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Phenetic variation in the Eucalyptus gunnii-archeri complex

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PHENETIC VARIATION IN THE *EUCALYPTUS GUNNII-ARCHERI* COMPLEX

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Abstract

A detailed study of phenetic variation in the *Eucalyptus gunnii-archeri* complex clearly indicates continuous variation between the taxa *E. archeri* Maiden and Blakely and *E. gunnii* Hook f. The complex comprises a multidimensional clinally varying series of highly differentiated populations. In part, population differentiation appears to result from the interaction of multicharacter clines paralleling at least two independent habitat gradients. These gradients are associated with, firstly, variation in exposure to the alpine environment and, secondly, the transition in the sub-alpine region from the open woodland, 'frost-hollow' habitat to the mixed eucalypt / rain-forest habitat. This multidimensional continuum is summarised by classification of populations into five main phenetic groups which are more or less geographically and ecologically defined and correspond well with the perception of the taxa in the literature.

1 - INTRODUCTION

The *Eucalyptus gunnii-archeri* complex encompasses a diverse assemblage of populations and comprises two main taxa, *E. gunnii* Hook f. and *E. archeri* Maiden and Blakely, often given specific status (e.g. Blakely 1934; Brett 1938; Jackson 1965; Hall *et al.* 1970; Hall and Brooker 1972; Curtis and Morris 1975), although treated as subspecies of *E. gunnii* in the latest revision of the genus (Pryor and Johnson 1971). Furthermore, the taxa described as *E. divaricata* Brett (Brett 1938) is included in the complex and is noted by Pryor and Johnson (1971) as a minor variant of ssp. *gunnii*. The close phylogenetic relationship of the Tasmanian endemics *E. gunnii*, *E. archeri*, *E. urnigera* and *E. morrisbyi* is recognised and along with the mainland species *E. glaucescens* they comprise the superspecies *Gunnii* (Subgenus *Symphyomyrtus*, Section *Maidenaria*, Series *Viminales*; Pryor and Johnson 1971).

2 - DISTRIBUTION AND ECOLOGY

With the exception of *E. morrisbyi*, the species in *E. supersp. Gunnii* occupy sub-alpine habitats and in terms of their principal occurrence, the endemics *E. urnigera*, *E. gunnii* and *E. archeri* form a geographic series. *E. urnigera* achieves maximum development on the mountains in the south-east of the island, *E. gunnii* on the Central Plateau and *E. archeri* on the northern scarp of the Central Plateau (along the Western Tiers) and on the north-eastern mountains. Major fault grabens isolate these highland areas yet populat-

ions ascribed to either taxa transcend these major habitat disjunctions. Small disjunct stands of *E. unnigera* extend as far north as Alma Tier (AH; Fig. 1) on the south-eastern edge of the Central Plateau and *E. gunnii* similarly extends as far south as the Mt. Wellington - Mt. Field ranges and the base of the Mt. Anne-Eliza Plateau. *E. archeri* and *E. unnigera* are allopatric and distinct forms of *E. gunnii* and *E. archeri* do not co-occur. Nevertheless on the Western Tiers north of Great Lake (P1 to Br), populations are more or less continuous and are clinally linked through geographically intermediate populations. In addition, allopatric populations further west in the upper Mersey Valley region are difficult to assign to either taxa. In contrast, *E. unnigera* and *E. gunnii* may occur together but are ecologically segregated. *E. gunnii* occupies the poorly drained marshy sites whereas *E. unnigera* occurs on the better drained slopes, often in association with *E. coccolera*. The boundary between stands is usually sharp and specific integrity is maintained except for the occurrence of occasional intermediates. Nevertheless, a degree of convergence in several allopatric populations of either species is apparent (i.e. SH, A1).

