



Wood anatomy of *Brabejum* and *Macadamia* (Macadamiinae, Proteaceae)

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ABSTRACT

Wood structure of *Brabejum stellatifolium* and *Macadamia integrifolia* (subtribe Macadamiinae, tribe Macadamieae, Proteaceae) is described for the first time. These species share exclusively simple perforation plates, minute to small alternate intervessel pits, non-septate libriform fibers, banded and unilaterally paratracheal axial parenchyma, and the rays of two distinct sizes, i.e. the suite of typical wood traits for many of Proteaceae. Our observations together with reported data suggest that the lineage comprising *Brabejum*, *Macadamia* and *Panopsis* is distinctive from closely related members of the tribe Macadamieae by the occurrence of vasicentric tracheids combined with the lack of fiber tracheids. More abundant axial parenchyma in *Macadamia* and *Panopsis* than in *Brabejum* is seemingly consistent with the global tendency to increase of amount of this tissue in the regions with warm climate. Libriform fibers in *Macadamia integrifolia* show one of the highest degrees of intrusiveness (F/V ratio = 3.98) reported within Proteaceae to date.

Key words: *Brabejum*, *Macadamia*, Proteaceae, wood anatomy, vasicentric tracheids

РЕЗЮМЕ

Степанова А.В., Оскольский А.А. Анатомия древесины *Brabejum* и *Macadamia* (Macadamiinae, Proteaceae). Впервые описано анатомическое строение древесины *Brabejum stellatifolium* и *Macadamia integrifolia* (подтриба Macadamiinae, триба Macadamieae, семейство Proteaceae). Для этих видов характерен набор признаков, типичных для многих протейных, таких как исключительно простые перфорационные пластинки, очень мелкие поры межсосудистой поровости, несептированные древесинные волокна, аксиальная паренхима односторонне-паратрахеальная и в тангентальных полосах, две отчетливых размерных группы лучей. Наши и литературные данные указывают на то, что монофилетическая группа, включающая роды *Brabejum*, *Macadamia* и *Panopsis*, отличается от других представителей Macadamieae наличием вазисентрических трахеид в сочетании с отсутствием волокнистых трахеид. Более обильная аксиальная паренхима у *Macadamia* и *Panopsis* по сравнению с *Brabejum* соответствует глобальной тенденции к увеличению количества этой ткани у растений в регионах с теплым климатом. Древесинные волокна *Macadamia integrifolia* характеризуются одним из самых высоких уровней интрузивности (отношение средней длины волокон к средней длине члеников сосудов равно 3,98), известным для протейных.

Ключевые слова: *Brabejum*, *Macadamia*, Proteaceae, анатомия древесины, вазисентрические трахеиды

Subtribe Macadamiinae L.A.S. Johnson & B.G. Briggs belonging to the tribe Macadamieae C. Venkata Rao of Weston & Barker's (2006) classification of Proteaceae Juss. comprises five genera with 36 species of evergreen trees and shrubs with mostly verticillate leathery leaves (Weston 2007). This small lineage is widespread across the southern hemisphere. The best known genus of this group is *Macadamia* F. Muell. with four species which are naturally distributed in subtropical regions of eastern Australia, two of which (*M. integrifolia* Maiden & Betche and *M. tetraphylla* L.A.S. Johnson and their hybrids) are widely cultivated for their edible seeds (macadamia nuts). The genus *Lasjia* P.H. Weston & A.R. Mast, that has recently been separated from *Macadmia* (Mast et al. 2008), comprises four tropical species from tropical rain forests of north-eastern Queens-

land and one species from Sulawesi. Monospecific *Nothorites* P.H. Weston, that has initially been described as a species of *Orites* R. Br. from the tribe Roupaleae (George & Hyland 1995), is also endemic of north-eastern Queensland. Unlike these three genera, 25 species of *Panopsis* Salisb. are widespread in shrublands, savannas, xerophytic woodlands, riparian forests and lowland to montane rainforests of tropical South and Central America (Prance et al. 2007, Weston 2007). Finally, *Brabejum stellatifolium* L., the only species of the genus *Brabejum* L., is a component of fynbos biome and Afrotropical forests restricted to the Cape region in South Africa with its Mediterranean climate (Mucina & Rutherford 2006, Weston 2007, Mast et al. 2008).

