PHYLOGENETIC RELATIONSHIPS WITHIN *APIALES*: EVIDENCE FROM WOOD ANATOMY

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Wood anatomical data confirm the close relationships of most *Araliaceae* to *Apiaceae*, but do not indicate any intermediate groups between the two families. *Heteromorpha* Cham. & Schltdl., *Bupleurum* L. and *Melanoselinum* Hoffm. form a well-delimited group distinguished from other woody *Apiaceae* by helical thickenings on their vessel walls, septate fibres, and mostly homogeneous rays. The woodiness in *Nirarathamnos* Balf.f. and *Myrrhidendron* J. M. Coult. & Rose is likely to be of secondary origin.

Keywords. *Apiaceae*, *Araliaceae*, systematic wood anatomy.

Introduction

Although *Araliaceae* and *Apiaceae* (*Umbelliferae*) are commonly accepted as two closely related taxa, different suggestions on their phylogenetic relationships have been proposed. Traditionally, the two families have been regarded as two separate lineages that arose from a common hypothetical ancestor. This was based mostly on morphological and anatomical data (e.g. Rodriguez, 1971). Alternatively, *Apiaceae* has been considered as an evolutionary successful group derived from within *Araliaceae*. This view was supported by occurrence of taxa within *Apiales* (e.g. *Myodocarpus* Brongn. & Gris., *Apiopetalum* Baill., *Stilbocarpa* (Hook.f.) Decne. & Planch., *Hydrocotyle* L.) that combine some traits of both *Araliaceae* and *Apiaceae* and are therefore regarded as intermediate links between the two families (e.g. Thorne, 1973). Recent results from morphological and biogeographical studies (Lowry, 1986a,b), and of cladistic analyses based on *mat*K and *rbc*L sequence data (Plunkett *et al.*, 1996a,b, 1997), suggest however that the majority of taxa in *Apiales* fall into one of two well-delimited groups which correspond largely to *Araliaceae* or *Apiaceae*, whereas others belong to a number of distinct ancient, paleotropical lineages (e.g. *Myodocarpus*, *Delarbrea* Vieill., *Apiopetalum*, *Mackinlaya* Hook.f). The objective of this study was to examine these hypotheses on the basis of an analysis of wood-structure diversity.

Wood Anatomy of *Araliaceae*

Published references and original data on the wood structure of *Araliaceae* (170 species of 44 genera have been examined) have been summarized by Oskolski (1994, 1996), Oskolski *et al.* (1997), and Oskolski & Lowry (2000). This family displays a considerable range of wood diversity and specialization (*sensu* Bailey, 1951). For example, average

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vessel element length, which is an important indicator of the level of xylem specialization, ranges within *Araliaceae* from 370 μm in *Oplopanax* (Torr. & A. Gray) Miq. to 1370 μm in *Schefflera* J. R. Forst. & G. Forst., but in most genera this parameter varies between 600–900 μm. Perforation plate type varies from exclusively scalariform (up to 56 bars in *Osmoxylon* Miq.) to exclusively simple (e.g. *Aralia* L., *Tetraplasandra* A. Gray).

