

Grevillea gilmourii Olde and *G. milleriana* Olde (Proteaceae: Grevilleoideae: Hakeinae), two species newly described from New South Wales

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Abstract

Grevillea gilmourii Olde and *G. milleriana* Olde, two species new to science, are described. They are putative members of the *Aspleniifolia/Hookeriana* Subgroup of the *Grevillea Pteridifolia* Group. *Grevillea gilmourii* is separated from *G. macleayana* (McGill) Olde & Marriott where it had previously been treated as the ‘*Deua form*’, a geographically disjunct, divided-leaf variant. The separate formal recognition of *G. gilmourii* here necessitates a revised delineation of *G. macleayana* to restrict it to populations with undivided leaves only, incorporating recent clarification to terminology in relation to leaf lobing. *Grevillea milleriana* is a recent discovery from the Maddens Plains area, south of Sydney. Known from a single plant, its recognition as a biological species rather than as a self-sown hybrid is discussed. All three species are linked morphologically and historically to the Victorian species *G. barklyana* F.Muell. ex Benth., which remains taxonomically unaltered from recent treatments. For the sake of convenience, all four species (*G. barklyana*, *G. macleayana*, *G. gilmourii* and *G. milleriana*) are grouped informally into an alliance, the *Grevillea barklyana* alliance, for which diagnostic characters are outlined and two identification keys are given. Both newly described species have divided leaves and are known from only small populations. Conservation recommendations are provided for both new species.

Introduction

Makinson (2000a) established the *Grevillea Pteridifolia* Group which corresponds broadly to Groups 31, 32, 33 and 35 *sensu* Olde and Marriott (1994). The *Grevillea Pteridifolia* Group was divided informally into 6 Subgroups, one of which was termed the *Aspleniifolia/Hookeriana* Subgroup. Forty-seven species in that Subgroup were included by Olde and Marriott (1994: 216–220) in their Group 35, although that number has subsequently increased to 54. All members of the *Aspleniifolia/Hookeriana* Subgroup have irregular, secund inflorescences, the abaxial surface of the perianth completely glabrous and follicles with red or purple-blotched exocarps. The four species recognised here, *G. barklyana*, *G. macleayana*, *G. gilmourii* and *G. milleriana*, appear to be more closely related to each other than to other species in the group and together form a subset of the *Aspleniifolia/Hookeriana* Subgroup, here termed for convenience the ‘*Grevillea barklyana* alliance’. This

alliance of species is closely linked to *G. laurifolia* Sieb. ex Spreng., *G. longifolia* R.Br. and *G. aspleniifolia* Knight but can be differentiated by the following combination of features:

- leaves broad (mostly ≥ 20 mm wide), elliptic, pinnatifid or with margins entire, the under-surface densely hairy except the midvein;
- inflorescences erect;
- pistils ≥ 18 mm long, the ovary stipitate, densely hairy;
- styles pink, glabrous except at base just above the ovary;
- style-end green or yellow.

Ferdinand Mueller (1860–61: 14) first mentioned his discovery of *Grevillea barklyana* in his annual report to the Victorian Parliament. ‘On my return to Melbourne I visited the Upper Tarwan, availing myself of a track formed by Mr. Devine’s prospecting party; the tall *Grevillea Barklyana* (sic) was discovered on this last occasion.’ Sir Henry Barkly, Toorak, then the Governor of Victoria, was noted (Mueller 1860–61: 3) in the same report as one of numerous donors to the Melbourne Botanic Gardens. It is somewhat surprising, given regular publication of new species in his *Fragmenta Phytographiae Australiae*, that Mueller neither described nor again mentioned this species until 1871, by which time Bentham (1870: 436–7) had published a description in *Flora Australiensis* based on Mueller’s collection, a duplicate of which he had selflessly remitted to Bentham sometime in 1870. Mueller (1871: 133) simply referred to it, (and in Latin), as a ‘shrub attaining a height of 12 feet’.

The next appearance of this ‘species’ came when flowering specimens of ‘*G. barklyana*’ collected by J.H. Maiden at Jervis Bay, New South Wales in July 1892 were displayed at the November meeting of the Linnean Society of New South Wales. Maiden showed them as ‘new’ for New South Wales, ‘hitherto recorded only from Gippsland’ (Maiden 1892: 404). However, according to correspondence cited by Olde (2005), Maiden was indeed well aware that the plant he collected was a new species and urged Mueller, with whom he corresponded on the matter, to name it after the recently deceased patron of science Sir William Macleay, M.P. However, the proposed taxonomic treatment lapsed after Mueller died in 1896 and Maiden did not progress the matter. Willis (1972) continued to recognise the Jervis Bay plants as a form of *G. barklyana*. Formal taxonomic recognition only eventuated when McGillivray (1986: 2) named it as *G. barklyana* subsp. *macleayana* McGill. In the diagnosis, he distinguished it from subsp. *barklyana* by its persistent floral [common] bracts, and its subvillous ovary.

In a fuller treatment of *G. barklyana*, McGillivray and Makinson (1993: 56) further elaborated differences between the two subspecies in their key which states, among other things, that subsp. *macleayana* has ‘leaves simple’. In a subsequent note on variation, it was stated that a collection from Diamond Creek, Deua National Park with ‘some divided leaves adjacent to the inflorescences’ ‘belongs to or is very closely allied to subsp. *macleayana*’ because of other shared floral features.

Olde and Marriott (1994: 185) regarded the stated floral differences between the subspecies as sufficient to enable recognition of *G. macleayana* as specifically distinct, while at the same time incorrectly interpreting embayments and some strong margin crenulation as leaf lobing, confounding it to some extent with *G. barklyana*, which has leaves with numerically more lobes. The species ranking was subsequently accepted in the *Flora of Australia* treatment (Makinson 2000a).

In their treatment of *G. macleayana*, Olde and Marriott (1995b: 9) recognised three forms, a ‘*Coastal form*’, a ‘*Woolly form*’ and a ‘*Deua form*’, all of which were stated to have various degrees of leaf lobing. More recently, leaf lobes have been more critically interpreted by Olde (2015: 99), with input unacknowledged until now, from Dr Peter Weston (NSW). ‘A leaf lobe is usually defined simply as part of a leaf enclosed by embayed or angular incisions in the margin. However, it is more strictly interpreted here as formed around a lateral or secondary vein that terminates at the margin in a short excurrent spine or mucro. Marginal teeth are short lobes formed from a higher order lateral vein or vein subsidiary to the intramarginal vein, but with a similar terminus. In a situation where both lobes and teeth are present, Crisp and Weston (1993, p. 56) have suggested that ‘the relative prominence of the vein leading to the lobe or tooth’ be used to differentiate them. Leaf-margin sinuation or crenulation differs in its lack of venation and is not therefore treated as a form of division.’

When we accept this definition, then neither the *Coastal form* (typical form), nor the *Woolly form* of *G. macleayana sensu* Olde and Marriott (1994) have lobed leaves. This sharpens and simplifies the conceptual distinction between populations with entire leaves only (all here included now in *G. macleayana*) and those sometimes with some divided leaves (here circumscribed as three separate distinct species: *G. barklyana*, *G. gilmourii*, and *G. milleriana*).

Subsequent collections from the Deua population at Diamond Creek, which is in steep country c. 100 km south-west from the nearest other populations of *G. macleayana*, confirm the other noted differences between the taxa outlined by McGillivray and Makinson (1993). These collections have been made by N. Taws *et al.* (NSW383047, NSW943097, NSW943098) and J. Knight *et al.* for the Eurobodalla Botanic Garden. This supports the decision taken here to separately recognise the ‘*Deua form*’ as a rare distinct species not only with its own distinctive morphology, but also different habitat and soil preference. Removing *G. gilmourii* from the previous circumscription of *G. macleayana* requires redefinition of the latter species with more concise morphological and ecological boundaries.

