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Sherwin Carlquist

*Santa Barbara Botanic Garden*

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## WOOD AND BARK ANATOMY OF RANUNCULACEAE (INCLUDING *HYDRASTIS*) AND GLAUCIDIACEAE

SHERWIN CARLQUIST

*Santa Barbara Botanic Garden  
1212 Mission Canyon Road  
Santa Barbara, California 93105<sup>1</sup>*

### ABSTRACT

Wood anatomy of 14 species of *Clematis* and one species each of *Delphinium*, *Helleborus*, *Thalictrum*, and *Xanthorrhiza* (Ranunculaceae) is compared to that of *Glaucidium palmatum* (Glaucidiaceae) and *Hydrastis canadensis* (Ranunculaceae, or Hydrastidaceae of some authors). *Clematis* wood has features typical of wood of vines and lianas: wide (earlywood) vessels, abundant axial parenchyma (earlywood, some species), high vessel density, low proportion of fibrous tissue in wood, wide rays composed of thin-walled cells, and abrupt origin of multiseriate rays. Superimposed on these features are expressions indicative of xeromorphy in the species of cold or dry areas: numerous narrow latewood vessels, presence of vasicentric tracheids, shorter vessel elements, and strongly marked growth rings. Wood of *Xanthorrhiza* is like that of a (small) shrub. Wood of *Delphinium*, *Helleborus*, and *Thalictrum* is characteristic of herbs that become woodier: limited amounts of secondary xylem, parenchymatization of wood, partial conversion of ray areas to libriform fibers (partial raylessness). Wood of Ranunculaceae other than *Clematis* has numerous narrow vessels, probably an adaptation to cold more than drought. *Glaucidium* has occasional scalariform perforation plates like those almost universally present in *Paeonia*, but the two genera differ strongly in other wood features. Wood of *Hydrastis* (scalariform perforation plates occasional in primary xylem, rare in secondary xylem) accords with the idea that *Hydrastis* is a lineage that separated from the base of Ranunculaceae. Features that ally Ranunculaceae with other families of Ranunculiflorae include presence of wide multiseriate rays (without accompanying uniseriate rays), vessel restriction patterns, and storied structure. Woodiness in Ranunculaceae is probably secondary, at least to some extent; the woodiness of *Xanthorrhiza*, thought by some to represent a primitive genus in the family, could be either primary or secondary.

Key words: Berberidales, *Glaucidium*, *Hydrastis*, *Paeonia*, Papaverales, Ranunculaceae, Ranunculiflorae, storied wood structure, vessel restriction patterns.

### INTRODUCTION

Phylogenetically, Ranunculaceae have been of interest because they have occupied a near-basal position in many systems. Most recently, the cladograms of Chase et al. (1993) follow this pattern on the basis of *rbcL* data. Currently, Ranunculaceae are also of interest in relation to the paleoherb hypothesis (Taylor and Hickey 1992). Anatomy of wood potentially offers character expressions that illuminate these concepts. Because Ranunculaceae contain a few woody genera as well as many herbaceous genera, it is a key family in understanding primary versus secondary woodiness, a chief concern of the paleoherb hypothesis.

Ranunculiflorae (a superorder that equates with the orders Berberidales, Papaverales, Ranunculales, or Rhoadales of earlier authors) consists of five main families: Berberidaceae, Lardizabalaceae, Menispermaceae, Papaveraceae, and Ranunculaceae, as well as some smaller satellite families. Studies on wood anat-

omy of these families may help understand the interrelationships of these taxa. The present essay continues a series begun with studies of Lardizabalaceae (Carlquist 1984) and Papaveraceae (Carlquist and Zona 1988; Carlquist et al. 1994).

Despite the fact that *Clematis* contains about 250 species of woody vines (Willis 1973), only a few species have been investigated with respect to wood anatomy. Accounts have been offered by Schmidt (1941), Metcalfe and Chalk (1950), Greguss (1959), Grosser (1977), Schweingruber (1978, 1992), and Sieber and Kucera (1980). However, these accounts are incomplete, contradictory, and offer some inaccuracies. Wood anatomy of two species of Ranunculaceae in genera other than *Clematis* has been briefly described by Schweingruber (1992), underlining the lack of wood data for the family. In order to compare wood anatomy of Ranunculaceae to that of other Ranunculiflorae, a more nearly complete and accurate understanding of wood in the family than currently at hand is required. In this connection, information is needed on wood of two genera traditionally included in Ranunculaceae (e.g., Prantl 1891): *Hydrastis* and *Glaucidium*. Recently excluded from Ranunculaceae as

<sup>1</sup> Address for correspondence with author: 4539 Via Huerto, Santa Barbara, CA 93110. This study was begun at the Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, CA 91711.

monogeneric families, *Glaucidium* and *Hydrastis* have been the objects of research, chiefly on embryology and floral anatomy (Tamura 1972; Tobe 1981; Tobe and Keating 1985). Keener (1993) has offered a summary of work to date on *Hydrastis*, and concludes that it can be regarded as a subfamily within Ranunculaceae. There is now general agreement that *Paeonia* should be excluded from Ranunculaceae as Paeoniaceae and perhaps placed near the families of Ranunculiflorae (e.g., Thorne 1992), although not within the group of families cited above as Ranunculiflorae. Wood anatomy may prove significant in comparing *Paeonia* with Glaucidiaceae, Hydrastidaceae, and Ranunculaceae.

Wood anatomy of Glaucidiaceae and Ranunculaceae is worthy of examination with respect to habits and habitats. The woody vine *Clematis* ranges from upland tropical to temperate alpine sites. The "woody herb" (herb, with various degrees of secondary xylem production in stems near the ground or beneath the ground surface) habits of some Ranunculaceae should be taken into account in studies of wood anatomy. Of the genera included in this study, only *Xanthorhiza* qualifies as a shrub or subshrub, an understory element in moist temperate forests. Some species of the North Temperate genus *Delphinium* have a short, upright, woody caudex. *Helleborus* (Mediterranean region to the Caucasus Mountains) can be a subshrub with moderately woody stems (*H. foetidus* L.), but most species, such as *H. viridis* studied here, have rhizomes with only a little secondary xylem. *Hydrastis* (two species of moist temperate forests: *H. canadensis* and *H. jezoensis* Sieb. & Zucc.) has succulent underground rhizomes. *Glaucidium* has a habit similar to that of *Hydrastis*, but with more condensed rhizomes; the single species is confined to montane northern Japan (Prantl 1891). Genera with minimal secondary xylem have been excluded from this study.

Are Ranunculaceae primarily or secondarily woody, or have both phyletic curricula occurred within the family? Wood anatomy examined in this context can cast light not only on this family but on others (such as Paeoniaceae or Papaveraceae) as well. Because Ranunculaceae might be close to the "paleoherbs" hypothesized to be primitive dicotyledons, this question has broader phyletic implications.

Because some of the samples studied here had intact bark portions, some data on bark anatomy are reported. These may be of interest both to systematics within the family and to considerations of familial interrelationships.

#### MATERIALS AND METHODS

Wood samples were available in dried form with the exception of specimens of *Clematis apiifolia*, *C. cir-*

*rhosa*, and *Glaucidium palmatum* (see Table 1); portions of these three were preserved in 50% aqueous ethyl alcohol. Wood of genera other than *Clematis*, *Glaucidium*, and *Thalictrum* were derived from specimens in the herbarium of the Rancho Santa Ana Botanic Garden. Some of the wood samples of *Clematis* were obtained from xylaria (see Table 1), and for these I am especially indebted to Dr. Regis Miller of the Forest Products Laboratory (MADw, SJRW) and to Dr. Roger Dechamps of the Musée Royale de l'Afrique Centrale, Tervuren, Belgium (Tw). The woods of *Clematis* documented by my collection numbers (Table 1) are all from cultivated specimens; herbarium specimens to document my collections are deposited at the Rancho Santa Ana Botanic Garden. I am grateful to the Municipal Botanic Garden, Dunedin, New Zealand, and to the Rancho Santa Ana Botanic Garden for wood from cultivated specimens included in this study. The stem of *Thalictrum polycarpum* was collected from cultivated plants in the Santa Barbara Botanic Garden.

The localities of noncultivated specimens are as follows: *C. dioscoriifolia*, ruderal, New York City; *C. haenkeana*, Ecuador; *C. iringaensis*, Shaba, Central Africa; *C. ligusticifolia*, dry riverbank near Yakima, Washington; *C. pauciflora*, Santa Ana Mountains, California; *C. pickeringii*, Fiji; *Delphinium elatum*, 83 miles from Novosibirsk on highway to Bernal, Siberia, Russia; *Glaucidium palmatum*, Mt. Shirano near Lake Chuzenji, Japan; *Helleborus viridis*, Montelupo, Italy; *Hydrastis canadensis*, Neversink, Berks Co., Pennsylvania; *Xanthorhiza apiifolia*, MacDowell Co., North Carolina. The identity of the specimen cited here as *C. haenkeana* was determined with the aid of comments from Dr. Frederick Essig and Dr. Nancy Moreno.

Dried wood samples of both *Clematis* and the remaining genera (incorporating bark portions) provided difficulties in sectioning because of wideness of vessels and (in bark) contrast between softness of phloem and hardness of fibers. These problems were solved by using a technique involving boiling the samples in water, softening them in ethylenediamine, embedding them in paraffin, and sectioning them on a rotary microtome (Carlquist 1982). Most sections were stained in a safranin-fast green combination. Some of the paraffin sections were affixed to SEM aluminum stubs exactly as paraffin sections are mounted on glass slides; the paraffin was then dissolved with xylene so that the sections could be studied by SEM. An ISI WB-6 scanning electron microscope was used. Macerations were prepared by means of Jeffrey's Solution and stained with safranin. Even though most wood samples had been dried rather than preserved in liquid, preservation of starch and of primary walls proves excellent with this method.

Table 1. Wood characteristics of Ranunculaceae and Glaucidiaceae.

Species	Collection	1 VG	2 VD	3 VM	4 VL	5 VW	6 TL	7 F/V	8 TW	9 AP	10 RW	11 M
<b>Ranunculaceae</b>												
<i>Clematis alpina</i> Mill.	Carlquist 8051	∞	13	783/1440	152	2-5	—	—	—	VSEW+IVLW	>20	1.4
<i>C. apiifolia</i> DC.	Carlquist 8050	8.3	37	67/121	198	2-5	378	1.91	2-4	VSEW+IVLW	6.5	7.9
<i>C. chrysocoma</i> Franch.	Carlquist 8056	>50	23	548/823	201	2-5	375	1.87	2-4	VSEW+IVLW	>15	5.6
<i>C. cirrhosa</i> L.	Carlquist 8053	>50	20	229/368	207	4-5	347	1.68	5	VSEW+IVLW	12.2	11.3
<i>C. dioscoriifolia</i> Lev. & Van.	MADw-2756	>50	23	261/422	244	2-6	423	1.73	6	VAEW+VSLW	>10	13.1
<i>C. haenkeana</i> Presl	SJRw-34198	8.3	37	67/121	245	3-11	520	2.12	7	VAEW+VSLW	11.8	74.9
<i>C. iringaensis</i> Engler	Tw-47313	1.7	97	18/36	225	2-6	501	2.23	5	VAEW+VALW	8.1	606.0
<i>C. lasiantha</i> Nutt.	cult. RSABG	>50	17	571/723	195	5-8	309	1.58	4	VSEW+IVLW	10.8	4.6
<i>C. ligusticifolia</i> Nutt.	MADw-45101	>50	26	394/471	198	2-5	306	1.55	4	VSEW+IVLW	11.0	10.9
<i>C. montana</i> Buch-Ham.	Carlquist 8049	>50	12	404/593	164	4	372	2.27	4	VSEW+IVLW	13.8	3.3
<i>C. pauciflora</i> Nutt.	Wolf 2296 (RSAw)	∞	20	524/654	195	2-5	364	1.67	5	VAEW+IVLW	8.1	6.0
<i>C. pickeringii</i> A. Gray	SJRw-28381	11.3	37	121/205	253	2-7	482	1.91	5	VAEW+VSLW	>10	45.7
<i>C. tangutica</i> Korsh.	Carlquist 8107	>50	15	500/569	181	4	338	1.87	4	VSEW+IVLW	13.1	4.8
<i>C. vitalba</i> L.	Carlquist 8109	>50	29	193/259	244	2-7	422	1.73	5	VAEW+IVLW	6.0	27.3
<i>Delphinium elatum</i> L.	Smirnov 392	2.8	31	55/112	135	2	312	2.31	2-7	VS, P	3.0	37.4
<i>Helleborus viridis</i> L.	Sinclair 8755	4.1	13	434/964	142	5	306	1.73	1	IV	>10	1.9
<i>Hydrastis canadensis</i> L.	Brumbach 8592	3.7	13	176/386	160	1	250	1.56	1	P	>10	5.4
<i>Thalictrum polycarpum</i> Wats.	cult. SBBG	3.2	15	331/482	204	2	373	1.83	3	VS	4.4	6.3
<i>Xanthorrhiza apiifolia</i> L'Her.	Thorne 19304	4.5	20	198/285	167	1	342	2.05	3	Rare	10.3	11.7
<b>Glaucidiaceae</b>												
<i>Glaucidium palmatum</i> S. & Z.	Carlquist 15726	4.5	34	101/149	159	2	313	1.97	5	P, IV	>10	36.3

Key to columns: 1 (VG), mean number of vessels per group; 2 (VD), mean vessel diameter,  $\mu\text{m}$ ; 3 (VM), mean number of vessels per  $\text{mm}^2$ —the first figure gives density of vessels in transections with rays included, the second the vessel density of fascicular areas only; 4 (VL), mean vessel element length,  $\mu\text{m}$ ; 5 (VW), vessel wall thickness,  $\mu\text{m}$ ; 6 (TL), mean length of imperforate tracheary elements (libriform fibers),  $\mu\text{m}$ ; 7 (F/V), ratio, imperforate tracheary element length divided by vessel element length; 8 (TW), wall thickness of imperforate tracheary elements (libriform fibers),  $\mu\text{m}$ ; 9 (AP), axial parenchyma types: EW = earlywood, LW = latewood, IV = intervacular, P = pervasive, VA = vascentric abundant, VS = vascentric scanty; 10 (RW), mean width of ray at widest point, cells; 11 (M), Mesomorphy ratio (vessel diameter times vessel element length divided by vessels per  $\text{mm}^2$ ).

