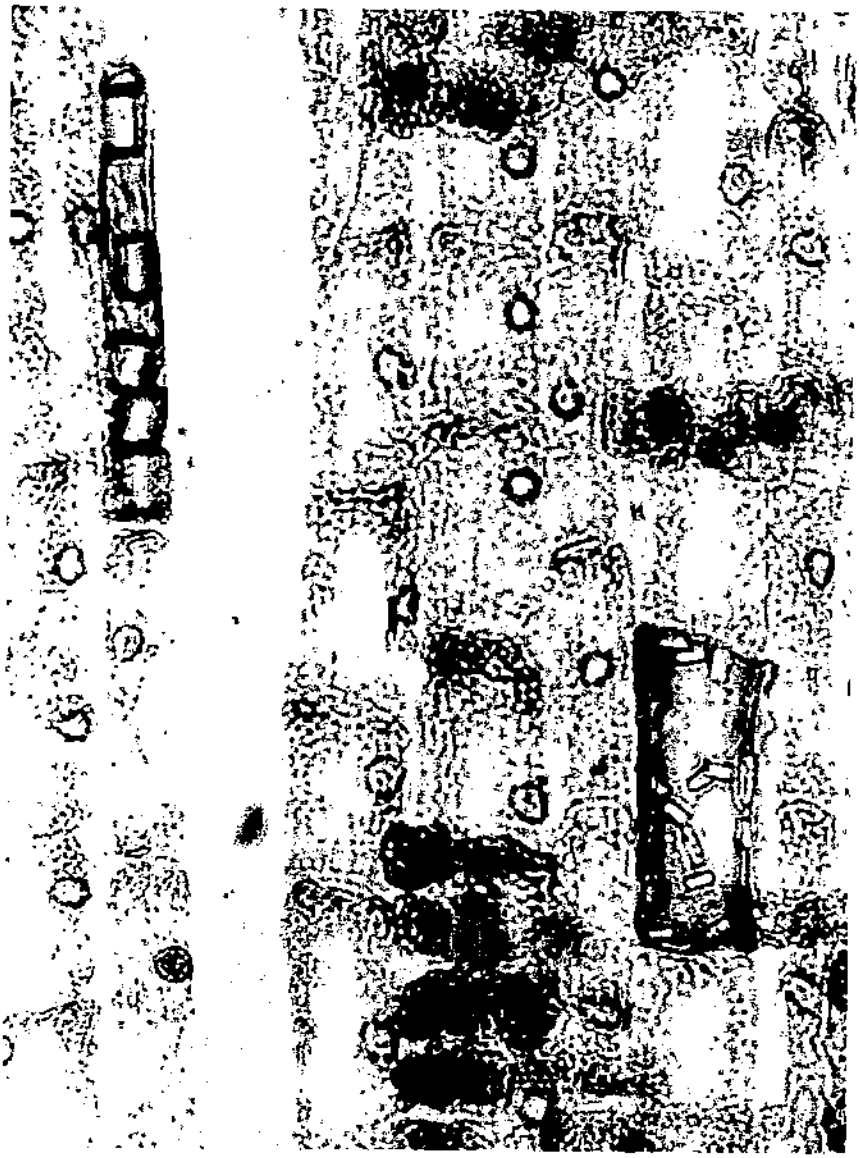

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FIGURE 15. *Pinus strobus.* This section was prepared by splitting inner bark boiled in water. Two sizes of crystals are shown in parenchyma cells; despite different sizes, they are all the type of rectangular-faced crystal that is characteristic of soft pine barks.

5 to 10 cells or 300 to 400 microns high, sometimes up to 25 cells or 700 microns; expansion of rays conspicuous in tangential width of rays and radial dimension of individual cells but height of rays not changed much. Cells in uniseriate rays contain abundant starch grains.

Marginal erect cells very common, appearing at almost every ray section close to cambium, usually a layer of single cells or occasionally of two cells in a vertical row or margin; individual albuminous cells about twice as high as ordinary ray cells, about one-half to one-third as large in radial dimension; with large nuclei; ordinary starch reaction tested with iodine-potassium iodide indistinct. Fusiform rays with horizontal resin canals; innermost canal borders formed by 3 to 4 thin-walled epithelial cells as shown on tangential section. Innermost epithelial cells usually larger than outer surrounding cells. No sclerenchyma cells observed in secondary phloem.

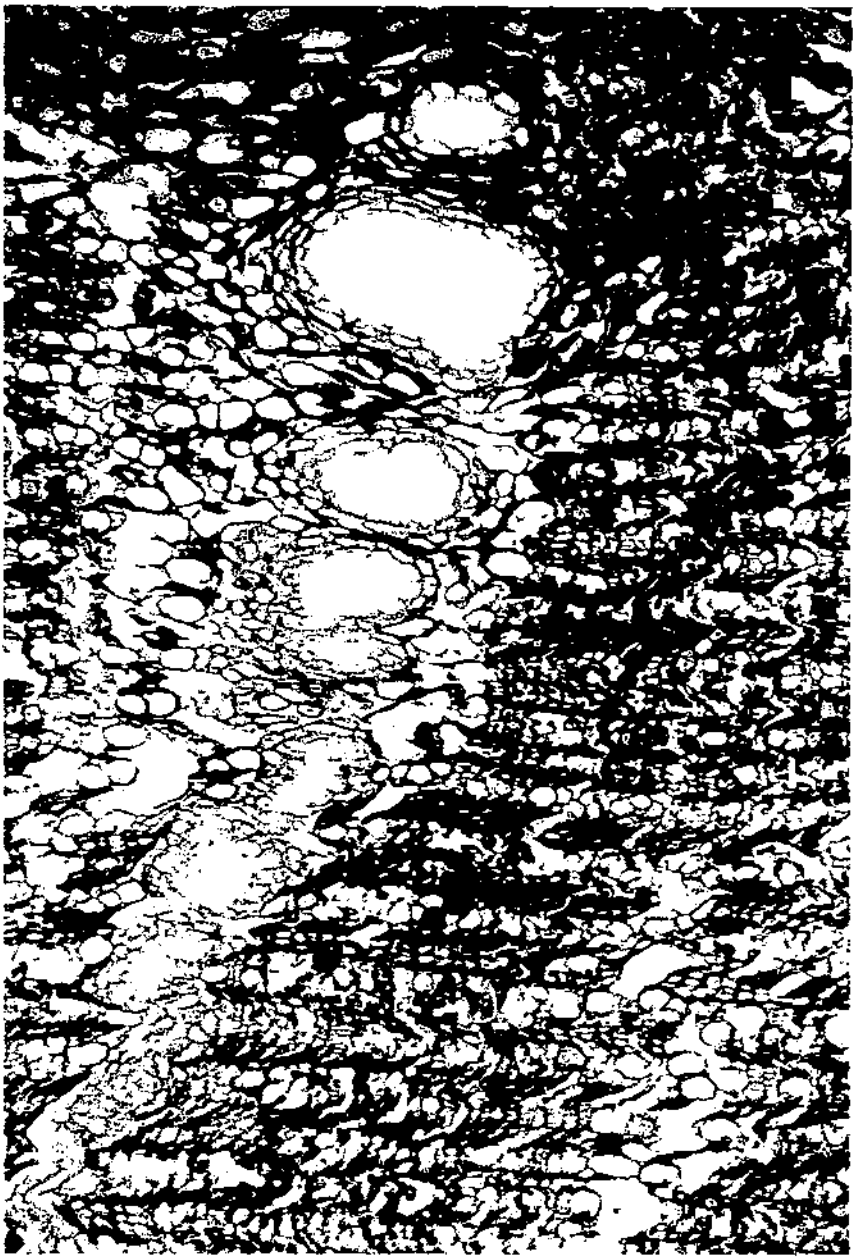
The bark structure of *Pinus monticola* is characterized by small-scaled rhytidome layers with grayish-brown outer surface, the outlines of the rhytidome layers often being curved in cross section, radially convex, and overlapping, with the intersecting regions more or less rounded; rather broad periderm, composed of both thin- and thick-walled cells; often 5 to 10 sieve cells in a continuous radial row; parenchyma cells containing crystals with rectangular lateral faces; no sclerenchyma cells in the secondary phloem.

Among the three important timber species in the Strobi subsection of *Pinus*, namely *P. strobus*, *P. monticola*, and *P. lambertiana*, the bark structures of *P. monticola* and *P. strobus* are very close. The bark of *P. lambertiana* differs from that of the eastern and western white pines by its wideness; deep reddish-brown color; short, broad parenchyma cells containing very large-sized starch grains; and long sieve cells, usually about 4.5 millimeters long. The thick and gelatinous extract obtained from sugar pine bark by acidic alcohol treatment is also very characteristic.

Small, tangentially short, and often curved periderm, only slightly expanded secondary phloem tissues in the outer bark, and the form of the parenchyma crystals are characteristics of the bark structure of the soft pines (compare figs. 12, 13, 14, 15, and 16). Resin canals are comparatively more abundant in these species than in the hard pines.

Within the soft pines subgenus *Haploxylon* it is rather difficult to establish definite sharp categories for separating species by their structures. Some soft pine species, however, do have particular features that could be useful for identification purposes; for instance, the characteristics of sugar pine previously pointed out. In addition, the bark of *P. bungeana* with its thin, white, and large flakes differs from that of all other native pines. This species has been introduced into this country and eventually may be widely cultivated as a beautiful ornamental tree. The barks of *P. balfouriana* and *P. aristata*, which have very thick and much-curved periderm and small-scaled rhytidome layers containing abundant resin canals, can easily be recognized by their general appearance. Bark scales of *P. cembroides* are tangentially longer than those of any other soft pines studied.

Abbe and Craft have contributed an important reference (*1*) on the phloem structure of white pine and related species.



89912 F

FIGURE 16.—*Pinus flexilis*. Cross section of outer part of inner bark showing a row of resin canals developed from phloem ray cells; canals are horizontal rather than vertical. Canals actually connected despite isolated appearance; this appearance is due in part to local expansion of canals in different directions and in part to canals not being cut at the same level in the radial direction.

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Pinus echinata Mill.

General features

Bark of available specimens from small trees about three-fourths inch thick; exfoliating into deep fissures and with comparatively thin scales; secondary phloem in rhytidomes reddish brown, periderm lighter colored with yellowish hue; periderm lines in two adjacent rhytidome scales parallel in most parts, about one-half to 1 inch in tangential dimension in cross section, and about 1½ to 2 inches high in radial sections; radial distance between two scales about one-sixteenth to one thirty-second inch in cross section. Tissues in newly formed rhytidome layers conspicuously expanded. Inner bark about one-sixteenth inch wide; light yellowish brown in dried specimens; fine tangential lines of ray cells and parenchyma visible under lens; resin canals inconspicuous.

Microscopic structure

Periderm composed of rather broad phellem, a layer of phellogen, and about 2 to 4 layers of phelloderm. Phellem cells are ordinarily thin walled like cork cells. Some thick-walled cells with narrow lumen and distinct pits were probably transformed from phelloderm. Usually about 2 to 5 layers of each kind of cell in alternate bands (fig. 17), or a total of 10 to 20 cells in a periderm layer; cells rectangular in cross section, about 50 microns in tangential dimension and 30 microns in radial dimension; number of layers and size of individual cells variable, especially of thick-walled cells.

Cell walls of last-formed phelloderm slightly thicker than those of ordinary corky phellem cells; simple pits distinct in walls; outer part of phloem parenchyma cells often merged into phelloderm layers. Both phellem and phelloderm cells often contain "resinous" substance.

Sieve cells alined in rather regular radial rows, often 4 to 6 cells, sometimes up to 10 cells, in a continuous radial row, interspersed by a layer of parenchyma cells as shown in cross section; rectangular in cross section, about 30 to 50 microns and 20 to 30 microns in tangential and radial dimensions, respectively; length variable in different specimens, ranging from 2.5 to 6.2 millimeters, mostly about 3.6 to 5.0 millimeters; ends chisellike and sometimes blunted.

Sieve areas unevenly spaced, not crowded at most places but often 2 or 3 areas close together, mostly alined in single rows on radial walls of sieve cells; slightly inclined to vertical axis of cell walls; oval to elliptic, about 10 to 15 microns in diameter. Pores and pore-group formation in sieve areas about same as in soft pines; both size of sieve areas and number of pores in a sieve area variable according to size and position of sieve cells.

Parenchyma strands consist of single cells or 2 to 3 cells in short radial rows alined more or less tangentially in continuous lines in cross section; strands about same length as adjacent sieve cells. Cells about same in cross-sectional area as sieve cells but slightly broader radially (conspicuously broader in outer part of inner bark), about 150 to 300 microns high; often contain large prismlike crystals, 50 to 70 microns long in lateral faces, with pointed front faces; starch grains and "resinous" substance abundant. Parenchyma cells at outer bark

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FIGURE 17.—*Pinus echinata*. Cross section of part of inner and outer bark with last-formed periderm between them. Periderm composed of phelloderm, phellogen, and phellem; the band of thin-walled typical phellem cells often occurs in alternation with the band of thick-walled cells which were probably transformed from phelloderm. Size and shape of cells in secondary phloem are in sharp contrast to those of cells in periderm.

conspicuously expanded, occupy most of a layer of rhytidome; cell walls "lignified"; simple pits distinct in walls and slightly enlarged compared to those in region close to cambium.

Rays of two sizes, uniseriate and fusiform. Uniseriate rays comparatively low, mostly about 8 or less cells or about 250 microns, sometimes up to 15 cells or 350 microns high; individual cells about 80 to 100 microns in radial dimension and about 20 to 30 microns high, expanded at outer part of inner bark, much enlarged at outer rhytidome layers; conspicuous albuminous cells usually appearing at every ray section close to cambial region, about twice as high as ordinary ray cells and about 20 to 30 microns in radial dimension (fig. 18); ordinary ray

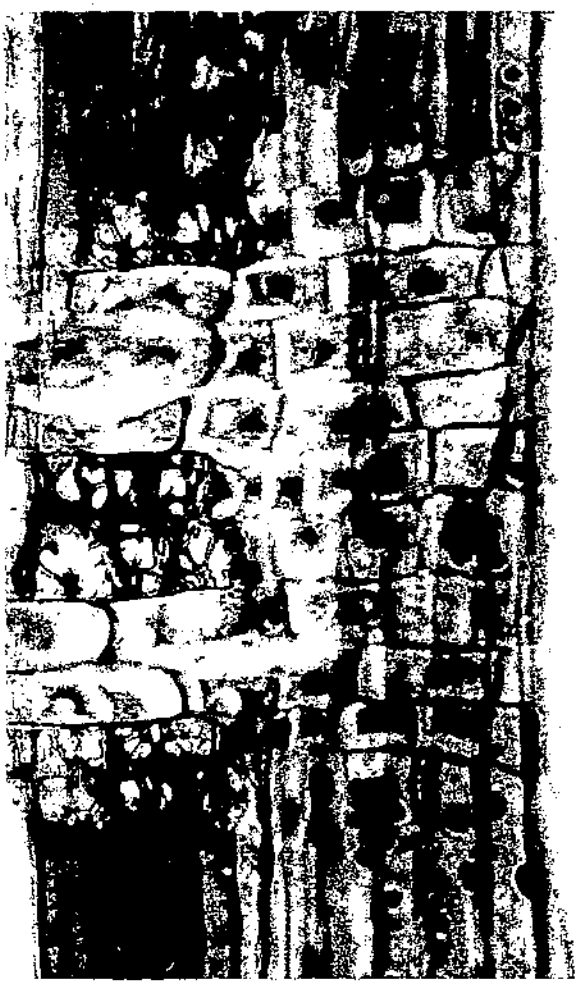

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FIGURE 18.—*Pinus echinata*. Radial section passing through cambial region; left side shows tracheids and xylem ray with newly differentiated ray tracheids immediately away from cambium; right side shows sieve cells and phloem ray cells. Albuminous cells or erect ray cells differentiated in position corresponding to ray tracheids.

cells contain rather abundant starch grains in inner bark region starting about 5 to 10 cells away from cambium. Fusiform rays usually about 70 microns wide and 500 microns high on tangential section, enlarged in outer part of inner bark; containing horizontal resin canals with well-defined border of usually 3 to 4 epithelial cells in the inside canal as shown in figure 19.

No sclerenchyma cells in secondary phloem.

