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Comparative bark anatomy of *Bursaria*, *Hymenosporum* and *Pittosporum* (Pittosporaceae)

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With 15 figures and 1 table

Abstract

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Bark anatomy in 3 species of *Bursaria*, 9 species of *Pittosporum*, and in the single species of monotypic genus *Hymenosporum* (Pittosporaceae) was examined. The members of these three genera resemble Araliaceae, Myodocarpaceae and Apiaceae in the occurrence of axial secretory canals in cortex and secondary phloem, the pattern of alternating zones in secondary phloem, and the absence of fibres in this tissue. We therefore confirm a relationship between Pittosporaceae and other Apiales (van Tieghem 1884, Dahlgren 1989, Takhtajan 1997, Plunkett et al. 1996, 2004) rather than its traditional placement into Rosales (Cronquist 1981). *Hymenosporum* differs markedly from *Bursaria* and *Pittosporum* in the presence of primary phloem fibres, in the cortical (v*s* subepidermal) initiation of the periderm and in the occurrence of numerous (more than 25) sieve areas on compound sieve plates. These features confirm the isolated position of *Hymenosporum* within Pittosporaceae, as suggested both by traditional taxonomy and gross morphology (Cayzer et al. 2000) and by molecular phylogenetics (Chandler et al. 2007).

Keywords: Pittosporaceae, *Hymenosporum*, *Bursaria*, bark anatomy, phylogenetics.

Introduction

Pittosporaceae is a small plant family with 9 genera and roughly 200–240 species. Eight of these genera are restricted to Australia or extended into nearby Malaysia, whereas the large genus *Pittosporum* is widely distributed within the tropical and subtropical zones of the Old World (Chandler et al. 2007). As Pittosporaceae is a very distinct taxon in its floral morphology (e.g. Erbar & Leins 1995, 2004), vegetative anatomy (Carlquist 1981, Wilkinson 1992), cytology (Gros 1965) and chemistry (Jay 1969) the monophyly of this family has commonly been recognized. Nevertheless, the position of Pittosporaceae within angiosperms has long been debatable. Traditionally, this family was placed within the rosids (sensu APG 2003) near the order Rosales (Cronquist 1981) but some authors (e.g. van Tieghem 1884, Dahlgren 1980, Takhtajan

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1997) suggested on anatomical and phytochemical grounds that Pittosporaceae are related to Apiales now being part of the euasterids II. The placement of this family within the Apiales was largely confirmed by recent phylogenetic analyses of molecular data (Plunkett et al. 1996, 2004, APG 2003, Chandler & Plunkett 2004).

Bark anatomy has made an important contribution to the taxonomy of Pittosporaceae: Van Tieghem (1884) first suggested a relationship between this family and the Apiales based on presence of secretory canals in the root cortex of *Sollya* (*Billarderia*) *heterophylla* Lindl. and three species of *Pittosporum*. However, knowledge of the bark structure of Pittosporaceae remains strictly limited. To date, published results come to nothing more than a brief review of bark anatomy within the family (Metcalfe & Chalk 1950) and a more detailed description of secondary phloem and periderm in a few *Pittosporum* species (Zahur 1959). The present study aims to examine the structure of the cortex and secondary phloem in *Bursaria*, *Hymenosporum* and *Pittosporum*, in order to analyse the variation of bark features in the context of recent taxonomic and phylogenetic treatments of Pittosporaceae (Cayzer et al. 2000, Chandler et al. 2007). As that sampling is very limited (only three of nine genera belonging to the family), we consider this work as part of a further survey of the bark anatomy throughout Pittosporaceae.

