VARIATION IN *EUCALYPTUS BARBERI* L. JOHNSON & BLAXELL

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(with three tables and four text-figures)

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Phenetic variation within *Eucalyptus barberi* L. Johnson & Blaxell was examined and compared to related Tasmanian species. "Typical" northern populations were morphologically distinct from the more diverse group of populations to the south. This phenetic disjunction did not correspond to the major geographic disjunction in the range of *E. barberi*. Detailed study of two morphologically aberrant populations indicated that they probably arose from *in situ* hybridisation; however, the exact identities of the progenitor species remains unclear. The type locality and several of the "southern" populations, as well as aberrant populations at Meredith Tier and Ponybottom Creek, deserve formal conservation.

Keywords: ***Eucalyptus barberi*, genetic variation, hybridisation, rare endemic, conservation, Tasmania.**

INTRODUCTION

The past environment of the east coast is less well understood than that of other regions of Tasmania (e.g. southwestern Tasmania, MacPhail & Colhoun 1985). In addition, the Eastern Tiers have received little botanical study until relatively recently (Duncan *et al.* 1981, Kirkpatrick 1981). Kirkpatrick & Brown (1984b) suggested that the geographic and habitat patterns of many species on the east coast result from limited radiation from separate glacial refugia. Their study of endemism in Tasmania suggested two centres of endemism on the east coast, implying at least two past glacial refugia (Kirkpatrick & Brown 1984b).

Eucalypts in this region exhibit interesting biogeographic and genetic patterns of uncertain origin. These include unexplained north–south range disjunctions (e.g. *Eucalyptus tenuiramis* – Wiltshire *et al.* 1991), absences from apparently suitable habitats in the northeastern mountains (*E. coccifera*, *E. urnigera*, *E. subcrenulata* and *E. johnstonii* – Potts 1990), and the unlikely presence of high-altitude species on low-altitude hills (*E. coccifera* – Shaw *et al.* 1984). In addition, species that are morphologically and ecologically distinct in the southeast appear to converge in both morphology and substrate preference in the east (*E. pulchella*, *E. amygdalina* and *E. tenuiramis* – Kirkpatrick & Brown 1984b). Other species exhibit marked genetic differentiation between eastern and southeastern populations (e.g. *E. cordata* – Potts 1989), and patches comprising individuals outside the typical phenotypic range of currently described species are regularly encountered (e.g. Potts 1989, Potts & Reid 1985b).

The present study examines population differentiation in the rare Tasmanian endemic *E. barberi*, that is distributed as a series of small, disjunct populations on the east coast of Tasmania (Kirkpatrick 1981, Pryor & Briggs 1981). In addition, several small, variable populations with some affinity to *E. barberi* are examined. *E. barberi* is restricted to the northern slopes of dry, low-altitude, dolerite ridges, most of which are unreserved crown or private land (Duncan 1989). *E. barberi* was first described informally by Barber (1954). It was formally described by Johnson & Blaxell (1972), who considered that it had obvious affinities to *E. ovata*, *E. camphora* and *E. yarraensis* and therefore placed it in the informal subseries *Ovatinae* (series *Ovatae*, section *Maidenaria*, subgenus *Symphyomyrtus*) of Pryor & Johnson (1971). Ladiges *et al.* (1981, 1984) included one population in phylogenetically oriented studies of juvenile and seedling characters within the series. Chippendale (1988) has since redefined the series *Foveolatae*, which also includes *E. aggregata*, *E. rodwayi* and *E. brookeriana* (Gray 1979). The affinities of *E. barberi* to other Tasmanian *Foveolatae* species are also examined.

MATERIALS AND METHODS

Sampling

Sites were chosen that encompassed the full geographic range of *E. barberi* (fig. 1, table 1), including the type locality (east Cherry Tree Hill; site 4). Representative samples of the other Tasmanian *Foveolatae* species (*E. brookeriana* A.M. Gray, *E. ovata* Labill. and *E. rodwayi* Baker & Smith) were also included for comparison with *E. barberi*.

Atypical phenotypes with some affinities to *E. barberi* grow at Meredith Tier (sites 10–11) and Ponybottom Creek (sites 12–13). At Meredith Tier, samples were located along a transect (4–8 trees from each of 7 sites) to capture a distinct spatial gradient of atypical phenotypes over about 1 km. Eleven trees were also sampled from an isolated stand, with apparent affinities to *E. barberi*, 1 km away (site 6). There was no evident spatial pattern of phenotypes at Ponybottom Creek. Consequently ten trees were sampled, in each of three subjective classes:
(1) narrow green foliage, resembling *E. barberi* (site 12),
(2) glaucous, broad-leaved phenotypes with apparent affinities to *E. gunnii* or *E. cordata* (site 13), and
(3) phenotypes intermediate between these extremes.
Nine trees were sampled from the nearest population with affinities to *E. barberi* (Ringrove Razorback, site 9), 1.5 km away. A range of eastern populations of *E. cordata*, *E. gunnii*, *E. archeri*, *E. johnstonii* and *E. subcrenulata* were sampled, including those proximal to the Meredith Tier (sites 10–11) and Ponybottom Creek (sites 12–13) sites, because

