Wood Anatomy of Trimeniaceae

By

Sherwin Carlquist

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Abstract: Four collections of three species of Trimenia and one collection of Piptocalyx were studied; early-formed and later-formed wood was analyzed for one Trimenia. Liquid-preserved material permitted analysis of mucilage and starch storage in wood of T. neocaledonica and P. moorei. Because Piptocalyx is scandent whereas Trimenia is arborescent, wood differences relative to evolution of a climbing habit could be examined. Piptocalyx contrasts with Trimenia in having wider vessels, more numerous per mm², resulting in a conductive area five times greater per unit area than that of the Trimenia woods averaged. Piptocalyx has appreciably fewer bars per perforation plate and thus much greater conductive area per perforation plate than have the species of Trimenia. Rays in Piptocalyx are much taller and wider than those of Trimenia. Wood of Trimeniaceae is highly primitive in its scalariform perforation plates, scalariform lateral wall pitting on vessels, relatively long vessels elements, and heterocellular rays. Imperforate tracheary elements are septate nucleate fiber-tracheids (or even libriform fibers) rather than tracheids, but loss of borders on pits (and thus lowered conductive function of the imperforate tracheary elements) can be explained by the development of these elements into starch-storing cells. Some fiber-tracheids in T. neocaledonica are enlarged mucilage-containing cells. Details of vessel structure in Trimeniaceae are similar to those of Monimiaceae (s. s.), but similarity to some other lauralean (annonalean) families may be found: in mucilage presence, Trimeniaceae resemble Lauraceae rather than Monimiaceae. Wood of Trimeniaceae may be regarded as highly mesomorphic, corresponding to the moist habitats in which all of the species occur.

With the support of morphological features cited by Money & al. (1950), the family Trimeniaceae, first recognized by Gibbs (1917), is now generally accepted as distinct from Monimiaceae. Two genera are included. Of these, Piptocalyx Oliv. has two species, P. moorei Oliv. from southeastern Australia and P. macrurus Gilg & Schlechter from

Wood of all three species of *Trimenia* and one of the species of *Piptocalyx*, *P. moorei*, was available. Because *Piptocalyx* has a vining tendency, whereas *Trimenia* is a small tree, wood anatomy of the two genera differs significantly and offers an unusually good instance of how wood structure shifts with evolution of the scandent habit. *Trimeniaceae* are of interest because of the numerous primitive features of wood anatomy. The affinities of the family, although generally conceded to be annonalean (lauralean), are not certain and wood anatomy offers evidence in this regard. Both pickled and dried wood specimens were utilized in an effort to explore for variation within the genus. Liquid preserved material of *T. neocaledonica* and *P. moorei* proved useful in the study of formation and storage of starch and mucilage in wood. The sample of *T. neocaledonica* also proved important because of its large size, permitting study of wood of a young stem and that formed many years later.

**Materials and Methods**

A dried wood sample of *T. papuana* was provided by the C.S.I.R.O. Division of Building Research, Highett, Australia. Although this sample was a small block and the stem diameter was therefore not known, angle of divergence of rays in the portion sectioned would make the sections comparable to those taken from the periphery of a stem 2 cm in diameter. A dried wood sample of *T. weinmanniiifolia* subsp. **weinmanniiifolia** from Fiji, **Parham** 770, was available through the kindness of the Herbarium, Department of Agriculture, Suva, Fiji. This wood sample was 1 cm in diameter. A dried wood sample of *T. weinmanniiifolia* subsp. **weinmanniiifolia** from Samoa, **SJRw-26069**, was provided by the Division of Forest Products, U.S.D.A., Madison, Wisconsin. This sample was 1.5 cm in diameter. The wood sample of *T. neocaledonica* was collected by **Gordon McPherson** (4356, MO) in New Caledonia. This sample, representing a stem 11 cm in diameter, was pickled in formalin acetic alcohol, drained, and shipped to me in a plastic bag. Upon arrival, the still-moist wood was immersed and stored in 50% ethyl alcohol.

