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TOWARDS A NATURAL CLASSIFICATION -
THE TAXONOMY AND EVOLUTION
OF <u>XANTHORRHOEA</u>

by

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of the requirements for the degree of

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DECLARATION

This thesis is entirely the result
of my own research work except
where otherwise indicated, and has
not been submitted for any other degree
at this or any other University.

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ABSTRACT

The taxonomy and evolution of <u>Xanthorrhoea</u> are investigated using phenetic and cladistic techniques in addition to a traditional taxonomic revision. Phenetic numerical and statistical techniques are used to investigate variability and poorly defined taxonomic boundaries in xanthorrhoeas growing in Queensland. The taxonomic uncertainty is resolved by recognition of a new species and clearing-up nomenclatural confusion. Intergradation and presumed hybridisation between a number of species on Quaternary sand deposits from Myall Lakes National Park in New South Wales to Beerwah in Queensland is analyzed using phenetic numerical classification and ordination techniques. The results are compared with measurements of a number of environmental factors. It is concluded that the data is consistent with a restricted distribution of intergradation due to hybridism and introgression between species along gradual ecoclines on the Quaternary sands. No evidence was found for hybridisation on other substrates. Phylogenetic relationships of species and of the genus are investigated by cladistic numerical analysis using PAUP and MacClade. The postulated phylogeny is used to examine the biogeography of the genus with a cladistic biogeographic interpretation. These results are drawn together, with the traditional morphological assessment of herbarium material, in a taxonomic revision of the genus, which also includes nomenclatural notes on the naming of the genus and a discussion of possible biological causes for some of the perceived taxonomic difficulty of the genus. Future research directions are suggested.

ACKNOWLEDGEMENTS

DEDICATION

This thesis is dedicated to my wife, Jennifer Stuerzl, for her encouragement and patience in enduring this apparently never ending study, and also for her keen <u>Xanthorrhoea</u>-spotting which has discovered many a valuable specimen.

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ABBREVIATIONS USED IN THE TEXT AND TABLES

(Many abbreviations are used by the numerical

analysis programs to fit into pre-determined constraints)

BR.	Bract.
COEFF.	Coefficient (used by TAXON).
Dissim.	Dissimilarity (used by TAXON).
DMUL	Disordered multistate characters (used by TAXON).
FNUM	Free format numeric characters (used by TAXON).
GP	Group produced by the TAXON classification program.
H.I.	Habitat index.
II	Number of individuals in a TAXON analysis.
IDM	Number of disordered multistate characters in TAXON.
IFN	Number of free-format numeric characters in TAXON.
ISS	Incremental sum of squares.
JUV.	Juvenile.
LEAFW	Leaf width.
Mtn	Mountain.
NGREQ	Number of groups a TAXON classification is to produce.
NQ52	Designates the 52 entity data set from Queensland.
NQ78	Designates the 78 entity data set from Queensland.
OBTRIANG	Obtriangular (used by TAXON).
OBTRULL	Obtrullate (used by TAXON).
QLD	Queensland.
Q-R	Quadrate-rhombic.
RBG	Royal Botanic Gardens, Sydney.
SCAPED	Scape diameter.
SCAPEL	Scape length.

ABBREVIATIONS USED - Continued.

SIG.   Significance (statistical, used by TAXON).

SORTSTRAT   Clustering strategy to be used by SAHN, e.g. UPG or ISS.

SPIKED   Spike diameter.

SPIKEL   Spike length.

SPSCRAT   Spike length divided by scape length (in DISCRIMINANT).

SP/SC   Spike Length divided by scape length (in TAXON).

ST.   Character state (used by TAXON).

Tas.   Tasmania.

TM   Trade mark.

TRIANG   Triangular (used by TAXON).

TRUNKHT   Trunk height.

UPG   Unweighted pair group, also known as group average.

VARS   Variables (used by TAXON).

Vic.   Victoria.

2°   Secondary.

CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION

1.1.1 Aims

The original impetus for this study arose out of observations of
Xanthorrhoea during University of Queensland undergraduate excursions
to wallum areas in south-east Queensland where the genus is a
prominent component of the vegetation. On those excursions it was
generally accepted that xanthorrhoeas were easy to identify to genus,
but difficult to identify to species. The botanists in charge of the
relevant courses, primarily Professor Trevor Clifford and Dr Rod.
Rogers, pointed-out the difficulties involved in identification and
the apparent blurring together of species, as well as mentioning the
work of Lee (1966 a and b).

These comments and observations led to the undertaking of an Honours
degree at that University to investigate the taxonomy of Xanthorrhoea
in south-east Queensland and northern New South Wales (Bedford, 1975).

That study revealed that much of the confusion concerning the
identification of species in the area studied could be eliminated by
careful observation and taxonomic technique.

However, even in the area studied in south-east Queensland there were
some doubts left as to the range of variation seen in some taxa. These
particularly involved what is now known as X. fulva, which had
inflorescences ranging in total length from 20 cm to 2.5 m, and what
was identified as X. johnsonii, where leaf dimensions and shape varied
from 1 mm wide by 1 mm thick to 3 mm wide by 2 mm thick, and some

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plants had scapes longer than spikes whilst others had spikes longer than scapes, which was not acceptable in other taxa. As well as these factors it appeared that in some sites the two taxa intergrade.

In addition Lee's published comments (locs cit., and discussed in more detail below) aroused my interest, as did her comments in correspondence (1973) to the effect that it was likely that X. johnsonii contained more than one taxon.

With field trips further afield (North Queensland, south into New South Wales and to Tasmania) the range of variation observed in the genus seemed to increase, with much difficulty in assigning specimens to the few described taxa, except in the Sydney region which had been intensively studied by Lee (locs cit.). Overall the perception gained from the wallum areas -- that it was easy to identify to genus but not to species level -- seemed to apply to the whole genus.

This research therefore began with the aim of clarifying the taxonomy of Xanthorrhoea through a study of variability within the genus, attempts to find additional reliable characters to aid identification and classification and a study of the evolutionary relationships of the species.

1.1.2 Background information - impediments to a natural classification

The paucity of good characters with which to distinguish taxa within Xanthorrhoea is one of the major difficulties in the way of taxonomic study within the genus. Lee (1966 a) found few characters she believed

constant enough to be useful to diagnose the differences between taxa. She commented on "the problem of discovering any positive diagnostic characters, a difficulty which arose from the fundamental uniformity of the flowering and vegetative parts and led to eventual reliance on indicative rather than absolute differences".

Whilst in previous studies I have found enough reasonably reliable characters, which if used in combination, do effectively distinguish the majority of taxa (Bedford 1975 and 1986 a and b), Lee's comments remain valid. There is an essential uniformity of characteristics for all species. In general, only small differences, many of them relative dimensions rather than absolute character changes, differ from taxon to taxon.

In terms of the number of characters recommended by Davis and Heywood (1965) and Sneath and Sokal (1973) for a satisfactory examination using phenetic methods, the number of "absolute difference" characters available in Xanthorrhoea fall far below their guidelines.

Various other impediments to the natural classification of the genus have been proposed -- primary amongst these was the "putative" hybridism (Lee, 1966 a and b; Johnson, Pers. comm., 1978). In particular Lee commented that nearly all species in New South Wales lacked discreteness "One by one the `species' were seen to lose their discreteness until only X. macronema maintained its discreteness to the degree usually acceptable in a species" (Lee, 1966 a).

Lee (1966 a) also suggested other impediments to classification. She noted that the intergradation between species "so commonly met with

in the genus appears to be partly due to inherent variation correlated with distribution, ...". Which appears to suggest clinal variation. In addition Lee commented that "certain phenotypes often show a strong correlation with soil or other habitat characters" and speculated whether the correlation is due to habitat preferences or environmental plasticity.

Some aspects of the group's biology also cause some difficulties. For example, flowering though strictly seasonal, is irregular and flowering or fruiting material is required for critical determination.

The latter problem is, however, alleviated by the fact that, for many species of Xanthorrhoea, flowering is more common in the next flowering season after fire (e.g. Rogers, 1975; Gill and Inwerson, 1978), thus occasionally providing a wealth of specimens for analysis.

Another impediment to a traditional classification is that, because Xanthorrhoea specimens are bulky, they have been under represented in herbarium collections in the past. Also, collectors have been uneven in their selection of which parts to collect and in their documentation of specimen dimensions, which means that many specimens are of little use.

1.1.3 Structure of the thesis

This thesis consists of four lines of research into the taxonomy of Xanthorrhoea, each line is contained in a separate chapter, though they are all, to some extent, interdependent and therefore cross-referenced. Chapters 2 and 3 use the same research approach (phenetic

numerical classification and analysis) to two different situations
which involve fundamental problems that had been identified as
inhibiting the natural classification of the genus (Lee 1966 a and b).
Both studies involve the considerable intraspecific morphological
variation which has inhibited a clear understanding of the taxonomy of
the group. In addition Chapter 2 examines the possibility of
interspecific hybridisation to determine whether this might be an
important feature of the genus which would affect its phylogeny and
classification. Chapter 5 is a traditional revision and
classification of the genus using, primarily, morphological
characters, based on the experience of examining the variation of
particular species in the preceding chapters. Chapter 5 is an
analysis of the phylogenetic relationships of <u>Xanthorrhoea</u> species but
also involves an ancillary and introductory examination of the
phylogenetic relationships of <u>Xanthorrhoea</u> at the generic level.

Taken together these studies represent a comprehensive examination of
the genus and provide a good basis for its classification.

Preliminary studies

A number of other approaches to the classification of the group were
originally considered and preliminary studies prepared, as it was
believed that the relatively small number of morphological characters
might prove inadequate for realistic taxonomic conclusions to be
drawn. These approaches were:

1/. Giemsa banding of chromosomes;

2/. Analysis of the flavonoid constituents of the leaves for chemotaxonomy (as per the studies of Mabry et al., 1970, Williams, 1975, Leach and Whiffen, 1978, Giannasa, 1978, etc.), and;

3/. Analysis of the chemicals of the resins for chemotaxonomy (Duewell, 1954, 1965, 1968, in press.).

The first two approaches were followed for some time, but for technical reasons failed to produce useful characters, as discussed below.

1/. Chromosome c banding with giemsa stain aims to reveal the patterns of heterochromatin and euchromatin banding (e.g. Vosa and Marchi, 1972; Schweizer, 1973 and 1974; Hadlaczky and Belea, 1975; Thomas, 1977 etc.). Some results were obtained, but this technique proved most unreliable on this material and, after repeated attempts and expert consultation (N. Darvey, pers. comm. 1979) the technique was abandoned since it was not providing consistent results. Essentially, the small size of Xanthorrhoea chromosomes and the unreliability of achieving banding made the approach inefficient.

2/. The second technique attempted was an analysis of the flavonoid constituents of leaves. Williams (1975) had included Xanthorrhoea leaves in a sampling of flavonoids in Monocotyledonous plants, and it was therefore hoped that these chemicals might be an aid to classification. The situation chosen to test the usefulness was however, an unfortunate one (Giannasa, 1981). Leaf extracts of 40 plants from Myall Lakes believed to be involved in a hybrid swarm were made and initially prepared as two dimensional paper chromatographs

using the techniques described in Mabry et al. (1970). As the large numbers of flavonoid compounds presented a confusing picture a sequence of single direction strip runs in a range of solvents was made to select out compounds for a clearer view (Quinn pers.com., 1979). However the resultant separations, coded as multi-state characters and analyzed using the CSIRO TAXON package did not clarify the situation.

The most probable reasons for the lack of success of this technique are: A. The technique was not sufficiently accurate to separate the numerous compounds present; B. The complexity of flavonoid interactions within an introgressive population is such that the result may not be clear cut (Giannasa, 1981). The analyses presented in Chapter 2 (Myall Lakes) show that the population there involves two taxa with their intermediates and probable backcrosses. In this situation Giannasa (loc. cit.) has indicated numerous patterns may arise including reversions and extensions of chemical pathways giving new compounds for the group coupled with additive or non-additive mixes of flavonoids. Some evidence for this possibility was the occasional occurrence of a yellow-fluorescing compound which appeared to be a new compound for the group as it was not seen in the majority of cases.

Whilst the complexity of interaction of the great number of phenolic compounds present in Xanthorrhoea which are extracted along with the flavonoids by the techniques of Mabry et al. (1970) meant that apparently random results were produced in the analyses attempted, it is possible that this technique would have been of use for the identification of good, discrete taxa. However, such groups do not

require extra characters to be distinguishable. In addition the chemotaxonomic work of Duewell (1954 and in press) and Bedford and Duewell (in prep.), using the resins, which are partially flavonoid, offer more promise than the flavonoid analyses as per Mabry et al (1970).

3/. Chemotaxonomic work using _Xanthorrhoea_ resins, as discussed above, is continuing. Duewell (1954, and in press) contends that the resins can be used to distinguish species. However, this assertion needs to be tested on a wider range of taxa before it can be trusted too far (Duewell and Bedford, in prep.). That is, this line of research shows promise, but has not yet come to fruition.

1.1.4 Conclusions from preliminary studies

At the same time that the above attempts were proving unsuccessful in providing additional characters, approaches using numerical and traditional classification techniques on, primarily, morphological characters were producing clear results which correlated well with intuitive classifications. Therefore these approaches were pursued rather than the alternatives above, and are detailed in chapters 2-5 below.

1.2 Literature survey

The taxonomic literature on _Xanthorrhoea_ is relatively sparse. The early discovery of Australia resulted in an initial flurry of activity in the late 18th Century, with illustrations and descriptions of the genus in accounts of the voyages, (e.g. Banks - Parkinson prepared an

illustration now titled X. resinosa, plate 334, for Banks circa 1788, but this was not published until the production of Banks Florilegium 1979-1988; Phillip, 1789; White, 1790), and in the (multiple) naming of the genus and type species (Kite 1795 a and b, Dryander 1797, Smith, 1798, Persoon 1805, Nelson and Bedford, in press, Nelson, in press).

This was followed in the early 19th century by the inaugural work towards an understanding of the genus by Brown, who described six additional species (X. arborea, X. australis, X. bracteata, X. media, X. minor, and X. pumilio) (Brown 1810). The family Xanthorrhoeaceae was named by Dumortier in 1829. There was no further concerted, comprehensive treatment of the genus until that undertaken by Lee during the 1960's (1966 a and b). During the remainder of the 19th century the main taxonomic work on the genus (apart from the flora treatments noted below) was the gradual increase in the number of species described as more of the Australian continent was discovered and settled. Workers during this period included Endlicher who described three species (X. brunonis, X. gracilis and X. preissii) in Lehmann's Plantae Preissianae (1846), Harvey who described X. drummondii (1855), and Mueller who described five species (X. pecoris, X. quadrangulata, X. semiplana, X. tateana (1864), X. macronema (ex Bentham, 1878)), and Tate, who described one species, X. thorntonii (1896).

This century the main workers of note have been Herbert, in Western Australia, who described three species during the 1920's: X. reflexa (1920) X. brevistyla (1921 a) and X. nana (1921 b); Cleland, who investigated the South Australian populations (1965 a and b), and; Lee

(1966 a and b) who prepared a comprehensive revision of the genus in New South Wales and prepared the ground for future work including the present study.

The most recent taxonomic treatment has been by Bedford, with preliminary studies in 1975, the description of X. acanthostachya in 1985, and a complete revision of the genus and Australia-wide flora treatment in 1986 (an up to date version of which is included here). Nomenclatural studies at the generic level have also recently been undertaken by Nelson and Bedford (in press).

Floras

The most numerous taxonomic works including reference to Xanthorrhoea are the various flora treatments for the whole or particular regions of Australia. The majority of these treatments naturally are based on previously published works (or the author or editor's interpretation of same) rather than a taxonomic assessment of the group by the relevant authors, and therefore do not add significantly to an understanding of the classification of the genus, although those included which have been published since 1985 are based on the taxonomic revision included in Bedford (1986 a). Indeed many of the earlier treatments are misleading because of numerous nomenclatural and taxonomic inaccuracies concerning Xanthorrhoea. They are included here solely for the sake of completeness.

C19th Flora Treatments

The major relevant flora treatment during the 19th century was

Bentham's <u>Flora Australiense</u> (1878) which drew primarily upon the
expertise of Mueller and the published treatment of the genus by Brown
(loc.cit.), rather than breaking new ground, as is common for such
treatments.

Other C19th floras with reference to the genus include:

Hooker, (1860), <u>The botany of the Antarctic voyage... Part III   Flora
Tasmaniae</u>. Vol. II.

Moore and Betche, (1893), <u>Handbook of the flora of New South Wales</u>.

C20th Flora Treatments

Bailey, (1902), <u>The Queensland Flora</u>.

Beadle, (1987), <u>Students Flora of North-eastern New South Wales</u>. Pt 6.

Beadle, Evans and Carolin, (1982), <u>Flora of the Sydney Region</u>.

Black, (1960), <u>Flora of South Australia</u>. 195-196.

Blackall and Grieve, (1974), <u>How to know Western Australian
Wildflowers</u>.

Burbidge and Gray, (1970), <u>Flora of the Australian Capital Territory</u>:
107.

George, (Ed.), (1986), <u>Flora of Australia</u> 46: 148-169.

Jessop, (Ed.), (1981), <u>Flora of Central Australia</u>: 424.

Jessop and Toelken, (Eds), (1987). <u>Flora of South Australia</u>.

Marchant et al., (Eds), (1987), <u>Flora of the Perth Region</u>.

Willis, (1970), <u>A handbook to plants in Victoria</u>. 2nd Edn, Vol. 1.

Other publications on <u>Xanthorrhoea</u>

In addition to the above there have been a number of studies specifically on, or including comments on, other aspects of <u>Xanthorrhoea</u> biology which are not directly relevant, or only partially relevant, to the present study. Some of these papers are:

Anatomy and Morphology: Fahn (1954); Waterhouse (1967); Staff (1968, 1970, 1974, 1975, 1976); Staff and Waterhouse (1981); Stebbins and Kush, (1961).

Biosystematics: Flavonoid patterns in leaves, Williams (1975); Resins, Duewell (in press).

Chromosomes: Darlington and Wylie, 1955; Briggs, 1966; Waterhouse, 1967; Keighery, 1984.

Ecology: Many ecological studies have included information on <u>Xanthorrhoea</u> biology, especially those dealing with the sand areas along the east coast where the genus is a prominent member of the flora (e.g. Specht, 1957 a; Rayson, 1957; Specht and Rayson, 1957 a and b; Specht, Rayson and Jackman, 1958; Coaldrake, 1961; Rogers, 1975; Clifford and Specht, 1976; Myerscough and Carolin, 1986).

Economic aspects and human uses of <u>Xanthorrhoea</u> discussed in the literature include: control of their growth (Anon, 1951); the uses made of the plants by people, e.g. Kite (1795), Maiden (1889 and 1894); species involved in stock poisoning, e.g. Cleland (1914),

Bedford (1986 a).

Growth and longevity: Investigators of growth, growth rates and flowering cycles in the genus have included Cleland (1913) on the rate of growth of the flowering spike, Lewis (1955), who extrapolated the age of the plants from the number of leaves produced by a seedling (and in doing so did not realise that the rate of leaf production of an adult plant was 100-200 times greater), Staff (1970; 1976) on rate of growth of shoots and inflorescences respectively, Gill and Inwerson (1976) on flowering in relation to fire and growth rate, Lamont and Downs (1979) on longevity, flowering and fire history, and B}low-Olsen et al. (1982) on growth and flowering history.

Resin: Xanthorrhoea have unique resins, and the formation and chemical nature of these have been studied by Maiden (1889 and 1894), Schober (1896), Osborne (1916), Birch and Hextall (1955), Duewell (1954; 1965; 1968; in press) and Duewell and Haig (1968).

Other, more peripheral, studies include:

Entomology of Xanthorrhoea: Froggatt (1896); Common (1963).

Microfungal associations: Sivanesan and Sutton (1985).

Xanthorrhoea resins have been used commercially as a
source of picric acid, and as a substitute for shellac,
but were not economically viable for either use (Maiden,
1894).

CHAPTER 2

ANALYSIS OF POPULATIONS OF *XANTHORRHOEA* IN QUEENSLAND USING PHENETIC AND STATISTICAL NUMERICAL TECHNIQUES

2.1 Introduction

It is difficult to distinguish between the three taxa _X. johnsonii_ Lee, _X. latifolia_ (Lee) Bedford and _X. pumilio_ R.Br. in Queensland. Lee has suggested that the name _X. johnsonii_ might represent more than one taxon (Lee 1966 a and b, and pers. comm. 1973) and Bedford has commented that the relationship between the three taxa needs clarification (Bedford 1986 a).

Indeed the types themselves present some difficulties. _X. pumilio_ was described by Robert Brown in 1810. The type specimen was collected by him in 1802 from Port Curtis, near Gladstone Queensland. The specimen is quite depauperate, with very short, sharply recurved leaves, and a small spike. From the specimen the plant appears to have been far from healthy, and therefore it may not have been the "normal" habit and size for its taxon. _X. latifolia_ was described by Lee in 1966 (as _X. media_ subsp. _latifolia_) (loc. cit.). The type specimen was collected by E.F. Constable in 1962 from a plant growing under a _Pinus elliottii_ plantation at Beerwah, Queensland (E.F. Constable, pers. comm. 1982). The plants in the population from which the type was collected were smaller in trunk height than usual for mature examples of the species in natural conditions, but are within the range of variation described for the species by Bedford (1986 a). _X. johnsonii_ was described by Lee, also in 1966 (a). The type specimen was collected by L. Johnson in 1962 from the sole roadside population between Dimbulah and Petford, Queensland (L. Johnson, pers. comm. 1976). The specimen is of the usual size and dimensions for plants in its vicinity, but is much smaller than many plants throughout N.S.W.

and Queensland, (especially the large populations in south-eastern Queensland) which are presently identified as this taxon.

Orthodox taxonomic methods have, up to the present time, failed to resolve the problems raised by these species. The analyses presented here are an attempt to investigate the status of, and if possible, to delimit any taxa in this complex using a combination of techniques of cluster analysis, ordination and discriminant analysis. The nomenclatural status of the groups/taxa which are produced is assessed.

Characters used (Table 2.1)

Fifteen morphological characters were measured for each specimen, except for those which had some missing data. The characters were chosen with reference to the morphological features described as varying between taxa by Lee (1966 a and b), and Bedford (1986 a).

Collections

Specimens for this study were collected on two field trips through Queensland in two successive years (Map, Figure 2.1, and list, Appendix 2.1). An attempt was made to sample both those areas for which previous collections were recorded in the literature and to search hitherto uncollected areas. Most populations were found in the coastal and coastal hinterland areas. A total of 78 specimens were available for analysis, 52 specimens collected specifically for this exercise, all from north of Maryborough, and 26 collections made primarily for other studies, from south-east Queensland (Figure 2.1).

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Table 2.1 Characters used in the analyses

<u>Numeric characters:</u>

1. Leaf width in mm
2. Scape length in cm
3. Scape diameter in mm
4. Spike length in cm
5. Spike diameter in mm
6. Ratio of spike length divided by scape length
7. Trunk height in cm

<u>Disordered multistate characters:</u>

1. Leaf shape in T.S.   State
    quadrate-rhombic   1
    narrowly quadrate-rhombic   2
    obtrullate to obtriangular   3
    concave   4

2. Leaf colour
    green   1
    glaucous   2

3. Prominence of cluster bracts
    absent (not prominent)   1
    shortly acute (just visible)   2
    base of spike only   3
    to 10 cm from base   4
    full length of spike (100%)   5

4. Juvenile cluster bracts
    absent   1
    shortly acute   2
    linear-triangular   3

5. Spike/bract colour/texture at flowering
    white to cream   1
    green   2
    brown   3
    light brown velvet   4
    dark brown velvet   5

6. Scape colour
    glaucous   1
    green   2

7. bract shape
    obtuse   1
    shortly acute   2
    acute   3

8. Bract indumentum
    glabrous   1
    short black hairs   2
    tomentose   3
    fringed   4
    densely hirsute   5

Figure 2.1   Specimen collection locations map

●   Collection sites
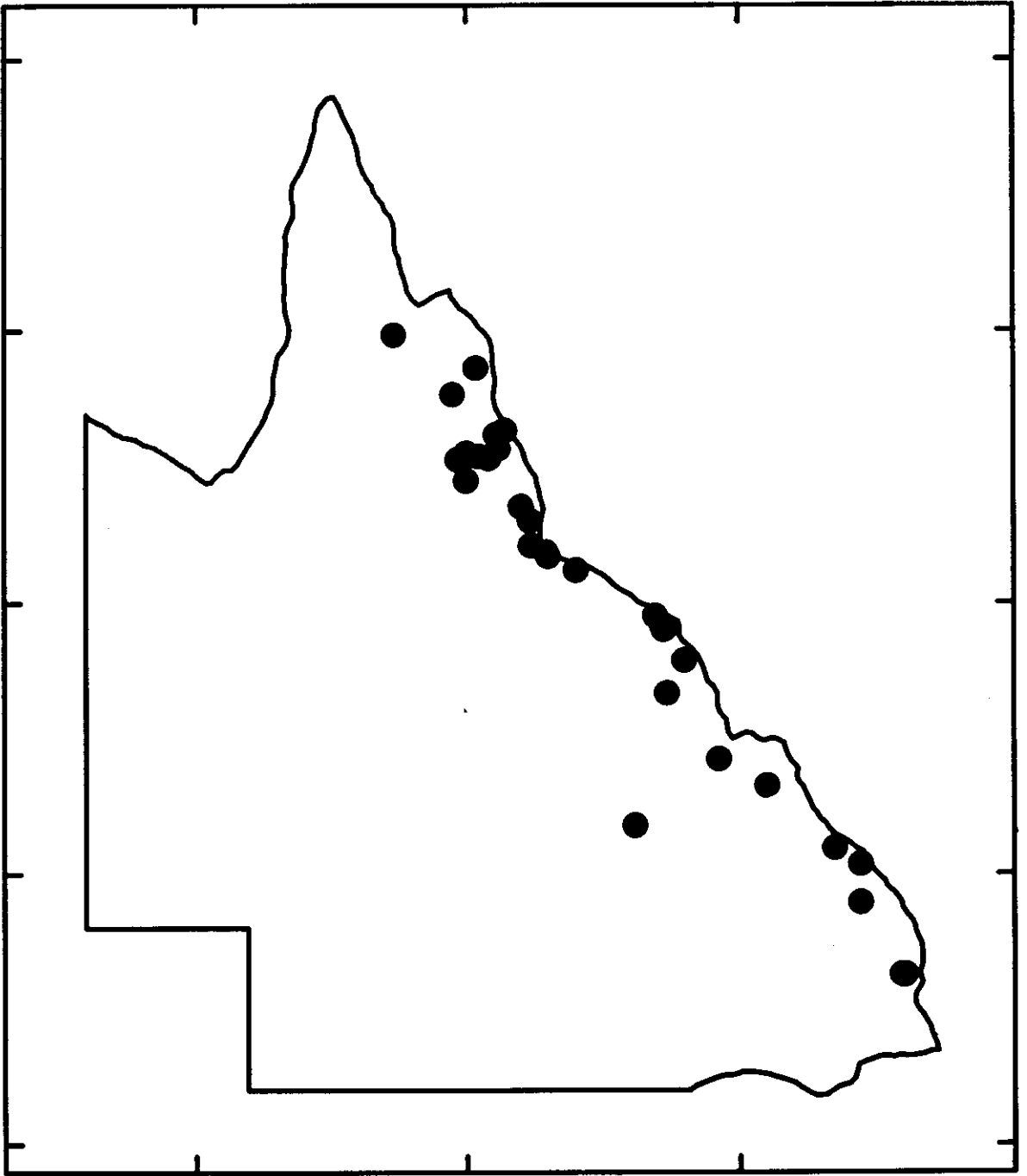
Wherever possible multiple specimens were collected from each population to represent the range of variation, however often only one flowering or fruiting specimen was available. In that case an attempt was made to re-sample the population on the second trip. Thus some populations are represented by samples from two years, and such specimens are marked with an * in the list in Appendix 2.1.

To provide known reference points for the classification, and thus assist in deciding the nomenclatural status of any groupings produced, the collections included specimens from the type localities of X. johnsonii and X. latifolia. Unfortunately the collection of specimens from the type locality of X. pumilio was not possible because of uncertainty in Brown's annotation as to the exact site. However, specimen numbers 3 and 7 were considered part of this taxon by Bedford (1986 a) (collection numbers 76-09, 41.7 km N of Townsville, and 76-12, 35 km S of Bowen respectively).

Due to practical constraints collecting was limited to areas accessible by road or 4 wheel drive track.

Analyses

Two suites of computer programs have been used to classify and analyze the data. The first suite is the TAXON Library of programs from the CSIRO Division of Computing Research as set out in the Taxon User's Manual Edition P4 (Ross et. al., 1986). The second suite of programs were chosen from the Statistical Package for the Social Sciences (SPSS) as run on the

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University of Sydney Cyber computer during 1987, and as set

out in the second edition of the SPSS Manual (Nie et al.,

1975) and the SPSS Update 7-9 (Hull and Nie, 1981). The basic

features and characteristics of the programs selected from these

suites are set out below under their respective headings.

CSIRONET TAXON Library

The programs for classification and ordination available from this

library were selected for a number of reasons.

(a) A phenetic rather than a phyletic (cladistic) classification

system was necessary since in my analyses the operational taxonomic

units (as defined by Sokal and Sneath, 1963) are individual specimens.

Therefore the underlying assumptions of a cladistic classification,

such as that the OTU's be separated by genetic barriers, can not be

met in these analyses.

(b) An ordination was also used because hierarchical classifications

can be poor representations of the phenetic relationships found in

nature. Far better representations of real situations are often

obtained by summarizing the data in an ordination of as few as three

dimensions (Sneath and Sokal 1973). Such a situation would arise if

there were one or more multivariate clines in the data instead of

clusters.

(c) The programs had important practical advantages as they:

(1) all used the same data format;

(2) could deal with the largest analyses likely to arise;

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(3) were proven programs operating reliably;

(4) could be run in a multiple-operation on the same data deck at the same time, and;

(4) were accompanied by diagnostic programs to help interpret the results from the analyses.

Both a classification and an ordination were carried out on all sets of data analyzed. The classification approach presupposes that the data is discontinuous whilst the ordination approach presupposes either that the data is continuous (Dale et al 1979) or, in the view of Clifford and Stephenson (1975), makes no assumptions about the existence or otherwise of groupings amongst the entities. Thus it would be expected that the classifications would be the most informative (the "best" resolution") where groupings or clusters exist, and that the ordinations would be the most informative analysis if there are no separate clusters, i.e. the data are ordered but continuous, such as in a multivariate (taxonomic) or univariate cline (possibly responding to a single environmental gradient). I applied both approaches because the structure of the data was not known. In such situations Sneath and Sokal (1973) considered it essential that both ordination and classification be run to examine the structure of a data set.

<u>i. Programs used:</u>

Classification (MSED + SAHN).

An agglomerative polythetic classification using the squared euclidean

distance dissimilarity measure (MSED), and two clustering algorithms

(in SAHN):

(a) Unweighted Pair Group, also known as Group Average (UPG);

(b) Incremental Sum of Squares (ISS).

Ordination (PCOA)

(c) In addition a Principal Co-ordinate Analysis ordination using the

same MSED dissimilarity matrix was carried-out for each data set.

Diagnostic programs GSTAT, GCOM and CRAMER and BACRIV were run to help

explain and quantify the results of the above programs.

Programs GSTAT, GCOM and CRAMER are used after a classification to

investigate the relationships between groups, and the attributes on

which those groups are based. They assist with the interpretation of

the results by giving details of the groups and indicating which

attributes were important in the formation of the hierarchy. BACRIV

is used after an ordination to interpret the axes in terms of the

original attributes.

Program Descriptions

MSED (Matrix generation using Standardized (squared) Euclidean
Distance) and SAHN (Sequential Agglomerative Hierarchical Non-
overlapping clustering program) provide an agglomerative polythetic
classification system with a choice of clustering algorithm. The
strategies for dealing with mixed data/character types developed by
Lance and Williams (1967) and Burr (1968) to include ordered and
disordered multistates and numeric data in the one dissimilarity
matrix are incorporated in both programs. Both programs are based on
the work of Lance and Williams (1966) (Ross et. al., loc. cit.).

Sokal (1986) discusses procedures for "the computation of a resemb-
lance matrix for each pair of OTU's". He notes that for continuous or
ordered multistate characters "one can compute taxonomic distances or
Manhattan distances", and that the former are preferred "where we wish
to focus attention on the gestalt of the organisms, i.e. linear
combinations of characters". However Sokal goes on to say that "all
distances measures are unduly influenced by the size of the organisms
being compared" and therefore recommends the use of "cosine
coefficients of shape".

For Xanthorrhoea intuitive classification indicates that size as well
as shape differences are important in the taxonomic groupings (e.g.
Bedford, 1986 a). It is therefore valid to use a metric of taxonomic
distance which reflects both shape and size such as Euclidean metric
(Euclidean distance squared). Previous experience also indicated that
this metric effectively reflected observed taxonomic differences

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(Bedford, 1975).

Clustering strategies

(a) The UPG (Unweighted Pair Group) Group Average clustering technique
was chosen because of its neutral clustering behaviour ("space
conserving" in the terminology of Lance and Williams 1967 a). As this
technique is one of the least likely to force clusters onto a group it
should give a realistic indication whether or not there are discon-
tinuities within the data (Dale et. al., 1979, Clifford and
Stephenson, 1975). Sokal (loc. cit.) comments that UPG clustering is
both the most commonly used approach, and frequently gives
classifications that are regarded as satisfactory by traditional
taxonomists. He also notes that UPG results are more stable and have
a higher predictive value (are more likely to accurately predict the
distribution of other characters not included in the classification)
than other clustering algorithms studied by him.

(b) The ISS (Incremental Sum of Squares) clustering technique was
chosen because it is an intensely clustering technique ("space
dilating", Lance and Williams 1967 a) which "artificially sharpens"
groups (Dale et. al., 1979). This technique is useful where the data
is relatively continuous as it separates out any centres of
discontinuity as discrete groups and segregates entities with weak
relationships as non conformist groups (Clifford and Stephenson,
1975). Conceptually this can be very useful as long as the
group-size-dependance characteristic is recognized and taken into
account.

Both classificatory algorithms were used on the full data sets to compare their different effects to test the stability of any groups found. It also provided an intuitive guide to how well structured the data set was, in that major changes in the composition of groups between the results of the two algorithms could indicate that discontinuities found by the classifications were artifacts of the classificatory process.

SAHN produces a table of entity and group fusion levels, output to a printer or plotter for a dendrogram (by DENDRO), and the composition of groups, (if such are specified) as well as output of the inter-element dissimilarity matrix for use by following programs.

GSTAT (Group STATistics) gives group summary statistics for each group - a table of the scores on multistate characters, and of minima, maxima, ranges and standard deviations for numeric characters.

GCOM (Group COMposition) shows which characters make up 50% of the difference between (in the case of the present comparisons of three main groups): (a.) the "most distinct" group and the other two groups combined and; (b.) the remaining two groups treated separately.

Because the program does not always choose the same group as being the "most distinct" the resulting comparisons are not always of the same pairs of groups and are therefore not directly comparable between runs. Whilst this lack of true pair-wise comparison of groups, and variable choice of combinations of groups, makes direct comparison of results difficult it is still possible to get an indication of group

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comparisons by a careful examination of the results presented.
CRAMER (Cramer statistic, Cramer, 1946) lists each character in the
order of its power to discriminate between groups, along with its
CRAMER value and other statistics. The program uses the Cramer
statistic as implemented by Lance and Williams (1977). Although an F
value is also included for each character, a message "caution F test
invalid" warns the user that it is not statistically valid to use an F
test on attributes that have been used in the classification because
the classification process has altered the statistical distribution of
the characters such that they no longer meet the requirements
underlying the F test (D. Ross, pers. comm. 1987).

(c) PCQA (Principal Co-Ordinate Analysis) operates on an inter-
element dissimilarity matrix, as described by Gower (1966, 1967). As
this ordination operates on the same dissimilarity matrix as MSED +
SAHN it can be run sequentially with those programs. This simplifies
the system both practically and also theoretically as it reduces or
eliminates sources of variability due to that part of the analytical
technique. PCQA results are output as two dimensional plots by
PTPLOT.

The PCQA ordination is the same for each MSED matrix (i.e. there are
only three matrices used here, two full data set analyses, (one with
52 individuals and one with 78 individuals) and one reduced data set
(subset of 39 individuals out of the full data set) and is therefore
presented once only for each data set, after the last classification
in each set with lines marked as per the groupings produced by each
different classification to show more clearly how each classification

relates to the relevant ordination.

BACRIV (BAck CoRrelation of Individuals on Vectors) is used to aid in the interpretation of the results produced by PCOA. BACRIV's output consists of a table for each vector. The table lists attributes sorted in order of their absolute correlation with the vector. That is, it lists which attributes have been important in the formation of each of the vectors, and the level of their contribution to that vector. It also gives the number of individuals on which this is based (in case of missing data) (Ross et. al., 1986). BACRIV results given here are lists of the correlations of characters and character states with the first three principal co-ordinates, which helps to explain the placing of groups and individuals along the co-ordinates in terms of their characteristics. Because BACRIV is calculated from PCOA, which uses the MSED matrix rather than the SAHN algorithm, it produces the same result independent of the classification algorithm. BACRIV results are therefore presented once only for each of the 3 data sets, with the UPG analyses.

Statistical Package for the Social Sciences (SPSS) Library

Statistical programs for further data analysis were selected from the SPSS library (Release 9), because of their ready availability and proven performance. In addition these programs were able to accept data input in a similar form to that required by TAXON, which reduced the need for data re-formatting and therefore the risk of simple data errors.

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The only statistical analytical procedures chosen for further data analysis were discriminant analysis and classification. These were used to provide information about the groups produced by the classifications, both in terms of (i) how well the groups can be discriminated, and (ii) which characters best showed any differences between the groups.

The discriminant analyses and classifications therefore provided assistance in assessing the TAXON classification both in terms of how recognizable the groups formed by the classifications are, and how the characters which best discriminate between the groups compare with the characters used in intuitive classification.

ii. Program used:

SPSS "subprogram" DISCRIMINANT was used for discriminant analyses and classifications. DISCRIMINANT does not accept disordered multistates data (it accepts only numeric or ordered multistate data) and this must be remembered in assessing the results.

DISCRIMINANT performs discriminant analysis either by entering all discriminating variables directly into the analysis or through a variety of "stepwise" methods selecting the "best" set of discriminating variables. The so called "stepwise" method was chosen here to identify differences between the characters as discriminating variables. The method chosen for the "stepwise" addition was METHOD = RAO, which uses Rao's V, a generalised distance measure. Variables are selected on the basis of whichever contributes the largest

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increase in Rao's V when added to the previous variables. This method
provides the greatest possible separation of the groups, and is
therefore the most powerful available (Klecka, 1975).

Klecka (loc. cit.) writes that discriminant analysis provides a means
of statistically distinguishing between predetermined groups. That is
to discriminate between the groups in the sense of being able to tell
them apart. The mathematical objective of discriminant analysis is to
weight and linearly combine the discriminating variables in a way that
the groups are forced to be as statistically distinct as possible i.e.
the discriminant functions are formed in such a way as to maximize the
separation of the groups.

To distinguish between the groups the researcher selects a collection
of variables characteristics on which the groups are expected to
differ. Usually no single variable will perfectly differentiate
between one group and another. By taking several variables and mathe-
matically combining them, we would hope to find a single dimension or
axis [discriminant function] on which one group is clustered at one
end of the axis and the other group at the other end of the axis.
The two implementations of this technique are analysis and
classification.

The analysis aspects of this technique provide several tools for the
interpretation of data. Among these are statistical tests for
measuring the success with which the discriminating variables actually
discriminate when combined into the discriminant functions.

The use of discriminant analysis as a classification technique comes after the initial computation. One can use classification in testing the adequacy of the derived discriminant functions. By classifying the cases used to determine the functions in the first place and comparing predicted group membership with actual group membership, one can empirically measure the success in discrimination by observing the proportion of correct classifications.

The higher the proportion of correctly classified cases the better the discriminant function discriminates between the groups. It is important to note that the discriminant classification does not provide a classification in the same way that TAXON does, but is only a test of the functions output by discriminant analysis.

If the discriminant function is formed from the more readily recognizable of the characters in the analysis, and the discriminant classification shows a high proportion of the entities as being correctly classified, then this could be interpreted as providing some empirical support to the relevant TAXON classification.

By examining which characters provide the best discrimination between groups it is also possible to gain an empirical comparison between classifications in terms of how recognizable the groups are.

The reasons why characters are not selected for inclusion in the DISCRIMINANT functions are not specified in the SPSS manual (Nie et al., 1975; Hull and Nie, 1981). There appear to be three possible reasons for non selection: (a) The character contains little or no

information, for example because it is often missing or is randomly distributed among the groups etc.;

(b) the character contains little or no additional information because it is strongly correlated with a character already included in the discriminant function, or;

(c) the character contains information contra indicative to the pre-determined groupings.

Other Statistical Procedures Considered

Standardization of the data for the analyses was considered. Sokal (1986) notes "Measurements or continuous characters must be scaled to avoid biasing the results by size factors." He continues "Scaling characters alters the resulting correlation or taxonomic distance matrixes between OTU's. It should always be undertaken, although the method of scaling -- whether by standardization or ranging -- seems to make very little difference in the results."

Trials were run of both raw data standardized only by the innate standardization of the euclidean distance algorithm, and of data separately standardized (by TAXON program DCV (Data ConVersion) to zero mean and unit variance. Sokal's statement that the method of scaling did not affect the results was supported, as analyses on raw data give exactly the same result as those on DCV standardized data.

It is clear that the MSED algorithm's squaring of the euclidean distance measure provides adequate standardization, with equivalent results to the specially developed standardization in the DCV program.

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Results printed in the same form as the raw data have a number of important advantages, such as conceptual simplicity and a reduced chance of error because of the ease of cross checking of the results by examination or statistical evaluation of tabulations of data of the component entities of each group. As program DCV produces results in the form of standardized data, with the disadvantages alluded to above, it was not used further. Therefore only the raw data results are considered here.

RESULTS

Three sets of analyses were carried out, as discussed below. Northern Queensland data only (2.2) and north and south Queensland data (2.3) used multiple analyses of the data set to test the robustness and stability of the groups generated by the classifications. The multiple analyses involved MSED + SAHN using the two clustering algorithms described, PCOA and a discriminant analysis and classification using DISCRIMINANT. The third set of analyses, Group β (2.4) used a subset of the data to examine internal dissimilarity in group β, one of the three groups produced by the full data set analyses. It involved MSED + SAHN, and the relevant diagnostic programs.

Data sets

The northern Queensland data set (52 entity, "NQ52") and the Group β set (39 entity) are subsets of the full north and south Queensland data set (78 entity, "NQ78") (Appendix 2.2)

So that the reader can judge the validity of the conclusions, appropriately numbered tables are provided to give the complete results for each analysis. Each set of results is summarised in the discussion in the relevant sections of the text.

2.2 Northern Queensland data (52 entities).

The first set of analyses used the 52 specimens collected from
Queensland north of Maryborough.

2.3 North and south Queensland data (78 entities).

After an examination of the above analysis it was decided   to extend
the geographic range and number of individuals in the data set and
analyses in an attempt to test the stability of the classification.
The data set was therefore expanded to include 26 collections from
south-east Queensland, including specimens of known identification as
X. latifolia and examples of the large populations of plants known as
X. johnsonii in south-east Queensland, (a total of 78 specimens).

2.4 Group β (39 entity data set).

The third set of analyses was on the group of individuals classified
into the largest group by the first set of analyses using the UPG
clustering algorithm on the Northern Queensland data (52 entities).
The NQ52 UPG dendrogram shows Group β to have two major and some minor
subdivisions. This analysis was undertaken to examine the causes of
these internal divisions.

This analysis was necessary because of the possibility that
there may be very dissimilar individuals included in the
larger matrices. Such inclusions could have distorted the
dissimilarity matrices sufficiently to hide smaller but
still significant discontinuities in the data. The removal
of the most dissimilar individuals from the matrix by
selecting this 39 entity subset should reveal the structure
of the data set more accurately.

2.2 Northern Queensland data set (52 entity) analyses.

2.2.1 TAXON SAHN Classification, UPG clustering strategy.

The dendrogram produced by this technique (Figure 2.2) shows three groups by the 1.0 dissimilarity level (SAHN dissimilarity levels are given in Appendix 2.3):

GP β WITH 39 MEMBERS - 1-3 5-12 15-21 23-26 31-33 35-39

41-42 44-46 48-49 51-52

GP θ WITH 9 MEMBERS - 13 14 22 27-28 40 43 47 50

GP Ω WITH 4 MEMBERS - 4 29 30 34

The groups are of very unequal size, though the levels of internal dissimilarity are more or less equivalent in all groups. The groups contain some elements of known taxa or have elements similar in general appearance to known taxa. GP β contains plants from the type locality of X. johnsonii in north Queensland, as well as the majority of the specimens in the analysis. The two smaller groups represent easily recognizable and distinctive growth forms. GP θ are robust plants with trunks, which are similar in appearance to plants identified as X. johnsonii in south-east Queensland. GP Ω are plants from north Queensland similar in appearance to the X. latifolia from south-east Queensland.

This grouping indicates that there are three distinct groups in the classification. Most individuals in the classification are placed in the one group, and may therefore be presumed to be similar to each

Figure 2.2 UPG Classification Dendrogram, Northern Queensland
data set (52 entities).

GP β shown β

GP θ shown θ

GP Ω shown Ω

Figure 2.2
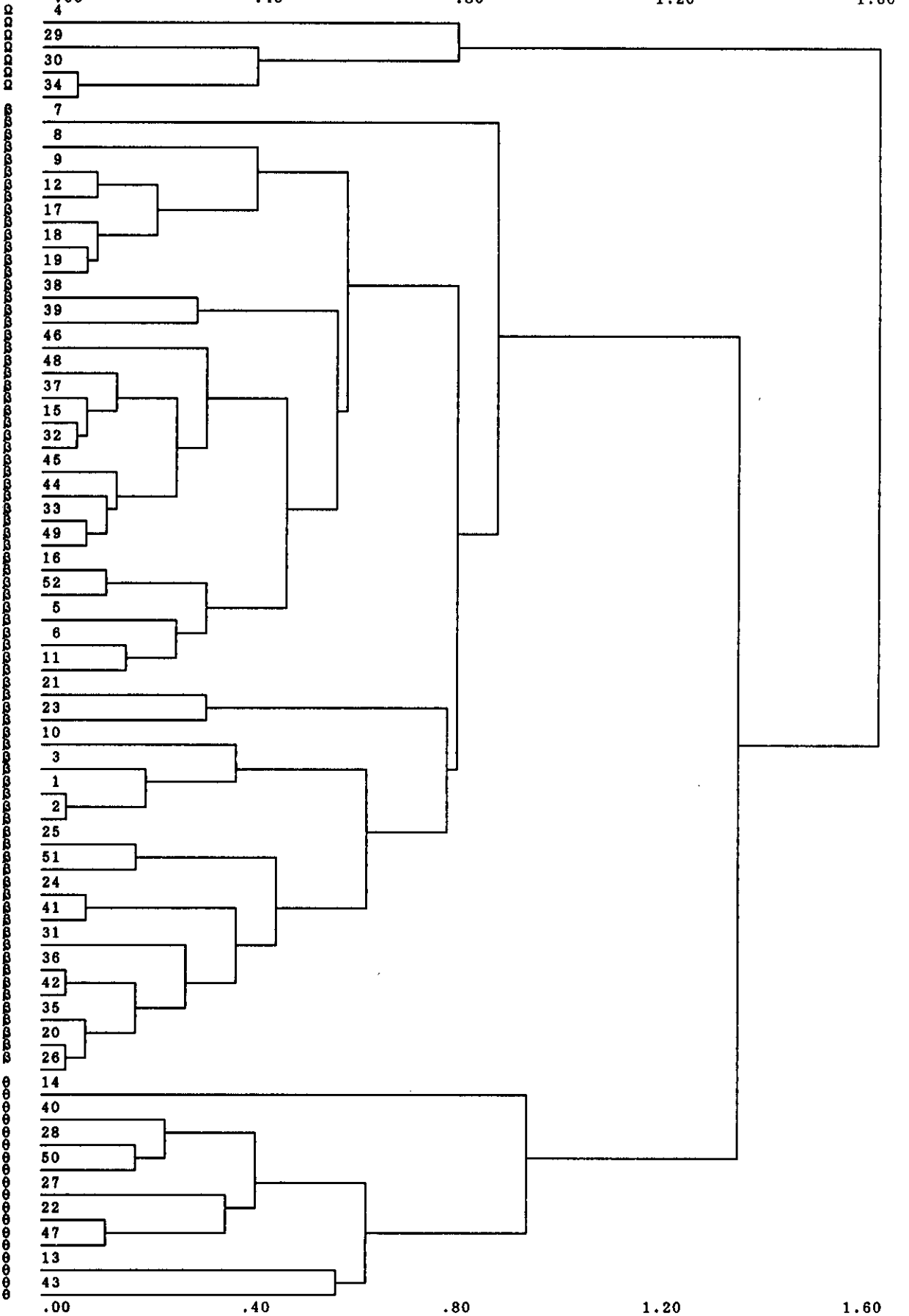
other, although the dendrogram shows that there are internal divisions into two subgroups and one singleton within the group.

Notable levels of dissimilarity in the dendrogram are: Three distinct groups are formed at the .9302 dissimilarity level; the first two groups to join together are GPs β and θ which join at the 1.3593 level; GP Ω then joins with those groups at the overall dissimilarity level of 1.6420.

Diagnostic Programs

GSTAT

The statistics for the three Groups indicate that two of the three are variable in many or most characters (Table 2.2).

GP β

Variable in most characters.

Disordered multistate characters: Leaf shape shows considerable variation with every possible shape represented; prominence of cluster bracts is also more variable than expected for one taxon in comparison to accepted variation in published classifications of the genus (Lee 1966 a and b, Bedford, 1986 a).

Numeric characters: Almost all characters are very variable, with wide ranges and high standard deviations, the latter as high as over 1/2 of the mean in the case of spike length.

Table 2.2 GSTAT, UPG Classification Groups, Northern Queensland data
set (52 entities).

Table 2.2

<pre>
            GP B WITH 39 MEMBERS
            ****
DISORDERED MULTISTATES NO.   NO. IN STATE
                        MIS   1   2   3   4   5

 1 LEAF SHAPE   0   21   12   4   2
 2 LEAF COLOUR   16   23   0
 3 CLUSTER BRACTS   0   18   7   12   2   0
 4 JUV. CLUSTER BR.   20   7   9   3
 5 BRACT COLOUR   28   0   11   0   0   0
 6 SCAPE COLOUR   28   11   0
 7 BRACT SHAPE   1   0   38   0
 8 BR. INDUMENTUM   0   0   0   0   39   0

NUMERIC ATTRIBUTES   NO.   NO   NO.   MIN.   MIN.   MAX.   MEAN   MEAN   S.D.   RANGE
     (FNUM)   MIS   =0 NOT 0   NOT 0   NOT 0
 1 LEAF WIDTH   0   0   39   130.0   130.0   350.0   204.1   204.1   53.41   220.0
 2 SCAPE LENGTH   0   0   39   59.00   59.00   296.0   147.5   147.5   55.21   237.0
 3 SCAPE DIAMETER   0   0   39   60.00   60.00   130.0   96.41   96.41   21.99   70.00
 4 SPIKE LENGTH   0   0   39   5.000   5.000   104.0   43.51   43.51   22.87   99.00
 5 SPIKE DIAMETER   1   0   38   16.00   16.00   28.00   22.21   22.21   3.112   12.00
 6 SP/SC RATIO   0   0   39   9.000   9.000   94.00   30.23   30.23   17.13   85.00
 7 TRUNK HEIGHT   0   10   29   0.   2.000   60.00   12.28   16.52   13.61   60.00

            GP C WITH 9 MEMBERS
            ****
DISORDERED MULTISTATES NO.   NO. IN STATE
                        MIS   1   2   3   4   5

 1 LEAF SHAPE   0   9   0   0   0
 2 LEAF COLOUR   2   7   0
 3 CLUSTER BRACTS   0   0   0   2   4   3
 4 JUV. CLUSTER BR.   2   0   2   5
 5 BRACT COLOUR   6   0   3   0   0   0
 6 SCAPE COLOUR   7   2   0
 7 BRACT SHAPE   0   0   9   0
 8 BR. INDUMENTUM   0   0   0   0   9   0

NUMERIC ATTRIBUTES   NO.   NO   NO.   MIN.   MIN.   MAX.   MEAN   MEAN   S.D.   RANGE
     (FNUM)   MIS   =0 NOT 0   NOT 0   NOT 0
 1 LEAF WIDTH   0   0   9   130.0   130.0   240.0   186.1   186.1   38.87   110.0
 2 SCAPE LENGTH   0   0   9   60.00   60.00   145.0   97.44   97.44   23.23   85.00
 3 SCAPE DIAMETER   0   0   9   120.0   120.0   200.0   153.3   153.3   34.64   80.00
 4 SPIKE LENGTH   0   0   9   55.00   55.00   140.0   88.44   88.44   31.34   85.00
 5 SPIKE DIAMETER   0   0   9   25.00   25.00   35.00   29.44   29.44   3.779   10.00
 6 SP/SC RATIO   0   0   9   61.00   61.00   150.0   92.22   92.22   28.60   89.00
 7 TRUNK HEIGHT   0   0   9   50.00   50.00   100.0   85.56   85.56   15.44   50.00

            GP Q WITH 4 MEMBERS
            ****
DISORDERED MULTISTATES NO.   NO. IN STATE
                        MIS   1   2   3   4   5

 1 LEAF SHAPE   0   0   4   0   0
 2 LEAF COLOUR   1   3   0
 3 CLUSTER BRACTS   0   4   0   0   0   0
 4 JUV. CLUSTER BR.   4   0   0   0
 5 BRACT COLOUR   2   0   2   0   0   0
 6 SCAPE COLOUR   1   3   0
 7 BRACT SHAPE   0   0   4   0
 8 BR. INDUMENTUM   0   0   0   0   4   0

NUMERIC ATTRIBUTES   NO.   NO   NO.   MIN.   MIN.   MAX.   MEAN   MEAN   S.D.   RANGE
     (FNUM)   MIS   =0 NOT 0   NOT 0   NOT 0
 1 LEAF WIDTH   0   0   4   300.0   300.0   450.0   361.5   361.5   66.52   150.0
 2 SCAPE LENGTH   0   0   4   165.0   165.0   285.0   240.0   240.0   52.12   120.0
 3 SCAPE DIAMETER   0   0   4   120.0   120.0   200.0   165.0   165.0   33.17   80.00
 4 SPIKE LENGTH   0   0   4   70.00   70.00   134.0   108.5   108.5   30.90   64.00
 5 SPIKE DIAMETER   0   0   4   27.00   27.00   37.00   32.00   32.00   4.082   10.00
 6 SP/SC RATIO   0   0   4   34.00   34.00   53.00   45.00   45.00   8.756   19.00
 7 TRUNK HEIGHT   0   1   3   0.   80.00   120.0   75.00   100.0   52.60   120.0

            STATISTICS FOR ENTIRE DATA
            ****
DISORDERED MULTISTATES NO.   NO. IN STATE
                        MIS   1   2   3   4   5

 1 LEAF SHAPE   0   30   16   4   2
 2 LEAF COLOUR   19   33   0
 3 CLUSTER BRACTS   0   22   7   14   6   3
 4 JUV. CLUSTER BR.   26   7   11   8
 5 BRACT COLOUR   36   0   16   0   0   0
 6 SCAPE COLOUR   36   16   0
 7 BRACT SHAPE   1   0   51   0
 8 BR. INDUMENTUM   0   0   0   0   52   0

NUMERIC ATTRIBUTES   NO.   NO   NO.   MIN.   MIN.   MAX.   MEAN   MEAN   S.D.   RANGE
     (FNUM)   MIS   =0 NOT 0   NOT 0   NOT 0
 1 LEAF WIDTH   0   0   52   130.0   130.0   450.0   213.6   213.6   68.43   320.0
 2 SCAPE LENGTH   0   0   52   59.00   59.00   296.0   145.9   145.9   50.22   237.0
 3 SCAPE DIAMETER   0   0   52   60.00   60.00   200.0   111.5   111.5   35.94   140.0
 4 SPIKE LENGTH   0   0   52   5.000   5.000   140.0   56.29   56.29   33.46   135.0
 5 SPIKE DIAMETER   1   0   51   16.00   16.00   37.00   24.26   24.26   4.824   21.00
 6 SP/SC RATIO   0   0   52   9.000   9.000   150.0   42.10   42.10   30.07   141.0
 7 TRUNK HEIGHT   0   11   41   0.   2.000   120.0   29.79   37.76   36.10   120.0
</pre>

(A detailed analysis of the internal variation in this group is given section 2.4).

GP θ

More uniform than GP β but still with considerable variation in the numeric characters.

Disordered multistate characters: All characters uniform or with consistent combinations of characters (e.g. prominent cluster bracts vary from slightly to very prominent).

Numeric characters: Reasonably uniform, except for the considerable variation in spike length and spike length : scape length ratio (in the latter the standard deviation is almost 1/3 of the mean).

GP Ω

The smallest and most uniform of the groups.

Disordered multistate characters: All characters are uniform.

Numeric characters: All characters are satisfactorily uniform, though the ranges of scape length, spike diameter and spike length reflect considerable variation.

GCOM, UPG Classification Groups, Northern Queensland data set (52 entities).

Table 2.3 reveals that leaf characters and, to a lesser extent, spike diameter make-up 50% of the difference between GP Ω and GPs $\beta+\theta$ combined:

GP Ω has broad, (mean 3.67 mm) narrowly quadrate-rhombic T.S. leaf shape and thicker spikes (mean 32 mm) than average for the other two GPs $\beta + \theta$ combined which have narrower leaves (mean 2.00 mm) of a range of shapes and narrower spikes (mean 23.5 mm).

The characters separating GP β from GP θ are spike to scape length ratio, trunk height and scape diameter:

GP β have a much shorter spike than scape whereas GP θ have spikes approximately the same lengths as scapes (mean values .30 and .92 respectively); GP β has shorter trunks than GP θ (mean trunk heights 12 cm and 85 cm respectively); GP β has thinner scapes than GP θ (means of 9.64 mm and 15.33 mm respectively). (Table 2.3).

CRAMER, UPG Classification Groups, Northern Queensland data set (52 entities) (Table 2.4).

The list of characters in order of their ability to distinguish between groups as indicated by CRAMER is:

1/. Trunk height, Cramer value .8508

2/. Spike length : scape length ratio, Cramer value .7812

3/. Spike diameter, Cramer value .7421

4/. Scape diameter, Cramer value .7401

Table 2.3 GCOM, UPG Classification Groups, Northern Queensland data

set (52 entities).

‡‡‡‡ COMPARISON NO. 1
‡‡‡‡ GROUP A = GP Ω
‡‡‡‡ GROUP B = GP β + GP θ

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 5.8813

		GROUP A 4 MEMBERS		GROUP B 48 MEMBERS		CONTRIBUTION			
ATTRIBUTE (STATE)	NAME	ATTRIBUTE MEAN	NO. PRESENT	ATTRIBUTE MEAN	NO. PRESENT	%	% (CUM)	ACTUAL VALUE	
FNUM 1	LEAF WIDTH	367.500	4	200.729	48	25	25	1.46	
DNUL 1	LEAF SHAPE		4		48	14	39	.822	
ST. 1	QUADRATE-RHOMBIC	.000		.625					
ST. 2	NARROWLY-Q-R	1.000		.250					
ST. 3	OBTRULL>OBTRIANG	.000		.083					
ST. 4	CONCAVE	.000		.042					
FNUM 5	SPIKE DIAMETER	32.000	4	23.596	47	13	52	.746	

6 ATTRIBUTES MADE NO CONTRIBUTION.

‡‡‡‡ COMPARISON NO. 2
‡‡‡‡ GROUP A = GP β
‡‡‡‡ GROUP B = GP θ

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 9.3616

		GROUP A 39 MEMBERS		GROUP B 9 MEMBERS		CONTRIBUTION			
ATTRIBUTE (STATE)	NAME	ATTRIBUTE MEAN	NO. PRESENT	ATTRIBUTE MEAN	NO. PRESENT	%	% (CUM)	ACTUAL VALUE	
FNUM 6	SP/SC RATIO	30.231	39	92.222	9	22	22	2.07	
FNUM 7	TRUNK HEIGHT	12.282	39	85.556	9	21	44	2.01	
FNUM 3	SCAPE DIAMETER	96.410	39	153.333	9	13	57	1.22	

5 ATTRIBUTES MADE NO CONTRIBUTION.

Table 2.4 CRAMER, UPG Classification Groups, Northern Queensland data set (52 entities).

Table 2.4 CRAMER, UPG Classification Groups, Northern Queensland data set (52 entities).

MEAN CRAMER VALUE FOR 15 ATTRIBUTES = .6387   SCALED CRAMER VALUE FOR 3 GROUPS = .3688

NO ATTRIBUTES ARE MISSING IN ALL GROUPS.

ATTRIBUTES DMUL 2 (LEAF COLOUR), DMUL 5 (BRACT COLOUR), DMUL 6 (SCAPE COLOUR),
DMUL 7 (BRACT SHAPE), DMUL 8 (BR. INDUMENTUM) (WHERE PRESENT) ARE THE SAME IN ALL GROUPS.

PNUM 7 (TRUNK HEIGHT)
++++++++++++++++++++++++
CRAMER VALUE = .8508

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP Q	4	4	75.00	BETWEEN GROUPS	.4812E+05	2	.2406E+05	64.21
GP P	39	39	12.28	WITHIN GROUPS	.1836E+05	49	374.7	
GP 8	9	9	85.56	TOTAL	.6648E+05	51		

GRAND MEAN = 29.73

PNUM 6 (SP/SC RATIO)
+++++++++++++++++++++++
CRAMER VALUE = .7812

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP Q	4	4	45.00	BETWEEN GROUPS	.2814E+05	2	.1407E+05	38.37
GP P	39	39	30.23	WITHIN GROUPS	.1797E+05	49	366.7	
GP 8	9	9	92.22	TOTAL	.4610E+05	51		

GRAND MEAN = 42.10

PNUM 5 (SPIKE DIAMETER)
++++++++++++++++++++++++++
CRAMER VALUE = .7423

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP Q	4	4	32.00	BETWEEN GROUPS	641.1	2	320.6	29.45
GP P	39	38	22.21	WITHIN GROUPS	522.5	48	10.89	
GP 8	9	9	29.44	TOTAL	1164.	50		

GRAND MEAN = 24.25

PNUM 3 (SCAPE DIAMETER)
++++++++++++++++++++++++++
CRAMER VALUE = .7401

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP Q	4	4	165.0	BETWEEN GROUPS	.3608E+05	2	.1804E+05	29.67
GP P	39	39	96.41	WITHIN GROUPS	.2980E+05	49	608.1	
GP 8	9	9	153.3	TOTAL	.6588E+05	51		

GRAND MEAN = 111.5

PNUM 4 (SPIKE LENGTH)
++++++++++++++++++++++++
CRAMER VALUE = .6818

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP Q	4	4	108.5	BETWEEN GROUPS	.2658E+05	2	.1329E+05	21.28
GP P	39	39	43.51	WITHIN GROUPS	.3059E+05	49	624.3	
GP 8	9	9	88.44	TOTAL	.5717E+05	51		

GRAND MEAN = 56.29

PNUM 1 (LEAF WIDTH)
++++++++++++++++++++++
CRAMER VALUE = .6633

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP Q	4	4	367.5	BETWEEN GROUPS	.1051E+06	2	.5253E+05	19.24
GP P	39	39	204.1	WITHIN GROUPS	.1338E+06	49	2730.	
GP 8	9	9	186.1	TOTAL	.2388E+06	51		

GRAND MEAN = 213.6

DMUL 3 (CLUSTER BRACTS)
++++++++++++++++++++++++++
CRAMER VALUE = .5836
CHI-SQ = 35.42, D.F. = 8

GROUP NAME	NO. MEMBERS	NO. PRESENT	NO. OF MEMBERS IN EACH STATE 1	2	3	4	5
GP Q	4	4	4	0	0	0	0
GP P	39	39	18	7	12	2	0
GP 8	9	9	0	0	2	4	3
	52		22	7	14	6	3

5/. Spike length, Cramer value .6818

6/. Leaf width, Cramer value .6633

7/. Prominence of cluster bracts, Cramer value .5836

The least important character listed, prominence of cluster bracts, shows that the GP β contains variation in this character in excess of that accepted elsewhere in the genus by Bedford (1986 a).

2.2.1.2 DISCRIMINANT ANALYSIS AND CLASSIFICATION, TAXON UPG Classification Groups, Northern Queensland data set (52 entities).