TABLE 1
Populations sampled for this study

Species	Sample location	Site code	AMG ref.* East	AMG ref.* North	Alt† (m)	Popn‡ (min)	Number sampled§ AP	JP	AH	JH
Eucalyptus barberi	Blindburn Hill North	1	6022	53678	220	400	12	22	12	22
	Blindburn Hill South	2	6024	53663	200	30	11	24	11	24
	Cherry Tree Hill West	3	5943	53528	180	40	9	23	9	23
	Cherry Tree Hill East	4	5948	53518	170	60	12	16	12	16
	Brushy Creek	5	5762	53478	440	60	10	18	10	18
	Meredith Tier	6	5770	53297	400	30	11	35	–	–
	Lily Flats (South of)	7	5718	53161	320	60	13	25	13	25
	Ravensdale Hill	8	5713	53079	140	18	9	22	9	22
	Ringrove Razorback	9	5735	52713	160	30	9	21	–	–
Uncertain	Meredith Tier green	10					7	29	7	29
	intermediate	–	5767	53301	440	200	–	–	25	96
	glaucous	11					6	37	6	37
	Ponybottom Ck green	12					10	37	10	37
	intermediate	–	5736	52723	180	60	–	–	13	42
	glaucous	13					10	41	10	41
E. brookeriana	Buckbys Road	14	3633	54602	120	–	4	–	–	–
	Elephant Pass	15	6020	53908	390	–	–	4	–	–
	E. brookeriana type ¶	16	5705	53420	600	–	1	1	–	–
	Rocka Rivulet	17	5700	53205	450	–	2	5	–	–
	Kellevie Plateau	18	5670	52663	340	–	1	5	–	–
Pooled *E. brookeriana*		BR	sites: 14 – 18			–	8	18	–	–
E. ovata	Robbins Road	19	3210	54855	20	–	5	–	–	–
	Bass Highway	20	3990	54575	10	–	6	–	–	–
	W Road	21	5727	52758	40	–	8	13	–	–
	Hobart College	22	5250	52480	280	–	9	15	–	–
Pooled northwest coast *E. ovata*		WO	sites: 19 – 20			–	8	13	–	–
E. rodwayi	Steppes	23	4910	53375	800	–	–	19	–	–
	M Road South	24	5698	53233	580	–	7	12	–	–
E. cordata	Bluestone Tier	25	5652	52932	350	–	10	18	10	18
	Brown Mt	26	5428	52837	710	–	7	13	7	13
	Perpendicular Mt top	27	5933	52766	340	–	–	–	10	–
	Perpendicular Mt low	28	5930	52765	240	–	–	–	10	–
	Square Mt	29	5506	52695	370	–	9	6	9	6
	Hospital Creek	30	5673	52660	240	–	–	–	10	–
	Chimney Pot Hill	31	5225	52476	430	–	–	–	10	–
	Cape Queen Elizabeth	32	5345	52109	100	–	–	–	10	–
E. archeri	Mt Maurice	33	5490	54260	1000	–	–	13	–	13
E. gunnii	Mt Arthur NE	34	5208	54283	500	–	–	–	10	–
	Mt Victoria	35	5687	54228	790	–	–	–	20	–
	Snow Hill	36	5693	53592	950	–	–	–	25	15
	Pensford	37	4837	53487	960	–	–	–	20	–
	M Road North	38	5732	53298	640	–	11	32	11	32
E. johnstonii	Springs, Mt Wellington	39	5190	52490	600	–	–	10	–	–
	Snug Plains	40	5133	52330	600	–	–	5	16	–
E. subcrenulata	Dove Lake	41	4135	53870	960	–	–	12	–	–
	Lake Charles	42	4367	53633	1070	–	–	10	–	–

* Australian Map Grid reference. † Altitude (metres). ‡ Minimum estimate of population size for *E. barberi* populations.
§ Number of individuals sampled for population studies: variation in *E. barberi* and related species (AP = adults, JP = juveniles); aberrant populations at Meredith Tier and Ponybottom Creek, sites 10–13 and intermediates (AH =adults, JH = juveniles).
¶ Seed collected from open pollinated offspring from type specimen of *E. brookeriana*, grown as an ornamental.

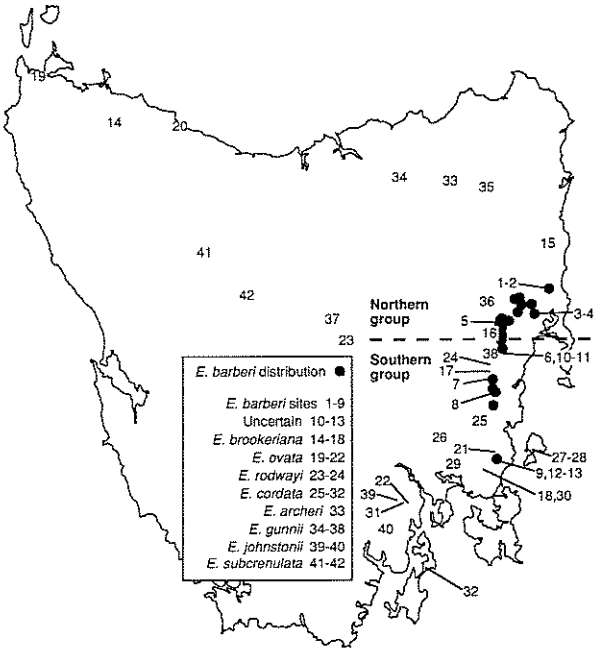

FIG. 1 — The known distribution of Eucalyptus barberi *(• — from Forestry Commission of Tasmania records) and locations of populations of all species sampled for this study (codes). (Location codes are detailed in table 1.) An explanation of "northern" and "southern" groups is given in the discussion.*

some atypical phenotypes showed affinities to these species. Adult data from previous studies were also used for *E. gunnii*, *E. archeri* (Potts & Reid 1985b) and *E. cordata* (Potts 1989). Open-pollinated seed, as well as three typical, mature canopy leaves and capsules, was collected from up to 13 trees, at least two tree-heights apart, from each *E. barberi* population (see table 1, AP).