The dried samples of *T. papuana* and *T. weinmanniiifolia* were boiled and sectioned on a sliding microtome. This treatment resulted in good sections which were stained in safranin (Figs. 15–19). A similar procedure with the liquid-preserved wood of *T. neocaledonica* however, did not prove successful. When the wood stored in alcohol was sectioned, a few portions of sections were sufficiently intact for study of presence of starch (Fig. 6) and mucilage. The sections were
Figs. 1–5. *Trimenia neocaledonica* (McPHerson 4356), sections of outer wood.—
1. Transection, vessels wide, thin walled.—2. Tangential section. The wide fiber-
tracheids are mucilage-bearing cells.—3. Radial section. Ray cells mostly square
to procumbent.—4. Thin-walled tyloses in vessel from radial section.—5.
Portion of perforation plate from radial section. Borders on bars vestigial.
Magnification scale for Figs. 1–3 above Fig. 1 (finest divisions = 10 μm), for
Fig. 4 above (division = 10 μm), and for Fig. 5 also above (divisions = 10 μm)
excessively fragmented because mucilage expanded during the sectioning process. Removal of mucilage from the wood samples was therefore attempted. Some, although not all, mucilage was dissolved away by treatment in a 2.5% aqueous NaOH solution for 4 hours in a 60 °C oven. After the wood was washed, sections could be cut with moderate success. Mucilage no longer resulted in swelling and fragmentation of the sections. However, the softness of the wood, a condition perhaps slightly aggravated by the use of NaOH, made sectioning on a sliding microtome still unsatisfactory because of fracturing of vessel walls and walls of other cells. Consequently, an alternative procedure for obtaining satisfactory sections was invoked at this point.

Wood of *T. neocaledonica* treated with NaOH was softened in a 4% ethylene diamine solution. Samples were then washed, infiltrated in a tertiary butyl alcohol series, embedded in paraffin, and sectioned on a rotary microtome. Soaking in water of the surface of the paraffin-embedded material prior to section minimized fracturing of walls during sectioning. These methods have been described in greater detail in a recent paper (CARLQUIST 1982 a). It has been successfully applied to vesselless woods with thin walls (CARLQUIST 1982 b, 1983) but is also applicable to a wide range of materials, such as bark and leaves, as well as to various types of wood which are not sufficiently stiff to section well on a sliding microtome without embedding. The photographs in Figs. 1–9 (excepting Fig. 6) represent sections obtained with this method. The sections illustrated in Figs. 10–14 represent material treated with NaOH, but sectioned on a sliding microtome without ethylene diamine treatment or embedding. The wood in Figs. 10–14, taken from near the center of the log of *T. neocaledonica*, has narrower vessels and slightly thicker walled cells and therefore tends to fracture less during sectioning (compare Fig. 1 and Fig. 10).

The sample studied of *Piptocalyx moorei* was collected at Stock Yard Creek, 81 km north of Walcha, New South Wales, Australia, by DONALD FORREMAN of the University of New England, Armidale, N.S.W., on September 19, 1982. These samples were kindly transmitted to me by Dr. F. B. SAMPSON, Botany Department, Victoria University of Wellington, New Zealand. These stems were preserved in formalin-propionic alcohol, and were 5 mm in diameter. After washing, these were sectioned on a sliding microtome. While these sections yielded information about distribution of starch (Fig. 25), they contained flaws related to the difficulty of sectioning large vessels. To obtain good sections, the ethylene diamine-paraffin method (CARLQUIST 1982 a) was used. This method provided excellent sections (Figs. 20–23). Mucilage was present in stems of *P. moorei*, but not in such large quantities that it interfered with sectioning and required special removal.

Macerations were prepared from all five collections by treatment with Jeffrey’s fluid. As with sections, macerations were prepared from both the periphery of the log of *T. neocaledonica* and from near the pith. Macerations were stained in safranin. Averages for quantitative features were derived from 25 measurements.

**Anatomical Descriptions**

*Trimenia neocaledonica* (McPHerson 4356), mature wood pattern at periphery of log 11 cm in diameter (Figs. 1–9). Growth rings absent (minor fluctuation in vessel diameters evident). Vessels mostly solitary, average 94 μm. in diameter. Vessels angular to rounded in transsectional outline (Fig. 1). Mean number of vessels per mm² = 18. Mean vessel
Figs. 6–9. *Trimenia neocaledonica* (McPherson 4356), sections of outer wood.—6. Spherical starch grains (unstained) in ray cells, from transection.—7. Scalariform perforation plate from radial section, showing borders on bars.—8. Scalariform (above) and alternate (below) pits on ray cells, from radial section.—9. Fiber-tracheids from radial section, showing vestigial nature of pit borders.

