

WOOD ANATOMY AND PHYLOGENY OF *PAEONIA* SECTION MOUTAN

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THE GENUS *Paeonia* consists of thirty-three species of herbaceous and woody plants. In his classic work on the taxonomy of *Paeonia*, Stern (1946) separated the genus into three sections: MOUTAN, PAEONIA, and ONAEPHA. The section MOUTAN contains four species of shrubs native to western China. The section PAEONIA has twenty-seven species of perennial herbs and occurs from Spain and North Africa through temperate Asia into Japan. The section ONAEPHA, also consisting of perennial herbs, contains two species native to western North America.

De Candolle (1824) placed *Paeonia* within the family Ranunculaceae. Bartling (1830), however, suggested that the genus belonged in a unigeneric family, Paeoniaceae, near the Magnoliaceae. Since then, the phylogenetic position of *Paeonia* has been the subject of considerable debate. Bartling's position has been supported by superficial studies of the wood anatomy (Worsdell, 1908; Kumazawa, 1935). Subsequent investigations of the cytology and floral anatomy, however, have indicated that a more natural position would be in the Dilleniales, near the Dilleniaceae or the Crossosomataceae (Corner, 1946; Lemesle, 1955; Eames, 1961).

Many authors have agreed on the need for more detailed studies on all aspects of this genus. In particular, there has been little study of the secondary wood anatomy. Previous anatomical studies have been concerned only with the amphicribal condition of the vascular bundles (Worsdell, 1908), or with the occurrence of secondary ray tissue and the presence of scalariform perforation plates in the vessels (Kumazawa, 1935).

The genus *Paeonia* is noteworthy in possessing a combination of both advanced and primitive characters. The most important of these combinations is the occurrence of both woody (primitive) and herbaceous (advanced) species. Also, the Paeoniaceae is the only family with herbaceous members (advanced) that possesses scalariform (primitive) vessel perforations (Eames, 1961). The gross morphology of the genus is predominantly primitive; however, a great number of advanced characters may be observed in the wood anatomy. Of special interest is the section MOUTAN, in which the ancestral woody habit has been retained. In addition, this section occurs in a region (western China) noted for its many relict taxa of great age.

MATERIALS AND METHODS

The secondary xylem of 59 samples of the four shrubby species of *Paeonia* section MOUTAN has been examined. Species of the section MOUTAN are distinguished from the other sections of the genus by their peren-

nial, woody stems and by thin petals which are much longer than the sepals.

The section is divided into two subsections (Stern, 1946):

I. Subsection VAGINATAE

1. *Paeonia suffruticosa* Andrews. Samples investigated: twenty-six. Native to the mountains of central China; Kansu, Szechwan, and Shansi provinces; elevation 2130–4270 meters (7,000–14,000 feet).

II. Subsection DELAVAYANAE

2. *Paeonia delavayi* Franchet. Samples investigated: ten. Native to the Likiang Ranges of Yunnan and southwest Szechwan provinces; elevation 3050–3660 meters (10,000–12,000 feet).
3. *Paeonia lutea* Delavay ex Franchet. Samples investigated: twelve. Native to the Tali Range, from northern Yunnan Province northwest into southeastern Tibet; elevation 2740–3660 meters (9,000–12,000 feet).
4. *Paeonia potaninii* Komarov. Samples investigated: seven. Native to the northern border of Yunnan north to western Szechwan Province, elevation 2740–3050 meters (9,000–10,000 feet).

In addition to the samples listed above, four hybrids were investigated: three of *Paeonia delavayi* \times *lutea* and one of *P. lutea* \times *potaninii*. All samples cited in this paper are identified by the senior author's numbers. Herbarium specimens, which have accompanied some of the wood samples, have been deposited in the herbarium of the University of California, Santa Barbara, California.

Five slides for microscopic examination were prepared from each sample, according to standard methods (Wetmore, 1932). Sections were softened in 48 percent hydrofluoric acid, embedded in celloidin, and cut on a sliding microtome at 15 μ m. Sections were stained in Heidenhain's iron alum haematoxylin and safranin. A complete collection of slides is filed with the herbarium sheets.

The terminology used in the anatomical descriptions complies with that approved by the Committee on Nomenclature, International Association of Wood Anatomists (1933, 1964). The choice of diagnostic characters was made largely from the lists prepared by Record and Chattaway (1939) and Tippo (1941). The most frequent range category in each case was arbitrarily determined. All measurements were taken at random. The classification of wood parenchyma distribution utilized here is a synthesis of the one presented by Metcalfe and Chalk (1950) as amended by the International Association of Wood Anatomists (1951).

ANATOMY OF THE SECONDARY XYLEM

An outline of the measurements recorded for the secondary xylem is presented in TABLE 1.

GROWTH RINGS. Growth rings are always present (FIGURE 23), although

TABLE 1. Secondary xylem of *Paconia*.

CHARACTER	RANGE	MOST FREQUENT RANGE	MEAN
I. Imperforate elements (Tracheids, fiber-tracheids)			
a. Length	160-1224 μm . (short-medium)	33-640 μm . (short)	541 μm . (short)
b. Wall thickness	very thin-thick	thin-thick	
c. Pit-pair horizontal diameters	2-8 μm .	3-5 μm .	4.1 μm .
II. Vessels			
a. Length	97-1191 μm . (short-medium)	250-500 μm . (short-medium)	380 μm . (medium)
b. Distribution	11-58/mm. ²	20-40/mm. ²	31/mm. ²
c. Transectional diameters	16-88 μm . (extremely small-moderately small)	28-44 μm . (very small)	36.4 μm . (very small)
d. Number of bars in scalariform perforation plates	1-7 (few-intermediate)	1-3 (few)	
e. Width between bars	6-20 μm . (narrow-wide)	8-12 μm . (wide)	
f. End wall angle from the vertical	4-45°	15-30° (very oblique)	
g. Intervascular pit diameters	2-10 μm . (minute-large)	5-7 μm . (small)	6 μm . (small)
III. Vascular rays			
a. Tangential frequency	3-16/mm.	6-10/mm.	
b. Width of multi-seriate rays	20-124 μm . (2-8 cells) (very fine-broad)	28-56 μm . (2 or 3 cells) (moderately fine)	
c. Width of uni-seriate rays	28-37 μm . (moderately fine)		
d. Height of uni-seriate rays	128-2430 μm . (1-75 cells) (extremely low-rather low)		570 μm . (very low)
e. Height of multi-seriate rays	160-3000 μm . (extremely low-rather low)		620 μm . (very low)

they are occasionally poorly defined. The annual increment varies from relatively narrow to wide.