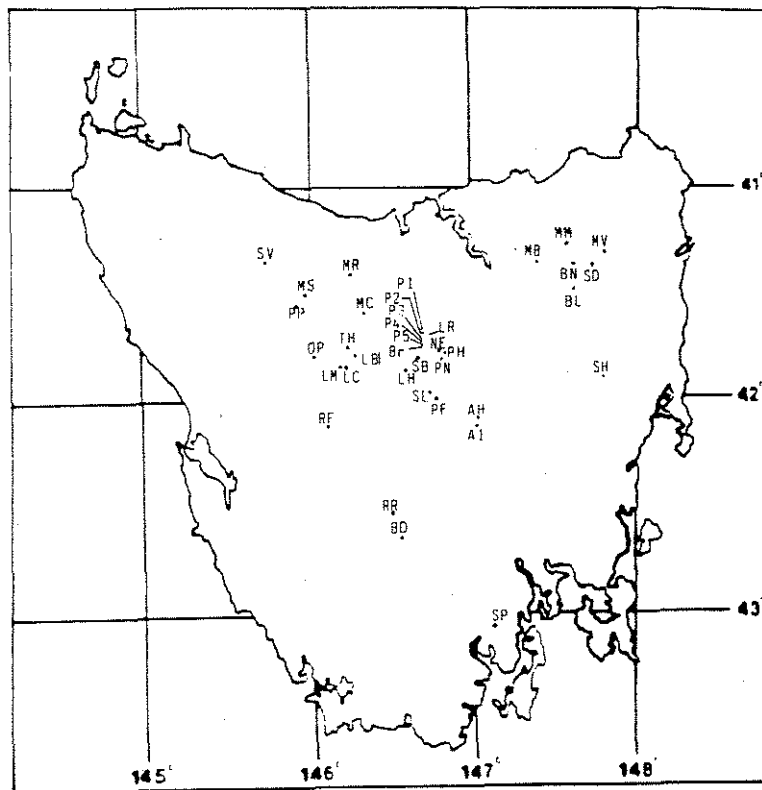


Figure 1 - Location of sampling sites. Population codes are detailed in table 1.



Figure 2 - Open woodland form of *E. gunnii* (site SL). This variant was described by Brett (1938) as *E. divaricata*.

The habitat in which *E. gunnii* is most commonly found is relatively open and defined by poor soil drainage and cold temperatures. The interaction of *E. gunnii* with surrounding eucalypt species is best explained by an ability to better tolerate this combination of factors, as well as a lower tolerance to summer drought. *E. gunnii* is one of the most frost tolerant eucalypt species (e.g. Hooker 1844; Martin 1948; Barber 1955; Marien 1979; Evans 1980; AFOCEL pub. 1982). On the Central Plateau, *E. gunnii* forms extensive open woodlands on the edges of 'frost hollows' (Fig. 2) between 1000 and 1100m. It is replaced on the better drained slopes at higher altitudes by *E. coccifera* and at lower altitudes by *E. delegatensis*, *E. pauciflora* and *E. dalrympleana*. On the southern slopes of the Central Plateau, in areas below 960m *E. gunnii* is only encountered sporadically and is replaced by *E. rodwayi* as the species tolerant of poor soil drainage (Jackson 1973). On these sheltered, low altitude forest sites *E. gunnii* may attain heights of over 30m (Fig. 3) but with increasing altitude and exposure tree height is reduced and in the open woodlands trees (12-20m) exhibit a marked divaricating branching pattern (hence *E. divaricata*; Fig. 2). At its upper altitudinal limit a variant of *E. gunnii* may extend with *E. coccifera* onto extremely exposed sites as a mallee or stunted single stemmed tree (Fig. 4). The disjunct populations of *E. gunnii* occurring south of the Central Plateau are at relatively low altitudes (600-850m) and are usually confined to button-grass plains (e.g. SP, BD). In the majority of these populations *E. gunnii* rarely exceeds 4-5m in height and often exhibits a mallee habit. However, in contrast to high altitude populations (e.g. Fig. 4) this habit appears to be maintained as a result of the high fire frequency associated with the sedge community (see Jackson 1968). *E. gunnii* extends westward as a series of small disjunct populations through the upper Mersey Valley (LM, LB, TH, LC, OP) and Cradle Mt. (MS, PP) region to the basalt plains near Guilford (SV). In the latter area, the distribution is patchy and small stands of *E. gunnii* (15-25m) occur at relatively low altitude (660m) and follow stream or rainforest margins, or occur in the open woodland habitat with such species as *E. delegatensis* and *E. rodwayi*.



← Figure 3 - Tall forest form
of *E. gunnii* (site PF).

Figure 4 - High altitude, mallee form
of *E. gunnii* (site LH).



