Systematic wood anatomy of *Myodocarpus*, *Delarbrea*, and *Pseudosciadium* (Araliaceae)

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ABSTRACT

Wood anatomical features examined in five species of *Myodocarpus*, four species of *Delarbrea*, and the single member of *Pseudosciadium* (Araliaceae) using light and scanning electron microscopy support the hypotheses that they are a closely related, monophyletic group, and that they form an ancient lineage that has survived and diversified on the island of New Caledonia, where all except two of the 17 species belonging to these genera are endemic. *Delarbrea* and *Pseudosciadium* have similar wood structure; the wood of *Myodocarpus* is distinctly more primitive (sensu Bailey). These genera differ markedly in wood structure from other Araliaceae in the presence of apotracheal (diffuse and diffuse-in-aggregates) axial parenchyma, and wood features do not support earlier suggestions that *Myodocarpus* is intermediate between Araliaceae and Apiaceae. Within *Myodocarpus* two groups of species can be distinguished on wood characters, which correspond to the species with simple vs. pinnately compound leaves. The wide-ranging *D. paradoxa* subsp. *paradoxa* is the only taxon studied with numerous vasicentric tracheids, often regarded as an adaptation to water stress.

KEY WORDS

*Myodocarpus*, *Delarbrea*, *Pseudosciadium*, Araliaceae, wood anatomy, vasicentric tracheids, phylogeny, New Caledonia.
RÉSUMÉ
Les caractères anatomiques du bois ont été examinés pour cinq espèces de Myodocarpus, quatre espèces de Delarbrea, et l'unique espèce de Pseudosciadium (Araliaceae) aux microscopes photonique et électronique à balayage. Les résultats obtenus confirment que ces genres sont proches, constituent un groupe monophylétique et forment une lignée ancienne qui a survécu et s'est diversifiée en Nouvelle-Calédonie, où 15 des 17 espèces de ces genres sont endémiques. La structure du bois de Delarbrea et Pseudosciadium est semblable ; celle de Myodocarpus est bien plus primitive (sensu Bailey). Ces trois genres ont une structure anatomique du bois nettement différente de celle des autres Araliaceae en raison de la présence d'un parenchyme axial apotrachéal (diffus à diffus-agrégé). L'ensemble des caractères observés n'est pas compatible avec l'idée que Myodocarpus occupe une position intermédiaire entre les Araliaceae et les Apiaceae. Chez les Myodocarpus deux groupes d'espèces peuvent être distingués par l'anatomie du bois : celles à feuilles simples et celles à feuilles composées. Delarbrea paradoxa subsp. paradoxa, à large répartition, est le seul taxon étudié à posséder de nombreuses trachéides vasicentriques, caractère souvent considéré comme une adaptation au stress hydrique.

INTRODUCTION
Myodocarpus, Delarbrea, and Pseudosciadium form a closely related group of genera centred in New Caledonia (Lowry 1986a, 1986b). All ten species of Myodocarpus and the single species of Pseudosciadium are endemic to this island, situated in the southwest Pacific. Moreover, four of the six species of Delarbrea are likewise restricted to New Caledonia; D. paradoxa Vieill. subsp. paradoxa also extends through Vanuatu and the Solomon Islands to the Moluccan and Lesser Sunda Islands, and D. michieana (F. v. Muell.) F. v. Muell., previously placed in the monotypic genus Porospermum F. v. Muell., is endemic to Queensland, Australia (Lowry 1986a, 1986b).

The plants of this alliance are monocious or sparsely branched treelets or trees ranging from ca. 1.5 to 20 m in height, with leaves that are densely clustered at the branch ends, and whose petiole bases are clasping, as in many other Araliaceae. The three genera share a number of other characters, including similar inflorescence structure and organization, articulated pedicels, an isomerous androecium, and a bicarpellate gynoecium, although each of these features also occurs individually elsewhere in the family. Their floral vasculature is also relatively primitive (Eyde & Tseg 1971). However, Myodocarpus, Delarbrea, and Pseudosciadium differ from all other Araliaceae by the presence of distinctive secretory oil ducts in the fruits (Eyde & Tseg 1971; Lowry 1986a, 1986b), which appear to represent a derived character (synapomorphy). Moreover, the apotracheal axial parenchyma found in the wood of the first two genera is also unknown among other members of the family (Rodriguez 1957; Oskolski 1994; but see below regarding Pseudosciadium).