Magnification scale for Figs. 6–9 above Fig. 5
element length, 920 µm. Mean vessel wall thickness, 3.0 µm. Perforation plates scalariform with many bars not bordered except at ends (Fig. 5). Mean number of bars per perforation plate = 23. Lateral wall pitting of vessels scalariform (Fig. 7), whether on interfaces with fiber-tracheids, ray cells, or other vessels. Fiber-tracheids with vestigial borders (Fig. 9). Mean fiber-tracheid length, 1471 µm; mean diameter at widest point, 55 µm; mean wall thickness, 4.6 µm. Fiber-tracheids septate (usually once) and nucleate at maturity. Fiber-tracheids septate and nucleate at maturity. Fiber-tracheids often thin-walled at center; some groups of fiber-tracheids have only thin walls separating them where their wider portions abut. This thin wall may be a portion of the same thin walls which form septa. Thin-walled fiber tracheids are occasionally seen to fracture (Fig. 1) in preparations. The large diameter of some of these fiber-tracheids make them easily confused with smaller vessels in wood transections (Fig. 1). At least the wider fiber-tracheids are filled with mucilage; starch is also present in them. Axial parenchyma scanty vasicentric, plus a very few diffuse cells. Axial parenchyma in strands of 4–6 cells. Rays both multiseriate and uniseriate (Fig. 2). Uniseriate wings present or absent on the multiseriate rays. Multiseriate rays wide (mean width, 6.9 cells). Multiseriate rays average 1887 µm in height; uniseriate rays average 562 µm in height. The multiseriate portions of multiseriate rays are composed mostly of procumbent cells (Fig. 3); a few square and erect cells are present. Uniseriate rays and uniseriate wings of multiseriate rays are composed of erect cells. Ray cells and axial parenchyma cells are rich in starch (Fig. 6) and mucilage. Pits on ray cells are circular and alternate or scalariform (Fig. 8). Predominantly the latter are on vessel-ray interfaces. Tyloses are present in some vessels, but are always thin-walled (Fig. 4). Wood non-storied.

*Trimenia neocaledonica* (McPherson 4356), inner wood (near pith in log 11 cm in diameter), Figs. 10–14. Features as in outer wood unless otherwise indicated. Mean vessel diameter, 40 µm. Mean vessel element length, 663 µm. Mean vessel wall thickness, 2.5 µm. Mean number of vessels per mm² = 48. Mean fiber-tracheid length, 1307 µm; diameter at widest point, 30 µm; wall thickness, 5 µm. Mean multiseriate ray height, 1307 µm. Mean uniseriate ray height, 408 µm. Mean ray width, 4.6 cells. Multiseriate portions of multiseriate rays are composed of erect cells with some square cells. Uniseriate rays and uniseriate portions of multiseriate rays composed of erect cells, often a little longer than the erect cells of the multiseriate portions of multiseriate rays. Dark-staining compounds evident in parenchyma cells (Figs. 10, 11, 14); these deposits are absent in photographs of outer wood because they were removed from samples of that portion by NaOH treatment. Some fiber-
Figs. 10–14. *Trimenia neocaledonica* (McPherson 4356), sections from center of log.—10. Transection. Compare vessel diameter to that in Figs. 1–11. Radial section. Ray cells erect, dark staining materials present.—12. Fiber-tracheids with gelatinous walls from transection.—13. Fiber-tracheids, mostly septate more than once, from radial section.—14. Ray cells with bordered pits from radial section. Magnification scales for Fig. 10 above Fig. 1, for Figs. 11 and 13, above Fig. 4, and for Figs. 12 and 14 above Fig. 5
tracheids have a gelatinous double wall, perhaps related to compression wood (Fig. 12). Nuclei and septa are evident in fiber-tracheids (Fig. 13). Some bordered pits may be seen in walls of thicker ray cells (Fig. 14).

