Morphological Variation Within the Genus *Blandfordia* (Liliaceae) in Relation to Its Environment

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Abstract

The taxa in *Blandfordia* are often difficult to separate morphologically. A multivariate morphometric analysis of data from both herbarium and field samples suggests that the genus consists of at least four polythetically distinct taxa, corresponding to the traditional concepts of *B. cunninghamii* Lindley, *B. grandiflora* R.Br., *B. nobilis* Smith, and *B. punicea* (Labill.) Sweet. The morphological boundaries between most of these species are arbitrary but are closely related to a number of environmental variables. Due to large intra-population variability, discrimination between these taxa is possible only on the basis of a combination of attributes, notably leaf width and margin sculpturing, and flower length and diameter. The morphological distinction between *B. punicea* and the other species is clear and seems to be maintained by its geographical isolation. The distinction between *B. grandiflora* and *B. cunninghamii* is based on vegetative rather than floral attributes and is made difficult by phenotypic response of *B. cunninghamii* plants to light intensity. Gene flow between these two species appears to be restricted by their separate habitats. The distinction between *B. grandiflora* and *B. nobilis* is based on floral rather than vegetative attributes and is related to latitude with the species being more distinct in the area of parapatry than in the area of allopatry. In the small area of sympatry there appears to be introgression of *B. nobilis* attributes into *B. grandiflora* populations.

Introduction

Blandfordia Smith (Liliaceae) is endemic in eastern temperate Australia, from coastal Queensland and New South Wales to Tasmania (Ingram 1965; Elliot and Jones 1982; Knees 1986; Henderson 1987). It is usually treated as a genus of four species (Henderson 1987): *B. cunninghamii* Lindley (Fig. 1), *B. grandiflora* R.Br. (Fig. 1), *B. nobilis* Smith (Fig. 1), and *B. punicea* (Labill.) Sweet (endemic in Tasmania). The plants are all tufted herbaceous perennials with a tuberous corm, and the brightly coloured flowers (popularly known as Christmas Bells) are exploited for both the domestic and overseas cut-flower markets (Stackhouse 1987). The genus is distinctive, and is sometimes recognised as a monogeneric family (e.g. Dahlgren *et al.* 1985).

However, in spite of the horticultural potential (Ingram 1965; Lamont and Maddock 1989; Johnson 1990*a*), the genus has been poorly studied ecologically and taxonomically. In particular, there is considerable morphological variation within the species, the morphological boundaries between the species are often not clear, and field hybridisation among some of the species has been postulated (Beadle *et al.* 1982; Elliot and Jones 1982; Henderson 1987).
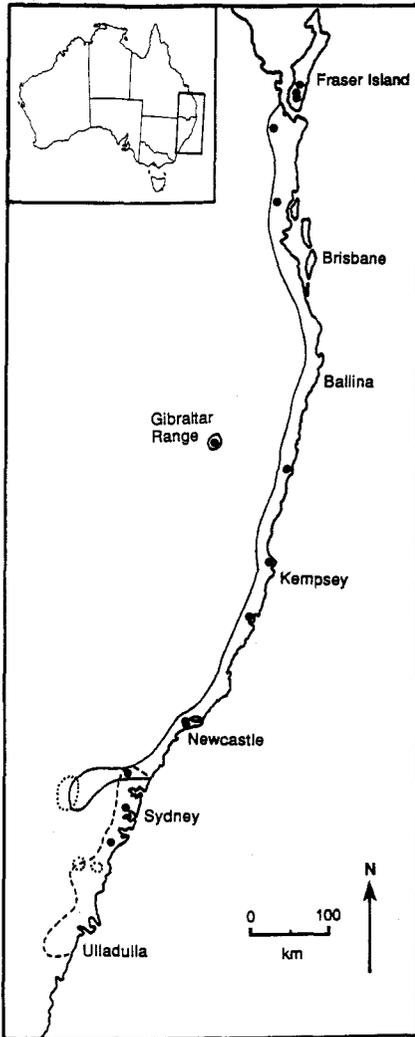
Fig. 1. Distribution of *Blandfordia cunninghamii* (dotted line), *B. grandiflora* (solid line) and *B. nobilis* (dashed line), as well as the location of the field sample sites (●) for the analysis of the relationship between *B. grandiflora* and *B. nobilis*.

Therefore, our study seeks to answer three questions:
(1) what is the pattern of morphological variation between the species of *Blandfordia*;
(2) what is the pattern of morphological variation within the variable species;
(3) does the morphometric separation between the similar species correlate with any environmental factors?

Materials and Methods

Blandfordia

In total, 106 dried herbarium specimens from the National Herbarium of New South Wales (NSW), the Australian National Botanic Gardens (CBG) and the Australian National Herbarium (CANB), were examined under a binocular dissecting microscope. Both the leaves and flowers were examined without further treatment.