The bark structure of *Pinus echinata* can be considered as typical of the hard pine group. This group differs in characteristics from

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FIGURE 19.—*Pinus banksiana*. Tangential section of secondary phloem showing abundant "resinous" substance in parenchyma cells and fusiform ray with horizontal resin duct. Notice pattern of epithelial cells.

the soft pine group by conspicuously expanded tissues in the rhytidome layers, which contrast strongly with those in the inner bark, and by periderm layers that are much longer tangentially than radially, with two adjacent periderm layers mostly parallel to each other. The gen-

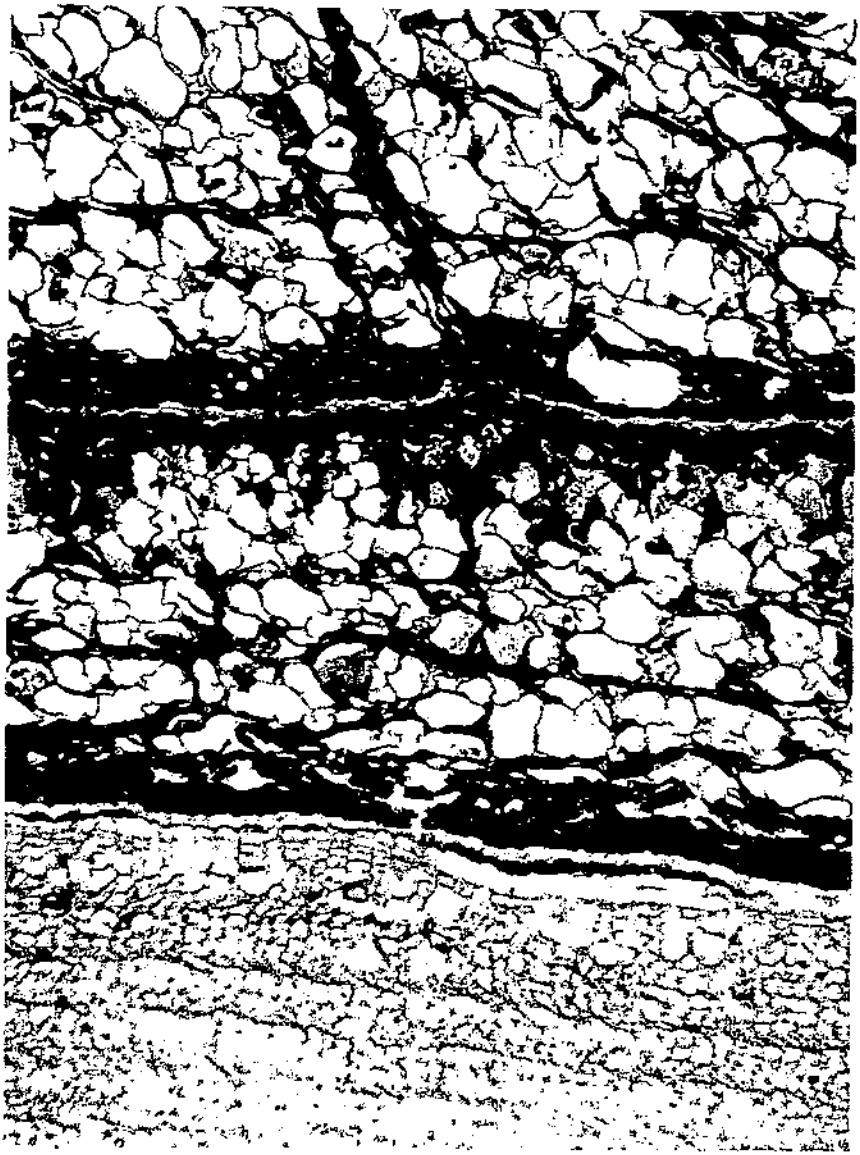

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FIGURE 20. *Pinus echinata*. Cross section with inner bark at lower part and two layers of rhytidome at upper part; illustrates conspicuous transformation from inner to outer bark; outlines of periderm are parallel to each other at most parts. These features are characteristic of hard pine barks (compare fig. 12*f*).

eral features of the bark structure are shown in figures 20, 21, and 22. The styloid parenchyma crystals (elongated lateral faces and pointed front faces) are also unique in this group of pines (fig. 23). Ohara (*41*) has used their presence as a basis for separating the Japanese hard and soft pines.

Bark structures of the various species in the hard pine subgenus *Diploxylon* mostly overlap in characteristics, as in the case of soft pines. Several species, however, do have some particular features that are rather useful for separating them. Barks of *P. resinosa* and

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FIGURE 21. *Pinus ponderosa*. Radial section of rhytidome, showing alternate layers of periderm and secondary phloem; expanded parenchyma cells make up most of a layer of rhytidome.

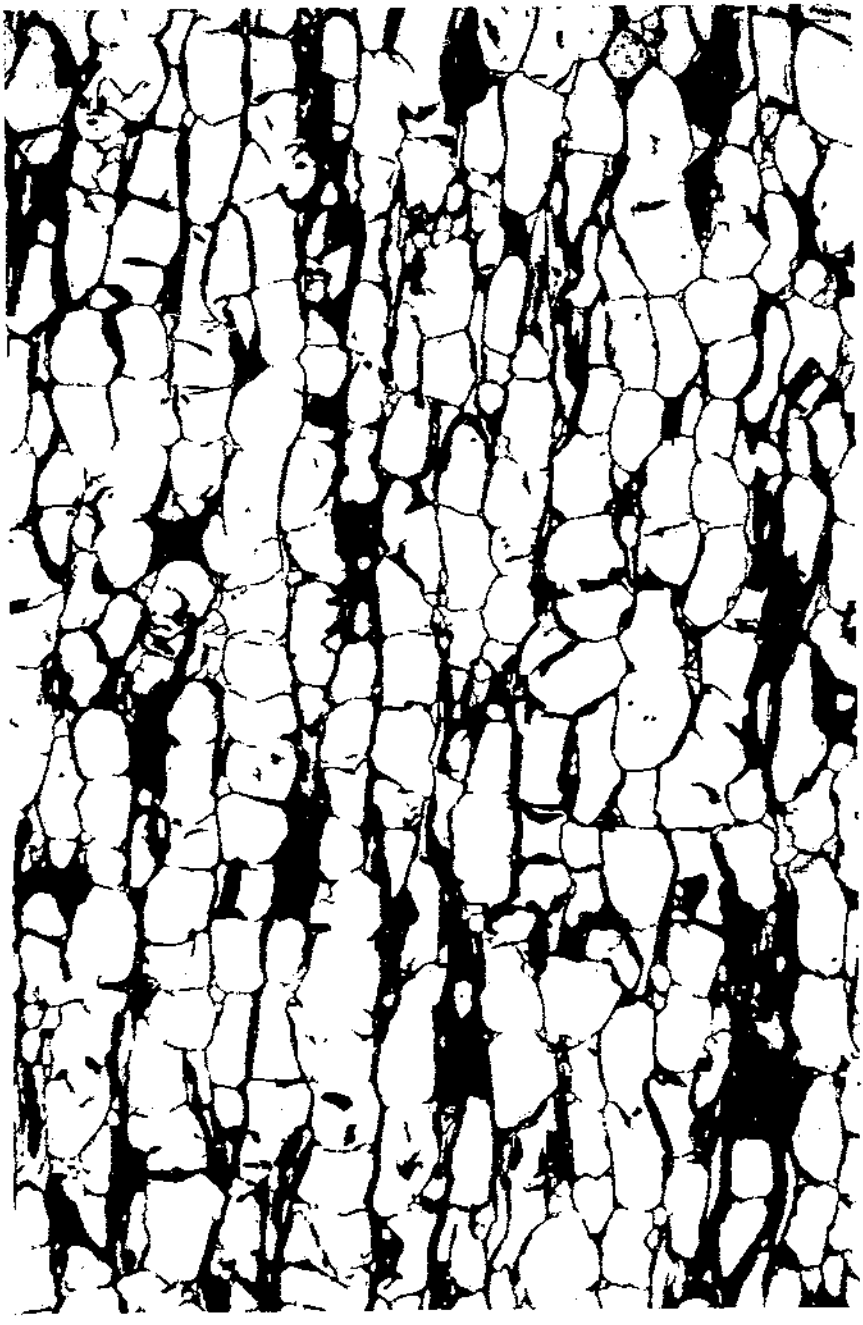

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FIGURE 22.—*Pinus serotina*. Tangential section of outer bark indicating that expanded parenchyma and ray cells are predominant tissues in this region; also showing traces of obliterated sieve cells and unexpanded ray cells scattered among large parenchymatous cells.

M 92402 F

FIGURE 23.—*Pinus radiata*. Tangential section showing styloid crystals in phloem parenchyma; this kind of crystal is characteristic of hard pine barks and hemlock bark.

P. sylvestris are characterized by their thin, papery scales with distinct reddish hue. *P. ponderosa* and *P. jeffreyi* both have yellowish periderm that is in sharp contrast to their reddish-brown secondary phloem. The scales of *P. contorta* are much smaller and shorter tangentially than any other hard pine observed in the present investigation, but the ratio of their tangential to radial dimensions is still large and follows the hard pine pattern.

Barks of the subsection Insignes mostly have a deeper color than the barks of the other hard pines and a strong reddish hue; their periderm has a pinkish hue. The length of sieve cells may be useful for separating small groups; for example, those in the bark of *P. palustris* and *P. echinata* are much longer than those in other hard pines.

To summarize the characteristics of bark structure in *Pinus* as a whole, the various species have the following diagnostic features in common: (1) Scalelike rhytidomes, with conspicuous periderm composed of both thin- and thick-walled cells; (2) sclerenchyma cells absent in the secondary phloem; (3) sieve cells often in radial rows of about 10 cells, and sieve areas often inclined to the vertical axis of the sieve cells; (4) albuminous cells conspicuous and present at almost every ray section close to the cambial region; (5) fusiform rays common, especially abundant and conspicuous in the soft pines, and containing horizontal resin canals with well-defined borders; (6) often 1 to 3 parenchyma cells in a short radial multiple, forming rather irregular tangential lines on cross section of inner bark, and containing crystals, small or large, but all with rectangular lateral faces.

De Vall (*54*) reports that the appearance of "cork cambium" is reliable for the indentification of native Florida pines, but this result could not be checked on an anatomical basis in the present investigation.

Pseudotsuga menziesii (Mirb.) Franco

General features

Bark mostly thick to very thick but highly variable in different localities, usually about 1 to 2 inches thick in thin-barked trees, about 5 to 6 inches, sometimes up to 1 to 2 feet thick in old or thick-barked trees. Outer surface of young trees rather smooth, grayish, slightly broken into scales and appearing brownish underneath; bark from old trees rather rough and broken into deep furrows with small scales that are mostly connected, grayish brown on outer surface.

Periderm in old or thick-barked trees well developed, rather thin in thin-barked trees or young stems; variable in cross section from fine lines to very broad bands, sometimes up to about one-half inch wide, composed of 15 or more layers of periderm cells and usually mingled with some comparatively narrow bands or lines; light creamy yellow in color, in contrast to deep, rather brilliant-brown secondary phloem tissues on cross and longitudinal sections; fibrous, with diffuse fibers visible to naked eye. Inner bark about one-eighth to one-fourth inch thick, lighter in color than outer bark; only diffuse fibers and parenchyma cells distinct under lens.

MICROSCOPIC STRUCTURE

Periderm usually composed of 2 to 3 layers of phelloderm, a layer of phellogen, and broad phellem variable in number of cells and formation of layers. Phellem cells mainly thin walled and uniform in thickness but occasionally with layers of, or sporadically distributed, thick-walled cells which were probably transformed from phelloderm; rectangular to nearly square in cross section, about 30 to 50 microns in tangential dimension and about 50 to 90 microns in radial dimension; often at least 30 cells in a layer. The last-formed phelloderm cells comparatively thick walled and mingled with parenchyma cells of secondary phloem; simple pits distinct in those cells in outer bark rhytidomes. Phelloderm and phellem often contain "resinous" substances; small crystals observed in phellem cells.

Sieve cells rather regularly arranged in cambial region, 2 to 6 cells, mostly about 3 cells in a radial row, interspersed by parenchyma cells; sieve cells in outer part of inner bark mostly obliterated and indistinct: active sieve cells about 20 to 30 microns and about 50 microns in radial and tangential dimensions, respectively, in cross section; length variable in different specimens, from 1.5 to 4.5 millimeters, mostly from 2.5 to 3.7 millimeters. Sieve areas usually partially crowded, not evenly spaced; alined mostly in single rows on radial surface of sieve cells, occasionally with pairs or a few cells close together vertically, and at a small angle to vertical axis of sieve cells; mostly oval to elliptic, sometimes nearly orbicular, but outline rather irregular; about 15 microns in diameter but variable in tangential dimension according to size of sieve cells. Connecting strands and definitive callus distinct in those sieve cells close to cambium of fresh bark. Pores distinct in those sieve cells in outer part of inner bark; usually about 15 small pore groups in a sieve area.

Fibers differentiated rather early and often only 15 cells away from cambium; solitary or sometimes 2 to 3 in small groups but without definite pattern, diffuse and rather crowded at certain locations; more or less circular and slightly irregular in cross section; about 50 microns in diameter and 600 microns to 1.5 millimeters long, mostly about 1 millimeter, tending to be longer in inner bark than in old outer bark. Cell walls thick with distinct lamellate layers and a very narrow lumen; simple pits rather distinct.

Parenchyma cells appear singly or 2 to 3 in short radial multiples in more or less discontinuous tangential lines, rather continuous lines in region close to cambium; more or less rectangular but slightly expanded radially, about same size as sieve cells in cross section, tending to be circular or oval in outer part of inner bark, and up to 50 microns in diameter and more expanded in outer bark. Some parenchyma strands about same length longitudinally as sieve cells. Individual cells about 100 to 200 microns high with flat to more or less rounded end walls; containing abundant "tanniferous" substance and crystals with rectangular lateral faces.

Rays of two sizes; uniseriate rays or occasionally partially biseriate rays and fusiform rays with horizontal resin canals. Uniseriate rays mostly about 8 cells or 200 to 250 microns high, sometimes up to 15 cells or 350 microns high in tangential section; about 100 microns in radial dimension and 20 microns high in radial section; marginal erect cells

or albuminous cells rather conspicuous on those rays in region from cambium to about 20 cells away from cambium, about 20 microns wide and 20 to 40 microns high, usually several occurring close together, with very large nucleus and no starch reaction as tested by iodine-potassium iodide; ordinary ray cells contain "resinous" substance and starch grains. Fusiform rays rather abundant, containing horizontal resin canals with distinct border formed by thin-walled epithelial cells; number of border cells variable according to size of canals. Both types of rays radially dilated at outer part of inner bark.

Transformation of secondary phloem tissues starting early at outer part of inner bark, with functionless sieve cells mostly obliterated and parenchyma and fibers becoming predominant tissues and forming main pattern of most of bark.

The bark structure of *Pseudotsuga menziesii* (figs 24–27) is quite distinguishable from that of the other species studied. The most sig-

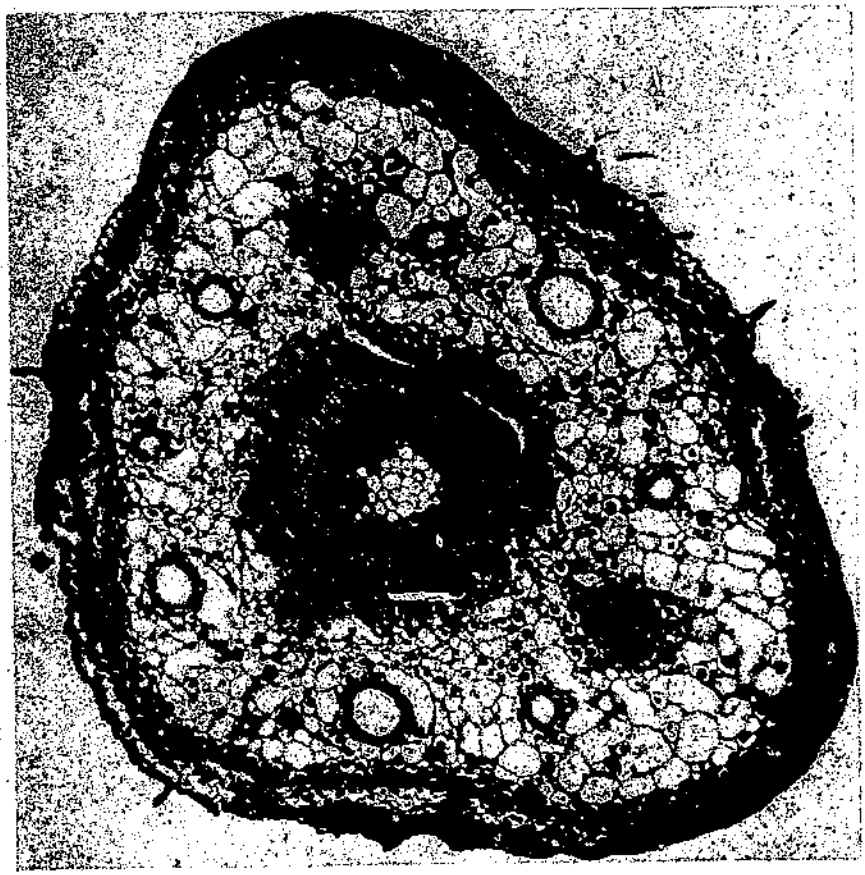

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FIGURE 24.—*Pseudotsuga menziesii.* Cross section of young branch. From center outward, pith, primary xylem, secondary xylem, secondary phloem, trace of primary phloem, cortical region with leaf trace and resin canals, periderm, and epidermis with hairs.

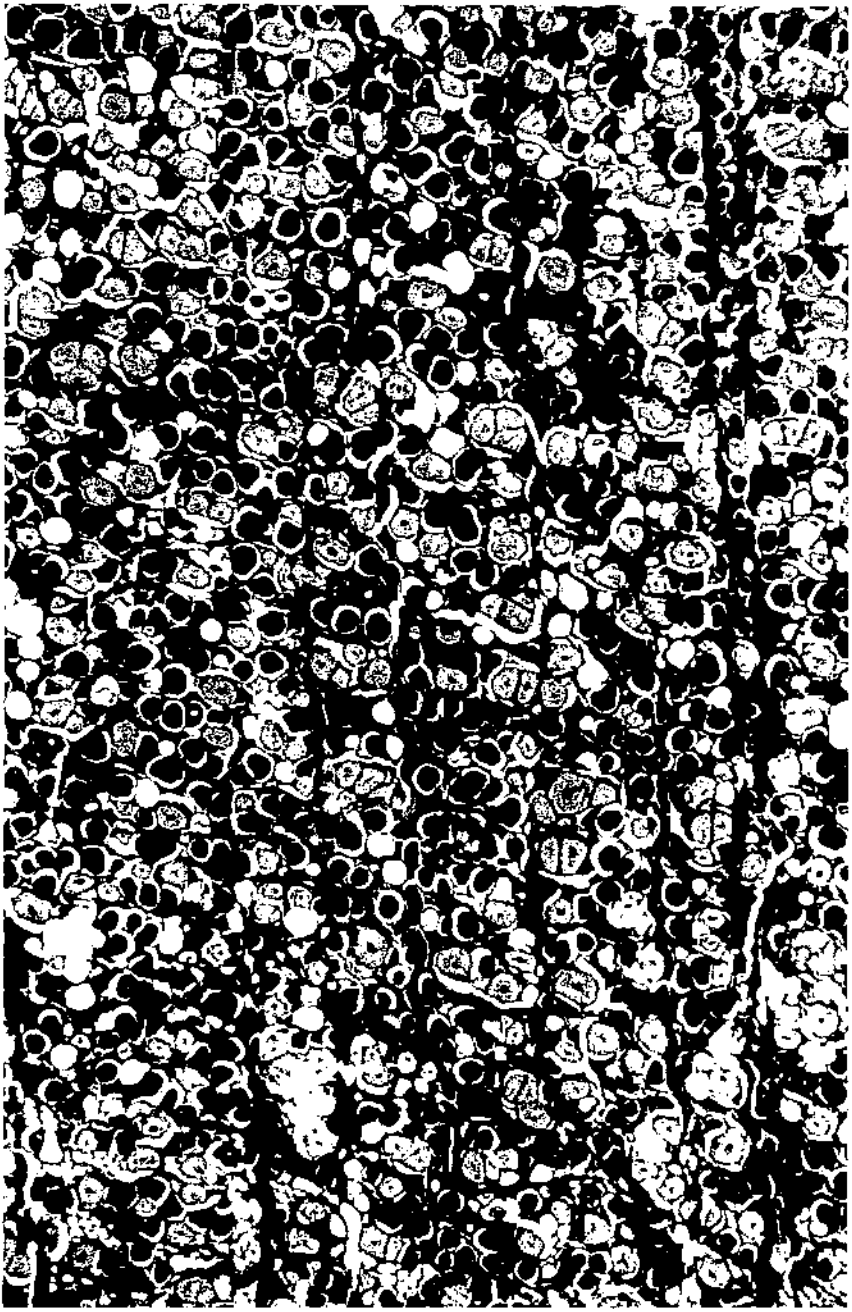

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FIGURE 25.—*Pseudotsuga menziesii.* Cross section of inner bark showing diffused fibers, solitary or often in small groups. Cells with dark contents are parenchyma cells. Sieve cells occur in continuous radial rows of about five cells, mostly obliterated.

nificant characteristics are the well-developed layers of phellem and the diffused short fibers starting close to the cambial region and distributed throughout the bark. The relative volume of periderm or cork in Douglas-fir bark is higher than that of other coniferous barks studied, but the percentage of cork varies considerably in trees grown in different localities. Grondal (*16*) classified Douglas-fir bark into four grades according to the formation of the periderm.