Analysis

Six characters were selected for inclusion in the two discriminant functions before the addition to Rao's V became non significant (Table 2.5). That is, the analysis selected the linear combination of the six characters listed below as being able to discriminate between the groups established by the TAXON NQ52 UPG classification. Scape diameter was the one character not selected. The order of selection of discriminating attributes in the "stepwise" analysis was:

1/. Trunk height

2/. Spike diameter

3/. Leaf width

4/. Scape length

5/. Spike length : scape length ratio

6/. Spike length

Trunk height was by far the most important discriminator between groups, with a change in Rao's V over twice that of the next most

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Table 2.5 DISCRIMINANT Analysis NQ52 UPG Groups

SUMMARY TABLE

STEP	ACTION ENTERED	VARS IN	WILKS LAMBDA	SIG.	RAO*S V	CHANGE IN V	SIG.
1	TRUNKHT	1	.277940	.0000	124.6993	124.6993	0
2	SPIKED	2	.197706	.0000	185.4682	60.7690	.0000
3	LEAFW	3	.113876	.0000	241.3510	55.8827	.0000
4	SCAPEL	4	.094099	.0000	282.9165	41.5655	.0000
5	SPSCRAT	5	.078804	.0000	303.2127	20.2963	.0000
6	SPIKEL	6	.062128	.0000	334.1989	30.9862	.0000

important character (Table 2.5). This combination of discriminating characters is only partly similar to the combination of (numeric) characters used in the traditional classification of <u>Xanthorrhoea</u> e.g. by Bedford (1986 a). In that classification trunk height is important, but is treated with care as it changes with age (in those species with trunks), and spike diameter is recorded but little used as a distinguishing character.

The use of a different set of diagnostic characters to that used in traditional classification could be expected to give the result that groups well defined on this set of characters would not be comparable to groups proposed elsewhere in the genus by traditional classification. This does not appear to be the case, since, as mentioned above, the groups contain elements of described taxa and of other consistent groupings. This suggests that the order of selection of characters, and their nominal discriminating value, as indicated by differences in changes in Rao's V, have less importance than the actual combination of characters. The column in Table 2.5 labelled SIG[significance] supports this hypothesis as all characters are shown as being significantly different between groups. The fact that there are differences between the characters used in this numerical classification and a traditional classification may, in any case, be beneficial as traditional taxonomic methods have failed to establish clear groupings in this complex.

The order and combination of characters chosen by DISCRIMINANT is different to the order chosen by CRAMER, most probably reflecting the different algorithms, as CRAMER is based on the Euclidean distance

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matrix and DISCRIMINANT is based on an overall similarity measure. Also the CRAMER analyses includes both continuous numeric characters and disordered multistate characters, whereas the discriminant analysis includes only the numerics.

Classification

The discriminant classification finds that the discriminant functions derived from the above six characters correctly classify 98.04% of the 52 entities (Table 2.6). The plot of the entities against the two discriminant functions (Figure 2.3) shows that the three groups are reasonably discrete, even though GPs β and θ have considerable spread, and one member of GP θ (2) is regarded as being misclassified because it is closer to an outlying member of GP Ω (3) than it is to its own group. These results indicate that the discriminant analysis has been highly successful in identifying an adequate combination of discriminating variables, and that the TAXON 52 UPG classification's groupings are well supported by the numeric characters in the analysis. This suggests that the three groups are valid groupings of the entities.

Table 2.6 DISCRIMINANT Classification Results NO52 UPG Groups

ACTUAL GROUP		NO. OF CASES	PREDICTED GROUP MEMBERSHIP 1	2	3
GROUP	β	38	38	0	0
			100.0	0	0
GROUP	θ	9	0	8	1
			0	88.9	11.1
GROUP	Ω	4	0	0	4
			0	0	100.0

PERCENT OF GROUPED CASES CORRECTLY CLASSIFIED - 98.04

CLASSIFICATION PROCESSING SUMMARY
        52 CASES WERE PROCESSED.
        1 CASE HAD ONE MISSING DISCRIMINATING VARIABLE.
        51 CASES WERE USED FOR PRINTED OUTPUT.

Figure 2.3 DISCRIMINANT Classification plot TAXON NQ52 UPG groups

SYMBOLS USED IN PLOTS   SYMBOL   GROUP   LABEL

                          ------   -----   ---------------------
                     ß   ß
                     θ   θ
                     Ω   Ω
                     ✳   GROUP CENTROIDS

                     CANONICAL DISCRIMINANT FUNCTION 1
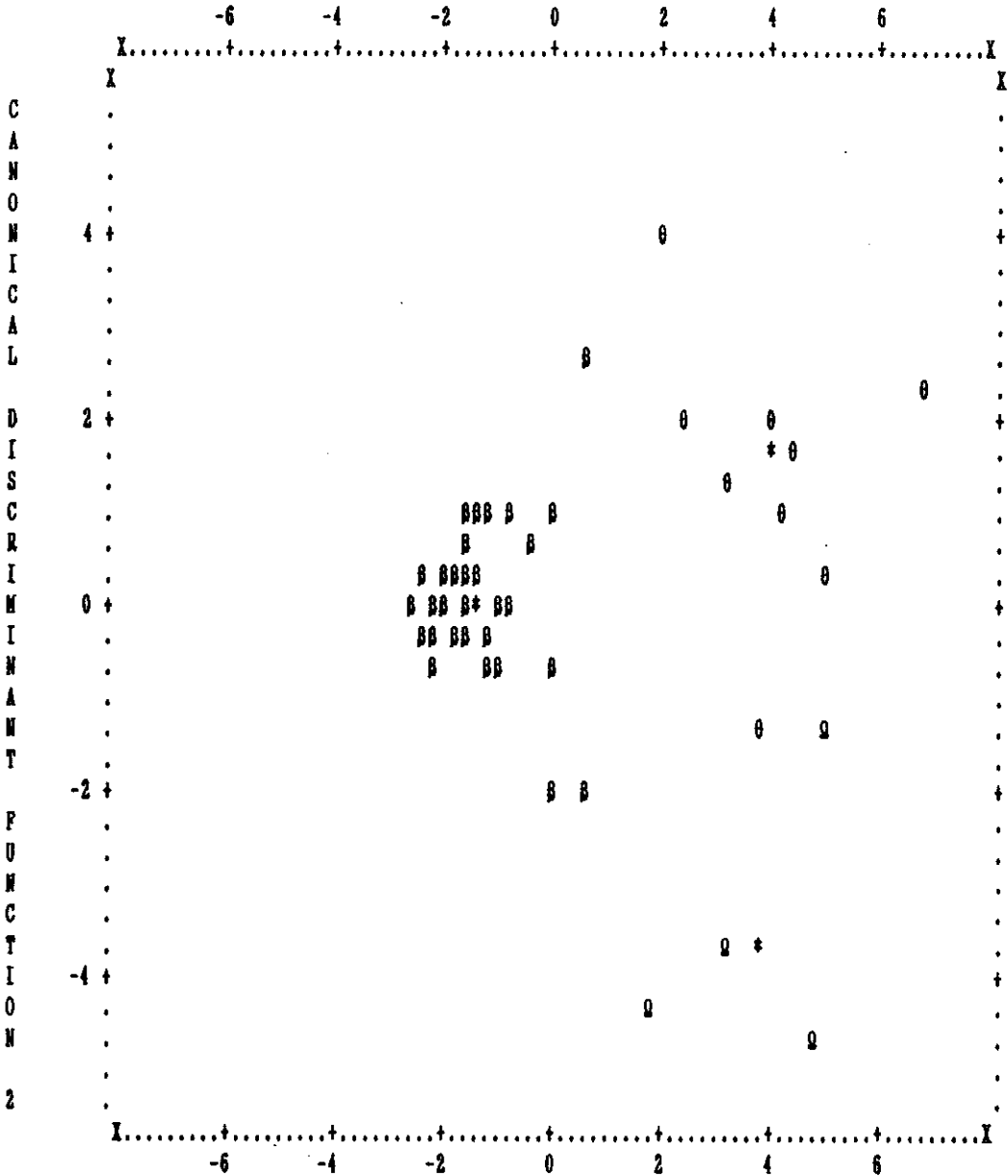
2.2.2.1 Northern Queensland data set (52 entities),

TAXON SAHN Classification, ISS Clustering strategy

This classification produces three groups by the 5.0 dissimilarity level (Figure 2.4, SAHN dissimilarity levels are given in Appendix 2.4):

GP β WITH   25 MEMBERS - 1-3 5-12 15-19 32 33 37 44-46 48 49 52

GP θ WITH   11 MEMBERS - 13 14 22 27-28 38-40 43 47 50

GP Ω WITH   16 MEMBERS - 4 20 21 23-26 29-31 34-36 41 42 51

The three groups contain sets of individuals in common with the UPG clustering technique, but GPs θ and Ω have been enlarged at the expense of GP β. This, and the fact that the levels of dissimilarity in the dendrogram are considerably higher than in the UPG analysis, are characteristic of the this algorithm, that is they are probably a by-product of the "group size dependency" characteristic described by Clifford and Stephenson (1975).

Dissimilarity levels are: There are three distinct groups at the 4.7452 level; the first two groups to join together are GP β and GP Ω which join at the 8.8490 level; GP θ joins with those groups at the overall dissimilarity level of 10.3645.

Figure 2.4 ISS Classification Dendrogram, Northern Queensland
data set (52 entities).

GP β shown β

GP θ shown θ

GP Ω shown Ω

Figure 2.4.
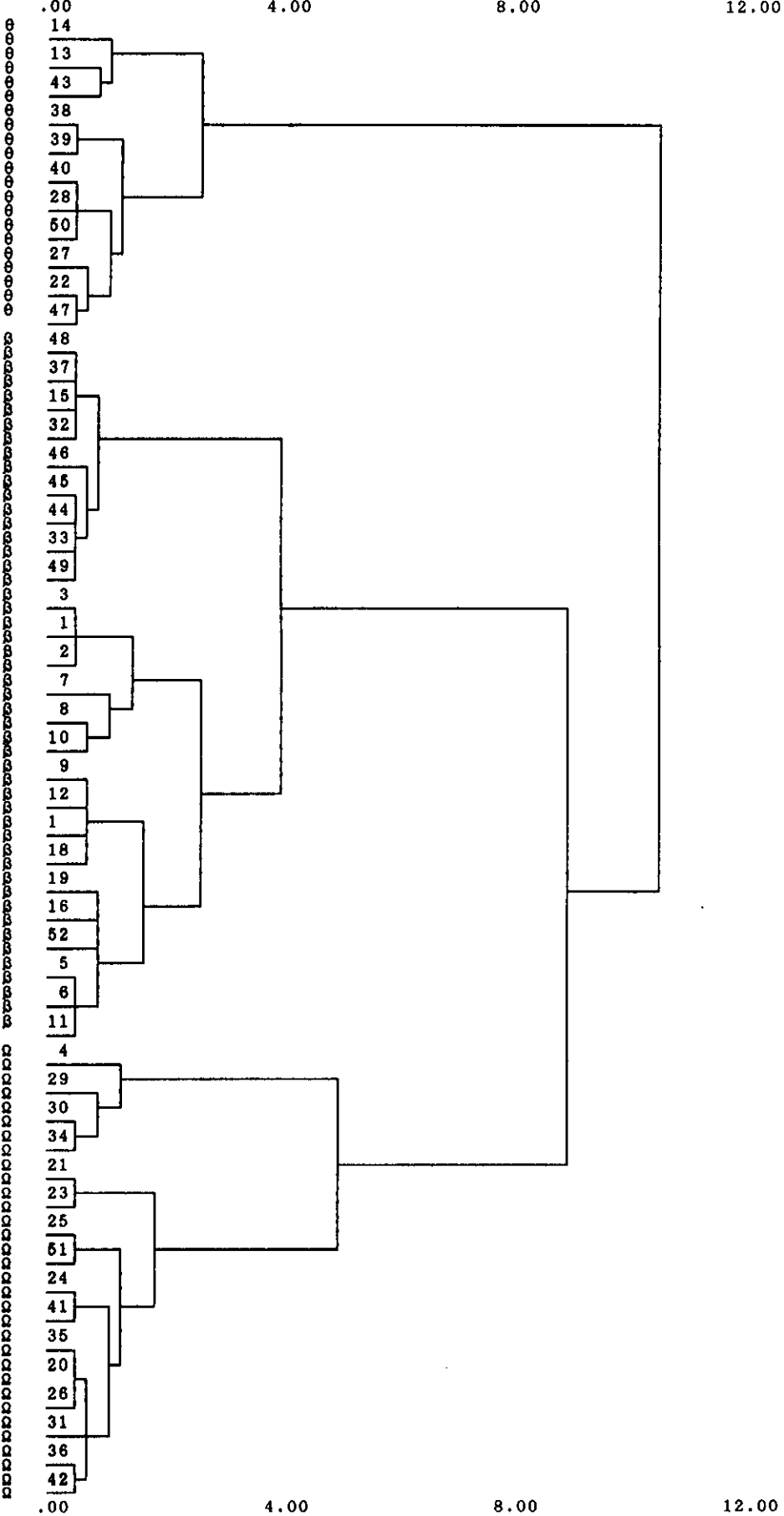
GSTAT, ISS Classification groups, Northern Queensland data set (52 entities)

The statistics for the three groups indicate that although GP β has slightly reduced included variation the other two groups have significantly increased variability (Table 2.7). Overall the three groups are now unsatisfactorily variable relative to satisfactorily circumscribed taxa elsewhere in the genus (e.g. in Bedford, 1986 a).

GP β

Variable in most characters, though more uniform than the UPG grouping.

Disordered multistate characters: Leaf shape is less variable than in the UPG analyses. However 3 of the 4 possible shapes are still represented, though the majority of the members are the one state (quadrate rhombic). Cluster bract characters are also less variable, c.f. the UPG analyses.

Numeric characters: A very similar situation to the UPG grouping, with almost all characters variable, wide ranges and high standard deviations.

GP θ

More variable than in the UPG analysis, but a more uniform group than GP β above.

Table 2.7 GSTAT, ISS Classification groups, Northern Queensland data set (52 entities).

Table 2.7

<pre>
                GP 8 WITH 25 MEMBERS
                ****
</pre>

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	19	0	4	2	
2 LEAF COLOUR	16	9	0			
3 CLUSTER BRACTS	0	9	7	9	0	0
4 JUV. CLUSTER BR.	11	7	6	1		
5 BRACT COLOUR	19	0	6	0	0	0
6 SCAPE COLOUR	23	2	0			
7 BRACT SHAPE	1	0	24	0		
8 BR. INDUMENTUM	0	0	0	0	25	0

NUMERIC ATTRIBUTES (PNUM)	NO. MIS	NO. =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	25	130.0	130.0	275.0	188.4	188.4	41.85	145.0
2 SCAPE LENGTH	0	0	25	59.00	59.00	208.0	138.7	138.7	45.40	149.0
3 SCAPE DIAMETER	0	0	25	60.00	60.00	130.0	97.60	97.60	21.46	70.00
4 SPIKE LENGTH	0	0	25	5.000	5.000	80.00	31.64	31.64	20.74	75.00
5 SPIKE DIAMETER	1	0	24	17.00	17.00	28.00	22.46	22.46	2.978	11.00
6 SP/SC RATIO	0	0	25	9.000	9.000	51.00	26.32	26.32	11.47	42.00
7 TRUNK HEIGHT	0	5	20	0.	2.000	40.00	13.16	16.45	12.65	40.00

<pre>
                GP 0 WITH 11 MEMBERS
                ****
</pre>

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	11	0	0	0	
2 LEAF COLOUR	2	9	0			
3 CLUSTER BRACTS	0	0	0	2	6	3
4 JUV. CLUSTER BR.	2	0	2	7		
5 BRACT COLOUR	6	0	5	0	0	0
6 SCAPE COLOUR	7	4	0			
7 BRACT SHAPE	0	0	11	0		
8 BR. INDUMENTUM	0	0	0	0	11	0

NUMERIC ATTRIBUTES (PNUM)	NO. MIS	NO. =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	11	130.0	130.0	240.0	182.7	182.7	36.43	110.0
2 SCAPE LENGTH	0	0	11	60.00	60.00	145.0	96.55	96.55	22.30	85.00
3 SCAPE DIAMETER	0	0	11	70.00	70.00	200.0	142.7	142.7	40.52	130.0
4 SPIKE LENGTH	0	0	11	21.00	21.00	140.0	81.64	81.64	34.57	119.0
5 SPIKE DIAMETER	0	0	11	22.00	22.00	35.00	28.27	28.27	4.292	13.00
6 SP/SC RATIO	0	0	11	28.00	28.00	150.0	84.64	84.64	32.31	122.0
7 TRUNK HEIGHT	0	1	10	0.	10.00	100.0	70.91	78.00	37.00	100.0

<pre>
                GP Q WITH 16 MEMBERS
                ****
</pre>

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	0	16	0	0	
2 LEAF COLOUR	1	15	0			
3 CLUSTER BRACTS	0	13	0	3	0	0
4 JUV. CLUSTER BR.	13	0	3	0		
5 BRACT COLOUR	11	0	5	0	0	0
6 SCAPE COLOUR	6	10	0			
7 BRACT SHAPE	0	0	16	0		
8 BR. INDUMENTUM	0	0	0	0	16	0

NUMERIC ATTRIBUTES (PNUM)	NO. MIS	NO. =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	16	160.0	160.0	450.0	274.1	274.1	81.10	290.0
2 SCAPE LENGTH	0	0	16	77.00	77.00	296.0	191.3	191.3	68.07	219.0
3 SCAPE DIAMETER	0	0	16	60.00	60.00	200.0	111.9	111.9	39.02	140.0
4 SPIKE LENGTH	0	0	16	23.00	23.00	134.0	68.00	68.00	33.69	111.0
5 SPIKE DIAMETER	0	0	16	16.00	16.00	37.00	24.19	24.19	5.890	21.00
6 SP/SC RATIO	0	0	16	20.00	20.00	94.00	37.50	37.50	20.07	74.00
7 TRUNK HEIGHT	0	5	11	0.	5.000	120.0	27.50	40.00	39.45	120.0

<pre>
              STATISTICS FOR ENTIRE DATA
              ****
</pre>

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	30	16	4	2	
2 LEAF COLOUR	19	33	0			
3 CLUSTER BRACTS	0	22	7	14	6	3
4 JUV. CLUSTER BR.	26	7	11	8		
5 BRACT COLOUR	36	0	16	0	0	0
6 SCAPE COLOUR	36	16	0			
7 BRACT SHAPE	1	0	51	0		
8 BR. INDUMENTUM	0	0	0	0	52	0

NUMERIC ATTRIBUTES (PNUM)	NO. MIS	NO. =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	52	130.0	130.0	450.0	213.6	213.6	68.43	320.0
2 SCAPE LENGTH	0	0	52	59.00	59.00	296.0	145.9	145.9	60.22	237.0
3 SCAPE DIAMETER	0	0	52	60.00	60.00	200.0	111.5	111.5	35.84	140.0
4 SPIKE LENGTH	0	0	52	5.000	5.000	140.0	56.29	56.29	33.48	135.0
5 SPIKE DIAMETER	1	0	51	16.00	16.00	37.00	24.25	24.25	4.824	21.00
6 SP/SC RATIO	0	0	52	9.000	9.000	150.0	42.10	42.10	30.07	141.0
7 TRUNK HEIGHT	0	11	41	0.	2.000	120.0	29.79	37.78	36.10	120.0

<u>Disordered multistate characters</u>: All characters are uniform or with consistent combinations of characters.

<u>Numeric characters</u>: The addition of two members to the UPG grouping has considerably extended the range and standard deviation figures for all characters except leaf width and scape length.

<u>GP Ω</u>

The greatly increased membership of this group (from 4 to 16 members) relative to the UPG grouping has caused a large and taxonomically significant increase in the included variation.

<u>Disordered multistate characters</u>: Uniform except for the cluster bract characters which vary from bracts absent to present at the base of the spike only. such a combination has been recorded as valid in some taxa elsewhere in the genus, but would not be valid for certain taxa.

<u>Numeric characters</u>: All characters are now significantly more variable than in the UPG classification, mainly due to lower minimum figures for most characters. This has caused large increases in the range and standard deviation figures.

GCOM, ISS Classification groups, Northern Queensland data set (52 entities)

The characters best separating GP θ from GPs β + Ω combined are spike length : scape length ratio, trunk height, cluster bracts and leaf

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shape (Table 2.8). GPs β and Ω are separated by leaf shape alone.
GP θ has spike length : scape length ratio much closer to 1:1 than do
GPs β + Ω combined (.84 c.f. .30), taller trunk (approximate figures
71 cm and 19 cm respectively), much more prominent cluster bracts and
uniformly quadrate-rhombic leaf shape compared to the range of leaf
shapes seen in GPs β + Ω combined. GP Ω is uniform in having narrowly
quadrate-rhombic leaf shape whereas GP β includes members with all
leaf shapes except narrowly quadrate-rhombic.

CRAMER List of characters in order of their ability to distinguish
between groups (Table 2.9):

1/. Spike length : scape length ratio, Cramer value .7577

2/. Leaf shape, Cramer value .7376

3/. Prominence of cluster bracts, Cramer value .7152

4/. Trunk height, Cramer value .6205

5/. Prominence of juvenile cluster bracts, Cramer value .6068

The least important character listed, prominence of juvenile cluster
bracts, shows that the GP β contains variation in this character in
excess of that accepted elsewhere in the genus by Bedford (loc. cit.).

2.2.2.2 DISCRIMINANT Analysis and classification, TAXON ISS
Classification groups, Northern Queensland data set (52 entities).

Analysis

Five characters were selected before the addition to Rao's V became
non significant (Table 2.10). That is, the analysis selected the

Table 2.8 GCOM, ISS Classification groups, Northern Queensland data

set (52 entities).

```
****    COMPARISON NO.  1     (TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 8.6877)
****    GROUP A = GP  θ
****    GROUP B = GP  β + GP  Ω
```

		GROUP A 11 MEMBERS		GROUP B 41 MEMBERS		CONTRIBUTION			
ATTRIBUTE (STATE)	NAME	ATTRIBUTE NO. MEAN	PRESENT!	ATTRIBUTE NO. MEAN	PRESENT!	% !	% !(CUM)!	ACTUAL VALUE	!
FNUM 6	SP/SC RATIO	84.636	11	30.683	41	21	21	1.86	
FNUM 7	TRUNK HEIGHT	70.909	11	18.756	41	14	35	1.21	
DMUL 3	CLUSTER BRACTS		11		41	13	48	1.11	
ST. 1	ABSENT	.000		.537					
ST. 2	SHORTLY ACUTE	.000		.171					
ST. 3	BASE OF SPIKE	.182		.293					
ST. 4	BASAL 10 CM	.545		.000					
ST. 5	100% SPIKE	.273		.000					
DMUL 1	LEAF SHAPE		11		41	10	59	.907	
ST. 1	QUADRATE-RHOMBIC	1.000		.463					
ST. 2	NARROWLY-Q-R	.000		.390					
ST. 3	OBTRULL>OBTRIANG	.000		.098					
ST. 4	CONCAVE	.000		.049					

```
  5 ATTRIBUTES MADE NO CONTRIBUTION.

****    COMPARISON NO.  2
****    GROUP A = GP  β
****    GROUP B = GP  Ω

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 6.9021
```

		GROUP A 25 MEMBERS		GROUP B 16 MEMBERS		CONTRIBUTION			
ATTRIBUTE (STATE)	NAME	ATTRIBUTE NO. MEAN	PRESENT!	ATTRIBUTE NO. MEAN	PRESENT!	% !	% !(CUM)!	ACTUAL VALUE	!
DMUL 1	LEAF SHAPE		25		16	53	53	3.63	
ST. 1	QUADRATE-RHOMBIC	.760		.000					
ST. 2	NARROWLY-Q-R	.000		1.000					
ST. 3	OBTRULL>OBTRIANG	.160		.000					
ST. 4	CONCAVE	.080		.000					

```
  5 ATTRIBUTES MADE NO CONTRIBUTION.
```

Table 2.9 CRAMER, ISS Classification groups, Northern Queensland data set (52 entities).

Table 2.9 CRAMER, ISS Classification groups, Northern Queensland data set (52 entities).

MEAN CRAMER VALUE FOR 15 ATTRIBUTES = .6123   SCALED CRAMER VALUE FOR 3 GROUPS = .3535

NO ATTRIBUTES ARE MISSING IN ALL GROUPS

ATTRIBUTES DMUL 2 (LEAF COLOUR), DMUL 5 (BRACT COLOUR), DMUL 6 (SCAPE COLOUR), DMUL 7 (BRACT SHAPE),
DMUL 8 (BR. INDUMENTUM) (WHERE PRESENT) ARE THE SAME IN ALL GROUPS

FNUM 6 (SP/SC RATIO)
****
     CRAMER VALUE = .7577

| | | | | | | | | F |
GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	STATISTIC
GP θ	11	11	84.64	BETWEEN GROUPS	.2647E+05	2	.1323E+05	33.02
GP β	25	25	26.32	WITHIN GROUPS	.1964E+05	49	400.8	
GP Ω	16	16	37.50	TOTAL	.4610E+05	51		

                    GRAND MEAN = 42.10

DMUL 1 (LEAF SHAPE)
****

     CRAMER VALUE = .7376
     CHI-SQ = 56.58, D.F. = 6

| | | | NO. OF MEMBERS IN EACH STATE | | | |
GROUP NAME	NO. MEMBERS	NO. PRESENT	1	2	3	4
GP θ	11	11	11	0	0	0
GP β	25	25	19	0	4	2
GP Ω	16	16	0	16	0	0
		52	30	16	4	2

DMUL 3 (CLUSTER BRACTS)
****
     CRAMER VALUE = .7152
     CHI-SQ = 53.20, D.F. = 8

| | | | NO. OF MEMBERS IN EACH STATE | | | | |
GROUP NAME	NO. MEMBERS	NO. PRESENT	1	2	3	4	5
GP θ	11	11	0	0	2	6	3
GP β	25	25	9	7	9	0	0
GP Ω	16	16	13	0	3	0	0
		52	22	7	14	6	3

FNUM 7 (TRUNK HEIGHT)
****

     CRAMER VALUE = .6205

                                              CAUTION: F TEST INVALID

| | | | | | | | | F |
GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	STATISTIC
GP θ	11	11	70.91	BETWEEN GROUPS	.2560E+05	2	.1280E+05	15.34
GP β	25	25	13.16	WITHIN GROUPS	.4088E+05	49	834.3	
GP Ω	16	16	27.50	TOTAL	.6648E+05	51		

                    GRAND MEAN = 29.79

DMUL 4 (JUV. CLUSTER BR.)
****

     CRAMER VALUE = .6068
     CHI-SQ = 19.15, D.F. = 4

| | | | NO. OF MEMBERS IN EACH STATE | | |
GROUP NAME	NO. MEMBERS	NO. PRESENT	1	2	3
GP θ	11	9	0	2	7
GP β	25	14	7	6	1
GP Ω	16	3	0	3	0
		26	7	11	8

Table 2.10 DISCRIMINANT Analysis TAXON NQ52 ISS Groups

SUMMARY TABLE

STEP	ACTION ENTERED REMOVED	VARS IN	WILKS LAMBDA	SIG.	RAO*S V	SIG.	CHANGE IN V	SIG.	LABEL
1	SPSCRAT	1	.429157	.0000	63.8472	.0000	63.8472	.0000	
2	LEAFW	2	.277488	.0000	90.1161	.0000	26.2689	.0000	
3	SCAPEL	3	.258498	.0000	97.3661	.0000	7.2500	.0266	
4	SCAPED	4	.219585	.0000	111.2777	.0000	13.9117	.0010	
5	TRUNKHT	5	.208029	.0000	117.8111	.0000	6.5333	.0381	

linear combination of the five characters listed below as being able to discriminate between the groups proposed by the TAXON NQ52 ISS classification. This implies that the two numeric characters not used in the formation of the discriminant functions, spike length and spike diameter, either contain no information or information contra indicative to the ISS groupings.

The order of selection in the "stepwise" analysis was:

1/.Spike length : scape length ratio

2/. Leaf width

3/. Scape length

4/. Scape diameter

5/. Trunk height

Spike length : scape length ratio was by far the most important discriminator between the groups, with a change in Rao's V nearly 2.5 times that of the next most important character (Table 2.10). As also noted for the UPG analyses, with the same probable explanation, the order and combination of characters selected here is different to the order and combination of characters selected by CRAMER.

This combination of characters is very similar to the combination of numeric characters used in the traditional classification of Xanthorrhoea, e.g. by Bedford (1986 a). This would lead one to expect that groups well discriminated on such a combination of characters would be of similar level to groups established elsewhere in the genus by such a traditional classification. However in this case no valid comparison can be made as the classification (below) shows that the

groups here are incompletely discriminated by this character combination.

Classification

The discriminant classification found that the discriminant functions derived from the above five characters correctly classify 84.62% of the 52 entities (Table 2.11, Figure 2.5). Whilst a high figure this is low relative to the situation in the UPG classification. This indicates that either the analysis has been less efficient in identifying an adequate combination of discriminating variables (an unlikely situation), or that the ISS groupings are not fully supported by the numeric characters in the analysis. It is not possible to tell how well the groupings are supported by the disordered multistate characters not included in this technique). As the groups are not well supported by the set of characters it is not possible to infer any similarity between them and groupings from traditional taxonomic classification as proposed above.

Table 2.11 DISCRIMINANT Classification Results TAXON NQ52 ISS Groups

ACTUAL GROUP		NO. OF CASES	PREDICTED GROUP MEMBERSHIP		
			1	2	3
GROUP	β	25	21	0	4
			84.0	0	16.0
GROUP	θ	11	1	10	0
			9.1	90.9	0
GROUP	Ω	16	1	2	13
			6.3	12.5	81.3

PERCENT OF GROUPED CASES CORRECTLY CLASSIFIED - 84.62

CLASSIFICATION PROCESSING SUMMARY

   52 CASES WERE PROCESSED.

   52 CASES WERE USED FOR PRINTED OUTPUT.

Figure 2.5 DISCRIMINANT Classification plot TAXON NQ52 ISS Groups

```
SYMBOLS USED IN PLOTS

SYMBOL  GROUP  LABEL
------  -----  --------------------
  β        β
  θ        θ
  Ω        Ω
  *              GROUP CENTROIDS
```


CANONICAL DISCRIMINANT FUNCTION 1
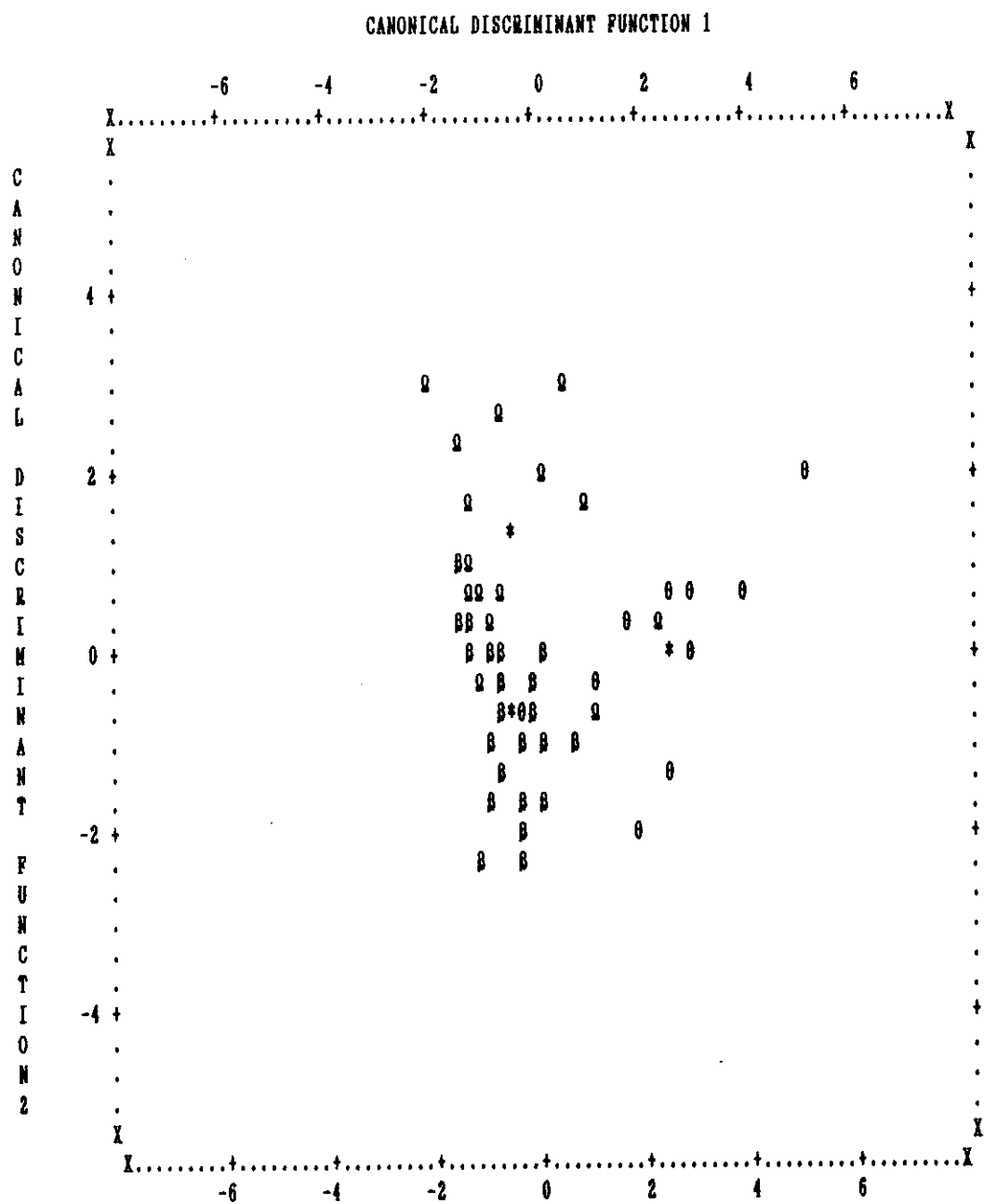
2.2.3 PCOA Ordination, Northern Queensland data set (52 entities).

The first three vectors represent 70% of the dissimilarity in the matrix (35%, 27% and 8% respectively). Appendix 2.5 shows the vector scores, and Figures 2.6.1, 2.6.2 and 2.6.3 give the plots of the entities against the first three vectors, with groupings as produced by the classifications.

The plot of the entities against the first and second vectors (Figure 2.6.1) is the only plot that aids in the interpretation of the data. It shows that the entities are distributed in a "horseshoe" (Kendall 1971) or an arched curve (Gauch 1982).

PCOA ordination relative to the NQ52 UPG classification groups.

The solid lines drawn on the plot (Figure 2.6.1) show the pattern and the relative distribution of the entities as classified by the NQ 52 UPG classification:

GP θ occupies the top end of the curved distribution of entities; GP β occupies the middle ground and slightly overlaps GP Ω, which falls at the bottom of the distribution.

None of the individual vectors provide a clear view of the groups, though the primary vector does show a tendency for GP β to occur towards the negative end of the vector and for GPs Ω and θ intermixed to occur towards the positive end of the vector, but there is not a clear separation between the groups. Vector two provides little

Figure 2.6.1 PCQA Ordination, Northern Queensland data set (52 entities), Vectors 1 and 2

Key: _____ UPG Groups; – – – – ISS Groups

Figure 2.6.1 Vectors 1 and 2
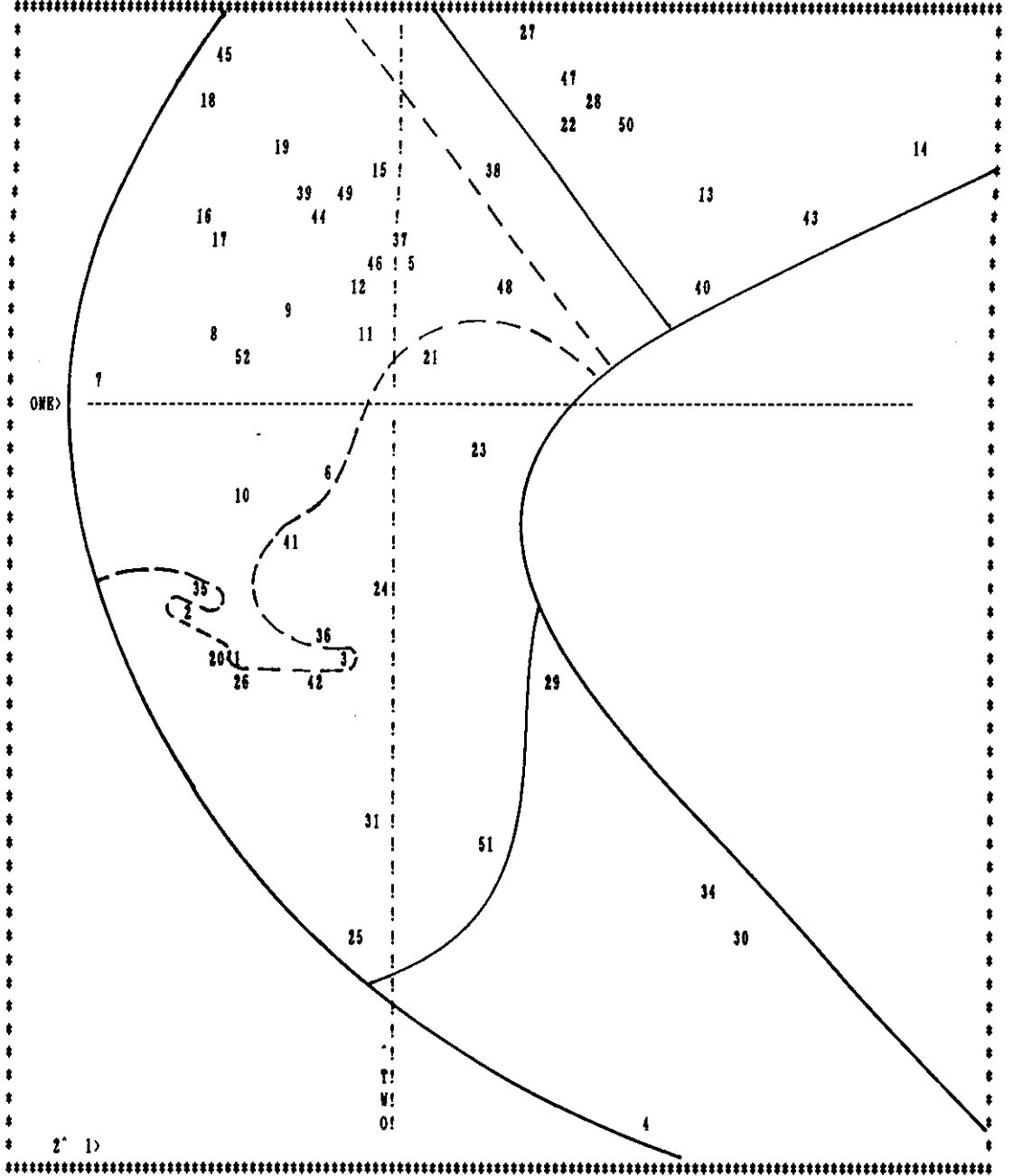
Figure 2.6.2 PCOA Ordination, Northern Queensland data set
(52 entities), Vectors 1 and 3

Taxa not separated by either classification,

therefore not demarcated on plot.

```
2.6.2   Vectors 1 and 3
*****************************************************************************************************
*                                                                                                 *
*                                                                                                 *
*                                                                                                 *
*                                                                                                 *
*                                                                                                 *
*                                         !                                                       *
*                             41          !                                                       *
*                                       24!                                                        *
*                                         !                                                       *
*                                         !                                                       *
*                                         !                                                       *
*                                49       ! 21                                                    *
*                             44        37     23                                                 *
*                     45        33      32                                                        *
*                  35                   !              48                                         *
*                   20 26               !                                                        *
*                                       !                       47                               *
*                        426            !       51      29                                       *
*                             2515      !                                                        *
*                        39        46   !              50      34        43                       *
* ONE>    7-------------------------------------27----------------------30-------------------     *
*                        52             !       38                                               *
*                                       !                                                        *
*                                       !             28                                         *
*                                       ! 5                                                      *
*               168                     !                       13                               *
*              2    1        6    11     !                               14                       *
*              18                        !                      40                               *
*                            3           !                                                       *
*                     19                 !                                                       *
*                17                      !                                                       *
*                    9        12         !                      4                                *
*                10                      !                                                        *
*                                        T                                                       *
*                                        H                                                       *
*                                        R                                                       *
*        3^  1>                          E                                                       *
*                                        E                                                       *
*****************************************************************************************************
```

Figure 2.6.3 PCOA Ordination, Northern Queensland data set
(52 entities), Vectors 2 and 3.

Key: - - - - - separates ISS group Ω from the other two ISS groups;
     UPG groups not separated.

```
‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡
‡                                                                                    ‡
‡                                                                                    ‡
‡                                                                                    ‡
‡                                                                                    ‡
‡                                                                                    ‡
‡                                                      !                             ‡
‡                                          41          !                             ‡
‡                                          24          !                             ‡
‡                 Group Ω                              !                             ‡
‡                                                      !                             ‡
‡                                                      !            /                ‡
‡                                                      !           /                 ‡
‡                                                      !  21      /      49          ‡
‡                                                  23  !        /    37 44           ‡
‡                                                      !       /    32  33        45 ‡
‡                                       35             !      /   48                 ‡
‡                                260                   !/                            ‡
‡                                                     /!                 22 47       ‡
‡                      51            42 36            / !                            ‡
‡                 25                                 /  !            15              ‡
‡                34    31                           /   !       46  4339 50          ‡
‡ TWO) ------------- 30----------------------------/---!------------------------ 27  ‡
‡                                                 /    !  52            38           ‡
‡                                                /     !                             ‡
‡                                               /      !                   28        ‡
‡                                              /       !         5   13              ‡
‡                                             /        !  8         16    14         ‡
‡                                    1 2     /      6  !  11   40                    ‡
‡                                           /          !                     18      ‡
‡                                    3     /           !  Groups β and θ mixed       ‡
‡                                         /            !               19            ‡
‡                                        /             !           17                ‡
‡               4                       /              !      9  12                  ‡
‡                                      /               !                             ‡
‡                                     /            10                                ‡
‡                                    /                 T                             ‡
‡                                   /                  H                             ‡
‡                                                      R                             ‡
‡               3^  2)                                 E                             ‡
‡                                                      E                             ‡
‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡
```
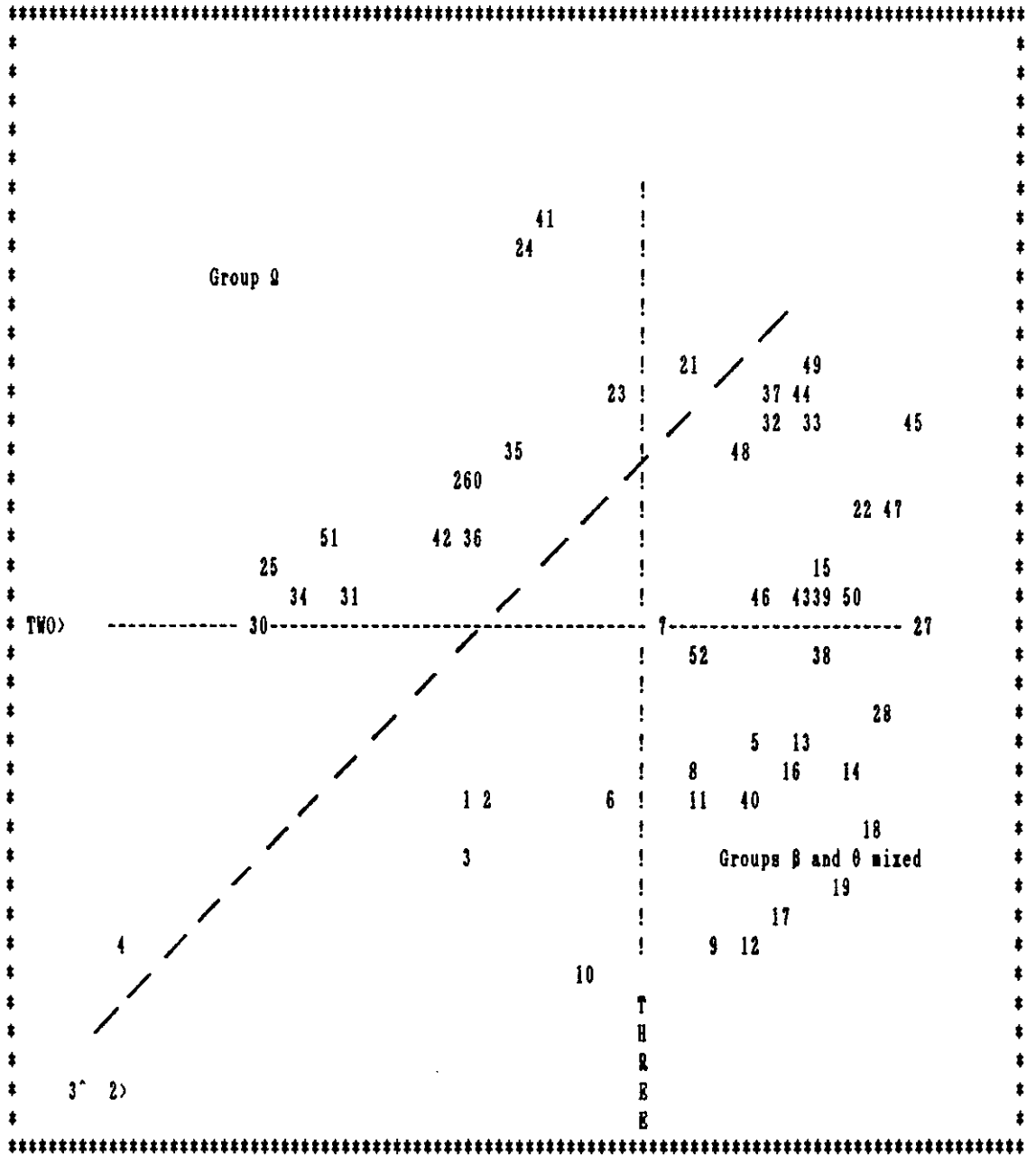
information when viewed in isolation. Vector three does not assist in the interpretation of the data.

The ordination plots of the first three vectors do not seem to have a clear message, or provide much information about the data set. They do not show random or continuous distribution of individuals or exceptionally clear-cut groups. Whilst none of the plots indisputably corroborates the groups proposed by the UPG classification it can be argued that there is some degree of corroboration in that the individuals classified together into groups tend to be placed together in the ordination plot of the first two vectors. In addition at least GP θ is separate, and GPs β and Ω may be separable in the plot of the first and second vectors.

PCOA Ordination relative to the NQ52 ISS classification groups

None of the plots (Figures 2.6.1-2.6.3) really corroborate the groups proposed by the NQ 52 ISS classification, although plot 1/2 (Figure 2.6.1) could be interpreted as showing GP θ as separate to the other groups. The plot of the entities against the first and second vectors shows some structure in the data. The dotted lines drawn on the plot show the pattern and the relative distribution of the groups produced by the ISS classification:

GP θ occupies the top end of the curved distribution of entities, and could be argued to be separate from the remainder of the entities; GP β occupies the middle ground with considerable overlap with GP Ω, which falls at the bottom of the distribution.

The plot of the entities against the second and third vectors can be divided with a diagonal line which separates GP Ω from the other two groups, which are intermixed. However this is a fairly artificial separation and cannot be interpreted as strong support for the separateness of the groups.

None of the individual vectors provide a clear view of the groups. The primary vector does not show any clear separation between the groups. Vectors two and three provide little information when viewed in isolation.

Diagnostic: BACRIV

BACRIV indicates that size factors are the most highly correlated with the primary vector (scape diameter, spike length, spike diameter and trunk height) although some shape factors are only slightly less correlated with it (spike length : scape length ratio and prominence of cluster bracts) (Table 2.12). For the second vector BACRIV indicates that a combination of size and shape factors are the most highly correlated (leaf width, leaf shape, scape length and prominence of cluster bracts).

Table 2.12 BACRIV for PCOA Ordination, Northern Queensland data set (52 entities).

Table 2.12 BACRIV, PCOA Ordination, Northern Queensland data set (52 entities).

CORRELATIONS FOR VECTOR 1

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	NO	STATE NAME
SCAPE DIAMETER	FNUM 3	.9116	52	--	----
SPIKE LENGTH	FNUM 4	.9004	52		
SPIKE DIAMETER	FNUM 5	.8569	51		
TRUNK HEIGHT	FNUM 7	.8229	52		
SP/SC RATIO	FNUM 6	.8127	52		
JUV. CLUSTER BR.	DMUL 4	-.5726	26	1	ABSENT
JUV. CLUSTER BR.	DMUL 4	.4144	26	3	LINEAR-TRIANG
CLUSTER BRACTS	DMUL 3	.3956	52	4	BASAL 10 CM
CLUSTER BRACTS	DMUL 3	.3759	52	5	100% SPIKE
CLUSTER BRACTS	DMUL 3	-.3212	52	2	SHORTLY ACUTE
LEAF SHAPE	DMUL 1	-.2738	52	4	CONCAVE
LEAF SHAPE	DMUL 1	-.2373	52	3	OBTRULL>OBTRIANG
LEAF WIDTH	FNUM 1	.2245	52		

23 ITEMS NOT PRINTED

CORRELATIONS FOR VECTOR 2

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	NO	STATE NAME
LEAF WIDTH	FNUM 1	-.8654	52	--	----
LEAF SHAPE	DMUL 1	.8376	52	1	QUADRATE-RHOMBIC
SCAPE LENGTH	FNUM 2	-.8219	52		
LEAF SHAPE	DMUL 1	-.7816	52	2	NARROWLY-Q-R
CLUSTER BRACTS	DMUL 3	-.7379	52	1	ABSENT
JUV. CLUSTER BR.	DMUL 4	.3836	26	3	LINEAR-TRIANG
SP/SC RATIO	FNUM 6	.3416	52		
CLUSTER BRACTS	DMUL 3	.3307	52	3	BASE OF SPIKE
JUV. CLUSTER BR.	DMUL 4	-.3300	26	2	SHORTLY ACUTE
CLUSTER BRACTS	DMUL 3	.3112	52	4	BASAL 10 CM
CLUSTER BRACTS	DMUL 3	.2345	52	5	100% SPIKE
LEAF SHAPE	DMUL 1	-.2190	52	3	OBTRULL>OBTRIANG
SPIKE LENGTH	FNUM 4	-.2151	52		

23 ITEMS NOT PRINTED

CORRELATIONS FOR VECTOR 3

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	NO	STATE NAME
JUV. CLUSTER BR.	DMUL 4	-.7445	26	1	ABSENT
JUV. CLUSTER BR.	DMUL 4	.7137	26	2	SHORTLY ACUTE
CLUSTER BRACTS	DMUL 3	.6506	52	3	BASE OF SPIKE
CLUSTER BRACTS	DMUL 3	-.5677	52	2	SHORTLY ACUTE
LEAF SHAPE	DMUL 1	.4115	52	2	NARROWLY-Q-R
LEAF SHAPE	DMUL 1	-.3646	52	3	OBTRULL>OBTRIANG
SPIKE DIAMETER	FNUM 5	-.2058	51		
SCAPE DIAMETER	FNUM 3	-.1910	52		
LEAF SHAPE	DMUL 1	-.1595	52	1	QUADRATE-RHOMBIC
LEAF WIDTH	FNUM 1	-.1465	52		

26 ITEMS NOT PRINTED

2.3 North and south Queensland data set (78) entity analyses

2.3.1 TAXON SAHN Classification, UPG Clustering strategy, North and
South Queensland data set.

The dendrogram (Figure 2.7) shows three groups by the 1.0 dis-
similarity level (data set, Appendix 2.2, SAHN dissimilarity levels,
Appendix 2.6)

GP β WITH   36 MEMBERS - 1-3 5-12 15-21 23 24 26 32 33 35-39 41 42

44-46 48 49 52

GP θ WITH   13 MEMBERS - 13 14 22 27 28 40 43 47 50 57-60

GP Ω WITH   29 MEMBERS - 4 25 29-31 34 51 53-56 61-78

It can be seen that GPs β and Ω are similar in size, and that GP θ is
between half and a third their size. The groups contain sets of
individuals in common with the groups produced by both the 52 entity
analyses. The 26 new individuals (i.e. those additional to the
original Northern Queensland data (52 entities)) have been classified
into two of the three groups: Four individuals (57-60) were placed
with GP θ and the remaining 22 individuals were placed with GP Ω; GP β
received none of the new individuals.

The groupings produced by this classification have aspects in common
with both the 52 UPG and the 52 ISS classifications. GP β is almost
exactly the same as the 52 UPG GP β except that three of its members
(25, 31 and 51 were classified to GP Ω in the 52 ISS classification)
have been transferred from it. GP θ is the same as the 52 UPG GP θ
with the addition of four south-east Queensland plants (57-60). GP Ω
combines the four individuals in the 52 UPG classification GP Ω plus

Figure 2.7 UPG Classification Dendrogram, North and
South Queensland data set.

GP β shown β

GP θ shown θ

GP Ω shown Ω

Figure 2.7.
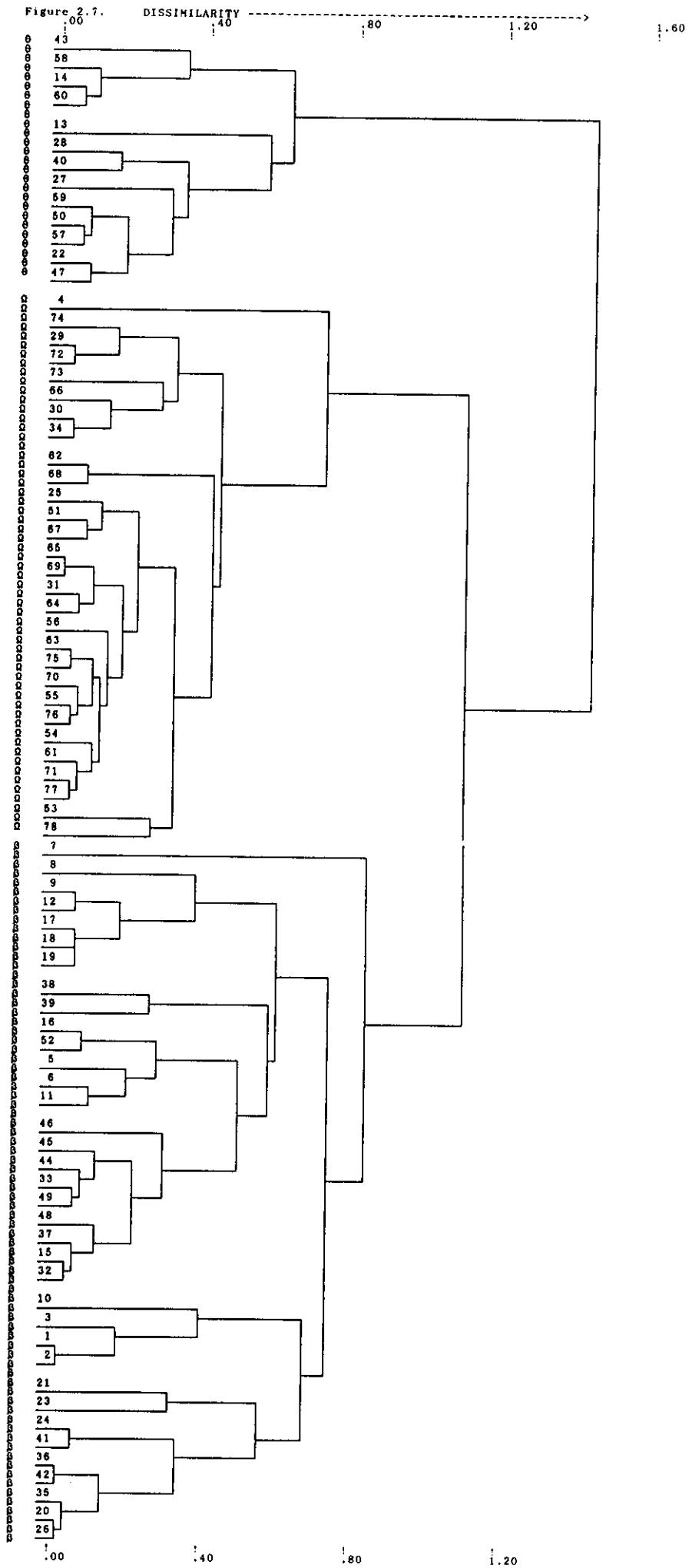
three of the twelve NQ 52 individuals added to it by the 52 ISS classification GP Ω, plus twenty two new individuals from south-east Queensland.

The levels of dissimilarity in the dendrogram are: Three distinct groups form at the .8472 level; the first two groups to join are GP β and GP Ω, which join at the 1.1001 level; GP θ then joins those groups at the overall dissimilarity level of 1.4489. It is interesting to note that these dissimilarity levels are lower than for the corresponding points in the NQ52 UPG dendrogram (Figure 2.2), even though there are twenty six additional individuals in this analysis. This must indicate that this is a more optimal resolution of the data than the earlier classification.

Diagnostic Programs

GSTAT, UPG Classification groups, North and South Queensland data set

The statistics for the three groups indicate that two groups are reasonably uniform and one is quite variable (Table 2.13).

GP β

Variable in most characters, very similar to NQ52 UPG classification result.

Disordered multistate characters: Leaf shape shows considerable variation with every possible shape represented; prominence of cluster bracts is also more variable than expected for one taxon.

Table 2.13 GSTAT, UPG Classification groups, North and South Queensland data set.

Table 2.13

GP 0 WITH 13 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	13	0	0	0	
2 LEAF COLOUR	2	11	0			
3 CLUSTER BRACTS	4	0	0	2	4	3
4 JUV. CLUSTER BR.	6	0	2	5		
5 BRACT COLOUR	6	0	7	0	0	0
6 SCAPE COLOUR	11	2	0			
7 BRACT SHAPE	0	0	13	0		
8 BR. INDUMENTUM	3	0	0	0	10	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	13	130.0	130.0	240.0	188.8	188.8	34.41	110.0
2 SCAPE LENGTH	0	0	13	60.00	60.00	145.0	94.77	94.77	21.48	85.00
3 SCAPE DIAMETER	0	0	13	120.0	120.0	200.0	156.3	156.3	31.29	80.00
4 SPIKE LENGTH	0	0	13	55.00	55.00	140.0	94.77	94.77	31.61	85.00
5 SPIKE DIAMETER	0	0	13	25.00	25.00	37.00	30.23	30.23	3.982	12.00
6 SP/SC RATIO	0	0	13	61.00	61.00	150.0	101.3	101.3	29.41	89.00
7 TRUNK HEIGHT	0	0	13	50.00	50.00	100.0	90.00	90.00	17.32	50.00

GP Q WITH 29 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	0	29	0	0	
2 LEAF COLOUR	1	28	0			
3 CLUSTER BRACTS	0	27	0	2	0	0
4 JUV. CLUSTER BR.	25	4	0	0		
5 BRACT COLOUR	23	0	2	4	0	0
6 SCAPE COLOUR	20	9	0			
7 BRACT SHAPE	0	0	29	0		
8 BR. INDUMENTUM	0	0	0	0	29	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	29	250.0	250.0	465.0	346.6	346.6	54.45	215.0
2 SCAPE LENGTH	0	0	29	152.0	152.0	296.0	227.1	227.1	42.70	144.0
3 SCAPE DIAMETER	0	0	29	90.00	90.00	210.0	136.4	136.4	26.94	120.0
4 SPIKE LENGTH	0	0	29	47.00	47.00	134.0	90.55	90.55	23.11	87.00
5 SPIKE DIAMETER	0	0	29	20.00	20.00	37.00	27.03	27.03	3.708	17.00
6 SP/SC RATIO	0	0	29	22.00	22.00	55.00	39.86	39.86	8.284	33.00
7 TRUNK HEIGHT	0	2	27	0.	10.00	150.0	45.17	48.52	37.07	150.0

GP 8 WITH 36 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	21	9	4	2	
2 LEAF COLOUR	16	20	0			
3 CLUSTER BRACTS	0	15	7	12	2	0
4 JUV. CLUSTER BR.	17	7	9	3		
5 BRACT COLOUR	25	0	11	0	0	0
6 SCAPE COLOUR	27	9	0			
7 BRACT SHAPE	1	0	35	0		
8 BR. INDUMENTUM	0	0	0	0	36	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	36	130.0	130.0	275.0	193.9	193.9	40.82	145.0
2 SCAPE LENGTH	0	0	36	59.00	59.00	210.0	139.2	139.2	46.70	151.0
3 SCAPE DIAMETER	0	0	36	60.00	60.00	130.0	95.56	95.56	21.71	70.00
4 SPIKE LENGTH	0	0	36	5.000	5.000	81.00	41.11	41.11	21.03	76.00
5 SPIKE DIAMETER	1	0	35	16.00	16.00	28.00	22.17	22.17	3.157	12.00
6 SP/SC RATIO	0	0	36	9.000	9.000	94.00	30.36	30.36	17.72	85.00
7 TRUNK HEIGHT	0	9	27	0.	2.000	40.00	11.22	14.96	11.42	40.00

STATISTICS FOR ENTIRE DATA
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	34	38	4	2	
2 LEAF COLOUR	19	59	0			
3 CLUSTER BRACTS	4	42	7	16	6	3
4 JUV. CLUSTER BR.	48	11	11	8		
5 BRACT COLOUR	54	0	20	4	0	0
6 SCAPE COLOUR	58	20	0			
7 BRACT SHAPE	1	0	77	0		
8 BR. INDUMENTUM	3	0	0	0	75	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	78	130.0	130.0	465.0	249.8	249.8	87.39	335.0
2 SCAPE LENGTH	0	0	78	59.00	59.00	296.0	164.4	164.4	65.74	237.0
3 SCAPE DIAMETER	0	0	78	60.00	60.00	210.0	120.9	120.9	35.68	150.0
4 SPIKE LENGTH	0	0	78	5.000	5.000	140.0	68.44	68.44	34.66	135.0
5 SPIKE DIAMETER	1	0	77	16.00	16.00	37.00	25.36	25.36	4.673	21.00
6 SP/SC RATIO	0	0	78	9.000	9.000	150.0	45.72	45.72	30.78	141.0
7 TRUNK HEIGHT	0	11	67	0.	2.000	150.0	36.97	43.04	37.63	150.0

Numeric characters: Almost all characters are very variable, with wide ranges and high standard deviations, the latter as high as over 1/2 of the mean in the case of spike length.

GP θ

More uniform than GP β but still with considerable variation in the numeric characters. Overall this is a reasonably consistent group.

Disordered multistate characters: All characters uniform or with consistent combinations of characters (e.g. prominent cluster bracts vary from slightly to very prominent).

Numeric characters: Reasonably uniform, except for the considerable variation in inflorescence characters: scape length, spike length and spike length : scape length ratio (in the latter two the standard deviation is almost 1/3 of the mean).

GP Ω

The most uniform of the groups.

Disordered multistate characters: All characters are uniform except for prominence of cluster bracts, which shows twenty seven members with obscure bracts and two members with cluster bracts at the base of the spike, (such a combination is recorded elsewhere in the genus by Bedford, 1986 a), and bract colour, which shows an anomalous combination of some individuals with green and some with brown bracts at time of flowering. As the majority of individuals were scored as missing this character it is difficult to form any realistic conclusions from this combination.

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<u>Numeric characters</u>: All characters are satisfactorily uniform, except for trunk height, which is extremely variable. However such variability is acceptable in a character which varies with the age of the plant (in those species that do develop trunks).

GCOM, UPG Classification groups, North and South Queensland data set (Table 2.14).

Inflorescence ratio, trunk height and leaf shape make-up 50% of the difference between GP θ and GPs $\Omega+\beta$ combined:
GP θ has spikes more or less equal in length to scapes (mean 1.01), tall trunks (mean 90 cm) and quadrate-rhombic leaf shape in T.S., whilst the average condition for GPs $\Omega + \beta$ combined is for spikes much shorter than scapes (mean .34), short trunks (mean 26 cm) and with a mixture of leaf shapes present.

The characters separating GP Ω from GP β are leaf shape and width, and to a lesser extent, spike length:
GP Ω has broad (mean width 3.46 mm) leaves with a narrowly quadrate-rhombic leaf T.S. shape and, on average, longer spikes (mean length 90 cm) than GP β, which has narrow leaves (mean width 1.93 mm), of a variety of T.S. shapes and short spikes (mean length 41 cm).

Table 2.14 GCOM, UPG Classification groups, North and South Queensland data set.

```
****    COMPARISON NO.  1
****    GROUP A = GP  θ
****    GROUP B = GP  Ω + GP  β
```

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 13.9714

ATTRIBUTE (STATE)	NAME	GROUP A 13 MEMBERS		GROUP B 65 MEMBERS		CONTRIBUTION		
		ATTRIBUTE MEAN	NO. PRESENT	ATTRIBUTE MEAN	NO. PRESENT	%	% (CUM)	ACTUAL VALUE
FNUM 6	SP/SC RATIO	101.308	13	34.600	65	24	24	3.39
FNUM 7	TRUNK HEIGHT	90.000	13	26.369	65	15	39	2.07
DMUL 1	LEAF SHAPE		13		65	14	53	2.02
ST. 1	QUADRATE-RHOMBIC	1.000		.323				
ST. 2	NARROWLY-Q-R	.000		.585				
ST. 3	OBTRULL>OBTRIANG	.000		.062				
ST. 4	CONCAVE	.000		.031				

4 ATTRIBUTES MADE NO CONTRIBUTION.

```
****    COMPARISON NO.  2
****    GROUP A = GP  Ω
****    GROUP B = GP  β
```

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 17.5887

ATTRIBUTE (STATE)	NAME	GROUP A 29 MEMBERS		GROUP B 36 MEMBERS		CONTRIBUTION		
		ATTRIBUTE MEAN	NO. PRESENT	ATTRIBUTE MEAN	NO. PRESENT	%	% (CUM)	ACTUAL VALUE
DMUL 1	LEAF SHAPE		29		36	19	19	3.41
ST. 1	QUADRATE-RHOMBIC	.000		.583				
ST. 2	NARROWLY-Q-R	1.000		.250				
ST. 3	OBTRULL>OBTRIANG	.000		.111				
ST. 4	CONCAVE	.000		.056				
FNUM 1	LEAF WIDTH	346.586	29	193.889	36	19	38	3.27
FNUM 4	SPIKE LENGTH	90.552	29	41.111	36	12	50	2.18

4 ATTRIBUTES MADE NO CONTRIBUTION.

CRAMER, UPG Classification groups, North and South Queensland data set (Table 2.15).

