

WOOD ANATOMY OF PAPAVERACEAE, WITH COMMENTS ON VESSEL RESTRICTION PATTERNS

by

Sherwin Carlquist and Scott Zona

Rancho Santa Ana Botanic Garden and Department of Biology, Pomona College,
Claremont, California 91711, U.S.A.

Summary

Qualitative and quantitative features are reported for *Bocconia*, *Dendromecon*, *Dicentra*, *Hunnemannia*, and *Romneya*. *Bocconia* differs from the other genera by its wide vessels, few per group, and few per mm²; it shows pedomorphosis in vessel element length and ray histology. In respects other than these, it agrees with features common to woody Papaveraceae; these features in turn occur in families of Papaverales (Berberidaceae, Lardizabalaceae, Ranunculaceae): vessels in diagonal groups; presence of both libriform fibres and vasicentric tracheids; nucleated nature of libriform fibres; rays almost exclusively multiseriate; rays wide, tall, and composed mostly of procumbent cells; wood storied to various degrees. Additional features show resemblance between one or more genera of Papaveraceae and other families of Papaverales. *Bocconia* is distinctive among Papaveraceae in its relatively mesomorphic wood, which may in part be explainable on the basis of stem succulence. The occurrence of a vessel restriction pattern – vessels in the centre of fascicular areas (axial portions of secondary xylem between rays) not in contact with rays – in *Dicentra* and *Hunnemannia* is like that of other genera of Papaverales such as *Nandina*. An explanation for the significance of vessel restriction, involving genera other than those of Papaverales (*Launea*, *Valeriana*), is attempted.

Key words: Ecological wood anatomy, systematic wood anatomy, vessel restriction patterns, Papaveraceae.

Introduction

Papaveraceae are not generally considered woody to any appreciable degree, although in

California, *Dendromecon* is a conspicuous shrub or small tree to 6 m (Munz 1974). *Bocconia*, native to montane Mesoamerican and Andean regions, is even taller (to 8 m: Fedde 1936, Cumbie 1983), although the succulent cortex and pith suggest a degree of herbaceousness. *Romneya* is a shrub to 2.5 m, in chaparral and coastal sage associations of California and northern Baja California (Munz 1974); the stems branch from the base, and last only for several years each, so that wood accumulation is less than in *Dendromecon*. *Hunnemannia*, which occurs on the Mexican Plateau, is a small to medium-sized shrub, woody at the base (the specimen in the present study was collected in Hawaii, where it is adventive). Much less woody is *Dicentra chrysantha*. Although most species of *Dicentra* are relatively herbaceous, the rhizomes and lower stems of *D. chrysantha* and *D. ochroleuca* Engelm. are conspicuously stout and woody; upright innovations from these rhizomes are woody at bases. Degree and kind of woodiness are relevant to the study of wood anatomy; Cumbie (1983), by studying wood ontogeny of *Bocconia vulcanica*, believes *Bocconia* wood to exemplify pedomorphosis. *Dendromecon* is, as Cumbie (1983) notes, probably not closely related to *Bocconia*, and therefore there is a possibility that it may be primarily rather than secondarily woody. This concept seems more plausible than the earlier phylogeny offered by Fedde (1936: 18, 58) in which he postulates a linear series leading from *Corydalis* to *Eschscholzia* to *Dendromecon* to *Bocconia* (and thence on to *Glaucium* and other herbaceous genera). In addition to primary versus secondary woodiness, degree of woodiness

is a concern; for example, the stems studied of *Dendromecon rigida* subsp. *rhamnoides* are much larger than those of *D. rigida* subsp. *rigida* (Table 1, column 1). Likewise, the differences between stem and root wood in *Dicentra* offer interesting comparisons. Papaveraceae that are essentially herbaceous, with only very thin woody cylinders at bases at most (e.g., *Argemone*) have not been included in the present study.

None of the Papaveraceae in the present study occur in wet forest habitats. *Bocconia* is a tree in shrubby montane forest; however, bark and pith succulence in *Bocconia* suggest the existence of features that modify xylary adaptation to dry conditions. The roots and stem bases of *Dicentra chrysantha* are also succulent and rich in starch. *Dendromecon* and *Romneya* are not at all succulent, and in these genera one may expect wood anatomy to reflect ecology more directly.

Although only a single species of *Dendromecon* is recognised here, in accordance with the treatment of Munz (1974), that species does possess considerable ecological amplitude. *Dendromecon rigida* subsp. *rhamnoides* occurs in the moderate climate of offshore islands of California, whereas *D. rigida* subsp. *rigida* can be found in summer-hot chaparral areas with less than 30 cm annual rainfall.

The term 'vessel restriction patterns' has been applied to those instances in which vessels are confined (to various degrees) to the central portions of fascicular areas and do not contact ray cells. Attention was called to an instance in *Valeriana* (Carlquist 1988). The phenomenon has been illustrated in *Launea* (Asteraceae), and the term invented in that instance (Carlquist 1988). The occurrence of vessel restriction in certain of the Papaveraceae studied here has led to an assessment of this phenomenon in terms of its occurrence systematically and with respect to habit. The phenomenon of vessel restriction does not seem related to the 'isolation' syndrome of rays (e.g., the wide or aggregate rays in *Fagaceae*), which Braun (1970) described from woody species quite unlike Papaveraceae in habit.

The systematic affinities of Papaveraceae and the constitution of an order that may be called Papaverales or Berberidales have near-

ly attained consensus, despite the presence of quite different views in earlier literature. The treatment of Dahlgren (1980), Takhtajan (1987), and Thorne (1976) group together the families Papaveraceae (including Fumariaceae in the present study), Berberidaceae, Circaeastraceae, Kingdoniaceae, Lardizabalaceae, Menispermaceae, Ranunculaceae, and Sargentodoxaceae (as well as such segregate families as Glaucidiaceae, Nandinaceae, and Podophyllaceae). Recent data are at hand on wood anatomy of some of these families, such as Lardizabalaceae (Carlquist 1984a) and Ranunculaceae (Sieber & Kučera 1980). Wood anatomy of Papaveraceae can be compared with that of these other families in an attempt to see to what degree wood anatomy reinforces the idea that the families named form a natural grouping.

Little data have been accumulated on wood anatomy of Papaveraceae. As the summary of Fedde (1936) shows, most work on the anatomy of the family emphasised study of laticifers or leaf anatomy. Harvey-Gibson and Bradley (1917) commented only briefly on features of wood anatomy (e.g., helical thickenings in tracheids of *Romneya*). The brief account of wood of Papaveraceae contains virtually all of what we know. Data on *Dendromecon* and *Romneya* were provided recently by Carlquist and Hoekman (1985).

