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A review of *Dendrobium kingianum* Bidwill ex Lindl. (Orchidaceae) with morphological and molecular-phylogenetic analyses

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Abstract

Populations of *Dendrobium kingianum* Bidwill ex Lindl. from near Newcastle, New South Wales to southern and central west Queensland and encompassing all regions of the distribution were studied using field observations, morphometric analysis and nrITS sequences. A total of 281 individuals were used to construct regional descriptions of *D. kingianum* and 139 individuals were measured for 19 morphological characters, and similarities and differences among specimens summarised using multivariate statistical methods. Patterns of morphological variation within *D. kingianum* are consistent with a single variable species that expresses clinal variation, with short-growing plants in the south and taller plants in the northern part of the distribution. The nrITS gene tree suggests two subgroups within *D. kingianum* subsp. *kingianum*, one comprising northern, the other southern individuals, which may overlap in the vicinity of Dorrigo, New South Wales. The disjunct *D. kingianum* subsp. *carnarvonense* Peter B. Adams in central west Queensland, which can be distinguished by a predominately subterranean habit and a narrower labellum midlobe, was resolved sister to *D. moorei* F.Muell., which renders *D. kingianum* paraphyletic in the nrITS gene tree, but this position was not supported. Regional descriptions documenting clinal variation are provided. All previously described varieties, including *D. kingianum* var. *pulcherrimum* Rupp, are colour and growth forms of *D. kingianum* subsp. *kingianum*.

Introduction

Dendrobium kingianum Bidwill ex Lindl. (sect. *Dendrocoryne*) is a lithophyte found mainly on the eastern seaboard in the northern half of New South Wales (NSW) and southern Queensland. There are also isolated and disjunct populations in inland central west Queensland. Across this broad distribution the species is variable in plant form and floral colour. *Dendrobium kingianum* was discovered by European explorers in the 1830s when opening up agricultural land north of Newcastle, and was described in 1844 by John Lindley from material sent by John Carne Bidwell, and named for Bidwell's friend Captain P.P. King of the Royal Navy. The collection location for type plants was not given but the description is consistent with those from the southern part of the range. Subsequently the known distribution was extended to the north as far as central Queensland. It has been widely cultivated in temperate zones. The species is of significant horticultural interest, and since the mid-20th century has been line bred and hybridised with other dendrobiums. There have been a number of taxa described, some separated at species level. This can create confusion for orchid hybrid registration.

There are a small number of studies of chromosome counts (Adams 1992), pollination (Adams 1988, Adams and Lawson 1988) and fragrance biochemistry (Adams 1988, Adams and Lawson 1995). Molecular phylogeny reconstruction using nuclear ITS for the 12 species in sect. *Dendrocoryne* (Burke *et al.* 2008) resolved *D. kingianum* as sister to *D. speciosum*, a relationship also recovered using AFLP data by Simpson *et al.* (2018).

The aims of this paper are to quantify variation within *D. kingianum* based on morphological and molecular phylogenetic analysis from populations across the distribution. In particular we are interested in morphological evidence relating to the potential existence of more than one species. Clements and Jones (2002) proposed that *D. kingianum* be split into three separate species under *Thelychiton*, namely, *T. kingianus*, *T. pulcherrimus* and *T. carnarvonense*. Neither *Thelychiton* nor these species have been accepted by the World Checklist of Selected Plant Families (WCSPF), *Genera Orchidacearum* Vol. 6 (Pridgeon *et al.* 2014) or a review of the systematics of Dendrobiinae (Adams 2011). We then formalise the results of this investigation, in conjunction with a taxonomic review of *D. kingianum*.

Historical review of taxonomy

Dendrobium kingianum is a variable species. In the late 19th and early 20th centuries, varietal status was proposed for particular plants with distinctive features, often flower colour and plant habit e.g. *D. kingianum* var. *pallidum* F.M.Bailey, *D. kingianum* var. *silcockii* F.M.Bailey, *D. kingianum* var. *aldersoniae* F.M.Bailey and *D. kingianum* var. *album* Williams. In 1943, Rupp described *D. kingianum* var. *pulcherrimum* Rupp for very short plants with comparatively large flowers from the upper Hastings River in the southern part of the range, and noted that few variations of the species were sufficiently constant to warrant even varietal rank. A description of the historical varieties and a subspecies are given below with comments.

***Dendrobium kingianum* Bidwill ex Lindl.**

The protologue of *D. kingianum* (Lindley 1844) was based on a single cultivated plant shipped from Australia to England by J.C. Bidwill, purchased by the Loddiges brothers possibly in 1842 (Lindley 1845), and cultivated. The plant's pseudobulbs were 4–5 inches long, bearing two leaves, and two-flowered inflorescences.

> *D.* (*Desmotrichum*) *Kingianum*; pseudobulbis ovatis in collum longum extensis apice bioliis, foliis ovalibus emarginatis, pedunculo terminali (2-floro foliis aequali ?), sepalis ovatis mento emarginato, petalis obovatis apiculatis duplo brevioribus, labelli trilobi pubescentis laciniis lateralibus acutis intermedia paulo longiore transverse rhombea angulis lateralibus rotundatis apiculi acuto axi elevata trilineata apice tridentata.
>
> This curious epiphyte was bought by the Messrs. Loddiges at the sale of Mr Bidwill's New Holland Plants. It has pseudo-bulbs between four and five inches long, tapered from an ovate base into a very long and narrow neck, on the top of which stand two oblong emarginate dark-green rather wavy leaves. Between these is a flower-stalk having two pink flowers gaily spotted with crimson in the inside. It will probably flower more profusely when in better health, and will then be a plant of considerable interest.

The following year Lindley (1845) published a longer treatment of the plant, including a colour illustration, and noted three flowered inflorescences and four-leaved canes.

Mueller (1862) provided a description including the same characters as Lindley's, but based on a specimen collected by Charles Stuart from the Severn River in New England, presumably from high altitude on the edge of the New England escarpment, where *D. kingianum* is common even today:

> Caulibus breviusculis pauciarticulatis basi sensim incrassatis, foliis 2-4 terminalibus ovato-lanceolatis, corymbo terminalia pauciflora, floribus roseo-purpureis, sepalis semilanceolato-ovatis petala ovato-lanceolata aequantibus, labello sepalis subaequilongo albo vittis purpureis striato trilobo, lobis lateralibus deltoideis, medio subreniformi apiculato integro, earinis tribus flavis usequ ad basin lobi medii extensis.
>
> In Nova Anglia haud procul a fluvio Severn. C. St.
>
> In indice orchidearum horti Schilleriani sequentes species Dendrobii Novo-Hollandicas nuperius enumerantur: D. calamiforme Lodd., D. lineolatum H.G.Rchb. (D. teres Lindl. nec R.Br.)
>
> Nondum vidi Dendrobium monoliforme (McLeay inedit), quod a viro reverendo R.L. King prope sinum Botany Bay in rupibus muscosis repertum et raritate minutie sicut caulibus subtiliter moniliformibus insigne dicitur. Hoc Forsan Bolbophyllis adscibendum est.

Bentham's description of *D. kingianum* in *Flora Australiensis* (1873: p. 280) encompassed more natural variation, with stems 3–6 inches tall, and 1–3 inflorescences per pseudobulb. He suggested Bidwill's plant may have come from Moreton Bay, and cited specimens collected at 'Biron' (possibly Byron Bay) by Leichardt, and at New England collected by C. Stuart, so encompassing the elevational range occupied by the species:

> Stems usually 3 to 6 in. high, striate with prominent angles, thickened at the base. Leaves at the summit of the stem 3 to 5, lanceolate or oblong-lanceolate, acute, 3 to 4 in. long. Racemes within or above the leaves 1 to 3, longer than the leaves. Flowers of a reddish purple, on pedicels of 1/4 to 1/2 in. Bracts very small. Sepals broadly lanceolate, the lower ones much falcate, 4 lines long in some specimens, fully 5 in others. Petals about as long, but narrower. Spur conical, slightly incurved, about 3 lines long. Labellum not much shorter than the sepals, not undulate, the lateral lobes very prominent, almost oblong, obtuse, the middle lobe scarcely longer, but very broad, almost reniform, the disk with 3 raised lines or plates extending to the base of the middle lobe, but not beyond.—Bot. Mag. t. 4527; F. Muell Fragm. iii. 60.
>
> Queensland, Morton bay ? Bidwill.
>
> N. S. Wales. On rocks and trees, Biron, *Leichhardt;* New England, *C. Stuart.*

The early descriptions do not encompass the full range of variation within *D. kingianum* there being, for example, no information about the number of flowers per raceme and little information about the colour or shape of the labellum.

***Dendrobium kingianum* var. *pallidum* F.M.Bailey**

A new variety of *D. kingianum* was described, in somewhat unusual circumstances, by F.M. Bailey. The summary of Bailey's paper presented to the Queensland Philosophical Society and printed in *The Brisbane Courier* (Anonymous 1883) actually fulfilled the requirements for valid publication of *D. kingianum* var. *pallidum*, a fact evidently of some embarrassment to Bailey, who noted in his more formal description of the taxon the following year (Bailey 1884) that the species was 'published in a newspaper report of the last meeting of the Queensland Philosophical Society, a publication scarcely meeting the requirements of scientific currency'. This was not the first orchid validly published in a newspaper. *Dendrobium fairfaxii* F.Muell & Fitzg. had been described in *The Sydney Mail*, the weekly edition of *The Sydney Morning Herald*, in 1872, and *D. falcorostrum* Fitzg. had been described in the *Sydney Morning Herald* in 1876.

Bailey (1884) described his new variety as follows:

> Stems clustered, often forming broad dense matted masses of several feet in diameter, the height of stem from 2 to 4 inches, slender except the base which is enlarged into pseudobulbs, all more or less covered by the torn bases of old leaves. Leaves 2 or 3 somewhat thin, 2–3 inches long, and about 1/2 inch broad near the base, oblong-lanceolate. Racemes slightly exceeding the leaves, slender and bearing about three or four white or lilac stained flowers.
>
> Habitat: On rocks Main Range, collected by B. Crow and C.H. Hartmann.

As first proposed, *Dendrobium kingianum* var. *pallidum* differed from *D. kingianum* var. *kingianum* by its smaller stature, pseudobulbs that formed dense masses, and by the white or pale pink colour of the flowers. However, Bailey later provided a slightly different description for his *D. kingianum* var. *pallidum*, including much taller plants, in the *Queensland Flora* (Bailey 1902):

> The clustered stems weaker than the typical form, often densely matted together and thus forming large patches on the rocks. Stems 2 to 9 inches high, the base enlarged in pseudobulbs. Leaves of a thin texture 2 to 3 inches long, about half an inch broad near the base, and tapering towards the apex. Racemes slightly longer than the leaves, bearing 3 or 4 pale lilac stained flowers.

This broadened description suggests that Bailey had seen a range of plants of different cane lengths between 1884 and 1902, and therefore indicated the range 2–9 inches in the later description. This effectively left flower colour as the only feature distinguishing *D. kingianum* var. *pallidum.*

***Dendrobium kingianum* var. *album* B.S.Williams**

A pure white form of what was thought to be *D. kingianum* was described and illustrated in Warner and Williams (1888), with the figure drawn from a plant that flowered in the collection of A.H. Smee, The Grange, Carshalton, Surrey, England. The flower spike bore 20 large white flowers whose labellum was freckled with a few reddish-brown lines and dots. The inflorescence length, flower number, labellum marking, and growth form all demonstrate that the plant was in fact *D.* × *delicatum* (F.M.Bailey) F.M.Bailey. Many white-flowered plants of *D. kingianum* are cultivated under the name *D. kingianum* var. *album*, but this name applies to *D.* × *delicatum* and not *D. kingianum.* Pure white and off-white flowers of *D. kingianum* with a trace of pale mauve are scattered throughout the distribution range in all growth forms.

***Dendrobium kingianum* subvar. *pallidum* J.H.Veitch**

Veitch in his *Manual of Orchidaceous Plants* fulfilled, perhaps inadvertently, the requirements for valid publication of a 'subvariety' of *Dendrobium kingianum* called 'pallidum' with 'white flowers with a few purple stripes on the labellum' (Veitch 1887). No type specimen was indicated, and none has been found for this brief description. *Dendrobium kingianum* subvar. *pallidum* may resemble, or be an example of the colour form known as 'silcockii', the flowers are off-white in colour with a few faint streaks of pale mauve in the labellum.

