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Sherwin Carlquist
Santa Barbara Botanic Garden

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WOOD ANATOMY OF BERBERIDACEAE: ECOLOGICAL AND PHYLOGENETIC CONSIDERATIONS

SHERWIN CARLQUIST¹

*Santa Barbara Botanic Garden
1212 Mission Canyon Road
Santa Barbara, California 93105*

ABSTRACT

Qualitative and quantitative data are presented for 21 collections of *Berberis* and one each of *Epimedium*, *Jeffersonia*, and *Nandina*. Most species of *Berberis* have large numbers of narrow vessels mixed with vasicentric tracheids. Scalariform perforation plates are reported here only for *Epimedium*, in which they are occasional. Berberidaceae have living fibers (*Berberis*), fiber-tracheids plus living fibers (*Nandina*), or tracheids (*Jeffersonia*) as imperforate tracheary elements. Axial parenchyma is reported here for *Jeffersonia* and one species of *Berberis*. Previous reports of axial parenchyma in *Berberis* and *Nandina* likely refer to undivided living fibers, mostly intermixed with vessels, which are slightly shorter and with thinner walls and larger pit apertures than living fibers elsewhere in the wood. Woods of *Berberis* and other Berberidaceae are remarkably xeromorphic. The wide, tall rays of Berberidaceae, other than *Jeffersonia*, resemble rays of *Clematis* (Ranunculaceae) and other Ranunculiflorae. In dimensions, these rays suggest herbaceousness, but abundance of procumbent cells in these rays is not juvenilistic. No consistent differences in wood separate the subgenera *Berberis* and *Mahonia* of *Berberis*, although the two subgenera differ modally in several respects. Wood anatomy of *Nandina* is very similar to that of *Berberis*, and segregation of Nandinaceae is unwarranted on the basis of wood anatomy.

Key words: Axial parenchyma, Berberidales, ecological wood anatomy, Papaverales, Ranunculales, Ranunculiflorae, systematic wood anatomy.

INTRODUCTION

The group of families currently termed Ranunculiflorae consists of five main families: Berberidaceae, Lardizabalaceae, Menispermaceae, Papaveraceae, and Ranunculaceae. The diversity of these families with respect to wood anatomy is very great, in part because of the diversity in habit within this group of families: herbs of various kinds, sympodial and monopodial shrubs, lianas, and even a few small trees. The relationship between wood anatomy and habit can be examined in the light of phylogenies constructed on the basis of macromorphology or of DNA analysis. These phylogenies have sufficient depth that they can be helpful in interpretation of evolutionary trends in wood, or else highlight problems in interpretation of wood evolution. The latter may be true in Berberidaceae, for the summary cladogram for the family offered by Loconte and Estes (1989) would require plesiomorphic woodiness (*Nandina*) to progress to herbaceousness (e.g., *Leontice*), only to turn to woodiness again (*Berberis*).

The two genera of Berberidaceae with the most numerous apomorphies (*Epimedium*, *Jeffersonia*) in the Loconte and Estes (1989) system appear to have re-

tained some primitive wood features. Can this be explained? Meacham (1980) and Terabayashi (1985) offer phylogenies that may fit wood evolution patterns better. If one compares systematic distribution of wood features, particularly degree of woodiness, to the cladogram of Qiu et al. (1993), based on *rbcL* data, additional interpretational problems arise.

The present paper is part of a series on wood anatomy of Berberidales that began with studies of Lardizabalaceae (Carlquist 1984a), Papaveraceae (Carlquist and Zona 1988; Carlquist et al. 1994), and Ranunculaceae and allied families (Carlquist 1995). Upon completion of this series, a summary of the wood anatomy of the families of Ranunculiflorae, together with evolutionary interpretations, will be offered. Recently, attention has been focused on families such as Chloranthaceae and Piperaceae as "paleoherbs" likely to be rich in plesiomorphic features (Taylor and Hickey 1992). Because Ranunculiflorae share many features with those families, Ranunculiflorae are of special interest, and data from wood need to be compared to the paleoherb hypothesis.

Within Ranunculiflorae, ideas on interrelationships of the families can be advanced by study of wood anatomy. The wood of Lardizabalaceae is notably primitive (Carlquist 1984a). Wood features can be used as markers of degree of phyletic advancement, perhaps advancing our knowledge of how the families

¹ This work was begun at the Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, CA 91711. Address for correspondence: 4539 Via Huerto, Santa Barbara, CA 93110.

have diverged. *Nandina* has been treated by some within Berberidaceae, but by others within a monogeneric family. Information from pollen ultrastructure stresses the distinctiveness of *Nandina* (Nowicke and Skvarla 1981). Evidence from wood is obviously needed to aid in resolution of this taxonomic problem. Similarly, *Berberis* and *Mahonia* have been variously treated as two genera or one. In Table 1, the species of the two genera are grouped in terms of two subgenera of *Berberis* to facilitate analysis of whether two genera or one should be recognized.

Wood of Berberidaceae is also of interest because the genera occupy a wide range of habitats: from understory in moist forests (*Epimedium*, *Jeffersonia*) to shrubs of arid regions, even deserts (several species of *Berberis* subgenus *Mahonia*). Quantitative data on woods (primarily vessel features) are clear indicators of ecological adaptations, and special attention is paid here to ecological interpretations of wood data.

Although a number of authors have contributed to knowledge of wood anatomy of Berberidaceae, information is still sparse and some descriptions contain errors. For example, Shen (1954) reports diffuse porosity, axial parenchyma, and aggregate rays for *Nandina*, but these reports may be due to incorrect interpretation; they are not substantiated here. Reports of axial parenchyma in *Berberis* by several authors are likely based on superficial examination, and consequently, the nature of living fibers in this genus is carefully examined. Resolution of this problem, in fact, helps understanding of wood evolution of Berberidaceae in relation to other families of Ranunculiflorae.

MATERIALS AND METHODS

The wood samples studied here are listed in Table 1. Material of *Berberis bealei* and *Nandina domestica* was preserved in aqueous 50% ethanol. Other samples were available in dried form. Liquid preservation of the two wood samples permitted demonstration of the nucleate nature of libriform fibers and of the starch in these fibers. Starch remnants could be seen in libriform fibers of dried samples, however. Most dried samples were boiled in water, stored in aqueous 50% ethanol, and sectioned on a sliding microtome. Material from herbarium specimens was used for *Epimedium pinnatum*, *Jeffersonia diphylla*, and *Leontice leontopetalum* L.; these samples were treated in warm 5% ethylenediamine, embedded in paraffin, and sectioned on a rotary microtome according to a method described earlier (Carlquist 1982). Sections to be mounted on slides, no matter how prepared, were stained in a safranin-fast green combination. Some sections prepared by means of the sliding microtome were dried between glass slides and examined with an ISI scanning elec-

tron microscope (SEM). Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Wood samples collected in Bolivia by Christopher Davidson proved especially important, because woods of equatorial and South American species of *Berberis* have been little studied. The identifications of his corresponding herbarium specimens (located at RSA) are mine, and these determinations should be considered tentative. My own collections are located at RSA, as are the specimens of *Epimedium*, *Jeffersonia*, and *Leontice*. Because quantitative data for *Leontice leontopetalum* were not feasible (the secondary xylem of the tuber consists of bundles augmented by secondary growth, in a parenchyma background), it is omitted from Table 1, but certain features are cited in the text.

Localities for the specimens studied are as follows. *Berberis* subgenus *Berberis*: *B. barbeyana*, Davidson 3796, on sandstone outcrop, altiplano scrub 7 km east of Caracolla on road to Cochabamba, Bolivia; *B. carinata*, Davidson 3717, Bolivia; *B. commutata*, Davidson 5082, Bolivia; *B. corymbosa*, Skottsberg 13, high ridges, Masatierra, Juan Fernandez Islands; *B. flexuosa*, PRFw-10316, Peru; *B. microphylla*, BAw-53035, Bahia Aguirre, Puerto Español, Tierra del Fuego, Argentina; *B. paniculata*, Davidson 5040, Bolivia; *B. thunbergii*, Carlquist 15897, cult. Orpet Park, Santa Barbara, California; *B. vulgaris*, Eidgenossische Technische Hochschule Institut für Mikrotechnische Holzforschung (ZTw), collected from a naturally occurring plant near Zürich, Switzerland. *Berberis* subgenus *Mahonia*: *B. aquifolium* var. *dictyota*, Thompson March 23, 1965, Big Sycamore Canyon, Tehachapi Mts., Kern Co., California; *B. bealei*, cultivated at Pomona College, Claremont, California; *B. fremontii*, Carlquist 8032, hilly thorn scrub, 17 miles from Magdalena del Kino on road to Curupé, Sonora, Mexico; *B. fremontii*, Wolf 10148, summit of east fork of Willow Springs, south side of Old Dad-Granite Range, San Bernardino Co., California; *B. haematocarpa*, Davidson 5806, New York Mountains, San Bernardino Co., California; *B. moranensis*, MADw-21940, moist *Alnus* cloud forest, 2 km SSW of La Cima Railroad Station on old Highway 95, on top of Serjana de Ajusco, D.F., Mexico; *B. nervosa*, Bissing 120, Del Norte Co., California; *B. nervosa*, Bissing 262, Del Norte Co., California; *B. nevinii*, cultivated at Rancho Santa Ana Botanic Garden, Claremont, California; *B. pinnata* subsp. *insularis*, Wallace in 1973, Santa Cruz Island, California; *B. piperiana*, Wheeler 2716, Hungry Creek, Siskiyou Mts., California; *B. trifoliata*, USw-14142, locality unknown. *Epimedium pinnatum*, McLean 19, heavily wooded limestone slopes in *Taxus-Buxus* Preserve, 3 km east of Costa above the Black Sea coast highway between Sochi and Gagra, Ukraine; *Jeffersonia diphylla*, Benke 53, Maniwoc, Wisconsin; *Leontice leontopetalum*, Davis 2131, Cyprus; *Nandina*

Table 1. Wood characteristics of Berberidaceae.