Progeny trial

Seeds were germinated on a 1:1 vermiculite:gravel mix covered with a surface (20 mm) of vermiculite. At the cotyledonary stage (three weeks) plants were transplanted into black plastic potting bags filled with potting mix. Plants were grown under glasshouse conditions (day 19°–24°C, night 12°–14°C) with the natural photoperiod extended to 18 h by a mixed incandescent and fluorescent light source.

Four seedlings from each of approximately 12 families were used in the progeny trial and were placed in a completely random design. Between 16 and 25 individuals were scored for each typical *E. barberi* population (numbers sampled from each populations are shown in table 1, JP). *E. brookeriana* samples (sites 14–18) were pooled (BR) for the purposes of the analysis. Similarly, northwest coast *E. ovata* populations (sites 19–20) were treated as one population sample (WO).

Morphometric data collection and analysis

The characters scored from adult and juvenile plants are listed in table 2. Capsule and adult leaf characters are the same as those described in Potts & Reid (1985b). Adult data analysis was performed on the means of three replicates from each tree. Seedlings were scored six months after planting. Measurement of the juveniles was based upon characters (table 2) recognised as distinguishing *E. barberi* from other members of the *Foveolatae* (LAML8, LAMW8, LWP8, PETL8, RUG, GLAND, CREN, LATLEN, LATRAT and INTLEN), *E. johnstonii* and *E. subcrenulata* (DIARAT, COLOUR), and *E. cordata* and *E. gunnii* (LOBE8, GLAU, INTRANOD, PETNODE; Chippendale 1988). Juvenile leaf characters were measured from a leaf removed from the eighth node (counting the cotyledonary node as node 0), and stem characters from the eighth internode (below node 8). Categorical multistate characters measured on relative scales were scored by comparison with standards (GLAND, CREN, RUG, GLAU, COLOUR). DIARAT (diameter ratio = widest width/narrowest width at the same height on the stem) represented the rectangularity of the stem. INTLEN (mean internode length) was calculated as the height/ the number of internodes. LATRAT (lateral ratio = number of nodes with laterals/number of nodes) represented the proportion of the plant bearing lateral branches.

The pooled within-population residuals for each variable were tested for normality, using the UNIVARIATE procedure of SAS (SAS 1988). The relationship between residuals and fitted values, derived from the one-way GLM analysis (SAS 1988), was inspected in bivariate plots. Where necessary, transformations were used that optimised the normality and homogeneity of variance criteria. Variables and transformations used in the analysis are shown in table 2. Stepwise discriminant analysis (STEPDISC procedure of SAS) found that all variables were significant ($p < 0.05$) in separating populations.

Parametric canonical discriminant analysis was performed using the CANDISC procedure of SAS; this produced discriminant functions, which maximised the separation of populations. Means and standard errors were calculated for each population from the individual scores along the discriminant functions. The relative importance of different characters in differentiating populations, and their direction of variation in the discriminant space, were summarised by plotting vectors, the lengths of which are proportional to the univariate F-values, the directions being determined by the standardised canonical coefficients of the relevant discriminant functions. Populations were also clustered, using average linkage cluster analysis (Sneath & Sokal 1973) based on the matrix of Mahalanobis' distances. Mahalanobis' distances between populations were calculated from the squared Euclidean distance between populations, in the space defined by the first nine discriminant axes (representing 99.3% of adult and 94.9% of juvenile variation for the populations shown in fig. 3). This procedure was applied to adult and juvenile (table 1: AP, JP respectively) *E. barberi* (sites 1–9) and other *Foveolatae* populations (*E. brookeriana* – BR; *E. ovata* – WO, sites 21–22; *E. rodwayi*, sites 23–24), including the green phenotypes resembling *E. barberi* from Meredith Tier (site 10) and Ponybottom Creek (site 12). For comparison with other species, this analysis was repeated, with the addition of samples from populations of *E. johnstonii* (sites 39–40), *E. subcrenulata* (sites 41–42), *E. gunnii-archeri*