In total, 16 morphological attributes of the leaves and flowers were scored for the 90 most complete specimens (Fig. 2; Table 1). These attributes include all of those used by previous workers to distinguish the four taxa (e.g. Ingram 1965; Beadle *et al.* 1982; Elliot and Jones 1982; Knees 1986; Henderson 1987), except that leaf length was excluded because too many of the leaves were incomplete, flower colour was not recorded because it was faded or absent on most specimens, and flower shape was
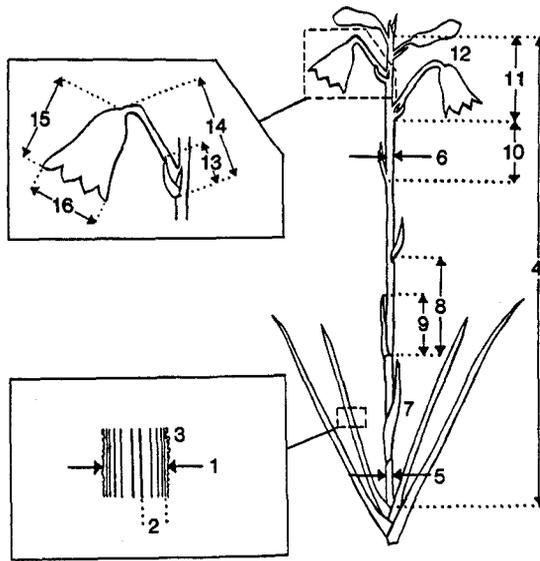
Fig. 2. *Blandfordia* attributes used in the morphometric analyses. Attribute code numbers as in Table 1. Not drawn to scale.

ignored because it was distorted by the pressing of the specimens. Three randomly chosen leaves and the lowest two flowers of each raceme were scored. Leaf width was measured at approximately half leaf length; leaf margins were coded as smooth (0) or crenulate (1); and stem diameter was recorded as the mean of measurements made at right angles with the stem bract at one of the angles.

B. grandiflora–B. nobilis

As a result of the analysis of the herbarium specimens of all four species (the generic analysis) the morphological distinction between these two species was examined in more detail at the population level in the field, since their discrimination was not straightforward. The relationship between the morphological patterns and latitude was also examined, this being the only environmental factor considered likely to influence the patterns observed.

Morphological data were collected in the field from 45 plants from five populations of *B. nobilis* during the summer of 1987–88, and from 100 plants from 11 populations of *B. grandiflora* during the summer of 1989–90, and a further 20 plants from two populations during the summer of 1990–91 (listed in Table 3). Based on the results of the generic analysis, the attributes measured on each plant were stem length (cm), number of flowers per raceme, flower length (mm), flower diameter (mm), and the presence of flowers with one of 10 possible colour forms (Table 4). These attributes do not appear to vary much between years within a population (personal observation).

B. cunninghamii–B. grandiflora

Also as a result of the generic analysis, the morphological distinction between these two species was examined in more detail at the population level in the field, since their discrimination was not straightforward. The relationship between the morphological patterns and several local environmental factors was also examined.

Morphological data were collected in the field from 27 plants from nine populations of *B. cunninghamii* and from 12 plants from four populations of *B. grandiflora* (from the Blue Mountains) during the summer of 1989–90 (listed in Table 5). Based on the results of the generic analysis, the attributes measured on each plant were stem diameter (mm), leaf width (mm), number of leaf veins and crenulation of leaf margins.

Eleven environmental variables were measured at each site (Table 5). Soil samples, each from the top 20 cm of the profile (excluding the A_0 horizon), were collected (with an auger) from adjacent to the three *Blandfordia* plants at each site. Three replicate analyses were performed on each soil sample using the methods of Allen (1989), and the data were averaged for statistical analysis. To examine the biotic effect of these environmental variables, the association of the *Blandfordia* individuals with the other species growing in the area was also measured by recording every other vascular plant species rooted within 1 m of each *Blandfordia* sampled.

Data Analyses

Non-metric multidimensional scaling (NMDS) with Gower dissimilarity (Belbin 1989) was used to analyse the pattern of variation among the morphological samples using all of the measured attributes. This non-linear ordination technique is usually superior to the other multivariate pattern analyses for taxonomic data (Hartman 1988), and the dissimilarity coefficient is a range-standardised separation-sensitive association measure particularly suitable for numerical taxonomy (Faith 1984). Two-dimensional analyses were used and each analysis was run 10 times to try to find the global stress minimum.