Species	Collection	1 VG	2 VD	3 VM	4 VL	5 PD	6 HE	7 TL	8 MR	9 MW	10 CR	11 FV	12 ME
<i>Berberis</i> subgenus <i>Berberis</i> :													
<i>B. barbeyana</i> Schneider	Davidson 3796	3.5	18	169	256	5	G/GT	530	6510	6.6	0	2.07	27.3
<i>B. carinata</i> Lechl.	Davidson 3717	10.2	14	422	217	4	T/T	381	1870	5.2	0	1.76	7.2
<i>B. commutata</i> Eichl.	Davidson 508	>15	12	476	250	5	T/T	502	861	7.0	0	2.01	6.3
<i>B. corymbosa</i> Hook. & Arn.	Skottsberg 13	5.6	17	128	272	5	O/T	508	776	5.7	+	1.87	36.1
<i>B. flexuosa</i> Ruiz & Pavon	PRFW-10316	3.5	19	90	173	5	G/T	370	1040	10.7	0	2.14	36.5
<i>B. microphylla</i> Forst.	BAW-53053	3.9	15	187	256	5	T/T	569	365	5.8	0	2.22	20.5
<i>B. paniculata</i> Juss.	Davidson 5040	2.4	24	69	254	4	SG/SG	371	1797	6.5	0	1.47	88.3
<i>B. thunbergii</i> DC.	Carlquist 15897	9.5	11	511	301	3	T/T	510	750	6.2	0	1.69	6.5
<i>B. vulgaris</i> L.	ZTw (s.n.)	6.6	13	407	201	6	GT/GT	424	1119	5.5	0	2.11	6.4
subgenus <i>Berberis</i> averaged		7.3	16	293	242			463	1676	6.6		1.92	26.1
<i>Berberis</i> subgenus <i>Mahonia</i> :													
<i>B. aquifolium</i> Pursh var. <i>dictyota</i> Jeps.	Thompson 1965	>15	9	820	167	4	G/T	327	>3000	4.6	0	1.96	1.8
<i>B. bealei</i> Fortune	cult. Claremont	11.8	13	488	272	4	GT/GT	541	2400	4.4	+	1.99	7.2
<i>B. fremontii</i> Torr.	Carlquist 8032	20.8	13	838	225	4	T/T	393	>3000	6.9	+	1.75	3.5
<i>B. fremontii</i> Torr.	Wolf 10148	32.0	9	689	209	4	T/T	386	1868	8.6	+	1.84	2.7
<i>B. haematocarpa</i> Woot.	Davidson 5806	7.7	12	491	209	3	G/GT	316	>3000	13.5	+	1.51	5.1
<i>B. moranensis</i> Schult. f.	MADw-21940	16.3	11	388	219	4	G/G	399	1451	7.0	0	1.82	6.2
<i>B. nervosa</i> Nutt., smaller stem	Bissing 120	4.4	12	137	272	4	T/T	406	985	2.9	0	1.49	23.8
<i>B. nervosa</i> Nutt., larger stem	Bissing 262	16.2	6	511	227	4	GT/GT	375	1084	7.9	0	1.65	2.7
<i>B. nevinii</i> A. Gray	cult. RSABG	5.6	9	576	209	5	T/T	422	3242	5.5	0	2.02	3.3
<i>B. pinnata</i> Lag. subsp. <i>insularis</i> Kunz	Wallace, 1973	13.9	9	534	217	5	G/T	404	1382	7.3	+	1.86	3.7
<i>B. piperiana</i> McMinn	Wheeler 2716	>20	8	759	190	5	G/T	336	329	3.9	+	1.73	2.0
<i>B. trifoliata</i> Hort ex DePpe	USw-14142	13.7	13	391	232	4	T/T	489	3579	8.2	+	2.11	7.7
subgenus <i>Mahonia</i> averaged		15.5	9	552	221			400	2110	6.7		1.97	5.8
<i>Epimedium pinnatum</i> Fisch.	McLean 19	2.8	15	323	400	4	O/T	439	>3000	10.3	0	1.55	17.3
<i>Jeffersonia diphylla</i> Pers.	Benke 53	1.2	17	438	156	4	O/O	239	164	2.0	0	1.53	6.1
<i>Nandina domestica</i> Thunb.	cult. Claremont	3.0	12	168	279	3	T/T	433	3322	4.5	+	1.55	19.9

Legend: 1 (VG), mean number of vessels per group; 2 (VD), mean lumen diameter of vessel elements, μm ; 3 (VM), mean number of vessels per mm^2 of transection; 4 (VL), mean length of vessel elements, μm ; 5 (PD), diameter of pit cavities, μm ; 6 (HE), helical sculpturing of vessels (wide vessels before slash, narrow vessels after slash, G = grooves interconnecting pit apertures, SG = short grooves, T = thickenings, 0 = no sculpturing); 7 (TL) mean length of imperforate tracheary elements; 8 (MR), mean height of multiseriate rays, μm ; 9 (MW), mean width of rays at widest point, cells; 10 (CR), occurrence of crystals in rays (0 = absent, + = present); 11 (FV) F/V ratio—imperforate tracheary element length divided by mean vessel element length; 12 (ME), mesomorphy ratio—mean vessel diameter times mean vessel element length divided by mean number of vessels per mm^2 .

domestica, cultivated at Pomona College, Claremont, California.

Terminology for anatomical features is according to the IAWA Committee on Nomenclature (1964). Ray terms are based on Kribs (1935) and Carlquist (1988). Quantitative data in Table 1 are means based on 25 measurements. Figures on vessel pit diameter and wall thickness cited in the text are based on observation of typical conditions. In Table 1, the species of *Berberis* are listed alphabetically under the two subgenera.

ANATOMICAL DESCRIPTIONS

Growth Rings

A typical condition for *Berberis* is shown for *B. nervosa* (Fig. 1, 3): vessels are larger in earlywood than latewood, but not strikingly so; most of a growth ring is latewood if one uses vessel diameter as a criterion. Although earlywood vessels are narrow (30–40 μm) by standards of dicotyledons at large, they are more than twice the mean diameter of latewood vessels in most species of *Berberis*, and if that criterion were applied, one could call these species ring porous. However, most workers would term most of those species semi-ring porous. Earlywood vessels wider than 30–40 μm —and therefore conspicuously wider than latewood vessels and clearly indicative of ring porosity—occur in *B. carinata*, *B. corymbosa*, *B. flexuosa* (Fig. 10), *B. thunbergii* (Fig. 11) and *B. vulgaris*. Schweingruber (1990) figures ring-porous woods for *B. hispanica* Boiss. & Reuter and *B. vulgaris*, and Gregg's (1959) figure for *B. vulgaris* also illustrates ring porosity. All of the species cited above as being ring porous belong to subgenus *Berberis*. The semi-ring porous nature of woods throughout subgenus *Mahonia* may be related to the evergreen habit of species in that subgenus. All species of subgenus *Berberis* that are not ring porous may be called semi-ring porous (Fig. 1, 3, 5, 9). In some species of subgenus *Mahonia*, growth rings begin with narrow vessels (Fig. 5). This behavior usually relates to onset of a growing season with a rise in temperature suitable for growth but with rainfall lacking, so vessels are narrow at first, then wider as rains occur. This often happens in the desert habitats of *Berberis haematocarpa*.

Wood of *Nandina* was reported by Shen (1954) to be diffuse porous. In fact, it can be semi-ring porous (Fig. 23); if one applied a criterion of earlywood vessels twice the mean diameter of latewood vessels, one could conceivably term this wood ring porous. Shen (1954) is incorrect in saying that all species of *Ber-*

beris are ring porous and thus contrast with *Nandina* in that respect.

The wood available for *Jeffersonia* (Fig. 25, 26) probably represents an accumulation of at least two years; the wood is diffuse porous. Material of *Epidendrum* (Fig. 27) does not have sufficient wood to permit a designation of growth ring presence or absence.

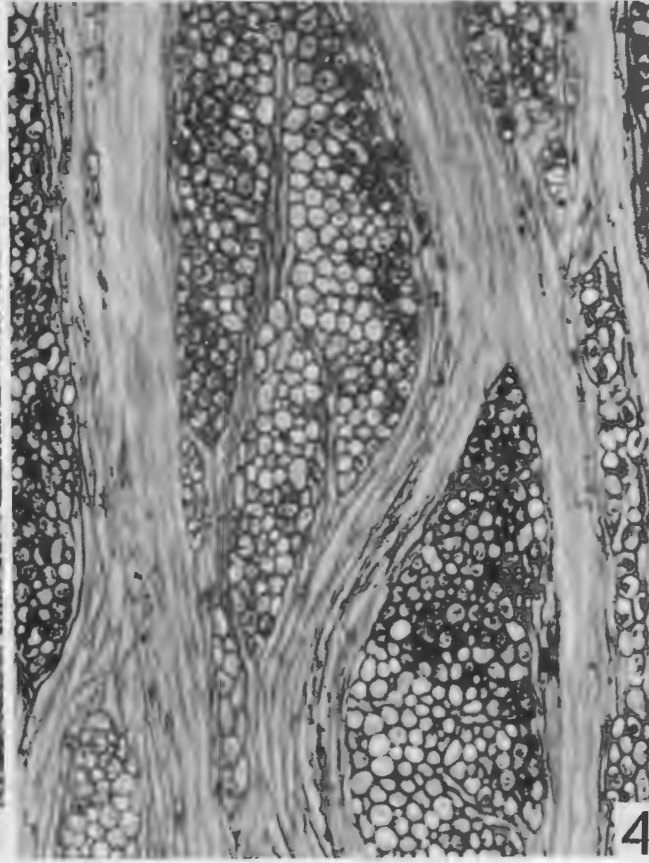
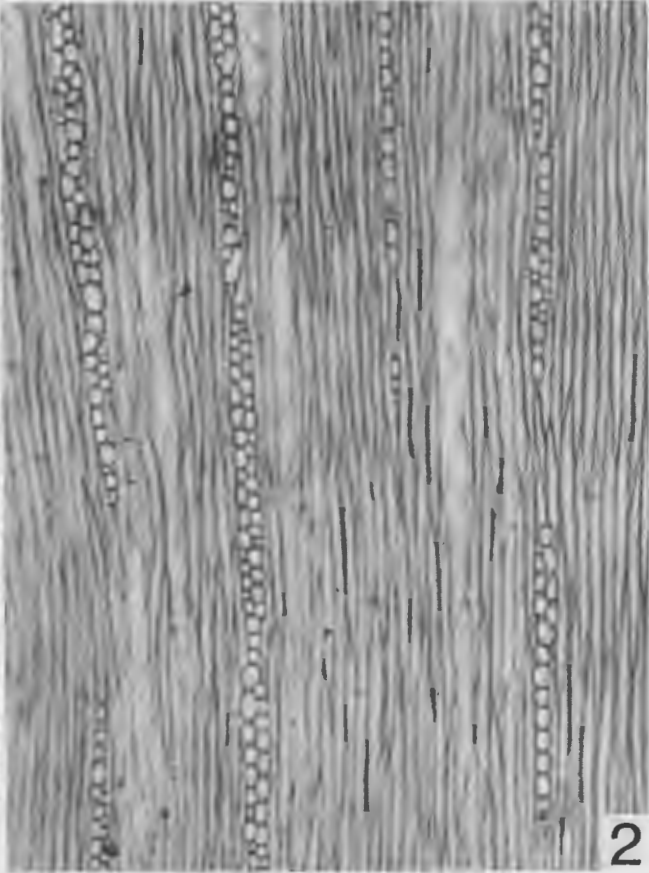
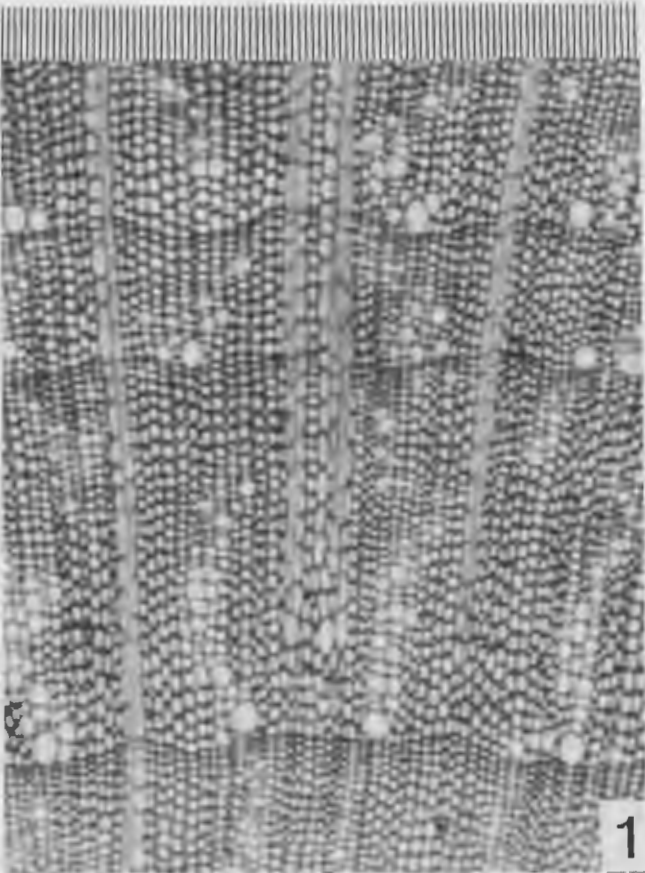
Vessel Restriction Patterns

Papaveraceae (Carlquist and Zona 1988; Carlquist et al. 1994) and Ranunculaceae (Carlquist 1995) show forms of what I have termed vessel restriction patterns. In Papaveraceae, vessels are often restricted to the central portions of fascicular areas of secondary xylem. In Ranunculaceae (notably *Clematis*), where vessels are more abundant, the phenomenon appears in terms of a ray-adjacent position for libriform fibers, which are scarcer in the central portions of fascicular areas. Such "ray-adjacent fibers" can be cited for *Berberis corymbosa* and *B. fremontii*. Restriction of vessels to the central portions of fascicular areas of woods is most characteristically shown by *Nandina* (Fig. 23). In some other Berberidaceae, such as *B. nervosa*, vessel restriction is clearer in earlier-formed wood (Fig. 1), but in the periphery of larger stems, vessels are more abundant and the restriction tends to disappear (Fig. 3). Lack of vessel restriction in some growth rings, together with vessel restriction in other growth rings was also observed in *B. thunbergii* (Fig. 11) and *B. trifoliata*. The vessel restriction pattern was visible in terms of at least one layer of fibers intervening between rays and vessels in *B. aquifolium* var. *dictyota*, *B. barbeyana*, *B. moranensis*, and *B. nevinii*. In *B. bealei* (Fig. 9), *B. carinata*, *B. flexuosa*, and *B. haematocarpa* (Fig. 5), no vessel restriction patterns were observed.

