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MORPHOLOGICAL VARIATION IN *EUCALYPTUS* L'Herit., SERIES : *DUMOSAE*

by

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ABSTRACT

Series Dumosae comprised the following 15 species from southern and western Australia prior to this study: Eucalyptus anceps, E. calcareana, E. clelandii, E. conglobata, E. cyanophylla, E. dongarraensis, E. dumosa, E. fraseri, E. georgei, E. kondininensis, E. lesouefii, E. pileata, E. sheathiana, E. striaticalyx, E. woodwardii. The series is noted for its high morphological variability with intergradation between many taxa often making identifications difficult. A survey of morphological characters revealed a lack of discrete differences in seed morphology, wood anatomy, leaf anatomy and leaf architecture, and indicated that differences between taxa result mainly from continuous variation in form rather than presence or absence of characters. Leaf surface texture and colour were examined by measuring height of cuticular sculpturing with epiflourescence microscopy and the contribution of glaucousness to leaf reflectance with a spectrophotometer.

A preliminary study was made on sessile-fruited forms using 202 specimens scored for six characters. A Canonical Variates Analysis (CVA) based on geographical groupings of South Australian specimens resulted in a new interpretation of E. conglobata and E. anceps as generally distinct entities in this state, both morphologically and geographically. However, classification of Western Australian specimens by the same CVA revealed much intergradation indicating that their current taxonomic status is unacceptable.

A set of 27 characters, mainly continuous metrics describing fruit, leaf and bud morphology, was chosen for analysis of all taxa and scored for 499 individuals. Two main numerical methods were used to objectively describe and analyse variation. Intergradation between groups was studied using CVA, and multivariate distance relationships between groups were determined using a multistate distance metric and Discriminant-distances between group centroids derived from CVA.

Existing taxa (including the undescribed "E. pterocarpa") were represented by 16 groups of 4 to 11 individuals collected from as near as possible to the type localities. Classification of unassigned individuals by CVA demonstrated much intergradation between taxa and geographical interspersion contrary to accepted distributional limits. Problems with existing species concepts were highlighted in a separate analysis on a subset of specimens derived from the South-eastern Region of South Australia. This CVA detected four species with strong intergradation within a single population.

In other analyses potential new taxonomic groups were tested. The recognition of several geographical groupings of South Australian large-fruited forms with affinities to E. cyanophylla was not supported. Distance relationships were examined between 31 populations of four or more individuals and most were found to be more distinctive than the most similar pair of groups representing existing species (E. calcareana and E. pileata). The five most distinctive groups were included with the 16 groups representing typical forms of existing species for further investigation of gradation and geographical relationships using CVA. A taxonomic system was derived on the basis of multivariate distance relationships, intergradation, and relative contributions of characters to group discrimination which is of practical importance for identification

by keys. Disparities between these three factors necessitated a subjective approach in deriving a new taxonomy from the evidence documented. Variation for each of the existing taxa is discussed in relation to evidence from the numerical analyses.A proposed taxonomic revision of the Dumosae is presented with a key to all taxa. Five taxa without substantial intergradation using the complete character set are recognized at the specific level. These are E. dumosa, E. kondininensis, E. lesouefii, E. woodwardii and a new taxon E. pterocarpa. Within E. dumosa five subspecies are recognized: ssp. dumosa, ssp. clelandii, ssp. conglobata, ssp. fraseri and ssp. georgei.

Cross-pollination trials, cases involving barriers to gene exchange within Dumosae, and evidence of inter-series and inter-section hybrids are described. The possible evolutionary and biogeographical development of series Dumosae is discussed. There is evidence that the widespread and taxonomically difficult E. dumosa complex arose from ancestors of the more distinctive tree forms in Western Australia, and underwent adaptive radiation and eastward migration relatively recently in conjunction with the development of sand dune systems in the mid-Pleistocene.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University. To the best of my knowledge and belief this thesis contains no material previously published or written by another person except where due reference is made in the text.

Peter J. Lang.

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CHAPTER 1

INTRODUCTION

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1.1 Purpose of study

The aims of this study are to describe and document the variation in series Dumosae of Eucalyptus and produce a more workable classification of the group. The name Dumosae is applied in this work in the sense of Pryor and Johnson (1971). Prior to this study sixteen species, one of which is undescribed, have been generally accepted. They are mallees or small trees with a wide distribution in southern Australia mainly, between the 200 and 500 mm rainfall isohyets. There is a decline in species diversity from west to east.

The Series was selected for study because it is noted for its complexity of variation and problems in identifying many taxa. Fortunately it is an apparently natural group that is clearly defined on the basis of seed characters. Its members are closely related and consequently the homology of attributes is not difficult to establish. On the other hand, the close relationship means that phylogenetic patterns are unclear and the presence of interbreeding makes phylogeny inherently complex and reticulate (Johnson,1968, p. 37). Thus the emphasis in this study is on phenetic relationships, which are amenable to analysis by numerical methods.

Problems in classifying the Dumosae were acknowledged by Burbidge (1947, p. 51) who described the difficulty in separating South Australian species. Burbidge noted intergradation between forms and the existence of relationships in several directions. She concluded : " An effort to reduce some of the forms to varieties proved unsatisfactory and they were retained as species to avoid adding to the existing confusion ". The

confusion is such that in the ecological and biogeographical studies of Parsons and Rowan (1968) and Parsons (1970) it was necessary to treat the E. dumosa complex as a single entity despite the possibility that three or four different species were involved. These authors pointed to the need for a taxonomic revision to overcome this limitation.

Although the Dumosae constitute only a small fraction of the large genus Eucalyptus (currently with about 500 recognized species (Pryor and Johnson, 1981)), it is clear that similar patterns of variation occur in other groups. Notable examples are the Grey Box complex studied by Gillison (1976) and the mallee complexes represented by the Series Torquatae and Oleosae which have not been subjected to critical analyses but appear to have many variation patterns that parallel those in the Dumosae. The results of this study are likely to have wider implications on species concepts within Eucalyptus.

1.2 Overview of approach taken in study

Numerical methods were employed as a taxonomic tool because there was no clear basis for any subjective definition of a priori groups. The limits of existing taxa were uncertain, their relationships multidimensional, and many specimens were difficult to assign - having affinities with several taxa. Evidence could easily be found for a number of different classification systems. It would be necessary to show the derivation of taxonomic groups from all the evidence, rather than proposing groups and testing them. To maximize nomenclatural stability, existing taxonomic concepts were reduced to the barest essential of a 'type population' and retained as reference points from which a new classification was built. The type populations were made up of individuals collected from as near as possible to the type localities.

Initially the study was planned as a revision of South Australian Dumosae species. The complex of sessile-fruited forms involving E. conglobata and E. anceps * was chosen as a starting point because it was an obvious case of intergradation that appeared to be relatively simple and involved a limited set of characters (chapter 3). Investigation of Western Australian occurrences of these forms revealed a different variation pattern to that in South Australia. Thus it was clear that the project needed to be expanded to cover the whole of the Dumosae. This meant the inclusion of a further seven existing taxa endemic to Western Australia, but fortunuately these are generally more distinct than those occurring in South Australia and required less sampling.

Before selecting a character set, investigations were made into aspects such as high-order leaf venation, chromatography of leaf extracts, wood anatomy, seed morphology, and leaf cuticular and epidermal features (chapter 2). Little useful taxonomic information was found in these areas and such characters were avoided because of the time and inconvenience involved. Numerical analyses were based on the classical characters of general morphology of leaves, fruits and buds. The resultant classification can not be expected to maximize phylogenetic 'naturalness' which is of doubtful value in such a small and closely related group.

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* Unless otherwise specified, the name Eucalyptus anceps is used throughout this thesis in its previously accepted but incorrect sense to refer to a part of the taxon E. dumosa ssp. conglobata. No alternative name has been proposed for it, since the final conclusion reached in this thesis is that it should not be regarded as a distinct taxon. Following its lectotypification (12.5.3, p. 302), E. anceps in the strict sense is actually a synonym of E. rugosa. (See chapter 13 for a detailed discussion.)

However, it is likely to facilitate phenetic interpretation, including field identification.

The approach used in the numerical analyses was to investigate relationships between small geographical groupings of specimens loosely referred to as 'populations'. This was done using the techniques of Canonical Variates Analysis (CVA) and a multistate distance measure, both of which take account of within-group variability. By comparing phenetic distances of type populations with other populations, significant centres of variation were identified for consideration as potential new taxa. The final decision on the taxa recognized was based not only on distance values but also on the degree of intergradation between groups and their ease of recognition using key characters.

1.3 Taxonomic history of the series Dumosae

Series Dumosae was originally understood in a much broader sense than that of Pryor and Johnson (1971). When first described by Blakely (1934) in his "Key to the Eucalypts" it incorporated 39 species. Blakely's classification of Eucalyptus at the level of sections and subsections was based entirely on stamen characters. He placed the Dumosae as the only series in subsection Subtruncatae of section Macrantherae. A single series was recognized because of the broad similarity in habit, bark type, juvenile leaves, mature leaves and general morphology of reproductive organs. These similarities are rather superficial and many species are now placed in other groups.

Carr and Carr (1969) proposed an informal group "Dumosae" comprising most of the species in Blakely's series Dumosae together with some members from his series: Anisomelae, Quadricostatae, Tetrapterae, Obliquae and Exsertae. The species were united by their entire, reniform or broad, emarginate cotyledons rather than bisected ones. Within the "Dumosae" four groups were recognized on the basis of testa characters, and three of these were found to be consistent for the presence of oil glands in the pith.

This work was followed up by Brooker (1971) who recommended modification of Blakely's Dumosae by the exclusion of seven species and the inclusion of eight from other series . Brooker gave more detailed descriptions for each of the four seed groups and described the distinctive features of anther shape and inflexion of stamens in bud which are common to all the groups.

In Pryor and Johnson's (1971) informal classification, the four seed groups were elevated to the the rank of series with the name Dumosae retained for the the group containing E. dumosa. With this narrower concept, the Dumosae corresponds to series Rufispermae of Maiden (1925 7(64), p. 152) which was based on the single species, E. woodwardii. The Dumosae and the other three series named Torquatae, Incrassatae and Dundasinae were grouped into Section Dumaria which corresponds to the previous concept of the Dumosae. The four series were described by Brooker (1979) together with a new one, the Merrickianae, split off from the Torquatae. An extended description of diagnostic seed characters and an account of other morphological characters is provided for the Dumosae in chapter 12 (12.2.1).

The recognition of the seed groups has enabled clarification of many taxonomic problems and improved the reliability of species identification.

The progress that has been made in clarifying variation is evident after considering Maiden's early concepts. Maiden (1904, 1(4), p.97) cited Luehman on E. incrassata: "E. dumosa seems to pass into it by almost imperceptible degrees". Maiden then concluded: "There is, in fact, an absolute series between E. incrassata and var. dumosa". The distinctness of these species is now beyond dispute and they can be separated readily, even without examination of seeds, by leaf texture and thickness. Burbidge interpreted some variation as resulting from gradation between Dumosae and Torquatae or Incrassatae which she regarded as part of a single complex. In the studies of Parsons and Rowan (1968) and Parsons (1970) mentioned earlier, members of Torquatae were included as part of the E. dumosa complex. I encountered many specimens in herbaria that had been incorrectly determined due to failure in distinguishing between series Dumosae and Torquatae - despite the presence of seeds in many cases. Confusion between some representatives of these series has persisted and promoted the view that these series intergrade. However, when the definition of taxa is constrained by seed characters to correspond to these series, there is no large scale intergradation between taxa of different series although occasional hybrids are known (14.4.1). This has allieviated much confusion, but major problems still lie within Dumosae s.str.

1.4 History of taxa belonging in series Dumosae

Eucalyptus dumosa was the first species decribed. It was described by Schauer in 1843 using the manuscript name applied by Alan Cunningham in 1817 to material he collected in central New South Wales on Oxley's expedition. The name presumably refers to the mallee habit and is derived from the Latin 'dumosus' meaning bushy. Bentham (1867) recognized several

varieties of E. dumosa including var. conglobata based on collections that Robert Brown had made on the South Coast voyage of Flinders in 1802-1803 and named "E. conglobata".

Maiden (1904, 1(4), p.97) transferred E. dumosa to E. incrassata but retained the two varieties dumosa and conglobata. This treatment had been implied earlier by Mueller (1879-1884) who described E. dumosa as representing the small-flowered state of E. incrassata. Maiden was aware of considerable variation in the Dumosae but considered it to be of low taxonomic significance. Descriptions and illustrations of forms and varieties included by Maiden under E. incrassata indicate that he had a very broad concept of this species. Represented in it are : Dumosae (E. dumosa ssp. dumosa , E. dumosa ssp. conglobata ; Torquatae (E. rugosa, E. concinna and E. griffithsii) ; Incrassatae (E. incrassata ssp. incrassata, E. incrassata ssp. angulosa) and possibly Merrickianae (E. merrickiae). Thus, Maiden's concept of a single species embraced much of what is now regarded as section Dumaria. In addition Maiden included E. goniatha and E. grossa which are now placed in section Bisectaria.

The next species recognized was E. striaticalyx, described by W. V. Fitzgerald (1904). Between 1910 and 1915 Maiden described E. woodwardii, E. lesouefii, E. clelandii and E. sheathiana, all from Western Australia. In 1922 Maiden reinstated E. dumosa as a species, raised var. conglobata to specific rank and described E. conglobata var. anceps based on "E. anceps" of Brown. Two more Western Australian species, E. dongarraensis and E. kondininensis, were described by Maiden and Blakely in 1925. Blakely's Key published in 1934 included two new species : E. anceps based on E. conglobata var. anceps of Maiden ; and E. pileata a new taxon from Western Australia. (For a history of the taxonomic interpretation of E. pileata, see section 11.3.5.)

No new taxa were described in the Dumosae for the next 38 years. In their "Classification of the Eucalypts", Pryor and Johnson (1971) made special provision for three undescribed species of which they were aware. They also proposed that E. pileata be made a subspecies of E. dumosa and E. anceps a subspecies of E. conglobata. No changes were made formally in this work and the classification from the level of superspecies to subgenus was explicitly divorced from the International Code. The authors reluctantly anticipated formalizing changes involving subspecies in a future publication. Eucalyptus anceps and E. pileata have been treated as species in subsequent works (Chippendale, 1973 ; Boomsma, 1981).

In 1972 Brooker described E. conglobata ssp. fraseri using the subspecies rank to give it taxonomic status equal to both "conglobata" and "anceps" in Pryor and Johnson's scheme. Later, he elevated it to E. fraseri and indicated its correspondence with the undescribed form designated SLE:J by Pryor and Johnson (Brooker,1976). The other two unnamed taxa, designated as SLE:L and SLE:O, are still undescribed and probably correspond to "E. redimiculiphloia" and "E. pterocarpa" respectively. The latter has been widely regarded as a species and received an informal treatment in a popular publication (Wallace, s.dat.).

Three more Dumosae species were described while this thesis was being researched. Eucalyptus cyanophylla (Brooker, 1977) and E. calcareana (Boomsma, 1979) were both described from South Australian forms previously included in E. dumosa or E. pileata. A more distinctive taxon, E. georgei was described from a remote area of Western Australia by Brooker and Blaxell (1978). Currently (Pryor and Johnson,1971 ; Boland et al, 1980) there are 15 taxa described within Series Dumosae.

1.5 Materials and methods

Details of materials and methods used for specific techniques are described in the text where relevant. Chapter 5 is devoted to a discussion of numerical methods of analysis. The work is based largely on herbarium specimens. These were derived mainly from my own collections made on field trips and supplemented by material made available by other workers (see acknowledgements) and by existing herbarium collections. In making collections I tried to avoid any bias toward localities with intermediate forms or a higher than usual degree of variability. However, differential sampling was practised within populations, so that more uniform populations were sampled by a single individual and more variable ones represented by four to six individuals.

All material of series Dumosae present at AD and ADW, and selected material from FRI, PERTH, MEL and NSW, was examined. Within the Dumosae there is a general decline in diversity of forms from west to east. Material from Victoria and New South Wales has been usually referred to only three species of the sixteen * : E. dumosa, E. cyanophylla and E. anceps. Variation in these two eastern States was not studied in detail because abundant evidence of gradation was known to occur in South Australia. A total of 499 individuals representing 248 localities were sampled for analysis. Brief locality data are given for these in appendix 1.

The abbreviations of herbaria used here are those given in Holmgren and Keuken (1974), except for "WF" and "ES" which designate the herbarium of the South Australian Woods and Forests Department and the herbarium of the Ecological Survey Unit of the South Australian Department of Environment

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* "E. pterocarpa" is regarded as the sixteenth 'accepted' species.

and Planning. Where no abbreviation is associated with specimens cited in the text or appendices, the material is present at the State Herbarium of South Australia (AD). Private collections have been lodged at AD and duplicates when available will be distributed to FRI and PERTH.

Throughout this work reference is made to "Regions" of South Australia and "Districts" (Beard, 1981) of Western Australia. These geographical subdivisions were chosen because they are adopted by the respective state herbaria. They are illustrated in figures 1 and 2 .

REGIONS OF SOUTH AUSTRALIA ADOPTED BY THE STATE HERBARIUM — ADELAIDE

1. North-western
2. Lake Eyre Basin
3. Nullarbor
4. Gairdner-Torrens Basin
5. Flinders Ranges
6. Eastern
7. Eyre Peninsula
8. Northern Lofty
9. Murray
10. Yorke Peninsula
11. Southern Lofty
12. Kangaroo Island
13. South-eastern

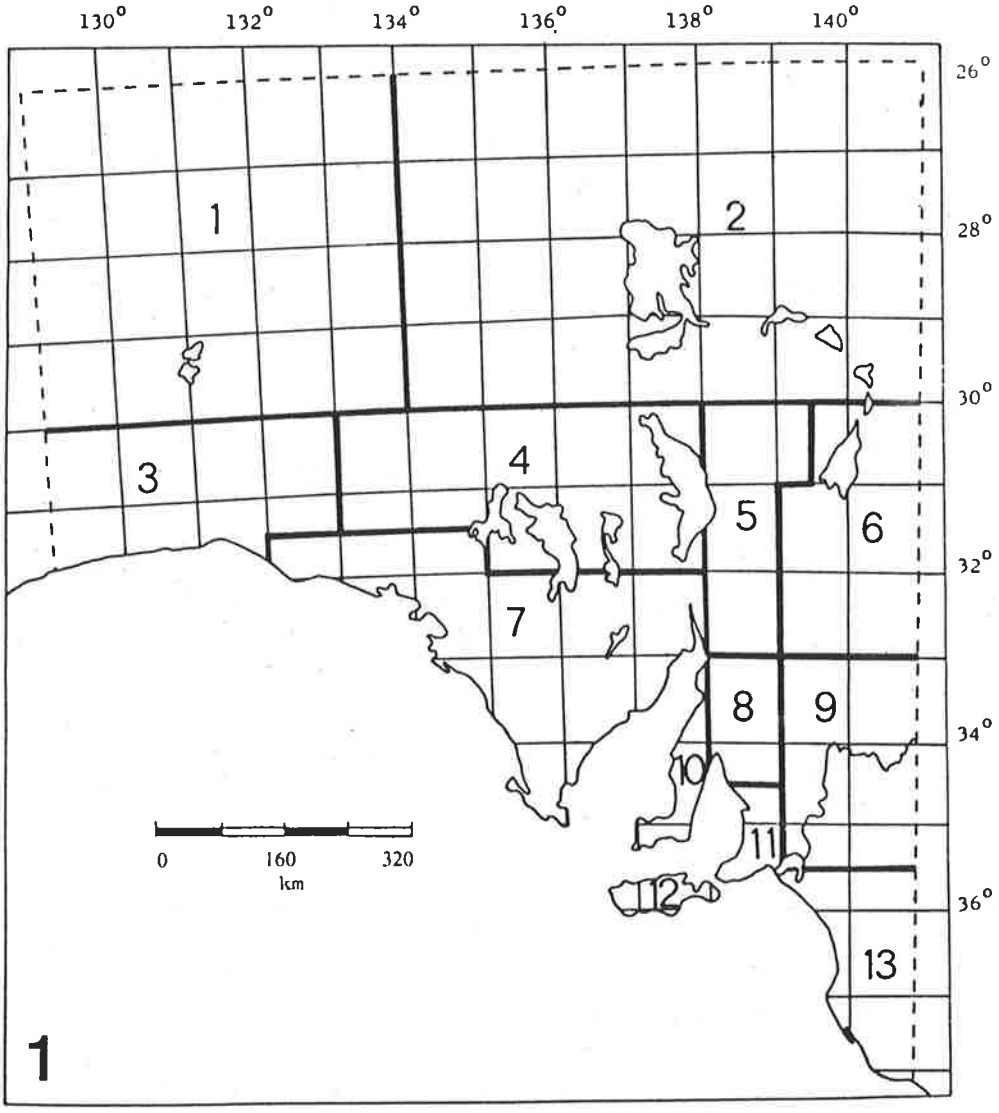


Figure 1: South Australian 'Regions'.

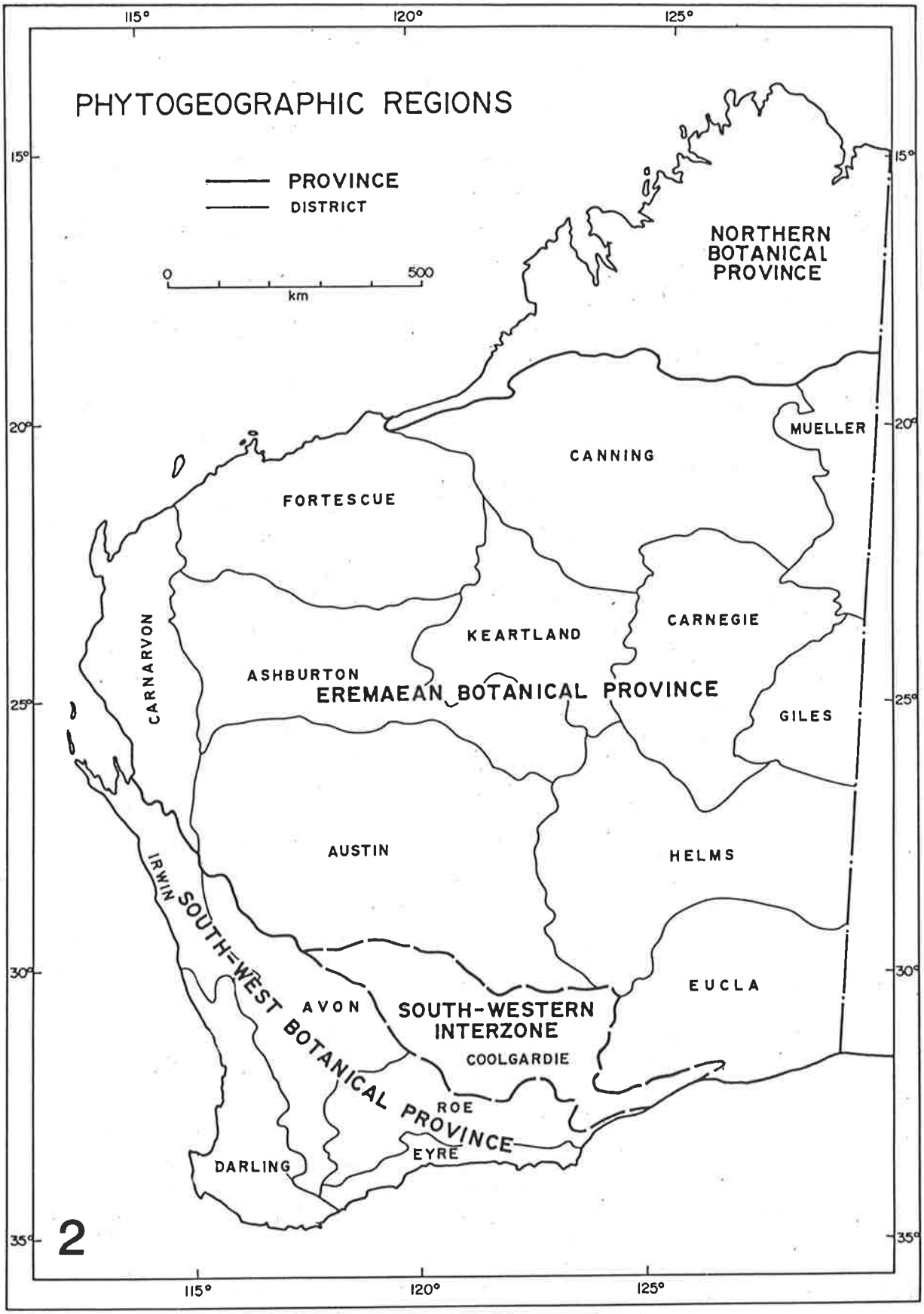


Figure 2: Western Australian 'Districts' of Beard (1981).

CHAPTER 2

VARIATION IN DUMOSAE: PRELIMINARY STUDIES

In this chapter a variety of investigations made to test for useful taxonomic information are described. These studies confirm the coherency of series: Dumosae. Seed morphology is considered first, as it forms the basis for recognition of Dumosae and the other four series in section Dumaria.

2.1 Seed morphology

Seeds were retained with all collections made for this study, to vouch for their identity at series level and to provide a potential source of taxonomic characters within Dumosae. Examination of representatives of the five series in section Dumaria confirmed the reliability of diagnostic seed characters. The descriptions provided for each series by Brooker (1979) were further elaborated in the light of these observations (12.2.2). Seeds of each series are well illustrated by Brooker (p. 186) and photographs of Torquatae seeds are included in this thesis in figures 229, 232, chapter 14. Minor variation was observed within Dumosae. Seeds vary in size, colour, height and size of reticulate sculpturing, and the extent to which surfaces are flat or irregularly facetted. Seed size has an obvious positive correlation with fruit size but no taxonomically significant patterns were apparent in the other attributes. Representative Dumosae seeds are illustrated in figures 3 to 5. (Further examples are provided by figures 227, 230 and 233). Quantitative analysis of minor differences in seed characters did not seem warranted. In a few cases atypical seeds were found but these were always associated with other morphological evidence for hybridization with an individual outside of the Series.

Figures 3 to 5: Representative Dumosae seeds.

(E. dumosa ssp. dumosa)

Scale bar: 2 mm

Right-hand seed of each figure is in ventral view; the others are shown in dorsal view.

3: R. Grandison 5.i.1980 C/8.2 km W Ungarie (NSW) (DUM)

4: PJL 1044/Carappee Hill (Eyre Peninsula) (CAR)

5: T.E. Dennis 191/136 km N Cook (North-western) (PCVH)



3



4



5

2.2 Wood anatomy

A preliminary survey of South Australian material was made to ascertain whether there was any geographic variation in wood anatomy that could be taxonomically useful. The following specimens representing four extremes of the E. dumosa complex and a member of series Torquatae (E. rugosa) were chosen for study:

1. PJL 757, Waitpinga (Southern Lofty Region)
2. PJL 1114, Spalding Cove (Eyre Peninsula Region)
3. PJL 1011, 18 km SW Yantanabie (Eyre Peninsula Region)
4. PJL 876, 26 km E Waikerie (Murray Region)
5. E. rugosa, PJL 664, Mt Thisbe (Kangaroo Is. Region).

Sections of stem 5-10 mm in diameter were softened by soaking in a 1:1 glycerine/alcohol mixture and sectioned by sledge microtome. Transverse sections were prone to splitting and could only be prepared at 40-60 µm thick compared to 10-15 µm for tangential and radial longitudinal sections. Sections were treated with "Eau de Javelle" to extract cellular contents, carbonized , and mounted in "xam" following the techniques used by Greguss (1955, p.10-11) and modified by M.D. Peters (pers. comm.)*.

No discrete differences in wood structure were found between these specimens and the only obvious difference between individuals was in the diameter of vessels and tracheids. The lack of distinctive features even in the representative of Torquatae, suggests that wood anatomy would be of no greater use for Dumosae taxa in Western Australia. As preparation of material was time consuming, further investigation of wood anatomy was abandoned in favour of more profitable characters.

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2.3 Leaf surface properties

2.3.1 Introduction

Leaf surfaces in series Dumosae vary widely in texture and colour. Workers have often given these characters a high weight for classifying and identifying taxa in the group. In the key to South Australian species of section Dumaria by Brooker (1977), *E. dumosa* and *E. cyanophylla* are separated from *E. anceps* and *E. pileata* by their green, more or less glossy leaves as opposed to the dull leaves of the latter. *Eucalyptus cyanophylla* and *E. dumosa* are then separated on the basis of bluish-grey leaves and grey-green leaves respectively. However, from an examination of South Australian material it appeared that these characters were are often unreliable. Obvious inconsistencies occurred in material from the Gawler and Flinders Ranges where forms with dull bluish-grey leaves occurred in the same populations as forms with dull green or even glossy green leaves. Much material from the Flinders Ranges has leaves that seem equally glaucous as those of *E. cyanophylla* although on other characters is most similar to *E. dumosa*. A major problem is the reliance on subjective assessments. The following studies were undertaken to enable more objective comparisons.

2.3.2 Cuticular relief

Differences in texture arise largely from variation in surface relief of cuticles. Low relief is associated with shiny leaves while sculptured cuticles result in leaves with a dull surface. Cuticular relief was studied using scanning electron micrographs of leaf surfaces taken on an ETEC Autoscan. Specimens were washed in chloroform to remove wax, mounted

on aluminium stubs with double-sided adhesive tape and coated with 80:20 gold/palladium in an evaporative coater. Micrographs were taken for 34 specimens representing series Incrassatae (E. incrassata, E. pimpiniana), Torqatae (E. rugosa, E. brachycalyx, E. concinna) and Dumosae (represented by 20 individuals from throughout South Australia).

Eucalyptus pimpiniana and E. incrassata were found to have very distinctive cuticles readily distinguishable from each other and all representatives of the other two series (figs 13, 14). The three members of Torquatae have surfaces that are almost entirely flat (fig. 12) or with only slight undulations. Except for E. torquata which has dull grey-green leaves, all species of Torquatae have shiny, non-glaucous, green leaves. Within Dumosae there is a wide range in degree of cuticular sculpturing from almost entirely flat to strongly undulate or papillate (figs 6 to 11). Light microscopy of isolated cuticles revealed that undulations or papillae correspond to either single underlying epidermal cells or groups of epidermal cells derived from the same mother cell. Cuticles of low relief are indistinguishable from those in Torquatae (figs 6, 12). The variation within Dumosae indicates that cuticular relief has potential taxonomic value. I found that it could be easily measured using epifluorescence microscopy of hand cut sections. This enabled its inclusion in the character set for numerical analysis.

2.3.3 Epicuticular waxes

The colour of leaves is affected by amount of epicuticular wax. Leaf colour may be green, grey-green, blue-green, blue-grey or almost white, depending on the density and nature of wax deposits. Dense wax deposits significantly alter microrelief of the cuticle and also result in a relatively dull surface.

Figures 6 to 14: Scanning electron micrographs of leaf surfaces.

Scale bar: 100 µm : figs 6 to 12
25 µm : fig. 13
100 µm : fig. 14

6: E. anceps *
(WF 212) Kingscote (Kangaroo Is)

7: E. dumosa **
(AD 97310217) Kondoolka HS, Gawler Rges (Eyre Peninsula)

8: E. dumosa
PJL 5/Pt Neil (Eyre Peninsula)

9: E. dumosa
(AD 97315259) Sliding Rock, Beltana (Flinders Ranges)

10: E. dumosa
(WF 277) Yankaninna Stn (Flinders Ranges)

11: E. striaticalyx **
(WF 1132) Victoria Desert (North-western)

12: E. rugosa
(WF 1297) American River (Kangaroo Is)

13: E. incrassata
(WF 492) Goolwa (Southern Lofty)

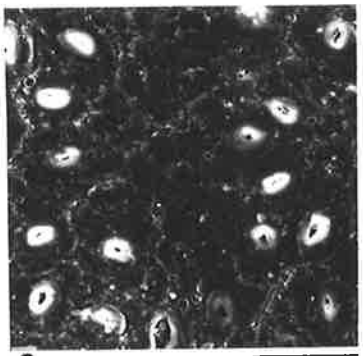
14: E. pimpiniana
(WF 965) Maralinga (Nullarbor)

* = E. dumosa ssp. conglobata
** = E. dumosa ssp. dumosa

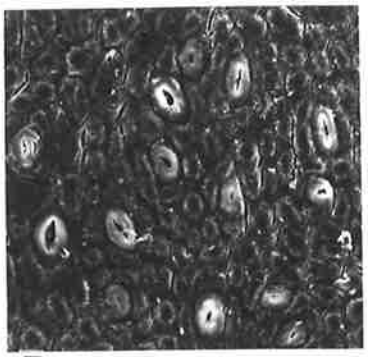
Figures 15, 16: Typical leaf venation pattern in Dumosae.

PJL 751 (E. dumosa ssp. conglobata)
Note secondary vein anastomoses and irregularity of tertiary veins.

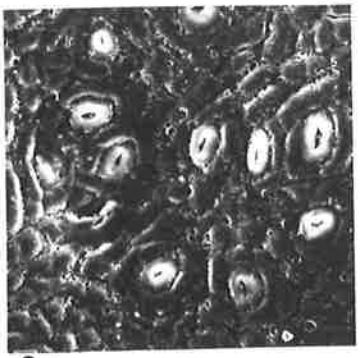
Scale bar: 5 mm : fig. 15
1 mm : fig. 16



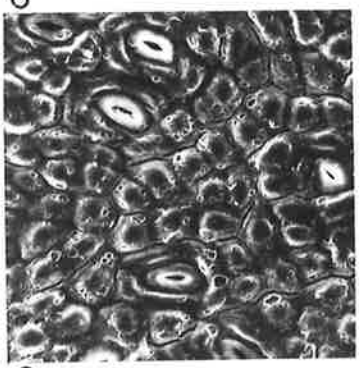
6



7



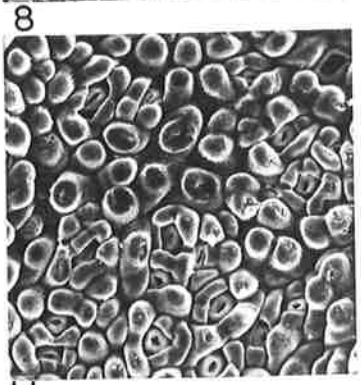
8



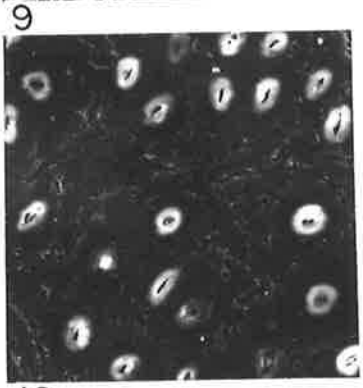
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10



11



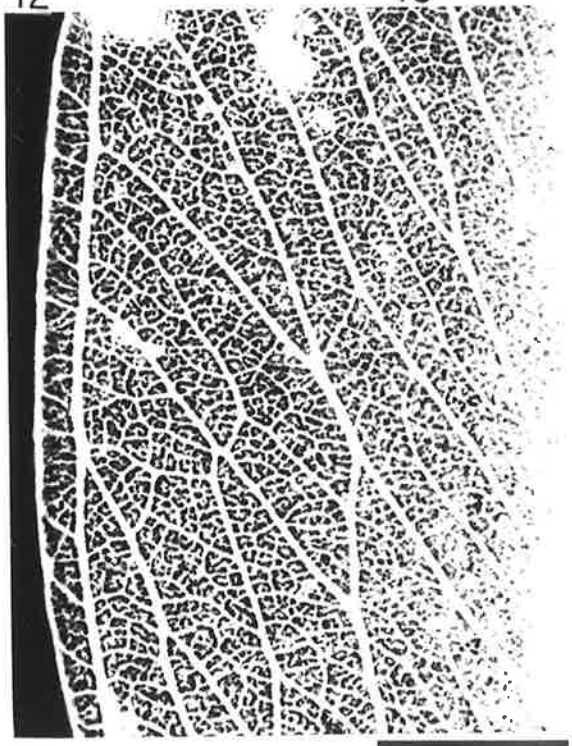
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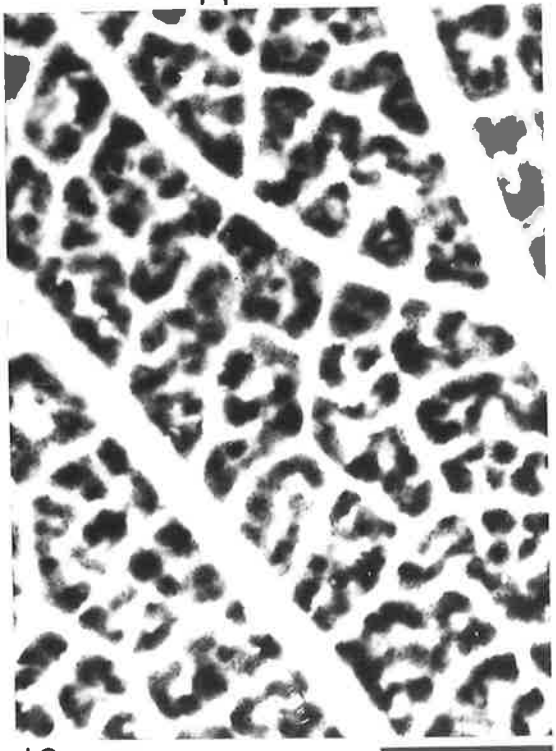
13



14



15



16

Hallam and Chambers (1970) surveyed leaf waxes in 315 species of Eucalyptus using scanning electron microscopy of carbon replicas of leaf surfaces. This work showed that epicuticular waxes are always present even on non-glaucous leaves where they are not visually apparent. Three main types of wax deposits were recognized: tube waxes (Group 1), plate waxes (Group 2) and a combination of plates and tubes (Group 3). According to Hallam and Chambers, tube waxes are responsible for an obvious white bloom that is easily removed by rubbing, whereas plate waxes generally give a dull, matt appearance and are difficult to remove completely by rubbing. In some cases plate waxes may be more effective in scattering light and thus would be expected to give a more obvious glaucous appearance. This would occur if they form a dense cover and are arranged irregularly, overlap, are orientated at an angle to the surface, or have digitate or strongly ornamented margins. The species E. clelandii, E. lesouefii and E. dongarraensis are known to show conspicuous glaucousness although they were found to have plate wax only.

Hallam and Chambers examined 10 species of Dumosae and found representatives in all three major wax groups. Their results, summarized in table 2.1, conflict with evidence of general morphology used as the basis for the new classification derived in this thesis. The grouping of E.conglobata with the distinctive species E. woodwardii rather than with E. anceps is surprising, considering its close affinities with the latter. Variation in margin type of wax plates does not correspond to related species within the "blackbutt complex" (7.3, p. 145; 10.6, p. 201). It would therefore seem to be unwise to attribute too much phylogenetic significance to wax type. The evidence is that these are relatively unstable characters in terms of recent evolutionary history. The inconsistency within the Dumosae is paralleled in other series of mallees in which both Group 1 and 2 waxes are represented, namely Foecundae,

Table 2.1: Summary of wax morphology data of Hallam and Chambers (1970) for members of Dumosae.

Species	No.[A]	Density[B]	Description of Wax
			GROUP 1
E. conglobata	1	1	Tubes : simple, branching at acute angles, rather blunt.
E. woodwardii	2	3-4	Tubes : simple, often branched at right-angles.
			GROUP 2
E. pileata	1	1	Plates : irregularly shaped, entire-edged.
E."pterocarpa"	1	2	Plates : irregularly shaped, entire-edged.
E. kondininensis	1	1	Plates : irregularly cresent-shaped, entire-edged.
E. clelandii	3	1	Plates : irregularly shaped, entire-edged.
E. lesouefii	1	4	Plates : irregularly shaped, sinuate-edged.
E. dongarraensis	2	4	Plates : irregularly shaped, crenate-digitate-edged.
			GROUP 3
E. anceps	1	?	Plates and tubes, plates : irregularly shaped, sinuate-edged.
E. dumosa	2	?	Plates and tubes, plates : irregularly shaped, sinuate-edged.

A : number of individuals sampled

B : density of wax cover

KEY :

1 = isolated
2 = sparse cover
3 = open cover
4 = complete cover

Calycogonae and Oleosae. There is also variation within the species E. calycogona (Groups 1 and 3) and E. oraria (Groups 1, 2 and 3). Due to the limited level of sampling within Dumosae species (table 2.1), the reliability of differences is unknown and may conceal much variation within species. As many of these species limits are artificial and poorly defined morphologically, one would not expect to find corresponding consistent differences in wax types. Hallam and Chambers work has demonstrated significant variation in wax characters and further study to investigate geographical variation would be profitable.

In this thesis, where the emphasis is on producing a phenetically based, workable classification, characters of wax morphology were not included because preparation techniques required are too involved for routine taxonomic use. However, epicuticular waxes were considered indirectly through measurements of leaf reflectance before and after wax removal. In this way it was possible to determine their contribution to the colour of leaves.

2.3.4 Leaf spectrophotometry

Reflectance and transmission measurements were made using a Shimadzu QR-50 spectrophotometer with Ubricht integrating sphere attachment. The apparatus was described in detail by Sinclair (1967) and by Sinclair and Thomas (1970). Fresh leaves were kept in airtight plastic bags below 5° C until ready for reading. Percentage values of reflectance are relative to a standard of six layers of Whatman's No. 1 filter papers. To accommodate the relatively narrow leaves of some individuals it was nescessary to reduce the window area of the sample holder to c. 1 x 2 cm, resulting in some loss of precision. To check the accuracy of the equipment, a leaf of Ligustrum ovalifolium (Privet) was tested as a

standard reference. A reflectance value of 13 % at 550 nm was obtained which is consistent with Sinclair (1967, p. 265). Measurements of Dumosae were made on abaxial surfaces using the most glaucous of the fully expanded leaves of adult form available.

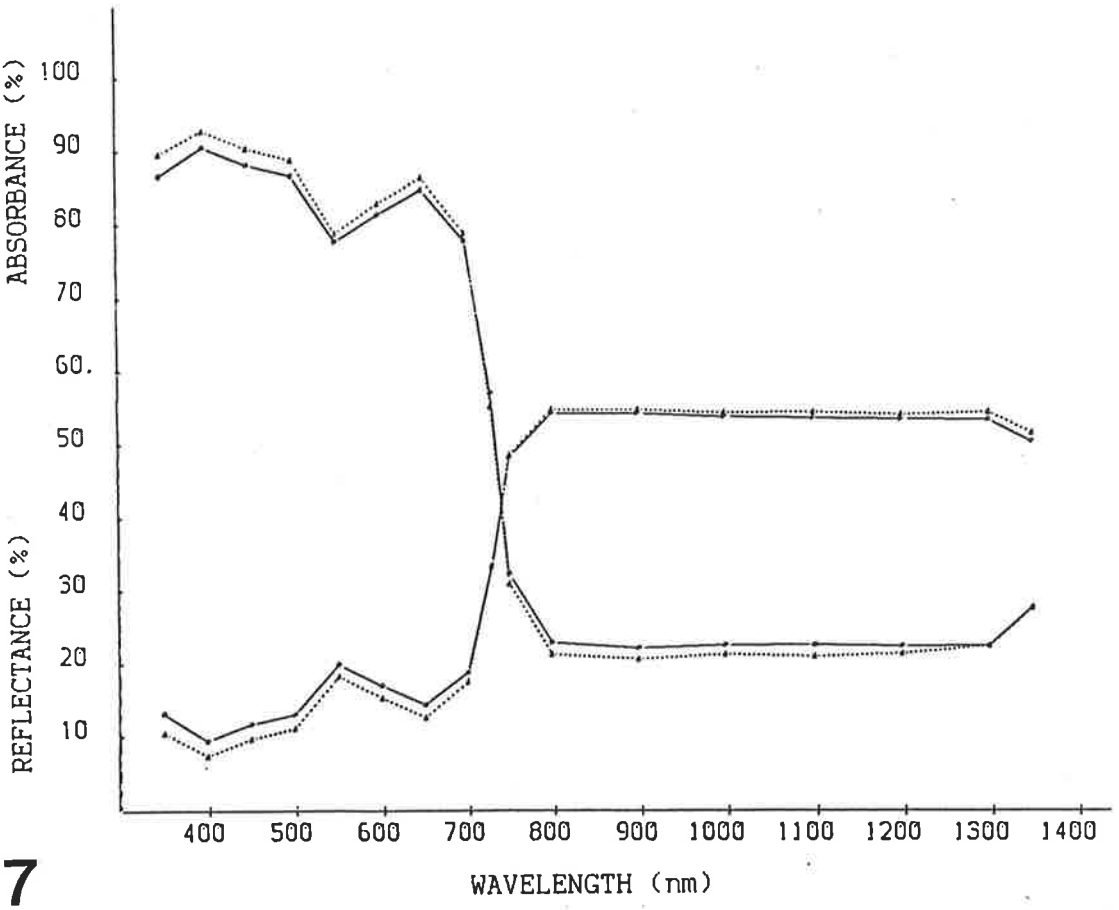
Readings were determined at 17 wavelengths across the visible and near infra-red section of the spectrum for a green-leaved individual and blue-leaved individual which were adjacent trees in a population in the Flinders Ranges (figs 17, 18). Wiping with chloroform reduced the reflectance of the green, non-glaucous individual by c. 2% throughout most of the visible region (350 - 730 nm). This agrees with Hallam and Chambers' observation that traces of wax are present on non-glaucous leaves even when not visually apparent. Removal of wax reduced reflectance of the glaucous individual by a value of more than 10% over most of the visible region, resulting in a spectrum of similar reflectance to the non-glaucous individual. The optical significance of the wax layer is shown by the fact that it approximately doubles reflectance at the 400 and 600 nm absorbtion peaks. In the near infra-red the effect of wax removal was less, and for the non-glaucous individual there was a slight increase in reflectance. This is probably an artifact of the treatment with chloroform. The absorbance spectra determined from reflectance and transmission measurements show that the wax causes a decrease in absorbance of a similar magnitude to the increase in reflectance. This conflicts with results of the study by Sinclair which compared optical properties of arid zone and mesophytic species. Sinclair found that although the arid zone species generally had higher surface reflectance this was associated with reduced transmission, and except for Atriplex vesicaria they did not have significantly lower absorption. However, the results here show that over the interval 350 - 1350 nm, which includes 92 % of incident solar energy, epicuticular wax can substantially lower

Figure 17: Spectrophotometer readings for non-glaucous individual, PJL 860/2 km SE Warraweena HS.

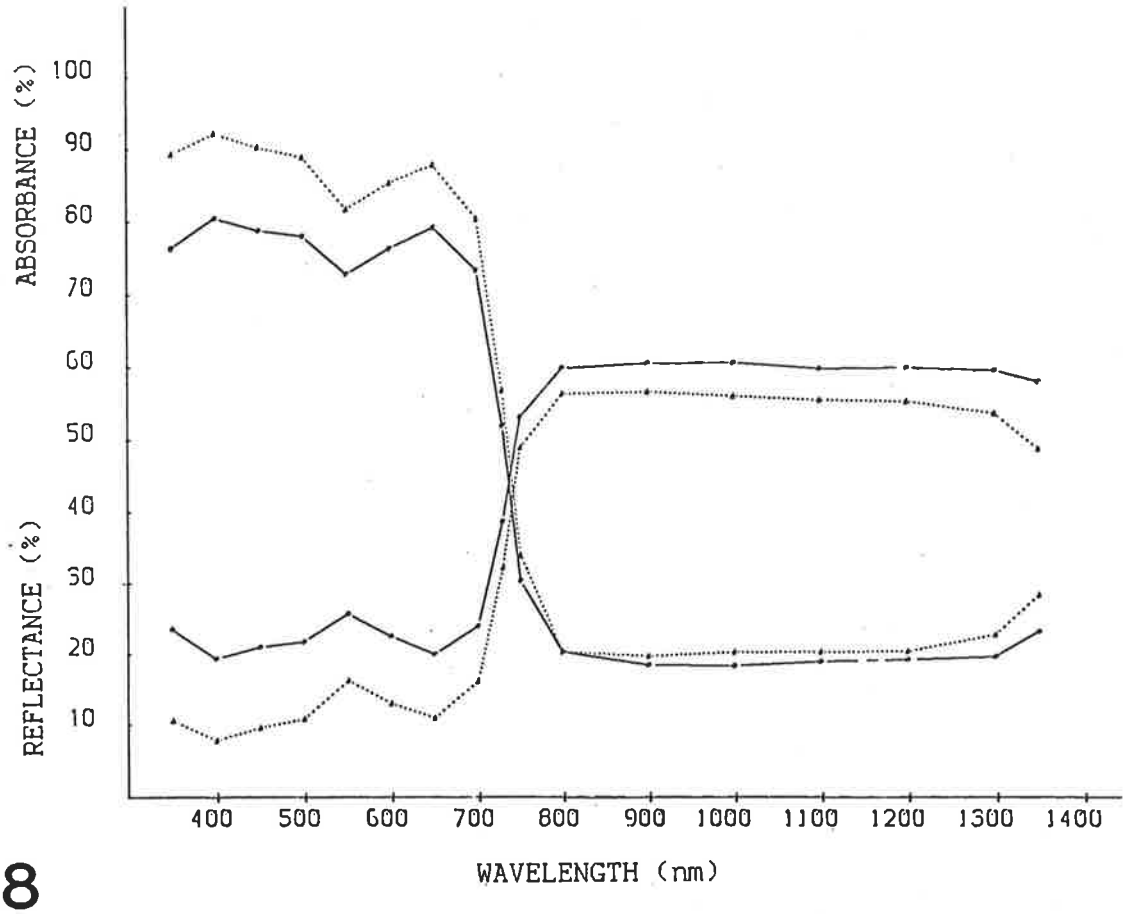
Figure 18: Spectrophotometer readings for glaucous-leaved individual, PJL 859/2 km SE Warraweena HS.

unwiped leaf

same leaf wiped with chloroform to remove wax


ABSORBANCE (%)
100
90
80
70
60
50
40
30
20
10
REFLECTANCE (%)
400
500
600
700
800
900
1000
1100
1200
1300
1400
WAVELENGTH (nm)

17


ABSORBANCE (%)
100
90
80
70
60
50
40
30
20
10
REFLECTANCE (%)
400
500
600
700
800
900
1000
1100
1200
1300
1400
WAVELENGTH (nm)

18

absorption and so reduce the energy load of leaves.

In this case the increase in reflectance caused by wax is relatively constant throughout the visible region so there is no major shift in colour but merely an increase in "whiteness". Readings at a single wavelength therefore provide a reasonable measure of the visible effect of the wax cover. Wax-contributed reflectance was determined at 400 nm for a sample of 54 leaves from 50 South Australian individuals of Dumosae. Readings obtained after removal of wax enabled investigation of the relationship between cuticular relief and reflectance. For non-glaucous leaves a strong association was apparent. Leaves found to have little or no cuticular relief often exhibit a strong sheen while leaves with high cuticular relief are always dull. It was thought that the shiny appearance of the former indicated a greater overall reflectance. (Lower reflectance in leaves with high relief might result from scattering of light within depressions between verrucae or papillae). To test this, reflectance values were plotted against scores of CS, a character expressing height of cuticular sculpturing (see 4.3, p.84) for definition). A negative correlation significant at the 0.01 level was obtained but the scatter of points was much broader than expected, with r = -0.47 (fig. 19). This may be due to the influence on reflectance of aspects of sculpturing other than height, such as closeness and steepness of papillae or undulations. Also the spectrophotometer only allowed measurements with incident light normal to the leaf surface but sculpturing may be more effective in reducing reflectance at acute angles.

The values obtained for wax-contributed reflectance are displayed in figure 20. In most cases, variation in replicates for individuals (different leaves) is limited, but wide variation often occurs between different individuals of a single population. Sessile-fruited forms representing E. conglobata and E. anceps, which consistently have

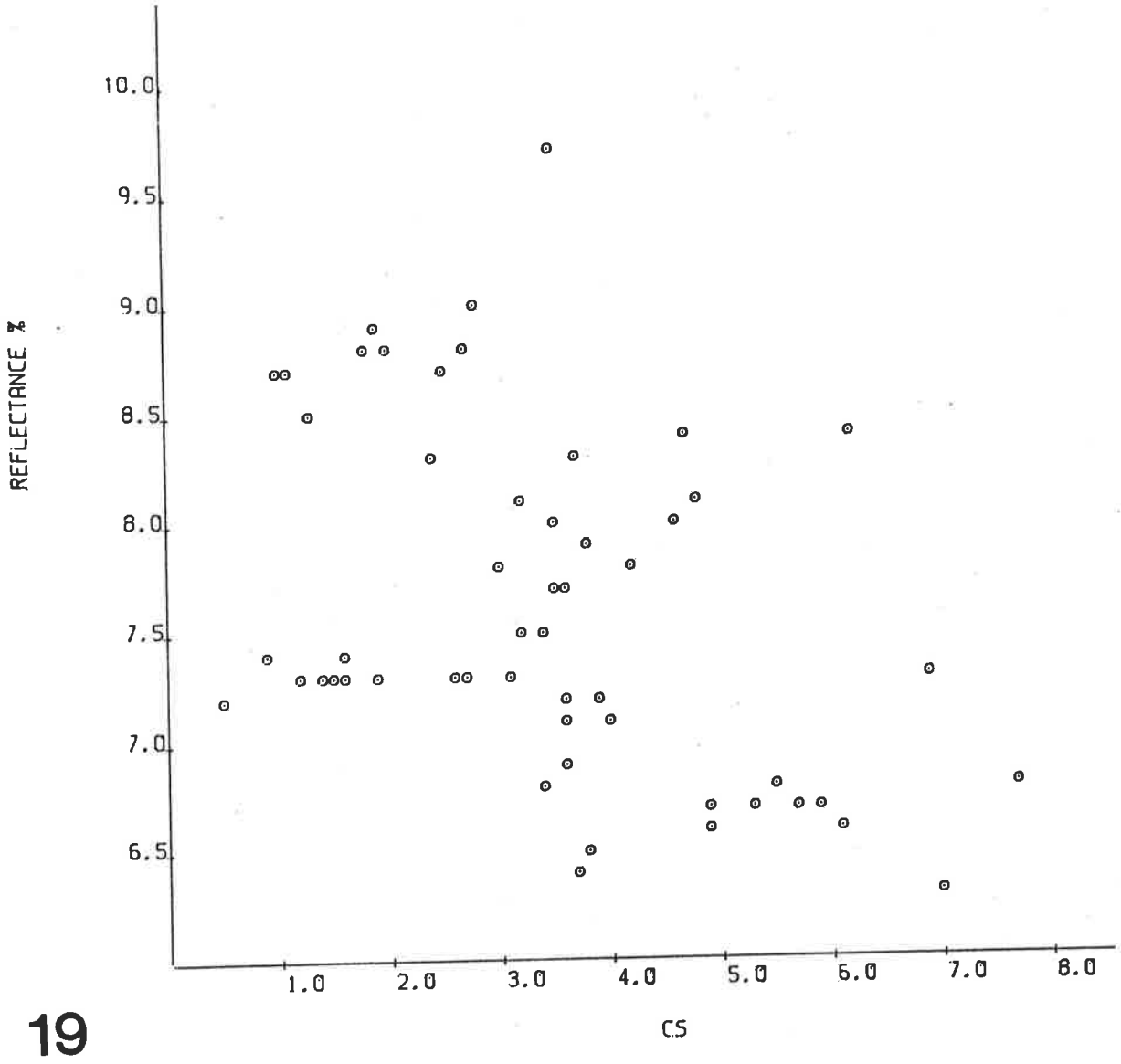


Figure 19: Relationship between leaf reflectance (after removal of wax) and the character CS (expressing height of cuticular sculpturing) for 50 South Australian individuals of the E. dumosa complex.

r = -0.47

Figure 20: Wax-contributed reflectance data.

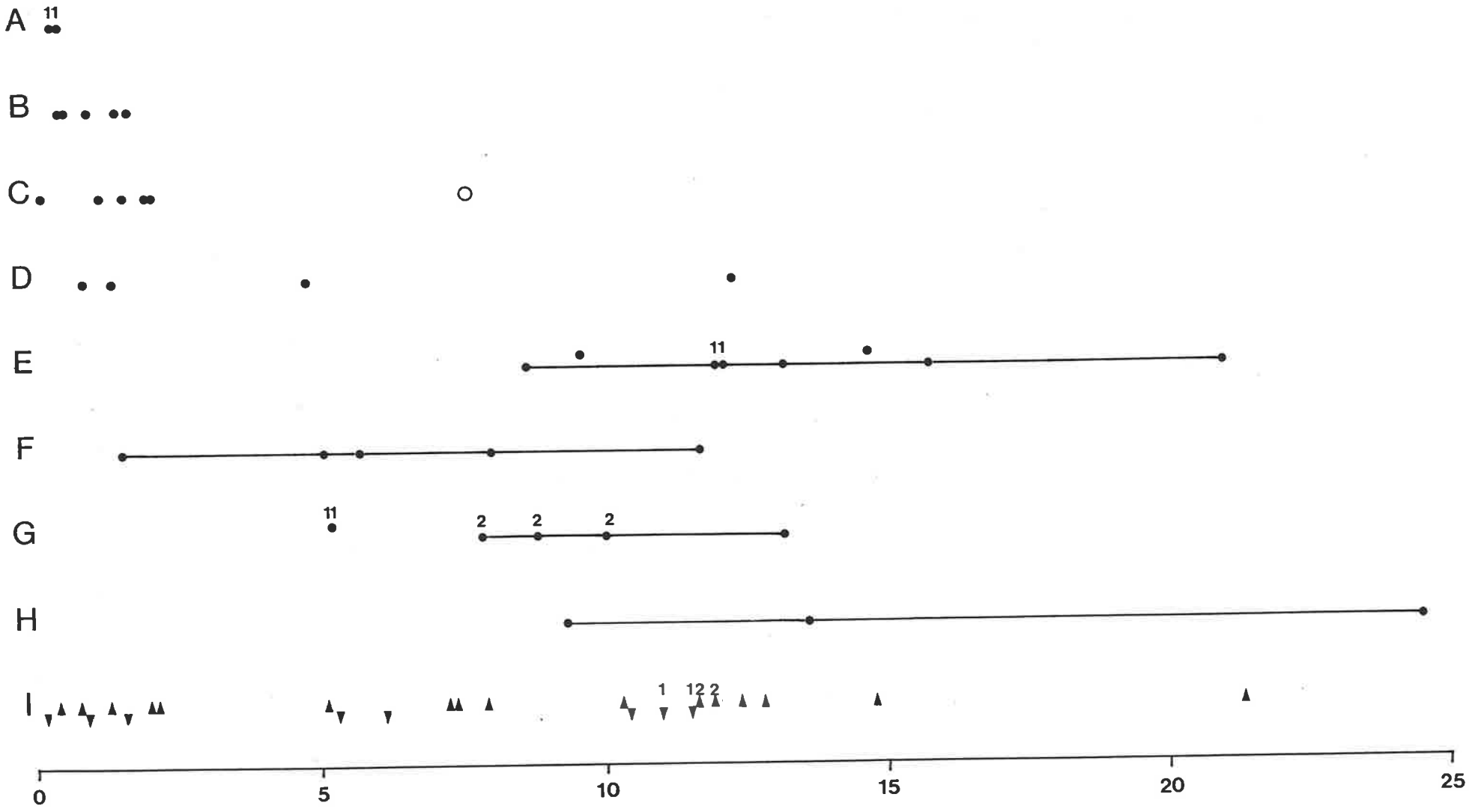
KEY:

A : E. conglobata, Eyre Peninsula Region
B : E. anceps, Eyre Peninsula and Yorke Peninsula Regions
C : E. dumosa complex, South-eastern Region
O coppice shoot
D : E. dumosa complex, Eyre Peninsula Region
E : E. cyanophylla, Murray Region (P28*)
F : E. dumosa complex (intergrade with E. cyanophylla), Murray Region (P30)
G : E. dumosa complex (Carappee Hill form), Eyre Peninsula Region (P73)
H : E. dumosa complex (affinity E. striaticalyx) Eyre Peninsula Region
I : E. dumosa complex
▲ Flinders Ranges
▼ Gawler Ranges

Within each group, replicate readings for a single individual are indicated by numerals 1 or 2.

Individuals from a single population are linked by lines for groups E,F,G,H.

* An index to population codes is provided in table 9.1.



20

% REFLECTANCE CONTRIBUTED BY WAX AT 400 nm

non-glaucous leaves, gave readings of less than 2 % wax contributed reflectance. Similar readings were obtained for material from the South-eastern Region representing intergrades between sessile and pedicellate forms. All Dumosae appear to retain the capacity for glaucousness in coppice or juvenile foliage and a coppice leaf from the above material showed a moderately dense cover of wax (7.6 %).

That the high degree of glaucousness characteristic of E. cyanophylla is not unique is supported by the data. A similar range of values was obtained in a population of large fruited forms with affinities to E. striaticalyx (POP: P57*) from sand dunes on northwestern Eyre Peninsula. The highest value of wax contributed reflectance (24.5%) was recorded in this population. The Flinders and Gawler Range material has values that overlap considerably with E. cyanophylla. A population that appears morphologically intermediate between E. cyanophylla and E. dumosa or E. anceps (POP: P28) has a range of wax contributed reflectance extending from the lower end of the range of E. cyanophylla to a value typical of non-glaucous forms.

The greatest variability is shown by the Flinders and Gawler Range material. Readings are clustered into three main groups but there is insufficient sampling to indicate whether these reflect genetically determined discontinuities. Nevertheless, class intervals for subjective assessment of wax cover were chosen to coincide with these groups.

The adaptive significance of the wax deposits is unclear. Association between glaucousness and distance from the coast evident in this material, also occurs in Western Australian Dumosae and other groups of eucalypts. In extreme coastal habitats non-glaucous leaves would have an advantage by

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* population measured for analysis (POP group) - see table 9.1, p. 157.

accumulating less salt on their leaf surfaces. Glaucousness may be advantageous in reducing: heat damage from absorption of solar radiation, frost damage, and cuticular transpiration (especially in young leaves). These are likely to be more significant factors in inland areas.

2.4 Leaf anatomy

The potential for leaf architectural characters in Eucalyptus taxonomy was demonstrated by Carr and Carr (1976) who recognized two sibling species in section Dumaria distinguished largely by differences in ultimate venation. Initially I planned to undertake a thorough analysis of leaf venation patterns in Dumosae but this was abandoned for the following reasons:

1. A cursory examination of fresh leaves with transmitted light and leaves cleared temporalily by dimethyl-sulphoxide or lactic acid for a range of Dumosae species did not reveal any discontinuities in characters such as used by Carr and Carr. Eucalyptus anceps could not be distinguished from E. rugosa (Torquatae) by a visual examination of venation, although it is possible that they might be separable by quantitative analysis.
2. Although a variety of methods for permanently clearing and staining eucalypt leaves were investigated, none were entirely satisfactory because fine veinlets were obscured by a layer of lignified parenchyma.
3. The venation patterns in Dumosae and many other eucalypts are highly irregular and not easily analyzed. Venation orders cannot be clearly defined and anastomoses often occur even in secondary veins (figures 15, 16).

However, one venation character, an estimate of the average angle of secondary veins in the central part of the leaf, was included in the final character set because it was easily measured and provided some taxonomically useful information.

Oil glands are abundant in leaves of Dumosae but they may be obscure when not located near the surface. Characters relating to oil glands were rejected for consideration when it was decided not to clear leaves. In retrospect this was unfortunate, as any data on oil gland size or frequency could be useful because of the potential economic value of eucalypt oil as a fuel.

In the survey of cuticular relief by scanning electron microscopy mentioned earlier, Dumosae cuticles were found to be basically similar in construction although there was continuous variation in height of verrucae or papillae. Cuticles were also studied by light microscopy to reveal details of epidermal cells and stomatal anatomy, but no obvious differences of taxonomic value were found. Although different arrangements of stomatal cavities and ledges were observed in series Incrassatae, all material of Dumosae and Torquatae was consistent.

2.5 Thin-layer chromatography of leaf extracts

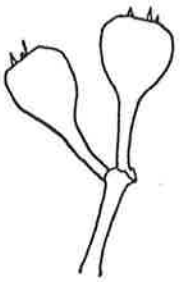
Numerous studies have shown that useful chemo-taxonomic information can be obtained from eucalypt leaves. The pioneering work in this field was carried out by Baker and Smith (1920) who analysed 'essential oils' distilled from leaves, and established major differences between groups that are now regarded as subgenera by Pryor and Johnson (1971). The potential for chemical taxonomic information at the infra-specific level was clearly demonstrated by Banks and Hillis (1969). In individuals of *E. camaldulensis* sampled from 103 localities, 47 polyphenols were detected and eight were regarded as taxonomically important. They were able to divide the individuals into six phyto-chemical provinces that correspond to major river drainage systems and correlate with groupings based on morphological characters.

I decided to use thin layer chromatography (TLC), a relatively rapid and simple technique, to investigate whether useful chemotaxonomic information could be obtained for series Dumosae and to search for chemical characters supporting the distinction between them and series Torquatae. The species E. striaticalyx (Dumosae) and E. concinna (Torquatae) were chosen for this initial study because a range of recently collected specimens from the Great Victoria Desert was available. Thus any gradual breakdown or modification of chemical constituents in fresh leaves would be minimized. In this area the species are sympatric but evidence from seed characters does not support intergradation. The two species show parallelism in gross morphology (figs 2.5, 2.6) and identification based on buds and fruits is often unreliable. However, they can be consistently identified on leaf characters. Shiny green to yellow-green leaves that are consistently non-glaucous are always associated with the Torquatae seed type while dull leaves that are variably glaucous (and green or grey-green if non-glaucous) are associated with the Dumosae seed type. The leaf colour characteristic of E. concinna is reflected in the name E. ocrophylla Maiden and Blakely (Yellow-leaved mallee) which is a synonym of E. concinna. Thus I expected that differences in leaf chemistry would be present between the two species.

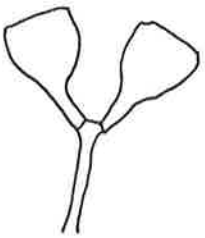
Nine individuals of each species were sampled. Dried pieces of mature leaves (c. 2 cm^2) were diced into fine fragments by razor blade to rupture all oil glands and were extracted with ether. The solutions were spotted onto TLC sheets with capillary tubes and run in a sealed jar saturated with solvent vapour. Aluminium oxide and silica-gel sheets were used with various solvent mixtures providing a range in polarity. The best separation of detectable compounds was achieved using silica-gel and a 60 : 40 diethyl ether : distilled petroleum mixture. Rf values were determined for visible pigments. Compounds not visible in daylight were

Figure 21: Outlines of fruit and bud shapes of E. concinna from north-western S.A.

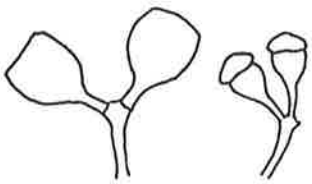
Actual size.



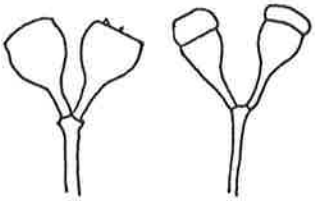
LDW 10720



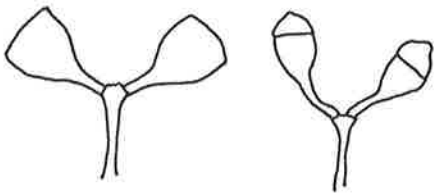
JD 12



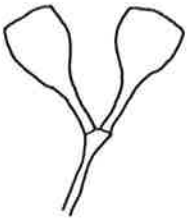
JD 64



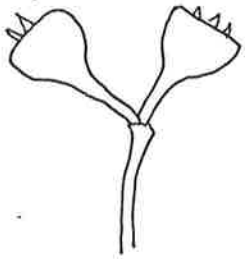
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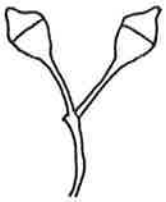
JD 65



JD 35



JD 50

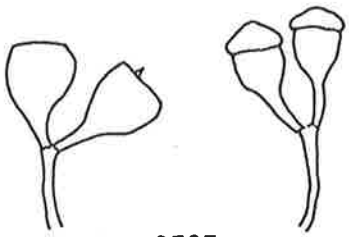




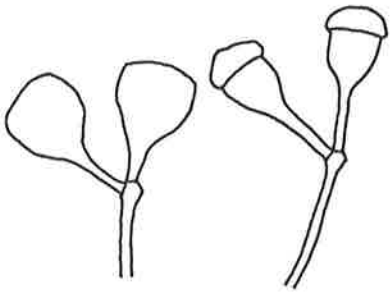
VJL 147



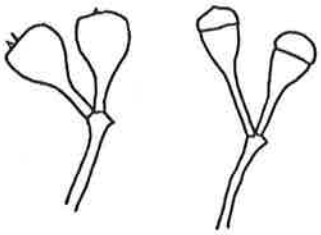
VJL 159



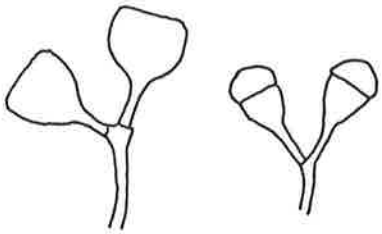
LDW 8787



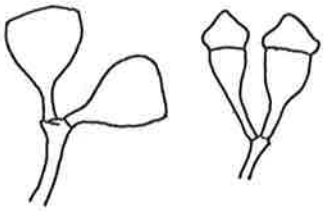
VJL 218



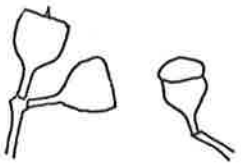
VJL 152



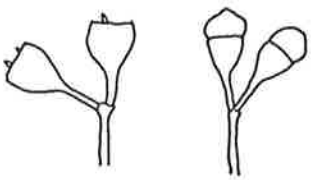
VJL 186



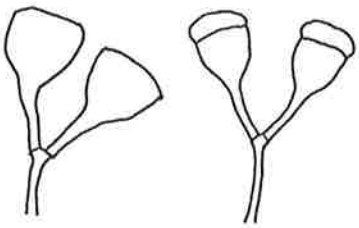
VJL 188



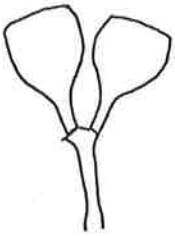
LDW 10595



LDW 10551



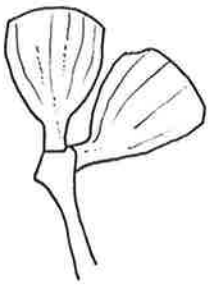
JD 51



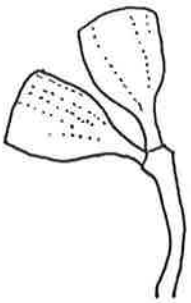
TED 186a

Figure 22: Outlines of fruit and bud shapes of E. striaticalyx from north-western S.A.

Actual size.



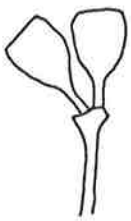
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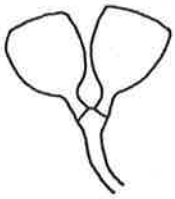
TED 188



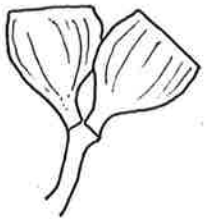
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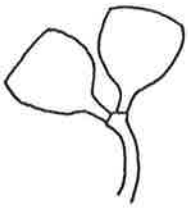
JJ 18.9.55

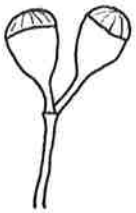


TED 186b

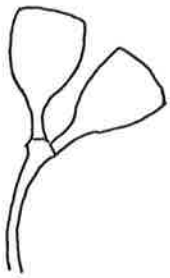


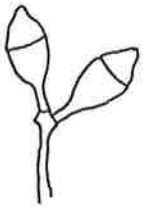
LDW 10492



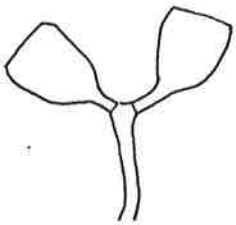


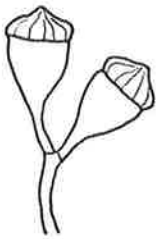
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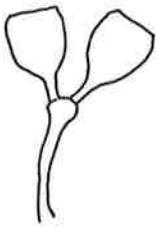


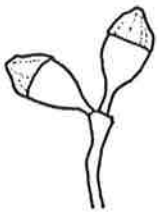
JD 34





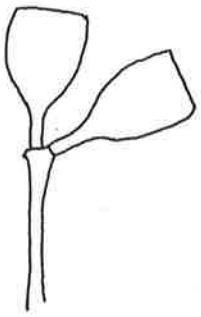
JD 27





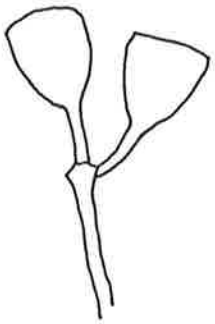
VJL 38





LDW 10573

LDW 10561

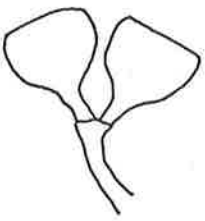


VJL 220





JJ & SR .7.70





JJ & SR 3.6.70

visualized under ultraviolet light at 254 and 305 nm and by spraying with 1 % vanillin in H_2SO_4.

There were 13 compounds that could be detected with certainty and their characteristics and distribution in the 18 specimens are shown in table 2.2 . Five are visible pigments identified as a carotenoid (no. 1), chlorophyll (no. 5, 9) and a flavonoid (no. 13). These were present in all specimens with no marked differences in intensity. Runs using different solvents or aluminium oxide sheets also did not reveal any difference in visible pigments. Thus the leaf colour difference between the two species is probably only a result of surface properties and cannot be explained in terms of pigmentation.

Six of the eight non-visible compounds were variable in their occurrence, but only one (no. 6) was confined to one species. As it was present in only two of the nine E. concinna specimens it is of limited taxonomic value and its absence from E. striaticalyx is less significant. The high proportion of compounds of secondary importance (indicated by their absence in some individuals) that are shared by the two species suggests a close phylogenetic affinity with little divergence.

For the material examined the method appears to be ideal for investigating genotypic variation and interchange at the level of small populations but is less likely to be useful as a taxonomic tool for analysing variation on the wider scale covered by this thesis.

Table 2.2: Thin-layer chromatography results.

Solvent : ether-petrol 60 : 40
Adsorbent : silica-gel

No	Rf	DAYLIGHT	UV_{254}	UV_{305}	VANILLIN
1	.96	o-y	x	y	p
2		-	x	l-y	p
3		-	x	-	-
4		-	-	-	p
5	.53	gr-y	x	r	b-g
6		-	-	pi	-
7		-	-	-	p
8		-	x	y	gr
9	.34	g	x	r	br-g
10		-	x	b	y-br
11		-	x	-	r
12	.18	ol-g	x	o	gr
13	.11	y	x	g	gr

	E. striaticalyx									E. concinna								
	TED 186b	LDW 10492	TED 188	TED 189	TED 191	LDW 10776	JD 34	JD 72	PJL 2065	TED 186a	TED 187	TED 193	LDW 10720	JD 35	JD 50	JD 64	VJL 186	PJL 1829
1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2	+	+	+	+	+	+	+	-	+	+	-	+	-	-	-	-	-	+
3	-	+	-	-	-	-	-	-	+	-	-	-	-	-	+	+	+	-
4	-	-	-	-	-	-	-	+	+	-	+	-	+	+	+	+	+	+
5	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
6	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+
7	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
8	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
9	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
10	-	-	-	-	-	+	-	+	+	-	-	-	-	-	-	-	-	+
11	+	-	-	-	-	+	-	-	+	-	+	+	+	+	+	-	+	-
12	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
13	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

KEY:

b	blue	o	orange
br	brown	ol	olive
g	green	p	purple
gr	grey	pi	pink
l	lemon	r	red

x opaque, non-flourescent

2.6 Flowering time

This section presents results of investigations into flowering time patterns in the Dumosae made for selected groupings of South Australian specimens from herbarium label records.

2.6.1 Bud and fruit stages

It is useful to define phenological stages for reference here and elsewhere in this thesis.

1. Developing buds are defined as those for which some floral bracts of the umbellaster* are still present, or those which still retain their calycine operculum and are small enough for it to obscure the greater part of the petalline operculum.
2. Immature buds covers a wide range in bud maturation, with buds of a size greater than developing buds and smaller than mature buds.
3. Mature buds are those which have reached their maximum size apart from some slight expansion of the operculum immediately prior to anthesis due to expansion of the stamens. In practice there was a subjective cut-off in sizes allowable for these stages. For non-flowering material it was necessary to guess whether buds were mature or not using fruit size as a guide.
4. Developing fruits are those in which stamens have been shed from the flower but are not sufficiently mature for the valves to separate at their tips (formed from the style base) nor split apart lower down on drying.
5. Immature fruits are those in which the valves split or separate in

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* following the terminology of Johnson (1972). Previously referred to as the "umbel" or "unit inflorescence".

their basal part on drying but do not properly open because they remain united at their tips. They often have a green epidermis and their seeds are straw-coloured to pale brown.

6. Mature fruits open freely and have red-brown seeds.

2.6.2 Flowering patterns

Developing buds were generally found to be present at any stage throughout the year and it appears that bud initiation can occur at any time when conditions allow vegetative growth. As a result immature and mature buds were also often present throughout the year even in populations with a regular fixed flowering period. The Dumosae have the capacity to retain the mature bud stage until the time is right for flowering. Sometimes two or even three generations of buds are present on an individual. Some individuals of E. dumosa ssp. conglobata (e.g. PJL 761, near Goolwa ; PJL 747, Mt Scrub - Mt Desert, Southern Lofty Region) were observed with two generations of buds flowering together.

Flowering on a single individual may last for only a few weeks but there seems to be genetically determined variation in the precise timing so that the flowering period is considerably longer for a given population or taxon. In the field, individual trees of a population were often observed at different stages of flowering or fruit development. At the Waite Institute arboretum, Adelaide, differences in the relative time of onset of flowering between individuals of the same species (E. woodwardii and E. dumosa) are consistent from year to year. Flowering spans for populations may be fixed or simply be a response to regular seasonal patterns. However, it is postulated that in arid areas there would be a strong selective advantage in having flowering coupled to infrequent and irregular rainfall events. Pollinators would be more abundant and active

after heavy rains and the tree would be less likely to be under stress during the sensitive stages of nectar flow, fertilization and maturation of seed and fruit.

For the selected groupings all available South Australian herbarium collections were recorded in one of four classes:

1. Flowers absent. (n)
2. Early in flowering period. (<)

At this stage there is a predominance of mature buds over flowers but developing fruits are absent or rare.

3. In full flower. (+)

At this stage there is a predominance of flowers or else significant numbers of both mature buds and developing fruits.

4. Late in flowering period. (>)

At this stage there is a predominance of developing fruits with mature buds being absent, rare or dead.

Initially, the other stages of buds and fruits were also recorded. An indication of flowering time can be obtained from the presence of immature fruits by extrapolation under the assumption of a uniform delevopment rate. However, this information was not considered to be worth the loss of clarity in interpreting the data.

Results are presented in a semi-graphical form (tables 2.3, 2.4) with months of the year divided into three sectors. This is a useful degree of resolution and enables the specifications of early-, late- and mid- month to be plotted or derived from the plots when describing the start or end of flowering. For groups A to E and G to I the degree of sampling probably does not justify this resolution and in interpreting the data it would be better to consider the months as single units. The results should be interpreted with caution taking numbers of non-flowering records into account. Absences of flowering records have little meaning when

Table 2.3: Herbarium flowering records.

Group: / Month	A	B	C	D	E
i	. 1 7	2 1 1	1 1 2	. 6 +++ . ++	. . 1
ii	3 . 1	. +++ . + . <	+ 1 + .	1 . .	. . .
iii	. . .	. . + 1 +++>>	. . .	1 . 1	1 . .
iv	2 1 .	1 > . .	. . 1	. . .	. < . + 2
v	. 1 .	. 2 1	1 2 > 1 >	. 7 .	1 1 .
vi	1 ++ 1 15	3 . 4 +>	5 +>> . + .	. 1 3	. . 4
vii	. . 1 ++++	. . 1 <	. + . 1	. . .	. . .
viii	1 +++ 3 < . +	. 2 >> 4	. 5 > 5 <+>	. 1 3	. . .
ix	. 8 1	1 1 1	. > 3 + 1	. 6 .	. . .
x	4 <<<+ 3 .	8 13 4	. +> 3 1	. 6 1	1 2 < 8
xi	. 1 <> .	. 1 .	. < 1 .	1 . .	. . .
xii	. . >> .	. . .	. . 1	. . 1 <<<	3 . .

Key:

A : 'E. cyanophylla' forms : Murray Region
B : 'E. dumosa' and intergrading forms : Murray Region
C : Sessile-fruited forms ('E. anceps') : Murray Region

D : Eyre Peninsula glaucous-stemmed forms : Carappee Hill - Darke Peak
E : " " " " Outliers.

< Early in flowering period
\+ In full flower
> Late in flowering period

numbers indicate non-flowering records.
months divided : 1-10 / 11-20 / 21-31.

Table 2.3 (cont.): Herbarium flowering records.

Group: Month	F	G	H	I
i	1 + . 4 <<++	1 . + .	. . 1	. . .
ii	2 <+++ 3 <+ .	1 <> 1 1	. 3 .	. . .
iii	3 <<<<<<<++++++++++++>>>>>>>> 1 <<++++++++++>>>> . <	7 <<+> 2 .	. . .	. . .
iv	. <<<<+> . < .	1 2 .	. . .	. 1 1
v	. 1 2 <	. 3 ++ 3	. . 1 <<++>	. 21 <<<+>>> 1
v	. . .	. 6 .	2 . 5	. > . .
v	2 > . 1	. 4 1	2 12 > 5	3 2 1 <
viii	. 2 + 2 +	2 3 1 +	2 7 << 2	. 26 >> 1 +
ix	1 . 1	1 3 + 1	2 + 1 2	2 <<<<< 6 2 +
x	1 +>> 6 <+> 29 <+++>>	4 +> 2 + 2	1 1 .	4 2 < .
xi	1 2 .	. + 3 +++ 2	. > 5 . <	. .+> .
xii	3 . 1 >	2 . + 1 +	. ++ . .	. . .

Key:

F : Sessile-fruited forms : southern regions (EP, YP, SL, KI, SE)
G : E. rugosa : " " " "

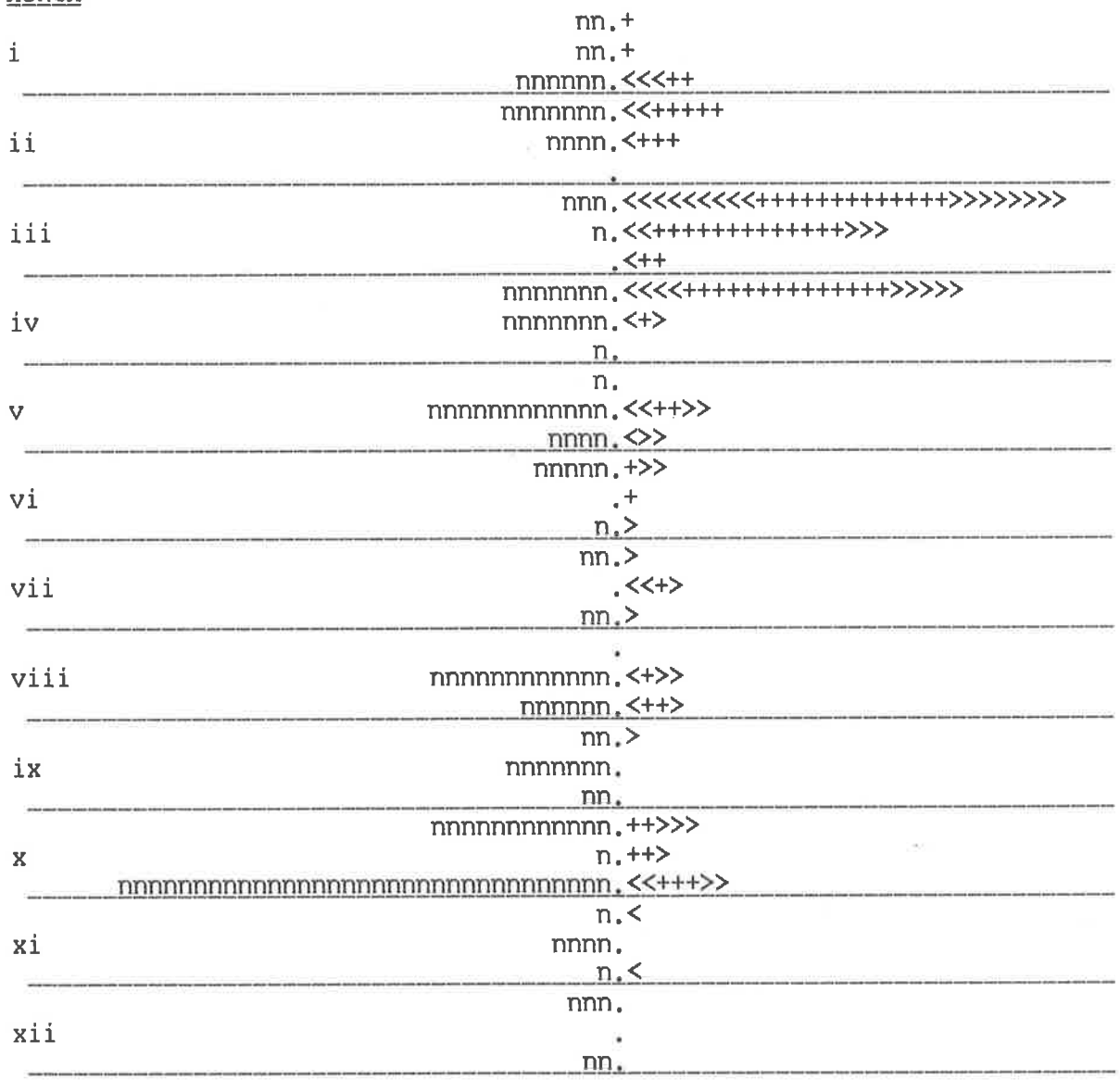
H : North-west desert dune forms (NW, NU)
I : Flinders Ranges forms (FR, NL)

< Early in flowering period
\+ In full flower
> Late in flowering period

numbers indicate non-flowering records.
months divided : 1-10 / 11-20 / 21-31.

Table 2.4: Herbarium flowering records.

Group:J
Month



Key:

J : E. dumosa ssp. conglobata : South Australia

n Not-flowering
< Early in flowering period
\+ In full flower
> Late in flowering period

months divided : 1-10 / 11-20 / 21-31.

non-flowering records are also absent, but are significant when non-flowering records are present because of the bias collectors undoubtedly have towards flowering material.

The irregularity of the distribution of records for most groups shows how unreliable isolated records can be, yet often inferences about flowering time can only be made in taxonomic treatments on the basis of one to several records. Due to uneven sampling with respect to time and geography, rather large samples of herbarium collections, as in group J (n = 293), are required before a more reliable picture of the flowering pattern emerges. The following conclusions about flowering times must therefore be regarded as tentative.

Groups A,B and C represent three different forms of the E. dumosa complex in the Murray Region of South Australia. The data demonstrates a major difference in the pattern of flowering times between E. cyanophylla and E. dumosa, generally confirming the winter-spring/summer-autumn distinction made by Brooker (1977). However, although the peak for E. dumosa is February-March, there is some overlap with E. cyanophylla in the three winter months. (Only one of the overlapping records was regarded as a morphological intermediate with E. cyanophylla.) The flowering of sessile-fruited forms in this area (group C) is spread over a longer period and overlaps with both of the previous two forms.

Group D from localities in the Carappee Hill - Darke Peak area has a more limited and regular flowering period beginning in December and reaching full-flower in January. It is likely that later stage flowering would continue into February. There is no evidence of a similar pattern in outlying glaucous forms (group E), but this is not surprising since they are interpreted as intergrades on morphological grounds.

Groups F and G were scored to examine the extent of flowering overlap between sessile-fruited forms (ultimately treated as E. dumosa ssp. conglobata in this thesis) and E. rugosa, a sympatric species of series Torquatae. For group E, E. dumosa ssp. conglobata was only sampled in areas where E. rugosa also occurred - namely the southern parts of Eyre and Yorke Peninsula, the Fleurieu Peninsula region, Kangaroo Island and the South-eastern Regions. In contrast to the Murray Region, sessile-fruited forms in these more coastal areas (group F) show a definite peak in flowering between late January and early March with only minor flowering at other times during the year. This pattern is maintained when records for other regions are included (group J). In March 92 % of 52 individuals sampled were in flower, while in October 19 % of 72 individuals sampled were in flower. Major flowering would not begin until January, as evident from the absence of late stage flowering (>) in January and February. With E. rugosa (group G) flowering is sporadic and overall a lower proportion of flowering individuals were collected. Flowering appears to occur throughout the year, possibly with a decline during winter. There is significant overlap with the sessile-fruited forms of Dumosae, so flowering time is unlikely to present a barrier to interbreeding.

Groups H and I are from more arid regions. Unfortunately sampling is poor during summer months when temperatures are high. Both groups have significant records in May and a scatter of records througout winter and spring. There is certainly no evidence of a limited and regular period (as in group D) in agreement with the prediction based on climate.

Overall, herbarium records indicate greater complexity in flowering patterns than expected on the basis of previous taxonomic treatments. Substantial geographic variation is exibited amongst forms here treated as E. dumosa ssp. conglobata (groups C, E, and I) and E. dumosa ssp. dumosa

(remaining groups). Systematic and regular sampling with respect to time and geography is required before definite conclusions can be made about the mechanisms and the taxonomic significance of variation in flowering periods. In this thesis information was derived mainly from herbarium records.

2.7 Summary

Preliminary investigations into aspects of variation covered in this chapter failed to reveal any fundamentally new characters readily applicable to taxonomic study. There is a general lack of discrete differences in seed morphology, wood anatomy, leaf anatomy and leaf architecture. Methods were developed to allow quantitative expression of leaf colour and texture by measuring height of cuticular sculpturing using epifluorescence microscopy and reflectances contributed by leaf glaucousness using a spectrophotometer. Major differences were found in the structure of cuticular and epidermal features within section Dumaria, but not within series Dumosae although the latter exhibited wide variation from flat to highly sculptured cuticles. A heavy wax bloom was shown to approximately double leaf reflectance in the visible spectrum and reduce the amount of energy absorbed. A wide range in glaucousness values was documented, with essentially non-glaucous individuals occurring in the same populations as individuals equally glaucous as E. cyanophylla. Thin-layer chromatography of leaf extracts revealed high variability between individuals but the compounds that separated out did not enable even the two species of series Dumosae and Torquatae to be distinguished. Study of herbarium specimen flowering records showed some significant geographic patterns but indicated only limited opportunity for reproductive isolation. There was greater irregularity than expected, and systematic records would be required for information of taxonomic value to be obtained.

CHAPTER 3

STUDY OF SESSILE FRUITED FORMS

(SESSDAT ANALYSES)

3.1 Introduction

A preliminary investigation of morphometric variation was made on individuals of series Dumosae with sessile fruits. These individuals form a subset of the Dumosae defined objectively but arbitrarily by the single character of pedicel length irrespective of species limits. Restricting the scope of study in this way meant that there were fewer components of variation to contend with and enabled character variation to be studied in more detail.

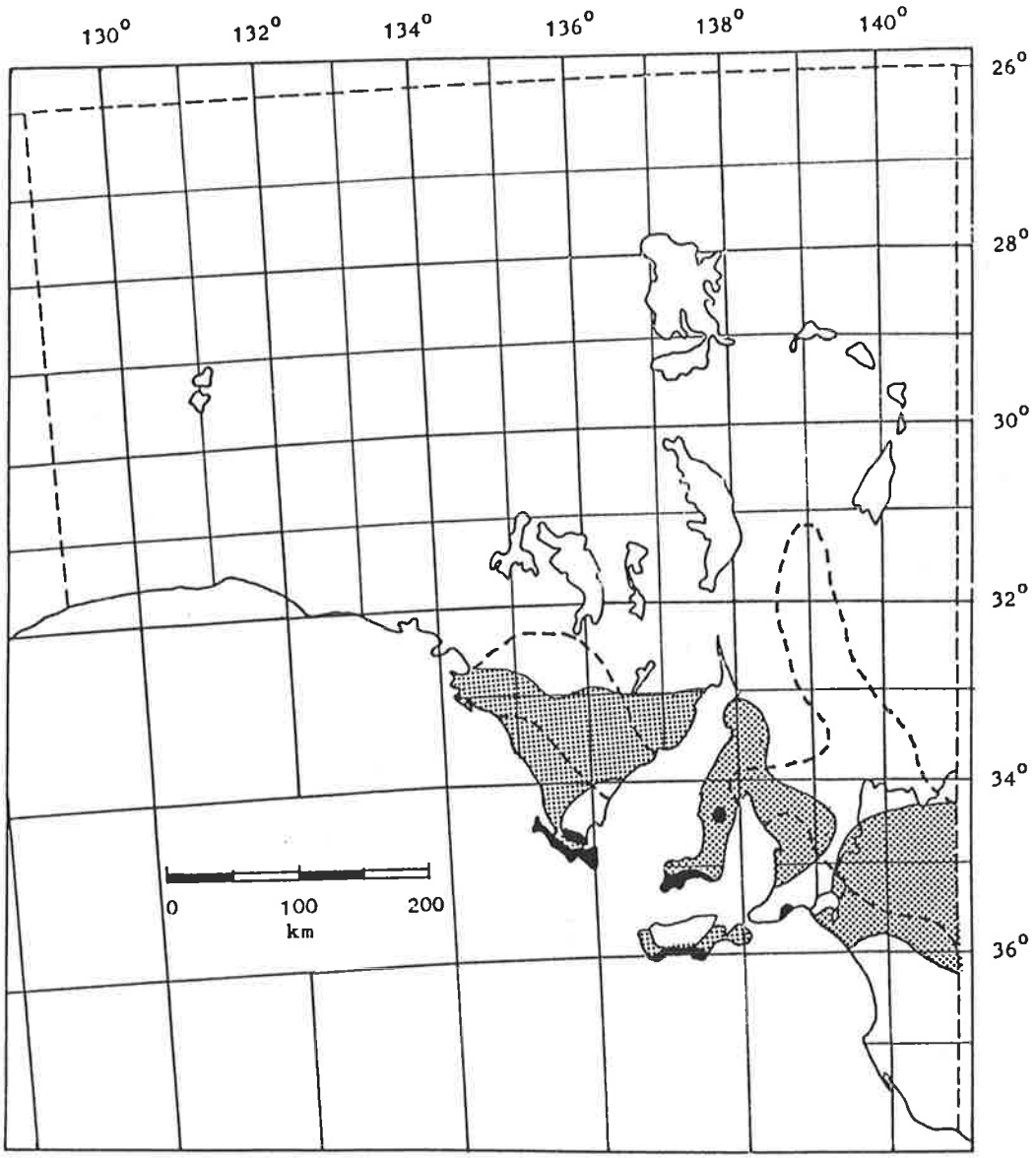
The only Dumosae taxa that have type specimens with completely sessile fruits are Eucalyptus conglobata and E. anceps. The original descriptions for both specify sessile flowers or buds although E. anceps * has sometimes been interpreted in a broader sense (Chippendale 1973, p. 151; Brooker 1976, p. 18) to include sub-sessile or shortly pedicellate forms. The Western Australian species E. kondininensis and E. fraseri are characterized by shortly pedicellate or sub-sessile fruits. Eucalyptus fraseri was originally described by Brooker (1972) as a subspecies of E. conglobata having either sessile or shortly pedicellate fruits. Brooker (1976) later elevated this taxon to specific rank and modified the description to exclude sessile forms which he considered were better placed in E. conglobata.

At the time of this study the most up to date information on the

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* see note regarding use of this name in section 1.2, p. 3

distribution of E. conglobata and E. anceps in South Australia was that of Boomsma (1972). Figure 23 is a composite of approximate distributions illustrated by Boomsma and shows occurrences of E. conglobata on Kangaroo Island, and the Fleurieu, Yorke and Eyre Peninsulas. Recently these distributions have been modified (Boomsma, 1981) following the results of this study (Boomsma, 1980, p.169; 1981, p.136)). Occurrences in all four regions are supported by computer-generated maps produced from the EUCALIST data bank of herbarium label information collated by Chippendale up to 1977. Boomsma's maps show E. conglobata as having the most southerly distribution and overlapping E. anceps in all regions except Fleurieu Peninsula. Further north E. anceps overlaps E. dumosa. The distribution pattern suggested the hypothesis that variation incorporating E. conglobata and E. anceps is a north-south, coastal-inland cline from sessile to pedicellate forms. Under this hypothesis the areas of overlap are not sympatric occurrences of distinct species but represent indistinct zones of intergradation. Pedicellate fruits are interpreted as resulting from the continuation of a trend in tapering of the hypanthium base associated with an increase in fruit length to width ratio. Comparison of type specimens and descriptions for E. conglobata and E. anceps indicated that the main differences between these taxa were a greater length to width ratio of fruits, peduncles and leaves for E. anceps. The simplest hypothesis is that these ratios are correlated with each other and increase in a northerly direction from E. conglobata to E. anceps to E. dumosa. Such a cline may be complicated by intergradation between sessile forms and pedicellate taxa other than E. dumosa. These include E. cyanophylla, E. calcareana or E. pileata, depending on the locality in an east-west direction. Effects of this complexity were minimized by testing only for part of a cline involving sessile forms.



23

Figure 23: Approximate South Australian distributions of three series Dumosae eucalypts according to Boomsma (1972).

E. dumosa

E. anceps

E. conglobata

3.2 Sampling of sessile forms in South Australia

A total of 127 individuals from 30 localities were sampled for numerical analysis. The localities are listed in appendix 4 and plotted in figure 24. Most specimens are taken from my own field collections. Up to five individuals were sampled from each locality within a radius of 1 km. Only localities with consistently sessile forms were selected for analysis and this limited the area of distribution covered. Localities were grouped into five geographically distinct regions isolated from each other by areas of sea, areas of higher rainfall uninhabited by any Dumosae, or areas occupied by pedicellate forms of Dumosae. Each of these regions will now be discussed.

