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The taxonomic web of the Grey Spider Flower: Grevillea buxifolia (Proteaceae)

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Abstract

Hart, J.M. and Henwood, M.J. (John Ray Herbarium, School of Biological Sciences, Macleay Building A12, The University of Sydney, NSW 2006). The taxonomic web of the Grey Spider Flower: Grevillea buxifolia (Proteaceae). Telopea 7(1): 65–76. The Grevillea buxifolia (Sm.) R. Br. species complex displays a wide range of morphological variation. The complex has undergone several taxonomic revisions in recent years, none of which has adequately accommodated the morphological variation within a robust classification. Principal component analysis and cluster analysis of 100 individuals and 35 characters were used to analyse the complex. These analyses indicated that the complex comprises four taxa. Two of the taxa are recognised as species; *G. phylicoides* R. Br. and *G. sphacelata* R. Br., and two are recognised as subspecies; *G. buxifolia* (Sm.) R. Br. subsp. *buxifolia* and *G. buxifolia* subsp. *ecorniculata* Olde & Marriott. *G. phylicoides* R. Br. sensu stricto is reinstated to specific rank and *G. buxifolia* subsp. *buxifolia* is redefined to accommodate *G. buxifolia* subsp. *phylicoides* pro parte and previously intermediate individuals. All of McGillivray's races are accommodated by this scheme.

Introduction

Species serve as the basis for describing and cataloguing diversity and are considered to be the basic entities of evolutionary theory (Cracraft 1989). Many species concepts have been put forward (Stuessy 1990), but they are generally of two types; those that emphasize processes (e.g. the 'biological species concept'), and those that are pattern based and emphasize the operational means by which species are recognized (Smith 1994).

The 'biological species concept' defines a species as 'an interbreeding community of populations that is reproductively isolated from other such communities' (Mayr 1992). It has been found by many biologists to be untenable in theory, and unworkable in practice, since it can normally only be applied subjectively. Rarely do plant taxonomists have sufficient data concerning reproductive behaviour of taxa for the concept's successful application. The ability to interbreed can transcend well-defined species and even generic boundaries, and thus cannot alone establish discrete, evolutionary boundaries (Cracraft 1989; Templeton 1989). The biological species concept has only been considered to be objective in cases of sympatry and reproductive isolation, yet in such cases, other species concepts would treat the situation in the same manner (Cracraft 1989).

In practice, species recognition is often based on patterns of morphological similarity, either intuitively or based upon some combination of multivariate statistical analyses (Crisp and Weston 1993; Smith 1994). Below the level of species, the definition of taxa is even more nebulous. Five infraspecific ranks are recognised by the Code of Botanical Nomenclature (Greuter et al. 1994). There is, however, little uniformity in the use and definition of infraspecific ranks by taxonomists (Stace 1989; Hamilton and Reichard 1992). The rank of subspecies is frequently applied to populations showing any degree of differentiation considered worthy of recognition by the worker (Cracraft 1989). However, there is a need for infraspecific variation to be expressed in taxonomic terms,

in order to draw attention to taxa and provide them with names, for communication and access to literature (Stace 1989).

Within *Grevillea*, there are a number of polymorphic species, some of which have been formally divided into subspecies or varieties, others informally into 'races' (McGillivray 1993). *Grevillea buxifolia* (Sm.) R. Br. s.lat. (Grey Spider Flower) is one such polymorphic 'species' that has received much recent attention. *Grevillea buxifolia* occurs in eastern New South Wales, in a coastal region centred on Sydney (Fig. 1), from Wollombi (c. 20 km south-west of Cessnock) in the north to Milton in the south, and west to Katoomba, in dry sclerophyll woodland, usually on sandy soils derived from Hawkesbury Sandstone (McGillivray 1993).

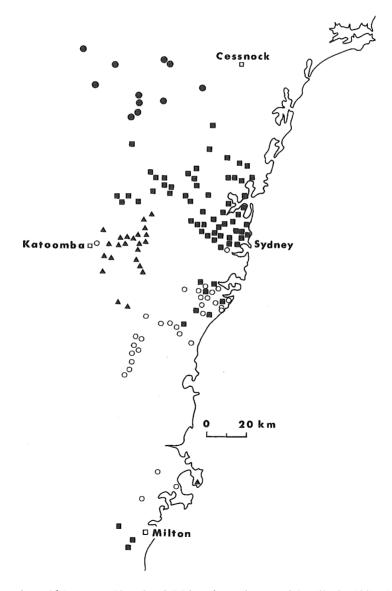


Fig. 1. Location within eastern New South Wales of populations of *Grevillea buxifolia* s.lat. and its segregates sampled for these analyses. \blacksquare *G. buxifolia* subsp. *buxifolia*, \bullet *G. buxifolia* subsp. *ecorniculata*, \blacktriangle *G. phylicoides*, \bigcirc *G. sphacelata*.

