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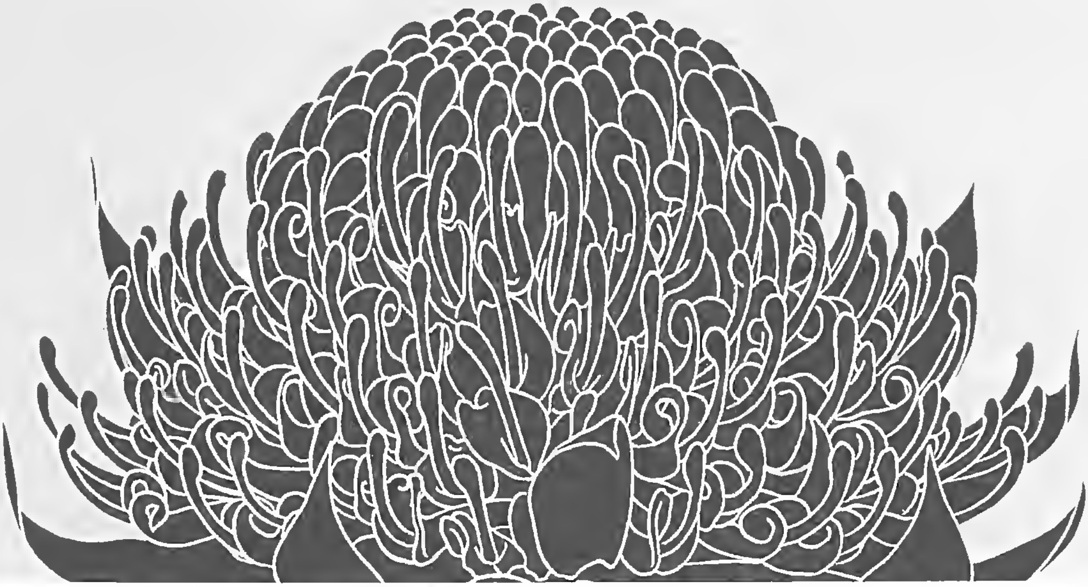

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Telopea Telopea 11(3) 246–251

Bazzania scalaris sp. nov. (Marchantiophyta: Lepidoziaceae) from Papua New Guinea

David Meagher

School of Botany, The University of Melbourne, Victoria 3010

Abstract

Bazzania scalaris sp. nov. (Marchantiophyta : Lepidoziaceae), a liverwort from the East Sepik District of Papua New Guinea, is described. The unpublished name 'Mastigobryum linearifolium' in Franz Stephani's *Icones* is recognised as this species.

Introduction

The genus *Bazzania* Gray comprises leafy liverworts with two rows of lateral leaves inserted incubously on the stem, a row of underleaves on the ventral side of the stem, and minutely leafy ventral flagella arising from the axils of underleaves. The cells in the outer layer of the stem are not differentiated from those of the inner stem. The branches are always of the *Frullania*- type; that is, the branch replaces the ventral half of a lateral leaf, leaving the other half of the leaf in the branch junction on the dorsal side. In almost all species the branches grow as strongly as the stem from which they arise, so that the branching is distinctly Y-shaped and resembles dichotomous branching. For this reason, such branching is called 'pseudodichotomous'.

The character trilobed lateral leaves is the normal condition in *Bazzania*, but a small number of bilobed or unlobed species are known. Bilobed species have been placed traditionally in section *Bidentatae*, which once included species now placed in genus *Acromastigum*. In that genus each flagellum replaces half an underleaf, the lateral leaves are never trilobed, and the stem in cross-section has an outer layer of enlarged, transparent cells. Other differences are described by Kitagawa and Grolle (1986). Species of both genera were once grouped together in the genus *Mastigobryum* Gottsche, Lindenb. & Nees, but most have now been transferred from that genus.

Several bilobed species of *Bazzania* are known from Asia and South East Asia, and are well documented in the literature (e.g. Meijer 1960, Pócs 1969, Kitagawa & Kodama 1975, Kitagawa 1980). None has the combination of characters seen in the current species.

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Bazzania scalaris **D.Meagher,** ***sp. nov.***

Diagnosis. *Bazzania* foliis suboppositis, subvittatis, asymmetrice oblongis, fragilis, apicibus asymmetrice 2-dentatis et saepe crenulatis; amphigastriis laceratis, plerumque 3–4-lobatis sed cum lobis minoribus additiciis; cellulis folii valde incrassatis et nodulosis; cellulis amphigastriorum similaribus sed minoribus; gynoecia et androecia desunt.

Type: Papua New Guinea, East Sepik: eastern ridge of Sumset (Mount Hunstein), 15 Aug 1966, R.D. Hoogland 11011 & L.A. Craven. Holotype: CANB 174151. Isotypes: COLO, F, MEL, MELU (the following replicates have not been examined – BM, JE, LAE, L, TNS).

Plants delicate, strongly anisophyllous, forming loose mats on rock. Branching infrequent, pseudodichotomous, the branches of *Frullania*-type; branch dorsal half-leaf ± symmetric, narrowly ovate, tapering to an acute, undivided apex; first branch underleaf 2-fid, often with one or two smaller lobes, adjacent to but not connate with the adjacent stem underleaf. Leaves mostly about 1.2–1.6 mm × 0.4–0.6 mm, subopposite to almost alternate, spreading widely whether moist or dry, fragile, often missing or broken; asymmetrically oblong, with arched dorsal and ventral margins that are often crenulate from projecting cell walls, cuticle smooth; subvittate, with a narrow region of distinctly elongate but not wider cells extending almost to the sinus of the lobes; apex not much narrower than the rest of the leaf, consistently 2-fid with widely to narrowly triangular lobes, sinus between lobes lunate to widely angular, margins often crenulate. Cells in mid-leaf mostly 25–35(–60) × 15–25(–35) µm, smaller near the margins, ± in regular longitudinal rows, thick-walled and strongly nodulose, with bulging and often confluent trigones. Oil bodies not seen. Underleaves mostly about 0.4–0.7 mm × 0.4–0.5 mm, narrowly to barely connate with leaves on one side only, lacerate, fundamentally 3–4-lobed but the lobes often further divided and additional smaller lobes always present. Cells of the underleaves similar to those of the leaves but slightly smaller. Flagella few, long and thin, sparsely and minutely leafy. Gynoecia and androecia not seen. Fig. 1.

Discussion

Of the small number of bilobed *Bazzania* species known, most have entire or weakly lobed underleaves, and their lateral leaf cells generally have evenly thickened walls and small trigones, or no trigones at all.

Stephani (1908, 1924) described a small number of bilobed *Bazzania* and *Mastigobryum* species from South East Asia and Australasia, and illustrated them in his unpublished *Icones* (Stephani 1985). However, not all the taxa illustrated in the *Icones* were published by Stephani, including one (no. 6857) labelled 'Mastigobryum linearifolium St. nsp, Nova Guiniae, Ledermann legit' and annotated 'Cellulae foliarum apice 18/18 µ parietibus validus, basales 18/36 µ trigonis majusculis acutis'. I am quite sure that this illustration represents *B. scalaris*, but as a description was never published the name 'Mastigobryum linearifolium' is not valid. Ledermann's herbarium is no longer in Genéve (G), and Kitagawa (1980) noted that Grolle believed it to have been burned in the destruction of the Berlin-Dahlem Herbarium during the Second World War. It is not yet clear whether any of Ledermann's collection of bryophytes from New Guinea survived.

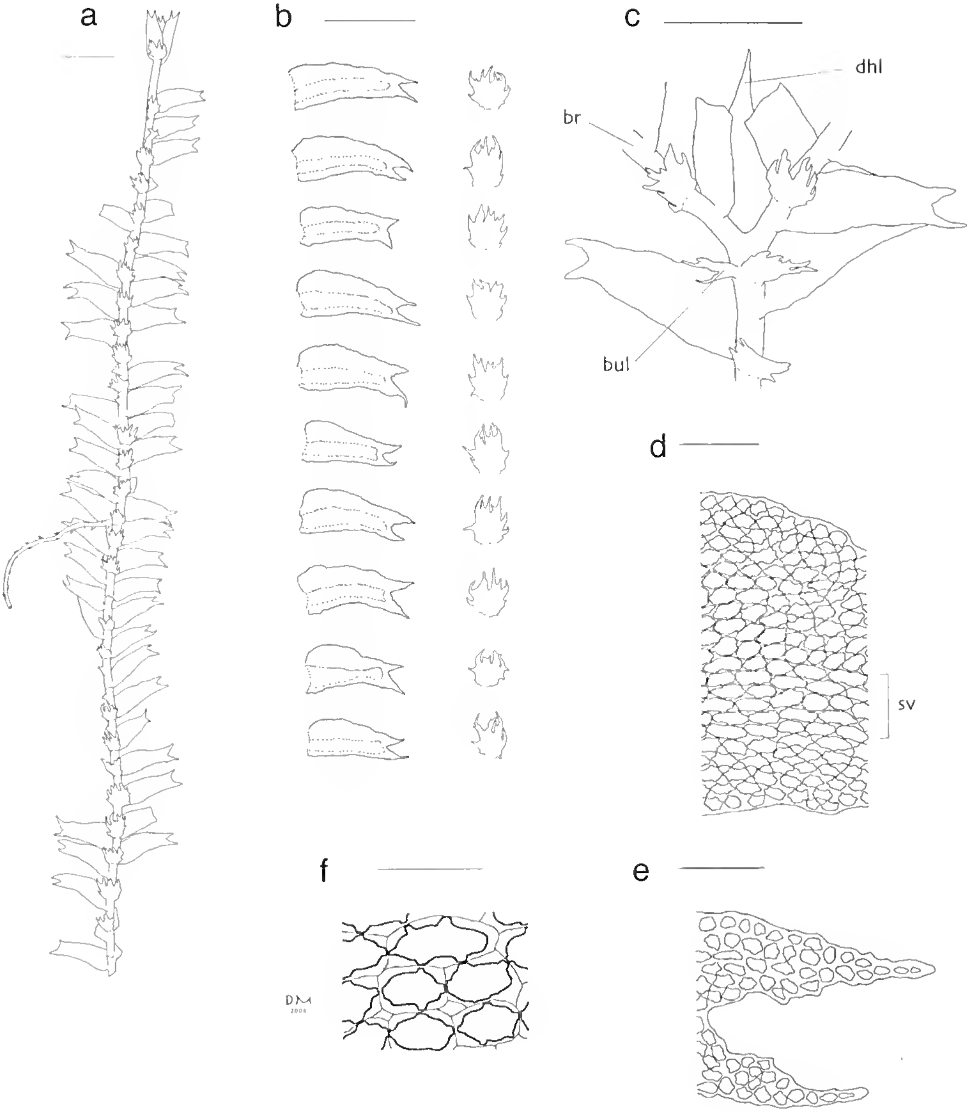

Fig.1. *Bazzania scalaris* **sp. nov. a**, ventral view of portion of moist plant; **b**, lateral leaves and underleaves; **c**, branching, showing branch (br), first branch underleaf (bul) and dorsal half-leaf (dhl) behind two fractured leaves; **d**, cells in mid-leaf, showing subvitta (sv); **e**, cells in leaf apex; **f**, detail of cells in mid-leaf.

Scale bars: a–c =1 mm, d, e = 100 µm, f = 50 µm.

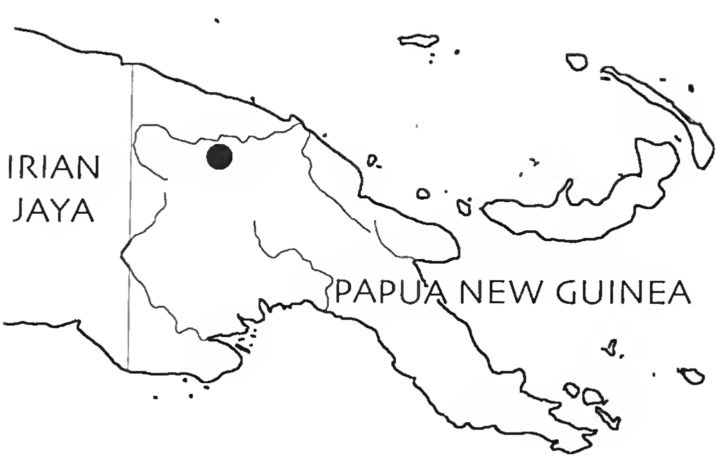

Fig. 2. Type locality (solid circle) of *Bazzania scalaris.*

Significant studies and reviews of the genus *Bazzania* have also been undertaken for South East Asia and Melanesia by Evans (1933), Grolle (1968, 1972), Herzog (1931, 1949, 1953), Kitagawa (1972, 1973, 1979, 1980), Meijer (1960) and Tixiér (1985), and for other nearby and distant regions of the world, e.g. Engel and Merrill (1994), Grolle and Schultze-Motel (1973), Hattori and Mizutani (1958), Jones (1975), Long and Grolle (1990), Mizutani (1967), Pócs (1969), Scott (1985).

Among the hundreds of species reported and described, only *Bazzania bhutanica* N.Kitag. & Grolle closely resembles the present species. However in that species, from Bhutan in the Himalaya, the cuticle is strongly asperous and often coarsely verruculose, the cells of the lateral leaves have evenly thickened walls and indistinct trigones, and the lobes of the lateral leaves are only weakly spreading. Furthermore, the leaves are much shorter and more or less contiguous to slightly imbricate (Kitagawa & Grolle 1986). Of the other Asian and Australasian *Bazzania* species with similar leaves, *B. linearis* Herzog, *B. bicrenata* N.Kitag., *B. bilobata* N.Kitag., *B. cadens* N.Kitag. and *B. distans* (Nees) Trevis., all have unlobed or weakly lobed underleaves, and all but the last have an asperous or verruculose cuticle on the lateral leaves (Herzog 1949; Kitagawa 1967, 1980). *B. friabilis* N.Kitag. & T.Kodama also has a distinctly verrucose cuticle and the margins of the leaves are quite crenulate, and *B. pseudovittata* N.Kitag. & T.Kodama has a very strongly asperous cuticle that gives the plant an overall frosty appearance, very weakly lobed leaves, and very weakly dentate underleaves (Kitagawa & Kodama 1975).

Bazzania scalaris is known at present only from the type collection (Fig. 2), but no doubt will turn up elsewhere. The specific epithet refers to the ladder-like appearance of intact shoots.

Acknowledgments

Many thanks are due to Dr Bill Weber (COLO) for providing a number of interesting specimens from New Guinea, among which this species was found. Thanks also to Nic Middleton and Kathy Vohs (MELU) for organising loans and laboratory facilities, and to Dr Elizabeth Brown (NSW) for correcting the original manuscript.

References

Arnell S (1963) *Hepaticae of South Africa*. (Swedish Natural Science Research Council: Stockholm)

Engel JJ & Merrill, GLS (1994) Studies of New Zealand Hepaticae. 8–13. *Bazzania* and *Acromastigum*. *The Bryologist* 97(3): 313–320.

Engel JJ & Schuster RM (1980) Studies of New Zealand Hepaticae. 1–6. *Brittonia* 40(2): 200–207.

Evans AW (1933) ['1932'] Some representative species of *Bazzania* from Sumatra. *Papers of the Michigan Academy of Science, Arts and Letters* 17: 69–118.

Fulford MH (1963) ['1962'] Manual of the leafy Hepaticae of Latin America—Part I. *Memoirs of the New York Botanical Gardens* 2(1): 1–172.

Grolle R (1968) Lebermoose aus Neuguinea. 7. Vierte Fundliste. *Journal of the Hattori Botanical Laboratory* 31: 1–12.

Grolle R (1972) *Bazzania* in Europa und Macronesien. Zur Taxonomie und Verbreitung. *Lindbergia* 1: 193–204.

Grolle R and Schultze-Motel, W (1973) Vorläufiges Verzeichnis der Lebermoose von Samoa. *Journal of the Hattori Botanical Laboratory* 36: 75–89.

Herzog, T (1931) II. Hepaticae. In Winkler H., Borneo-Pflanzen. *Mitteilungen aus den Institut für allgemeine Botanik in Hamburg* 7(3): 182–216.

Herzog T (1949) Hepaticae Borneenses (Oxford University Expedition to Sarawak, 1932). *Transactions of the British Bryological Society* 1(3): 275–326.

Herzog T. (1953) Lebermoose aus Neukaledonien gesammelt von Dr. O.H. Selling. *Arkiv för Botanik* (ser. 2, band 3) 3: 43–61.

Hodgson EA (1954) New Zealand Hepaticae (Liverworts)—VIII. A review of the New Zealand species of the genera *Bazzania* and *Acromastigum*. *Transactions of the Royal Society of New Zealand* 82(1): 7–24.

Jones EW (1975) African Hepatics XXVII. *Bazzania*. *Journal of Bryology* 8: 71–75.

Kitagawa N (1967) Studies on the Hepaticae of Thailand I. The genus *Bazzania*, with general introduction. *Journal of the Hattori Botanical Laboratory* 30: 248–270.

Kitagawa N (1972) Notes on little-known species of Hepaticae, 1–25. *Journal of the Hattori Botanical Laboratory* 36: 444–454.

Kitagawa N (1973) Miscellaneous notes on little-known species of Hepaticae, 26–50. *Journal of the Hattori Botanical Laboratory* 37: 263–273.

Kitagawa, N (1979) Studies on Asian species of *Bazzania*, Hepaticae, II. *Bulletin of the Nara University of Education* 28(2): 71–83.

Kitagawa N (1980) New Guinean species of the genus *Bazzania*, I. *Journal of the Hattori Botanical Laboratory* 47: 127–143.

Kitagawa N & Grolle R (1986) A new *Acromastigum*-like species of *Bazzania* S. Gray from Bhutan. *Journal of the Hattori Botanical Laboratory* 61: 269–272.

Kitagawa N & Kodama T (1975) Two new species of *Bazzania* with an unusual habitat in Sabah (North Borneo). *Journal of the Hattori Botanical Laboratory* 61: 269–272.

Long DG and Grolle R (1990) Hepaticae of Bhutan. II. *Journal of the Hattori Botanical Laboratory* 68: 381–440.

Meijer W (1960) Note on the species of *Bazzania* (Hepaticae) mainly of Java. *Blumea* 10(2): 367–366.

Mizutani M (1967) Studies of the Himalayan species of *Bazzania*. *Journal of the Hattori Botanical Laboratory* 30: 71–90.

Pócs, T (1969) A short survey of the *Bazzania* of North Viet-Nam. *Journal of the Hattori Botanical Laboratory* 32: 79–94.

Pócs T (1994) Taxonomic results of the BRYOTROP expedition to Zaire and Rwanda. 27. Lepidoziaceae, II. *Tropical Bryology* 9: 123–130.

Scott GAM (1985) *Southern Australian Liverworts.* Flora and Fauna Bulletin 2. (AGPS: Canberra)

Stephani F (1908) *Species Hepaticarum*, vol. 3. (George & Cie: Genéve & Bale)

Stephani F (1924) *Species Hepaticarum*, vol. 6. (Université de Genéve: Genéve)

Stephani F (1985) *Icones Hepaticarum*, microfiche. (International Documentation Company: Leiden)

Tixiér P (1985) A propos du genre *Bazzania* en Nouvelle-Calédonie. Récoltes de H.S. MacKee. *Cryptogamie, Bryologie-Lichénologie* 6: 177–180.

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Telopea 11(3) 252–259

New species of *Prostanthera* section *Prostanthera* (Labiatae) from New South Wales

Barry J. Conn

National Herbarium of New South Wales, Mrs Macquaries Road, Sydney 2000, Australia

Abstract

Prostanthera petraea and ***P. stenophylla*** are described for the first time. Although these species have very restricted distributions, they are regarded as adequately protected because they both occur within National Parks.

Introduction

The two species of *Prostanthera* that are formally named in this paper have been well known for a long time. *Prostanthera petraea* appears to have first been collected by J.F. Thomas from Boonoo Boonoo during July 1936, whereas *Prostanthera stenophylla* was first recognized as a possible undescribed species when it was collected by George W. Althofer in 1952 from an area that has since become part of the Wollemi National Park. An earlier collection by Lindsay D. Pryor (December 1937) from the Canberra district also appears to be this latter species. Subsequently, *P. stenophylla*, under the unpublished name 'Prostanthera rylstonii', has been promoted as a suitable Australian species for horticulture and is now occasionally grown in gardens.

An identification guide (key) to these species, under their unpublished informal names, is included in Conn (1992). Terminology follows Conn (1984), except inflorescence terminology, particularly podial features (replacing the more typical terminology of 'pedicel'), are based on Conn (1995).

Taxonomy

Prostanthera petraea B.J.Conn, ***sp. nov.***

P. lasiantho Labill. affinis, a qua inflorescentiis botryoidalibus, foliis olivaceis integris differt.

Holotype: New South Wales: Northern Tablelands: Bald Rock National Park: Bungoona Walking Track, *B.J. Conn 3668 & E.A. Brown*, 11 Oct 1992, (NSW 260615); isotypes: BRI, CANB, K, MEL.

Prostanthera species B sensu Conn, in Harden (ed.) *Flora of New South Wales*, vol. 3: 656 and fig. (1992); PlantNET (http://plantnet.rbgsyd.nsw.gov.au) (accessed March 2006) as '*Prostanthera* sp. B sensu Conn (1992)' and *Prostanthera* sp. 'Boonoo Boonoo' (T.D. Stanley 78/76).

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Shrub to small tree, 1–3(–5) m high, branching from up to 1 m above base. *Branches* laterally 2-ridged or on older branches becoming more equally spaced 4-ridged, moderately to densely hairy (20–40 hairs/mm^2), mostly restricted to ridges and area between ridges; hairs ± curved, antrorse, sub-appressed, 0.5–1 mm long, white, moderately glandular (10–20 hairs/mm^2); glands hemispherical. *Leaves* dull, olive-green above, much paler below, faintly but pleasantly aromatic when crushed.; *petiole* (5–)7–12 mm long, hairy at base; *lamina* ovate, (25–)35–50(–70) mm long, (12–) 15–25(–27) mm wide (length to width ratio (1.9–)2–2.6, length of maximum width from base to total lamina length ratio 0.4–0.5), glabrous, distinctly and moderately glandular (10–15 hairs/mm^2); base attenuate and shortly decurrent; margin entire, slightly recurved; apex obtuse to sub-acuminate; venation indistinct or not visible, midrib slightly raised basally. *Inflorescence* a frondose (at base) dibotryoid conflorescence, uniflorescence botryoid; 5–13-flowered (per uniflorescence, up to c. 30-flowered per conflorescence). *Podium* 1–2 mm long, glabrous or with an occasional hair, densely glandular. *Prophylls* not persistent, usually only base persisting, inserted just below calyx (a_1 axis to anthopodium ratio 10–20), opposite, narrowly elliptic, 2.5–3 mm long, 0.2–0.3 mm wide (length to width ratio 1–1.3, length of maximum width from base to total lamina length ratio c. 0.5), glabrous or with an occasional hair, densely glandular; base attenuate; margin entire; apex attenuate; venation not visible. *Calyx* light green; outer surface glabrous, moderately glandular; inner surface glabrous, except margin shortly fimbriate; *tube* 4.5–5 mm long; *abaxial lobe* broadly to very broadly ovate, 3.5–4 mm long, 3.5–5 mm wide at base (length to width ratio 0.8–1.2), apex rounded, slightly irregular, often slightly retuse; *adaxial lobe* transversely ovate, 2.5–3.3 mm long, 4.4–5 mm wide at base (length to width ratio 0.5–0.7), apex obtuse to rounded (adaxial lobe length to abaxial lobe length ratio 0.7–0.8). *Corolla* 8–12 mm long, white, lacking markings, once recorded with pale mauve dots in throat (*Jobson 5225*); outer surface glabrous, sparsely glandular; inner surface glabrous in tube and distally on lobes, sparsely hairy (6–12 hairs/mm^2) near base of lobes, especially near sinus between adaxial and abaxial lobes; *tube* 5–6 mm long; *abaxial median lobes* spathulate, 5.5–7 mm long, 4.5–5.5 mm wide (length to width ratio 0.8–1.3), apex irregular and rounded, usually bilobed (sinus c. 1 mm long, 1–1.5 mm wide distally); *lateral lobes* elliptic, 5–6 mm long, 3–3.5 mm wide (length to width ratio 1.6–1.7), apex slightly irregular, rounded to slightly retuse; *adaxial median lobe-pair* depressed ovate to very depressed ovate, 4–5 mm long, 10–12 mm wide (length to width ratio c. 0.6), apex rounded, irregular, bilobed (sinus 2–4 mm long, median margin of lobes usually overlapping). *Stamens* inserted 1.5–2 mm above base of corolla; filaments 4–5 mm long; anthers 1.3–1.5 mm long, lobes slightly cristate on basal dorsal surface (narrowly triangular trichomes 0.1–0.2 mm long) with small acumen basally, connective extended to form a basal appendage 0.5–0.8 mm long, terminating in a few (up to c. 6) narrowly triangular trichomes 0.1–0.2 mm long. Disc 0.4–0.6 mm long. *Pistil* 8–9 mm long; *ovary* cylindrical obovoid, 0.4–0.5 mm long, diameter at base 0.5–0.6 mm, lobes 0.1–0.2 mm long; *style* c. 4 mm long; *stigma lobes* 0.6–0.8 mm long. *Fruiting calyx* not or only slightly enlarged *Mericarps* 1.3–2 mm long, distally 0.5–1 mm extended beyond base of style, distal diameter 2.3–2.6 mm; seeds ellipsoid-cylindrical to slightly obovoid, c.1 mm long, 0.6–1 mm diameter (slightly flattened). Figure 1.

Flowering: late Spring – early Summer. **Fruiting:** Summer.

Fig. 1. *Prostanthera petraea* **a**, branchlets showing leaves, flowers and developing fruits; **b**, flower (ventral view), with adaxial lobe-pair dissected to show androecium and gynoecium; **c**, flower (ventral view) showing corolla, androecium and gynoecium; **d**, flower (side view) showing calyx, corolla, style and stigma; **e**, stamen (ventral view) showing connective and anther appendages; **f**, stamen (dorsal view) showing connective and anther appendages; **g**, detail of adaxial surface of leaf showing hemispherical glands; **h**, detail abaxial surface of petiole showing hairs and hemispherical glands (a–g from *Conn 3670 & Brown*; h from *Conn 3668 & Brown*; both NSW). Scale bar: a=55 mm, b–d=15 mm; e & f=3 mm; g & h=20 mm. Illustration by Catherine Wardrop.

Selected specimens examined (17 seen): New South Wales: Northern Tablelands: Bald Rock National Park: Bungoona Walking Track, *Conn 3670 & Brown*, 11 Oct 1992 (AD, BRI, MEL, NSW); Boorook State Forest: Bridge on Boorook Creek, *Copeland 586*, 22 Oct 1997 (NE, NSW); summit of Bald Rock, *Jobson 5225 & Mills*, 25 Oct 1997 (BRI, NSW); Boonoo Boonoo National Park: 4 miles from Boonoo Boonoo Falls, *Williams s.n.*, 19 Nov 1965 (BRI, NE, NSW).

Distribution: this species is restricted to the Boonoo Boonoo-Bald Rock area (north-east of Tenterfield), New South Wales. Since *P. petraea* is more or less restricted to areas that have not been subjected to fires, such as amongst large granite boulders and along water-courses, this intolerance to frequent bushfires may explain why it is not more widespread.

Habitat: *Prostanthera petraea* grows in *Callitris—Eucalyptus* woodland and *Leptospermum novae-angliae* heath with *Philotheca myoporoides*, *Oxylobium arborescens*, *Phebalium ambiens*, *Styphelia* and *Leucopogon* understorey. Growing amongst granite boulders in skeletal black peaty sand or shallow coarse sand.

Etymology: the specific epithet (viz. *petraea*) refers to the habitat of large granite boulders amongst which this species grows. The epithet also acknowledges the aboriginal place name 'Boonoo Boonoo' (which means 'large rocks'), one of the areas in which this species occurs.

Notes: the affinities of this species appear to be with *Prostanthera lasianthos* with both having similar shaped flowers and white corollas. However, *P. lasianthos* has a more elaborate, paniculate inflorescence (cf. botryoidal in *P. petraea*); corolla with markings on the inner surface (cf. *P. petraea* that almost always lacks corolla markings); and mid-green, more or less glossy leaves which are usually shortly toothed (cf. *P. petraea* which has pale olive-green, dull leaves with margin entire).

Conservation status: this species is probably adequately conserved within the Bald Rock National Park, Boonoo Boonoo National Park and the Boorook State Forest. However, it is likely to be a vulnerable species because of its very restricted distribution.

Prostanthera stenophylla B.J.Conn, *sp. nov.*

P. graniticae Maiden & Betche affinis, a qua foliis angustis (1.5–2 mm. latis), indumento molli differt.

Holotype: New South Wales: Central Tablelands: Dunns Swamp area, Wollemi National Park, *P.C. Jobson 4354*, 28 Sep. 1996, (NSW 619013); isotypes: AD, B, BM, BRI, CANB, E, K, MEL, NSW 619015, NY, US.

Prostanthera species A sensu Conn, in Harden (ed.) *Flora of New South Wales*, vol. 3: 650 and fig. (1992); PlantNET (http://plantnet.rbgsyd.nsw.gov.au) (accessed March 2006) and images as '*Prostanthera* sp. A sensu Conn (1992)'; 'Prostanthera rylstonii' sensu Nursery Trade (in use 2005), nom. nud.; *Prostanthera* sp. 'Rylstone' in Australian Plant Name Index (APNI) (http://www.anbg.gov.au/cpbr/databases/apni.html) (accessed June 2006).

Erect slender shrub, 1.5–2.5 m high. *Branchlets* terete, densely hairy (35–48 hairs/mm^2); hairs patent or slightly retrorse to antrorse, 0.1–0.2 mm long, straight to slightly curved, white; glands hemispherical, subsessile, moderately dense to sparse (on older branchlets) (10–36 glands/mm^2). *Leaves* dull green above, slightly paler below, strongly aromatic (when crushed); *petiole* very short, c. 0.5 mm long (often appearing absent),

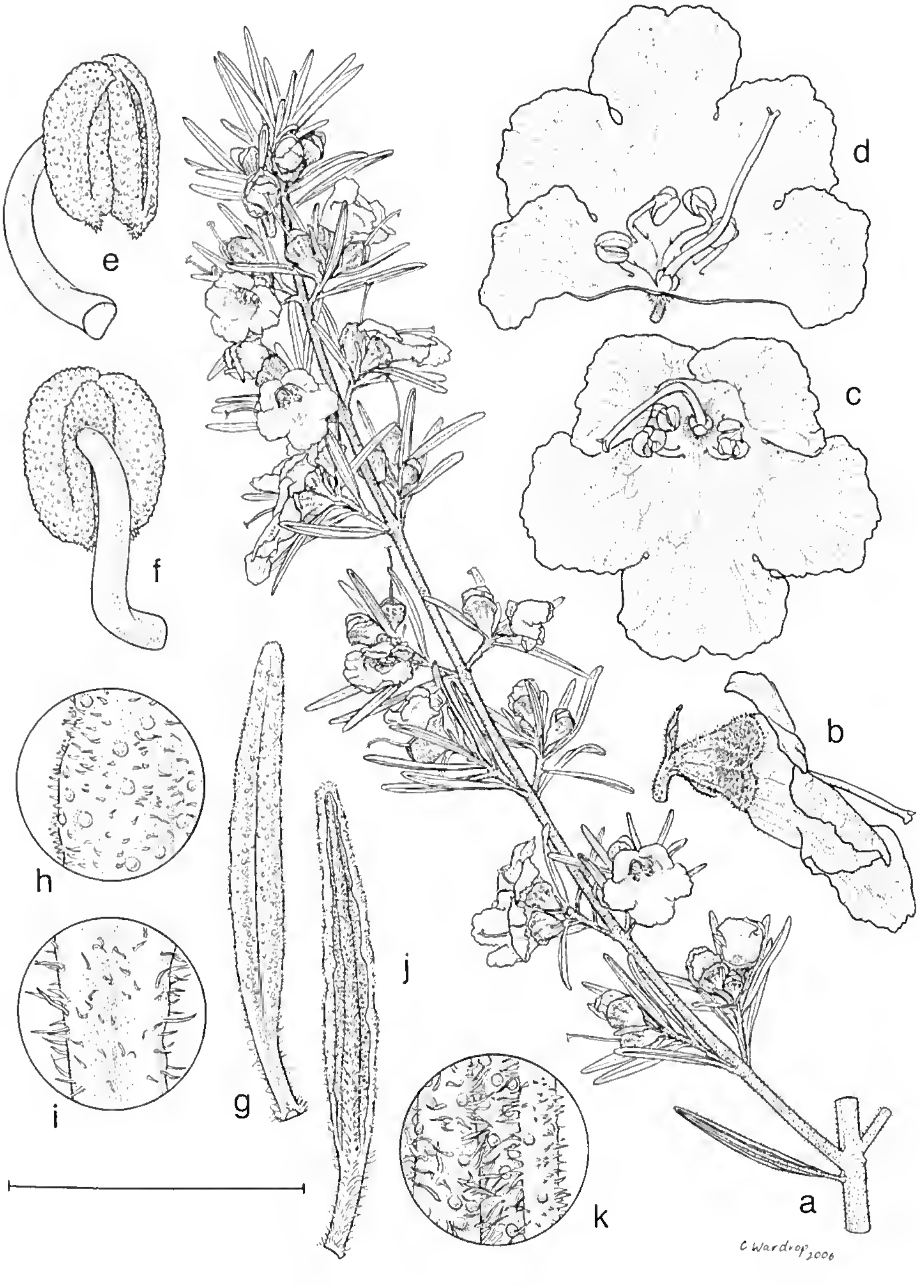

Fig. 2. *Prostanthera stenophylla* **a**, branchlets showing leaves and flowers; **b**, flower (side view) showing prophyll, calyx, corolla, style and stigma; **c**, flower (ventral view) showing corolla, androecium and gynoecium; **d**, flower (ventral view), with adaxial lobe-pair dissected to show androecium and gynoecium; **e**, stamen (ventral view); **f**, stamen (dorsal view); **g**, leaf (adaxial view); **h**, detail of adaxial surface of leaf showing hairs and hemispherical glands; **i**, detail of abaxial surface of petiole showing hairs; **j**, leaf (abaxial view); **k**, detail of abaxial surface of leaf showing hairs and hemispherical glands (from *Jobson 4354*, NSW). Scale bar: a=30 mm, b & c=12 mm; d=15 mm; e & f=3 mm; g & j=10 mm; h, i, k=2.1 mm. Illustration by Catherine Wardrop winner of the Margaret Flockton Award for 2006.

± grading into base of lamina; *lamina* narrowly ovate to narrowly elliptic, appearing oblong to narrowly oblong because margin revolute to strongly recurved, 7–14 mm long, 1.5–2 mm wide (length to width ratio 5–7, length of maximum width from base to total lamina length ratio 0.3–0.4), densely hairy, hairs c. 0.1 mm long, patent (abaxial surface), slightly antrorse (adaxial surface), densely glandular (as for branchlets); base attenuate; margin entire, strongly recurved such that only midvein of abaxial surface visible; apex obtuse; venation indistinct, midrib slightly raised on abaxial surface. *Inflorescence* a frondose racemiform conflorescence (on short side shoots), uniflorescence monadic; 4–6-flowered (per conflorescence). *Podium* 0.5–0.7 mm long, densely hairy and glandular. *Prophylls* ± persistent, inserted just below the calyx (a_1 axis to anthopodium ratio c. 3), opposite, narrowly oblong to slightly narrow-elliptic to -obovate, 1.2–1.6 mm long, c. 0.4 mm wide (length to width ratio c. 4, length of maximum width from base to total lamina length ratio 0.5–0.6), densely hairy (hairs as for abaxial surface of leaf lamina), densely glandular; base attenuate; margin entire; apex obtuse; venation not visible. *Calyx* green basally, strongly maroon distally, especially on lobes; outer surface densely hairy throughout, slightly less dense distally, with hairs white, patent to slightly retrorse, c. 0.5 mm long, moderately to densely glandular; inner surface of tube glabrous, lobes densely hairy, with hairs c. 0.1 mm long, ± patent; *tube* 2–2.8 mm long; *abaxial lobe* transversely broad-elliptic to very broadly ovate, 1.4–2.2 mm long, 2.5–3.8 mm wide at base (length to width ratio 0.4–0.8), apex rounded, very slightly irregular; *adaxial lobe* transversely ovate to transversely oblong, 1–2.5 mm long, 2.2–4 mm wide at base (length to width ratio 0.5–0.6), apex rounded to almost truncate (adaxial lobe length to abaxial lobe length ratio 1–1.3). *Corolla* 8–12 mm long, pale bluish mauve, lacking markings; outer surface glabrous basally, distally sparsely hairy (7–9 hairs/mm^2), hairs 0.6–1.2 mm long, ± spreading, sparsely glandular on distal parts of tube and base of lobes (2–5 glands/ mm^2); inner surface glabrous; *tube* c. 4 mm long; *abaxial median lobes* transversely broad-spathulate, 4–5 mm long, 4.5–5 mm wide (length to width ratio 0.8–1), apex irregular and rounded, usually bilobed (sinus c. 0.4 mm long, c. 2.5 mm wide distally); *lateral lobes* oblong to slightly elliptic, 3–3.5 mm long, 3–3.8 mm wide (length to width ratio 0.8–1), apex rounded to slightly retuse, slightly irregular; *adaxial median lobe-pair* depressed ovate to very depressed ovate, 3.8–4.2 mm long, 8.5–10 mm wide (length to width ratio c, 0.4), apex rounded, irregular, bilobed (sinus 2.5–3 mm long, median margin of lobes usually touching or overlapping). *Stamens* inserted 2–2.5 mm above base of corolla; filaments 2–2.3 mm long; anthers 1–1.2 mm long, base of lobes glabrous or with a few narrowly triangular trichomes (up to 0.1 mm long), usually with small acumen basally, connective appendage absent or minute and indistinct, with a few narrowly triangular trichomes up to 0.1 mm long. Disc c. 0.2 mm long. *Pistil* 5.5–6 mm long; *ovary* cylindrical obovoid, 0.4–0.5 mm long, diameter at base 0.5–0.7 mm, lobes 0.1–0.2 mm long; *style* 8.5–9.5 mm long; *stigma lobes* 0.8–1 mm long (unequal in length). *Fruiting calyx* not or only slightly enlarged. *Mericarps* 1–1.4 mm long, distally c. 1 mm extended beyond base of style, distal diameter 1.8–2 mm; seeds ellipsoid-cylindrical, c. 1 mm long, c. 0.5 mm diameter. Figure 2.

Flowering: throughout the year, but mostly in Spring. **Fruiting:** mostly late Spring to early Summer.

Selected specimens examined (22 seen): New South Wales: Central Tablelands: Wollemi National Park: *Althofer 2*, pre-June 1952 (MEL); *Althofer s.n.*, 1953 (NSW); *Carrick 3240* & *3242*, 27 Oct 1972 (AD, NSW); *Conn 823*, 26 Aug 1980 (MEL); *Ford 619*, 19 Oct 1991 (NSW, SYD); *Johnstone 823 & Jobson*, 16 Oct 1999 (NSW); *Weston 2607*, 29 Aug 2003 (NSW); *Washington s.n.*, May 1998 (NSW). Locality uncertain: Southern Tablelands: Canberra district, *Pryor s.n.*, Dec 1937 (NSW).

Distribution: the only confirmed populations of this species occur in the western parts of the Wollemi National Park, New South Wales. The herbarium collection by Lindsay D. Pryor from the imprecisely described 'Canberra District' is regarded as unlikely to be correct.

Habitat: this species occurs in sandy loamy soil, amongst sandstone outcrops ('pagodas') in dry sclerophyll forest dominated by *Eucalyptus piperita*, *E. rossii* and *Callitris endlicheri*.

Etymology: the specific epithet (viz. *stenophylla*) refers to the narrow leaves characteristic of this species.

Notes: this species is characterised by having leaves that are strongly aromatic, densely hairy, revolute to strongly recurved, hence appearing narrow. The flowers have anthers that either lack connective appendages or they are minute and indistinct. The affinities of this species are unclear, but it is morphologically similar to *P. granitica*, being readily distinguished from the latter by its relatively soft indumentum compared to the coarse, rough (to touch) hairs of *P. granitica*. Furthermore, although both species have revolute leaves, those of *P. granitica* are generally less strongly revolute and broader (2–5 mm wide) than those of *P. stenophylla* (1.5–2 mm wide). The margin of the leaf lamina appears to be usually entire, but occasionally, all the leaves of a plant (*Althofer s.n.*) or an occasional leaf, of a plant with otherwise entire leaves (*Jobson 4354*), is slightly or distinctly lobed to sub-crenate with lobes porrect (up to c. 0.4 mm long).

This species was recognized as an undescribed species by George W. Althofer in 1952 who quickly promoted this species as suitable for horticulture. Cuttings of *P. stenophylla* were broadly distributed amongst home-gardeners interested in the cultivation of Australian native plants. This species is now available from commercial plant nurseries under the unpublished name 'Prostanthera rylstonii'.

Conservation status: although this species occurs in the Wollemi National Park, it appears to have a very restricted distribution and so should, at least, be considered as vulnerable.

Acknowledgments

I thank the late George Althofer (then Wellington, N.S.W.) for informing me of the presence of both species and his brother, the late Peter Althofer (also from Wellington), who accompanied me on a field visit to the main population of *Prostanthera stenophylla*. I gratefully acknowledge advice on the Latin diagnoses provided by Dr Peter Wilson (NSW) and thank Catherine Wardrop (NSW) for preparing the detailed illustrations.

Peter Jobson (NSW) kindly re-collected suitable type material of *P. stenophylla*. Elizabeth Brown (NSW) assisted with the collection of the type material of *P. petraea*. Additional herbarium collections held at AD, BRI, MEL and NE were examined during the taxonomic evaluation of these species. I thank the directors, curators and staff for allowing me access to these important collections.

References

Conn BJ (1984) A taxonomic revision of *Prostanthera* Labill. Section *Klanderia* (F.v. Muell.) Benth. (Labiatae). *Journal of the Adelaide Botanic Gardens* 6: 207–348.

Conn BJ (1992) *Prostanthera*. Pp. 646–662 in Harden GJ (ed.) *Flora of New South Wales*, vol. 3. (New South Wales University Press: Kensington)

Conn BJ (1995) Description of inflorescence axes in the genus *Logania* R.Br. (Loganiaceae). *Kew Bulletin* 50: 777–783.

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Boronia boliviensis (Rutaceae series Erianthae), a new rare granite outcrop endemic from north-eastern New South Wales

John B. Williams†[1] and John T. Hunter[2]

[1]*Botany, Centre for Ecology, Evolution and Systematics, University of New England, Armidale NSW 2351, Australia*
[2]*School of Human & Environmental Studies, University of New England, Armidale, NSW 2351, Australia*

Abstract

Boronia boliviensis J.B.Williams & J.T.Hunter, a new rare granite outcrop restricted species from the Bolivia Hill area of the Northern Tablelands of New South Wales is described and notes are provided on its distribution, ecology and conservation status.

Introduction

The rock outcrop environment of the New England Batholith has recently been a fruitful area for the discovery and description of narrow-endemic species (Hunter & Williams 1994; Hunter 1997, 1998; Hunter & Bruhl 1999; Hunter & Copeland 2001; Williams & Hill 2001). In particular Bolivia Hill, a granite area between Tenterfield and Deepwater, has yielded a number of plant species restricted to the hill and nearby surrounds (*Acacia pycnostachya* F.Muell., *Eucalyptus boliviana* J.B.Williams & K.D.Hill, *Homoranthus croftianus* J.T.Hunter and *Pimelea venosa* Threlfall). Bolivia Hill also contains a number of other rare or threatened vascular plants with restricted distributions (*Babingtonia odontocalyx* A.R.Bean, *Brachyloma saxicola* J.T.Hunter, *Callistemon pungens* Lumley & R.D.Spencer, *Cryptandra lanosiflora* F.Muell., *Daviesia elliptica* Crisp, *Hibbertia patens* Toelken, *Kunzea bracteolata* Maiden & Betche, *Olearia gravis* (F.Muell.) F.Muell. ex Benth., *Philotheca conduplicatus* (Paul G.Wilson) P.I.Forst., *Plectranthus suaveolens* S.T.Blake, *Pultenaea pycnocephala* Benth., *Thesium australe* R.Br. and *Thelionema grande* (C.T.White) R.J.F.Hend.) and was duly listed as a hotspot for conservation initiatives by Quinn et al. (1995). In October 1989 the senior author collected specimens of a *Boronia* from Bolivia Hill. The taxon is clearly a member of the section *Valvatae*, however it did not match with any presently known species. While awaiting formal publication the entity has been recognised and included in cladistic and systematic revisions of the section *Valvatae* as *Boronia* aff. *granitica* (Duretto &

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† Deceased 31 July 2005

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Ladiges 1999; Duretto 1999). These investigations have firmly placed this taxon within the series *Erianthae*. This new taxon is described here at specific rank and represents yet another species restricted to Bolivia Hill.

Taxonomy

Boronia boliviensis J.B.Williams & J.T.Hunter, ***sp. nov.***

Similis B. graniticae Maiden & Betche sed indumento ramuli et foliorum longo, arachnoideo, non denso differt.

Holotype: New South Wales: Northern Tablelands: Bolivia Hill, c. 33 km south of Tenterfield (29°20'S 151°20'E), *Williams 89556*, 2 Oct 1989 (holo: NSW; iso: BRI, CANB, NE, MEL, HO.)

Boronia sp. J, sensu Quinn et al. (1995, p. 72); Hunter & Clarke (1998, p. 591).

Boronia aff. *granitica*, sensu Duretto & Ladiges (1999, p. 647, 649, 652, 653, 655, 656, 661 & 663).

Boronia aff. *granitica* (Bolivia Hill), sensu Duretto (1999, p. 11 & 47).

Boronia boliviensis J.B.Williams ms. (Williams 89556), sensu Weston & Duretto (2002, p. 272).

Much-branched *shrub* to 1.5 (–2.2 m) tall, odoriferous; branchlets with a dense covering of very short, sessile, multi-angular yellowish stellate hairs, becoming glabrous with age. *Leaves* pinnate with mostly 7–11 leaflets, rarely with 1–5 leaflets on some leaves (especially on flowering branchlets); rachis 2–12 (–20) mm long, jointed, 8–15 mm wide, narrowly winged, rachis wings flat or recurved; leaflets narrow-elliptic, sessile, 3.8–9 mm long, 0.5–1.5 mm wide, apex acute to sub-obtuse, broadest above the middle, margins entire and closely revolute, rarely only recurved, upper surface deep green with a sparse indumentum of stellate hairs or ± glabrous, the surface and margin dotted with large, sunken oil glands, lower surface often hidden by revolute margins but when visible markedly paler, usually glabrous; petiole 1–3 mm long. *Inflorescences* axillary, 1–3-flowered; prophylls unifoliate; peduncle 1.5–2 mm long; pedicels 2–3 mm long. Calyx lobes deep red, narrow-deltate, acute or acuminate, 2.5–3.8 mm long, 1–2 mm wide, shortly stellate-hairy abaxially. Petals pink, 4–9 mm long, 3–4 mm wide, valvate in bud, very shortly stellate-tomentose abaxially, glabrous or almost so with fine simple hairs adaxially, persistent in fruit. *Filaments* 1–2 mm long, glandular to tuberculate; anther with erect apiculum. *Style* glabrous or sparsely hairy. *Fruit* with cocci glabrous, 4–5 mm long, 2–3 mm wide. Seed 3–4 mm long, 1–2 mm wide. Flowers mainly September to November but flowers also recorded in May, August and December.

Etymology: the epithet *boliviensis* refers to the location of all known populations on the Bolivia Range (south of Tenterfield, on the Northern Tablelands of New South Wales).

Distribution: the known populations are all restricted to the higher parts of the Bolivia Range, particularly on Bolivia Hill south of Tenterfield in the Northern Tablelands Botanical District of New South Wales and the New England Tablelands Bioregion.

Notes: in a cladistic analysis of *Boronia* section *Valvatae*, Duretto & Ladiges (1999) demonstrated that *Boronia boliviensis* (*Boronia* aff. *granitica*) was most closely related

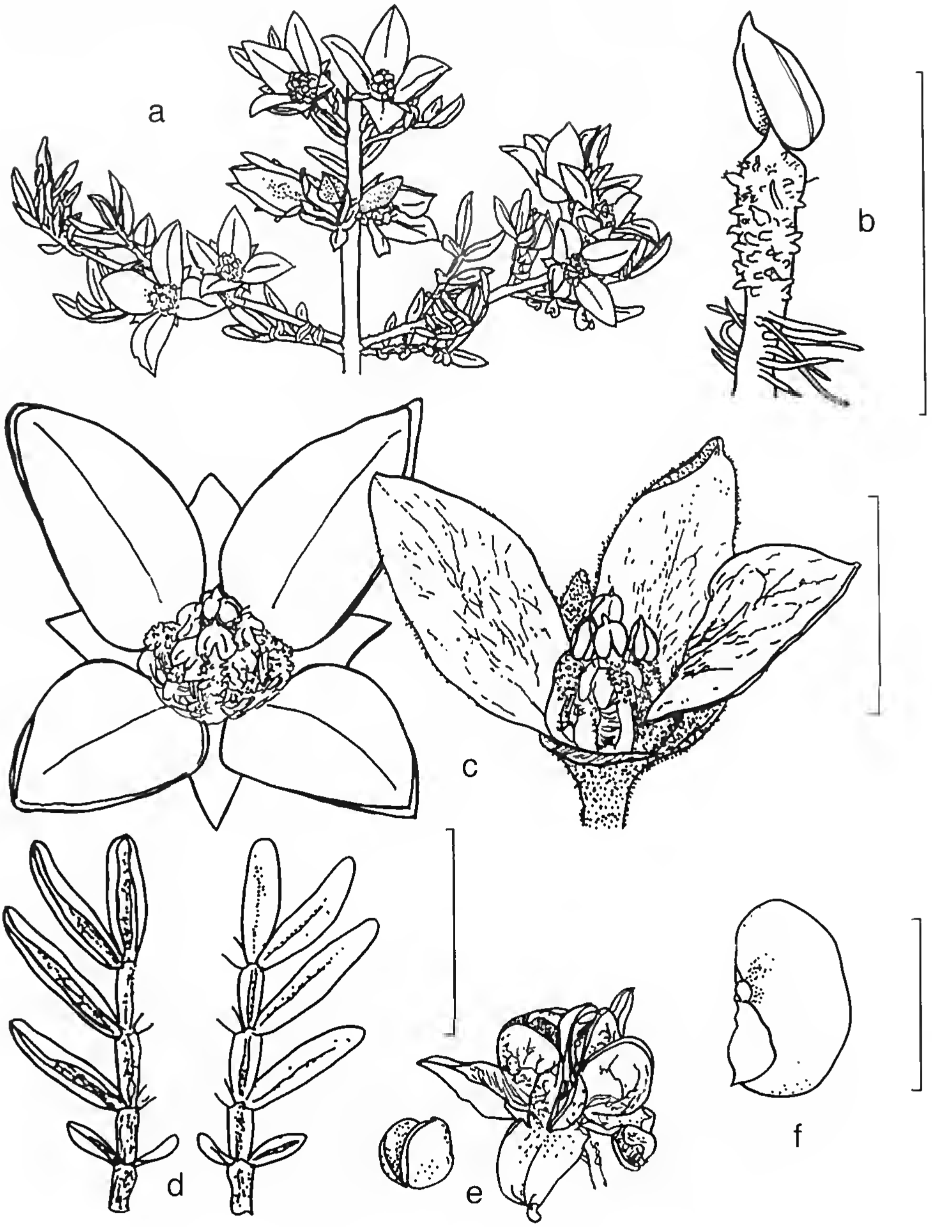

Fig. 1. *Boronia boliviensis* J.B.Williams & J.T.Hunter **a**, branchlet; **b**, filament and anther , showing anther apiculum and glandular hairs on the filament; **c**, mature flower showing staminal arrangement; **d**, foliage morphology; **e**, mature cocci; **f**, mature seed.

Scale bar: a & b, a = 50 mm, b = 2 mm; c, d & e = 10 mm; f = 2 mm.

to *B. granitica* Maiden & Betche and *B. ruppii* Cheel. These three taxa were placed along with *Boronia eriantha* Lindl. and *B. warrumbunglensis* P.H.Weston within the series *Erianthae*. *Boronia granitica* can be distinguished by its branchlets and leaves lacking long, slender (arachnoid) multi-angular stellate hairs and by its deltate red sepals. The species has been commonly known as Bolivia Hill Boronia.

Habitat: *Boronia boliviensis* is currently known from altitudes between 900 to 1200 m which receive a mean annual rainfall between 800–900 mm. The species occurs in Low Shrublands and Heaths on granite rock outcrops, described as Element 4 by Hunter & Clarke (1998), which is dominated by *Leucopogon neoanglicus* and *Micromyrtus sessilis* but commonly includes other shrub species such as *Acacia pycnostachya, Boronia anethifolia, Brachyloma saxicola, Kunzea bracteolata, Leptospermum nova-eangliae, Leptospermum brevipes, Melichrus urceolatus* and *Cryptandra lanosiflora* all of which are associated with *Boronia boliviensis. Boronia boliviensis* may also occur within adjacent low forest and woodlands on shallow rocky soils surrounding exposed granite sheets and is here associated with *Acacia adunca, Callitris endlicheri, Eucalyptus andrewsii, Eucalyptus prava* and *Eucalyptus youmanii.*

Conservation status: the species is currently listed as Endangered on Schedule 1 of the *NSW Threatened Species Conservation Act* as Endangered. This species is currently known from an estimated 3000 individuals within 12 discrete populations, all of which are included within the boundaries of Bolivia Hill Nature Reserve (Hunter & Earl 1999; Hunter 2002). Threats to the species include fires of too high a frequency, browsing by goats and prolonged drought and climate change.

Specimens examined: Northern Tablelands: Bolivia Hill, *c.* 34 km south of Tenterfield, *Williams 95231 & Quinn*, 7 May 1995 (NE, NSW, BRI, MEL); Bolivia Hill, *Hunter 3066*, 30 Apr. 1995 (NE); Bolivia Hill, *Hunter 3040* (NE); Bolivia Hill, *c.* 35 km south of Tenterfield, *Falconer & Morsley*, 2 Dec 1996, plants in fruit (BRI, NE, NSW, CANB, MEL, AD); Bolivia Hill, *Williams*, Nov. 1996 (NE, NSW, CANB, MEL).

Acknowledgments

We wish to thank Barrie McGowan for allowing access to Bolivia Hill while it was under his ownership. Marco Duretto is thanked for providing advice on the Section *Valvatae* of *Boronia*. Jeremy Bruhl, Frances Quinn and Peter Weston are thanked for their discussions and the directors of BRI, NSW and NE kindly provided access to specimens under their care. Steve Falconer and Richard Morsley provided assistance in the field and David Mackay and Vanessa Hunter are thanked for providing the drawings for Fig. 1, which were initially paid for by the World Wide Fund for Nature.

References

Duretto MF (1999) Systematics of *Boronia* section *Valvatae* sensu lato (Rutaceae). *Muelleria* 12: 1–132.

Duretto MF & Ladiges PY (1999) A cladistic analysis of *Boronia* section *Valvatae* (Rutaceae). *Australian Systematic Botany* 11: 635–665.

Hunter JT (2002) *Vegetation and floristics of the Tenterfield Nature Reserves (Bluff River, Bolivia Hill, Curry's Gap, Gibraltar and Mt McKenzie)*. Report to the New England Region of the New South Wales, National Parks and Wildlife service.

Hunter JT (1997) *Acacia williamsiana* (Fabaceae: Juliflorae): a new granitic outcrop species from northern New South Wales. *Journal of the Royal Society of Western Australia* 80: 235–237.

Hunter JT (1998) Two new rare species of *Homoranthus* (Myrtaceae: Chamelaucieae) from the Northern Tablelands of New South Wales. *Telopea* 8: 35–40.

Hunter JT & Bruhl JJ (1999) Two new species of *Eucalyptus* (Myrtaceae) from northern New South Wales (series *Viminales* section *Maidenaria*). *Telopea* 8: 257–263.

Hunter JT & Clarke PJ (1998) The vegetation of granite outcrop communities on the New England Batholith of eastern Australia. *Cunninghamia* 5: 547–618.

Hunter JT & Copeland LM (2001) *Homoranthus binghiensis* (Myrtaceae: Chamelaucieae), a new species from the North Western Slopes of New South Wales. *Telopea* 9: 431–433.

Hunter JT & Earl J (1999) *Field surveys to determine the location and distribution of the threatened plant* Pimelea venosa *Threlfall.* Report to the Northern Directorate, New South Wales, National Parks and Wildlife Service.

Hunter JT & Williams JB (1994) A new species of *Brachyloma* and three new subspecies of *B. daphnoides* (Epacridaceae) from south-eastern Australia. *Telopea* 6: 1–7.

Quinn FC, Williams JB, Gross CL & Bruhl JJ (1995) *Report on rare and threatened plants of north-eastern New South Wales.* Report to the Northern Region, New South Wales National Parks & Wildlife Service, Coffs Harbour.

