Multivariate analysis of morphological variation in *Eucalyptus* series *Psathyroxyla* Blakely (Myrtaceae): taxonomic implications

B.E. Pfeil and M.J. Henwood

Abstract

B.E. Pfeil[1] and M.J. Henwood (John Ray Herbarium, School of Biological Sciences, Heydon-Laurence Building (A08), The University of Sydney, NSW 2006, Australia; [1]Present Address: Department of Plant Biology, 228 Plant Science Bld., Cornell University, Ithaca NY 14853, U.S.A.) 2004. Multivariate analysis of morphological variation in Eucalyptus *series* Psathyroxyla *Blakely (Myrtaceae): taxonomic implications.*Telopea *10(3): 711–724.* Characters used in recent treatments to separate members of *Eucalyptus* series *Psathyroxyla* Blakely (scribbly gums) show a considerable degree of overlap. Multivariate analyses of 79 individuals were used to examine morphological variation in up to 35 characters, in order to resolve this problem. These analyses revealed the presence of three taxa, not five as previously described. Furthermore, two of these taxa show significant morphological overlap which is best explained by introgression. Problems regarding the type specimens are discussed. *Eucalyptus haemastoma* Smith, *E. racemosa* Cav. ssp. *racemosa* and **E. racemosa** subsp. **rossii** (R.T. Baker & H.G. Smith) B.E.Pfeil & Henwood **comb. et stat. nov.** are recognised here.

Introduction

Four species of *Eucalyptus* were recognised by Blakely (Blakely 1934) as constituting the series *Psathyroxyla*. The series became commonly known as the scribbly gums, on account of the characteristic insect 'scribbles' that cover their otherwise smooth bark. Apart from the markings on the bark, the scribbly gums are further distinguished by their raised fruit disc, mostly hemispherical fruit, and their small seed (Ladiges et al. 1992). Despite Chippendale's (1988) more inclusive definition of the series, Ladiges et al. (1992) confirmed that the scribbly gums constituted a monophyletic group. The most recent flora treatment of the group (Hill, 1991) recognises five species: *Eucalyptus haemastoma* Smith, *E. racemosa* Cav., *E. rossii* R.T. Baker & H.G. Smith, *E. sclerophylla* (Blakely) L.A.S.Johnson & Blaxell, and *E. signata* F. Muell.

Scribbly gums are trees or mallees restricted to woodlands on the coast of southern Queensland (south from Fraser Island) and New South Wales (north from Jervis Bay), and the tablelands and south-western slopes of N.S.W. (Figs 1 and 2). The western geographic limit of the scribbly gums is near Wagga Wagga on the N.S.W. south-western slopes (Fig. 2). Whilst the group is geographically relatively widespread, species are locally frequent but patchy in their distribution. They are usually confined to infertile, sandy or stony soils on ridge tops or rises with rare occurrences on sandy and sometimes swampy flats in coastal N.S.W. (Hill 1991).

The most recent taxonomic treatments of the scribbly gums are those by Hill (1991) and by Bean (Bean 1997). Hill (1991) recognised five species, the diagnostic characters of which overlap, e.g. fruit length and width, and adult leaf width. In Hill's key, leaf glossiness, fruit width and the location of populations are used to separate the species. Bean (1997), however, found that leaf glossiness can vary within a population, and is thus not diagnostic. The overlap of many morphological characters has meant that the geographic location of an individual is the primary method of positive identification.

Bean (1997) included *E. signata* and *E. sclerophylla* within the circumscription of *E. racemosa*, but did not provide a formal analysis of character variation for this action. He stated that "there appear to be no significant differences between the entities *E. racemosa*, *E. sclerophylla* and *E. signata*" (Bean 1997, p.133).

As with many species complexes, one must always be aware of the possibility that phenotypic plasticity might be masking otherwise diagnostic characters in at least some individuals of some taxa. Testing the extent of phenotypic plasticity in adults by way of traditional common garden experiments is particularly problematic in relatively long-lived taxa like the scribbly gums. However, the use of seedlings can provide an environmentally independent set of characters by which to assess the taxonomic limits of species under consideration (Wiltshire et al. 1992). The character differences (or similarities) which may be present should, therefore, be due more to underlying genetic differences than to phenotypic plasticity. A preliminary assessment of scribbly gum seedling characters has indicated that a range of morphological variation exists within the group (Brooker & Kleinig 1990; Chippendale 1988; Hill 1991).

The current study aims to provide an empirical analysis of the character variation encountered in the scribbly gums, with the aim of assessing the taxonomic distinctness of any entities present. Multivariate analysis of morphological (and thereby phenotypic) variation is a suitable method to accomplish this aim.

Methods

Sampling

Twenty-five populations were sampled, covering the geographic range of the species (Fig. 1, Table 1). Over half of the populations (14 of 25) were drawn from the central coast and central tablelands, as these regions are where scribbly gums species with the most narrow circumscriptions (Hill, 1991) have the greatest overlap in their distributions. An ambiguous population from the Bruxner highway in the northern tablelands was also targeted, as individuals from this area have been alternatively assigned to *E. signata* and *E. rossii*, the only suspected area of overlap between those species. Other populations were spread over the range of scribbly gum species to maximise capture of the variation among populations over a wide geographic range, although the furthest extremes of the distribution were not sampled due to practical limitations.