Quantitative data are offered in Table 1. Because many vessels are flattened radially, tangentially, or otherwise, a compromise lumen diameter (intermediate between widest and narrowest measurement) was estimated for vessels noncircular in outline as a way of representing conductive capacities more accurately. Exceptional care was taken to differentiate accurately among narrow vessels, vasicentric tracheids, and libriform fibers as seen in transection; the stains used aided cellular identification. Macerations permitted identification of vasicentric tracheids, which cannot be distinguished from narrow vessel elements with certainty in longisections. Vasicentric tracheids have been overlooked in *Clematis*, since there are no previous reports of them in the genus other than mine (Carlquist 1985). These tracheids are called vasicentric rather than vascular for reasons given there (Carlquist 1985, p. 47). Terms for vessel restriction patterns, ray types, and axial parenchyma types are based on Carlquist (1988). For other terms, the IAWA Committee on Nomenclature (1964) has been used because of its accuracy and applicability to purposes other than data computerization. For each quantitative feature described, means were derived from 25 measurements except for vessel wall thickness, libriform fiber wall thickness, and dimensions of lateral wall pits on vessels; for these features, typical conditions were selected for measurement.

#### ANATOMICAL DESCRIPTIONS

The assumption inherent in most descriptions of wood anatomy is that imperforate tracheary elements ("fibers") are distributed randomly. Likewise, descriptions of vessel distribution, other than those that relate to growth rings, lead one to assume random distribution of vessels. In *Clematis*, however, libriform fibers are commonly in a pattern that can be called ray-adjacent, along the edges of fascicular areas. Thus, vessels are infrequently adjacent to rays, and one could view this phenomenon as a vessel restriction pattern. Ray-adjacent distribution of libriform fibers is present in all of the *Clematis* species studied here except for *C. alpina*, in which libriform fibers are absent (Fig. 4). Ray-adjacent fiber distributions are illustrated here for *C. apiifolia* (Fig. 5), *C. chrysocoma* (Fig. 6), *C. cirrhosa* (Fig. 8), *C. dioscoriifolia* (Fig. 3), *C. haenkeana* (Fig. 2), *C. iringaensis* (Fig. 1), *C. pickeringii* (Fig. 7), and *Xanthorhiza apiifolia* (Fig. 20). In the illustrations of Greguss (1959) and Schweingruber (1992) for

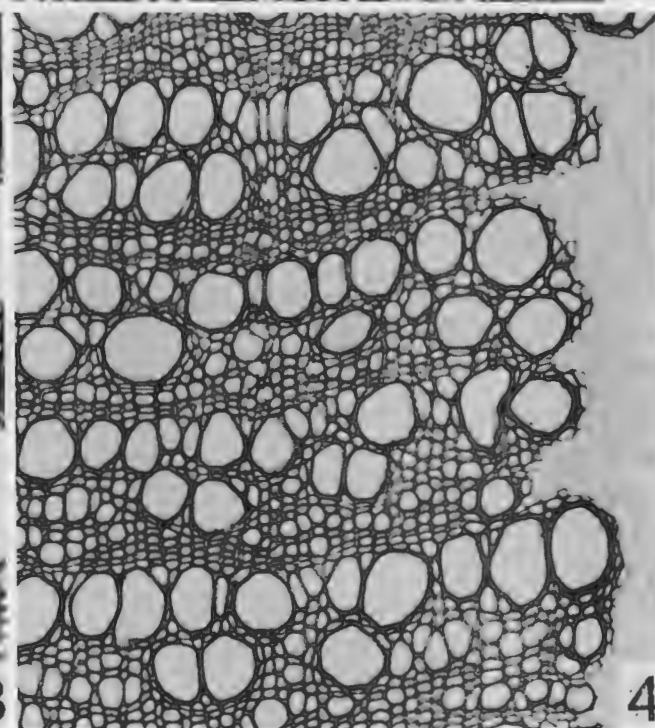
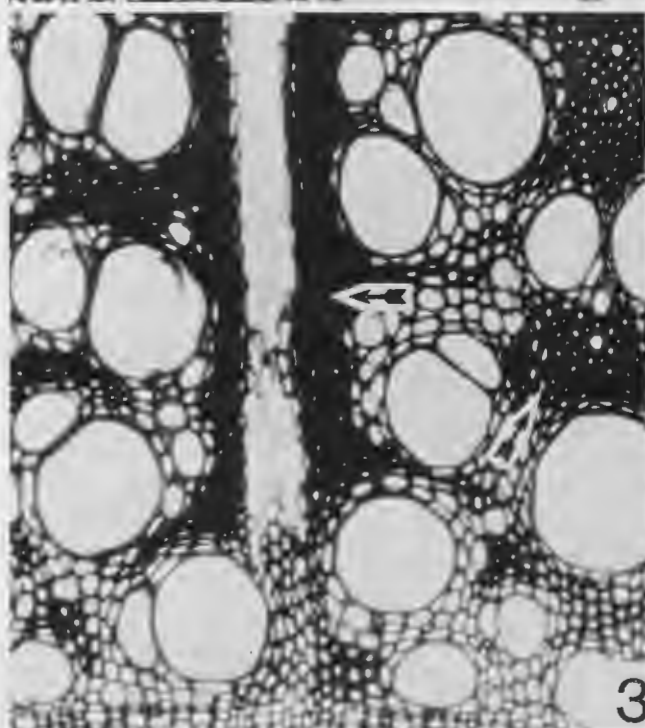
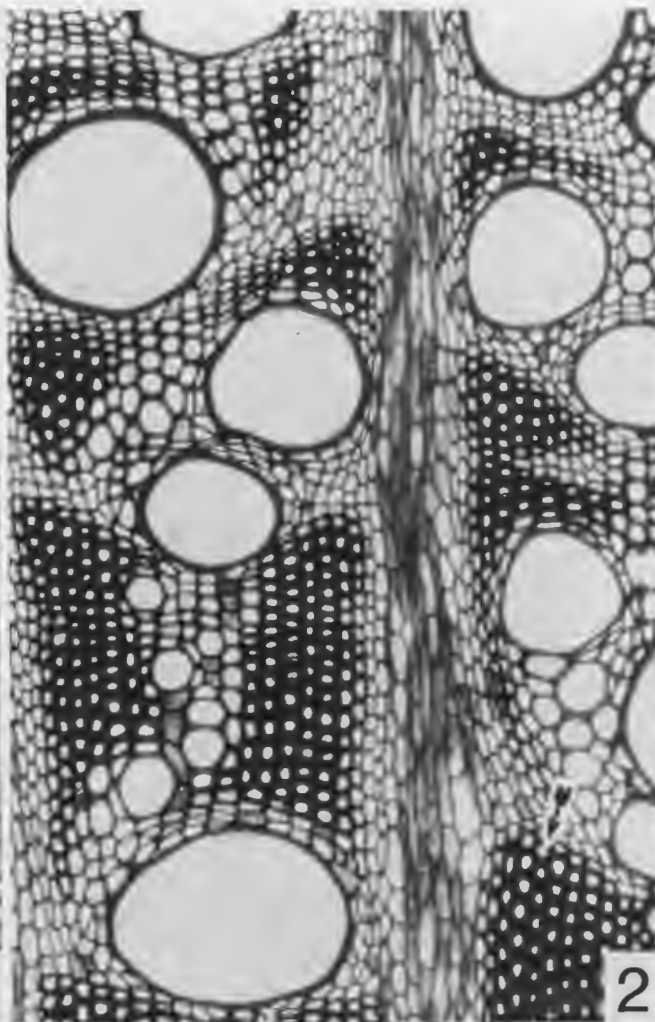
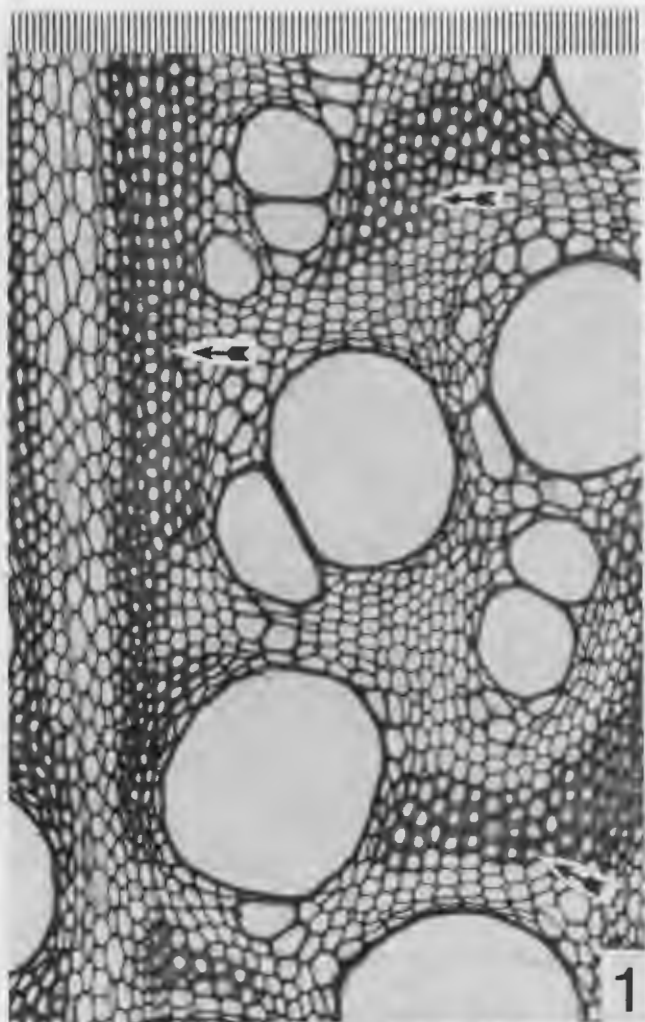
*C. vitalba* as well as by Schweingruber (1992) for *C. campanulata*, *C. cirrhosa*, and *C. viticella* L., ray-adjacent libriform fibers are evident, but these authors do not mention this phenomenon. Ray-adjacent fibers are also present prior to origin of a multiseriate ray, as in *C. chrysocoma* and *C. vitalba*. Libriform fibers are also present in a mid-growth-ring position (comparatively infrequent earlier or later in growth rings) in fascicular areas of wood of *C. dioscoriifolia* (Fig. 3), *C. cirrhosa*, and *C. iringaensis* (Fig. 1). Libriform fibers in positions abaxial to vessels were observed in *C. apiifolia* (Fig. 5) and *C. ligusticifolia*. Libriform fibers are very scarce in *Helleborus viridis*, but are always present in a ray-adjacent position. In *Delphinium elatum* (Fig. 16) and *Glaucidium palmatum* (Fig. 22), libriform fibers are abundant in earlywood, chiefly absent in latewood (some patchy or irregular distributions may be found, however), and tend to be more abundant in the earlier growth rings (which are wider) than in the later ones, as shown for *Glaucidium* (Fig. 22). In latewood of *Delphinium elatum* and *Glaucidium palmatum*, axial parenchyma tends to substitute for libriform fibers. The distribution of libriform fibers in *Hydrastis canadensis* is similar (Fig. 26), but the fibers are in the middle of growth rings.

If one looks at the above phenomenon from the aspect of vessel distribution rather than libriform fiber distribution, a clear example of restriction of vessels to the central portions of fascicular xylem portions is seen in *Xanthorhiza apiifolia* (Fig. 20, 21).