Material and methods

Bark structure in 3 species of *Bursaria*, 9 species of *Pittosporum* and in the single species of monotypic genus *Hymenosporum* (Pittosporaceae) was examined (Table 1). Most of the bark samples examined were collected by G.M. Plunkett and the second author in Queensland, Australia. The samples of *P. rehderianum* and *P. anomalum* were taken by the second author from plants cultivated outdoors in the Kuban Subtropical Botanic Garden in Sochi, Russia and the sample of *P. viridiflorum* was collected by him from a tree growing on the campus of the University of Johannesburg, South Africa. Specimens 2–3 cm long were cut from branch tips without a visible periderm layer as well as from other stem parts distinguished as mature bark with more or less thick periderm and were fixed in FAA (Barykina et al. 2004). Transverse, radial, and tangential sections 15–30 μm thick were made by the freezing microtome and stained with a 1% aqueous solutions of Safranin and 1% Light Green in concentrated picric acid. For scanning electron microscopy (SEM), dry pieces of bark were sputter-coated with Au or Au/Pd and examined by the scanning microscopes CamScan S–2 and JSM.

Results

The epidermis on the young parts of the stems consists of a single layer of isodiametric, rounded and thin-walled cells. Multicellular trichomes on the epidermal surface are found in all the species except *B. incana*, *P. revolutum*, *P. rubiginosum*, *P. venulosum* and *P. wingii*. Trichomes are unbranched and uniseriate (*B. spinosa*, *B. tenuifolia*, *H. flavum* (Fig. 1) and *P. ferrugineum*), two-armed (*B. tenuifolia*, *P. anomalum*, *P. ferrugineum* and *P. rehderianum*; Fig. 2) or 2–3-seriate (*P. spinescens*; Fig. 3) and capitate glandular with multiseriate stalks (P. *viridiflorum*; Fig. 4).

The periderm is initiated in the subepidermal layer (Fig. 13) in all species examined except *H. flavum*, where it is initiated in the third or fourth layer of cortical cells

Table 1. Source of material studied.

Species	Voucher	Habit, height	Stem diameter (mm)	Provenance
Bursaria incana Lindl.	G.M. Plunkett 1530	shrub 4 m	35	Australia, Queensland, Goldsborough Rd, open forest, alt. 140 m, 30.12.1997
B. spinosa Cav.	G.M. Plunkett 1524	shrub 3 m	30	Australia, Queensland, N of Watsonville, 28.12.1997
B. tenuifolia F.M. Bailey	G.M. Plunkett 1523	treelet 4,5 m	>100	Australia, Queensland, N of Watsonville, 27.12.1997
Hymenosporum flavum F. Muell.	G.M. Plunkett 1528	treelet 2 m	40	Australia, Queensland, Gilles Lookout Rd., private garden. 29.12.1997.
Pittosporum anomalum Laing & Gourlay	A.A. Oskolski 18-07	shrub 1,5 m	5	Russia, Sochi, Kuban Subtropical Botanic Garden, 07.07.2007
P. ferrugineum Ait. f.	G.M. Plunkett 1529	tree 5 m	>80	Australia, Queensland, Goldsborough Rd, open forest, alt. 140 m, 30.12.1997
P. rehderianum Gowda	A.A. Oskolski 15-07	shrub 3 m	40	Russia, Sochi, Kuban Subtropical Botanic Garden, 07.07.2007
P. revolutum Dryand.	G.M. Plunkett 1531	shrub 2 m	25	Australia, Queensland, near Atherton, 31.12.2007
P. rubiginosum A.Cunn.	G.M. Plunkett 1503	tree 4 m	70	Australia, Queensland, Bellenden Ker Park, 27.12.1997
P. (Citriobatus) spinescens (F. Muell.) L.W. Cayzer, Crisp & I.R.H. Telford	G.M. Plunkett 1534	shrub 4 m	45	Australia, Queensland, Forty Miles Scrub National Park, alt. 800 m, 31.12.1996
P.venulosum F. Muell.	G.M. Plunkett 1518	tree 5 m	40	Australia, Queensland, near road Herbuton – Atherton – Ravenshoe, 28.12.1997
P. viridiflorum Sims	A.A. Oskolski 01-07	tree 8 m	30	South Africa, Johannesburg, campus of the University of Johannesburg, 10.05.2007
P. wingii F. Muell.	G.M. Plunkett 1543	tree 5 m	50	Australia, Queensland, Gadgarra state forest, alt. 670 m, 02.01.1997