TABLE 2
Morphological characters measured for this study

Code	Description	Scale*	Trans.†	Significance‡	
Adult leaf characters				$F_{15,140}$	Pr>F
LL	Lamina length	mm	log	8.42	0.0001
LW	Lamina width	mm	log	13.9	0.0001
LWP	Length to widest point	mm	log	4.73	0.0001
PET	Petiole length	mm	log	8.93	0.0001
Adult capsule characters					
PEDI	Pedicel length	mm	log	9.39	0.0001
PEDU	Peduncle length	mm	log	6.71	0.0001
CAPL	Capsule length	mm	log	19.2	0.0001
MAXW	Capsule max. width	mm	log	13.8	0.0001
PTMW	Length to max. width	mm	log	6.69	0.0001
RIMW	Rim width	mm	square	5.18	0.0001
VPOS	Valve thickness	(1–4)	square	2.92	0.0005
VSIZE	Valve size	(1–4)	log	1.97	0.0212
Juvenile leaf characters				$F_{15,333}$	
LAML8	Lamina length	mm	–	4.85	0.0001
LAMW8	Lamina width	mm	–	13.2	0.0001
LWP8	Length to widest point	mm	–	5.81	0.0001
PETL8	Petiole length	mm	–	1.58	0.0001
LOBE8	Lobe length from leaf base to bottom of lobe	mm	–	7.63	0.0001
GLAND	Gland density on leaf	(1–4)	–	8.27	0.0001
CREN	Crenulation of margin	(1–3)	–	5.51	0.0001
Juvenile stem characters					
RUG	Rugoseness	(1–3)	log	14.7	0.0001
DIARAT	Stem rectangularity	–	–	2.53	0.0014
Juvenile whole plant characters					
INTRANOD	Node 1st intranode	–	–	10.6	0.0001
PETNODE	Node of 1st petiole	–	–	9.32	0.0001
INTLEN	Mean internode length	mm	–	7.04	0.0001
LATLEN	Length longest lateral	mm	–	4.13	0.0001
LATRAT	Lateral ratio	–	–	3.14	0.0001
GLAU	Glaucousness	(0–8)	–	3.12	0.0001
COLOUR	Max. node where anthocyanin occurs on the undersurface of the leaf				
	0–10 × Depth of colour (0, 1, … 3)	(0–30)	–	2.15	0.0079

* *Numbers in parentheses represent relative scales.*
† Transformation used.
‡ Univariate significance of variation in each character between populations in the series *Foveolatae.*

(sites 33, 36, 38), *E. cordata* (sites 25–26, 29), and the most glaucous phenotypes from Meredith Tier (site 11) and Ponybottom Creek (site 13).

For analysis of the Meredith Tier and Ponybottom Creek samples, quadratic discriminant functions were calculated for both adult and juvenile data sets, which maximised the separation between typical populations of *E. barberi* (sites 1–5, 7–8), *E. gunnii* (sites 34–38) and *E. cordata* (sites 25–32). The latter procedure takes into account the differences in variance/covariance structures between species. Mean discriminant scores and 95% confidence intervals for individuals from the reference groups were calculated. Discriminant scores for individuals from Meredith Tier (sites 10–11 and intermediates) and Ponybottom Creek (sites 12-13 and intermediates) were also calculated on the two discriminant functions derived from this analysis.

In order to determine whether an individual falls within the range of variation encompassed by each reference species (*E. barberi, E. gunnii, E. cordata*), the generalised distance of each individual tree from the centroid of each species, and its significance were calculated according to equations 5.1 and 5.2b in Orlóci (1978), using separate variance–covariance matrices for each species (and equal sample sizes). An individual was classified as falling within the range of variation encompassed by a species if the probability of obtaining the observed generalised distance due to chance alone was greater than 0.05 (i.e. the individual falls within the multivariate 95% confidence interval of the species). For each of the three reference species, the proportions of adult individuals in each population that matched the reference species phenotype were calculated, as well as the proportion of individuals whose phenotype did not match

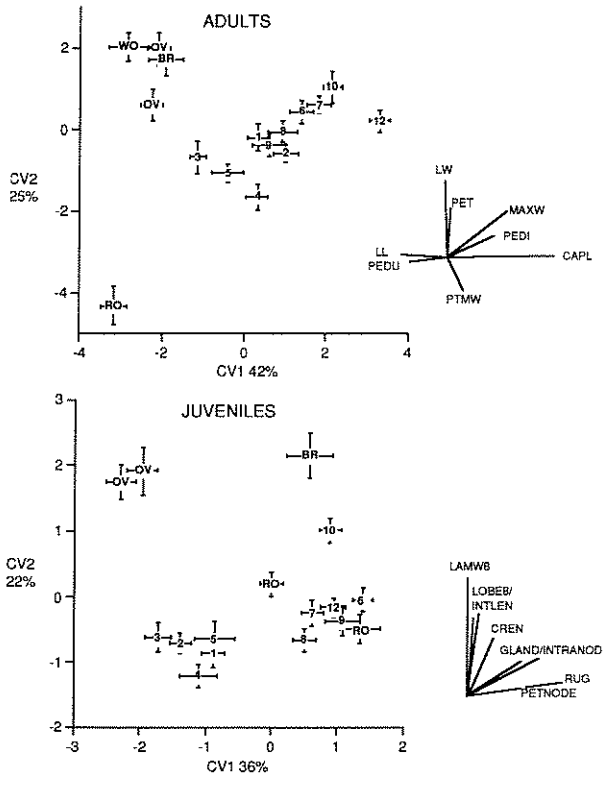

FIG. 2 — Population means and standard errors along the two major discriminant functions (CV1, CV2) derived from the analysis of adult (upper) and juvenile (lower) population samples from northern (sites 1–5) and southern (sites 6–9) populations of Eucalyptus barberi, E. brookeriana *(BR),* E. ovata *(OV, WO),* E. rodwayi *(RO) and green phenotypes resembling* E. barberi *from Meredith Tier (site 10) and Ponybottom Creek (site 12). Vectors represent the direction (derived from the standardised discriminant function coefficients) and magnitude (derived from the univariate F-values) of variation in characters between populations. The percentage of the total variance explained by each discriminant function is indicated. (Location codes detailed in table 1.)*