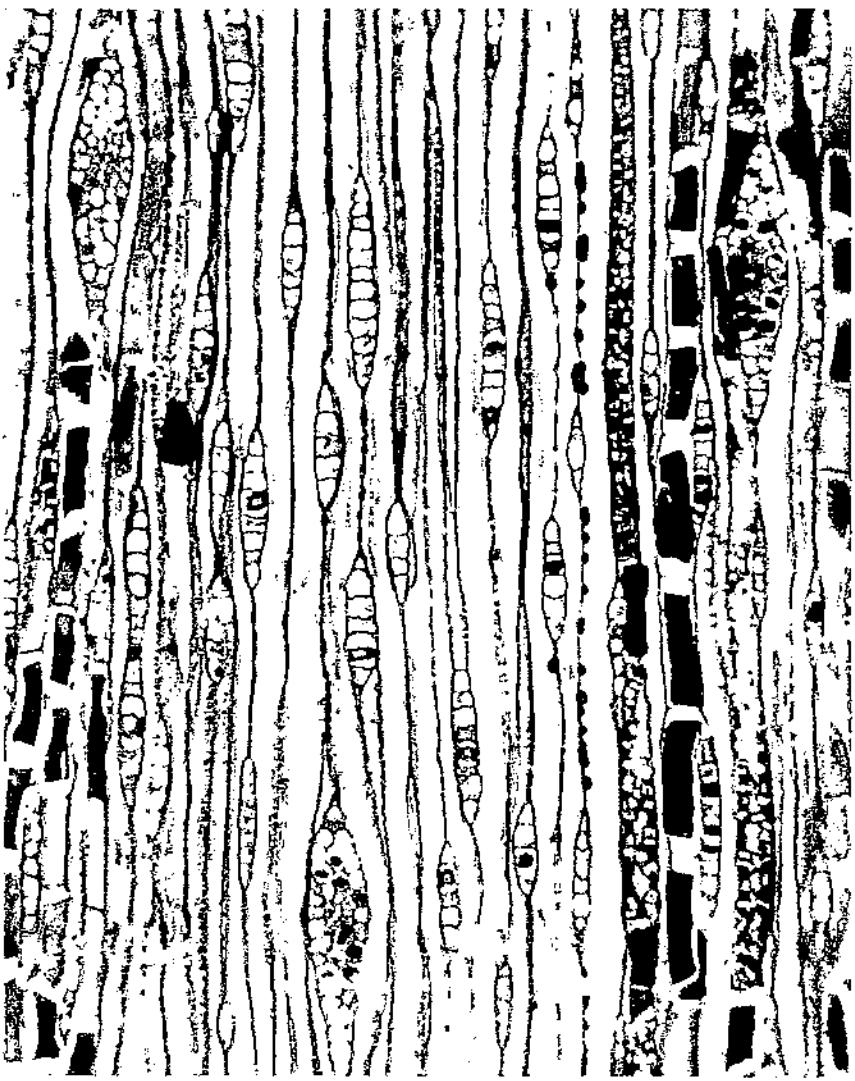

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FIGURE 26. *Pseudotsuga menziesii.* Tangential section of inner bark close to cambial region. On right side, two rows of sieve cells show distinct definitive callus attached. Differentiation of horizontal resin canals in fusiform ray has not yet been completed. Parenchyma cells contain "resinous" substance and crystals.

ZM 92400 F

FIGURE 27.—*Pseudotsuga menziesii.* Macerated inner bark showing short fibers, sieve cells, and parenchyma cells.

Tsuga heterophylla (Raf.) Sarg.

GENERAL FEATURES

Bark about 1 inch thick in available specimens, deeply fissured, with rather large and firm scales; reddish brown with purplish red hue at those regions with exposed periderm; scales formed by alternate layers of periderm about one-half to three-fourths inch in tangential dimension, with one-sixteenth to one-eighth inch between scales in cross sec-

tion, and gradually pointed, overlapping ends. Inner bark about one-fourth inch thick with yellowish hue in fresh bark, turning pink after exposure; strongly reddish hue in outer bark. Diffused sclereid groups starting very close to cambium and occurring throughout inner bark, visible to naked eye; parenchyma and rays indistinct.

MICROSCOPIC STRUCTURE

Periderm composed of 2 to 3 layers of phelloderm, a layer of phellogen, and usually over 10 layers of phellem, but rather variable in different rhytidomes; about 15 to 20 or more layers of phellem in last-formed periderm layer. Phellem cells rectangular in cross section, about 30 to 50 microns in tangential dimension and 15 to 40 microns, mostly about 20 microns in radial dimension, usually about 20 to 50 microns high in radial section; mainly thin walled and uniform in thickness, walls comparatively thicker in regions of overlap; abundant "tanniferous" substance in newly differentiated cells. Phelloderm cells slightly larger than phellem cells and comparatively thicker walled; simple pits distinct in cell walls; cells usually merged into parenchyma cells of secondary phloem but sometimes there is distinct border between these two types of cells.

Sieve cells differentiated rather regularly, about 10 cells in a radial row, and interspersed by more or less tangentially alined parenchyma cells; sieve cells in region up to about 20 cells away from cambium usually retained in good shape but most old cells become obliterated because of the presence of sclereid groups; rectangular in cross section, about 10 to 15 microns and 15 to 30 microns in radial and tangential dimensions, respectively, length variable from 1.5 to 4 millimeters, mostly about 2.5 millimeters.

Sieve areas usually alined in a vertical row or radial surface of sieve cell walls, not evenly spaced, sometimes rather crowded locally, slightly oblique to vertical axis of cell body; elliptic to nearly orbicular; size variable according to size of sieve cells, mostly about 8 microns in diameter. Connecting strands and definitive callus distinct in those sieve cells close to cambial region. Pores in sieve areas distinct in inactive cells: small pores form groups, usually about 5 groups to a sieve area with 2 to 5 pores in each group. Network of cell walls retained within a sieve area distinct; borderline of sieve area distinct.

Sclereids forming diffused small groups distributed throughout most of inner bark region about 20 cells away from cambium; mature sclereid groups usually composed of 10 or more sclereids of varying size, usually about 500 microns in diameter, as shown in cross section: groups rather high in longitudinal section, mostly about 1 millimeter but up to 2.5 millimeters high. Individual cells in sclereid groups branched and twisted; short, usually about 400 microns long; thick walled with distinct lamellate and narrow lumen; distinct simple pits in cell walls; often containing "resinous" substances.

Parenchyma strands alined more or less in continuous tangential lines usually of single cells or two cells in a radial row. Newly formed parenchyma cells about same size and shape as sieve cells in cross section, becoming enlarged and radially expanded nearer outer bark; rather short vertically, about 20 to 100 microns high, mostly about 50 microns high in those strands close to cambium; small simple pits distinct and enlarged with expansion of cell walls. Cells contain

abundant "tanniferous" granules and "resinous" substance and styloid crystals with elongated lateral faces and pointed front faces, about 50 microns high.

Phloem rays mainly uniseriate, about 10 to 15 cells or 300 microns high, but sometimes up to 25 cells or 600 microns high in tangential section; individual cells about 30 to 50 microns in radial dimension and about 10 microns high in those rays close to cambial region, end walls usually rounded. Marginal ray cells or albuminous cells present at almost every ray close to cambial region: about 10 microns wide and about 2 to 3 times height of ordinary ray cells; in layer of single cells or, occasionally, of two cells in vertical row on ray margin.

Expansion of ray cells distinct in outer part of inner bark; cells enlarged, often partially paired. No fusiform rays observed. No pocket-like resin passages present in inner bark; indistinct in outer bark because of abundant sclereid groups and "resinous" and "tanniferous" content.

Transformation of secondary phloem tissues starting early from inner bark; phenomena about same as those in *Abies* and *Picea*.

The bark structure of *Tsuga heterophylla* is characterized by thick, roughened outer bark; rather broad periderm composed mainly of thin-walled phellem cells; abundant diffused sclereid groups that start early at the inner bark (fig. 28); absence of fusiform rays; and parenchyma containing elongated crystals and "tanniferous" granules. Its general appearance and some of its microscopic structures are rather similar to those of *Abies grandis*. *Tsuga canadensis* has a bark structure generally like that of *T. heterophylla*. No special distinction between these two species was established in the present study.

TAXODIOIDEAE

Sequoia sempervirens (D. Don) Endl.

Isenberg has described the anatomy of redwood bark (*27*). Although it is not necessary to repeat a full description of the bark structure of this species here, some supplementary notes should be added. The following points are based upon observations made on specimens collected from California and Hawaii.

The arrangement of the secondary phloem tissues in redwood should be mentioned first. Generally, phloem fibers, sieve cells, and parenchyma cells were differentiated in a regular order in the specimens observed and occurred in continuous alternating sequence throughout the entire bark. Local irregularities did occasionally occur, however, and the significant variation often appeared in the diameter of the phloem fibers, especially in the Hawaiian specimens.

Fibers close to the cambial region were mostly uniform in size and shape, in cross sections of the California specimens, and usually radially flattened; outward from the inner bark the fibers tended to be square. Mature fibers appeared in every unit of the alternate layers of the secondary phloem tissues. Fibers in the Hawaiian barks were mostly square in cross section, and about every 5 to 7 units a row of extraordinarily radially elongated fibers occurred. Their radial dimension was often up to 90 microns in contrast with about 20 to 30 microns for regular-sized fibers.

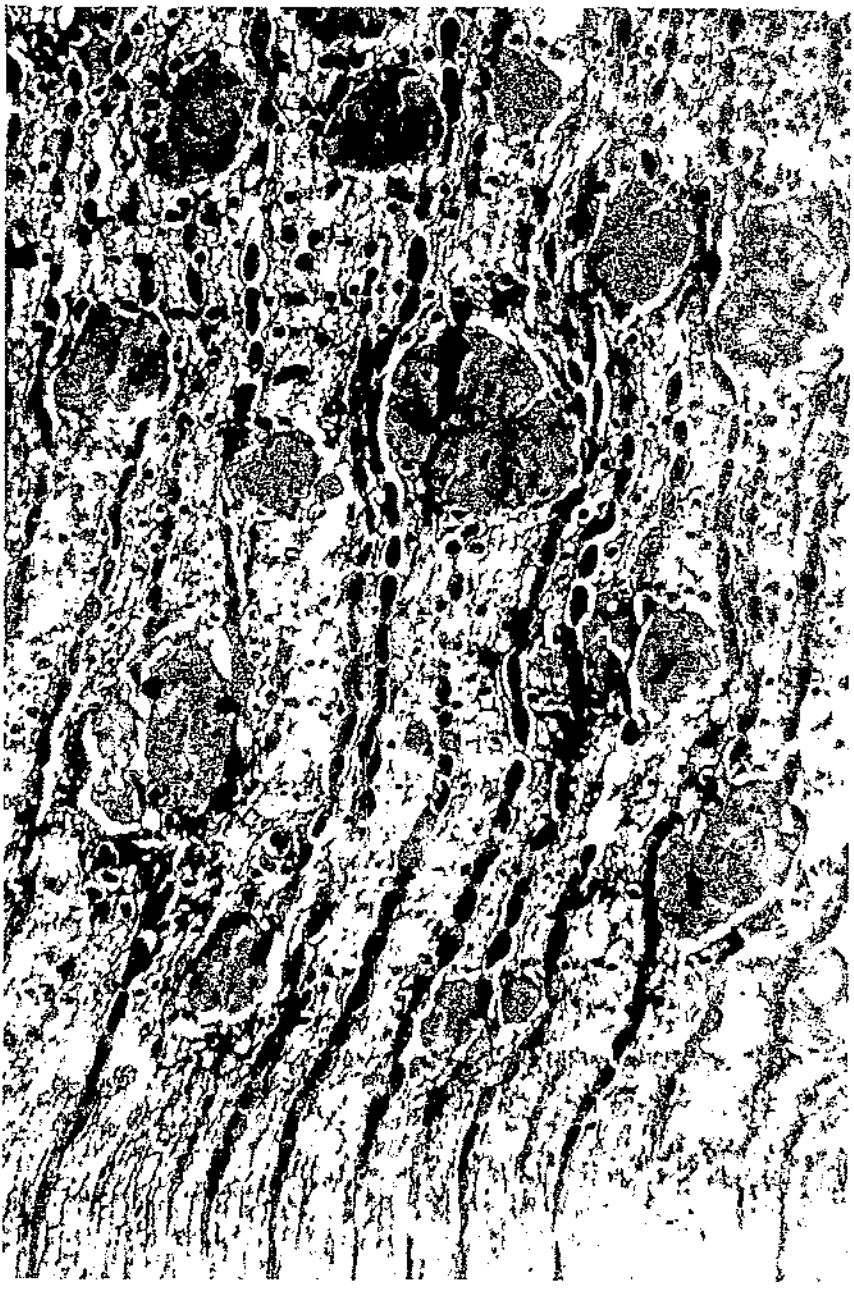

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FIGURE 25. *Tsuga heterophylla.* Cross section of inner bark indicating pattern of arrangement and distribution of secondary phloem tissues similar to that of *Abies grandis* illustrated in figure 4 but with less crowded sclereid groups and more sieve cells in a continuous radial row.

Although the dimensional variation of the redwood phloem fibers might be caused by environmental factors, some constant tendencies of their development can be generalized. As a rule, the fibers close to the cambium or in the inner part of the inner bark are mostly radially flattened and rather regular in shape and size. Square fibers and especially radially elongated ones occur mostly in the outer part of the inner bark and in the rhytidomes of the outer bark at rather constant intervals. The variation and general tendencies of fiber development are important from the following standpoints: The morphological significance of the transformation of bark structure, and the relative volume of fibers in a given bark, which is one of the interesting points involved in practical applications of bark.

Although Isenberg proposed and discussed the term "reinforced area," he did not make a definite conclusion about its real nature. "Reinforced area" should be defined as a zone of transformed tissue composed of expanded phloem parenchyma, phloem ray cells, and some deformed sieve cells between two adjacent fiber lines, or it may be extended to a number of fiber lines. It may appear in a whole rhytidome layer or only at those regions close to the periderm. Depending upon the degree of transformation, parenchyma cells, which predominate in such regions, may expand only slightly or expand extensively and occupy the main area. Although the walls of the parenchyma cells mostly become thick, it is not uncommon for them to remain thin or only slightly thickened. The parenchyma cell cavities are much enlarged over their original size, and the cells are often less compact.

This structure does not seem to be formed exactly in the mechanical sense of "reinforced." From the standpoint of expressing the real nature of the physical function of such areas or indicating the anatomical origin of the cell types, the writer agrees with Isenberg's original intention that the term "reinforced area" should be used tentatively. It would be better to say "transformed area" in a general sense and refer to the original cell types accordingly. Such areas are a common phenomenon in all coniferous barks but occur in different patterns and are not confined to the outer bark. Their differences are due to the original arrangement of the secondary phloem tissues and the degree of transformation.

A few additional characteristic features of redwood bark will be mentioned here. The periderm layers of redwood bark usually overlap each other for a short distance in the tangential direction. This pattern was more pronounced in the California than in the Hawaii specimens. In the regularly alined layers of the secondary phloem tissues, the individual parenchyma cells always are more or less oval in cross section and the middle portion of the cell walls tends to be convex. If a little iodine-potassium iodide is applied to the sections, especially those from fresh material, the appearance of starch grains in the parenchyma cells will be very helpful for distinguishing them from sieve cells and the underdeveloped fibers. Starch grains are wanting or inconspicuous, however, in newly differentiated parenchyma cells, which are in a region usually about 15 cells away from the cambium.

Phloem rays become dilated at the outer part of inner bark, as was shown very conspicuously in the Hawaiian specimens. Erect ray cells or albuminous cells are inconspicuous, often wanting in the whole

section, but occasionally a few erect cells are observed close to the cambial region, sometimes 4 or 5 close together. The erect cells are about half as wide in radial dimension as the ordinary ray cells and slightly higher.