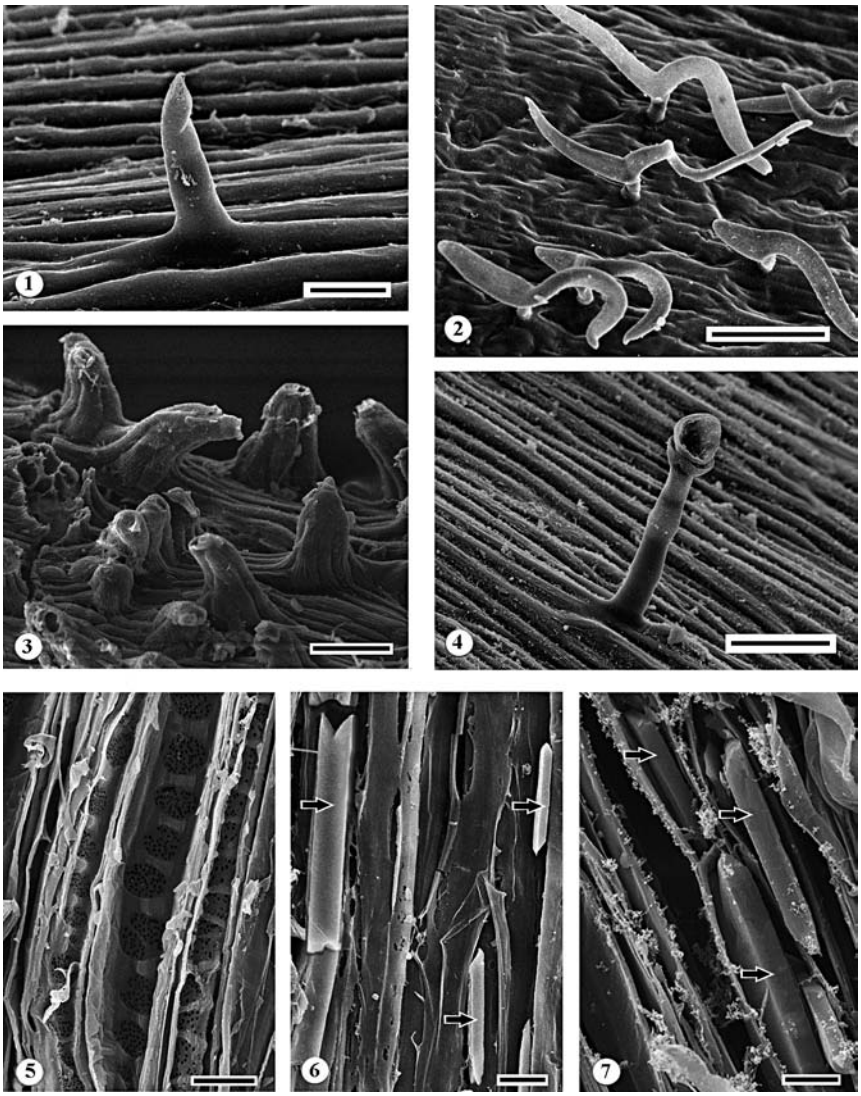

Fig. 1–7, SEM graphs. — 1, Unbranched 2–3-seriate trichomes of *Pittosporum spinescens*. Scale bar = 100 μm. –2, Two-armed trichomes of *Pittosporum rehderianum*. Scale bar = 100 μm. — 3. Unbranched uniseriate trichome of *Hymenosporum flavum*. Scale bar = 20 μm. — 4, Capitate trichome of *Pittosporum viridiflorum*. Scale bar = 50 μm. — 5, Sieve tube member with compound sieve plates in secondary phloem of *Pittosporum rehderianum*. Scale bar = 10 μm. — 6–7, Calcium oxalate styloids (black arrows) in axial parenchyma cells of secondary phloem. Scale bars = 10 μm. — 6, *Bursaria spinosa*. — 7, *Pittosporum viridiflorum*.