*Trimenia papuana* (C.S.I.R.O. Division of Building Research H-6891). Growth rings absent. Vessels mostly solitary (1.08 vessels per group); mean vessel diameter, 70 μm. Vessels angular to rounded in transsectional outline. Mean number of vessels per mm² = 40. Mean vessel element length, 1345 μm. Mean vessel wall thickness, 3.5 μm. Perforation plates scalariform with many bars not bordered except at ends. Mean number of bars per perforation plate = 60. Lateral wall pitting of vessels scalariform, whether on interfaces with fiber-tracheids, ray cells, or other vessels. Fiber-tracheids with vestigial borders but some pits observed to lack discernible borders (and the elements bearing them therefore libriform fibers). Mean fiber-tracheid length, 1894 μm; mean diameter at widest point, 38 μm; mean wall thickness, 5.3 μm. Fiber-tracheids septate once or twice. Axial parenchyma very scanty, chiefly vasicentric. Rays both multiseriate and uniseriate. Uniseriate wings present or absent on the multiseriate rays. Multiseriate rays wide (mean width at widest point, 4.6 cells). Multiseriate rays average 1649 μm in height; uniseriate rays average 653 μm in height. The multiseriate portions of multiseriate rays are composed mostly of erect cells; a few square and procumbent cells also are present. Pits on ray cells are circular and alternate or else scalariform, predominantly the latter on vessel-ray interfaces. Some pits on ray cells are bordered. Tyloses were not observed. Wood non-storied.

*Trimenia weinmaniiifolia* subsp. *weinmaniiifolia* (Fiji, Parham 770). Growth rings absent (Fig. 15). Vessels mostly solitary. Mean vessel diameter, 65 μm. Vessels angular to somewhat rounded in transection (Fig. 15). Mean number of vessels per mm² = 55. Mean vessel element length, 860 μm. Mean vessel wall thickness, 3.5 μm. Perforation plates scalariform (Fig. 18), borders present to a limited extent on bars (Fig. 19), more obvious at ends of the perforations. Some apparent perforations at ends of perforation plates seem to have faintly-staining pit membranes and must therefore be termed pits (Fig. 19). Mean number of bars per perforation plate = 29. Lateral walls of vessels scalariformly pitted, whether facing other vessels, fiber-tracheids, or parenchyma cells. Fiber-tracheids with vestigial borders on pits. Mean fiber-tracheid length, 1115 μm; mean diameter at widest point, 30 μm; mean wall thickness, 4.0 μm. Axial parenchyma almost absent, a few vasicentric cells seen. Rays both multiseriate and uniseriate (Fig. 16). Uniseriate wings present or absent on multiseriate rays. Multiseriate rays average 3.3 cells wide at widest points of rays.
Figs. 15–19. *Trimenia weinmaniifolia* (Parham 770), sections of wood.—15. Transection. Vessels moderately narrow. 16. Tangential section. Rays narrow, dark-staining deposits present.—17. Radial section, showing erect to square shape of ray cells.—18. Perforation plate from radial section.—19. Portion of perforation plate; uppermost pits have borders and appear to have pit membranes by virtue of staining. Magnification scale for Figs. 15 and 16 above Fig. 1, for Figs. 17 and 18 above Fig. 4, and for Fig. 19 above Fig. 5
ray height, 1.275 μm. Mean uniseriate ray height, 440 μm. Uniseriate rays and uniseriate portions of multiseriate rays composed of erect and square cells, very few procumbent cells present (Fig. 17). Dark-staining deposits present in ray cells (Figs. 15–17). Spherical holes in the deposits in ray cells (Fig. 17) probably represent sites of starch grains lost during boiling of the wood sample. Tyloses not observed. Wood non-storied.