Materials and Methods

Wood samples were available in dried form except for *Dendromecon rigida* subsp. *rigida* and *Dicentra chrysantha*; portions of these were preserved in formalin-acetic-alcohol. Woods were sectioned on a sliding microtome except for *Dicentra*. Sections of greater thickness (e.g., 30 µm) were prepared for *Bocconia* and *Hunnemannia* in order to minimise collapse of vessels in transections. Thick sections were not disadvantageous because cell size is greater in these genera than in the other genera. For the stems and roots of *Dicentra chrysantha*, an alternative method involving softening in ethylene diamine followed by sectioning portions in paraffin on a rotary microtome (Carlquist 1982a) was employed. Sections were stained in safranin; for most collections, sections were also counterstained in fast green. Macerations were

prepared with Jeffrey's fluid and stained with safranin. Photographs utilising scanning electron microscopy (SEM) were derived from sliding microtome sections with the use of an ISI WB-6 electron microscope. The mottled appearance of SEM photographs presented here is not the result of charging; it represents natural depositions on the vessel walls illustrated.

The means in Table 1 are based upon 25 measurements per feature except for vessel wall thickness, libriform fibre diameter at widest point (as seen in transection), libriform fibre wall thickness, and diameter of pits on lateral walls of vessels. For these features, means were derived from a few carefully selected measurements. Vessel diameter was taken at widest point within a vessel and is the lumen diameter. The presence of very narrow vessels that are close to vasicentric tracheids in diameter presented a problem, and some narrow vessels may have been inadvertently omitted from calculations. Terminology follows the IAWA Committee on Nomenclature (1964), except for vasicentric tracheids, where the usage of Carlquist (1985) and Carlquist and Hoekman (1985) is followed; this usage is much like that of Metcalfe and Chalk (1950). If the usage of Metcalfe and Chalk (1950) and Carlquist (1985) is not entirely uniform, that is because the representation of vasicentric tracheids varies somewhat from one family to another. The reader's attention is called to the fact that some authors apply the term 'vascular tracheids' to what are called vasicentric tracheids here. Vascular tracheids, in the usage of Carlquist and Hoekman (1985) and Carlquist (1985) are restricted to latewood and do not tend to surround vessels. Reasons for adoption of the terminology employed here will be found discussed by Carlquist (1985).

Preparation of many of the sections and collection of quantitative data represent the work of the junior author; the senior author prepared photographs, text, and made additional observations on wood characteristics. Some of the samples were collected by the senior author in Peru with the aid of a grant from the National Science Foundation, BSR-8109910. The taxonomy of *Dendromecon* and *Romneya* follows Munz (1974).

Anatomical results

Growth rings

Growth rings are absent or nearly so in *Bocconia* (Fig. 1), *Dicentra* (Fig. 10), and *Hunnemannia* (Fig. 15). In contrast, *Dendromecon* (Fig. 11) and *Romneya* (Fig. 16) are ring-porous to varying degrees. The ring porosity of these two genera takes the form of larger vessels in earlywood; the larger vessels tend to be in smaller groupings than the latewood vessels, and vasicentric tracheids are less abundant in earlywood than in latewood, although they are present throughout growth rings in *Dendromecon* and *Romneya*.

Quantitative vessel features

The number of vessels per group has been computed in Table 1, column 2. A difference between *Bocconia* (2.1 or fewer vessels per group; Fig. 1) and the other genera (3.6 or more vessels per group) is evident. Because very narrow vessels may have been missed during measurements, the number of vessels per group in *Dendromecon* and *Romneya* may be slightly higher than those recorded in Table 1. The large groupings of vessels in the latewood of *Dendromecon* (Fig. 11) contain an almost indefinite number of vessels per group.

Vessels wider than 100 μm in diameter characterise *Bocconia* (Fig. 1). Next in mean vessel diameter of the genera is *Dicentra* (Fig. 10), in which vessel diameter is greater in roots than in stems (Table 1, column 3). Lowest in vessel diameter are *Dendromecon rigida* subsp. *rigida* (Fig. 11) and *Romneya coulteri* (Fig. 16). The vessels of *Hunnemannia* (Fig. 15) are narrow but fluctuate seasonally in diameter less than do those of *Dendromecon* and *Romneya*. The small vessel diameter of large numbers of latewood vessels in the latter two genera account for the low figures (Table 1, column 3). Similar results were obtained for *Dendromecon* and *Romneya* earlier (Carlquist & Hookman 1985).

Vessel density (Table 1, column 4) is roughly inversely proportional to vessel diameter in dicotyledons at large; this tends to be illustrated also in Papaveraceae. *Bocconia* (Fig. 1) has the lowest number of vessels per mm^2 , whereas *Dendromecon rigida* subsp.

Table 1. Wood characteristics of Papaveraceae.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12
		thickness of woody cylinder (mm)	mean number of vessels per group	mean diameter of vessels at widest point (µm)	mean number of vessels per mm ²	mean vessel element length (µm)	mean vessel wall thickness (µm)	mean diameter of libriform fibres at widest point (µm)	mean libriform fibre length (µm)	mean libriform fibre wall thickness (µm)	mean height multiseriate rays (µm)	mean width multiseriate rays at widest point (cells)	Mesomorphy ratio *
<i>Bocconia arborea</i> S. Watson	Carlquist 2393 (RSA, RSAw)	18	2.0	132	13.5	357	3.5	23	726	2.8	1758	7.9	3491
	Wiens 2535 (RSA, RSAw)	4	2.1	127	24.1	409	3.5	19	598	3.5	1067	4.7	2155
<i>B. frutescens</i> L.	Davidson 5131 (RSA, RSAw)	24	2.0	129	9.2	269	2.6	30	715	4.0	1730	11.0	3772
<i>B. integrifolia</i> H. & B.	Carlquist 7044 (RSA, RSAw)	25	1.7	135	11.6	241	3.4	16	614	3.0	1404	6.0	2805
	Carlquist 7068 (RSA, RSAw)	17	1.9	143	6.7	360	3.5	32	711	3.5	1443	5.0	7684
	Carlquist 7111 (RSA, RSAw)	14	1.5	144	7.7	386	3.4	19	731	4.0	1533	4.3	7219
	Davidson 5046 (RSA, RSAw)	11	1.7	107	17.4	270	3.5	19	585	3.0	1556	8.9	1660
<i>B. vulcanica</i> Donn. Smith	Davidson 3317 (RSA, RSAw)	18	2.0	182	9.2	308	2.7	29	677	3.7	1213	5.7	6093
<i>Dendromecon rigida</i> Benth.	Thome 34845 (RSA, RSAw)	38	6.4	63	89.3	330	2.5	19	514	3.5	1385	5.1	233
subsp. <i>rhamnoides</i> (Keell.) Raven	R.S.A.B.G. prop. no. 5865	6	14.7	43	256.0	302	2.5	13	474	3.2	1630	4.5	51
<i>D. rigida</i> subsp. <i>rigida</i>	STEM Carlquist 15940 (RSA)	15	3.6	87	36.2	200	2.4	17	294	2.1	> 1 cm	> 10	481
<i>Dicentra chrysantha</i> (H. & A.) Walp.	ROOT Carlquist 15940 (RSA)	10	5.0	100	38.6	277	2.6	24	514	2.5	> 1 cm	> 10	718
<i>Hunnemannia fumariifolia</i> Sweet	Carlquist 2392 (RSA, RSAw)	14	14.4	54	80.0	142	3.5	19	307	2.0	> 1 cm	> 10	96
<i>Romneya coulteri</i> Harv.	R.S.A.B.G. prop. no. 6549	4	17.4	37	227.8	196	2.5	12	391	2.8	> 1 cm	> 10	32