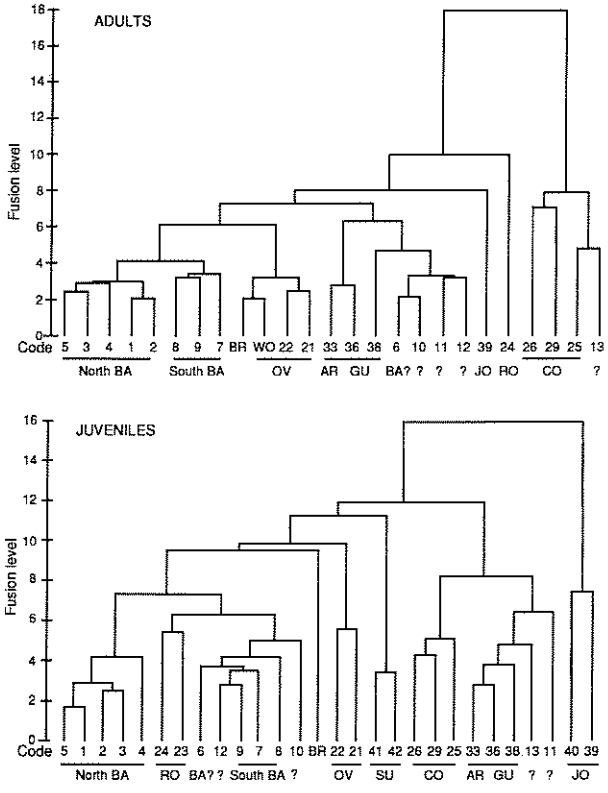

FIG. 3 — Dendrogram from average linkage clustering of adults (upper) and juveniles (lower) from populations of Eucalyptus barberi *(BA),* E. brookeriana *(BR),* E. ovata *(OV),* E. rodwayi *(RO),* E. archeri *(AR),* E. gunnii *(GU),* E. cordata *(CO),* E. johnstonii *(JO),* E. subcrenulata *(SU) and aberrant populations (?). (Location codes detailed in table 1.)*

any of the three species. Where there is phenetic overlap between species, some individuals may fall within the 95% confidence intervals of more than one species; hence, the proportions may sum to more than 100%. In the juveniles, only the proportion that matched the phenotype of *E. barberi* was calculated, since samples sizes of juvenile *E. gunnii* and *E. cordata* were insufficient to represent the species' full phenetic ranges.

RESULTS

The mean scores of the series *Foveolatae* populations on the first two discriminant axes derived from the adult and juvenile data are shown in figure 2. Clusters produced from this analysis proved to be subsets of those produced by the analysis including other species (fig. 3).

E. barberi (sites 1–9) and green samples from Meredith Tier and Ponybottom Creek with apparent affinities to *E. barberi* (sites 10, 12) were well separated from the other *Foveolatae* species (BR, OV, WO, RO) in the discriminant space derived from the analysis of adult morphological traits. However, they were not well differentiated from *E. rodwayi* (RO) in the juvenile analysis (figs 2 & 3). *E. ovata* (OV, WO) was quite distinct from *E. barberi* and *E. rodwayi* (RO) in adult and juvenile morphology. *E. brookeriana* is closer to *E. ovata* in adult morphology, particularly the northwestern samples (WO, fig. 3), but equidistant and distinct from other species in juvenile morphology.

On juvenile morphology, *E. barberi* populations fell into two distinct groups: sites 1–5 and sites 6–9, 10, 12 (fig. 3). These correspond geographically to a northern and a southern group (fig. 1). In the cluster analysis, which incorporates a larger proportion of variation than the ordination, this pattern is also apparent in the adults (fig. 3). Southern populations (sites 6–9, 10, 12) exhibited greater variation in adult than juvenile morphology. In particular, the green samples with apparent affinities to *E. barberi* from Meredith Tier (sites 6, 10) and Ponybottom Creek (site 12) were separated from other southern populations of *E. barberi* (fig. 3). The northern and southern *E. barberi* populations differed in capsule traits (larger, more pedicellate capsules in southern populations), and seedlings from southern populations retained the juvenile foliage longer than northern populations (expressed as higher node of first intranode and petiole; fig. 2).

At Meredith Tier (sites 10–11) and Ponybottom Creek (sites 12–13), phenotypes varied from narrow, green-leaved individuals with seven medium-sized fruit per umbel, typical of *E. barberi,* to individuals with broad, glaucous leaves and three large fruit per umbel, resembling *E. cordata.* The

TABLE 3
Comparison of samples with the phenotypic ranges of three eucalypt species*