Multiple discriminant function (or canonical variate) analysis (Wilkinson 1987) was used to analyse the extent of morphological separation between defined groups. This analysis was used to assess which attributes most closely define the groups, and to test the integrity of these groupings (Reyment *et al.* 1984). For the herbarium data the groups used were the species as determined using Henderson (1987); for the field data the groups were each of the populations sampled. The leaf margin attribute was excluded from these analyses because it is invariant within all groups.

To assess the possible effect of latitude on the general morphological pattern within *B. grandiflora* and *B. nobilis* the relationship between latitude and the scores from the NMDS ordinations was examined. This was done separately for the morphological data from both the herbarium specimens and the field plants. The axis 2 scores from the first ordination and the axis 1 scores from the second ordination were chosen because these axes most effectively summarised the morphological separation of the two

Table 1. Means and ranges of the morphological data from the *Blandfordia* herbarium specimens

n, number of specimens examined

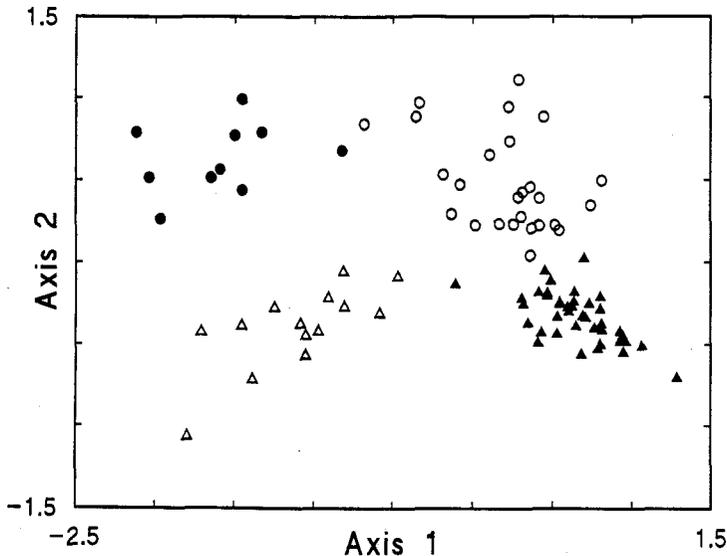| Attribute	*Blandfordia* cunninghamii [*n* = 10]	punicea [*n* = 14]	nobilis [*n* = 40]	grandiflora [*n* = 26]
1 Leaf width (mm)	8·4	7·7	1·5	2·4
	6·0–10·5	5·5–9·3	0·8–2·2	1·5–3·5
2 No. of leaf veins	7	7	3	4
	6–8	5–8	1–4	3–5
3 Leaf margins (see text)	0	1	1	1
	0	1	1	1
4 Stem length (cm)	54·4	63·7	49·0	73·6
	27·0–71·0	31·5–114·5	16·8–75·2	48·0–123·0
5 Lower stem diameter (mm)	6·9	6·4	2·6	4·6
	4·8–8·8	4·0–9·3	1·2–5·2	3·1–8·4
6 Upper stem diameter (mm)	3·8	4·1	1·7	2·5
	2·7–4·6	2·3–6·5	1·0–3·3	1·7–4·5
7 No. peduncle bracts	6	5	4	5
	4–8	4–7	3–6	3–10
8 Stem length 2nd–3rd bract (mm)	74·7	100·2	108·2	151·0
	39·9–117·6	41·7–160·1	41·5–186·7	74·2–339·1
9 2nd bract length (mm)	158·2	106·0	33·4	69·6
	59·1–338·0	63·9–192·4	11·5–144·3	26·1–201·3
10 Stem length peduncle bract to pedicel bract (mm)	56·2	71·6	64·4	103·6
	22·0–106·4	20·4–152·9	27·4–154·5	49·3–206·2
11 Raceme length (mm)	58·7	90·2	28·8	26·9
	26·4–89·7	43·4–187·5	6·4–56·0	2·4–50·7
12 No. of flowers/raceme	17	19	8	6
	8–27	9–35	3–16	2–23
13 Pedicel bract length (mm)	19·5	28·5	10·5	14·2
	12·8–30·4	22·6–37·2	5·9–16·1	9·6–22·8
14 Pedicel length (mm)	32·1	33·9	23·0	26·0
	22·6–45·6	20·4–50·1	9·6–37·0	12·6–38·6
15 Flower length (mm)	51·3	36·7	28·6	47·4
	42·6–63·0	28·6–42·7	21·5–37·2	38·8–65·6
16 Flower diameter (mm)	23·8	15·7	8·9	25·4
	18·1–27·5	11·7–20·4	4·3–14·6	12·7–36·7

Fig. 3. Non-metric multidimensional scaling ordination of the morphological data from the herbarium specimens of *B. cunninghamii* (●), *B. grandiflora* (○), *B. nobilis* (▲) and *B. punicea* (△).

taxa. The relationship between latitude and each morphological attribute of *B. grandiflora* was also statistically tested using non-parametric Spearman rank correlations for both data sets (Wilkinson 1987).