The time of radiation of the subtribe Macadamiinae is estimated as the late Oligocene – early Miocene. Disjunct

distribution of this group is seemingly a result of long-distance dispersal of their buoyant diaspores from Australia to South America and Africa by the Antarctic Circumpolar Current that has also developed in the Oligocene. The evolutionary shifts from the early fruit and seed maturity found in *Macadamia* and other Australian members of this group to the tardy dehiscence at the seed germination, which is shared by extra-Australian taxa are well consistent with this scenario (Mast et al. 2008).

The subtribe Macadamiinae is poorly explored by wood anatomists: the detailed information on wood structure has been published to date only for two species of *Panopsis* (Mennega 1966, Detienne & Jacquet 1983). Brief wood anatomical description and microphotos are available also for *Macadamia ternifolia* F. Muell. (Chattaway 1948, InsideWood 2004–onwards). Quantitative data on wood density, diameter of vessel lumina and vessel wall thickness in the *Brabejum* wood have been reported by Crous et al. (2012). The aim of the current study is the detailed examination of wood structure of *Brabejum* and *Macadamia*, and its comparisons with related groups of Proteaceae.

MATERIAL AND METHODS

Wood sample of *Brabejum stellatifolium* was collected by Alexei Oskolskii on 05.09.2016 in afrotemperate forest on the eastern slope of Table Mountain near the Kirstenbosch Botanical Garden, Cape Town, South Africa. Wood sample of *Macadamia integrifolia* was taken by him on 10.04.2019 from the tree cultivated in Pretoria, South Africa. Both wood samples were collected from large branches. Herbarium vouchers (A.A. Oskolskii # 98 for *B. stellatifolium* and # 281 for *M. integrifolia*) are deposited in JRAU; wood samples are deposited in the Xylarium of the Komarov Botanical Institute, St. Petersburg, Russia (LEW).

Transverse, radial, and tangential microtome sections of 20–30 µm in thickness were stained with alcian blue/safranin (Jansen et al. 2004), dehydrated in gradient series of alcohol, and then mounted in Euparal. Macerations were made using Jeffrey's solution (Johansen 1940). Descriptive terminology followed the recommendations of the IAWA Committee (1989). The quantitative data are summarized in Table 1. Details of the microstructure of intervessel pits were investigated by scanning electron microscopy (SEM TESCAN, soft – VegaTS) at Spectrum, University of Johannesburg. For the SEM examination, dried wood samples were mounted on aluminum stubs with double-sided carbon tape and coated with gold.

Evolution of selected wood anatomical features was clarified by mapping discrete characters on a subsample of the tree recovered from the Bayesian analyses of a data set of three chloroplast DNA and four nuclear DNA sequences as well as morphological data for the tribe Macadamieae (Mast et al. 2008). Character optimization along the branches of the tree was illustrated using the parsimony reconstruction method of the Character History Tracing option in the computer package Mesquite 2.75 (Maddison & Maddison 2011).

RESULTS

Wood anatomy of *Brabejum stellatifolium* (AO 98-16)

Wood diffuse-porous. Growth ring boundaries indistinctly marked by 3–6 rows of weakly flattened fibres. Vessels few (up to 25 per mm²), medium to wide (67–178 µm in tangential diameter), solitary, in clusters and in tangential multiples of 2–8 (up to 12), thin-walled (wall thickness 2.8–5.3 µm) (Fig. 1a). Vessel lumina round to slightly angular. Vessel elements relatively long (average length 710 µm, range 299–987). Perforation plates simple. Intervessel pits alternate, minute to small (3.1–5.9 µm in vertical size), non-vestured, with oblique oval apertures (Fig. 1b,c). Vessel-ray pits distinctly bordered (occasionally with reduced borders or simple), similar to intervessel pits in size and shape. Solitary vascentric tracheids occur in vessel groups. Helical thickenings not found.

