Comparative wood anatomy of some shrubwoods native to the northern Rocky Mountains

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COMPARATIVE WOOD ANATOMY OF SOME SHRUBWOODS NATIVE TO THE NORTHERN ROCKY MOUNTAINS

By

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Introduction

The goal of the present study was the formulation of a key for identification of the shrubby plants native to the Northern Rocky Mountains. This key supplements those already in existence which are based on plant organs: flowers, leaves, fruits and other macroscopic characters. In contrast, the characters upon which this key is based are those of the wood, or technically, the xylem. Such a key seemed necessary for several reasons: (1) to identify the remains of plants left after fires, (2) to substantiate identifications made by means of the ordinary keys of plants which, because of some environmental factor such as shade, do not exhibit typical gross morphology, and (3) to aid in the identification of plants when flower, leaves, and fruits are not available.

Fifty-five species, representing thirty-five genera, have been incorporated in this key. No attempt has been made to arrange the species in their usual taxonomic groupings. Where certain characters were held in common by all genera of a family, such an arrangement occurs; where such characters were not, the arrangement does not. Where characters permitted, identification is to the species level. In some cases, identification is to the genus level while in others, as in Rosaceae, the key terminates in a group of possible genera. On the basis of present knowledge, such seeming incompleteness of identification is unavoidable.
Literature Review

A review of the literature concerning wood anatomy indicates a change in emphasis has occurred within the past twenty years. This change has been from a heavy reliance on quantitative data in distinguishing among woods to the use of qualitative characters. This change has been caused by increased understanding of the extent and causes of variations within a species. No longer is it assumed that a single specimen accurately represents a species. Some authors, such as Panshin (13) fail to stress this new perspective in wood anatomy; others, such as Jane (9) emphasize it. While making the formulation of a key more time-consuming, knowledge of wood variability increases the probability of the key's accuracy.

Previous studies in comparative wood anatomy have dealt with either a varied assemblage of commercial timbers or a small taxonomic group, such as a genus or family. Keys based on wood anatomy have been in existence for many years for those trees which are common sources of timber (13,14). Such keys have utilized macroscopic and microscopic characters in addition to taste, odor, touch, and other traits. Some authors have published simultaneously a pair of keys, one based entirely on microscopic characters, and the other based on characters which can be noted with a hand lens and on color, taste, odor, and feel (13).

The investigations of small taxonomic groups are comparisons of several of their species. They are attempts to study in a de-
tailed fashion the group's variability in wood characters. Whereas the studies of timbers have as their end the identification of unknown woods, studies of small taxonomic groups have as their goal the understanding of the inter-relationships of the species. Consequently, these latter studies take the form of synopses rather than keys. Distinguishing characters are limited to microscopic ones. Carlquist, in his study of the Heliantheae, selected the following characteristics as being diagnostic: vessel diameter, vessel element length, number of vessels per group, helical striae on vessels, vessel pitting, vascular tracheids, apotracheal parenchyma, storied elements, ray cell wall thickness, ray height, and ray composition. Other characters, though studied, failed to distinguish among the species. In expressing averages for quantitative data, Carlquist presents figures in p (1). Chattaway, among others, advocates the use of size classes rather than strict numerical distinctions; these size classes may be based on either the average or the maximum size (2). The basic interest of these investigators is phylogeny rather than identification.

A key may function for identification, for description, or for both these purposes. In an artificial key, no attempt is made to follow natural or phylogenetic groupings. Such a key is designed for identification purposes only. At each step in the key, a single, easily observable trait is employed. The trait chosen may not necessarily be the most important or consistent difference between the two groups. In contrast, in a synoptic or natural key,
species are aligned in their normal taxonomic order. Each step in the key summarizes the characteristics for the group of species which follows. The characteristics enumerated, which may or may not be easily apparent, are those judged to be the accurate distinctions between the groups. The artificial key provides a means of identifying an unknown, disregarding its genetic relationships to other plants; the natural key, while allowing identification of unknowns, strives to illustrate phylogenetic relationships among the species (7). Most keys, as the one presented here, are not strictly one or the other; they are a compromise.

Methods and Materials

Specimens were collected for over sixty species of shrubs. Because they were represented by only one specimen, several of these species were rejected from consideration in this study; others were rejected because the specimens collected were only one year of age. While some species were represented by as many as five specimens, the typical number was two. Most of the collections and all of the identifications were made by Mr. Peter F. Stickney, Associate Plant Ecologist, Intermountain Forest and Range Experiment Station, U. S. Forest Service. Western Montana

*Identifications were made by means of the following:
Hitchcock, C.L., A. Cronquist, M. Owenby, and J. W. Thompson.

and northern Idaho were the sites of the collections. Ultimately fifty-five species were selected for inclusion in the key.

The paraffin-embedding method was employed in preparing the microscopic slides from the specimens. Small pie-shaped pieces were cut from the specimens, aspirated, dehydrated through a tertiary butyl alcohol series, and embedded in Paraplast. The embedded specimens were sectioned at thicknesses of from six to twenty μ on a rotary microtome; for most of the material a thickness of eight or ten μ was optimum. The paraffin ribbons were affixed to slides with Haupt's adhesive. After removal of the paraffin by xylene, the sections were run through an ethyl alcohol series into water, stained by means of the Fuelgen reaction, dehydrated in a second alcohol series, and counter-stained with fast green. They were mounted in Harleco's Synthetic Resin. From a minimum of two specimens for each species, cross, radial, and tangential sections were cut.