For the *B. cunninghamii* and *B. grandiflora* environmental data each variable was analysed using a one-factor analysis of variance, after first testing for homogeneous variances using Bartlett's test (Wilkinson 1987).

Results

Blandfordia

All the morphological attributes show considerable variation within and between the species (Table 1), except for the leaf margins which are invariant within each species. There is considerable overlap between species for most of the attributes.

However, the ordination analysis (Fig. 3) indicates that the four species as currently defined form four non-overlapping morphological groups. Three of the species are morphologically variable, but *B. nobilis* is less so. *B. punicea* is morphologically relatively discrete from the other three species, but the morphological distinction between *B. grandiflora* and *B. nobilis* and between *B. cunninghamii* and *B. grandiflora* could be interpreted as arbitrary. These three species were therefore investigated at the population level in the field.

The discriminant function analysis gave a good separation of the four species, with three functions necessary to separate the species effectively (Table 2). Function 1 (canonical correlation coefficient [CCR] = 0·98) separated the specimens of *B. grandiflora* and *B. nobilis* from those of *B. cunninghamii* and *B. punicea*, with leaf width contributing most to this discrimination (Table 2); the latter group has wider leaves than the former (Table 1). Function II (CCR = 0·94) mainly separated the specimens of *B. grandiflora* from those of *B. nobilis* with flower diameter, flower length and pedicel length contributing most to this discrimination (Table 2); *B. grandiflora* has the larger flowers (Table 1). Function III (CCR = 0·81) mainly separated the specimens of *B. cunninghamii* from those of *B. punicea* with pedicel bract length, flower number and stem diameter contributing most to this discrimination (Table 2); *B. punicea* is larger in all these attributes (Table 1) and *B. cunninghamii* also has entire leaf margins (Table 1).

The four species have very high integrity as all of the specimens were correctly reclassified into their respective groups by the discriminant function analysis. Their presumed identity is thus confirmed.

Table 2. Results of the discriminant function analysis of the morphological data from the herbarium specimens, and correlation of the *B. grandiflora* morphological data with latitude

Attribute codes as in Table 1. —, not calculated; * $P < 0.01$

Attribute	Standardised discriminant function coefficient			Spearman correlation coefficient	
	Function: I	II	III	Herbarium specimens	Field plants
1	1·031	− 0·107	− 0·226	0·212	—
2	0·311	− 0·281	− 0·302	0·298	—
4	− 0·314	0·096	0·255	0·210	− 0·231
5	− 0·331	0·017	0·120	0·519	—
6	− 0·130	0·403	0·811	0·594 *	—
7	− 0·208	0·391	0·208	0·434	—
8	0·114	0·154	0·239	0·030	—
9	0·277	− 0·357	− 0·428	0·332	—
10	0·076	0·201	− 0·094	0·072	—
11	0·200	− 0·353	0·182	0·159	—
12	0·008	0·052	− 0·861	0·331	0·209
13	0·201	0·044	0·957	0·343	—
14	− 0·087	− 0·506	− 0·025	0·561 *	—
15	0·249	0·472	− 0·627	0·628 *	0·265 *
16	0·152	0·807	0·235	− 0·040	0·259 *

B. grandiflora–B. nobilis

The ordination analysis (Fig. 4) indicates that even when intra-population variation is taken into account these two species as currently defined form almost non-overlapping morphological groups. However, the morphological boundary between the two species is rather arbitrary.

The discriminant function analysis gave a good separation of the two species, with only one function (CCR = 0·94) necessary to separate most of the plants. The attributes contributing most to this separation were flower colour forms 1 and 3, these reddish colours occurring predominantly in populations of *B. nobilis* (Table 3), indicating there is also differentiation in flower colour between these two species (Table 3). The two species have relatively high integrity, as all except one plant were correctly re-classified
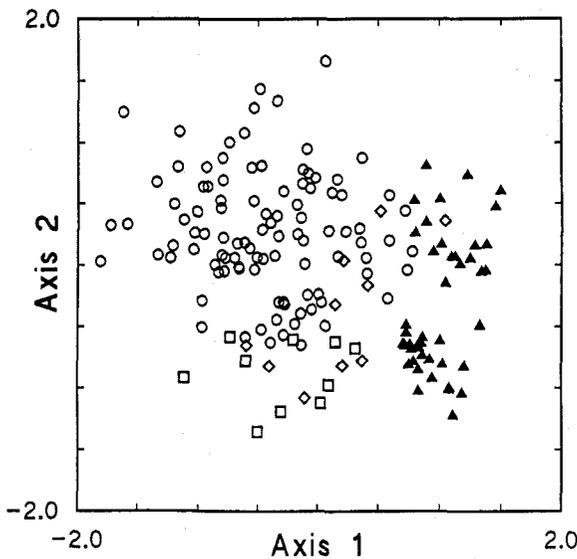

