WOOD ANATOMY OF DAPHNIPHyllACEAE: ECOLOGICAL AND PHYLOGENETIC CONSIDERATIONS, REVIEW OF PITOSPORALEAN FAMILIES

SHERWIN CARLQUIST

Carlquist, Sherwin (Rancho Santa Ana Botanic Garden, Claremont, CA 91711). Wood anatomy of Daphniphyllaceae: Ecological and phylogenetic considerations, review of pittosporalean families. Brittonia 34: 252–266. 1982.—Wood anatomy of 16 collections representing three species containing eight subspecies of the single genus Daphniphyllum is analyzed quantitatively and qualitatively. Daphniphyllum has vessels angular to roundish in transection, scalariform perforation plates, scalariform to opposite lateral wall vessel pitting, tracheids with fully bordered pits, heterocellular multiseriate and uniseriate rays, diffuse axial parenchyma and, in one taxon, chambered crystals in axial parenchyma cells. Growth rings, narrower vessels, and more numerous vessels per square mm characterize taxa from cooler habitats. All of the taxa have highly mesomorphic woods. Comparisons are made between Daphniphyllaceae and the other families of Thorne's Pittosporales (Balanopaceae, Bruniaceae, Buxaceae, Byblidaceae, Geissolomataceae, Grubbiaceae, Myrothamnaceae, Pittosporaceae, Roridulaceae, and Tremandraceae). These families are most comparable to hamamelidoid or rosoid families; other similarities or relationships for these families may exist, but are less conspicuous or less close. The families cited may form a plexus, characterized by primitive xylary and other features, comparable to Annonales (Magnoliaceae) as products of an early radiation of dicotyledons.

Daphniphyllum Blume is worthy of investigation on account of the apparent primitiveness of many of its features. A survey of wood features is needed, and can aid in understanding the phylogenetic position of this genus, the affinities of which have been disputed. As part of a monograph of Daphniphyllaceae, a brief account of wood anatomy is given by Huang (1966a). A detailed account has been attempted in the present paper.

While wood only offers a limited series of features, it may be used to clarify the systematic position of Daphniphyllaceae. In this regard, the families grouped with Daphniphyllaceae by Thorne (1968, 1976) into the order Pittosporales are especially pertinent. With the present paper, a wood anatomy survey of these families reaches completion (Hydrostachyaceae, a group of aquatic plants devoid of secondary xylem or nearly so, has not been included). Hamamelidaceae and Saxifragaceae (sensu lato) also are pertinent and are included in a tabular summary.

Although Daphniphyllaceae can be said to occupy mesic habitats, they range into cool climatic zones from the tropics and are worthy of consideration with regard to relationship between wood anatomy and ecology.

Daphniphyllaceae consists of the single genus Daphniphyllum. Huang (1966b) recognizes nine species, some with numerous subspecies and varieties. Daphniphyllum ranges from Himalayan India across China to northern Honshu (Japan) in the north and to southern India, Ceylon, Indonesia, and New Guinea in the south (Huang, 1966b). The genus does not occur in Australia. Huang has reduced the large number of species formerly recognized, undoubtedly with justification. The genus appears to form populations each slightly distinct from the other;

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grouping these populations into subspecies and species is not an easy task, and Huang appears to have produced a workable scheme. The genus ranges from sea level (*D. laurinum* (Benth.) Baill.) to subalpine zones. The sea level habitat of *D. laurinum* apparently is not saline, but in areas with non-saline groundwater. However, the wood of *D. laurinum* unfortunately was not available for study.

**Materials and Methods**

Although the author was able to collect wood samples of two taxa of *Daphniphyllum* in the wild (Table I), the majority of wood samples were provided by wood collections, listed in Table I with the xylarium abbreviations of Stern (1978). The sources of these specimens are as follows: *D. glaucescens* subsp. *borneense*, Carlquist 15500, 3450 m, Mt. Kinabalu, Sabah, Malaysia; *D. glaucescens* subsp. *borneense*, CLPw s.n., Sabah, Malaysia (no further locality); *D. glaucescens* subsp. *buchananfolium*, CLPw s.n., Philippines (no further locality); *D. glaucescens* subsp. *oldhamii*, MADw-3250 and MADw-24889, Taiwan (no further locality); *D. glaucescens* subsp. *scortechinii*, Carlquist 4404, 1200 m, Ulu Kali (Genting Highlands), Malaya; *D. glaucescens* subsp. *scortechinii*, KEPw-1078, 1600 m, Cameron Highlands, Malaya; *D. glaucescens* subsp. *teijsmannii*, KYO-905, Okinawa; *D. glaucescens* subsp. *teijsmannii*, MADw-8318, Chiba Univ. Forest, Japan; *D. glaucescens* subsp. *teijsmannii*, TWTw-3380, Japan (no further locality); *D. gracile*, FPAw-NGF-4407, FPAw-NGF-6765, MADw-25314, New Guinea (voucher for MADw-25314, Vink 17303); *D. himalayense* subsp. *himalayense*, RBHw-13077, 2800 m, Hwlong Ridge north of Mt. Victoria, Burma (8 m tree); *D. himalayense* subsp. *macropodum*, KYOw-110, Japan (no further locality); *D. himalayense* subsp. *macropodum*, PRFw-14678, W. Szechuan, China. The wood of *B. himalayense* subsp. *macropodum* illustrated in Figs. 12–13 was obtained from a cultivated specimen in the Vavra Estate, near U.C.L.A., a garden temporarily owned by U.C.L.A. I am grateful to the curators of the above-mentioned collections for the use of their materials.

