Wood Anatomy of Aextoxicaceae and Berberidopsidaceae Is Compatible with Their Inclusion in Berberidopsidales

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ABSTRACT. In recent DNA-based cladograms of dicotyledons, Aextoxicaceae (one sp., Chile) and Berberidopsidaceae (three spp., Chile and Australia) form an isolated clade, Berberidopsidales, basal to rosids and asterids. Until recently, Aextoxicaceae had been placed in Euphorbiales, Berberidopsidaceae in Violales. Light microscopy and scanning electron microscopy (SEM) studies of wood of the two families show numerous shared primitive features: perforation plates with numerous bars and extensive pit-membrane remnants, lateral wall pitting of vessels scalariform to transitional, tracheids present; long vessel elements and tracheids, low F/V ratio; diffuse axial parenchyma; and Heterogeneous Type I rays. Features reported for the first time include crystals with various degrees of encapsulation in ray cells (Aextoxicaceae), pit membrane remnants in perforations (Berberidopsis, previously reported in Aextoxicaceae), and presence of narrow latwood vessels the perforation plates of which can bear pit membranes (Berberidopsis). Probable synapomorphies of the two families include marked difference between multiseriate parts (cells procumbent only) and uniseriate parts (cells square to upright), and presence of dark-staining deposits in axial parenchyma and rays. Cladistics does not use symplesiomorphies, which are numerous between the two families, to group closely-related families at clade tips. Ecological and habitat adaptations of woods of the two families are briefly considered.

Aextoxicaceae and Berberidopsidaceae exemplify families the ordinal assignment of which remained stable for decades, but which, with the availability of DNA studies, have been subjected to radical reassigments. The single species of Aextoxicaceae, sole genus of Aextoxicaceae, was considered by most authors (including Takhtajan 1987) to belong to Euphorbiales (see table of treatments of 11 phylogenists in Goldberg 1986). Two authors who demurred include Hutchinson (1973) and Cronquist (1981), who placed Aextoxicaceae in Celastrales. Thorne (1992, 2000) cited Aextoxicaceae as a genus incertae sedis.

A similar history has characterized Berberidopsidaceae. The Gilg (1925) treatment of Flacourtiaceae was modified by Hutchinson (1967), who placed two genera now referable to the family (Berberidopsis and Streptothamnus) along with several other genera in a tribe of Flacourtiaceae. Miller (1975), who stressed the probability that Flacourtiaceae was a polyphyletic and unnatural family, suggested that Berberidopsis (along with the closely related Streptothamnus) should be placed in a family of its own. This action was taken by Takhtajan (1985), who still retained Berberidopsidaceae within Violales along with Flacourtiaceae (Takhtajan 1987). Thorne (2000) considered Berberidopsis a genus incertae sedis.

One of the striking realignments yielded by cladograms in molecular systematic studies was the grouping of Aextoxicaceae and Berberidopsidaceae in a new order, Berberidopsidales (Savolainen et al. 2000, Solits et al. 2000; paired as sister families but without an ordinal name in Nandi et al. 1998). The Berberidopsidales clade, according to these authors, is not close to any other existing order, but is basal to the line leading to asterids and is also close to the base of rosids. The purpose of the present study is to compare wood of Aextoxicaceae with that of Berberidopsis in order to see whether wood anatomy reflects the relationship claimed between the two genera on the basis of molecular data. The single species of Aextoxicaceae, A. punctatum Ruiz & Pav. occurs in central Chile as a tree to 25 m tall "relict in the forest of Fray Jorge and Talinay in Coquimbo... and is found from Colchagua to Chiloe in the mountains" (Rancusi et al. 1987). Takhtajan (1985, 1987) recognized Berberidopsidaceae as a family containing Berberidopsis corallina Hook.f. (Chile) and two species of Streptothamnus, S. moorei F. Muell. and S. beckleri F. Muell. (Australia). Veldkamp (1984) and Baas (1984) recognized two species of Berberidopsis by virtue of the transfer of an Australian Streptothamnus species as B. beckleri (F. Muell.) Veldkamp, thereby making Berberidopsis a trans-Pacific genus. A third possibility, inclusion of both Streptothamnus species in Berberidopsis, which thereby would consist of three species, is suggested as a possible treatment by van Heel (1984), who studied seeds and pollen morphology of Berberidopsidaceae. Although Streptothamnus moorei has apparently not yet been recombined as a species of Berberidopsis, Berberidopsis as a genus containing S. moorei as well as the other two species could be termed "Berberidopsis s. l." Regardless of whether Berberidopsis includes one, two, or all three of these species, they are all scendent shrubs of montane forest (for localities, see Veldkamp 1984), a feature of importance, because wood of scendent shrubs has characteristics different from those of self-supporting trees (Carlquist 1985), differences that should not be regarded as phylogenetically significant in the present context.