Fig. 4. Non-metric multidimensional scaling ordination of the morphological data from the field plants of *B. grandiflora* (○,□,◇) and *B. nobilis* (▲). Single populations indicated are Gibraltar Range (□) and Mangrove Mountain (◇).

Table 3. Field populations of *B. grandiflora* and *B. nobilis* sampled, and frequency distribution of the flower colour forms

Flower colour codes as in Table 4

Population	Colour form										No. of plants sampled
	1	2	3	4	5	6	7	8	9	10	
B. grandiflora											
Fraser Island	-	-	-	-	-	5	-	4	-	1	10
Fraser Island	-	-	-	-	-	2	1	7	-	-	10
Fraser Island	-	-	-	-	-	2	-	3	-	5	10
Toolara State Forest	-	-	5	-	-	4	-	1	-	-	10
Beerwah	-	-	3	-	7	-	-	-	-	-	10
Gibraltar Range	2	7	1	-	-	-	-	-	-	-	10
Wooli	-	-	-	-	2	2	-	-	-	6	10
Wooli	-	-	1	-	4	1	-	-	-	-	6
South West Rocks	-	-	1	-	2	1	1	2	1	2	10
Lake Innes Reserve	-	-	2	1	5	2	-	-	-	-	10
Lemon Tree Passage	1	-	3	-	-	-	-	-	-	-	4
Tomago	4	1	1	4	-	-	-	-	-	-	10
Mangrove Mountain	2	4	3	1	-	-	-	-	-	-	10
B. nobilis											
Davidson Park	1	-	9	-	-	-	-	-	-	-	10
Davidson Park	3	-	6	-	-	-	1	-	-	-	10
Davidson Park	5	-	4	-	-	-	1	-	-	-	10
Davidson Park	5	-	4	-	-	-	1	-	-	-	10
Heathcote National Park	2	1	2	-	-	-	-	–	-	-	5

into their respective species. The exception was a plant in the Mangrove Mountain population (Fig. 4) which had very short flowers (*c.* 32 mm long).

However, the discriminant function analysis failed to effectively separate most of the populations within either of the two species, and only 54% of the *B. grandiflora* plants and 51% of the *B. nobilis* plants were correctly re-classified into their respective populations. This indicates that there is as much morphological variation within any one population as there is between populations for each of these species.

This analysis also highlighted two of the *B. grandiflora* populations (see Fig. 3). Firstly, the Mangrove Mountain population was very variable and only one plant was correctly re-classified. Secondly, the Gibraltar Range population was morphologically differentiated from the other populations and all the plants were correctly re-classified.

The morphological variation within *B. grandiflora* and *B. nobilis* is at least partially related to latitude (Fig. 5), and all the attributes that most effectively separate the two species are significantly positively correlated with latitude within *B. grandiflora* (Table 2). Therefore, most of the morphologically similar plants of *B. grandiflora* and

