

Wood anatomy of *Ranunculiflorae*: a summary

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Abstract: Recent surveys of wood anatomy of *Berberidaceae*, *Glaucidiaceae*, *Lardizabalaceae*, *Menispermaceae*, *Papaveraceae*, and *Ranunculaceae* reveal that wood anatomy is more closely related to habits than to systematic distinctions. The families can, however, be ranked from primitive to specialized in terms of vessel element length and “F/V ratio” (length of imperforate tracheary elements divided by length of vessel elements) as well as in terms of morphology of imperforate tracheary elements. *Lardizabalaceae* – especially the genus *Decaisnea* – rank as the family of *Ranunculiflorae* with the most primitive wood features. Wood characters that are of prime importance in determining relationship of *Ranunculiflorae* to other families include vessel restriction patterns, storring, and ray type; characters of less value include helical sculpturing in vessels, axial parenchyma type, and mode of crystal occurrence. The families of *Piperales*, (*Aristolochiaceae*, *Lactoridaceae*, *Piperaceae*) show more numerous resemblances to the families of *Ranunculiflorae* than do families of other orders. *Paeoniaceae*, thought by some closely related to *Glaucidiaceae*, have wood unlike that of *Glaucidium* or other families of *Ranunculiflorae*. The wood of *Eupteleaceae* is similar to that of *Decaisnea*, but this resemblance may derive merely from similarity in phylogenetic level. Wood anatomy supports inclusion of *Hydrastis* in *Ranunculaceae* and *Nandina* in *Berberidaceae*.

In an attempt to provide new information on wood anatomy of the families of *Ranunculiflorae*, a series of papers leading to the present summary has been constructed. This series includes studies on *Lardizabalaceae* (CARLQUIST 1984), *Papaveraceae* (CARLQUIST & ZONA 1988, CARLQUIST & al. 1994), *Ranunculaceae* (including *Hydrastis*) and *Glaucidiaceae* (CARLQUIST, unpubl.), *Berberidaceae* (CARLQUIST, unpubl.), and *Menispermaceae* (CARLQUIST unpubl.). *Kingdonia* and *Circaea* have not been studied here because their xylem is too limited for comparison even to herbaceous *Ranunculiflorae* with some secondary growth. *Sargentodoxa* has not been studied in the series leading to this summary because material was not available to me. However, data on wood anatomy of *Sargentodoxa* (LEMESLE 1943) and information on pollen ultrastructure (NOWICKE & SKVARLA 1982) seem to place that genus in *Lardizabalaceae*. The series of papers on wood anatomy of *Ranunculiflorae* includes many species not hitherto studied, and includes

new reports of anatomical features, such as those on storied cambia and axial parenchyma types. New information on wood anatomy of other families, such as *Piperales* (e.g., *Aristolochiaceae*, *Lactoridaceae*, *Piperaceae*) and *Chloranthales* (CARLQUIST 1992, 1993) provide data that prove vital in comparisons of *Ranunculiflorae* with other orders.

Wood is often valuable with relation to demonstration of systematic affinities of dicotyledonous genera and families, so a review of wood data of *Ranunculiflorae* is of value. If kinds of data other than those on wood give clear ideas of phyletic relationships within *Ranunculiflorae*, however, those interpretations may help interpretations of patterns of wood evolution. The present paper is divided into three parts. The first deals with phyletic sequences of wood features within *Ranunculiflorae*. The second discusses wood features of greatest value for understanding relationships of *Ranunculiflorae* to families of other orders, and indicates which of those relationships are most likely. In a third section, distributions of wood features that tend to define particular groups within *Ranunculiflorae* are discussed. In fact, relationships between wood anatomy and ecology or habit are often more persuasive than those that seem to link wood anatomy with systematic distinctions. Because detailed descriptions of habits and ecological preferences of taxa require much space, relationships at the generic and specific level between these features and wood character expressions are largely covered in individual papers earlier in this series.

Comparisons at the familial level with respect to habit are, however, of concern in this summary. For example, are *Ranunculiflorae* primitively lianoid, as OGANEZOWA (1975) claimed? The system of QIU & al. (1993) places the arboreal family *Eupteleaceae* near the base of the ranunculid clade, but *Papaveraceae* is lower and the remainder of the order higher, so that one might have to hypothesize a conversion from herbaceous to arboreal to lianoid; is this possible? *Ranunculiflorae* have a number of features regarded as primitive, and may be close to families that are predominantly herbaceous, such as *Piperales*; if the "paleoherb" hypothesis (TAYLOR & HICKEY 1992), based on groups such as the *Piperales* is valid, are *Ranunculiflorae* primitively herbaceous or relatively nonwoody? Even if these questions cannot be answered satisfactorily at present, the close relationship between wood anatomy and habit is evident. For example, *Cocculus trilobus* (THUNB.) DC. has only a single cambium, has libriform fibers, and has only upright and square cells in rays, in contrast to the successive cambia, tracheids, and predominantly procumbent ray cells in lianoid *Menispermaceae* (CARLQUIST, unpubl.). These contrasts are related to the sprawling subshrub habit of *Cocculus trilobus*.