The list of characters in order of their ability to distinguish between groups, as indicated by CRAMER is:

1/. Leaf width, CRAMER value .8576

2/. Spike length : scape length ratio, CRAMER value .8251

3/. Scape length, CRAMER value .7749

4/. Trunk height, CRAMER value .7564

5/. Spike length, CRAMER value .7357

6/. Scape diameter, CRAMER value .6877

It is notable that only numeric characters are listed as able to distinguish between the groups set up by this classification.

2.3.1.2 DISCRIMINANT Analysis and Classification, TAXON UPG Classification groups.

Analysis

Five characters were selected for inclusion in the two discriminant functions before the addition to Rao's V became non significant (Table 2.16). Two characters were not selected (scape length and spike diameter). The order of selection of discriminating attributes in the "stepwise" analysis was:

1/. Leaf width

2/. Spike length : scape length ratio

3/. Spike length

4/. Trunk height

Table 2.15 CRAMER, UPG Classification groups, North and South Queensland data set.

Table 2.15 CRAMER, UPG Classification groups, North and South Queensland data set.

MEAN CRAMER VALUE FOR 15 ATTRIBUTES = .6948

SCALED CRAMER VALUE FOR 3 GROUPS = .4012

NO ATTRIBUTES ARE MISSING IN ALL GROUPS.

ATTRIBUTES DMUL 2 (LEAF COLOUR), DMUL 6 (SCAPE COLOUR), DMUL 7 (BRACT SHAPE), DMUL 8 (BR. INDUMENTUM)
(WHERE PRESENT) ARE THE SAME IN ALL GROUPS.

PNUM 1 (LEAF WIDTH)
*******************   CRAMER VALUE = .8576

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP θ	13	13	188.8	BETWEEN GROUPS	.4325E+06	2	.2162E+06	104.28
GP Ω	29	29	346.6	WITHIN GROUPS	.1555E+06	75	2074.	
GP β	36	36	193.9	TOTAL	.5880E+06	77		

GRAND MEAN = 249.8

PNUM 6 (SP/SC RATIO)
*******************   CRAMER VALUE = .8251

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP θ	13	13	101.3	BETWEEN GROUPS	.4966E+05	2	.2483E+05	79.96
GP Ω	29	29	39.86	WITHIN GROUPS	.2329E+05	75	310.5	
GP β	36	36	30.36	TOTAL	.7295E+05	77		

GRAND MEAN = 45.72

PNUM 2 (SCAPE LENGTH)
*******************   CRAMER VALUE = .7749

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP θ	13	13	94.77	BETWEEN GROUPS	.1998E+06	2	.9992E+05	56.37
GP Ω	29	29	227.1	WITHIN GROUPS	.1329E+06	75	1773.	
GP β	36	36	139.2	TOTAL	.3328E+06	77		

GRAND MEAN = 164.4

PNUM 7 (TRUNK HEIGHT)
*******************   CRAMER VALUE = .7564

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP θ	13	13	90.00	BETWEEN GROUPS	.6238E+05	2	.3119E+05	50.15
GP Ω	29	29	45.17	WITHIN GROUPS	.4664E+05	75	621.9	
GP β	36	36	11.22	TOTAL	.1090E+06	77		

GRAND MEAN = 36.97

PNUM 4 (SPIKE LENGTH)
*******************   CRAMER VALUE = .7357

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP θ	13	13	94.77	BETWEEN GROUPS	.5008E+05	2	.2504E+05	44.25
GP Ω	29	29	90.55	WITHIN GROUPS	.4244E+05	75	565.8	
GP β	36	36	41.11	TOTAL	.9251E+05	77		

GRAND MEAN = 68.44

PNUM 3 (SCAPE DIAMETER)
****

CRAMER VALUE = .6877

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP θ	13	13	156.3	BETWEEN GROUPS	.4637E+05	2	.2319E+05	33.65
GP Ω	29	29	136.4	WITHIN GROUPS	.5168E+05	75	689.1	
GP β	36	36	95.56	TOTAL	.9805E+05	77		

GRAND MEAN = 120.9

Table 2.16 DISCRIMINANT Analysis TAXON NQ78 UPG Groups

SUMMARY TABLE

STEP	ACTION ENTERED	REMOVED	VARS IN	WILKS LAMBDA	SIG.	RAO*S V	SIG.	CHANGE IN V	SIG.	LABEL
1	LEAFW		1	.263714	.0000	206.6072		0206.6072	0	
2	SPSCRAT		2	.086663	.0000	360.2147		0153.6075	0	
3	SPIKEL		3	.068421	.0000	437.8702	0	77.6555	.0000	
4	TRUNKHT		4	.052908	.0000	502.1601	0	64.2899	.0000	
5	SCAPED		5	.048547	.0000	530.8912	0	28.7311	.0000	

5/. Scape diameter

The figures in Table 2.16 show that leaf width and spike length : scape length ratio were the most important discriminators between groups, with a discriminating power, as measured by a change in Rao's V, of two to three times that of the next most important character.

This combination of discriminating characters is quite similar to the combination of characters used for field identification of Xanthorrhoea, and used in traditional taxonomic treatments of the genus, e.g. Bedford (1986 a). It would be expected that groups well defined by this set of characters would be comparable to groupings established by traditional taxonomic means elsewhere in the genus. As discussed in the conclusions, this does seem to be the case.

Classification

The discriminant classification (Figure 2.8, Table 2.17) found that the discriminant functions derived from the above five characters correctly classifies 98.72% of the 78 entities. This indicates that the discriminant analysis has been highly successful in identifying an adequate combination of discriminating variables, and that the TAXON 78 UPG classification's groupings are well supported by the numeric characters in the analysis. This corroborates the hypothesis that the three groups formed by the 78 UPG classification are valid groupings of the entities.

Table 2.17 DISCRIMINANT Classification TAXON NQ78 UPG Groups

ACTUAL GROUP		NO. OF CASES	PREDICTED GROUP MEMBERSHIP 1	2	3
GROUP	β	36	35	1	0
			97.2	2.8	0
GROUP	θ	13	0	13	0
			0	100.0	0
GROUP	Ω	29	0	0	29
			0	0	100.0

PERCENT OF GROUPED CASES CORRECTLY CLASSIFIED - 98.72

CLASSIFICATION PROCESSING SUMMARY   78 CASES WERE PROCESSED.

78 CASES WERE USED FOR PRINTED OUTPUT.

Figure 2.8 DISCRIMINANT Classification plot TAXON NQ78 UPG groups

SYMBOLS USED IN PLOTS   SYMBOL GROUP LABEL

    β   β
    θ   θ
    Ω   Ω
    *   GROUP CENTROIDS
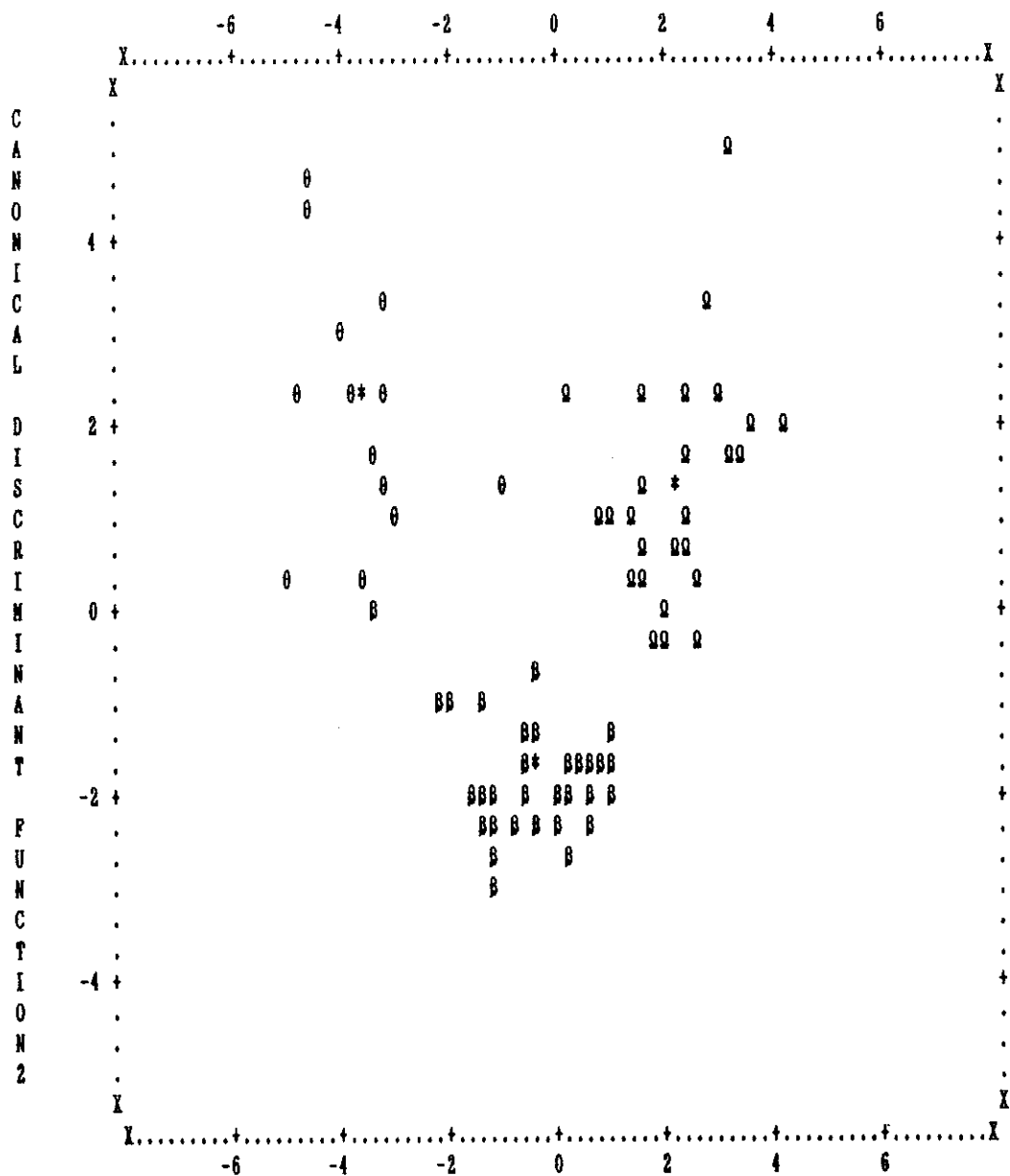
2.3.2 TAXON SAHN Classification, ISS Clustering strategy, North and South Queensland data set.

The ISS clustering algorithm produces three groups by the 5.0 dissimilarity level (Dendrogram Figure 2.9, SAHN dissimilarity figures in Appendix 2.7):

GP β WITH 38 MEMBERS – 1-3 5-12 15-21 23 24 26 32 33 35-39 41 42
                                           44-46 48 49 52 62 68

GP θ WITH 13 MEMBERS – 13 14 22 27 28 40 43 47 50 57-60

GP Ω WITH 27 MEMBERS – 4 25 29-31 34 51 53-56 61 63-67 69-78

The three groups are very similar to those produced by the 78 UPG classification, with the only change being the transfer of two individuals (no.s 62 and 68) from the 78 UPG GP Ω to GP β. GP θ is exactly the same as the 78 UPG GP θ. The levels of dissimilarity are higher than for the 78 UPG analysis, as is characteristic of the different techniques, and they are also higher than in the 52 ISS analysis, in contrast to the relationship between the relative dissimilarity levels of the NQ 52 UPG and the NQ 78 UPG analyses mentioned above. The exact dissimilarity figures are: Three discrete groups form at the 4.9827 level; the first two groups to join together are GPs β and θ which join at the 17.4474 level; GP Ω then joins with those to give an overall dissimilarity of 19.6701.

Figure 2.9 ISS Classification Dendrogram, North and

South Queensland data set.

GP β shown β

GP θ shown θ

GP Ω shown Ω

Figure 2.9.   DISSIMILARITY --------------------------------------->
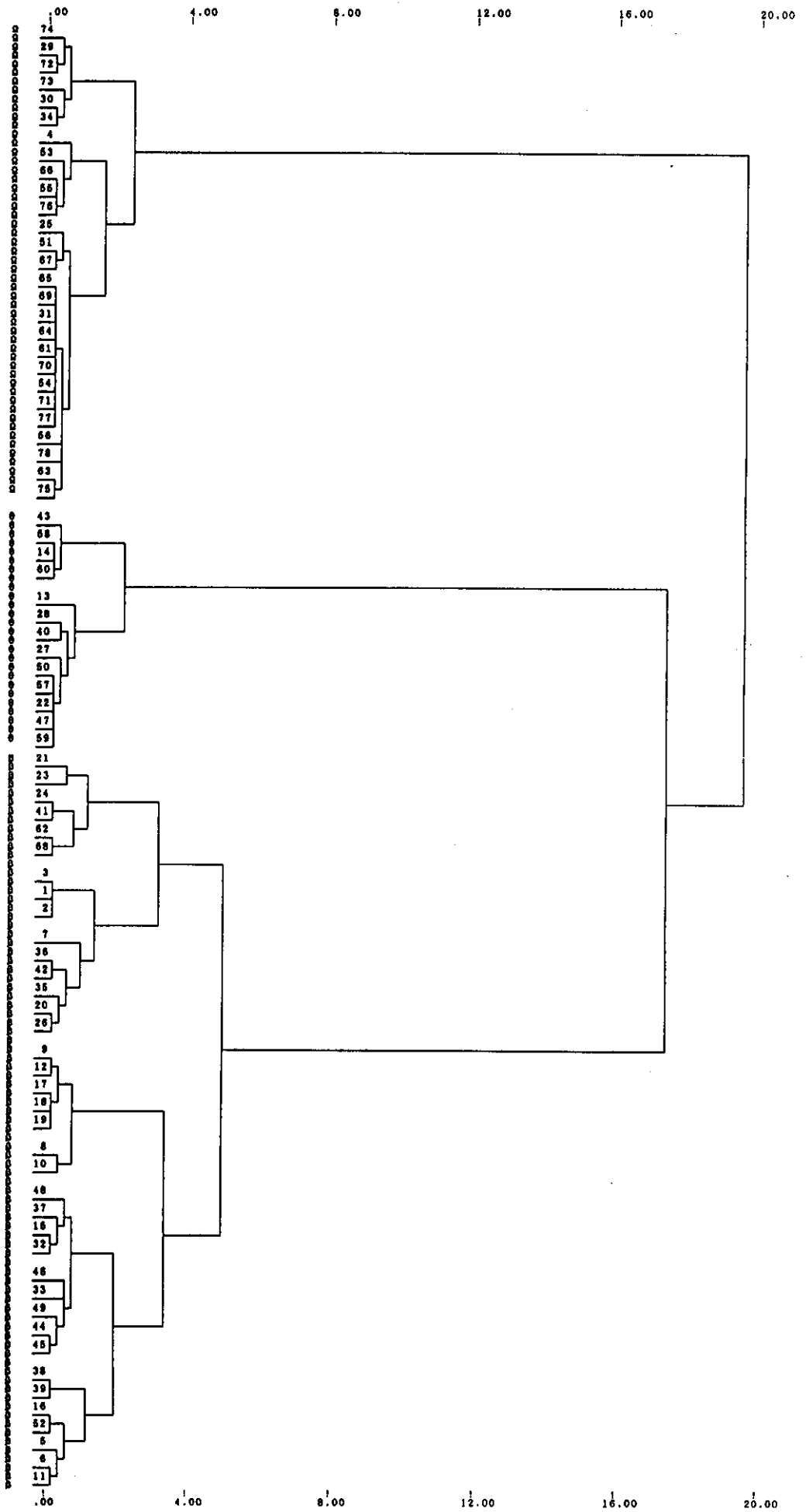
GSTAT, ISS Classification groups, North and South Queensland data set

The statistics for the three groups indicate that two groups are reasonably uniform and one is quite variable (Table 2.18).

GP β

Variable in most characters, more variable than the same group in the 78 UPG classification result.

Disordered multistate characters: Leaf shape shows considerable variation with every possible shape represented; prominence of cluster bracts is also more variable than expected for one taxon.

Numeric characters: Almost all characters are very variable, with wide ranges and high standard deviations, the latter as high as over 1/2 of the mean in the case of spike length, spike length : scape length ratio and trunk height.

GP θ

More uniform than GP β but still with considerable variation in the numeric characters. Overall a reasonably consistent group.

Disordered multistate characters: All characters uniform or with consistent combinations of characters (e.g. prominent cluster bracts vary from slightly to very prominent).

Table 2.18 GSTAT, ISS Classification groups, North and South Queensland data set.

Table 2.18

GP 8 WITH 38 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	21	11	4	2	
2 LEAF COLOUR	16	22	0			
3 CLUSTER BRACTS	0	15	7	14	2	0
4 JUV. CLUSTER BR.	19	7	9	3		
5 BRACT COLOUR	27	0	11	0	0	0
6 SCAPE COLOUR	29	9	0			
7 BRACT SHAPE	1	0	37	0		
8 BR. INDUMENTUM	0	0	0	0	38	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	38	130.0	130.0	350.0	201.1	201.1	50.46	220.0
2 SCAPE LENGTH	0	0	38	59.00	59.00	218.0	142.8	142.8	48.14	159.0
3 SCAPE DIAMETER	0	0	38	60.00	60.00	150.0	97.63	97.63	23.18	90.00
4 SPIKE LENGTH	0	0	38	5.000	5.000	120.0	44.47	44.47	25.29	115.0
5 SPIKE DIAMETER	1	0	37	16.00	16.00	28.00	22.43	22.43	3.262	12.00
6 SP/SC RATIO	0	0	38	9.000	9.000	94.00	31.39	31.39	17.83	85.00
7 TRUNK HEIGHT	0	9	29	0.	2.000	40.00	12.74	16.69	12.87	40.00

GP 9 WITH 13 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	13	0	0	0	
2 LEAF COLOUR	2	11	0			
3 CLUSTER BRACTS	4	0	0	2	4	3
4 JUV. CLUSTER BR.	6	0	2	5		
5 BRACT COLOUR	6	0	7	0	0	0
6 SCAPE COLOUR	11	2	0			
7 BRACT SHAPE	0	0	13	0		
8 BR. INDUMENTUM	3	0	0	0	10	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	13	130.0	130.0	240.0	188.8	188.8	34.41	110.0
2 SCAPE LENGTH	0	0	13	60.00	60.00	145.0	94.77	94.77	21.48	85.00
3 SCAPE DIAMETER	0	0	13	120.0	120.0	200.0	156.3	156.3	31.29	80.00
4 SPIKE LENGTH	0	0	13	55.00	55.00	140.0	94.77	94.77	31.61	85.00
5 SPIKE DIAMETER	0	0	13	25.00	25.00	37.00	30.23	30.23	3.982	12.00
6 SP/SC RATIO	0	0	13	61.00	61.00	150.0	101.3	101.3	29.41	89.00
7 TRUNK HEIGHT	0	0	13	50.00	50.00	100.0	90.00	90.00	17.32	50.00

GP 2 WITH 27 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	0	27	0	0	
2 LEAF COLOUR	1	26	0			
3 CLUSTER BRACTS	0	27	0	0	0	0
4 JUV. CLUSTER BR.	23	4	0	0		
5 BRACT COLOUR	21	0	2	4	0	0
6 SCAPE COLOUR	18	9	0			
7 BRACT SHAPE	0	0	27	0		
8 BR. INDUMENTUM	0	0	0	0	27	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	27	250.0	250.0	465.0	347.8	347.8	56.03	215.0
2 SCAPE LENGTH	0	0	27	152.0	152.0	296.0	228.4	228.4	43.94	144.0
3 SCAPE DIAMETER	0	0	27	90.00	90.00	210.0	136.5	136.5	29.74	120.0
4 SPIKE LENGTH	0	0	27	47.00	47.00	134.0	89.48	89.48	23.25	87.00
5 SPIKE DIAMETER	0	0	27	20.00	20.00	37.00	27.04	27.04	3.848	17.00
6 SP/SC RATIO	0	0	27	22.00	22.00	53.00	39.11	39.11	7.968	31.00
7 TRUNK HEIGHT	0	2	25	0.	10.00	150.0	45.56	49.20	38.44	150.0

STATISTICS FOR ENTIRE DATA
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	34	38	4	2	
2 LEAF COLOUR	19	59	0			
3 CLUSTER BRACTS	4	42	7	16	6	3
4 JUV. CLUSTER BR.	48	11	11	8		
5 BRACT COLOUR	54	0	20	4	0	0
6 SCAPE COLOUR	58	20	0			
7 BRACT SHAPE	1	0	77	0		
8 BR. INDUMENTUM	3	0	0	0	75	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	78	130.0	130.0	465.0	249.8	249.8	87.39	335.0
2 SCAPE LENGTH	0	0	78	59.00	59.00	296.0	164.4	164.4	65.74	237.0
3 SCAPE DIAMETER	0	0	78	60.00	60.00	210.0	120.9	120.9	35.68	150.0
4 SPIKE LENGTH	0	0	78	5.000	5.000	140.0	68.44	68.44	34.66	135.0
5 SPIKE DIAMETER	1	0	77	16.00	16.00	37.00	25.36	25.36	4.673	21.00
6 SP/SC RATIO	0	0	78	9.000	9.000	150.0	45.72	45.72	30.78	141.0
7 TRUNK HEIGHT	0	11	67	0.	2.000	150.0	36.97	43.04	37.63	150.0

<u>Numeric characters</u>: Reasonably uniform, except for the considerable variation in inflorescence characters: scape length, spike length and spike length : scape length ratio (in the latter two the standard deviation is almost 1/3 of the mean).

<u>GP Ω</u>

The most uniform of the groups.

<u>Disordered multistate characters</u>: All characters are uniform except for bract colour, which shows an anomalous combination as some individuals have green and some have brown bracts at flowering time. As the majority of individuals were scored as missing this character it is difficult to form any realistic conclusions from this combination.

<u>Numeric characters</u>: All characters are satisfactorily uniform, except for trunk height, which is extremely variable. However such variability is acceptable in a character which varies with the age of the plant (in those species that do develop trunks).

GCOM, ISS Classification groups, North and South Queensland data set

Leaf characters and scape length make-up 50% of the difference between GP Ω and GPs θ + β combined (Table 2.19):

GP Ω has broad (mean 3.48 mm) leaves, uniformly narrowly quadrate-rhombic in T.S., and long scapes (mean 228 cm), whilst the average condition for GPs θ + β combined is for narrower leaves (mean 1.98

Table 2.19 GCOM, ISS Classification groups, North and South Queensland data set.

```
****   COMPARISON NO.  1
****   GROUP A = GP  Ω
****   GROUP B = GP  θ + GP  β
```

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 17.2630

ATTRIBUTE (STATE)	NAME	GROUP A 27 MEMBERS ATTRIBUTE NO. MEAN PRESENT		GROUP B 51 MEMBERS ATTRIBUTE NO. MEAN PRESENT		CONTRIBUTION %	% (CUM)	ACTUAL VALUE
DNUL 1	LEAF SHAPE		27		51	25	25	4.36
ST. 1	QUADRATE-RHOMBIC	.000		.667				
ST. 2	NARROWLY-Q-R	1.000		.216				
ST. 3	OBTRULL>OBTRIANG	.000		.078				
ST. 4	CONCAVE	.000		.039				
FNUM 1	LEAF WIDTH	347.815	27	197.941	51	20	45	3.46
FNUM 2	SCAPE LENGTH	228.407	27	130.588	51	15	60	2.61

4 ATTRIBUTES MADE NO CONTRIBUTION.

```
****   COMPARISON NO.  2
****   GROUP A = GP  θ
****   GROUP B = GP  β
```

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 13.1923

ATTRIBUTE (STATE)	NAME	GROUP A 13 MEMBERS ATTRIBUTE NO. MEAN PRESENT		GROUP B 38 MEMBERS ATTRIBUTE NO. MEAN PRESENT		CONTRIBUTION %	% (CUM)	ACTUAL VALUE
FNUM 6	SP/SC RATIO	101.308	13	31.395	38	25	25	3.33
FNUM 7	TRUNK HEIGHT	90.000	13	12.737	38	21	46	2.72
FNUM 5	SPIKE DIAMETER	30.231	13	22.432	37	14	59	1.79

5 ATTRIBUTES MADE NO CONTRIBUTION.

mm) of the whole possible range of shapes, and with shorter scapes (mean 131 cm).

The characters separating GP θ from GP β are spike length : scape length ratio, trunk height and spike diameter:
GP θ has spikes more or less equal in length to scapes (mean 1.01), tall trunks (mean 90 cm) and thicker spikes (mean 30 mm) than GP β which has much shorter spikes than scapes (mean .31) shorter trunks (mean 13 cm) and thinner spikes (mean 22 mm).

CRAMER, ISS Classification groups, North and South Queensland data set.

The list of characters in the order of their ability to distinguish between groups, as indicated by CRAMER (Table 2.20) is:
1/. Leaf width, CRAMER value .8227
2/. Spike length : scape length ratio, CRAMER value .8208
3/. Scape length, CRAMER value .7587
4/. Trunk height, CRAMER value .7472
5/. Prominence of cluster bracts, CRAMER value .6948
6/. Spike length, CRAMER value .6801

The first four characters are listed in the same order, and with similar values to the 78 UPG classification CRAMER results. Character five, prominence of cluster bracts, shows that GPs Ω and θ are uniform or consistent in this character, but that GP β has a combination of bracts obscure to bracts quite prominent. Such a combination is uncommon in the genus and is not accepted in most taxa, but is recorded for X. johnsonii as presently circumscribed (Bedford 1986 a).

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Table 2.20 CRAMER, ISS Classification groups, North and South
Queensland data set.

Table 2.20 CRAMER, ISS Classification groups, North and South Queensland data set.

MEAN CRAMER VALUE FOR 15 ATTRIBUTES = .6809   SCALED CRAMER VALUE FOR 3 GROUPS = .3931

NO ATTRIBUTES ARE MISSING IN ALL GROUPS. ATTRIBUTES DNUL 2 (LEAF COLOUR), DNUL 6 (SCAPE COLOUR),
DNUL 7 (BRACT SHAPE), DNUL 8 (BR. INDUMENTUM) (WHERE PRESENT) ARE THE SAME IN ALL GROUPS.

PNUM 1 (LEAF WIDTH)
*******************   CRAMER VALUE = .8227

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP 150	27	27	347.8	BETWEEN GROUPS	.3980E+06	2	.1990E+06	78.53
GP 149	13	13	188.8	WITHIN GROUPS	.1900E+06	75	2534.	
GP 153	38	38	201.1	TOTAL	.5880E+06	77		

GRAND MEAN = 249.8

PNUM 6 (SP/SC RATIO)
*******************   CRAMER VALUE = .8208

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP 150	27	27	39.11	BETWEEN GROUPS	.4915E+05	2	.2457E+05	77.44
GP 149	13	13	101.3	WITHIN GROUPS	.2380E+05	75	317.3	
GP 153	38	38	31.39	TOTAL	.7295E+05	77		

GRAND MEAN = 45.72

PNUM 2 (SCAPE LENGTH)
*******************   CRAMER VALUE = .7582

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP 150	27	27	228.4	BETWEEN GROUPS	.1913E+06	2	.9565E+05	50.70
GP 149	13	13	94.77	WITHIN GROUPS	.1415E+06	75	1887.	
GP 153	38	38	142.8	TOTAL	.3328E+06	77		

GRAND MEAN = 164.4

PNUM 7 (TRUNK HEIGHT)
*******************   CRAMER VALUE = .7472

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP 150	27	27	45.56	BETWEEN GROUPS	.6086E+05	2	.3043E+05	47.40
GP 149	13	13	90.00	WITHIN GROUPS	.4816E+05	75	642.1	
GP 153	38	38	12.74	TOTAL	.1090E+06	77		

GRAND MEAN = 36.97

DNUL 3 (CLUSTER BRACTS)
*******************   CRAMER VALUE = .6948
   CHI-SQ = 71.44, D.F. = 8

GROUP NAME	NO. MEMBERS	NO. PRESENT	NO. OF MEMBERS IN EACH STATE				
			1	2	3	4	5
GP 150	27	27	27	0	0	0	0
GP 149	13	9	0	0	2	4	3
GP 153	38	38	15	7	14	2	0
		74	42	7	16	6	3

PNUM 4 (SPIKE LENGTH)
*******************   CRAMER VALUE = .6801

CAUTION: F TEST INVALID

GROUP NAME	NO. MEMBERS	NO. PRESENT	MEAN		SUM SQUARES	D.F.	MEAN SQUARE	F STATISTIC
GP 150	27	27	89.48	BETWEEN GROUPS	.4279E+05	2	.2140E+05	32.27
GP 149	13	13	94.77	WITHIN GROUPS	.4972E+05	75	662.9	
GP 153	38	38	44.47	TOTAL	.9251E+05	77		

GRAND MEAN = 68.44

2.3.2.2 DISCRIMINANT Analysis and Classification, TAXON ISS
Classification groups, North and South Queensland data set.

Analysis

Six characters were selected for inclusion in the two discriminant
functions before the addition to Rao's V became non significant (Table
2.21). The one character not selected was spike diameter. The order
of selection was:

1/. Leaf width

2/. Spike length : scape length ratio

3/. Trunk height

4/. Spike length

5/. Scape diameter

6/. Scape length

Table 2.21 shows that leaf width and spike length : scape length ratio
were, almost equally, the most important discriminators between groups
with a discriminating power, as measured by change in Rao's V, of over
three times that of the next most important character.

These results are very similar, though not identical to the results
for the discriminant analysis on the NQ78 UPG classification
groupings, and the comments made there apply here also.

Classification

The discriminant classification (Figure 2.10, Table 2.22) found that

Table 2.21 DISCRIMINANT Analysis TAXON NQ78 ISS Groups

SUMMARY TABLE

	ACTION		VARS	WILKS				CHANGE		
STEP	ENTERED	REMOVED	IN	LAMBDA	SIG.	RAO*S V	SIG.	IN V	SIG.	LABEL
1	LEAFW		1	.323060	.0000	155.0598		0155.0598	0	
2	SPSCRAT		2	.108657	.0000	309.6443		0154.5845	0	
3	TRUNKHT		3	.086117	.0000	360.4476		0 50.8033	.0000	
4	SPIKEL		4	.071998	.0000	415.5879		0 55.1403	.0000	
5	SCAPED		5	.065845	.0000	443.6821		0 28.0942	.0000	
6	SCAPEL		6	.062814	.0000	455.8279		0 12.1457	.0023	

Table 2.22 DISCRIMINANT Classification Results TAXON NQ78 ISS Groups

CLASSIFICATION RESULTS -

		NO. OF	PREDICTED GROUP MEMBERSHIP		
ACTUAL GROUP		CASES	1	2	3
GROUP	1	38	35	1	2
			92.1	2.6	5.3
GROUP	2	13	1	12	0
			7.7	92.3	0
GROUP	3	27	0	0	27
			0	0	100.0

PERCENT OF GROUPED CASES CORRECTLY CLASSIFIED - 94.87

Figure 2.10 DISCRIMINANT Classification TAXON NQ78 ISS groups

SYMBOLS USED IN PLOTS
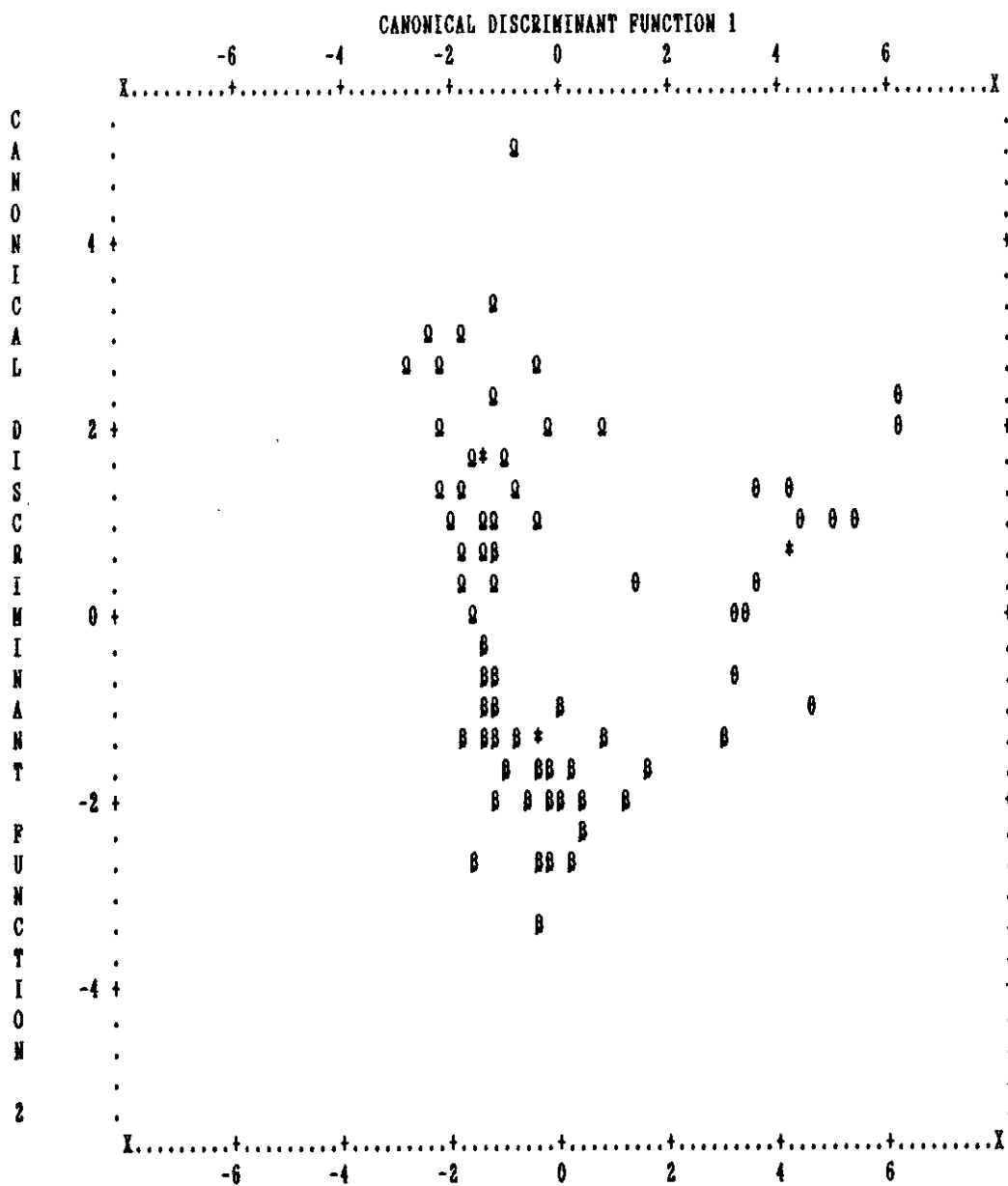
SYMBOL   GROUP   LABEL
------   -----   --------------------
  β   β
  θ   θ
  Ω   Ω
  ‡   GROUP CENTROIDS

```
                          CANONICAL DISCRIMINANT FUNCTION 1
                  -6        -4        -2         0         2         4         6
             X.........+.........+.........+.........+.........+.........+.........+.........X
         C   .                                                                              .
         A   .                              Ω                                               .
         N   .                                                                              .
         O   .                                                                              .
         N  4+                                                                              +
         I   .                                                                              .
         C   .                            Ω                                                 .
         A   .                         Ω  Ω                                                 .
         L   .                       Ω  Ω        Ω                                          .
             .                            Ω                                           θ     .
         D  2+                         Ω        Ω    Ω                                θ     +
         I   .                        Ω‡ Ω                                                  .
         S   .                       Ω Ω    Ω                        θ  θ                   .
         C   .                       Ω  ΩΩ   Ω                         θ  θ θ               .
         R   .                       Ω  Ωβ                             ‡                    .
         I   .                       Ω   Ω               θ              θ                   .
         M  0+                       Ω                              θθ                      +
         I   .                      β                                                      .
         N   .                      ββ                                                     .
         A   .                      ββ          β                        θ                 .
         N   .                   β  ββ β  ‡        β            β                          .
         T   .                        β  ββ β          β                                   .
           -2+                        β  β ββ β     β                                      +
         F   .                            β                                                .
         U   .                   β     ββ β                                                .
         N   .                                                                             .
         C   .                      β                                                      .
         T   .                                                                             .
         I  -4+                                                                            +
         O   .                                                                             .
         N   .                                                                             .
             .                                                                             .
         2   .                                                                             .
             X.........+.........+.........+.........+.........+.........+.........+.........X
                  -6        -4        -2         0         2         4         6
```

the discriminant functions derived from the above six characters correctly classifies 94.87% of the 78 entities. This indicates that the discriminant analysis has been quite successful in identifying an adequate combination of discriminating variables. It also indicates that the TAXON NQ78 ISS groups are quite well supported by the numeric characters in the analysis. This partially corroborates the hypothesis that the NQ78 ISS three groups are valid groups of the entities.

2.3.3 PCOA ordination, North and South Queensland data set.

The first three vectors represent 76% of the dissimilarity in the matrix (35%, 33% and 7% respectively). Appendix 2.8 gives the vector scores and Figures 2.11.1-2.11.3 show the plot of the entities on the first three vectors.

The plots of the entities against the first and second vectors (Figure 2.11.1) and against the second and third vectors (Figure 2.11.3) are the only plots showing interpretable pattern. Figure 2.11.1 shows that the entities are distributed in an arched or horseshoe shaped curve, as in the ordinations for the classifications treated above. A comparison of the ordination plots with how individuals are allocated to groups by the UPG and ISS classifications gives a very similar, though not identical, result for the two classifications.

PCOA ordination showing NQ78 UPG groups

The solid lines drawn on the plot (Figure 2.11.1) show the distribution of groups in the pattern. It can be seen that GP θ falls

93

Figure 2.11.1   NQ78 PCQA Ordination Vectors 1 and 2

Key: _____ UPG Groups; - - - - ISS Groups.

ONE>

TWO

GP 0

58
60
14
43
59
57
13
50 28
40
47 27
22
38
48
37 15
46 33 19
5 49 39
44
45
21 12
18
23
11
34 62 29
9 17
30
68
16
73
24 6 52
10 8
782 63
41
75
3
66 76 56 69
65 36
70 77
4
67 42
53 55 61 7
54 31
1 20
352
26
25

2^ 1>
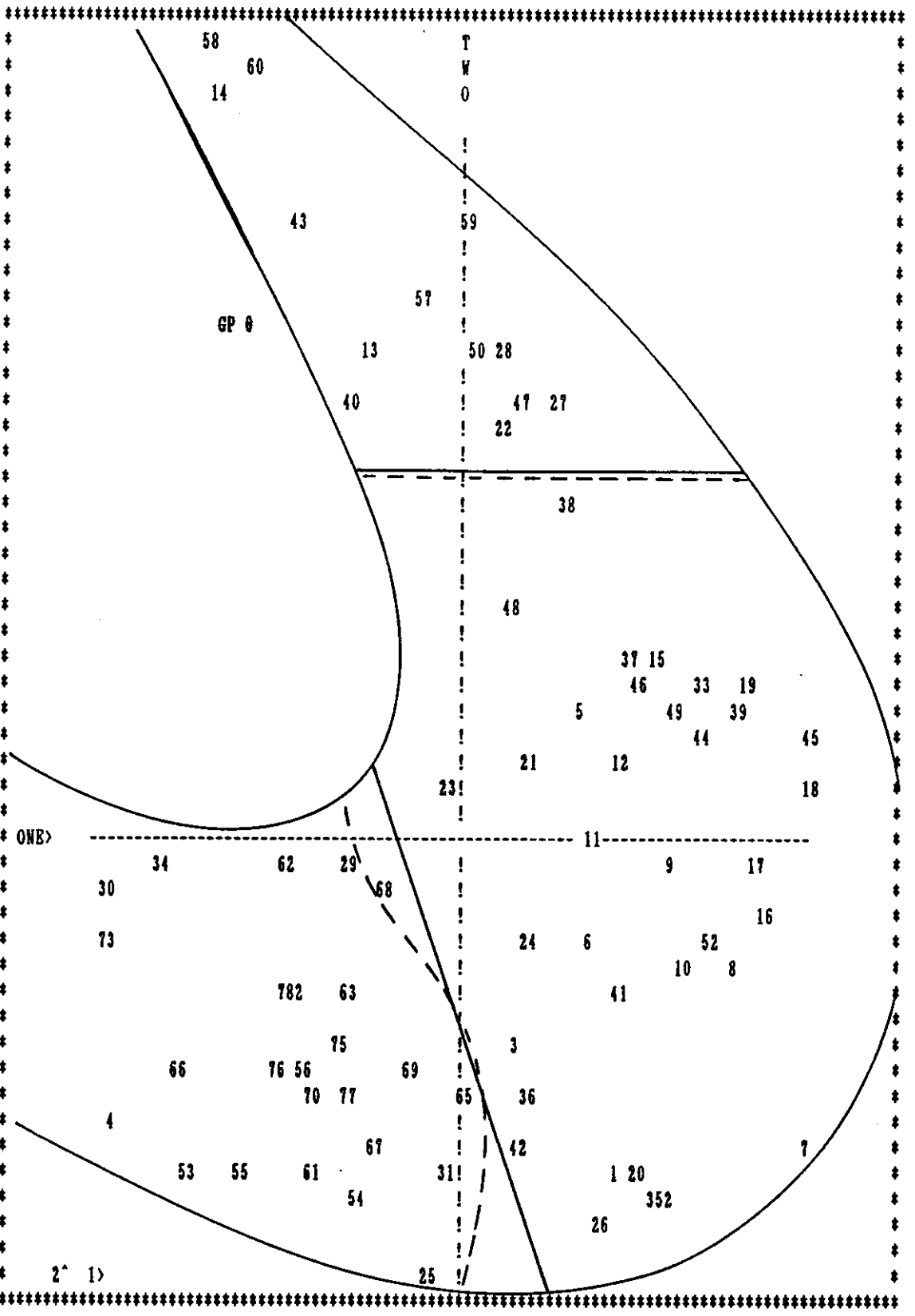
Figure 2.11.2, Vectors 1 and 3,

taxa not separated, so not demarcated.

```
************************************************************************

                                      !                41
                                      !          24
                                      !
                                      !
                                      !
                                      !
                                      !
                                      !                37
                                      !                32
                            68        !            20      33
                   62                 !
                          29          !   4821          49
                                      !              46    44
        34                            !                              45
                          51          2523!        26      35
   73              7472        67     !  65    47        15
   30                    61         69 !  50 22 36              39
 ONE> -------- 66----- 60---- 70 757--- 64-- 3 59----------------------
                58      783          57 !        38
                                      !  28                        7
                                      !                52
                                      !      27    1    2
                          40          !              10    8
                           13         !    3
     4                                !        11          19
           14              54         !
              55                      !                16   18
        53                            !                17
                56                    !        12    9
                                      T
                                      H
                                      R
     3^  1>                           E
                                      E

************************************************************************
```

Figure 2.11.3, Vectors 2 and 3

Key: .... Separation of Group θ from other
two groups in both UPG and ISS Classifications

```
*****************************************************************************
*                                                                         *
*                                                                         *
*                                                                         *
*                                                                         *
*                                                                         *
*                                                                         *
*                41          !                                            *
*                     24     !                                            *
*                            !                                            *
*                            !                          .                 *
*                            !                          .                 *
*                            !                          .                 *
*                            !                          .                 *
*                            !           37            .                  *
*                       68 !            32             .                  *
*            20              62         33             .                  *
*            GPs B/Q         29      21 49    48       .   GP θ           *
*                            !        44 46            .                  *
*                            34       45               .                  *
*      25  2 35     51        !    23                  .                  *
*            67 65     742 73 !         15             .   47             *
*            61 36 69      30 !         39             .   22  50         *
* TWO)  -------- 31  77 75163-------------------------.------------ 59--------- 60  *
*                  76  78      !                38  .            57  43        58 *
*            7                 !                     .      28                *
*                        52    !                     .                       *
*            2 1               !                     .    27                 *
*                        10    !                     .    40                 *
*                  3           !                     .         13            *
*              4           6      11    5 19        .                        *
*            54                !                     .                   14   *
*            55           16 !  18                  .                        *
*            53                17                    .                       *
*                  56          9!    12             .                        *
*                              T                                            *
*                              H                                            *
*                              R                                            *
*            3^   2)           E                                            *
*                              E                                            *
*****************************************************************************
```

at the top end of the distribution, without overlap, GP β occupies the middle ground and could also be interpreted as being without overlap, GP Ω falls at the end of the curved distribution. Figure 2.11.3 shows that GP θ are distributed at one end of the second vector, separate from the other two groups which are interspersed with each other. In terms of the individual vectors: The primary vector shows some incomplete separation between GP Ω and GP β; the second vector shows GP θ at one end, separated from the other groups; the third vector does not assist with the interpretation of the data.

PCOA ordination NQ78 ISS groups.

The dotted lines drawn on the plot of vectors 1 and 2 (Figure 2.11.1) show the distribution of groups in the pattern. As for the UPG groupings, it can be seen that GP θ falls at the top end of the distribution, without overlap. But in contrast to the UPG groupings, ISS GP β, while it still occupies the middle ground now slightly overlaps GP Ω which falls at the lower end of the curved distribution, and is therefore not marked separately. Figure 2.11.3 shows that GP θ are distributed at one end of the second vector, separate from the other two groups which are interspersed with each other. In terms of the individual vectors: The primary vector shows some incomplete separation between GP Ω and GP β; the second vector shows GP θ at one end, separated from the other groups; the third vector does not assist with the interpretation of the data.

BACRIV

BACRIV (Table 2.23) indicates that the size of parts (spike length,

100

Table 2.23 BACRIV for PCOA Ordination, North and South Queensland data
set.

Table 2.23 BACRIV PCOA Ordination, North and South Queensland data set.

CORRELATIONS FOR VECTOR 1

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	STATE NO	STATE NAME
SPIKE LENGTH	FNUM 4	-.8963	78		
SCAPE DIAMETER	FNUM 3	-.8027	78		
SPIKE DIAMETER	FNUM 5	-.7481	77		
LEAF WIDTH	FNUM 1	-.7064	78		
SCAPE LENGTH	FNUM 2	-.5819	78		
LEAF SHAPE	DMUL 1	-.5768	78	2	NARROWLY-Q-R
TRUNK HEIGHT	FNUM 7	-.5695	78		
BRACT COLOUR	DMUL 5	.4808	24	2	GREEN
BRACT COLOUR	DMUL 5	-.4808	24	3	BROWN
SP/SC RATIO	FNUM 6	-.4353	78		
CLUSTER BRACTS	DMUL 3	-.4257	74	1	ABSENT
LEAF SHAPE	DMUL 1	.4187	78	1	QUADRATE-RHOMBIC
CLUSTER BRACTS	DMUL 3	.4017	74	2	SHORTLY ACUTE
CLUSTER BRACTS	DMUL 3	.2777	74	3	BASE OF SPIKE
LEAF SHAPE	DMUL 1	.2564	78	4	CONCAVE

21 ITEMS NOT PRINTED

CORRELATIONS FOR VECTOR 2

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	STATE NO	STATE NAME
SP/SC RATIO	FNUM 6	.7962	78		
LEAF SHAPE	DMUL 1	.7786	78	1	QUADRATE-RHOMBIC
CLUSTER BRACTS	DMUL 3	-.7481	74	1	ABSENT
LEAF SHAPE	DMUL 1	-.6533	78	2	NARROWLY-Q-R
JUV. CLUSTER BR.	DMUL 4	-.6522	30	1	ABSENT
SCAPE LENGTH	FNUM 2	-.6330	78		
BRACT COLOUR	DMUL 5	.5848	24	2	GREEN
BRACT COLOUR	DMUL 5	-.5848	24	3	BROWN
LEAF WIDTH	FNUM 1	-.5736	78		
TRUNK HEIGHT	FNUM 7	.5621	78		
JUV. CLUSTER BR.	DMUL 4	.5405	30	3	LINEAR-TRIANG
CLUSTER BRACTS	DMUL 3	.5230	74	4	BASAL 10 CM
SPIKE DIAMETER	FNUM 5	.4414	77		
CLUSTER BRACTS	DMUL 3	.4230	74	5	100% SPIKE
SCAPE DIAMETER	FNUM 3	.3724	78		
CLUSTER BRACTS	DMUL 3	.3194	74	3	BASE OF SPIKE

20 ITEMS NOT PRINTED

CORRELATIONS FOR VECTOR 3

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	STATE NO	STATE NAME
JUV. CLUSTER BR.	DMUL 4	-.7406	30	1	ABSENT
JUV. CLUSTER BR.	DMUL 4	.6875	30	2	SHORTLY ACUTE
BRACT COLOUR	DMUL 5	-.6598	24	3	BROWN
BRACT COLOUR	DMUL 5	.6598	24	2	GREEN
CLUSTER BRACTS	DMUL 3	.6267	74	3	BASE OF SPIKE
CLUSTER BRACTS	DMUL 3	-.4408	74	2	SHORTLY ACUTE
LEAF SHAPE	DMUL 1	.2909	78	2	NARROWLY-Q-R
SCAPE DIAMETER	FNUM 3	-.2418	78		
LEAF SHAPE	DMUL 1	-.1848	78	1	QUADRATE-RHOMBIC
LEAF SHAPE	DMUL 1	-.1799	78	3	OBTRULL>OBTRIANG
CLUSTER BRACTS	DMUL 3	-.1587	74	1	ABSENT

25 ITEMS NOT PRINTED

scape diameter, spike diameter, leaf width, scape length and trunk height) are the most highly correlated with the primary vector, with leaf shape and bract colour the next most highly correlated. For the second vector BACRIV shows that shape factors are the most highly correlated (inflorescence ratios, leaf shape, and the prominence of cluster bracts).

2.4.1 A detailed analysis of the structure of NQ52 UPG GP β with 39 members.

TAXON SAHN Classification, UPG Clustering strategy, NQ52 GP β - a 39 entity subset of NQ52.

The dendrogram (Figure 2.12, SAHN dissimilarity levels Appendix 2.9) shows five "subgroups" by the 1.0 dissimilarity level. There are two major subgroups connected to a chain of singletons with one small subgroup adding to the mass at higher levels:

GP 70 WITH 12 MEMBERS 1-3 20 24-26 31 35 36 41 42

GP 72 WITH 3 MEMBERS 21-23

GP 73 WITH 22 MEMBERS 5 6 8-12 15-19 32-33 37 39 44-46 48 49 52

ENTITY 7 1 MEMBER 7

ENTITY 51 1 MEMBER 51

The membership of these subgroups is mostly similar to the membership of the subgroups of NQ52 UPG GP β: GP 70 is similar to NQ52 UPG GP 96 except that entities 10 and 51 have been lost; GP 72 is the same as NQ52 UPG GP 81 with the addition of entity 38; GP 73 is similar to NQ52 UPG GP 94, with the only changes being the loss of entity 38 and

102

Figure 2.12 TAXON SAHN Classification, UPG Clustering strategy, Dendrogram, NQ52 GP β (39 entity) data set.

Figure 2.12
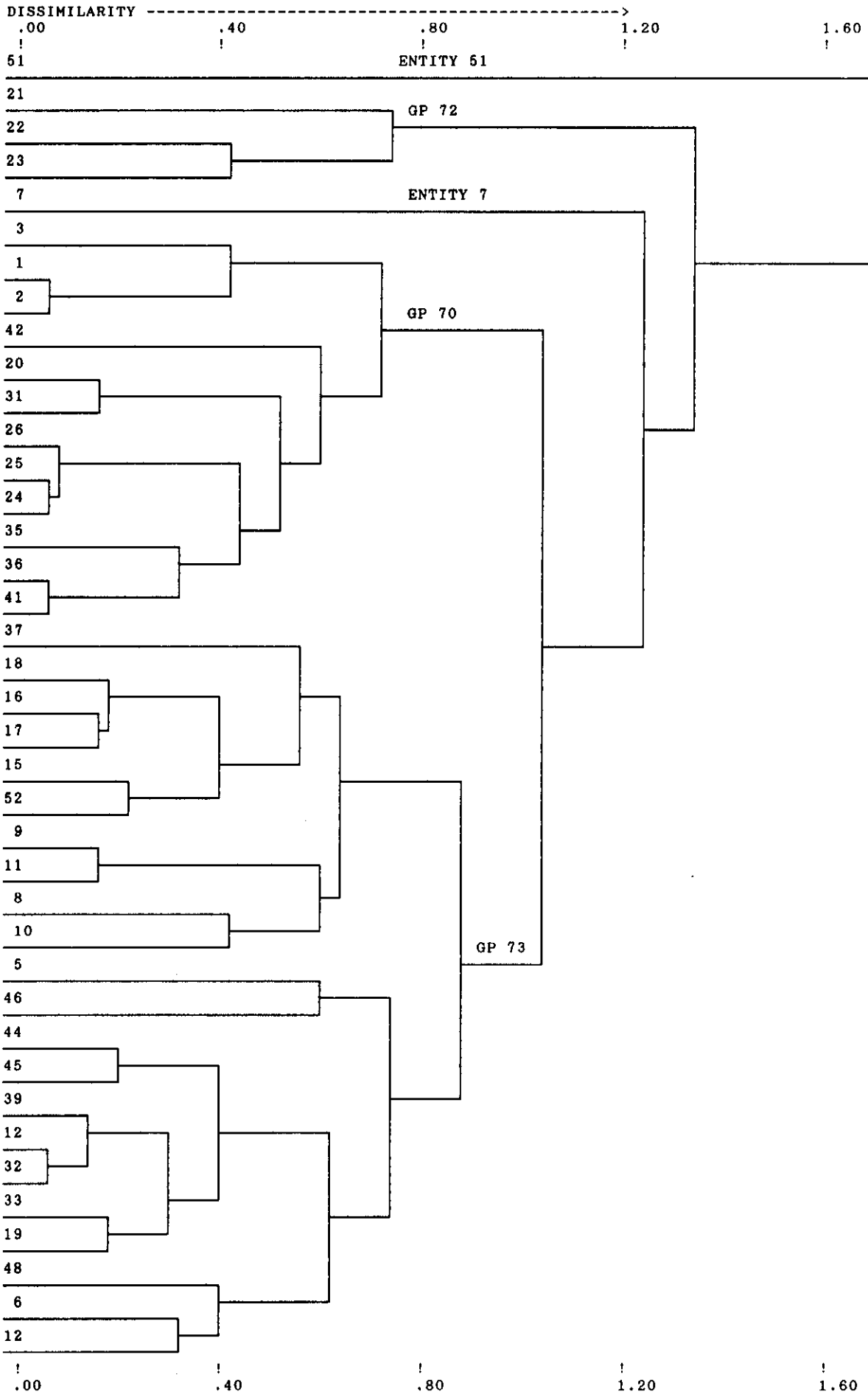
the addition of entity 10; ENTITY 7 was also a singleton within NQ52 UPG GP β. The separation of entity 51 as a singleton is a new, and unexpected, change in this classification. Such a change is hard to explain with certainty, but could be due to distortions in the current dissimilarity matrix of unknown cause, or to distortions in the NQ52 UPG matrix. In the latter case the distortions could be due to the presence of very dissimilar individuals in the matrix. The changes would then be caused by the removal from the matrix of individuals which were equally dissimilar to entity 51 as to the rest of GP β. The presence of such individuals could have resulted in forcing 51 and the rest of GP β together even though they were not very similar.

GSTAT, NQ52 GP β - a 39 entity subset of NQ52

The statistics for the subgroups indicate that some are still quite variable and others fairly uniform (Table 2.24).

GP 70

In some respects a consistent and reasonable group, but in other respects still quite variable.

Disordered multistate characters: Leaf shape is reasonably consistent; prominence of cluster bracts also shows a consistent combination.

Numeric characters: Many characters have wide ranges and or high variability. In particular the ranges for leaf width and scape length, though less than for NQ52 UPG GP β as a whole, are excessive, and spike length is highly variable with a standard deviation of over 1/3 of the mean.

Table 2.24 GSTAT, NQ52 GP β – a 39 entity subset of NQ52, page 1.

Table 2.24

INDIVIDUAL NO. 51
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	0	1	0	0	
2 LEAF COLOUR	0	1	0			
3 CLUSTER BRACTS	0	1	0	0	0	0
6 SCAPE COLOUR	0	1	0			
7 BRACT SHAPE	0	0	1	0		
8 BR. INDUMENTUM	0	0	0	0	1	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO. =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	1	300.0	300.0	300.0	300.0	300.0	0.	0.
2 SCAPE LENGTH	0	0	1	265.0	265.0	265.0	265.0	265.0	0.	0.
3 SCAPE DIAMETER	0	0	1	110.0	110.0	110.0	110.0	110.0	0.	0.
4 SPIKE LENGTH	0	0	1	104.0	104.0	104.0	104.0	104.0	0.	0.
5 SPIKE DIAMETER	0	0	1	22.00	22.00	22.00	22.00	22.00	0.	0.
6 SP/SC RATIO	0	0	1	39.00	39.00	39.00	39.00	39.00	0.	0.
7 TRUNK HEIGHT	0	0	1	60.00	60.00	60.00	60.00	60.00	0.	0.

GP 72 WITH 3 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	1	2	0	0	
2 LEAF COLOUR	0	3	0			
3 CLUSTER BRACTS	0	1	0	1	1	0
4 JUV. CLUSTER BR.	1	0	1	1		
5 BRACT COLOUR	2	0	1	0	0	0
6 SCAPE COLOUR	2	1	0			
7 BRACT SHAPE	0	0	3	0		
8 BR. INDUMENTUM	0	0	0	0	3	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO. =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	3	150.0	150.0	180.0	163.3	163.3	15.28	30.00
2 SCAPE LENGTH	0	0	3	77.00	77.00	110.0	90.00	90.00	17.58	33.00
3 SCAPE DIAMETER	0	0	3	120.0	120.0	120.0	120.0	120.0	0.	0.
4 SPIKE LENGTH	0	0	3	54.00	54.00	81.00	69.33	69.33	13.87	27.00
5 SPIKE DIAMETER	0	0	3	24.00	24.00	27.00	25.67	25.67	1.528	3.000
6 SP/SC RATIO	0	0	3	65.00	65.00	94.00	77.33	77.33	14.98	29.00
7 TRUNK HEIGHT	0	0	3	10.00	10.00	20.00	13.33	13.33	5.774	10.00

INDIVIDUAL NO. 7
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	0	0	0	1	
3 CLUSTER BRACTS	0	1	0	0	0	0
7 BRACT SHAPE	0	0	1	0		
8 BR. INDUMENTUM	0	0	0	0	1	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO. =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	1	220.0	220.0	220.0	220.0	220.0	0.	0.
2 SCAPE LENGTH	0	0	1	59.00	59.00	59.00	59.00	59.00	0.	0.
3 SCAPE DIAMETER	0	0	1	60.00	60.00	60.00	60.00	60.00	0.	0.
4 SPIKE LENGTH	0	0	1	5.000	5.000	5.000	5.000	5.000	0.	0.
5 SPIKE DIAMETER	0	0	1	17.00	17.00	17.00	17.00	17.00	0.	0.
6 SP/SC RATIO	0	0	1	9.000	9.000	9.000	9.000	9.000	0.	0.

Table 2.24 GSTAT, NQ52 GP β – a 39 entity subset of NQ52, page 2.

GP 70 WITH 12 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	0	9	3	0	
2 LEAF COLOUR	3	9	0			
3 CLUSTER BRACTS	0	10	0	2	0	0
4 JUV. CLUSTER BR.	10	0	2	0		
5 BRACT COLOUR	9	0	3	0	0	0
6 SCAPE COLOUR	6	6	0			
7 BRACT SHAPE	0	0	12	0		
8 BR. INDUMENTUM	0	0	0	0	12	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	12	200.0	200.0	350.0	255.4	255.4	47.60	150.0
2 SCAPE LENGTH	0	0	12	100.0	100.0	296.0	186.6	186.6	45.07	196.0
3 SCAPE DIAMETER	0	0	12	60.00	60.00	110.0	89.17	89.17	16.21	50.00
4 SPIKE LENGTH	0	0	12	16.00	16.00	75.00	43.25	43.25	17.06	59.00
5 SPIKE DIAMETER	0	0	12	16.00	16.00	28.00	21.17	21.17	3.538	12.00
6 SP/SC RATIO	0	0	12	9.000	9.000	35.00	22.58	22.58	6.317	26.00
7 TRUNK HEIGHT	0	6	6	0.	5.000	15.00	4.583	9.167	5.418	15.00

GP 73 WITH 22 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	20	0	1	1	
2 LEAF COLOUR	12	10	0			
3 CLUSTER BRACTS	0	5	7	9	1	0
4 JUV. CLUSTER BR.	7	7	6	2		
5 BRACT COLOUR	15	0	7	0	0	0
6 SCAPE COLOUR	19	3	0			
7 BRACT SHAPE	1	0	21	0		
8 BR. INDUMENTUM	0	0	0	0	22	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	22	130.0	130.0	230.0	176.6	176.6	31.11	100.0
2 SCAPE LENGTH	0	0	22	60.00	60.00	195.0	132.7	132.7	42.62	135.0
3 SCAPE DIAMETER	0	0	22	70.00	70.00	130.0	98.18	98.18	21.96	60.00
4 SPIKE LENGTH	0	0	22	11.00	11.00	80.00	39.14	39.14	20.38	69.00
5 SPIKE DIAMETER	1	0	21	19.00	19.00	28.00	22.57	22.57	2.619	9.000
6 SP/SC RATIO	0	0	22	16.00	16.00	51.00	28.55	28.55	10.51	35.00
7 TRUNK HEIGHT	0	3	19	0.	2.000	40.00	14.73	17.05	12.68	40.00

STATISTICS FOR ENTIRE DATA
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	21	12	4	2	
2 LEAF COLOUR	16	23	0			
3 CLUSTER BRACTS	0	18	7	12	2	0
4 JUV. CLUSTER BR.	20	7	9	3		
5 BRACT COLOUR	28	0	11	0	0	0
6 SCAPE COLOUR	28	11	0			
7 BRACT SHAPE	1	0	38	0		
8 BR. INDUMENTUM	0	0	0	0	39	0

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	39	130.0	130.0	350.0	204.1	204.1	53.41	220.0
2 SCAPE LENGTH	0	0	39	59.00	59.00	296.0	147.5	147.5	55.21	237.0
3 SCAPE DIAMETER	0	0	39	60.00	60.00	130.0	96.41	96.41	21.09	70.00
4 SPIKE LENGTH	0	0	39	5.000	5.000	104.0	43.51	43.51	22.87	99.00
5 SPIKE DIAMETER	1	0	38	16.00	16.00	28.00	22.21	22.21	3.112	12.00
6 SP/SC RATIO	0	0	39	9.000	9.000	94.00	30.23	30.23	17.13	85.00
7 TRUNK HEIGHT	0	10	29	0.	2.000	60.00	12.28	16.52	13.61	60.00

From the multistate data this appears an odd assortment of individuals, but the numeric characters indicate that the plants concerned have very similar dimensions.

Disordered multistate characters: Very variable – leaf shape varies from quadrate rhombic to narrowly quadrate rhombic; the prominence of cluster bracts shows an unacceptable combination.

Numeric characters: All characters are acceptably uniform relative to taxa in the genus (Bedford, 1986 a).

GP 73

Some characters are satisfactorily uniform, others are variable.

Disordered multistate characters: Leaf shape is reasonably consistent with the majority of members scored quadrate-rhombic, though one member is scored obtrullate to obtriangular and another as concave; prominence of cluster bracts is quite variable – from bracts obscure to prominent for the basal 10 cm of the spike (an unusual but not necessarily unacceptable combination).

Numeric characters. Many characters are quite variable but some are within acceptable ranges: Leaf width, scape diameter and spike diameter have acceptable range and standard deviation figures; scape and spike lengths have large ranges and high variability, with high standard deviations of 1/3 to 1/2 their ranges; spike length : scape length ratio and trunk height also appear very variable, but may be within the range of acceptable figures as

other groups in the genus with similar amounts of variation are valid taxa (Bedford, 1986 a).

The singletons. 7 and 51 are obviously uniform and without internal variability.

To assist with comparisons of the subgroups with each other, and therefore with the understanding of the significance of the subdivisions within GP β, full word descriptions of their characteristics as given by GSTAT were prepared.

Descriptions of groups (characters listed in ascending order from soil level):

GP 70

Trunk absent to short, 0 - 15 cm; leaves narrowly quadrate rhombic or, less commonly, obtrullate to obtriangular; medium width to broad, 2.0 - 3.5 mm; scape 100 - 296 cm long and 6 - 11 mm diam.; spike 16 - 75 cm long and 16 - 28 mm diam.; spike always much shorter than scape, ratio .09 - .35; cluster bracts obscure, or rarely, prominent at the base of the spike only.