Fibres libriform, non-septate, long (fiber length 1082–2056 µm), with moderate intrusiveness (F/V ratio = 2.3), with simple to minutely bordered pits on very thin walls (2.8–3.7 µm thick).

Table 1. Wood anatomical characters of *Brabejum stellatifolium* and *Macadamia integrifolia*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Brabejum stellatifolium</i> [AO 98-16]	110±4.7 67–178	23.1 14–37	2.3/12	12	4.5 3.1–5.9	710±30.2 299–987	1657±46.0 1080–2060	2.33 18.6–33.9	24.4±0.82 18.6–33.9	2.8–3.7	2.8–5.3	2–4	1–2/7–20	304 33–475	3266 409–5729	1.3±0.14 1.0–2.1	1.1±0.22 0–2.1	2.3±0.21 1.0–3.2
<i>Macadamia integrifolia</i> [AO 281-19]	66±2.5 25–99	23.4 17–30	2.2/8	17	4.2 3.4–5.0	376±11.4 201–523	1494±28.6 1080–1890	3.98 8.1–22.2	15.9±0.43 8.1–22.2	3.8–10.5	2.9–5.8	2–6	1–3/7–34	279 38–750	1123 229–2893	1.2±0.07 0.8–1.9	3.1±0.14 1.9–4.9	4.3±0.13 3.4–5.7

1 – Tangential diameter of vessels (mean ± standard error, min–max, µm); 2 – number of vessel lumina per sq.mm (mean, min–max); 3 – mean/ max number of vessel lumina per group; 4 – percent of solitary vessels; 5 – diameter of intervessel pits (mean, min–max, µm); 6 – length of vessel elements (mean ± standard error, min–max, µm); 7 – length of fibres (mean ± standard error, min–max, µm); 8 – F/V ratio; 9 – tangential diameter of fibres (mean ± standard error, min–max, µm); 10 – fibre wall thickness (min–max, µm); 11 – vessels wall thickness (min–max, µm); 12 – number of axial parenchyma cells per strand; 13 – width of narrow/ broad rays (cell number); 14 – width of multiseriate rays (mean, min–max, µm); 15 – height of multiseriate rays (mean, min–max, µm); 16 – number of multiseriate rays per mm; 17 – number of uniseriate rays per mm; 18 – total number of rays per mm