Populations classified as *E. archeri* usually occur on talus slopes at or above the upper altitudinal limit of the sub-alpine *E. delegatensis* / *E. dalympleana* forest (Fig. 6). Moreover, in the north-eastern mountains (BL, MB, BN, MM), *E. archeri* forms the tree-line species due to the absence of *E. coccifera*, the normal tree-line species on similar dolerite-capped mountains in the rest of the island. In contrast, *E. gunnii* is frequently found at the inverted tree-line in other areas. *E. archeri* is confined to high rainfall areas (>1200mm / year) and may extend into sub-alpine mixed forest with temperate rainforest species (e.g. *Nothofagus cunninghamii*). While *E. archeri* is usually a mallee or a small tree (Fig. 5), examples of relatively tall (20-30m), overmature *E. archeri* protruding above a dense rainforest canopy can be found (e.g. P1).



Figure 5 - Tree-line habitat of *E. archeri* on Ben Lomond (site BL).

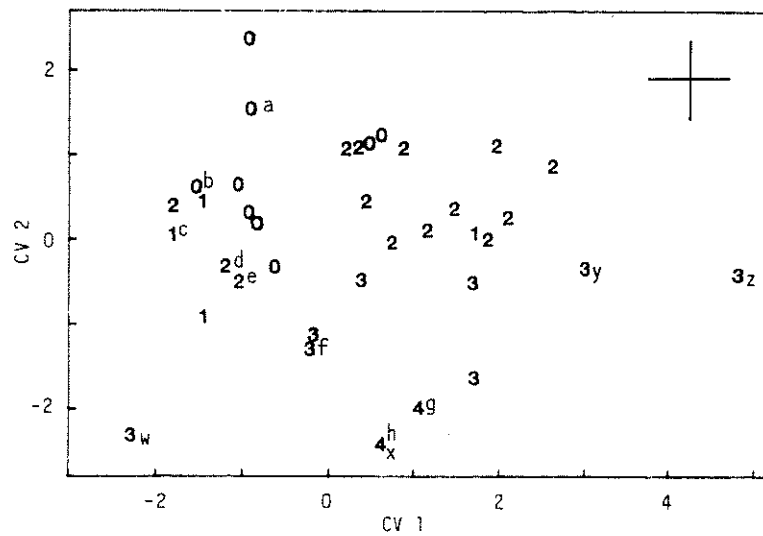


Figure 6 - Variation in glaucousness in relation to the main directions of morphometric differentiation. CV1 (40 %) and CV2 (17 %) are derived from canonical variates analysis of the 15 morphometric characters given in Table 2. Population glaucousness values correspond to the average glaucousness score rounded to the nearest integer (0 = green, 4 = highly glaucous). Populations sampled along a geographical transect over the Western Tiers (a to h, Table 1) and along an exposure gradient on the Central Plateau (w to z, Table 1) are indicated. The 95 % confidence limits are based on $n = 20$.

POPULATION	PHENETIC GRID REFERENCE					% GLAUC=0/1	
	CODE	CLASS	E/W	N/S	ALTITUDE (m)	N	
a Projection Bluff low	P1	1	476	5883	980	20	100
b Projection Bluff high	P2	1	477	5381	1100	20	100
c Pine Lake 1	P3	2	476	5378	1150	20	75
d Pine Lake 2	P4	2	477	5377	1140	20	40
e Mickey's Creek	P5	2	476	5375	1150	20	20
f Breona	Br	3	475	5374	1040	20	0
g South Brandum	SB	3	474	5368	1040	20	0
xh Shannon Lagoon	SL	3	480	5351	1050	20	0
w Liawenee	LN	3	468	5361	1150	20	0
z Scrummies Marsh	A1	4	504	5335	930	20	0
y Jimmy's Marsh	AH	3	504	5340	1010	10	0
Pensford	PF	4	484	5349	960	20	0
Middlesex Plains	MS	5	416	5400	760	8	12
Pencil Pine Creek	PP	5	411	5400	870	6	0
St. Valentines Peak	SV	5	396	5417	660	10	60
Mole Creek	MC	1	446	5391	1140	10	100
Mt. Rufus	RF	4	428	5334	1050	6	0
Broad River	BD	4	466	5278	830	9	0
Trapper's Hut	TH	5	438	5373	1130	10	0
Lake Ball	LB	5	442	5370	1150	9	0
Lake Charles	LC	5	437	5363	1070	10	0
Lake Myrtle	LM	5	434	5364	1030	10	0
Pelion Plains	OP	5	420	5369	960	10	0
Liffey River	LR	2	477	5380	980	10	60
Mt. Roland	MR	1	440	5410	1120	20	100
Ben Lomond	BL	1	553	5404	1230	20	100
Mt. Barrow	MB	1	534	5417	1200	20	100
Ben Nevis	BN	1	553	5417	1140	20	100
Mt. Maurice	MM	1	549	5426	1000	20	100
Mt. Saddleback	SD	1	563	5417	1180	18	100
Mt. Victoria	MV	5	569	5423	790	20	30
Snow Hill	SH	4	569	5359	950	26	19
Snug Plains	SP	4	513	5233	600	16	6
Repulse River	RR	5	461	5289	760	6	0
Poatina Highway	PH	2	488	5371	1080	6	50
Poatina Inlet	PN	3	486	5368	1040	6	0
NE Plateau	NE	2	485	5372	1120	15	0