Grevillea milleriana represents a recent discovery known from only a single plant. Although a small population is inferred from previous anecdotal information, it has claims to being Australia’s rarest *Grevillea* species. It was first included notionally in *G. macleayana* as a geographically disjunct extension of range (c. 110 km from Nowra at the northern end of the distribution). However, its divided leaves and other characters distinguish it morphologically and its preference for dense vegetation in upland swamp heath differentiate it ecologically. It is therefore affirmed here as specifically distinct.

The four species circumscribed here in the *Grevillea barklyana* alliance can be separated morphologically based on the features presented in Table 1 and comparative illustrations of styles and inflorescences represented in Figure 1.

Table 1. A comparison of morphological features of species in the *Grevillea barklyana* alliance.

	<i>G. barklyana</i>	<i>G. macleayana</i>	<i>G. gilmourii</i>	<i>G. milleriana</i>
HABIT	small tree to 8 m	shrub (0.3–)2–3(–4) m	small tree to 7 m	low shrub to 0.5 m
LEAVES	lobed and entire	entire	lobed and entire	lobed and entire
length	(4.5–)10–30 cm	4–15 cm	7.5–19.2 cm	5–8.5 cm
lobes	triangular	absent	obovate to narrow-triangular	broadly triangular
lobe number	0–11	0	0–6	0–8
abaxial surface	minutely velutinous	curly tomentose	curly tomentose	sericeous
FLORAL RHACHIS length	50–100 mm	25–45 mm	25–45 mm	40–50 mm
COMMON BRACTS	oblong ovate–angularly ovate	depressed ovate–triangular	ovate	ovate
length	2.5–3 mm	0.8–2.3 mm	1.8–2.5 mm	2–2.5 mm
persistence	caducous before anthesis of any flowers	persistent to anthesis	persistent to anthesis	persistent at or just before anthesis
PEDICEL length	1.75–2 mm	1.5–2.5 mm	1–1.5 mm long	3.25–3.5 mm
indumentum	white-sericeous	white-tomentose to villous	white-tomentose to pubescent	white-sericeous with some coloured hairs
NECTARY	inconspicuous	inconspicuous	inconspicuous	prominent
PISTIL length	18.5–25 mm	22–28.5 mm	22–23 mm	18–19 mm
GYNOPHORE length	0.6–2 mm	2–2.5(–3) mm	1.5 mm	1–1.25 mm
indumentum	sericeous	tomentose–sub-villous	tomentose–sub-villous	sericeous
POLLEN-PRESENTER at anthesis	green	green	green soon yellow	yellow
shape	subconical	flat to broadly convex	flat to broadly convex	subconical
PERIANTH LIMB	fawn brown-sericeous	white-tomentose	white-tomentose	rusty-sericeous
POLLEN at anthesis	pale pink	white or pale pink to translucent	dark maroon-purple	yellow
ANTHER length	1 mm	1.2 mm	1–1.2 mm	0.5 mm

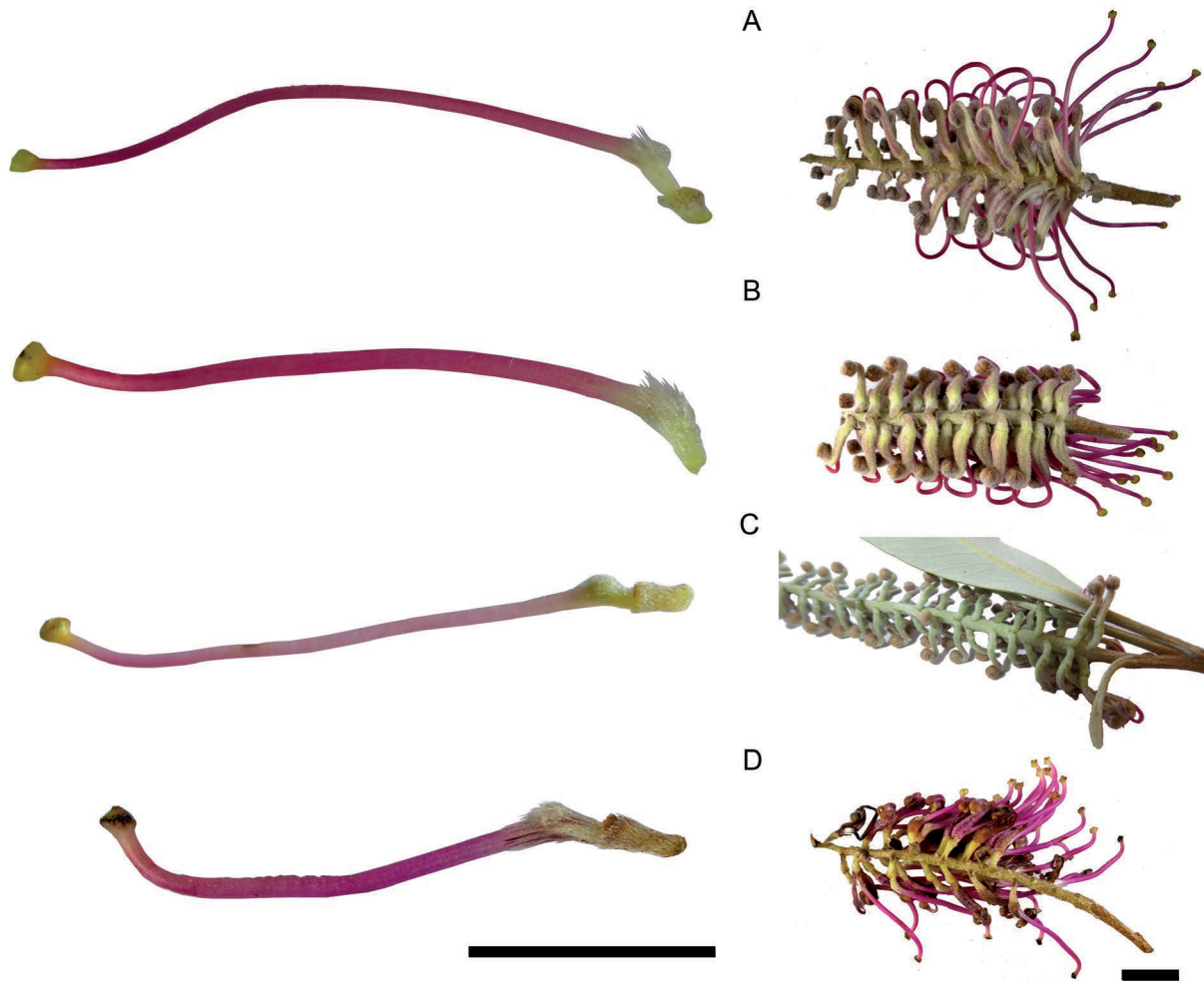


Fig. 1. A. *Grevillea gilmourii*, B. *G. macleayana*, C. *G. barklyana*, D. *G. milleriana*. Left: Comparison of ovary indumentum and style. Right: Comparison of conflorescence from below showing bract delapsus. Composite and images by M. Noake.