IMPERFORATE ELEMENTS. The imperforate elements are tracheids and fiber-tracheids. No libriform wood fibers or gelatinous or septate fibers were observed. The walls of the imperforate elements vary from very thin to thick, but are most frequently within the limits of thin to thick (FIGURE 24).

The pit-pairs are bordered and generally circular. The inner apertures of all pits are elongated, and those of the pit-pairs are crossed. The elongated inner apertures do not ordinarily extend beyond the outline of the borders (FIGURES 25, 31).

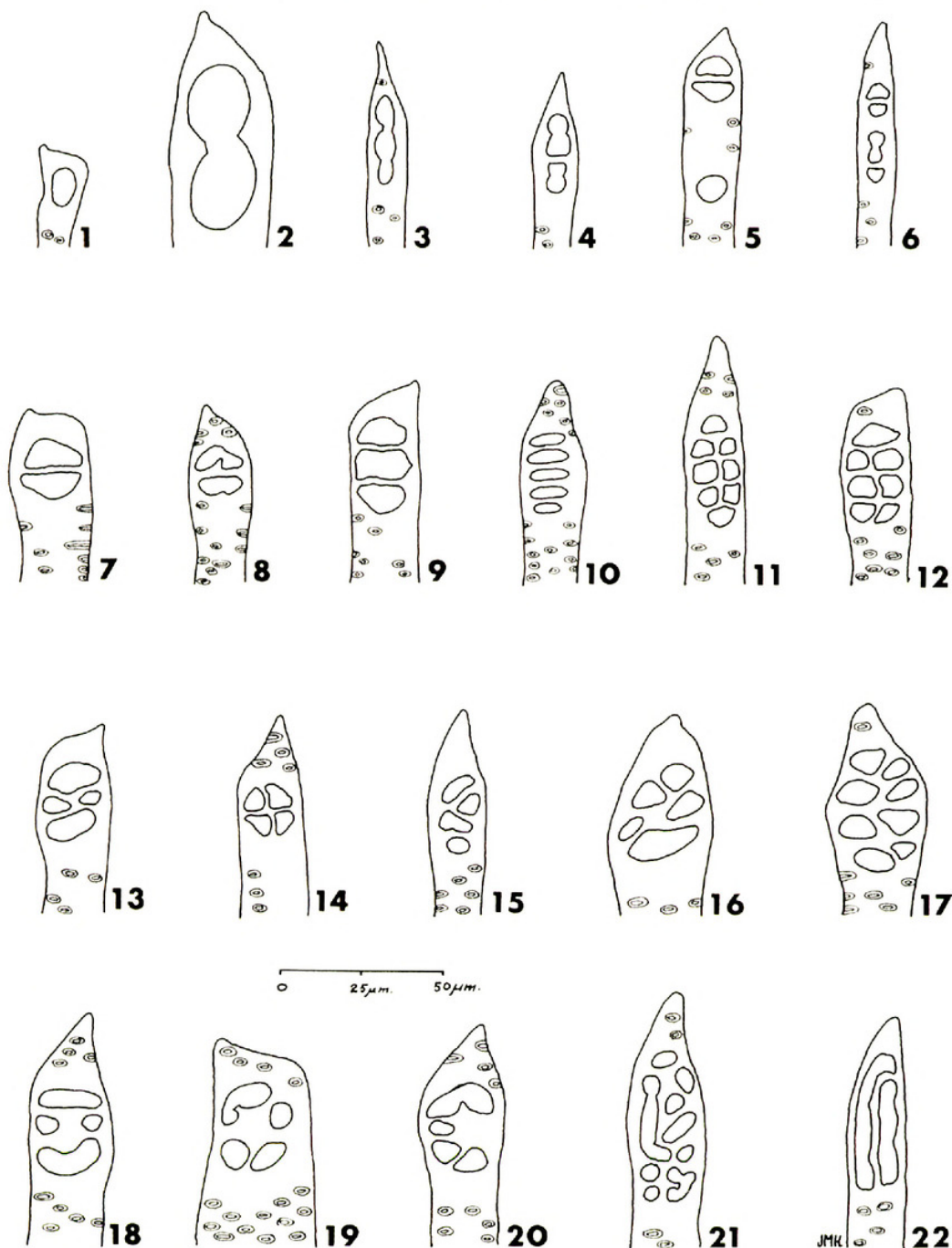
One hundred length measurements of the imperforate cells of each of the 59 samples were taken at random. The lengths of the elements vary from 160 (short) to 1224 μm . (medium sized). The most frequent range is from 33 to 640 μm . (short), and the mean for the genus is 541 ± 7.04 μm . (short), with a standard deviation of 89.7 ± 1.16 μm . The proportion of elements with spiral thickenings is quite variable from sample to sample. In some samples, most of the elements have spiral thickenings; in others, this condition is rare or absent. Occasionally, the thickening is a double one, with one coil pitched in one direction and the other one in the opposite direction.

VESSELS. The number of vessels per square millimeter in transverse aspect was calculated from 10 microscopic fields of each sample. Vessel distribution is predominantly of solitary and chain arrangements, but multiples also occur frequently (FIGURE 23). Pore clusters occur occasionally or rarely in 36 of the samples.

Paeonia is usually distinctly ring porous (FIGURE 23), although some rings are indistinct or are only semi-ring porous. The early wood characteristically has larger and more frequent pores than are found in the late wood. The late wood has small pores which are usually fairly evenly distributed. In all species, the vessels are angular in cross section (FIGURES 23, 24). Exceptions were observed in scattered vessels in a few samples of *P. lutea*, where some of the larger vessels were circular or nearly so.

Perforation plates in the end walls of the vessel elements are most commonly of the scalariform type, but other multiperforate forms, as well as simple perforation plates, also occur (FIGURE 31). The number of bars in typical scalariform perforation plates varies from 1 to 7 (few to intermediate) (FIGURES 7-10), and varies most frequently from 1 to 3 (few). The widths of the openings among the bars vary from 6 (narrow) to 20 μm . No borders occur around the perforations.

Of a random count of 2950 perforation plates, 3.7 percent were found to be simple (FIGURES 1-3). The simple perforation plates usually occur in vessels with relatively narrow diameters, and are of three main types. The first type (FIGURE 1) has typically round openings which are most often encountered in the more advanced dicotyledons ("simple perforations" *sensu* Esau, 1965). These perforations occur in vessels with end



FIGURES 1-22. Perforation plates as seen in radial section: 1-4, 6-8, 10-15, 17-20, *Paeonia suffruticosa*; 5, 9, 21, *P. delavayi* \times *lutea*; 16, *P. potaninii*; 22, *P. lutea*.

walls most closely approaching the horizontal. The second type of simple perforation is vertically elongate (FIGURE 3). The last type appears similar to a scalariform perforation with the cross bar partially unformed (FIGURES 2, 31). In rare instances, a vessel end wall appears to have two distinct perforation groups, of which one might be simple and the other multiple (FIGURE 5). This latter type might be considered a single scalariform perforation plate, however.