Five individuals were sampled from each apparently monomorphic population, with the exception of two populations where only single individuals (represented by herbarium specimens with viable seed) were available. Populations with a range of morphotypes (e.g. those potentially containing two or more species) were sampled more intensively in order to capture the range of observable morphological variation (up to ten individuals). Generally, one branch, consisting of numerous branchlets, was sampled for each individual. From each branch, numerous fully expanded leaves and a range of available reproductive material were collected and dried. Seed was subsequently removed from the fruit and stored at room temperature in paper bags. A total of 130 individuals were sampled in this way.

Table 1: Population localities.

Population Name	Region	Latitude S		Longitude E	
		Deg	Min	Deg	Min
Bungendore Turnoff	ST	35	10	149	17
Marulan	ST	34	44	149	51
Tallong	ST	34	43	150	03
Jerrabomberra Hill	ST	35	22	149	12
Black Mountain (ACT)	ST	35	16	149	06
Penrose	CT	34	40	150	15
Sutton Forest	CT	34	28	150	19
Mudgee*	CT	32	26	149	50
Running Stream	CT	33	04	149	56
Bruxner H'way	NT	28	56	152	13
Nowra Air Base	SC	34	57	150	31
North Nowra	CC	34	51	150	34
Wilton	CC	34	17	150	43
Mount White	CC	33	27	151	12
Somersby	CC	33	21	151	18
Bucketty	CC	33	09	151	12
Mandalong	CC	33	07	151	28
Nord's Wharf	CC	33	08	151	36
Munmorah SRA	CC	33	11	151	35
Charmhaven	CC	33	14	151	29
Hornsby Heights	CC	33	31	151	07
Nabiac	NC	32	07	152	25
Copperabung Ck	NC	31	13	152	49
Red Rock	NC	29	59	153	13
Queensland*	-	26	24	153	06

*Populations represented by a single herbarium sheet.

Character selection

A data set comprising 18 adult leaf, bud, fruit and seed characters was generated (Table 2). Data included characters used traditionally in the identification of these species (eg. fruit width) as well as additional characters such as bud dimensions. The appropriate sample size for fruit characters was determined by plotting the variances of these measurements against sample size for each of five individuals. Variance estimates become more accurate as sample size increases, although the rate of accuracy-gain is reduced simultaneously. The estimate of the variance of all the individuals was found to peak at a sample size of about 50 fruit. A sample size of 30 fruit per individual was considered to be a reasonable combination of morphological variation captured for time expended.

Six fully expanded leaves, each subtending a floral bud, were selected to represent the foliar characters for each individual. Leaves at the apex of a growing shoot were not used. Five unopened buds on an umbellaster with at least one open flower (to minimise ontogenetic variation) were chosen for hand-sectioning.

Twenty seeds from each individual were sorted from the chaff and sown into five replicate pots each containing four, equally spaced seeds. Pots were randomly arranged within a single glasshouse. A variation of Hoagland's Solution (after Mowatt 1981) was used to fertilise the seedlings. Four to five seedlings per individual were subsequently chosen at random, and these were used to derive a total of 17 seedling characters for each individual (Table 3). Pots were randomised once a month, and each pot was rotated by 90° at this time.