1. Kangaroo Island (KI)

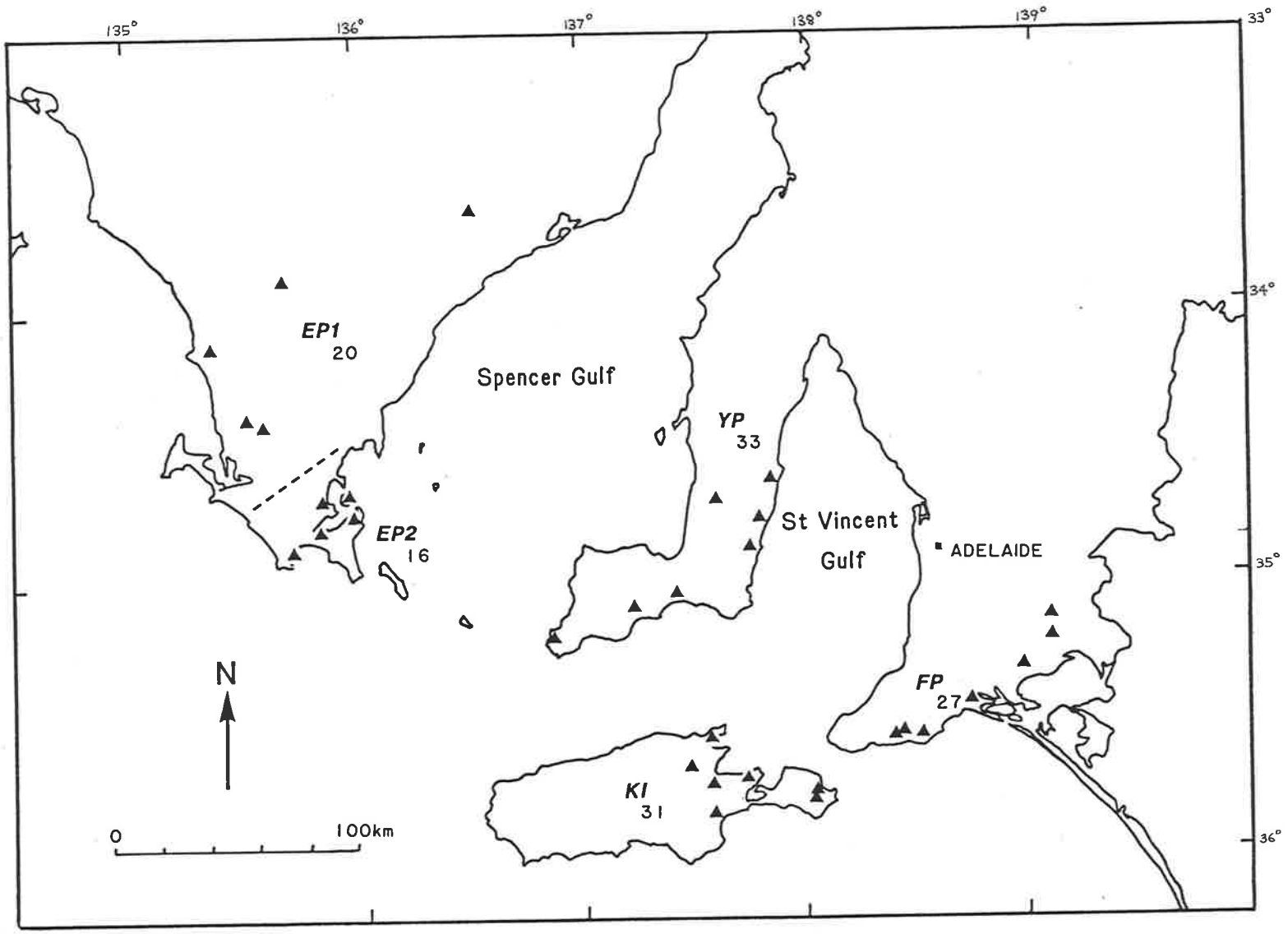
Sessile-fruited forms are the only Dumosae present on Kangaroo Island. Previously they were poorly collected here, being represented by only three collections at AD. Field surveys for this study revealed an easterly rather than southerly distribution and no observations were made west of longitude 137° 25′ E (13.1, p.333). The occurrences are on duplex loamy soils derived from schist and quartzite, lateritic soils, and calcarenite. All these soil types are present in the west but a higher annual average rainfall (> 600 mm) is probably the limiting factor. Kangaroo Island is isolated from Fleurieu Peninsula by Investigator Strait but it was connected as recently as about 10,000 years ago (Lampert, 1979).

2. Fleurieu Peninsula Region (FP)

There are only limited occurrences of sessile fruited Dumosae on the peninsula itself. These are disjunct and appear to be relict populations related to the more common occurrences on the plains and eastern slopes of

Figure 24: Map showing regions and localities for sampling of sessile-fruited forms in South Australia.

The total number of individuals represented by the localities is shown beside each region.


135°
136°
137°
138°
139°
33°
34°
35°
36°
EP1
20
EP2
16
Spencer Gulf
YP
33
St Vincent
Gulf
ADELAIDE
FP
27
KI
31
N
0
100km

the southern Mt Lofty Ranges to the northeast. The higher rainfall of the Ranges would provide a barrier to westward exchange. There is intergradation with pedicellate forms on the Murray plains to the north and east. Unlike the other regions this grouping does not correspond to a Region defined by the State Herbarium of South Australia (fig. 1), but incorporates material from the Murray and Southern Lofty Regions.

3. Yorke Peninsula (YP)

Occurrences on Yorke Peninsula are isolated from those of the Fleurieu Peninsula region by the Mt Lofty Ranges which have a higher rainfall and by areas inhabited by pedicellate Dumosae - on the Adelaide Plains (extending up the northeast side of St Vincent's Gulf) and at the top of Yorke Peninsula. Consistently sessile-fruited populations are known on the northern part of Yorke Peninsula from near Sandilands, Arthurton and Ardrossan. Although this area was not sampled in this study, material from further south is of a similar form and was well represented.

4. Upper Eyre Peninsula (EP1)

Occurrences on Eyre Peninsula are isolated from Yorke Peninsula by an area of low annual average rainfall (< 250 mm) in the north and northwest part of Spencer Gulf. This supports a low open woodland of Acacia papyrocarpa (Western Myall) rather than a mallee community. Sessile-fruited forms often intergrade with pedicellate forms on Upper Eyre Peninsula but consistently sessile populations do occur in disjunct localities. These are usually associated with inselbergs or ranges rather than the intervening dune-covered plains which are occupied by pedicellate forms of Dumosae.

5. Lower Eyre Peninsula (EP2)

This region in the vicinity of Port Lincoln is isolated from EP1 by the Koppio Hills to the north which are inhabited by pedicellate Dumosae and by a zone of higher annual rainfall (to 600 mm) to the northwest where no Dumosae have been recorded. Most of the the occurrences are on calcarenite and could be cut off under a higher sea level by the infilling of Sleaford Mere, a salt lake to the west.

3.3 Measurement of characters

The following six characters were measured for numerical analysis:

FL : fruit length

FW : maximum fruit width

PL : peduncle length

PW : maximum peduncle width

LL : leaf length (long axis of lamina from base to apex)

LW : maximum leaf width (perpendicular to midrib)

The fruit and peduncle characters were measured to the nearest 0.1 mm using dial calipers. Leaf characters were measured to the nearest 1.0 mm for LL and 0.5 mm for LW using a millimeter ruler. Each individual was represented by a mean score from a sample of fruits, peduncles, and leaves. Consideration was given to the effect of sample size on the ability to distinguish individuals statistically. Estimates of the population individual variance were made from samples of 10 measurements for each of about 10 individuals. Assuming that this is a good estimate applicable for all individuals, then the magnitude of a true difference in means that is detectable by a t-test can be determined by the formula given by Simpson et al. (1960, p. 194). For example, using a sample of 14

fruits to determine mean FW scores means that it is possible to detect differences between individual means of 1.0 mm with 95 % reliability using a t-test at the .05 level. To detect a difference of only 0.5 mm required a sample size of 54 fruits. This approach for optomizing sample sizes for measurements is still subjective as it requires an arbitrary decision on the magnitude of difference that is desirable for a given character. It does, however, demonstrate that there is no real meaning in statistically significant differences of mean character scores without reference to the degree of sampling.

Measurements for South Australian material were based on 14 fruits, 10 peduncles and seven leaves. These sample sizes enable detection of the following differences for the most variable character of each organ: 1.0 mm for FW, 3.0 mm for PL and 15 mm for LL. For Western Australian material sample sizes were reduced to seven, seven and five respectively. The reduction was necessary because of the need to reduce measurement time and the difficulty in obtaining sufficient organs on mounted herbarium specimens. This reduced the confidence interval for mean scores and thus increased between-individual variation. However, it was shown empirically that this was insufficient to affect the relatively high within-locality variance. It was tested using random sub-samples with the reduced sample sizes taken from the existing measurements for South Australian individuals. This was done for each region, for the locality with the highest ratio of mean individual variance to total locality variance.

3.4 Analysis of Variance

The suitability of the data for a Multivariate Analysis of Variance was tested using the SPSS subprogram MANOVA (Cohen and Burns, 1977). The data satisfied the requirement for non-orthogonality of variables according to

Bartlett's test of sphericity. However, the requirement of homogeneity of variances among character measurements was not met according to the Pearson and Hartley maximum variance/minimum variance statistic, Fmax ($P < 0.001$).

Univariate Analysis of Variance (AOV's) were therefore performed for each character, using SPSS* subprogram ONEWAY. For each character Bartlett's test of homogeneity of group variances was satisfied ($P > 0.05$). This test is also sensitive to departures from normality (Sokal 1965, p. 35).

The data is represented by three levels of sampling: individuals, localities and regions. The variation at the level of the individual reflects phenotypic variation resulting from the expression of a particular genotype. It is of no taxonomic interest per se and was removed by representing individuals by mean character scores. The within-locality variation is significant as it indicates the genetic variability present in an essentially uniform environment. For an intra-breeding population this can be treated as an error term underlying any variation of taxonomic importance. The within-region variation reflects differences between localities which may or may not be taxonomically significant.

Results of AOV's using within-locality variance as the error term revealed significant differences between localities within regions for FL and FW ($P < .001$) but not for PL, PW, LL and LW ($P > .05$). It is notable that differences were detected at the locality level considering the small locality sample sizes and generally high within-locality variation.

The AOV's using between locality variation as the error term revealed significant differences between regions ($P < .001$) for all characters.

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* SPSS is used throughout this study and refers to the Statistical Package for the Social Sciences (Nie et al, 1975).

The effect of different sample sizes for the region and locality levels was taken into account by partitioning the total variance by expectation mean squares, following the procedure used by Burley, Wood and Hans (1971). For all characters the greater portion of variation was contributed by regions (table 3.1).

Character	Percentage of total variation:	
	Localities within regions	Regions
FL	45.5	55.5
FW	31.6	69.4
PL	20.6	79.4
PW	20.7	79.3
LL	42.0	58.0
LW	17.3	82.7

Table 3.1: Components of variance partitioned using expectation mean square.

3.5 Correlation analysis

Values of the Pearson product-moment correlation coefficient (r) were computed for all 15 combinations of character pairs using SPSS subprogram PEARSON CORR. The results are shown in table 3.2. The first three pairs are length - width combinations describing the same organ. A positive correlation between length and width indicates variation expressing absolute size of the organ while a negative correlation indicates variation in length/width ratio expressing organ shape. For fruits and leaves significant positive correlations were obtained thus indicating dominance of the size component of variation. For PL and PW there was no significant correlation indicating that size and shape components were in

Table 3.2: Pearson correlation coefficients for data of South Australian sessile forms.

Characters	r
FL,FW	.35 *
PL,PW	-.04
LL,LW	.62 *
FW,PW	.71 *
FW,LW	.64 *
PW,LW	.59 *
FL,PL	.66 *
FL,LL	.03
PL,LL	.03
FL,PW	.01
FL,LW	.00
PL,FW	.16
PL,LW	-.06
LL,FW	.40 *
LL,PW	.31 *

* indicates significant correlations ($P < 0.01$)

balance. Correlation coefficients for the next six character pairs describe the coherence between similar attributes of different organs. All width characters are significantly correlated with other width characters and length characters behave similarly excepting LL which does not correlate with FL or PL. The remaining six character pairs show that lengths and widths of different organs are not correlated, again with the exception of LL which correlates significantly with FW and PW. These results disagree with the hypothesis of clinal variation in shape attributes which predicts that, for all organs, shape variation would dominate with strong coherence between length/width ratios.

3.6 Relationship with some environmental parameters

The following variables were determined for each locality and assigned to individuals:

ALT : Altitude (5 to 210 m)

TH : Maximum height in population (3.0 to 5.16 m)

RF : Mean annual average rainfall (375 to 700 mm)

DC : Distance from coast (0 to 56 km)

LAT : Latitude

LONG: Longitude

Correlation coefficients were computed for all possible pair-wise combinations of these variables and the six morphological characters. The results are shown in tables 3.3 and 3.4. The highest correlation is between LAT and LONG resulting from the northwest - southeast trend of localities sampled (fig. 24). LONG does not correlate significantly with other environmental parameters but there are significant correlations involving LAT, showing the tendency for higher rainfall and more coastal situation to the south. ALT correlates with higher rainfall but not

Table 3.3: Pearson correlation coefficients for environmental parameters.

**	LAT	LONG	DC	RF	ALT
LONG	.69 *				
DC	-.37 *	.12			
RF	.52 *	.11	-.38 *		
ALT	-.10	.02	.21	.40 *	
TH	.42 *	.09	-.38 *	.11	-.31 *

Table 3.4: Pearson correlation coefficients showing relationships between environmental parameters and morphological characters.

	FL	FW	PL	PW	LL	LW
LAT	.40 *	.46 *	.48 *	.13	.15	.23
LONG	.33 *	-.01	.35 *	-.27 *	-.08	-.17
DC	.02	-.46 *	-.07	-.36 *	-.12	-.26
RF	.37 *	.47 *	.26	.20	.12	.25
ALT	.13	-.05	.02	-.18	-.19	-.10
TH	.20	.51 *	.25	.33 *	.49 *	.35 *

* indicates significant correlations ($P \leq .001$)

** see description of environmental parameters, p. 55

geographic position and coefficients for TH indicate that the highest trees are associated with southern, coastal localities of low altitude. Relationships with morphological characters are complex. Individuals with large leaves (high LL and LW) tend to be higher trees. The association between RF and fruit size may result from the correlation between RF and LAT rather than being a direct effect of RF.

3.7 Univariate analysis of geographical relationships

Scattergrams of length on width were plotted for fruits, peduncles and leaves locality by locality and region by region. No simple pattern of clinal variation was detected and it was clear that subtle geographic trends would be overridden by the relatively large intra-locality variation. Larger scale regional differences were apparent with EP2 being strongly differentiated on the FL/FW and PL/PW plots (figs 25, 26). The values for FL and FW given in the original species descriptions are plotted on figure 25. The values given for E. conglobata by Maiden (1922, 6(56), p. 273) are typical for EP2 individuals in terms of both magnitude and ratio (0.6). The values for E. anceps (Blakely, 1934) are atypical being too large both in magnitude and ratio (=1.1). A length/width ratio of 1.0 is closer to the mean ratio for non-EP2 individuals. However, this ratio has been taken as the boundary for distinguishing E. conglobata (fruits wider than long) from E. anceps (fruits longer than wide), (Boomsma 1972, p. 28). This approach results in occurrences for E. conglobata in all regions and a distribution sympatric with E. anceps. Alternatively if a geographically based distinction between the taxa is applied, E. conglobata (EP2) can be distinguished from E. anceps (non-EP2) by a critical FL/FW ratio of 0.8. This value minimizes overlap between the two groups and results in fewer borderline cases. It is notable that on Eyre Peninsula complete separation of E. conglobata (EP2) and E. anceps

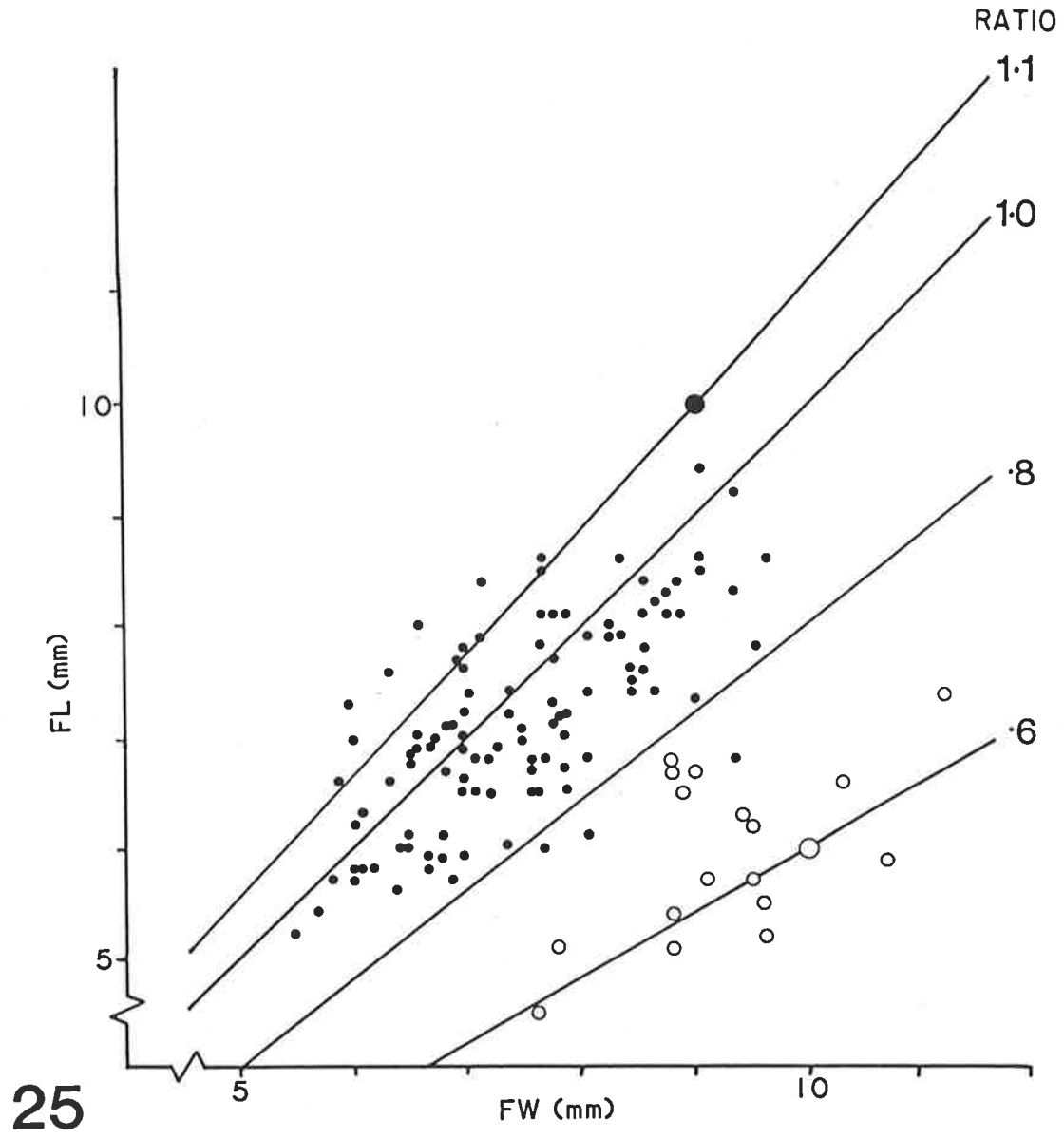


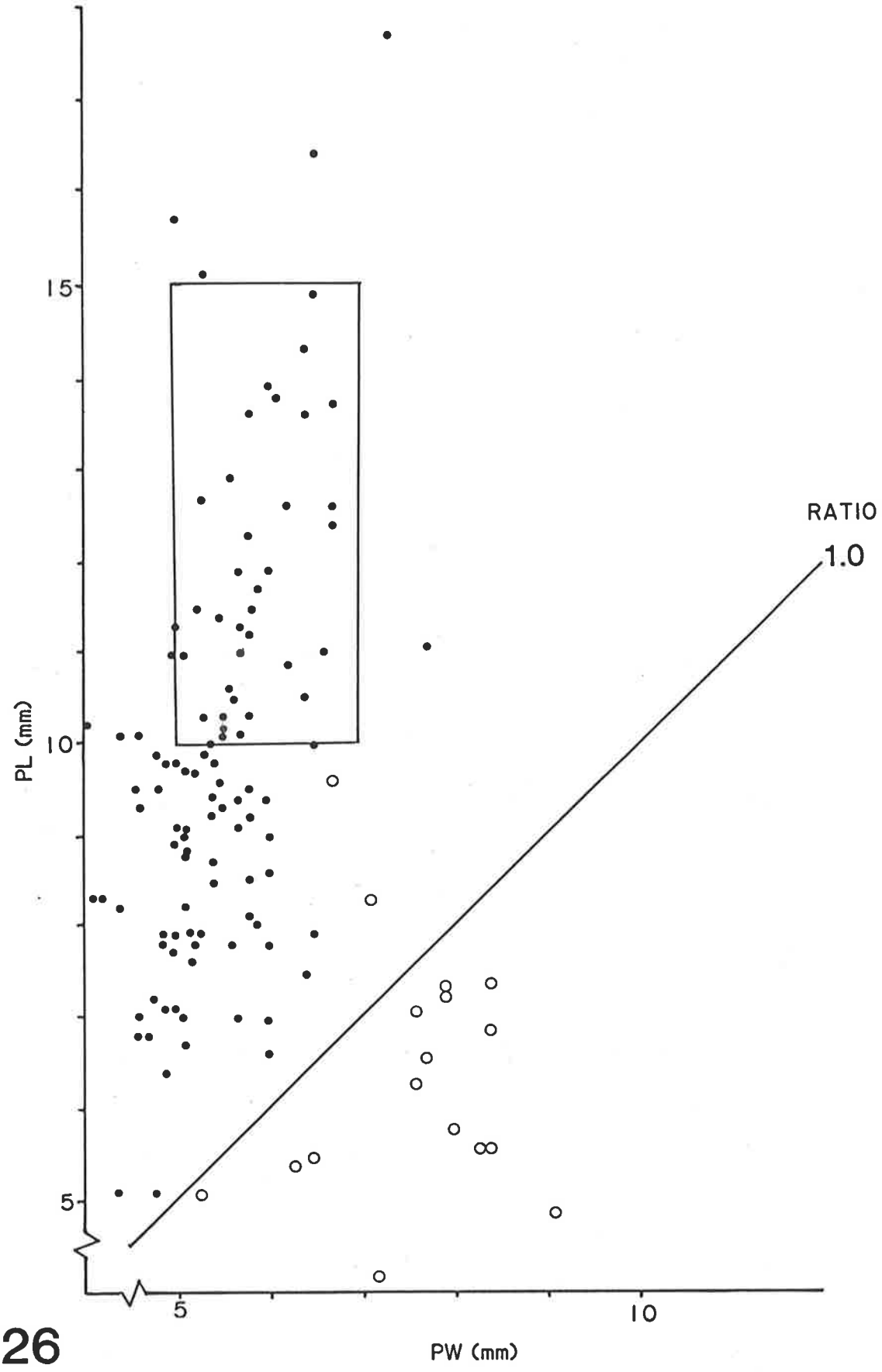
Figure 25: Scattergram of fruit length (FL) against fruit width (FW) for South Australian sessile-fruited Dumosae.

- • individuals sampled from Regions: KI, FP, YP, EP1
- o individuals sampled from Region: EP2
- ● measurements for E. anceps specified by Blakely (1934)
- ○ measurements for E. conglobata specified by Maiden (1922)

Figure 26: Scattergram of peduncle length (PL) against peduncle width (PW) for South Australian sessile-fruited Dumosae.

- • individuals sampled from Regions: KI, FP, YP, EP1.
- o individuals sampled from Region: EP2.

Rectangle indicates range for *E. anceps* specified by Blakely (1934).


15
10
5
PL (mm)
5
10
PW (mm)
RATIO
1.0

(EP1) can be achieved using FL/FW ratio alone. The PL/PW plot shows that EP2 individuals mostly have a ratio less than 1.0 which is exceeded by all non-EP2 individuals. However, only 34 % of non-EP2 individuals fall within the range of peduncle dimensions given in Blakely's description of E. anceps. Individuals from KI show better agreement with 65 % falling within this range. Although Kangaroo Island individuals are partially differentiated by longer peduncles, the major differentiation with minimal overlap occurs between EP2 and non-EP2. Regional differentiation was further investigated using multivariate analysis.

3.8 Multivariate analysis of South Australian sessile-fruited forms

Canonical Variates Analysis (CVA) has been used extensively in this study and is described more fully in section 5.2. Analyses were performed using SPSS sub-program DISCRIMINANT. CVA requires an a priori classification of individuals into groups. Linear compound functions are derived from these groups by weighting characters positively or negatively relative to their contribution to the polarity defined by groups. Functions can be used to test the distinctiveness of these groups or classify other individuals on the same basis.

A CVA was performed on 127 South Australian individuals divided into five groups defined by the five geographical regions. This generated four canonical variate functions. The first two together account for 96 % of the total variation and so include nearly all the information carried by the six characters. The plot of individual's scores on these two functions (fig. 27) shows that the EP2 region is completely disjunct from the other four regions all of which overlap each other to some extent. The degree of distinctness of each region can be expressed as the percentage of the individuals assigned to a region that are correctly classified by functions derived from the CVA (table 3.5). These results show

Figure 27: Canonical Variates Analysis for 127 individuals of South Australian sessile-fruited forms with groups defined by the five Regions.

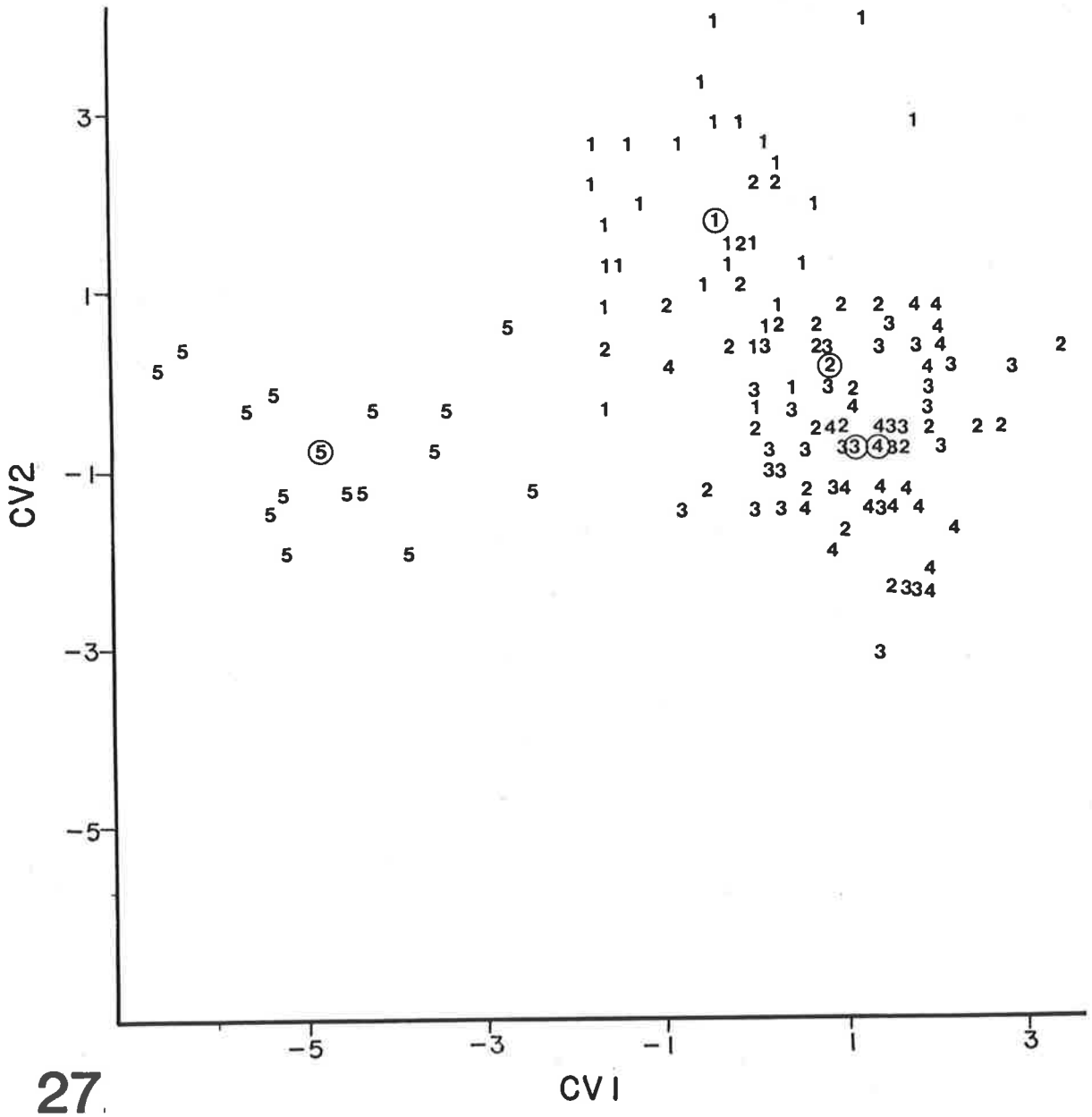
Group:	Region:	
1	KI	(Kangaroo Island)
2	FP	(Fleurieu Peninsula)
3	YP	(Yorke Peninsula)
4	EP1	(Upper Eyre Peninsula)
5	EP2	(Lower Eyre Peninsula)

○ indicates group centroid

CV1 : canonical variate 1 (75 % of variation)
principal loadings: -FW, +FL, (-PW)

CV2 : canonical variate 2 (21 % of variation)
principal loadings: +PL (+FW)

(total variation expressed by plot: 96 %)



27.

that E. conglobata and E. anceps are morphologically discrete if interpreted to correspond to the geographical grouping of EP2 versus non-EP2 regions. Consideration was given to treating E. anceps in a more strict sense, confining it to KI which includes its type locality. However, this was unsatisfactory because of the overlap between KI and other non-EP2 individuals, particularly FP. The overlap was maintained when the other non-EP2 individuals were defined as a third group in another CVA.

Region	% correct
EP2	100
KI	74
YP	61
EP1	55
FP	37
Overall	63

Table 3.5: Classification of individuals to regions by CVA. "% correct" represents the percentage of individuals in a defined group (= region) that are correctly classified by CVA into that group.

The conclusion reached using CVA assumes that the variation of greatest taxonomic importance is based on regional units. The validity of this assumption is supported by the greater variance attributed to regions compared to localities in the partitioning of variance and by the fact that in plotting bivariate scattergrams no major disjunctions were observed that were independent of region boundaries. To further test the

assumption, a Principal Component Analysis (PCA) was performed on the data using SPSS subprogram FACTOR. With PCA the data is interpreted in terms of major independent axes of variation which involves no a priori assumptions about groupings within the data. There were no major disjunctions found on any of the five principal component axes. However, when the two groups EP2 and non-EP2 were identified on plots of factor scores (SPSS option FACSCORES), the first two components produced an ordination with minimal overlap (fig. 28). The distinction between EP2 and non-EP2 is expressed by a large part of these components which together account for 73 % of the total variance.

Four additional individuals, unassigned to groups, were classified using unstandardized classification fuctions (output by SPSS DISCRIMINANT, option 11) derived for the CVA. Two of these represent character values derived from modal values of original descriptions and mean measurements from illustrations of associated material for each of E. conglobata and E. anceps. Also included were measurements for a specimen collected from Kangaroo Is in a survey by Lange (1979, p. 74) and a specimen I collected from near Minlaton, Yorke Peninsula (PJL 803). The Kangaroo Island individual was correctly classified but the Yorke Peninsula individual was assigned to EP1. The cases representing 'typical' E. conglobata and E. anceps were classified to EP2 and KI respectively. These regions include the type locality for each species, so this supports the region-based classification of these taxa.

The tentative conclusion suggested by the South Australian material is that E. conglobata and E. anceps are morphologically and geographically distinct taxa. The interpretation of these taxa according to the EP2/non-EP2 grouping of South Australian specimens will be designated by 'CON' and 'ANC' respectively.

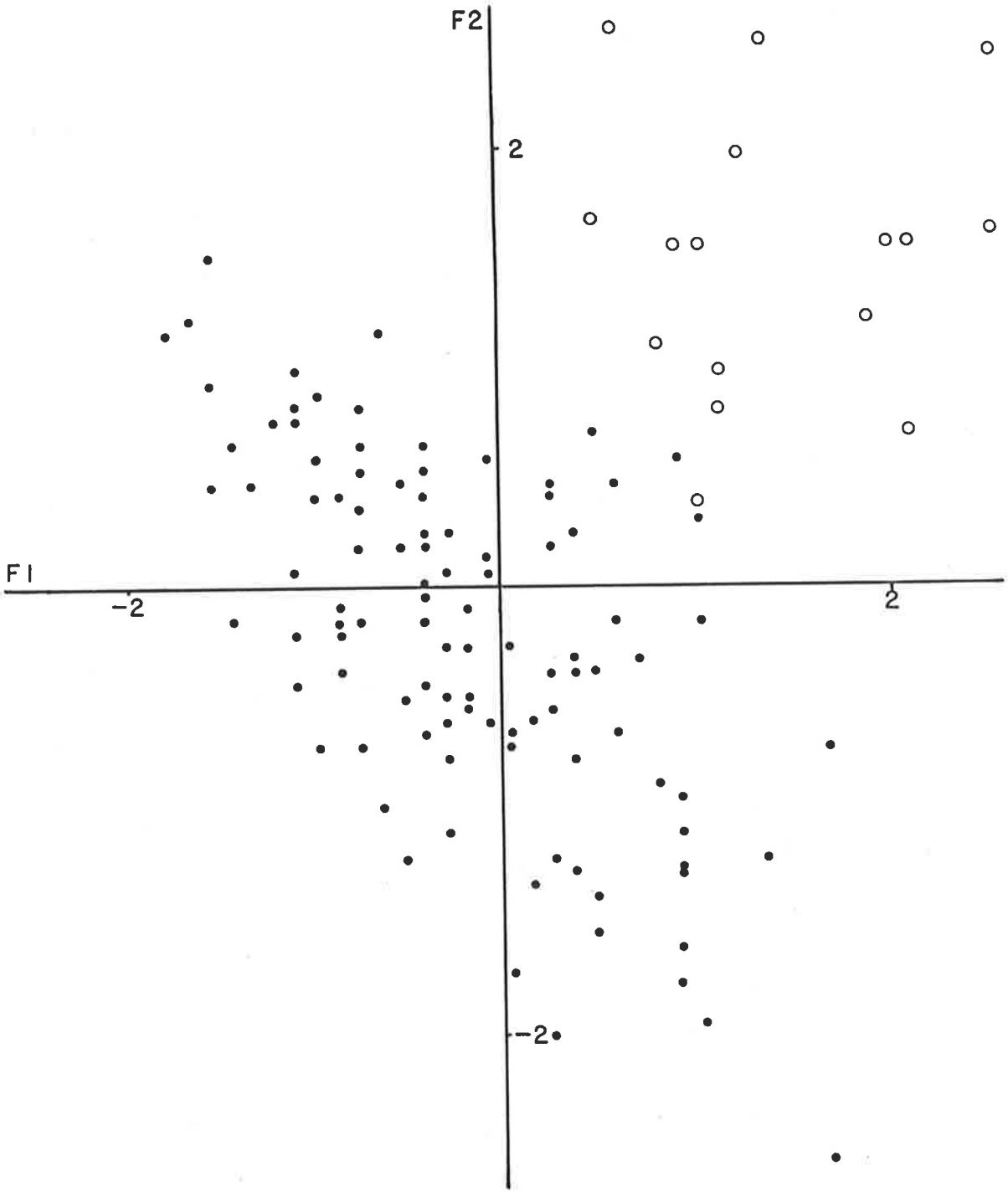
Figure 28: Principal Component Analysis of the 127 South Australian sessile-fruited individuals.

o classified to CON (= EP2) by CVA

• classified to ANC (= non-EP2) by CVA

F1 : 1st principal component (45 % of variation)
loadings: +FW, +PW, +LW, +LL, (+FL, +PL)

F2 : 2nd principal component (28 % of variation)
loadings: +FL, +PL (+FW, -PW, -LL, -LW)



28

This study indicates a distribution pattern differing markedly from the previously accepted one in that the E. conglobata occurrences on Kangaroo Is, Fleurieu Peninsula and Yorke Peninsula should now be treated as E. anceps. Subsequent to this study, two collections were found which are an exception to this pattern and extend the range of E. conglobata from Eyre Peninsula to include a limited, disjunct occurrence on Fleurieu Peninsula. The specimens involved are: J.B. Cleland s.n., 27.i.1933/Road across Upper Willow Creek, Waitpinga; and J.B. Cleland 19, -.ii.1946/Scrub near Bluff, Encounter Bay. The latter is represented by a sheet at AD with specimens from two different individuals both clearly referable to the group CON. From the same locality there is also a sheet of J.B. Cleland 18, -.ii.1946 with two different individuals, both clearly referable to ANC. Duplicates of J.B. Cleland 18 and 19 at NSW provide further material representing E. anceps. Although intermediates are not present amongst the individuals from this locality, there is considerable variation in the critical characters of peduncle length and fruit length/width ratio as well as in fruit size. However, the sample is too limited to prove whether or not the two forms occurred together without intergradation at this locality. Other Cleland collections from this district are referable to ANC. The area near the Bluff (Rosetta Head) has been extensively cleared, and despite careful searching of small remnants of native vegetation, no Dumosae could be located. It seems that typical E. conglobata forms are now extinct on Fleurieu Peninsula. Forms referred to this taxon by Boomsma (1980, 1881) from the Waitpinga Creek basin were classified to ANC by the CVA, but their canonical variate scores showed that they were amongst specimens of this group closest to CON.

The results of the CVA (fig. 27) provide further information on morphological relationships. The first canonical variate has the character weighted so that it describes mainly FL, FW and to a lesser degree PW.

This is the major pole of variation which separates CON and ANC but it is also expressed to a lesser extent within the ANC cluster. The centroids of KI, FP, YP and EP1 have progressively higher scores on this function. Individuals of ANC from KI are most similar to CON and those from EP1 are least similar despite being geographically closest. The second canonical variate is weighted predominantly on PL. It does not contribute to the separation of CON and ANC, and although there is some variation within the CON cluster, it is mainly expressed within the ANC cluster with the regions falling into the same sequence as on the first function. The distances between the centroids of each group in multivariate space defined by all the canonical variate axes are equivalent to D. D^2 is the Mahalanobis distance between groups, a measure that scales differences according to within-group variation. Distances were tested using F ratios and group centroids were found to be significantly different ($P < .001$) for all regions except EP1 and YP ($P > .05$).

The analysis was repeated defining two groups (CON and ANC) instead of five. This produced a single discriminant function with a weight for each character corresponding to its importance in separating CON and ANC (table 3.6). PW is the most useful character and LL the least. The signs indicate that CON is distinguished from ANC by wider and shorter peduncles and fruits and by leaves that are wider but also longer. The deviation of LL from the pattern between length and width characters agrees with the result from correlation coefficients. The PCA ordination on the groups CON and ANC (fig. 28) displays a low degree of clustering in that there is only a limited zone of overlap or contact. This indicates that the variation between CON and ANC, as expressed by the discriminant function of Table 3.6 and the first canonical variate of figure 27, is not trivial but is a significant component of the overall variation.

Table 3.6: Discriminant function coefficients for CVA to separate groups CON (-ve pole) and ANC (+ve pole).

Character	Sign	Weight
PW	-	.90
FL	+	.74
PL	+	.61
FW	-	.60
LW	-	.38
LL	-	.15

Table 3.7: Effect of reducing the character set for CVA on the percentage of individuals correctly classified. (CVA based on 127 S.A. individuals.)

Variables in discriminant function	% correct
PW, FL, PL, FW, LW, LL	100
PW, FL, PL, FW	100
PW, FL, PL	98
PW, FL	96
PW	84
FL	75
PL	76
FW	79
LW	71
LL	73
FL, FW	98
PL, PW	96
LL, LW	88

To further investigate the value of characters in identifying the two taxa, a series of CVA's were performed with reduced character sets (table 3.7). Complete discrimination can be achieved without the leaf characters. Using the two characters with highest weights, PW and FL, discrimination is only reduced to 96 % correct classification. If a single character was used in a key to separate CON and ANC the best result (84 % correct classification) would be obtained using PW. The best result for a discriminant function based on two characters is 98 % using FL and FW. Even with only two characters such a function would be too cumbersome to use in a key. However, the same discriminating power (98 %) can be obtained when FL and FW are combined as a ratio rather than a vector sum. Using the critical FL/FW ratio of 0.8, only three individuals of ANC would be misclassified in figure 25.

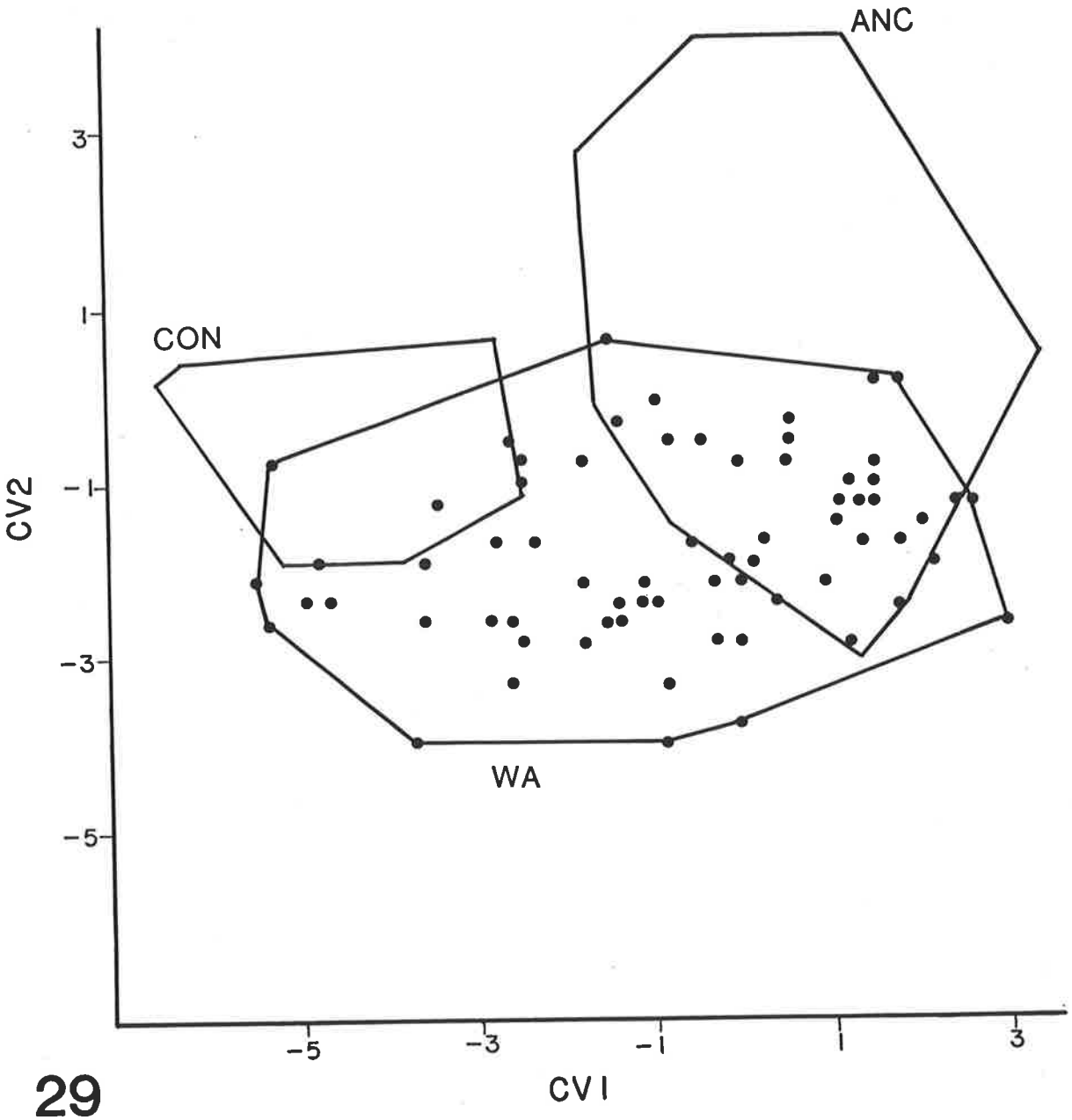
3.9 Analysis of Western Australian sessile-fruited forms

The characters were scored for 75 individuals from Western Australia (WA). Most of this material was from my own field collections but 28 specimens were a selection of herbarium specimens from PERTH, FRI and AD. Out of a total of c. 150 available herbarium specimens only 28 were sufficiently complete to provide satisfactory material for the required seven fruits, seven peduncles and five leaves. The data were input as unassigned cases for classification by the CVA of South Australian (SA) material based on regions. It is clear from the plot of function scores (fig. 29) that much of the WA material is intermediate between CON and ANC. Compared to SA individuals, WA specimens generally have much lower scores on the second canonical variate. This reflects the trend for shorter peduncles and to a lesser extent narrower fruits for WA. Using the territorial map overlay (appendix 5) it is apparent that most of the WA individuals are classified with regions EP1 and YP. Their mean score on the second canonical variate

Figure 29: Canonical variate scores for 75 unassigned Western Australian sessile-fruited individuals classified by the CVA of South Australian material (fig. 27).

Classification of individuals with respect to the five South Australian Regions may be determined using the overlay territorial map (appendix 5).

NOTE: Information from the overlay territorial map transparency has been added to Figure 29



29

is below that of EP1 and YP. Thus there is a continuation of the trend KI - FP - YP - EP1 further westwards to WA.

The taxa defined by CON and ANC clearly intergrade in WA. However, the possibility of an alternative classification that might result in more distinct taxa was considered. CVA's were performed treating WA individuals as a separate taxon. When the two groups SA and WA were defined, 80 % of specimens were classified correctly to their state of origin. The discriminant function weights (table 3.8) show the principal differences involved. Defining three groups (WA, ANC and CON) the same overall level of discrimination was achieved (80 %) but only 73 % of the WA individuals were correctly classified (fig. 30). This does not support the recognition of WA material as a separate taxon.

The taxonomic significance of the classification of WA specimens according to the SA analysis, is supported by the existence of a geographic pattern (fig. 31). Individuals nearer to CON occur in the east and in a coastal fringe to the west, while those nearer to ANC occur mainly in the west and extend further inland. An exception to this is an eastern outlier of specimens classified as ANC, growing on limestone south of Caiguna. Intergradation is exhibited by localities that have intermediate probability values for classification to CON or ANC. Four localities have a mixture of individuals classified to each taxon. There are no major geographic disjunctions in the distribution of sessile-fruited forms that could be used as a basis for groups in any alternative classification.

Further support for the application of the SA concept of CON and ANC is provided by the results of a PCA on the 75 WA individuals (fig. 32). The CON-ANC distinction is well represented by the first principal component which accounts for 64 % of the total variation.

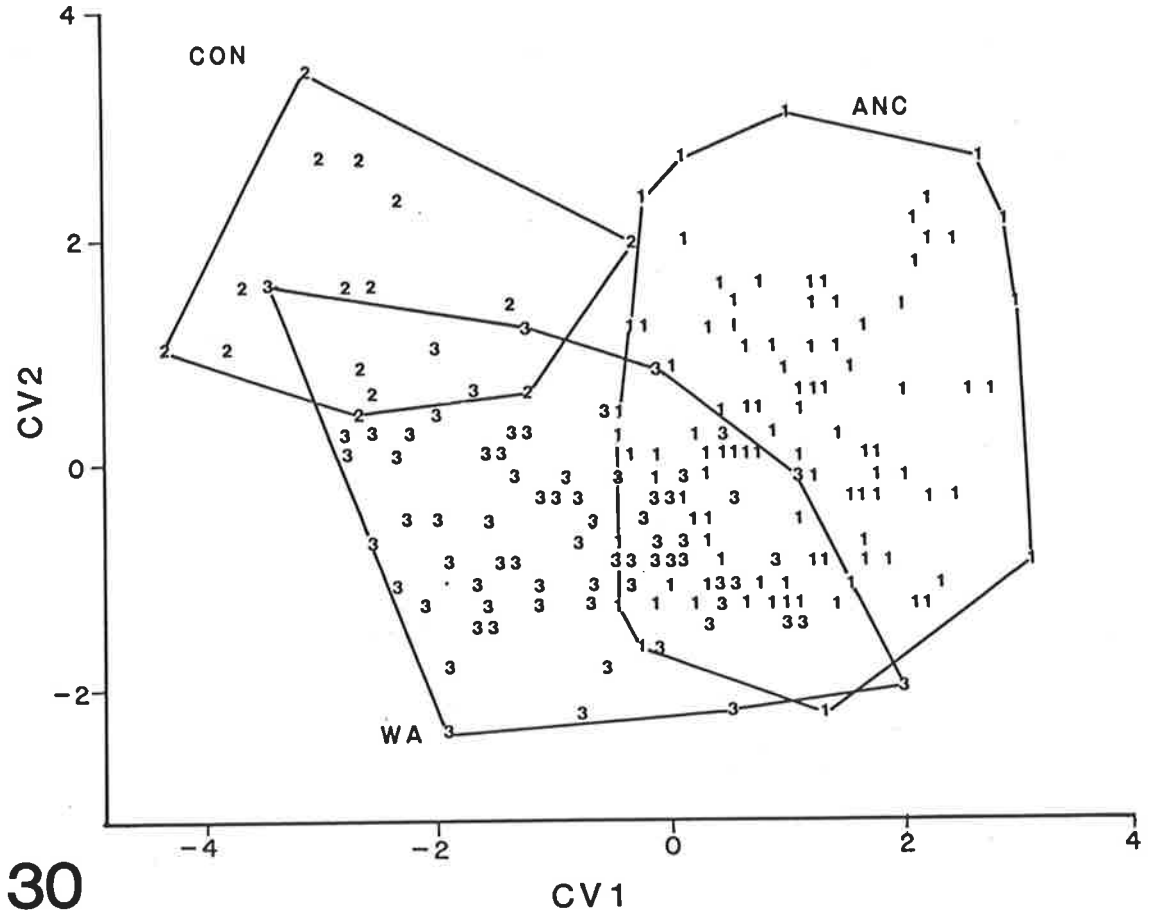


Figure 30: Canonical Variate Analysis of 202 sessile-fruited individuals based on three regional groupings.

South Australia:

1 : ANC (= Regions KI, FP, YP, EP1)

2 : CON (= Region EP2)

Western Australia

3 : WA

Figure 31: Distribution of Western Australian sessile-fruited forms showing classification results for CVA based on groups CON and ANC.
Line lengths are proportional to P(CON/X), the probability that an individual belongs to group CON.

- indicates position of localities sampled by more than one individual.

Line length	Range for P(CON/X) *	
shortest (1)	< .1000	
2	.1000 - .1999	
3	.2000 - .2999	classified to
4	.3000 - .3999	ANC
5	.4000 - .4999	
6	.5000 - .5999	
7	.6000 - .6999	
8	.7000 - .7999	classified to
9	.8000 - .8999	CON
longest (10)	.9000 -1.0000	

* Probability values for P(ANC/X) are complementary.

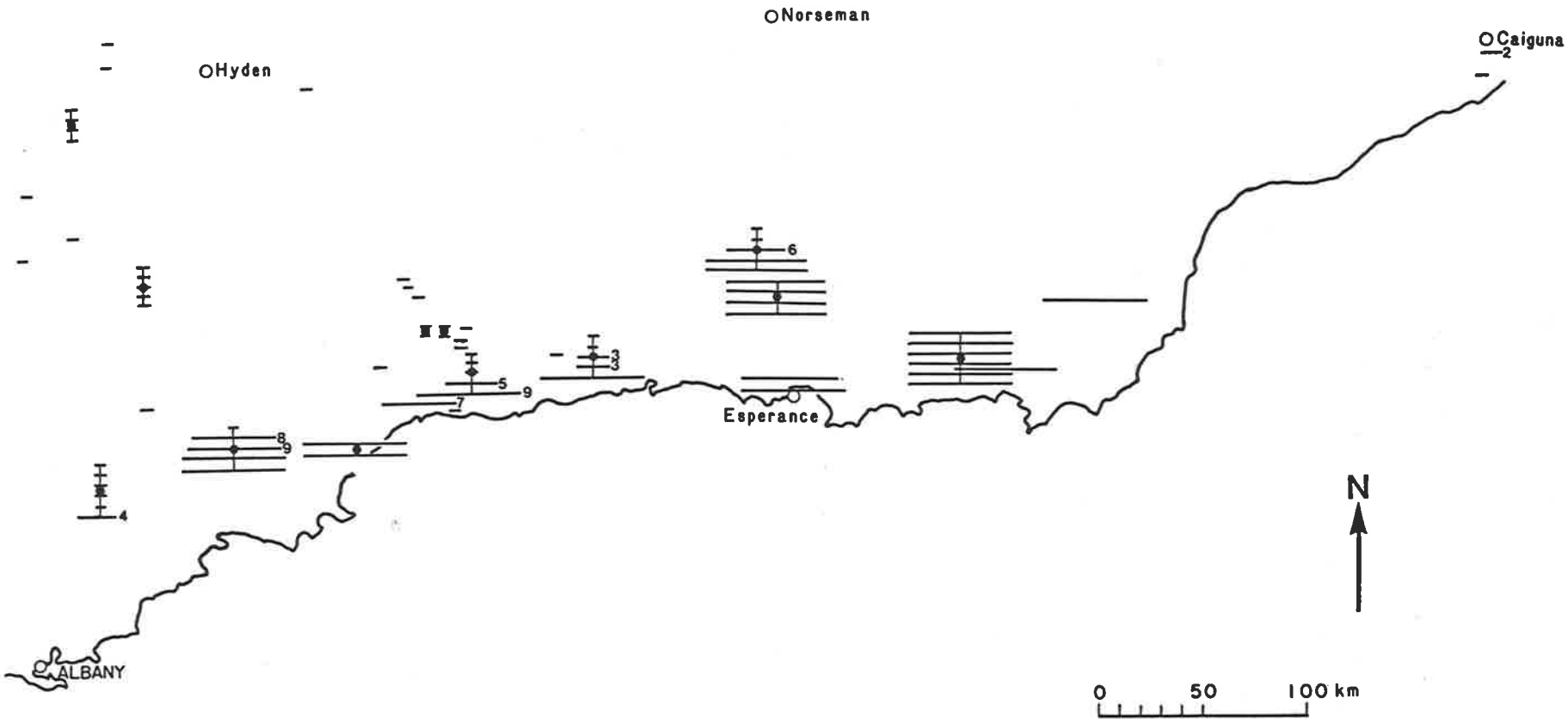

Norseman
Caiguna
Hyden
Esperance
ALBANY
N
0
50
100 km

Figure 32: Principal Component Analysis of the 75 Western Australian sessile-fruited individuals.

- o classified to CON by CVA
- • classified to ANC by CVA

F1 : 1st principal component (64 % of variation)
loadings: -PL (+ all others)

F2 : 2nd principal component (17 % of variation)
loadings: +PL, +LL, +FL, -PW (-LW)

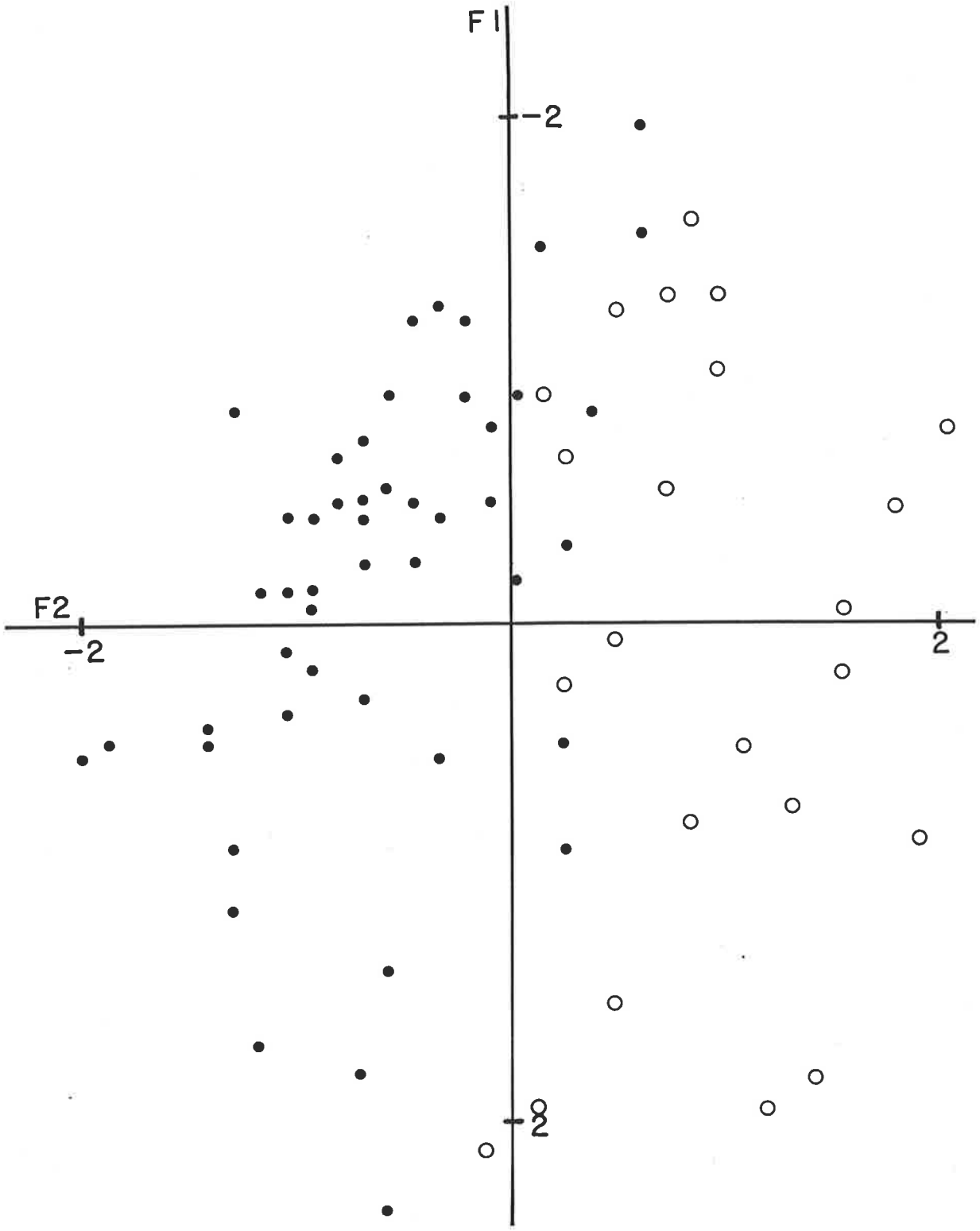

F1
-2
F2
-2
2
2

Table 3.8: Discriminant function coefficients for CVA to separate groups WA (-ve pole) and SA (+ve pole).

Character	Sign	Weight
FW	-	1.01
PL	-	.88
PW	+	.65
LL	+	.37
LW	-	.10
FL	+	.02

Table 3.9: Discriminant function coeficients for CVA's based on alternative groupings of 28 W.A. specimens scored from herbarium sheets.

Groups defined by classification to CON (-ve pole) or ANC (+ve pole) by CVA of S.A. individuals.

Character	Sign	Weight
PW	-	1.31
FL	+	1.11
PL	+	.68
LL	-	.64
FW	-	.48
LW	-	.05

Groups defined by most recent determination on sheet: *E. conglobata* (-ve pole) or *E. anceps* (+ve pole).

Character	Sign	Weight
FL	+	1.23
FW	-	1.14
LW	-	.37
PL	+	.06
LL	-	.04
PW	+	.02

Both the names E. conglobata and E. anceps have been applied to the WA material. To test the existing concept used in classifying WA material, the subset of 28 specimens measured from herbarium sheets was subjected to two further CVA's. In the first CVA, two groups were defined according to classifications of the 28 specimens by the SA analysis to CON or ANC. This resulted in 100 % correct classification and generated the discriminant function shown in table 3.9. For the second CVA the groups were defined according to the most recent determination made on the herbarium sheet. This resulted in 82 % (23/28) correct classification. The five individuals misclassified were labelled E. conglobata but classified to ANC on the basis of their discriminant function scores. This indicates an inconsistency in the distinction between the taxa which would be expected if workers have uncertain or conflicting concepts of them. Despite the misclassification (or overlap), the discriminant function generated by this analysis (table 3.9) represents a polarity which best corresponds to the way WA specimens are classified overall. The function loads mainly on the characters FL and FW, and in contrast to the function for the first analysis, the other characters carry very little weight. This suggests that workers have based determinations solely on FL and FW ignoring peduncles and leaves. Also of interest is the fact that the misclassifications were determinations to E. conglobata. According to the herbarium determinations the two taxa are represented in equal proportions while under the SA view ANC forms predominate over CON 19 to 9. There may be a tendency for taxonomists to split intergrading material into groups which have a similar number of representatives or area of occurrence. In this way E. conglobata would be over-represented. This idea is supported by the results of the SA analysis which shows that E. conglobata and E. anceps are best treated as uneven groups with E. conglobata restricted in concept and not extending far from its type locality when previously it was treated as being more widespread but less distinct.

Based on the failure of CVA to adequately separate the two taxa in Western Australia, it is concluded that E. anceps and E conglobata should not be distinguished at the specific level.

CHAPTER 4

SELECTION OF CHARACTER SET

4.1 Introduction

Following the analysis of sessile-fruited forms, numerical analysis of the entire Dumosae was initiated. The selection of characters for this analysis was made in two stages. Following an examination of morphological variation in Eucalyptus, series Dumosae, a subjective choice of characters was made. These characters were then scored on a test set of specimens and were further selected and modified according to quantitative attributes.

The initial character set was derived after subjective appraisal of specimens representing all existing taxa. In addition to the special investigations described in chapter 2, careful examinations were made for basic macro-morphological differences of taxonomic potential. Taxa were found to differ mainly by continuous vaiation in form rather than presence or absence of discrete characters. There are no distinctive features confined to a single taxon but only unique character combinations, or in some taxa, extreme or disjunct values of character states.

The initial selection of characters was made to satisfy the following criteria:

1. The character must be capable of quantitative expression to be suitable for numerical analysis. Some diagnostic characters used in descriptions and keys, such as leaf colour and texture, were avoided since they can not directly be expressed as objective measurements.
2. The character must be either a continuous metric or an ordered multistate character but not a non-ordered multistate character. The use of non-ordered states implies independent causality. Such characters

should be resolved into uni-dimensional component characters to achieve a linear measure of resemblance obeying the rule of additivity. Preference was given to high-order multistate characters over low-order multistate or binary characters since the former contain more information on the degree of resemblance between OTU's.

3. The character must be capable of measurement in a reasonable time with available apparatus. Cost of measurement must be weighed against amount of useful information contributed.

4. The character must contribute sufficient information that is potentially useful taxonomically. It must either exhibit significant differences between geographically separate populations or else a disjunction in its variation within specimens from the same locality.

5. The character must be capable of being scored from herbarium collections. It was necessary to use some existing herbarium collections because of the difficulty in visiting remote areas in northwestern South Australia and western Western Australia. This restriction is advantageous in that taxonomic conclusions will result in a new classification readily applicable to herbarium material.

4.2. Definition of characters

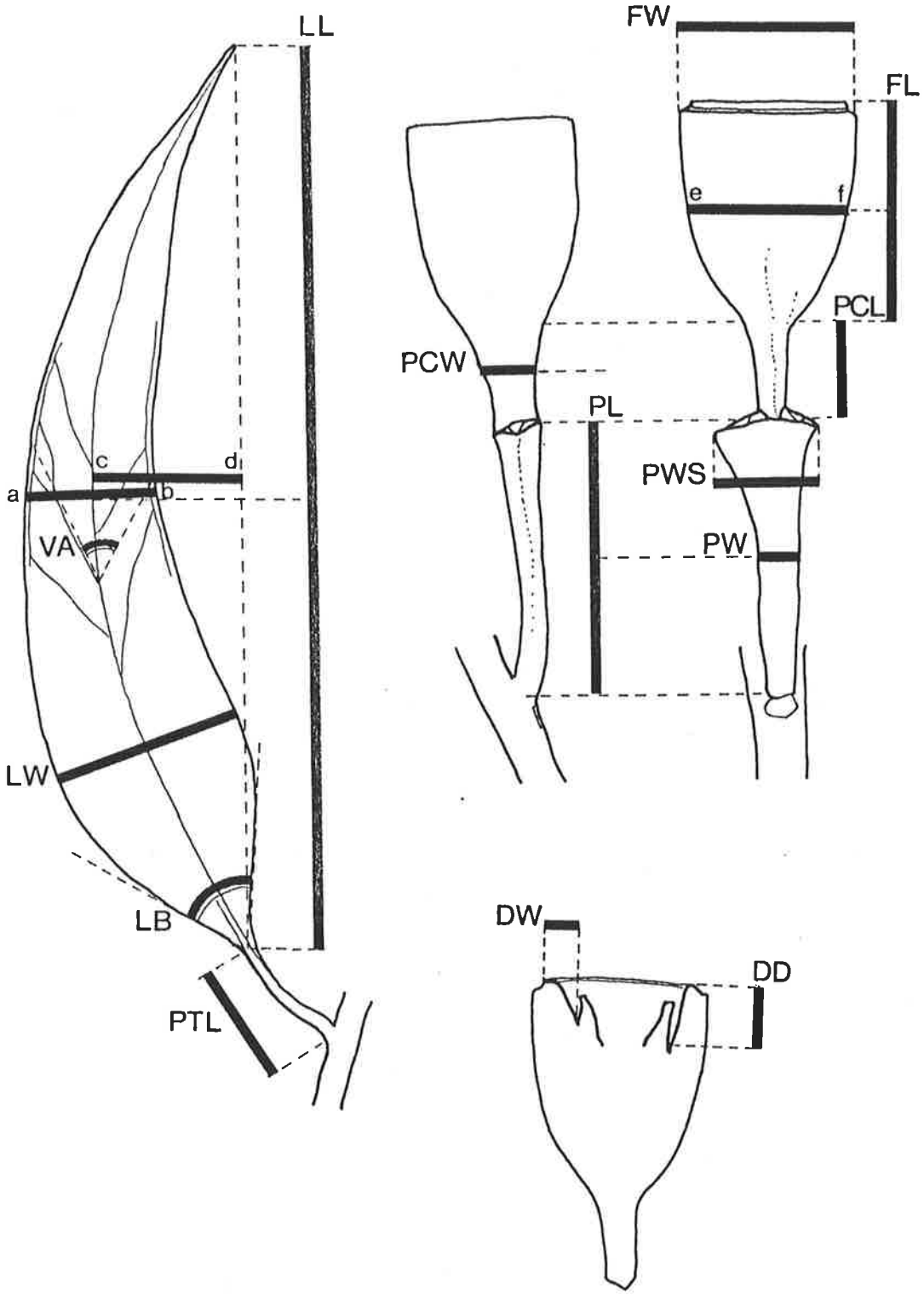
It is important to define character measurements in detail so that they can be applied by other workers to additional material or be validly compared with existing data. The following descriptions of character measurements refer to figure 33. Characters will be referenced by abbreviations for which an alphabetic key is provided in table 4.1.

Measurements were made from specimens that were in a dry, and in most cases, pressed state. Extreme pressure during pressing can result in distortion of buds and even quite robust fruits. Where compression occurred it was usual to find some buds or fruits which escaped

Table 4.1: Key to alpha-numeric symbols for characters.

* indicates characters excluded from the final set.

	Symbol	Meaning	Precision
	BB	Presence of blackbutt	2 states
	CS	Height of cuticular sculpturing	-
*	CU	Leaf curvature (midrib deviation from long axis/LL)	1 mm
*	DD	Disc depth	0.1mm
	DDR	DD/FL	0.1mm
	DW	Disc width	0.1mm
	FL	Fruit length (excluding pedicel)	0.1mm
	FR	Depth of regular ribbing on fruit	0.05mm
*	FW	Fruit width at base of rim	0.1mm
	FWL	FW/FL	0.1mm
	FWM	Fruit width at mid-fruit length	0.1mm
	FWMR	FWM/FW	0.1mm
*	LB	Leaf base angle	5°
	LG	Leaf glaucousness	3 states
	LL	Leaf length	1 mm
	LTH	Leaf thickness	0.01mm
	LW	Leaf width at widest point	0.5mm
	LWM	Leaf width at mid-length/LW	0.5mm
	NPU	Maximum number of buds per umbel	5 states
	OLW	Operculum length/operculum width at base	0.1mm
	OPR	Depth of ribbing on operculum	0.05mm
	OWM	Operculum width at mid-length/ operculum width at base	0.1mm
	PCL	Pedicel length	0.1mm
	PCW	Pedicel width at mid-length	0.1mm
	PL	Peduncle length	0.1mm
	PTL	Petiole length	1 mm
	PW	Peduncle width at mid-length	0.1mm
	PWS	Peduncle width at summit/PW	0.1mm
	SG	Stem glaucousness	2 states
	VA	Angle between pair of secondary veins at mid-length	5°
	VN	Number of valves per fruit	-



33

Figure 33: Definition of the principal leaf and fruit characters.

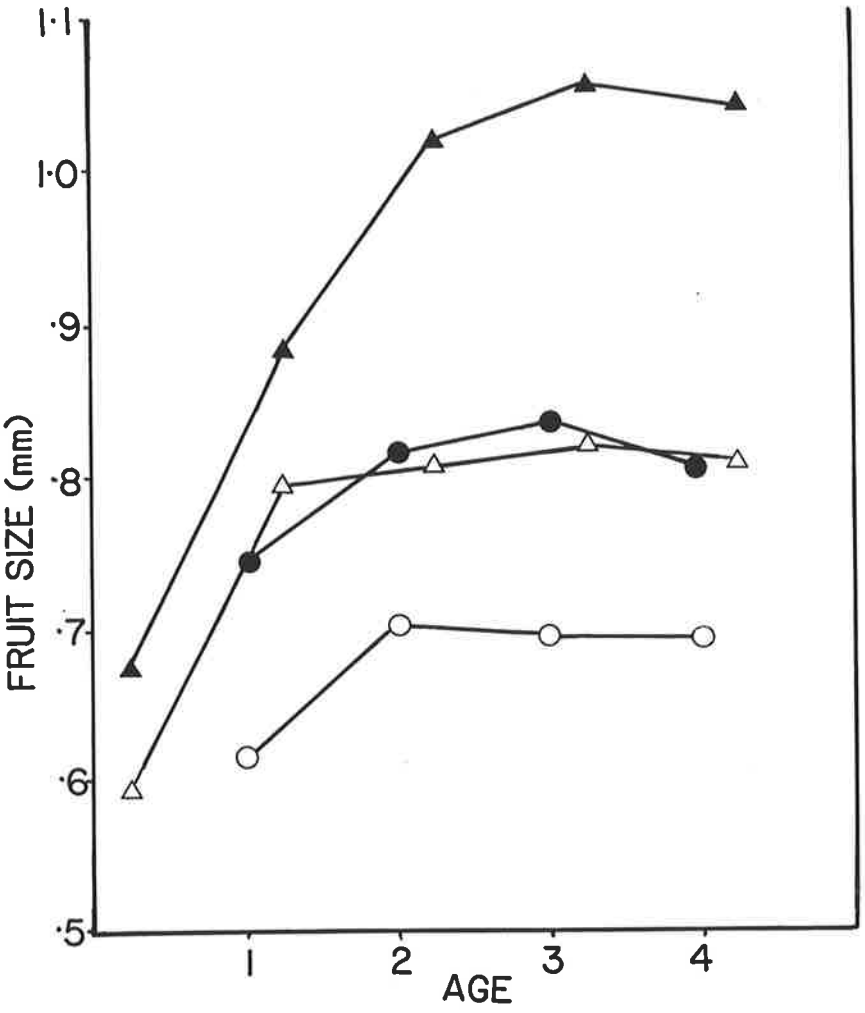
compression owing to their position in the umbel or protection by thicker stems. Measurements were only made on uncompressed organs. Scores for all characters, except when indicated otherwise, were determined as a mean value for the individual based on a sample of five organs (leaves, fruits, peduncles or buds). The degree of precision for each measurement is shown in table 4.1.

4.2.1 Leaf characters

The first nine characters were measured on mature, fully expanded leaves. Those not mis-shapen and of most adult form in the sequence juvenile - intermediate - adult were selected. Excepting when otherwise indicated, leaf measurements were made by overlaying a transparent ruler graduated in millimetres.

4.2.2 Reproductive characters

The remaining characters describe the morphology of fruits, peduncles and buds. Except where indicated otherwise, measurements were made using dial calipers graduated to 0.5 mm. A high degree of repeatability of measurements was obtained when a specific orientation of the organ was prescribed. Measurement of fruits and peduncles were made on umbels bearing mature fruits. Mature fruits are those which on drying release ripe seed (red-brown rather than pale-brown or straw coloured) and have valves completely separated (2.6.1). This stage is reached about a year after flowering. Most changes in fruit dimensions occur before this but there is a tendency for some swelling to continue if the fruit is retained on a growing branch (fig. 34). The peduncle also becomes engulfed at its base. These problems were avoided by selecting fruits from low order branches. As older fruits are weathered the disc may become indistinct and the epidermis breaks up causing irregularities, loss of ribbing and a



34

Generations after flowering

Figure 34: Relationship between fruit size and age.

Plot of characters FL and FW (mean of 10 fruits) for successive generations of fruits in two sessile-fruited individuals. Fruits were taken from branches that had continued as axes of growth after flowering.

▲ FWM PJL 660

△ FL PJL 660

● FWM PJL 757

○ FL PJL 757

reduction in fruit size. Fruits with signs of swelling or excessive weathering were avoided.

Only three characters describing bud morphology were included for measurement. The number of bud characters was minimized to reduce problems associated with missing data in analyses. It is usually possible to obtain mature fruits on fertile individuals of series Dumosae at any time of year. However, mature buds may only be present for a short period prior to flowering unless flowering is delayed by unfavourable conditions. All characters excepting the three bud characters were scored on all individuals. Buds are often attacked by weevils belonging to a group with at least three closely related species in the mallee areas of South Australia and Western Australia. The larvae feed on the enclosed stamens. Infected buds develop to maturity but do not open and are retained on the branch in a dead condition after the flowering period. Any mature buds of this type were collected for measurement. In cases where normal mature buds were also present comparable scores were obtained. The use of bud characters was complicated by the effect of maturity on size and shape. It was not possible to assess objectively if buds were mature but a visual assessment was made based on the relative sizes of hypanthium of bud and fruit. Some variation in scores for bud characters is therefore likely to be due to differences in bud ages of OTU's.

4.3 Description of characters

1. LL Leaf length is the long axis measured from the apex to the base of lamina. LL is related to midrib length according to the degree of leaf curvature.

2. LW Leaf width is the maximum width perpendicular to the midrib.

3. LWM is leaf width perpendicular to midrib at the intersection of the mediator of LL (line a-b, fig. 33) divided by LW.

4. PTL is petiole length. The distinction between petiole and base of lamina was defined by the point of maximum change in curvature, but where the lamina base tapered very gradually or was asymmetric, the petiole was defined as that portion of the leaf having no more than 0.5 mm of tissue either side of the midrib vein.

5. VA is the angle between a pair of secondary veins which intersect mid-width (line a-b) of leaf. If secondary veins forked or deviated from a straight line, a line of best fit was estimated. Measurements were made with a flexible piece of transparent cellulose-acetate marked with 5° angles.

6. LB is the angle between tangents of the lamina base, measured in the same way as VA.

7. CU is the degree of leaf curvature. This was determined as the deviation (line c-d) of the midrib from the long axis (LL) at the mid-length, expressed as a percentage of LL.

8. LTH is leaf thickness of the central third of the leaf and is the greater of two measurements, one on each side of the midrib. Measurements were made with dial calipers taking care to avoid scars or other irregularities.

9. CS equals the height of cuticular sculpturing (undulations or papillae) on abaxial leaf surfaces, measured on a transverse section from the central third of a leaf. This character was costly in measurement time but proved to have a high information content. Time required for cutting and mounting sections was reduced by using epiflourescence rather than normal transmitted light. Leaves were placed abaxial surface uppermost and sectioned perpendicular to the midrib with a sharp razor blade. Strips several millimetres wide were mounted upright in plasticine on a slide and examined at 500 X magnification. Measurements were made in eyepiece micrometer units equivalent to .011 mm. Between 5 and 10 measurements were made per individual by measuring the highest regular undulation or

papilla of a regular form for each field of view in a series spaced between the margins and the midrib.

10. LG is leaf glaucousness. This is a visual estimate of reflectance contributed by epicuticular wax. Individuals were assigned to one of three classes defined on reflectance values at 400 nm. Disjunctions in the distribution of values obtained using a spectrophotometer with integrating sphere (fig. 20, section 2.3.4) made it convenient to define states with the following intervals: 0-5 %, 5-10 %, >10 %. The most glaucous, fully expanded leaves closest to adult form were selected. If there was a detectable difference in the degree of glaucousness on the two surfaces. The most glaucous (usually the abaxial) surface was chosen. The surface was wiped with paper tissue dipped in chloroform to remove the wax bloom. The wax-contributed reflectance was estimated by comparing wiped and non-wiped areas. Where necessary, comparisons were made with a reference set of chloroform-wiped leaves that had been measured with the spectrophotometer. The first class interval usually corresponded to leaves with no visually detectable wax.

Although leaf glaucousness appeared to vary continuously across a set of individuals, it was not treated as a metric character for two reasons. Firstly measurement by spectrophotometer was too time consuming and was difficult and less accurate for narrow leaves. Secondly there were significant non-genetic components of variation in the amount of wax present on leaves. On a given individual older leaves had less wax. Selection of the most glaucous leaves present does not completely overcome this problem since leaf production does not occur at a constant rate and specimens can differ in their ranges of leaf age.

11. SG or stem glaucousness is the presence or absence of epicuticular wax on stems, excluding coppice shoots or shoots with intermediate foliage. As with LG, there seemed to be continuous variation in the amount

of wax-contributed reflectance between individuals. Some populations consistently had light stem glaucousness that was only detectable by close examination, while in others wax gave the stems an opaque, white coating. Consideration was given to recognizing three rather than two character states but again greater precision was unwarranted due to the unreliability of visual estimation and variation in SG caused by other factors. These include differences in the uniformity of distribution of wax retained, the degree of underlying dark stem pigmentation, the bark texture and degree of lenticel development, and the age of stems present at the time of picking the specimen. As with LG, there was evidence of a loss in glaucousness with increasing age. Marked differences in degree of glaucousness were sometimes observed between branchlets of a similar age from different limbs of the same tree. This was notable in the collection PJL 1472 (from group P160, table 9.1). Despite such variation, field observations indicate complete reliability in determining presence or absence of SG. If a tree showed stem glaucousness, this could always be detected by traces of SG on a herbarium specimen collected from it.

12. BB is the presence or absence of blackbutt. Blackbutt refers to a zone of dark, rough, persistent bark extending from the base of the trunk and sometimes reaching major branches. At its upper limit there is an abrupt change to pale, smooth, deciduous bark. (This feature is apparent for trees illustrated in figures 101 to 104, chapter 11). This character was determined by field observation or from herbarium labels. It is a conspicuous feature and reference is usually made to it in annotations by collectors. Determinations were sometimes difficult with some individuals of mallee habit (e.g. forms with affinity to E. striaticalyx in northwestern South Australia and inland Western Australia) having varying degrees of bark coarseness and persistency. However, blackbutts are inherited as a discrete feature in a number of tree species in Western Australia, and for the majority of OTU's there is no intergradation.

13. FW is fruit width at the rim base. This was measured perpendicular to the direction of maximum pedicel width or maximum fruit width for sessile fruits. In fruits with prominent regular ribbing, the measure was made exclusive of ribs.

14. FWMR is fruit width at mid-point of FL (line e-f) divided by FW. It was measured in the same orientation as FW and was also exclusive of ribbing.

15. FL or fruit length is length from the fruit summit to the junction with pedicel. The distinction between fruit and pedicel was defined by the point of inflexion in curvature.

16. PCL is pedicel length.

17. PCW or pedicel width is the maximum width at mid-point of PCL. For sessile fruits the maximum width at the fruit base was measured.

18. DW is the maximum disc width measured perpendicular to the long axis of the fruit.

19. DD or maximum disc depth is the vertical distance from the fruit summit to the junction of valve base and fruit wall. To measure DD, the sliding arm of the dial calipers was modified by grinding the end to a point which could be inserted between the valve base and fruit wall. With the base of the immovable part of the calipers held flat across the fruit summit, the central sliding arm was inserted until the valve base was reached and a maximum reading obtained.

20. FR is depth of regular fruit ribbing. Regular ribs are defined to exclude irregular wrinkling of the epidermis associated with drying out of some fruits and the one to four major ribs continuous with the pedicel (appearing as wings on sessile fruits). To avoid confusion these major ribs will henceforth be referred to as costae to distinguish them from regular ribbing. The presence or prominence of costae appears to be linked to the angularity of the peduncle. This variation between terete and flat peduncles is expressed by the characters PW and PWS. Regular ribs were

measured just below rim level. For rib depths greater than 0.3-0.4 mm measurements were made with dial calipers to the nearest 0.5 mm. Below this, readings were inconsistent so scores were estimated. Consequently FR was treated as a multistate rather than continuous character. Character states for mean scores (determined to the nearest .01 mm when measurements were made) were defined with 3 class intervals of .158 mm between 0 and .475 mm and class intervals of .125 mm for higher states.

21. VN is number of values (= no. carpels) per fruit. A mean value was determined from a sample of 20 fruits.

22. PL or peduncle length is the maximum length from a pedicel junction to the fusion of the peduncle centre with the stem.

23. PW is maximum peduncle width at mid-point of PL.

24. PWS is maximum peduncle width at summit, divided by PW.

25. NPU is the maximum number of buds or fruits per umbel represented on a collection. This is an ordered multistate character with the scores 3, 5, 7, 9, 11, 13 comprising six equal states. NPU was determined by counting pedicels and/or scars left on peduncles. Because it was difficult to discern some scars, only definite determinations were included in a tally for each peduncle. Consequently some lower scores would be doubtful, so rather than allowing them to contribute to a mean, the maximum value was used as the character score for an individual.

26. OLW is operculum length from plane of junction with hypanthium to summit, divided by operculum width at its base. Operculum widths were measured perpendicular to widest face of pedicel (or maximum width of hypanthium in sessile fruits) and were inclusive of ribbing.

27. OWM is operculum width at mid-point of operculum length divided by operculum width at base.

28. OPR is the depth of operculum ribbing. This was measured as for FR except that the largest rib on each bud was selected for measurement. Regular ribbing is generally more pronounced on operculae than on fruits

and costae are rarely present on smooth operculae. A distinction between costae (continuation of angles on pedicels) and regular ribs was not necessary.

4.4 Criteria for evaluation of characters

A character set was required that would be suitable for two types of analysis: Canonical Variates Analysis (CVA) with groups representing taxa or localities; and analyses involving clustering of OTU's based on distance measures. Characters were evaluated using two statistics: F ratios from an Analysis of Variance (AOV) with groups corresponding to each taxon; and Pearson product-moment correlation coefficients (r) calculated for all pairs of characters.

The assumption behind using AOV was that if characters conveyed useful variation then this would be expressed in significant differences between described taxa. This criterion was also applied subjectively in the initial choice of characters. Consideration was given to the possibility of populations with new and significant variation not represented by individuals typical of described taxa, but there was no evidence for this. Populations considered as candidates for new taxa never differed in unique characters and, although they sometimes had more extreme scores, the characters still showed significant differences between existing taxa. F ratios give some indication of discriminating power in CVA and correlate with values of Wilks λ, a statistic that measures this directly. Characters with low F ratios can contribute little information in a CVA, so time is wasted measuring them. More importantly, in a distance measure they may obscure relationships unless a measure is used which takes account of within OTU variation and weights characters accordingly. There are grounds with both types of analyses for rejection of characters with low F values.

The problem with highly correlated characters is that they may share redundant information which will receive a biased weighting in analyses. However, it is important to distinguish between characters that are correlated because they express in different ways the same fundamental attribute and those that express distinct attributes and are correlated for some other reason. In this study the former will be termed 'intrinsic' and the latter 'extrinsic' correlations. Intrinsic correlations include the logical and partial logical correlations described by Sneath and Sokal (1973, p. 103) and the less obvious pleiotropic effects. Pleiotropy is to be expected when one considers that the number of observable characters is infinite while the number of genes that control development is limited. It follows that many genes must affect more than a single character. A character will correlate with another character that is influenced by the same gene(s), but it can also show some independent variation if it is influenced by other genes that are not shared. Intrinsic correlations will be expressed at all levels of sampling including within-population variation (fig. 35 a). Any component of independent variation will reduce the level of correlation overall but may not affect all levels. For the theoretical model illustrated (fig. 35 b), the independent component is evident only at the between-population level. A pattern like this was found in the analysis of SESS specimens (sections 3.5, 3.7). The overall correlation for FL and FW was r = .35 and positive correlations were also present within geographical regions (r = .54 to r = .75). However, the variation of most taxonomic significance was an independent component expressed largely as differences between regional groups.

Extrinsic correlations may result from gene linkage, or selection favouring particular gene combinations. The effect of these influences has been demonstrated by examining character correlations in hybrids between different species (Anderson 1939). Pleiotropy is indicated if there is no

Figure 35: Hypothetical patterns of correlation.

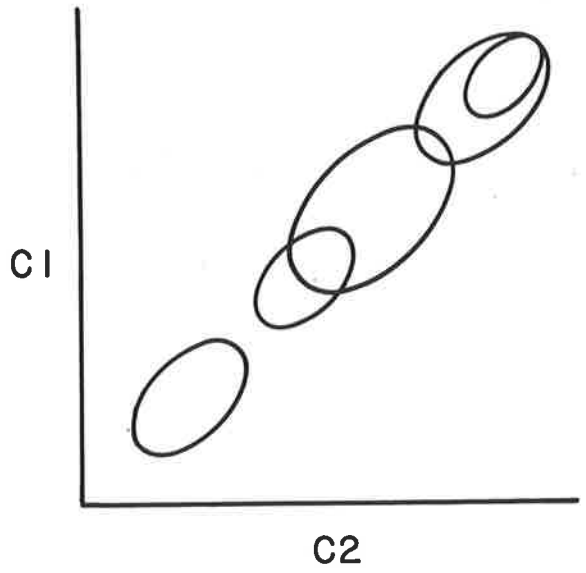
Circles and ellipses represent distributions of scores in correlated characters C1 and C2 for allopatric populations.

A : characters intrinsically correlated without independent variation

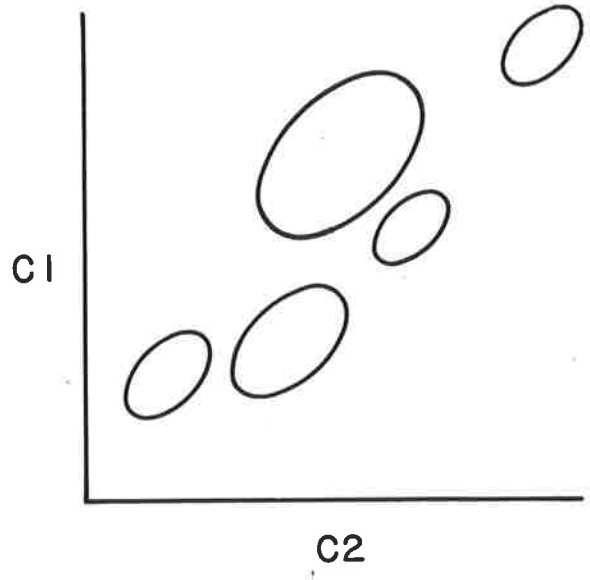
B : characters intrinsically correlated with independent variation component

C : characters not intrinsically correlated

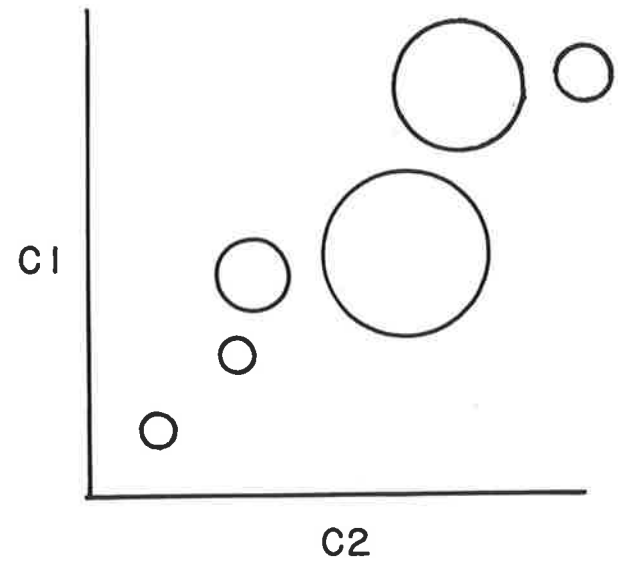
A



B



C



recombination for a character pair and F2 hybrids show the same degree of correlation as the F1 hybrids. In most cases Anderson found recombination between characters but it was extremely restricted compared to the total range of possible combinations of states. In a scatterplot of a pair of characters, F2 recombinants were limited to an ellipse extending between parental types. Anderson explained this by a system of partial linkage resulting from multiple gene control of characters. Continuous metric characters, expressing variation mainly of genetic origin, require the action of genes at a number of loci and so will be subject to this effect. Restriction of recombination in Eucalyptus has been attributed to such linkage by Hartley (1965), who found significant correlations in F2 hybrids between characters including petiole length, leaf shape and glaucousness. The direction of these correlations (the sign of r) corresponded to the parental combinations. Whatever mechanism restricts recombination, natural selection may channel variation at the inter-population level so that character combinations in different species or geographically separate populations are constrained within physiologically or ecologically acceptable limits. Correlations expressed at this level may reflect evolutionary trends or geographic clines where a number of characters respond to the same environmental factor. Such a correlation does not preclude independent variation within populations or between some pairs of populations (fig. 35 c).

Analyses based on distance measures usually assume that each character contributes an equal amount of unique variation. The inclusion of characters with intrinsic correlations clearly violates this, but when a component of independent variation is present the value of its contribution must be weighed against distortion in the distance metric caused by the redundant information. Sneath and Sokal (p. 105) advocate erring in favour of including new information so that characters are

excluded only where there is no evidence for at least some independent sources of information. This approach will be followed here excepting that consideration will be given to the significance of the independence variation. Regardless of whether correlation is intrinsic, extrinsic or a combination of both, when significant independent variation is expressed at any level in a sample, characters should be retained. The independent variation is considered significant if it is possible to remove high correlations by restricting sample size in a way that maintains taxonomically significant variation for the characters.

Correlated characters are of no consequence for CVA, which takes correlations into account by using variance-covariance dispersion matrices for groups when deriving discriminant funtions. Correlated characters share loadings in discriminant functions and so influence the relative contribution of characters to the separation of groups, but they do not directly affect ease of separation or 'distance' between groups which is related to group variance. A group represented by an elongate cluster of points in space defined the correlated characters approaches circularity in two-dimensional D-space of CVA.

In Principal Components Analysis (PCA) a new set of variables (components) are derived by a transformation which expresses the total variation and covariation of the original variables. As each character contributes to the ordination the same amount of information as previously, inherent character correlations are unacceptable for the same reason as for distance measure analyses.

4.5 Test data

The 28 characters described previously were scored for a test set of 69 individuals representing 14 of the 15 existing taxa. Individuals for each

taxon correspond to the TYP groups defined in chapter 7 which are collections taken from one or more localities as close as possible to the type locality. This data is a subset from that of the 100 individuals used for the TYPDAT analyses presented in chapter 7. It differs in lacking the groups representing E. dumosa and the undescribed taxon "E. pterocarpa" and having a smaller sample size (n) for some of the groups. Eucalyptus georgei was represented by a single individual and E. woodwardii by four, but for the remaining groups sample size was between five and seven.

4.6 Analysis of variance

All variables were found to have F ratios greater than 1.0 at the .001 level of significance except CU (P = .060). As there was no evidence that leaf curvature had a different pattern of variation in the two missing TYP groups or any other populations observed, this character was excluded.

4.7 Correlation analysis

Computation of Pearson correlations for all pairs of 28 characters produced a matrix of 378 r values. Some criterion to select significantly high correlations was required. Probability values for r are unsuitable as these test departures from circularity in a bivariate scatter. With a sample of n = 69 small departures from circularity are significant but the correlations of significance to numerical taxonomy are those where a bivariate scatter approaches linearity. The procedure adopted was that of Hills (1969) involving half-Normal plotting of z-transformed r values. This method detects correlation coefficients which are numerically too large to come from a random sample of a Normal distribution with mean of zero. Such coefficients will have z values which deviate from a straight line in the half-Normal plot. The results (fig. 36) showed departure from

a straight line commencing in the vicinity of z values corresponding to r = 0.7 . This is the same cut-off as obtained by Blackburn (1978, p. 132) using this method to investigate correlations in a set of 13 leaf characters. The 10 character pairs with r > 0.7 are listed in table 4.2.

Character pairs	r
LB - LW	.89
LG - CS	.74
PW - PCW	.96
PW - PWS	-.81
PWS - PCW	-.80
DD - FL	.79
FW - DW	.81
FW - VN	.74
FW - LW	.72
FW - FL	.77

Table 4.2: Pearson correlation coefficients for character pairs of initial set correlated at r > 0.7.

Scatter diagrams were plotted for each pair and examined for independent variation. The scatter for LB-LW (fig. 37) showed a lack of independent differences between TYP populations and a tendency for elongate population clusters suggesting that these characters are intrinsically correlated. A logical correlation between leaf base angle and leaf width would be expected if there was some physical restraint on length of the transition zone from lamina to petiole. LB was chosen for rejection from the character set because it had a lower F ratio (8.8) than LW (12.0).

Figure 36: Half-Normal plot of correlation coefficients with $|r| \geq 0.4$.

upper line : based on all coefficients

middle line : plot after excluding coefficients with $|r| \geq 0.7$

lower line : hypothetical plot for Normal distribution $N(0, \sigma^2)$ of coefficients with slope :
$= 0.123 \left(1/ n-3 \right)$

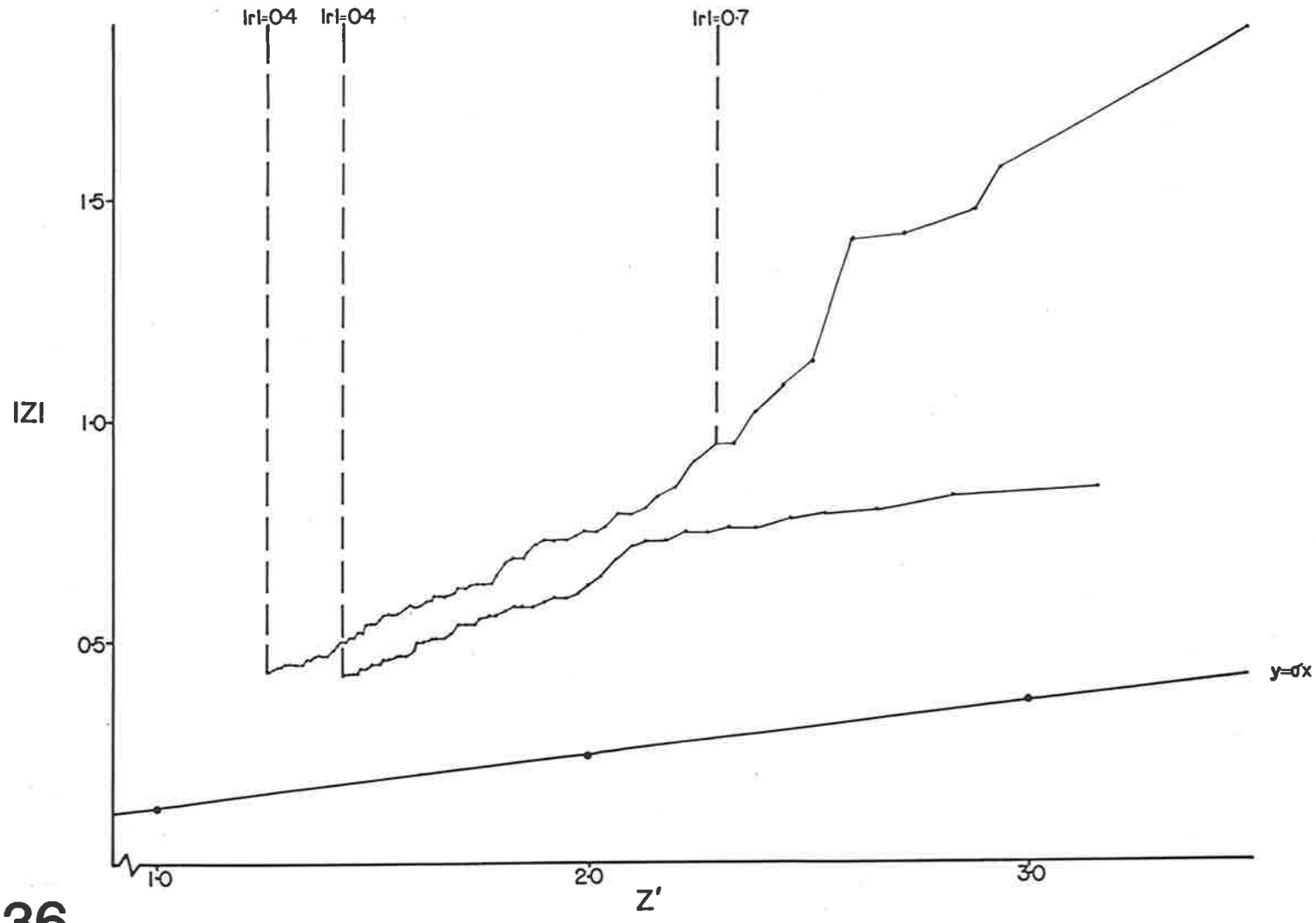

|r|=0·4
|r|=0·4
|r|=0·7
1·5
1·0
0·5
|Z|
y=σx
1·0
2·0
3·0
Z'

Figure 37: Scattergram of character LB (leaf base angle) against LW (maximum leaf width).

correlation: r = 0.88

Figure 38: Scattergram of PCW (pedicel width) against PW (peduncle width).

