Wood Anatomy of Akaniaceae and Bretschneideraceae: 
a Case of Near-identity and its Systematic Implications

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ABSTRACT. Wood anatomy is described in detail for the single-species families Akaniaceae and Bretschneideraceae, placed close together in most phylogenetic systems. Both families have simple perforation plates with occasional scalariform plates, alternate lateral wall pitting, helical sculpturing on vessel walls, septate fibers with pits simple or nearly so, scanty vasicentric axial parenchyma, and wide tall multiseriate rays composed mostly of procumbent cells. Differences between the genera are relatively few and minor compared with resemblances; close relationship is indicated. Wood anatomy of the two families resembles that of Sabiaceae and, to a lesser extent, that of other Sapindales. The wood is distinctive within Capparales whether that order is defined traditionally or in the light of molecular studies. Wood data are compatible with an interpretation that Akaniaceae and Bretschneideraceae diverged from near the base of Sapindales.

The families Akaniaceae and Bretschneideraceae, each with a single species, have been placed next to each other in Sapindales (including Rutales of some authors) by Dahlgren (1980), Cronquist (1981), and Thorne (1992); Takhtajan's (1987) treatment includes them in Sapindales with only a single family (Melianthaceae) intervening between them. The families differ in that Akaniaceae have hypogynous flowers and are alleged to lack myrosin cells (which are usually thought to contain glucosinolate compounds), whereas Bretschneideraceae have perigynous flowers and myrosin cells (Cronquist 1981). Although Akania may lack myrosin cells, both families contain glucosinolates (Ettlinger and Kjaer 1968); some families that contain glucosinolates apparently lack myrosin cells (Metcalfe and Chalk 1950) but all possess some portion of this chemical syndrome. Recently, similarity in embryology between Akaniaceae and Bretschneideraceae has been demonstrated (Tobe and Peng 1990; Tobe and Raven 1995).

The glucosinolate-bearing families, once scattered among seven orders (Batales, Capparales, Celastrales, Euphorbiales, Geraniales, Sapindales, and Violales; Cronquist 1981), were included in an expanded Capparales by Dahlgren (1980) on the basis of certain character distributions and then by Rodman (1991a, b), on the basis of phenetics and cladistics. Excluded from Dahlgren's (1980) revised Capparales were the glucosinolate families Caricaceae and Pentadiploandraceae (often placed in Violales), as well as Bretschneideraceae (usually included in Sapindales). Drypetes, alone among Euphorbiaceae, has been reported to possess glucosinolates, but no author has suggested that either Drypetes or Euphorbiaceae as a whole is close to the other glucosinolate families. The arrangement of Dahlgren (1980) was altered on the basis of molecular data by Gadek et al. (1992), Rodman et al. (1993), Rodman et al. (1994) and Conti et al. (1996), who find that a monophyletic clade is formed by the families Akaniaceae, Bataceae, Brassicaceae, Bretschneideraceae, Capparaceae, Caricaceae, Gyrostemonaceae, Koeberliniaceae, Limnanthaceae, Moringaceae, Resedaceae, Tovariaceae, and Tropaeolaceae. Outgroups relatively close to these glucosinolate families include Geraniales, Myrtales, and Sapindales, according to the data of these papers.

The intriguing redefinition of the glucosinolate families (which might tentatively still be termed Capparales) by Rodman et al. (1993), Rodman et al. (1994), and Conti et al. (1996) invites comparison of their cladograms with data from wood anatomy. I have examined wood of Bataceae (Carlquist 1978), Brassicaceae (Carlquist 1971), Gyrostemonaceae (Carlquist 1978), Tovariaceae (Carlquist 1985), and Limnanthaceae and Tropaeolaceae (Carlquist and Donald 1996). Numerous papers contain data on wood anatomy of Capparaceae (see Gregory 1994). Wood descriptions have been furnished for Koeberliniaceae (Gibson 1979) and Salvadoraceae (den Outer and van Veenendaal 1981). I plan papers on wood anatomy of other glucosinolate families to supplement this picture. Some information on wood anatomy has been offered for Akaniaceae by Dadswell and Record (1936), Heimsch (1942), Ilic (1991), and for Bretschneideraceae by Cheng (1980),
Cheng et al. (1992), Heimsch (1942), Luo (1989), and Tang (1935). The present account is offered as a way of offering supplementary quantitative and qualitative data, using both light microscopy and scanning electron microscopy (SEM). The material of Bretschneidera studied by Heimsch (1942) was from a twig, and thus may represent juvenile wood expressions. By placing descriptions of the woods of Bretschneidera and Akania together, the idea that they are closely related, common to both traditional phylogenetic systems as well as those based on molecular data (e.g., Rodman et al. 1994), can be assessed.