Dendrobium kingianum var. *silcockii* F.M.Bailey

This name is widely used today in reference to plants with white tepals which contrast with the purple coloured labellum. *Dendrobium kingianum* var. *silcockii* was described as follows (Bailey 1902):

> Stem and leaves firm as in the typical form. Flowers pure white except the labellum and of thick substance. Pedicels white 1/2 inch long. Ovary green, two lines long. Dorsal sepal five lines long three lines broad., cymbiform, lateral ones broad, falcate, from point to point seven lines quite enclosing the elongated base of the column (spur). Petals long as dorsal sepal but not so broad, incurved and meeting over the column. Labellum about as long as the sepals, lateral lobes spreading, pointed at the ends and reaching above the column, marked with lilac lines, middle lobe broadly cordate, apiculate, lilac lined with white. The disk bearing three thick ridges ending in points at the base of the middle lobe. Column thick and short. Anther lid ciliate in front. Pollen masses amber coloured.

'Silcockii' has been used for colour forms with pure white sepals and petals, and a purple and white speckled or patterned labellum. It is sometimes applied to flowers that are a pale mauve with purple speckled lip, but it should be reserved for flowers with white tepals, as per the protologue. Plants with 'silcockii'-type flower colouration occur sporadically in many areas of the distribution range with a wide variety of growth forms and variable floral size, shape and other characteristics (Adams and Lawson 1995). It is therefore a colour form only. Selfings and sibling crosses breed plants with flowers that have shades of mauve, mainly pale and only occasional true 'silcockii', indicating the presence of genes for mauve, which are expressed in 'silcockii' itself.

Dendrobium kingianum var. *aldersoniae* F.M.Bailey

Bailey (1905) provided the following brief description:

> Habit of the typical form. Flowers fragrant as in other forms, pure white except sometimes a very faint purple stain on the back of the sepals; and the labellum very faintly dotted with purple, the disk plates yellowish.
>
> Collected in the Blackall Range. Mrs. G.W. Alderson.

The original material has not been found. The original spelling by Bailey was *aldersonae,* subsequently corrected to *aldersoniae* by other authors. There is no evidence to suggest that this is a distinct variety. The description could match plants from many parts of the distribution range.

Dendrobium kingianum var. *pulcherrimum* Rupp

Rupp (1943) described *D. kingianum* var. *pulcherrimum* as

> Pseudobulbs crowded, all short, not exceeding 9cm. Leaves as long as the pseudobulbs, tinged with red. Flowers comparatively large, the sepals and petals deep mauve. Labellum white on the undersurfaces and the margins'.

He commented 'There are many varieties in this species chiefly of colour, but few appear to be sufficiently constant to warrant varietal rank.' This variety was described from plants collected in the Upper Hastings River with congested short (<9 cm) pseudobulbs and relatively large, deep mauve flowers with a white margin. Other treatments (Dockrill 1992, Upton 1989) have listed the variety, recording 1–3 or few flowers per raceme, blue-green leaves, with a distribution from the Macleay River down to the southern limit of the species.

Plants agreeing with this description are seen occasionally in the Hastings River region and less commonly elsewhere (see descriptions for Hastings, Comboyne and Coffs Harbour/Dorrigo). Although plants are generally short (<11 cm), there is a wide range of floral colour, white-purple, flowers per raceme (2–8), midlobe shapes and leaf lengths. Grey-green leaves are a feature of the southern region in most populations, and very few plants in each population could be ascribed to Rupp's description. In this study, three plants meeting the description were recorded in the northern part of the range, and eight plants meeting the description from the three southern-most regions. At Bulahdelah, approximately the southern limit, plants are very short (4–8 cm), may have 1–5 flowers which are small, not larger in all aspects, and of a pale mauve, rarely if ever deep purple, and not meeting Rupp's description. The populations in the Upper Hastings contain significant numbers of large mauve flowering forms mixed with smaller and paler flowering individuals, with a wide range of stem heights, mostly longer than seen in *D. kingianum* var. *pulcherrimum*.

Dendrobium kingianum **subsp.** ***carnarvonense*** **Peter B. Adams**

This subspecies was described in Adams and Lawson (1995) for unusual forms of *Dendrobium kingianum* growing in disjunct sandstone gorges of Central Queensland, between the Carnarvon region and Isla Gorge, usually in secluded, shaded situations near streams.

The plants have slender pseudobulbs, up to 15 cm long, the older ones and lower portions of newer pseudobulbs covered by decomposing sandstone and leaf litter, the upper portions emergent and bearing frequent aerial growths, with small flowers having a rounded outline, 1.6 by 2.2 cm in vertical and horizontal dimensions. The forelobe and midlobe of the labellum are unusually curved to form a narrow open tube approximately 0.35 – 0.5 cm wide, and the labellum callus is green without any raised keels. Subspecies rank was chosen for these plants to reflect their geographic isolation, and the relatively subtle nature of differences from other *D. kingianum*.

Material and Methods

Field Survey and Population Sampling

Populations in all regions of the distribution (Fig. 1) were studied in the flowering season during September to October, between 1980 and 2019. Plants in 52 main locations were selected to represent the variation in each location (Table 1). Numerical and morphological data from 281 specimens was obtained from wild plants *in situ* and used to describe plants from regions 1–8.

Table 1. Vouchers and sources for sequences used in nrITS gene tree reconstruction.

New South Wales	Subspecies	Region	Coordinates
Mt Alum	kingianum	1	32°24´S 152°13´E
Middle Brother	kingianum	3	33°15´S 149°17´E
Comboyne	kingianum	3	31°36´S 152°28´E
Yarras	kingianum	3	31°26´S 156°20´E
Haystack/Little Nellie	kingianum	3	31°24´S 152°30´E
Jollynose	kingianum	3	31°35´S 152°47´E
North of Wauchope	kingianum	3	31°28´S 152°43´E
Cairncross	kingianum	3	31°20´S 152°40´E
Hastings	kingianum	3	32°24´S 152°13´E
Kundebung	kingianum	3	31°12´S 152°51´E
No. 1626 Gibraltar Range	kingianum	5	29°32´S 152°17´E
Dorrigo	kingianum	4	30°20´S 152°43´E
Russell's Red	kingianum	2	32°02´S 151°57´E
Gibraltar Range/Hanging Rock Station	kingianum	4	29°32´S 152°17´E
Busby's Flat	kingianum	6	29°02´S 152°50´E
Grafton	kingianum	4	29°40´S 152°56´E
Coledale	kingianum	5	34°17´S 150°57´E
Clouds Creek	kingianum	4	30°05´S 153°37´E
Sherwood Road, Coffs Harbour	kingianum	4	30°06´S 153°03´E
Korora	kingianum	4	30°14´S 153°06´E
Stanton, Bucketts	kingianum	2	32°01´S 151°57´E
Farley, Bucketts	kingianum	2	32°01´S 151°57´E
Bucketts	kingianum	2	32°01´S 151°57´E
Benny's Tops	kingianum	2	32°01´S 151°07´E
Bald Rock	kingianum	5	28°57´S 152°01´E
Rocky River	kingianum	6	29°02´S 152°29´E
Boonoo Boonoo	kingianum	6	28°56´S 152°06´E
Lamington	kingianum	6	28°15´S 153°05´E
Tunglebung	kingianum	6	28°50´S 152°41´E
Glenreagh Ridge	kingianum	5	30°03´S 152°59´E

New South Wales	**Subspecies**	**Region**	**Coordinates**
Stewart Creek, Lansdowne	kingianum	3	31°46´S 152°32´E
Glenreagh	kingianum	3	30°03´S 152°59´E
Dungog	kingianum	2	32°24´S 151°45´E
Rowley's Ridge, Gloucester	kingianum	2	32°01´S 151°07´E
Paterson	kingianum	1	32°35´S 151°36´E
Morgan's Camp	kingianum	5	34°17´S 150°57´E
Pinnacle	kingianum	6	28°26´S 153°06´E
Plants Queensland			
Tarlington 1	kingianum	6	28°03´S 153°14´E
Tarlington 2	kingianum	6	28°03´S 153°14´E
Main Creek	kingianum	6	28°07´S 153°11´E
Coongara	kingianum	7	25°40´S 151°59´E
Mt. Tamborine	kingianum	6	27°56´S 153°11´E
Tallai	kingianum	6	28°04´S 153°19´E
Cedar Creek	kingianum	6	27°49´S 153°10´E
Carnarvon Gorge	carnarvonense	8	25°03´S 148°13´E
Carnarvon Gorge 2	carnarvonense	8	25°03´S 148°13´E
Robinson Gorge	carnarvonense	8	25°17´S 149°08´E
Mt. Tavingah	kingianum	7	26°25´S 152°18´E
Mothar Mountain	kingianum	7	26°14´S 152°46´E
Nimbin	kingianum	6	28°36´S 153°11´E
Ngun Ngun	kingianum	7	26°54´S 152°58´E
Beerwah	kingianum	7	26°15´S 152°57´E

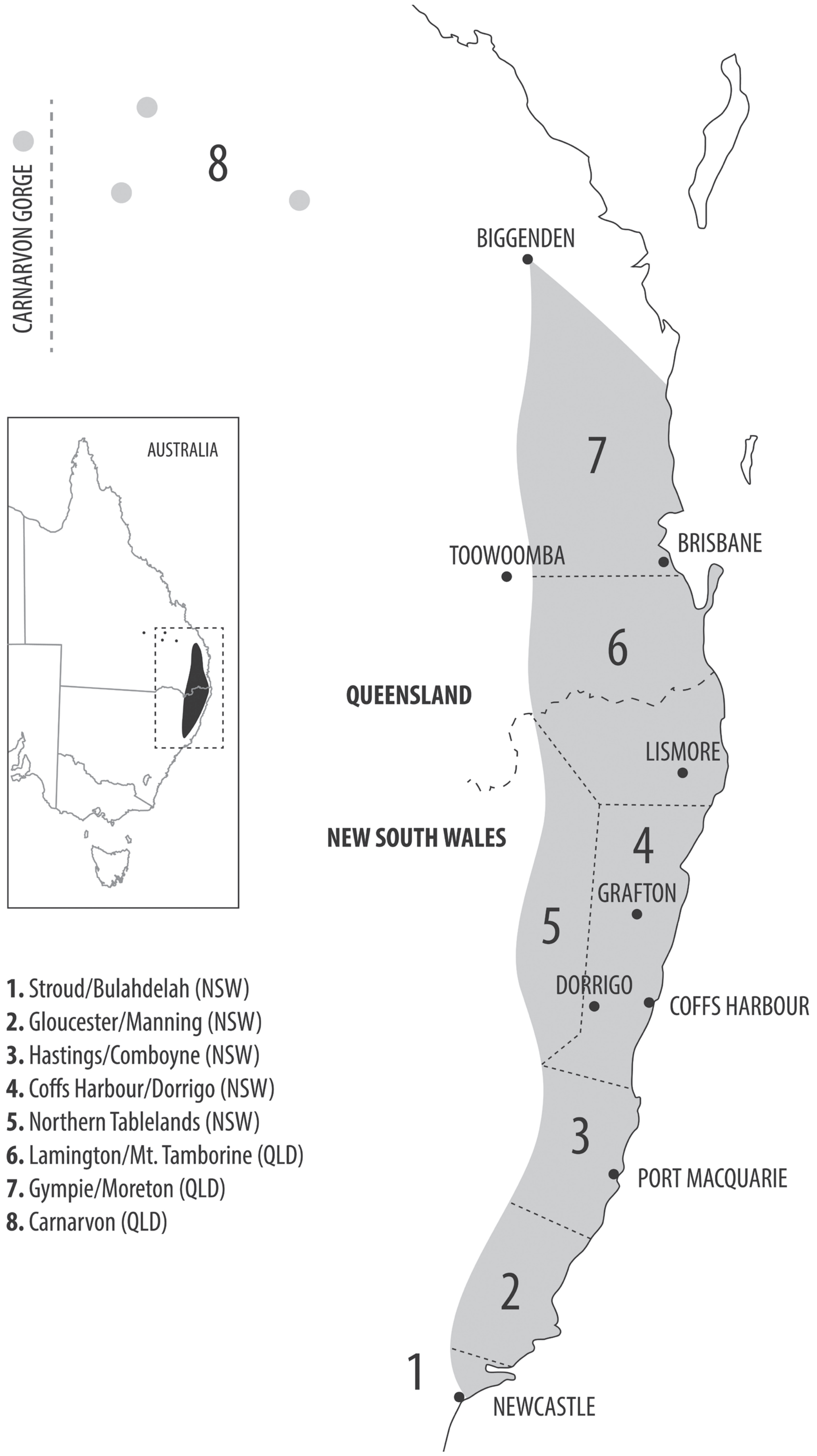

Figure 1. Distribution of *Dendrobium kingianum* showing regions used as a factor in the morphological analysis.

