WOOD ANATOMY AND RELATIONSHIPS OF PENTAPHYLACACEAE: SIGNIFICANCE OF VESSEL FEATURES

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WOOD ANATOMY AND RELATIONSHIPS OF PENTAPHYLACACEAE: SIGNIFICANCE OF VESSEL FEATURES

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Abstract

Three wood samples of Pentaphylax, representing a range of habitats and ages, were examined. They agree in qualitative features: vessels angular in transsectional outline; perforation plates scalariform and long; vessel elements long; intervacular pitting scalariform; vessel-to-tracheid pits alternate and sparse; vessel-ray pitting scalariform; spirals present in vessel element tips (one collection); pits on tracheids fully bordered; axial parenchyma diffuse to diffuse-in-aggregates; rays beginning as uniseriates but becoming multiseriate with age (Heterogeneous I of Kribs); dark-staining deposits in rays; and a few crystals in axial parenchyma (one collection). These features are those of a primitive wood, and seem to place the family in Theales along with Clethraceae, Cyrillaceae, and Theaceae; such thelean families as Aquifoliaceae are also close. The ecological correlations of vessel diameter, vessel element length, and number of vessels per sq. mm are discussed. All of these are doubtless valid as indicators of xeromorphy or mesomorphy. The mesomorphy index indicates that the wood of Pentaphylax collections covers a wide range for a single species.

Wood anatomy of Pentaphylax has been presented in a condensed form by Heimsch (1942) and Metcalfe & Chalk (1950). The present study was undertaken because the available materials of Pentaphylax wood showed appreciable diversity for a single species (the treatment of the family offered by van Steenis 1955)

The diversity of the wood samples offers a problem for interpretation in ecology and ontogeny. Also the wood anatomy of these species could probably suggest whether Pentaphylax is composed of a single species, as claimed by van Steenis (five species have been named in the genus, which is the only genus of the family).

Pentaphylacaceae have generally been conceded to be related to Theaceae by recent authors, but many earlier systematists had placed it in Celastrales (see van Steenis 1955), where it was grouped with Aquifoliaceae, Corynocarpaceae, and Celastraceae. Aquifoliaceae, probably, should be placed near Theaceae, as was perceptively done by Thorne (1968). Corynocarpaceae and Celastraceae are not close to each other, and have affinities elsewhere. Thus, Pentaphylacaceae can be regarded as thelean no matter which view is considered. Study of wood

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anatomy is, however, of potential importance in confirming this.

### Material and Methods

Wood of *Pentaphylax euryoides* Gardner & Champion, was collected in the Malayan Highlands (Gunung Ulu Kali, also known as Genting Highlands), where it is a dominant element in the cloud forest. A wood sample, 8 cm in diameter, representing a reasonably mature wood pattern, was taken. Material from Hong Kong (Taam 2251) was less mature (6 mm in diameter) and was obtained from an herbarium specimen. It represents an unusual ecological site for the species. Although van Steenis (1955) mentions Hong Kong in the distribution of *Pentaphylax*, he does not take that locality into account in his elevational distribution (mountain forests and subalpine scrub forest, 1200-3000 m), for the Hong Kong specimen is from near sea level (Repulse Bay Road); his distribution map also excludes Hong Kong from the range of the genus. The third sample was provided by the Forest Research Institute of Malaysia at Kepong. Although the Institute could not offer information on the provenance of this wood sample, it seems (by virtue of angle of rays) to come from a fully mature and relatively large trunk.

All the samples were available in dried form, and were boiled prior to sectioning. The specimens, Carlquist 4387 and Taam 2251, were sectioned on a sliding microtome; the former was treated briefly with ethylene diamine (Kukachka 1977). The material from Kepong proved difficult because it contained large thin-walled vessels mixed with very thick-walled tracheids. This problem was solved by means of the technique suggested earlier (Carlquist 1982a), with longer than normal treatment in ethylene diamine. Sections of all collections were stained with safranin. Macerations were prepared by means of Jeffrey’s Fluid and stained with safranin. Quantitative data are based on 25 measurements per feature, except where the structure was infrequent or where only a few intact structures (long vessel elements break easily in macerations) were present.