Myodocarpus stands out by being the only genus of Araliaceae with a dry, laterally compressed, schizocarpic fruit with a central carpophore, whose overall morphology is at least superficially similar to the fruits of many Apiaceae (by contrast, the fruits of Delarbrea and Pseudosciadium are terete drupes). On this basis, Baumann (1946) regarded Myodocarpus as a possible link between Araliaceae and its traditional sister group, Apiaceae (see also Thorne 1973), which together are widely recognized as comprising the order Araliales. More recently, however, a number of studies have questioned such an intermediate position for the genus (Rodriguez 1957, 1971; Eyde & Tseg 1971; Lowry
Wood anatomy of Araliaceae

1986a, 1986b; Oskolski 1994; Plunkett 1994; Plunkett et al. 1996). Lowry (1986a) points out that the fruits of all three genera share a single basic anatomical plan, with each tissue present in the fleshy fruits of Delarbrea and Pseudosciadium having a direct homologue in those of Myodocarpus, including the characteristic oil ducts.

The close relationship between Delarbrea and Myodocarpus was first pointed out by Vieillard (1865). Bentham (1867), and later Harms (1894-97), Hutchinson (1967), and Tseng & Hoo (1982) placed these genera in the tribe Araliaceae Benth., whereas Viguié (1906) and Takhtajan (1987) treated them as members of a segregate tribe Myodocarpeae (erroneously referred to as Myodocarpineae by Viguié). The systematic placement of Pseudosciadium has a somewhat more complex history. When Bailon (1878, 1879) first described Pseudosciadium balansae, he indicated that it was closely related to both Delarbrea and Myodocarpus, and further suggested that it was intermediate between them. In later treatments of Araliaceae (Harms 1894-97; Viguié 1906, 1925; Hutchinson 1967), however, Pseudosciadium was separated from both genera, and included in the tribe Mackinlayeae, which was rigidly (and artificially) defined by valvate, clawed petals. The close relationship of Pseudosciadium to Delarbrea and Myodocarpus initially suggested by Bailon was confirmed when oil ducts were observed in the fruits of Pseudosciadium by Lowry (1986a, 1986b), who concluded on the basis of this and other characters that these three genera comprise a monophyletic group. He further suggested that they represent the relics of an ancient araliaceous lineage forming part of a floristic ensemble that was able to survive in the relatively equable climates of New Caledonia, but was in large part eliminated from Australasia and elsewhere as a result of changing climatic conditions in Neogene times (see also Raven & Axelrod 1972, 1974; Raven 1980; Lowry in press). More recently, Plunkett (1994 and Plunkett et al. 1996), using molecular and morphological characters to examine relationships within Araliaceae, concluded that the available data support the hypothesis that Delarbrea (the only one of the three genera under consideration here that was included in his study) is part of an ancient group from which both Araliaceae and Apiaceae evolved.

Structural features of wood offer a useful tool for improving our understanding of the systematic position of Myodocarpus, Delarbrea, and Pseudosciadium within Araliaceae, as well as the relationships among these three genera. Previously published data on the wood structure of these taxa are scanty, and hence insufficient to develop any conclusive interpretations. Only four species of Myodocarpus have been studied previously [M. simplicifolius Brongn. & Gris (Kribs 1937; Oskolski 1994); M. pinnatus Brongn. & Gris (Sarlin 1954); M. fraxinifolius Brongn. & Gris and M. involucratus Dubard & Vig. (Rodriguez 1957); Myodocarpus sp. (Record & Hess 1944; Metcalfe & Chalk 1950)], while only a single member of Delarbrea had been examined [D. paradoxa subsp. paradoxa (Oskolski 1994)].