The key was first outlined from photomicrographs of the sections and then checked with the slides and with published accounts of wood anatomy. Since in many cases the original photographs did not show the characters sought, the slides for each species had to be examined several times. Each character used to distinguish a species was checked in all specimens representing that species. The characters used to distinguish among the species are not in all cases the same; vessel distribution, perforation plates, rays, and axial parenchyma are the characters most often utilized. Where information about wood anatomy for a
species was available, it was consulted as a check against the specimens used in this study. These accounts, with few exceptions, confirmed the conclusions outlined. In a number of cases, particularly in the Rosaceae, no reliable separation could be obtained with the information available.

Results

There are few characters which are common to all genera of a family, and fewer still, if any, that are limited to a single family. Although one type may be found in most of its species, each family has a considerable range in any particular character. For example, rays of one to two cells in width are most commonly found in species of the Rosaceae, but some of its species also have rays of three to many cells in width. Of the families studied here, none possessed an exclusive trait. What distinguishes a family is not a single unique trait but a combination of traits. Because of the wide variety in characters found within the family, enumeration of its typical traits is often difficult. The species of a family may be united by floral organs, but their wood anatomy provides little unity.

The information gained in this study is presented in three forms: (1) photographs, (2) an artificial key, and (3) synopses for all species. A number has been assigned to each species which is used in all three presentations. For example, D16 refers in photographs, key and synopsis to Rosa gymnocarpa. The letter prefix indicates the family in which the species is placed; family D is Rosaceae. The photographs and synopses are arranged in numer-
ical sequence. One to four photographs are given for each species and have letter suffixes of a, b, c, and d to distinguish them. The characters listed in the synopses are only those which are actually used as key characters. A glossary and diagrams of the more pertinent characters are included. The terms vessel, tracheid and fiber are used in the general sense as delimited by Esau (5). Also given are a list of the families involved in the study, with their letter designations, and an alphabetical listing of the species.
KEY TO SOME SHRUBWOODS NATIVE TO THE NORTHERN ROCKY MOUNTAINS

1 Vessels present.................................3
1 Vessels not present..............................2
   2 Tracheids with spiral thickenings...Taxus brevifolia (A 1 ab)
   2 Tracheids without spiral thickenings....................................Juniperus spp. (B 2 a, B 3 a)
3 Rays 3 to many cells in width, often massive, dispersed between uniseriate rays.........................4
3 Rays 1 or 2 cells in width (rarely 3)..17
4 Vessels grouped in patterns forming radial or concentric bands or arcs..5
4 Vessels predominantly solitary or in pairs, except for initial vessels of growing season which may be contiguous.................................8
5 Vessel bands radial..................................Prunus spp. (D 12 ab, D 13 ab)
5 Vessel bands concentric or vessels forming arcs..................................6
6 Band of cork tissue initiating each growth ring..................................Artemisia tridentata (C 4 ab)
6 Band of cork not present as above...7
7 Vessels in concentric bands, alternating with bands of tracheids and fibers...Chrysothamnus nauseosus (C 5 ab)
7 Vessels in slight arcs rather than in concentric bands..................................Chrysothamnus viscidiflorus (C 6 ab)
8 Perforation plates simple ..........9
8 Perforation plates scalariform ......11

9 Growth ring distinct; vessels decreasing in size from early to late wood;
   vessels relatively numerous ..........10

9 Growth ring indistinct; vessels not
   changing in size or spacing from
   early to late wood; vessels rela-
   tively few and far apart ............ Holodiscus discolor
   (D 10 ab) or Rubus sp.
   (D 17 ab, D 18 ab, D 19 ab)

10 Vessels markedly larger in early
   than in late wood .................. Rosa woodsii (D 16 ab)

10 Vessels not markedly larger in
   early than in late wood ............ Rosa gymnocarpa (D 15 ab)

11 Tracheids and fibers alternating in
   radial bands ...................... Philadelphus lewisii (E 22 ab)

11 Tracheids not alternating with
   fibers as above ....................12

12 Vessels forming complete or short
   concentric bands within growth
   ring, usually 1 vessel in width ...13

12 Vessels not forming such bands,
   instead being more in diagonal
   bands or diffuse ..................14
13 Bands complete; vessels of successive bands in any one growth ring are of similar size. \textit{Ribes aureum} (E 23 ab)

13 Bands tending to be interrupted not forming complete bands; vessels of successive bands in any one growth not similar in size; the initial vessels usually are markedly larger than succeeding ones. \textit{Ribes cereum} (E 24 ab)

14 Vessels mostly solitary with some small clusters of vessels; these vessels or clusters are randomly dispersed, with no clear pattern evident. \textit{Ribes} 15

14 Vessels arranged in diagonal bands or arcs with a few short, tangential bands. \textit{Ribes lacustre} (E 27 abc)

15 Growth ring initiated with a band of larger vessels; the vessels become progressively smaller through the growing season; vessels relatively few. \textit{Ribes lacustre} (E 27 abc)
15 Growth ring not initiated with a band of larger vessels although the vessels of the last-formed wood are noticeably smaller than the initial vessels, making the growth rings discernible......Ribes hudsonianum (E 25 ab)

16 Vessels forming a zig-zag pattern, radially aligned......................Ribes viscosissimum (E 29 ab)

16 Vessels may be diagonally aligned, in short tangential bands, and/or diffuse, with none of these found exclusively; there is not the regularity of alternating diagonal bands as in the above......................Ribes irriguum (E 26 abc) or Ribes setosum (E 28 ab)

17 Vessels commonly in radial multiples; often spring wood vessels are closely spaced singles or in irregular clusters (some appearing as subdivisions of a single vessel), the vessels progressing toward formation of radial multiples from early to late wood......18