GP 72

Trunk short, 10 - 20 cm; leaves quadrate rhombic or narrowly quadrate-rhombic; narrow to medium width, 1.5 - 1.8 mm; scape 77 - 110 cm long and 12 mm diam.; spike 54 - 81 cm long and 24 - 27 mm diam; spike about half as long to the same length as scape, ratio .65 - .94;

cluster bracts obscure, prominent at the base of the spike only or for the basal 10 cm of the spike.

GP 73

Trunk short, 0 - 40 cm; leaves quadrate-rhombic or, rarely, obtrullate to obtriangular or concave; narrow to medium width, 1.3 - 2.3 mm; scape 60 - 195 cm long and 7 - 13 mm diam; spike 11 - 80 cm long and 19 - 28 mm diam.; spike very much shorter than to about half as long as scape, ratio .16 - .51; cluster bracts obscure, prominent - shortly acute in shape, prominent at the base of the spike only or, rarely, prominent for the basal 10 cm of the spike.

Entity 7

Trunk absent; leaves concave; medium width, 2.2 mm; scape 59 cm long and 6 mm diam.; spike 5 cm long and 17 mm diam; spike very much shorter than scape, ratio .09; cluster bracts obscure.

Entity 51

Trunk medium height, 60 cm; leaves narrowly quadrate-rhombic; broad, 3.0 mm; scape 265 cm long and 11 mm diam.; spike 104 cm long and 22 mm diam.; spike much shorter than scape, ratio .39; cluster bracts obscure.

The groups compared, in order of most dissimilar pair comparison to least dissimilar pair (Table 2.25) show:

Comparison 1. Individual 51 from the remaining members.

The characters separating individual 51 as a singleton (with 61% of the differences) are the possession of the highest trunk and longest spike in this analysis.

Such a separation is somewhat artificial as the difference between the dimensions of this plant and the largest in the range present in the remaining 38 plants is not very great, and would not normally be regarded as being of taxonomic significance in this genus. This appears to be a case of "a large fish in a small pond".

Comparison 2. GP 72 and the remaining 35 members.

The single character most different between GP 72 and the remaining 35 members in the analysis (with 52% of the differences) is spike length : scape length ratio.

This difference may be of taxonomic significance, as it is an important character elsewhere in the genus, though the average for the group of .77 is not very different to the highest value elsewhere (in GP 73) of .51.

Table 2.25 GCOM, NQ52 GP β – a 39 entity subset of NQ52

Table 2.25 GCOM, NQ52 GP β - a 39 entity subset of NQ52

```
####    COMPARISON NO. 1  (MOST DISSIMILAR PAIR OF GROUPS)
####    GROUP A = GP  51
####    GROUP B = GP  72 + GP  7 + GP  70 + GP  73
```

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 2.1555

ATTRIBUTE (STATE)	NAME	GROUP A 1 MEMBERS ATTRIBUTE NO. MEAN PRESENT		GROUP B 38 MEMBERS ATTRIBUTE NO. MEAN PRESENT		CONTRIBUTION %	% (CUM)	ACTUAL VALUE
FNUM 7	TRUNK HEIGHT	60.000	1	11.026	38	39	39	.841
FNUM 4	SPIKE LENGTH	104.000	1	41.921	38	22	61	.479

6 ATTRIBUTES MADE NO CONTRIBUTION.

```
####    COMPARISON NO. 2
####    GROUP A = GP  72
####    GROUP B = GP   7 + GP  70 + GP  73
```

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 3.1860

ATTRIBUTE (STATE)	NAME	GROUP A 3 MEMBERS ATTRIBUTE NO. MEAN PRESENT		GROUP B 35 MEMBERS ATTRIBUTE NO. MEAN PRESENT		CONTRIBUTION %	% (CUM)	ACTUAL VALUE
FNUM 6	SP/SC RATIO	77.333	3	25.943	35	52	52	1.66

5 ATTRIBUTES MADE NO CONTRIBUTION.

```
####    COMPARISON NO.  3
####    GROUP A = GP   6
####    GROUP B = GP  70 + GP  73
```

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 1.1809

ATTRIBUTE (STATE)	NAME	GROUP A 1 MEMBERS ATTRIBUTE NO. MEAN PRESENT		GROUP B 34 MEMBERS ATTRIBUTE NO. MEAN PRESENT		CONTRIBUTION %	% (CUM)	ACTUAL VALUE
DMUL 1	LEAF SHAPE		1		34	24	24	.288
ST. 1	QUADRATE-RHOMBIC	.000		.588				
ST. 2	NARROWLY-Q-R	.000		.265				
ST. 3	OBTRULL>OBTRIANG	.000		.118				
ST. 4	CONCAVE	1.000		.029				
FNUM 2	SCAPE LENGTH	59.000	1	151.706	34	15	40	.183
FNUM 3	SCAPE DIAMETER	60.000	1	95.000	34	15	55	.178

6 ATTRIBUTES MADE NO CONTRIBUTION.

Comparison 3.   Individual 7 with the remaining 34 members.

The characters most different between individual 7 and the remaining 34 members (55% of the differences) are shown as leaf shape, scape length and scape diameter.

These differences are highly artificial if viewed singly, as none of the dimensions of individual 7 are outside the range of the other 34 members.   This separation must then depend on the possession of this combination of characters. In taxonomic terms this is a poor basis for the separation of this individual

Comparison 4.   GP 70 with GP 73.

The characters separating these groups (63% of the differences) are leaf shape and leaf width.

Reference to the GSTAT tables and descriptions shows that there is considerable overlap between the dimensions of these groups. The range of leaf widths for GP 70 is from 2.0 mm to 3.5 mm, and for GP 73 from 1.3 mm to 2.3 mm, giving an overlap of .3 mm.

There is also some overlap in leaf shape, as both groups have members with obtrullate to obtriangular leaves. As such, although there may be some real differences between the groups, it would be difficult to distinguish between them in practice.

Conclusions from 39 entity analyses.

At this stage of knowledge the differences present in NQ52 UPG GP β are not taxonomically reliable enough to support the formal recognition of any taxa within this group.

2.5 GENERAL DISCUSSION

Characters

Many of the multistate characters in the data set do not vary significantly between the groups. This is most probably because:

(a) the character set was devised to cover the range of variation in the genus as a whole rather than only the perceived differences in the taxa involved in the analyses, and;

(b) the taxa involved here are difficult to distinguish (hence the need for these analyses), and it is therefore to be expected that they will have many features in common.

Testing the Results

A classification produces an hypothesis that there are a number of valid groupings or nested subsets present in the total set of individuals or taxa in the classification. It is desirable to test or corroborate such an hypothesis in some manner.

It may be thought that it would be possible to test the statistical significance of classifications produced by SAHN and similar programs

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by using one of the available analysis of variance (ANOVA) statistics such as an F test. However such an exercise is essentially tautological, i.e. circular in logic, and does not provide a test of the significance in such a situation (J. Robinson, pers. comm., 1987). This apparent anomaly may be explained by reducing the situation to its simplest possible form--a classification based on one variable. When a classification establishes an hypothesis that there are n subsets or groups in the data set it has done so by clustering together, around centres of difference, n sets of those entities or taxa with like values for that variable.

The ANOVA is usually a test of the null hypothesis that the means of the n groups do not differ significantly, i.e. that the groups are samples of the one population. As the classification has already used an analogous process to determine centres as different as possible from one another in producing the n groups, the use of these two techniques as a test of each other is obviously not logical. The classification has altered the statistical distribution of the data set (by clustering around centres of difference) such that it no longer meets the underlying statistical requirements for validity upon which the ANOVA is based. Thus in the situation of a classification based on one variable the use of an ANOVA has no validity (J. Robinson, pers. comm. 1987).

In a more usual situation where multiple variables have been used in a classification an ANOVA still has no validity as a test of significance of the classification, but will show which variables were used by the classification in the formation of the groups. Where the ANOVA results in a high value ("highly significant") the correlation

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of the classification and the variable is high, i.e. that variable was used in the formation of the groups. Where a low ("not significant") value is found, the classification did not make use of the variable informing the groups. Another way of expressing this is that, in this situation, the ANOVA null hypothesis is that the variable played no part in the grouping process of the classification.

As the TAXON programs used here incorporate diagnostic procedures to provide an assessment of the contribution of each variable to the formation of groups it was not necessary to use the ANOVA technique in this study.

There is no test of the <u>statistical significance</u> of a classification in existence (J. Robinson pers. comm.). It is however, possible to "test" the hypothesis by examining the usefulness and effectiveness of the classification in the real world, for example by adding more samples to see if they "fit" the proposed groups, or by examining characters not previously included in the classification to see if they follow the same pattern. These are not tests of significance in statistical terms, but may help to corroborate or support a classification.

Ordinations

There are at least two possible interpretations of the ordination results, depending on the perceived causes of and explanations for the distinctive distribution of the plotted individuals on the plots of the first and second vectors.

Interpretations of the Ordination results

1. At face value the curved distributions appear to indicate that there is not a simple linear relationship between the individuals or groups. The tendency for individuals assigned to particular groups in the classifications to be plotted closer to each other than to members of other groups would also suggest that there is a closer relationship between the individuals in those groups than to other individuals or groups. It could therefore be argued that GP θ is always separable, and that GP β and GP Ω are more or less separable in the NQ52 UPG and NQ78 classifications.

Such an interpretation would suggest that:

(i) The groups proposed by the classifications are at least partly corroborated by the ordination results;

(ii) As there appear to be at least some discontinuities within the data set, classification provides a better resolution than ordination.

2. However there is also an alternative interpretation for the distinctive curved distribution of the plotted individuals on the plots of the first and second vectors. In ecological and mathematical literature this curve is seen as an artifact of the ordination process (arch effect of Gauch, 1982; Gauch et. al. 1977, or horseshoe effect of Kendall 1971). This is primarily because the curve has been observed both in artificial and natural data sets where individuals are known or believed to vary only along a single axis/vector (a single straight line sequence exists or is believed to exist). Mathematically the curve is regarded as being caused by there being a strong quadratic relationship between the first and second axes. This

interpretation of the curve observed in the plots presented here would mean that a single linear sequence could exist in this data set.

In taxonomic terms such a sequence could be a clinal or perhaps an evolutionary relationship of gradual change from individuals at one end of the primary vector to individuals at the other end of the vector.

In terms of the groupings in the classifications (names as in the present nomenclature in brackets) this would mean that there is a gradual change from GP Ω (X. latifolia) through GP β (X. pumilio syn. X johnsonii) to GP θ (presently identified as X. johnsonii).

The geographic distribution of the individuals rules out the existence of a major geographical cline, because the members of the group are to some extent interspersed with one another (see map page 2). The possibility that there may be a gradual change in response to an environmental gradient such as rainfall or precipitation/evaporation balance is not as easily checked or excluded .

It is not clear whether this simple explanation of a curved distribution holds true in a taxonomic situation. In the ecological and artificial data sets described above (Gauch et. al. 1977, Kendall 1971) it is known in advance that the second vector is not a valid one (since a single linear sequence is known or presumed to exist). However in a taxonomic situation the validity or otherwise of the second vector cannot be known (as no single linear sequence can be assumed, or even expected). In fact the second vector may be, and from the BACRIV results presented here it seems reasonable to propose,

is, a valid vector. As such the effect of that vector on the distribution of the individuals should not be ignored or explained away.

This interpretation, coupled with the stability of the groupings produced by the classifications and the corroboration of the discriminability of those groups by DISCRIMINANT leads to the conclusion that the first of the two possible interpretations of the ordination results mentioned above (i.e. that there is not a simple linear relationship between the individuals or groups) is the most supportable. That is, discontinuities exist in the data set; the classifications are the most biologically valid representations of the data.

Summary of Ordination results and interpretations:

The curve of the distributed entities, presence of at least some discontinuities and the tendency of individuals to group i.e. individuals placed into groups by the classification are located closer to other members of the same group than to members of other groups, indicates that there is not a simple linear transitional relationship between the entities or the groups of entities as would be seen in a clinal situation. As such a situation is normally best resolved and described by classification (Sneath and Sokal, 1973 etc.) one would not expect the ordination to be the optimal expression of the relationship between the groups or entities.

In real life situations it may also be possible to find variation that is not well described by either classification or ordination, and at

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the moment such situations can only be investigated to the limit of present day techniques. It may well be that the variation present in Xanthorrhoea fits into such a category, so that whilst the classification approach gives the "best" interpretation at the present time, future techniques will give a more optimal resolution of the situation.

Relationships Between Results of the Different Classification Techniques

The UPG classification groupings are more easily interpretable as discrete groups in the PCOA plots (of the first and second vectors), and are better corroborated in their respective DISCRIMINANT analyses and classifications than are the ISS classifications groupings.

The Groups Compared

Figures 2.13 and 2.14 show a graphical representation of the groups in the NQ52 and the NQ78 classifications respectively.

GP θ is a particularly consistent group as it is either the same or consistent in three of the four classifications: It is exactly the same in both of the 78 entity classifications and that grouping is consistent with the NQ52 UPG result as the 78 entity classifications GP θ is made up of the 52 entity GP θ with the addition of a set of four of the 26 "new" individuals from south-east Queensland added to the Northern Queensland data (52 entities) to make the North and South Queensland data set (78 entities).

Figure 2.13 A graphical representation of the groups in the
NQ52 classifications.
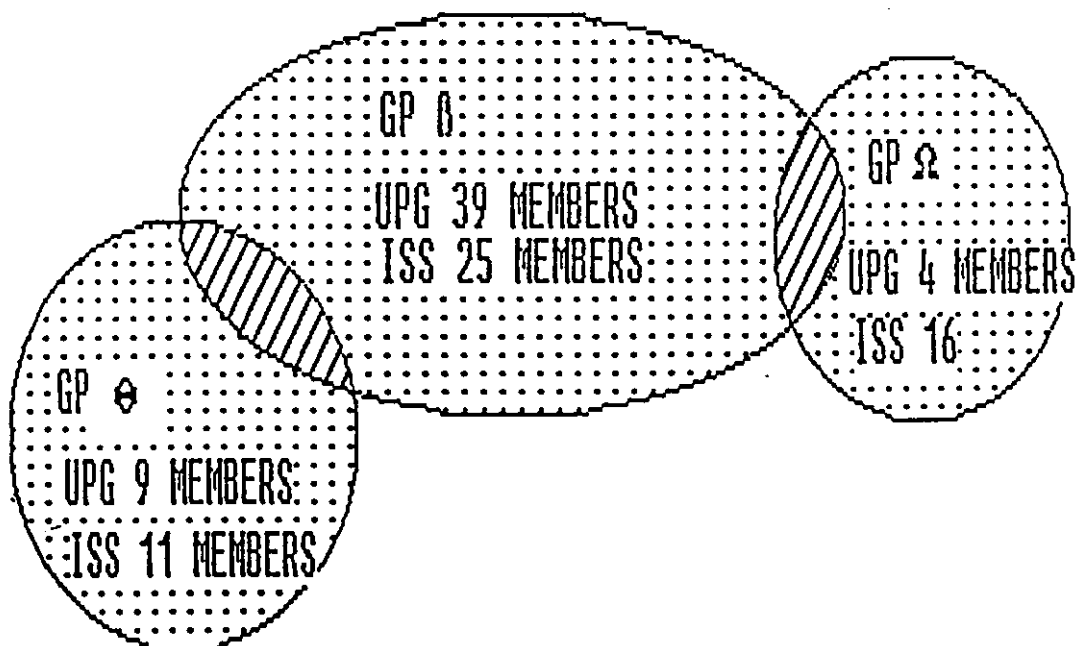
GP θ

UPG 39 MEMBERS
ISS 25 MEMBERS

GP Ω

UPG 4 MEMBERS
ISS 16

GP θ

UPG 9 MEMBERS
ISS 11 MEMBERS

```
[::]  MEMBERSHIP IN AGREEMENT  ⎫  between classification
[//]  MEMBERSHIP IN DISPUTE    ⎬  strategies
                               ⎭
```

A comparison of the groups produced

by the UPG and ISS clustering strategies.

Figure 2.14 A graphical representation of the groups in the NQ78 classifications.

NQ78 CLASSIFICATION
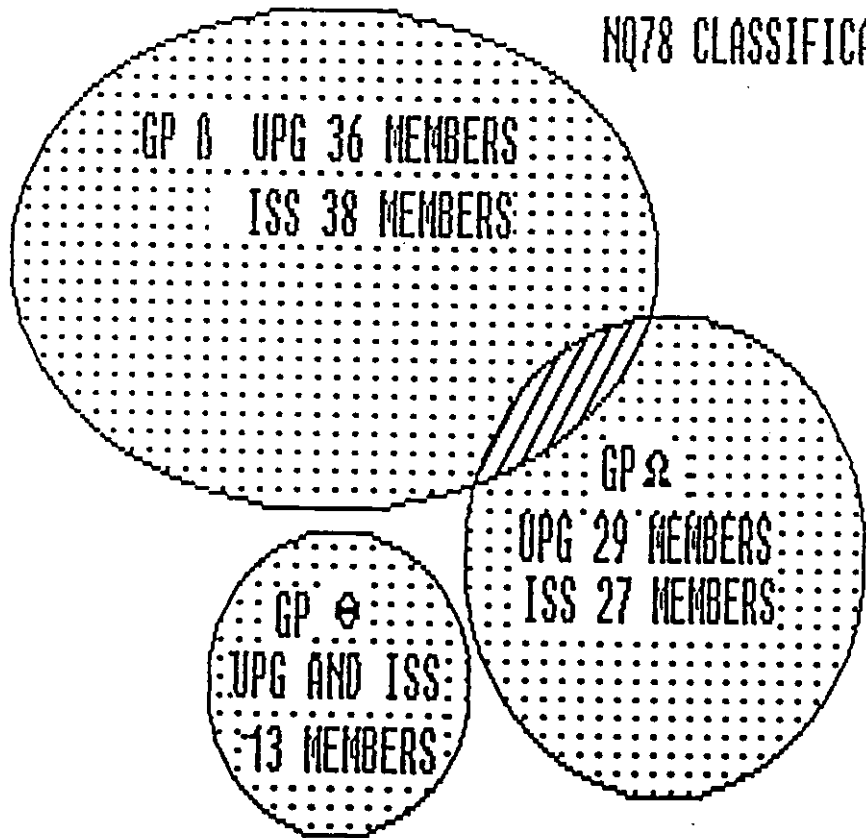
GP δ UPG 36 MEMBERS
ISS 38 MEMBERS

GP Ω
UPG 29 MEMBERS
ISS 27 MEMBERS

GP θ
UPG AND ISS
13 MEMBERS

▦ MEMBERSHIP IN AGREEMENT ⎫ between classification
▨ MEMBERSHIP IN DISPUTE ⎬ strategies

A comparison of the groups produced

by the UPG and ISS clustering strategies.

GP Ω and GP β vary somewhat between the classifications. In the 52 entity analyses there are a considerable number of transfers from GP β to GP Ω, as well as some transfers to GP θ in the ISS classification c.f. the UPG classification. Some of the transfers to GP Ω are supported by the inclusion of some of the same individuals in the 78 entity UPG classification GP Ω, but none of the transfers to GP θ are supported by either of the 78 entity classifications.

Northern Queensland and North and south Queensland Analyses

All four classifications indicate that there are three groups of individuals in the data set. Each group is similar though not identical in the different classifications. That is, each group contains a set of the same "core" individuals in all classifications. Within each classification matrix, as expressed in the dendrograms, each of the groups contains more or less equivalent levels of internal euclidean distance dissimilarity. However the statistics for each group given by GSTAT show that one of the groups (GP β) is quite variable in all classifications, especially in regard to the disordered multistate characters. The subsequent investigation of the internal structure of this group in the 36 and 39 entity analyses has so far failed to find any clear cut distinctions within the group.

CONCLUSIONS

These analyses indicate that there are three valid taxa in the complex investigated, each representing one of the three major groups consistently produced by all the full data set analyses.

One taxon (GP Ω) represents <u>X. latifolia</u> (Lee) Bedford, and its nomenclatural status is undisputed, one taxon (GP β) contains a range of variation which includes two types - <u>X. pumilio</u> R.Br. and <u>X. johnsonii</u> Lee.

There is no type that falls within the range of variation of GP θ and therefore this group requires a new name.

The classifications all indicate that the three taxa are of more or less equal rank. As the specific rank presently applying to <u>X. latifolia</u> appears satisfactory (Bedford, 1986 a), it is appropriate that the other two groups also be accorded specific rank.

The nomenclatural position of GP β is simply resolved according to the rules of botanical nomenclature giving precedence to the earliest valid publication (Stafleu 1983). The correct name for GP β is therefore <u>X. pumilio</u> R.Br. The subdivisions in this group apparent in the dendrograms do not appear to be discrete enough to justify formal nomenclatural recognition. However the status of this considerable internal variation may be clarified by further studies, most probably based on newer investigative techniques, such as protein or isoenzyme electrophoretic analyses.

GP θ requires a name. I propose to name this species after Alma T. Lee. Although the practice of naming plants after people means the loss of a valuable opportunity to convey a concise description of the species, the discovery of this species owes its start, to a considerable extent, to Mrs Lee, who first mentioned the possibility of its existence many years ago (Lee, pers. comm. 1973).

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In addition, Mrs Lee's clear thinking and astute and effective practice of taxonomy have provided an excellent example to many botanists, including myself, and is therefore deserving of permanent recognition. The species will be formally published as a paper arising from this thesis (an English description is in Chapter 5).

Formal descriptions of all these three taxa are given in chapter 5, but are included here in an abbreviated form for easier reference:

18. **Xanthorrhoea pumilio** **R.Br.**

Trunk none or up to 60 cm long; stem simple or branched; crown 1; leaves broadly spreading or recurved. Leaves transverse-linear to very depressed-obtrullate or very depressed-cuneate in T.S., 1.7-2.3 mm wide, 0.7-1.2 mm thick, green, not glaucous. Scape 50-180 cm long, rarely to 210 cm, 5-11 mm diam. Spike less than 1/4 as long as scape, 5-40 cm long, 14-23 mm diam. Cluster-bracts obscure. Packing-bracts obtuse to shortly acute, glabrous to subglabrous. Sepals shortly acute, without beak or beak very short, sometimes with a short median abaxial ridge, without proboscis, glabrous. Petals recurved, with proboscis, glabrous except hirsute apex.

20. **Xanthorrhoea latifolia** **(A. Lee) Bedford**

Trunk none or up to 3.6 m long; stem branched or single; crowns 1 to many, each with spreading mature leaves; young leaves in ± erect tuft. Leaves narrowly transverse-rhombic to very depressed-cuneate in T.S., 2.4-10 mm wide, 0.7-3.5 mm thick, bright-green, not glaucous. Scape 75-210 cm long, 7-20 mm diam. Spike shorter than or almost equal to scape, 30-150 cm long, 18-41 mm diam. Cluster-bracts obscure. Packing-bracts obtuse, shortly acute to acute, glabrous to fringed with hairs, sometimes abaxially hirsute. Sepals shortly acute to acute, without proboscis, with short beak and median abaxial ridge, subglabrous to slightly hirsute. Petals recurved, with proboscis, glabrous except at apex.

23. **Xanthorrhoea almae** **sp. nov.**

Trunk 10 cm to 5 m long, usually 30 cm to 2 m; stem and crown usually 1; young leaves in spreading upright tuft; old leaves often strongly reflexed. Leaves ± quadrate-rhombic to transverse-rhombic in T.S., 1-2.5 mm wide, 0.8-1.8 mm thick, green, not glaucous. Scape 75-190 cm long, 7-20 mm diam. Spike 0.75-1.25 as long as scape, 20-120 cm long, rarely to 225 cm, 20-40 mm diam. Cluster-bracts prominent only in lower portion of spike, acute to narrowly triangular, subglabrous to moderately hirsute. Packing-bracts shortly acute to acute, the distal 1/3 subglabrous to moderately hirsute. Sepals shortly acute, beak absent or very short, sometimes with proboscis, often with median abaxial ridge, glabrous to subglabrous. Petals erect to recurved, with proboscis, glabrous except some hairs abaxially at apex.

CHAPTER 3

STUDIES IN INTERGRADATION

BETWEEN XANTHORRHOEA SPECIES

3.1 Introduction

Both hybridism and, to a lesser extent, clinal variation have been proposed to explain the apparent blurring of taxonomic boundaries and the occurrence of individuals intermediate between recognized taxa (Lee, 1966 a and b). Many of these apparent intermediates have since been recognised as distinct, though often "cryptic", species (Bedford, 1986 a and b). However, some reported examples of intermediacy remain unresolved, as discussed below.

The taxa involved include: (a) X. fulva; (b) X. glauca subsp. glauca; (c) X. almae; (d) X. arborea, and; (e) X. latifolia. Bedford (1986 a) discusses intergradation between (a), (b) and (c), and Lee (1966 a and b) mentions intergradation between all of the above taxa.

3.1.2 X. fulva and X. glauca subsp. glauca

These taxa are distinguished from each other by the diagnostic characters: trunk height; leaf T.S. shape; leaf thickness; scape length and diameter; spike length and diameter; colour; shape and hairiness of the packing-bracts; presence/absence of prominent cluster-bracts.

These two taxa are not usually sympatric and occupy distinct habitats. X. fulva is restricted to poorly drained, periodically waterlogged sites on the Quaternary sands, along the coastal strip from Wyong in New South Wales to Maryborough in Queensland. X. glauca is restricted to well drained soils and is also usually on more fertile soils further inland than X. fulva, most often occurring west

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of the dividing range from the Snowy Mountains in N.S.W. to Gayndah in
Queensland.

However, in a number of sites along the coast, including Myall
Lakes National Park, Hat Head N.P., Limeburners Creek Reserve and the
coastal sands near Byron Bay, both species occur close together on the
coastal sand masses. When this happens, morphological intergradation
is occasionally observed and this has for some time been interpreted
as hybridization, e.g. Lee (1966 a and b) and Johnson (pers. comm.
1978).

The New South Wales coast from the Queensland border to the Hunter
River has many examples of Quaternary sand deposits protected by rocky
headlands. There are many sites in these extensive sand deposits
where the same taxa that meet at Myall Lakes occur adjacent to each
other. A survey of these populations was conducted to test whether
similar situations to that found at Myall Lakes occurs in these sites.

3.1.3 Intermediacy between X. fulva and X. almae

In south-east Queensland there are extensive sand deposits along the
coast such as at Cooloola and Beerwah, as well as the offshore islands
of Stradbroke Is, Fraser Is etc. Although X. glauca is not found on
these sands, another species, X. almae (fairly closely related - see
Chapter 4) takes its ecological niche, and is also sometimes seen to
appear to intergrade with X. fulva.

X. arborea and X. latifolia on the other hand are species found only
on older soils, i.e., sandstones and pre-Quaternary, "less

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consolidated" sediments respectively. These two species are very similar in appearance. They do not usually meet, but where they do they seem to merge into one another (Lee, 1966 a). An example of such a situation is behind Pearl Beach in Brisbane Waters National Park.

In discussions about causative factors and distribution patterns for hybrids in the relevant literature the concept that hybrids occupy intermediate habitats is a well accepted one, whether it is postulated that the intermediacy is due to disturbance "hybridization of the habitat" (e.g. Anderson, 1949) or natural causes (e.g. Leach and Whiffen, 1978).

It appears then, that hybridisation possibly does occur in Xanthorrhoea but is restricted in distribution to particular localities and environmental conditions, probably only along the east coast of Australia.

To test this hypothesis four sites of contact between species which were thought to hybridise were examined. Two sites, at Myall Lakes and at Pearl Beach, were examined in detail, as the major analyses, and two sites, northern New South Wales and Beerwah in south-east Queensland, in somewhat less detail, as subsidiary analyses.

3.1.4 Voucher specimens

In all studies samples were collected as voucher specimens kept at SYD.

3.2 Site 1: Myall Lakes.

3.2.1.1 Materials and Methods

A mass flowering of Xanthorrhoea occurred in a swamp heath east of the
sand mining road north of Bombah Broadwater in Myall Lakes National
Park in 1978 (Plate 3.1 and Figure 3.1) following an earlier bushfire.
Plants growing on low dunes had a completely different growth habit
and morphology from plants growing in the swamp. However along some
gentle gradients there is an apparent continuum of habit and
morphology from small plants in the swamp, through intermediate sized
plants, to tall trunked plants on top of the hill. On steeper
gradients there were no intermediate plants observed.

Five transects of varying length were run from one side to the other
of this population of Xanthorrhoea covering the sand rise and adjacent
wet heath swamp (Figure 3.2). All plants within one metre each side
of the transect line were measured, making the areas surveyed each two
meters wide. Forty plants occurred in the area covered by the five
transects.

Four transects (A, C, D, E) ran from the top of the rise into the
swamp, one (B) ran through a slight depression to an adjacent rise.
The distance from the origin was recorded for each plant.

Carolin (1971) and Myerscough and Carolin (1987) have discussed
zonation of vegetation with small changes in elevation at Myall Lakes,
and other similar situations have been reported elsewhere on the east
coast (Clifford and Specht, 1979) and on other sand systems

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Plate 3.1 Myall Lakes Study Area. Tagged spikes along one of the five transects in the mid ground.

Figure 3.1 Myall Lakes Study area location map.

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LOCATION MAP AND SAMPLE AREA
ROCKY HILLS SHOWN WITH CONTOURS AT 10M INTERVALS

Pigeon Point

BOOLAMBAYTE

LAKE

PALMERS BAY

Lemon
Tree
Point

Sheep
Island

VIOLET HILL PASSAGE

Goat
Island

BOOLAMBAYTE

LAKE

Bombah
Point

Howks Nest Seal Rocks Road

The Bombah Sands (dunes)

PACIFIC OCEAN

BOMBAH BROADWATER

MARKWELL

WOOTTON

Forster

CHARL-
OTTE
BAY

Bulandelah
BULAHDELAH

MYALL
LAKE

SEAL
ROCKS

THE BRANCH

BOMBAH
POINT

Mungo Point

STUDY AREA

Port Stephens

KEY:

SAMPLE AREA

Figure 3.2 Study area and transect lay-out, Myall Lakes.

(1) Five transects are shown on a contour map of the site
layout. A1-A12 mark the positions of the first and last
plants on transect A. Transects B-D are similarly depicted.

STUDY AREA IN BOMBAH SWAMP , MYALL LAKES NATIONAL PARK
DIAGRAMMATIC PLAN VIEW OF TRANSECTS WITH
APPROXIMATE CONTOURS AT 10 CM. INTERVALS
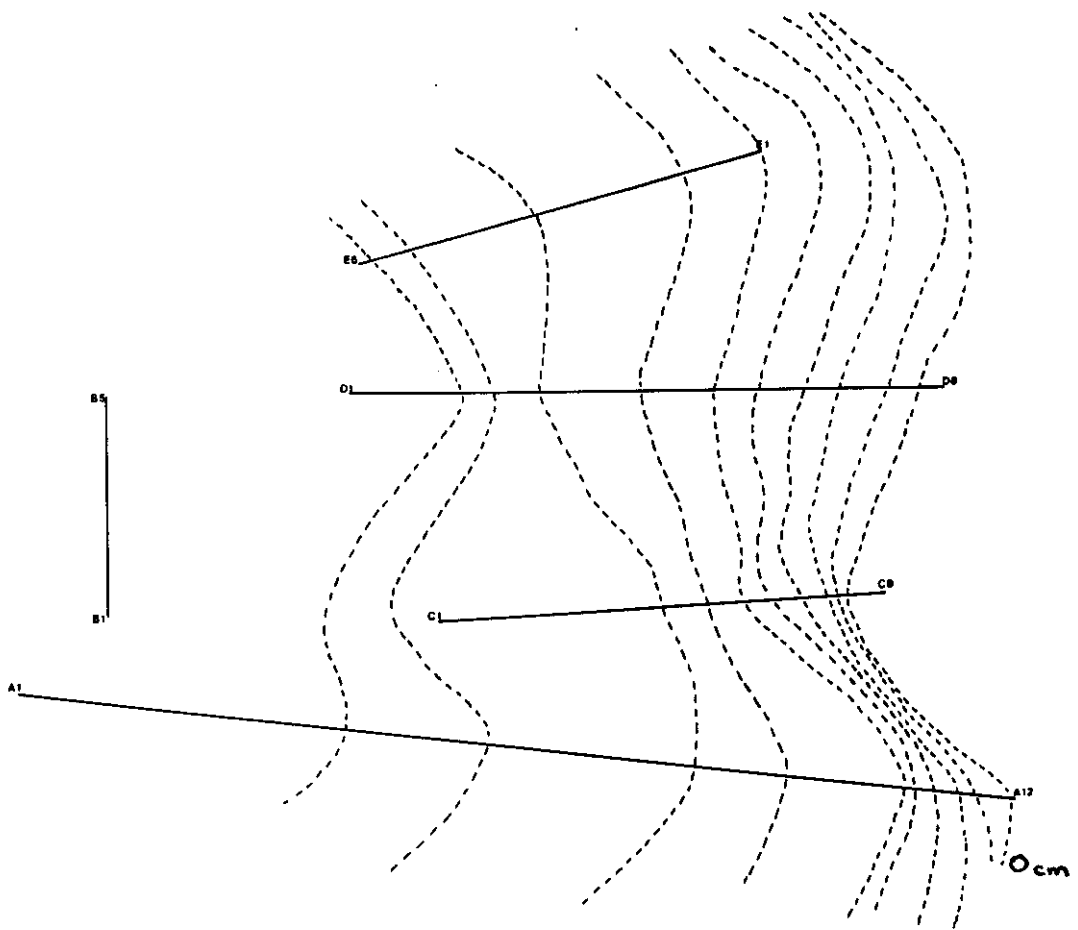
(e.g. Wiedmann, 1966, cited in Newman, 1983; Whittaker, 1975; Groves and Specht, 1978). The conclusion has also been drawn that the depth from the sand surface to the water-table is a critical factor in determining the distribution of many species at Myall Lakes (Myerscough and Carolin, 1987; Clements, 1988) and in similar sand dune environments elsewhere (Willis et al., 1959 a and b; Ranwell, 1959 and 1960; Onyekwelu, 1972; Newman, 1983).

Two analytical techniques have been used in the study: (a) The numerical classification and ordination of morphological characters using the TAXON library of programs on CSIRONET, and these were compared with; (b) measurements of three ecological site factors.

3.2.1.2 Numerical Analyses of Plant Morphology.

Characters

Fourteen separate morphological features were scored for each plant, either as continuous characters (C) or as disordered multistate characters (DM) (Table 3.1). Characters 1- 9 were recorded in the field, and 10 - 14 were measured or calculated in the laboratory. These characters were chosen because they have previously been proved useful in the delimitation of taxa (Lee, 1966 a and b, Bedford, 1986 a).

Numerical Analytical Techniques

A similar suite of programs to that used in chapter 2 was applied. However as these analyses were carried-out at an earlier date to the

Table 3.1   Morphological characters used in the analyses

1.	Trunk height	C
2.	Leaf width	C
3.	Leaf thickness	C
4.	Leaf T.S. shape	DM
5.	Leaf colour	DM
6.	Scape length	C
7.	Scape diameter	C
8.	Spike length	C
9.	Spike diameter	C
10.	Ratio of spike length to scape length	C
11.	Prominence of cluster bracts	DM
12.	Bract colour at flowering	DM
13.	Density of bract hairs	C
14.	Bract shape	DM

Key C = continuous, DM = disordered multistate

Table 3.2   Equivalent names for programs in different versions of the
TAXON package

Version Number
  1   4

MULCLAS = MSED+SAHN+DENDRO

GROUPER = GSTAT+GCOM+CRAMER

GOWER   = PCOA+PTPLOT

GOWECOR = BACRIV

final analyses for chapter 2, an earlier version of the TAXON package, (V.1), was used (Dale et al., 1979). This version used the same algorithms in very similar analyses to those used in Version 4 as described in full in chapter 2 but had different names for the programs as well as a somewhat different output format. Equivalent program names are given in Table 3.2 (above). Because of the essential similarity of techniques used, readers are referred to the rationale and detailed explanations in chapter 2 for further information about these analyses.

The 40 plants were analyzed on the 14 equally weighted characters in both a MULCLAS classification and in the principal co-ordinate analysis (GOWER), with the diagnostic programs GROUPER and GOWECOR respectively. These were all based on the same Euclidean Distance dissimilarity matrix, using the strategies developed for mixed data/character types by Lance and Williams (1967) and Burr (1968). Both Group Average (GA) and Incremental Sum of Squares (ISS) clustering techniques were used in the classifications to test the reliability and stability of the clusters (Clifford and Stephenson, 1975).

3.2.1.3 Ecological Measurements

At first sight the features of the habitat most obviously related to the distribution of the two taxa and their intermediates were their relative locations and altitudes and the colour of the soil; the last apparently due to variation in organic matter content. Measurements were therefore made of these features together with the depth to the water-table, which clearly relates to the altitude in these sands

(Myerscough and Carolin, 1987).

The following site variables were measured:

(1). percentage of organic matter in the soil by the loss on ignition technique. This seems to reflect the overall water-logging of the soils since water-logging reduces the rate of organic decay and thus prevents the leaching of humates

Soil organic matter was estimated using loss on ignition (Chapman, 1976). Soil samples were processed by the standard technique in use at the University of Sydney School of Biological Sciences, i.e. oven-dried at 105 °C then placed in a muffle furnace at 400 °C for 16 hours. The loss in weight is expressed on a dry weight basis (Table 3.3).

(2). the depth to the water-table below the surface.

Measurements of the depth to the water-table below the ground surface were made with a 100 mm diameter soil auger beside each plant. The depth to the water below the soil surface was measured with a metre rule (Table 3.3). Measurements were all made within a 24 hour period to ensure consistency of results. Thus this is a measure of the depth of the water-table relative to the soil surface at each point at which it was taken but not a measure of average water-table over a long period.

H.I. = habitat index C.H.I = cumulative total of the habitat index. The individual habitat indices were calculated by scaling the environmental variables such that their lowest figure became equal to zero and their highest figure became equal to 100, then expressing individual measurements in terms of a range from 1-100 (except that for the organic matter in the soil habitat index the scale was inverted to maintain the pattern of the other indexes, i.e. the lowest figure became 100, and the highest became 0). The cumulative habitat index was calculated adding the 3 index figures for each plant.

Table 3.3 Environmental Measurements (* means missing data).

Individuals sampled no.	Transect no.	Distance from origin	% Organic component of soil	H.I.	Altitude cm	H.I.	Water-table depth cm	H.I.	Cum. Habitat Index (C.H.I.) (total)
1	A1	0.0	4.7	98.8	112	100.0	97	94.4	293.2
2	A2	0.6	4.7	98.8	112	100.0	97	94.4	293.3
3	A3	21.9	3.7	100.0	100	89.3	87	75.9	265.2
4	A4	22.2	4.0	99.7	100	89.3	87	75.9	264.9
5	A5	26.5	4.3	99.3	102	91.1	90	81.5	271.9
6	A6	57.0	22.5	77.8	74	66.1	63	31.5	175.4
7	A7	57.5	22.5	77.8	74	66.1	66	37.0	180.9
8	A8	58.0	22.5	77.8	74	66.1	69	42.6	186.5
9	A9	60.5	14.2	87.6	65	58.0	63	31.5	177.1
10	A10	64.0	22.5	77.8	58	51.8	59	24.1	153.7
11	A11	65.0	31.0	67.8	50	44.6	58	22.2	134.6
12	A12	68.0	39.9	57.3	15	13.3	50	7.4	78.0
13	B1	0.0	6.4	96.9	95	84.8	*	*	*
14	B2	1.4	7.5	95.5	81	72.3	*	*	*
15	B3	5.2	*	*	60	*	*	*	*
16	B4	10.2	*	*	56	*	*	*	*
17	B5	15.4	*	*	87	*	*	*	*

Table 3.3 Environmental Measurements continued (* means missing data).

| Individuals sampled | | | ENVIRONMENTAL FACTORS MEASURED | | | | | | Cum. Habitat |
no.	Transect no.	Distance from origin	% Organic component of soil	H.I.	Altitude cm	H.I.	Water-table depth cm	H.I.	Index (C.H.I.) (total)
18	C1	0.0	7.8	95.2	85	75.9	77	57.4	228.5
19	C2	6.0	6.6	96.6	85	75.9	77	57.4	229.9
20	C3	12.0	6.6	96.6	79	70.5	71	46.3	213.4
21	C4	14.8	13.3	88.7	87	77.7	80	63.0	229.4
22	C5	16.0	13.3	88.7	82	73.2	77	57.4	219.3
23	C6	17.6	16.9	84.4	77	68.8	75	53.7	206.9
24	C7	18.3	16.9	84.4	75	67.0	78	59.3	210.7
25	C8	20.5	25.6	74.2	65	58.0	75	53.7	185.9
26	C9	30.5	88.4	0.0	5	4.5	46	0.0	4.5
27	D1	0.0	*	*	105	93.8	93	*	*
28	D2	6.6	*	*	102	91.1	*	*	*
29	D3	11.0	*	*	88	78.6	*	*	*
30	D4	14.9	*	*	80	71.4	*	*	*
31	D5	31.1	*	*	53	47.3	*	*	*
32	D6	35.7	*	*	53	47.3	*	*	*
33	D7	36.0	*	*	50	44.6	*	*	*
34	D8	42.0	*	*	0	0.0	*	*	*
35	E1	28.0	15.5	86.1	65	58.0	63	31.5	175.6
36	E2	26.8	6.3	96.9	65	58.0	66	37.0	191.9
37	E3	17.6	4.6	98.9	81	72.3	82	67.0	238.2
38	E4	16.0	4.6	98.9	81	72.3	82	67.0	238.2
39	E5	5.9	4.4	99.2	86	76.8	84	70.4	246.4
40	E6	0.0	4.1	99.6	103	92.0	100	100.0	291.6

(3). the relative altitudes of plants (topography).

Elevation above an arbitrary datum was measured using a surveyors Alidade. The levels were measured in cm above or below the arbitrary benchmark and are given corrected to cm above the lowest point (Table 3.3).

Environmental factors (1) and (2) were presumed to be site variables and were therefore measured across the site rather than for every transect. Measurements were made for every plant on three of the transects (A, C and E - one transect at each edge of the study area and one in the centre), making twenty nine measurements for each of these characters. Forty measurement were taken for character (3), i.e. for all of the plants for all transects.

3.2.1.4 RESULTS - Numerical Analyses of morphological characters of individual plants

Group Average clustering (GA). The dendrogram of the Group Average classification (Figure 3.3, and Appendix 3.1) has two major clusters at about the 0.80 level of dissimilarity. However, the six subgroup level (MULCLAS groups 64, 68, 71, 72, 73 and 74 on the dendrogram by the .65 level of dissimilarity) was chosen for the GROUPER analysis to examine the high levels of dissimilarity in the major groups.

The plants are divided into two main groups, 76 and 78, at about the 1.8 level of dissimilarity. The average plant described by GROUPER for group 76 has characteristics of X. glauca subsp. glauca, while

Figure 3.3 GROUP AVERAGE Classification Dendrogram, Myall Lakes.

Key: ▦▦ X. fulva; //// X. glauca; XXXX Intermediates.

A1, A2, ETC. ARE PLANT TRANSECT POSITION NUMBERS.

Figure 3.03 MYALL 40 UPG ANALYSIS DENDROGRAM WITH TAXA AND TRANSECTS MARKED
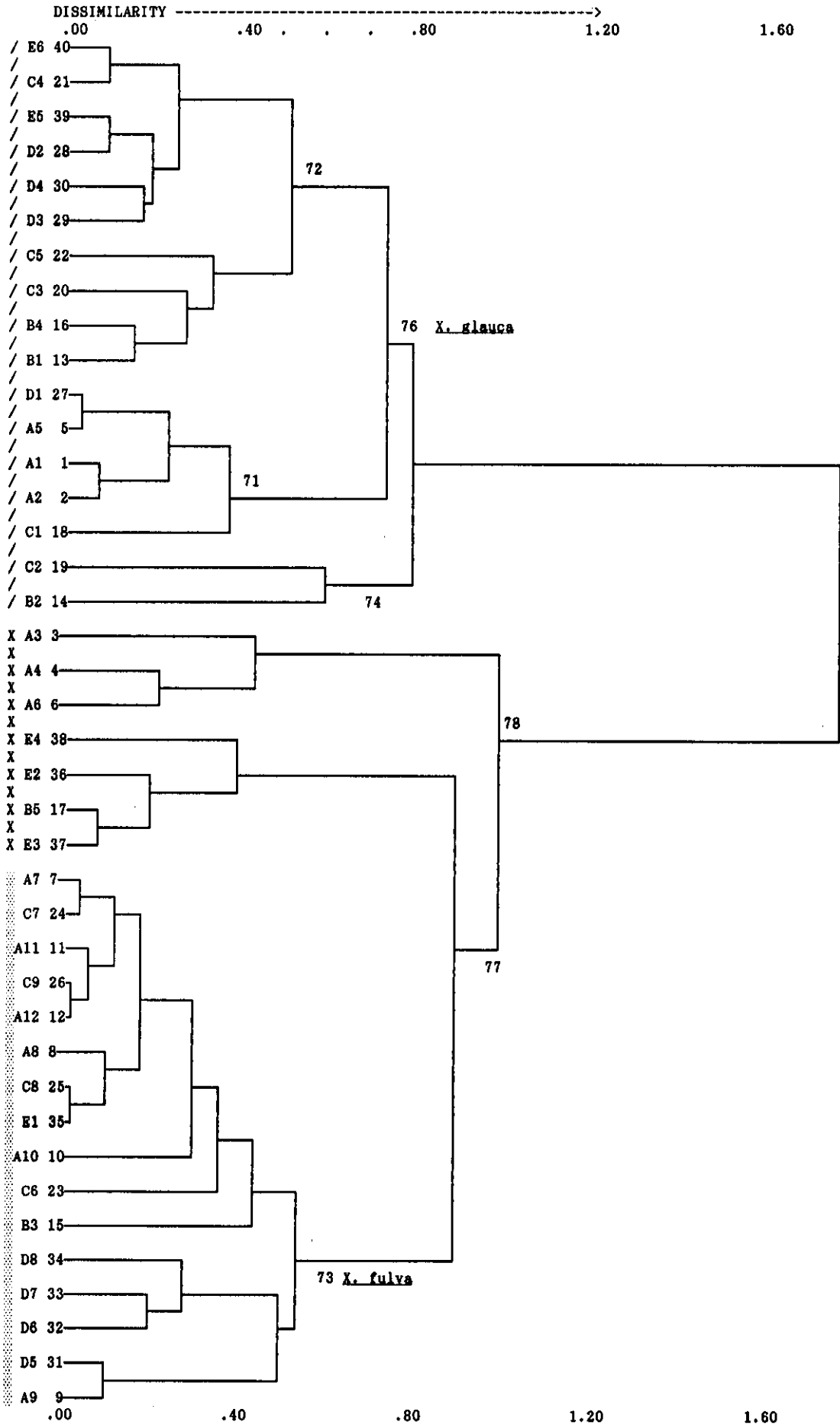
that for group 78 has most of the characteristics of X. fulva (Table 3.4). However, as is obvious from the dendrogram, both subgroups (i.e. 76 and 78) contain significant levels of dissimilarity and can be further subdivided.

It is of note that the characters used by GROUPER include the diagnostic characters separating the two species. In the X. glauca subsp. glauca group (76), there are three major MULCLAS subgroups (71, 72 and 74). These subgroups have predominantly the characteristics of X. glauca subsp. glauca with a small admixture of the characteristics of X. fulva, as well as characteristics intermediate between these two. In the X. fulva group (78) there are also three distinct divisions, MULCLAS subgroups 68, 73, and 64. GROUPER indicates that subgroup 73 has mostly the characteristics of X.fulva with only a very small number of X. glauca subsp. glauca characters. Subgroup 68 represents plants with intermediate morphology between the two taxa, they have inflorescence characters similar to both taxa and are intermediate in other characters such as leaf T.S. shape. The characteristics of subgroup 64 are also intermediate between X.fulva and X. glauca subsp. glauca. In this case, however, the dimensions of the plants and their vegetative morphology are closer to the pure X. glauca subsp. glauca form, though still distinctly intermediate, whilst some bract characters are closer to X. fulva.

Incremental Sum of Squares clustering (ISS).

(Figure 3.4 and Appendix 3.2)

Once again there is a major division into two groups representing, on the one side, predominantly X. glauca subsp.

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Table 3.4   GROUPER Group Average classification, Myall Lakes.

order	Characters	Group 76 (X.glauca)	Group 78 (X. fulva and "intermediates")	% Dissim.
1	Bract colour at flowering	green	light to dark-brown	13.6
2	Bract shape	most triangular	most obtuse	13.0
3	Prominence of cluster-bracts	most more than at base-only	most absent some base-only	11.0
4	Bract hairiness	glabrous to sparse	very hairy	10.0
5	Trunk height	Av. 79.5 cm	Av. 5.7 cm	8.2
6	Scape diam.	Av. 43 mm	Av. 18 mm	8.0
7	ratio of spike length - scape length	Av. 5.4:1	Av. 1:1	8.0
8	Spike diam.	Av. 59 mm	Av. 30 mm	7.0
9	Scape length	Av. 45 cm	Av. 95 cm	7.0
10	Spike length	Av. 239 cm	Av. 90 cm	6.0

Figure 3.4   ISS Classification Dendrogram,   Myall Lakes.

Key: ▦▦   X. fulva;   ////   X. glauca;   XXXX   Intermediates.

XX■ ■XX   individuals added to the intermediates group

in this classification strategy c.f. the UPG strategy.

Figure 3.04 MYALL ISS DENDROGRAM
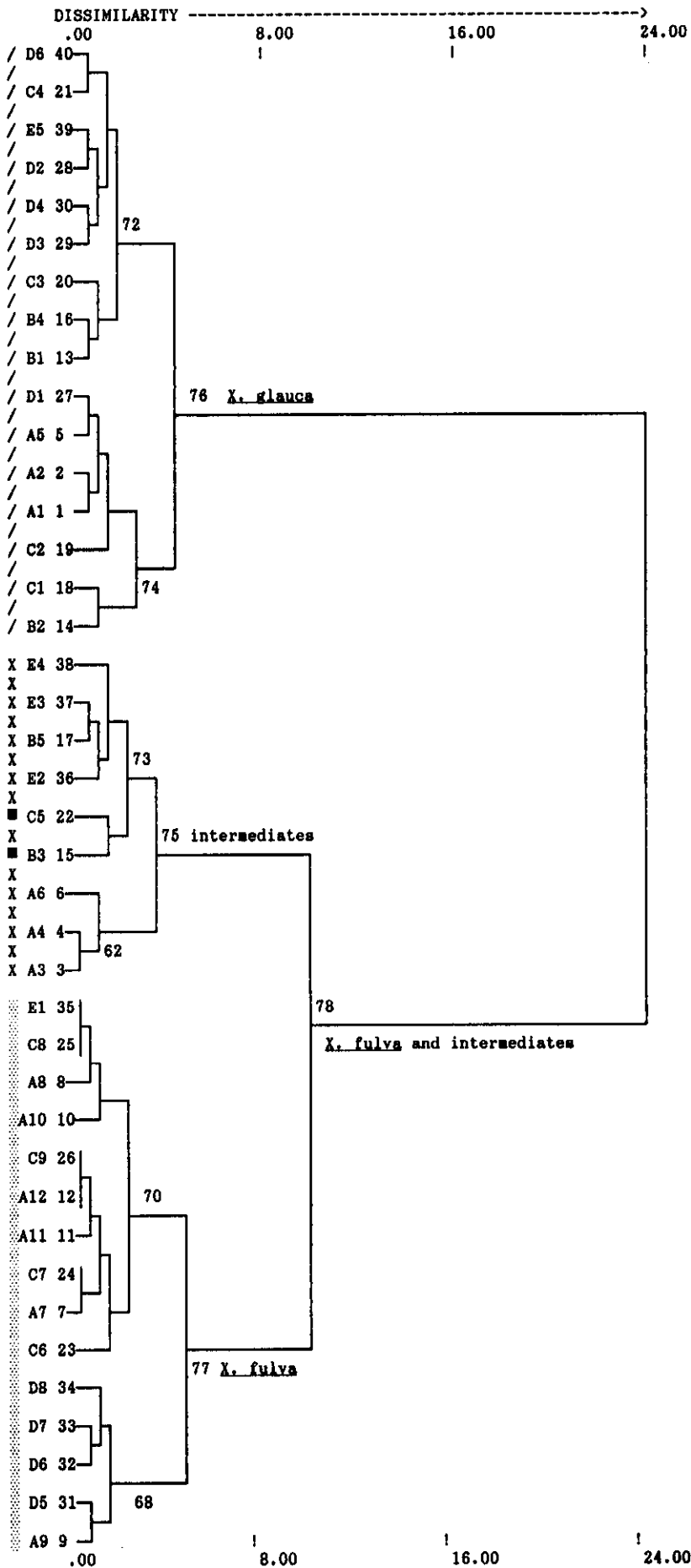
glauca (group 76) and, on the other side, a mixture of X. fulva

and plants intermediate between the two taxa (group 78). However, as

a direct consequence of the ISS algorithm the dissimilarity levels in

this classification are much higher than those in the Group Average

classification. This is due to the intensely clustering nature of the

ISS classification, not a reflection of higher levels of dissimilarity

between the plants (Dale et al., 1979; Clifford and Stephenson, 1975).

Ordination - GOWER and GOWECOR

(Plots of the three major vectors are presented in Figure 3.5.1-3.5.3,

entity/vector scores are in Appendix 3.3, GOWECOR results Table 3.5)

The first vector in GOWER represents 60 percent of the total

dissimilarity in the matrix, vector 2 represents a further 10.5

percent and vector 3 a further 7.6 percent. The first three

vectors together represent 78.1 percent of the total

dissimilarity indicating that the ordination is a very

successful representation of the data in this situation

(Clifford and Stephenson, 1975).

The first vector shows the widest distribution of entities in

the data, with individuals separated by the classifications

placed at opposite ends of the primary axis, and the third group of

individuals - the apparent intermediates - spaced between

them along the axis. The second and third vectors indicate only

minor additional influences on the data and as such are only of

use in combination with the first vector.

Figure 3.5.1 GOWER Ordination, Myall Lakes,

Plot of Vectors 1 and 2.

Key: ▦ <u>X. fulva</u>; //// <u>X. glauca</u>; Intermediates

in the middle, unassigned.

Putative ecocline shown <<═══════════>>

(This is a reflection of the ecocline through its

selection effect on the taxonomic morphological

characters used for the ordination)

Figure 3.5.1 Myall lakes GOWER Plot Vectors 1 and 2.

Figure 3.5.2 GOWER Ordination, Myall Lakes,

Plot of Vectors 2 and 3.

Taxonomic groupings less well defined,

therefore not marked.

Vectors 2 and 3.

```
************************************************************************
*                                          T                          *
*                                          H                          *
*                                          R                          *
*                                          E                          *
*                                          E                          *
*                           19             !                          *
*                                          !                          *
*                                          !                          *
*                                          !                          *
*                                          !                          *
*                                          !                          *
*               24                         !                          *
*                                          !                          *
*                  23                       !   20                     *
*                           7              !                          *
*                           11             !                          *
*                                          !   33                      *
*                                          !       40                  *
*                        12                !                          *
*                                          !                          *
*                                          22              21          *
*                             26           !                          *
*               2                          8!          39  29    31    *
*                             14           !                  28        *
* TWO    --------------------------------------- 27----------- 30------- TWO *
*                                  15      !                          *
*                                          !                          *
*                                 25  350  13      32                  *
*                                          !                16    9    *
*                                          !                  34        *
*               1                          !                          *
*                                          !                          *
*                                          !          3717            *
*                                          !                  36        *
*        6                                 !                      38    *
*                                          !                          *
*                                          !                          *
*                             5            !                          *
*        4           18                    !                          *
*                                          !                          *
*                                          !                          *
*                  3                       T                          *
*                                          H                          *
*                                          R                          *
*                                          E                          *
*    3^   2>                                E                          *
************************************************************************
```
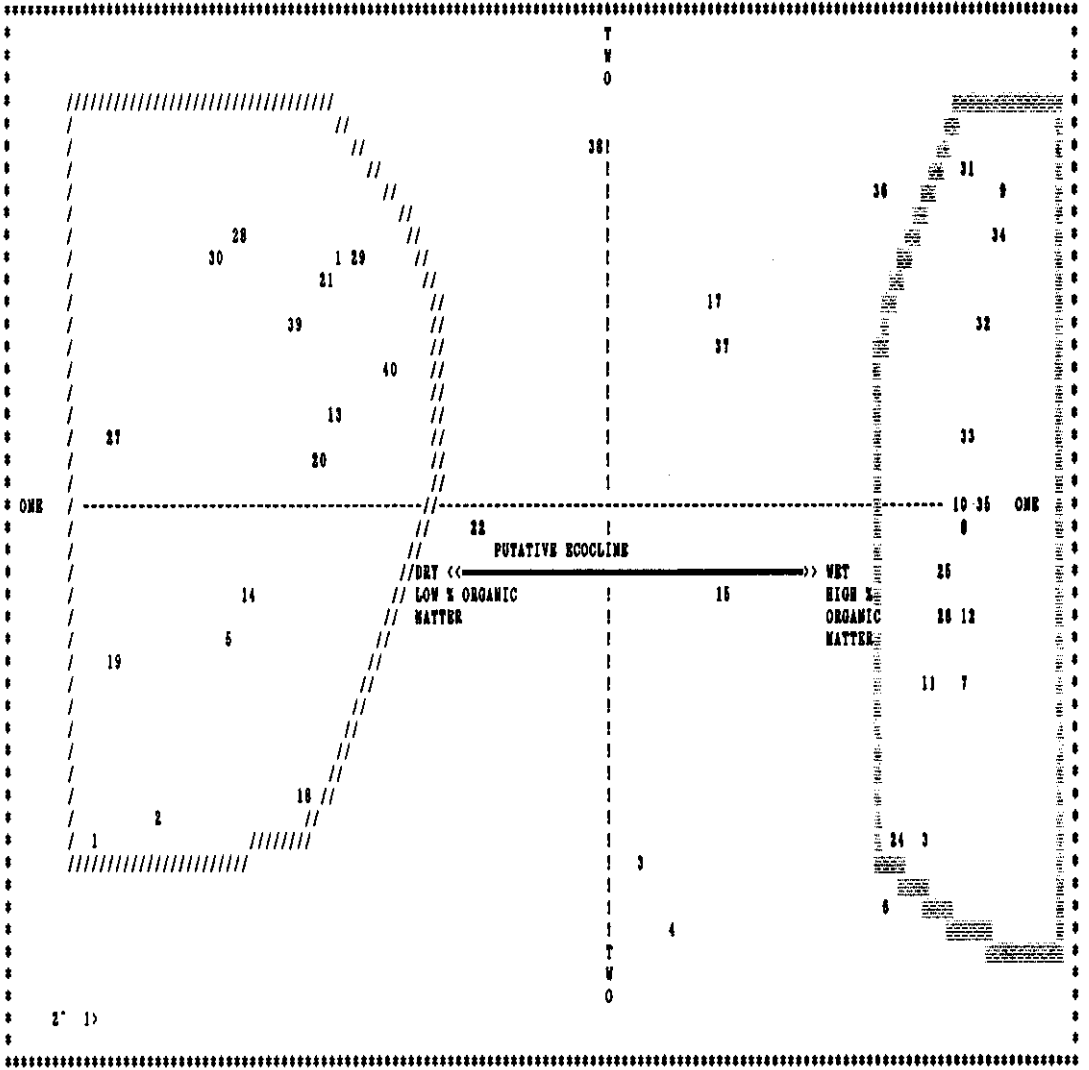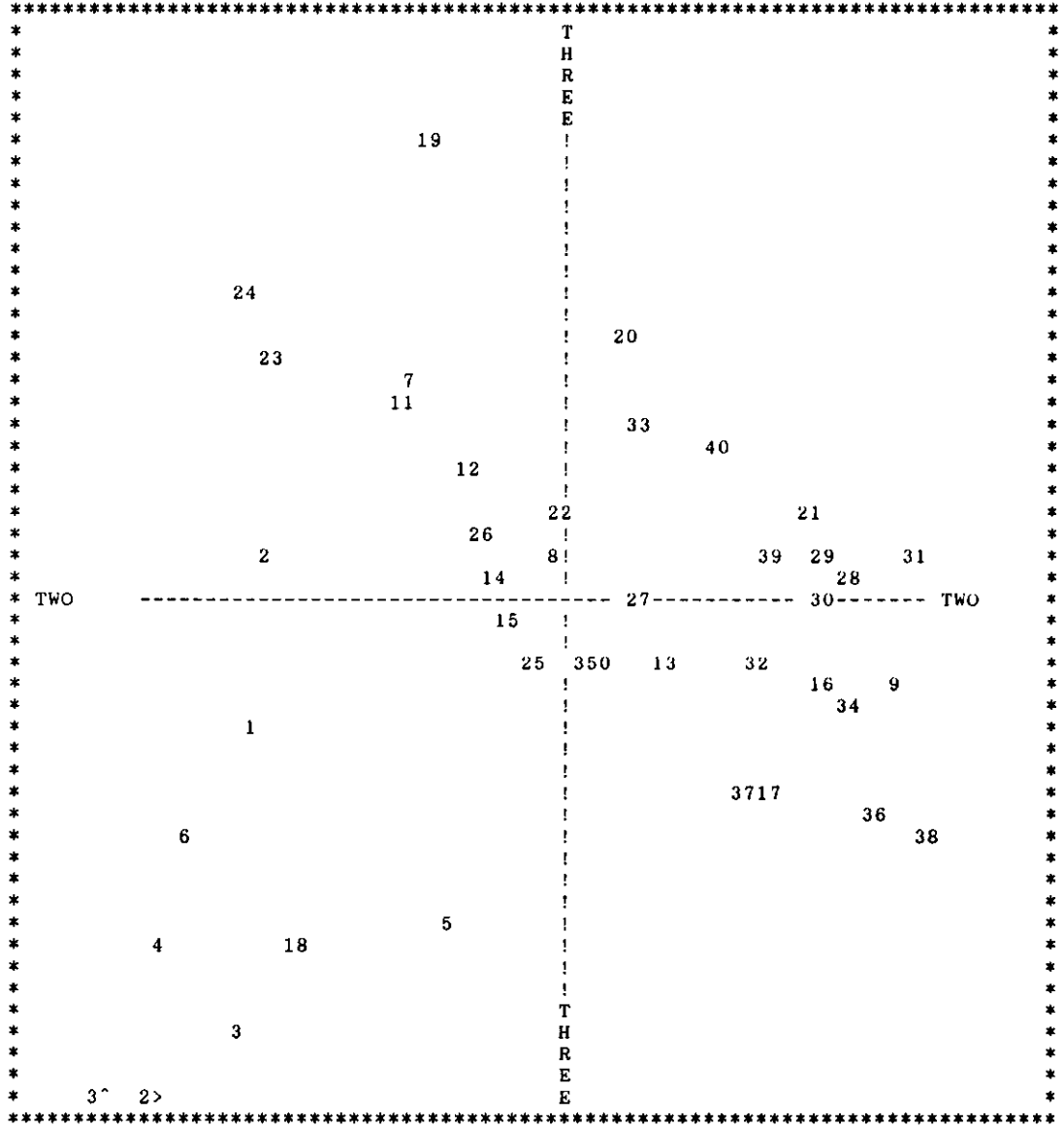
Figure 3.5.3 GOWER Ordination, Myall Lakes,

Plot of Vectors 1 and 3.

Taxonomic groupings not separated so not marked.

Vectors 1 and 3.
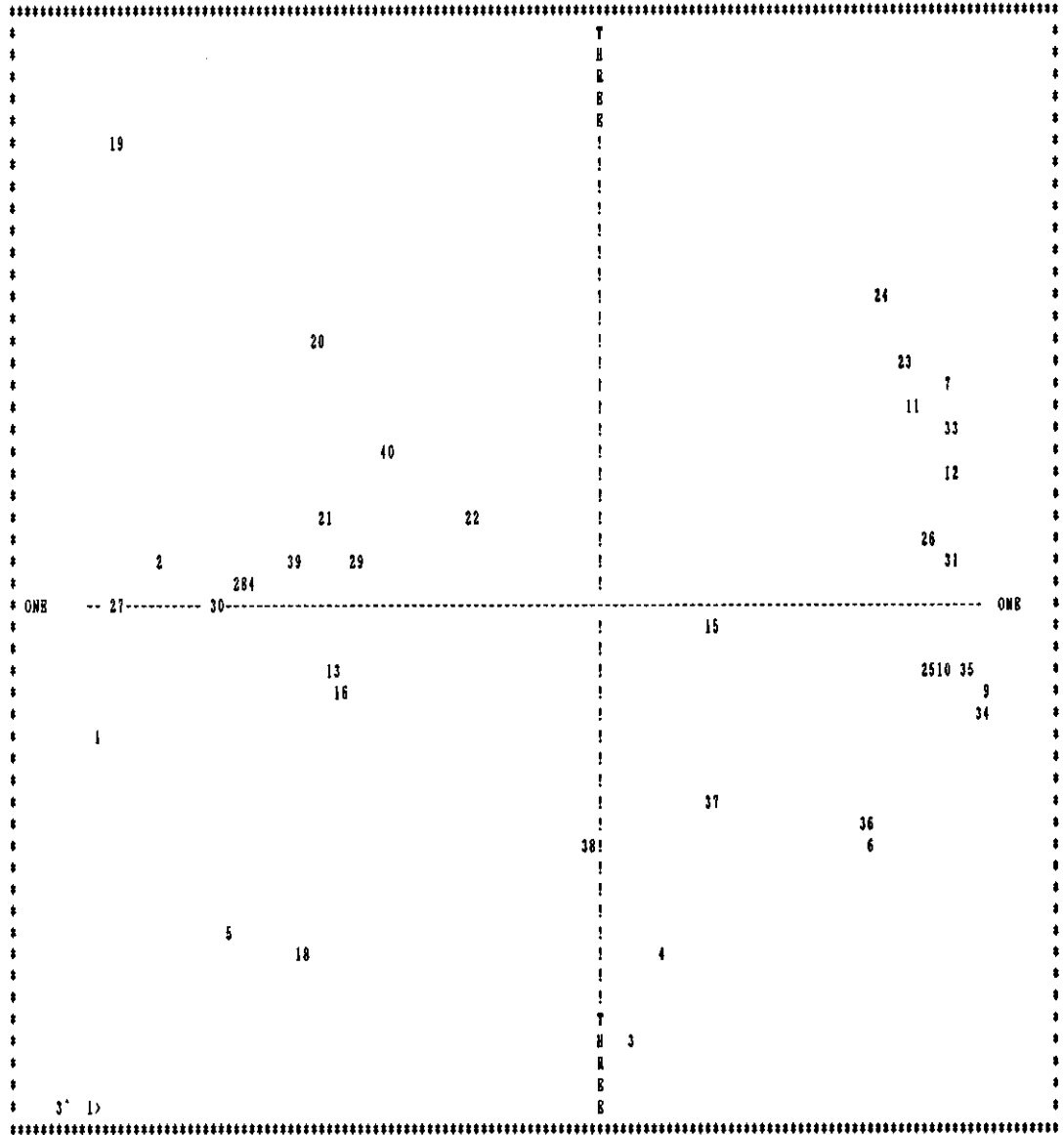
Table 3.5 GOWECOR (Gower Correlation Co-efficients) Results for Myall Lakes analysis.