**Key to species in the *Grevillea barklyana* alliance and some closely related species
(modified from Olde and Marriott 1994: 219–220)**

- 59 Leaf under-surface tomentose with hairs chaotically oriented, curled or wavy, semi-appressed or spreading 60
- 60 Most leaves ≤ 15 mm wide *G. aspleniifolia*
- 60: Most leaves ≥ 20 mm wide 61
- 61 Ovary sericeous; all common bracts caducous before anthesis of any flowers in the raceme; small tree to 8 m with up to 11 triangular lobes (Vic) *G. barklyana*
- 61: Ovary pubescent-tomentose; common bracts persistent at anthesis; plants prostrate to small trees 61A
- 61A All leaves simple and entire; habit of plant semi-prostrate to shrubby (NSW) *G. macleayana*
- 61A: Some or all leaves divided; habit of plants a small tree (NSW) *G. gilmourii*
- 59: Leaf under-surface sericeous with hairs mutually aligned, straight, appressed 62
- 62 All leaves simple and entire 63
- 63 Most leaves ≥ 20 mm wide; habit prostrate (NSW) *G. laurifolia*
- 63: Most leaves < 12 mm wide; habit shrubby (NSW) *G. longifolia*
- 62: Some or all leaves divided or toothed 63A

- 63A** Common bracts 2–2.5 mm long, persistent at anthesis; pedicels > 3 mm long; pistils 18–19 mm long; most or all leaves <8.5 cm long; low-growing shrub <60 cm high (NSW) **G. milleriana**
- 63A:** Common bracts c. 1 mm long; caducous; pedicels 1.5–3 mm long; pistils 21–24 mm long; most or all leaves > 12 cm long; shrub 1.5–3 m high (NSW) **G. longifolia**

Alternative key to the *Grevillea barklyana* alliance

- 1** Abaxial surface of leaves sericeous **2**
- 2** All leaves simple and entire; styles red or black-red; habit of plant prostrate..... **G. laurifolia**
- 2:** Some or all leaves toothed or shallowly lobed; styles pink; habit of plant low-growing but not prostrate..... **G. milleriana**
- 1:** Abaxial surface of leaves tomentose **3**
- 3** All leaves simple and entire; habit a decumbent to spreading shrub **G. macleayana**
- 3:** Some or all leaves divided; habit a tree-like shrub 4–10 m high **4**
- 4** Common bracts 1.8–2.5 mm long, mostly persistent at anthesis; hairs on ovary ascending to spreading; leaves 10–20 cm long, with 0–6 lobes; pollen dark maroon-purple (NSW) **G. gilmourii**
- 4:** Common bracts 2.5–3 mm long, all caducous before anthesis of any flowers in the raceme; hairs on ovary tightly appressed; leaves 12–30 cm long with 0–11 lobes; pollen pale pink (Vic)..... **G. barklyana**

Taxonomy and Nomenclature

1. *Grevillea macleayana* (McGill.) Olde & Marriott, *The Grevillea Book* 1: 185 (1994e). *Grevillea barklyana* subsp. *macleayana* McGill., *New Names in Grevillea*: 2 (1986). *Hakea macleayana* (McGill.) Christenh. & Byng, *Global Flora* 4: 85 (2018).

Type: New South Wales: 0.3 miles [0.5 km] E. of Bream Beach, *R. Coveny* 3777, 14 Oct 1971 (holo: NSW 544140; iso: A 00589619).

Seedlings not seen. *Mature plants* spreading, seed-obligate, self-compatible, non-lignotuberous *shrubs* usually 1.5–2.5 m high, 1.5–5 m wide, usually bushy, rarely almost prostrate and 0.3 m high, 2–3 m wide or decumbent to 0.5 m high, 1 m wide, occasionally a sub-arborescent to 4 m tall, 2–3 m wide. *Branchlets* angular in cross-section, subglabrous, reddish or overlain by a white-tomentose evanescent indumentum often with brown striations. *New growth* bronze pink. *Adult leaves* dorsiventral, simple, (1–)4–13(–15) cm long, (10–)15–45 mm wide, ascending to spreading, not crowded (internodes to 100 mm long), petiolate, ovate to elliptic or oblong-elliptic; *petioles* 5–10 mm long; *leaf base* cuneate; *leaf apex* acute to obtuse, mucronate, the mucro decurved, non-pungent; *leaf margins* entire, flat or slightly recurved, often sinuous to crenulate; *venation* brochidodromous; *adaxial surface* glabrous or nearly so, dull, the midvein discolorous, conspicuous, impressed; *lateral veins* and *intramarginal veins* similar; *lateral veins* evident but narrower, widely angled at c. 60–70° to midvein; *edge-vein* sometimes evident, not enlarged, glabrous; *abaxial surface* densely white-tomentose except the prominently raised midvein greenish, subglabrous, the secondary venation and reticulum also raised but densely hairy; *texture* coriaceous. *Conflorescences* (25–)35–50 mm long, 25–30 mm wide, terminal or sub-terminal, leaf-opposed, erect, unbranched, acropetal, conical-secund to oblong-secund; *conflorescence buds* cylindrical to narrowly ovoid, pedunculate; *peduncles* 5–10 mm long, brown-black- or reddish-tomentose; *floral rachises* 25–45 mm long, 1.5 mm thick, white or brown, discolorous, sericeous-tomentose, with an apical flowerless extension c. 3 mm long; *common bracts* (0.8–)1.2–1.8(–2.3) mm long, 1.5–1.6 mm wide, ovate, concavo-convex, tomentose outside, glabrous inside or a few hairs towards the tip, most persistent to anthesis, a solitary bract subtending the proximal flower pair up to 10 mm long, leaf-like. *Flower colour*: perianth pinkish white outside, pale pink inside; limb white or sometimes brownish in the distal half; style pale or dark pink; pollen-presenter green to yellow. *Flowers* zygomorphic, inodorous, nectariferous, acroscopic; *pedicels* 1.5–2.5 mm long, 1.2 mm wide, white-tomentose to tomentose-villous; *torus* 1–1.5 mm across, transverse; *nectary* semi-annular, rising c. 0.1 mm above the toral rim, the margin uneven to minutely toothed; *pistils* 22–25(–28.5) mm long; *gynophore* 2–2.5(–3) mm long, tomentose-villous; *ovary* tomentose to sub-villous, prominent ventrally; *style* glabrous except for ascending hairs at base above ovary, undulate, strongly retrorse after anthesis and almost parallel to the rachis; *style-end* abruptly

divergent from style, unguiform; *pollen-presenter* 1.2 mm long, 1.2 mm wide, oblique to almost transverse, round to ovate-elliptic, the surface flat to broadly convex; *perianth* 8–10 mm long, 1.5–2.5 mm maximum width, oblong-sigmoid, narrowed to 1 mm wide at the curve, tomentose outside, glabrous inside, the inner surface scarcely visible, after anthesis, falling as a coherent unit; *tepals* attached to the toral rim; *limb* 2.5 mm long, 2 mm wide, white, ovoid, declined, densely sericeous-tomentose to tomentose-villous, tightly enclosing the style-end; *anthers* 1.2 mm long; *pollen* translucent to white or pink, sometimes abundant. *Fruit* 12–19 mm long, 8 mm wide, on inflexed pedicel, laterally compressed, oblong/ovoid, the apex attenuate; *style* persistent; *pericarp* c. 0.5 mm thick; *exocarp* tomentose, purple-striped or in irregular patches, ridged on dorsal side; *mesocarp* crustaceous; *endocarp* smooth. *Seed* 15 mm long, 5 mm wide, elliptic, rugose. (Figs 1B, 2)



Fig. 2. *Grevillea macleayana*. A. Flowers and foliage from a medium spreading shrub near Point Perpendicular lighthouse. B. A prostrate plant from near Racecourse Creek, Ulladulla, in cultivation. C. Decumbent shrub near Currarong on track to Abrahams Bosom. D. Sub-arborescent shrubs near Blenheim Beach. Photos: A, C, D: P. Olde; B: M. Noake.

Distribution: From the South Coast of New South Wales, between Nowra and the Jervis Bay area, Green Patch, Honeymoon Bay, Point Perpendicular, Currarong, Hyams Beach, Blenheim Beach, Bream Beach, Vincentia, extending patchily west of Nowra to Bundanoon and then south c. 65 km to Ulladulla.

Phenology: Flowers from May to February with spasmodic flowers at other times.