Sieve areas are not crowded and are often alined in a vertical row on the radial surface of sieve cells. They are oval to nearly orbicular and about 8 to 10 microns in diameter. Connecting strands and definitive callus are distinct in those sieve cells close to the cambial region. Pores become distinct in the inactive sieve areas. The cell walls in the network retained among the pores are usually coarser in the central portion of a sieve area, somewhat similar to those in sieve areas in *Taxodium*.

Taxodium distichum (L.) Rich.

General features

Bark thin, that of the available specimens measuring up to three-fourths inch thick (reported as up to 1 or 2 inches thick in old trees). Outer surface exfoliating into long fibrous strips; broken into horizontal checks in comparatively young trees, giving scalelike appearance; yellowish brown to deep brown tinged with reddish hue in those regions with exposed periderm. Inner bark narrow, about one-sixteenth to one-eighth inch thick; light yellowish brown after exposure to air; fine tangential fiber lines and rays visible under lens.

Microscopic structure

Periderm thin, usually composed of 2 to 5 layers of phellem cells, a layer of phellogen, and about 2 layers of phelloderm. Phellem cells thin walled and uniform in thickness; rectangular in cross section, about 15 microns in radial dimension and 30 microns in tangential dimension; vertically about 50 to 80 microns high on radial section. Phelloderm cells usually wider and with thicker walls than phellem cells; sometimes mingled with parenchyma cells of secondary phloem; simple pits distinct on those cells becoming "lignified." Both phellem and phelloderm cells often contain "resinous" substance. Rhytidome layers rather narrow because only about 18 cells of secondary phloem tissue included.

Sieve cells differentiated regularly in alternate layers with phloem parenchyma and fibers (fig. 29); about 15 to 20 microns and 50 microns in radial and tangential dimensions, respectively, in cross section; mostly about 4 millimeters long but variable from 2 to 5.5 millimeters.

Sieve areas not crowded and rather evenly spaced in a vertical row on radial surface of sieve cells; oval to nearly orbicular, about 15 microns in diameter. Connecting strands and definitive callus distinct in those sieve areas close to cambium. Pores in functionless sieve areas distinct, not crowded; network of cellulose walls retained among pores usually very distinct, with walls often rather broad in central part of sieve area.

Fibers differentiated rather regularly, usually flattened radially and about same shape and size throughout most of inner bark;

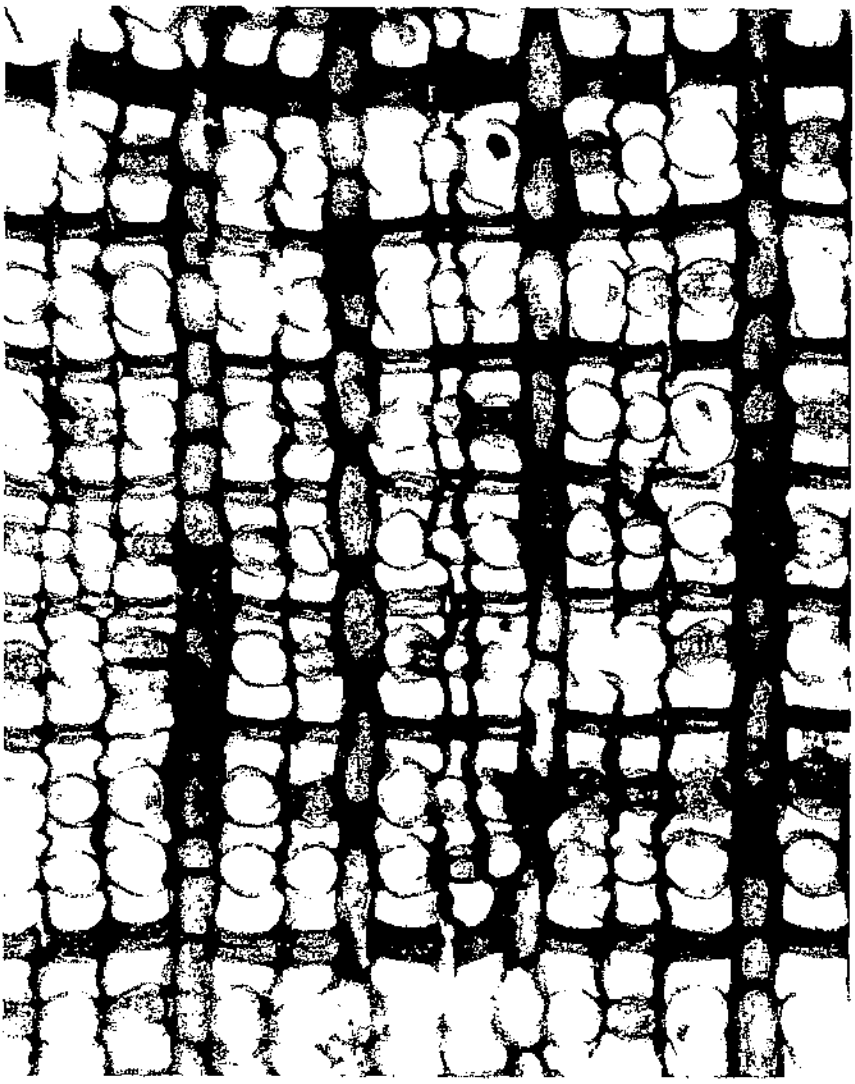

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FIGURE 29. *Taxodium distichum*. Cross section of inner bark showing regularly alternating layers of fibers, sieve cells, and parenchyma. Fibers are conspicuously flattened radially, but parenchyma cells are expanded. This regular differentiation of tissues is characteristic of barks of Taxodiaceae and some Cupressaceae.

occasionally some fibers not much lignified or some tending to be square in cross section; about same length as adjacent sieve cells but fibers at outer bark comparatively shorter than those in inner bark; simple pits distinct in cell walls. Extremely large pits in many fibers in outer bark; variable in size, up to 10 microns in diameter; oval to orbicular; probably abnormal growth or defect rather than any defi-

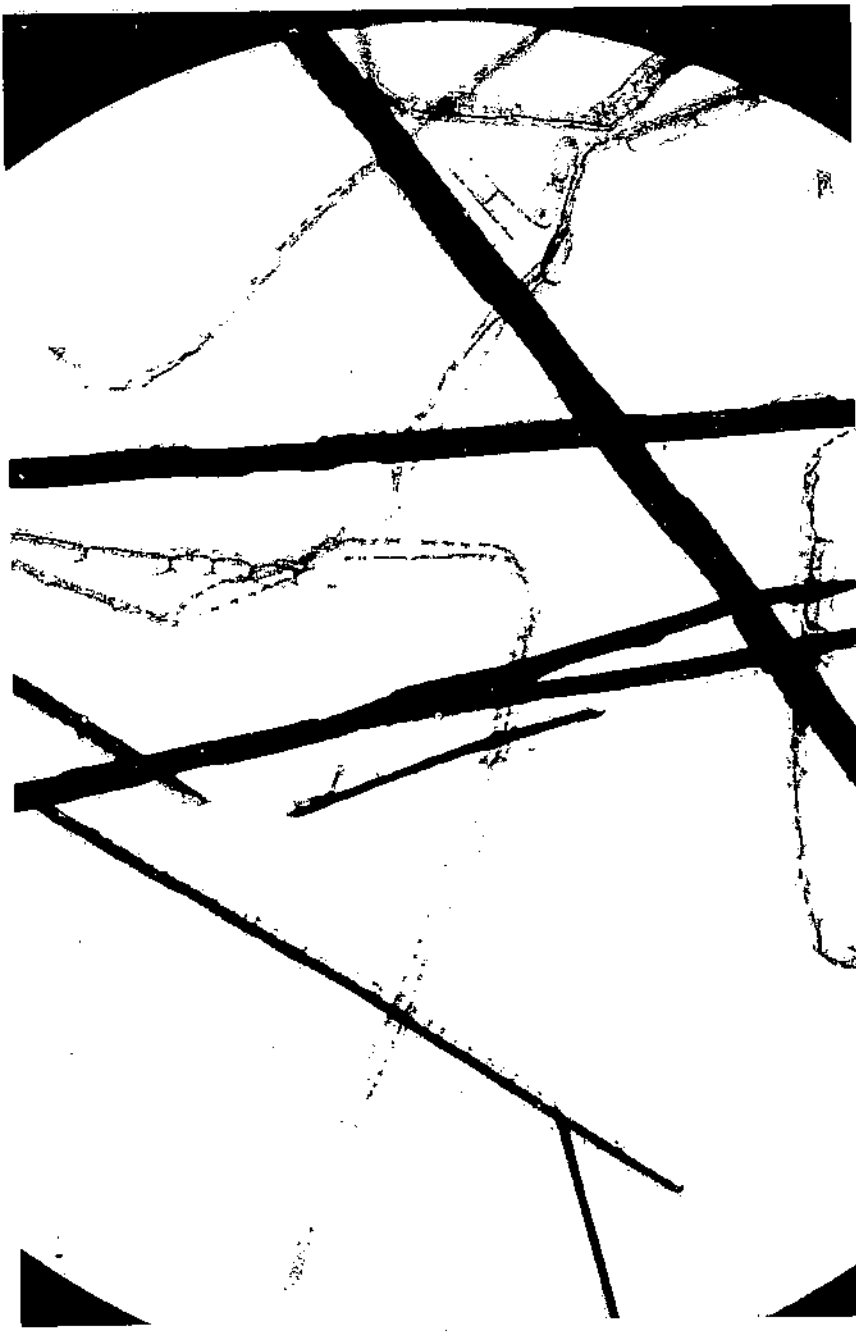

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FIGURE 30.—*Taxodium distichum*. Macerated inner bark showing typical long phloem fibers, sieve cells, and parenchyma strands.

nite morphological form of pitting, except possibly characteristic of fibers of this kind.

Parenchyma strands about same length as sieve cells and fibers. Individual cells mostly 50 to 100 microns high, occasionally up to 180 microns; about 30 to 50 microns in tangential dimension and usually about 35 microns in diameter radially; contain starch and sometimes abundant "resinous" substance.

Phloem rays mainly uniseriate, occasionally partially biseriate; mostly 10 to 15 cells or 200 to 300 microns, sometimes up to 30 cells or 500 microns high; not much dilated at outer part of inner bark. Individual cells rather small, about 50 to 80 microns in radial dimension and 20 microns high on radial section; marginal erect cells rarely observed in prepared specimens.

No resin canals observed.

Transition from inner bark to outer bark gradual; expanded cells conspicuous at newly formed rhytidomes; cells generally become "lignified." Because of early formation of periderm at innermost rhytidome layers, underdeveloped fibers often present in some of those layers; sieve cells mostly obliterated in outer rhytidomes.

In general appearance, the bark structure of *Taxodium distichum* is very close to that of redwood, but differences are evident in their microscopic structures. The rather constant range of variation of their fiber length and the manner of transformation from inner to outer bark are quite useful for separating these two species.

Types of cells occurring in the secondary phloem of the inner bark of *T. distichum* are illustrated in figure 30.

CUPRESSOIDEAE

Chamaecyparis thyoides (L.) B. S. P.

General features

Bark on collected specimens comparatively thin; total thickness of inner and outer bark about three-eighths inch, with one-sixteenth inch of inner bark. Outer bark exfoliating into shallow furrows and long, irregular ridges often partially connected to each other; deep brown with reddish hue on those regions with exposed periderm; tangentially alined resin canals conspicuous in cross section, chalky colored in dried specimen. Inner bark light yellowish brown, much lighter than outer bark; resin canals present; tangential lines of fibers distinct under lens, rather closely spaced. Periderm inconspicuous in cross section; deep reddish color on longitudinal surface.

Microscopic structure

Periderm thin, usually composed of about 5 layers of phellem, a layer of phellogen, and usually about 1 to 2 layers of phelloderm. Phellem cells thin walled, uniform in thickness; mainly rectangular on radial and cross sections; about same size as other phloem tissues in cross section, but narrower, about 40 to 80 microns high; suberized cells usually containing "resinous" substances. Phelloderm slightly broader than phellem; cell walls comparatively thicker, with distinct simple pits.

Sieve cells differentiated regularly and alternately with parenchyma and fibers; about 40 microns in tangential dimension and about 15 microns in radial dimension; radially comparatively narrower than adjacent tissues because of expansion of parenchyma and formation of fibers; about 2.6 to 3.8 millimeters long, mostly about 3.4 millimeters. Sieve areas in single row on radial walls of sieve cells, rather evenly spaced and not crowded; oval to orbicular, about 10 microns in diameter. About 3 to 6 pore groups in a sieve area, each group containing 2 to 5 pores; cell walls retained among pores form branched network; border of sieve area distinct. Sieve cells often contain abundant granules or crystal sands.

Mature fibers appearing rather close to cambium and alternating regularly with sieve cells and parenchyma strands; sometimes underdeveloped or immature fibers, slightly "lignified" with comparatively thin walls, present. All fibers mainly radially flattened, in cross section about 20 to 30 microns in tangential dimension and about 10

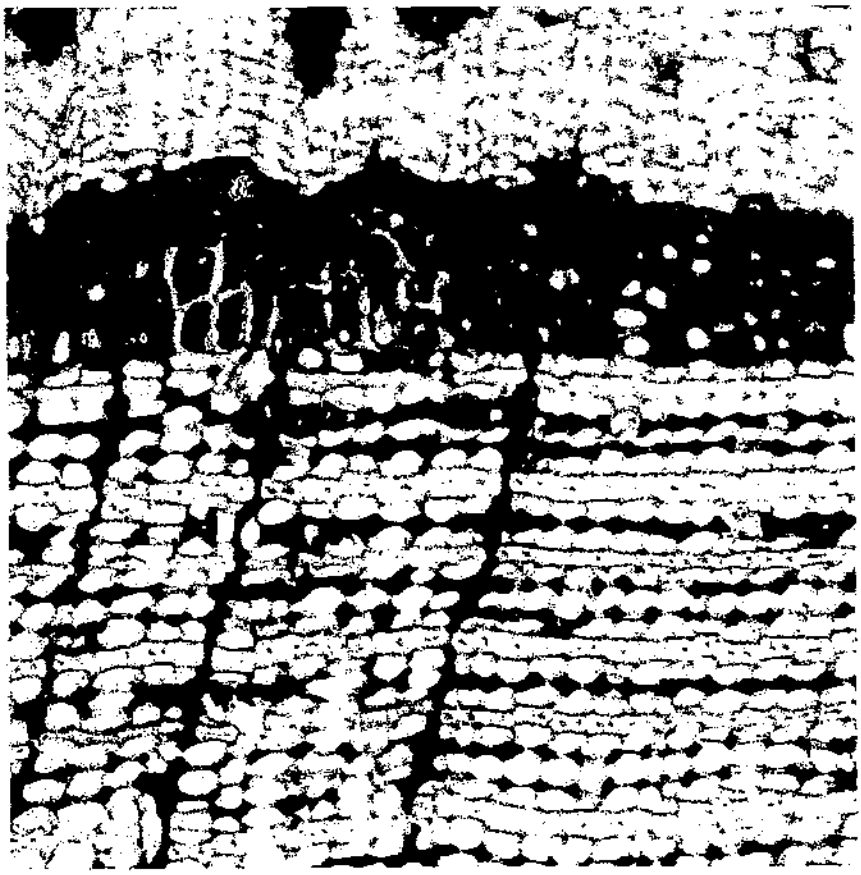

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FIGURE 31.—*Chamaecyparis lawsoniana*. Cross section of a part of inner bark and periderm, showing broad band of phellem cells and transformed cells at the boundary between the regular phloem cells and phellem.

to 20 microns in radial dimension. Mature fibers occasionally square or slightly radially elongated, about same length as adjacent sieve cells and parenchyma strands; ends pointed gradually, sometimes blunt; simple pits distinct on cell walls.

Phloem parenchyma quite different from that of other coniferous barks investigated. Strands usually about same length as adjacent

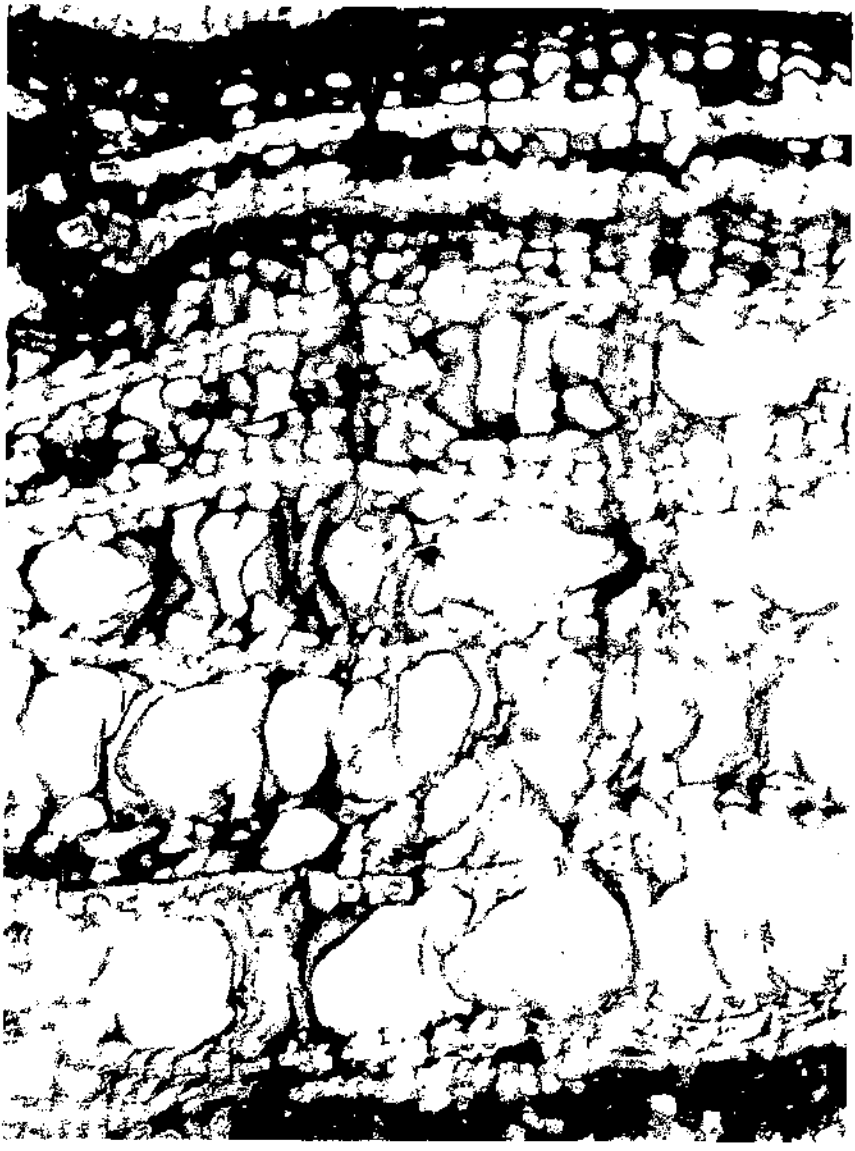

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FIGURE 32.—*Chamaecyparis lawsoniana*. Cross section of outer bark, showing transformed parenchyma cells; only fibers in this region still retain their original shape.