Vessel Grouping

Degree of vessel grouping is calculated by the mean number of vessels per group (Table 1, column 1). The number of vessels per group is very high in most species of Berberidaceae, and difficult to determine accurately because narrow vessels cannot be distinguished from vasicentric tracheids as seen in transection. Moreover, vasicentric tracheids are most abundant in the species that have abundant narrow vessels, a fact demonstrated by study of macerations. The indefinite figures (">15") in Table 1 result from the difficulty in determining the limits of a vessel group

Fig. 1–4. Wood sections of *Berberis nervosa*.—1–2. Small stem, Bissing 120.—1. Transection; vessels are restricted to center of fascicular areas.—2. Tangential section; rays are all multiseriate or biseriate, but narrow.—3–4. Large stem, Bissing 262.—3. Transection; growth rings are semi-ring porous.—4. Tangential section; rays are multiseriate, wide. (Fig. 1–4, scale above Fig. 1 [divisions = 10 μm].)



as seen in transection. Relatively low numbers of vessels per group (<5) were observed in *B. barbeyana*, *B. flexuosa*, *B. microphylla*, and *B. paniculata*. All of these collections are from relatively mesic localities in South America.

In genera other than *Berberis*, the figure for number of vessels per group is low. In *Jeffersonia diphylla*, the very low number of vessels per group is due to the fact that this species has tracheids exclusively as its imperforate tracheary element type. Thus, the wood of *Jeffersonia* exemplifies the correlation between tracheids and the solitary vessel habit hypothesized earlier (Carlquist 1984b). *Epimedium* and *Nandina* have a relatively low number of vessels per group when they are compared with *Berberis*, the other genus that has libriform fibers (as opposed to tracheids).

The very high number of vessels per group in *Berberis* and *Nandina* exceeds what one finds in Lardi-zabalaceae and Papaveraceae, and Ranunculaceae, with the exception of some species of *Clematis* of the Ranunculaceae (Carlquist 1995) and *Argemone*, *Dendromecon*, and *Romneya* of the Papaveraceae (Carlquist and Zona 1988; Carlquist et al. 1994). Ecological interpretations of vessel grouping are included in a later section of this paper.

The patterns of vessel groupings as seen in wood transections vary within Berberidaceae. Diagonal groupings of vessels are conspicuous in *B. bealei* (Fig. 9), *B. carinata*, *B. corymbosa*, *B. haematocarpa* (Fig. 5), *B. nervosa* (Fig. 1), and *B. thunbergii* (Fig. 11). Diagonal patterns of vessels are not clear in *B. flexuosa* (Fig. 10) or *B. moranensis*, *B. nervosa* (larger stems only: Fig. 3), *Epimedium pinnatum* (Fig. 27), and *Nandina domestica* (Fig. 23). The extent of these patterns can be judged well only from study of an entire section; a given photographed portion may not be entirely representative.

Quantitative Vessel Features

Mean vessel diameter (Table 1, column 2) is remarkably low in Berberidaceae: the figures are very low compared with dicotyledons at large (Metcalf and Chalk 1950) but close to what one finds in desert shrubs (26 μm) or chaparral shrubs (29 μm). Narrow vessel diameter characterizes not only Berberidaceae from moderately to markedly dry areas (Fig. 1, 3, 5, 9, 11) but also those from moist forest floor habitats (Fig. 25, 26, 27). One must remember that in transection, one cannot see presence or absence of perforation

plates, so that vasicentric tracheids or even libriform fibers may inadvertently be measured as narrow vessels and therefore figures for vessel diameter are least reliable in species in which narrow vessels are abundant.

Vessel density (Table 1, column 3) in Berberidaceae is comparable to figures for southern California desert shrubs (361 vessels per mm^2) or chaparral shrubs (299) (Carlquist and Hoekman 1985). The figure for the *Ma-honia* species of *Berberis* (552) is higher than that reported for any of the ecological categories in the southern California flora, including alpine shrubs (Carlquist and Hoekman 1985).

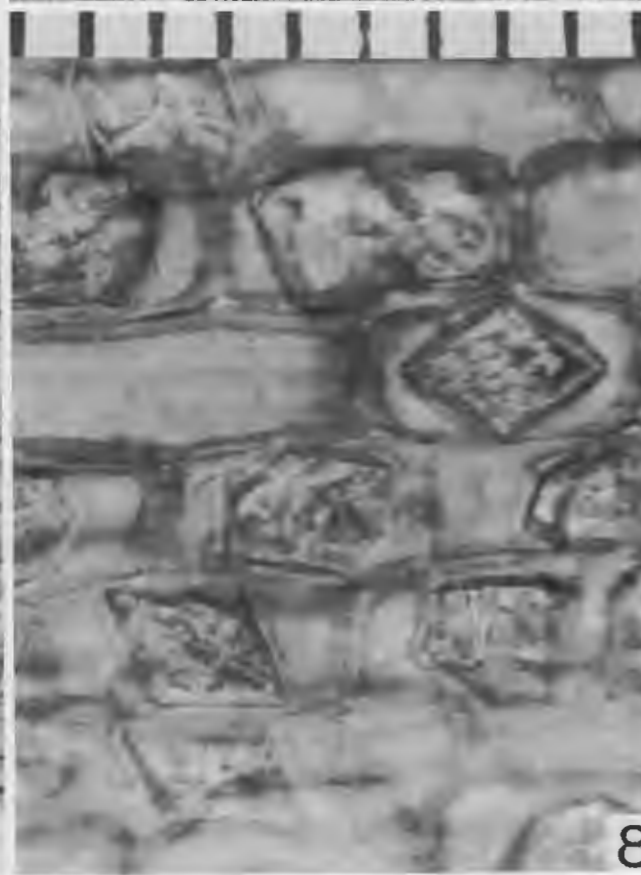
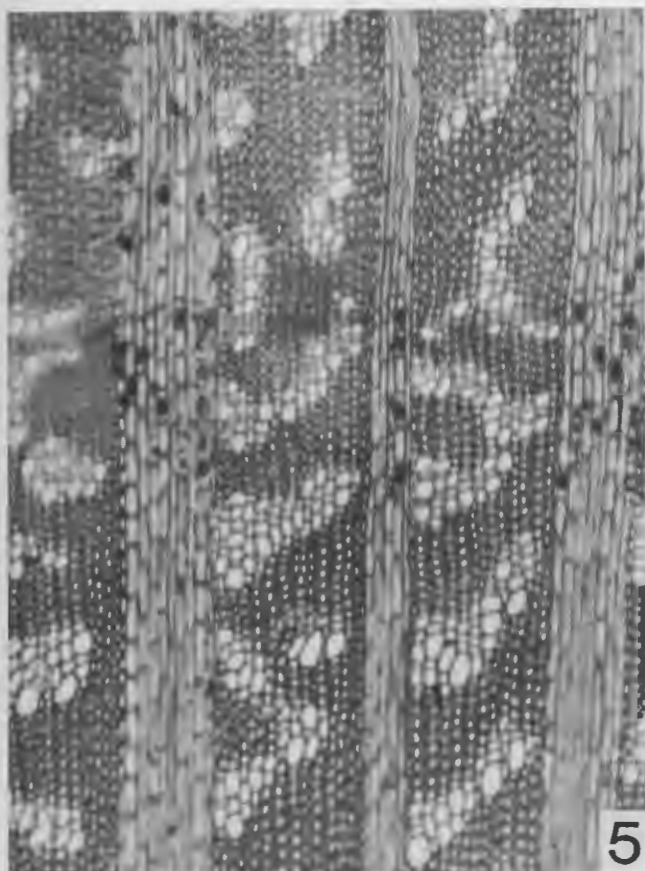
Vessel element length (Table 1, column 4) is relatively uniform in Berberidaceae. Although mean lengths from 167 μm to 400 μm are reported, the latter figure is for *Epimedium pinnatum*, in which the woods studied were relatively juvenile, and if that specimen is omitted, the greatest mean is only 301 μm . More than half of the species of *Berberis* have a mean vessel element length between 200 and 250 μm . The relatively short vessel elements of Berberidaceae should be taken into account when considering the phenomenon of storying, since storying occurs only in woods with relatively short fusiform cambial initials and, therefore, short vessel elements (Bailey 1923).

Pits in vessels of Berberidaceae are alternate, circular to oval, with the exception of *Epimedium pinnatum* and *Leontice leontopetalum*. In *Leontice* (Fig. 30) the pitting is pseudoscalariform. Pseudoscalariform pitting can be defined as alternate pits that are much widened laterally, but in which the ends of the pits do not correspond to the face of a vessel (they do correspond to vessel faces in scalariform pitting). The stem studied for *Epimedium pinnatum* has vessel-to-vessel and vessel-to-fiber pitting that is alternate as well as, in earlier-formed secondary xylem, scalariform and transitional. Vertical pit cavity diameter is shown in Table 1, column 5. Pit cavity diameter is relatively small, ranging from 3 to 50 μm .

Vessel Morphology

Although Solereder (1908) reported occasional scalariform perforation plates in *Berberis* (no species given), no subsequent report of scalariform plates for the genus has been made except for Tupper's (1927) statement that in *Berberis*, perforation plates are scalariform exclusively. Tupper's (1927) statement may be based on misidentified material. In the present study,

Fig. 5–8. Wood sections of *Berberis haematocarpa*.—5. Transection; diagonal aggregations of vessels conspicuous.—6. Tangential section; storying evident in vessel elements and in some fibers (lower left).—7–8. Crystals as seen in radial section of rays.—7. Lower magnification, to show that crystals are most abundant where earlywood meets latewood in a growth ring.—8. Higher magnification, to show size and shape of crystals. (Fig. 5, 6, scale above Fig. 1; Fig. 7, scale above Fig. 7 [divisions = 10 μm]; Fig. 8, scale above Fig. 8 [divisions = 10 μm].)



scalariform perforation plates were seen in secondary xylem only in *Epimedium pinnatum*. In this specimen, scanning of one radial section revealed four scalariform plates (with 1, 4, 5, and 5 bars respectively), but all other perforation plates were simple. As noted elsewhere, the sample of *Epimedium pinnatum* studied had relatively little secondary xylem (Fig. 27), so occurrence of scalariform perforations, which would be more likely to occur in primary xylem than in secondary xylem, might be understandable if paedomorphosis is operative in this wood; the ray structure (see below) definitely suggests paedomorphosis. This interpretation is also supported by the fact that in radial sections of a species that included primary as well as secondary xylem, *B. paniculata*, I located in late metaxylem a few perforation plates with several bars, although secondary xylem had only simple perforation plates in this species.

Helical sculpture is almost omnipresent in vessels of the Berberidaceae studied (Table 1, column 6); only in *Jeffersonia diphylla* was some form of helical sculpture not observed. Berberidaceae is a key group for showing that grooves interconnecting pit apertures ("coalescent pit apertures") and helical ("spiral") thickenings can both be present in vessels of a genus, and are, in fact, interrelated forms of helical sculpture, as shown earlier for *Clematis* (Carlquist 1988). For example, grooves may be present in wider vessels of *B. aquifolium* var. *dictyota*, *B. barbeyana*, *B. bealei*, *B. flexuosa*, *B. haematocarpa*, *B. pinnata* subsp. *insularis*, and *B. piperiana*, but in the narrow vessels in this list of species, helical thickenings are present. In *B. paniculata* (Fig. 17), only occasional short grooves interconnect pit apertures. In *B. commutata* (Fig. 18), grooves are longer; in the vessel wall illustrated, inconspicuous helical thickenings also are present. In some specimens, grooves do not run precisely parallel to the pit apertures within the groove; the apertures are at an angle somewhat divergent from the grooves. This condition was figured for *Melia* earlier (Carlquist 1988). Light microscopy is actually better than SEM for distinguishing between grooves and helical thickenings, because helical thickenings stain more darkly; on vessel walls shaved away by the sectioning process, grooves can be seen readily by light microscopy.

