WOOD AND STEM ANATOMY OF RHABDODENDRACEAE IS CONSISTENT WITH PLACEMENT IN CARYOPHYLLALES SENSU LATO

by

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SUMMARY

Qualitative and quantitative data are given for two species of Rhabdodendron. Newly reported for wood of the family are vestured pits in vessels and tracheids, nonbordered perforation plates, abaxial axial parenchyma, and presence of sphaerocrystals. Although treated variously in phylogenetic schemes, Rhabdodendron is placed in an expanded Caryophyllales in recent cladograms based on molecular data. This placement is consistent with features characteristic of most families of the order, such as nonbordered perforation plates and successive cambia. Primitive character states in Rhabdodendron (tracheids, diffuse axial parenchyma, ray type) are shared with Caryophyllales s.l. that branch near the base of the clade: Agdestis, Barbeuia, Simmondsia, and Stegnosperma. Presence of vestured pits in vessels and silica bodies in wood, features not reported elsewhere in Caryophyllales s.l., are shared by Rhabdodendron and Polygonaceae. Wood of Rhabdodendron has no features not found in other Caryophyllales, and is especially similar to genera regarded as closely related to it in recent phylogenetic hypotheses. Successive cambia that are presumably primitive in the clade that includes Rhabdodendron are discussed. Distinctions between sphaerocrystals and druses are offered.

Key words: Caryophyllales, druses, perforation plates, Rhabdodendron, sphaerocrystals, vestured pits, successive cambia.

INTRODUCTION

Rhabdodendraceae consist of a single genus, Rhabdodendron, which contains two or possibly three species of shrubs from tropical America (Prance 1968; Thorne 1992). The affinities of Rhabdodendraceae have been controversial, and families claimed to be related include Rutaceae, Chrysobalanaceae, and Phytolaccaceae (for a review, see Prance 1968). After surveying these possibilities, Prance opted for a caryophyllalean position for Rhabdodendraceae, although various workers disagreed (Cronquist 1981; Thorne 1992). However, in recent years, cladograms based on DNA data have placed Rhabdodendraceae in Caryophyllales (Lledó et al. 1998; Soltis et al. 2000). Note should be taken that Caryophyllales sensu stricto (see Thorne 1992 or Cronquist 1994) has now been expanded (Williams et al. 1994; Fay et al. 1997; Soltis et al. 2000) so as to include Ancistrocladaceae, Droseraceae, Frankeniaceae, Nepenthaceae, Plumbaginae,
ceae, Polygonaceae, Simmondsiaceae, and Tamaricaceae (this resultant larger order termed Caryophyllales s.l. here).

Data on wood anatomy often reflect the systematic position of a given group of dicotyledons. In view of the diverse placements claimed for Rhabdodendraceae, data on wood anatomy, as well as other data sets, are of especial interest. However, one must also take into account that Rhabdodendraceae are shown to branch from near the base of the caryophyllalean clade, and thus comparison to presumptively more specialized Caryophyllales is not as phylogenetically informative as comparison to families close to the root of the clade.


Successive cambia are present in *Rhabdodendron amazonicum* (Benth.) Huber, but apparently absent in *R. macrophyllum* (Spruce ex Benth.) Huber (Heimsch 1942). Successive cambia are widespread in Caryophyllales s.s. (Metcalfe & Chalk 1950), raising the question of whether the feature is a plesiomorphy or an apomorphy in that clade. In families that branch from near the base of Caryophyllales s.l. (Lledó et al. 1998; Soltis et al. 2000) – Plumbaginaceae, Polygonaceae, Rhabdodendraceae, Simmondsiaceae – successive cambia are present in at least one genus per family. The possibility is thereby raised that the capability to form successive cambia might be ancestral to at least most Caryophyllales s.l. In any case, each genus with successive cambia offers some information on the histological aspects of this feature. Authors differ considerably with respect to terminology and interpretation of successive cambia, their origin and products. Each study of a genus with this cambial variant contributes to clarification of how successive cambia originate and produce derivatives.

MATERIALS AND METHODS

Data on *Rhabdodendron amazonicum* are based on a set of slides given me by Dr. Charles Heimsch, a duplicate set of slides from his thesis work. The wood samples of this species studied are Y-21237 and Y-23601 (these would now be represented by the SJRw collections in the Forest Products Laboratory, Madison WI; “Brazil”, Ducke 25466). These sections were stained with safranin. The wood sample of *R. macrophyllum* was derived from a branch on an herbarium specimen, Prance 23549, km 16, Manaus-Itacoatiara, Amazonas, Brazil (RSA).