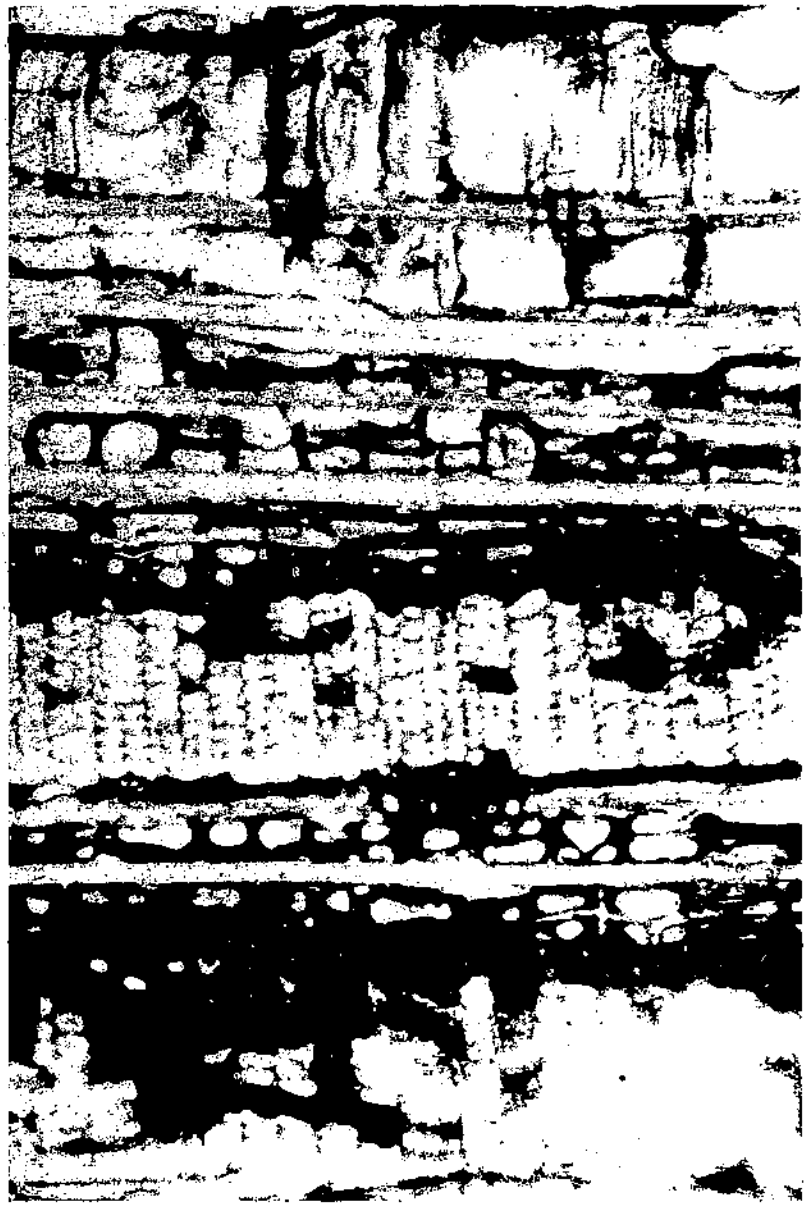

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FIGURE 33.—*Chamaecyparis lawsoniana*. Radial section of outer bark, showing expanded cells of secondary phloem and alternate layers of periderm.

ZM 92386 F

FIGURE 34. *Chamaecyparis thyoides*. Cross section of inner bark showing conspicuously expanded parenchyma cells.

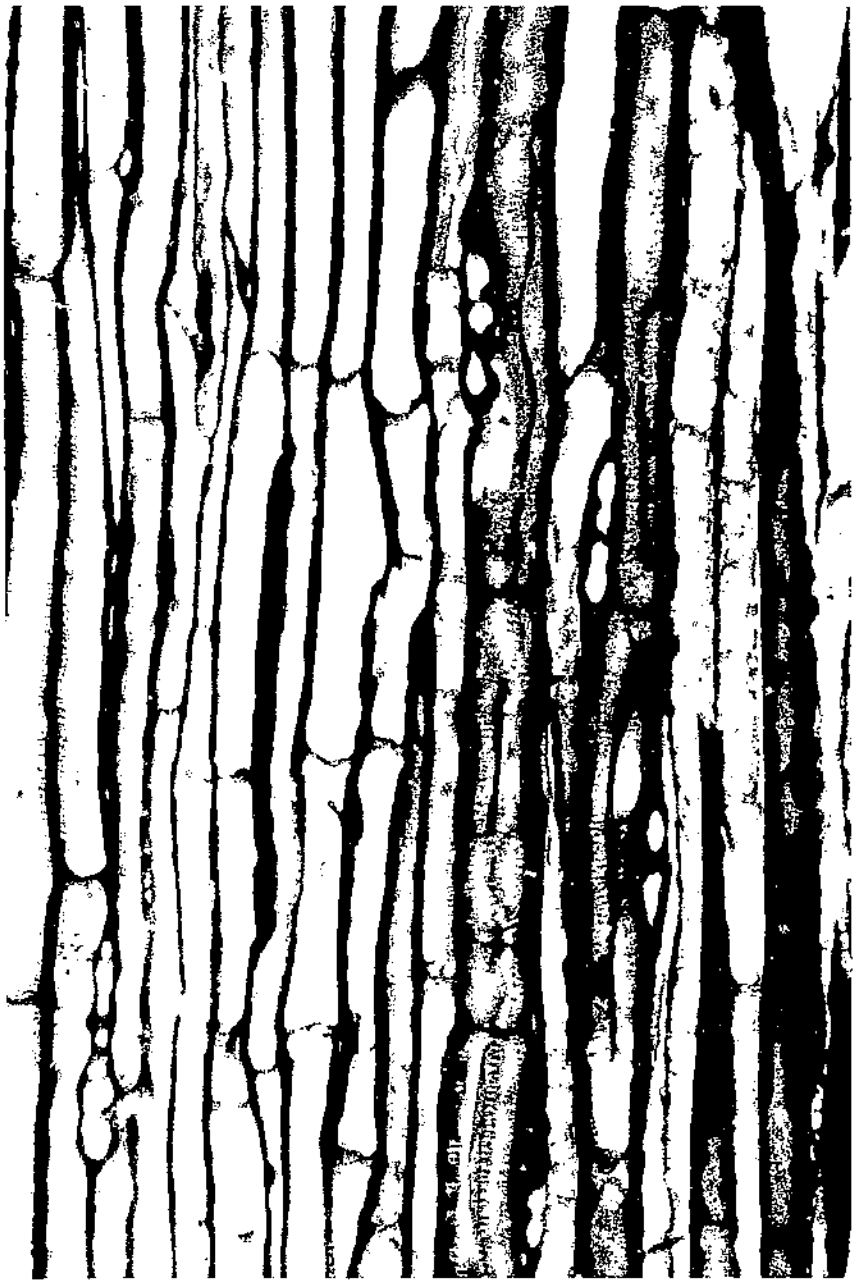

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FIGURE 35.—*Chamaecyparis thyoides*. Tangential section of inner bark showing significant pattern of simple pits on parenchyma cell walls.

fibers and sieve cells. Individual cells vary from 200 to 300 microns in height, mostly about 250 microns; in cross section usually about same shape and size as sieve cells but very often radially expanded to about twice usual size, expansion occurring in inner bark and sometimes even very close to cambial region. Simple pits in cell walls very characteristic and abundant, appearing on both radial and tangential sections; oval pits tending to be elliptic to linear and horizontally extended; alined in a single vertical row or sometimes 2 to 3 rows on radial surface of a single cell; sometimes pits extremely enlarged and extend full width of radial wall to give general appearance somewhat like scalariform pitting or perforation; occasionally up to 15 enlarged pits in a row. Sometimes cell walls with partially thickened portions, irregularly spaced, and without definite position. Cells often contain "resinous" substance.

Phloem rays mainly uniseriate, rarely partially biseriate; not much dilated at outer bark; rather low and narrow on tangential section, mostly about 5 to 10 cells or 100 to 200 microns high. Individual cells about 70 microns in radial dimension and about 50 microns high in radial section; often containing "resinous" substances. No specially formed erect marginal cells comparable to albuminous cells observed.

Resin canals present without definite location, usually several alined in a tangential row, some very close to cambial region; rather big in size, varying from one-half to 1 millimeter in diameter in cross section, and vertically up to several millimeters long; distinct border around canals formed by thin-walled parenchyma cells.

Transition from inner bark to outer bark gradual; expansion of parenchyma cells and "lignification" of fibers starting early in inner bark.

Chamaecyparis lawsoniana (figs. 31–33) often retains comparatively thicker bark than *C. thyoides* (figs. 34 and 35). Structurally, it differs from *C. thyoides* by having conspicuously expanded layers of parenchyma that are thicker than usual and mixed with the regular layers in most of the bark; its parenchyma cells also have less conspicuous pits. Other distinguishing characteristics are the conspicuously transformed layers of secondary phloem tissues that are mainly composed of expanded parenchyma cells and the broad periderm composed of 15 or more cells filled with abundant "tanniferous" or "resinous" substances.

Cupressus macrocarpa Hartw.

General features

Bark usually less than 1 inch thick; about one-half inch thick in specimen studied. Outer surface rather firm and in shallow, narrow furrows and ridges mostly connected to each other; grayish brown with deep reddish-brown periderm as observed on longitudinal surface; outer bark in cross section dull brown with yellowish hue, tissues rather compact, periderm indistinct. Inner bark narrow, lighter in color than outer bark, transition gradual; rather closely spaced tangential lines of fibers visible under lens; rays indistinct. Resin canals present in both inner and outer bark; in tangential section chalky-yellow dots of resins visible to naked eye.

MICROSCOPIC STRUCTURE

Periderm thin, composed of 3 to 10 layers of phellem, a layer of phellogen, and about 2 to 6 layers of phelloderm. Phellem usually includes 3 to 6 layers of thin-walled cells; cells uniform in thickness; rectangular in cross section, about 20 to 30 microns and 50 microns in radial and tangential dimensions, respectively; about 50 microns high in radial sections. Phelloderm cells about same shape and size as phellem cells, slightly broader radially, and with thicker walls. Both phellem and phelloderm cells contain "resinous" substance.

Sieve cells differentiated regularly in every unit of alternate layers of secondary phloem tissues; about 30 microns in tangential dimension and 20 microns in radial dimension in cross section, about 1.2 to 3 millimeters long, mostly about 2.5 millimeters; ends chisellike but not very pointed. Sieve areas appear only on radial walls of sieve cells, not crowded, and evenly spaced; mostly about 10 microns in diameter; nearly orbicular to oval. Connecting strands and definitive callus distinct in those sieve cells close to cambial region. About 2 to 5 pore groups in each sieve area with 2 to 5 pores in each group; border surrounding sieve area and network of cell walls within area rather distinct. Sieve cells contain abundant granules of unknown nature.

Maturation of fibers rather variable in different parts of inner and outer bark, but with a more or less generalized tendency in variation. Mature fibers usually appear at an interval of 2 to 4 units of alternate layers of secondary phloem tissues, mostly square or radially elongated in cross section; underdeveloped fibers slightly "lignified" or unlignified, square or radially flattened in cross section. Fibers about same width tangentially as other phloem tissues; varying from 20 to 35 microns in diameter radially and from 1.2 to 3.0 millimeters in length, mostly about 2.4 millimeters; ends gradually pointed, sometimes blunt.

Cell walls very thick in mature fibers, with a very narrow lumen; underdeveloped fibers with thin walls similar to parenchyma cells; simple pits distinct, especially on slightly lignified fibers, in single row or occasionally double, with slitlike apertures. Fibers in outer bark mostly about 2 millimeters long, although range in length about same as in inner bark.

Parenchyma strands about same length as adjacent sieve cells and fibers, but slightly expanded radially in cross section. Individual cells about 50 to 150 microns high, mostly about 100 microns; simple pits, similar to small sieve areas, distinct in parts of strands passing ray cells, becoming enlarged and 2 or 3 connected together with barlike septations in cells of outer bark; cells contain abundant granules, reaction of starch test indistinct.

Phloem rays mostly uniseriate but very frequently partially biseriate; mostly about 6 cells or 90 microns, occasionally up to 15 cells or 250 microns high in tangential section; about 40 to 50 microns in radial dimension and 20 to 40 microns high in radial section. Typical marginal ray cells comparable to albuminous cells not observed in specimens studied; some cells slightly higher than ordinary ray cells but with same cell content. Ray cells becoming "lignified" and slightly expanded at outer bark region.

Vertical resin canals present in both inner and outer bark; in cross section, elliptical and tangentially elongated, about 300 microns in diameter; vertically up to several millimeters long; border of canals well formed by thin-walled epithelial cells. General features of canals same as those of other cupressaceous barks; often 3 to 5 alined close together in a tangential row; sometimes appear very close to cambium.

Transition from inner bark to outer bark rather gradual as far as nature of cell composition is concerned; significant changes are expansion of parenchyma cells and slightly expanded phloem ray cells, "lignification" of all tissues in outer bark, crushing of most sieve cells, although some retain their original shape. Usually inner bark composed of 20 to 30 units of alternate layers of differentiated secondary phloem tissues from cambium to last-formed periderm.

The frequently biseriate phloem rays and the distribution of the mature fibers in the secondary phloem of the bark of *Cupressus* are its major differences from other barks studied in this family. Sinz (*49*) has reported a brief study on the cupressaceous barks.

Juniperus virginiana L.

General features

Bark thin, usually about one-fourth inch thick in ordinary-sized trees. Outer bark very easily shredded into long, narrow, fibrous strips; yellowish brown, with reddish brown exposed regions of periderm. Inner bark about one-eighth inch wide, light creamy yellow with pinkish tinge; lines of broad fibers distinct under lens, visible to naked eye; phloem rays and periderm indistinct under lens. Resin canals present in both inner and outer bark, alined more or less in tangential rows, visible to naked eye.

Microscopic structure

Periderm thin, composed of 2 to 5 layers of phellem, a layer of phellogen, and 2 to 5 layers of phelloderm. Phellem cells rectangular in cross section, about 10 microns and 20 microns in radial and tangential dimensions, respectively; vertically about 30 to 50 microns high; thin walled and rather uniform in thickness. Phelloderm cells slightly broader than phellem cells; usually "lignified," with distinct simple pits on those cells at outer bark. Both phellem and phelloderm often contain "resinous" substances, especially in outer bark region.

Sieve cells differentiated regularly at every unit of alternate layers of secondary phloem tissues; rectangular in cross section, about 20 to 30 microns and 10 microns in tangential and radial dimensions, respectively, mostly about 2 to 3 millimeters long; ends gradually pointed, sometimes blunt. Sieve areas not crowded, rather evenly spaced; oval to nearly orbicular; mostly about 10 or less microns in diameter. Pores forming small groups, usually 3 to 6 groups in a sieve area; borderlines and cell wall network within an area rather fine. Sieve cells contain abundant granules of unknown nature.

Fibers differentiated at every unit of alternate layers of secondary phloem tissues; conspicuous difference between mature and underdeveloped fibers. Tangentially alined mature fibers appear at every 3

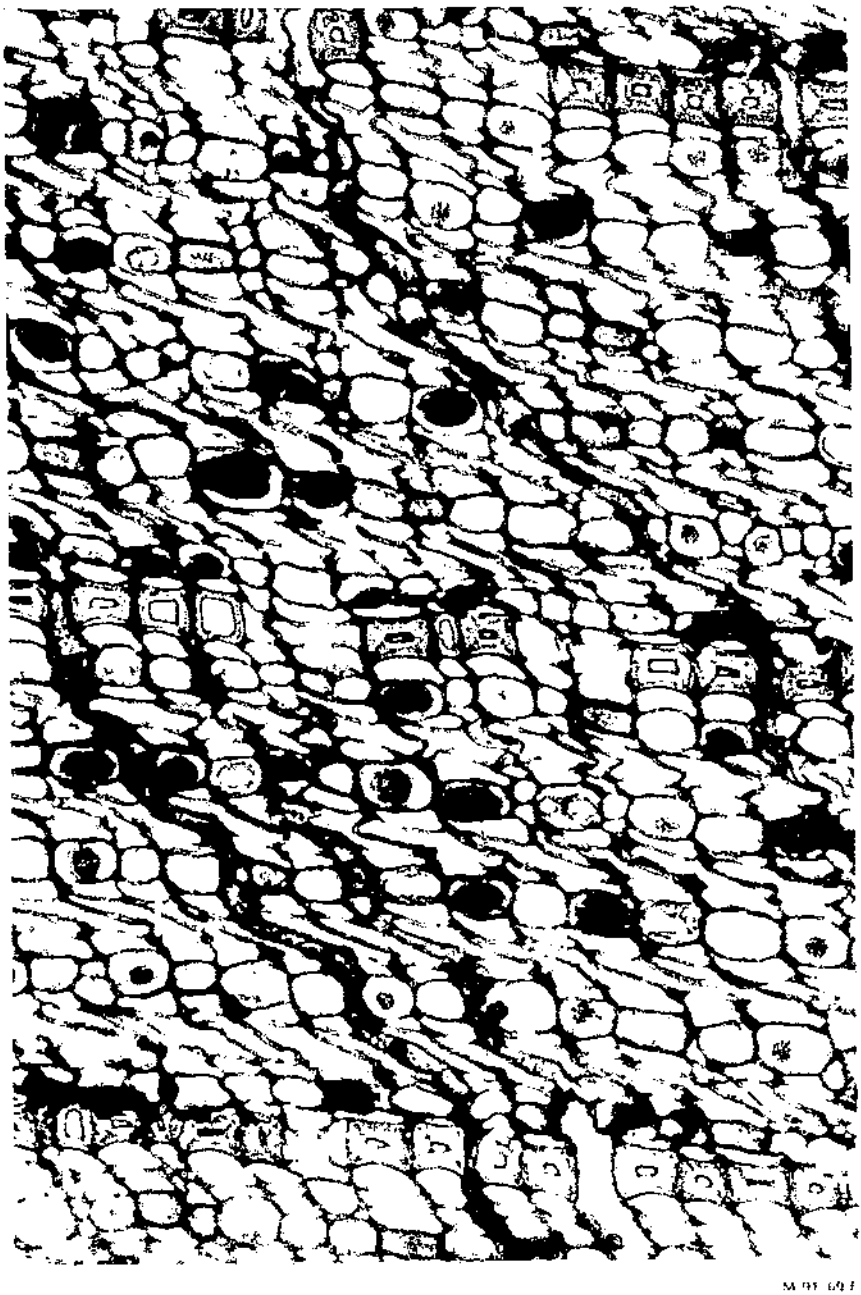

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PLATE 21.—*Juniperus virginiana*.—Cross section of inner bark showing nearly square mature fibers appearing at every 1 to 5 units of alternate layers of secondary phloem tissues (compare fig. 20).

to 6 units of alternate layers of secondary phloem tissues; within tangential lines of mature fibers, some immature fibers commonly occur. All fibers nearly square or radially elongated in cross section; mature fibers with thick, conspicuously "lignified" cell walls and narrow lumen, underdeveloped fibers much thinner walled (fig. 36).