Collected as		Code (Site)		Classification†				
				E. barberi %	*E. cordata* %	*E. gunnii* %	None test sp. %	n
E. barberi		1	adults	100	0	17	0	12
			juveniles	100	–	–	–	22
		2	adults	100	0	18	0	11
			juveniles	96	–	–	–	24
		3	adults	100	0	0	0	9
			juveniles	100	–	–	–	23
		4	adults	100	0	0	0	12
			juveniles	94	–	–	–	16
		5	adults	100	0	0	0	10
			juveniles	83	–	–	–	18
		6	adults	45	0	27	36	11
			juveniles	63	–	–	–	35
		7	adults	100	0	8	0	13
			juveniles	92	–	–	–	25
		8	adults	100	0	11	0	9
			juveniles	91	–	–	–	22
		9	adults	89	0	11	11	9
			juveniles	86	–	–	–	21
Meredith Tier	green	10	adults	57	0	43	29	7
			juveniles	59	–	–	–	29
	intermediate	–	adults	43	0	30	44	23
			juveniles	27	–	–	–	96
	glaucous	11	adults	13	0	13	88	8
			juveniles	14	–	–	–	37
Ponybottom Ck	green	12	adults	30	0	40	50	10
			juveniles	51	–	–	–	37
	intermediate	–	adults	0	0	0	100	13
			juveniles	45	–	–	–	42
	glaucous	13	adults	0	10	0	90	10
			juveniles	12	–	–	–	41
Summary:								
E. barberi		all	adults	93	0	10	5	96
			juveniles	88	–	–	–	206
E. cordata		all	adults	0	100	0	0	76
			juveniles	0	–	–	–	37
E. gunnii		all	adults	11	0	96	3	76
			juveniles	7	–	–	–	46
Meredith Tier		all	adults	39	0	30	50	38
			juveniles	30	–	–	–	162
Ponybottom Ck		all	adults	9	3	12	82	33
			juveniles	36	–	–	–	120

* The percentage of individuals in each sample which were not significantly different ($p > 0.05$) from *E. barberi*, *E. cordata* and *E. gunnii*, and the percentage matching none of the reference species. The percentage of individuals of the reference species which were not significantly different from the reference groups is shown, for comparison with samples from Meredith Tier and Ponybottom Creek. Dash (–) indicates sample not tested. Due to overlap between reference groups, percentage may not total 100%.
† Based on generalised distance.

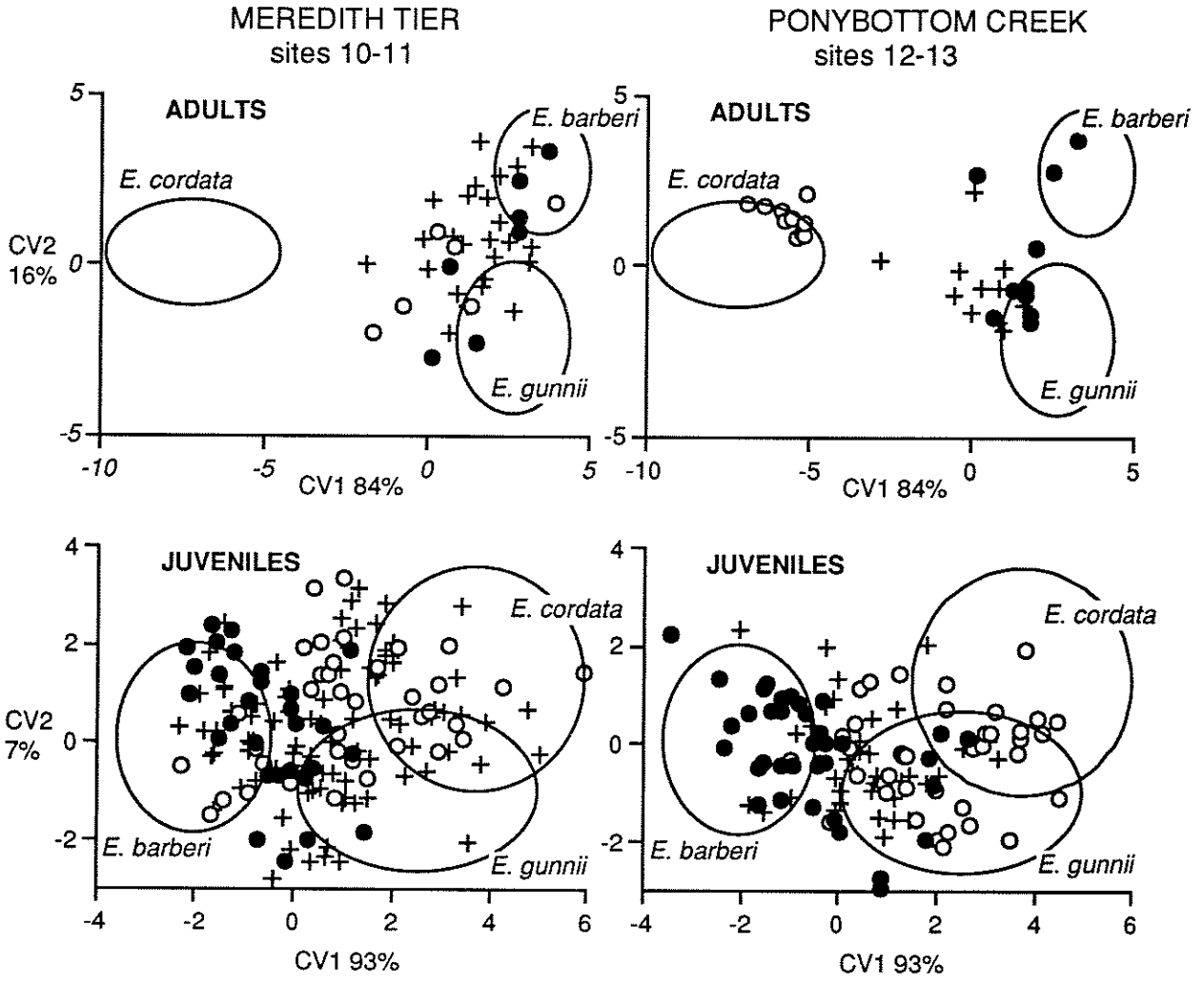

FIG. 4 — Plots of adults (upper) and juveniles (lower) from Meredith Tier (left) and Ponybottom Creek (right) on the axes derived from the discriminant analysis of typical Eucalyptus barberi, E. cordata *and* E. gunnii *samples. The percentage of variance represented by each discriminant function is shown. Ellipses represent the 95% confidence intervals for individuals of the three reference species.* ● *– green adults resembling* E. barberi *(upper), and their juvenile progeny (lower).* ○ *– glaucous adults and their juvenile progeny.* + *– intermediate adults and their juvenile progeny.*