17 Vessels solitary, in pairs, or in various aggregates, including sometimes radial vessel chains but not vessel multiples.......................24
18 Perforation plates simple
19 Rays composed of procumbent cells only
19 Rays composed of both procumbent and upright cells
20 Vessels with spiral thickenings; rays mainly uniseriate but some 2 to 4 cells wide
20 Vessels without spiral thickenings; rays uniseriate only
21 Rays 1 cell in width
21 Rays 2 to 4 cells in width
22 Rays uniseriate only
22 Rays both 1 and 2 cells in width
23 Axial parenchyma forming tangential bands at short intervals between rays
23 Axial parenchyma sparse and diffuse
24 Vessel perforation plates scalariform
24 Vessel perforation plates simple
25 Vessels regular in size and spacing throughout growth ring

Acer glabrum (F 30 abcd)
Populus spp. (G 31 ab G 32 ab)
Salix scouleriana (G 33 abc)
Sambucus spp. (M 51 ab M 52 ab)
Betula spp. (H 36 ab H 37 ab)
Alnus incana (H 34 ab)
Alnus sinuata (H 35 abc)
Cornus stolonifera (I 38 abc)
25 Vessels not regular in size or spacing as above........................26
26 Rays 1 to several cells wide..............Vaccinium spp. (J 42 ab
J 43 ab)
26 Rays uniseriate only.....................27
27 Growth ring initiated by a single row of large, closely spaced vessels.............................Menziesia ferruginea (J 41 abc)
27 Growth ring not initiated as above; no clear line of large vessels.............Ledum glandulosa (J 40 ab)
28 Annual ring initiated by a definite band of large vessels; other vessels are much smaller and sparse, giving a two-banded appearance to the growth ring........29
28 Annual ring not initiated by band of large vessels as above; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size..30
29 Axial parenchyma numerous, paratracheal and diffuse, often encircling the larger vessels.................................Symphoricarpos albus (M 53 ab)
29 Axial parenchyma few, if in contact with a vessel, a single cell rather than an encircling band. Arctostaphylos uva-ursi (J 39 abc)

30 Axial parenchyma predominantly paratracheal.

30 Axial parenchyma predominantly terminal or diffuse.

31 Axial parenchyma distributed as 2 to several cells on the periphery of each vessel group; vessels solitary or in clusters of a few cells in the early wood progressing to radial files which are grouped secondarily to form tangential bands in the late wood. Rhus glabra (K 44 ab)

31 Axial parenchyma distributed as an occasional single cell adjacent to a vessel; vessels diffuse, not grouped as above. Pachistima myrisinites (O 55 ab)

32 Axial parenchyma predominantly terminal.

32 Axial parenchyma predominantly diffuse or absent.
33 Vessels decreasing gradually in size from early to late wood; vessels smooth in outline, solitary or in occasional pairs. *Physocarpus malvaceus* (D 11 ab)

33 Vessels not decreasing gradually in size as above; vessels angular in outline. 34

34 Vessels arranged in diagonal and/or radial lines. *Rhamnus alnifolia* (L 47 ab)

34 Vessels solitary or in occasional multiples of a few cells. *Rhamnus purshiana* (L 48 abc)

35 Vessels occurring in patterns of radially aligned S curves in mature wood; tannins occurring in even the young ray parenchyma. *Ceanothus* spp. (L 45 ab L 46 ab)

35 Vessels not in patterns as described above; tannins, if present, occurring in ray parenchyma only in the more mature cells. 36

36 Axial parenchyma numerous. 37

36 Axial parenchyma absent or sparse. 39

37 Vessel walls composed of five or six facets, giving the vessel a definitely angular appearance. 38
Vessel walls, although composed of several facets, giving a smoother, more rounded outline than above............... **Amelanchier alnifolia** (D 7 abc)

Vessels tending to form concentric bands within the growth ring; vessels relatively few and large....................... **Shepherdia canadensis** (N 514 ab)

Vessels diffuse in distribution with no particular alignment; vessels relatively small and numerous...................... **Crataegus douglasii** (D 9 ab)

Spring wood vessels large, numerous and solitary (although closely spaced); vessels of late wood not greatly smaller than those of early wood, but much more widely spaced; vessels markedly angular, with concave facets......................... **Sorbus scopulina** (D 20 ab)

Spring wood vessels not as above; if vessel spacing is as above, then vessels are rounded, with convex facets; if vessel shape is as above, then spacing differs...........
Early wood with a few large vessels; vessel size decreases greatly from early to late wood, but spacing of vessels remains similar. \textit{Cercocarpus ledifolius} (D 8 ab)

Early wood may have a few large vessels, but, if so, then the vessel size and spacing differ from the above. \textit{Spiraea betulifolia} (D 21 ab)

Axial parenchyma absent. \textit{Spiraea betulifolia} (D 21 ab)

Axial parenchyma present although few in number. \textit{Purshia tridentata} (D 14 ab)

Vessels angular in outline. \textit{Purshia tridentata} (D 14 ab)

Vessels rounded in outline. \textit{Purshia tridentata} (D 14 ab)

Ray cells squared in outline in cross section. \textit{Lonicera involucrata} (M 49 abc)

Ray cells radially elongated in cross sections. \textit{Lonicera involucrata} (M 49 abc)
LEGEND FOR PLATES

All photographs are of cross sections unless otherwise noted:

* = radial

** = tangential

PLATE I

Ala  Taxus brevifolia
Alb*  

B2a  Juniperus communis
B3a  scopulorum

Clia  Artemisia tridentata
Clib  


PLATE II

05a  Chrysothamnus nauseosus
05b  "    "
06a  Chrysothamnus viscidiflorus
06b  "    "
PLATE III

D7a Amelanchier alnifolia
D7b " "
D7c* " "
D8a Cercocarpus ledifolius
D8b " "
PLATE IV

D9a  Crataegus douglasii
D9b   "   "
D10a Holodiscus discolor
D10b   "   "
PLATE V