With the exception of the herbaceous Paeoniaceae, scalariform perforation plates in dicotyledons are found exclusively in woody taxa (Eames, 1961). Scalariform vessels have been observed by the writers in *Paeonia californica*, a perennial herb with fleshy roots. The most common pattern in *Paeonia* section MOUTAN could be classified as "typically scalariform" (FIGURES 9, 10); in this form the horizontal bars are arranged in a ladder-like series along the flattened, oblique end wall. This corresponds to the form occurring most frequently in dicotyledonous vessel perforation plates ("scalariform" *sensu* Esau, 1965).

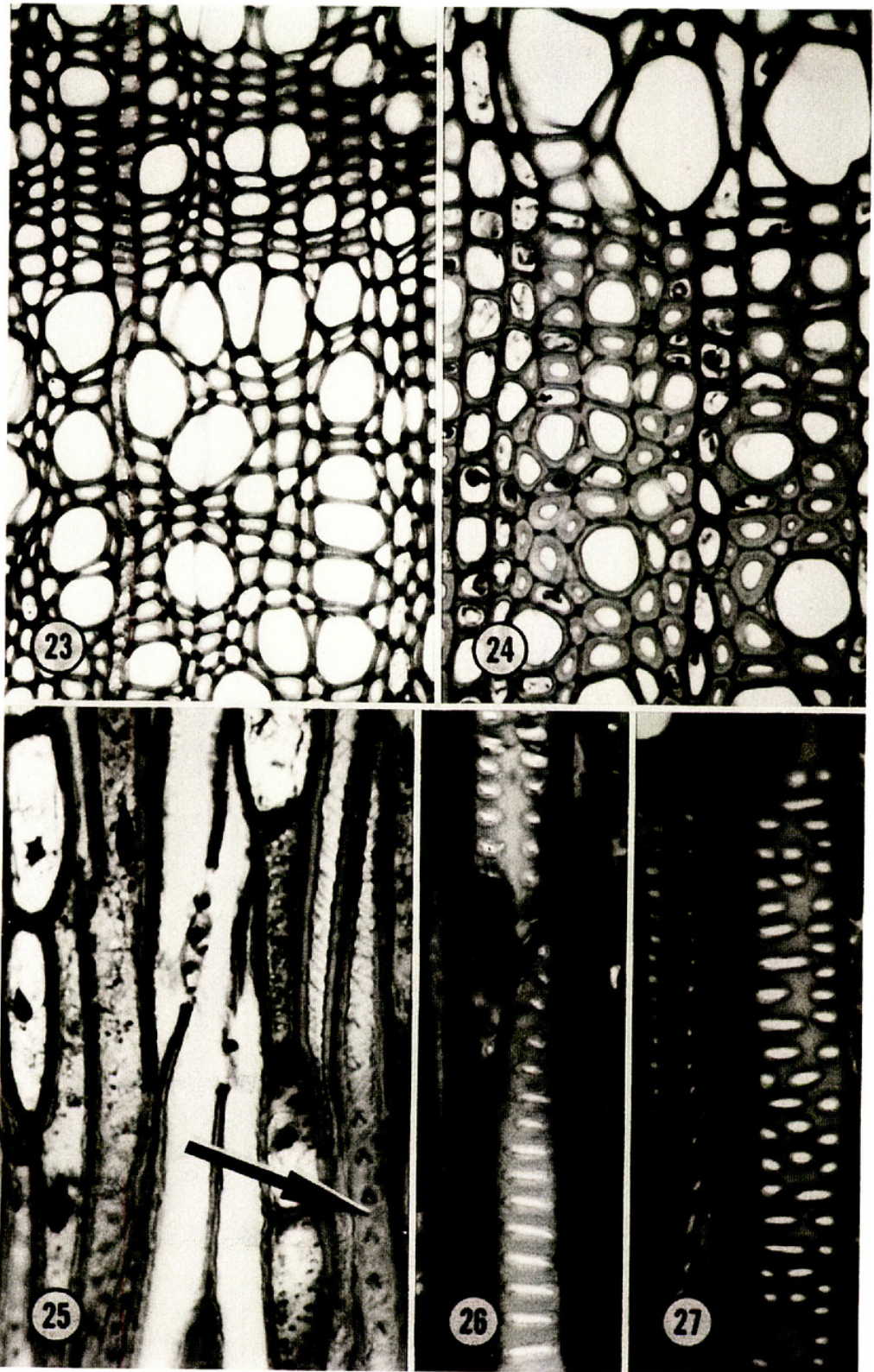
Ten percent of the perforation plates examined were atypical multiperforate forms. These occur in four basic types. The first, and most common, type includes typically scalariform bars with the addition of vertical bars or bar-fragments (FIGURES 8, 11–14). We have named this type modified scalariform. The second type has some plates including irregularly reticulated perforation patterns in oval to circular (FIGURES 15, 18–20), scattered (FIGURE 21), or elongate (FIGURE 22) configurations. In the third type the plates approach foraminate configurations (Gray & de Zeeuw, 1974) (FIGURES 16, 17). The fourth type includes forms transitional between scalariform and simple perforation plates (FIGURES 2–6). Both the first and second types would be considered irregular reticulate plates according to Gray and de Zeeuw (1974).

A similar and distinctive perforation pattern tends to appear in successive end walls, *ad seriatim*, of several members (five to ten) of a single vessel. Distinctive patterns were not observed to be repeated in radially successive vessel members; that is, in derivatives of the same cambial initial. This indicates that a particular perforation pattern may be expressed in a vessel as a unit, rather than in the successive derivatives of a single cambial initial.

The end walls of the vessel elements in tangential aspect are generally quite oblique, ranging from 4 to 45° off the vertical, but vary most frequently from 15 to 30° off the vertical (very oblique) (FIGURES 25, 26).