Most fibers about 30 microns and 20 to 35 microns in tangential and radial dimensions, respectively; underdeveloped fibers usually larger in diameter than mature fibers; mature fibers usually about 2.5 millimeters but up to 3.4 millimeters long, underdeveloped fibers slightly shorter, usually about 2 to 2.5 millimeters and seldom over 3 millimeters long. Ends of mature fibers often pointed, those of underdeveloped fibers tend to be blunt; simple pits distinct, with long slitlike apertures in cell walls of underdeveloped fibers; thin-walled fibers retain the same structure after being transformed in outer bark.

Parenchyma strands about same length as adjacent sieve cells and fibers; radial dimension up to 30 microns in cross section. Individual cells about 50 to 150 microns high; end walls often rounded; small simple pits often in groups of 2 to 3, usually in a vertical row, distinct in those parts passing through ray cells; cells contain "resinous" substance and starch grains.

Phloem rays mainly uniseriate; narrow and low, mostly about 5 to 8 cells or 100 microns but up to 15 cells or 160 microns high in tan-

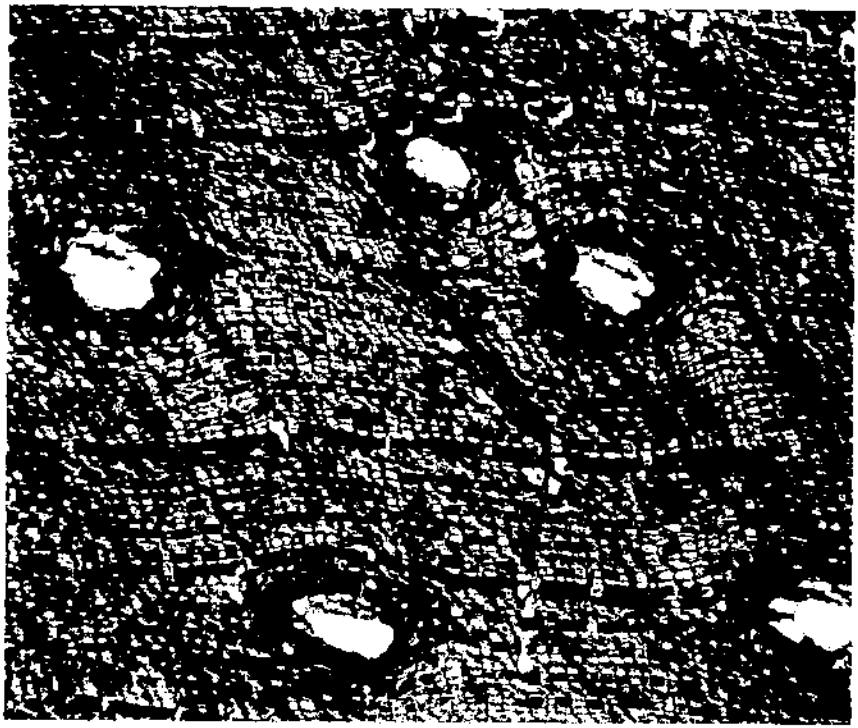

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FIGURE 37.—*Juniperus virginiana*. Cross section of inner bark showing tangentially alined vertical resin canals with well-defined border, and general arrangement of secondary phloem tissue.

gential section. Individual cells rather small, about 12 microns high and 50 microns in radial dimension; contain "resinous" substance and starch. Marginal erect cells equivalent to typical albuminous cells not observed in specimens studied.

Resin canals present in both inner and outer bark regions, alined more or less in tangential rows, elliptic and tangentially elongated in cross section; diameter usually about 200 microns radially, up to 600 or more microns tangentially; vertically rather long, mostly over one-half centimeter long; well-formed border of thin-walled epithelial cells in 2 to 5 or more layers (fig. 37); traces of crushed tissues, due to formation of canals, sometimes remain at border or in canals.

Transformation from inner bark to outer bark rather distinct. Tissues in outer bark contain mainly radially expanded parenchyma and ray cells, but all become thick walled and "lignified"; fibers and sieve cells occasionally remain at corner of expanded cells, crushed or still in their original shape. "Lignification" and slight expansion of secondary phloem tissues also occur at outer part of inner bark close to last-formed periderm.

Barks of *Juniperus monosperma* and *J. scopulorum* both show widely spaced mature phloem fiber lines and about the same structure, on the whole, as *J. virginiana*. According to the general features of the available specimens of these species, their barks are very similar, with only slight differences in the predominant colors. The alligator juniper (*J. deppeana* Steud.) with thick, scaled bark like the back of an alligator is quite distinguishable by its bark.

Libocedrus decurrens Torr.

General features

Bark thick, usually about 2 to 3 inches (reported as often up to 6 to 8 inches in old trees). Outer bark exfoliating into fibrous flakes or shreds; yellowish brown and tinged with purplish red on exposed regions of periderm; rather loose and soft because expanded parenchyma cells occupy most of rhytidome. Inner bark mostly about one-fourth inch wide; much lighter in color than outer bark; expanded parenchyma layers occur in outer part of inner bark, usually about 2 to 4 expanded layers mixed with regular compact layers of secondary phloem tissues, distinct under lens. Phloem rays and broad fiber lines distinct under lens and visible to naked eye. Resin canals sporadic in inner bark, rather conspicuous in outer bark; visible to naked eye.

Microscopic structure

Periderm narrow, composed of about 5 layers of phellem, a layer of phellogen, and 2 to 5 layers of phelloderm. Phellem cells thin walled and uniform in thickness; newly formed cells small in size, varying from 15 to 40 microns in tangential dimension, in cross section, and about 20 to 50 microns high. Phelloderm cells about same shape as phellem cells but smaller in size; simple pits distinct in cells of old bark, which often become "lignified" and contain "resinous" substance.

Sieve cells differentiated regularly in between a layer of parenchyma and a layer of fibers; about 40 to 50 microns in tangential dimension and 30 microns in radial dimension; varying from 2.6 to 4.5 milli-

meters in length, mostly about 3.7 millimeters; ends gradually pointed, chisellike, or sometimes blunt. Sieve areas rather evenly spaced and not crowded, mainly solitary; orbicular to oval and vertically flattened; mostly about 15 to 20 microns in diameter. Connecting strands and definitive callus distinct in those sieve cells close to cambium of fresh specimen. Pores appear in sieve areas of inactive sieve cells; usually about 2 to 5 pores in a small group and about 10 groups in an area; pores rather evenly distributed. Cellulose walls retained in sieve area form network; border of sieve area distinct. Small granules of unknown nature present in sieve cells in inner bark.

Phloem fibers appear regularly in every unit of alternate layers of secondary phloem tissues; slightly variable in size and thickness of cell walls. In young stems, fibers regular and uniform in size and shape, conspicuously flattened radially. In old barks, mature fibers appear every two units of alternate layers of secondary phloem tissues; flattened radially in those cells close to cambium, becoming square and tending to be elongated radially in those cells at outer part of inner bark; underdeveloped fibers "lignified" but comparatively thin walled and remain flattened radially.

Fibers in inner bark about same length as sieve cells; ends usually pointed but slightly curved and blunt ends not uncommon; simple pits very distinct in immature fibers; cell walls very thick and with very narrow lumen in mature fibers. Fibers in outer bark comparatively shorter than those in inner bark, mostly about 3 millimeters long; mainly square or slightly elongated radially in cross section.

Parenchyma strands differentiated regularly in alternating sequence with sieve cells and phloem fibers; cells about same shape and size as in other phloem tissues in cross section, except end walls tend to be round; about 100 to 150 microns high; pits in cell walls about shape of small sieve areas but with only 2 or 3 pores; cells contain "resinous" substance and starch grains. Conspicuously radially expanded parenchyma cells occur in outer part of inner bark, mixed with layers of regularly grown tissues; expansion may extend to 5 or 10 times original radial dimension and 2 to 4 times original tangential dimension, as shown in cross section; adjacent tissues obliterated; cell walls of expanded cells comparatively thicker than usual, simple pits more conspicuous.

Phloem rays mainly uniseriate, occasionally partially biseriate; mostly 10 to 15 cells or 300 microns but up to 25 cells or 600 microns high, tangentially about 15 microns wide in inner bark, not much dilated towards outer bark. On radial section individual cells about 40 to 60 microns high and about 150 to 200 microns in radial dimension; contain "resinous" substance and starch grains. Albuminous cells occasionally occur on rays close to cambium, sometimes 3 or 5 together or 2 marginal cells in a row; about 15 microns in radial dimension and slightly higher than regular ray cells.

Resin canals occur in both inner and outer bark; oval to elliptic in cross section, with tangential diameter about 500 microns; canal borders well defined by thin-walled epithelial cells.

Transformation from inner bark to outer bark accomplished by conspicuous radial expansion of parenchyma cells, slight dilation of phloem ray cells, obliteration of sieve cells, "lignification" of all tissues in the secondary phloem and occasionally of phelloderm. Color of

outer bark much deeper than that of inner bark because of changes in cell walls and cell chemical content; change of color does not exactly correspond, however, to real demarcation of inner and outer bark, because expanded cells occur in light-colored "inner bark."

The bark structure of *Libocedrus* differs from that of other cupressaceous barks in its thickness, often early expansion of cells in inner bark, and comparatively long fibers.

Thuja occidentalis L.

General features

Bark thin, usually less than 1 inch thick; in specimens studied only about one-fourth inch thick. Outer surface grayish brown, reddish-brown hue in regions of exposed periderm, generally with brown as predominant color, and less reddish as compared with barks of *Juniperus* and *Cupressus*; exfoliating into shallow fissures and shredded into long fibrous strips. Periderm very thin, distinguishable from longitudinal surface by its reddish-brown color; visible under lens in cross section. Inner bark narrow, usually about one-sixteenth to one-eighth inch thick; creamy yellow after exposure to air for short period; fine fiber lines and phloem rays barely visible under lens. Resin canals present in both inner and outer bark; alined more or less in tangential rows; visible to naked eye.

Microscopic structure

Periderm narrow, composed of 2 to 5 layers of phellem, a layer of phellogen, and about 2 to 5 layers of phelloderm. Phellem cells thin walled, uniform in thickness; rectangular in cross section, about same in tangential dimension as parenchyma cells but narrower radially, vertically about 40 to 50 microns high in radial section. Phelloderm cells about same size as phellem cells but slightly broader radially, simple pits distinct in those cells at outer bark. Both phellem and phelloderm cells often contain "resinous" substance.

Sieve cells differentiated regularly at every unit of alternate layers of secondary phloem tissues; rectangular in cross section, mostly about 15 and 30 microns in radial and tangential dimensions, respectively, and about 2.5 millimeters long; usually with chisellike ends. Sieve areas not crowded, evenly distributed; oval to nearly orbicular, about 15 or less microns in diameter. Connecting strands and definitive callus distinct. Pores in sieve areas grouped; borders of sieve areas and cellulose network within sieve area rather narrow. Sieve cells contain abundant granules of unknown nature.

Fibers differentiated regularly, mature fibers appear at every unit of alternate layers of secondary phloem tissues and remain rather flattened radially throughout inner and outer bark regions; underdeveloped fibers present occasionally, but quite distinguishable from other tissues and about same shape and size as mature fibers. Fibers mostly about same diameter and length as adjacent sieve cells; ends gradually pointed; cell walls of mature fibers rather thick with a very narrow lumen, simple pits distinct.

Parenchyma strands about same length as adjacent sieve cells. Individual cells about 100 to 150 microns high; usually 2 or 3 simple pits close together in cell walls, somewhat similar to small sieve areas; pits distinct in those regions passing through phloem rays as shown

in radial section. Cells often contain "resinous" substance and starch.

Phloem rays mainly uniseriate; narrow and low, mostly about 6 cells or 150 microns but up to 12 cells or about 200 microns high in tangential section; not much dilated at outer bark. Cells somewhat rounded on radial end walls; about 20 microns high and 50 microns in radial dimension; albuminous cells rare in specimens studied.

Vertical resin canals present in both inner and outer bark, alined more or less in tangential rows; well-defined border formed by thin-walled epithelial cells in 2 to 5 layers. Canals elliptic and tangentially elongated in cross section: some large-sized ones up to 2 millimeters in tangential dimension, most about 300 microns in radial dimension, vertically rather high, usually several millimeters long.

Transformation from inner to outer bark rather distinct; conspicuously radially expanded parenchyma and ray cells usually occupy full space between two fiber layers; most cells in outer bark region becoming "lignified."

The bark structure of *Thuja plicata* is quite similar to that of *T. occidentalis*. It has slightly longer phloem fibers, mostly about 2.5 to 3.0 millimeters long. Mature fibers are squarer in cross section than the fibers in the bark of *T. occidentalis*.

DIAGNOSTIC FEATURES OF BARK AND THEIR APPLICATION TO IDENTIFICATION

The structure of coniferous barks is comparatively simple, and there are many similarities in features among the barks of different species and genera. After careful evaluation of their structural characteristics and variations, however, the generic differences of the North American coniferous barks studied were established. The artificial keys and table 1 are based upon both the gross features and microscopic structure of these barks and should be helpful in separating genera. The table and keys should be considered as only a simplified form of data, however, and for comparison of detail and characteristics of some species, it will be necessary to refer to the description and discussion of the particular genus.

Artificial Keys to Families and Genera

Key to Genera of North American Conifers, Based Upon Macroscopic Structure of Their Barks

1. Periderm conspicuous, in uniform, fine lines or broad corky bands, distinct to naked eye. Rhytidomes formed by alternate layers of periderm and enclosed secondary phloem tissues brittle and exfoliating into small scales or large flakes. Secondary phloem tissues in outer rhytidomes mainly in a diffused pattern; no distinct tangential lines of phloem fibers.
   2 (PINACEAE, subfamily Abietoideae)

1. Periderm inconspicuous, barely visible to distinct under lens. Rhytidomes fibrous and peeling into longitudinal strips or thin, coriaceous scales (as in *Taxus brevifolia* and some young stems of *Cupressus* and *Juniperus*). Rather regularly alined tan-

TABLE 1.—*Features to be used as basis for the separation of North American coniferous barks (families Taxaceae and Pinaceae)*

[+ Denotes features present constantly; − denotes features present occasionally]

Type of feature	Appearance of features														
	Family Taxaceae		Subfamily Abietoideae						Subfamily Taxodioideae		Subfamily Cupressoideae				
	Taxus	*Torreya*	*Abies*	*Larix*	*Picea*	*Pinus*	*Pseudotsuga*	*Tsuga*	*Sequoia*	*Taxodium*	*Chamaecyparis*	*Cupressus*	*Juniperus*	*Libocedrus*	*Thuja*
General features of rhytidomes:															
Peeling into fibrous strips		+							+	+	+	+	+	+	+
Exfoliating into scales	+		+	+	+	+	+	+							
Periderm:															
Mainly thin-walled phellem cells	+	+	+				+	+	+	+	+	+	+	+	+
Bands of thin-walled and thick-walled cells			−	+	+	+	−	−			−	−		−	
Phellem narrow, 5 to 50 layers in a peridern layer	+	+		+	+	+		+	+	+	+	+	+	+	+
Phellem broad, often up to about 100 layers in a periderm layer			+				+								
Sieve cell arrangement:															
Single or occasionally 2 to 3 in short radial multiples	+	+							+	+	+	+	+	+	+
5 to 15 or more in radial rows			+	+	+	+	+	+							
Types of sclerenchyma in secondary phloem:															
Absent						+									
Typical fiber about same length as adjacent sieve cells; cross-sectional area rectangular to square	+	+							+	+	+	+	+	+	+
Fiber form but much shorter than sieve cells; cross-sectional area oval to irregularly rounded				+			+								
Short, branched, and twisted sclereids in group			+		+			+							
Crystals in parenchyma:															
Absent	+	+							+	+	+	+	+	+	+
Mainly isodiametric			+	+	+										
Distinct rectangular lateral faces						+	+								
Much elongated lateral faces with pointed front face						+		+							