TABLE 1 Population codes, phenetic class, grid reference, altitude, number per sample and percentage of green or subglaucous individuals (GLAUC=0/1). Grid references (1 unit = 1 km) are based on the 1: 100,000 TASMAP series (Lands Dept., Hobart). Population series a to h and w to z correspond to samples along a geographical transect over the Western Tiers and along an exposure gradient on the Central Plateau respectively (see Figs 1 and 6). The phenetic classes correspond to '*E. archeri*' (1), 'Pine Lake intermediates' (2), '*E. divaricata*' (3), 'southern *E. gunnii*' (4) and 'NW *E. gunnii*' (5) (see Fig. 7).

3 - PHENETIC VARIATION

The present paper summarises the patterns of phenetic variation in the *E. gunnii*-*archeri* complex and examines the phenetic relationship of the two taxa in an area of parapatry. These results are based on a population survey involving 37 populations and samples of over 550 mature trees (see Fig. 1; Table 1). The set of 16 characters scored (Table 2) included the majority of characters emphasised in the literature as defining or discriminating *E. gunnii* from *E. archeri*.

-
1. Lamina length
 2. Lamina width
 3. Length to the widest point of the lamina
 4. Petiole length
 5. Lamina thickness
 6. Lamina curvature
 7. Peduncle length
 8. Capsule length
 9. Pedicel length
 10. Capsule rim width
 11. Maximum capsule width
 12. Distance from the capsule rim to the point of the maximum width
 13. Disk level
 14. Valve size
 15. Valve position relative to the capsule rim
 16. Degree of glaucousness
-

TABLE 2 Characters scored from adult samples.

The degree of waxy glaucousness on the adult and juvenile foliage is one of the main characters used to differentiate the two taxa and in this respect their relationship bears similarities to that between the green and glaucous variants of *E. urnigera* (e.g. Barber and Jackson 1957; Thomas and Barber 1974). Barber (1955) treats this difference in glaucousness as an adaptive clinally varying character of both adult and juvenile *E. gunnii*. The maximum development of glaucousness on the adult foliage occurs in open woodland populations skirting 'frost-hollows' on the Central Plateau (e.g. SL, SB) and declines radially at varying rates from this area. Most northern populations including those recorded as *E. archeri* in the literature (e.g. P1, P2, BL, MB) are dominated by trees with green or at most subglaucous adult foliage. However, populations exhibiting extreme levels of glaucousness are more or less continuous on the Central Plateau and are clinally linked through a series of geographically intermediate populations (P1 to SL; Table 1). Ordination studies clearly indicate marked morphological differentiation between the green and the more glaucous populations (e.g. Fig. 6). Nevertheless, when the full geographic range of the complex is considered these populations appear as extremes of a morphological continuum and encompasses a broad array of morphologically differentiated populations.