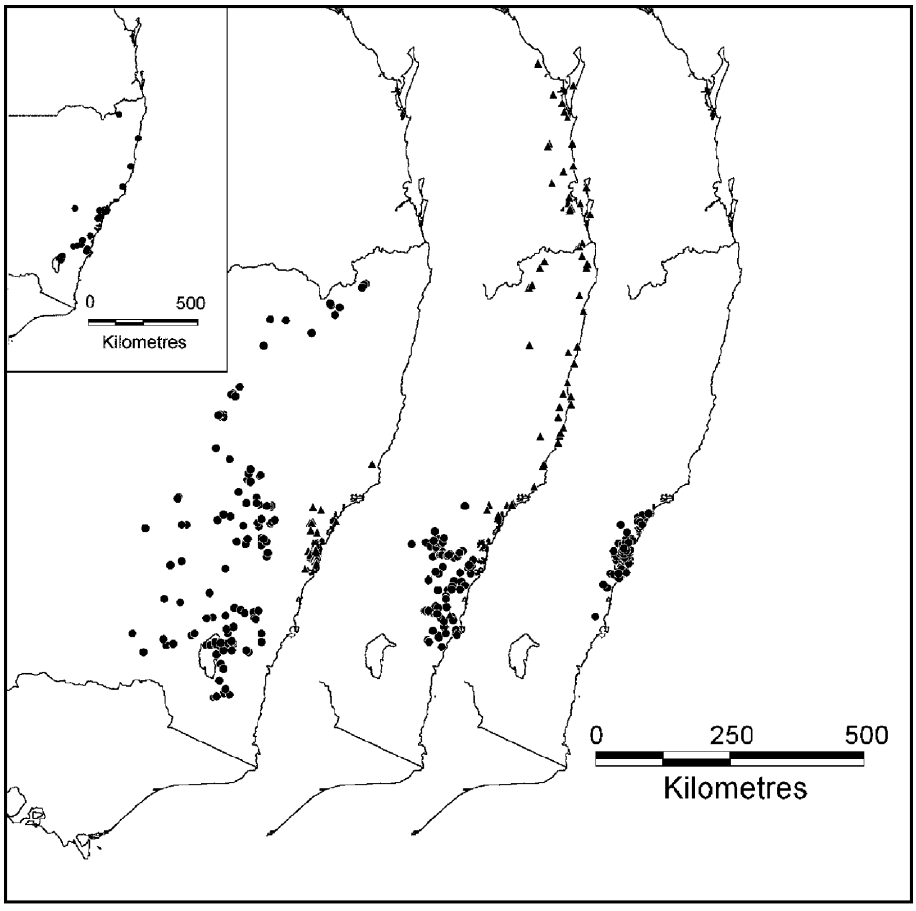

Fig. 1. Distribution of scribbly gums *sensu* Hill (1991). Left: *Eucalyptus rossii* (●), *E. racemosa* (▲). Centre: *E. sclerophylla* (●), *E. signata* (▲). Right: *E. haemastoma* (●) . Inset: sites sampled in this study

Table 2. Adult characters.

Character name	Abbreviation	Sample size
Leaf characters		
Petiole Length	(LPE)	6
Leaf Length	(LLN)	6
Maximum Width	(LMW)	6
Length to Width Ratio	(LLW)	6
Fruit Characters		
Maximum Width	(FMW)	30
Width of Disc	(FDW)	30
Fruit Length	(FLE)	30
Degree of Disc Emergence	(FDE)	30
Shape of Base	(FSB)	30
Length to Width Ratio	(FLW)	30
Fruit Width to Disc Width Ratio	(FWD)	30
Seed Characters		
Seed Colour	(SCO)	1*
Chaff Colour	(SCC)	1*
Bud Characters		
Ovary Chamber Height	(BOC)	5
Floral Chamber Height	(BFH)	5
Floral Chamber Width	(BFW)	5
Style Length	(BSL)	5
BSL/BFH	(BSF)	5

* seed and chaff were pooled for each individual.

Data analysis

There is wide agreement that multi-dimensional scaling (MDS), and, in particular, the non-metric form (N-MDS), is recommended above Principle Component Analysis (PCA) for taxonomic studies (Crisp 1991; Faith et al. 1987; Pimentel 1981). In contrast with PCA, N-MDS assumes a much less restrictive model of relationships between an association measure and the ordination space (Coxon 1982; Austin 1985).

The program PATN (Belbin 1991) was used for all analyses. In the case of MDS, PATN uses a semi-strong monotonic transformation (a type of N-MDS), with the option of using a linear transformation (M-MDS) for smaller association matrix ranks (i.e. for smaller distances between individuals). This scaling - termed hybrid scaling - is most appropriate for ecological data. The hybrid nature of the scaling refers the linear relationship between values in an association matrix (based on robust association measures) and the distance between points in an ordination when distances are small. When distances become large, a monotonic relationship holds, over a number of different species response models (Faith et al. 1987).

Table 3: Seedling characters.

Character name	Abbreviation	Sample Size
At 1st bud emergence		
Cotyledon Maximum Width	(CMW)	5
At 3rd bud emergence		
1st Leaf Pair Maximum Width	(1W3)	4
1st Leaf Pair Length	(1L3)	4
Length / Width Ratio of 1st Leaf Pair	(1LW)	4
2nd Leaf Pair Maximum Width	(2W3)	4
Internode Trichome Type	(TC1)	4
2nd Leaf Margin Trichome Type	(T2M)	4
1st Leaf Primary Vein Trichome Type	(T1P)	4
At 6th bud		
2nd Leaf Pair Maximum Width	(2W6)	4
2nd Leaf Pair Length	(2L6)	4
Length / Width Ratio of 2nd Leaf Pair	(2LW)	4
3rd Leaf Pair Maximum Width	(3W6)	4
3rd Leaf Pair Length	(3L6)	4
Length / Width Ratio of 3rd Leaf Pair	(3LW)	4
2nd Leaf Pair Margin Undulation	(MU2)	4
3rd Leaf Pair Margin Undulation	(MU3)	4
3rd Leaf Pair Base Contact	(BC3)	4

No such models for taxonomic data have been assessed in this way (an exception being the limited study by Pimentel 1981). Therefore, for the current study it was decided to initially employ the least restrictive transformation available in PATN (semi-strong monotonic scaling) to transform the association matrix values into ordinations.

Shepard plots (Shepard 1974) based on 2-dimensional N-MDS ordinations were examined for each of the analyses. The shape of these plots indicated that a linear relationship existed between the inter-item distances in the association matrix and the inter-item distances in the ordinations ($n=3080$, $r=0.95$, $p<0.05$). Therefore, M-MDS was used in all subsequent analyses. In all cases Gower's metric (Gower 1971) was used as the association metric.

Three analyses were conducted. After removing individuals for which insufficient material was available to score characters (due to seedling mortality, insufficient fully expanded adult foliage, etc.), most populations were represented by three individuals, with the variable populations represented by up to ten individuals. The analyses, therefore, used a total of 79 individuals.