Habitat and ecology: Grows generally in relatively small, isolated populations of scattered plants, occasionally in numerically large populations. Usually found in elevated coastal scrub, heath or woodland in well-drained, acid sand derived from sandstone. Associated species include *Banksia serrata*, *B. ericifolia*, *B. integrifolia*, *Hakea sericea* and other common coastal species.

Conservation status: Although not currently considered to be endangered, *G. macleayana* is mostly restricted to an area < 70 km long, 20 km wide, in areas that receive considerable tourist traffic in summer. Although it is

contained in several Nature Reserves and National Parks, some of these areas are close to habitation and have been degraded by over-use.

Etymology: A suggestion of J.H. Maiden in 1892 that Mueller should honour Sir William Macleay (1820–1891), pastoralist, MP and ‘promoter of Science in New South Wales’, in the epithet was not at the time brought into effect. However, D.J. McGillivray (1986) later acted within the same spirit in choosing the epithet, though using a different specimen on which to base the name.

Variation: McGillivray and Makinson (1993: 56) drew attention to two variants, then known from single specimens, notable for their morphological variation and geographic disjunction from the main areas of occurrence of *G. macleayana*. The plants from Diamond Creek in Deua National Park, the first variant recognised, are here treated as *Grevillea gilmourii*, a separately distinct species. The specimen from the Bundanoon area (NSW 1281169) was treated as a second variant, the ‘Woolly form’, by Olde and Marriott (1995b: 9), because of its slightly larger common bracts and the ‘rather more profuse and woolly indumentum on the flowers’ (McGillivray and Makinson (1993: 56). The ‘Woolly form’ continues to be recognised informally here as a geographically disjunct variant (c. 40 km north-west of, and inland from, the nearest other occurrence of the typical populations) but warrants further study. Should the morphological variation and geographic disjunction be corroborated by plants in a viable population, then the status of this form will need review. It is currently still known only from a single collection made in 1963 (*Coveny s.n.*, NSW 1281169).

Olde and Marriott (1995b: 9) also recognised a ‘Coastal form’ which is more or less co-occurring with the main or typical populations. Among them a plant near Ulladulla (Olde 93/01 – NSW 899105; Orme 410 *et al.* – NSW 617990) was noted as being prostrate and has been introduced into cultivation where it maintains a ground-hugging, spreading habit. A similar, slightly larger plant c. 0.5 m high, 1 m wide, was found on the main walking track at Abraham’s Bosom, near Currarong by the author and a study party in 2020.

Ayre (1994) found that an unusually large population comprising hundreds of plants at Honeymoon Bay consisted of atypically tall plants more than 4 m high. These were found as understorey plants within a eucalypt woodland, an uncommon ecotone at variance with populations typically co-dominant in heath or low woodland.

Discussion: Between 1993 and 2009, honours, post-doctoral students and lecturers at the University of Wollongong have focused on *G. macleayana* in a series of ecological, pollination and genetic studies.

Harriss and Whelan (1993) found that *G. macleayana* was self-compatible and that there was virtually no difference in fruit set resulting from autogamy, geitonogamy and xenogamy. Ayre *et al.* (1994) reported that in most populations (3 out of 4) the plants were almost all completely selfed or inbred. In the remaining population, the plants were highly xenogamous. Although the mode of pollination is highly variable, the species appears to well-tolerate high levels of inbreeding. Edwards and Whelan (1995) investigated the soil-stored seed bank and found no seeds outside the existing canopy of living plants. Seeds found were small in number and germinated erratically. 75% of all seed was innately dormant. Vaughton (1995) studied whether *G. macleayana* engaged in selective abortion of less vigorous progeny to enhance the average quality of its seed crop but found that, notwithstanding high levels of fruit abortion in early development, there was no difference between fruits arising from differing modes of pollination. Vaughton (1996) followed up this study with a pollinator comparison in which she found that European honeybees were less efficient pollinators than nectar-feeding birds in *G. macleayana*. Vaughton (1998) next turned to a study of the size and dynamics of the soil seed bank in order to identify fire frequencies that might threaten population survival. Although plants began flowering only 2 years after fire, maximum seed production did not occur for about 15–16 years when plants reached full size, after which senescence set in and seed production declined. More than 95% of flowers failed to develop fruits. Of the initiated fruits, 60% aborted, 27% were attacked by parrots and only 13% matured. Mature seeds were also consumed and dispersed by rodents after falling to ground. Seed recruitment was negligible without fire but after fire, seedlings outnumbered adults 20:1 and there was a 90% survival rate in years with above average rainfall. Vaughton (1998) concluded that population numbers are limited by the size and dynamics of the seed bank if fire intervals are less than 10 years or greater than 25 years.

Hogbin *et al.* (1998) looked at genetic variation and reproductive success of road-verge populations. They found that three road verge populations under study produced significantly more inflorescences and seed than three nearby non-verge populations. They also detected similar levels of genetic variability within and among road-verge and non-verge populations. They concluded that all three road-verge populations had relatively great conservation value, as all were apparently as fecund and as genetically diverse as conspecific non-verge populations. England *et al.* (2001) found that honeybee activity is so high that the contribution of birds to pollination in *G. macleayana* is sometimes relatively trivial. England *et al.* (2002) argued that natural patterns of pollen and seed dispersal, coupled with a patchy, fire-shaped distribution, may have restricted long-distance

gene flow in the past. England *et al.* (2003) studied the effect of anthropogenic disturbance to the seed bank on the genetic structure of populations. They found that at two sites, disturbed by road building, mixing of the seed bank was evident, countering naturally low dispersal and elevated selfing due to honeybees. Pollinator activities may be expected to fluctuate from one flowering season to the next, as well as between populations. Whelan *et al.* (2009) concluded that the characteristics of bird visits to *G. macleayana* are sufficient to produce significant variation in outcrossing rates among sites, especially in the presence of honey-bees, which are likely to be responsible for rapid pollen removal from flowers and little pollen deposition on flowers of distant plants. In addition to these summarised studies, Lloyd (2006) presented an extensive doctoral thesis to the University of Wollongong concerning the pollination ecology and reproductive success of *Grevillea macleayana*.