### Observations

**CARLQUIST 4387** — Vessels angular in transection, mostly solitary (Fig. 1). Mean vessel diameter, 65 µm. Mean number of vessels per sq. mm = 103. Mean vessel wall thickness, 2.5 µm. Vessels with long scalariform perforation plates, mean number of bars per perforation plate = 37. Perforations narrowly bordered in middle of bars, more fully bordered at ends of bars (Figs. 3, 4). Some perforation plates have forked bars or a meshwork-like pattern (Fig. 5). Vessel-ray pitting scalariform (Fig. 7). Vessel-to-vessel pitting scalariform but mostly limited to tips of vessel elements because vessels are almost all solitary. Vessel-to-tracheid pitting sparse, alternate. No spirals seen in tips of vessel elements. Mean vessel element length, 1189 µm. All imperforate tracheary elements are tracheids with fully bordered pits (Fig. 6). Mean tracheid length, 1456 µm. Mean tracheid diameter, 30 µm. Mean tracheid wall thickness, 9 µm. Axial parenchyma diffuse, with some tendency to diffuse-in-aggregates (Fig. 1), parenchyma in strands of 6-9 cells. Rays predominantly uniseriate; a few rays 2-3 cells wide (Fig. 2). Mean height multiseriate rays, 551 µm. Mean height uniseriate rays, 645 µm. Some pits on ray cells bordered (Fig. 7). Ray cells erect to procumbent, the latter mostly in the central portions of rays, even if the rays are uniseriate (Heterogeneous Type I of Kribs, 1935, although this type is more typically demonstrated in the Kepong collection below, where multiseriate rays are more abundant). Dark-staining compounds in ray cells (Figs. 2, 4) and in small amounts among tracheids (Fig. 6). Crystals absent. Wood nonstoried.

**KEPONG COLLECTION** — Features the same as in Carlquist 4387, except as follows: Mean vessel diameter, 121 µm. Mean vessel wall thickness, 3 µm. Mean number of bars per perforation plate = 53. Mean vessel element length, 2221 µm. Mean tracheid
length, 3143 \mu m. Mean tracheid diameter, 48 \mu m. Mean tracheid wall thickness, 14 \mu m. Rays both multiseriate and uniseriate, but the multiseriate rays are more common (Fig 8). Mean multiseriate ray width = 3-4 cells. Mean multiseriate ray height, 1542 \mu m. Mean uniseriate ray height, 676 \mu m. Erect ray cells compose the uniseriate rays and the uniseriate wings of the multiseriate rays; the central portions of the multiseriate rays are composed of procumbent cells with a few erect sheathing cells (Fig. 8). Dark-staining deposits not observed.

TAAM 2251 — Some fluctuation in vessel diameter and abundance indicative of mild growth ring activity evident (Fig. 9). Mean vessel diameter, 28 \mu m. Mean vessel wall thickness, 1-2 \mu m. Mean number of bars per perforation plate = 31, bars narrowly bordered (Fig. 10). Spirals present in tips of vessel elements (Fig. 11). Scalariform intervacular pitting observed. Mean vessel element length, 829 \mu m. Mean tracheid length, 865 \mu m. Mean tracheid diameter, 18 \mu m. Mean tracheid wall thickness ranges from 2-4 \mu m, related to growth ring activity. Rays almost all uniseriate. Mean uniseriate ray height, 387 \mu m. Ray cells mostly erect, procumbent cells tending to be present in central portions of rays. Some dark-staining deposits present in ray cells. Crystals seen in a few axial parenchyma cells (Fig. 12).