#### Growth Rings

Growth rings are present in all Ranunculaceae studied, despite the fact that three species of *Clematis* are from tropical latitudes: *C. haenkeana* (Fig. 2, 15), *C. iringaensis* (Fig. 1), and *C. pickeringii* (Fig. 7). Seasonality in rainfall rather than temperature may influence growth ring formation in these species. Vasicentric tracheids are absent in these tropical upland species. In the temperate species of *Clematis*, all of which have vasicentric tracheids, growth rings are highly pronounced and vasicentric tracheids (intermixed with narrow vessels) occur in latewood but at least a few very wide vessels are in earlywood. All of the temperate species of *Clematis*, as well as *Xanthorhiza apiifolia* and *Thalictrum polycarpum*, have growth rings of this nature, which are illustrated here for *C. alpina* (Fig. 4), *C. apiifolia* (Fig. 5), *C. chrysocoma* (Fig. 6), *C. cirrhosa* (Fig. 8), *C. dioscoriifolia* (Fig. 3), and

Fig. 1–4. Transections of *Clematis* wood.—1. *C. iringaensis*; ray-adjacent fibers flank the ray at left; axial parenchyma is abundant.—2. *C. haenkeana*; strands of fibers occur at various points in the growth rings.—3. *C. dioscoriifolia*; cells of ray near center have thicker lignified walls below, but distal part of ray has thin primary walls on ray cells (some collapsed due to drying of wood sample).—4. *C. alpina*; five growth rings are shown. Collections given in Table 1. Arrows indicate zones of libriform fibers. (Scale for Fig. 1–4 above Fig. 1 [divisions = 10  $\mu$ m].)





*Xanthorhiza apiifolia* (Fig. 20). The abundance of narrow latewood vessels in these species accounts for the fact that they have much smaller mean vessel diameter (Table 1, column 2) as compared to *C. haenkeana*, *C. iringaensis*, and *C. pickeringii*. Growth rings are extremely narrow in *C. alpina* (Fig. 4). Lack of vessels characterizes latewood in *Helleborus foetidus* according to Schweingruber (1992). Latewood of *Delphinium elatum* (Fig. 16) and *Glaucidium palmatum* (Fig. 22) features axial parenchyma instead of libriform fibers. If one views transections of fascicular areas of *Clematis alpina* (Fig. 4) and *C. pickeringii* (Fig. 7), one sees apparent "indentations" in their outline. These are due to presence of thin-walled axial parenchyma in latewood, adjacent to thin-walled ray cells.

### Vessel Grouping

Mean number of vessels per group (Table 1, column 1) ranges from 1.7 in *C. iringaensis* (Fig. 1) to an infinite number in *C. alpina* (Fig. 4), in which the entirety of a fascicular secondary xylem area except for scattered vasicentric tracheids and a few axial parenchyma cells consists of vessels. In most species of *Clematis*, the number of vessels per group averages more than 50 and cannot be counted exactly (Table 1, column 1). Species with such extensive groupings include *C. apiifolia* (Fig. 5), *C. chrysocoma* (Fig. 6), *C. cirrhosa* (Fig. 8), and *C. dioscoriifolia* (Fig. 3). Vessel grouping is least in the species of tropical latitudes: *C. haenkeana* (Fig. 2), *C. iringaensis* (Fig. 1), and *C. pickeringii* (Fig. 7). Relatively low numbers of vessels per group (2.8–4.5) characterize the genera studied other than *Clematis*. All of these genera are woody herbs of moist forest, whereas *Clematis* is a woody vine of varied habitats. Correlations between quantitative vessel features and ecology are considered at the end of this paper.

### Vessel Diameter

Mean vessel diameter (Table 1, column 2) is not a good indicator of the diversity of vessel diameter within a *Clematis* wood section. As the transections (Fig. 1–8) show, vessels exceeding 200  $\mu\text{m}$  may be found in the early wood of most species. Vessels that wide do not occur in *C. alpina* (Fig. 4), *C. cirrhosa* (Fig. 8), *C. montana*, *C. pauciflora*, or *C. tangutica*, but the widest vessels in these species are at least 100  $\mu\text{m}$  in diameter. In macerations, very wide vessels are mostly wider than long. The discrepancy between the wide-

ness of earlywood vessels and the relatively small mean vessel diameter in the various species of *Clematis* is explained by the large number of narrow latewood vessels. In this respect, *Clematis* contrasts with the other genera: although the other genera have mean vessel diameters much like those in *Clematis*, they have relatively uniform vessel diameter and lack notably wide vessel elements (Fig. 16, 18, 20, 22). The three tropical species of *Clematis* have relatively wide mean vessel diameters; these species have relatively few narrow latewood vessels compared to the temperate species.

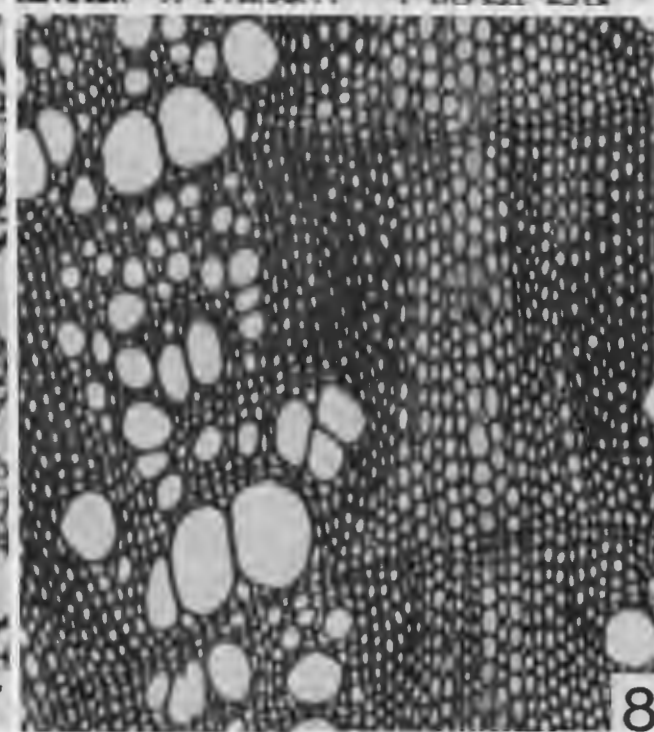
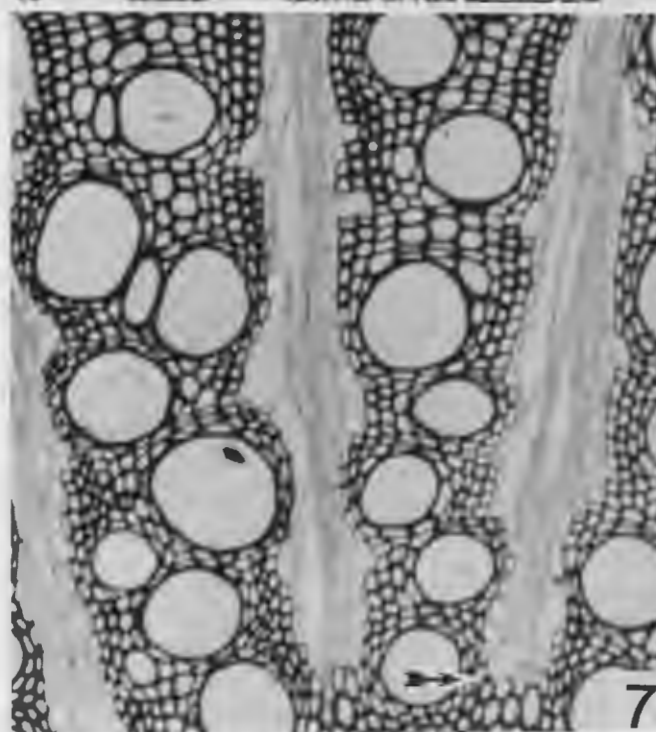
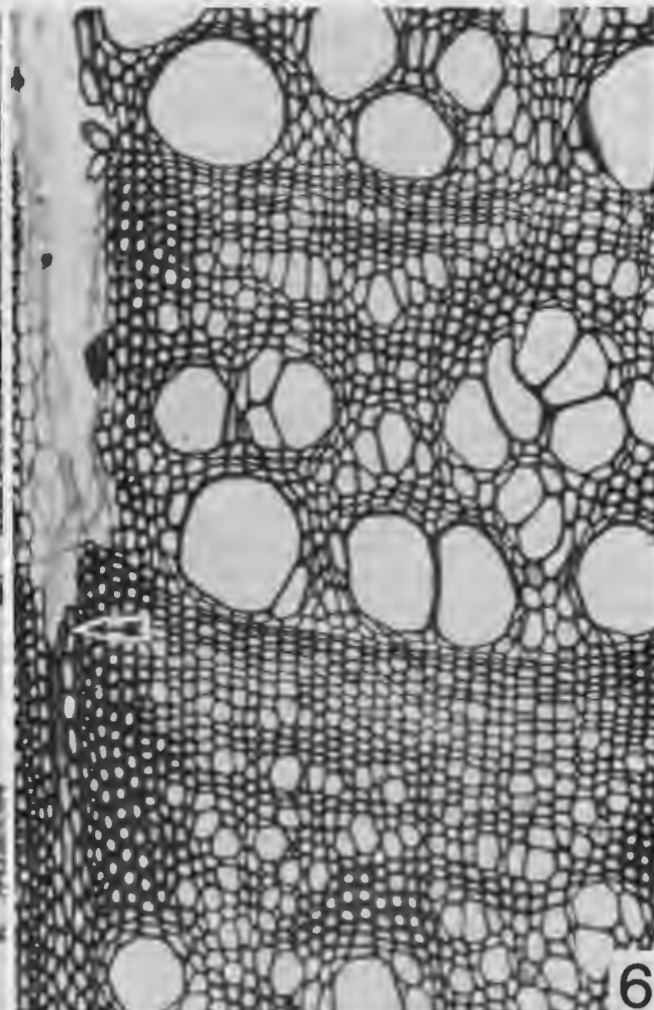
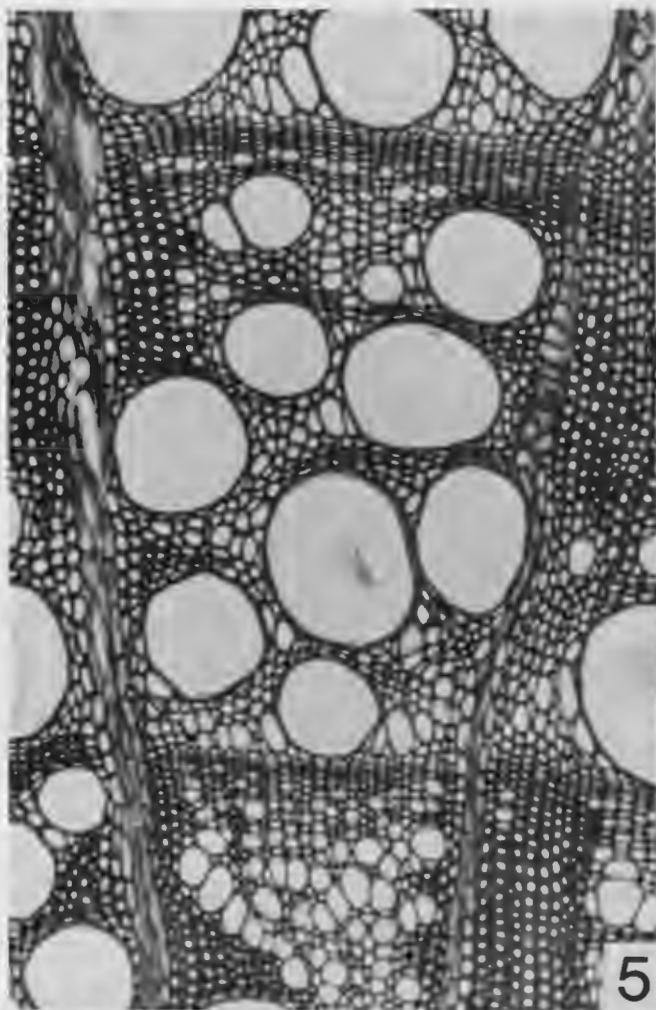
### Vessel Density

Mean vessel density is estimated in most studies of dicotyledon wood by averaging the vessel number as seen in random scans of transections. Such scanning does not avoid rays, which do not comprise a large percentage of a transection in most dicotyledon woods. In the genera studied here, however, rays are large, and so vessel density has been calculated in Table 1, column 3, in two ways: the first value is based on scans that include rays, the second figure is based on scans of fascicular xylem only. A high value for vessel density is evident in *Clematis*. The presence of large numbers of narrow latewood vessels accounts for this. The genera other than *Clematis* have relatively low vessel density, in part because large patches of axial parenchyma are present in some of them (Fig. 16, 22, 26). In *Helleborus viridis* (Fig. 18), there are no large patches of axial parenchyma but numerous narrow vessels, so vessel density is relatively high.