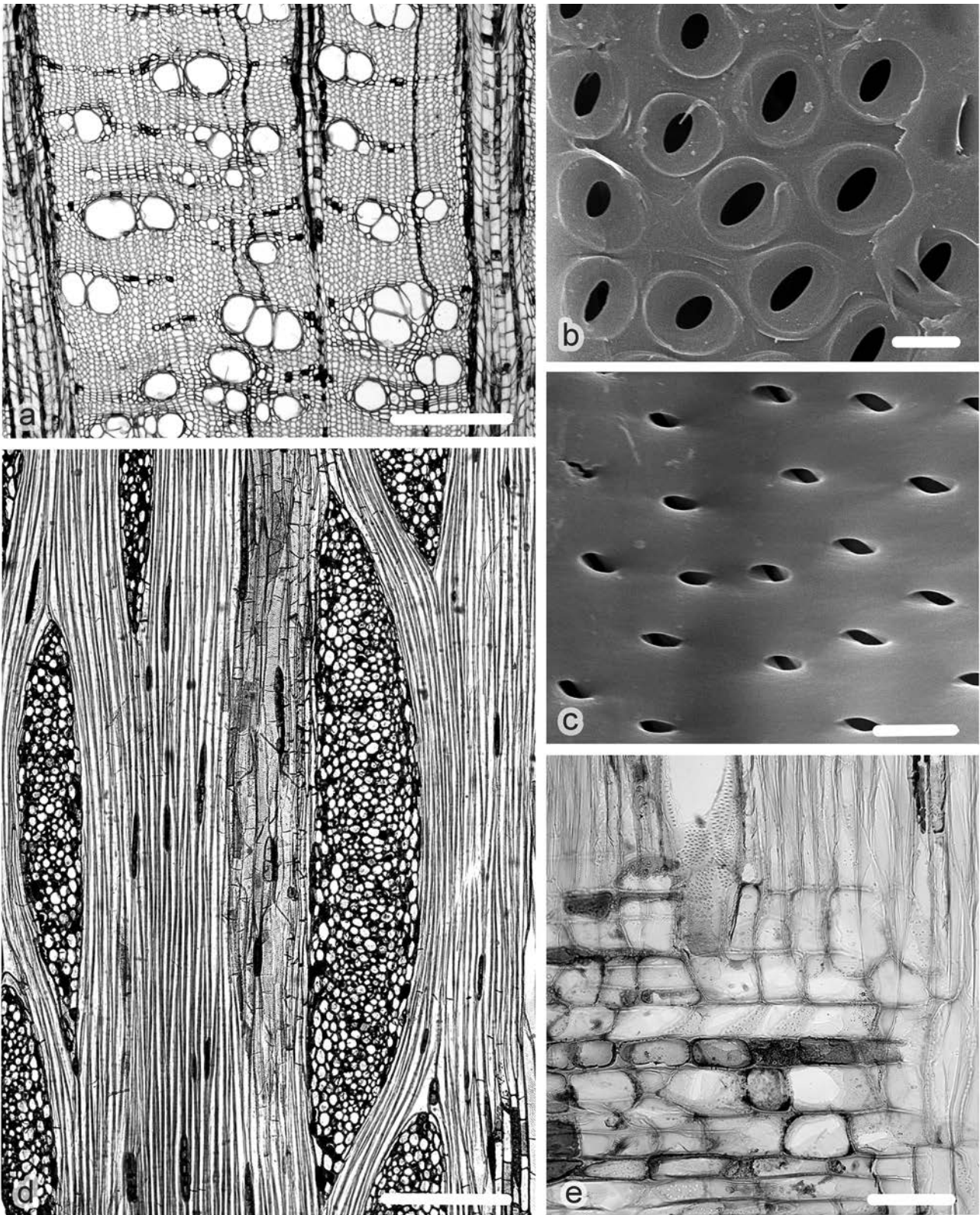


Figure 1 Wood structure of *Brabejum stellatifolium* L. [AO 98-16]: (a) vessels in short tangential multiples and clusters, thin-walled libriform fibres, axial parenchyma unilateral paratracheal and in 1–3-seriate tangential line, light microscopy (LM), transverse section (TS); (b) alternate intervessel pits with chambers lacking warty layer (SEM, RLS); (c) apertures of intervessel pits without groove-like wall sculptures, scanning electron microscopy (SEM), radial longitudinal section (RLS); (d) rays of two distinct sizes (uniseriate and 8–15-seriate ones), strands of axial parenchyma (LM, TLS); (e) procumbent, square and upright ray cells, vessel-ray pits (LM, RLS). Scale bars = 500 μm (a,d), 100 μm (e), 5 μm (b,c)

Axial parenchyma unilateral paratracheal, winged aliform and banded (Fig. 1a), in lines and narrow (up to 5-seriate) bands associated with vessels and vessel groups in unilateral pattern (i.e. vessels and vessel groups mostly attached to axial paren-

chyma bands with their outer sides, but occasionally embedded into the bands). Axial parenchyma strands consist of 2–6 cells.