Table 3.5 GOWECOR Results Myall Lakes.

<u>Vector 1</u>

-.9843	Bract colour: green		.9843	Bract colour: light-brown
-.9483	Scape diameter		.9470	Bract indumentum: densely
-.9448	Ratio of scape length to			hirsute
	spike length		.9143	Bract shape: obtuse
-.9143	Bract shape: linear-		.8502	Scape length
	triangular		.6379	Cluster bracts: not
-.9138	Spike diameter			prominent
-.8923	Spike length		.2997	Leaf shape: obtriangular
-.8833	Trunk height		.2499	Cluster-bracts: prominent
-.8423	Cluster bracts: prominent			only at base of spike
	for whole of spike			
-.4237	Leaf shape: quadrate-			
	rhombic			
-.2958	Leaf thickness			
-.2179	Leaf width			
-.1398	Bract shape: shortly acute			

<u>Vector 2</u>

-.7622	Leaf thickness		.6401	Leaf shape: obtriangular
-.5335	Cluster bracts: not		.5085	Cluster bracts: prominent
	prominent			only at base of spike
-.3881	Leaf shape: quadrate-		.3052	Bract shape: shortly acute
	rhombic		.1753	Cluster bracts: prominent
-.3556	Leaf width			for whole of spike
-.2564	Juvenile bract colour:		.1705	Bract shape: linear-
	dark-brown			triangular
-.1705	Bract shape: obtuse		.1292	Bract colour:
-.1696	Scape length			light-brown
-.1292	Bract colour: green		.0548	Trunk height
-.1195	Bract indumentum			
-.1054	Scape diameter			
-.0962	Spike length			

Vector 3

-.3204	Bract shape: shortly acute
-.2941	Cluster bracts: prominent only at base of spike
-.1394	Spike length
-.1081	Spike diameter
-.0944	Bract colour: green
-.0919	Bract indumentum
-.0903	Ratio of spike length to scape length
-.0603	Bract shape: obtuse
-.0265	Scape diameter
-.0153	Leaf shape: quadrate rhombic

.7756	Leaf width
.5776	Leaf shape: obtriangular
.2421	Bract colour: dark-brown
.2357	Leaf thickness
.2283	Cluster bracts: prominent for whole of spike
.1402	Trunk height
.0944	Juvenile bract colour: light-brown
.0933	Scape length
.0603	Bract shape

The GOWECOR results for the first vector showed that the strongest elements at each end of the scale are those bract and inflorescence characters most distinct between the two taxa involved. Characters less distinct or intermediate between the two taxa (e.g. leaf dimensions and shortly acute bract shape) are less strongly correlated with this vector and so are close to the centre of the axis.

For the second vector, the strongest elements at the negative end of the axis are a combination of large transversely rhombic leaf T.S. shape and absence of prominent cluster-bracts and, at the positive end of the axis, obtriangular leaf T.S. shape, shortly acute bracts and prominent cluster bracts at the base of the spike. Both of these combinations represent a mixture of characteristics of the taxa involved. As such, this vector reflects the diversity of combinations of characters within the plants with intermediate characteristics.

In the third vector the strongest correlations at the negative end of the axis are with shortly acute bract shape and prominent cluster bracts at the base of the spike only, both intermediate characteristics. The strongest correlations at the positive end of the axis are broad, obtriangular leaf T.S. shape and, to a lesser extent, dark brown bracts, leaf thickness and prominent cluster-bracts present on the spike. This combination represents a mixture of $\underline{X}$. fulva and $\underline{X}$. glauca subsp. glauca characters. This vector therefore shows a further separation of intermediates not revealed by the first two vectors.

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Table 3.3 and Figures 3.6-3.10 show that there are gradients across the site in all three factors measured. In addition a habitat index figure is calculated for each of the factors and a cumulative total of the habitat index figures is shown as the right-hand column, and in Figure 3.11. The individual habitat indices were calculated by scaling the environmental variables such that their lowest figure became equal to zero and their highest figure became equal to 100, then expressing individual measurements in terms of a range from 1-100 (except that for the organic matter in the soil habitat index the scale was inverted to maintain the pattern of the other indexes, i.e. the lowest figure became 100, and the highest became 0). The cumulative habitat index was calculated adding the 3 index figures for each plant .

3.2.1.5 DISCUSSION

Numerical analyses.

Although GA and ISS classifications differ in several finer details, as discussed below, both give basically the same result. The two most important differences are (i) the intermediates group contains two more members (C5 and B3) in the ISS classification than in the GA classification. One new member coming from each of the other two major groups in the GA classification, and (ii) whether the two subdivisions of the intermediates subgroup unite with each other before uniting with $\underline{X}$. fulva (e.g. ISS 75) or whether they each unite separately with that subgroup to form the overall group (e.g. GA 78).

Figure 3.6 Environmental Gradients, Myall Lakes.

(1) Transect A:

Altitude of soil surface and water-table level

 (elevations above an arbitrary benchmark),

taxonomic classification of individual plants

along the transect, and % organic matter in the soil.

KEY

▨ X. glauca   ▢ X. fulva   ▨ Intermediates

─────── ALTITUDE ABOVE ARBITRARY BENCHMARK

─ ─ ─ ─ WATER-TABLE

--------- % ORGANIC MATTER IN SOIL

A4
──┴─── MARKS POSITION OF PLANTS ON TRANSECTS

(2) Key (Applies to figures 3.6-3.11)

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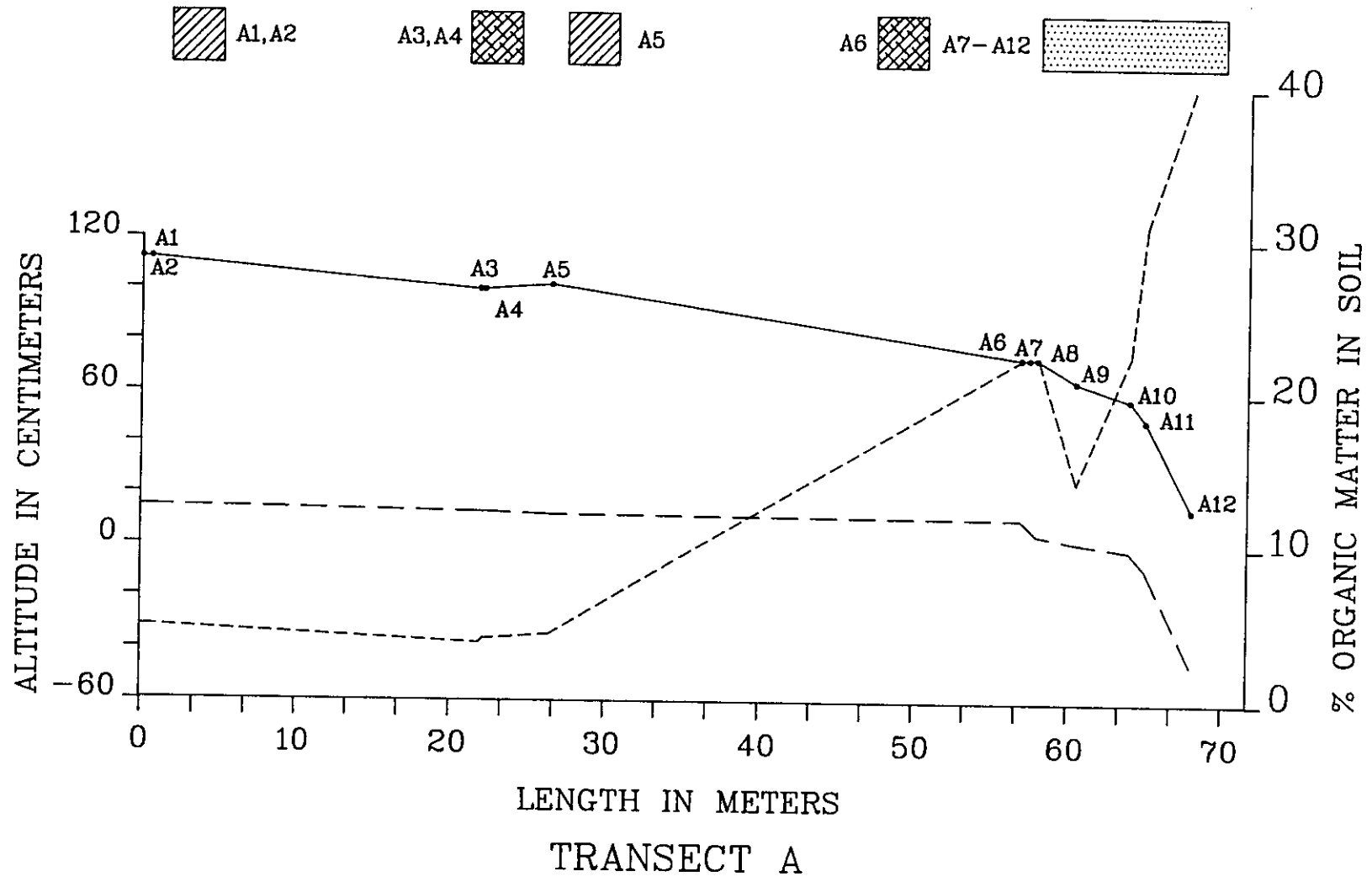
TRANSECT A

Figure 3.7 Environmental Gradients, Myall Lakes - continued -

Transect B:

Altitude of soil surface and taxonomic

classification of individual plants along

the transect (no data for water-table or

organic matter). Key with Figure 3.6.
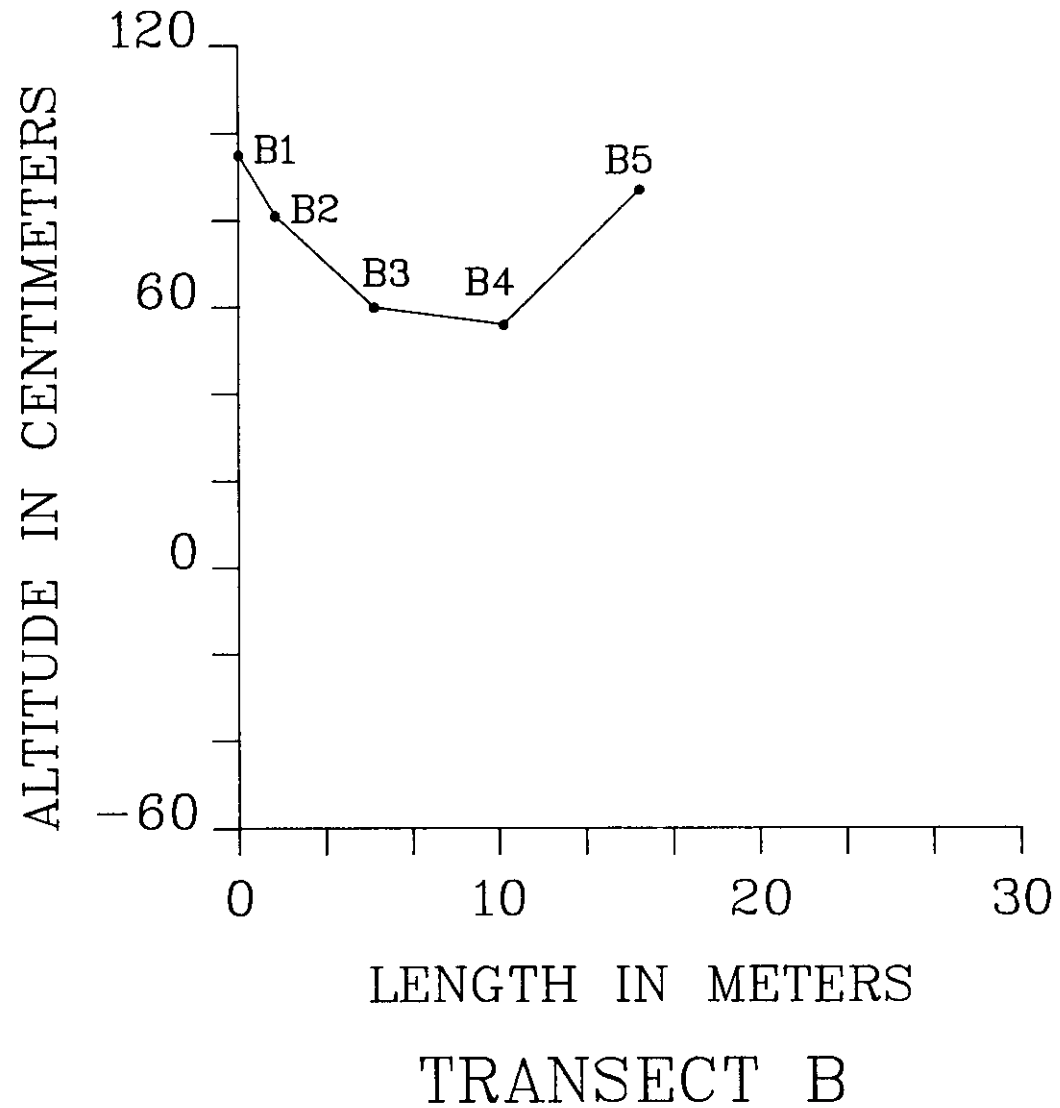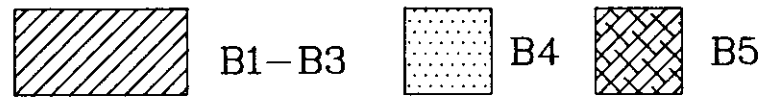
TRANSECT B

Figure 3.8 Environmental Gradients, Myall Lakes - continued -

Transect C:

Altitude of soil surface and water-table level,

taxonomic classification of individual plants

along the transect, and % organic matter in the

soil. Key with Figure 3.6.
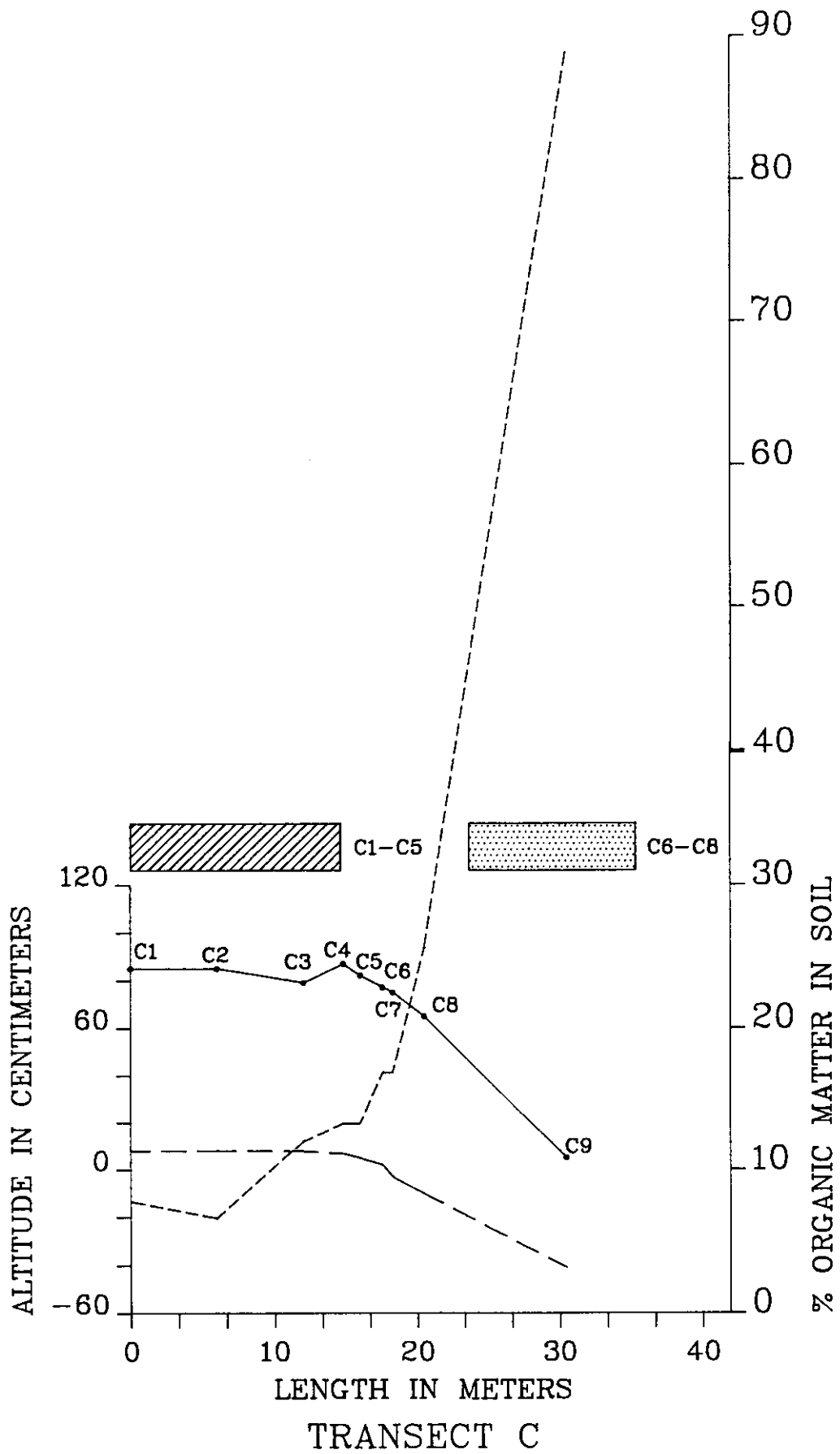
TRANSECT C

Figure 3.9 Environmental Gradients, Myall Lakes – continued.

Transect D:

Altitude and taxonomic classification of individual

plants along the transect (no data for water-table or

organic matter). Key with Figure 3.6.
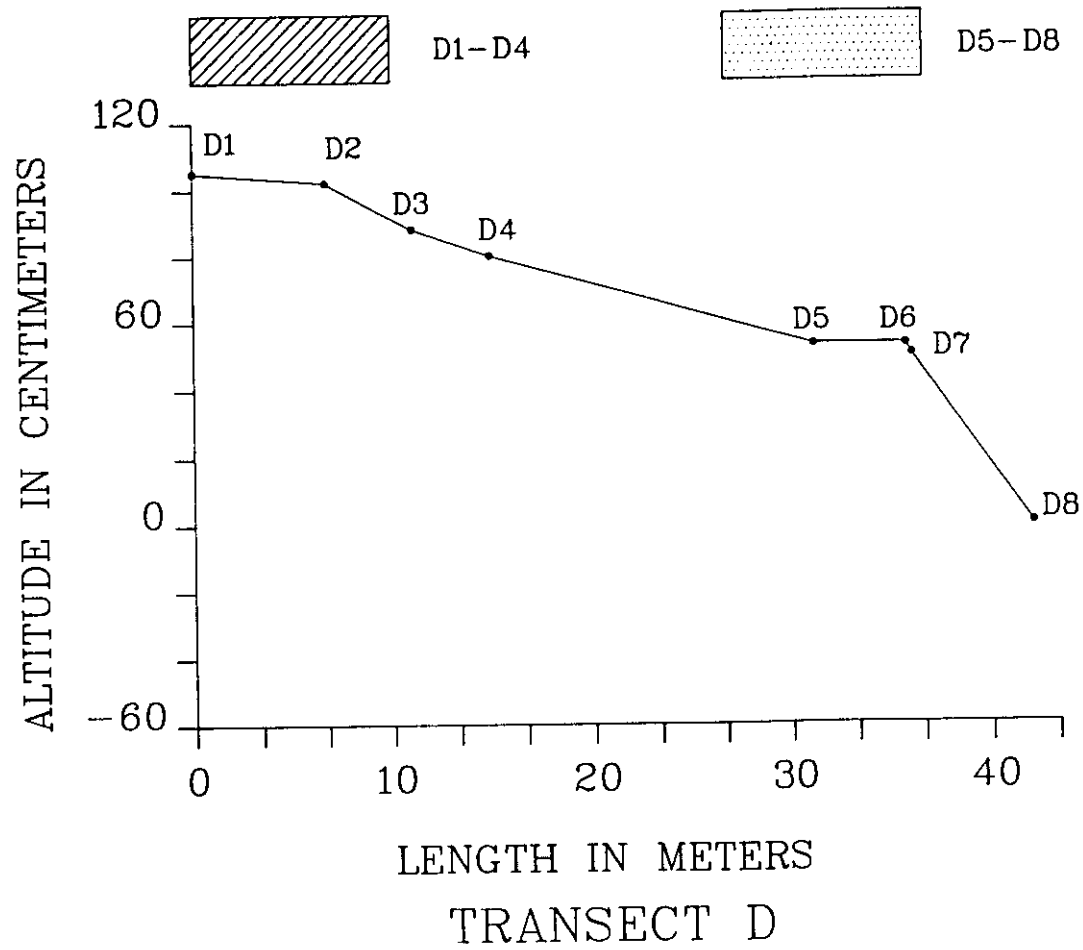
TRANSECT D

Figure 3.10 Environmental Gradients, Myall Lakes – continued.

Transect E:

Altitude of soil surface and water-table level,
taxonomic classification of individual plants
along the transect and % organic matter in the
soil. Key with Figure 3.6.

TRANSECT E
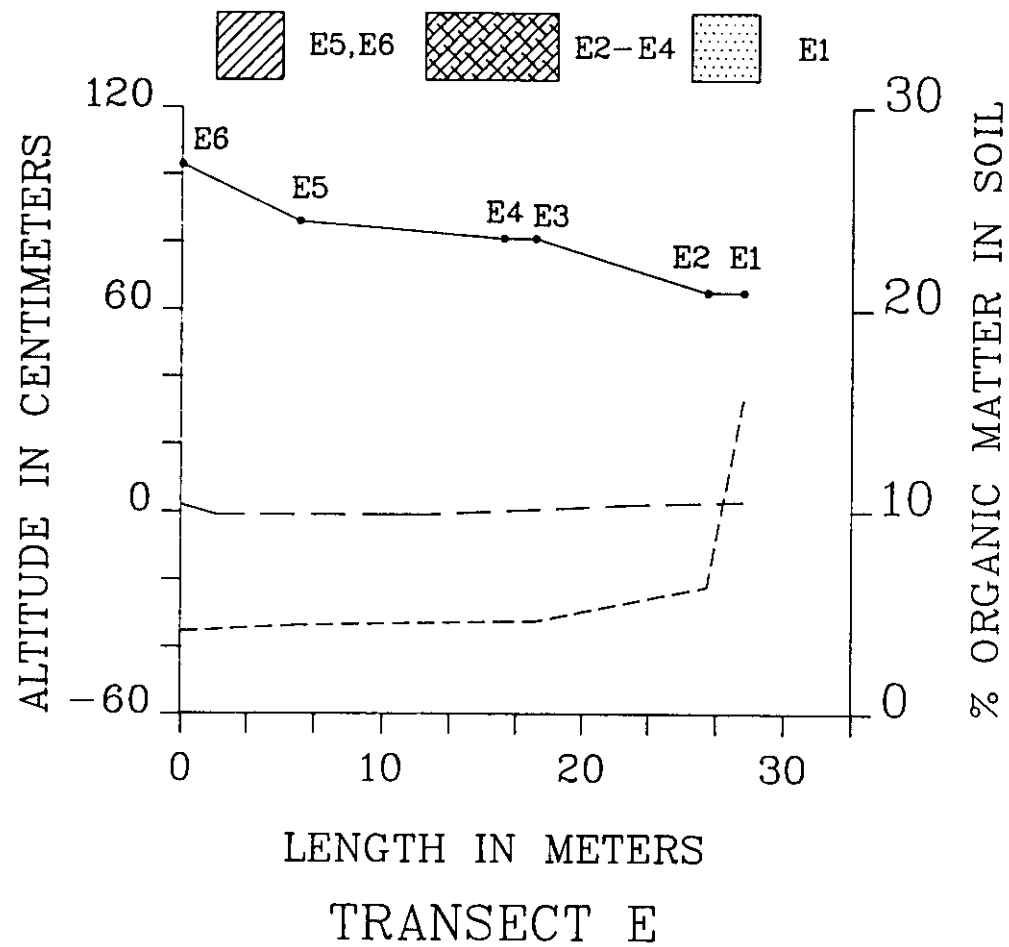
Figure 3.11 Cumulative habitat index diagram showing relative

habitat indices for the two species and the intermediates.

Key with Figure 3.6.

TAXON

HABITAT INDEX

300   240   180   120   60   0
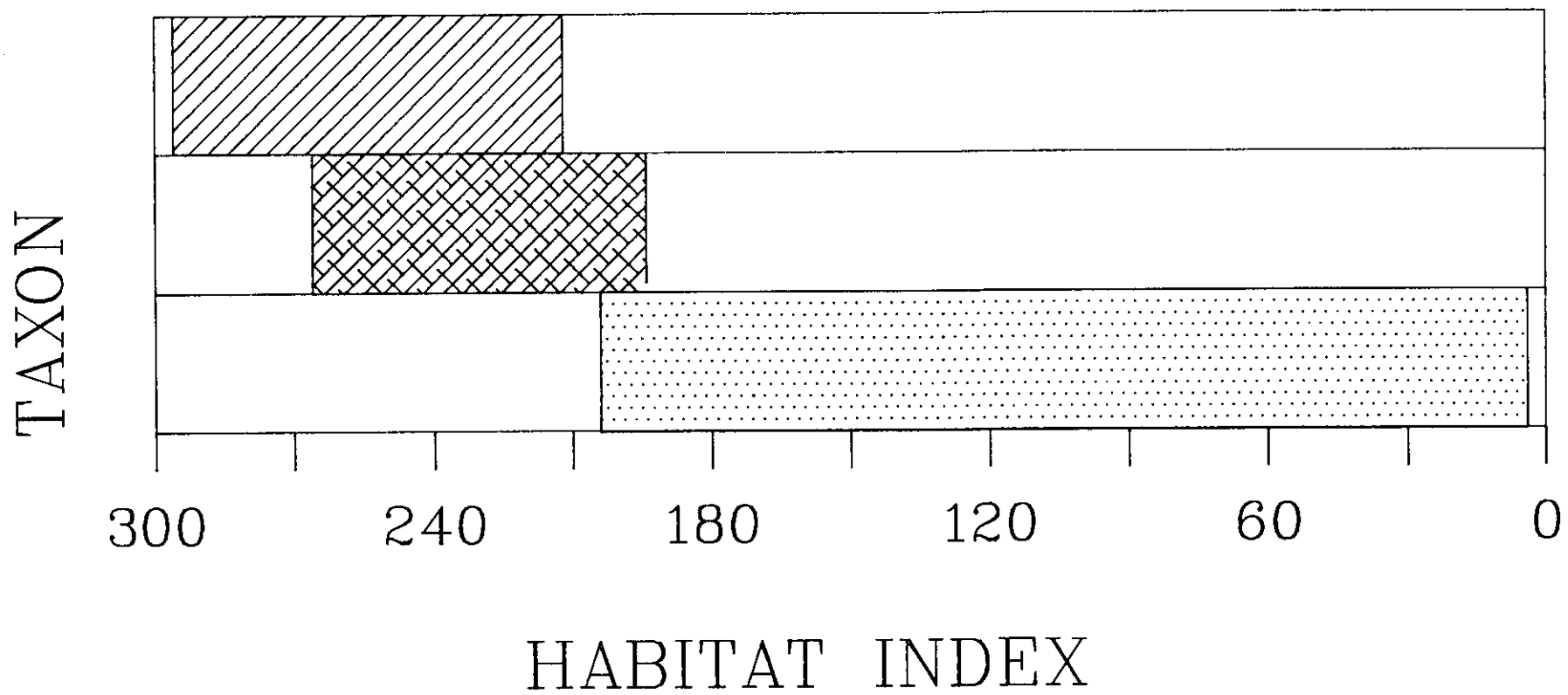
The ISS situation is a clearer representation of two taxa and intermediates and also agrees more closely with the GOWER ordination than does the GA classification.

The high percentage of the total dissimilarity brought out in the first 3 vectors of the GOWER ordination indicate that this technique is very successful in the interpretation of this data. Clifford and Stephenson (1975) state that such a result implies that the data is weakly structured, i.e. the data tends towards continuous distribution. However this assumption is not supported by these results as the plot of the first and second vectors of the GOWER ordination shows that the individuals are mostly grouped to either end of the primary axis, with only a few individuals scattered in the middle. The ordination result agrees well with the results of the classifications. The most important characters indicated by GOWECOR for the formation of the primary vector are those morphological characters traditionally used to distinguish the taxa and also found most useful by MULCLAS. That is, both the two classifications and the ordination indicate that there are two taxa and some individual plants intermediate between the taxa present.

Environmental measurements.

There are three clear, positively correlated environmental gradients across the site: soil water-holding capacity; depth to the water-table, and; the topographic gradient (Table 3.3, Figures 3.6-3.10).

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Combined results - conclusions.

A comparison of the results of the numerical analyses and the measured environmental gradients, shown graphically in Figures 3.6-3.10 reveals a relationship between the habitats of the taxa and the intermediates with their position along the environmental gradients. X. fulva always occupies the lower sites, which are much closer to the water-table and have a much higher proportion of organic matter in the soil. X. glauca subsp. glauca always occupies the higher sites, on the sand rises, further from the water-table and with a lower proportion of organic matter in the soil. In the same way, the plants with intermediate morphology occupy the middle ground, with intermediate environmental conditions (also see Figure 3.6).

This is also demonstrated by the cumulative habitat index figures (Table 3.3 and Figure 3.11). Plants identifiable as X. glauca subsp. glauca grow in sites with cumulative index figures of 213-293, X. fulva 4.5-207, and hybrids 192-265. The cumulative habitat index for X. glauca subsp. glauca and X. fulva sites do not overlap, however the values for sites with intermediates are intermediate, and overlap both taxa.

The relationship between the environmental results and the ordinations is a particularly interesting one. As indicated above the ordination vectors can be seen to represent the taxonomic separation of taxa. Vector 1 also reflects the environmental factors, because the distribution of the taxa reflects those factors. It can be seen to reflect the three environmental gradient, as indicated on the plot in Figure 3.5.1. Vectors 2 and 3 however do not appear to reflect any

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specific environmental factors.

In those transects such as C and D where the gradients were slightly steeper however, there are no intermediate plants, probably because there is inadequate intermediate environment for them to establish. Anderson and Noy-Meir (1971) have indicated that there is little justification for interpreting primary vectors as "main environmental gradients" in most circumstances. Whilst this is true because the vector should only be interpreted in terms of the morphological characters it represents, in this situation the primary vector clearly shows the taxonomic and morphological gradient which follows the putative environmental gradient, as indicated by figures 3.6-3.10.

The situation of hybrid plants in a "hybrid" environment demonstrated here is similar to the numerous examples (for other taxa) in the literature, eg. Anderson and Hubricht (1938), Briggs (1962), Leach and Whiffen (1978).

It is difficult to determine whether the observed intermediacy of the habitat is due to "hybridization" by the actions of man, by natural disaster as proposed by Anderson (1949) or is naturally occurring. As these populations are well established plants, they are a minimum of 10 years old and are more probably in the order of 50 - 100 years old (Gill and Inwerson (1976); and observations on cultivated plants by the present author). As such any man-made or natural disturbance connected with the establishment of the hybrids would have had to have occurred many years ago. There are no signs of any such disturbance. The nearest man-made disturbance is the sand-mining access road to Seal Rocks. However this is both too recent to be of significance and

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is also on a different slope of the sand rise which should reduce its effect on the area studied. It therefore appears that the intermediate habitat is of natural origin.

3.2.2 SUBSIDIARY ANALYSES:

3.2.2.1 NORTHERN NEW SOUTH WALES COASTAL POPULATIONS – Materials and Methods.

Thirty six flowering or fruiting specimens were collected from sand areas near Lennox Head, Coffs Harbour Airport (the type locality for X. fulva), Hat Head, Limeburners Creek Reserve, Diamond Head and a few kilometers south of Diamond Head (Map, Figure 3.12). These specimens were analysed using 14 morphological characters and the TAXON package V.4. (Data set and full results in Appendix 3.4). Because of the essential similarity of results obtained by the UPG and ISS classification strategies in the Myall Lakes study only one classification technique, the UPG strategy, was used in the subsidiary analyses. In a similar way the PCOA ordination results as plotted by PTPLOT are only presented for vectors 1 and 2.

3.2.2.2 RESULTS

The dendrogram (Figure 3.13), ordination (Figure 3.14) and character of the groupings of individuals produced by SAHN (as shown by GCOM and GSTAT, Tables 3.6 and 3.7) show very similar patterns to those seen in the Myall Lakes data set analyses.

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Figure 3.12 Map of Quaternary sand deposits

and study locations in N.S.W. and south-east

Queensland.   Scale = 1:1,000,000.

Page 1.

Thick black lines/and arrows along the coast mark the

distribution of post-Pleistocene, mainly Holocene,

sand deposits.   Pleistocene sand deposits are marked

with a P inside a line bordering the area of the deposit.

(From D. Chapman, Geography Department, University of

Sydney).

Locations of collections for this study are marked with

a ▲

BYRON BAY

Lennox Head

COFFS HARBOUR

Hat Head

Limeburners Creek

PORT MACQUARIE

Diamond Head

Myall Lakes

NEWCASTLE
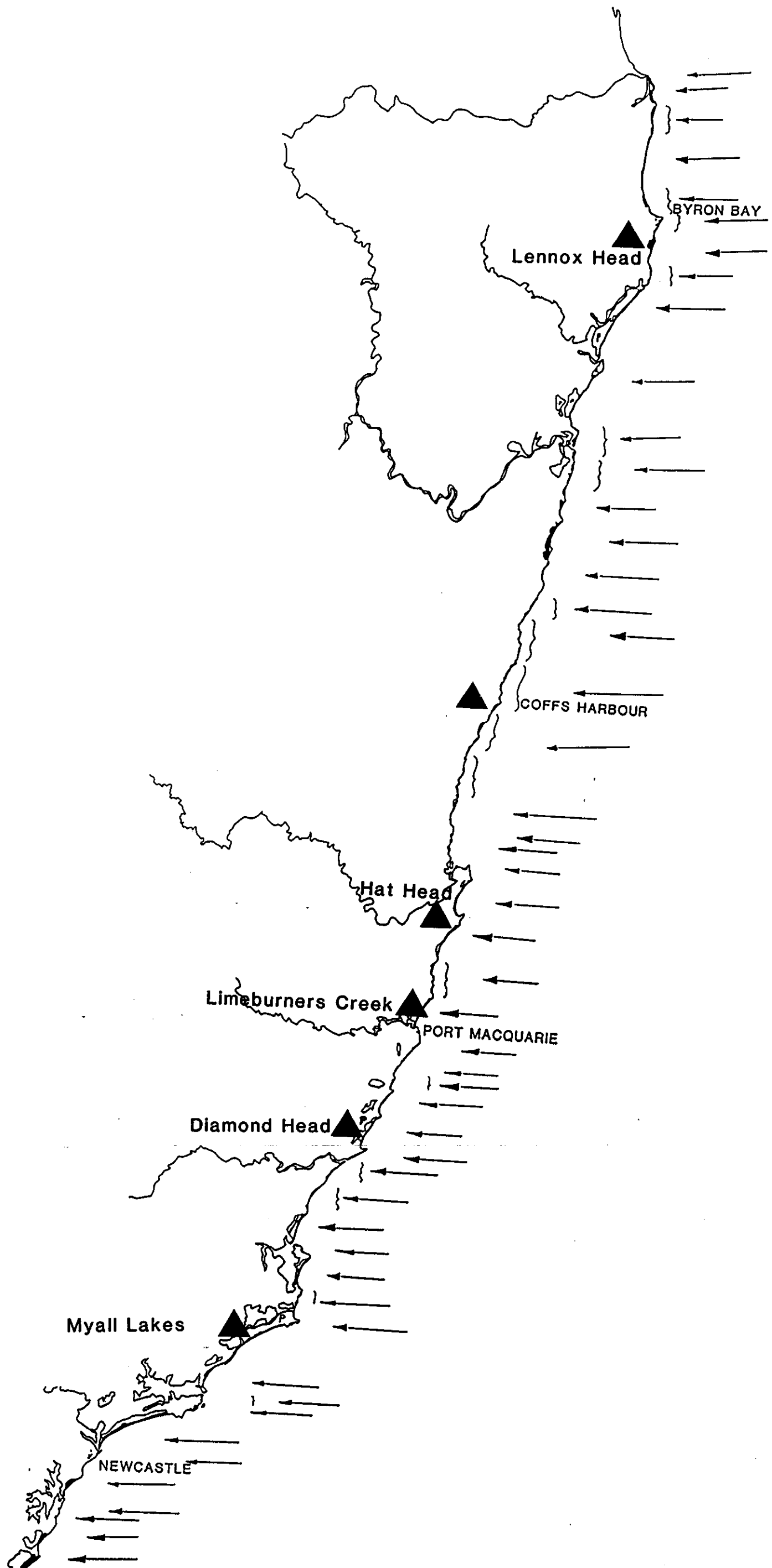
Figure 3.12 Map of Quaternary sand deposits

and study locations in N.S.W. and south-east

Queensland. Page 2.

                                and arrows
Thick black lines/along the coast mark the

distribution of post-Pleistocene, mainly Holocene,

sand deposits. Pleistocene sand deposits are marked

with a P inside a line bordering the area of the deposit.

(From D. Chapman, Geography Department, University of

Sydney).

Locations of collections for this study are marked with

a ▲
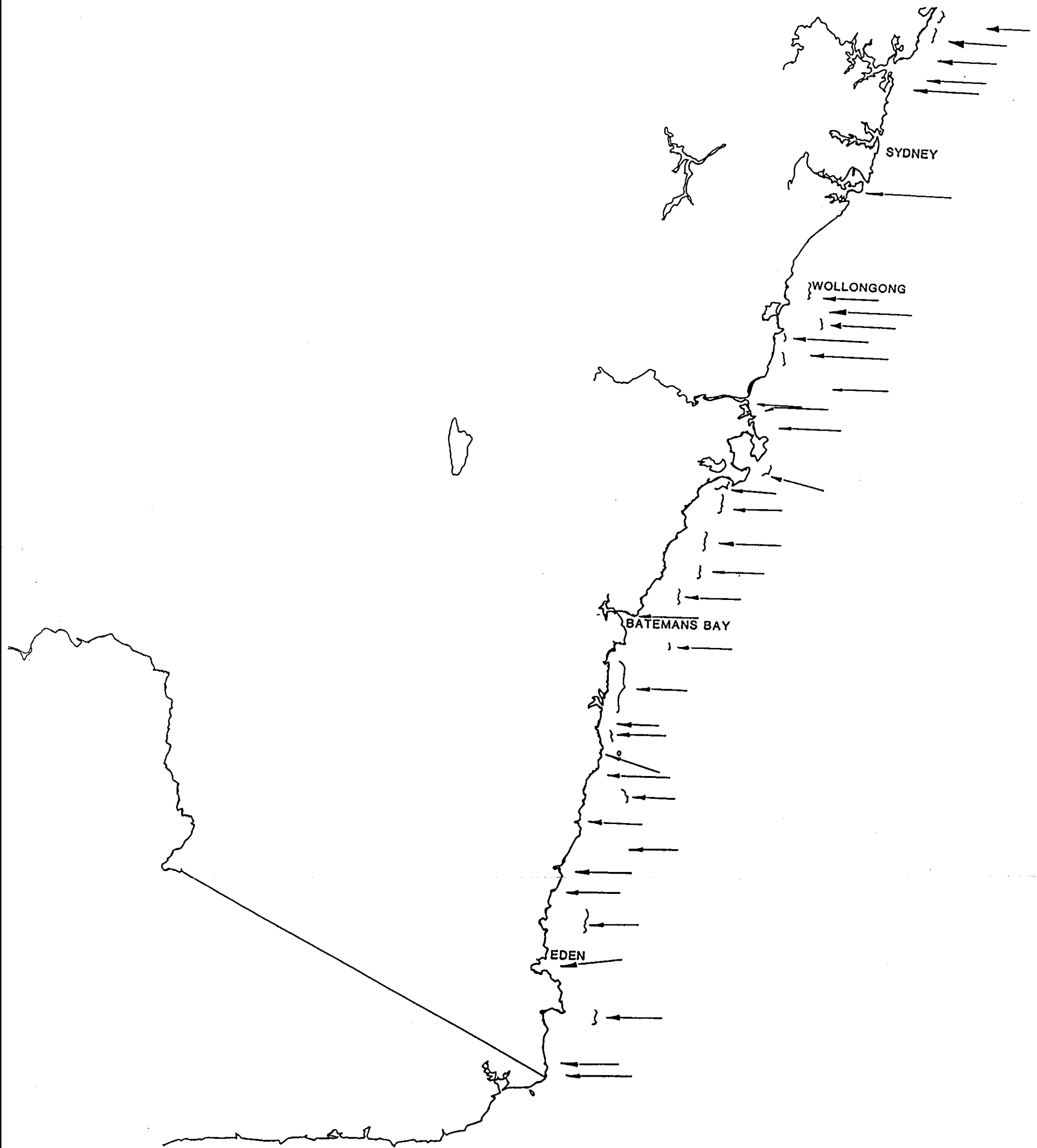
SYDNEY

WOLLONGONG

BATEMANS BAY

EDEN

Figure 3.13 SAHN UPG Classification Dendrogram,

Northern N.S.W data set.

Key: ▦▦ X. fulva; //// X. glauca; XXXX Intermediates.

DISSIMILARITY LEVEL ------------------------------------->
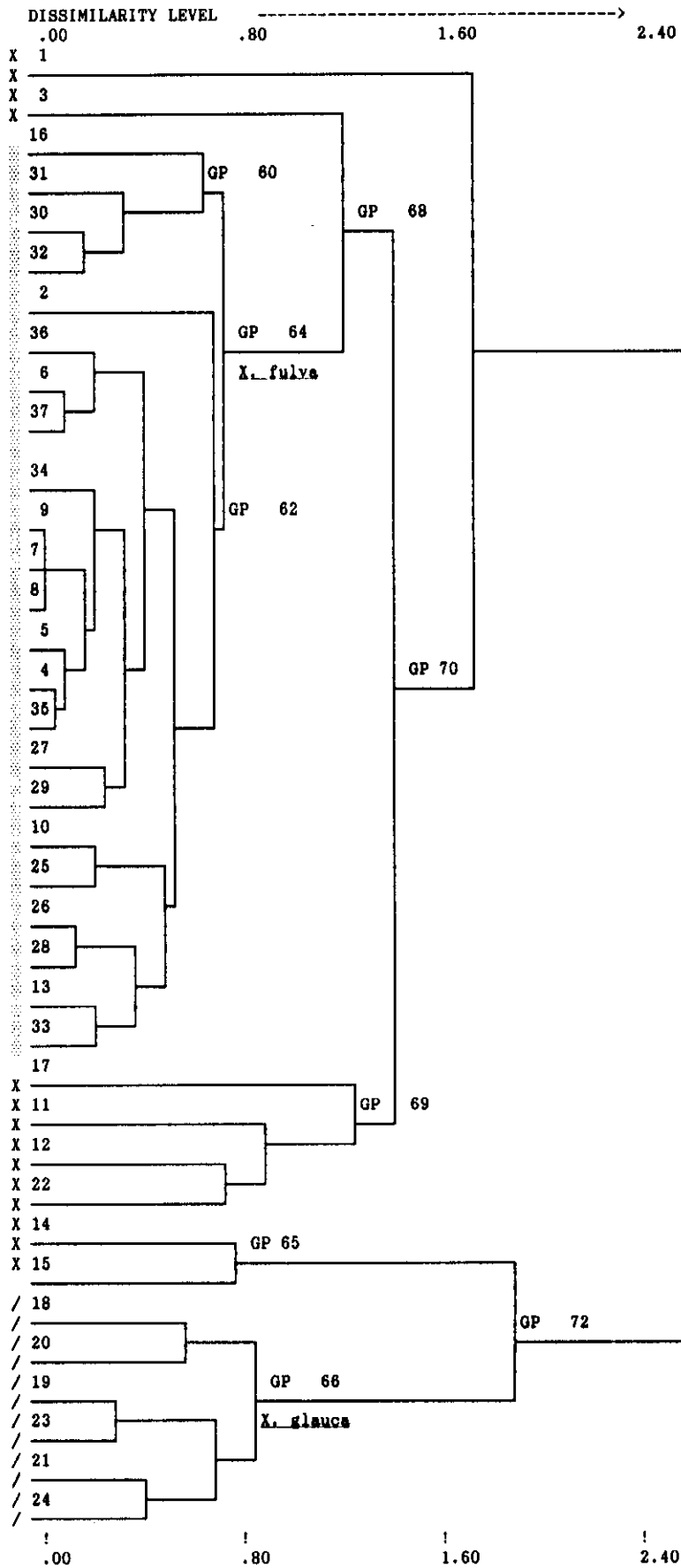
Figure 3.14 PCOA Ordination, Northern N.S.W. data set,
PTPLOT plot of Vectors 1 and 2, showing taxonomic
and putative environmental factors.

Key: ▦ X. fulva; //// X. glauca;

Intermediates between, unassigned.

Putative moisture gradient <<═══>>

Figure 3.14

Vectors 1 and 2.
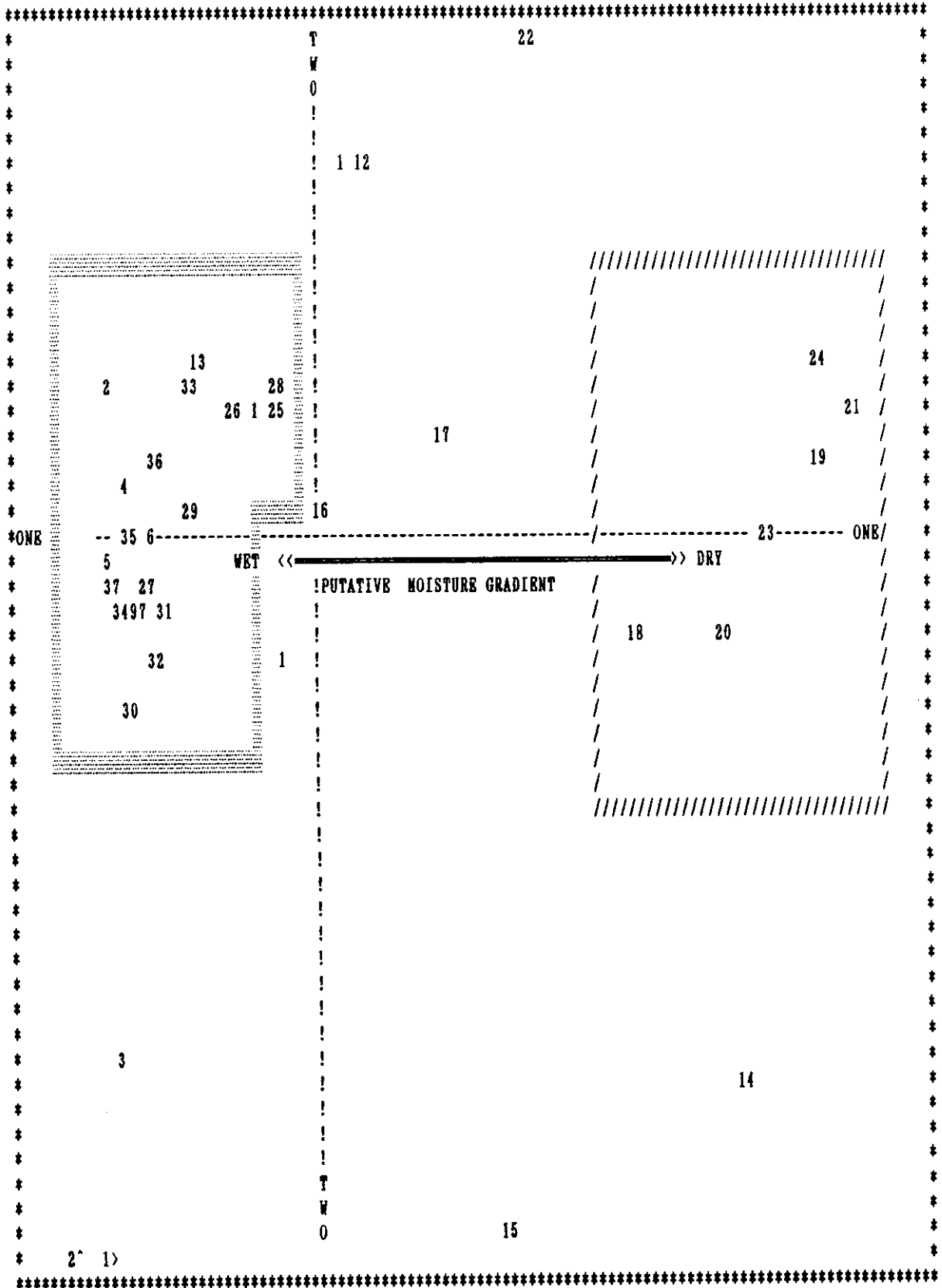
Table 3.6 GCOM, SAHN UPG classification, Northern N.S.W.

**** COMPARISON OF MAJOR GROUPS PRODUCED BY SAHN
**** GROUP A = GP 1 + GP 68 + GP 69 (_X. fulva_ and intermediates)
**** GROUP B = GP 65 + GP 66 (_X. glauca_ and backcrosses)

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 20.0042

ATTRIBUTE NAME (STATE)	GROUP A 29 MEMBERS		GROUP B 8 MEMBERS		CONTRIBUTION		
	ATTRIBUTE MEAN	NO. PRESENT	ATTRIBUTE MEAN	NO. PRESENT	%	% (CUM)	ACTUAL VALUE
DMUL 6 BRACT INDUMENTUM		29		8	22	22	4.38
ST. 1 GLABROUS	.000		1.000				
ST. 2 SLIGHTLY HIRSUTE	.069		.250				
ST. 3 TOMENTOSE	1.000		.000				
DMUL 5 CLUSTER BRACTS		29		8	20	41	3.91
ST. 1 OBSCURE	.966		.000				
ST. 2 BASE OF SPIKE	.172		.000				
ST. 3 100% SPIKE LENGTH	.000		1.000				
DMUL 4 BRACT COLOUR		29		6	11	52	2.17
ST. 1 GREEN	.000		1.000				
ST. 2 LIGHT BROWN	.759		.000				
ST. 3 DARK BROWN	.448		.000				

Table 3.7 GSTAT, SAHN UPG Classification 5 Groups,

Northern N.S.W. data set.

Table 3.7 Northern New South Wales SAHN UPG Classification groups GSTAT 5 Groups

INTERMEDIATES: (GP 1) WITH 1 MEMBERS
                   ****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	0	0	1	0	
2 LEAF COLOUR	0	1	1			
3 BRACT SHAPE	0	1	0	0	0	0
4 BRACT COLOUR	0	0	1	0		
5 CLUSTER BRACTS	0	1	0	0		

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	1	315.0	315.0	315.0	315.0	315.0	0.	0.
2 SCAPE LENGTH	0	0	1	166.0	166.0	166.0	166.0	166.0	0.	0.
3 SCAPE DIAMETER	0	0	1	32.00	32.00	32.00	32.00	32.00	0.	0.
4 SPIKE LENGTH	0	0	1	183.0	183.0	183.0	183.0	183.0	0.	0.
5 SPIKE DIAMETER	0	0	1	43.00	43.00	43.00	43.00	43.00	0.	0.
6 SP/SC RATIO	0	0	1	110.0	110.0	110.0	110.0	110.0	0.	0.

X. PULVA AND INTERMEDIATES: (GP 68) WITH 24 MEMBERS
                            ****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	10	0	21	0	
2 LEAF COLOUR	0	1	24			
3 BRACT SHAPE	0	20	0	4	0	0
4 BRACT COLOUR	0	0	19	11		
5 CLUSTER BRACTS	0	24	3	0		

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	24	265.0	265.0	490.0	352.9	352.9	56.16	225.00
2 SCAPE LENGTH	0	0	24	75.00	75.00	150.0	115.0	116.0	21.13	75.00
3 SCAPE DIAMETER	0	0	24	11.00	11.00	22.00	15.42	15.42	3.229	11.00
4 SPIKE LENGTH	0	0	24	18.00	18.00	131.0	61.79	61.79	31.24	113.0
5 SPIKE DIAMETER	0	0	24	18.00	18.00	34.00	26.46	26.46	4.314	16.00
6 SP/SC RATIO	0	0	24	20.00	20.00	118.0	52.83	52.83	25.75	98.00
7 TRUNK HEIGHT	0	20	4	0.	5.000	20.00	1.875	11.25	4.848	20.00

INTERMEDIATES: (GP 69) WITH 4 MEMBERS
                   ****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	4	0	1	0	
2 LEAF COLOUR	0	0	4			
3 BRACT SHAPE	0	3	0	1	0	0
4 BRACT COLOUR	0	0	2	2		
5 CLUSTER BRACTS	0	3	2	0		

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	4	295.0	295.0	385.0	342.5	342.5	44.25	90.00
2 SCAPE LENGTH	0	0	4	72.00	72.00	149.0	107.8	107.8	31.50	77.00
3 SCAPE DIAMETER	0	0	4	21.00	21.00	34.00	27.50	27.50	5.323	13.00
4 SPIKE LENGTH	0	0	4	117.0	117.0	217.0	180.5	180.5	43.97	100.0
5 SPIKE DIAMETER	0	0	4	35.00	35.00	48.00	43.25	43.25	5.909	13.00
6 SP/SC RATIO	0	0	4	110.0	110.0	300.0	181.5	181.5	86.23	190.0
7 TRUNK HEIGHT	0	1	3	0.	40.00	65.00	42.25	56.33	30.46	65.00

BACKCROSSES TO X. GLAUCA: (GP 65) WITH 2 MEMBERS
                          ****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	2	0	1	0	
2 LEAF COLOUR	0	2	2			
3 BRACT SHAPE	0	0	0	2	0	0
5 CLUSTER BRACTS	0	0	0	2		

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	2	330.0	330.0	345.0	337.5	337.5	10.61	15.00
2 SCAPE LENGTH	0	0	2	34.00	34.00	81.00	57.50	57.50	33.23	47.00
3 SCAPE DIAMETER	0	0	2	16.00	16.00	22.00	19.00	19.00	4.243	6.000
4 SPIKE LENGTH	0	0	2	89.00	89.00	160.0	124.5	124.5	50.20	71.00
5 SPIKE DIAMETER	0	0	2	24.00	24.00	34.00	29.00	29.00	7.071	10.00
6 SP/SC RATIO	0	0	2	109.0	109.0	470.0	289.5	289.5	255.3	361.0
7 TRUNK HEIGHT	0	0	2	5.000	5.000	10.00	7.500	7.500	3.536	5.000

X. GLAUCA: (GP 66) WITH 6 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	6	0	0	0	
2 LEAF COLOUR	0	0	6			
3 BRACT SHAPE	0	0	0	2	1	3
4 BRACT COLOUR	0	6	0	0		
5 CLUSTER BRACTS	0	0	0	6		

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	6	225.0	225.0	370.0	269.2	269.2	54.17	145.0
2 SCAPE LENGTH	0	0	6	30.00	30.00	67.00	44.17	44.17	14.65	37.00
3 SCAPE DIAMETER	0	0	6	21.00	21.00	33.00	28.00	28.00	4.899	12.00
4 SPIKE LENGTH	0	0	6	69.00	69.00	145.0	118.3	118.3	31.51	76.00
5 SPIKE DIAMETER	0	0	6	33.00	33.00	50.00	43.00	43.00	6.957	17.00
6 SP/SC RATIO	0	0	6	102.0	102.0	476.0	296.7	296.7	122.6	374.0
7 TRUNK HEIGHT	0	0	6	5.000	5.000	100.0	50.50	50.50	37.41	95.00

STATISTICS FOR ENTIRE DATA
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4	5
1 LEAF SHAPE	0	22	0	24	0	
2 LEAF COLOUR	0	4	37			
3 BRACT SHAPE	0	24	0	9	1	3
4 BRACT COLOUR	2	6	22	13		
5 CLUSTER BRACTS	0	28	5	8		

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	37	225.0	225.0	490.0	336.4	336.4	59.51	265.0
2 SCAPE LENGTH	0	0	37	30.00	30.00	166.0	101.0	101.0	36.40	136.0
3 SCAPE DIAMETER	0	0	37	11.00	11.00	34.00	19.41	19.41	6.890	23.00
4 SPIKE LENGTH	0	0	37	18.00	18.00	217.0	90.46	90.46	53.60	199.0
5 SPIKE DIAMETER	0	0	37	18.00	18.00	50.00	31.54	31.54	9.014	32.00
6 SP/SC RATIO	0	0	37	20.00	20.00	476.0	120.6	120.6	123.2	456.0
7 TRUNK HEIGHT	0	22	15	0.	5.000	100.0	14.38	35.47	26.52	100.0

GCCM (Table 3.6) reveals there is one major group produced by SAHN (64) which contains those plants most resembling X. fulva, a smaller group (66) which contains plants and which have the characteristics of X. glauca subsp. glauca, and a number of smaller groups and singletons which have characteristics intermediate between these two taxa in a pattern consistent with hybridisation and introgression.

The PCOA ordination results in the PTPLOT plot of vectors 1 and 2 (Figure 3.14) also show a similar pattern to the ordinations of the Myall Lakes data, with a concentration of individuals identifiable as the parent taxa at opposite ends of the first vector, and individuals with intermediate characteristics spread-out between them.

Environmental factors

Although environmental measurements were not made for these subsidiary studies the environmental conditions were very obvious and appear to be directly comparable with those at the Myall Lakes site. For example, both at the Limeburners Creek Reserve site and at Hat Head the specimens of X. fulva grew in distinctly swampy conditions, surrounded by free water at the lowest extreme of the populations, while X. glauca grew on sand hills at the edge of the swamp in obviously well-drained conditions. A comparison of the observed wet-dry ecocline with vector 1 appeared to show a similarly close reflection of the gradient to that seen at Myall Lakes.

3.2.2.3 BEERWAH SCIENTIFIC PURPOSES AREA.

Materials and Methods

In the Queensland Forestry Commission Scientific Purposes Area near Beerwah in south-east Queensland (location map, Figure 3.15) situation similar in appearance to that described for Myall Lakes was found. A number of Xanthorrhoea species occur close to each other in the mosaic of environments created by the varying depth of a layer of Quaternary sand overlying older substrates, mainly clays, and a varying degree of periodical waterlogging due to a low relief swale/dune topography.

In periodically waterlogged areas of the deeper sand deposits are found X. fulva, while X. almae occupies the drier rises on both sand and older substrates. There are a number of low relief dunes and swales throughout the area where these two species come into close contact, and where that happens plants with characteristics between the two species are sometimes found. One such population flowered profusely in 1978. Measurements were made and have since been analysed as detailed below.

Forty four flowering plants were measured for 14 morphological characters and analysed using the same numerical techniques as for the Northern New South Wales analyses. Summarised results are given below, the data set and results in full are given in Appendix 3.5.

3.2.2.4 RESULTS

The dendrogram Figure 3.16 and ordination Figure 3.17 show similar patterns to those seen in the study areas analysed above, and results

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Figure 3.15 Beerwah Study Area location map.

GYMPIE

NAMBOUR

LANDSBOROUGH

Glass
House **BEERWAH**
Mts.

*BRIBIE
ISLAND*

CABOOLTURE

*MORETON
ISLAND*

Moreton

Bay

B R I S B A N E

*NORTH
STRADBROKE
ISLAND*

N

10   20   km
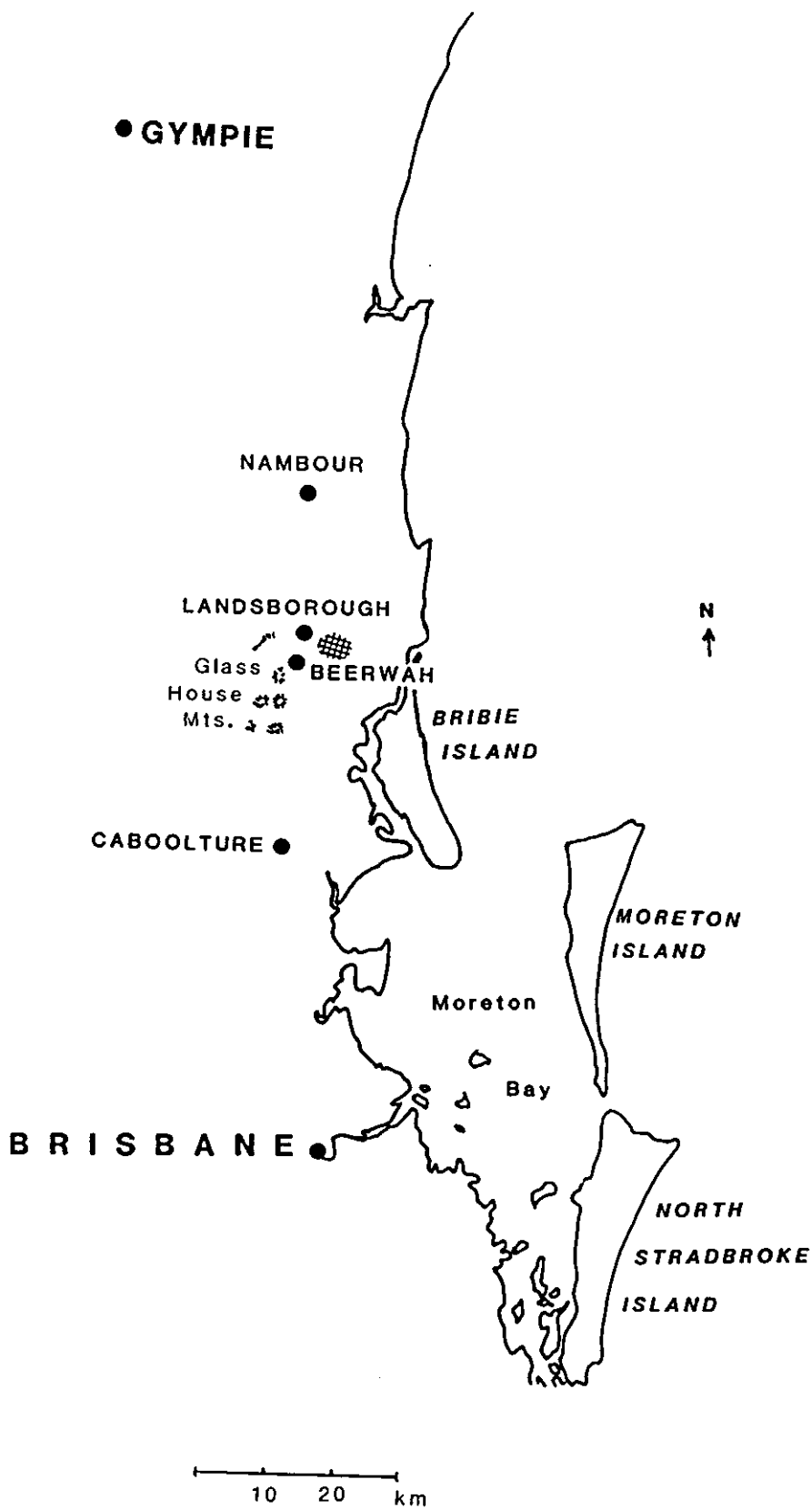
KEY:
SAMPLE AREA

Figure 3.16 SAHN UPG Classification dendrogram, Beerwah.

Key: ▦ X. fulva; ▉ X. almae; XXXX Intermediates.

Combination / mixture shown: ▉XXX▉XXX.