Twig wood of the Australian species of Berberidop-
sidaceae has been studied by Baas (1984). Miller (1975) studied twig wood of S. moorei, but Miller (1975) studied a mature stem of B. corallina (also studied here), whereas Baas (1984) studied a twig of that species. These materials seem to provide sufficient data for an informative comparison of Berberidopsidaceae with Aextoxicaceae. Wood of Aextoxicacae has been studied on several occasions (see Gregory 1994), but the most complete description is probably that of Rancusi et al. (1987). I have studied mature wood of both A. punctatum and B. corallina by both light microscopy and SEM in order to extract as much systematically useful information as possible. A side-by-side comparison of wood of the two families has not been provided previously.

In any examination of wood anatomy with relation to systematics, wood features that likely are primarily influenced by habit and by ecology must be considered. Although Aextoxicaceae and Berberidopsidaceae share similar ecology, the difference in habit between the two families must be taken into account.

**MATERIALS AND METHODS**

Wood samples were available in dried condition. Data on A. punctatum are primarily from Carlquist 7222 (RSA), 7 km N of Concepción, Chile, on the coast road. Sections of this species from the collection Aw-2483 were also studied. The material of Berberidopsis corallina, F. G. Meyer 9766 (NA), provided by the wood collection of the National Museum of Natural History (as USW-34057) was studied; another portion of this specimen had independently been studied by Miller (1975).

Wood was boiled in water and stored in 50% aqueous ethyl alcohol. Sections were prepared on a sliding microtome Some radial sections were dried between clean slides, mounted on aluminum stubs, sputter-coated, and examined by SEM. Transverse, tangential, and radial sections for study by light microscopy were stained with safranin and fast green and mounted in Canada balsam. Macerations were prepared with Jeffrey’s Fluid and stained with safranin and fast green and mounted in Canada balsam. Sputter-coated, and examined by SEM.

**RESULTS**

**Aextoxicacae (Fig. 1-10).** Growth rings inconspicuous (latwood = bottom third of photograph, Fig. 1); vessels fewer and narrower in latwood, tracheids narrower. Vessels angular in transection (Fig. 1). Mean number of vessels per group, 1.16. Mean vessel lumen diameter, 44 μm. Mean number of vessels per mm², 112. Mean vessel element length, 1357 μm. Mean vessel wall thickness, 2.0 μm. Perforation plates scalariform (Fig. 3, 7-10) with bordered bars, mean number of bars per plate, 66 (range 49-84). Perforations bear various degrees and forms of pit membrane remnants (Fig. 7-10), no perforation plates completely devoid of such remnants; remnants vary from sheetlike (Fig. 7) to weblike (Fig. 8) or threadlike (Fig. 9, 10). Helical thickenings in vessels absent. Mean axial diameter of lateral vessel wall pits, 3.5 μm. Vessel-to-vessel pits (seen on vessel tips) scalariform. Vessel-to-ray pits scalariform to transitional or even alternate. Tracheids present as the sole type of imperforate tracheary element. Pits of tracheids about 3.5 μm in diameter, pit cavities circular in outline, pit apertures narrow and slitlike (Fig. 3, right). Mean tracheid length, 1528 μm. Mean tracheid wall thickness, 4.1 μm. Axial parenchyma diffuse, moderately common. Strands of axial parenchyma composed of 7-10 axially elongate cells. Multiseriate rays more common than uniseriate rays. Central portion of multiseriate rays composed of markedly procumbent cells (Fig. 3, 4) which are notably different from the square to upright cells that compose the uniseriate portion of these rays (Fig. 2, 4). Uniseriate rays composed of upright cells. Some multiseriate rays have uniseriate portions connecting with two or more multiserate portions and are therefore termed interconnected rays (Carlquist 2001).