Data on wood anatomy are of particular interest because there are such diverse growth forms (trees, shrubs, stem succulents, annuals) among the glucosinolate families. The cladogram of Rodman et al. (1994) places Tropaeolaceae basal to Akaniaceae and Bretschneideraceae, thereby offering the intriguing possibility, acknowledged by those authors, that there may have been marked shifts in habit during the hypothesized divergence of the herbaceous family Tropaeolaceae from the arboreal sister-families Akaniaceae and Bretschneideraceae. The nature of wood anatomy of these families should be considered in connection with the hypothesized shift in habit from herbaceous to woody hypothesized by Rodman et al. (1994).

Some degree of divergence of Akaniaceae and Bretschneideraceae in wood anatomy would be expected because of the marked geographical separation of the two families. Akania bidwillii (Hogg) Mabb., formerly known as A. hillii Hook. f. and A. lucens (F. Muell.) Airy-Shaw, is the sole species of Akaniaceae and is native to southeastern Australia (Cronquist 1981). Bretschneidera sinensis Hemsl., the only species of Bretschneideraceae, occurs in China and Taiwan (Lu et al. 1986).

**RESULTS**

**Akania bidwillii** (Fig. 1–8). Growth rings inconspicuous, most latewood vessels only slightly narrower than earlywood vessels. Vessels solitary or in small clusters or multiples (Fig. 1), mean number of vessels per group = 1.74. Vessels rounded in transsectional outline. Vessels mostly with simple circular to elliptical perforation plates; a few perforation plates basically scalariform but with numerous aberrations (interconnections between bars) present (Fig. 3). Vessel to vessel pitting alternate, pits about 5 µm in diameter (Fig. 5). Inconspicuous grooves interconnecting pit apertures (coalescent pit apertures) present on vessel walls (Fig. 5, below; Fig. 6). Vessel to axial parenchyma pitting (Fig. 8) and vessel to ray pitting scalariform or transitional. Mean vessel diameter, 82 µm. Mean vessel wall thickness, 2.5 µm. Mean number of vessels per mm², 63. Mean vessel element length, 730 µm. Imperforate tracheary elements with very small inconspicuous borders (Fig. 7), the borders visible in face view and in transections. The imperforate tracheary elements mostly septate one to three times each, and thus are septate fibers. Mean wall thickness of septate fibers length of septate fibers, 1488 µm. Axial parenchyma scanty paratracheal (vasentric) with a few terminal cells at ends of growth rings. Axial parenchyma in strands of 4–8 (mostly 5) cells. Ray cells multiseriate (Fig. 2), heterocellular, composed mostly of procumbent cells, with upright cells at

**MATERIALS AND METHODS**

Wood samples were obtained from xylaria (wood sample collections). The Forestry Commission of New South Wales provided the samples of Akania bidwillii (SFCw-D10096). The Samuel J. Record collection of the U. S. Forest Products Laboratory supplied the wood samples of Bretschneidera sinensis (SJRw-21841, 22016). Locality data for these samples were not available for these specimens other than their country of origin (Australia and China, respectively).

Sections were prepared on a sliding microtome and stained with a safranin-fast green combination (Carlquist 1978). A few radial sections of *Bretschneidera sinensis* wood were left unstained and were examined with SEM. Macerations were prepared with Jeffrey's Fluid and stained with safranin (Carlquist 1985).