Molecular phylogenetic analysis

New sequences for the nuclear internally transcribed spacer (nrITS) were generated from eight *D. kingianum* samples using the extraction, PCR, and sequencing methods described by Burke *et al.* (2008). Consensus sequences were assembled using Sequencher v.4.0 (Gene Codes Corporation, U.S.A.) and manually aligned using SeA1 Sequence Alignment Editor V. 2.0a11 (Rambaut 1996). These were combined with 82 published nrITS sequences from *Dendrobium* downloaded from GenBank, representing 39 species with an emphasis on the Australian region. In total fourteen samples of *D. kingianum* were included, so that all major regional variants (Adams and Lawson 1995) were represented. A number of accessions from *D. speciosum* J.Sm. and *D. tetragonum* F.Muell. were included from those available on GenBank for purposes of comparing the levels of nrITS haplotype diversity within each species. Voucher details and GenBank accession numbers are provided in Table 2. The sequences were aligned by MUSCLE, as implemented in Geneious Prime 2020.0.5 (BioMatters Ltd), with all default options. The MUSCLE alignment was then manually edited to compensate for localised over alignment of some indels.

We estimated a nrITS gene tree as a basis for inferring the relationships of *Dendrobium kingianum*, and variation within *D. kingianum*. The optimal substitution model was estimated with jModelTest 2.1.10 (Darriba *et al.* 2012). We estimated the most likely nuclear ITS gene tree and branch support in a single run implemented by RAxML v.8.0.0 (Stamatakis 2014), with a GTR+G model, 2 threads, and 1000 likelihood bootstrap replicates. We also used Bayesian inference to estimate the gene tree with a Markov Chain Monte Carlo search of the posterior probability distribution of tree space implemented by MrBayes (Ronquist and Huelsenbeck 2003; Ronquist *et al.* 2012). Bayesian analysis had two runs of four chains, and 3 million generations, a GTR plus G substitution model, and no partitions. Convergence and mixing were assessed with Tracer v.1.6, and a burn-in of 25% was excluded before estimating the majority rule consensus tree as a summary of the sample of trees from the posterior probability distribution. The most likely tree is presented as output by RAxML, with *D. thyrsiflorum* and *D. cunninghamii* in a sister relationship to the remainder of the *Dendrobium* species included, which is in reasonable agreement with the topology of previously published phylogenies for *Dendrobium* (Burke *et al.* 2008).

Morphological analyses

A total of 139 plants, being a subset of the 281 individuals measured and scored for the purposes of description, from 52 locations throughout the distribution of *D. kingianum* (Table 1) were selected to capture the breadth of morphological and geographical variation expressed by this lineage. The number of plants from each region used in morphological analysis were: Region One: Stroud/Bulahdelah – nine plants; Region Two: Gloucester/Manning – 24 plants; Region Three: Hastings/Comboyne – 25 plants; Region Four: Coffs Harbour/Dorrigo – 32 plants; Region Five: Northern tablelands New South Wales – 15 plants; Region Six: Lamington/Mt. Tamborine – 17 plants; Region Seven: Gympie/Moreton – 9 plants; Region Eight: Carnarvon Gorge area – 8 plants.

Fresh living material was used for all measurements, which were made in the field when complete data were obtainable, otherwise samples were taken by removing a small number of pseudobulbs together with roots from the side of the plant, which were then grown in aged pine bark in raised beds or pots under greenhouse conditions. Height, width and mode of tapering vary to a differing degree in many populations over the distribution range. There is a general trend toward taller canes in the northern part of the range and shorter canes in the southern part, but dwarf forms may occur in all areas. Leaves vary in width, length, and number per cane. Flower count per raceme, and flower size vary among individuals. Flower colour and flower shape also vary, but these were not included in the analysis.

The core dataset comprised nineteen logically independent characters, including 7 vegetative and 12 floral characters: pseudobulb length; pseudobulb base width; pseudobulb apex width; leaves per cane; leaf length; leaf width; number of pseudobulb segments; number of flowers per raceme; peduncle length; flower length; dorsal sepal length; dorsal sepal width; raceme length; lateral sepal length; lateral sepal width; petal length; petal width; mid lobe width; fore lobe width. For each plant, three measurements from representative organs were made, and the mean value calculated. Where it was not possible to obtain three measurements, due to damaged or missing parts, mean values were calculated from two measurements. The lowermost leaf of the pseudobulb was used for all leaf measurements, and a flower of average appearance used for measurement. This core dataset was used for analysis of variance, and principal components analysis. For multidimensional scaling, an expanded dataset with additional metric and nominal variables was used, see details below. The plants were assigned to one of three taxa following the circumscriptions proposed by Clements and Jones (2002), and were scored for their region of origin, regions defined as illustrated in Figure 1.

Table 2. Specimen or reference details and GenBank accession numbers for sequences included in nrITS gene tree. Sequences newly generated for this study are indicated in bold. Vouchers for these specimens are destined for NSW herbarium, their deposition has been hampered by the COVID-19 pandemic.

Species	GenBank accession	Reference
Dendrobium adae	EU430371	Burke et al. (2008)
Dendrobium aemulum	EU430372	Burke et al. (2008)
Dendrobium amboinense	AB894133	Takamiya et al. (2018)
Dendrobium (Grastidium) baileyi	AY240016	Clements (2003)
Dendrobium bifalce	EU430373	Burke et al. (2008)
Dendrobium bigibbum var bigibbum	KP142215	Adams (2015)
Dendrobium bigibbum var bigibbum	KP142214	Adams (2015)
Dendrobium bigibbum var bigibbum	KP142212	Adams (2015)
Dendrobium bigibbum var superbum	KP142211	Adams (2015)
Dendrobium bigibbum var superbum	KP142213	Adams (2015)
Dendrobium callitrophilum	EU430374	Burke et al. (2008)
Dendrobium canaliculatum	EU430375	Burke et al. (2008)
Dendrobium carrii	EU430376	Burke et al. (2008)
Dendrobium (Flickingeria) cognatum	AY240015	Clements (2003)
Dendrobium cunninghamii	AY240019	Clements (2003)
Dendrobium falcorostrum	EU430377	Burke et al. (2008)
Dendrobium finniganense	EU430378	Burke et al. (2008)
Dendrobium fleckeri	EU430380	Burke et al. (2008)
Dendrobium fractiflexum	AY239949	Clements (2003)
Dendrobium furcatopedicellatum	AF521611	Tsai et al. (2004)
Dendrobium gracilicaule	EU430382	Burke et al. (2008)
Dendrobium haemoglossum	HM054638	Singh et al. (2012)
Dendrobium ischnopetalum	AY240007	Clements (2003)
Dendrobium jonesii var. magnificum	EU430383	Burke et al. (2008)
Dendrobium kingianum subsp. kingianum	**MW521085**	Haystack_269
Dendrobium kingianum subsp. kingianum	**MW521086**	Casino_699
Dendrobium kingianum subsp. kingianum	**MW521087**	Gloucester_PA8
Dendrobium kingianum subsp. kingianum	**MW521088**	Coongara_PA11
Dendrobium kingianum subsp. kingianum	**MW521089**	Lamington_PA7
Dendrobium kingianum subsp. kingianum	**MW521090**	Cloud_Ck_PA9
Dendrobium kingianum subsp. kingianum	**MW521091**	Mt_Tavingha_PA10
Dendrobium kingianum subsp. kingianum	**MW521092**	Mt_Alum_PA6
Dendrobium kingianum subsp. carnarvonense	EU430384	Burke et al. (2008)
Dendrobium kingianum subsp. kingianum	EU430386	Burke et al. (2008)
Dendrobium kingianum subsp. kingianum	AB894138	Takamiya et al. (2018)
Dendrobium kingianum subsp. kingianum	KJ672680	Hou, Luo and Ding, unpublished
Dendrobium kingianum subsp. kingianum	AF521075	van den Berg et al. (2005)
Dendrobium kingianum var. pulcherrimum	EU430385	Burke et al. (2008)
Dendrobium linguiforme	AF321593	Perkins and Weston, unpublished
Dendrobium macrophyllum	AY239979	Clements (2003)
Dendrobium macrophyllum	AB894131	Takamiya et al. (2018)
Dendrobium (Cadetia) maidenianum	AY239948	Clements (2003)
Dendrobium moorei	EU430388	Burke et al. (2008)
Dendrobium nindii	AY239985	Clements (2003)
Dendrobium oppositifolium	LC227998	Takamiya et al. (2018)
Dendrobium plicatile	KY966573	Li et al. (2018)

Species	**GenBank accession**	**Reference**
Dendrobium pugioniforme	AF321594	Perkins and Weston, unpublished
Dendrobium racemosum	EU430389	Burke et al. (2008)
Dendrobium salaccense	JN388577	Li et al. (2012)
Dendrobium schoeninum	EU430390	Burke et al. (2008)
Dendrobium shiraishii	AB894132	Takamiya et al. (2018)
Dendrobium somae	EU840692	Takamiya et al. (2011)
Dendrobium somae	HM590380	
Dendrobium speciosum	AY239998	Clements (2003)
Dendrobium speciosum	AB894143	Takamiya et al. (2018)
Dendrobium speciosum var. blackdownense	EU430391	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811539	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811541	Burke et al. (2013)
Dendrobium speciosum var. boreale	EU430392	Burke et al. (2008)
Dendrobium speciosum var. boreale	KC811542	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811538	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811534	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811531	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811532	Burke et al. (2013)
Dendrobium speciosum var. capricornicum	KC811545	Burke et al. (2013)
Dendrobium speciosum var. capricornicum	KC811543	Burke et al. (2013)
Dendrobium speciosum var. capricornicum	KC811544	Burke et al. (2013)
Dendrobium speciosum var. capricornicum	EU430393	Burke et al. (2008)
Dendrobium speciosum var. carnarvonense	EU430394	Burke et al. (2013)
Dendrobium speciosum var. curvicaule	KC811533	Burke et al. (2013)
Dendrobium speciosum var. curvicaule	EU430395	Burke et al. (2008)
Dendrobium speciosum var. curvicaule	KC811535	Burke et al. (2013)
Dendrobium speciosum var. grandiflorum	EU430396	Burke et al. (2008)
Dendrobium speciosum var. hillii	EU430397	Burke et al. (2008)
Dendrobium speciosum var. pedunculatum	KC811540	Burke et al. (2013)
Dendrobium speciosum var. pedunculatum	EU430398	Burke et al. (2008)
Dendrobium speciosum var. pedunculatum	KC811536	Burke et al. (2013)
Dendrobium speciosum var. pedunculatum	KC811537	Burke et al. (2013)
Dendrobium speciosum var. speciosum	EU430399	Burke et al. (2008)
Dendrobium taurinum	AB894142	Takamiya et al. (2018)
Dendrobium teretifolium var. fasciculatum	AY240008	Clements (2003)
Dendrobium tetragonum subsp. giganteum	KC811548	Burke et al. (2013)
Dendrobium tetragonum subsp. giganteum	KC811546	Burke et al. (2013)
Dendrobium tetragonum subsp. giganteum	EU430400	Burke et al. (2008)
Dendrobium tetragonum subsp. giganteum	KC811549	Burke et al. (2013)
Dendrobium tetragonum subsp. giganteum	EU430401	Burke et al. (2008)
Dendrobium tetragonum subsp. giganteum	KC811547	Burke et al. (2013)
Dendrobium tetragonum subsp. tetragonum	KC811551	Burke et al. (2013)
Dendrobium tetragonum subsp. tetragonum	KC811552	Burke et al. (2013)
Dendrobium tetragonum subsp. tetragonum	EU430403	Burke et al. (2008)
Dendrobium tetragonum subsp. tetragonum var. melaleucaphilum	EU430402	Burke et al. (2008)
Dendrobium tetragonum subsp. tetragonum var. serpentis	KC811550	Burke et al. (2013)
Dendrobium thyrsiflorum	AY24001	Clements (2003)

The distribution of some variables exhibited right skew, and while parametric multiple analysis of variance (manova) is generally robust to such violations (Olson 1974), we used permutational manova to test the null hypothesis that taxa, and regions, were no more different than expected by chance. All variables were standardised to unit variance by subtracting the variable mean from each observation and dividing by the variable standard deviation; this equalised variate contribution to pairwise distance among individuals, which was calculated using a Euclidean measure of association. Because we were interested in the contribution to overall variance by factors, not just the rank dissimilarities, we performed a permutational multivariate analysis of variance using distance matrices (Anderson 2001), implemented by the adonis function of package vegan 2.5-6 (Dixon 2003). We analysed a design with taxon and region treated as independent factors with an interaction term, and the significance of observed statistics estimated was estimated from 999 permutations to reduce Type 1 error.

Multidimensional Scaling (MDS) provides a means of visually representing the similarities and differences among samples. The same representative sample of 139 plants was analysed. Combined floral and vegetative data were analysed for all regions to determine differences and similarities between plants from different locations and from plants in areas described as different taxa. Morphometric analysis was conducted based on the characters in Table 3 using NTSYS pc Version 2.21. Data for each character were range standardised, such that the range of all characters equalled one unit, giving all characters equal weight. Pairwise distances between specimens were calculated using the Manhattan Metric, and the distance matrix subjected to ordination using non-metric MDS (Kruskal 1964). Ordinations were performed in three dimensions, to give an acceptable level of "stress" in the analysis, i.e. a good level of fit between the visual representation and the original distance matrix (Sneath and Sokal 1973, Milligan and Cooper 1988).