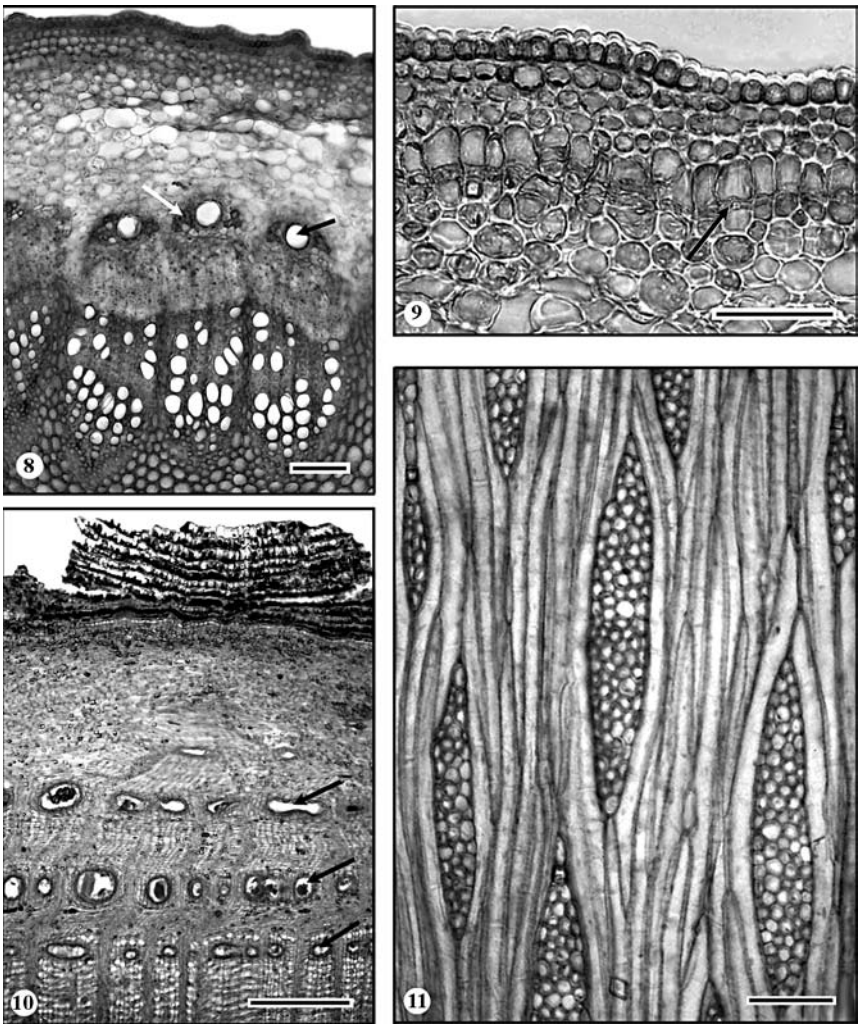

Fig. 8–11, *Hymenosporum flavum*. — 8, Primary bark with axial secretory canals (arrows) and primary phloem fibres. Transsection, scale bar = 500 μm.– 9, Epidermis and outer region of primary bark showing initiation of phellogen in 3–4 layer of cortical cells (arrow). Transsection, scale bar = 50 μm. — 10, Periderm and dilated secondary phloem with axial secretory canals (arrows). Transsection, scale bar = 500 μm. — 11, Multiseriate rays in non-dilated secondary phloem. Tangential section, scale bar = 100 μm.

(Fig. 9). The phellem is composed of 5–25 (up to 50 in *P. spinescens*) layers of isodiametric to radially flattened cells with thin nonsclerified walls. The tannin contents commonly occur in phellem cells in all species examined except *B. incana*, *P. spinescens*, and *P. viridiflorum*. The phelloderm is composed of 2–8 (up to 18 in *P. rubiginosum*) layers of radially flattened cells which are thin-walled and nonsclerified in the

outer layers, and thick-walled and sclerified in the deeper layers (sclerified phelloderm cells are not found in *P. anomalum* and *P. viridiflorum*). Some phelloderm cells contain prismatic calcium oxalate crystals.