Study of woods of *Ranunculiflorae* has highlighted distinctive modes of wood structure. The problem of *Jeffersonia*, which has wood features different from those of other *Berberidaceae*, is one of these (CARLQUIST, unpubl.). In some instances, (*Glaucidium*, *Hydrastis*), wood formulas can be used in helping to decide whether a genus should be segregated or recognized within a larger family. A distinctive wood pattern would support segregation.

The terminology, materials and methods, and raw data that support conclusions in the present paper are given in the series of papers cited above; space does not permit the inclusion of these details here. Literature is also cited more extensively in those papers.

Wood anatomy and phylogenetic sequences

Only one species of *Ranunculiflorae*, *Decaisnea fargesii* FRANCH. has long scalariform perforation plates in vessels of the secondary xylem (CARLQUIST 1984). The primitiveness of these perforation plates is underlined by the fact that lateral walls of vessels of *Decaisnea* have a primitive pitting configuration, scalariform to transitional, on intervacular contacts. The remainder of *Ranunculiflorae* have much more specialized vessel elements, and the only occurrences of primitive character states that can be cited are much more advanced than those of *Decaisnea*. Occasional perforation plates with one of three bars occur in secondary xylem of *Epimedium* and *Glaucidium*, but most perforation plates are simple. In *Hydrastis*, only simple plates plus a very few with a single bar can be seen in secondary xylem.

There are reports of scalariform perforation plates in vessels of primary xylem of some *Ranunculiflorae*, however. BIERHORST & ZAMORA (1965) list scalariform perforation plates (mixed with simple plates) in species of *Menispermaceae* and *Ranunculaceae*. Primary xylem contains a scattering of scalariform perforation plates also in *Lardizabalaceae* (SOLEREDER 1908), *Hydrastis* (LEMESLE 1948, TOBE & KEATING 1985), and *Glaucidium* (TAMURA 1972). BAILEY (1944) thought of the primary xylem as a refugium for primitive vessel features phylogenetically, and this concept appears justified on the basis of numerous studies, so that one might expect more primitive perforation plates in primary xylem than in secondary xylem in particular species.

LEMESLE (1943) figures "tracheids with areolate pits" for vessel elements he observed in *Sargentodoxa* (*Sargentodoxaceae*; included in *Lardizabalaceae* by some authors); these should be called fibriform vessel elements. Narrow vessel elements of lianas are occasionally or commonly fibriform, so occurrence of such cells in *Sargentodoxa* is not surprising.

The length of vessel elements of families of *Ranunculiflorae* is given in Table 1. These mean lengths are based on averages of mean vessel elements lengths of all species studied in the respective families of the series of papers cited earlier. The families in Table 1 have been arranged in order of descending length of vessel elements. According to BAILEY & TUPPER (1918), long vessel elements (which have virtually the same length as the fusiform cambial initials from which they were

Table 1. Quantitative wood features of *Ranunculiflorae*¹

	Vessel element length	F/V ratio
<i>Lardizabalaceae</i>	411	1.51
Lianoid <i>Menispermaceae</i>	318	3.20
<i>Nandina</i>	279	1.55
<i>Papaveraceae</i>	272	1.82
<i>Berberis</i> (including <i>Mahonia</i>)	246	1.74
<i>Ranunculaceae</i>	195	1.91
<i>Glaucidiaceae</i>	159	1.97

¹ Sources for data given in introduction, further explanation in text.