Williams JB & Hill KD (2001) *Eucalyptus boliviana* (Myrtaceae), a new distinctive species of stringybark from New England, New South Wales. *Telopea* 9: 409–414.

Weston PH & Duretto MF (2002) *Boronia.* Pp. 265–276 in Harden GJ (ed.) *Flora of New South Wales*, vol. 2, 2nd edition. (New South Wales University Press: Kensington)

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A Revision of *Cymbonotus* (Compositae: Arctotideae, Arctotidinae)

A.E. Holland[1] and V.A. Funk[2]

[1]Queensland Herbarium EPA, Brisbane Botanic Gardens Mt Coot-tha, Mount Coot-tha Rd, QLD, Australia
Author for correspondence: Ailsa.Holland@epa.qld.gov.au
[2]US National Herbarium, Smithsonian Institution MRC 166, Washington D. C. 20013–7012 USA

Abstract

A revision of the Australian endemic genus *Cymbonotus* Cass. is presented, including keys and descriptions for the three recognised species. A new combination, ***Cymbonotus maidenii*** (Beauverd) A.E.Holland & V.A.Funk is made, based on *Arctotis maidenii* Beauverd.

Introduction

The Arctotideae is one of 35 tribes in the flowering plant family Compositae. Within the tribe there are two subtribes, and several taxa that are difficult to assign. Previous work (Funk et al. 2004; submitted) has shown that the limits of the subtribe Arctotidinae are well defined and that, except for the Australian genus *Cymbonotus*, the subtribe is restricted to southern Africa. The genus *Cymbonotus* is, however, a strongly supported monophyletic clade embedded within this subtribe (Funk et al. submitted).

For at least 20 years it has been known that a possible undescribed species of *Cymbonotus* was present in New South Wales and Queensland (Stanley & Ross 1986, Murray 1992, Henderson 2002). Our paper provides a new combination based on an earlier name assigned to this species, *Arctotis maidenii* Beauverd. Formal descriptions, and a key to the three species of *Cymbonotus* are presented.

Cymbonotus Cass., in F. Cuvier *Dict. Sci. Nat.* ed. 2, 35: 397 (1825)

Arctotis subg. *Cymbonotus* (Cass.) Beauverd, *Bull. Soc. Bot. Geneve* ser. 2, 7: 49 (1915)

Arctotis sect. *Cymbonotus* (Cass.) Baillon, *Hist. Plates* 8: 198 (1882).

Type: *Cymbonotus lawsonianus* Gaudich. (**here designated**)

Annual herbs, stems short. Latex absent. Leaves all basally rosetted, with a narrow tapering base. Leaf blades entire, toothed to deeply pinnatisect, flat. Indumentum of felted cottony hairs mixed with longer spreading hairs, or nearly glabrous. Most parts of the plant (except achenes) with glandular hairs. Capitula broadly campanulate, radiate, terminal, solitary (rarely branched), pedunculate; involucral bracts free,

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2- or 3-seriate, herbaceous throughout or with scarious margins, cottony hairy and glandular; receptacle slightly convex, pitted, with scarious scales. Corollas yellow, sometimes purplish. Ray florets pistillate, 1-seriate, "ligulate" with 4 veins and 3 triangular lobes at apex. Disc florets bisexual, fertile; corollas tubular or campanulate, glandular, deeply 5-lobed; anthers sagittate at base, not tailed, with apical appendage ovate; style minutely pubescent about a slight swelling 1/3 below apex; style branch apices 2, ovate in ray florets, obtuse in disc florets, smooth. Achenes asymmetrically oblong to obovoid, ridged, ribbed or grooved on adaxial side, glabrous or minutely pubescent; pappus absent.

Three species, all endemic to Australia (Figs 1–3).

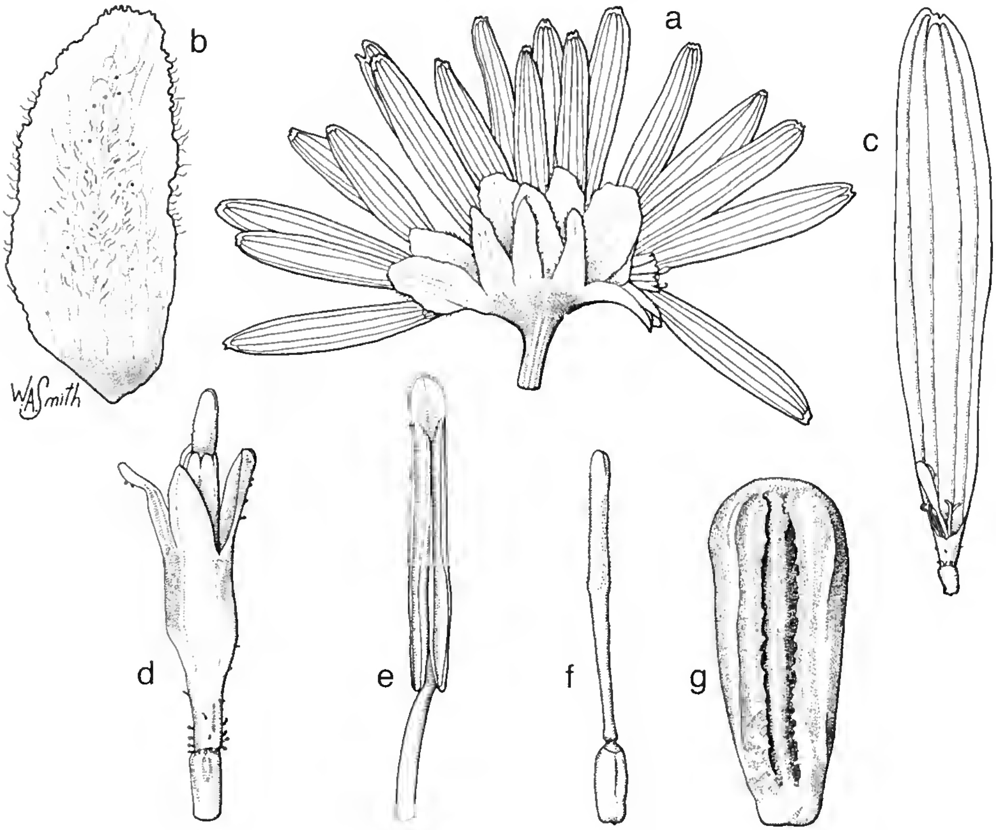

Fig. 1. *Cymbonotus maidenii* (Beauverd) A.E.Holland & V.A.Funk **a**, capitula × 1.5; **b**, involucral bract × 4; **c**, ray floret × 3; **d**, disc floret × 6; **e**, stamen × 12; **f**, style × 6; **g**, mature achene, adaxial view × 8. a–f from *Menkins 0075* (BRI), g from *Bean 14509* (BRI).

Key to the species of *Cymbonotus*

1. Abaxial surface of leaves green or greenish-grey, sparsely to moderately cottony hairy; achenes 4.5–5.9 mm long; outer involucral bracts not expanded and not spreading at apex .... ***C. maidenii***

   Abaxial surface of leaves white or grey, densely hairy with matted cottony hairs; achenes 2–4 mm long; outer involucral bracts expanded and spreading at apex 2

2. Achenes strongly curved, smooth or tuberculate, puberulous, adaxial side deeply cavernous .... ***C. lawsonianus***

   Achenes straight or slightly curved, transversely wrinkled, glabrous or glabrate, or adaxial side with 2 longitudinal ridges either side of a shallow central groove .... ***C. preissianus***

Cymbonotus maidenii (Beauverd) A.E.Holland & V.A.Funk, ***comb. nov.***

Type: New South Wales. North West Plains: Nully-Toorale, *J.H. Maiden s.n.*, Sept 1913 (**lectotype here designated**: G).

Venidium maidenii Beauverd, *Bull. Soc. Bot. Geneve* ser. 2, 7: 7 (1915) nomen nudum.

Cymbonotus sp. (Mitchell, RW Johnson 2237) sensu Queensland Nature Conservation Act 1992.

Cymbonotus sp. A sensu Murray, in Harden (ed.) *Fl. NSW* 3: 319 (1992)

Cymbonotus sp. 1 sensu Stanley & Ross, *Fl. SE Qld* 2: 579 (1986)

Cymbonotus sp. (Mitchell R.W.Johnson 2237) in Henderson (2002).

Arctotis maidenii Beauverd, *Bull. Soc. Bot. Geneve* ser. 2, 7: 47 (1915).

Illustrations: Beauverd, *Bull. Soc. Bot. Geneve* 7: 48, fig. 5 (1915); Murray, in Harden (ed.) *Fl. NSW* 3:319 (1992) as *Cymbonotus* sp. A; Stanley & Ross, *Fl. SE Qld* 2:578, fig. 81F_1 & F_2 (1986) as *Cymbonotus* sp. 1.

Annual herbs 10–40 cm high. Leaf indumentum of sparse to dense white cottony hairs and scattered longer hairs. Leaves erect, lanceolate, 10–40 cm long, 3–9 cm wide, pinnatisect; lobes triangular to oblong, irregularly toothed or further divided, with apical points sometimes spur-tipped; adaxial surface dark green, sparsely hairy, glabrescent; abaxial surface light green or greenish-grey, with sparse to moderately dense cottony hairs, with glandular hairs present. Capitula 15–30 mm diam.; florets 45–100; mature receptacle to 15 mm diam. Peduncle 2–30 cm long, longitudinally striate with lines of cottony hairs. Involucral bracts cottony hairy and glandular on outer face, with or without a scarious margin to 2 mm wide; outer involucral bracts triangular, 2–8 mm long, 2–3 mm wide, with apex blunt or acute; inner bracts lanceolate, elliptic or obovate, 11–13 mm long, 4–7 mm wide, with apex rounded or bluntly acute. Ray florets 15–20; corolla laminae elliptic, 15–28 mm long, 3–6 mm wide, yellow, glandular; corolla lobes c. 1 mm long. Disc florets 30–85; corollas dilated distally from a narrow base, 4–5 mm long, yellow, glandular; lobes c. 1.4 mm long. Anther appendages broadly ovate, c. 0.2 mm long and wide, rounded or broadly acute at apex. Style branches 0.5–1 mm long. Achenes obovoid, 4.5–5.9 mm long, 2.4–2.8 mm wide, brown to nearly black, straight or slightly curved, with corolla insertion slightly acentric; surface more or less smooth or slightly rugose; abaxial side rounded; adaxial side with 2 inflated ridges on either side, curved inwards to a deep central groove, sometimes with scattered hairs. Figure 1.

Selected specimens examined: Queensland: Darling Downs District: c. 12 km SE of Dalby, *Bott s.n.*, 21 Dec 1973 (BRI AQ012804); near Norwin, *Everist s.n.*, 11 Sep 1951 (BRI AQ245137); Millmerran, 9.3 km along Pittsworth-Millmerran road (off Toowoomba-Cecil Plains road) between "Merlewood" entrance and road 31, *Menkins ILM5*, 28 Oct 2000 (BRI); Toowoomba, *Morwood 13*, 21 Nov 1940 (BRI); Just N of Worthington's road on W side of the Dalby-Cecil Plains road, *Story JS0001*, Jan 2000 (BRI); cultivated at Oakey, from seed collected by Menkins from the Dalby-Cecil Plains Road, just NW of intersection with Worthington's Road, *Holland 1339 & Fechner*, 28 Oct 2000 (US, BRI). Maranoa District: 6 km W of Mitchell, *Johnson 2237*, 25 Apr 1961 (BRI); 7 miles [11 km] W of Roma, *Everist 3518*, 13 Oct 1948 (BRI, CANB); Mitchell, *White 11834*, 6 Apr 1941 (BRI). Leichhardt District: Ivy Vale, Gindie, 2 miles [3 km] S of Gindie siding, *Bisset E331*, 20 Aug 1962 (BRI). **New South Wales**: North Western Plains: 15.1 km SW of Goodooga, *Bean 14509*, 29 Dec 1998 (BRI); Jew's Lagoon, 50 miles [80 km] W of Narrabri, *Blakely s.n.*, Aug 1936 (NSW25514); Near Beemery, Brewarrina, *Milthorpe s.n. & Cunningham 5405*, 13 Sep 1978 (NSW); c. 5 miles [8km] SSE of Wee Waa, *Cutting s.n.*, 31 Oct 1962 (NSW589905); Brenda-Weilmoringle road, *Jones s.n. & McBarron 16516*, 7 May 1969 (NSW); Goodooga, *McBarron 16060*, 17 Oct 1968 (NSW); 12 km from Louth on Wanaaring road, Darling River flood plain, *Moore 9011*, 22 Jan 1990 (CANB); near "Langboyd", SE of Weilmoringle, *Mulham 1145*, Aug 1977 (CANB); 80 miles [128 km] NW of Walgett, *Roe AR525*, 27 Aug 1948 (CANB); 1 km W of Beemery, *Short 3020*, 31 Oct 86 (MEL).

Distribution: *C. maidenii* grows in isolated patches, in New South Wales north of the Darling and Barwon rivers, and in Queensland in southern inland districts as far west as Mitchell (Fig. 2).

Ecology: this species occurs on black, brown, or grey heavy cracking clay, usually in open grassland, along roadsides or beside waterholes or watercourses. It flowers throughout the year, probably in response to rain, but most commonly in spring.

Conservation status: this species is currently known only from two populations: a few individuals at one roadside locality on the Darling Downs, and another population that is thought to still exist near Roma (Ian Menkins pers. comm. 2006). It is therefore recommended for listing as (E) Endangered under the schedules of the Queensland Nature Conservation Act 1992. The status of populations in New South Wales is not known.

Typification: Beauverd states in his protologue "typus in herb. nat. N.S.W. et in herb. Barbey-Boissier" and the type citation " next to springs near Nulty-Toorale, leg. cl. J.H. Maiden, after whom this significant species has been named." One sheet with two specimens collected by J.H. Maiden from Nulty-Toorale in September 1913 has been located at G (herb. Barbey-Boisser). This sheet was seen by Beauverd and includes his illustrations as well as correspondence from Maiden (addressed to Beauverd) requesting an identification. One other specimen has been located from Nulty – Toorale, collected by J.L. Boorman 1064 in Sep 1912 (NSW25517). A portion of correspondence kept with this specimen indicates that Boorman was also in correspondence with Beauverd about the identity of this plant a year earlier.

The sheet held at G is here designated as the lectotype. Although there appear to be two specimens on this sheet, Beaverd's illustration of the material suggests that one specimen has been divided after being drawn.

Notes: this species differs from the other two species in the erect pinnatisect leaves, the usually longer peduncles up to 30 cm, the involucral bracts not spreading or expanded at the apex, and the larger and more or less straight achenes. The leaves are usually greener and less hairy than those of the other species.

Cymbonotus lawsonianus Gaudich., *Voy. Uranie* 462, t. 186 (1829).

Type: Port Jackson, Bathurst, *C. Gaudichaud 166* (G).

Arctotis lawsoniana (Gaudichaud) Beauverd, *Bull. Soc. Bot. Geneve* ser. 2, 7: 50 (1915).

Arctotis australiensis Beauverd, *Bull. Soc. Bot. Geneve* ser. 2, 7: 44, fig. 4 (1–9) (1915). Type: Dubbo, *J.L. Boorman*, August 1903 (**lectotype here designated:** G – right hand specimen on sheet).

Venidium australisense Beauverd, *Bull. Soc. Bot. Geneve* ser. 2, 7: 7 (1915) nomen nudum.

Illustrations: Gaudichaud, *Voy. Uranie,* plate 86 (1826); Beauverd, *Bull. Soc. Bot. Geneve* ser. 2, 7: 45, fig. 4 (1915); Murray, in Harden (ed.) *Fl. NSW* 3:319 (1992); Jeanes, in Walsh & Entwistle (eds) *Fl. Vic.* 4:718, fig. 138e (1999); Stanley & Ross, *Fl. SE Qld* 2:578, fig. 81E (1986).

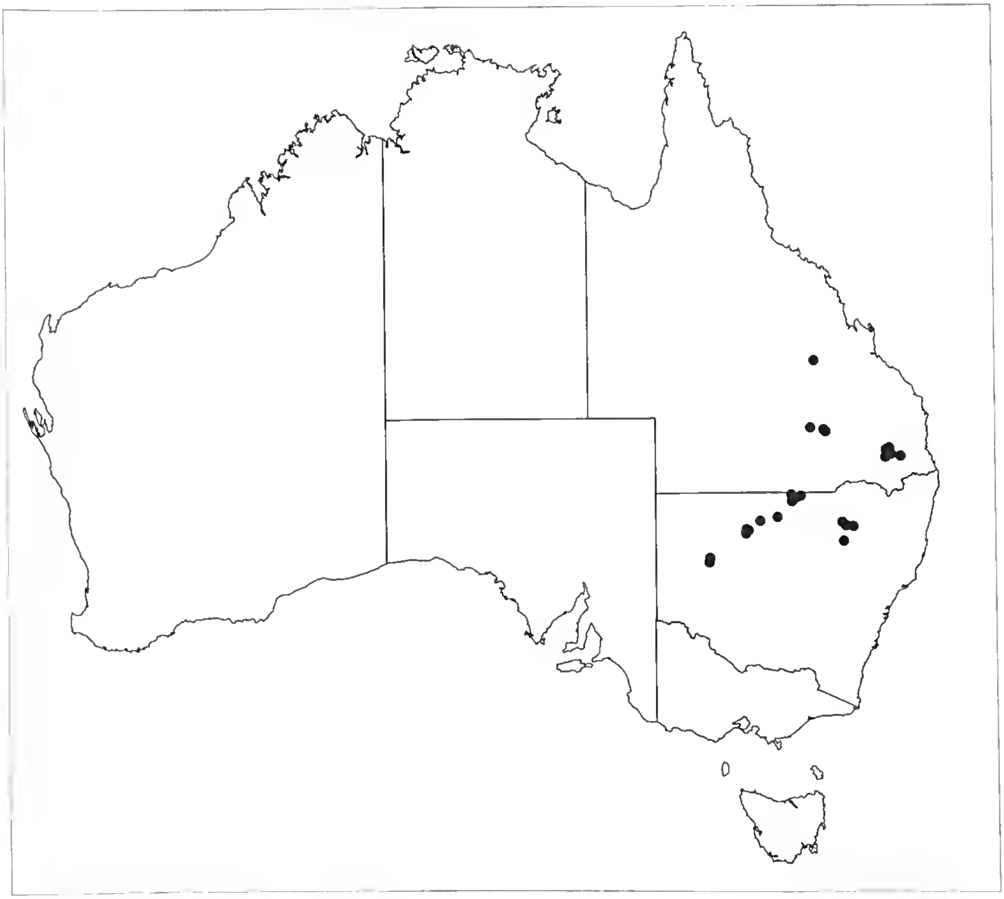

Fig. 2. Distribution of specimens of *Cymbonotus maidenii* in Australia based on BRI, NSW and CANB specimens.

Annual herbs to 30 cm high. Leaf indumentum of sparse to very dense felted white hairs, especially on the abaxial leaf surface. Leaves erect or spreading, ovate, lanceolate or elliptic, 2–25 cm long, 2–9 cm wide, entire or shallowly or coarsely toothed; lobes triangular, up to 2 cm wide and long, with secondary teeth sometimes present, and apices spur-tipped; adaxial surface dark green, sparsely hairy with short coarse hairs or nearly glabrous; abaxial surface densely covered with white matted hairs, with glands usually obscured. Capitula 10–20 mm diam.; florets 20–50; mature receptacle to 10 mm diam. Peduncle 0–9 cm long, cottony hairy. Involucral bracts with dense cottony hairs on outer face, often obscuring glands; outer involucral bracts spreading, herbaceous, linear or expanded towards the acute or acuminate apex, 5–10 mm long, 1–3 mm wide, often purplish; inner bracts ovate, elliptic or obovate, 5–10 mm long, 2–6 mm wide, rounded or bluntly acute at apex, with a scarious irregular margin to 1.5 mm wide. Ray florets 10–20, corolla laminae linear to oblanceolate, 4–11 mm long, 0.7–1.3 mm wide; corolla lobes 0.2–1 mm long, yellow, with abaxial surface sometimes brownish purple. Disc florets 10–30; corollas dilated distal to narrow base, 2–3.5 mm long, yellow, glandular; lobes triangular 0.5–1.0 mm long. Anther appendages ovate, acute, c. 0.1 mm long and wide. Style branches c. 0.3 mm long. Achenes obovoid, 2.0–2.8 mm long, 1.1–1.5 mm wide, brown to black, strongly curved, with corolla insertion acentric; surface smooth or tuberculate, puberulous; adaxial side deeply cavernous.

Selected specimens examined: Queensland: Darling Downs District: 6 km from Mt Colliery towards Gambubal SF, E of Warwick, *Bean 14803*, 11 Apr 1999 (BRI); 2.2 km E of Allora along Forest Plain road, *Bean 10850*, 4 Oct 1996 (BRI); c. 4 km along The Head Road from Spring Creek road, Condamine Gorge, NE of Killarney, *Phillips 1040*, 12 Apr.2003 (BRI). Moreton District : Gladvale grazing property on Emu Creek, on New England highway, *McIntyre SM98241*, 8 Sept 1998 (BRI). **New South Wales:** North Coast: 12 miles [9.2 km] SSW of Curricabark on Scone road, *Blaxell & Coveny 580*, 22 Sep 1968 (NSW); Barrington River, near Gloucester, *Heron s.n.*, Aug 1909 (NSW25540). Northern Tablelands: Long Ridge road, Dalmorton SF, E of Glen Innes, *Bean 20136*, 23 Mar 2003 (BRI, NSW); 2 miles [3.2 km] N of Dumaresq, *Jessup & Gray s.n.*, 19 Oct 1952 (NSW61690). North West Slopes: Warrumbungle Ranges, 22 km WSW of Coonabarabran, 0.8 km NW of Burrumbuckle Rock, *Crisp 4382*, 11 Oct 1978 (CANB); Killarney Gap, Mount Kaputar NP, 35 km from Narrabri towards Bingara, *Dalby 86/128*, 2 Oct 1986 (BRI, NSW); Coonabarabran, *Boorman s.n.*, ix 1916 (US). North West Plains: Cobar, *Abrahams s.n.*, 7 Sep 1911 (NSW25526); Cuttabri, *Jensen s.n.*, Aug 1911 (NSW25541). Central Coast: R.C.Cemetery, Cawdor road, Camden, *McBarron s.n.*, 16 Sep 1967 (NSW616039); Glen Davis, *Salasoo s.n.*, without date (NSW514412). Central Tablelands: Above Coxe's River, 4 km S of Hartley, *Benson 1801 & Keith*, 23 May 1984 (NSW); "Cherter", Clandulla, *Bray & McBarron s.n.*, 6 May 1967 (NSW590407). Central West Slopes: Dubbo, *Betche s.n.*, Sep 1885 (NSW25547); Gilgandra, *Simon s.n.*, Sep 1915 (NSW25523). Southern Tablelands: Monga, *Bauerlen s.n.*, Sep 1898 (NSW25533). South West Plains: Near Eremaran turnoff, on Gigunnia road, *Cunningham 1465 & Milthorpe*, 17 Nov 1973 (NSW). Hunter River, US Exploring Expedition, *Wilkes, s.n.*, without date (US). Australian Capital Territory: Stromlo Forest, *D'Arnay 746*, 25 Nov 1975 (CANB, NSW); Lyneham, Canberra, *Gray 6402*, 16 Mar 1969 (CANB); open country to NE of Black Mountain, Canberra, *Pullen 2197*, 10 Sep 1960 (CANB). **Victoria:** Kamarooka State Park, *Beauglehole 69612*, 31 Oct 1981 (MEL); East Gippsland, Junction of Snowy and Deddick Rivers near McKillop bridge, *Beauglehole 33842 & Rogers*, 28 Aug 1970 (MEL).

Distribution: *C. lawsonianus* occurs in south-eastern Queensland in the Darling Downs district from Toowoomba to the NSW border, throughout NSW, in northern Victoria, South Australia and Tasmania. Fig. 3.

Ecology: the species grows in a range of situations on roadsides, in open forest and woodlands, and in disturbed areas often near water. Soils are variable, including skeletal soil over sandstone, grey sand on old dunes, clay loam, sandy loam and red earth. Sometimes it also occurs in lawns and gardens. It flowers throughout the year, probably in response to rain, but most commonly in spring.

Conservation status: this species is not considered to be threatened.

Typification: in his protologue, Beauverd describes the achenes of *Arctotis australiensis* as glabrescent or glabrous, winged, the wings lateral, inflexed, with whole margins, very similar to *C. lawsonianus*. His illustration of an achene of *A. australiensis* on page 45, Fig. IV (3) looks like *C. lawsonianus*. What is curious is that an illustration on the same plate Fig. IV (10) is supposed to be an achene of *C. lawsonianus* but looks more like *C. preissianus* Steetz, although this name is not mentioned anywhere in his study. Further, he goes on to distinguish *A. australiensis* (from *C. lawsonianus*) by the achene that has

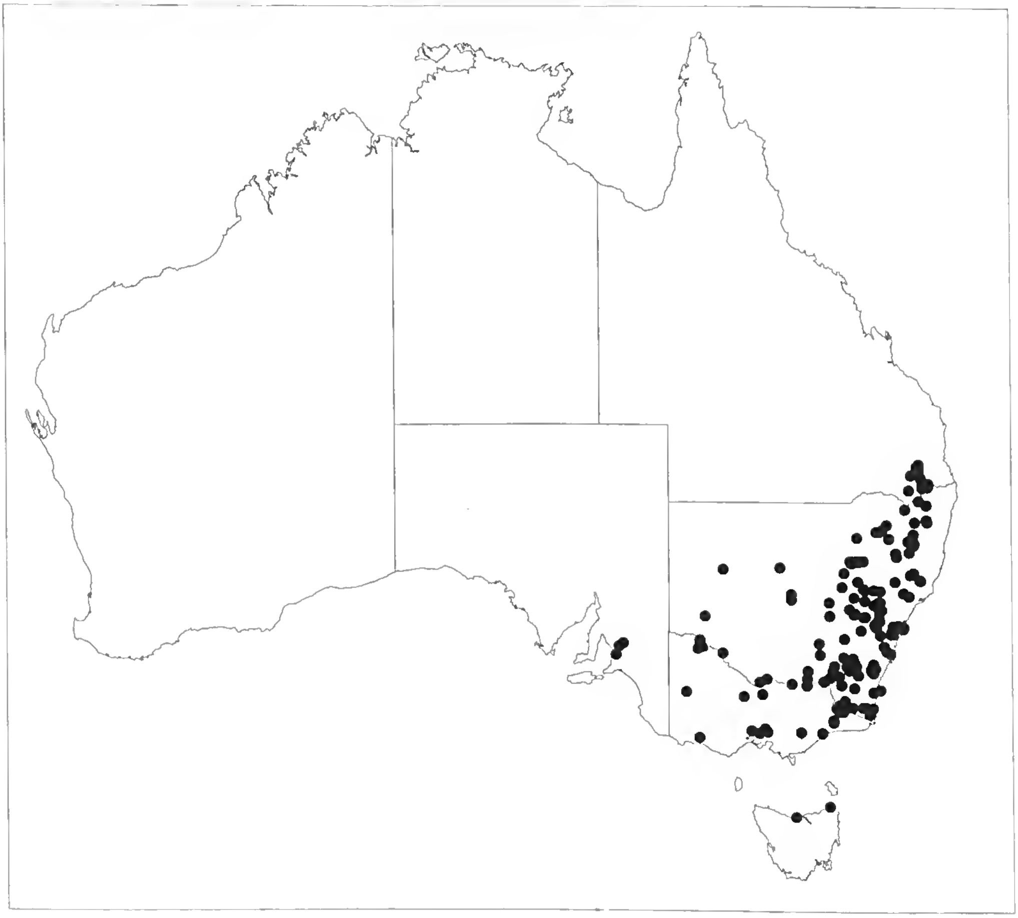

Fig. 3. Distribution of specimens of *Cymbonotus lawsonianus* in Australia. (data courtesy Australias Virtual Herbarium)

two wings inflexed against the median ribs creating two strong longitudinal cavities, while the achene of *C. lawsonianus* is lacking in apparent cavities and has a horizontal apex (rather than oblique as in *A.australiensis*). On this basis, I suggest that Beauverd was probably unaware of the existence of *C. preissianus* and mistakenly assumed that his material was *C. lawsonianus*. Correspondence (kept with the type material) from J.H. Maiden (to Beauverd), indicates that he too was mystified as to why a new name was being formulated for this species "for it is identical with the whole series of *C. lawsonianus* in this Herbarium… and closely resembles Gaudichaud's figure". *Arctotis australiensis* Beauverd is therefore considered to be a synonym of *C. lawsonianus*.

The lectotype of *Arctotis australiensis* is here chosen as the right hand specimen on the sheet held at G. The illustration by Beauverd appears to have been drawn from this specimen. No achenes are present on either specimen or in the attached packet, so it is possible that the left hand specimen may represent *C. preissianus*.

Cymbonotus preissianus Steetz in Lehmann., *Pl. Preiss.* 1: 486 (1845).

Type: Western Australia. In Nova Hollandia (Swan River Colonia), *J.A.L. Priess 13* (**lectotype here designated:** MEL 727579).

Illustrations: Murray, in Harden (ed.) *Fl. NSW* 3:318 (1992); Jeanes, in Walsh & Entwistle (eds) *Fl. Vic.* 4: 718, fig. 138f (1999).

Annual herbs to 30 cm high. Leaf indumentum of sparse to very dense felted white hairs, especially on the abaxial leaf surface. Leaves erect or spreading, petiole-like at base, ovate, lanceolate or elliptic, 2–30 cm long, 2–10 cm wide, coarsely toothed or pinnatisect; lobes triangular, up to 2.5 cm wide and long, with secondary teeth sometimes present, and apices spur-tipped; adaxial surface dark green, sparsely hairy with short coarse hairs or nearly glabrous; abaxial surface densely covered with white matted hairs, with glands usually obscured. Capitula 12–30 mm diam.; florets 20–60; mature receptacle to 15 mm diam. Peduncle 0–15 cm long, cottony hairy. Involucral bracts with dense cottony hairs on outer face, often obscuring glands; outer involucral bracts spreading, herbaceous, linear or expanded towards the acute or acuminate apex, 5–10 mm long, 1–3 mm wide, often purplish; inner bracts ovate, elliptic or obovate, 5–10 mm long, 2–4.5 mm wide, rounded or bluntly acute at apex, with a scarious irregular margin to 1 mm wide. Ray florets 10–20; corolla laminae linear to oblanceolate, 6–20 mm long, 1–4 mm wide; corolla lobes 0.2–1 mm long, with adaxial surface yellow, and abaxial surface brownish purple. Disc florets 10–40, dilated above a narrow base, 2–4 mm long, yellow, glandular; lobes triangular, 0.5–1.0 mm long. Anther appendages ovate, acute, c. 0.1 mm long and wide. Style branches c. 3 mm long. Achenes obovoid, 2.5–4.0 mm long, 1.0–1.4 mm wide, brown to black, straight or slightly curved, with corolla insertion slightly acentric; surface transversely wrinkled throughout; adaxial side with 2 narrow ridges either side of a shallow central groove.

Selected specimens examined: New South Wales. Central Tablelands: 10 km SW of Orange, Boree Creek, Federal Falls, *Barnsley 1123*, 5 Nov 1979 (CANB); Jenolan State Forest, *Benson 1689 & Keith*, 30 Mar 1984 (NSW). Southern Tablelands: c. 4 km SE of Tumut, Tumut State Forest, *Jones 7625 & Broers*, 23 Aug 1991 (CANB); Cave Creek, 18 miles (28.8 km) NNE of Kiandra, *Rodd & Coveny 2634* , 11 Dec 1969 (NSW); Gurrangorambla Creek, Currango Plain, N of Tantaugoara Dam, *Thompson 771*, 19 Jan 1971 (NSW). South West Slopes: Wagga, *Breakwell s.n.*, Oct 1912 (NSW25551); 1 km NNE of Mt Ulandra, *Crawford 6575*, 26 Oct 2001 (CANB); Ulandra Nature Reserve, c. 29 km directly ENE of Junee, at summit of Mt Ulandra, *Parris 9916*, 6 Oct 1991 (CANB). South Western Plains: Deniliquin, *Mulham S387*, 17 Sep 1965 (CANB, NSW). Australian Capital Territory: Tidbinbilla Flora and Fauna Reserve, *Canning 3067*, 16 Dec 1969 (CANB); Black Mountain, *McKee 8955*, 15 Feb 1962 (CANB, NSW); beside Paddys River road, c. 1 km from Cotter Reserve, *Ward 19 & Hughes*, 1 Sep 1983 (CANB). **Victoria**: Boweya Flora and Fauna Reserve, *Beauglehole 80373*, 13 Sep 1985 (MEL); Morphett Swamp Wildlife Reserve, *Beauglehole 80497*, 15 Sep 1985 (MEL); Splitters Range Forest Block, 12.7 km NNW of Swifts Creek township, Splitters Range road, 1.2 km E of Omeo Gap road, *Carr 10205*, 7 Dec 1984 (CANB); SW of Hepburn, Tipperary Track, S of Bruces Flat, E of Sailors Creek, *Ross 3984*, 26 Sep 1997 (MEL); Mouth of Aire River, 4.5 miles [7.2 km] NW of Cape Otway, *Willis s.n.*, 13 Sep 1969 (MEL2159321). **Tasmania**: Penquite, *Gunn 509*, 13 Sep 1841 (NSW61712); Summit of Mt Nelson, *Lord H509*, 18 Jan 1930 (CANB); Deal Island, *Whinray 1264*, 18 Dec 1970 (CANB).

Fig. 4. Distribution of specimens of *Cymbonotus preissianus* in Australia. (data courtesy Australias Virtual Herbarium)

South Australia: Morialta near Adelaide, *Cheel s.n.*, Aug 1924 (NSW61695); Mt. Lofty Range, Tarma, ca. 90 km NNE of Adelaide, *Kraehenbuehl 2250*, 17 Aug 1968 (US).

Distribution: *C. preissianus* occurs in the southern half of New South Wales, throughout Victoria, in southern South Australia east from Eyre Peninsula, in Tasmania and in south-western Western Australia. Fig. 4.

Ecology: the species grows in a range of open forest and woodland habitats, in disturbed areas, often in drainage lines. Soils include shallow loams, coastal sandhills, loams, sandy loams and red earths. Flowers have been collected between August and February.

Conservation status: this species is not considered to be threatened.

Typification: the specimen held at MEL: In Nova Hollandia (Swan River Colonia), *J.A.L. Preiss 130* (MEL 727579) is here designated as the lectotype. According to the annotation on the specimen, it was part of the Steetz herbarium, and was seen by Bentham. No other authentic material was found at MEL or LD.

Acknowledgments

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References

Funk VA, Chan R & Keeley S (2004) Insights into the evolution of the tribe Arctotideae (Compositae) using *trn*L, *ndh*F, and ITS. *Taxon* 53: 637–655.

Funk VA, Holland AE & Chan R (submitted) *Cymbonotus* (Compositae: Arctotideae, Arctotidinae): an endemic Australian genus embedded in a southern African clade. *Botanical Journal of the Linnean Society.*

Henderson RJF (ed.) (2002) *Names and distribution of Queensland plants, algae and lichens.* (Environmental Protection Agency: Brisbane)

Murray L (1992) *Cymbonotus.* Pp. 318–319 in Harden GJ (ed.) *Flora of New South Wales*, vol 3. (New South Wales University Press: Kensington)

Stanley TD & Ross EM (1986) *Flora of South-eastern Queensland*, vol. 2. (Queensland Department of Primary Industry: Brisbane)

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New Australian species and typifications in *Veronica* sens. lat. (Plantaginaceae)

Barbara G. Briggs[1] and Friedrich Ehrendorfer[2]

[1]*Botanic Gardens Trust Sydney, Mrs Macquaries Road, Sydney NSW 2000, Australia.*
Email: barbara.briggs@rbgsyd.nsw.gov.au
[2]*Institute of Botany, University of Vienna, Rennweg 14, A–1030, Vienna, Austria.*
Email: friedrich.ehrendorfer@univie.ac.at

Abstract

Four Australian species of *Veronica* sens. lat. are newly described and illustrated; lectotypes are selected for other species and synonyms. In *V.* 'sect. *Derwentia*' (Raf.) B.G.Briggs (in Garnock-Jones et al. submitted) we informally recognise three clades: the *Derwentia* clade, the *V. formosa* clade and the *V. calycina* clade. A second species of the *V. formosa* clade, ***V. continua***, is newly described; both *V. continua* and *V. formosa* being Tasmanian endemics. New Australian mainland taxa of the *V. calycina* clade are ***V. grosseserrata***, ***V. sobolifera*** and ***V. subtilis***; types and synonyms are listed for *V. brownii*, *V. calycina*, *V. distans*, *V. gracilis*, *V. hillebrandii*, *V. notabilis*, *V. novae-hollandiae*, *V. parnkalliana* and *V. plebeia*. From *V.* sect. *Hebe*, typification and synonyms are provided for *V. densifolia*.

Introduction

Veronica and related genera of the Veroniceae were, until recently, regarded as members of the Scrophulariaceae. The results of DNA analyses have, however, led to drastic changes in the circumscription of the family and the reclassification of *Veronica* as a member of the Plantaginaceae (Olmstead & Reeves 1995, Olmstead et al. 2001, Albach et al. 2005). Such analyses have also made clear that *Veronica* is paraphyletic if Southern Hemisphere genera such as *Derwentia*, *Parahebe*, *Hebe* and *Chionohebe* are recognised (Albach & Chase 2001, Wagstaff et al. 2002). A greatly enlarged genus *Veronica* is therefore now accepted by Albach et al. (2004), Garnock-Jones et al. (submitted) and Albach et al. (submitted), although Bayly and Kellow (2006), in their comprehensive account of *Hebe* and *Leonohebe*, continue to recognise these at generic level 'as segregates of the larger, mostly northern hemisphere genus *Veronica*' and Brummitt (2006) regards a satisfactory classification of *Veronica* as incompatible with the recognition of only monophyletic taxa. The main consequences of an expanded *Veronica* for species native in Australia are the inclusion of all the Southern Hemisphere clades of *Veronica* in one subgenus that includes three sections: 'sect. *Detzneria* (Schltr. ex Diels) Albach' (in Garnock-Jones et al. submitted), 'sect. *Derwentia* (Raf.) B.G.Briggs' (in Garnock-Jones

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et al. submitted; both sectional names to be formally published in that paper and a choice to be made there between the competing subgeneric names), and sect. *Hebe* (Juss.) G.Don.

The first of these sections includes only '*V.* (= *Detzneria*) *tubata* (Diels) Albach' (Garnock-Jones et al. submitted) in New Guinea. The second section, '*V.* sect. *Derwentia*', consists of

(1) all the somewhat woody Australian taxa treated under *Derwentia* by Briggs and Ehrendorfer (1992) together with *Parahebe lithophila* B.G.Briggs & Ehrend., here informally referred to as the *Derwentia* clade,
(2) the relatively isolated *Veronica formosa* clade with two species from Tasmania, and also
(3) a number of herbaceous and predominantly Australian taxa listed under *Veronica* sect. *Chamaedrys*, group *Calycina* by Römpp (1928).

The latter taxa, treated as the *V. calycina* clade in the present study, are represented in the analyses of DNA data (Wagstaff & Garnock-Jones 1998, 2000; Wagstaff et al. 2002) by two species reported as *V. calycina* and *V. arguta* (a synonym of *V. brownii*), and these changes clearly support their placement within '*V.* sect. *Derwentia*'. Indeed, the phylogeny presented by Wagstaff et al. (2002) suggests that the *calycina* clade is embedded in the *Derwentia* clade. With respect to their morphology, the taxa of the *V. calycina* clade correspond with Northern Hemisphere *Veronica* sens. strict. (particularly *V.* sect. *Chamaedrys*, $x = 8$). They are polyploids with $2n = 36$ (rarely $2n = 34$) and $2n = 72$ and thus exhibit a secondary base number of $x = 18$ (rarely 17) in contrast to all other members of the '*Hebe* complex' of *Veronica* (Heads 1992, Bayly & Kellow 2006, and other authors) which have secondary base numbers of $x = 21$, 20 and 19 (Briggs & Ehrendorfer 2006).

Together with Albach et al. (submitted), we interpret all these secondary base numbers as derived from hexaploid ancestors and descending dysploidy. A hexaploid number of $2n = 48$ was reported (Borgmann 1964) in the monospecific New Guinean '*V.* sect. *Detzneria*' but our studies (Briggs & Ehrendorfer 2006), although giving only a very approximate count, show $2n = 38$–42. There may have been hexaploidy from a primary base number of $x = 8$ (as in *V.* sect. *Chamaedrys*) or hexaploidy may have followed dysploid change to $x = 7$. The closely related *V.* sect. *Hebe* (with $x = 21$ and 20) includes the former genera *Hebe*, *Heliohebe*, *Leonohebe*, *Chionohebe* and most of *Parahebe* and has its greatest species diversity in New Zealand but extends to New Guinea, French Polynesia and South America; it is represented on the Australian mainland only by *V. densifolia* and in Tasmania by the species that has been known as *Chionohebe ciliolata* (Hook.f.) B.G.Briggs & Ehrend. Bayly and Kellow (2006) observe that in sect. *Hebe* 'it seems likely that independent origins of polyploidy have been relatively common', given that polyploidy 'is found in taxa with both $x = 20$ and 21 chromosomes, morphologically divergent taxa with the same base chromosome number, and within at least some species'.

In accordance with the new phylogenetic concept of *Veronica* sens. lat., we provide descriptions and illustrations for four new Australian species. With respect to '*V.* sect. *Derwentia*', including the clades of *V. calycina* and *V. formosa*, lectotypes are selected for four species and the types of seven other species are listed. Types are also indicated for synonyms of the species now recognised, and one of these is lectotypified. Citations of the types of the species classified under *Derwentia* and *Parahebe* by Briggs and Ehrendorfer (1992) are not repeated here. Of the two species that have been included in *Chionohebe* (now in *V.* sect. *Hebe*) and that are common to Australia and New Zealand, *V. densifolia* is lectotypified here, but the other is discussed by Garnock-Jones et al. (submitted). With respect to *V.* subgenus *Beccabunga* subsect. *Serpyllifolia*, it is probable that the occurrences of *V. serpyllifolia* L. sens. lat. in Australia are partly native to this country and partly naturalised introductions (Briggs & Barker 1999); they are not included in this study.

'*Veronica* sect. *Derwentia*': *V. formosa* clade

Veronica formosa, a somewhat woody species from Tasmania, was discussed in our study of the Australian representatives of *Derwentia* and *Parahebe* (Briggs & Ehrendorfer 1992). It shows $2n = 42$, $x = 21$, but was provisionally left in *Veronica* as of uncertain position. DNA data available now (Wagstaff et al. 2002: listed as *Hebe formosa*) clearly demonstrate that it is a basal and relatively isolated member of '*V.* sect. *Derwentia*', a group that links the Northern with the Southern Hemisphere clades of the genus. We now provide a description and illustration of a second species of the clade, *V. continua*, and lectotypification of *V. formosa*.

Veronica continua B.G.Briggs, ***sp. nov.***

A *Veronica formosa* combinatione characterum sequentium distinguitur: caules vix ramificantes; folia majora, (12–)15–30(–35) mm longa, (3.5–)5–9(–11) mm lata, oblonga vel lanceolata; racemi non nisi ad nodos supremos; racemi longiores, racemi fructiferi (2–)4–10 cm longi, flores 15–30 gerentes; capsulae majores, 5–7.5 mm longae, 6–9 mm latae.

Holotype: Tasmania: 2.4 km NW of Cranbrook Rd, on road to Hardings Falls, W of Bicheno (41° 52′ S 148° 02′ E), *B.G. Briggs 9149*, 24 Jan 1993 (HO). Isotypes NSW, CANB, MEL.

Erect woody herb to 1.5 m tall. *Stems* 1–8 per plant, with few branchings, continuing growth (usually without branching) after flowering for several seasons before falling and being replaced by new shoots from the perennial base, terete, the longest internodes 0.4–1.2 cm long, 1.5–3.5 mm diam., hirsute with spreading hairs in a longitudinal band below the leaf sinus; hairs 0.3–1.3 mm long, of 3–6 cells; surface of the old stems clothed in old flaking leaf bases. *Leaves* opposite, decussate, entire, sessile, stem-clasping, firm textured, smooth, oblong to lanceolate, spreading or strongly reflexed, (12–)15–30(–35) mm long, (3.5–)5–9(–11) mm broad, glabrous except for rigid white cilia on margin towards the base, acute, apex often recurved, midvein deeply impressed above and prominent below, secondary venation discernable on abaxial surface; base of young leaf fused with the opposite leaf base but splitting apart with age. *Racemes* arising in the uppermost axils of the season's growth or a few on a short bracteose lateral branch in an upper axil, (2–)4–10 cm long, most of the length floriferous; with 15–30 flowers. *Flowers* in the axils of linear bracts that are (3–)5–8(–9.5) mm long. *Fruiting pedicels* 4–9 mm long. *Calyx lobes* narrow triangular, acuminate, 3.5–4.7 mm long and 1–1.5 mm broad in fruit, with short hairs on margin. *Corolla* blue, 8–9.5 mm long; adaxial lobe broad ovate, obtuse, 6–9.5 mm long, 5–7.6 mm broad; abaxial lobe obtuse, ovate but narrower than the adaxial lobe, 5.5–9.5 mm long, 3–6 mm broad; lateral lobes elliptical to obovate, not folded, c. 6 mm long, 3.5–4.5 mm broad; the tube very short and broad, glabrous. *Stamens*: filaments 3.5–5.5 mm long; anthers 1.8–3.2 mm long.

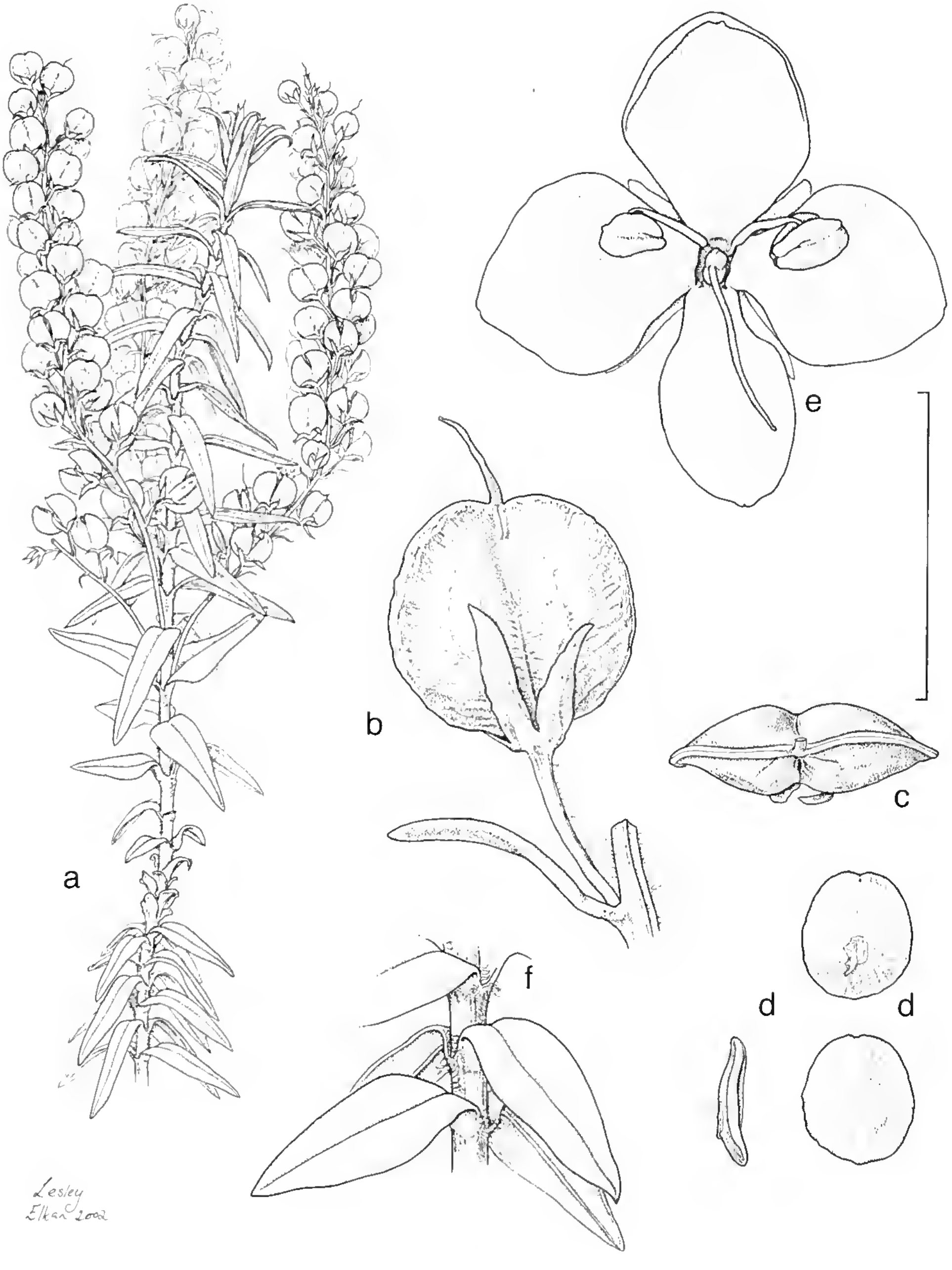

Fig. 1. *Veronica continua.* **a**, leafy branch with fruiting racemes; **b**, capsule, lateral view; **c**, capsule, apical view; **d**, seed, adaxial, abaxial and lateral views; **e**, flower; **f**, leaf and stem detail (a–d, f from type collection; e from *Collier 3793*). Scale bar: a = 5 cm; b, c = 0.75 cm; d = 0.6 cm; e = 1 cm; f = 2 cm.

Capsule strongly flattened, with a narrow septum, glossy, glabrous, broad ovate, 5–7.5 mm long, 6–9 mm broad, apex slightly emarginate to truncate; dehiscing by a septicidal split, initially 1/4 to 1/3 to the base, eventually splitting to base; style ± persistent, 4.5–5.5 mm long, glabrous. *Seeds* to 12 in number, almost circular in outline, thin, smooth, flat or slightly concavo-convex, 2–2.5 mm long, 1.6–2.4 mm broad. (Fig. 1).

Distinguished from *V. formosa*, which is widely distributed in the eastern half of Tasmania, by the stems less branched; leaves larger, lanceolate to narrow elliptic, often strongly reflexed (less often spreading); racemes developed only at the uppermost nodes of the current season's growth; racemes longer with more flowers; larger capsules. In *V. formosa* the leaves are (5–)10–18(–21) mm long and (2–)3–5(–7) mm wide, ovate to narrow elliptic, spreading or less often recurved; racemes are mostly on short lateral branches developed at most of the nodes of a previous season's growth; racemes (0.2–)0.5–3 cm long with 2–12(–18) flowers; capsules 3.5–6 mm long, 3.5–5.5 mm broad. Occasional departures from the normal mery have been noted in *V. continua*, with a small proportion of 3- and 4- locular capsules and rarely one of the lateral corolla lobes divided into two. *Veronica continua* shows many similarities to the more variable *V. formosa* which has a more shrubby and compact form, well adapted to the less sheltered habitats of mountain areas in Tasmania where it commonly occurs. Altogether, the small *V. formosa* clade in its morphology and karyology is clearly related to the Australian taxa formerly included in *Derwentia* (Briggs & Ehrendorfer 1992).

The epithet is from the Latin *continuus* = continuous, unbroken; referring to the stems continuing growth after flowering for several seasons with little or no branching.

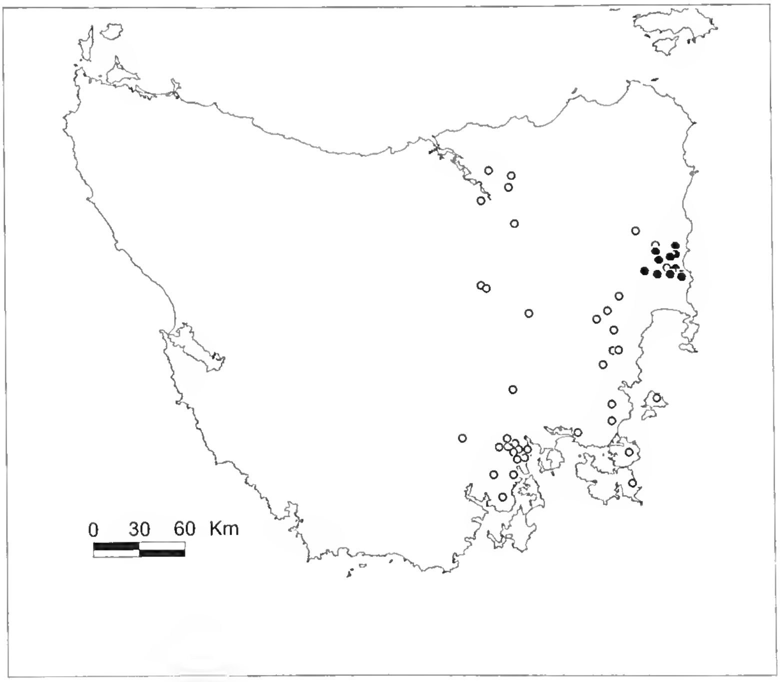

Fig. 2. Distribution of *V. continua* ● and *V. formosa* ○ in Tasmania.

Distribution: towards the north-east of Tasmania, growing on rocky hillsides, pebbly ground in a riverine flood zone, cliff ledges; sometimes in wet sclerophyll forest, mostly on dolerite (Fig. 2).

Conservation status: restricted in distribution, occurring in an area managed as native forest and perhaps not currently endangered. *Veronica continua* is found in rocky areas, or sites with sparse undergrowth, suggesting that the species is confined to sites with some protection from wildfires. Its present region of occurrence was a refugium during colder and drier glacial times (Coates et al. 1999; Kirkpatrick & Brown 1984a). The region includes a considerable number of endemic Tasmanian species, especially in fire-protected sites such as cliff faces, rocky gorges and alpine plateaus (Kirkpatrick & Brown 1984b). This handsome species has, for more than two decades, been in cultivation and marketed by plant nurseries specialising in species native to Tasmania.

Selected specimens examined: Tasmania: East Coast: Marshes Hd of Douglas River, *Milligan*, 12 Dec 1851 (K); Coal Marsh near Apsley River, *Collier 3793*, 13 Nov 1988 (HO); Nichols Cap, W of Seymour Beach, *Harris*, 25 Jan 1979 (HO); Organ Hill near Bicheno, *Moscal 192*, 20 Mar 1980 (HO); Blindburn Creek, NW of Bicheno, *Gray 600*, 9 May 1982 (HO); Hardings Falls, Swan River, WNW of Bicheno, *Briggs 9148*, 24 Jan 1993 (NSW); Apsley River, *Collier 922*, 2 Nov 1985 (HO); Lilla Villa Bridge, SW of Bicheno, *Simmons*, 20 May 1982 (HO); Lilla Villa Bridge, Apsley River, *Buchanan 222*, 23 Jan 1980 (HO); Apsley River, by main road bridge, S of Bicheno, *Gordon*, 19 Nov 1942 (HO).

Veronica formosa R.Br., *Prodr.* 434 (1810).

≡ *Hebe formosa* (R.Br.) Cockayne, *Trans. & Proc. New Zealand Inst.* 60: 470 (1929).

≡ *Parahebe formosa* (R.Br.) Heads, *Bot. J. Linn. Soc.* 115: 69 (1994).

≡ *Derwentia formosa* (R.Br.) Bayly in Bayly & Kellow, *Illustrated Guide to New Zealand Hebes.* 328 (2006).

Lectotype (**here designated**): [Tasmania] Ad rupes saxosas fluvii Cataract R., in Porta Dalrymple [near Georgetown], *R. Brown*, 10 Jan 1804 (BM!, marked 'A' on the sheet, photo NSW). Probable isolectotypes: MEL 21612!, 21613! and NSW 6234!, which are in similar fruiting condition but lack locality notes. Residual syntypes: `In montibus prope fluv. Derwent. In collibus supra Sullivan Cove. In monte Tabulari' [Mt Wellington], *R. Brown*, 27 Feb. 1804 (BM!, photo NSW, isosyntype K!). The residual syntypes in BM are mounted on the same sheet as the lectotype; of the five pieces on the sheet, only piece 'A' can be readily matched to a locality.

'*Veronica* sect. *Derwentia*': *V. calycina* clade

As presently known, the *Veronica calycina* clade is made up of 12 perennial, herbaceous Australian species of which one (*V. plebeia*) also occurs in New Zealand, where its native or naturalised status is unclear (Sykes 1988). There is considerable polymorphism, associated with the polyploid and reticulate nature of the clade. Chromosome numbers are all polyploid, mostly on the secondary and reduced hexaploid base number $x = 18$, ($2n = 36$ or 72), only *V. plebeia* appears further reduced to $2n = 34$, i.e. $x = 17$ (Briggs & Ehrendorfer 2006). No comprehensive survey of the clade is yet available, but treatments in the floras of South Australia (Barker 1986), New South Wales (Briggs et al. 1992) and Victoria (Briggs & Barker 1999) supply partial information, including brief descriptions and keys for the identification of the new taxa described here. Three new species, *V. grosseserrata*, *V. sobolifera* and *V. subtilis*, are described and illustrated below. We also provide notes on the typification of the other nine species recognised within the *V. calycina* clade and their synonyms.