Initiation of a second periderm was observed in *B. spinosa* and *P. spinescens*. A thick (up to 15 mm) rhytidome of 4–6 successive periderms was found in *B. tenuifolia* where the phellem of successive periderms in the latter species cosists of 6–10 layers of thin-walled (mostly tanniferous) cells. The clusters of dilated secondary phloem and 3–8-layered fragments of phelloderm — composed of thick-walled cells commonly containing prismatic crystals with facets of 10–20 μm in length — occur between the successive periderms.

The cortical collenchyma is lamellar or angular-lamellar of 2–5 cell layers with a tangential diameter of collenchyma cells of 10–45 μm. Cortical parenchyma is composed of 3–8 (up to 15 in *H. flavum* and *P. rehderianum*, and up to 20 in *P. viridiflorum*) layers of isodiametric or tangentially-elongated, thin-walled cells. The tangential diameter of cortical parenchyma cells varies from 10 to 60 μm. Druses (12–30 μm in diameter) are present in the cortical parenchyma cells of *H. flavum*, *P. spinescens*, *P. rehderianum*, *P. revolutum*, *P. venulosum* and *P. wingii*. Prismatic crystals occur in the cortical parenchyma cells of all species except *B. spinosa*, *P. ferrugineum*, *P. rehderianum* and *P. spinescens*. Axial secretory canals are arranged in a single ring in the innermost part of the cortical parenchyma. Lumina of the axial secretory canals are 20–90 μm (up to 120 in *P. venulosum*) in tangential diameter, lined by a single layer of 7–18 (12–22 in *P. venulosum*) epithelial cells.

Primary phloem fibres occur only in *H. flavum* (Fig. 8, 12). They are thick-walled and aggregated into small clusters 2–5 tangential layers deep, or are sometimes solitary.

Dilatation of the cortical tissue is effected mostly by tangential stretching of cells, but sometimes by anticlinal division of the cortical collenchyma and parenchyma cells. Tangentially elongated sclereids up to 100 μm in length and isodiametric, thick-walled sclereids 20–60 μm in diameter commonly occur in the outermost region of the dilated cortical parenchyma (only tangenially-elongated sclereids 20–80 μm in length are present in *H. flavum* and *B. tenuifolia*). These sclereids tend to aggregate into continuous band in the oldest cortex regions. No sclereids were found in *P. anomalum*, *P. rehderianum* and *P. viridiflorum*.

The secondary phloem is composed of tangential zones of 10–50 cell layers, consisting of sieve elements, companion cells and axial phloem parenchyma cells, alternating with tangential rows (4–8 cell layers deep) of axial secretory canals surrounded by axial sheath parenchyma (excepting *P. wingii* and *P. revolutum* where no axial canals are found in the secondary phloem). This pattern of alternating zones is obscured in the outermost region where phloem parenchyma is greatly dilated (Fig. 10, 14). The transition from noncollapsed to collapsed secondary phloem is gradual.

Sieve tube members are 8–30 μm wide and 150–600 μm long. Sieve plates are compound, with 10–20 sieve areas (Fig. 5; up to 25 in *P. rehderianum* and up to 35 in *H. flavum*) located on the vertical or slightly oblique end walls.

The axial parenchyma associated with conductive elements is fusiform, or in strands of 2–10 cells. Some axial parenchyma cells in the noncollapsed secondary phloem