Hart & Henwood, Taxonomic web of Grevillea buxifolia

The G. buxifolia complex has been traditionally regarded as consisting of three closely related species: G. buxifolia, restricted to Sydney and northwards, Grevillea phylicoides R. Br. in the Blue Mountains, and *Grevillea sphacelata* R. Br. on the Woronora Plateau. In McGillivray's revision of the genus (1986, 1993) the three species were treated as one, each being reduced to subspecies of G. buxifolia. In 1986 McGillivray formally described and named *Grevillea acerata*, a species that had previously been regarded as a northern 'form' of G. sphacelata R. Br., and which is restricted to the Gibraltar Range, New South Wales. McGillivray (1993) also informally recognised five 'races' within G. buxifolia, two within subsp. buxifolia ('a' and 'c'), two within subsp. phylicoides ('b' and 'd'), and subsp. *sphacelata* ('e'). McGillivray (1993), further identified three groups of populations which did not fit into his classification, since they shared features of more than one of the 'races'. Intermediates occur between races 'b' and 'c', 'b' and 'd', and 'c' and 'd' (McGillivray 1993). However, the morphologically extreme races, 'c' and 'e', occur sympatrically at a number of locations, without apparent signs of interbreeding (McGillivray 1993; Olde and Marriott 1994a; pers. obs.). Such populations are known to occur in the O'Hares Creek Catchment, around Woronora Dam, Lucas Heights, Royal National Park, Illawong and, possibly, Gladesville.

Olde and Marriott (1993a, b; 1994a, b, c; 1995) have revised a number of taxa that had been previously regarded by McGillivray as subspecies or forms. Olde and Marriott (1994a), drawing partly on McGillivray's work, formally described and named McGillivray's race 'a' as *G. buxifolia* subsp. *ecorniculata* Olde & Marriott, and reinstated subspecies *sphacelata* to species rank. Olde and Marriott (1994a) did not, however, address the taxonomic status of the intermediate entities within the complex.

Thus, as the taxonomy currently stands, *G. buxifolia* comprises three subspecies: *buxifolia, ecorniculata* and *phylicoides* — each with one or two forms — and with some intermediates. *Grevillea buxifolia* appears to be most closely allied to both *G. sphacelata* and *G. acerata*. McGillivray's concept of a species is morphological, whereas Olde and Marriott (1993b) have defined their own biologically-based species concept. Thus the *G. buxifolia* complex serves as an ideal model with which to investigate the ideas and techniques involved in the delimitation and ranking of species and infraspecific taxa.

The current study attempts to clarify the taxonomic position of the intermediate individuals present in the *G. buxifolia* complex by way of principal components analysis and cluster analysis, and in doing so reassesses the status of the currently recognised taxa.

Methods

A total of 100 flowering specimens (OTUs) of *G. buxifolia* s.lat. were chosen to represent the geographic range and morphological variation exhibited by the complex. Of the 100 *G. buxifolia* individuals used in the analyses, 12 were from *G. buxifolia* subsp. *ecorniculata* (race 'a'), 8 were from *G. buxifolia* subsp. *phylicoides* pro parte (race 'b'), 22 *G. buxifolia* subsp. *buxifolia* (race 'c'), 17 *G. buxifolia* subsp. *phylicoides* sensu stricto (race 'd'), 28 *G. sphacelata* (race 'e'), and 13 could not be assigned to a race. An additional three specimens of *G. acerata* were included in the analysis, because of this taxon's previous inclusion within *G. sphacelata*.

Specimens were collected in the field (vouchers lodged at SYD), or were sampled from herbarium specimens from the John Ray Herbarium (SYD) and National Herbarium of NSW (NSW). Prior to measurement the fresh leaves and flowers were stored in a 5% glycerine in 65% alcohol mixture, whereas material sampled from herbarium specimens was rehydrated prior to measurement by heating in a weak detergent solution. Where possible, character reliability of both spirit preserved and rehydrated organs was checked by reference to fresh material.