Mean height of multiserate rays, 1849 μm. Mean width of multiserate rays at widest point, 3.8 cells. Mean height of uniseriate rays, 599 μm. Mean wall thickness of ray cells 1.1 μm, but varying widely. Tangential walls of upright ray cells bear some bordered pits on tangential walls as seen in sectional view (Fig. 6). Crystals present in enlarged upright ray cells (Fig. 4), sometimes in a pair of cells subdivided from an upright cell (Fig. 4, left). Rhomboidal crystals often covered with secondary walls of various thicknesses ("encapsulated crystals"); some ray cells occluded by the secondary walls covering the crystals. Droplets or amorphous deposits of a dark-staining substance common in ray cells (especially procumbent cells (Fig. 1, 2, 4). Starch not observed in wood. Tyloses present in vessels, most tyloses with secondary walls (Fig. 5). Wood nonstoried.

**Berberidopsis corallina (Fig. 11-19).** Growth rings present (Fig. 11), characterized by numerous narrower vessels in latewood (Fig. 11). Vessels circular to oval or angular in outline (Fig. 11). Mean number of vessels per group, 1.04. Mean vessel lumen diameter, 57 μm. Mean number of vessels per mm² 94 (narrow latwood vessels not included). Mean vessel element length, 1490 μm. Mean vessel wall thickness, 2.2 μm. Perforation plates scalariform (Fig. 13, 15-17), bars sometimes anastomosing and variously bordered. Mean number of bars per plate, 24 (range 18-41). Bars tenuous (Fig. 15, right) in wider vessels to wide (Fig. 17) in the narrow vessels or “imperforate vessels.” Pit membranes present in ends of perforations (Fig. 15) or absent (Fig. 16). Membranes present in end-wall pitting (potential
Fig. 1-6. Wood sections of *Aextoxicon punctatum*. 1. Transection, showing narrowness of vessels. 2. Tangential section; upright sheathing cells are absent on the multiseriate portions of multiseriate rays. 3. SEM photograph of perforation plate from radial section; two tracheids at right. 4. Radial section to show crystals (arrows) and difference between upright cells (top, bottom) and procumbent cells (darker) of a multiseriate ray. 5. Radial section; tyloses in vessel in right half of photograph. 6. Tangential wall of upright ray cell from radial section, some pits bordered as shown in sectional view. Fig. 1, 2, scale above Fig. 1 (divisions = 10 μm); Fig. 3, scale bar = 20 μm; Fig. 4, 5, scale above Fig. 3 (divisions = 10 μm); Fig. 6, scale above Fig. 6 (divisions = 10 μm).
Fig. 7-10. SEM photographs of portions of perforation plates of *Aextoxicon punctatum*, to show presence of pit membrane remnants. 7. Laminar portions of pit membranes fill large portions of perforations (disjunction between pit membrane and perforation edge in some is due to tearing). 8. Portions of two perforations to show weblike pit membrane remnants. 9. Pit membrane remnants form coarse threads. 10. Pit membrane remnants form fine threads in some perforations, membrane remnants shrink to knoblike vestiges on the edges of other perforations. Scale bars in Fig. 7, 9, 10 = 10 μm; bar in Fig. 8 = 30 μm.
Fig. 11–14. Wood sections of *Berberidopsis corallina*. 11. Transection, showing wide ray (right), growth ring (latewood ends 1/3 distance from top of photograph). 12. Tangential section, portion of wide ray at left. 13, 14, SEM photographs from radial section. 13. Perforation plate, center, shows some anastomosing bars; inside of vessel, left, shows alternate oval pits. 14. Inside of vessel, showing vessel-ray pitting; tracheid at right. Fig. 11, 12, scale above Fig. 1. Fig. 13, scale bar = 20 μm; Fig. 14, scale bar = 10 μm.
Fig. 15–19. Wood of Berberidopsis corallina. 15–17. SEM photographs of perforation plates from radial section. 15. Perforation plate with pit membrane remnants at ends of bottom four perforations. 16. Portion of perforation plate almost devoid of pit membrane remnants; outside surface of tracheid at left. 17. "Potential" perforation plate of narrow latewood vessel in which pit membranes have been retained. 18. Tip of vessel element from maceration (pp placed over top of perforation plate; h pointer indicates helical thickenings in element tip. 19. SEM photograph of two druses in phloem parenchyma from radial section of stem. Fig. 15–17, 19, scale bars = 20 μm; Fig. 18, scale above Fig. 4.
perforations) of very narrow vessels (Fig. 17), which may perhaps be termed imperforate vessels. Mean axial diameter of vessel lateral wall pit cavities, 6 μm, apertures relatively wide (Fig. 14). Vessel-to-ray pitting scalariform, less commonly transitional to alternate (Fig. 14). Vessel to tracheid pitting composed of axial rows of circular pits. Helical thickenings faint or absent in most portions vessels (most frequently seen on unpitted lateral wall faces), but more prominent in vessel element tips (Fig. 18). The use of the term “helical” may be misleading, because some of the thickenings are mere lines or arcs rather than continuous helices. Tracheids present as the sole imperforate tracheary element type (excepting the few latewood imperforate vessels). Mean tracheid length, 1653 μm. Mean tracheid wall thickness, 3.0 μm. Pit cavities about 6 μm in diameter, apertures narrowly elliptical (Fig. 16, left). Axial parenchyma inconspicuous but present; mostly diffuse, but some cells in contact with rays or vessels. Axial parenchyma strands mostly single, but rarely in groups of two or three cells as seen in transection. Multiseriate rays more common than uniseriate rays; a moderate number of exceptionally wide multiseriate rays present (Fig. 11, right; Fig. 12, portion of wide ray at left). Multiseriate portions of multiseriate rays composed of procumbent cells only, the distal uniseriate portions composed of upright cells. Uniseriate rays composed of upright cells. Both multiseriate and uniseriate rays very tall, accurate measurements not possible because so few rays are entirely contained within the limits of a tangential section. Mean width of multiseriate rays at widest point >10 cells. Crystals absent or else very rare in ray cells, occasional crystal chips seen in ray cells are probably dislodged from crystals elsewhere in the stem; small druses common in parenchyma of secondary phloem (Fig. 19). Droplets or amorphous deposits of dark-staining material common in rays (especially procumbent cells). Starch present in some procumbent ray cells. Tyloses present, but infrequent. Wood nonstoried.