Veronica grosseserrata B.G.Briggs & Ehrend., ***sp. nov.***

A *Veronica notabilis* combinatione characterum sequentium distinguitur: pili indumentorum rigentiores; laminae foliorum ad basim truncatae, grosse serratae; lobi calycis acutiores, densius ciliati; capsulae truncatae, apicem versus latae.

Holotype: New South Wales: Mt Boss (lower slope), 43 km NW of Wauchope. (Mt Boss State Forest at Camerons Forest Camp), alt. 1096 m., *R.G. Coveny, P.D. Hind & R. Hancock*, 15 Feb 1975 (NSW). Isotypes BRI, CANB, K, MEL, NY.

Herbs with procumbent stems and ascending to erect flowering stems, the procumbent stems commonly becoming ascending to erect distally, or sometimes the flowering stems becoming procumbent and continuing vegetative growth into the next season. *Flowering stems* (8–)12–30(–45) cm long; longest internodes 2–7(–9) cm; stem hairs mostly short, 0.2–1 mm long, stiff, yellowish, scattered, multicellular, to 8 cells long, the cell walls mostly not collapsed when dry, antrorsely curved, very rarely with glandular heads. *Leaves*: petioles 5–12(–17) mm; laminae angular-ovate to almost triangular, broadest towards base, 30–55(–90) mm long, (9–)11–20(–35) mm broad, base broadly cuneate or truncate, apex acute, margins grossly serrate with 6–12 apiculate, uneven, spreading teeth on each side, the largest teeth toward the base, texture thin, green to dark brown or somewhat blackish when dry, ± palmately nerved with 5–7 nerves from near the base and 2–3 major nerves higher up on each side of the midvein, the margin slightly revolute and scarcely thickened, with short curved hairs on the upper surface and on the veins of the lower surface and the margin, but the lower surface glabrous or with sparse hairs between the veins. *Racemes* single or mostly paired at 2–4 nodes on the upper 1/2 of the stem but sometimes ± irregularly distributed, (45–)60–140(–160) mm long, with (6–)10–16(–20) flowers; peduncle (10–)15–40(–60) mm long. *Bracts* narrow-obovate, 4–6 mm long. *Fruiting pedicels* 6–13 mm long. *Calyx lobes* obovate, acute to obtuse, almost doubled in size from flower to fruit, finally 5–8 mm long, 1.5–3.5 mm broad, with short curved hairs on the margins (including the apex) and scattered on the outer surface and veins. *Corolla* at first white, becoming mauve, 3–6(–8) mm long; lobes obovate to very broad obovate, not folded. *Capsule* glabrous or with a few short hairs on and near upper margins, somewhat glossy, slightly emarginate, 4–5 mm long, breadth slightly greater than length; style ± equal to fruit length. *Seeds* broadly ovoid, flattened, very slightly rugulose and somewhat glossy, light brown, 1–1.5 mm long. (Fig. 3, a–c).

Veronica grosseserrata is octoploid ($2n = 72$) (Briggs & Ehrendorfer 2006). It can be distinguished from *V. notabilis* F.Muell. ex Benth. (tetraploid, $2n = 36$) by its indumentum of more rigid hairs, with the cells not collapsed when dry; more truncate and more deeply serrate leaves with sparser hairs on lower surface; more strongly ciliolate calyx lobes; capsules that are more truncate and broader toward the apex. Despite the reported difference in ploidy level, some collections suggest that there is hybridisation between the two taxa. *Veronica grosseserrata* was referred to as '*Veronica* sp. C' in Briggs et al. (1992, p. 580), and as '*Veronica* sp. 1' in Briggs and Barker (1999, p. 515).

The epithet is from the Latin and refers to the deep serration of the leaves.

Distribution: South-eastern Queensland, North and Central Coast and Tablelands of New South Wales, and in the eastern half of Victoria. In moist eucalypt forest and openings in rainforest. (Fig. 4).

Conservation status: widespread and common.

Selected specimens examined: Queensland: Mt Merino, McPherson Range, *Blake 15371*, 9 Dec 1943 (BRI); Wilsons Peak, *Forster 15702 & Leiper*, 21 Aug 1994 (BRI). **New South Wales:** North Coast:Clarence River, [*Beckler*] (MEL 17933); Moonan Brook, *Carter*, 1884 (MEL 17935); Mt Boss State Forest, c. 15 miles [25 km] NW of Wauchope, *Constable*, 31 Oct 1956 (NSW 42216); Gloucester Tops, *Coveny*, 1 Jan 1967 (NSW 95319); c. 32 miles [50 km] SW of Gloucester, *Coveny*, 30 Nov 1967 (NSW 98194); Dorrigo, *Heron*, May 1912 (NSW 5966); Timbarra, New England, *Stuart 682*, (MEL); Mt Warning, *White & Brass*, 1 Jan 1938 (K); Gibraltar Range, c. 42 miles [65 km] NE of Glen Innes, *Williams*, Feb 1961 (NE). Northern Tablelands: Mt Spirabo summit, E of Deepwater, *Constable*, May 1961 (NSW 57445); Point Lookout, New England National Park, *Williams*, 4 Jun 1967 (NSW 96612). Central Tablelands: Base of Scenic Railway, Katoomba, *Ehrendorfer & Briggs*, 22 Oct 1966 (NSW 94525); Katoomba, *Briggs*, 26 Dec 1967 (NSW 101559); Blue Mountains, *Bufton*, 1893 (MEL 17937); Blue Mountains, *Lamont 328*, Mar 1888 (BM). Southern Tablelands: Wark's Road A.C.T., *Gray*, 21 Mar 1959 (CANB 168031); Sugarloaf Mountain, *Gauba*, 23 Feb 1951 (CANB); Humes River (MEL 17934). **Victoria:** Mountain Creek, near turn-off to Trapper's Gap, Tawonga district, *Rodd 380*, 27 Dec 1966 (NSW); Dividing Ranges, *Walter*, Nov 1898 (NSW 5985).

Veronica sobolifera B.G.Briggs & Ehrend., ***sp. nov.***

A *Veronica gracilis* combinatione characterum sequentium distinguitur: caules florentes longiores (plerumque 10–40 cm longi); folia majora latioraque, 13–30 mm longa, 8–15(–22) mm lata, dentibus 6–16; racemi flores 6–20 gerentes; lobi calycis majores latioresque.

Holotype: Gloucester Tops, New South Wales, *R.G. Coveny*, 1 Jan 1967 (NSW 98196). Isotypes BRI, K, MO.

Herbs with subterranean rhizomes and erect stems, without surface runners. *Rhizomes* extensively developed and with small scale-like leaves, finally bending upwards to produce erect flowering stems. *Flowering stems* (6–)10–40 cm long, often with leafy lateral branches below the inflorescence; longest internodes (10–)15–60 mm long; stem hairs fine but rigid, mostly antrorsely curved, to 0.7–1 mm long, cells not collapsed when dry, hairs usually confined to lateral bands towards base of stems but scattered (often densely) over whole stem in upper parts. *Petioles* 1–2(–5) mm long. *Leaf laminae* broadly ovate, 13–30 mm long, 8–15(–22) mm broad; the base truncate; apex acute, margins serrate with 3–8 somewhat uneven, apiculate teeth on each side, the lower ones larger than the upper and spreading; texture relatively thick; greenish to blackish when dry; ± palmately nerved with 3–5 nerves from near the base and 2–4 major nerves higher up on the midrib; upper surface glabrous except for very small papillose hairs towards the margin; lower surface with scattered antrorsely-curved hairs on and between the nerves. *Racemes* single or paired on 1–3 nodes of the upper 1/3–1/2 of the stem, (30–)40–70(–130) mm long with 6–20 flowers; peduncle 15–35 mm long. *Bracts* broadly ovate, often rather large, to 8 mm long. *Pedicels* 8–20 mm long, ascending to erect, rather stiff. *Calyx lobes* elliptic to broad obovate, acute, almost doubled in size

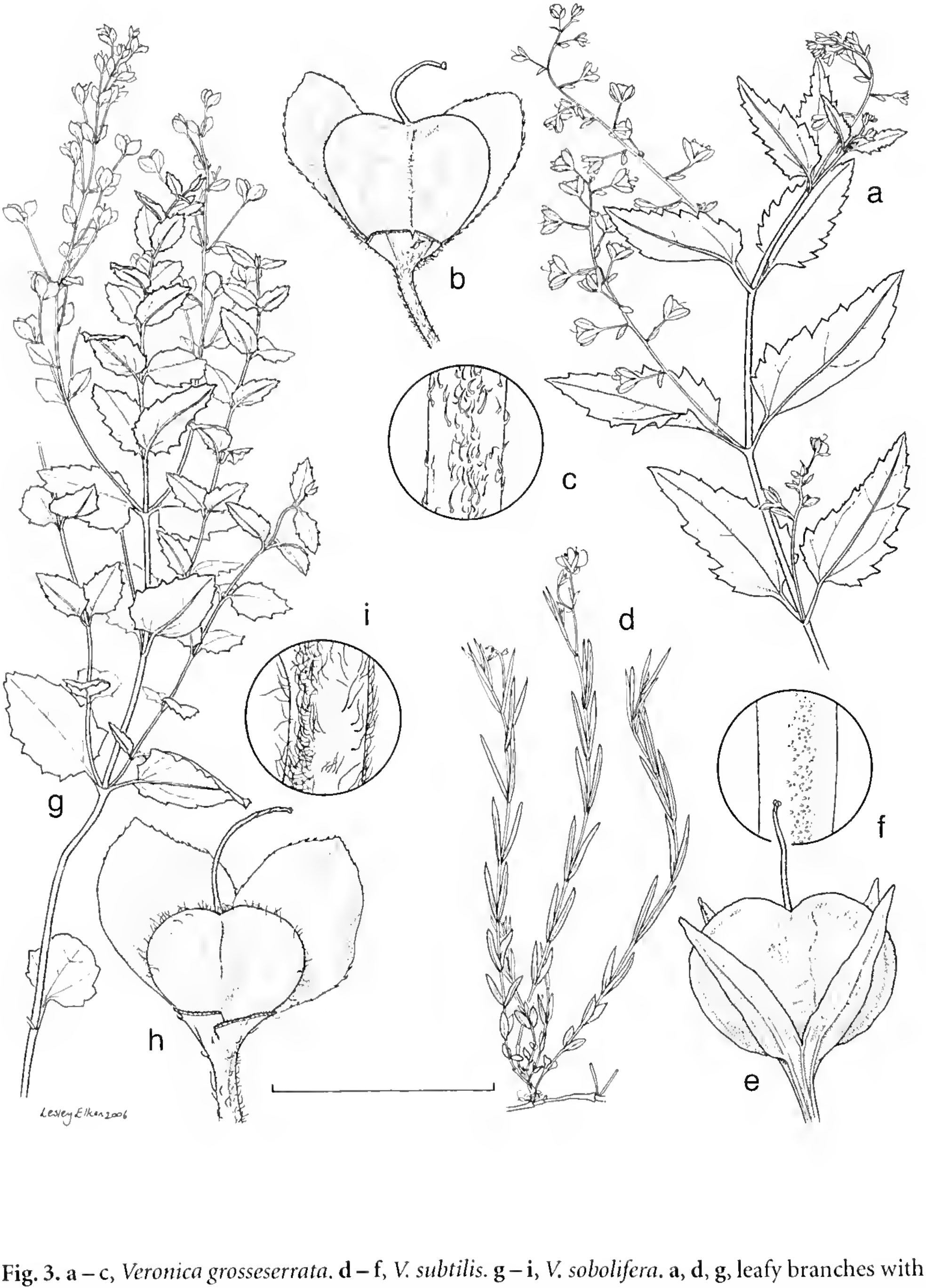

Fig. 3. a – c, *Veronica grosseserrata*. **d – f**, *V. subtilis*. **g – i**, *V. sobolifera*. **a**, **d**, **g**, leafy branches with flowering or fruiting racemes; **b**, **e**, **h**, capsule with calyx (calyx partly removed in b and h); c, **f**, **i**, stem indumentum (a – d, f, g, i, from holotypes; e, from *Coveny 16355*; h, from NSW 283785). Scale bar: a, d, g = 5 cm; b, e, h = 6.5 mm; c, i = 5 mm; f = 2.5 mm.

from flower to fruit and finally 6–7 mm long, 2.5–4 mm broad, with both long and short hairs on the margins near the base and short hairs extending to the apex; outer surface of the lobes almost glabrous. *Corolla* white tinged with mauve, length 5–6 mm; anterior lobe broad obovate; posterior and lateral lobes almost circular, not folded. *Capsule* broader than long, 2–3 cm long, 2.5–3.5 mm broad, slightly emarginate, with short fine hairs on the margin; style 4–5 mm long. *Seeds* broad ovoid, c. 1.5 mm long. (Fig. 3, g–i).

Veronica sobolifera has a chromosome number of $2n = 72$ (Briggs & Ehrendorfer 2006) and can be distinguished from *Veronica gracilis* R.Br., also octoploid, especially by its taller stems, larger and broader leaves with more serrations, racemes with more numerous flowers, and larger and broader calyx lobes. In *V. gracilis* stems are mostly 4–25 cm long, leaves 1–4.5 mm broad, entire or with 1–2 teeth on each side, racemes have 2–8 flowers, and calyx lobes are up to 2.5 mm broad. *Veronica sobolifera* was referred to as '*Veronica* sp. B' in Briggs et al. (1992, p. 580).

The epithet is from the Latin *soboles* [= *suboles*] = a sprout or shoot, growing from below, and *fero* = to bear; referring to the flowering stems arising from extensive rhizomes.

Distribution: Northern Tablelands of New South Wales, in moist eucalypt woodland and grassland, or in swampy sites (Fig. 5).

Conservation status: of restricted range but common in several conserved areas.

Selected specimens examined: New South Wales: North Coast: Gloucester Tops, *Briggs*, 2 Nov 1968 (NSW 118254); Gloucester Tops, *Coveny*, 1 Jan 1967 (NSW 98196), 30 Sept 1967 (NSW 101612); Barrington Tops National Park, *Coveny*, 30 Sept 1967 (NSW 283785); Tubrabucca and Tugalo Top, Barrington Tops, *Earp*, 1 Dec 1954 (NSW 39755); below Carey's Peak, Barrington Tops, *Fraser & Vickery*, 8 Jan 1934 (NSW 6085, SYD); Barrington Tops, *Harrison*, Jan 1925 (NSW 6084). Northern Tablelands: c. 1 mile [1.7 km] NW of Point Lookout, *Williams*, Dec 1961 (NE).

Veronica subtilis B.G.Briggs & Ehrend., *sp. nov.*

A *Veronica gracilis* combinatione characterum sequentium distinguitur: pili caulium brevissimi (c. 0.1 mm longi); folia intergra, plerumque linearia, 0.8–2 mm lata; flores parvi, corolla 3.5–5(–8) mm longa; ovarium glabrum.

Holotype: New South Wales: Rocky Plain Creek, 3 miles [c. 5 km] SE of Kiandra, c. 1300 m alt., *B.G. Briggs 2531*, 9 Feb 1969 (NSW). Isotypes AD, CHR, K, MEL, MO, W.

Herbs with erect flowering stems and long slender rhizomes, surface runners absent. *Rhizomes* with long internodes and small scale-like leaves. *Flowering stems* very slender or almost filiform (4–)10–25(–35) mm long; the longest internodes between well-developed leaves (8–)12–40(–60) mm long; stem hairs very short (ca. 0.1 mm) papillose, in lateral bands or rarely absent. *Leaves* entire, mostly linear (those near base of stem or on vegetative shoots sometimes ovate or reduced and scale-like), sessile, narrowed gradually toward apex and base, (7–)11–25(–30) mm long, (0.5–)0.8–2 (–2.5) mm broad, the apex acuminate and apiculate, the margins somewhat revolute and thickened, the lateral veins scarcely visible, green or brown when dry, glabrous except for very short antrorse hairs on the upper side at and near the margins. *Racemes* single or paired at 1–2 nodes of the uppermost part of the stem, clearly overtopping the main axis, (6–)15–55(–80) mm long with (1–)2–4(–6) flowers; peduncle

(3–)10–35(–40) mm. *Bracts* linear, to 6 mm long. *Fruiting pedicels* 10–20 mm long. *Calyx lobes* broad-linear, acute, in young fruit ca. 4–5 mm long, 0.6–1 mm broad; margins and inner surface with very short antrorse papillose hairs. *Corolla* mauve or pale blue, 3.5–5(–8) mm long; anterior lobe obovate; posterior and lateral lobes broad obovate to almost circular, not folded. *Capsule* glabrous, emarginate, slightly broader than long, ca. 2 mm long, 4.5 mm broad. (Fig. 3, d–f).

Veronica subtilis is tetraploid ($2n = 36$: Briggs & Ehrendorfer 2006) and can be distinguished from the octoploid *V. gracilis* by the very short hairs on the stem, the entire and generally narrower leaves, very slender peduncles and pedicels, the smaller flowers and glabrous ovaries. In *V. gracilis* the stem hairs are up to 0.5 mm long, leaves lanceolate or linear and 1.5–4 mm wide, leaves entire or often with 1–2 serrations on each side, ovaries with dense hairs on margins and apex. *Veronica subtilis* was referred to as '*Veronica* sp. A' in Briggs et al. (1992, p. 581), and as '*Veronica* sp. 2' in Briggs and Barker (1999, p. 516). The presence of a linear-leaved species allied to *V. gracilis* was mentioned by Willis (1973) and Barker (1986).

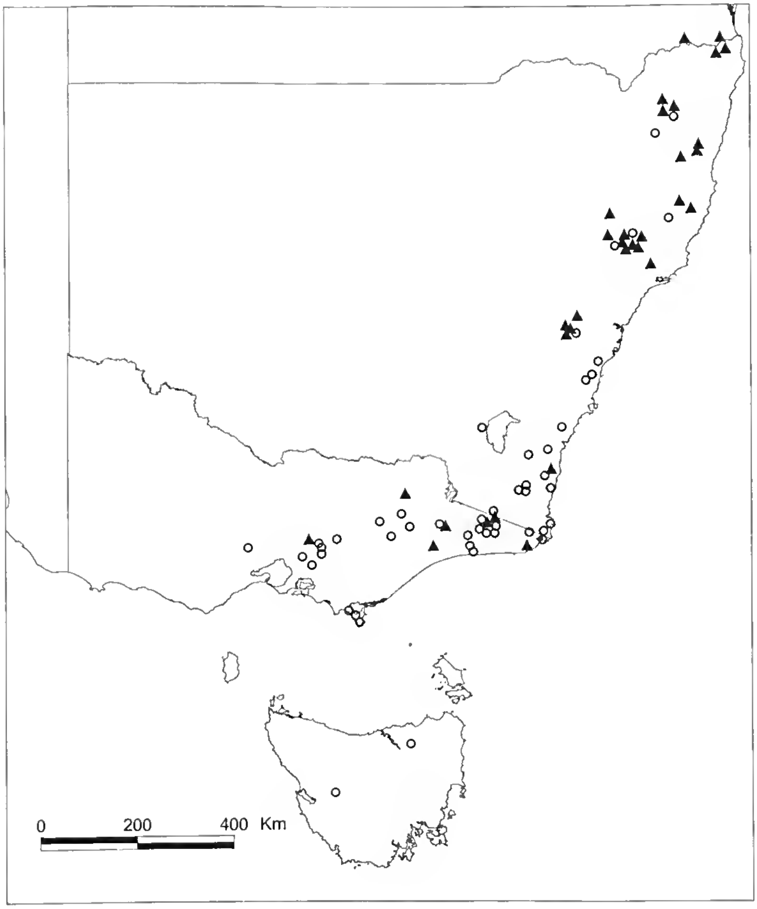

Fig. 4. Distribution of *V. grosseserrata* ▲ and *V. notabilis* ○ in south-eastern Australia.

The epithet is from the Latin *subtilis* = fine, slender or delicate, referring to the stems and leaves.

Distribution: Central and Southern Tablelands of New South Wales, widespread at both high and low altitudes in eastern and south western Victoria and collected from Honans Scrub in the south east of South Australia. In moist sites in swamps, *Sphagnum* bogs, grassland and grassy forests. Mostly in moister sites than *V. gracilis*, and on less acidic soils of higher nutrient status (Fig. 5).

Conservation status: widespread and common, occurring in several conserved areas.

Selected specimens examined: New South Wales: Central Tablelands: Brown Mtn, near Littleton, *Betche*, Feb 1893 (NSW 5962); Tomat Swamp, 8 miles [13 km] SSW of Yerranderie, *Briggs 1082 & Johnson*, 29 Nov 1966 (NSW); Bindook Swamp, Colong to Mt Werong, *Cambage 3201*, 5 Dec 1911 (SYD); edge of Fitzroy Falls Reservoir, *Coveny 16355*, 8 Jan 1993 (NSW). Southern Tablelands: Sawpit Creek, Mt Kosciusko, *Briggs*, 31 Jan 1954 (NSW 39758); Upper Cotter Homestead, *Burbidge* 6368, 24 Feb 1959 (CANB); Upper Cotter, *Cambage 3420*, 15 Jan 1912 (NSW). **Victoria**: Genoa, *Bauerlen*, Feb 1885 (MEL 18017); Surrey R., near Portland, *Beauglehole*, 26 Nov 1944 (MEL 18013); Gorae West, *Beauglehole 8401*, Oct 1946 (NSW); Wannon River, E of Mirranatwa Gap, Grampians, *Beauglehole 16353*, 9 Nov 1967 (NSW); between The Link Road turn-off and Matlock, *Johnson*, 22 Jan 1967 (NSW 84493); S sources of the Goulburn R. and the N sources of the Yarra R., *Mueller* (MEL 18011); Ranges of the Macallister R., *Mueller*, Jan 1863 (MEL 18012); Moroka River Heads on The Big Plain, 2 miles [c. 3 km] NW of Mt Wellington, *Muir* 3162, 5 Jan 1964 (MEL); Upper Yarra, *Walter* (BM, NSW 5944); Bullace Glen, Grampians, *Warcup*, 20 Jan 1961 (AD). **South Australia**: Honans Scrub, *Bates 4835*, 20 Jan 1978 (AD).

Veronica brownii Roem. & Schult., *Syst. Veg.* 1: 118 (1817), as '*brownei*'.

≡ *V. arguta* R.Br., *Prodr.* 435 (1810) non Schrad. (1803).

≡ *V. gracilis* R.Br. var. *arguta* (R.Br.) C.Moore & Betche, *Handb. Fl. N.S.W.* 341 (1893). Holotype: [New South Wales] Ad ripas fluvii Grose, *R. Brown*, Nov 1803 (BM!, photo NSW).

Veronica calycina R.Br., *Prodr.* 435 (1810).

Lectotype (**here designated**): [Tasmania] In summitati montis primaevi rotundati prope Mount Tabular, *R. Brown*, Mar 1804 (BM!). The type material of *V. calycina* at BM includes five of Brown's Australian collections, four from Tasmania and one from Victoria, mounted on two sheets:

A "In summitati montis primaevi rotundati prope Mount Tabular [now Mount Wellington], March 1804"
B "Near outer Cove in Port Dalrymple, Jan. 4, 1804"
C Port Dalrymple
D Prince of Wales, Derwent
E Port Philip [Victoria]

It is evident that Brown's description of this species was based on collection 'A' which is therefore here designated as lectotype. Further syntypes and duplicates from Brown's collections are the sheet at K! shown in photo 2639 (CANB), which includes further material of 'E' and probably 'D' and NSW 6233! (which is probably 'D'). Another of Brown's collections, "Summ. Mount., Derwent (K!, photo 2640 CANB p.p., lower specimens on sheet, and also MEL 17955!) was originally labelled "*Veronica calycina* var. *alpina*" and is probably not to be regarded as isotype material.

= *Veronica calycina* R.Br. var. *parviflora* Benth. in DC., *Prodr.* 10: 477 (1846). Holotype: Tasmania, Circular Head, *R. Gunn 1218 p.p.*, 12 Jan 1838 (K!, photo 2643, 2643a CANB, the upper specimens on the sheet). Isotypes NSW 6076!, HO 696A p.p.!

= *Veronica gunnii* Benth. in DC., *Prodr.* 10: 477 (1846). ≡ *Veronica calycina* var. *gunnii* (Benth.) Hook.f., *Fl. Tasman.* 1, 294 (1857). Lectotype (**here designated**): Tasmania, Cathedral Rocks, *Gunn 723*, 1836 (K! 'ex Herb. Benth.', photo 2641 CANB). Residual syntype VDL [Van Diemens Land], *Gunn* (NSW!, K!, CANB photo 2642).

Veronica distans R.Br., *Prodr.* 435 (1810).

Holotype: [Western Australia] Bald Head, King Georges Sound, *R. Brown* (Bennett No. 2702), 10 Dec 1801 (BM!, photo NSW).

= *Veronica stolonifera* Lehm., *Sem. Hort. Hamburg* (1824, p. 20). ≡ *V. calycina* R.Br. var. *stolonifera* (Lehm.) Ostenf., in *Dansk. Vidensk. Biol. Medd.* 3: 115 (1921). Type (holotype or syntype?): [Western Australia] In arenosis umbrosis prope urbiculam Freemantle, *Preiss 2329*, 15 Aug [18]39 (LD!).

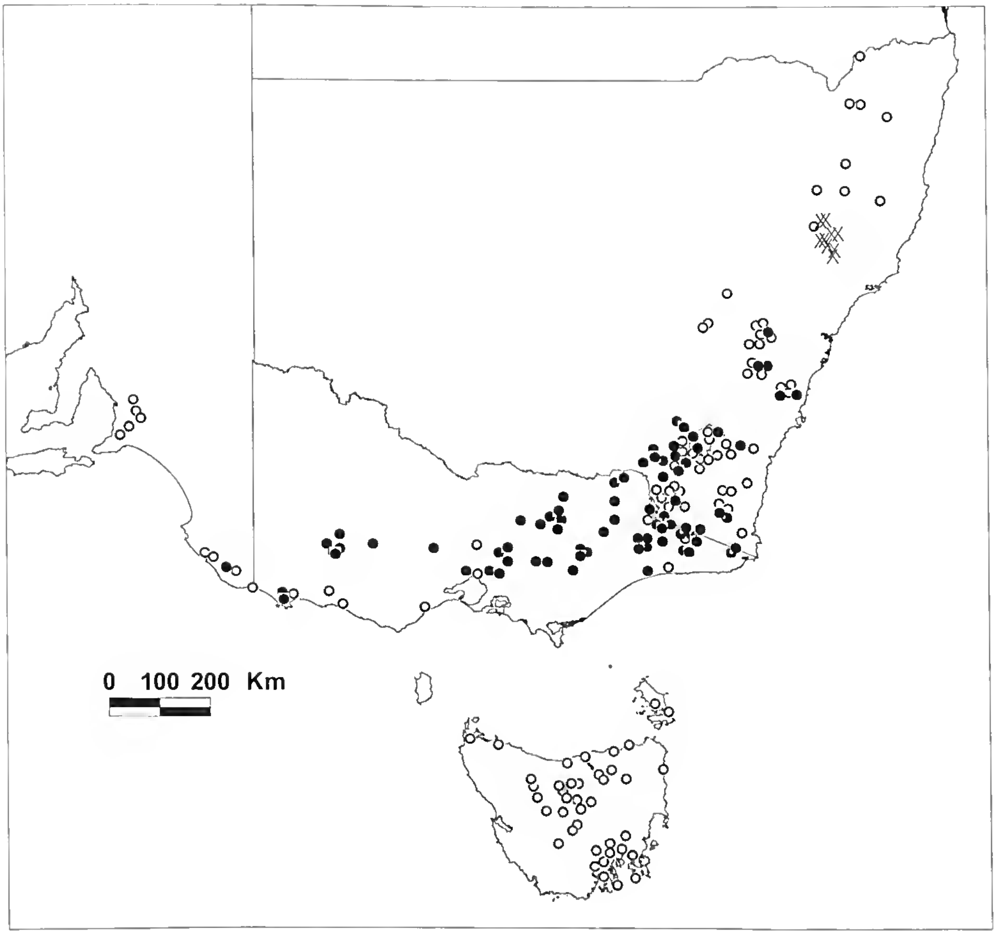

Fig. 5. Distribution of *V. sobolifera* ×, *V. subtilis* • and *V. gracilis* ○ in south-eastern Australia

= *Veronica cycnorum* Miq. ex Bartl. in Lehm., *Pl. Preiss.* 1, 342. (1845). Type (holotype or syntype?): [Western Australia] Australia occidentali, *Preiss 2414* (LD!).

= *Veronica drummondii* Benth. in DC., *Prodr.* 10: 478 (1846). Holotype: [Western Australia] Swan River, *Drummond*, 1839 (K!, CANB photo 2637).

Veronica gracilis R.Br., *Prodr.* 435 (1810).

Holotype: [Tasmania] Port Dalrymple, *R. Brown* (Bennett No. 2704), 1804 (BM!, photo NSW).

Veronica hillebrandii F. Muell., *Trans. Philos. Soc. Victoria 1*: 49 (1855).

Holotype: [South Australia] Limestone cliffs at Lake Alexandrina, *Mueller*, Oct 1848 (MEL). The protologue cites 'Barren ridges along the Coorong and on limestone rocks around Lake Alexandrina' but appears to refer to a single gathering.

Veronica notabilis F.Muell. ex Benth., *Fl. Austral. 4*: 511 (1869).

Lectotype (**here designated**): [Victoria] Secus rivos umbrosos montium Dandenong-range", *F. Mueller*, Jan 1853 (MEL 18102!). Probable isotypes (collection details are not given in full on the specimens): K! (photo 2646 CANB); MEL 18099!, 18118!, 18101!, 18103!; Dandenong Ranges, *Mueller* (LD!). The lectotype bears Mueller's handwritten label and is annotated as having been examined by Bentham. Residual syntypes: Berwick, *G.W. Robinson* (MEL 18117!, presumably from c. 11 km ESE of Dandenong, Victoria, rather than from New South Wales as cited by Bentham); Sealer's Cove [Wilson's Promontory, Vic.], *F. Mueller*, May 1853 (MEL!); St. Patricks R., Tas., *R. Gunn 174*, 1 Apr 1845 (NSW 5980, 5981!); Clarence River, [*Beckler*] (MEL 17933!); the last mentioned is a specimen of *V. grosseserrata*.

The collection 'Five Islands District, N.S.W. *Cunningham* 1819 (BM)' may be that cited by Bentham as from 'Illawarra' (which refers to the same region); it may therefore be a further syntype. It resembles *V. notabilis* but its features show some approach to those of *V. grosseserrata* and it may be hybrid.

Bentham cites 'Grose River, *R. Brown*' under both *V. notabilis* and *V. arguta* R.Br. Only one specimen has been located with these particulars, i.e. the holotype of *V. brownii* Roem. & Schult. (1817), a *nom. nov.* for *V. arguta* R.Br. non. Schrad., and so it must be concluded that Bentham cited the same specimen under both *V. notabilis* and *V. arguta*. In the protologue of *V. notabilis* Bentham states 'This species, which had been determined by A. Cunningham to be the *V. arguta* of Brown, and was included under that name by myself in the 'Prodromus' [DC., *Prodr.*] and by Hooker in the 'Tasmanian Flora', proves to be very different from Brown's plant, and apparently as distinct a species as any of the *Chamædrys* group in Australia except *V. nivea*.' Also the description in the protologue of *V. notabilis* does not match Brown's specimen, especially in respect of leaf size and indumentum. Clearly Bentham has excluded the Grose River specimen (the type of *V. brownii*) from his concept of *V. notabilis* and so it can be assumed that its citation was simply an error and the name *V. notabilis* is therefore legitimate.

Veronica novae-hollandiae Poir., *Encycl.* 8: 526 (1808).

Type citation: 'recueillie, dans la Novelle Hollande, per M. Labillardière (v. s. in herb. Desfont.)'.

Holotype: [Tasmania] labelled 'Veronica Nova hollandiae Poir encycl.' and 'Herb Webbianum ex Herb. Desfontaines' (FI!, photo NSW). Probable isotype (K!, photo 2638, 2638a CANB).

= *V. calycina* R.Br. var.? *longifolia* Benth., *Fl. Austral.* 4: 510 (1869). Holotype: Tasmania, Hampshire Hills, *Gunn 174/1837*, Feb 1887 (K!).

Veronica parnkalliana J.M.Black, *Fl. S. Austral.* 3: 512 (December 1926); also in *Trans. & Proc. Roy. Soc. South Austral.* 50: 286 (23 December 1926).

Holotype: Near Port Lincoln, *H.H.D. Griffith*, 10 Oct 1909 (AD 96645025!, photo NSW; iso K).

Veronica plebeia R.Br., *Prodr.* 435. 1810.

Holotype: [New South Wales] in humidis prope Sydney, *R. Brown*, May 1802 (BM!). The collection from Williams and Hunter's Rivers, *R. Brown*, Nov 1804 (BM!, K!, CANB photo 2644) was used for a description of an unpublished variety and is not regarded as a syntype.

= *V. deltoidea* Spreng., *Syst. Veg.* 4 (2) 17. 1827. Type (holotype or syntype?): [New South Wales] *Sieber, Pl. Nov. Holl.* 483 (K!, CANB photo 2645 p.p.).

= *V. vitifolia* Sm. ex Walp., *Repert. Bot. Syst.* 3: 367. 1844. Type (syntype?): Port Jackson, New South Wales, collector not stated, (LIV! ex herb. [J.E.] Smith).

= *V. elongata* Benth. in DC., *Prodr.* 10: 478. 1846. Typification: Bentham cites "in New Zeelandia, (*A. Cunningham*! *Sinclair*! *Edgerley*!)". The sheet in K (!) bears a label "No. 382, Bay of Islands, New Zealand 1838" and the name "Allan Cunningham" is written on the sheet near this label; a separate label on the sheet reads "B. of Islds. Dr Sinclair". It is not clear how much of the material should be attributed to each of these collectors.

Veronica sect. *Hebe*: *Chionohebe* clade

From this small clade, centred on New Zealand, only the typification of *V. densifolia* is considered here.

Veronica densifolia (F.Muell.) F.Muell., *Fragm.* 2: 137 (1861),

≡ *Paederota densifolia* F.Muell., *Trans. Philos. Soc. Victoria* 1: 107 (1855).

≡ *Chionohebe densifolia* (F.Muell.) B.G.Briggs & Ehrend., *Contr. Herb. Austral.* 25: 2 (1976).

≡ *Leonohebe densifolia* (F.Muell.) Heads, *Bot. Soc. Otago Newslett.* 5: 4 (1987).

≡ *Hebejeebie densifolia* (F.Muell.) Heads, *Bot. Soc. Otago Newslett.* 36: 11 (2003).

Type citation: On the highest rocky summits of the Munyang Mountains (6–6500 feet) [*F. Mueller*].

Lectotype (**here designated**): Munyang Mountains, Mount Coskiusko [=Kosciusko], 6000–6500 ft., Mueller, Jan 1855 (MEL 21502!). Residual syntypes: Munyang Mountains, 6000 ft, [Mueller] (MEL 21503!); Munyang Mtns 6000′, F v Mueller (K!, two sheets: one from Hooker herbarium, the other from Linnean Society); Mount Coskiusko 6000', F v Mueller (K!). Possible syntype: Mount Coskiusko, [Mueller?] (MEL 21504!).

Acknowledgments

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References

Albach DC & Chase MW (2001) Paraphyly of *Veronica* (Veroniceae; Scrophulariaceae): evidence from the internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA. *Journal of Plant Research* 114: 9–18.

Albach DC, Martinez-Ortega MM, Delgado L, Weiss-Schneeweiss H, Özgökce F & Fischer MA (submitted) Chromosome numbers in Veroniceae: Review and several new counts. *Annals of the Missouri Botanical Garden.*

Albach DC, Martínez-Ortega MM, Fischer MA & Chase MW (2004) A new classification of the tribe Veroniceae – problems and a possible solution. *Taxon* 53: 429–52.

Albach DC, Meudt HM & Oxelman B (2005) Piecing together the "new" Plantaginaceae. *American Journal of Botany* 92: 297–315.

Barker WR (1986) *Scrophulariaceae*. Pp. 1275–1313 in Jessop JP & Toelken HR (eds) *Flora of South Australia*, vol. 3, 4th edition. (South Australian Government Printer: Adelaide)

Bayly MJ & Kellow AV (2006) *An illustrated guide to New Zealand Hebes*. (Te Papa Press: Wellington)

Borgmann E (1964) Anteil der Polyploiden in der Flora des Bismarckgerbirges von Ostneuguinea. *Zeitschrift für Botanik* 52: 118–172.

Briggs BG & Barker WR (1999) *Veronica*. Pp. 509–516 in Walsh NG & Entwisle TJ (eds) *Flora of Victoria*, vol. 4. (Inkata Press, Melbourne)

Briggs BG & Ehrendorfer F (1992) A revision of the Australian species of *Parahebe* and *Derwentia* (Scrophulariaceae). *Telopea* 5: 241–87.

Briggs BG & Ehrendorfer F (2006) Chromosome numbers of Australian and New Guinean species of *Veronica* (Plantaginaceae). *Telopea* 11(3): 294–298.

Briggs BG, Wiecek B & Whalen AJ (1992) *Veronica*. Pp. 578–582 in Harden GJ (ed.) *Flora of New South Wales*, vol. 3. (New South Wales University Press, Kensington)

Brummitt RK (2006). Am I a bony fish? *Taxon* 55: 268–269.

Coates F, Kirkpatrick JB & Minchin D (1999) Towards an explanation of the causes of the rarity of two Tasmanian *Spyridium* species. *Australian Journal of Ecology* 24: 11–17.

Garnock-Jones PJ, Albach D & Briggs BG (submitted) Botanical names in *Veronica* sect. *Derwentia*, sect. *Detzneria* and sect. *Hebe* (Plantaginaceae). *Taxon.*

Heads MJ (1992) Taxonomic notes on the *Hebe* complex (Scrophulariaceae) in the New Zealand mountains. *Candollea* 47: 583–595.

Kirkpatrick JB & Brown MJ (1984a) The palaeogeographic significance of local endemism in Tasmanian higher plants. *Search* 15: 112–113.

Kirkpatrick JB & Brown MJ (1984b) A numerical analysis of Tasmanian higher plant endemism. *Botanical Journal of the Linnean Society* 88: 165–183.

Olmstead RG, dePamphilis CW, Wolfe AD, Young ND, Elisons WJ & Reeves PA (2001) Disintegration of the Scrophulariaceae. *American Journal of Botany* 88: 348–361.

Olmstead RG & Reeves PA (1995) Evidence for the polyphyly of the Scrophulariaceae based on chloroplast *rbc*L and *ndh*F sequences. *Annals of the Missouri Botanical Garden* 82: 176–193.

Römpp H (1928) Die Verwandtschaftsverhältnisse in der Gattung *Veronica*. *Repertorium species novarum regni vegetabilis*. Beihefte 50: 1–172.

Sykes WR (1988) Scrophulariaceae. Pp. 1175–1214 in Webb CJ, Sykes WR, Garnock-Jones PJ *Flora of New Zealand*, vol. 4. (Botany Division, D.S.I.R.: Christchurch)

Wagstaff SJ & Garnock-Jones PJ (1998) Evolution and biogeography of the *Hebe* complex (Scrophulariaceae) inferred from ITS sequences. *New Zealand Journal of Botany* 36: 425–37.

Wagstaff SJ & Garnock-Jones PJ (2000) Patterns of diversification in *Chionohebe* and *Parahebe* (Scrophulariaceae) inferred from ITS sequences. *New Zealand Journal of Botany* 38: 389–407.

Wagstaff SJ, Bayly MJ, Garnock-Jones PJ & Albach DC (2002) Classification, origin, and diversification of the New Zealand hebes (Scrophulariaceae). *Annals of the Missouri Botanical Garden* 89: 38–63.

Willis JH (1973) *A handbook to plants in Victoria*, vol.2. (Melbourne University Press: Carlton)

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Chromosome numbers of Australian and New Guinean species of *Veronica* (Plantaginaceae)

Barbara G. Briggs[1] and Friedrich Ehrendorfer[2]

[1]*Botanic Gardens Trust Sydney, Mrs Macquaries Road, Sydney NSW 2000, Australia.*
Email: barbara.briggs@rbgsyd.nsw.gov.au
[2]*Institute of Botany, University of Vienna, Rennweg 14, A–1030, Vienna, Austria.*
Email: friedrich.ehrendorfer@univie.ac.at

Abstract

New records of chromosome numbers are presented for eleven Australian species of *Veronica* sens. lat. Reference is also given to records previously published for ten species that have been referred to *Derwentia*, *Parahebe* or *Chionohebe*, but that are now included in a widely circumscribed *Veronica*. The species formerly included in *Derwentia*, *Parahebe* or *Chionohebe* exhibit secondary base numbers of $x = 21$, 20 or 19, whereas those formerly retained in *Veronica* have $x = 18$ (or 17). For the species formerly referred to *Detzneria*, from New Guinea, we present only a very approximate count of $2n = 38–42$ which, however, differs from the previous report of $2n = 48$.

Introduction

Differences in chromosome number have long been regarded as an important feature in characterising genera within Veroniceae (Frankel 1941, Frankel & Hair 1937, Garnock-Jones 1993). Chromosome numbers for most of the Australian and one New Guinean species are presented here (Table 1), making them available for a compilation of karyological data for Veroniceae (Albach et al. submitted). Information on the New Zealand taxa is given by Dawson (2000) while Bayly and Kellow (2006) provide a revised and updated list of chromosome numbers for species formerly included in *Hebe* or *Leonohebe*. New taxa and taxonomic notes on these Australian taxa are presented by Briggs and Ehrendorfer (2006) in this issue of *Telopea*. Chromosome numbers for most of the Australian species formerly included in *Derwentia* or *Parahebe* have been reported already by Briggs and Ehrendorfer (1992); references to these reports are included here, giving the names and authorities (as in Garnock-Jones et al. submitted), now that they will be included in an enlarged *Veronica*. For four species (‘*V. arcuata*’, ‘*V. blakelyi*’, ‘*V. lithophila*’ and ‘*V. tubata*’), as well as the subspecies of *V. derwentiana* and most of the Southern Hemisphere sections within *Veronica*, valid publication of the new combinations will await Garnock-Jones et al. (submitted).

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Methods

The new counts are mostly somatic numbers, determined on root-tip material, using 130 minutes of pre-fixation treatment with saturated aqueous *p*-dichlorobenzene and staining with alcoholic carmine (Snow 1963). Plants transplanted from the wild were grown at the Royal Botanic Gardens Sydney. In most cases, the number reported was counted from several cells. For '*V. tubata*', however, only a small amount of wild-collected stem and leaf meristematic tissue was available and only approximate counts were obtained. In that case, the chromosomal spreads (of several cells) were far from ideal but the result is included since it differed from what had been previously reported.

Results

The new findings and reference to previous reports are presented in Table 1. Voucher specimens and their collectors are cited.

Discussion

The findings are mostly consistent with previous reports (Briggs & Ehrendorfer 1992), in that the species formerly included in the genera *Derwentia* ('*V. arcuata*', *V. arenaria*, '*V. blakelyi*', *V. decorosa*, *V. derwentiana*, *V. nivea*, *V. perfoliata*, '*V. velutina*'), *Parahebe* ('*V. lithophila*'), *Chionohebe* (*V. densifolia*) and one previously of uncertain generic position (*V. formosa*) have numbers of $x = 19, 20$ or 21. These species are here referred to the *Derwentia* clade and the *V. formosa* clade within '*Veronica* sect. *Derwentia*' and the *Chionohebe* clade within sect. *Hebe* (Briggs & Ehrendorfer 2006, Garnock-Jones et al. submitted). By contrast, all records for the Australian species formerly retained in *Veronica* show secondary base numbers of $x = 17$ or 18 and are placed in the *V. calycina* clade of 'sect. *Derwentia*'. For *Veronica tubata,* the sole member of '*V.* sect. *Detzneria*', only a very approximate count of $2n = 38–42$ is reported, but it is a finding different from the previously reported count of $2n = 48$ (Borgmann 1964).

Wagstaff et al. (2002) showed that, from analysis of ITS DNA data, '*Veronica lithophila*' (then known as *Parahebe lithophila*) grouped more closely with species of *Derwentia* than with *V. calycina* or with the New Zealand species then placed in *Parahebe* and that are now referred to *Veronica* sect. *Hebe*. The chromosome number $2n = 42$ does not assist in resolving its subgeneric position, but supports its placement in the *Derwentia* clade, rather than the *V. calycina* clade, within *Veronica* 'sect. *Derwentia*'. We take this opportunity to correct a previous error concerning *V. lithophila*. Garnock-Jones has drawn attention to the folded lateral corolla lobes of *Parahebe* as a distinguishing feature of the genus. When describing this species (Briggs & Ehrendorfer 1992) we included a photo supposedly illustrating this feature in newly-opened flowers of *P. lithophila* and we considered this feature to be among those identifying it as a species of *Parahebe*. We were later advised that the photo was not of this species, as we had understood, but of cultivated plants of a New Zealand species. *Veronica lithophila* has flat lateral corolla lobes, as in *Derwentia* species.

In agreement with Albach et al. (submitted), we hypothesise that the chromosome numbers of the Southern Hemisphere *Veronica* species of sect. '*Derwentia*' and sect. *Hebe* have been derived from $x = 8$, characteristic for the most closely related Northern Hemisphere *V.* subgenus *Chamaedrys*. If the previous record of $2n = 48$ for the monospecific *V.* 'sect. *Detzneria*' (formerly *Detzneria tubata*) in New Guinea is correct, the secondary hexaploid base number $x = 24$, is still maintained. Our finding, of $2n = 38–42$ for this species, however, although only approximate, suggests that dysploid change ($x = 8 \rightarrow 7$) may have preceded polyploidy or that only dysploid levels may now exist. From the hexaploid level, stepwise descending dysploidy could have resulted in $x = 21 \rightarrow 20 \rightarrow 19 \rightarrow 18 \rightarrow 17$, the secondary base numbers found in the remaining Southern Hemisphere sections of *Veronica*. The evolutionary history may, however, be somewhat more complex since a number of reports deviate from multiples of these base numbers. Also, Bayly and Kellow (2006) observe that polyploidy is found 'within at least some species [of the New Zealand species of *V.* sect. *Hebe* and] it seems likely that independent origins of polyploidy have been relatively common'.

The patterns of different chromosome numbers tend to be obscured by inclusion of all these clades in an enlarged *Veronica*, but the previous classification was untenable if only monophyletic groups are to be recognised, as discussed by Garnock-Jones et al. (submitted).

References

Albach, DC, Martínez-Ortega MM, Delgado L, Weiss-Schneeweiss HF, Özgökce F & Fischer MA (2006 submitted) Chromosome numbers in Veroniceae: review and several new counts. *Annals of the Missouri Botanical Garden*

Bayly MJ, Kellow AV (2006) *An illustrated guide to New Zealand Hebes*. (Te Papa Press: Wellington)

Borgmann E (1964) Anteil der Polyploiden in der Flora des Bismarckgerbirges von Ostneuguinea. *Zeitschrift für Botanik* 52: 118–172.

Briggs BG & Ehrendorfer F (1992) A revision of the Australian species of *Parahebe* and *Derwentia* (Scrophulariaceae). *Telopea* 5: 241–287.

Briggs BG & Ehrendorfer F (2006) New Australian species and typifications in *Veronica* s. lat. (Plantaginaceae). *Telopea* 11(3): 276–292.

Briggs BG & Makinson RO (1992) *Parahebe*. P. 574 in Harden GJ (ed.) *Flora of New South Wales*, vol. 3. (New South Wales University Press: Kensington)

Dawson MI (2000) Index of chromosome numbers of indigenous New Zealand spermatophytes. *New Zealand Journal of Botany* 38: 47–150.

Frankel OH (1941) Cytology and taxonomy of *Hebe*, *Veronica* and *Pygmaea*. *Nature* 146: 117.

Frankel OH & Hair JB (1937) Studies on the cytology, genetics, and taxonomy of New Zealand *Hebe* and *Veronica* (Part 1). *New Zealand Journal of Science and Technology* 18: 669–687.

Garnock-Jones PJ (1993) Phylogeny of the *Hebe* complex (Scrophulariaceae; Veroniceae). *Australian Systematic Botany* 6: 457–479.

Garnock-Jones PJ, Albach DC and Briggs BG (2006 submitted). Botanical names in *Veronica* sect. *Derwentia*, sect. *Detzneria* and sect. *Hebe* (Plantaginaceae). *Taxon*.

Snow R (1963) Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. *Stain Technology* 38: 9–13.

Table 1. Chromosome numbers reported for Australian and a New Guinean species of *Veronica*, new findings and reference to previous records. Combinations at sectional, species and subspecies rank indicated as 'ined.' will be published in Garnock-Jones et al. (submitted).

Taxon	*n*	2*n*	Voucher (Herb. NSW)	Collector	Locality or reference
			'*Veronica* sect. *Derwentia* (Raf.) B.G.Briggs' ined.		
			***V. calycina* clade**		
Veronica brownii Roem. & Schult.		72	118260	*B. Briggs*	Blackheath Glen, NSW
Veronica calycina R.Br.		36	84539	*L. Johnson & B. Briggs 1058*	near Mt Werong, NSW
Veronica distans R.Br.		72	95339	*F. Ehrendorfer 17601*	Hamelin Bay, WA
Veronica gracilis R.Br.		c. 72	97476	*R. Coveny 903*	Wingecarribee Swamp, NSW
Veronica grosseserrata B.G.Briggs & Ehrend.		72 72	95319 95276	*R. Coveny* *A. Rodd 380*	Gloucester Tops, NSW Mountain Creek, Vic.
Veronica hillebrandii F.Muell.		36	101772	*A. Rodd*	cultivated ex South Australia
Veronica notabilis F.Muell. ex Benth.		36	255756	*B. Briggs 3989*	Brown Mountain, NSW
Veronica plebeia R.Br.		34 34 34	240439 118263 95314	*F. Ehrendorfer 18301* *B. Briggs* *R. Coveny*	Porongorup Mts, WA Megalong Valley, NSW Copeland, NSW
Veronica sobolifera B.G.Briggs & Ehrend.		72	98196	*R. Coveny*	Gloucester Tops, NSW
Veronica subtilis B.G.Briggs & Ehrend.		36	95757	*B. Briggs 1082*	Tomat Swamp, NSW
			***Derwentia* clade**		
'*Veronica arcuata* (B.G.Briggs & Ehrend.) B.G.Briggs' ined.		42	96611	*J. Williams*	Bullock Creek, E of Armidale, NSW
Veronica arenaria A. Cunn. ex Benth.	19	38	95685	*F. Ehrendorfer et al.*	Briggs & Ehrendorfer (1992), as *Derwentia arenaria*
'*Veronica blakelyi* (B.G.Briggs & Ehrend.) B.G.Briggs' ined.		42	101598	*B. Briggs 1058*	Clarence, NSW
Veronica decorosa F.Muell.	19	38	97485	*Hj. Eichler*	Briggs & Ehrendorfer (1992), as *D. decorosa*

Taxon	***n***	**2*n***	**Voucher (Herb. NSW)**	**Collector**	**Locality or reference**
Veronica derwentiana, subsp. not recorded, probably subsp. *derwentiana*	20			*O. Frankel*	Briggs & Ehrendorfer (1992), as *D. derwentiana*
'*Veronica derwentiana* subsp. *homalodonta* (B.G.Briggs & Ehrend.) B.G.Briggs' ined.		40	118325	*McArthur*	Briggs & Ehrendorfer (1992), as *D. derwentiana* subsp. *homalodonta*
'*Veronica derwentiana* subsp. *subglauca* (B.G.Briggs & Ehrend.) B.G.Briggs' ined.		40	101605	*B. Briggs 1011 & L. Johnson*	Briggs & Ehrendorfer (1992), as *D. derwentiana* subsp. *subglauca*
'*Veronica lithophila* (B.G.Briggs & Ehrendorfer) B.G.Briggs' ined.		42 42	84562 98192	*B. Briggs 1125* *A. Rodd 517*	Briggs & Ehrendorfer (1992), as *Parahebe lithophila*
Veronica nivea Lindl.		40		*F. Ehrendorfer*	Briggs & Ehrendorfer (1992), as *D. nivea*
Veronica perfoliata R.Br.	20	40	854491	*L. Johnson*	Briggs & Ehrendorfer (1992), as *D. perfoliata*
'*Veronica velutina* (B.G.Briggs & Ehrend.) B.G.Briggs' ined.		40†	258899	*B. Briggs 4298 & L. Johnson*	Mt Kaputar plateau, NSW
			***V. formosa* clade**		
Veronica formosa R.Br.	21	42 42		*O. Frankel* *M. Phillips*	Briggs & Ehrendorfer (1992)
			***Veronica* sect. *Hebe* (Juss.) G.Don**		
			***Chionohebe* clade**		
Veronica densifolia (F.Muell.) F.Muell.		42†	124420	*B. Briggs 2631*	Mt Northcote, NSW
			'*Veronica* sect. *Detzneria*' (Schltr. ex Diels) Albach ined.		
'*Veronica tubata* (Diels) Albach' ined.		38–42 48	249793	*B. Briggs 3747*	Mt Wilhelm, Papua New Guinea Borgmann (1964)

† Chromosome numbers that were reported by Briggs & Ehrendorfer (1992), but without citation of the voucher specimen.

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Dianella tenuissima (Hemerocallidaceae), a remarkable new species from the Blue Mountains, New South Wales, Australia

G.W. Carr

Ecology Australia Pty Ltd, 88B Station Street, Fairfield, Victoria 3078, Australia
Email: gcarr@ecologyaustralia.com.au

Abstract

A highly distinctive, taxonomically isolated new species, ***Dianella tenuissima*** G.W.Carr, confined to sandstone cliff habitats in the Blue Mountains of New South Wales, Australia, is described and illustrated. Its reproductive biology, ecology, taxonomic affinities and conservation status are discussed. The species is regarded as Data Deficient according to IUCN conservation-status criteria.

Introduction

As presently understood, the genus *Dianella* Lam. ex Juss. (Hemerocallidaceae) (Clifford et al. 1998) in Australia contains approximately 48 validly described, currently recognised taxa (Henderson 1987, 1991; Carr & Horsfall 1995; Carr 2004 unpubl.; Green 1994) of which only a few extend beyond these shores. Henderson (1987) and Carr and Horsfall (1995) indicated that other species remain to be described, the taxonomic status resolved, or the taxonomic rank of others re-evaluated, particularly the varieties of *D. caerulea* Sims, *D. revoluta* R.Br., *D. longifolia* R.Br. and *D. pavopennacea* R.J.F.Hend., described by Henderson (1987). Approximately 32 extra-Australian taxa are known (Carr 2004 unpubl.). Taxonomic studies by G. Carr and P. Horsfall (unpubl. data) in the field and the herbarium, and utilising our extensive living collections from all Australian states and territories, and some countries in Malesia, indicate that numerous taxa await description. In addition, almost all taxa have been very inadequately circumscribed, causing many problems in nomenclature (e.g. Henderson 1988) and leading to radical 'lumping', notably by Jessop (1979) and to a lesser extent by Henderson (1987). It is now evident that far more taxa exist than currently described in Australia and elsewhere, and that the genus is much more morphologically, anatomically, chemically and perhaps cytologically diverse than hitherto acknowledged.

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In 1996 my attention was drawn to a *Dianella* species collected from Newnes Plateau in the Blue Mountains, New South Wales, by Robert T. Miller. It was immediately apparent that it was an undescribed species. Subsequent studies of *Dianella* material held at NSW revealed one collection of the species and I found it to be locally common on cliffs at Wentworth Falls in 1997. In January 2004 fruiting material was observed and collected at Wentworth Falls and at Katoomba Falls. The cultivated plants flowered in September 2004, providing material to enable the new species to be described and illustrated in this paper.

Terminology in the following description follows Henderson (1987, 1991) or Clifford et al. (1998), and colour determination of organs *in vivo*, frequently diagnostic and of great weight in *Dianella* taxonomy (Carr & Horsfall 1995) are given according to the 1986 reprint of the Royal Horticultural Society Colour Chart (RHS London, and Flower Council of Holland, Leiden). The dimensions of the leaves are those of fertile shoots on mature plants, and measurements of vegetative and fertile material were made from fresh and wet specimens.

Dianella tenuissima G.W.Carr, ***sp. nov.***

Species valde distincta, taxonomia sejuncta, in Montibus Caeruleis (NSW) endemica. Planta parva dense caespitosa. Folia linearia angustissima, flavo-virentia, ad 86 cm longa, 5–7 mm lata. Culmi foliis 2–4; inflorescentia gracillima floribus 3–10, cymulis distantibus floribus1–3. Flores penduli minuti pedicellis capillaribus, cleistogami vel apertione tarda; tepala late elliptica ad suborbicularia cucullata, dilute hinnulea vel dilute malvina, 3.5–4 mm longa, 2.3–4.4. mm lata; antherae dilute ad saturate violaceae, ovoideo-cuneatae, 0.9–1.5 mm longae; ovarium parvum depresso-globulare, ovula in quoque loculo 5; stylus violaceus, ad 2 mm longus; filamenta violacea; strumae parvae luteolae; bacca ellipsoidea, ad 10 mm longa, 7 mm lata.