The stems of *R. amazonicum* were treated with hydrofluoric acid prior to sectioning. Sections were stained with safranin. I sectioned wood of *R. macrophyllum* with a sliding microtome without prior softening in order to preserve cellular contents, espe-
cially silica bodies, despite the tearing inevitably involved. These sections were stained with a safranin-fast green combination. Some radial and tangential sections were studied with an ISI WB-6 scanning electron microscope (SEM) (Fig. 9 & 10), others with a Bausch & Lomb Nanolab SEM (Fig. 11–14). The stem diameter of the *R. macrophyllum* specimen studied was 1.5 cm. Macerations were prepared with Jeffrey’s solution and stained with safranin.

Vessel diameter is measured as lumen diameter. For a vessel oval in transection, the wide and narrow chords were averaged. Terms are used in accordance with the IAWA Committee on Nomenclature (1964), except for the terms successive cambia and conjunctive tissue, which accord with definitions in Cariquist (1988). The number of vessels per mm² in *R. amazonicum* was determined by excluding conjunctive tissue and phloem from the transection areas surveyed.

**RESULTS**

*Rhabdodendron amazonicum*, Y-21237 (Fig. 1–6). Growth rings absent (Fig. 1). Vessels mostly solitary (Fig. 1), mean number of vessels per group, 1.07; mean lumen diameter, 75 μm; mean wall thickness, 2.3 μm; mean number of vessels per mm², 2.13. Mean vessel element length, 430 μm. Perforation plates simple, perforation plates nonbordered. Lateral wall pitting of vessels composed of oval pits 4 μm in axial diameter; pit apertures slit-like, vestured. Grooves interconnect two or more pit apertures. Imperforate tracheary elements are all tracheids, with pit cavities circular in outline and 4 μm in diameter (Fig. 5, 6), the pits markedly bordered (Fig. 5, arrow; Fig. 6). Tracheid pit apertures vestured. Mean tracheid length, 1036 μm; mean wall thickness, 5 μm (Fig. 5). Axial parenchyma sparsely diffuse (vertical arrow, Fig. 3), but mostly paratracheal, usually abaxial in distribution (horizontal arrow, Fig. 3), in strands of two to three cells. Multiseriate rays about as common as uniseriate rays (Fig. 4). Rays conform to Heterogeneous Type IIA of Kribs (1935), with upright cells in uniseriates, as sheathing cells on multiseriate portions and in the wing-like tips of multiseriate rays. Ray cell wall thickness about 2 μm, pits mostly simple. Mean height multiseriate rays, 985 μm; mean width at widest point, 3.8 cells. Mean height of uniseriate rays, 308 μm. Wood nonstoried. Successive cambia present, the vascular bands composed of cells with relatively thin but lignified walls (Fig. 2). A few nests of thick-walled sclereids present in conjunctive tissue. In the specimen studied, strands of tracheids (identifiable by bordered pits) present exterior to phloem poles in one conjunctive tissue band (Fig. 2, arrows). Silica bodies present in rays (evident as remnants because of hydrofluoric acid treatment). Dark-colored amorphous deposits present in ray and axial parenchyma (Fig. 4).