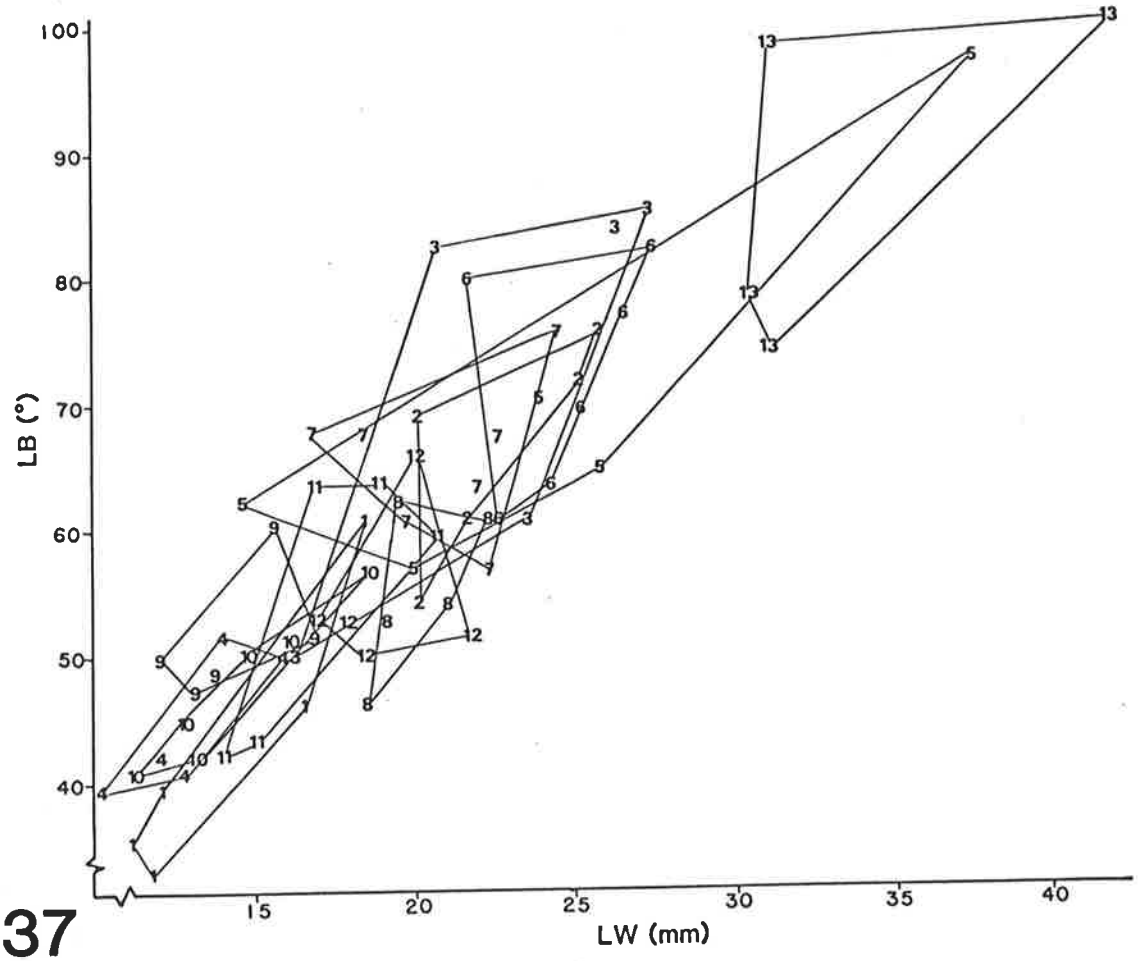
correlation: r = 0.96

Key to TYP* groups:

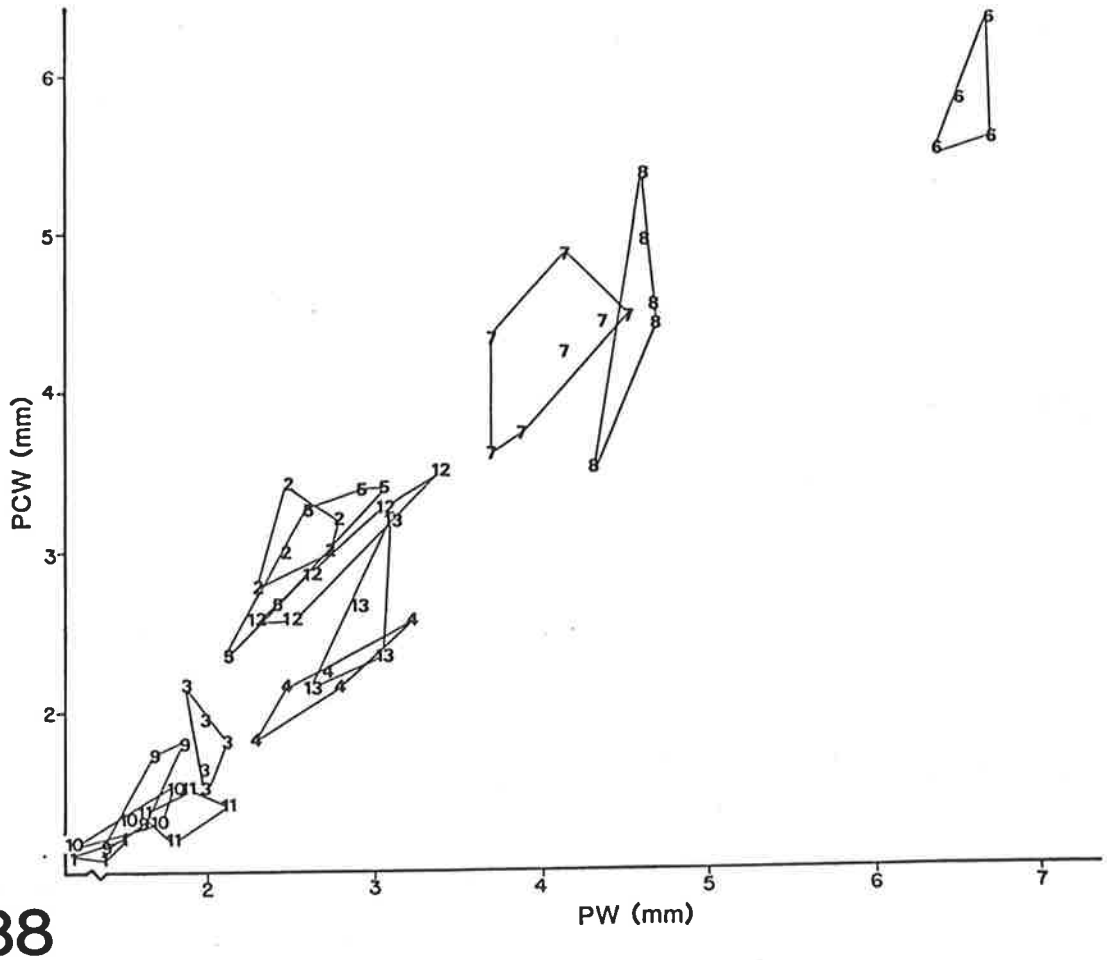
1 : SHE
2 : DON
3 : STR
4 : PIL
5 : CYA
6 : CON
7 : ANC
8 : FRA
9 : KON
10 : CLE
11 : LES
12 : CAL
13 : WOO

Outermost points for each group are linked to show extent of clusters.

* typical populations representing species (chapter 7)


LB (°)
LW (mm)
100
90
80
70
60
50
40
15
20
25
30
35
40

37


PCW (mm)
PW (mm)
6
5
4
3
2
2
3
4
5
6
7

38

The nine remaining character pairs all showed some independent variation between TYP populations. This was evident even for PW-PCW, the pair with the highest correlation (fig. 38). The tendency for elongate population clusters suggests an intrinsic correlation component, but the within-group variation is much less than in the LB-LW plot. This is reflected in higher F ratios for PW and PCW (161.3 and 82.6 respectively). Lower within-group variation facilitates separation of TYP populations. Thus in the plot of PW-PCW it is possible to distinguish groups such as PIL and DON or LES and STR on PCW scores even though they overlap on PW scores.

The pattern of correlation between LG and CS was difficult to interpret because LG was scored as a 3-state character. Continuous measurements of LG determined by spectrophotometer were available for leaf samples representing 58 individuals. Determinations of CS were made for each sample and the resulting scatterplot with r = 0.62 is shown as figure 39. There is no apparent reason why these characters should be intrinsically correlated, but extrinsic correlation might be expected if cuticular sculpturing does significantly increase energy absorption of the leaf due to its apparent affect on reflectance (2.3.4, p.24). Where such absorption is disadvantageous there may be selective pressure in favour of leaf glaucousness to increase leaf reflectance. The causual independence of these two characters is demonstrated by populations in the Flinders Ranges where individuals with extremes in LG grow side by side. If the sample size of the scatter is reduced to the 12 individuals from localities in the Flinders Ranges, the correlation falls dramatically to r = -0.24.

4.8. Investigation of discriminatory information using CVA

The characters describing pedicel and peduncle widths, (PCW, PW, PWS) have high correlations for all three pair-wise combinations. Although they all

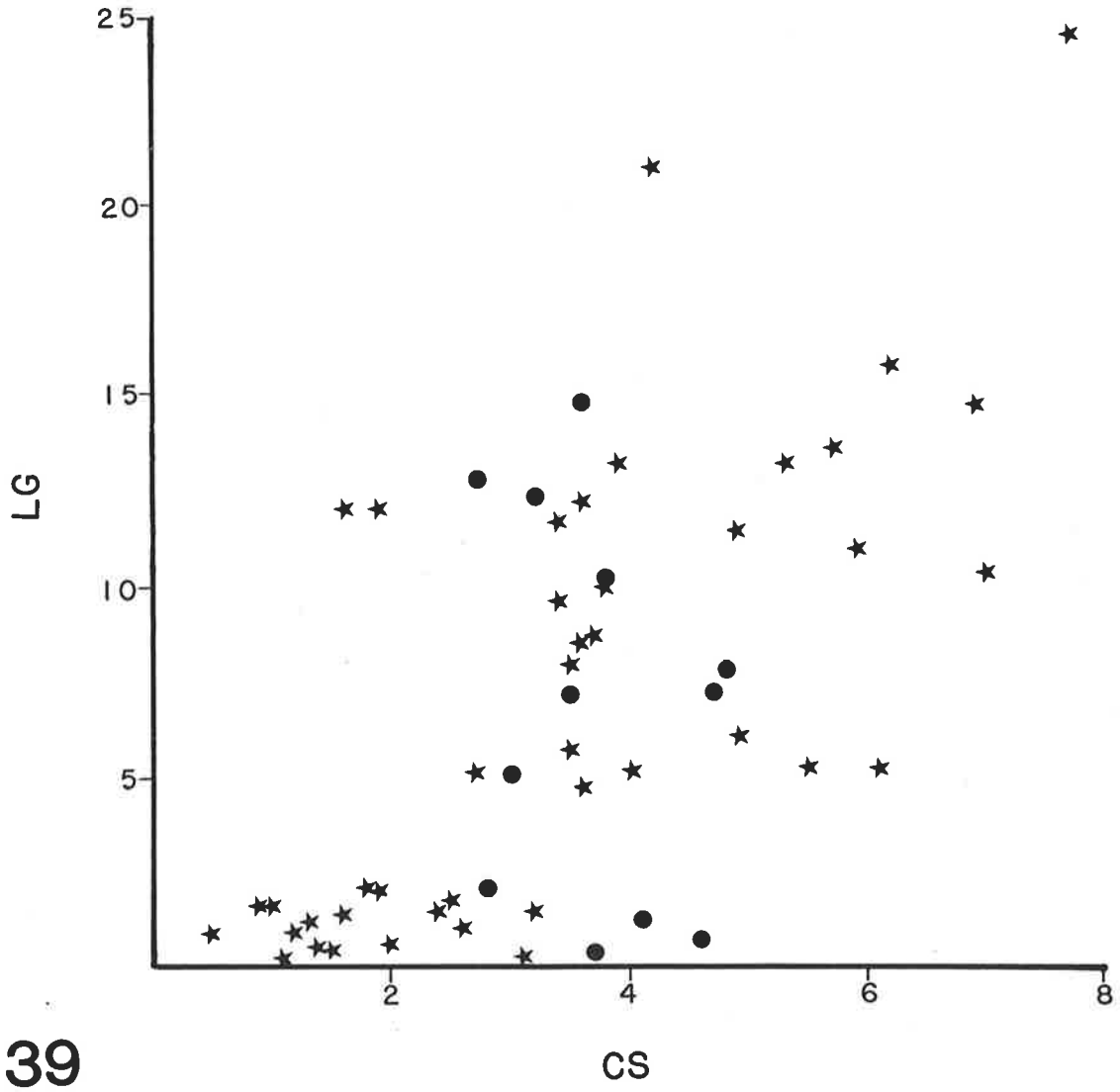


Figure 39: Scattergram of LG (leaf glaucousness) against CS (cuticular sculpturing) for n = 55 individuals for which leaf optics were measured by spectrophotometer.

LG measured as wax-contributed reflectance
(% incident light)

CS is an upper limit measure for height of ornamentation
(1 unit = .011 mm)

correlation: r = 0.62

★ miscellaneous South Australian localities

● specimens from localities in the Flinders Ranges
(n = 12, r = -0.24)

exhibited some independent variation in their scatter plots this information may be shared between pairs. Thus it may be possible to remove one character and reduce intrinsic correlation but maintain a similar level of independent information. To test this CVA's were performed on TYP groups for various combinations of characters. Since discriminant functions do not use the redundant information, the success in identifying the TYP groups is a result of the amount of unique information present in the characters used. The results of these analyses (table 4.3) indicate that removal of any of the three characters causes a reduction in discriminatory information, so all were maintained.

Characters used	No. (of 68) individuals correctly classified.
PCW, PWS, PW	51
PCW, PWS	45
PWS, PW	43
PCW, PW	41

Table 4.3: Results of CVA based on TYP groups using various combinations of pedicel and peduncle characters.

A further strategy used in an attempt to reduce intrinsic correlation without loss of independent information was to replace characters with new ones defined as ratios of existing characters. Five ratio characters were intuitively employed in the original set when there were grounds for expecting very high intrinsic correlations between characters describing the same organ. The ratio character OLW was used to minimize variation relating to the maturity of buds and to avoid correlation with absolute size measures of fruits. The other four ratio characters (LWM, FWMR, PWS, OWM) describe organ shape in terms of two width measures that would logically be highly correlated. In less extreme cases when there was a

possibility that significant independent variation might be lost if ratio characters were not chosen. Two new ratio characters were defined from the highly correlated characters of table 4.2 (DDR = DD/FL and FWL = FW/FL), and their effect on discriminatory information tested. Compared to DD, DDR has a much lower correlation with FL, but the discriminatory power when used in combination with FL was actually slightly greater than with DD (table 4.4). DD was therefore replaced by DDR.

Character pair	r	No. (of 68) individuals correctly classified
DD, FL	.79	33
DDR, FL	.29	35

Table 4.4: Correlations and results of CVA based on TYP groups for disc depth and fruit length characters.

Substitution of FWL for FW was found to remove high correlations with DW, VN, LW and FL (table 4.5).

Characters:	FWL	FW	FWM	FL
DW	.10	.81	.62	.64
VN	.06	.74	.67	.63
LW	.18	.72	.75	.56
FL	-.44	.77	.73	-

Table 4.5: Correlation coefficients (r) for combinations of fruit characters and DW, VN, LW, FL.

Discriminatory information for FWL and FW was considered in combination with a subset of characters highly correlated with, or (in the case of FWMR) logically related to, FW, since only information beyond that already carried in the character set is of importance.

Characters	No. (of 68) cases correctly classified
S (= FL, FWMR, LW, VN, DW)	55
FW + S	59
FWL + S	59
FWM, FWL + (FWMR, LW, VN, DW)	61
FWM, FWL + S	63

Table 4.6: Results of CVA based on TYP groups with sets of variables related to fruit width.

The results of CVA's (table 4.6) shows that FW does contain discriminatory information beyond that of the related subset (S) and that this level is maintained if FWL is substituted for FW. This substitution was made, leaving FL as the only measure of absolute fruit size. Observations of fruit morphology suggested that fruit width had lower within-population variation than FL. An absolute measure of fruit width, FWM (equivalent to FWMR without division by FW) was considered. FWM was found to have a higher F ratio (50.7) than FL (28.4). Replacement of FL by FWM results in an increase in the high character correlations (table 4.5) but except for LW, the correlation levels with FWM are still significantly lower than with FW. As there is also an increase in discriminatory power (table 4.6), this change is advantageous. However, the addition of FWM without removing FL was found to further increase discriminatory power. Although this contributed another high correlation (FL-FWM, $r = 0.73$) it seems that there is sufficient unique information in FL to warrant its retention.

The four fruit characters FL, FWM, FWMR, FWL included in the final set are logically related to the extent that it is possible to determine any one from the other three. Nevertheless a fourth character is not redundant as the ratio characters carry additional information not expressed by FL, FWM or FW separately.

4.9 Summary

A preliminary set of characters was defined precisely and measured on a test set of specimens representing most of the existing Dumosae taxa. Most characters are continuous metrics describing morphological attributes of leaves, fruits or buds. The set was then examined critically and modified for numerical analysis. Following an AOV one character (CU) was excluded on the grounds of a low F ratio indicating that it contributed little between-group variation. Correlation coefficients were determined for all 378 pairs of the 28 characters. On the basis of a half-Normal plot of Z-transformed r values, characters in the 10 pairs correlated at $r > 0.7$ were considered for exclusion, subject to a consideration of their independent variation. Taxonomic groups were identified in scattergrams of these highly correlated pairs and one character (LB) was rejected because of an excessive instrinsic (within-group) component of correlation. Groups of related, highly correlated characters were subjected to CVA's to investigate the amount of discriminatory information contributed when certain characters were excluded. All characters contributed unique discriminatory information. It was found that by employing new ratio characters (DDR and FWL) defined from existing characters, correlations could be reduced without loss of discriminatory power.

The final character set comprised 27 characters (indicated in table 4.1) with 6 pairs correlated at $r > 0.7$. Overall, lower correlations were obtained for these pairs in data sets of subsequent analyses than in the test set (table 4.7).

Data set:	Test set	Subsequent analyses		
	TYPDAT.1	TYPDAT.2	ALLDAT.1	LGFDAT
Sample size:	n = 69	n = 100	n = 499	n = 111
Characters				
FWM - LW	.75	.71	.73	.60
FWM - FL	.73	.65	.78	.82
PCW - PWS	-.81	-.74	-.64	-.60
PCW - PW	.96	.95	.92	.79
PWS - PW	-.80	-.71	-.60	-.54
LG - CS	.74	.61	.61	.64

Table 4.7: Correlation coefficients (r) showing effect of different data sets on highly correlated character pairs.

This result supports the retention of the highly correlated characters. The test set provided a good cover of the extremes of variation within the Dumosae but in subsequent analyses there was more detailed sampling of variation within this framework. Thus there is a greater capacity for independent variation to be expressed at smaller geographical levels as opposed to the overall extrinsic correlations that may be imposed by evolutionary relationships. Differences between TYPDAT.1 and TYPDAT.2 can be attributed mainly to increased sampling within TYP populations for TYPDAT.2, while differences between POPDAT and TYPDAT.2 result from sampling additional populations in POPDAT. The lowest correlations were

obtained with LGFDAT which was based on populations from South Australia characterized by large fruits. This demonstrates the capacity for independent variation within taxonomically meaningful subsets from a larger sample.

CHAPTER 5

METHODS FOR NUMERICAL ANALYSIS

5.1 Introduction

Ideally a numerical analysis is performed without a priori grouping of data. Usually this means using individuals as the operational taxonomic units (OTU's) and computing a measure of resemblance between all pairs of individuals. The resulting similarity matrix is then simplified by a cluster analysis and taxa are determined directly from the clusters derived.

However, this approach was not followed here. The 499 individuals scored for the complete character set would have produced an unwieldly similarity matrix difficult to handle with computer programs that were available. Furthermore, uneven sampling of individuals means that cluster analyses would be unreliable. In this study, populations rather than individuals were used as OTU's. Intra-population variation was treated as background variation to enable more significant taxonomic differences to be identified.

Originally I planned to sample five individuals from each locality but this proved to be impractical. At many sites individuals were rare or there was insufficient suitable material with mature fruits and undamaged leaves. A major restriction was rate of measurement, which averaged about four individuals per day for the complete character set. As a result of time-costing, some populations were represented by a single individual which was chosen either at random or because of the presence of operculum data. A total of 47 localities, each represented by four or more individuals, were used for numerical analysis.

5.2 Canonical Variates Analysis and intergradation

Canonical Variates Analysis (CVA) is a form of Discriminant Analysis where differences among a number of groups are maximized and expressed in as few dimensions as possible. Although often referred to as Discriminant Analysis, CVA differs from this in a strict sense (Pimental 1979, p. 218) in that it involves an eigenvalue-eigenvector solution. A CVA is equivalent to performing a Principle Co-ordinate Analysis on a D^2-matrix (Sneath and Sokal 1973, p. 249).

In a Discriminant Analysis performed on two groups the Mahalanobis distance (D^2) is equal to the difference in scores of the group centroids on the discriminant function. D^2 indicates inter-group distance scaled according to the degree of intra-group variation. Sneath and Sokal described a discriminant function as a linear-combination of all characters weighted relative to their contributions to the polarity between groups so that as many as possible of the members in one group score high values and as many as possible of the other groups score low values. The discriminant function is likely to discriminate better between the two groups than any individual character.

The space defined by discriminant functions (D-space) is a transformation of multivariate character space (A-space) achieved by rotating and stretching character axes to make group clusters maximally hyperspherical (thus removing the effect of character correlations) and equal in diameter (thus standardizing distance to within-group variance). When there are more than two groups, separate discriminant functions apply to each pair, and a generalized solution defining the D-space can be obtained by deriving canonical variates using a pooled within-groups variance-covariance matrix. This requires the assumption of a multivariate

Normal distribution and homogeneity of within-group variance and covariance matrices. No gross departures from either assumption were observed when allocating means, standard deviations and ranges of character scores to classes for the multistate distance metric. In practice CVA is a robust technique so that strict adherence to these assumptions does not seem to be critical for a meaningful result (Klecka 1975, p. 434; Blackith and Reyment 1971, p. 49).

With n groups and $\geq$ n characters, n-1 canonical variate functions are derived which define D-space when plotted as orthogonal axes. Generally each successive canonical variate axis portrays less of between-group differences than the preceeding axis. These orthogonal axes are distinct contrasts of form but unlike principal component axes the polarities they represent are correlated. Canonical variates can be used to classify individuals to groups on the basis of their scores in the same way as with discriminant functions. This is achieved indirectly through special classification functions.

All CVA's were performed using subprogram DISCRIMINANT of the SPSS package (Nie et al, 1975), with the 'DIRECT' rather than 'stepwise' method of variable entry. The latter was found to produce a different result only if some variables were automatically excluded from the analysis, a situation which occurred only rarely. Classification functions were derived from the pooled within-groups variance-covariance matrix according to the default OPTION. Under the assumption of a multivariate Normal distribution, classification scores are converted into probabilities of group membership (designated in SPSS as P(G/X)) and individuals are assigned to the group for which this value is highest. When interpreting the classification results for unassigned individuals, it is important to keep in mind that the individuals are assumed to belong to one of the defined groups whereas they may be better classified with some other group not defined in the

analysis.

The values for P(G/X) can be used to indicate intergradation in discriminant space, but the relationship is not linear. Individuals that are half-way between two group centroids will have P(G/X) = 0.5, but small deviations from this position can produce a large change in the P(G/X) values so that the individuals are significantly closer to one or other of the groups. Two levels of gradation were defined by arbitrarily chosen P(G/X) values for the classified group:

$$\text{Level 1: } .9000 \leq P(G/X) \leq .9900$$

$$\text{Level 2: } .9000 < P(G/X) < .5000$$

The above ranges of P(G/X) values for the two levels were found to detect individuals that were displayed as obvious intergrades on canonical variate axes of the SEDAT study (8.2). In all CVA analyses, individuals belonging to the defined groups were nearly always classified correctly and without gradation at either level but in the range .9900 < P(G/X) < 1.0000 (table 9.2). Missing data is a problem for CVA as there is no way that canonical variates can be adjusted for individual cases when characters weighted in the function are absent. For defined groups (TYP, LGF and POP groups) missing data was filled with group mean values of operculum characters. For unassigned individuals entered in CVA for classification, two approaches were developed. The first follows OPTION 2 of SPSS subprogram DISCRIMINANT in which a mean value of all cases is substituted for missing values. This was modified so that a mean value based on each of the group means was substituted using the RECODE facility. Thus substituted missing values will not contribute information biased towards any particular group on account of group size. The second approach involves performing two CVA's for each analysis: one for cases with complete data in which the whole character set is included in the

analysis, and another for the cases with missing data in which the missing characters (OLW, OWM, OPR) are deleted. The classification results are then pooled. Both methods were tried with the TYPDAT data and were in agreement for most classifications of cases with missing data. Where they differed the second method gave results more in line with subjective expectations. This can be explained by the fact that for groups with distinctive operculae, canonical variates loading highly on operculum characters will be important for discrimination and cases with mean values may be 'incorrectly' assigned with regard to the other characters. With the second method this cannot occur since the missing operculum characters will not be weighted at all in the canonical variates. The second method was therefore used for analyses presented in this study.

5.3 Measures of distance between groups

5.3.1. Multistate distance metric

A generalized semi-Euclidean distance metric known as the multistate distance (DI) was devised by Blackburn (1978, 1980) to accommodate within-OTU variability in character scores. The Fortran program TAXON written by Blackburn was used in this study to compute values of DI. It allows a maximum of eight states for defining a continuous range of values displayed by an OTU for each character. The range in states can be used to express any suitable measure of dispersion of the character scores. The multistate distance is determined according to the degree of overlap or separation in the ranges of states for a pair of OTU's and is dependent on the size of these ranges. With greater variability within OTU's there is a greater opportunity for overlap and thus a smaller distance, DI.

The formula for multistate distance is:

$$DI = \frac{\left|2Cv - Tj - Tk + \sum_{-m}^{+m} 2(m-1)\right|}{Tj + Tk}$$

where: m = order of match or mismatch, given by the number of character states overlapping (+ve m) or separating (-ve m) the two OTU's.

Tj and Tk = total number of states across all characters possessed by OTUj and OTUk respectively.

Cv = total number of characters for which OTU's j and k are validly scored.

Worked examples for pairs of OTU's with various ranges of states revealed anomalous behaviour of the metric (table 5.1). If a constant overlap (m > o) is maintained, then increasing variability results in an increase in DI as expected. However, variability has no effect on DI if the ranges for the two OTU's are adjacent. Where Cv = 1 and m = 0 the above equation becomes:

$$DI = \frac{|-Tj - Tk|}{Tj + Tk} = 1$$

In the third situation where there is a constant disjunction in ranges (m < o), increasing variability results in a decrease in DI. This effect is undesirable and runs contrary to the trend in median character scores which increase their distance of separation. It results from the fact that DI is determined from the match in the central part of available character states and the number of states scored positively but not from the unscored states at the ends or the total number of possible states. Attempts to overcome this problem by modifying the formula for DI were unsuccessful. Blackburn (1980, p. 325) noted that computation of Euclidean distances requires that there is no missing data, a single datum type is

used, and characters have no variability or equal variability in OTU's. The examples of table 5.1 show a non-Euclidean effect when variability is changed, although individual pairs of OTU's may have the same variability. The reversed relationship between distance and variability for non-overlapping OTU's is not as significant as it first appears. The relationship was demonstrated by holding the order of matching (m) constant and varying the OTU character ranges. However, in practice m will be strongly influenced by within-OTU variability. As this increases there will be a greater opportunity for overlap (or a reduction of separation) and thus a smaller distance value. The effect of including within-OTU variation on distance values is demonstrated in table 5.3. The mean distance and its coefficient of variation are greatly reduced since variability restricts the maximum achievable distance for a comparison.

Departure from Euclidean distances also occurs for the data in this study because the three operculum characters have missing values and because mixed data will result from the two and three state characters (LG, SG and BB) which cannot be treated as 'continuous' 8-state characters. For binary characters applied to variable OTU's, the two states must be represented by adjacent states in an 8-state system to prevent discontinuity in the range occupied by an OTU that scores both states. This means that $m \leq 0$ and the maximum distance obtainable is 1 unit compared to 7 for a continuous 8-state character. For a 3-state character such as LG the maximum distance is 2 units. However, for the data analysed this potential for differential weighting of characters had little affect. This was because the 8-state characters had overlapping scores for most pairs of OTU's and the resulting distance values were always less than 1 unit.

A method was devised to enable an increased weight for binary or multistate characters with fewer than the maximum number of states scored. Although not necessary here, the technique is presented for use in studies

with characters that are less variable within OTU's. It is demonstrated for a binary character in table 5.2. When a single binary state is scored for an OTU this is represented by a single state on the 8-state scale. The state is positioned so that a mismatch will result in the desired distance equal to |m-1|, in this case chosen to be 4 units. When an OTU scores both binary states it is represented by a continuous range extending between the two single state positions which enables meaningful distances to be calculated by the TAXON program.

Continuous metric characters were assigned states by the following method. A measure of dispersion, either the range or an interval of two standard deviations each side of the mean was determined for each OTU. The overall range occupied by these intervals for all OTU's was divided into eight equal class intervals and each OTU interval was scaled accordingly. The characters are thus standardized to common range from state 1 to state 8. Blackburn (1981) advocated the use of variable class intervals adjusted so that states have equal frequencies to reduce distortions imposed by "distributional artifacts of the data set". However, the validity of this approach is questionable. It assumes that the importance of variation in a character will be reflected in the number of occurrences sampled. Even if sampling of variation is uniform there is still the question whether abundance or distribution should influence taxonomic characters. It is possible for natural selection towards an extreme character value to be confined in extent or for a large number of individuals with an intermediate condition for a character to become extinct. In these cases extreme values for a character, although rare, represent real phenetic or 'evolutionary' distance and would be under-weighted if states were assigned to equal frequency classes. Unless theoretical grounds such as with a logarithmic growth factor or a specific frequency distribution for character values can be demonstrated for a single locality, it would seem

Table 5.1: The effect of within-OTU variability on the multistate distance (DI) for a constant order of match (m).

m	OTU	States scored	DI
+2	j	- - + + + - - -	
	k	- + + + - - - -	0.33
+2	j	- - + + + + - -	
	k	- + + + - - - -	0.43
+2	j	- - + + + + - -	
	k	+ + + + - - - -	0.50
0	j	- + + + - - - -	
	k	- - - - + + + -	1.00
0	j	+ + + + - - - -	
	k	- - - - + + + +	1.00
-2	j	- - + - - - - -	
	k	- - - - - + - -	3.00
-2	j	- + + - - - - -	
	k	- - - - - + + -	2.00
-2	j	+ + + - - - - -	
	k	- - - - - + + +	1.67

Table 5.2: Method of scoring a binary character to enable DI > 1.

OTU	Binary score	States scored for DI	DI
j	+ -	- + - - - - - -	
k	- +	- - - - - + - -	4.00
j	+ -	- + - - - - - -	
k	+ +	- + + + + + - -	0.67
j	+ -	- + - - - - - -	
k	+ -	- + - - - - - -	0.00
j	+ +	- + + + + + - -	
k	+ +	- + + + + + - -	0.00

Table 5.3: A comparison of the similarity matrices resulting from four separate analyses of the LGFDAT data.

Distance measure	Mean D value	CV* of D values (%)	Ratio Dmax/Dmin
Multistate distance based on mean values, $\bar{x}$	2.87	21.5	2.53
Multistate distance with dispersion defined by: $\bar{x} \pm$ S.D.**	0.36	1.6	2.33
Multistate distance with dispersion defined by: $\bar{x} \pm 2$(S.D.)	0.30	1.1	2.21
Discriminant distance	0.93	22.4	2.61

* CV = Coefficient of variation.

** S.D. = Standard deviation.

best to treat character scores as being of equal phenetic weight.

5.3.2 Discriminant distance

In CVA the canonical variate axes are scaled in D units which are effectively within-taxon average standard deviations in the transformed space (Sneath and Sokal, 1973, p. 407). This means that distances in multidimensional D-space can be derived from canonical variate scores by Pythagorean principles. A computer program DISCD (p. 117) was written to compute distances in D-space between all pairs of group centroids. The program is written in Fortran 4.8 for use on a Cyber computer. The distances indicate the ease of discrimination of groups and will be referred to as discriminant distances (D-distances).

Like the multistate distances, D-distances are based on weighted characters. With CVA, weighting is applied directly to characters and is not constrained by a maximum range of character states. This enables more effective weighting of important characters than with the multistate metric.

D-distances are considered preferable to multistate distances when the aim, as in this study, is to derive a practical classification rather than reveal relationships expressed by overall similarities. Canonical variates are only concerned with information for distinguishing groups whereas the distance metric is a summation of all the character differences. The addition of a number of characters with low F ratios will not decrease the ability to distinguish groups using CVA but with a multistate distance analysis the relative distance of the more distinctive groups will be reduced. This effect, together with the more limited weighting of characters, explains the lower variation in distance values obtained with the multistate metric compared to CVA. This is demonstrated by the

```
PROGRAM DISCD                    FTN 4.8+538          81/11/11

      PROGRAM DISCD (INPUT=/200,TAPE1=INPUT,OUTPUT=/200,
     1TAPE2=OUTPUT,TAPE3)
C DISCD COMPUTES EUCLIDEAN DISTANCES (D) IN D-SPACE
C FROM DISCRIMINANT(CVA) SCORES FOR GROUP CENTROIDS.
C THE MAHALHANOBIS DIST. BETWEEN GROUPS = D**2

C**** ADJUST FOLLOWING 3 LINES
C     SCORE(NT,NF),TAX(NT)
C     NF=NO. OF FUNCTIONS
C     NT=NO. OF TAXA ****:

      DIMENSION SCORE(3,6),TAX(3)
      NF=6
      NT=3

      N=NT-1
C L1 READ DATA
      DO 34 J=1,NT
      READ(1,999) TAX(J),(SCORE(J,K),K=1,NF)
   34 CONTINUE
C L2 ECHO-PRINT DATA
      DO 35 J=1,NT
      PRINT(2,999) TAX(J),(SCORE(J,K),K=1,NF)
  999 FORMAT(X,A5,99(X,F6.2))
RECORD LENGTH EXCEEDS 137 COLUMNS -- MAY EXCEED I/O DEVICE
   35 CONTINUE
      PRINT*,≠TAX1  TAX2  DDIST≠
C L3 SELECT TAX1
      DO 13 L=1,N
      LL=L+1
C L4 SELECT TAX2
      DO 14 L2=LL,NT
      DIST=0
C L5 COMPUTE DIST.
      DO 15 M=1,NF
      D=SCORE(L,M)-SCORE(L2,M)
      D=D*D
      DIST=DIST+D
   15 CONTINUE
      DIST=SQRT(DIST)
      PRINT(2,101) TAX(L),TAX(L2),DIST
C**** REMOVE ≠C≠ TO OUTPUT RESULTS ON TAPE3 ****
      WRITE(3,101) TAX(L),TAX(L2),DIST
  101 FORMAT(2(X,A5),X,F6.2)
   14 CONTINUE
   13 CONTINUE
      STOP
      END
```

```
SHE      -.54  -3.06   -.46   2.58  -1.54   -.54
DON       .95  -1.58   1.85    .06  -2.54   2.08
STR    -11.01  -3.33   1.77  -2.22    .12    .07
```

```
TAX1  TAX2  DDIST
SHE   DON     4.90
SHE   STR    11.87
DON   STR    12.74
```

coefficients of variation derived for similarity matrices in table 5.3. A further advantage of D-distances is that they are unaffected by correlation between characters.

D-distance values differ fundamentally from multistate distances in that differences are only measured along certain polarities. This means it is theoretically possible for two individuals with different sets of character scores to receive the same score on a canonical variate. Such individuals will always be treated as different by the semi-Euclidean multistate metric.

The use of CVA is limited by the fact that it is statistically invalid to practise discriminant topology where there are more groups than characters (Blackith and Reyment 1971, p.38). A further disadvantage of CVA over the distance metric is that a D-distance is not uniquely defined by a pair of groups but is influenced by other groups that help determine the canonical variates. Results of the SEDAT analysis (chapter 8) show that with a larger number of groups the discriminant distance between specific pairs of groups is lower. Multistate distances were therefore used in conjunction with many of the CVA's. For the POPDAT analysis, where the large number of groups exceeded the number of characters, the multistate metric was used in place of a CVA.

5.4 Clustering methods

The lack of uniform or random sampling of Dumosae specimens is evident in the distribution maps (figs 218 to 226, chapter 12). There is heterogeneity both in the spacing of localities and the intensity of sampling within them. This partly resulted from the need to rely on herbarium material for remote areas where special collections could not be made as for *E. woodwardii* and *E. georgei*. However, some areas such as the

Eyre Peninsula and South-eastern Regions of South Australia were collected more intensively because complex variation or intergradation was apparent. In other areas such as the Goldfields district around Kalgoorlie in Western Australia, Dumosae were common but taxa appeared more distinct, and sampling was less intense.

Uneven sampling has serious consequences for many commonly used clustering strategies. Similar individuals that are over-represented in a cluster contribute excessive information concerning fusion with other clusters or individuals. These will be more likely to link in if they resemble the over-represented type. With increasing similarity of individuals this approaches the problem of uneven group size using identical replicates of OTU's. Correll (1973) considered nine clustering stratigies and found that eight were affected by the inclusion of similar entities. These include the frequently used UPGMA and Ward's Error Sum of Squares. The problem can be avoided by using WPGMA (Sneath and Sokal, 1973) which gives the most recently joined OTU an equal weight to pre-existing cluster members. However, this method has disadvantages. Intuitively, it would be expected to lead to the phenomenon of chaining because as a group grows it would be easier for less similar individuals to join. Also, Sokal and Sneath (p. 228-229) note that there is greater distortion in comparing phenograms with original distance matrices when weighted clustering is used.

The weight given to a single OTU that is relatively different from all others should depend on whether it is a geographically isolated occurrence or is an atypical variant within a population of typical forms. Weighted clustering is desirable for the first case and unweighted clustering for the second. If a locality is represented by a single individual it can only be assumed that this is typical and could be replicated by further sampling. This may be evident from other material collected but not measured for the analysis. The weighting of poorly sampled forms needs to

be given careful consideration in numerical analyses and perhaps is better done subjectively rather than by applying a rigid algorithm.

Another criterion applied by Correll to clustering strategies is the stability of the classification resulting from the similarity matrix, discussed further by Jardine et al. (1967). A high stability requires a continuous transformation from the matrix to a dendrogram and means that small changes in the matrix will produce only a small change in the classification. Of the nine strategies considered by Correll, only nearest neighbour clustering satisfied this requirement.

Cluster analyses were not emphasized for this study but were used in conjunction with evidence of intergradation between forms. The clustering principles applied were based on Nearest Neighbour and Graph Theory clustering.

5.4.1 Nearest Neighbour clustering

This method requires the nearest neighbours of each OTU to be determined from the similarity matrix. This task was made easier by ranking distance values using the SPSS procedure SORT. Nearest neighbour dendrograms were constructed by the method of Blackburn (1978, pp. 245-247) in which OTU's joining clusters are linked directly to their nearest neighbour. This conveys more information than the usual method termed Single Linkage clustering (Sneath and Sokal, p. 217) in which added OTU's are linked to the centre of the cluster containing their nearest neighbour. The same information as in a nearest neighbour dendrogram can be displayed by a Nearest Neighbour Network (Blackburn, p. 247). This method was also used (9.1.3, fig. 54) as it shows the structure of clusters more clearly but it has the disadvantage that comparisons between distances are made more difficult due to different orientations of linkages. Further information

can be conveyed by incorporating second nearest neighbour distances into a nearest neighbour plot following a method given by Blackburn (1978, p. 258 ff) which is similar to that shown by Sneath and Sokal (1973, p. 268). With this method, triangulation from two previously plotted neighbours fixes two alternative positions for a joining OTU. A choice between these was made with regard to the simplicity of the overall structure of the plot by minimizing overlapping links and avoiding close placement of OTU's. This is more useful than attempting to minimize distortion at the next neighbour level (generally 3rd-nearest neighbours) since this often leads to even greater distortions at lower levels. When interpreting a nearest neighbour or a 1st and 2nd-neighbour plot, it is important to keep in mind that the only true distances are those represented by linkages and that distances between unlinked OTU's have no meaning.

Nearest neighbour clustering was advocated by Correll (1973, p. 54) because of its independence of replicates and stability resulting from the simple, continuous transformation from the similarity matrix. Its main disadvantage is that it is space-contracting and results in poorly defined clusters by forming chains of OTU's linked together via intermediates.

5.4.2 Graph Theory clustering

This clustering is based on a model in Graph Theory by Estabrook (1966). It satisfies the criteria of independence of replicates and stability. With this method OTU's are linked together if they have a distance value less than or equal to a specified value, Dc. The size and number of clusters defined vary according to the value of Dc. A value for Dc can be chosen to optimize the following cluster properties described by Estabrook. The cohesion of a cluster is determined by the ratio of the number of acutal links to the maximum number of possible links. This is

expressed by the 'normalized connectedness' (Nc) for a cluster which varies between 0 and 1. This is calculated as:

$$Nc = \frac{2A - 2(n-1)}{(n-1)(n-2)}$$

where:

A = number of actual links

n = number of cluster members

The stability of a cluster is measured by its moat (m), which is the difference between the minimum distance defining the cluster and the maximum distance which maintains the same cluster. This means that an OTU within the cluster is at least 'm' more similar to an OTU within it than to one outside it.

The Graph Theory approach described by Clifford and Williams (1980) was applied in most of the cases where 1st and 2nd-neighbour plots were used. It is a closely related method and did not produce substantially different clustering.

5.5 Outline of main numerical analyses

Five main analyses are presented in the following chapters. They were all performed using the chosen character set but each had its own set of individuals arranged in specially defined groups:

1. LGFDAT analysis. This tests hypotheses concerning potential taxa based on geographical groupings of forms characterized by large fruits.

2. TYPDAT analysis. This examines relationships between groups defined by currently recognized taxa. The TYP groups comprise individuals collected from as near as possible to the type localities.

3. SEDAT analysis. This was performed to demonstrate intergrades occurring in the Southeast region of South Australia between four of the TYP groups.

4. POPDAT analysis. All localities sampled by four or more individuals are investigated to identify centres of variation not adequately encompassed by the TYP groups for consideration as potential new taxa.

5. DPOPDAT analysis. Relationships of groups selected in the POPDAT analysis are investigated to form a basis for modifying the taxonomy of the Dumosae.

The whole set of 499 measured individuals (ALLDAT) was subjected to classification, with and without 2 and 3-state characters, by the TYPDAT and DPOPDAT CVA's. The results for this are presented in appendix 1.

CHAPTER 6

ANALYSIS OF LARGE FRUITED FORMS

(LGFDAT ANALYSES)

6.1 Introduction

The recently described Eucalyptus cyanophylla was distinguished from E. dumosa and other pedicellate Dumosae by larger fruits and leaves together with other characters such as heavy leaf glaucousness and winter-spring flowering period (Brooker, 1977). In South Australia it appears to be a rather distinctive, well delineated taxon within the confines of its given distribution in Murray Region, mainly to the south of the Murray River (Brooker, p. 17, fig. 3). However, it has complex affinities with a number of other large-fruited forms in other areas. At one stage Brooker (pers. comm.) had considered including some other forms under E. cyanophylla. For instance, material from the South-eastern Region to the south of E. cyanophylla s.str. occurrences differs from this taxon in lacking leaf glaucousness and intergrades with forms of the E. dumosa complex with smaller and sessile fruits. Material on Eyre Peninsula, although geographically isolated, appears very similar in form to E. cyanophylla but differs in having glaucous stems. The LGFDAT analysis was proposed to test the relationships between these and other large-fruited forms in South Australia.

As in the SESSDAT analyses of chapter 3, the forms considered constitute an arbitralily defined subset of variation within the E. dumosa complex. Fruit size appears to be the most important morphological character for justifying recognition of E. cyanophylla. It has been demonstrated that the leaf glaucousness character causing the distinctive bluish colour of

foliage is highly variable in the E. dumosa complex, even within single populations (2.3.4). Following the recognition of E. cyanophylla, Boomsma modified his concept of E. dumosa by specifying fruit width to be ≤ 6 mm (Boomsma, 1972; 1981). Boomsma and Brooker both gave fruit width for E. cyanophylla as ≥ 7 mm. For this study a lower limit for fruit width of 6.6 mm applies. Within an arbitrarily limited sample it is feasible to use CVA to test some initial hypotheses about nodes of variation that may warrant taxonomic recognition. On the basis of fruit size, other forms may deserve equal status to E. cyanophylla and be treated as taxonomically separate from E. dumosa. If analyses show them to be distinct from E. cyanophylla they could be treated as new species or as subspecies of E. cyanophylla. The status of these forms needs to be considered in relation to two existing species E. striaticalyx and E. calcareana which have similar but larger fruits than E. dumosa, so these are represented by groups in the analysis.

6.2 Definition of LGF groups

The LGF groups were selected where possible to be geographically distinct entities to avoid the problem of having to subjectively assign interspersed or intergrading forms. Consequently this analysis does not cover all the large-fruited forms in South Australia. A brief description of characteristics for each group is given below. The group sample size is given in brackets.

LCYA (22)

This group incorporates the TYP group (CYA) of 12 individuals representing E. cyanophylla. Leaves are typically a light blue-green colour ('cyanose') due to heavy glaucousness (LG = 1,2) and cuticular sculpturing. Stems are non-glaucous.

LCAL (13)

This includes the TYP group for E. calcareana (CAL) and also some forms with larger fruits from further west near Coorabie. A narrow concept of the species was applied here so that the distribution is consistent with that of Boomsma (1979) in extending no further east than Ceduna. Similar material occurs on Eyre Peninsula but there is interspersion and intergradation with other forms. LCAL is characterized by non-glaucous stems and leaves and broadly pedicellate fruits.

LSTR (38)

This group was measured entirely from existing herbarium collections originating from the northwest part of South Australia except for one specimen from Blackstone Range in Western Australia. Material from the northwest has been referred to E. striaticalyx (Boomsma, 1972), a species which has its type locality much further west in Western Australia. Group STRL is variable in leaf glaucousness and stem glaucousness and is characterized by very large fruits with elongate pedicels.

LCAR (6)

This group comprises individuals collected from the slopes or base of Carappee Hill, Eyre Peninsula. It has fruits of a similar form to LCYA but differs in having variably glaucous leaves and consistently glaucous stems which suggests affinites with LSTR.

LDAR (6)

These individuals were collected east of Carappee Hill on flat country (occasionally with sand dunes) in the vicinity of Darke Peak. LDAR was originally included within LCAR but it was found that these adjacent geographical groups could be easily separated morphologically.

A Discriminant Analysis performed on these two groups resulted in 100 % correct classification and group centroids were 16 units apart on the discriminant function. The LDAR individuals differ from LCAR mainly in having wider fruits and longer leaves.

LCUM (8)

This group is associated with the range of hills on the southeastern part of Eyre Peninsula between Cummins and Tumby Bay. CUML individuals are consistently non-glauous.

LKIM (4)

These individuals are from the vicinity of Kimba on Eyre Peninsula and differ from LCUM in having minor leaf glaucousness and duller leaves due to higher cuticular relief. It is postulated that they may be intermediate between LCUM and LSTR or LCAR.

LBOR (14)

Nine of the LBOR individuals originate from a single locality at Comet Bore, 60 km N of Bordertown and the remainder occur at various localities closer to Bordertown. This group had to be defined morphologically as well as geographically because of intergradation and intermixing with smaller fruited forms. Individuals were excluded if they had a mean fruit width (FW) less than 6.6 mm. This was the minimum for the other seven groups excepting a single anomalous individual in LCYA. The LBOR individuals have non-glaucous stems and mostly non-glaucous leaves.

6.3 Canonical Variates Analyses

A CVA was performed on the eight LGF groups with missing operculum data filled with the means of group mean scores. All but one of the 111

individuals were classified to their correct group. The misclassified individual belongs in LCAL but was assigned to LBOR.

When the characters describing glaucousness (LG and SG) were removed, misclassification was increased to seven individuals, with all groups except LSTR having some overlap. This shows the significance of the glaucousness characters in the analysis. This result is not surprising because these characters provide the most obvious difference between the groups. Nevertheless, the fact that correct classification was achieved for the majority of individuals indicates that much discriminatory information can be contributed by the other characters even though they do not show clear cut differences between groups.

Important variation was carried by the first five of the seven canonical variates. A simple display of relationships by plotting canonical variate scores is not possible with this number of dimensions. Therefore D-distances were determined for group centroids and a 1st and 2nd-neighbour network plotted (fig. 40). Distance values range from 3.8 for LCUM - LBOR to 10.0 for LSTR - LCAL. For groups accommodated by existing taxa (LCYA, LCAL and LSTR), the pair LCYA - LCAL is the least distinct being separated by a distance of 6.5 units. The other five 'undescribed' groups are all less than this distance from LCYA, LCAL or LSTR. Thus the recognition of all LGF groups as taxa would mean a general decrease in the ease of discrimination. The nearest neighbour network (defined by solid lines in fig. 40) has two clusters. The groups characterized by glaucous stems (LSTR, LCAR and LDAR) are joined to other groups only by lower order neighbour links. Since these are comparable in magnitude to many of the nearest neighbour links, the clustering is poorly developed according to the principles of Graph Theory.

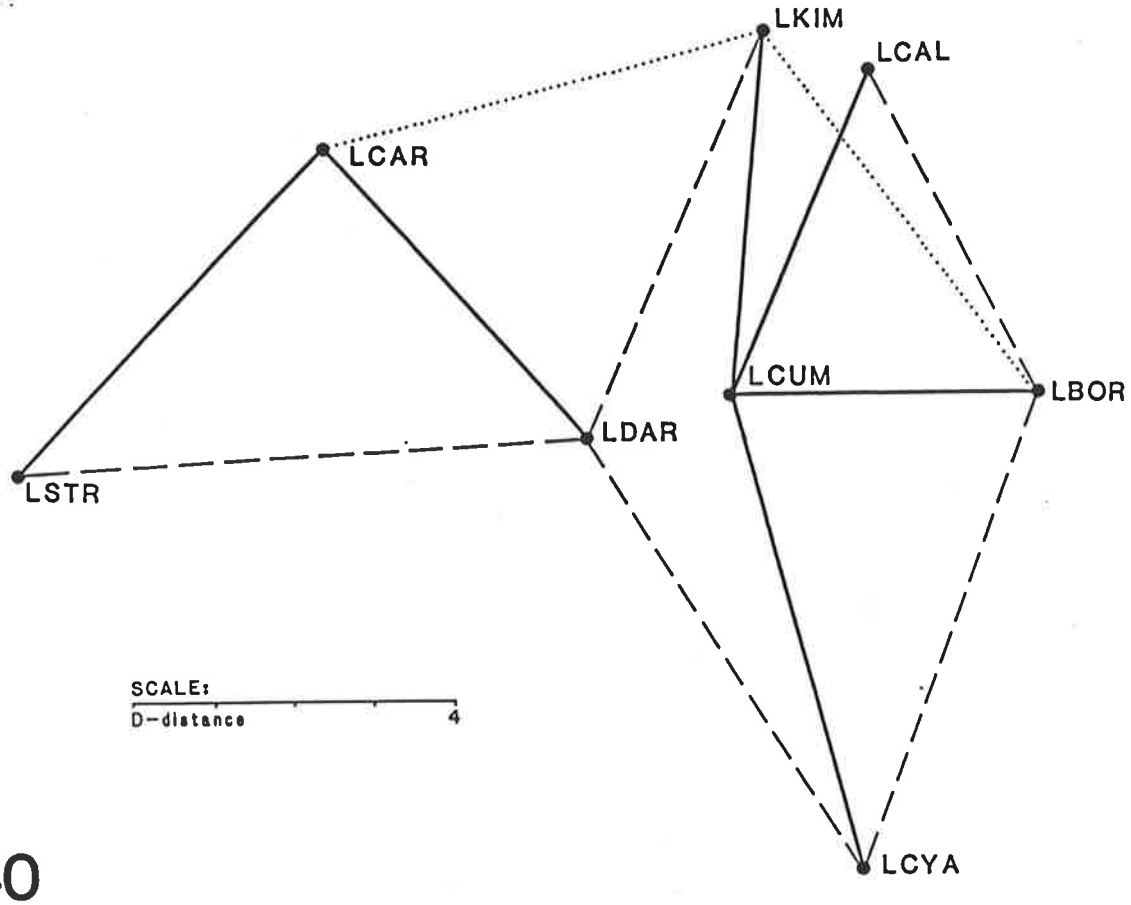
Figure 40: 1st and 2nd-neighbour plot based on D-distances for CVA of LGF groups.

Figure 41: 1st and 2nd-neighbour plot based on the multistate distance metric (DI) for the LGF groups.

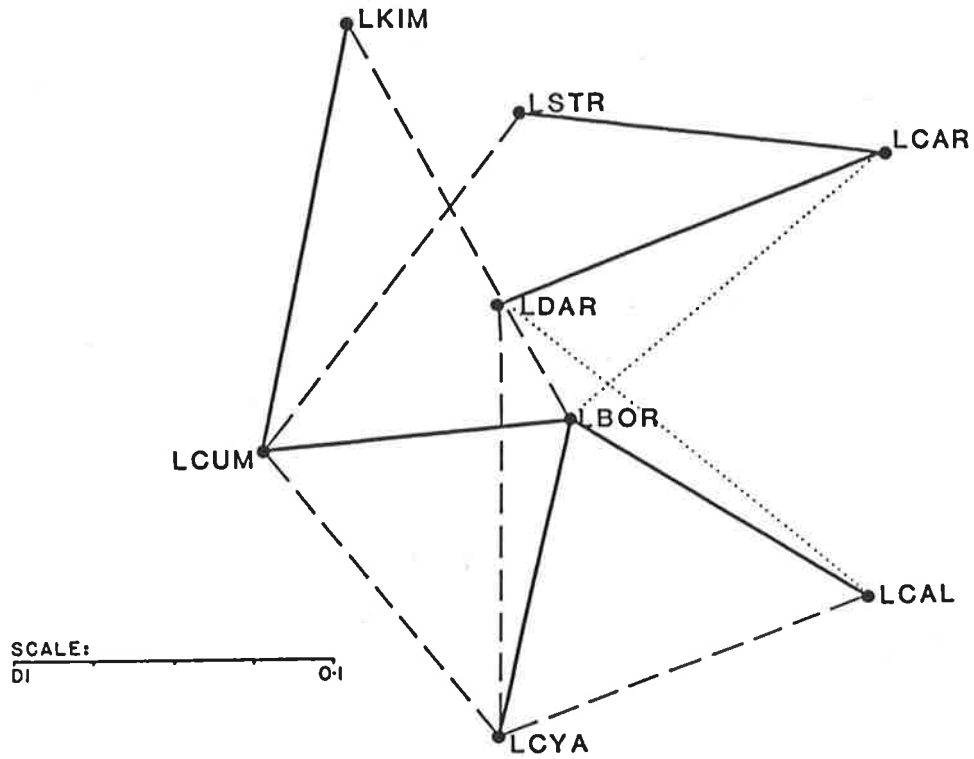
———— nearest neighbour link

- — — — 2nd-nearest neighbour link

..... 3rd- " " "


LKIM
LCAL
LCAR
LCUM
LBOR
LDAR
LSTR
LCYA
SCALE:
D-distance
4

40


LKIM
LSTR
LCAR
LDAR
LBOR
LCUM
LCAL
LCYA
SCALE:
DI
0·1

41

6.4 Multistate Distance Analysis

The distance analysis was performed using LGF groups as OTU's with their variability represented by intervals of two standard deviations either side of the mean. The 1st and 2nd-neighbour plot (fig. 41) is similar in structure to that for D-distances but the variation in distances is less (table 5.3). The same two clusters are defined by nearest neighbour links. The closest pair overall is still LCUM - LBOR, and LCYA - LCAL is the closest for existing taxa. This analysis provides further support for the relationships expressed by CVA.

6.5 Conclusion

Groups representing potential new taxa provide some inter-group distances smaller than those occurring between the groups representing existing taxa. Despite the variation in D-distances, the lack of misclassification in the first CVA indicates that geographical groups including the most similar pair (LCUM - LBOR) are morphologically distinct. However, the taxonomic significance of this distinctness is complicated by the need to practically distinguish individuals without using compound functions. The groups LCYA and LCAL differ markedly in leaf colour and texture as measured by the characteristics LG and CS respectively and they can be separated on either of these characters alone. In contrast the groups LCAL, LBOR and LCUM, which according to both distance measures are not much less distinct from each other than LCYA and LCAL, appear superficially similar. They have typically non-glaucous leaves with low cuticular relief and there are no characters to enable easy recognition. Subtle differences can be detected such as: shorter pedicels and shorter, wider leaves for LBOR; longer fruits with a more deeply inserted disc and

less fruit ribbing for LCUM; and broader fruits spreading more at the summit for LCAL. Such differences are tendencies only and there is considerable overlap between groups on any individual character. The distance between these groups is a result of smaller differences across a number of characters that are unsuitable for keying out.

Even without information on intergradation between LGF groups, results of the LGFDAT analysis provide grounds against recognition of new taxa. It can be seen that this would involve a decrease in the actual distinctiveness of taxa (distance-wise) as well as difficulties distinguishing some of them in practice. The 1st and 2nd-neighbour distances indicate that with maintenance of the taxonomic status quo, LCAR and LDAR are best included with STRL under E. striaticalyx and LKIM, LCUM and LBOR with LCAL under E. calcareana. This result was followed by Boomsma (1981) in his treatment of the Carappee Hill material under E. striaticalyx.

CHAPTER 7

ANALYSIS OF GROUPS BASED ON EXISTING TAXA (TYPDAT ANALYSES)

7.1 Introduction

Morphometric relationships of all existing taxa were investigated using groups of individuals derived from as close as possible to type localities. These TYP groups are used in the TYPDAT, SEDAT, POPDAT and DPOPDAT analyses. The theory behind this approach is as follows. It is usual to accept a particular circumscription when the aim is to test an established taxonomy. This means that limits of variation must be defined and a level of sampling for various forms or geographical areas determined. These *a priori* assumptions may artificially create or blurr distinctions between existing taxa and obscure possible new taxa that might be incorporated within an accepted range of variation. However, these problems can be overcome if comparisons are based on type material. In *Eucalyptus*, types usually comprise material taken from an individual plant. Thus by definition this is the only individual belonging to a given taxon with absolute certainty. More meaningful comparisons can be made if this concept is expanded to include the population from which the type is derived. This is reasonable on the grounds that an interbreeding population within a limited geographical area ought not be subdivided taxonomically. Comparing populations rather than single individuals is advantageous in allowing elimination of some of the more trivial aspects of variation that constitute random background noise in the population gene pool.

7.2 Definition of TYP groups

This section documents precise localities for specimens comprising the groups and shows the extent to which the aim of sampling type locality populations was successful. In some cases type localities which apply are uncertain and interpretations for these are presented here. Original locality information as cited in the protologue, herbarium sheet labels of types, and discussions of typification are provided in chapter 12.

The TYP group names are derived from the first three letters of the epithet of the species which they represent and are arranged alphabetically below. Sample sizes range from 4 to 12 and are indicated by numbers in brackets. Representative herbarium specimens are illustrated among figures 56 to 77 in chapter 9. Figures illustrating material from these groups in more detail may be found in chapters 10 and 11 marked with group names.

ANC (7) fig. 63

E. anceps type locality: Kangaroo Island, near the north coast between Kingscote and American River (Kangaroo Is. Region).

(4) 1.0 km W of main American River to Kingscote road, on road linking Point Morrison with Birchmore Hwy (c. 5 km NW of American River) /PJL 672-675.

(3) On road from American River to Red Banks, 0.8 km NW of road linking Point Morrison with Birchmore Hwy (c. 15 km W of American River) /PJL 667-669.

A collection made by Robert Brown (on Mathew Flinders' south-coast voyage in 1802) from Kangaroo Island has been regarded as the type material of E. anceps. (For a reassessment of this material, see chapter 13.) Flinders

anchored on the north coast of Kangaraoo Island on March 22-23 (Stearn, 1960) and again near the same locality on April 2-6 Maiden, 1908, p. 7-8). According to Maiden (1909, p. 107), the anchorage was at "Kangaroo Head, near the modern Hog Bay", which is near Penneshaw. However, after studying Brown's localities, Burbidge (1955) identified the site as "Kangaroo Head, west end of Nepean Bay", which lies south of Kingscote and northwest of American River. Brown went ashore on both occasions and travelled by small boat to American River where he climbed the nearby Prospect Hill (Mt Thisbe).

With this itinerary and the time available, the material could have been collected anywhere between Kingscote and American River and need not have come from right on the coast. The two localities of the ANC group are located south of Nepean Bay at distances of 5 km and 0.5 km from the coast respectively.

CAL (7) fig. 75

E. calcareana type locality: 43 km W of Nundroo (Nullarbor Region).

(5) 44.1 km by road W of Nundroo on Hwy 1/PJL 1321-1325
--- 40 km E of Head of Bight/G.C.Cornwall s.n. 16.vi.1976
--- 90 km along Eyre Hwy W of Nundroo/G.C.Cornwall 288

The second locality is approximately the same as the type and the collection of the third is a paratype.

CLE (6) fig. 60

E. clelandii type locality: Goongarie, 65 miles N of Kalgoorlie (Austin District).

(5) 5.9 km by road N of Goongarie, c. 0.5 km W of road to Menzies /PJL 1530, 1539-1542

--- 3.7 km by road S of Goongarie on E side of Kalgoorlie-Menzies road /PJL 1543

CON (5) fig. 62

E. conglobata type locality: Vicinity of Memory Cove and Port Lincoln Bay (Eyre Peninsula Region).

(5) Lincoln National Park, roadside 2 km S of Pt Lincoln-Sleaford road /PJL 1123-1127

The CON locality is at the west end of Port Lincoln proper which is a bay south of Port Lincoln township. Missing bud data was filled with mean scores derived from an individual from this locality and another individual (4 km W of Port Lincoln PO on road to Coffin Bay/PJL 1112).

CYA (12) fig. 72

E. cyanophylla type locality: 3 km N of Berri (Murray Region).

(5) 10 km NNE of Berri on road to Renmark/PJL 886-890

(5) 1 km by road W of main Renmark-Berri highway on main road to Monash [= c. 3 km N of Berri]/W.R.Barker 4034A-4034E & R.M.Barker

--- Berri Nursery area of Woods and Forests Dept/C.D.Boomsma s.n., 24.i.1976

--- Springcart Gully, Berri/B. Dangerfield s.n., 20.x.1962

DON (5) fig. 66

E. dongarraensis type locality: Dongara, not far from beach (Irvin District)

(5) 22 km by road S of Hwy 1 into Dongara on road to Eneabba [ca. 20 km SE of Dongara]/PJL 1463 to 1467

No material of Dumosae could be located in the immediate vicinity of Dongara and it is probably now extinct here as a result of vegetation clearance. Although the population sampled was about 20 km from Dongara, there is agreement with the type material in its proximity to the coast (occurring behind coastal dunes) and the character of slight stem glaucousness which is absent in most material referred to E. dongarraensis.

DUM (9) fig. 73

E. dumosa type locality: c. 13 km WSW of Ungarie (New South Wales).

(4) 8.2 km W by road from Ungarie towards Youngareen/R. Grandison s.n., 5.i.1980

(2) 7.5 km W of Ungarie/P.L.Milthorpe & G.M. Cunningham 4, 5

--- 9 km W of Ungarie/P.L.Milthorpe & G.M. Cunningham 2

--- 6.6 km SW of Yalgogrin on Mid-Western Hwy/G.M.Chippendale 945 & M.J. Beeston

--- 66 km W of West Wyalong towards Rankin Springs/J.D.Turner 83

It is important to establish the type locality more precisely because E. dumosa, being the first described taxon within the Dumosae, is the name under which other taxa will be synonymized in this study *. Furthermore, within the above area there is considerable variation in fruit size which has a bearing on the relationship between E. dumosa and other taxa. All collections representing DUM fall within the area bounded by 33 to 34° S and 146 to 147° E. According to Maiden (1904, 1(4), p. 98), this is the area Oxley's expedition would have been in between May 23 and June 10 1817 when Alan Cunningham was most likely to have collected the type specimen. Maiden chose the date of June 10 because of an entry in Oxley's journal describing mallee vegetation featuring E. dumosa. However, I consider that May 23 is the likely date for the collection of the type material because of an entry under this date in Cunningham's diary quoted by Lee (1925, p. 219-220). There is a reference to having made a collection of E. dumosa together with a brief morphological account. Cunningham describes the habitat as "a stony ascent" in a "rugged sterile tract covered with a tall thick brush". This agrees with a label on the type specimen, Cunningham 206 at BM, which reads "Eucalyptus species from back of the ..?.. found on the high barren lands of the interior observed to flower in July". The label is in the handwriting of Charles Fraser, Cunningham's assistant on the expedition. A second label by Fraser on the same sheet reads "Eucalyptus species from back of the interior found in flower and bud in July, habit a tree 7 feet high". The reference to flowers and buds in July, is unlikely to refer to the date of collecting this material as no buds are present, but is probably a later observation or a mismatched label.

Taking May 23rd as the probable date of collection for Cunningham 206, the

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* However, see notes in section 12.5.1, p.292, 293.

type locality was defined more precisely by plotting Oxley's route through the area on the Cargelligo 1: 250,000 map using information from Cunningham's diary provided by Lee (1925). The following points are significant:

1. A course due southwest from the Lachlan River passing close by Mt Maud puts Oxley's camp on May 21 near Ungarie. It was "five miles east of water in lagoons" which would probably have been associated with Euglo (Humbug) Creek.

2. The camp on May 23 was 10 miles from the previous locality in a major channel after a descent from the rise on which E. dumosa had been collected. This compares well with a low ridge defined by drainage tributaries on the Cargelligo map extending northwest and southeast of 'Bibbijolee' and bounded on the southwest by Euglo (Humbug) Ck.

3. The location of Oxley's route across this rise is constrained by the fact that the next camp was 11 miles southsouthwest and at the foot of a rocky mountain. This must have been Narriah Mountain as it is the only prominent peak for many miles.

The third fact is inconsistent with the type locality of 6.5 miles SE of Ungarie given by Hall and Brooker (1974). From the evidence presented the type locality of E. dumosa is most likely to be approximately 13 km WSW of Ungarie and 3 km S of Youngareen.

FRA (5) fig. 64

E. fraseri type locality: 14 miles (22.5 km) W of Balladonia (Coolgardie District).

(5) 8 km by road WNW of Balladonia Roadhouse on S side of Eyre Highway /W.R.Barker 2599A-2599E

GEO (4) fig. 61

E. georgei type locality: 159 km E of Hyden along the track to Norseman (Roe District).

--- 159 km E of Hyden on Norseman track/M.I.H.Brooker 4989

--- 315 mile peg Hyden-Norseman road = N end of Bremer Range /L.F.Allan 29

--- Junction of Bremer Range road and Hyden track/A.Kessell 947

--- 315-332 mile pegs on Hyden-Norseman track/A.Kessell 424

The above four collections are all paratypes.

KON (5) fig. 59

E. kondininensis type locality: Kondinin (Roe Dostrict)

(5) 0.5 km S of Kondinin, near junction of road to Lake Kondinin /PJL 1440-1444

LES (6) fig.57

E. lesouefii type locality: Kalgoorlie (Coolgardie District).

(5) Binduli, 5.2 km by road SW of Kalgoorlie P.O. on Great Eastern Hwy /PJL 1523-1527

--- 8.4 km by road N of Kalgoorlie on road to Menzies/PJL 1528

PIL (5) figs 74,76

E. pileata type locality: Desmond, near Ravensthorpe (Eyre District).

(5) 0.6 km S of Desmond, which is 10 km SE of Ravensthorpe on road to Hopetoun/PJL 1379-1383

PTE (5) fig. 56

"E. pterocarpa" type locality: Northwest of Norseman (Coolgardie District).

--- 10 miles NWW of Norseman/G.E.Brockway s.n., -.x.1942
--- Norseman 16 km occidentalem versus/C.A.Gardner s.n., 20.vii.1963
--- 9 miles NW of Norseman/G.E.Brockway s.n., 20.viii.1963
--- 5.4 miles W on road 6.8 miles NW of Norseman/G.M.Chippendale 154
--- 6.4 miles W along (L)turn-off, 6.4 miles N of Norseman/D.Boland J345

Although undescribed, "E. pterocarpa" was treated as an existing taxon and included as the basis for a TYP group. It had been regarded as a species by foresters and nurserymen for some time and clearly warranted investigation as a distinct entity. The above collections are later (12.5.9) proposed as the holotype and four paratypes.

SHE (10) fig. 68

E. sheathiana type locality: (cultivated tree - origin uncertain) (Avon District ?)

(5) Nungarin, 0.5 km S of Nukarni RS, E of road/PJL 1447, 1448, 1449A-1449C
(5) 1.7 km by road W of Carrabin on Great Eastern Hwy/PJL 1492-1496

The type for this species is from a cultivated tree grown from seed at Kings Park, Perth. The seed was sent to Mr J. Sheath at Kings Park as originating from the "Eastern Goldfields near the South Australia border". However, no specimens referrable to E. sheathiana are known from near the border. Further doubt is cast on the locality because the seed had been sent labelled as E. erythronema which is also not known to occur this far east.

Two populations about 30 km apart in the Avon District were chosen to represent E. sheathiana on the basis of their morphological similarity to the type material. Buds were present only in the first population and agree with the type in their conoidal shape and consistent absence of ribbing. The mean scores of OLW and OW2 compare favourably with measurements taken from illustrations of type collections by Maiden (1922, 6(51), p.61) and Gardner (Aplin, 1979, p.115, fig. 38a) and with a specimen at PERTH derived from the type tree. The similarity in bud form was later confirmed by type specimens sent on loan (figs. 87, 168). Other specimens from the same area which are illustrated by Gardner have consistent bud morphology. More hemispherical buds with regular ribbing are common in much material elsewhere that has been referred to E. sheathiana. The second locality, although lacking buds, was included because there were larger fruits closer to the type in size. These still maintained the characteristic narrow disc, which again is not found in much other material referred to E. sheathiana. Missing bud data was filled with mean values derived from material at the first locality and from illustrations of the type.

STR (5) fig. 65

E. striaticalyx type locality: Milly's Soak, near Cue (Austin District).

--- Creek crossing S of Millie Well, 4.3 km W along track 19.3 kmm NNE of Cue/PJL 1481-1485

Reference to the type locality by Boomsma (1969) as " Milly's Soak four miles east of Nannine" is misleading and results from confusion with another locality cited in the protologue (12.5.1, p. 287, 290). A local inhabitant at Cue confirmed that the 'Millie Well' marked on the Cue 1: 250,000 national map is at the place known as Milly's Soak.

WOO (4) fig. 58

E. woodwardii type locality: 120 km E of Kalgoorlie on transcontinental railway (Coolgardie District).

--- 60 miles S from Victoria Spring,W.A./R. Helms 15
--- cultivated, Waite Agricultural Research Institute arboretum, Adelaide. NW corner of mallee section/PJL 1562.
--- cultivated, loc. cit., W side of mallee section/PJL 1563
--- cultivated, Burnside, Adelaide/PJL 1564

The inaccessabilty of the type locality means that there are only limited suitable collections to sample variabilty there. Thus it was necessary to use cultivated material. Eucalyptus woodwardii has a quite restricted occurrence (Pryor, 1981), so there is less scope for geographic variation and cultivated material could be reasonably representative.

7.3 Canonical Variates Analysis

The 16 TYP groups described above were subjected to CVA with their missing operculum characters filled with group mean values (except where otherwise indicated in the description of TYP groups). Subsequently all 499 measured specimens (ALLDAT) were incorporated in the analysis for classification. Missing data in unassigned individuals was taken into account by separate runs with operculum data excluded as described in section 5.2, p.109,110. Finally, separate analyses were performed with the 2- and 3-state characters pertaining to blackbutt and glaucousness removed.

Classification results for the TYP groups are summarized in table 9.1 a. Classification functions assigned all members correctly, meaning that there was no overlap between groups. No gradation was detected as correct classifications were made with a high degree of certainty (table 9.1). The results demonstrate the distinctiveness of the existing species concepts when applied in their narrowest sense. Relationships between taxa are displayed by the 1st and 2nd-neighbour plot for TYP groups (fig. 42). This has a three-lobed structure marked by three relatively distinctive groups, CON, WOO and PTE at the apices. In terms of nearest neighbours alone, the lobes represent distinct clusters. These are linked together by lower-order neighbour relationships in a central hub. Since the central links are more uniform and relatively smaller distances, the clusters overlap and are better interpreted as trends emanating from a central complex. The trends are clearly displayed because of the way the plot was constructed by choosing between each two points of triangulation to minimize overlap. The structure is not merely an artifact of this method but results because members of a nearest neighbour cluster (particularly the more extreme members) have next-highest order links within the cluster more frequently than with groups from the other clusters. The three clusters correspond to combinations of the three

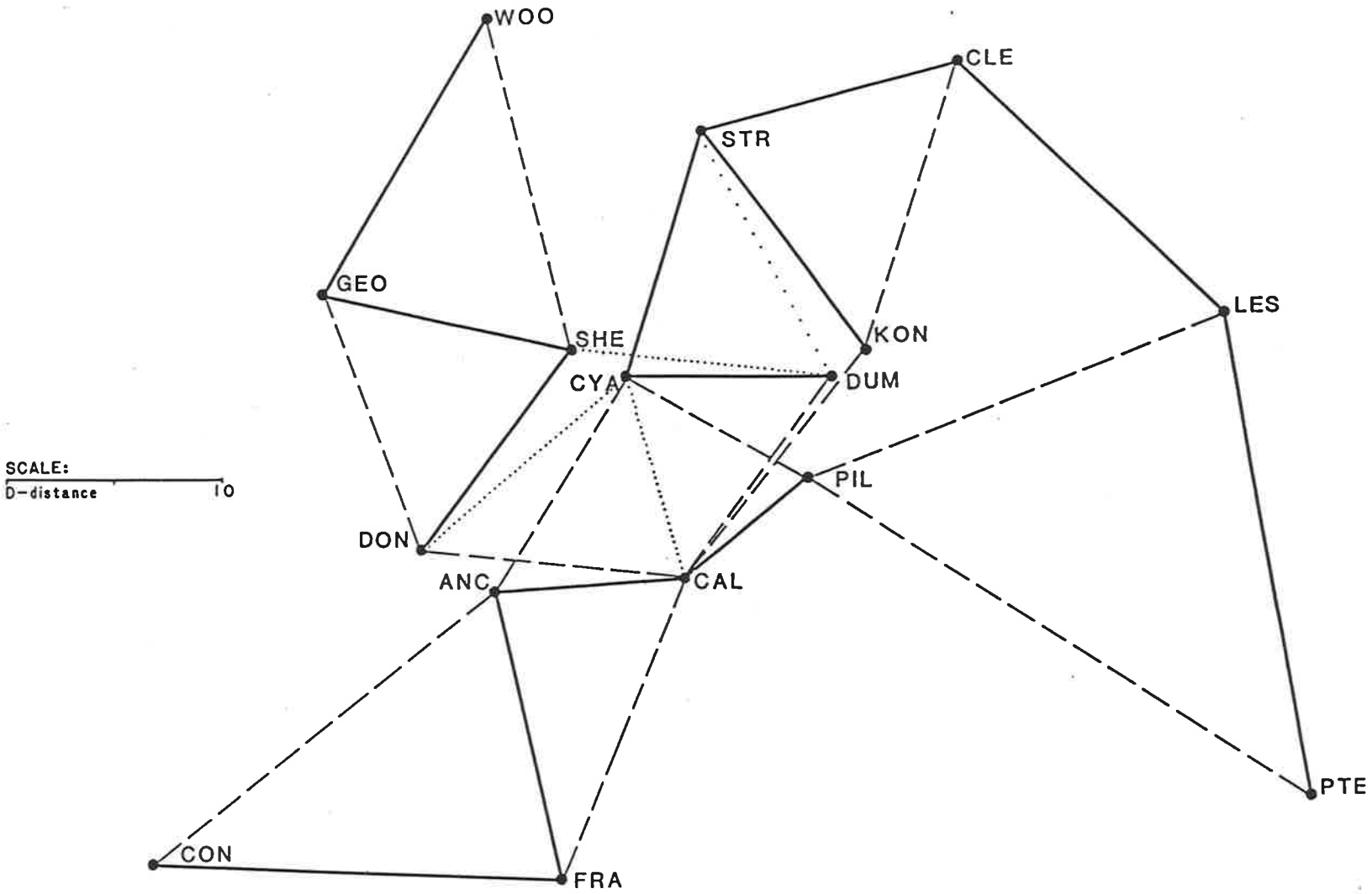
Figure 42: 1st and 2nd-neighbour plot based on D-distances for CVA of TYP groups.

———— nearest neighbour link

– — — – 2nd-nearest neighbour link

..... 3rd- " " "

. . . . . 4th- " " "


WOO
CLE
STR
GEO
LES
SHE
KON
CYA
DUM
SCALE:
D-distance
10
PIL
DON
ANC
CAL
PTE
CON
FRA

low-state characters (LG, SG and BB) which indicates the importance of these characters as discriminators. The groups of the first cluster, CON, FRA, ANC, CAL, and PIL, are all characterized by non-glaucous leaves and have an associated low cuticular relief. They also lack stem glaucousness and blackbutts. Groups of the second cluster, DON, SHE, GEO and WOO, have stem glaucousness and lack blackbutts but vary in leaf glaucousness. The third cluster contains the remaining groups which, with the exception of PTE, have a blackbutt and/or glaucous leaves and vary in stem glaucousness.

It is notable that PIL and CAL are the most similar pair. Eucalyptus calcareana (represented by CAL) is the most recently described taxon in the Dumosae. Boomsma (1979) noted its affinites with E. pileata and (represented by PIL) and the difficulty of separating the two species.

For members of defined groups there was a slight reduction in distinctiveness reflected by P(G/X) values after removal of blackbutt and glaucousness characters (table 9.1). However, the absence of misclassification demonstrates that these characters are not necessary to distinguish typical representatives of the taxa. More significantly, with removal of the three operculum characters, a member of group CAL was misclassified to PIL. This indicates that the the two most similar species, even when confined to populations from the type localities, can not be distinguished with complete reliability if buds are unavailable.

Classification of unassigned individuals to TYP groups resulted in a large number of intergrades. Gradation at levels 1 and 2* was confined to groups of the central part of the 1st and 2nd-neighbour ordination. The most evident gradation occurred between the following pairs of groups which

---

* Level 1: $.5000 < P(G/X) < .9000$, Level 2: $.9000 \leq P(G/X) \leq .9900$

were represented by seven or more individuals intermediate at level 2: CAL-PIL, CAL-ANC and DUM-CYA. For each unassigned individual, the classified group and its nearest neighbour, if a level 2 intergrade, were recorded for comparison with subjective determinations made prior to numerical analyses (appendix 1). The determinations were in agreement with the closest assigned group in less than 40 % of the classifications. This result was not surprising because of the uncertainty with which many of the subjective determinations were made. The most marked discrepancy occurred with the 38 individuals corresponding to the LGF group LSTR, none of which were classified to the TYP group STR. This is attributed to the high weight given to the character BB. Blackbutts were scored for members of the TYP group but are lacking in the LGF material from the northwest of South Australia. When the character BB was removed from the analysis 15 individuals were classified to the group STR. Repeating the analysis with the glaucousness and blackbutt characters removed resulted in a greater degree of intergradation and a greater geographical intermixing of groups in classifications of the unassigned individuals.

7.4 Multistate Distance Analysis

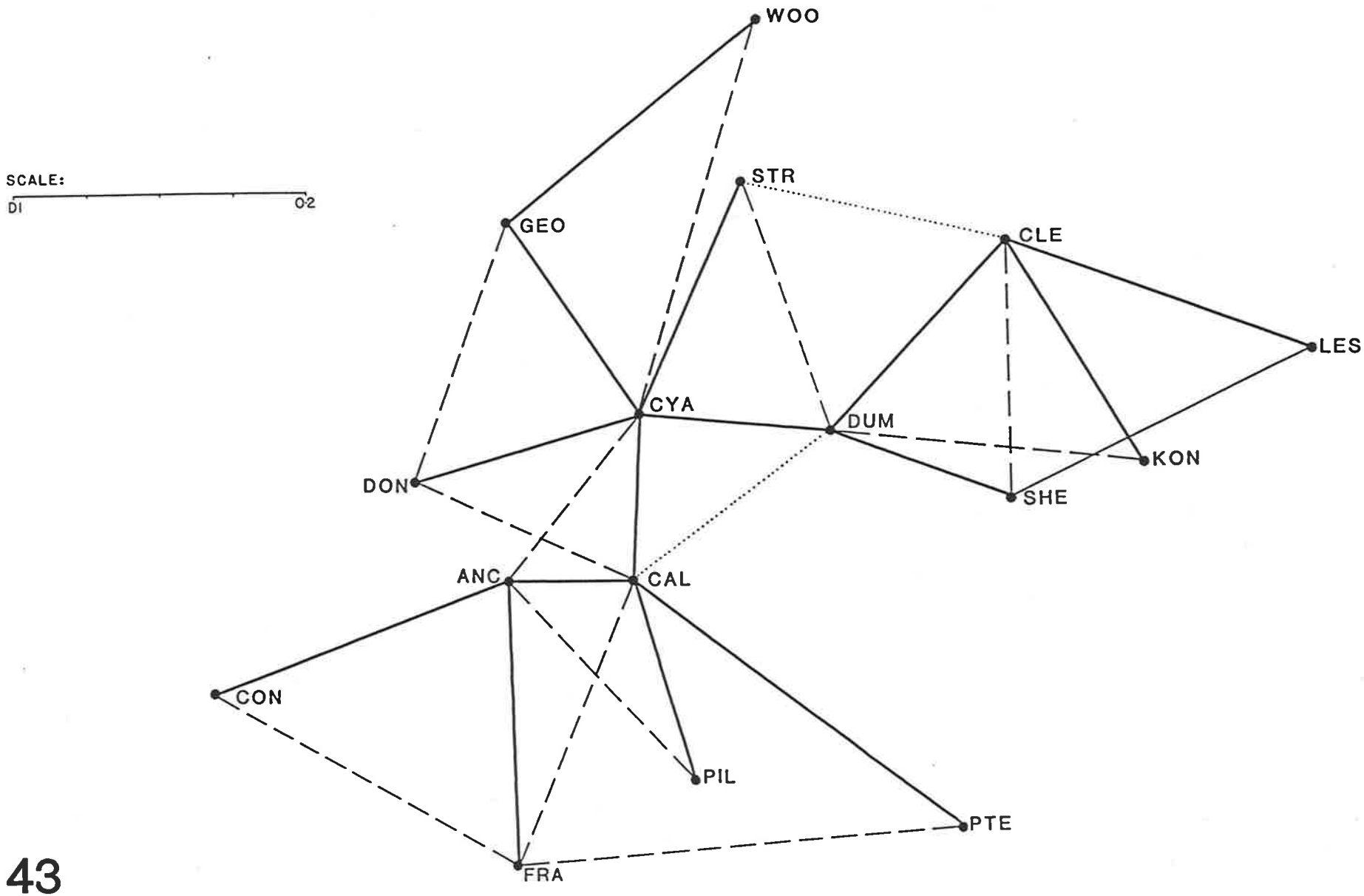
The nearest neighbour network (fig. 43) differs from that derived with D-distances in being a single cluster and having a greater degree of branching. The three-lobed structure relating to the low-state characters is not as well defined since these characters are no longer weighted. The greater degree of branching reflects the reduced variation in distance values produced by the metric (table 5.3). The more even weighting of characters also results in major changes for the neighbours of PTE and SHE. However, the overall ordination of TYP groups obtained with the 1st and 2nd-neighbour network (fig. 43) is broadly similar to that of the CVA.

Figure 43: 1st and 2nd-neighbour plot based on the multistate distance metric (DI) for the TYP groups.

———— nearest neighbour link

– — — — 2nd-nearest neighbour link

..... 3rd- " " "


SCALE:
DI
0·2
WOO
STR
GEO
CLE
LES
CYA
DUM
KON
DON
SHE
ANC
CAL
CON
PIL
PTE
FRA

The results of these analyses, and their taxonomic significance, are considered further in chapters 10 and 11 together with the results of the DPOPDAT analyses (chapter 9).

CHAPTER 8

ANALYSIS OF SOUTH-EASTERN POPULATIONS

(SEDAT ANALYSES)

8.1 Introduction

Separate analyses were performed on a smaller set of specimens from the South-eastern Region of South Australia to demonstrate the extent and complexity of variation that could occur within a limited geographical area. A total of 38 individuals were sampled from 11 localities in this area. One locality, Comet Bore, 55 km south of Pinnaroo, was sampled by 20 individuals. Collection data is listed in appendix 1 for the South-eastern Region under '*E. dumosa* ssp. *conglobata*', 'Intergrades between ssp. *conglobata* and ssp. *dumosa*', and '*E. dumosa* ssp. *dumosa*'.

8.2 Canonical Variates Analysis

In the TYPDAT CVA described in the previous chapter, the 38 individuals were classified to the groups CYA, ANC, CAL and DUM with considerable intergradation indicated by P(G/X) values. By restricting defined groups in the SEDAT CVA to these four TYP groups, relationships of the 38 unassigned individuals could be displayed completely by scores on only three canonical variate functions.

Results are presented as two scattergrams (figs 44 and 45) with the first canonical variate repeated, to avoid the complexity of a three dimensional plot. It is evident that the unassigned individuals do not overlap with any of the TYP groups in D-space. (Although there is some overlap with CYA on the first two canonical variates, these individuals are clearly distinct on the third function.) This can be interpreted as indicating that material typical of *E. cyanophylla*, *E. anceps*, *E. calcareana*

Figure 44: Canonical Variates Analysis based on four TYP groups with classification of 38 unassigned individuals from the South-eastern Region.

CV1 : canonical variate 1 (45 % of variation)

CV2 : canonical variate 2 (35 % of variation)

TYP groups:

□ ANC

◇ CAL

○ CYA

△ DUM

unassigned individuals:

● miscellaneous localities

✱ Comet Bore population (P111)

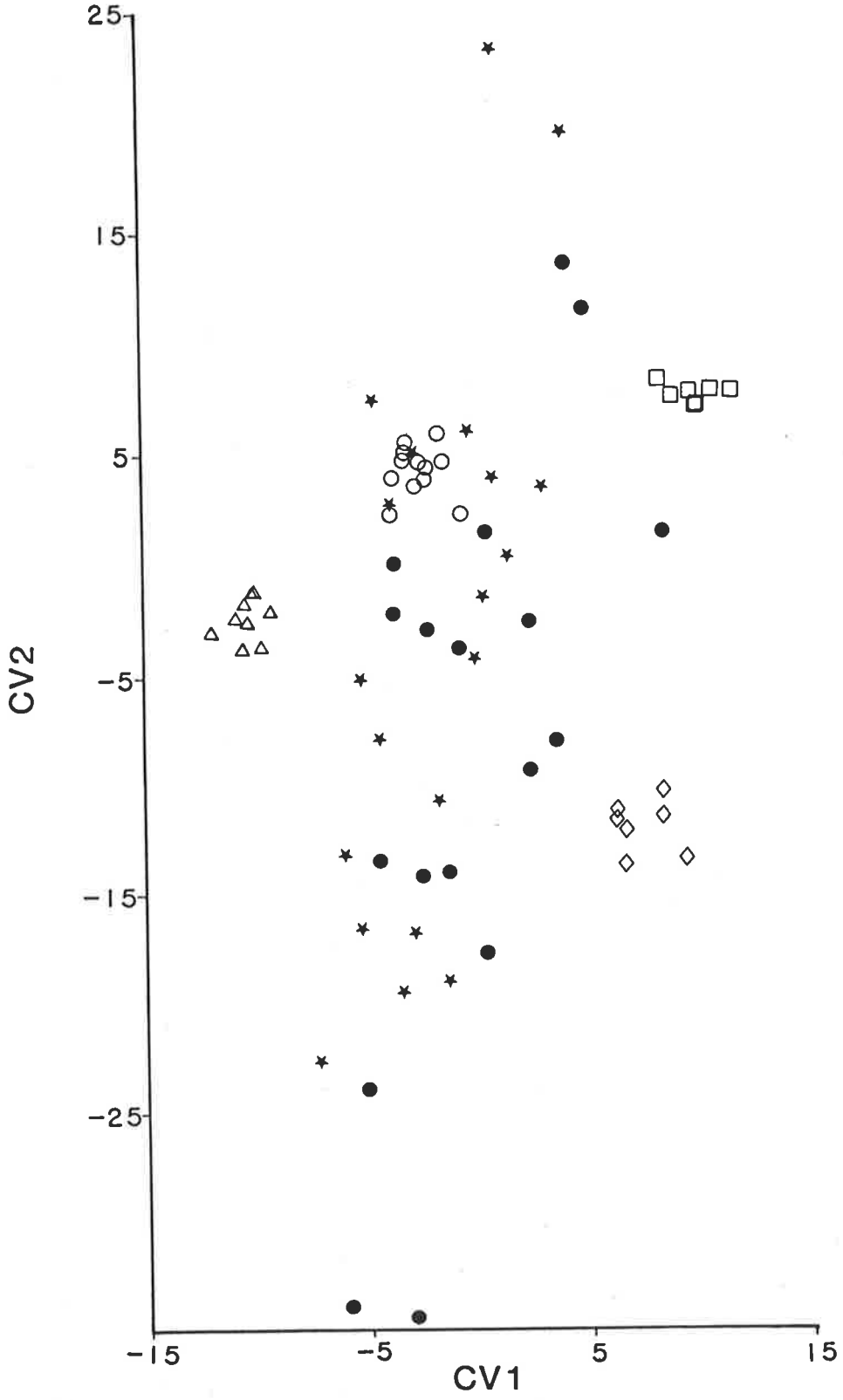

25
15
5
-5
-15
-25
CV2
-15
-5
5
15
CV1

Figure 45: Canonical Variates Analysis based on four TYP groups with classification of 38 unassigned individuals from the South-eastern Region.

CV1 : canonical variate 1 (45 % of variation)

CV3 : canonical variate 3 (20 % of variation)

Total variation expressed by both plots (figs 44 and 45): 100 %

TYP groups:

□ ANC

◇ CAL

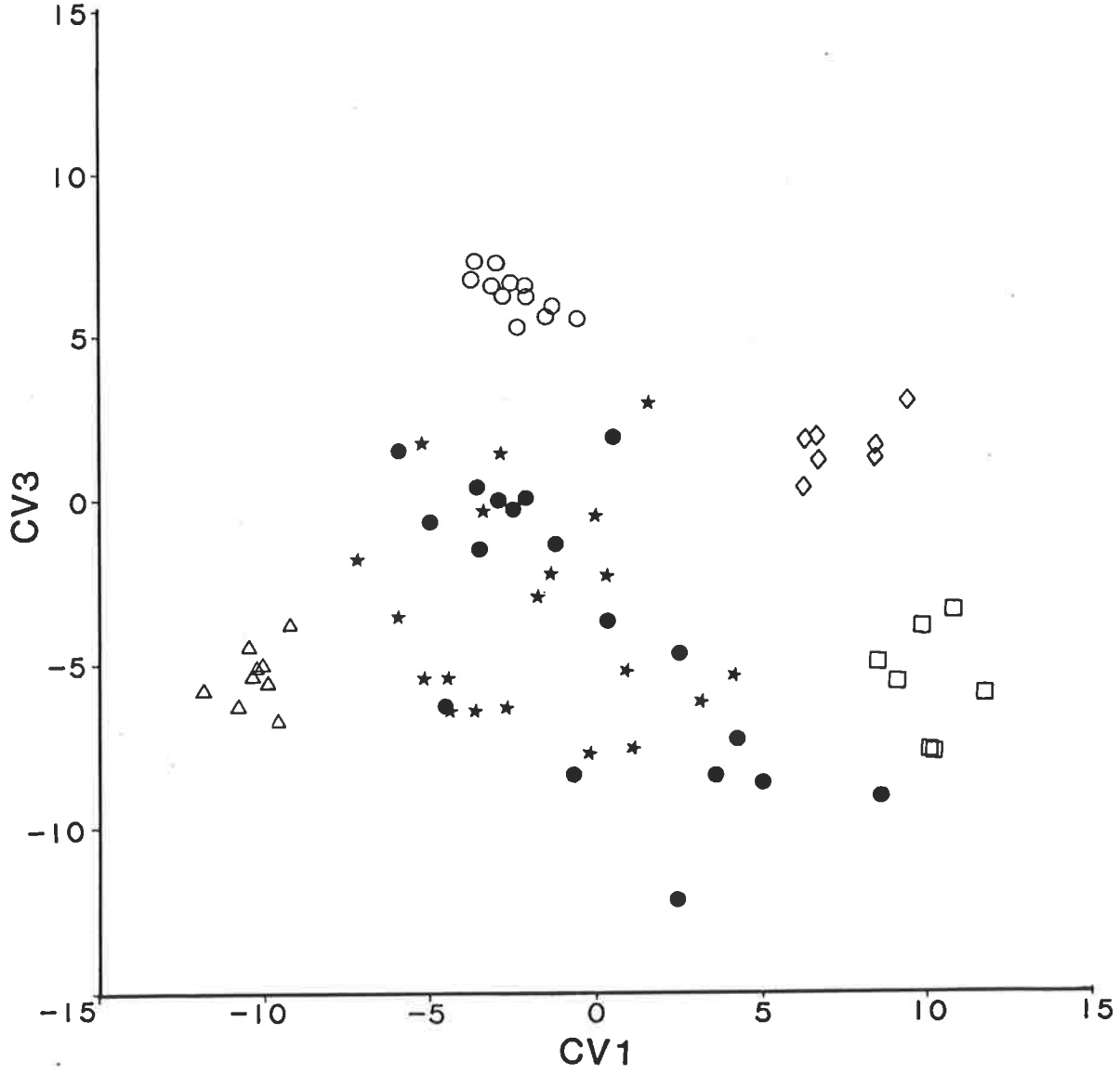
○ CYA

△ DUM

unassigned individuals:

● miscellaneous localities

★ Comet Bore population (P111)



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or E. dumosa in a strict sense, does not occur in this area. Another observation is that the scatter of points is much greater for the unassigned individuals than for any of the TYP populations. This remains true even for the single Comet Bore locality. This indicates that a large amount of the between-groups variation is expressed within a single population. Diagnostic characters distinguishing the four taxa must exhibit much greater variation here than within the TYP populations. The scores for some individuals, mainly on the second canonical variate, are more extreme than for the TYP populations. However, most individuals are intermediate and fall within the region of D-space bounded by the four TYP groups. Thus the canonical variate scores indicate substantial intergradation between all four TYP groups.

The P(G/X) values were found to be very conservative indicators of this intergradation and only five of the 38 individuals were classed as intergrades using the two levels defined in chapter 5 (p.109). Two exhibited level 1 gradation and three, level 2 gradation. A greater extent and degree of intergradation for the same individuals was obtained with classification by the TYPDAT CVA based on all 16 TYP groups. In this case, 11 individuals were recognized as exhibiting significant gradation, six at level 1 and five at level 2. The canonical variates are better able to discriminate between the four groups when the other groups are excluded. This is expressed by the larger D-distances between group centroids in the SEDAT CVA.

8.3 Principal Component Analysis

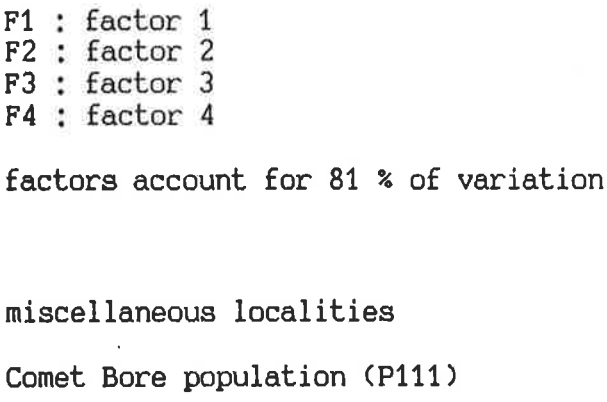
This was performed to test for any clustering or discontinuities in variation independent of polarities defined by the four TYP groups. The 38 unassigned individuals were subjected to Principal Component Analysis

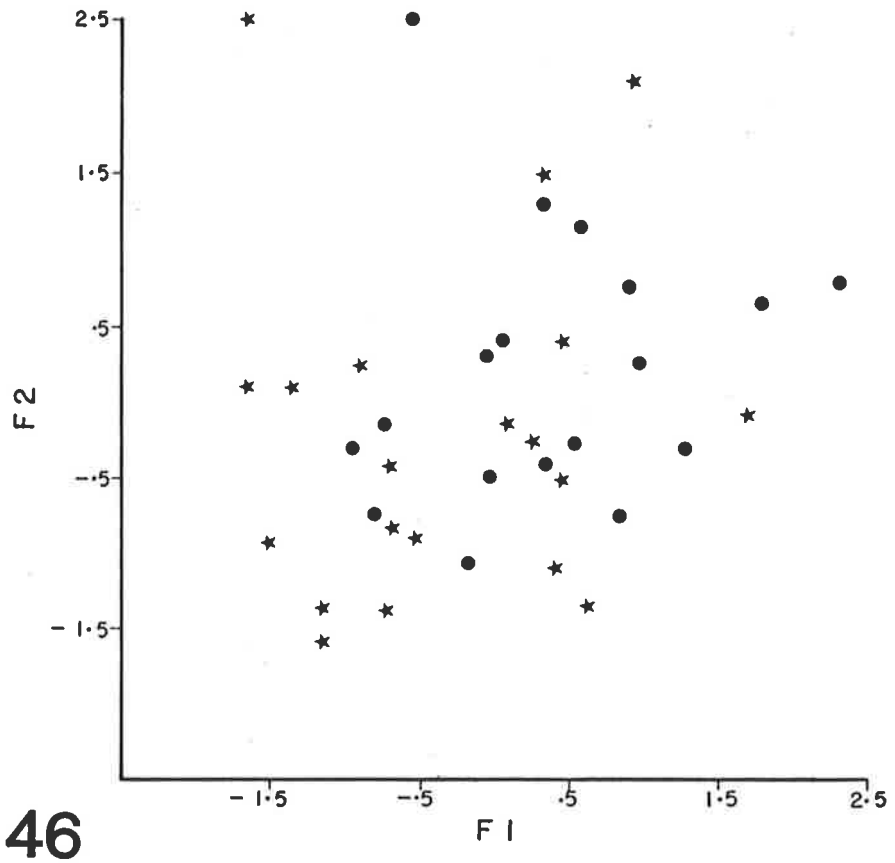
(SPSS FACTOR: PA2), repeated with orthogonal and oblique rotation of factors. Operculum characters were excluded due to missing data. To avoid problems arising from the mixing of low-state and continuous metric data, the three low-state characters were also excluded. This is not a serious omission. Only a little information expressed by LG (leaf glaucousness) was lost, and SG and BB were constant. Factor loadings for characters resulting from these analyses could not be related to existing taxa and were difficult to interpret morphologically as they were widely distributed even after oblique rotation. Factor scores plotted for the first four factors, which together account for 81 % of the total variation, failed to reveal any significant clustering of individuals (figs 46, 47).

8.4 Conclusion

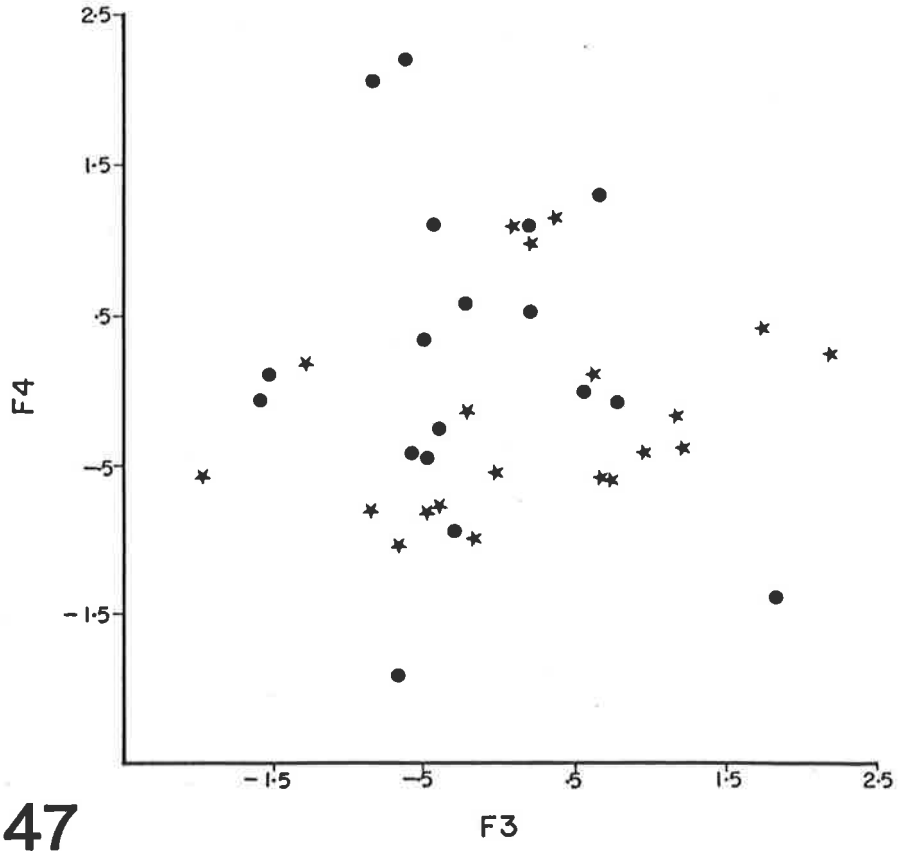
The SEDAT analyses demonstrate the problems in attempting to apply existing taxa to material from the South-eastern Region. Of the 20 individuals sampled at Comet Bore, the CVA classified 2 to CYA, 5 to ANC, 6 to DUM, and 7 to CAL. However, based on function scores these do not represent discrete morphological entities but are largely intermediate forms. They were all sampled from the same fairly uniform habitat on clayey soils around a clay-pan depression. There is no evidence of different flowering periods and they are interpreted as part of a single interbreeding population with a large pool of genetically-determined morphological variation. The recognition of four closely related species in this area under the existing concept involving a high degree of 'splitting' is not supported.