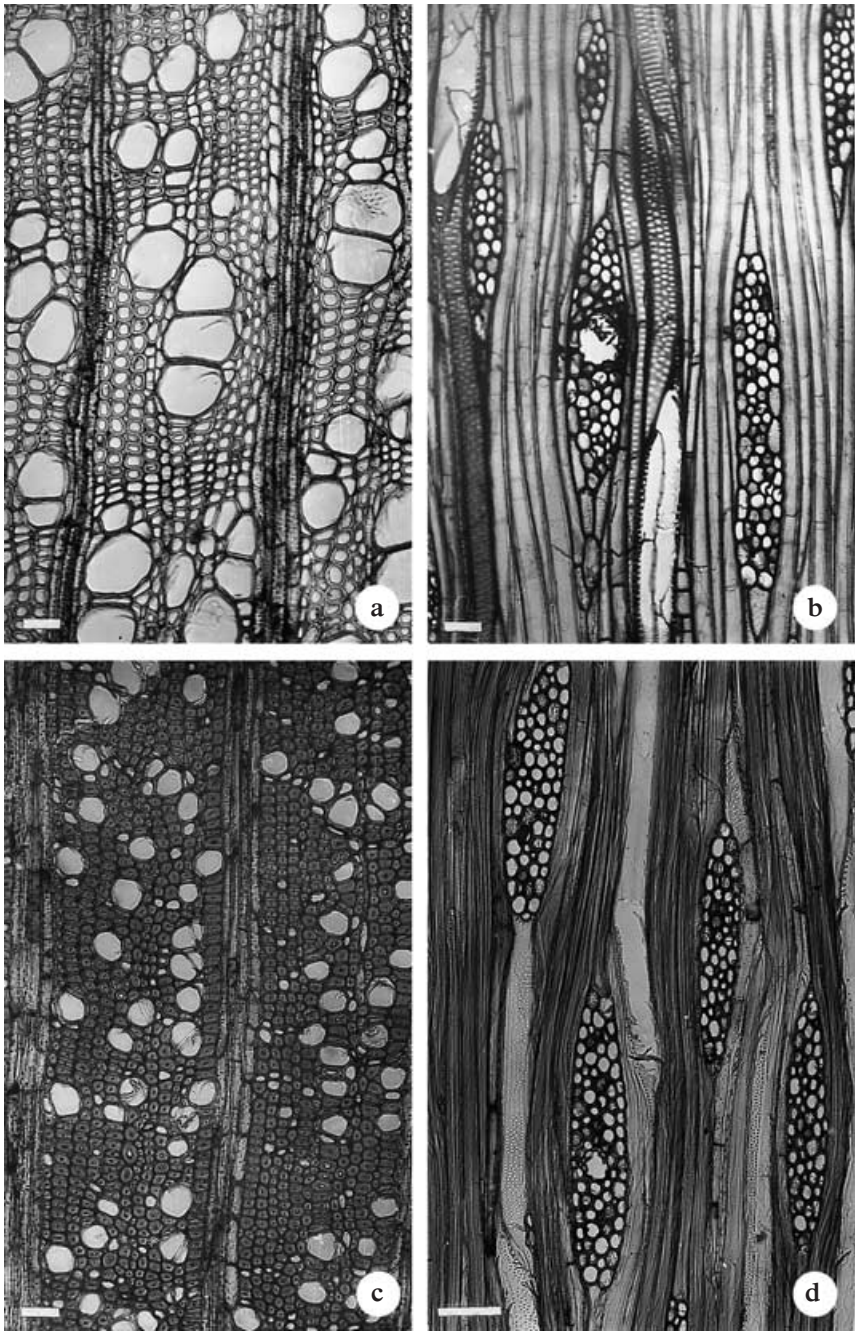
The most important diagnostic wood characters for the family are the axial parenchyma type, the occurrence of septate fibres and/or of radial canals, and the intervessel pit size. Core *Araliaceae* (40 genera examined) share relatively large intervessel pits, scanty paratracheal axial parenchyma, and the presence of septate fibres (which can be secondarily lost) and of radial canals (Fig. 1a,b) in the most primitive genera. *Myodocarpus* (Fig. 1c,d), *Delarbrea* and *Pseudosciadium* Baill. form a well-delimited assemblage, which is sharply distinguished from other *Araliaceae* by relatively small intervessel pits, apotracheal diffuse-in aggregates axial parenchyma, and also by non-septate fibres (Oskolski *et al.*, 1997). *Apiopetalum* and *Mackinlaya* comprise another well-delimited assemblage, characterized by relatively small intervessel pits, presence of both paratracheal and apotracheal (diffuse and diffuse-in-aggregates) axial parenchyma, non-septate fibres, and absence of radial canals (Oskolski & Lowry, 2000).

Wood Anatomy of *Apiaceae*

Shrubs or small trees occur in c.20 apiaceous genera (out of c.300 in this mostly herbaceous family), representing all three traditionally recognized subfamilies (*Hydrocotyloideae* Link, *Saniculoideae* Burnett and *Apioideae* Drude). Wood anatomical study of 10 species in nine genera (*Arracacia* DC., *Bupleurum* L., *Eryngium* L., *Heteromorpha* Cham. & Schltdl., *Melanoselinum* Hoffm., *Myrrhidendron* J. M. Coult. & Rose, *Nirarathamnos* Balf.f., *Platysace* Bunge and *Steganotaenia* Hoscht.) has added to data published by Metcalfe & Chalk (1950) and Schweingruber (1990), but Rodriguez (1957) remains the most important and extensive data source on the family.