Analysis 1: Combined adult and seedling characters

Analysis 2: 17 seedling characters

Analysis 3: 18 adult characters

Results

Analysis 1: All characters

Figure 2 shows two distinct groups (group 1 and 2). Individuals from each population are contained entirely within either group 1 or group 2 and are connected by lines. Variation in group 1 can be summarised as fruit ≥ 8 mm wide, whereas group 2 can be characterised as having fruit ≤ 7 mm wide. The morphological distinctness of each group is paralleled by a congruent geographic distribution. Group 1 forms a geographically cohesive group, the four populations all being located on the central coast of NSW, between Botany Bay and Lake Macquarie. The populations of group 2 span a broader geographic area than those of group 1. Group 2 ranges from the coast of southern Queensland to southern NSW, and from the coast to the western slopes in NSW.

Populations with small fruit (group 2) form two sub-groups (groups 2a and 2b; Fig. 2). Sub-group membership is defined primarily by a combination of mean adult leaf width (sub-group 2a = 5–13 mm; sub-group 2b = 11.5–24 mm) and mean adult leaf

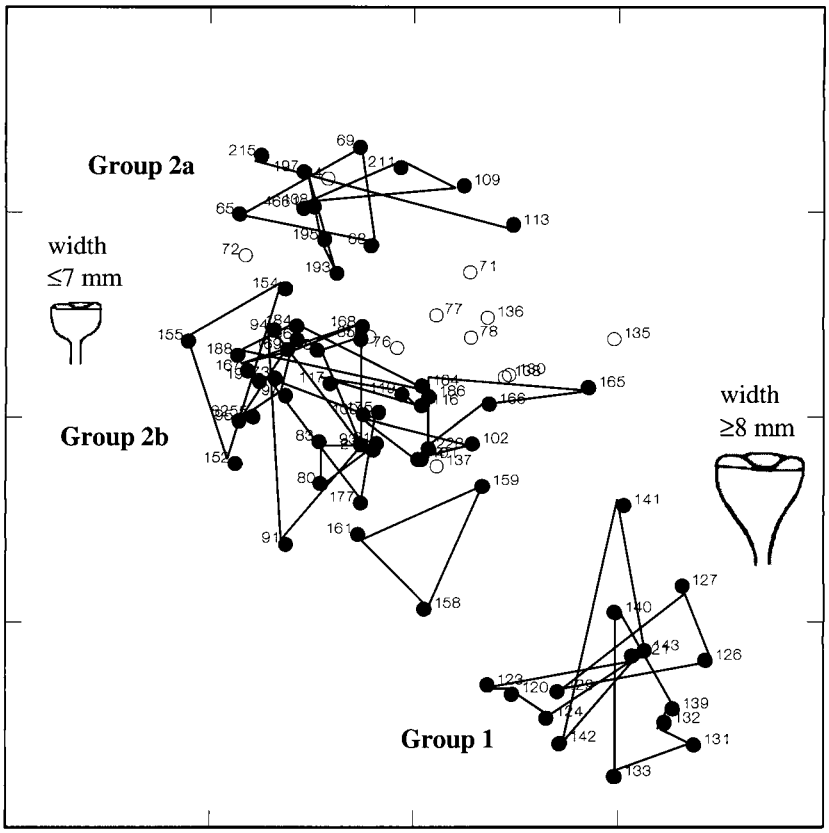

Fig. 2. A 2-dimensional M-MDS ordination based on Analysis 1 (35 characters, 79 individuals). Stress = 0.17. Individuals from any one population are connected by lines. Groups of morphologically similar populations (overlapping in the ordination) discussed in text are labelled. Individuals marked by open circles (○) come from two intermediate populations as discussed in text. Relative fruit size for large vs. small fruited groups is shown diagrammatically.

length (2a = 5–9.5 cm; 2b = 8–13.5 cm). These differences are diagrammatically represented on Fig. 3. Each sub-group, however, is linked by individuals from populations of mixed morphology. These 'linking' populations are also from geographically intermediate localities. The morphologically heterogeneous populations contain individuals that fall within either sub-group, as well as individuals that fall between the sub-groups. We were only able to locate two such populations in the field; one from near Bucketty (central coast, NSW) and the other from near Marulan (southern highlands, NSW). Individuals from these populations are shown by open circles (Fig. 2).

Analysis 2: Seedling characters only

Analysis of seedling data, revealed two non-overlapping groupings of morphological homogenous populations (Fig. 3). In contrast with the analysis of all characters (Fig. 2), the seedling data did not strongly separate individuals with large fruit (group 1 of Fig. 2, shown as stars in Fig. 3) from those with small fruit (group 2 of Fig. 2, other symbols in Fig. 3). Individuals from the morphologically heterogeneous populations cross the previously identified sub-group boundaries (shown as open circles, Fig. 3).