Figures 46, 47: Principal Component Analysis (followed by oblique rotation of axes) for the 38 unassigned individuals from the South-eastern Region.





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CHAPTER 9

ANALYSIS OF POTENTIAL NEW TAXA

9.1 POPDAT Analysis

9.1.1 Aim of analysis

The two preceding analyses have investigated the way that variation in Dumosae can be accommodated by existing taxa. The aim of the POPDAT analysis was to identify significant centres of variation for consideration as potential new taxa. A group of individuals that are treated as intergrades by a CVA may be characterized by a unique combination of character scores. If defined for the analysis such a group would lie on a new pole of variation and may be as distinct as other groups in D-space. Alternatively a group with a similar pattern of character scores may be as distinct as other groups if it lies on the same polarity midway between two widely separated groups. Thus individuals treated as intergrades, or even assigned to TYP groups without detectable gradation in the TYPDAT CVA, may contribute to distinct new groups in the POPDAT analyses.

9.1.2 Definition of POP groups

The 33 POP groups listed in table 9.1, were investigated together with the 16 TYP groups. Two of the POP groups were based on potential taxa recognized by Gardner. RED is represented by a single specimen labelled by Gardner with the unpublished name "Eucalyptus redimiculiphloia". The group ZAN comprises two specimens from near Zanthus on the Nullarbor Plain, Western Australia representing a form of E. lesouefii referred to by Gardner (Aplin, 1979, p. 186). The remaining POP groups are represented by four or more individuals collected from a single locality or nearby sites

as specified in table 9.1.

The POP and TYP groups were subjected to a multistate distance analysis. Use of CVA was invalid because the number of groups exceeded the number of characters. Variation within groups was represented by absolute ranges for character scores except for RED which was represented by an interval equal to the mean range for each character centred on the character scores for the RED specimen.

9.1.3 Results

Multistate distance values were used to construct a nearest neighbour tree, and a Graph Theory network using the approach of Clifford and Williams (1980). The latter incorporated all the second neighbour links, many of which joined individuals widely separated in the plot by nearest neighbour links. This indicates a tight structure in multidimensional space. This plot was complex and difficult to interpret, so the nearest neighbour tree is illustrated (fig. 48) to display relationships in less detail. Clustering is poorly developed although some patterns are evident. For instance P12, P92, P27, P20, and P121 are characterized by small fruits and generally non-glaucous leaves, and except for P121 occur near the upper part of the gulfs in South Australia. Groups P22, P53, and P35 are joined by mutual nearest neighbour links and are from the Flinders and Gawler Ranges, as are P109 and P52 which link indirectly via P30. The group PTE is clearly the most distinct.

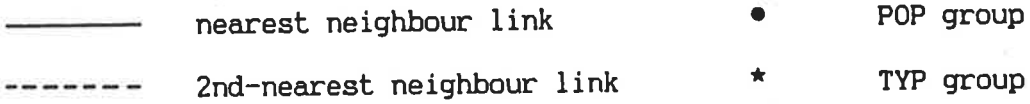
The closest pair of TYP groups is CAL-ANC, separated by .19 units. It is evident that most POP groups have nearest neighbours more distant than this. This demonstrates the uniqueness of populations and shows how little of the overall variation is described by the TYP groups. Applying nearest neighbour clustering on these distances with a phenon line at .19 units would produce an impractically large number of potential new taxa.

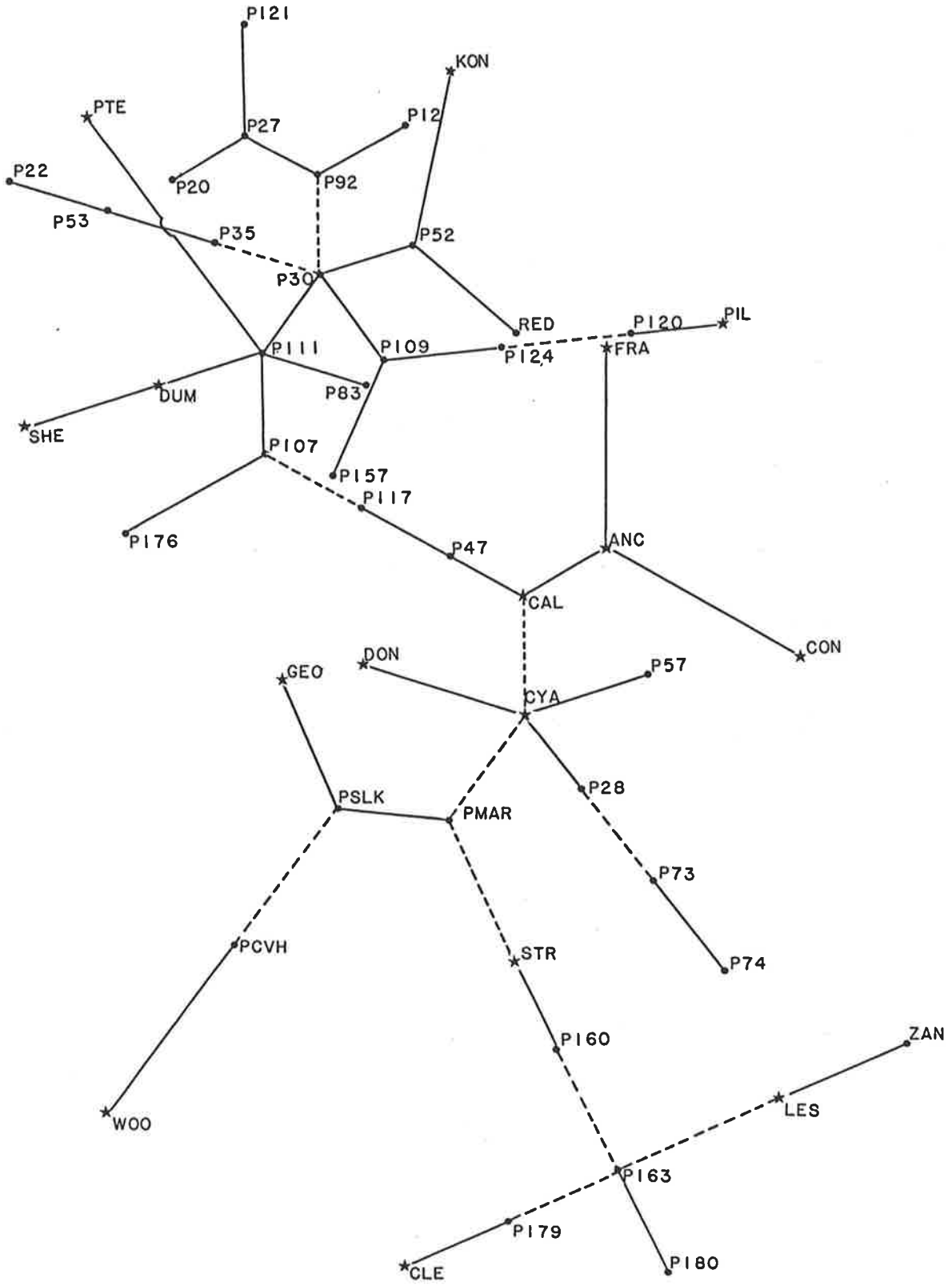
Table 9.1: Key to POP groups

POP	n	NT	d	locality (state : Region/District)
PCVH	9	WOO	.40	125-136 km N Cook (SA : North-western)
PMAR	6	CYA	.26	Maralinga (SA : Nullarbor)
PSL	6	CYA	.27	Serpentine Lakes near WA border (SA : North-western)
P12	6	DUM	.24	Folland Park, Enfield (SA : Southern Lofty)
P20	5	PIL	.32	3 km N Bute (SA : Northern Lofty)
P22	7	DUM	.24	0.5-6.0 km SW Mt Hack (SA : Flinders Ranges)
P27	4	PIL	.30	3 km S Lochiel (SA : Northern Lofty)
P28	5	CYA	.18	9 km W of Kingston (SA : Murray)
P30	6	DUM	.24	22 km WSW Waikerie (SA : Murray)
P35	4	DUM	.28	1 km NE Devils Peak (SA : Flinders Ranges)
P47	5	CAL	.16	25 km NW Lock (SA : Eyre Peninsula)
P52	6	DUM	.24	Kokodo Hill, Gawler Rges (SA : Eyre Peninsula)
P53	4	DUM	.27	Scrubby Peak, Gawler Rges (SA : Eyre Peninsula)
P57	5	CYA	.25	24.0-26.5 km NE Yantanabie (SA : Eyre Peninsula)
P73	6	CYA	.23	Carappee Hill (SA : Eyre Peninsula)
P74	5	CYA	.26	0.5-4.0 km NE Darke Peak PO (SA : Eyre Peninsula)
P83	5	CAL	.28	4.3-6.9 km WNW Edillilie (SA : Eyre Peninsula)
P92	5	CAL	.33	54 km SW Whyalla (SA : Eyre Peninsula)
P107	6	CAL	.22	2 km SE Coonalpyn (SA : South-eastern)
P109	6	DUM	.25	1 km W Loves Mine Rge (SA : Flinders Ranges)
P111	20	DUM	.21	Comet Bore, 55 km s Pinnaroo (SA : South-eastern)
P117	6	CAL	.26	Madura (WA : Eucla)
P120	5	PIL	.18	39.4 km S Norseman (WA : Coolgardie)
P121	4	PIL	.35	Peak Charles (WA : Roe)
P124	5	PIL	.24	18.0 km W Bullabulling (WA : Coolgardie)
P157	5	DUM	.28	6.2 km N Coorow (WA : Avon)
P160	6	STR	.19	2 km N Mt Magnet (WA : Austin)
P163	4	CLE	.27	14.5 km NE of Mt Gibson HS turn-off (WA : Austin)
P176	4	SHE	.32	14.7 km E Lake Grace (WA : Roe)
P179	5	CLE	.21	1.3 km W Bullabulling (WA : Coolgardie)
P180	5	CLE	.27	15.1 km S Menzies (WA : Austin)
RED	1	PIL	.28	13 km NW Norseman (WA : Coolgardie)
ZAN	2	LES	.32	Zanthus - Cundeelee district (WA : Coolgardie)

KEY:
n : sample size of POP group
NT : nearest TYP group
(nearest neighbours are shown in fig. 48)
d : distance of NT from POP

Figure 48: Nearest-neighbour tree based on the multistate distance metric (DI) for the 33 POP groups and 16 TYP groups.




P121
KON
PTE
P27
P12
P22
P20
P92
P53
P35
P52
P30
RED
P120
PIL
P111
P109
P124
FRA
DUM
P83
SHE
P107
P157
P117
P176
P47
ANC
CAL
CON
DON
GEO
P57
CYA
P28
PSLK
PMAR
P73
PCVH
STR
P74
P160
ZAN
LES
WOO
P163
P179
P180
CLE

SCALE :

DI 0.4

9.2. DPOPDAT Analysis

9.2.1 Modification of POP groups

To reduce the groups to a manageable number, POP groups were excluded if their nearest TYP group was closer than the arbitrarily chosen value of .26 units. In cases where POP groups formed chains or clusters linked at less than .26, these were represented by a single population chosen on account of its central position in a cluster or presence of bud data. In two cases constituent groups of nearest-neighbour pairs were geographically close and were pooled to form a single group. The groups P73 and P74 (which virtually correspond to the LGF groups LCAR and LDAR) linked at .23 units and were combined as PCAR. Although possible (6.2, p. 126, 127), it was clearly impractical to distinguish these as separate taxa. The localities are mostly adjacent with some overlap. The morphological differences are best regarded as ecotypic, corresponding to skeletal soils on the inselbergs and alluvial or sandy soils on the plains. Groups P20 and P27 (from near Bute and Lochiel respectively) linked at .16 units and were combined as a single group representing the Northern Lofty Region, PNLR. A further modification was to remove the group RED from subsequent analyses. Although RED is fairly distinct, being .28 units from PIL its nearest TYP neighbour, there was insufficient consistent material suitable for measurement to justify recognizing it as a new taxa on the basis of numerical analysis. (See discussion of "E. redimiculipholia" in section 11.4.2 .) This left eight POP groups which were then subjected to a CVA as defined groups together with the TYP groups. For each POP group, the distance in discriminant space to the nearest TYP group was derived. Three groups, PNLR, P83, and P163, had D-distance links to a TYP group less than that of the nearest TYP neighbours PIL-CAL. Since recognition of new taxa that are more difficult

to distinguish than this pair is undesirable, these three were excluded, leaving five POP groups for inclusion in the DPOPDAT analyses.

9.2.2 Definition of DPOP groups

The groups used for the DPOP analyses include the 16 TYP groups defined in section 7.2 as well as the following five groups. The number of individuals sampled is indicated in brackets. Localities for individual collections can be obtained by consulting the appropriate Region in South Australia or District in Western Australia under E. dumosa ssp. dumosa in appendix 1. Representative specimens are illustrated among figures 56 to 57. Group names are also marked on figures of fruits and buds in chapters 10 and 11.

PCAR (12) fig. 71

Carappee Hill, Darke Peak Range and the intervening plain between Darke Peak and Carappee Hill (Eyre Peninsula Region).

These forms were represented in the LGFDAT analysis by LCAR and LDAR. There are strong affinities with CYA and the principal difference is the presence of glaucous stems. Well developed operculum ribbing is also characteristic.

PCVH (9) fig. 70

124-136 km N of Cook on the road to Vokes Hill, and in an area northwest of this (North-western region).

This group is associated with a system of tall sand dunes and a dune-field to the north. It is characterized by extremely large fruits and variable stem glaucousness. Similar forms occur at scattered localities elsewhere in the Great Victoria Destert.

PMAR (7) fig. 69

Vicinity of Maralinga (Nullarbor Region).

Associated with smaller dunes from the same system as above. It has relatively large, elongate fruits but they are smaller than in PCVH and stem glaucousness is less frequent. It differs from STR mainly in the lack of a blackbutt and presence of stem glaucousness. Similar forms are known to extend eastwards across the Nullarbor near the transcontinental railway line.

P35 (4) fig. 76

1 km NE Devil's Peak, near Quorn (Flinders Ranges Region).

This group has strongly ribbed operculae of similar shape to PIL but differs principally in having leaves which may be glaucous and shortly pedicellate fruits. Similar forms occur further south in the southern Flinders Ranges at Mt Remarkable National Park, Telowie Gorge Conservation Park and Beetaloo.

P157 (5) fig. 67

6.2 km N Coorow (Avon District).

This group differs from DON most notably in the absence of stem glaucousness, smaller fruits and narrower pedicels. It is more typical of most material referred to E. dongarraensis than is DON which appears to represent a coastal form.

9.2.3 Results

The aim for the DPOPDAT analyses was to examine relationships between the five selected POP groups, the TYP groups and the unassigned specimens to form a basis for taxonomic conclusions. Four CVA's were performed on the 21 groups with various combinations of the character set. Using all characters, CVA achieved discrimination of all groups without overlap. As for the TYPDAT analysis, the minimum D-distance is between PIL and CAL, which demonstrates the comparable distinctiveness of the five remaining POP groups.

The 1st and 2nd-neighbour network (fig. 49) shows that addition of the five POP groups results in considerable modification of the three-lobed structure of the TYPDAT plot. There is still a distinctive lobe (STR, KON, CLE, LES, PTE) characterized by groups with blackbutts and the lobe containing groups with non-glaucous leaves and stems (PIL, CAL, ANC, FRA, CON) is hardly changed. The third lobe, previously characterized by stem glaucousness alone, includes the five POP groups and is now merged with the central complex to form a complex cluster of groups characterized by stem glaucousness and/or leaf glaucousness. A nearest neighbour dendrogram plotted from the D-distance values (fig. 50) shows a large cluster of 12 groups (ANC to SHE) linked together at a distance less than 8.3 units.

Graph Theory plots were made using the ordination of groups produced by the 1st and 2nd-neighbour plot. Without 1st and 2nd-neighbour linkages the ordination has little meaning but is used merely to provide a spatial separation of groups. By maintaining the same underlying ordination, comparisons between different analysis are facilitated. The major cluster recognized from the nearest neighbour dendrogram is defined by the lowest 16 values and is the only Graph Theory cluster defined for Dc=8.3. This network (fig. 52) includes six links not included in the nearest neighbour

Figure 49: 1st and 2nd-neighbour plot based on D-distances for CVA of 21 DPOP and TYP groups.

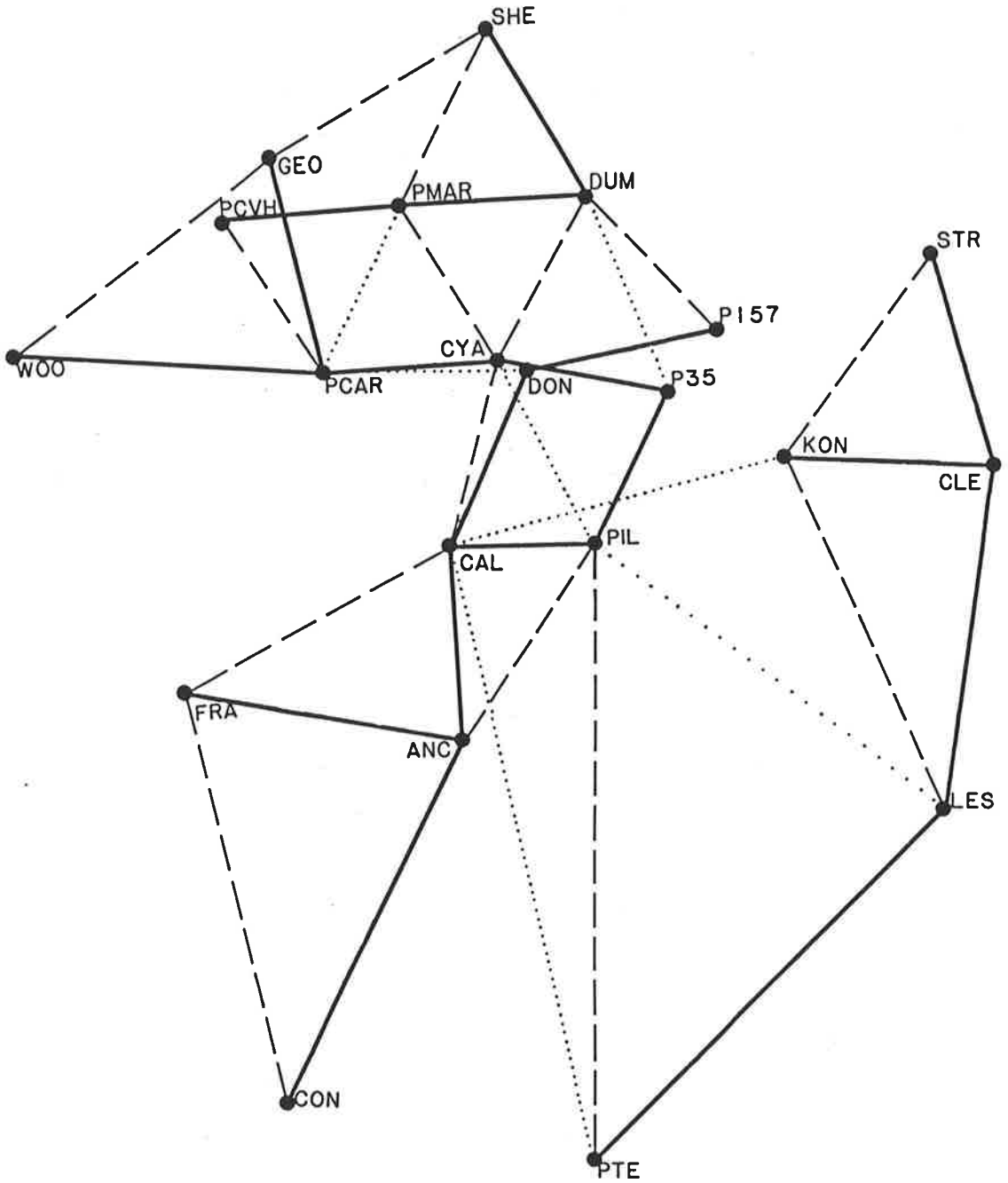


nearest neighbour link

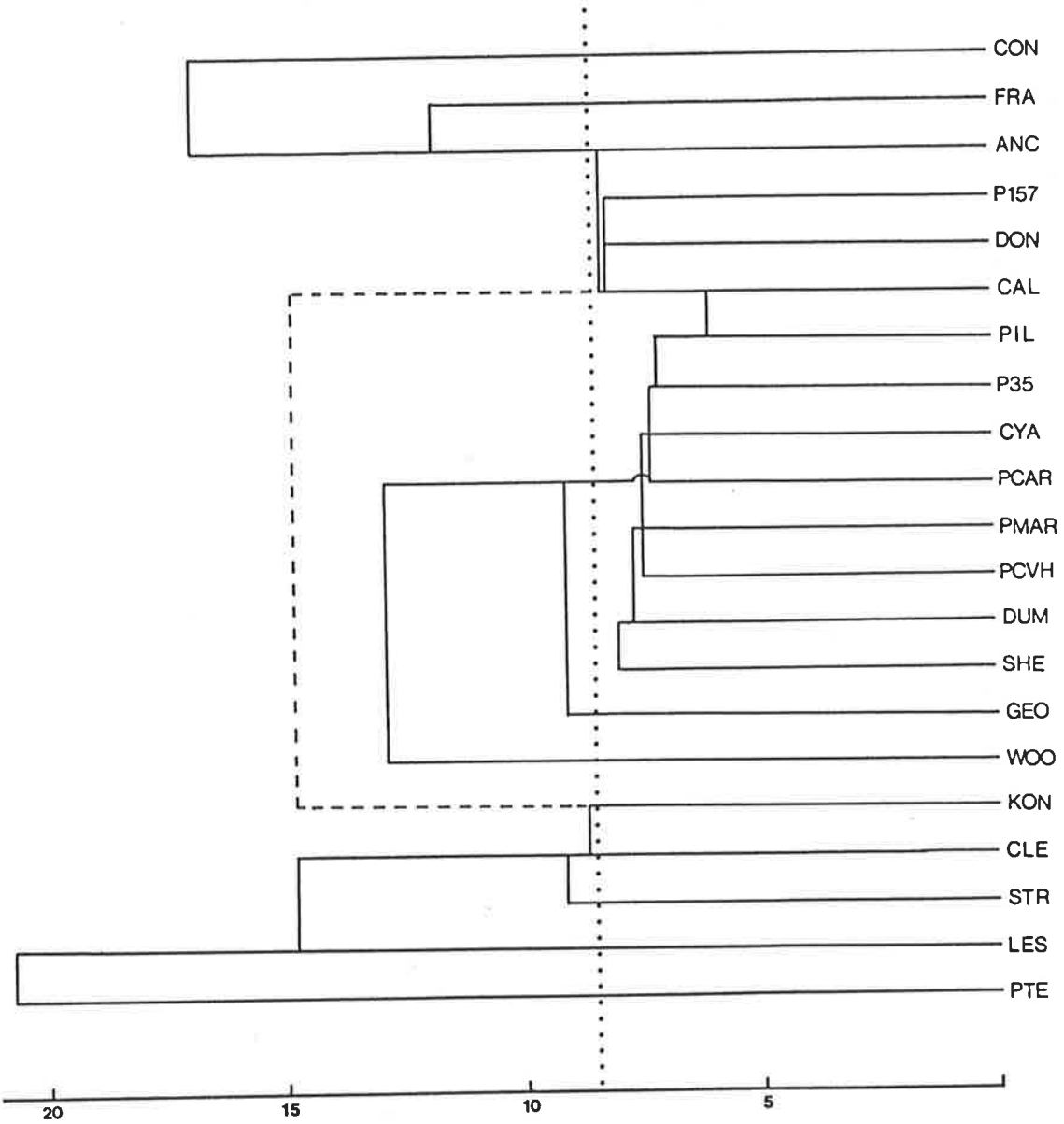
2nd-nearest neighbour link

3rd- " " "

4th- " " "



SCALE:
D–distance 10 20



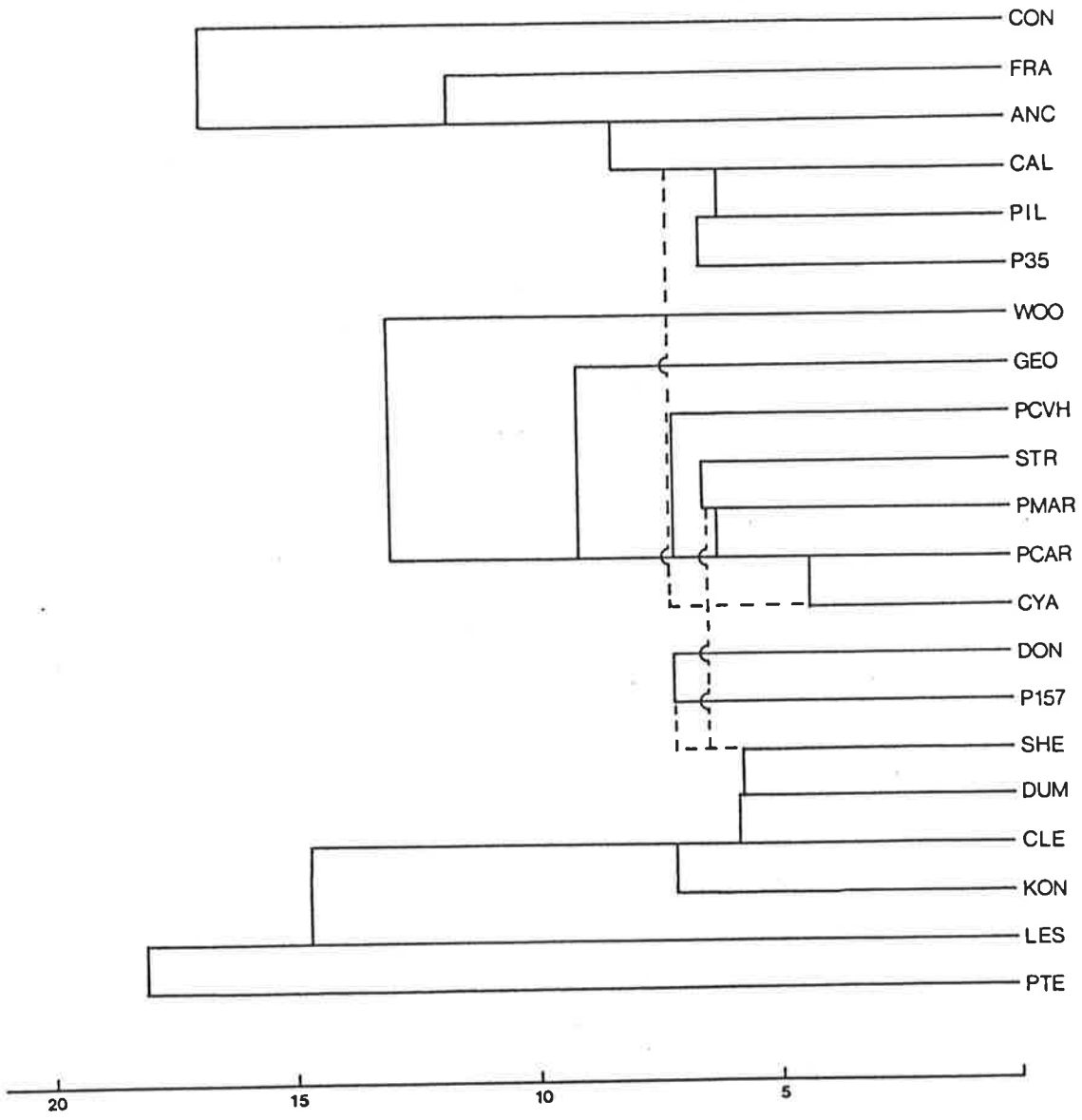
50

Figure 50: Nearest neighbour dendrogram based on D-distances for CVA of 21 DPOP and TYP groups.
(Complete character set)

———— nearest neighbour link

- - - - - - - - 2nd-nearest neighbour link

. . . . . 8.5 unit phenon line



51

Figure 51: Nearest neighbour dendrogram based on D-distances for CVA of 21 DPOP and TYP groups with 2- and 3-state characters (LG, SG, BB) deleted from character set.

——— nearest neighbour link

- - - - - - 2nd-nearest neighbour link

dendrogram. As all of these are 2nd and 3rd neighbour links represented in the 1st and 2nd neighbour plot, they portray actual distances. The cluster is moderately stable and has a moat of 0.9. With increasing distance values, a further 10 internal links are made before GEO links in. This relatively low degree of cross-linking (normalized connectedness = 0.27) conceals considerable anisotropy in the structure of the cluster. Although there is little variation in distances of links defining the cluster this does not mean that the groups are approximately equidistant in hyperspace. This is demonstrated by the fact that the distance for SHE-ANC (15.5) greatly exceeds that for ANC-CAL (8.3) which is the maximum link defining the cluster.

The CVA was repeated without the low-state characters (LG, SG and BB). The D-distance relationships are portrayed by a nearest neighbour dendrogram (fig. 51). Notable differences from the previous dendrogram are the close linking of CLE to the central complex via DUM and the new minimum distance between PCAR and CYA. Significant gradation was detected between the members of the last two groups (table 9.2).

The results of classification of unassigned individuals by CVA to the 21 groups are presented in appendix 1. Figures 78 to 93 mainly illustrate some forms that show substantial departures from typical material of the defined groups. They are incorporated here to facilitate comparisons with the preceeding figures representing the TYP and DPOP groups. Intergradation between groups is displayed on the 1st and 2nd neighbour ordination for comparison with distance relationships (fig. 53). Most intergrades occurred between groups of the central cluster but there is otherwise little correspondence between distance and intergradation. Removal of LG, SG and BB increased the level and extent of intergradation and many of the outlying groups distinct distance-wise are linked into the central complex (fig. 54). For groups with distinctive operculum

Table 9.2: Summary of CVA classification results for TYP and DPOP groups

(a) TYPDAT CVA

Characters deleted	Misclassification	Intergradation
None	None	P(G/X) > .9999
LG, SG, BB	None	P(G/X) > .9990
OLW, OWM, OPR	CAL : PIL(CAL)	P(G/X) > .9999
LG, SG, BB, OLW, OWM, OPR	CAL : PIL(CAL)	SHE(DUM)

(b) DPOPDAT CVA

Characters deleted	Misclassification	Intergradation
None	None	CAL(pil)
LG, SG, BB	None	CYA(PCAR) PCAR(cya) PCAR(CYA) PCAR(pcvh)
OLW, OWM, OPR	CAL : PIL(CAL)	DUM(P157) PMAR(SHE)
LG, SG, BB, OLW, OWM, OPR	CAL : PIL(CAL) DUM : P157(DUM) PCAR : CYA(PCAR)	SHE(dum) CYA(pcar) CYA(PCAR) CYA(PCAR) CYA(PCAR) DUM(she) DUM(cle) P35(dum) P157(dum) PCAR(cya) PCAR(cya) PCAR(CYA) PCAR(pcvh)

Figure 52: Graph Theory Network of DPOP and TYP groups based on ordination of figure 49.

———— D-distance linkages ≤ 8.3 units

. . . . . D-distance linkages > 8.3 and ≤ 9.1 units

All the links for Dc = 8.3 correspond to those on the 1st and 2nd-neighbour plot (fig. 49) and therefore their lengths represent actual distances.

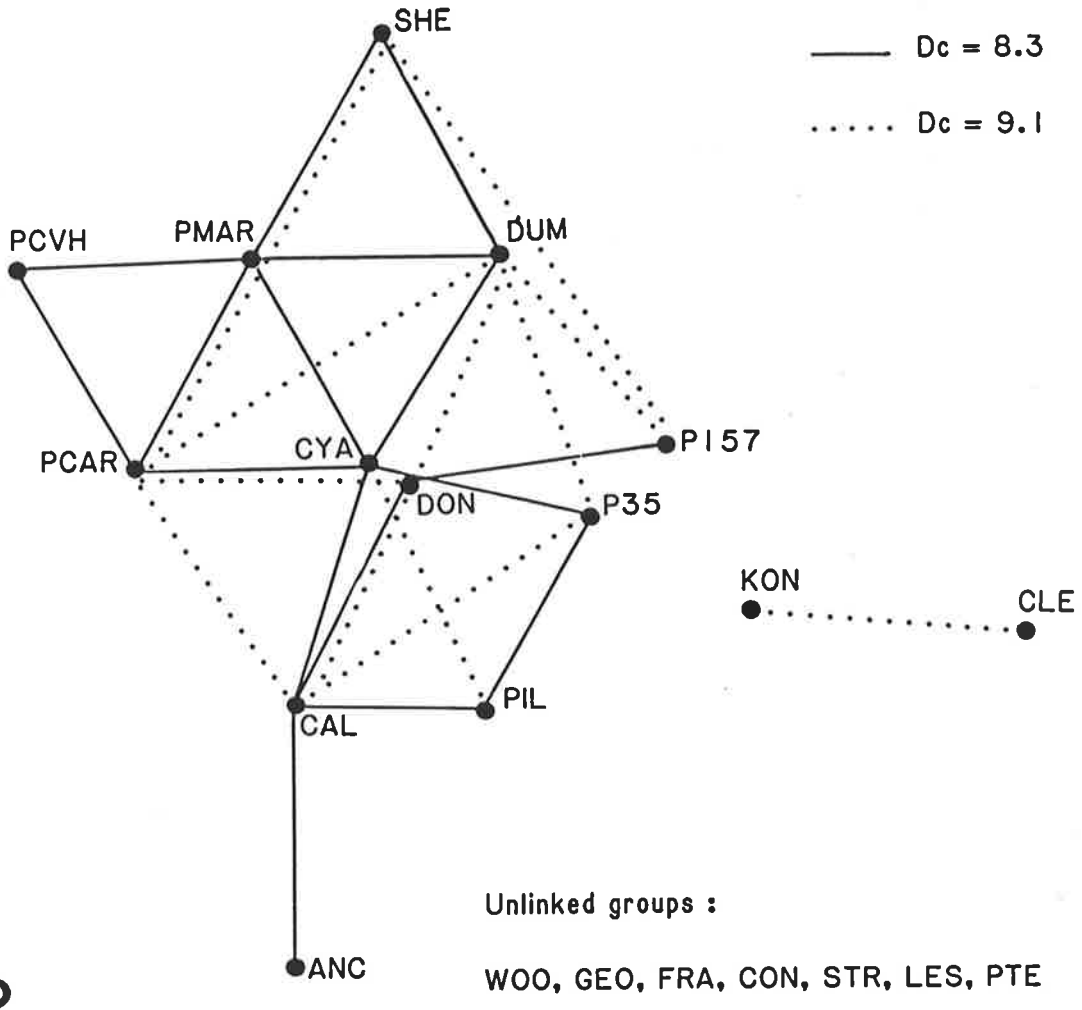
Figure 53: Representation of major gradations detected by CVA amongst DPOP and TYP groups using complete character set.

Underlying ordination is that of figure 49.

———— 7 or more pairs of individuals with level 2 gradation

— — — — 1 to 4 " " " " "

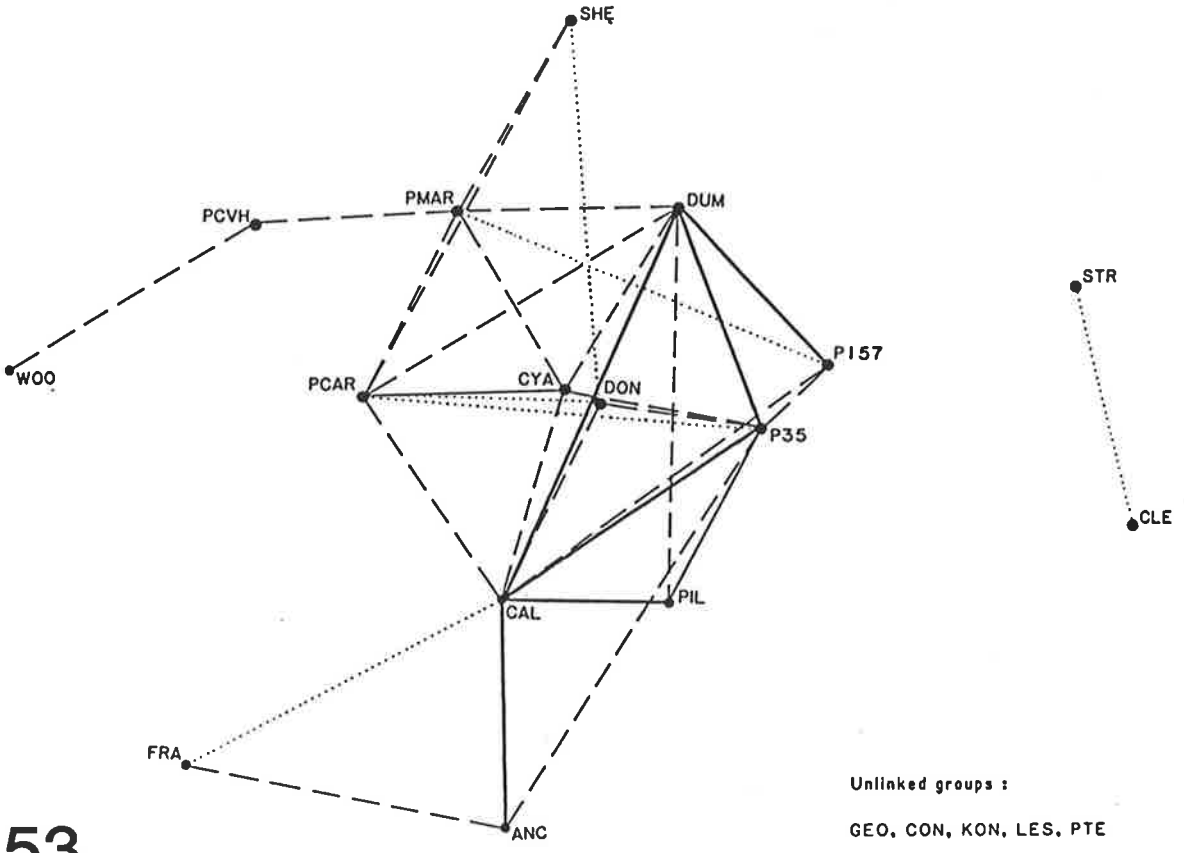
..... 1 or more " " " level 1 "



Unlinked groups :

WOO, GEO, FRA, CON, STR, LES, PTE

52



Unlinked groups :

GEO, CON, KON, LES, PTE

53

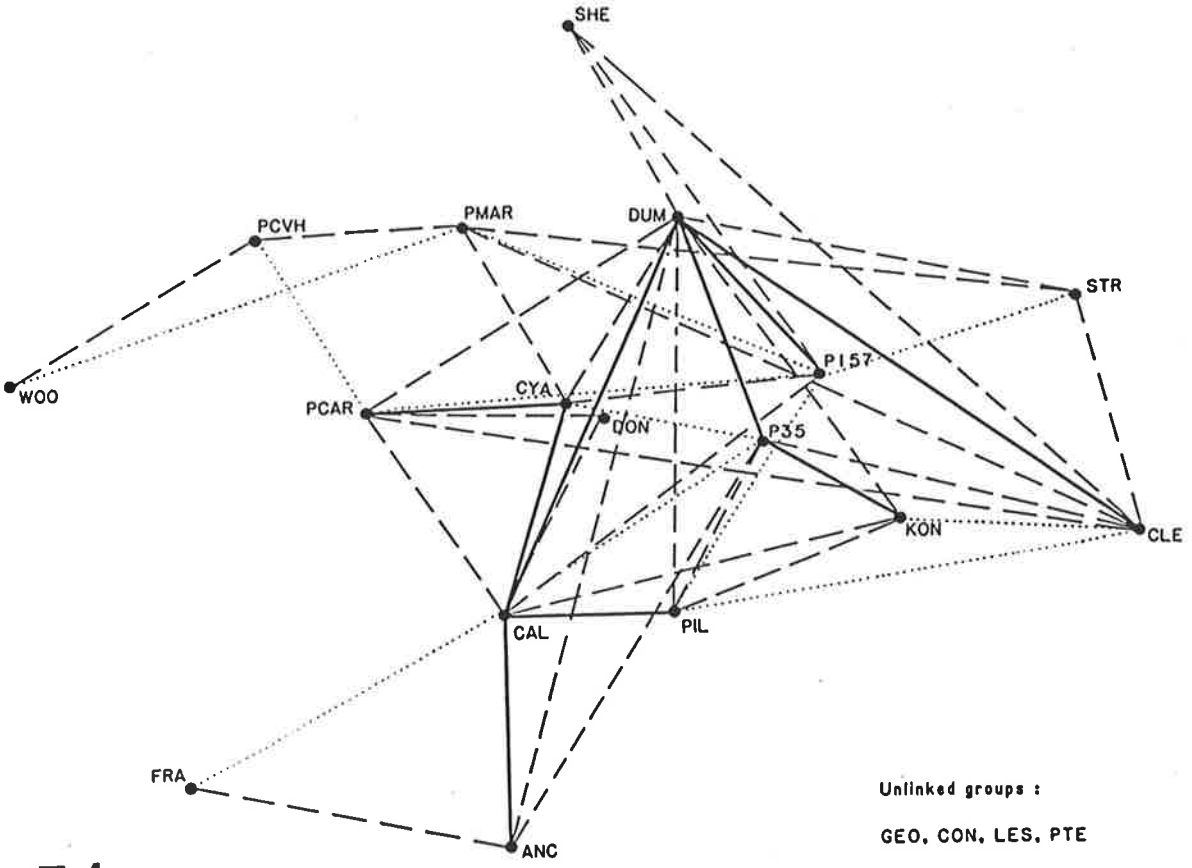
Figure 54: Representation of major gradations detected by CVA amongst DPOP and TYP groups using character set with 2- and 3-state characters (LG, SG, BB) deleted. Underlying ordination is that of figure 49.

Figure 55: Representation of major gradations detected by CVA amongst DPOP and TYP groups using complete character set. Only shows gradation for cases when the three operculum characters were scored for both individuals. Underlying ordination is that of figure 49.

———— 7 or more pairs of individuals with level 2 gradation

– — — – 1 to 4 " " " " "

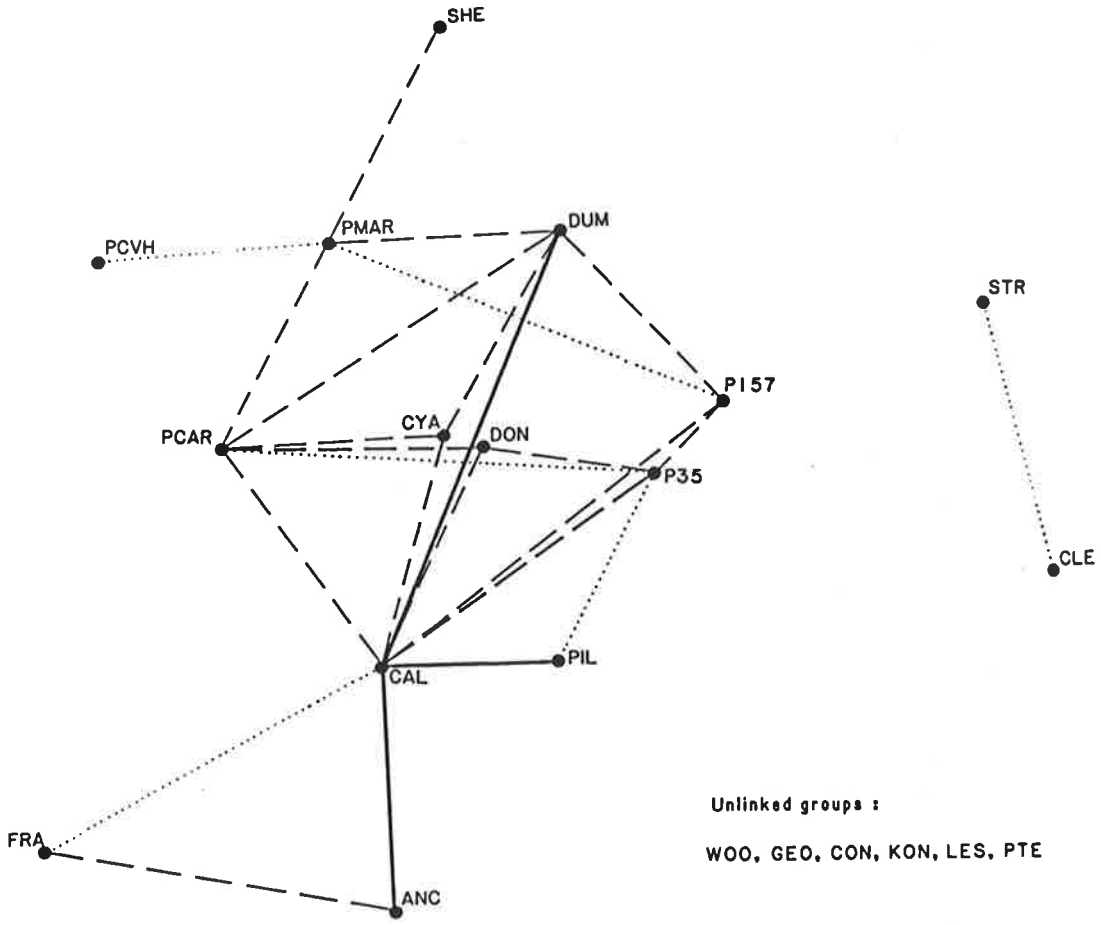
..... 1 or more " " " level 1 "



Unlinked groups :

GEO, CON, LES, PTE

54



Unlinked groups :

WOO, GEO, CON, KON, LES, PTE

55

characters, evidence of intergradation is more meaningful for the individuals without missing data. Large numbers of individuals were classified to the groups DUM, P35 and PIL both with and without operculum data, but intergradation between these groups was greatly reduced when cases with missing data were excluded (fig. 55). This occurred both with and without the low state characters. The results of these analyses and their taxonomic significance for each group are discussed in more detail in the next two chapters.

Figures 56 to 77: Representative specimens of TYP and DPOP groups.

Scale bar: 1 cm
(applies to all figures)

Figure 56: PTE
G.M. Chippendale 154

E. pterocarpa

Figure 57: LES
PJL 1526

E. lesouefii



56

PTE



57

LES

Figure 58: WOO
PJL 1563

E. woodwardii

Figure 59: KON
PJL 1440

E. kondininensis



58 WOO



59 KON

Figure 60: CLE
PJL 1530

E. dumosa ssp. clelandii

Figure 61: GEO
M.I.H. Brooker 4989

E. dumosa ssp. georgei



60

61

Figure 62: CON
PJL 1126

E. dumosa ssp. conglobata

Figure 63: ANC
PJL 673

E. dumosa ssp. conglobata


62
CON
63
ANC

Figure 64: FRA
W.R. Barker 2599E

E. dumosa ssp. fraseri

Figure 65: STR
PJL 1481

E. dumosa ssp. dumosa (aff. ssp. clelandii)



64 FRA



65 STR

Figure 66: DON
PJL 1467

E. dumosa ssp. dumosa

Figure 67: P157
PJL 1459

E. dumosa ssp. dumosa


66
DON
67
P157

Figure 68: SHE
PJL 1447

E. dumosa ssp. *dumosa*

Figure 69: PMAR
O.H. Turner, 1.xi.1959

E. dumosa ssp. *dumosa*


68
SHE
69
PMAR

Figure 70: PCVH
T.E. Dennis 213

E. dumosa ssp. dumosa

Figure 71: PCAR
PJL 1044

E. dumosa ssp. dumosa



70

71

Figure 72: CYA
PJL 890

E. dumosa ssp. dumosa

Figure 73: DUM
P.L. Milthorpe & G.M. Cunningham 6

E. dumosa ssp. dumosa


72
CYA
73
DUM

Figure 74: PIL
PJL 1380

E. dumosa ssp. dumosa

Figure 75: CAL
G.C. Cornwall, 16.vi.1976

E. dumosa ssp. dumosa



74

PIL



75

CAL

Figure 76: P35
R. Sinclair, 1.xi.1977 C

E. dumosa ssp. dumosa

Figure 77: PIL
PJL 1381

E. dumosa ssp. dumosa


76
P35
77
PIL

Figures 78 to 93: Photographs for a selection of herbarium material mainly to provide examples of deviations from typical forms represented by TYP and DPOP groups.

Scale bar: 1 cm
(applies to all figures)

Figure 78: PJL 1359/1.2 km S Grass Patch (Roe)

E. dumosa ssp. conglobata

Figure 79: PJL 1400/8 km N Stirling Ranges NP (Roe)

E. dumosa ssp. conglobata


78
79

Figure 80: R.D. Royce 5338/1.6 km N Cundeelee Mission (Coolgardie)

E. lesouefii

Figure 81: PJL 967/Kododo Hill, Gawler Ranges (Eyre Peninsula)

E. dumosa ssp. dumosa


80
81

Figure 82: PJL 1546/22.1 km N Norseman (Coolgardie)

E. dumosa ssp. dumosa, aff. ssp. clelandii

Figure 83: PJL 1547/22.1 km N Norseman (Coolgardie)

E. dumosa ssp. dumosa aff. ssp. clelandii



82



83

Figure 84: PJL 1431/25 km E Hyden (Roe)

E. dumosa ssp. dumosa aff. ssp. georgei

Figure 85: PJL 1418/14.7 km E Lake Grace (Roe)

E. dumosa ssp. dumosa



84



85

Figure 86: T.E. Dennis 218/W of Wyola Lake (North-western)

E. dumosa ssp. *dumosa*

Figure 87: Isolectotype of *E. sheathiana*


86
87

Figure 88: T.E. Dennis 215/W of Wyola Lake (North-western)

E. dumosa ssp. dumosa

Figure 89: T.E. Dennis 223/W of Wyola Lake (North-western)

E. dumosa ssp. dumosa



88

89

Figure 90: T.E. Dennis 189/131 km N Cook (North-western)

E. dumosa ssp. dumosa

Figure 91: M.I.H. Brooker 1996/Lake Austin (Austin)

E. dumosa ssp. dumosa


90
91

Figure 92: PJL 1330/Madura (Eucla)

E. dumosa ssp. dumosa

Figure 93: PJL 1192/9 km SW Coorabie (Nullarbor)

E. dumosa ssp. dumosa



92

93

CHAPTER 10

DERIVATION OF TAXONOMIC CONCLUSIONS

10.1 Introduction

In deriving a taxonomic system to accommodate the groups considered in the preceding analyses three aspects were taken into account:

1. multivariate distance relationships between groups;
2. degree of intergradation between groups;
3. ease with which groups could be distinguished by key characters.

The problems associated with the first two aspects have been objectively documented. However, it was necessary to use a subjective approach to make an assessment of the third and to reach a taxonomic conclusion based on all three. There are many disparities between intergroup relationships expressed by the various aspects. This means that an ideal objectively derived classification is not possible because there is no objective criterion for weighing up opposing factors. Thus in this study the quantitative results do not lead directly to a classification. Rather they are used to document and describe complex variation before deriving a workable taxonomic system. It is therefore to be expected that the analyses will provide evidence both for and against the proposed taxa.

My initial approach was to propose complex hierachies of subspecies and varieties corresponding to most of the DPOP groups. However, these suffered from many inconsistencies and the taxa were difficult to key out. To separate most of the DPOP groups by key required the use of strings of characters with overlapping ranges in opposing lines of couplets. The difficulty in identifying such taxa is even greater when intergrades and other individuals outside the typical groups are considered. This problem was minimized by sacrificing some information displayed by the taxonomic system in the recognition of a relatively small number of taxa.

In the final classification now proposed, the 21 DPOP groups are placed into five species and five subspecies as listed in table 10.1 . These nine taxa correspond to nine clusters of DPOP groups which can be defined by an arbitrary phenon line at 8.5 units on the nearest-neighbour dendrogram of D-distances (figure 50). One group, STR, is intersected by the phenon line but was not recognized as a separate taxon for reasons discussed later. The allocation of species and subspecies ranks to the nine taxa was based largely on evidence of intergradation and the ease with which the taxa could be defined. On the dendrogram, which displays distance relationships alone, it is not possible to draw a straight phenon line that intersects species but not subspecies.

A full description of variation in each taxon is presented in chapter 12. The following sections discuss evidence from numerical analyses concerning relationships between groups and the taxonomic conclusions reached. Classification results from CVA, and relationships in D-space, refer to DPOPDAT analyses on the the complete character set unless otherwise specified. Taxa are considered in sequence from the most to least distinctive.

10.2 Eucalyptus pterocarpa

The group PTE was determined as the most distinctive by the multistate analysis and all the CVA's. Its distinctiveness is greater for the CVA's than for the multistate analysis. This is because its extreme degree of fruit and operculum ribbing, which suffice to distinguish it from all other groups, receive a high weighting in the CVA's. In all CVA's the nearest neighbour of PTE is LES, the group with the next highest degree of ribbing. In the multistate analysis however, its nearest neighbour is CAL with which it shares the the absence of leaf glaucousness, stem

Table 10.1: Relationship between DPOP groups and taxa recognized in the new classification. The DPOP groups are ranked according to a subjective assessment of their distinctness based on nearest neighbour D-distances and evidence of intergradation.

DPOP group	Taxon
PTE	*Eucalyptus pterocarpa* sp. nov.
LES	*E. lesouefii*
WOO	*E. woodwardii*
KON	*E. kondininensis*
CLE	*E. dumosa ssp. clelandii*
GEO	*E. dumosa* ssp. *georgei*
CON	*E. dumosa* ssp. *conglobata*
ANC	" "
FRA	*E. dumosa* ssp. *fraseri*
STR	*E. dumosa* ssp. *dumosa* aff. ssp. *clelandii*
DON	*E. dumosa* ssp. *dumosa*
P157	" "
SHE	" "
PMAR	" "
PCVH	" "
PCAR	" "
CYA	" "
DUM	" "
P35	" "
PIL	" "
CAL	" "

glaucousness and blackbutt. The relationship with LES is more consistent with the treatment of Gardner (Aplin, 1979, p. 186) who referred to material corresponding to PTE as a 'form' of E. lesouefii. Phylogenetic considerations support a closer relationship with LES than with CAL. The weighting of ribbing characters is justifiable since within the Dumosae the high degree of ribbing is unique to PTE and LES. In contrast, the character states shared by PTE and CAL occur in other groups within the Dumosae and have a widespread geographical distribution. Furthermore, PTE occurs within the area of distribution of E. lesouefii but is disjunct from material referable to E. calcareana.

Despite the relationship between PTE and LES, the numerical analyses show that these are relatively distant groups. This is supported by the fact that PTE and LES have non-overlapping ranges for 10 characters, namely: LTH, SG, FWMR, FWL, PCL, PCW, PWS, PW, FR and OPR (defined in table 4.1).

As well as being distant, PTE is distinct in lacking intergradation. No gradation at level 1 or level 2 * was detected between PTE and any other group. Although there is evidence of limited gradation towards PTE in specimens classified to LES, this gradation was not sufficient to be detected by the CVA's (10.3). The group PTE is clearly worthy of the highest rank applied within the Dumosae at species level or below. In this classification it will therefore be treated as a distinct species.

10.3 E. lesouefii

LES is the next most distant group in D-space regardless of the inclusion of the two and three-state characters relating to glaucousness and blackbutt (LG, SG, BB). Although less pronounced, it shares with PTE

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* level 1: $.9000 \leq P(G/X) \leq .9900$, level 2: $.5000 < P(G/X) < .9000$

prominent fruit and operculum ribbing (figs 95, 150) which contribute greatly to its separation from other groups by CVA. However, LES can be easily distinguished from PTE by the 10 characters listed above, and its nearest neighbour is CLE rather than PTE. As with PTE, no significant gradation with other groups at levels 1 or 2 was detected by the CVA's. However, two cases of limited gradation involving LES were detected. The first involves two specimens of E. lesouefii from the Zanthus - Cundeelee area (R.D.Royce 5362 & 5338) (fig. 80). These are disjunct from the the main area of distribution of E. lesouefii and approach PTE morphologically in several characters. Out of the 10 characters for which LES and PTE have overlapping ranges, these two individuals have scores overlapping those of PTE in two characters (PCW and OPR) and scores intermediate between LES and PTE for two others (PWS and FR). In most characters they are consistent with LES and were classified by the CVA's to LES without significant gradation. Even though the probability for classification to LES exceeds .9999 (i.e. P(G/X) = 0.0000 for PTE), a tendency towards PTE was detected since the Zanthus specimens differ from most material classified to LES by having PTE rather than CLE as the second closest group.

The second case of limited gradation occurs in some specimens classified by the analyses to CLE. These have a greater degree of ribbing than usual for material referred to E. clelandii (fig. 99) and may be interpreted as showing limited gradation towards E. lesouefii. The absence of more intermediate gradation (level 1 or 2) in this and other material indicates a reasonable discontinuity between LES and other groups, and supports the retention of E. lesouefii as a separate species. Using the character of fruit ribbing there is no difficulty in keying out these first two species based on PTE and LES.

10.4 E. woodwardii

In terms of multistate and D-distances WOO is also a very distinctive group. In fact its distance from other groups is likely to be underestimated by the analyses because some unique features were omitted from the character set. Eucalyptus woodwardii differs from the usual condition in the Dumosae for white or cream coloured filaments by consistently having bright yellow flowers. A less reliable character is the occurrence in many individuals of pendulous branchlets. This character can be inferred from herbarium specimens by the presence of reflexed peduncles (fig. 58). Chippendale (1973) presumably refers to the pendulous condition when he describes an "untidy habit" which he attributes to the weight of fruits or flowers. However, it is more reasonable to regard this as a result of stem plasticity because E. woodwardii does not always have an obvious pendulous condition and the character does not often occur in other Dumosae such as PCVH which can have fruits of a similar size. The habit of E. woodwardii is also often distinctive, being a small, usually erect and single-stemmed tree in contrast to the mallee or more spreading tree form of other Dumosae.

In multistate A-space, WOO is closest to GEO, while in D-space its nearest neighbour is PCAR with GEO as the second nearest neighbour. There is no good evidence of intergradation between these or any other populations and WOO. A specimen from the Mt Holland area (A. Kessell 408) approaches WOO in its large fruit size and operculum shape but its affinities are unclear as it has operculum ribbing and other features not found in either WOO or GEO (fig. 119). Gradation towards WOO in this specimen was not detected for any of the CVA's.

There was no material sampled for analysis apart from the TYP group WOO, that I consider could be referred to as E. woodwardii. One specimen from the northwest of South Australia (N.N.Donner 3982) was assigned to WOO by CVA with level 2 gradation to PCVH and this is the sole basis for the line linking WOO and PCVH in figure 53. However, I consider that this specimen is consistent with the other material from the northwest and has no close affinity with E. woodwardii. The most distinctive characters used in the analysis to separate PCVH and WOO are operculum characters which are lacking in this specimen. The fruits of this specimen and other large-fruited individuals of PCVH can be distinguished from those of WOO by a slight difference in shape not expressed by the two width measurements in the character set. The fruits of WOO have a somewhat campanulate shape with a slight inflexion in the outline not present in PCVH (figs. 96, 176 to 178). In the absence of flowers and buds, this is the only character consistent enough to separate the groups by key. In contrast to WOO, the material from the northwest has been well sampled with 38 specimens measured for analysis and many more examined. There is no tendency for the large-fruited forms in this region to have smooth and rostrate operculae, yellow flowers, or habit characters of WOO. Thus good evidence of intergradation is lacking. It is possible that intergrades may occur in the inaccessible and poorly collected country towards the region of known occurrences of E. woodwardii.

In conclusion, E. woodwardii is distinct distance-wise and is disjunct from other Dumosae both geographically and morphologically, although this may be an artifact of inadequate sampling. On the available evidence it is maintained as a species.

10.5 E. kondininensis

In terms of D-distance, KON is much less distinct than the preceding three groups. This is evident from the deviation required in a hypothetical phenon line on figure 50 for its recognition at species rank. However, KON is a very distinct group in terms of intergradation. Its nearest neighbour in D-space is CLE but no gradation at levels 1 or 2 occurred between CLE or any other group using the full character set. In the nearest neighbour dendogram (fig. 50) KON is grouped with a cluster (KON, CLE, STR, LES, PTE) that is characterized largely by the presence of a blackbutt. This cluster is linked via KON at a rather high distance value to the remaining groups. With removal of glaucousness and blackbutt characters, this distinctiveness breaks down (fig. 51), and KON intergrades with CAL, P35 and DUM (fig. 54). This is maintained even when cases with missing data are excluded. The groups P35 and DUM share non-glaucous stems with KON, while CAL shares both non-glaucous stems and leaves. Thus the separation between KON and P35 or DUM can be attributed to the characters of leaf glaucousness and blackbutt, while the separation between KON and CAL must be solely a result of blackbutt. Despite the importance of these few characters in distinguishing KON, in other characters it is a morphologically consistent group. This is shown by the CVA classification results. Of the eight individuals assigned to KON, only one was misclassified when the glaucousness and blackbutt characters were removed.

There is some evidence for affinity between KON and ANC. Sessile-fruited forms similar to ANC approach the southern part of the distribution of E. kondininensis in the Pingrup-Lake Grace area. These individuals have narrow leaves which are uncharacteristic of ANC, small fruits and sometimes a tree habit. Three such individuals were included in the analysis, and with removal of 2 and 3-state characters one was classified

to KON. In addition to the absence of a blackbutt, they differ from KON in other characters such as VN, PCL and FWMR. Although affinities are evident, significant intergradation between KON and other groups does not occur, and E. kondininensis is maintained as a species.

10.6 E. dumosa ssp. clelandii

While the previous taxa clearly deserve specific status, I regard this taxon as being better placed at sub-species rank. Although the weight of evidence favours relegation to subspecies, there are nevertheless substantial arguments for a species ranking. The mutual nearest neighbour of CLE is KON, so that in terms of D-distance it is equally distinct as KON. No significant gradation was detected by CVA between CLE and KON, but one individual classified to CLE showed gradation towards STR at level 1. This individual is from a population at Mt Magnet (P160) represented by six individuals (fig. 123). The fact that four of these were classified as CLE and two as STR, adds to the evidence of intergradation between these groups. With removal of glaucousness and blackbutt characters, only one remains classified to CLE, one is classified to PMAR and four to STR. Thus without the two and three-state characters, the Mt Magnet population is morphologically closest to STR (fig. 122). However, the presence of stem glaucousness and blackbutt is probably derived from individuals morphologically close to CLE. A similar pattern occurs in a population (P163) from near Mt Gibson where four individuals (fig. 124), originally classified to CLE with the entire character set, were reclassified to DUM and SHE without glaucousness and blackbutt characters. The group CLE has variable leaf glaucousness (LG=0,1,2) but is consistent for possession of a blackbutt and stem glaucousness. The latter two characters are weighted highly in the functions used by CVA to separate CLE.

However, the specimens classified to CLE by the CVA are quite consistent morphologically on their other characters. There are 21 individuals that were originally classified to CLE by the CVA. Deletion of the two and three-state characters only resulted in the reclassification of five individuals. These are from the Mt Magnet and Mt Gibson populations, which are northern outliers from the main occurrence of more typical CLE forms. There is a substantial area, mainly to the south of the TYP group CLE, where material is consistent in form and lacks intergradation with other groups.

In the POPDAT distance analysis where low state characters were not weighted, the five populations with individuals assigned to CLE by CVA are associated in the nearest neighbour network (fig. 48). The three populations that have CLE as their nearest TYP group form a cluster with CLE. This is better defined than shown on the plot because of additional links not required to specify the network but relevant from the Graph Theory approach. There are two mutual nearest neighbour links (CLE - P179 and P163 - P180), one mutual second-neighbour link (P179 - P163), and one additional nearest neighbour link (CLE - P180). This cluster is situated between E. lesouefii (represented by mutual neighbours LES and ZAN) and part of the complex referred to E. dumosa ssp. dumosa to which it links via mutual neighbours P160 and STR.

As described previously, some individuals within the main area of occurrence appear to have affinities with E. lesouefii, most notably in fruit ribbing. These occur in populations from south of Menzies (P180, P181). The CVA classified all such material to CLE without detectable gradation (P(G/X)=1.0000). Although some gene transfer may have occurred, there is no continuity of variation between the forms represented by CLE and LES.

The contribution of the blackbutt and stem glaucousness characters to the distinctiveness of CLE is demonstrated by the effects of their deletion from the character set. Removal of the two and three-state characters changes the nearest neighbour of CLE in D-space from KON to DUM. This links at a distance of 5.7 units which is less than many of the linkages within the central cluster (fig. 51). A similar situation occurs for intergradation. Based on all characters CLE is distinct having only minor gradation with STR, but without the two and three-state characters there are numerous intergrades between CLE and groups of the central complex (figs 53, 54).

The value of the blackbutt character is questionable because of some populations at the south-eastern limits of the distribution of E. clelandii where its independence from other characters is exhibited. Although individuals classified to CLE are mostly morphologically consistent, their form is not uniquely associated with the presence of a blackbutt. Eleven individuals lacking blackbutts and previously classified to other groups using the full character set, were classified to CLE with removal of two and three-state characters. Six of these are from South Australia and differ from CLE in lacking glaucous stems as well as blackbutts. The other five from Western Australia have glaucous stems and are similar to material named by Gardner as "E. redimiculiphloia". One isolated population 22.1 km N of Norseman W.A., comprises individuals which lack blackbutts but are up to 13 m tall with a tree habit like CLE rather than a mallee habit typical of SHE (figs 104, 108, 109, 111). Using all characters the two individuals sampled (figs 82, 83, 120, 121) were classified to SHE and DUM, but without two and three-state characters they were classified to CLE with level 2 gradation to DUM.

In a second population 13 km W of Bullabulling W.A. (P179), individuals with and without blackbutts (fig. 105) occur together but there are no other obvious morphological differences associated with the state of the blackbutt character (fig. 174). Based on all characters, the two individuals sampled without blackbutts were classified to SHE and the other three with blackbutts assigned to CLE. With removal of the 2 and 3-state characters, all were classified to CLE except one without a blackbutt that was classified as a level 2 intergrade between DUM and CLE. This is similar to the situation in the TYP population of LES where two individuals were observed without blackbutts. It demonstrates the breakdown of the diagnostic blackbutt character in an otherwise morphologically consistent population.

Taxonomic status given to CLE depends on the significance attributed to the blackbutt. If there are grounds for regarding it as a generally unreliable and trivial character, then CLE is best grouped with DUM and the other members of the central complex with recognition only at subspecies rank. Specific status might be justified considering the significance of the blackbutt in a broader taxonomic context. There are strong similarities between CLE and the group LES which clearly represents a distinct species. Both groups occur in the Goldfields district of Western Australia, and are virtually identical in their habit and field appearance (figs 101, 104). Within the central area of distribution they behave as equally distinct entities and the limited gradation they show is with each other rather than any other groups in Dumosae. Presence of a blackbutt is a major characteristic for a cluster of groups detected by the analyses. These groups have the following features in common: a well developed tree habit (not included in the character set); operculae that are both rostrate and ribbed; and a distribution confined to Western Australia. Within the confines of this cluster, CLE appears distinct and

possibly worthy of species status. The cluster may have some phylogenetic basis, but the groups within it are very diverse, and the common features could be a result of introgression rather than divergence from a common ancestry. Considered alone, it appears that the blackbutt character has not been sufficiently conservative in evolution to indicate a close phylogenetic relationship. This is evident from: its absence in PTE despite this group's strong affinity with LES; its inconsistent occurrence in E. dumosa ssp. fraseri (figs 106, 107); its absence in two individuals at the LES locality; and its unreliable nature in the populations described above. More importantly, from a practical viewpoint it is unsatisfactory to have to use presence of a blackbutt as a key character for identification to species. When information on this character is missing, E. clelandii is difficult to separate from other taxa such as E. sheathiana or E. striaticalyx. Confusion between E. striaticalyx and E. clelandii is a problem for many collections in outlying, northern areas not measured for analyses in this study. For these reasons I consider that CLE is best treated as a subspecies of E. dumosa.

10.7 E. dumosa ssp. georgei

The group GEO is rather distinct in D-space with its nearest neighbour being PCAR at a distance of 9.1 units. As GEO and PCAR share the same scores for LG, SG, and BB, the removal of these characters from the character set does not influence this relationship (figs 50, 51). The second nearest neighbour of GEO is SHE, but in the TYPDAT CVA where the group PCAR is not defined, SHE is the nearest neighbour. PCAR occurs on central Eyre Peninsula and there is a large disjunction from GEO or similar forms with glaucous stems in Western Australia. On the other hand SHE occurs in an adjacent area to the west of GEO and is thus a likely candidate for intergradation with GEO. A population 25 km E of Hyden, to

the west of the GEO type locality, has individuals that appear intermediate between SHE and GEO (figs 112, 113, 169). The main difference from SHE is in the coarser fruits, leaves and habit (figs 68, 84, 110, 111). The three individuals sampled were classified to PCAR without significant gradation, but in the CVA using only TYP groups, they were classified to SHE with one individual showing level 2 gradation to GEO.

Taxa based on GEO proved difficult to distinguish from other groups such as SHE, PCAR, PCVH, and PMAR in a key. This contributed to the decision to treat GEO as a subspecies. The distinctness of GEO in D-space partly results from the limited variabilty in the TYP population which may reflect the very restricted distribution of the four TYP specimens sampled. Two additional specimens from the vicinity of Mt Holland were measured for analysis but were excluded from the TYP group. Although these are paratypes of E. georgei they were excluded because they are outliers with obvious morphological differences from material near the type locality. Compared to GEO, one specimen (A.Kessell 408) received significantly higher scores on the following characters: LL, PTL, FWM, FWL, PCW, PW, OLW, and OPR (figs. 112, 119). It was classified by CVA to ANC rather than GEO. If further sampling of GEO forms extends the range of variation to be continuous with forms such as this, then GEO would be virtually impossible to key out and its distinctiveness in D-space would be greatly reduced. As a result it would be necessary to sink it within E. dumosa ssp. dumosa. Alternatively, more extensive occurrences with a consistent morphology would reduce the significance of the limited evidence for gradation, and may justify species status. Like E. woodwardii, this taxon has been collected from only a few localities in a remote area which makes the treatment of GEO as a subspecies somewhat tentative.

10.8 E. dumosa ssp. conglobata

Group CON is the second most distinctive in D-space irrespective of the inclusion of two and three-state characters. However, it also represents one of the most strongly intergrading forms and is therefore treated as a subspecies rather than a species. Group CON (fig. 102) intergrades strongly via ANC (fig. 103) with members of the central complex. This is illustrated by the examples in figures 138 to 141. In the DPOPDAT analyses gradation is established between ANC and members of the central complex but not between ANC and CON (fig. 53). The latter was studied in the SESSDAT analyses (chapter 3) and consequently sampling of unassigned sessile-fruited individuals was reduced for the main analyses. The SESSDAT analyses demonstrated substantial intergradation between ANC and CON in Western Australia. Group ANC is incorporated into ssp. conglobata because it is seen to be part of a cline connecting the central complex with an extreme of variation. The fact that ANC is the nearest neighbour of CON is consistent with this treatment.

Despite the strong intergradation between sessile-fruited forms (ssp. conglobata) and pedicellate forms in the central complex (ssp. dumosa), recognition of a taxon based on sessile forms is supported by the existence of a number of populations where they occur together as distinct entities without detectable gradation (14.3).

10.9 E. dumosa ssp. fraseri

Although FRA is intermediate between CON and ANC in the magnitude of its nearest neighbour D-distance value (fig. 50), it is not entirely intermediate between these groups in morphology. It has a number of features not present in either CON or ANC such as its elongate operculae

(high OLW) and pedicellate or subsessile fruits (PCL > 0) as opposed to strictly sessile fruits. However, FRA is related to these groups by being the the second nearest neighbour of CON and having ANC as its nearest neighbour. To some extent it is morphologically intermediate between them. It is similar to CON in its short and wide peduncles and similar to ANC in its relatively high fruit length/width ratio (FWL). On the first canonical variate of the DPOPDAT CVA, FRA has an ordination intermediate between CON and ANC, while on the second canonical variate it is distinct from both (fig. 94).

Sampling of unassigned individuals with affinities to FRA was limited, but level 1 gradation, supported by operculum data, was recognized between ANC and FRA and between FRA and CAL. Intergrades between E. fraseri and E. conglobata were recognized by Brooker (1976) in the area south of Norseman. Brooker redefined his concept of E. fraseri so that forms with sessile fruits were transferred to E. conglobata. One specimen, from a population 6.8 km E of Scadden which was transferred to E. conglobata by Brooker, was nevertheless classified to FRA by the CVA. However, Brooker's treatment is followed here because of the need to use the sessile/non-sessile distinction to reliably key out FRA. This distinction is artificial and is not weighted as highly by the CVA, thus resulting in some discrepancy or 'misclassification' with respect to the original and final determinations in appendix 1. (Similarly, many forms comparable to ANC were classified to CAL and other groups by the CVA's because of characters other than pedicel length. On the basis of their sessile fruits, and non-glaucous stems and leaves, they are assigned to ssp. conglobata in the key (12.3).)

Gradation exists between FRA and CON to the south of Norseman and between forms included in spp. dumosa to the east. CAL is the closest group in this complex and large-fruited forms similar to CAL may be keyed out to

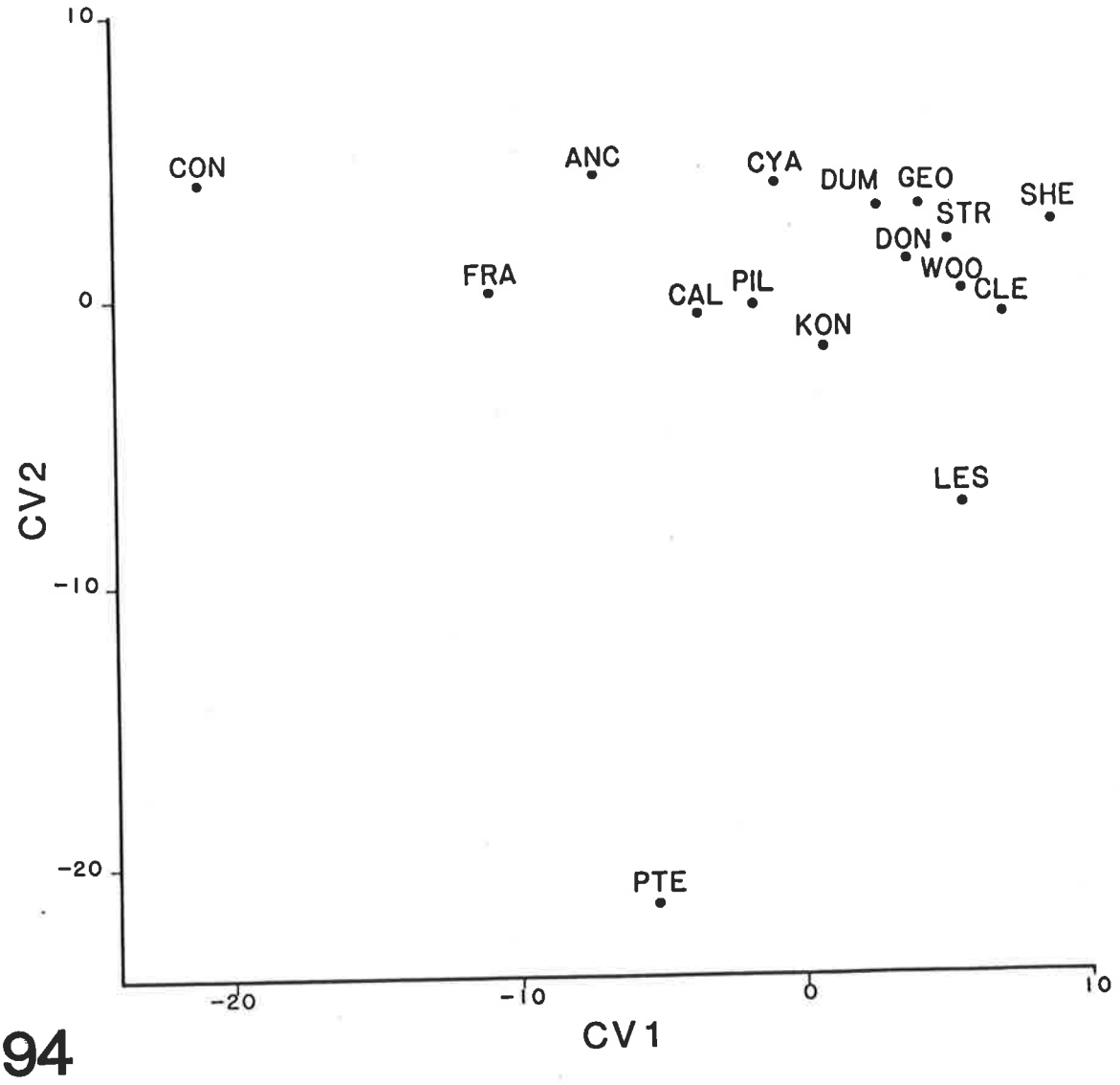


Figure 94: Canonical Variates Analysis based on the 16 TYP groups.

Plot shows position of group centroids on the first two canonical variates.

CV1 : canonical variate 1 (36 % of variation)
principal loadings : -PWM, +DW, -FWL

CV2 : canonical variate 2 (22 % of variation)
principal loadings : -FL, -FR

ssp. fraseri in the absence of buds. One intergrade (from about 70 km east of the type locality) was recognized between ssp. fraseri and ssp. dumosa from amongst the three unassigned specimens included for analysis (appendix 1). It was classified to FRA (with level 1 gradation to CAL) by both the DPOPDAT CVA's and to CAL in both TYPDAT CVA's. There are also some specimens of ssp. dumosa * which appear to exhibit affinities between FRA and PIL. Intergradation, and the paucity of useful diagnostic characters, lead to the recognition of FRA at the subspecies rather than species rank.

10.10 E. dumosa ssp. dumosa

The remaining groups are included in ssp. dumosa. They are linked by nearest neighbour distances of less than 8.3 units except for STR which has its nearest neighbour outside the cluster of remaining groups and links in at a distance of 14.2 units. I believe that STR is best treated as an intergrade between E. dumosa ssp. dumosa and ssp. clelandii. The inclusion of STR (in part) within ssp. dumosa is discussed in the following chapter.

Based on all characters STR is grouped within the blackbutt cluster, but with removal of the two and three-state characters its nearest neighbour is PMAR. This link is at a distance of 6.4 units which is less than the nearest neighbour linkages for many of the other remaining groups included in E. dumosa (fig. 51). The relationship with PMAR is significant since Dumosae representatives from the vicinity of Maralinga and elsewhere in

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* 64.9 km E Norseman/PJL 1552 (fig. 193)
70 km E Norseman, 3 km E of Heartbreak Ridge/C.D. Boomsma 352
N of Pine Hill/A.S.George 7408

the northwest of South Australia have often been referred to E. striaticalyx. In the CVA based on all characters, STR is a much more distinctive group than PMAR. The only consistent difference between STR and PMAR populations for two and three-state characters is the presence of a blackbutt for STR and its absence for PMAR. The high weighting of the blackbutt in CVA therefore contributes to the separation of STR in D-space. However, field evidence suggests that this character results from intergradation with the group CLE. In the ssp. clelandii the character is more widespread and is consistently associated with a suite of other morphological characters over a substantial area.

There is good evidence for a close affinity between STR and the material from northwest South Australia represented by 41 specimens in the CVA. In an analysis based on TYP groups, none of these were classified to STR with the full character set, but with the removal of the blackbutt character alone, 15 were classified to STR. Further evidence is provided by the classification in the DPOPDAT CVA of two individuals from Western Australia that were scored as not having a blackbutt. One specimen from a gypsum dune near Lake Annean (PJL 1478) was classified to SHE and the other from Wongawol Station (F.M. Bennet 192) was classified to PMAR. Affinities are also evident in material from the Fortescue and Giles Districts (11.3.3, p. 10).

The two states of the blackbutt character are not as discrete for STR and related forms, as for other groups in the blackbutt cluster. LES, CLE and KON consistently have a tree habit and their blackbutt is usually confined to the trunk. The persistent bark is dark and rough in appearance with the pale, smooth bark of the decorticating zone in stark contrast. The STR population has forms intermediate between a mallee and a tree, with branching often close to the ground (figs 125, 126). Although the two bark types are well defined, the persistent bark extends to a height

greater than in ssp. clelandii, often onto minor branches (fig. 104, 125).

The original description of E. striaticalyx was based on occurrences said to cover four to five square miles at two localities: Milly's Soak, which is the location of the holotype and of STR; and "4 miles east of Nannine". Fitzgerald (1904) states: "So far as observed the new plant is confined to calcareous areas, with a permanent supply of water at shallow depths." The Nannine locality is probably also a soak or watercourse since E. rostrata (= E. camaldulensis, River red gum) was given as an associate at this locality and the maps indicate that there are watercourses draining into Lake Annean in the vicinity.

The concept of E. striaticalyx was later expanded by the inclusion of other populations in the same region. Gardner (Aplin, 1979) recognised three forms represented by populations at the following locations:

1. Milly's Soak;
2. sand hills at Lake Annean near Nannine;
3. a watercourse just north of Mt Magnet.

He states: "The three forms exhibit differences in stature and in the nature of the bark, but all have the same pendulous grey leaves." Representatives of the Mt Magnet population (P160) were classified by the CVA's in a way that indicates this population to be intermediate between STR or E. striaticalyx s.lat. and CLE. (See discussion under ssp. clelandii, 10.6, p. 198.) This is supported by the POPDAT nearest neighbour network (fig. 48). There is a close mutual nearest neighbour link between STR and P160, and P160 also links less closely to the CLE cluster. It is the most southerly of the three forms and the most similar to ssp. clelandii. Features in common with ssp. clelandii include a smaller fruit size, glaucous stems, and a similar tree habit. Compared to the Milly's Soak population (STR), there is less tendency for branching at or near ground level, generally a larger trunk, and a shorter blackbutt.

The fact that these characteristics of the trunk are also most like those of CLE suggests that the blackbutt is derived from intergradation with ssp. clelandii.

The other form mentioned by Gardner occurs on consolidated gypsum dunes associated with Lake Annean (figs 127, 128) and Lake Austin. These areas are edaphically distinctive and much dryer than those of the type description. As in the Milly's Soak population (STR), individuals consistently have non-glaucous stems, but differ morphologically, most notably in narrower leaves and smaller fruits. Their habit is mallee or mallee-like with branching close to the ground, and they have a variable, often indistinct, zone of persistent rough bark at the base. This bark is less coarse than in a typical blackbutt and paler, being grey-brown rather than black. The habit and bark type of this material contribute to the link between STR and material from the northwest of South Australia. The northwest individuals are mostly mallees or occasionally small, low-branching trees (fig. 203). They are smooth-barked to the base or may retain some rough basal bark which is never very dark or sharply defined as in the blackbutt condition. Material in this region has also been collected from dunes and other habitats with gypsum (e.g. B. Lay 525).

In conclusion, the evidence provided by:

1. the reduction in distinctiveness of STR in D-space after removal of the blackbutt character;
2. intermixing of classifications between Western Australian and South Australian material;
3. variation in habit and bark type;

supports the view that STR is an atypical population within a complex of forms that usually lack blackbutts. It is therefore not given separate taxonomic status.

The other groups all fall within the central cluster and show little variation in nearest neighbour distances, although distances of lower order neighbours are more variable (9.2.3, p. 166). Attempts to define subspecies and/or varieties within this cluster were unsuccessful because of the impossibilty of imposing complex multidimensional relationships on a taxonomic hierachy. Furthermore, it was not possible to produce simple, practicable keys to identify taxa based on the groups because of overlapping character ranges. Taxa could not be defined independently of groups by dividing character ranges into discrete intervals, without ignoring inconsistencies with other characters that varied across the taxa. The lumping of the remaining groups into a single taxon is supported by the following evidence:

1. Intergradation demonstrated between groups in the CVA results (figs 53 to 55).
2. Populations with intergradation and interspersion of groups (appendix 1).
3. Interspersion of groups between regions (appendix 1 and table 11.1).
4. Close relationships established in the LGFDAT analysis between LGF groups. In the DPOPDAT analyses all the members of these groups are classified to these remaining DPOP groups.
5. Intergradation and interspersion of DUM, CYA and CAL within a single district and locality as demonstrated in the SEDAT analysis.
6. The lack of cases where distinct forms classified or referable to these groups are maintained at a single locality (14.3).

The complex relationships between these groups are considered in more detail in the next chapter, which further substantiates the evidence for grouping them within E. dumosa ssp. dumosa.

Figures 95 to 128: These mainly illustrate variation in Dumosae taxa as discussed in chapter 10. In collections of fruits and buds, each umbellaster represents a different randomly sampled individual unless otherwise indicated.

Scale bars: 1 cm

Figure 95: Eucalyptus lesouefii

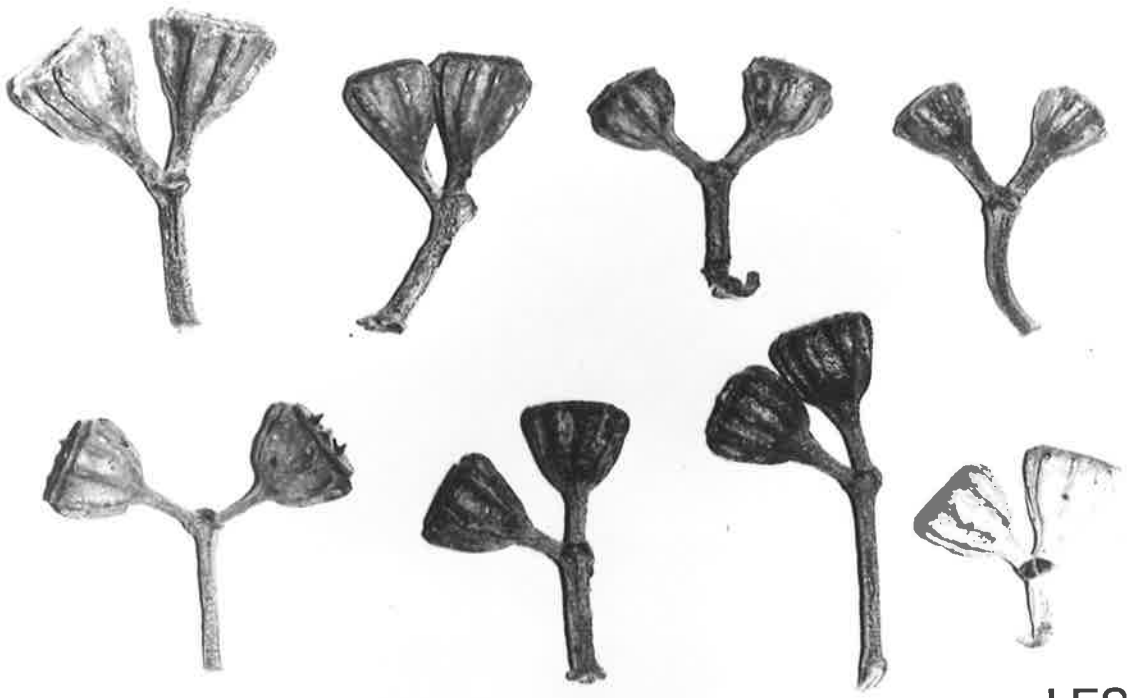
A selection of fruits from five localities to illustrate range of variation.

row 1 : PJL 1556, 1549, 1551, 1557
row 2 : PJL 1544, 1545, 1559, 1521

Figure 96: E. woodwardii fruits.

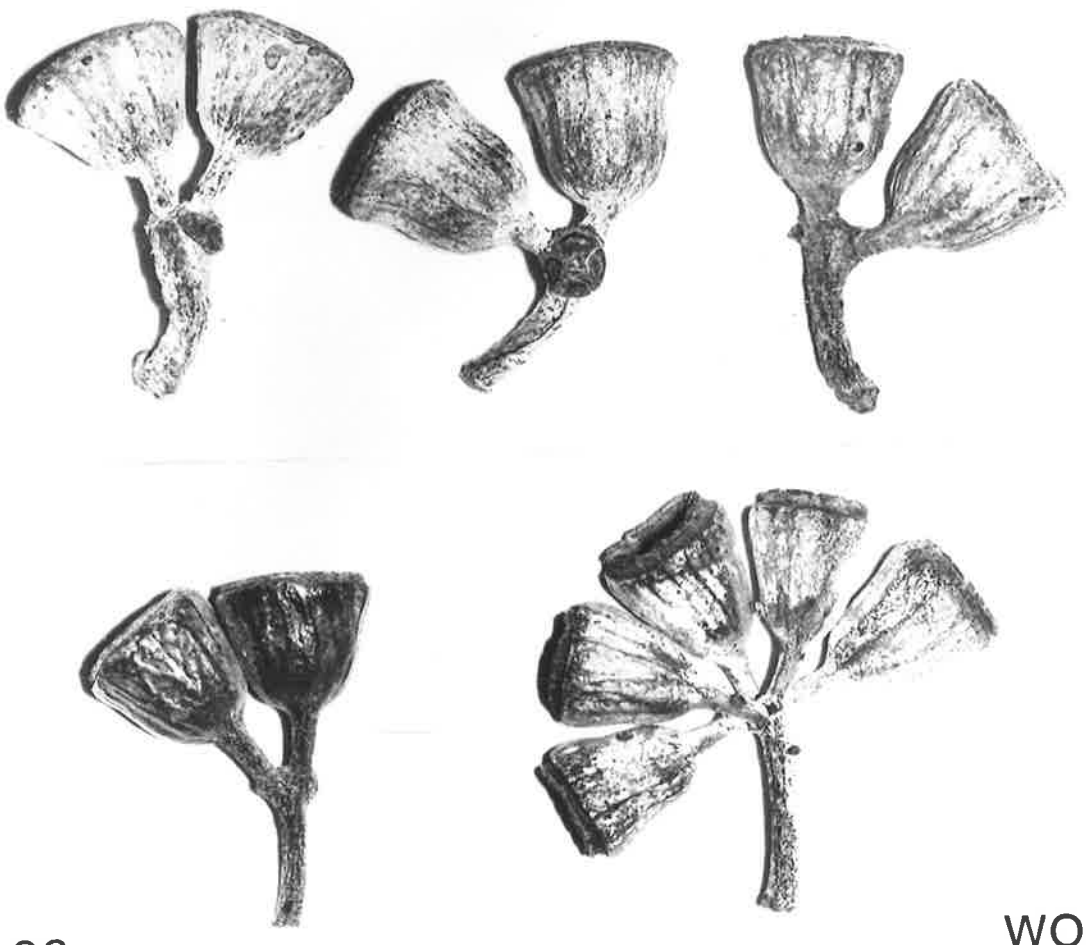
row 1 : PJL 1562, 1563, 1564
cultivated trees

row 2 : R. Helms 15/97 km S Victoria Spring



95

LES



96

WOO

Figures 97 to 99: E. dumosa ssp. clelandii

97: 5.9 km N Goongarrie (CLE)
Population from near the type locality.

row 1 : fruits PJL 1530, 1539 to 1542
row 2 : buds PJL 1530, 1539, 1540

98: 4.9 km NW Coolgardie
Random collection of one umbellaster per tree (n = 8).

99: 3.9 km S Menzies (P181)

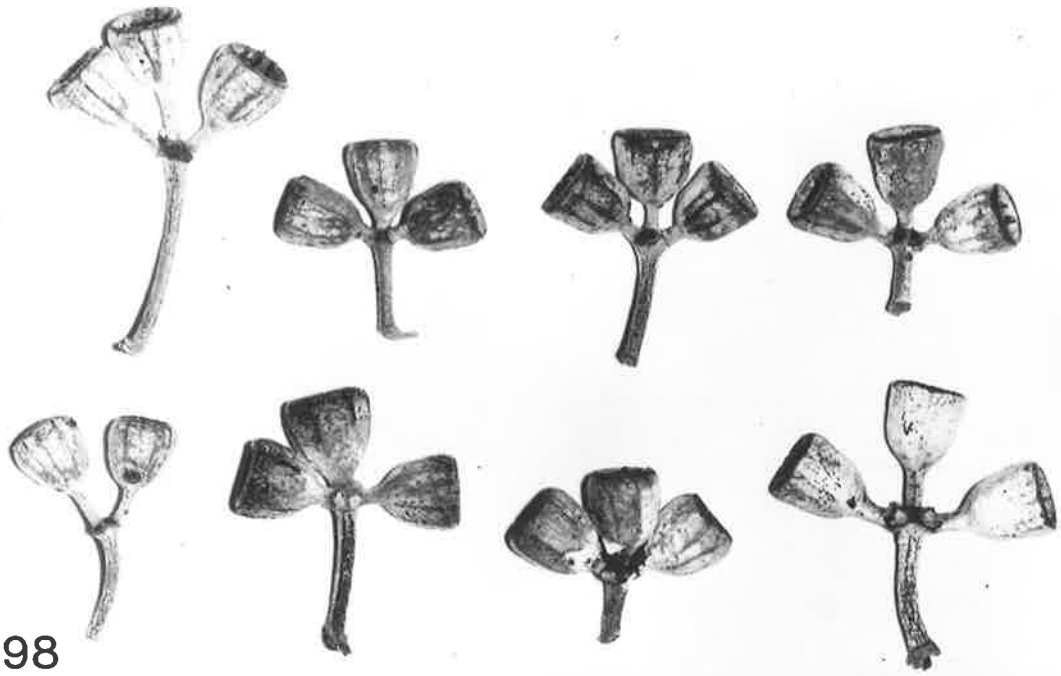
fruits: row 1 : PJL 1534 to 1536
row 2 : PJL 1537, 1538 (random sample);
the third umbellaster is an extreme variant
(non-random selection).

buds (top to bottom): PJL 1534, 1535, 1537

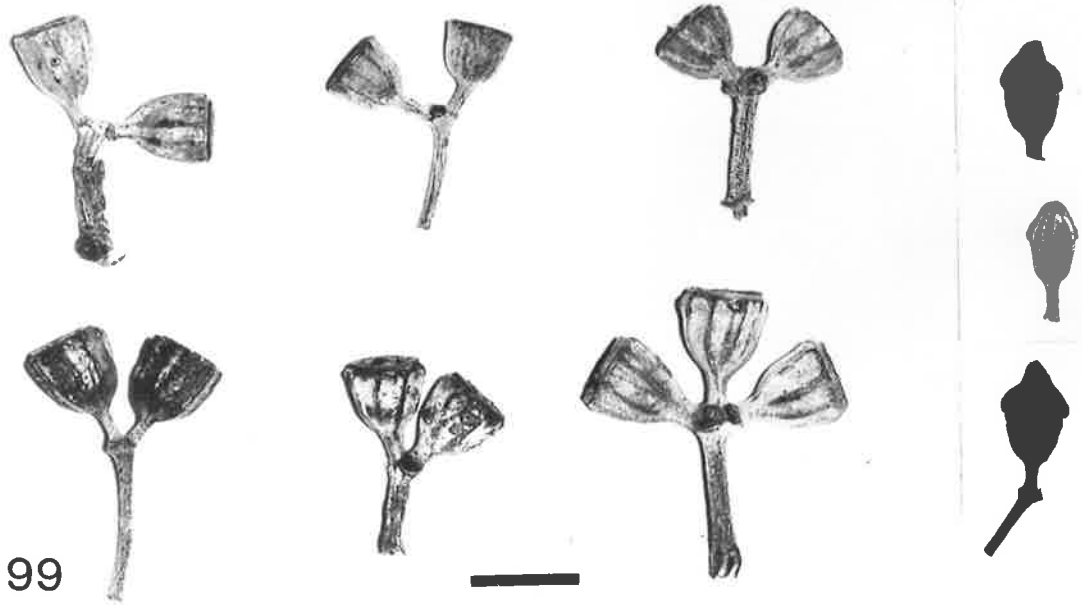


97

CLE



98



99

Figures 100 to 105: Habit photographs for Western Australian Dumosae in the 'blackbutt group'.

100: E. pterocarpa

c. 18 km WNW Norseman (PTE)
Trees at the type locality. Photograph from herbarium specimen: G.M. Chippendale 154.
Blackbutts not present.

101: E. lesouefii

PJL 1521/Kurrawang RS
Height: 13 m, blackbutt: 0.9 m

102: E. kondininensis

0.5 km S Kondinin (KON)
Trees near the type locality. Height: 12 m, blackbutt: 3.3 m

103: E. kondininensis

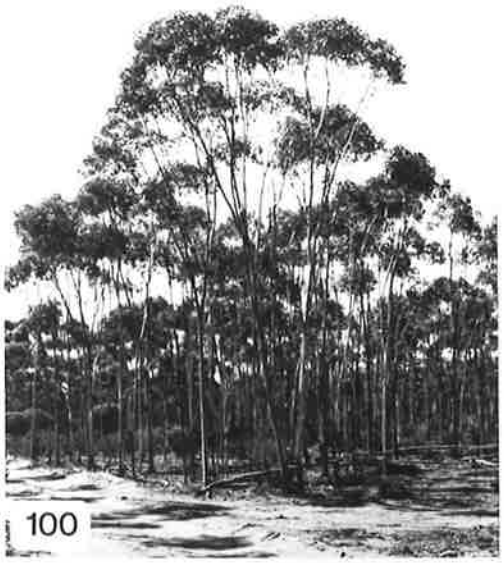
1.0 km E Newdegate
Height: 13 m, blackbutt: 5 m

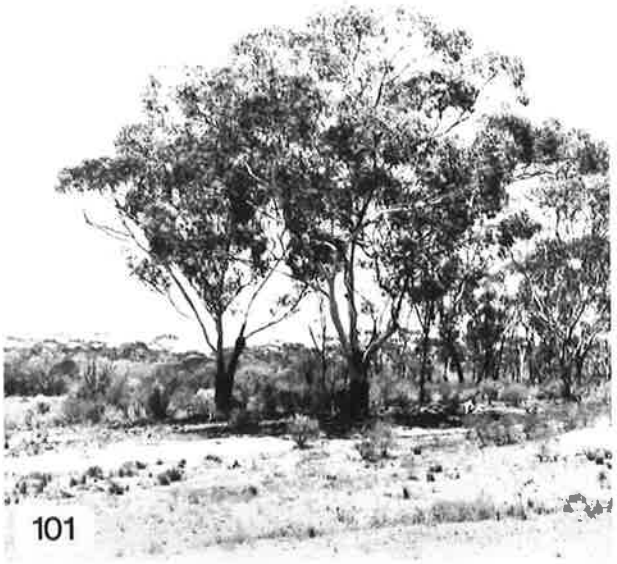
104: E. dumosa ssp. clelandii

5.9 km N Goongarrie (CLE)
Tree near the type locality. Height: 8.5 m, blackbutt: 1 m

105: E. dumosa ssp. clelandii intergrade ssp. dumosa

PJL 1516/1.3 km W Bullabulling (P179)
Tree with habit of ssp. clelandii, but without blackbutt.
Height: 8.5 m


100


101


102


104


103


105

Figure 106: E. dumosa ssp. fraseri

8 km W Balladonia motel (FRA)
Tree near the type locality. Height: 11 m, trunk: 5 m

Figure 107: E. dumosa ssp. fraseri

E side Fraser Range pass, 84 km W Balladonia motel
Form with blackbutt. Height: 17 m, blackbutt: 6 m

Figure 108: Intergrades between E. dumosa ssp. clelandii and ssp. dumosa

21.1 km N Norseman (P154)
Height: to 13 m, trunks: 4 to 6.5 m

Figure 109: Detail of trunk from above population showing bark decorticating to base.