### Vessel Element Length

Mean vessel element length (Table 1, column 4) is greater in the tropical species of *Clematis* (*C. haenkeana*, *C. iringaensis*, *C. pickeringii*) than in the temperate species. The species with the shortest vessel element length (152  $\mu\text{m}$ ) is *C. alpina*. Except for this species and *C. montana*, the genera other than *Clematis* mostly have shorter vessel elements than do *Clematis* species. However, these differences between *Clematis* and the other genera with respect to vessel element length is not very great. For one species, *C. pauciflora*, vessel element length was calculated separately for wide earlywood vessel elements (vessel elements as wide as long or wider as seen in macerations) and narrow latewood vessel elements (a mean combining all vessel elements is shown in Table 1). In

Fig. 5–8. Transections of *Clematis* wood.—5. *C. apiifolia*; note marked contrast in vessel diameter between earlywood and latewood vessels.—6. *C. chrysocoma*; bands of fibers flank ray, left.—7. *C. pickeringii*; no growth rings are evident.—8. *C. cirrhosa*; ray cells resemble fibers in wall thickness; libriform fibers are adjacent to ray. Collections given in Table 1. Arrows indicate points at which ray cell walls change from lignified to unlignified. (Scales for Fig. 5–8 above Fig. 1.)





this species, mean length of wide vessel elements = 162  $\mu\text{m}$ , mean length of narrow vessel elements = 217  $\mu\text{m}$ , and mean length of vasicentric tracheids = 218  $\mu\text{m}$ . These data suggest that there is some intrusive growth in narrow vessel elements compared to wide vessel elements as they mature.

#### Vessel Wall Thickness

In *Clematis*, vessel wall thickness (given in Table 1, column 5) shows a range: less in narrow vessels, much more in wider vessels. This can be seen at lower magnifications in Fig. 1 and 2, but is much more evident in Fig. 15. The genera other than *Clematis* have uniformly thin vessel walls except for *Helleborus viridis*, in which the vessel walls are notably thick (Fig. 18).

#### Vessel Morphology

Simple perforation plates exclusively were observed in all species except *Glaucidium palmatum* (Fig. 25) and *Hydrastis canadensis*. In *H. canadensis*, a single plate with one bar was seen, all other plates were simple. Tobe and Keating (1985) figure scalariform plates with 3–10 bars in *H. canadensis*, but these are metaxylem perforation plates; they report that most perforation plates in the species are simple. Among the species studied here, only in *Glaucidium palmatum* are scalariform perforation plates found in appreciable numbers, and even in my material of this species, only one of about 25 secondary xylem plates was observed to have a single bar. The perforation plate shown in Fig. 25 was the only one observed to have more than one bar. A similar perforation plate of *Glaucidium palmatum* is figured by Tamura (1972), who terms it “reticulate,” although that plate would be termed scalariform by most workers. Tamura (1972) reports that most perforation plates in *Glaucidium palmatum* are simple; thus, his observations are in accord with mine.

Lateral wall pitting of vessels (intervascular pitting) consists of alternate circular to oval pits in all species studies except *Glaucidium palmatum*. In that species (Fig. 25), lateral wall pitting is either scalariform or pseudoscalariform. Scalariform pits are defined as having a horizontal dimension extending the entire width of a vessel wall face (vessels angular in transectional outline are assumed). Pseudoscalariform pits are basically alternate but laterally widened, and their horizontal axes do not coincide with vessel wall faces. The vertical height of lateral wall pits is 8  $\mu\text{m}$  in *Clematis*

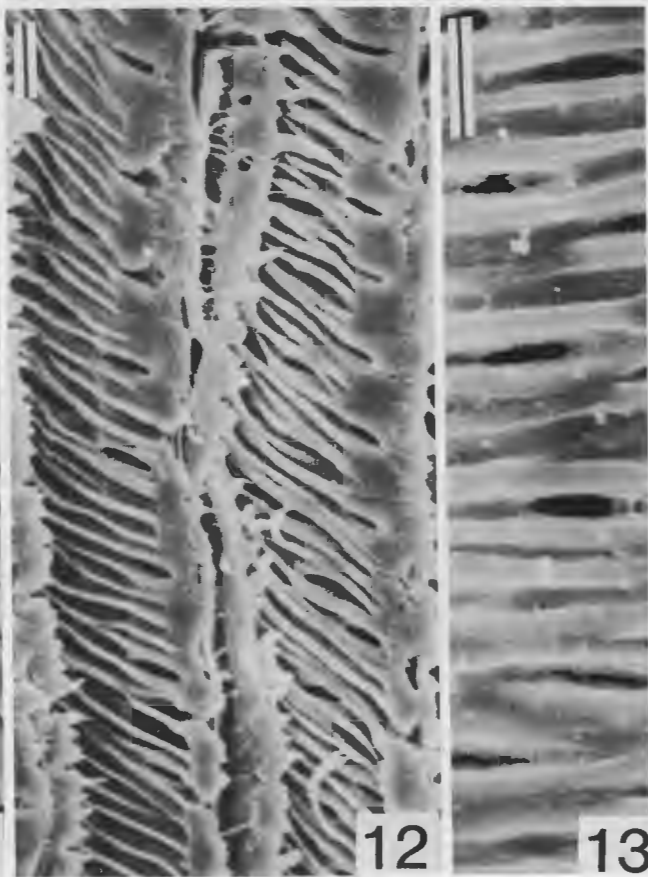
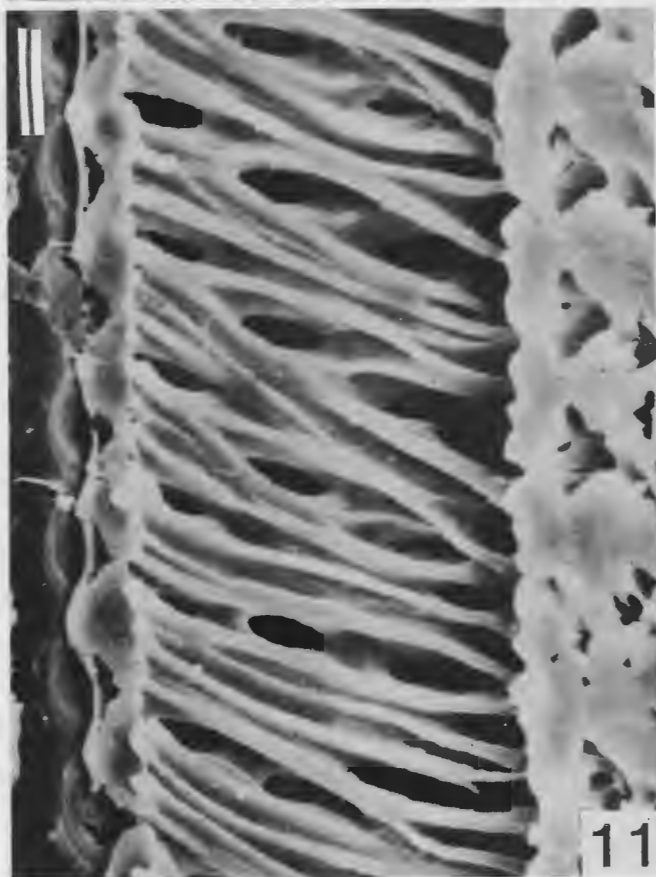
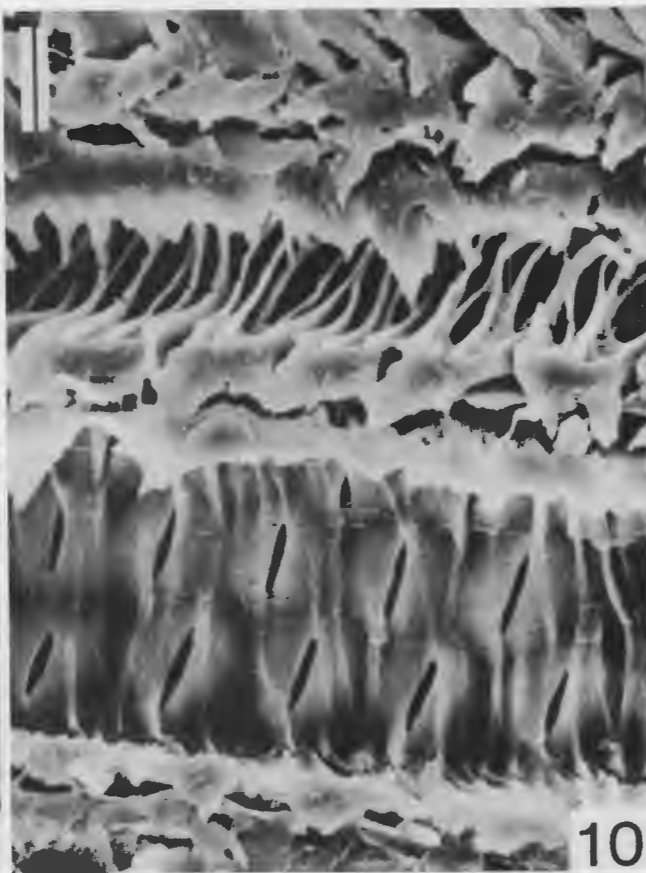
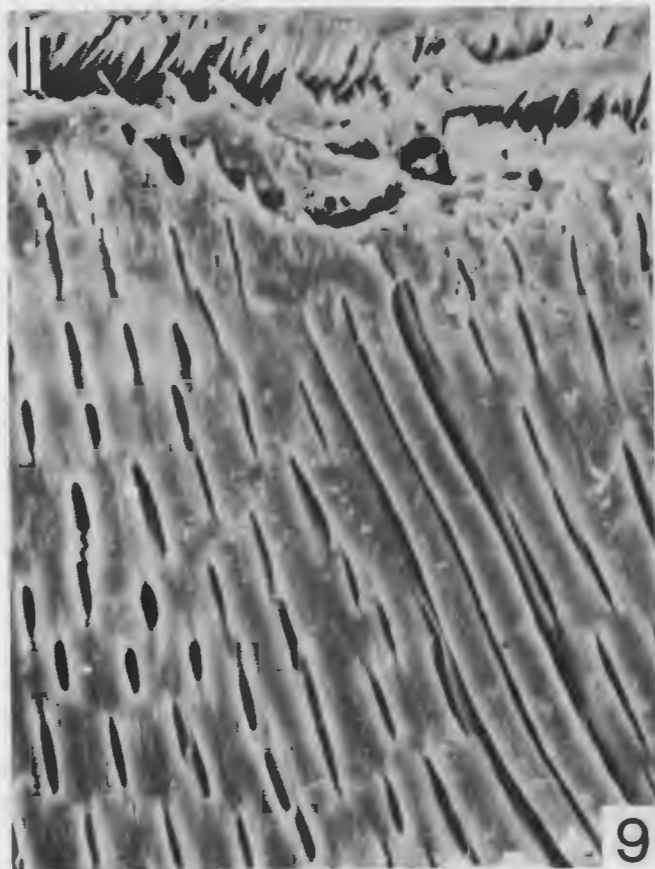
*alpina*, *C. apiifolia*, *C. dioscoriifolia*, *C. haenkeana*, *C. tangutica*, and *C. vitalba*. The vertical axis of pits is about 5  $\mu\text{m}$  in *Clematis chrysocoma*, *C. cirrhosa*, *C. iringaensis*, *C. lasiantha*, *C. ligusticifolia*, *C. pauciflora*, *C. pickeringii*, *Delphinium elatum*, *Helleborus viridis*, and *Hydrastis canadensis*. The vertical axis of pits is about 3  $\mu\text{m}$  in *Thalictrum polycarpum* and *Xanthorhiza apiifolia*.

Vessel wall sculpturing is prominent in most species of *Clematis*. In most species, the patterns include grooves interconnecting pit apertures (“coalescent pit apertures”) in wide vessels, combined with helical thickenings—usually fine rather than coarse—in narrow vessels and vasicentric tracheids. This combination is shown for *C. montana* in Fig. 9, 10. The grooves may be shallow, as at left in Fig. 9. The combination of grooves in wide vessels plus fine helical thickenings in narrow vessels and vasicentric tracheids was observed in *C. apiifolia*, *C. chrysocoma*, *C. cirrhosa*, *C. dioscoriifolia*, *C. lasiantha*, *C. ligusticifolia*, *C. montana*, *C. pauciflora*, *Helleborus viridis* (Fig. 19), and *Thalictrum polycarpum*. Grooves in wide vessels only, and no sculpture in narrow vessels, were observed in *C. pickeringii*. Grooves in both wider and narrower vessels were observed in *C. haenkeana* and *C. iringaensis*. Coarse helical thickenings in both wide and narrow vessels (slightly finer in the narrower vessels) were observed in *C. vitalba* (Fig. 11–13). The presence of helical thickenings in this species does not exclude the presence of grooves interconnecting pit apertures; pairs of thickenings flanking grooves interconnecting pit apertures could be seen on walls of wider vessels (Fig. 13). In *Delphinium elatum*, *Glaucidium palmatum*, *Hydrastis canadensis*, and *Xanthorhiza apiifolia*, no helical sculpture was observed on vessel walls.