*Rhabdodendrum macrophyllum* (Fig. 7–14). Growth rings present but inconspicuous, evident as alternating rings of wide and narrow vessels (Fig. 7). Vessels mostly solitary, mean number of vessels per group, 1.26; lumen diameter, 32 μm; mean number per mm², 225; mean wall thickness, 2.5 μm. Mean vessel element length, 359 μm. Perforation plates simple, nonbordered. Lateral wall pits of vessels with oval aper-
Fig. 1–4. Stem sections of *Rhabdodendron amazonicum*. – 1: Transection of secondary xylem, showing solitary nature of vessels. – 2: Stem transection to illustrate portions of successive vascular bands, separated by conjunctive tissue in which strands of secondary xylem (arrows) occur abaxial to phloem strands of the preceding band. – 3. Transection of secondary xylem, to show sparse diffuse axial parenchyma (vertical arrow) and paratracheal axial parenchyma chiefly abaxial in distribution (horizontal arrow). – 4. Tangential section; multiseriate and uniseriate rays about equally frequent. — Fig. 1, 2 & 4, magnification scale above Fig. 1 (divisions = 10 μm); Fig. 3, scale above Fig. 3 (divisions = 10 μm).
Fig. 5–9. Wood sections of *Rhabdodendron*. — 5 & 6: *R. amazonicum*, sections to show tracheids, ray cells at left in each. — 5: Transection; pit cavity outlined by dark-staining deposit (arrow); to the left of that pair of tracheids an axial parenchyma cell. — 6: Tangential section; density and size of pits on tracheids visible because pit cavities contain dark-staining material. — 7 & 8: *R. macrophyllum*. — 7: Transection; arrow indicates band of parenchyma that becomes more prominent toward left edge of photograph (another parenchyma band further up); vessel diameter fluctuates. — 8: Tangential section to show a patch of axial parenchyma cells from a band (arrow) and rays. — Fig. 5 & 6, scale above Fig. 5 (divisions = 10 μm); Fig 7 & 8, scale above Fig. 1.
Fig. 9–12. SEM photographs of vessel portions from radial section of wood of *Rhabdodendron macrophyllum*. – 9: Oval pits seen from lumen side to show vesturing. – 10: Oval pits seen from outside of vessel, showing outlines of pit cavities and vested pit apertures. – 11: Oval pits seen from lumen side to illustrate vesturing of pit apertures, grooves interconnecting pit apertures, and striate wall surface. – 12: Scalariform and transitional pits; pit apertures are vested. — Scales in each figure = 10 μm.
Fig. 13 & 14. SEM photographs of cell contents from ray cells of radial section of *Rhabdodendron macrophyllum*. – 13: Silica body, showing characteristic surface. – 14: Section of sphaerocrystal to show central hilum-like structure, component prismatic crystals, and smooth outer surface of the sphaerocrystal. — Scales in each figure = 10 μm.

Figures (Fig. 9–11) on intervascular faces, but predominantly scalariform to transitional (Fig. 12) on vessel–parenchyma faces. Axial diameter of pit cavities about 4 μm. Pit apertures vestured (Fig. 9–12). Vessel walls smooth (Fig. 9, 12) or finely striate (Fig. 11). Grooves interconnect some pit apertures (Fig. 11). Imperforate tracheary elements all tracheids; pit cavities 4 μm in diameter, apertures vestured as seen with SEM. Mean tracheid length, 580 μm; mean wall thickness, 5 μm. Axial parenchyma in tangential bands (Fig. 7, arrow) of various lengths; vessels present both within and outside of axial parenchyma bands, which are therefore apotracheal. Axial parenchyma in strands of two to four cells. Multiseriate rays about equal to uniseriates in frequency (Fig. 8). Rays composed of procumbent cells almost exclusively, intermediate between Heterogeneous Type IIB and Homogeneous Type I of Kribs (1935). Mean ray cell wall thickness, 2 μm, pits nonbordered. Mean height of multiseriate rays, 554 μm; mean width at widest point, 2.6 cells. Mean height of uniseriate rays, 81 μm. Wood nonstoried. Successive cambia absent. Silica bodies in most ray cells, usually only one per cell (Fig. 13), but some cells contain smaller bodies in addition to a medium-sized one. Sphaerocrystals present in most pith cells and in some ray cells, especially ray cells closer to the pith. Sphaerocrystals one, rarely two, per cell (Fig. 14), composed of numerous prism-like crystals radiating from a small central sphere. The surface of the sphaerocrystal mass is relatively smooth. As seen in sectional or optical sectional view, two or three concentric rings are present.
DISCUSSION AND CONCLUSIONS

Several features are newly reported here: some of these are of systematic significance. The vestured pits in vessels and tracheids of both species of *Rhabdodendron* have been reported elsewhere in Caryophyllales only in Polygonaceae (Ter Welle 1976; Kucera et al. 1977). Polygonaceae and Rhabdodendraceae are adjacent in the cladogram of Soltis et al. (2000).

Interestingly, silica bodies occur in both Rhabdodendraceae and Polygonaceae (Ter Welle 1976; Carlquist 1988). They also occur in Plumbaginaceae (Carlquist & Boggs 1996), a family adjacent to Polygonaceae in cladograms (Lledó et al. 1998; Soltis et al. 2000). Silica bodies have also been reported in Ancistrocladaceae and Dioncophyllaceae (Gottwald & Parameswaran 1968), two families that are currently included in Caryophyllales s.l. (Soltis et al. 2000).