derived) are primitive and short ones are specialized. Of the families in Table 1, *Lardizabalaceae* have the longest vessel elements. In certain dicotyledons with particular growth forms (e.g., rosette trees that appear to have been derived from herbs), paedomorphosis occurs in wood, and one finds longer vessel elements than one would expect on the basis of degree of phyletic specialization of a particular plant (CARLQUIST 1962). However, the *Ranunculiflorae* studied, except for some with herbaceous characteristics (e.g., *Bocconia* of the *Papaveraceae* and relatively non-woody species in several families), do not possess indicators of paedomorphosis in wood to any appreciable extent. In fact, the herbaceous species of *Ranunculaceae* have shorter vessel elements than the woody species of the family. Lianoid species do not on the average have vessel elements longer than those of nonlianoid woody dicotyledons (CARLQUIST 1975). Therefore, one can use the vessel element lengths of Table 1 as accurate indicators of degree of phyletic advancement. The vessel elements of *Lardizabalaceae* are markedly longer than those of the other families, followed by *Menispermaceae*, then by *Papaveraceae*, *Berberidaceae*, and *Ranunculaceae*. This sequence is close to that in recent phylogenetic treatments (TAKHTAJAN 1987, THORNE 1992). The cladogram of QIU & al. (1993), based on *rbcL* evidence, is similar, except that *Papaveraceae* is accorded a basal position. Families are by no means uniform in vessel element length, and shortening of fusiform cambial initials has occurred polyphyletically. Nevertheless, the sequences of Table 1 are useful preliminary indicators of phyletic advancement.

The F/V ratio (Table 1) is another key to phyletic advancement. After origin of vessels in dicotyledons, there is progressive division of labor between vessel elements and imperforate tracheary elements. With phyletic advance, vessel elements become progressively shorter, as noted above, but intrusiveness of imperforate tracheary elements (before they form secondary walls) increases, so they become progressively longer than the vessel elements they accompany. This phenomenon of increasing division of labor, accompanied by length divergence between vessel elements (V) and the imperforate tracheary elements ("fibers," F) they accompany has been documented in detail earlier (CARLQUIST 1975). The F/V ratio does not increase indefinitely with phyletic advance: ratios above 4.0 are rare. Moreover, the increase in the ratio may be affected in some groups by factors other than phyletic advancement. The basal position of *Lardizabalaceae* in this series is notable. The high F/V ratio in *Menispermaceae* is perhaps related to the occurrence of successive cambia in that family. Except for *Menispermaceae*, the sequence of families is identical with the sequence for vessel element length. The families putatively more primitive for two categories given in Table 1 are woody, with a progressive increase in herbaceousness in the families lower on the list. This could be interpreted as evidence that *Ranunculiflorae* are primitively woody, but I do not regard the evidence as conclusive. In *Chloranthaceae* and *Piperales*, a sympodial habit appears to have preceded a monopodial habit (CARLQUIST 1992), and a similar phenomenon may have occurred in *Ranunculiflorae* as a whole or in parts of it. Certainly the habits of *Nandina* and *Mahonia* are sympodial, as are the habits of various herbaceous genera, and this growth form should be considered in phyletic analysis. The sympodial habit can occur in somewhat woody species, but is much more common in less woody *Chloranthales* and *Piperales* than in arboreal ones.

Wood anatomy and relationships of *Ranunculiflorae*

Vessel restriction patterns. Vessels in dicotyledons are not always distributed randomly in fascicular areas (areas of vertical cells) of wood. Vessels may be confined to the central portions of fascicular areas, with very few or no vessels touching rays. Such phenomena have been termed vessel restriction patterns (CARLQUIST & ZONA 1988). Vessel restriction patterns are not common in dicotyledons at large. Aside from *Ranunculiflorae*, they have been reported only from *Valeriana* of *Valerianaceae* (CARLQUIST 1983), *Launea* of *Asteraceae* (CARLQUIST 1988) and *Isomeris* of *Capparaceae* (new report). In addition, vessel restriction is newly reported for *Aristolochiaceae* and *Piperaceae* in Table 2. Vessel restriction patterns occur in all families of *Ranunculiflorae* (Table 2, column 1), although vessel restriction is not conspicuous in all species. In *Lardizabalaceae*, I was able to observe it clearly only in *Boquila trifoliata* DECAISNE. Although my materials of *Menispermaceae* did not reveal vessel restriction clearly, the phenomenon was evident in that family to METCALFE & CHALK (1950: 56), who state, "Vessels ... seldom in contact with the rays." In *Glaucidium*, vessels are most conspicuously confined to central portions of fascicular areas in fiber-containing bands, less obviously confined in zones in which vessels occur within a ground tissue of axial parenchyma.