Phenetic variation in the *E. gunnii*-*archeri* complex is summarised by classification of populations into five main phenetic groups which can be conceived as broad reference points in a multidimensional continuum (Fig. 7). The geographical distribution of these five clusters is indicated in Fig. 8 and there is clearly reasonable congruence between geographic location and phenotype. This is indicative of a significant correlation ($P < 0.001$) between

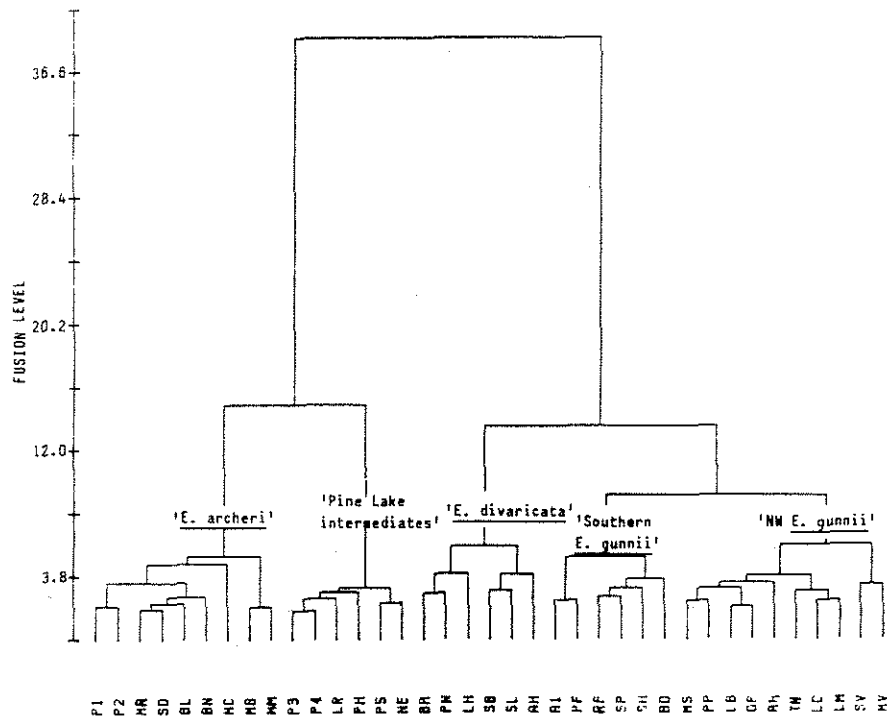


Figure 7 - Dendrogram from Ward's minimum variance clustering of populations based on the 16 characters indicated in table 2.

geographic and phenetic distance (Mahalanobis'D) throughout the complex which, at least partly, reflects a similarity of habitat with geographic proximity. The main phenetic clusters exhibit predominantly northern ('*E. archeri*', 1; 'Pine Lake intermediates', 2), central ('*E. divaricata*', 3), southern ('southern *E. gunnii*', 4) and north-western ('NW *E. gunnii*', 5) distribution patterns. Furthermore, there is close agreement between clusters and the perception of the taxa in the literature. One of the northern clusters (1) corresponds to *E. archeri*, the central cluster (3) to *E. divaricata* and the southern (4) and north-western (5) clusters together appear to encompass Bretts' (1938) conception of *E. gunnii*. These phenetic clusters are genetically differentiated although continuity is apparent for both adult and seedling character sets.

In part, population differentiation appears to result from the interaction of multicharacter clines paralleling at least two major habitat gradients. These relate to a complex set of factors associated with variation in firstly, exposure to the alpine environment (e.g. LH, SL, PF, AI; Figs 1,2,3, 4) and secondly, a transition in the sub-alpine region from the open woodland to the mixed eucalypt / rainforest habitat (e.g. P1 to SL; Fig. 1). The '*E. divaricata*' and 'southern *E. gunnii*' populations are clinally differentiated with respect to the former gradient and the '*E. divaricata*' and '*E. archeri*' populations with respect to the latter gradient. Major differentiation occurs within the more or less continuous stands on the Central Plateau (Fig. 7)