Type: New South Wales: Central Tablelands: Wentworth Falls Reserve, Blue Mountains, *G.W. Carr 0401-30a* and *C.P. Gibson*, 6 Jan 2004 (holo NSW; iso MEL).

Densely to loosely *caespitose perennial herb* to c. 50 cm high and c. 10 cm wide at base; shoots very slender, touching or up to c. 2 cm apart, shoots ± erect or slightly inclined. *Rhizomes* very short, slender, to c. 3 mm in diameter, cortex yellow, cataphylls encircling and embracing rhizome, to c. 20 mm long. *Roots* fibrous, very slender, to 1.5 mm in diameter (Greyed-Orange 163C). *Fertile shoots* with 2–3(–4) leaves, subtended by 1–several reduced, sheathing, acuminate (non-laminate) leaves (cataphylls) to 12.5 cm long x 4 mm wide at base, these dull crimson or reddish-purple (Greyed-Red 181B or paler); *lamina of leaves* very narrow-linear, lax, very thin, moderately to strongly arcuate, to 86 cm long x (2.5–) 3–4 (–5.7) mm wide, long-attenuate, acuminate, long-carinate at apex, hypostomatous; lamina ± plane or slightly channelled; *leaf sheaths* ± fully occluded at the summit, to 4.5 mm wide each side of midrib, smooth to minutely hispid with dense, colourless, patent, acute, straight to slightly curved trichomes to c. 1/20 mm long on abaxial surface; leaf sheaths and lamina obscurely striate with 8–12 unequal, parallel veins on each side of midrib, which are conspicuously paler than intervening lamina. *Margins of leaf sheaths* smooth, edges of lamina smooth almost throughout, or with very small, scattered, colourless, strongly antrorse, straight or curved marginal 'teeth' to 0.4 mm long and up to 10 mm apart, distally increasing in frequency, most abundant at apex; midrib costate, subactute, similarly armed in distal 1–4 cm with minute cuticular 'teeth' at the apex. Leaf sheath and elongate cataphylls strongly and uniformly marked abaxially deep to pale crimson (Greyed-Red 181B)

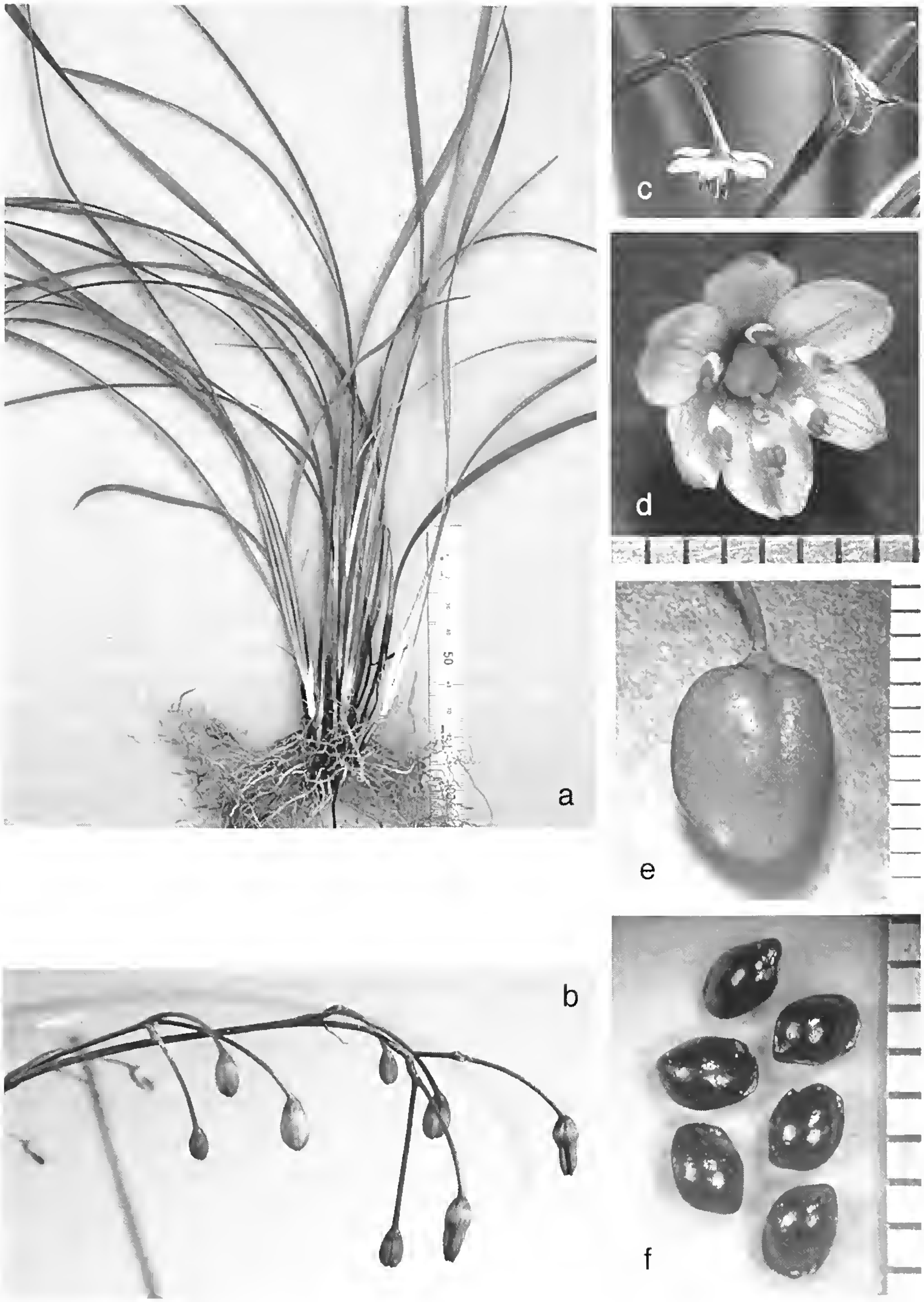

Fig. 1. *Dianella tenuissima* **a,** plant from the holotype location in vivo (*Carr 0401-30b*); **b,** inflorescence with cleistogamous flowers and developing post-anthesis ovaries (right) (*Carr 0401–30*); **c,** flower showing typical opening of perianth and a developing fruit (right) embraced by the hyaline remains of the dead perianth (*Carr 0401-30*); **d,** fully opened flower (*Carr 0401-30*); **e,** fruit (*Carr 0401-30a*); **f,** seeds (*Carr 1401-30a*). Scale bar: a = cm and mm; d, e and f = 1 mm divisions; b, central cleistogamous flower 4.5 mm long; c, open flower 8.5 mm in diameter.

fading upwards into yellow-green adaxial lamina (Yellow-Green 147A), lamina slightly paler abaxially, faintly glaucous abaxially and adaxially when very immature.

Inflorescence paniculate, extremely reduced and much shorter than the leaves, 10–36 cm long, interrupted and very slender; flowers 3–10 per inflorescence; *scape* ± erect to arcuate, 8–20 cm long, 0.7–1.0 mm in diameter, terete throughout, reddish green or reddish brown; cymules (bostryces) 1–3 flowered, racemosely and distantly arranged on the axis. *Flowers* extremely small, pendant, on terete capilliforme pedicels 8–18 mm long, the same colour as scape or paler, articulated below the torus, subtended by pale reddish-brown herbaceous-membranous, acute to acuminate, linear, involute bracts the same colour as scape, decreasing in size upwards, from 1–14 mm long. Flowers facultatively cleistogamous (and autogamous) but most opening to allow pollination, 8–9 mm diameter at full anthesis; floral fragrance not detectable. *Tepals* remaining tightly to loosely closed, or opening through c. 25–90° from bud (and then ± horizontal), subcampanulate to ± flat; torus prominent. *Outer tepals* shallowly cucullate, broadly elliptical or rotund, 3.5–4.0 mm long x 2.3–4.4 mm wide, apex subacute with tuft of minute white trichomes; 5-veined to apex; outer tepals abaxially very pale violet-buff or buff (nearest Greyed-Yellow 161D) with faint to pronounced yellow-green tinge at apex and a tinge of greyed-purple, veins darker reddish-violet; margins of tepals very pale violet (Violet 85D); lamina adaxially Violet 85D, veins pale violet or yellow-green, ± tinged pale yellow-green at apex. *Inner tepals* cucullate, broadly-elliptic to sub-orbicular 3.6–4.0 mm long x 2.5–3.8 mm wide, emarginate with minute tuft of white hairs in sinus; 5-veined with 3 complete inner veins and 2 shorter outer veins; inner tepals translucent, thinly membranous with crystalline texture, abaxially and adaxially very pale violet (Violet Group 85D, Violet-Blue 92A), much more intensely violet-coloured at base, with pale reddish-violet veins. *Stamens* 6, rarely fewer or with some anthers aborted, 3.0–3.5 mm long, ± erect; filaments subterete, 1.5–1.8 mm long, markedly sigmoid-geniculate below strumae, translucent, pale to deep violet-blue (Violet Blue 93A at base or uniformly Violet-Blue 94B), tinged brownish-yellow below strumae. *Strumae* obovoid, dorsiventrally compressed, microscopically papillose; very pale lemon-yellow (Yellow 10B; Greyed-Yellow 160B, C), 0.8–1.0 mm long x 0.6–1.0 mm wide and c. 0.5 mm thick near summit. *Anthers* ovoid-cuneate, 0.9–1.5 mm long x 0.6–0.8 mm wide at base, contracting in apical 25% into a blunt beak, dehiscing by terminal latrorse slits 0.3–0.5 mm long, pale to deep violet throughout (Violet Blue 92C, 94C). *Ovary* depressed-globular or globular-ellipsoid, shallowly 3–lobate, 1.2–1.4 mm long x 1.3–1.6 mm wide, yellow-green (Yellow-Green 144A); ovules 5 per loculus. *Style* 1.8–2.0 mm long, straight or flexuose, translucent (Violet-Blue 92B, 94C), stigma punctiforme, minutely papillose. *Berry* ovoid to narrowly ellipsoid, 5–10 mm long x 3–7 mm wide, obscurely 3–lobate, each loculus delineated by a vertical suture, fruits iridescent violet (Violet Group 94A). *Seeds* irregularly lenticular-ovoid, 2.3–2.5 mm long x 1.6–1.8 mm wide, black, smooth and very glossy. (Fig. 1a–f).

Notes: *Dianella tenuissima* is remarkable in its habitat, in morphological features and colour of floral organs, and in its reproductive biology. Its taxonomic relationships are obscure and it is taxonomically isolated with no known close relatives. The distinguishing features of this taxon include: the tussock forming habit, narrow leaves to 5.7 mm wide, the reduced few-flowered inflorescence with 1–3 flowers per cymule, very pale violet perianth and cucullate tepals, violet filaments, very pale yellow strumae and berries that are ovoid to narrowly-ellipsoid and have longitudinal sutures. Other features are uncommon in other species, e.g. the few-leaved fertile shoots (Henderson

1987, 1991; Carr & Horsfall 1995, unpubl. data), pale to deep mauve-violet anthers (Green 1994) and the small number of ovules per locule.

The breeding biology of *D. tenuissima* is very unusual. Flowers are facultatively cleistogamous (Fig. 1b), a condition not previously reported in *Dianella* which is uniformly melittophilous, that is buzz-pollinated by solitary bees (Bernhardt 1995, Duncan et al. 2004, Carr and Horsfall unpubl. data). Apomixis has also been reported once in *D. tasmanica* Hook.f. sens. lat. (Curtis 1952) but may be much more common (Carr unpubl. data).

Microscopic examination of cleistogamous *D. tenuissima* flowers from several plants showed dehisced anthers with gaping terminal latrorse slits approximately one third the length of the anther, and numerous pollen grains on the well-developed outer papillae of the stigma. These observations support cleistogamy, rather than apomixis, and it is likely that autogamy is routine, even in flowers that open 'normally' (Fig. 1c). In the early part of the 2–3 week flowering period in cultivated plants maintained by me (Melbourne) and by Colin Gibson and Robert Miller (Sydney and Bulli), all flowers were cleistogamous and all produced fruit (unless damaged). In the cultivated plants, including the type, maintained by me indoors, flowers opened partially or fully (perianth reflexed through 90°) (Fig. 1c) in the mid to late morning yet all flowers produced fruit (Fig. 1e) in the absence of insects, including thrips. It is apparent that flowers open to allow exogamous pollination but that the stigmas have already collected pollen via autogamy in bud. There is no reason to believe that autogamy precludes geitonogamy or xenogamy in individual flowers and there is no morphological evidence to suggest that flowers are not buzz pollinated as typical for *Dianella*, albeit by small bees.

All flowers examined had five ovules per loculus and the maximum number of seeds recorded per fruit, in the largest examined, was 12. Nothing is known about seed dispersal in *D. tenuissima*. The genus is routinely and predominantly ornithochorous (e.g. Rose 1973, Carr unpubl. data) and saurochory has been documented in Victoria in one species (Carr unpubl. data). The fruits of *D. tenuissima* generally conform in size and colour with most *Dianella* taxa, and the dispersal agent is perhaps most likely to be the Grey or Pied Currawong (*Strepera versicolor* and *S. graculina*). Currawongs are implicated in the dispersal of numerous *Dianella* species (Carr unpubl. data).

Dianella tenuissima occupies an unusual habitat and apparently has unusual habitat fidelity (see Ecology).

Ecology: *Dianella tenuissima* is known only from Triassic, lithic and quartz sandstone and conglomerate geology of the Narrabeen Group, forming the Blue Mountains Plateau (Bembrick 1980). It occurs at altitudes between c. 800–1200 m ASL where average annual rainfall is 1200–1400 mm (Commonwealth of Australia 1988). It occurs on escarpment cliffs and ledges and pockets and fissures in sandstone rocks, often with minimal soil development, and also in deeper soils of the plateau forest and ravines at the edges of escarpments. Soils are very well-drained, low-nutrient, gradational, fine-textured sandy or stony loams, which are often humic, or (in seepage zones) with a high peat content. Plants grow in heavily shaded to very exposed situations of southerly or easterly aspect and soils are ± permanently moist; the plants often occur in seepage zones. There has been some drought death in recent years and the very thin roots, to 1.5 mm diameter – the thinnest recorded in Australian *Dianella* (Carr unpubl. data) probably indicate permanently moist environments and relative drought intolerance in the species.

Dianella tenuissima occurs in at least two of the vegetation types described and mapped by Keith and Benson (1988) and Benson et al. (1996) for the Blue Mountains: 9i Blue Mountains Sandstone Plateau Forest, and 21c Montane Heath (open heath and cliffs). Associated plant species in Sandstone Plateau Forest include *Banksia cunninghamii* subsp. *cunninghamii*[1], *Blechnum wattsii, Callicoma serratifolia, Ceratopetalum apetalum, Cissus hypoglauca, Eucalyptus fastigata, E. mannifera* subsp. *gullickii, E. oreades, E. piperita* subsp. *piperita, E. sieberi, Gahnia sieberiana, Hakea dactyloides, H. salicifolia, Lycopodium deuterodensum, Olearia myrsinoides, Persoonia mollis, Pittosporum undulatum, Pteridium esculentum* and *Stylidium productum.*

Associated species in montane heath of cliffs and rock-faces include *Acacia obtusifolia, Alania endlicheri, Allocasuarina littoralis, A. nana, Amperea xiphoclada, Banksia cunninghamii* subsp. *cunninghamii, Callicoma serratifolia, Dracophyllum secundum, Epacris longiflora, E. reclinata, Eucalyptus cunninghamii, E. stricta, Gahnia sieberiana, Gleichenia dicarpa, G. rupestris, Goodenia bellidifolia, G. decurrens, G. rostrivalvis, Hakea dactyloides, Leptospermum polyanthum, L. trinervium, Marsdenia suaveolens, Mitrasacme* sp., *Patersonia sericea, Pimelea linifolia* subsp. *linoides, Platysace lanceolata, Smilax glyciphylla, Sprengelia monticola, Stylidium productum, Todea barbara, Tristaniopsis collina, Woollsia pungens and Xanthorrhoea* sp.

The species has also been collected in very shaded *Ceratopetalum apetalum* forest in steep-sided ravines associated with *Acacia elata, Blechnum ambiguum, Dracophyllum secundum, Gahnia sieberiana, Lomandra montana, Quintinia sieberi, Sticherus lobatus* and *Tristaniopsis collina.*

Several species of *Dianella* are sympatric with *D. tenuissima* at its known locations (Carr unpubl. data): *D. tasmanica* Hook.f. sens strict., *D.* sp. aff. *caerulea* Sims (Blue Mountains), *D.* sp. aff. *caerulea* Sims (Katoomba Falls), *D. prunina* R.J.F.Hend. and *D. revoluta* R.Br. All of these species are taxonomically distant from *D. tenuissima.*

Conservation status: IUCN criteria indicate that insufficient information is available and that the conservation status of *D. tenuissima* cannot be adequately evaluated; it therefore remains Data Deficient (IUCN 2001). Given its high-quality habitat and very steep to vertical terrain in an area little modified by human influence, the species is not currently regarded as threatened. There is a need however for further studies to determine its distribution, population status and potential threats.

Etymology: from the superlative of the Latin *tenuis*, slender, in reference to the exceptionally gracile habit, very narrow leaves and capilliforme scapes and pedicels.

Specimens examined: New South Wales: Central Tablelands: Blackfellows Hand Rock, Newnes Plateau, Blue Mountains, *Miller s.n.* (Mar 1993) (NSW); Wentworth Falls, Blue Mountains, *Coveny 17363 & Hind*, 17 Nov 1996 (NSW).

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I am indebted to Colin Gibson (Fairfield, NSW) and Robert Miller (Bulli, NSW) for drawing my attention to this species, for valuable information on its ecology and

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[1] Taxonomic nomenclature follows Harden (1990–1993) and Harden and Murray (2000).

behaviour in cultivation, and stimulating discussion. Neville Walsh (MEL) kindly provided the Latin diagnosis and Fig. 1d; Deborah Lau, CSIRO, Melbourne, produced SEM images of leaves; Jamie McMahon, Beverley Mussen, and Carole McWilliam (Ecology Australia Pty Ltd) provided valuable assistance; Lawrie Conole (Ecology Australia Pty Ltd) provided Figs. 1b and 1c. The director of NSW is acknowledged for providing access to collections; editorial comments were kindly provided by Dr Elizabeth Brown.

References

Bembrick C (1980) Geology of the Blue Mountains, Western Sydney basin. Pp. 134–161 in Herbert C & Helby R (eds) *A guide to the Sydney basin*. Geological Survey of New South Wales Bulletin 26. (Department of Mineral Resources: Sydney)

Benson D, Howell J & McDougall L (1996) *Mountain Devil to Mangrove: a guide to natural vegetation in the Hawkesbury-Nepean catchment*. (Royal Botanic Gardens: Sydney)

Bernhardt P (1995) The floral ecology of *Dianella caerulea* var. *assera* (Phormiaceae). *Cunninghamia* 4: 9–20.

Carr GW & Horsfall PH (1995) Studies in Phormiaceae (Liliaceae) 1: New species and combinations in *Dianella* Lam. ex Juss. *Muelleria* 8(3): 365–378.

Carr GW (2004) A world checklist of *Dianella* (Hemerocallidaceae). Unpublished ms. (Ecology Australia Pty Ltd: Fairfield)

Clifford HT, Henderson RJF & Conran JG (1998) Hemerocallidaceae. Pp. 245–253 in Kubitzki K (ed.) *The families and genera of vascular plants: III Flowering plants. Monocotyledons: Lilianae (except Orchidaceae)*. (Springer-Verlag: Berlin)

Commonwealth of Australia (1988) *Climatic averages, Australia*, Bureau of Meteorology. (Australian Government Publishing Service: Canberra)

Curtis WM (1952) Variation in certain Tasmanian plants. *New Phytologist* 51(3): 398–414.

Duncan DH, Nicotra AB & Cunningham SA (2004) High self-pollen transfer and low fruit set in buzz-pollinated *Dianella revoluta* (Phormiaceae). *Australian Journal of Botany* 52: 185–193.

Green PS (1994) *Dianella*. Pp. 505–506 in Wilson AJG (ed.) *Flora of Australia*, vol. 49. (Australian Government Publishing Service: Canberra)

Harden GJ (ed.) (1990–1993) *Flora of New South Wales*, vols 1–4. (New South Wales University Press: Kensington)

Harden GJ & Murray LJ (2000) *Flora of New South Wales*, vol. 1 supplement. (New South Wales University Press: Kensington)

Henderson RJF (1987) *Dianella*. Pp. 194–225 in George AS (ed.) *Flora of Australia*, vol. 45. (Australian Government Publishing Service: Canberra)

Henderson RJF (1988) Nomenclatural studies in *Dianella* Lam. ex Juss. (Phormiaceae) 1. *Austrobaileya* 2(5): 419–426.

Henderson RJF (1991) Studies in *Dianella* Lam. ex Juss. (Phormiaceae) 2. *Austrobaileya* 3(3): 473–480.

James TA (ed.) (1994) *An assessment of the world heritage values of the Blue Mountains and surrounding plateaus*. (Royal Botanic Gardens: Sydney)

IUCN (2001) *Red list categories and criteria: version 3.1*. (IUCN: Species Survival Commission. IUCN: Gland & Cambridge)

Jessop JP (1979) *Dianella*. Pp. 206–209 in van Steenis CGGJ (ed.) *Flora Malesiana*, vol. 9(1). (Sijthoff & Noordhoff: Alphen aan den Rijn)

Keith DA & Benson DH (1988) The natural vegetation of the Katoomba 1:100 000 map sheet. *Cunninghamia* 2(1): 107–144.

Rose AB (1973) Food of some Australian birds. *Emu* 73: 177–183.

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Chromosome numbers in some species of *Dicranoloma* from Australia, New Zealand and Papua New Guinea

Helen P. Ramsay

National Herbarium of New South Wales, Royal Botanic Gardens, Sydney NSW 2000, Australia
Email:hpramsay@ozemail.com.au

Abstract

Chromosome numbers have been added or confirmed for a number of Australasian species of *Dicranoloma* based on studies of New Zealand (and several Australian) collections. These are n = 7 for *D. dicarpum, D. platycaulon, D. robustum*; n = 8 for *D. plurisetum*; New Zealand populations of *D. menziesii* had n = 7 and lacked the *m*-chromosome found in Australian populations where n = 8 (7 + m). *D. billarderii* has n = 12 chromosomes. The chromosome number of n = 7 is confirmed for *D. dicarpum* in Papua New Guinea. The chromosome number of n = 9 (7 + 2 m) recorded for *D. serratum* in Ramsay (1985) is now referred to *D. leichhardtii* with which *D. serratum* has been synonymised (Klazenga 2003).

Introduction

The family Dicranaceae is well represented in Australia and New Zealand where the genus *Dicranoloma* is prominent in wet forests. The species are erect, with almost unbranched stems and form tall turfs or small cushions on soil, fallen tree trunks or are sometimes epiphytic. The genus has been revised by Klazenga (2003) who recognises 15 species from Australasia with 10 species and 2 endemics in New Zealand (Beever et al 1992, Fife 1995, Klazenga 2003) and 13 species with 3 endemics in Australia (Klazenga 2003).

Chromosome numbers have been published previously for five Australian species – *D. billarderii*[1] n = 12, *D. dicarpum* n = 7, *D. menziesii* n = 8 (7 + m), *D. robustum* n = 7 and *D. leichhardtii* n = 9 (7 + 2m; as *D. serratum*) (Ramsay 1974, 1985; Fritsch 1982, 1991). A mitotic count of n = 12 from New Zealand material of *D. billarderii* (as *Dicranum billarderi*) has also been made (Przywara et al. 1992).

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[1] The spelling of this epithet has been the subject of much debate. The original spelling was *billarderii*, indicating that Bridel's intended latinisation of La Billardière's name was Billarderius, a form also reflected in his germanicised version of the name (W. Greuter and J. McNeill, pers. comm.). The name should, therefore, remain as published (ICBN Art. 60.7) and not be modified either to *billardierei*, following Art.60.7(b), Ex.15, or to *billarderi*, following Art. 60.11.

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Materials and Methods

The chromosome numbers obtained are based on meiotic studies of fresh material collected in the field, transported to the laboratory and maintained under cool conditions until capsules reached the correct stage of development. The methods used follow those outlined by Ramsay (1982) using aceto-carmine stain and slides made permanent using dry ice and mounting in euparal (Ramsay 1974). Permanent slides using this technique are still clear and are able to be examined 20 years later. A total of 30 populations from Australia and/or New Zealand and two from Papua New Guinea were examined. Voucher specimens have been lodged at NSW and detailed locality information can be obtained upon request, citing the number codes in Table 1.

Chromosome numbers

Meiotic studies of six New Zealand species have been made while numbers for additional populations of various species in Australia are confirmed. Two populations of *Dicranoloma dicarpum* in Papua New Guinea were also examined for the first time (Table 1).

1. ***Dicranoloma billarderii*** (Brid. ex Anon.) Paris, n = 12, Fig. 1

Two cytotypes n = 12 and n = 13 (12 + m) from meiotic studies were reported on Australian material by Ramsay (1974, 1985). Przywara et al (1992) recorded the chromosome number n = 12 on the basis of mitotic material for a population from New Zealand. In the present studies, the meiotic chromosome number was determined as n = 12 (Fig. 1) for one population from New Zealand (21/87) and from an additional Australian population (12/80; Table 1).

2. ***Dicranoloma dicarpum*** (Nees) Paris, n = 7, Figs 2–8.

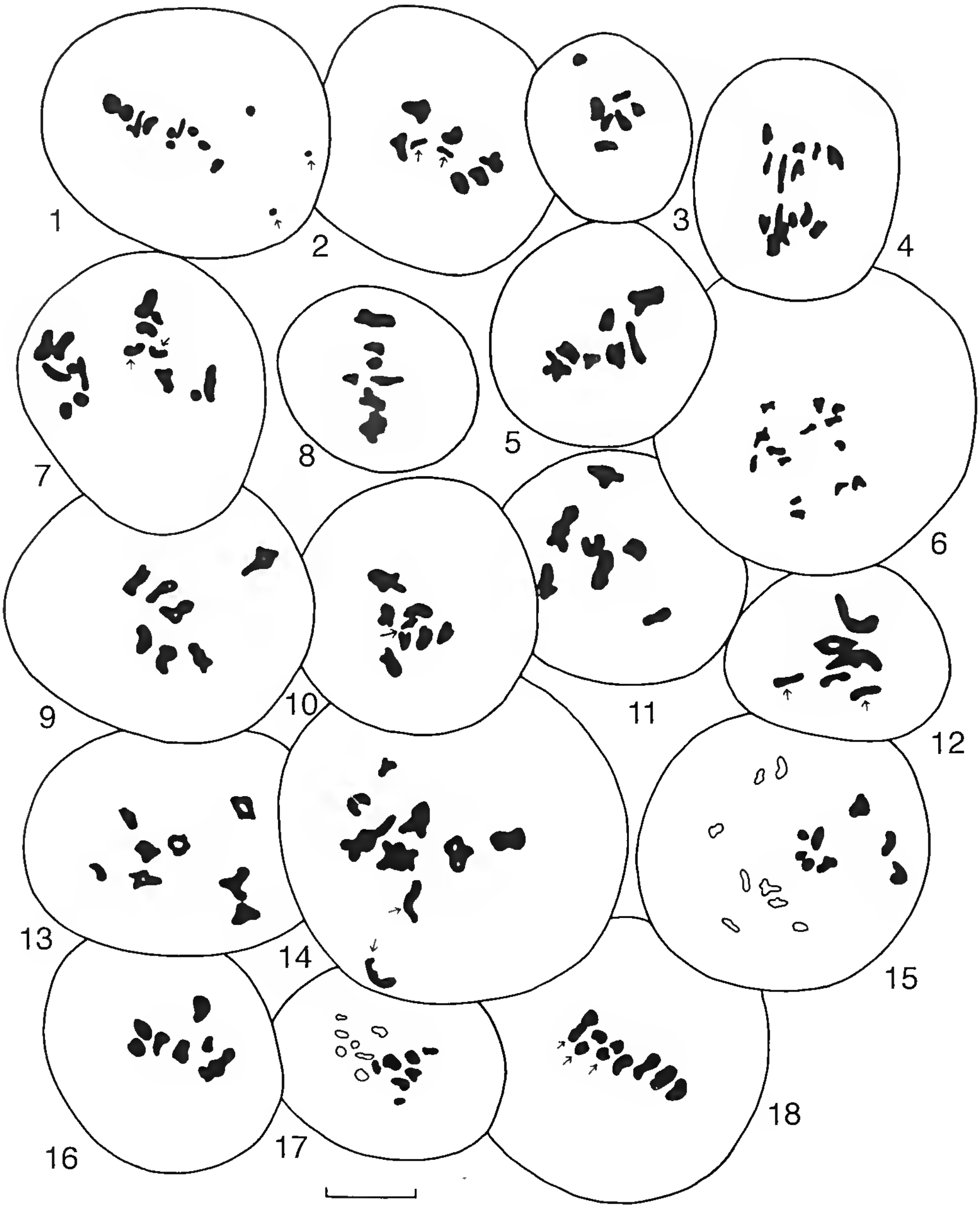
The chromosome number n = 7 was obtained here for the first time for three populations in New Zealand (30/87, 25/87, 83/82, Figs 7 & 8) (Table 1). The same chromosome number, n = 7, was also recorded for the first time for two populations from separate locations in Papua New Guinea (18/82, 66/82, Figs. 2–5) (Table 1). This agrees with the previously recorded chromosome number of n = 7 for Australian populations (Ramsay 1974, 1985; confirmed also by a further two populations from New South Wales, 6/72, 7/82).

Figures 1–18. Various stages of meiosis in *Dicranoloma* species.

1. *D. billarderii* n = 12 (NZ 21/87), MI meiosis note bivalents of various sizes present, one is separating early (arrows);

2–8. *D. dicarpum* n = 7, 2.(PNG 18/82) MI showing early separation of one bivalent (arrows), 3. (PNG 66/82) MI note seven bivalents of various sizes, 4. (PNG 18/82) AI note the 7 chromosome pairs moving to opposite poles, 5. (PNG 18/82) MI note seven bivalents present, 6. (Aust. 7/82) AI note the 7 half bivalents moving to opposite poles, 7. (NZ 83/82) AI note the 7 half bivalents moving to opposite poles, 8. (NZ 25/87) seven bivalents of various sizes present;

9 & 10. *D. menziesii* n = 7 (14/83 NZ), 9. MI note seven bivalents present, no m-bivalent detected in the NZ populations studied, 10. MI note one bivalent disjoining early;



11 & 12. *D. platycaulon* n = 7, 11. (NZ 39/87) MI note the seven bivalents of various sizes, 12. (NZ 68/84) MI showing the two half bivalents of one bivalent are separating;

13–15. *D. plurisetum* n = 8, 13. (NZ 71/84) MI, 14. (NZ 87/84) MI one bivalent has separated early, 15. (NZ 87/84) MII showing the eight half bivalents of each plate;

16–18. *D. robustum* n = 7, 16. (NZ 19/87) MI note seven bivalents, one larger than the others, 17. (NZ 22/87) AI note the 14 half-bivalents moving apart, 18. (NZ 58/84) note the 7 bivalents on the metaphase plate, 3 beginning to separate.

Table 1. Chromosome numbers in *Dicranoloma* species in Australia (Aust), New Zealand (NZ) and Papua New Guinea (PNG) reported in these studies. Unless otherwise stated collections were made by the author. Other abbreviations; HS = Heinar Streimann, NI = North Island, NSW = New South Wales, SI = South Island

Species	Chromosome number (n =)	Country	Voucher details
D. billarderii	12	Aust	*12/80*, NSW, Megalong Valley
D. billarderii	12	NZ	*21/87*, SI, Red Hills
D. dicarpum	7	NZ	*30/87*, SI, Lake Rotoroa track; *25/87*, *A. Fife*, SI, Red Hills; *83/82*, *A. Fife*, SI, Cora Lynn Station
D. dicarpum	7	Aust	*6/72*, NSW, Royal National Park; *7/82*, NSW, Wattagan State Forest
D. dicarpum	7	PNG	*18/82*, *HS 22528*, Upper Nawata Banda *66/82*, *HS 25833*, Bulolo-Watut Divide
D. menziesii	7	NZ	*14/83*, SI, Mt Cargill; *15/83*, ibid.
D. menziesii	8 (7 + m)	Aust	*33/84*, NSW, Mt Wilson
D. platycaulon	7	NZ	*28/87*. SI, Lake Rotoroa track; *39/87*, ibid. *68/84*, NI, Akatarawas
D. plurisetum	8	NZ	*71/84*, NI, Akatarawas; *94/84*, NI, ibid. *87/84*, NI, Mt Ruapehu; *26/87*, SI, Red Hills; 38/87, ibid.
D. robustum	7	NZ	*57/84*, NI, Mt Ruapehu; *58/84*, ibid.; *81/84*, ibid.; *19/87*, SI, Lake Rotoroa; *27/87*, SI, ibid.; *22/87*, SI, Red Hills; *23/87*,ibid.; *24/87*, ibid.

3. *Dicranoloma menziesii* (Taylor) Renauld, n = 7, Figs 9 & 10

Counts for two populations from New Zealand (14/83,15/83) had the chromosome number n = 7 (Figs 9 & 10). The chromosome complement lacked the *m*-chromosome found in the Australian populations (n = 8 (7 + m); Ramsay 1974, 1985, figs 1–4), a count reconfirmed here by one additional Australian population (33/84; Table 1).

4. *Dicranoloma platycaulon* Dixon, n = 7, Figs 11 & 12

The chromosome number, n = 7, was obtained from studies of three populations in New Zealand, (28/87; 39/87, Fig. 11; 68/84, Fig. 12). The bivalents were large and of various sizes with one, medium in size, that disjoined first at early anaphase I (Fig. 12; Table 1).

5. ***Dicranoloma plurisetum*** Dixon, n = 8, Figs 13–15.

Five populations examined for the first time had the chromosome number n = 8 (87/84, 94/84, 71/84, 26/87, 38/87, Fig. 13). The bivalents varied in size, most being relatively large with several often separating early at anaphase I (Fig. 14) but no *m*-bivalent was seen. The number was confirmed at anaphase I (Fig. 15; Table 1).

6. ***Dicranoloma robustum*** (Hook.f. & Wilson) Paris, n = 7, Figs 16–18.

The chromosome number was determined as n = 7 (Figs 16–18) from eight separate New Zealand collections (23/87, 19/87, 22/87, 24/87, 81/84, 57/84, 58/84, 27/87). Of these several (19/87, 22/87, 23/87, 24/87) originally identified as *D. cylindrothecium* but now in synonymy with *D. robustum* had bivalents comparable with the latter. These counts are consistent with those found for Australian populations (Ramsay 1974, 1985).

Chromosome numbers reported for the related genus *Dicranum* include n = 11, 12, 13, 14 to 24 with the number n = 12 being most frequent. The number n = 7, found in a number of species of *Dicranoloma*, is rarely recorded for *Dicranum* (Fritsch 1991) and only from Russia. Ramsay (1985) noted that the chromosomes in *Dicranoloma* species with n = 7or 10, are relatively larger than those of *D. billarderii* with n = 12. Alignment of chromosomes for Australian species suggests that *D. billarderii* is likely to be polyploid in origin (Ramsay 1985). It has been suggested that the basic number for the genus is x = 7 (Ramsay 1974).

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References

Beever JE, Allison KW & Child J (1992) *The mosses of New Zealand*. (University of Otago Presss: Otago)

Fife A (1985) Biosystematics of the cryptogamic flora of New Zealand: Bryophytes. *New Zealand Journal of Botany* 23:645–662.

Fritsch R (1982) *Index to plant chromosome numbers - Bryophyta*. Regnum Vegetabile 108. (Scheltema & Holkema: Utrecht)

Fritsch R (1991). *Index to bryophyte chromosome counts*. Bryophytorum Bibliotheca 40. (J. Cramer: Berlin)

Klazenga N (2003) A revision of the Australasian species of *Dicranoloma* (Bryophyta, Dicranaceae). *Australian Systematic Botany* 16: 427–471.

Przywara L, Kuta E & Ochyra R (1992) Chromosome numbers in some New Zealand Bryophytes: 1. *Fragmenta floristica et geobotanica* 37(2): 395–405.

Ramsay HP (1974) Cytological studies of Australian mosses. *Australian Journal of Botany* 22: 293–348.

Ramsay HP (1982) The value of karyotype analysis in the study of mosses *Journal of the Hattori Botanical Laboratory* 53: 51–71.

Ramsay HP (1983) Cytology of mosses. Pp.149–221 in Schuster RM (ed.) *New Manual of Bryology*, vol. 2. (Hattori Botanical Laboratory: Nichinan)

Ramsay HP (1985) Cytological and sexual characteristics of the moss *Dicranoloma* Ren. Pp. 93–110 in Crosby MR (ed.) *Studies in systematic botany dedicated to Lewis E. Anderson.* Monographs in Systematic Botany from the Missouri Botanical Garden 11.

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A new suprageneric classification of the Proteaceae, with an annotated checklist of genera

Peter H. Weston[1] and Nigel P. Barker[2]

[1]*National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney NSW 2000, Australia*
[2]*Department of Botany, Rhodes University, Grahamstown 6140, South Africa*

Abstract

A new suprageneric classification of the Proteaceae is presented that takes account of available molecular systematic results, synthesised as a phylogenetic supertree. Subfamilial, tribal and subtribal names are recircumscribed or created, where necessary, to ensure the putative monophyly of named higher taxa. Subfamilies, tribes and subtribes are briefly described. One new subfamily, **Symphionematoideae**, two new tribes, **Petrophileae, Leucadendreae**, and four new subtribes, Leucadendreae subtribe **Isopogoninae**, Leucadendreae subtribe **Leucadendrinae**, Macadamieae subtribe **Malagasiinae** and Macadamieae subtribe **Virotiinae** are named. Information is provided on the number of species currently recognised in, and distribution of, each genus, and the most recent generic taxonomic treatments are cited. Challenges to the monophyly of some genera are briefly discussed.

Introduction

The most recent, complete suprageneric classification of the Proteaceae was published over thirty years ago, as part of a highly influential monograph on the evolution and biogeography of the family (Johnson & Briggs 1975). The phylogenetic analysis that this classification reflected was based primarily on morphological, anatomical and cytological characters, as well as a few micromolecular attributes (such as the ability to accumulate aluminium in the leaves) and biotic associations (pollinators). Johnson and Briggs described their analytical procedure as 'admittedly less "repeatable" or formally "objective"' than 'cladistic taximetric approaches' but 'no less likely to represent the truth' (Johnson & Briggs 1975: 98). Their philosophical approach to classification is more accurately described as 'gradistic' than 'cladistic': 'grades, when sufficiently well characterised and presumably monophyletic, are recognised as taxa, and the practical impossibility as well as the theoretical difficulties of pure cladism are acknowledged' (Johnson & Briggs 1975: 88).

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Johnson and Briggs' classification was amended slightly by Douglas (1995) in response to the discovery of a new genus, *Eidothea*, and the recognition that no morphological evidence supported the inclusion of *Bellendena* in the subfamily Persoonioideae. Nevertheless, Johnson and Briggs' classification has served as the systematic framework for a generation of researchers working on the comparative biology of the Proteaceae, including those interested in taxonomy (e.g. Rourke 1984a), phylogeny reconstruction (e.g. Midgley 1987), morphology (e.g. Douglas 1996), historical biogeography (e.g. Weston & Crisp 1996), anatomy (e.g. Catling & Gates 1995), cytology (e.g. Wiltshire & Stace 1997), palynology (e.g. Feuer 1990), paleobotany (e.g. Hill et al. 1995), reproductive biology (e.g. Collins & Rebelo 1987) and ecology (e.g. Cowling & Lamont 1998). However, much has changed since 1975 in the way that phylogenies are reconstructed and in the way they are used to justify higher level classifications. DNA sequences are now used routinely as a source of characters for phylogenetic analysis and explicit algorithms are routinely used to analyse them. Although a few systematists continue to advocate a gradistic or phenetic approach to classification (see e.g. Brummitt 1996) we agree with Hennig (1966), Nelson and Platnick (1981) and many others, who argue that cladistic classification is preferable. In making taxonomic changes to maximise the number of named higher taxa for which there exists good evidence of monophyly, we agree with Backlund and Bremer (1998) and Entwisle and Weston (2005) that nomenclatural stability should be a primary criterion in the choice of appropriate ranks for putative clades.

In recent years, several phylogenetic analyses of members of the Proteaceae have been conducted using DNA sequence data and algorithmic phylogenetic methods. Some of these analyses have been published while others are still in preparation. Hoot and Douglas (1998) is an analysis of representatives of most genera of Proteaceae, based on an alignment of DNA sequences for the chloroplast loci *atp*β and the *atp*β-*rbc*L intergenic spacer. Mast and Givnish (2002: fig. 2) is an analysis of 28 species of *Banksia* plus five species of *Dryandra* and representatives of 12 outgroup genera, based on an alignment of cpDNA sequences for the *rpl16* intron, *trnL* intron and *trnL-trnF* intergenic spacer. Barker et al. (2002) is an analysis of representatives of 19 genera of the subfamily Proteoideae, with particular emphasis given to African taxa, based on an alignment of ITS1–5.8S–ITS2 nrDNA sequences. Analyses of a sample of most genera of Proteaceae, based on ITS1–5.8S–ITS2 nrDNA and *rbc*L cpDNA sequences, by P.H. Weston, N.P. Barker and K. Downs (hereafter cited as WB&D ITS and WB&D *rbc*L, respectively) are still being prepared for publication. These analyses are largely congruent with one another in corroborating the monophyly of some of Johnson and Briggs' suprageneric taxa but also indicate that others are probably not monophyletic.

Only a small fraction of the species of Proteaceae have been sampled in the molecular systematic studies mentioned above, so it is fair to say that classification of the family is still based primarily on morphology, at least at the generic level. Although monophyly of a number of genera has been minimally tested using molecular data, only *Banksia* has been subject to detailed sampling at the species level (Mast 1998, Mast & Givnish 2002) and was shown to be non-monophyletic by inclusion of *Dryandra*, the genus that was previously thought to be its sister group (Thiele & Ladiges 1996). Barker et al. (2002) also showed that several of the African genera (*Mimetes, Sorocephalus, Spatalla* and *Paranomus*) could potentially be non-monophyletic, but with less comprehensive sampling of species. The main advances that molecular analyses have made resolve clades at the ranks of subtribe, tribe and subfamily in Johnson and Briggs' classification.

Although we expect further taxonomic changes at generic and higher levels in the Proteaceae, it is timely to update its classification by recircumscribing subfamilies, tribes and subtribes where molecular analyses strongly indicate that change is required.

One of us (PHW) has prepared a treatment of the Proteaceae for 'Families and Genera of Vascular Plants', and a supra-generic classification is required as part of this treatment. The primary purpose of this paper is to formalise the names of several clades that had not been named previously. In order to present these new names in a meaningful context, we have synthesised the results of molecular systematic analyses using supertree analysis (see e.g. Bininda-Emonds et al. 2002, 2004) to provide as complete a supra-generic classification as phylogenetic knowledge available to us allows. Presenting this classification required a complete listing of currently recognised genera, so we also took the opportunity to present some additional information on each genus that users are likely to find helpful: the number of species presently recognised; a verbal description of the geographic distribution; references to general taxonomic treatments (revisions and/or regional flora accounts) and more recently named species; plus comments on any challenges to the accepted taxonomic circumscription of the genus.

Methods

A supertree analysis using matrix representation and parsimony ('MRP' – Bininda-Emonds et al. 2002, 2004) was conducted that synthesised the results of published and unpublished molecular phylogenetic analyses of the Proteaceae (Hoot & Douglas 1998, Mast & Givnish 2002, Barker et al. 2002 (Analysis 1), WB&D ITS and WB&D *rbc*L – see above). The terminal taxa were currently recognised genera of Proteaceae. Each character was a component (sensu Nelson & Platnick 1981) of a bootstrap majority rule consensus tree for one of the molecular phylogenies. A total of 136 components were coded as characters in the data matrix. The states for each character were the membership (1) or non-membership (0) of a genus in the relevant component.

Generic membership of several components of the bootstrap consensus tree of Hoot and Douglas (1998) was modified to exclude dubiously or wrongly identified samples. The genera *Protea*, *Roupala* and *Floydia* were excluded from the coding of their tree for the following reasons. Hoot and Douglas (1998) reported *Leucadendron* to be more closely related to *Protea* than to either *Adenanthos* or *Isopogon*, contrary to our results (Barker et al. 2002, WB&D *rbc*L). We checked the identity of their DNA sequences of *Protea neriifolia* by examining a digital image of their voucher specimen and it is definitely a specimen of *Leucadendron*, although we could not identify it to species. The DNA sequences that Hoot and Douglas (1998: 317) reported for *Roupala* and *Floydia* were identical. This result is incredible, given that these genera are morphologically quite dissimilar and occur on different continents. We strongly suspect that one or other sequence was obtained from misidentified material. We requested a loan of the relevant voucher specimens from MEL, but these could not be found, so we took the cautious approach of excluding both taxa from our coding of Hoot and Douglas' tree.

Each character was weighted according to the bootstrap value of its component as shown in Table 1. Note that the relationship between these weights and bootstrap support is curvilinear, in recognition of the fact that the bootstrap index is a ratio and does not vary linearly with the number of uncontradicted synapomorphies supporting a group. It is easy to estimate the expected bootstrap percentages equivalent to various

Table 1: Character weighting scheme used in supertree analysis. The boundaries, in bootstrap percentages, delimiting the lower and upper bounds of each integral character weight, correspond to equivalent numbers of uncontradicted synapomorphies (1 = 64.1%, 2 = 88.3%, 3 = 96.4%, 4 = 99.0%, 5 = 99.4%).

Range of bootstrap values of component	Character weight
<64.1%	1
64.1–88.3%	2
88.4–96.4%	3
96.5–99.0%	4
99.1–100%	5

numbers of uncontradicted synapomorphies by constructing an artificial, ideal data set consisting of absolutely congruent "characters". We made such a matrix and subjected it to a bootstrap analysis with 100,000 replicates, conducted using the branch and bound search option of PAUP* version 4.0b10. The following equivalences were shown by this exercise: one uncontradicted synapomorphy is equivalent to a bootstrap percentage of 64.1%, two to 88.3%, three to 96.4%, four to 99.0%, and five to 99.4%. The boundaries, in bootstrap percentages, delimiting the lower and upper bounds of each of our integral character weights were based on these equivalences.

An all-zero outgroup was included to root the tree. The character matrix was subjected to parsimony analysis in PAUP* version 4.0b10 using default settings (heuristic search with TBR branch-swapping). Equally parsimonious trees were summarised as a strict consensus tree. An undesirable property of the MRP method is that some of the groupings that it produces may not be represented in any of the input trees (see e.g. Bininda-Emonds 2003, Goloboff 2005). We inspected the groupings on our consensus tree to identify those that were not components of any of the molecular phylogenies that our supertree was meant to synthesise.

Results

186630 equally parsimonious trees were found, the strict consensus of which is shown in Fig. 1. Of 59 components that constitute this tree, only one, the cluster of *Eucarpha* with *Floydia* and *Darlingia*, is not found in any of the input trees. This appears to be the spurious result of interactions between lowly weighted components of the ITS and *rbc*L input trees. This grouping was eliminated from consideration as a potential named taxon. This supertree was used as the basis for our suprageneric classification described below. Bootstrap support indices for the components of our supertree, from the original phylogenetic analyses, are shown in Table 2.

Fig. 1. MRP supertree of genera of Proteaceae, produced by taking the strict consensus of 186630 equally parsimonious trees resulting from an analysis of weighted components from available molecular phylogenies for the Proteaceae (see Methods and Results sections for details). Numbered rectangles on the right hand side of the figure refer to named higher taxa recognised here, signified by their numbers in the taxonomic treatment (subfamilies by digits 1–5 in the left-hand column, tribes by numbers 2.1–5.4 in the middle column and subtribes by numbers 4.1.1–5.4.4 in the right-hand column of rectangles).

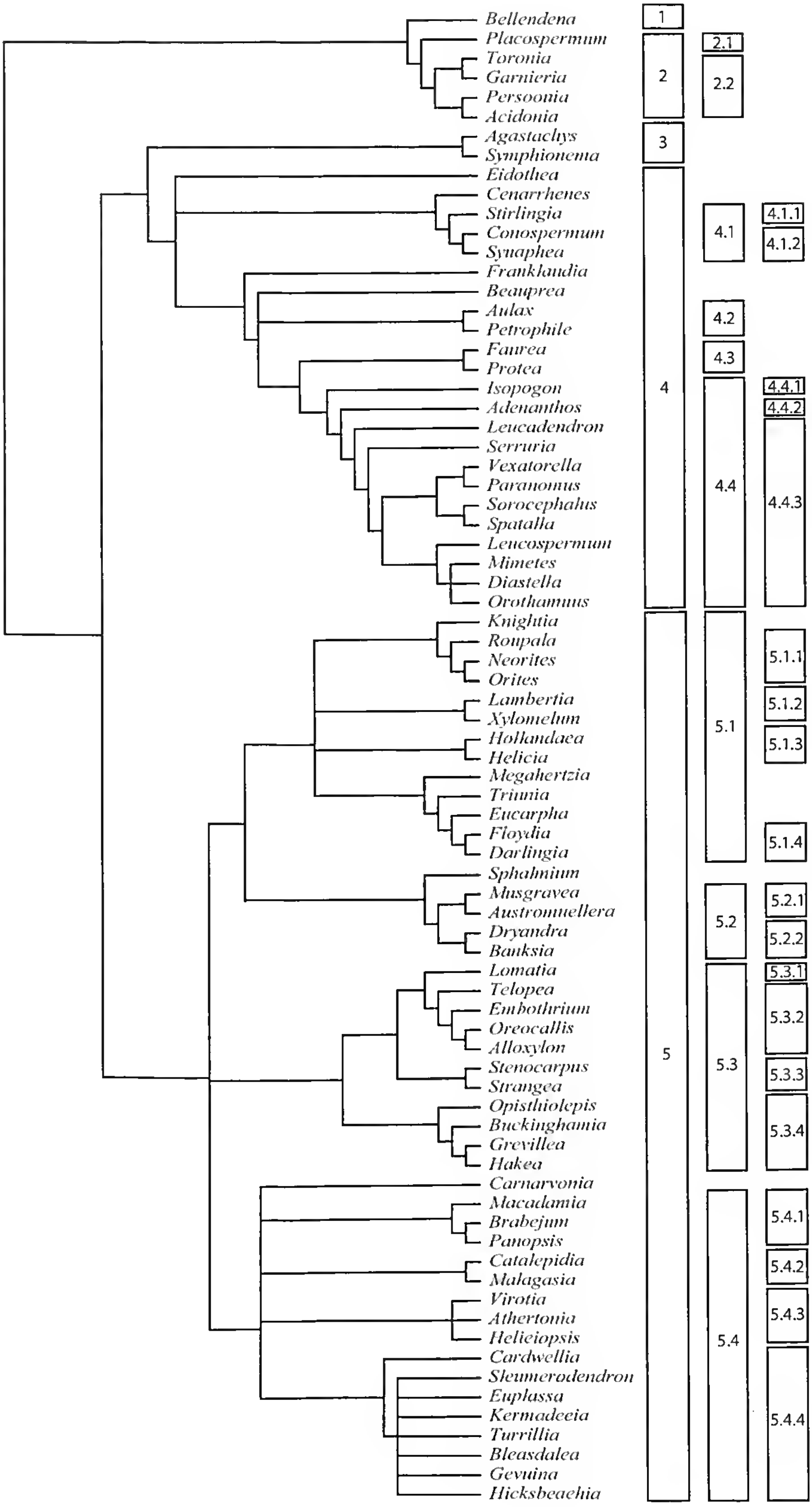
Bellendena
Placospermum
Toronia
Garnieria
Persoonia
Acidonia
Agastachys
Symphionema
Eidothea
Cenarrhenes
Stirlingia
Conospermum
Synaphea
Franklandia
Beauprea
Aulax
Petrophile
Faurea
Protea
Isopogon
Adenanthos
Leucadendron
Serruria
Vexatorella
Paranomus
Sorocephalus
Spatalla
Leucospermum
Mimetes
Diastella
Orothamnus
Knightia
Roupala
Neorites
Orites
Lambertia
Xylomelum
Hollandaea
Helicia
Megahertzia
Triunia
Eucarpha
Floydia
Darlingia
Sphalmium
Musgravea
Austromuellera
Dryandra
Banksia
Lomatia
Telopea
Embothrium
Oreocallis
Alloxylon
Stenocarpus
Strangea
Opisthiolepis
Buckinghamia
Grevillea
Hakea
Carnarvonia
Macadamia
Brabejum
Panopsis
Catalepidia
Malagasia
Virotia
Athertonia
Helicieopsis
Cardwellia
Sleumerodendron
Euplassa
Kermadecia
Turrillia
Bleasdalea
Gevuina
Hicksbeachia
1
2
3
4
5
2.1
2.2
4.1
4.2
4.3
4.4
5.1
5.2
5.3
5.4
4.1.1
4.1.2
4.4.1
4.4.2
4.4.3
5.1.1
5.1.2
5.1.3
5.1.4
5.2.1
5.2.2
5.3.1
5.3.2
5.3.3
5.3.4
5.4.1
5.4.2
5.4.3
5.4.4

Table 2: Bootstrap support indices for the named higher taxa that we have recognised, from the original phylogenetic analyses. A bootstrap support index of 0 indicates that the group was not resolved but that the highest bootstrap support for any incongruent clades was <50%. A negative bootstrap support index indicates the highest bootstrap support index greater than 50% for any group that was incongruent with the group in question.

Component	Bootstrap support in Hoot & Douglas 1998	Bootstrap support in Mast & Givnish 2002	Bootstrap support in Barker et al. 2002	Bootstrap support in WB&D ITS	Bootstrap support in WB&D rbcL
Bellendenoideae	monotypic	monotypic	monotypic	monotypic	monotypic
Persoonioideae	100	not tested	not tested	not tested	0
Placospermeae	monotypic	monotypic	monotypic	monotypic	monotypic
Persoonieae	not tested	not tested	not tested	100	97.7
Symphionematoideae + Proteoideae	65	not tested	not tested	0	0
Symphionematoideae	94	not tested	not tested	not tested	81.3
Proteoideae	85	not tested	not tested	0	0
Conospermeae	98	not tested	-72	76.5	<50
Stirlingiinae	monotypic	monotypic	monotypic	monotypic	monotypic
Conosperminae	100	not tested	72	90.5	64.9
Franklandia + *Beauprea* + Petrophileae + Proteeae + Leucadendreae	<50	not tested	not tested	0	0
Beauprea + Petrophileae + Proteeae + Leucadendreae	<50	not tested	66	0	0
Petrophileae	82	not tested	not tested	not tested	<50
Proteeae + Leucadendreae	not tested	not tested	59	not tested	0
Proteeae	not tested	not tested	100	not tested	91.1
Leucadendreae	100	not tested	100	100	78.2
Isopogoninae	monotypic	monotypic	monotypic	monotypic	monotypic
Adenanthinae + Leucadendrinae	92	not tested	60	-54.1	
Adenanthinae	monotypic	monotypic	monotypic	monotypic	monotypic
Leucadendrinae	not tested	not tested	90	95.1	<50

Serruria + *Vexatorella* + *Paranomus* + *Spatalla* + *Sorocephalus* + *Leucospermum* + *Mimetes* + *Diastella* + *Orothamnus*	not tested	not tested	100	87.4	<50
Vexatorella + *Paranomus* + *Spatalla* + *Sorocephalus* + *Leucospermum* + *Mimetes* + *Diastella* + *Orothamnus*	not tested	not tested	64	<50	0
Vexatorella + *Paranomus* + *Spatalla* + *Sorocephalus*	not tested	not tested	67	66.1	0
Vexatorella + *Paranomus*	not tested	not tested	73	not tested	0
Spatalla + *Sorocephalus*	not tested	not tested	59	not tested	0
Leucospermum + *Mimetes* + *Diastella* + *Orothamnus*	not tested	not tested	82	0	0
Mimetes + *Diastella* + *Orothamnus*	not tested	not tested	94	not tested	0
Grevilleoideae	89	not tested	not tested	<50	58
Roupaleae	0	94	not tested	51.5	0
Knightia + Roupalinae	<50	not tested	not tested	57.3	not tested
Roupalinae	96	98	not tested	64.4	<50
Lambertiinae	83	not tested	not tested	91.7	0
Heliciinae	100	not tested	not tested	100	0
Megahertzia + *Triunia* + *Eucarpha* + Floydiinae	Not tested	not tested	not tested	62.0	0
Triunia + *Eucarpha* + Floydiinae	Not tested	not tested	not tested	<50	0
Eucarpha + Floydiinae	not tested	not tested	not tested	-68.0	0
Floydiinae	not tested	not tested	not tested	100	97.7
Sphalmium + Banksieae	0	not tested	not tested	76.7	0

Component	Bootstrap support in Hoot & Douglas 1998	Bootstrap support in Mast & Givnish 2002	Bootstrap support in Barker et al. 2002	Bootstrap support in WB&D ITS	Bootstrap support in WB&D rbcL
Banksieae	98	87	not tested	-51.5	0
Musgraveinae	100	not tested	not tested	not tested	96
Banksiinae	not tested	100	not tested	100	91
Embothrieae	0	100	not tested	77.2	0
Stenocarpinae + Lomatiinae + Embothriinae	0	98	not tested	-53.2	0
Lomatiinae + Embothriinae	-68	not tested	not tested	91.7	0
Lomatiinae	monotypic	monotypic	not tested	monotypic	monotypic
Embothriinae	99	not tested	not tested	99.5	0
Embothrium + *Oreocallis* + *Alloxylon*	57	not tested	not tested	<50	0
Oreocallis + *Alloxylon*	not tested	not tested	not tested	<50	0
Stenocarpinae	not tested	not tested	not tested	53.8	0
Hakeinae	100	99	not tested	98.7	<50
Buckinghamia + *Grevillea* + *Hakea*	99	99	not tested	not tested	0
Grevillea + *Hakea*	not tested	not tested	not tested	not tested	99.4
Carnarvonia + Macadamieae	0	not tested	not tested	68.0	0
Macadamieae	70	not tested	not tested	-68.0	0
Macadamiinae	100	not tested	not tested	99.4	0
Brabejum + *Panopsis*	99	not tested	not tested	0	0
Malagasiinae	not tested	not tested	not tested	100	78.3
Virotiinae	not tested	not tested	not tested	98.1	70.9
Gevuininae	100	not tested	not tested	100	0
Sleumerodendron + *Euplassa* + *Kermadecia* + *Turrillia* + *Bleasdalea* + *Gevuina* + *Hicksbeachia*	99	not tested	not tested	64.4	<50

Subfamilies, tribes and subtribes. Only two of the seven subfamilies recognised in Douglas' (1995) slightly modified version of Johnson and Briggs' (1975) classification, subfamilies Bellendenoideae and Persoonioideae, are monophyletic, according to our supertree. Moreover, one of these, the Bellendenoideae, is monospecific and thus monophyletic by definition. However, a set of five, putatively monophyletic subfamilies can be formed with only minor changes to the circumscriptions of existing named taxa.