Helical sculpturing in vessels. In Table 2, column 2, forms of helical sculpturing in vessels are listed. Grooves interconnecting pit apertures (G) and helical thickenings (T) are sometimes interrelated (CARLQUIST 1988). In *Clematis* and other genera, one can see in some vessels that grooves interconnecting pit apertures are flanked by vessels. Helical sculpturing tends to be more pronounced in narrower vessels, less obvious or absent in wider vessels. Although these forms of helical sculpturing occur in numerous families of dicotyledons, their occurrence in all major families of *Ranunculiflorae* is noteworthy. Absence of helical sculpturing in vessels of *Glaucidium* is probably related to the highly mesic preference of that species; also, herbs tend to have less helical sculpturing (e.g., it is lacking in *Delphinium* and *Hydrastis*) than in woody representatives of a family. The widespread occurrence of helical sculpturing in vessels of *Ranunculiflorae* is probably a better indicator of ecology than of relationship, because this feature has been found mostly in species of habitats with marked dry or cold seasons (CARLQUIST 1975).

Imperforate tracheary elements. Table 2, column 3 lists distribution of types of imperforate tracheary elements in *Ranunculiflorae* and some other families (data on the latter from CARLQUIST 1990, 1992, 1993). One can see that tracheids occur in all but one species of *Menispermaceae*, in some *Lardizabalaceae*, and in *Jeffersonia* of the *Berberidaceae*. Tracheids are generally interpreted as the primitive type of imperforate tracheary element; fiber-tracheids are considered intermediate in specialization, and libriform fibers most specialized (BAILEY 1944; CARLQUIST 1975, 1988). Therefore, one might expect tracheid presence is a plesiomorphy in the genera that have them. There is another possibility, however; tracheids might result from an evolutionary diversification of fiber-tracheids, a process termed fiber-tracheid dimorphism (CARLQUIST 1988: 109). The fiber-tracheids themselves do not, of course, diverge: the genetic information for fiber-tracheid formation is modified so that a plant produces both fiber-tracheids and tracheids. As a result of fiber-tracheid dimorphism, a wood would contain both tracheids (which are vasicentric in this

Table 2. Qualitative wood features of *Ranunculiflorae*. ¹Data from CARLQUIST papers cited in text and from NAST & BAILEY (1946); further explanation in text. Understanding of the phyletic status of a character state (e.g., plesiomorphic, synapomorphic) is essential to use of that character state as an indicator of relationship.

Abbreviations: + or a letter: presence of a feature in at least some members of a family (for families with more than one genus, parentheses indicate the feature occurs in only one genus), 0 absence of feature, *G* grooves interconnecting pit apertures, *T* thickenings, *F* fiber-tracheids, *L* libriform fibers, *T* tracheids, *VT* vasicentric tracheids, *D* diffuse, *DA* diffuse-in-aggregates, *IV* intervacular, *P* pervasive, *VS* vasicentric scanty, *MP* multiseriate and paedomorphic with cells mostly upright, *MS* multiseriate with upright cells only as sheathing cells, *U* uniseriate rays present, *AP* rhomboidal crystals in axial parenchyma, *D* druses in rays, *R* rhomboidal crystals in rays

	Vessel restriction patterns	Helical sculpturing in vessels	Imperforate element types	Axial parenchyma types	Ray histology	Storied structure	Crystal occurrence
<i>Lardizabalaceae</i>	+	T	F, T	VS + D	MS (+U)	+	(R)
<i>Menispermaceae</i>	+	G	T, (L)	D, DA, VS	MS	+	AP, R
<i>Nandina</i>	+	T	L + T	0	MS	+	R
Other <i>Berberidaceae</i>	+	G, T	L	(VS), 0	MS	+	R
<i>Papaveraceae</i>	+	T	L, VT	VS	MP	+	0
<i>Ranunculaceae</i>	+	G, T	L, VT	P, IV, VS	MS	+	(R)
<i>Glaucidiaceae</i>	+	0	L, (T)	IV, P	MS	0	0
<i>Eupteleaceae</i>	0	0	F	D + DA	MS, (U)	0	0
<i>Chloranthaceae</i>	0	0	F, T	D, DA, VS	MS, MP + U	0	0
<i>Aristolochiaceae</i>	+	0	F, T	D, DA	MP	+	D
<i>Lactoridaceae</i>	0	0	F	VS	MP	+	F
<i>Piperaceae</i>	+	0	F, T	VS	MP	+	0

case) plus fiber-tracheids (distal from the vessels). This situation is actually represented in *Boquila* and *Lardizabala* (*Lardizabalaceae*). If such a phylad then progressed further and lost the fiber-tracheids, a wood containing tracheids only would be evolved as an apomorphy. This might have happened in the ancestors of *Akebia*, *Holboellia*, *Sinofranchetia*, and *Stauntonia*. Alternatively, these genera might have retained tracheids from tracheid-bearing ancestors as a plesiomorphy, in which case *Decaisnea* may have shifted from tracheid to fiber-tracheid presence in response to selection for greater mechanical strength in the wood of this self-supporting shrub. The difference is relatively minor, because the shift from tracheids to fiber-tracheids (or back again) is not a huge one. The presence of libriform fibers in *Berberidaceae*, *Glaucidiaceae*, *Papaveraceae*, and *Ranunculaceae* is definitely a specialization, however. The level of these four families in imperforate tracheary elements parallels the ranking of families in the features considered in Table 1.

