WOOD ANATOMY OF CEPHALOTACEAE

by

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Summary

Wood anatomy of *Cephalotus* is described for the first time. Vessel elements are short and narrow, with simple perforation plates. Lateral wall pitting is scalariform on vessel–parenchyma contacts but alternate on intervascular areas. Scalariform perforation plates occur only in primary xylem vessel elements. Imperforate tracheary elements are all tracheids. Rays are predominantly uniseriate. Axial parenchyma ranges from diffuse to more abundant states. All wood details are in accord with the hypothesis that Cephalotaceae is a family related to Saxifragaceae and allied families.

Introduction

Wood anatomy of *Cephalotus follicularis* Labill., sole species of Cephalotaceae, is of interest for several reasons. The wood anatomy has not been described hitherto; Schweiger's (1909) description was probably based on primary xylem, or only a small accumulation of secondary xylem. Schweiger's claim that vessel elements of *Cephalotus* have scalariform perforation plates is regarded by Metcalfe and Chalk (1950) as in need of confirmation. The habitat of *Cephalotus* is an unusual one: bogs which are decidedly wet in the winter, but which can dry appreciably during summer months. The nature of wood anatomy in a rhizomatous herb from such an environment is of potential interest. Cephalotaceae has been generally regarded as allied to Saxifragaceae or other families near Saxifragaceae. This view has been disputed by only a few, and such dissenting opinions have diminished since Schweiger's (1909) study, in which various ideas about relationships are reviewed. The nature of wood anatomy should be pertinent in an assessment of systematic relationships of the genus.

Materials and Methods

Wood of *Cephalotus* was collected in a bog near Two Peoples Bay, Western Australia, in 1974 (Carlquist 5682, RSA). An effort was made to select older rhizome portions so as to secure maximal secondary xylem accumulation. Probably rhizomes persist for only three or four years before the older end becomes inactive or rots away. Rhizomes collected were fixed in formalin-acetic-alcohol. Portions to be sectioned were treated for a month in commercial strength hydrofluoric acid. This treatment permitted sectioning in paraffin. Stems would have been very difficult to manage on a sliding microtome because of their small size and softness. Sections were stained in safranin and fast green, preceded by a tannic acid-ferric chloride series, corresponding to Northen's modification of Foster's tannic acid-ferric chloride method (Johansen, 1940). This technique permits enhanced staining of primary walls. The ferric tannate permits one to discriminate between pits and perforations on vessel elements. Macerations were also prepared; these were stained with safranin.

Results

The cylinder of secondary xylem in *Cephalotus* is, at maximum, not notably thick (Fig. 1). The composition of this ring varies greatly with respect to parenchymatization. Secondary xylem may contain only diffuse parenchyma cells, or parts of the cylinder may be composed of vessel elements embedded in a background of axial parenchyma cells. The portion shown in Figure 1 includes, in its upper left sector, a highly parenchymatous zone of secondary xylem. In the upper right quadrant, tracheids are present instead of the parenchyma. Highly parenchymatized xylem can be found within a single stem early, late, or in a central zone in secondary xylem within a single stem. No explanation for this behaviour can be offered at present, other than the possibility that axial parenchyma tends to substitute for imperforate tracheary elements in more succulent stems, such as those of *Brighamia insignis* or *Crassula argentea* (Carlquist, 1962). Where xylem is not highly parenchymatized, axial parenchyma may be said to be diffuse. As might be expected in a semi-succulent perennial, there is no evidence of growth rings in the secondary xylem of *Cephalotus*.