Vessel diameter is measured as lumen diameter; an attempt is made to estimate the average diameter of each vessel (e.g., the average between widest and narrowest diameter), since that average would be the most significant measurement with respect to conductive capacity of a vessel. Terms are according to the IAWA Committee on Nomenclature (1964). The ray types of Kribs (1935) have been accepted here. The term "imperforate tracheary elements" is used in a wide sense, including the range from tracheids to libriform fibers, because of the continuous nature of this range and because this usage is common among recent authors on wood anatomy. Scale bars in all Figs. represent 10 µm units.
Figs. 1–4. Wood sections of Akania bidwillii. 1. Transection; margin of growth ring across middle of photograph. 2. Tangential section; multiseriate rays tall, wide, uniseriate rays absent. 3. Aberrant scalariform perforation plate from radial section. 4. Transection, growth ring margin vertically down the middle of the photograph. Two rhomboidal crystals shown in the ray cells. Figs. 1–2, scale above Fig. 1; Fig. 3, scale above Fig. 3; Fig. 4, scale above Fig. 4; divisions in all scales = 10 μm.
FIGS. 5–8. Details of wood of *Akania bidwillii*. 5. Alternate vessel to vessel pitting from vessel in radial section; grooves interconnecting pit apertures evident as pale diagonal streaks between pits in lower half of photograph. 6. Portion of vessel wall from radial section to show diagonal grooves interconnecting pit apertures. 7. Pits on septate fibers from radial section; septa out of focus above right and below left. 8. Scalariform and transitional vessel to axial parenchyma pitting from radial section. Figs. 5–8, scale as in Fig. 3.
the tips of rays and as sheathing cells on sides of rays (Fig. 2, arrow). Ray cells radially shorter at margins of growth rings (Fig. 4, center). Ray cell wall thickness about 1.8 μm. Pits in ray cells nearly all simple. Mean height of multiseriate rays, 2,793 μm. Mean width of multiseriate rays at widest point, 7.1 cells (range: 3–10). Wood nonstoried. Rhomboidal crystals are present singly in occasional ray cells (Fig. 4, arrows).

Occasional perforation plates that are near-scalariform in disposition of bars, grooves in vessel walls, and crystals in ray cells are three features newly reported for Akania. In other respects, features in the above description are very similar to those reported by Heimsch (1942). The ray type of Akania is not really referable to any of the ray types of Kribs (1935). Multiseriate rays are heterocellular with elongate tips and therefore correspond to Heterogeneous Type IIA, but uniseriate rays are absent in Heterogeneous Type II of Kribs (1935). This condition has been reported in Sabiaceae (Carlquist et al. 1993).

**Bretschneidera sinensis** (SJRw-22016) (Figs. 9–18). Wood with inconspicuous growth rings (Figs. 9, 11). Latewood vessels slightly narrower than earlywood vessels (compare Fig. 11, below center, with Fig. 11, above center). Vessels solitary or in clusters, mean number of vessels per group = 1.96. Vessels rounded in transsectional outline. Perforation plates mostly simple; occasional scalariform perforation plates present, the bars sometimes fused (Fig. 15). Lateral walls of vessels with pits alternate or opposite (Fig. 12), about 6 μm in vertical diameter. Helical thickenings present on vessel walls (Figs. 13, 14). Thickening slender, occasionally anastomosing (Fig. 13, upper left) and sometimes with shallow grooves between thickenings in close pairs (Fig. 14). Mean vessel diameter, 81 μm. Mean number of vessels per mm², 87. Mean vessel element length, 624 μm. Imperforate tracheary elements have simple pits and septate once or twice (Fig. 16). Mean wall thickness of septate fibers, 6.0 μm. Mean length of septate fibers, 1,182 μm. Axial parenchyma scanty paratracheal (vasicentric) and terminal. Vessel to axial parenchyma pitting scalariform. Vessel to ray pitting scalariform, transitional, or opposite (Figs. 17, 18). Rays multiseriate and uniseriate (Figs. 9, 10, 11), Heterogeneous Type IIA of Kribs (1935), tip cells and some sheathing cells of multiseriate rays upright, all cells of uniseriate rays upright; ray cells otherwise procumbent (Fig. 10). Ray cell wall thickness varied (Fig. 18), mostly about 3.0 μm. Borders present on pits of tangential walls of ray cells (Fig. 18, arrows). Mean height of multiseriate rays, 1,654 μm. Mean width of multiseriate rays at widest point, 5.8 μm. Mean height of uniseriate rays, 173 μm. Wood nonstoried. No crystals observed. Ray cells and axial parenchyma cells with dark-staining contents (Figs. 10, 11).