#### Vasicentric Tracheids

Vasicentric tracheids have been reported for one *Clematis* species earlier (Carlquist 1985), but they occur in all of the species studied here except for the three tropical species *C. haenkeana*, *C. iringaensis*, and *C. pickeringii*. In genera other than *Clematis*, vasicentric tracheids were observed only in *Thalictrum*. Vasicentric tracheids in *Clematis* and *Thalictrum* occur mostly in latewood. Latewood distribution of these cells might lead one to designate them as vascular tracheids, but that term is reserved for instances in which tracheids (in a wood that also contains libriform fibers

Fig. 9–13. Scanning electron micrographs of vessel walls of *Clematis* from tangential sections.—9–10. *C. montana*.—9. Earlywood vessel wall has grooves interconnecting pit apertures.—10. Two latewood vessels have fine helical thickenings.—11–13. *C. vitalba*.—11. Wall of vessel of intermediate diameter; helical thickenings are coarse; grooves interconnect some of the pit apertures.—12. Two latewood vessels; helical thickenings are numerous.—13. Portion of wall of earlywood vessel; thickenings tend to occur as pairs of bands flanking pit apertures. Collections given in Table 1. (Scales shown at upper left in each figure [bars = 10  $\mu\text{m}$ ].)



or fiber-tracheids) form terminal layers in latewood, layers that do not include vessel elements to any appreciable extent. In *Clematis* and *Thalictrum*, tracheids in latewood are intermixed with narrow vessels, so the term vasicentric must be applied. Sieber and Kucera (1980) are correct in saying that Greguss (1959) errs in figuring helical thickening in a libriform fiber (with obviously simple pits) for *C. vitalba*. Possibly Greguss combined the helical thickenings seen in vessels or vasicentric tracheids with features of a libriform fiber.

### Libriform Fibers

The imperforate tracheary element type (excepting vasicentric tracheids) of all Ranunculaceae studied is the libriform fiber. Only simple pits were seen in these cells. Libriform fibers are lacking in my material of *Clematis alpina* (Fig. 4): the tissue in which vessels are embedded consists of vasicentric tracheids and, to a lesser extent, axial parenchyma. In *Helleborus viridis*, libriform fibers are very scarce and are adjacent to ray areas. Libriform fibers in *Clematis* contain starch (observed most clearly in wood samples that were liquid-preserved: see Materials and Methods). Septate libriform fibers were observed in *C. pickeringii*. Starch and septa are indications of prolonged longevity of libriform fibers, and these features accord with Wolkinger's (1969) report of nucleated fibers in *Clematis*.

Mean length of libriform fibers (Table 1, column 6) ranges from 250 to 520  $\mu\text{m}$ . The longest libriform fibers occur in the tropical species: *Clematis haenkeana*, *C. iringaensis*, and *C. pickeringii*. The genera other than *Clematis* have relatively short libriform fibers. The "F/V ratio" (ratio of length of imperforate tracheary elements—libriform fibers in the case of Ranunculaceae—to vessel elements) has been calculated for the species studied (Table 1, column 7). The values range from 1.55 to 2.31. The average figure for all species studied is 1.87. Such a range is typical for a species with libriform fibers; lower F/V ratios (closer to 1.0) would be expected for woods with tracheids or fiber-tracheids.

Libriform fiber wall thickness is given in Table 1, column 8. In *Clematis*, notably thick (5–7  $\mu\text{m}$ ) walls occur in *C. cirrhosa* (Fig. 8), *C. dioscoriifolia* (Fig. 3), *C. haenkeana* (Fig. 2, 15), *C. pauciflora*, *C. pickeringii* (Fig. 7), and *C. vitalba*. Libriform fibers were relatively thin walled in the other genera except for

*Glaucidium* (Fig. 22). Libriform fibers in *Delphinium elatum* range in wall thickness from 2 to 7  $\mu\text{m}$ ; the thicker-walled fibers occur in local patches.

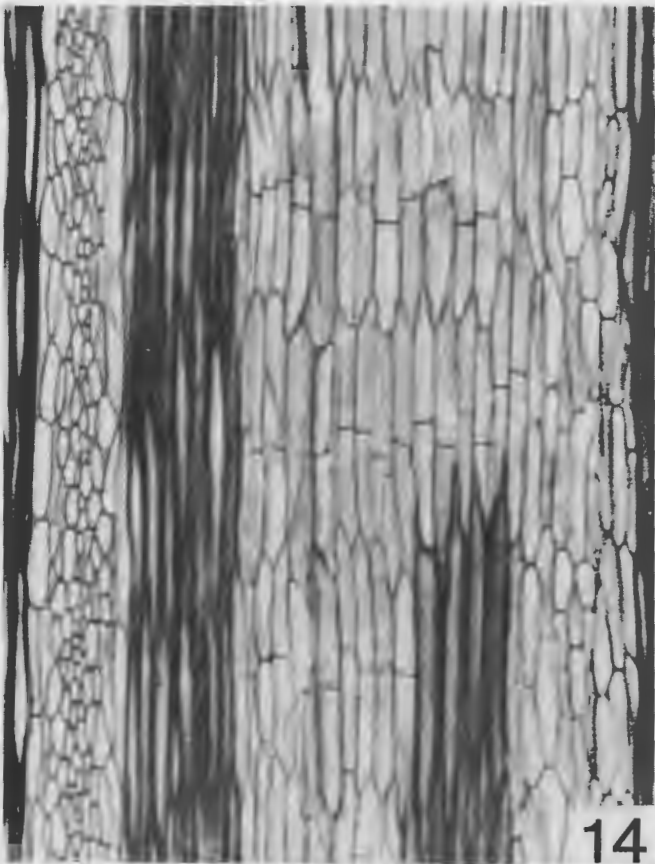
### Axial Parenchyma

Axial parenchyma in *Clematis* has been described as apotracheal (Greguss 1959; Grosser 1977). Schmidt (1941), Metcalfe and Chalk (1950), and Schweingruber (1978) consider the axial parenchyma in *Clematis* to be paratracheal. Sieber and Kucera (1980) and Schweingruber (1992) designate axial parenchyma in *Clematis* as both paratracheal and apotracheal. Sieber and Kucera (1980) suspect that Greguss (1959) may have mistaken narrow vessels for libriform fibers and therefore declared axial parenchyma in contact with the alleged fibers to be apotracheal. In fact, when macerations and sections were carefully examined, narrow vessels were found to be very abundant in most species, and vasicentric tracheids were present in appreciable numbers in all species of *Clematis* except the three tropical ones. Vasicentric tracheids may have been mistaken for libriform fibers by some workers. Axial parenchyma in contact with vasicentric tracheids probably should be classified as paratracheal, although I know of no worker who has considered this question. In any case, I failed to find any axial parenchyma that as individual cells or as part of larger parenchyma aggregations was not in contact with vessels. The large masses of libriform fibers adjacent to rays (e.g., Fig. 1, 2, 3, 8) do not contain axial parenchyma. Thus, I was unable to convince myself that any apotracheal parenchyma was present in the specimens of *Clematis* studied.

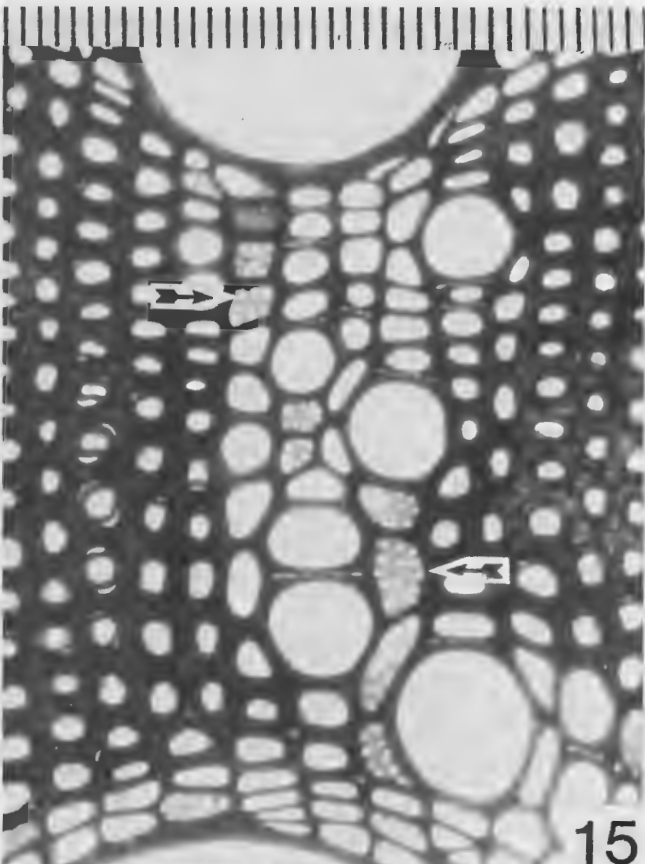
An unusual form of axial parenchyma is represented in *C. alpina* (Fig. 4). In this species, the dark-staining fascicular xylem areas have an indented rather than straight outline in contact with the rays. The apparent indentations are, in fact, strands of thin-walled axial parenchyma adjacent to the rays in latewood areas.

In Table 1, column 9, the axial parenchyma types observed are shown. I have termed scattered axial parenchyma cells, distributed as single cells among narrow vessels (or vasicentric tracheids) "intervascular axial parenchyma" in accord with earlier definitions (Carlquist 1988). Where more than one axial parenchyma cell, as seen in transection, is in contact with a vessel, the term paratracheal scanty or vasicentric scanty (the latter from Kribs 1937) is used. In early-

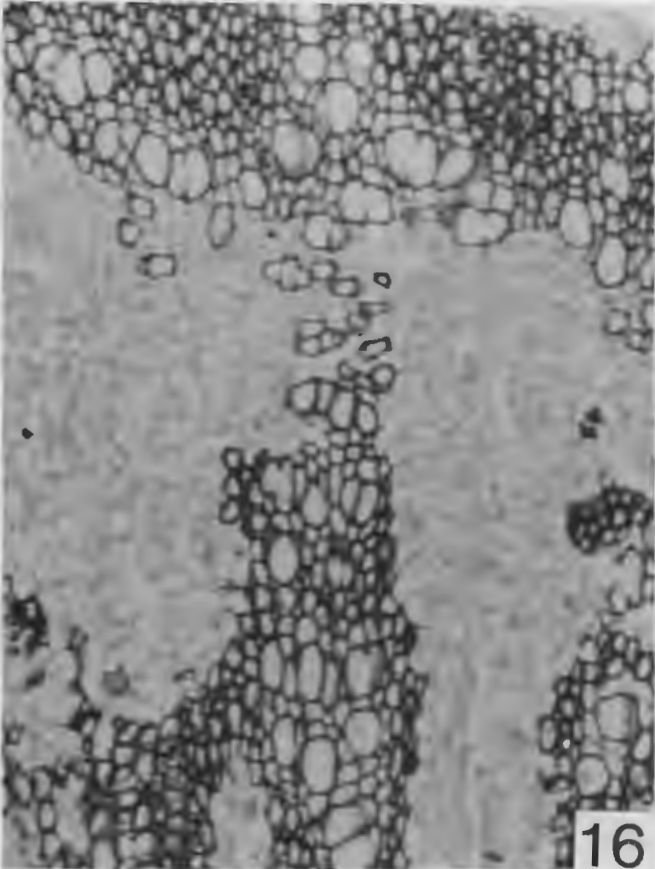
Fig. 14–17. Wood sections of Ranunculaceae.—14–15. *Clematis haenkeana*.—14. Tangential section; ray at left; storied libriform fibers (dark) and axial parenchyma (light, in strands of two cells) shown.—15. Transection; axial parenchyma is more abundant near earlywood vessel (below), less abundant near latewood vessels (center); transverse walls in axial parenchyma indicated by arrows.—16–17. *Delphinium elatum*.—16. Transection; this portion is rayless, and has large, irregular patches of axial parenchyma.—17. Tangential section; the central third may be interpreted as a ray with markedly upright ray cells or a ray area converted to short libriform fibers. Collections given in Table 1. (Scale for Fig. 14, 16, 17 above Fig. 1; scale for Fig. 15 above Fig. 15 [divisions = 10  $\mu\text{m}$ ].)