Principal component analysis (PCA) provides an effective means of extracting the main parameters of morphological variation (Dryden and Mardia 1998), by building linear and uncorrelated combinations of morphometric variables to maximise the sample variance explained by the first axis. Remaining axes were orientated orthogonally, with the same aim, and sequentially explain all the remaining variance. Principal components analysis was performed by the prcomp function in stats v.3.5.2 package (R Core Team 2018), again with variables scaled to have unit variance, and Euclidean pairwise distance between individuals, and analyses were conducted in R v.3.5.2 (R Core Team 2018).

Results

Gene tree reconstruction

The 14 *D. kingianum* nrITS sequences belonged to 11 haplotypes, due to differences at 14 variable sites, involving G-C, G-A, and C-T substitutions; 4 deletions of 1 or 2 bases, and an insertion of variable length involving a GA tandem repeat, which was longest in the individual from Cloudy Creek.

In the Bayesian analyses of nrITS sequences, the tree likelihood, base frequencies, and substitution matrix parameters all had effective sample sizes greater than 600 in the single runs, and marginal probability distributions overlapped with shared peaks, suggesting stationarity and convergence in the replicate searches.

In both the most likely tree and the Bayesian Majority Rule (MJ Rule) tree the individuals of *Dendrobium kingianum* group within a strongly supported lineage, but the species was rendered paraphyletic by *D. moorei* (Fig. 2). However, this paraphyly was not supported. Aside from *D. kingianum* subsp. *carnarvonense,* the other samples of *D. kingianum* formed two strongly supported monophyla, one containing individuals from the southern part of the distribution from Casino south, the other containing plants from northern part of the range from Dorrigo (Cloudy Creek) north. Three individuals of *D. kingianum* var. *pulcherrimum* formed a supported monophylum within the southern lineage.

Dendrobium kingianum was resolved sister to *D. speciosum* with strong support, as reported by Burke *et al* (2008). The monophyly of *D. speciosum* was unsupported, in contrast to the full support for the three nrITS lineages resolved within that species. Northern varieties including *D. speciosum* var. *curvicaule*, *D. speciosum* var. *boreale,* and *D. speciosum* var. *pedunculatum* were resolved among two lineages, and the southern lineages were resolved in a monophylum sister to the northern lineage containing the sampled individuals of *D. speciosum* var. *curvicaule.*

Table 3. Morphological characters used in morphological analyses.

Vegetative Characters
Pseudobulb length (cm)
Pseudobulb width at base (cm)
Pseudobulb width at midpoint (cm)
Pseudobulb width at top (cm)
Number of segments along pseudobulb
Collum[A]0/0.25/0.5/0.75/1.0 0= absent 1= strongly present
Number of leaves
Leaf length (cm)
Leaf width (cm)
Leaf thickness (mm)
Aerial roots [A] 0/1/2/3/4 0 = absent 4 = strongly present
Pseudobulb – midpoint width/base width
Floral Characters
Number of flowers per inflorescence
Rachis length (cm)
Peduncle length (cm)
Peduncle width (mm)
Flower length (dorsal sepal tip – lateral sepal tips) (cm)
Flower length (dorsal sepal tip – mentum) (cm)
Flower width across petals (as presented) (cm)
Flower width across petals (flattened) (cm)
Flower width at mentum (as presented) (cm)
Flower width at mentum (flattened) (cm)
Dorsal sepal length (cm)
Dorsal sepal width at base (cm)
Petal length (cm)
Petal width at base (mm)
Petal width at widest point (mm)
Individual lateral sepal width at base (cm)
Width of lateral sepals at widest point (as presented) (cm)
Width of lateral sepals at widest point (flattened) (cm)
Distance between lateral sepal tips (as presented) (cm)
Distance between lateral sepal tips (flattened) (cm)
Inner width of lateral sepals at widest point (flattened) (cm)
Pedicel length (cm)
Ovary length (cm)
Flower stalk length (cm)
Labellum length (cm)
Midlobe length (cm)
Midlobe width (cm)
Forelobe length (cm)
Forelobe width (cm)
Forelobe presentation width (mm)
Dorsal sepal length:width
Dorsal sepal length:labellum length
Flower length:labellum length ratio
Peduncle length:rachis length
Labellum length:midlobe length

[A] denotes nominal character

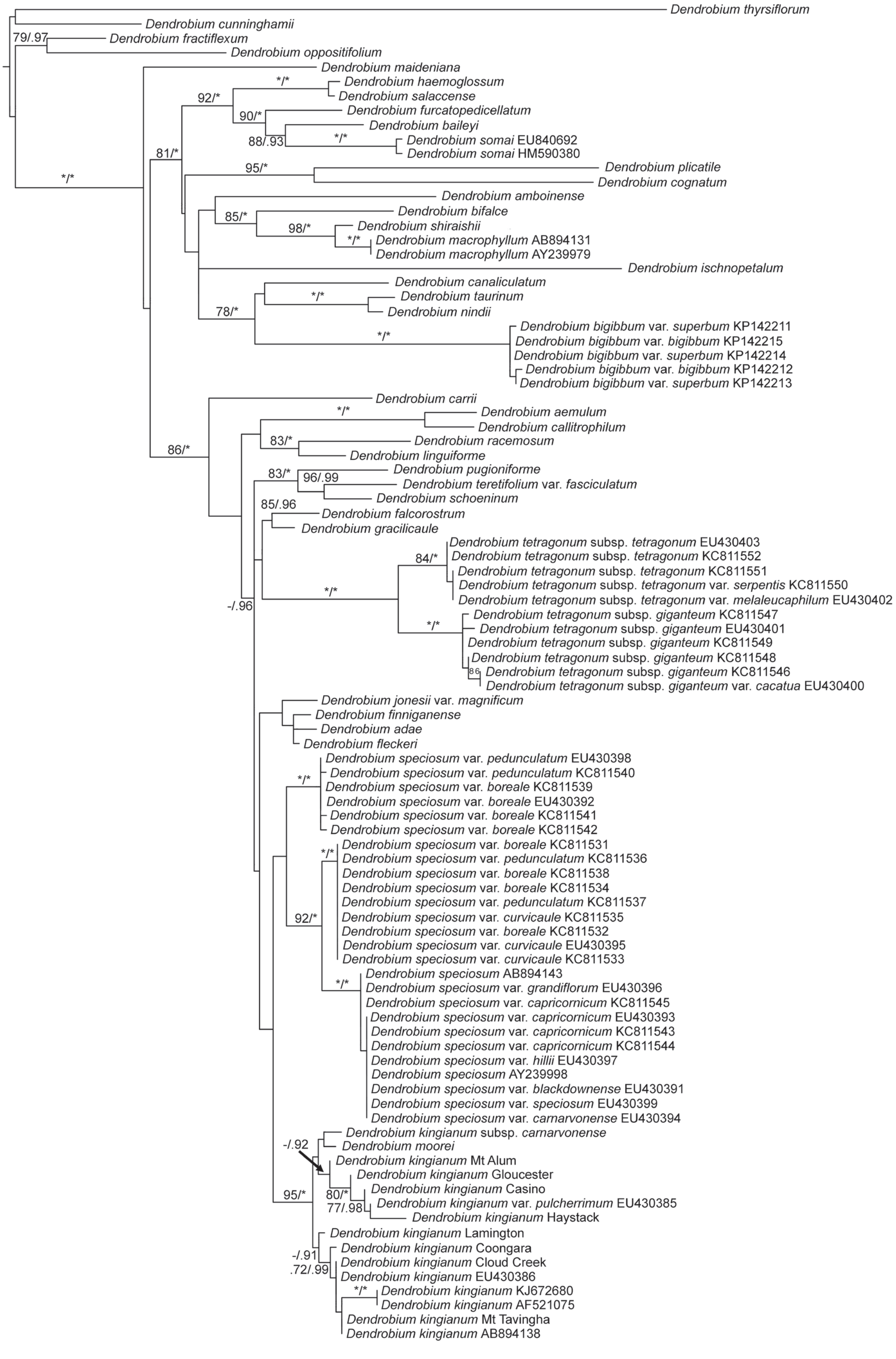

Figure 2. The most likely tree estimated for the nrITS sequences. Numbers associated with branches show likelihood bootstrap and posterior probability values, the latter from Bayesian analysis of the same dataset, respectively with * representing full support (100% and 1.0).

Morphological Analysis – Multidimensional Scaling

All plants ordinate within the space occupied by *D. kingianum* subsp. *kingianum*, with no isolated subgroups (Fig. 3). Plants ascribed to *D. kingianum* var. *pulcherrimum sensu* Rupp, being three plants from northern NSW and eight plants from the three southernmost regions of the distribution, occupy a broad central area of the ordination space, admixed with *D. kingianum* subsp. *kingianum*. Plants described as *D. kingianum* subsp. *carnarvonense* group towards one side of the ordination space. Some ordinate with tall straggly plants with narrow leaves from the northern and western limits of distribution where conditions are more extreme, for example the coastal southern Queensland area (Region 7).

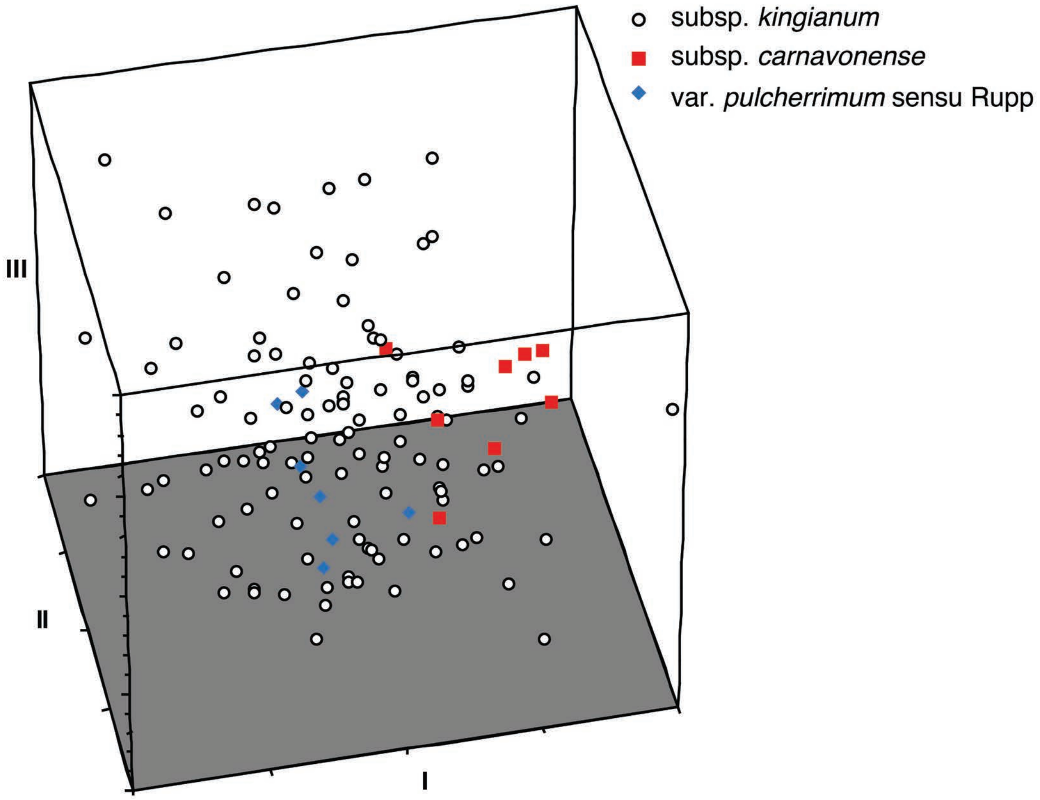

Figure 3. Ordination summarising variation among individuals in 19 morphological characters, summarising variation among individuals belonging to three commonly recognised taxa.

Plants of all regions overlap. Region 8 plants ordinate in the same space as some plants from regions 5, 6 and 7. Taller plants tend to ordinate towards one end of the space, and shorter ones at the other, with much overlap. Shorter plants from regions 1, 2 and 4 that correspond to *Dendrobium kingianum* var. *pulcherrimum* are mixed within the larger group.