D11a  Physocarpus malvaceus
D11b
D12a  Prunus emarginata
D12b
D12c#
PLATE VI

D13a  **Prunus virginiana**
D13b  "  "
D14a  **Purshia tridentata**
D14b  "  "
PLATE VII

D15a  

Rosa gymnocarpa

D15b  

D16a  

Rosa woodsii

D16b  


PLATE VIII

D17a  Rubus idaeus
D17b  "    "
D17c** "    "
D18a  Rubus leucodermis
D18b  "    "
PLATE IX

D19a Rubus parviflorus
D19b " "
D20a Sorbus scopulina
D20b " "

PLATE X

D21a  *Spiraea betulifolia*
D21b  
E22a  *Philadelphus lewisii*
E22b  

PLATE XI

E23a  Ribes aureum
E23b  "  "
E24a  Ribes cereum
E24b  "  "
PLATE XII

E25a  Ribes hudsonianum
E25b  "    "
E26a  Ribes irriguum
E26b  "    "
PLATE XIII

E27a  Ribes lacustre
E27b  "  "
E28a  Ribes setosum
E28b  "  "

PLATE XIV

E29a Ribes viscosissimum
E29b " "
E26c* " irriguum
E27c** " lacustre
PLATE XV

F30a  Acer glabrum
F30b  
F30c  
F30d  

PLATE XVI

G31a  *Populus tremuloides*

G31b  

G32a  *trichocarpa*

G32b  


PLATE XVII

G33a  Salix scouleriana
G33b  "    "
G33c* "    "
G32c* Populus trichocarpa
PLATE XIX

H36a  *Betula glandulosa*

H36b  "  "

H37a  "  *occidentalis*

H37b  "  "
PLATE XX

I38a  Cornus stolonifera
I38b
I38c
H35c  Alnus sinuata
PLATE XXI

J39a  Arctostaphylos uva-ursi
J39b  "    "
J39c* "    "
J40a  Ledum glandulosum
J40b  "    "
PLATE XXII

J41a Menziesia ferruginea
J41b  
J41c*  
J42a Vaccinium membranaceum
J42b  

PLATE XXIII

\( J_{43a} \) Vaccinium scoparium

\( J_{43b} \) " "

\( J_{43c} \) " "

\( Kl_{4a} \) Rhus glabra

\( Kl_{4b} \) " "

PLATE XXIV

145a Ceanothus sanuineus

145b " "

146a Ceanothus velutinus

146b " "
PLATE XXV

L47a  Rhamnus alnifolia
L47b  "   "
L48a  Rhamnus purshiana
L48b  "   "
L48c* "   "
PLATE XXVI

M49a  Lonicera involucrata
M49b  "    "
M49c* "    "
M50a  "    utahensis
M50b  "    "
<table>
<thead>
<tr>
<th>M51a</th>
<th>Sambucus caerulea</th>
</tr>
</thead>
<tbody>
<tr>
<td>M51b</td>
<td>&quot;</td>
</tr>
<tr>
<td>M52a</td>
<td>&quot; racemosa</td>
</tr>
<tr>
<td>M52b</td>
<td>&quot;</td>
</tr>
</tbody>
</table>
PLATE XXVIII

M53a  Symphoriocarpos albus
M53b   "     
M52c*  Sambucus racemosa
M52d** "     

PLATE XXIX

NS4a  Shepherdia canadensis
NS4b  "  "
O55a  Pachistima myrsinotes
PLATE XXX. A, (a) procumbent rays cells in radial view. (b) Upright ray cells in radial view. B, (a)简单 perforation plate. (b) scalariform perforation plate. C, (a) procumbent ray cells in tangential view. (b) Upright ray cells in tangential view. D, (a) cross or transverse view. (b) radial view. E, xylem elements as seen in cross view. (a) vessel. (b) axial parenchyma. (c) ray parenchyma. (d) tracheid. (e) fiber.
SYNOPSES

**Taxus brevifolia**

A1  vessels absent; tracheids with spiral thickenings.

**Juniperus communis B2 and Juniperus scopulorum B3**

vessels absent; tracheids without spiral thickenings.

**Artemisia tridentata**

C4  vessels present, grouped in patterns forming concentric bands; rays three to many cells in width, often massive, dispersed between uniseriate rays; band of cork tissue initiating each growth ring.

**Chrysothamnus nauseosus**

C5  vessels present, grouped in patterns forming concentric bands; rays three to many cells in width, often massive, dispersed between uniseriate rays.

**Chrysothamnus viscidiflorus**

C6  vessels present, grouped in patterns forming slight arcs; rays three to many cells in width, often massive, dispersed between uniseriate rays.
Amelanchier alnifolia

D7 vessels present, solitary or in pairs; annual ring not initiated by band of large vessels; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessel walls giving a smooth, rounded outline to vessel in cross section; vessel perforation plate simple; axial parenchyma numerous, diffuse; rays one to two cells in width (rarely three).

Cercocarpus ledifolius

D8 vessels present, solitary, in pairs or various aggregates; annual ring not initiated by a band of large vessels; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; early wood with a few large vessels; vessel size decreases greatly from early to late wood, but spacing of vessels remains similar; perforation plate simple; axial parenchyma absent or sparse and diffuse; rays one or two cells in width (rarely three).

Crataegus douglasii

D9 vessels present, diffuse in distribution with no particular alignment; vessels relatively small and numerous; vessel walls composed of five or six facets, giving the vessel a definitely angular appearance; vessels grade into smaller sizes as the growing season progresses
Crataegus douglasii (Cont.)
D9 without an abrupt change in size; vessels solitary or in pairs, or in various aggregates; vessel perforation plates simple; axial parenchyma absent or sparse, diffuse; rays one or two cells in width (rarely three).