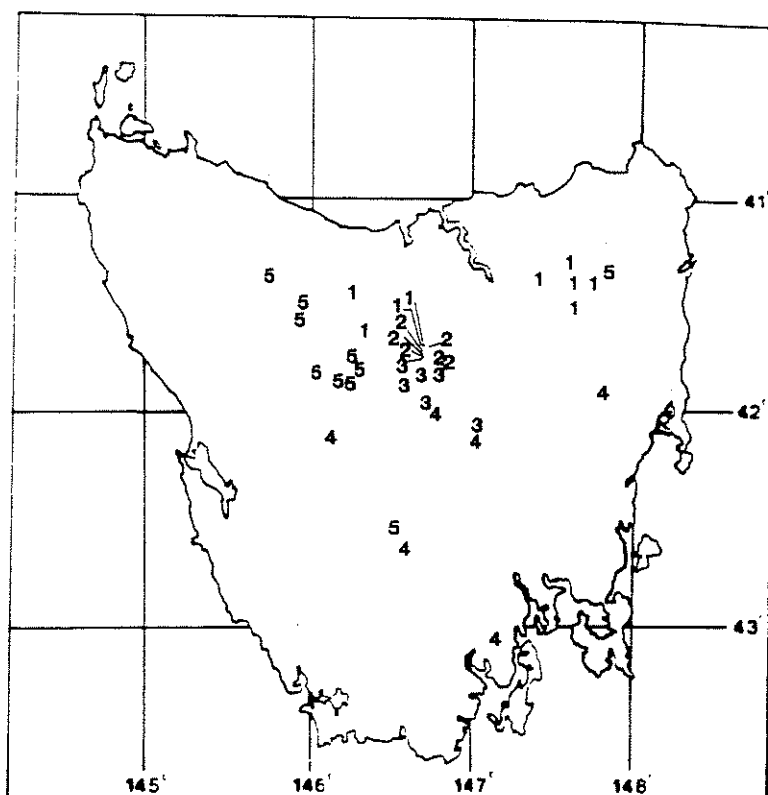


Figure 8 - Geographical distribution of the clusters defined at the five group level by the Ward's minimum variance classification shown in Fig. 7. Populations are grouped into phenetic classes corresponding to '*E. archeri*' (1), 'Pine Lake intermediates' (2), '*E. divaricata*' (3), 'southern *E. gunnii*' (4) and 'NW *E. gunnii*' (5).

and in this area '*E. divaricata*' and '*E. archeri*' morphs are clinally linked through the 'Pine Lake intermediate' populations. On morphological criteria alone, these intermediate populations have closer affinities to the local '*E. archeri*' populations (P1 and P2) than populations from any other cluster and are best considered as glaucous forms of *E. archeri*. Furthermore, these populations flower more or less concurrently with the local *E. archeri* and differ in mean flowering time from the '*E. divaricata*' populations by nearly three months. This difference would act as a major barrier to gene flow along this continuum and appears to be partly a result of the steep topographic transition between erosion surfaces (i.e. between sites P5 and Br).

4 - DISCUSSION

Reciprocal transplant trials on the Central Plateau indicate that variation in the more or less continuous stands is at least partly maintained by spatially varying selective forces. Nevertheless, it is suggested that the '*E. archeri*' and '*E. divaricata*' morphs on the Central Plateau have different-

iated in allopatry. The occurrence of relatively low altitude disjunctions in the north and south of the geographical range (e.g. MV, SP, SV; Fig. 1) provide circumstantial evidence for northern and southern distributions during the last glacial. The '*E. archeri*' and north-western populations are probably derived from a northern glacial distribution whereas the 'southern *E. gunnii*' populations are possibly the remnants of a distribution in a south-eastern glacial refugia and from which the '*E. divaricata*' populations originated. The high altitude sites on the Western Tiers currently occupied by intermediate populations (P3, P4, P5) would be amongst the last areas to have become available to arboreal taxa following deglaciation. It is suggested that the continuum between the '*E. divaricata*' and '*E. archeri*' morphs in this area is a result of secondary contact between northern and southern populations following a retreating glacial tree-line. Nevertheless, all morphs appear to be extensions of the same gene pool and the inclusion of *E. archeri* as a subspecies of *E. gunnii* by Pryor and Johnson (1971) is consistent with their treatment of other variable species (e.g. *E. pauciflora*, *E. verrucosa* and *E. globulus*). While emphasising the clinal nature of the variation between morphs, it is suggested that a more equitable and comprehensive partition of the variation in the complex could be achieved by recognition of the five phenetic clusters indicated in Fig. 7 as subspecies or varieties of *E. gunnii*.

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