Nandina is more primitive than other *Berberidaceae* in retaining fiber-tracheids – but this proves to be the only difference between *Nandina* and *Berberis* in wood anatomy. The presence of vasicentric tracheids in *Clematis* can best be explained as an apomorphy, the result of a process termed vessel dimorphism (CARLQUIST 1988: 109). In vessel dimorphism, both wide and very narrow vessels are formed; among the latter are sometimes so narrow that they lack perforation plates and thus are, by definition, tracheids. Wherever this process has happened, the tracheids are in contact with vessels and thus must be termed vasicentric tracheids. The presence of tracheids in *Jeffersonia* might be a plesiomorphy, or it might be explained by fiber-tracheid dimorphism or vessel dimorphism. Further investigation of *Jeffersonia* and genera close to it is necessary to understand this. The work of KIM & JANSEN (1995) shows that *Jeffersonia* is closer to a basal position than hitherto thought. KIM (pers. comm.) considers *Jeffersonia* “definitely not the terminal group of the *Berberidaceae*.” *Vancouveria*, a genus close to *Jeffersonia*, has vessels (with scalariform or pseudoscalariform lateral wall pitting) and libriform fibers.

Axial parenchyma. Axial parenchyma types are given in Table 2, column 4. The generally accepted scheme of KRIBS (1937) indicates that diffuse parenchyma is the most primitive character state, followed by diffuse-in-aggregates; the only other type present in *Ranunculiflorae*, vasicentric scanty, is considered more specialized than diffuse-in-aggregates (KRIBS 1937). All three types can occur together in some species (notably *Menispermaceae*). Aggregation of diffuse cells into either diffuse-in-aggregates or vasicentric axial parenchyma is apparently about equally easy to achieve genetically. However, absence of the most primitive type, diffuse, in the families of *Ranunculiflorae* other than *Lardizabalaceae* and *Menispermaceae* accords with the rankings of Table 1. Intervascular parenchyma (axial parenchyma cells scattered among vessel elements, rather than surrounding groups of vessel elements) is a relatively recently recognized type, as is pervasive parenchyma (parenchyma that comprises the background tissue of a fascicular area, or at least large tangential bands of it, to the exclusion of imperforate tracheary elements. In the wood of *Clematis*, latewood contains numerous narrow vessels but few or no libriform fibers, so axial parenchyma is inevitably intervascular in distribution – although this is an expression related to vasicentric, since all axial parenchyma cells are in contact with vessels. Pervasive parenchyma is related to herbaceous habits: It likely serves for storage in stems that overwinter.

Berberidaceae have largely departed from the remainder of *Ranunculiflorae*; vasicentric parenchyma was observed in one species each of *Berberis* and *Jeffersonia*. In all other species of the family (including *Nandina*), axial parenchyma is absent but functionally replaced by living (nucleated) libriform fibers.

Rays. Wide, tall multiseriate rays little altered during ontogeny, relatively intact extensions of primary rays, are characteristic of the families of *Ranunculiflorae* (Table 2, column 5). These contrast with multiseriate rays in most dicotyledons, in which the large primary rays are rapidly broken into smaller segments during growth of the stem or root. In most *Ranunculiflorae*, the multiseriate rays are composed of procumbent cells except for one or two layers of sheathing cells, which are upright. These rays would come close to Homogeneous Type II of KRIBS, except that the presence of upright cells – at least where most abundant, as in *Papaveraceae* – is indicative of pedomorphosis, and rays with a large proportion of upright cells would be termed Paedomorphic Type II (CARLQUIST 1988). Some rays, therefore, can be considered intermediate between these two types. Paedomorphic rays, as in *Cocculus trilobus* (*Menispermaceae*) as well as *Epimedium* and *Jeffersonia* of the *Berberidaceae*, *Glaucidium*, and the more nearly herbaceous genera of *Ranunculaceae*, characterize plants with less woody habits. Uniseriate rays are abundant only in *Decaisnea* and *Jeffersonia*. Because presence of both multiseriate and uniseriate rays is more primitive than presence of multiseriate rays only (KRIBS 1935), the ray configuration of *Decaisnea* may be one more indication of the primitive status of that genus. In *Jeffersonia*, the rays are paedomorphic and may have another explanation. In *Delphinium*, ray areas can be abruptly converted largely to zones of fibers, leaving a series of uniseriate and biseriate rays; this process may happen in *Jeffersonia* also. Uniseriate rays are uncommon in *Lardizabalaceae* other than *Decaisnea*.