Where appropriate, the characters employed by McGillivray (1993) and Olde and Marriott (1994a) were included in the data set. In total, twenty-four floral and eleven foliar characters were measured (Appendix 1). Each character was measured from three flowers or from three leaves per specimen; the means were subsequently used to represent each specimen in the analysis. The leaves were removed from the fifth, sixth and seventh nodes below an open conflorescence to reduce allometric differences between individuals.

Computerised image analysis was utilised in the measurement of six of the leaf characters. Unscaled leaves were digitised using a Tracor Northern TN-8502 computer (IPA85 imaging software, Tracor Northern 1987) fitted with a Sony DXC-3000P CCD colour video camera. Measurements of floral characters were made directly using an eye-piece graticule on a dissecting microscope.

Numerical analyses were performed using 'A MultiVariate Statistical Package' (MVSP Ver. 2.1, Kovach 1993) computer program, run on an IBM-compatible PC. The data were range-coded to prevent those characters with the greatest range from dominating the analysis (Sneath and Sokal 1973). Principal components analysis was undertaken using Euclidean distance. The cluster analysis employed Gower's similarity metric (Gower 1971), and was combined with a UPGMA (unweighted pair-group method using averages) clustering strategy (Sneath and Sokal 1973).

The chromosome numbers of all races of *G. buxifolia* s.lat. were determined from studies of meiosis, obtained from pollen mother cells fixed in 1:3 acetic-alcohol and stained in aceto-carmine.

Results

The observed chromosome numbers indicated that all races of *G. buxifolia* s.lat. are diploid. The chromosome number of all races was n = 10 (Table 1).

Ordination of the first three principal components (Fig. 2) resulted in the resolution of five main groups: *G. acerata, G. sphacelata, G. buxifolia* subsp. *phylicoides* sensu stricto (race 'd'), *G. buxifolia* subsp. *ecorniculata* (race 'a') and a group comprising *G. buxifolia* subsp. *buxifolia*, *G. buxifolia* subsp. *phylicoides* pro parte (race 'b') and all of the unassigned OTUs. The first three principal components accounted for 68.2% of the total variance (Table 2).

Grevillea acerata and *G. sphacelata* are separable from the other OTUs in the first principal component (Fig. 2a) based on the extent of stem and petiole trichome appression (characters 25 & 26). The second principal component separates *G. buxifolia* subsp. *phylicoides* sensu stricto (race 'd') from the other OTUs (Fig. 2a & c) on the basis of the erect trichomes on its abaxial leaf surfaces (character 35). *Grevillea buxifolia* subsp. *ecorniculata* formed an identifiable subgroup of the *G. buxifolia* complex (races 'c', 'b' and unassigned OTUs) in the third principal component (Fig. 2b) because of its lack of a stylar appendage (character 23).

Cluster analysis (Fig. 3) resulted in the resolution of the same five groups as determined by Principal Components Analysis (PCA). The only conflict between the PCA and cluster analysis involved the apparent affinities of the unassigned OTUs. In contrast with the PCA, four of the 13 unassigned OTUs were placed with *G. buxifolia* subsp. *phylicoides* sensu stricto (race 'd'). All race 'b' OTUs and the nine remaining unassigned OTUs were nested within the race 'c' OTUs in the cluster analysis, however, it is clear from the ordination that all of the unassigned OTUs are unequivocally associated with a group dominated by *G. buxifolia* subsp. *buxifolia* (races 'b' and 'c').