The intervacular pitting of the vessels varies from transitional to alternate (FIGURES 25–27). Often there is a single staggered row of pit-pairs in the vessel wall (FIGURES 25, 30). The scalariform arrangement was observed in two samples of *P. suffruticosa*, although rarely so even in these cases (FIGURE 26). The size of the intervacular pit-pairs varies from 2 (minute) to 10 μm . (large), but ranges most frequently from 5 to 7 μm . (small), with a mean of 6 μm . Twenty pit-pairs from each of the samples were measured. The intervacular pit-pairs are predominantly circular in outline, but are occasionally elongate, oval, or scalariform. Generally, the pit-pairs have elongate and crossed apertures which in face view do not extend beyond the outlines of the pit borders.

VESSEL-RAY PITTING. The pitting between the vessel elements and the vascular ray cells is variable. Alternate and opposite pitting are the most common, but the transitional arrangement was found frequently in most samples (FIGURE 28). The vessel-ray pits are without borders.



FIGURES 23-27. 23, *Paeonia suffruticosa*, transverse section showing a distinct growth ring boundary (distinctly ring-porous), the angular vessel elements in solitary, chain, and multiple arrangements (Keefe 2322), $\times 185$. 24, *P. lutea*, transverse section demonstrating thick- to thin-walled imperforate tracheary elements, a growth ring boundary, and axial wood parenchyma (Keefe 2351), \times

VESSEL LENGTH. One hundred length measurements of vessel elements were taken at random from macerated wood of each of the 59 samples. The length of the elements from the tip of one "tail" to the other varies from 97 (short) to 1190 μm . (medium). The most frequent range is from 250 to 500 μm . (short to medium), and the mean for the genus is $380 \pm 4.95 \mu\text{m}$. (medium) with a standard deviation of $89.7 \pm 1.16 \mu\text{m}$. The vessel elements are often storied (FIGURE 28). Spiral thickenings occur frequently in the vessel elements, and, as in the imperforate elements, they are often double. These occur most often in smaller vessels.

VASCULAR RAYS. The frequency of rays occurring horizontally across a tangential section is from 3 to 16 per mm., and more commonly from 6 to 10 per mm. The vascular rays are both uniseriate and multiseriate. No compound or aggregate rays occur. The ray type is not constant for the section MOUTAN, or for a particular species. The rays, furthermore, do not closely agree with the classical patterns as set down by Kribs (1935). The rays are often heterocellular, but the vertically elongate cells occur randomly throughout a particular ray, rather than exclusively in the wings or distal portions of the ray (FIGURE 30). The classical pattern with elongate cells only at the distal portion of a ray was not observed in any of the samples.

Three basic types of rays were observed. The most common was a modified Heterogeneous Type II (all names of ray types taken from Kribs, 1935). These consist of 40 to 99 percent uniseriate rays, which were in the low or extremely low class in height (FIGURE 30). Generally speaking, the samples which possess a greater percentage of uniseriates tend to have the higher uniseriate rays. The multiseriate rays are most commonly bi- or triseriate. Again, the samples with the higher percentage of uniseriate rays tend to have a greater proportion of biseriate rays than of wider ones.

One sample of *Paeonia suffruticosa* (Keefe 1301) has Homogeneous Type I rays. In this sample the uniseriate rays comprise 20 to 30 percent of the total number of rays. The multiseriate rays are almost entirely biseriate with very long wings. The height is in the extremely low class. Although these rays are fairly homocellular, the individual ray cells as seen in face view on tangential sections are intermediate between the traditionally defined round and rectangular-shaped cells.

Three samples, two of *Paeonia suffruticosa* (Keefe 1051, 1504) and one of *P. potaninii* (Keefe 1268), would agree with Kribs's classification of

280. 25, *P. suffruticosa*, tangential section illustrating imperforate tracheary elements with circular-bordered pit-pairs and crossed apertures (arrow), vessel elements having oblique end walls and scalariform perforation plates, uniseriate vascular rays, spiral thickenings in imperforate elements, and fusiform axial wood parenchyma (Keefe 2332), $\times 360$. 26, *P. delavayi*, tangential section showing vessel element with scalariform intervacular pitting, and portion of vessel element with opposite to alternate intervacular pitting (Keefe 2359), $\times 340$. 27, *P. delavayi*, tangential section showing vessel element with transitional intervacular pitting (Keefe 2359), $\times 340$.



FIGURES 28-31. 28, *Paeonia lutea*, radial section showing storied vessel elements and vascular rays with square and upright cells (Keefe 2351), $\times 60$. 29, *P. potaninii* forma *alba*, tangential section showing Homogeneous Type II vascular rays, with infrequent uniseriate and nearly homocellular multiseriate vascular rays, and 3-celled strand axial wood parenchyma (arrow) (Keefe 1268), \times

Homogeneous Type II rays. These samples have uncommon uniseriate rays (10 to 20 percent of the total number of rays), and frequent multiserial rays which are usually wingless (FIGURE 29). The rays are homocellular, being composed entirely of angular to nearly rounded cells as seen in tangential section.

For the section MOUTAN as a whole, the widths of the multiserial rays vary from 20 to 124 μm . (very fine to broad) or from 2 to 8 cells, as measured horizontally in tangential sections. The majority of multiserial rays vary within the range of 28 to 56 μm . (moderately fine) or 2 or 3 cells wide, with the exception of the three samples with Homogeneous Type II rays. The uniseriate rays most frequently range from 28 to 37 μm . in width (moderately fine).

Ray height for the genus has a mean of 620 μm . (very low) for the multiserial rays, with a range of 160 to 3000 μm . (extremely low to rather low). The mean height for the uniseriate rays is 570 μm . (very low), and the range is 128 to 2430 μm . (extremely low to rather low). In number of cells, the uniseriate rays vary commonly from 1 or 2 cells to 75 cells high.

AXIAL WOOD PARENCHYMA. Both strand and fusiform types of axial wood parenchyma occur in all four woody species of *Paeonia*. The most common type is strand parenchyma, with each strand consisting of two cells (FIGURE 30, arrow). Strands with three cells (FIGURE 29, arrow) or fusiform cells (FIGURE 31, arrow) occur less commonly. The axial wood parenchyma is apotracheal and sparse, and occurs in a scattered diffuse pattern among the imperforate elements. In both shape and wall thickness, the axial wood parenchyma is often very similar to the imperforate elements.

DISCUSSION

TAXONOMIC HISTORY. The relationship of the genus *Paeonia* has long been problematic. The genus has been placed in the families Ranunculaceae, Berberidaceae, and Paeoniaceae (and included in the orders Ranales, Paeoniales, Dilleniales, Theales, and Guttiferales) by various authors (TABLE 2).