Storying. Storying of fusiform cambial initials occurs in all families of *Ranunculiflorae* other than *Glaucidiaceae*. In *Glaucidiaceae*, as in herbaceous *Ranunculaceae*, accumulation of secondary xylem may be insufficient for storying to appear; where present in dicotyledons, it appears only after an appreciable number of divisions leading to increase in girth of the cambium.

Where present, storying is often not revealed in imperforate tracheary elements, because these elongate to various degrees compared with length of fusiform cambial initials from which they were derived, and the varied nature of the elongation prevents storying from becoming evident. If numerous vessel elements are present side by side tangentially, storying is evident in them, but this is not true in some *Ranunculiflorae* (e.g., *Lardizabalaceae*). Storying is, however, quite evident in secondary phloem of *Lardizabalaceae* (and *Menispermaceae*), because the numerous sieve tube elements lie side by side tangentially and reflect the storied nature of the fusiform cambial initials well. Given the absence of storying in herbaceous species, *Ranunculiflorae* as a whole do have storied cambia, and therefore varying degrees of storied wood structure.

Crystals. Rhomboidal calcium oxalate crystals are not rare in wood of dicotyledons, but such crystals still have been reported in a minority of the genera of woody dicotyledons (see CARLQUIST 1988). In *Ranunculiflorae*, calcium oxalate crystals were observed in rays in all families except *Glaucidiaceae* and *Ranunculaceae*. One must remember that only a small portion of each family was surveyed, so conceivably crystals might yet be found in wood of *Ranunculaceae*. Crystals were

observed in ray cells of only one species of *Lardizabalaceae* (*Stauntonia hexaphylla* DECAISNE); this example shows that we should attach more significance to presence of a feature than absence. In the case of crystals in wood, one should also take into account phloem; crystals present in phloem rays of a species do not always occur in the xylem rays, or are less common in xylem rays.

Synthesis of features indicating relationship. Wood features are of highest value in systematic significance if they are not easily evolved with respect to ecological conditions, and if they characterize relatively few families. For example, vestured pits occur almost universally in woods of *Myrtales*, but also in a small number of woods from other orders (see listing in CARLQUIST 1988). If several features of restricted distribution in dicotyledon woods are common to a group of families, the likelihood that they are valid indicators of close relationship increases accordingly. One should also be able to find suites of features (e.g., pollen ultrastructure, embryology) that link families in which wood features seem to demonstrate close relationship.

The wood features that appear most promising as indicators of relationships of *Ranunculiflorae* by virtue of the above considerations are vessel restriction patterns, ray histology, and storying. To be indicators of relationship, the character states described should be synapomorphic, and all conceivably are in *Ranunculiflorae*. Features of subsidiary importance as indicators of relationships include axial parenchyma type and distribution, crystal occurrence in wood, imperforate tracheary element type, and helical sculpturing occurrence. The character state distributions outside of *Ranunculiflorae* for the features listed as most significant point primarily to *Piperales* (*Aristolochiaceae*, *Lactoridaceae*, *Piperaceae*).

Can similarities in these character state distributions result from similarity in habit or evolutionary level? Vessel restriction patterns appear unrelated to either of these considerations (the significance of vessel restriction patterns has not as yet been elucidated). Storying is more likely to occur in dicotyledons with short fusiform cambial initials (and thus could be related to evolutionary level), but there are many groups of dicotyledons with short fusiform cambial initials but no indications of storying. The peculiar nature of multiseriate rays in *Ranunculiflorae* (cells procumbent except for 1–2 layers of sheath cells; uniseriate rays absent in most species) is not matched in very many families, and few “woody herbs” have this ray type.

In addition to the wood features, there are some remarkable similarities in bark anatomy that link *Ranunculiflorae* and *Piperales*. In inner bark of some species, one finds a cylinder of large brachysclereids (in which phloem fibers may also be included); a single large rhomboidal crystal may be found in at least some of these sclereids. From the cylinder of sclereids, sclereid plates may extend radially into the outer xylem rays of the woody cylinder. Sclereid cylinders with all of the features mentioned have been observed and figured in *Lardizabalaceae* (CARLQUIST 1984), *Menispermaceae* (CARLQUIST, unpubl.), and, in *Piperales*, *Aristolochiaceae* (CARLQUIST 1993). To be sure, all of these families are lianoid, but bark sclereids corresponding to the formula cited are not present in bark of most lianoid families of dicotyledons.