Figure 110: Intergrade between E. dumosa ssp. georgei and ssp. dumosa

25 km E Hyden
Small tree to mallee habit (background). Height: 7 m

Figure 111: E. dumosa ssp. dumosa

0.5 km S Nukarni RS (SHE)
Slender mallee, previously referred to E. sheathiana.
Height: 7 m



106



107



108



109



110



111

Figure 112: E. dumosa ssp. georgei

c. 160 km E Hyden (GEO)
Paratype individuals from near the type locality.

fruits: M.I.H Brooker 4989, L.F. Allan 29,
A. Kessell 947, A. Kessell 424
buds: " " " "
" " " "

Figure 113: Intergrades between E. dumosa ssp. georgei and ssp. dumosa

25 km E Hyden

fruits PJL 1431 to 1433; buds PJL 1431

Figure 114: E. dumosa ssp. conglobata

Lincoln NP, 2 km S of Sleaford rd (CON)
Population from near the type locality.

PJL 1123 to 1127

Figure 115: E. dumosa ssp. conglobata

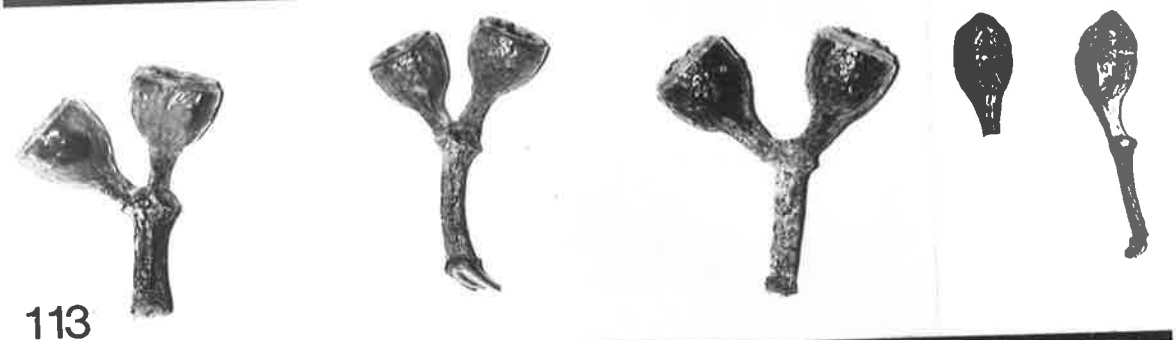
c. 15 km W American River (ANC)
Population from the vicinity of the type locality for E. anceps.

fruits: PJL 672 to 676
buds: " "



112

GEO



113



114

CON



115

ANC

Figures 116 to 118: Variation in habit of E. dumosa ssp. conglobata

116: Spalding Cove
Tree form on shallow grey sand over calcrete. Height: 9 m

117: 6.5 km E Scadden
Erect form on grey-white sand. Height: 6.5 m

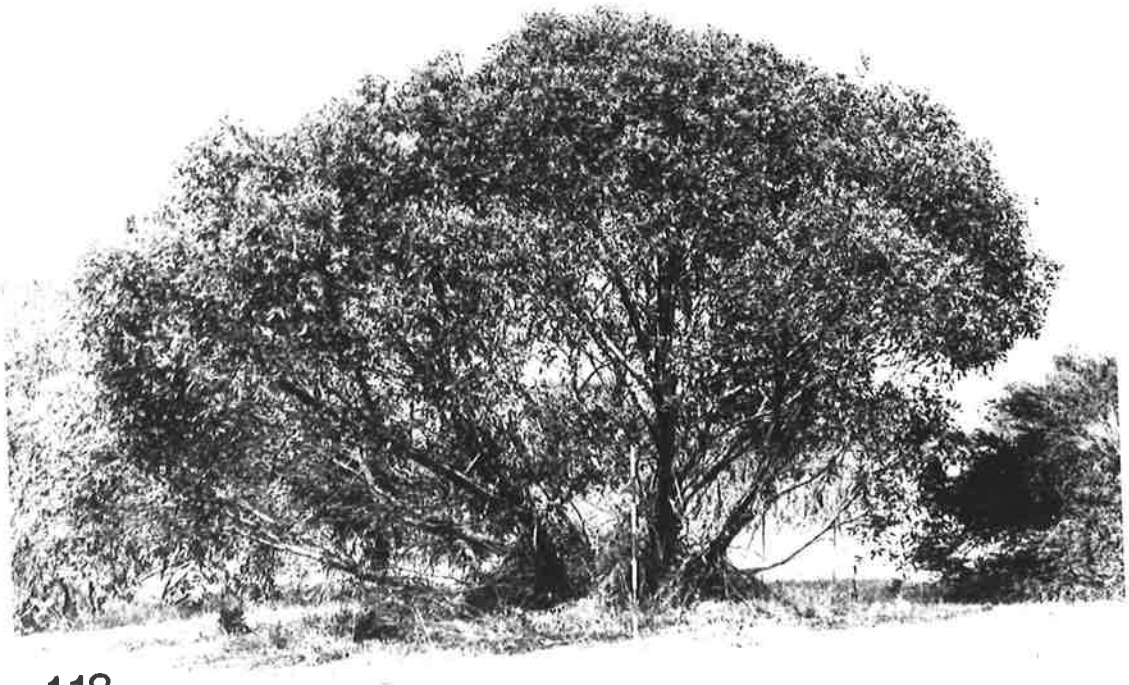
118: 4 km W Pt Lincoln PO
Mallee form on loam with lateritic and calcareous gravel.
Height: 4 m



116



117



118

Figure 119: E. dumosa ssp. georgei intergrade.

A. Kessell 408/Mt Holland Area

Figures 120, 121: E. dumosa ssp. clelandii intergrade ssp. dumosa.

22.1 km N Norseman (P154)

120: PJL 1546

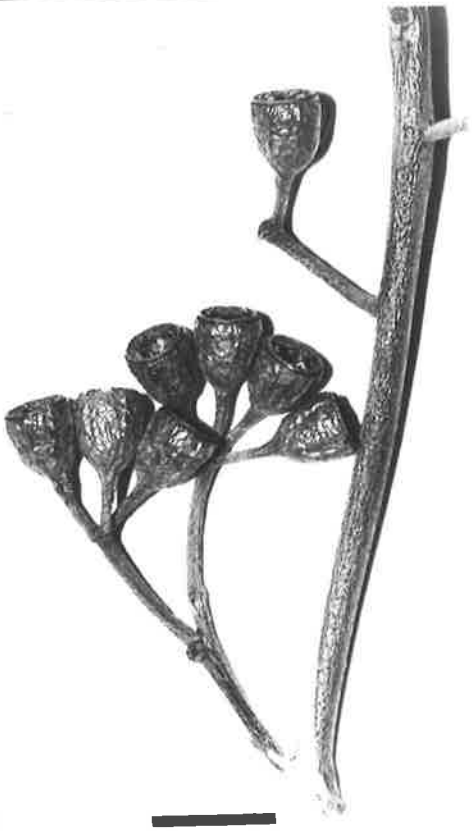
121: PJL 1547



119



120



121

Figures 122 to 123: Fruits and buds in populations displaying affinities between taxa previously referred to as E. striaticalyx and E. clelandii.

122: E. dumosa ssp. dumosa (aff. ssp. clelandii)

Millie Well, 15 km N Cue (STR)
Population from the type locality of E. striaticalyx.

PJL 1481 to 1485

123: E. dumosa ssp. clelandii intergrade ssp. dumosa

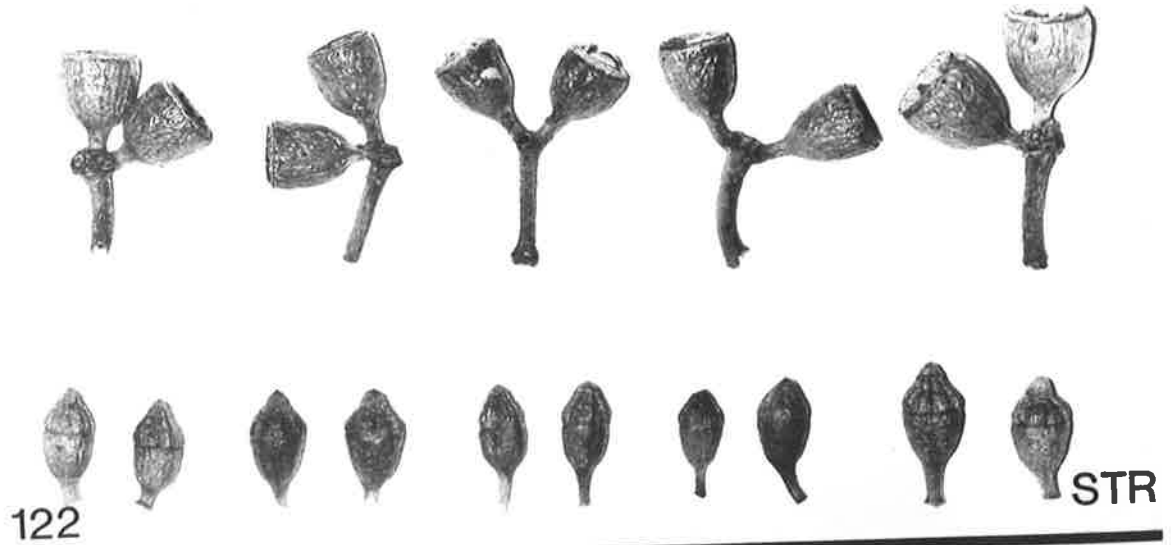
2 km N Mt Magnet (P160)

row 1 : fruits PJL 1472 to 1476
row 2 : buds PJL 1472 to 1476; fruits from an extreme variant (non-random collection)

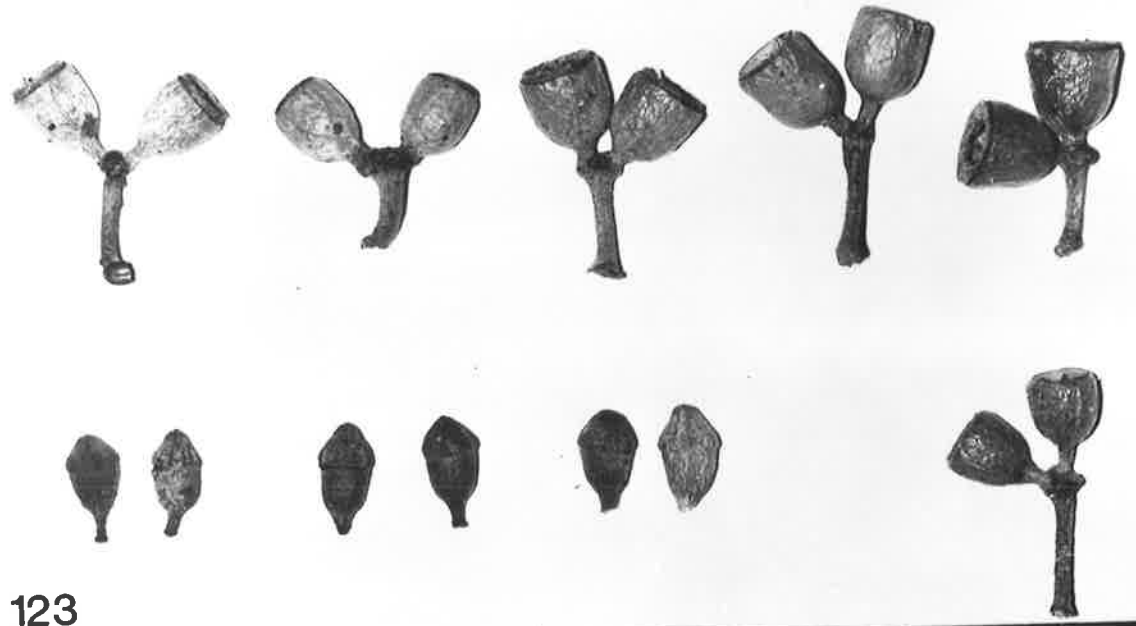
124: E. dumosa ssp. clelandii (aff. ssp. dumosa)

14.5 km NE Mt Gibson HS turn-off (P163)

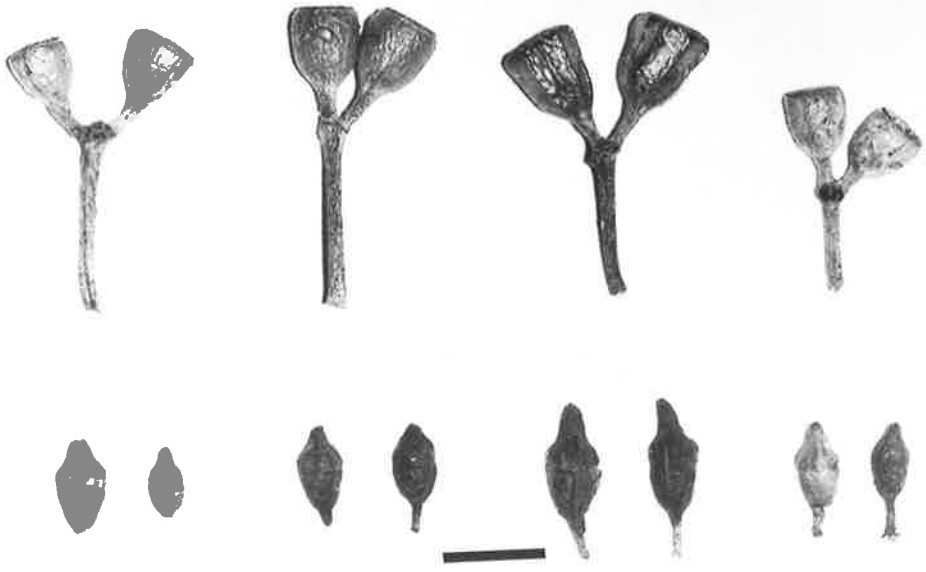
PJL 1486 to 1489



122



123



124

Figures 125 to 128: Habit of 'E. striaticalyx' (E. dumosa ssp. dumosa) at two localities in the Austin District, W.A.

125: PJL 1481/Millie Well, 20 km NNE Cue (STR)
Tree at the type locality of 'E. striaticalyx' with rough bark extending well up major branches.
Height: 11.5 m, trunk: 1.3 m

126: Mallee forms at Millie Well.
Height: 10 m

127: PJL 1479/73 km NNE Cue (P161)
Height: 7 m

128: 73 km NNE Cue (P161)
Habitat: kopi (gypsum) dune on the margin of Lake Annean



125



126



127



128

CHAPTER 11

VARIATION WITHIN EUCALYPTUS DUMOSA SSP. DUMOSA

This chapter uses the framework of pre-existing species concepts to describe some of the variation incorporated within Eucalyptus dumosa ssp. dumosa. In this way further evidence is presented on the limitations and inconsistencies in these concepts and supports the lumping of these taxa in the new classification derived in chapter 10. Species names referred to here are now regarded as synonyms of E. dumosa ssp. dumosa.

11.1 Within-population variation

A notable feature of the Dumosae is the high variability in size and shape of leaves, fruits, and buds in a single population. Figures 135 to 137, and 155 illustrate the degree of variation in fruits that can occur in subspecies dumosa at a single locality. This demonstrates the impracticability of defining taxa on a small scale. In many populations the variation is less extreme and some characters such as fruit size or pedicel length are more consistent (figs 142 to 145). Some populations include a continuum of forms between ssp. conglobata and ssp. dumosa (figs 138 to 141).

The four Dumosae species endemic to Western Australia all have operculae that are rostrate or umbonate and never entirely convex or hemispherical. In E. dumosa there is a wider range of operculum shapes, and extreme forms often occur together in the same populations (figs 146 to 149).

The within-population variability enables finger-printing of individuals. Subtle differences in bud characters are evident between all individuals

in the group DUM (figs 153, 154). Such variation makes it possible to match disarticulated buds or fruits with their tree of origin. This was useful when supplementing collections with old bud material from the ground.

11.2 Geographic variation

Despite the background of high variability, many geographic patterns are evident. For example a short, blunt operculum is a consistent feature within the main area of distribution for E. dongarraensis; and high leaf glaucousness is fixed in areas of the Murray region where material has been referred to E. cyanophylla.

The distribution of group classifications in appendix 1 is far from random. Classification results for the DPOPDAT CVA are summarized on a geographical basis in table 11.1. Significant geographical correlations are shown by the distributions of PCVH and PMAR which are restricted to more arid areas, and by the absence of SHE in South Australia. It is notable that there are no individuals in Western Australia classified to CYA or PCVH and only a few to DUM. The lack of DUM and CYA reflects the fact that in Western Australia glaucous leaves are nearly always associated with glaucous stems. The Gawler Ranges and the Flinders Ranges are similar in that most material is classified to DUM or P35, with the majority classified to DUM.

Eyre Peninsula is the most intensely sampled region because it was known to have complex variation and material was readily available. Nine groups from within E. dumosa ssp. dumosa were represented in classifications of Eyre Peninsula material by the DPOPDAT CVA. Distributions of the four major groups classified by the TYPDAT CVA's are shown in figures 129 to

Table 11.1: Classification results of DPOPDAT CVA for E. dumosa ssp. dumosa according to geographical areas.

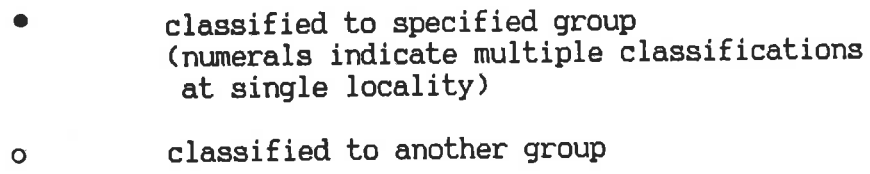
Areas	DPOP Groups											
	CAL	PIL	P35	DUM	CYA	PCAR	PCVH	PMAR	SHE	P157	DON	STR
Western Australia												
1. Eremaean Province												
Eucla District	4/1	1/0	2/0	3/0								
other Districts								2/2	1/1		1/1	5/5
2. South-western Interzone	6/6	8/1		1/1					2/2			
3. South-west Province	3/2	11/7	2/2			1/1			12/11	10/8	10/7	
TOTAL	13/9	20/8	4/2	4/1		1/1		2/2	15/14	10/8	11/8	5/5
South Australia												
1. Northwestern area *						1/1	11/10	26/15		2/2		
2. Eyre Peninsula Region	45/31	8/0	11/1	13/4	11/6	22/19		3/1		3/2	1/0	
Gawler Ranges	1/1		5/0	8/4	1/0			2/1				
3. Flinders Ranges **			8/5	14/5		2/2				3/1		
4. Murray Region	2/2		1/0	2/2	20/18	1/1						
5. South-eastern Region	7/2		10/0	6/1	1/0					1/0		
6. other Regions	9/9			7/7								
TOTAL	63/44	8/0	30/6	42/19	32/24	26/23	11/10	29/16		9/5	1/0	
Victoria					2/1							
New South Wales				11/10								

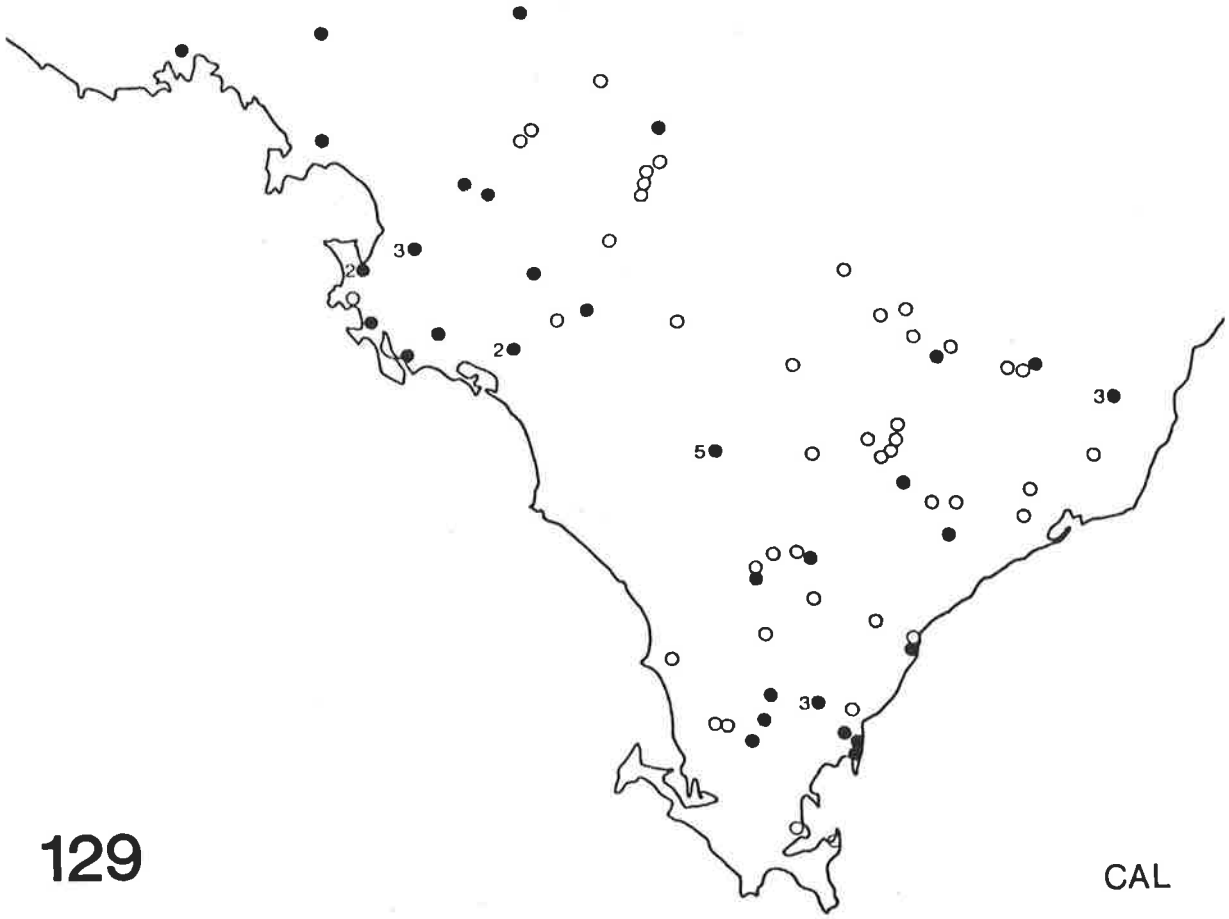
* includes North-western, Gairdner-Torrens Basin and northern part of Nullarbor Regions

** includes Flinders Ranges Region and northern part of Northern Lofty Region (= 'Southern Flinders Ranges')

KEY: a/b a: total no. classifications
b: classifications without missing operculum data

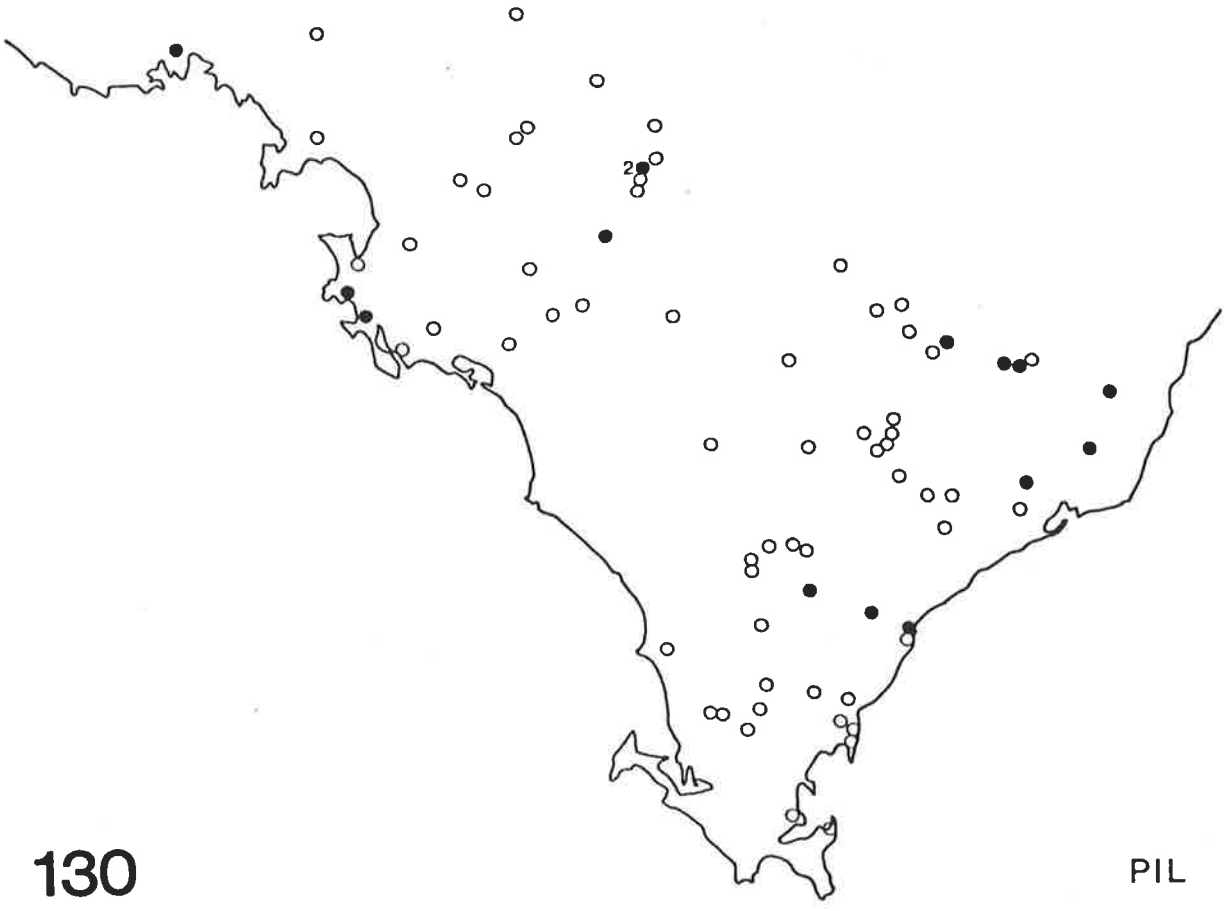
Figures 129, 130: Distribution of unassigned individuals from Eyre Peninsula classified to groups CAL and PIL by the TYPDAT CVA.





129

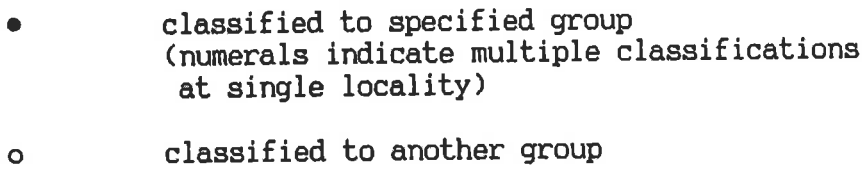
CAL

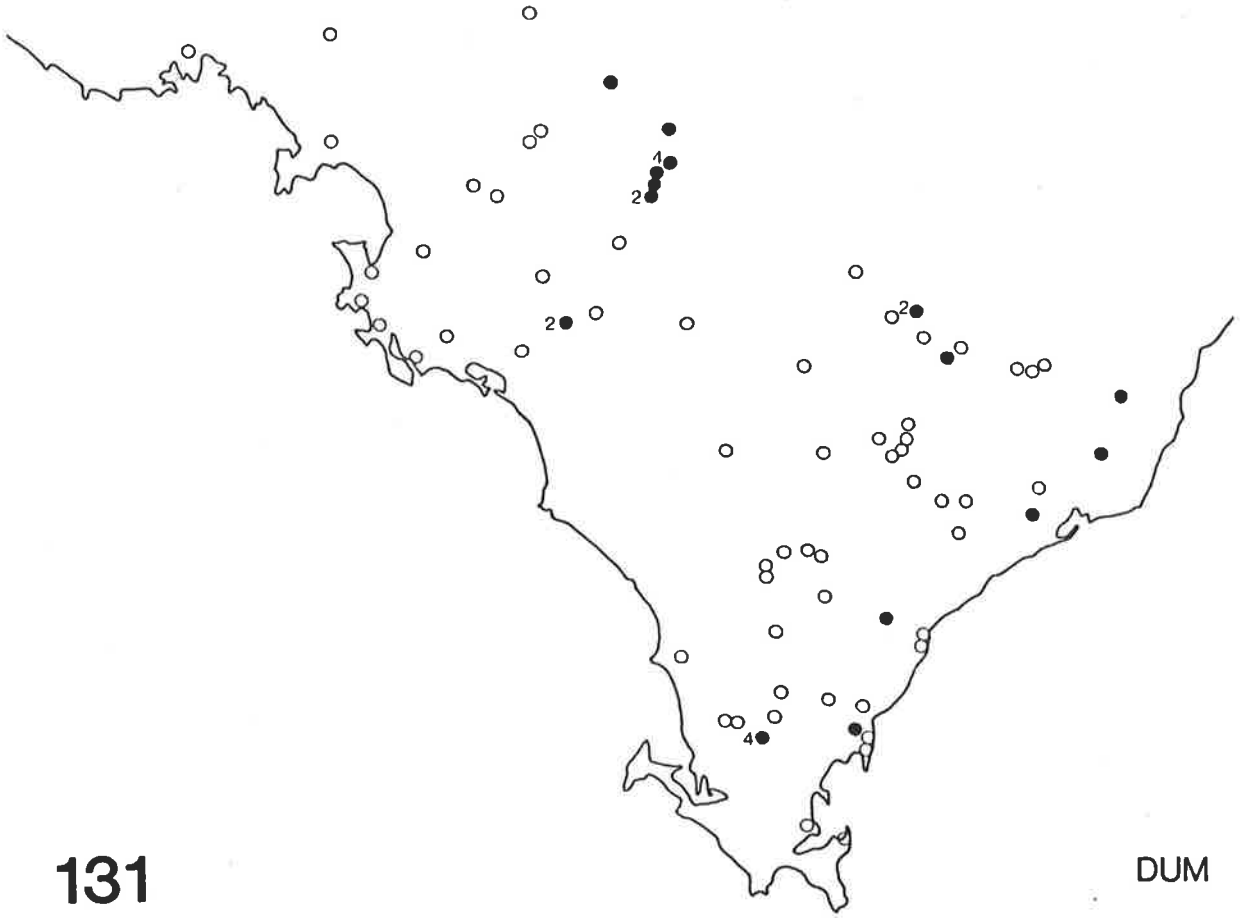


130

PIL

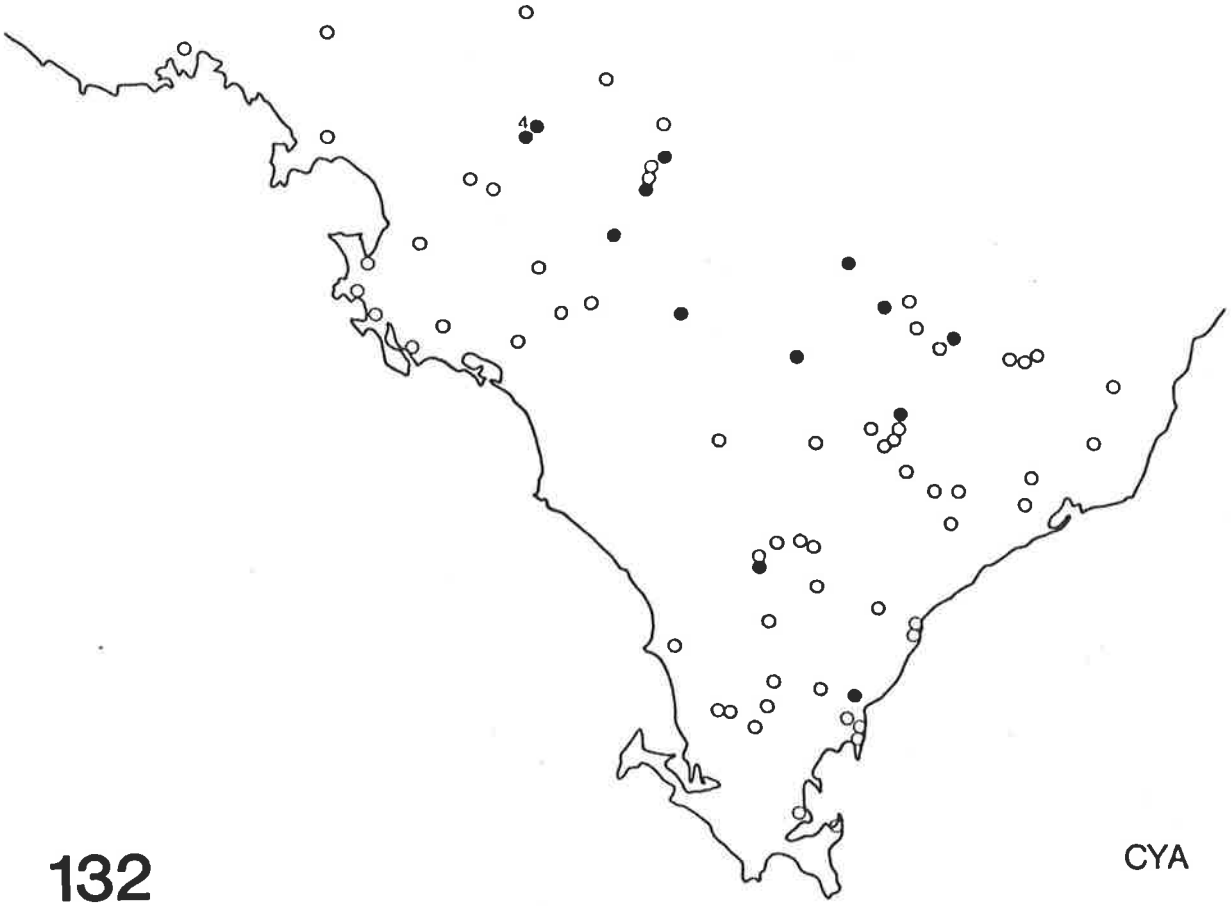
Figures 131, 132: Distribution of unassigned individuals from Eyre Peninsula classified to groups DUM and CYA by the TYPDAT CVA.





131

DUM



132

CYA

132. There is a high level of overlap and lack of any clearly defined geographical groupings. Although there are some trends such as the high representation of DUM in the Gawler Ranges and the occurence of CYA in a central zone away from the coast, overlap and intermixing predominates. Gawler Range material is certainly not consistently referable to E. dumosa s. str. As well as DUM, four other groups are represented (table 11.1), and there is a wide range in leaf glaucousness (fig. 20) and cuticular sculpturing (CS : 1.3 - 7.1), together with much variation in fruit size and shape (figs 155, 156).

On Eyre Peninsula, as in much of South Australia, the three groups PIL, DUM and CAL form a closely related complex with a particularly high degree of gradation and spatial intermingling.

11.3 Relationships of synonyms of E. dumosa ssp. dumosa

11.3.1 E. dongarraensis

The group DON * comprises five individuals three of which were scored as having glaucous stems, although this was only slight. In the other two, glaucousness persisted only on small stems (< 3mm diam.) bearing intermediate foliage. The only other material referred to E. dongarraensis and known to have glaucous stems is the type material collected at Dongara. Maiden (1927, 7(68), p.372) compares it with E. dumosa as: " ..more glaucous, especially in the juvenile leaves and buds". An examination of the type material at PERTH confirmed that the buds were glaucous as stated in the type description and that the stems were also glaucous. DON is included by the TYPDAT CVA in a cluster of groups

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* The groups are defined in sections 7.2 and 9.2.2.

characterized by glaucous stems and has SHE as its nearest neighbour. In the DPOPDAT CVA it is most closely linked to CAL and P157, and is clustered amongst groups lacking glaucous stems. With removal of two and three state characters, DON and P157 are mutual nearest neighbours and form a relatively isolated cluster in the nearest neighbour dendrogram (fig 51). P157 differs from DON mainly in the absence of glaucous stems. The relationship between DON and P157 parallels that between STR and PMAR. DON is interpreted as an atypical, coastal population with sub-glaucous stems within a complex of largely non-glaucous forms that has been referred to as E. dongarraensis.

Eucalyptus dongarraensis has been regarded as a geographically well delimited taxon (Chippendale, 1973) with occurrences confined to a coastal/sub-coastal zone between Perth and Shark Bay in Western Australia. This incorporates the northern part of Avon, Irwin, and the southern part of Carnarvon, Botanical Districts. The classification results of the DPOPDAT CVA indicate that it is an easily distinguishable taxon in this area (appendix 1). The six unassigned individuals determined as E. dongarraensis were all classified to P157 or DON. The only Western Australian material classified to these groups is from this area, except for four individuals from the Roe District determined as E. sheathiana but classified to DON. A further 10 individuals from South Australia were also classified to DON or P157 , indicating inability to distinguish E. dongarraensis from material outside its accepted geographic limits.

An apparently unique feature of E. dongarraensis within the the Dumosae is the occurrence of an elongated, sometimes pyriform, fruit with a poorly defined base that is confluent with a dilating pedicel. This feature is well represented in the DON population but is not as well developed in the remaining material sampled (figs 158, 160). It is obvious in the specimens PJL 1469 (P159) and C.D.Boomsma, WA 45/76 (P182), but many fruits from

other localities have well-defined bases and are difficult to separate from those of DUM or other forms included in ssp. dumosa.

The most distinctive feature of DON and P157 within the complex of groups placed in ssp. dumosa is the flattened operculum, represented by low scores for OLW and high scores for OWM (figs 161 to 163, 165). Although these characters are highly variable in most of ssp. dumosa, they are genetically fixed in the area that is the accepted distribution for E. dongarraensis. No individual is known from this area with a conical, umbonate or rostrate operculum.

However, when operculum characters are missing it is impossible to distinguish E. dongarraensis in a key from much of the material that has been referred to E. dumosa or similar forms. Material outside the area may have similar bud morphology. The collection PJL 1154 from 54 km SW of Whyalla has buds that show strong convergence with those of P157 although the fruits are uncharacteristic (figs 162 to 164). Operculum data were present for half of the 14 individuals outside the prescribed area of E. dongarraensis that were classified to DON or P157. Thus even when operculum data are available, E. dongarraensis does not stand up as a geographically discrete group.

The relationships of DON and P157 are further complicated by gradation. In the southern part of the distribution of E. dongarraensis, there is good evidence of gradation with E. sheathiana. Individuals from 5.3 km W of Wyalkatchem seem to be intermediate between DON and P157 on one hand and SHE on the other (figs 165 to 168). The four populations form a geographical sequence trending inland southeast from the coast. The corresponding morphological trend involves an increase in OLW, a decrease in OWM, and decrease in PCW and PW .

11.3.2 E. sheathiana

A wide range of forms have been referred to this name. It seems to have been used as a "carry-all" taxon in the same way as E. dumosa from which it differs principally in having glaucous stems and being restricted to Western Australia. The relationship with E. dumosa is evident from the fact that DUM is the nearest neighbour of SHE in D-space irrespective of the inclusion of two and three state characters. Level 2 gradation occurs with PMAR and PCAR using all characters, and with DUM, P157 and CLE with removal of two and three state characters. With both operculum and the two and three-state characters removed, there was even a level 2 intergrade between SHE and DUM for a TYP group (table 9.2).

The doubt about the origin of the cultivated type material has probably contributed to the difficulty in defining this taxon. Information on within-population variability at a type locality can be used to indicate a range of forms that should be regarded as belonging to the same taxon as the type. The SHE populations only represent material that is consistent with the type. These populations are distinctive in their slender peduncles and pedicels, their relatively elongate fruits contracted towards the rim (low values of FWMR), and their narrow disc (fig. 169). Fruits of other populations, however, are often indistinguishable in form from those of PCAR , or if stem glaucousness is ignored, from much material referred to E. dumosa, E. dongarraensis and E. pileata (figs 170, 171, 173).

In the western part of Roe Province there are major occurrences of individuals both with and without glaucous stems. The former have traditionally been referred to E. sheathiana and the latter to E. pileata. Although often in proximity , the two forms are only known to occur in a mixed population at one locality, 0.4 km E of Burngup (P177). Here there

is only limited gradation between the forms and it is apparent only in those with glaucous stems. One specimen (PJL 1421) has only faint stem glaucousness and buds more like those of E. pileata than typical E. sheathiana, having a rounded more hemispherical operculum with weak but well defined ribs. Another (PJL 1427) has fruits reminiscent of E. pileata in the short disc depth and expanded shape (low FWM). Buds and fruits are illustrated in figure 172. Examination of character scores showed that substantial differences between SHE and PIL are maintained. The three individuals sampled with glaucous stems all have longer, narrower peduncles and pedicels and narrower discs than the non-glaucous forms. Also, two of the three glaucous forms have umbellasters of 11 flowers. This is common in material referred to E. sheathiana but unknown in material referred to E. pileata which has a maximum of seven flowers. The glaucous form with all seven-flowered umbellasters, was classified to SHE by all CVA's, but the other individuals show various affinities with PIL, CAL, and DON (appendix 1). It is concluded that there is probably some barrier preventing complete gene exchange between the two forms in this population. Flowering time is a possible mechanism as buds were abundant on the non-glaucous forms but absent on all but one of the glaucous forms where they were rare.

Elsewhere, gene exchange between the two forms is more evident. For example, a population 10.6 km E of Southern Cross (P152) has only very lightly glaucous stems and some operculum and fruit shapes approaching those of eastern forms referred to E. pileata (fig. 171). Populations from 2.6 km NW of Kulin (P178) and 14.7 km E of Lake Grace (POP: P176) have fruit shapes more like those of non-glaucous forms and approach PIL in their high degree of operculum ribbing (fig. 170). None of the four individuals sampled from the latter population were classified to SHE when the two and three state characters were removed. It was not possible to

separate this population from PCAR and other glaucous material on Eyre Peninsula using diagnostic characters suitable for a key.

The recognition of a taxon in Western Australia based primarily on the presence of stem glaucousness, is also not supported by the variation this character shows in members of the E. dumosa complex in South Australia. There is no good evidence of association with other morphological characters in material from the northwest and Eyre Peninsula Regions. If E. sheathiana were maintained as a taxon, many South Australian forms would have to be included or excluded solely on the basis of stem glaucousness.

11.3.3 E. striaticalyx

For a long time E. striaticalyx was thought to be rare and confined to the Cue-Nannine area in Western Australia. Relationships of the forms occurring in this district were discussed in the previous chapter together with the treatment of STR as an intergrade between E. dumosa ssp. dumosa and ssp. clelandii. Initially, South Australian material that was later referred to E. striaticalyx, was determined as E. pileata. Under the latter name Black (1952, p.629) cited Ooldea as a locality in his his Flora of S.A. This interpretation remained unaltered by Eichler's (1965) revisions. Eucalyptus striaticalyx was first identified from South Australia by L.A.S. Johnson in 1965 (Boomsma 1969). Boomsma reported several dispersed collections giving it a wide potential distribution " from the Transcontinental Railway northwards to the Musgrave Ranges ... and westwards to Western Australia". Subsequent floristic treatments (Boomsma 1974, 1981) included this species for South Australia, but Hall and Brooker (1973) did not recognize occurrences outside of Western Australia.

The northwest part of South Australia comprising the North-western, Gairdner-Torrens and northern Nullarbor Regions contains a wide diversity of forms that can be referred to E. striaticalyx in its broadest sense. They may be regarded as desert-adapted forms with the following features in common: large fruits, well defined pedicels (not dilating into the base of the fruit) and dull leaves (high cuticular relief). Unlike the population of the type in Western Australia which has consistently non-glaucous stems, they are variable for both leaf and stem glaucousness. Most of the 41 individuals sampled were classified by CVA to PCVH and PMAR which are defined from within the same area. The group PCVH was initially based on only five specimens (L.D. Williams 10492; T.E. Dennis 188, 189, 191; J. Johnson and S. Reid 3, 3.vi.1970) collected on the Cook-Vokes Hill track between 124.5 and 136 km north of Cook *. In this section the track intercepts a series of tall sand dunes that are associated with a low calcrete rise and form part of the Barton Dune System and a continuation of the Ooldea Range. This system extends northwest from just south of Maralinga and veers west near the Cook-Vokes Hill track to merge with west trending dunes south of Serpentine Lakes. Other dunes are encountered elsewhere along the track but in this section they are taller, more erratic and less consolidated; and blue-leaved, glaucous mallees are a notable feature on them (L.D. Williams, pers. comm.). The five specimens are characterized by glaucous stems and very large, broad fruits. A striking feature of some individuals is the presence of strong fruit ribbing (figs 176, 178). The only buds present are those of the Johnson and Reid specimen and one eroded bud of T.E.Dennis 191. The operculae are sub-hemispherical, barely rostrate and, unlike the type population of STR,

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* Note: the locality given for this collection of Johnson and Reid represented at WF, AD, MEL, and WRSL was corrected after consultation of the field log book with Mr S. Reid.

strongly ribbed. Although stem-glaucousness was known to vary in smaller fruited forms, it seemed that it may be fixed in large-fruited forms in this region. The limited evidence available suggested the possibility of recognizing a taxon based on PCVH and characterized by glaucous stems, large and broad fruits, and sub-hemispherical, strongly ribbed operculae. Further collections were requested from T. E. Dennis to ascertain whether there was any significant breakdown in these characters. Subsequent collections from just north of the main dune belt revealed large-fruited forms with non-glaucous stems and: elongated fruits (fig. 89); conical and weakly ribbed operculae (fig. 89); hemispherical operculae (fig. 88); and strongly rostrate operculae (fig. 86). The breakdown in stem glaucousness is demonstrated by the specimens T.E.Dennis 213 and 215 (figs 70, 88) which are virtually identical morphologically apart from this character.

With PCVH expanded by the inclusion of four non-glaucous forms, six cases involving gradation between PCVH and PMAR were detected by CVA. One of these , L.D.Williams 10776, is illustrated in figure 175. Affinities with PCVH are suggested by fruit and operculum shapes, but the smaller fruit size (approaching that of PMAR) and smooth surface, are more typical of E. striaticalyx. Material collected by D.E.Symon from the Great Victoria Desert in August 1980 further demonstrates the breakdown in fruit size. One specimen from Western Australia (D.E.Symon 12674) has fruits equally large as PCVH while a number of specimens from the main dune belt are smaller.

The distribution of glaucous-stemmed forms is widespread but not random. No individuals with glaucous stems were present in six collections from the vicinity of Maralinga township, nor in seven collections from near the junction of Serpentine Lakes and the track to Emu. The latter population is also characterized by relatively large, elongate fruits. Some geographic patterns are evident but the variation is complex and does not

support the recognition of separate taxa in the northwestern regions.

Material collected in the vicinity of Tom Price in the Hamersley Ranges of Western Australia (Fortescue District) was not available in time for numerical analysis but appears to have strong affinities with northwestern material. The stems are consistently non-glaucous and fruits are elongate. Individuals are usually smooth-barked but occasionally some decorticated bark persists at the base (C. B. Boomsma, pers. comm.). Similar material with glaucous stems has also been collected from the Blackstone Range in the Giles Province (D.E.Symon 8403 (ADW)). These widely spaced collections further support the link proposed between STR and the broader concept of E. striaticalyx that includes PMAR and PCVH.

On northern Eyre Peninsula there appears to be intergradation with other forms of ssp. dumosa. Scattered individuals are indistinguishable from some northwestern forms. This is supported by CVA which classified three individuals to PMAR and detected six cases involving intergradation with PMAR. Affinities with E. striaticalyx are recognizable in some forms from the Gawler Ranges with large fruits and elongate pedicels (figs 155, 156). Large-fruited, glaucous-leaved forms are also common on sand dunes at places such as near Yantanabie, Minnipa, Koongawa (fig. 143) and Buckleboo. Although many of these were classified to CYA, gradation with STR was detected in five individuals from northeast of Yantanabie (fig. 144).

The concept of E. striaticalyx is made even less workable by the inclusion of forms from Carappee Hill and Darke Peak on Eyre Peninsula (11.4.1), represented by the group PCAR. Previously this material has been referred to E. pileata (11.3.5, p. 241) and E. clelandii (Eichler, 1965). Stem glaucousness is fixed at these localities and despite the tendency for smaller fruits, broader pedicels and deeper operculum ribbing, some

specimens are extremely similar to glaucous northwestern forms (fig. 181). Problems in defining limits for E. striaticalyx are exemplified by two extreme forms referred to this taxon under existing concepts (figs 90, 91).

11.3.4 E. cyanophylla

In describing E. cyanophylla Brooker (1977) lists the following features to distinguish it from E. dumosa:

1. broader,bluer leaves;
2. coarser buds and fruits;
3. winter-spring flowering time compared to late summer-autumn in E. dumosa.

From the following discussion it will be apparent that none of these provide a clear or consistent distinction between the two taxa.

Spectrophotometer readings of leaves before removal of wax indicate that the blue colour is not a special character of E. cyanophylla. The proportion of visible light reflected at the blue end of the visible spectrum was found to be no greater for E. cyanophylla than for leaves of E. dumosa with heavy glaucousness. Determinations of wax-contributed reflectance for a sample of representatives of the E. dumosa complex reported in chapter 2 (fig. 20) demonstrate considerable overlap with E. cyanophylla in degree of glaucousness. Concepts of E. dumosa with regard to fruit size have altered since the description of E. cyanophylla (fig. 133). Photographs of type material of E. dumosa obtained from KEW and BM revealed that individuals had larger immature fruits than expected. One specimen at KEW (ex BM) labelled "Interior of Australia - A. Cunningham" was notable for its broad leaves and coarse buds. Consequently, through the assistance of R. Grandison and C. Boomsma, further collections were

Figure 133: Fruit size in E. dumosa and E. cyanophylla.

FL : fruit length

FW : fruit width
(measured at mid-length for TYP groups)

★ individuals of group DUM (from near type locality)

● individuals of group CYA (from near type locality)

E. dumosa (prior to description of E. cyanophylla):

- - - - - range specified by Boomsma (1972)

. . . . . range specified by Hall and Brooker (1974)

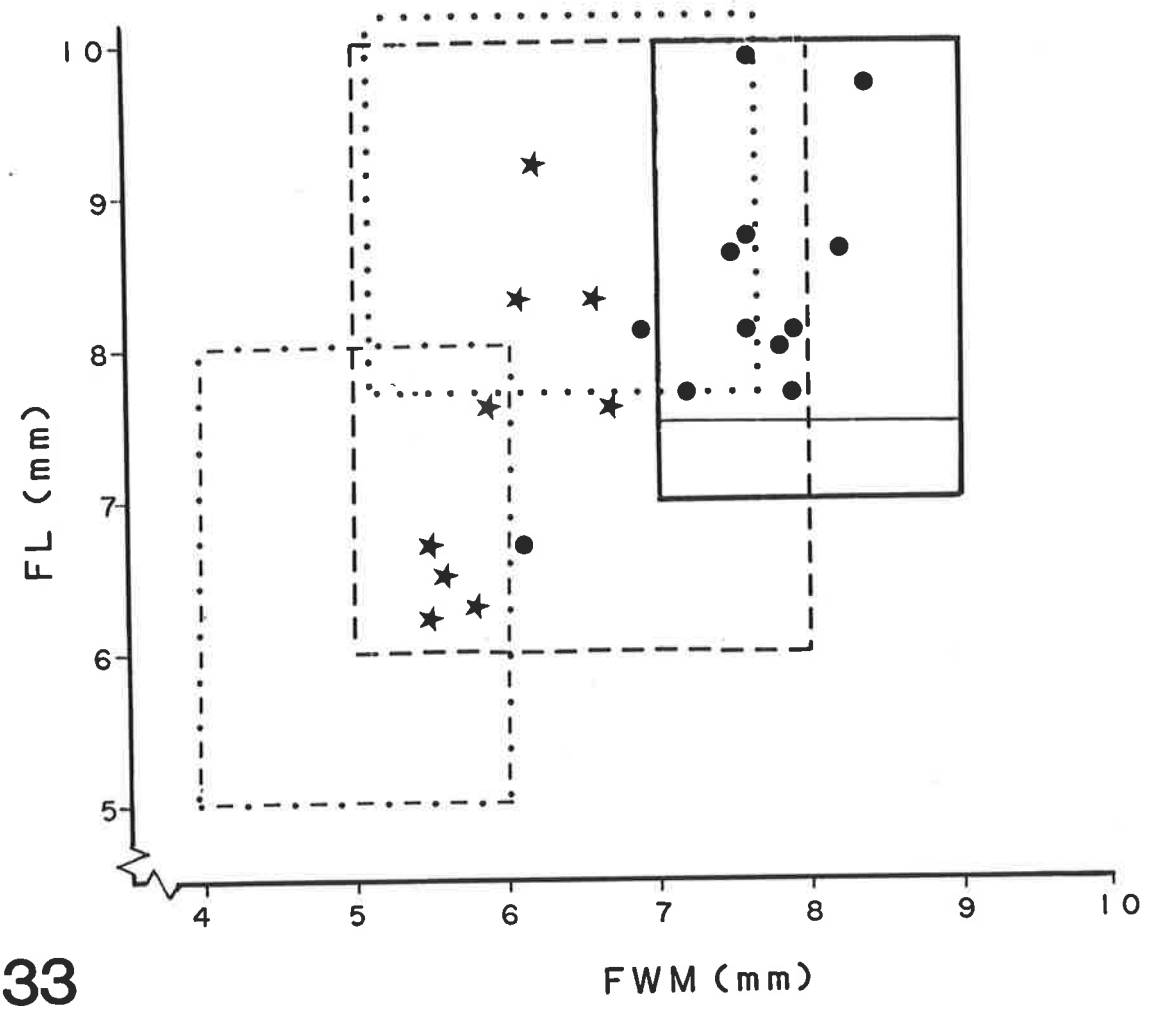
E. dumosa (after description of E. cyanophylla):

_ . _ . _ . range specified by Boomsma (1981)

E. cyanophylla:

——— range specified by Brooker (1977)

——— range specified by Boomsma (1981)
(limits as for Brooker (1977) except lower limit of FL)


10
9
8
7
6
5
FL (mm)
4
5
6
7
8
9
10
FWM (mm)

obtained from near the type locality. These exhibit wide variation in leaf glaucousness and have fruits much closer in size and shape to E. cyanophylla than for material previously regarded as 'typical' E. dumosa (figs 153, 154, 180). Leaves of a bluish colour and equally glaucous as CYA (SG = 2) are present, and there is overlap between DUM and CYA on scores for leaf length and width. A scatter plot of the character scores of FL and FWM for DUM and CYA (fig. 133) shows considerable overlap in fruit length although separation is better on FWM. However, there is a real disjunction in values of PCW, with DUM being 1.3-2.0 mm and CYA 2.4-3.4 mm. The DUM population was found to be flowering in early March, contrary to the annotation of July flowering on the type (7.2, p. 137) that had suggested affinities with E. cyanophylla.

Flowering records from the Murray Region (table 2.3) support the winter-spring flowering time for forms referable to E. cyanophylla but other forms of ssp. dumosa (referred in the past to E. dumosa s.str.) show some overlap although flowering predominantly in autumn. There is also the possibility of indirect gene exchange via E. anceps, here treated as E. dumosa ssp. conglobata. Flowering records for ssp. conglobata generally peak in autumn (table 2.4) as for E. dumosa forms, but in the Murray Region there is a substantial overlap with the flowering of E. cyanophylla forms (table 2.3). Both forms exhibit morphological intergradation with ssp. conglobata. Contrary to the claim by Brooker (1977), distinct forms clearly referable to E. dumosa forms do occur within the area occupied by E. cyanophylla (appendix 2a). There are also intermediate forms amongst material included for numerical analysis and in other collections listed in appendix 2b. Field observations indicate that there is an extensive breakdown in diagnostic characters between Waikerie and Blanchetown. A population sampled from this area (POP: P30) had classifications to both DUM and CYA. Despite the presence of some intergrades, many forms referred

to E. cyanophylla in the Murray Region were classified to the group CYA with a high degree of reliability by all four analyses in appendix 1. Within this region, E. cyanophylla represents a fairly coherent group exibiting definite intergradation in some areas. This is consistent with observed flowering patterns. Although flowering time differences would provide a partial barrier to gene exchange between E. cyanophylla and other forms of the E. dumosa complex, there are sufficient overlaps between some individuals to allow substantial intergradation to occur.

However, with a wider perspective E. cyanophylla is difficult to define taxonomically. Classification results of DPOPDAT analyses provide further evidence of gradation between CYA and DUM outside the Murray Region. There is also gradation with other groups (figs 53,54), consistent with the central position of CYA in the nearest neighbour ordination (fig. 49). CYA has two equal nearest neighbours in D-space: PCAR and P35. Its affinities with PCAR have already been noted (9.3.2, p. 166) and are discussed further in section 11.4.1 . There is level 1 gradation with P35, and in practice E. cyanophylla is sometimes difficult to separate from glaucous-leaved forms in the Flinders Ranges (e.g.: PJL 851, 566; J.B. Cleland, s.n., 25.viii.1966; and J.Z. Weber 2450). The classification of 11 individuals on Eyre Peninsula to CYA shows that E. cyanophylla is not a geographically coherent entity. In the absence of two and three-state characters there is much intermixing of classifications to CYA, PCAR and CAL (appendix 1). These three groups are very similar in morphology apart from the glaucousness characters (figs 179 to 181) and taxonomic segregation is unwarranted.

11.3.5 E. pileata

E. pileata was described by Blakely (1934) from material from Desmond near Ravensthorpe in Western Australia. This locality is the only distribution information that was provided. Blakely claimed: "It is readily distinguished from E. dumosa, with which it has been confused, by the different shaped buds and fruits, particularly in the broad, pileiform corrugated operculum". Later,in 1960, Gardner (Aplin, 1979, p.166) recognized a number of forms with differences in sharpness of hypanthium and operculum ribbing, habit and flowering time. In addition to the common occurrences on clay soils of the Ravensthorpe district, he included forms to the east from the district around Esperance northwards to Salmon Gums and forms to the north from around Boorabbin and Karalee. He distinguished E. pileata from its closest relatives by the following features:

1. it is never a tree but always a mallee;
2. the operculum is broader and shorter than the hypanthium;
3. the operculum is corrugated or ribbed;
4. the fruit is never deeply ribbed or corrugated.

A more extensive distribution was given by Chippendale (1973) who highlighted as a distinctive feature the hemispherical, slightly corrugated operculum that is wider than the hypanthium .

The occurrence of E. pileata in South Australia has been a contentious issue for a long time. The type material of E. dumosa and E. pileata form two reference points in a vast array of complex gradation and variation. The problem is essentially one of defining limits within this variation. The status of E. pileata has varied according to the characters that are emphasized and the placement of cut-off points in the distribution of character states. The following history of the interpretation of this species in South Australia is presented to illustrate the difficulty of

achieving a stable definition within the E. dumosa complex.

The South Australian distribution of E. pileata given by Burbidge (1947) comprises Eyre Peninsula, Yorke Peninsula, Murray Mallee, Encounter Bay,and Kangaroo Island. This interpretation involved a narrow concept of E. dumosa based on material with smooth or almost smooth cylindrical buds collected at Wyalong near the type locality. This view is not supported by a recent collection with conspicuous operculum ribbing from near the type (fig. 215). Burbidge regarded E. dumosa as rare in South Australia, occurring only along the eastern border and near the Murray River. She says: "In this State most of the material classed as E. dumosa has buds with ribbed conical opercula. This agrees with the Western Australian species, E. pileata. There are intermediates in the eastern part of the State, but on the whole the two are reasonably distinct".

Black (1952) followed Burbidge's treatment for E. pileata but not for E. dumosa which he also gave a wide distibution in South Australia, extending as far west as the Great Australian Bight. Black referred to the glaucous-stemmed material on Eyre Peninsula under E. pileata and applied the name "var. argentea" to one herbarium specimen: J.M.Black s.n., 30.i.1951 (AD 97631412). Ooldea was also cited as a locality for E. pileata.

Boomsma (1960) followed Burbidge's more restricted interpretation of E. dumosa with the statement: "Smooth-budded specimens are found in eastern localities of South Australia, but specimens which are not smooth-budded are usually referable to other species". He also referred to occasional specimens of E. pileata collected from the far north of South Australia.

Later, Boomsma (1969) reported that L. A. S. Johnson in 1965 did not accept E. pileata for this State on the grounds that: " this species has a characteristic pileate bud and that South Australian material is not in

agreement with that from the type locality in Western Australia". Later, Pryor and Johnson (1971) proposed treating E. pileata as a subspecies of E. dumosa and indicated its occurrence in South Australia.

Boomsma (1972, p.8) excluded E. pileata from his handbook due to lack of satisfactory records for South Australia. He stated that he included the large-fruited form which was previously referred to E. pileata by Burbidge in 1947, under E. dumosa.

Chippendale (1973) believed that most South Australian records of E. pileata may refer to a related undescribed species, but accepted several records as being authentic. He listed two localities for these:

1. 32 km W of Colona H.S. (Nullarbor Region);
2. between Kimba and Iron Knob (Eyre Peninsula Region).

Brooker (1977) placed large-fruited forms from the Murray Region that had been included in E. pileata, into a new species, E. cyanophylla. In this paper he regarded E. pileata as extending to southern and eastern Eyre Peninsula and interpreted material on Yorke Peninsula as intergrades between E. pileata and E. dumosa. In a key to South Australian Dumosae, he distinguished E. pileata from E. dumosa by its green and more or less glossy leaves compared to grey-green or bluish dull leaves in E. dumosa.

A wider distribution for E. pileata in South Australia is implicit in some recent determinations and confirmations made by L.A.S Johnson & D. Blaxell (-.viii.1982 and -.ix.1982). Of twelve South Australian collections of Dumosae from the Woods and Forests Herbarium, selected by Mr C.D. Boomsma because of difficulties in their identification, three were determined as E. pileata and another three as intergrades between E. pileata and E. anceps or E. dumosa. Eyre Peninsula Region was represented by collections of E. pileata from Talia, Cummins area, and near Kimba. Determinations as intergrades between E. pileata and E. anceps were applied to

collections from near Tarlee in the Northern Lofty Region (C.D. Boomsma s.n., 22.x.1947) and at Goolwa in the Southern Lofty Region (C.D. Boomsma s.n., 22.vi.1946). A specimen from Wanbi in the Murray region (C.D. Boomsma s.n., 5.iv.1947) was also determined as E. pileata. This has dull glaucous foliage (contrary to E. pileata in Brooker's (1977) key) and closely resembles E. cyanophylla apart from the smaller leaves and fruits. These determinations of Johnson and Blaxell denote a much wider circumscription of E. pileata than that of Boomsma or Chippendale.

A wide range of non-glaucous material in Western Australia has been referred to E. pileata. In considering this material, occurrences are excluded east of the western margin of the Nullarbor plain at about longitude 124° (following Parsons' (1970) use of a geomorphological definition of the Nullarbor). This avoids confusion with E. calcareana or other forms associated with calcareous soils.

A pileate operculum is not a consistent feature of this material. Even within the PIL population there are more conical and sub-rostrate operculae as well as hemispherical ones (figs 191, 192). Elongate,conical operculae are present on a specimen (PJL 1552) from 64.9 km E of Norseman (fig. 193). Together with the shortly and broadly pedicellate fruits this suggests affinities with ssp. fraseri. Many of the northern and eastern populations have operculae not conspicuously wider than the hypanthium and lacking deep ribbing (figs 194, 189). Fruits vary greatly in size and shape (figs 182 to 187). Compared to other forms of ssp. dumosa, there is a tendency for fruits that expand toward their rim (reflected in lower scores of FWMR), but this character is unreliable. Small-fruited forms (PJL 1354, 1353) growing on Peak Charles, an inselberg southwest of Norseman, are morphologically very similar to some individuals in the Gawler Ranges of South Australia, for example PJL 967 (figs 188 to 190). At Peak Charles there are also forms with fruits more typical of the

eastern E. pileata populations (PJL 1348, 1349). Habit ranges from low mallees 3-4 m tall in the PIL population at Desmond (fig. 201), to trees of 11 m (reported in error as 15 m by Boomsma (1979)) with trunks 3 m tall in a population 14 km NW of Norseman (fig. 202). The mallees at Desmond have foliage held more or less erect on the branches. This was regarded as a significant character by Chippendale (1973) and Brooker (1977, p.17). However, erect foliage is not a feature in the eastern and northern populations. The colour of the operculum, stated to be red by Chippendale, was found to vary. The mature operculae of some individuals in the PIL population were yellow.

The CVA classification results indicate that E. pileata overlaps with other groups even within the limits of the Western Australian region defined above. Only 12 of the 23 unassigned individuals determined as E. pileata were classified to PIL. Nine of the remainder were classified to CAL, eight of these being supported by operculum data (appendix 1).

Some South Australian specimens are more similar to the type material of E. pileata in bud morphology than much of the Western Australian material. This is the case in P35 and other populations with deeply ribbed operculae (figs 197 to 200) from between Quorn and Telowie Gorge in the southern Flinders Ranges. Group P35 differs from PIL principally in having variable leaf glaucousness (LG : 0,1,2) rather than consistently non-glaucous leaves. In the TYPDAT CVA, two of the four P35 individuals were classified to PIL. Unassigned individuals classified to P35 in the DPOPDAT CVA cover a wide area in South Australia and Western Australia (table 11.1), but few are supported by operculum data. A taxon based on P35 would not be geographically discrete nor easily recognizable without bud material.

Many individuals classified to P35 in the DPOPDAT analysis were classified to PIL in the TYPDAT analysis where P35 was not defined. Fifteen individuals from Eyre Peninsula were classified to PIL by the TYPDAT CVA although none are supported by operculum data. Hence E. pileata cannot be excluded from South Australia on the basis of fruit and leaf morphology. Some specimens with buds from Eyre Peninsula that were not measured for analysis appear closer to PIL than any other group, (e.g. PJL 636/10 km S Tumby Bay). The specimen: PJL 1225/2.2 km N Mt Hall, Western Eyre Peninsula, also has strong affinities with PIL, particularly in the operculum that is wider than the hypanthium (fig. 216).

11.3.6 E. calcareana

The problems in defining E. dumosa and E. pileata were compounded by the description of a new species, E. calcareana by Boomsma (1979) which is to a large degree intermediate between them. The description was based on South Australian material from between the southern boundary of the Nullarbor Plateau and the Great Australian Bight. Recently Boomsma (1981) gave a wider distribution extending from Cocklebiddy near the western margin of the Nullarbor in Western Australia to near Pt Kenny on the central west coast of Eyre Peninsula. Boomsma (1979) admitted that E. calcareana was close to E. pileata but avoided subspecific treatment due to "its distinctive features". He made or implied the following distinctions between E. calcareana and E. pileata respectively:

1. usual tree habit compared to usual mallee habit;
2. fresh leaves scarcely shining or glossy rather than lustrous;
3. fruit markedly costate rather than smooth;
4. leaf length/breadth ratio (6-) 7 (-9) compared to (5-) 6 (-9);
5. operculum not always wider than hypanthium rather than consistently so.

Variation in habit within the E. dumosa complex does not deserve taxonomic significance. Forms referable to E. calcareana show a similar range in habit to that described above for E. pileata, and mallee forms are not uncommon within the distribution given by Boomsma. In a population sampled on limestone near the coast at the Western Australia-South Australia border, mature mallees only attain a height of 2 - 4.5 m. Although both CAL and PIL have consistently non-glaucous leaves, no distinction can be made on leaf texture. The TYP groups and similar material classified to them, have overlapping ranges for values of cuticular sculpturing (CS). The range for E. calcareana is CS : 1.0 - 2.4 , and for E. pileata, 1.1 - 3.4 . The distinction on fruit ribbing (FR) is unreliable, as fruits without regular ribbing (FR : 0) were present in CAL and much similar material. Data obtained from the scores for LL and LW do not support a higher length/width ratio for E. calcareana. A mean ratio of 5.8 was obtained for CAL compared to 6.7 for PIL. No distinction can be made on operculum width compared to hypanthium because this character is also variable in E. pileata.

Group CAL has intermediate scores for 8 of the 11 characters that I consider to exhibit major differences between DUM and PIL, confirming its intermediate position between these groups (table 11.2). In D-space CAL is closer to PIL, and CAL-PIL is by far the closest nearest neighbour pair. Gradation at levels 1 and 2 was detected between CAL and PIL in 24 unassigned individuals. One defined individual was misclassified, and CAL is the only TYP group showing misclassification with the full character set (table 9.2). The TYPDAT results indicate a much wider distribution than that given by Boomsma. Classifications to CAL are represented throughout the whole of Eyre Peninsula (fig. 129) as well as in many other regions of South Australia and Western Australia (table 11.1). In practice, it is impossible to distinguish much material in the

Table 11.2: Mean character scores for the TYP groups: PIL,CAL and DUM. Characters exhibiting major differences between PIL and DUM, and the more intermediate values for CAL, are underlined. (Table 4.1 provides key to character codes and to units of measurement.)

Character:	LL	LW	PTL	VA	LTH	LWM	CS	LG	SG	BB
PIL:	86	13.0	14.4	82	.47	.87	2.5	0	0	0
CAL:	105	18.2	21.3	65	.50	.86	1.3	0	0	0
DUM:	97	18.7	18.4	57	.40	.80	3.8	1.3	0	0

FWM	FL	FWL	FWMR	PCL	PCW	DW	DDR	VN
6.5	6.8	1.08	.89	3.3	2.2	1.2	.12	4.16
6.9	7.3	1.00	.95	3.7	2.9	.9	.12	4.04
6.0	7.4	.79	1.05	3.3	1.7	.7	.16	4.03

PL	PWS	PW	FR	NPU	OLW	OWM	OPR
10.7	1.68	2.7	.6	2.0	.86	.92	7.6
12.1	1.70	2.8	1.6	2.0	.87	.86	5.5
13.6	1.85	1.8	.2	2.1	.96	.58	2.4

South-east Region from E. calcareana as described by Boomsma. Not only is E. calcareana not a discrete geographical entity, but there is great morpholgical variation in Dumosae occurring within the distribution ascribed to it by Boomsma (figs 205 to 207). Although similar in field habit, extreme differences in fruit size and other characters are evident between forms on calcarenite dunes near Coorabie in South Australia and those growing on calcrete at the base of the Hampton Scarp at Madura (figs 92, 93).

A wide interpretation of E. pileata, as adopted by Johnson and Blaxell (11.3.5, p. 242), makes it difficult to accommodate E. calcareana as a separate species since other forms equally distinct are placed in E. pileata. Analyses were performed excluding CAL as a defined group. This resulted in many more classifications to PIL but there was still substantial gradation and interspersion with other groups. On Eyre Peninsula the spatial intermixing of DUM and PIL was maintained and no meaningful geographic patterns were apparent.

There are no major disjunctions in the variation pattern for leaf surface texture (CS), operculum shape, operculum ribbing, fruit shape, or pedicel width, to permit anything more than arbitrary subdivisions to be made within this complex. Recognition of species within the complex is made even more difficult by the strong intergradation of sessile-fruited forms referred to as E. anceps.

11.4 Relationships of informal taxa

11.4.1 Carappee Hill form

Material from Carappee Hill and Darke Peak on Eyre Peninsula, which is represented in this study by the group CAR, has often been determined as a

new species. It has also been previously treated as E. clelandii (Eichler, 1965), as a form of E. pileata by Black (11.3.5, p. 241) or even as E. rugosa in some determinations. The results of analyses performed here indicate that its closest affinities are with E. cyanophylla and E. striaticalyx . The link with E. striaticalyx is geographically plausible, but there are stronger affinities with E. cyanophylla if stem glaucousness is ignored. A comparison of fruits (figs 180, 181) reveals strong similarity of form between PCAR and CYA. The close relationship is demonstrated by the following results of CVA after removal of the two and three state characters:

1. PCAR and CYA are the closest nearest neighbour pair;
2. there is a high degree of gradation between them in the classification of DPOP groups (table 9.2);
3. there is much gradation and intermixing of them in unassigned individuals from Eyre Peninsula and Murray regions (appendix 1).

The proposed treatment of the glaucous-stemmed Eyre Peninsula material as a subspecies of E. cyanophylla (6.1) is consistent with these affinities. However, it is not supported by the complex relationships revealed in the LGFDAT analysis, nor by the characters of leaf glaucousness and flowering time. Leaf glaucousness is generally not as heavy in the PCAR populations as in E. cyanophylla. Nine of the 12 CYA individuals were scored as LG = 2 while eight of the 11 PCAR individuals were scored as LG = 1. Unlike typical E. cyanophylla which has a winter-spring flowering period, flowering in the PCAR populations is probably restricted to the period December-January. Flowering has been recorded for outliers in April and October (table 2.3).

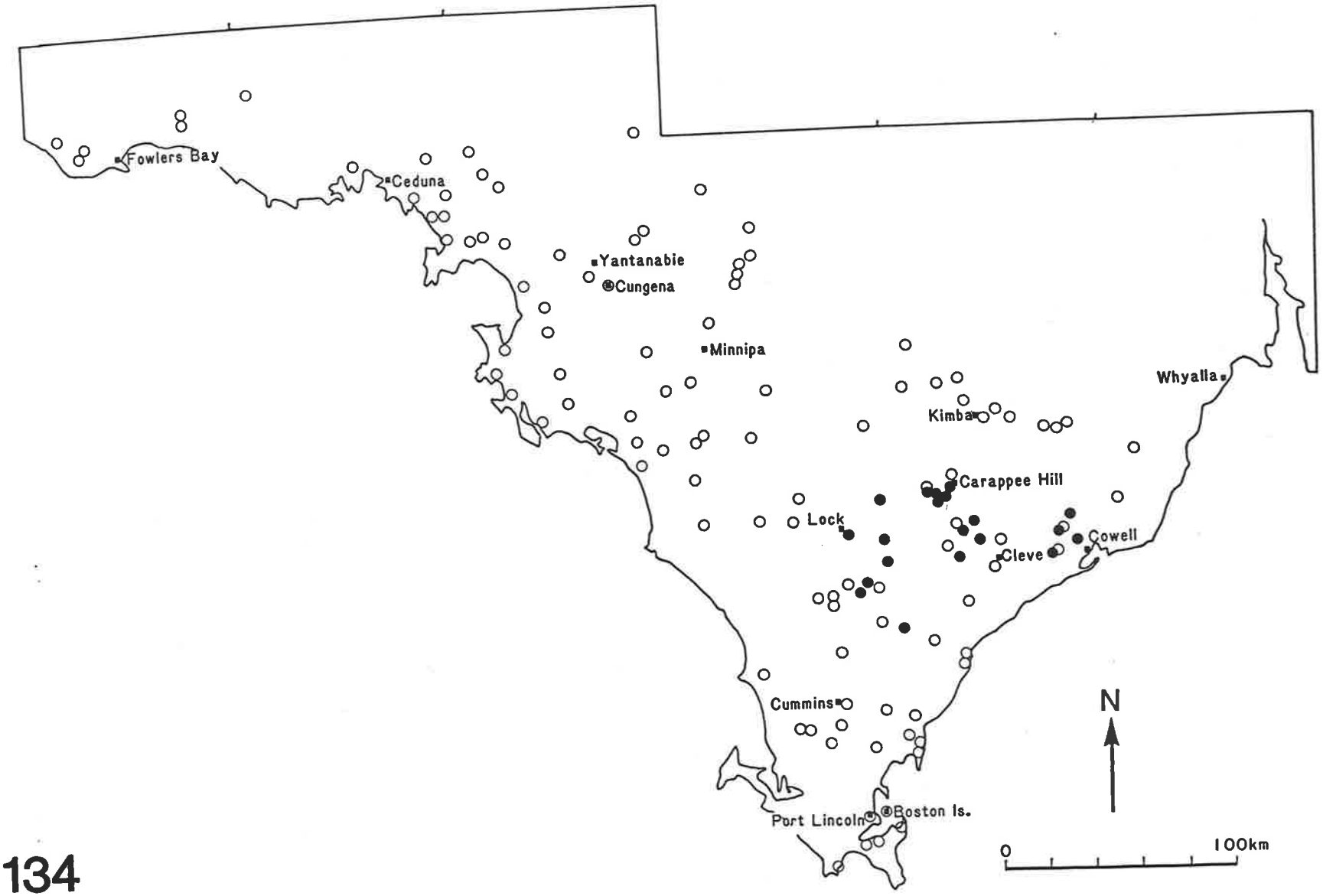
I believe the treatment of the PCAR populations as a new species is also unacceptable due to the wide diversity of forms with glaucous stems, particularly in the large number of outlying occurrences (fig. 134,

Figure 134: Distribution records for E. dumosa on Eyre Peninsula showing extent of occurrences of glaucous-stemmed forms.

Records are based on collections in appendix 1, together with other herbarium specimens and field records of P.J. Lang.

o forms without stem glaucousness (SG = 0)

● forms with stem glaucousness (SG = 1)


Fowlers Bay
Ceduna
Yantanabie
Cungena
Minnipa
Whyalla
Kimba
Carappee Hill
Lock
Cowell
Cleve
Cummins
Port Lincoln
Boston Is.
N
100km

appendix 3). Large-fruited forms on the plain west of Carappee Hill (often with prominent fruit ribbing) are in marked contrast to small-fruited forms occurring in many outlying populations (figs 208 to 210). Habit varies from straggly thin-stemmed mallees on the slopes of Carappee Hill, to robust small tree forms with coarse foliage on the adjoining plain, or mallees that are indistinguishable from typical ssp. dumosa at outlying localities (figs 211 to 214). Stem glaucousness is consistent for PCAR and all other material of ssp. dumosa from the same localities, although two collections are known with only very light glaucousness (PJL 1045; D.E.Symon 9012,(ADW)). However, it is not consistent in most of the outlying populations. In one population 12 km NW north of Cleve, stem glaucousness was present in only five individuals out of a sample of 52 . This variation gives the impression of a 'floating gene' for stem glaucousness as the principal link between these populations. (See section 15.2.)

11.4.2 "E. redimiculiphloia"

The name "E. redimiculiphloia" has been used for a rather heterogenous assemblage of of Western Australian collections from the Coolgardie District. Gardner first applied the name on several herbarium sheets in 1953. One specimen (J.K.Frank s.n.,-.vii.1928), from Bullabulling is recorded as being 25-30 ft (7.6-9.1 m) tall with white bark. After the name "E. redimiculiphloia" Gardner added the note: " The obvious approach is with E. clelandii". This collection differs from the others in its non-glaucous stems and leaves, larger campanulate fruits and hemispherical operculae. I believe it has more obvious affinities with E. pileata and is consistent with some northern forms that have been referred to this name. However, it is outside Gardner's concept of E. pileata which he regarded as being always a mallee and only reaching a height of four metres

(Gardner, 1960). The collection: M.I.H. Brooker 4539, determined by Brooker as possibly "E. redimiculiphloia", is also most similar to E. pileata. The locality is given as 9.7 km from the Norseman - Coolgardie road, 10.6 km from Norseman. This is probably near the population of tree forms similar to E. pileata that includes PJL 1550 (p. 234). The Brooker 4539 specimen was classified to PIL by all the CVA's.

The other collections determined by Gardner have glaucous stems and rostrate operculae. They appear very similar to E. dumosa ssp. clelandii but differ presumably in the absence of a blackbutt. One of these (C.A.Gardner 11153/13 km NW of Norseman) was classified by the DPOPDAT CVA to PIL and, after removal of the 2 and 3-state characters, to KON (fig. 217). The other two (Gardner s.n.,-.ix.1955; 11187) occur between Southern Cross and Coolgardie: at Yellowdine and 1.6 km W of Bullabulling respectively. Bullabulling is within a few kilometres of the population P179 where there is a breakdown in the presence of blackbutts that was interpreted as result of gradation between CLE and SHE (10.6, p. 201).

More recently, the determination "E. redimiculiphloia nom. mss. C.A. Gardner" was applied by Chippendale to the collection: G.M.Chippendale 360 , from 6.1 km NNE of Butcher Bird Battery, 155 km N of Southern Cross. This specimen is almost identical with material of the CLE population. As with most material referred to "E. redimiculiphloia", no information is provided on habit or bark characters, making identification uncertain. Material without a blackbutt and referable to "E. redimiculiphloia" can be easily accommodated in the complex of forms treated here as E. dumosa ssp. dumosa.

11.5 Conclusion

The variation encompassed by the forms discussed in this chapter is complex. Although there are some obvious nodes of variation and geographical clustering of similar forms, the multidirectional relationships and exceptions to geographical patterns preclude any simple taxonomic groupings even if a high level of intergradation is permitted. The evidence is that the existing species have not been, and can not be, applied consistently.

Figures 135 to 217: These mainly illustrate variation within Eucalyptus dumosa ssp. dumosa as discussed in chapter 11. This name applies to all the material illustrated here unless otherwise indicated.

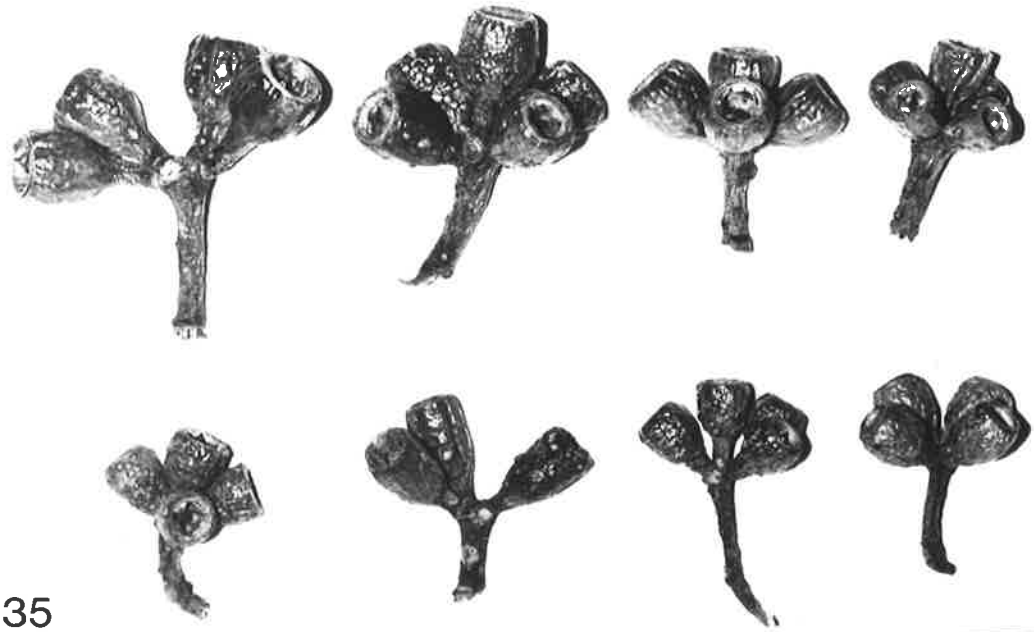
Scale bars: 1 cm

Figures 135 to 137: Within-locality variation in fruit morphology on Eyre Peninsula.

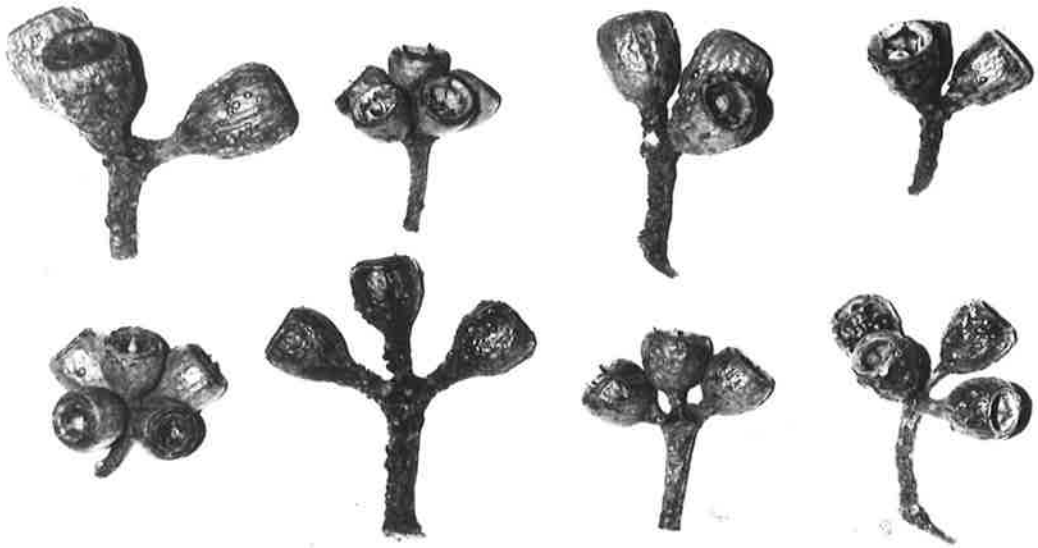
135: 2.8 km SE Cummins (P82)
Selected extremes in fruit shape and size from a random collection of umbellasters representing n = 35 individuals.

136: c. 12 km NW Cleve (P77)
Selected extremes in fruit shape and size from a random sample of n = 37 individuals.

137: S of Pt Kenny
Selected extremes showing variation in fruit shape and exsertion of valves from a random sample of n = 24 individuals.



135



136



137

Figures 138 to 141: Gradation between sessile and pedicellate forms of E. dumosa.

(E. dumosa ssp. conglobata, ssp. dumosa and intergrades)

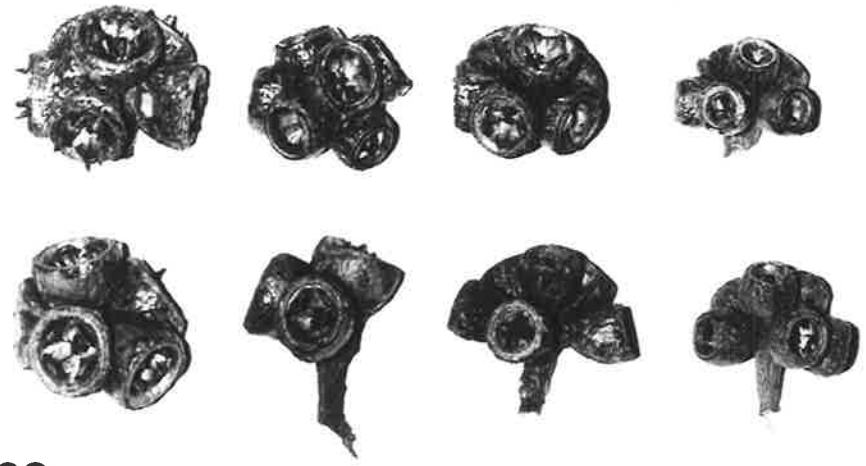
138: 4 km W Pt Lincoln PO
Selected extremes from a random collection of umbellasters, n = 25 individuals.

row 1: variation in fruit size
row 2: PJL 1109; three individuals with longer peduncles (note greater length/width ratio fruits in middle specimen)

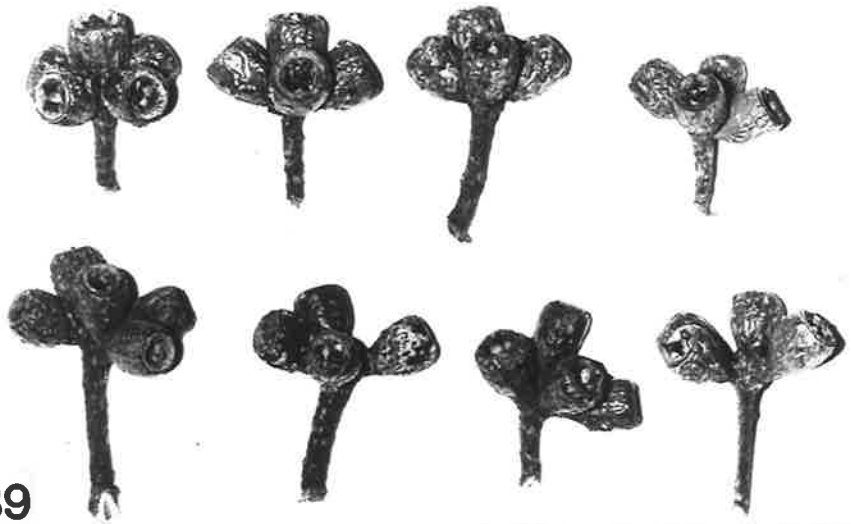
139: 2 km SE Coonalpyn
Umbellasters showing gradation from sessile to shortly pedicellate fruits. Selected from a random sample of n = 25 individuals.

140: Folland Park, Enfield
Umbellasters showing gradation from sessile to pedicellate fruits. Selected from a random sample of n = 22 individuals.

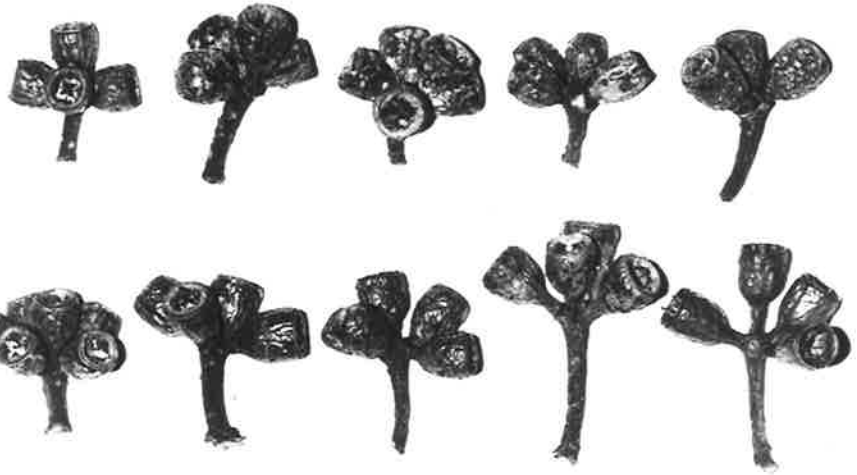
141: Cungena
As above. Selected from a random sample of n = 26 individuals.



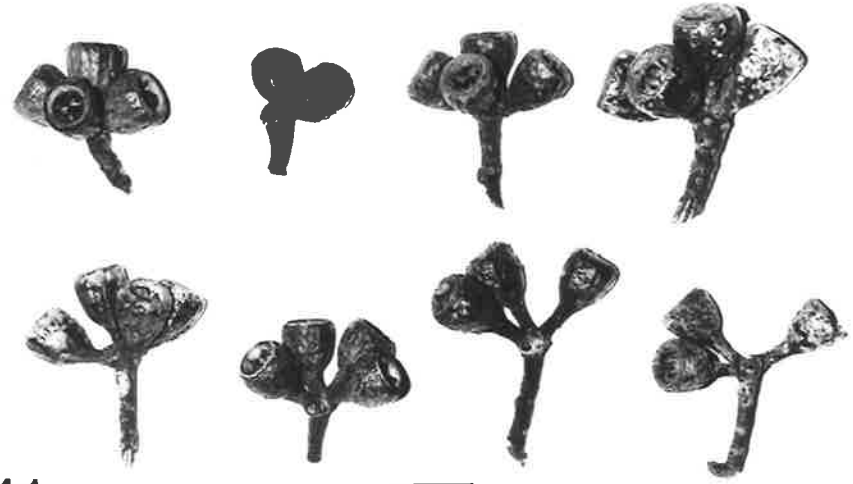
138



139



140



141

Figures 142 to 145: Between-locality variation in fruit size on Eyre Peninsula.

142: 20.5 km N Cummins (P81)
Selected large-fruited forms from a random sample of n = 17 individuals

143: Koongawa (P105)
Selected large-fruited forms from a random sample of n = 21 individuals

144: 26.5 km NE Yantanabie (P57)

PJL 998 to 1002

145: 54 km SW Whyalla S (P92)

PJL 1153 to 1157

Populations P81 and P92 have green non-glaucous leaves with low cuticular relief, while P57 and P105 have glaucous leaves with high cuticular relief. Individuals of P57 have the most sharply delineated pedicels and displayed affinities with group STR in classification results.



142



143



144



145

Figures 146 to 149: Extremes of variation in operculum shape of E. dumosa ssp. dumosa between individuals of the same populations.

146: Telowie Gorge (Northern Lofty)

R.J. Davies s.n., A, B

147: Gammon Ranges (Flinders Ranges):

left : R.J. Davies 12.x.1980 A/Mainwater Pound
right : R.J. Davies 12.x.1980 B/Sambot waterhole

148: 6 km SW Coorabie (Eyre Peninsula)

individual adjacent to PJL 1193; PJL 1193

149: W of Wyola Lake (North-western)

T.E. Dennis 215, 223

Figure 150: E. lesouefii

5.2 km SW Kalgoorlie (LES)

buds : PJL 1526, 1523
showing variation in operculum shape from strongly to weakly rostrate

fruits : PJL 1526
showing depth of ribbing

Figure 151: E. dumosa ssp. conglobata.
K. Holden, 23.8.73/Boston Island (WF)

Conglomerate umbellaster with compressed fruits.

Figure 152: E. dumosa ssp. dumosa
PJL 1380/0.6 km S Desmond (PIL)

Umbellaster bearing normal and dwarf fruits.



146



147



148



149



150



151



152

Figures 153, 154: Fruits and buds of individuals from near the type locality of E. dumosa.

153: 8.2 km W Ungarie

fruits: R. Grandison, 5.i.1980, A to B
buds: " " " " "

154: 7.5 to 9.0 km W Ungarie

fruits: P.L. Milthorpe & G.M Cunningham 1, 2, 3, 4
" " " " 5, 6, 7

buds: " " " " 1, 2, 6



153



154

Figures 155 to 156: Gawler Ranges and Flinders Ranges forms previously referred mainly to E. dumosa.

155: Scrubby Peak, Gawler Ranges (P53)

Fruits from a highly variable population comprising non-glaucous (LG = 0) and glaucous-leaved forms (LG = 1,2).

PJL 975, 976, 977, 978, 979, 980

(LG: 2, 0, 0, 1, 0, 2)

156: Kododo Hill, Gawler Ranges (P52)

PJL 966, 967, 968, 969, 970, 971, 972

(LG: 2, 0, 2, 2, 1, 1, 1)

157: 2 km SE Warraweena HS, Flinders Ranges (P25)

PJL 853, 854, 856, 859, 860

(LG: 0, 0, 2, 2, 0)



155



156



157

Figure 158 to 161: Fruits of forms previously referred to E. dongarraensis.

158: 22 km S Dongara (DON)
(in the vicinity of the type locality for E. dongarraensis)

PJL 1463 to 1467

159: 6.2 km N Coorow (P157)

PJL 1457 to 1461

160: miscellaneous localities

row 1: 13.5 km WSW Yuna
PJL 1469, 1470

row 2: Pithara
PJL 1451, 1452

row 3: 20 km S Overlander
C.D. Boomsma WA 45/76



158

DON





159



160

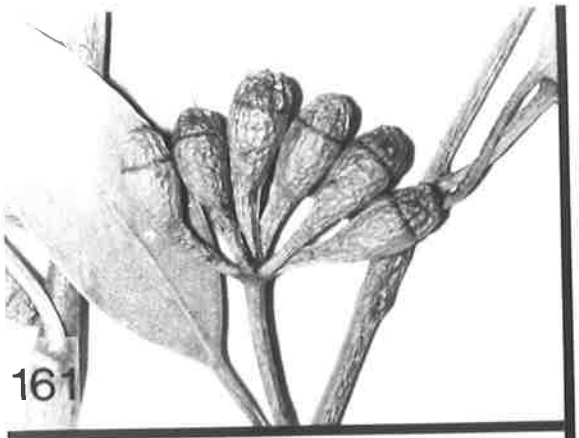
Figures 161 to 163: Forms previously referred to E. dongarraensis.

161: C.D. Boomsma WA45|76/20 km S Overlander

162: PJL 1452/Pithara

163: PJL 1451/Pithara

Figure 164: South Australian form with bud morphology convergent with E. dongarraensis.



161



162





163



164

Figures 165 to 168: Gradation between forms previously referred to *E. dongarraensis* and *E. sheathiana*.

165: PJL 1463/22 km S Dongara (DON)

Form from the vicinity of the type locality of *E. dongarraensis*.

166: PJL 1543/Pithara

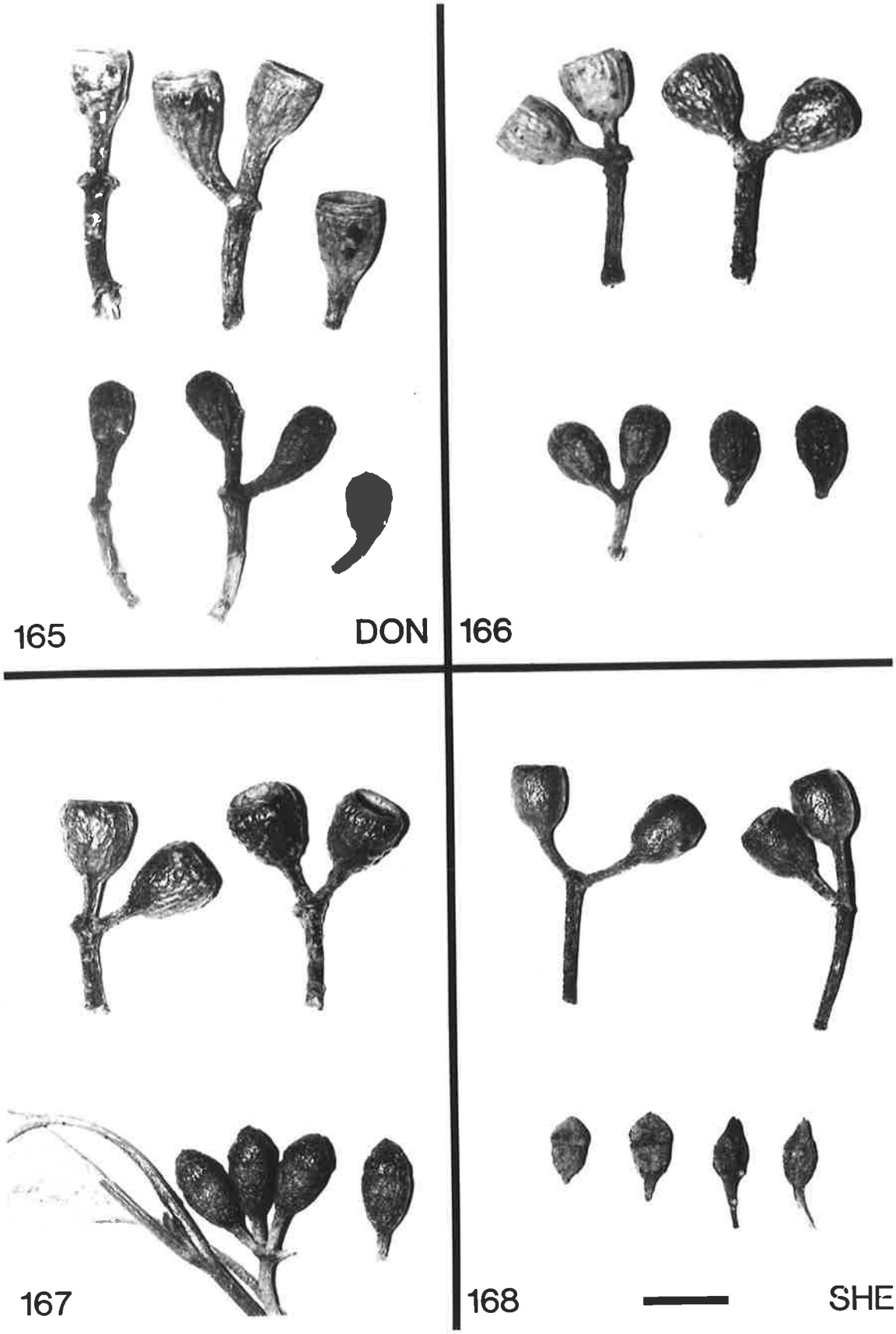
Form similar to group P157.

167: PJL 1450/5.3 km W Wyalkatchem

Intermediate form.

168: PJL 1447/0.5 km S Nukarni RS (SHE)
(right pair of buds from adjacent individual)

Form representing typical *E. sheathiana*.


165
DON
166
167
168
SHE

Figures 169 to 171: Forms previously referred to E. sheathiana.