* vessel diameter times vessel element length divided by number of vessels per mm².

rigida and *Romneya coulteri* have the highest values.

Vessel element length (Table 1, column 5) ranges from 409 μm in *Bocconia arborea* to 142 μm in *Hunnemannia fumariaefolia*. Vessel elements in Papaveraceae are relatively short compared to those in dicotyledons at large (mean = 649 μm : Metcalfe & Chalk, 1950: 1360). The majority of Papaveraceae have vessel elements ranging from 200 to 360 μm in length. In view of the ontogenetic changes in vessel element length found by Cumbie (1983) in *Bocconia vulcanica*, these results are worthy of examination.

Vessel wall thickness (Table 1, column 6) ranges from 2.4 μm to 3.9 μm in Papaveraceae. This range is small. *Bocconia*, the genus with the widest vessels, also has the greatest vessel wall thickness, although not conspicuously so (Fig. 1).

Qualitative vessel features

Perforation plates are simple throughout Papaveraceae. Lateral wall pitting consists of alternate circular to somewhat elliptical pits. Intervascular pits are similar in size to vessel-parenchyma pits; mean diameters for the former are shown in parentheses in the following: *Dendromecon* (6 μm); *Dicentra* (7 μm); *Hunnemannia* (6 μm); *Romneya* (5 μm). In *Bocconia*, vessel-parenchyma pits are about 50% greater in horizontal length than the intervascular pits (compare Fig. 3 with Figs. 4, 5); intervascular pits are as follows in mean diameter: *B. arborea* (8 μm); *B. frutescens* (14 μm); *B. integrifolia* (11 μm : Fig. 3); *B. vulcanica* (15 μm). In *Bocconia*, vessel-parenchyma pits have much wider apertures (Figs. 3, 4) than do intervascular pits (Fig. 3). Intervascular pits in Papaveraceae have pit aperture shape that ranges from nearly circular to markedly elliptical.

Some pits on lateral vessel walls of *Bocconia vulcanica* appear to be vested when viewed with a light microscope. Examination of these with SEM reveals that these pits have somewhat irregular outlines to their margins, and a tendency of pit aperture margins to be bent into the pit cavities (Fig. 9). This has also been figured (with a different photograph) for this species elsewhere (Carlquist 1988).

Forms of helical sculpture occur on vessel walls of Papaveraceae. In *Dicentra* and *Hunnemannia*, shallow grooves interconnect pit apertures. These grooves are not readily visible, and can be demonstrated where portions of vessel walls are shaved away by sectioning in such a way that depressions on the inner wall surface are revealed as slitlike appearances in the wall sections. In *Dendromecon* and *Romneya*, pronounced thickenings occur on vessel walls. In *Dendromecon*, these thickenings may be wide (Fig. 13) or narrow (Fig. 14), and may tend to anastomose (Fig. 14). The thickenings do not tend to run predominantly between pit apertures; rather, the thickenings may overlie pits (Fig. 13, thickenings overlie most pits; Fig. 14, thickenings over some pits). Pit apertures do not penetrate the thickenings. In *Romneya*, the thickenings are more densely crowded (Fig. 18), so that only slitlike portions of the wall are not covered by them. No helical sculpture was observed on vessel walls of *Bocconia*.

Thin-walled tyloses were observed in three collections of *Bocconia integrifolia* (Fig. 1).

Imperforate tracheary elements

As reported by Metcalfe and Chalk (1950), borders are not present on pits of the ordinary imperforate tracheary elements; following the IAWA Committee on Nomenclature (1964) usage, these cells are termed libriform fibres here. In Table 1, column 7, mean diameter of libriform fibres at widest point (as seen in transection) is given. The figure for *Bocconia* (Fig. 1) ranges upward from 19 μm , whereas *Dendromecon* (Fig. 11) and *Romneya* (Fig. 16) have libriform fibres less than 19 μm in diameter. *Hunnemannia* (Fig. 15) is intermediate. Libriform fibres are wider in roots (Fig. 10) of *Dicentra chrysantha* than in stems.

With respect to libriform fibre length (Table 1, column 8), one finds the range in *Bocconia* is from 585 μm to 731 μm . The shortest libriform fibres occur in *Dicentra chrysantha* roots and in the stems of *Hunnemannia* and *Romneya*. The fact that libriform fibres are nearly twice as long in stems as they are in roots of *Dicentra chrysantha* is noteworthy, because the difference in length of vessel elements between the two organs in this species is not so great.

Libriform fibre wall thickness is shown in Table 1, column 9. Although fibre walls are thickest in *Bocconia* (Fig. 1), these fibres do not appear thick because the diameter of libriform fibres in *Bocconia* is relatively great. Relatively thin walled libriform fibres can be seen in *Dendromecon* (Fig. 11), *Dicentra* (Fig. 10), *Hunnemannia* (Fig. 15) and *Romneya* (Fig. 16).

With the aid of liquid preserved material, one can demonstrate nuclei in the libriform fibres of *Dendromecon rigida* subsp. *rigida*. One can find starch in libriform fibres of *Bocconia* (not liquid preserved) and *Dicentra* (liquid preserved). Thus, living (or nucleated) fibres can be claimed for three genera. The fact that materials of *Hunnemannia* and *Romneya* were dried may account for absence of contents in libriform fibres of these two genera. A small amount of fibre dimorphism occurs in *Bocconia* and *Hunnemannia*, in which shorter, wider fibres (resembling narrow vessel elements in length and diameter at widest point) occur near vessels.