Table 4. Flower colour forms in *Blandfordia*

| Colour code	Description of flower phenotype
1	Deep burgundy red with red markings on every second lobe
2	Deep red striped
3	Deep red with yellow lobes
4	Combination of type 1 and type 3
5	Lighter red with streaks and red dots on lobes
6	Predominantly yellow with a few red stripes or red dots
7	Pale orange
8	Yellow flowers with green peduncle
9	Yellow flowers with red peduncle
10	Buttercup
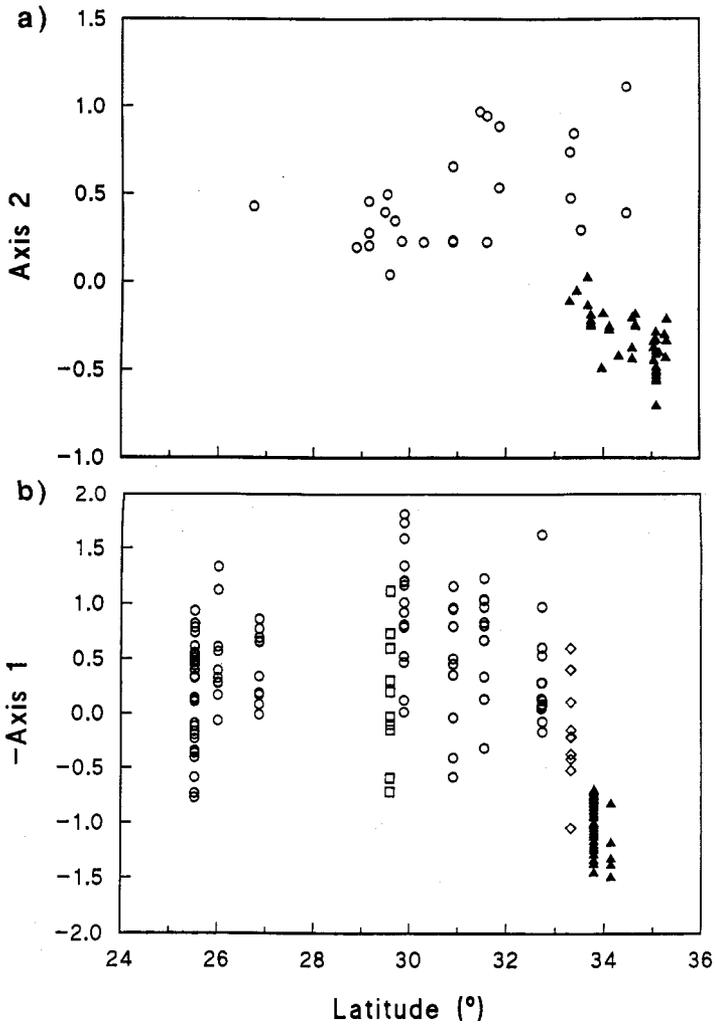
Fig. 5. Relationship between latitude and the score from the ordination analyses of the morphological data from the (*a*) herbarium specimens and (*b*) field plants of *B. grandiflora* and *B. nobilis*. Symbols as for Fig. 3.
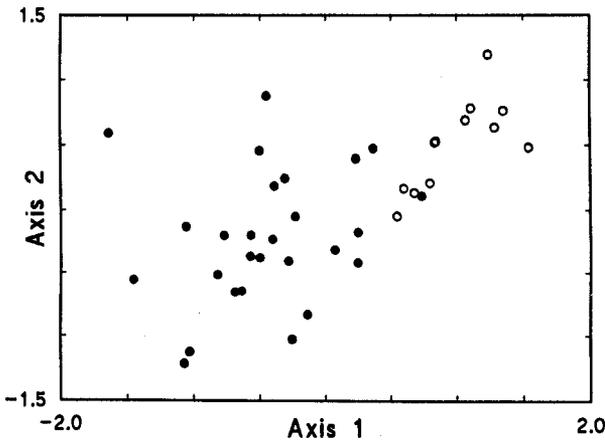

Fig. 6. Non-metric multidimensional scaling ordination of the morphological data from the field plants of *B. cunninghamii* (●) and *B. grandiflora* (○).

B. nobilis are in geographically separate areas. The exception is the Mangrove Mountain population which mainly has typical *B. grandiflora* plants but also has several plants with some *B. nobilis* attributes.

B. cunninghamii–B. grandiflora

The ordination analysis (Fig. 6) indicates that even when intra-population variation is taken into account these two species as currently defined form two almost non-overlapping morphological groups. Furthermore, *B. cunninghamii* is morphologically variable relative to *B. grandiflora* in their area of sympatry, and the morphological boundary between the two species is somewhat arbitrary.

The discriminant function analysis gave a reasonable separation of the two species, with only one function (CCR = 0·87) necessary to separate most of the plants. The attribute contributing most to this separation was the number of leaf veins (which is closely related to leaf width), these being greater in populations of *B. cunninghamii*. The two species have relatively high integrity, as all except one plant were correctly re-classified into their respective species. The exception was a plant in a *B. cunninghamii* population that had relatively narrow leaves (*c.* 5 mm wide).

However, the discriminant function analysis failed to effectively separate most of the *B. cunninghamii* populations and only 30% of the plants were correctly re-classified into their respective populations. This indicates there is as much morphological variation within any one population as there is between populations for this species. On the other hand, all except one of the *B. grandiflora* plants were correctly re-classified.

The analyses of the environmental data indicate that the two species generally occur in different habitats (Table 5). The *B. cunninghamii* plants tend to occur in areas at higher altitudes, with more southerly aspects, on steeper slopes, and in less sandy soils than the *B. grandiflora* plants (Table 5).