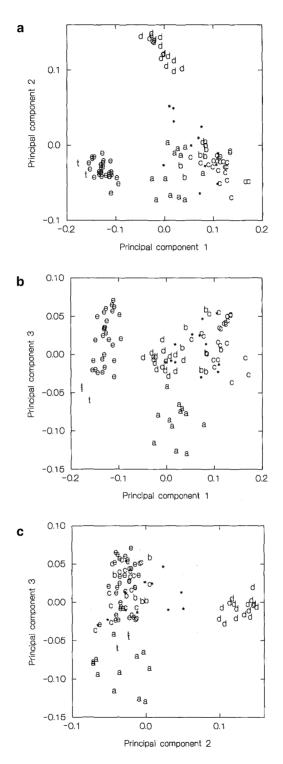


Fig. 2. Ordination of the first three principal components. **a**, principal components 1 and 2; **b**, principal components 1 and 3; **c**, principal components 2 and 3. ($\mathbf{a} - G$. *buxifolia* subsp. *ecorniculata*, $\mathbf{b} - G$. *buxifolia* subsp. *phylicoides* pro parte race 'b', $\mathbf{c} - G$. *buxifolia* subsp. *buxifolia*, $\mathbf{d} - G$. *buxifolia* subsp. *phylicoides* pro parte race 'b', $\mathbf{c} - G$. *buxifolia* subsp. *buxifolia*, $\mathbf{d} - G$. *buxifolia* subsp. *phylicoides* pro parte race 'd', $\mathbf{e} - G$. *sphacelata*, $\mathbf{t} - G$. *acerata*, * – unassigned OTUs).

Discussion

These analyses indicated that *G. buxifolia* comprises two entities: (1) *G. buxifolia* subsp. *ecorniculata* and (2) *G. buxifolia* subsp. *buxifolia*, *G. buxifolia* subsp. *phylicoides* pro parte (race 'b') and all of the previously unassigned OTUs. *Grevillea buxifolia* and *G. phylicoides* sensu stricto (race 'd'), as defined here, are separable from *G. acerata* and *G. sphacelata*.

A significant amount of the phenetic pattern of variation within the *Grevillea buxifolia* complex was found to be size-related. The flowers of *G. buxifolia* subsp. *buxifolia* (race 'c') are noticeably larger than those of the other races, suggesting the possible presence of polyploidy. However, chromosome counts determined that polyploidy is not, apparently, present within the *G. buxifolia* complex.

Chromosome number alone is also uninformative as to the possible reproductive isolation of any of the taxa. To prove reproductive isolation is difficult, if not impossible in a genus

Taxon	Chromosome no.	Voucher
race 'a'	n = 10	Staircase Hill, 7.9km S of Putty turnoff, on the Putty Road, NSW. J.M.Hart 94023 9/4/1994
race 'b'	n = 10	c.32km N of Windsor on the Putty Road, NSW. J.M.Hart 94019 9/4/1994
race 'c'	n = 10	Oxford Falls Road, 0.8km W of Oxford Falls, NSW. J.M.Hart 94050 21/8/1994
race 'd'	n = 10	Bruce Road, Glenbrook, NSW. A.J.Perkins s.n. 10/4/1994
race 'e'	n = 10	Woronora Dam Road, 5.6km from Princes Hwy, NSW. J.M.Hart 94004 26/1/1994

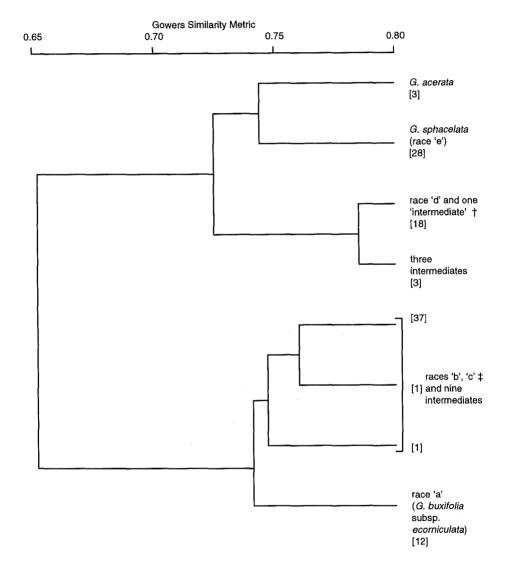
Table 1. Chromosome numbers in the Grevillea buxifolia complex. Voucher specimens lodged at SYD.

Table 2. Character loadings of the major characters and percentages of total variation for the first three axes of the principal components analysis.