In chloroplast DNA analyses, *Bellendena* is either resolved as sister group to the rest of the family ("the rest" receiving 61% bootstrap support, Hoot & Douglas 1998), or left in an unresolved, basal position (WB&D *rbc*L). Our ITS analysis (WB&D ITS) was rooted at its midpoint, which resulted in *Bellendena* being resolved as sister group to the Persoonioideae in Fig. 1. An anatomical character that supports the position of *Bellendena* as sister group to the rest of the Proteaceae is its possession of laterocytic stomata, in common with *Platanus* and unlike all other Proteaceae, which have brachyparacytic stomata (Carpenter et al. 2005). Putative autapomorphies of the Bellendenoideae include the mostly ebracteate flowers, winged fruit and chromosome number of $n = 5$ (Johnson & Briggs 1975).

The monophyly of subfamily Persoonioideae, is either strongly supported (Hoot & Douglas 1998) or weakly contradicted (WB&D *rbc*L) by molecular analyses (Table 2). The unusually large chromosomes are probably a synapomorphy for the subfamily (Johnson & Briggs 1975, Weston 1994, Stace et al. 1998). The sister group relationship of the Persoonioideae to the rest of the Proteaceae is either moderately supported in molecular analyses ("the rest" receiving 81% bootstrap support in Hoot & Douglas 1998) or weakly contradicted by them (WB&D *rbc*L).

One of the two tribes of Persoonioideae recognised by Douglas (1995), the Placospermeae, is monospecific and thus monophyletic by definition. Its putative autapomorphies include andromonoecy, and sterilisation of anterior and lateral stamens. Follicular fruits, containing numerous transversely oriented seeds, are also likely to be autapomorphic given that the fruits of *Nelumbo*, *Platanus*, Symphionematoideae, Proteoideae and Persoonieae are indehiscent. The other tribe, Persoonieae, is monophyletic in our supertree and was strongly supported in the two analyses in which it has been tested (WB&D ITS, WB&D *rbc*L, see Table 2). The drupaceous fruit, in which the endocarp develops from proliferation of the inner epidermis of the carpel (Johnson & Briggs 1975, Stroeschen 1986), is likely to be a synapomorphy for this tribe (Weston 1994).

Douglas' monogeneric subfamily Eidotheoideae is nested within the subfamily Proteoideae sensu Douglas according to Fig. 1 and sinking the former into the latter would render the Proteoideae monophyletic and so we have done this. However, we have also chosen to recognise the clade of *Symphionema* and *Agastachys*, which is sister group of the rest of the Proteoideae, as a new subfamily, the Symphionematoideae, for several reasons. Firstly, the monophyly of the Symphionematoideae was corroborated in both of the analyses in which it was tested. Secondly, the monophyly of the more narrowly circumscribed Proteoideae is more strongly supported than that of Proteoideae sensu lato (Table 2). Thirdly, excluding Symphionematoideae from the Proteoideae allows the straightforward morphological diagnosis of both of these subfamilies from Persoonioideae. Symphionematoideae differs from Persoonioideae in having dry indehiscent fruits, while Proteoideae s.s. differs from Persoonioideae in possessing cluster roots (in all taxa examined).

Our subfamily Symphionematoideae is diagnosed by a combination of the following character states: absence of cluster roots (Lee 1978) and possession of dry, indehiscent fruits. Given the presence of cluster roots in *Bellendena*, their absence in Symphionematoideae is likely to represent secondary loss. Loss of cluster roots is therefore a putative synapomorphy for this subfamily, albeit one paralleled in subfamily Persoonioideae.

Subfamily Proteoideae as circumscribed here is diagnosed by a combination of the following character states: presence of cluster roots, ovule solitary (with rare, biovulate flowers in some species of *Isopogon* and *Petrophile*) and possession of indehiscent fruits. Reduction in ovule number from two to one could be a synapomorphy for the Proteoideae, but with parallels in Persoonioideae (some species of *Persoonia*), Symphionematoideae (*Agastachys*) and Grevilleoideae (some species of *Strangea*).

Neither *Dilobeia* nor *Beaupreopsis* have been sampled in any molecular phylogenetic analyses of the Proteaceae, nor have they been screened for presence of cluster roots. Their membership in subfamily Proteoideae is thus highly provisional. Their drupaceous fruits suggest a possible relationship with *Eidothea*, *Cenarrhenes* and *Beauprea* and although these genera do not form a clade in any of the molecular analyses, their possible monophyly is not strongly contradicted either.

We have recognised four tribes in the subfamily Proteoideae: Conospermeae, Petrophileae, Proteeae and Leucadendreae. The tribe Conospermeae, as broadly circumscribed by Johnson and Briggs (1975) and Douglas (1995), is strongly contradicted by all of the molecular analyses in which it has been tested and appears to be polyphyletic. However, a more narrowly circumscribed Conospermeae, as recognised here, and earlier as an unnamed group by Johnson and Briggs (1963), was supported in three of the four analyses in which it has been tested (Hoot & Douglas 1998, WB&D ITS, WB&D *rbc*L). The analysis in which it was found to be paraphyletic (Barker et al. 2002) included only two non-Proteoid outgroups and this result is likely to be a sampling artifact. Coherence of fertile anther loculi to the fertile loculi of adjacent anthers is a putative synapomorpy supporting this clade.

Within the Conospermeae, *Conospermum* and *Synaphea* are resolved as sister groups in every analysis in which the three genera have been represented (Hoot & Douglas 1998, WB&D ITS, WB&D *rbc*L). The grouping of the latter two genera was formally recognised by Johnson and Briggs (1975) as subtribe Conosperminae and they placed *Stirlingia* in a monogeneric subtribe Stirlingiinae. Those authors noted that *Conospermum* and *Synaphea* "show perianth zygomorphy, partial sterilisation of the androecium and unusual pollination mechanisms, but these must be of independent origin in view of the opposite direction of the zygomorphy in the two genera. Nevertheless they share a common reduced chromosome number of $n = 11$, true gamotepaly and suppression of the intersporangial septum in each anther lobe" (Johnson & Briggs 1975: 104). Apart from the zygomorphic features, all of these character states are putative synapomorphies for the Conosperminae.

The tribe Petrophileae is resolved as monophyletic in both published (Hoot & Douglas 1998) and unpublished (WB&D *rbc*L) analyses in which both genera have been represented. However, *Petrophile* and *Aulax* share no obvious morphological synapomorphies nor even a simple diagnostic combination of morphological character states. Moreover, *Petrophile* is superficially very similar to *Isopogon*, with which it has previously been grouped (Johnson & Briggs 1963, 1975; Venkata Rao 1971;

Douglas 1995). Nevertheless, the Petrophileae do possess at least one putative, non-macromolecular synapomorphy, the shared synthesis of pinitol, a polyol sugar, which is found elsewhere in the Proteaceae only in Persoonioideae tribe Persoonieae (Bieleski & Briggs 2005). *Petrophile* plus *Aulax* are a putative clade for which a formal name would be useful, especially given their biogeographically significant, disjunct distribution spanning the Indian Ocean, so we have recognised this group as a new tribe.

The monophyly of the tribe Proteeae, as broadly circumscribed by Johnson and Briggs (1975) and Douglas (1995), is strongly refuted by all of the molecular analyses in which it has been tested (Hoot & Douglas 1998, Barker et al. 2002, WB&D ITS, WB&D *rbc*L). However, a much more narrowly circumscribed Proteeae, including only *Protea* and *Faurea*, as recognised here, and earlier as an unnamed grouping by Johnson and Briggs (1963, 1975), is strongly supported as monophyletic (Barker et al. 2002, WB&D ITS, WB&D *rbc*L). These genera share a form of floral zygomorphy in which the perianth splits into two lobes, the anterior tepal being free or basally connate to the others and the 3 posterior tepals being completely connate or almost so. This feature is a putative synapomorphy for the Proteeae, albeit with a parallel, similar synapomorphy in *Leucospermum*. Other putative non-macromolecular synapomorphies include the shared production of high concentrations of polygalatol, a polyol sugar (Bieleski & Briggs 2005) and shared production of xylose-rich nectar (Nicolson & van Wyk 1998).

The tribe Leucadendreae is newly named here to signify a clade that includes most of the South African genera of Proteaceae, together with the Australian genera *Adenanthos* and *Isopogon*. This clade is moderately to strongly supported in all of the molecular analyses in which it has been tested (Hoot & Douglas 1998, Barker et al. 2002, WB&D ITS, WB&D *rbc*L, Table 2) but possesses no obvious morphological synapomorphies. It is a large, morphologically diverse group that is difficult to diagnose. Nevertheless, a formal name will be useful for this clade because of its biogeographic significance.

Within tribe Leucadendreae, the Australian genus *Adenanthos* is resolved as sister group to a large clade of southern African genera that have been informally dubbed the "Cape Clade" (Barker et al. 2002) and, together, they are the sister group of *Isopogon*. Here we formally name the "Cape Clade" as subtribe Leucadendrinae. This group is characterised by no morphological synapmorphies but can be diagnosed from other taxa by a combination of symplesiomorphous character states. *Adenanthos* was placed in its own monogeneric subtribe by Johnson and Briggs (1975) and we recognise it in our classification, together with a new monogeneric subtribe Isopogoninae. We acknowledge that such monotypic subtribes have no information content and can thus be regarded as taxonomically redundant. However, they have traditionally been used in botanical nomenclature as an alternative to listing genera as *incertae sedis* and it is this tradition that we follow here.

Johnson and Briggs (1975) recognised two monospecific subfamilies, the Sphalmioideae and Carnarvonioideae, which are nested within the subfamily Grevilleoideae according to our supertree. Sinking the former two taxa into the Grevilleoideae renders the latter a well supported monophyletic subfamily, so we have done this.

The monophyly of Grevilleoideae sensu lato is supported by the shared possession of auriculate cotyledons by the great majority of taxa that have been sampled for this character, including *Sphalmium* and *Carnarvonia*. Cotyledon auricles are apparently connate (i.e. the cotyledons are peltate) in *Panopsis cinnamomea* and are obscure in

Hollandaea and *Cardwellia*, apparently due to thickening and widening, respectively, of the cotyledons in these taxa. All other subfamilies of Proteaceae, as well as *Platanus*, have non-auriculate cotyledons, so auricles seem likely to be a synapomorphy for the Grevilleoideae. Follicular fruits may also be a synapomorphy for the Grevilleoideae, contrary to the suggestion of Johnson and Briggs (1975) that follicles are plesiomorphous within the Proteaceae. Our interpretation relies on three hypotheses of homology. Firstly the dry, indehiscent fruits of Symphionematoidae and most Proteoideae must be homologous with the very similar ones of the outgroup *Platanus* but non-homologous with the very dissimilar indehiscent fruits of some Grevilleoideae. Secondly, the follicles of *Placospermum* must be non-homologous with the quite dissimilar ones of the Grevilleoideae. Thirdly, the indehiscent fruits of some Grevilleoideae must be modified follicles, an argument put in some detail and with great force by Johnson and Briggs (1975: 133–138).

We have recognised four tribes in the subfamily Grevilleoidae, all of which are resolved in some molecular analyses but only one of which, the Banksieae, is strongly supported in all analyses in which it has been tested (Hoot & Douglas 1998, Mast & Givnish 2002, WB&D ITS, WB&D *rbc*L). We have recognised these groups at tribal rank in part to maintain nomenclatural stability of a number of better supported subtribes already recognised by Johnson and Briggs (1975) and Douglas (1995) and in the expectation that phylogenetic research currently in progress (by Austin Mast and co-workers) will resolve clades at the tribal level with greater confidence in the near future.

The tribe Roupaleae is an assemblage that is difficult to diagnose morphologically from the Macadamieae. It is largely composed of genera that were previously included in Johnson and Briggs' (1975) tribes Oriteae, Knightieae and Helicieae. Most of these genera have actinomorphic perianths (but in *Triunia* and most species of *Lambertia* they are zygomorphic), hemitropous to anatropous ovules (but in *Roupala*, *Floydia* and *Lambertia* they are orthotropous), follicular fruits (but in *Triunia*, *Helicia* and *Floydia* they are indehiscent) and flattened, winged seeds (but in *Triunia*, *Helicia* and *Floydia* they are globose and wingless). While monophyly of Johnson and Briggs' Oriteae is not strongly rejected in any molecular analyses, their tribes Knightieae and Helicieae are both strongly shown to be polyphyletic. It would not be surprising if future discoveries also demonstrated our Roupaleae to be polyphyletic, thus necessitating further taxonomic change at tribal level. However, our Roupaleae is better supported than alternative tribal circumscriptions in this part of the family, given available evidence.

The name Roupaleae, which was published by Meisner (1841) as "Rhopaleae", has nomenclatural priority over the other tribal names that are available for this group. The name was ignored by late twentieth century taxonomists (e.g. Johnson and Briggs 1963, 1975; Venkata Rao 1971, Douglas 1995), presumably because they thought it was illegitimate. Meisner listed the previously published tribal name Grevilleeae as a synonym of his "Rhopaleae", thus rendering his name superfluous when published.

We are confident of the identity of the *Roupala* sequences that were included in two analyses (Mast & Givnish 2002, WB&D ITS) and in both of these *Roupala* was weakly to strongly grouped with *Orites* and *Neorites* (Table 2). These three genera constitute our subtribe Roupalinae. They share no putative morphological synapomorphies but are similar enough to have been a source of some confusion at the generic level (Prance et al. in press). The name Roupalinae was published by Johnson and Briggs (1975) to refer to their grouping of *Roupala* and *Kermadecia*, two quite distantly related genera according to our unpublished ITS analysis (WB&D ITS).

The name Lambertiinae was created by Johnson and Briggs (1975) as a monogeneric subtribe within the tribe Macadamieae. However, all analyses that have included samples of both *Lambertia* and *Xylomelum* (Hoot & Douglas 1998, WB&D ITS, WB&D *rbc*L) have clustered them as sister taxa with moderate to strong support (Table 2), outside the Macadamieae. Consequently, we have placed them together in the subtribe Lambertiinae. The only putative morphological synapomorphy that they share is opposite to whorled foliar phyllotaxis, a character state that has evolved repeatedly in several different lineages of Proteaceae.

The subtribe Heliciinae was named by Johnson and Briggs (1975) to group *Helicia* with *Xylomelum*. However, this grouping is strongly contradicted in all three analyses in which both genera have been sampled and is highly likely to be polyphyletic. Instead, *Helicia* is strongly clustered with *Hollandaea* in two of the three analyses in which both the genera were sampled (Hoot & Douglas 1998, WB&D ITS, Table 2) a result that is neither supported nor contradicted by the third analysis (WB&D *rbc*L). Consequently, we have used this available subtribal name for the *Helicia-Hollandaea* clade. *Helicia* and *Hollandaea* have similar, rather non-descript vegetative and floral morphology but have dramatically different fruits. However, they share fleshy, wingless seeds and anatropous ovules, both of which are probably synapomorphies for the subtribe, albeit homoplasious ones.

The subtribe Floydiinae was published by Johnson and Briggs (1975) as a monogeneric subtribe in their tribe Macadamieae. This tribal placement seemed to make sense morphologically because *Floydia* shares two orthotropous ovules, and an indehiscent fruit containing a globose, wingless seed with many members of that tribe. However, the two molecular analyses in which we were confident of the identity of the *Floydia* DNA sequences (WB&D ITS, WB&D *rbc*L) both strongly grouped this genus with the two species of *Darlingia* (Table 2), a member of Johnson and Briggs' (1975) Knightieae. Although these genera differ spectacularly in their ovule, fruit and seed morphology (*Darlingia* has four hemitropous ovules, follicular fruits and flat, winged seeds), their flowers are very similar, albeit lacking any shared, novel character states.

Members of the tribe Macadamieae are superficially similar to some members of the Roupaleae but are almost uniformly characterised by having two, orthotropous ovules, and indehiscent or very tardily dehiscent fruits, each containing a solitary, globose to ellipsoidal, unwinged seed. The only genus that lacks these character states, the monospecific *Cardwellia*, has numerous hemitropous ovules, and massive follicular fruits, each containing numerous, flat, prominently winged seeds. Despite these morphological differences, membership of *Cardwellia* in the tribe Macadamieae is weakly to strongly supported in all of the molecular analyses in which it has been sampled (Hoot & Douglas 1998, WB&D ITS, WB&D *rbc*L). Our circumscription of Macadamieae is similar to that of Johnson and Briggs (1975), but differs in excluding *Floydia*, *Roupala* and *Lambertia* (to Roupaleae) and including *Cardwellia* (from Johnson and Briggs' tribe Knightieae).

In our supertree (Fig. 1), the genus *Carnarvonia* was included within the Macadamieae as part of a basal polytomy, the other lineages of which we have recognised as subtribes. Despite this result, we decided not to include *Carnarvonia* as a monotypic subtribe in our circumscription of Macadamieae because, for several reasons, we have little confidence in the veracity of this placement. Firstly, only one of the three analyses in which *Carnarvonia* was represented (WB&D ITS) resolved this genus as belonging to the Macadamieae, with less than 50% bootstrap support, as sister group to the subtribe Gevuininae. Secondly, *Carnarvonia* was placed in its own subfamily by Johnson and Briggs on the grounds that it lacked what they regarded as the most distinctive synapomorphy of their subfamily Grevilleoideae, inflorescences with grevilleoid flower pairs. Douglas (1996), in a detailed study of inflorescence and flower development in *Carnarvonia*, confirms the complete absence of even a vestige of the development of flower pairs in *Carnarvonia*. These observations are more consistent with a basal position of *Carnarvonia* within the Grevilleoideae than membership of the Macadamieae. Thirdly, *Carnarvonia* lacks the morphological character states that are typical of most other members of the Macadamieae: orthotropous ovules, fleshy cotyledons, unwinged seeds and indehiscent or tardily dehiscent fruits. We have thus chosen to retain *Carnarvonia* in the subfamily Grevilleoideae as a genus incertae sedis.

Monophyly of the subtribe Gevuininae, as newly circumscribed here, is strongly supported in two of the three molecular analyses in which it has been tested (Hoot & Douglas 1998, WB&D ITS, Table 2) and was neither supported nor contradicted by the third (WB&D *rbc*L). To the three genera included by Johnson and Briggs (1975) in their more narrowly defined Gevuininae are added *Bleasdalea* and *Turrillia* (not formally recognised when Johnson and Briggs submitted their paper for publication but both implicitly included in *Gevuina* by them), *Cardwellia* (from their polyphyletic tribe Knightieae), *Hicksbeachia* (from their polyphyletic Macadamieae: Hicksbeachiinae) and *Kermadecia* (from their polyphyletic Macadamieae: Roupalinae). All taxa of Gevuininae for which floral development has been investigated in detail (*Cardwellia sublimis*, *Sleumerodendron austrocaledonicum*, *Gevuina avellana*, *Bleasdalea bleasdalei*) are characterised by carpels oriented so that the ventral suture faces the abaxial tepal (Douglas & Tucker 1996). The only other species in which this condition has been observed is *Xylomelum salicinum* (Roupaleae: Lambertiinae). Moreover, most members of the Gevuininae share a novel form of floral zygomorphy in which the style is abaxially hooked through 180° and the adaxial tepal is straight, in contrast to the other three, recurved tepals. These morphological features are likely to form a syndrome of synapomorphies for the Gevuininae.

The subtribe Macadamiinae as circumscribed by Johnson and Briggs (1975) and Douglas (1995) is strongly corroborated as monophyletic in two of the three molecular analyses in which it has been tested (Hoot & Douglas 1998, WB&D ITS, Table 2). This result is neither supported nor contradicted by our unpublished *rbc*L analysis (WB&D *rbc*L) in which its three genera form part of a large polytomy. In all three genera the nectary forms a cup or collar-like structure surrounding the ovary, a condition that seems most likely to have resulted from connation of four free hypogynous glands. A similar condition is found elsewhere in the Macadamieae only in *Virotia*, in which it seems likely to have evolved convergently. Johnson and Briggs (1975: 110) add that the group is characterised by 'a strong tendency to opposite or whorled phyllotaxy, lacking only in some species of *Panopsis*', a feature that is likely to be synapomorphous for the subtribe, given its absence in other taxa of Macadamieae.

The subtribe Virotiinae, newly recognised here, is moderately to strongly supported as monophyletic in the two molecular analyses in which it has been tested (WB&D ITS, WB&D *rbc*L). Its three genera, *Virotia*, *Athertonia* and *Heliciopsis*, all share a distinctive reticulate to foveate surface sculpturing of the woody inner mesocarp of the drupe-like fruits. This contrasts with the smooth surface sculpturing of the inner mesocarp in other members of the Grevilleoideae with drupe-like fruits.

The subtribe Malagasiinae, also newly recognised here, is moderately to strongly supported as monophyletic in the two molecular analyses in which it has been tested (WB&D ITS, WB&D *rbc*L). Its two genera, *Malagasia* and *Catalepidia*, do not share any distinctive morphological characters states but nor do either of them share any such states with other genera.

The tribe Banksieae, as circumscribed by Johnson and Briggs (1975) and Douglas (1995) is weakly to moderately corroborated as monophyletic in three of the four molecular analyses in which it has been tested (Hoot & Douglas 1998, Mast & Givnish 2002, Barker et al. 2002, WB&D ITS). The only analysis in which its monophyly was unsupported was our unpublished analysis of *rbc*L sequences (WB&D *rbc*L), where the two subtribes formed part of a large polytomy. Putative morphological synapomorphies for the tribe include biporate pollen grains (otherwise found in the Proteaceae only in *Embothrium coccineum* and in atypical grains of a few other species, see e.g. Dettmann & Jarzen 1998), the presence of trichomes with unusually long, thin terminal cells, and 'banksioid' leaf venation (Johnson & Briggs 1975, Thiele & Ladiges 1996).

The two subtribes of the Banksieae, which were first recognised at this rank by Johnson and Briggs (1975), are moderately to strongly supported as monophyletic in all of the molecular analyses in which they have been tested (Table 2). The subtribe Banksiinae is characterised by four morphological and anatomical synapomorphies according to Thiele and Ladiges (1996): follicles with a bony endocarp, the presence of an interseminal false dissepiment, presence of vascular tissue in the wood rays, and a condensed conflorescence axis. The subtribe Musgraveinae is characterised by reduction in the number of hypogynous nectary glands from four to three (Johnson & Briggs 1975), a putative synapomorphy that is paralleled in *Lomatia*. Another novel morphological character state shared by *Musgravea* and *Austromuellera* is the antrorse-appressed cotyledons of their seedlings (Hyland 1999, Sankowsky et al. 1988).

Our tribe Embothrieae results from combining two of Johnson and Briggs' (1975) tribes: their Embothrieae and Grevilleeae. Molecular phylogenetic analyses consistently show that a paraphyletic doublet of two genera of Johnson and Briggs' Embothrieae, *Buckinghamia* and *Opisthiolepis*, are most closely related to their Grevilleeae. Molecular analyses have been less consistent in corroborating the monophyly of our Embothrieae as a whole, with only two out of four analyses in which this tribe was tested weakly to moderately supporting it (Mast & Givnish 2002, WB&D ITS, Table 2). However, the dissenting analyses (Hoot & Douglas 1998, WB&D *rbc*L) neither support nor contradict its monophyly. Although this group possesses no obvious morphological synapomorphies the chromosome numbers found in these taxa, $n = 11$ and $n = 10$ were interpreted as synapomorphic by both Johnson and Briggs (1975) and Stace et al. (1998), relative to the $n = 12–15$ found in other Grevilleoideae.

Our tribe Embothrieae contains four subtribes, three of which are circumscribed as by Johnson and Briggs (1975). The monogeneric subtribe Lomatiinae was grouped by Johnson and Briggs with the Embothriinae in an unnamed putative clade, a position that is consistent with our supertree but which is contradicted by one of the molecular analyses. Hoot and Douglas (1998) found *Lomatia* to cluster with *Stenocarpus* with 68% bootstrap support, so retaining *Lomatia* in its own subtribe rather than sinking it into the Embothriinae maintains nomenclatural stability at the same time as acknowledging conflicting information concerning its closest relatives.

The subtribe Embothriinae was strongly supported as monophyletic in two of the three molecular analyses in which it was tested (Hoot & Douglas 1998, WB&D ITS, Table 2). This result was weakly contradicted by our unpublished *rbc*L analysis (WB&D *rbc*L) in which *Alloxylon* was grouped with other members of the Embothrieae, with less than 50% bootstrap support. The four genera of Embothriinae share several morphological synapomorphies (Johnson & Briggs 1975, Weston & Crisp 1994), all of which are paralleled in other grevilleoid lineages.

The subtribe Stenocarpinae consists of *Stenocarpus* and *Strangea*, two genera that Johnson and Briggs (1975) grouped together on the basis of the novel, envelope-like morphology of their outer seed wing. To that putative synapomorphy can be added the umbel-like inflorescence shared by all species of *Stenocarpus* and *Strangea stenocarpoides*, the only species of *Strangea* in which the inflorescence has not been reduced to one or two flowers.

The subtribe Hakeinae, newly recognised here, combines Johnson and Briggs' (1975) Embothrieae subtribe Buckinghamiinae with their tribe Grevilleeae. The genus *Finschia*, which has not been sampled yet in any molecular analysis, is closely related to *Grevillea* and *Hakea* on the basis of shared, apomorphous, morphological and cytological character states (Johnson & Briggs 1975) such as diagonally oriented zygomorphic flowers, biramous trichomes, reduction in ovule number to two and reduction in chromosome number to $n = 10$. All of these states are convergently derived in other lineages of Proteaceae but *Finschia* seems most unlikely to be more closely related to any other genera. Monophyly of the Hakeinae is weakly to strongly corroborated in all four of the molecular analyses in which it has been tested.

Taxonomy

Family Proteaceae Juss.
(Jussieu 1789: 78)

1. Subfamily Bellendenoideae P.H.Weston
(Weston 1995b: 472)

Cluster roots present. Cotyledons not auriculate. Inflorescence a mostly ebracteate raceme. Staminal filaments free. Hypogynous glands absent. Ovules 2. Fruit dry, indehiscent, 2-winged. Chromosomes n = 5, mean length 6.7 µm.

1. *Bellendena* R.Br.
One sp. (*B. montana* R.Br.), Tasmania (Weston 1995b).

2. Subfamily Persoonioideae L.A.S.Johnson & B.G.Briggs
(Johnson & Briggs 1975: 170)
Cluster roots absent. Cotyledons not auriculate. Inflorescence a bracteate raceme or spike or panicle of racemes. Staminal filaments largely or completely adnate to tepals; anthers free or basally (or completely) adnate to tepals. Hypogynous glands present. Fruit not winged. Chromosomes n = 7 or rarely n = 14; mean length 9.1–14.4 µm.

2.1 Tribe Placospermeae C.T.White & W.D.Francis
(White & Francis 1924: 79)
Andromonoecious trees. Cotyledons obreniform, shortly stalked, flat. Leaves entire in the seedling phase, deeply lobed in the juvenile phase, entire in the adult phase.

Inflorescence a raceme or more commonly a panicle of racemes. Stamens dimorphic; posterior stamen fertile, prominently apiculate; anteriors and lateral stamens sterile. Ovary sessile; ovules 15–22. Fruit follicular; endocarp leathery, not penetrating between the seeds. Seeds 15–22, flat, transversely oriented, bilaterally winged.

2. ***Placospermum*** C.T.White & W.D.Francis

One sp. (*P. coriaceum* C.T.White & W.D.Francis), NE Australia (Weston 1995a: 47–49).

2.2. Tribe Persoonieae Rchb.

(Reichenbach 1828: 81)

Bisexual trees or shrubs. Cotyledons elliptic to linear, sessile, semicircular to semi-ellipsoidal to triangular in cross-section. Leaves entire. Inflorescence a raceme or spike (often leafy and auxotelic in *Persoonia*). Stamens monomorphic (abaxial anther sterile and adnate to abaxial tepal in *Persoonia hakeiformis*). Ovary shortly stipitate; ovules 1–7. Fruit a drupe; endocarp stony, penetrating between the seeds. Seeds 1–2, ovoid, not winged.

Drupaceous fruits are likely to be a synapomorphy for this tribe (Weston 1994).

3. ***Toronia*** L.A.S.Johnson & B.G.Briggs

One sp. (*T. toru* (A.Cunn.) L.A.S.Johnson & B.G.Briggs), North Island, New Zealand (Allan 1961: 299, as *Persoonia toru* A.Cunn.).

4. ***Garnieria*** Brongn. & Gris

One sp. (*G. spathulifolia* (Brongn. & Gris) Brongn. & Gris), New Caledonia (Virot 1968: 74–78).

5. ***Acidonia*** L.A.S.Johnson & B.G.Briggs

One sp. (*A. microcarpa* (R.Br.) L.A.S.Johnson & B.G.Briggs), SW Australia (Weston 1995a: 49–50).

6. ***Persoonia*** Sm.

100 spp., widespread in Australia, including Tasmania (Weston 1994, 1995a: 50–125, Weston & Johnson 1997, Weston 1999).

Persoonia appears to be polyphyletic, with *Toronia*, *Garnieria* and *Acidonia* nested amongst its basal subclades (P.H. Weston and C. Porter, unpublished analysis).

3. Subfamily Symphionematoideae P.H.Weston & N.P.Barker **subfam. nov.**

Fasciculi radicum absentes. Cotyledones non auriculatae. Inflorescentiae bracteatae, spicatae sed in *Symphionema* saepe complexae. Filamenta staminalia basaliter tepalis adnata. Glandes hypogynae absentes. Ovula 1–2. Fructus indehiscens, siccus, tribus alis vel non alatus. Chromosomatum numerus haploideus 10 vel 14. Genus typicum: *Symphionema* R.Br.

Cluster roots absent. Cotyledons not auriculate. Inflorescence bracteate, spicate but often compound in *Symphionema*. Staminal filaments basally adnate to tepals. Hypogynous glands absent. Ovules 1–2. Fruit indehiscent, dry. Chromosomes n = 10 or 14, mean length 3.1 μm.

7. ***Agastachys*** R.Br.

One sp. (*A. odorata* R.Br.), Tasmania (Telford 1995a).

8. ***Symphionema*** R.Br.

Two spp., SE Australia (Telford 1995b).

4. Subfamily Proteoideae Eaton
(Eaton 1836: 30)
Synonym: subfamily Eidotheoideae A.W.Douglas & B.Hyland (Douglas & Hyland 1995: 472)
Cluster roots present. Cotyledons not auriculate. Inflorescence bracteate, basically racemose but often compound and often condensed to form spikes or capitula, sometimes with different orders of branching differing qualitatively in structure (conflorescences of Johnson & Briggs 1975). Staminal filaments very slightly to completely adnate to tepals. Ovule 1 (2 in a few flowers of some species of *Petrophile* and *Isopogon*). Fruit indehiscent. Chromosomes n = 10–14, mean length 1.2–3.4 μm.

Genera incertae sedis
9. *Eidothea* A.W.Douglas & B.Hyland
Two spp., E Australia (Douglas & Hyland 1995, Weston & Kooyman 2002).
10. *Beauprea* Brongn. & Gris
13 spp., New Caledonia (Virot 1968: 20–74, 247–250).
11. *Beaupreopsis* Virot
One sp. (*B. paniculata* (Brongn. & Gris) Virot), New Caledonia (Virot 1968: 14–19).
12. *Dilobeia* Thou.
Two spp., E Madagascar (Bosser & Rabevohitra 1991: 49–58).
13. *Cenarrhenes* Labill.
One sp. (*C. nitida* Labill.), Tasmania (Telford 1995c).
14. *Franklandia* R.Br.
Two spp., SW Australia (George 1995a).

4.1 Tribe Conospermeae Endl.
(Endlicher 1837: 338)
Synonym: tribe Stirlingieae Baill. (Baillon 1870: 405, 427)
Involucral bracts absent. Floral bracts inconspicuous, not imbricate, scale-like, not thickening or hardening during fruit development. Flowers sessile. Perianth actinomorphic or zygomorphic. Tepals basally to almost wholly connate. Anther loculi coherent with fertile loculi of adjacent anthers. Hypogynous glands absent. Style tip not functioning as pollen presenter.

4.1.1 Subtribe Stirlingiinae L.A.S.Johnson & B.G.Briggs
(Johnson & Briggs 1975: 171)
Plants andromonoecious. Perianth actinomorphic. Anthers all bilocular, fertile.
17. *Stirlingia* Endl.
Seven spp., SW Australia (George 1995b).

4.1.2 Subtribe Conosperminae L.A.S.Johnson & B.G.Briggs
(Johnson & Briggs 1975: 171)
Plants bisexual. Perianth zygomorphic or rarely actinomorphic (some species of *Conospermum*). Lateral anthers unilocular; adaxial or abaxial stamen sterile.
18. *Conospermum* Sm.
53 spp., S Australia including Tasmania (Bennett 1995).
19. *Synaphea* R.Br.
50 spp., SW Australia (George 1995c).

4.2 Tribe Petrophileae P.H.Weston & N.P.Barker **trib. nov.**
Inflorescentia involucro bractearum subtenta (*Petrophile*) vel involucro bractearum et inflorescentiarum sterilifactarum complanatarum subtenta (*Aulax*). Bracteae

indurescentes per maturationem fructus (praeter *Aulax pallasia*), persistentes post liberatio fructuum. Tepala basaliter connata (sed in floris masculinis *Aulacis* libera). Antherae liberae. Glandes hypogynae absentes. Genus typicum: *Petrophile* R.Br. ex Knight.

Inflorescence subtended by an involucre of bracts (*Petrophile*) or an involucre of bracts and sterilised, flattened inflorescences (*Aulax*). Floral bracts hardening during fruit development (except in *Aulax pallasia*), persistent until after fruit fall. Tepals basally connate (free in the male flowers of *Aulax*). Anthers free. Hypogynous glands absent.
15. ***Petrophile*** R.Br. ex Knight
53 spp., S Australia (Foreman 1995a).
16. ***Aulax*** Berg.
Three spp., Cape region of South Africa (Rourke 1987).

4.3 Tribe Proteeae

Floral bracts persistent until after fruit fall. Flowers sessile. Perianth zygomorphic, splitting into two lobes, the anterior tepal free or basally connate to the others, the 3 posterior tepals completely connate or almost so. Anthers free. Style tip functioning as pollen presenter.
20. ***Protea*** L.
114 spp. (according to Rourke 1980 and Beard 1992) or 103 spp. (according to Rourke 1980 and Brummitt & Marner 1993: 8–30), widespread in sub-Saharan Africa.
21. ***Faurea*** Harvey
About 15 spp., widespread in sub-Saharan Africa and Madagascar (Brummitt & Marner 1993: 2–8, Bosser & Rabevohitra 1991: 58–63).

4.4 Tribe Leucadendreae P.H.Weston & N.P.Barker trib. nov.

Bracteae involucrales praesentes (absentes in speciebus aliquis *Leucadendri*, *Vexatorellae*). Flores sessiles. Tepala basaliter connata (libera in speciebus aliquis *Diastellae*). Antherae liberae. Apex styli plerumque palynophorio fungens. Genus typicum: *Leucadendron* R.Br.

Involucral bracts present (absent in some species of *Leucadendron*, *Vexatorella*). Flowers sessile. Tepals basally connate (free in some species of *Diastella*). Anthers free. Style tip functioning as pollen presenter (not so in a few species of *Leucadendron*).

4.4.1 Subtribe Isopogoninae P.H. Weston & N.P.Barker subtrib. nov.

Inflorescentia multiflora; bracteae florales caducae ubi fructus liberati. Glandes hypogynae absens. Ovulum orthotropum. Genus typicum: *Isopogon* R.Br. ex Knight.

Inflorescence multiflowered; floral bracts caducous when fruits are released. Hypogynous glands absent. Ovule orthotropous.
22. ***Isopogon*** R.Br. ex Knight
35 spp., S Australia (Foreman 1995b).

4.4.2 Subtribe Adenanthinae L.A.S.Johnson & B.G.Briggs

(Johnson & Briggs 1975: 171)

Inflorescences one-flowered; floral bract persistent. Hypogynous glands 4, basally adnate to perianth. Ovule hemitropous.
23. ***Adenanthos*** Labill.
33 spp., S Australia (Nelson 1978).

4.4.3 Subtribe Leucadendrinae P.H.Weston & N.P.Barker **subtrib. nov.**

Inflorescentia plerumque multiflora (uniflora in speciebus aliquis *Spatallae*); bracteae florales persistentes. Glandes hypogynae 4, liberae, vel absens (speciebus aliquis *Leucadendri* et *Diastellae*). Ovulum hemitropum. Genus typicum: *Leucadendron* R.Br.

Inflorescence usually multiflowered (one-flowered in some species of *Spatalla*); floral bracts persistent. Hypogynous glands 4, free, or absent (some species of *Leucadendron* and *Diastella*). Ovule hemitropous.

24. *Leucadendron* R.Br.
80 spp., Cape region, South Africa (Williams 1972).

25. *Serruria* Salisb.
51 spp., SW Cape region of South Africa (Rebelo 1995).

26. *Paranomus* Salisb.
18 (+1 excluded by Levyns) spp., Cape region of South Africa (Levyns 1970, Rebelo 1995).

27. *Vexatorella* Rourke
Four spp., SW Cape region of South Africa (Rourke 1984a).

28. *Sorocephalus* R.Br.
11 spp., SW Cape region of South Africa (Rourke 1969).

29. *Spatalla* Salisb.
20 spp., SW Cape region of South Africa (Rourke 1969).

30. *Leucospermum* R.Br.
48 spp., Cape region of South Africa, NE to the Chimanimani Mountains, Zimbabwe (Rourke 1972).

31. *Mimetes* Salisb.
13 spp., Cape region of South Africa (Rourke 1984b). *Mimetes* appears to be polyphyletic, including both *Diastella* and *Orothamnus* as subclades (Barker et al. 2002).

32. *Diastella* Salisb.
Seven spp., SW Cape region of South Africa (Rourke 1976).

33. *Orothamnus* Pappe ex Hook.
One sp. (*O. zeyheri*), Cape region of South Africa (Rebelo 1995).

Subfamily Grevilleoideae Engl.

(Engler 1888: 128)
Synonym: subfamily Carnarvonioideae L.A.S.Johnson & B.G.Briggs (Johnson & Briggs 1975: 172)
Synonym: subfamily Sphalmioideae L.A.S.Johnson & B.G.Briggs (Johnson & Briggs 1975: 172)
Cluster roots present. Cotyledons auriculate or rarely peltate (auricles obscure in a few genera due to thickening or widening of the cotyledons). Inflorescence bracteate, a raceme of flower pairs or a panicle of such racemes (grevilleoid conflorescences of Johnson & Briggs 1975) (occasionally a simple raceme or panicle of racemes or a highly reduced grevilleoid conflorescence). Staminal filaments basally to completely adnate to tepals.. Fruit not winged. Chromosomes $n = 10–14$, mean length 1.0–2.6 μm.

Genera incertae sedis

34. *Sphalmium* B.G.Briggs, B.Hyland & L.A.S.Johnson
One sp. (*S. racemosum* (C.T.White) B.G.Briggs, B.Hyland & L.A.S.Johnson), NE Australia (Briggs et al. 1975).

35. *Carnarvonia* F.Muell.
One sp. (*C. araliifolia* F.Muell.) with two subspp., NE Australia (Hyland 1995a).

5.1 Tribe Roupaleae Meisn.

(Meisner 1841: Tab. Diagn. 332, Comm. 245, as Rhopaleae)
Synonym: tribe Oriteae Venkata Rao ex L.A.S.Johnson & B.G.Briggs (Johnson & Briggs 1975: 172)
Synonym: tribe Knightieae L.A.S.Johnson & B.G.Briggs (Johnson & Briggs 1975: 172)
Synonym: tribe Helicieae L.A.S.Johnson & B.G.Briggs (Johnson & Briggs 1975: 173)
Anthers apiculate (inapiculate in *Neorites* and some species of *Orites*). Pollen grains triporate. Ovary sessile; style tip functioning as pollen presenter (not so in *Neorites* and some species of *Orites*); stigma terminal to subterminal (oblique in *Neorites*).

Genera incertae sedis
36. *Megahertzia* A.S.George & B.Hyland
One sp. (*M. amplexicaulis* A.S.George & B.Hyland), NE Australia (George & Hyland 1995).
37. *Knightia* R.Br.
One sp. (*K. excelsa* R.Br.), New Zealand (Allan 1961: 299–300).
38. *Eucarpha* (R.Br.) Spach
Two spp., New Caledonia (Virot 1968: 236–246, as *Knightia*).
39. *Triunia* L.A.S.Johnson & B.G.Briggs
Four spp., E Australia (Foreman 1995c).

5.1.1 Subtribe Roupalinae L.A.S.Johnson & B.G.Briggs

(Johnson & Briggs 1975: 174)
Adult leaves spiral. Ovules orthotropous to hemitropous. Fruit a leathery follicle; seeds winged.
40. *Roupala* Aubl.
33 spp., widespread in tropical South and Central America (Sleumer 1954: 141–175 but see Prance & Plana, 1998 and Prance et al., in press, regarding the number of species).
41. *Neorites* L.S.Sm.
One sp. (*N. kevediana* L.S.Sm.), NE Australia (Hewson 1995).
42. *Orites* R.Br.
Eight spp., E Australia including Tasmania, Chile (Sleumer 1954: 140–141, George 1995d).

5.1.2 Subtribe Lambertiinae (C.VenkataRao) L.A.S.Johnson & B.G.Briggs

(Venkata Rao 1968: 23; Johnson & Briggs 1975: 174)
Adult leaves opposite-decussate or whorled. Ovules 2, orthotropous to hemitropous. Fruit a woody follicle; seeds winged.
43. *Lambertia* Sm.
10 spp., SW and SE Australia (Hnatiuk 1995a).
44. *Xylomelum* Sm.
Six spp., SW and E Australia (Foreman 1995d).

5.1.3 Subtribe Heliciinae L.A.S.Johnson & B.G.Briggs

(Johnson & Briggs 1975: 173)
Synonym: subtribe Hollandaeinae L.A.S.Johnson & B.G.Briggs (Johnson & Briggs 1975: 173)
Adult leaves spiral (rarely opposite in *Helicia*). Ovules anatropous. Seeds not winged.
45. *Helicia* Lour.
About 100 spp., S India, Sri Lanka, China and Japan to SE Australia, with centre of diversity in New Guinea (Sleumer 1955a: 164–190, Foreman 1995e, 1995i: 234–268, Pham 1992: 86–109, Chung 2002: 170–189).

46. *Hollandaea* F.Muell.
Two spp., NE Australia (Hyland 1995b).

5.1.4. Subtribe Floydiinae L.A.S.Johnson & B.G.Briggs
(Johnson & Briggs 1975: 174)
Adult leaves spiral. Ovules orthotropous to hemitropous.
47. *Darlingia* F.Muell.
Two spp., NE Australia (Hyland 1995c).
48. *Floydia* L.A.S.Johnson & B.G.Briggs
One sp. (*F. praealta* (F.Muell.) L.A.S.Johnson & B.G.Briggs), E Australia (Foreman 1995f).

5.2 Tribe Banksieae Reichb.
(Reichenbach 1828: 82)
Floral bracts present (absent in a few species of *Dryandra*). Flowers sessile (shortly pedicellate in *Austromuellera*). Anthers apiculate. Pollen grains biporate. Ovary sessile; style tip functioning as pollen presenter; stigma terminal, oblique or abaxial; ovules 2, hemitropous (anatropous in some species of *Banksia* and *Dryandra*). Fruit follicular; seeds winged.

5.2.1 Subtribe Musgraveinae L.A.S.Johnson & B.G.Briggs
(Johnson & Briggs 1975: 174)
Common peduncle of flower pairs present. Tepals not connate. Hypogynous glands 3. False dissepiment scarcely formed between seeds.
49. *Musgravea* F.Muell.
Two spp., rainforest, NE Australia (Hyland 1999a).
50. *Austromuellera* C.T.White
Two spp., NE Australia (Hyland 1999b).

5.2.2 Subtribe Banksiinae L.A.S.Johnson & B.G.Briggs
(Johnson & Briggs 1975: 174)
Common peduncle of flower pairs absent. Tepals basally connate. Hypogynous glands 4. False dissepiment formed between seeds.
51. *Banksia* L.f.
76 spp., widespread in Australia including Tasmania, one sp. extending to S New Guinea (George 1999a).
Banksia is paraphyletic, including *Dryandra* as a subclade (Mast & Givnish 2002).
52. *Dryandra* R.Br.
93 spp., shrublands, woodlands and sclerophyll forests, SW Australia (George 1999b).

5.3 Tribe Embothrieae Reichb.
(Reichenbach 1828: 82)
Synonym: tribe Grevilleeae Endl. (Endlicher 1837: 340)
Common peduncle of flower pairs absent. Floral bracts absent. Flowers pedicellate (except in a few species of *Grevillea*) Perianth zygomorphic (except in some species of *Grevillea* and *Hakea*). Anthers inapiculate (or minutely apiculate). Pollen grains triporate (biporate in *Embothrium*). Ovary stipitate (sessile in some species of *Grevillea*); style tip functioning as pollen presenter, usually swollen; ovules hemitropous. Fruit dry, follicular (rarely dry and indehiscent: a few species of *Grevillea* or drupaceous, with fleshy outer mesocarp and hard inner mesocarp: *Finschia*); seeds winged (rarely wingless: *Finschia*, a few species of *Grevillea*).

5.3.1 Subtribe Lomatiinae L.A.S.Johnson & B.G.Briggs (1975: 173)

Inflorescence a raceme of flower pairs or a panicle of such racemes. Hypogynous glands 3. Carpel orientation diagonal.

53. *Lomatia* R.Br.

12 spp., E Australia including Tasmania, Chile, Argentina, Peru and Ecuador (Sleumer 1954: 196–200, Wilson et al. 1995).

5.3.2 Subtribe Embothriinae Endl.

(Endlicher 1837: 342)

Inflorescence a raceme of flower pairs. Hypogynous gland solitary, crescentic to horseshoe-shaped. Carpel orientation diagonal..

54. *Embothrium* J.R.Forst. & G.Forst.

One sp. (*E. coccineum* R.Forst. & G.Forst.), Chile, Argentina (Sleumer 1954: 204–207).

55. *Oreocallis* R.Br.

One or two spp., Peru and Ecuador (Sleumer 1954: 200–203, omitting *O. wickhamii*, *O. pinnata* and *O. brachycarpa*).

56. *Alloxylon* P.H.Weston & Crisp

Four spp., E Australia, S New Guinea and Aru Is (Weston & Crisp 1991).

57. *Telopea* R.Br.

Five spp., SE Australia including Tasmania (Crisp & Weston 1995).

5.3.3 Subtribe Stenocarpinae L.A.S.Johnson & B.G.Briggs

(Johnson & Briggs 1975: 172)

Inflorescence an umbel of flower pairs or a panicle of such umbels (reduced to a solitary flower pair or solitary flower in some species of *Strangea*). Hypogynous gland solitary, oblong to horse-shoe-shaped (*Stenocarpus*) or absent (*Strangea*). Carpel orientation antero-posterior.

58. *Stenocarpus* R.Br.

21 spp., N & E Australia, New Guinea, Aru Is., New Caledonia (Virot 1968: 176–236, Foreman 1995g). *Stenocarpus* is probably paraphyletic, including *Strangea* as a subclade (Weston, Barker and Downs unpublished analysis).

59. *Strangea* Meisn.

Three spp., SW & E Australia (Hnatiuk 1995b).

5.3.4 Subtribe Hakeinae Endl.

Endlicher (1837: 340), as Hakeaeae

Synonym: subtribe Buckinghamiinae L.A.S.Johnson & B.G.Briggs (Johnson & Briggs 1975: 173)

Inflorescence a raceme or umbel of flower pairs or a panicle of such racemes or umbels (rarely reduced to a single flower in a few species of *Grevillea* and *Hakea*). Hypogynous gland solitary, (rarely absent).

60. *Opisthiolepis* L.S.Sm.

One sp. (*O. heterophylla* L.S.Sm.), NE Australia (Foreman 1995h).

61. *Buckinghamia* F.Muell.

Two spp., NE Australia (Foreman & Hyland 1995).

62. *Hakea* Schrad. & J.C.Wendl.

149 spp., widespread in Australia including Tasmania (Barker et al. 1999).

63. *Grevillea* R.Br. ex Knight

362 spp., widespread in Australia including Tasmania, New Caledonia, New Guinea and Sulawesi (Olde & Marriott 1994, 1995a,b, Makinson 2000). *Grevillea* is probably polyphyletic, including both *Hakea* and *Finschia* as subclades.

64. *Finschia* Warb.
Three spp., New Guinea with one sp. extending NW to Palau Is. and SE to Vanuatu (Foreman 1995i: 228–232).

5.4 Tribe Macadamieae C.VenkataRao

(Venkata Rao 1968: 23)
Anthers apiculate. Pollen grains triporate. Ovary sessile; style tip functioning as pollen presenter); ovules 2 (numerous in *Cardwellia*), orthotropous (hemitropous in *Cardwellia*). Seeds wingless (winged in *Cardwellia*).

5.4.1 Subtribe Macadamiinae L.A.S.Johnson & B.G.Briggs

(Johnson & Briggs 1975: 174)
Common peduncle absent. Floral bracts absent. Flowers pedicellate. Perianth actinomorphic or slightly zygomorphic. Staminal filaments basally to almost completely adnate to tepals. Hypogynous gland solitary, cylindrical to cup like, irregularly lobed, surrounding base of ovary. Carpel orientation antero-posterior or diagonal (polymorphic from flower to flower). Fruit dry, tardily dehiscent or indehiscent, with radially oriented vascular bundles or bundles of fibres in the outer mesocarp. Seed globose or ellipsoidal.

65. *Macadamia* F.Muell.
Nine spp., E Australia, Sulawesi (Sleumer 1955a: 194–198, Gross 1995, McDonald & Ismail 1995). *Macadamia* appears to be paraphyletic, including both *Panopsis* and *Brabejum* as subclades (Weston & Downs unpublished analysis).

66. *Panopsis* Salisb.
25 spp., widespread in tropical South and Central America (Sleumer 1954: 176–184, Hernandez & Enrique 1991, Edwards & Prance 1993, Prance et al. in press).

67. *Brabejum* L.
One sp. (*B. stellatifolium* L.), SW Cape region of South Africa (Rebelo 1995).

5.4.2 Subtribe Malagasiinae P.H. Weston & N.P.Barker subtrib. nov.

Pedunculus communis praesens. Bracteae florales squamiformes. Flores pedicellati. Perianthium actinomorphum. Filamenta staminalior tepalis praeter apices adnatis. Glandes hypogynae 4, liberae. Cursus carpelli incognitus ; ovula 2, orthotropa. Fructus drupaceus; mesocarpus interior durus, pagina laevis; mesocarpus exterior succulentus, fasciculis vascularibus radialibus et fasciculis fibrarum radialibus absentibus. Semen globosum. Genus typicum: *Malagasia* L.A.S.Johnson & B.G.Briggs

Common peduncle present. Floral bracts scale like. Flowers pedicellate. Perianth actinomorphic. Staminal filaments adnate to tepals except at tips. Hypogynous glands 4, free. Carpel orientation unknown. Fruit drupaceous; inner mesocarp hard, with a smooth surface; outer mesocarp succulent, lacking radially oriented vascular bundles or bundles of fibres; Seed globose.

68. *Malagasia* L.A.S.Johnson & B.G.Briggs
One sp. (*M. alticola* (Capuron) L.A.S.Johnson & B.G.Briggs), Madagascar (Bosser & Rabevohitra 1991: 64–67).

69. *Catalepidia* P.H.Weston
One sp. (*C. heyana* (F.M.Bailey) P.H.Weston), NE Australia (Weston 1995c).

5.4.3 Subtribe Virotiinae P.H.Weston & N.P.Barker subtrib. nov.

Pedunculus communis praesens. Bracteae florales squamiformes. Flores pedicellati. Perianthium actinomorphum. Filamenta staminales tepaliis adnatis. Glandes hypogynae 4, liberae vel glans hypogyna solitaria, annularis, quadrilobata vel denticulata

(*Virotia*). Cursus carpelli incognitus. Fructus drupaceus; mesocarpus interior durus, pagina foveolata ad reticulata; mesocarpus exterior succulentus, fasciculis vascularibus radialibus vel fasciculis fibrarum radialibus. Semen ellipsoideum vel compressum-ellipsoideum. Genus typicum: *Virotia* L.A.S.Johnson & B.G.Briggs

Common peduncle present. Floral bracts scale like. Flowers pedicellate. Perianth actinomorphic. Staminal filaments adnate to tepals. Hypogynous glands 4, free or solitary, annular, 4-lobed or denticulate (*Virotia*). Carpel orientation unknown. Fruit drupaceous; inner mesocarp hard, with pitted to reticulate surface sculpturing; outer mesocarp succulent, with radially oriented vascular bundles or bundles of fibres; seed ellipsoid or compressed-ellipsoid.

70. *Virotia* L.A.S.Johnson & B.G.Briggs

Six spp., New Caledonia (Virot 1968: 109–140, as *Macadamia*, omitting the treatment of *M. integrifolia* as *M. ternifolia auct. non* F.Muell.).

71. *Athertonia* L.A.S.Johnson & B.G.Briggs

One sp. (*A. diversifolia* (C.T.White) L.A.S.Johnson & B.G.Briggs), NE Australia (Weston 1995d).

72. *Heliciopsis* Sleumer

Fourteen spp., Burma and SE China to Malesia, west of Wallace's Line (Sleumer 1955b: 79–86, Kochummen 1973, Pham 1992: 109–112, Kochummen 1973, Chung 2002: 189–201).

5.4.4 Subtribe Gevuininae L.A.S.Johnson & B.G.Briggs

(Johnson & Briggs 1975: 173)

Synonym: subtribe Cardwelliinae L.A.S.Johnson & B.G.Briggs (Johnson & Briggs 1975: 172)

Synonym: subtribe Hicksbeachiinae L.A.S.Johnson & B.G.Briggs (Johnson & Briggs 1975: 173)

Common peduncle present or absent. Floral bracts absent. Flowers pedicellate or sessile. Perianth zygomorphic (actinomorphic in *Hicksbeachia*). Staminal filaments adnate to tepals. Hypogynous glands 4, free (*Cardwellia*, *Sleumerodendron*, *Hicksbeachia*, some species of *Euplassa*) or 2, anterior, free (*Gevuina*, *Bleasdalea papuana*), or solitary, annular and 4-lobed (some species of *Euplassa*) or solitary, anterior, crescentic to bilobed-oblong (*Kermadecia*, *Turrillia*, *Bleasdalea bleasdalei*). Fruit drupaceous with a hard inner mesocarp with smooth surface and succulent outer mesocarp usually with radially oriented vascular bundles or bundles of fibres (or dry, follicular: *Cardwellia*); seed globose to ellipsoid or compressed-ellipsoid, not winged (flat, winged, elliptical in *Cardwellia*).

73. *Cardwellia* F.Muell.

One sp. (*C. sublimis* F.Muell.), NE Australia (Hyland 1995d).

74. *Sleumerodendron* Virot

One sp. (*S. austrocaledonicum* (Brongn. & Gris) Virot), New Caledonia (Virot 1968: 101–109).

75. *Euplassa* Salisb.

20 spp., widespread in tropical South America (Sleumer 1954: 185–196, Plana & Prance 1998, Prance et al. in press).