Wood samples of *Daphniphyllum* were available dried; they were boiled, sectioned on a sliding microtome, and stained with safranin. The wood samples which were harder were treated with ethylene diamine (Kukachka, 1977) prior to sectioning. Woods of *Daphniphyllum* provide difficulties not because of their hardness but because of the gelatinous nature of tracheids (and other cells) and because of the very thin-walled (less than 2 μm often) nature of vessels, which tend to collapse during sectioning.

**Anatomical Features**

**Vessel elements.**—Vessels of *Daphniphyllum* are generally angular as seen in transection (Figs. 1, 7, 12, 16). However, in *D. gracile* (Fig. 15), vessels are more nearly rounded in outline. Vessel walls are mostly between two and three microns thick. Although vessels in pairs can be seen occasionally (Fig. 16), vessels may be said to be characterized as solitary.

Perforation plates are long (Fig. 10) throughout the genus. Bars may be forked (Fig. 3) or with interconnections (Fig. 11) in all taxa, although the majority of bars in any taxon are not so altered. The number of bars per perforation plate (Table I, column 4) is large throughout the genus, although somewhat smaller bar numbers seem to characterize the temperate taxa *D. glaucescens* subsp. *oldhamii*, *D. glaucescens* subsp. *teijsmannii*, and *D. himalayense* (both subspecies). Bars bear borders at edges of the perforation plate (Fig. 3, left and right), and sometimes (notably *D. glaucescens* subsp. *teijsmannii*, Fig. 11) along the length of the bars as well.
TABLE I

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* Legends for columns: 1, mean vessel diameter, \( \mu \text{m} \); 2, mean number of vessels per square mm transection; 3, mean vessel element length, \( \mu \text{m} \); 4, mean number of bars per perforation plate; 5, mean tracheid diameter, \( \mu \text{m} \); 7, mean tracheid wall thickness, \( \mu \text{m} \); 8, mean height multiserrate rays, \( \mu \text{m} \); 9, mean height uniseriate rays, \( \mu \text{m} \); 10, mean ray width, cells; 11, mean tracheid length divided by mean vessel element length; 12, “vulnerability” ratio (vessel diameter divided by vessels per square mm); 13, “mesomorphy” ratio (vulnerability ratio multiplied by vessel element length).

Lateral wall pitting of vessels is predominantly scalariform on vessel-ray contacts (Fig. 6), with some pitting transitional to opposite. On other vessel contacts (Fig. 4), pitting is scalariform (vessel to vessel) to sparse (vessel to tracheid, vessel to axial parenchyma cells).

Vessel diameter (Table I, column 1) does not fluctuate widely in the genus, but narrower vessels characterize temperate taxa, especially \( D. \text{ himalayense} \) (compare Fig. 12 to Figs. 1 and 7). Vessel density (Table I, column 2) varies inversely with vessel diameter in a rough way; the variations will be discussed with relation to ecology in a later section of this paper. Vessel element length ranges upward from 1000 \( \mu \text{m} \) (Table I, column 3), but not with distinctive patterns within the genus. Species with longer vessel elements have means which exceed the range given for the genus (‘1000–1640 \( \mu \text{m} \)”) by Metcalfe and Chalk (1950).

Tracheids.—As shown in Table I (column 5) tracheid length in \( D. \text{aphyllum} \) ranges from means of 1331 \( \mu \text{m} \) to 2207 \( \mu \text{m} \). Means must be considered approximate because of the wide variance in tracheid length within a single wood sample. Likewise, the ratio produced by dividing tracheid length by vessel length (Table I, column 11) fluctuates considerably within the genus. However, the ratio for the genus as a whole is rather low (average of the means = 1.23) and this would rank the wood of \( D. \text{aphyllum} \) as highly primitive according to the interpretations of this ratio (Carlquist, 1975a). Longer vessel elements and tracheids tend to occur in larger wood samples. This accords with the length-on-age curves showing gradual increase in length of tracheary elements with age (Bailey &
The shortest vessel elements were observed in the smallest of the wood samples studied here (xylem cylinder 2.8 cm in diameter), *D. glaucescens* subsp. *borneense*, Carlquist 15500.