COMPARATIVE ANATOMY OF THE SECONDARY XYLEM. The following characters of the secondary xylem of *Paeonia* are strictly primitive: (1) presence of tracheids and fiber-tracheids, but absence of libriform wood fibers (Bailey & Tupper, 1918; Bailey, 1936, 1953; Reinders, 1935); (2) absence of septate imperforate elements (Tippo, 1938; Metcalfe & Chalk,

400. 30, *P. suffruticosa*, tangential section showing vessel elements with oblique end walls; essentially Heterogeneous Type II vascular rays with heterocellular uniseriate and multiserial rays; multiserial rays almost entirely two cells wide; and 2-celled strand axial wood parenchyma (arrow) (Keefe 2332), $\times 275$. 31, *P. suffruticosa*, radial section showing vessel with typical scalariform perforation plates with 1 and 2 bars, vessel with atypical simple perforation plate, and fusiform axial wood parenchyma (arrow) (Keefe 817), $\times 240$.

TABLE 2. Summary of systematic treatments of the genus *Paeonia*.

De Candolle, 1824	Ranunculaceae, near Magnoliaceae
Bartling, 1830	Ranunculaceae
Bentham & Hooker, 1862	Ranunculaceae
Baillon, 1867	Ranunculaceae
Engler & Prantl, 1887, 1915	Ranunculaceae
Hallier, 1905	Berberidaceae
Worsdell, 1908	Paeoniaceae, in Ranales, between Ranunculaceae and Magnoliaceae- Calycanthaceae
Lotsy, 1911	Berberidaceae
Engler & Gilg, 1924	Ranunculaceae
Rendle, 1925	Ranunculaceae, between Lauraceae and Berberidaceae
Heintze, 1927	Paeoniaceae, in Paeoniales, with Ranunculaceae, Berberidaceae, Lardizabalaceae and Menispermaceae
Langlet, 1928	Berberidaceae (including Berberidoideae, Podophylloideae, and Paeonioideae)
Kumazawa, 1935	Paeoniaceae, in Ranales, near Magnoliaceae
Engler & Diels, 1936	Ranunculaceae
Corner, 1946	Paeoniaceae, in Dilleniales, with <i>Actinidia</i>
Lawrence, 1951	Ranunculaceae, in Ranales
Lemesle, 1955	Paeoniaceae, in Ranales, between Magnoliaceae and Calycanthaceae- Crossosomataceae
Benson, 1957	Ranunculaceae, between Hernandiaceae and Berberidaceae
Hutchinson, 1959	Paeoniaceae, in Ranales, between Magnoliaceae and Helleboraceae
Eames, 1961	Paeoniaceae, in Dilleniales, near Crossosomataceae
Melchior, 1964	Paeoniaceae, in Guttiferales, near Dilleniaceae
Dickison, 1967	Paeoniaceae, in Dilleniales, near Dilleniaceae
Thorne, 1968, 1974	Paeoniaceae, in Theales, under Dilleniaceae
Cronquist, 1968	Paeoniaceae, in Dilleniales, with Dilleniaceae and Crossosomataceae
Takhtajan, 1969	Paeoniaceae, in Paeoniales, between Dilleniales (including Dilleniaceae and Crossosomataceae) and Theales

1950); (3) moderately to very numerous vessels per square millimeter (Frost, 1930a); (4) vessel elements typically angular (Frost, 1930a); (5) vessel elements very small in diameter (Frost, 1930a); (6) vessel elements with scalariform perforation plates (Bailey & Tupper, 1918; Bailey, 1944; (Frost, 1930a, 1930b); (7) vessel elements with oblique end walls (Frost, 1930a; Bailey, 1944); (8) presence of uniseriate and multiseriate rays (Heterogeneous Type IIa) (Kribs, 1935; Barghoorn, 1940, 1941); and (9) axial wood parenchyma scattered, diffuse, and apotracheal (Kribs, 1937; Metcalfe & Chalk, 1950; Carlquist, 1961).

The following characters of the secondary xylem of *Paeonia* are relatively advanced: (1) imperforate elements most frequently with thin to thick walls (intermediate categories) (Bailey, 1936, 1953; Reinders, 1935); (2) imperforate elements and vessels typically with circular-bordered pit-pairs having crossed inner apertures which do not extend beyond the border outlines (Bailey, 1936; Eames & MacDaniels, 1947); (3) length of imperforate elements ranging most frequently from 330 to 640 μm . (short) (Bailey & Tupper, 1918; Chattaway, 1936; Bailey, 1953); (4) vessel distribution commonly of pore chains and multiples in addition to the more primitive solitary condition (Tippo, 1946); (5) ring porosity or semi-ring porosity, ring porosity predominant (Frost, 1930a); (6) number of bars composing the scalariform perforation plates most frequently 1 to 3 (few) (Frost, 1930b); (7) the common presence of wide and (8) non-bordered perforations in the scalariform perforation plates (Frost, 1930b); (9) occasional simple perforation plates (Bailey & Tupper, 1918; Bailey, 1944; Frost, 1930a, 1930b); (10) opposite as well as alternate intervacular pitting (Bailey & Tupper, 1918; Frost, 1931); (11) alternate and opposite as well as transitional pitting between rays and vessels (Bailey & Tupper, 1918; Frost, 1931); (12) length of vessel elements ranging from 250 μm . (short) to 500 μm . (medium) (Bailey & Tupper, 1918; Chattaway, 1936; Bailey, 1953); (13) homogeneous rays (Types I and II) (Kribs, 1935; Barghoorn, 1941); (14) presence of strand axial wood parenchyma, most commonly composed of two cells, rarely accompanied by true fusiform axial parenchyma (Metcalfe & Chalk, 1950); (15) reduced vascular ray structure, with uni- or biseriate rays predominating (Metcalfe & Chalk, 1950); and (16) storied vessel elements (Metcalfe & Chalk, 1950).

The following characters are specialized, but it has not been shown that they represent an advanced condition: (1) occurrence of spiral thickenings in the imperforate elements (Tippo, 1946); (2) presence of spiral thickenings in the vessel elements (Frost, 1931); and (3) presence of atypical multiperforate perforation plates in the vessel elements (MacDuffie, 1921; Chalk, 1933; Gottwald & Parameswaran, 1964).

The preceding lists support the hypothesis that the secondary xylem of *Paeonia* cannot be considered primitive. Although several characters are of a primitive nature, a greater number are moderately specialized, and a few are highly specialized. In view of this evidence, one must tentatively

conclude that the family Paeoniaceae has reached a moderate level of specialization.