Woody *Apiaceae* (except some hydrocotyloids with anomalous stem structure, e.g. *Azorella* Lam.) resemble core *Araliaceae* in their wood structure, but differ by their distinctly shorter vessel elements (average length from 240 μm in *Eryngium* to 500 μm in *Heteromorpha*, but Rodriguez, 1957, noted that in the hydrocotyloids *Asteriscium* Cham. & Schltdl., *Gymnophyton* Clos and *Trachymene* Rudge, this parameter varies from 170–240 μm), and also by exclusively simple perforation plates. Wood

FIG. 1. Wood structure in some *Araliaceae*. Scale bar = 100 μm. a, b, *Aralia soratensis* Marchal (= *Pentapanax angelicifolius* Griseb.): Argentina, Kw 10714. An example of the typical wood structure for the core *Araliaceae*; a, trans-section – thin-walled libriform fibres, scanty paratracheal axial parenchyma; b, tangential section – septate libriform fibres, heterogeneous rays of Kribs' IIB type, radial canal. c, d, *Myodocarpus fraxinifolius* Dubard & R. Vig.; New Caledonia, Lowry 3679; c, trans-section – thick-walled libriform fibres, apotracheal (diffuse-in-aggregates) axial parenchyma; d, tangential section – non-septate libriform fibres, homogeneous rays, radial canal.


a
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anatomical data confirm the close relationships of core *Araliaceae* to *Apiaceae*, but do not support ideas of linear phylogenetic sequence of the two families because no intermediate groups have been identified. *Myodocarpus*, *Delarbrea* and *Pseudosciadium*, as well as *Apiopetalum* and *Mackinlaya*, often regarded as 'bridging taxa' between the families, differ distinctly from both core *Araliaceae* and *Apiaceae*. Instead, wood anatomical data support the view (Lowry, 1986a,b; Plunkett *et al.*, 1996a,b, 1997) that these assemblages are separate, isolated lineages.

Within *Apiaceae*, *Apioideae* are characterized by less advanced (*sensu* Bailey, 1951) wood structure than *Hydrocotyloideae* and *Saniculoideae*, as indicated by the longer length of their vessel elements. However, relationships within these three subfamilies remain obscure for wood anatomists. A woody habit appears to have arisen secondarily from herbaceous ancestors in several *Apiaceae* genera such as the hydrocotyloids *Asteriscium*, *Azorella* and *Mulinum* Pers. (Rodriguez, 1957), and the apioids *Nirarathamnos* and probably *Myrrhidendron* (Downie *et al.*, 1998). Secondary woodiness in these taxa can be recognized by an anomalous stem structure, as in *Azorella* (Rodriguez, 1957) or by such paedomorphic wood features (*sensu* Carlquist, 1962) as the combination of simple perforation plates, scalariform intervessel pitting, and a predominance of upright and square cells in ray composition, and also the tendency to raylessness in *Myrrhidendron* (Fig. 2c,d).

Three apioid genera, *Heteromorpha*, *Bupleurum* and *Melanoselinum*, form a well-delimited group distinguished from other woody *Apiaceae* by having helical thickenings on their vessel walls, septate fibres, and mostly homogeneous rays (Fig. 2a,b). The presence of septate fibres links these genera to *Araliaceae*, where this character is very common; no *Araliaceae* can, however, be regarded as their close relatives. Available data therefore confirm Drude's (1898) idea of close relationships among these three genera, as well as the view (Plunkett *et al.*, 1996a,b; Downie *et al.*, 1998) on their basal position in the Apioideae clade.