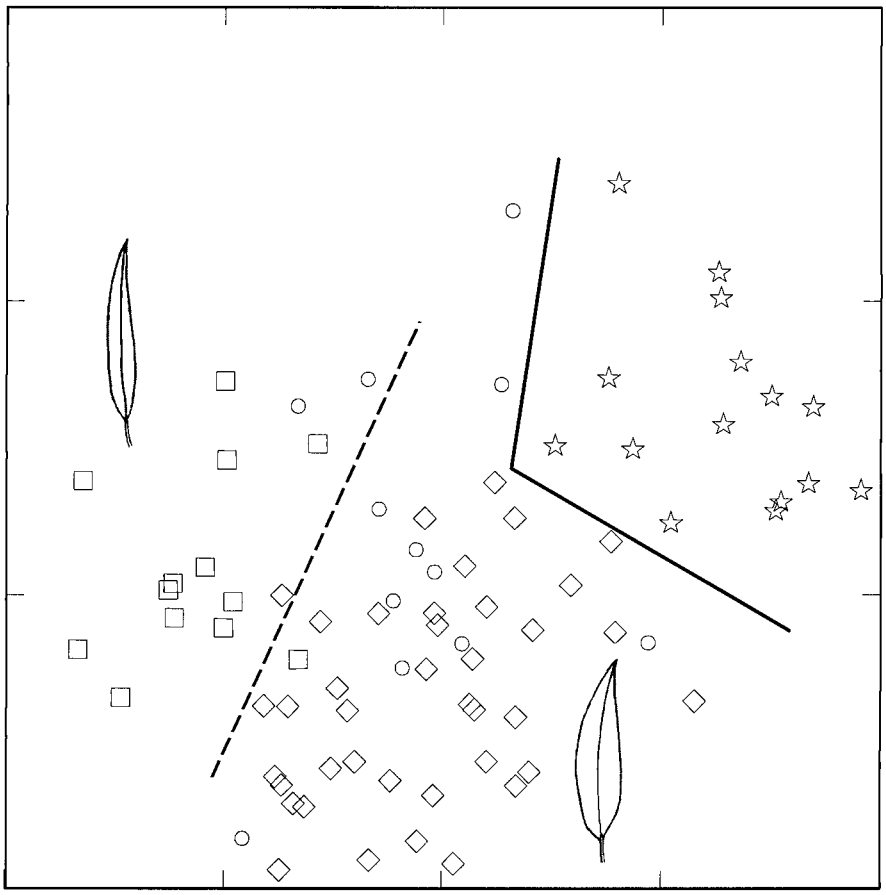

Fig. 3. A 2-dimensional M-MDS ordination based on Analysis 2 (17 seedling characters, 79 individuals). Stress = 0.15 Stars (★) = large-fruited (≥ 8 mm wide) individuals. Diamonds (◆), squares (■) and circles (●) = small-fruited (≤ 7 mm wide) individuals. Relative adult leaf size for large vs. small leaved sub-groups (within the small-fruited group) is shown diagrammatically.

Analysis 3: Adult characters

As with seedling data, the adult data (Fig. 4) mostly maintained the group membership observed in Figure 2 (all characters). An exception to this pattern is that one individual from one population (Charmhaven), previously clustered within group 2, is now located amongst group 1 individuals (shown as a diamond in Fig. 4). This population is located in the same general area as group 1 populations (central coast, NSW).

Discussion

Our results reveal the presence of two distinct groups of scribbly gums, characterised by large and small fruit (group 1 and 2 respectively, Fig. 2). Furthermore, the group with small fruit is divisible into two sub-groups with small and large adult foliage (group 2a and 2b respectively, Fig. 2).

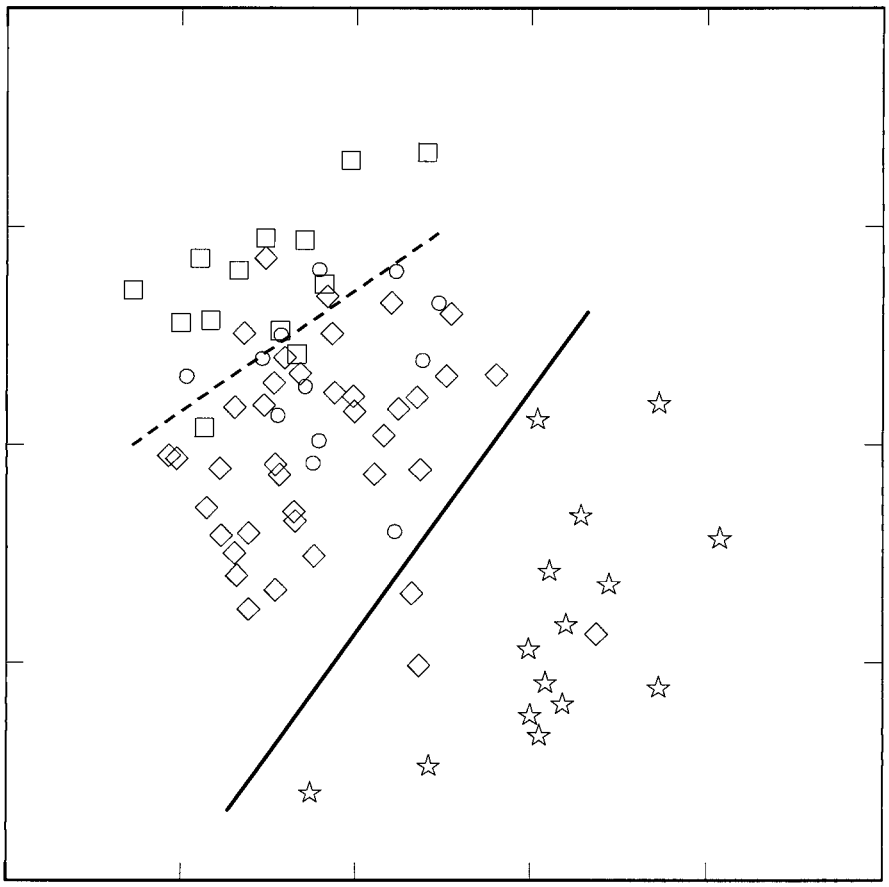

Fig. 4. A 2-dimensional M-MDS ordination based on Analysis 3 (18 adult characters, 79 individuals). Stress = 0.22 Stars (★) = large-fruited (≥ 8 mm wide) individuals. Diamonds (◆), squares (■) and circles (●) = small-fruited (≤ 7 mm wide) individuals.