slightly isolated populations at Meredith Tier (site 6) and Ringrove Razorback (site 9) resembled *E. barberi* in leaf characters, but varied in bud number, from three to seven per umbel. *E. gunnii*, which occurs in the vicinity of the Meredith Tier population, has narrow adult leaves similar to *E. barberi*, but has three small buds per umbel.

Samples from Meredith Tier and Ponybottom Creek were ordinated in the discriminant space differentiating core populations of *E. barberi*, *E. cordata* and *E. gunnii* (fig. 4). Overlap of the juvenile discriminant scores of the reference *E. cordata* and *E. gunnii* populations (fig. 4, ellipses) indicates that these species were less distinct from one another in the juvenile than adult stages. Tests of the significance of the generalised distance between individuals and the centroids of the three reference species are shown in table 3. It is expected, in theory, that 95% of typical species' samples would not differ significantly from the corresponding reference group. In this case, 93–100% of adults of the three species and 88% of *E. barberi* juveniles were correctly classified. There was some overlap in the ranges of *E. barberi* and *E. gunnii* adults, with 8–10% of adults of both species falling within the 95% confidence intervals of the other species.

The pattern observed for the reference populations contrasts markedly with the classification results from the anomalous populations at Meredith Tier and Ponybottom Creek. Most adults from Meredith Tier fell outside the 95% confidence intervals of all three reference species; 50% overall and 88% of the glaucous individuals were outside the confidence intervals of all the reference species (table 3). Those that did match were similar to *E. barberi* and *E. gunnii* in approximately equal proportions (39% and 30% respectively) and, overall, the Meredith Tier population showed similarities to *E. gunnii* in the cluster analysis (fig. 3). The adults from Meredith Tier deviated slightly toward, but were not within the phenotypic range of *E. cordata* (fig. 4). A large proportion of the juveniles from Meredith Tier were also outside the ranges of all three reference species and most were intermediate between the reference species (fig. 4). Cluster analysis of the juveniles placed the green sample

from Meredith Tier (site 10) as an outlier to the *E. barberi* populations and the glaucous sample (site 11) closest to *E. gunnii* (fig. 3).

In the full multidimensional space, 82% of the Ponybottom Creek adults were outside the 95% confidence intervals of all three reference species (table 3), with a small proportion of the remainder ascribed to each species. The green individuals (site 12) were divided between *E. barberi* (30%) and *E. gunnii* (40%). Only one individual from the intermediate and glaucous (site 13) samples matched a reference species (*E. cordata*), but the glaucous individuals appeared closest to the *E. cordata* populations in the cluster analysis (fig. 3), and were very close to the adult phenotype of *E. cordata* (fig. 4). A greater proportion of Ponybottom Creek juveniles matched the phenotype of *E. barberi* (36%) compared with the adults (9%, table 3). Most juveniles appeared intermediate between *E. barberi* and *E. gunnii*, but there was overlap with, and deviation toward the phenotypic range of *E. cordata* (fig. 3).

The range of variants observed in the juvenile progeny from both Meredith Tier and Ponybottom Creek (from all phenotypic classes collected) and the intermediate phenotypes of the parents strongly suggested parental heterozygosity rather than simple outcrossing. For example, recombination of leaf shape and glaucousness was very apparent in progeny of one intermediate individual from Meredith Tier.

DISCUSSION

Significant differentiation, in both adult and juvenile characters, was found between most populations of *E. barberi*. A seedling trial clearly indicated that this differentiation has a strong genetic basis. There appeared to be a primary division between a northern group of populations that may be designated "typical" *E. barberi* and other, southern, populations which deviated toward the phenotype of other species (fig. 1). There was no clear clinal or consistent spatial pattern of variation within each group. The "typical" group comprised populations from Cherry Tree Hill (sites 3–4), Brushy Creek (site 5) and the vicinity of Blindburn Creek (sites 1–2, in the Douglas-Apsley National Park). Within this group, phenetic distance was poorly correlated with geographic distance. The southern group comprised *E. barberi* populations from Ravensdale Hill (site 8), 1.5 km south of Lily Flats (site 7) and the green phenotypes resembling *E. barberi* from Meredith Tier (6, 10), Ponybottom Creek (site 12) and Ringrove Razorback (site 9). Some southern populations showed affinities to juvenile *E. rodwayi* but were quite distinct on adult traits. Conversely, several of the southern populations (sites 6, 10, 12) showed affinities toward *E. gunnii* in their adult morphology (fig. 3) but were clearly differentiated from *E. gunnii* and *E. archeri* on juvenile morphology. In most cases, they would also have been differentiated from these species on the basis of the number of buds per inflorescence, which was not included in the analysis (and was greater than the typical three of *E. gunnii* and *E. archeri*). They, therefore, appear to have closest affinities to *E. barberi*.