If thickenings are present in both wide and narrow vessels in a particular species, the thickenings tend to be more pronounced in the narrow vessels, as shown for *B. microphylla* (compare Fig. 19 and 20). This is even more clearly shown in the pair of SEM photographs of *B. haematocarpa*: inconspicuous thickenings

occur in the wider vessels (Fig. 13), more pronounced thickenings in the narrower vessel (Fig. 14). Two vessels are shown for *B. vulgaris* in Fig. 16; in these vessels, thickenings are short and tend to fade into the wall at many points. By contrast, the three vessels shown for *B. fremontii* in Fig. 15 have very pronounced thickenings that do not fade into the wall at intervals. The differences just cited between *B. vulgaris* and *B. fremontii* likely represent characteristics of species.

Vasicentric Tracheids

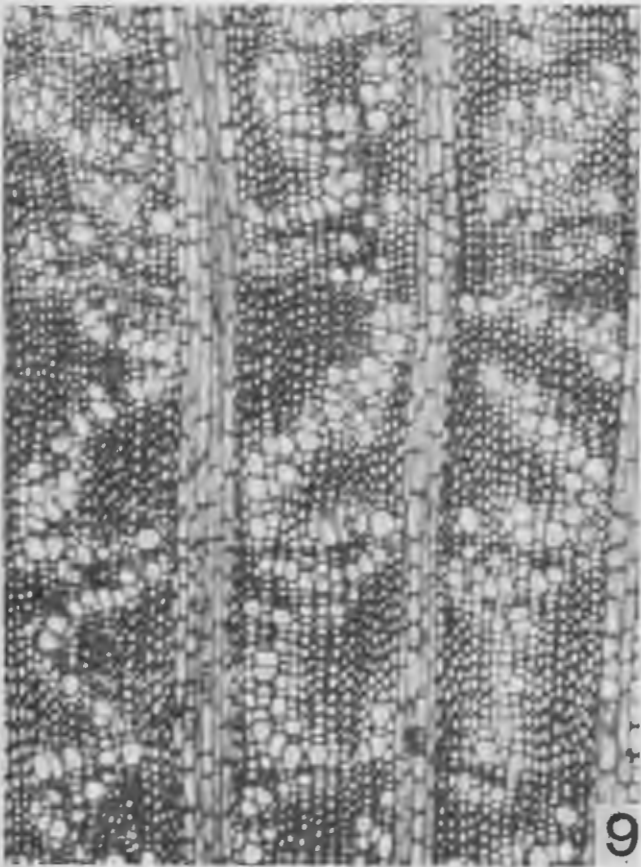
Vasicentric tracheids are intermixed with vessels in most species of *Berberis*. Helical thickenings are characteristic of vasicentric tracheids in the species in which helical thickenings are reported in vessels. The only species in which vasicentric tracheids were not observed are *Berberis barbeyana*, *Epimedium pinnatum*, and *Jeffersonia diphylla*. In the species of *Berberis* in which narrow vessels are abundant (low mean vessel diameter also characterizes these species), vasicentric tracheids are also abundant. Vasicentric tracheids can be identified with certainty only when macerations, as well as sections, are studied, because one must be sure that fusiform cells with bordered pits do not bear perforations, and perforations can easily be missing from a fusiform cell because of the sectioning process.

Imperforate Tracheary Elements

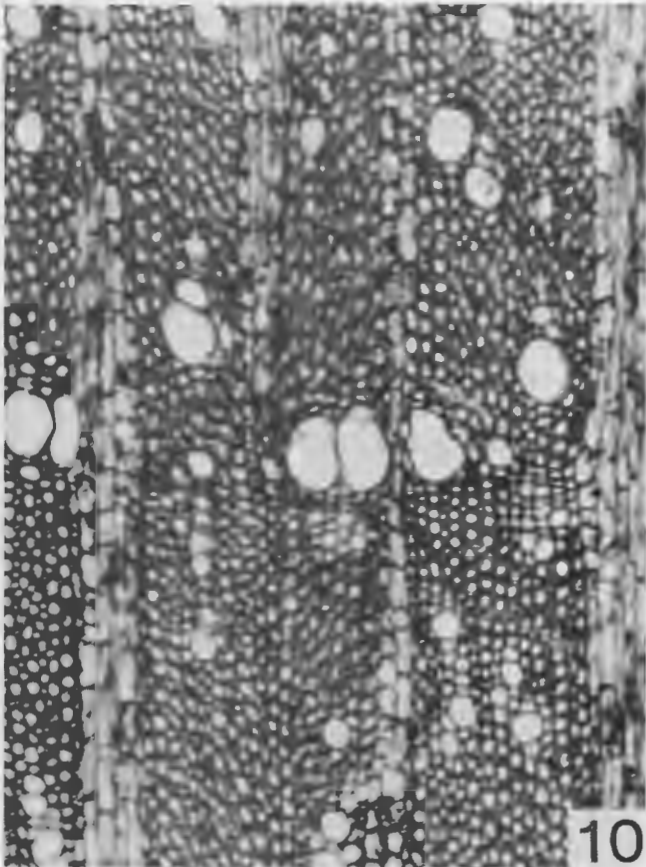
As stated by Metcalfe and Chalk (1950), the imperforate tracheary elements of *Berberis* have simple pits and are therefore libriform fibers. The narrow elliptical pit apertures of a libriform fiber are illustrated with SEM for *B. microphylla* (Fig. 19, top). The cells termed "tracheids" in *Nandina* by Solereder (1908) and "imperfect vessel members" in Berberidaceae by Metcalfe and Chalk (1950) are undoubtedly vasicentric tracheids, which are discussed above. Likewise, what Greguss (1959) terms tracheids and fiber-tracheids in *Berberis vulgaris* are vasicentric tracheids. *Nandina* does, however, have fiber-tracheids, as noted by Shen (1954). The fiber-tracheids of *Nandina* have bordered pits with pit cavities 2.0–2.5 μm in diameter. There are also libriform fibers in *Nandina*, often rich in starch, adjacent to rays, whereas the fiber tracheids are distal to the rays.

Jeffersonia diphylla has tracheids as its sole type of imperforate tracheary element. The bordered pits in

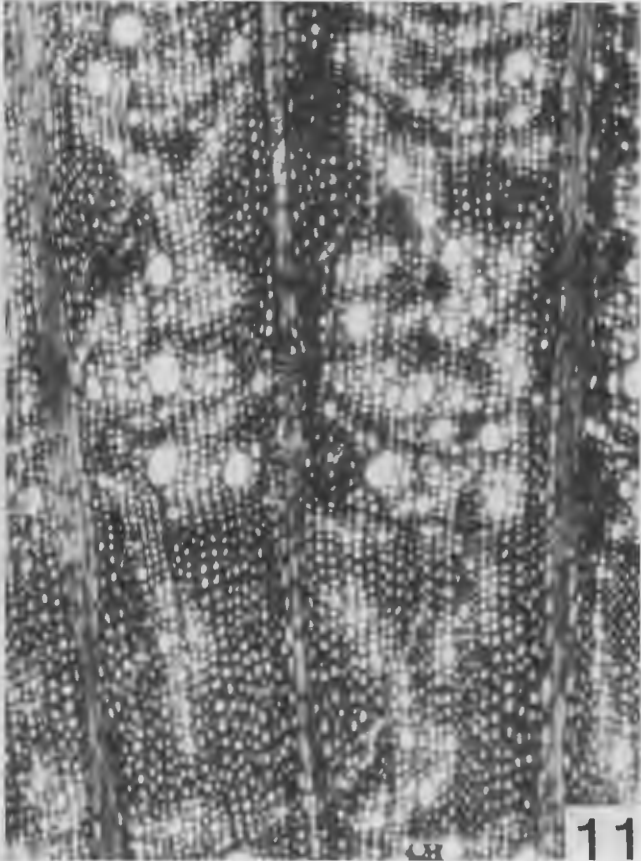
Fig. 9–12. Wood sections of *Berberis*.—9. *B. bealei*. Transection; diagonal aggregations of vessels are evident.—10. *B. flexuosa*. Transection; large earlywood vessels, middle.—11–12. *B. thunbergii*.—11. Transection; wood is semi-ring porous.—12. Tangential section; rays are multiseriate, tall. (Fig. 9–12, scale above Fig. 1.)



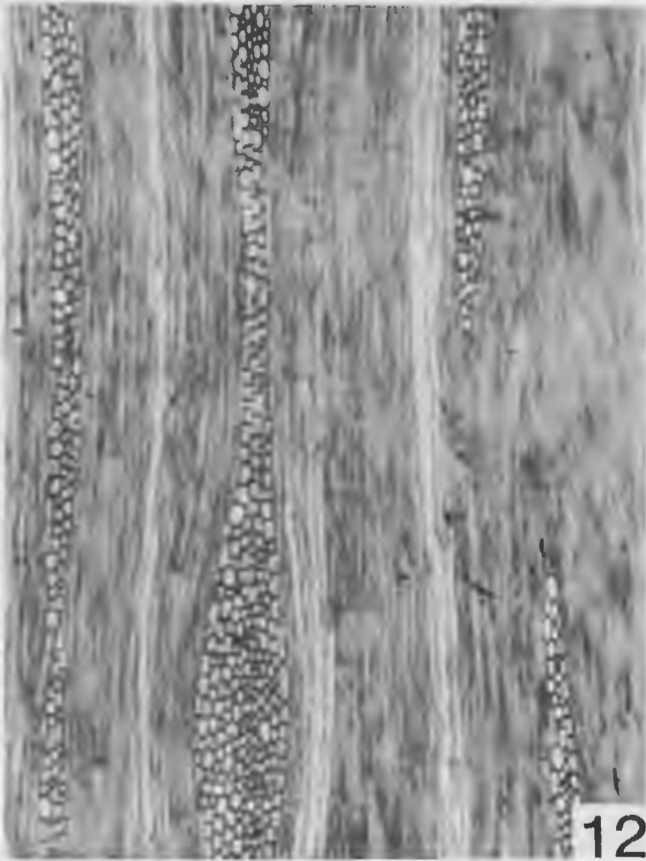
9



10



11



12

these cells are densely placed; pit cavities are 3 μm in diameter.

Mean imperforate tracheary element length is given for the species studied in Table 1, column 7. The range is from 237 μm (*Jeffersonia diphylla*) to 569 μm (*Berberis microphylla*). Septate fibers were observed in *B. barbeyana*, *B. microphylla*, *B. paniculata*, and *B. vulgaris*. In *B. paniculata*, some cells of axial parenchyma strands contain septa, and septate fibers are more common adjacent to vessels, as they are in *Clematis* (Metcalf and Chalk 1950; Carlquist 1995). All of the species with septate fibers belong to subgenus *Berberis*. Metcalf and Chalk (1950) report septate fibers for wood of *Nandina*. My material of *Nandina* showed septate fibers located between primary xylem and pith, but no septate fibers in the wood itself. Solereder (1908) reports "prosenchyma with simple pits" in *Nandina*. There are starch-containing fibers of this description adjacent to rays in *Nandina*, as noted above.

Histological details of nucleate libriform fibers that contain starch are illustrated for *Berberis vulgaris* by Wolkinger (1970a). In reviewing the systematic occurrence of living fibers in dicotyledons, Wolkinger (1970b) cites eight species of *Berberis* subgenus *Berberis*, three species of subgenus *Mahonia*, and the single known species of *Nandina*. Presence of starch or starch remnants was noted in libriform fibers of all collections of *Berberis*, *Epimedium*, and *Nandina* in the present study. The tracheids of *Jeffersonia diphylla* have no contents and are very likely dead at maturity, as conductive cells typically are.