Rays few (1.1–3.2 per mm), of two distinct sizes (Fig. 1d). Narrow rays uniseriate (occasionally 2-seriate),

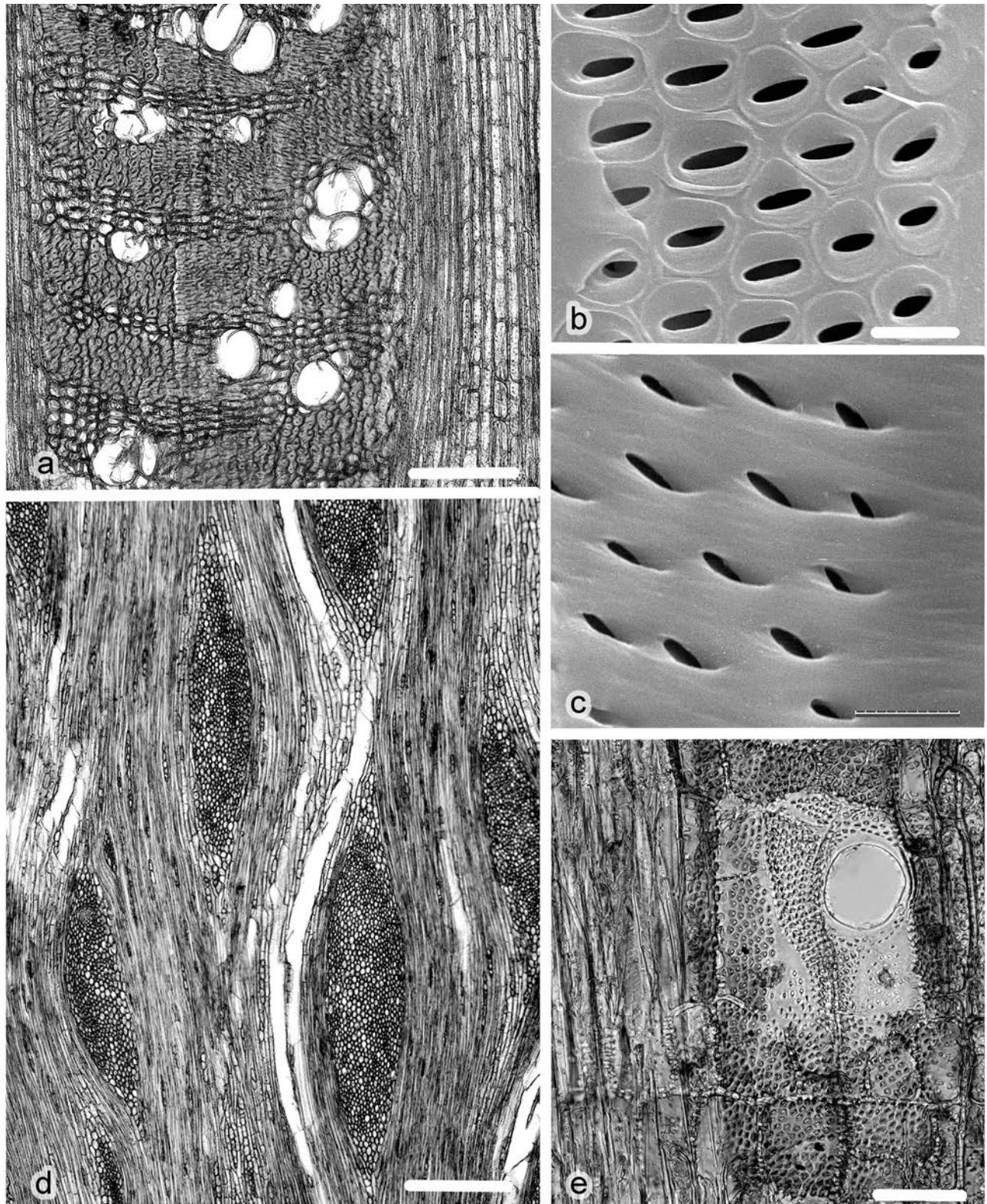


Figure 2 Wood structure of *Macadamia integrifolia* Maiden & Betche [AO281-19]: (a) vessels solitary and in clusters, thick-walled libriform fibres, 3–7-seriate bands of axial parenchyma in reticulate arrangement (LM, TS); (b) chambers of intervessel pits lacking warty layer (SEM, RLS); (c) apertures of alternate intervessel pits surrounded and occasionally interconnected by groove-like wall sculptures (SEM, RLS); (d) rays of two distinct sizes (1–2-seriate and 5–25-seriate ones) (LM, TLS); (e) simple perforation plates, band of axial parenchyma, mostly procumbent ray cells (LM, RLS). Scale bars = 500 μ m (a), 200 μ m (d), 50 μ m (e), 5 μ m (b,c)