It is difficult to attach any phyletic importance to the presence of the atypical multiperforate perforation plates. Atypical plates have been reported in many unrelated families. Aldridge (1964) described a definite abnormality of the regular perforation in tomatoes. This is the phenotypic expression of a genetic aberration. Chalk (1933) and Gottwald and Parameswaran (1964) found plates composed of very numerous isodiametric openings which are similar in both size and shape to the bordered pits on the side walls of the vessels. There is no evidence reported of fusion between these perforations within a plate. Multiperforate plates may occur intermittently in a plant and are usually found in taxa with otherwise simple perforation plates. This type undoubtedly has no significance in the evolution of the vessel as a whole, but rather is an anomaly in which the pattern of the intervacular pitting is imposed on the end walls.

The atypical perforation plates found in *Paeonia* represent modifications of scalariform or reticulate plates or are retentions of more primitive perforation plates like those described for other taxa (Thompson, 1923; Dickison, 1967; Gray & de Zeeuw, 1974). Gottwald and Parameswaran (1964) described similar forms as occurring in the Dipterocarpaceae and believed that they were intermediate steps in the evolution of simple perforation plates from scalariform ones.

This is very possibly the case in *Paeonia*, where both scalariform and simple perforation plates exist. In his study on the secondary xylem of the Compositae, Carlquist (1959, 1960) occasionally found multiperforate plates, often in radial series, associated with the normally occurring simple perforation plates. This fact indicates that a single cambial initial tends to produce a series of atypical perforation plate patterns. This situation is different from the condition in *Paeonia*, where similar atypical patterns were found to occur in successive end walls of a single vessel, rather than in radial series.

Atypical multiperforate plates have been reported sporadically, but not infrequently, in scattered families of angiosperms, including both primitive and advanced taxa, as well as in ferns and other lower groups. MacDuffie (1921) states that this condition is particularly prevalent in dicotyledons with herbaceous and climbing habits, but this is not confirmed by a search of other papers treating the subject (Chalk, 1933; Thompson, 1923; Webber, 1936; Bailey & Howard, 1941; Heimsch, 1942; Young, 1955; Carlquist, 1959, 1960, 1961; Eames, 1961; Gottwald & Parameswaran, 1964; Dickison, 1967).

TABLE 3 shows a comparison of the various characters of the secondary xylem of *Paeonia* with those of other taxa with which it has been variously allied in the past. In summary, on the basis of the secondary wood anatomy alone, the woody species of *Paeonia* are similar to, but more advanced than, the Dilleniaceae and Actinidiaceae, and are similar to, but slightly more primitive than, the Calycanthaceae and Annonaceae. Borderline taxa, in which there is a possibility of relationship, but much less than in com-

TABLE 3. Comparison of secondary xylem of *Paeonia* and other taxa.

	Magnoliaceae	Winteraceae	Cannellaceae	Annonaceae	Myristicaceae	Calycanthaceae	Ranunculaceae (Clematis)	Berberidaceae	Dilleniaceae	Crossosomataceae	Rosaceae	Spiraeoideae	Rosoideae	Maloideae	Prunoideae	Theaceae	Actinidiaceae	Saurauaceae	Guttiferae
IMPERFORATE ELEMENTS																			
Type	+	P	A	A	A	A	A	A	+	A	±	A	+	+	+	+	+	A	A
Length	P	P	P	P	P	P	+	+	P	O	P	P	P	P	P	P	O	P	P
Spiral thickenings	P	P	P	P	P	+	P	P	P	P	+	+	+	+	+	P	P	P	P
VESSELS																			
Porosity	+		P	+	P	A	A	+	P	A	±	P	+	+	P	+	P	P	P
Pore distribution	P		P	+	P	A	A	P	+	P	P	P	P	P	P	P	P	P	P
Pore diameter	A		P	+	A	+	O	+	+	+	A	A	A	A	A	A	+	A	A
Cross-sectional outline	+		+	A	A	+	O	+	A	+	A	A	A	A	A	+	O	+	A
Perforation plates	P		P	A	+	A	A	A	+	A	A	A	A	A	A	P	A	P	A
Number of bars	P		P	O	+	O	O	A	P	O	O	O	O	O	O	P	P	P	P
Intervascular pitting	P		P	+	P	A	A	A	P	A	A	A	A	A	A	P	O	P	A
Ray-vessel pitting	P		P	A	P	A	A	A	P	A	A	A	A	A	A	P	O	P	P
Ray-vessel pits bordered	+		P	+	P	+	+	+	+	+	+	+	+	+	+	P	O	+	+
Length	P		P	+	P	+	+	A	P	O	P	P	P	P	P	P	P	P	P
Spiral thickenings	+		P	+	+	+	+	+	P	P	P	P	+	+	+	+	+	+	P
VASCULAR RAYS																			
Type	P	P	A	A	+	+	P	A	P	P	+	+	+	+	+	P	P	P	P
Widths of multiseriata	A	A	+	A	+	+	A	A	A	A	A	A	A	A	A	+	A	A	A
Sheath cells common	+	A	+	+	+	+	A	A	A	+	+	+	+	+	+	A	+	+	+
AXIAL WOOD PARENCHYMA																			
Type	+	+	+	+	+	O	A	P	+	O	+	+	+	+	+	O	+	O	O
Number of cells in strand	P	P	P	P	P	+	P	P	O	P	O	O	O	O	O	O	P	O	O
Parenchyma distribution	A	A	A	A	A	A	A	P	+	A	A	A	A	A	A	A	+	A	A
Percentage of characters identical to those of <i>Paeonia</i>	33	10	19	50	29	50	33	33	37	25	45	21	26	32	32	26	38	21	11
Percentage of characters of a lower phyletic level than those of <i>Paeonia</i>	52	60	65	15	52	11	11	24	47	31	25	37	26	26	32	58	50	58	52
Percentage of characters of a higher phyletic level than those of <i>Paeonia</i>	15	30	16	35	19	39	56	43	16	44	30	42	48	42	36	16	12	21	37

+ Family in question has essentially the same secondary xylary feature as found in *Paeonia*P Character of the family in question is less specialized than that of *Paeonia*A Character in question is more specialized than that of *Paeonia*

O Knowledge of character is lacking, or phyletic nature not understood

parison to the families noted above, are the families Magnoliaceae and Berberidaceae, the rosaceous subfamilies Maloideae and Prunoideae, and the ranunculaceous genus *Clematis*. About one-third of the secondary xylary characters of these latter taxa lie at a phyletic level similar to those of *Paeonia*.