169: Populations similar to type material of E. sheathiana.

row 1 : 0.5 km S Nukarni RS (SHE)
PJL 1447, 1448, 1449A, 1449B, 1449C

row 2 : 1.7 km W Carrabin (SHE)
PJL 1492 to 1496

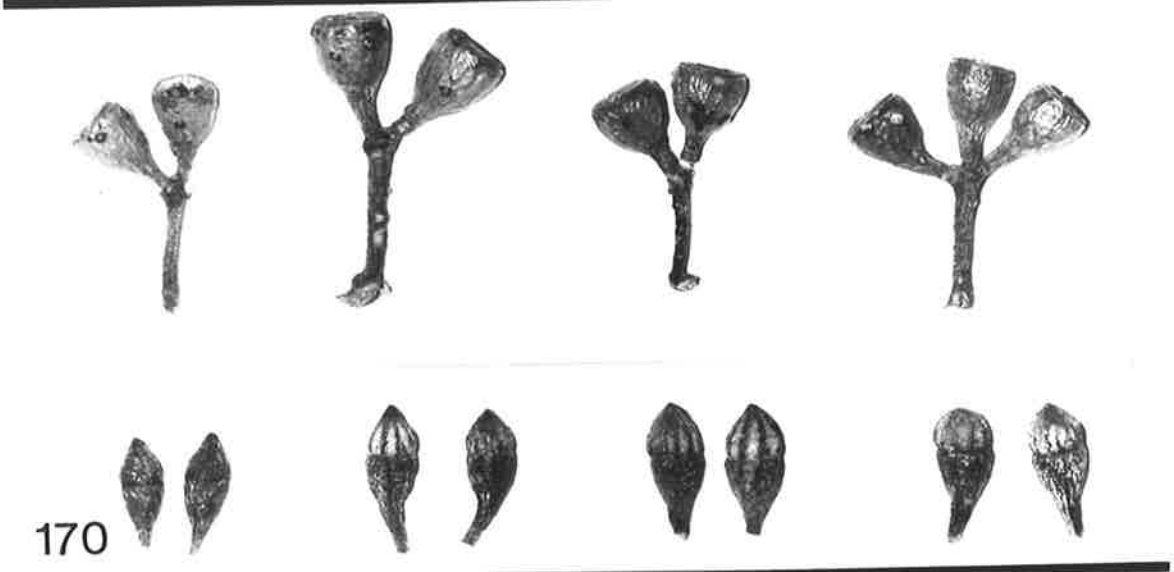
170: 14.7 km E Lake Grace (P176)

PJL 1416 to 1419

171: 10.6 km E Southern Cross (P152)

PJL 1497 to 1501


169
SHE


170


171

Figure 172: Mixed population of non-glaucous (SG = 0) and glaucous-stemmed forms (SG = 1) previously referred to *E. pileata* and *E. sheathiana* respectively.

0.4 km N Burngup (P177)

row 1 : fruits PJL 1421, 1425, 1426, 1423
row 2 : buds " " " "
(SG: 0, 0, 0, 0)

row 3 : buds PJL 1422;
fruits 1422, 1427, 1428
(SG: 1;
1, 1, 1)

Figure 173: Forms from miscellaneous localities previously referred to *E. sheathiana*.

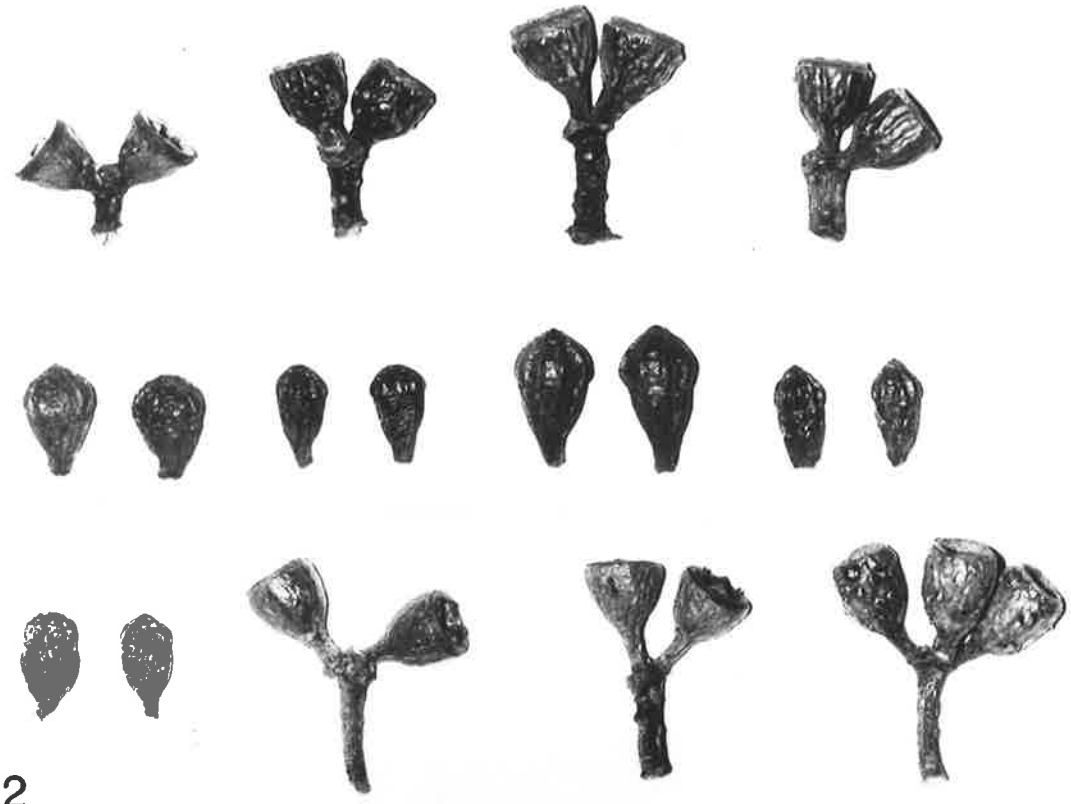
PJL 1420/8.9 km S Burngup
PJL 1505/1.3 km E Ghooli
PJL 1426/2.6 km NW Kulin

Figure 174: Mixed population of forms with and without blackbutts (BB = 1, 0) previously referred to *E. clelandii* and *E. sheathiana* respectively.

(*E. dumosa* ssp. *clelandii* intergrade ssp. *dumosa*)

1.3 km W Bullabulling (P179)

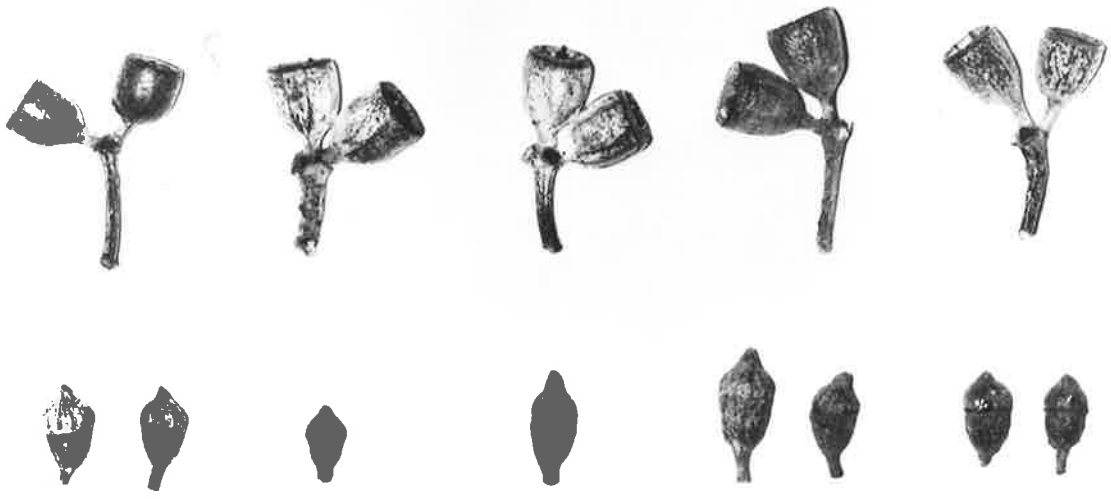
fruits: PJL 1514, 1515, 1518, 1516, 1517
buds: " " " " "
(BB: 1, 1, 1, 0, 0)



172



173



174

Figures 175 to 178: Large-fruited forms from Victoria Desert sand dunes previously referred to E. striaticalyx.

175: L.D. Williams 10776/20 km SW Vokes Junction

176: L.D. Williams 10492/130 km N Cook (PCVH)

177: T.E. Dennis 188/131 km N Cook (PCVH)

178: T.E. Dennis 189/131 km N Cook (PCVH)





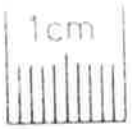
175



176

PCVH





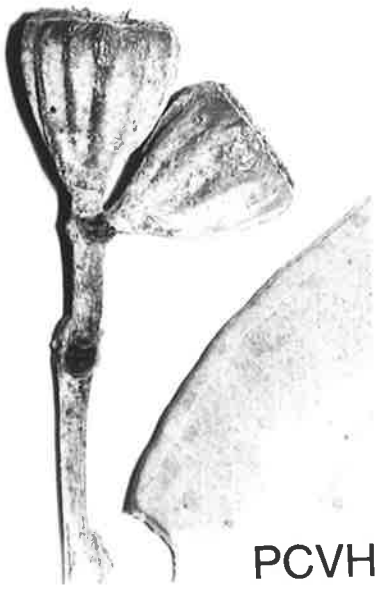


177

PCVH



178



PCVH

Figure 179: 44.1 km W Nundroo (CAL)
Population from near type locality of E. calcareana.

PJL 1321 to 1325

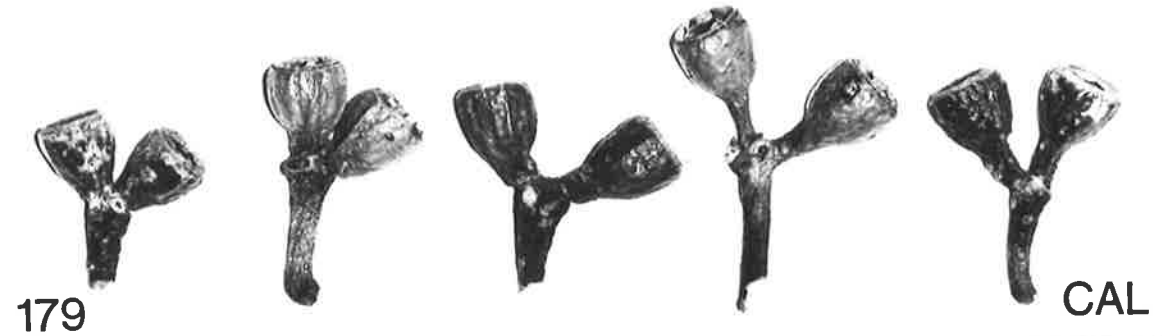
Figure 180: c. 3 km N Berri (CYA)
Population from near type locality of E. cyanophylla.

row 1 : R.M. & W.R. Barker 403A to 403E
row 2 : " " " 403F

Figure 181: Eyre Peninsula glaucous-stemmed forms from populations represented in group PCAR.

row 1 : Carappee Hill (PCAR)
J.P. Conquest 24.x.1977;
PJL 1044, 1045, 1047, 1048

row 2 : Localities between Darke Peak and Carappee Hill (PCAR)
PJL 1050; C.D. Boomsma 420A, 420B, 423; PJL 1051



179

CAL





180

CYA





181

CAR

Figures 182 to 187: Fruits of forms previously referred to E. pileata and occurring west of the Nullarbor Plain.

182: 0.6 km S Desmond (PIL)
Population from near the type locality of E. pileata.

PJL 1379 to 1383

183: Fruits from miscellaneous localities in eastern part of Roe District.

184: 18.0 km W Bullabulling (P124)

PJL 1509 to 1513

185: 39.4 km S Norseman (P120)

PJL 1343 to 1347

186: Peak Charles (P121)

PJL 1348, 1349, 1353, 1354

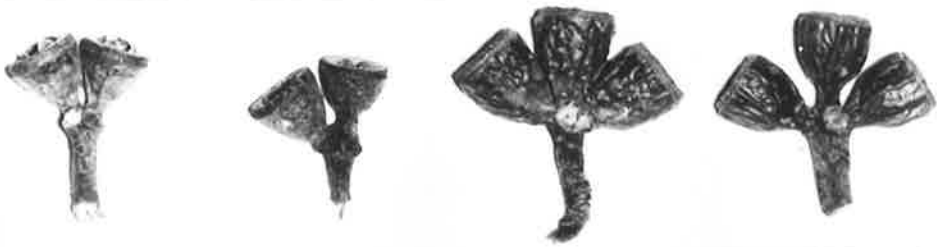
187: Miscellaneous collections from Coolgardie District.

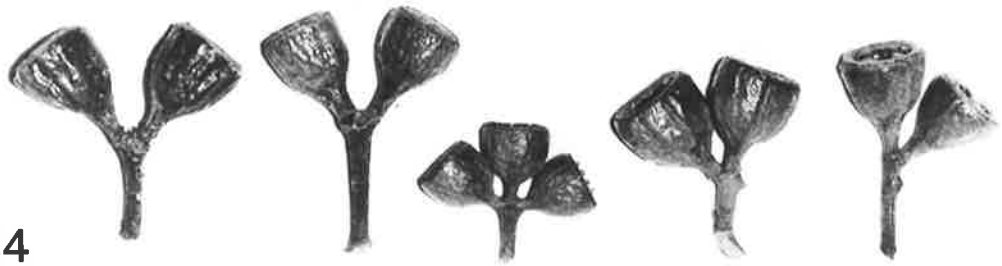
64.9 km E Norseman
PJL 1552, 1553

13.5 km NW Norseman
PJL 1550

3.1 km E Boorabbin
PJL 1508


182
PIL


183


184


185


186


187

Figures 188 to 190: Similarity between small-fruited forms from Gawler Ranges (Eyre Peninsula Region) and Peak Charles (Roe District).

188: PJL 967/Kododo Hill, Gawler Ranges

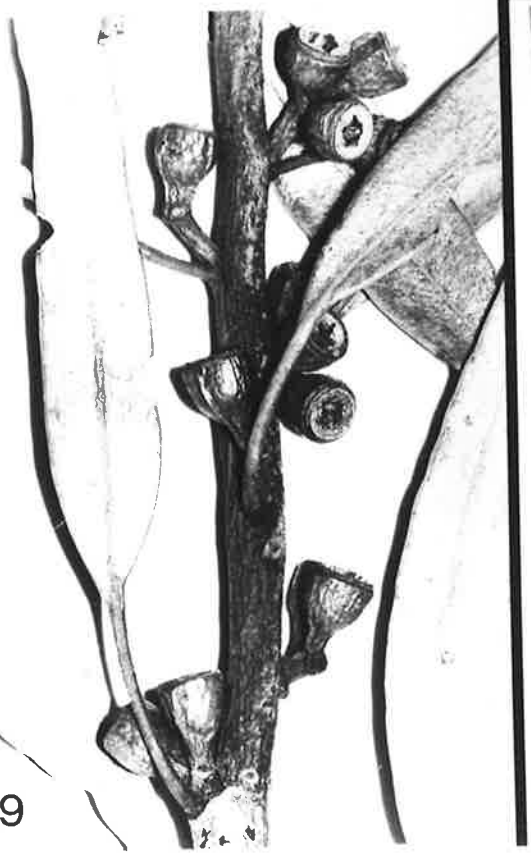
189: PJL 1353/Peak Charles

190: PJL 1354/Peak Charles



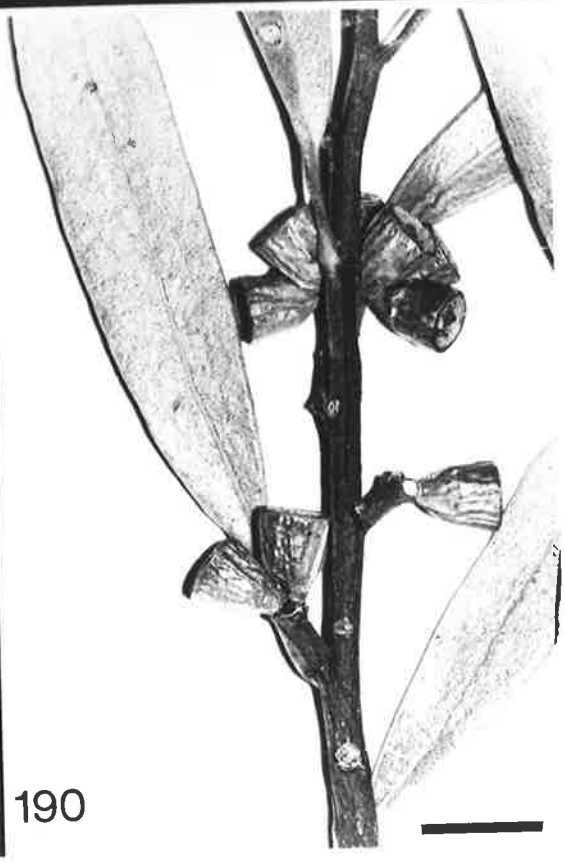
188





189





190

Figures 191 to 196: Some Western Australian forms previously referred to E. pileata and occurring west of the Nullarbor Plain, showing variation in operculum characters.

191: PJL 1380/0.6 km S Desmond (PIL)

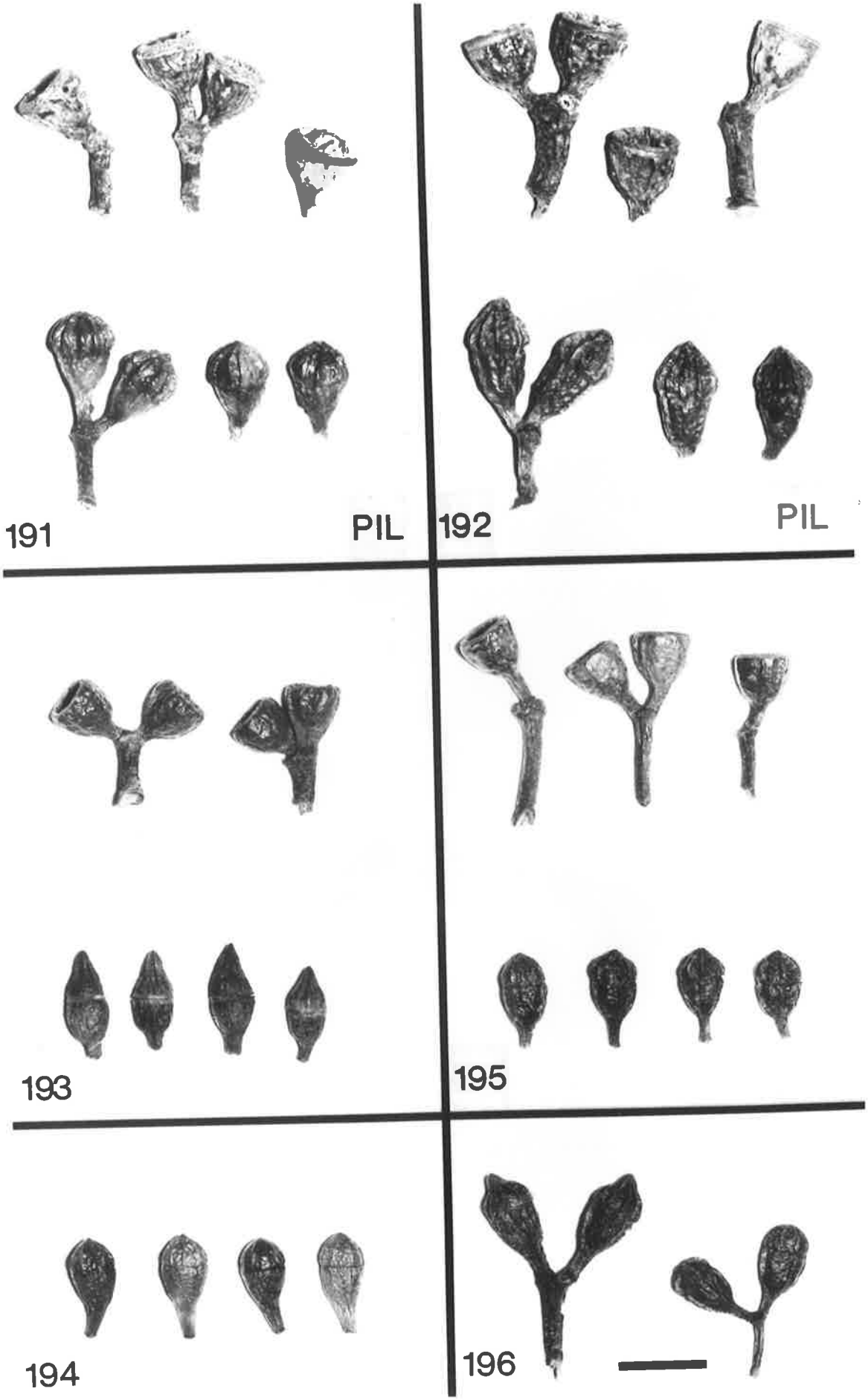
192: PJL 1381/0.6 km S Desmond (PIL)

193: PJL 1552/64.9 km E Norseman

194: PJL 1343/39.4 km S Norseman

195: PJL 1550/13.5 km NW Norseman

196: Buds from two other individuals at above locality.


191
PIL
192
PIL
193
195
194
196

Figures 197 to 198: Some South Australian forms from the Southern Flinders Ranges with strong affinities in bud and fruit morphology to forms previously referred to E. pileata.

197: R. Sinclair 1.ix.1977 D/1 km NE Devils Peak (P35)

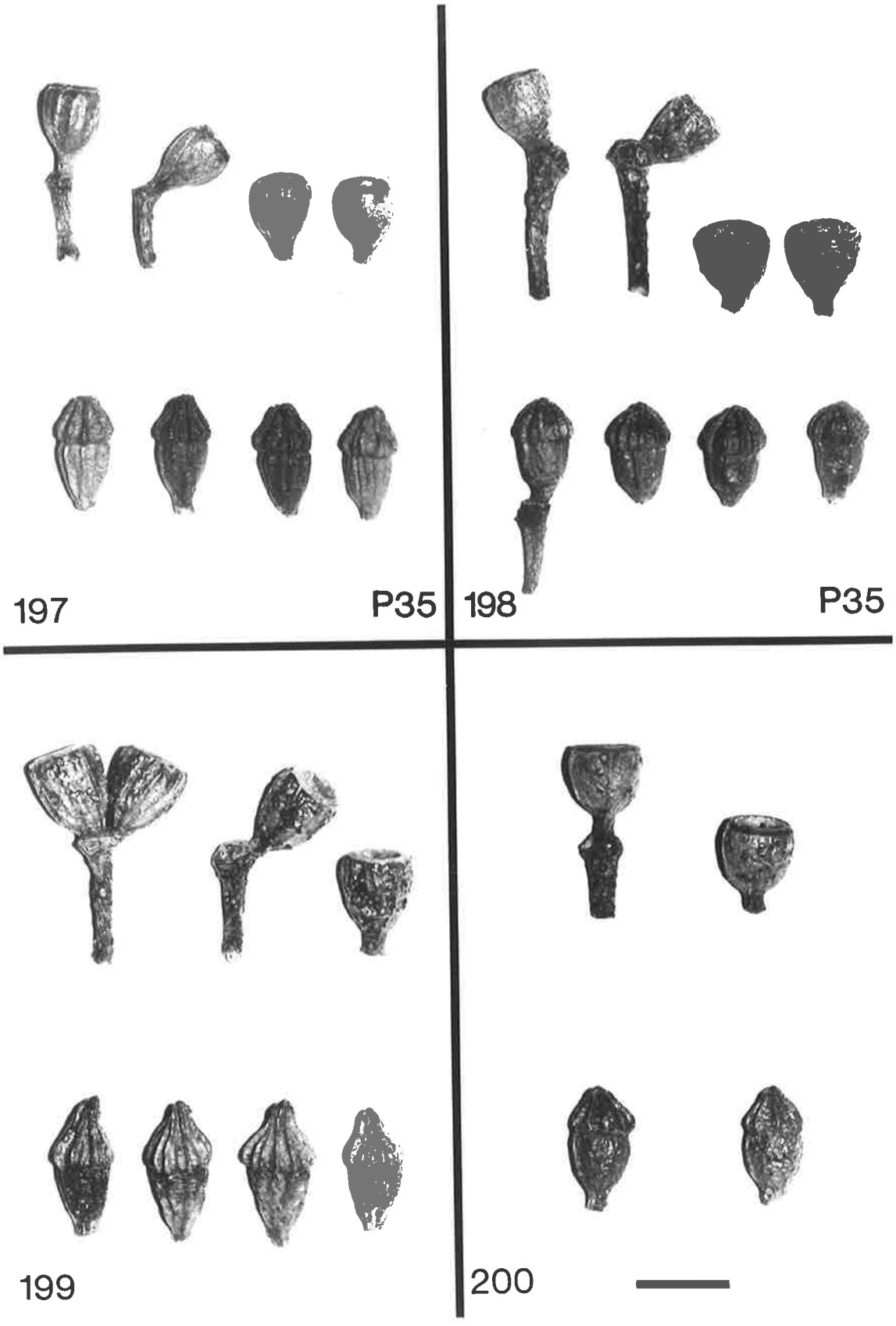
Glaucous-leaved form (LG = 2).

198: R. Sinclair 1.x.1977 C/1 km NE Devils Peak (P35)

Glaucous-leaved form (LG = 2).

199: R.J. Davies s.n. /Telowie Gorge CP

200: C.D. Boomsma 16.ix.1977/The Bluff, Beetaloo Valley


197
P35
198
P35
199
200

Figures 201, 202: Extremes of habit in forms previously referred to E. pileata.

201: PJL 1379/0.6 km S Desmond (PIL)
Example of low mallee forms near the type locality of E. pileata.
Height: 3.5 m

202: 13.5 km NW Norseman
Tree forms. Height: 10 m

Figure 203: F. Mollemans 800/Commonwealth Hill Stn
(North-western)
Small tree forms growing in sand on the margin of a salt pan. Height: 5.5 m

Figure 204: Loves Mine Range (P109)
Mallee form growing on rocky slope in the Flinders Ranges. Height: 5 m


201


202


203


204

Figures 205 to 207: Forms previously referred to E. calcareana.

205: 16 km WNW Coorabie

fruits: PJL 1194 to 1196
buds: PJL 1194, 1195

206: 9 km SW Coorabie

fruits: PJL 1191, 1192
buds: " "

6 km SW Coorabie

fruits: PJL 1193
buds: "

207: Madura

PJL 1331 to 1335; 1330 (individual with smallest fruits observed - non-random selection)



205



206



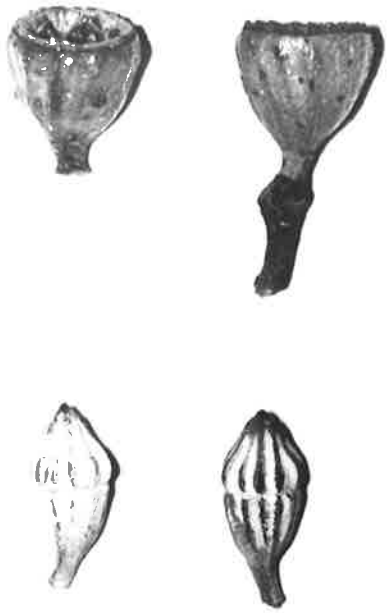
207

Figures 208 to 210: Glaucous-stemmed forms from Eyre Peninsula.

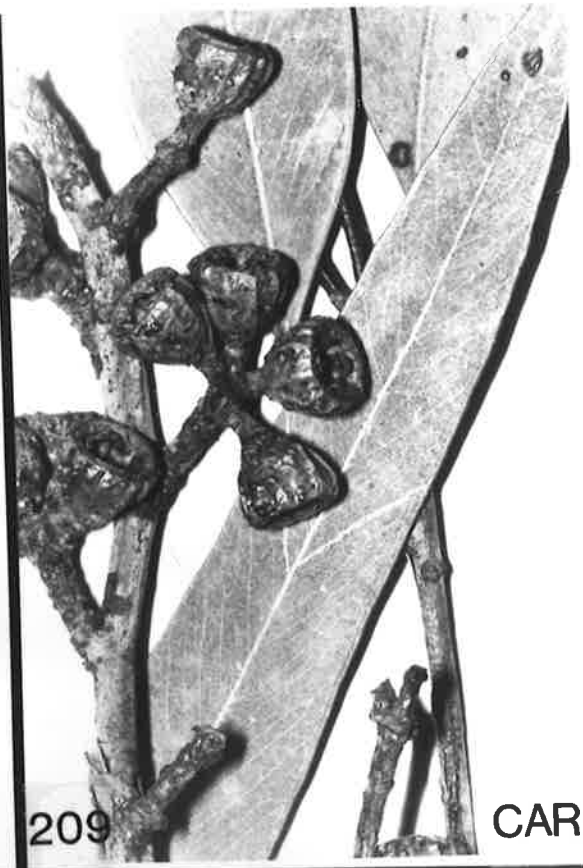
208: C.D. Boomsma 423/3 km SW Carappee Hill

209: C.D. Boomsma 420B/3 km SW Carappee Hill
Individual with strong fruit ribbing.

210: PJL 1072/6 km E Tooligie Hill
Form with stem-glaucousness from outlying population.



208 CAR



209 CAR



210

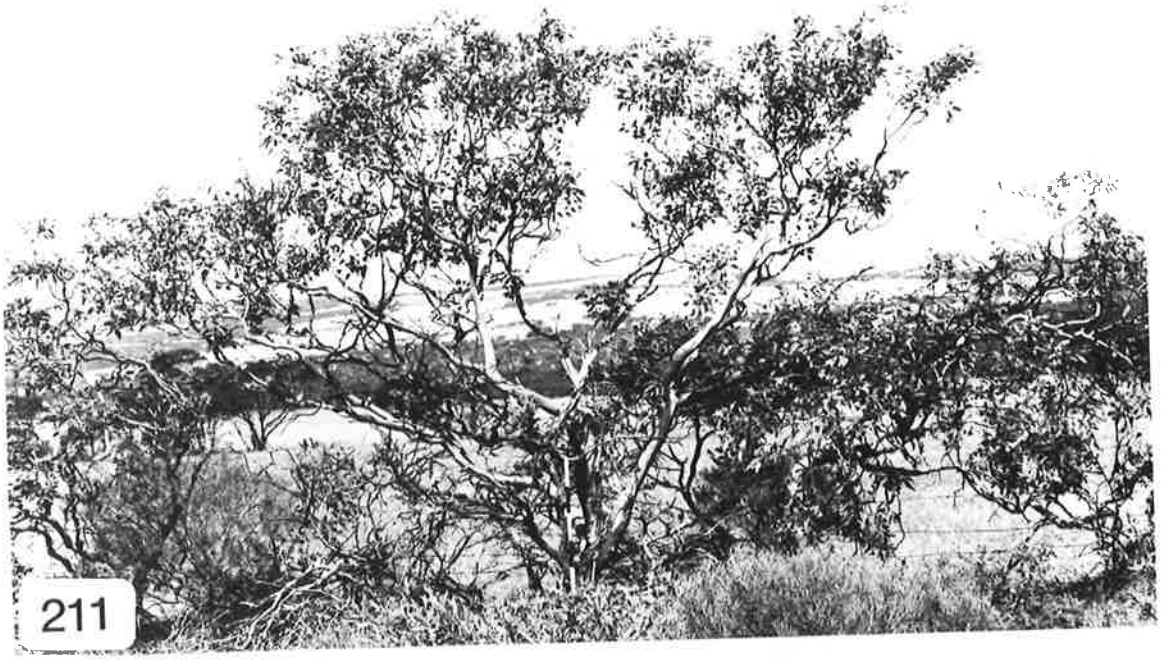
Figures 211 to 214: Habit photographs of glaucous-stemmed forms from Eyre Peninsula.

211: Small tree form near the base of Carappee Hill. Height: 5 m

212: PJL 1072/6 km E Tooligie Hill
Mallee form in outlying population. Height: 3.8 m

213: Open scrub to open heath of E. dumosa ssp. dumosa and Melaleuca uncinata associated with granitic outcrops on the slopes of Carappee Hill.

214: Thin-stemmed mallee form on Carappee Hill. Height: 3.5 m



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Figure 215: P.L. Milthorpe & G.M. Cunningham 6/W Ungarie
Form from near the type locality of E. dumosa showing prominent ribbing on buds.

Figure 216: PJL 1225/2.2 km N Mt. Hall
South Australian form with strong affinities to type material of E. pileata in bud and fruit morphology. It also has non-glaucous foliage (LG =0).

Figure 217: C.A. Gardner 11153/13 km NW Norseman
Glaucous-stemmed form labelled by Gardner as "E. redimiculiphloia".



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CHAPTER 12

TAXONOMY

12.1 Introduction

A new taxonomy of the Dumosae is proposed here on the basis of evidence from analyses discussed in the two previous chapters, and an examination of additional specimens. Before these proposed changes are published, it is planned to make a complete survey of all collections of Dumosae taxa at NSW, MEL and PERTH herbaria. This will enable precise limits for distributional, flowering and ecological data to be compiled and may indicate further morphological patterns. I wish to emphasize that there is already sufficient evidence to warrant the taxonomic changes and that nomenclature is likely to remain stable with further information because type material and variation centred geographically on it has been given thorough consideration. Only one new taxon, E. pterocarpa, has been described and all available collections for this have been studied. The other changes all involve a reduction in rank. New information from outlying occurrences can not negate the existing evidence, but may add to it or perhaps indicate new taxa.

Previous taxa relegated to synonymy have been lectotypified in this treatment so that names can be applied correctly and with certainty by workers who may wish to accept narrower taxonomic circumscriptions than advocated here. All types cited have been seen unless designated 'n.v.' (non vide) or 'photo.' (photograph only examined). To mimimize unavoidable damage to dried eucalypt specimens in transport only a selection of type material was requested after consultation with Dr. J. Jessop of the S.A. State Herbarium.

Where necessary, modifications have been made to the code designations ("PJ Codes") of the Pryor and Johnson (1971) system. Measurements given in descriptions are based on data from the numerical analyses modified to varying degrees by other material studied. Specimens regarded as intergrades were not taken into account. Ranges not enclosed by brackets should be taken to apply to at least 90 % of individuals and the measurements refer to average or typical values for an individual. Bracketted values are extremes either within an individual or the taxon. Precise definitions for the measurement of characters are given in section 4.3. Many characters presented in descriptions by other workers were rejected. Some were found to be too variable, some were noted only for a few taxa, and others were redundant. For instance, the conspicuousness of venation and oil glands in leaves appears directly related to glaucousness. The term 'adult leaves' is used to refer to fully expanded leaves on a mature individual that are the most advanced in the sequence from juvenile, intermediate to adult. On some individuals all leaves are intermediate and never attain the adult form, although it is unclear to what extent this is genetically fixed or environmentally induced. The definition used to distinguish trees and mallees is that the former are single-stemmed, the latter multi-stemmed.

Lists of specimens examined are not presented here but a representative list for each taxon is provided in Appendix 1. The following additional material has been considered for this taxonomic treatment:

1. Specimens from my personal collections in W.A. and S.A. which were not measured for analysis.
2. A representative sample of 2 - 3 specimens for each of the previous taxa, selected by Mr. M.I.H. Brooker from PERTH.
3. All Dumosae collections at AD and ADW. These are mainly South Australian occurrences but include some duplicate collections from other

states.

4. Various type specimens from interstate herbaria as cited below.

5. Loans of all collections available at the time for various taxa: E. conglobata and E. anceps from PERTH and FRI (with selected duplicates from MEL), and E. pterocarpa, "E. redimiculiphloia", E. georgei and E. striaticalyx from PERTH.

12.2 Series Dumosae

12.2.1 Description

Mallees or trees to 20 m tall, entirely smooth-barked or with a variable amount of brown or grey, rough, fibrous bark from the base rarely extending to major branches, or with a distinct blackbutt of persistent dark grey to black, thick, rough , flaky bark; the smooth bark deciduous in strips, pale and white or cream, grey, pink, yellow or brown, often in streaks or patches. Branchlets with oil glands in pith, non-glaucous or glaucous, quadrangular as primary stems, after secondary growth becoming terete or remaining angular until growing beyond branchlet stage. Wood: pale to dark brown, straight-grained and durable. Seedling: cotyledons reniform (with distal margin concave or sometimes convex in outline) or elliptical, under-surface pink, red or purple; hypocotyl pink to red; stem with oil gland verrucae; leaves for first 2 -4 pairs decussate, petiolate, grading from elliptical or lanceolate to broad-lanceolate or ovate, subsequent leaves subopposite to alternate, grading to ovate or lanceolate. Adult leaves alternate, petiolate, lamina narrow- to broad-lanceolate or sometimes ovate, often falcate, thin and flexible to thick and rigid, glossy to dull, non-glaucous to densely glaucous, concolourous, yellow-green, grey-green, greenish-blue or whitish, midrib convex to flat on abaxial side, slightly concave or channelled on adaxial

side, secondary veins irregular, 15 - 50 to midrib, cuticular surfaces smooth to highly sculptured with verrucae or papillae up to .09 mm high; stomata in crypts with outer stomatal ledges and a lenticular ostiole in thin outer layer of cuticle, stomatal bars absent, subsidiary cells anomocytic. Umbellasters axillary, 3-, 5-, 7-, 9-, 11- or 13-flowered, with pairs of deciduous bracts corresponding to nodes of condensed compound dichasium and the major outer pair enclosing the other bracts and developing buds, non-glaucous or glaucous; peduncles terete, angular or compressed. Buds bi-operculate, the outer calycine operculum being shed from developing or immature buds or sometimes remaining attached to summit of inner petaline operculum, filaments erect basally then inflexed downwards around style; operculum contracted or concave in outline to convex in outine, smooth to striate or corrugated with ribs or 'wings'. Flowers: staminodes absent; filaments white, cream, pale yellow or bright yellow; anthers with a large dorsal oil gland, sub-basifixed, versatile, obovoid to oblong, with cells distinct and opening by longitudinal slits; ovary with 3 -7 locules, placentae with ovules and ovulodes in four vertical rows. Fruit variable in shape, cylindroid, obconoid, or less often sub-hemispherical or campanulate; smooth, sub-rugose, costate or regularly ribbed or winged; valves, including persistent base of style, splitting at dehiscence. Seeds: lenticular or ovoid and often somewhat irregular in shape, 1.5 - 4.0 mm long, the surface even or with irregular facets and depressions, red-brown or dark ruby-red, lustrous, shallowly sculptured with obscure or prominent reticulum of polygonal or elongate areolae arranged more or less in rows, areolae walls opaque and rather thick and obtuse, hilum ventral and not distinctly coloured, not winged but sometimes with narrow flange of testaceous material on margin where adjoined to adjacent seeds. Chaff: 'D-shaped' to acicular, often irregular in shape, yellow-brown, brown or red-brown, smooth, lustrous, with a pattern of closed polygonal to elongate areolae.

Type species: E. dumosa A. Cunn. ex Schau.

12.2.2 Other series of section Dumaria.

Most of the above characters apply equally to the other series of section Dumaria. Within this section the principal diagnostic characters are those of the seeds, although there are some significant differences in anther shape and filament thickness (Brooker, 1979), and leaf and stem glaucousness. A formal treatment of section Dumaria is outside the scope of this thesis. However, to aid in distinguishing material of the other series from Dumosae and enable recognition of some hybrids, descriptions of seeds for the other series are provided.

Torquatae

Ovoid or less often lenticular, usually even-surfaced, brown to dark grey, deeply sculptured, appearing dull to the naked eye, deeply sculptured with prominent reticulum of polygonal to elongate areolae arranged more or less in rows, areolae walls translucent, testaceous and thin, hilum indistinct, areolae deeper around circumference and often forming an indistinct wing.

Incrassatae

Lenticular to pyramidal and often irregular in shape, ventral surface with ridges and facets radiating from the hilum, brown to dark grey, shallowly sculptured with distinct reticulum of mostly elongate areolae arranged irregularly sometimes in rows, hilum indistinct, testa flattened into a prominent circumferential wing with a translucent flange.

Dundasinae

Ovoid, with even surface, brown, sculptured with prominent reticulum of polygonal to elongate areolae arranged more or less in rows, hilum distinct and dark brown to almost black, not winged.

Merrickianae

Lenticular, the surface uneven with irregular depressions and facets, brown or dark grey with varying amounts of a pale grey to straw-coloured scurvy deposit, shallowly sculptured with prominent reticulum of elongate areolae more or less in rows, hilum same colour as underlying testa, often flattened around circumference into an indistinct wing.

12.3 Key to species and subspecies of series Dumosae

1a Fruits corrugated with ribs or 'wings' of maximum depth at least 1.0 mm ; operculum rostrate ; tree habit. ____ 2

1b Fruits not corrugated, without regular ribbing or with ribs of maximum depth less than 1.0 mm ; operculum rostrate, umbonate, or not contracted ; tree or mallee habit. ____ 3

2a Fruits > 11 mm long, with 'wings' up to 2.5 - 4.0 mm deep, branchlets non-glaucous ; umbellasters 3-, 5-, (7-) -flowered. ____ *Eucalyptus pterocarpa*

2b Fruits < 11 mm long, with ribs up to 1.0 - 2.5 mm deep, branchlets usually glaucous ; umbellasters 7-, (9-), (11-) -flowered. ____ *E. lesouefii*

3a Branchlets glaucous ____ 4

3b Branchlets non-glaucous ____ 7

4a Flowers with filaments bright yellow ; operculum ± hemispherical with distinct rostrum, mid-width/base-width ratio 0.25 - 0.50, smooth or faintly striate ; fruits > 11.0 mm long and > 9.5 mm wide at mid-length, campanulate or with slight contraction in outline. (Restricted to W.A., Coolgardie District). ____ *E. woodwardii*

4b Flowers with filaments white or cream, rarely pale yellow; operculum with or without rostrum, if rostrate then mid-width/base-width ratio 0.50 - 1.00, smooth to deeply ribbed; fruits usually < 11.0 mm long or < 9.5 mm wide at mid-length, if larger then not campanulate but straight-sided or convex in outline. ____ 5 (*E. dumosa*)

5a Tree with distinct blackbutt; fruit 4.5 - 7.5 mm long; operculum always ribbed and contracted with rostrum or umbo. (Restricted to W.A.)._____E. dumosa ssp. clelandii

5b Mallee or sometimes a small tree, entirely smooth-barked or with some rough basal bark but never with a distinct blackbutt; fruit 5.5 - 13.5 mm long; operculum sometimes smooth or not contracted._____6

6a Operculum (truncate-)hemispherical, not contracted or minutely umbonate, up to 3.5 mm long, smooth; leaves thick and rigid, 25 - 45 mm wide. (Restricted to W.A., Roe District).
_____E. dumosa ssp. georgei

6b Operculum conoidal or hemispherical(-compressed), not contracted to strongly rostrate, up to 8.0 mm long, smooth or ribbed; leaves sometimes thin and flexible, 10 - 45 mm wide.
_____E. dumosa ssp. dumosa

7a Leaves non-glaucous. _____8
7b Leaves glaucous. _____E. dumosa ssp. dumosa

8a Fruits and buds strictly sessile._____E. dumosa ssp. conglobata

8b Fruits and buds pedicellate to subsessile._____9

9a Fruits 4.0 - 5.0 mm wide at mid-length and 3.5 - 6.5 mm long, with pedicels up to 2.5 mm long and up to 2.5 mm wide at mid-length, 3- or 4-valved (often with more than 50% of fruits on an individual 3-valved);tree with blackbutt. (Restricted to W.A., Avon & Roe Districts)_____E. kondininensis

9b Fruits 5.0 - 12.5 mm wide at mid-length and 5.0 - 13.5 mm long, with pedicels up to 7.5 mm long and up to 6.0 mm wide at mid-length, (3-), 4-, 5-, (6-), (7-) -valved (never with more than 50% of fruits on an individual 3-valved); tree or mallee, never with a blackbutt if fruits < 6.5 mm long._____10

10a Fruiting peduncles 3.5 - 6.0 mm wide at mid-length and 4 - 8 mm long,compressed-angular; operculum length/base-width ratio usually 1.10 -2.25; fruits relatively large, 7.0 - 11.0 mm long and 7.0 - 11.0 mm wide at mid-length, tapering into short, broad pedicels or subsessile,pedicels never longer than wide, up to 3.0 mm long and 3.0 - 6.0 mm wide at mid-length._____E. dumosa ssp. fraseri

10b Fruiting peduncles 1.0 - 3.5 mm wide at mid-length and 6 - 22 mm long, compressed, angular or terete; operculum length/base-width ratio usually 0.50 - 1.10; fruits small to large, 5.0 - 13.5 mm long and 5.0 - 12.5 mm wide at mid-length, distinctly pedicellate or tapering into indistinct pedicels or subsessile, pedicels often longer than wide, up to 7.5 m long and 1.0 - 4.5 mm wide at mid-length._____E. dumosa ssp. dumosa

12.4 Systematic treatment for Eucalyptus dumosa

(incorporating all subspecies)

Eucalyptus dumosa A.Cunn. ex Schau.

Synonyms: (for full citations see treatment of each subspecies):

E. lamprocarpa F.Muell. ex Miq. 1856
E. muelleri Miq. 1856
E. dumosa A.Cunn. ex Schau. var. conglobata R.Br. ex Benth. 1867
E. dumosa A.Cunn. ex Schau. var. rhodophloia Benth. p.p. 1867
E. incrassata Labill. var. dumosa (A.Cunn. ex Schau.) Maiden 1904
E. incrassata Labill. var. conglobata (R.Br. ex Benth.) Maiden 1904
E. glomerata Tausch. ex Maiden 1904 nom. nud.
E. striaticalyx W.V.Fitzgerald 1904 syn. nov.
E. goniatha Turcz. var. clelandii Maiden 1910
E. clelandii (Maiden) Maiden 1912 syn. nov.
E. sheathiana Maiden 1915 syn. nov.
E. conglobata (R.Br. ex Benth.) Maiden 1922 syn. nov.
E. dongarraensis Maiden & Blakely 1925 syn. nov.
E. pileata Blakely 1934 syn. nov.
E. conglobata (R.Br. ex Benth.) Maiden ssp. fraseri Brooker 1972
E. fraseri (Brooker) Brooker syn. nov.
E. cyanophylla Brooker 1977 syn. nov.
E. georgei Brooker & Blaxell 1978 syn. nov.
E. calcareana Boomsma 1979 syn. nov.

Common name: various names - see subspecies.

PJ Code: SLE:G

Description

Mallee or tree to 20 m tall, with fine to coarse foliage, entirely smooth-barked or with a variable amount of rough, brown to grey, fibrous bark from the base rarely extending to major branches, or with a distinct blackbutt of persistent, dark, thick, rough, flaky bark ; smooth bark deciduous in strips, pale and white, cream, grey, pinkish, yellow-brown or brown, often in streaks or patches. Branchlets non-glaucous to heavily

glaucous, terete to strongly quadrangular. Seedling leaves: first (2 -) 4 pairs decussate, elliptical to lanceolate, broad-lanceolate or ovate, green or grey-green, subsequent pairs subopposite to alternate, ovate to broad-lanceolate, non-glaucous to densely glaucous ; juvenile and coppice leaves broad-lanceolate to broad-ovate. Adult leaves: lamina narrow- to broad-lanceolate, rarely ovate, thin and flexible to thick and rigid, (50-)75 - 155(-175) mm long, 9 - 38(-48) mm wide, (.30-).35 - .70(-.75) mm thick, glossy to dull with cuticular relief .010 - .090 mm high, non-glaucous to densely glaucous, yellowish-green to grey-green, greenish-blue or whitish, angle between secondary veins (30-)35 - 90(-100) ; petioles (10-)13 - 31(-38) mm long. Umbellasters (3-), (5-), 7-, 9-, 11-, (13-) -flowered, non-glaucous or glaucous ; fruiting peduncles 3 - 18(-24) mm long, (1.0-)1.2 - 7.3(-8.3) mm wide at mid-length, terete, angular or compressed. Mature buds: hypanthium cylindrical, obconical,turbinate or hemispherical, smooth to slightly ribbed or striate, sometimes with 2 - 4 costae ; operculum coniodal, turbinate, hemispherical, compressed- or truncate-hemispherical, with distinct rostrum or umbo, slightly contracted, or convex and not contracted, flush to markedly wider than hypanthium, 2.5 - 10 mm long by 4 - 8 mm wide, length/base-width ratio (.40-).45 - 2.00(-2.25), mid-width/base-width ratio (.40-).45 - 1.05(-1.10), sometimes becoming yellow or red before anthesis, smooth to striate or deeply corrugated, ribs up to 0 - 1.2 mm deep. Flowers: filaments white, cream or sometimes pale yellow. Mature fruits cylindroidal -- cylindrical, doliform, obovoidal-truncate, obconoidal, pyriform, sub-hemispherical or discoidal, truncate at base and sessile, or tapering gradually or abruptly into pedicel, (3.0-)4.5 - 13.0(-13.5) mm long, midwidth 4.5 - 11.5(-12.5) mm wide, rim-width/length ratio (.45-).55 - 1.90(-2.10), mid-width/rim-width ratio (.80-).85 - 1.35(-1.40), smooth, striate or with regular ribs 0 - 1.0 mm deep, sometimes with 2 -4 costae, sometimes sub-rugose ; disc 0.3 - 2.0 mm wide,

sloping inwards to 0.2 - 2.8 mm below rim level, flat, or rarely slightly raised ; valves (3), 4, 5, (6) per fruit (average 3.1 - 5.0), tips well below rim level to well exserted ; pedicels absent or (0.0-) 0.9 - 7.7(-9.7) mm long, (0.9-)1.1 - 5.4(-6.0) mm wide.

Notes

E. dumosa is a highly variable taxon. The bulk of the variation is contained within the typical subspecies and the other four subspecies are more narrowly defined and represent extreme forms which have a more restricted distribution. Details of distribution, ecology etc. are provided under each subspecies.

12.5 Systematic treatment for individual taxa

The five subspecies of E. dumosa are considered in their order of publication and followed by the other four species in order of publication. Where necessary, comments are made on new synonyms of subspecies under their old species names in the sections on typification.

12.5.1 Eucalyptus dumosa A.Cunn. ex Schau. ssp. dumosa

E. dumosa A. Cunn. ex Schauer, Walp. Rep. Bot. Sys. 2: 925 (1843); Bentham, Fl. Austral. 3: 230 (1867) p.p. (as to var. dumosa only); --E. incrassata Labill. var. dumosa (A.Cunn. ex Schau.) Maiden, Crit. Rev. Gen. Euc. 1(4): 97, pl. 16, figs 1,2,3,5, pl. 19, fig. 1, pl. 21, fig. 3 (1904) p.p. (excl. syn. E. lamprocarpa F. Muell., E. muelleri Miq.); --E. dumosa: Maiden, loc. cit. 4(38): 220 (1919) p.p (as to var. dumosa only); Blakely, Key Euc. 118 (1934); Burbidge, Trans. Roy. Soc. S. Aust. 71(2): 152 (1947);Black, Fl. S. Aust. edn.2: 630 (1964) p.p. (excl. Kangaroo Is.); Hall & Brooker, For. Timb. Bur. Forest Tree Series No. 131, figs (1974);

Boomsma, Native Trees S. Aust. edn.2: 147, fig. (1981).

Type: " A. Cunn., Herb., No. 206, 1817."

Holotype: n.v. Isotype: A. Cunningham 206, Back of the interior, s.dat. (BM photo.). Probable isotypes: A. Cunningham s.n., Interior of Australia, s.dat. (BM n.v.); s.leg. s.n., Euryalean scrub, s.dat. (K photo.).

[E. lamprocarpa F. Mueller ex Miquel, Nederl. Kruidk. Arch. 4: 129 (1856) p.p. typo excluso (pedicellate forms only (12.5.3, p. 305))]

E. glomerata Tausch ex Maiden, Crit. Rev. Gen. Euc. 1(4): 100 (1904). nom. nud.

E. striaticalyx W.V. Fitzgerald, J. W. Aust. Nat. Hist. Soc. 2(1): 20 (1904) syn. nov.; Maiden, Crit. Rev. Gen. Euc. 6(51): 3, pl. 208, figs 2,3 (1922); Blakely, Key Euc. 121 (1934); Gardner (1965) in Aplin, Euc. W. Aust. 247, fig. 101 (1979) p.p. [excl. Mt Magnet population here regarded as intergrades between E. dumosa ssp. dumosa and ssp. clelandii]; Boomsma, Native Trees S. Aust. edn. 1: 174, fig. (1972); Hall & Brooker, For. Timb. Bur. Forest Tree Series No. 83, figs (1973); Boomsma, loc. cit., edn. 2: 232, fig. (1981), Chippendale in Jessop, Fl. Cent. Aust. 247 (1981).

Type: " Milly's Soak, and four miles east of Nannine, Sept., 1903 --W. V. F. "

Lectotype (here designated): W.V. Fitzgerald s.n., Milly's Soak, -.9.1903 (NSW, ex herb. W.V.F). Isolectotypes: ibid. -.-.1903 (PERTH 2 sheets)

[E. clelandii auct. non. (Maiden) Maiden: Chippendale in Jessop, Fl. Cent. Aust. 247 (1981)]

E. sheathiana Maiden, J. Roy. Soc. N.S.W. 49: 312 (1915) syn nov; republished in Crit. Rev. Gen. Euc. 6(51): 1,60,61, pl. 208, fig. 1 (1922);Blakely, Key Euc. 114 (1934); Gardner (1955) in Aplin, Euc. W.

Aust. 114, fig. 38 (1979); Chippendale, Euc. W. Aust. Goldf. 144, figs (1973).

Type: " a cultivated specimen in the King's Park, Perth, W.A. .. The late Mr J. Sheath, Superintendent up to 1913 .... additional specimens from the same plant from Mr Sidney William Jackson, of Sydney, and from Dr. F. Stoward, Government botanist of Western Australia..."

Lectotype (here designated): J. Sheath s.n., Cult. King's Park, Perth, W.A. -.xii.1910 (NSW 177992). Probable isolectotypes: ((PERTH,K,BM) n.v.). Syntype: W. Jackson s.n., King's Park, Perth, W.A. -.ii.1913 (NSW 151284).

*E. dongarraensis Maiden & Blakely, J. Roy. Soc. N.S.W. 59: 184 (1925) syn. nov.; Maiden, Crit. Rev. Gen. Euc. 7(68): 371, pl. 278, fig. 1 (1927);Blakely, Key Euc. 121 (1934); Gardner (1961) in Aplin, Euc. W. Aust. 219, fig. 88 (1979); Chippendale, Euc. W. Aust. Goldf. 146, figs (1973). Type: " It has only been seen at Dongarra [= Dongara] in Western Australia, .."

Lectotype (here designated): J.H. Maiden s.n., Dongara, -.x.1909 (NSW 42723, one specimen in bud). Isolectotypes: (NSW 42723, other specimens; PERTH, 2 sheets). Probable isolectotypes: ((K,MEL) n.v.). Possible isolectotype: (PERTH 1227A).

E. pileata Blakely, Key Euc. 120 (1934) syn. nov.; Burbidge, Trans. Roy. Soc. S. Aust. 71(2): 152 (1947) p.p. [excl. " Kangaroo Island "]; Black, Fl. S. Aust. edn. 2: 629 (1964), p.p. [excl. " Kangaroo Island "];

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*This name is probably a synonym of:

E. obtusiflora DC, Prodromus 3: 220 (1828), syn. nov. (misapplied name). Type: Australia on the eastern coast.

(See p. 292, 293.)

Gardner (1959) in Aplin, Euc. W. Aust. 166, fig. 64 (1979); --E. dumosa ssp. [pileata]: Pryor & Johnson, Classif. Euc. 85 (1971); --E. pileata: Chippendale, Euc. W. Aust. Goldf. 147, figs (1973).

Type: " Desmond, near Ravensthorpe (J.H. Maiden, November, 1909) ". Holotype: J.H. Maiden s.n., loc. cit. -.xi.1909 (NSW 17794). Isotypes: (PERTH, (K,BM) photo.).

E. cyanophylla Brooker, Trans. R. Soc. S. Aust. 101(1): 15, figs 1,2 (1977) syn. nov.; Boomsma, Native Trees S. Aust., edn. 2: 140, fig. (1981).

Holotype: B. Copley 3799, c. 3 km northeast of Berri, South Australia (34 15 S 140 37 E) 5.viii.1972 (AD). Isotype: (FRI n.v.).

E. calcareana Boomsma, J. Adelaide Bot. Gard. 1(6): 361, fig. 1 (1979) syn. nov.; Native Trees S. Aust. edn. 2: 122, fig. (1981).

Holotype: G.C. Cornwall, s.n., South Australia, 43 km along Eyre Highway W. of Nundroo (31 29 S 131 53 E) 11.iii.1977 (AD).

Common name: White Mallee

PJ Code: SLE:GA

Diagnosis

Mallee or small tree to 12 m tall, entirely smooth-barked or with a variable amount of rough bark from the base rarely extending to major branches, but never with a distinct blackbutt. Branchlets angular becoming terete. Umbellasters: fruiting peduncles 6 - 18(-24) mm long, 1.1 - 3.6(-4.2) mm wide at mid-length. Mature fruits distinctly or obscurely pedicellate, (4.5-)6.0 - 13.0(-13.5) mm long, mid-width (4.5-)5.0 - 11.5(-12.5) mm wide; pedicels (0.0-)1.5 - 7.7(-9.7) mm long, 1.0 - 4.0(-4.9) mm wide.

(Figs: 110, 111, 125 to 128, 201 to 204, 211 to 214 (habit);
65 to 77, 81 to 93, 113, 120 to 122, 135 to 137,
139 to 149, 152 to 200, 205 to 210, 215 to 217.)

Typification

1. E. dumosa

The holotype has not been seen, but is presumably located at a herbarium where Schauer (the author of the species) worked. Collections at K and BM, of which photographs were examined, bear no evidence of having been examined by Schauer, and are therefore treated as isotypes.

2. E. striaticalyx

The protologue includes reference to two localities followed by the author's initials which can be taken to designate both as collections. Although sometimes confused (7.2, p. 142), these are two disjunct occurrences. No collection by Fitzgerald is known from the second locality, but it would be a syntype if it exists. Maiden (1922, 6(51): 60) refers to a tree at the first locality which produced the type. Although this does not constitute the selection of a type specimen, it supports the choice of lectotype made here. Since the type material is the author's own collection, it would all be familiar to him and form part of the basis of the description. Thus all duplicates can be regarded as syntypes. The NSW and one PERTH sheet have labels from Fitzgerald's herbarium. These specimens at least were probably in his possession when the description was made. The NSW sheet was chosen as the lectotype on the grounds of completeness of material. It has two branchlets, one with buds attached and the other with fruits, and is the only sheet providing both organs.

3. E. sheathiana

I believe that specimens of the three collectors Sheath, Jackson and Stoward, all constitute the type and are therefore syntypes, contrary to Johnson's (pers. comm., 1982) statement that Sheath material is holotype. The reference to "a specimen" of Sheath followed by "additional specimens", does not unambiguously designate the former as type although it may attribute greater significance to it. In other cases (E. kondininensis and E. clelandii (p. 319 and 298)), Maiden has subsequently indicated the second rather than the first specimen cited in the protologue as being "the type". For E. sheathiana, Maiden also makes a later indication of the type (Maiden, 1922, 6(51): 60) and this complicates determination of type status for the collections. Maiden's reference is in an illustration label which reads: "From a cultivated plant in the King's Park, Perth, Western Australia (J. Sheath). The type." It is unclear from the Code whether such a reference should be treated as valid lectotypification. It certainly does not make the Sheath collection a holotype since it was not expressed at the time of the original publication of the name of the taxon (I.C.B.N., Guidelines for Determination of Types, no.1). Acceptance of the Sheath material as a lectotype chosen by Maiden is doubtful for the following reasons: he has not explicitly stated that he was making a selection among types; there is no stated rejection of the other material as types; "the type" may loosely mean 'this is part of the type'; it is unlikely that he would have deliberately meant to clarify and make more precise his own earlier indication of the type in such a casual way; there is no evidence that the 'choice' is not arbitary (Art. 8). I believe that it is more likely that the reference reflects Maiden's original unstated intention rather than a changed concept of the type. Consequently, a Sheath specimen is here selected as lectotype, following Guideline 4d which states: "When choosing a lectotype, any indication of intent by the author of a name should be

given preference unless such indication is contrary to the protologue".

Any interpretation of the Sheath material as being the holotype or a lectotype of Maiden, is further complicated by the fact that the figures referred to by the label do not appear to be of this collection. Rather, they support the syntype status of material from the other two collectors. The illustration has figures of a twig bearing mainly flowers and a twig with fruits, whereas the J. Sheath (NSW) collection has buds and lacks flowers and fruits. The fruits illustrated are of the same form and development as those on the collection: F. Stoward s.n., King's Park Perth W.A. -.iv.1916 (NSW 151282). Its folder is annotated: " fruits drawn 5.8.20 M.F. " indicating that they were probably drawn by Flockton for this illustration published by Maiden in 1922. The collection W. Jackson -.ii.1913 (NSW 151284) has a branchlet at the same stage of flowering as that in the illustration . The illustration of Stoward's and Jackson's collections as " the type " may mean that Maiden only refers to J. Sheath in the label for having grown the type tree. This would imply that he had a broad understanding of the type that included all material that he had been sent from this tree.

It should be noted that the above Stoward collection and another one, F.Stoward, Perth Cult. -.vi.1916 (NSW 151283), cannot be syntypes unless there is an error in dating, as the collection dates exceed that given for the publication of the original description. Only Stoward's material referred to in the protologue in 1915 would be a syntype, but it is now unknown.

4. E. dongarraensis

Brooker (pers. comm., Dec. 1982) believed that the type specimen of E. obtusiflora DC is the same taxon as E. dongarraensis, based on his examination of De Candolle's specimen in the Geneve herbarium (G). The

single specimen of E. obtusiflora there is presumably the holotype. This observation was too late to be fully pursued and taken into account for this thesis. I have examined microfiche of this specimen, a branchlet with mature leaves and buds, and agree with Brooker's determination on this evidence. A final judgement will not be made until I have examined the specimen. The name E. obtusiflora has been applied to eastern Australian material placed in series Obliquae of subgenus Monocalyptus. The leaves of the type specimen, however, have relatively obtuse bases and certainly do not belong in this subgenus. There is good agreement with the type collection of E. dongarraensis in the blunt, hemispherical operculum that is shorter and broader than the hypanthium. These features are noted in the type description. If E. obtusiflora is the same taxon as E. dongarraensis, then these features indicate that it must have been collected on the west, not the east coast of Australia as stated in the protologue and on the specimen label. As E. obtusiflora was published before E. dongarraensis, it has priority and would be the correct name for the taxon. However, for the taxonomic treatment proposed here the consequences would be more serious because E. obtusiflora also preceded the publication of E. dumosa. Thus the name E. dumosa would be rejected and the previous taxa would be sunk into E. obtusiflora with four of the five subspecies names retained and the type subspecies replaced by ssp. obtusiflora.

For E. dongarraensis, material at NSW could be accepted as the holotype (as labelled by L.A.S. Johnson) if the duplicates had been distributed elsewhere before Blakely could have studied them for the description. However, one sheet at PERTH (CSIRO neg. no. 3478) has a NSW label with a determination and the word 'Type' written by Blakely. This specimen at least is a syntype and candidate for lectotypification. It has only a few buds, adult leaves and juvenile leaves. There is a much better

representation of material at NSW including fruits, and this is therefore chosen for lectotype. Because this material is not attached to a sheet, a single branchlet (in bud) has been chosen as the lectotype specimen. This will avoid confusion when the collection is eventually mounted, as two sheets would be needed.

5. E. pileata

The duplicates of Maiden's E. pileata collection have all been distributed from NSW herbarium. This was probably done prior to Blakely's description, as the only evidence of Blakely's study of the material is the determination in his handwriting on this NSW sheet. It is therefore accepted as the holotype.

Flowering period: Throughout the year, varying with different forms and regions. Flowering periods in summer - autumn months are most common.

Distribution (fig. 219): W.A., Fortesque, Carnarvon, Ashburton, Austin, Irwin, Avon, Roe, Eyre, Coolgardie, Giles, Helms and Eucla Districts; S.A., North-western, Nullarbor, Gairdner-Torrens Basin, Eyre Peninsula, Yorke Peninsula, Flinders Ranges, Northern Lofty, Southern Lofty, Eastern, Murray, South-eastern Regions; Victoria; New South Wales.

It is widespread throughout arid and semi-arid southern Australia. The most northerly occurrences are in the Hamersley Ranges. South of this in the arid central region there are scattered occurrences confined to specialized habitats. It is abundant throughout the semi-arid wheatbelt and Goldfields region of the southwest and extends eastwards into South Australia along the southern margin of the Nullarbor plain. North of the Nullarbor it is prevalent in sand dunes of the Great Victoria Desert. There are records in the Blackstone and Musgrave Ranges, so E. dumosa ssp.

dumosa probably extends across the border to similar areas in southern Northern Territory. It is found in greatest abundance in the mallee areas of semi-arid South Australia, in particular on Eyre Peninsula and the Murray Mallee, but is absent from Kangaroo Island. It occurs in the Gawler Ranges to the north of Eyre Peninsula, in the Olary Spur of the Eastern Region, and extends north into the arid region up the entire length of the Flinders Ranges in areas with suitable edaphic conditions. From the Murray mallee it extends through northwestern Victoria to western and central New South Wales.

Ecology

Habitat: highly variable but compared to other mallees it often shows a preference for more fertile and heavier-textured soils. Eucalyptus dumosa ssp. dumosa occurs: in the Hamersley Range on residual caps of calcrete or ironstone and on areas of calcrete between sand dunes; in the central desert area restricted to soakages, depressions, creek beds, consolidated gypseous dunes on salt lake margins, calcrete tables and sand dunes; throughout much of semi-arid southwestern Western Australia on coastal plain, alluvial slopes, dissected laterites, lateritic sand plains, low sand dunes, calcareous loam plains and rarely on inselbergs or small ranges; along the Nullarbor mainly on the plain at the base of the scarp or on the limestone plateau in depressions or slopes of narrow valleys; in the Great Victoria Desert often in the interdune corridors, on dune slopes or crests, sand plains, margins of salt lakes or depressions; in the semi-arid mallee areas of the eastern states on coastal plains, alluvial slopes, sand dunes (swales, slopes or crests), calcareous loam plains, calcrete and sometimes on inselbergs; on lateritic remnants on southern Eyre Peninsula; on alluvial and skeletal soils derived from quartzite, porphyritic rhyaodacite (Gawler Ranges), quartz-feldspar gneisses

(Carappee Hill, Cleve Hills etc. on Eyre Peninsula), low granitic domes (near the type locality in New South Wales) and, in the Flinders Ranges, siltstone, limestone, a variety of soft metamorphics (exposed in the Blinman Dome and elsewhere), sandstone and sometimes quartzite. Occurrences associated with quartzite in the Gammon Ranges (northern Flinders Ranges) are confined to saddles and depressions in the level-bedded strata where clay soils accumulate. Soils range from sand to loam to clay and include: gravelly sand or loam with quartzite, laterite, or limestone gravel; calcareous or gypseous sands, loams and clays; and duplex soils with a lower clay horizon.

Average annual rainfall: 150 - 500 mm

Associated species: In the Hamersley Ranges E. dumosa ssp. dumosa is often found with E. kingsmillii, and in the central desert area it is frequently in pure stands or with E. camaldulensis or E. microtheca. Throughout the semi-arid regions that make up most of its distribution, it occurs in woodland or mallee communities usually with several other species from a large number of associate eucalypts. The most common and widespread of these are E. gracilis, E. socialis and E. oleosa. Melaleuca species, including M. uncinata and M. lanceolata, are often present and the understorey varies from heath-like and sclerophyllous to chenopodiaceous. In semi-arid Western Australia important associates include: E. eremophila, E. flocktoniae, E. redunca, E. wandoo, E. salubris, E. salmonophloia, E. erythronema, E. loxophleba, E. diptera and E. oleosa. In the vicinity of the Nullarbor the main associates are E. oleosa, E. gracilis and E. yalatensis. In the Victoria Desert and elsewhere on desert sand dunes E. yalatensis is replaced by E. socialis, E. yumbarana and E. concinna. The main mallee areas of South Australia containing E. dumosa ssp. dumosa can be divided into two principal community types. These often occur as a mosaic of distinct communities within a limited

area although intermediate communities with representative species from both do occur. The first type occurs on sandy areas that are sometimes calcareous, dunes and well-drained soils and is characterized by E. incrassata, E. socialis, E. foecunda, E. diversifolia, E. calycogona, Melaleuca uncinata and Triodia sp.. The second type occurs in loamy soils, sometimes in depressions or swales and often with limestone. It is characterized by E. gracilis, E. oleosa, E. brachycalyx, E. odorata, Melaleuca lanceolata, M. pauperiflora, Geijera linearifolia, Olearia muelleri , O. decurrens, and Westringia rigida.

Notes

Eucalyptus dumosa ssp. dumosa is a highly variable taxon. Inland desert forms are characterized by large fruits with distinct and often elongate pedicels,and variable leaf and stem glaucousness. Semi-arid mallee and woodland forms generally have fruits of medium size, and variable leaf glaucousness with variable stem glaucousness in the west and non-glaucous stems in the east. Those near the coast or on lateritic soils in areas of higher rainfall have fruits with broad sometimes indistinct pedicels and non-glaucous leaves and stems. Forms growing in the Gawler and Flinders Ranges tend to have fruits of small size with distinct but often short pedicels, variable leaf glaucousness and non-glaucous stems. Operculum shape and and degree of ribbing varies greatly in many of these forms.

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12.5.2 Eucalyptus dumosa A. Cunn. ex Schau. ssp. clelandii (Maiden) Lang , comb. et stat. nov.

E. goniatha Turcz. var. clelandii Maiden, J. W. Aust. Nat. Hist. Sc. Soc. 3(1): 176 (1910) as " Clelandi ", basionym; --E. clelandii (Maiden) Maiden, Crit Rev. Gen. Euc. 2(16): 189, pl. 69, fig. 8 (1912) syn. nov.; loc. cit. 8(75): 274 (1931) seedlings; Blakely, Key Euc. 123 (1934); Gardner (1961) in Aplin, Euc. W. Aust. 225, fig. 91 (1979); Chippendale, Euc. W. Aust. Goldf. 153, figs (1973).

Type: " Lannin's Timber Camp, nearly 70 miles north of Kurrawang .... Goongarrie, 54 miles north of Kalgoorlie. ". Lectotype (here designated): J.H. Maiden s.n., 65 miles N. of Kalgoorlie, -.ix.1909 (NSW 47518) branchlet with fruits and buds. Isolectotype: ibid (NSW 47518) other specimens, (PERTH). Probable isolectotype: (K, n.v.). Syntype: J.H. Maiden s.n., 70 miles N. of Kurrawang, -.ix.1909 (NSW 47545). Probable syntype: (K, n.v.).

Common name: Cleland's Blackbutt

PJ Code: SLE:GM

Diagnosis

Tree to 12 m tall with a blackbutt of persistent, dark, thick, rough, flaky bark for 0.2 to 1.5 m. Branchlets densely glaucous, quadrangular becoming terete. Adult leaves narrow lanceolate, dull, moderately to densely glaucous, grey-green or greenish-blue. Mature buds: operculum rostrate or umbonate, ribbed to 0.3 - 0.7 mm deep. Mature fruits relatively small, 4.5 - 7.0 mm long, midwidth 4.5 - 6.5 mm wide, smooth or with shallow ribs less than 0.5 mm deep, distinctly pedicellate, pedicels

(1.5-)2.0 - 3.4(-4.3) mm long, (0.9-)1.1 - 1.7(-1.9) mm wide.

Figs: 104 (habit); 60, 97 to 99.)

Typification

In the original description of the variety Maiden mentions having collected it and gives observations made when standing before trees at two localities. Both are represented by extant herbarium specimens including sheets at NSW labelled by Maiden as E. goniatha var. Clelandi then altered to E. Clelandi. As Maiden is both collector and author all duplicates are treated as syntypes. This is contrary to annotations on the NSW sheets by Johnson who regards the Goongarrie specimen as holotype because of a later statement by Maiden when describing the taxon as a species. However, the Code states that a new name formed from a previously published legitimate epithet is, in all cases, typified by the type of the older name (Art. 7, para. 10). Maiden's later reference to the second collection as Type (1912, Crit. Rev. Gen. Euc. 2(16): 190) could be considered lectotypification. The case for this is better than that for E. sheathiana because reference is made at the same time to Lannin's Timber Camp material as another collection but clearly not the type. Nevertheless, it does not appear that Maiden was aware of making an explicit choice from among types. The best solution is to follow Maiden's apparent intention and choose a lectotype from the Goongarrie collection. The NSW sheet was chosen in preference to the PERTH one for the following reasons:

1. The former has branchlets bearing buds and fruits whereas in the latter the fruits are detached.
2. It is a more complete collection with bark and coppice leaves present
3. It is labelled by Maiden.

A single branchlet with five umbellasters of fruits is designated from the

loose material.

Flowering period: Mainly September to February but also at other times throughout the year.

Distribution (fig. 222): W.A.: Coolgardie, Austin and Helms Districts.

The principal occurrence is centred on the Goldfields district of Kalgoorlie and Coolgardie with a number of northerly outlying populations.

Ecology

Habitat: on slopes of low ironstone or schistose hills, on flat terrain or in depressions. The soil is sandy-, clay- or gravelly-loam with quartzite, laterite or limestone.

Average annual rainfall: 220 - 280 mm

Associated species: E. celastriodes, E. campaspe, E. salmonophloia, often with Atriplex spp. in the understorey.

Successfully cultivated in Adelaide and Perth under annual rainfall of at least up to 800 mm.

Notes

This taxon is an extreme form of the E. dumosa complex that approaches E. lesouefii in its habit, possession of a blackbutt and ribbing of fruits but does not intergrade continuously with it. Some forms of ssp. clelandii near Menzies could be interpreted as phantom hybrids with E. lesouefii. Intergrades with ssp. dumosa are common and there are intermediate

populations in outlying areas. There is often misidentification between ssp. dumosa (determined as 'E. striaticalyx') and ssp. clelandii and further material needs to be examined to clarify limits of the taxa.

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12.5.3 Eucalyptus dumosa A.Cunn. ex Schau. ssp. conglobata (R.Br. ex Benth.) Lang stat. nov.

E. dumosa A.Cunn. ex Schau. var. conglobata R.Br. ex Bentham, Fl. Austral. 3: 230 (1867), basionymn; --E. incrassata Labill. var. conglobata (R.Br. ex Benth.) Maiden, Crit. Rev. Gen. Euc. 1(4): 100, pl. 17, figs 1,2,5,6 (1904); Trans. Roy. Soc. S. Aust. 3(3): 281 (1908); Crit. Rev. Gen. Euc. 4(38): 220 (1919); --E. conglobata (R.Br. ex Benth.) Maiden, loc. cit. 6(56): 273 (1922) syn. nov.; Maiden, loc. cit. 8(75): 270 (1931) seedlings;Blakely, Key Euc. 117 (1934); Burbidge, Trans. Roy. Soc. S. Aust. 71(2): 151 (1947); Black, Fl. S. Aust., edn 2: 628 (1964); Chippendale, Euc. W. Aust. Goldf. 149, figs (1973); Boomsma, Native Trees S. Aust., edn 2: 136, fig. (1981).

Type: " Port Lincoln, Wilhelmi; S. Coast, R. Brown." Lectotype (here designated): R. Brown s.n., Bays 9 & 10 [Memory Cove (34 58 S 133 59 E) & Port Lincoln c. (34 44 S 135 52 E) , S. Aust.] s. dat. [22.ii.1802 & -.iii.1802] (K photo., right specimen). Isolectotypes: ibid (K, left specimen); s. nom. [C. Wilhelmi] s.n., Port Lincoln, s.dat. (K photo.); Carl Wilhelmii s.n., Port Lincoln proper, s. dat. (MEL 80653)); R. Brown (4749), South Coast Bays 9 & 10, s.dat. ((BM,K) photo., FRI(ex BM) 2 sheets, MEL 80652). Possible isolectotype: R. Brown s.n., s.loc., 1802-5 (MEL 80654).

[E. conglobata (R.Br. ex Benth.) Maiden var. anceps (auct. non R.Br.) ex Maiden, Crit. Rev. Gen. Euc. 6(56): 274 (1922) p.p [typo excluso (see 13.1)]; --E. anceps (R.Br. ex Maiden) Blakely, Key Euc. 118 (1934); Burbidge, Trans. Roy. Soc. S. Aust. 71(2): 151 (1947); Black, Fl. S. Aust., edn 2: 629 (1964); --E. conglobata [ssp. anceps]: Pryor & Johnson, Classif. Euc. 58, 65 (1971); --E. anceps: Chippendale, Euc. W. Aust. Goldf. 150, figs (1973); Boomsma, Native Trees S. Aust., edn 2: 112, fig. (1981).]

Type: "..the type which comes from Kangaroo Island "

Lectotype (here designated): R. Brown (4748), Kangaroo Island -.-.1802-5 (NSW sheet with JHM annotation (CSIRO neg. no. 4229)) [= E. rugosa R. Br. ex Blakely]. Isolectotypes: (NSW (CSIRO neg. no. 4168), (K sheets '1,2,3' ,BM 2 sheets) photo., (MEL 80646, FRI).

E. lamprocarpa F.Mueller ex Miquel, Nederl. Kruidk. Arch. 4: 129 (1856) p.p. [pedicellate specimens excluded]; Maiden, Crit. Rev. Gen. Euc. 1(4): 100 (1904).

Type: " In desertis Murray Scrub, Salt's Creek, Traveller's Rest, Ponindi, Angus park, &c. Novae Holl. Austr. (F.Muller)."

Probable syntypes: F. Mueller s.n., Murray Scrub, Salt Creek, Angas park ...?, s.dat. (U 63655B photo.); Mueller s.n. Murray Scrubs s.dat. (Herb. Vindob. n.v. - fide Maiden). Possible syntypes: Mueller s.n., Murray s.dat. (K photo.); s.leg. s.n., Desert, S. Austr. s.dat. (K (CSIRO neg. no. 617) photo.).

E. muelleri Miquel, Nederl. Kruidk. Arch. 4: 130 (1856) fide Maiden, loc. cit.

Type: " ad fl. Murray (F. Muller). "

Holotype?: F. Mueller s.n., ad fl. Murray in modum Pepper-Menth, Nova Holl. Aust. s.dat. (U 63667B photo.)

E. dumosa A.Cunn. ex Schau. var. rhodophloia Bentham, Fl. Austral. 3: 320 (1867) p.p. [type collection - excl. specimen in fruit]; Maiden, Crit. Rev. Gen. Euc. 1(4): 98, 123, pl. 21, fig. 1b (1904), under E. incrassata var. dumosa; Pryor & Johnson, Classif. Euc. 89 (1971), as "E. rhodophloia".

Type: " W. Australia, Phillips Bluffs, near Eyre's Relief, Maxwell. "

Syntype: (K n.v.) fide: illus. Maiden, loc. cit., pl. 21, fig. 1b; Brooker, Brunonia 2: 132 (1979).

[E. incrassata Labill. var. dumosa auct. non A.Cunn ex Schau: Maiden, Crit. Rev. Gen. Euc. 1(4): 97 (1904) p.p. [as to pl. 16, fig. 6 & p. 105 " sand plains north from the Stirling Range" only]]

Common name: Cong Mallee

PJ Code: SLE:GI

Diagnosis

Mallee or tree to 15m tall, entirely smooth-barked or with some basal rough bark but never a distinct blackbutt; branchlets non-glaucous, remaining slightly to strongly quadrangular. Adult leaves narrow to broad lanceolate, rarely ovate, with a dull sheen or glossy, non-glaucous, green or yellowish-green. Umbellasters: fruiting peduncles (3-)4 - 15 mm long, 3.6 - 7.3(-8.3) mm wide at mid-length, compressed or angular. Mature buds sessile; hypanthium smooth, not ribbed but often with 3 -4 costae; operculum conoidal, rarely hemispherical, with ribs 0.5 - 0.9 mm deep. Mature fruits cylindrical, doliform, truncate-hemispherical or discoidal, (3.0-)4.5 - 9.0(-10.0) mm long, midwidth (5.0-)6.5 - 9.5(-10.5) mm wide, sessile.

(Figs: 116 to 118 (habit); 62, 63, 78, 79, 114, 115, 138, 151, 240)

Typification

1. E. conglobata

This name was first used by Robert Brown on his own collections. Sheets at K and BM have labels in his handwriting: " 9th Eucalyptus conglobata Bays 9 and 10 South Coast". It was first validly published as a variety of E. dumosa in Flora Australiensis by Bentham who gave a brief description and cited the collections: "Port Lincoln, Wilhelmi; S. Coast, R. Brown". Bentham worked at Kew so sheets of these collections there would have been seen by him are therefore syntypes. I believe one sheet with the locality "Port Lincoln" and the name "E. pachyphylla F. Muell." is from the first collection despite its lack of a collector's name. It is labelled as having been named by Bentham in Flora Australiensis as a variety of E. dumosa. Maiden (p. 101) notes that the invalid name E. pachyphylla F. Muell. was applied to the Wilhelmi collection. The specimen matches a Port Lincoln specimen of Wilhelmi at MEL and agrees with the illustration of Maiden (1909, pl. 17, fig. 2a) in lacking buds and fruits and being at a late flowering stage with some stamens detached. The second locality is ambiguous and could refer to various specimens marked "South Coast", "South Coast Bays 9 and 10" (Port Lincoln proper and Memory Cove), or "Island vii, South Coast" (Kangaroo Is.) that are all consistent with Bentham's brief description. For lectotypification it would be best to consider material from Bays 9 and 10 only, since this is closest to the more specific Wilhelmi collection both geographically and morphologically, and unlike the Kangaroo Island material, is distinct from the subsequently described var anceps of Maiden. The sheet at Kew with the label Bays 9 and 10 by Brown has two substantial branchlets. Both have developing buds but one has mature fruits while the other has developing fruits. Since they could be derived from different trees, and more importantly, different localities on separate occasions, they are treated as individual syntypes.

The right hand specimen was chosen as lectotype due to the mature fruits which I consider provide the most definitive diagnostic characters.

When Maiden (1922, 6(56) p. 273) described the species E. conglobata, Bentham was not included in the author citation and a new type specimen (W. Gill Port Lincoln, South Australia, Dec. 1901) was designated as the type (p. 275). Maiden's illustration of this collection is consistent with Bentham's types and it does not seem that Maiden intended the name for a new taxon. He refers to Bentham's treatment and lists E. dumosa A. Cunn. var. conglobata (R. Br.) Benth. as a synonymn. Bentham's variety is therefore the basionymn and the selection of a new type is invalid.

2. E. anceps

See discussion in chapter 13.

3. E. lamprocarpa

Type status of the collections is unclear and there is no sign of determination or labels by Miquel. The material ranges from distinctly pedicellate, shortly pedicellate-subsessile to sessile. Sessile material should be chosen for a lectotype in accordance with the type description which states: " floribus sessilibus ". The only specimen of those seen which appears to be sessile is the left branchlet of U 63655B . No choice will be made until a search for further collections is made and actual specimens have been seen.

4. E. muelleri

I treat this as a synonym of ssp. conglobata since its type description also states: " floribus sessilibus ". This is supported by photographic evidence but the clarity is not good and it should be confirmed by examination of the specimen at Utrecht herbarium (U).

Flowering period: Mainly in February to April, with some flowering at anytime throughout the year (table 2.4).

Distribution (fig. 218): W.A.: Darling, Avon, Roe, Eyre and Coolgardie Districts; S.A.: Eyre Peninsula, Yorke Peninsula, Kangaroo Island, Southern Lofty, Northern Lofty, Murray and South-eastern Districts; Victoria.

The subspecies has a wide distribution in coastal and subcoastal areas of southern Australia with a major disjunction across the Great Australian Bight. It occurs in the Little Desert National Park and probably other areas in western Victoria but these are minor occurrences and are associated with intergradation to ssp. dumosa, as is the case with the more inland occurrences in South Australia. It is present on Boston and Taylors Island off the coast of southern Eyre Peninsula.

Ecology

Habitat: Grows on coastal plains in loams and sandy loams, sand dunes overlying clay, calcareous sand or calcrete; on dissected lateritic plateaus or other areas with lateritic soil; and sometimes on hillsides with skeletal soils or nearby areas of alluvial clay-loam.

Annual average rainfall: 300 - 700 mm

Associated species: Major associates include E. uncinata, E. tetragona and E. eremophila in Western Australia and E. rugosa, E. diversifolia, E. cneorifolia and E. foecunda in South Australia. It often occurs in mallee communities which have a sclerophyllous and not a chenopodiaceous understorey. Melaleuca uncinata (Broombush) is often present.

Notes

This is a somewhat artificial group embracing a wide range of forms which have sessile fruits. In particular fruit size and shape, peduncle shape, and leaf width show great variation. In addition to sessile fruits it is defined by the presence of non-glaucous leaves and angular or compressed peduncles, thus excluding sessile forms which occur occasionally in Flinders Range populations of ssp. dumosa. The most extreme forms occur in southern coastal areas and are very distinctive, having inflorescences that are highly conglomerate (fig. 151) with short peduncles and fruits. In more inland areas where its distribution overlaps that of ssp. dumosa it is less distinctive and often intergrades strongly with that subspecies. The taxonomic segregation of this group within the E. dumosa complex is meaningful on an ecological basis relating to water availability. This is apparent from the tendency for coastal habitats, high rainfall, and specialized sites of relict occurrences (with heavier-textured soils and/or greater catchment of run-off water).

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12.5.4 Eucalyptus dumosa A. Cunn. ex Schau. ssp. fraseri (Brooker) Lang, comb. nov.

E. conglobata (R.Br. ex Benth.) Maiden ssp. fraseri Brooker, Nuytsia 1: 251, figs 7,8 (1972) basionymn , p.p. [excl. sessile-fruited forms west and south of Fraser Range]; --E. fraseri (Brooker) Brooker, Aust. For. Res. 7: 66, fig. 2 (1976) syn. nov.

Holotype: M.I.H. Brooker 2472, 14 miles west of Balladonia, W.A., 14.ii. 1970 (PERTH). Isotypes: (AD, (ANU,BRI,CANB,FRI,GAUBA,K,MEL,NSW) n.v.)

Common name: I suggest the name Fraser Range Gum.

PJ Code: SLE:GJ

Diagnosis

Tree to 20 m tall, usually entirely smooth barked, but sometimes with some basal rough bark or a distinct blackbutt; foliage coarse. Branchlets non-glaucous, remaining quadrangular. Adult leaves thick and rigid, 25 - 45 mm wide, non-glaucous. Umbellasters: fruiting peduncles short and broad, (4-)5 - 7(-8) mm long, (3.2-)3.6 - 4.7(5.4) mm wide at mid-length, compressed-angular. Mature buds shortly pedicellate; operculum elongate, conoidal, often weakly contracted, 7 - 10 mm long, 5 - 6 mm wide, length/base-width ratio (1.25-)1.45 - 2.00(-2.25), with ribs 0.5 - 0.9 mm deep. Mature fruits relatively large, cylindroidal to obconoidal or doliform, (8.0-)9.0 - 12.0(-12.5) mm long, mid-width (6.5-)7.0 - 9.0(-9.5) mm wide, shortly pedicellate to subsessile, pedicels, broader than long, (0.7-)0.9 - 2.4(-2.9) mm long, (3.1-)3.5 - 5.4(-6.0) wide.

(Figs: 106,107 (habit); 64)

Flowering period: reported to flower in February.

Distribution (fig. 220): W.A.: Coolgardie district.

Ocurrs in isolated populations from Fraser Range to Balladonia HS, possibly further eastwards, and southwards to Mt Ragged.

Ecology

Habitat: on flat terrain in sandy loam.

Annual average rainfall: c. 250 mm

Associated species: E. oleosa , Melaleuca sp.

Notes

It intergrades with E. dumosa ssp. conglobata to the southwest and ssp. dumosa to the east. Brooker has determined material in the far west of South Australia as this taxon (pers. comm., 1982) but I know of no distinctive populations there. Large-fruited forms of ssp. dumosa in this area (previously regarded as forms of 'E. calcareana') may approach ssp. fraseri in a number of features but have narrower peduncles and usually lack an elongate operculum. There is a distinctive population with blackbutts near Fraser Range.

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12.5.5 Eucalyptus dumosa A. Cunn. ex Schau. ssp. georgei (Brooker & Blaxell) Lang , comb. et stat. nov.

E. georgei Brooker & Blaxell, Nuytsia 2: 224, fig. 3 (1978) syn. nov., basionymn.

Holotype: D.F. Blaxell W75/45, 159 km E of Hyden along the track to Norseman, Western Australia (32 15 S 120 23 E) 3.x.1975 (NSW n.v.).

Isotypes: (K n.v., FRI,PERTH).

Common name: Hyden blue gum.

PJ Code: SLE:GB

Diagnosis

Thin-stemmed mallee or slender tree to 6m tall, with smooth, whitish bark from the base and coarse foliage. Branchlets densely glaucous, reddish beneath wax, terete from an early age. Seedling leaves intensely glaucous. Adult leaves broad-lanceolate, thick and rigid, dull, moderately glaucous, pale blue-green or yellowish-green, with midrib often densely glaucous towards leaf base. Umbellasters: fruiting peduncles more or less terete. Mature buds: operculum short, hemispherical, 2.4 - 3.5 m long, length/base-width ratio (.40-).45 - .65 , with a short, obscure umbo often retaining calycine operculum, smooth or with slight striations less than 0.2 mm deep. Mature fruits relatively large, cylindrical to obconoidal, with relatively short and broad pedicels, (8.0-)0.9 - 12.0(-12.5) mm long, (6.5-)7.0 - 9.0 mm wide.

(Figs: 61, 112)

Flowering period: not known.

Distribution (fig. 221): W.A.: Roe District.

It has a restricted distribution in small isolated populations in the vicinity of the Johnston Lakes and westwards towards Hyden.

Ecology

Habitat: on low lateritic or sandy rises.

Annual average rainfall: 275 - 300 mm

Associated species: growing in pure stands with Casuarina sp., Acacia sp. and Triodia scariosa at the type locality.

Notes

This subspecies represents an extreme of the E. dumosa complex which approaches E. woodwardii in its relatively large fruits, coarse wide and thick leaves, heavy stem glaucousness and rather smooth buds, but there is no evidence of continuous gradation with this species. Towards Hyden it intergrades with E. dumosa ssp. dumosa.

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12.5.6 Eucalyptus woodwardii

E. woodwardii Maiden, J. W. Aust. Nat. Hist. Sc. Soc. 3(1): 42 (1910) as "Woodwardi"; republished in Crit. Rev. Gen. Euc. 2(16): 213, pl. 72, fig. 3 (1912); loc. cit. 7(64): pl. 261, fig. 19 (1925) seeds; loc. cit. 8(75): 274 (1931) seedlings; Blakely, Key Euc. 104 (1934); Gardner in Aplin, Euc. W. Aust. 42, fig. 11 (1979); Chippendale, Euc. W. Aust. Goldf. 143, figs (1973); Pryor, Aust. Endangered Sp.,Euc. 134, fig. (1981).

Type: " ... 120 miles east of Kalgoorlie, Transcontinental Railway Survey. Collected by Henry Deane ... May, 1909. ".

Lectotype (here designated): H. Deane s.n., ibid. (NSW 146917) branchlet with buds and fruits attached. Isolectotypes: (PERTH 4 sheets). Probable isolectotype: (K n.v.).

Common name: Lemon-flowered gum

PJ Code: SLE:A

Description

Slender, erect tree to 15m tall with straggling or pendulous branches supporting coarse foliage; entirely smooth-barked or with a little rough, brown bark at the base of the trunk, smooth bark deciduous, pale and whitish, grey, yellowish or pinkish-brown, sometimes in streaks or patches. Branchlets heavily glaucous, quadrangular, becoming terete. Seedling leaves: first (3) - 4 pairs decussate, elliptical grading to lanceolate, grey-green, subsequent leaves alternate, broad lanceolate, becoming glaucous; juvenile and coppice leaves ovate, densely glaucous. Adult leaves: lamina lanceolate or broad-lanceolate, sometimes ovate, thick and rigid, (90-)125 - 145(-160) mm long, (28-)31 - 42(-50) mm wide, (.45-).50 - .55(-.60) mm thick, dull with cuticular relief .035 - .060 mm high, moderately to densely glaucous, grey-green to greenish-blue or whitish, angle between secondary veins (65-)75 - 100(-110); petioles (21-)24 - 29(-31) mm long. Umbellasters 7- or 9-flowered, glaucous; fruiting peduncles (10-)14 - 22(-32) mm long, (2.0-)2.6 - 3.1(-3.6) mm wide at mid-length, thick and more or less terete, often reflexed. Mature buds smooth or only faintly striate; hypanthium obconical; operculum hemispherical with distinct rostrum, flush with hypanthium, 8 - 10 mm long by 8 - 11 mm wide, length/base-width ratio .90 - 1.05(-1.15), mid-width/base-width ratio .30 - .40(-.50), smooth or faintly striate with ribs less than 0.2 mm deep. Flowers: filaments bright yellow, stiff. Mature fruits campanulate (obconoid or cylindrical with a slight contraction in outline), (11.0-)11.5 - 12.5(-14.5) mm long, mid-width (9.5-)10.5 - 11.5(-12.5) mm wide, rim-width/length ratio (.85-).95 - 1.10(-1.25), mid-width/rim-width ratio (.75-).80 - .85(-.90), smooth or with faint undulate ribbing less than 0.6 mm deep; disc (1.5-)1.9 - 2.2(2.5) mm wide, sloping obliquely inwards to 1.6 -4.1 mm below rim

level;valves 4 - 6(-7) per fruit (average 4.6 - 5.3), tips exserted or just below rim level; pedicels (2.5-) 3.5 - 6.5(-7.0) mm long, 2.0 - 3.0(-4.0) mm wide.

(Figs: 58, 96)

Typification

Three of four sheets of duplicates at PERTH have labels denoting their origin from NSW or Sydney Botanic Gardens and can be assumed to have been seen by Maiden. Distribution of the collection back to its state of origin prior to Maiden's description is most unlikely. The sheet at NSW bears no marking by Maiden to give it special status as a type, so all the sheets with NSW labels are regarded as syntypes. The material at NSW was chosen for lectotype as it includes more complete specimens. As they are unmounted, the largest piece, which has both buds and fruits attached, is specified as the lectotype.

Flowering period: throughout the year, principally in July - December.

Distribution (fig. 223): W.A., Coolgardie District.

It is only known to occur in small stands at several disjunct localities between Karonie and Xanthus, to the east of Kalgoorlie.

Ecology

Habitat: low sandy ridges, in deep sandy loam or clay flats.

Annual average rainfall: c. 200 - 250 mm

Associated species: grows in pure stands.

It has been extensively cultivated in a range of soils under rainfall up to at least 700 mm p.a. and is tolerant of limestone. Blake (1981) classsed it has having a high salt tolerance on the basis of seedling survival in liquid culture of increasing salt concentration. In fact it had the highest tolerance of the 52 species tested (LD50 in liquid culture = 450 mM NaCl). It flowers from an early age, sometimes when less than a year old.

Notes

E. woodwardii is a distinctive taxon most closely related to E. dumosa ssp. georgei.

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12.5.7 Eucalyptus lesouefii

E. lesouefii Maiden, Crit, Rev. Gen. Euc. 2(16): 187, pl. 69, figs 5, 6, 7 (1912); Blakely, Key Euc. 123 (1934); Gardner in Aplin, Euc. W. Aust. 186, fig. 74 (1979); Chippendale, Euc. W. Aust. Goldf. 155. figs (1973).
Type: "Kalgoorlie" (J.H. Maiden) ". Lectotype (here designated): J.H. Maiden s.n., Kalgoorlie -.ix.1909 (NSW 47517) branchlet with buds and fruits. Isolectotypes: ibid (NSW 47517) other specimens,(PERTH). Probable isolectotypes: ((MEL,BM,K) n.v.)

Common name: Goldfields Blackbutt

PJ Code: SLE:N

Description

Tree to 14 m tall, trunk with a blackbutt of persistent, dark, rough, thick, flaky bark for 0.3 to 3.0 m, the remainder of trunk and branches with deciduous, smooth bark pale and whitish, grey, orange or brown, often in streaks or patches. Branchlets lightly to moderately glaucous, usually reddish beneath wax, quadrangular becoming terete. Seedling leaves: first four pairs decussate, elliptical grading to ovate, grey-green above, purple below, subsequent pairs alternate, grading to lanceolate and glaucous; juvenile and coppice leaves alternate, ovate to broad-lanceolate, thick and glaucous. Adult leaves: lamina narrow-lanceolate, thin, (95-)110 - 170(-200) mm long, (11-)14 - 21(-23) mm wide, .35 - .60(-.65) mm thick, glossy to dull, with cuticular relief .009 - .034 mm high, non-glaucous to moderately glaucous, sometimes densely glaucous, green, grey-green or greenish-blue, angle between secondary veins (35-)45 - 70(-80); petioles (17-)20 - 28(-32) mm long. Umbellasters 7-, sometimes 9- or 11-flowered, glaucous; fruiting peduncles (7-)9 - 18(-23) mm long, (1.4-)1.6 - 2.3(-2.6) mm wide at mid-length, terete to slightly flattened. Mature buds: deeply corrugated with narrow ribs; hypanthium obconical; operculum conical or turbinate, bluntly to prominently rostrate, sometimes with long beak, wider than hypanthium, 6 - 16 mm long by 5 - 9 mm wide, length/base-width ratio (1.00-)1.10 - 1.70(-2.05), mid-width/base-width ratio (.35-).40 - .65(-.70), sometimes becoming yellowish before anthesis, with ribs up to 1.5 - 3.0(-4.4) mm deep. Flowers: filaments creamy white, sometimes pale yellow. Mature fruits obconical to hemispherical, (6.5-)7.0 - 10.0(-11.5) mm long, midwidth (excluding ribs) 6.0 - 7.5(-8.0) mm wide, rim-width/length ratio (.75-).85 - 1.20(-1.25), mid-width/rim-width ratio (.70-).75 - .90, with ribs up to (0.9-)1.0 - 2.6 mm deep; disc 1.0 - 1.7 mm wide, nearly flat or

sloping inwards to 0.4 - 1.4 mm below rim level; valves (3), 4, (5) per fruit (average 3.7 - 4.6), tips exserted or below rim level; pedicels (2.0-) 2.5 - 6.4(-7.2) mm long, 1.2 - 1.8(-3.0) mm wide.

(Figs: 101 (habit); 57, 80, 95, 150, 236, 237)

Typification

As Maiden is both collector and author the duplicates are syntypes. Furthermore the PERTH material (and probably the other duplicates) is derived from NSW herbarium. A single large branchlet with buds and fruits attached is chosen as lectotype from the loose collection at NSW in preference to the PERTH sheet which has smaller more immature fruits.

Flowering period: October to March, also recorded in late August.

Distribution (fig. 224): W.A., Coolgardie, Austin, and Helms Districts.

The principal occurrence is in the goldfields area and particularly between Kalgoorlie and Norseman. There are isolated outlying populations to the west near Zanthus and at scattered localities to the north.

Ecology

Habitat: usually in flat areas in sandy-, calcareous- or gravelly- loam with quartzite, laterite or limestone gravel; sometimes on greenstone hills.

Annual average rainfall: c. 230 - 300 mm

Associated species: May be found with a wide range of eucalypts including E. corrugata, E. griffithsii, E. oleosa, E. flocktoniae, E. salmonophloia, E. torquata, E. dundasii and E. brockwayii. The understorey is often dominated by chenopods.

It has been widely cultivated in areas with rainfall from 200 to 700 mm p.a. Blake (1981) classed it as having low salt tolerance (LD50 = 190 mM NaCl).