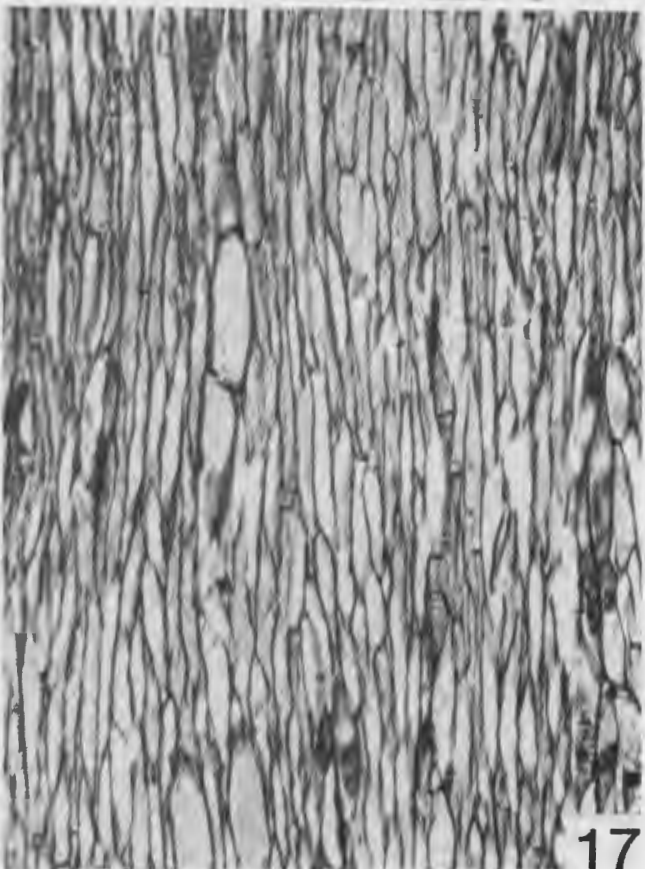
14



15



16



17



wood of *Clematis*, the vessels are larger and therefore each tends to be in contact with a few or even many axial parenchyma cells (Fig. 1, 2, 15); where many cells surround a vessel, the parenchyma may be termed vasicentric abundant. Axial parenchyma is very scarce in *Xanthorrhiza apiifolia* (Fig. 20). In *Delphinium elatum* (Fig. 16), *Glaucidium palmatum* (Fig. 22), and *Hydrastis canadensis* (Fig. 26), large patches of axial parenchyma are present in some areas of fascicular secondary xylem, whereas libriform fibers characterize other zones of fascicular secondary xylem. Such extensive patches of axial parenchyma are termed "pervasive" in accordance with an earlier usage (Carlquist 1995). In *Helleborus viridis* (Fig. 18), axial parenchyma is so common among vessels, rather than in groupings around vessels or vessel groups, that the term "intervascular" appears appropriate. The terms intervascular parenchyma and pervasive parenchyma were not placed in usage in earlier decades because they are found chiefly in secondary xylem of relatively herbaceous dicotyledons, and wood of arboreal and shrubby species has formed the basis for most works in wood anatomy until recently.

Sieber and Kucera (1980) report axial parenchyma in strands of either two or three cells in *Clematis vitalba*. I agree with that designation, and certainly strands of two are common in most wood samples of *Clematis*, as shown in Fig. 14. Strands of two cells exclusively were also observed in *C. tangutica*. However, careful examination of other *Clematis* woods revealed wide fibriform cells with circular simple pits, thereby exactly like parenchyma in strands but formed as undivided cells. Thus, strands of one to two cells are reported here as constituting axial parenchyma of all species of *Clematis* except *C. tangutica* and *C. vitalba*; strands of three or four cells, in addition to one or two, were observed in *C. haenkeana* wood.

Axial parenchyma in strands of single undivided cells characterizes *Delphinium elatum* (Fig. 17), *Glaucidium palmatum* (Fig. 23), *Helleborus viridis*, and *Xanthorrhiza apiifolia*. In *Hydrastis canadensis*, strands of one to two cells were observed; in *Thalictrum polycarpum*, the strands consist of two to five cells.

### Rays

Ray histology in *Clematis* has been characterized as belonging to Heterogeneous Type III of Kribs (1935) according to Sieber and Kucera (1980). This is clearly a mistake, because Kribs (1935, p. 551) defines Het-

erogeneous Type III as uniseriate only, whereas rays in *Clematis* are wide multiseriate exclusively. Rays in all Ranunculaceae studied are rather wide (Table 1, column 10).

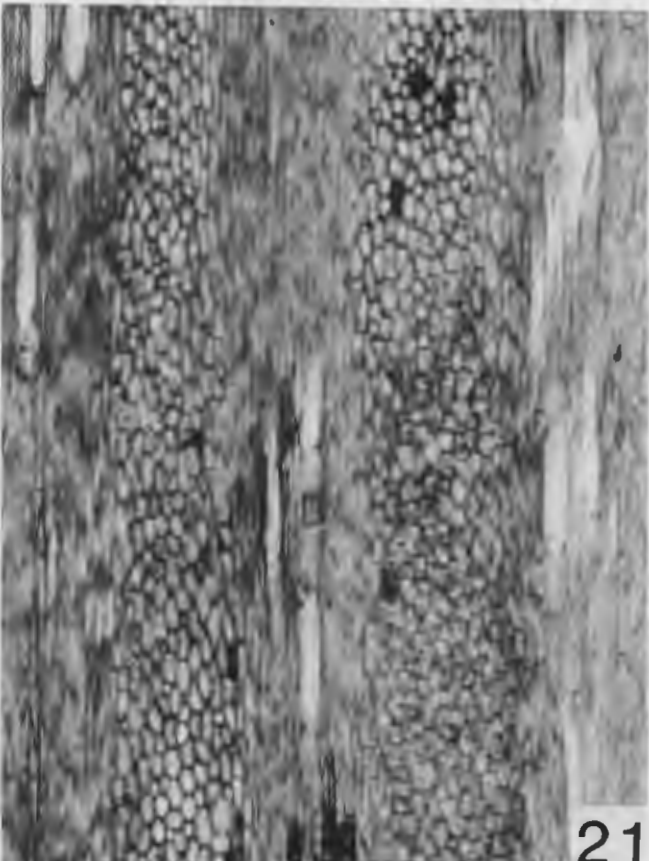
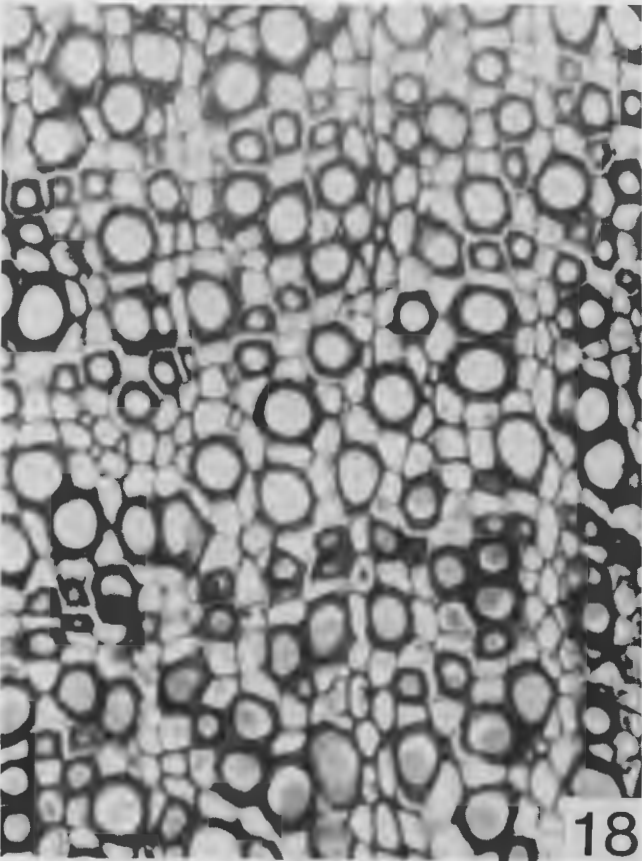
Rays in most species of *Clematis* consist mostly of procumbent cells, but have one to two layers of upright sheath cells. In some species such as *C. alpina*, *C. haenkeana* (Fig. 14), and *C. iringaensis*, three to four layers of sheath cells may be present, so that most of the ray tissue consists of upright cells. In fact, rays of *Clematis* do not fit any of the Kribs types. The rays of *Clematis* are best described as intermediate between Homogeneous Type II (multiseriate, all cells procumbent) and Paedomorphic Type II (multiseriate, upright cells only). Paedomorphic Type II rays characterize *C. pickeringii*, and, judging from Schweingruber's (1992) illustrations, *C. viticella*. Curiously, Schweingruber (1992) uses the term "Heterogeneous" for rays that consist wholly of upright cells as well as for those in which both upright and procumbent cells are present. Rays that consist wholly or predominantly of upright cells should be termed Paedomorphic (Carlquist 1988). Paedomorphic Type II rays of this type were observed in *Delphinium elatum*, *Helleborus viridis*, *Glaucidium palmatum* (Fig. 24), *Hydrastis canadensis*, and *Thalictrum polycarpum*. Rays of *Xanthorrhiza apiifolia* (Fig. 21) consist of upright plus some square cells, and thus clearly qualify as Paedomorphic Type II, because square cells are, by common consent, considered equivalent to upright cells morphologically.

In *Clematis*, new rays originate abruptly as wide multiseriate rays rather than as narrow rays that widen later. This may be related to the scandent habit, because it also occurs in woody climbers in two other families, neither closely related to Ranunculaceae: Cucurbitaceae (Carlquist 1992) and Aristolochiaceae (Carlquist 1993). Another feature that may be related to the vining habit is the tendency in some species of *Clematis* for rays to have at first cells that have lignified walls, then cells that are thin walled and nonlignified. This, which is shown (some thin-walled ray cells collapsed, to be sure) for *C. chrysocoma* (Fig. 6, left), *C. dioscoriifolia* (Fig. 3, below), and *C. pickeringii* (Fig. 7, below), was also observed in *C. montana*. Only thick-walled cells with lignified walls 1–4  $\mu\text{m}$  thick were observed in *C. apiifolia* (Fig. 5), *C. cirrhosa* (Fig. 8), *C. haenkeana* (Fig. 2), *C. lasiantha*, *C. pauciflora*, and *C. vitalba*. Bordered pits on tangential walls (and sometimes on other walls) were observed

→

Fig. 18–21. Wood sections of Ranunculaceae.—18–19. *Helleborus viridis*.—18. Transection; axial parenchyma is scattered among vessels rather than surrounding vessel groups.—19. Tangential section; inconspicuous helical thickenings are present on vessels (arrow).—20–21. *Xanthorrhiza apiifolia*.—20. Transection; vessels are confined to a central position in the fascicular areas.—21. Tangential section; rays are composed of square to upright cells with secondary walls. Collections given in Table 1. (Fig. 18–19, scale above Fig. 15; Fig. 20, 21, scale above Fig. 1.)





in *C. iringaensis*, *C. pauciflora*, and *C. vitalba*. Such bordered pits are often overlooked by workers because they view pits in face view, whereas the borders are best seen in sectional view.

The rays in *Delphinium*, *Glaucidium*, *Helleborus*, *Hydrastis*, *Thalictrum*, and *Xanthorhiza* are really only extensions of primary rays. There can be histological changes in these rays during ontogeny, however. In *Delphinium*, *Glaucidium*, and *Thalictrum*, some (but not all) of the ray areas are soon converted to axial tissue; vertically elongate ray initials become almost the same length as fusiform cambial initials, and yield fusiform cells that qualify as libriform fibers rather than ray cells (Fig. 23). The central third of the tangential section portion of *Delphinium elatum* shown in Fig. 17 is likely an area that began as a ray and was replaced with wide libriform fibers not very different from ray cells. This "partial raylessness" is a phenomenon not often encountered, and I am not able to cite other examples. The relatively small width of rays in *Thalictrum polycarpum* (Table 1, column 10) is due to replacement of some ray areas with axial cells, much as shown for *Delphinium elatum* in Fig. 17. The figures and descriptions of Schweingruber (1992) for *Thalictrum minus* L. indicate only biseriate or uniseriate rays. This condition is in contrast to other Ranunculaceae—and Ranunculiflorae, in fact—that one is tempted to question the determination of the wood sample. However, the transections Schweingruber (1992) illustrates for this species seem to show rapid conversion of ray tissue to fascicular tissue, achieving a rayless condition, followed by initiation of narrow rays. This is a sequence that has been observed in some other woods, such as *Plantago arborescens* Poir. (Carlquist 1970). Instances such as these are worthy of further investigation.

Quantitative data on ray width (Table 1, column 10) show that in both *Clematis* and the remaining genera, the rays are relatively little altered extensions of primary rays, as indicated in the comments of Sieber and Kucera (1980) for *C. vitalba*. The relatively narrow ray widths given in the tabular data for *Delphinium elatum* and *Thalictrum polycarpum* are related to the "partial raylessness" described above.

### Cell Contents

Large quantities of an unidentified yellowish material (often staining darkly in my material) were observed in vessels of *Glaucidium palmatum* (Fig. 22,

upper half), *Helleborus viridis* (Fig. 18, lower half), *Hydrastis canadensis* (Fig. 26), and *Xanthorhiza apiifolia* (Fig. 20, 21).

In *Clematis*, starch grains occur in libriform fibers, axial parenchyma, and ray cells. Likely any species of *Clematis* might be expected to contain starch in these wood cells, but starch might be expected to vary in presence according to season and according to method of wood sample preservation. Starch was observed clearly in *C. apiifolia*, *C. cirrhosa*, *C. iringaensis*, and *Xanthorhiza apiifolia*. No crystals were observed in any wood cells in any of the Ranunculaceae studied.