Holodiscus discolor
D10 vessels present; vessels predominantly solitary or in pairs, except for initial vessels which may be contiguous; growth ring indistinct; vessels not changing in size or spacing from early to late wood; vessels relatively few and far apart; perforation plates simple; rays three to many cells in width, often massive, dispersed between uniseriate rays.

Physocarpus malvaceus
D11 vessels present; vessels decreasing gradually in size from early to late wood; vessels smooth in outline, solitary or in occasional pairs; vessel perforation plates simple; axial parenchyma predominantly diffuse or absent; rays one or two cells in width (rarely three).

Prunus emarginata D12 and Prunus virginiana D13 vessels present; vessels grouped in radial bands; rays three to many cells in width, dispersed between uniseriate rays.
Purshia tridentata

D14 vessels present; vessels rounded in outline; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessels solitary, in pairs, or in various aggregates; perforation plates simple; axial parenchyma present although few in number, diffuse; rays one or two cells in width (rarely three).

Rosa gymnocarpa

D15 vessels present; vessels not markedly larger in early than in late wood; growth ring distinct; vessels decreasing in size from early to late wood; vessels relatively numerous; vessels predominantly solitary or in pairs, except for initial vessels which may be contiguous; perforation plates simple; rays three to many cells in width, dispersed between uniseriate rays.

Rosa woodsii

D16 vessels present; vessels markedly larger in early than in late wood; growth ring distinct; vessels decreasing in size from early to late wood; vessels relatively numerous; vessels predominantly solitary or in pairs, except for initial vessels which may be contiguous; perforation plates simple; rays three to many cells in width, dispersed between uniseriate rays.
Rubus idaeus D17, Rubus leucodermis D18, and Rubus parviflorus D19 vessels present; vessels predominantly solitary or in pairs, except for initial vessels which may be contiguous; growth ring indistinct; vessels not changing in size or spacing from early to late wood; vessels relatively few and far apart; perforation plates simple; rays three to many cells in width, dispersed between uniseriate rays.

Sorbus scopulina

vessels present; spring wood vessels large, numerous and solitary (although closely spaced); vessels of late wood not greatly smaller than those of early wood, but much more widely spaced; vessels markedly angular, with concave facets; perforation plate simple; axial parenchyma absent or sparse and diffuse; rays one or two cells in width (rarely three).

Spiraea betulifolia

vessels present; vessels grade into smaller sizes as the growing season progresses; without an abrupt change in size; vessels solitary, in pairs, or in various aggregates; perforation plates simple; axial parenchyma absent; rays one or two cells in width (rarely three).
Philadelphus lewisi

E22 vessels present; vessels predominantly solitary or in pairs, except for initial vessels which may be contiguous; perforation plates scalariform; rays three to many cells in width, often massive, dispersed between uniseriate rays; tracheids and fibers alternating in radial bands.

Ribes aureum

E23 vessels present; vessels forming complete concentric bands within the growth ring, usually one vessel in width, vessels of successive bands in any one growth ring are of similar size; vessels predominantly solitary or in pairs, except for initial vessels which may be contiguous; perforation plates scalariform; rays three to many cells in width, often massive, dispersed between uniseriate rays.

Ribes cereum

E24 vessels present; vessels forming interrupted concentric bands within the growth ring, usually 1 vessel in width; vessels of successive bands in any one growth ring not similar in size; the initial vessels are usually markedly larger than succeeding ones; vessels predominantly solitary or in pairs, except for initial vessels which may be contiguous; perforation plates scalariform; rays three to many cells in width; often massive, dispersed between uniseriate rays.
Ribes hudsonianum

E25 vessels present; vessels mostly solitary with some small clusters of vessels; these vessels or clusters are randomly dispersed with no clear pattern evident; growth ring not initiated with a band of larger vessels although the vessels of the last-formed wood are noticeably smaller than the initial vessels, making the growth rings discernible; perforation plates scalariform; rays three to many cells in width, often massive, dispersed between uniseriate rays.

Ribes irriguum E26 and Ribes setosum E28

vessels present; vessels may be diagonally aligned, in short tangential bands, and/or diffuse, with none of these found exclusively; perforation plate scalariform; rays three to many cells in width, often massive, dispersed between uniseriate rays.

Ribes lacustre

E27 vessels present; growth ring initiated with a band of larger vessels; the vessels become progressively smaller through the growing season; vessels relatively few; vessels predominantly solitary, in pairs, or in various aggregates; perforation plate scalariform; rays three to many cells in width, often massive, dispersed between uniseriate rays.
Ribes viscosissimum

E29 vessels present; vessels predominantly solitary, in pairs, or in various aggregates; vessels forming a zig-zag pattern, radially aligned; perforation plates scalariform; rays three to many cells in width, often massive, dispersed between uniseriate rays.

Acer glabrum

F30 vessels present; vessels commonly in radial multiples; often spring wood vessels are closely spaced singles or in irregular clusters (some appearing as subdivisions of a single vessel), the vessels progressing toward formation of radial multiples from early to late wood; vessels with spiral thickenings; perforation plates simple; rays composed of procumbent cells only; rays mainly uniseriate but some two to four cells wide.

Populus tremuloides G31 and Populus tricocarpa G32

vessels present; vessels commonly in radial multiples; often spring wood vessels are closely spaced singles or in irregular clusters (some appearing as subdivisions of a single vessel), the vessels progressing toward formation of radial multiples from early to late wood; vessels without spiral thickenings; perforation plates simple; rays composed of procumbent cells only; rays uniseriate only.
Salix scouleriana

G33 vessels present; vessels commonly in radial multiples; often spring wood vessels are closely spaced singles or in irregular clusters (some appearing as subdivisions of a single vessel), the vessels progressing toward formation of radial multiples from early to late wood; vessel perforation plates simple; rays composed of both procumbent and upright cells; rays uniseriate only.