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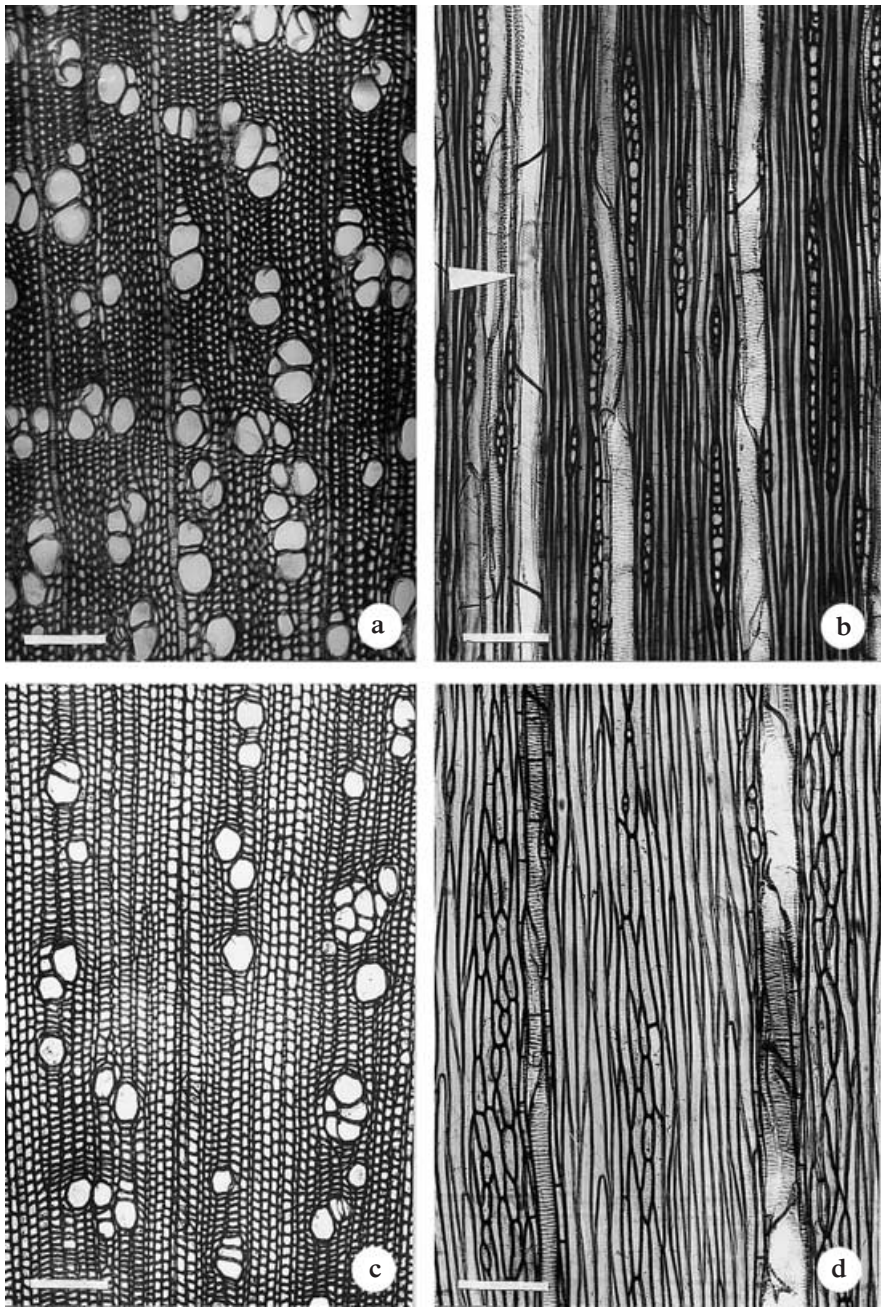
FIG. 2. Wood structure in some woody *Apiaceae* (subfam. Apioideae). Scale bar = 100 μm. a, b, *Heteromorpha arborescens* Cham. & Schltdl., Tanzania, Kw 10606; a, trans-section – thin-walled libriform fibres, scanty paratracheal axial parenchyma; b, tangential section – alternate intervessel pitting, helical thickenings on the vessel walls (arrow), septate libriform fibres, uni- and 2-seriate homogeneous rays. c, d, *Myrrhidendron pennellii* J. M. Coult. & Rose: Columbia, Uw 20765; c, trans-section – thin-walled libriform fibres, scanty paratracheal axial parenchyma, rays poorly distinguished; d, tangential section – scalariform intervessel pitting, non-septate libriform fibres, rays composed of upright cells (tendency to raylessness).



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