Notes

E. lesouefii is a distinctive taxon related to the E. dumosa complex via E. dumosa ssp. clelandii. Leaf surfaces are often glaucous and dull, but are non-glaucous and shiny in the Norseman district and in forms from near Zanthus. The strongest affinity is with E. pterocarpa, particularly in the deeply ribbed Zanthus form. In the Menzies region there may be a breakdown in the diagnostic character of stem-glaucousness which helps to distinguish it from E. pterocarpa. Two individuals, (S.G.M. Carr 529, 530 - known to me from herbarium labels only) are reported to have non-glaucous buds and fruits except on reversion shoots.

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12.5.8 Eucalyptus kondininensis

E. kondininensis Maiden & Blakely, J. Roy. Soc. N.S.W. 59: 189 (1925); Maiden, Crit. Rev. Gen. Euc.7(69): 404, 448, pl. 280, fig. 3 (1928): Blakley, Key Euc. 122 (1934); Gardner (196?) in Aplin, Euc. W. Aust. Goldf. 152, figs (1973).

Type: " Kondinin ...(C.A. Gardner, Nos. 1843, 1966)". Lectotype (here designated): C.A. Gardner 1966, Kondinin, W.A. 9.vii. 1923 (NSW 47525)

large fruiting branchlet. Isolectotypes: ibid (NSW 47525) other specimens, (PERTH 4 sheets); C.A. Gardner 1843, ibid (NSW 146916, PERTH 4 sheets). Probable isolectotype: (MEL n.v.).

Common name: Kondinin Blackbutt

PJ Code: SLE:K

Description

Tree to 20 m tall, with a blackbutt of persistent, dark, rough, thick, flaky bark for up to 4 m, sometimes extending onto base of major branches, the remainder of trunk and branches with deciduous, smooth bark, pale and whitish, grey, yellowish or light brown, often in streaks or patches. Branchlets non-glaucous, quadrangular becoming terete. Seedling leaves pale green, non-glaucous, first 3 - 4 pairs decussate, elliptical, subsequent pairs alternate, grading to lanceolate; juvenile and coppice leaves alternate, ovate, thin and green. Adult leaves: lamina narrow-lanceolate or lanceolate, thin, (75-)95 - 110(-125) mm long, (8-)10 - 17(-20) mm wide, (.30-).35 - .40(-.45) mm thick, glossy or with dull sheen, rarely dull, with cuticular relief .009 - .034 mm high, non-glaucous, yellowish-green or green, angle between secondary veins (50-)60 - 75(-90); petioles (13-)16 - 19(-22) mm long. Umbellasters 7-flowered, non-glaucous; fruiting peduncles (5-)9 - 11(-13) mm long, 1.3 - 2.0(-2.3) mm wide at mid-length, flattened or angular. Mature buds: hypanthium cylindroidal or obconical, smooth to slightly striate; operculum conical, rostrate with long beak, flush to only slightly wider than hypanthium, 4 - 6 mm long by 3 - 5 mm wide, length/base-width ratio (1.05-)1.15 - 1.35(-1.45), mid-width/base-width ratio (.45-).60 - .75(-.80), often becoming yellow before anthesis, striate or ribbed, with

ribs up to .3 - .7 mm deep. Flowers: filaments white. Mature fruits obconical, (3.5-)4.0 - 6.0(-6.5) mm long, midwidth 4.0 - 5.0 mm wide, rim-width/length ratio (.80-).90 - 1.25(-1.35), mid-width/rim-width ratio (.80-).85 - .95(-1.00), smooth or with ribs less than 0.2 mm deep; disc 0.3 - 0.9 mm wide, sloping steeply inwards to 0.4 - 1.3 mm below rim level;valves 3 or 4 per fruit (average 3.1 - 4.0), tips slightly exserted; pedicels (0.5-) 0.7 - 2.2(-2.6) mm long, (0.9-) 1.2 - 2.2(-2.6) mm wide.

(Figs: 102, 103 (habit); 59)

Typification

The two collections cited in the protologue are here regarded as containing syntypes. Maiden's subsequent reference to the second collection as " the type " in a figure caption (1928, 7(69): 448) is not accepted as lectotypification for reasons discussed for E. sheathiana (p. 291). The two NSW sheets are labelled and named by Blakely and are clearly syntypes. One sheet at PERTH is a duplicate from NSW and, as it is unlikely to have been distributed back to Western Australia prior to the description, it is regarded as a probable syntype. Another seven duplicates of Gardner's two collections retained at PERTH are unlikely to have been seen by Maiden and Blakely and are isosyntypes. Two of these which have the collection numbers 1343 and 1466, I still accept as types. They are probably numbered in error since they match material of 1843 and 1966 respectively and there is a note by Gardner on one sheet stating that both 1343 and 1466 constitute the type.

Both of the syntypes have a good representation of material. Gardner 1966 is selected as lectotype in accordance with Maiden's possible intention and because its buds are more mature than those of 1843. As this is loose material a single branchlet is specified.

Flowering period: November and December, possibly continuing to February.

Distribution (fig. 225): W.A., Avon and Roe Districts.

It is confined to an area in the wheat-belt of southwestern Western Australia, southeast of Quairading to Newdegate and Pingrup.

Ecology

Habitat: typically found in a zone around the margin of salt lakes, or in clay flats or depressions. Soils range from heavy clay-loams to sandy or gravelly loams with limestone nodules.

Annual average rainfall: 330 - 380 mm

Associated species: in pure stands or with other eucalypts including E. melanoxylon, E. loxophleba or E. salmonophloia. Melaleuca sp. and chenopods are often in the understorey.

E. kondininensis is reputably highly salt tolerant and slow-growing. Gardner (Aplin, 1979) claimed it was the most salt tolerant of all Western Australian eucalypts, but this is not supported by recent experimental work of Blake (1981). Based on the survival of seedlings in a liquid culture of increasing concentration he classed it as having low tolerance (LD50 = 185 mM NaCl). It has been successfully cultivated at Adelaide, and at Ardrossan on coastal limestone.

Notes

This taxon shows affinities with two rather different extremes of the E. dumosa complex, namely E. dumosa ssp. clelandii and ssp. conglobata.

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12.5.9 Eucalyptus pterocarpa Gardner ex Lang , sp. nov.

Species nova Seriei Dumosarum affinis Eucalypto lesouefii Maiden a quo differt cortice trunci ubique laevi, foliis adultis nitidis flavido-viridibus non glaucis, ramulis inflorescentiisque non glaucis, operculo 1.4 - 2.1-plo longiore quam latiore, fructu alati latioibus ferenti, et inflorescentiis ex floribus 3, 5 vel raro 7 constantibus.

Holotype: G.M. Chippendale 154, 5.4 mi (8.7 km) W on road 6.8 mi (10.9 km) NW of Norseman 32 08 S 121 36 E, 12.iii.1967 (FRI 14482); Isotypes: (AD 967510517, PERTH s.n., (NSW, MEL, BRI) n.v.) .

E. pterocarpa is a new species in series Dumosae (see description, p. 279) with affinity to Eucalyptus lesouefii Maiden from which it differs principally in the following features.

1. The trunk is smooth-barked to the base, lacking the blackbutt of E. lesouefii.
2. Adult leaves are glossy, yellowish-green, and non-glaucous whereas in E. lesouefii they are green, grey-green or greenish-blue and may be dull and non-glaucous.
3. Branchlets and umbellasters are non-glaucous rather than glaucous as is usual in E. lesouefii.
4. The operculum is more elongate with a length/width ratio of 1.4 - 2.1 compared to 1.05 - 1.65 in E. lesouefii.
5. The fruits are larger with a length of 12.0 - 15.5 mm compared to 7.0 - 10.5 mm in E. lesouefii.
6. The ribbing on buds and fruits is extended to form "wings" and the maximum width (= 'depth') of wings on a fruit is 2.4 - 4.1 mm. In E. lesouefii fruits have ribs with a maximum depth of 1.6 - 2.1 mm.
7. Umbellasters are 3-, 5- or rarely 7-flowered whereas in E. lesouefii

they are usually 7-, and sometimes 9- or 11-flowered.

Common name: I suggest the name " Norseman Gum ".

PJ Code: SLE:O

Description

Tree to 13.5 m tall with slender, erect branches supporting flat canopy; entirely smooth-barked; bark deciduous, and whitish, light to dark grey or grey-brown in mottled streaks. Branchlets non-glaucous, remaining quadrangular. Seedling leaves grey-green, non-glaucous, first four pairs decussate, elliptical grading to ovate, subsequent pairs alternate, broad lanceolate; juvenile and coppice leaves not seen. Adult leaves: lamina lanceolate, thick and rigid, (95-)100 - 125(-145) mm long, (12-)13 - 24(-28) mm wide, .50 - .55(-.60) mm thick, glossy with cuticular relief .015 - .025 mm high, non-glaucous, yellowish-green, angle between secondary veins (45-)55 - 75(-90); petioles (19-)21 - 26(-28) mm long. Umbellasters 3-, 5- or rarely 7-flowered, non-glaucous; fruiting peduncles (6-)8 - 11(-15) mm long, (2.2-)2.6 - 2.9(-3.3) mm wide at mid-length, somewhat flattened. Mature buds deeply corrugated or winged; hypanthium obconical; operculum conical, rostrate with long beak, slightly wider than hypanthium, 11 - 20 mm long by 7 - 12 mm wide, length/base-width ratio (1.40-)1.45 - 2.00(-2.10), mid-width/base-width ratio .35 - .55(-.60), becoming yellow before anthesis, with wings up to 2.3 - 3.2 mm deep. Flowers: filaments creamy-white. Mature fruits obconical to hemispherical, (12.0-)12.5 - 14.5(-15.5) mm long, midwidth (excluding ribs) (6.5-)7.0 - 8.5(-9.5) mm wide, rim-width/length ratio (.65-).70 - .75(-.80), mid-width/rim-width ratio .70 - .85(-.90), with 9 -12 wings up to 2.4 - 4.1 mm deep; disc 1.3 - 1.8 mm wide, sloping inwards to 1 -2 mm below rim level; valves (3), 4, (5) per fruit (average 3.8 - 4.2), tips below rim level or slightly exserted; pedicels (5.5-) 8.0 - 10.5(-12.0) mm long,

(1.6-) 1.8 - 3.0(-4.1) mm wide.

(Figs: 100 (habit); 56)

Flowering period: includes October.
(Of the five collections of natural occurrences examined, only one, G.E. Brockway -.x.1942, was in flower.) A tree growing at the Waite Arboretum, Adelaide was observed in flower in late January and early February.

Distribution (fig. 226): Western Australia, Coolgardie district.

Eucalyptus pterocarpa has a very restricted distribution with known occurrences being confined to a small area under 20 km west to northwest of Norseman.

Ecology

Habitat: on flat terrain in heavy soils of clay, brown sandy loam or rocky red sand.

Altitude: c. 300m

Annual average rainfall: c. 275 mm

Associated species: Eucalyptus griffithsii, E. brockwayii and E. calycogona.

Eucalyptus pterocarpa has been widely cultivated and grows well in arid areas with a rainfall of 200 mm p.a. (Broken Hill, N.S.W.; Woomera, S.A.) and wetter areas with a rainfall of 500 - 600 mm p.a. (Glenmorgan, Qld.; Adelaide, S.A.).

Notes

This taxon has been known as an undescribed species for many years and corresponds to the code designation SLE:0 in the clasification of Pryor and Johnson (1971). The name E. pterocarpa was first used by C.A. Gardner on the herbarium specimen G.E. Brockway s.n.,-.x.1942 (FRI). In a later undated determination of this specimen he used the name E. corrugata var. pterocarpa. Apparently Gardner did not describe E. pterocarpa because of uncertainty about its status and affinities. In 1960 he referred to it as a form of E. lesouefii (Aplin, 1979, p.186). Gardner's opinion is expressed in a letter sent from the Conservator of Forests Mr B.H. Bednall to Dr Hj. Eichler in 1963 that was found associated with a specimen at AD. It quotes Mr R. Perry, Forestry Dept., Perth: " Gardner tells me that ... it seems to him that " pterocarpa " will not stand up as a distinct species and is possibly a variety of E. corrugata or E. lesouefii " . However, despite similarities to E. corrugata in the shiny,non-glaucous foliage, the non-glaucous stems and strong ribbing, it clearly belongs in series Dumosae with E. lesouefii on the basis of seed morphology. The Chippendale collection was chosen for the type in preference to the single sheet originally determined by Gardner because it has a better representation of fruits, a more precise locality and a number of duplicates.

Eucalyptus pterocarpa has been rarely collected, but herbarium annotations indicate that it is common in its area of occurrence. Trees are frequent over a distance of at least half a mile (0.8 km) and therefore would not be F1 hybrids. Although it is closely related to E. lesouefii and is included within the southern part of its range, the two species do not occur side by side and they show no intergradation. I observed E. lesouefii c. 10 km to the west of the E. pterocarpa locality but it did

not approach any closer than at least c. 5 km. Eucalyptus pterocarpa appears to be a discrete genetically isolated population and not a hybrid swarm involving E. lesouefii. Material of E. lesouefii that is closest in form to E. pterocarpa occurs in an isolated population near Cundeelee c. 120 km to the northeast. The nature of the barrier that has prevented gene exchange between E. pterocarpa and E. lesouefii is unknown. There are no obvious ecological factors that would account for habitat isolation. Flowering time does not appear to be the mechanism as records for E. pterocarpa overlap with the flowering period of E. lesouefii.

Specimens examined

D. Boland J345 10.3 km W along (L) turn-off, 10.3 km N of Norseman (= 14.6 km NW of Norseman), 11.xi.1970 (FRI) -- G.E. Brockway s.n., 16 km WNW Norseman, .x.1942 (PERTH,FRI) -- G.E. Brockway s.n., 14.5 km NW of Norseman, 20.viii.1963 (PERTH) -- G.M. Chippendale 154, 8.7 km W on road 10.9 km NW of Norseman (= 18 km WNW of Norseman), 12.iii.1967 (FRI holotype, AD, PERTH isotypes) -- C.A. Gardner s.n., 16 km W of Norseman, 20.vii.1963 (PERTH).

Figures 218 to 226: Distribution maps for Dumosae taxa.



Distribution of individuals sampled and included for numerical analysis in this study. These localities are listed in appendix 1.

resolution : grid cells of 0.5 degrees latitude
x 0.5 degrees longitude



Intergrade with E. dumosa ssp. dumosa
(as above)

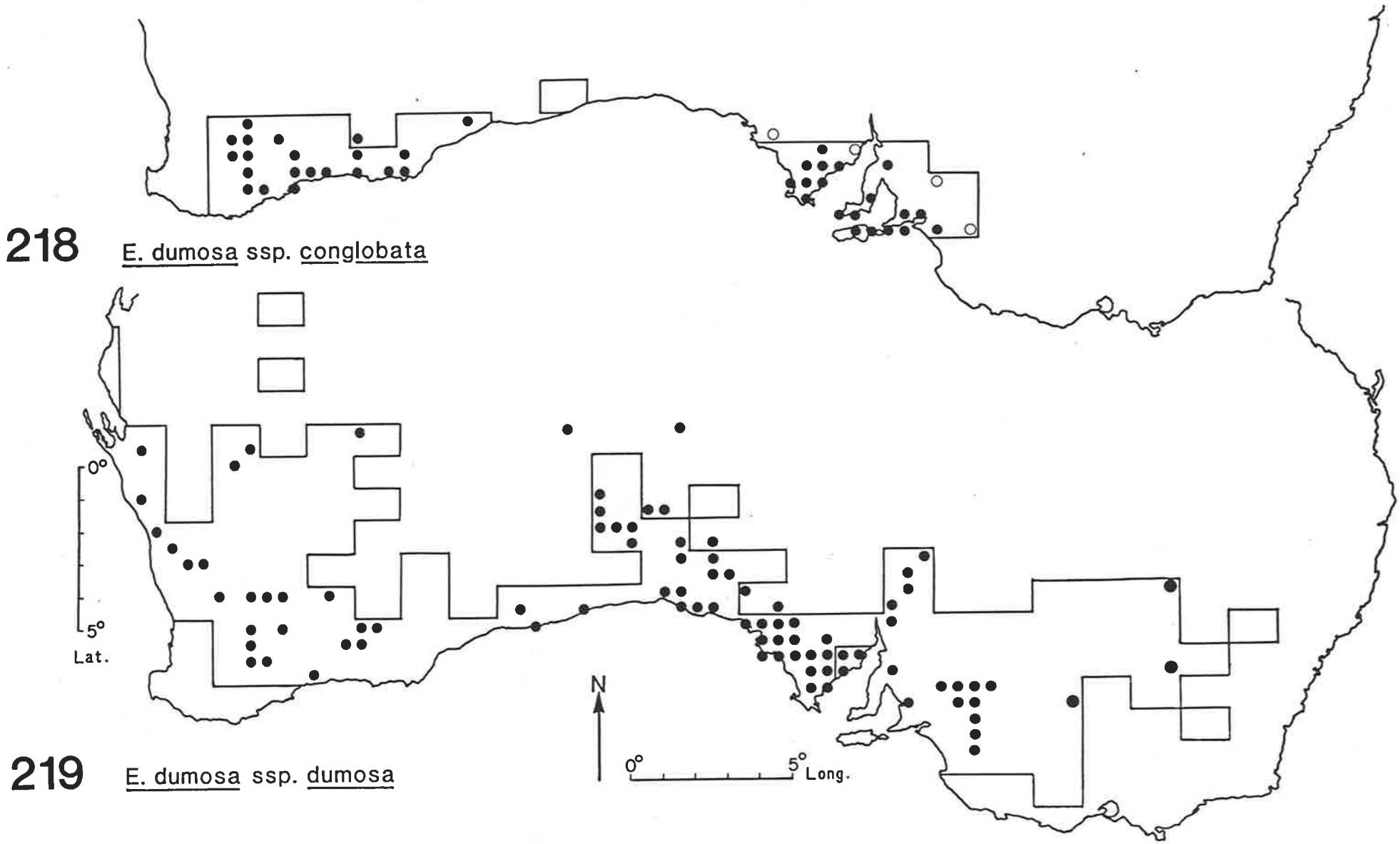


Outline of distribution given by Chippendale (1980) for equivalent taxa.

resolution : grid cells of 1 degree latitude
and 1.5 degrees longitude

SCALE:

1 degree latitude approximates 110 km
1 degree longitude approximates 95 km


218
E. dumosa ssp. conglobata
0°
5°
Lat.
N
0°
5°
Long.
219
E. dumosa ssp. dumosa

Figures 220 to 222: Distribution maps for Dumosae taxa.



Distribution of individuals sampled and included for numerical analysis in this study. These localities are listed in appendix 1.

resolution : grid cells of 0.5 degrees latitude
x 0.5 degrees longitude



Intergrade with E. dumosa ssp. dumosa
(as above)

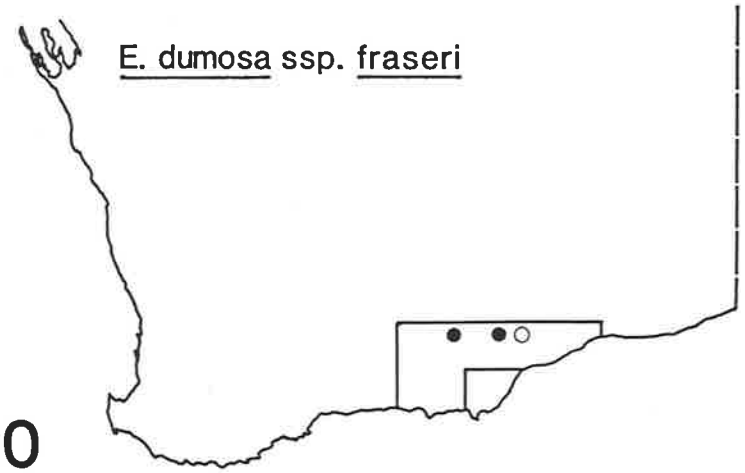


Outline of distribution given by Chippendale (1980) for equivalent taxon.

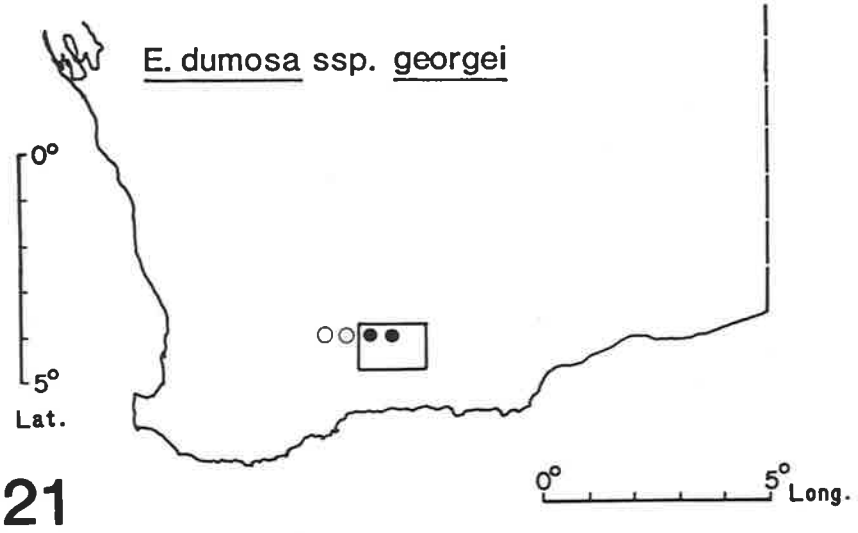
resolution : grid cells of 1 degree latitude
and 1.5 degrees longitude

SCALE:

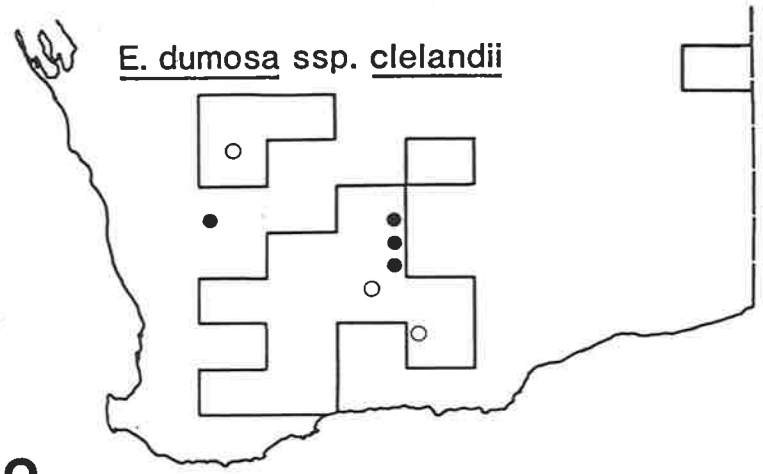
1 degree latitude approximates 110 km
1 degree longitude approximates 95 km


E. dumosa ssp. fraseri

220


E. dumosa ssp. georgei
0°
5°
Lat.
0°
5°
Long.

221


E. dumosa ssp. clelandii

222

Figures 223 to 226: Distribution maps for Dumosae taxa.



Distribution of individuals sampled and included for numerical analysis in this study. These localities are listed in appendix 1.

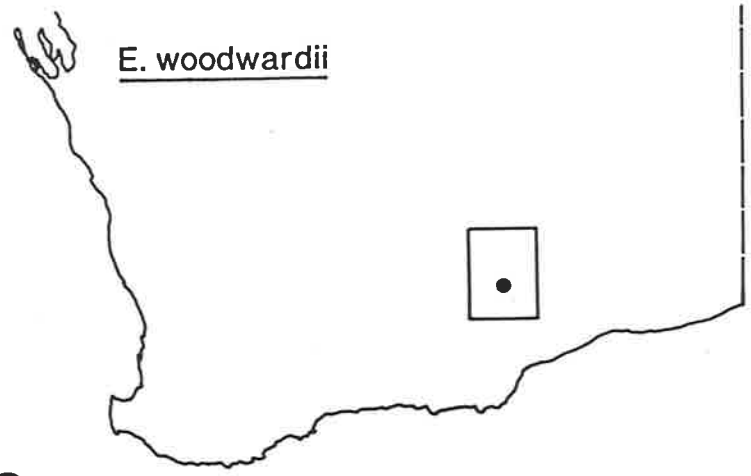
resolution : grid cells of 0.5 degrees latitude
x 0.5 degrees longitude

Outline of distribution given for taxa by Chippendale (1980).

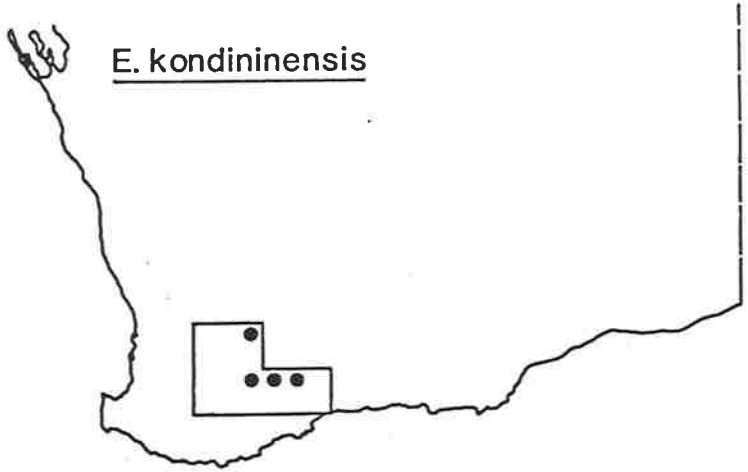
resolution : grid cells of 1 degree latitude
and 1.5 degrees longitude

SCALE:

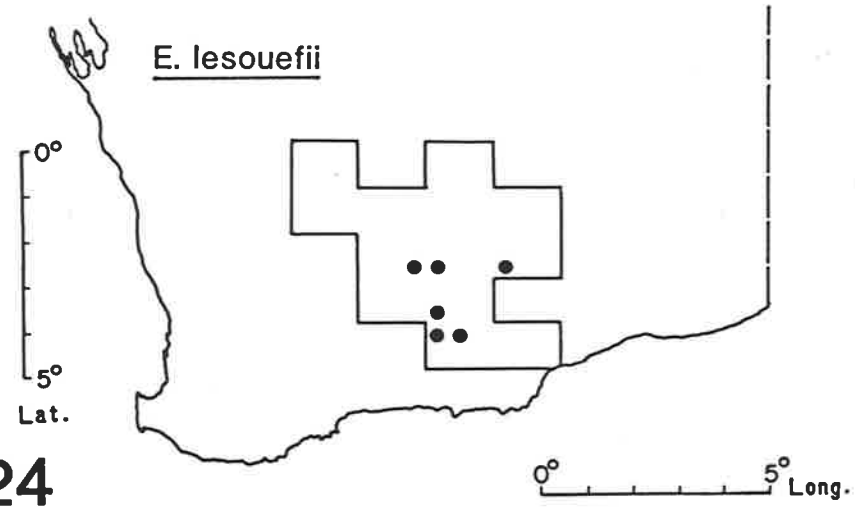
1 degree latitude approximates 110 km
1 degree longitude approximates 95 km



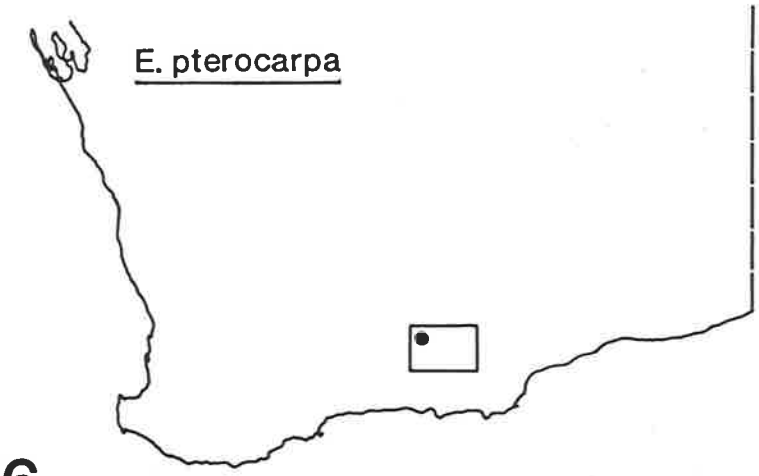
223



225



224



226

CHAPTER 13

NOMENCLATURAL PROBLEMS.

In this chapter problems involving type material are discussed for two taxa not considered in the the formal taxonomic treatment of chapter 12 . In both cases difficulties are compounded by confusion between series Dumosae and Torquatae.

Eucalyptus anceps was not treated in chapter 12 because I concluded that the entity to which it referred did not warrant taxonomic recognition. I have included most material determined as E. anceps, under E. dumosa ssp. conglobata. The choice of a lectotype for this name is discussed here as it is important to establish its status for use in synonymy or by other workers who may continue to recognize the taxon.

Eucalyptus rugosa belongs to series Torquatae, which is outside the scope of the taxonomic revision, but is discussed because it is frequently confused with members of Dumosae. It is not lectotypified here but problems are pointed out so that confusion can be minimized in any future revision.

13.1 Eucalyptus anceps

The name Eucalyptus anceps was first used by Robert Brown on herbarium labels for material he collected from Kangaroo Island in 1802, but was never published by him. The first description using the name "anceps" was published by Maiden in September 1922. This description is unusual as it is not set out formally but is included in the middle of a formal treatment for the new combination, Eucalyptus conglobata. Maiden (1922,

6(56), p. 274) cited "E. anceps R.Br." as a synonym of E. conglobata and then provided additional notes under this citation. He gave a brief description and diagnosis, referred to a "type (which comes from Kangaroo Island)" and established its known range by citing seven collections. The use of the name by Maiden as a synonym of E. conglobata, and earlier as a synonym of E. incrassata var. conglobata (Maiden, 1904, 1(4), p.100-101), does not constitute valid publication (I.C.B.N., Art. 34(4)). However, before continuing with his formal treatment of E. conglobata, Maiden concluded his discussion of the synonym E. anceps with the following statement:

"E. anceps is too near to E. conglobata and E. dumosa to be retained as a species, but it is worthy of discrimination and I propose the name E. conglobata var. anceps for it".

This is more than an incidental mention of the new name (I.C.B.N., Art. 34(3)) and the use of the word "propose" can be interpreted as indicating that Maiden was actually putting forward a new name rather than expressing intention to do so at a later date, thus satisfying part (2) of Article 34. Although there is no evidence for Maiden subsequently publishing this name, his acceptance of it is supported by his similar treatment of E. celastriodes Turcz. Maiden (1902) listed this as a synonym of E. calycogona and concluded by proposing the name of var. celastriodes for it. Subsequently, Maiden (1909, vol. I, p.80) cited this work as the original publication of the new combination E. calycogona var. celastriodes. Thus it is reasonable to treat E. conglobata var. anceps as a new name with the preceding discussion as the protologue.

The description of the species E. anceps by Blakely (1934) is also irregular and poses further nomenclatural problems due to his failure to include Maiden's name in the author citation "E. anceps (R. Br.) Blakely" or refer to a type specimen. The usual procedure would be to select a

lectotype for E. anceps on the basis of Maiden's protologue for E. conglobata var. anceps, but with these omissions in Blakely's treatment there is the possibility of choosing a type from Blakely's protologue instead. This could occur if Blakely's treatment is understood as being independent from Maiden's variety (and possibly based on different type material). In such a case use of the name "anceps" would be permissible, since a name must be of the same rank to be illegitimate as a later homonymn (I. C. B. N. Art. 64(1)). Blakely may have divorced his treatment from Maiden's in order to present a different, although obviously overlapping, taxonomic concept. This is difficult to evaluate because Maiden's description is so brief. Under this view it may be necessary to select an illustration cited by Blakely as the type, unless a specimen annotated by Blakely prior to publication in 1934 can be located. However, Blakely's intention is unclear and three other possibilities need to be considered.

1. Blakely may have incorrectly regarded E. anceps as an existing valid name from its use by Brown and believed that he was merely providing a description for it. Reference to Maiden's subsequent treatment at a lower rank would thus be unnecessary. There would be no need to provide a type which would obviously be Brown's material. In this publication ("A Key to the Eucalypts") Blakely frequently omitted to designate types for new taxa but usually cited one, or sometimes more, specimens clearly intended as types. This interpretation of Blakely's intention is supported by the absence of the designation 'sp. nov.' which he used when elevating other varieties to specific rank (e.g. E. punticulata and E. rhodophloia).

2. Blakely may have intended to create a species consistent with Maiden's variety but because of the format of Maiden's protologue did not recognize it as a valid description. Although he referred to Maiden's treatment with the words "as E. conglobata var. anceps", he may have rejected this as a valid name and therefore deliberately omitted Maiden

from the author citation.

3. Blakely may have merely intended to elevate Maiden's variety to a species but omitted citing Maiden in error. It is clear that he was familiar with the practice of citing the author of the basionymn in parentheses because he refers to "E. scyphocalyx (F.v.M.) Maiden and Blakely" together with the synonym "E. incrassata var. scyphocalyx ,F.v.M" in the same work. However, he also omitted author citations for "E. punticulata sp. nov." and "E. rhodophloia sp. nov.", so it is unclear whether it is likely to have been accidental or not.

Blakely's acceptance of Maiden's concept is supported by his reference to illustrations in Maiden's work and his use of the same six localities in indicating the range. As he made no explicit comparisons with Maiden's taxon, I conclude that the above three alternatives provide a better explanation than the view that Blakely rejected Maiden's concept. Thus in considering lectotypification of E. anceps it is necessary to return to Maiden's treatment of E. conglobata var. anceps. Clarification of the type specimen applying to this taxon is critical because the taxonomic identity of the currently accepted type material (R. Brown (Bennett) No. 4748, Kangaroo Is, South Coast) is in doubt. This problem will be described before discussing the choice of a type.

Negatives were obtained of the type material of E. anceps at KEW and BM. These included one specimen of Brown 4748 from BM which was not labelled as a type and lacked other annotations. However, it had been determined as E. rugosa by M.I.H. Brooker in 1977 and this prompted me to question the identity of the rest of Brown's collection.

Eucalyptus anceps and E. rugosa have been confused on Kangaroo Island for a long time. Nevertheless, the two taxa represented by these names can be readily distinguished by examining seeds to determine whether they belong

to Dumosae or Torquatae respectively. There is only one case known on Kangaroo Island (PJL 658) where there is a breakdown in seed morphology indicating hybridization. Most forms of E. rugosa are quite distinct from E. anceps in having well defined pedicels and a constriction at the operculum-hypanthium junction. No specimens of pedicellate Dumosae are known on Kangaroo Island. Reference to E. dumosa by Wood (1936) (as a co-dominant with E. oleosa in a major mallee association) and Lange (1979, p.74) probably refer to forms of E. rugosa. Distribution maps also indicate the confusion between E. anceps and E. rugosa. Boomsma's (1972) map for E. anceps showed a southern distribution across the whole island. Field observations and collections that I made on Kangaroo Island in 1977 established that, while E. rugosa is widespread, E. anceps does not occur west of longitude 137° 25' E, and its distribution was subsequently modified by Boomsma (1981). The confusion between E. conglobata and E. anceps was clarified by the SESSDAT study (chapter 3) which demonstrated that the Kangaroo Island material is better referred to E. anceps. A record of E. conglobata on the western end of the island at Yacca Flat near Cape de Couedic (C.M. Eardley s.n., ADW 5554) is the basis for a western occurrence on EUCALIST maps. This specimen has sessile fruits, but affinities with E. rugosa are evident in finer details of buds and fruits. Some material of E. rugosa on Dudley Peninsula and at West Bay is difficult to distinguish from E. anceps (or E. conglobata) without seed evidence. A population with a high proportion of strictly sessile specimens of E. rugosa occurs at West Bay - only 22 km northwest of Cape de Couedic. Fortunately I was able to extract a single seed from the Eardley specimen and verify determination as E. rugosa.

Recently Brooker (pers. comm. 1981) examined type material of E. anceps in London and concluded that the Brown 4748 collection is the same as E. rugosa and not the taxon referred to by current usage of E. anceps.

Subsequently I have studied duplicates of Brown 4748 obtained from FRI, MEL and NSW which confirm this determination. The buds are shortly and broadly pedicellate, costate with two major ribs, and are on broad, flat peduncles in groups of up to 11 (fig. 243, p. 359). In seven individuals sampled for the TYPDAT analysis of this study from the vicinity of Nepean Bay (in the region where Brown 4748 was collected - see 7.2, p. 134), the maximum number of buds per umbellaster was seven in all but one case where it was nine. In contrast, E. rugosa commonly has 11 or more buds.

It is evident from photographs that buds of most of the KEW and BM type specimens are consistent in form and development and suggest sampling of the same individual of E. rugosa, with two possible exceptions. One sheet at BM (identifiable by its FRI negative number: 372) has buds which appear more sessile and different in shape and may be E. anceps. The other exception involves a sheet at KEW labelled "sheet 2" by Chippendale which has to my knowledge the only fruits present for Brown 4748. Unfortunately these are not attached to fragments with bud material clearly belonging to E. rugosa that are also on this sheet. I believe the identity of the fruits is eqivocal. I can match them fairly well from my collections of E. anceps from the Nepean Bay area. They are smoother than usual for E. rugosa, but without seed a definite determination is impossible. The material could be mixed, as E. rugosa and E. anceps often occur in mixed stands on Kangaroo Island. I do not expect that examination of the actual specimens would enable either of these uncertainties to be resolved.

The reference by Maiden to "the type" from Kangaroo Island specifies the Brown 4748 collection, as no other specimens of the taxa are known from Kangaroo Island before 1909. To "represent" E. anceps, Maiden refers to to illustrations of Brown's specimens (Maiden, 1922, 6(56), figs 3a, 3b, 4). Figure 4 is of a Brown collection labelled "Island viii, South Coast". This is consistent morphologically with Brown 4748 and the locality is

probably Kangaroo Island, since this is the eighth of the island anchorages for Flinder's South Coast voyage listed by Maiden (1909). Figures 3a and 3b match exactly the specimens in bud and fruit on "sheet 2" at KEW. This sheet was inscribed by Maiden in 1901 as: "The only specimen of 4748 I have seen in fruit so far".

Two major alternatives for lectotypification of E. conglobata var. anceps have been considered. The first possibility is to choose a lectotype from the Brown 4748 collection. It can be argued that Maiden's reference to a type when discussing E. anceps can be taken as applying to E. conglobata var. anceps through the concluding statement proposing the new name. Logically this is consistent with the referral of the preceding description and diagnosis of E. anceps to E. conglobata var. anceps, which is necessary for the publication to be valid. With Brown 4748 as the lectotype, E. conglobata var. anceps would be a synonym of both the new name E. rugosa R.Br. ex Blakely and the new combination E. anceps (R.Br. ex Maid.) Blakely which were published together in 1934. Current usage could be maintained for E. rugosa by treating E. anceps as a synonym of the former rather than vice versa. A new name would only be required for what is currently referred to as E. anceps, whereas the reverse treatment would involve two changes.

According to an alternative argument, the seven collections used by Maiden to illustrate the range of E. anceps are also syntypes. With this view, although Maiden has obviously based his concept on Brown's material, Maiden is incorrect in referring to a type for E. anceps since it is not a valid name. Eucalyptus anceps cannot be a valid basionym (which is a "name" according to the definition of the Code) and its "type" therefore has no status for E. conglobata var. anceps. Technically, Maiden has not designated a type specimen for his description. This second view allows two further possibilities in choosing a lectotype. The choice of a Brown

4748 specimen has the advantage that it has the same outcome as the previously discussed alternative and any uncertainty about the validity of the other syntypes becomes irrelevant. The other possibility is to choose the lectotype from among the other seven collections cited. This has the advantage that a type can be chosen so as to maintain current usage for E. anceps as well as E. rugosa. Thus there is a conflict between technical correctness and maintaining nomenclatural stability. The seven collections cited by Maiden were obtained from NSW to assess their suitability for lectotypification. All belong to Dumosae and are determined in Maiden's handwriting as "E. conglobata (R. Br.) Maiden var. anceps Maiden". The two specimens of J.B. Cleland 19/Scrub near Bluff, Encounter Bay, are consistent with E. anceps despite the absence of peduncles noted by Maiden (1922, p. 274). This feature is associated with the phenomenon of 'twin umbellasters' which occurs occasionally throughout the Dumosae, and the specimens have some peduncles of normal length for E. anceps. However, apart from this abnormality, there is another reason for avoiding this sheet in choosing a lectotype: it is part of a mixed collection including two specimens consistent with E. conglobata s. str. on a sheet at AD (3.8). The collection: W. Gill, 3.vi.1903/near Murray Bridge, should also be avoided due to the presence of some subsessile fruits. Maiden implied in his diagnosis no difference from the sessile condition of E. conglobata. The remaining five collections are completely consistent with this diagnosis and with the existing concept of E. anceps which is represented by the group ANC in this study. I believe that the collection: J.H. Maiden, -.i.1907/Pt. Lincoln to Coffins Bay has the most suitable material for a lectotype. This sheet bears a "co-type" label and an annotation by L.A.S. Johnson dated 23.ix.1959 stating the view that the Brown specimen is the holotype.

Further light was thrown on this subject by Dr Hj. Eichler of Herbarium Australiense (pers. comm.) who expressed the opinion that it would best to follow Maiden's clearly expressed intention to base his taxon on the Brown collections and therefore treat the seven collections as paratypes. This stance was followed here and a lectotype chosen from R. Brown 4748 (12.5.3, p. 302) with the following considerations in mind.

1. Although it is tempting to choose in favour of maintaining nomenclatural stability, the two specimens that I regard as possibly being E. anceps are unsuitable candidates for lectotype because their identity is likely to remain uncertain.
2. Two sheets at NSW and another at K that are annotated or labelled by Maiden are definite syntypes and are given preference for lectotypification.

Material is equally well represented on these sheets and the annotated NSW sheet was chosen because Maiden worked at NSW herbarium and it makes the type more accessible to Australian taxonomists.

As E. anceps is designated as a synonym of E. rugosa, Dumosae material previously referred to as E. anceps requires a different name*. Fortunately the inconvenience and confusion that this outcome would have caused is avoided because of the conclusion in this study that such material is best treated as part of the same taxon as E. conglobata.

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* If E. anceps is regarded as being worthy of recognition as a separate taxon, contrary to the stance taken here, then it would be necessary to choose a lectotype from E. lamprocarpa and E. muelleri, two synonyms of E. dumosa ssp. conglobata (12.5.3).

13.2 E. rugosa

A similar case involving confusion between series Dumosae and Torquatae as described for E. anceps may also apply to syntype specimens of E. rugosa. This name was also applied by Brown as a manuscript name but was not validly described until Blakely's Key in 1934. In the protologue a Maiden specimen is designated as" co-type" but no other specimens are cited. Blakely may have neglected to mention another type specimen, either in error, or because he thought it was implicit in his treatment. If the latter is correct, then it is a R. Brown specimen that is implied. With the absence elsewhere of Brown's use of the name in writing, the author citation "(R. Br., Mss.) Blakely" becomes an indirect reference to this material. There are three sheets at KEW and BM of: R. Brown, South Coast (Bennett No. 4764) which are labelled as E. rugosa in Brown's handwriting. The possibility of the KEW material being implied as a syntype through the citation "R. Br. Mss.", was stated in an annotation on the KEW sheet by G. Chippendale, 19.i.1973. Blakely also referred indirectly to the Brown collections by citing an illustration provided by Maiden of a R. Brown specimen from "southern coast of Australia", and possibly by listing the locality of Fowlers Bay. Furthermore, it can be argued that Brown's material should be treated as including the type rather than just being syntypes of equal status to the designated co-type. It is unclear what Blakely meant to convey by the term co-type. The prefix "co" implies equal status with some other type specimen(s) making it equivalent to the current term syntype. However, this is contrary to Blakely's use of the term for E. apodophylla Blakely and Jacobs (Blakely, 1934, p.166). Here he referred to a specimen as "the type" and another as "a co-type". This usage makes co-type equivalent to a paratype.

Irrespective of the intended meaning of co-type, specimens on the three sheets labelled by Brown can be regarded as syntypes. All three present

problems for lectotypification. Although assigned the same number by Bennett (4674), Brown's labels refer to different collections. One sheet at BM is labelled "Memory Cove" (which is near Port Lincoln) and is clearly consistent with E. rugosa as currently applied. The other two sheets represented at KEW and BM are labelled "Bay III, South Coast" which corresponds to Fowlers Bay. The problem is that I believe the material on these two sheets is consistent with E. calcareana C.Boom. It has a strong resemblance to the Dumosae specimens (PJL 1194, 1191, 1193 - see figs 205, 206) collected near Coorabie, northwest of Fowlers Bay. I have observed E. rugosa (in the accepted sense) in this district but it is less common than Dumosae mallees referable to E. calcareana. Several features of the Brown material are more characteristic of E. calcareana than E. rugosa. The buds lack a constriction at the junction of operculum and hypanthium. This is extremely rare in Dumosae but common in E. rugosa. The KEW specimen has a single fruit with even striations (small ribs), and a truncate base with a well-defined pedicel. Usually in E. rugosa (and less commonly in Dumosae species) two or three ribs are developed more strongly into costae that are continuous with a more flattened, less distinct pedicel. These observations from photographs were confirmed by M.I.H. Brooker who, at my request, examined the KEW specimen while serving as Australian Liason Officer at Kew. Unfortunately no seed was present. Brooker (pers. comm.) pointed out that in the KEW specimen the operculum is slightly broader than the hypanthium. Based on his collecting experience confirmed by seed examination, he concluded that E. rugosa can have the operculum broader but it is more often narrower. This is consistent with Blakely's description where he says "Operculum ...broader than the calyx tube" and is further evidence supporting the status of R. Brown 4764 as a syntype. The specimens from Memory Cove are consistent with current usage of E. rugosa but have the operculum distinctly narrower, thus favouring the Fowlers Bay material for choice of

lectotype. However, Blakely is again ambiguous since, as Brooker noted, the latin diagnosis states "Operculum ...calycis tubo brevius" (operculum shorter than calyx tube). If Blakely made a slip of the pen it could be in the latin or english, but strictly the latin diagnosis should be followed. This is consistent with all the material.

From the protologue it appears that none of the potential type material is without problems. Before selecting a lectotype, duplicates of the Brown and Maiden collections should be sought from NSW herbarium. Any collections that have been seen and annotated by Blakely could resolve these ambiguities. If possible the Fowlers Bay material should be avoided for a lectotype as its identity must be regarded as uncertain without seed.

CHAPTER 14

INTERBREEDING AND RELATIONSHIPS WITH OTHER TAXA

14.1 Artificial Pollination Trials

These trials were performed to test for incompatibility mechanisms acting as a barrier to self-fertilization or gene exchange between different taxa. Pryor (1976, p.27) stated that self-incompatibility was general throughout the genus with a gene-controlled system being present in the few eucalypts critically examined. He noted that the extent of incompatibility was variable and that some species such as E. pulverulenta could contain self-incompatible, weakly self-compatible and some completely self-compatible individuals. From other cases reported in the literature it appears that self-compatibility is rather common in Eucalyptus. Isozyme analysis has indicated a significant rate of self-fertilization in natural populations of E. obliqua (Brown et al, 1975) and E. pauciflora (Phillips and Brown, 1977). Pryor (1951) showed that E. maidenii, E. blakelyi, and E. bicostata were self-fertile by artificial selfing of emasculated flowers and bagging experiments. Frequencies of lethal, recessive marker genes in seedlings of several E. leucoxylon individuals reported by Boland (1977) indicate that self-fertilization occurs under natural conditions. Self-fertilization varied from being predominant to less frequent than cross-fertilization. An individual of E. pilularis with a marker gene was reported by Florence (1969) where fertilization resulted almost entirely from self-pollination. Fruit set on isolated trees suggests that the extent of self-compatibility varies in different species and systematic groups throughout the genus (Pryor, 1976). From my own observations of isolated trees in cultivation it appears that self-compatibility is a common feature in section Dumaria.

It is important to remember that the existence of self-compatibility need not result in inbreeding due to the promotion of cross-pollination by protandry.

Incompatibility is only one of a variety of mechanisms that may operate to prevent or inhibit hybridization between different eucalypt taxa. Stigmatic secretions have been implicated in the inhibition of pollen tube growth. Pryor and Willing (1974) found that a light treatment of the stigma prior to pollination with an organic solvent such as hexane increases the likelihood of producing hybrids between incompatible pairs of Eucalyptus species.

Crossing experiments were made in mid-December on trees growing at the Waite Institute Arboretum, Adelaide. The following observations were based on trees of E. dumosa ssp. dumosa, E. dumosa ssp. clelandii and E. woodwardii at the Arboretum. Anther dehiscence (when pollen can first be shaken from anthers) occurs one day after the operculum becomes detached from the hypanthium. At this stage the stamens have unfolded from their inflexed position but are usually still bent at the middle of their filaments. Three to four days after operculum detachment the stigma begins to exude a sticky secretion. Pollen placed on it at this time is capable of germinating and growing into the style. This is similar to timing of stigma receptivity reported for other species of subgenus 'Symphomyrtus' by Griffin and Hand (1979).

Flowers on which the operculum was starting to separate were selected for emasculation. This was performed by cutting through the hypanthium collar just below the the staminal ring, taking care not to injure the style, then lifting the 'tube' of infolded stamens up and over the style. The flowers were then enclosed in glassine bags sealed with masking tape. Pollination was carried out four days after emasculation and flowers were

harvested after another four days. Transverse sections c. 1 mm thick were sliced from the top of the style and stained using the callose flourochrome reaction method described by Martin (1959) and Lalouette (1967). Successful results were obtained without adding K_3PO_4 or KOH. Sections were placed in 0.1 % aqueous aniline blue for two hours then examined under UV light using a microscope with epiflourescence optics. A bright green flourescence was obtained throughout pollen tube walls due to the presence of callose. The pollen exine flouresced pale yellow and an assessment of the success of pollination and pollen germination was made by examining the stigmatic surface on the uppermost section. In subsequent sections pollen tubes penetrating the style appeared as rings or sometimes as oblique cylindrical sections. Some of the tubes reached the base of the style.

Results are displayed in table 14.1. From the absence of germination in the emasculated controls it is apparent that the glassine bags provided an effective barrier to stray pollen. Thus all pollen and tubes observed are likely to have been derived from the manipulated pollen donor. The importance of natural pollinating agents is demonstrated by the second treatment where the opening buds were bagged without emasculation. Pollination was rather ineffective after the eight days tested. For E. dumosa and E.woodwardii no pollen grains or tubes were present except for a single tube in the former and one germinating grain in the latter. In E. torquata there was a small amount of pollen that had begun to germinate and only several tubes. In the third treatment with artificial pollination of emasculated flowers it is clear that the individuals of E. dumosa ssp. clelandii and E. torquata are self-compatible. Successful cross-pollinations were made between various species representing series Dumosae, Torquatae, and Tetrapterinae of section Dumaria, and sections Bisectae and Adnataria of sugenus 'Symphomyrtus'. Evidence of

Table 14.1: Results of artificial pollination trials.

Flower	Pollen donor	Germination	Penetration
1. Control (emasculated)			
E. dumosa	--	-	-
E. torquata	--	-	-
2. Not emasculated			
E. dumosa	self	-	(+)
E. woodwardii	self	(+)	-
E. torquata	self	(+)	(+)
3. Emasculated			
E. clelandii	self	+	+
E. torquata	self	+	+
4. Cross-pollination			
**E. dumosa* (a)	*E. lesouefii*	+	+
* "	*E. concinna*	(+)	-
* "	*E. tetraptera*	+	+
"	*E. foecunda*	+	+
"	*E. eremicola*	+	(+)
E. dumosa (c)	*E. torquata*	+	+
**E. woodwardii*	*E. clelandii*	+	+
* "	*E. torquata*	+	+
* "	*E. lansdowneana* (b)	+	+
E. torquata	*E. clelandii*	+	+
* "	*E. woodwardii*	+	+

* indicates replicate for fruiting

(a): ssp. *dumosa*
(c): ssp. *clelandii*

(b): ssp. *lansdowneana*

incompatibility was found only in two cases. In the E. dumosa ssp. dumosa X E. concinna cross some germination occurred but no pollen tubes developed sufficiently to penetrate the style. Without testing over a longer period this result is inconclusive. In the E. dumosa ssp. dumosa X E. eremicola cross pollen tubes were much narrower than in the others, were sinuous to irregularly convoluted, and had either no penetration or only shallow penetration within the the top millimetre section. It seems unlikely that fertilization could occur in this case. Eucalyptus eremicola has been placed in series Oleosae of section Bisectae (Boomsma, 1975). There is no evidence of hybridization between Dumosae and Oleosae species in the field despite the fact that they are freqently codominant. In the remaining crosses the results should be interpreted as indicating the absence of chemically induced barriers in the style. However, gene exchange may still be prevented by failure of fertilization or by post-zygotic mechanisms. The compatibility between E. woodwardii and E. lansdowneana (series Odoratae, section Adnataria) is not surprising because several natural hybrids between Dumosae and Odoratae are known (14.4.2).

Replicates of seven of the crosses (indicated in table 14.1) were retained on the trees but fruit set was achieved in only two of these: E. dumosa ssp. dumosa X E. lesouefii and E. woodwardii X E. torquata. Seed from the latter cross germinated and seedlings were raised that were intermediate between parental types in leaf glaucousness , thickness, and length/width ratio. Failure of fruit set for most crosses may have been caused by failure of fertilization or abortion of the zygote or embryo. However, there is insufficient evidence to infer the existence of reproductive isolation mechanisms. Abortion of fruits may also have resulted from very high ambient temperatures at the time of the crossings, injury or dessication due to to emasculation; or it may be a natural loss in

'thinning' the number of fruits developed.

Although limited in extent, these crossing trials have provided evidence of compatibility with some species of other series and sections.

14.2 Possible isolating mechanisms in series Dumosae

14.2.1 Pre-zygotic mechanisms

Three important pre-zygotic mechanisms are geographical isolation, flowering time differences, and pollen incompatibility. Distributions of Dumosae taxa are characterized by major disjunctions and isolated outlying populations. Even within their main areas of occurrence they frequently exist as series of isolated populations many kilometres apart. Maintenance of discontinuities over time is enhanced by the poor dispersal ability of seeds (15.2). The high level of morphological differentiation between the 'populations' noted in section 9.1.3 may be a result of geographical isolation restricting gene exchange and enabling divergence to occur. Within these populations (arbitrarily defined to be within a diameter of 1 km), distance would not present a barrier to pollination. Like most eucalypts, Dumosae are not adapted to specific pollinators and their open flowers with copious nectar attract a wide range of potential vectors. Various species of flies, bees, wasps, beetles (especially chafers (Scarabaeidae) and jewel beetles (Buprestidae)), lorikeets and honeyeaters have been observed feeding in flowers of Dumosae. Birds and the stronger fliers of the insects would be able to transport pollen over distances of one kilometre and more. As the pollen grains are small and non-clumping, some long distance wind pollination may occur. Rare dispersal events could enable gene transfer and provide effective migration of genotypes that would compensate for poor seed dispersal ability. For this to be successful it is probably necessary for the new

genetic information present in the hybrid and subsequent generations to have a definite selective advantage in order to become established amongst more numerous existing forms. There would be a high level of competition because of the high fecundity of the Dumosae which results in large seed crops, and their long life span which is associated with a low frequency of regeneration by seed in natural communities. Where there is no positive selective pressure and cross-pollinations are infrequent, distance could provide an effective barrier to gene exchange.

Pryor (1951) tested viability of stored pollen for artificial pollinations and concluded that separation of flowering times by as much as three months, and probably more, is not likely to be an obstacle to successful pollination. However, nothing is known about the survival of stray pollen from earlier flowering in the field or its availability to pollinating agents. Again, rare cross-pollination events will have little significance without a positive selective pressure because of the high level of competition. Higher levels of cross-pollination between populations could result in limited intergradation without entirely eliminating discontinuities of variation. This situation is suggested to explain the maintenance of '*E. cyanophylla*' forms in the Murray Region (11.3.4). Apart from this, flowering records of South Australian forms of *E. dumosa* presented in chapter 2 generally show too much overlap to maintain morphological disjunctions over a wide area.

There is no direct evidence for the operation of genetically controlled incompatibility systems within Dumosae. Only two crosses were made between pairs of Dumosae taxa in pollination trials (14.1) and further investigations are desirable. The abundance of intergradation within *E. dumosa* indicates that incompatibility is not a widespread barrier.

14.2.2 Post-zygotic mechanisms

Two important post-zygotic mechanisms involve the fitness of the resultant hybrid. Hybrids may abort soon after fertilization due to genic disharmony, or exhibit reduced viabilty, sterility or reduced fertility. Habitat or ecological isolation is a special case where hybrid fitness is critical in relation to specific environments. In hybrid offspring new gene combinations that deviate significantly from that of the parent may be unable to establish or survive in the parental habitat and new 'intermediate' habitats may not exist. Gene exchange will be constrained by selection favoring parental combinations. Habitat isolation assumes that there is a close link between genotype and environment, although this link may not be obvious. Part of the genotype is expressed in the morphological characters which are the basis for the classification. For many characters such as stem glaucousness, fruit ribbing and operculum shape, it is difficult to envisage any current adaptive signficance, and invisible biochemical and physiological attributes may be more important. It is apparent that the Dumosae, like many other eucalypt taxa, are able to tolerate a wide range of edaphic and climatic conditions. In arboreta and plantations many different taxa and forms of Dumosae are able to grow well under the same conditions. This seems to counter field evidence of adaptation to specific habitats. However, survival may be critical at the seedling stage which is usually nurtured even in plantations otherwise relying on natural rainfall. Another difference in natural communities is the factor of competition which heightens the influence of selection. These considerations show that habitat isolation may be difficult to demonstrate. Where habitats are not discrete, incomplete isolation may occur. A study of clinal variation in E. urnigera on Mt. Wellington by Barber and Jackson (1957) provides an excellent example of this. There was a complete change in frequency of glaucous individuals from 0 % to 100 %

over an altitudinal change of 400 - 500 feet (0.8 - 1.6 km ground distance). Clinal variation in numerous other characters was associated with this. Examination of seedling progeny showed that there was some cross-pollination of glaucous and non-glaucous forms over a much greater distance but natural selection reduced the cline to a narrow zone of intergradation separating the two forms. Habitat isolation may also involve pre-zygotic isolation by a reduction in cross-pollination due to spacial separation of habitats within the one region.

14.2.3 Coherence

Another mechanism restricting gene exchange is the phenomenon of coherence whereby random recombination between characters in hybrid populations is restricted so that hybrids tend to resemble one or other of the parents. Hartley (1965) attributed this to a system of partial linkage resulting from multiple gene control of characters. Hartley suggested that this could enable considerable maintenance of specific identity, which coupled with ready interspecific hybridization would allow for extensive introgression and account for the high genetic component of variance common in Eucalyptus .

14.3 Sympatric populations of series Dumosae

The abundant intergradation in morphology described for E. dumosa ssp. dumosa in chapter 11, and to a lesser degree for the other taxa in chapter 10, is indicative of a general lack of isolating mechanisms within the Dumosae. Some of the taxa have distributions with partial overlap when considered on a broad scale. For example, E. lesouefii, E. pterocarpa and E. dumosa ssp. dumosa all occur near Norseman, and E. woodwardii and E. lesouefii occur near Zanthus. However, on a local scale at distances of

only several kilometres there is little intermingling and truly sympatric populations do not occur in these cases. Zones of overlap comprise isolated populations separated by at least several kilometres. Distribution overlaps for some of the forms previously recognized as taxa (Chippendale and Wolf, 1981) do not involve distinct forms but are areas with complex intergradation. However, there are some notable exceptions to these patterns. For this thesis over 200 populations of Dumosae were sampled with each population being contained within a diameter of one kilometre. Only six of these could be regarded as comprising more than one interbreeding group (or population in a strict sense). These were the only cases encountered where distinct forms (differing in more than just a low-state character - LG, SG, or BB) occurred together without a breakdown in morphological variation indicative of local intergradation. The six cases of sympatric populations are listed in table 14.2 as evidence for the existence of intrinsic barriers to gene exchange within the Dumosae. In the taxonomy proposed in this thesis the distinct forms are recognized as different species in one case, as different subspecies in three cases but are not taxonomically recognized in two cases. The possible role of the above mechanisms in these cases will now be considered.

Firstly it is necessary to assume that the concurrence of distinct forms is <u>not</u> a result of recent migration of one form from a separate area. In this situation the absence of intergrades may merely mean that conditions have not yet been suitable for establishment of new progeny. This is a reasonable assumption because of the poor dispersal ability. A chance migration from a disjunct area would most likely involve one or a few individuals in a given area and would not produce a stand of normally spaced trees until the second generation. Most forms are represented by at least 10 individuals. The exceptions are case 6 where there was only a

Table 14.2: Sympatric occurrences of distinct forms.

Locality/collection Taxon	Determination (DPOP group)
1/ 14.0 km E Lake Grace (Roe District)/PJL 1415	
E. kondininensis	KON
14.7 km E Lake Grace/PJL 1416-1419	
E. dumosa ssp. *dumosa*	SHE
2/ 13.6 km N Minnipa (Eyre Peninsula Region)/PJL 1033	
E. dumosa ssp. *dumosa*	PIL
14.2 km N Minnipa/PJL 1032	
E. dumosa ssp. *dumosa*	CYA
3/ 0.4 km E Burngup (Roe District)/PJL 1421, 1423, 1425, 1426	
E. dumosa ssp. *dumosa*	PIL
/PJL 1422, 1427, 1428	
E. dumosa ssp. *dumosa*	SHE
4/ 19.3 km N Pingrup (Roe District)/PJL 1407-1410	
E. dumosa ssp. *conglobata*	ANC
/PJL 1406, 1411	
E. dumosa ssp. *dumosa*	PIL
5/ Carappee Hill (Eyre Peninsula Region)/D.E. Symon 8856 (ADW)	
E. dumosa ssp. *conglobata*	ANC
/PJL 1044, 1045 et al	
E. dumosa ssp. *dumosa*	CAR
6/ 2.6 km NW Kulin (Roe District)/PJL 1435-1439	
E. dumosa ssp. *conglobata*	ANC
/PJL 1436	
E. dumosa ssp. *dumosa*	SHE

single individual of E. dumosa ssp. dumosa, and case 5 where the abundance of E. dumosa ssp. conglobata is unknown.

For all cases, geographical isolation can be eliminated as the factor maintaining morphological disjunction. Only in cases 1 and 2 is there significant spatial separation between forms, but less frequent cross-pollination could not account for the total absence of intergradation in these cases. Differences in flowering time are possible mechanisms at two localities: case 3 which was discussed earlier (section 11.3.2, p. 230, 231), and case 4. When the latter site was visited in late November the pedicellate forms (PIL) were flowering whereas the sessile forms (ANC) only had buds that were not quite mature. Similar forms of E. dumosa ssp. dumosa and ssp. conglobata occur northwest of Ravensthorpe. On collections of E. pileata (= ssp. dumosa) from this area by C.D. Boomsma, E. conglobata is cited as an ecological associate. The population of ssp. dumosa representing the type locality of E. pileata at Desmond is situated between occurrences of ssp. conglobata northwards near Ravensthorpe and as close as 8.3 km to the south. Other herbarium collections support the distinctness of ssp. conglobata and ssp. dumosa in the Ravensthorpe district. The maintenance of these forms in this wider area also suggests that some factor other than spatial isolation has been involved in past. In another state (South Australia) these two subspecies frequently intergrade morphologically on a wide scale. The barrier is therefore probably a mechanism under genetic control such as incompatibility or flowering time. This is supported by case 5 which provides is a further example of inconsistent behaviour for ssp. conglobata. Since I have not found it in my survey of Carappee Hill, and as there is only a single collection from this intensively collected locality, it must be restricted in distribution compared to the abundant glaucous-stemmed forms of ssp. dumosa. Another equally distinctive

specimen of ssp. conglobata from Darke Peak (leg. S. Culic, L.D. Williams 9056) is likely to have been growing near these forms. However, at two outlying localities where there are intergrades of the glaucous-stemmed forms with other ssp. dumosa forms, gradation with ssp. conglobata is also apparent (PJL 1071, C.D.Boomsma 408).

There were no observable differences in soils or topography which suggested habitat isolation as a factor except in the two cases with a spatial separation of forms. In case 1, the two species were clearly associated with different habitats. There was a stand of E. kondininensis trees confined to a narrow zone near the edge of a salt pan. About 700 m away E. dumosa occurred as a slender mallee form on low sand dunes. Case 2 was less obvious because the two forms are from the same taxon and can not even be confidently referred to pre-existing species. The first form has relatively narrow, non-glaucous leaves and small fruits, and was growing in loam with scatttered calcrete gravel on a small flat in association with E. brachycalyx and E. diversifolia. The single individual sampled from this population was classified to the group PIL by all CVA's of appendix 1. The second form has broad, glaucous leaves and large fruits, and was growing on the crest of a small dune of loamy sand overlying sandy clay loam at a depth of 50 cm. The single individual sampled from this population was classified to CYA by all CVA's. It also shows affinities to some of the forms occurring on desert dunes further northwest which have been referred to E. striaticalyx. The characteristics differentiating these forms are not environmentally induced since they are retained by 'E. pileata', 'E. cyanophylla' and 'E. striaticalyx' growing in the Waite Institute Arboretum, Adelaide. The above two habitats are representatives of the two major plant community types in mallee areas of South Australia as described in section 12.5.1, p. 296, 297. A similar case was observed at Koongawa and probably occurs

elsewhere on Eyre Peninsula where these two habitat types are prevalent. However, the concurrence of the two distinct forms is only one facet of the total variation pattern. Elsewhere the two habitat types may be separated sufficiently for geographical isolation or occur in proximity without morphological differentiation of E. dumosa forms. Sometimes E. dumosa may be absent from one of the habitats or there may be intermediate habitats with intermediate forms or a gradation of forms. Even without maintaining distinct entities by reproductive isolation, natural selection is responsible for maintaining much morphological variation.

Case 3 is also of interest because of the possibity of limited gradation (11.3.2). The forms most similar to group SHE approach PIL in some features although a discontinuity in variation is maintained. This may be a case where a strong coherence is maintained by correlation between the stem glaucousness character and other morphological features either under current intergradation or past introgression. This possibility could be tested by studying character segregation in artificial hybrids of the two forms.

14.4 Hybridism between Dumosae and other series

From experimental crosses and occurrences of natural hybrids it is clear that each of the subgenera of Eucalyptus is genetically isolated from all the others, whereas within them hybrids are frequent and fertile. Inter-sectional hybrids are much less common than intra-sectional crosses but are known in quite a number of cases (Johnson, 1976).

The best known hybrid involving series Dumosae is the cross E. woodwardii X E. torquata which is widely cultivated as an ornamental tree known as 'Torwood'. The hybrid first arose from two adjacent parent trees planted at Kalgoorlie (Wallace, s.dat.). This is an indisputable case of

hybridism because of the distinctiveness of the parent species and the known history of crossing. It is useful to consider the way that seed testa characters are inherited in a known hybrid, since intermediate seed types are important as evidence of naturally occurring putative hybrids. Several Torwood trees planted in Adelaide were found to produce only occasional seeds of variable morphology, with some trees having fruits that were completely barren (PJL 1575 to 1577, 1580, 1581). The source for seed supplied to nurseries in South Australia was tracked down to two individual Torwoods in the town of Three Springs in Western Australia. These produced abundant seed which was intermediate between the Dumosae and Torquatae types in structure and colour but variable in their approach to each type. By contrast, hybrid seed that I produced by pollinating E. woodwardii with E. torquata pollen (14.1) was typical of series Dumosae in structure but was uniform and approached Torquatae seed by being brown rather than reddish in colour. Its hybrid nature was confirmed by seedling morphology. The reason that hybridity was not expressed in structural features of the testa may be a result of dominance of Dumosae characters in the F1 generation or determination by ovary wall in parent tree. However, it is clear from an examination of Torwood seeds that hybrid trees do produce intermediate seeds. Where natural hybridism was suspected on the basis of morphological features of buds and fruits, seeds were found to be intermediate between the typical forms for the parent series described in section 12.2.2. Seven cases of putative hybrids were discovered and are listed in table 14.3. Some evidence is illustrated here from buds and fruits (figs 236 to 242) and seed morphology (figs 237 to 235).

Table 14.3: Occurrences of putative hybrids.

Locality/collection Parent taxa	PJ Codes *
1/ c. 8 km WNW Cape Willoughby (Kangaroo Is.)/PJL 658 *E. dumosa* ssp. *conglobata* X *E. rugosa*	SLE:GI X SLI:A
2/ 10 km SE Warooka (Yorke Peninsula)/PJL 799 *E. dumosa* ssp. *conglobata* X *E. rugosa*	SLE:GI X SLI:A
3/ 3 km S Lochiel (Northern Lofty)/PJL 870 *E. dumosa* ssp. *conglobata* X *E. rugosa*	SLE:GI X SLI:A
4/ 18.3 km SE Widgiemootha (Coolgardie)/PJL 1558 *E. lesouefii* X *E. torquata*	SLE:N X SLI:M
5/ 7 km NW Victor Harbour (Southern Lofty)/PJL 1595, 1596 *E. conglobata* ssp. *conglobata* X *E. incrassata*	SLE:GI X SLOAB
6/ Folland Park, Enfield (Southern Lofty)/PJL 774 *E. dumosa* ssp. *dumosa* X *E. odorata*	SLE:GA X SUNEB
7/ 5 km NW Goolwa (Southern Lofty)/PJL 767 *E. dumosa* ssp. *conglobata* X *E. odorata*	SLE:GI X SUNEB
8/ 2 km N Finniss (Southern Lofty)/PJL 85 *E. dumosa* ssp. *conglobata* X *E. odorata*	SLE:GI X SUNEB

* PJ Codes indicate proximity in taxonomic hierachy. Successive letters indicate taxa for categories: subgenus, section, (subseries), species and subspecies.

Figures 227 to 235: Seed morphology in putative hybrids.

Scale bar: 2 mm

The right hand seed of each figure is in ventral view; the others are shown in dorsal view.

227: E. dumosa ssp. conglobata
PJL 659/8 km WNW Cape Willoughby, Kangaroo Is.

228: E. rugosa X E. dumosa ssp. conglobata
PJL 658/l.c.

229: E. rugosa
PJL 728/Kangaroo Is.

230: E. lesouefii
PJL 1545/18.3 km SE Widgiemootha

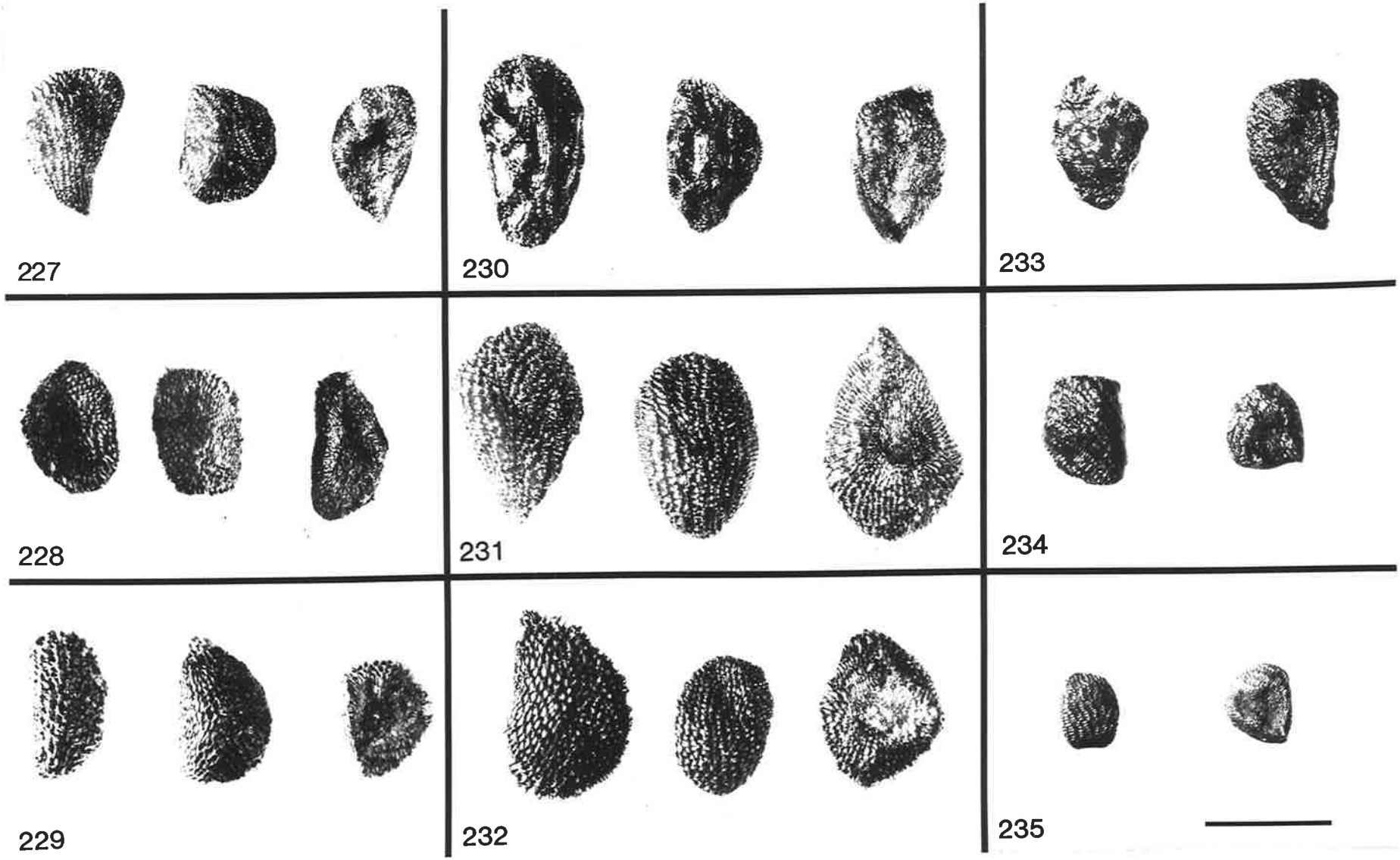
231: E. lesouefii X E. torquata
PJL 1558/l.c.

232: E. torquata
PJL 1560/l.c.

233: E. dumosa ssp. conglobata
PJL 763/5 km NW Goolwa

234: E. dumosa ssp. conglobata X E. odorata
PJL 767A/l.c.

235: E. odorata
PJL 765/l.c.


227
230
233
228
231
234
229
232
235

Figures 236 to 239: Putative hybrid between species from series Dumosae and Torquatae.

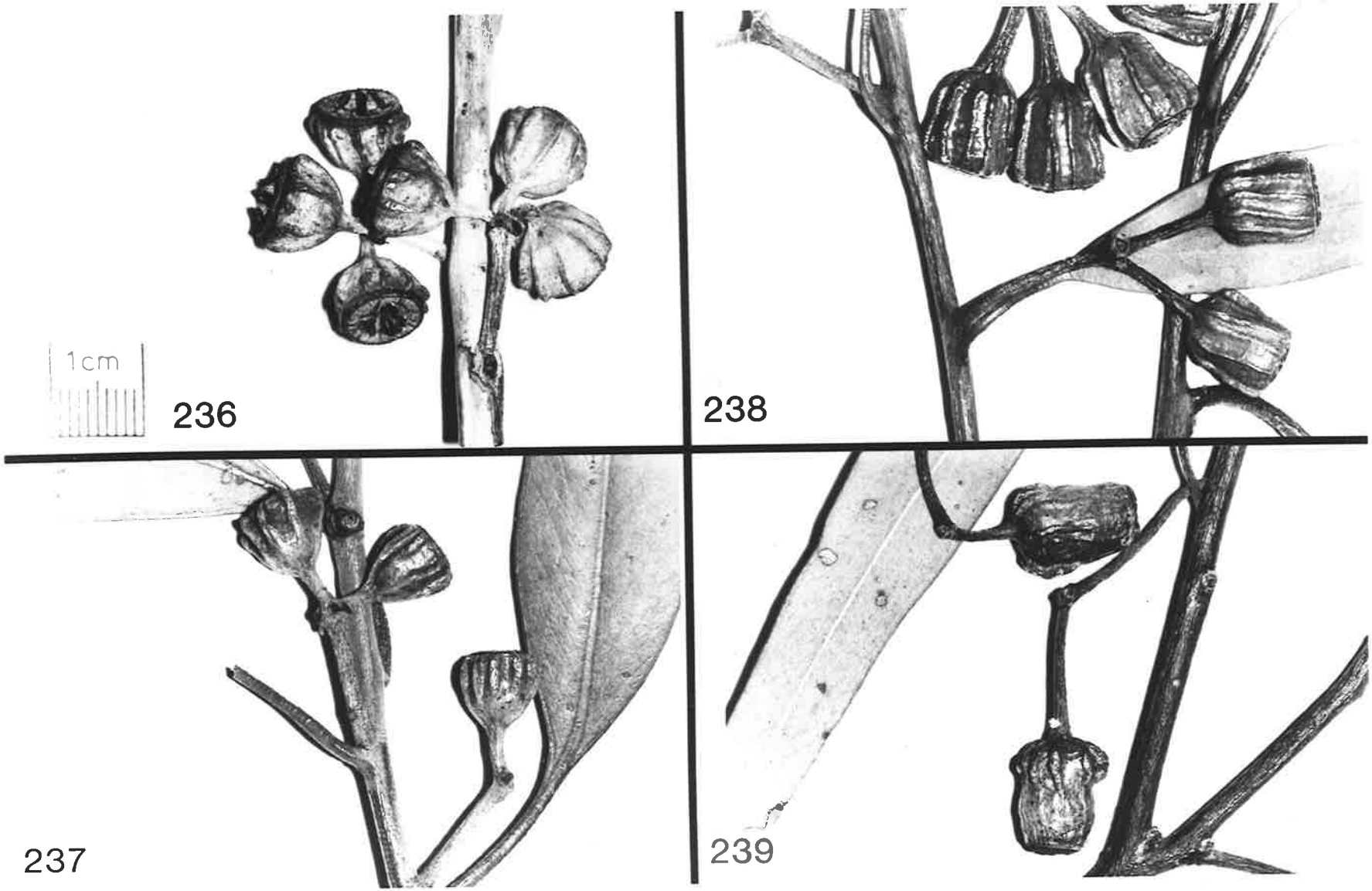
Scale bar: 1 cm

236: E. lesouefii
PJL 1544/18.3 km SE Widgiemootha

237: E. lesouefii
PJL 1545/l.c.

238: E. lesouefii X E. torquata
PJL 1558/l.c.

239: E. torquata
PJL 1560/l.c.


1cm
236
238
237
239

Figures 240 to 242: Putative hybrid between species from series Dumosae and Odoratae.

Scale bar: 1 cm

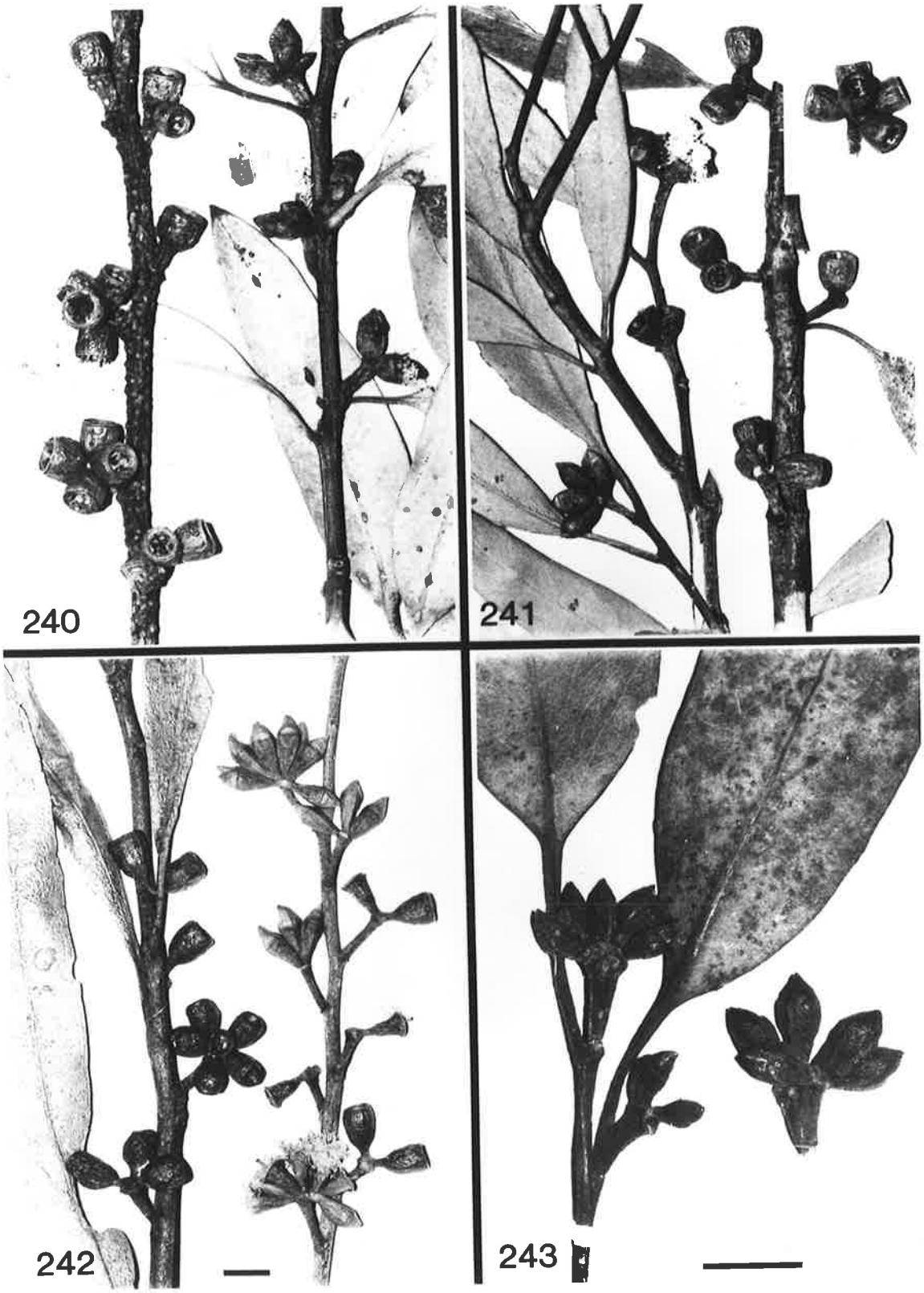
240: E. dumosa ssp. conglobata
PJL 763/5 km NW Goolwa

241: E. dumosa ssp. conglobata X E. odorata
PJL 767A/1.c.

242: E. odorata
PJL 765/1.c.

Figure 243: Isolectotype of E. anceps (MEL 80646) showing presence of short broad pedicels, costae, and wide peduncle which are characteristic of E. rugosa.

Scale bar: 1 cm


240
241
242
243

14.4.1 Inter-series hybrids

In general, Dumosae taxa are reproductively isolated from Torquatae although there are a few exceptions which suggest a breakdown in the operative mechanism. The absence of incompatibilty in the case of the Torwood cross is not surprising since E. woodwardii and E. torquata are geographically isolated and there can be no selective advantage for incompatibilty where there is no contact. Elsewhere members of these two series occur together as distinct forms and there must be some barrier to prevent merging. The existence of a few cases of hybridism indicates potential for gene exchange in that the two taxa have not diverged sufficiently to make their genotypes incompatible. In all cases the hybrids are represented by one or only a few individuals; there are no hybrid swarms or zones of intergradation. This suggests that breakdown in the reproductive barrier is uncommon, introgression is prevented by the same mechanism, and that there is a reduction of fitness or fertility in the hybrid offspring. In most cases habitat isolation can be eliminated because of the association of the parent species in communities. This means that habitat disturbance and creation of 'hybrid' niches can be discounted.

In the three cases of hybrids discovered between E. dumosa ssp. conglobata and E. rugosa, the seeds are lustrous and red-brown to brown in colour. They have more pronounced areolae than Dumosae seeds (figs 227, 228) with thin translucent walls which are not as deep as in Torquatae. In each case only single hybrid trees were found. In South Australia E. dumosa spp. conglobata frequently occurs in major communities or small mixed stands in association with E. rugosa (Torquatae). This intermingling indicates that habitat isolation is not a factor. Flowering time barriers can be eliminated as a mechanism maintaining isolation on a broad scale because of the overlaps displayed by herbarium records (2.6.2, p. 41, 42).

A reduction in hybrid fitness or fertility is not likely to be the mechanism because of the rarity of hybrids found. The most likely explanation is a breakdown in a genetically controlled incompatibility system.

In more arid areas E. dumosa ssp. dumosa replaces ssp. conglobata and E. brachycalyx replaces E. rugosa. Further north in desert sand dune country E. concinna replaces E. brachycalyx. Although the latter two Torquatae species frequently occur in mixed communities with E. dumosa, no putative hybrids are known.

The E. lesouefii X E. torquata hybrid occurred as a young tree in a small natural woodland community comprising both parent species. Although these are often segregated into flat and hillside habitats respectively, this site does not represent a rare ecotone. Chippendale (1973, p. 5) regarded these species as co-dominants on rocky ridges in this region. Habitat isolation cannot be responsible for maintaining their usual distinctness. The hybrid appears most similar to E. lesouefii. The seeds are red-brown in colour and although they have more prominent sculpturing than in nearby E. lesoufeii it is not markedly different from that in Dumosae forms elsewhere (figs 230 to 232). Affinity with E. torquata is evident in the absence of stem glaucousness and the elongate fruits with deep discs and slightly twisted ribbing (figs 238, 239). The existence of this hybrid is interesting because other members of Torquatae grow in close proximity to E. torquata but are not known to hybridize with it. Eucalyptus torquata is quite distinct from these species and the absence of hybrids indicates that it has developed virtually complete incompatibility with them (Brooker, 1979b, p. 162).

Eucalyptus incrassata (series Incrassatae) has a similar distribution to E. dumosa ssp. conglobata and is frequently found in association with it.

Late in this study apparent hybrids between these species were discovered in a small relict mallee community containing a few individuals of E. incrassata (Ridge-fruited mallee) and E. foecunda (Slender-leaved mallee) surrounded by open scrub of E. baxteri (Brown stringybark) and E. cosmophylla (Cup gum). The paucity of the hybrids and the absence of the suspected parent E. dumosa ssp. conglobata is inconclusive, as native vegetation is now confined mainly to roadside verges. There are records of this taxon within at least 10 km. The specimen PJL 1595 shows affinities with E. dumosa ssp. conglobata in its relatively small fruit size and sessile fruits, and affinities with E. incrassata in the strong fruit ribbing and thick glossy leaves. Two generations of fruit were present but no properly formed seeds or chaff could be extracted. The tree is well-shaped and vigorous in appearance but apparently barren. The other specimen (PJL 1596) has shortly pedicellate fruits reminiscent of E. dumosa ssp. dumosa but with some recognizable affinities to E. incrassata. This individual produced seeds intermediate in morphology between those of series Dumosae and Incrassatae. They are red-brown to dark-brown and somewhat lustrous with very narrow areolae.

14.4.2 Inter-section hybrids

Three cases of putative hybrids between E. dumosa and E. odorata constitute the first reported evidence of hybridism between Dumosae and another section. Cases 6 and 7 (table 14.3) are supported by seed morphological evidence but seed was not collected in case 8. Seed shape as well as colour and sculpturing is intermediate in the hybrids (figs 233 to 235). All are clearly intermediate in obvious morphological characters of leaves, buds and fruits. Case 7 is illustrated in figures 240 to 242). Leaves of this hybrid are intermediate in width, colour, prominence of oil glands on the leaf surface, and leaf base angle. The last character is

evident in these figures. Further morphological evidence is provided by anther structure observed in cases 7 and 8. The hybrids within section Dumaria involve series with the same anther type but the above two species are from groups with different anther types. The hybrids have anthers intermediate in size but irregular in shape and with irregular apertures. This is similar to the pattern of inheritance for anther characters observed in section Adnataria in a hybrid (PJL 88) between E. leucoxylon (Melliodorae) and E. microcarpa (Moluccanae).

The capacity for hybridization between sections Dumaria and Adnataria is also supported by good morphological evidence in an apparent hybrid swarm between E. incrassata (Torquatae) and E. leucoxylon (Melliodorae) collected by L.D. Williams 4528 to 4538 and M.D. Crisp, 1 km south of Meningie.

14.5 Parallelism and convergence

14.5.1 Relationship between series Dumosae and Oleosae

The absence of of hybridism between sections Dumaria and Bisectaria was noted by Pryor and Johnson (1981) who suggested that they could be regarded as genetically well on the way to a separation comparable with that of the 'subgenera'. Despite this, there are strong similarities between these groups and the two sections appear to have evolved in parallel. Both have their centre of diversity in south-western Australia and they comprise mainly semi-arid and arid species with a high proportion of mallees. Within section Bisectaria, members of series Oleosae exhibit the most similarities with Dumosae in terms of habit and superficial morphological characters. However, diagnostic characters important at the section and series level, like seed, anther and filament features, are

always maintained. On this basis there is no evidence of gene exchange in the field, and in the cross-pollination trial, pollen tube incompatibilty was detected between a representative of Oleosae and E. dumosa (14.1).

Variation in series Oleosae approaches that of Dumosae in its degree of intergradation and complexity. Many species in Oleosae could be regarded as 'forms' in the E. socialis complex. These are often associated with forms of E. dumosa and correspond in habit and morphology. Pryor and Johnson (1971) included E. socialis and E. dumosa as an example of a number of unrelated species pairs of eucalypts with a striking convergence in general field appearance. These species commonly occur together in the Flinders and Gawler Ranges. Their fruits are usually similar in size and glaucous-leaved forms of E. dumosa ssp. dumosa are often difficult to separate from E. socialis in the field without examination of buds or fruits. Both occur here as white-stemmed mallees and although E. socialis has a greater tendency to retain basal rough bark this is not a reliable difference. At 31 km east of Kimba (Eyre Peninsula Region) a small-fruited and small-leaved form of E. dumosa ssp. dumosa (PJL 1038) occurs with a similarly small-fruited and small-leaved form of E. socialis (PJL 1039). Glaucous-stemmed forms of E. dumosa ssp. dumosa growing at Coonarie, 8 km northwest of Cowell on Eyre Peninsula (PJL 1593, 1594) are accompanied by morphologically similar forms of E. socialis with glaucous stems (PJL 1595) even though this character is usually only well developed on northern forms of that species.

On the southern limit of desert sand dunes country between Yantanabie and Hiltaba HS on Eyre Peninsula, E. dumosa ssp. dumosa (POP: P57) grows on dune crests amongst forms intermediate between E. socialis and E. yumbarrana ssp. yumbarrana (PJL 997, 1004). These forms are very similar in habit and both have relatively broad glaucous leaves and large fruits. Further north these features are more extreme in E. yumbarrana and forms

of E. dumosa ssp. dumosa often previously referred to E. striaticalyx. On sand dunes between Cook and Vokes Hill E. dumosa ssp. dumosa often exhibits stem glaucousness. Again this is paralleled in the Oleosae. Stem glaucousness is a characteristic feature of E. yumbarrana ssp. striata (Boomsma, 1980) which is endemic to this area.

Similarities are also evident between E. dumosa ssp. dumosa and forms referable to E. flocktoniae (or intergrades to E. socialis) growing in Hincks Conservation Park (Eyre Peninsula Region) and at 3 km NW of Kulin (Roe District). At the latter locality the two taxa were indistinguishable by their slender and erect habit and shared narrow, shiny, non-glaucous leaves and relatively small fruits.

14.5.2 Similarities with other series

Cases of parallelism or convergence are not confined to sympatric species of series Dumosae and Oleosae. For example, the tendency for sessile fruits and wide peduncles characteristic of E. dumosa ssp. conglobata is found in other species which have a southern coastal distribution and high rainfall requirement relative to the remainder of their series. Eucalyptus uncinata (Foecundae) is consistently sessile while E. rugosa (Torquatae) is often subsessile or sometimes strictly sessile in populations unrelated to rare instances of hybridism with E. dumosa ssp. conglobata. Eucalyptus lansdowneana ssp. albopurpurea (Odoratae) is usually sessile and one population found on limestone cliffs at Fishery Bay on southern Eyre Peninsula (PJL 1119, 1120) has short broad leaves and could be confused with forms of E. dumosa ssp. conglobata without close examination.

The intergrading complex of Torquatae species E. rugosa - E. brachycalyx - E. concinna and concurring Dumosae forms in E. dumosa ssp. conglobata and

ssp. dumosa show parallel trends in size and shape of fruits, pedicels, peduncles and leaves. Similarity in fruits and some operculae between E. dumosa ssp. dumosa and E. concinna is illustrated in figures 21, 22 (2.5). There is also a notable resemblance between E. corrugata (Torquatae) and E. lesouefii or E. pterocarpa. Eucalyptus corrugata occurs in an adjacent area to the west of E. lesouefii and shares large, strongly ribbed buds and fruits and sometimes a blackbutt.

There are strong similarities in many of the morphological characters of buds, fruits, umbellasters, and leaves emphasized in this study for taxa from distinct reproductively isolated groups which occur together or in comparable habitats. The independent retention (parallelism) or evolution (convergence) of these characters in different groups supports the weight they have been given in the analyses and new classification of this study. They may be direct adaptations, although the possibilty that they are merely pleiotropic effects or the result of gene linkage involving ecologically significant characters cannot be disproved. Certainly it discounts the possibilty that occurrences of these morphological features are simply historical anomalies, having arisen originally in isolated populations by genetic drift.

CHAPTER 15

PHYTOGEOGRAPHY AND EVOLUTION

15.1 Introduction.

15.1.1 Climatic change and evolution of *Eucalyptus*.

It is important to take account of past changes in climate and sea level in considering the possible evolutionary development of Dumosae taxa and their current distribution patterns. Evidence of climatic changes and their affect on the southwestern flora has been considered by Hopper (1979) and the development of aridity in Australia from the late Tertiary and Quaternary examined in detail by Bowler (1976; 1982). Recently, Galloway and Kemp (1981) have reviewed late Cainozoic environments in Australia, and Nelson (1981), the phytogeography of southern Australia. There is widespread evidence of a humid subtropical aspect in Tertiary faunas and sedimentary facies extending even to southern Australia. Fossil faunas in inland South Australia and western Victoria indicate the continuation of conditions wetter than now until Pliocene time. As further evidence Bowler cites the large abandoned river channels (sometimes remaining as salt-lake chains) of the Western Australia Plateau. The overall trend from the middle Miocene onwards has been one of increasing dryness with wetter phases occurring only as relatively brief interruptions. This is associated with a change from dominantly rainforest to xerophytic forms in fossil floras.

The earliest reliable eucalypt fossil (Pryor and Johnson, 1981) is wood dated as Oligocene (Gill, 1975, p. 226) but no reliable fruits or leaves are known prior to the Miocene (D.C. Christophel, pers. comm., 1983). One would expect these woody and sclerophyllous organs to be readily preserved

and represented in fossil deposits if eucalypts were prominent in the flora. Abundant eucalypt fruits and leaves are present in a silicified flora from Stuart Creek, near Woomera in the arid zone of South Australia (Lange, 1978). Lange noted resemblance between several fossils and extant Dumosae taxa. Two are umbels with sessile fruits and broad peduncles, and one of these displays unequal growth of fruits with dwarf capsules present in the cluster. Lange noted this feature in a Kangaroo Island specimen of E. dumosa ssp. conglobata. I have also encountered it in this taxon as well as a number of forms of E. dumosa ssp. dumosa (e.g. fig. 152), but do not know whether it occurs outside of Dumosae. There is also a fossil bud with a ribbed hypanthium and overlapping 'pileate' operculum. Lange noted similarities between this specimen and various species of section Dumaria, including E. pileata and E. lesouefii in the Dumosae. These similarities are superficial and because of the wide degree of parallelism and convergence in Eucalyptus, I regard their relationship to Dumaria taxa as inconclusive. Stratigraphic control for the Stuart Creek deposit is not precise and its age could be either Eocene-Oligocene or Miocene (Ambrose et al, 1979). The latter is more consistent with other evidence that aridity first became a feature in the landscape in the Miocene (Barlow, 1981; Bowler, 1976). Nelson cited geomorphologic studies of laterite formation in southwestern Australia and karst features in the Nullarbor region as evidence that a climate similar to that pertaining today may have been substantially accomplished by the time of the emergence of the Nullarbor plain from the sea in the mid-Miocene. Bowler (1982) challenged this date claiming that the actual emergence of the Nullarbor may have been considerably later. According to Bowler the earliest severely arid conditions are likely to have been encountered in the Nullarbor region about 6 million years ago in the mid-Pliocene. The available evidence certainly indicates that Eucalyptus first diversified some time in the upper Tertiary with the onset of arid conditions.

Burbidge (1952) suggested that many of the mallee eucalypts are a much more recent development and evolved their distinctive habit during a 'Great Arid' period believed to be mid-Holocene in age. However, the hypothesis of the 'Great Arid' period is now no longer regarded as tenable and instead there is strong palynological and geomorphological evidence that several arid phases of varying severity occurred throughout the Tertiary and Quaternary. The major period of aridity experienced in southern Australia in the past 100,000 years extended from 26,000 to 11,000 BP with a peak at 18,000 - 16,000 corresponding to the time of the last glacial optimum (Bowler 1976, Dodson 1977). In the last 10,000 years the climate has been relatively stable although there are indications that temperature and rainfall were marginally higher than now between 8,000 and 5,000 BP . Bowler states that the causes of aridity involved a greatly intensified atmospheric circulation aided by increased continental extent resulting from glacial low sea levels. This is supported by the correspondence between glacial maxima and dune building episodes. Thus it appears that lower sea levels were associated with periods of more arid climate.

15.1.2 Sand dune formation

Sand-dominated landscapes with longitudinal dunes and sand sheets are a prominent feature in arid and semi-arid Australia (Galloway and Kemp, 1981, p.58, fig. 2). The occurrence of dune systems outside of arid areas is good evidence that their formation entailed greater aridity than present today. For example, Beard (1982) describes a dune system on the Esperance plains with a similar configuration to that of the Great Sandy Desert. The Nullarbor-Spencer dune system which extends across Eyre Peninsula northwestwards into the Great Victoria Desert, is particularly relevant to the biogeography of the Dumosae. The apparent source for the

sand in this system was calcareous aeolianite deposited on the Nullarbor Plain and western side of Eyre Peninsula and ultimately derived from the continental shelf at a time of lower sea level (Crocker, 1946). In these regions there are now extensive deposits of calcareous aeolianite and Ripon calcrete of the Bridgewater Formation which represent the original B-horizon left behind after sand was deflated and deposited as dunes to the north and west. Ripon calcrete and Bridgewater Formation Members are also present in most other mallee areas of South Australia in the St Vincent, Spencer and Murray Basins. They are placed in the mid-Pleistocene (Parkin, 1969). The major period of dune formation was originally thought to be in a recent severe arid period about 3,000 to 6,000 years ago (Crocker). Recently the initial dune formation events have been placed at about 300,000 BP or earlier (Bowler,1976; Barlow, 1981), possibly 700,000 years BP (Barlow), indicating a similar age to the calcareous aeolianite formation. According to Bowler (1982), rapid hydrologic oscillations meant that the threshhold of low humidity necessary for dune building was first reached after 400,000 BP. The period of maximum aeolian activity was more recent and coincided with the glacial maximum 18,000 to 16,000 BP. During this time the Australian desert expanded, with the construction of longitudinal dunes as far south as Kangaroo Island.