Heimsch is correct in saying that scalariform perforation plates are only occasional in Bretschneidera, whereas the description of Tang (1935) suggests that scalariform perforation plates are characteristic in the species. Heimsch (1942) calls the imperforate tracheary elements (which he observed in twig material) fiber-tracheids, but I was unable to locate any borders on pits of imperfect tracheary elements. Otherwise, my descriptions agree with those of Heimsch (1942). Terminal parenchyma may not be present in the ordinary sense; it may be vasicentric parenchyma associated with the small latewood vessels. Borders on ray cell pits of Bretschneidera are newly reported.

**DISCUSSION**

**Resemblances Between Woods of Akania and Bretschneidera.** Some features in the above descriptions are widespread in wood of dicotyledons (e.g., scanty paratracheal axial parenchyma) and thus are not likely to be synapomorphies for the two families. However, other features are not common (perforation plates predominantly simple but scalariform plates occasional in mature secondary xylem) and are likely synapomorphies for at least the two families, and possibly some closely related families as well. The list of features in which Akania and Bretschneidera woods agree is surprisingly extensive. This list includes inconspicuous growth rings, occasional perforation plates with bars numerous but often in aberrant arrangements, vessel to vessel lateral wall pitting predominantly alternate, vessel to axial parenchyma pitting scalariform, vessel to ray pitting scalariform to opposite, vessels relatively long, imperforate tracheary elements all septate fibers with borders very vestigial or absent, axial parenchyma scanty paratracheal (possibly with a few terminal cells in growth rings) in strands of 4–5 cells, multiseriate rays tall and composed predominantly of procumbent cells, wood nonstoried and with sparse dark deposits in cells.

Akania and Bretschneidera differ in minor ways. Vessel to vessel pitting is alternate in Akania, but is sometimes alternate, sometimes opposite in
Figs. 9–12. Wood sections of Bretschneidera sinensis (SJRw-22016). 9. Transection; growth ring terminus about ½ the distance from the top of the photograph, where rays widen. 10. Tangential section; in addition to wide, tall multiseriate rays, several uniseriate rays are visible. 11. Transection to show nature of latewood: a layer of terminal axial parenchyma is present at the end of the growth ring, middle, just below the wide vessels. 12. Vessel-to-vessel pitting from radial section; opposite pitting is shown. Figs. 9, 10, scale above Fig. 1; Fig. 11, scale above Fig. 4; Fig. 12, scale above Fig. 3.
FIGS. 13–16. Wood details of *Bretschneidera sinensis*. 13–14. Helical thickenings from vessels of radial sections (SJRw-22016). 15. Portion of a scalariform perforation plate from radial section (SJRw-21841). 16. Septate fibers from radial section (SJRw-22016). Figs. 13–15, bars = 10 μm; Fig. 16, scale above Fig. 3).
Bretschneidera. Bretschneidera has helical thickenings on vessel walls, whereas in Akania vessels there are grooves interconnecting pit apertures; these two features might be homologous; however, they can co-occur in some families of dicotyledons, such as Asteraceae (Carlquist 1966). The pits of Akania septate fibers are vestigially bordered, whereas I was unable to find any borders on pits of septate fibers in Bretschneidera. Bretschneidera has uniseriate rays, Akania lacks them. Crystals were observed in rays of Akania but not in those of Bretschneidera. When one compares these differences in character states (some of which are merely differences of degree) to resemblances between the two genera, one finds the similarities much more numerous, and many resemblances are features not widespread in dicotyledons, so that the resemblances are likely not all homoplasies. The differences between the two genera are of a kind and degree one can easily find within a family or even within a genus such as Meliosma (Carlquist et al. 1993). Akania and Bretschneidera are similar even in quantitative features.