Tracheid diameter fluctuates within the genus (Table I, column 6), but the narrower tracheids occur in the temperate to subtropical taxa, the wider tracheids in the tropical taxa. Tracheids can vary in diameter within a sample in those species with growth rings (Fig. 16). Tracheid wall thickness varies somewhat (Table I, column 7), but notably thick-walled tracheids occur in one collection of *D. glaucescens* subsp. *borneense* (Fig. 1). The thicker tracheids in these bands may represent reaction wood. However, all of the taxa of *Daphniphyllum* have notably gelatinous tracheids. Distinctive wall shrinkage patterns are evident in the prepared slides.

Pits on tracheids are all fully bordered (Fig. 5). Pit apertures are elliptical and lie within the circles formed by the pit cavities as seen in face view. In some tracheids in most taxa, splits occur in such a way as to lengthen the apparent pit aperture (Fig. 6, left). These splits are to be interpreted as dehydration artifacts related to the gelatinous wall structure, and are not part of the basic pit structure in the genus. The same phenomenon is common in Buxaceae (Carlquist, in press b).

**Axial parenchyma.**—As Metcalfe and Chalk (1950) note, parenchyma strands are formed of long cells, often in strands of seven, in *Daphniphyllum*. However, axial parenchyma may be characterized as relatively scarce in *D. glaucescens* subsp. *borneense* and in *D. himalayense* (both subspecies). Groupings of axial parenchyma slightly greater than what a random pattern would dictate can be observed in some taxa. A tendency toward diffuse-in-aggregates was noted in *D. glaucescens* subsp. *teijsmannii* (notably in latewood) and in *D. gracile*. A tendency toward abaxial groupings (one to three cells on the abaxial sides of vessels) was noted in *D. glaucescens* subsp. *borneense*, *D. glaucescens* subsp. *teijsman-
Figs. 1–6. Wood sections of *Daphniphyllum glaucescens* subsp. *scortechinii*, Carlquist 4404 (RSA). 1. Transection, showing band of thick-walled tracheids, center. 2. Tangential section; biseriate and uniseriate rays present. 3. Portion of perforation plate from radial section, showing narrowness of bars. 4. Intervascular pitting on vessel above perforation plate, from radial section. 5. Pits on tracheid from radial section. 6. Portion of a radial section showing tracheid with splits in wall, left, and scalariform vessel-ray pitting, right. Figs. 1–2, magnification scale above Fig. 1 (finest divisions = 10 μm); Figs. 3–6, scale above Fig. 3 (divisions = 10 μm).
Vascular rays.—Rays are both multiseriate and uniseriate in all species. Multiseriate rays are mostly two cells wide at their widest points (Figs. 2, 8), resulting in the figures offered in Table I, column 10. The central portion (biseriate or multiseriate) of multiseriate rays is composed of procumbent cells predominantly (Fig. 9), with only a few erect sheathing cells (Figs. 2, 8). Uniseriate wings occur on many multiseriate rays. The wings are identical to uniseriate rays histologically, and are composed predominantly of erect ray cells. In no species were all uniseriate rays devoid of procumbent cells, but taller uniseriate rays tend to have procumbent cells whereas shorter uniseriate rays may lack them.

Taller rays (Table I, columns 8 and 9) tend to occur in larger wood samples, whereas shorter rays tend to occur in smaller ones. The shortest rays were observed in *D. glaucescens* subsp. *borneense* (Carlquist 15500, sample 2.8 cm in diameter). Ray length appears to be governed by age, therefore, and to follow the same patterns mentioned above under tracheids.

In *D. himalayense* subsp. *macropodum* (Fig. 13) and in *D. himalayense* subsp. *himalayense* (Fig. 14), uniseriate rays outnumbered multiseriate rays. In all other species of *Daphniphyllum*, multiseriate rays outnumber uniseriate rays or are about equally abundant. Apparently the secondary xylem of *D. himalayense* originates ontogenetically with rays uniseriate or mostly so. This has been judged a specialized feature in *Illicium* by Bailey and Nast (1948). It only holds true for some species of *Illicium* (Carlquist, in press a), but it may also be observed in *Sarcococca* of the Buxaceae (Carlquist, in press b). The ray histology of *Daphniphyllum* could be described as Heterogeneous Type I in the typology of Kribs (1935), with the exception of the earlier-formed secondary xylem of *D. himalayense*, which corresponds to his Heterogeneous Type III. Ray width does not appear to correlate with taxonomic divisions within *Daphniphyllum*.