Discussion

RELATIONSHIPS OF PENTAPHYLACACEAE

The wood of Clethraceae resembles that of Pentaphylacaceae, differing only in the occurrence of growth rings in temperate species; spirals in vessel element tips occur in both families (Giebel & Dickson 1976). These authors discuss relationship of Clethraceae to Ericaceae. Although that relationship is not ruled out by wood anatomy, both Clethraceae and Pentaphylacaceae match Theaceae more closely (cf. Metcalfe & Chalk 1950), and the grouping of Pentaphylacaceae with Clethraceae and Cyrillaceae in Theales (Thorne 1968) seems consonant with information from wood anatomy. Wood anatomy of Aquifoliaceae, described in detail by Baas (1973), can also be cited in support of Thorne's concept of Theales, for he includes Aquifoliaceae in that order and the wood of Aquifoliaceae proves, in sum, more thealean than similar to wood of other orders. Wood of Pentaphylacaceae is very primitive compared to that of dicotyledons at large. Naturally there is a tendency to compare such a wood with equally primitive woods in dicotyledons, some of which may not be close to Pentaphylacaceae. Rays which begin as uniseriate, predominantly or exclusively, but become multiseriate with increase in stem diameter, as in Pentaphylax, are known in random dicotyledonous families. Some of these are families with primitive wood features, such as Illiciaceae (Carlquist 1982b) and Buxaceae (Carlquist 1982c). Rays with this ontogenetic pattern are probably more widespread than presently reported because many comparative studies do not take ontogenetic stages into account.

INTERPRETATION OF VESSEL ELEMENT FEATURES — The genus Pentaphylax presumably consists of a single species, in agreement with van Steenis (1955). The

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Figs. 1-7 — Wood sections (Carlquist 4387; RSA). Fig. 1. Transection; axial parenchyma is diffuse and diffuse-in-aggregates. Fig. 2. Tangential section; most ray are uniseriate. Figs. 3-5. Perforation plates from radial sections. Fig. 3. Typical perforation plate. Fig. 4. Portion of plate showing presence of borders at ends of perforations. Fig. 5. Meshwork-like perforation plate portion. Fig. 6. Transection, showing borders on pits of tracheids. Fig. 7. Ray cells from radial section, illustrating scalariform vessel-ray pitting. Figs. 1, 2. Magnification scale above Fig. 1 (finest divisions = 10 \mu m). Fig. 3. Magnification scale above Fig. 3 (divisions = 10 \mu m). Figs. 4-7. Magnification scale above Fig. 4 (divisions = 10 \mu m).
Figs. 8-12 — Fig. 8. Tangential section (Kepong, s.n.) showing multiseriate rays. Figs. 9-12. Sections of Taam 2251 (UC). Fig. 9. Transection; vessels narrow. Fig. 10. Perforation plate from radial section; bars are narrowly bordered. Fig. 11. Spirals in tip of vessel element from radial section. Fig. 12. Portion of transection; dark cell, centre, is axial parenchyma cell containing crystal.

Figs. 8, 9. Magnification scale above Fig. 1. Figs. 10-12. Magnification scale above Fig. 4.
three collections studied here represent different-sized samples, but all the anatomical differences cannot be ascribed to ontogenetic variations: some must have an ecological basis, and are presumably heritable. The smallest stem is that of Taam 2251, the intermediate is Carlquist 4387, and the largest is the unnumbered Kepong collection. If we range the collections in this series, we find that in anatomical terms also the series corresponds to: increase in vessel diameter; decrease in number of vessels per sq. mm transection; increase in vessel element length; increase in tracheid diameter; increase in ratio of length between tracheids and vessel elements.

Differences in lengths of conductive cells correspond to those described by Bailey & Tupper (1918), in which lengths of tracheary elements in secondary xylem increase with age; Bailey & Tupper figure more rapid increase for imperforate tracheary elements than for vessel elements, accounting for the increase in the ratio mentioned in the above listing. Changes in the length of tracheary elements with age, are based on an increase in the length of fusiform cambial initials, evidently a rather deep-seated feature, which shifts slowly during growth of a stem. Ontogenetic change in vessel diameter is not based on length of fusiform cambial initials, but on degree of cell enlargement. The independence of diameter from length is clearly shown in growth rings of various dicotyledons.