Vasicentric tracheids were reported earlier for *Dendromecon* and *Romneya* (Carlquist 1985; Carlquist & Hoekman 1985). Vasicentric tracheids occur in the collections of these two genera in the present study. Vasicentric tracheids occur in smaller numbers in the woods of *Dicentra* and *Hunnemannia*, and were not observed in *Bocconia*. In *Dendromecon* and *Romneya*, vasicentric tracheids are more abundant in latewood than in earlywood, although present in appreciable numbers in earlywood.

Axial parenchyma

Paratracheal axial parenchyma forming sheaths one to three cells in thickness occurs in *Bocconia* (Fig. 1). In *Dendromecon*, *Dicentra*, *Hunnemannia*, and *Romneya*, axial parenchyma is sparser and is scattered among the vessels, which are typically in large groups in these genera; the distribution can be considered vasicentric scanty (this term used by Kribs, 1937, and other authors).

Axial parenchyma most commonly occurs in strands of two cells in Papaveraceae; parenchyma not subdivided into strands was encountered commonly only in *Dendrome-*

con rigida subsp. *rigida*, in which strands of two cells are also common.

Quantitative features of rays

In Table 1, column 10, multiseriate ray height is given. Within *Bocconia*, the range is from 1067 μm to 1758 μm – a relatively small range. The rays shown for *B. integrifolia* (Fig. 2) are typical for the genus. The height of multiseriate rays in *Dendromecon* (Fig. 12) lies within the range given for *Bocconia*. The rays of *Dicentra*, *Hunnemannia*, and *Romneya* (Fig. 17) are much taller; estimating the height of rays in these genera proved difficult because many rays in the sections studied are longer than the section; this accounts for the approximate values in Table 1.

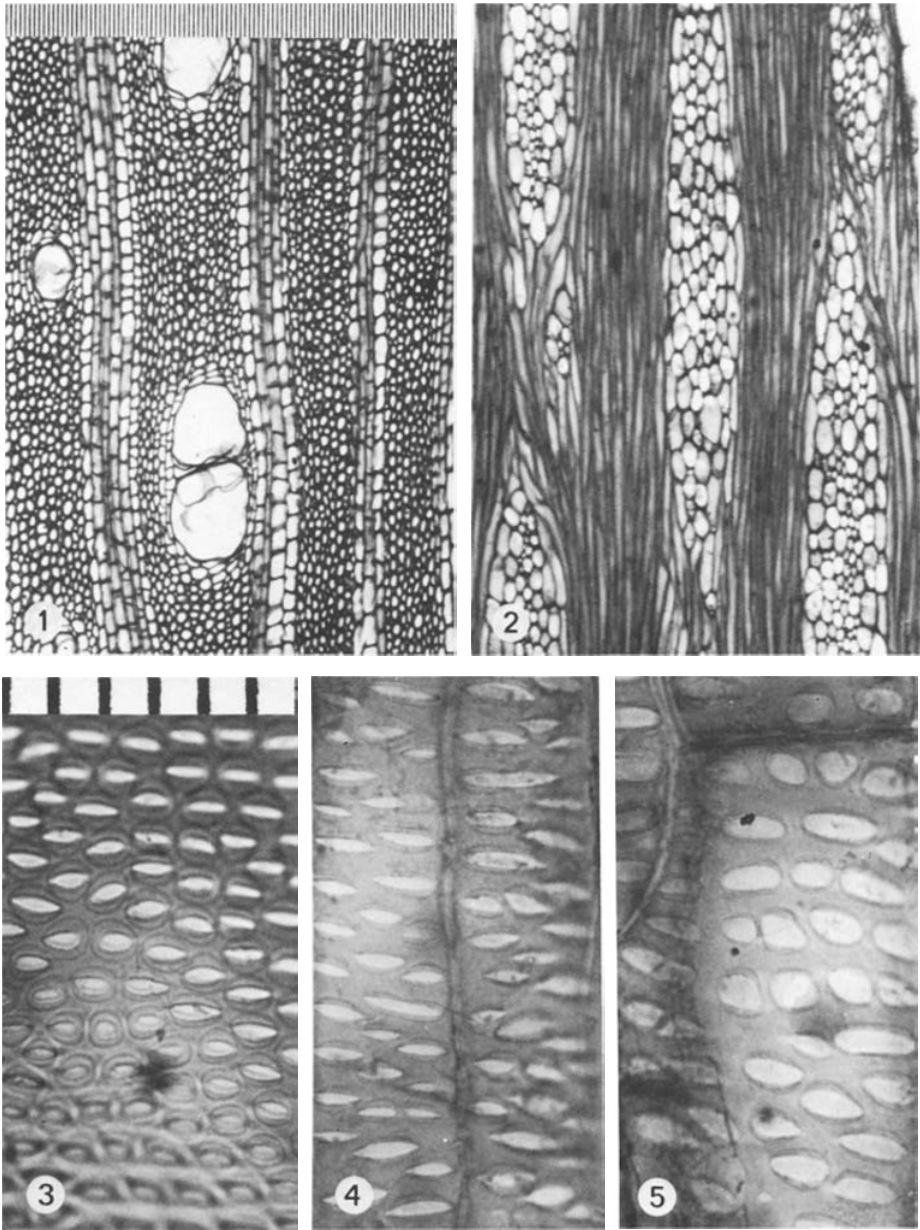
If one computes multiseriate ray width in terms of cell number at widest point (Table 1, column 11), one obtains figures for the species of Papaveraceae that tend to parallel ray height. Multiseriate rays of *Bocconia* (Fig. 2) and *Dendromecon* (Fig. 12), which range from 5.0 to 8.9 cells, are less wide than those of *Dicentra*, *Hunnemannia*, and *Romneya* (Fig. 17), in which mean ray width at widest point exceeds 10 cells.

Uniseriate rays are so scarce in Papaveraceae that they have been omitted from Table 1.