In radial sections, bordered pits may be observed on ray cells in all of the *Daphniphyllum* taxa studied. However, the bordered pits are confined to the tangential walls only, and are most conspicuous on the procumbent cells. The occurrence of bordered pits on these walls seems related to probable conduction patterns in ray cells. If, as hypothesized earlier (Carlquist, 1975a), ray cells (especially procumbent ray cells) function in horizontal transport of photosynthates, not only is a procumbent cell of selective value (fewer tangential walls per unit length of stem radius) but also bordered pits (greater wall strength compromised with maximal pit membrane surface area) are of selective value. In this hypothesis, one must assume that ray cells are conferring appreciable mechanical strength to the wood. That seems a reasonable assumption in view of the relatively thick lignified walls common on ray cells.

Crystals.—Janssonius (1934) reported axial parenchyma subdivided into crystalliferous strands (chambered crystals) in what would be *D. glaucescens* subsp. *glaucescens* in Huang's (1966b) treatment. There is no reason to question Janssonius's report, although I could not observe crystals in my materials of *Daphniphyllum*, which did not include the taxon Janssonius studied.

Amorphous deposits.—Deposits of unidentified material in the form of droplets (Fig. 9) or fine granular accumulations may be seen in ray axial parenchyma cells of *Daphniphyllum*. Perhaps these deposits are related to the distinctive bitter scent given off by crushed foliage of *Daphniphyllum*. The report by Huang (1966a) of "tanniniferous tubules" in the wood of *Daphniphyllum* must be discredited. Examination of his photographic figures reveals the structures so designated to
Figs. 7–11. Wood sections of *Daphniphyllum glaucescens* subsp. *teijsmannii*, FPAw-13212. 7. Transection; end of growth ring visible, center. 8. Tangential section. Uniseriate wings present on many multiseriate rays. 9. Multiseriate ray from a radial section; dark-staining droplets in ray cells. 10. Four perforation plates from radial section. 11. Portion of perforation plate from radial section, showing interconnections between bars. Figs. 7–8, magnification scale above Fig. 1; Figs. 9–10, scale above Fig. 9 (divisions = 10 μm).
be the melanin-rich walls of fungal hyphae, an all-too-common component of soft woods which cannot be dried easily under humid conditions. Huang’s figures claiming “tanniniferous tubules” in a leaf of *Daphniphyllum* likewise illustrate fungal hyphae.

**Growth rings.**—No growth rings were observed in most taxa of *Daphniphyllum*. Growth rings were observed in *D. glaucescens* subsp. *teljsmannii* (Figs. 7, 16), *D. himalayense* subsp. *himalayense*, and *D. himalayense* subsp. *macropodum* (Fig. 12). In these three taxa, earlywood is not strongly different from latewood. Earlywood vessels are wider than latetwood vessels, and earlywood tracheids are wider than latewood tracheids (Fig. 16). In *D. himalayense* subsp. *himalayense*, vessels in latewood were somewhat fewer than those in earlywood, and the last several layers of latewood were nearly devoid of vessels in some rings. Thus, growth rings in *Daphniphyllum*, where present, would correspond to Type ID (Carlquist, 1980a), with *D. himalayense* subsp. *himalayense* representing Type VD. The taxa of *Daphniphyllum* which have growth rings represent stations in high latitudes (*D. glaucescens* subsp. *teljsmannii* and *D. himalayense* subsp. *macropodum* are both from Japan) or high altitudes (the *D. himalayense* subsp. *himalayense* sample was collected at 2800 m, about 21°N latitude).

**Ecological Summary**

The woods of *Daphniphyllum* qualify as primitive in having long vessel elements with scalariform perforation plates associated with tracheids, diffuse axial parenchyma, and Heterogeneous Type I rays. These are wood characters associated with mesic preferences in dicotyledons; also, they indicate probable unbroken occupancy of such habitats, for more specialized woods may also be found in such habitats, probably representing phylesis into mesic areas from drier ones by particular groups. The mesomorphic wood features vary little within the genus *Daphniphyllum*. One may note fewer bars per perforation plate in the taxa from colder areas (Table I), but the difference between 40 and 60 bars is probably not an appreciable one where function is concerned. One may say with respect to the genus as a whole that all of the localities where *Daphniphyllum* is found must qualify as mesic.