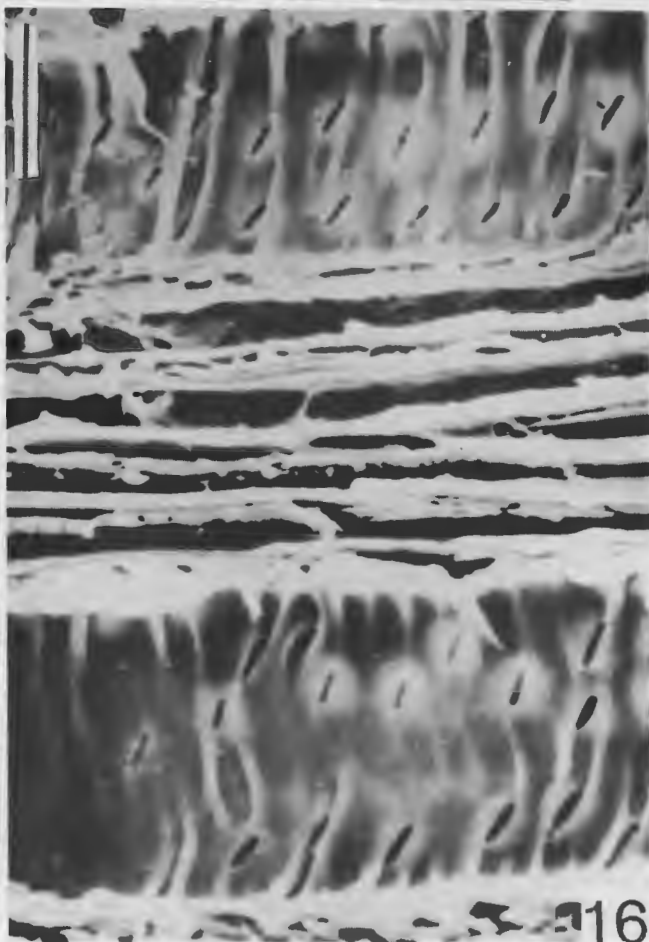
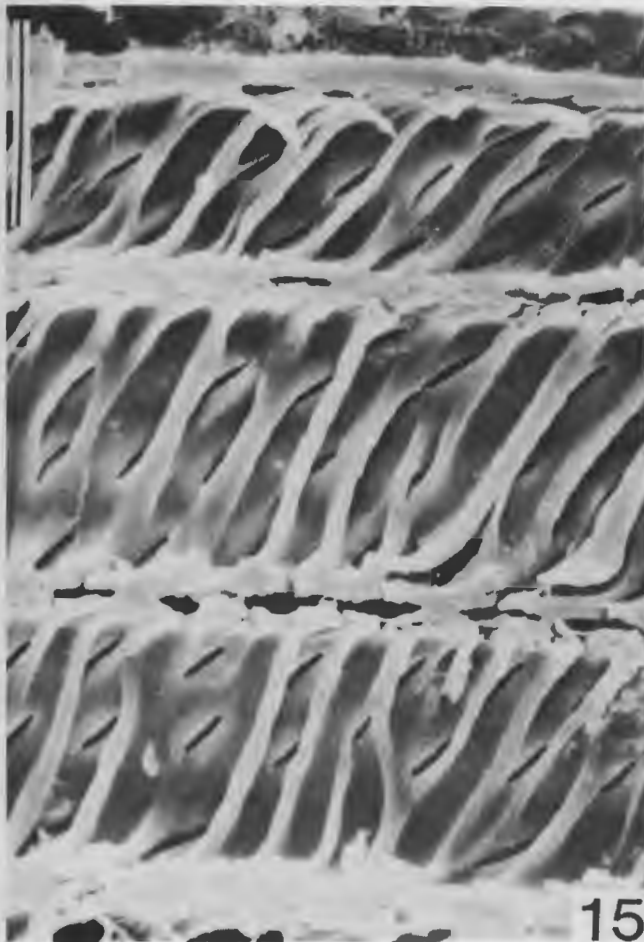
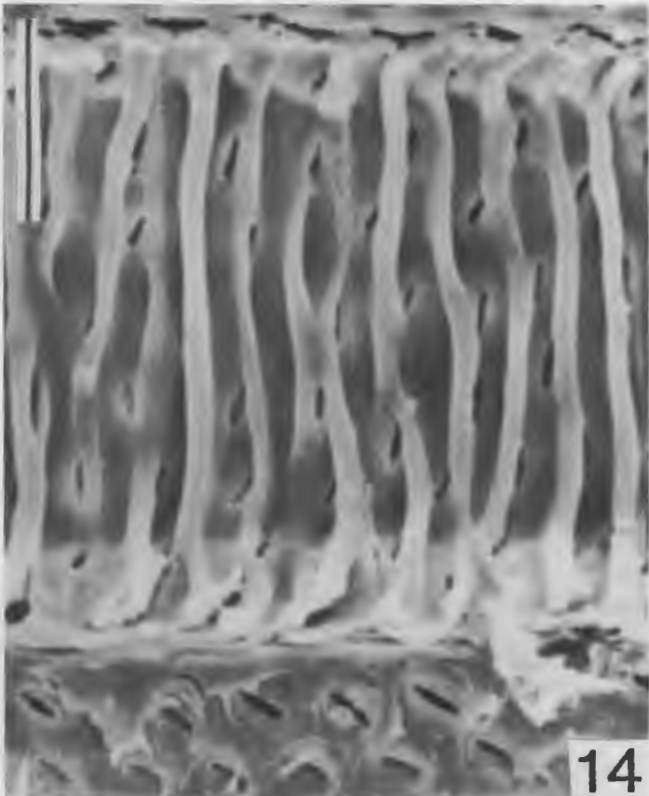
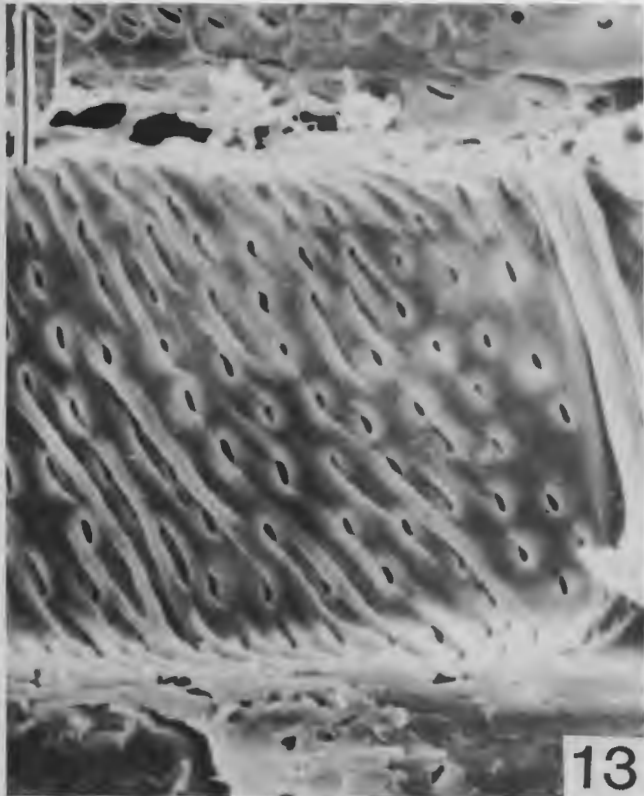
Axial Parenchyma

Axial parenchyma is scarce or absent in woods that have living fibers, and the Berberidaceae other than *Jeffersonia* certainly exemplify this principle. There have been reports that axial parenchyma is present in Berberidaceae (Shen 1954; Rancusi et al. 1987; Schweingruber 1990). Rancusi et al. (1987) and Schweingruber (1990) claim that in *Berberis*, axial parenchyma is apotracheal and diffuse. Shen (1954) claims that in *Nandina*, axial parenchyma is both apotracheal and paratracheal. None of these authors offer any details concerning the alleged axial parenchyma, and one can be accordingly skeptical about these reports, since both Solereder (1908) and Metcalf and Chalk (1950) report axial parenchyma to be absent from the family. Likewise, Greguss (1959) reports axial parenchyma to be absent from the wood of the three species of Berberidaceae he studied.

Because of the above contradictory reports, I examined wood of Berberidaceae with special attention to this feature. As a result, I can report that axial parenchyma in the ordinary sense—strands of cells—occurs only in one species of *Berberis*, *B. paniculata* (Fig. 21), in which parenchyma is scanty paratracheal, and strands of two to four cells are present, as seen in radial sections. Some cells of parenchyma strands in that species contain septa, so that there appears to be some intergradation between axial parenchyma and septate fibers. In *Jeffersonia* (not studied by Solereder 1908 or Metcalf and Chalk 1950), axial parenchyma is also present; paratracheal strands consisting of one or, more commonly, two cells, are present, and the walls are thin and primary, in contrast to the tracheids in this wood. The scanty paratracheal nature of axial parenchyma in *B. paniculata* and *Jeffersonia diphylla* accords with the scanty paratracheal parenchyma reported for *Clematis* and other Ranunculaceae (Carlquist 1995). Despite Shen's (1954) claim that both apotracheal and paratracheal axial parenchyma can be found in *Nandina*, I was unable to locate any (in the sense of strands of cells), and Shen (1954) does not illustrate or describe any axial parenchyma for *Nandina* in his paper.

However, living libriform fibers functionally form a cell type equivalent to parenchyma (Wolkinger 1970a). The living fibers of *Berberis* and *Nandina* that are embedded in groups of vessels and vasicentric tracheids have simple or slightly bordered pits with oval apertures that contrast with the narrow slitlike pits of libriform fibers elsewhere in the wood. These parenchymalike fibers in vessel groups are about the same length as vessel elements or vasicentric tracheids, in contrast to the other libriform fibers, which are typically about twice as long as vessel elements in the family (Table 1, column 11). Could these fibers be termed axial parenchyma? Perhaps, but I prefer to consider them a kind of libriform fiber, as Metcalf and Chalk (1950) evidently do, because *Berberis paniculata* and *Jeffersonia diphylla* do have true axial parenchyma in the sense of cells subdivided into strands, each cell of the strand surrounded by a lignified secondary wall. The parenchymalike fibers of *Berberis* and *Mahonia* can be considered a product of fiber dimorphism, a process described originally in Asteraceae, where bands of apotracheal parenchyma have this type of origin (Carlquist 1958, 1961). In any case, the reports of apotracheal parenchyma in Berberidaceae (Rancusi et al. 1987; Schweingruber 1990) appear

Fig. 13–16. SEM photomicrographs of vessels from radial sections of *Berberis* wood.—13–14. *B. haematocarpa*.—13. Wide vessels; showing grooves and moderate thickenings.—14. Narrow vessel; thickenings are pronounced, but fade into walls in places.—15. *B. fremontii*, Wolf 10148. Three vessels; pit apertures deviate in their angle from that of the thickenings.—16. *B. vulgaris*. Two vessels; thickenings are rather faint, and fade into walls at various places. (Magnifications shown by bars at upper left of figures; each bar = 10 μm .)



likely to have been based on examination of transections rather than on examination of longisections and macerations.

Axial parenchyma is pervasive in the succulent caudices of *Leontice leontopetalum*. Grouped vessels without imperforate tracheary elements are embedded in a background of parenchyma cells in this species (Fig. 29).

Rays

Rays in *Berberis* (Fig. 2, 4, 6, 12) and *Nandina* (Fig. 24) are almost exclusively multiseriate. Uniseriate rays (one of which appears in Fig. 6) are so infrequent as to be negligible except in *Jeffersonia diphylla*, in which uniseriate rays (mean height = 90 μm) are far more abundant than multiseriate rays. Rancusi et al. (1987) cite the rays of *Berberis* as Homogeneous Type II of Kribs (1935). This designation is close: Kribs specifies procumbent cells in Homogeneous Type II, but some upright sheathing cells occur on the multiseriate rays of all Berberidaceae studied (Fig. 2, 4, 6, 12). In some species, upright cells form at least a single layer of cells, especially in earlier-formed wood (Fig. 2), but upright cells decrease in abundance as wood is added (Fig. 4). Upright cells were relatively abundant in the rays of *B. barbeyana*, *B. corymbosa*, *B. nervosa*, *B. paniculata*, *B. pinnata* subsp. *insularis*, and *B. vulgaris*.