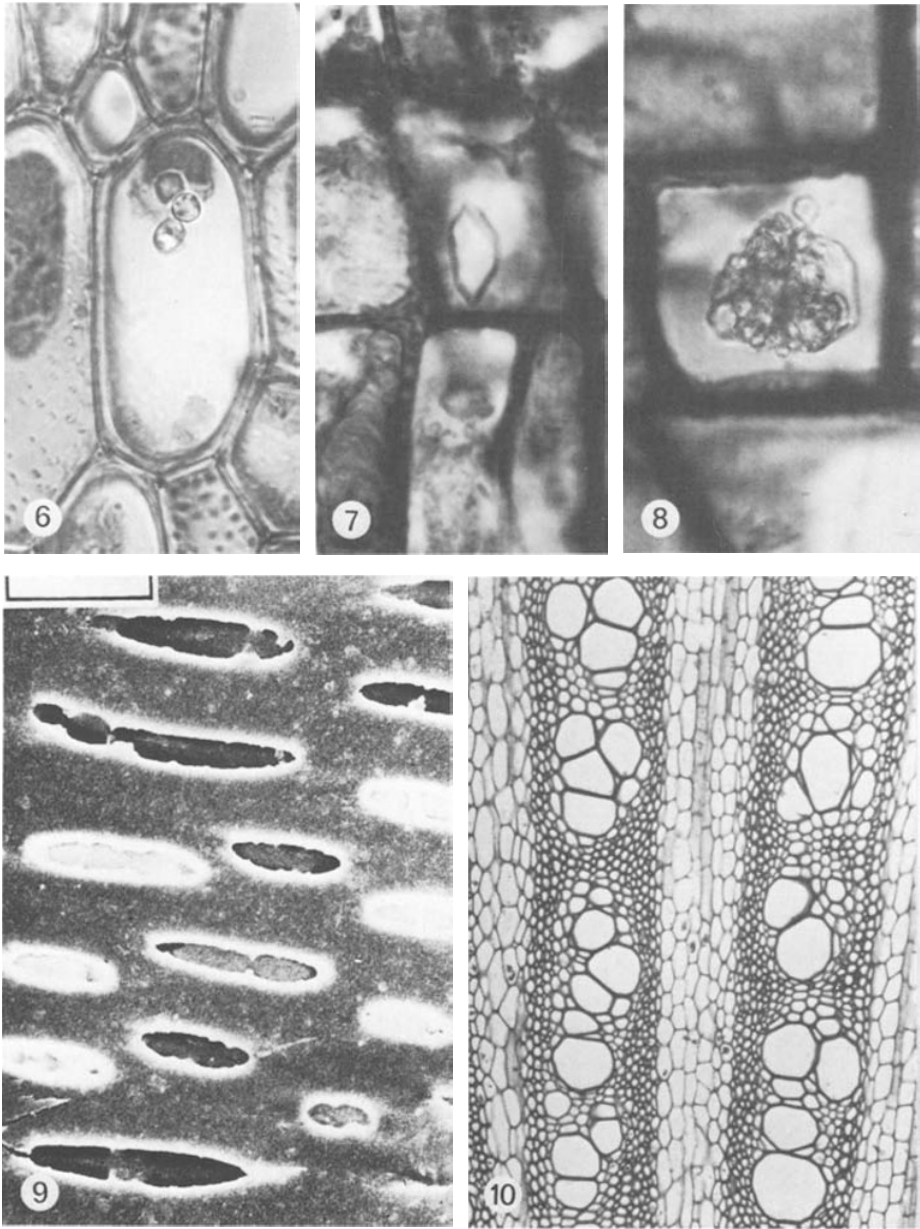
Qualitative ray features

Multiseriate rays in Papaveraceae consist of upright or square cells on lateral surfaces (sheathing cells) of the rays (Figs. 12, 17). Upright cells are more common in rays of *Bocconia* (Fig. 2), where they are present not merely on surfaces but throughout rays; some procumbent cells are present in small numbers in *Bocconia* rays. In *Hunnemannia*, markedly elongate cells form the central portion of a ray, while upright cells comprise the periphery and square to moderately procumbent cells occur between. The abundance of upright cells in rays of most Papaveraceae exceeds that specified in the definition by Kribs (1935) of Heterogeneous Type II; uniseriate rays, present in that type, are absent or nearly so in Papaveraceae. Because of the abundance of upright cells in rays in Papav-

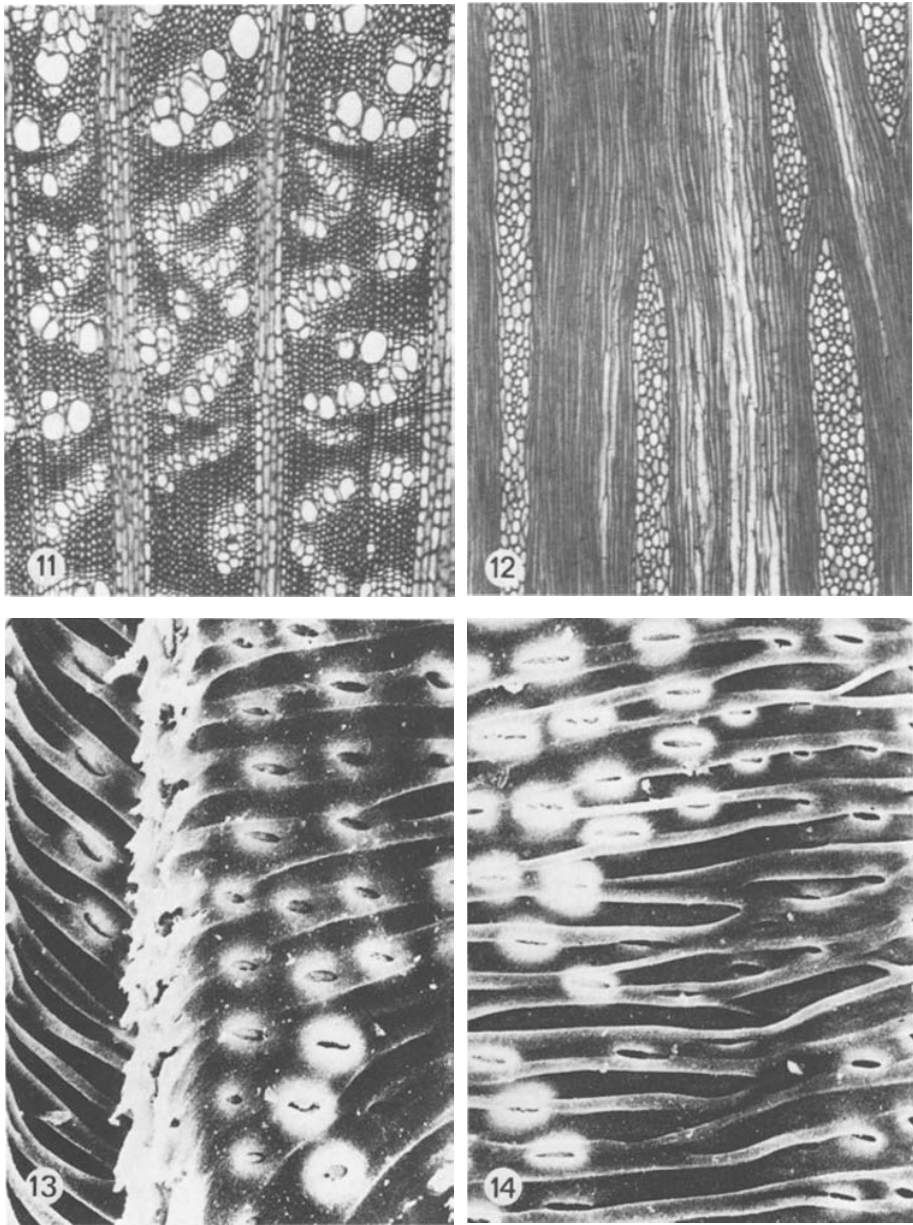
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Figs. 1–5. Wood section of *Bocconia integrifolia*, Carlquist 7111. — 1: Transection; tyloses present in vessels. — 2: Tangential section; rays contain a large proportion of upright cells. — 3–5: Pitting in vessel walls from radial sections. — 3: Intervascular pitting. — 4: Vessel-axial parenchyma pitting with narrowly elliptical pit apertures. — 5: Vessel-axial parenchyma pitting with wide apertures. — Figs. 1, 2, magnification scale above Fig. 1 (divisions = 10 μ m); Figs. 3–5, scale above Fig. 3 (divisions = 10 μ m).