Selected specimens: New South Wales: Fauna Reserve, just past Ulladulla, *J.Basset s.n.*, 19 Nov 1971 (NSW 544133); Nowra–Nerriga, *J.Boorman s.n.*, Feb 1910 (NSW 544128); Nowra–Turpentine, *J.Boorman s.n.*, 1915 (NSW 92417); Nowra Airfield, *R.F.Brown* 2310 & *P.M.Olde*, 20 Aug 1988 (NSW); cnr Hames and Braidwood Rds, West of Nowra, *R.F.Brown* 2416 & *P.M.Olde*, 20 Aug 1988 (NSW); Ulladulla, *R.H.Cambage* 3495, 28 Dec 1911 (NSW 617990); Jindelara Creek, Milton, *R.H.Cambage s.n.*, 1 Jan 1918 (NSW 92430, SYD); ‘Hell Hole’ between Tomerong and Nerriga Road, *J.Cole s.n.*, 5 Oct 1943 (NSW 92418); 0.5 mi [0.8 km] NW of lighthouse, Pt Perpendicular, *E.F.Constable s.n.*, 7 Oct 1960 (MO, NSW 52340); Pt Perpendicular Beecroft Peninsula Jervis Bay, *J.Cosh s.n.*, 17 Sep 1984 (WOLL); Bundanoon area, *R.Coveny s.n.*, 5 Oct 1963 (NSW 1281169); Cave Beach Rd., 4.5 km SW of Jervis Bay, *R.Coveny* 3707, 12 Oct 1971 (NSW 544131); Jervis Bay and Cruckadille, *C.W.Darley s.n.*, 1895 (NSW 92427); Cave Beach Rd., 1 km N of ANBG Annexe entrance, *F.W.Howe* 54, 12 Sep 1983 (AD, CANB 8317598, LE, MEL 713984, NSW 473989, NY, PRE); Along road to Green Point, 2 km from junction of Green Point Road and Point Perpendicular Road, Beecroft Peninsula, Jervis Bay, *M.Kennedy* 576 & *D.West*, 28 Sep 1993 (NSW 277638); Jervis Bay, *J.H.Maiden s.n.*, 28 Jul 1892 (MEL 98862; NSW 544130); Jervis Bay, *J.H.Maiden s.n.*, Jul 1899 (NSW 92420); Hyams Beach, Jervis Bay NP, *T.Mason s.n.*, 10 Nov 2002 (WOLL 11459); Parma Creek Nature Reserve, beside Braidwood–Nowra Road, SW of Albatross Navy Base, *K.L.McDougall* 955, 5 Sep 2001 (MEL 2210127, NSW); Behind Blenheim Beach, Vincentia, *J.Millott s.n.*, 7 Sep 2002 (WOLL 7593); Abrahams Bosom Reserve, Currarong, *K.Mills s.n.*, 4 Sep 1987 (NSW544132); Ettrema Gorge, Morton National Park, *K.Mills s.n.*, 5 Jun 1987 (WOLL 807); Princes Highway, Racecourse Creek, Ulladulla, *P.M.Olde* 93/01, 22 Jan 1993 (BRI, MEL, NSW 899105); Around the water tower, Vincentia, *P.M.Olde* 97/24, 24 Oct 1997 (BRI, NSW 535288); 50 m along Kings Point Road from Princes Highway, Ulladulla, *A.E.Orme* 410, *P.M.Olde*, *N.R.Marriott*, 31 Oct 2003 (NSW 617990); at entrance to Jervis Bay Botanic Gardens Annexe, Jervis Bay National Park, *B.Rann* 1, 5 Aug 1993 (NSW 274778); Jervis Bay Beach, near Naval College, *F.A.Rodway s.n.*, Oct 1923 (NSW 92425); 1.5 km W of Commonwealth Naval Base, *J.H.Willis s.n.*, 20 Mar 1954 (MEL 98864); South Pacific Heathland Reserve, Coral Crescent, 1.4 km S of Ulladulla Post Office, *P.H.Weston* 3192, 20 Jun 2008 (CANB 703191, NSW 768982).

2. *Grevillea gilmourii* Olde, *sp. nov.*

Type: New South Wales: Diamond Ck., NW of Coondella Trig., Deua National Park, *P.Gilmour* 4832, 16 Oct 1984 (holo: NSW 473991; iso: CBG 8413639 (2 sheets), ERBG-8783).

Grevillea macleayana ‘Deua form’ *sensu* Olde & Marriott (1995b: 9)

Seedlings not seen. *Mature plants* erect, seed-obligate, probably self-compatible, non-lignotuberous trees 4–7 m high with spreading crown. *Branchlets* angular in cross-section, rusty-tomentose with subglabrous brown striations. *New growth* dull pink. *Adult leaves* dorsiventral, simple and divided, 7.5–19.2 cm long, 20–75 mm wide, ascending to spreading, not crowded (internodes to 100 mm), petiolate, coriaceous; *simple leaves* 7.5–15 cm long, 20–40 mm maximum width, narrow-elliptic to oblong-elliptic; *divided leaves* 10–19.2 cm long, 55–75 mm maximum width, obovate in outline, bifid or irregularly pinnatifid with 2–3(–6) lobes; *leaf lobes* 5–8 cm long, 16–25 mm wide, broadly to narrowly subtriangular to broadly obovate; *petioles* 5–10 mm long; *leaf base* cuneate, sometimes unequal; *apex of leaves and lobes* acute to obtuse, mucronate, the mucro decurved, non-pungent; *leaf margins* entire or lobed, flat to shortly recurved, sometimes undulate; *venation* mixed, mostly brochidodromous but usually a few lateral veins terminating in an excurrent mucro or spine; *adaxial surface* glabrous or almost so, dull, midvein discolourous, clearly evident, impressed; *lateral veins* and *intramarginal veins* narrower, similar; *lateral veins* widely angled at 60°–70° to the midvein; *edge-veins* sometimes evident, enlarged or not, green, glabrous; *reticulum* fine, very faintly evident; *abaxial surface* densely white-tomentose, or with scattered rusty hairs, a ferruginous indumentum covering the prominently raised, discolourous midvein; secondary veins and anastomosing penninervation faintly evident; *texture* coriaceous. *Conflorescence* 3.5–4 cm long, 20–25 mm wide, terminal or subterminal, leaf-opposed, erect, unbranched, acropetal, broadly secund; *conflorescence buds* narrowly ovoid, exerted bracts evident, pedunculate; *peduncles* 5–15 mm long, rusty-tomentose; *floral rachises* 25–45 mm long, 1.5 mm thick, discolourous, white-tomentose, with an apical flowerless extension *c.* 3 mm long; *common bracts* 1.8–2.5 mm long, 1.5 mm wide, ovate,

shallowly concavo-convex to flat, tomentose-villous outside, glabrous inside, persistent at anthesis. *Flower colour*: perianth greenish white becoming pale pink outside, pink inside; limb white; style pale pink; style-end green becoming yellow. *Flowers* zygomorphic, inodorous, nectariferous, acroscopic; *pedicels* 2 mm long, 1–1.5 mm thick, white, pubescent-tomentose; *torus* 1.5 mm across, slightly oblique; *nectary* semi-annular, rising 0.4 mm above the toral rim, the margin uneven to minutely toothed; *pistils* 22–23 mm long; *gynophore* 1.5 mm long, openly tomentose-villous; *ovary* villous, prominent ventrally; *style* glabrous except for ascending hairs at base above the ovary, straight or undulate, oblique immediately after anthesis, ultimately strongly retrorse; *style-end* abruptly divergent from style, unguiform; *pollen-presenter* 1.25 mm long, 1 mm wide, oblique, elliptic, the surface flat to broadly convex; *perianth* 10 mm long, 1.5 mm maximum width, oblong-sigmoid, not dilated at base, narrowed to 1 mm wide at the curve, openly subsericeous on the abaxial surface, the hairs white or red intermixed, the adaxial surface partly visible at anthesis, glabrous, falling as a coherent unit; *tepals* attached to the toral rim; *limb* 2.5 mm long, 2 mm wide, white, ellipsoid, nodding to declined, densely tomentose-villous, tightly enclosing the style-end; *anthers* 1.2 mm long; *pollen* maroon–dark purple, abundant. *Fruit and Seed* not seen. (Fig. 3)

Diagnostic characters: Closely related to *Grevillea macleayana* (McGill.) Olde & Marriott, but differing in its taller, tree-like habit (4–7 m high) with spreading crown versus a spreading shrub [(0.3–)1.5–2.5(–4) m high], and in its leaves both simple and divided versus all simple and entire.

Distribution: Known only from the type location in Deua National Park, New South Wales, which is c. 100 km south-west of the nearest known population of *G. macleayana*.

Phenology: Cultivated plants and specimen records indicate flowering from late winter to summer.

Habitat and ecology: Found on a terrace at a bend in the creek. Soils are deep brown clay derived from volcanic rhyolite mixed with Silurian porphyry, formed in this area as part of the Comerang Volcanic Series. It occurs in open forest with upper storey including *Acacia sylvestris*, *Allocasuarina littoralis* in association with a dense understorey of *Hakea macraeana*, *Phebalium squamulosum* subsp. *squamulosum*, *Prostanthera lasianthos* and *P. incisa*. Recorded summer temperatures range from 6.6°–44.8°C. Lowest winter minimum is –5.6°C. Rainfall varies from 480–1160 mm annually. Cultivated plants at Eurobodalla Botanic Garden have regenerated from seed after fire impacted the site.