The potential significance of the wood resemblances between *Ranunculiflorae* and *Piperales* is underlined by the cladogram of QIU & al. (1993), based on analysis of *rbcL*. In that cladogram, *Piperales* occur in a clade adjacent to and basal to that including the families of *Ranunculiflorae*. This placement is pertinent because the

families of *Piperales* figure prominently in the paleoherb hypothesis of TAYLOR & HICKEY (1992).

Chloranthaceae, interpreted here as the sole family of *Chloranthales*, possess fewer similarities to *Ranunculiflorae* than do *Piperales*. The rays of *Chloranthaceae* are like those of the allegedly primitive *Decaisnea* of *Lardizabalaceae*. *Chloranthaceae* have relatively tall fusiform cambial initials, so one would not expect storying in that family. Vessel restriction patterns are not thus far evident in *Chloranthaceae*. The long scalariform perforation plates, scalariform to transitional wall pitting, and fiber-tracheids of *Decaisnea* are similar to those of *Chloranthaceae*.

Eupteleaceae are placed in the clade that includes *Ranunculiflorae* according to the results of QIU & al. (1993). Although this placement is unprecedented in phylogenies based primarily on macromorphology (e.g., TAKHTAJAN 1987, THORNE 1992), it should be given consideration. The wood of *Euptelea*, which has been described by NAST & BAILEY (1946), is actually rather similar to that of *Decaisnea* or *Chloranthaceae*: long scalariform perforation plates, scalariform to transitional lateral wall pitting of vessels, fiber-tracheids present as the imperforate tracheary element type, axial parenchyma diffuse to diffuse-in-aggregates, rays Heterogeneous Type II. All of these features occur in *Decaisnea*. *Eupteleaceae* do not have crystals in ray cells, nor do they have vessel restriction patterns.

Resemblances between wood of *Decaisnea* and that of *Euptelea* can be claimed to be based mostly on similarity in evolutionary level, and one should keep this possibility in mind. LOCONTE & ESTES (1989) accord a basal position to *Decaisnea* in their cladogram of the genera of *Lardizabalaceae*. Interestingly, NAST & BAILEY (1946) cite transitions between tricolpate and polycolpate pollen as characteristic not only of *Eupteleaceae*, but also *Berberidaceae* and *Ranunculaceae*. The possibility that *Eupteleaceae* might be related to and basal to *Ranunculiflorae* needs to be examined in detail; that idea stands in contradiction to the paleoherb hypothesis of TAYLOR & HICKEY (1992).

Most workers now exclude *Glaucidium* from *Ranunculaceae* (or other families). TOBE (1981) stresses similarity of *Glaucidium* to *Paeoniaceae*. In terms of wood anatomy, however, the resemblances are very few (data on wood of *Paeonia* based on KEEFE & MOSELEY 1978). Wood of *Paeonia* characteristically has scalariform perforation plates with 1–7 bars (only 37% of perforation plates are simple); wood of *Glaucidium* has mostly simple plates, and only occasionally plates with 1–3 bars. Lateral wall pitting on vessels of *Paeonia* is transitional to alternate; lateral wall pitting on vessels of *Glaucidium* appears in part scalariform, but the pattern is probably basically pseudoscalariform (a basically alternate pattern with pits much widened laterally). Imperforate tracheary elements of *Paeonia* are tracheids; those of *Glaucidium* are libriform fibers. Axial parenchyma of *Paeonia* is apotracheal and sparse; in *Glaucidium* it is paratracheal and pervasive. Rays in *Paeonia* are narrowly multiseriate (2–8 cells wide) plus uniseriate, and have lignified cell walls; those of *Glaucidium* are tall and wide, multiseriate only, and have thin nonlignified cell walls. Thus, the resemblances in wood between *Paeonia* and *Glaucidium* are minimal. On the contrary, wood of *Glaucidium* resembles that of *Delphinium* or *Hydrastis*. *Hydrastis* has been separated as a monogeneric family from *Ranunculaceae* or *Berberidaceae* by various authors (e.g., TOBE & KEATING 1985), but KEENER (1993), reviewing all available data, concludes that *Hydrastis* is best placed in

Ranunculaceae. Wood data show that *Hydrastis* agrees with herbaceous or minimally woody *Ranunculaceae* in all features, differing only in having in secondary xylem a very small number of scalariform perforation plates with a single bar – a minor difference when one considers that scalariform plates can be found in primary xylem of a number of *Ranunculaceae* (BIERHORST & ZAMORA 1965). The concepts of KEENER (1993) and the wood data cited here agree with the treatment of HOOT (1991), who, in a cladistic analysis of *Ranunculaceae*, accords *Hydrastis* a near-basal position in the family.