Morphological analysis - Principal Components Analysis

Dendrobium kingianum subsp. *kingianum*, *D. kingianum* var. *pulcherrimum* and *D. kingianum* subsp. *carnarvonense* all have different centroids in multivariate morphological space (Fig. 4). Just over 9% of variation contributed by differences among taxa. Centroids are also significantly different among regions, which contributed 28% of residual sums of squares (Table 4). There was no significant interaction between putative taxon and region, implying the putative taxa are not geographically segregated. The first principal component (PC) explained 33% of variation among individuals. Characters with highest loading on the first PC were all associated with flower size, suggesting this axis broadly summarises differences in flower size among individuals (Table 5). *Dendrobium kingianum* subsp. *carnarvonense*, to which individuals from region 8 belong, are the only plants that separate along this axis, forming a distinct but not discrete cluster at the negative end (Fig. 4a). *Dendrobium kingianum* subsp. *carnarvonense* overlap with some individuals of *D. kingianum* subsp. *kingianum* from regions 4, 5, and 7. The distribution of individuals along PC1 suggests wide variation in flower size is a feature of most regions, with the largest flowers being found in regions 2, 3, and 6.

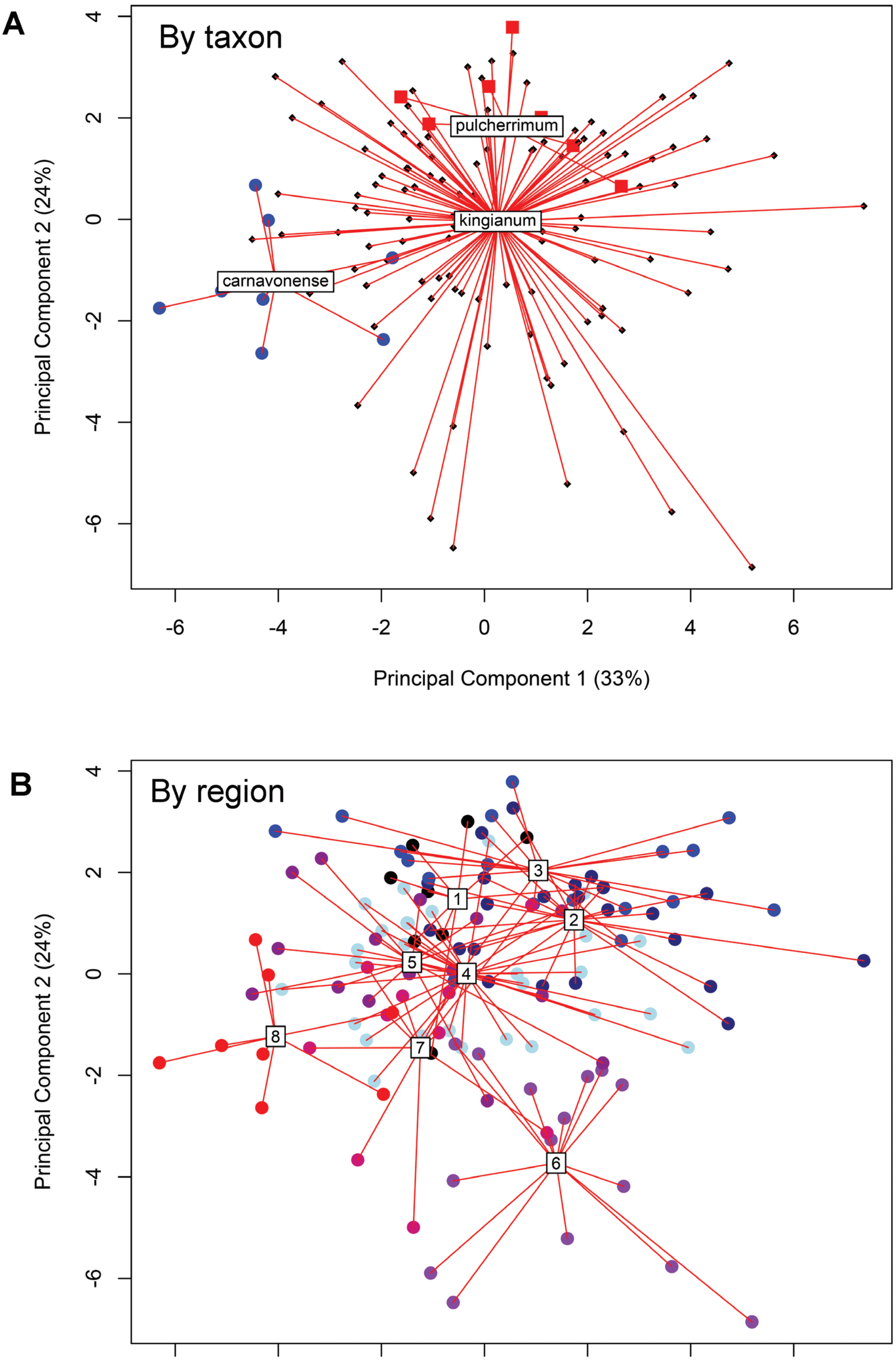

Figure 4. Principal components plot summarising variation among individuals in 19 morphological characters, showing centroids and distribution of individuals belonging to (A) three commonly recognised taxa; and (B) the eight regions in which *D. kingianum* occurs.

Table 4. Summary statistics from permutational MANOVA of morphological data.

	Df	SumsOfSqs	MeanSqs	F.Model	R^2	Pr(>F)	
Taxa	2	220.24	110.120	8.6195	0.09127	0.001	***
Region	6	676.66	112.776	8.8274	0.28042	0.001	***
Taxa : Region	2	21.35	10.675	0.8355	0.00885	0.573	
Residuals	117	1494.75	12.776		0.61946		
Total	127	2413.00			1.00000		

Table 5. Character loadings on principal components analysis.

	PC1	PC2	PC3	PC4	PC5
pseudobulb length	0.0726	-0.3931	0.0027	-0.2367	0.0611
pseudobulb base	0.1737	-0.0614	-0.5153	0.1055	0.2286
pseudobulb apex width	0.1944	-0.0704	-0.5350	0.1533	0.0824
leaves per cane	0.0122	-0.3628	-0.0737	-0.0571	-0.3961
leaf length	0.0494	-0.3619	0.0682	-0.0173	0.2296
leaf width	0.1657	-0.3423	-0.1854	-0.1334	-0.1688
number of pseudobulb segments	-0.0342	-0.3876	0.0842	-0.3772	0.0122
number of flowers per raceme	0.1850	-0.2714	0.0521	0.1997	-0.4692
peduncle length	0.1220	-0.2438	0.1676	0.4954	0.3781
flower length	0.3048	0.0145	0.2064	-0.1803	0.2484
doral sepal length	0.3027	0.0621	0.2918	-0.0359	0.0298
dorsal sepal width	0.2648	0.0264	-0.1923	-0.3165	0.1492
raceme length	0.2284	-0.2508	0.1703	0.3895	0.1539
lateral sepal length	0.3311	0.0987	0.1781	0.0110	-0.2537
lateral sepal width	0.2408	0.1617	-0.1270	0.3136	-0.3865
petal length	0.3267	0.0836	0.2431	-0.0079	0.0428
petal width	0.2882	0.1772	-0.2418	-0.0695	0.0882
midlobe width	0.3120	0.1194	0.0781	-0.1791	-0.0623
forelobe width	0.2912	0.1321	-0.0254	-0.1979	0.0002

The second PC explained 24% of variation among individuals. Characters with high loading on this axis were predominantly associated with pseudobulb and leaf size, but also the number of flowers per raceme and the peduncle length, which are all positively correlated with one another, and negatively correlated with PC2. Plants of *D. kingianum* var. *pulcherrimum* cluster toward the positive end of PC2, but they do not fall beyond the range of *D. kingianum* subsp. *kingianum*, whose individuals are more or less continuously distributed along this axis (Fig. 4A). Some separation among regions was achieved along PC2, plants from southern regions 1, 2 and 3 have centroids closest to the positive end of the axis, while plants from south-east Queensland and far north-east New South Wales have their centroid closest to the negative end (Fig. 4B). Individuals from region 7, and regions 1, 2, and 3 occupy non-overlapping subsets of multivariate morphological space, due to differences in vegetative morphology, flower count, and flower peduncle length.

Discussion

The nuclear ITS gene tree resolved *D. kingianum* paraphyletic with respect to *D. moorei*, but with no positive support for this topology, because the relationships of *D. moorei* within the *D. kingianum* clade are unsupported. Splits networks from AFLP data have also recovered a close relationship between *D. kingianum* and *D. moorei,* but resolved a single cluster corresponding with *D. kingianum* (Simpson *et al.* 2018). More nrITS haplotypes were detected among a smaller number of individuals of *D. kingianum* than within *D. speciosum*, suggesting *D. kingianum* may contain relatively higher levels of haplotype diversity in this marker, which may indicate lower effective gene flow among populations of the latter species. Where the sample of 26 individuals of *Dendrobium speciosum* yielded 7 haplotypes separated by 1–3 base differences and short indels, the sample of 14 *D. kingianum* returned 11 nrITS haplotypes. These 11 haplotypes exhibit a geographic pattern of relationships suggesting that geographic partitioning may contribute to the high haplotype diversity within *D. kingianum*.

Dendrobium kingianum is an inhabitant of rock outcrops, rock pavements, boulder fields, bluffs, cliff lines, gullies, gorges and ravines, and occurs as a mosaic of populations within the Australian landscape as a function of the existence of suitable habitat. Orchid populations may supply the majority of their own recruits, and gene flow among populations by pollen and seed transport may be limited, despite the apparent dispersability of small dust-like orchid seeds (Kotilínek *et al.* 2020). The lack of genetic panmixis that results from populations inhabiting relatively isolated habitat patches may contribute to the accumulation of regional differences in haplotype diversity, as known in other rainforest taxa (Heslewood *et al.* 2014). This regionalisation could be promoted by fluctuation in population sizes, such that shared ancestral haplotypes were purged from populations by stochastic processes during periods of small effective population size, as might result from glacial-interglacial cycling. Environmental niche modelling for the southern lineage of *Dendrobium speciosum* has predicted contraction of core habitat during the last glacial maximum (Simpson *et al.* 2018), consistent with the contraction of other species associated with rainforest habitats (Das *et al.* 2019). *Dendrobium kingianum* may exhibit a similar response. During glacial interglacial climate cycling through the Quaternary, rainforests have repeatedly contracted to core refugia (Van Der Waal *et al.* 2009) and have expanded in range and extent of occurrence since the last glacial maximum (Fahey *et al.* 2019; Whitehead *et al.* 2019). The results from the nrITS gene tree are suggestive, but the geographically structured genetic diversity may have a climatic component. The geographic distribution of genetic diversity within *D. kingianum* warrants further investigation, particularly with respect to establishing the dynamics of recruitment, and the potential existence and distribution of refugia.

In turn, there is a strong geographic component to the partitioning of morphological variation. During periods of climatic stress and small population size, selection may promote adaptive morphological divergence, as may have been the case at the southern end of the distribution, and indeed at higher elevations where short stature, clump-forming morphotypes predominate. These morphotypes may be adaptive in water-limited or cold environments. Studies from bryophytes demonstrate reduced water loss associated with clump forming habit due to reduced surface area to volume ratio, and activation of a boundary-layer effect that slows evaporation (Sand-Jensen and Hammer 2012; Zotz *et al.* 2000). Clumping may also facilitate warming, and slow the rate of cooling after dark, which may be especially important if *Dendrobium kingianum* is a C_4 plant. Cushion-forming alpine plants are known to warm at the same rate as the air, but cool at a slower rate than air (Sklenar *et al.* 2016). Both rates may be important at the southern end of *D. kingianum*'s distribution during periods of historical climate-induced stress, as may have occurred during glacial maxima. Conversely, we may be witnessing a peak in the extent and abundance of *D. kingianum* distribution, where the species currently occupies most of the suitable sites throughout its range, in which context many of the previously effective distance-based barriers to gene flow have been reduced or removed.

At the northern end of *D. kingianum* distribution we see a pattern that may be different from that observed at the south – a population currently confined to a mesic refugium within a canyon system. The climate currently constraining the distribution of *D. kingianum* in Carnarvon Gorge may be the result of longer-term cooling and drying of the Australian continent (Martin 2006). Today, conditions at the north-western limits of *D. kingianum* distribution may be promoting the unusual subterranean growth habit of *D. kingianum* subsp. *carnarvonense*, as the population shelters from climatic extremes by growing partially underground. Interactions with climate at two very different temporal and spatial scales, one a continent scale cooling and drying that has occurred millions of years, the other glacial-interglacial cycling that occurs over tens of thousands of years and likely has more pronounced impacts in the south of Australia, may contribute to the morphological diversity seen in contemporary *D. kingianum* populations.