The main differences among the species in quantitative features occur with respect to the indices or ratios (Table I, columns 12 and 13) termed “vulnerability” and “mesomorphy” (Carlquist, 1977c). These ratios, despite criticism (Vliet, 1979; see Carlquist, 1980a), prove to be very accurate indicators of habitat where wood is a primary tool in water relations management by plants. Where succulent or leathery leaves serve as intermediate buffers in the water relations of the plant, wood details are not as sensitive indicators of habitat. Vessel elements in *Daphniphyllum* show no clear evolutionary trend with respect to length, other than all being relatively long. Evolutionary alteration of vessel element length is not easy, based as it is on length of fusiform cambial initials. If, as Slatyer (1967) avers, air embolisms within vessels do not spread the length of a vessel, but often tend to stop at end walls (perforation plates), then one may hypothesize that shorter vessel elements, which better localize air embolisms formed under drought or frost conditions, would be advantageous to plants in dry habitats. *Daphniphyllum*, which is uniformly mesic in preferences, does not exhibit any appreciable trend toward shortening of vessel elements. However, vessel diameter and vessels per square mm do fluctuate within the genus with respect to ecology. Narrow vessels, more numerous per square mm, may be found in the taxa from high-montane Burma and from Japan. Narrow vessels may connote
Figs. 12–16. Wood sections of *Daphniphyllum*. Figs. 12–13. *D. himalayense* subsp. *macropodum*, Carlquist s.n., from Vavra Estate. 12. Transection, showing two weak growth rings. 13. Tangential section, illustrating predominance of uniseriate rays. 14. *D. himalayense* subsp. *himalayense*, RBHw-13077, tangential section showing paucity of multiseriate rays. 15. *D. gracile*, FPAm-13212, transection, showing end of growth ring (center), angular nature of vessels. Figs. 12–15, magnification scale above Fig. 1; Fig. 16, scale above Fig. 9.
low air entry capabilities, as Slatyer (1967) claims, and thus one may hypothesize that air embolisms would enter woods with such formulations, in localities prone to drought and frost, less readily. Numerous vessels per unit transection offer greater redundancy than few vessels per unit transection. Under conditions where vessels are blocked by air embolisms, more numerous vessels are therefore advantageous. Both vessel diameter and vessel density can be easily changed evolutionarily, in contrast to vessel element length. Changes within a single growth ring in these respects can be seen readily. Vessel diameter and vessel density are independent of each other, within limits. Therefore they can be independent indications of mesomorphy and xeromorphy, and their independence justifies use of both measures in the construction of the “vulnerability” and “mesomorphy” ratios. The vulnerability ratio of Table I (column 12) shows variation among the taxa. The taxa from colder areas (where frost tends to occur in winter) have vulnerability values below 0.50. Vulnerability values below 0.50 typify more xeric species in such a group as Pittosporaceae (Carlquist, 1981). By “xeric” one should connote both drought and physiological drought produced by freezing. The pattern shown by *Daphniphyllum* (little variation in vessel element length, but with appreciable variation in vessel diameter and in vessel density) can be seen also in Illiciaceae (Carlquist, in press a) and Buxaceae (Carlquist, in press b). These two families have woods similar in primitiveness to *Daphniphyllum*. The wood pattern in these three families shows that adaptation to more xeric habitats is possible in terms of vessel diameter and vessel density; these shifts are evidently frequent compared to the rather slow alteration of other wood features in groups which have retained primitive wood features over long periods of time.

**Relationships of Daphniphyllaceae; Summary for Pittosporales**

In his monograph, Huang (1966a) discussed the relationships of Daphniphyllaceae. The orders most frequently cited as possible placements for the family have been Euphorbiales, Hamamelidales, Rosales, and Pittosporales. Huang merely opts for a separate order, Daphniphyllales, without discussing what groups have closer or more remote resemblances in any detail. While Daphniphyllaceae is a distinctive family, it can be said to have relationships. The work of Mohana Rao (1974) on seeds and the study of Bhatnagar and Garg (1977) on pollen of *Daphniphyllum* express clear similarities between Daphniphyllaceae and Hamamelidaceae. A recent proponent of this viewpoint is Cronquist (1981).