Conservation status: *Grevillea gilmourii* is known from a single population which is infrequently monitored. Because of its restricted distribution and low population number, it must be treated as critically endangered in the wild. Feral goats, deer, climate change, increased fire frequency, lower precipitation and other stochastic events are all seen here as potential threats to regenerating seedlings and therefore to its ongoing viability. Like many other species that occur in steep habitats with volcanic origins, *G. gilmourii* is known from a single population.

Etymology: This species is named for its discoverer Phillip ‘Phil’ Gilmour (fl. 1970–), an ecologist whose collections from remote areas of this difficult south-coast terrain are worthy of greater recognition.

Variation: A reasonably uniform species but with considerable variation in the number and shape of leaf lobes. Some plants have most leaves entire with only a few lobed. Others have most leaves divided and only a few entire.

Discussion: McGillivray and Makinson (1993: 56) have noted the closer morphological similarity of *Grevillea gilmourii* to *G. macleayana*, in preference to *G. barklyana*, which differs in its ovary and gynophore with a close sericeous indumentum, its leaves longer and with more numerous lobes, and in its pollen-presenter subconical. From its comparator *G. macleayana*, which is now circumscribed as having only entire leaves, *G. gilmourii* also differs in being geographically disjunct, in its occurrence at higher elevations (130 m) and on volcanic soils, in its riparian habitat in tall wet sclerophyll forest. *Grevillea gilmourii* differs morphologically from *G. macleayana* in its arborescent habit 4–7 m high with a spreading crown and in having some to most of its leaves always divided. Its pollen is noticeably maroon-red coloured whereas that of *G. macleayana* is transparent to pink. *Grevillea macleayana* is also distinguished by its mostly shrubby habit (to c. 2 m high, rarely to 4 m in Eucalypt woodland). The differences provide clear evidence of lineage divergence between *G. macleayana* and *G. gilmourii*.

Specimens seen: New South Wales: Deua National Park, Diamond Creek, 600 m upstream from junction with Coondella Creek, *N.Taws* 360, 2 Jan 1994 (CBG 9400110, NSW 943097); Deua National Park, Diamond Creek, 600 m upstream from junction with Coondella Creek, *N.Taws* 361, *A.Scott*, *W.Marsden*, 2 Jan 1994 (CBG 9400008, NSW 9430098, NSW 383047).



Fig. 3. *Grevillea gilmourii*. A. Young plant in cultivation, Moruya, NSW. B. Conflorescence and new growth in cultivation. Photos: M. Noake.

3. *Grevillea milleriana* Olde, *sp. nov.*

Type: New South Wales: Heathcote Soaring League Model airfield, crown lease adjacent to Dharawal Nature Reserve, Old Princes Highway, Maddens Plains, Central Coast, NSW, P.M. Olde 21/01 & G.P. Phillips, 22 Sep 2021 (holo: NSW 1115010; iso: CANB *distribuendus*).

Seedlings not seen. *Mature plants* spreading, subprostrate, seed-obligate, probably self-compatible, non-lignotuberous *shrubs*, c. 0.3 m high, 0.5 m wide with lower branches trailing on ground. *Branchlets* angular in cross-section, openly brown-tomentose with brown striations. *New growth* not seen. *Adult leaves* dorsiventral, simple and divided, (0.7–)5–8.5 cm long, (0.7–)15–35 mm wide, ascending to spreading, not crowded (internodes to 20 mm), petiolate, leathery; *simple leaves* 5–6 cm long, 20 mm wide, elliptic or oblong-elliptic; *divided leaves* 6–8.5 cm long, 20–30 mm wide, obovate to elliptic, usually with 1–8 lobes; *leaf lobes* 2–6 mm long, 5–10 mm wide at base, broadly triangular; *petioles* 5–6 mm long; *leaf base* broadly cuneate; *leaf apex* obtuse, mucronate, the mucro decurved, non-pungent; *leaf margins* entire or lobed, flat or slightly recurved, slightly undulate; *venation* mixed, mostly brochidodromous but usually a few lateral veins terminating in an excurrent mucro or spine; *adaxial surface* glabrous or nearly so, dull, the midvein discolorous, conspicuous, impressed; *lateral veins* and *intramarginal veins* narrower, similar; *lateral veins* acutely-angled at c. 45° to midvein; *edge-veins* obscure; *reticulum* obscure to faintly evident; *abaxial surface* densely white-sericeous, the midvein and lateral veins prominently to slightly raised, the midvein discolorous, subglabrous, green; secondary veins and anastomosing penninervation faintly evident; *texture* coriaceous. *Conflorescences* 35–45 mm long, 15 mm wide, sub-terminal, leaf-opposed, erect, unbranched, acropetal, conico-secund; *conflorescence buds* cylindrical to narrowly ovoid, pedunculate; *peduncles* 5–12 mm long, white-sericeous; *floral rachises* 40–50 mm long, 1.2–1.8 mm thick, concolorous, white-sericeous, with apical, flowerless extension c. 3.5 mm long; *common bracts* 2–2.5 mm long, 2 mm wide, ovate, strongly incurved from just above base, sericeous outside, glabrous or with a few scattered hairs inside, caducous at or just before anthesis. *Flower colour*: perianth pink outside, purple-pink inside; limb brown-sericeous; style reddish-pink; pollen-presenter yellow. *Flowers* zygomorphic, inodorous, nectariferous, acroscopic; *pedicels* 3.25–3.5 mm long, 0.5–0.75 mm thick, openly white-sericeous with some hair contents coloured; *torus* 0.8–1.5 mm across, oblique; *nectary* semi-annular, rising 0.2–0.4 mm above the toral rim, the margin uneven to minutely toothed; *pistils* (14–)18–19 mm long; *gynophore* 1–1.25 mm long, white-sericeous with scattered red hairs interspersed; *ovary* white-sericeous with scattered red hairs intermingled, prominent ventrally; *style* glabrous except for appressed hairs at base above the ovary, ascending to erect after anthesis; *style-end* abruptly divergent from style, unguiform; *pollen presenter* 1.2–1.5 mm long, 1.2–1.5 mm wide, slightly oblique, round to broadly elliptic, the surface broadly conical, the stigma c. 0.5 mm above base; *perianth* 6–7 mm long, 1.2–1.8 mm maximum width, narrowly ovoid-sigmoid, 0.6–1.2 mm wide at the curve, sparingly white-sericeous outside, glabrous inside, the adaxial surface partly visible at anthesis, after anthesis falling as a coherent unit; *tepals* attached to the toral rim; *perianth limb* 1.25–1.8 mm long, 1.75–2 mm wide, ovoid to depressed-globose, declined to revolute, densely ferrugineo-sericeous, tightly enclosing the style-end; *anthers* 0.5 mm long; *pollen* yellow. *Fruits and Seeds* not seen. (Figs 4, 5)

Diagnostic characters: Differs from *G. macleayana* (McGill) Olde & Marriott in some of its leaves shallowly 1-8-lobed or toothed versus always entire, the abaxial surface sericeous versus curly-tomentose, its pedicels longer (3.25–3.5 mm versus 1.5–2.5 mm), its pistils shorter (14–)18–19 mm long versus 22–28.5 mm long, its perianth limb rusty-sericeous versus white-tomentose, its anthers 0.5 mm long versus 1.2 mm long, its pollen white to yellow versus translucent to white or pale pink, its ovary and gynophore sericeous versus tomentose.

Distribution: New South Wales. Confined to a small area near Darkes Forest, c. 60 km S of Sydney.

Phenology: Flowering commences at the end of August and continues probably throughout spring.