This study, which is part of a general survey of wood anatomy throughout the family (Oskolski 1994, 1995, 1996; Oskolski & Lowry in prep.), examines the wood structure of a much larger sample of Myodocarpus, Delarbrea, and Pseudosciadium, and considers the results with regard to the systematic relationships of the group. The conclusions from such systematic analyses of wood structural features represent an important contribution to an overall understanding of the family, and will assist in preparing further revisions of Araliaceae for the Flore de la Nouvelle-Calédonie (Lowry 1986a, 1986b, in prep.) and other regions in the Pacific (Lowry 1987, 1988, 1989, 1990, in prep.; Lowry et al. 1989). Moreover, this type of study provides additional morphological information for ongoing comparative phylogenetic analyses based largely on molecular data (Plunkett 1994; Plunkett et al. 1996).

MATERIALS AND METHODS

Most of the wood specimens examined were collected by the second author during field investigations
conducted in New Caledonia (voucher herbarium specimens are deposited at MO, NOU, P, and various other institutions). Some additional material was obtained from the wood collection of the Smithsonian Institution (USw), and one sample was taken from an individual growing in cultivation at the Botanical Garden of the V.L. Komarov Botanical Institute, St. Petersburg. Specimens examined in this study were mostly taken from trunks or stems with a secondary xylem radius of more than 10 mm (8 mm in D. montana Vieill. ex R. Vig. subsp. arborea (Vieill. ex R. Vig.) Lowry, and in Delarbrea paradoxa Vieill. subsp. paradoxa, and 5 mm in D. michieana F. v. Muell.).

Standard procedures for the study wood structure were employed to prepare sections and macerations for light microscopic studies. Specimens for scanning microscopy were prepared according to Exley et al. (1977). Descriptive terminology and measurements follow Carlquist (1988) and the I.A.W.A. List of Microscopic Features for Hardwood Identification (1989), except for the diameter of intervessel pits, for which the vertical dimension is recorded.

RESULTS

The wood anatomical data for Myodocarpus simplicifolius (USw W-4736) and Delarbrea paradoxa subsp. paradoxa (cult, in St. Petersburg) published earlier in Russian (Oskolski 1994) are included in the following descriptions.

**MYODOCARPUS** (Fig. 1A-B, 2A-B, 4A-D, 5A-B, 5B-D, 6A-D, 7F-H; Table 1).


Growth rings absent (*M. fraxinifolius* (Fig. 1A), *M. sp. nov.*, ined. (Lowry 3772)) or indistinctly marked by zones of more abundant axial parenchyma tending to form long tangential lines (*M. pinnatus, M. elegans*), and also of more numerous vessels (*M. simplicifolius*, Fig. 1B).

Vessels rounded, rarely angular in outline, rather small (tangential diameter < 100 μm in *M. pinnatus*, and < 70 μm in the other species) and numerous (up to 282 per mm² in *M. elegans*); solitary mixed with few radial multiples of 2–3 (up to 7 in *M. elegans* and *M. fraxinifolius*). Vessel walls 2–6 μm thick. Tyloses not observed. Vessel elements (400–)830–1240 (–1470) μm in length. Perforation plates scalariform (Fig. 4A–C) with numerous bars (up to 20 in *M. elegans* and *M. simplicifolius*) and reticulate (Fig. 4D); rarely simple (observed in *M. fraxinifolius* only), in more or less oblique end walls. Intervessel pits alternate, opposite, and rarely scalariform (*M. elegans*, *M. sp. nov.*, ined. (Lowry 3772), Fig. 5A), 4–6 μm in vertical diameter, rounded or oval, with slit-like apertures surrounded and/or interconnected by shallow, groove-like wall sculptures (Fig. 5B, D). Vessel-ray pits similar to intervessel pits in size and shape (*M. pinnatus* (Fig. 6B), *M. fraxinifolius*) or predominantly scalariform (*M. simplicifolius* (Fig. 6A, C), *M. elegans*, *M. sp. nov.*, ined. (Lowry 3772), Fig. 6B). Helical thickenings absent.

Vasicentric and vascular tracheids not observed. Fibres libriform, walls very thick (5–15 μm, up to 20 μm in *M. elegans* and *M. sp. nov.*, ined., Lowry 3772), non-septate and septate (the latter few and located in immediate vicinity of rays in *M. pinnatus* only), with few simple to minutely bordered pits with slit-like apertures primarily in radial walls.