In *Epimedium pinnatum* (Fig. 28), rays are multiseriate exclusively, but ray cells are square to upright. Because the stem studied was relatively young, this ray cell histology might differ from what one would find in older stems: procumbent cells typically increase in abundance as secondary growth proceeds in dicotyledons at large. In *Jeffersonia diphylla*, ray cells are mostly square or upright, but a few procumbent cells are present. If multiseriate rays in this species are so infrequent as to be considered negligible, the ray type in *Jeffersonia* is intermediate between Heterogeneous Type III of Kribs and Paedomorphic Type III (Carlquist 1988).

Figures for mean height of multiseriate rays are given in Table 1, Column 8. Measurement of rays is difficult in *Epimedium*, *Nandina*, and some collections of *Berberis* because the rays are so tall that they often are not included entirely within a tangential section (Fig. 2, 4, 6, 12, 24, 28). If one measures only rays that are included within a given tangential section, the mean figure is skewed downward, so I have preferred

to estimate probable length of very tall rays in obtaining means; I have obtained this estimate by determining the proportion of rays that are completely included within a section and adjusting accordingly the figure based on rays entirely included within a section.

Mean width of multiseriate rays at widest point is given in Table 1, column 9. *Berberis nervosa* shows a divergence in ray width between juvenile wood (Fig. 2), *Bissing 120*, and adult wood (Fig. 4), *Bissing 262*. Rays typically do increase in width as stems increase in diameter in dicotyledons at large, so that example is understandable. However, as seen in transection, in which ray width changes can be traced to some degree, rays of *Berberis* begin as multiseriate, not uniseriate or biseriate.

Shen (1954) states that the rays of *Nandina* (Fig. 24) are "very broad aggregate rays, mixed with parenchyma and fibers, while the rays of *Mahonia* and *Berberis* are simple and nearly homogeneous." In Betulaceae and Fagaceae, rays that originated separately may become fused into aggregate rays. In at least a few of the *Berberis* species studied, by contrast, ontogenetic breakup of larger rays into smaller segments was readily apparent, and likely Shen (1954) confused this with formation of aggregate rays, which are restricted to a few families of dicotyledons; aggregate rays have not been hitherto reported in the families of Ranunculiflorae by authors other than Shen (1954).

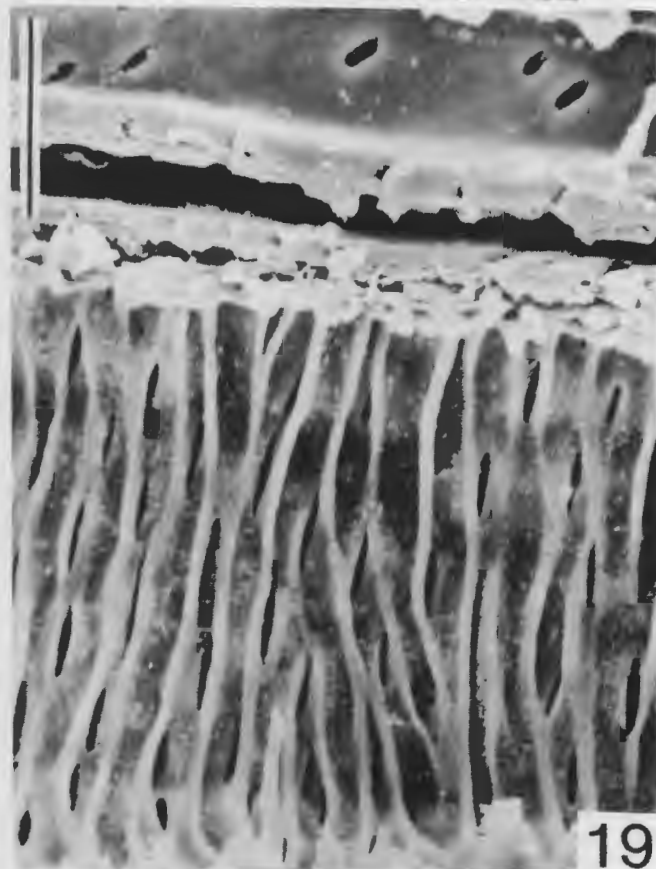
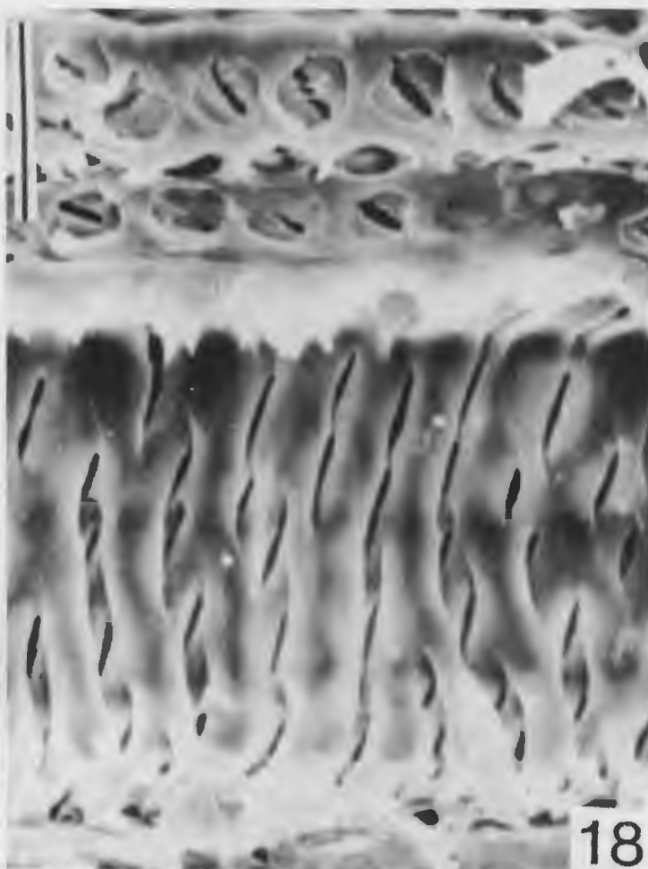
Ray cell wall thickness is typically 1.8 to 2.2 μm in most species of Berberidaceae (Fig. 22); slightly thinner ray cell walls occur in *B. barbeyana* (1.4 μm), *B. flexuosa* (1.5 μm), *B. moranensis* (1.2 μm), and *B. piperiana* (1.5 μm). Ray cell walls are also thin in *Epimedium pinnatum* (1.3 μm ; Fig. 27, 28), *Jeffersonia diphylla* (0.3 μm ; Fig. 26), and *Nandina domestica* (1.1 μm ; Fig. 24). All species have lignified secondary walls on ray cells except for *Jeffersonia diphylla* (Fig. 25, 26), in which ray cell walls are primary only.

Pitting is sparser on radially oriented ray cell walls (both vertical and horizontal) than on tangentially oriented walls. If one views the pitting of ray cells in sectional view rather than in face view, one sees that bordered pits are common, especially on tangentially oriented walls, although simple pits are also present. Viewing of ray cell walls in face view in dicotyledons at large often fails to reveal pit borders which prove to be quite conspicuous in sectional view.

Wood Cell Contents

Starch is present in living fibers (libriform fibers) and in ray cells of all Berberidaceae studied. Starch

Fig. 17–20. SEM photographs of vessels from radial section of *Berberis* wood.—17. *B. paniculata*. Wide vessel; a few short grooves interconnect some pit apertures.—18. *B. commutata*. Long grooves interconnect indefinite numbers of pit apertures.—19–20. *B. microphylla*.—19. Wide vessel; fine thickenings are present.—20. Narrow vessel; thickenings are relatively coarse. (Magnifications shown by scales at upper left of figures; each bar = 10 μm .)



presence is more obvious in the liquid-preserved specimens, but either starch grains or starch-grain remnants were observed in libriform fibers and ray cells of all collections.

Prismatic calcium oxalate crystals are present in ray cells of some species of *Berberis* and in ray cells of *Nandina* (Table 1, column 10). Crystals are figured here for *B. haematocarpa* (Fig. 7, 8). Crystals are most abundant near the interface between earlywood and latewood (Fig. 7, right; Fig. 5, slightly above center—right, left, middle). Crystals are large, rhomboidal in shape, and formed singly within ray cells (Fig. 8). The distribution shown in Table 1, column 10, shows that crystals were observed in six species of *Berberis* subgenus *Mahonia* (but not in three species of that subgenus), and only in one species (*B. corymbosa*) of subgenus *Berberis*. However, Rancusi et al. (1987) report crystals as occasional in ray cells of another species of subgenus *Berberis*, *B. chilensis* Gill. Consequently, the statement by Metcalfe and Chalk (1950) that crystals are present in rays of subgenus *Mahonia* but absent in rays of subgenus *Berberis* is no longer tenable.

Shen (1954) reports crystals as absent in wood of *Nandina domestica*, but in my material of this species, crystals are abundantly present in ray cells. Presence or absence of crystals in rays may not be a deep-seated character: crystals can readily be observed in pith of certain species of subgenus *Berberis*, species in which crystals are absent in rays of the secondary xylem. The genetic information for formation of crystals is therefore present, so modification of the distribution of the crystals within the plant body seems relatively easy.

Storying

Storying of at least some vessel elements and vasicentric tracheids was observed in all species of *Berberis* (Fig. 22) and in *Nandina*. In addition, storying of at least some libriform fibers was observed in *B. barbeyana*, *B. carinata*, *B. corymbosa*, *B. fremontii*, *B. haematocarpa* (Fig. 6; storying of fibers clearest at lower left), *B. nervosa* (Fig. 2), and *B. vulgaris*. In any species that shows storying in vessel elements, fusiform cambial initials may be expected to be mostly storied; lack of storying in libriform fibers results from their elongation. In Berberidaceae, libriform fibers are about double the length of vessel elements (the latter a good indication of fusiform cambial initial length), but deviation of any given libriform fiber from the mean F/V ratio for a species (Table 1, column 11) is

considerable, resulting in obliteration of the storied pattern in libriform fibers. Vasicentric tracheids are typically storied in *Berberis*, because they are about the same length as vessel elements.