Alnus incana

H34 vessels present; vessels commonly in radial multiples; often spring wood vessels are closely spaced singles or in irregular clusters (some appearing as subdivisions of a single vessel), the vessels progressing toward formation of radial multiples from early to late wood; vessel perforation plates scalariform; axial parenchyma forming tangential bands at short intervals between rays; rays uniseriate only.

Alnus sinuata

H35 vessels present; vessels commonly in radial multiples; often spring wood vessels are closely spaced singles or in irregular clusters (some appearing as subdivisions of a single vessel), the vessels progressing toward formation of radial multiples from early to late wood; vessel perforation plates scalariform; axial parenchyma sparse and diffuse; rays uniseriate only.
Betula glandulosa H36 and Betula occidentalis H37

text continues...
**Ledum glandulosa**

$J_{40}$ vessels present; vessels solitary, in pairs, or in various aggregates; vessel perforation plates scalariform; rays uniseriate only.

**Menziesia ferruginea**

$J_{41}$ vessels present; growth ring initiated by a single row of large, closely spaced vessels; vessels solitary, in pairs, or in various aggregates; perforation plate scalariform; rays uniseriate only.

**Vaccinium membranaceum $J_{42}$ and Vaccinium scoparium $J_{43}$**

vessels present; vessels solitary, in pairs, or in various aggregates; perforation plate scalariform; rays one to several cells wide.

**Rhus glabra**

$K_{44}$ vessels present; vessels solitary, in pairs, or in various aggregates; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessels solitary or in clusters of a few cells in the early wood progressing to radial files which are grouped secondarily to form tangential bands in the late wood; perforation plate simple; axial parenchyma distributed as two to several cells on the periphery of each vessel group; rays one or two cells wide (rarely three).
Ceanothus sanguineus \textit{L.f} and Ceanothus velutinus \textit{L.f}

vessels present; vessels solitary, in pairs, or in various aggregates; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessels occurring in patterns of radially aligned S curves in mature wood; perforation plates simple; axial parenchyma predominantly diffuse; rays one or two cells in width (rarely three); tannins occurring in even the young ray cells.

\textbf{Rhamnus alnifolia}

\textit{L.f}

vessels present; vessels solitary, in pairs, or in various aggregates; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessels arranged in diagonal and/or radial lines; vessels angular in outline; perforation plates simple; \textbf{axial} parenchyma predominantly terminal; rays one or two cells in width (rarely three).

\textbf{Rhamnus purshiana}

\textit{L.f}

vessels present; vessels solitary, in pairs, or in various aggregates; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessels solitary or in occasional multiples of a few cells; vessels angular in outline; perforation plates
Rhamnus purshiana (Cont.)

L48 simple; axial parenchyma predominantly terminal rays; one or two cells in width (rarely three).

Lonicera involucrata

M49 vessels present; vessels angular in outline; vessels solitary, in pairs, or in various aggregates; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessel perforation plates simple; axial parenchyma present though sparse and diffuse; rays one or two cells in width (rarely three), ray cells radially elongated in cross sections.

Lonicera utahensis

M50 vessels present; vessels angular in outline; vessels solitary, in pairs, or in various aggregates; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessel perforation plates simple; axial parenchyma present though sparse and diffuse; rays one or two cells in width (rarely three); ray cells squared in outline in cross sections.

Sambucus coerulea M51 and Sambucus racemosa M52

text continues...
Sambucus cœerulea M51 and Sambucus racemosa M52 (Cont.)
a single vessel), the vessels progressing toward formation of radial multiples from early to late wood;
vessel perforation plates simple; rays composed of both procumbent and upright cells; rays two to four cells in width.

Symphoricarpos albus

M53 vessels present; vessels solitary, in pairs, or in various aggregates; annual ring initiated by a definite band of large vessels; other vessels are much smaller and sparse, giving a two-banded appearance to the growth ring; perforation plates simple; axial parenchyma numerous, paratracheal and diffuse, often encircling the larger vessels; rays one or two cells wide (rarely three).

Shepherdia canadensis

M54 vessels present; vessels solitary, in pairs, or in various aggregates; vessels tend to form concentric bands within the growth ring; vessels relatively few and large; vessel walls composed of five or six facets, giving the vessel a definitely angular appearance; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessel perforation plates simple; axial parenchyma absent or sparse, diffuse; rays one or two cells in width (rarely three).
Pachistima myrsinites

055 vessels present; vessels solitary, in pairs, or in various aggregates; vessels grade into smaller sizes as the growing season progresses without an abrupt change in size; vessels diffuse; perforation plate simple; axial parenchyma distributed as an occasional single cell adjacent to a vessel; rays one or two cells wide (rarely three).
Discussion

The limits on time and sampling in this study of fifty-five species made adequate treatment impossible. Investigation of only a small number of characters occurring in woods could be accomplished. Several publications list numerous characters which can be used to describe and distinguish woods. In this study these lists had to be dismissed as impractical for application to all the species to be studied. Only those characters which were essential in separating species were noted. Once a trait had been found to separate groups, no further trait was sought. Continued study of the specimens undoubtedly could have contributed several confirmatory characters at each step in the key. The information presented in this study should not be interpreted as representing reliably the species studied; two specimens are not an adequate basis for generalizations on the species as a whole. Because of the unsatisfactory sampling of the species and the inadequate time allotted for study of the specimens, this key is of doubtful value for identifying unknown plants.