Habitat and ecology: Grows in wet, sandy grey loam in densely vegetated upland swamp heath dominated by low-growing clumps of *Hakea teretifolia* and sedges, associated with *Actinotus minor*, *Banksia paludosa*, *Isopogon anemonifolius*, *Petrophile pulchella*, *Bauera microphylla*, *Allocasuarina paludosa*, *Lepidosperma forsythii*, *Epacris obtusifolia*, *Xanthorrhoea resinosa*, *Xyris* sp. The nectariferous flowers are ornithophilous, a pollination syndrome discussed by Carolin (1961) and defined here as flowers with the following characteristics: bright coloration, inodorous, tube-shaped with strong tepal structure and coherence, prominently displayed, and borne on branches sufficiently strong, and with stigmas on overarching pistils capable both of depositing pollen on a probing nectarivore and receiving transferred pollen. Honey-eaters (Meliphagidae) are the common suspect pollinators in Australia but none have yet been observed on *G. milleriana*.

Conservation status: Presently known from a single individual plant although other sightings have been reported elsewhere in the Darkes Forest area. The only confirmed ‘population’ is adjacent to a regularly mown airfield which will provide considerable challenges for conservation management.



Fig. 4. *Grevillea milleriana*. A. Plant in natural habitat. Photo: P. Olde.



Fig. 5. *Grevillea milleriana*. A. Conflorescence. B–D. Leaf variation. Photos: G. Phillips.

Etymology: The epithet recognises the joint discovery of this species in August 2021 by ecologists Robert T. Miller (R.T.Mill.) (1950–) and Janice Miller, née Peters (1953–).

Discussion: This species was first brought under notice by Mr Nathan Kirkwood (Olde 2002) who reported that he had seen various *Grevillea* species of interest in association with *G. longifolia* while mountain-bike riding as a youth in the Darkes Forest area many years earlier. An area, subsequently confirmed as wrong, was searched by a party which included Mr Robert Miller, Richard Johnston (then seed collector, Australian Botanic Garden, Mt Annan) and the author but no plants were located (Olde 2004). Mr Miller subsequently spent much time searching the area in a private capacity without results. However, more recently, he and his wife Jan, chanced upon a single plant, from which we infer a small population that is not extant in the immediate vicinity. Although the species is known currently from only one living plant, it is expected that further populations will be located in the coming years. The plant from which the type specimen was collected has been previously slashed to ground level and has regenerated from branches spreading below the level of the mower blade.

A follow-up visit to the site with Mr Kirkwood resulted in positive recognition of *G. milleriana* that he now admits to having mis-identified as a youth as *G. caleyi* (Olde 2004). He then pointed to a second site, where he remembered seeing plants: a track heading south off Darkes Forest Rd that leads towards a branch of Waratah Rivulet, the same watercourse on which *G. milleriana* occurs. An immediate search could not be conducted because the area has been made inaccessible by Sydney Water environmental exclusion fencing. Mr Kirkwood also advised that he saw the same plant along O'Hare's Creek, also yet to be searched. The anecdotal existence of *G. milleriana* at multiple sites suggests that it is not a hybrid.

Although the possibility that *G. milleriana* represents the successful establishment of a self-sown seedling arising from horticulture or the wild cannot be eliminated, it is nonetheless considered to be highly improbable. Based on floral morphology, at least one of its putative parents would have been drawn from a species in the *G. barklyana* alliance, the nearest wild source being *G. macleayana*, 100 km to the south. If *G. milleriana* is a self-sown hybrid seedling then distance strongly mitigates the likelihood of wild plants of *G. macleayana* as a putative parent. Furthermore, almost 60% of fertile seed of *G. macleayana* examined by Lloyd (2006) was found to selfed, so it is not a wildly promiscuous species.

Grevillea macleayana has been sold in native nurseries during the 1980s but it is not generally long-lived in the Sydney region, is not widely planted, and has never been used successfully as a landscape plant. Furthermore, there is no human habitation or home landscaping in the immediate area of the type locality, although a school is located further to the south and a golf club is opposite.

Grevillea macleayana has figured putatively in two hybrid cultivars, *G. 'Coastal Glow'* = *G. 'Frampton's Hybrid'* = *G. longifolia* × *G. macleayana*, and *G. 'Brookvale Letitia'* (*G. macleayana* × *G. acanthifolia*). The latter cultivar arose in Queensland in horticulture and was never sold in New South Wales. It has not been seen or cultivated in over 40 years. The former is a robust shrub to 3 m in height, requiring good garden conditions, rarely cultivated and not known for its fertility or the production of garden seedlings. Moreover, a planting of neither cultivar was found on the adjacent golf course. *Grevillea longifolia* cannot be entirely ruled out as a possible parent of a putative hybrid with *G. macleayana*. However, the likelihood of a natural connect is ruled out by geography and the low-growing habit of *G. milleriana* is not really a conceivable product of hybridisation between these two robust shrubby species.

The possibility that *G. milleriana* is a hybrid between *G. laurifolia* and *G. macleayana*, neither of which occur nearby in nature, has been entertained but rejected because of the unlikely chance that two entire-leaved species would produce a plant with divided leaves. However, *G. laurifolia* is known to hybridise with *G. acanthifolia* with which it co-occurs in the wild. *Grevillea* × *gaudichaudii* was named from a hybrid swarm still extant in the upper Blue Mountains and there are a couple of hybrids with it as putative parent including *G. 'Grassfire'* and *G. 'Hunter Beauty'*. However, these latter two are either manipulated hybrids or occur in botanical collections with both parents present. Neither of these cultivars have set seed in cultivation and are therefore presumed to be of low fertility.

Grevillea barklyana, or a hybrid thereof, is grown in horticulture. Seedlings emanating from this species are always robust shrubs 2–4 m high and produce wide leaves with multiple, deeply incised, triangular lobes. They tend to arise only when the parent plant dies. *Grevillea 'Copper Rocket'* and *G. 'Taminga'* are the only known daughter cultivars of this species and they are not widely cultivated to my knowledge in the Sydney region, if at all. The likelihood of seed arising from further afield, such as from the Illawarra Grevillea Park, Bulli is also highly doubtful and speculative, as there is no self-sown seedling similar to *G. milleriana* known to have arisen there.

Anecdotal reports of additional wild plants that have been seen and reported since 2002 are given added weight by the discovery of the plant at Maddens Plains. The lack of a reasonable parental source of *G. milleriana* as a

self-sown hybrid, coupled with its own unique morphology unrepresented even closely in hybrid horticulture, and its adaptation to a unique, harsh ecological situation induces me to accept this plant as a biological species worthy of recognition.

Additional specimen seen: New South Wales: Maddens Plains, *P.M.Olde* 21/01, *R.Miller*, *J.Miller*, 2 Sep 2021 (NSW).