Wood anatomy and familial definitions. In many respects, wood anatomy of *Ranunculiflorae* is like a continuum, with distinctive modes of structure relating to particular habits and, to a lesser extent, ecological conditions, rather than to systematic distinctions. For example, *Cocculus trilobus* differs from lianoid *Menispermaceae* by having libriform fibers rather than tracheids, vasicentric axial parenchyma rather than diffuse and diffuse-in-aggregates, and relatively narrow rays with upright cells rather than very wide, tall rays with cells procumbent except for a few sheathing cells (CARLQUIST, unpubl.). These differences seem related to habit primarily: *Cocculus trilobus* is a sprawling subshrub. In addition, the mean vessel diameter of *C. trilobus* is smaller than that of any other *Menispermaceae* in the study cited, a fact related to the dryland tropical island sites where this species grows. Yet *C. trilobus* unquestionably belongs in the same genus as large upright shrubs and scandent shrubs that become true lianas with age.

Although one should note with caution the above example, there are instances where wood features are restricted to a particular family. For example, wood of *Lardizabalaceae* is like that of *Menispermaceae* in many respects, but the occurrence of successive cambia is restricted to *Menispermaceae*, and likely successive cambia occur in the vast majority of genera and species in that family.

The genus *Berberis* (including *Mahonia*) is distinctive in that true axial parenchyma is almost entirely absent – it has been reported in one species (CARLQUIST, unpubl.), although in view of the size of the genus, the possibility that axial parenchyma may occur in more than one species is considerable. Nucleated fibers substitute functionally for axial parenchyma; there even appears to be incipient dimorphism between the fibers located distal to vessel groups and those within vessels groups; the latter fibers are somewhat more parenchymalike in pits and wall thickness.

The wood of *Nandina* is very similar to that of *Berberis*. *Nandina* has fiber tracheids plus (adjacent to rays) nucleated libriform fibers; otherwise, *Nandina* wood has no features not also found widely in *Berberis*. Differences between the genera claimed by SHEN (1954) are likely the results of misinterpretations. *Nandina* has been listed separately in Tables 1 and 2. The data given there as well as other information cited elsewhere (CARLQUIST 1995c) show that *Nandina* does not warrant segregation into a monogeneric family, although some authors recognize such a family. The presence of fiber-tracheids in *Nandina*, and the fact its values in Table 1 rank as slightly more primitive than those of *Berberis* justify a basal position for the genus within the family *Berberidaceae*, as shown in the cladistic study of LOCONTE & ESTES (1989). One is tempted to characterize the family *Berberidaceae* on the basis of *Berberis*, because wood samples of that genus are so much more readily available than wood portions of the other genera, most of which are relatively nonwoody.

However, modes of wood structure other than that shown by *Berberis* occur in the family. In particular, the wood of *Jeffersonia* is distinctive, and more intense study of wood of the subfamily (*Epimedioideae*), to which *Jeffersonia* belongs, is recommended.

Our concepts of wood anatomy of *Ranunculaceae* are influenced by the fact that *Clematis* has been the source of most wood samples studied thus far for the family. When wood of herbaceous genera with some degree of woodiness (e.g., *Delphinium*, *Helleborus*) is added, a much more diverse picture emerges. As with *Berberidaceae*, we need a survey of wood of more of the herbaceous genera, particularly those species with some appreciable degree of woodiness in rhizomes. The likelihood that *Hydrastis* should be included in *Ranunculaceae* on the basis of wood anatomy is discussed above. Although wood anatomy of *Glaucidium* shares many features with wood of *Hydrastis* and *Delphinium*, those features may be due to similarity in habit and ecology, and other features of *Glaucidium* may well be of overriding significance in segregating it as a monogeneric family.

Woods of *Papaveraceae* are separable from those of other *Ranunculiflorae*—particularly those with more specialized xylem (*Papaveraceae* all have libriform fibers). The juvenilism in rays of *Papaveraceae* is much more pronounced than in other families of *Ranunculaceae*, although one can cite selected genera from those families that are like *Papaveraceae* in ray structure (e.g., *Epimedium*, *Xanthorhiza*). Adaptation of the various genera and species of *Papaveraceae* to particular habits and ecological conditions (especially xeric conditions) is of overriding importance in explaining the xylary character states of the component genera of the family.

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