Resemblances of Akania and Bretschneidera. Conceding that woods of Akania and Bretschneidera, respectively, are close to each other, does the wood of this family pair resemble that of the other glucosinolate families? Because relevant monographs of some of these families are not at hand, conclusions based on an adequate data base must await further studies. Even so, analysis will not be easy, because differences attributable to habit (e.g., stem succulence of Caricaceae; herbaceousness of Tropaeolaceae) mostly do not indicate phyletic relationship.

Do the wood patterns of Akania and Bretschneidera support the idea, widely held by several leading phylegenists, that these two genera are sapindalean or at least not far from Sapindales? If one excludes Sabiaceae from Sapindales, a number of wood features common to Akania and Bretschneidera contrast with those of most but not all Sapindales.
The wide, tall rays of *Akania* and *Bretschneidera* differ from the rays of most sapindalean families, which have relatively narrow multiseriate rays. A scattering of Aceraceae and Anacardiaceae have rays that are of medium width, but these do not approach the rays of *Akania* and *Bretschneidera* in width (Heimsch 1942; Metcalfe and Chalk 1950). Interestingly, occasional scalariform perforation plates, reported here for both *Akania* and *Bretschneidera*, have been reported for 10 genera of Rutaceae, two genera of Anacardiaceae, and for the latewood of *Ailanthus* of the Simaroubaceae (Metcalfe and Chalk 1950). Fabaceae are now regarded as a family of Sapindales (e.g., Thorne 1992). Such a large family might be expected to have such a wide range of character state expressions that matches of character states with those of *Akania* and *Bretschneidera* could be found, but these are more likely homoplasies than synapomorphies with *Akania* and *Bretschneidera* (e.g., helical thickenings in vessels). Such features of those two genera as septate fibers, imperforate tracheary elements with vestigial or simple pits and scanty vasicentric axial parenchyma can be found widely in Sapindales, but without phylogetic analysis, one must assume the possibility that these features are synapomorphies.

However, wood anatomy of Sabiaceae (Carlquist et al. 1993) offers more numerous similarities than do other families placed in Sapindales. Sabiaceae are often regarded as near Sapindales (e.g., Thorne 1992), so they might be expected to retain some features seen in *Akania* and *Bretschneidera* if this family pair and Sapindales had a common ancestry. One can neglect Sabia in this comparison because *Sabia* is a liana and thus wood of the arboreal *Meliosma* is more pertinent for comparison. Notable in *Meliosma* is occurrence of scalariform perforation plates, characteristic of some species, whereas others have only simple plates and some have both simple and scalariform perforation plates (Carlquist et al. 1993). The multiseriate rays of *Meliosma* are Heterogeneous Type IIA and often wide, as in *Akania* and *Bretschneidera*, and in some species of *Meliosma*, as in *Akania*, uniseriate rays are lacking. Hexagonal crystals, formed singly per cell, are found in *Meliosma*, as they are in *Akania*. Features more commonly found in Sapindales, such as septate fibers (with either vestigially bordered of simple pits), scanty vasicentric axial parenchyma, and presence of dark-staining compounds in rays and axial parenchyma, are also resemblances between *Meliosma* and *Akania* and *Bretschneidera* (Carlquist et al. 1993). If, as the cladograms of Rodman et al. (1993) and Conti et al. (1996) indicate, Sapindales may lie close to the glucosinolate families (Capparales in a new and expanded sense), Sabiaceae may deserve attention with respect to features in addition to those from wood anatomy.

**Literature Cited**


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