In assessing what relationships Daphniphyllaceae may have in terms of xylary data, comparisons may be made to the families of Thorne’s (1976) Pittosporales. Using Thorne’s grouping as a premise for a research program, I have investigated wood anatomy of these families without any bias. However, all of these families do prove to have rather primitive xylem. Hydrostachyaceae, which lacks secondary xylem, is omitted from the discussion below. Discussions are based on secondary xylem only. For a review of the varied views on relationships of these families based on gross morphology and other characteristics, the papers cited below may be consulted. Table II lists wood features of the pittosporalean families in alphabetical order. To these are appended Hamamelidaceae and Saxifragaceae sensu lato (in the case of the Saxifragaceae, the woody segments often known as Hydrangeaceae, Brexiaceae, Escalloniaceae, etc., not the herbaceous groups, are cited). One must assess these wood features knowledgeabley. For example, the predominance of upright cells in multiseriate rays may simply indicate a small accumulation of secondary xylem (as with Byblidaceae), because subdivision of cambial initials leading to production of procumbent cells occurs over time. He-
Table II
WOOD FEATURES OF SELECTED DICOTYLEDON FAMILIES

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<td>T</td>
</tr>
<tr>
<td>Myrothamnaceae</td>
<td>M</td>
<td>S</td>
<td>A</td>
<td>S</td>
<td>T</td>
</tr>
<tr>
<td>Pittosporaceae</td>
<td>(F)-S</td>
<td>A</td>
<td>R</td>
<td>S-8.73 (FT)-LF</td>
<td></td>
</tr>
<tr>
<td>Roridulaceae</td>
<td>M</td>
<td>S-O-A</td>
<td>A-AR</td>
<td>S</td>
<td>T</td>
</tr>
<tr>
<td>Tremandraceae</td>
<td>S</td>
<td>S-O-A</td>
<td>AR-R</td>
<td>S-2.2 LF</td>
<td></td>
</tr>
<tr>
<td>Hamamelidaceae</td>
<td>M</td>
<td>S-O</td>
<td>A-AR</td>
<td>S-?</td>
<td>T</td>
</tr>
<tr>
<td>Saxifragaceae</td>
<td>M-F-S</td>
<td>S-O-A</td>
<td>AR</td>
<td>S</td>
<td>T</td>
</tr>
</tbody>
</table>

* Key to table: 1 = perforation plates of vessel elements (M = many bars, F = 1–10 bars, S = simple); 2 = lateral wall pitting of vessels (S = scalariform, O = opposite, A = alternate); 3 = vessel outline in transection (A = angular, AR = intermediate, R = round); 4 = vessel grouping (S = solitary, fewer than 1.5 vessels per group); 5 = imperforate tracheary elements (T = tracheids with fully bordered pits, FT = fiber-tracheids with vestigial borders on pits, LF = libriform fibers); 6 = helical sculpturing on vessel walls (+ = present, 0 = absent); 7 = Axial parenchyma distribution (D = diffuse, DA = diffuse in aggregates, AB = abaxial, V = vasicentric); 8 = transverse septa in upright ray cells (+ = present, 0 = absent); 9 = multiseriate ray histology, 10 = uniseriate ray histology (9 & 10, U = upright, S = square, P = procumbent); 11 = ray width (N = narrow, W = wide, greater than 3 cells in widest portion typically); 12 = erect sheathing cells on multiseriate rays (+ = present, 0 = absent); 13 = axial parenchyma strands subdivided into crystalliferous strands of chambered crystals (+ = present, 0 = absent); 14 = rhomboidal crystals in ray cells. Parentheses around symbols indicate only a few taxa within the family have the character. Boldface indicates the predominant condition.

lices on vessel walls (column 6) undoubtedly are not indicative of relationship, but may occur independently, probably as a response to drought or frost, in the evolution of many groups of dicotyledons. Where upright cells in rays are predominant, sheathing cells are present by definition on the multiseriate portion of the multiseriate ray.

Data in Table II are from the following of my papers: Balanopaceae (Carlquist, 1980a); Bruniaceae (1978); Buxaceae (in press b); Byblidaceae (1976a); Geissolomataceae (1975b); Grubbiaceae (1977a); Myrothamnaceae (1976b); Pittosporaceae (1981); Roridulaceae (1976c); and Tremandraceae (1977b). Data on wood anatomy of Hamamelidaceae and Saxifragaceae sensu lato are from Metcalfe and Chalk (1950). A somewhat wider range of characters than cited may be expected on account of the large size of Saxifragaceae and because of the families close to Hamamelidaceae (Cercidiphyllaceae, Eupelelelaceae, etc.) which should be considered with it. In the various papers of mine just cited, comparisons to “rosoid” families are often mentioned. By “rosoid” one can connote “Rosales” or even a larger group such as the Rosiflorae of Thorne (1968), which also includes Pittosporales. Hamamelidaceae, mentioned prominently in the monograph of Balanopaceae (Carlquist, 1980b) is also very pertinent to at least some of these families. Indeed, Hamamelidales and Rosales can be considered very close to each other, and these two orders are often placed close to each other in systems.