*Trimenia weinmaniifolia* subsp. *weinmaniifolia* (SAMOA, SJRW-26069). Growth rings absent. Vessels mostly solitary (1.24 vessels per group), mean vessel diameter, 64 μm. Vessels angular to somewhat rounded in transection. Mean number of vessels per mm² = 55. Mean vessel element length, 1331 μm. Mean vessel wall thickness, 3.5 μm. Perforation plates scalariform, borders present on ends of bars but borders less to absent on central portions of bars. Mean number of bars per perforation plate = 34. Lateral walls of vessels scalariformly pitted, whether facing other vessels, fiber-tracheids, or parenchyma cells. Mean fiber-tracheid length, 1650 μm; mean diameter at widest point, 35 μm; mean wall thickness, 40 μm. Axial parenchyma scanty vasicentric. Rays both multiseriate and uniseriate. Uniseriate wings present or absent on multiseriate rays. Multiseriate rays average 3.6 cells wide at widest point. Mean multiseriate ray height, 2173 μm; mean uniseriate ray height, 603 μm. Uniseriate rays and uniseriate portions of multiseriate rays composed of erect cells, very few square or procumbent cells present. Pitting on ray cells alternate to scalariform, predominantly the latter on vessel-ray interfaces, Dark-staining deposits present in ray cells. Spherical holes in deposits in ray cells probably represent sites of starch grains lost during boiling of the wood sample. Tyloses not observed. Wood non-storied.

*Piptocalyx moorei* (New South Wales, D. Foreman IX-29-1982). Growth rings absent. Vessels mostly grouped (mean number of vessels per group, 1.85), groupings mostly radial (Fig. 20). Mean vessel diameter, 102 μm. Vessels rounded, only slightly angular in outline (Fig. 20). Mean number of vessels per mm² = 63. Mean vessel element length, 1050 μm. Vessel wall thickness, 2.8 μm. Perforation plates scalariform (Fig. 24). Borders present at ends of bars, but also along the length of bars on many plates. Mean number of bars per perforation = 8.7. Lateral walls of vessels scalariformly pitted (Fig. 24), whether facing other vessels or parenchyma cells; pitting between vessels and fiber-tracheids sparse. Mean fiber-tracheid length, 1350 μm; mean diameter at widest point, 25 μm; mean wall thickness, 3.5 μm. Fiber-tracheids with well-marked borders on pits (Fig. 23). Fiber-tracheids once or twice septate (Fig. 22). Axial parenchyma scanty vasicentric. Rays both multiseriate and uniseriate (Fig. 21), uniseriate
Figs. 20—25. *Piptocalyx moorei* (D. Foreman, Sept. 29, 1982), preparations of wood. —Fig. 20. Transection, showing wide vessels, many per unit area.—Fig. 21. Tangential section; a multiseriate ray at right; vessels and uniseriate rays at left.—Fig. 22. Portion of a multiseriate ray, showing an enlarged cell which is probably a mucilage idioblast.—Fig. 23. Portion of a fiber-tracheid, showing borders on pits.—Fig. 24. Perforation plate of a typical vessel element, from maceration.—Fig. 25. Portion of a transection to show starch grains in ray cells (at left) and in fiber-tracheids (at right). Magnification scale for Figs. 20 and 21 above Fig. 1, for Figs. 22 and 24 above Fig. 4, and for Figs. 23 and 25 above Fig. 5.
rays more common than multiseriate rays. Uniseriate wings present on multiseriate rays. Multiseriate rays average 6.1 cells wide at widest point. Mean multiseriate ray height about 1 cm, too great to provide enough measurements for a reliable mean; uniseriate rays correspondingly tall. Uniseriate rays and uniseriate portions of multiseriate rays composed mostly of procumbent cells, a few square cells present also. Presumptive mucilage cells present in some multiseriate rays (Fig. 22), similar cells also present in phloem rays and in secondary phloem. Starch grains abundant in ray cells and in fiber-tracheids (Fig. 25). Tyloses not observed. Wood non-storied.

Discussion

The tendency of vessels in Trimenia to be angular in transsectional outline and their tendency to be solitary should probably be regarded as primitive features, in accordance with the criteria of Frost (1930 a). The perforation plates of Trimenia are certainly primitive on the basis of Frost’s (1930 b) criteria. Vessel-bearing dicotyledons with more primitive perforation plates with respect to more numerous bars or more fully bordered bars may be found, however. Within Trimenia, T. papuana would rank as more primitive with respect to number of bars per perforation plate. Scalariform pitting on vessels is primitive (Frost 1931).