Character	AXIS 1	AXIS 2	AXIS 3
6. Limb length	0.204	-0.131	-0.134
7. Limb length:Perianth height	0.093	-0.049	-0.243
8. Perianth length	0.215	-0.145	-0.007
14. Style length	0.200	-0.129	0.125
16. Style length: width	0.068	-0.029	0.281
18. Pollen-presenter width	0.153	-0.145	-0.260
20. Appendage length (no trichomes)	0.219	-0.043	0.264
21. Appendage length (with trichomes)	0.237	-0.051	0.276
22. Appendage trichome length	0.212	-0.062	0.210
23. Appendage shape	0.169	0.014	0.529
25. Stem indumentum	0.403	0.253	-0.245
26. Petiole indumentum	0.385	0.387	-0.001
34. Leaf abaxial trichome density	-0.236	-0.432	0.054
35. Leaf abaxial trichome state	-0.015	0.561	-0.060
% variation	43.22	16.69	8.29
cumulative % variance	43.22	59.91	68.20

in which there exists widespread self-compatibility (McGillivray 1993), and many naturally occurring hybrids between otherwise distinct species (e.g. McLuckie 1930).

According to the biological species concept, reproductive isolation is the process which delineates species. Use of reproductive isolation to define plant species makes their identification largely conjectural since morphological disparity or similarity has no necessary place in the definition of the biological species. The mismatch between reproductive isolation and morphological distinctness is evident from the literature on cryptic, sibling and polytypic species (Cracraft 1989; Smith 1994), and the common occurrence of hybridization between morphologically and evolutionarily distinct



† race 'd' (= G. buxifolia subsp. phylicoides sensu stricto)

‡ race 'b' (= G. buxifolia subsp. phylicoides pro parte), race 'c' (= G. buxifolia subsp. buxifolia)

Fig. 3. Dendrogram resulting from the cluster analysis, indicating the presence of four groups within the *Grevillea buxifolia* complex. NB. clusters above 0.80 similarity not shown. Number of OTUs in each cluster given in square brackets.

plant species (Stuessy 1990). Reproductive isolation is merely a subset of the numerous possible consequences of the more general process of differentiation (Cracraft 1989). Thus, in practice, the biological species complex is difficult to apply successfully.

The morphological species concepts are commonly employed. It is assumed that morphological relationships do reflect genetic and reproductive relationships. Morphological data are the most easily obtained, and phenetic methods can handle large data sets in which there are complex patterns of variation. However, defining species morphologically also has faults, and critics believe that this approach is too subjective. Users of the phenetic species concept have to decide which phenetic unit is the one to be called a species (Stuessy 1990). A specific level of dissimilarity, above which two taxa should be recognised as separate species, subspecies, or other rank, cannot be determined and applied uniformly. In addition to this, there are a number of examples in which biochemical and molecular techniques are in absolute disagreement with morphological species, or with each other (King 1993). Thus, the biological species concept and morphological species concepts each carry their own sets of implications and limitations (Smith 1994).

Here, the taxonomy of the *Grevillea buxifolia* species complex is based upon morphological data.

Taxonomic conclusions

It is clear from these analyses that *G. buxifolia* subsp. *phylicoides* is divisible into two groups: race 'b' and race 'd'. Individuals conforming to race 'b' and the previously unassigned individuals are easily accommodated within *G. buxifolia* subsp. *buxifolia* whereas those conforming to race 'd' merit recognition at the species level. Race 'd' conforms precisely to Brown's concept of *G. phylicoides* as lectotypified by Makinson (1997 *ined.*), and, therefore, requires reinstatement to species level and a redefinition of the concept of *G. buxifolia* subsp. *buxifolia*. *Grevillea buxifolia* subsp. *ecorniculata* (race 'a') forms an identifiable, but phenetically similar, subgroup of *G. buxifolia* based only on a single character; the lack of the stylar appendage. Thus on the basis of these analyses, continued recognition of *Grevillea buxifolia* subsp. *ecorniculata* is recommended. *Grevillea buxifolia* as defined here consists of two subspecies: *buxifolia* and *ecorniculata*, and is separable at the species level from *G. acerata*, *G. phylicoides* and *G. sphacelata* as outlined in Table 3 and below.

Table 3: Recent taxonomic concepts in the *Grevillea buxifolia* complex and taxonomic recommendations. — species boundaries, — subspecies boundaries, …… race boundaries.