* Only four species were studied in the paper on Tremandraceae; one of these, “Tetraphetha sp.,” from the Tutanning Reserve, Western Australia, could not be identified because a monograph was in preparation. That collection may now be called T. retrorsa” Thompson (Thompson, 1976).
To be sure, wood anatomy offers only a limited series of features usable in systematics. For this reason, an exhaustive series of comparisons is not offered. Relationships to groups other than the above are still currently advocated by various authors: for example, Daphniphyllaceae and Buxaceae are claimed to be related to Euphorbiaceae, Grubbiaceae to Ericaceae, Pittosporaceae to Araliaceae, Tremandraceae to Polygalaceae, etc. While some of these are not negated by the evidence from wood anatomy (indeed, by postulating hypothetical common ancestors, one could hypothesize a wide variety of relationships), the similarities between the pittosporalean families and Saxifragaceae sensu lato or Hamamelidaceae are sufficiently close that similarities of a more remote nature (which are, in fact, considered in the above-mentioned papers) are not included in the present account. If data from wood offered more definitive evidence or if I had studied a wide range of features other than wood so that relatively secure opinions could be voiced, a wider range of comparisons would have been undertaken. I must stress that data from wood anatomy do not by themselves offer a sufficient basis for attempting to relate the pittosporalean families to each other or to other groups.

With these limitations in mind, a few commentaries may be offered. In using wood anatomy, one can separate characters into those dealing with phylogenetic level (e.g., number of bars per perforation plate) and those unrelated to broad phyletic lines but possibly indicative of relationship (e.g., modes of crystal occurrence, such as shown in columns 13 and 14 of Table II). Most wood characters fall into the former set; if these features could be evolved independently in every group, one could easily dismiss them as useless in assessing relationship. However, there is more than a passing chance that when two families have wood features markedly different in phyletic level, the families probably are not closely related. For example, Daphniphyllaceae has wood markedly more primitive than Euphorbiaceae. One can say with reasonable certainty that Daphniphyllaceae has not been derived from Euphorbiaceae. To say that Daphniphyllaceae in terms of wood represents a relictual type ancestral to Euphorbiaceae is theoretically possible, but such an interpretation would call for such massive extinction of pre-Euphorbiaceae and more primitive Euphorbiaceae as to be relatively unlikely. Families closely related (using gross morphology as the criteria for relationship) often tend to have wood anatomy similar in evolutionary level, and therefore more numerous wood characters in common.

One close alliance, on the basis of the data shown in Table II, appears to be
the trio of South African families Bruniaceae, Geissolomataceae, and Grubbiaceae. Aside from the greater diversity which Bruniaceae as a large family presents, the three families are virtually identical in wood patterns. Axial parenchyma subdivided into crystalliferous strands does not occur in Geissolomataceae or Grubbiaceae, but it does not occur in all Bruniaceae—only a scattering of species, in fact. These are three of the families grouped by Thorne (1968, 1976) as suborder Brunineae of Pittosporales (all the families of Brunineae are South African essentially). The other two families of Brunineae, Myrothamnaceae and Roridulaceae, are not so close to that trio. Myrothamnaceae are distinctive in having uniseriate rays exclusively; this feature occurs in young (but not old) stems of Sarcococca (Buxaceae) and Daphniphyllum himalayense, as well as in a scattering of unrelated families (e.g., Illicium; Carlquist, in press a). Mniottamnea bullata of the Bruniaceae does come close to the ray condition in Myrothannus, however. Some Hamamelidaceae also have only uniseriate rays. Roridulaceae are similar in ray structure to Myrothannus. However, the ontogenetic dimension must not be forgotten: narrow rays yield to wider ones as stems grow in diameter in most taxa. Both Myrothannus and Roridula have stems of relatively finite diameter.

Those who have seen similarity between Byblidaceae and Roridulaceae in gross morphology can claim wood features as another indicator of possible relationship. Perforation plates of Byblidaceae are nearly all simple, but they may well represent rapid adaptation to seasonally dry areas compared to the perpetually wet habitats in which Roridula grows. Both families have tracheids as imperforate elements, whereas Pittosporaceae and Tremandraceae (grouped with Byblidaceae by Thorne into a predominantly Australian suborder of Pittosporales, Pittospo-nineae) have libriform fibers (fiber-tracheids like libriform fibers in a few Pittosporaceae).