CORRELATION OF TAXONOMIC AND MORPHOLOGICAL FEATURES WITH XYLEM

CHARACTERS. It is unwise to speculate concerning phyletic relationship solely on the basis of secondary wood anatomy (Bailey, 1951, 1953). Considering that similar structures appear in quite distantly related taxa due to the frequent occurrence of parallel evolution, no single line of evidence should be considered conclusive. Since a taxon which retains primitive secondary wood characters cannot be derived from one which is uniformly advanced, Bailey (1957) has pointed out that the evidence obtained from secondary wood anatomical studies is often more helpful in negations than in positive assertions of close alliance.

Bailey (1951, 1953, 1957) has also stressed that meaningful phylogenies can be constructed only when comprehensive studies, taking into account evidence from all organs and parts of the plant body, have been evaluated. For this reason, TABLE 4 has been prepared to show differences and similarities of features other than those of the secondary wood, between *Paeonia* and each of the taxa with which it has been linked.

As familial taxonomic descriptions are readily available, they are not included here. The principal works used in compiling TABLE 4 are those by Rendle (1925), Gunderson (1950), Lawrence (1951), Hutchinson (1959), and Melchior and Werdermann (1964). The characters chosen for comparison are those for which information is available in these standard works.

The morphological characters of the Paeoniaceae that have been shown to be primitive (Hutchinson, 1959; Eames, 1961; Davis & Heywood, 1963) include: woody and perennial habit (section MOUTAN); spiral arrangement of leaves; bisexual, solitary, and actinomorphic flowers with many free parts, spirally arranged; hypogynous stamens; several free carpels; and follicular fruit. Those characters of *Paeonia* which are commonly considered advanced or specialized include herbaceous habit (sections PAEONIA and ONAEPHA); deciduous and pinnately compound leaves; absence of stipules; fasciculate stamens; and tricolporate pollen. In addition, Camp and Hubbard (1963) found an abundant vascular supply subtending the ovules of *Paeonia lactiflora* (section PAEONIA). From this they suggest that the ovules in *Paeonia* are specialized through reduction from an ancestral type.

It can be seen, therefore, that the Paeoniaceae may be considered to have predominantly primitive characters. The relatively specialized wood anatomy, however, possibly invalidates the placement of the family in the traditional positions near families that have similar primitive morphology, but that possess dissimilar primitive wood anatomy.

Members of the family Dilleniaceae possess the highest number of morphological characters similar to those of *Paeonia* (85 percent, TABLE 4). In addition, it is one of the five families most possibly related to *Paeonia* on the basis of the secondary wood anatomy alone. Morphologically, the families are extremely similar, differing, in characters considered, only by the presence in Dilleniaceae of occasional climbing forms, usually simple leaves, a free stigma, a basic chromosome number of $n = 8$ to 13, and the absence of a disc and nectaries. *Paeonia* can be seen to be more specialized than species in the family Dilleniaceae, especially in its deciduous habit and in its secondary wood, which exhibits such specialized features as ring or semi-ring porosity, short imperforate and vessel elements, a reduction in the number of bars in the scalariform perforation plates (from 20 to 130 down to 1 to 3), and a reduced vascular ray structure (TABLE 3).

Takhtajan (1969) considers *Paeonia* the component of an unigeneric family and order, thereby separating it somewhat more from the Dilleniaceae than do the present writers. His separation is based upon the following morphological characters: (1) thick, fleshy carpels, (2) broad stigmas, (3) a lobed and unusually prominent staminal nectariferous disc, (4) a massive outer integument, (5) seed coat characters, and (6) the peculiar embryogeny described by Yakolev and Yoffe (1957), Cave, Arnott, and Cook (1961), and Walters (1962).

Because of the frequency with which *Paeonia* has been placed within the Ranunculaceae, a discussion of the relationship between these two taxa seems appropriate. The similarities between the Paeoniaceae and Ranunculaceae (and often with the "Ranales" in general) include: usually perennial and herbaceous habit; alternate, more or less divided leaves; bisexual flowers with free and spiral or spirocyclic parts; numerous stamens; free and numerous carpels; follicular or achenial fruits; and seeds containing copious, oily endosperm with a small embryo at the apex.

The separation of *Paeonia* from the Ranunculaceae, however, is strongly indicated in TABLE 5, in which the major and fundamental differences between the two taxa are listed.

Of the differences separating *Paeonia* and the Ranunculaceae, several characters of *Paeonia* also separate that genus from the "Ranales" in general (*sensu* Eames, 1961): amphicribal vascular bundles, fasciculate and centrifugal stamens, and several characters of the ovule, pollen, and secondary wood.

The "Ranalian" families that are most similar to the Paeoniaceae on the basis of the secondary wood anatomy (TABLE 2) are the Calycanthaceae and the Annonaceae, with one-half of the total characters used similar to those found in *Paeonia*. The Calycanthaceae, however, are quite dissimilar to *Paeonia* in morphological features (TABLE 4) and are therefore unlikely to be related.

The family Annonaceae is chiefly tropical and seems to be a reduced or specialized taxon closely related to the Magnoliaceae. Characters which show this relationship are the whorled perianth, exstipulate leaves, and ruminant endosperm. In these features, the Annonaceae are most closely

TABLE 5. Comparison of *Paeonia* and Ranunculaceae.

CHARACTER	<i>Paeonia</i>	<i>Ranunculaceae</i>
1. Habit	Woody and herbaceous perennials	Herbaceous perennials, woody vines (<i>Clematis</i>), or rarely shrubs (<i>Xanthorrhiza</i>)
2. Vascular bundles	Amphicribal	Frequently amphivasal
3. Perianth delimitation	Gradation gradual from leaves through bracts, sepals, and petals	Perianth sharply delimited from leaves and bracts
4. Receptacle	Somewhat concave	Convex
5. Vascular supply to perianth	Sepals and petals receiving few to several vascular traces	Sepals typically receiving three traces, petals receiving one trace
6. Petal derivation	From bracts	Probably from stamens
7. Sepals	Persistent	Fugacious
8. Stamens	Fasciculate, developing centrifugally	Free, developing centripetally
9. Subgynoecial disc	Present	Absent
10. Ovule development	With outer integument strongly developed and thick; nucellus crushed, embryo sac enclosed by inner integument, hypostase invariably present; antipodal cells ephemeral	Outer integument similar to the inner integument; nucellar epidermis persisting and enclosing the embryo sac, hypostase rarely present; antipodal cells persistent
11. Seed	Aril present	Aril absent
12. Pollen	3-colporate	3-colpate
13. Seed germination	Hypogeal	Epigeal (except in part of <i>Clematis</i>)
14. Basic chromosome number	$n = 5$	$n = 7, 8, 9$
15.* Imperforate elements	Xylary fibers and fiber-tracheids	Libriform wood fibers
16.* Vessels	Small and often solitary, with scalariform and simple perforation plates	Large and usually clustered, with simple perforation plates only
17.* Sheath cells	Absent in vascular rays	Common in vascular rays
18.* Axial wood parenchyma	Apotracheal	Paratracheal
19. Phloem	With little or no sclerenchyma	With many fiber and stone cells
20. Accessory cortical bundles	Present	Absent