76. *Gevuina* Molina

One sp. (*G. avellana* Molina), Chile and Argentina (Sleumer 1954: 184–185, Prance et al. in press).

77. *Bleasdalea* F.Muell.

Two spp., NE Australia and New Guinea (Foreman 1995i: 225–228, Weston 1995e, as *Gevuina*).

Recent floristic treatments have placed these two Australasian species in a variety of genera, including *Turrillia* (Smith 1985) and *Gevuina* (Weston 1995). On the basis of morphology they seem to be closely related sister species. So far it has not been possible to obtain DNA of *B. papuana* but molecular systematic analyses (Weston, Barker and Downs unpublished) of *B. bleasdalei* do not strongly resolve its relationships to other genera of Gevuininae, other than to include it in a clade that excludes *Cardwellia.*

78. *Hicksbeachia* F.Muell.

Two spp., E Australia (Weston 1988).

79. *Kermadecia* Brongn. & Gris

Four spp., New Caledonia (Virot 1968: 78–101).

Weston and Crisp (1996) asserted, on the basis of floral morphology, that *K. pronyensis* is misplaced in *Kermadecia*. However, molecular systematic analyses (Weston, Barker and Downs unpublished) strongly group it with other species of *Kermadecia*.

80. *Turrillia* A.C.Sm.

Three spp., Vanuatu, Fiji (Smith & Haas 1975 as *Bleasdalea*, but omitting *B. papuana* and *B. bleasdalei*).

Recent taxonomic and floristic treatments have placed these three species in a variety of genera, including *Bleasdalea* (Smith & Haas 1975). On the basis of morphology they seem to form a clade of closely related species. So far it has been possible to obtain DNA of only *T. lutea* from Vanuatu and molecular systematic analyses (Weston, Barker and Downs unpublished) weakly group it with *Kermadecia.*

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References

Allan HH (1961) *Flora of New Zealand*, vol. 1. (Government Printer: Wellington)

Backlund A & Bremer K (1998) To be or not to be – principles of classification and monotypic plant families. *Taxon* 47: 391–400.

Baillon HE (1870) *Histoire des plantes. Monographie des Protéacées.* (L. Hachette et Cie: Paris)

Barker NP, Weston PH, Rourke JP & Reeves G (2002) The relationships of the southern African Proteaceae as elucidated by internal transcribed spacer (ITS) DNA sequence data. *Kew Bulletin* 57: 867–883.

Barker W, Haegi L & Barker R (1999) *Hakea*. Pp. 1–170 in Wilson A (ed.) *Flora of Australia*, vol. 17B. (CSIRO Publishing: Melbourne)

Beard JS (1992) *The proteas of tropical Africa.* (Kangaroo Press: Kenthurst)

Bennett EM (1995) *Conospermum*. Pp. 224–271 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Bieleski RL & Briggs BG (2005) Taxonomic patterns in the distribution of polyols within the Proteaceae. *Australian Journal of Botany* 53: 205–217.

Bininda-Emonds ORP (2003) Novel versus unsupported clades: assessing the qualtitative support for clades in MRP supertrees. *Systematic Biology* 52: 839–848.

Bininda-Emonds ORP (2004) The evolution of supertrees. *Trends in Ecology and Evolution* 19: 315–322.

Bininda-Emonds ORP, Gittleman JL & Steel MA (2002) The (super)tree of life: procedures, problems, and prospects. *Annual Review of Ecology and Systematics* 33: 265–289.

Briggs BG, Hyland BPM & Johnson LAS (1975) *Sphalmium*, a distinctive new genus of Proteaceae from North Queensland. *Australian Journal of Botany* 23: 165–172.

Bosser J & Rabevohitra R (1991) Protéacées. Pp. 47–69 in Morat P (ed.) *Flore de Madagascar et des Comores*, Familles 45, 57, 93, 94, 107. (Muséum National d'Histoire Naturelle: Paris)

Brummitt RK (1996) In defence of paraphyletic taxa. Pp. 371–384 in van der Maesen, LJG, van der Burgt XM & van Medenbach de Rooy JM (eds) *The biodiversity of African plants.* (Kluwer: Dordrecht)

Brummitt RK & Marner SK (1993) Proteaceae. Pp. 1–30 in Polhill RM (ed.) *Flora of Tropical East Africa*. (A.A. Balkema: Rotterdam)

Carpenter RJ, Hill RS & Jordan GJ (2005) Leaf cuticular morphology links Platanaceae and Proteaceae. *International Journal of Plant Sciences* 166: 843–855.

Catling DM & Gates PJ (1995) Leaf anatomy in *Hakea* Schrader (Proteaceae). *Botanische Jahrbucher fur Systematik Pflanzengeschichte und Pflanzengeographie* 117: 153–172.

Chung RCK (2002) Proteaceae. Pp. 169–201 in Soepadmo E, Saw LG & Chung RCK (eds) *Tree flora of Sabah and Sarawak*, vol. 4. (Forest Research Institute Malaysia: Selangor Darul Ehsan)

Collins BG & Rebelo T (1987) Pollination biology of the Proteaceae in Australia and southern Africa. *Australian Journal of Ecology* 12: 387–422.

Crisp MD & Weston PH (1995) *Telopea*. Pp. 386–390 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Douglas AW & Hyland BPM (1995) Subfamily Eidotheoideae. Pp. 127–129, 472–473 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Dettmann ME & Jarzen DM (1998) The early history of the Proteaceae in Australia: the pollen record. *Australian Systematic Botany* 11: 401–438.

Douglas AW (1995) Affinities. Pp. 6–14 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Douglas AW (1996) Inflorescence and floral development of *Carnarvonia* (Proteaceae). *Telopea* 6: 749–774.

Douglas AW & Tucker SC (1996a) Inflorescence ontogeny and floral organogenesis in Grevilleoideae (Proteaceae), with emphasis on the nature of the flower pairs. *International Journal of Plant Sciences* 157: 341–372.

Douglas AW & Tucker SC (1996b) The developmental basis of diverse carpel orientations in Grevilleoideae (Proteaceae). *International Journal of Plant Sciences* 157: 373–397.

Eaton A (1836) *Eaton's botanical grammar and dictionary, modernised down to 1836* (Oliver Steele: Albany)

Edwards KS & Prance GT (1993) New species of *Panopsis* (Proteaceae) from South America. *Kew Bulletin* 48: 637–662.

Endlicher SL (1837) *Genera Plantarum*, part 5. (Fr. Beck: Vienna)

Engler A (1888) *Die Natürlichen Pflanzenfamilien*, Teil III, vol. 2, fascicle 29. (Wilhelm Engelmann: Leipzig)

Entwisle TJ & Weston PH (2005) Majority rules, when systematists disagree. *Australian Systematic Botany* 18: 1–6.

Feuer S (1990) Pollen morphology of the Embothrieae (Proteaceae) II. Embothriinae (*Embothrium, Oreocallis, Telopea*). *Grana* 29: 19–36.

Foreman DB (1995a) *Petrophile*. Pp. 149–193 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Foreman DB (1995b) *Isopogon*. Pp. 194–223 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Foreman DB (1995c) *Triunia*. Pp. 404–407 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Foreman DB (1995d) *Xylomelum*. Pp. 399–403 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Foreman DB (1995e) *Helicia*. Pp. 393–399 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Foreman DB (1995f) *Floydia*. Pp. 417–419 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Foreman DB (1995g) *Stenocarpus*. Pp. 363–369 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Foreman DB (1995h) *Opisthiolepis*. Pp. 373–374 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Foreman DB (1995i) Proteaceae. Pp. 221–270 in Conn BJ (ed.) *Handbooks of the flora of Papua New Guinea*, vol. 3. (Melbourne University Press: Melbourne)

Foreman DB & Hyland BPM (1995) *Buckinghamia*. Pp. 371–373 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

George AS (1995a) *Franklandia*. Pp. 316–317 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

George AS (1995b) *Stirlingia*. Pp. 136–140 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

George AS (1995c) *Synaphea*. Pp. 271–315 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

George AS (1995d) *Orites*. Pp. 346–352 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

George AS (1999a) *Banksia*. Pp. 175–251 in Wilson A (ed.) *Flora of Australia*, vol. 17B. (CSIRO Publishing: Melbourne)

George AS (1999b) *Dryandra*. Pp. 251–363 in Wilson A (ed.) *Flora of Australia*, vol. 17B. (CSIRO Publishing: Melbourne)

George AS & Hyland BPM (1995) *Megahertzia*. Pp. 355, 497–498 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Goloboff PA (2005) Minority rule supertrees? MRP, compatability and minimum flip may display the least frequent groups. *Cladistics* 21: 282–294.

Gross CL (1995) *Macadamia*. Pp. 419–425 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Hennig W (1966) *Phylogenetic systematics*. (Illinois University Press: Urbana)

Hernandez G & Enrique L (1991) Revision de las especies Colombianas del genero *Panopsis* (Proteaceae). *Caldasia* 16: 459–484.

Hewson HJ (1995) *Neorites*. Pp. 352–353 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Hill RS, Scriven LJ & Jordan GJ (1995) The fossil record of Australian Proteaceae. Pp. 21–30 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Hnatiuk RJ (1995a) *Lambertia*. Pp. 425–436 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Hnatiuk RJ (1995b) *Strangea*. Pp. 360–363 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Hoot SB & Douglas AW (1998) Phylogeny of the Proteaceae based on *atp*β and *atp*β–*rbc*L intergenic spacer region sequences. *Australian Systematic Botany* 11: 301–320.

Hyland BPM (1995a) *Carnarvonia*. Pp. 343–345 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Hyland BPM (1995b) *Hollandaea*. Pp. 391–393 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Hyland BPM (1995c) *Darlingia*. Pp. 356–357 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Hyland BPM (1995d) *Cardwellia*. Pp. 358–359 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Hyland BPM (1999a) *Musgravea*. Pp. 170–172 in Wilson A (ed.) *Flora of Australia*, vol. 17B. (CSIRO Publishing: Melbourne)

Hyland BPM (1999b) *Austromuellera*. Pp. 173–175 in Wilson A (ed.) *Flora of Australia*, vol. 17B. (CSIRO Publishing: Melbourne)

Johnson LAS and Briggs BG (1975) On the Proteaceae — the evolution and classification of a southern family. *Botanical Journal of the Linnean Society* 70: 83–182.

Jussieu AL (1789) *Genera plantarum*. (Vidnam Herissant: Paris)

Kochummen KM (1973) Notes on the systematy of Malayan Phanerogams XXII. *Heliciopsis* (Proteaceae). *The Gardens' Bulletin Singapore* 26: 286–287.

Lee HM (1978) Studies of the family Proteaceae II. Further observations on the root morphology of some Australian genera. *Proceedings of the Royal Society of Victoria* 90: 251–256.

Levyns MR (1970) A revision of the genus *Paranomus* (Proteaceae). *Contributions from the Bolus Herbarium* 2: 3–48.

McDonald JA & Ismail R (1995) *Macadamia erecta* (Proteaceae), a new species from Sulawesi. *Harvard Papers in Botany* 7: 7–10.

Makinson RO (2000) *Grevillea*. Pp. 1–460 in Wilson AJG (ed.) *Flora of Australia*, vol. 17B. (CSIRO Publishing: Melbourne)

Mast AR (1998) Molecular systematics of the subtribe Banksiinae (*Banksia* and *Dryandra*; Proteaceae), based on cpDNA and nrDNA sequence data: implications for taxonomy and biogeography. *Australian Systematic Botany* 11: 321–342.

Mast AR & Givnish TJ (2002) Historical biogeography and the origin of stomatal distributions in *Banksia* and *Dryandra* (Proteaceae) based on their cpDNA phylogeny. *American Journal of Botany* 89: 1311–1323.

Meisner CF (1841) *Plantarum vascularium genera*, Fasc. 10. (Libraria Weidmannia: Leipzig)

Midgley JJ (1987) The derivation, utility and implications of a divergence index for the fynbos genus *Leucadendron* (Proteaceae). *Botanical Journal of the Linnean Society* 95: 137–152.

Nelson EC (1978) A taxonomic revision of the genus *Adenanthos* (Proteaceae). *Brunonia* 1: 303–406.

Nelson G & Platnick N (1981) *Systematics and biogeography: cladistics and vicariance*. (Columbia University Press: New York)

Nicolson SW & Van Wyk B-E (1998) Nectar sugars in Proteaceae: patterns and process. *Australian Journal of Botany* 46: 489–504.

Olde P & Marriott N (1994) *The Grevillea Book*, vol. 1. (Kangaroo Press: Kenthurst)

Olde P & Marriott N (1995a) *The Grevillea Book*, vol. 2. (Kangaroo Press: Kenthurst)

Olde P & Marriott N (1995b) *The Grevillea Book*, vol. 3. (Kangaroo Press: Kenthurst)

Pham HH (1992) Proteaceae. Pp. 82–114 in Morat P (ed.) *Flore du Cambodge du Laos et du Vietnam*, vol. 26. (Muséum National d'Histoire Naturelle: Paris)

Plana V & Prance GT (1998) A new species of *Euplassa* (Proteaceae) from Brazil. *Kew Bulletin* 53: 967–971.

Prance GT & Plana V (1998) The American Proteaceae. *Australian Systematic Botany* 11: 287–299.

Prance GT, Plana V, Edwards KS & Pennington RT (in press) Proteaceae. *Flora Neotropica*.

Rebelo AG (1995) *SASOL proteas: a field guide to the proteas of southern Africa* (Fernwood Press: Vlaeberg)

Reichenbach HG (1828) *Conspectus regni vegetabilis*. (Carolum Cnobloch: Leipzig)

Rourke JP (1969) Taxonomic studies on *Sorocephalus* R.Br. and *Spatalla* Salisb. *Journal of South African Botany*, Supplementary Volume 7: 1–124.

Rourke JP (1972) Taxonomic studies of *Leucospermum* R.Br. *Journal of South African Botany, Supplementary Volume* 8: 1–194.

Rourke JP (1976) A revision of *Diastella* (Proteaceae). *Journal of South African Botany* 42: 185–210.

Rourke JP (1980) *The proteas of southern Africa.* (Purnell: Cape Town)

Rourke JP (1984a) *Vexatorella* Rourke, a new genus of the Proteaceae from southern Africa. *Journal of South African Botany* 50: 373–391.

Rourke JP (1984b) A revision of *Mimetes* Salisb. (Proteaceae). *Journal of South African Botany* 50: 171–236.

Rourke JP (1987) The inflorescence morphology and systematics of *Aulax* (Proteaceae). *South African Journal of Botany* 53: 464–480.

Sankowsky G, Sankowsky N, Radke P & Radke A (1988) *A field guide to the rainforest Proteaceae of North Queensland*, 2nd edition. (published by the authors: Tolga & Walkamin)

Sleumer H (1954) Proteaceae americanae. *Botanischer Jahrbucher* 76: 139–211.

Sleumer H (1955a) Proteaceae. *Flora Malesiana* (series 1) 5: 147–206.

Sleumer H (1955b) Studies in Old World Proteaceae. *Blumea* 8: 1–95.

Smith AC (1985) *Flora Vitiensis nova: a new flora of Fiji (spermatophytes only).* (Pacific Tropical Botanical Garden: Lawai)

Smith AC & Haas JE (1975) Studies of Pacific island plants XXIX. *Bleasdalea* and related genera of Proteaceae. *American Journal of Botany* 62: 133–147.

Stace HM, Douglas AW & Sampson JF (1998) Did 'paleo-polyploidy' really occur in Proteaceae? *Australian Systematic Botany* 11: 613–629.

Stroeschen B (1986) Contributions to the biology of useful plants 6. Anatomical studies of fruit development and fruit classification of *Persoonia pinifolia* R.Br. *Angewandte Botanik* 60: 257–265.

Telford IRH (1995a) *Agastachys.* P. 131 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Telford IRH (1995b) *Symphionema.* Pp. 133–135 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Telford IRH (1995c) *Cenarrhenes.* Pp. 131–133 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Thiele K & Ladiges PY (1996) A cladistic analysis of *Banksia* (Proteaceae). *Australian Systematic Botany* 9: 661–733.

Venkata Rao C (1968) Studies in the Proteaceae XI. Morphology, floral anatomy and embryology of *Lambertia* Sm. with a discussion on the taxonomic position of the genus. *Proceedings of the Indian Academy of Science.* 48B: 11–24.

Venkata Rao C (1971) *Proteaceae.* (Council of Scientific & Industrial Research: New Delhi)

Virot R (1968) Protéacées. Pp. 5–254 in Aubreville A (ed.) *Flore de la Nouvelle Calédonie et Dépendances*, vol. 2. (Muséum National d'Histoire Naturelle: Paris)

Weston PH (1988) A revision of *Hicksbeachia* (Proteaceae). *Telopea* 3: 231–239.

Weston PH (1994) The Western Australian species of subtribe Persooniinae

(Proteaceae: Persoonioideae: Persoonieae). *Telopea* 6: 51–165.

Weston PH (1995a) Persoonioideae. Pp. 47–124, 471–472 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Weston PH (1995b) Bellendenoideae. Pp. 125–127, 472 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Weston PH (1995c) *Catalepidia.* Pp. 415–416, 499 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Weston PH (1995d) *Athertonia.* Pp. 413–415 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Weston PH (1995e) *Gevuina.* Pp. 408–410 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Weston PH & Johnson LAS (1997) *Persoonia hindii* (Proteaceae), a new species from the Newnes Plateau, New South Wales. *Telopea* 7: 199–203.

Weston PH (1999) *Persoonia pauciflora* (Proteaceae), a new species from the Hunter Valley, New South Wales. *Telopea* 8: 159–164.

Weston PH & Crisp MD (1991) *Alloxylon* (Proteaceae), a new genus from New Guinea and eastern Australia. *Telopea* 4: 497–507.

Weston PH & Crisp MD (1994) Cladistic biogeography of Waratahs and their allies (Embothrieae: Proteaceae) across the Pacific. *Australian Systematic Botany* 7: 225–249.

Weston PH & Crisp MD (1996) Trans-Pacific biogeographic patterns in the Proteaceae. Pp. 215–232 in: Keast A & Miller SE (eds) *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes* (SPB Academic Publishing: Amsterdam)

Weston PH & Kooyman RM (2002) Systematics of *Eidothea* (Proteaceae), with the description of a new species, *E. hardeniana*, from the Nightcap Range, north-eastern New South Wales. *Telopea* 9: 821–832.

White CT & Francis WD (1924) Contributions to the Queensland Flora. No. 2. *Proceedings of the Royal Society of Queensland* 35: 63–84.

Williams I (1972) A revision of the genus *Leucadendron* (Proteaceae). *Contributions from the Bolus Herbarium* 3: 1–425.

Wilson AJG, Hewson HJ & Mowatt J (1995) *Lomatia*. Pp. 374–382 in McCarthy P (ed.) *Flora of Australia*, vol. 16. (CSIRO Australia: Melbourne)

Wiltshire RJE & Stace HM (1997) The cytotaxonomy of four Tasmanian genera of Proteaceae. *Telopea* 7: 181–185.

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Pollen morphology of some rainforest taxa occurring in the Illawarra region of New South Wales, Australia

Phillip G. Kodela

National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney NSW 2000, Australia

Abstract

Pollen morphological descriptions and photographic illustrations based on light microscope analyses are provided for over 60 angiosperm taxa that occur in rainforest and wet sclerophyll forest communities in the Illawarra region of New South Wales. The resulting pollen taxonomy contributes to the study of Holocene mesotherm rainforest floras in coastal and tableland New South Wales and, because many species are or will have been shared with other vegetation types in the past, also to the floras of other botanical regions. Taxonomic relationships assessed on pollen morphology are discussed for several taxa.

Introduction

Pollen representing over 60 taxa occurring in rainforests and wet sclerophyll forests in the Illawarra region, including the Robertson–Moss Vale plateau and the Illawarra escarpment and coastal plain, were investigated and described. The aim was to assist the identification of pollen types found in moss/lichen cushions used in modern pollen rain studies (Kodela 1990a, b) and in swamp deposits investigating vegetation history of the region (Kodela 1992, 1996). Due to the under-representation of many rainforest taxa by their pollen it was important to be able to identify as many rainforest pollen types as possible in order to investigate the history and dynamics of the rainforest vegetation in the region. The morphological descriptions and illustrations will also be available for use in pollen flora keys, atlases and taxonomic studies. This study contributes to both neobotanical taxonomy and rainforest palaeoecology.

Methods

Modern reference pollen was obtained from flowers of plant specimens collected in the field or from herbarium material. Plant specimen vouchers are housed in the John T. Waterhouse Herbarium at the University of New South Wales (UNSW). The taxa investigated occur in the Illawarra region of New South Wales, however, the reference

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pollen representing these taxa have often been extracted from plant specimens collected from elsewhere in the State. An exception is *Cyclophyllum protractum*, which is a species occurring in northeastern Queensland.

Flowers or mainly just the anthers underwent standard hydroxide, acetolysis and alcohol dehydration treatments prior to mounting in silicone oil (Faegri & Iversen 1975, Moore & Webb 1978). Pollen morphological descriptions are based on features recognised at 500× and sometimes 1250× magnifications using a Wild Heerbrugg light microscope. Photographs of pollen grains were taken mainly at 500× magnification. Terminology used in the pollen descriptions follows Erdtman (1966, 1969), Faegri and Iversen (1975), Moore and Webb (1978) and Boyd (1992). Features characteristic of Myrtaceae pollen are also provided by Chalson and Martin (1995). A useful glossary of palynological terms is available on the web (Hoen et al. 1999). Nomenclature follows the *New South Wales FloraOnline* (http://plantnet.rbgsyd.nsw.gov.au/floraonline.htm).

A limitation of light microscope (LM) observations is the level of detail discernable for pollen grain surface sculpture and other features; detail that is available from SEM or TEM and often required for taxonomic studies. With LM it is often difficult to distinguish micro-projections versus micro-pits, and therefore define a sculpturing type. Ornamentation may not only be less distinct under LM but can appear different to the type of sculpture revealed by SEM analyses.

Features used in the pollen descriptions

Symmetry

Symmetric pollen grains may be radially symmetric (= radiosymmetric, with more than two vertical planes of symmetry and the equatorial axes equilong) or bilateral (with only two vertical planes of symmetry and the equatorial axes not equilong) (Erdtman 1966). Asymmetric grains are either fixiform or nonfixiform (without fixed shape).

Size

The size of pollen grains for a taxon may vary naturally, i.e. within flowers or between individual plants. Size may also be affected by the means of preservation, chemical treatments or the degree of pollen maturity. Impact of the mounting medium on size can be considerable, for example, grains mounted in silicon oil may be up to one third smaller than equivalent grains mounted in glycerol jelly (Drs A.H.R. Martin, formerly of University of Sydney, & M.K. Macphail, Australian National University, pers. comm.). Pollen grains tend to swell over time in the latter medium.

For radiosymmetric pollen types a minimum of 30 grains were measured for each taxon to calculate mean lengths and standard deviations of both the polar and equatorial axes. The longest axis was measured for most other pollen types. Qualitative descriptions for size follow Erdtman (1966) and are based on the length of the longest axis, not including appendages such as spines, i.e. very small: < 10 µm, small: 10–25 µm, medium: 25–50 µm, large: 50–100 µm, very large: 100–200 µm.

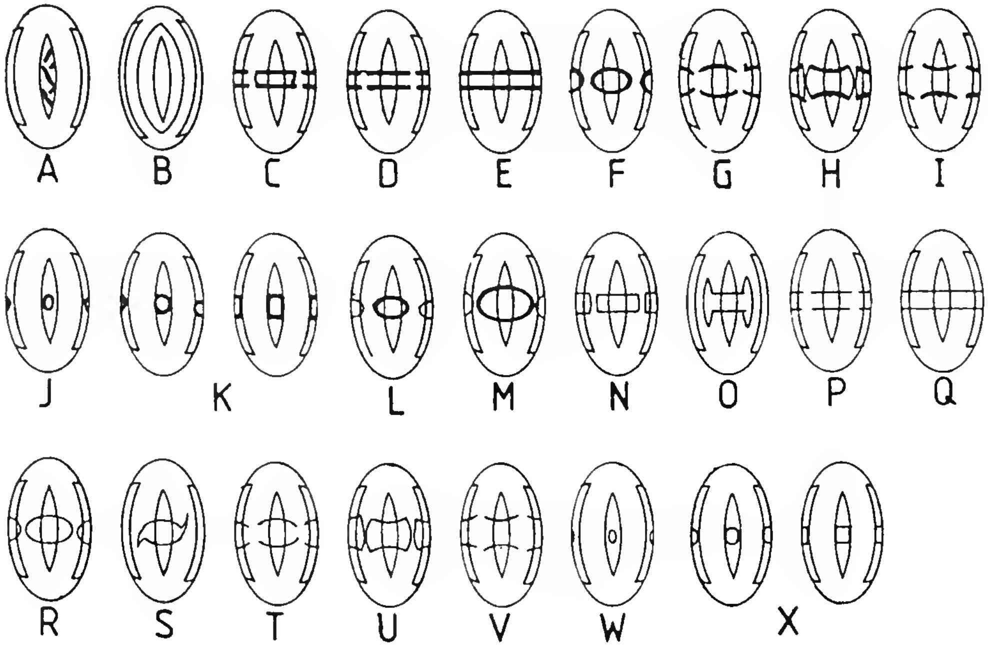

Fig. 1. Line illustrations of pollen grain apertures in equatorial view (from El Ghazali 1990)

A, endoapertures with endocracks; B, endoapertures meridionally elongated; C, endoapertures with parallel transverse costae, meridional edges encircling; D, endoapertures with parallel transverse costae, meridional edges lacking or indistinct; E, pollen grains with costae equatorialis; F, endoapertures with converging transverse costae, meridional edges encircling; G, endoapertures with converging transverse costae, meridional edges lacking or indistinct; H, endoapertures with diverging transverse costae, meridional edges encircling; I, endoapertures with diverging transverse costae, meridional edges lacking or indistinct; J, endoapertures with closed costae, diameter of endoapertures less than the width of the ectoapertures; K, endoapertures with closed costae, diameter of endoapertures ± equal to the width of the ectoapertures; L, endoapertures with closed costae, diameter of endoapertures broader than the width of the ectoapertures, length of endoapertures ≤ ½ the length of the ectoapertures; M, endoapertures with closed costae, diameter of endoapertures broader than the width of the ectoapertures, length of the endoapertures ≥ ⅔ the length of the ectoapertures; N, endoapertures with transverse parallel edges, meridional edges encircling, endoapertures rectangular; O, endoapertures with transverse parallel edges, meridional edges encircling, endoapertures H-shaped; P, endoapertures with transverse parallel edges, meridional edges lacking or indistinct; Q, pollen grains with colpus transversalis equatorialis; R, endoapertures with transverse converging edges, meridional edges encircling, without horns; S, endoapertures with transverse converging edges, meridional edges encircling, with horns; T, endoapertures with transverse converging edges, meridional edges lacking or indistinct; U, endoapertures with transverse diverging edges, meridional edges encircling; V, endoapertures with transverse diverging edges, meridional edges lacking or indistinct; W, endoapertures with closed edges, diameter of endoapertures less than the width of the ectoapertures; X, endoapertures with closed edges, diameter of endoapertures ± equal to the width of the ectoapertures.

Shape

The shapes of the polar and equatorial views of radiosymmetric tricolp(or)ate grains are described mainly following the scheme of Kuyl et al. (1955; see Fig. 1 in Faegri & Iversen 1975, p. 20). In prolate grains the polar axis (i.e. the axis of rotation) is greater than the equatorial axis while in oblate grains the equatorial axis is the longer axis. In spherical pollen grains both axes are ± equal. Radiosymmetric pollen grains described as oblate to prolate oval include spherical shapes. The above terms can be further divided according to the degree of eccentricity (ratio of polar axis length to equatorial axis length) (see Erdtman 1966), however this was not attempted given the variability of many taxa and the information already provided by the quantitative size data.

The term 'apiculate' is used to define pollen grains with somewhat abruptly and slightly protruding polar caps as illustrated by Kuyl et al. (loc. cit.), rather than other common uses of the term to refer to ending abruptly with a distinct, short, sharply pointed tip or having small pointed projections (= minutely echinate). 'Amb' refers to the outline shape of a grain in polar view.

Apertures

Pollen grains without apertures are referred to as inaperturate (= non-aperturate), while the terms pore, colpus and sulcus are used mostly in this study when describing apertures in aperturate grains. Colpi are elongated apertures (or furrows) where the length/breadth ratio is greater than two. A sulcus is another type of furrow and has the same general shape as a colpus, but differs in orientation, being an essentially latitudinal aperture situated at the distal or proximal pole whereas colpi are essentially longitudinal apertures (Hoen et al. 1999). Apertures are described by their position (polar, equatorial, global), shape, structure, size and number. The system described by Erdtman (1966) in which pores and furrows are differentiated according to their distribution and position was not applied here.

In radiosymmetric pollen grains apertures are normally arranged equally distanced around the equator, i.e. equidistantly and meridionally if colpi are present (Moore & Webb 1978). Pores are described as lalongate when they are equatorially (= transversely) elongated or lolongate when longitudinally (= meridionally) elongated. When two or more colpi meet at the poles the pollen grains are described as syncolpate. In some of the pollen descriptions endoapertures (often = pores) are defined using the coded letters from the scheme of El Ghazali (1990, p. 229; see Fig. 1). The term 'annulus' (adj. annulate) is used to refer to an area of the exine surrounding a pore that is sharply differentiated from the remainder of the exine, either in ornamentation or thickness (Hoen et al. 1999). When it is a thickening of the nexine bordering the pore it is called a costa.

Exine stratification

The exine refers to the chemically resistant outer layer of the wall of pollen and spores, and is primarily composed of sporopollenin. Various terms have been used to define the layers that make up the exine. Following Erdtman (1966), the inner, non-sculptured layer is the nexine lying below the outer, usually sculptured sexine. The sexine is usually stratified, consisting of sculpture elements on the outer surface of a layer called the tectum which overlies a layer of columellae (rod-like elements supporting the tectum) or a combination of these three layers. Layers in the sexine, such as the tectum, may be complete (continuous), partially present (discontinuous) or completely absent, resulting in characteristic surface patterns (sculpturing types). When a columellae layer is present the exine can be described as columellate. Further terms relating to the exine are defined within the text where they are relevant.

Sculpturing types (Ornamentation)

Differences in the exine structure, in the way various layers are structured and the elements arranged, are responsible for the different types of sculpture or ornamentation seen in pollen grains. The main terms used in this study to describe exine surface sculpturing follow Faegri and Iversen (1975) and Moore and Webb (1978) and include smooth or psilate, perforate (surface pitted with holes < 1 µm diam.), granulate or scabrate, striate, rugulate and reticulate ornamentation. Reticula are further defined as fine, medium or coarse when the lumina (i.e. the spaces between the muri or walls) are < 1 µm, 1–2 µm or > 2 µm wide, respectively. The ornamentation is microreticulate when the muri and lumina are smaller than 1 µm.

When pollen grains have projections or spines these may be: rod-shaped where the elements are of even thickness and longer than broad (baculate); wart-like where the elements are equal or broader than high and not constricted at the base (verrucate); club-shaped where the elements are longer than broad and narrowed towards their base (clavate); drumstick-shaped with a short shaft and swollen top (pilate); short, globular and basally constricted (gemmate); or sharply pointed (echinate). Echinae are referred to as spinules when they are ≤ 3 µm long or spines when > 3 µm long.

Results

Pollen descriptions are provided in alphabetical order by family, genus and species. Features that are less common and may represent extremes of range are given in brackets. Exine sculpturing types are based mainly on appearance under LM. Key to abbreviations: S = qualitative size based on longest axis; EV = shape in equatorial view; PV = shape in polar view; σ = one standard deviation; *n* = sample number of pollen grains measured.

Adoxaceae

Sambucus australasica (Lindl.) Fritsch Fig. 2a

(2)3-colporate, isopolar, radiosymmetric. S: small (to medium); EV (oblate to) prolate oval; PV circular to inter-hexagonal, colpi intruding to open; colpi constricted equatorially, the pores inconspicuous, slightly protruding; exine 0.5–0.8(–1) µm thick, finely reticulate. Polar axis, mean value: 20.1 µm, σ = 1.5 µm, range 18.0–21.6(–25.2) µm; equatorial axis, mean value: 18.9 µm, σ = 1.5 µm, range 17.4–20.4(–25.2) µm; *n* = 31.

Voucher: Mt Keira near Scout Camp, 15 May 1975, *Howard & Quinn* (UNSW5325).

Note: *Sambucus* is sometimes placed in the family Caprifoliaceae or Sambucaceae.

Anacardiaceae

Euroschinus falcatus Hook.f. Fig. 2b

3-colporate, isopolar, radiosymmetric. S: medium; EV prolate oval; PV semi-angular to circular, colpi open; apertures with ragged margins, endoapertures D (or G), the pores lalongate, ± oblong, usually exceeding the colpi rims, 3–5(–8.4) µm long, 7.2–12 µm wide; colpi maintain ± even width until reaching polar areas where they have obtuse, often poorly defined apices, the colpus membrane ± smooth; exine < 1.5 µm thick at equator, slightly thicker (i.e. 2–2.5 µm) at poles, 2.4–3.6 µm thick at pores, distinctly columellate, with a medium reticulum becoming slightly coarser at poles. Polar axis, mean value: 30.1 µm, σ = 1.5 µm, range (26.4–)28.8–32.4 µm; equatorial axis, mean value: 25.7 µm, σ = 1.8 µm, range 22.8–28.8 µm; *n* = 30.

Voucher: Treachery Headland, 6 Dec 1983, *Adam* (UNSW16403).

Aphanopetalaceae

Aphanopetalum resinosum Endl. Fig. 2c

(2)3-colpor(oid)ate (often appears tricolpate due to poorly defined pores), isopolar, radiosymmetric; S: small; EV (oblate to) prolate oval; PV semi-angular with convex sides to ± circular, colpi open; endoapertures X_l (or W), pores ± indistinct, the colpi slightly constricted at equator; exine 0.8–1 µm thick, smooth to faintly or vaguely granulate-rugulate. Polar axis, mean value: 19.6 µm, σ =1.1 µm, range 17.4–21.6 µm; equatorial axis, mean value: 17.0 µm, σ = 1.1 µm, range (13.8–)15.6–19.2 µm; *n* = 32.

Voucher: behind Oaky Beach, 24 Nov 1983, *Więcek & Stricker* (UNSW15520).

Polar axis, mean value: 17.4 µm, σ = 1.4 µm, range (13.8–)15.6–19.2 µm; equatorial axis, mean value: 15.1 µm, σ = 1.1 µm, range 12.0–17.4 µm; *n* = 30.

Voucher: Tantawangalo State Forest, near Bega, Oct 1987, *Kodela* (UNSW).

Notes: *Aphanopetalum* was previously placed in Cunoniaceae. The larger, usually 3-colporate pollen of *A. resinosum* differs from the small to very small, 2-colporate pollen of Cunoniaceae species examined in this study. This finding supports anatomical and molecular studies which excluded *Aphanopetalum* from Cunoniaceae (Dickison et al. 1994, Bradford & Barnes 2001, Fishbein et al. 2001, Hilu et al. 2003).

Apocynaceae

Parsonsia brownii (Britten) Pichon Fig. 2d

(2)3(4)-porate, apolar. S: small to medium; shape spheroidal to ellipsoidal; pores ± circular to elliptical, annulate with a raised rim-like border, the annuli c. 1 µm wide and often fragmented, the orifice (2.4–)3.6–6.6(–7.2) µm in diam.; exine 0.6–0.9 µm thick, 1.8–2.4(–3) µm thick around pores, smooth or often finely wrinkled. Longest axis, mean value: 28.9 µm, σ = 3.1 µm, range (16.8–)21.6–34.2(–36.0) µm; *n* = 60.

Voucher: near Wingecarribee Swamp, Robertson, 10 Feb 1986, *Kodela* (UNSW).

Notes: an obscure shallow surface pattern appears at higher magnifications. See also Sampson and Anusarnsunthorn (1990).

Parsonsia straminea (R.Br.) F.Muell. Fig. 2e

3- or 4-porate, occasionally with 5 or 6 pores, apolar. S: medium; shape spheroidal to ellipsoidal; pores ± circular to elliptical, annulate, the annuli usually fragmented and with irregular outline, the orifice 2.4–6.6 µm in diam.; exine 0.5–0.8 µm thick, 1.8–2.4(–3) µm thick at pores, almost smooth, appearing finely wrinkled especially at higher magnification when the surface may appear vaguely granulate to shallowly rugulate. Longest axis, mean value: 32.7 µm, $\sigma = 3.5$ µm, range 26.4–40.2 µm; $n = 30$.

Notes: pollen sample from Minnamurra Estuary (no voucher). Smaller, 17.4–25.2 µm diam., 2- or 3-porate, darker, possibly immature grains were observed. See also Sampson and Anusarnsunthorn (1990).

Araceae

Gymnostachys anceps R.Br. Fig. 3a

1-sulcate (= monosulcate). S: small to medium; shape variable, ± boat-shaped to ellipsoidal; sulcus with ragged margins; exine 0.8–1 µm thick, minutely and distinctly reticulate, becoming finer near sulcus margins. Polar axis, mean value: 18.3 µm, $\sigma = 2.4$ µm, range (13.2–)15.6–21.6(–24.0) µm; longitudinal equatorial axis (following furrow), mean value: 25.6 µm, $\sigma = 2.1$ µm, range (20.4–)24.0–27.6(–31.2) µm; $n = 30$.

Voucher: Bola Creek, Royal National Park, 27 Mar 1958, *Evans & Blaxell* (UNSW).

Bignoniaceae

Pandorea pandorana (Andrews) Steenis Fig. 3b

(2)3-colpate, isopolar, radiosymmetric. S: medium; EV oblate to prolate oval; PV circular to rounded inter-hexagonal, colpi open; colpi high on the poles with acute apices almost meeting, mostly 2.5–7(–12) µm wide at equator, colpus membrane often with ladder-like arrangement of rupture patterns (i.e. endoapertures with endocracks = A in Fig. 1); exine 0.8–1.3(–1.5) µm thick, with distinct medium reticulum, becoming finer towards colpi. Polar axis, mean value: 28.4 µm, $\sigma = 1.6$ µm, range 25.2–30.6(–33.6) µm; equatorial axis, mean value: 27.4 µm, $\sigma = 2.1$ µm, range 22.8–30.0(–32.4) µm; $n = 39$.

Voucher: North Wilson Camp, Mount Boss State Forest, 26 Aug 1975, *Waterhouse* (UNSW4444).

Notes: abnormal, syncolpate (mostly 2-colpate) grains were observed. See also Suryakanta (1973, *n.v.*), Buurman (1977) and James and Knox (1993).

Boraginaceae

Ehretia acuminata R.Br. Fig. 3c

3(4)-colporate, isopolar, radiosymmetric. S: small; EV spherical to slightly oblate or prolate oval; PV inter-hexagonal with ± straight to slightly convex or sometimes concave sides; aperture margins ragged, the pores lalongate, conspicuous when elliptical or may be indeterminable where constriction of colpus occurs at the equator; exine c. 1 µm thick, with fine to medium reticulum. Polar axis, mean value: 20.8 µm, σ = 1.5 μm, range 18.0–24.0 μm; equatorial axis, mean value: 19.9 μm, σ = 2.1 μm, range (10.8–)18.0–23.4 μm; *n* = 31.

Voucher: Dyke Forest on the Dyke River, Kempsey–Armidale road, 14 Nov 1978, *Hindmarsh & Waterhouse* (UNSW8036).

Note: *Ehretia* is sometimes placed in the family Ehretiaceae.

Celastraceae

Celastrus australis Harv. & F.Muell. Fig. 3d

(2)3(4)-colporate, isopolar, radiosymmetric. S: small to medium; EV oblate to prolate oval; PV circular, colpi open; endoapertures K_1, the pores conspicuous, mostly confined within the margins of colpi, lalongate, ± elliptical, 1.5–3(–3.6) μm long, 3.1–4.2(–5) μm wide, the colpi tapering with conspicuous margins to acute or obtuse apices, the colpus membrane ± smooth; exine 1.3–1.8 μm thick, sometimes thicker (to 2.6 μm) at the poles, distinctly columellate, with a distinct fine to medium reticulum, becoming finer near colpi. Polar axis, mean value: 22.4 μm, σ = 2.4 μm, range (18.0–)20.4–24.0(–31.8) μm; equatorial axis, mean value: 21.7 μm, σ = 2.5 μm, range 18.0–24.0(–30.0) μm; *n* = 30.

Voucher: 3.5 km S of Albion Park on the road to Jamberoo, 23 Nov 1982, *Hindmarsh & Waterhouse* (UNSW11583).

Polar axis, mean value: 18.8 μm, σ = 1.5 μm, range 16.2–21.6 μm; equatorial axis, mean value: 19.1 μm, σ = 1.8 μm, range (14.4–)16.2–21.6(–23.4) μm; *n* = 30.

Voucher: downhill of 'Sunny View', S of East Kangaloon, 17 Nov 1987, *Kodela* (UNSW).

Cunoniaceae

Ceratopetalum apetalum D.Don Fig. 4a

2-colporate, isopolar, bilateral. S: very small to small; shape ± ellipsoidal with an encircling groove where longitudinal colpi intrude; pores minute, inconspicuous, mostly defined by small protrusions at the equator; colpi almost meet at poles; exine 0.5–0.6 μm thick, finely reticulate (to rugulate), smooth near colpi. Longest axis, mean value: 9.9 μm, σ = 1.1 μm, range 8.4–12.0 μm; *n* = 30.

Voucher: Rocky Ck Crossing, Gordon, 17 Nov 1977, *Waterhouse* (UNSW5076).

Notes: *Ceratopetalum* has very similar pollen to *Bauera* species (formerly in Baueraceae), *Callicoma serratifolia*, *Eucryphia moorei* (formerly in Eucryphiaceae) and *Schizomeria ovata*. Pollen morphology supports a phylogenetic study of molecular and morphological data by Bradford and Barnes (2001) which places these genera together in Cunoniaceae.

Eucryphia moorei F.Muell. Fig. 4b

2-colp(or)ate, isopolar, bilateral. S: very small; shape ± ellipsoidal with narrow grooves where longitudinal colpi intrude, the colpi almost meeting at the poles, with some grains appearing ± syncolpate, the pores minute, inconspicuous, absent or appear as very slight protrusions; exine c. 0.5 µm thick, very finely reticulate, the pattern disappearing towards the colpi. Longest axis, mean value: 6.7 µm, σ = 0.4 µm, range 6–7.8 µm; n = 52.

Voucher: Milo Rd, via Milo via Princes Hwy, Ulladulla/Batemans Bay, 18 May 1983, *Bruhl & Wood* (UNSW14737).

Notes: the pollen of *Eucryphia moorei* is relatively smaller with more obscure pores and surface ornamentation than *Ceratopetalum apetalum* pollen. Pollen morphology is consistent with molecular studies (Bradford & Barnes 2001) which place *Eucryphia* in Cunoniaceae rather than Eucryphiaceae.

Schizomeria ovata D.Don Fig. 4c

2-colporate, isopolar, bilateral. S: very small to small; shape ± ellipsoidal with longitudinal grooves where colpi intrude; pores distinctly protrude at the equator, oblong or irregularly shaped when open, to 2 µm long; colpi taper and almost meet at poles, the colpus membrane smooth; exine c. 0.5 µm thick, finely reticulate (to rugulate), becoming obscure and then smooth before reaching the colpi margins. Longest axis, mean value: 9.8 µm, σ = 0.6 µm, range 8.4–11.4 µm; n = 30.

Voucher: Dog Trap Rd, 8.9 km E from Central Mangrove road, 8 Nov 1978, *Waterhouse & Quinn* (UNSW7874).

Note: the pores and surface ornamentation in pollen of *Schizomeria ovata* are more pronounced than in *Ceratopetalum apetalum*.

Dilleniaceae

Hibbertia scandens (Willd.) Gilg Fig. 4d

3-colporate, isopolar, radiosymmetric. S: small; EV (oblate to) prolate oval; PV circular, colpi open; endoapertures ± X_2, the pores lolongate, oblong to narrowly oblong, not exceeding margins of the colpi, (4–)6–11 µm long, 2–6 µm wide, open or with a rough membrane; colpi with ragged margins, ± smooth membrane except where pores occur, tapering to acute apices; exine 1.3–1.5 µm thick, distinctly columellate, with a fine (to medium) reticulum. Polar axis, mean value: 17.9 µm, σ = 1.2 µm, range 15.6–20.4 µm; equatorial axis, mean value: 16.3 µm, σ = 0.9 µm, range 14.4–18.6 µm; n = 32.

Voucher: Liguria Street, Lurline Bay, Coogee, 3 Nov 1981, *Francis & Więcek* (UNSW12730).

Polar axis, mean value: 19.6 µm, σ = 1.1 µm, range 16.8–22.2 µm; equatorial axis, mean value: 18.6 µm, σ = 2.2 µm, range 15.0–24.0 µm; n = 35.

Voucher: Robertson Cemetery, 9 Feb 1988, *Kodela* (UNSW).

Note: the pore length:width ratio varies, often being 2:1, 3:1 or 4:1 and ratios intermediate between these.

Ebenaceae

Diospyros australis (R.Br.) Hiern. Fig. 4e

3-colporate, isopolar, radiosymmetric. S: medium; EV prolate oval; PV circular to rounded inter-hexagonal, colpi open; endoapertures D, the pores lalongate, exceeding margins of the colpi; colpi narrow, with granulate membrane, the margins and apices distinct; exine c. 1 µm thick (1.2–2.4 µm thick at pores), smooth to minutely scabrate. Polar axis, mean value: 36.9 µm, σ = 2.0 µm, range 33.0–40.8 µm; equatorial axis, mean value: 29.7 µm, σ = 1.3 µm, range 27.0–32.4 µm; *n* = 31.

Voucher: Mungo Brush, 20 Jan 1977, *Hindmarsh & Waterhouse* (UNSW6404).

Elaeocarpaceae

Elaeocarpus reticulatus Sm. Fig. 4f

3-colporate, isopolar, radiosymmetric. S: very small to small; EV prolate oval to almost circular; PV circular, colpi intruding; pores minute, slightly protruding; exine c. 0.5 µm thick, smooth. Polar axis, mean value: 8.7 µm, σ = 0.8 µm, range 7.2–10.2 µm; equatorial axis, mean value: 7.9 µm, σ = 0.5 µm, range 7.2–9.6 µm; *n* = 35.

Voucher: Hotel Ck Rd, Wallingat State Forest, 5 Dec 1981, *Francis & Więcek* (UNSW12750).

Euphorbiaceae

Baloghia inophylla (G.Forst.) P.S.Green Fig. 4g
(syn. *Baloghia lucida* Endl.)

Inaperturate, apolar. S: medium; shape ± spheroidal to ellipsoidal; exine 2–2.6 µm thick; very coarsely reticulate with the 'croton pattern', which is described by Erdtman (1966, p. 173) and Lieux (1983, p. 345). Longest axis, mean value: 33.0 µm, σ = 2.6 µm; range 27.6–37.2 µm; *n* = 37.

Voucher: Fountaindale Rd, on Saddleback Mountain, 25 Jan 1978, *Hindmarsh & Waterhouse* (UNSW7697b).

Breynia oblongifolia Muell.Arg. Fig. 5a

8-colpate with 1 or 2 pores in each colpus (occasionally 3 or no pores in some colpi). S: small; EV slightly oblate oval; PV circular, colpi slightly intruding; endoapertures L, the pores annulate, ± circular with an orifice c. 1.5 µm in diam., often arranged irregularly and not located on equator, annuli smooth, the colpi ± closed, with distinct margins; exine 1.3–1.5 µm thick, with a distinct medium reticulum. Polar axis, mean value: 20.2 µm, σ = 0.7 µm, range 19.2–21.6 µm; equatorial axis, mean value: 21.7 µm, σ = 0.8 µm, range 20.4–23.4 µm; *n* = 30.

Voucher: Diamond Hill, at the junction of Blue Gum and Little Wheeney Creeks, Kurrajong, 13 Nov 1978, *Quinn* (UNSW7767).

Note: pollen of *Breynia* and related genera in Euphorbiaceae are described by Sagun and van der Ham (2003).

Homalanthus populifolius Graham Fig. 5b
(syn. *Omalanthus populifolius* Graham)

3-colporate, isopolar, radiosymmetric. S: medium; EV oblate to prolate oval, often ± spherical; PV inter-subangular, colpi intruding to open; endoapertures D, the pores lalongate, oblong or elliptical, 1.8–3.6 µm long, 8.4–12.6 µm wide, the colpi narrow, tapering to pointed apices; exine 2–2.6 µm thick, usually thicker (to 3.1 µm) at the poles, finely reticulate (to rugulate). Polar axis, mean value: 33.0 µm, σ = 1.5 µm, range 29.4–36.0 µm; equatorial axis, mean value: 32.8 µm, σ = 1.5 µm, range 30.0–36.0 µm; *n* = 34.

Voucher: Scarborough Beach, 9 Nov 1982, *Więcek & Stricker* (UNSW14160).

Flacourtiaceae

Scolopia braunii (Klotzsch) Sleumer Fig. 5c

3-colporate, isopolar, radiosymmetric. S: small; EV prolate oval; PV circular, colpi intruding to open; endoapertures W, the pores very small, 1–2.5 µm long, indistinct, the colpi equatorially constricted; exine c. 1 µm thick, with a very fine reticulum. Polar axis, mean value: 17.1 µm, σ = 1.2 µm, range 14.4–19.8 µm; equatorial axis, mean value: 12.0 µm, σ = 1.0 µm, range 10.2–13.8 µm; *n* = 42.

Voucher: Cape Hawke, 7 Dec 1981, *Waterhouse & Quinn* (UNSW12839).

Lauraceae

Cryptocarya glaucescens R.Br. Fig. 5d

Inaperturate, apolar. S: small to medium; shape ± spheroidal, often irregularly shaped due to wrinkling and folding, very thin-walled, the exine ≤ 0.5 µm thick, smooth (may appear striated due to wrinkling). Longest axis, mean value 24.1 µm, σ = 2.2 µm, range 19.2–28.8 µm; *n* = 44.

Voucher: Ourimbah Ck Rd, 9 km from turn-off from Pacific Hwy, 17 Oct 1975, *Waterhouse & Hindmarsh* (UNSW5055a, b).

Note: Sampson (2000) provides a synopsis of Lauraceae pollen.

Cryptocarya microneura Meisn. Fig. 5e

Shape and exine features similar to those of *Cryptocarya glaucescens*. Longest axis, mean value: 28.6 µm, σ = 2.8 µm, range 21.6–34.8 µm; *n* = 39.

Voucher: Ourimbah Ck Rd, 1.6 km from turn-off, 17 Oct 1975, *Waterhouse & Hindmarsh* (UNSW4475b).

Endiandra sieberi Nees Fig. 5f

Inaperturate, apolar. S: small to medium; shape ± spheroidal to ellipsoidal, often irregularly shaped due to folding; exine < 1 µm thick, the surface echinate with spinules to 1.3 µm but mainly < 1 µm high, smooth between spinules. Longest axis, mean value: 25.4 µm, σ = 3.2 µm, range (16.8–)22.8–31.2 µm; *n* = 46.

Voucher: Bass Point, 21 Jul 1983, *Adam, Więcek & Stricker* (UNSW15128).

Neolitsea dealbata (R.Br.) Merr. Fig. 5g

Inaperturate, apolar. S: small (to medium); shape spheroidal to ellipsoidal, often folded and/or wrinkled; very thin-walled, the exine c. 0.5–0.8 µm thick, minutely echinate with spinules to c. 1 µm high (sometimes with short baculae). Longest axis, mean value: 20.8 µm, σ = 2.3 µm, range 16.8–25.2 µm; *n* = 55.

Voucher: Narara Ck, Ourimbah, 22 May 1958, *Evans & Blaxell* (UNSW).

Luzuriagaceae

Eustrephus latifolius R.Br. ex Ker Gawl. Fig. 6a

Trichotomosulcate (the trifid furrow occurring as a 3-armed slit opening on the proximal face), heteropolar. S: small to medium; shape of amb triangular with straight or very slightly concave or convex sides and rounded, obtuse angles that are slightly notched where the furrow intrudes, the distal face rounded convex, the proximal face concave to convex, the trifid furrow often open; exine 0.5–0.6 µm thick, finely reticulate to rugulate-reticulate. Polar axis, mean value: 14.0 µm, σ = 1.4 µm, range 10.8–16.8 µm; equatorial axis, mean value: 24.5 µm, σ = 1.5 µm, range 21.6–27.0 µm; *n* = 30; base of amb to angle, mean value: 22.5 µm, σ = 1.5 µm, range 19.8–25.8 µm; *n* = 42.

Voucher: Hotel Ck Rd, 1 km outside Wallingat State Forest, 5 Dec 1981, *Więcek & Francis* (UNSW12752).

Note: *Eustrephus* is sometimes placed in the family Philesiaceae.

Geitonoplesium cymosum (R.Br.) A.Cunn. ex Hook. Fig. 6b

Trichotomosulcate, heteropolar. S: small to medium; shape of amb triangular with straight or slightly convex or concave sides and broadly rounded, obtuse angles that are often slightly notched where the furrow intrudes; trifid furrow often open; exine c. 0.8 µm thick, finely reticulate to rugulate-reticulate. Base of amb to angle, mean value: 21.9 µm, σ = 1.5 µm, range 19.2–24.0 µm; *n* = 30.

Voucher: Dog Trap Rd, 8.9 km E from Central Mangrove Rd, 13 Oct 1978, *Waterhouse & Hindmarsh* (UNSW7743).

Notes: the pollen surface ornamentation of *Geitonoplesium cymosum* is finer than that of *Eustrephus latifolius*. Erdtman (1966, p. 240) describes pollen from a specimen of *G. cymosum* from New Caledonia as being monosulcate and distinctly reticulate while pollen from an Australian specimen was trichotomosulcate with a ± obscure pattern. The pollen sample investigated in this survey was clearly trichotomosulcate and was distinctly ornamented. *Dianella* pollen grains and the pollen of some other liliaceous taxa (Liliaceae s. lat.) are very similar to Luzuriagaceae pollen. *Geitonoplesium* is sometimes placed in the family Philesiaceae.

Meliaceae

Synoum glandulosum (Sm.) A.Juss. Fig. 6c

4-colporate, isopolar, radiosymmetric. S: medium; EV spherical to slightly prolate oval (sometimes ± depressed oval when the sides are slightly flattened); PV obtuse straight-convex quadrangular (Moore & Webb 1978); endoapertures L or F, the pores lalongate, ± elliptical, exceeding margins of the colpi, 1.8–3 μm long, 4.2–6.6 μm wide, the nexine markedly thickened around pores (i.e. costate), the colpi narrow, with rough margins, not reaching the poles, sometimes diagonal; exine 1–1.5 μm thick (3.6–4.1 μm thick at pores), (smooth to) granulate. Polar axis, mean value: 27.6 μm, $\sigma = 1.5$ μm, range 25.2–31.2 μm; equatorial axis, mean value: 26.4 μm, $\sigma = 1.9$ μm, range 24.0–31.8 μm; $n = 31$.

Voucher: Scotchman Range, S of Bellingen, 17 Jun 1985, *Kodela & Dodson* (UNSW).

Toona ciliata M.Roem. Fig. 6d
(syn. *T. australis* (F.Muell.) Harms)

(3)4-colporate, isopolar, radiosymmetric. S: small; EV circular to slightly prolate oval (often ± depressed or compressed oval, i.e. poles or sides slightly flattened), rarely oblate; PV circular or broadly rounded quadrangular inter-hexagonal, with colpi intruding to open; endoapertures K or L, the pores often lalongate, circular to elliptical or oblong, within or slightly exceeding width of colpi, 1.2–2.4 μm long, 2.4–3.6(–6) μm wide, distinctly costate, the colpi narrow, tapering to acute or obtuse ends not reaching the poles, the colpus membrane slightly granulate; exine to c. 1 μm thick (1.8–2.0 μm thick at pores), smooth, though slightly granulate near colpi margins. Polar axis, mean value: 21.0 μm, $\sigma = 2.4$ μm, range (14.4–)18.0–24.0 μm; equatorial axis, mean value: 20.0 μm, $\sigma = 2.5$ μm, range (13.8–)16.8–23.4 μm; $n = 34$.

Voucher: Dykes Forest on the Dyke River, Kempsey to Armidale road, 14 Nov 1978, *Hindmarsh & Waterhouse* (UNSW8037).

Notes: pores may be torn-like (and ragged) when exceeding the colpi margins. *Toona ciliata* pollen differs from *Synoum glandulosum* grains in the polar view being less angled with the apertures intruding more deeply into the angles, as well as generally being smaller and thinner-walled.

Menispermaceae

Legnephora moorei (F.Muell.) Miers Fig. 7a

3(4)-colporate, isopolar, radiosymmetric. S: small; EV prolate oval; PV circular with intruding colpi; pores often slightly lolongate, circular to elliptical, exceeding the ± closed faint colpi, 2–3 μm long, 1–2 μm wide; exine 0.8–1.0 μm thick, distinctly columellate, very finely reticulate. Polar axis, mean value: 17.6 μm, $\sigma = 1.2$ μm, range 15.6–19.8(–21.6) μm; equatorial axis, mean value: 15.8 μm, $\sigma = 1.1$ μm, range 14.4–18.6 μm; $n = 30$

Voucher: Seal Rocks opposite the Post Office, 23 Feb 1981, *Quinn & Waterhouse* (UNSW10400).