consists mostly of square and upright cells, occasionally also with procumbent cells. Broad rays 7–20 seriate, up to 2.9 mm in height, composed mostly of procumbent cells, with upright and square cells in 1–3 marginal rows and in incomplete sheaths (Fig. 1e). No sclerified ray cells found.

Brown content occur in axial parenchyma and ray cells. Crystals and silica bodies not found.

Note: Crous et al. (2012) reported much smaller diameter of vessel lumina in *Brabejum stellatifolium* (average 39.6–42.5 μ m) than we found in this species.

Wood anatomy of *Macadamia integrifolia* (AO 281-19)

Wood diffuse-porous. Growth rings absent. Vessels not numerous (up to 30 per mm²), moderately wide (25–100 µm in tangential diameter), solitary and mostly in small clusters and tangential multiples of 2–4 (up to 8) vessels associated with tangential bands of axial parenchyma, thin-walled (wall thickness 2.9–5.6 µm) (Fig. 2a). Vessel lumina round to slightly angular. Vessel elements relatively short (average length 376 µm, range 200–520 µm). Perforation plates simple. Intervessel pits alternate, minute to small (3.4–5.0 µm in vertical size), non-vestured (Fig. 2b), with oblique to horizontal oval apertures, sometimes interconnected by shallow grooves (Fig. 2c). Vessel-ray pits distinctly bordered (occasionally with reduced borders or simple), similar to intervessel pits in size and shape. Solitary vasicentric tracheids occur in vessel groups. Helical thickenings not found.

Fibres libriform, non-septate, long (1000–1900 µm in length), with high intrusiveness (F/V ratio = 3.98), with simple to minutely bordered pits on thick to very thick-walled (3.8–10.5 µm).

Axial parenchyma (Fig. 2a) abundant in 3–7-seriate tangential bands associated with vessels and vessel groups in unilateral paratracheal pattern (i.e. vessels and vessel groups mostly attached to axial parenchyma bands with their outer sides, but occasionally embedded into the bands). Axial parenchyma strands consist of 2–6 cells.

Rays of two distinct sizes (Fig. 2d). Narrow rays uniseriate (occasionally 2–3-seriate), consists mostly of square and upright cells, occasionally also with procumbent cells. Broad rays 7–34-seriate, up to 2.9 mm in height, composed mostly of procumbent cells, with upright and square cells in 1–3 marginal rows (Fig. 2e) and in incomplete sheaths. No sclerified ray cells found. Brown content occur in axial parenchyma and ray cells. Crystals and silica bodies not found.

Character evolution within the Macadamieae

Analysis of wood trait evolution based on results of our observations together with other available anatomical data (Chattaway 1948, Mennega 1966, Kribs 1968, Detienne & Jacquet 1983, Sosef et al. 1998, InsideWood 2004–onwards) showed that the patterns of variation in two wood features, namely the occurrence of distinctly bordered pits on fiber walls (Fig. 3a) and the presence of vasicentric tracheids (Fig. 3b) are apparently consistent with the topology of the phylogenetic tree of the tribe Macadamieae (Mast et al. 2008). Although no clear tendencies in evolution of these traits were revealed, the character mapping suggested that the loss of bordered pits on fiber walls as well as the gain of vasicentric tracheids (Fig. 3a,b) are associated with diversification of the subtribe Macadamieae.