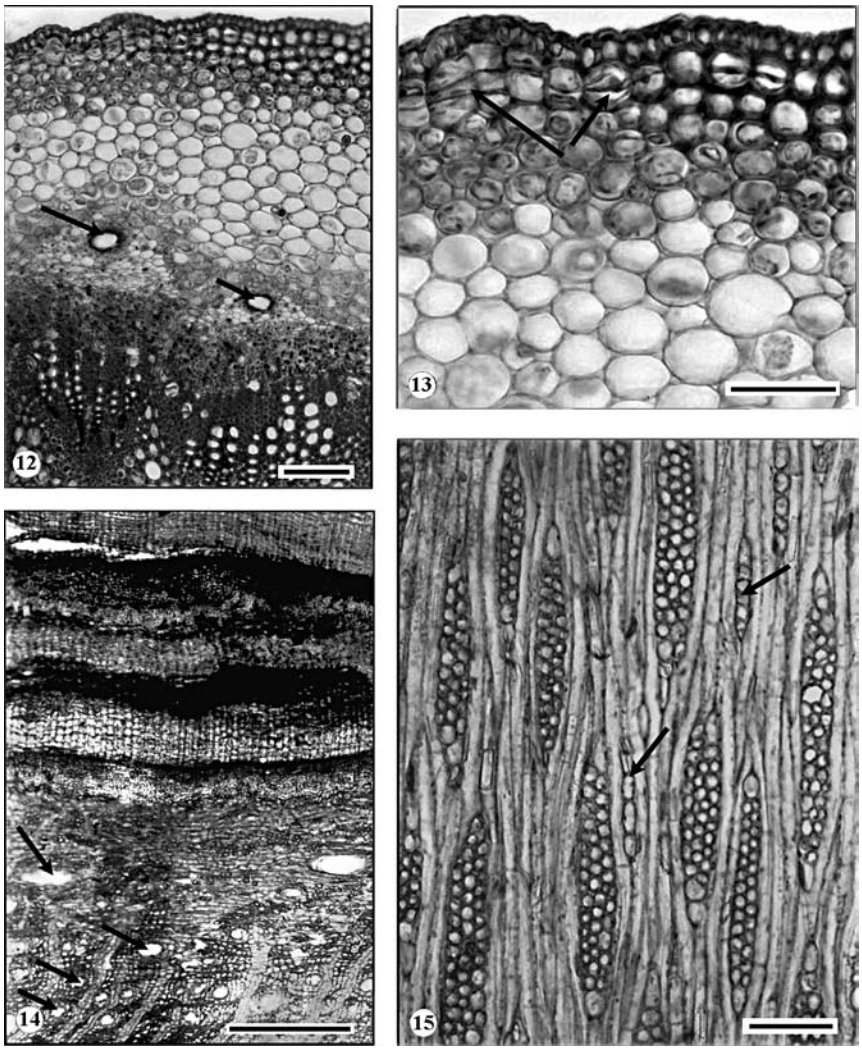

Fig. 12–15. — 12, Primary bark of *Pittosporum viridiflorum* with axial secretory canals (arrows) but without primary phloem fibres. Transsection, scale bar = 100 μm. — 13, Epidermis and outer region of primary bark of *P. viridiflorum* showing subepidermal initiation of phellogen (arrow). Transsection, scale bar = 50 μm. — 14, Periderm and dilated secondary phloem of *Pittosporum spinescens* with axial secretory canals (arrows). Transsection, scale bar = 500 μm. — 15, Uni- and multiseriate rays in non-dilated secondary phloem of *P. spinescens*. Tangential section, scale bar = 100 μm.

contain calcium oxalate styloids (3–14 μm wide and 15–60 μm long; Fig. 6, 7) or — rarely — prismatic crystals (7–15 μm long). Crystals were not found in the noncollapsed secondary phloem of *H. flavum*, *P. ferrugineum*, *P. rubiginosum* and *P. wingii*.

Axial parenchyma cells in the collapsed secondary phloem have thin to thick sclerified walls but are nonsclerified in *B. tenuifolia*, *H. flavum*, *P. anomalum* and *P. rehde-*

rianum. Some axial parenchyma cells contain prismatic or irregular crystals (no crystals were found in *P. rubiginosum*); small druses (10–15 μm in diameter) rarely occur in *P. anomalum*.

Axial secretory canals in the secondary phloem are lined by a single layer of 6–18 epithelial cells, and accompanied by 1–3-seriate sheaths of axial parenchyma. Axial parenchyma sheaths near the secretory canals consist of strands of 3–12 thin-walled cells. Axial secretory canals are not found in *P. revolutum* and *P. wingii*.