The morphologically heterogeneous populations at geographically intermediate locations are particularly informative with respect to the relationships between the two sub-groups of group 2 (plants with small fruit). In adult, seedling and combined analyses, the presence of both intermediate individuals as well as individuals closely resembling 'core' members of both sub-groups strongly suggests that introgression is occurring at these sites. This pattern of variation is inconsistent with the presence of a cline, where all individuals would be expected to possess a morphology intermediate between both sub-groups.

The population at Bucketty, the only population that unambiguously contains members of group 1 and group 2, shows clear separation between individuals of both groups in all analyses. No introgression or cline between groups 1 and 2 appears to be present at this site.

One population (Charmhaven), however, occupies an ambiguous morphological position in relation to groups 1 and 2 (Fig. 2). This population is in the same region as all of group 1 (central coast, NSW). One individual from this population appears to have adult morphology of the large-fruited group, whereas its seedlings are more similar to those of the small-fruited group. It is possible that this population is mixed, with only a few group 1 individuals introgressing with a larger pool of group 2 individuals. This would give an overall position that is intermediate between group 1 and 2, but closer to group 2. It is also possible that the adult morphology is convergent due to the similar environment, whereas the seedling morphology more accurately reflects genetic affinities. Both processes may be operating together. Despite this single ambiguous population, there is no strong evidence that widespread introgression is occurring between individuals of group 1 and group 2. Furthermore, herbarium specimens and field observations indicated that populations within a morphological group, as determined in these analyses, do not flower synchronously.

Thus, rather than the five species recognised by Hill, our analyses have indicated the presence of only three taxa. Whilst this broadly corresponds with Bean's treatment (1997), we consider that the entities revealed here are not of equivalent taxonomic rank to those of Bean. These differences in concept are the result of several factors. Firstly, the use of a larger number of characters to resolve taxa; secondly, the use of seedling characters grown under controlled conditions; and thirdly, the use of multivariate statistics to summarise character information.

Prior treatments have relied upon an intuitive interpretation of a limited number of adult morphological characters. However, the overlap of many 'diagnostic' characters which led to the use of geographic location of an individual to make identifications is a clear sign that the complex variation in this group was not adequately dealt with by intuitive taxonomic methods. The power of multivariate analyses to accurately summarise morphological information from a large number of characters is particularly useful as an aid to taxonomic decision-making in such situations.

Furthermore, whilst neither adult nor seedling data sets alone provided resolution of component taxa with any certainty, the combination of these data led to the clear resolution of three taxa in this group. Our conclusions are strengthened by the fact that our data set contains information from two independent sources, of which the seedling information should be significantly less susceptible to phenotypic plasticity. Seedling data can only be expected to have these properties when derived from an appropriate sampling strategy coupled with germination and growth under controlled environmental conditions. Only then can environmentally induced effects be teased from genotypic variation.

Scribbly gums with large fruit (group 1) are here assigned the rank of species, as is the group with small fruit (group 2, Fig. 2). The two sub-groups of group 2 are assigned

sub-specific rank. The types of all species of series *Psathyroxyla* were examined, with the exception of that of *E. rossii* which could not be located at NSW where it is believed to be held (Chippendale 1988).

The isotype of *Eucalyptus haemastoma* has smaller fruit than that of members of the large-fruited species (to which the name has been thus far applied). Examination of additional specimens from the northern suburbs of Sydney revealed a number of plants with morphology intermediate between the large- and small-fruited species of scribbly gum. The fruit of the *E. haemastoma* isotype fell within this intermediate set of specimens. The large number of intermediate collections found suggests that our sampling regime may have missed a critical zone of genetic exchange between the large- and small-fruited species. As such, we are reluctant to suggest any alteration to the name of the large-fruited group, despite the type not being entirely consistent with this group.

The small-fruited species currently has the names *E. racemosa* and *E. rossii* applied to it. *Eucalyptus racemosa* has priority at the rank of species as it was published in 1797. As the type of *Eucalyptus rossii* is currently missing, a specimen from Bungendore in N.S.W. discussed by the authors (Baker & Smith 1920) as being chemically and morphologically similar to the holotype is here chosen as the lectotype. This specimen is a very close match for our subspecies and for *E. rossii* as described by Baker and Smith (1920).

Descriptions of taxa

The taxa found here are accommodated by Bean's (1997) circumscriptions, although the exact limits of *E. haemastoma* are uncertain (as discussed above). Our sampling found a more narrowly definable core group of individuals (centred around Lake Macquarie), but the uncertainties in being able to assign specimens from northern Sydney reliably to either species makes this narrow concept difficult to justify. The uncertainties revealed here must await resolution after further study.