Axial parenchyma apotracheal, rather abundant, diffuse and diffuse-in-aggregates, forming short and longer, occasionally anastomosing tangential lines (Fig. 1A–B, 2A); strands composed of (3–)5–7–(9) cells.

Rays 3–5 per mm, uni- and multiseriate of 2–5 (up to 6 in *M. elegans* and *M. simplicifolius*) cells in width (Fig. 2B). Ray height commonly less than 1 mm. Both multiseriate and uniseriate rays mostly composed of procumbent cells, occasionally with 1–2 marginal rows of square cells (Kribs' Homogenous I, occasionally Heterogeneous III). Pits on tangential walls of ray cells (Fig. 7F–H) mostly rounded and oval, rather large (2–5(8) μm in diameter). Radial canals present, bordered by thin-walled epithelial cells. Crystals not observed.
Fig. 1.—Transverse sections: A. *Myodocarpus fraxinifolius*, Lowry 3679, growth rings absent.—B. *M. simplicifolius*, Lowry 3216, growth rings marked by zones of more numerous vessels and more abundant axial parenchyma tending to form longer tangential rows.—C. *Delarbrea harmsii*, Lowry 3685, growth rings marked by zones of scarce axial parenchyma and lower vessel frequency (arrows).—D. *Pseudosciadium balansae*, Lowry 3799, growth rings marked by zones of scarce axial parenchyma and by incomplete rows of wider vessels (arrows). Scale bars = 100 µm.
DELARBREA AND PSEUDOSCIADIUM (Fig. 1C-D, 3A-D, 4E-G, 5C-E-G, 6E-G, 7A-E; Table 1).

The wood structure of these genera is very similar, and a combined description is therefore given.


Growth rings absent (D. harmsii (Lowry 3909), D. paradoxa) or indistinct, marked by zones of scarce axial parenchyma and lower vessel frequency (D. harmsii (Lowry 3685), Fig. 1C), and also by incomplete rows of wider vessels (in the other taxa, Fig. 1D).

Vessels rounded, rarely angular in outline, small (tangential diameter < 70 μm) and numerous (up to 242 per mm² in D. montana); solitary with variable portions of radial and tangential multiples of 2-3 (up to 12 in D. montana); vessel multiples predominantly tangential in D. michieana and D. montana. Vessel walls 2-6 μm thick. Tyloses not observed. Vessel elements (310-)540-890(-1300) μm in length. Perforation plates exclusively simple, in more or less oblique end walls (Fig. 4E-G). Intervessel pits alternate, occasionally opposite, 3-6 μm in vertical diameter, rounded, with slit-like apertures surrounded and/or interconnected by shallow, groove-like wall sculptures (Fig. 5C,E-G).
Fig. 3.—A, Delarbrea harmsii, Lowry 3685, transverse section: axial parenchyma, diffuse-in-aggregates and diffuse, thick-walled fibers.—B, D. paradoxa subsp. paradoxa, Lowry 3750, tangential section: multiseriate rays up to 5 rows wide, radial canal (arrow).—C-D, Pseudosciadium balansae, Lowry 3799; C, transverse section: parenchyma diffuse-in-aggregates and diffuse, thick-walled fibers; D, tangential section: multiseriate rays up to 3 rows wide, radial canals. Scale bars = 100 μm.
Vessel-ray pits similar to intervessel pits in size and shape (Fig. 6E-G). Helical thickenings found only in one sample of *D. harmsii* (Lowry 3909, Fig. 5F, 6F), but absent in others (including the second sample of *D. harmsii* studied, Lowry 3685, Fig. 5G, 6E).

Vasicentric tracheids rather numerous in *D. paradoxa* subsp. *paradoxa* but absent in the other species.

Fibres libriform, thick-walled (4-10 μm, up to 16 μm in *D. harmsii*), non-septate (occasionally septate in *D. paradoxa*), with small to rather large (> 3 μm) bordered pits in both radial and tangential walls.

Axial parenchyma apotracheal diffuse and diffuse-in-aggregates, rather abundant, often forming anastomosing, discontinuous tangential lines (Fig. 1C-D, 3A,C), strands composed of (2-)3-5(-7) cells.