Original taxonomy	McGillivray, 1986	McGillivray, 1993	Olde & Marriott, 1994	Taxonomic Recommendations
Grevillea	Grevillea buxifolia subsp. buxifolia	race 'a'	Grevillea buxifolia subsp. ecorniculata	<i>Grevillea buxifolia</i> subsp. ecorniculata
buxifolia	Grevillea buxifolia subsp. buxifolia	race 'c'	<i>Grevillea buxifolia</i> subsp. <i>buxifolia</i>	<i>Grevillea buxifolia</i> subsp. <i>buxifolia</i>
Grevillea	<i>Grevillea buxifolia</i> subsp. <i>phylicoides</i>	race 'b'	<i>Grevillea buxifolia</i> subsp. <i>phylicoides</i>	<i>Grevillea buxifolia</i> subsp. <i>buxifolia</i>
phylicoides	Grevillea buxifolia subsp. phylicoides	race 'd'	Grevillea buxifolia subsp. phylicoides	Grevillea phylicoides
Grevillea sphacelata	Grevillea buxifolia subsp. sphacelata	race 'e'	Grevillea sphacelata	Grevillea sphacelata

Hart & Henwood, Taxonomic web of Grevillea buxifolia

Nomenclature

Grevillea buxifolia (Sm.) R. Br., Trans. Linn. Soc. London 10: 174 (1810).

Embothrium buxifolium Sm., A Specimen of the Botany of New Holland: 29 t.10. (1794).

Stylurus buxifolia (Sm.) Knight, *On the Cultivation of Plants Belonging to the Natural Order of the Proteeae*: 115 (1809).

Grevillea buxifolia Sm. (R.Br) subsp. **buxifolia**, see McGillivray, *New Names in* Grevillea (*Proteaceae*): 3 (1986).

Embothrium genianthum Cavanilles, Ic. & Descr. Pl. 4: 60 t.387 (1798).

Grevillea buxifolia race 'b' (informal) McGillivray, Grevillea (*Proteaceae*): A taxonomic revision: 312–314 (1993).

Grevillea buxifolia race 'c' (informal) McGillivray, Grevillea (*Proteaceae*): A taxonomic revision: 312–314 (1993).

Geographic distribution: Central Coast: from north of Gosford, south to Port Jackson and inland to Bucketty, Culoul Range and Bilpin, as well as south of the Georges River to Appin and Bulli Pass on the Woronora Plateau.

South Coast: Restricted to Pigeon House Mountain near Milton.

Apparently intergrading populations with *Grevillea phylicoides* occur in the Bilpin–Kurrajong area. *Grevillea buxifolia* subsp. *buxifolia* co-occurs with *Grevillea sphacelata* without intergrading at Gladesville, Illawong, Royal National Park, Lucas Heights, Woronora Dam and the O'Hares Creek Catchment.

Grevillea buxifolia subsp. ecorniculata Olde & Marriott, Telopea 5(4): 709 (1994).

Grevillea buxifolia race 'a' (informal) McGillivray, Grevillea (Proteaceae): A taxonomic revision: 312–314 (1993).

Geographic distribution: Central Coast: In the region around the town of Putty, between Howes Mountain to Wollombi and Mount Coricudgy.

Grevillea phylicoides R. Br., Trans. Linn. Soc. London 10: 174 (1810).

Grevillea scabrifolia Gandoger, Bull. Soc. Bot. France 66: 231 (1919).

Grevillea buxifolia subsp. *phylicoides* (R. Br.) McGillivray, *New Names in* Grevillea (*Proteaceae*): 3 (1986) pro parte.

Grevillea buxifolia race 'd' (informal) McGillivray, Grevillea (*Proteaceae*): A taxonomic revision: 312–314 (1993).

Geographic distribution: Central Coast: Lower Blue Mountains from Glenbrook to Lawson, north to Grose Wold and south to Oakdale.

South Coast: Known from a single collection on Beecroft Peninsula.

This species apparently intergrades with *Grevillea buxifolia* subsp. *buxifolia* in the Kurrajong–Bilpin area.

Grevillea sphacelata R. Br., Trans. Linn. Soc. London 10: 174 (1810).

Grevillea walteri Gandoger, Bull. Soc. Bot. France 66: 231 (1919).

Grevillea buxifolia subsp. sphacelata (R. Br.) McGillivray, New Names in Grevillea (Proteaceae): 3 (1986).

Grevillea buxifolia race 'e' (informal) McGillivray, Grevillea (*Proteaceae*): A taxonomic revision: 312–314 (1993).

Geographic distribution: Central Coast: From Gladesville in the coastal region south to Bulli and inland to Picton and Mittagong.