DISSIMILARITY --------------------------------->

.00 .40 .80 1.20 1.60

GP 63   X. fulva

GP 73

GP 70
backcrosses to
X. fulva

GP 84

GP 77

GP 79
Intermediates

GP 75

GP 78

GP 83

GP 80

GP 74

GP 85

GP 81

GP 86
A mixture of
X. almae and
backcrosses

GP 82

.00 .40 .80 1.20 1.60
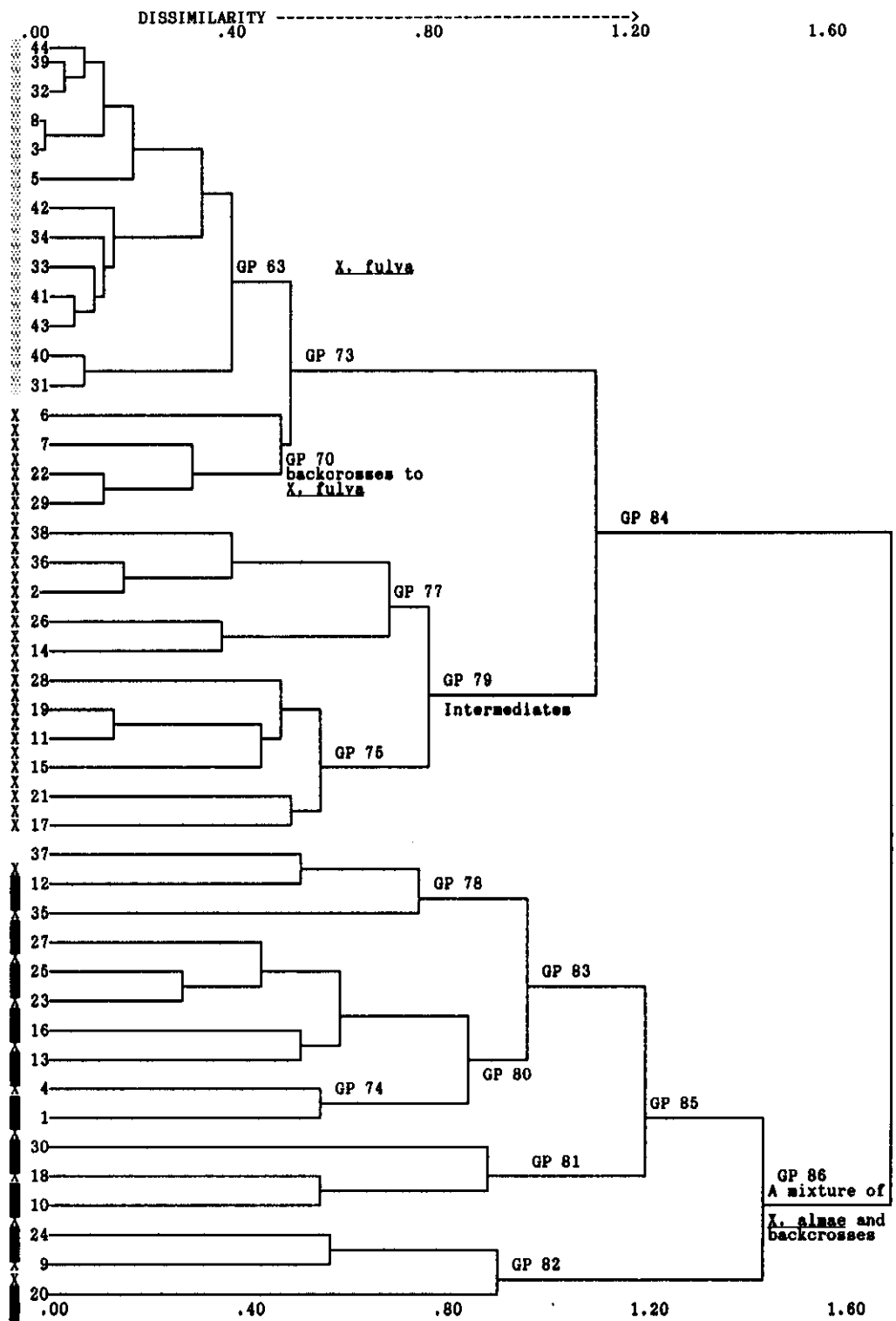
Figure 3.17   PCQA Ordination 1st and 2nd Vectors, Beerwah.

Key: ▦▦ <u>X. fulva</u>; ███ <u>X. almae</u>

Putative moisture gradient <<═══════>>

TWO

2

36

37

38

14   21

28   17

Putative moisture gradient

DRY <<   >> WET

12
1
35   19   34

ONE   43-------- ONE

11
9   24   2013   26   15   22

16   29

4

27

10
30

23

25

18   TWO

2 13
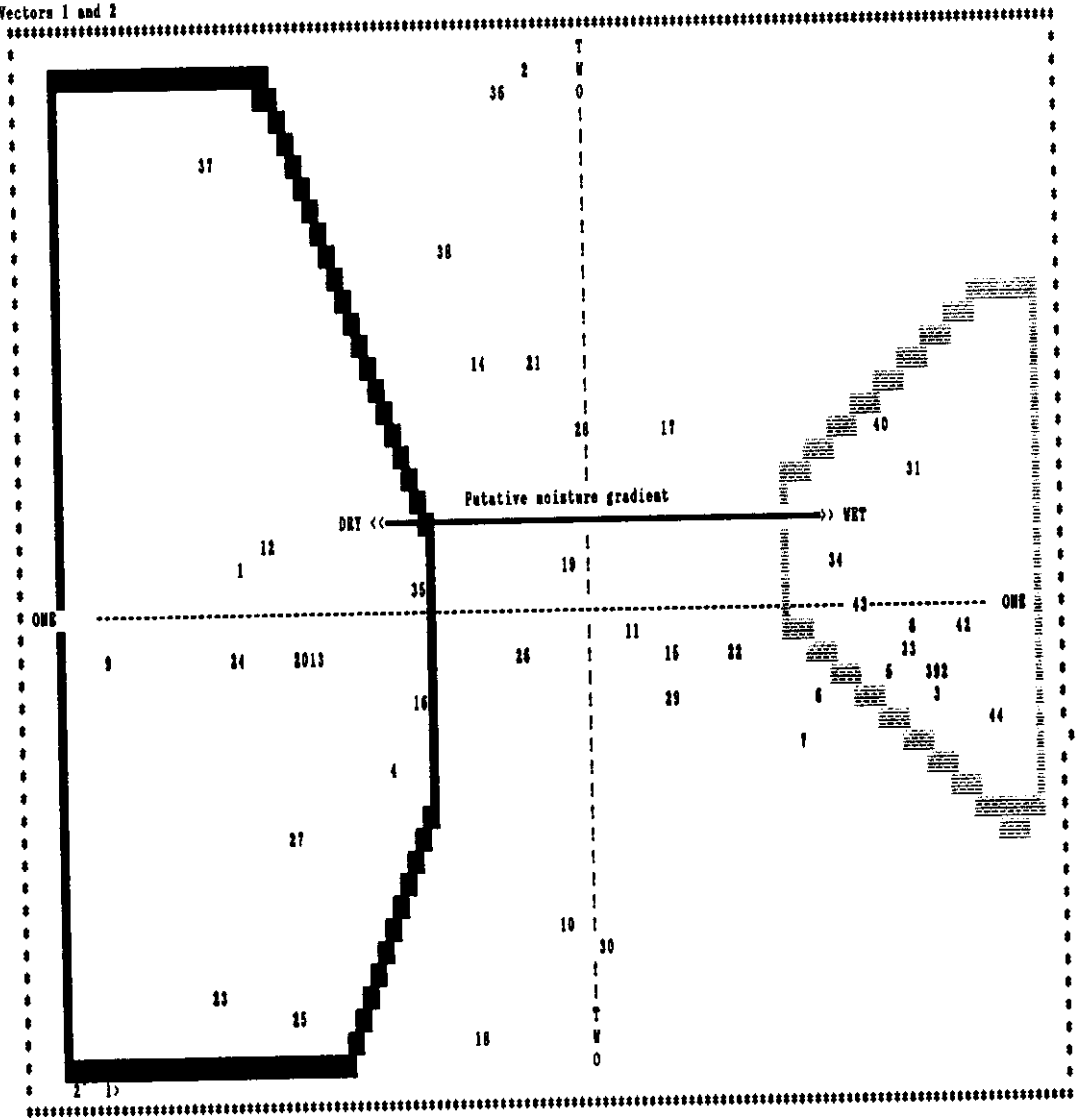
and can therefore be interpreted in the same way, i.e. that there are two separate taxa and a number of intermediates present.

GSTAT and GCCM (Tables 3.8 and 3.9, Appendix 3.6) reveal that the characteristics of the five major groups in the dendrogram are those of the separate species involved, i.e. X. fulva and X. almae, as well as a range of intermediates between these two consistent with the many levels of backcrosses between parents and hybrids characteristic of introgressive hybridisation. The comparison between the two main groups produced by SAHN is given in Table 3.8.

The PCOA ordination plot of vectors 1 and 2 shows the individuals spread-out along vector 1, with individuals at one end ascribable to X. almae and at the other end as X. fulva, with intermediate plants at one end. Plants with primarily the characteristics of X. fulva but some characters of X. almae, which are therefore presumed to be backcrosses from hybrids to X. fulva (SAHN GP 67) can be seen to be closer to the X. fulva group than most of the other intermediates such as SAHN GP 79. There is a considerably wider distribution of individuals along the vectors compared with the Myall and Northern New South Wales studies, where there was more concentration at the ends of the primary vector. This may represent a situation with more backcrosses, or possibly a more gentle environmental gradient. There is also a greater separation of the intermediate plants along vector 2, in this analysis, in comparison with the above analyses.

Table 3.8 GCOM, SAHN UPG Classification Major Groups, Beerwah.

**** GROUP A = GP 73 + GP 79 (X. fulva, backcrosses and intermediates)
**** GROUP B = GP 82 + GP 83 + GP 81 (X. almae and backcrosses)

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 16.1423

ATTRIBUTE (STATE)	NAME	GROUP A 28 MEMBERS ATTRIBUTE MEAN	NO. PRESENT	GROUP B 16 MEMBERS ATTRIBUTE MEAN	NO. PRESENT	CONTRIBUTION X	X (CUM)	ACTUAL VALUE
DMUL 4	BRACT COLOUR		26		15	14	14	2.21
ST. 1	GREEN	.200		1.000				
ST. 2	LIGHT BROWN	.733		.091				
ST. 3	DARK BROWN	.067		.000				
FNUM 9	TRUNK HEIGHT	7.656	28	54.000	16	13	26	2.04
FNUM 7	SP,SC RATIO	.367	28	1.051	16	11	38	1.85
FNUM 6	SPIKE DIAMETER	21.875	28	30.333	16	10	48	1.62
FNUM 4	SPIKE LENGTH	42.719	28	93.667	16	9	57	1.40

Table 3.9 GSTAT, SAHN UPG Classification 5 Groups, Beerwah.

Table 3.9 Beerwah Analysis SAHN UPG Classification GSTAT 5 groups

X. PULVA AND BACKCROSSES (GP 72) WITH 17 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	2	0	17	0
2 LEAF COLOUR	1	2	16		
3 BRACT SHAPE	0	17	3	0	
4 BRACT COLOUR	1	0	14	2	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	17	2.000	2.000	3.200	2.629	2.629	.3241	1.200
2 LEAF THICKNESS	11	0	6	1.400	1.400	2.000	1.750	1.750	.2000	.6000
3 SCAPE LENGTH	0	0	17	90.00	90.00	150.0	110.1	110.1	16.06	60.00
4 SPIKE LENGTH	0	0	17	10.00	10.00	55.00	29.29	29.29	13.21	45.00
5 SCAPE DIAMETER	0	0	17	7.000	7.000	13.00	10.29	10.29	1.724	6.000
6 SPIKE DIAMETER	0	0	17	15.00	15.00	23.00	20.29	20.29	2.339	8.000
7 SP,SC RATIO	0	0	17	*	*	.5400	.2653	.2653	.1233	.4400
8 PCB'S	0	13	4	0.	1.000	1.000	.2353	1.000	.4372	1.000
9 TRUNK HEIGHT	0	15	2	0.	5.000	10.00	.8824	7.500	2.643	10.00
10 BRACT INDUMENTUM	0	0	17	4.000	4.000	5.000	4.941	4.941	.2425	1.000

INTERMEDIATES (GP 79) WITH 11 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	7	0	8	0
2 LEAF COLOUR	0	11	0		
3 BRACT SHAPE	1	10	5	0	
4 BRACT COLOUR	1	2	8	0	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	11	1.750	1.750	2.500	2.068	2.068	.2348	.7500
2 LEAF THICKNESS	2	0	9	1.200	1.200	1.700	1.400	1.400	.1132	.5000
3 SCAPE LENGTH	0	0	11	85.00	85.00	136.0	115.9	115.9	15.65	51.00
4 SPIKE LENGTH	0	0	11	22.00	22.00	100.0	62.73	62.73	22.08	78.00
5 SCAPE DIAMETER	0	0	11	10.00	10.00	17.00	13.82	13.82	2.183	7.000
6 SPIKE DIAMETER	0	0	11	18.00	18.00	27.00	23.55	23.55	3.387	9.000
7 SP,SC RATIO	0	0	11	.2500	.2500	.7500	.5291	.5291	.1623	.5000
8 PCB'S	1	2	8	0.	1.000	5.000	2.400	3.000	2.271	5.000
9 TRUNK HEIGHT	0	1	10	0.	4.000	30.00	15.91	17.50	9.833	30.00
10 BRACT INDUMENTUM	1	0	10	3.000	3.000	5.000	4.550	4.550	.6852	2.000

INTERMEDIATES (GP 80) WITH 4 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	0	0	4	0
2 LEAF COLOUR	0	3	1		
3 BRACT SHAPE	0	0	4	1	
4 BRACT COLOUR	0	4	0	0	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	4	1.800	1.800	2.600	2.163	2.163	.3351	.8000
2 LEAF THICKNESS	1	0	3	1.350	1.350	1.600	1.450	1.450	.1323	.2500
3 SCAPE LENGTH	0	0	4	104.0	104.0	144.0	127.0	127.0	17.01	40.00
4 SPIKE LENGTH	0	0	4	27.00	27.00	77.00	44.75	44.75	22.16	50.00
5 SCAPE DIAMETER	0	0	4	11.00	11.00	17.00	13.00	13.00	2.708	6.000
6 SPIKE DIAMETER	0	0	4	21.00	21.00	31.00	24.00	24.00	4.761	10.00
7 SP,SC RATIO	0	0	4	.2000	.2000	.5700	.3525	.3525	.1559	.3700
8 PCB'S	0	1	3	0.	1.000	5.000	2.750	3.667	2.630	5.000
9 TRUNK HEIGHT	0	1	3	0.	5.000	30.00	13.75	18.33	13.77	30.00
10 BRACT INDUMENTUM	0	0	4	1.000	1.000	4.000	2.750	2.750	1.258	3.000

INTERMEDIATES OR BACKCROSSES TO X. ALMAE

(GP 82) WITH 3 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	0	0	3	0
2 LEAF COLOUR	0	3	1		
3 BRACT SHAPE	0	3	3	0	
4 BRACT COLOUR	0	3	0	0	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	3	2.000	2.000	2.250	2.150	2.150	.1323	.2500
2 LEAF THICKNESS	0	0	3	1.500	1.500	1.600	1.567	1.567	.5774E-01	.1000
3 SCAPE LENGTH	0	0	3	73.00	73.00	128.0	98.67	98.67	27.68	55.00
4 SPIKE LENGTH	0	0	3	110.0	110.0	150.0	131.0	131.0	20.07	40.00
5 SCAPE DIAMETER	0	0	3	21.00	21.00	23.00	22.00	22.00	1.000	2.000
6 SPIKE DIAMETER	0	0	3	33.00	33.00	39.00	35.33	35.33	3.215	6.000
7 SP,SC RATIO	0	0	3	.8500	.8500	1.820	1.413	1.413	.5036	.9700
8 PCB'S	0	0	3	5.000	5.000	5.000	5.000	5.000	0.	0.
9 TRUNK HEIGHT	0	0	3	12.00	12.00	100.0	60.67	60.67	44.74	88.00
10 BRACT INDUMENTUM	0	0	3	2.000	2.000	5.000	3.667	3.667	1.528	3.000

X. ALNAE AND BACKCROSSES 5 (GP   83) WITH 9 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	4	0	6	0
2 LEAF COLOUR	0	9	0		
3 BRACT SHAPE	0	3	9	4	
4 BRACT COLOUR	1	8	1	0	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	9	1.800	1.800	2.200	1.967	1.967	.1299	.4000
2 LEAF THICKNESS	2	0	7	1.200	1.200	1.500	1.336	1.336	.1107	.3000
3 SCAPE LENGTH	0	0	9	56.00	56.00	120.0	89.44	89.44	19.69	64.00
4 SPIKE LENGTH	0	0	9	44.00	44.00	115.0	81.22	81.22	22.30	71.00
5 SCAPE DIAMETER	0	0	9	11.00	11.00	19.00	15.11	15.11	2.713	8.000
6 SPIKE DIAMETER	0	0	9	24.00	24.00	33.00	28.67	28.67	3.082	9.000
7 SP,SC RATIO	0	0	9	.5100	.5100	1.300	.9300	.9300	.2757	.7900
8 PCB'S	1	2	6	0.	1.000	5.000	3.250	4.333	2.435	5.000
9 TRUNK HEIGHT	0	0	9	32.00	32.00	81.00	51.78	51.78	15.83	49.00
10 BRACT INDUMENTUM	0	0	9	1.000	1.000	5.000	2.556	2.556	1.236	4.000

STATISTICS FOR ENTIRE DATA
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	13	0	38	0
2 LEAF COLOUR	1	28	18		
3 BRACT SHAPE	1	33	24	5	
4 BRACT COLOUR	3	17	23	2	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	44	1.750	1.750	3.200	2.278	2.278	.3827	1.450
2 LEAF THICKNESS	16	0	28	1.200	1.200	2.000	1.482	1.482	.2127	.8000
3 SCAPE LENGTH	0	0	44	56.00	56.00	150.0	108.1	108.1	20.26	94.00
4 SPIKE LENGTH	0	0	44	10.00	10.00	150.0	56.61	56.61	33.98	140.0
5 SCAPE DIAMETER	0	0	44	7.000	7.000	23.00	13.20	13.20	3.708	16.00
6 SPIKE DIAMETER	0	0	44	15.00	15.00	39.00	24.18	24.18	5.244	24.00
7 SP,SC RATIO	0	0	44	.1000E+00	.1000E+00	1.820	.5534	.5534	.3968	1.720
8 PCB'S	2	18	24	0.	1.000	5.000	1.905	3.333	2.250	5.000
9 TRUNK HEIGHT	0	17	27	0.	4.000	100.0	20.30	33.07	25.63	100.0
10 BRACT INDUMENTUM	1	0	43	1.000	1.000	5.000	4.058	4.058	1.292	4.000

Environmental factors

Once again, although measurements of the environment were not recorded for this study, the population was spread-out across an easily discernable gentle slope from swampy conditions to a drier rise. This gradient, as well as the taxonomic gradient, appears to be reflected in vector 1. Vector 2 can not easily be correlated with any environmental gradient, but is revealed by BACRIV (Appendix 3.5) to represent a number of intermediate morphological features of the plants.

3.2.2.5 DISCUSSION OF SUBSIDIARY ANALYSES RESULTS

The subsidiary analyses of populations of _Xanthorrhoea_ on Quaternary sand deposits in both northern New South Wales and at Beerwah in south-east Queensland show very similar patterns of variation to the patterns seen in the populations at Myall Lakes.

It is therefore reasonable to infer that these populations are also examples of two species with different habitat preferences hybridising with each other where they meet in the "hybrid" environmental conditions on ecoclines between their habitats of preference.

It is clear that vector 1 of the ordinations can be interpreted as a taxonomic gradient which appears to reflect a wet-dry environmental gradient.

Thus this phenomenon is clearly not restricted to the Myall Lakes region but rather occurs on many of the Quaternary sand deposits along

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the east coast.

3.3 - AN EXAMPLE OF OVERLAPPING BUT DISCRETE SPECIES

3.3.1 Pearl Beach

Another example of intergradation proposed by Lee (1966 a) concerns four taxa: X. latifolia; X. arborea; X. media; X. minor. Lee notes "... two species [X. arborea and X. media] ... seem to give place to a population in which their characters, perhaps with those of X. minor also are merged, namely X. media subsp. latifolia [X. latifolia]". (Lee also commented that X. latifolia (as X. media subsp. latifolia) sometimes develops a trunk higher than its normal 1 m limit "but perhaps only in hybrid derivatives", which she also notes occur as "large populations of presumed hybrid derivatives ... in the coastal ranges near Wyong, N.S.W.". However, specimens of X. latifolia close to its type locality (Beerwah, Qld) have trunks up to 2 m tall, Bedford (1986 a). Thus Lee's hypothesis that hybridism is a necessary precursor to the development of tall trunks in this taxon is not supported.)

X. latifolia and X. arborea are the most similar in appearance of the above listed taxa, but are distinguishable on a number of characters, the most obvious of which are leaf width, scape length and ratio of scape length to spike length. The two taxa are not usually sympatric and usually occur on different substrates, with X. arborea restricted to the sandstones in the Sydney region and X. latifolia growing on a range of substrates, mostly other than sandstone, north of the Sydney region to about Townsville in Queensland. The taxa also have some differences in flowering patterns, with different peak flowering times

and limited overlap in range of flowering times, with X. arborea flowering January-April and X. latifolia flowering March-October.

A site in Brisbane Waters National Park behind the University of Sydney Crommelin Research Station at Pearl Beach (Figure 3.18) provided an opportunity to investigate an apparent transition between X. arborea and X. latifolia to see if Lee's hypothesis was supported. The site consists of a north facing sandstone slope which tapers out to the sandy valley floor. Tall X. arborea grow from the top of the sandstone slope down to, and apparently intergrade with, X. latifolia growing on the valley floor.

An unusually productive overlap in flowering times of these two taxa at this site in Autumn 1979 meant that there were 21 plants with spikes at the one time, which provided a reasonable number of fertile (complete) plants for a numerical analysis. All 21 plants were measured and scored for characters.

3.3.1.2 CHARACTERS AND METHODS

The same fourteen separate morphological features were scored for each plant, either as continuous characters (C) or as disordered multistate characters (DM) as were used in the Myall analyses (Table 3.1).

The 21 plants were analysed on the 14 equally weighted characters as for the Northern New South Wales analyses. That is both a TAXON (V.4)

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Figure 3.18 Location map for Pearl Beach Study area.

GOSFORD   ETTALONG BEACH

UMINA

BRISBANE WATER

NATIONAL PARK

Ettalong Creek

Umina Beach

Ocean Beach

Ettalong Beach

Lobster Beach

Green Point Creek

Pearl Beach

CROMMELIN
NATIVE
ARBORETUM

Green Point

Warrah▲

N

Middle Head

LION ISLAND

BROKEN   BAY

|0   1   2 km

Barrenjoey Head

West Head
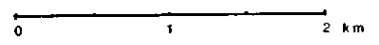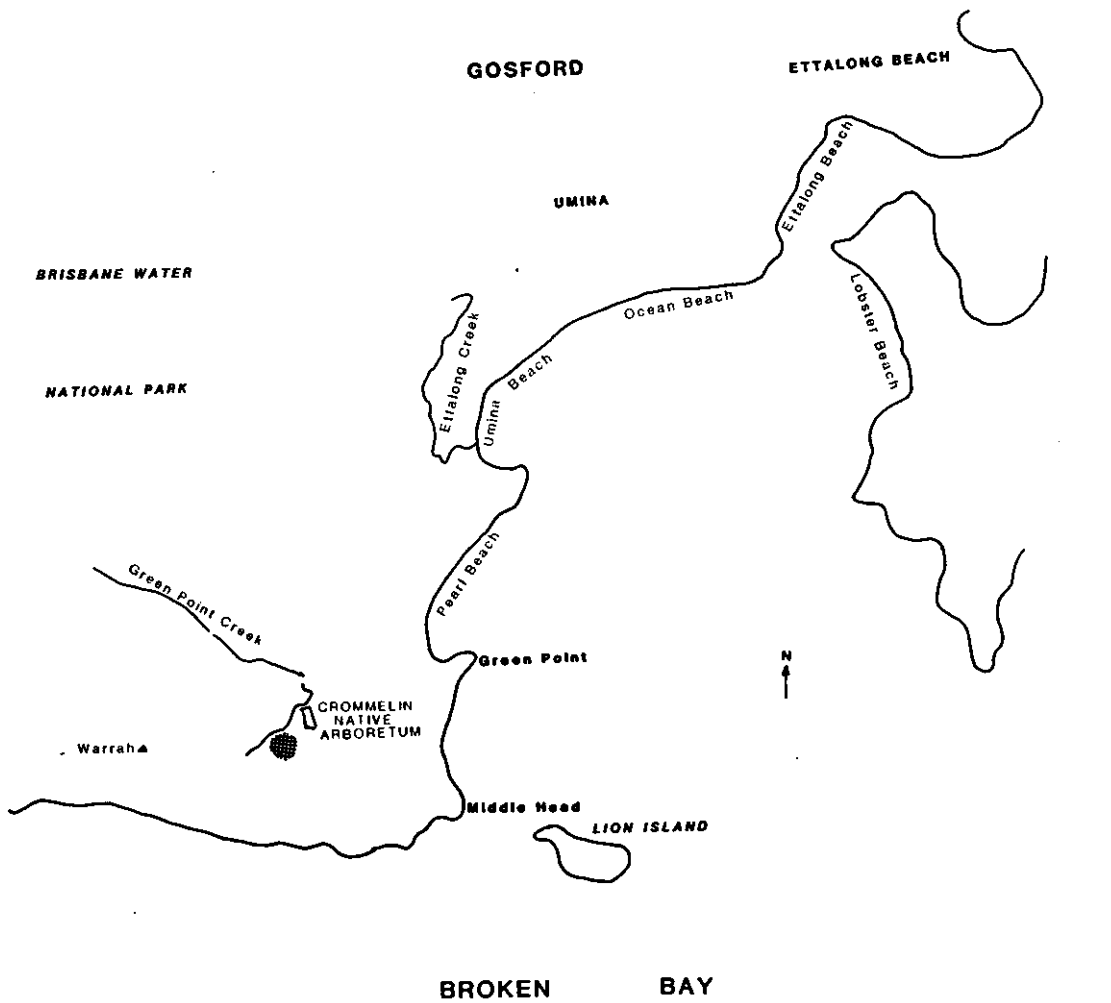
KEY:
SAMPLE AREA

classification (MSED+SAHN) and principal co-ordinate analysis (PCOA+PTPLOT) with their respective diagnostic programs (GCOM+GSTAT+CRAMER and BACRIV) were performed. Both Group Average (UPG) and Incremental Sum of Squares (ISS) clustering techniques were used in the classifications to test the stability of the clusters.

3.3.1.3 RESULTS

Group Average clustering (UPG) (dendrogram, Figure 3.19, data set and dissimilarity levels in Appendix 3.6) .

By the .9 dissimilarity level there are two main clusters and one singleton, entity 15. Entity 15 joins the smaller of the two clusters at the 1.27 level of dissimilarity, to form two clusters in the data. Individuals in the larger of the two clusters have the characteristics of X. arborea and those in the smaller cluster have the characteristics of X. latifolia.

The three-group level was chosen for further analysis by GCOM and GSTAT to examine the high level of dissimilarity of entity 15. These programs (Tables 3.10 and 3.11) show that entity 15 has most of the characteristics of X. latifolia but differs from that taxon in having a relatively short scape (80 cm) which is equal in length to its spike, giving a spike length to scape length ratio of 1:1. As this scape length is also shorter than usual for X. arborea in these analyses however, this can not be taken to infer that this plant is intermediate between the two taxa. It is most likely that this is a "runt" plant.

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Figure 3.19 SAHN Classification UPG Dendrogram, Pearl Beach.

Key: **** <u>X. arborea</u>; ■ ■ ■ ■ <u>X. latifolia</u>.
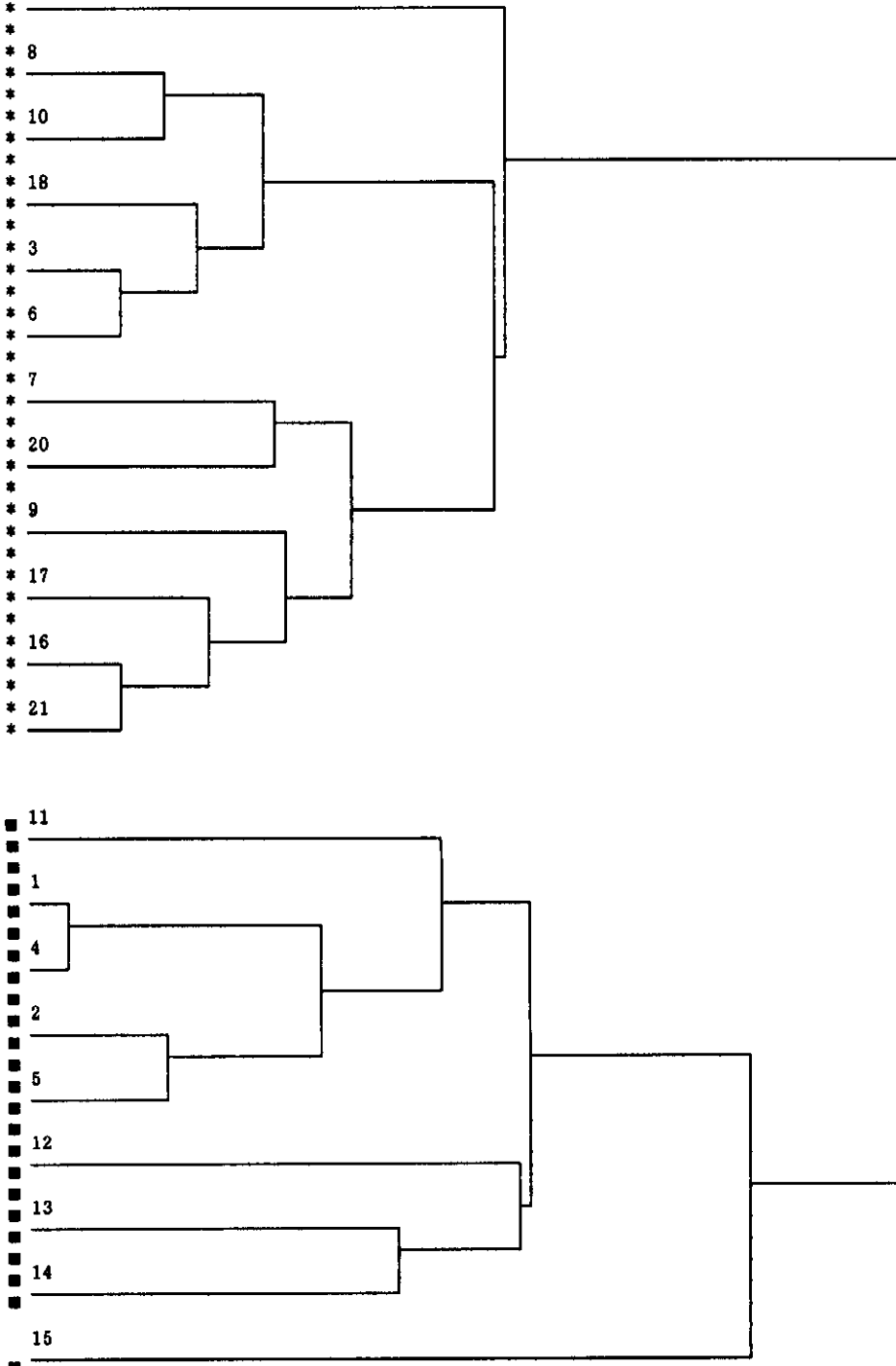
Table 3.10 GCOM, UPG Classification 3 Groups, Pearl Beach.

```
####   COMPARISON NO.  1
####   GROUP A = GP 37 (X. arborea)
####   GROUP B = INDIVIDUAL 15 + GP 39 (X. latifolia)
```

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 8.1527

ATTRIBUTE (STATE)	NAME	GROUP A 12 MEMBERS ATTRIBUTE NO. MEAN PRESENT		GROUP B 9 MEMBERS ATTRIBUTE NO. MEAN PRESENT		CONTRIBUTION %	% (CUM)	ACTUAL VALUE
DMUL 2	LEAF COLOUR		12		9	31	31	2.50
ST. 1	GREEN	.000		1.000				
ST. 2	GLAUCOUS	1.000		.000				
DMUL 1	LEAF SHAPE		12		9	19	50	1.59
ST. 1	NARROWLY Q-R	.000		.444				
ST. 2	OBTRULLATE	.000		.556				
ST. 4	TRANSVERSE LINEAR	1.000		.000				

1 ATTRIBUTES MADE NO CONTRIBUTION.

```
####   COMPARISON NO.  2
####   GROUP A = GP   15 (ANOMALOUS MEMBER OF X. latifolia)
####   GROUP B = GP   39 (X. latifolia)
```

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 1.6094

ATTRIBUTE (STATE)	NAME	GROUP A 1 MEMBERS ATTRIBUTE NO. MEAN PRESENT		GROUP B 8 MEMBERS ATTRIBUTE NO. MEAN PRESENT		CONTRIBUTION %	% (CUM)	ACTUAL VALUE
FNUM 7	SP/SC RATIO	1.000	1	.445	6	29	29	.469
FNUM 3	SCAPE LENGTH	80.000	1	207.750	8	27	56	.436

4 ATTRIBUTES MADE NO CONTRIBUTION.

Table 3.11 GSTAT, SAHN UPG Classification 3 Groups, Pearl Beach.

Table 3.11   Warrah SAHN UPG Classification GSTAT   3 Groups.

X. ARBOREA   (GP   37) WITH 12 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	0	0	0	12
2 LEAF COLOUR	0	0	12		
3 BRACT SHAPE	0	0	12		
4 BRACT COLOUR	8	4	0		
5 CLUSTER BRACTS	2	1	2	7	
6 JUV. CLUSTER BR.	3	0	1	8	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	12	4.800	4.800	11.00	7.342	7.342	1.568	6.200
2 LEAF THICKNESS	0	0	12	1.500	1.500	2.500	1.992	1.992	.3081	1.000
3 SCAPE LENGTH	0	0	12	130.0	130.0	275.0	210.0	210.0	40.93	145.0
4 SPIKE LENGTH	0	0	12	80.00	80.00	227.0	143.6	143.6	43.80	147.0
5 SCAPE DIAMETER	0	0	12	15.00	15.00	38.00	26.33	26.33	5.883	23.00
6 SPIKE DIAMETER	0	0	12	29.00	29.00	50.00	36.92	36.92	6.529	21.00
7 SP,SC RATIO	0	0	12	.4400	.4400	.9500	.6775	.6775	.1338	.5100
8 PCB'S	0	10	2	0.	.5000	1.000	.1250	.7500	.3108	1.000
9 TRUNK HEIGHT	0	0	12	60.00	60.00	200.0	118.3	118.3	41.08	140.0
10 BRACT INDUMENTUM	0	0	12	.5000	.5000	3.000	1.292	1.292	.7821	2.500

ANOMALOUS MEMBER OF X. LATIFOLIA

(INDIVIDUAL 15)
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	1	0	0	0
2 LEAF COLOUR	0	1	0		
3 BRACT SHAPE	0	0	1		
5 CLUSTER BRACTS	0	0	1	0	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	1	3.350	3.350	3.350	3.350	3.350	0.	0.
2 LEAF THICKNESS	0	0	1	2.250	2.250	2.250	2.250	2.250	0.	0.
3 SCAPE LENGTH	0	0	1	80.00	80.00	80.00	80.00	80.00	0.	0.
4 SPIKE LENGTH	0	0	1	80.00	80.00	80.00	80.00	80.00	0.	0.
5 SCAPE DIAMETER	0	0	1	23.00	23.00	23.00	23.00	23.00	0.	0.
6 SPIKE DIAMETER	0	0	1	34.00	34.00	34.00	34.00	34.00	0.	0.
7 SP,SC RATIO	0	0	1	1.000	1.000	1.000	1.000	1.000	0.	0.
9 TRUNK HEIGHT	0	0	1	70.00	70.00	70.00	70.00	70.00	0.	0.

X. LATIFOLIA   (GP   39) WITH 8 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	3	5	0	0
2 LEAF COLOUR	0	8	0		
3 BRACT SHAPE	0	0	8		
4 BRACT COLOUR	2	4	2		
5 CLUSTER BRACTS	2	3	1	2	
6 JUV. CLUSTER BR.	6	1	1	0	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	8	2.750	2.750	3.500	3.231	3.231	.2463	.7500
2 LEAF THICKNESS	0	0	8	1.250	1.250	2.000	1.700	1.700	.2632	.7500
3 SCAPE LENGTH	0	0	8	150.0	150.0	242.0	207.8	207.8	32.22	92.00
4 SPIKE LENGTH	2	0	6	54.00	54.00	115.0	91.83	91.83	27.62	61.00
5 SCAPE DIAMETER	0	0	8	13.00	13.00	26.00	19.38	19.38	4.749	13.00
6 SPIKE DIAMETER	0	0	8	26.00	26.00	43.00	36.25	36.25	5.849	17.00
7 SP,SC RATIO	2	0	6	.2700	.2700	.6000	.4450	.4450	.1167	.3300
8 PCB'S	0	4	4	0.	1.000	1.000	.5000	1.000	.5345	1.000
9 TRUNK HEIGHT	0	0	8	10.00	10.00	60.00	33.75	33.75	16.85	50.00
10 BRACT INDUMENTUM	0	0	8	.1000E+00	.1000E+00	2.000	.9500	.9500	.5398	1.900

STATISTICS FOR ENTIRE DATA
****

DISORDERED MULTISTATES	NO. MIS	1	2	NO. IN STATE 3	4
1 LEAF SHAPE	0	4	5	0	12
2 LEAF COLOUR	0	9	12		
3 BRACT SHAPE	0	0	21		
4 BRACT COLOUR	11	8	2		
5 CLUSTER BRACTS	4	4	4	9	
6 JUV. CLUSTER BR.	10	1	2	8	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D.	RANGE
1 LEAF WIDTH	0	0	21	2.750	2.750	11.00	5.586	5.586	2.386	8.250
2 LEAF THICKNESS	0	0	21	1.250	1.250	2.500	1.893	1.893	.3218	1.250
3 SCAPE LENGTH	0	0	21	80.00	80.00	275.0	203.0	203.0	45.60	195.0
4 SPIKE LENGTH	2	0	19	54.00	54.00	227.0	123.9	123.9	45.74	173.0
5 SCAPE DIAMETER	0	0	21	13.00	13.00	38.00	23.52	23.52	6.210	25.00
6 SPIKE DIAMETER	0	0	21	26.00	26.00	50.00	36.52	36.52	5.988	24.00
7 SP,SC RATIO	2	0	19	.2700	.2700	1.000	.6211	.6211	.1875	.7300
8 PCB'S	0	15	6	0.	.5000	1.000	.2619	.9167	.4364	1.000
9 TRUNK HEIGHT	0	0	21	10.00	10.00	200.0	83.81	83.81	52.49	190.0
10 BRACT INDUMENTUM	0	1	20	0.	.1000E+00	3.000	1.100	1.155	.7280	3.000

The lower levels of dissimilarity were not investigated further because they did not appear to correlate with any visible pattern of variation in the population.

Incremental Sum of Squares clustering (ISS) (Dendrogram, Figure 3.20, dissimilarity levels, GCOM and GSTAT in Appendix 3.7).

This classification shows the entities divided into the same two groups as for the UPG classification, although the order of joining is different. As is usual for this clustering algorithm the dissimilarity levels are considerably higher and the result is apparently more "clean-cut". For example entity 15 is no longer placed as a high dissimilarity level singleton, although it is still placed as the most dissimilar individual in the whole analysis.

Ordination - PCOA and BACRIV (Figures 3.21.1-3.21.3, Table 3.12, Appendix 3.8).

The first three vectors account for 71% of the dissimilarity in the matrix: Vector 1 = 44%; Vector 2 = 15%; Vector 3 = 11%. According to the guidelines in Clifford and Stephenson (1975) such a high percentage indicates that the ordination is a reasonable representation of the data.

The first vector shows the widest distribution of individuals and the most information, in combinations with the other two vectors it shows a clear structure in the data. In the first two plots which show the combinations of vector 1 with the other two vectors, there is a clear division between the groupings of individuals indicated by the

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Figure 3.20 SAHN Classification ISS Dendrogram,
Pearl Beach.

Key: **** <u>X. arborea</u>; ■ ■ ■ ■ <u>X. latifolia</u>.
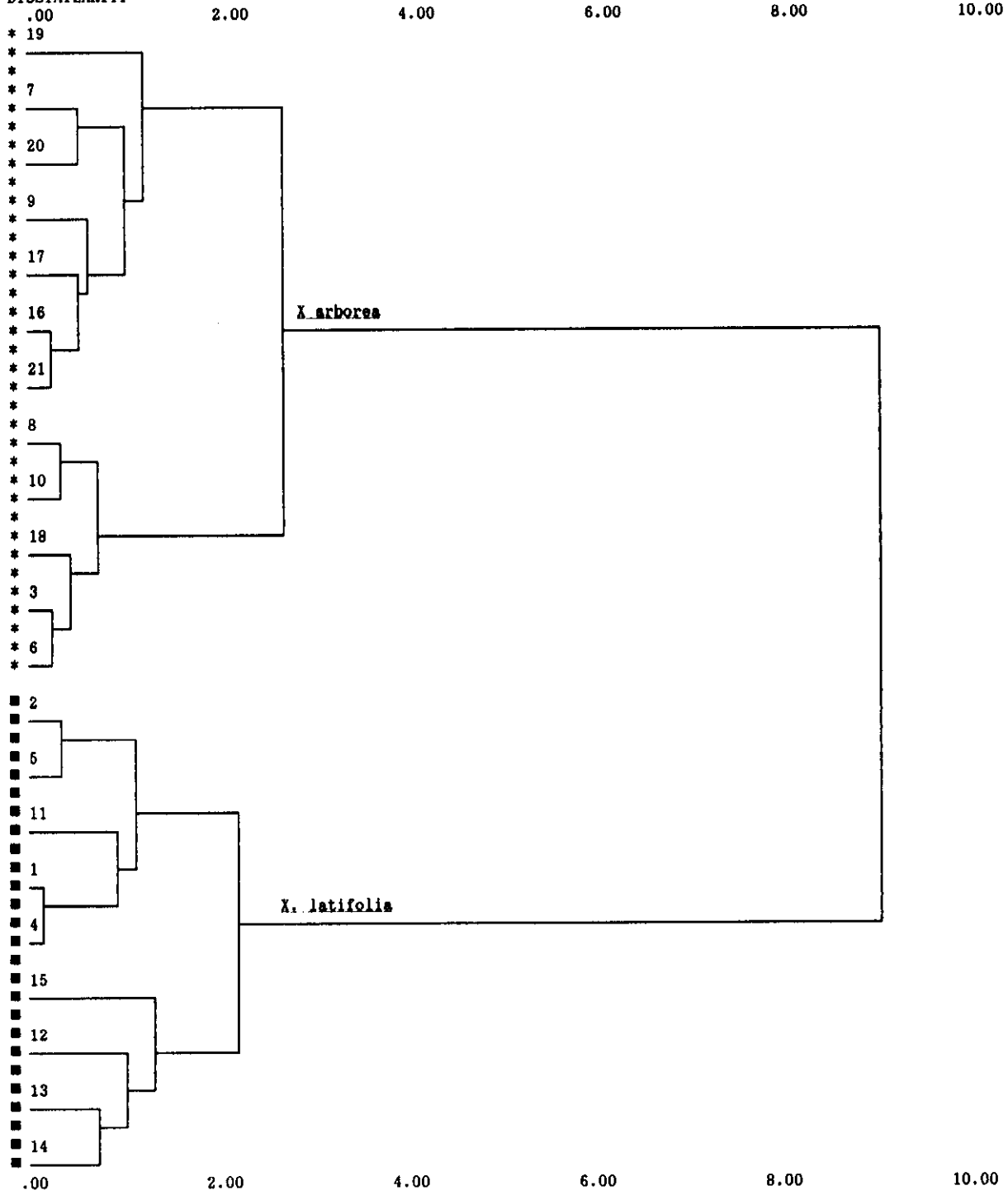
Figure 3.21.1 PCQA Ordination, Pearl Beach,

Vectors 1 and 2.

Key: **** <u>X. arborea</u>; ■ ■ ■ ■ <u>X. latifolia</u>;

   entity 15 highlighted by − − − − .
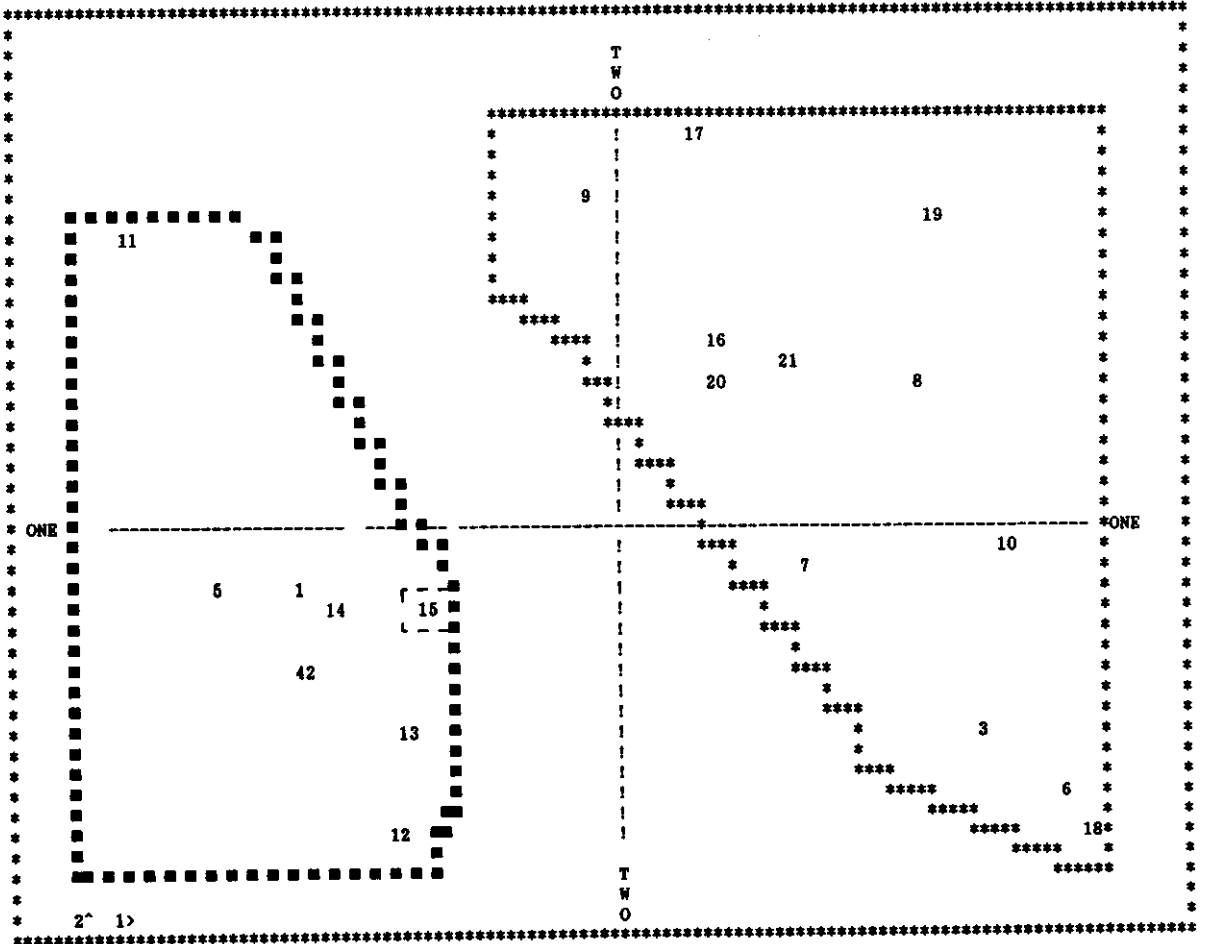
Figure 3.21.2 PCOA Ordination, Pearl Beach,

Vectors 1 and 3.

Key: **** <u>X. arborea</u>; ■ ■ ■ ■ <u>X. latifolia</u>.

Vectors 1 and 3
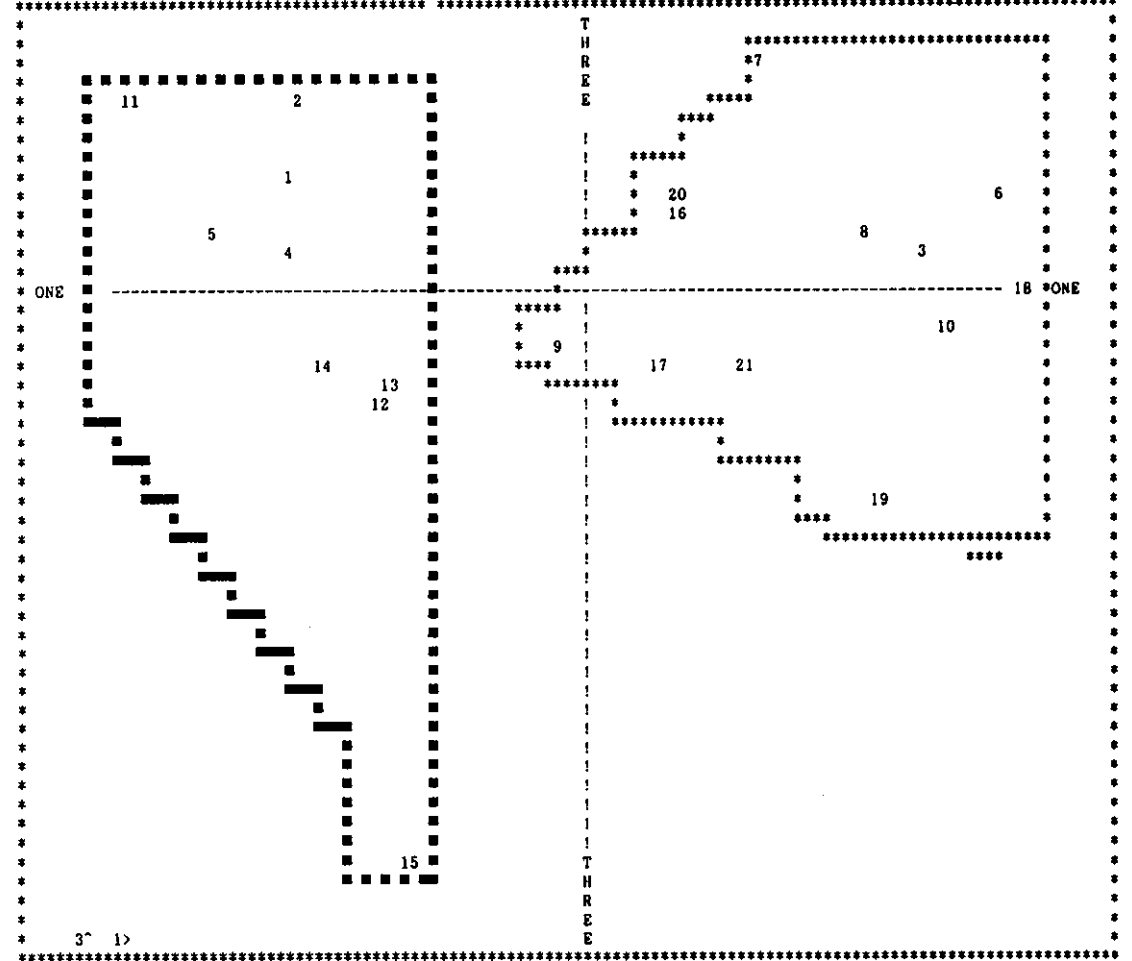
Figure 3.21.3 PCQA Ordination, Pearl Beach,

Vectors 2 and 3.

Taxa not separated.

Vectors 2 and 3.

```
Vectors 2 and 3.
*************************************************************************
*                                T                                     *
*                           7    H                                     *
*                                R                                     *
*                    2           E                    11               *
*                                E                                     *
*                                !                                     *
*                           1    !                                     *
*           6                    !           20                        *
*                                !              16                     *
*                           5    !          8                          *
*         3      4               !                                     *
*                                !                                     *
*  TWO          18---------------+------------------------- TWO        *
*                                !                                     *
*                               10                                     *
*                                !                        9            *
*                      14        !            21              17       *
*              13                !                                     *
*        12                      !                                     *
*                                !                                     *
*                                !                                     *
*                                !                        19           *
*                                !                                     *
*                                !                                     *
*                                !                                     *
*                                !                                     *
*                                !                                     *
*                                !                                     *
*                                !                                     *
*                                !                                     *
*                                !                                     *
*                                !                                     *
*                                !                                     *
*                      15        T                                     *
*                                H                                     *
*                                R                                     *
*                                E                                     *
*      3^   2>                   E                                     *
*************************************************************************
```

Table 3.12 PCOA Ordination BACRIV results, Pearl Beach.

Table 3.12 PCOA Ordination BACRIV results, Pearl Beach.

NOTE: CORRELATIONS PRINTED ARE THE CORRELATIONS OF THE ATTRIBUTE VALUES WITH THE SCORES FOR THE VECTOR

CORRELATIONS FOR VECTOR 1

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	NO	STATE NAME
LEAF WIDTH	FNUM 1	.9250	21		
JUV. CLUSTER BR.	DMUL 6	.9055	11	3	
LEAF SHAPE	DMUL 1	.8989	21	4	
LEAF COLOUR	DMUL 2	-.8989	21	1	
LEAF COLOUR	DMUL 2	.8989	21	2	
SPIKE LENGTH	FNUM 4	.8318	19		
SCAPE DIAMETER	FNUM 5	.7882	21		
TRUNK HEIGHT	FNUM 9	.7846	21		
LEAF SHAPE	DMUL 1	-.6939	21	2	
JUV. CLUSTER BR.	DMUL 6	-.6696	11	2	
LEAF THICKNESS	FNUM 2	.6284	21		
SP,SC RATIO	FNUM 7	.6257	19		

14 ITEMS NOT PRINTED

CORRELATIONS FOR VECTOR 2

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	NO	STATE NAME
SPIKE DIAMETER	FNUM 6	-.8139	21		
BRACT INDUMENTUM	FNUM 10	.7188	21		
SCAPE LENGTH	FNUM 3	-.5433	21		
SPIKE LENGTH	FNUM 4	-.4540	19		
SCAPE DIAMETER	FNUM 5	-.4408	21		
TRUNK HEIGHT	FNUM 9	.3890	21		
LEAF SHAPE	DMUL 1	-.3846	21	1	
LEAF SHAPE	DMUL 1	.3613	21	4	
LEAF COLOUR	DMUL 2	.3613	21	2	
LEAF COLOUR	DMUL 2	-.3613	21	1	
BRACT COLOUR	DMUL 4	-.3452	10	2	
BRACT COLOUR	DMUL 4	.3452	10	1	
LEAF THICKNESS	FNUM 2	-.2739	21		

13 ITEMS NOT PRINTED

CORRELATIONS FOR VECTOR 3

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	NO	STATE NAME
CLUSTER BRACTS	DMUL 5	-.6591	17	2	
SCAPE LENGTH	FNUM 3	.6419	21		
LEAF SHAPE	DMUL 1	-.6100	21	1	
SP,SC RATIO	FNUM 7	-.4883	19		
LEAF THICKNESS	FNUM 2	-.4696	21		
PCB'S	FNUM 8	.4315	21		
LEAF SHAPE	DMUL 1	.4068	21	2	
CLUSTER BRACTS	DMUL 5	.3546	17	3	
BRACT COLOUR	DMUL 4	-.3066	10	2	
BRACT COLOUR	DMUL 4	.3066	10	1	
JUV. CLUSTER BR.	DMUL 6	-.2753	11	1	

15 ITEMS NOT PRINTED

classifications. The plot of vector 2 against vector 3 does not show any clear structure or trends, reflecting the lower information content of these vectors.

It is interesting that entity 15, which is shown to be a somewhat anomalous member of the X. latifolia group by the UPG classification, is shown as an outlier to that group by the plot of vector 1 against vector 3, and by the plot of vector 2 against vector 3. It appears that vector 3 has been considerably influenced by this individual. These plots therefore also suggest that entity 15 is not an intermediate plant but is most likely a somewhat anomalous member of the X. latifolia group.

BACRIV (Table 3.12) indicates that leaf width, leaf shape transverse linear and leaf colour are the characters most highly correlated with vector 1. For vector 2 spike diameter and bract indumentum characters are the most highly correlated, while for vector 3 scape length, cluster bracts and leaf shape 1 (narrowly transverse rhombic) are the most highly correlated.

From these results it is not surprising that vector 1 provides the best separation of the two taxa within the ordination, as it represents those characteristics most diagnostically different between the two taxa. It is also not surprising that vectors 2 and 3 do not provide good separation as they represent characters not reliably differing between the taxa.

Environmental factors

The obvious environmental factors at this site are the slope and change in soil type (Figure 3.22). Although no specific measurements were made of the environment the obvious factors are, to some extent, reflected in the results, though significantly less so than in the previous three analyses. For example, it is possible to interpret vector 1 in the ordinations as reflecting a combination of the slope and soil change, as well as the obvious taxonomic change. Plants placed at each end of vector 1, as well as being separate taxa, are from areas towards the top and bottom of the slope. However this analogy can not be extended too far as the distribution of the plants was almost continuous, with a cluster of plants around the slope/soil boundary, whereas ordination vector 1 shows the plants quite well separated. Also individual 15, which is shown in between the other groups on vector 1, but as an outlier on vector 3 did not occupy the environmental mid ground but was amongst other plants of its own species.

3.3.1.4 DISCUSSION

The results of this analysis indicate that these two species do not intergrade or hybridise at this site, even though they do overlap in their distribution. The one individual which does not fall easily into either group can be seen not to be intermediate between the taxa but rather an example of the considerable occasional variation that can occur in many Xanthorrhoea taxa.

Figure 3.22 Diagrammatic representation of location of plants at the Pearl Beach study area in relation to slope and soil type.

DIAGRAMMATIC DISTRIBUTION OF TAXA
RELATIVE TO SOIL TYPE AND SLOPE

A = *X. arborea*

L = *X. latifolia*

SANDSTONE

SAND

ALTITUDE

DISTANCE ALONG TRANSECT
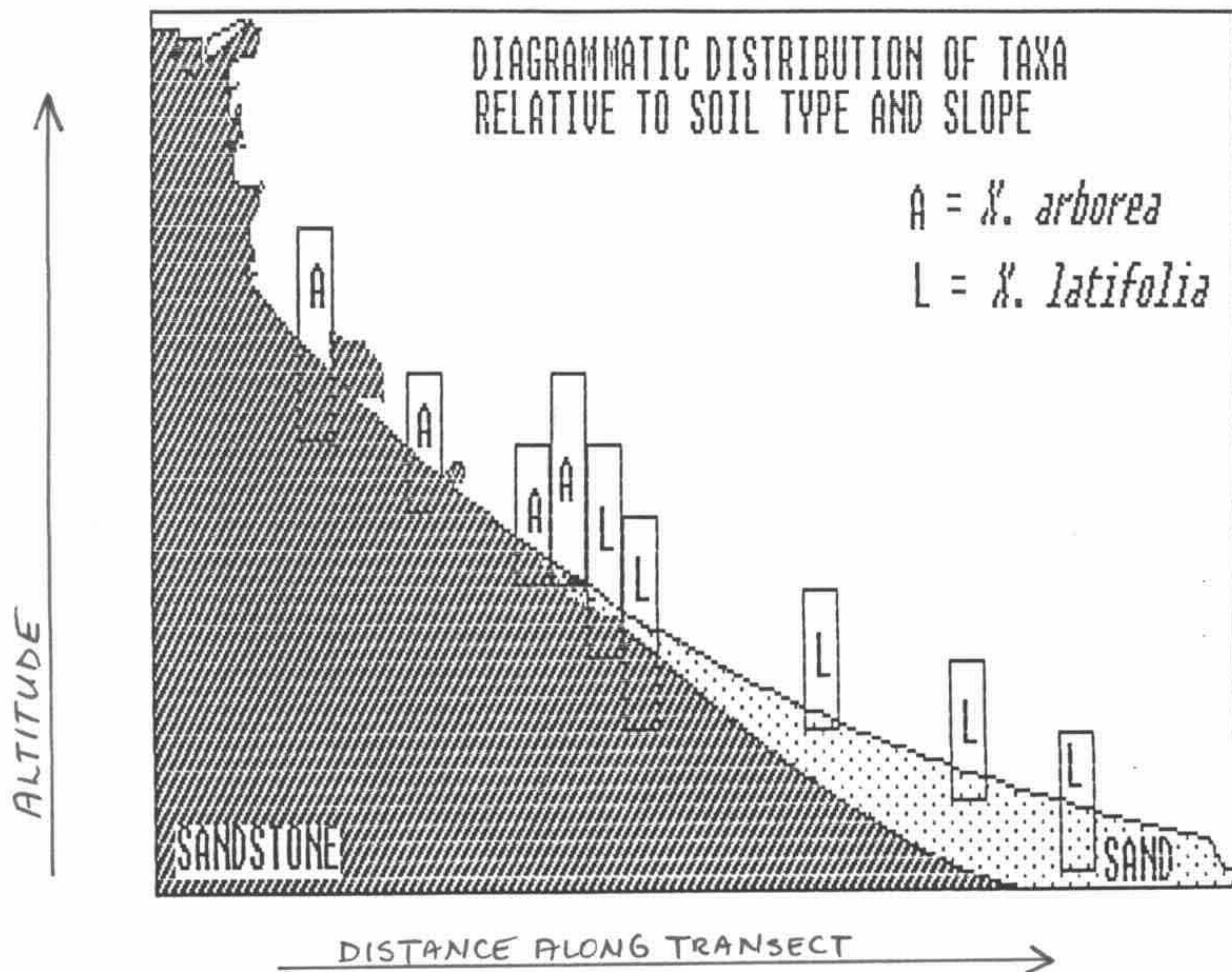
3.4 GENERAL DISCUSSION AND CONCLUSIONS

Lee (1966 a and b) termed all examples of intermediacy "putative hybrids" and Bedford (1986 a) has commented that hybrids only seem to exist on the coastal sand dunes from Beerwah in Queensland to Newcastle in N.S.W., although they may also be present in similar situations further south. He noted however that "most other plants presumed to be hybrids are probably either taxa not yet recognised or examples of the considerable variation that often occurs in Xanthorrhoea species.

This belief was reflected by the formal description in Bedford (1986 a and b) of a number of taxa which had previously been referred to purported hybrids.

Examples of the hybrid swarms referred to by Bedford (1986 a) and Lee (1966 a and b) have now been observed and documented on the Quaternary sand masses along the east coast of Queensland and New South Wales

The studies above therefore support the hypothesis that hybridisation does occur in Xanthorrhoea. Also, the extensive studies throughout Australia conducted for the taxonomic revision of the genus (Chapter 5), support the hypothesis that hybridism is restricted to habitats on the Quaternary age sand deposits along the east coast of Australia.

Figure 3.12 shows the distribution of Quaternary sands along the New South Wales coast.

Figure 3.23 shows the Xanthorrhoea species of eastern Australia with

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Figure 3.23 Diagrammatic representation of gene flow and species habitat preferences.

The circles representing the species are placed in the concentric zones representing the substrates on which they occur, and in the sector of the circle representing the relative water-logging of their habitat as indicated by the patterns in the sectors of the inner circle. Thick lines join those taxa documented here as hybridising, thin lines join taxa in similar situations which show signs of intergradation, but have not yet been fully documented.