Note: see also Erdtman (1966, p. 270).

Sarcopetalum harveyanum F.Muell. Fig. 7b

3-colporate, isopolar, radiosymmetric. S: small; EV prolate oval; PV circular with intruding colpi; pores conspicuous, often slightly lolongate, circular to elliptical, the orifice 1.8–2.6 μm long, 1–2 μm wide, the colpi with ± conspicuous margins and pointed apices almost meeting at the poles; exine 0.8–1.0 µm thick, very finely reticulate. Polar axis, mean value: 13.5 µm, σ = 0.6 µm, range 12.6–14.4 µm; equatorial axis, mean value: 11.2 µm, σ = 0.6 µm, range 10.2–12.0 µm; *n* = 31.

Voucher: Cattai Creek, Cattai, 13 Nov 1963, *Blaxell* (UNSW).

Stephania japonica var. ***discolor*** (Blume) Forman Fig. 7c

3-porate, isopolar, radiosymmetric. S: small; EV oblate oval; PV circular to semi-angular (slightly rounded triangular); pores lalongate to lolongate, circular to elliptical (often appearing slit-like at lower magnification), with ragged margins, 1.5–2.5 µm long, c. 1 µm wide; exine 1.3–1.5 µm thick, with fine (to medium) reticulum. Polar axis, mean value: 11.7 µm, σ = 0.5 µm, range 10.2–12.0 µm; equatorial view, mean value: 13.7 µm, σ = 0.6 µm, range 12.0–14.4 µm; *n* = 30.

Voucher: Mungo Brush, 20 Jan 1977, *Hindmarsh & Waterhouse* (UNSW5983).

Monimiaceae s. lat.

Doryphora sassafras Endl. Fig. 7d

2-sulcate, isopolar, bilateral. S: medium to large; shape variable, (± spheroidal to) ellipsoidal; furrows open or with granulate membrane, the margins often torn-like and ragged when furrows open, the ends almost meeting (sometimes the grains syncolpate); exine 1.5–2 µm thick (sexine thicker than nexine), thinning towards margins of furrows, columellate, with a fine to medium reticulum becoming finer and disappearing towards furrow margins. Axis following the furrows (usually the longest axis), mean value: 43.2 µm, σ = 3.9 µm, range 34.8–52.8 µm; width, mean value: 37.1 µm, σ = 3.9 µm, range (25.2–)30–42 µm; *n* = 40.

Notes: pollen sample from Jamberoo Mountain road below Barren Grounds (no voucher). Sampson and Foreman (1988) describe the two elongated apertures being centred and widest at the poles and tapering at their ends, to terminate, without meeting, near the equator of the grain. As well as having disulcate pollen with the above type of aperture, *Doryphora sassafras* can have meridionosulcate pollen where there is a median encircling aperture that narrows markedly or slightly in two regions opposite one another near the equator of the grain (Sampson 2000). See also Erdtman (1966, p. 271), and a synopsis of pollen of Monimiaceae s. lat. by Sampson (2000). *Doryphora* is sometimes placed in the family Atherospermataceae.

Hedycarya angustifolia A.Cunn. Fig. 7e

Inaperturate, acalymmate tetrads (the sexine of each monad is well differentiated, but does not form a single continuous envelope around the tetrad unit). S: medium. Pollen in permanent tetrads, usually with isobilateral (tetragonal) or decussate arrangement, sometimes T-shaped or intermediate between these types. Exine thin (c. 0.5 µm thick), finely granulate; under SEM the exposed surfaces of the grains have a verrucose warty configuration (Sampson 1997). Polar axis, mean value: 26.3 µm, σ = 2.5 µm, range 20.4–30.0 µm; longitudinal equatorial axis, mean value: 34.7 µm, σ = 2.5 µm, range (27.6–)31.8–36.0(–40.8) µm; transverse equatorial axis, mean value: 31.3 µm, σ = 2.0 µm, range 27.6–36.0 µm; *n* = 30.

Voucher: Mt Tomah, Blue Mtns, near Bells Line of Road, 4 Oct 1982, *Winterhalder* (UNSW13985).

Notes: Sampson (1997) reports 37–44 µm diameter tetragonal tetrads (measured along the polar axis). See also Sampson (1977, 1982) and Foreman and Sampson (1987).

Palmeria scandens F.Muell. Fig. 7f

Inaperturate, apolar. S: small to medium; shape ± spheroidal, grains often folded; echinate with spinules to c. 1 µm long; exine c. 0.5 µm thick. Longest axis (± equal to diam.), mean value: 24.1 µm, $\sigma = 3.0$ µm, range 18.0–32.4 µm; $n = 30$.

Notes: Pollen sample from Dorrigo National Park (no voucher). See also Foreman and Sampson (1987), Sampson and Foreman (1990) and Sampson (2000).

Myoporaceae

Myoporum boninense subsp. ***australe*** Chinnock Fig. 8a

3-colpate and diorate (= diploporate, with 2 pores in each colpus arranged north and south of the equator), fossaperturate, isopolar, radiosymmetric. S: small (to medium); EV usually prolate oval, sometimes circular or oblate oval; PV circular, colpi open; pores lalongate, frequently exceeding the rims of the colpi, elliptical to slit-like with jagged edges, 0.5–1.8(–7.4) µm long, 5.1–9.2 µm wide, without thickened margins, the colpi taper to acute apices high on the poles, with a smooth to granular membrane persistent except at the pores where it is broken; exine 1.0–1.3 µm thick, distinctly columellate, finely reticulate, becoming slightly finer at the poles. Polar axis, mean value: 23.1 µm, $\sigma = 1.2$ µm, range 20.4–25.2 µm; equatorial axis, mean value: 21.4 µm, $\sigma = 1.0$ µm, range 19.2–22.8 µm; $n = 41$.

Voucher: Dee Why Head, 25 Jun 1982, *Więcek & Stricker* (UNSW13056).

Note: see also Niezgoda and Tomb (1975).

Myrsinaceae

Myrsine howittiana (F.Muell. ex Mez) Jackes Fig. 8b
(syn. *Rapanea howittiana* (F.Muell.) Mez)

3-colporate, isopolar, radiosymmetric. S: very small to small; EV prolate oval, rarely circular; PV circular or inter-subangular, colpi intruding to open; pores small (≤ 1 µm diam.), indistinct, protruding at equator where colpi are slightly constricted, the colpi narrow; exine 0.5–0.8 µm thick, smooth. Polar axis, mean value: 14.8 µm, $\sigma = 1.5$ µm, range 10.8–16.8 µm; equatorial axis, mean value: 10.9 µm, $\sigma = 1.0$ µm, range 8.4–12.6 µm; $n = 38$.

Voucher: Smiths Lake Field Station, 20 Aug 1982, *Adam* (UNSW14101).

Notes: recently transferred to the genus *Myrsine* (Jackes 2005). See also Vasanthy and Pocock (1981) who describe abnormalities in '*Rapanea*' pollen.

Myrtaceae

Acmena smithii (Poir.) Merr. & L.M.Perry Fig. 8c

3-colporate, syncolpate, without apocolpia or polar islands, angulaperturate (i.e. apertures are situated at the angles of the amb), radiosymmetric, isopolar. S: small; EV oblate (often depressed) oval, the polar areas often slightly concave or more rarely raised; PV rounded triangular with the sides of the amb ± straight to slightly concave or convex (semi-angular to semi-lobate); pores lalongate, slit-like, exceeding the width of the colpi, the vestibulum absent or very narrow with a concave floor; exine 1–1.5 µm thick, surface ± smooth. Polar axis, mean value: 11.8 µm, $\sigma = 0.9$ µm, range 9.6–13.2 µm; equatorial axis, mean value: 16.0 µm, $\sigma = 1.0$ µm, range (13.8–)15.6–18.0 µm; $n = 42$; base of amb to angle, mean value: 14.9 µm, $\sigma = 0.8$ µm, range (12.0–)14.4–16.8 µm; $n = 32$.

Voucher: 6 km along Ourimbah Ck Rd from turn-off on Pacific Hwy, 6 Nov 1975, *Waterhouse* (UNSW5250).

Notes: employing SEM, Patel et al. (1984) found intercolpar concavities that are equatorially elongated and elliptic in shape clearly defined in *Acmena smithii* pollen grains. Chalson (1991) found the vestibulum of *A. smithii* pollen indistinct with a straight floor. *A. smithii* grains have a less angular amb and thicker walls than pollen grains of *Backhousia myrtifolia* and *Syncarpia glomulifera*. See also Pike (1956). Craven et al. (2006) have recently adopted a broader circumscription of *Syzygium*, including *Acmena*. If accepted this will resurrect the name *Syzygium smithii* (Poir.) Nied. for the taxon investigated here.

Backhousia myrtifolia Hook. & Harv. Fig. 8d

3(4)-colporate, syncolpate without apocolpia, angulaperturate, isopolar, radiosymmetric. S: small; EV ± depressed oblate oval, the polar regions concave; PV rounded triangular amb with slightly concave sides (angular to semi-lobate); pores lalongate, slit-like, exceeding the width of the colpi, the vestibulum absent or very narrow with a concave floor; exine c. 1 µm thick, smooth. Polar axis, mean value: 7.9 µm, $\sigma = 0.8$ µm, range 6.6–9.6 µm; equatorial axis, mean value: 16.1 µm, $\sigma = 0.9$ µm, range 14.4–18.0 µm; $n = 33$; base of amb to angle, mean value: 14.3 µm, $\sigma = 0.7$ µm, range 12.6–16.2 µm; $n = 38$.

Voucher: 8 km S of Albion Park on the road to Jamberoo, 23 Nov 1982, *Hindmarsh & Waterhouse* (UNSW11591).

Note: see also Pike (1956), Gadek and Martin (1981) and Chalson (1991).

Syncarpia glomulifera (Sm.) Nied. subsp. ***glomulifera*** Fig. 9a

(2)3(4)-colporate, syncolpate, angulaperturate, isopolar, radiosymmetric. S: small; EV oblate (often depressed) oval, polar areas slightly concave or sometimes raised; PV rounded triangular amb with straight or slightly concave sides (angular to semi-lobate); pores lalongate, exceeding colpi width, the margins distinct due to slight thickening of nexine around pores, the costa vaguely elliptical in outline, the orifice elliptical to slit-like, 0.5–1.5 µm long, 2–3.6 µm wide, the vestibulum often able to be delimited, to 1.1 µm high, with a concave floor; exine 0.6–1.0 µm thick (c. 2–3 µm thick at pores), smooth to finely granulate. Polar axis, mean value: 11.0 µm, $\sigma = 0.8$ µm, range

9.6–13.2 µm; equatorial axis, mean value: 18.2 µm, σ = 1.2 µm, range 15.6–21.0 µm; base of amb to angle, mean value: 16.0 µm, σ = 1.0 µm, range 14.4–17.4(–19.2) µm; *n* = 35.

Voucher: Coops Creek Crossing on Comenarra Parkway, Wahroonga, 21 Oct 1975, *Waterhouse* (UNSW3758).

Notes: sometimes one polar face is concave while the other is slightly raised. Chalson (1991) describes *Syncarpia glomulifera* pollen grains that are parasyncolpate with the apocolpium < 2 µm wide, and the exine with a faint granular/scabrate pattern. See also Pike (1956) and Gadek and Martin (1981).

Tristaniopsis collina Peter G.Wilson & J.T.Waterh. Fig. 9b

3(4)-colporate, syncolpate, isopolar, radiosymmetric. S: (very small to) small; EV oblate (often depressed) oval, the polar regions ± flat or raised; PV rounded triangular amb with slightly concave sides; pores very small and poorly defined, ± circular, the colpi indistinct; exine 0.5(–0.8) µm thick, smooth. Polar axis, mean value: 6.9 µm, σ = 0.4 µm, range 6.0–7.2 µm; equatorial axis, mean value: 12.1 µm, σ = 0.9 µm, range 9.6–13.8 µm; *n* = 30; base of amb to angle, mean value: 10.9 µm, σ = 0.5 µm, range 10.2–12.0 µm; *n* = 34.

Voucher: not recorded.

Notes: Chalson (1991) reports *Tristaniopsis collina* pollen with convex sides and rounded to blunt angles in the amb. See also Gadek and Martin (1981), where this species is treated as *Tristania* sp. aff. *laurina*.

Oleaceae

Notelaea venosa F.Muell. Fig. 9c

3(4)-colporate, isopolar, radiosymmetric. S: small; EV circular, otherwise slightly prolate or oblate oval; PV circular, colpi open; pores small, often indistinct, defined by protrusions at the equator, colpi of ± even width in equatorial view, tapering to obtuse ends; exine 0.5–0.8 µm thick, microreticulate. Polar axis, mean value: 12.7 µm, σ = 0.8 µm, range 10.8–14.4 µm; equatorial axis, mean value: 12.4 µm, σ = 0.6 µm, range 10.8–14.4 µm; *n* = 48.

Voucher: Minnamurra Falls Reserve, 25 Jan 1978, *Hindmarsh & Waterhouse* (UNSW7673).

Pennantiaceae

Pennantia cunninghamii Miers Fig. 9d

3(4)-colporate, isopolar, radiosymmetric. S: small; EV prolate oval; PV circular, colpi intruding; pores very small (< 1 µm diam.), often appearing costate; exine 0.5–0.8 µm thick, smooth. Polar axis, mean value: 13.0 µm, σ = 0.9 µm, range 10.2–14.4 µm; equatorial axis, mean value: 11.2 µm, σ = 0.9 µm, range 9.6–13.2 µm; *n* = 33.

Voucher: Long Gully Rd, 15 miles [24 km] W of Tabulam, no date, *Blaxell* (UNSW).

Notes: *Pennantia* was previously placed in Icacinaceae. See also Lobreau-Callen (1972).

Peperomiaceae

Peperomia tetraphylla (G.Forst.) Hook. & Arn. Fig. 9e

Inaperturate, apolar. S: very small to small; shape variable, ± ellipsoidal, circular in some views; exine 1–1.5 µm thick, the surface rough (appearing verrucate to reticulate or pitted depending on depth of field focus). Longest axis, mean value: 10.8 µm, σ = 1.3 µm, range 8.4–13.2 µm; *n* = 30.

Voucher: Minnamurra Falls, 22 May 1961, *Blaxell* (UNSW).

Note: *Peperomia* pollen is reported to have granules below a thick tectum (Walker 1976, per Sampson 2000).

Piperaceae

Piper novae-hollandiae Miq. Fig. 9f

l-sulcate. S: very small to small. Shape very variable, ± ellipsoidal with a sunken furrow/pore (i.e. concave on side with aperture and rounded-convex on the distal face); exine 0.8–1.0 µm thick, at some magnifications the surface appears finely reticulate in the depressed aperture region (which may rupture out) but this is possibly a granulate sulcus membrane (appearing reticulum-like under LM); rest of the surface appears smooth to shallowly ornamented. Longest axis, mean value: 10.4 µm, σ = 0.8 µm, range 8.4–12 µm; *n* = 30.

Voucher: Mt Kiera Scout Camp, 20 May 1974, *Waterhouse & Howard* (UNSW2415).

Note: Sampson (2000) illustrates the large ornamented aperture occurring in pollen of *Macropiper excelsum* using SEM.

Pittosporaceae

Bursaria spinosa Cav. subsp. ***spinosa*** Fig. 9g

(2)3-colporate, isopolar, radiosymmetric. S: small; EV circular to prolate oval, sometimes slightly oblate; PV circular with colpi intruding to open; pores circular to elliptical, within or exceeding width of colpi, 1.8–3.1 µm long, (2.3–)3.1–3.6 µm wide, the colpi tapering to acute apices, the colpus membrane smooth, persistent except at pores; exine 0.8–1.0(–1.5) µm thick, with a distinct, (fine to) medium reticulum, finer near colpi margins. Polar axis, mean value: 14.2 µm, σ = 1.1 µm, range 12.0–16.8 µm; equatorial axis, mean value: 13.8 µm, σ = 0.8 µm, range 12.0–15.6 µm; *n* = 30.

Voucher: Kalang River, near Bellingen, 17 Jun 1985, *Kodela & Dodson* (NSW804257, UNSW).

Note: see also Erdtman (1966, p. 323).

Pittosporum multiflorum (A.Cunn. ex Loudon) L.W.Cayzer, Crisp & I.Telford (syn. *Citriobatus pauciflorus* A.Cunn. ex Ettingsh.) Fig. 10a

3- or 4-colporate, isopolar, radiosymmetric. S: small to medium; EV circular to slightly prolate oval, rarely slightly oblate; PV circular to ± inter-hexagonal, colpi open; pores irregularly shaped, confined within margins of colpi or appearing broken and exceeding margins of the colpi, 1.5–4.1 µm long, 1.5–2.3(–5.1) µm wide, the colpi slightly constricted at equator, with somewhat ragged margins and acute to obtuse ends; exine 0.6–1.0 µm thick (to c. 1.3 µm at pores, c. 1.5 µm at poles), very finely reticulate, becoming finer and indistinguishable at colpi margins. Polar axis, mean value: 24.3 µm, σ = 1.6 µm, range 21.6–27.6 µm; equatorial axis, mean value: 23.6 µm, σ = 1.7 µm, range (18–)21–25.8 µm; *n* = 30.

Voucher: Robertson Nature Reserve, 28 Oct 1986, *Kodela* (UNSW).

Polyosmaceae

Polyosma cunninghamii Benn. Fig. 10b

3-porate, rarely with 4 pores, isopolar, radiosymmetric. S: medium; EV oblate oval; PV semi-angular, a triangular amb with convex sides; pores mostly elliptical when lalongate (sometimes ± circular or irregularly shaped), 2.4–3.6(–5.4) µm long, (2.4–)3.6–6.0(–7.2) µm wide, costate, with a coarse granulate pattern to 8.4 µm wide surrounding each pore; exine 1–1.5(–2) µm thick, granulate to faintly rugulate-reticulate. Polar axis, mean value: 31.7 µm, σ = 2.2 µm, range 28.2–36.0 µm; equatorial axis, mean value: 44.1 µm, σ = 2.7 µm, range 38.4–49.2 µm; *n* = 30; base of amb to angle, mean value: 41.7 µm, σ = 2.5 µm, range (36.0–)38.4–46.8 µm; *n* = 34.

Voucher: Mt Keira Scout Camp, 14 May 1975, *Howard & Quinn* (UNSW5316).

Polar axis, mean value: 33.3 µm, σ = 2.4 µm, range 28.8–36.0(–38.4) µm; equatorial axis, mean value: 42.4 µm, σ = 2.6 µm, range (37.2–)39.6–45.6(–48.0) µm; base of amb to angle, mean value: 41.2 µm, σ = 2.6 µm, range 37.2–45.6 µm; *n* = 30.

Voucher: Robertson, Jun 1987, *Kodela* (UNSW).

Notes: *Polyosma* was previously placed in Escalloniaceae.

Proteaceae

Stenocarpus salignus R.Br. Fig. 10c

3-porate, (sub)isopolar, radiosymmetric. S: medium; EV oblate, rhomboidal to apiculate; PV triangular amb with slightly convex sides, the arms pronounced and protruding, angulaperturate; pores conspicuous, ± circular, the orifice 2.8–3.6 µm in diam., often maintaining a thin membrane cap protruding to 3 µm; exine 1.8–2.0 µm thick, thicker (2.3–2.6 µm) near pores due to thickening of nexine, tectate-perforate (Feuer 1989; referring to the tectum having perforations smaller than 1 µm in diam.), appearing like a shallow reticulum under certain magnifications, granulate around the pores. Polar axis, mean value: 18.7 µm, σ = 0.9 µm, range 16.8–20.4 µm; equatorial axis, mean value: 29.7 µm, σ = 1.2 µm, range 26.4–32.4 µm; base of amb to angle, mean value: 25.4 µm, σ = 1.1 µm, range 24.0–27.6 µm; *n* = 30.

Voucher: Ourimbah Ck Rd, 26 Dec 1975, *Waterhouse* (UNSW5422).

Notes: some *Stenocarpus* pollen grains are subisopolar when one polar face is slightly more rounded convex than the opposite face. In equatorial view the arms sometimes appear to be very slightly orientated towards one pole. See also Erdtman (1966, p. 368).

Quintiniaceae

Quintinia sieberi A.DC. Fig. 10d

(3)4(5)-colporate, isopolar, radiosymmetric. S: small; EV (circular to) prolate oval; PV circular, colpi intruding; pores small, to c. 2 µm long, appearing as protrusions interrupting the colpi at the equator, the colpi equatorially constricted; exine c. 1 µm thick, smooth (obscurely granulate at higher magnification). Polar axis, mean value: 15.5 µm, σ = 1.1 µm, range (10.8–)14.4–17.4 µm; equatorial axis, mean value: 14.3 µm, σ = 0.9 µm, range 12.0–15.6 µm; n = 41.

Voucher: 6.2 km from Ulong on road to Coramba, 22 Oct 1978, *Waterhouse* (UNSW7850).

Notes: *Quintinia* was previously placed in Escalloniaceae. Most modern and fossil *Quintinia* pollen grains recorded by Kodela (1996) were 5-colporate.

Ranunculaceae

Clematis glycinoides DC. Fig. 10e

3-colpate, isopolar, radiosymmetric. S: small to medium; EV oblate oval, sometimes circular or very slightly prolate; PV circular, colpi intruding to open; colpi with finely granulate membrane; exine 0.8–1.0 µm thick, echinate to baculate, the projections to 1 µm high. Polar axis, mean value: 21.4 µm, σ = 1.7 µm, range 18.0–24.0 µm; equatorial axis, mean value: 23.1 µm, σ = 1.6 µm, range 20.4–26.4(–28.2) µm; n = 37.

Voucher: Mirrabooka, c. 6 km E of Morisset, Lake Macquarie, 1986, *Kodela* (UNSW).

Note: very similar to pollen of *Clematis aristata* and some species of *Ranunculus.*

Rhamnaceae

Alphitonia excelsa (Fenzl) Benth. Fig. 11a

3-colporate, angulaperturate, isopolar, radiosymmetric. S: small; EV oblate to prolate oval to slightly rhomboidal-apiculate; PV triangular with amb sides slightly concave, straight or slightly convex, colpi open in the angles; endoapertures J–K_p, the pores small, ± circular to slightly elliptical, costate; exine 1.5–2.0 µm thick, smooth to faintly scabrate. Polar axis, mean value: 16.7 µm, σ = 1.1 µm, range 14.4–19.2 µm; equatorial axis, mean value: 17.2 µm, σ = 0.9 µm, range 15.0–19.2 µm; n = 39; base of amb to angle, mean value: 16.0 µm, σ = 1.0 µm, range 14.4–18.0 µm; n = 36.

Voucher: Minnamurra Falls Reserve, 25 Jan 1978, *Waterhouse* (UNSW7665).

Rosaceae

Rubus moluccanus var. ***trilobus*** A.R.Bean Fig. 11b
(formerly *Rubus hillii* F.Muell.)

3(4)-colporate, isopolar, radiosymmetric. S: medium; EV usually prolate oval, sometimes circular or more rarely oblate oval; PV circular to semi-angular, colpi open; pores circular to elliptical, often bulging, very variable in size (may be small and poorly defined to large, torn-like ruptures), the colpus membrane granulate (colpi may be constricted at a small pore); exine 1.3–1.5 µm thick, the surface striated to striate-rugulate. Polar axis, mean value: 29.3 µm, σ = 1.4 µm, range (25.8–)27.6–31.2 µm; equatorial axis, mean value: 28.1 µm, σ = 1.5 µm, range (24.0–)26.4–30.0 µm; *n* = 30.

Voucher: Bulahdelah State Forest, 19 Jan 1961, *Blaxell* (UNSW).

Rubus rosifolius Sm. Fig. 11c

3-colporate, isopolar, radiosymmetric. S: small; EV prolate oval; PV circular, colpi intruding to open; pores protruding, the orifice poorly defined, the colpi equatorially constricted; exine 1.0–1.4 µm thick, the surface finely striate. Polar axis, mean value: 21.9 µm, σ = 1.4 µm, range 18.6–24.6 µm; equatorial axis, mean value: 16.8 µm, σ = 0.8 µm, range 15.6–19.2 µm; *n* = 30.

Voucher: Mt Keira near Scout Camp, 15 May 1975, *Howard & Quinn* (UNSW5322).

Rubiaceae

Coprosma quadrifida (Labill.) B.L.Rob. Fig. 11d

3-colporate, brevicolpate, isopolar, radiosymmetric. S: small to medium; EV oblate oval; PV circular, colpi open; endoapertures D or G, the pores lalongate, exceeding the colpi rims, ± elliptical when the transverse sides merge to pointed ends or may have poorly defined meridional edges, 2.0–3.8 µm long, 7.7–13.8 µm wide, the orifice irregularly shaped, slit-like or often oblong, usually confined within margins of the colpus, a patterned membrane maintained over rest of the pore; colpi very narrowly elliptical to slit-like, 0.5–2.0 µm wide at equator, 7.7–12.8 µm long, with pointed apices not reaching the poles; exine c. 1 µm thick, granulate to minutely reticulate. Polar axis, mean value: 23.3 µm, σ = 1.4 µm, range (19.2–)21.6–24.6(–26.4) µm; equatorial axis, mean value: 27.5 µm, σ = 1.3 µm; range 24.0–30.0 µm; *n* = 32.

Voucher: Tantawangalo State Forest, near Bega, Sep 1987, *Kodela* (UNSW).

Note: the pore length:width ratio is often 3:1 or greater, in which case the pores may be referred to as transverse colpi.

Cyclophyllum protractum S.T.Reynolds & R.J.F.Hend. Fig. 12a
(previously included as part of *Canthium coprosmoides* F.Muell.)

3-porate, isopolar, radiosymmetric. S: medium; EV oblate oval; PV rounded triangular, amb sides convex; pores ± circular, 4.8–10.8 µm in diam., sometimes lolongate, with ragged margins; exine c. 1.5 µm thick, coarsely suprareticulate with lumina of variable shape and (< 1–) 2–10.7 µm wide, muri wide and verrucate between lumina, the verrucae merging and becoming ± granulate around pores (i.e. at annulus). Polar axis, mean value: 32.0 µm, σ = 2.4 µm, range 26.4–36.0 µm; equatorial axis, mean value: 38.3 µm, σ = 1.6 µm, range 34.8–41.4 µm; *n* = 33.

Voucher: State Forest 143, Little Mossman Logging Area, Qld, 1 Oct 1978, *Moriarty 2470* (UNSW).

Note: distinguished by its bimodal sculpturing consisting of a suprareticulum and a finer ornamentation, as well as having large ± circular pores.

Morinda jasminoides A.Cunn. Fig. 12b

3-colporate, isopolar, radiosymmetric. S: medium; EV oblate oval; PV circular or very rounded inter-semi-angular to inter-hexagonal; pores ± circular to elliptical (orifice 1.8–7.2 µm in diam. and surrounded by a granular margin), occurring within transverse, elliptical colpi with more prominent margins on the polar sides (8.4–16.8 µm long, 13.2–20.4 µm wide); longitudinal colpi often faintly delimited, tapering to irregular, acute or bluntly obtuse ends, the colpus membrane granulate, persistent except at pore orifice; exine 1.5–2.0 µm thick, distinctly thickened near pores, rugulate to irregularly very finely reticulate. Polar axis, mean value: 27.9 µm, σ = 2.6 µm, range 22.8–32.4 µm; equatorial axis, mean value: 32.5 µm, σ = 2.6 µm, range (26.4–)28.8–36.6(–39.0) µm; *n* = 35.

Voucher: Buds Crossing, on Eungai Ck, Collombatti State Forest, Kempsey, 17 Nov 1978, *Hindmarsh & Waterhouse* (UNSW8059).

Note: see also Johansson (1987).

Sapindaceae

Alectryon subcinereus (A.Gray) Radlk. Fig. 12c

3(4)-colporate, parasyncolpate with polar islands, angulaperturate, isopolar, radiosymmetric. S: small; EV oblate oval; PV obtuse triangular (semi-angular) amb with convex sides and broadly rounded angles, sometimes almost circular; pores conspicuous, mostly lalongate, elliptical or oblong, the orifice 1.5–3.8 µm long, 2.6–5.1 µm wide; vestibulum poorly defined or to c. 1 µm high with a concave floor; exine 1.0–1.5 µm thick, very finely reticulate. Polar axis, mean value: 16.8 µm, σ = 2.1 µm, range 13.2–19.2(–22.8) µm; equatorial axis, mean value: 20.9 µm, σ = 1.8 µm, range 17.4–24.0 µm; *n* = 34; base of amb to angle, mean value: 20.7 µm, σ = 1.8 µm, range 16.8–24.6 µm; *n* = 32.

Voucher: 1.1 km below Watsons picnic area on the road to Gloucester Tops, 21 Jan 1977, *Hindmarsh & Waterhouse* (UNSW6432).

Note: size of the triangular-shaped polar islands often slightly different on opposing poles.

Sapotaceae

Pouteria australis (R.Br.) Baehni Fig. 12d
(syn. *Planchonella australis* (R.Br.) Pierre)

4-colporate, isopolar, radiosymmetric. S: medium; EV prolate oval to compressed prolate oval; PV obtuse, convex ± quadrangular, colpi mostly positioned between the angles, intruding to slightly open; endoapertures L, the pores circular or elliptical when lalongate or more rarely lolongate, slightly protruding, the orifice 2.3–3.6 µm ×(2.3–) 3.3–4.8 µm, the colpi narrow, with ragged margins, often with vague ends not reaching the poles; exine 1.5–2.0 µm thick, with nexine markedly thickened at pores where exine to 3.5 µm thick, the surface scabrate to shallowly rugulate. Polar axis, mean value: 33.3 µm, σ = 1.5 µm, range 30.6–37.8 µm; equatorial axis, mean value: 25.9 µm, σ = 1.4 µm, range 22.8–28.8 µm; *n* = 34.

Voucher: specimen was not retained.

Smilacaceae

Smilax australis R.Br. Fig. 13a

Inaperturate, apolar. S: small; shape ± spheroidal; exine very thin (c. 0.5 µm thick), the surface finely echinate with minute spinules (< 1 µm long) irregularly arranged, otherwise smooth. Diameter, mean value: 17.4 µm, σ = 0.9 µm, range 15.6–19.2 µm; *n* = 30.

Voucher: Pacific Hwy 1.2 km S of Wootton, 23 Sep 1978, *Waterhouse* (UNSW7818).

Solanaceae

Duboisia myoporoides R.Br. Fig. 13b

3-colporoidate, isopolar, radiosymmetric. S: small (to medium), EV mostly prolate oval, sometimes circular to oblate oval; PV circular, colpi intruding to open; pores often indistinct or appear as irregular ruptures in the colpi (occasionally the grains are diploporate with two slit-like pores/transverse furrows in the colpi), the colpi with distinct (sometimes fragmented) margins, tapering to pointed apices almost meeting at the poles, the colpus membrane smooth to slightly granulate; exine c. 1 µm thick, rugulate to striate. Polar axis, mean value: 22.0 µm, σ = 1.8 µm, range (16.8–)20.4–25.2 µm; equatorial axis, mean value: 19.5 µm, σ = 1.4 µm, range 16.8–22.8 µm; *n* = 36.

Voucher: specimen was not retained.

Sterculiaceae

Brachychiton acerifolius (A.Cunn. ex G.Don) Macarthur & C.Moore Fig. 13c

3-colporate, isopolar, radiosymmetric. S: medium; EV prolate oval; PV circular to ± inter-hexagonal, colpi intruding to open; pores conspicuous, exceeding the colpi rims without definite or distinct meridional edges and equatorial limits (c. 7.7–12.2 µm wide), the open orifice oblong, usually confined within rims of the colpus, 2.0–5.1 µm long, (0.5–)1.5–5.9 µm wide, the colpi widest at the equator, tapering to blunt or acute apices, the smooth to slightly granular colpus membrane persistent except at pores; exine c. 1.8 µm thick, slightly thicker at the poles where to 2.5 µm thick, distinctly columellate, with fine to medium reticulum. Sample 1: Polar axis, mean value: 35.2 µm, σ = 1.5 µm, range 32.4–37.2 µm; equatorial axis, mean value: 30.0 µm, σ = 1.5 µm, range 28.2–33.6 µm; *n* = 31. Sample 2: polar axis range 30.0–34.2 µm; equatorial axis range 22.8–28.8 µm; *n* = 30.

Vouchers: specimens were not retained.

Symplocaceae

Symplocos stawellii F.Muell. Fig. 13d

3(4)-colporate (2-aperturate grains occupied 30 % of a sample studied by van der Meijden 1970), brevicolpate, angulaperturate, (sub-)isopolar, radiosymmetric. S: medium; EV oblate oval; PV obtuse/rounded triangular (semi-angular) amb with convex sides, sometimes almost circular; pores ± elliptical, ± lalongate, with granulate membrane (around orifice) often difficult to distinguish from the surrounding sexine, with costa formed from thickening of bordering nexine; colpi slit-like to narrowly open, within boundary of irregular, fragmented annulus, 4.8–7.2 µm long, 1–2.4 µm wide; exine 1–1.5 µm thick, following van der Meijden (1970) the sexine would be described as finely verrucate above a ± distinct columellae layer; surface sculpturing may appear irregularly finely reticulate (–rugulate) at certain magnifications. Polar axis, mean value: 19.8 µm, $\sigma = 1.1$ µm, range 17.4–21.6 µm; equatorial axis, mean value: 27.9 µm, $\sigma = 1.7$ µm, range 24.6–31.2 µm; $n = 29$; base of amb to angle, mean value: 26.6 µm, range (22.2–) 24–28.8 µm; $n = 39$.

Voucher: between Port Macquarie and Crescent Head, 5.6 km N of Hastings River, 21 Aug 1973, *Waterhouse* (UNSW3059).

Notes: in New South Wales, *Symplocos stawellii* occurs north from Royal National Park, while *S. thwaitesii* F.Muell. occurs north from Victoria and is present in the Illawarra region. The pollen of both species are described and illustrated by van der Meijden (1970). *Symplocos* is a ± eurypalynous genus (Erdtman 1966), meaning there is much diversity in the pollen of this genus. See Barth (1979) for aperture features in *Symplocos* pollen.

Ulmaceae

Trema tomentosa var. ***viridis*** (Planch.) Hewson Fig. 14a
(formerly *Trema aspera* (Brongn.) Blume)

2-porate, isopolar, ± bilateral. S: small; shape ± ellipsoidal with slightly protruding pores; pores usually arranged ± equidistant on the equator (and therefore ± opposite), circular to slightly elliptical, distinctly annulate, 4.1–5.6 µm in diam. (including margin), orifice 2–3.1 µm in diam., annulus width c. 1 µm; exine c. 1 µm thick (2.3–3.1 µm around pores), the surface appears granulate. Longest axis, mean value: 21.4 µm, $\sigma = 1.4$ µm, range 19.2–24.6 µm; $n = 30$.

Voucher: [Royal] National Park, 14 Feb 1958, *Blaxell* (UNSW).

Notes: in the following Urticaceae species the pores of the pollen are minute and barely protruding while in *Trema tomentosa* var. *viridis* pollen the pores are more pronounced. See also Erdtman (1966, p. 442). Zavada's (1983) study found: (1) wall structure and exine sculpturing were the best diagnostic pollen characteristics for determining subfamilial affinities in Ulmaceae; (2) the pollen morphological characteristics of the subfamily Celtidoideae (which includes *Trema*) are more like those of Moraceae than of subfamily Ulmoideae; and (3) the pollen morphology supports family status for Celtidoideae, which would occupy a phylogenetically intermediate position between the Ulmaceae (Ulmoideae) and the Moraceae.

Urticaceae

Australina pusilla Gaudich. Fig. 14b

3-porate, ± isopolar, radiosymmetric. S: very small to small; EV oblate oval; PV ± circular (overall the grains appear ellipsoidal); pores ± equally distanced on the equator, ± circular, minute and often indistinct, 1.5–2.4 µm in diam. (including margin), the orifice 0.5–1.1 µm in diam., the margin to 0.5 µm wide; exine 0.5–0.6 µm thick, slightly thicker around pores; surface appears ± smooth at 500× magnification, however 1250× magnification reveals an obscure pattern that appears shallowly rugulate. Polar axis, mean value: 9.4 µm, σ = 0.7 µm, range 7.7–10.8 µm; equatorial axis, mean value: 11.2 µm, σ = 1.0 µm, range 9.0–13.8 µm; *n* = 45.

Voucher: 'Doradell', c. 1.5 km S of Robertson, 9 Feb 1988, *Kodela* (UNSW).

Notes: Moar (1993) reported *Australina pusilla* pollen c. 18 µm in size with a scabrate pattern (from a New Zealand specimen).

Elatostema reticulatum Wedd. Fig. 14c

2-porate. S: very small to small; shape ± ellipsoidal, probably oblate oval in equatorial view and ± circular in polar view; pores mostly not equally distanced on the equator, ± circular or occasionally elliptical, 2.0–2.8 µm in diam. (including margin), the orifice 0.8–1.5 µm in diam, the margin c. 0.5 µm wide; exine 0.5–0.8 µm thick, slightly thicker around pores; surface appears obscurely rugulate to reticulate, especially at higher magnification. Longest axis, mean value: 11.0 µm, σ = 0.8 µm, range 9.0–12.9 µm; *n* = 30.

Vouchers: (mixed pollen preparation): Minnamurra Falls, 22 May 1961, *Blaxell* (UNSW); Barrengarry Mt at head of Kangaroo Valley, 20 Jan 1969, *Barber* (UNSW).

Note: *Elatostema reticulatum* pollen is distinguished from *Australina pusilla* and *Urtica incisa* by being 2-porate and having a more pronounced surface ornamentation.

Urtica incisa Poir. Fig. 14d

3-porate, isopolar, radiosymmetric. S: small; EV oblate oval; PV ± circular; pores positioned ± equally distanced on the equator, ± circular, 2.3–3.3 µm in diam. (including prominent margin), the orifice 1.0–1.5 µm in diam., the margin to 0.8 µm wide; exine 0.5–0.6 µm thick; surface smooth at 500× magnification, appearing faintly and minutely reticulate at 1250× magnification. Polar axis, mean value: 12.7 µm, σ = 0.8 µm, range 10.8–14.3 µm; equatorial axis, mean value: 14.7 µm, σ = 1.0 µm, range 12.0–15.9 µm; *n* = 45.

Note: pollen sample from Robertson area (no voucher).

Verbenaceae

Lantana camara L. Fig. 15a

3(4)-colporate, isopolar, radiosymmetric. S: medium; EV oblate to prolate oval, PV rounded semi-angular, a triangular amb with obtuse angles and convex sides when 3-colporate, ± square when 4-colporate; pores lalongate, 7–11 µm long, to 20 µm wide, with granulate membrane where exceeding colpus margins, often with a distinct ± oblong–square orifice (to c. 8.5 µm) within colpus margins; colpi with granulate membrane except at pore opening, with tapering ends; exine c. 2 µm thick, thicker (to c. 4 µm) at pores, appearing ± rugulate–reticulate or variably patterned under some magnifications but under SEM shown to be tectate-perforate (Raj 1983). Polar axis, mean value: 33.4 µm, σ = 6.6 µm, range 24.6–49.2 µm; equatorial axis, mean value: 33.6 µm, σ = 4.8 µm, range 26.4–44.4 µm; *n* = 37.

Notes: *Lantana camara* is a naturalised species in Australia. The pollen sample is from Lane Cove, Sydney (no voucher specimen was retained). The pollen of *Lantana camara* is also described and illustrated by Raj (1983) and Willard et al. (2004).

Violaceae

Hymenanthera dentata R.Br. ex DC. Fig. 15b

(2)3-colporate, isopolar, radiosymmetric. S: small; EV oblate to prolate oval, PV circular, colpi intruding; pores small, defined by protrusions where the colpi are constricted equatorially, occasionally seen with large oblong orifices; exine c. 0.8 µm thick, the surface smooth. Polar axis, mean value: 15.5 µm, σ = 0.9 µm, range 13.8–17.4 µm; equatorial axis, mean value: 14.6, µm, σ = 1.1 µm, range 12.6–16.8 µm; n = 30.

Voucher: Tantawangalo State Forest, near Bega–Eden, Oct 1987, *Kodela* (UNSW).

Vitaceae

Cissus hypoglauca A.Gray Fig. 15c

3-colporate, isopolar, radiosymmetric. S: medium; EV prolate oval; PV semi-lobate (triangular with concave sides and cavities at angles); endoapertures L, the pores lalongate, slightly elliptical, 3.6–5.1 µm long, 4.1–6.1 µm wide, the colpi narrowly open; exine 1.3–1.5 µm thick, often thicker (to 3.6 µm) at poles, distinctly columellate, with a medium reticulate ornamentation, in colpi region finely reticulate. Polar axis, mean value: 41.7 µm, σ = 1.3 µm, range 38.4–43.8 µm; equatorial axis, mean value: 30.6 µm, σ = 1.2 µm, range (27.0–)28.8–32.4 µm; n = 30.

Voucher: Bola Creek, Royal National Park, 14 Jan 1963, *Blaxell* (UNSW).

Discussion

Investigation of pollen morphology revealed, as would be expected, similarities between species in the same genus, e.g. species of *Cryptocarya* and *Parsonsia*. Using the light microscope it would be difficult, or impossible, to differentiate pollen at the species level for most genera in fossil or modern pollen rain studies with a satisfactory degree of certainty. However, it is possible to differentiate the pollen of some plant groups to species level after detailed analyses of the regional pollen flora, e.g. an investigation of Myrtaceae pollen morphology (particularly *Eucalyptus* species) for a study of the vegetation history of the Blue Mountains (Chalson 1991, Chalson & Martin 1995). Determining the species likely to be represented in a modern or fossil pollen study will also be assisted by a regional vegetation survey, e.g. an investigation of rainforest history and dynamics in the Robertson area (Kodela 1990a, b, 1996). These types of study benefit from establishing reference pollen sets to compare morphologies. It is important however to recognise the potential problems and limitations when relating pollen morphology of existing taxa from actual plant specimens ('actuo' pollen morphological pollen classification and nomenclature) to palaeopalynological pollen, as discussed by Joosten and de Klerk (2002). These authors concluded that fossil pollen cannot, beyond reasonable doubt, be ascribed to recent and native taxa that produce the same kind of pollen. Hence their argument to refer to pollen types defined by a limitative collection of morphological properties rather than identifying fossil pollen as that of a taxon which involves interpretation.

This study shows that it would be difficult to differentiate *Ceratopetalum, Callicoma* and *Eucryphia* pollen in sediments, especially if the fossil pollen is damaged (eroded, folded, broken). This would also be the case for many Myrtaceae genera and some tricolporate taxa. Monimiaceae s. lat. is a very eurypalynous family with the genera investigated here having distinctly different pollen types, which adds support to recent evidence from molecular and morphological data (Renner 1999) indicating the polyphyletic nature of the family.

The pollen of *Parsonsia brownii, P. straminea, Pandorea pandorana, Legnephora moorei, Doryphora sassafras, Hedycarya angustifolia, Palmeria scandens, Acmena smithii, Backhousia myrtifolia, Syncarpia glomulifera, Tristaniopsis collina, Bursaria spinosa, Stenocarpus salignus, Morinda jasminoides, Symplocus stawellii, Trema tomentosa, Australina pusilla* and *Lantana camara* in this study generally agree with previously published descriptions, with size being one of the most variable features, and shape and sculpturing type sometimes described differently by different researchers. Some of the differences might be accounted for by methodologies, including: (a) pollen preparation, e.g. chemical pre-treatment or mounting medium (glycerine jelly versus silicone oil) may affect size and shape of pollen; (b) light microscope versus scanning electron microscope (SEM) or transmission electron microscope (TEM) observations, e.g. SEM is particularly useful when studying external features such as surface sculpturing and ornamentation for taxonomic research; and (c) degree of magnification which influences the type of surface sculpturing or other features revealed. Differences in pollen descriptions of the same taxon will also result from natural differences in samples (particularly size) and possibly due to the different interpretations and terminologies of investigators.

In some taxa the shape of the pollen appears to vary widely, for example, radiosymmetric tricoporate pollen taxa that are oblate to prolate in equitorial view, or the shape of the amb in species of Myrtaceae (whether the sides are concave, straight or convex). Apertures can also vary, including the degree of 'openness' of colpi, or whether pores exceed the colpi margins due to 'tearing of the wall' in some tricolporate grains.

This study provides some insight into the features useful for pollen identification, as well as problems that may be encountered when differentiating pollen of related taxa. The pollen morphological descriptions and illustrations are available for use in palynological investigations and plant taxonomic studies. Pollen taxonomy is essential for the identification of fossil pollen and spores to reconstruct past floras and palaeoenvironments. While acknowledging the limitations of relating 'actuo' pollen morphology to palaeopalynological studies (see Joosten & de Klerk 2002), palaeoenvironmental and plant history investigations still benefit from the knowledge of modern pollen for comparison. This assists the interpretation of pollen types and the taxa they are likely to represent. In the case of vegetation and environmental history studies it is particularly important to have an understanding of the variability, as well as the similarities, in the pollen flora to assist the interpretation of fossil pollen records. Superficially similar pollen types from the same family may represent genera or species with very different habits and/or habitat/environmental conditions. Pollen morphological studies integrated with modern pollen rain studies greatly assist the interpretation of pollen representation in palaeo-investigations.

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References

Barth OM (1979) Pollen morphology of Brazilian *Symplocos* species (Symplocaceae). *Grana* 18: 99–107.

Boyd WE (1992) A pollen flora of the native plants of South Australia and southern Northern Territory, Australia. *South Australian Geographical Papers* No. 3.

Bradford JC & Barnes RW (2001) Phylogenetics and classification of Cunoniaceae (Oxalidales) using chloroplast DNA sequences and morphology. *Systematic Botany* 26: 354–385.

Buurman J (1977) Contribution to the pollenmorphology of the Bignoniaceae, with special reference to the tricolpate type. *Pollen et Spores* 19: 447–519.

Chalson, JM (1991) The Late Quaternary vegetation and climate history of the Blue Mountains, N.S.W., Australia. Unpublished PhD thesis. (University of NSW: Sydney)

Chalson JM & Martin HA (1995) The pollen morphology of some co-occurring species of the family Myrtaceae from the Sydney region. *Proceedings of the Linnean Society of New South Wales* 115: 163–191.

Craven LA, Biffin E & Ashton PS (2006) *Acmena, Acmenosperma, Cleistocalyx, Piliocalyx* and *Waterhousea* formally transferred to *Syzygium* (Myrtaceae). *Blumea* 51: 131–142.

Dickison WC, Hils MH, Lucansky TW & Stern WL (1994) Comparative anatomy and systematics of woody Saxifragaceae. *Aphanopetalum* Endl. *Botanical Journal of the Linnean Society* 114: 167–182.

El Ghazali GEB (1990) An illustrated key to endoaperture morphology. *Review of Palaeobotany and Palynology* 63: 227–231.

Erdtman G (1966) *Pollen morphology and plant taxonomy: Angiosperms.* (Hafner: New York)

Erdtman G (1969) *Handbook of palynology.* (Hafner: New York)

Faegri K & Iversen J (1975) *Textbook of pollen analysis,* 3rd edn. (Munksgaard: Copenhagen)

Feuer S (1989) Pollen morphology of the Embothrieae (Proteaceae). I. Buckinghamiinae, Stenocarpinae and Lomatiinae. *Grana* 28: 225–242.

Fishbein M, Hibsch-Jetter C, Soltis DE & Hufford L (2001) Phylogeny of Saxifragales (angiosperms, eudicots): analysis of a rapid, ancient radiation. *Systematic Biology* 50: 817–847.

Foreman DB & Sampson FB (1987) Pollen morphology of *Palmeria scandens* and *Wilkiea huegeliana* (Monimiaceae). *Grana* 26: 127–133.

Gadek PA & Martin HA (1981) Pollen morphology in the subtribe Metrosiderinae of the Leptospermoideae (Myrtaceae) and its taxonomic significance. *Australian Journal of Botany* 29: 159–184.

Hilu KW, Borsch T, Müller K, Soltis DE, Soltis PS, Savolainen V, Chase MW, Powell MP, Alice LA, Evans R, Sauquet H, Neinhuis C, Slotta TAB, Rohwer JG, Campbell CS & Chatrou LW (2003) Angiosperm phylogeny based on *matK* sequence information. *American Journal of Botany* 90: 1758–1776.

Hoen P, Punt W, Blackmore S, Nilsson S & Le Thomas A (1999) *Glossary of pollen and spore terminology*, 2nd edn, http://www.bio.uu.nl/~palaeo/glossary/glos-int.htm.

Jackes BR (2005) Revision of *Myrsine* (Myrsinaceae) in Australia. *Australian Systematic Botany* 18: 399–438.

James EA & Knox RB (1993) Reproductive biology of the Australian species of the genus *Pandorea* (Bignoniaceae). *Australian Journal of Botany* 41: 611–626.

Johansson JT (1987) Pollen morphology of the tribe Morindeae (Rubiaceae). *Grana* 26: 134–150.

Joosten H & Klerk P de (2002) What's in a name? Some thoughts on pollen classification, identification, and nomenclature in Quaternary palynology. *Review of Palaeobotany and Palynology* 122: 29–45.

Kodela PG (1990a) Pollen–tree relationships within forests of the Robertson–Moss Vale region, New South Wales, Australia. *Review of Palaeobotany and Palynology* 64: 273–279.

Kodela PG (1990b) Modern pollen rain from forest communities on the Robertson plateau, New South Wales. *Australian Journal of Botany* 38: 1–24.

Kodela PG (1992) Rainforest, pollen and palaeoecological studies in the Robertson area. *Eucryphia (Newsletter of the Robertson Environment Protection Society)* 5: 5–8.

Kodela PG (1996) The vegetation of the Robertson Plateau, New South Wales: historical and contemporary issues. Unpublished PhD thesis. (University of NSW: Sydney)

Kuyl OS, Muller J & Waterbolk HT (1955) The application of palynology to oil geology with reference to Western Venezuela. *Geologie en Mijnbouw*, new ser., 17: 49–75.

Lieux MH (1983) An atlas of pollen of trees, shrubs, and woody vines of Louisiana and other southeastern states, Part V. Lythraceae to Euphorbiaceae. *Pollen et Spores* 25: 321–350.

Lobreau-Callen D (1972) Pollen des Icacinaceae 1. – Atlas. *Pollen et Spores* 14: 345–388.

Meijden R van der (1970) A survey of the pollenmorphology of the Indo-Pacific species of *Symplocos* (Symplocaceae). *Pollen et Spores* 12: 513–551.

Moar NT (1993) *Pollen grains of New Zealand dicotyledonous plants.* (Manaaki Whenua Press: Lincoln, Canterbury, New Zealand).

Moore PD & Webb JA (1978) *An illustrated guide to pollen analysis.* (Hodder and Stoughton: London)

Niezgoda CJ & Tomb AS (1975) Systematic palynology of tribe Leucophylleae (Scrophulariaceae) and selected Myoporaceae (1). *Pollen et Spores* 17: 495–516.

Patel VC, Skvarla JJ & Raven PH (1984) Pollen characters in relation to the delimitation of Myrtales. *Annals of the Missouri Botanical Garden* 71: 858–969.

Pike KM (1956) Pollen morphology of Myrtaceae from the south-west Pacific area. *Australian Journal of Botany* 4: 13–53.

Raj B (1983) A contribution to the pollen morphology of Verbenaceae. *Review of Palaeobotany and Palynology* 39: 343–422.

Renner SS (1999) Circumscription and phylogeny of the Laurales: evidence from molecular and morphological data. *American Journal of Botany* 86: 1301–1315.

Sagun VG & Ham RWJM van der (2003) Pollen morphology of the Flueggeinae (Euphorbiaceae, Phyllanthoideae). *Grana* 42: 193–219.

Sampson FB (1977) Pollen tetrads of *Hedycarya arborea* J.R. et G. Forst. (Monimiaceae). *Grana* 16: 61–73.

Sampson FB (1982) Variation in position of the nascent generative cell in pollen of *Hedycarya* (Monimiaceae). *Grana* 21: 9–14.

Sampson FB (1997) Pollen morphology and ultrastructure of Australian Monimiaceae – *Austromatthaea, Hedycarya, Kibara, Leviera, Steganthera* and *Tetrasynandra*. *Grana* 36: 135–145.

Sampson FB (2000) Pollen diversity in some modern magnoliids. *International Journal of Plant Sciences* 161: S193–S210.

Sampson FB & Anusarnsunthorn V (1990) Pollen of Australian species of *Parsonsia* (Apocynaceae). *Grana* 29: 97–107.

Sampson FB & Foreman DB (1988) Pollen morphology of *Atherosperma*, *Daphnandra* and *Doryphora* (Atherospermataceae [Monimiaceae]). *Grana* 27: 17–25.

Sampson FB & Foreman DB (1990) Pollen morphology of *Peumus boldus* (Monimiaceae) – comparison with *Palmeria scandens*. *Grana* 29: 197–206.

Suryakanta (1973) Pollen morphological studies in the Bignoniaceae. *Journal of Palynology* 9: 45–82.

Vasanthy G & Pocock SAJ (1981) A comparative study of anomalous and normal pollen of *Rapanea*: morphology, elemental analysis, sterility and fungal parasitism. *Pollen et Spores* 23: 349–379.

Walker JW (1976) Evolutionary significance of the exine in the pollen of primitive angiosperms. Pp. 251–308 in Ferguson IK & Muller J (eds) *The evolutionary significance of the exine*. (Academic Press: London)

Willard DA, Bernhardt CE, Weimer L, Cooper SR, Gamez D & Jensen J (2004) Atlas of pollen and spores of the Florida Everglades. *Palynology* 28: 175–227.

Zavada M (1983) Pollen morphology of Ulmaceae. *Grana* 22: 23–30.

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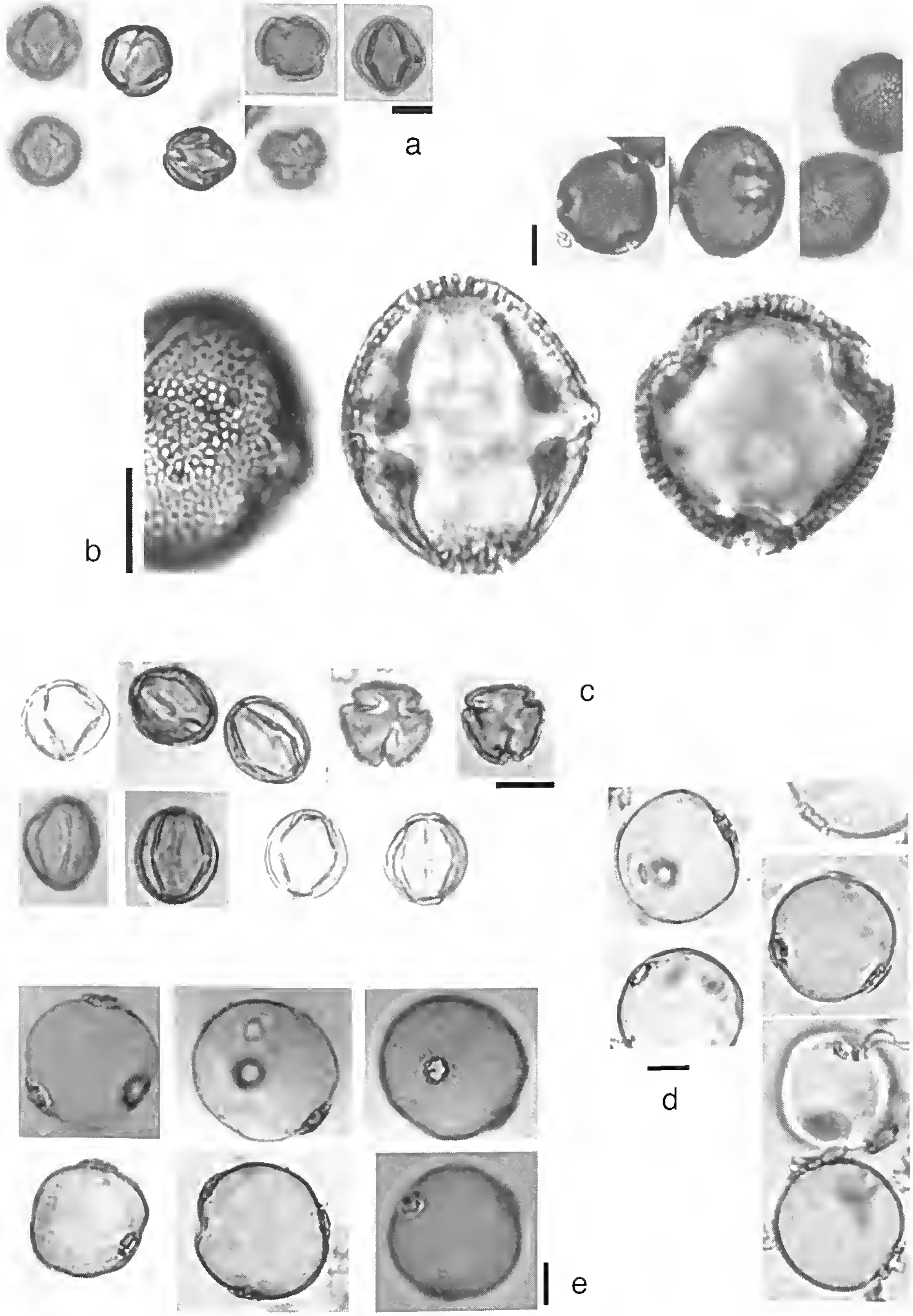

Fig. 2. Light micrographs of pollen: **a**, *Sambucus australasica*; **b**, *Euroschinus falcata*; **c**, *Aphanopetalum resinosum*; **d**, *Parsonsia brownii*; **e**, *Parsonsia straminea*. Scale bars = 10 µm.