### Storied Structure

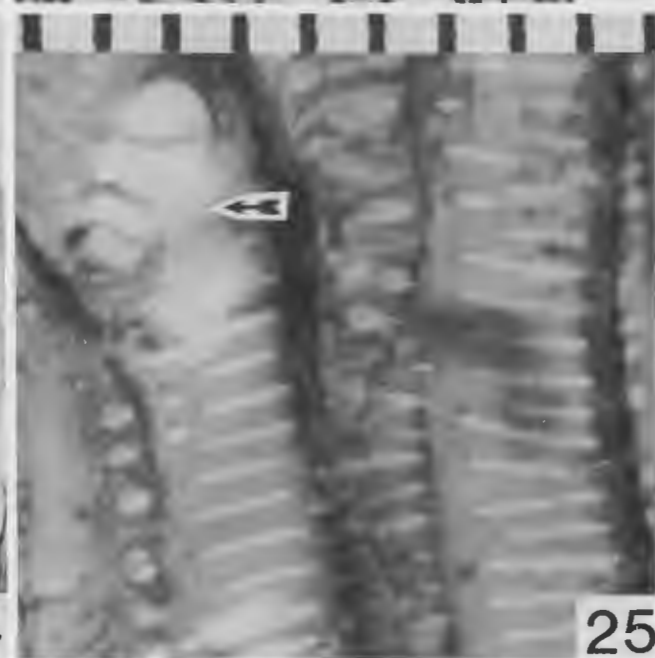
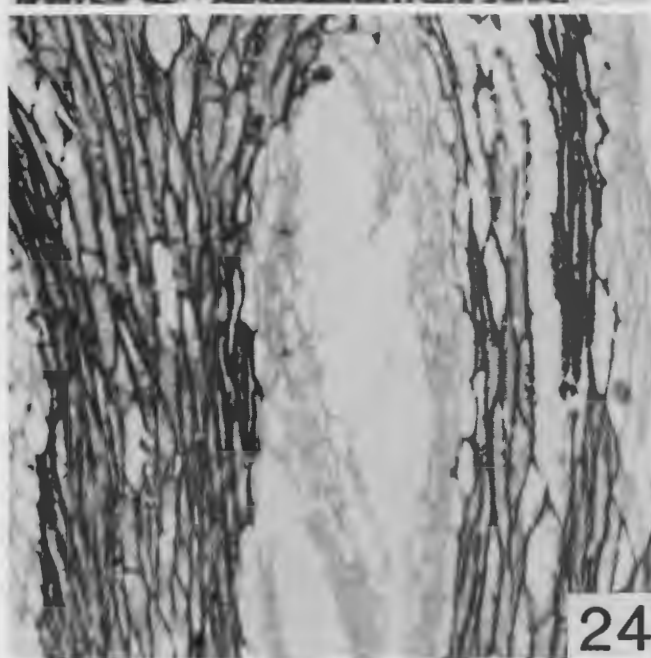
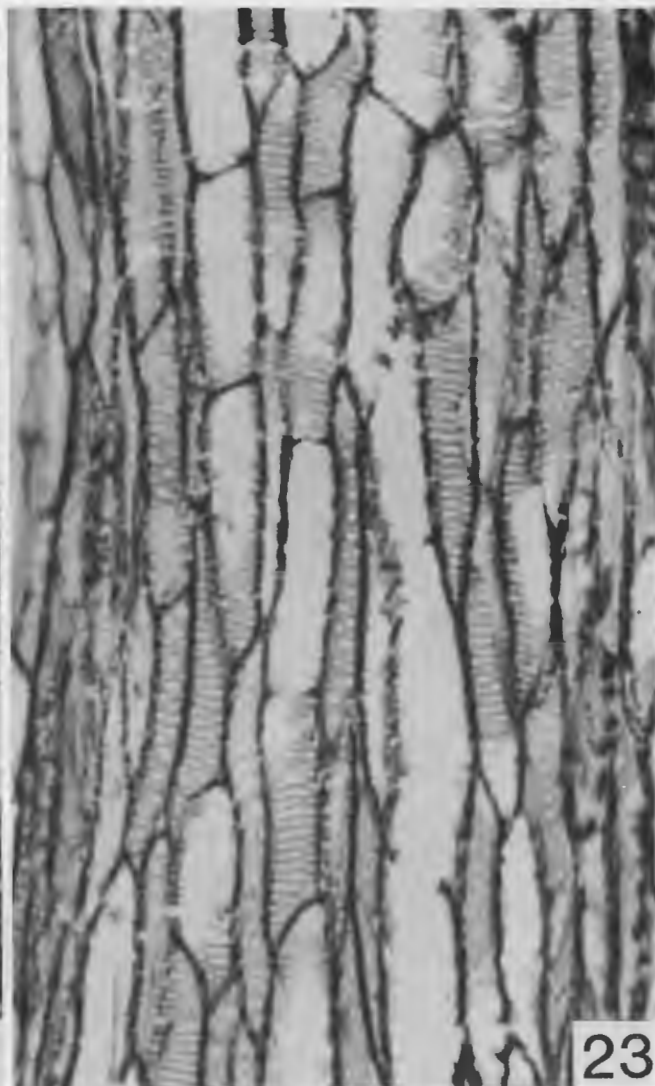
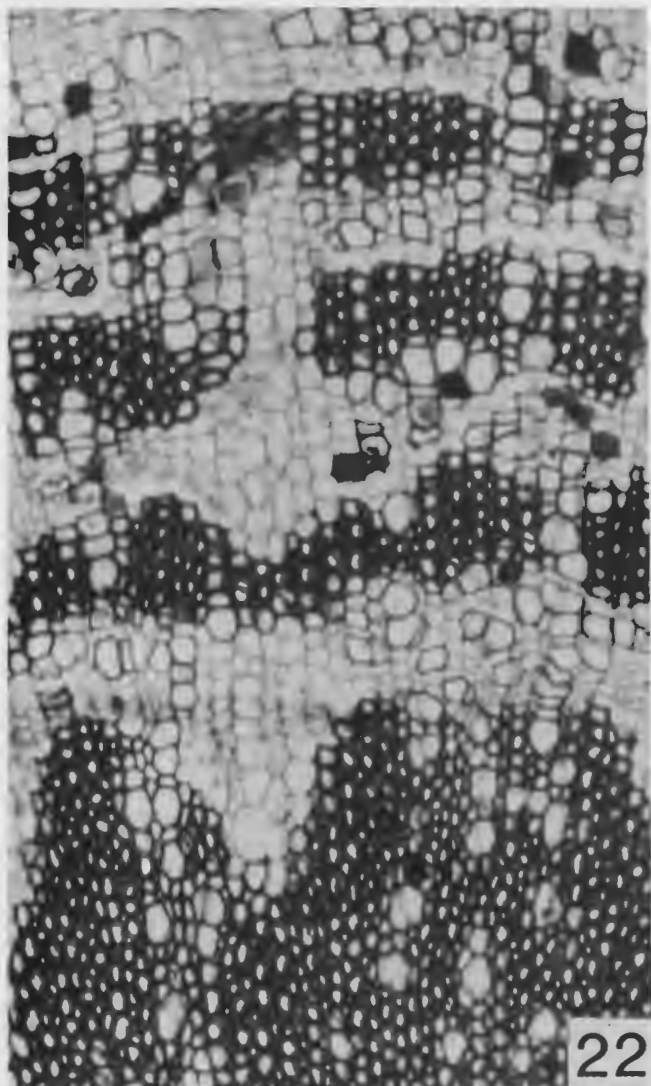
In older stems of *Clematis*, storying is evident. Storying can be seen in all of the axial cell types: vessel elements, axial parenchyma, vasicentric tracheids, and even libriform fibers (Fig. 14). The storying of libriform fibers is less evident than that of the other cell types because of the elongation of the fibers, to about twice the length of vessel elements (Table 1, column 7). The younger stems of *Clematis* I examined showed less storying, in accord with what one finds elsewhere in dicotyledons. No storying in axial xylem cells was observed in the genera of Ranunculaceae other than *Clematis*.

Rays themselves are not storied in *Clematis*, but in *C. alpina*, storied ray cells may be seen in tangential sections. The rays in this species are markedly dilated (noticeable especially in the low power transection photograph by Schweingruber 1992). The storying of ray cells in *C. alpina* seems likely the result of multiplicative divisions in the ray initials of the cambium, but studies to confirm this were not undertaken.

### Bark Anatomy

Only moderate amounts of phellem form on stems of *Clematis* (Fig. 27, 28). Periderms are successive (Fig. 27). In the cortex, a few parenchyma cells may enlarge into brachysclereids, as in *C. pickeringii* (Fig. 28). Protophloem fibers form in all the species for which bark was available (Fig. 28, upper right). In most species of *Clematis*, annual increments of secondary phloem are completely encircled by a ring of fibers (Fig. 28). Other phloem increments are incompletely encircled, with fibers formed laterally and adaxially to each year's secondary xylem (Fig. 27, 29). In most species, phloem fibers do not form in central

Fig. 22–25. Wood sections of *Glaucidium palmatum*.—22. Transection; the portion shown is rayless, and axial parenchyma is mostly in latewood zones.—23. Tangential section showing a fascicular xylem portion; vessel elements are relatively short and have scalariform or pseudoscalariform pitting.—24. Tangential section showing a wide ray that consists of thin-walled cells, many of which have collapsed.—25. Vessels from a radial section showing scalariform and pseudoscalariform lateral wall pitting; the perforation plate (arrow) has three bars. (Scale for Fig. 22, 24 above Fig. 1; scale for Fig. 23 above Fig. 15; scale for Fig. 25 above Fig. 25 [divisions = 10  $\mu$ m].)



portions of phloem increments, but an exception is illustrated for *C. apiifolia*, in which strands of fibers of various sizes occur (Fig. 27). Notably large diameter characterizes the sieve tube elements of *Clematis* (Fig. 28, 29).

In *Xanthorrhiza apiifolia*, bark is like that illustrated for *Clematis iringaensis* (Fig. 29), but with much smaller increments of secondary phloem and with much narrower sieve tube elements. The stems of *Glaucidium* studied were relatively old, and showed thick phellem, but with no sclerenchyma; secondary phloem also lacks sclerenchyma in this genus.

#### CONCLUSIONS

##### *Habit and Ecology in Relation to Wood Anatomy*

Differentiating between adaptations of wood that are related to ecology and those that correspond to habit is not possible in all instances. Certainly in *Clematis* wood adaptations are primarily due to the climbing habit; on those adaptations are superimposed those of climate, for *Clematis* ranges from tropical to temperate conditions.

The scandent habit of *Clematis* is correlated with presence of limited numbers of wide thick-walled vessels in earlywood and with a greater density of vessels (in the wood as a whole) than found in all but dicotyledons with very xeromorphic wood. Libriform fibers are not randomly distributed throughout the wood, but rather mostly at the margins of fascicular areas, adjacent to rays. The rays are unusually wide and tall in *Clematis* (compared with those of dicotyledons at large), and are relatively infrequently subdivided during growth. Vasicentric tracheids are present in latewood and, less commonly, elsewhere in growth rings. There is a tendency for rays to begin with cells that have thick lignified walls, but over time these yield to thin-walled cells that have only primary walls (e.g., Fig. 3, 6, 7). New rays are multiseriate from their origin, and are initiated abruptly (rather than as narrow rays that gradually increase in width), as in Cucurbitaceae (Carlquist 1992) or Aristolochiaceae (Carlquist 1993). All of the above features tend to characterize wood of scandent taxa when those taxa are compared to nonscandent relatives (Carlquist 1991).