Despite its incompleteness, this study contributes some new information, further extending the knowledge of wood anatomy for the families included. In some cases, the key, outlining the information gained, may allow identification of plants when standard keys cannot be utilized. Also, when tentative identification of a plant has been made from organs, confirmation of identity may be obtained from wood characters. With continued study, wood anatomy will increase in value as a means of identifying plants.
REFERENCES


GLOSSARY

Cell. — A chamber or compartment at some time containing a protoplast; cells form the structural units of plant tissues.

Fibre, Fiber (Am.). — A general term of convenience in wood anatomy for any long, narrow cell of wood or bast other than vessels and parenchyma. Note: Often further qualified as wood fibres or bast fibres; the former including both the tracheids of gymnosperms and the libriform wood fibres and fibre-tracheids of woody angiosperms. Also used loosely for wood elements in general.

Growth layer. — A layer of wood or bark produced apparently during one growing period; frequently, especially in woods of the temperate zones, divisible into early and late wood or bark (IAWA).

Parenchyma. — Tissue composed of cells that are typically brick-shaped or isodiametric and have simple pits; formed in wood from (a) fusiform cambial initials by later transverse divisions of the daughter cells (axial parenchyma), or (b) ray initials (ray or radial parenchyma). Syn. Soft tissue, Storage tissue. See also Parenchyma cell, fusiform. Note: Primarily concerned with the storage and distribution of food materials. Termed wood parenchyma or xylem parenchyma if occurring in the xylem, and phloem parenchyma if in the phloem.

Parenchyma, apotracheal. — Axial parenchyma typically independent of the pores or vessels. Note: This includes Terminal, Diffuse, and Banded apotracheal parenchyma.


Parenchyma, diffuse. — Single apotracheal parenchyma strands or cells distributed irregularly among fibres, as seen in cross section (IAWA modif.).

Parenchyma, paratracheal. — Axial parenchyma associated with the vessels or vascular tracheids (IAWA modif.). Note: This includes Scanty paratracheal, Vasicentric, Aliform and Confluent parenchyma.

1Excerpts from "International Glossary of Terms Used in Wood Anatomy", published by the Committee on Nomenclature International Association of Wood Anatomists (3).
Parenchyma, ray. — Parenchyma composing the rays wholly or in part. (IAWA modif.). Syn. Radial parenchyma.

Parenchyma, terminal. — Apotracheal parenchyma cells occurring either singly or forming a more or less continuous layer of variable width at the close of a season's growth. Note: Before a distinction was made between "terminal" and "initial" parenchyma, this term was used to include both forms and is still used in this sense as a term of convenience.

Perforation, simple. — A single and usually large and more or less rounded opening in the perforation plate, cf. Perforation, multiple (IAWA).

Perforation, vessel. — An opening from one vessel member to another (IAWA).

Perforation plate. — A term of convenience for the area of the wall (originally imperforate) involved in the coalescence of two members of a vessel (IAWA).

Perforation plate, scalariform. — A plate with multiple perforations elongated and parallel. The remnants of the plate between the openings are called Bars (IAWA).

Pit. — A recess in the secondary wall of a cell, together with its external closing membrane; open internally to the lumen. Note: Essential components are the pit cavity and the pit membrane (IAWA modif.).

Pore. — A term of convenience for the cross section of a vessel or of a vascular tracheid (IAWA).

Pore, solitary. — A pore completely surrounded by other elements (IAWA).

Pore chain. — A series or line of adjacent solitary pores (IAWA).

Pore multiple. — A group of two or more pores crowded together and flattened along the lines of contact so as to appear as subdivisions of a single pore (IAWA). Note: The most common type is a Radial pore multiple, in which the pores are in radial files with flattened tangential walls between them. Another type is a Pore cluster, in which the grouping is irregular.

Protoplast. — The mass of protoplasm enclosed by a cell wall.
Ray. — A ribbon-like aggregate of cells formed by the cambium and extending radially in the xylem and phloem (IAWA modif.). Note: The terms Medullary ray and Pith ray are now restricted to the parenchyma connecting the primary cortex with the pith.

Ray, multiseriate. -- A ray two or more cells wide as seen in tangential section.

Ray, uniseriate. -- A ray one cell wide as seen in tangential section.

Ray cell, procumbent. -- A ray cell with its longest axis radial (IAWA).

Ray cell, upright. -- A ray cell with its longest dimension axial (IAWA modif.). Note: Such cells compose certain uniseriate rays and parts, typically the margins, of some multiseriate rays.

Ring, annual. -- In wood and bark, a growth layer of one year as seen in cross section (IAWA modif.), cf. Ring, growth.

Ring, growth. -- In wood and bark a growth layer as seen in cross section (IAWA modif.).

Spiral thickening. -- Helical ridges on the inner face of, and part of, the secondary wall (IAWA). See Cell wall. Note: Often erroneously called tertiary spirals to distinguish them from the spirals of primary xylem.

Storied (storeyed). -- A term applied to the axial cells and rays in wood when these are arranged in horizontal series on tangential surfaces. Note: The term is applied to particular tissues, e.g., "storied parenchyma" or used in a general sense, as in "woods with storied structure." The presence of storied structure is the cause of the ripple marks visible with the unaided eye.

Tannins. -- A heterogenous group of phenol derivatives; they appear as yellow, red or brown substances within the cell, commonly in the vacuoles, but also within the cytoplasm.*

Tracheid. -- An imperforate wood cell with bordered pits to congeneric elements (IAWA modif.).

Vessel. -- An axial series of cells that have coalesced to form an articulated tube-like structure of indeterminate length;

*Description from Esau, 1965.
Vessel. (Cont.) — the pits to congeneric elements are bordered (IAWA modif.). Syn. Trachea.

Vessel member or element. — One of the cellular components of a vessel (IAWA). Syn. Vessel segment (deprec.).