Pittosporaceae and Tremandraceae resemble each other in crystal occurrence, presence of septate fibers, and, to some extent, axial parenchyma type. Pittosporaceae is unusual among the roster of families in having scanty vasicentric axial parenchyma, with small quantities of diffuse parenchyma in a few species. Pittosporaceae is now known to have one species with scalariform perforation plates in vessels of secondary xylem (Carlquist, 1981); other species of Pittosporaceae have scalariform perforation plates in primary xylem (Bierhorst & Zamora, 1965). Tremandraceae have simple plates exclusively, even in primary xylem as far as I have been able to ascertain from my admittedly limited material. Thus Tremandraceae is rather strongly specialized in both vessel elements and tracheary elements, and in these respects is unusual among the families listed, but one may still think of it as being related to Pittosporaceae. The poricidal anthers of Tremandraceae, terminating as they do in long tubes, have been thought to relate Pittosporaceae to Tremandraceae, Byblidaceae, and Roridulaceae. Pittosporaceae are probably not primitively poricidal, however; the oft-cited Cheiranthera is exceptional within Pittosporaceae in its poricidal anthers. Whether or not poridical anthers represent adaptations to particular pollination schemes should be investigated; the Australian Thysanotus (Liliaceae) is certainly noteworthy for such anthers.

Balanopaceae has been compared closely to Hamamelidaceae (Carlquist, 1980b), but it also is very similar to some of the above families. One possible conclusion is that Hamamelidales and Rosales are related to each other closely, as well as to the roster of families discussed here. Both of the two types of crystal occurrence in wood may be found in Rosales (Brexia, Carpodetus) and Hamamelidales (Distylium, Rhodoleia).
Thorne related Balanopaceae to Daphniphyllaceae by constituting the pair as a suborder, Daphniphyllineae, of Pittosporales. The data from wood anatomy are not opposed to this. Daphniphyllaceae lack crystals in rays, but do have them in axial parenchyma strands (Janssonius, 1934); Balanopaceae have crystals in both cell types. Daphniphyllaceae have true tracheids with gelatinous walls; Balanopaceae have tracheids with more massive, but still gelatinous walls. Thus the resemblances between the two families, and with Hamamelidaceae and allied families, seem close.

More curious, perhaps, is Buxaceae, because the relatively wide span of features in wood anatomy is exceptional for such a small family. Buxaceae have no crystals in wood, and lack sheaths on the central portions of multiseriate rays except for Stylloceras, easily the most primitive genus in the family with respect to wood features. Despite the range from many to few bars on perforation plates of vessels, imperforate tracheary elements of Buxaceae are all tracheids with fully bordered pits. A mild range in axial parenchyma types may be found, but the diffuse-in-aggregate and abaxial conditions in Buxaceae represent mild departures from the diffuse condition. Among orders other than Hamamelidales, Rosales, and Pittosporales, Celastrales (especially Celastraceae) show some resemblances to Buxaceae, but Euphorbiales, a traditional site for Buxaceae, do not seem close to Buxaceae on the basis of wood anatomy. *Simmondsia*, sometimes included in Buxaceae, differs from Buxaceae with respect to wood anatomy (Carlquist, in press b), may be considered a separate family, Simmondsiaceae, which may well have affinities with Euphorbiaceae (Scogin, 1980; Cronquist, 1981). Daphniphyllaceae do not appear properly included in Euphorbiales, despite the retention of that treatment by some authors; as noted above, more numerous resemblances with Hamamelidaceae have been claimed by various authors in recent years.

The families of Thorne's Pittosporales mostly have quite primitive wood structure. The retention of such wood by this curious roster of families is remarkable. While the features of ranalean families (variously Annonales, Magnoliales, and Laurales) have captured the attention of phylogenists, that order by no means has uniformly primitive woods. Some botanists are surprised to learn how specialized woods of such families as Annonaceae, Hernandiaceae, Calycanthaceae, Lactoridaceae, Myristicaceae, and Piperaceae are. Hamamelidales contain two families with primitively vesselless wood (Tetracentraceae and Trochodendraceae), and other families (Cercidiphyllaceae, Eupteleaceae, and Hamamelidaceae itself) with strongly primitive woods. The woody saxifragoid families also have remarkably primitive woods predominantly: some botanists are surprised to learn that *Philadelphus* or *Cunonia* has wood more primitive than one finds in Degeineriaceae, Himantandraceae, or Magnoliaceae. Although the hamamelidoid-rosoid plexus (into which we may tentatively include various of the pittosporalean families, perhaps all of them) has some groups with specialized wood, such as Tremandraceae (in which the specialized wood coordinates with the xeric habitats these shrubs or subshrubs occupy), these assemblages of families have a remarkable degree of primitiveness in wood features. Thus the annonalean (magnoliaceous, lauraceous) radiation was not the only radiation of primitive angiosperms, and our views of early angiosperms could well afford a more inclusive look.

**Literature Cited**