**DISCUSSION**

Using the description by Rancusi et. al. (1987) as a baseline for wood of *Aextoxiciscorallina* as a baseline, features are newly reported here for *B. corallina*: growth rings present, with numerous narrow vessels (some apparently imperforate) in latewood, pit membrane remnants present in at least some perforations, bars in perforation plates nonbordered and tenuous to bordered and moderately wide, wall thickenings present in vessel tips and on some nonpitted lateral wall areas, bordered pits present on some tangential walls of upright ray cells; dark-staining depaosits present in axial parenchyma and ray cells, and starch present in ray cells. Baas (1984) reported axial parenchyma in Berberidopsidaceae without mentioning whether it was seen in one or all three species of the family. Axial parenchyma was not reported in wood of *B. corallina*.

Differences in wood anatomy of Aextoxicaceae and Berberidopsidaceae are very few. Crystals are present in rays of *A. punctatum* but absent in rays of Berberidopsidaceae although present elsewhere in stems of the three species of the family according to Baas (1984). However, Miller (1975) reported infrequent crystals in rays of *Streptothamnus moorei*. Helical thickenings may be found in vessels of *B. corallina*, but are absent in other species of Berberidopsidaceae (Miller 1975; Baas 1984). Thus, the only differences that can be cited do not apply to all Berberidopsidaceae. I do not regard the wider vessels with fewer bars per perforation plate and the wider rays in Berberidopsidaceae (as compared to Aextoxicaceae) as systematic differences between the two families, because these features relate to habit (see below).

Similarities between wood of the two families are, on the contrary, numerous: presence of long vessel elements with long end walls bearing scalariform perforation plates with numerous bordered bars and pit membrane remnants in at least some perforations; scalariform to transitional lateral wall pitting on vessels; angular outline of vessels as seen in transection; low degree of vessel grouping (related to presence of tracheids and not an independent feature: Carlquist 1984a); imperforate tracheary elements all tracheids with fully bordered pits; low F/V ratio; axial parenchyma diffuse; rays Heterogeneous Type I, tall. All of the features listed here are considered primitive in dicotyledons (for criteria, see Carlquist 2001). Synapomorphies are useful for indicating degree of relationship of genera within families, or families within or-
ders. There is one notable resemblance between wood of the two families that would have to be interpreted as a synapomorphy: the marked differentiation between the strongly procumbent cells of the multiseriate portions of multiseriate rays and the square to upright cells of the uniseriate portions of multiseriate rays. The multiseriate portions of multiseriate rays almost invariably are sheathed by at least a few upright cells in dicotyledons (Kribs 1935). Presence of crystals in rays and presence of dark-staining material in rays are shared features of the two families, but they occur in so many dicotyledons that they may well be homoplasy by most workers. Presence of tyloses and presence of inconspicuous growth rings are almost certainly parallelisms throughout dicotyledons.