The imperforate tracheary elements of Trimenia, in contrast, are fiber-tracheids with very small remnants of borders on pits. According to concepts of division of labor in angiosperm woods, fiber-tracheids of this description must be considered rather specialized (see MEICALFE & CHALK 1950, p. xlv). The ratio between fiber-tracheid length and vessel element length has been claimed to be an indication (within limits) of specialization within woods of dicotyledons (CARLQUIST 1975). According to these ideas, the ratios in Trimenia are not exceptionally primitive (T. neocaledonica, 1.6; T. papuana, 1.37; T. weinmaniifolia, 1.30, 1.24). In Trimenia, division of labor between vessel elements and fiber-tracheids is well marked in terms of lack of borders on the pits of the fiber-tracheids. Also, the fiber-tracheids no longer function as conductive elements, if presence of nuclei, protoplasts, and septa are criteria. Very likely loss of borders on pits of the imperforate elements has occurred concomitant with their function in storage rather than in conduction. As suggested by Money & al. (1950), these septate fiber-tracheids may be regarded as a substitute for axial parenchyma, which is present in very limited quantity in the three species of Trimenia examined.

The fiber-tracheids of T. neocaledonica deserve special mention. There is a dimorphism in them with respect to diameter and contents. As transections of T. neocaledonica wood show, some fiber-tracheids are
exceptionally wide. Where several such fiber-tracheids occur together, only a very thin wall separates them. This accounts for the breakages among cells in Fig. 1. In untreated or moderately treated pickled wood samples of *T. neocaledonica*, these fiber-tracheids prove to be filled with mucilage. Thus, the wide fiber-tracheids can be termed mucilage cells. Money & al. (1950) noted that the *Trimeniaceae* differ from the *Monimiaceae* but agree with *Lauraceae* in the presence of mucilage cells in leaves and stem cortex; wood may now be added to this organographic distribution.

With respect to wood characters other than mucilage cells, *Monimiaceae* sensu stricto show numerous resemblances to *Trimenia*. If one reviews the data of Garratt (1934) and Metcalfe & Chalk (1950), one finds that *Trimenia* resembles the *Monimiaceae* in having scalariform perforation plates, scalariform lateral wall pitting, tyloses, axial parenchyma quite sparse and vasicentric, fiber-tracheids with vestigial borders on pits, and rays as described above for *Trimenia*. The range of expressions reported for *Monimiaceae* is understandably wider than for *Trimeniaceae*. *Monimiaceae* is a moderately large family, whereas *Trimeniaceae* contains five species. The wood of *Monimiaceae* matches wood of *Trimenia* and *Piptocalyx* just as closely as does that of *Lauraceae*, a family in which scalariform perforation plates are not frequent, however. If a small group of families is ranked around *Trimeniaceae*, groupings such as the order *Laurales* (Cronquist 1981) or *Laurinae* of Thorne (1976) seem justified on the basis of wood anatomy.

The ray cells of *Trimenia* were reported to be predominantly erect by Money & al. (1950). This proves to be true of the relatively small stems of *T. papuana* and *T. weinmanifolia* studied here. It is also true of wood in the center of the log of *T. neocaledonica*, but it is not true of wood at the periphery of that log. Predominance of procumbent cells in rays in outer wood of that sample is understandable, however. As noted by Bargohorn (1941) and other authors, subdivision of ray initials over time tends to result in a higher proportion of procumbent cells in outer wood as compared to inner wood of large stems. Despite the comparatively small diameter of *Piptocalyx* stems, however, ray cells are predominantly procumbent and thus do not show any evidence of juvenilism. Perhaps vines show accelerated adolescence in ray cell types, although the large size of rays can be said to betoken retarded breakup of large rays in vines, and thus retarded rather than accelerated adulthood could be claimed. However, as noted below, larger rays in vines represents an adaptive feature regardless of whether or not it can be termed juvenilistic.

The ray cells of *T. neocaledonica* and *P. moorei* prove to be notably rich in starch grains. This fact may be related to seasonality in flowering
and fruiting, as well as the tendency for shoots to leaf out in a series of growth events rather than in a continuous fashion.