DISCUSSION

Our observations together with the wood anatomical data reported for two species of *Panopsis* (Mennega 1966, InsideWood 2004–onwards) suggest that three genera of the subtribe Macadamieae share exclusively simple perforation plates, minute to small alternate intervessel pits, non-septate libriform fibers, banded and unilaterally para-

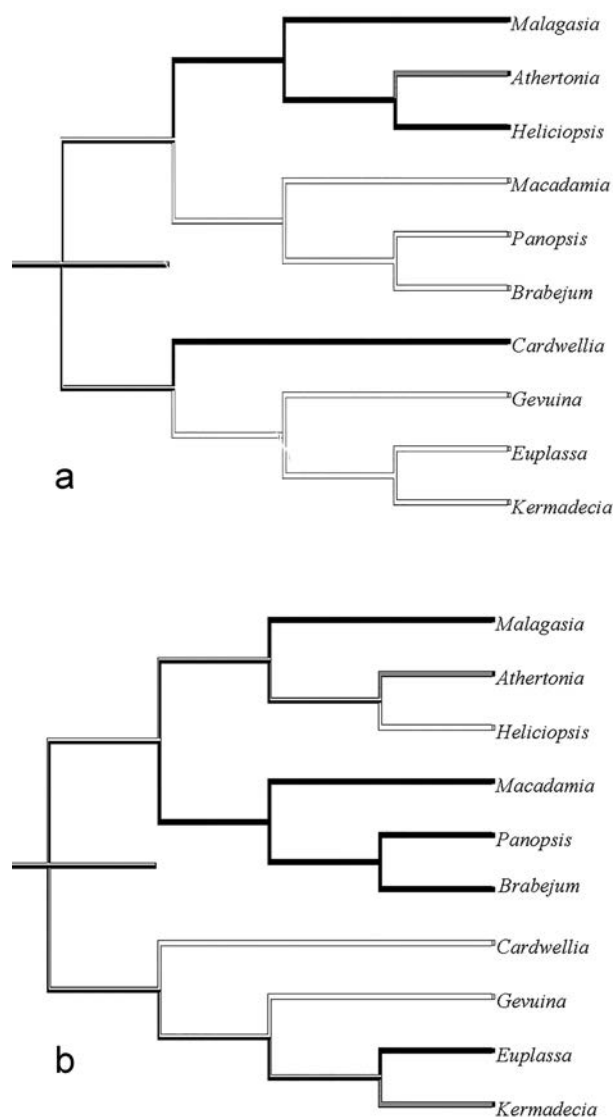


Figure 3 Distribution of the wood character states within the Macadamieae mapped onto a subsample of phylogenetic tree, recovered from the Bayesian analyses of a data set of three chloroplast DNA, four nuclear DNA sequences and morphological data (Mast et al., 2008). (A) the presence of distinctly bordered pits on fiber walls (white – absent, black – present, gray – unknown); (B) the presence of vasicentric tracheids (white – absent, black – present, gray – unknown)

tracheal axial parenchyma, and the rays of two distinct sizes (mostly uniseriate rays combined with >6-seriate ones). This suite of traits is typical for many other genera of Proteaceae (Chattaway 1948, Metcalfe & Chalk 1950, InsideWood 2004–onwards). The lineage comprising *Brabejum*, *Macadamia* and *Panopsis* is distinctive, however, from closely related members of the tribe Macadamieae by the combination of the occurrence of vasicentric tracheids and the lack of fiber tracheids, i.e. the fibers with distinctly bordered pits on their walls.

Both these traits are variable within Proteaceae, and even within Macadamieae. The presence of bordered pits on fiber walls has been reported in *Placospermum* C.T. White & W.D. Francis (Lanyon 1979) and *Persoonia* Michx. (Patel 1982) belonging to the subfamily Persoonioideae, *Dilobeia*