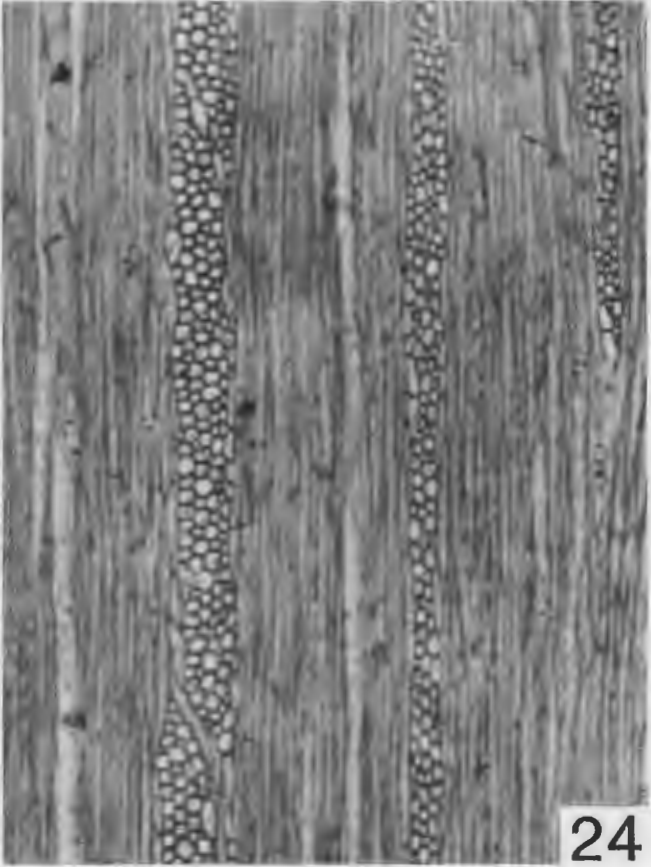
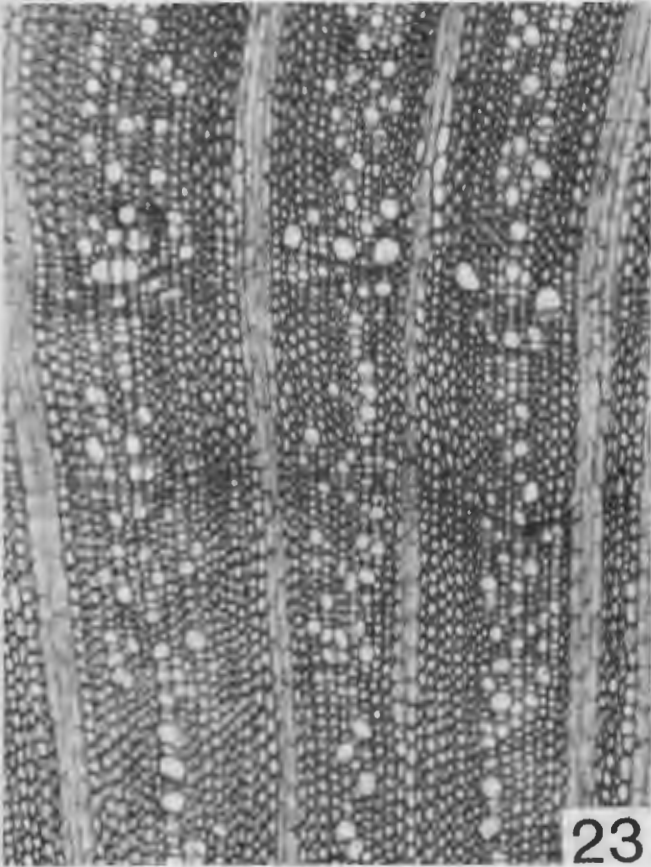
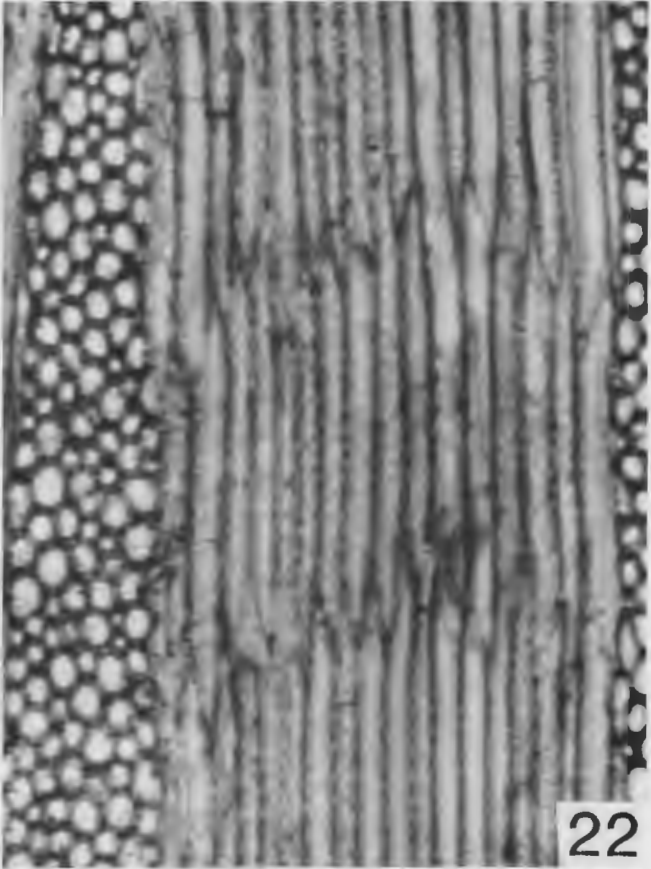
No storying is evident in any axial elements of *Epi-medium pinnatum* (Fig. 28) or *Jeffersonia diphylla*. No storying was observed in rays of any Berberidaceae.

ECOLOGICAL AND HABITAT CORRELATIONS

In Table 1, column 12, figures are presented for the Mesomorphy ratio, which combines three quantitative vessel features (definition for the ratio given in legend, Table 1). The value for this ratio is much greater in the species of subgenus *Berberis* (26.1) than in the species of subgenus *Mahonia* (5.8); the former are comparable to southern California desert shrubs (Mesomorphy value = 20.9: Carlquist and Hoekman 1985). Indeed, the figures for *Mahonia* species as a whole would have been even lower had the juvenile stem of *B. nervosa* been omitted. The greater xeromorphy of wood of subgenus *Mahonia* is likely related to the evergreen nature of leaves in that subgenus; in subgenus *Berberis*, deciduous leaves occur in at least some species (e.g., *B. vulgaris*). In a species with evergreen leaves, air embolisms in vessels are not tolerable if foliage is to be maintained, so greater wood xeromorphy is to be expected in a species with evergreen leaves.

The presence of large groupings of vessels, especially in latewood, is a xeromorphic feature of wood in Berberidaceae. Large groupings of vessels are indicative of xeromorphy in species in which vessels are accompanied by fiber-tracheids or libriform fibers rather than a background tissue of tracheids (Carlquist 1966, 1984b). Tracheids are associated with minimal vessel grouping because they are such an effective subsidiary conductive system that vessel grouping is a less effective strategy for achieving safety of conductive pathways. Therefore, wood with tracheids as the imperforate tracheary element type have evolved patterns that feature only minimal grouping of vessels (Carlquist 1984b). This principle is shown by *Jeffersonia diphylla*, in which tracheids are present and vessel grouping is minimal. The vasicentric tracheids in *Berberis* and *Nandina* are insufficient in number to deter vessel grouping; the much more abundant vasicentric tracheids of *Quercus* do apparently, deter vessel grouping, because the vessels in *Quercus* are solitary. The principle that tracheids deter vessel grouping

Fig. 21–24. Wood sections of Berberidaceae.—21. *B. paniculata*, radial section showing axial parenchyma strand (right) and septate fibers (left).—22. *B. haematocarpa*. Tangential section; narrow vessels and vasicentric tracheids are storied.—23–24. *Nandina domestica*.—23. Transection showing semi-ring porous condition.—24. Tangential section; rays are simple, multiseriate, tall. (Fig. 21, magnification scale above Fig. 8; Fig. 22, scale above Fig. 7; Fig. 23, 24, scale above Fig. 1.)



can be illustrated with *Jeffersonia* (Fig. 25, 26) in which tracheids are present and vessels are minimally grouped (vessel contacts in that species are likely the result of random placement of vessels). Wood in *Jeffersonia* has wood features other than vessel grouping that clearly indicate xeromorphy.

Although some species of *Berberis* are ring porous and the remaining species are semi-ring porous, the striking feature of the growth rings is the brevity of production of earlywood vessels within each growth ring. The extensive latewood in all of these species in which narrow vessels are intermixed with vasicentric tracheids is ideally designed for resistance to drought.

Many species of Berberidaceae—notably *Nandina domestica* and the *Mahonia* species of *Berberis*—produce rapid flushes of growth. This habit may be related to the storage of large quantities of starch in libriform fibers. Only *B. paniculata* has true axial parenchyma, but even this species has starch in libriform fibers. In the remaining species of *Berberis* and in *Nandina*, libriform fibers embedded in vessel groupings are the same length as vessel elements and with larger pit apertures and more pits than libriform fibers typically have. This is evidently the result of fiber dimorphism (Carlquist 1958, 1961) rather than modification of axial parenchyma of ancestral Berberidaceae. *Jeffersonia* has true axial parenchyma, as do the tubers of *Leontice*, in which fascicular secondary xylem consists of vessels and axial parenchyma without fibers. In *Jeffersonia* and *Leontice*, axial parenchyma likely plays a role in storage of starch during dry or cold seasons.

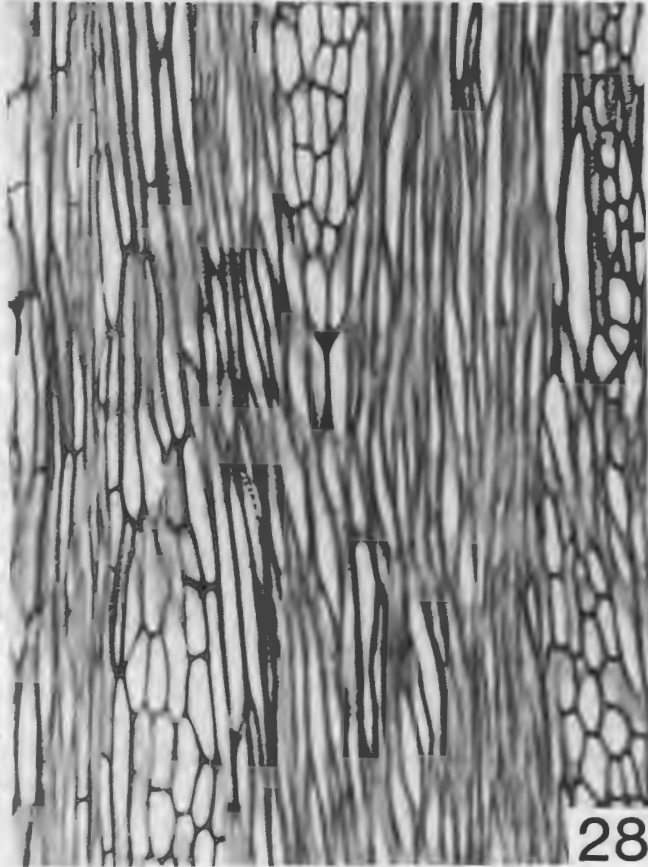
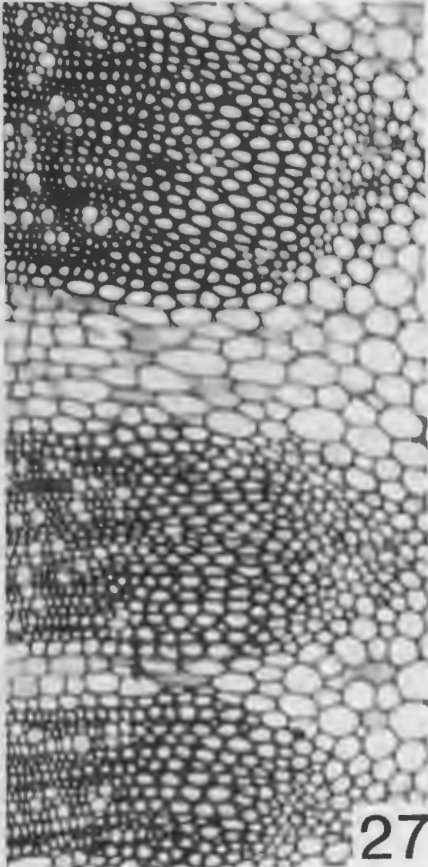
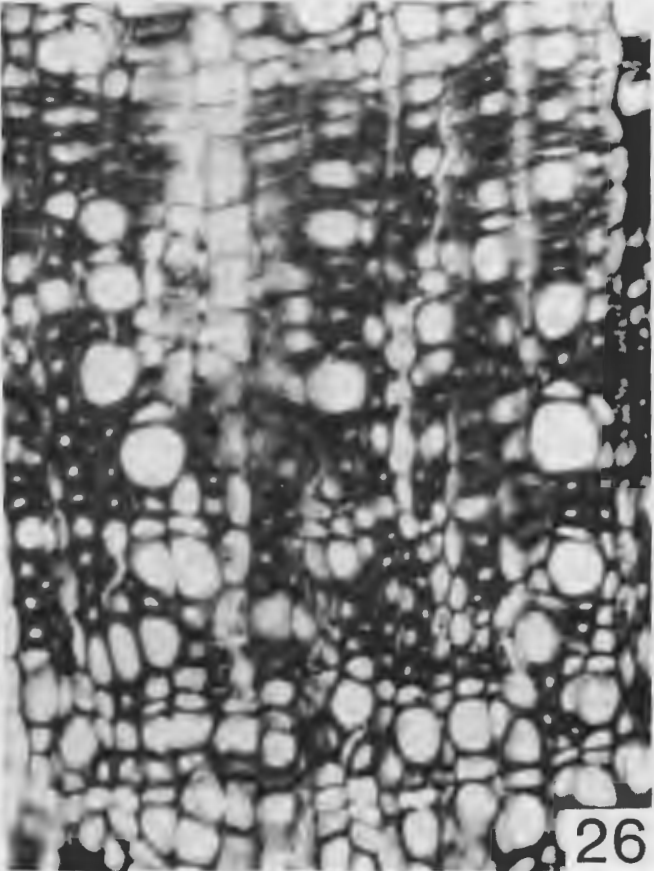
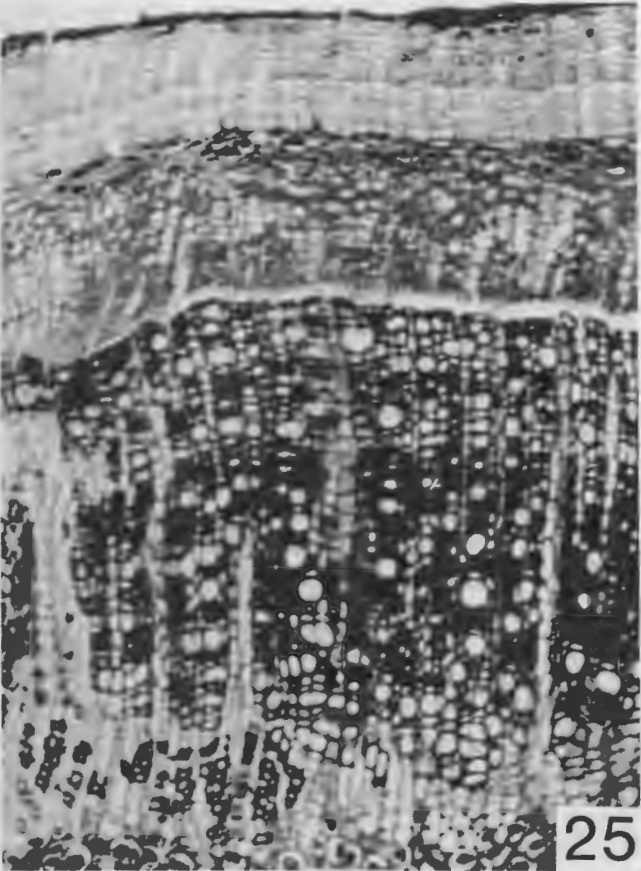
The wide, tall rays of *Berberis* and *Nandina* are reminiscent of those of Ranunculaceae (Carlquist 1995), Lardizabalaceae (Carlquist 1984a), and Papaveraceae (Carlquist and Zona 1988; Carlquist et al. 1994). The rays of Berberidaceae suggest little altered extensions of primary rays, but with procumbent cells predominant. Predominance of upright cells is to be expected in primary rays and early in the rays of secondary xylem, as exemplified by *Epimedium*, in which the available wood sample was from a twig. Although the more mature wood samples studied of *Berberis* and *Nandina* have fewer upright cells (which might be indicators of herbaceous ancestry) in rays than in, say, *Clematis*, *Helleborus*, or *Xanthorhiza* (Ranunculaceae), the width and height of rays in Berberidaceae could be cited as evidence of an herbaceous ancestry of Berberidaceae. The cladogram of Loconte and Estes