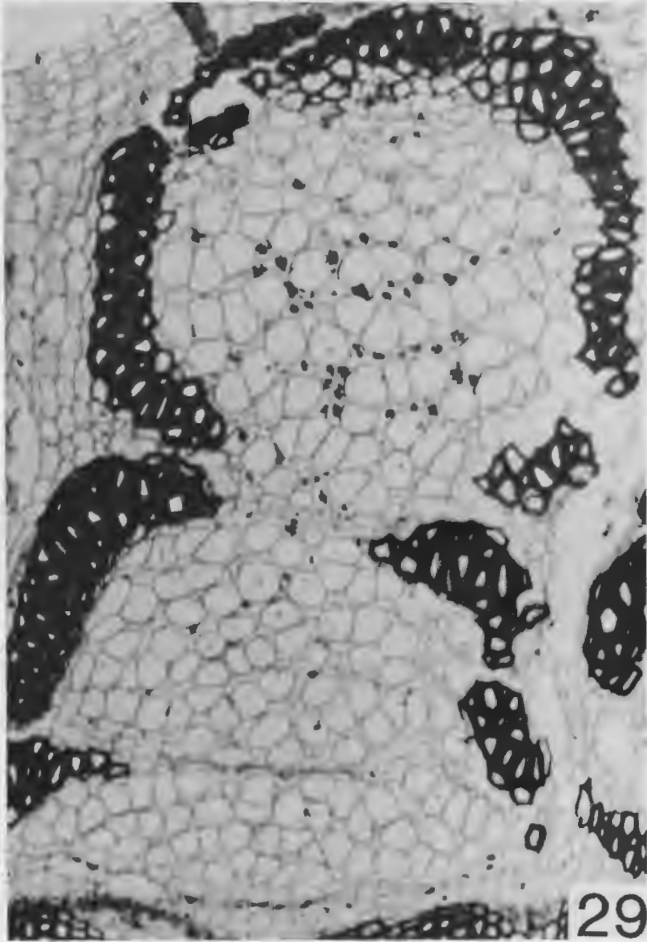
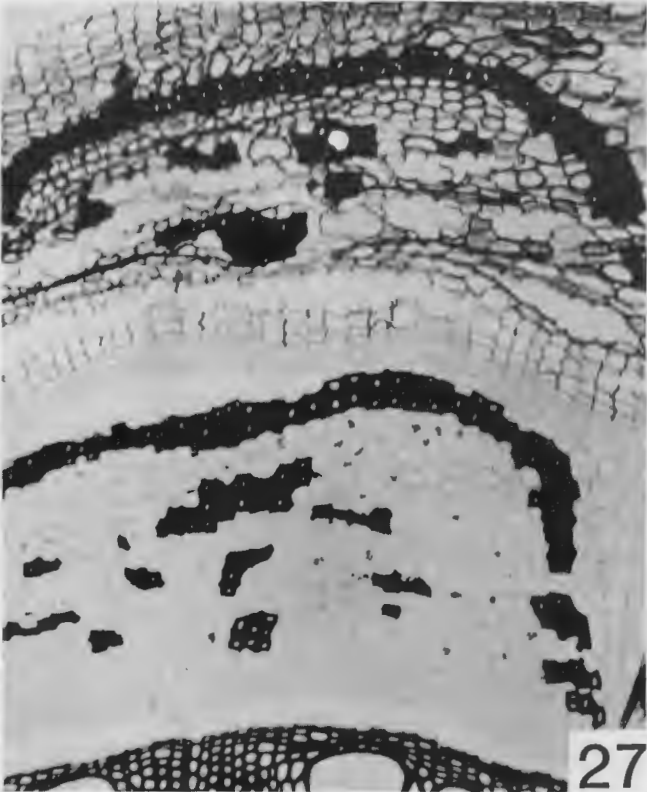
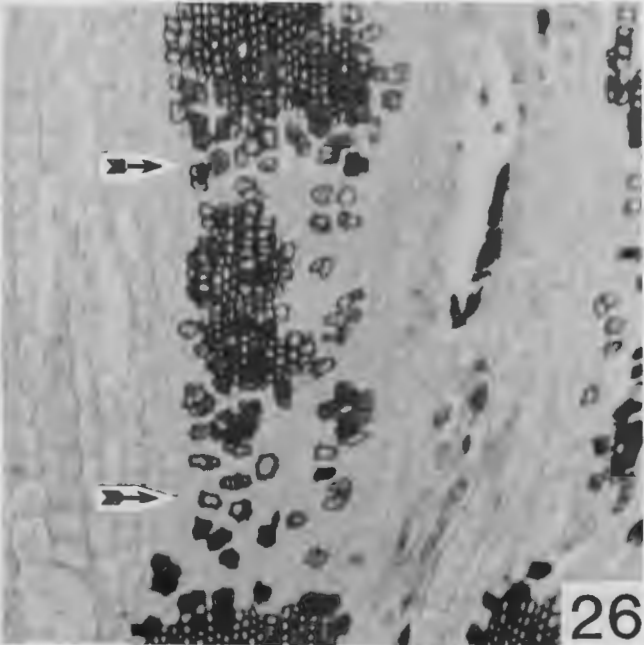
Superimposed on the abovementioned wood features in *Clematis* are character expressions that relate to ecology. The three tropical species (*C. haenkeana*, *C. iringaensis*, and *C. pickeringii*) have relatively great

mean vessel diameter, relatively few vessels per mm<sup>2</sup> of transection, and relatively long vessel elements. These three features have been combined as the Mesomorphy ratio in Table 1, column 11; the tropical species show values from 45.7 to 606, higher than the values for any of the temperate species. Other features characteristic of the tropical species are a relatively low number of vessels per group and an absence of vasicentric tracheids. Conditions alternative to those of the tropical species characterize the temperate species. The Mesomorphy ratio is lowest for the montane temperate species *C. alpina* and *C. montana*. Only slightly less xeromorphic are the woods of *Clematis* species from the Californian chaparral: *C. lasiantha* and *C. pauciflora*. Montane localities have physiological drought due to freezing of soil; the chaparral species experience soil dryness due to lack of rain during the six summer and autumn months. Vasicentric tracheids, present in the temperate species of *Clematis*, are characteristic of woods from dry and cold areas (Carlquist 1985).

The genera studied other than *Clematis* are all from moist-temperate forest localities in which freezing of soil can occur in winter. Relatively narrow, short vessel elements, numerous per mm<sup>2</sup> of transection, as found in these genera are characteristic of xeromorphic woods. The xeromorphy here is related to winter freezing, in all likelihood. These quantitative vessel features, combined as the Mesomorphy ratio, range from 1.9 to 37.4 (Table 1, column 11). Moist-temperate shrubs would be expected to have values from 100 to 500, and tropical wet-forest trees values above 1000, so the subherbaceous genera other than *Clematis* have a degree of xeromorphy equivalent to that of desert, alpine, or chaparral shrubs (Carlquist and Hoekman 1985). The low number of vessels per group in the genera other than *Clematis* is probably explained by the relative abundance of parenchyma in these woods, often occupying large patches ("pervasive axial parenchyma"). The rays are also wide in these genera. Abundance of both axial and ray parenchyma in the genera other than *Clematis* is likely related to their subherbaceous habit, which features storage of photosynthates in underground stems or basal portions of stems during the winter months. Partial raylessness in *Delphinium* and *Glaucidium* is seen here as a mechanism for rapid production of more fibrous (and therefore mechanically strong) tissue, which can be of value in supporting tall upright stems that last only one year.

Fig. 26–29. Transections of stems of Ranunculaceae.—26. Secondary xylem of *Hydrastis canadensis*; axial parenchyma occurs in earlywood and latewood (arrows), libriform fibers are in an intermediate position in the growth rings.—27–29. Sections of bark of *Clematis*.—27. *C. apiifolia*; strands of fibers occur within secondary phloem.—28. *C. pickeringii*; each increment of secondary phloem is sheathed in fibers; cortical sclereids, upper right and left.—29. *C. iringaensis*; fibers incompletely sheathe increments of secondary phloem; note wide sieve tube elements. Collections given in Table 1. (Scales for Fig. 26–29 above Fig. 1.)







### Systematic Implications of Wood Anatomical Data

Of the genera treated here, the one most commonly considered not to belong to Ranunculaceae is *Glaucidium*. Authors such as Tamura (1972) and Tobe (1981), who have studied various aspects of this monotypic genus, make it the basis for a monogeneric family, Glaucidiaceae, and notice more resemblances between Glaucidiaceae and Paeoniaceae than between Glaucidiaceae and Ranunculaceae. These ideas are reflected in recent phylogenies, such as that of Thorne (1992), who assigns only Glaucidiaceae and Paeoniaceae to Paeoniales, but who assigns Ranunculaceae and Hydrastidaceae to Berberidales. This treatment is in agreement with the concepts of Tobe (1981), but Tamura (1972) assigns Paeoniaceae (and therefore also Glaucidiaceae) to Dilleniales, a treatment that is certainly current in some treatments (e.g., Cronquist 1988); Dilleniales is close to Theales or combined with it by some systems.

Is wood of *Glaucidium* like that of *Paeonia*? *Glaucidium* does have scalariform perforation plates, but these are quite uncommon; plates with one bar are rare (about 1 in 25; the remainder of the plates are simple). In *Paeonia*, by contrast, most perforation plates have 2–11 bars, and only 3.7% of the perforation plates are simple (Keefe and Moseley 1978). Lateral wall pitting in *Paeonia* is transitional or alternate (very rarely scalariform), whereas in *Glaucidium* it is scalariform or pseudoscalariform. The imperforate tracheary elements of *Paeonia* are tracheids, whereas they are always libriform fibers in *Glaucidium*. The axial parenchyma of *Paeonia* is apotracheal and sparse, whereas in *Glaucidium* it is paratracheal and pervasive. Rays in *Glaucidium* are tall and wide and composed of cells with primary walls only, with no uniseriate rays present. In *Paeonia*, rays are relatively narrow multiseriate (2–8 cells wide) plus uniseriate; the ray cells have lignified secondary walls. Thus, there are numerous contrasts between *Paeonia* and *Glaucidium* with respect to wood anatomy. If Glaucidiaceae are indeed close to Paeoniaceae, as embryological and other features have suggested to the authors cited earlier, the two families have diverged markedly with respect to wood anatomy.

Hydrastidaceae are recognized as a monogeneric family separate from Ranunculaceae by some recent authors (e.g., Tobe and Keating 1985; Thorne 1992) but not others (e.g., Cronquist 1988; Keener 1993). Nowicke and Skvarla (1982) treated Hydrastidaceae as a member of Berberidales, which they are considering as an order separate from Ranunculales. Tobe and Keating (1985) conclude that *Hydrastis* diverged early from the basal stock of Ranunculaceae, and therefore represents a kind of relict element. The cladograms of Hoot (1991), which incorporate data from macromor-

phology and from epidermal micromorphology, show much the same pattern, although resolution of several basal lineages in Ranunculaceae is poor in Hoot's (1991) scheme. According to Hoot, *Hydrastis*, *Xanthorhiza*, and *Coptis* share the "T-type" small chromosomes, in contrast to the "R-type" large chromosomes elsewhere in the family. Wood of *Hydrastis* is not, however, like that of *Xanthorhiza*, although one must keep in mind the differences in habit: *Xanthorhiza* is a woody subshrub whereas *Hydrastis* is an herb with succulent, minimally woody prostrate stems. These differences could account for the differences in wood between these two genera. The presence in *Hydrastis* metaxylem of some scalariform perforation plates, combined with presence in secondary xylem of rare single-bar perforation plates (most plates are simple) is noteworthy. These xylary conditions are marginally more primitive than those of Ranunculaceae s.s., in which scalariform perforation plates have been reported for primary xylem of two species of *Clematis* and one of *Ranunculus* (Bierhorst and Zamora 1965); these authors report simple perforation plates exclusively for primary xylem of one species each of *Anemone* (now *Thalictrum*) and *Ranunculus*. Zamora (1966) listed 12 genera of Ranunculaceae in which metaxylem contains "... 2 of the following kinds of perforation plates throughout the protoxylem-metaxylem transition: scalariform, transitional, simple." Scalariform perforation plates would be expected to persist in primary xylem, as they do in *Glaucidium* and *Hydrastis*, in a phylad with simple perforation plates in secondary xylem, if primary xylem is a "refugium" for primitive vessel features, as Bailey (1944) hypothesized. The position of *Hydrastis* as a genus close to Ranunculaceae and basally divergent from it appears justified; Keener (1993) makes a case for inclusion of *Hydrastis* in Ranunculaceae. The helical sculpturing of vessels of *Hydrastis* is a feature reminiscent of similar sculpture in vessels of *Clematis* and *Thalictrum*. Molecular evidence may offer further evidence on whether *Hydrastis* should be segregated from Ranunculaceae or retained within it.

On the basis of data presented above for Ranunculaceae and Glaucidiaceae, as well as data in the literature for wood anatomy of families of Ranunculiflorae, three unusual wood features are worthy of mention as potential indicators of relationship. These are: presence of vessel restriction patterns (vessels confined to central portions of fascicular areas); presence of wide multiseriate rays exclusively (not accompanied by uniseriate rays); and presence of storied wood structure. Storied wood (and storying in fusiform cambial initials and axial phloem cells), seen in *Clematis*, may also be seen in Lardizabalaceae (Carlquist 1984) and Papaveraceae (Carlquist and Zona 1988; Carlquist et al. 1994), for example. Vessel restriction patterns, shown

well in *Clematis* and *Xanthorhiza*, occur in Papaveraceae, as do the wide multiserial rays (Carlquist and Zona 1988, Carlquist et al. 1994). A summary paper is planned in order to map distribution of these key features, as well as other wood features in Berberidaceae, Lardizabalaceae, Menispermaceae, Ranunculaceae and several other families claimed by particular authors to belong to Ranunculiflorae (e.g., Eupteleaceae).

The phylogenetic relationships of Ranunculaceae are important to the question of whether woodiness is primary or secondary in Ranunculaceae—or, if both, in which genera. At present, one should note that Ranunculaceae have very short fusiform cambial initials (as indicated by the length of vessel elements) as compared to Lardizabalaceae (Carlquist 1984) or Menispermaceae (Metcalf and Chalk 1950); both of these families are woody. Herbaceous phylads of dicotyledons typically have short fusiform cambial initials in comparison to those of their woody relatives. Short fusiform cambial initials in herbaceous dicotyledons may represent phyletic specialization of most herbaceous phylads rather than a feature related to the herbaceous habit per se. If any genus of Ranunculaceae were primitively woody, one would expect it to retain longer fusiform cambial initials. Whether or not *Xanthorhiza* might be derived from woody ancestors is not clear because cell size in *Xanthorhiza* wood is small in every respect. The rays of the specimen studied were paedomorphic, suggesting the possibility of interpreting the wood as secondarily woody. However, a stem of maximal diameter for this genus was not available for the present study. An older stem is needed to see whether the rays remain paedomorphic. Judging from the relatively basal position of *Xanthorhiza* in Hoot's (1991) cladograms for Ranunculaceae, this is the genus to which attention should be paid in assessing whether the family is primitively woody or herbaceous.

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