Typical phloem fibers:															
Approximate length (average):															
2 to 3 millimeters	+	+										+	+		+
3 to 5 millimeters										+	+			+	
5 to 7 millimeters									+						
Occurrence of matured fibers in alternate units of tissue layers:															
Mainly regular in every unit									+	+					+
Often every 2 to 3 units	+	+									+	+	+	+	
Every 4 to 5 units, or irregular	+	+											+		
Crystals present															
Albuminous cells:															
Present in every ray close to cambial region			+	+	+	+	+	+							
Wanting to very sporadic	+	+							+	+	+	+	+	+	+
Resin passages:															
Normally absent	+	+						+	+	+					
Horizontal canals in fusiform rays				+	+	+	+								
Vertical canals											+	+	+	+	+
Expansion of ray cell, passage without definite border			+												

gential lines of phloem fibers remain in rhytidome, distinct under lens.
8 (TAXACEAE; PINACEAE, subfamilies Taxodioideae and Cupressoideae)

2. Fine dots of phloem fibers or larger spots of sclereid groups diffused in inner or outer bark or both, visible to distinct to naked eye. Inner bark usually about one-eighth to one-fourth inch thick, usually broader than last-formed layer of outer bark---4
2. No fine dots of fibers nor scattered spots of sclereid groups present in inner and outer bark. Inner bark often about one-sixteenth inch but less than one-eighth inch thick, often about same width as last-formed layer of outer bark---3 *Pinus*
3. Periderm short tangentially in cross section, often convex radially, and outline of overlapped region often rounded. Secondary phloem tissues in outer bark not much expanded, indistinct under lens. Resin canals often abundant throughout inner and outer bark, visible to naked eye---Subgenus *Haploxylon*
3. Periderm much elongated tangentially in cross section, main portions of two adjacent layers usually parallel to each other, outlines of overlapping regions chisellike and gradually pointed. Secondary phloem tissues in outer bark conspicuously expanded radially, even in last-formed layer of rhytidome, distinct under lens---Subgenus *Diploxylon*
4. Diffused phloem fibers forming scattered fine dots in cross section, distinct only under lens---5
4. Grouped sclereids forming large spots in cross section, usually flattened radially, scattered to crowded, visible to distinct to naked eye---6
5. Periderm with well-developed cork in narrow lines or broad bands with laminated layers, light brownish yellow, very contrasting to brilliant-brown secondary phloem---*Pseudotsuga*
5. Periderm without conspicuous corky layers; color difference between periderm and secondary phloem not sharp---*Larix*
6. Periderm soft and comparatively broad, often over one-thirty-second inch and sometimes up to one-sixteenth to one-fourth inch wide. Sclereid groups abundant, often alined in discontinuous tangential rows---*Abies*
6. Periderm compact and brittle, comparatively thin but in some parts up to one-thirty-second inch thick. Sclereid groups sporadic or absent in inner bark---7
7. Bark with strong reddish hue, especially periderm; comparatively thick, often over 1 inch, even in small-sized trees usually over one-half inch thick---*Tsuga*
7. Bark with light to dull brown as predominant color, color of periderm not very contrasting to that of secondary phloem; comparatively thin, usually less than one-half inch thick.
Picea
8. Tangentially alined vertical resin canals always shown on outer bark and usually in inner bark, chalky to light yellow.
9 Cupressoideae
8. Tangentially alined vertical resin canals absent.
13 (TAXACEAE; Taxodioideae)

9. Bark thick, usually over 2 inches. Expanded phloem tissues in inner and outer bark distinct to naked eye.....*Libocedrus*
9. Bark comparatively thin, usually less than 1 inch. Expanded phloem tissues absent or indistinct..... 10
10. Old bark rather compact. Cross section of outer bark light brown, with yellowish hue.....*Cupressus*
10. Old bark usually easily peeling into thin layer. Cross section of outer bark deep brown and often with reddish hue..... 11
11. Inner bark with very closely spaced fine lines, barely visible under lens.....*Thuja*
11. Inner bark with comparatively widely spaced and coarse tangential lines, distinct under lens..... 12
12. Bark dark in color; resin-filled periderm often forming irregular bands (*C. lawsoniana*); sometimes with fine lines of expanded parenchyma cells (*C. thyoides*).....*Chamaecyparis*
12. Bark comparatively light in color; irregular bands of periderm or expanded parenchyma lines indistinct.....*Juniperus*
13. Surface of outer bark firm and smooth, or forming shallow furrows with short scales. Tangential lines of phloem fibers inconspicuous and occasionally irregular; often lustrous in cross section because of presence of crystals.....14 (TAXACEAE)
13. Outer bark in deep fissures and exfoliating into long strips, very fibrous. Tangential lines of phloem fibers conspicuous and regular, not lustrous in cross section.....15 (Taxodioideae)
14. Outer bark forming large flakes, firm and smooth. Inner and outer bark with reddish hue.....*Taxus*
14. Outer bark in shallow furrows with short scales, comparatively fibrous. Inner and outer bark with distinct yellowish hue.....*Torreya*
15. Bark thick, usually over several inches to 1 foot thick in old trees. Rhytidomes in cross section comparatively shorter tangentially, overlapping regions distinct.....*Sequoia*
15. Bark comparatively thin, usually about 1 inch or less in thickness. Rhytidomes mostly regular and running in long parallel lines in cross section.....*Taxodium*

Key to Genera of North American Conifers, Based Upon Microscopic Structure of Their Barks

1. Tissues in secondary phloem differentiated into alternate layers of parenchyma, sieve cells, and fibers; only occasionally with partial irregularities. Typical fibers always present; cross-sectional area square or rectangular; total length about same as adjacent sieve cells. Phloem rays not much dilated in inner bark; albuminous cells wanting or very sporadic..... 8
1. Tissues in secondary phloem not arranged in definite alternate layers; sieve cells usually in radial rows of about 5 to 15 or more cells; parenchyma often alined in more or less continuous tangential lines of single cells or of 2 to 4 cells in short, radial multiples. Sclerenchyma may be entirely wanting in secondary phloem or occur in form of sclereids or fibers, but only about one-third as long as adjacent sieve cells; cross-sectional area

usually oval to irregular. Phloem rays often very dilated in outer bark or even in inner bark; albuminous cells conspicuous and present in almost every ray close to cambial region. 2 (PINACEAE, subfamily Abietoideae).

2. Secondary phloem with sclereids or fiber-formed sclerenchyma cells. Crystals in parenchyma cells nearly cubic, with isometric faces. Horizontal resin canals present or absent; innermost epithelial cells usually over 6 in number and about the same size as, or smaller than, the outer surrounding cells as shown in tangential section 4

2. Secondary phloem without sclerenchyma. Crystals in parenchyma mainly with rectangular or much elongated faces. Horizontal resin canals always present; innermost epithelial cells usually 3 to 4 in number and much larger than outer surrounding cells as shown in tangential section ..... 3 *Pinus*

3. Tissues in newly transformed outer bark not much expanded radially, sometimes even inconspicuous in outer rhytidomes. Periderm in cross section comparatively short and distinctly curved, very often overlapping. Crystals in parenchyma mainly with rectangular faces. Resin canals abundant. Subgenus *Haploxylon*

3. Parenchyma and rays in newly transformed layer of outer bark conspicuously expanded radially, sieve cells mostly obliterated. Periderm layers parallel to each other in most parts of rhytidomes. Comparatively long styloid crystals with pointed front faces in parenchyma. Resin canals sporadic to wanting. Subgenus *Diploxylon*

4. Sclerenchyma in fiber form, solitary or 2 to 3 in small groups 5

4. Sclerenchyma in form of grouped sclereids: cells twisted and branched; often 10 or more cells in a group 6

5. Phloem fibers abundant and rather crowded, often 2 to 3 in small groups. Periderm often very thick; composed mainly of thin-walled phellem cells; some thick-walled cells sporadically distributed but not in definite band formation ..... *Pseudotsuga*

5. Phloem fibers very sporadic and mainly solitary. Periderm thin, with conspicuously alternate bands of thin- and thick-walled cells ..... *Larix*

6. Sclereid groups very sporadic and often wanting or immature in inner bark of young trees. Fusiform phloem rays abundant, horizontal resin canals with well-defined border. Periderm comparatively thin but with conspicuous bands of thick-walled cells ..... *Picea*

6. Sclereid groups crowded and often appear very close to cambium. Phloem rays mainly uniseriate or with partially paired cells; fusiform phloem rays wanting and no horizontal resin canals with definite border. Periderm often well developed but mainly with thin-walled phellem cells 7

7. Parenchyma with isodiametric crystals, often very abundant. Resin passage in secondary phloem, forming pocketlike cysts without epithelial cells, very common in *A. balsamea*, *A. lasiocarpa* and its variety *arizonica*, and *A. fraseri*, rare in other species ..... *Abies*

7. Parenchyma with long styloid crystals and rather abundant "tanniferous" granules. No pocketlike resin passage developed. *Tsuga*

8. Abundant small crystals embedded in cell walls of phloem fibers. Fibers often differentiated in irregular sequence; mature fibers appear usually in discontinuous tangential lines. 9 (TAXACEAE)

8. Phloem fibers without crystals. Differentiation of tissues in secondary phloem mainly in regularly alternated layers------ 10

9. Phloem rays low, mostly less than 10 cells or less than 100 microns high. Crystalliferous fibers mature early, often appear very close to cambium; comparatively large in size, mostly about 2.6 millimeters long------ *Torreya*

9. Phloem rays high, mostly over 10 cells or 150 microns and occasionally up to 25 cells or 300 microns high. Mature fibers appear sporadically at outer part of inner bark; comparatively small in size, mostly about 2 millimeters long------ *Taxus*

10. Vertical resin canals always present in secondary phloem and with distinct border; usually several canals alined in a tangential row. Sieve cells and fibers seldom over 4 millimeters long. Phloem rays comparatively low, rarely over 20 cells high. 12 (PINACEAE, subfamily Cupressoideae)

10. Vertical resin canals wanting in secondary phloem; traumatic canals rarely occur. Sieve cells and fibers long, often vary from 4 to 7 millimeters long. Phloem rays comparatively high, often over 30 cells high--11 (PINACEAE, subfamily Taxodioideae)

11. Phloem fibers mostly over 5 millimeters and up to 7 or more millimeters long. Transition from inner to outer bark rather abrupt; layers of rhytidomes comparatively broad and with conspicuously expanded parenchyma cells------ *Sequoia*

11. Phloem fibers comparatively short, mostly about 4 to 5 millimeters long. Transition from inner to outer bark gradual; layers of rhytidomes narrow and parenchyma not much expanded. *Taxodium*

12. Mature fibers appear regularly in every unit or every other unit of alternate layers of secondary phloem tissues; cell walls of underdeveloped fibers comparatively thin but quite distinguishable from other tissues; fibers conspicuously flattened radially or square in cross section; radially elongated fibers mainly appear at outer part of inner bark------ 13

12. Mature fibers appear irregularly, usually at an interval from 2 to 6 units of alternate layers of secondary phloem tissues; underdeveloped fibers usually remain thin walled; most fibers, even newly formed ones, often square or radially elongated in cross section------ 15

13. Mature fibers appear regularly at every unit of alternate layers of secondary phloem tissues, conspicuously flattened radially, only occasionally square in cross section. Parenchyma not expanded in inner bark. Phloem fibers comparatively short, mostly about 2.7 millimeters long------ *Thuja*

13. Mature fibers appear mostly at every other unit of alternate layers of secondary phloem tissues; cells flattened radially or square

in cross section. Inner bark often with expanded parenchyma mingled with ordinary growth of alternate layers of secondary phloem tissues. Phloem fibers comparatively long, mostly about 3.5 millimeters long----------14

14. Expanded phloem parenchyma often extends through 1 or 2 entire units of alternate layers of secondary phloem tissues in inner bark. Tissues in rhytidomes of outer bark mostly much expanded and very contrasting to normal tissues in inner bark. Simple pits on parenchyma cells sporadic and mainly appear on radial walls----------*Libocedrus*

14. Inner bark occasionally with expanded parenchyma, but expansion not much extended to adjacent cells. Tissues in newly transformed outer bark not conspicuously expanded and not very contrasting to those in inner bark. Parenchyma with well-developed simple pits, often crowded and alined in 1 or 2 vertical rows, appearing on both tangential and radial walls, or sometimes a few pairs of very large pits----------*Chamaecyparis*

15. Phloem rays very frequently partially biseriate. Mature fibers appear at an interval of 2 to 4 units of alternate layers of secondary phloem tissues, mostly about every 3 units----*Cupressus*

15. Phloem rays mainly uniseriate. Mature fibers appear at an interval varying from 3 to 6 units of alternate layers of secondary phloem tissues, mostly about every 4 to 5 units----------*Juniperus*

NOTES ON RANDOM CHEMICAL MEANS FOR IDENTIFICATION

Identification of woods according to their anatomical structure is still the most reliable method, and the same is true for barks. The closely related species, however, are often similar to each other in structure, and chemical methods sometimes are very useful for distinguishing them. Phytochemical findings from plants are increasing in number and becoming more conclusive. Research contributions directed either simply toward *materia phytochemica* or toward the more fundamental consideration of structural relationships of phytochemistry, which have already been analyzed and summarized by J. A. Hall (*19*), provide some interesting hints that apply to the identification of biological species. Chemical analyses of bark are, of course, also valuable for identification purposes.

Although the well-known Maule reaction (*35*) was the earliest application of chemical means for distinguishing wood, notably wood of Angiosperms from that of Gymnosperms, the first special contribution to the chemical identification of coniferous wood was made by Schorger (*45*) in this country. Recently, Stearns and Hartley (*50*) prepared a very interesting review of the physicochemical methods for wood diagnosis, although the information given is not complete, especially in regard to histochemistry. Most of the findings from wood or higher plants would be worth trying for bark identification. Perhaps chemical methods might be more suitable for identification of barks, since the chemical contents of bark cells are more strongly marked than those of wood cells.

Comparing the color of extracts seems the simplest chemical method of identifying barks, and various methods of extraction applied to wood were considered in this study. Japanese investigators, such as Fujioka (*15*), Kanehira (*29*), and Miyoshi (*38*), have done a great deal of this work on wood. Their methods were later improved and made more specific by Indians, such as Krishna and Chowdhury (*31*); by Australians, such as Cohen (*6*) and Dadswell (*9*); and by Americans, such as Isenberg (*28*) and Marteny (*34*). Although they modified the solvents, observed the extracts under different light, and used different standards for recording color, they followed the same principles, and none of the specified procedures could be effectively used for a large group of woods. On the other hand, it is quite understandable that certain chemicals will be specially useful for certain small groups of wood.

Among the contributions mentioned, the method used by Miyoshi and later intensified by Isenberg was found especially favorable for separating eastern and western white pine barks. Adding 10 cubic centimeters of methanol and 2 drops of concentrated hydrochloric acid to 0.5 gram of bark chips produced an intensive color within 15 minutes. The color of the extracts was very stable so far as general observation showed. When 2 drops of ferric chloride were added to the extracts, those from western white pine became a much deeper brownish red and those from eastern white pine remained the same color. More than 5 dry specimens, collected from different localities, and 1 fresh specimen from each species were tested. The colors of the extracts of these two species always showed the same degree of difference. Seven species of southern pines and a few western pines were also tried by the same method. Their extracts did show special colors in different species, but further comparison of extracts from additional material is needed.

The spectra of the extracts were compared with the recording infrared spectrophotometer. Only one solvent, carbon tetrachloride, was used. The curves produced by the extracts of 6 different kinds of pine bark and 2 kinds of cypress bark all followed the same pattern.

No special microchemical tests were attempted in the present investigation, but some common chemicals and aqueous stains, such as iodine-potassium iodide, ferric chloride, and aniline blue, were constantly used during the course of microscopic observations.

DISCUSSION

Significance of Coniferous Bark Structure

The fundamental cell types and their arrangement in each generic representative have been described. Based upon these observations, the specific and generic characteristics were compared and those of diagnostic value evaluated for identification of barks. From this information, we may summarize the significant characteristics in the group of coniferous barks studied.

The generic characteristics of all species studied are rather constant, and the distinction among the four families is quite clear.

The bark structure of typical Pinaceae (subfamily Abietoideae) differs from that of the family, Taxaceae and also from that of the other two Pinaceae subfamilies, Taxodioideae and Cupressoideae, mainly by the well-developed periderm and lack of typical libriform fibers. The absence of sclerenchyma in the secondary phloem of *Pinus* distinguishes it from all other genera.

The structure of barks of Cupressoideae and Taxodioideae is very different from that of other Pinaceae. The family Taxaceae is intermediate between these two groups as far as bark structure is concerned. The similarities of bark structure in Cupressoideae and Taxodioideae appear in the regularly alined alternate layers of sieve cells, fibers, and parenchyma. Barks of Cupressoideae are distinguished by the presence of tangentially alined vertical resin canals in the secondary phloem. Although the bark structure of the Taxaceae studied is in a position between that of typical Pinaceae and those of the other two subfamilies, most of its characteristics are closer to those of the Cupressoideae and Taxodioideae, based on the differentiation of secondary phloem tissues. The tendency towards irregularity in the secondary phloem tissues and scalelike formation of rhytidomes in some species, however, leads in the direction of typical Pinaceae. The presence of crystalliferous fibers in the barks of Taxaceae confines them to a distinct group among the coniferous barks studied.

The generic distinction of barks in Cupressoideae is not so sharp as in Taxaceae and its two fellow subfamilies. Bark structures of genera in this subfamily show more affinity than in other groups. In general, however, on the basis of the data from this investigation, the author feels that the generic, subfamily, and family characteristics of the North American coniferous barks are very distinct and constant and could be naturally classified in a manner corresponding to other taxonomical systems.

Although some diagnostic features of coniferous secondary phloem have been reported by such authors as Holdheide (*21*, *22*), Huber (*23*), Miyoshi (*39*), Moeller (*40*), Shimakura (*47*), and Takamatsu (*53*), a few points concerning the specific tissues in the group of barks studied may be interesting.