Secondary phloem rays are uni- and multiseriate (Fig. 15) or only multiseriate (in *B. incana*, *B. tenuifolia*, *H. flavum* (Fig. 11), *P. ferrugineum*, *P. rehderianum* and *P. viridiflorum*). Uniseriate rays consist of 2–8 cell rows, composed mostly of square and upright cells. Multiseriate rays are composed of procumbent body cells with upright and square cells forming 1(2) marginal rows. Nondilated phloem rays are 2–5-seriate (4–6-seriate in *B. tenuifolia*) and up to 40 cells in height.

Cells of the dilated rays are enlarged by tangential expansion and also by anticlinal divisions (ray width increasing up to 8-seriate during dilatation). Dilated ray cells are rarely sclerified. Druses are found only in *P. anomalum* but prismatic crystals are present in the dilated ray cells of all the species examined. Radial secretory canals are not found.

Discussion

As our results show, *Bursaria*, *Hymenosporum*, and *Pittosporum* resemble the members of Araliaceae, Myodocarpaceae and woody Apiaceae (Viguier 1906, Metcalfe & Chalk 1950, Holdheide 1951, Kolalite et al. 2003, Oskolski et al. 2007, Kotina & Oskolski 2007, Kotina 2008) in their overall bark structure. Three genera studied share with these families such remarkables features such as the occurrence of the axial secretory canals in cortex and secondary phloem, distinctive pattern of secondary phloem (alternation of tangential zones of conductive elements with rows of axial secretory canals sheathed by axial parenchyma) and absence of fibres in this tissue. Conversely, the members of the families belonging to the order Rosales sensu APG (2003), i.e. Rosaceae, Rhamnaceae, Moraceae, Urticaceae and Ulmaceae are commonly characterized by the occurrence of fibres and absence of axial secretory canals in the secondary phloem (Metcalfe & Chalk 1950, Roth 1981, Metcalfe 1983, Furuno 1990, Lotova 1998, Lotova & Timonin 2005). Therefore, we confirm a relationship between Pittosporaceae and Apiales (van Tieghem 1884, Dahlgren 1980, Takhtajan 1997, Plunkett et al. 1996, 2004) rather than its traditional placement into Rosales (Cronquist 1981).

The genera examined, however, are distinguished by the common occurrence of styloids in the axial parenchyma of the secondary phloem. Crystals of this type are not at all common within Apiales: they have only been reported in *Delarbrea harmsii* R. Vig. and *Myodocarpus vieillardii* Brongn. & Gris from Myodocarpaceae (Kotina 2008). Occurrence of this feature in Pittosporaceae and Myodocarpaceae, as distinct from other Apiales, points to a relationship between these two families suggested by molecular phylogenetics (Chandler & Plunkett 2004, Plunkett et al. 2004).

The absence of primary phloem fibres in *Bursaria* and *Pittosporum* is also a rather distinctive character. This condition rarely occurs within Apiales: it has been reported only in *Neopanax*, *Oplopanax* and in a single species of *Polyscias* (Araliaceae; Kotina 2008). Primary phloem fibres are, however, present in *Hymenosporum*; thus this character is of diagnostic value at generic level only.

Hymenosporum differs markedly from *Bursaria* and *Pittosporum* not only in the presence of primary phloem fibres but also in the cortical (*vs* subepidermal) initiation of the periderm and by the occurrence of numerous (more than 25) sieve areas on compound sieve plates. These features confirm the isolated position of *Hymenosporum* within Pittosporaceae as suggested both by traditional taxonomy and gross morphology (Cayzer et al. 2000) and by molecular phylogenetics (Chandler et al. 2007). We cannot, however, distinguish between *Bursaria* and *Pittosporum* on the basis of bark anatomical characters.

Our results therefore show that some bark characters are valuable for taxonomy and phylogenetics of Pittosporaceae. However, the bark structure remains to date poorly known for the most genera of this family (i.e. *Auranticarpa*, *Rhytidosporum*, *Marianthus*, *Bentleya*, *Cheiranthera*, *Billarderia*). Further anatomical studies in these taxa could be important to clarify the relationships within Pittosporaceae as well as to the pathways of their bark evolution.

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