X. glauca subsp. *glauca*

X. glauca subsp. *angustifolia*

X. almae

X. latifolia subsp. *maxima*

X. australis

X. malacophylla

X. arborea

X. macronema

X. acaulis

X. media

X. resinifera sp. aff. *resinifera* (Vic.)

X. latifolia subsp. *latifolia*

X. fulva

X. pumilio
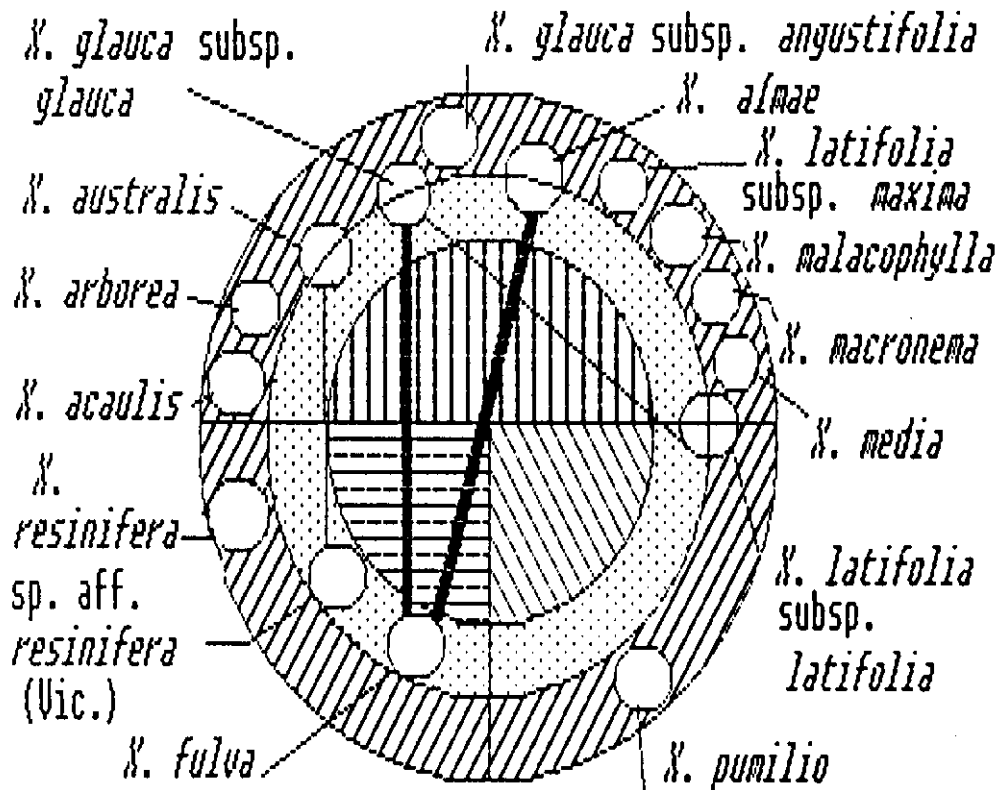
KEY :
━━━━ hybridising species;
──── species presumed to hybridise

PRE-QUATERNARY SUBSTRATES

QUATERNARY SANDS

WELL DRAINED HABITATS

PERIODICALLY WATERLOGGED HABITATS

INTERMEDIATE DRAINAGE HABITATS
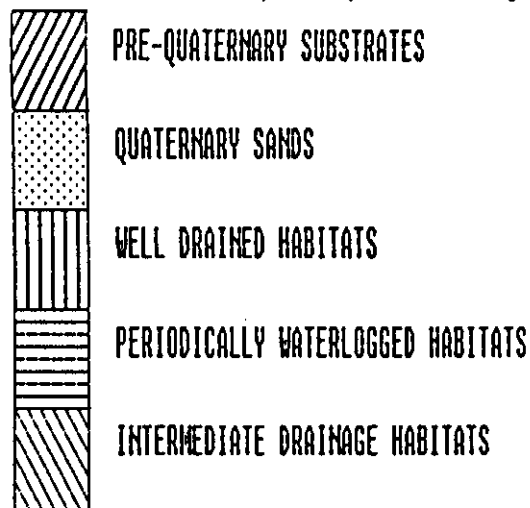
links between those species believed to hybridise and indicates their soil type and drainage preferences. It can be seen that all documented examples of hybrids occur on the Quaternary sands between species with opposite wet and dry habitat preferences. Such a situation is also mentioned in the case of the possible hybridism indicated between X. australis and X. resinifera as indicated by annotations on specimens in herb. NSW that a range of intermediates between the taxa existed in the area where the specimens were collected. The other example of apparent hybridism marked on Figure 3.23 occurs between X. glauca, a "well drained" species and X. latifolia subsp. latifolia where it grows in intermediate drainage conditions at Nelson Bay, New South Wales (Bedford, unpub. data), also occurs on an apparent ecotonal situation, with X. glauca on a sand dune and X. latifolia at the edge of the dune where sand overlies the older soils preferred by that species.

The studies above also show that hybridism is only found where two species meet on an ecocline (usually apparently from wet-dry) such that there is an intermediate habitat with conditions not preferred by either parent. It appears that the hybrids have environmental preferences (?habitat drainage) intermediate to those of their parents and are therefore able to more effectively colonise the intermediate habitat of the ecocline than are their parents.

The causative factors for such a restricted distribution of hybrids are not clear. Possible factors that could be considered include the possibility that changes in moisture conditions such as increased or decreased rainfall may be causing the development of the intermediate habitat.

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However, other species with different moisture preferences on different, older soils, do sometimes meet without hybridisation occurring. For example, on the Sydney sandstones, species with a preference for conditions with seasonally impaired drainage, such as X. resinosa, often abut species which prefer good drainage, such as X. media, without intermediates or hybrids ever having been found.

The Quaternary sands are relatively new, (mostly less than 130,000 years B.P., Galloway and Kemp, 1981, and judging from sea level records which show peak sea levels about 240,000, 200,000, and with the highest some 130,000 years ago according to Chappell, 1983 and Chappell and Shackleton 1986). The habitat they provide, however, might well be older since similar sand systems may have been formed during the interglacials of the Pleistocene, i.e. 1,000,000 years B.P. Such habitats may have been more limited during the warmer conditions which appear to have prevailed before that, as there is no evidence for pre-Quaternary coastal dunes in Australia (B.G. Lees, pers. comm.). Thus the sand systems represent a younger habitat than the inland rock-based soils. Moreover, they are habitats which have undergone a series of sharp changes, advances and retreats depending upon the changing size of the ice caps, and therefore sea levels, during the Pleistocene. These two conditions, relative youth and fluctuating changing environment, are the kind of conditions that are postulated to be the cause of inefficient barriers to gene flow, and thus increase the likelihood of intermediates or hybrids (e.g. Anderson, 1949; Stebbins, 1959; Levins, 1964; Lewis, 1966).

There is some evidence in the literature to support the proposal that hybridism should be limited to ecotones on the Quaternary sands.

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Bobrov (1982) documented hybridism in _Picea_ which he believed to be connected with the change of climate of "the Quaternary and Holocene periods", a direct parallel with the postulated timing for the onset of hybridisation in _Xanthorrhoea_. Also Levins (1964) has noted that changing habitats favour increased gene flow between species, which is relevant because the Quaternary sands are a changing habitat, as noted above.

Chapter 4

PHYLOGENETIC RELATIONSHIPS

OF XANTHORRHOEA

4.1   Introduction

The cladistic taxonomic techniques enumerated by Hennig (1966) and refined by subsequent authors (e.g. Eldredge and Cracraft 1980, Wiley 1981 and Farris 1983) have been used to infer phylogenetic relationships between organisms. These principles are now generally accepted by biologists (e.g. Kluge and Farris, 1969; Nelson, 1973, 1978 and 1982; Johnson and Briggs, 1985; Humphries and Parenti, 1986; Ladiges and Humphries, 1983 and 1986; Weston and Crisp, 1987; etc.).

These principles state, in part, that the only satisfactory way to determine sister group relationships is on the basis of shared advanced characters (synapomorphies). Further, when, in grouping some taxa, the characters contradict each other in terms of direction of change of characters or states, the principle of parsimony is applied (Fitch, 1977; Eldredge and Cracraft, 1980 ; Farris, 1982; 1983). That is, the grouping which involves the least number of character changes (changes from one state to another in any direction) is the most preferred (theoretically sound) phylogenetic arrangement.

In the present study no evidence to oppose the principle of parsimony has appeared and it has consequently been used throughout the following analyses.

Phylogenies inferred/proposed by algorithms operating on the above cladistic criteria can be used to develop taxonomic hierarchies.

One prerequisite of cladistic analyses is the determination of the direction of evolutionary change -- the polarity of character states

for at least some of the characters in the analyses. There are two well accepted ways of determining such polarity:

(1) by following the principle of generality of character states to determine which are shared primitive character states (symplesiomorphies) (Nelson, 1973 a, 1978, Crisp and Weston 1987);

(2) by using the characteristics of an "outgroup" to choose which state is symplesiomorphic (Stevens 1980; Nelson and Platnick 1981; Maddison et al. 1984). An outgroup is a closely related group to that being studied, often the sister group, which has enough characters and character states in common to determine which of them are shared primitive states (symplesiomorphic) and which are advanced states.

The outgroup method was the primary technique used here, with the principle of generality applied as noted in the text.

A review of the literature on <u>Xanthorrhoea</u> and associated groups was undertaken for:

(a) an analysis of the families considered to be close to Xanthorrhoeaceae, to determine a suitable outgroup;

(b) the outgroup was then used to infer the direction of evolutionary change in <u>Xanthorrhoea</u>, and;

(c) as background information on <u>Xanthorrhoea</u> to augment the present authors data on <u>Xanthorrhoea</u>/species.

4.2 Analytical Techniques Used

Three programs were used:

(1) PAUP V. 2.4.1, (Phylogenetic Analysis Using Parsimony), (Swofford, 1985);

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(2) CONTREE V. 1.3, (consensus tree), (Swofford, 1985);

(both run on an IBM PC-AT compatible computer)

(3) MacClade V. 2.1, (Madison and Madison, 1987), run on an Apple

Macintosh computer. (for the Xanthorrhoea analysis only)

PAUP

All the initial cladistic analyses were run using PAUP (using the most
exhaustive options available for the number of taxa in each analysis)
because of its ready availability on the range of computer equipment
available to me, and its proven performance.

PAUP Options

Exact solutions

PAUP includes two options designed to find all possible trees, and
therefore guaranteed to find the shortest possible tree, for small
numbers of taxa:

(a) ALLTREES (produce all possible trees), and;

(b) BANDB (the branch and bound algorithm of Hendy and Penny 1982).

Because these options are very computation intensive the program has
preset limits to limit the number of taxa used. ALLTREES can only be
used up to 9 taxa, BANDB can be used for up to 16 taxa. Wherever
possible, it is more efficient to use ALLTREES rather than BANDB
(Swofford, 1985).

The number of taxa involved in the outgroup analysis is within the

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preset limit, so that analysis was run using ALLTREES.

Heuristic procedures

The number of taxa in the _Xanthorrhoea_ analysis was in excess of the limits for both BANDB and ALLTREES algorithms, requiring the use of alternative options. These options primarily involve branch-swapping, or rearranging tree topologies in search of shorter trees.

(c) The "global branch-swapping" algorithms are the next most exhaustive options available in PAUP and "more often than not ... do as well as the exact solution" (Swofford 1985). This is especially true when used in conjunction with the HOLD, MAXTREE and MULPARS options set to their maximum values. These ensure that the maximum possible number of trees are retained to be input into branch swapping at each step, in case one of them can produce a more parsimonious tree than can branch swapping on the shortest tree from the previous step.

(2) CONTREE

Where multiple equally parsimonious trees were found by PAUP they were then input to the program CONTREE to produce a strict consensus tree, so that all possible equally parsimonious trees could be included in further consideration of the phylogeny of the group. A consensus tree is one which takes into account the variability of all of the component trees, a strict consensus tree is a consensus tree constructed using the Rohlf (1982) algorithm. Where component trees disagree the consensus tree shows a polychotomy, indicating that the situation is not fully resolved.

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(3) MacClade

MacClade V. 2.1 (Maddison and Maddison 1987) runs on an Apple
Macintosh computer, and makes use of the graphics abilities of that
machine to interactively create and manipulate phylogenetic trees and
to allow an interactive study of character evolution. Character
information and tree topologies are entered to MacClade using the
built-in editor or other appropriate program. There are numerous
options to allow the interactive manipulation of tree topologies which
allows the user to search for a shorter tree or investigate the
effects of changes in topology, rooting and character constraints.
Individual characters can be "painted" on to the tree to trace their
evolution along the branches or the "Show total changes" mode used to
trace character evolution along the tree.

4.3. Outgroup Determination

Choice of an outgroup -- Inter-familial relationships of
Xanthorrhoeaceae: Information from the literature.

4.3.1 Method

To determine the polarity of character changes within <u>Xanthorrhoea</u> it
is necessary to compare it with its nearest relative, i.e. its sister
group. In these circumstances the sister group is known as the
outgroup.

In the case of <u>Xanthorrhoea</u> there are a number of groups reported in

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the literature as being related to the genus. A cladistic analysis of the groups recorded as the most closely related of these was used to determine which was the most closely related, and therefore the sister group.

The literature, with the one major exception discussed below, offers little direct evidence on the close phylogenetic relationships of Xanthorrhoea which might help in the choice of an appropriate out-group. Most modern authors agree in placing Xanthorrhoea in a monogeneric family in the Asparagales, but do not offer opinion or evidence as to the closer familial affinities (Huber 1969, Dahlgren and Clifford 1982, Dahlgren and Rasmussen 1983, Dahlgren et al. 1985).

The most direct suggestions as to the close relatives of Xanthorrhoea, and therefore towards choice of an outgroup, place the group next to the Agavaceae (e.g. Fahn 1954, Waterhouse 1967, Dahlgren et al. 1985). Waterhouse (1967) in particular offered some cogent arguments for the Agavaceae as a "co-ordinal" and therefore a possible sister group to the Xanthorrhoeaceae because both of these families possess a set of similar anatomical characters of the stem, and morphological characters in flowers and leaves. He further commented that the possession of the set of characters making up the monocotyledonous secondary thickening meristem is a basic feature of those plants that possess it, and therefore suggested that those groups should be regarded as being more closely related than had been thought. The characters listed by Waterhouse (1967) as shared characteristics of Xanthorrhoea and the Agavaceae are given below (Table 4.1).

Waterhouse (1967) and Dahlgren and Clifford (1985) also noted that

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Table 4. 1 SHARED CHARACTERISTICS OF XANTHORRHOEA AND AGAVACEAE

AS GIVEN BY WATERHOUSE (1967).

(In cladistic terms i-vi, xi-xii are synapomorphic, and vii-x are symplesiomorphic characters/states for the combined clade relative to their common outgroup of the monocotyledons as a whole.)

Secondary thickening, comprising:

i. Tissue produced externally by the cambium is simple parenchyma, although it ultimately becomes suberized.

ii. Tissue produced internally by the cambium consists of collateral or amphivasal vascular bundles embedded in parenchyma.

iii. The cells of the parenchyma between the bundles are arranged in radial rows (as seen in T.S.), each row being continuous with a cambial initial. That is, these secondary parenchyma cells mature directly from a cambial derivative.

iv. A single vascular cell-element (either xylem or phloem) is not formed directly from the maturation of one cambial derivative as in dicotyledonous secondary tissues. Instead, one, two or three adjacent derivatives undergo numerous periclinal and anticlinal divisions to produce the many cells that differentiate into a vascular bundle.

v. The sieve-tube cells are about the same length as the cambial initials, i.e. they do not elongate during maturation.

vi. The tracheary elements are tracheids and in any one tier not more than a few cells of the provascular strand become tracheids. The large number (15 to 20) of tracheids seen in transverse section of a mature bundle are the result of considerable elongation (15 to 40 times the initial length) and intrusive growth of the pro-tracheary element as it differentiates.

Floral characters:

vii. The pedicel contains 2 to 3 concentric rings of bundles (sometimes more or less scattered), or a ring of bundles.

viii. Both outer and inner perianth segments have similar vasculatures and are one or three trace phyllomes. In either case the number of veins in the lamina may be more than the original trace number as a result of division of the traces. This is especially common in the single trace condition.

ix. Stamens are one trace and one veined segments. The traces may be adnate with perianth traces at the early stages of their separation from the stele.

x. Carpels are usually three-trace phyllomes. Quite frequently two or more lateral traces and veins are also present; these may have a separate origin from the stele or they may be formed by branching of the median trace or bundle.

xi. Septal glands, which are a development of the epidermis of the intercarpellary fissures are present.

Leaf characters:

xii. Presence of inverted vascular bundles in <u>Xanthorrhoea</u> and <u>Agave</u>.

cytological characters "allow for some affinity" between Agavaceae and Xanthorrhoeaceae in that both have dimorphic chromosome complements.

There are also other, obvious, shared characteristics of the two groups such as spiral phyllotaxis and inflorescences borne on a long bare peduncle or scape.

According to Waterhouse (1967) neither _Kingia_ nor _Dasypogon_, (which are included in the Xanthorrhoeaceae by Hutchinson, 1959) conform to the set of characters in Table 4.1, and he therefore believed them to be not closely related to _Xanthorrhoea_. (Although, without differing from Waterhouse's conclusions, it will be realised that as some of these characters are almost certainly symplesiomorphies of the Monocotyledons as a whole, as noted below, it seems probable that at least some of the individual characters would in fact be held in common).

Staff and Waterhouse (1981) agree that neither _Kingia_ or _Dasypogon_ possess monocotyledonous secondary thickening, and also state that _Xanthorrhoea_ is the only genus in Australia with such thickening. However Fahn (1954), Dahlgren and Clifford (1982) and Waterhouse (1987) list _Lomandra_ as one of the groups with dracaenoid secondary thickening (Table 4.2).

The most recent treatment of the Monocotyledons, by Dahlgren et al. (1985) notes that "The phylogenetic connections [of Xanthorrhoeaceae] are still unsettled". They do, however, give useful information towards an understanding of the relationships of families within the Asparagales in their key to families, which they note "is meant to

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Table 4.2   Families identified as possessing dracaenoid secondary thickening, and their distributions.   From Waterhouse (1987).

TABLE 4.2   Distribution of the taxonomic groups displaying
dracaenoid thickening (from Waterhouse 1987, p. 135)

Generic Group	Distribution
Agave and Yucca	Central America
Nolina	North America
Xanthorrhoea	Australia
Aloe	South Africa
Lomandra	Australia, New Zealand, Hawaii
Cordyline and Dracaena	Australia, New Zealand, widespread in the tropics
Aristeae (Iridaceae)	South Africa

reflect the structure of the order". This key brings out subfamily Yuccoideae of the Agavaceae as the adjacent group to the Xanthorrhoeaceae. The series of key leads gives an indication of the basis for this result (Table 4.3). Although this key brings out the two subfamilies of the Agavaceae separately the authors do not appear to be arguing for a paraphyletic development of the family.

There are some apparent anomalies in the leads in this key. The characters in brackets of lead 26, which lead to <u>Xanthorrhoea</u>, state "inflorescence generally not scapose, rarely spicate" are incorrect for <u>Xanthorrhoea</u> which always has scapose and spicate inflorescences. Also there is more commonality between Xanthorrhoeaceae and Yuccoideae than appears as all members of Xanthorrhoeaceae also have linear leaves, and some members have yellowish flowers. However the overall conclusions are not challenged here, as they are supported by other evidence presented in the work and elsewhere (Table 4.4).

A combination of the concepts of Waterhouse (1967 and 1987), Dahlgren and Rasmussen (1982), Dahlgren and Clifford (1983) and Dahlgren et al. (1985) (Table 4.4) were used in the choice of families to include in the outgroup comparison. Where the scoring could not be determined from those publications, information on character states was sought in Trealease (1902), Cheadle, (1942, 1943 a and b), Reynolds (1950), Fahn (1954), Huber (1969), Tomlinson (1974), Wagner (1977), Staff and Waterhouse (1981), Gentry (1982), and Bedford (1986 a).

Table 4.3   SUBSET OF KEY TO FAMILIES, FROM DAHLGREN ET AL. (1985).

(information in [] is added by the present author.)

(1) Ovary superior   8
(8) Fruit hard or leathery, generally capsular,
    rarely a nutlet 17 (17)
Seeds with phytomelan   23
(23) Pollen grains not spiraperturate   24
(24) Pollen grains not trichotomo-sulcate   25
(25) Non twiners   26
(26)   Plants   non   bulbous, generally rhizomatous (inflorescence
    generally not scapose, rarely spicate) 28
(28) Chromosome complement strongly dimorphic (x = 30; 5 large and 25
small) 29
(28) Chromosomes   more uniform in size and not as above [x = 11; 1
    large and 10 small] 30
(29) Generally large, with short or tall woody trunk; leaves
linear, flowers white to yellowish, in panicles or racemes
Agavaceae (subfamily Yuccoideae)
(30) Large rosette plants, often with a tall woody trunk, stomata
    paracytic, (flowers small, numerous, white, densely crowded
in a spike; aril lacking)   Xanthorrhoeaceae

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Table 4.4 Characteristics of Woody Monocotyledonous Plants with Dracaenoid Secondary Thickening.

TABLE 4.4 CHARACTERISTICS OF WOODY MONOCOTYLEDONOUS PLANTS RECORDED AS POSSESSING DRACAENOID SECONDARY THICKENING

FAMILY	DISTRIB.	ARBORES.	HERB.	VESSELS: ROOT	STEM	LEAF	PHYLLOTAXY: SPIRAL	DISTYCH.	LEAF SHAPE: LINEAR	BROAD	SPINES	STOMATES	STOMATE POSITION: SURFACE	IN PITS	CHANNELS	INFLORES POSITION	FLOWERS	CAPSULES	PHYTOMEL.	RAPHIDES
SCORE		0 ABSENT 1 PRESENT	0 ABSENT 1 PRESENT	0 SIMPLE 1 ABSENT	0 SCALAR 1 ABSENT	0 ABSENT 1 SCALAR 2 SIMPLE	0 ABSENT 1 PRESENT	0 PRESENT 1 ABSENT	0 ABSENT 1 PRESENT	0 PRESENT 1 ABSENT	0 ABSENT 1 PRESENT	0 ANOMOC 1 PARACY	0 PRESENT 1 ABSENT	0 ABSENT 1 PRESENT	0 ABSENT 1 PRESENT	0 AXIAL 1 TERMIN	0 ARTIC 1 SESSIL	0 ABSENT 1 PRESENT	0 ABSENT 1 PRESENT	0 PRESENT 1 ABSENT
XANTHO	AUSTRAL	1	1	0	0	2	1	1	1	0	1	1	0	1	1	1	1	1	0	0
AGAV	AMERICA	1	1	0	0	*	1	1	1	1	1	0	1	1	0	1	0	1	0	1
ASTEL	S HEMI	1	1	1	1	0	1	0	1	1	0	1	*	*	*	*	0	1	0	*
NOLIN	AMERICA	1	1	*	1	1	1	1	1	0	1	*	1	1	1	*	0	0	1	1
DRACAE	OLDWTROP	1	1	0	1	1	1	1	1	1	0	0	*	*	*	0	0	0	1	0

(* = MISSING DATA, XANTHO = Xanthorrhoeaceae, AGAV = Agavaceae, ASTEL = Asteliaceae, NOLIN = Nolinaceae, DRACAE = Dracaenaceae, AUSTRAL = Australia, S HEMI = Southern Hemisphere, OLDWTROP = Old World Tropics)
(DATA FROM Dahlgren and Clifford (1982), Dahlgren and Rasmussen (1983), Dahlgren et al. (1985) and Bedford, unpub. observations).

Waterhouse (locs. cit.) argued strongly for a monophyletic development of "Dracaenoid" secondary thickening. If this concept is combined with the perceived importance of the presence of phytomelan in the seed coat (Dahlgren et al. 1985), Asteliaceae, Agavaceae and Xanthorrhoeaceae would be brought close together, perhaps as "sister" groups, with other families with secondary thickening somewhat more distantly related.

As detailed under results and discussion the listing and preferred cladogram support the hypothesis that the Xanthorrhoeaceae and the Agavaceae are closely related, and postulates an order of decreasing phylogenetic affinity with other families.

It therefore appears reasonable that, if one family were to be chosen as an outgroup, the Agavaceae (and in particular the Yuccoideae) would be the most appropriate outgroup for a cladistic examination of evolution within Xanthorrhoea. However, as proposed by Madison et al. (1984), Johnson and Briggs (1985) and Johnson (in press) it is not intended here to chose a single family as outgroup, because of the inevitable difficulty with autapomorphies in such a restricted group comparison, but rather to choose a generalised outgroup. The outgroup chosen here represents the generalised condition of the set of closely related families: Agavaceae, Asteliaceae, Nolinaceae and Dracaenaceae, and sometimes of a larger group, the Asparagales when a character trend is not clear in the narrower clade represented by the former four families.

The family circumscriptions given by Dahlgren et al. (l.c.) are used here in the construction of an higher order cladogram of the

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Xanthorrhoeaceae and related families (Figure 4.1).

As discussed below in more detail Xanthorrhoeaceae is here regarded as consisting of only Xanthorrhoea. Genera such as Lomandra, Dasypogon, Calectasia and Kingia, included in other circumscriptions of the family Xanthorrhoeaceae are clearly very significantly different to Xanthorrhoea in many features, including anatomy, and therefore would not be suitable, on their own, as outgroups, although as part of the Asparagales they may be relevant (references below).

Character choice and coding were carried-out for each of the groups and a data set (listed below and also part of Table 4.4) was run using PAUP analysis.

4.3.2 Character coding for the cladistic analysis of the Asparagales

Unless otherwise noted information as to characters and character states was found from Dahlgren and Clifford (1982), Dahlgren and Rasmussen (1983) and Dahlgren et al. (1985). Other sources are noted under the relevant character(s). Symplesiomorphic states are coded as 0 and apomorphies as successively higher integers. Missing data for any character was coded as 9. Appendix 4.1 contains the data set.

1. Dracaenoid secondary growth (a) Arborescence.

There is considerable discussion above which leads to the conclusion that arborescence resulting from dracaenoid secondary growth is a synapomorphy for those plants possessing the character. There are also some members of some groups which appear to have secondarily

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developed the herbaceous habit, as they have a ± inactive secondary cambium. As the criterion for inclusion in these analyses was the possession of arborescence with secondary growth this character was a constant feature of the group and was therefore not scored. The apomorphic secondary development of herbaceous habit was scored as noted below.

(b) Herbaceous habit with the remnants of 2° growth.

Plants which have dracaenoid secondary growth but are none-the-less herbaceous are treated here as secondarily and independently developed for this characteristic and are therefore scored as autapomorphic. Because information was lacking as to whether herbaceous members of families other than Xanthorrhoeaceae possessed dracaenoid secondary thickening they were scored as missing this character.

Herbaceous plants present in group (remnants of 2° growth)

absent	0
present	1

2/3/4 Vessel type.

The type of vessel in various organs and direction of evolutionary change of this character were researched from a number of sources. The most informative sources other than those already cited were Cheadle (1942, 1943 a and b) Fahn (1954) and Wagner (1977). In some instances sources differed concerning presence and type of vessel, and in those cases either the best supported reference or, if all else was equal the most recently researched source was followed.

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2. Vessel type - roots

simple	0
scalariform	1

3. Vessel type - stem

scalariform	0
absent	1

4. Vessel type - leaf

absent	0
scalariform	1
simple	2

5. Phyllotaxy.

The monocots as a whole have varied phyllotaxy. Dahlgren and Clifford (1982) p. 64 comment that "the condition of spirally set (non distichous) leaves may be either primitive or advanced". Spiral phyllotaxy is present in all groups in the analysis so was not included in the analysis. Distichous phyllotaxy was only present in some members and was coded as plesiomorphic as a working hypothesis.

Distichous phyllotaxy in group:

present	0
absent	1

6. Leaf Shape.

Broad leaves (here arbitrarily defined as greater than 20 mm wide, or having a ratio of width to length of less than or equal to 1:10) are

more common throughout the plant kingdom than narrow leaves and this state is therefore coded as plesiomorphic. All groups in the analysis have some members with linear leaves so this character was not considered separately.

Broad leaves in group

present	0
absent	1

7. Spines or processes on leaves.

The monocots as a whole lack spines or processes on the leaves so that has been scored as the plesiomorphic state. An homology has been assumed between the minute hairs on <u>Xanthorrhoea</u> leaf margins (macroscopic only in <u>X. gracilis</u>), the processes on the margins of other groups such as <u>Nolina</u> and the spines on many agaves (but not of the fine hairs on the margins of many yuccas as these can be seen to be due to a fraying of the edge of the leaf--an inherently different process to the previous categories). Whilst evidence to support such an assumption is lacking it was proposed merely as a working hypothesis. The results of the analysis do not dispute such an homology, though they cannot be taken as support because of the tautological nature of such an argument.

Spines or processes on leaves

absent	0
present	1

8. Stomate type.

There are two possible classifications for stomates in the
monocotyledons, (a) using the "traditional" groupings and terminology
used above and (b) as proposed by Tomlinson (1974) based on the
divisions in cells adjacent to the stomates, which is discussed below.
In this study the classification shown was used for the purely
pragmatic reason that the relevant literature was most complete in
these terms. Dahlgren and Clifford (1982, diagram p. 98) indicates
that anomocytic stomates are the most common form in the Asparagales
and the Liliiflorae as a whole so that state was chosen as
plesiomorphic.

There is considerable disagreement about the validity and accuracy of
classification of monocotyledonary stomates into the above states and
Tomlinson (1974) argued strongly and convincingly for an alternative
classification based on the pattern of dividing walls in neighboring
cells. Dahlgren and Clifford (1982 p. 101-104) discuss this
classification and note that most of the combined clade of dracaenoid
secondary thickened plants fall into the same group (group 4) i.e.
with neighboring cells with oblique divisions. As Asteliaceae and
Nolinaceae are not mentioned in the publications which were searched
their position re this classification is not known.

It is clear that such a character should be treated with care and
therefore one analysis was run with this character masked as a
comparison. The results showed a tree with similar topology
(differing only in being two steps shorter because the character was
not counted), indicating that this character scoring is not

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detrimental to the analysis.

Stomates

anomocytic	0
paracytic	1

9. Stomate position.

There are three possible stomate positions recorded for these groups:

a. <u>Stomates at leaf surface present in group.</u>

Stomates at the same level as the epidermis is logically the most primitive state (the most common, and simplest condition throughout the plant kingdom);

b. <u>Stomates in pits present in the group.</u>

Where stomates in pits are present this has been regarded as a development from the plesiomorphic state;

c. <u>Stomates in papillae-lined channels present in the group.</u>

Where stomates in channels are present this has been regarded as a further development from the plesiomorphic state (see <u>Xanthorrhoea</u> analysis character 8). It is difficult to know in advance whether this is a synapomorphy or a series of autapomorphies. Fahn (1954) noted significant differences in the anatomy of the leaves of members of the Xanthorrhoeaceae (as circumscribed by Hutchinson, 1959), which indicates that such a structure may have arisen independently [perhaps as an adaption restricting water loss]. The resulting cladogram should reveal the status of these characters (but see under results).

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All groups either had some members with stomates in pits or had not been investigated for such and therefore had to be scored as missing for this character. The combinations present were:

Dracaenaceae and Asteliaceae - missing information on these characters;

Agavaceae - lacking both stomates at the surface and stomates in channels but with stomates in pits;

Nolinaceae - lacks stomates at the surface but has stomates in pits and in channels;

Xanthorrhoeaceae - has all three conditions, i.e. stomates at the surface and in pits and in channels.

These combinations are difficult to compare as to evolutionary advancement--is a group which has secondarily lost stomates at the surface more or less advanced than a group which has both? As a working hypothesis these groups were scored on the basis that both the development of an apomorphic character and the loss of a plesiomorphic character constitute evolutionary advancement. As such Nolinaceae is scored as more advanced than Xanthorrhoeaceae because Nolinaceae has lost the most primitive state. Combinations that do not occur are not included.

Stomates	Surface	Pits	Channels	Score
	Present	Absent	Absent	0
	Absent	Present	Absent	1
	Present	Present	Present	2
	Absent	Present	Present	3

10. Inflorescence position.

As a working hypothesis axillary inflorescence position was chosen as the plesiomorphic condition because the restriction of inflorescence formation to the terminal position would appear to be a specialisation from the more general state and is therefore likely to be the most primitive.

axillary	0
terminal	1

This hypothesis was supported in the analysis to the extent that this coding was better correlated with the other characters in the analysis than the alternatives.

The alternative coding (axillary as the apomorphic condition) was run as analysis 2 (Appendix 4.2) resulting in two 24 step trees, one of which produced the same result as the above coding, showing Agavaceae and Xanthorrhoeaceae as sister groups, and the other produced a different topology with Agavaceae and Xanthorrhoeaceae as adjacent clades.   Analysis 3 (Appendix 4.3) shows the results with this character deleted, 2 trees each 23 steps long were produced - one tree was of similar topology to the preferred cladogram, the other showed Agavaceae and Xanthorrhoea as adjacent clades.   In analysis 4 (Appendix 4.4) this character was not polarised, and also resulted in 2 equal length trees (24 step) as in the above two alternative analyses.

11. Flowers.

Flowers articulated was chosen as the plesiomorphic condition because
it is hypothesised that, at least within this group, sessile flowers
are the result of a reduction in pedicel length.

articulated	0
sessile	1

12. Fruit.

The coding below followed the theory of Huber (1969) (cited in
Dahlgren and Clifford, 1982) who argued that the capsules in most
Asparagales may be interpreted as secondarily derived from berries.

not a capsule	0
a capsule	1

Dahlgren and Clifford (1982) however also note that capsules "show a
central and wide distribution in the monocotyledons" and "represent a
more original state ... in relation to berries in most cases in the
Liliiflorae". This alternative view was run as analysis 5 (Appendix
4.5) giving 4 equal length trees, each with a different topology, one
showed the same topology as the preferred cladogram, another showed
Agavaceae and Xanthorrhoeaceae as sister groups but in a different
topology to the preferred cladogram and the other two brought them out
as adjacent clades.

13. Seeds.

Dahlgren et al. (1985) regard the presence of phytomelan as a
synapomorphic character for the Asparagales.

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phytomelan not in seed coat 0

phytomelan in seed coat   1

14. Rhaphides in leaves.

Huber (1969), (cited in Dahlgren et al., 1985) noting that raphides are commonly present in the Asparagales, but uncommon elsewhere, so this character has been scored as a synapomorphy for this group of the Asparagales.

absent   0

present   1

4.3.3 Analyses

The groups chosen for the analysis were scored according to the above character set, and the resultant data matrix was run using PAUP V. 2.4.1. A series of exhaustive analyses were performed using the ALLTREES option. Since many of the polarisations listed above are rather speculative, numerous analyses were tried with alternative character polarities, character deletions and characters un-polarised, to examine the effects of the various alternatives.

4.3.4 Results

4.3.4.1 Cladogram

The PAUP analysis using ALLTREES produced the single tree shown in Figure 4.1 (Appendix 4.1). The tree has 24 steps and a consistency

Figure 4.1 Asparagales analysis cladogram

<u>Figure 4.1   Single tree produced by PAUP with ALLTREES on data set 1.</u>
Superscript numbers are character states achieved at the relevant point on the cladogram.
Negative numbers indicate reversals.
Statistics for tree
    Length =   24.000
    Consistency index = 0.708

```
  ┌********************** OUTGROUP
  │                   ┌─14¹── DRACAENACEAE
  │            ┌4¹,5¹─┤                    ┌1¹,-3⁰,4²,12¹,13¹─┐ ┌-6⁰,-9¹── AGAVACEAE
  │           ─┤      └6¹,7¹,10¹─┤                            └8¹,-11⁰,14── XANTHORRHOEACEAE
  └─ 3¹,9¹────┤                  └NOLINACEAE
             └2¹,8¹,12¹,13¹─ ASTELIACEAE
```
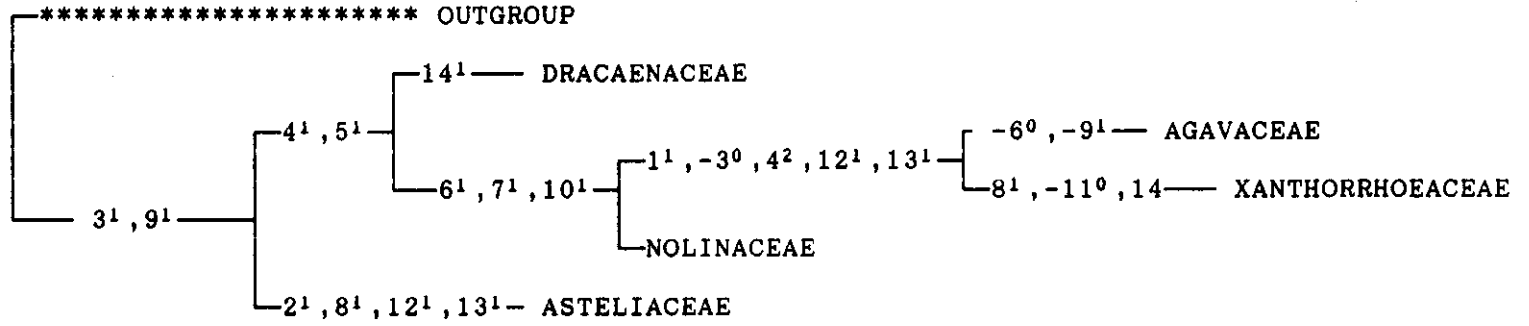
index of 0.708 as calculated by PAUP using the Kluge and Farris (1969) algorithm. (Data set, full results, and lists of character changes and apomorphies are in Appendix 4.1)

The tree was rooted using a hypothetical ancestor with all plesiomorphic states (representing the generalised monocotyledonous plant) defined as the outgroup in the analysis. The preferred cladogram shows Xanthorrhoeaceae and Agavaceae as a sister-group-pair as the most advanced clades, with progressively less close relationship with Nolinaceae, Dracaenaceae, Asteliaceae and the hypothetical ancestor outgroup. This topology was the most common result of all manipulations of the data set, and is in good agreement with other modern concepts of the relationships within the Asparagales.

There were numerous alternative possible cladogram topologies resulting from, in some cases, relatively minor manipulations of character polarisations and scoring in the data set (appendices 2-5). This indicates that the preferred result is not quite as reliable as one would otherwise expect from the production of a single tree by a PAUP ALLTREES analysis. However the detailed examination of homologies of all the characters involved in this analysis is not relevant to the main thrust of this thesis, which is primarily concerned with the evolution of Xanthorrhoea itself. The important conclusion as far as the present work is concerned is that the analyses do support the hypothesis that there are a number of synapomorphies for the woody asparagales with dracaenoid secondary thickening. In addition the majority of resulting cladograms (over all manipulations of the data set) support the hypothesis that the Agavaceae and Xanthorrhoeaceae are sister groups.

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4.3.4.2 Characters

A number of characters are indicated to have parallel development, that is, to not be homologous single characters as scored. These are (character numbers shown in brackets): (a) Stomate type (8), which is shown to change to state 1 – paracytic – both on the branch leading to the Asteliaceae and the branch leading to Xanthorrhoeaceae; (b) Fruit a capsule (12), which develops both on the branch leading to Asteliaceae and the branch leading to the Agavaceae and Xanthorrhoeaceae, and; (c) Phytomelan present (13) which develops two times, on the branch leading to the Asteliaceae and on the stem leading to the Agavaceae and xanthorrhoeaceae (d) Raphides present (14), which also develops twice, once on the branch leading to Dracaenaceae and on the branch leading to Xanthorrhoeaceae. The earlier comments under three of these characters indicated that the codings used were merely as a working hypothesis because of a shortage of evidence or conflicting opinions concerning their status. These results lend support to, respectively, (a) Tomlinson's alternative classification of stomate types (Tomlinson 1974), (b) Huber's contention that there may be more than one development of capsular fruit in the monocotyledons Huber (1969 (cited in Dahlgren and Clifford, 1982), (d) The uncertainty concerning the status of rhaphides, Huber (1969) (cited in Dahlgren et al., 1985). However the parallel development of phytomelan is not expected considering the view of Dahlgren et al. (1985) that phytomelan is synapomorphous for the Asparagales. If Dahlgren et al. (l.c.) and this analysis are both correct then the Asteliaceae may not belong in the Asparagales. Alternatively either this assumption or the present analysis need to be questioned. Further examination of these concepts is necessary, but are outside the priorities of the

present work.

The status of stomates in pits and stomates in channels were discussed earlier (section 4.3.2, character 9) as their being some uncertainty as to whether they are synapomorphic or autapomorphic. Their status is not fully resolved in these analyses, although the cladogram shows that the achievement of state 1 is by reversal, which may indicate that this coding of these characteristics needs further work.

4.4 Relationships of _Xanthorrhoea_ Species

4.4.1 Method

The family Xanthorrhoeaceae

In the past, most authors appear to have either lumped _Xanthorrhoea_ with other perennial hard-leaved groups they found difficult to classify, such as _Lomandra_ and _Acanthocarpus_ (e.g. Engler, 1892), or which had a similar pachycaulous habit, such as _Kingia_ and _Dasypogon_ (Hutchinson, 1959, Cronquist, 1981).

However, there is a growing body of evidence that _Xanthorrhoea_ is not closely related to any of these groups, and some authors indicate that some of these taxa should not be placed in the same, or even closely related, families (Fahn, 1954, Waterhouse, 1967 and 1987, Chanda and Ghosh, 1976, Huber, 1969, Dahlgren and Clifford, 1982, Dahlgren and Rasmussen, 1983 and, Dahlgren et al., 1985). Waterhouse (1987) went so far as to state "Hutchinson's family Xanthorrhoeaceae is monstrously unnatural", mostly on the basis of his research which

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found "that the pachycaulous habit in members of the Xanthorrhoeaceae [sensu Hutchinson] is the expression of two fundamentally different processes".

The most modern and supportable circumscription of the family Xanthorrhoeaceae is that of Dahlgren et al. (1985) and restricts the family to solely Xanthorrhoea. This family circumscription is followed here.

Direction of evolutionary change

In general the polarity of characters (direction of evolutionary change) is determined by the determination of the outgroup(s) and therefore the hypothetical ancestor of the group under discussion. One character, Dracaena-like secondary thickening, is of particular note because of its importance as recognised by a number of authors-as discussed elsewhere (both above and below) - and some apparently conflicting views of its nature as it is variously discussed in the literature as being either advanced, (either homologous or independently developed) (Dahlgren and Rasmussen 1983), or primitive (Waterhouse 1987).

Waterhouse (1987) argued that the development of those groups possessing this character is monophyletic, and that the character is an "ancient" feature for the group. Dahlgren and Rasmussen (1983) comment that "the woody habit in combination with secondary thickening constitutes a synapomorphy for some of the woody Asparagales with a thick trunk.". They also, somewhat contradictorily, say that "... secondary thickening may have arisen separately in each ..." of the

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groups (which would make this feature an autapomorphy in each group). This latter is her considered to be highly unlikely, and this character is therefore regarded as having a monophyletic development, and as constituting an homologous character held in common. Thus it is "primitive feature" within Xanthorrhoea (a symplesiomorphy), though it is an advanced feature held in common (a synapomorphy) for the combined clade of the woody Asparagales with that character state. Evidence for this view comes primarily from Waterhouse (1967 and 1987) but also from the observation that all groups that possess Dracaena-like secondary thickening have members which have secondarily reduced development of the cambium and woody trunk.

4.4.2 Character coding for cladistic analysis of Xanthorrhoea.

Unless otherwise specified 0 represents the plesiomorphic state with reference to either the combined clade Agavaceae/Asteliaceae/Xanthor-rhoeaceae, or to the Asparagales as a whole, and progressively higher states represent successive apomorphic changes. Missing data is coded as 9.

CHARACTER	STATE	CODE
1. Trunk	tall >60 cm	0
	medium > 0 $\leq$ 60	1
	none (ever)	2

Waterhouse (1967, p. 68) notes that "The arborescent habit is .... considered a primitive condition within the genus, and the herbaceous habit derived." He argues this on the basis of the presence in Xanthorrhoea of Dracaena-like secondary thickening, (which he says has a "whole set of features that are not found elsewhere"). This character is found in a number of groups and is therefore unlikely to have

evolved separately in _Xanthorrhoea_ as a parallel development. He further argues (p. 71) that secondary thickening is intimately correlated with arborescent habit ("a fundamental feature of this habit is the contribution of a cambium to its development"). Such an assertion is supported by evidence in _Xanthorrhoea_ where arborescent species have a well developed cambium and herbaceous species have a poorly developed cambium ("vestigial").

For these reasons, in these analyses arborescence has been coded as the plesiomorphic state. Observations of the genus have identified two levels of arborescence. Some species that have the ability to develop trunks never exceed a medium short height of about 60 cm, while other species can become truly arborescent with trunks to 5 or rarely 6 meters.

[Note: Agavaceae, Asteliaceae and Dracaenaceae all have some members which are arborescent and other members with short or absent aerial trunks. The argument that secondary thickening and arborescence are fundamentally linked and are the symplesiomorphic condition (within the combined clade Agavaceae/Asteliaceae/Xanthorrhoeaceae) for all those groups possessing this character has significant implications for these groups also. The examination of this hypothesis is, however, outside the scope of this study].

Ease of development and reversibility of arborescence.

If as Waterhouse argued, arborescence is causally related to an active cambium then, as all species of _Xanthorrhoea_ possess a cambium, it appears likely that this character could undergo multiple developments

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and reversals by switching the cambial activity on or off.

2. Stem branching
   position   above ground   0
                   below ground   1
                   un-branched   9

This character was not polarised in the analyses, because the

symplesiomorphic state could not be established.

3. No. of crowns   one   0
                   two or three   1
                   more than three   2

The symplesiomorphic form in the combined clade (also the simplest and

most common condition) is for single main stems, sometimes with few

branches above ground level.

4. Leaf shape   obtrullate   )
                   obtriangular)   0
                   concave   )
                   narrowly quadrate-
                   rhombic   1
                   quadrate-rhombic   2
                   irregularly rounded 3

The symplesiomorphic leaf shape in the monocotyledons as a whole is

for broad leaves of various shapes. Common leaf shapes in the

combined clade are concave, obtrullate and obtriangular, so these have

been regarded as being equivalent plesiomorphic states, with

successive apomorphic states being the trend towards a narrower leaf

shape. State 3 is coded as the most advanced because it is quite

different from the other shapes, which can be seen to be more closely

related to each other than to state 3.

Whether a <u>Xanthorrhoea</u> leaf with one of the broader shapes is truly

homologous with a broad leaf of the same shape in the combined clade

is unknown. The anatomical structure of leaves in the different groups is most probably different, Fahn (1954) certainly found significant differences in anatomy within Hutchinson's Xanthorrhoeaceae, and there are many obvious differences in that many of the Agavaceae have specialised succulent leaves. It is therefore possible that leaf shape in _Xanthorrhoea_ has secondarily and independently developed the broader leaf shapes from the simplest form—the quadrate-rhombic leaf shape.

5. Leaf width   broad >4 mm   0
                   medium 2-4 mm   1
                   narrow <2 mm   2

See leaf shape above.

6. Leaf thickness thick >2.5 mm   0
                   medium $\geq 1.5 \leq 2.5$ 1
                   thin <1.5 mm   2

See leaf shape above.

7. Leaf colour   glaucous, i.e.
                   gray or blue green   0
                   green   1

Glaucous leaves are a common state in the Agavaceae, and could therefore be presumed to be the plesiomorphic state for the combined clade. However non-glaucous leaves are the plesiomorphic state for the Monocotyledons as a whole. Because it is unknown which state is plesiomorphous this character was left unpolarised.

8. Leaf stomatal   superficial or in pits   0
   arrangement   in channels   1

Stomates at or near the leaf surface are the plesiomorphic condition for the Monocotyledons as a whole, and are also the most common state

in the combined clade. However stomates in subsurface channels over-arched by papillose hairs have also been recorded elsewhere - in Lomandra and Acanthocarpus, by Fahn (1954), and have been observed in specimens of Nolina growing at the Royal Botanic Gardens, Sydney, by the present author. It is not clear whether these occurrences are homologous, or parallel developments, however the latter is a possibility as Fahn (l.c.) has noted that such an arrangement is one means of reducing water loss from the plant.

9. Scape length   <1 m   0
                   >1 m <2 m   1
                   >2 m   2

Both long and short scape lengths are found in the combined clade, so that comparison does not assist with determining the direction of evolutionary change in this character. The longer scape lengths would appear to have a functional adaption towards wider seed distribution, and may therefore be an advanced state. Both long and short scapes are present in the Agavaceae so that comparison does not assist in coding for these analyses. Trial runs of the analyses indicated that the most parsimonious choice was as coded above, however because of the doubt about which state is plesiomorphic this character was left unpolarised. See also comments under ratio.

10. Scape diameter >1 cm   0
                   <1 cm   1

The direction of evolutionary change is not clear for this character either, as both thin and thick scapes are found in the combined clade. The thinner scapes are more flexible, and therefore may help in seed dispersion, and because they are less strong would also tend to

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restrict successful pollination events to those involving the smaller pollinators. As such one line of logic would suggest that these are the more specialised. However, to avoid prejudicing the results the character was left unpolarised.

11. Ratio of
    Spike length divided
    by scape length

>2	0
>1.5<2	1
~ 1	2
<1 > .5	3
<.5>.2	4
<.2	5

There is a clear trend from one extreme of the range of proportions to the other, but the direction of the trend is not clear.

The species of Xanthorrhoea with the most primitive trunk characters, e.g. X. australis also have the highest spike length divided by scape length ratios, as they have long spikes and short scapes, which implies that these may be the most primitive conditions. However, as above this character was left unpolarised.

This character is divided into states after a examination of the pattern of variation in the genus, however because of the variability inherent in the genus the division is, to some extent, an arbitrary one.

12. Spike length   >2 m   0
                         >1 m<2 m   1
                         <1 m   2

Both long and short spike lengths are found in the combined clade, so that comparison does not assist with determining the direction of evolutionary change in this character. The longer spike lengths would appear to have a functional adaption towards greater seed production,

but this could be either a primitive or an advanced state. Many species of Agavaceae also have long spikes or inflorescence lengths, so the possibility exists that this is the plesiomorphic state. As above this character was run unpolarised - see also comments under ratio.

13. Spike diameter ≥ 20 mm   0
                < 20 mm   1

The direction of change of this character is not clear so it was not polarised.

Bract characters

These characters are scored on the premise that bracts are derived from leaves and that therefore the most leaf-like bracts are the most primitive. Thus bracts that are green, glabrous and the most leaf-like shape are scored as the plesiomorphic state. This situation is seen clearly in the combined clade in subtending or cluster bracts, which are often very similar to the leaves, and appear to function as reduced leaves, as they are green. Supporting evidence is also found in Xanthorrhoea where the more massive plants, such as X. australis, which, it is argued, are the most primitive species, also have the most massive spikes, and most prominent subulate glabrous bracts. It is therefore argued that these are the plesiomorphic states.

14. Cluster bracts very prominent (100%)   0
       prominence   slightly prom (10 cm) 1
                 base only   2
                 obscure   3

15.   - shape   subulate   0
                 linear triangular 1
                 acute   2
                 shortly acute   3
                 obscure   9

16. – indumentum glabrous 0
subglabrous 1
fringed 2
hirsute 3
densely hirsute 4

Packing bracts

Because it is difficult to judge the homologies of characters 17 and 18 with characteristics of members of the outgroup these characters were not polarised.

17. – shape subulate 0
linear triangular 1
acute 2
shortly acute 3
obtuse 4

18. – indumentum glabrous 0
subglabrous 1
fringed 2
hirsute 3
tomentose 4

19. – colour green 0
dark 1
dark or)
pale hairs) 9

Floral characters

An outgroup comparison reveals that large "hooded" or "beaked" tepals (the latter term from Bedford, 1986 a), glabrous except for papillose hairs on and in the beak, which sometimes form a proboscis-like structure, are present as the most common form in other taxa of the Agavaceae (from Gentry, 1982, Dahlgren et al., 1985 and an examination of flowers of <u>Yucca</u> and other genera growing at the Royal Botanic Gardens, Sydney). It is not known if such structures are homologous

with petals in Xanthorrhoeaceae, but that is the most parsimonious
hypothesis.

Sepals

20. – beak   present   0
                 absent   1

21. – proboscis present   0
                 absent   1

22. – indumentum glabrous   0
                  subglabrous   1
                  partly hirsute   2
                  hirsute   3

Petals

23. – size   large / prominent   0
                 small   1

24. – shape   erect   0
                 erect to
                 slightly recurved   1
                 recurved   2

25. – proboscis present   0
                 absent   1

26. – indumentum glabrous   0
                  hirsute   1

4.4.3 Analyses.

PAUP was used for the initial examination of the evolutionary
relationships of Xanthorrhoea taxa.

The program was run in the most exhaustive options available for this
number of taxa: i.e global branch-swapping with MULPARS and the

maximum settings for the MAXTREE and HOLD options of 100 and 25 respectively, run in batch mode so that MULPARS would automatically be switched off to allow branch-swapping to continue if the maximum value for MAXTREE was exceeded (Data set and full results in Appendix 4.6).

The trees found by this analysis were then input to the program CONTREE to produce a strict consensus tree, so that all possible equally parsimonious trees could be included in a synthesis.

The topology for the consensus tree was then used in MacClade to investigate the position and direction of character changes on the tree. This was accomplished using the "SHOW TOTAL CHANGES" mode. These changes were then incorporated/superimposed on the consensus tree diagram to show a tree in which the length of the branches reflect the amount of change along the branch, and the position and direction of character change are clear.

Most MacClade options are duplications in one way or another of PAUP options. The main option not in PAUP is the ability to interactively investigate the effects of moving branches from one clade to another, to see if a shorter tree can be found. This option was not relevant to this analysis as PAUP had already produced the most parsimonious individual trees, which had then been used to produce the consensus tree. MacClade was therefore used only to trace the evolution of characters, as these are more easily observed in MacClade than by using PAUP output.

4.4.4 Results

4.4.4.1 Cladogram

The PAUP analysis gave 18 equally parsimonious trees, each 181 steps long (appendix 4.6). Figure 4.2 shows the consensus tree and Figure 4.3 the same tree with branch lengths reflecting the number of character changes on each branch by each branch being "painted" with the characters and their changes. Two trees are presented because they are complementary: Figure 4.2 shows the branching pattern most clearly; Figure 4.3 carries additional information about character evolution. In the discussions below the number of the taxon in the analysis is given in brackets after its name, e.g. (1) stands for the first taxon in the data matrix, or shown in the nested bracketed format used to designate tree structure in cladograms, e.g. (1(2,3) shows taxon 2 and 3 to be a sister-group-pair with taxon 1 the next branch on the cladogram (Swofford, 1985, Madison and Madison, 1987).

The consensus tree produced from these 18 trees (Figures 4.2 and 4.3) shows that there is a high degree of congruence of the input trees. That is, the majority of the taxa were always assigned to the same clades in all trees.

The main differences between the 18 equally parsimonious trees involve only a small proportion of the taxa. Only X. brevistyla, X. latifolia subsp. latifolia, X. latifolia subsp. maxima, X. arborea, X. acanthostachya and X. australis varied in their position in the different analyses, causing the three polychotomies on the consensus tree. X. brevistyla (8) had the most variable placements with three

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Figure 4.2   _Xanthorrhoea_ analysis consensus tree 1

Figure 4.2 XANTHORRHOEA CONSENSUS TREE DERIVED FROM 18 TREES EACH 181 STEPS
THE NUMBERS BESIDE TAXON NAMES REFER TO THE POSITION OF THAT TAXON IN BEDFORD (1986).
Strict consensus tree
****

```
                                            ┌──── 1   MACRONEMA
                                       ┌────┤
                                  ┌────┤    └──── 2   GRACILIS
                             ┌────┤    └───────── 3   CONCAVA
                        ┌────┤    └────────────── 4   FULVA
                   ┌────┤    └─────────────────── 5   RESINIFERA
                   │    │              ┌────────── 6   BRUNONIS BRUNONIS
                   │    │         ┌────┤
                   │    │    ┌────┤    └────────── 7   BRUNONIS SEMIBARBATA
                   │    └────┤    └─────────────── 8   BREVISTYLA
                   │         │         ┌────────── 24  ACAULIS
                   │         │    ┌────┤
                   │         │    │    └────────── 29  ARENARIA
              ┌────┤         │    │         ┌───── 25  MINOR MINOR
              │    │         └────┤    ┌────┤
              │    │              │    │    └───── 26  MINOR LUTEA
              │    │              └────┤    ┌───── 27  BRACTEATA
              │    │                   └────┤
              │    │                        └───── 28  CAESPITOSA
              │    └────────────────────────────── 14  NANA
         ┌────┤    ─────────────────────────────── 11  DRUMMONDII
         │    │         ┌──────────────────────── 9   PLATYPHYLLA
         │    │    ┌────┤
         │    │    │    └──────────────────────── 10  PREISSII
         │    └────┤    ┌──────────────────────── 12  QUADRANGULATA
         │         │    │         ┌──────────────── 15  PUMILIO
         │         └────┤    ┌────┤
    ┌────┤              │    │    └──────────────── 16  MEDIA
    │    │              └────┤    ┌──────────────── 18  LATIFOLIA  LATIFOLIA
    │    │                   │    │─────────────── 19  LATIFOLIA MAXIMA
    │    │                   └────┤
    │    │                        └──────────────── 20  ARBOREA
    │    └─────────────────────────────────────── 13  THORNTONII
┌───┤    ┌──────────────────────────────────────── 17  ALMAE
│   │    │──────────────────────────────────────── 21  MALACOPHYLLA
│   └────┤    ┌───────────────────────────────────── 22  GLAUCA GLAUCA
│        └────┤
│             └───────────────────────────────────── 23  GLAUCA ANGUSTIFOLIA
│        ───────────────────────────────────────── 32  ACANTHOSTACHYA
│        ───────────────────────────────────────── 33  AUSTRALIS
*** ┌──────────────────────────────────────────── 30  SEMIPLANA SEMIPLANA
  * │
  * └──────────────────────────────────────────── 31  SEMIPLANA TATEANA
  *
****************************************************** 34  Asparagales
```

Statistics derived from consensus tree
****

    Consensus fork index (component count) =   28
    CF (normalized) =   0.875
    Term information =259
    Total information =287
    Mickevich's consensus information (CI) = 0.482
    Weighted consensus fork = 0.512
    Levels sum = 2789
    Rohlf's CI(1) = 0.792
    Rohlf's -log CI(2) =0.10121E+03

Figure 4.3 _Xanthorrhoea_ analysis consensus tree 2

Figure 4.3 XANTHORRHOEA CONSENSUS TREE DERIVED FROM 18 TREES EACH 181 STEPS - WITH CHARACTER CHANGES SHOWN - NEGATIVE NUMBERS INDICATE REVERSALS AND SUPERSCRIPT NUMBERS ARE THE CHARACTER STATE NUMBER ACHIEVED AT THAT POINT. THE LETTERS A-M ARE USED TO DESIGNATE SUCCESSIVE APOMORPHIC STEPS ON THE MAIN EVOLUTIONARY STEM OF THE TREE.

Strict consensus tree
****

M
L $4^3,7^1,8^1,11^5,13^1,-18^3,-23^0$ $-18^0,-22^0,-24^0$ — X. macronema
10^1 X. gracilis
K
1^2 $-5^0,-9^0$ — X. concava
J
$17^3,18^4,22^3$ $6^2,17^4$ — X. fulva
$-3^0,4^1,20^1,26^1$ — X. resinifera
I
2^1 $7^1,25^1$ -18^0 — X. brunonis subsp. brunonis
X. brunonis subsp. semibarbata
$-5^0,24^2$ — X. brevistyla
-22^1 $-1^1,5^2$ — X. acaulis
$11^3,-15^0,-21^0$ $-16^0,-17^0,-18^0$ — X. arenaria
H $6^2,10^1$ 17^3 — X. minor subsp. minor
$1^1,3^2,-4^0,11^2,12^2$ $7^1,13^1,24^2$ $14^1,-23^0$ 14^2 — X. minor subsp. lutea
$1^2,-14^0$ $-16^0,-18^0,-25^0$ — X. bracteata
G
$18^2,22^2$ $-5^0,-17^0,25^1$ — X. caespitosa
F
-22^1 -24^0 — X. nana
$-3^0,4^2,18^3,22^3$ — X. drummondii
$1^1,-3^0,-4^0,-5^0,-14^2,17^3$ X. platyphylla
-11^0 $7^1,-12^0,-18^0,20^1$ — X. preissii
$15^2,24^2$
E $4^2,5^2$ X. quadrangulata
14^3 $6^2,11^3,19^1$ $-4^0,13^1,17^4,20^1,-22^0$ X. pumilio
$1^1,10^1,11^4,-18^0$
$7^1,9^1$ -14^2 — X. media
9^2 — X. latifolia subsp. latifolia
D $-5^0,18^2$ $9^2,3^2,11^4$ — X. latifolia subsp. maxima
14^1 $-4^0,-6^1$ — X. arborea
C
$15^1,16^1,17^2,18^1$ $4^2,-17^1,-24^0$ — X. thorntonii
$-3^0,15^2,20^1$ — X. almae
$7^1,9^1,11^2$
$3^2,-4^0,19^1,24^2$ — X. malacophylla
B (22) X. glauca subsp. glauca
$4^1,5^1,6^1$ $3^2,6^2,-11^0$
X. glauca subsp angustifolia

A
12^1 $11^3,12^2$ — X. acanthostachya
3^1
23^1 $-11^0,$ — X. australis
****
   * 9^1 — X. semiplana subsp. semiplana
24^2
3^0 * -12^0 — X. semiplana subsp. tateana
23^0*

** 34 OUTGROUP -- Asparagales with dracaenoid secondary thickening

quite dissimilar alternatives, each of equal frequency (six of each alternative): as adjacent clade to the two subspecies of X. brunonis (6)+(7), i.e. (6,7)8); as three steps removed from the sister group of X. acaulis (24) and X. arenaria (29), i.e. (8(((24,29); and as two steps removed from X. caespitosa (28), , i.e. 28))8). There was much less variation in the placement of X. latifolia subsp. latifolia, X. latifolia subsp. maxima and X. arborea with two alternate equally frequent groupings: with X. latifolia subsp. latifolia (18) and X. latifolia subsp. maxima (19) as a sister-group-pair and X. arborea (20) as adjacent clade i.e. (18,19)20); and X. latifolia subsp. latifolia and X. arborea as a sister-group-pair with X. latifolia subsp. maxima as the adjacent clade, i.e. (18,20)19). There were two alternative positions for X. acanthostachya (32) and X. australis (33): these were resolved as adjacent clades twelve times, i.e. 32)33); and as a sister-group-pair clade six times i.e. (32,33).

Although their exact position within their clade is not resolved, four of the six taxa involved in polychotomies are part of larger clades, and are thus reasonably well resolved in terms of the overall analysis. X. acanthostachya (32) and X. australis (33) are also better resolved than is apparent from the consensus diagram as the individual trees show them to be closely associated only with each other, not with any other taxon.

Thus there are nine clear clades in Figure 4.2, as well as the unresolved X. acanthostachya and X. australis, which form either one sister-group-pair clade or two adjacent clades, in the analysis. These clades, named after the most "advanced" member (the member with the most changes in its lineage) are listed below in order from that

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with the most character changes, i.e. apomorphies (most advanced) to
that with the least changes (most primitive):

X. macronema clade   - comprising X. macronema, X. gracilis,

                          X. concava, X. fulva, and X. resinosum;

X. minor clade   - comprising both subspecies of X. minor

                          X. bracteata, X. acaulis, X. arenaria,

                          X. caespitosa, X. brevistyla and both

                          subspecies of X. brunonis;

X. nana clade   - solely X. nana;

X. drummondii clade   - solely X. drummondii;

X. pumilio clade   - X. platyphylla, X. preissii,

                          X. quadrangulata, X. pumilio, X. media,

                          both subspecies of X. latifolia and

                          X. arborea;

X. thorntonii clade   - solely X. thorntonii;

X. malacophylla clade   - X. malacophylla and X. almae;

X. glauca clade   - both subspecies of X. glauca;

X. semiplana clade   - both subspecies of X. semiplana;

with X. acanthostachya and X. australis occurring above the X.
semiplana clade as either one sister-group-pair clade or two adjacent
clades.

4.4.4.2 Character Evolution

The consensus tree with the character changes revealed by MacClade's
"show changes" function demonstrates the evolution of individual
characters along the tree. There are, however, some limitations in
MacClade which mean that this process may not reveal all character

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changes. Some portions of the tree are shown as having "no unambiguous changes". This does not necessarily mean that there are no changes along this section of the tree, but only that the program is unable to "be sure" what is there. This situation can arise on a branch which leads to two terminal taxa with conflicting states for a character. However, for the majority of the characters, the program does allow a clear graphic representation of character evolution, and the results are detailed below. Positions of change on the main stem are marked with letters A-M on Figure 4.3.

1. Trunk height.

This character shows (a) three parallel changes to state 1 - medium trunk height - (on the main stem of the tree at `H`; on the branch leading to X. pumilio and X. media; on the branch leading to X. platyphylla), (b) two parallel changes to state 2 - no above ground trunk ever developing - (on the main stem at `K`; on the main branch leading to the X. minor clade. There are no reversals.

This character is therefore not one homologous character, but rather a number of parallel superficially similar characters. Such a result is not surprising considering the discussion above of the purported interrelationship between arborescence and degree of activity of the secondary thickening cambium, and tends to confirm such a relationship.

2. Stem branching position.

This character is shown to be a reliable single-development character

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with a single change to state 1 - branching below ground - (at `I` on the main stem), and no reversals.

3. Number of crowns.

There are multiple parallel changes and reversals. The character changes to state 1 - two or three crowns - at the root of the tree, but has numerous reversals to state 0 - a single crown. There are five separate parallel changes to state 2 - more than three crowns.

The pattern of change of this character indicates that the number of crowns is of little evolutionary significance and may be controlled by a simple physiological mechanism such as switching on or off of the development of the axillary shoot meristems.

4. Leaf Shape.

There are multiple parallel changes and reversals of this character. This may indicate that this character has not evolved from the leaf shapes common to the outgroups as hypothesised by this scoring pattern. An alternative hypothesis is that leaf shape may evolve in response to environmental conditions, and as such could be expected to have multiple separate developments.

4. Leaf width.

This character has a single change to state 1 - medium width leaves- (at `B` on the main stem), but two parallel changes to state 2- narrow leaves - (at X. acaulis; X. quadrangulata). There are five

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reversals to state 0 – broad leaves.

This result indicates (a) that the narrow leaf state is not truly homologous, and (b) the multiple reversals to state 0 may indicate that, similar to character 4, the character has evolved in response to environmental conditions.

6. Leaf thickness.

There is a single change to state 1 – medium thickness leaves – on the main stem at `B`, but four parallel changes to state 2 – thin leaves. There is one reversal to state 1 on the branch leading to <u>X. arborea</u>. That is, the change from thick to medium leaves happens only once, and is part of the main evolutionary line of the genus, but the change from medium to thin leaves is a localised phenomenon with parallel changes to four non homologous thin leaved forms.

This character therefore shows a similar pattern to the two leaf characters above, indicating that, at least in its final step, the change may be in response to localised, possibly environmental, pressures.

7. Leaf colour.

State 1 – green leaves – has arisen six times as a parallel development. That is, green leaves in different groups are not homologous. There are no reversals to the symplesiomorphous state.

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8. Leaf stomatal arrangement.

This is a reliable character, with a single change to state 1- stomates in channels - on the branch leading to X. macronema and X. gracilis.