Among the stem tissues in woody plants as a whole, the structural variation of periderm is comparatively much less significant than that of other tissues. In certain morphologically conservative tissues, such as periderm, however, if changes do occur through a long course of natural development, they often provide reliable characteristics of diagnostic value. As described herein, the structure of periderm is useful not only for separating families and genera, but also for separating the two subgenera of *Pinus*. The alternate bands of thick-walled cells and of the ordinary thin-walled phellem cells within a layer of periderm are especially interesting. The thick-walled cells are most likely transformed from the phelloderm.

Anatomical study of periderm is mostly concerned with the structure of mature phellem and the origin of phellogen at a certain age of a branch or stem. The successive development of phellogen in a tree and the transformation of phelloderm are not well understood. Study of coniferous periderm is also comparatively meager. Messeri has reported (*37*) that the periderm of *Pinus pinea* was of superficial origin. Miscellaneous information concerning cork structure can be

obtained by checking the bibliography by Watrous and Barnes (*55*), although it is primarily for cork oak. The different colors of periderm in different barks, which come from the chemical content of the cells and the nature of the cell walls, are quite constant in certain genera and species. In this investigation, only the color of the bark was noted and no further microchemical differentiation was attempted.

Features shown in the cross section of barks, especially the distribution and arrangement of sclerenchyma, are important and practical for identification of barks. Their diagnostic importance and its interpretation were discussed by the author in his study of rubiaceous barks (*4*). In the present study, these features were particularly useful for separating the barks of Pinaceae.

Within the group of coniferous barks studied, establishment of the salient lines of the specialization of sieve cells based simply upon their cell structure is rather difficult, since the shape of the cells and the structure and arrangement of sieve areas are quite similar in different genera. Although there are some minor differences, the sieve cells are primarily modified as a result of the formation of their surrounding tissues or physiological requirement. For this reason, no attempt was made to consider their phylogenetic relationship.

Albuminous cells, which were first described by Strasburger (*52*), are one of the special structures of coniferous phloem. Their development and distribution have been studied by Chrysler (*5*), Bannan (*2*), Barghoorn (*3*), and others. The present study supports the general conclusions of these recent authors, but it is rather difficult to specify a definite percentage of albuminous cells as presented by Bannan. At any rate, albuminous cells are conspicuous in all the Pinaceae, subfamily Abietoideae genera studied, but not in any of the other three families and subfamilies. The morphological distinction of the vertical parenchyma system, which is supposed to be physiologically equivalent to albuminous cells, could not be clearly defined in the present study, although many newly differentiated parenchyma layers close to phloem rays have individual cells similar to albuminous cells.

The structure of cell walls in ordinary phloem ray cells in different species and genera is similar, having a smooth surface and a lack of conspicuous pits, but careful observation under very high magnification may be helpful for identification. Because of this similarity, the diagnostic value of such features as the ray cell walls and the pits on tracheid and ray crossing fields, which are very useful for distinguishing coniferous xylem, is considerably lessened.

Most anatomists suspect that the chemical contents of plant cells vary according to variation of the soil or other physiological and environmental factors and are therefore not quite reliable in diagnostic value. Judging by the regular occurrence of certain observable chemical substances in the coniferous barks, however, that conception seems rather inconclusive. The presence of starch grains, "tanniferous" granules, and "resinous" substance in parenchyma and ray cells; the different types of calcium oxalate crystals in parenchyma and fibers, the conspicuous granules or crystal sands of unknown nature in sieve cells and parenchyma cells of the Cupressoideae barks; and the different types of resin passages are all anatomically significant and constant. They are worthy of further study in detail.

Although the transformation from inner to outer bark is morphologically characterized by the expansion of parenchymatous cells, such as parenchyma strands and phloem rays, and modification of their cell walls, the patterns of transformation in different barks are greatly influenced by the surrounding tissues, especially the sclerenchyma cells. The significant difference is best demonstrated by comparing the manner of expansion in rhytidomes of pine barks with that in the Cupressoideae. Within the typical Pinaceae, there is also a marked distinction between the barks with early matured sclerenchyma cells and those without sclerenchyma cells. The expansion of "bast cells" was reported by Shimakura (*48*) and others, but they did not particularly consider the original surrounding tissues.

In comparison with barks of other woody plants, the most significant features of the structure of coniferous barks are the formation of sieve cells and the universal presence of uniseriate rays with special albuminous cells or physiologically equivalent parenchyma cells. In general, the structure of coniferous barks has its own category, with well-defined distinctions among its small groups. These distinctions are useful for identification as well as for purely anatomical considerations.

Correlation of Coniferous Bark Structure to Wood Structure

The structural variation in bark and wood indicates valid relationships that may be demonstrated in different phases. It may be that both bark and wood confirm the constancy of generic characteristics. On the other hand, close relationship between genera as demonstrated by wood structure may seem less close as a result of bark comparison or vice versa. Instead of a full-scale discussion, the present comparison will be limited to those significant features of diagnostic value. The information given on wood structure is based upon miscellaneous information from wood anatomists, especially from Phillips (*42*) and from Kukachka of the Forest Products Laboratory staff. In considering correlations, similarities are as important as differences. Since no parts homologous to periderm and cortex exist in wood, this discussion is confined to the comparison of secondary phloem and secondary xylem. Significant correlations of some important cell types and tissues are enumerated briefly in the following paragraphs.

Tracheids and sieve cells.—In coniferous stems, tracheids and sieve cells are the conductive tissues in xylem and phloem, respectively. They have many morphological structures in common that distinguish them from the corresponding tissues in the dicotyledons, such as vessels and sieve tubes. From the phylogenetic viewpoint, the tracheids and sieve cells are supposed to be on the same level of evolution. Nevertheless, in the artificial way of comparison, they are different.

The greatest differences are in the nature of the cell walls, strongly cellulosic in the sieve cells as against lignified in the tracheids; and the means for passage of solutes, such as bordered pits as against sieve areas. The approximate average length of sieve cells, as meas-

ured in this study, is comparatively less than that of the corresponding tracheids of the same species. The tendency towards increase in length of late-formed sieve cells, however, seems to parallel the general growth condition of tracheids in wood. The relative volume of sieve cells per area of secondary phloem is less than that of tracheids in xylem.

Xylem rays and phloem rays.—The formation of rays in xylem and phloem is quite similar and related particularly by the universal presence of uniseriate rays. Fusiform rays are present in the xylem and phloem of only a few genera of Pinaceae, such as *Cedrus, Larix, Picea, Pseudotsuga.* The distinct correlation between the differentiations of ray tracheids and albuminous cells has been studied by many botanists, as mentioned previously in this report. One interesting point should be mentioned here. Rather abundant albuminous cells occur in all the barks of the typical Pinaceae studied, including *Abies*, which rarely has ray tracheids. The relative height and number of cells in a uniseriate ray are very alike in the xylem and phloem, although often the cells are higher and more cells are differentiated in a phloem ray.

The structure of phloem ray cell walls is very similar in the different species. The walls have no special thickenings nor distinct pits. Their chemical content is usually abundant, but no definite crystal formation is reported in the xylem rays of the wood of *Abies, Cedrus, Ketelceria, Picea,* and *Pseudolarix.* The dilation of rays in the phloem, especially the manner in which it occurs in the barks of Pinaceae, is seldom or very inconspicuously found in the secondary xylem.

Phloem parenchyma and xylem parenchyma.—Parenchyma has not been reported in the secondary xylem of *Picea, Pinus, Torreya,* and *Taxus.* Phloem parenchyma strands, however, were well developed in all the 15 genera studied. The usually regularly alined parenchyma in the bark of Taxodioideae, Taxaceae, and Cupressoideae seems correlated to the trend in some woods of Taxodioideae and Cupressoideae towards discontinuous zonate formation of xylem parenchyma. Phloem parenchyma differs from xylem parenchyma in the different chemical content of the cells and the structure of pits as observed under a microscope. It may be that phloem parenchyma serves in part as conducting tissue, especially in Taxaceae, Taxodioideae, and Cupressoideae.

Phloem parenchyma containing well-defined large crystals was observed in all the typical Pinaceae barks studied, but not in barks of the other three families and subfamilies. Crystals of styloid form were confined to the barks of hard pines and hemlock. Crystals have never been reported in xylem parenchyma of the four families.

Resin passages.—The occurrence of horizontal resin canals is quite similar in xylem and phloem of the genera studied. The presence of vertical resin canals, however, is an entirely different story. No typical vertical resin canals were observed in the secondary phloem of the typical Pinaceae studied, which is the only group with vertical resin canals in the xylem. On the other hand, only Cupressoideae barks had well-differentiated vertical canals in the secondary phloem. The vertical and horizontal resin canals in the coniferous barks studied had the

same kind of thin-walled epithelial cells; but the horizontal resin canals in the barks of Pinaceae can be distinctly separated into two types according to the shape and number of their epithelial cells.

The resin passages in the bark of some species of *Abies*, which are quite different from those in other species, are formed by the enlargement of a single ray cell without further differentiation of border cells. Normal resin canals or definite formed passages are absent in both the phloem and xylem of Taxodioideae, Taxaceae, and *Tsuga*.

Seasonal growth.—Seasonal growth in bark tissues is not so sharply demarcated as in xylem, although Huber (*23*, *25*) and Holdheide (*21*, *22*) often found definite annual rings in the coniferous barks. In the barks of Pinaceae, there are distinctly crushed tangential lines approximately between two parenchyma lines that could be presumed to be the demarcation of seasonal growth. The author rather hesitates to confirm this, however, without checking fresh material collected from the same trees in successive seasons. At any rate, theoretically, there must be a corresponding growth layer in phloem as well as in xylem.

Inner bark and outer bark.—Transformation from inner to outer bark seems comparable to heartwood formation. The main difference in bark is that the outer bark formation is primarily forced by the development of periderm, which cuts off the physiological connection from the inner bark. In this respect, there is no comparison with heartwood and sapwood. Besides, there is no conspicuous enlargement of cells or change in their shape in the heartwood.

Sclerenchyma.— Sclerenchyma cells occur in the secondary phloem of all coniferous barks except those of the pines, but not in the secondary xylem of any conifers.

Relation of Bark Structure to Other Research

In considering the properties and utilization of barks or in other research on bark, the following fundamental differences between bark and wood should be kept in mind, in addition to knowledge of their structures.

(1) Most bark tissues serve different physiological functions than the tissues in wood, and, therefore, their cell walls and chemical contents are quite different.

(2) Transformation of bark due to growth is complicated. Only a limited narrow zone in the inner bark is the actual physiological functioning tissue, and its duration is variable in different genera or species. The outer bark comes from the old inner bark as well as from the periderm, which also has the ability of differentiation. The rhytidomes of the outer bark may persist or become exfoliating very quickly. In any case, the outermost part of bark is subject to more environmental changes than the inner part. The structural transitions from cambium to the outermost layer of attached bark are more complicated than those from sapwood to heartwood.

(3) Mechanically, bark serves as a protective layer for a tree rather than to support it. The suberized and "lignified" tissues are usually mingled with very delicate and deforming tissues. In evaluating data on the physical properties and strength of a bark, or any specified tissue in bark, the interpretation should be modified from that applied to wood.

Bearing these facts in mind, a few considerations regarding bark in the field of forest products will be mentioned. These considerations relate primarily to the structure of bark.

Bark structure, in general, is a natural design for insulation board. Since most parts of bark serve for protection of the tree, the manner of cell arrangement, the nature of the cell walls, and the cell contents can serve as a guide for the composition of insulating constructions. This does not mean that bark is necessarily the best material for making insulation board, although the bark periderm is suitable for this purpose. Rather, a comparative survey of barks grown in different altitudes and different climates will certainly give us some hints for insulating material from their natural design. Stickel's report (*51*) on the relation of thermal conductivity and thickness of bark may be of interest in this respect.

Utilization of cork from coniferous bark does not seem practical because the quantity of cork obtainable is small, so far as is known. A search for coniferous species that would yield a considerable amount of periderm, the source of cork, should be limited to those in Pinaceae, subfamily Abietoideae. It is well known that natural cork is comparably more abundant in the barks of *Abies* and *Pseudotsuga* than in other genera. Periderm in Taxaceae, Taxodioideae, and Cupressoideae (except some species of *Chamaecyparis*) is too thin even to be detached.

For pulp making, the main drawbacks of bark are its heterogeneous composition and deformed tissue elements, and the colored substances present. Although the secondary phloem of pines has no sclerenchyma, the periderm often contains thick-walled, "lignified" phellem cells. The heterogeneous nature of bark pulp, which has been called multifibrous by Crossley (*8*), may make it comparable to hardwood pulp in general. Structurally, the difference between pulps made from coniferous barks and woods is likely to be greater than the difference between pulps made from hardwood barks and woods. For direct use of bark tissues in pulp making, if coniferous barks with long fibers and rather uniform cell length are desired, the barks of Taxodioideae and Cupressoideae are better than those of Abietoideae and Taxaceae. Bark of *Abies* species is perhaps least suitable because it contains abundant branched, short, brittle sclereids and short sieve cells. To eliminate trouble from such complicated structures, making modified board or such products as "dissolving pulp" from the bark might be considered.

There is very limited reference in the literature to fundamental study on the cell wall structure of matured bark tissues as compared with the voluminous contributions on tracheids, vessel elements, and xylem fibers. The presence of secondary walls in sieve cells in Pinaceae is known, and Preston (*44*) and others have reported some fine structure of random types of phloem cells. The phenomenon of conspicuous transformation of secondary phloem tissues and the universal "lignification" of tissues in the outer bark are also of considerable interest.

Although there are a number of publications on physiology, pharmacognosy, and pure chemistry concerning barks, the field of bark chemistry is just opening. Reviews in this field have been prepared by Hardwood and Purves (*20*), Kurth (*32*), and Segall and Purves

(*46*). One point should be emphasized with respect to the structure of bark and bark chemistry. Since bark structure is very heterogeneous in nature and the transformation resulting from growth is complicated, chemical analysis of bark constituents should be referred to specified parts or tissues. Unfortunately, most of the published data on bark analysis are based upon the whole bark.

Besides the well-known bark tannin, which is still one of the important sources of natural tannin, mention of other products derived from barks through extraction, hydrolysis, distillation, or other processes is increasing in the literature. Interest in obtaining insulation and plastic materials and antibiotic substances from barks is growing.

The basic physical properties of barks have not yet been systematically studied. Important properties such as shrinkage and specific gravity values for different kinds of bark should be explored because they are closely related to the structure of barks. Kapur (*30*) has reported that tree barks behave similarly to wood with regard to sorption of water vapor.

Debarking is a problem of the wood-using industry, especially in pulp making. Fobes (*13*, *14*) and others have reported on development of bark peeling machines and methods. Peeling bark from the standing trees by the application of chemicals such as sodium arsenite is another significant approach to the problem. Important contributions in this field have been reported by Cook (*7*), Hale (*18*), McIntosh (*36*), and others. Popp (*43*) and Huber (*24*) have also reported the peelability of some timber trees with some considerations of their bark structure. So far, however, no special correlation between bark structure and bark peelability has been established.

Much is still unknown about bark structure, and many important barks have not been studied. Purely anatomical study of barks should be intensified. In addition to the comparative study of mature barks, developmental and physiological investigations would supply more basic knowledge.

The study of tree growth would be more reliable if it were based upon the facts from both wood and bark rather than from any part alone. In this respect, phloem growth might be more important than that of xylem. Checking the seasonal growth rings is one of the common methods applied in this field, however, and in bark the demarcation of growth rings is usually not well defined. If this problem could be solved, investigation of bark growth would be especially helpful in studying tree growth of those softwoods which often have indistinct growth rings in the wood, such as *Cupressus*, *Juniperus*, and *Libocedrus*. Comparison of the relative vigor of tree growth based upon general observation of the bark surface of standing trees has been reported by Guttenberg (*17*). Thorough information should be obtained by extending his study to an anatomical basis.

In conclusion, knowledge of bark is too meager and needs systematic studies on every basic phase. Where the integrated utilization of timber is sought, it would be wise to take advantage of those characteristics and properties of barks that are different from or "superior" to those of wood, rather than trying to force bark to be useful by applying the same pattern as that applied to wood. The usefulness of bark depends upon how we evaluate it and how far our knowledge applies to it.

SUMMARY

This study, which was a 1951–52 project of the U. S. Forest Products Laboratory, dealt with the comparative anatomy of North American coniferous barks. Its general objectives were essentially the following: (1) To determine the basic anatomical structure of all tissues outside the cambium of matured barks; (2) to evaluate the features of bark structure of diagnostic value and other related findings from bark as means for identification of species; and (3) to induce the viewpoints that would correlate bark structure to related research in the field of forest products.

Material used for this study included old specimens from the collection of the U. S. Forest Products Laboratory and fresh material cut at breast height and from young branches on the same trees and sent to the Laboratory by various Forest Experiment Stations of the U. S. Forest Service. All together, 57 timber species distributed in 15 genera of North American conifers were examined. Permanent slides of sections and macerated material from the representative species were prepared. To obtain better observations, an attempt was made to cut the brittle barks into thin series sections. Sections of fresh material were also prepared for checking cell walls and cell contents. Important structural features and patterns of tissues arrangements were recorded on photomicrographs.

Using the modern accepted terms in plant anatomy and the universally adopted pattern of describing wood structure, full descriptions of bark of representative species in each genus are given in this bulletin. Supplementary summaries of the characteristics and differences among the important species in each genus follow each description.

The comparison table and artificial keys to families and genera presented in this bulletin are based upon both the gross features and the microscopic structures of diagnostic value. Recognizing the limitations of bark identification by structure alone, the author briefly reports supplementary random preliminary chemical tests, especially the coloration of bark extracts.

The significances of various tissues and the characteristics of bark in each genus of North American conifers are discussed. In general, their family and generic characteristics are quite distinct, constant, and rather naturally classified according to the suggested scheme. Somewhat overlapping diagnostic features are encountered only in the barks of Cupressoideae.

The important structural correlations of wood and bark are summarized, primarily on the basis of comparisons between secondary xylem and secondary phloem of the conifers studied.

The relation of bark structure to other research problems in the field of forest products is briefly discussed. Some general suggestions are offered in regard to bark utilization and desirable chemical, physical, and pure anatomical studies.

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