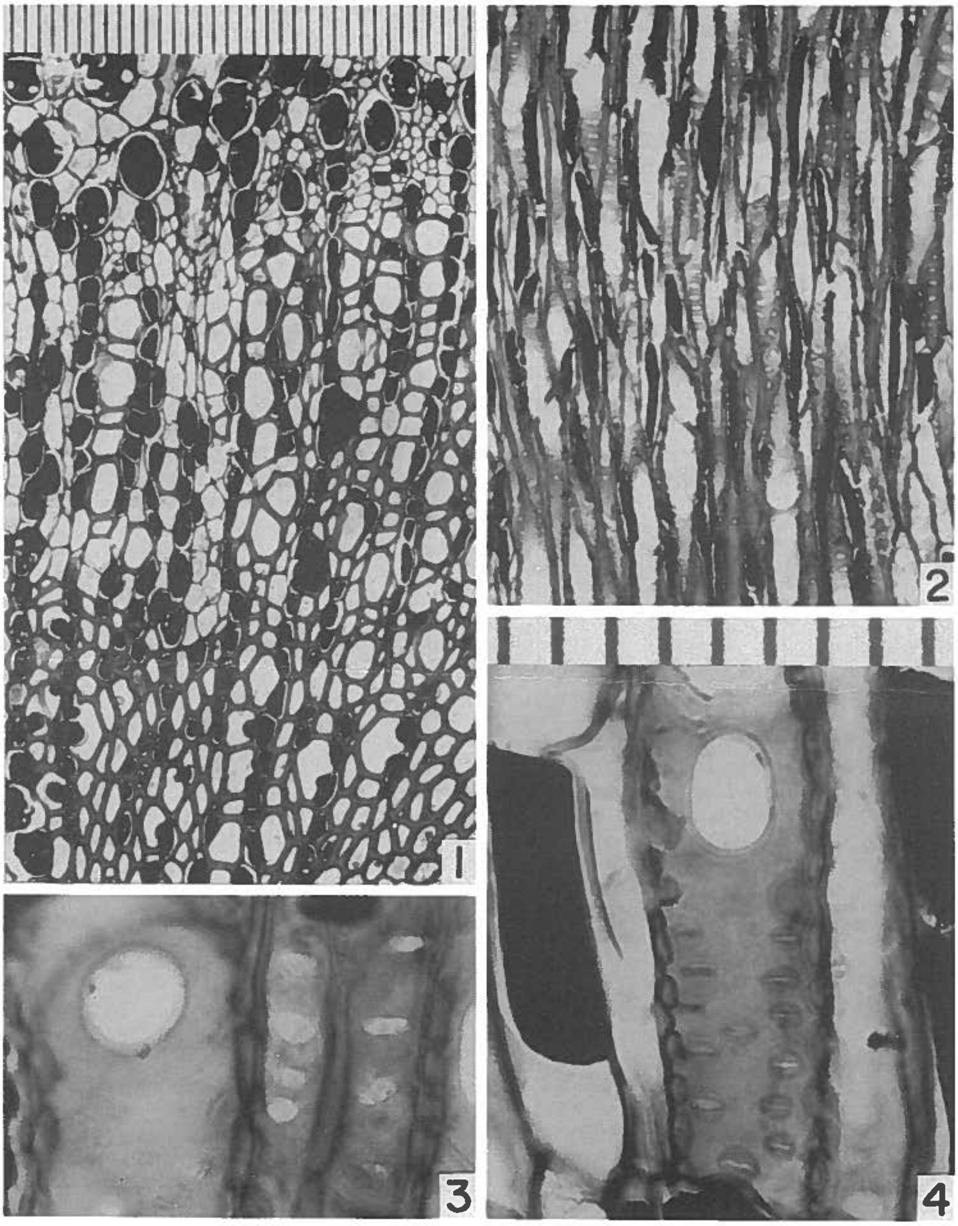

Fig. 1–4. Wood sections of *Cephalotus follicularis*. – 1: Transection, phloem at top; pith begins lower right. – 2: Tangential section, showing tannin-filled ray and axial parenchyma cells. – 3: Perforation plate of vessel (left) and portions of two tracheids (right). – 4: Vessel element, showing alternate circular bordered pits on an intervascular interface. – Magnification scale for 1 and 2 is above Fig. 1 (divisions = 10 μm). Scale for 3 and 4 above Fig. 4 (divisions = 10 μm).