(1989, p. 572) hypothesizes a woody ancestry for the family, followed by a shift to herbaceousness, with a reversion to woodiness in the branch that terminates in *Berberis*–*Mahonia*. The cladistic scheme of Qiu et al. (1993, p. 594) place Papaveraceae as basal to the order, and thus by inference they might hypothesize an herbaceous ancestry for the order. However, the next branch that departs above Papaveraceae in their cladogram is Eupteleaceae (an arboreal family not put in Ranunculiflorae in other systems), then Lardizabalaceae (woody), Menispermaceae (woody), then Berberidaceae, and finally two Ranunculaceae, *Xanthorhiza* (woody) and *Caltha* (herbaceous). The cladograms of Loconte and Estes (1989) and Qiu et al. (1993) could both be interpreted as regarding *Berberis*–*Mahonia* as secondarily woody. Whether the family as a whole is herbaceous or woody is not so clear from phylogenetic studies done thus far. *Nandina* can be considered a basal genus in the family, in agreement with Loconte and Estes (1989), by virtue of its presence of fiber-tracheids rather than libriform fibers only, as in *Berberis*. *Nandina* is undeniably woody, but its habit of sympodial branching, with the production of canes of limited (a few years) duration rather than monopodial (single-trunked) stems with indefinite woodiness is very similar to habits found in Chloranthaceae (e.g., *Chloranthus*) and Piperaceae. Aristolochiaceae, Chloranthaceae, Piperaceae, and Saururaceae are among the families regarded as “paleoherbs,” the primitively herbaceous plants (or “diminutive rhizomatous to scrambling perennial herbs”) thought to be ancestral in angiosperms according to Taylor and Hickey (1992). Certainly several genera of Berberidaceae, such as *Caulophyllum*, *Jeffersonia*, and *Vancouveria*, are minimally woody herbs with sympodial habits. If *Nandina* were only a little less woody, it would conform to the paleoherb model. The fact that Berberidaceae are basically sympodial, like Chloranthaceae or Piperaceae, has not been generally noticed. This habit has important phylogenetic implications (see Carlquist 1992), especially in view of the paleoherb hypothesis.

SYSTEMATIC CONCLUSIONS

Berberis and *Mahonia* differ in the pinnate evergreen leaves of the latter; the former subgenus has simple leaves with an articulate petiole that suggests derivation from a pinnate-leaved ancestry. The materials

Fig. 25–30. Sections of secondary xylem of Berberidaceae.—25–26. *Jeffersonia diphylla*, transection of stem.—25. Lower magnification, showing diffuse porous condition (pith below; periderm and secondary phloem above).—26. Higher magnification; axial parenchyma is adjacent to some vessels.—27–28. *Epimedium pinnatum*.—27. Transection, pith at right; vessels are narrow.—28. Tangential section; ray cells are upright.—29–30. *Leontice leontopetalum*, sections of secondary xylem from succulent tuber.—29. Transection; fascicular xylem consists of vessels and parenchyma, no imperforate tracheary elements are present.—30. Tangential section; lateral wall pitting of vessel is pseudoscalariform. (Fig. 25, 27, 28, scale above Fig. 1; Fig. 26, 29, scale above Fig. 7; Fig. 30, scale above Fig. 8.)



of these two subgenera examined by Metcalfe and Chalk (1950) led them to claim that crystals are absent in rays of *Berberis*, present in rays of *Mahonia*. When more material is studied, neither subgenus is consistent in this regard (see above and Table 1, column 10). Subgenus *Berberis* has some ring porous woods (probably related to deciduous leaves in these species), but semi-ring porous woods may be found in both subgenera. The greater wood xeromorphy (as judged from quantitative vessel features) in subgenus *Mahonia* is likely related to the evergreen leaves of that subgenus, because water columns must be able to supply leaves during the most extreme days of a season. Thus, the two subgenera differ modally, but there are no characters in the wood that differentiate the subgenera in a binary way. The presence in one species of the supposedly more derived subgenus, *Berberis*, of true axial parenchyma is curious, but not incomprehensible; an exhaustive survey of the genus might provide explanations. Nowicke and Skvarla (1981) found that pollen grains of the two subgenera showed the same ranges of expression, and thus concluded that a single genus rather than two was justified.

The basal position of *Nandina* in the family, as claimed by the cladogram of Loconte and Estes (1989), receives support from the presence in *Nandina* of fiber-tracheids near the rays (plus libriform fibers distal to the ray margins), rather than libriform fibers only, as in *Berberis*. This is really the only difference between *Nandina* and *Berberis* in wood anatomy. The dramatic differences between the genera listed by Shen (1954), mentioned above, are likely based on error or incomplete information. Consequently, Shen's conclusion that *Nandina* should be segregated as Nandinaeae is not supported on the basis of wood anatomy, although Nowicke and Skvarla (1981) find that the pollen of *Nandina* is distinctive on the basis of its thick endexine. A single most parsimonious tree, based on *rbcL* sequence data by Dr. Youngdong Kim (personal communication), shows that *Nandina* does not branch from near the base of Berberidoideae, but rather is one of the branches within the subfamily Berberidoideae. His study encompasses only eight genera of Berberidaceae, and needs to be expanded to clarify phyletic interrelationships of berberidaceous genera further.

The *Epimedium* wood sample studied here had a few scalariform perforation plates. Although only simple plates were observed in the other Berberidaceae studied, the presence of scalariform plates in *Epimedium* should not be stressed. Scalariform perforation plates can be found in primary xylem of Menispermaceae and Ranunculaceae in which secondary xylem has only simple perforation plates (Bierhorst and Zamora 1965). This situation was found (see above) in *Berberis paniculata*. The wood sample of *Epimedium* was from a twig and therefore was likely to have some

juvenile characteristics (as it does in ray histology), characteristics of primary xylem that appear in earlier-formed secondary xylem. Therefore, the scalariform perforation plates in *Epimedium* do not necessarily contradict the derived position it is accorded in the cladogram of Loconte and Estes (1989).

The presence of tracheids in *Jeffersonia*, rather than fiber-tracheids or libriform fibers, is striking. Also noteworthy are the uniseriate (rarely biseriate) rays, which contrast with the wide, tall rays elsewhere in the family. Presence of vessels plus tracheids (but no libriform fibers) in *Clematis alpina* (L.) Miller (Carlquist 1995) is likely the result of great abundance of vasicentric tracheids. Vasicentric tracheids occur in other species of *Clematis*, with various quantities of libriform fibers (few fibers in some species). The condition in *C. alpina* appears to be the result of extinction of the fibers; the tracheids are the same length as vessel elements, so this fact, together with the various quantities of vasicentric tracheids in species of the genus, argues that the tracheids in *C. alpina* are vasicentric tracheids. In *Jeffersonia*, the tracheids are 1.53 times the length of vessel elements, and are not associated with fiber-tracheids or libriform fibers. Thus, one would be tempted to call the tracheids of *Jeffersonia* true tracheids (in the sense of Carlquist 1988) rather than vasicentric tracheids in species of the genus, argues that the tracheids in *C. alpina* are vasicentric tracheids. The apparently plesiomorphic nature of these tracheids runs counter to the derived position accorded *Jeffersonia* in the cladogram of Loconte and Estes (1989). The phylogenetic scheme of Terabayashi (1985), summarized by Loconte and Estes (1989, p. 56), shows a position for Epimedioideae (the subfamily to which *Jeffersonia* belongs) more basal than in the cladogram of Loconte and Estes. Studies by Dr. Youngdong Kim (personal communication) on phylogeny of genera of Berberidaceae and Ranunculaceae using *rbcL* sequence data show that *Jeffersonia* branches from the Berberidaceae clade more basally than any of the other genera he studied (single most parsimonious tree). Detailed study of wood anatomy of herbaceous Berberidaceae would be desirable for clarifying the significance of the distinctive wood reported here for *Jeffersonia*. The data of Nowicke and Skvarla (1981) underline the distinction between the subfamilies Berberidoideae and Epimedioideae. Wood data support this to the extent data from Epimedioideae are available. The difficulty in developing wood data from Epimedioideae lies in the herbaceous nature of most of the genera in this subfamily: features of primary xylem and juvenile wood, which are not directly comparable with the adult wood of *Berberis*, must be used in analysis of xylem of Epimedioideae. The anatomy of xylem with respect to habit is worthy of study in Epimedioideae, but the possible retention of primitive

features in this subfamily is also potentially very interesting.

Discussion of the relationships of Berberidaceae to other families, mentioned above in connection with evolution of habit, would be premature on the basis of the present evidence. When the present series of papers is concluded with a study of Menispermaceae, detailed analysis of the wood of Ranunculiflorae will be at hand, and conclusions about the interrelationships of the component families can be attempted.

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