These habitat differences are also reflected in the other plant species associated with each of the two *Blandfordia* species. Of the 69 species recorded at more than one site, 29 were recorded at *B. cunninghamii* sites only and 8 at *B. grandiflora* sites only. Thus, only 46% of these species occurred with both of the *Blandfordia* taxa. The *B. cunninghamii* individuals occur with species commonly found in moist habitats, particularly damp rock faces, often being associated with *Acacia elata*, *Callicoma serratifolia*

Table 5. Field populations of *B. cunninghamii* and *B. grandiflora* sampled, environmental characteristics, and results of analyses of variance

B. cunninghamii populations: Mount Tomah, Pierces Pass, Blackheath, Katoomba, Leura, Leura, Wentworth Falls, Wentworth Falls, Mount Kembla. *B. grandiflora* populations: Lawson, Linden, Linden Ridge, Springwood. * $P < 0.01$

Characteristic	Means and (standard error)		Analysis of variance F
	B. cunninghamii	*B. grandiflora*	
Altitude (m)	798·0(48·7)	515·0(71·7)	10·57 *
Aspect (°)	180·6(11·6)	323·5(41·9)	20·23 *
Slope (°)	53·4 (6·0)	19·3 (2·7)	13·31 *
Soil depth (cm)	22·6 (3·1)	19·0 (4·0)	0·44
pH	4·6 (0·1)	4·8 (0·1)	2·67
Total water content (%)	22·2 (2·6)	12·4 (1·6)	5·91
Loss on ignition (%)	9·2 (1·2)	5·2 (1·2)	4·06
Gravel (> 2·0 mm) (%)	6·5 (1·2)	4·3 (1·2)	1·68
Sand (0·05–2·0 mm) (%)	59·4 (2·5)	76·1 (0·9)	17·85 *
Silt (0·002–0·05 mm) (%)	15·6 (1·3)	7·6 (0·2)	17·41 *
Clay (< 0·002 mm) (%)	19·5 (1·2)	12·1 (0·5)	15·41 *

and *Ceratopetalum apetalum* in the overstorey, and with an understorey of *Dianella caerulea, Epacris pulchella, Gonocarpus teucrioides, Hakea dactyloides, Leptospermum flavescens, Stylidium productum* and *Styphelia triflora* (all species' nomenclature follows Beadle *et al.* 1982). The *B. grandiflora* plants occur with species more common in drier, more exposed areas, often with *Banksia serrata* in the overstorey, and an understorey of *Daviesia mimosoides, Entolasia stricta, Grevillea buxifolia* and *Platysace linearifolia*. A further 42 species occurred at one *B. cunninghamii* site only and 29 at one *B. grandiflora* site only.

Discussion

We conclude from our analyses that there are four phenetically differentiated morphometric groups within the genus *Blandfordia*, corresponding to the traditional concepts of *B. cunninghamii, B. grandiflora, B. nobilis* and *B. punicea* (Fig. 3). The ordination and discriminant function analyses suggest that these are coherent polythetic taxa but the morphological boundaries between them are somewhat arbitrary. The vast majority of the plants can be assigned unambiguously to one of the four taxa, but the intra-population variation is large and therefore identifying the occasional plant is more problematic.

All of the taxa overlap for most of the attributes measured (Table 1), due principally to the large intra-population variation. Consequently, no exclusive or 'key' attribute could be found to distinguish the four taxa. Any of the traditional diagnostic attributes may break down in a particular plant, and this can make it difficult to assign the plant to one taxon or another. Instead, these species are best distinguished by using a combination of attributes, notably leaf width (and therefore number of veins) and margin sculpturing (although this is not useful for juvenile plants), and flower length and diameter. Attributes previously used to discriminate between these taxa that we found to be inadequate include, most notably, leaf length and the number of flowers per raceme.

Our data indicate that the four taxa are best distinguished as follows.

	Leaf width (mm)	Leaf margins	Flower length (mm)	Flower diameter (mm)
B. cunninghamii	6–15	Entire	42–63	18–28
B. grandiflora	1–6	Crenulate	38–66	12–37
B. nobilis	0–3	Crenulate	21–38	4–15
B. punicea	5–12	Crenulate	29–43	11–21

Other characters that may be of use in distinguishing some of the taxa include the laxity or erectness of the leaves, leaf cross-section shape, and leaf colour.

The morphological variation within each taxon and the overlap between them for many of the attributes measured suggest that there is a low degree of genotypic constancy within each of the taxa. Most of the phenotypic variability appears to be at the intra-population level, suggesting that there is considerable gene flow between populations. However, the morphological discrimination between the species indicates that they maintain their reproductive integrity and therefore represent 'good' biological species (Mayr 1986). Furthermore, the taxa do not appear to lose their distinguishing features in cultivation (personal observation), suggesting that they are genotypically distinct. These hypotheses could be further tested by, for example, isozyme analysis.