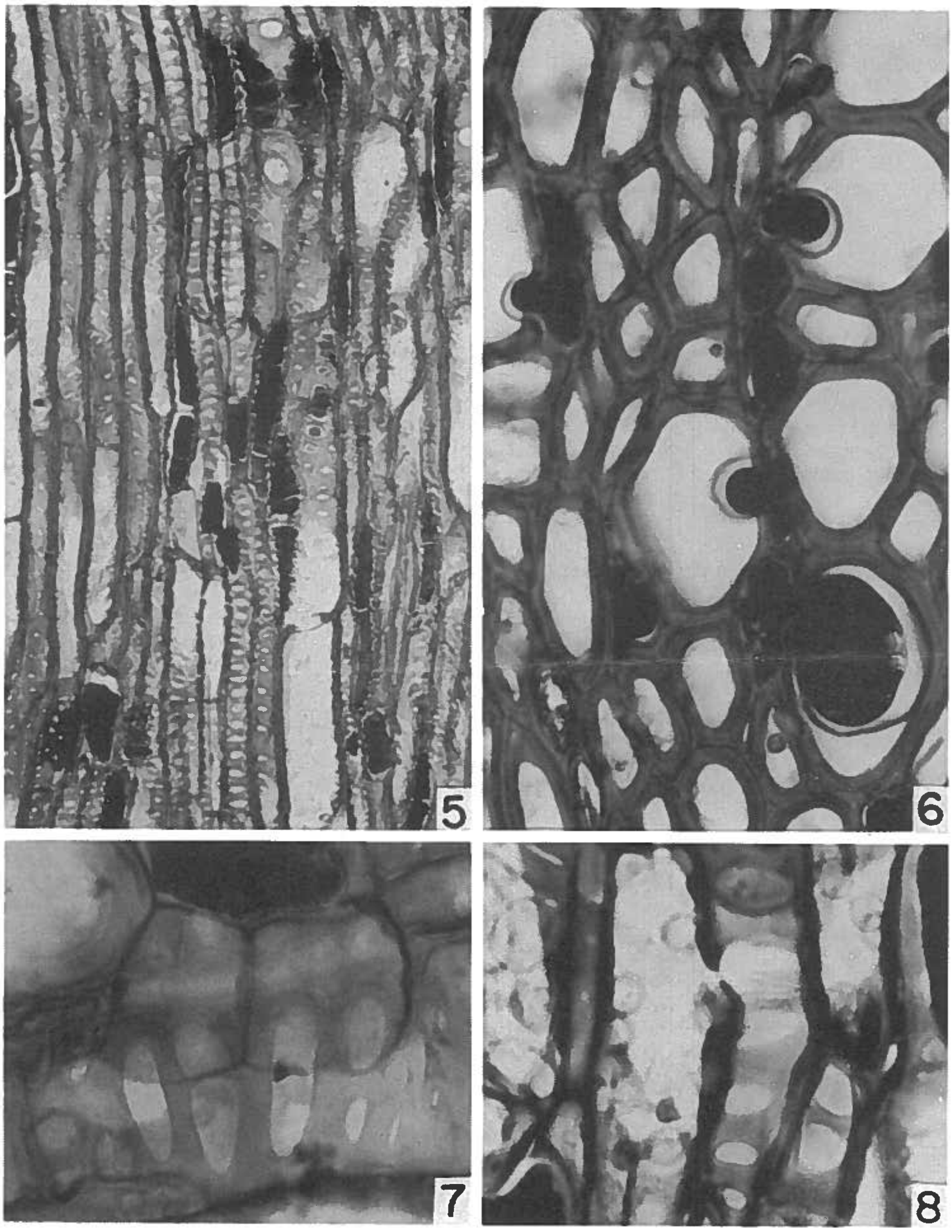

Fig. 5–8. Wood sections of *Cephalotus follicularis*. – 5: Radial section; erect cells of rays filled with tannins, near top and bottom. – 6: Transection, showing tyloses from ray and axial parenchyma cells in vessels. – 7: Portion of radial section (vessel shown horizontally), illustrating scalariform vessel–ray pitting. – 8: Tangential section, showing a narrow vessel with scalariform pitting on its contacts with axial parenchyma cells. – Magnification scale for 5 above Fig. 1; scale for 6–8 above Fig. 4.

Vessel elements are of small size: they average 43 μm in diameter (widest diameter, wall included), and 183 μm in length. Vessel elements of the secondary xylem have simple circular perforation plates (Figs. 3, 4). Very infrequently a pair of perforation plates occurs at one end of a vessel element; such pairs very likely represent branching of a vessel. The report of Schweiger (1909) that scalariform perforation plates occur in *Cephalotus* certainly does not apply to secondary xylem. What might appear to be scalariform perforation plates on secondary xylem vessels prove to have pit membranes and are, in fact, scalariform lateral wall pitting. Scalariform perforation plates were observed only on metaxylem vessel elements. Primary xylem contains helically-thickened tracheary elements with scalariform perforation plates as well as a few with no perforation plates; the latter thus qualify as tracheids. Occurrence in primary xylem of both tracheids and vessel elements with scalariform perforation plates has been reported for species of Saxifragaceae by Bierhorst and Zamora (1965).

Vessel elements have alternate circular bordered pits on intervascular contacts (Fig. 4). Vessel–ray contacts have scalariform pitting (Fig. 7), as do vessel–axial parenchyma contacts (Fig. 8). Scalariform lateral wall pitting is abundant where vessels are surrounded by parenchyma, but elliptical pits may be found where vessels contact tracheids (Figs. 3, 5). The abundance of such pits on *Cephalotus* tracheids and vessel elements seems related not merely to parenchymatization of the wood, but to lack of selective pressure for mechanical strength as well.

Vessel elements are angular as seen in transection, and mostly wider radially than tangentially (Fig. 1). The angular shape can be related to the fact that vessel elements are narrow in diameter, so that a small number of cells abutting on a vessel element tends to make its shape more angular. Tracheids average 234 μm in *Cephalotus* secondary xylem. Walls of tracheids are thin but lignified (Fig. 6). A few tracheids are septate (Fig. 5, centre left).

Rays are mostly uniseriate; a few are biseriate (Fig. 2). They are composed of cells square to erect as seen in radial section (Fig. 5). Both ray cells and axial parenchyma cells are mostly filled with tannins. Tylosis formation is active in the stems studied here (Fig. 6). The tyloses observed ranged from those minimal in size to some large enough to occlude vessels. The tannins deposited in parenchyma cells are also found in tyloses. Parenchyma cells and tyloses have thin primary walls, which are not visibly birefringent.

Phloem contains tannin-filled parenchyma cells in addition to sieve-tube elements and companion cells. Sieve tube elements have simple sieve plates. No fibres occur in the secondary phloem. Pith and cortex cells of *Cephalotus* are rich in starch and tannins, as described by Schweiger (1909).

Vessel elements with simple perforation plates, small in size, accompanied by narrow rays and tanniniferous cells are all features present in *Cephalotus* which are also reported for herbaceous Saxifragaceae by Metcalfe and Chalk (1950). Because anatomical characteristics of the wood of *Cephalotus* are congruent with those of herbaceous Saxifragaceae, there seems no reason from this standpoint to question the prevailing view that Cephalotaceae and Saxifragaceae are related.

References

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