Wood, diffuse-porous. — Wood in which the pores are of fairly uniform or only gradually changing size and distribution throughout a growth ring (IAWA).


Wood, ring-porous. — Wood in which the pores of the early wood are distinctly larger than those of the late wood and form a well-defined zone or ring, cf. Wood, diffuse-porous (BSI modif.).

Xylem. — See Wood.
ALPHABETICAL LISTING OF SPECIES

Acer glabrum Torr.                    - - - - - - - - - - - - - - - - - - - - - F30
Alnus incana (L.) Moench.             - - - - - - - - - - - - - - - - - - - - - H34
A. sinuata (Regel) Rydb.             - - - - - - - - - - - - - - - - - - - - H35
Amelanchier alnifolia Nutt.          - - - - - - - - - - - - - - - - - - - - D7
Arctostaphylos uva-ursi (L.) Spreng. - - - - - - - - - - - - - - - - - - - - J39
Artemisia tridenta Nutt.              - - - - - - - - - - - - - - - - - - - - C4
Betula glandulosa Michx.             - - - - - - - - - - - - - - - - - - - - H36
B. occidentalis Hook.                - - - - - - - - - - - - - - - - - - - - H37
Ceanothus sanguineus Pursh.           - - - - - - - - - - - - - - - - - - - - L45
C. velutinus Doug.                   - - - - - - - - - - - - - - - - - - - - L46
Cercocarpus ledifolius Nutt.          - - - - - - - - - - - - - - - - - - - - D8
Chrysothamnus nauseosus (Pall.) Britt. - - - - - - - - - - - - - - - - - - - - G5
C. viscidiflorus (Hook.) Nutt.        - - - - - - - - - - - - - - - - - - - - G6
Cornus sericea f. stolonifera (Michx.) Fosberg - - - - - - - - - - - - - - - - - - - - I38
Crataegus douglasii Lindl.            - - - - - - - - - - - - - - - - - - - - D9
Holodiscus discolor (Pursh) Maxim.   - - - - - - - - - - - - - - - - - - - - D10
Juniperus communis L. var. montana Ait. - - - - - - - - - - - - - - - - - - - - B2
J. scopulorum Sarg.                  - - - - - - - - - - - - - - - - - - - - B3
Ledum glandulosum Nutt.              - - - - - - - - - - - - - - - - - - - - J40
Lonicera involucrata (Richards) Banks  - - - - - - - - - - - - - - - - - - - - M49
L. utahensis Wats.                   - - - - - - - - - - - - - - - - - - - - M50
Menziesia ferruginea Sm.             - - - - - - - - - - - - - - - - - - - - J41
Pachistima myrsinites (Pursh) Raf.   - - - - - - - - - - - - - - - - - - - - O55
Philadelphus lewisii Pursh            - - - - - - - - - - - - - - - - - - - - E22
Physocarpus malvaceus (Greene) Kuntze - - - - - - - - - - - - - - - - - - - - D11
Populus tremuloides Michx.           - - - - - - - - - - - - - - - - - - - - G31
P. tricocarpa T. and G.              - - - - - - - - - - - - - - - - - - - - G32
Prunus emarginata (Dougl. ex Hook.) D. Dietr. - - - - - - - - - - - - - - - D12
P. virginiana L. var. demissa (Nutt.) Torr. - - - - - - - - - - - - - - - D13
P. virginiana L. var. demissa (Nutt.) Torr. - - - - - - - - - - - - - - - D14
Rhamnus alnifolia L/ Her              - - - - - - - - - - - - - - - - - - - - L47
R. purshiana D. C.                   - - - - - - - - - - - - - - - - - - - - L48
Rhus glabra L. Samac                  - - - - - - - - - - - - - - - - - - - - K48
Ribes aureum Pursh                   - - - - - - - - - - - - - - - - - - - - E23
R. cereum Doug.                      - - - - - - - - - - - - - - - - - - - - E24
R. hudsonianum Rich.                 - - - - - - - - - - - - - - - - - - - - E25
R. irrugum Doug.                     - - - - - - - - - - - - - - - - - - - - E26
R. lacustre (Pers.) Poir             - - - - - - - - - - - - - - - - - - - - E27
R. setosum Lindl.                    - - - - - - - - - - - - - - - - - - - - E28
R. viscoissimum Pursh.               - - - - - - - - - - - - - - - - - - - - E29
Rosa woodsii Lindl.                  - - - - - - - - - - - - - - - - - - - - D15
R. gymnocaarpa Nutt.                 - - - - - - - - - - - - - - - - - - - - D16
Rubus idaeus L.                      - - - - - - - - - - - - - - - - - - - - D17
R. leucoedermis Doug.                - - - - - - - - - - - - - - - - - - - - D18
R. parviflorus Nutt.                 - - - - - - - - - - - - - - - - - - - - D19
Salix scouleriana Barratt.           - - - - - - - - - - - - - - - - - - - - G33
Sambucus caerulea Raf.                - - - - - - - - - - - - - - - - - - - - M51
S. racemosa L.                       - - - - - - - - - - - - - - - - - - - - M52
<table>
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<tr>
<th>Species</th>
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<tr>
<td>Shepherdia canadensis (L.) Nutt.</td>
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<td>Sorbus scopulina Greene</td>
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<td>Spiraea betulifolia Pall.</td>
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<td>Symphoricarpos albus (L.) Blake</td>
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<td>Taxus brevifolia Nutt.</td>
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<tr>
<td>Vaccinium membranaceum Doug.</td>
<td>J42</td>
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<tr>
<td>V. scoparium Leiberg.</td>
<td>J43</td>
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(1) As classified in Lawrence 1951 (11).