Individuals from the southern end of *D. kingianum*'s distribution look different vegetatively from individuals in the coastal districts at the northern end of the distribution, although there are no qualitative character differences. A number of quantitative character differences could be used to circumscribe the morphotypes most frequent in each region, and these could be considered for recognition as different taxa. However, the proposition of species status for plants from different regions would overlook two critical factors integral to the utility of species. The first is that explaining a difference in morphology among individuals by the existence of different species neglects a hierarchy of variance components that may also explain those differences among individuals. The second is the broader geographic and climatic context that has resulted in those patterns. Species often preserve a signature of dynamic interaction with their environmental and ecological context, from which we can infer aspects of species history and life history (Rossetto *et al.* 2008; Rutherford *et al.* 2018; Whitehead *et al.* 2019). That signature often manifests in the form of intra-specific morphological variation.

Data from field observations of variation over the whole distribution range support a single species with wide variability of plant form and flowers. Two morphological and geographic sub-groups can be recognised. These have been formalised as subspecies which are now widely accepted (WCSPF 2018). Within the typical subspecies, morphological variation is more or less continuous, and exhibits a strong signature of regionalisation, at the same time as regions exhibit overlap and continuity in their parameters of morphological variation. Short, very clumped plants with small flowers represent one end of a continuum in morphological variation at the southern end of the distribution. Plants with relatively large flowers fitting the description of *D. kingianum* var. *pulcherrimum*

Rupp are scattered and very occasional over the southern half of the range. The geographic partitioning of a continuous spectrum of clinal variation, and nestedness of individuals of *D. kingianum* var. *pulcherrimum* within *D. kingianum* in the nrITS gene tree, both support the interpretation that individuals with the *D. kingianum* var. *pulcherrimum* morphotype are one expression of a variable *D. kingianum* subsp. *kingianum.*

Morphological data from PCoA and MDS support recognition of a single morphologically variable species, with a morphologically distinct subspecies in the north-west (Figures 3, 4). These results are compatible with the occurrence and distribution of molecular diversity recovered by this and previous studies of variable section *Dendrocoryne* species such as *Dendrobium speciosum* (Burke *et al.*, 2008, Simpson *et al.* 2018). No subgroups that could provide support for separate species within *D. kingianum* could be found in either the molecular or morphological data sets. The diminutive midlobe and partially subterranean habit of *D. kingianum* subsp. *carnarvonense*, together with the disjunct distribution supports the circumscription of the subspecies as initially described by Adams (Adams and Lawson 1995), in addition to the characters included in the morphological analysis completed here. Subspecies is appropriate for the Carnarvon Gorge plants because of their disjunct distribution, membership of a broader lineage corresponding with *D. kingianum,* and broad morphological overlap with *D. kingianum* subsp. *kingianum*. However, there are some plants at the western distribution limit of *D. kingianum* subsp. *kingianum* that may exhibit a similar degree of subterranean habit, as in typical *D. kingianum* subsp. *carnarvonense*. Unlike many orchid species, the labellum shape varies considerably in *D. kingianum*, in most regions and even in a single population (Table 6), and is not useful in circumscribing intra-specific taxa.

Table 6. Variation in Flower Colour and Midlobe Types in a population of *Dendrobium kingianum* at Gloucester, New South Wales

Plant No.	Flower Colour	Midlobe Type	Midlobe Point*
1.	purple	spade	-
2.	midmauve	oval	+
3.	midmauve	broadheart	+
4.	pale mauve	spade and	+/-
	pointed spade		
5.	midmauve	oval and spade	-
6.	midmauve	oval	-
7.	midmauve	broadheart	+
8.	deep mauve	broadheart	+
9.	pale mauve	broadheart	+
10.	midmauve	spade	-
11.	splash purple	broadheart	+
12.	pale mauve	pointed spade	
13.	pale mauve	broadheart	+
14.	splash mauve	broadheart	+
15.	midmauve	oval and spade	+/-
16.	midmauve	large globular	+
17.	pale mauve	broadheart	+

*

+ midlobe point present

- midlobe point absent or diminutive

Field studies coupled with analyses of morphological and molecular variation allow consideration of the status of all previously proposed taxa informed by morphological and molecular data. Firstly, this study of the whole distribution revealed no evidence to support the proposed segregate taxa of Clements and Jones (2002) with variation being continuous and best explained by a single species. Secondly, the historic varieties *Dendrobium kingianum* var. *aldersoniae*, *D. kingianum* var. *pallidum*, *D. kingianum* var. *pulcherrimum* and *D. kingianum* var. *silcockii* are all retained in synonymy with *D. kingianum* subsp. *kingianum* as recommended by Adams and Lawson (1995), as these varieties all represent colour and growth forms of a single variable species (Fig. 5).

Figure 5. A representative range of flowering individuals of *Dendrobium kingianum* from each region, illustrating diversity in vegetative and floral form expressed by this morphologically variable species; (A) Region 1. Mt. Alum. (B) Region 2. Gloucester (a triploid). (C) Region 3. Haystack (*D. kingianum* var. *pulcherriumum* Rupp). (D) Region 3. Stony Creek. (F) Region 4. Cloud Creek (*D. kingianum* var. *silcockii* F.M.Bail.).(E) Region 3. (*D. kingianum* var. *pulcherriumum* Rupp). (G) Region 6. Busby's Flat. (H) Region 6. Tarlington. (I) Region 7. Mt. Timbeerwah. (J) Region 8. Robinson Gorge (*D. kingianum* subsp. *carnarvonense*).

Taxonomic treatment

Dendrobium kingianum Bidwill ex Lindl. *Edwards' Botanical Register* 30: misc. 11 (1844)

Original material: 'This curious plant was bought by the Messers. Loddiges at the sale of Mr Bidwill's New Holland Plants'

Type: K 001089618 *fide* Clements (1989)

Callista kingiana (Bidwill ex Lindl.) Kuntze. *Revis. Gen*. pl. 2:654 (1891)

Dendrocoryne kingiana (Bidwill ex Lindl.) Brieger, in Schlechter *Die Orchideen* Ed. 3 (11/12): 724 (1981)

Tropilis kingiana (Bidwill ex Lindl.) Butzin, *Willdenowia* 12(2): 250 (1982)

Tropilis kingiana (Bidwill ex Lindl.) Rauschert, *Feddes Repert*. 94(78): 470 (1983) *nom. superfl.*

Thelychiton kingianus (Bidwill ex Lindl.) M.A.Clem. & D.L.Jones *The Orchadian* 13(11): 491 (2002)

General description based on all geographic regions

Plants growing together and forming large congested clumps or growing as separate individuals, of widely variable habit from miniature, short compact forms to medium and tall, upright urn shapes or spreading, scrambling plants with horizontal and downward arching pseudobulbs. Aerial growths absent, occasional or common, especially on older and leafless pseudobulbs. Pseudobulbs very variable, from very short (4 cm) to long (30 cm, rarely to 60 cm), broadest (up to 2.5 cm) at the base and tapering upwards to a narrow apex (0.25–0.7 cm), segments 2–7, most commonly 3–5; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green, brown or purple surface with longitudinal grooves. Leaves apical, 2–7 per pseudobulb, most commonly 3 or 4, narrow, elliptical to ovate, 3.5–12 cm long, 1.1–3.9 cm wide. Colour usually mid green or grey green with or without red purple tints, the tints pronounced when plants are exposed to strong light. There is a tendency in some plants towards very narrow leaves produced in a single plane, or variably twisted about the long axis. Plants variably floriferous, either one raceme per pseudobulb or multi-racemed pseudobulbs with dense floral displays. Floral racemes 1–3, green to deep purple in colour, arising terminally from the pseudobulbs and occasionally from a variable number of lateral nodes between and below the origin of the leaves, racemes erect to semipendulous; peduncle variable from 3.5–14.5 cm long, inflorescence 8–22 cm long.. One to fifteen flowers per raceme, on pedicels 1.0–1.5 cm long. Flower colour variable even within small populations, from pure white to solid purple, tending most commonly to splash purple and pale to mid mauve with a mid to deep purple speckled labellum. Occasionally the labellum is almost solid purple, rarely it is pure white. Flowers presenting cupped to planar, more commonly cupped and of medium substance (firmness of the plant tissue), occasionally with a deeper colour on the reverse side (northern plants). The mentum may be tinged with pale green or mauve-purple. Dorsal sepal keel 1.3–3.0 cm long, dorsal sepal 1.0–2.2 cm long, 0.3–0.8 cm wide, lateral sepals spanning 2.2–4.1 cm, 0.9–1.7 cm wide, petals 0.9–1.0 cm long, 0.2–0.7 cm wide. Floral segments from acute to rounded. Labellum c.1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; three lobed, very narrow at the base, lateral lobes narrow, usually erect or curved, and column embracing but occasionally flared outwards away from the column. Midlobe shape variable, sometimes two or three distinct shapes on the same plant, including oval, pointed spade, spade, bilobed spade, narrow-cordate, broadly cordate and occasionally rotund (similar to Table 6). Midlobe presentation width (diameter of midlobe in naturally presented flowers) 0.6–1.1 cm, forelobe presentation width (distance between lateral lobes in naturally presented flowers) 0.4–0.85 cm. Callus on lamina green, yellow, colourless or white, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column c. 0.4 long by 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, varying from yellow to green in colour, most commonly green.

Representative specimens examined are listed in Table 7 and lodged at MELU and NSW.

Table 7. *Dendrobium kingianum* specimens lodged at Herbaria

Name	Collection No.	Region	Herbarium	DNA sampled
subsp. *kingianum*				
Mt. Alum	1088	1	NSW	+
Mt. Alum	1188	1	NSW	-
Main Creek Dungog	861	1	NSW	-
Waukivory Pink	865	2	NSW	-
Gloucester Shell Pink	1867	2	NSW	-
Rowleys Ridge	893		NSW	-*
Ha Ha (No. 21)	1922/549	2	NSW	+
AF22	669	2	NSW	-
Gloucester Red No.1	290	2	NSW	-
Gloucester Red No.2	563	2	NSW	-
Haystack	490	3	NSW	+ *
Mt. Boss	1282	3	NSW	-
Tunstead’s Pink	426	3	NSW	-
Lansdowne	850	3	NSW	-
Stony Creek	167	3	NSW	-
Yarras White	1281/1196	3	NSW	-
Port Macquarie	136	3	MELU	EU430385
Dorrigo Red	1421	4	NSW	-
Len Archer Pulcherrimum	699	4	NSW	+*
Cloud Creek Dorrigo	889	4		+
Keith Preston	288	4	NSW	-
Lipstick	296	4	NSW	-
Gibraltar Range Rock Top	1626	4	NSW	-
Walkerie Rock Pulcherrimum	1983	4	NSW	-
Coledale Morgans Camp	1634/?1636	4	NSW	-
Gibraltar Range R&R	10	5	NSW	-
Boonoo Boonoo Falls	1644	5		-
Boonoo Boonoo	1632	5	NSW	-
Boonoo Boonoo	1605	5	NSW	-
Rocky River 1.	1029	5	NSW	-
Rocky River 2.	1022	5	NSW	-
Busby’s Flat White	449	6	MELU	EU430386
Tarlington	640	6	NSW	-
Tarlington	642	6	NSW	-
Lamington Plateau	216	6	NSW	+ ?MELU
Wine Creek	514	6	NSW	-
Busby’s Flat Pink Stars	509		NSW	-
Pikapene White	740	6	NSW	-
Corrigan’s Red	240	6	NSW	-
Mothar Mountain	926	7	NSW	-
Coongara	268	7	NSW	+?MELU
Tavinghi	1967	7	NSW	+ PA10
Tibrogargan or Timberwah	?961	7	NSW	-
Yangan Toowoomba	896	7	NSW	-
Yangan Toowoomba	917	7	NSW	-
subsp. *carnarvonense*				
Robinson Gorge	1981	8	NSW	-
Carnarvon Gorge	1982	8	NSW	+?MELU
Carnarvon Gorge	1983	8	NSW	-

*pulcherrimum

Key to subspecies

1a. Plants erect to spreading, but not consistently partially subterranean, flowers variable in colour, midlobe greater than 0.6 cm in width with a callus on the labellum bearing conspicuous keels ending in three prominences anteriorly. Plants of southern Queensland and New South Wales.. *D. kingianum* subsp. *kingianum*

1b. Plants consistently partially subterranean, pseudobulbs forming an underground mat with narrow emergent upper portions, leaves long 8.2–13.5 cm and narrow 0.85–1.9 cm, flowers white to pale mauve with very small purple-streaked midlobe, midlobe diameter 0.4–0.5 cm, low callus on labellum with no bluntly-ending anterior keels. Plants of Central Queensland sandstone country ....*D. kingianum* subsp. *carnarvonense*

Dendrobium kingianum* subsp. *kingianum

=*Dendrobium kingianum* var. *album* B.S.Williams, *The Orchid Album* 7: 332 (1887)

Original material: 'For the opportunity of figuring this rare plant we are indebted to A.H. Smee, Esq., The Grange, Carshalton, in whose well-known collection it bloomed in the early part of the present year.'