Rays 2-5 per mm, mostly multiseriate of 2-3
(up to 5 in *D. montana*, and to 6 in *D. paradoxa*) cells in width (Fig. 3B,D); uniseriate rays scantly in *Delarbrea* (except *D. michieana*), more numerous in *Pseudosciadium*; in *D. michieana* rays considerably more numerous (9-10 per mm) than in others. Both multiseriate and uniseriate rays composed of procumbent cells, occasionally with 1-2 marginal rows of square cells (Kribs’ Homogenous I, occasionally Heterogeneous III). Pits on the tangential walls of ray cells (Fig. 7A-E).

rounded, oval, elongate, 1-3 µm in diameter (up to 5 µm in D. harmsii and D. paradoxa). Radial canals present, bordered by thin-walled epithelial cells. Crystals not observed.

DISCUSSION

These results strongly support the idea (LOWRY 1986a, 1986b) that Myodocarpus, Delarbrea (including D. michieana originally described as a separate genus Porospermum), and Pseudosciadium form a closely related monophyletic group. This alliance differs sharply from other Araliaceae by the presence of apotracheal (diffuse and diffuse-in-aggregates) axial parenchyma. Moreover, members of the genera studied have several other wood characters that are unusual for Araliaceae, including small intervessel pits (3-6 µm), exclusively thick- to very thick-walled libriform fibres, and large bordered fibre pits (the last feature occurs in Delarbrea and Pseudosciadium only). These data do not support BAUMANN's (1946) view that Myodocarpus is a link between Araliaceae and Apiaceae, since apotracheal axial parenchyma of this type has not been found in either family except in the three taxa studied here (METCALFE & CHALK 1950; RODRIGUEZ 1957, 1971; OSKOLSKI & LOWRY in prep.). As for other plant groups usually regarded as possible relatives of Araliaceae, the wood features of Myodocarpus, Delarbrea, and Pseudosciadium are in some respects similar to those found in certain Cornalean families (Cornaceae sensu lato, Alangiaceae) based on the presence of the axial parenchyma type, and also the occurrence of large bordered fibre pits. However, the genera studied here differ markedly from the latter by their predominantly homogeneous rays and by the presence of radial canals (ADAMS 1949;

<table>
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<th>Taxon (voucher collection number)</th>
<th>Character</th>
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<tr>
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<tr>
<td>Myodocarpus fraxinifolius (Lowry 3679)</td>
<td>35 1239 57 41/7 101 10/0-18 1580 5 0.4 2.5</td>
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<td>M. fraxinifolius (USw 20844)</td>
<td>50 1050 52 51/5 75 8/5-14 1376 5 1.0 3.2</td>
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<tr>
<td>M. elegans var. gracilis (Lowry 3377)</td>
<td>16 1160 33 34/7 282 8/6-20 1093 6 2.8 2.5</td>
</tr>
<tr>
<td>M. sp. nov., ined. (Lowry 3771)</td>
<td>15 832 41 62/5 138 14/7-18 1159 4 2.3 2.3</td>
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<tr>
<td>M. pinnatus (Lowry 3318)</td>
<td>25 995 61 40/5 93 9/5-20 1398 5 2.2 3.1</td>
</tr>
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<td>22 1042 46 52/5 157 10/8-20 1555 6 2.6 2.2</td>
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<tr>
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<td>50 1132 54 49/5 108 15/8-29 1343 6 1.9 2.9</td>
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<tr>
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<td>45 870 47 54/4 114 0 1320 3 0.4 3.2</td>
</tr>
<tr>
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<td>50 890 55 50/4 100 0 1423 3 0.2 3.8</td>
</tr>
<tr>
<td>D. michieana (Lowry 3626)</td>
<td>15 638 34 40/5 217 0 857 3 2.5 7.0</td>
</tr>
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<td>10 789 32 28/12 242 0 1079 5 0.3 3.4</td>
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<tr>
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<td>30 573 49 58/5 89 0 1093 6 0.4 3.8</td>
</tr>
<tr>
<td>D. paradoxa subsp. paradoxa (cult. in SPb Bot. Gard.)</td>
<td>10 540 46 56/4 157 0 814 5 1.6 4.4</td>
</tr>
<tr>
<td>Pseudosciadium balansae (Lowry 3799)</td>
<td>25 640 32 61/4 119 0 1080 3 1.0 2.5</td>
</tr>
</tbody>
</table>