The high level of population differentiation found within *E. barberi* is typical of the population genetic structure that would be predicted by theory for a species distributed as a series of small disjunct populations (due to factors such as genetic drift – Falconer 1986) and has been observed in other eucalypt species with comparable distribution patterns (e.g. *E. caesia*, *E. pendens* – Moran & Hopper 1987; *E. crucis* – Sampson *et al.* 1988). Prober *et al.* (1990) suggest that such restricted distributions may result from recent divergence (with insufficient time for geographical radiation), barriers to dispersal (e.g. unsuitability of habitat, competition), or contraction of the range of an older species due to environmental factors (e.g. habitat specificity, climatic change). In this case, the degree and pattern of phenetic differentiation between *E. barberi* populations and the large disjunctions in its geographical range support Williams' (1990) contention that *E. barberi* is not a recently diverged species. *E. barberi* appears to be a relic species and has possibly been displaced from intervening sites by competition with more rapidly growing species.

It is only possible to speculate on the cause of differentiation in *E. barberi*. Genetic drift, localised selection, hybridisation and historical factors may all be involved. Kirkpatrick & Brown (1984a, b) and Potts & Reid (1985c) suggested that the present east coast flora may have originated from populations which differentiated in two glacial refugia. Such separation could explain differentiation of the northern and southern populations of *E. barberi*. However, the disjunct distribution of *E. barberi* does not appear to have been caused by insufficient time for radiation, as the major disjunction in the geographical distribution of *E. barberi* does not correspond to the phenetic disjunction (fig. 1). This contrasts with the coincidence of marked genetic differentiation with geographic disjunction in *E. tenuiramis* in the same area (Wiltshire *et al.* 1992). Disjunctions in the geographical distribution of *E. barberi* may not be as extensive as is shown by current records. Paucity of sampling may have occurred, due to the small population sizes (and area), inaccessibility and small size of the trees. There are, for example, unverified reports of other populations west of Triabunna (between sites 12–13 and site 8).

"Confusing intermediacy" (Kirkpatrick & Brown 1984b) is an apt description of the Meredith Tier and Ponybottom Creek populations. At both sites, the pattern of high diversity and intermediacy of parents and progeny, coupled with the high variability within some families, was consistent with a hybrid swarm, several generations old (e.g. Potts & Reid 1985a). The magnitude of the differences between extreme phenotypes was strongly suggestive of hybridisation, as was the distribution of extreme phenotypes at Meredith Tier. Although this may have been produced by disruptive selection from the gene pool of one species, no selective agency of sufficient magnitude was evident, particularly at Ponybottom Creek. At both localities, trees with close affinities to *E. barberi* appeared to be one of the parents. The exact identity of the other parent remains unclear. *E. cordata*, *E. gunnii* and possibly *E. morrisbyi* are the only plausible extant species. *E. morrisbyi* was not included in the progeny trial because of its extremely limited distribution (Wiltshire *et al.* 1990), and the fact that its juveniles would be difficult to distinguish from *E. gunnii* in hybrid combination (e.g. Potts 1989). At both Meredith Tier and Ponybottom Creek, extreme phenotypes did not resemble other members of the *Foveolatae*, and the involvement of *E. johnstonii* or *E. subcrenulata*, which has been reported from near Ponybottom Creek and on the Eastern Tiers (Brown *et al.* 1983), is unlikely, as the juveniles of these taxa are clearly differentiated from those of *E. barberi* and populations at Meredith Tier and Ponybottom Creek (fig. 3).

The unusual characteristics of the latter populations may have resulted from hybridisation between atypical populations of the species suggested. Such small, atypical populations of both *E. cordata* (Potts 1989) and *E. gunnii* (Potts & Reid 1985b) are numerous on the east coast and are still being found (e.g. *E. cordata* near Wielangta Hill, between site 12–13 and site 8). However, it remains to be ascertained whether the variation found at Meredith Tier and Ponybottom Creek and the deviation of these populations from typical *E. barberi* are due to past introgression or reflect genetic variation within *E. barberi* at these localities. Molecular techniques may best be able to resolve the identity of these populations.

Conservation status

At present one, albeit relatively large population of *E. barberi* is securely reserved, in the Douglas-Apsley National Park (sites 1–2). Another of the northern populations (Brushy Creek, site 5) is in the proposed Bluemans Creek state reserve (Williams 1989). Other populations, including the type locality (site 4), are unreserved. The type locality also contains other rare species (*Spyridium microphyllum, Helichrysum lycopodioides, Melaleuca pustulata, Cyathodes pendulosa* and *Gahnia graminifolia* – Duncan & Duncan 1984) and has been previously recommended for reservation (Duncan & Brown 1985).

There is a need to extend conservation measures to encompass the full range of variability in this species. In particular, the type locality, representatives of the southern phenetic group (e.g. "south of Lily flats" – site 7; "Ravensdale Hill" – site 8) and outlying populations such as Meredith Tier (sites 6, 10–11), Ringrove Razorback (site 9) and Ponybottom Creek (site 12-13) should be formally reserved. The latter populations are also of scientific interest. *E. barberi* populations are generally small, particularly the southern populations (table 1), which would argue for reservation of multiple representatives of each of the major phenetic groups.

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