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References

- Ayre DJ, Whelan RJ, Reid A (1994) Unexpectedly high levels of selfing in the Australian shrub *Grevillea barklyana* (Proteaceae). *Heredity* 72: 168–174. <https://doi.org/10.1038/hdy.1994.24>
- Bentham G, Mueller F von (1870) *Grevillea*. *Flora Australiensis* 5: 417–489. (Lovell Reeve: London) <https://www.biodiversitylibrary.org/item/42576#page/443/mode/1up>
- Briggs JD, Leigh JH (1995) *Rare or threatened Australian plants*. (Australian National Parks and Wildlife Service: Canberra)
- Carolin RC (1961) Pollination in the Proteaceae. *Australian Museum Magazine* Sept. 1961: 371–374.
- Edwards W, Whelan RJ (1995) The size, distribution and germination requirements of the soil-stored seed bank of *Grevillea barklyana* (Proteaceae). *Australian Journal of Ecology* 20: 548–555. <https://doi.org/10.1111/j.1442-9993.1995.tb00574.x>
- England PR, Ayre DJ, Whelan RJ (1999) Microsatellites in the Australian shrub *Grevillea macleayana*. (Proteaceae) *Molecular Ecology* 8: 689–690. <https://doi.org/10.1046/j.1365-294x.1999.00873.x>
- England PR, Beynon F, Ayre DJ, Whelan RJ (2001) A molecular genetic assessment of mating-system variation in a naturally bird-pollinated shrub: contributions from birds and introduced honeybees. *Conservation Biology* 15: 1645–1655. <https://doi.org/10.1046/j.1523-1739.2001.00236.x>
- England PR, Usher AV, Whelan RJ, Ayre DJ (2002) Microsatellite diversity and genetic structure of fragmented populations of the rare, fire-dependent shrub *Grevillea macleayana*. *Molecular Ecology* 11: 967–977. <https://doi.org/10.1046/j.1365-294X.2002.01500.x>
- England PR, Whelan RJ, Ayre DJ (2003) Effects of seed bank disturbance on the fine-scale genetic structure of populations of the rare shrub *Grevillea macleayana*. *Heredity* 91: 475–480. <https://doi.org/10.1038/sj.hdy.6800308>
- Harriss F, Whelan RJ (1993) Selective fruit abortion in *Grevillea barklyana* (Proteaceae). *Australian Journal of Botany* 41: 499–509. <https://doi.org/10.1071/BT97046>
- Hermanutz L, Innes D, Denham A, Whelan RJ (1998) Very low fruit : flower ratios in *Grevillea* (Proteaceae) are independent of breeding system. *Australian Journal of Botany* 46: 465–478. <https://www.publish.csiro.au/bt/BT97046>
- Hickey LJ (1973) Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* 60: 17–33. <https://doi.org/10.1002/j.1537-2197.1973.tb10192.x>
- Hogbin PM, Ayre DJ, Whelan RJ (1998) Genetic variation and reproductive success of road verge populations of the rare shrub *Grevillea barklyana* (Proteaceae). *Heredity* 80: 180–186. <https://doi.org/10.1046/j.1365-2540.1998.00271.x>
- JSTOR Global Plants (2000 onwards) <http://plants.jstor.org/page/global-plants> (accessed April 2022)
- Keith DA, Lindenmayer D, Lowe AJ, Russell-Smith J, Barrett S, Enright NJ, Fox BJ, Guerin G, Paton DC, Tozer MG, Yates CJ (2014) Heathlands. In Lindenmayer D, Burns E, Thurgate N, Lowe A (eds) *Biodiversity and environmental change: monitoring challenges and direction*. pp. 213–282. (CSIRO Publishing: Melbourne)
- Keith DA, Myerscough PJ (1993) Floristics and soil relations of upland swamp vegetation near Sydney. *Australian Journal of Ecology* 18: 325–344. <https://doi.org/10.1111/j.1442-9993.1993.tb00460.x>
- Lloyd S (2006) The pollination ecology and reproductive success of the Australian shrub *Grevillea macleayana*. Thesis. University of Wollongong. <https://ro.uow.edu.au/theses/579/>
- MacArthur Sir William (1817–73), Horticultural correspondence and lists of plants, Unpublished papers, ms nos A2943, A2945, A2947, A2949. Mitchell Library, Sydney.

- McGillivray DJ (1986) New names in *Grevillea*. (Private: Castle Hill)
- McGillivray DJ, Makinson RO (1993) *Grevillea*, *Proteaceae*. (Melbourne University Press: Carlton, Victoria)
- McNeill J (2014) Holotype specimens and type citations: general issues. *Taxon* 63: 1112–1113. https://www.iapt-taxon.org/historic/Congress/IBC_2017/holotype.pdf
- Maiden JH (1892) Notes and exhibits. *Proceedings of the Linnean Society of New South Wales* (2nd Series Vol 7) 17: 404. <https://www.biodiversitylibrary.org/item/29776#page/426/mode/1up>
- Makinson RO (1991) Revised (2002) *Grevillea*. In Harden G (Ed.) *Flora of New South Wales* Vol. 2: 31–55. (New South Wales University Press: Kensington)
- Makinson RO (1996) Updated by Stajsic V (2016) *Grevillea barklyana*. In Walsh NG, Entwisle TJ (eds), *Flora of Victoria* Vol. 3, *Dicotyledons Winteraceae to Myrtaceae*. (Inkata Press: Melbourne) <https://vicflora.rbg.vic.gov.au/flora/taxon/92da312f-6c64-420d-be00-ba915f9da836>
- Makinson RO (2000a) *Proteaceae* 2, *Grevillea*. *Flora of Australia Volume 17A*. (CSIRO Publishing: Melbourne) <https://www.environment.gov.au/system/files/pages/9956603b-17a1-4fe2-b47a-3addcd924fc0/files/flora-australia-17a-proteaceae-2-grevillea.pdf>
- Makinson RO (2000b) *Grevillea*. In Harden GJ, Hardin DW, Godden DC (eds) *Proteaceae of New South Wales*: 117–151. (University of New South Wales Press: Kensington)
- Mast AR, Olde PM, Makinson RO, Jones E, Kubes A, Miller E, Weston PH (2015) Paraphyly changes understanding of timing and tempo of diversification in subtribe Hakeinae (Proteaceae), a giant Australian plant radiation. *American Journal of Botany* 102: 1634–1646. <https://doi.org/10.3732/ajb.1500195>
- Mueller FJH (1860–61) *Annual report of the Government Botanist and Director of the Botanical and Zoological Garden*. (Government Printer: Melbourne) <https://www.biodiversitylibrary.org/item/217350#page/16/mode/1up>
- Mueller FJH von (1871) *Grevillea barklyana*. *Fragmenta Phytographiae Australiae* 7 (Fascicle 56): 133 (Government Printer: Melbourne) <https://www.biodiversitylibrary.org/page/761094#page/134/mode/1up>
- Olde PM (2002) Bits 'n Pieces. *G. caleyi* and *G. macleayana* near Helensburgh. *Grevillea Study Group Newsletter* 62: 18. <http://anpsa.org.au/grevSG/grev62.pdf>
- Olde PM (2004) A southern distribution for *Grevillea caleyi*. *Grevillea Study Group Newsletter* 69: 6. <http://anpsa.org.au/grevSG/grev69.pdf>
- Olde PM (2005) Naming *Grevillea macleayana*. *Grevillea Study Group Newsletter* 72: 13. <http://anpsa.org.au/grevSG/grev72.pdf>
- Olde PM, Marriott NR (1994) *The Grevillea Book, Volume 1*. (Kangaroo Press: Kenthurst, New South Wales)
- Olde PM, Marriott NR (1995a) *The Grevillea Book, Volume 2*. (Kangaroo Press: Kenthurst, New South Wales)
- Olde PM, Marriott NR (1995b) *The Grevillea Book, Volume 3*. (Kangaroo Press: Kenthurst, New South Wales)
- Vaughton G (1995) No evidence for selective fruit abortion in the Australian shrub *Grevillea barklyana*. (Proteaceae). *International Journal of Plant Sciences* 156: 417–424. <https://www.jstor.org/stable/2475059>
- Vaughton G (1996) Pollination disruption by European honeybees in the Australian bird-pollinated shrub *Grevillea barklyana*. (Proteaceae). *Plant Systematics and Evolution* 200: 89–100. <https://www.jstor.org/stable/23642841>
- Vaughton G (1998) Soil seed bank dynamics in the rare obligate-seeding shrub, *Grevillea barklyana*. (Proteaceae). *Australian Journal of Ecology* 23: 375–384. <https://doi.org/10.1111/j.1442-9993.1998.tb00742.x>
- Whelan RJ, Ayre DJ, Beynon FM (2009) The birds and the bees: pollinator behaviour and variation in the mating system of the rare shrub *Grevillea macleayana*. *Annals of Botany* 103: 1395–1401. <https://doi.org/10.1093/aob/mcp091>
- Willis JH (1972) *A Handbook to Plants in Victoria*. Vol. 2: 38–48. (Melbourne University Press: Carlton)