1: Radius of wood sample (mm).—2: Average length of vessel elements (µm).—3: Average tangential diameter of vessels (µm).—4: Percentage of solitary vessels / the greatest number of vessels in a vessel group.—5: Vessel and vasicentric tracheid frequency (per sq. mm).—6: Usual / min.-max. number of bars per perforation plate.—7: Average length of libriform fibres (µm).—8: Width of multiseriate rays (maximum, cells).—9: Number of uniseriate rays per mm.—10: Number of multiseriate rays per mm.
Myodocarpus (Fig. 7F-H) differs from both Myodocarpus, while in wood is indicated by the type of Myodocarpus. Although the wood of walls of adjacent ray cells are also of important Pseudosciadium. Vely scalariform perforations, thicker-walled transitional, and alternate pitting is found in longer vessel elements (Table 1), almost exclusively to differences in the vessel element morphology, the more primitive nature of Apiopetalum. When the full set of features examined is taken into consideration, the wood structure of Myodocarpus is distinctly more primitive (sensu Bailey) than that of the other two genera. The wood anatomy of Myodocarpus differs from that of Delarbrea. While the wood anatomy of the Myodocarpus species examined is rather uniform, two groups can tentatively be distinguished based on the shape of their intervessel and vessel-ray pits. Group 1, which includes M. pinnatus and M. fraxinifolius, has only oval and rounded vessel-ray and intervessel pits. Group 2, comprising M. simplicifolius, M. elegans, and M. sp. nov., includes (Lowry 3772), has scalariform as well as oval and rounded vessel-ray pits, and its intervessel pits are occasionally also scalariform. The delimitation of these two groups is consistent with a fundamental difference in leaf morphology: the two members of Group 1 have pinnately compound leaves, while the Group 2 species (and indeed all other species of Myodocarpus) have exclusively simple leaves.

The qualitative wood structural features of the species of Delarbrea and Pseudosciadium examined are also uniform, including the shape of the intervessel and vessel-ray pits. Based on the limited sample studied here, two species groups can, however, be tentatively distinguished within this alliance: D. harmsii, D. michieana, and P. balansa, with rays up to 3 cells wide; and D. montana subsp. arborea and D. paradoxa subsp. paradoxa, with rays up to 5-6 cells wide. The inter-ray pits of D. paradoxa and D. harmsii are slightly larger than in D. montana subsp. arborea and Pseudosciadium balansa, but this is considered a less reliable basis for discriminating species groups. It would be useful to examine these features in a larger set of samples of these taxa. The presence of vasicentric tracheids was recently considered by the first author (Oskolski 1994, 1996) as a generic character of Delarbrea, based on the study of a single sample of Delarbrea paradoxa subsp. paradoxa. While a second sample of this taxon also possesses vasi-
centric tracheids, all other species of Delarbreia examined to date lack this feature. Moreover, although OSKOLSKI (1994, 1996) made no distinction between vascular and vasicentric tracheids in D. paradoxa subsp. paradoxa, they should be referred to the second type because of the absence of the growth rings in this taxon, whereas vascular tracheids are always associated with latewood vessel clusters in species that exhibit growth rings (I.A.W.A. Committee, 1989).

CARLQUIST (1985, 1988) considers vasicentric tracheids as an adaptation to ensure adequate water conduction in conditions of extreme water stress. This idea suggests a hypothesis to explain the adaptive importance of the vasicentric tracheids in D. paradoxa subsp. paradoxa, which is most common and wide-ranging member of the genus, and indeed of any Araliaceae in the Malesian region (LOWRY 1986a, 1986b, 1989), with at least some populations occurring in areas that periodically undergo dry conditions. It would be interesting to analyze a larger sample of D. paradoxa subsp. paradoxa, and also to determine whether vasicentric tracheids occur in D. paradoxa subsp. depauperata, whose distribution is restricted to northeastern New Caledonia, the driest part of the island.

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