Narrow vessels are positively correlated with xeromorphy in any given group of dicotyledons which has radiated into various habitats (Carlquist 1966). Narrow vessels, more numerous per sq. mm, offer greater safety (Zimmermann 1983). The narrow diameter of the vessels of wood of branches, as opposed to main stems, has been noted in several groups (Carlquist 1969, 1980): this feature is mentioned in relation to the much smaller diameter of vessels in the collection of Taam 2251, taken from a branch. Vessel diameter and vessel length (not to be confused with vessel element length) are closely correlated (Zimmermann 1982) statistically and not morphologically. A similar parallel occurs between vessel diameter and vessel element length. Although Baas (1982) and Zimmermann (1983) regarded patterns of vessel element length as "functionless trends imposed by correlative restraints", vessel element length could not possibly parallel so precisely vessel diameter and number of vessels per sq. mm (three features governed by different factors), and yet be functionless. Baas (1982) and Zimmermann (1983) did not consider the hypothesis (Carlquist 1982b), based upon Slatyer’s (1976) observation that spread of air embolisms tends to be localized or minimized by occurrence of perforation plates, even simple perforation plates: evidently, the spread of an air embolism tends to be stopped at a constriction rather than in the middle of a vessel element. According to this idea, if the vessel elements are shorter, air embolisms are more likely to be localized. Consequently, just as short vessels offer a form of safety (Zimmermann 1982), short vessel elements also offer safety. Vessel element length does not run parallel to plant height (Carlquist 1975, Baas 1982), so it cannot be merely a by product of particular lengths of mechanical cells; the basis must be sought elsewhere in most cases (longer mechanical cells may be hypothesized to offer greater mechanical support). Numerous vessels per sq. mm of transection are correlated with xeric habitats, and offer a form of safety (Carlquist 1975, Zimmermann 1983).

If vessel diameter, vessel element length, and vessel number per sq. mm are all related to the degree of safety woods possess under water stress, the three dimensions (all easily computed) can be combined, for any given species, into an index, termed Mesomorphy (Carlquist 1977). The collection Taam 2251 has a mesomorphy value of 54; the collection Carlquist 4387 has a value of 75; and that of the Kepong sample is much higher, 8218. A similar range in mesomorphy values was found in Pittosporaceae (Carlquist 1981). Both Pentaphylax and Pittosporum are evergreen shrubs to small trees, and the scope of variation in the habitats for the two genera is similar (although Pittosporum can occur
in much drier and colder habitats than Pentaphylax). Whereas some of the numerical differences among the three Pentaphylax collections can be related to ontogeny, there is evidently an independent ecological component also. The habitat occupied by Taam 2251 is subject to more ecological extremes, and thus the lower mesomorphy value is to be expected.

The spirals in vessel element tips of Taam 2251 could also be an indication of xeromorphy, since spirals in vessels increase with xeromorphy (Carlquist 1966; Baas 1982). The reason why spirals should occur in the tips and not in the central portions of vessel elements, is not evident at present.

Crystals are present only in the Taam collection. Although it cannot be generalized on such a narrow basis, crystals have been reported to be more abundant or present in mesic species of a genus, less abundant or absent in more xeric species: this holds in Balanops (Carlquist 1980) and the New Caledonian species of Pittosporum (Carlquist 1981). Investigation of more groups is advised to see if this tendency proves true more widely in dicotyledons. If it is so, one might look for a correlation with increased herbivore pressure, since occurrence crystals may be regarded as one of the many herbivore deterrence mechanisms in angiosperms.

**Literature Cited**

Carlquist S 1982a Wood anatomy of Buxaceae: correlations with ecology and phylogeny; *Flora Jena* 172 483-491


Heimsch C Jr 1942 Comparative anatomy of the secondary xylem of the "Gruinales" and "Terebinthales" of Wettstein with reference to taxonomic groupings; *Lilloa* 8 83-198

Kribs D A 1935 Salient lines of structure specialization in the wood rays of dicotyledons; *Bot. Gaz.* 96 547-557

Kukachka B F 1977 Sectioning refractory woods for anatomical studies; *Microscopica Acta* 80 301-307


Steelins C G G & Van 1955 Pentaphylacaceae; *Flora Malesiana Ser. 1* (5) 121-124

Thornew R F 1968 Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* 6(4) 57-66


Zimmermann M H 1983 Xylem Structure and the Ascent of Sap; (Berlin, Germany: Springer Verlag)