B. punicea is the most morphologically distinctive of the four taxa (Fig. 3), and presumably maintains this by its extreme geographical separation from the other species. However, it may be more morphologically variable than our limited data suggest. For example, Moscal (1979) reports a more robust variant from wind-pruned shrublands, which was not included in our analysis. However, this variant is certainly no more similar to the other three taxa than are any of our samples. Moscal (1979) also describes

another *Blandfordia* population from Maatsuyker Island that is even more distinctive and which may warrant recognition as a separate species. These populations deserve more detailed examination.

The distinction between *B. grandiflora* and *B. nobilis* is based on floral but not vegetative attributes and it is problematic at the intra-population level, as individual plants from each taxon can be rather similar morphologically. However, at the inter-population level there is little taxonomic difficulty, as any one population can easily be assigned to one taxon or the other. More importantly, these species are shown not to be simply latitudinal extremes of a morphological gradient. The plants in the area of parapatry are morphologically more distinct in flower size than are the plants in the area of allopatry, since it is some of the *B. grandiflora* plants on Fraser Island that are morphologically most similar to the *B. nobilis* plants of the Sydney region (Fig. 5). However, in the small area of sympatry (see below) there is some evidence of intermediates, and thus it is only in this area that there is any chance of taxonomic confusion.

Only in the relatively small area between the Hawkesbury River and Gosford are these two taxa sympatric (Fig. 1), as *B. nobilis* occurs in the coastal part of the Sydney region and along the coast south of there, while *B. grandiflora* occurs in the Blue Mountains to the west of the Sydney region and along the coast north of there. The Mangrove Mountain population was the only one sampled from the area of sympatry, and three of the 17 plants examined in this population are morphologically intermediate between the two species. All the other plants were typical of *B. grandiflora* (cf. Fig. 4, Fig. 5*b*), so the intermediates appear to be the result of introgression of *B. nobilis* attributes into a population of *B. grandiflora*. However, this hypothesis remains to be tested experimentally.

The apparent exception to these generalisations is the population sampled from the Gibraltar Range. Both the ordination and discriminant function analyses indicate that this entire population is morphologically differentiated from the rest of the *B. grandiflora* plants (Fig. 4). For the 61 plants examined in this population, both flower length (46–71 mm) and diameter (17–38 mm) are similar to those of typical *B. grandiflora*, flower colour (colours 1, 2 and 3; see Table 4) is typical of *B. nobilis*, and stem length (41–92 cm) is in the area of overlap between the two species. Flower number (1–3 per raceme) is extremely low compared with that of either species.

This population is one of several known from the area, all of which are morphologically similar (M. Ramsey, personal communication). These populations are allopatric to the rest of the species' range and are the only non-coastal (altitude *c*. 1000 m) populations north of Sydney (Fig. 1). It is therefore unclear whether or not these morphological differences are simply a phenotypic response to altitude. However, no such effect is apparent in the non-coastal (altitude 500 m) plants near Sydney. If these morphological differences have a genetic basis then this population would be worthy of recognition as a separate subspecific taxon. This could be tested by cultivation of offspring under standardised conditions, which would be difficult because growth to reproductive maturity is very slow (Parry 1962; Johnson 1990*b*; Johnson and Burchett 1991), or possibly by isozyme analysis. Breeding system studies suggest that the Gibraltar Range plants are partially self-compatible while the nearby coastal populations are self-incompatible (M. Ramsey, personal communication).

B. cunninghamii is the least known of the four species, as it is currently recorded from only 11 populations in the Blue Mountains and Illawarra areas of the Sydney region (Fig. 1; Porter 1992), and is rated 3RC by Briggs and Leigh (1988). The morphological distinction between it and *B. grandiflora* in their area of sympatry (Fig. 1) is also problematic at the intra-population level, as individual plants from both taxa can be similar morphologically. These taxa are vegetatively but not florally distinct, the principal difference being in their leaf width. However, the width of the leaves on the *B. cunninghamii* plants appears to be related to shading, as they do not always produce particularly wide leaves when growing in very low light intensities. Growth

of plants under glasshouse conditions suggests that this response is phenotypic. Nevertheless, at the inter-population level there is little taxonomic difficulty, as any one population can easily be assigned to one taxon or the other.

B. cunninghamii and *B. grandiflora* are clearly separated ecologically, with the former occurring in damper more sheltered habitats than the latter, so that the two taxa are never locally sympatric or parapatric. Our samples cover the known morphological variation within these taxa and we found no evidence of hybridisation between them as no plant was encountered that resembled a morphological intermediate. However, artificial cross-pollinations in the glasshouse do produce viable seeds (personal observation). Therefore, it seems likely that gene flow between these two species is restricted mainly by their ecological habitat separation as none of the other reproductive isolation mechanisms (Grant 1981) appear to apply.

Acknowledgments

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