If one views other vessel-bearing dicotyledons with highly primitive wood (e.g., Cornaceae, Hamamelidaceae, Illiciaceae) like that of the two families, one finds synapomorphic character states that may be small in number but are clearly character states of features different from those shared by the two families of Berberidopsidales (notably pollen morphology and ultrastructure; Walker 1976). Therefore, the primitive features of Berberidopsidales can be used to distinguish the order from other orders with a large number of primitive features. Wood anatomy can be of some use as a phylectic indicator even in groups with primitive woods. However, in groups with highly primitive wood, molecular data will very likely be especially valuable in assessing relationships.

The tribe Berberidopsideae of Flacourtiaceae as recognized by Miller (1975) contains a number of genera other than Berberidopsis and Streptothamnus, although Veldkamp (1984) restricts the tribe to those two genera and Veldkamp's tribe was converted into Berberidopsidaceae by Takhtajan (1975). Is there evidence from wood anatomy for exclusion of various genera of Flacourtiaceae from Berberidopsidaceae? Conceding that Flacourtiaceae is now no longer a tenable family (the name Salicaceae takes precedence for the new family that includes some of the traditional Flacourtiaceae), and subtracting the three species of Berberidopsidaceae from Flacourtiaceae, the remaining Flacourtiaceae (sensu Gilg 1925) have fiber-tracheids or libriform fibers rather than tracheids, they lack axial parenchyma, and they have upright cells sheathing the multiseriate portions of multiseriate rays (Miller 1975). Most genera of Flacourtiaceae have simple perforation plates, a few mixed simple and scalariform plates, and a small number of scalariform plates only. These differences between Berberidopsidaceae and Flacourtiaceae s. s. may be few in number, but they are important, particularly in view of the highly heterogeneous nature of Flacourtiaceae, which will undoubtedly be subdivided into several families (Miller 1975). Molecular data now place Flacourtiaceae in Malpighiales, well away from Berberidopsidales (e.g., Soltis et al. 2000). However, only a few genera of Flacourtiaceae have been included in these studies, and more molecular data are likely to refine the groupings.

The antiquity of Berberidopsidales is suggested by the fact that although Aextoxicon is restricted to Chile, Berberidopsidaceae are split between Chile and Australia (Veldkamp 1984). In this respect, Berberidopsidaceae resemble families represented in Chile but with trans-Pacific localities also, such as Cordiariaceae, Cupressaceae, Donatiaceae, Gunneraceae, Nothofagaceae, Lardizabalaceae, Stylidiaceae, and Winteraceae.

Primitive dicotyledons are nearly all found in habitats that could be considered moist or highly mesic (Carlquist 1975). One can calculate a Mesomorphy Ratio for dicotyledon woods (vessel diameter times vessel element length divided by vessels per mm²). The values obtained here were Aextoxicon punctatum (533) and Berberidopsis corallina (903). These figures typify dicotyledons of cloud forest or other moist forest types, judging by the species with such values in families that occupy a diverse range of ecological situations, such as Pittosporaceae (Carlquist 1981) and Solanaceae (Carlquist 1992b). Vessel elements have greater average lumen width in Berberidopsis corallina (57 μm) than in Aextoxicon punctatum (44 μm), although the difference is not a great one. Mean number of bars per perforation plate is fewer in B. corallina (24) than in A. punctatum (66). These differences are consistent with quantitative data for vessel elements in families with characteristically scalariform perforation plates that contain both scandent and nonscandent genera, such as Trimeniaceae (Carlquist 1994b) and Dilleniaceae (Metcalfe and Chalk 1950), in which vessel elements of the nonscandent genera are narrower and have fewer bars per perforation plate.

Accelerated loss of bars per perforation plate in scandent species as compared to their nonscandent relatives (Carlquist 1975) is shown by comparison of Berberidopsidaceae with Aextoxicaceae. In addition, the notably wide and tall rays of Berberidopsis, and the dimorphism in vessel diameter of Berberidopsis are features typical of lianas as compared to nonscandent relatives (Carlquist 1984b, 1985).

LITERATURE CITED


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