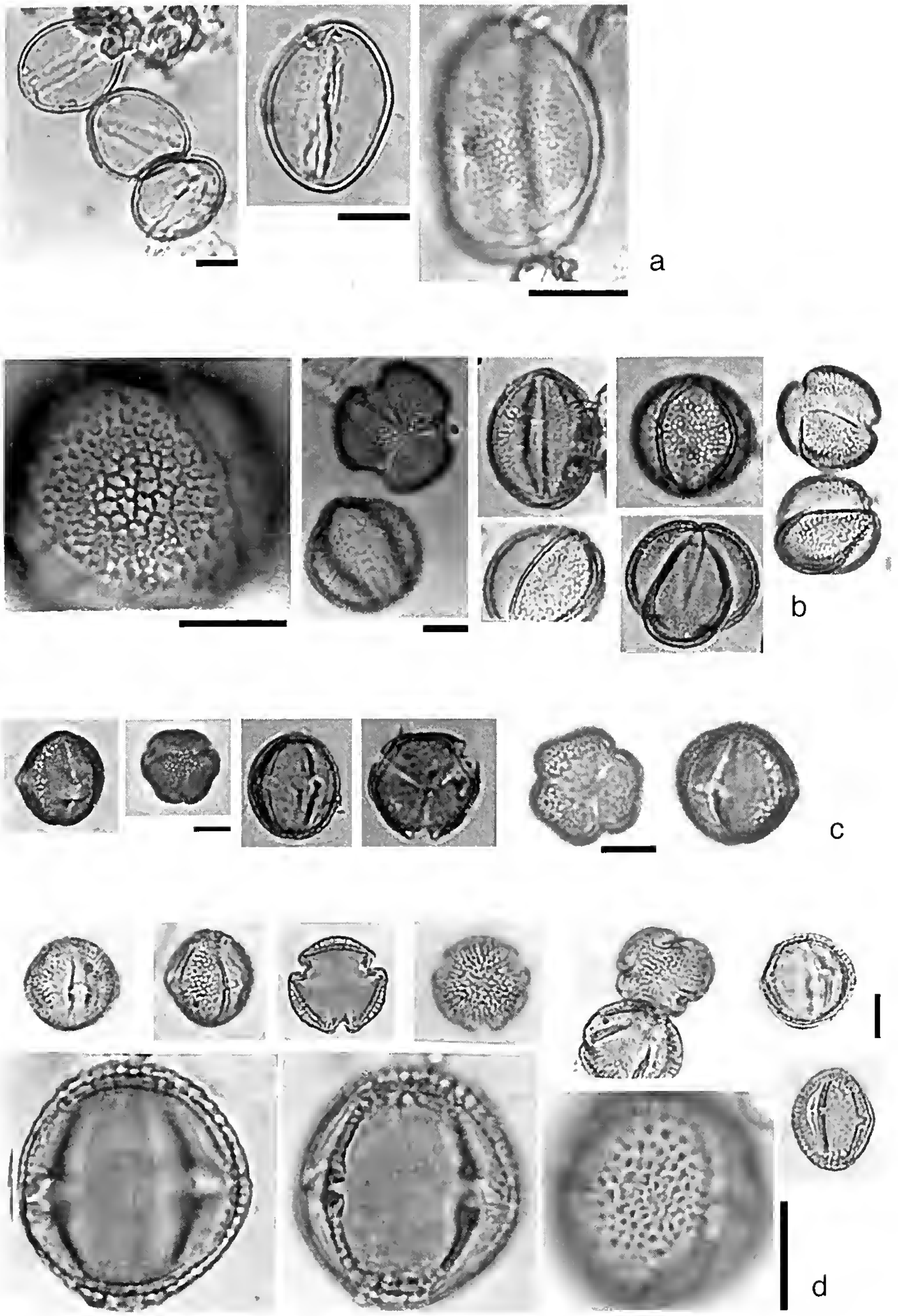

Fig. 3. Light micrographs of pollen: **a**, *Gymnostachys anceps*; **b**, *Pandorea pandorana*; **c**, *Ehretia acuminata*; **d**, *Celastrus australis*. Scale bars = 10 µm.

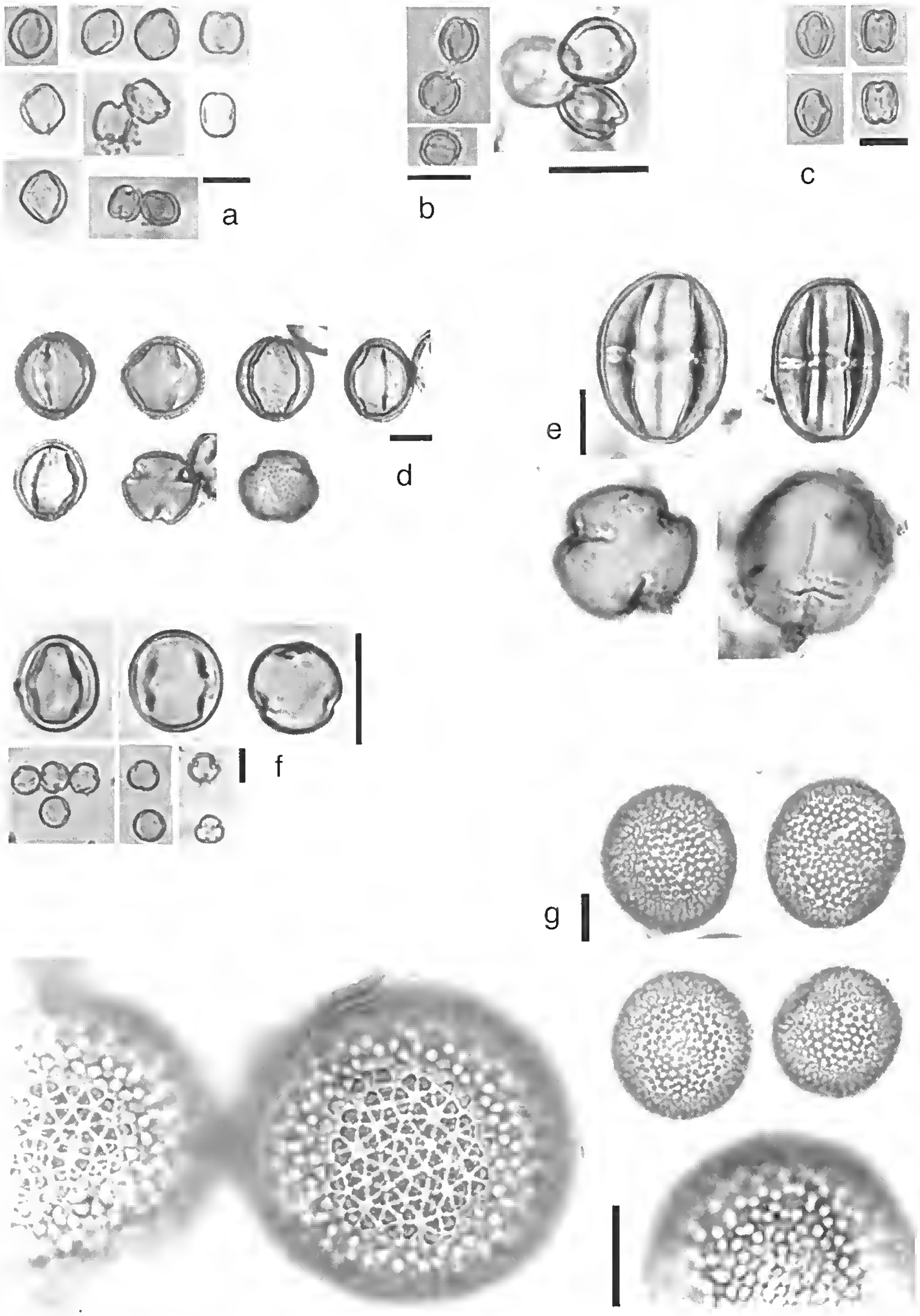

Fig. 4. Light micrographs of pollen: **a**, *Ceratopetalum apetalum*; **b**, *Eucryphia moorei*; **c**, *Schizomeria ovata*; **d**, *Hibbertia scandens*; **e**, *Diospyros australis*; **f**, *Elaeocarpus reticulatus*; **g**, *Baloghia inophylla*. Scale bars = 10 µm.

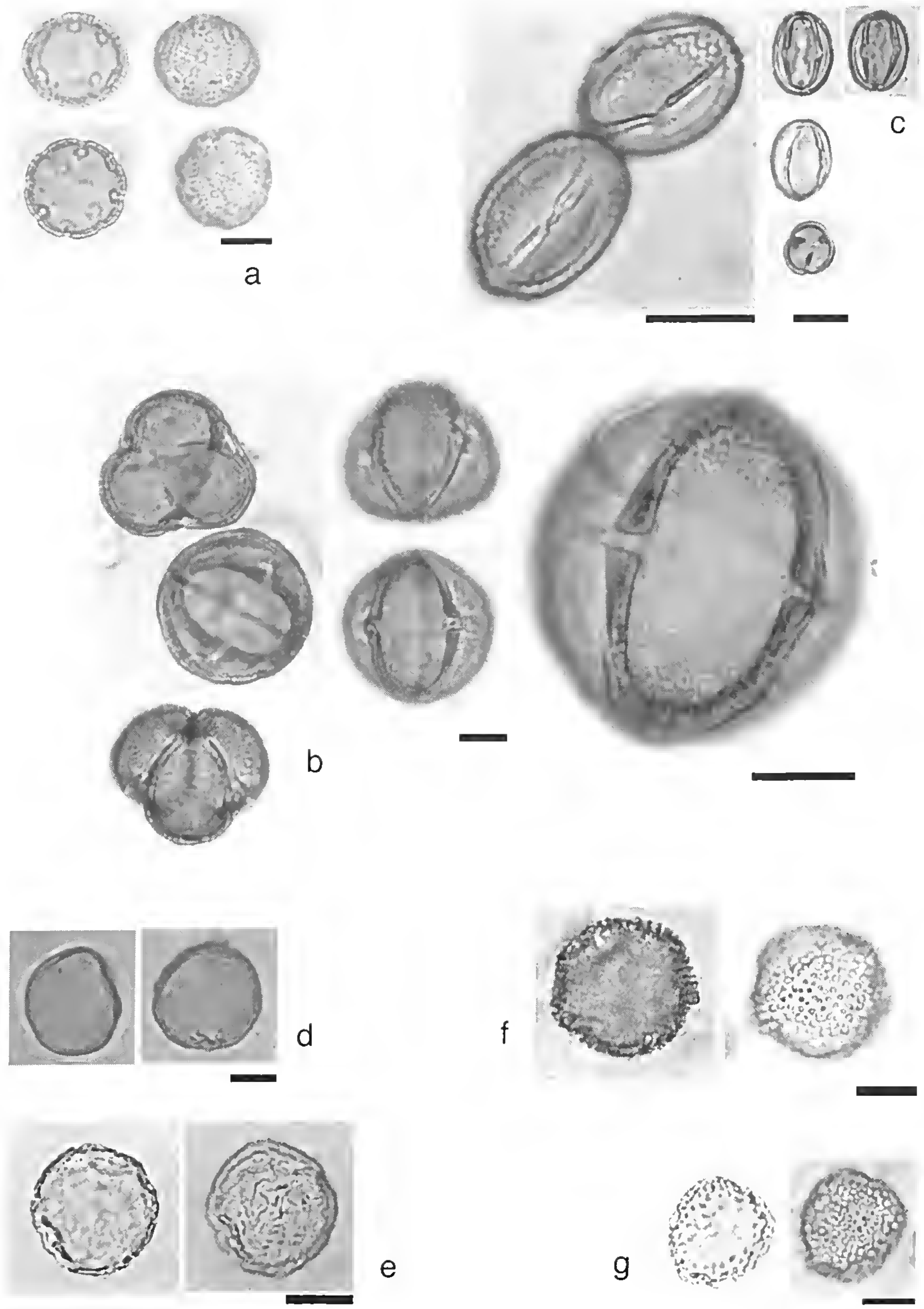

Fig. 5. Light micrographs of pollen: **a**, *Breynia oblongifolia*; **b**, *Homalanthus populifolius*; **c**, *Scolopia braunii*; **d**, *Cryptocarya glaucescens*; **e**, *Cryptocarya microneura*; **f**, *Endiandra sieberi*; **g**, *Neolitsea dealbata*. Scale bars = 10 μm.

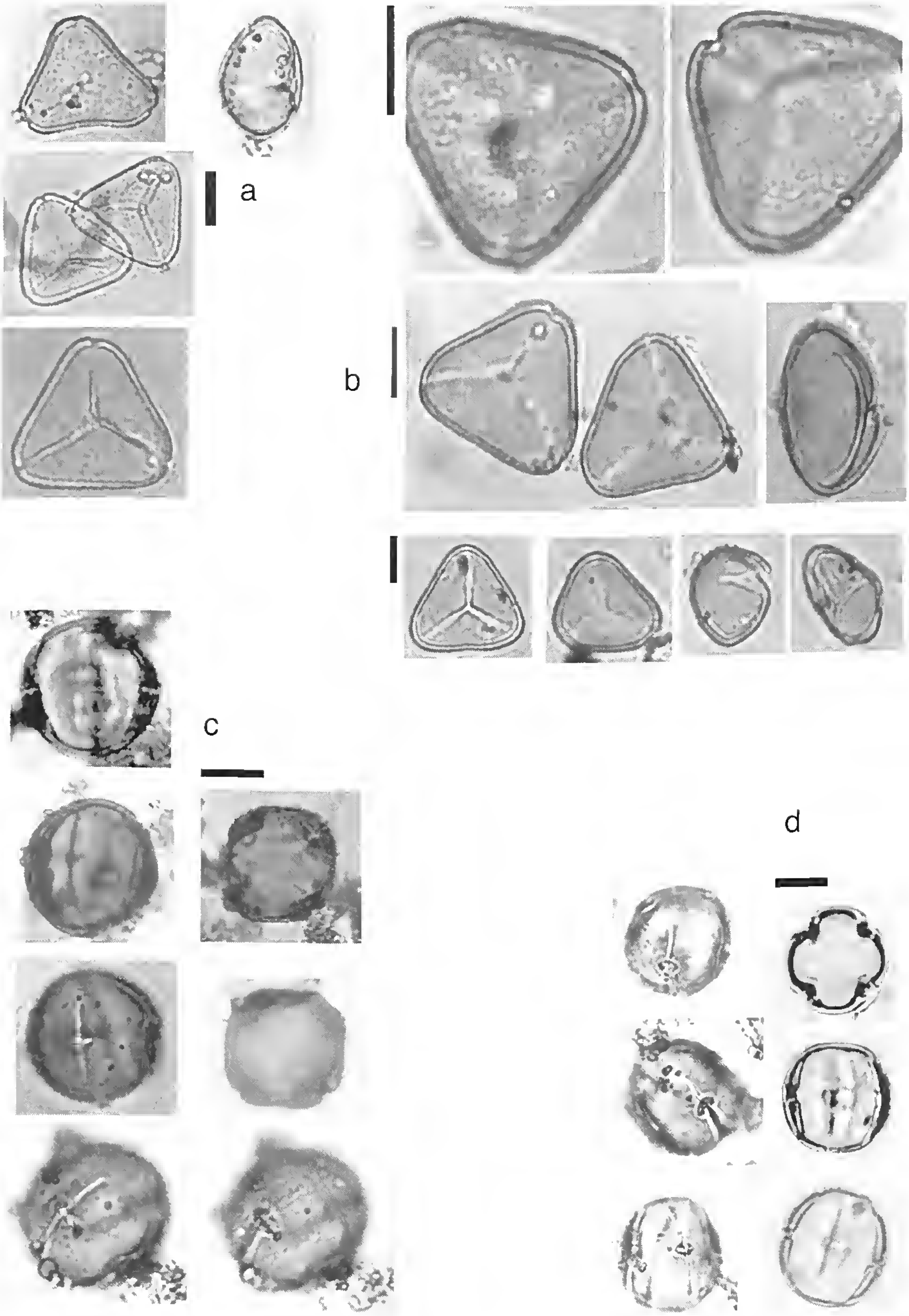

Fig. 6. Light micrographs of pollen: **a**, *Eustrephus latifolius*; **b**, *Geitonoplesium cymosum*; **c**, *Synoum glandulosum*; **d**, *Toona ciliata*. Scale bars = 10 µm.

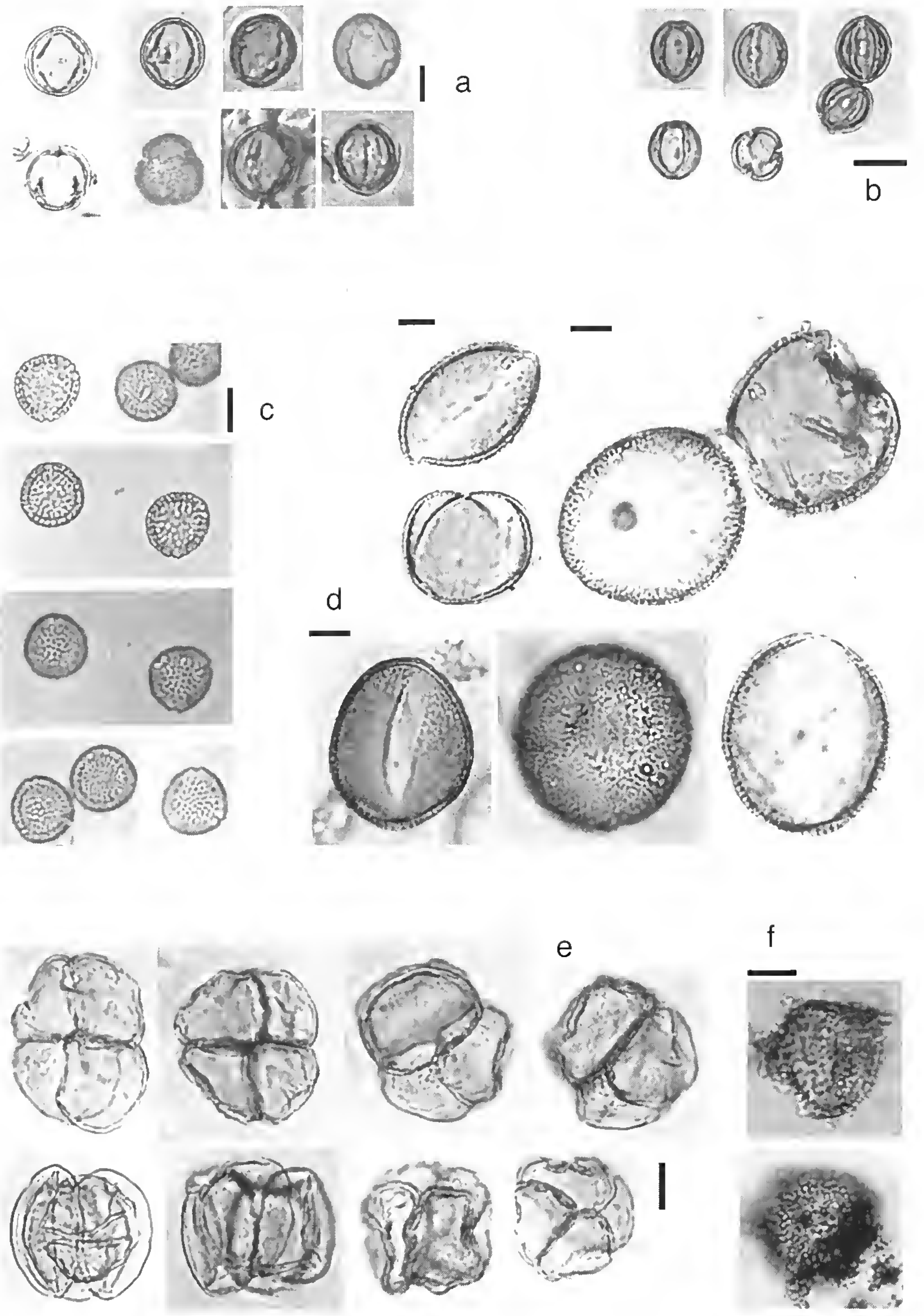

Fig. 7. Light micrographs of pollen: **a**, *Legnephora moorei*; **b**, *Sarcopetalum harveyanum*; **c**, *Stephania japonica* var. *discolor*; **d**, *Doryphora sassafras*; **e**, *Hedycarya angustifolia*; **f**, *Palmeria scandens*. Scale bars = 10 µm.

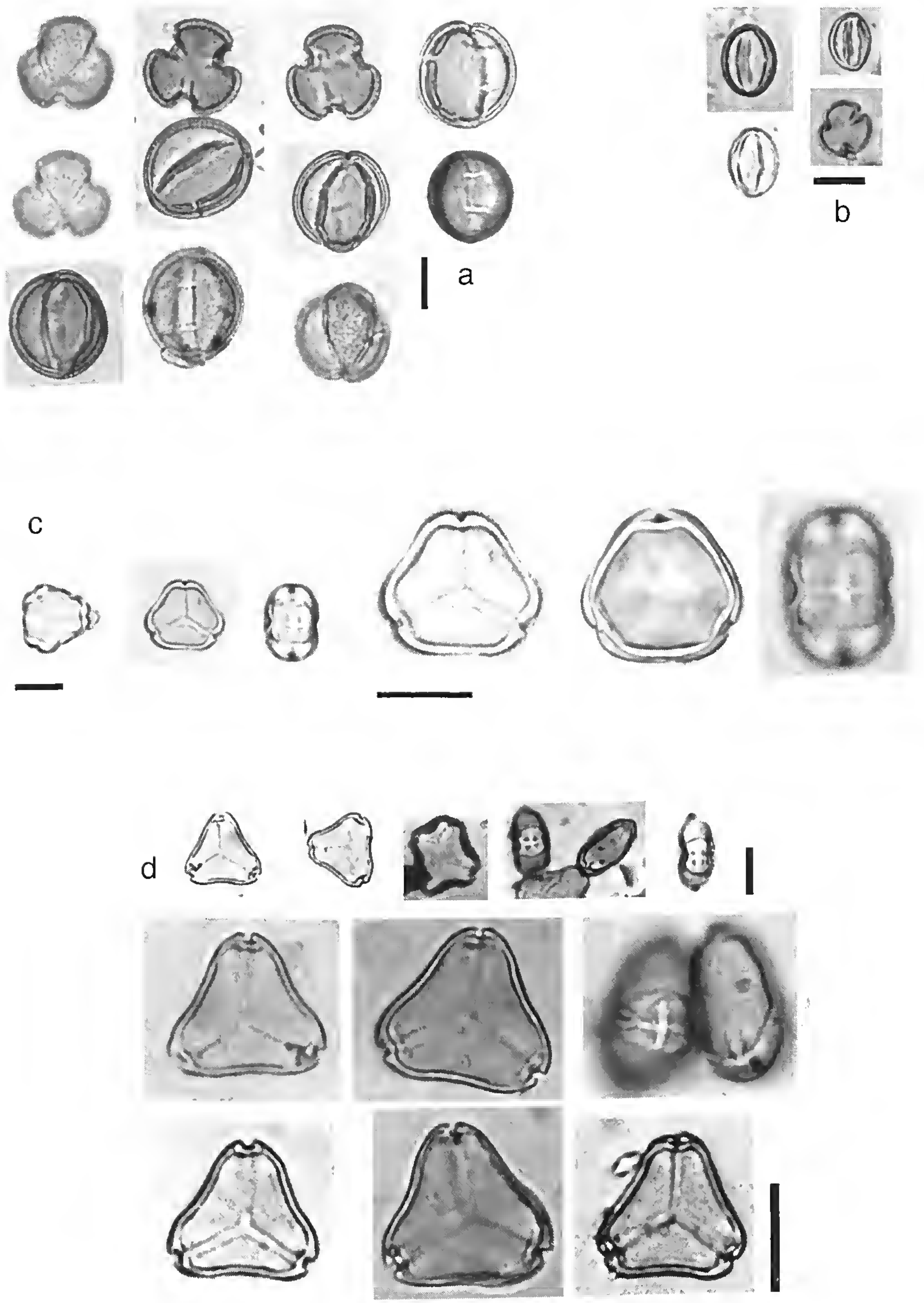

Fig. 8. Light micrographs of pollen: **a**, *Myoporum boninense* subsp. *australe*; **b**, *Myrsine howittiana*; **c**, *Acmena smithii*; **d**, *Backhousia myrtifolia*. Scale bars = 10 µm.

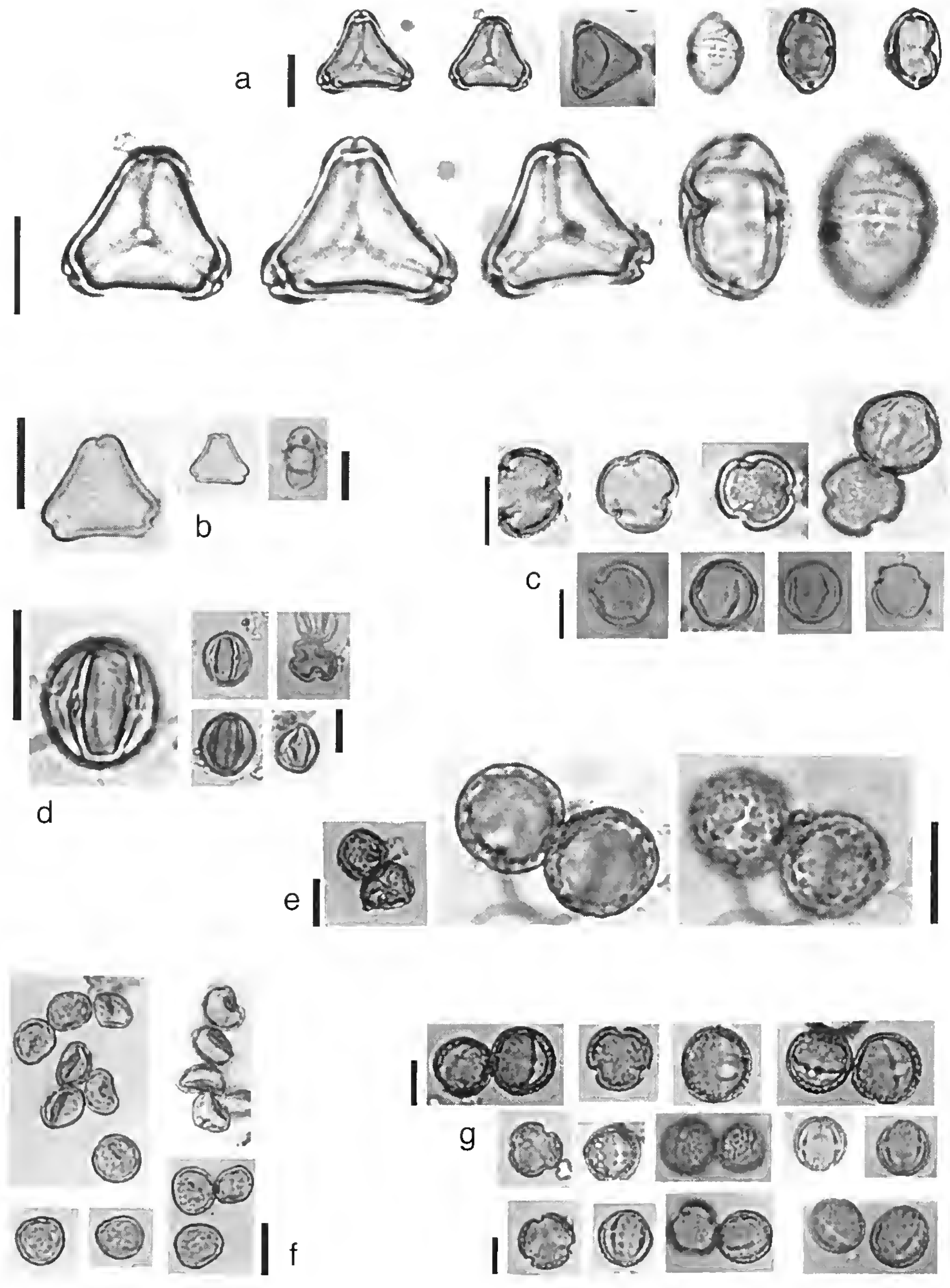

Fig. 9. Light micrographs of pollen: **a**, *Syncarpia glomulifera* subsp. *glomulifera*; **b**, *Tristaniopsis collina*; **c**, *Notelaea venosa*; **d**, *Pennantia cunninghamii*; **e**, *Peperomia tetraphylla*; **f**, *Piper novae-hollandiae*; **g**, *Bursaria spinosa* subsp. *spinosa*. Scale bars = 10 µm.

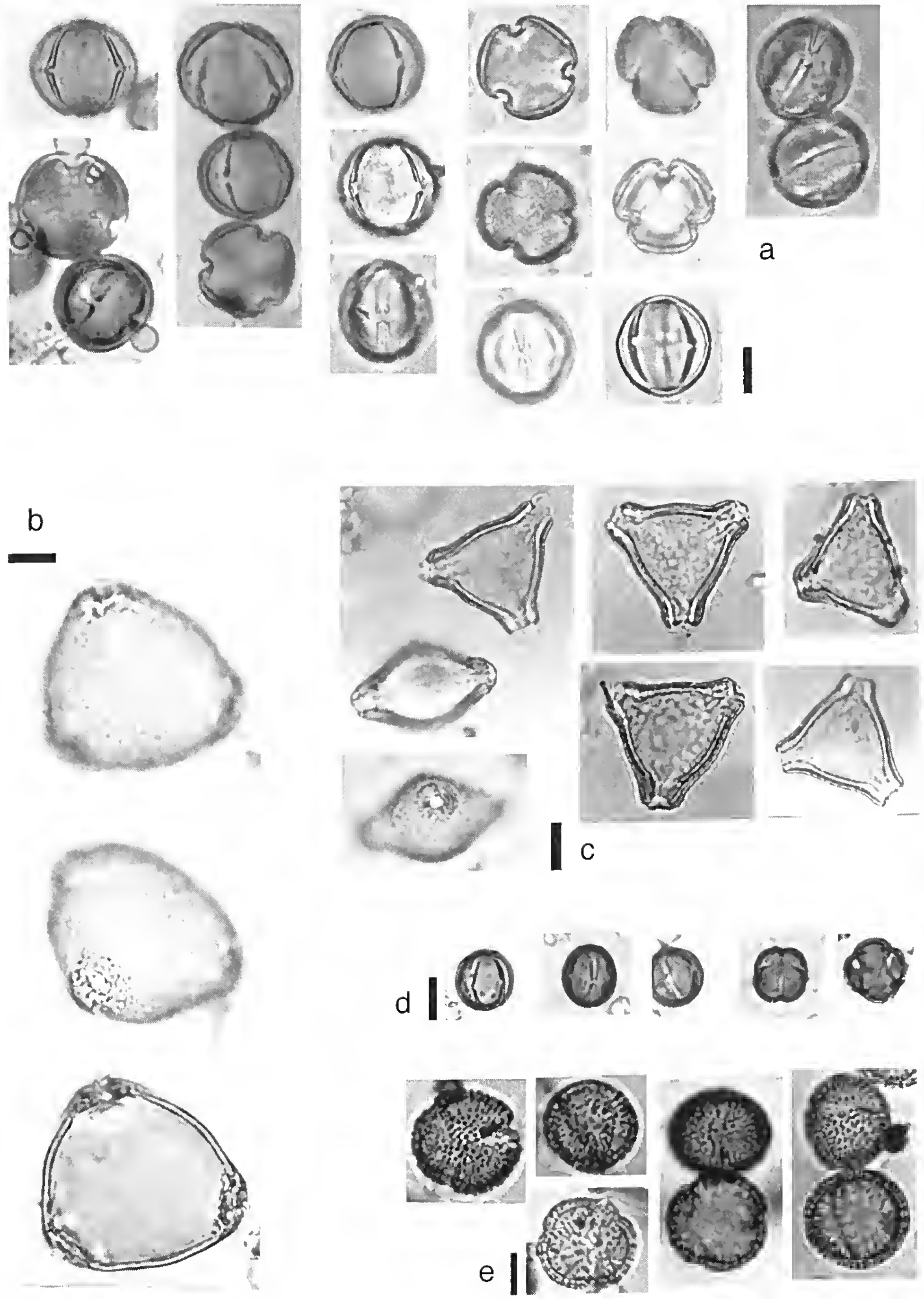

Fig. 10. Light micrographs of pollen: **a**, *Pittosporum multiflorum*; **b**, *Polyosma cunninghamii*; **c**, *Stenocarpus salignus*; **d**, *Quintinia sieberi*; **e**, *Clematis glycinoides*. Scale bars = 10 µm.

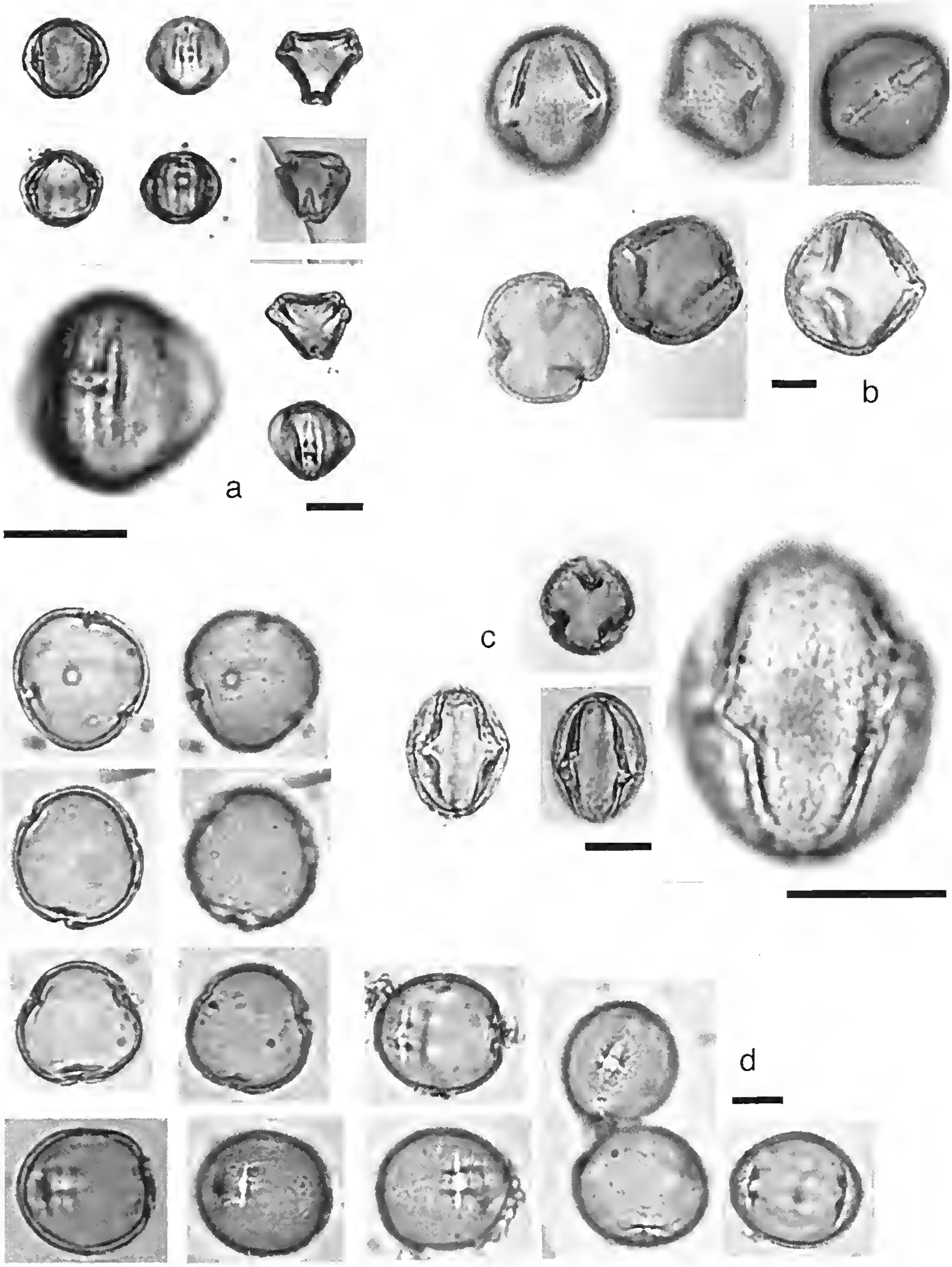

Fig. 11. Light micrographs of pollen: **a**, *Alphitonia excelsa*; **b**, *Rubus moluccanus* var. *trilobus*; **c**, *Rubus rosifolius*; **d**, *Coprosma quadrifida*. Scale bars = 10 µm.

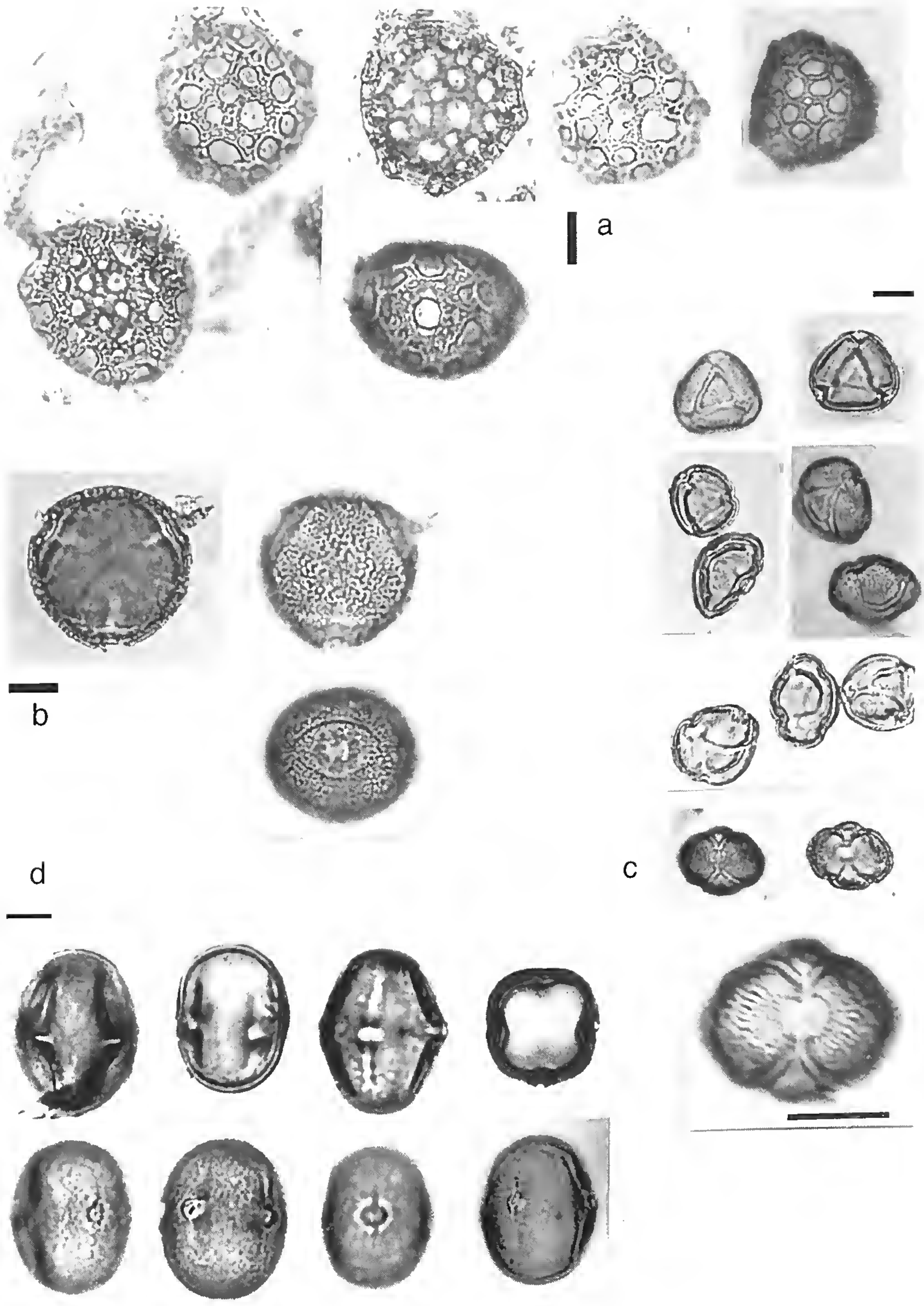

Fig. 12. Light micrographs of pollen: **a**, *Cyclophyllum protractum*; **b**, *Morinda jasminoides*; **c**, *Alectryon subcinereus*; **d**, *Pouteria australis*. Scale bars = 10 µm.

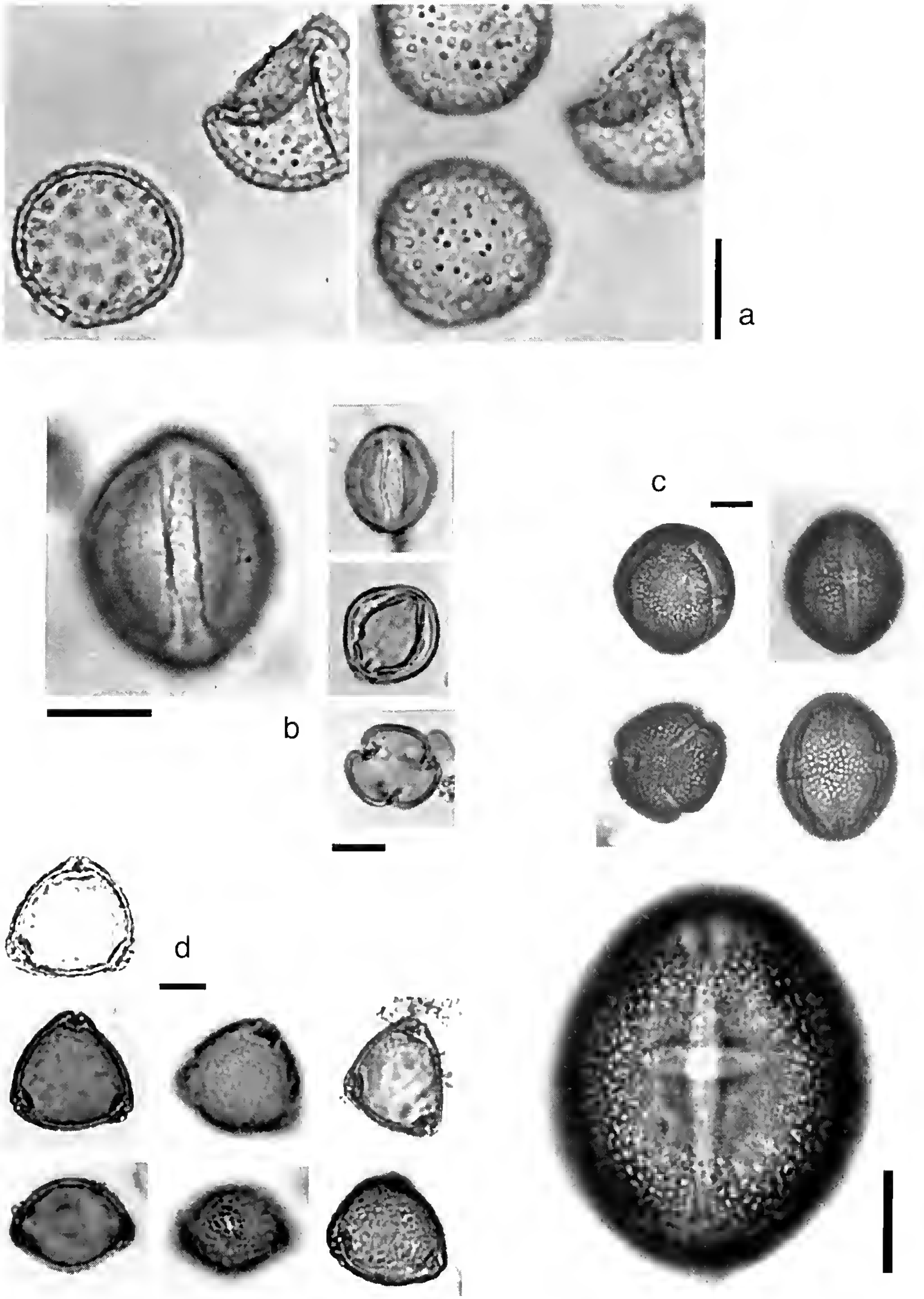

Fig. 13. Light micrographs of pollen: **a**, *Smilax australis*; **b**, *Duboisia myoporoides*; **c**, *Brachychiton acerifolius*; **d**, *Symplocos stawellii*. Scale bars = 10 µm.

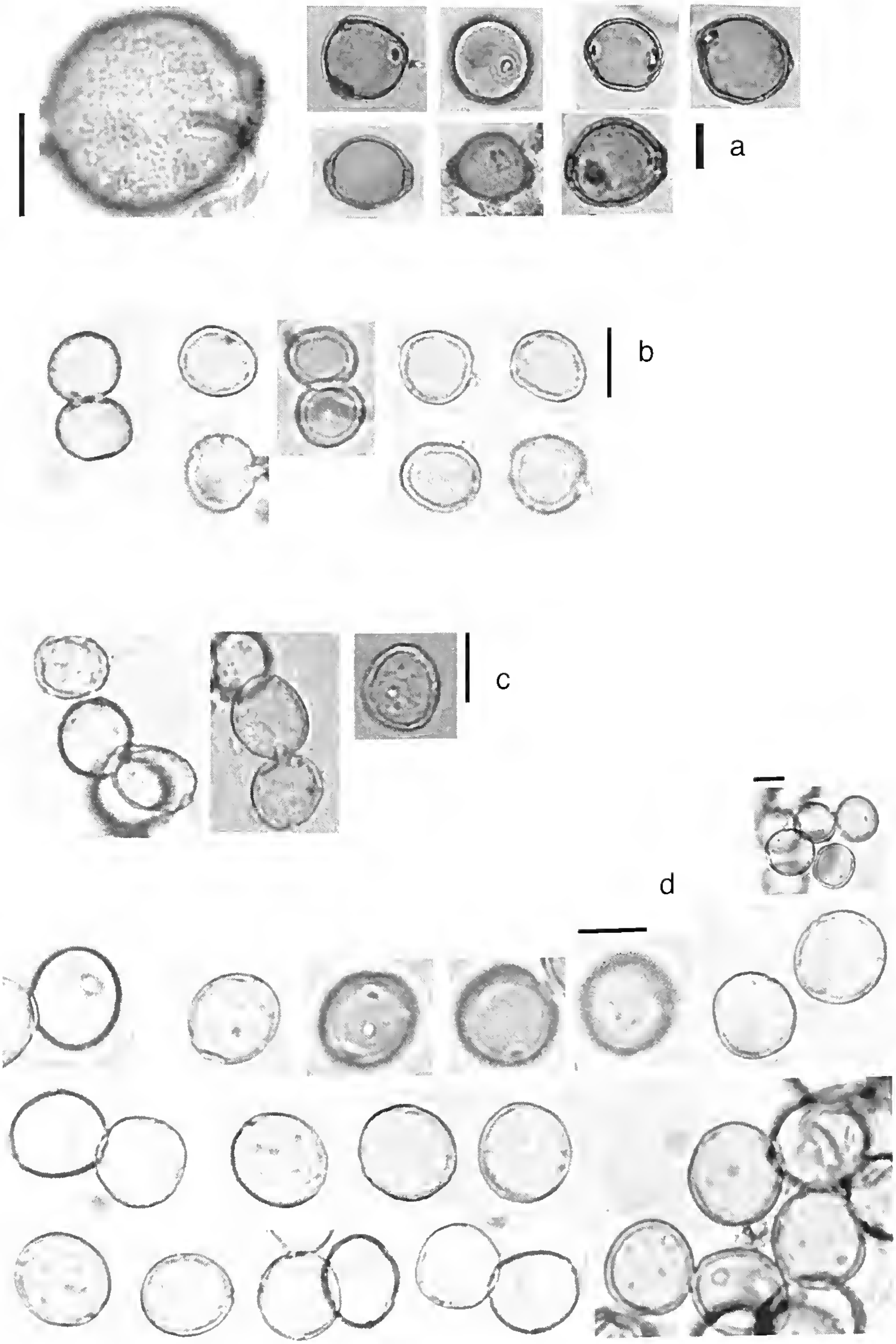

Fig. 14. Light micrographs of pollen: **a**, *Trema tomentosa* var. *viridis*; **b**, *Australina pusilla*; **c**, *Elatostema reticulatum*; **d**, *Urtica incisa*. Scale bars = 10 µm.

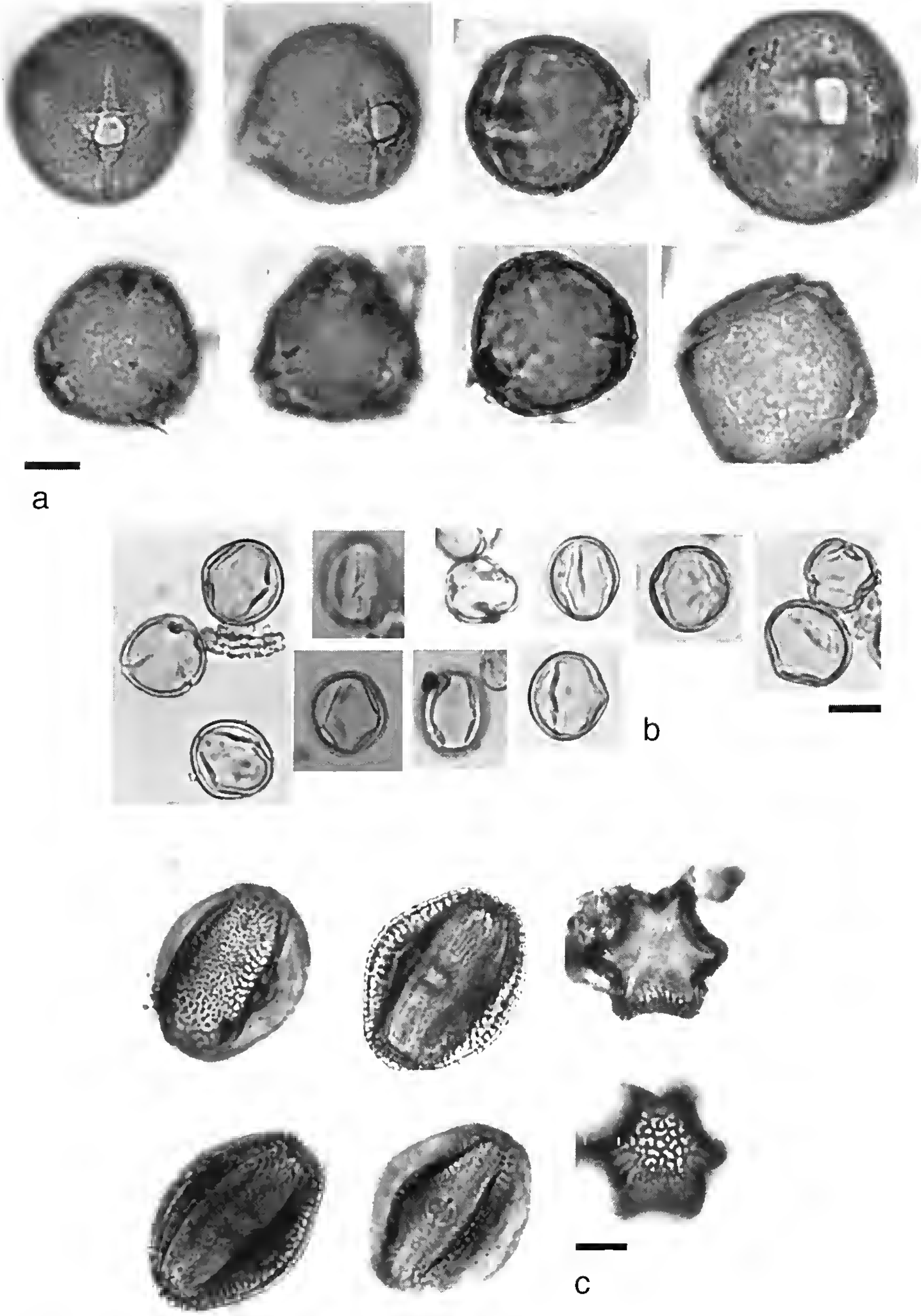

Fig. 15. Light micrographs of pollen: **a**, *Lantana camara*; **b**, *Hymenanthera dentata*; **c**, *Cissus hypoglauca*. Scale bars = 10 µm.

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Short Communication

A new combination in *Clematicissus* Planch. (Vitaceae)

Betsy R. Jackes[1] and Maurizio Rossetto[2]

[1] *School of Tropical Biology, James Cook University, Townsville, Qld 4811, Australia*
[2] *National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney NSW 2000 Australia.*

When the genus *Cissus* was revised (Jackes 1988) the decision was made to retain the species *Cissus opaca* F.Muell. in the genus until molecular studies indicated its true affinities. *Cissus opaca*, an eastern Australian species, shares a number of morphological features with the Western Australian species *Clematicissus angustissima* (F.Muell.) Planch., and with the South American species *Cissus tweedieana* (Baker) Planch. These features are: a vine or sprawling shrub; tuberous roots; great variation in size and shape of adult leaves even within the same population; inflorescences arise from one or both branches of a leaf-opposed tendril and flowers are 5-merous. Many of these characteristics are also exhibited by both subspecies of *Rhoicissus tridentata* (L.f.) Wild & Drumm (Urton et al. 1986). *Clematicissus angustissima* can be distinguished from *Cissus* by the 5-merous flowers, the presence of the inflorescence arising on the tendrils and the structure of the endosperm., as well as from most species of *Cissus*, as currently circumscribed, by the compound leaves and the fruit which often has more than 1 seed; features also shared by *C. opaca*. *Cissus opaca* also exhibits considerable variation in leaf morphology between juvenile and adult leaves in young plants arising from seed as well as in aerial parts developing from the resprouting of the underground tuber; this leaf polymorphism is particularly noticeable for individuals growing in moist situations.

Phylogenetic analyses by Rossetto et al. (2002) using sequence data from plastid (the *trnL* intron) and nuclear (ITS1) DNA strongly supported a clade comprising *Cissus opaca* and *Clematicissus angustissima* as being separate from the other Australian species analysed. Thus a new combination is required. Subsequent studies indicate that *Cissus tweedieana* forms a clade sister to *Clematicissus* along with *Cissus striata* Ruiz & Pav., another South American species (Rossetto et al. submitted). A study by Soejima & Wen (2006) indicated that *Cissus striata* was closely related to several species of *Rhoicissus*. Further studies, particularly molecular and developmental, are required to resolve these relationships.

Clematicissus opaca (F.Muell.) Jackes & Rossetto ***comb. nov.***

Basionym: *Cissus opaca* F.Muell., *Trans. & Proc. Philos. Inst. Victoria* 3: 23 (1859). Holotype: Brigolow [sic] scrub of eastern Australia (MEL 539836).

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Key to the species of *Clematicissus*

Flowers in a loose umbel, endosperm in transverse section W-shaped, New South Wales and Queensland .... ***C. opaca***

Flowers in a contracted umbel or head, endosperm in transverse section U-shaped, Irwin District Western Australia .... ***C. angustissima***

Both species are illustrated in Austrobaileya 2(5): 497 (Jackes 1988) and Austrobaileya 3(1): 102 (Jackes 1989) respectively.

References

Jackes BR (1988) Revision of the Australian Vitaceae, 3 *Cissus* L. *Austrobaileya* 2: 481–505.

Jackes BR (1989) Revision of the Australian Vitaceae, 4 *Clematicissus* Planchon. *Austrobaileya* 3: 101–102.

Rossetto M, Jackes B, Scott KD & Henry RJ (2002) Is the genus *Cissus* (Vitaceae) monophyletic: evidence from plastid and nuclear ribosomal DNA. *Systematic Botany* 27: 522–533.

Rossetto M, Crayn DM, Jackes BR & Porter C (submitted) Molecular evolution of the Australian Vitaceae. *Canadian Journal of Botany*.

Soejima A & Wen J (2006) Phylogenetic analysis of the grape family (Vitaceae) based on three chloroplast markers. *American Journal of Botany* 93: 278–287.

Urton NR, Olivier MC & Robertson BL (1986) The taxonomy of the *Rhoicissus tridentata* (Vitaceae) complex in southern Africa. *South African Journal of Botany*: 52:389–396.

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- References in the text should be made by giving the author's name with the year of publication in parentheses. For reference list at end of paper see papers in the latest issue for style. Titles of journals should be given in full.
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- Cite no more than 20 (except for very widely distributed species) and arrange by Botanical Divisions. Use accepted format: locality, collector & number, date (herbarium code plus institutional number if there is no collector's number) Only latitudes and longitudes on the original labels should be included. Give dates in the following format: 12 Jan 1987, 2 Jun, 30 Jul, 10 Dec etc.

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SHORT COMMUNICATION

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