Central Tablelands: Known from a single collection at Leura.

South Coast: From Jervis Bay inland to Conjola.

Co-occurs with *Grevillea buxifolia* subsp. *buxifolia* without intergrading at Gladesville, Illawong, Royal National Park, Lucas Heights, Woronora Dam and the O'Hares Creek Catchment.

Name of uncertain application

Grevillea collina (Knight) Sweet, Hortus Suburbanus Londonensis: 22 (1818).

Stylurus collina Knight, *On the Cultivation of Plants Belonging to the Natural Order of the Proteeae*: 116 (1809).

This name may be applicable to either *Grevillea sphacelata* or *Grevillea phylicoides*, however the protologue in the absence of a specimen or illustration, is insufficient for the purposes of circumscription.

Key to Grevillea buxifolia and morphologically similar species

1 Stem covered by an appressed, subsericeous to subvillous indumentum

	2	Flowers with sutures adaxially oriented G. acerata				
	2*	Flowers with sutures abaxially oriented				
		3 Conflorescences borne terminally and in leaf axils G. occidentalis				
		3* Conflorescences borne terminally only G. sphacelata				
ł	Ste	tem covered by a spreading, villous to tomentose indumentum				
	4	Leaves covered by erect hairs below, linear-oblong to narrowly elliptic, 7–30 mm long, 3–5 mm wide; pollen-presenter elliptic to narrow elliptic, 1–1.6 mm wide G. phylicoides				
	4*	* Leaves covered by appressed hairs below, elliptic to ovate, 5–25 mm long, 2–6.5 mm wide; pollen-presenter round to elliptic, 1.4–3.3 mm wide				
		5 Stylar appendage > 1.4 mm long G. buxifolia subsp. buxifolia				
		5* Stylar appendage absent or rarely to 1.3 mm long				

1*

Hart & Henwood, Taxonomic web of Grevillea buxifolia

Acknowledgments

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Appendix 1. Character List

Definition

Floral characters 1. Floral orientation 0 – adaxial, 1 – abaxial, 2. Pedicel length 3. Pedicel colour 0 - rusty trichomes sparse/absent, 1 - rusty trichomes present 4. Torus width 5. Perianth height 6. Limb length 7. Limb length/Perianth height ratio 8. Perianth length Sum of the perianth height and limb length 9. Perianth height/length ratio 10. Nectary height 11. Nectary trichomes 0 – absent, 1 – present. 12. Stipe length The distance from the torus to the base of the ovary. 13. Ovary length The distance from the base to the top of the ovary. 14. Style length The distance from the top of the ovary to the base of the pollen-presenter. 15. Style width at midpoint 16. Style length/width ratio 17. Pollen-presenter length including the rim (if present). 18. Pollen-presenter width including the rim (if present). 19. Pollen-presenter length/width ratio 20. Appendage length (no trichomes) exclusive of trichomes. 21. Appendage length (with trichomes) inclusive of trichomes 22. Appendage trichome length the difference between characters 20 and 21 23. Appendage shape 0 – absent, 1 – obtuse, 2 – acute. 24. Trichome length/Appendage (no trichomes) The ratio of character 22 : character 20 Leaf and stem characters 25. Stem indumentum 0 – appressed, 1 – spreading. 26. Petiole indumentum 0 - appressed, 1 - spreading 27. Leaf length maximum leaf projection 28. Leaf width The maximum leaf projection perpendicular to the maximum projection 29. Aspect ratio The ratio of leaf length to leaf width 30. Leaf area Measured from the number of pixels in a leaf image 31. External leaf perimeter leaf image perimeter measured from pixel centre to pixel centre 32. Leaf circularity a measure of deviation from a circle (circle value = 1), calculated from the equation: $circ = \frac{(external perimeter)^2}{2}$ $4\pi \times \text{area}$ 33. Leaf rectangularity deviation of leaf shape from a rectangle rectangularity = $\frac{1}{\text{length} \times \text{width}}$ (rectangle value = 1), (West and Noble, 1984) 34. Leaf abaxial trichome density 1 - space between trichomes > 4 times the width of the trichomes 2 - space between trichomes 2 to 4 times the width of the trichomes 3 -space between trichomes < 2 times the width of the trichomes 4 – trichomes almost always touching along their whole length

Character

35. Leaf abaxial trichome state

0 - appressed, 1 - spreading