* Items 15 through 18 present a comparison of the secondary xylem of *Paeonia* with that of *Clematis*. The latter genus provides the only basis for comparison in this respect.

related to the more advanced genera of the Magnoliaceae, such as *Liriodendron*. The Magnoliaceae and Annonaceae resemble one another in so many ways that the two families are doubtless derived from the same ancestral stock, with the Annonaceae being somewhat more advanced. This advancement has brought the Annonaceae within its alliance up to a phylogenetic level similar to that of *Paconia*. Because of the basic differences between *Paconia* and the "Ranales", and the probability of close relationship between the Magnoliaceae and the Annonaceae, the similarities of *Paconia* and the Annonaceae are probably the result of parallel evolution, rather than of close relationship.

According to TABLE 3 (wood anatomy), the Theales, including the Theaceae, Actinidiaceae, and Saurauaceae, seem to be closely related to the Dilleniales. Morphologically, the family Theaceae represents a direct syncarpous derivative from the more primitive order Dilleniales. The alliance of the Dilleniaceae to the Theaceae (Thorne, 1968, 1974) is supported by anatomical considerations. The greatest agreement between the anatomy of the two families exists between the subfamily Dillenioidae and the tribes Actinandrieae and Ternstroemiaceae in the Theaceae (Dickson, 1967).

The Guttiferae are most often placed in their own order in close association with the Theales. The Guttiferae (Theales and Dilleniales) are also seen as advanced syncarpous types, with opposite leaves, and free or variously connate stamens. The stamens are often united into specialized bundles (phalanges). Morphologically, the Guttiferae show little relationship to *Paconia*, and the secondary wood anatomy is completely dissimilar (TABLE 3).

These two orders, the Theales and the Guttiferales, were more likely derived from a dilleniaceous stock in one evolutionary direction. The secondary wood of the Actinidiaceae shows a phylogenetic level similar to that of the secondary wood in *Paconia*, but this is not necessarily indicative of close relationship. The different direction taken by these taxa may be seen in the development of carpels and stamens that are more united, a lianous habit (in *Actinidia* and several genera of the Dilleniaceae), and opposite leaves (Guttiferae).

Members of the family Rosaceae are characterized by the usual presence of stipules, a generally pentamerous flower, a hypanthium (in most genera), and the near absence of endosperm in the seed. This family represents a large and eminently successful modification from the "Ranales" by the development of a hypanthium. It has been suggested that the Dilleniales represent the link between the "Ranales" and the Rosales (Porter, 1959). This view, however, is questionable on the basis of specializations found in the Dilleniales which apparently have been retained by other taxa arising from the same ancestral stock, but which are not found in the Rosales (e.g., the centrifugal stamens which are found in the Dilleniales and Theales, but not in the Rosales). Characters found in the Rosaceae which show no similarities to any condition in the Dilleniaceae or in *Paconia* include the hypanthium, leaves with stipules, free and centripetal

stamens, axile placentation, nearly absent endosperm, and the absence of arillate seeds. In total number of morphological characters, *Paeonia* and the Rosaceae might be considered somewhat similar (TABLE 4), but the important differences already mentioned do not support such a conclusion. Also, treating the four subfamilies separately, as was done in the anatomical treatment, reduces the number of morphological similarities to less than that shown by the family as a whole. Although the Maloideae and Prunoideae exhibit fewer morphological characters similar to those in *Paeonia* than do the other subfamilies, they are anatomically closer to the Paeoniaceae than are the Spiraeoideae or Rosoideae. This is further evidence of the probability that the two taxa are not closely related.

The monogeneric family Crossosomataceae has been included either in the Rosales (Gunderson, 1950; Thorne, 1968) on the basis of the hypanthium, or in the Dilleniales (Hutchinson, 1959; Eames, 1961) on the basis of the free follicular carpels and strongly arillate seeds. Metcalfe and Chalk (1950) and Dickison (1967), however, question the placement of *Crossosoma* within the Dilleniales because of their rather dissimilar anatomy. This view is supported by the lack of similarities between the secondary xylary anatomy of *Paeonia* and that of *Crossosoma* (TABLE 3). In general, the secondary wood of *Crossosoma* contains more highly advanced features than does that of *Paeonia*. Both of these taxa are probably northern derivatives and end-line specializations of larger tropical groups.

CONCLUSIONS

The secondary wood of *Paeonia* shows both primitive and advanced features, with the majority of characters being relatively specialized or advanced. The comparative morphology of the taxa previously held to be related to *Paeonia* clearly indicates that relationship to the Dilleniaceae is very close. The secondary wood anatomy does not negate this conclusion, but further suggests that *Paeonia* is most probably best placed as a valid and distinct unigeneric family within the Dilleniales, somewhat more specialized than the Dilleniaceae. There is a great deal of evidence from morphology, wood anatomy, and cytology to show that *Paeonia* should not be linked with the Ranunculaceae; furthermore, similar evidence nearly as strongly negates close relationship with the other taxa discussed above except for the Theales.

It is noteworthy that the authors' association of *Paeonia* with the Dilleniaceae agrees with the concepts of Corner (1946), Eames (1961), Melchior and Werdermann (1964), Dickison (1967), Thorne (1968, 1974), Cronquist (1968), and Takhtajan (1969). The evidence assembled by the writers, however, does not indicate that the relationship of *Paeonia* with the Crossosomataceae is as significant as is implied by the systems of Eames (1961), Cronquist (1968), and Takhtajan (1969). Closer to our views are those of Corner (1946), Dickison (1967), and Thorne (1968, 1974) that suggest a relationship of *Paeonia*, Dilleniales, and Theales, excluding Crossosomataceae. The proportions of similar anatomical and

morphological-taxonomic characters assembled in TABLES 3 and 4 indicate that *Paeonia* should be included as a distinct family within the Dilleniales. Our assemblage of characters also shows the probability of a close relationship between the Dilleniales (including only the Dilleniaceae and Paeoniaceae) and the Theales.

The Paeoniaceae probably arose from dilleniaceous ancestors in the Indo-Malayan region, the present center of distribution of the Dilleniaceae, and migrated northward into western China. The ancestral types still persist in the higher mountains of western China as the section MOUTAN. The more specialized herbaceous forms have spread west across temperate Eurasia and northeast into western North America.

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