Sphaerocrystals are reported for the first time in *Rhabdodendron*. In literature on dicotyledon anatomy, sphaerocrystals are not always considered a category separate from druses, although this distinction has now been advocated (Carlquist 1988). Sphaerocrystals have been defined variously, both in morphology and in chemistry, judging from the listing of Metcalfe and Chalk (1950: 1346). In the usage proposed here, sphaerocrystals (Fig. 14) are composed of a large number of slender prismatic crystals radiating from a spherical kind of hilum in the center of the group. Sphaerocrystals form a globe with a relatively smooth surface. Concentric rings may be seen in sections and optical sections of sphaerocrystals; these rings may represent pauses in crystal deposition, a kind of growth ring. By contrast, druses are composed of relatively few crystals. Crystals in druses retain rhomboidal shapes, and thereby the druse has a surface on which angles of the component crystal project conspicuously. To be sure, there may be crystal aggregations that do not conform to the distinctions offered above. Additional studies are needed. Plant anatomists are unlikely to test chemistry of crystals in plants, so morphology is considered of prime importance here. Ultimately, chemical tests and better crystallographic analyses on crystals in a wide range of dicotyledon families will hopefully refine our concepts.

The near-basal position of Rhabdodendraceae in the caryophyllalean clade (Lledó et al. 1998; Soltis et al. 2000) is interesting in connection with the presence of successive cambia in Rhabdodendraceae. At least some genera of families close to Rhabdodendraceae in the clades of those authors have successive cambia: Plumbaginaceae (*Aegialitis*), Polygonaceae (*Antigonon*), and Simmondsiaceae (*Simmondsia*). *Stegnosperma* is claimed to be relatively primitive in Caryophyllales s.s. (Manhart & Rettig 1994; Rodman 1994). *Stegnosperma* has successive cambia, although the initiation of a second or third cambium may be tardy (Horak 1981). Successive cambia are present in all of the families cited above, as well as in families of Caryophyllales s.s. (except for Achatocarpaceae, Cactaceae, Didieriaceae, Portulacaceae, and some Phyllocladaceae). One can more easily hypothesize loss of successive cambia in the genera of Caryophyllales s.s. in which they are absent than hypothesize independent acquisition of this feature in branches of this clade – fewer character state reversions would be required. However, the tardiness with which a second or third cambium develops
in *Stegnosperma* opens the possibility that the genetic basis for successive cambium formation may be present, but those genes may be partially or wholly suppressed by modifier genes in some genera and families. This may explain absence of successive cambia in *Rhabdodendron macrophyllum* (as reported thus far by several authors). Perhaps older stems or roots of this species may possess the phenomenon; my material did not represent the stem or main branch of an adult plant.

The presence of tracheids is a primitive feature when dicotyledons as a whole are analyzed (e.g., Metcalfe & Chalk 1950: xlv, “fibres with distinctly bordered pits”). Tracheids occur not only in *Rhabdodendron*, but also in the ‘basal’ families listed above: Simmondsiaceae (Carlquist, unpublished data), Stegnospermateaceae (Carlquist 1999a), Agdestidaceae (Carlquist 1999b), and Barbeuiaceae (Carlquist 1999c). Thus, presence of tracheids may be a symplesiomorphy in Caryophyllales. The very low degree of vessel grouping in *Rhabdodendron* correlates with presence of tracheids in this genus, in accord with the hypothesis for dicotyledons as a whole (Carlquist 1984).

Diffuse axial parenchyma, present in *Rhabdodendron*, also occurs in *Agdestis, Barbeua*, and *Stegnosperma* (Carlquist 1999a, 1999b, 1999c). Diffuse axial parenchyma was demonstrated to be a primitive character state in wood of dicotyledons as a whole (Kribs 1937).

One further feature, apparently a symplesiomorphy in Caryophyllales s.l., is newly reported for Rhabdodendraceae: presence of nonbordered perforation plates. The pervasiveness of this feature in the order has been stressed earlier (Carlquist 1999c, 2000b).

Some of the features cited above are characteristic of Rhabdodendraceae plus families considered primitive in recent phylogenies of Caryophyllales. Nonbordered perforation plates and successive cambia are widespread in Caryophyllales (but not in dicotyledons at large), and may be indicative of a caryophyllalean placement for Rhabdodendraceae. More significantly, there is no feature in wood of Rhabdodendraceae that contradicts placement of Rhabdodendraceae in Caryophyllaceae.

REFERENCES


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