Taxonomy

E. haemastoma Smith, *Trans. Linn. Soc. London* 3: 286 (1797). Type: *J. White s.n.*; holo: LINN, iso: G!.

Eucalyptus racemosa Cav., *Icones* 4: 24 (1797).

Type: *L. Née s.n.*; holo: MA; iso: MEL (photo BRI!).

E. haemastoma var. *capitata* Maiden, *Crit. Revis. Eucalyptus* 1: pp.319 (1909). Type: *J.H. Maiden s.n.*; holo: NSW!; iso: FRI.

E. haemastoma var. *sclerophylla* Blakely, *Key Eucalypts* pp. 218 (1934). Type: *J.H. Maiden s.n.;* holo: NSW!; iso: FRI.

E. micrantha DC., *Prodr*. 3: pp. 217 (1828). Type: *F.W. Sieber 497*; holo: G; iso: G, W.

E. signata F. Muell., *J. Proc. Linn. Soc., Bot*. 3: pp. 85 (1859). Type: *F. Mueller s.n.*; holo: MEL!; iso: K.

Eucalyptus racemosa *ssp.* **rossii** *(R.T. Baker & H.G. Smith) B.E.Pfeil & Henwood* **comb. et stat. nov.**

E. rossii R.T. Baker & H.G. Smith, *Res. Eucalyptus* 70 (1902). Type: *R.T. Baker s.n.*, March 1901, Cow Flat, Bathurst; holo: NSW (missing); **lectotype here chosen**: *Baker and Smith s.n.*, Bungendore, N.S.W., March 1899; NSW!.

Distribution of taxa

Maps of the distributions of these taxa based on CANB and NSW collections, and the collections made during this study, are presented in Figure 5.

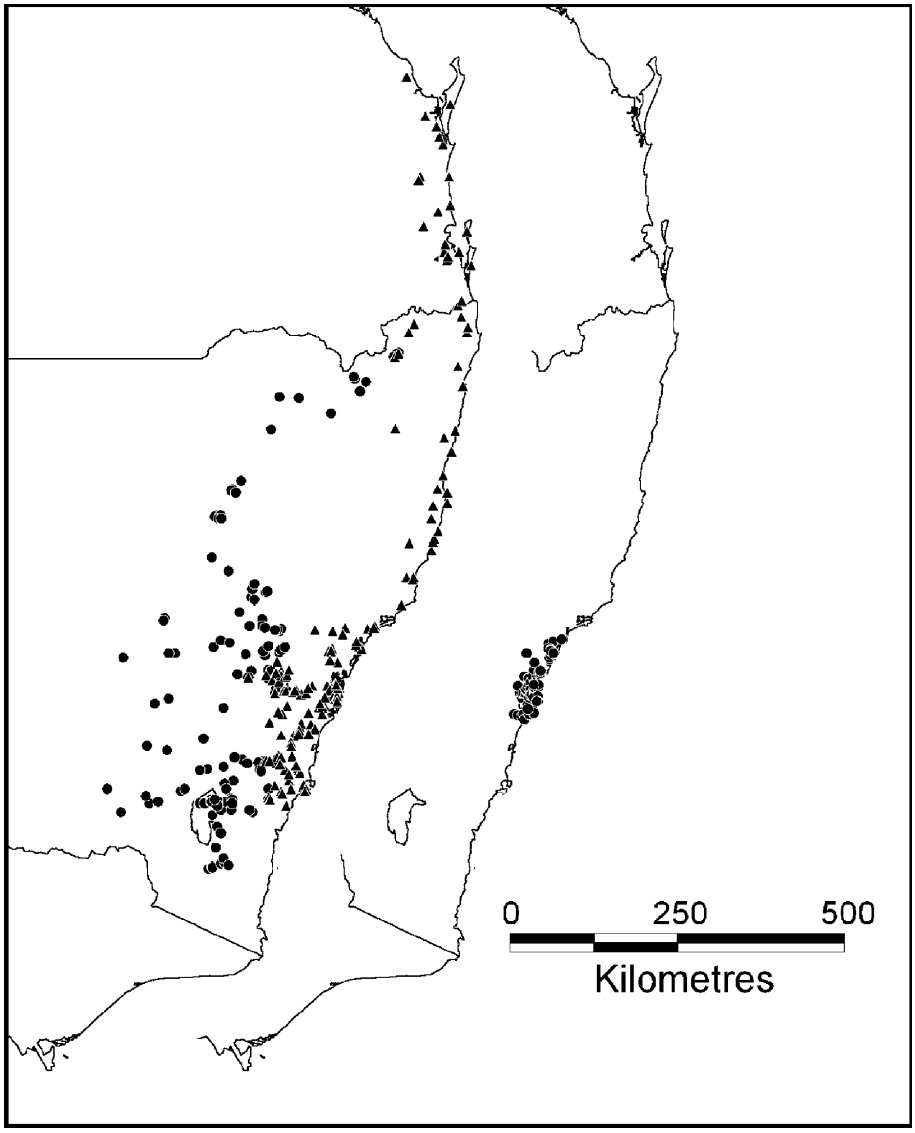

Fig. 5. Distribution of scribbly gums *sensu* Pfeil and Henwood. Left: *Eucalyptus racemosa* subsp. *rossii* (●), *E. racemosa* subsp. *racemosa* (▲). Right: *E. haemastoma* (●).