15.1.3 Past sea levels

There is evidence that sea levels were low in relation to the continent for substantial periods in the late Tertiary (Galloway and Kemp) and several periods of lower levels of uncertain duration and date have occurred since the beginning of the Quaternary (Nelson, 1981, p.752). Throughout the period from 120,000 to c. 10,000 BP the sea in southern Australia remained significantly lower than the present level although it fluctuated considerably during the cycle of Pleistocene glaciations. The

highest level during this time was 15 m below present level at 83,000 BP and the lowest level reached was about 125 - 150 m below present between 20,000 and 17,000 BP (Lampert, 1981). During this last glacial maximum the sea is thought to have been near to the continental shelf edge which is marked by several giant submarine canyons in the gulf region (Sprigg, 1947) corresponding to old river outlets. In effect this would have provided a land bridge between Kangaroo Island and Eyre Peninsula and south-western Australia. To the south of the Nullarbor a 200 km belt of land would have been exposed. Subsequently in the Holocene transgression there was a rapid rise in sea level to reach the present level at c. 6,500 B.P (Belperio, Hails, and Gostin, 1982). According to Lampert (1981) Kangaroo Island has been connected to the mainland for most of the last 80,000 years and last became isolated at c. 9,500 - 9,300 B.P.

15.2 Dispersal ability and migration

As in most Eucalypts, Dumosae seeds are relatively small and have no special adaptations for dispersal. Wind is likely to be the major agent involved. Cremer (1977) found a relationship between wind speed, tree height and seed weight for a range of eucalypt seeds. Assuming a seed weight of 1 mg (which is at the lower end of the range for Dumosae) and a tree height of 10 m, a distance of c. 50 m is predicted by his equation for a wind of 60 kph. This would be a generous estimate of the distance that seeds would travel. Onans and Parsons (1980) studied regeneration of mallee vegetation in south-eastern Australia and found no eucalypt seedlings more than 10 m from a seed source. Seed fall may be completely absent at distances of twice tree height and in two forest eucalypt species the bulk of the seed falls within a distance equal to the height of the tree (Cremer, 1977).

Parsons (1968) reported that a mallee community of E. incrassata and E. foecunda first carried a new crop of fruits seven years after a fire. In this case regeneration was from the lignotuber, so a generation time of at least five years for seedlings, which have slower initial growth rates, is a reasonable estimate. (E. woodwardii is exceptional in the Dumosae for its ability to flower within periods as short as one year.) Under current conditions seedling recruitment is rare in mallee communities and individuals regenerate from rootstocks which appear to be long-lived. Studies by Wellington and Noble (1981) indicate that normal seedfall is kept in check by ant predation. (This is consistent with the finding of Barbour and Lange (1967) that no Eucalyptus seeds were present in the seed population of the topsoil of a E. gracilis - E. dumosa - E. oleosa mallee community.) The half-life for seeds on the ground was found to be less than two days. Significant seedling establishment only takes place if predation is satiated by the sudden release of seeds from all fruits (as occurs after fire), and if suitable rains follow. The coincidence of fire and favourable years results in infrequent, episodic recruitment. Thus the spread of mallee communities is much slower than would occur with immediate establishment of successive generations. An upper limit for generation length is suggested by C14 dating which indicates that extant lignotuber tissues are less than 200 years old. However, at the time of initial colonization and migration of mallee taxa, adapted communities of seed predators are not likely to have been established and less arid conditions may have prevailed. Assuming a 50 m dispersal distance and a 5 year generation time, it would still take 100,000 years to spread 1,000 km with immediate establishment of each generation.

Mention should be made of the possibility of dispersal by water in the case of E. kondininensis. Present occurrences are associated with salt lake chains which are remnants of old river systems (Bettenay and Mulcahy,

1972). Eucalyptus kondininensis is confined to the southern branch of the Avon palaeo-drainage system and is absent from similar salt lakes in the adjoining Blackwood and Monger systems. Similarly, in inland areas E. dumosa ssp. dumosa is often associated with extant creeks or salt lakes representing ancient drainage lines such as Serpentine Lakes in the North-western Region of South Australia.

Finally there is the possibility of migration by introgression through pollen transport as suggested in section 14.2.1. Pollen is much more mobile than seeds and may travel distances of several kilometres in a single dispersal event. This would mean much faster migration rates than predicted above.

15.3 Biogeographical implications of distribution patterns

15.3.1 Eucalyptus dumosa ssp. dumosa

Eucalyptus dumosa ssp. dumosa is the taxon in Dumosae able to grow in areas of lowest rainfall. Significantly it is also the most widespread, occurring on both sides of the Nullarbor Plain. The Nullarbor region presents a major biogeographical barrier which is at present both climatic and edaphic. No eucalypt species are shared between the more mesic south-west corner of Western Australia and south-eastern Australia (Pryor, 1976, p.4). Crocker and Wood (1947) concluded that the floras of these zones indicated continuous isolation since the formation of the Nullarbor in the Miocene. This pattern is confirmed in the recent review by Nelson (1981, p.753) although a few taxa seem to have circumvented the barrier. The aridity of the region is accentuated by the porous nature of limestone which allows water to drain away rapidly. Rainfall decreases progressively northwards on the Plain so the coastal strip provides the most likely migration route. Along the coast rainfall is lowest between

the Head of the Bight and Eucla. (At Nullarbor HS near the Head of the Bight it is only 236 mm p.a.) The distribution of mallee eucalpts shows how critical water availablity is. Mallee vegetation occurs along the southern part of the Plain in South Australia except for a gap of c. 25 km just west of the Head of the Bight (Parsons, 1970). Eucalyptus dumosa ssp. dumosa tends to occur in moister sites associated with the Plain. It is common in linear depressions or narrow valleys on the fringe of the southeastern sector of the Plain (Boomsma, 1979). In Western Australia I have observed it along the base and in gullies of the Hampton Scarp and on sands of the Roe Plain to the south. The only major gap in the known distribution around the Bight is an area extending west from the the head of the Bight for about 130 km (Boomsma). This coincides with the dryest habitat. The fringe of occurrences around the coast would probably be completely connected under slightly higher rainfall conditions. Occurrences in the Victoria Desert to the north of the Nullarbor indicate another possible link between ssp. dumosa in western and eastern Australia. The major gap in the Western Australian part of the Desert (fig. 219) probably reflects the lack of botanical collection in this area. Scattered occurrences may have been linked under higher rainfall periods of the mid-Holocene.

The edaphic barrier of the Nullarbor region results from the prevalence of calcareous soils, with Miocene limestone and Ripon calcrete on the Plain itself and associated coastal calcarenite dunes to the south in Western Australia. Eucalyptus dumosa ssp. dumosa is the only Dumosae taxon with forms able to tolerate both these substrates under semi-arid conditions. Its frequent occurrences on calcareous aeolianite and shallow loam over Ripon calcrete (travertine limestone) down most of the west side of Eyre Peninsula demonstrate how well adapted it is. Eucalyptus dumosa ssp. dumosa is also the only taxon that is widespread on sand dune ridges

characteristic of much of arid and semi-arid Australia. Eucalyptus woodwardii is also found in this habitat but has a very limited distribution. The dune systems have their own adapted plant associations and have probably existed for 300,000 years (Barlow, 1981). This is a relatively short time compared to the last 15 million years for which Barlow claims there is reasonable evidence indicating the evolution of Eremean flora in Australia. This may explain the high variability in E. dumosa ssp. dumosa compared to other taxa. Many of the forms in the complex comprising this taxon may have been derived from one or more Western Australian taxa during the mid-Pleistocene in response to the formation of calcareous soils of the Bridgewater Formation and the major inland sand dune systems. Even with a conservative estimate of migration rate, there would be ample time for Dumosae to spread eastwards into South Australia, Victoria and New South Wales. This hypothesis explains the progressively lower diversity of taxa from west to east and the high variability in ssp. dumosa which suggests incipient speciation. Variabilty is probably maintained because of the dynamic nature and inherent instabilty of the sand dune habitat as well as its spatial heterogeneity with crests, swales, interdune areas, irregular dunefields varing in depth of sand, water catchment and wind exposure. Evidence of breeding barriers within E. dumosa ssp. dumosa is very limited (14.3), and possibly this reflects a lack of time for their evolution compared to the other taxa. The alternative explanation - that the E. dumosa ssp. dumosa forms were derived from ssp. conglobata or less arid forms of ssp. dumosa already present in southern latitudes of Western Australia and South Australia - seems less likely. It does not explain the west-east decline in diversity and requires the independent evolution of characters associated with inland arid forms, such as glaucous leaves and stems, highly sculptured cuticles and slender pedicels from progenitors lacking these features.

In arid areas in particular, E. dumosa ssp. dumosa has a discontinuous distribution and is frequently confined to specialized habitats such as hills, dunes, soakages, depressions, salt pans or calcrete tables where water availability is greater. Given the poor dispersal ability, this requires previously continuous distributions or migrations and suggests the existence of wetter conditions in the past. For instance, under a higher rainfall the occurrences in the Hamersley Range could be connected with those in specialized habitats to the south (in the Austin district) which are at present surrounded by shrubland dominated by Acacia and Eremophila. Populations on consolidated gypsum dunes fringing Lake Austin and Lake Annean (figs 127, 128) appear out of step with the existing environment and are certainly outliers in drier areas than currently occupied by the major populations of this taxon. Rainfall approaches the lower limit of 150 mm p.a. and the trees survive in an extreme environment with a hard gypsum crust that would no longer permit their establishment. Only one other plant species (identified as Selenothamnus helmsii, Malvaceae) was observed growing in substantial numbers on these dunes. Trees extend for several kilometres along the dunes and all are old-aged in appearance. There was no sign of reproductive organs except for some rather weathered fruits under a few trees. Such low fecundity has not been observed elsewhere in the Dumosae and is presumably a result of adverse conditions. These observations are more consistent with a declining population than an expanding one and suggest a recent decrease in water availabilty.

Within E. dumosa ssp. dumosa the distribution of forms exhibiting stem glaucousness is worthy of comment. In Western Australia this character state is found in many of the other taxa and is widespread in ssp. dumosa. The eastern limit of stem glaucousness is a disjunct area of occurrence on central Eyre Peninsula (fig. 134). This is isolated from populations of

ssp. dumosa with stem glaucousness at Maralinga and in the Great Victoria Desert to the northwest, by non-glaucous forms north of Kimba and in the Gawler Ranges. While the adaptive significance of this character is unknown, it is not possible to be certain whether its absence in the east is a result of natural selection or geographic isolation. Occasional individuals exhibiting stem glaucousness occur in populations in the Flinders and Gawler Ranges.* These vary in intensity and distribution of waxy bloom. In some, glaucousness is confined either to immature buds, to bud pedicels or to stems and peduncles. This suggests that the character may readily arise from independent mutations. The Eyre Peninsula stem glaucous forms may have evolved independently from those in Western Australia in response to habitat peculiarities in that area. The absence of the character state further east would simply reflect the lack of suitable habitat to confer a selective advantage. In central Eyre Peninsula the most distinctive habitat, and the one where the glaucous forms are most abundant, is the rocky slopes of Carappee Hill on skeletal soil derived from Archaean quartz-feldspar gneiss. They also occur on the north end of Darke Peak Range and on the intervening plain on clayey soils derived from the basement rocks where the Range has blocked the easterly spread of sand dunes. The shadow effect of the Range on the distribution of dunes is illustrated by Crocker (1946, fig. 3, p. 87). In addition to these major occurrences there are outliers in the Cleve Hills on gneissic or schistose outcrops and elsewhere on similar habitats as well as some unrelated ones (appendix 3). However, there are no obvious differences in habitat near the type area of E. dumosa in central New

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* 1 km NE Devil's Peak/R.Sinclair s.n.,1.ix.1977

Wilpena Pound/A.Robinson s.n.,15.ix.1977

Kokodo Hill/PJL 968

Peterby Yards/PJL 987

South Wales where the material sampled was associated with granitic domes but stem glaucousness was absent. The alternative hypothesis is that stem glaucousness on Eyre Peninsula was derived from Western Australian forms and its absence further east is due to the inability of Dumosae to migrate further prior to the development of the sand dune systems. The process leading to the formation of dunes would then have isolated Eyre Peninsula glaucous forms to refuges in ranges and other specialized habitats free from the sand sheets and with better water availability. Similarly, refuges in the Musgrave and Blackstone Ranges may have enabled the spread of this character to forms of the Ooldea-Barton dune system in the Great Victoria Desert and at Maralinga. It is unclear why the character is present in these desert dunes but it may be due to their higher loam content compared to those in the south. An origin from older Western Australian taxa is more consistent with other evidence for a west - east evolution, but the first hypothesis of an independent origin cannot be discounted.

Whichever hypothesis is correct, most of the scattered occurrences of glaucous forms on Eyre Peninsula are probably remnants from a continuous distribution there prior to disruption by the dune systems. However, an alternative explanation may apply to some outliers which appear to intergrade with non-glaucous forms and may occur with low frequency in mixed populations (section 11.4.1). Outliers near Tooligie Hill (PJL 1071, 1072, 1076) have light stem-glaucousness but approach non-glaucous forms of E. dumosa in their mallee habit, small fruits, and habitat with substrate of calcareous loam containing kunkar limestone. (figs. 212, 210). Such intermediate outliers may be explained as phantom hybrids (Pryor and Johnson, 1971; Kirkpatrick et al, 1973) or the result of 'floating genes'. Under the first explanation distinct forms would originally have been present in the area. Possibly they occurred on

Tooligie Hill itself, and although it has only non-glaucous forms now, it may have provided suitable habitat under earlier climatic conditions. With reduction of the distribution to relict areas they may have become extinct there but genes responsible for stem-glaucousness could have been preserved in the vicinity by introgression. Under the second explanation introgression has occurred following long distance transport of pollen from areas such as Carappee Hill where distinctly glaucous forms are now established. Once again it is not possible to distinguish between these two alternatives.

15.3.2 Eucalyptus dumosa ssp. conglobata

Eucalyptus dumosa ssp. conglobata is notable in being the Dumosae taxon adapted to the highest rainfall conditions. Since it would be the most severely affected by recent aridity, it is not surprising that its distribution exhibits the greatest disjunction of all the Dumosae taxa. More interesting is that of the remaining taxa it is the only one to occur east of the Nullarbor Plain and has the widest distribution.

The major disjunction corresponds to the dryest part of the coastline centred on the Great Australian Bight. There is a gap of c. 1300 km from the principal occurrences near Israelite Bay in Western Australia and Mt Hope on the southern part of Eyre Peninsula, South Australia. If occasional outliers occuring in populations with pedicellate forms are considered then the disjunction is c. 900 km. The eastern limit in Western Australia is south of Caiguna and in South Australia the limit is at least as far west as Cungena on northwestern Eyre Peninsula. Two main hypotheses are proposed to explain this major disjunction. Firstly, ssp. conglobata may have evolved independently from pedicellate forms in both the east and west. This is not inconceivable because of the heterogenous

array of sessile forms grouped in this taxon. Secondly, it may previously have had a continuous distribution. Eucalyptus dumosa ssp. conglobata tolerates a variety of soil types including shallow soils on calcrete or calcareous sands, so the barrier presented in the Nullarbor region is probably climatic rather than edaphic. Based on rainfall limits for principal occurrences, an increase in rainfall of about 150 mm p.a. would probably be required for a continuous distribution around the present coastline. Alternatively, Parsons (1969), in explaining similar but lesser disjunctions for E. incrassata and E. diversifolia, pointed out that drops in sea level during Pleistocene glacials would produce an extensive coastal lowland south of the Nullarbor which would obviate the need to postulate a major climatic change. The current climatic pattern would mean higher rainfall from the winter south-westerly airstreams at more southerly latitudes, but this could be offset by an increase in aridity associated with lower sea levels (15.1). A further complication is the fact that the glacial maxima were also periods of lower temperature (Bowler, 1976; Nelson, 1981). A consequent reduction in evaporation rate may have increased the effectiveness of rainfall. However, Martin's (1973) pollen studies at Eucla provide specific evidence of increased aridity in this district when the sea was at its last glaciation low level of 90 m below present level at c. 18,000 BP. Pollen spectra indicate a southerly extension of treeless chenopod shrubland which was subsequently replaced by mallee communities when sea levels rose.

The spread of ssp. conglobata could not have occurred during the the arid dune-building phase that was suggested as leading to the radiation of ssp. dumosa. Although there is sufficient time for it to have occurred subsequently, this is unlikely as there would have been ample opportunity during periods of wetter climate earlier in the Pleistocene. Under this hypothesis the greater distinctness of these two taxa in Western Australia

compared to South Australia where they intergrade substantially is consistent with a west to east migration of ssp. dumosa. This provides a longer period of contact in the west and thus more time for evolution of barriers to interbreeding.

Smaller disjunctions within the distribution of E. dumosa ssp. conglobata were noted for the gulf region of South Australia (3.2). During periods of lower sea level these disjunctions could be connected in the south. Connections where the maximum depth of intervening sea floor is greatest would require greater falls in sea level. Examination of a bathymetric map of this area (Boland, 1974, fig. II.3) shows that with a progressive fall in sea level the peninsulas would link to Kangaroo Island in the order: Fleurieu Peninsula, Yorke Peninsula and Eyre Peninsula. For Fleurieu Peninsula a drop of only 37 m is required, compared to a drop of 75 - 100 m for a direct link between the west end of Kangaroo Island and Eyre Peninsula. A maximum fall in sea level to the edge of the continental shelf would still only provide an indirect link at more northerly latitudes with Western Australia. The trend in morphological variation of groups (KI - FP - YP - EP1 - WA) noted in the SESSDAT analysis (3.8, 3.9) parallels these geographical relationships. Groups which would have been most closely linked with Kangaroo Island for the longest periods show greatest affinity with the Kangaroo Island group in the aspect of morphological variation expressed by the second canonical variate. The overlap between the function scores for different geographical groups indicates that this is a fairly weak pattern of racial affinities. However, it does not provide evidence on the direction (from east or west) or on the timing of migration. The link between Kangaroo Island and Fleurieu Peninsula is probably accentuated because of the fact that the west end of the Island is currently too wet for Dumosae to occur.

There is no evidence of speciation in the Dumosae on Kangaroo Island and the peninsulas as a result of the recent and intermittent isolation provided by the gulf waters. This is supported by other eucalypt taxa. Of the five eucalypts endemic to southern South Australia, only E. remota is endemic to Kangaroo Island. This could be a relict of a wider distribution since its nearest relatives (the other members of subseries Considenianinae) do not occur in this State. The other four species have distributions reflecting wider distributions in the gulf region independent of the present configuration of land and sea. Eucalyptus cneorifolia and E. cosmophylla are confined to Kangaroo Island and Fleurieu Peninsula consistent with the close link based on a sea level fall. Eucalyptus lansdowneana and E. cladocalyx are absent on Fleurieu Peninsula but demonstrate a past link between Kangaroo Island and Eyre Peninsula.

The major component of variation within E. dumosa ssp. conglobata corresponds approximately to the previous taxa E. conglobata and E. anceps. The distribution of groups CON and ANC which represent these taxa in analyses is difficult to interpret biogeographically. In South Australia these groups are generally distinct and CON has a more southerly distribution confined to the southern parts of Eyre and Fleurieu Peninsula. Early collections at Encounter Bay on Fleurieu Peninsula (3.8) indicate that there was a minor occurrence here as a mixed population with ANC forms. In Western Australia the two forms are indistinct with substantial intergradation and intermixing (3.9) but there is still a tendency for a more southerly distribution in forms closest to CON. So far this suggests that CON simply represents an extreme form maintained by natural selection in the more southern, coastal habitats. However, the absence of CON forms on Yorke Peninsula and Kangaroo Island, and the geographical separation between most CON and ANC occurrences on Eyre

Peninsula, are difficult to explain with this hypothesis and suggest that historical factors may be involved. On southern Eyre Peninsula there is the possibility of isolation of CON populations by Sleaford Mere which appears to have been formed by the retreat of a higher sea level. There is evidence of Holocene sea levels in upper Spencer Gulf up to c. 4 m above present level (Belperio, Hails and Gostin, 1982) and sea levels were also probably higher in the interglacial before 120,000 BP (Lampert, 1981, p.18). Except for an uncertain record at Fishery Bay which may represent a more recent migration, all the Eyre Peninsula occurrences of CON forms would be confined to an island produced by the formation of a marine channel at Sleaford Mere.

On an even smaller scale, discontinuities in the distribution of E. dumosa ssp. conglobata on Eyre Peninsula imply previously more favorable conditions. Like the glaucous-stemmed forms of ssp. dumosa, ssp. conglobata occurs in scattered localities frequently associated with inselbergs or ranges, but is more widespread. For example it has been collected or observed at the following localities: Curtinye Hill, northwest of Kimba; Carappee Hill; Mt Shannan, north of Cleve; vicinity of Tooligie Hill; lateritic hills near Koppio; pass between North and South Block; and Mt Hope. Compared to the sand dune plains where ssp. dumosa is virtually ubiquitous, the above localities could act as refuges due to slightly higher rainfall, catchment of run-off water or the better water holding capacity of heavier-textured soils derived from basement rocks. Independent evolution of ssp. conglobata at all these localities is implausible. The distribution patterns of these two subspecies concur with the earlier hypothesis that ssp. conglobata migrated to South Australia before rather than after the major development of sand dune systems and spread of ssp. dumosa.

Evidence of more arid conditions in the past is provided by outliers of ssp. conglobata on Fleurieu Peninsula. These occur in non-mallee communities under a rainfall greater than the upper limit for major occurrences of c. 575 mm p.a. Two isolated patches containing a total of about ten trees occur in strips of roadside vegetation between Mt Scrub and Mt Desert, c. 15 km WSW of Encounter Bay. They are surrounded by an open scrub of E. obliqua (Messmate stringybark) and E. cosmophylla (Cup gum) and the rainfall is nearly 700 mm p.a. Chance dispersal from major occurrences northeast of Encounter Bay can be excluded as an explanation since E. incrassata (Ridge-fruited mallee) and E. foecunda (Slender-leaved red mallee) are also present, suggesting the previous existence of a mallee community. At Waitpinga, 8 km WSW of Encounter Bay two trees are known amongst woodland with E. fasiculosa (Pink Gum). The hybrid population involving E. incrassata described in section 14.4.1 (p. 362) is another similar case. Outlying distributions indicative of a previously dryer climate are also evident for other mallee species. Brooker (1979b) suggested that a population of E. foecunda at Black Hill, Athelstone was a relict as the western foothills of the Mt Lofty ranges are not an expected habitat.

Another case nearby is the occurrence of E. rugosa (Kingscote mallee) in the Torrens Gorge west of Castanbul under a rainfall of about 800 mm p.a. Here several individuals occur on calcareous soil with Melaleuca lanceolata and Lasiopetalum baueri, which are typical understorey species of mallee communities. The closest known E. rugosa occurrences are c. 40 km to the east near Monarto.

15.3.3 Other taxa

Of the remaining taxa, E. lesouefii and E. dumosa ssp. clelandii are relatively widespread. Both have a number of outlying occurrences in more arid areas, indicating wetter conditions in the past. The other taxa have rather restricted distributions which do not overlap with each other (figs 220, 221, 223, 225, 226). Since these taxa are closely related and clearly of monophyletic origin, they or their progenitors must have been previously more widespread. The distributions are on the Great Plateau or Archaean Shield of Western Australia (Mulcahy, 1973) which has low relief and has been tectonically stable since the Tertiary. It has residual lateritic soils preserved in many places. Hopper (1979) considered that this contributed to the development of high species richness and endemism in southwest Western Australia. Certainly these conditions would be advantageous in enabling survival of relicts for long periods. Existing patterns may therefore be the result of climatic fluctuations causing expansions and contractions in relatively old taxa which have ultimately been reduced to relict areas. Breakdown in variation with E. dumosa ssp. dumosa apparent in some cases would be a more recent phenomenon. The alternative hypothesis - that the Western Australian taxa are a complex of recently evolved and evolving species - does not agree with these distribution patterns. Although current conditions are probably suitable to allow much wider distributions, this may be prevented by competition with other eucalypts. However, migration and associated invasion of new habitat may require higher and more reliable rainfall or other conditions not necessary for mere survival.

Burbidge (1952) noted that the chemical and morphological characteristics of the major mallee groups exhibit a high degree of specialization, and argued that the mallee habit is a derived condition, possibly representing the retention of a multi-stemmed juvenile state. Dumaria has a higher

proportion of mallees and of Eremaean species than any other section of Eucalyptus s.lat. Its primary centre of diversity is still mostly in the dryish but scarcely Eremaean parts of the south-west, and the mallee habit appears to be secondary (Pryor and Johnson, 1981, p.525). A similar pattern applies for series Dumosae alone. Eucalyptus dumosa ssp. dumosa and ssp. conglobata are the most common and widespread of the taxa recognized here and the only ones to extend east of the Nullarbor plain and outside of Western Australia. In these taxa a mallee habit predominates. In contrast the other seven taxa are endemic to Western Australia and generally have a tree habit. Biogeographical considerations support the view that these are the more primitive taxa. Present climatic and edaphic conditions alone do not explain their absence in South Australia. Most have been cultivated in this state and grow vigorously if planted in suitable habitats. In trial plantations six and seven years old made by the South Australian Woods and Forests Department at Monarto, trees from the semi-arid zone of Western Australia were grown together with a wide selection of South Australian taxa under natural rainfall (c. 400 mm p.a.) after their initial establishment. Endemic Western Australian taxa with a tree habit generally exhibit the highest growth rates. Eucalyptus spathulata (Swamp mallet), E. gardneri (Blue mallet), E. transcontinentalis (Redwood), and E. lesouefii even out-perform E. dumosa ssp. conglobata from the Murray Region, which is an indigenous mallee at this site.

The semi-arid zone of Western Australia is notable for its diverse sclerophyll woodland and forest communities comprising eucalypts of tree form that are found principally between the 250 and 400 mm rainfall isohyets. These include the remaining Dumosae taxa and numerous other taxa mostly in section Bisectaria. One example is E. salmonophlioa (Salmon gum) which may grow to 24 m tall. In contrast, areas of the same

rainfall in southeastern Australia are mostly covered in mallee scrub. This can be explained partly by soil differences between these two regions. The best development of forests and woodlands in the semi-arid is on deep loamy soils - in the Kalgoorlie area on sandy loams often with calcareous sandy clay loams in the lower horizon and in the Norseman area on loams derived from basement rocks. On the other hand, the semi-arid in South Australia is notable for the prevalence of limestone and sand dunes. Mallee forms are well adapted to growing on soils with calcrete or dunes and although they also grow well on more limited areas of loamy soils in South Australia this is probably due to the absence of tree forms better adapted to this niche. Tree forms have either become extinct here or have been unable to migrate from the west. Favorable conditions for tree forms may have been more widespread in South Australia prior to the development of the sand dune systems. Their subsequent extinction would not be surprising given the relict nature of distributions in the more stable environment in Western Australia. Eucalypts with lignotubers often have the capacity for variation in habit from tree to mallee forms and vice versa. Eucalypts which are normally trees are often reduced to a mallee habit under extreme conditions (Carolan, 1959). Although habit variation can be merely a phenetic effect, observations of eucalypts in cultivation suggest habit is under genetic control to a large extent. If E. dumosa ssp. dumosa, ssp. conglobata or other Dumosae had been in South Australia as long as in the west it would be unlikely for tree forms not to have evolved. However, assuming a western origin for the Dumosae, the absence of tree forms adapted to deep loamy soils in the east can be explained by the edaphic barriers of the Nullarbor region. Easterly migration would have been blocked by marine incursions in the Oligocene - Miocene and then by the Nullarbor karst which developed in the Miocene. Geologic and geomorphical studies of karst features suggest that there have been generally low absolute values of rainfall ever since (Nelson, 1981, p.737,

748). During periods of lower sea level, the exposed shelf would have been unsuitable as a migration route since fossil dunes and aeolian calcarenites beneath the present sea indicate that it was covered in sand (Nelson; Parsons, 1969). Although suitable soils may have existed in the Great Victoria Desert prior to formation of dunes there, this area is in a zone even more arid than the Nullarbor. Nelson argued that it would only be feasible as a migration route if climatic conditions were substantially wetter than the present for a long period. However, he pointed out that there is no evidence for long moist regimes since the late Tertiary, and there are no relict populations in the northern regions providing evidence of floristic interchange.

15.3.4 Summary

The simplest hypothesis - that the Dumosae evolved in the west along with the other series of section Dumaria and spread eastwards - is supported by phytogeographical evidence, although other more complex explanations can not be discounted. Series Dumosae seems to have evolved some time after the Eocene-Miocene incursions. Tree forms were probably prevented from reaching South Australia by sandy or highly calcareous soils in the Great Australian Bight region. These soils would not pose a barrier to E. dumosa ssp. conglobata which could have migrated into South Australia under conditions of higher rainfall or lower sea level. It appears that more recently in the Pleistocene there was a phase of adaptive radiation and spread of E. dumosa ssp. dumosa mallee forms associated with the development of calcareous soils and major sand dune systems. The distributions of various taxa provide evidence of past climates both wetter and dryer than at present. Most of the disjunctions probably reflect the most recent arid phase which peaked at about 17,000 BP.

15.4 Possible evolutionary relationships between taxa

The determination of phylogenetic relationships within the Dumosae was not an aim of this study. It is difficult to infer phylogeny in a group of closely related taxa where the differences are largely a matter of degree (continuous variation in character states) with some simple characters for which the primitive and derived conditions within the group are equivocal. Nevertheless, phenetic relationships between groups used in developing the classification suggest possible evolutionary pathways when considered in conjunction with phytogeographical aspects. The following conjecture follows a minimum pathway of evolution approach. Past relationships are inferred directly from existing patterns using the simplest hypotheses. These should not be given too much weight due to the possibility of complex historical developments evident from the the preceding sections.

Eucalyptus dumosa ssp. clelandii is possibly the closest extant taxon to the ancestral form. It is a tree form, has a relatively wide distribution in Western Australia and is central morphologically in that it is the easiest to hypothetically derive all the other taxa from. Although it belongs in the blackbutt group it also has strong affinities with ssp. dumosa in its morphological characters. The three major lobes evident in the nearest neighbour networks (7.3, p. 143 to 145) may correspond to three major lines of evolution culminating in the extreme taxa E. pterocarpa, E. woodwardii and E. dumosa ssp. conglobata. With loss of blackbutt and ribbing, ssp. clelandii may have given rise to ssp. georgei and E. woodwardii. This lobe is the most similar to the E. dumosa ssp. dumosa complex and more direct links are evident in the groups RED and SHE. With further development of ribbing and increase in fruit size, ssp. clelandii links to E. lesouefii and then to E. pterocarpa in which the blackbutt and glaucousness is suppressed. With loss of leaf and stem

glaucousness and a reduction in pedicel length, ssp. clelandii links directly to E. kondininensis and then to ssp. conglobata with loss of blackbutt. Forms of ssp. conglobata currently occurring close to E. kondininensis are very similar apart from their absence of a blackbutt. The origin of E. dumosa ssp. dumosa may be polyphyletic, being derived as several lines from ssp. clelandii. To the north ssp. clelandii grades into STR forms which link to PSL, PCVH and PMAR in the east and DON in the west. To the southeast ssp. clelandii grades into the groups RED and SHE from which PIL, CAL, DUM and CYA can be derived moving further eastwards. The group CAL may also be derived in part from ssp. conglobata with a link through ssp. fraseri.

15.5 Conclusion

In this study a pragmatic approach to classification has been adopted. Johnson (1968) argued strongly for using phylogeny as a basis for classification but admitted that taxa may be too closely related to show clear phylogenetic patterns (p. 29). Phylogeny tends to be obscure and untestable in a group where divergence is limited and a multitude of pathways could be proposed on the basis of morphological relationships. Johnson's statement that "Phylogeny cannot be perfectly elucidated, and it is inherently complex and reticulate at those levels of grouping at which interbreeding among groups still occurs" is an appropriate description of the situation in the Dumosae. The phylogenetic relationships proposed above are conjectural and were not considered in deriving the taxonomy. A taxonomy built on these would be far too unstable.

This investigation has described and demonstrated objectively the very complex pattern of morphological variation in series Dumosae. Although it is convenient to use a detailed taxonomy with many names as reference

points to describe this complexity, it is difficult to apply these names consistently to all material. The taxonomic revision proposed here involves placing many existing taxa in synonymy and will increase the reliability of information conveyed by a name. This is done at the expense of detail - there is a reduction in the amount of information conveyed. However, this is not a problem so long as taxa are not seen to be the ultimate units of genetic or ecological significance. The classification only organizes that information which can be readily identified or keyed out with reasonable certainty. It is envisaged that for the Dumosae the most important areas in which the classification will be applied are in conservation of naturally occurring communities (for recreation purposes and as a genetic resource) and cultivation for amenity purposes or fuel production in arid areas. The high level of variation present indicates that the ultimate unit for consideration should not be at the level of taxa but populations and provenances.

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Appendix 1: Classification results for the TYPDAT and DPOPDAT canonical variate analyses.

LOCALITY / COLLECTION: Individual collections are arranged firstly according to the taxa recognized in this thesis, then according to state, then botanical district or region. Where possible the arrangement is from west to east and north to south.

DETERMINATIONS : Specimens were assigned subjectively to TYP groups (representing existing species) prior to performing the analyses. Code names in brackets indicate other groups with nearly intermediate status or strong affinities (upper case), or with weak or uncertain affinities (lower case). Where collections belong to TYP or DPOP groups defined for the analyses the appropriate codes are underlined.

OP : This column indicates whether the three operculum characters were present (+) or absent (-).

CLASSIFICATIONS : The remaining four columns tabulate the outcome of CVA classifications. The assigned TYP or DPOP group is the one with the closest centroid in multi-dimensional discriminant space. Any significant intergradation is indicated by including the name of the second nearest neighbour group in brackets. Upper case letters are used for level 2 intergrades ($.50 < P(G/X) < .90$) and lower case letters for level 1 intergrades ($.90 \leq P(G/X) \leq .99$).

The results for the TYPDAT analysis (column 1) are the most directly comparable with prior determinations, being based on the same 16 TYP groups. The classifications indicate similarities based solely on the variation expressed in the defined TYP groups, whereas the determinations in the preceeding column are subjective and reflect existing taxonomic concepts with biased weighting of key characters and consideration to geographical occurrence. The results for the DPOPDAT analysis (column 2) may further differ because there is the potential for classification to an additional five DPOP groups. Both the analyses were repeated with the three low-state characters (LG,SG,BB) excluded (columns 3 and 4). These results reveal affinities in basic morphology irrespective of glaucousness or the possession of a blackbutt.

LOCALITY / COLLECTION	DETERMINATION (TYP affinities)	OP	CLASSIFICATIONS 1 TYPDAT	2 DPOPDAT	3 TYPDAT -(LG,SG,BB)	4 DPOPDAT -(LG,SG,BB)
Eucalyptus pterocarpa						
WESTERN AUSTRALIA						
Coolgardie District						
16 km WNW Norseman/G.E.Brockway -.x.1942	PTE	+	PTE	PTE	PTE	PTE
16 km W Norseman/C.A.Gardner 20.vii.1963	PTE	+	PTE	PTE	PTE	PTE
14.5 km NW Norseman/G.E.Brockway 20.viii.1963	PTE	+	PTE	PTE	PTE	PTE
18 km WNW Norseman/G.M.Chippendale 154	PTE	+	PTE	PTE	PTE	PTE
14.6 km NW Norseman/D.J.Boland J345	PTE	+	PTE	PTE	PTE	PTE
Eucalyptus lesouefii						
WESTERN AUSTRALIA						
Coolgardie District						
5 km SW Coolgardie/PJL 1523	LES	+	LES	LES	LES	LES
" " /PJL 1524	LES	+	LES	LES	LES	LES
" " /PJL 1525	LES	+	LES	LES	LES	LES
" " /PJL 1526	LES	+	LES	LES	LES	LES
" " /PJL 1527	LES	+	LES	LES	LES	LES
8.4 km N Kalgoorlie/PJL 1528	LES	+	LES	LES	LES	LES
Kurrawang RS/PJL 1521	LES	+	LES	LES	LES	LES
23.3 SE Kalgoorlie/PJL 1556	LES(pte)	+	LES	LES	LES	LES
18.3 km SE Widgiemootha/PJL 1557	LES(cle)	-	LES	LES	LES	LES
" " "/PJL 1544	LES	-	LES	LES	LES	LES
1.6 km N Cundelee Mission/R.D Royce 5338	LES(PTE)	+	LES	LES	LES	LES
Goddard Creek/R.D.Royce 5362	LES(PTE)	+	LES	LES	LES	LES
7.7 km NNW Norseman/PJL 1549	LES	+	LES	LES	LES	LES
36.4 km E Norseman/PJL 1551	LES	-	LES	LES	LES	LES

Eucalyptus woodwardii

WESTERN AUSTRALIA					
Coolgardie District					
97 km S Victoria Spring/R.Helms 15	WOO	+ WOO	WOO	WOO	WOO
cultivated, Waite Institute,Adelaide/PJL 1562	WOO	+ WOO	WOO	WOO	WOO
cultivated, Waite Institute,Adelaide/PJL 1563	WOO	+ WOO	WOO	WOO	WOO
cultivated, Burnside,Adelaide/PJL 1564	WOO	+ WOO	WOO	WOO	WOO

Eucalyptus kondininensis

WESTERN AUSTRALIA					
Roe District					
0.5 km S Kondinin/PJL 1440	KON	+ KON	KON	KON	KON
" " /PJL 1441	KON	+ KON	KON	KON	KON
" " /PJL 1442	KON	+ KON	KON	KON	KON
" " /PJL 1443	KON	+ KON	KON	KON	KON
" " /PJL 1444	KON	+ KON	KON	KON	KON
14.0 km E Lake Grace/PJL 1415	KON	+ KON	KON	KON	KON
1.0 km E Newdegate/PJL 1429	KON	- KON	KON	KON	P35(KON)
" " /PJL 1430	KON	+ KON	KON	KON	KON
5.1 km W Lake Grace/PJL 1414	KON	+ KON	KON	KON	KON

Eucalyptus dumosa ssp. clelandii

WESTERN AUSTRALIA					
Austin District					
5.9 km N Goongarrie/PJL 1530	CLE	+ CLE	CLE	CLE	CLE
" " /PJL 1539	CLE	+ CLE	CLE	CLE	CLE
" " /PJL 1540	CLE	+ CLE	CLE	CLE	CLE
" " /PJL 1541	CLE	+ CLE	CLE	CLE	CLE
" " /PJL 1542	CLE	+ CLE	CLE	CLE	CLE
3.7 km S Goongarrie/PJL 1543	CLE	+ CLE	CLE	CLE	CLE
26.3 km N Kalgoorlie/PJL 1529	CLE	+ CLE	CLE	CLE(kon)	CLE

15.1 km S Menzies/PJL 1531	CLE(LES)	+ CLE	CLE	CLE	CLE
" " /PJL 1533	CLE(LES)	+ CLE	CLE	CLE	CLE
3.9 km S Menzies/PJL 1534	CLE(LES)	+ CLE	CLE	CLE	CLE
" " /PJL 1535	CLE(LES)	+ CLE	CLE(KON)	CLE	CLE
" " /PJL 1536	LES(CLE)	+ CLE	CLE	CLE	CLE
" " /PJL 1537	LES(CLE,str)	+ CLE	CLE	CLE	CLE
" " /PJL 1538	LES(CLE)	- CLE	CLE	CLE	CLE
14.5 km NE Mt Gibson HS turn-off/PJL 1486	CLE	+ CLE	CLE	CLE(DUM)	DUM(CLE)
" " " /PJL 1487	CLE(SHE)	+ CLE	CLE	SHE	SHE
" " " /PJL 1488	STR(CLE,LES)	+ CLE	CLE	CLE	CLE
" " " /PJL 1489	CLE	+ CLE	CLE	CLE(DUM)	CLE(DUM)
Coolgardie District					
4.9 km NW Coolgardie/PJL 1519	CLE(les)	+ CLE	CLE	CLE	CLE(she)
" " /PJL 1520	CLE(les,str)	+ CLE	CLE	CLE	CLE

Intergrades between ssp. clelandii and ssp. dumosa

Austin District					
2 km N Mt Magnet/PJL 1472	STR(CLE)	+ CLE	CLE(str)	STR	STR(PMAR)
" " /PJL 1473	STR(CLE)	+ CLE	STR	STR	STR
" " /PJL 1474	STR	+ CLE	CLE	STR	STR
" " /PJL 1475	STR	- CLE	CLE	STR(cle)	PMAR(CLE)
" " /PJL 1476	STR	+ STR	STR	STR(cle)	STR(cle)
" " /PJL 1477	SHE	- CLE	CLE	CLE(SHE)	CLE(SHE)
Coolgardie District					
1.3 km W Bullabulling/PJL 1514	CLE	+ CLE	CLE	CLE(STR)	CLE(STR)
" " /PJL 1515	CLE	+ CLE	CLE	CLE	CLE(PCAR)
" " /PJL 1518	CLE	+ CLE	CLE	CLE(DUM)	CLE(DUM)
" " /PJL 1516	CLE(SHE,STR)	+ SHE	SHE	CLE	CLE
" " /PJL 1517	CLE(SHE,DUM)	+ SHE	SHE	CLE(kon)	DUM(CLE)
12.9 km NW Norseman/C.A.Gardner 11153	RED/CLE(SHE,PIL ?)	+ LES	PIL	KON(pil)	KON(PIL)
22.1 km N Norseman/PJL 1546	CLE(SHE,str)	+ SHE(dum)	DUM(PCAR)	DUM	CLE(DUM)
" " /PJL 1547	SHE	- SHE(DON)	SHE	CLE(KON)	CLE(DUM)

Eucalyptus dumosa ssp.georgei

Roe District					
c.160 km E Hyden/M.I.H.Brooker 4989	GEO	+ GEO	GEO	GEO	GEO
" " /L.F.Allan 29	GEO	+ GEO	GEO	GEO	GEO
" " /A.Kessell 947	GEO	+ GEO	GEO	GEO	GEO
" " /A.Kessell 424	GEO	+ GEO	GEO	GEO	GEO
E of Mt Holland/C.A.Gardner -.6.1930	GEO(SHE)	+ GEO	GEO	GEO	GEO

E. dumosa ssp. georgei intergrades

Roe District					
Mt Holland area/A.Kessell 408	GEO(WOO?)	+ GEO	ANC(FRA)	ANC(FRA)	ANC(FRA)
25 km E Hyden/PJL 1431	SHE(GEO)	+ GEO	PCAR	GEO	PCAR
" " /PJL 1432	SHE	- GEO(SHE)	PCAR	CLE(CYA)	PCAR(CLE)
" " /PJL 1433	SHE(GEO)	- GEO	PCAR	CYA	PCAR

Eucalyptus dumosa ssp. fraseri

WESTERN AUSTRALIA					
Coolgardie District					
8 km WNW Balladonia motel/W.R.Barker 2599A	FRA	+ FRA	FRA	FRA	FRA
" " " " 2599B	FRA	+ FRA	FRA	FRA	FRA
" " " " 2599C	FRA	+ FRA	FRA	FRA	FRA
" " " " 2599D	FRA	+ FRA	FRA	FRA	FRA
" " " " 2599E	FRA	+ FRA	FRA	FRA	FRA
Afgan Rocks, Balladonia motel/PJL 1554	FRA	+ FRA	FRA	FRA	FRA
E side Fraser Range pass/PJL 1340	FRA	+ FRA	FRA	FRA	FRA

Intergrade between ssp. fraseri and ssp. dumosa

WESTERN AUSTRALIA					
Eucla District					
58.9 km E Balladonia HS/PJL 1339	FRA(CAL)	+ CAL(ANC)	FRA(cal)	CAL(ANC)	FRA(cal)

Eucalyptus dumosa ssp. conglobata

WESTERN AUSTRALIA					
Avon District					
12.2 km NE Dumbleyung/PJL 1412	ANC(kon)	+ CAL(anc)	CAL(ANC)	KON	KON
Roe District					
35.2 km SW Lake Grace/PJL 1413	ANC(KON)	- CAL	P35	KON	P35
18 km N Pingrup/PJL 1405	ANC(kon)	+ CAL	CAL	CAL	CAL
19.3 km N Pingrup/PJL 1407	ANC	- CAL(PIL)	P35	KON	P35(kon)
2.6 km NW Kulin/PJL 1437	ANC	- CAL	CAL	CAL	CAL(pil)
6.8 km E Scadden/PJL 1360	CON(fra)	+ CON	FRA	CON(fra)	FRA
1.2 km S Grass Patch/PJL 1356	CON(fra,anc)	+ FRA	FRA	FRA	FRA
" " /PJL 1359	ANC(CON,fra)	+ FRA	FRA	FRA	FRA
Eyre District					
Kundip, 19.8 km S Ravensthorpe/PJL 1386	CON(ANC)	+ ANC	ANC	ANC	ANC
1.3 km N Howick Hill/PJL 1368	CON	+ FRA	ANC(fra)	FRA	ANC(FRA)
SOUTH AUSTRALIA					
Eyre Peninsula Region					
Lincoln NP, 2 km S of Sleaford road/PJL 1123	CON	+ CON	CON	CON	CON
" " " " /PJL 1124	CON	+ CON	CON	CON	CON
" " " " /PJL 1125	CON	+ CON	CON	CON	CON
" " " " /PJL 1126	CON	+ CON	CON	CON	CON
" " " " /PJL 1127	CON	+ CON	CON	CON	CON
Spalding Cove/PJL 1117	CON	- CON	CON	CON	CON
4 km W Pt Lincoln PO/PJL 1113	CON	+ CON	CON	CON	CON
Pass between North and South Block/PJL 1101	ANC	+ ANC	ANC	ANC	ANC
3 km W North Block/PJL 1097	ANC	+ ANC	ANC	ANC	ANC
1 km W Mt Hope summit/PJL 1086	ANC(dum)	- ANC	ANC(P35)	ANC	P35(ANC)
1.7 km N Tooligie/PJL 1062	ANC	+ ANC	ANC(CAL)	ANC	ANC(CAL)
2 km E Mt Hill RS/C.D.Boomsma 432	ANC(cal)	- PIL(CAL)	PIL(P35)	PIL(CAL)	P35(pil)
" " " 433	ANC(dum)	- DUM	P35	DUM	P35
Mt Shannon, 7.4 km N Cleve/PJL 1138	ANC	+ ANC(CAL)	ANC(cal)	ANC(cal)	ANC(cal)
6 km ENE Kielpa/PJL 1146	ANC	- CAL	CAL	CAL	CAL

Coolanie/PJL 1150	ANC	- PIL(CAL)	P35(DUM)	KON(PIL)	P35(pil)
Carappee Hill/D.E.Symon 8856	ANC	+ ANC(CAL)	CAL(ANC)	ANC(cal)	CAL(ANC)
Yorke Peninsula Region					
4 km NE Pondalowie/PJL 942	ANC	+ ANC	ANC	ANC	ANC
2.5 km W Pt Vincent/PJL 806	ANC	+ CAL	CAL(DUM)	CAL	DUM(CAL)
Southern Lofty Region					
Mt Scrub - Mt Desert road/PJL 745	ANC	+ ANC	ANC	ANC	ANC
8 km SE Strathalbyn/PJL 1163	ANC	+ ANC(cal)	ANC(CAL)	ANC(CAL)	ANC(DUM)
Kangaroo Island Region					
5 km NW American River/PJL 672	ANC	+ ANC	ANC	ANC	ANC
" " /PJL 673	ANC	+ ANC	ANC	ANC	ANC
" " /PJL 674	ANC	+ ANC	ANC	ANC	ANC
" " /PJL 675	ANC	+ ANC	ANC	ANC	ANC
15 km W American River/PJL 667	ANC	+ ANC	ANC	ANC	ANC
" " /PJL 668	ANC	+ ANC	ANC	ANC	ANC
" " /PJL 669	ANC	+ ANC	ANC	ANC	ANC
Murray Region					
Monarto/J.Venninng C	ANC	+ CAL(ANC)	ANC(CAL)	CAL(ANC)	ANC(CAL)
South-eastern Region					
2 km SE Coonalpyn/PJL 1266	ANC	- ANC(cal)	ANC	ANC	ANC
Northern Lofty Region					
3 km S Lochiel/PJL 1158	ANC	+ CAL	P35(cal)	CAL(kon)	P35
" " /PJL 1159	ANC	+ ANC(dum)	ANC	ANC(DUM)	ANC
Intergrades between ssp. conglobata and ssp. dumosa					
SOUTH AUSTRALIA					
Eyre Peninsula Region					
Cungena RS/PJL 1198	ANC(dum)	+ CAL	CAL	CAL(CYA)	P35
5 km WNW Edillilie/PJL 1105	ANC(DUM)	- DUM	P35	DUM	P35
Tooligie/C.D.Boomsma 450	ANC(DUM)	- CAL(ANC)	ANC(CAL)	CAL(ANC)	ANC(CAL)
" " 451	ANC(cal)	- CYA(cal)	CYA(CAL)	CYA	CYA(p35)
Tooligie Range/PJL 1068	ANC(cal)	+ ANC(CAL)	CAL(anc)	ANC(CAL)	CAL(anc)
10.4 km SW Cleve/PJL 1137	ANC(DUM,CAL)	- CAL	CAL	CAL	CAL(pil)

54 km SW S side Whyalla/PJL 1155	ANC(DUM,KON)	- DUM	P35(dum)	KON(dum)	P35(KON)
Northern Lofty Region					
3.5 km N Bute/P.Copley A	ANC(DUM,KON)	+ CAL	CAL(p35)	KON	KON(P35)
" " B	ANC(DUM,PIL)	+ DUM	P157(P35)	KON(dum)	P35(p157)
Murray Region					
22 km WSW Waikerie/PJL 892	CYA(ANC)	+ CYA	CYA	CAL(cya)	CAL(CYA)
" " /PJL 895	ANC(CYA)	+ CAL(CYA)	CAL(CYA)	CYA(CAL)	CYA(CAL)
South-eastern Region					
2 km SE Coonalpyn/PJL 1261	ANC(DUM)	+ DUM	CAL(DUM)	DUM	DUM(cal)
" " /PJL 1262	ANC(DUM)	+ CAL	P35	KON	KON
" " /PJL 1263	DUM(ANC)	+ CAL	CAL	CAL	CAL(DUM)
" " /PJL 1264	ANC(DUM)	+ CYA	CYA	CYA	CYA
Comet Bore, 55 km S Pinnaroo/C.D.Boomsma 4.10.1977 E	ANC(cya)	- CYA(anc)	CYA(cal)	CYA(anc)	CYA(pcar)
" " " /J.G.West 2314	ANC(dum)	- DUM	P35(dum)	DUM	P35
" " " " 2315	ANC(dum)	- DUM	P35(dum)	DUM	P35(dum)
" " " " 2321	CYA(ANC)	- DUM	P35	DUM	P35
" " " " 2322	ANC(DUM)	- DUM	P35	DUM	P35
" " " " 2325A	ANC(dum)	- DUM	P35(dum)	DUM	P35(dum)

Eucalyptus dumosa ssp. dumosa

WESTERN AUSTRALIA					
Carnarvon District					
20 km S Overlander/C.D.Boomsma WA45/76	DON	+ DON(cal)	DON	DON	DON
Ashburton District					
8 km NE Wongawol HS/F.M.Bennet 192	STR	+ DUM	PMAR	SHE(dum)	PMAR
Austin District					
73 km NNE Cue/PJL 1478	STR	+ DUM	SHE	CLE	CLE
Millie Well, 20 km NNE Cue/PJL 1481	STR	+ STR	STR	STR	STR
" " " PJL 1482	STR	+ STR	STR	STR	STR
" " " PJL 1483	STR	+ STR	STR	STR	STR
" " " PJL 1484	STR	+ STR	STR	STR	STR
" " " PJL 1485	STR	+ STR	STR	STR	STR

Irvin District					
13.5 km WSW Yuna/PJL 1468	DON(str)	- -	P157	-	PCAR(DON)
" " PJL 1469	DON	- CAL	DON(cal)	DON(cal)	DON
20 km SE Dongara/PJL 1463	DON	+ DON	DON	DON	DON
" " PJL 1464	DON	+ DON	DON	DON	DON
" " PJL 1465	DON	+ DON	DON	DON	DON
" " PJL 1466	DON	+ DON	DON	DON	DON
" " PJL 1467	DON	+ DON	DON	DON	DON
1.3 km N Watheroo/PJL 1456	DON(SHE,STR)	- DUM	P157	DUM(she)	P157(dum)
Avon District					
6.2 km N Coorow/PJL 1457	DON/P157	+ DON(DUM)	P157	SHE(DON)	P157
" " PJL 1458	DON(SHE)/P157	- DUM	P157	DUM(SHE)	P157
" " PJL 1459	DON/P157	- DUM	P157	DUM	P157(she)
" " PJL 1460	DON(DUM)/P157	- DUM	P157	DUM	P157
" " PJL 1461	DON(SHE,DUM)/P157	- DUM	P157	DON	P157(dum)
Pithara/PJL 1451	DON(pil,she)	+ DON(DUM)	P157	DON	P157
" PJL 1452	DON(SHE)	+ DUM(don)	P157	SHE(DON)	P157
5.3 km W Wyalkatchem/PJL 1450	SHE(DON)	+ DUM	P157	SHE	SHE(P157)
0.5 km S Nukarni RS/PJL 1447	SHE	+ SHE	SHE	SHE	SHE
" " PJL 1448	SHE	+ SHE	SHE	SHE	SHE
" " PJL 1449A	SHE	+ SHE	SHE	SHE	SHE
" " PJL 1449B	SHE	+ SHE	SHE	SHE	SHE
" " PJL 1449C	SHE	+ SHE	SHE	SHE	SHE
1.7 km W Carrabin/PJL 1492	SHE	+ SHE	SHE	SHE	SHE
" " PJL 1493	SHE	+ SHE	SHE	SHE	SHE
" " PJL 1494	SHE	+ SHE	SHE	SHE	SHE
" " PJL 1495	SHE	+ SHE	SHE	SHE	SHE
" " PJL 1496	SHE	+ SHE	SHE	SHE	SHE
Roe District					
12.4 km E Bendering/PJL 1445	PIL(SHE)	- PIL(cal)	PIL(CAL)	PIL(dum)	DUM(PIL)
33.9 km E Hyden/PJL 1434	PIL(SHE)	- CAL(pil)	CAL(PIL)	CAL(PIL)	CAL(PIL)
2.6 km NW Kulin/PJL 1436	SHE	- SHE	DON(she)	DUM(SHE)	P157(DUM)

0.4 km N Burngup/PJL 1421	PIL	+ CAL	CAL(PIL)	CAL(kon)	CAL(PIL)
" " PJL 1426	PIL	+ CAL	CAL(PIL)	CAL	CAL(PIL)
" " PJL 1423	PIL(anc)	+ PIL(CAL)	P35(PIL)	DON(pil)	P35
" " PJL 1422	SHE(pil)	+ DON	DON(CAL)	CAL	CAL(pil)
" " PJL 1427	SHE(pil)	- DON(she)	DON(CAL)	PIL(cal)	DUM(PIL)
" " PJL 1428	SHE	- SHE	SHE	SHE	SHE
14.7 km E Lake Grace/PJL 1416	SHE	+ SHE	PCAR(SHE)	DUM	DUM(kon)
" " PJL 1417	SHE	+ SHE(don)	SHE	DUM(CAL)	DUM
" " PJL 1418	SHE(pcar)	+ DON	P35	KON	KON(P35)
" " PJL 1419	SHE	+ DON	DON(P35)	CAL(PIL)	P35
19.3 km N Pingrup/PJL 1411	PIL	+ PIL	PIL	PIL	PIL(p35)
Peak Charles/PJL 1348	PIL(CAL,DUM)	- PIL	PIL(cal)	PIL(cal)	PIL(cal)
" " PJL 1349	PIL(DUM,CAL)	- PIL(CAL)	PIL(CAL)	PIL(DUM)	PIL(CAL)
" " PJL 1353	PIL(DUM,anc)	+ CAL(PIL)	PIL(CAL)	CAL(KON)	CAL(PIL)
" " PJL 1354	PIL(DUM)	+ PIL(cal)	PIL(CAL)	PIL(KON)	PIL(CAL)
Eyre District					
10.5 km SE Ravensthorpe/PJL 1379	PIL	+ PIL	PIL	PIL	PIL
" " PJL 1380	PIL	+ PIL	PIL	PIL	PIL
" " " PJL 1381	PIL	+ PIL	PIL	PIL	PIL
" " " PJL 1382	PIL	+ PIL	PIL	PIL	PIL
" " " PJL 1383	PIL	+ PIL	PIL	PIL	PIL
Coolgardie District					
10.6 km E Southern Cross/PJL 1498	SHE(?)	+ SHE	SHE(pcar)	DUM(she)	DUM
" " " PJL 1499	SHE	+ SHE	SHE	SHE(DUM)	SHE(DUM)
3.1 km E Boorabbin/PJL 1508	PIL(CAL)	+ CAL	CAL	CAL	CAL
18.0 km W Bullabulling/PJL 1509	PIL(les?)	+ CAL	CAL(DUM)	KON(CAL)	DUM(KON)
" " PJL 1510	PIL	+ CAL	CAL	CAL	CAL
" " PJL 1511	PIL(DUM)	- PIL(cal)	PIL(dum)	KON	KON
" " PJL 1512	PIL	- PIL(cal)	PIL	PIL	PIL(cle)
" " PJL 1513	PIL	- PIL(cal)	PIL(CAL)	PIL(kon)	PIL(CAL)
14.4 km NW Norseman/M.I.H.Brooker 4539	PIL(DUM)	- PIL(cal)	PIL(CAL)	PIL(cal)	PIL(CAL)
13.5 km NW Norseman/PJL 1550	PIL(les?)	+ PIL(cal)	PIL(CAL)	PIL(cal)	PIL(CAL)
64.9 km E Norseman/PJL 1552	PIL(fra,cal)	+ CAL	CAL	KON	CAL(KON)
" " PJL 1553	PIL(kon,dum,cal)	+ DUM	DUM(CAL)	KON(DUM)	KON(DUM)

39.4 km S Norseman/PJL 1343	PIL	+ CAL	CAL	CAL	PIL(cal)
" " PJL 1344	PIL(str)	- PIL	PIL	PIL	PIL
" " PJL 1345	PIL(kon)	- PIL	PIL	PIL	PIL
" " PJL 1346	PIL	- PIL	PIL	PIL	PIL
" " PJL 1347	PIL	+ CAL	CAL(pil)	CAL	CAL(pil)
Eucla District					
Madura/PJL 1331	CAL	- PIL(dum)	PIL(DUM)	CLE(cya)	CLE(p35)
" PJL 1332	CAL	- CAL(PIL)	P35	KON(CLE)	P35
" PJL 1333	CAL	- CAL(pil)	P35(CAL)	KON(cal)	P35(KON)
" PJL 1334	CAL	- CAL(dum)	CAL	CAL(DUM)	CAL(p35)
" PJL 1335	CAL(DUM)	- DUM	DUM(p35)	CLE(DUM)	CLE(DUM)
" PJL 1336	CAL(?)	- CAL	DUM(P35)	KON	KON(cle)
19 km S Madura/PJL 1555	CAL	+ CAL	CAL	CAL	CAL
0.4 km SSW B.P. Village (SA border)/PJL 1327	CAL(DUM)	- DUM	DUM(p35)	DUM(cle)	DUM(P35)
" " " " PJL 1328	CAL	- CAL	CAL	CAL	CAL
" " " " PJL 1329	CAL	- CAL(PIL)	CAL	CAL(PIL)	CAL
Giles District					
Wurgelina,Blackstone Range/D.E.Symon 8403	STR	- SHE	PMAR	STR	PMAR
SOUTH AUSTRALIA					
North-western Region					
Serpentine Lakes on WA border/J.Johnson Stn 26	STR	- CYA	PMAR	CYA(SHE)	PMAR(pcar)
" " " " 27	STR	+ DUM(cya)	PMAR	STR(GEO)	PMAR
Serpentine Lakes near WA border/L.D.Williams 10573	STR	- CYA(geo)	PMAR(pcvh)	STR(GEO)	PCVH(PMAR)
" " " " 10561	STR	- CYA	PMAR	WOO	WOO(pmar)
" " " /V.J.Levitzke 38	STR	+ CYA	PMAR	STR	PMAR(STR)
" " " /J.Douglas 34	STR	+ DUM(CYA)	PMAR	GEO	PMAR
" " " " 72	STR	+ CYA	PMAR	STR	PMAR
29 12 S 129 21.5 E/V.J.Levitzke 220	STR	- DON	PMAR(PCVH)	WOO	PMAR(PCVH)
155 km NW Hughes/R.C.Shearer 137	STR	- CYA(DUM)	PMAR	SHE	PMAR
124.5 km N Cook/J.Johnson & S.Reid 3	STR/PCVH	+ CYA	PMAR	CYA	PMAR
130 km N Cook/L.D.Williams 10492	STR/PCVH	- WOO	PCVH	WOO	PCVH
131 km N Cook/T.E.Dennis 189	STR/PCVH	- WOO	PCVH	WOO	PCVH
" " " 188	STR/PCVH	- GEO	PCVH	WOO(GEO)	PCVH

136 km N Cook/T.E.Dennis 191	STR/PCVH	-	WOO	PCVH	WOO	PCVH
W of Wyola Lake, 29 15 S 130 13 E/T.E.Dennis 215	STR/PCVH	+	-	PCVH	-	PCVH
" " 29 15 S 130 00 E/T.E.Dennis 218	STR/PCVH	+	-	PCVH	-	PCVH
" " 29 15 S 129 55 E/T.E.Dennis 220	STR/PCVH	+	-	PCVH	-	PCVH
" " 29 15 S 129 50 E/T.E.Dennis 223	STR/PCVH	+	-	PCVH	-	PCVH
Vokes Corner/N.N.Donner 3904	STR	+	SHE	PCAR	CYA(STR)	PMAR(pcar)
20 km SW Vokes Junction/L.D.Williams 10776	STR	+	SHE	PMAR(pcvh)	STR	PMAR
95 km S Vokes Corner/N.N.Donner 3982	STR	-	WOO	WOO(PCVH)	WOO	PCVH(WOO)
103 km N Cook/T.E.Dennis 110	STR	+	DON(SHE)	PCVH	CYA	PCVH
78 km S Wyola Lake/T.E.Dennis 186B	STR	-	CYA	PMAR(pcvh)	WOO	PMAR(PCVH)
105 km S Vokes Hill/T.R.N.Lothian 5701	STR	-	CYA	PCVH	CYA(woo)	PCVH
N L.Maurice 131 02 28 55/J.Johnson & S.Reid WF 1133	STR	+	SHE	PMAR(pcvh)	SHE	PMAR
Between Ernabella & Mt Woodroofe/J.Johnson WF 1124-5	STR	-	SHE	PMAR(SHE)	STR(cya)	PMAR
40 km NE Maralinga/R.C.Shearer 15.ii.1972	STR	-	WOO	PMAR(PCVH)	CYA(STR)	PMAR
W Dog fence, Commonwealth Hill Stn/B.Lay 525	STR	-	SHE	PMAR	STR	PMAR
Gairdner-Torrens Basin Region						
Barton/E.H.Ising 1340	STR	-	DUM(CYA)	PMAR	SHE(CYA)	PMAR
S of Lake Bring/D.E.Symon 3398	STR	-	CYA	PMAR	SHE(CYA)	PMAR
Cultivated Waite Inst.(D.E.S 3398)/PJL 1180	STR	+	CYA(don)	P157(pmar)	DON(she)	P157(pmar)
16 km W Mt Christy/F.A.Mowling 70	STR	+	CYA	PMAR	GEO	PMAR(p157)
76 km NE Kalanbi/L.D.Williams 8781	STR	+	CYA(dum)	PMAR	STR	PMAR
Nullarbor Region						
Maralinga/O.H.Turner	STR/PMAR	+	DUM	PMAR	DUM	PMAR
" /J.Johnson & S.Reid 8	STR/PMAR	+	SHE	PMAR	SHE	PMAR
Near Maralinga/S.Warne 20113	STR/PMAR	-	CYA	PMAR	CYA(GEO)	PMAR
33.2 km E Maralinga/O.H.Turner E5	STR/PMAR	+	CYA	PMAR	SHE(STR)	PMAR
Maralinga bombsite/P.Aitken (AD 97548142)	STR/PMAR	-	CYA	PMAR	STR(CYA)	PMAR
1 km S Maralinga checkpoint/T.R.N.Lothian 4012	STR/PMAR	-	CYA	PMAR	CYA(STR)	PMAR
4.8 km S Maralinga/B.Copley 2691	STR/PMAR	+	CYA	PMAR	STR	PMAR
27 km N Watson/M.I.H.Brooker 5607	STR	+	DON(dum)	P157	DUM(CYA)	SHE(p157)
90 km W Nundroo/G.C.Cornwall 288	CAL	+	CAL	CAL(pil)	CAL	CAL
40 km E Head of Bight/G.C.Cornwall 16.vi.1976	CAL	+	CAL	CAL	CAL	CAL

44.1 km W Nundroo/PJL 1321	CAL	+ CAL	CAL	CAL	CAL
" " /PJL 1322	CAL	+ CAL	CAL	CAL	CAL
" " /PJL 1323	CAL	+ CAL	CAL	CAL	CAL
" " /PJL 1324	CAL	+ CAL	CAL	CAL	CAL
" " /PJL 1325	CAL	+ CAL	CAL	CAL	CAL
Eyre Peninsula Region					
16 km WNW Coorabie/PJL 1194	CAL	+ CAL	CAL	CAL	CAL
" " /PJL 1195	CAL	- CAL(PIL)	P35(cal)	KON(cal)	P35(kon)
" " /PJL 1196	CAL	+ ANC	ANC(CAL)	ANC	ANC(CAL)
6 km SW Coorabie/PJL 1193	CAL	+ CAL	CAL	CAL	CAL
9 km SW Coorabie/PJL 1191	CAL	+ CAL	CAL(pil)	CAL(cya)	CAL(pcar)
" " /PJL 1192	CAL	+ CYA(CAL)	CAL	CYA	CAL(CYA)
20 km WNW Ceduna/PJL 1199	CAL	- CAL(pil)	CAL	CAL(pil)	CAL
" " /PJL 1200	CAL	- PIL(CAL)	CAL(pil)	CAL(PIL)	CAL(DUM)
N Puntabie RS, Hd Guthrie/PJL 1205	CAL	- CAL	CAL	CAL	CAL
12 km E Smoky Bay/PJL 1207	CAL	+ CAL	CAL	CAL	CAL
(Gawler Ranges:)					
Hills NE Kondoolka HS/J.Z.Weber	DUM(PIL)	+ CAL	CAL(P35)	KON	KON
13.4 km SE Hiltaba HS/PJL 995	DUM	- DUM	P35(DUM)	KON(CLE)	P35(CLE)
Peltabinna Hill/PJL 992	DUM	- DUM	P35	KON	KON(P35)
" " /PJL 993	DUM	+ CAL(dum)	DUM	KON	KON
Kododo Hill/PJL 967	DUM	+ DUM	DUM	KON(dum)	KON(DUM)
" /PJL 968	DUM	- SHE	P35(pcar)	DUM	DUM(P35)
" /PJL 969	DUM	- DUM	DUM	DUM(str)	DUM(STR)
" /PJL 970	DUM	+ DUM	DUM(pmar)	DUM(CLE)	DUM(CLE)
" /PJL 971	DUM	- DUM	DUM(p35)	DUM	DUM(P35)
" /PJL 972	DUM	- CYA	CYA(p35)	CYA	PCAR(CYA)
Peterby Yards/PJL 987	DUM	- DUM(cya)	PMAR(dum)	SHE(cle)	SHE(CLE)
" " /PJL 988	DUM(STR)	- DUM	DUM(PMAR)	CLE	CLE
Petersby Gate fence line/F.A.Mason -.ix.1975	STR(DUM)	+ CYA	PMAR	STR	PMAR
E side Scrubby Peak/PJL 976	DUM	- PIL(cal)	P35(PIL)	PIL(cal)	P35(PIL)
" " /PJL 977	DUM	- PIL	P35(pil)	KON	KON
" " /PJL 980	DUM(STR)	- DUM	DUM	DUM	DUM
5 km S Scrubby Peak/L.Haegi 761	DUM	+ DUM	DUM(cal)	DUM(kon)	DUM(kon)

(Eyre Peninsula:)					
26.5 km NE Yantanabie/PJL 998	STR	- CYA	CYA(PMAR)	STR	PCAR(str)
" " /PJL 999	CAL(STR)	- CYA	CYA	CYA(str)	PCAR(CYA)
" " /PJL 1001	CAL(STR)	+ CYA	CYA	CYA(str)	CYA
" " /PJL 1002	STR(CAL)	+ CYA	CYA	STR	STR(p157)
23.9 km NE Yantanabie/PJL 1005	CAL(STR)	- CYA	CYA(pmar)	CYA(str)	PCAR(CYA)
5.4 km SW Yantanabie/PJL 1011	CAL(PIL,dum)	+ CAL	CAL	CAL	CAL
13.6 km N Minnipa/PJL 1033	DUM(pil)	- PIL	PIL(P35)	PIL(kon)	PIL(p35)
14.2 km N Minnipa/PJL 1032	STR(cal)	+ CYA	CYA	CYA	CYA(pcar)
14 km SSE Poochera/PJL 1219	DUM(cal)	+ CAL	CAL	DUM(cal)	CAL
Piednippie/PJL 1023	CAL(dum,pil)	+ CAL	CAL	CAL	CAL
" /PJL 1024	CAL	- CAL(PIL)	CAL	CAL(pil)	CAL
" /PJL 1025	DUM(PIL)	+ CAL	CAL	CAL	CAL(PIL)
Streaky Bay/PJL 1013	CAL	+ CAL	CAL	CAL	CAL
" /PJL 1014	CAL	+ CAL	CAL(CYA)	CAL	CAL(cya)
16.4 km SSW Streaky Bay/PJL 1021	CAL	- PIL	PIL(cal)	PIL	PIL(CAL)
23 km S Streaky Bay/PJL 1220	CAL	+ CAL(pil)	CAL	CAL	CAL
" " /PJL 1222	CAL(ANC)	- PIL(cal)	PIL(cal)	PIL(cal)	PIL(P35)
Calca Hill/PJL 1224	CAL	- CAL(pil)	CAL(pil)	CAL(pil)	CAL(p35)
2.2 km N Mt Hall/PJL 1225	PIL	+ CAL	CAL(P35)	CAL(cya)	P35(cal)
14.2 km NE Pt Kenny/PJL 1027	CAL	- CAL(PIL)	CAL(PIL)	CAL(PIL)	CAL(pil)
" " /PJL 1028	CAL(ANC)	+ CAL	CAL	CAL	CAL
21 km ENE Colley Hill/PJL 1214	STR(DUM)	- DUM(CYA)	DUM(CYA)	CYA(DUM)	CYA(DUM)
" " /PJL 1215	DUM(STR,CAL)	- DUM(cal)	P35(DUM)	DUM(PIL)	P35(DUM)
14.1 km SW Minnipa/PJL 1030	CAL(STR)	+ CAL	CAL	CAL	CAL
5.1 km NW Wudina/PJL 1320	CAL(STR)	- CYA(dum)	PMAR(DUM)	CYA	PCAR(pmar)
Koongawa WR/PJL 1227	CAL(STR)	+ CYA	CYA	CYA	CYA
6.7 km SSE Buckleboo HS/PJL 1035	CAL(STR)	+ CYA	CYA	CYA	PCAR(CYA)
24 kmk NW Kimba/PJL 1036/	DUM(CYA?)	+ CYA	CYA(DUM)	CYA(CLE)	PCAR(CLE)
Cortilinye WR, 7 km NW Kimba/C.D.Boomsma 425	DUM	- DUM	DUM(p35)	CLE(dum)	CLE(dum)
" " " " 426	DUM	- DUM	DUM(P157)	DUM(cle)	DUM(cle)
1 km SE Kimba PO/PJL 1043	CAL(DUM,CYA)	- DUM(CYA)	DUM(P35)	DUM(CYA)	P157(DUM)
" " /PJL 1042	CAL(DUM)	+ CAL	CAL(p157)	CAL(DON)	PCAR(CAL)
8 km ENE Kimba/PJL 1242	CAL(DUM,CYA)	- CYA(DUM)	PCAR(DUM)	CYA	PCAR
" " /PJL 1241	CAL(DUM,str)	- PIL(cal)	DON(CAR)	DON(pil)	PCAR(DON)
27.6 km E Kimba towards Whyalla/PJL 1041	DUM(CAL)	- PIL(DUM)	PIL(DUM)	DUM(cle)	DUM(CLE)

34 km E Kimba towards Whyalla/PJL 1040	DUM(ANC,kon)	- PIL	PIL(p35)	KON	P35(KON)
Secret Rocks, 31 km E of Kimba/PJL 1038	DUM	+ CAL	P157(CAL)	DUM(CAL)	DUM(pcar)
54 km SW Whyalla S/PJL 1153	CAL(pil,kon)	- CAL	CAL	CAL(KON)	CAL(p35)
" " /PJL 1154	CAL(DUM,DON)	+ CAL	CAL(p157)	CAL	CAL(p157)
" " /PJL 1156	DUM(CAL)	- CAL	CAL	CAL(pil)	CAL(p35)
" " /PJL 1157	DUM(CAL,anc)	- PIL	PIL(cal)	KON(CLE)	CLE(P35)
30 km N Cowell/C.D.Boomsma 452	DUM(anc,kon)	- PIL(DUM)	P35	KON	P35(KON)
" " " 453	DUM	- DUM	P157(DUM)	DUM	DUM(P157)
25 km NW Lock/PJL 1053	CAL(ANC)	+ CAL	CAL	CAL	CAL
" " /PJL 1054	DUM(ANC,CAL)	+ CAL	CAL	CAL	CAL
" " /PJL 1055	CAL(ANC)	+ CAL	CAL	CAL	CAL
" " /PJL 1056	CAL(DUM)	+ CAL	CAL	CAL	CAL
" " /PJL 1057	CAL	+ CAL	CAL	CAL	CAL
Waddikee/C.D.Boomsma 419	DUM(CAL)	- CYA	CYA(P35)	CYA(CLE)	CYA(PCAR)
Carappee Hill/PJL 1044	CYA(STR)/PCAR	+ SHE	PCAR	CYA	PCAR(cya)
" " /PJL 1045	CYA(STR)/PCAR	+ GEO	PCAR	GEO	PCAR
" " /PJL 1047	CYA(STR)/PCAR	- GEO	PCAR	CYA	PCAR
" " /PJL 1048	CYA(STR)/PCAR	- SHE	PCAR	CYA	PCAR(CYA)
" " /K.D.Rohrlach 445	CYA(STR)/PCAR	+ SHE	PCAR	CYA(str)	PCAR
" " /D.E.Symon 9008	CYA(STR)/PCAR	+ SHE	PCAR	DUM(CYA)	PCAR
4 km NE Darke Peak PO/PJL 1050	CYA(STR)/PCAR	+ DON(GEO)	PCAR	CAL	PCAR
3 km SW Carappee Hill/C.D.Boomsma 420A	CYA(STR)/PCAR	- GEO	PCAR	CYA	PCAR
" " " 420B	CYA(STR)/PCAR	- DON(GEO)	PCAR	CLE(CYA)	PCAR
" " " 423	CYA(STR)/PCAR	+ DON	PCAR	CYA	PCAR(pcvh)
0.7 km NE Darke Peak PO/PJL 1051	CYA(STR)/PCAR	+ DON	PCAR	CYA	PCAR
NW corner Darke Peak Range/L.D.Williams 5202	CYA(STR)/PCAR	+ DON	PCAR	CYA	PCAR
E Prominent Hill, Hambidge CP/D.Krahlenbuel 2074	CYA(STR,CAL)	- DON(she)	PCAR	CYA	PCAR(CYA)
12 km NW Cleve/PJL 1142	CYA(STR)	+ DON(SHE)	PCAR	CYA	PCAR(cya)
" " /PJL 1143	CYA(STR,CAL)	+ SHE	PCAR(CAL)	CYA(CAL)	CAL(cya)
" " /PJL 1144	CYA(STR,CAL)	+ SHE(DON)	PCAR	CAL	CAL(PCAR)
0.3 km SW Coolanie/PJL 1149	CYA(STR,DUM)	+ DON	PCAR(DON)	CYA	CAL(CYA)
8 km E Yabmana/C.D.Boomsma 408	DUM(ANC)	- DUM	P35(DUM)	DUM	P35(dum)
" " " 410	CYA(STR,DUM)	- SHE	PCAR	DUM	DUM(P157)
4.7-5.1 km E Tooligie Hill PO/PJL 1071	CYA(STR,ANC)	+ DON	PCAR	CYA	CYA(CAL)
" " " /PJL 1072	CYA(STR,DUM)	+ DON(she)	PCAR	DUM(cal)	PCAR(p157)
" " " /PJL 1073	CYA(STR,?)	+ SHE	PCAR	CYA	CYA

Hincks CP, W margin/PJL 1074	CAL	- CAL	CAL	CYA(CAL)	CAL(CYA)
Hincks CP, NW corner peninsula/C.D.Boomsma 444	CAL	- PIL(CAL)	PIL(CAL)	PIL(cal)	PIL(cal)
4 km N Pt Neil/PJL 1136	CAL(dum)	- PIL(cal)	PIL(cal)	PIL(cal)	PIL(cal)
W Pt Neil, on Lincoln Hwy/C.D.Boomsma 429	DUM(CAL)	- CAL(pil)	CAL(PIL)	CAL(KON)	CAL(PIL)
20.5 km N Cummins/PJL 1077	CAL	+ ANC(cal)	CAL(ANC)	ANC(CAL)	PCAR(CAL)
2.8 km SE Cummins/PJL 1078	ANC(CAL)	- ANC(CAL)	CAL(ANC)	CAL(DUM)	P35(ANC)
" " /PJL 1079	CAL	- CAL	CAL	CYA(CAL)	CYA(CAL)
Pillana RS/C.R.Alcock 1378	CAL	- CAL	CAL	CAL	CAL(p35)
Stokes/PJL 640	CAL	+ CAL	CAL	CAL	CAL(p35)
" /PJL 1128	CAL	+ CAL	CAL	CAL	CAL
" /PJL 1129	CAL	+ CAL	CAL	CAL	CAL
3.5 km NW Tumby Bay/PJL 1130	CAL	+ CYA	P35	CYA	P35(cya)
4.5 km SW Tumby Bay silos/PJL 1134	CAL(DUM,PIL)	- CAL	CAL(p35)	KON	P35(CAL)
" " " /PJL 1135	CAL(DUM)	+ DUM	DUM(cal)	DUM	DUM(p35)
10 km S Tumby Bay/PJL 638	CAL(PIL)	+ CAL	CAL	CAL	CAL
3.5 km W Thuruna/PJL 1132	CAL	+ CAL	CAL	CAL	CAL
5 km WNW Edillilie/PJL 1103	CAL	+ CAL	CAL(pil)	CAL	CAL(pil)
" " /PJL 1104	CAL(anc)	- DUM	P35(cal)	DUM	P35(dum)
" " /PJL 1106	DUM(anc,cal)	+ DUM(ANC)	CAL(ANC)	DUM(anc)	CAL(anc)
" " /PJL 1107	DUM(anc)	+ DUM	P157	DUM	P157
Flinders Ranges Region					
1.4 km WSW Freeling Heights summit/PJL 566	DUM(CYA,STR)	+ DUM	DUM(P157)	SHE(DUM)	P157(dum)
" " " /PJL 568	DUM	+ DUM	DUM	DUM(SHE)	DUM(she)
S side Octopus Hill, Gammon Rges/PJL 1281	DUM(PIL)	+ PIL(cya)	P157(p35)	CYA	P35(p157)
" " " /PJL 1282	DUM	- DUM(CYA)	DUM(CYA)	DUM(CYA)	PCAR(CYA)
0.5 km SW Mt Hack summit/PJL 843	DUM	+ DUM	DUM(P157)	DUM(STR)	P157(str)
" " " /PJL 844	DUM	+ DUM	DUM	DUM(SHE)	DUM(KON)
2 km SW Mt Hack/PJL 848	DUM	- DUM	DUM	DUM	DUM
" " /PJL 849	DUM(ANC)	+ SHE	PCAR	DUM	PCAR(DUM)
4 km WSW Mt Hack/PJL 851	DUM	+ DON	PCAR(p35)	CYA	CYA(P157)
2 km SE Warraweena HS/PJL 859	DUM	- DUM	P35(dum)	CLE(dum)	CLE(P35)
" " /PJL 860	DUM	+ DUM	DUM(p35)	DUM	DUM(P35)
1 km NE Mt Elkington/PJL 913	DUM	- DUM	DUM	DUM	DUM(p157)
0.5 km W junction Parachilna & Blinman Ck/PJL 918	DUM(ANC)	- DUM	P157(DUM)	DUM(cle)	CLE(DUM)
" " " " /PJL 920	DUM	- DUM	P157(dum)	DUM	P157(DUM)

1 km W Loves Mine Rge/PJL 1271		DUM	- DUM(pil)	DUM(P35)	CLE(dum)	CLE(DUM)
" " /PJL 1273		DUM(CYA,STR)	- DUM	DUM(p35)	DUM	DUM(PCAR)
" " /PJL 1274		DUM	- DUM	DUM(p35)	DUM(cle)	DUM(CLE)
" " /PJL 1275		DUM(ANC)	- DUM	P35	DUM	P35(dum)
" " /PJL 1276		DUM	- DUM	P35(DUM)	DUM	P35(dum)
" " /PJL 1279		DUM	- DUM	DUM	DUM	DUM(p35)
Yourambulla Range, W of Hawker/PJL 865		DUM	- DUM	DUM	DUM(cle)	DUM(CLE)
" " " /PJl 866		DUM	+ DUM	DUM	DUM(SHE)	DUM(she)
1 km NE Devils Peak/R.Sinclair 1.ix.1977	A	PIL(ANC)/P35	+ PIL(CYA)	P35	CYA	P35
" " " "	B	DUM(PIL)/P35	+ PIL	P35	PIL	P35
" " " "	C	PIL(DUM)/P35	+ CYA	P35	PIL	P35
" " " "	D	PIL(DUM)/P35	+ SHE(don)	P35	PIL(CYA)	P35
Northern Lofty Region						
The Bluff, Beetaloo Valley/C.D.Boomsma 16.ix.1977		PIL(CYA)	+ PIL	P35(pil)	PIL	P35
3 km N Bute/P.Copley -.iv.1977 C		ANC(DUM,PIL)	+ CAL	CAL(PIL)	CAL(pil)	CAL(PIL)
3 km S Lochiel/PJL 872		DUM(ANC,CAL)	+ CAL	CAL	KON(cal)	CAL
" " /PJL 1160		DUM(KON,ANC)	+ DUM	DUM	KON(DUM)	DUM(KON)
Southern Lofty Region						
Folland Park, Enfield/PJL 768A		DUM(anc)	+ DUM	DUM	KON	KON
" " /PJL 767, 1186		DUM	+ DUM	DUM(p157)	DUM	DUM
" " /PJL 768B		DUM(anc)	+ DUM	DUM	DUM(CLE)	DUM(cle)
" " /PJL 769, 1188		DUM	+ DUM	DUM	DUM	DUM
" " /PJL 770		DUM(anc)	+ DUM	DUM	DUM	DUM
" " /PJL 1187		ANC(DUM)	+ DUM	DUM	DUM	DUM
Murray Region						
22 km WSW Waikerie/PJL 891		DUM(CYA)	+ CYA	CYA	CYA	CYA
" " /PJL 893		CYA(DUM)	+ DUM	DUM(CAL)	DUM(kon)	DUM(CAL)
" " /PJL 894		DUM	+ CAL(dum)	CAL(dum)	CAL(DUM)	CAL(DUM)
" " /PJL 896		CYA(ANC)	+ CAL	CAL	CAL	CAL
10 km W Kingston/J.Thompson 21.ix.1979		CYA	- CYA	CYA	CYA	CYA
9 km W Kingston/PJL 876		CYA	+ CYA	CYA	CYA	CYA
" " /PJL 880		CYA	+ CYA	PCAR(CYA)	CYA	PCAR
" " /PJL 881		CYA	+ CYA	CYA	CYA	CYA(pcar)
" " /PJL 883		CYA	+ CYA	CYA	CYA	CYA

14 km SE Barmera/L.D.Williams 7631		CYA	+ CYA	CYA	CYA(GEO)	PCAR
c. 3 km N Berri/R.M.& W.R.Barker 4034A		CYA	+ CYA	CYA	CYA	CYA
" " " 4034B		CYA	+ CYA	CYA	CYA	CYA
" " " 4034C		CYA	+ CYA	CYA	CYA	CYA
" " " 4034D		CYA	+ CYA	CYA	CYA	CYA
" " " 4034E		CYA	+ CYA	CYA	CYA	CYA
Berri/C.D.Boomsma 24.i.1976		CYA	+ CYA	CYA	CYA	CYA
Springcart Gully, Berri/B.Dangerfield 20.x.1962		CYA	+ CYA	CYA	CYA	CYA
10 km NE Berri/PJL 886		CYA	+ CYA	CYA	CYA	CYA
" " /PJL 887		CYA	+ CYA	CYA	CYA	CYA(PCAR)
" " /PJL 888		CYA	+ CYA	CYA	CYA	CYA
" " /PJL 889		CYA	+ CYA	CYA	CYA	CYA
" " /PJL 890		CYA	+ CYA	CYA	CYA	CYA
10 km E Wanbi/J.Thompson 20.8.1979		CYA	- CYA	CYA	CYA	CYA(PCAR)
1 km N Alawoona/G.W.Anderson (AD 97026076)		CYA	+ CYA	CYA	CYA	CYA
N Billiat CP/B.J.Warren 33		CYA	- CYA(PIL)	P35(CAL)	CYA(CAL)	P35(cal)
Pinnaroo/M.I.H.Brooker B4908		DUM	+ DUM	DUM	DUM	DUM
South-eastern Region						
2 km SE Coonalpyn/PJL 1265		DUM(ANC)	+ DUM	DUM	DUM	DUM(PCAR)
Box Flat, 34 km SSW Lameroo/J.G.West 2448		DUM	- DUM	DUM(P35)	DUM	DUM(P35)
" " " " 2449		DUM	- DUM	P35(DUM)	DUM(kon)	P35(DUM)
" " " " 2450		DUM(ANC)	- DUM(CAL)	P35(DUM)	DUM	P35(dum)
Comet Bore, 55 km S Pinnaroo/C.D.Boomsma 4.x.1977	A	DUM	- DUM	P35(DUM)	DUM	P35(DUM)
" " " " "	C	DUM	- DUM	P157(DUM)	DUM	P35(DUM)
" " " /J.G.West 2313		DUM(ANC)	- CAL(dum)	P35(CAL)	KON(DUM)	P35(cal)
" " " "		DUM(ANC)	- DUM	P35(DUM)	DUM	P35(DUM)
" " " " 2323		DUM(CYA,ANC)	- DUM	P35(DUM)	DUM	P35(DUM)
" " " /C.D.Boomsma 4.x.1977		CYA(CAL,DUM)	- ANC(CAL)	CAL(anc)	ANC(CAL)	CAL(ANC)
" " " /J.G.West 2318		CYA(CAL,DUM)	- DUM	P35(CAL)	DUM	P35(dum)
" " " " 2319		CYA(CAL,DUM)	- CYA	CYA	CYA	CYA
" " " " 2324A		CYA(CAL,DUM)	- DUM(CAL)	DUM(cal)	CAL(P35)	P35(CAL)
" " " " 2325		CYA(CAL,DUM)	- DUM	P35(DUM)	DUM	P35(dum)
" " " /C.D.Boomsma 4.x.1977	B	CYA(CAL,DUM)	- DUM(cal)	DUM(P35)	DUM	P35
" " " " "	F	CYA(ANC)	- DUM	DUM(P35)	DUM	DUM
" " " /J.G.West 2320		CYA(CAL,DUM)	- DUM	DUM(P35)	DUM	DUM
" " " " 2324		CYA(CAL,DUM)	- CAL	CAL	CAL	CAL

2.2 km ESE Mt Shaugh/J.G.West 2274	CYA(ANC)	- DUM(cya)	P35	CYA(dum)	P35
25 N along Senior rd, Bordertown/C.D.Boomsma (WF)	CYA(CAL,DUM)	- DUM(CAL)	CAL	DON	DON(CAL)
15 km N Bordertown/C.D.Boomsma 24.9.1977	CYA(CAL,DUM)	- CAL	CAL	CAL	CAL
6 km NE Bordertown/C.D.Boomsma 24.9.1977 A	DUM(ANC,CYA)	+ DUM	CAL(DUM)	DUM	DUM(cal)
" " " " D	CYA(CAL,DUM)	- DUM	P35(DUM)	DUM	P35(dum)
" " " " C	CYA(CAL,DUM)	- CAL	CAL	CAL	CAL
15 km E Bordertown/C.D.Boomsma WF 1059	CYA(CAL)	+ DUM(cal)	CAL(DUM)	DUM	DUM(CAL)
VICTORIA					
2 km E SA border towards Mildura/M.I.H.Brooker B4904	CYA	- CYA	CYA	CYA	PCAR(cya)
110 km W Mildura/H.Vos & J.D.Turner 8	CYA	+ CYA	CYA	CYA	CYA(PCAR)
NEW SOUTH WALES					
3 km W Balranald/C.W.E.Moore 3717	DUM	- DUM	DUM(p157)	DUM	DUM
Coolabah/J.L.Boorman -.10.1904	DUM	+ DUM	DUM	DUM	DUM
66 km W West Wyalong/M.J.Beeston & J.Turner 83	DUM	+ DUM	DUM	DUM	DUM
6.6 km SW Yalgogrin/G.M.Chippendale 945	DUM	+ DUM	DUM	DUM	DUM
9 km W Ungarie/P.L.Milthorpe & G.M.Cunningham 2	DUM	+ DUM	DUM	DUM	DUM
8.2 km W Ungarie/R. Grandison 5.i.1980 A	DUM	+ DUM	DUM	DUM	DUM
" " " " B	DUM	+ DUM	DUM	DUM	DUM
" " " " C	DUM	+ DUM	DUM	DUM	DUM
" " " " D	DUM	+ DUM	DUM	DUM	DUM
7.5 km W Ungarie/P.L.Milthorpe & G.M.Cunningham 4	DUM	+ DUM	DUM	DUM	DUM
" " " " " 5	DUM	+ DUM	DUM	DUM	DUM

Appendix 2: Additional records relating to E. cyanophylla.

(a) Sympatric occurrences of E. dumosa forms in Murray Region, S.A.

c.1 km NW Berri/W.R. (& R.M.) Barker 4034F
35.6 km E of Morgan towards Berri/M.I.H.Brooker 5573
Alawoona/E.H.Ising s.n., 22.i.1938
9.8 km N Alawoona/L.D.Williams 7633
Karoonda/E.H.Ising s.n., 9.i.1937
Near Karoonda/J.B.Cleland s.n., 22.v.1954
W Lameroo/M.I.H.Brooker B4910

(b) Intergrades between E. dumosa and E. cyanophylla forms not included in analyses.

Loxton/C.D.Boomsa s.n. 5.iv.1947 (WF)
Karoonda/E.H.Ising s.n. 9.i.1937
Paruna/F.van der Sommen s.n., 24.vii.1975
18 km SSW Pinnaroo/L.D.Williams 7152
Mt Hope, Euabalong, Yarra Stn, N.S.W./Walker ANU 1317, -.ii.1964

(c) Intergrade between E.anceps and E.cyanophylla forms not included in analyses.

Marne Valley C.P./R.Davies s.n., 28.x.1980

Appendix 3: Collection localities and habitat information for glaucous-stemmed forms in Eyre Peninsula Region.

Carappee Hill, SE side/PJL 1044, 1045, 1047, 1048
- on granite slopes in gravelly dark brown loam (pH 7.0); at base of hill in gravelly dark red-brown loam (pH 7.0) over medium clay (pH 9.0)

Carappee Hill, S side/K.D.Rohrlach 455
Carappee Hill, N and NE side/A.Sampson s.n., 20.i.1980, (WF)
Carappee Hill, W end/D.E. Symon 8940
- on sand abutting granite

3-4.5 km SW Carappee Hill/C.D.Boomsma 420, 423; PJL 1050
- in depressions on light grey-brown sandy loam

Darke Peak (Range), NW corner/L.D.Williams 5202, (ES)
3.2 km N Darke Peake (town)/B.Copley 2962-2964
Darke Peake (town), near school/PJL 1051; C.R.Alcock 532
Kimba/C.D.Boomsa s.n., -.vi.1964 (WF)
E of Prominent Hill, Hambidge CP/D.N. Kraehenbuel 2074
- on small clay-pan depression

5.7-6.1 km E Tooligie Hill P.O./PJL 1071-1072, 1076
- on dark red-brown calcareous sandy clay-loam (pH 8.8) over red calcareous heavy clay (pH 9.0)

Sn 9, Hd Tooligie (c. 9 km NE Tooligie)/R.L.Specht 2252
- on stony limestone soil

5 km SW Lock/R.Wilkins s.n., 1.iii.1981 (Private herb.)
Sn 12, Hd Molong (c. 20 km ESE Lock)/R.French s.n., 5.v.1958, (WF)
Sn 21, Hd Murlong (c. 25 km SE Lock)/R.L.Specht 2240
- low lying areas in sand dunes

Hincks CP, 2 km N of southern boundary/J.R.Wheeler 965
5 km E of Rudall/T.R.N.Lothian s.n., 28.vi.1959
?Cummins/R.French s.n., -.vi.1958, (WF)
1-5 km W Poolalie H.S., 12 km NW Cleve/PJL 1142-1144
Miltalie/R.Pearce s.n., 28.i.1965 (ADW); J.R.N.Lothian s.n., -.iv.1972
- on rocky hillside

0.3 km SW Coolanie church/PJL 1149
6.5 km E Kielpa/PJL 1145
Kielpa-Mangalo road, 1.5 km ENE of junction of road to Konanda/PJL 1147
Mangalo road, 0.2 km NW from junction with Coolanie-Yabmana road/PJL 151
Sn 39, Hd Playford (c.8 km NW Cowell)/PJL 1589, 1593, 1594
- rocky hillside with limestone

8 km E Yabmana/C.D.Boomsma 410, 412
- on slope of red-brown acidic clay with gneissic granite

Appendix 4: Collection localities for E. dumosa ssp. conglobata included in analysis of sessile-fruited forms (SESSDAT).

WESTERN AUSTRALIA

Avon District

Harrismith/C.A.Gardner 1603 (PERTH)
12.2 Km by road NE of Dumbleyung towards Lake Grace/PJL 1412

Roe District

9.2 km S of South Kumminin/G.C.Chippendale 245 (PERTH)
Bendering/C.A.Gardner 9481 (PERTH)
2.6 km by road NW of Kulin towards Corrigin/PJL 1435-1439
10 km NW of Holt Rock towards Hyden/M.I.H. Brooker 2674 (PERTH)
35.2 km by road SW of Lake Grace towards Dumbleyung/PJL 1413
19.3 km by road N of Pingrup towards Lake Grace/PJL 1407-1410
18 km N Pingrup towards Lake Grace/PJL 1405
8.7 km by road N of Ongerup/PJL 1403
8 km by road N of Stirling Ranges N.P. towards Borden/PJL 1398-1402
8 km N of Stirling Range/R.D. Royce 8155 (PERTH)
1 km W of Norseman-Esperance road on Lake King road/M.I.H.Brooker 5658 (FRI)
Grass Patch/S.G.M. Carr 632 (PERTH)
1.2 km by road S of Grass Patch/PJL 1356-1359
6.8 km by road E of Scadden/PJL 1360-1363
Mt Ragged/P.Wilson 2906

Eyre District

16.5 km by road S of Jerramungup/PJL 1392-1396
Fitzgerald Inlet, Fitzgerald Reserve (N side)/M.I.H. Brooker 2702 (FRI)
Fitzgerald River, Reserve/A.S.George 9918 (PERTH)
23 km W of Hopetown towards Hamersley Inlet/M.I.H. Brooker 2312 (PERTH)
8.8 km E of East Mount Barren/J.W. Green 4582 (PERTH)
13 km E of Hamersley River crossing/M.I.H. Brooker 2352 (PERTH)
35 km N of Ravensthorpe/B.A. Rockel (FRI)
Ravensthorpe, 32 km N/C.A.Gardner 13658 (PERTH)
Between Mt Madden and Ravensthorpe/M.I.H.Brooker 3599 (FRI)
Ravensthorpe/Ralph & Stamford s.n., 26.vi.1924 (PERTH)
Ravensthorpe Caravan Park/PJL 1391
4.0 km S of Ravensthorpe/A.S. George 7269 (PERTH)
4.0 KM SE of Ravensthorpe/G.M.Chippendale 414 (FRI)
12.6 km by road E of Ravensthorpe towards Esperance/PJL 1378
11.9 km S of Ravensthorpe/G.M.Chippendale 2207 (FRI)
Desmond battery, 1 km S/H.Demarz D.6335 (PERTH)
Kundip/PJL 1386-1390
Oldfield River, 65.8 km E of Ravensthorpe/G.M.Chippendale 196 (FRI)
5 km N of Esperance/R.D.Royce 4114 (PERTH)
Esperance/J.B.Cleland s.n., 5.ix.1950
1.3 km by road N of Howick Hill/PJL 1366-1370
92 km E of Esperance on Fisheries road/M.I.H.Brooker B4479 (FRI)
Thomas River, Cape Arid National Park/R.D.Royce 10004 (PERTH)

Coolgardie District

10 km S of Caiguna/R.Parsons 171
23 km S of Caiguna/R.Parsons 167

SOUTH AUSTRALIA

Eyre Peninsula Region

7.4 to 8.6 km N of Cleve/PJL 1138-1141
1.7 km N of Tooligie/PJL 1601-1605
1 km E of Mt Hope summit/PJL 1084-1088
7 km by road SE of Warrow towards Edillilie/PJL 1095-1098
Pass between North and South Block, 11 km SE from Warrow/PJL 1100, 1101
4 km by road W of Pt Lincoln P.O. towards Coffin Bay/PJL 1109, 1110, 1112, 1113
Boston Island/K.Holden s.n., 23.viii.1973 (WF)
Spalding Cove/PJL 1114-1118
Lincoln N.P., 2 km by road S of Pt Lincoln-Sleaford road/PJL 1123-1127
Fishery Bay/C.D.Boomsma s.n., -.ix.1958 (WF)

Yorke Peninsula Region

3 km WNW of Pt Julia/PJL 560, 561, 792-794
2.5 km W of Pt Vincent/PJL 805-809
E of Pt Rickaby towards Curramulka, 1.5 km E of Maitland to Minlaton road /PJL 787-790, 796A
S of Warooka/PJL 797-801
6 km S from Warooka-Stenhouse Bay road towards Foul Bay/PJL 929-930, 935, 936.
4 km NE of Pondalowie on road to Brown's Beach/PJL 937-942

Kangaroo Island Region

c.20 km SW of Kingscote on Playford Highway, 1.1 km SW of Emu Bay road junction/PJL 732-736
Bay of Shoals, 4.0 km NE of Wisanger road/PJL 680-683
c. 20 km W of American River, 1.0 km W of road to Kingscote/PJL 672-676
16 km SW by road from American River/PJL 686-689
c. 5 km NW of American River on road to Red Banks, 0.8 km NW of Pt Morrison road/PJL 666-670
1.6 km by road NW of Chapman River/PJL 652-656
0.5 km W towards Wilson River from Cape Willoughby road/PJL 659-662

Southern Lofty Region
Mt Scrub-Mt Desert road, 1 km E of junction with road to Weymouth Hill /PJL 743-747
0.5 km ENE of ford on Coolawang Ck on Mt Scrub-Mt Desert road/PJL 750-753
0.5 km NE of junction of Dennis Road to Waitpinga beach towards Victor Harbor/PJL 757, 758
0.5 km SSW of junction of Goolwa-Strathalbyn and Goolwa-Mt Compass roads /PJL 760-764
8 km SE of Strathalbyn/PJL 1161, 1163
Monarto/J.Venning, s.n.
Braendler's Scrub, Monarto South/PJL 900-903

Appendix 5 - Territorial map for CVA classifications - transparency overlay

NOTE: Information from the transparency overlay has been added to Figure 29