The indices "vulnerability" and "mesomorphy" (Carlquist 1977) have proved quite useful (Carlquist 1980). In Trimeniaceae, the vulnerability ratio is quite high (P. moorei, 1.13; T. neocaledonica outer wood, 5.2; inner wood, 0.83; T. papuana, 1.75; T. weinmanii, 1.18, 1.15). The mesomorphy values are correspondingly high (P. moorei, 1708; T. neocaledonica outer wood, 4804; inner wood, 552; T. papuana, 2356; T. weinmanii, 1.18, 1.15). These figures show an increase for vulnerability and mesomorphy from the inside to outside of the stem in T. neocaledonica. Where inner and outer wood of a large stem are compared, an increase of this sort is often found; young stems have wood apparently more xeromorphic than that of older stems. In part, the greater apparent mesomorphy of outer portions of stems may represent accommodation to greater rates of conduction when the plant has a larger crown of foliage, more exposed to sunlight. The mesomorphy values for Trimenia are exceptionally high. If one compares values for Trimenia with those for a large genus distributed in various habitats, Pittosporum (Carlquist 1981), this is dramatized. Species of Pittosporum with mesomorphy values as high as those of Trimenia collections are found in the rain forests of Fiji, the Solomon Islands, and the Philippines—notably mesic localities much like those where Trimenia occurs. In New Caledonia, T. neocaledonica is restricted to the Panié-Ignambi-Colnett massif of northern New Caledonia, the wettest region of that island. Thus, correlations between vulnerability and mesomorphy indices for particular species and habitats occupied by those species continue to be very close. Within the genus Trimenia, T. papuana rates high in these index values, a fact which seems corroborated by the greater number of bars per perforation plate in that species.

Because Piptocalyx is scandent, it offers an excellent opportunity to compare the wood anatomy of a vining genus to that of a non-vining genus which is its closest relative. To be sure, Piptocalyx may be regarded as an incipient vine, not so highly pronounced in this habit as other vines one might cite, such as Vitis or Akebia. However, a marked difference is in figures between quantitative wood features of Piptocalyx and the species of Trimenia grouped (omitting inner wood of T. neocaledonica) is evident. Vessel diameter in Piptocalyx is 102 µm (mean in Trimenia, 72 µm), vessels per mm² = 63 (mean in Trimenia, 42). Thus the average conductive area per mm² is 0.16 mm² in Piptocalyx, compared to 0.05 mm² in Trimenia. Thus there is a threefold increase in conductive capacity in Piptocalyx compared to Trimenia. Another accommodation to increased conductive rates is represented by the low number of bars per perforation plate in Piptocalyx (8.7) as compared
with the combined collections of *Trimenia* (36.5). The reduced number of bars on plates of *Piptocalyx*, combined with greater area of perforation plates in that genus (a function of greater vessel diameter) means that each perforation in *Piptocalyx* is, on the average, much larger than each perforation in *Trimenia*, and thus plates in *Piptocalyx* have much less friction. The gains in conductive rate potential in *Piptocalyx* may be regarded as compensatory for the smaller area of a typical liana stem as compared to a typical tree or shrub stem which supports the equivalent amount of foliage. Obviously in a vine or liana, the transsectional area devoted to mechanical tissue (imperforate tracheary elements usually) is lowered, compared to the area of mechanical tissue in tree or shrub wood. In *Piptocalyx* this is true as a result of the higher area devoted to vessels (ray tissue is roughly comparable). Lowered mechanical strength in *Piptocalyx* mechanical tissue is also seen in the thinner walls of fiber-tracheids (3.4 µm, compared to 4.5 µm in *Trimenia*).

Also probably related to the scandent habit of *Piptocalyx* is that the rays are taller and wider than in *Trimenia*. Vines tend to have a cable-type construction in which flexibility is enhanced by presence of soft-walled rays between the relatively hard fascicular areas.

Presence of idioblastic mucilage cells in *Piptocalyx* rays is probably related to the large size of those multiseriate rays, as compared to multiseriate rays in *Trimenia*. Mucilage cells also occur in phloem rays and in secondary phloem of *Piptocalyx*. In all of these locations, mucilage cells represent enlargement of parenchyma cells. The occurrence of mucilage in parenchyma cells of *Piptocalyx* rather than in fiber-tracheids (as in *T. necaledonica*) may be related to minimal development of fiber-tracheids in stems of *Piptocalyx*.

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Address of the author: Dr. SHERWIN CARLQUIST, Rancho Santa Ana Botanic Garden, Claremont, CA 91711, U.S.A.