Thouars and *Faurea* Harv. (InsideWood 2004–onwards) of the subfamily Proteoideae as well as in several lineages of the subfamily Grevilleoideae, i.e. in *Helicia* Pers. (Sosef et al. 1998) of the tribe Roupaleae, in *Lomatia* R. Br. (Tortorelli 1956), *Stenocarpus* R. Br. (Chattaway 1948, InsideWood 2004–onwards), and *Embothrium* J.R. Forst. & G. Forst. (Detienne & Jacquet 1983) of the tribe Embothriaceae, in *Cardwellia* F. Muell. (Kribs 1968), *Heliciopsis* Sleumer (Sosef et al. 1998), *Euplassa* Salisb. (Detienne & Jacquet 1983) and *Malagasia* L.A.S. Johnson & B.G. Briggs (InsideWood 2004–onwards) belonging to the tribe Macadamieae, and in *Knightia* R. Br., the genus insertae sedis, as well (Patel 1982). Within Macadamieae, the loss of fiber tracheids is synapomorphic for the subtribe Macadamiineae comprising *Brabejum*, *Macadamia* and *Panopsis*, and, independently, for the crown group of the subtribe Gevuiniinae comprising *Gevuina* Molina, *Euplassa* and *Kermadecia* Brongn. & Gris (Fig. 3a).

Within the tribe Macadamieae, the vasicentric tracheids found in *Malagasia* (InsideWood 2004–onwards), *Euplassa* (Mennega 1966, Detienne & Jacquet 1983), *Panopsis* (Mennega 1966), *Macadamia* (Chattaway 1948) and in *Brabejum*. Apparently, the gain of these tracheary elements is characteristic for the subtribe Macadamiineae (Fig. 3b). As for other Proteaceae, this feature has been reported in the genera of all there subfamilies, i.e. in *Persoonia*, *Dilobeia*, *Faurea*, *Floydia* L.A.S. Johnson & B.G. Briggs, *Hakea* Schrad. & J.C. Wendl., *Stenocarpus*, *Xylomelum* Sm., *Roupala* Aubl., and *Knightia* (Chattaway 1948, Metcalfe & Chalk 1950, Mennega 1966, Detienne & Jacquet 1983, Patel 1992, InsideWood 2004–onwards). No large-scale patterns in evolution of this trait were revealed.

Brabejum is distinctive from *Macadamia* and *Panopsis* (Mennega 1996, InsideWood 2004–onwards) in the thickness of libriform fiber walls as well as in the abundance and distribution of axial parenchyma. Unlike its closely related genera having axial parenchyma mostly in wide bands commonly arranged into reticular pattern, *Brabejum* has mostly unilaterally paratracheal axial parenchyma, occasionally with tangential lines and narrow bands in irregular arrangement. More abundant axial parenchyma in *Macadamia* and *Panopsis*, naturally distributed in regions with warmer climates than *Brabejum* (Queensland and The Guianas vs Western Cape, respectively) is seemingly consistent with the global tendency to increase of amount of axial parenchyma in wood in the regions with higher mean annual temperature (Morris et al. 2016).

High intrusiveness of libriform fibers found in *Macadamia integrifolia* ($F/V = 3.98$) is noteworthy: this species shows on of the highest F/V ratio (3.98) reported within Proteaceae to date. This family is considered by Carlquist (2001) as one of the groups (together with Bignoniaceae Juss., Boraginaceae Juss., Malvaceae Juss., Moraceae Gaudich., Santalaceae R. Br., Scrophulariaceae Juss., Solanaceae Juss., Ulmaceae Mirb., Urticaceae Juss., and Verbenaceae J. St.-Hil.) with exceptional elongation of libriform fibers. The available data on lengths of vessel members and imperforate elements in wood (Bailey & Tupper 1918, Mennega 1966, Lanyon 1979, Patel 1982) show, however, that the F/V ratio in most Proteaceae does not exceed 3.

Greater intrusiveness has been reported (Bailey & Tupper 1918, Mennega 1966) only in *Roupala montana* Aubl. ($F/V = 3.66$), *Banksia verticillata* R. Br. ($F/V=3.75$), *Grevillea robusta* A. Cunn. ex R. Br. ($F/V=4.0$) and *Hakea leucoptera* R. Br. ($F/V=5.0$). More comprehensive data are required to clarify the evolutionary and/or ecological patterns of variation of this interesting trait within Proteaceae.

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