Figs. 6–10. Wood sections of *Bocconia* and *Dicentra*. — 6: *B. arborea*, Carlquist 2393, crystals in ray cell, tangential section. — 7: *B. frutescens*, Davidson 5131, rhomboidal crystal in ray cell, radial section. — 8: *B. integrifolia*, Carlquist 7111, cluster of crystals, radial section. — 9: *B. vulcanica*, Davidson 3317, vessel-axial parenchyma pitting from tangential section, showing irregular pit margins. — 10: *D. chrysantha*, Carlquist 15940, transection of root; vessels are restricted to centre of fascicular zones. — Figs. 6–8, scale above Fig. 3; Fig. 9, scale at upper left (bracket = 10 μ m); Fig. 10, scale above Fig. 1.



Figs. 11–14. Sections of *Dendromecon rigida* subsp. *rigida*, R.S. A.B.G. prop. no. 5865. — 11: Transection; vessels in diagonal aggregations. — 12: Tangential section; upright, square, and procumbent cells present in about equal numbers. — 13 & 14: SEM photographs of vessel walls from tangential section; mottled appearance is caused by deposits on wall. — 13: Wider helical thickenings in wide vessel plus (left) narrow vessel. — 14: Narrower helical thickenings in wide vessel. — Figs. 11 & 12, scale above Fig. 1; Fig. 13 & 14, bracket in Fig. 9.

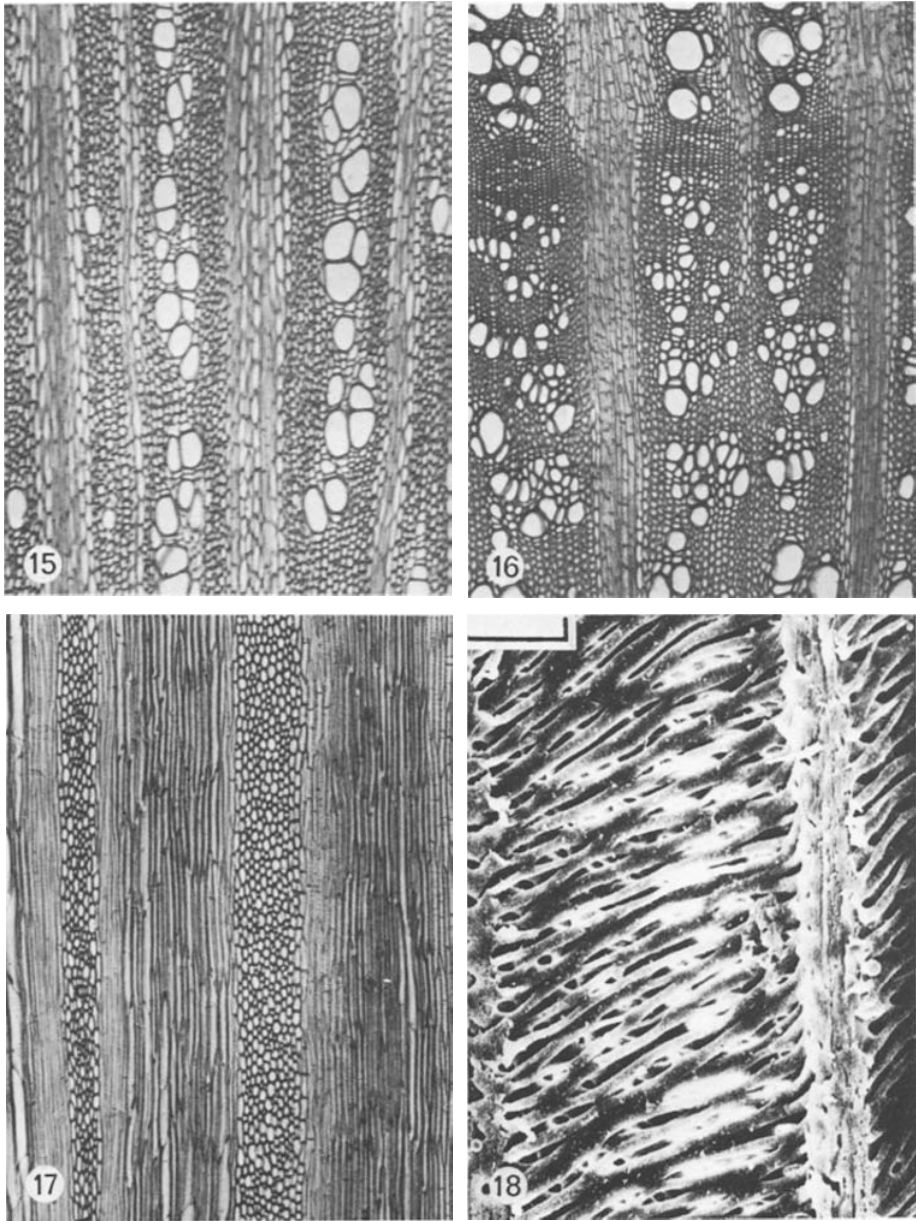


Fig. 15. Wood section of *Hunnemannia fumariaefolia*, Carlquist 2392; vessels restricted to central portions of fascicular areas. — Figs. 16–18: Wood sections of *Romneya coulteri*, R.S.A.B.G. prop. no. 6549. — 16: Transection; latewood with many narrow vessels and vasicentric tracheids 1/5 distance from top of photograph. — 17: Tangential section; narrow vessels and vasicentric tracheids (darker staining areas) are stored. — 18: SEM photograph of vessel from tangential section; helical thickenings are narrow, crowded. — Figs. 15–17, scale above Fig. 1; Fig. 18, bracket = 10 μm .

eraceae, they should be designated Paedomorphic Type II, according to the scheme offered by Carlquist (1988), or transitional to that type.