Key to species of *Eucalyptus* series *Psathyroxyla*

1 Fruit ≥ 8 mm wide, pyriform (occasionally almost hemispherical), discs ≥ 1.6 mm wide. Raised oil glands of seedling internodes (at 2nd leaf pair stage) usually adorned with small stellate hairs, raised oil glands of the 2nd leaf pair margin prominent and those nearest the petiole often adorned with small stellate hairs ..... ***Eucalyptus haemastoma***

1* Fruit ≤ 7 mm wide, hemispherical (rarely almost pyriform), discs ≤ 1.6 mm wide. Raised oil glands on seedling internodes (of the 2nd leaf pair stage) usually unadorned or rarely adorned with small stellate hairs; raised oil glands on 2nd leaf absent or present ..... ***E. racemosa … 2***

2 Leaves subtending buds 5–13 mm wide × 50 mm–95 mm long; usually more than 7 times as long as wide; raised oil glands on 2nd leaf margin usually absent, if present then unadorned ..... ***E. racemosa* subsp. *rossii***

2* Leaves subtending buds 11.5–24 mm wide × 80 –135 mm long; usually less than 7.5 times as long as wide; raised oil glands on the 2nd leaf margin usually present and occasionally adorned with small stellate hairs near the petiole .... ***E. racemosa* subsp. *racemosa***

Aknowledgments

We thank curators of the following herbaria for access to collections in their care: CANB, G, MEL, NSW. Special thanks are due to Ian Brooker, Andrew Slee and John Connors of CANB for their helpful advice and discussion. We also thank Lee Belbin for assistance with PATN.

References

Austin, M. P. (1985) Continuum concept, ordination methods, and niche theory. *Annual Review of Ecology and Systematics* 16, 39–61.

Baker, R.T. and Smith, H.G. (1920) *A research on the Eucalypts, especially in regard to their essential oils*. 2nd edn Sydney, The Government of the State of New South Wales.

Beadle, N.C.W., Evans, O.D. and Carolin, R.C. (1962) *Handbook of the Vascular Plants of the Sydney District and Blue Mountains.* (Published by the authors: Armidale).

Bean, A. R. (1997) Notes on *Eucalyptus* ser. *Psathyroxyla* Blakely (Myrtaceae) and other 'Ash group' eucalypts. *Autrobaileya* 5: 125–135.

Belbin, L. (1991) *PATN; Pattern Analysis package*. (Division of Wildlife and Ecology, CSIRO: Canberra, Australia).

Bentham, G. (1866) *Flora Australiensis*. Vol 3. (Lovell Reeve: London).

Blakely, W.F. (1934) *A Key to the Eucalypts.* (The Worker Trustees: Sydney).

Brooker, M.I.H. and Kleinig, D.A. (1990) *Field Guide to Eucalypts. South-eastern Australia.* (Inkata Press: North Ryde).

Carolin, R.C. and Tindale, M.D. (1994) *Flora of the Sydney Region*. 4th ed. (Reed: Chatswood).

Chippendale, G.M. (1988) *Eucalyptus*, *Angophora* (Myrtaceae). in *Flora of Australia*. A. S. George (ed.) (Australian Government Printing Service: Canberra).

Coxon, A.P.M. (1982) *User's Guide to Multi-dimensional Scaling.* (Heinemann: London).

Crisp, M.D. (1991) Contributions towards a revision of *Davesia* Smith (Fabaceae: Mirbelieae). II. The *D. latifolia* group. *Australian Systematic Botany* 4: 229–298.

Faith, D.P., Minchin, P.R. and Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57–68.

Gower, J.C. (1971) A general coefficient of similarity and some of its properties. *Biometrics* 27: 857–867.

Greuter, W. et al. (2000) International Code of Botanical Nomenclature (St Louis Code). *Regnum Vegetabile* 131. (Koeltz Scientific Books: Königstein).

Hill, K.D. (1991) Eucalyptus. in *Flora of New South Wales*. G.J. Harden (ed.) (New South Wales University Press: Kensington).

Ladiges, P.Y., Prober, S.M. and Nelson, G. (1992) Cladistic and biogeographic analysis of the 'blue ash' Eucalypts. *Cladistics* 8: 103–124.
Moore, C. (1893) *Handbook of the Flora of New South Wales*. (Charles Potter: Sydney).
Mowat, J. (1981) *Comparative ecology of scribbly gums and angophoras*. Unpublished PhD thesis, University of Sydney.
Pimentel, R.A. (1981) A comparative study of data and ordination techniques based on a hybrid swarm of sand verbenas (*Abronia* Juss.). *Systematic Zoology* 30: 250–267.
Shepard, R.N. (1974) Representation of structure in similarity data: problems and prospects. *Psychometrika* 39: 373–421.
Wiltshire, R.J.E., Potts, B.M. and Reid, J.B. (1992) A paedomorphocline in *Eucalyptus*. II. Variation in seedling morphology in the *E. risdonii*/ *E. tenuiramis* complex. *Australian Journal of Botany* 40: 789–805.

Manuscript received 1 July 2002
Manuscript accepted 9 December 2003