=*Dendrobium kingianum* var. *pallidum* F.M.Bailey, *The Brisbane Courier* 38(8000): 7 (1883)

Original material: 'Hab. on rocks Main Range, collected by B. Crow and C.H. Hartmann'

Type: Main Range, *B. Crow and C.H. Hartmann* (BRI-AQ0025296, K)

=*Dendrobium kingianum* subvar. *pallidum* J.H.Veitch, *A Manual of Orchidaceous Plants* 1(3): 52 (1887)

Original material: (none cited)

Type: not located

=*Dendrobium kingianum* var. *silcockii* F.M.Bailey, *The Queensland Flora* 5: 1528 (1902)

Original material: 'Found towards the Tweed River, 24th Sept. 1901. P. Silcock.'

Type: Collected from towards the Tweed River, Sept 24th 1901, *P. Silcock* (BRI-AQ0025295; K).

=*Dendrobium kingianum* var. *aldersoniae* F.M.Bailey, *The Queensland Agricultural Journal* 15: 781 (1905).

Original material: Blackall Range, Mrs G. W. Alderson

Type: not located

Dendrobium kingianum var. *aldersonae* F.M.Bailey, *orth. var.*

=*Dendrobium kingianum* var. *pulcherrimum* Rupp, *Orchids of New South Wales*: 116 (1943)

Thelychiton pulcherrimus (Rupp) M.A.Clem. & D.L.Jones, *The Orchadian* 13(11): 492 (2002)

Original material: In Herb. Rupp: Northbridge (cult. plant from the Upper Hastings River, Fieldsend 1937), Rupp 9.1943, Holotype.

Type: Cult. Northbridge, N.S.W. 9. 1943 (HMRR). Plant originally from the Upper Hastings River, N.S.W. (coll. F. Fieldsend) (holotype: NSW 87427!).

Queensland and Border Ranges forms

Description: Plants of variable habit, generally tall, upright, urn shaped with open structure in exposed areas, and scrambling cascades on shaded creek sides. Aerial growths common on most plants. Pseudobulbs usually robust and tending to a vertical orientation with an expanded basal third anchored to rocks in leaf litter or grass; short (10 cm) to long (27 cm), an occasional plant to 60 cm, broadest (up to 2.5 cm) at the base and tapering upwards to a broad apex (0.3–0.7 cm), segments 5–10, most commonly 6–7; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a brown or purple surface with longitudinal grooves. Leaves apical, 3–7 per pseudobulb, most commonly 4–6, narrow, elliptical to ovate, 6.2–12 cm long, 1.8–3.9 cm wide. Colour usually mid green with or without red purple tints, the tints pronounced when plants are exposed to strong light. Plants variably floriferous, including multi-racemed pseudobulbs with dense floral displays. Floral racemes 1–3, arising terminally from the pseudobulbs and occasionally from lateral nodes between and below the origin of the leaves, racemes erect, semierect or pendulous; bearing 3–15 flowers per raceme, commonly 8–10, on pedicels 1–1.5 cm long. Peduncle variable from 5–12 cm long, rachis 7–13 cm, inflorescence 11–22 cm long. Flower colours pure white to solid purple, tending most commonly to splash purple and pale to mid-mauve with a mid to deep purple speckled labellum. Occasionally the labellum is almost white or solid purple. Flowers presenting cupped to planar, more commonly cupped and of medium to heavy substance, commonly with a deeper colour or strong purple lines on the reverse side. The mentum may be tinged with pale green or mauve purple. Dorsal sepal 1.2–1.7 cm long, 0.55–0.75 cm wide, keel 1.6–2.6 cm long, lateral sepals spanning 2.4–3.4 cm, 1.0–1.3 cm wide, petals 1.0–1.6 cm long, 0.3–0.55 cm wide. Floral segments are usually acute. Labellum approximately 1.5 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple; three lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing. Midlobe shape widely variable, occasionally two or three distinct shapes on the same plant, including oval, pointed spade, spade, broad heart and occasionally globular or narrow heart (similar to Table 6). Midlobe presentation 0.6–0.95 cm wide, forelobe presentation 0.4–0.65 cm wide. Laminar callus green, yellow or colourless to white, with three low to distinctly elevated ridges, often conspicuously divided into three prominent lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column generally c. 0.4 cm long, 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, from yellow to green in colour, usually green.

Distinctive aspects: In general, there is a trend towards aerialization and longer upright pseudobulbs and raceme habit. Flowers have medium to heavy substance and pointed segments, imparting a starry appearance.

Notes: Characteristics intergrade with those of plants on the Great Dividing Range through the Border Ranges (Queensland, New South Wales) to Gibraltar Range and the Dorrigo region (New South Wales).

Chromosome number: All plants tested were diploid (2n=38) (Adams 1992).

Dorrigo and Gibraltar Range forms

Description: Plants growing together and forming large clumps or growing as separate individuals, of widely variable habit from tall upright urn shape to spreading, scrambling plants with horizontal and downward arching pseudobulbs. Aerial growths are common, especially on older and leafless pseudobulbs. Pseudobulbs variable, from short (7 cm) to long (20 cm), broadest (up to 1.5 cm) at the base and tapering upwards to a narrow apex (0.25–0.4 cm), segments 4–5, most commonly 4; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green, brown or purple surface with longitudinal grooves. Leaves apical, 3–5 per pseudobulb, most commonly 3 or 4, narrow, elliptical to ovate, 4.5–9 cm long, 1.4–2.1 cm wide. Colour usually mid green with or without red purple tints, the tints pronounced when plants are exposed to strong light. In some plants there is a tendency towards very narrow leaves produced in a single plane, or variably twisted about the long axis. Plants variably floriferous, including multi-racemed pseudobulbs with dense floral displays. Floral racemes 1 or 2, occasionally 3, arising terminally from each pseudobulb and occasionally from lateral nodes between and below the origin of the leaves, racemes erect to semierect; bearing 3–10 flowers per raceme, median 6, on pedicels 1.0–1.5 cm long. Peduncle variable 5–14.5 cm long, rachis 4–9 cm long, inflorescence 9.5–20 cm long. Flower colour pure white to solid purple, or splashed with purple and pale to mid-mauve with a mid to deep purple speckled labellum, occasionally with a deeper colour on the reverse side; the labellum may be almost solid purple. Flowers presenting cupped to planar, more commonly planar and of light to medium substance. The mentum may be tinged with pale green or mauve purple. Dorsal sepal 1.3–1.8 cm long, 0.5–0.6 cm wide, keel 2.1–2.8 cm long, lateral sepals spanning 2.5–3.3 cm, 1.1–1.2 cm wide, petals 1.2–1.7 cm long, 0.3–0.5 cm wide. Floral segments from strongly pointed (sharply acute) to rounded. Labellum 1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; three-lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing but occasionally flared outwards away from the column. Midlobe shape widely variable, occasionally two or three distinct shapes on the same plant, including oval, pointed spade, spade, broad heart and occasionally globular (similar to Table 6). Midlobe presentation 0.75–1.0 cm wide, forelobe presentation 0.4–0.65 cm wide. Callus on lamina green, yellow or colourless to white, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column about 4 mm long, 3 mm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, from yellow to green in colour, most commonly green.

Distinctive aspects: There is a trend towards flowers with light to average substance and acute segments (starry), but there are some examples of large rounded flowers with heavy substance.

Notes: Characteristics intergrade with plants in the adjacent Coffs Harbour and Grafton areas at lower altitude, where pseudobulbs are shorter, and with plants at the western limit that are smaller and shorter, with diminutive flowers. Intergrades with forms in the Border Ranges and with more southerly forms from the NSW north coast.

Chromosome number: Most plants diploid (2n=38); occasionally triploid (3n=57) (Adams 1992).

Grafton to Coffs Harbour forms

Description: Plants of variable habit, from compact to short or medium height, and widely open structure, either erect or spreading and scrambling. Aerial growths common. Pseudobulbs variable from very short (7 cm) to medium (14 cm) height, often narrow in the upper portion and at the apex, without specific identifying features, broadest (up to 1.4 cm) at the base and tapering upwards to a narrow apex (0.25–0.4 cm),segments 3–6, most commonly 5, when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal green, brown or purple surface with longitudinal grooves. Leaves apical, up to 3–5 per pseudobulb, narrow, elliptical to ovate, 5–10 cm long, 1.3–2.1 cm wide. Colour usually mid green with or without red purple tints, the tints pronounced when plants are exposed to light; in erect plants there is a tendency towards very narrow leaves produced in a single plane, or variably twisted about the long axis. Plants variably floriferous, including multi-racemed pseudobulbs with dense floral displays. Flowers generally of moderate form and quality, with some attractive splash petal and pale mauve forms. Floral racemes 1 or 2, occasionally 3, arising terminally from the pseudobulbs and from lateral nodes between and below the origin of the leaves, racemes erect, semi-erect or semi-pendulous. Flowers 4–8 per raceme, median 6, on pedicels 5–10.5 cm long, peduncle variable from 5–10.5 cm long, rachis 3–8.5 cm long, inflorescence 8–20 cm long. Flower colour pure white to solid purple, most commonly splashed with purple and pale to mid-mauve with a mid to deep purple speckled labellum. Occasionally the labellum is almost solid purple. Flowers presenting cupped to planar, more commonly cupped and of light to medium substance, occasionally with a deeper colour on the reverse side. The mentum may be tinged with pale green or mauve-purple. Dorsal sepal 1.3–1.8 cm long, 0.5–0.6 cm wide, keel 1.5–2.6 cm long, lateral sepals spanning 2.3–3.2 cm, 0.9–1.3 cm wide, petals 1.0–1.5 cm long, 0.3–0.55 cm wide. Floral segments strongly pointed (sharply acute) to rounded. Labellum c. 1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; three lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing but occasionally flared outwards away from the column. Midlobe shape widely variable, occasionally two or three distinct shapes on the same plant, including oval, pointed spade, bilobed spade, spade, broad heart and occasionally globular (similar to Table 6). Midlobe presentation 0.65–0.95 cm wide, forelobe presentation 0.4–0.75 cm wide. Callus on lamina green, yellow or colourless to white, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column generally 0.4 cm long, 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, from yellow to green, but most commonly green.

Distinctive aspects: There is a trend towards narrow upper portions of pseudobulbs and flowers with light to average substance and pointed segments, but there are some examples of large rounded flowers.

Notes: Characteristics intergrade with those of plants in the adjacent Dorrigo Gibraltar Range areas at higher altitude. Intergrades also occur with northern plants in the Border Ranges and with more southerly plants of the Hastings Region.

Chromosome number: Most plants diploid (2n=38); very occasionally triploid (3n=57) (Adams 1992).

Hastings to Comboyne forms

Description: Plants of miniature (very short) or short and compact habit or occasionally to medium height, often interweaving to form a mat with closed canopy over rocky outcrops, individual plants upright or spreading with widely radiating pseudobulbs. Aerial growths occasional. Pseudobulbs variable, from very short (4 cm) to medium (11 cm) height, usually robust, but sometimes more slender in the apical portion, broadest at the base (up to 1.4 cm diam.) and gradually tapering upwards to the apex (3–4 mm), segments 2–4, most commonly 3; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green, brown or purple surface with longitudinal grooves. Leaves apical, up to 3 or 4 per pseudobulb, narrow, elliptical to ovate, 3.5–10 cm long, 1.1–2.3 cm wide; colour usually grey green occasionally with a few red purple tints. Plants variably floriferous, usually with a medium density of flowers. Floral raceme(s) 1, sometimes 2, arising terminally from the pseudobulbs and rarely from lateral nodes between and below the origin of the leaves, racemes erect, semierect or pendulous. Flowers 2–8 per raceme, usually 4 or 5, on pedicels 1.0–1.5 cm long, peduncle variable from 3.5–8.3 cm long, rachis 3.5–9 cm long, inflorescence 8–14 cm long. Flowers pure white to deep mauve, occasionally *silcockii* colour (having white sepals and petals and purple markings on the labellum) and lavender. Flowers presenting cupped to planar, more commonly cupped and of medium to heavy substance. The mentum may be tinged with pale green or mauve. Dorsal sepal 1.1–1.9

cm long, 0.3–0.8 cm wide, keel 1.5–3.0 cm long, lateral sepals spanning 2.4–3.6 cm, 1.0–1.4 cm wide, petals 1.1–1.7 cm long, 0.3–0.7 cm wide. Floral segments from strongly pointed (sharply acute) to rounded, mostly tending to a relatively broad apex. Labellum approximately 1.5 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; three lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing but occasionally flared outwards away from the column. Midlobe shape widely variable, often two or three distinct shapes on the same plant, including oval, pointed spade, spade, broad heart and occasionally globular or narrow heart (similar to Table 6). Midlobe presentation 0.6–1.1 cm wide, forelobe presentation 0.4–0.85 cm wide. Laminar callus green or yellow, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column about 0.4, 0.3 cm, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, from yellow to green, most commonly green.