Mean ray cell wall thickness is moderate in Papaveraceae: *Bocconia*, 1.6–2.2 μm ; *Dendromecon*, 2.2 μm ; *Dicentra*, 1.4 μm (root) to 2.0 μm (stem); *Hunnemannia*, 2.3 μm ; *Romneya*, 2.0 μm . Pits among ray cells are predominantly simple, although some bordered pits were observed on ray cells of all genera except *Dicentra*.

Starch was seen in ray cells of *Bocconia* and *Dicentra* (root, lower stem, but not upper stem). Crystals (nature confirmed with polarised light), are present in ray cells of *Bocconia*, but were not seen in wood of the other genera. In *B. arborea* (Fig. 6), various numbers of smaller rhomboidal crystals occur in a minority of ray cells. They vary from clearly angular to somewhat rounded in outline; rounded outlines of crystals have occasionally been observed in various dicotyledons. In *B. frutescens*, slightly larger and clearly rhomboidal crystals occur in solitary fashion in a scattering of ray cells (Fig. 7). A few ray cells of *B. integrifolia* have minute rhomboidal crystals, which tend to be grouped (Fig. 8). The difference between modes of occurrence in *B. arborea* and *B. integrifolia* is not great. Crystals have not been reported hitherto in wood of Papaveraceae, although Metcalfe and Chalk (1950) report crystals in plant portions other than wood for the family.

Dadswell and Record (1936) report a few large open radial canals in rays of *Bocconia*. No such canals were observed in the present study, despite abundance of material; the possibility must be taken into account that the canals reported by Dadswell and Record were traumatic in nature or the result of shrinkage patterns due to drying. No laticifers were observed in rays of any of the Papaveraceae studied here, nor have any been found in wood of the family previously.

Storied structure

In *Romneya* (Fig. 17), one finds storying in narrow vessels and vasicentric tracheids as well as in vessels and axial parenchyma in zones where tracheids are abundant. Small numbers of storied cells were observed in

very limited local portions of tangential sections in *Bocconia* and *Hunnemannia*. Storied cells in these two genera may include wider fibres, axial parenchyma, narrow vessels, and vasicentric tracheids.

Conclusions

Vessel restriction patterns

The term 'vessel restriction patterns' was devised to describe instances in *Valeriana* of the Valerianaceae (Carlquist 1983) and *Lauanea* of the Asteraceae (Carlquist 1988) in which vessels occur in central portions of fascicular secondary xylem, and thus only libriform fibres but not vessel elements are in contact with rays. The occurrence of this phenomenon in *Dicentra* (Fig. 10) and, to a lesser extent (occasional vessels touching rays), in *Hunnemannia* (Fig. 15) leads one to ask if this occurs in other genera of the order Papaverales. Most Berberidaceae have large vessel groupings which come into contact with rays here and there. However, in *Nandina domestica* Thunb., several layers of libriform fibres lie between the groupings of vessels (including some vasicentric tracheids) and the rays. A figure of a wood transection of *Berberis darwinii* Hook. by Metcalfe and Chalk (1950: 60) shows no vessels in contact with rays. The photographs by Sieber and Kucera (1980) of *Clematis vitalba* L. and my own materials of *C. lasiantha* Nutt. indicate few vessels in contact with rays in that genus of Ranunculaceae.

However, the occurrence of vessel restriction patterns in Asteraceae and in Valerianaceae may indicate that vessel restriction patterns are less of phyletic than of physiological significance. If one compares the species that show vessel restriction patterns most clearly, all have stems of limited diameter or duration; they are either woody herbs, short-lived shrubs, or, as in the case of *Nandina*, a shrub with canelike stems each of which lasts for only a few years. In vessel restriction, vessels contact axial parenchyma but do not have direct contact with radial parenchyma. If contacts between axial and ray parenchyma, common in most dicotyledonous woods, form a system for transferring photosynthates both radially and vertically within the wood,

vessel restriction may represent minimal selective value for radial translocation of photosynthates in a plant. Minimal contact between vertical and horizontal parenchyma systems is assumed here because the parenchyma in Papaveraceae (as in the other groups with vessel restriction patterns) is vasicentric; thus the radial photosynthate-conduction system (rays) is unlikely to form contacts with the vertical photosynthate-conducting system (axial parenchyma). This is reminiscent of raylessness, in which radial translocation of photosynthates must be very low (axial parenchyma is not prominent either in most instances of raylessness). If there is not a selective value for radial translocation of photosynthates in taxa with vessel restriction patterns, one would still need to explain why vessel restriction is of any value. One possibility is found in the tendency of vessels to be sheathed by libriform fibres in certain plants. For example, in scandent species of *Thunbergia*, rays may be absent, but axial parenchyma (which may contain phloem strands) occurs as islands or strips in the secondary xylem; the vessels, however, are invariably sheathed by fibres. Vessel restriction may have the same effect as sheathing of vessels by fibres. One can imagine that sheathing of vessels by fibres might have some positive value. For example, in a vine such as *Thunbergia*, the wide vessels are relatively vulnerable and might experience fewer failures in their water columns when sheathed by fibres (Carlquist & Zona 1988). Alternatively, one could imagine that if vessels were restricted to the central portion of a fascicular area of secondary xylem (axial secondary xylem zones between rays), there would be a greater tendency for radial chains of vessels to form, increasing the potential degree of vessel grouping, which is claimed to enhance conductive safety (Carlquist 1984b). The concept of isolation rays entirely composed of procumbent cells (Braun 1970) represents a different phenomenon (one which may enhance efficient radial conduction of photosynthates), and should not be confused with vessel restriction.

Paedomorphosis

The theory of paedomorphosis (Carlquist 1962) was devised to explain occurrence in

secondary xylem for various periods of time of features characteristic of metaxylem; this phenomenon occurs in particular herbs and herblike growth forms such as succulents, rosette trees, and annuals. Cumbie (1983) has rightly identified features of the wood of *Bocconia vulcanica* as exemplifying paedomorphosis; he uses the age-on-length curve (Carlquist 1962) which shows a descending length of vessel element length in instances of paedomorphosis (as opposed to an ascending pattern for typical woody species). Length of libriform fibres in *Bocconia vulcanica* neither increases nor decreases. Cumbie (1983) also identifies as paedomorphic the tendency in *B. vulcanica* for few rays to be initiated after the onset of secondary growth, and the tendency for few horizontal divisions to occur in ray initials (thus upright cells continue to predominate in rays and procumbent cells remain comparatively few). The present study confirms these features and their interpretation in *Bocconia*. Although the present study has not developed length-on-age curves, it is notable that the collection of *Bocconia* with the longest vessel elements, *B. arborea*, Wiens 2535, has the least accumulation of secondary xylem. The large pit apertures of vessel-parenchyma pits in *Bocconia* may be associated with lowered mechanical strength of wood, which appears to characterise certain woods with paedomorphosis (Carlquist 1975).

Dendromecon, *Hunnemannia*, and *Romneya* show relatively few features related to paedomorphosis, and Cumbie (1983) is justified in suggesting that *Dendromecon* could have had a woody ancestry, whereas *Bocconia* may have had herbaceous or more nearly herblike ancestors and may not be closely related to *Dendromecon*. The storied wood pattern of *Romneya* is probably an indication of a nonpaedomorphic wood, because storying is not common in woods with paedomorphosis (although Piperaceae are an exception: Carlquist 1962). Storying may develop over time in a wood, rather than shortly after onset of secondary growth. Although woody relatives of Papaveraceae, such as Berberidaceae and *Decaisnea* (Lardizabalaceae), are shrubs branched from the base rather than subarborescent, they must be classified as woody, just as must *Dendromecon*.

Relationships

As cited in the Introduction, Papaveraceae are generally conceded by recent phylogenists to be closely related to Berberidaceae, Lardizabalaceae, Menispermaceae, Ranunculaceae, and Sargentodoxaceae, as well as several families that are herbaceous (Circaeastraceae, Glaucidiaceae, Kingdoniaceae). The wood anatomy of Papaveraceae contains a series of features that validate this relationship (data from Metcalfe & Chalk 1950; Sieber & Kuceira 1980; Carlquist 1984a): vessels with simple perforation plates (scalariform in *Decaisnea*); lateral wall pitting of vessels alternate (intervascular pitting similar to vessel-ray pitting); helical thickenings present in vessels (present in *Berberis* of Berberidaceae, *Akebia* of Lardizabalaceae, *Clematis* of Ranunculaceae); libriform fibres present (fibre-tracheids in Lardizabalaceae, tracheids in Menispermaceae); libriform fibres nucleated (some septate); axial parenchyma vasicentric scanty (absent in Berberidaceae); rays exclusively multiseriate or nearly so, tall and wide, composed mostly of procumbent cells.

Several wood features unite Papaveraceae with some but not all of the woody families cited above. For example, vasicentric tracheids, common in *Dendromecon* and *Romneya*, occur in *Berberis* (including *Mahonia*), *Nandina*, and *Clematis* (Carlquist 1985). Crystals occur in ray cells of *Stauntonia* (Lardizabalaceae) as well as those of *Bocconia*. In addition to *Dendromecon* and *Romneya*, papaveralean genera with diagonal aggregations of vessels include *Berberis*, *Nandina*, and *Clematis*.

If one is to rank Papaveraceae with respect to degree of primitiveness in Papaverales on the basis of wood features, one finds that two families have somewhat more primitive wood features: fibre-tracheids may be found in Lardizabalaceae (one genus of which, *Decaisnea*, has scalariform perforation plates); true tracheids are present in Menispermaceae. Papaveraceae retains axial parenchyma, the absence of which in Berberidaceae must be counted a specialisation. Thus, Papaveraceae can be considered of medium advancement within Papaverales. The hypothesis that Papaverales as an order is primitively woody seems to be supported by the distribution of

primitive wood features among the families and genera.

Ecology

Within Papaveraceae, computation of the Mesomorphy ratio (Table 1, column 12) reveals that *Bocconia* and *Dicentra* have relatively mesomorphic woods. Both of these genera have markedly succulent cortex and pith, as well as, to a limited extent, rays. *Dendromecon* and *Romneya* show wood xeromorphy in ways other than the density of vessel elements and their narrowness and shortness, as reflected in the Mesomorphy ratio. Degree of grouping of vessels has been cited, in families with libriform fibres or fibre-tracheids (as opposed to true tracheids) as indicative of degree of xeromorphy (Carlquist 1966, 1984b). Using vessel grouping figures (Table 1, column 2) as an indicator of xeromorphy, one can arrange the genera of Papaveraceae from most mesomorphic to most xeromorphic: *Bocconia*, *Dicentra*, *Hunnemannia*, *Dendromecon*, *Romneya*. This series corresponds to ecology of these genera: *Dendromecon* and *Romneya* occur in chaparral or coastal sage. *Dicentra chrysantha* does occur in sites that are like these, but its relatively mesomorphic wood can be explained on the basis of the succulence of roots and lower stems, and the fact that upper stems die back annually.

Vasicentric tracheids are abundant in *Dendromecon* and *Romneya*, supporting the idea that these genera should be regarded as the most xeromorphic in the family. Vasicentric tracheids and narrow vessels are moderately common in *Hunnemannia*, less common in *Dicentra*. Vasicentric tracheids prove to be a key to understanding diagonal aggregations of vessels (Baas *et al.* 1984; Carlquist 1987). The occurrence of these vessel aggregations can be considered a maximal form of xeromorphy (or conductive safety) in phylads that possess vasicentric tracheids (Carlquist 1987, 1988).

The systematic and ecological distribution of helical thickenings in vessels of dicotyledons suggests adaptation both to cold (as in *Ilex*: Baas 1973) and drought (Carlquist 1982b). Helical thickenings are present in vessels of *Dendromecon* even in frost free

localities, such as Santa Catalina Island, and in montane areas where frost occurs, but one must note that even in the most extreme *Dendromecon* and *Romneya* localities with respect to winter cold, frost is probably too mild to account for selective value of helical thickenings in vessels. Adaptation to drought may explain these cases of helical sculpture. Presence of helical thickenings does not seem to be a relictual feature in dicotyledons because one can find many families (even genera) in which some species possess helical thickenings (the species of colder or drier areas) whereas the species from less extreme sites lack the thickenings.

Thus, Papaveraceae show a wide diversity in ecological adaptation. The wood features of *Dendromecon* and *Romneya* are much like those of *Berberis* (including *Mahonia*) from comparable habitats. *Bocconia*, however, is notably more mesomorphic, and does not correspond to any other genus of Papaverales in its growth form. Comparable in habit and degree of wood xeromorphy are such genera as *Wigandia* (Hydrophyllaceae) or arborescent species of *Nicotiana* (Solanaceae). These two examples are very pertinent because in both cases, the plants have an Andean habitat much like that of localities where *Bocconia* could be found.

The fact that *Dendromecon rigida* subsp. *rigida* from cultivation has wood that ranks as much less mesomorphic on a quantitative basis than that of a specimen of *D. rigida* subsp. *ramnoides* collected from the wild shows that the genetic nature of wood in these two subspecies is well fixed, and cultivation (with water availability greater than in the wild) evidently has not altered the xeromorphic nature of the wood appreciably.

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