Distinctive aspects: The grey green leaves are conspicuous in most but not all locations in this region, and the colour is relatively uniform in each population of plants.

Notes: The grey green leaf colour is distinctive at many locations in the region, but grades to mid green in adjacent regions, and is of variable intensity. Deep purple colour is uncommon. Flowers rarely have a significantly deeper colour on the reverse side. Characteristics intergrade with plants in the adjacent Coffs Harbour - Grafton areas to the north. Characteristics are usually distinguishable from inland plants of the Grafton - Manning region, but not in all cases.

Chromosome number: All plants tested have been diploid (2n=38) (Adams 1992).

Gloucester to Manning forms

Description: Plants short to medium height, infrequently tall and forming large congested clumps or growing as separate individuals, of widely variable habit, urn shaped to spreading, scrambling with horizontal and downward arching pseudobulbs. Aerial growths are common on some plants, but infrequent or absent on most. Pseudobulbs without specific identifying features, variable and usually robust, from short (6.5 cm) to long (35 cm), broadest (up to 2.8 cm) at the base and tapering upwards to a narrow apex (0.4 cm diam.), segments 2–5, most commonly 4; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green, brown or purple surface with longitudinal grooves. Leaves apical, 3–4 per pseudobulb, narrow, elliptical to ovate, 4.5–9 cm long, 1.4–2.1 cm wide. Colour usually mid green with or without red purple tints, the tints pronounced when plants are exposed to strong light. No absolute distinguishing leaf features, a tendency in many plants to robust leaves, variably twisted about the long axis. Plants variably floriferous, including a few multi-racemed pseudobulbs with dense floral displays. Flowers generally of moderate to excellent form and quality, with some outstanding forms in most of the main colours. Floral racemes 1–3, arising terminally from the pseudobulbs and occasionally from lateral nodes between and below the origin of the leaves, racemes erect to semierect. Three to ten flowers per raceme, median 6, on pedicels 1.0–1.5 cm long. Peduncle variable from 5–11.5 cm long, rachis 9–20 cm, total inflorescence 9–20 cm long. Flower colours pure white to solid purple, tending most commonly to pale to mid-mauve rarely with a slightly deeper colour on the reverse side, mid to deep purple speckled labellum. Occasionally the labellum is almost solid purple. Flowers presenting cupped to planar, more commonly cupped and of medium to very heavy substance. The mentum may be tinged with pale green or mauve purple. Dorsal sepal keel 1.9–3.0 cm long, dorsal sepal 1.1–2.2 cm long, 0.55–0.8 cm wide, lateral sepals spanning 2.2–4.1 cm, 1.1–1.4 cm wide, petals 1.1–1.8 cm long, 0.35–0.65 cm wide. Floral segments from pointed (acute) to rounded. Labellum approximately 1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple; three lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing but occasionally flared outwards away from the column. Midlobe shape widely variable, often two or three distinct shapes in a population and sometimes on the same plant, including oval, pointed oval, pointed spade, spade, bilobed spade, broad heart and globular (Table 6). Midlobe presentation 0.7–1.1 cm wide, forelobe presentation 0.45–0.75 cm wide. Callus on lamina green, yellow or colourless, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column c. 0.4 cm long, 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–1.0 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, yellow to green, but most commonly green.

Distinctive aspects: There is a trend towards round shaped flowers with heavy substance and robust leaves which have a marked twist.

Notes: Characteristics intergrade with those of plants in adjacent areas to the north, and towards Bulahdelah in the south. Some plants of robust type are identifiable as coming from the region, but many are not.

Chromosome number: Most plants diploid (2n=38); occasionally triploid (3n=57) or tetraploid (4n=76). In some areas, purple flowering plants are exclusively triploid (Adams 1992).

Bulahdelah area forms

Description: Short compact plants crowded together forming large mats or growing as separate individuals. Aerial growths are occasional. Pseudobulbs variable, very short (4 cm) to short (8 cm), broadest at the base (up to 1.5 cm diam.) and tapering upwards to a variable apex (0.25–0.4 cm diam.), segments 2 or 3, most commonly 3; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green or brown surface with longitudinal grooves. Leaves apical, up to 4 per pseudobulb, most commonly 3, narrow, elliptical to ovate, 5.1–7.6 cm long, 1.3–2.0 cm wide. Colour usually mid green. Plants often with few flowers. Floral racemes, usually one, arising terminally from the pseudobulbs, rarely from lateral nodes between and below the origin of the leaves, racemes erect to semierect. Flowers 1–5 per raceme, median 3, on pedicels 1.0–1.4 cm long. Peduncle 4–8 cm long, rachis 3.5–7.0 cm long, inflorescence 8–14 cm long. Flowers pure white to mid mauve, most commonly pale mauve with a mid-purple speckled labellum and without deeper colour on the reverse side. Flowers presenting cupped, or occasionally planar and of medium substance. The mentum may be tinged with pale green or yellow. Dorsal sepal 1.2–1.7 cm long, 0.55–0.7 cm wide, keel 1.8–2.3 cm long, lateral sepals spanning 2.2–3.4 cm, 1.1–1.3 cm wide, petals 1.1–1.6 cm long, 0.3–0.5 cm wide. Floral segments pointed (sharply acute) to rounded. Labellum c. 1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; 3-lobed, very narrow at the base, lateral lobes narrow, usually erect, or curved and column embracing. Midlobe shape widely variable, often 2 or 3 distinct shapes on the same plant, including oval, pointed spade, spade, narrow heart, broad heart and occasionally globular (similar to Table 6). Midlobe presentation 0.6–0.8 cm wide, forelobe presentation 0.4–0.6 cm wide. Callus on lamina green or yellow, with three low ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously. Column c. 0.4 cm long, 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, yellow to green, but most commonly green.

Distinctive aspects: There is a trend towards very short plants with few small flowers of average substance and with rounded segments.

Notes: Characteristics intergrade with those of plants in the adjacent Hastings, Comboyne and Gloucester areas, where pseudobulbs are longer and flowering more prolific. Wide variations occur in this southern region, especially in the intergrading ranges between Bulahdelah and Gloucester, in flower colour, form, and plant growth habit.

Chromosome number: All plants tested have been diploid (2n=38) (Adams 1992).

Distribution and ecology: *Dendrobium kingianum* subsp. *kingianum* occurs in and around sclerophyll forest and rainforest from central coast NSW to the Sunshine Coast, north of Brisbane, Queensland. It is scattered and discontinuous due to its restricted habitat. At its northern limit it is found on the volcanic plugs of the Glasshouse Mountains and isolated communities north to Biggenden. Limiting factors in the north and west are likely the high temperatures or limited day length variation between summer and winter, restricting flowering, and the lower rainfall in the west. At the southern limit, lower winter temperatures may restrict growth. *Dendrobium kingianum* subsp. *carnarvonense* has a disjunct distribution well separated from subsp. *kingianum* and is found in sheltered gorges inland at the extreme north of the range, with relatively low evaporation rates, fairly constant humidity and adequate water.

Dendrobium kingianum grows as a lithophyte and rarely as an epiphyte in Eastern Australia from just north of the Hunter River (32°30'S) near Newcastle (Central NSW) to the Tropic of Capricorn (23°26'S) in central west Queensland. Small colonies at Isla Gorge, Biggenden, and the Monto area partially fill the gap in the range which was previously thought to exist between the Gympie and Biggenden area to the east and Carnarvon Gorge. The western limit follows the New England Highway in northern NSW and southern Queensland.

There are unconfirmed reports of *D. kingianum* (Clemesha 1965) outside of the substantiated range. These are possibly due to planting *D. kingianum* plants from private collections into the bush in areas south of the Hunter River and even in southern NSW and Victoria. Reports of plants of the “Bulahdelah form” south of the Hunter River at Ourimbah, Bucketty and Burragorang Valley prior to flooding by the Warragamba Dam, for example, may represent relocated plants.

Under favourable conditions *D. kingianum* forms extensive colonies on cliff faces and rocks in open forests or along forest creeks. There are places where it is the dominant plant species, covering north facing hillsides with plants up to several metres in diameter. Colonies may grow on rocky bluffs within a few kilometres of the sea, and at elevations of 3,000 feet in the Great Dividing Range. At the western limit small isolated colonies survive as moss embedded plants in dry country 100km west of the Great Divide and in an isolated population at Carnarvon Gorge (central Queensland) 450 km from the coast. Habitats include warm temperate rainforest, wet sclerophyll forests and dry forest types dominated by *Eucalyptus* species. Isolated restricted occurrences in the western and northern parts of the range suggest that the distribution was much more widespread in the past under wetter climates.

Dendrobium kingianum* subsp. *carnarvonense Peter B.Adams in P.B. Adams and S.D. Lawson, *Dendrobium kingianum*: *a unique Australian orchid*: 16 (1995)

Thelychiton carnarvonensis (P.B. Adams) M.A.Clem. & D.L.Jones, *The Orchadian* 13(11): 491 (2002)

Type: Carnarvon Gorge, Queensland, 14 Sep. 1994, *P.B. Adams 1135*; holo: BRI, iso: MEL.

Plants lithophytic and semiterrestrial, rarely epiphytic, with slender pseudobulbs, up to 15cm long, the older ones and lower portions of newer pseudobulbs covered by decomposing sandstone and leaf litter, the upper portions emergent and bearing frequent aerial growths, narrow at the apex. Leaves lanceolate, 8–14 cm long, 0.85–1.9 cm wide. Racemes erect or semierect, bearing 2–7 flowers groups towards the apex, segments curved to form a cup shaped flower, with purple blushing or striae on the reverse of sepals and on the labellum. Flowers small and round, 1.6 cm high 2.2 cm wide. Segments acute or subacute, forelobe and midlobe of labellum curved to form a narrow tube approximately 0.35–0.5 cm wide. Midlobe oval or broadly heart shaped, ending in a small point anteriorly, callus pale green without raised keels, ending bluntly or with three small nodules at the base of the midlobe.

Description: Plants forming dense mats of leafless pseudobulbs fully covered by sandy soil and debris, with the upper portions of more recent pseudobulbs emergent, bearing frequent aerial growths. Roots ramifying through soil and attached to rocks. Plants occasionally epiphytic. Pseudobulbs generally narrow at the base, 0.7–1.2 cm diam., and narrow to very narrow, 0.25–0.4 mm diam., at the apex; 9.0–15 cm long, curving irregularly in many different directions, segments 4–6, green in colour if aerial, yellow if subterranean, partly covered by a pale brown papery velum. Leaves apical, up to 3–4 per pseudobulb, narrow, lanceolate, 8.2–14 cm long, 0.85–1.9 cm wide, colour mid green with no purple tints. Plants variably floriferous, not usually forming dense displays. Floral racemes 1 or 2, arising from lateral nodes between and below the origin of the leaves, racemes erect or semierect. Flowers two to seven per raceme, median 4, clustered toward the floral apex on short pedicels 0.4–0.7 cm long. Peduncle 4.6–12 cm long, rachis 2.5–5 cm long, inflorescence 7–15 cm long. Flowers white anteriorly with purple striae or blush areas on reverse side of sepals. Labellum c. 1.2 cm long, 0.8 cm wide, curved, three lobed, narrow at the base, lateral lobes embracing the column. Labellum coloured mid purple or deep mauve speckles on a white background. Presenting cupped, round, of moderately heavy substance. Mentum white or tinged with pale green or mauve-purple. Dorsal sepal dorsal sepal 0.8–1.3 cm long, 0.4–0.6 cm wide, keel 1.65–2.2 cm long, lateral sepals spanning 1.6–2.2 cm, 0.85–1.0 cm wide, petals 0.7–1.2 cm long, 0.2–0.4 cm wide. Floral segments acute to subacute, sepals sometimes obtuse. Midlobe shape broad heart, oval, or pointed spade. Midlobe very narrow, 0.45–0.5 cm wide, forelobe also narrow, 0.35–0.4 cm wide. Callus on lamina pale green or yellow, a broad plate of tissue without clearly distinct keels, ending bluntly or with a suggestion of three nodules which may have a faint purple colouration. Apex of midlobe small, pointed. Column, anther, pollinia and stigma as for *D. kingianum* from other areas. Nectary at base of column foot, pale green or yellow.

Distinctive aspects: Partially subterranean habit, long narrow leaves, small and uniformly pale coloured flowers (occasionally with dark purple markings on the labellum), cup shaped with very narrow mid and fore lobe, and callus without keels or ridges.

Notes: Distinct from plants from other areas, most similar to the long-caned plants of southern Queensland and northern New South Wales, which have pale flowers with purple on the reverse side.

Chromosome number: unknown.

Distribution and ecology: Sandstone gorges of Central Queensland, between the Carnarvon region and Isla Gorge, usually in secluded, shaded situations near streams.

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