9. Scape length.

There are three parallel changes to state 1 - medium length scapes- all on minor branches of the tree. There is some uncertainty about the change to state 2 - long scapes - which is shown as a parallel change on two adjacent taxa X. latifolia subsp. latifolia and X. latifolia subsp. maxima because of disagreement in the constituent individual trees that make-up the consensus tree. As discussed more fully elsewhere some trees show these taxa as a sister-group-pair and other trees show them as adjacent single taxon clades. Parsimony would tend to support a single development of the character, but there are obviously considerations from changes in other characters for which the most parsimonious change requires this to be a parallel development. It is easy to imagine the parallel development of this character if the mechanism of its formation is a simple one such as elongation of tissues. Unfortunately, however, it is not possible to make a decision on this because the mechanism of elongation is unknown. (Staff (1976) discussed the growth rate of the inflorescence of one species but did not investigate whether elongation is due to cell multiplication, cell expansion or other means.)

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10. Scape diameter.

There are three parallel changes to state 1 -thin scapes - all close to the level of terminal taxa, indicating that there are three non homologous types of thin scapes in the genus. It would be interesting to test this conclusion by examining the anatomy of these scapes to see if any consistent differences exist between the groups. The character is not of major evolutionary significance.

11. Ratio of spike length divided by scape length.

There are numerous parallel developments at all except one of the five states (except that any changes to state 1 were not shown by MacClade, and, as such, is an example of the problem with the "no unambiguous changes" result from MacClade, as mentioned above). In addition the patterns of change do not follow the pattern proposed by the scoring. State 2 - ratio of spike length divided by scape length approximately 1:1 - developed three times in parallel, each case representing a change from state 0 directly to state 2. State 3 - ratio of spike length divided by scape length greater than .5:1 bit less than 1:1- arose two separate times, one change being state 1-> 2-> 3 the other being state 0 -> 3. State 4 - ratio of spike length divided by scape length less than .5:1 but greater than .2:1 - also arose two separate times, both representing a transition from state 3 to state 4. State 5 - ratio of spike length divided by scape length less than .2:1- arose only once: on the branch leading to X. macronema and X. gracilis, as a change from state 2 -> state 5. There are three reversals to the plesiomorphous state 0.

It is clear that more than one evolutionary state (character) is represented here, as although similar in appearance, occurrences coded here as states 2, 3 and 4 are not homologous.

12. Spike length.

The change to state 1 - medium length spikes -occurs at the first step on the main stem: `A`. The second state - short spikes - occurs twice, in parallel: at `H` on the main stem, and; on the terminal branch leading to <u>X. acanthostachya</u>. There are two reversals to the plesiomorphic state, both of single taxa.

Apart from the single, non homologous occurrence of this character at <u>X. acanthostachya</u>, it appears to represent a reliable evolutionary transition.

13. Spike diameter.

This character has three parallel developments to state 1 - thin spikes - all close to terminal branches. The evolution of this characteristic roughly parallels that of scape diameter, and similar conclusions can be drawn as for that character.

14. Cluster bract prominence.

State 1 - slightly prominent cluster bracts - depending on interpretation shows one or two forward developments, the first is clearly such: at `D` on the main stem, but the second may be interpreted as a "reversal": on the penultimate branch leading to <u>X.</u>

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minor to which it takes an indirect route: state 1→ 3→ 4→ 1. That is, it is a forward development but only after an earlier reversal. State 2 - prominent cluster bracts restricted to the base of the spike - also has two possible interpretations concerning forward development because of the change before X. minor subsp. lutea. This development is not a direct one, rather it is by a round-about route: state 1→ 4-> 0-> 1-> 2, and may therefore be interpreted either as a forward development or a reversal. The reversals to state 2 are clear: before X. platyphylla and X. media. State 3 - obscure cluster bracts- develops only once: on the main evolutionary stem at `E`. There is one other reversal: to state 0 before X. caespitosa in the X. minor clade.

The evolution of this character is thus quite complex, and therefore difficult to interpret. If the character does represent one evolutionary characteristic it is an easily reversible one, and could therefore be regarded as being of lower value than other, more reliable characters.

15. Cluster bract shape.

State 1 - linear-triangular - develops only once: on the main stem at `E`. State 2 - acute - develops twice, in parallel: below the X. latifolia clade; before X. almae. The change to state 3 was not revealed by MacClade, which indicates that it was hidden by the "no unambiguous changes" problem mentioned above. There is one reversal to the plesiomorphous state: on the penultimate branch leading to X. arenaria and X. acaulis.

The change to state 1 is therefore a reliable evolutionary indicator, but the change to state 2 is actually two separate changes to non homologous characters.

16. Cluster bract indumentum.

Only one apomorphic change is revealed by MacClade, to state 1-subglabrous bracts - which occurs on the main stem at C. There are two reversals to the symplesiomorphic state: on the ultimate branch to X. arenaria and on the ultimate branch leading to X. bracteata. Thus the character is a reliable indicator of evolutionary change.

17. Packing bract shape.

The only occurrence shown for state 1 - linear triangular bracts - is as a reversal: at X. thorntonii. State 2 - acute bracts - is achieved at `C` on the main stem of the tree. There are three parallel changes to state 3 - shortly acute: on the main stem at `J`; at X. minor subsp. minor; at X. platyphylla. State 4 is reached twice: at X. fulva; at X. pumilio. There are two reversals to state 0 - subulate bracts: at X. arenaria; at X. caespitosa.

The evolutionary pattern of this character is different to that proposed by the scoring pattern used in the analyses. The pattern of evolution on the tree is:

$$
\begin{array}{c}
17^1 \\
| \\
17^0 - 17^2 \equiv 17^3 - 17^4 \\
| \\
17^4
\end{array}
$$

So that linear triangular bracts are "more advanced" than acute bracts, there are three different types of shortly acute bracts and two different types of obtuse bracts. Such a result is not surprising as the bracts are difficult to classify into what are, after all, artificial concepts of similarity of shape, (a common feature of morphological characters).

18. Packing bract indumentum.

State 1 – subglabrous bracts – develops once: on the main stem at `C`. State 2 – fringed bracts – develops twice, in parallel: on the main stem at `G`; on the branch leading to X. latifolia and X. arborea. State 3 – hirsute bracts – occurs twice: once as a forward change before X. drummondii; once as a "reversal" at `M` before X. macronema and X. gracilis. State 4 – tomentose bracts – develops once on the main stem at `J`.

From the pattern of change it appears possible that the "reversal" to state 3 at `M` noted above is really a forward development to a state non homologous with state 3.

$$
\begin{array}{c}
18^2 \\
| \\
18^0 - 18^1 - 18^2 - 18^4 - 18^3 \\
| \\
18^3
\end{array}
$$

The parallel change to state 2 indicates that there are two different

types of fringed bracts present in the genus.

19. Packing bract colour.

There are two changes, in parallel, to state 1 – dark bracts: before X. quadranqulata in the X. latifolia clade; at X. malacophylla. There are no reversals to the plesiomorphic state.

That is, there are two different types of dark bracts in the genus.

20. Sepals – beak.

There are four parallel changes to state 1 – beak absent, all at close to the taxon level. Such a result indicates that this character, as well as being a misinterpretation of four different characters, is of little significance to the overall evolution of the genus.

21. Sepals – proboscis.

The apomorphic state was not revealed by MacClade. There was one reversal to the plesiomorphous state: before X. acaulis and X. arenaria.

This character would also appear to be of little significance to the overall evolution of the genus.

22. Sepals – indumentum.

State 1 – subglabrous sepals – is reached twice: once as a forward

development on the main stem at `F`; once as a reversal on the main branch to the X. minor clade. State 2 - partly hirsute sepals- occurs on the main stem at `G`. State 3 - hirsute sepals - is reached twice, in parallel. The main change is at `J` on the main stem, but there is also a non homologous change at X. drummondii. There are two reversals to the symplesiomorphous state - glabrous sepals: at X. macronema, and; at X. pumilio.

The character thus appears to be a fairly reliable character which is part of the main line of evolution of the genus, with only the one occurrence of a similar but non homologous state at X. drummondii.

23. Petal size.

The analyses do not confirm large petals as the plesiomorphic state. Rather they show species with small petals at the base of the tree and the large petal state arising twice, separately, in X. macronema/X. gracilis and in X. minor (coded here as "reversals").

This means that either the genus developed from small petalled stock or that the development of the genus was accompanied by the development of this feature. In the latter case, as large petals arise in parallel in the genus, it is most likely that they are not true reversals to the plesiomorphic state, but rather are autapomorphies.

24. Petal shape.

The change to state 1 - erect to slightly recurved petals - is not

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revealed by MacClade. State 2 - recurved petals - is shown as arising five times in parallel. There are three "reversals" to the postulated plesiomorphic state - erect petals - shown.

It appears most likely that the evolution of this character is also not as scored. Rather it seems likely that apparently similar, but not homologous, petal shapes have arisen multiple separate times, i.e. as autapomorphies.

25. Petal proboscis.

State 1 - proboscis absent - develops twice, in parallel: below X. brunonis, and; below X. caespitosa. There is one reversal to the plesiomorphic state at X. bracteata.

The two non homologous developments of lack of a proboscis are not surprising, in that it is difficult to assess the homology of the lack of a feature. It is difficult however to draw many conclusions from this evolutionary pattern, except that the character is not involved in the main evolutionary line of the genus.

26. Petal indumentum.

State 1 - hirsute petals - arises only once, and only in the development of one species, X.resinosa. As such it does not contribute significantly to the evolution of the genus as a whole, and could indeed have been excluded from the analysis.

4.5 Discussion

4.5.1 Characters

Five characters (2, 8, 12, 16 and 22) were reliable evolutionary in-dicators, six characters (5, 6, 9, 15, 17 and 21) were partially reliable, and fifteen (1, 3, 4, 7, 10, 11, 13, 14, 18, 19, 20, 23, 24, 25 and 26) were shown as having parallel development or a pattern of change in conflict with the character scoring. That is, only the minority of the characters in the analysis were good or reasonable indicators of the main evolutionary thrust of the genus. Thus many of the apparent similarities in the genus are postulated to be non homologous parallel developments.

This situation could not be regarded as a reliable resolution of the evolution of the genus, and indicates that more work is needed to accurately determine homologies within the group.   Once such homologies have been determined the evolutionary pattern postulated by this cladogram could be reassessed.

4.5.2 Taxonomic implications of the cladogram

Hennig (1966) states that in phylogenetic systematics each taxon must be monophyletic, that is, it must include an ancestor and all its descendants.   If this principle is applied to <u>Xanthorrhoea</u> some significant conceptual changes are necessary within the genus.

The hypothesised close relationship between X. resinosa, X. fulva X. concava and X. gracilis with X. macronema, is a new concept as X. macronema had long been regarded as a species quite distinct from other xanthorrhoeas (Lee 1966 a and b). The close relationship proposed for X. macronema and X. gracilis on the other hand, whilst only established before by their being placed together on intuitive grounds in the revision by Bedford (1986 a), is obvious to even the casual observer of plants of both species.

The polychotomy involving the two subspecies of X. latifolia and X. arborea, reflects the uncertainty of whether the two subspecies are closer to each other than X. latifolia subsp. latifolia is to X. arborea (there is a 50% probability each way). This indicates that there is some evidence that either X. latifolia subsp. maxima should be considered a taxon of species rank, (albeit closely related to both other taxa), or that the three taxa should be considered as subspecies of X. arborea (since that is the oldest name). X. arborea and X. latifolia subsp. latifolia are taxonomically and geographically distinct, with different ecological niches, and, as indicated in Chapter 1, can be distinguished even where their distributions overlap.

The two subspecies of X. latifolia are also quite geographically distinct, with different ecological niches, but are very similar morphologically. Few specimens are known of X. latifolia subsp. maxima, which looks rather like a larger version of subsp. latifolia, and occurs only in a few, restricted localities (Bedford, 1986 a). One possible action is to revise the level of X. latifolia subsp.

maxima to give it specific rank, i.e. as X. maxima. However, the sparsity of collections and knowledge about this taxon, together with its apparent close similarity to subsp. latifolia, mean that it would be unwise to segregate it as a species at this time.

The lack of resolution of position of X. acanthostachya and X. australis indicates an uncertainty as to the exact relationship between these species. It is clear is that they are closely related, but not whether they are a true sister-group-pair (2/3 of the 18 most parsimonious trees) or adjacent clades (1/3 of the most parsimonious trees). Their very separate geographic distributions, south-west of Western Australia and south-eastern Australia respectively would lead one to expect that there might be considerable evolutionary differences between them, even if they did represent a sister-group-pair, and thus helps to explain how such an ambivalent situation in the cladograms could arise.

In many cladistic analyses the divisions of the genus into clades (e.g. as shown in Figures 4.2 and 4.3) are considered formal subgeneric groupings of the species. Such a decision for Xanthorrhoea would result in nine well defined subgenera as well as one or two subgenera for the unresolved taxa X. acanthostachya and X. australis.

It is my view that the development of a formal subgeneric classification should only be made after a very thorough examination of a group from many different aspects.

In this context, it is suggested that before taking such an action a number of important questions must be answered, including at least the

following three inter-related questions:

(a) will such a classification reflect all present knowledge about the group?

(b) how thorough is our knowledge of the group?

(c) are the groupings corroborated by more than one type of information source.

In the case of <u>Xanthorrhoea</u> the answers are (a) yes, to (b) not very, and to (c) no. That is, the present classification does represent all the presently available taxonomic information on the group, but the information is solely of a morphological nature.

Thus this classification should not be adopted as a formal subgeneric classification at this stage. Rather it should be regarded as a first approximation, which needs to be tested by comparison with data from other aspects of the group, possibly such as protein or isoenzyme analyses, before it could be regarded as a reliable subgeneric classification. However such analyses require specialised knowledge, equipment and materials, as well as considerable preliminary work to identify suitable analytical techniques. As such they represent a possible future direction for research, but could not be incorporated in the present study.

It is of note that there has been some chemotaxonomic work on flavonoid compounds in the genus which has not been successful in clarifying the situation (Bedford, unpublished data, Chapter 1). Also work is continuing on the taxonomic value of the resins (Duewell, in press, and Bedford and Duewell, in prep) which shows promise.

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4.5.3 Biogeographic implications of the preferred cladogram.

Rosen (1978), Nelson and Platnick (1981) and Humphries and Parenti (1986) describe the use of cladistic concepts in the study of biogeography, which they describe as cladistic biogeography. These concepts have been followed here to examine the biogeographic consequences and implications of the preferred cladogram. This procedure produces an area-cladogram by, in its simplest form, replacing the species names on the ends of branches with the geographic distributions of the species. The area cladogram (Figure 4.4) postulates historical relationships between areas, at least as far as these species are concerned (Humphries and Parenti, 1986, Rosen, 1978, Nelson and Platnick, 1981, Weston and Crisp, 1987). To extract the maximum possible information from such a procedure it is necessary to construct a reduced area cladogram (Figure 4.5) which incorporates all of the biogeographic information from Figure 4.4 in a simpler form (Humphries and Parenti, 1986). The process of creating a reduced area cladogram is complicated by the necessity to make decisions about the way in which widespread taxa should be treated and to delineate the biogeographic areas to use as the basic units (Humphries and Parenti, 1986, Nelson and Platnick, 1981).

Widespread taxa, i.e. those which occur in one or more of the biogeographic regions chosen for the study, may be treated under any of three assumptions (termed 0, 1 and 2) as to the relationships of the relevant areas, (Nelson and Platnick 1981; Nelson 1982; Humphries and Parenti 1986; Weston, pers. comm. 1988).

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Figure 4.4 Full-Area-Cladogram

Figure 4.4 XANTHORRHOEA CONSENSUS TREE WITH DISTRIBUTION OF SPECIES SHOWN IN TERMS OF MAP 1.

```
                                          ┌─── South-east temperate Australia (6) and Macpherson Macleay overlap
                                       ┌──┤
                                       │  └─── Temperate south-west Western Australia (5)
                                    ┌──┤
                                    │  ├─────── South-east temperate Australia (6)
                                    │  │
                                  ┌─┤  ├─────── South-east temperate Australia (6) and Macpherson Macleay overlap
                                  │ │  │
                                  │ │  └─────── South-east temperate Australia (6)
                                  │ │
                                  │ │        ┌─── Temperate south-west Western Australia (5)
                                  │ │     ┌──┤
                                  │ │     │  └─── Temperate south-west Western Australia (5)
                                  │ ├─────┤
                                  │ │     └────── Temperate south-west Western Australia (5)
                                  │ │
                                ┌─┤ │        ┌─── South-east temperate Australia (6)
                                │ │ │      ┌─┤
                                │ │ │      │ └─── Tasmania (7)
                                │ │ └──────┤
                                │ │        │ ┌─── South-east temperate Australia (6)
                                │ │        └─┤
                              ┌─┤ │          └─── South-east temperate Australia (6)
                              │ │ │
                              │ │ │        ┌───── Tasmania (7)
                              │ │ └────────┤
                              │ │          └───── South-east temperate Australia (6)
                              │ │
                              │ └─────────────── South-west Western Australian interzone (1)
                            ┌─┤
                            │ └───────────────── Temperate south-west Western Australia (5)
                            │
                            │        ┌────────── South-west Western Australian interzone (1)
                            │     ┌──┤
                            │     │  └────────── Temperate south-west Western Australia (5)
                          ┌─┤   ┌─┤
                          │ │   │ └───────────── South-east temperate Australia (6)
                          │ │   │
                          │ │   │        ┌────── Tropical north-eastern Australia (4)
                          │ └───┤      ┌─┤
                          │     │      │ └────── South-east temperate Australia (6)
                          │     │    ┌─┤
                        ┌─┤     │    │ └──────── South-east temperate Australia (6) and Tropical NE Australia (4)
                        │ │     └────┤
                        │ │          │ ┌──────── South-east temperate Australia (6)
                        │ │          └─┤
                        │ │            └──────── South-east temperate Australia (6)
                      ┌─┤ │
                      │ │ └───────────────────── Eremaean central Australia (8)
                    ┌─┤ │
                    │ │ │        ┌────────────── South-east temperate Australia (6) and Tropical NE Australia (4)
                    │ │ └────────┤
                  ┌─┤ │          └────────────── South-east temperate Australia (6) and Macpherson Macleay overlap
                  │ │ │
                  │ │ │          ┌────────────── South-east temperate Australia (6) and Macpherson Macleay overlap
                  │ │ └──────────┤
                ┌─┤ │            └────────────── South-east temperate Australia (6)
                │ │ │
                │ │ └──────────────────────────── Temperate south-west Western Australia (5)
              ┌─┤ │
            **│ │ └──────────────────────────── South-east temperate Australia (6) and Tasmania (7)
           ***│ │
            # │ │              ┌──────────────── South-east temperate Australia (6)
            # └─┤──────────────┤
            #   │              └──────────────── South-east temperate Australia (6)
            #
************************************************************** Southern Africa, North and South America
```

Figure 4.5 Reduced-Area-Cladogram

Areas numbered as per Figure 4.4. Letters represent hypothetical
vicariance events, and are referred to in the text.
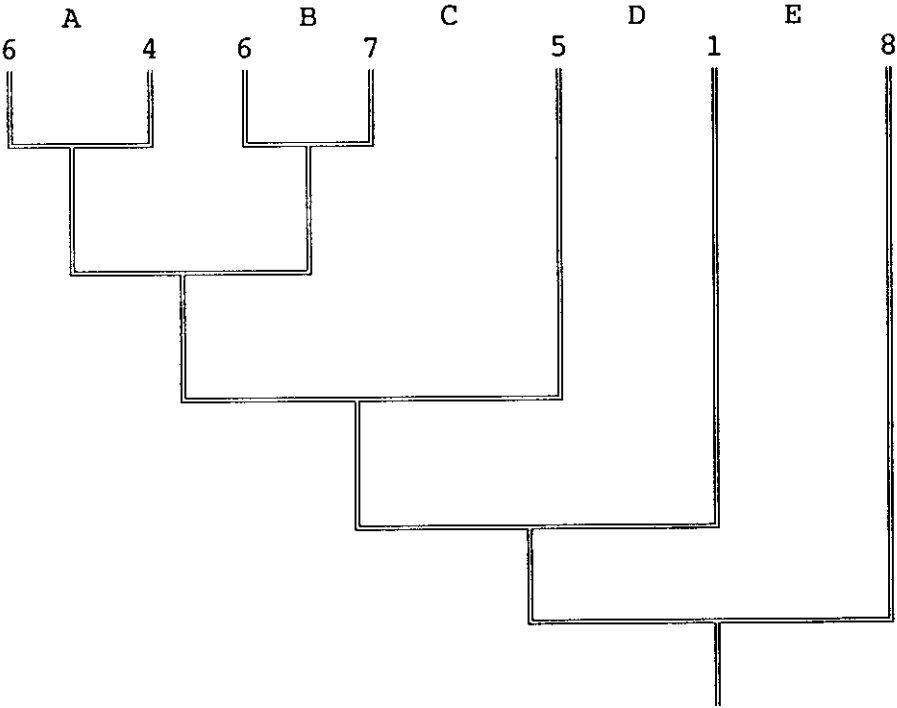
A = the separation of tropical north-eastern Australia (4) and
temperate south-eastern Australia (6).

B = the separation of temperate south-eastern Australia (6) and
 Tasmania (7).

C = the separation of eastern temperate Australia and temperate
south-west Australia (5).

D = the separation of Eremaean (8) and Eremaean south-west
interzone (1) areas from temperate and tropical Australia.

E = the separation of the central Australian Eremaean area (8)
from the south-west interzone and rest of Australia.

Assumption 0 states that the areas covered by a widespread taxon may not be related to each other at all (Weston pers. comm. 1988) and is thus the least rigorous and least useful of the three. It is not investigated further in this study.

Nelson and Platnick (1981) and Nelson (1982) discuss the full theoretical aspects of assumptions 1 and 2 under which widespread taxa can be treated. Under assumption 1 whatever is true of a widespread taxon in one part of its range must be true of the same taxon in another part of its range (i.e. the taxon is uniform). Assumption 2 states that whatever is true for a widespread taxon in one part of its range need not be true for the same taxon in another part of its range(i.e. the taxon is not necessarily uniform).

The implications of assumption 1 are that a widespread taxon C will never be distinguished as two or more separate taxa. So if species A and B are more closely related to each other than they are to C in one part of its range then A and B are also more closely related to each other than they are to C in another part of its range.

The implications of assumption 2 are that the widespread taxon C might at some time be recognised as two or more separate taxa, so that whatever is true of one occurrence may not be true of another. Thus it may be possible that A and B are more closely related to each other than either is to C in one location 1, but that A is more closely related to C in location 2 than it is to B (Humphries and Parenti 1986).

Humphries and Parenti (1986) argue that assumption 2 gives the most

informative resolutions when cladograms of two or more unrelated groups from the same geographic range are combined/compared, but will usually result in more than one hypothesis. Further, they state that assumption 1 will only give informative results when there is no overlap or conflict in the original area cladogram.

There are also a number of different ways to delineate the basic unit areas for consideration in the study. The technique chosen here has been to divide the continent into biogeographic areas using a modification of Burbidge (1960) as shown in Figure 4.6, and to allocate the taxa distributions into these areas prior to preparing the reduced area cladograms. Burbidge delineates one area as the Macpherson-Macleay overlap, in which she comments that species which are primarily tropical in distribution extend into tropic-like habitats south of the tropics, and species which are primarily temperate extent into temperate-like habitats north of the temperate region. If one takes this literally it is possible to treat some taxa which appear to overlap both regions as being restricted to the region of their primary distribution. This approach, although at variance with some of the precepts of cladistic biogeography as espoused by Humphries and Parenti (1986) has some similarities with the approach of Rosen (1978), and has been adopted here solely for the practical reason that it greatly simplifies the preparation of reduced area cladograms without (in this case, in this author's opinion) significant loss of information. The reduced-area-cladogram was prepared by combining the informative resolutions of component analysis (using assumption 2) of each separate clade.

The most rigorous way to prepare reduced area cladograms would have

Figure   4.6   Australia   divided into phytogeographic regions used in
analyses.

TROPICAL ZONE ....
EREMAEAN ZONE ....
TEMPERATE ZONE ....
INTERZONE AREAS ....

N.E. focal area

4

MACPHERSON
MACLEAY
overlap

5

S.W. focal area

8

SUMMER RAIN
WINTER RAIN

6

TASMANIAN
focal area

7
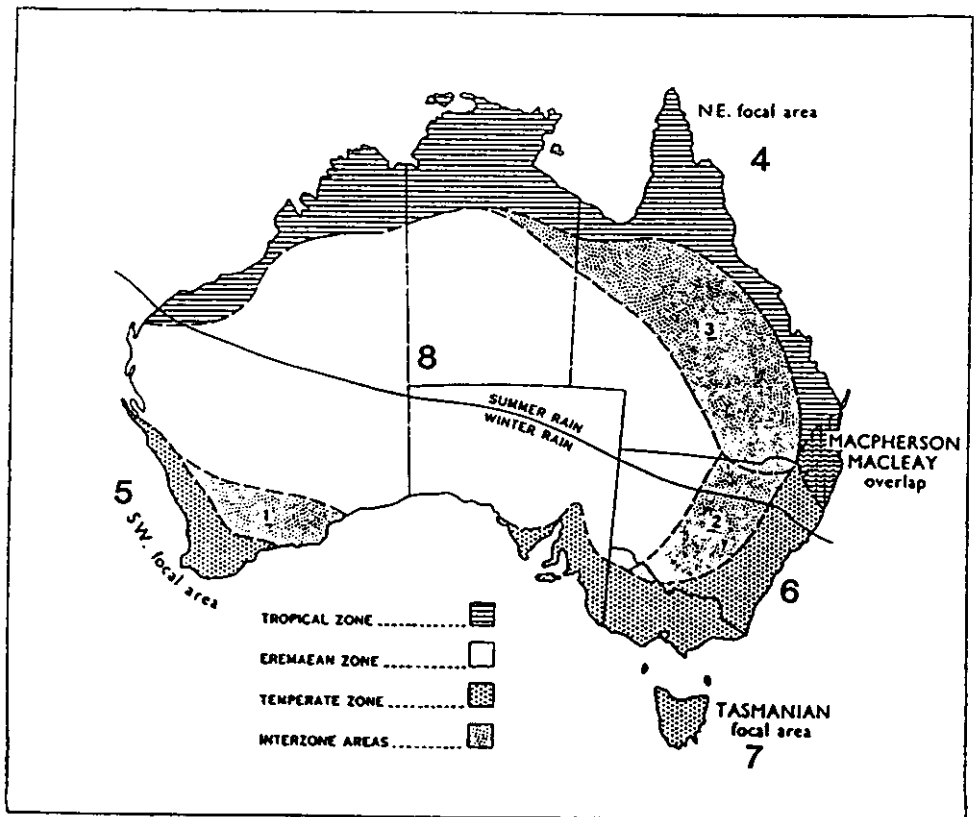
been to prepare large scale maps of the distribution of taxa and identify both the basic areas and areas of overlap (Humphries and Parenti 1986; Weston pers. comm. 1988). This method is, however, because of its complexity, more suited to a methodological study of vicariance biogeographical techniques than to this more generalised study of Xanthorrhoea. It is intended to continue this work using such an approach, outside the confines of the present study.

Figure 4.4 shows the consensus cladogram with the geographic distribution of taxa replacing the species names. Figure 4.5 shows the reduced area cladogram created from Figure 4.4. Figure 4.6 gives the phytogeographic areas used.

Area-Cladograms

An examination of both area-cladograms reveals that they are slightly different, though complementary, in information content. The full area-cladogram can be used to examine more detailed species-specific distributional hypotheses for one of the clades whereas the reduced area-cladogram presents more general overall hypotheses concerning the evolution of the genus. Results are therefore presented and discussed (as far as is informative) for both area-cladograms.

Full-Area-Cladogram (Figure 4.4)

The uppermost clade in Figure 4.4 shows eastern Australia joining with Western Australia before joining with three other eastern Australian branches. There are a number of points of biogeographical interest to this situation. Firstly that the closest two branches of the clade

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are so widely geographically separated. In biological terms this infers that the genus is older than the biological isolation of eastern Australia from western Australia. Secondly that an eastern Australian branch is classified more closely to a Western Australian branch than to other eastern Australian branches.

A possible explanation for this result is that both X. gracilis and X. macronema occupy well drained open eucalypt forest habitats, which are very similar in structural appearance, whereas the other three taxa in the clade, X. concava, X. fulva and X. resinifera all occupy periodically waterlogged, more open environments than the first two taxa in the clade. It is therefore possible to interpret this classification as reflecting the similarity of the different ecosystems. That is, ecological factors as well as areas appear to be relevant to these results.

The lower clades are most informative when examined as part of the reduced-area-cladogram.

Reduced-Area-Cladogram (Figure 4.5)

Component analysis of the full area-cladogram yields only one possible resolved cladogram for all the areas in which taxa occur. The resulting reduced-area-cladogram specifies a series of historical area relationships which can then be interpreted in biological terms for the evolution of the genus.

The uppermost clade in Figure 4.5 shows two equally likely close relationships: (a) temperate south-eastern Australia (6) and north-

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eastern tropical Australia (4); (b) temperate south-eastern Australia (6) and Tasmania (temperate) (7). The whole of the above are more closely related than they are to the next most closely related area-temperate south-western Australia (5). All of these are more closely related than they are to the next most closely related area - the south-western Australian "interzone" between the temperate and eremaean regions (1). The most distantly related area from all the above is the eremaean central Australian region.

Such a conclusion indicates that the biological separation of eastern Australia and Western Australia is of fundamental importance to the evolution of Xanthorrhoea. Furthermore the separation between the essentially coastal temperate and tropical areas and the more inland drier areas argues that evolution has been greatly influenced by the availability of water.

That is, the historical relationship proposed is for the earliest separations to have been of eremaean Australia and inland Western Australia from the rest of the clade, which can be attributed to an early vicariance event leading to the separate evolution of the more or less coastal conditions of the former and semi-arid conditions of the latter. Later vicariance events have separated firstly east from west and most recently the double separation of north-east tropics and Tasmania from temperate south-east.

Humphries and Parenti (1986) note the importance of comparing the reduced area-cladogram for one taxonomic group with that derived from other unrelated taxonomic groups. These results have therefore been compared with the relevant parts of the reduced area cladogram

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prepared for the eucalypts by Ladiges and Humphries (1983). These authors use a very similar biogeographical grouping to that used here (Figure 4.6) in that it is also a modification of Burbidge (1960), mainly differing in that they do not distinguish the south-western interzone. As the geographic groupings are so similar the results are directly comparable.

An examination of the two cladograms reveals that the results for Xanthorrhoea are fully concordant with the relevant part of the results for the eucalypts which Ladiges and Humphries summarise "south-western Australia is sister group to south-eastern and north-eastern Australia". This result is not surprising considering that both Xanthorrhoea and the eucalypts comprise parts of Australia's distinctive sclerophyllous flora which are believed to have a considerable evolutionary history in Australia, and which could therefore be expected to show at least some common patterns.
Other comparisons with the results for analyses of different groups of eucalypts by the same authors are discussed below.

The area-cladograms of taxa above can be compared with known or presumed events in the geological history of Australia in order to establish hypotheses about possible vicariance events involved in the separation of areas in the area-cladogram. It is therefore necessary to examine the literature on possible vicariance events in Australia's geological history. The relevant literature is summarised in Table 4.5 and Appendix 4.7.

Most recent (in geological time) vicariance events for Australia are generally presumed to have primarily been related to changes in sea

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Table 4.5 Summary chronology of vicariance events in Australia.

Appendix 4.7 contains a more detailed summary with references.

I. PHYSICAL CHANGES

Mesozoic and Tertiary

East-west physiographic division of the Australian land mass

Late Cretaceous-early Paleocene (80-60 m.y. B.P.)

Separation of New Zealand and New Caledonia from Australia.

Late Paleocene (60-53 m.y. B.P.)

Separation of Australia from Antarctica, and from the Papua New
Guinea mobile belt.

Eocene (Mid at 45 m.y. B.P.)

A time of major marine transgression across southern Australia.

Miocene (Mid at 15 m.y. B.P.)

Ended in large expansion of the Antarctic ice sheet with
corresponding low sea levels.

Pleistocene

Sea levels fluctuated repeatedly (range -200 m to +43 m), in the
lows, Tasmania, Australia and New Guinea joined.

Holocene

Severing of the land bridge to Tasmania 12,000-13,500 years ago

II. CLIMATIC CHANGES

Early Tertiary to middle Eocene

Humid and relatively warm climate with a tropical flora.

Mid-Tertiary - late Eocene

Development of a north-south disjunction, SE colder. Some evidence for persistence of tropical conditions in south west Australia.

Mid-Oligocene

Reduced temperatures. Reduction in floristic diversity in south.

Miocene

Early warm wet conditions followed by relative aridity.

Pliocene

Marked warming (? wetter), followed by cooling and dryness.

Pleistocene

Predominantly dry, sand dune areas showed mobile dunes.

Late Pleistocene and Holocene climates

123,000-40,000 years B.P.

NE had tropical conditions, rainfall at least as high as at present. SE drier and cooler than present.

40,000-30,000 years B.P.

Drier (c. half present levels), glacial activity in Tasmania.

30,000-26,000 years B.P.

Dry conditions persisted in the north, glaciers in the SE. Some conflicting evidence for warm conditions in western N.S.W.

26,000-16,000 years B.P.

Increasing aridity with "peak" achieved 16,000-17,500 B.P. 16,000-10,000 years B.P.

Dry conditions persisting, gradual warming increased rainfall. 10,000 years B.P. to the present

Early return of tropical conditions in north Queensland, followed by decline to essentially the same conditions as today for the last 2,000 yrs.

levels due to changes in the Earth's temperature and to increasing aridity, associated both with temperature changes and the northward drift of the Australian tectonic plate. Galloway and Kemp (1981) state that climate is the most significant environmental factor for Australian biogeography.

How then are the known or presumed vicariance events related to those involved in the area evolution demonstrated for Xanthorrhoea? It is not possible to answer this question definitively because of the considerable unknowns involved. For example it would be necessary to accurately date the development of the genus Xanthorrhoea as we know it. This is not possible at this time as there are no fossil Xanthorrhoea plant specimens known. (Microfossils (pollen) believed to be of Xanthorrhoea have been reported in 30,000 year old deposits at Cooloola in Queensland (pers. comm. C. Bell, 1975). However Xanthorrhoea pollen can be difficult to distinguish from the pollen of some other monocots, so this report must be treated with caution, and certainly cannot be taken as a dating for the emergence of the group.)

As such it is only possible to compare the sequences of vicariance events hypothesised by the Xanthorrhoea area-cladogram with the sequence of known or presumed vicariance events from the geological and paleo-botanical etc. records to determine if any sequence of the latter has occurred in the corresponding order.

Depending on certain assumptions one or more such sequences can be found in the biogeographic literature.

Galloway and Kemp (1981) note that south-west Western Australia and

eastern Australia have been isolated throughout the late Quaternary, which places a <u>minimum</u> time on vicariance event C (the separation of east and west) as not being more recent than that time. Unfortunately they do not give any more exact estimated date for the event isolating east and west.

If we hypothesise this as vicariance event C in our sequence it is clear that vicariance events D and E must have been earlier events, and we could hypothesise that these were the periods of aridity during the Miocene and Pleistocene. Event E would be hypothesised to be the first period of aridity at the end of the Miocene, which could have separated off the eremaean area from all others, and event D being a second, (possibly more severe?) period of aridity during the Pleistocene causing a more extensive retreat of the south-west temperate area, and, in so doing, isolating the south-west interzone.

As noted above, vicariance event C may be hypothesised to have been the most recent separation of east and west. Such a separation may be attributed to the onset of aridity during the period 80,000-40,000 years ago (which culminated in maximum aridity about 16,000 years ago).

Galloway and Kemp (1981) note that Bass Strait originated as far back as the Miocene but that the last severing of the land bridge was only about 12,000-13,500 years ago. They note that Bass Strait is wide, deep and stormy and has therefore presumably been an effective barrier. They comment that even before the flooding of the strait "Dunes developed on the exposed floor of Bass Strait during the last glaciation and the resulting sandy surface would have restricted

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migration of many species while major contrasts between the environments of Tasmania and Victoria would also have helped to preserve differences between their biota." But it is notable in this latter context that <u>Xanthorrhoea</u> often occupy sandy habitats and so (except for mobile dunes) would not necessarily have been affected by this factor, and may have been present on the land bridge. As such it is hypothesised that vicariance event B, is the recent development of Bass Strait circa 12,000-13,500 years ago.

The last vicariance event, A, the separation of tropical north-east Queensland and temperate south-east Australia is hypothesised to be caused by the gradual warming of the continent, resulting in the re-development of tropical conditions in North Queensland, but continuing temperate conditions in the south which began 10,000 years ago.

This schema requires (a) that the Miocene aridity was less extreme in the south-west of Western Australia than the more recent "peak" aridity of about 16,000 years ago, and (b) that there was an effective link between east and west in the early quaternary. However, Nelson (1981) argued that there was unlikely to have been an effective corridor between east and west to the north of the Nullarbor since the emergence of the Nullarbor karst in the mid-Miocene, which argues against the second of these requirements, and detailed information about temperatures and severity of aridity of particular areas of Australia is not available (Kemp, 1981) so that no decision can be made concerning the first.

Other alternative schemas based on an earlier starting point for vicariance event C of the Miocene marine incursion are possible, at

least to a certain extent. Such a schema could take into consideration the evidence that the late Eocene aridity was less extreme in south-west Western Australia than in south-eastern Australia (Hos, 1975), which would possibly correspond with vicariance event E, which separated eremaean Australia from both the south-west temperate and interzone areas. However this proposal does not supply any known possible vicariance event for our proposed event D, separating the south-west interzone from the south-west temperate areas. Events A and B could continue to be attributed to the same events as in schema one, above, or to earlier events. Ladiges and Humphries (1986) found a north-south separation in the stringybark eucalypts which has some similarity to the north-south disjunction found here. However they ascribe the separation to the temperature decrease in the late Eocene, which timing does not agree with the position of proposed vicariance event A if the Miocene is proposed for event C. This suggests that the later events proposed in schema one are more feasible in this case.

Neither schema unequivocally leads to any series of known events which definitely corresponds with the series hypothesised by the Xanthorrhoea area-cladogram. However both schemas have their better aspects. The major doubt concerning schema one is about the date of the last separation between east and west. As the areas were joined (at least by sand) during the periods of low sea level during the Pleistocene and the continent enjoyed tropical conditions from 123,000-80,000 years B.P., it is possible there was a continuous connection between these areas. (Galloway and Kemp (1981) say "Lowered sea level during glacial times could also have affected the role of the Nullarbor as a barrier between the south west and east of

Australia. A 200 km wide belt of different (sandier?) soils would have been exposed on what is now the continental shelf."). Nelson (1981), in raising doubt about the possibility of a "recent" connection based his argument partially on the distribution of species that cannot grow on lime soils. Some Xanthorrhoea species do grow on lime soils and therefore may not have been separated by the expanses of limestone on the Nullarbor under higher rainfall conditions.

In support of schema two is that vicariance event C might have been expected to be one of the more physical breaks between east and west, such as one of the major marine transgressions of the present day Nullarbor area during the Eocene and Miocene. This argument would agree well with the original proposals of Diels (1906) and paleobotanical evidence quoted in Nelson (1981). It is also in agreement with the evolutionary pattern and area-evolution proposed for Western Australian eucalypts by Ladiges et al. (1987).

4.5.4 Conclusions of biogeographic discussion

The vicariance events for Xanthorrhoea hypothesised by the area-cladogram for the genus corresponds (with some reservations) to a series of climatic and physical vicariance events during the Quaternary. As such the genus can be presumed to be a relatively young group, with relatively recent evolution, in common with much of the Australian flora (Kemp 1981).

CHAPTER 5

A REVISION OF

XANTHORRHOEA

5.1 Introduction

The following revision has been adapted from Bedford (1986 a and b), which were prepared as a result of the research for the present work. The major changes from that publication are the organisation of the species to reflect their relationships following cladistic analysis (chapter 5), and the description of new taxa discovered as part of the analysis of Xanthorrhoea in Queensland (chapter 2). In addition recent research into the nomenclatural status of the name Xanthorrhoea is reported in section 5.3. The format adopted here is the standard for flora treatments in the Flora of Australia.

As part of the taxonomic revision for Bedford (1986 a) a number of new species were described, and nomenclatural clarifications were made. These were published in the appendix of the same volume (46), of the Flora of Australia (Bedford, 1986 b) and, for completeness, are included here as an associated publication in Appendix 5.1. Another species, X. acanthostachya, was published earlier, in 1985, and is also included here as above, in Appendix 5.2.

5.2 Generic description of Xanthorrhoea

Xanthorrhoea J.E. Smith ex Dryander, Cat. bibl. Banks, 3: 486 (1797). (Nelson and Bedford, in press, and discussed below).

Stems arborescent or subterranean, woody, covered with packed leaf-bases. Leaves crowded in a terminal crown, narrowly linear, tapered, rhombic to cuneate in T.S.; margins with microscopic

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trichomes, rarely hairy; leaf-base broad, sometimes thickened. Inflorescence cylindrical, spike-like, on a woody scape; flowers bisexual, in spirally-arranged clusters surrounded by packed bracts. Sepals free, chartaceous or scarious. Petals free, membranous; apices exerted. Stamens exerted; filaments flattened; anthers dorsifixed, dehiscing by slits. Ovary 3-locular; ovules several per locule; style simple; stigma entire, sometimes grooved. Capsule obtuse or pointed, the hardened style base ± exerted. Seeds 1 or 2 per locule, ovate and semi-matt black, rarely ovoid and shining.

Common names: Blackboy, Grass-tree, Yacca.

Xanthorrhoea is named from the Greek xanthos (yellow) and rhoea (flowing), in reference to the yellow resin noted in the type species.

Chromosome number n=22 (several species counted), Darlington and Wylie (1955), Briggs (1966), Keighery (1984).

A genus of 28 species endemic in Australia. One species, X. almae, (as X. johnsonii) is sometimes involved in stock poisoning in Qld.

All species have contractile roots and a secondary thickening meristem, the latter character absent from the other genera of the Xanthorrhoeaceae as circumscribed here. The flowers are protandrous, having a style that is short at anthesis and elongates with age.

With the exception of X. thorntonii all species occur in regions receiving more than 250 mm annual rainfall, and most in regions receiving more than 500 mm.

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5.3 Nomenclatural considerations

5.3.1 The generic name _Xanthorrhoea_

Smith has for some time been regarded as the authority for the name _Xanthorrhoea_ (e.g. Lee, 1966 a), however recent research has revealed that the name was published by Dryander on 3 October 1797, six months previous to Smith's publication on 24 May 1798. Moreover, there is an earlier valid name for the genus, _Acoroides_ Kite (1795), (Nelson and Bedford, in press).

Because the earlier name does not have, and has never been, accepted usage it is intended to conserve the name _Xanthorrhoea_ against the earlier name, to ensure stability of nomenclature (Nelson and Bedford, in press).

5.3.2 Type species for the genus

The Type species for the genus has been regarded as _X. resinosa_ Pers., since Lee (1966 a) took this name to have priority over the name _X. hastile_. However recent research by Nelson (in press) has found that the name _X. hastile_ was published earlier, in Dryander (1797), although Dryander attributed the name to Smith, making the correct attribution for the name _X. hastile_ Smith ex Dryander. The situation is further complicated in that the earlier publication of _Acoroides_ as a valid name for the genus we know as _Xanthorrhoea_ was accompanied by the publication of a specific epithet, which, under the rules of botanical nomenclature, is the correct name for the type species for the genus. This epithet is _resinifera_, which, will,

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unfortunately, cause some unavoidable confusion with the name _resinosa_ which must be rejected as superfluous (_resinosa_ was first published 1798) (Nelson, in press; Nelson and Bedford, in press).

5.3.3 Nomenclatural conclusions

It is clear that the nomenclatural situation for the genus and type species are in a state of flux, with research and publication still underway to determine and document the validity of recently discovered names and to conserve the name _Xanthorrhoea_ against such names. This situation has arisen through two main developments: (a) the historical "accident" of Brown (1810) taking up the name _Xanthorrhoea_ and thus setting the pattern for all later authors, and; (b) the changes made to the International Code of Botanical Nomenclature (Stafleu 1983) at the Nomenclature session of the 1987 International Botanical Congress in Berlin, which removed the provisions to invalidate a name on the basis of "incidental mention". Nelson (pers. comm.) has commented that, if not for this change, it is possible that the name _Acoroides_ may not have been validly published.

5.4 Taxonomic notes - impediments to a natural classification.

5.4.1 Hybridism

Although A.T. Lee, (1966 a and b), discussed hybrid swarms of _Xanthorrhoea_, documented examples indicate that hybrids are scarce and restricted (chapter 2). All have been on the coastal sand dunes from Beerwah, south-eastern Qld, to Newcastle, N.S.W., in restricted

ecotonal conditions. The species known to be involved are X. glauca, X. resinifera, X. fulva, X. johnsonii, and X. latifolia. Hybrids probably also occur in similar conditions elsewhere on the east coast and this is certainly indicated by specimens from coastal sand dunes in Vic. Most other plants presumed to be hybrids are probably either taxa not yet recognised or examples of the considerable variation that often occurs within Xanthorrhoea species. A number of new taxa described here have been referred to purported hybrids, e.g. X. caespitosa and X. arenaria, both as X. minor x X. australis, (Lee, 1966 a, p. 54 and p. 46 respectively).

5.4.2 Floral and reproductive biology

During some initial experiments to investigate the possibility of breeding experiments with Xanthorrhoea, it was found that it is possible that some aspects of the floral and reproductive biology of the genus contribute to the impediments to their natural classification.

Initial experiments for breeding and artificial pollination research into the purported hybridisation in the genus involved finding whether the flowers were self fertile within the one spike (Bedford, unpub. data).

Seed production by spikes of X. glauca subsp. glauca covered with cloth bags, from prior to flowering until seed set, to prevent cross fertilization, was variable. Some spikes produced no seed at all, but the majority produced a considerable number of seeds, with seed set per spike ranging from 0 to 1000. These numbers represent a

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considerable reduction from the estimated number reported for X. australis and actual numbers recorded for X. resinifera in Victoria by Staff (1975). Staff reported seed set for the latter ranging from 336 to 2,600 seeds per spike, and his single estimate for the former species was 7,500 seeds. The spike lengths of X. glauca measured were comparable to the range of specimens recorded by Staff (loc. cit.).

It therefore appears possible that X. glauca (?and other species) may be to some degree facultatively self fertile. The actual proportion of selfed seed to open pollinated seed can not be estimated from these experiments, partially because no data were obtained for seed set on open pollinated spikes of X. glauca so the percentage reduction in seed set is not known.

When collecting Xanthorrhoea it quickly becomes apparent that they have a patchy distribution, with many isolated populations. Such a distribution may be partly an artifact of the land clearing since white settlement, but is found even in relatively undisturbed areas such as Cape York. In these circumstances the possibility of facultative self fertilization helps to explain some of the considerable variation seen from one population of Xanthorrhoea to another, as there would be a tendency for isolated populations to become inbred, and thus slightly different from other populations.

Another result of these initial experiments was the discovery that some of the seed set by selfed plants have more than one embryo. Germination tests were undertaken to test if the seed set were fertile. It was found that the majority were fertile, and that some have more than one embryo (Figure 5.1).

Figure 5.1   Seed of <u>X. glauca</u> subsp. <u>glauca</u> with

two embryonic seedlings. (seed approx 6 mm long).

Seed from specimen growing on the Queensland

margin of Levers Plateau, collected by D.J. Bedford 1978.
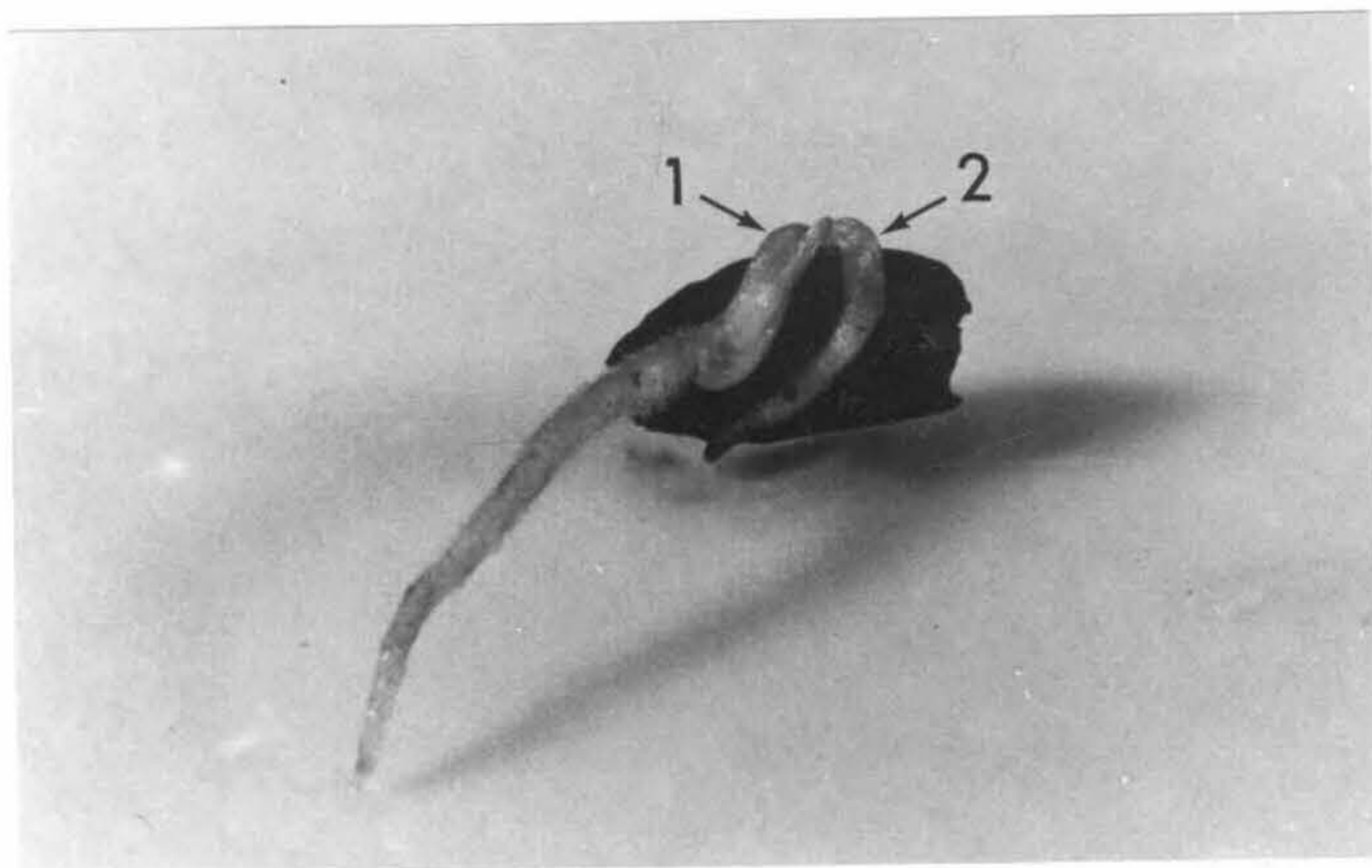
It is known that many apomictic plants are polyembryonic (e.g.in somatic apospory), as are plants with some other asexually seed forming processes (e.g. sporophytic embryony) (Barlow, 1958; Davis, 1972), and thus the discovery of polyembryony in Xanthorrhoea opens the possibility that it may be partly apomictic.

As apomixis, and asexual reproduction in general, works to stabilise variation within populations, but increases variation between populations. This phenomenon in Xanthorrhoea would explain some of the difficulties in the classification of taxa within the genus.

However, as these experiments were only a preliminary investigation no firm conclusions can be drawn as to whether self fertilization or apomixis are present. It is clear that considerable further research to test these hypotheses is needed.

5.4.3 Taxonomic conclusions

The restricted distribution of hybridism in the genus, in conjunction with an awareness of the taxa and ecotonal conditions involved, mean that hybridism is not a significant impediment to the natural classification of the genus. The possibility of facultative inbreeding and apomixis in the genus are also not a significant impediment to a natural classification, though their effects would help to explain some of the variation found in the genus.

That is, notwithstanding the problems noted above, it has been found possible to prepare a classification which appears to take into account the majority of the variation found in the genus, and which

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allows the majority of complete specimens to be classified with like specimens.

5.5 Characters Used (Figures 5.2-5.4).

A number of characters and terms are used as in Bedford (1986 a). The term packing-bracts is used for the mass of small bracts that cover the axis (e.g. Figure 5.2, M-R).   These are densely packed, filling out the space between the flowers and giving the surface of the spike its distinctive appearance.   There is a considerable range of shape and size of packing-bracts on ever spike; only the largest and most mature are described here, since immature bracts are very variable in every species.   Cluster-bracts subtend the clusters of fertile and aborted flowers.   All species possess cluster-bracts though in some species they are obscure at maturity, i.e. not distinguishable from the packing-bracts. The terms used for the shape of the bracts are as in Bedford (1986 a), as defined below. The shortest and least pointed bracts are obtuse (Figure 5.2, M) followed by shortly acute (Figure 5.2, N), acute (Figure 5.2, O), triangular (Figure 5.2 P), narrowly triangular (Figure 5.2 Q) to the most pointed form subulate (Figure 5.2 R) which tapers directly from the base to the apex without the distal enlargement evident in the other categories.

Sepals and petals are described variously as beaked (Figure 5.3, R), and/or with proboscis (Figure 5.3, S), and/or with median abaxial ridge, or recurved (Figure 5.3, P-Q). A beak is a continuation of the sepal or petal into a terminal appendage, it contains a small tuft of papillose hairs. A proboscis is a small adaxial projection from the

Figure 5.2 Xanthorrhoea leaf characters and habit of X. nana

(From Bedford, 1986 a).

Xanthorrhoea. A–L, T.S. leaf shapes, all ×8. A–B, depressed-cuneate. A, *X. fulva* (D.Blaxell NSW89530, NSW). B, *X. minor* (H.McKee 789, NSW). C, *X. macronema*, rounded depressed-cuneate (H.Salasoo 1542, NSW). D, *X. minor*, very depressed-cuneate (H.McKee 789, NSW). E, *X. fulva*, depressed-obtrullate (E.Constable NSW6166, NSW). F–G, very depressed-obtrullate. F, *X. semiplana* subsp. *tateana* (D.Bedford 104, NSW). G, *X. arborea* (L.Johnson NSW61355, NSW). H, *X. drummondii*, quadrate-rhombic (D.Bedford 41 & T.Macfarlane, NSW). I, *X. media*, transverse-rhombic (J.Camfield NSW59863, NSW). J, *X. latifolia* subsp. *latifolia*, narrowly transverse-rhombic (I.Telford 5517, NSW). K, *X. arborea*, transverse-linear (E.Constable NSW39982, NSW). L, *X. concava*, concave (J.Waterhouse NSW81659, NSW). M–R, packing bract shapes, × c. 3.5–5. M, *X. fulva*, obtuse (E.Constable NSW 6166, NSW). N, *X. arborea*, shortly acute (L.Johnson NSW61355, NSW). O, *X. media*, acute (J.Camfield NSW59863, NSW). P, *X. preissii*, triangular (L.Preiss 1620, MEL). Q, *X. acanthostachya*, narrowly triangular (T.Macfarlane 659, PERTH). R, *X. australis*, subulate (D.Martin NSW67463, NSW). S, *X. macronema*, sub-epidermal stomatal chamber, diagrammatic ×330. T, *X. johnsonii*, leaf surface and stomate arrangement, diagrammatic ×170. U, *X. nana*, habit ×0.1 (D.Bedford 67, 70 & T.Macfarlane, NSW).

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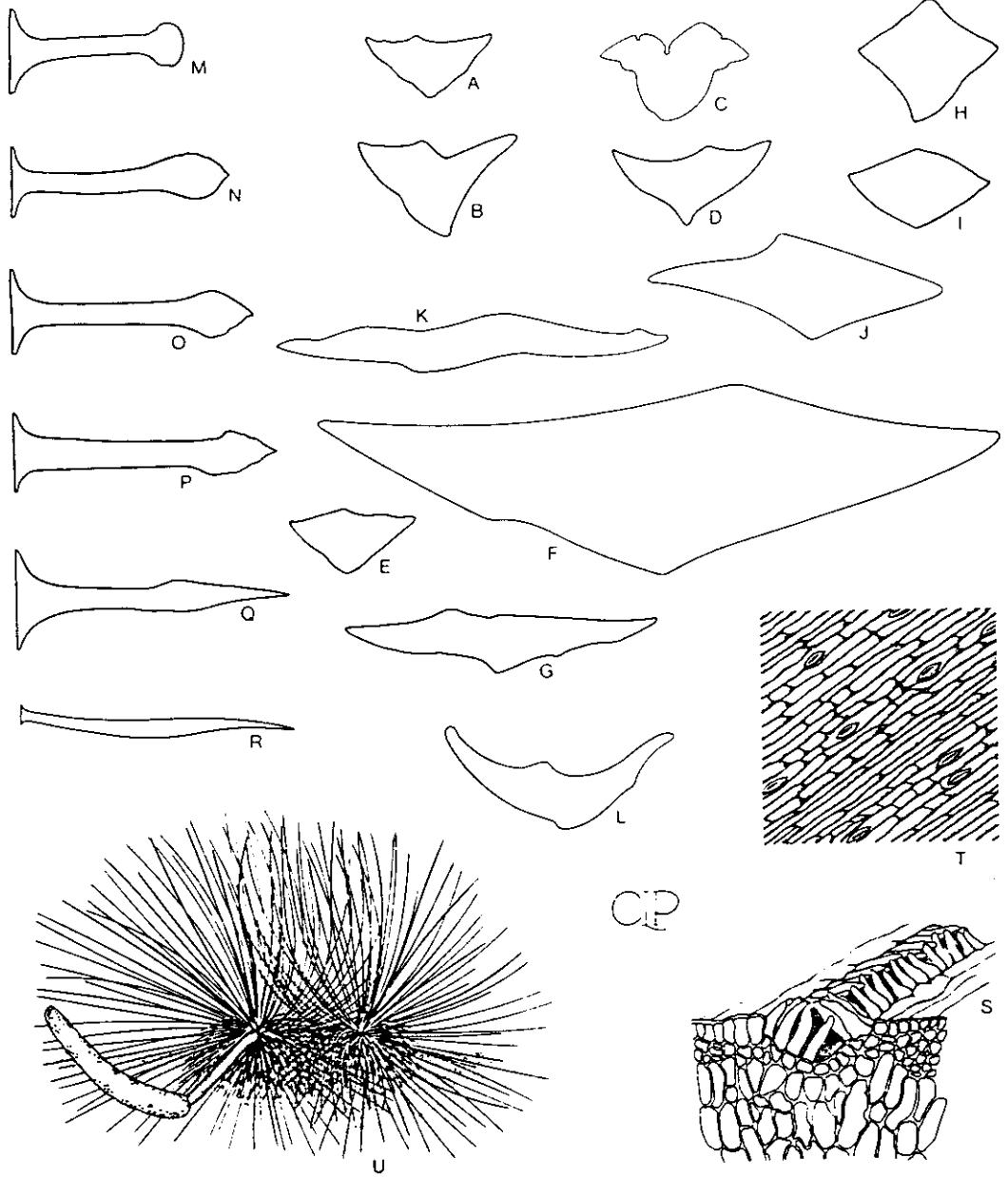
Figure 5.3 Xanthorrhoea bract and floral characters, and habit of X. resinifera. (From Bedford, 1986 a).

Xanthorrhoea. A–G, *X. fulva*. A–B, sepals ×5; C–D, packing bracts ×5; E, surface view of spike ×10; F–G, petals ×5 (E.Constable NSW 6166, NSW). H–K, *X. bracteata*. H–I, packing bracts ×5; J, sepal ×5; K, cluster bract ×5 (R.Brown *Iter Australiense* 5772, BM). L–Q, *X. arborea*. L–M, packing bracts ×5; N–O, sepals ×5; P–Q, petals, showing strongly recurved distal portion, ×5 (L.Johnson NSW 61355, NSW). R–S, *X. australis*, sepals (k, beak, p, proboscis) ×5 (D.Martin NSW 673567, NSW). T, *X. resinifera* habit (a, spike, b, scape) ×0.02 (Sydney, photo D.Bedford).

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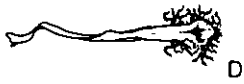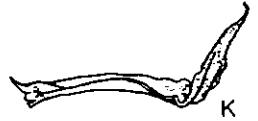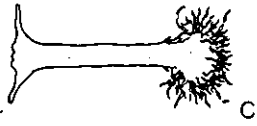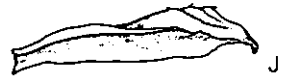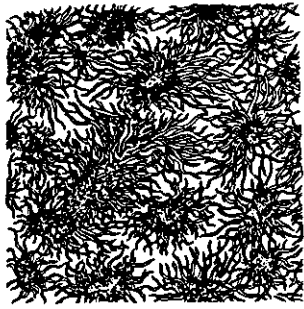
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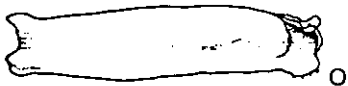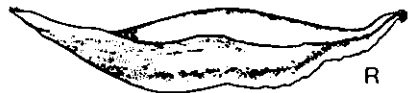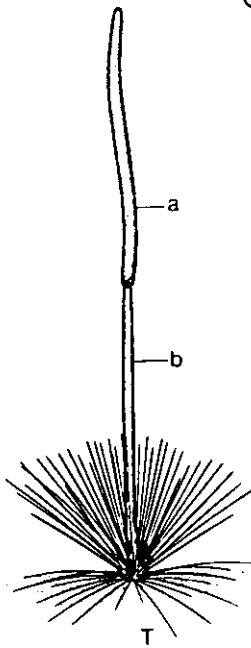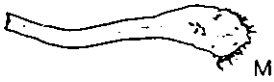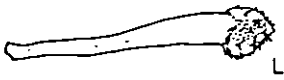
Figure 5.4 Xanthorrhoea bract, floral and spike characters
(From Bedford, 1986 a).

Xanthorrhoea. A–B, *X. drummondii*, packing-bracts ×5 (D.Bedford 41 &
T.Macfarlane, NSW). C–D, *X. preissii*, packing-bracts ×5 (L.Preiss 1620, MEL). E–F, *X.
nana*, packing-bracts ×5 (K.Allan 815, PERTH). G–L, *X. acanthostachya*. G, small
cluster-bract of aborted ·floral cluster ×5; H–I, packing-bracts ×5; J, sepal ×5; K–L,
petals (p, proboscis) ×5 (G–L, T.Macfarlane 659, PERTH). M, *X. preissii*, surface view
of spike showing bract apices ×10 (L.Preiss 1620, MEL). N–O, *X. drummondii*, surface
view of spikes showing variation in hairiness of bract apices ×10 (N, D.Bedford 59 &
T.Macfarlane, NSW; O, D.Bedford 41 & T.Macfarlane, NSW).

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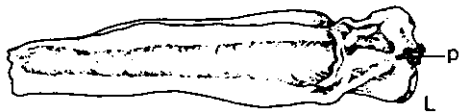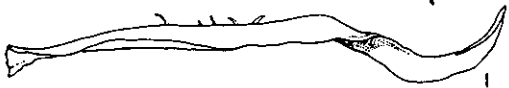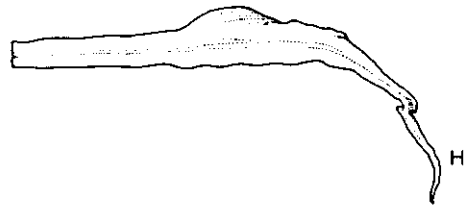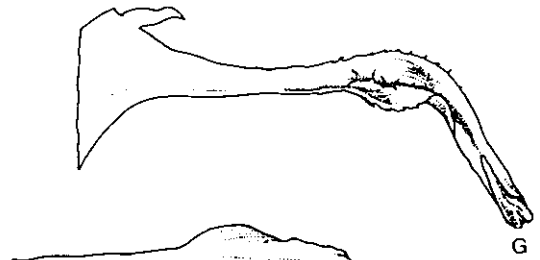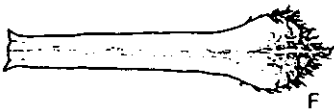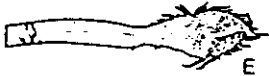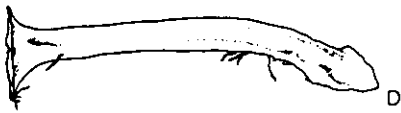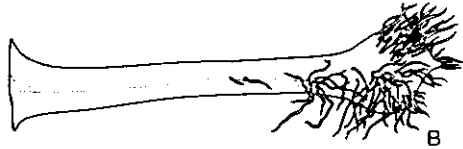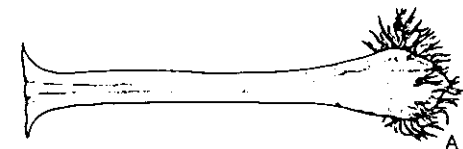
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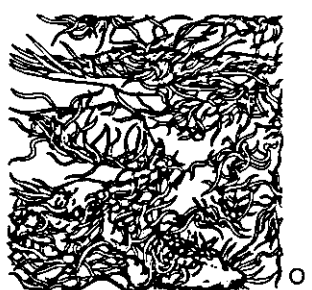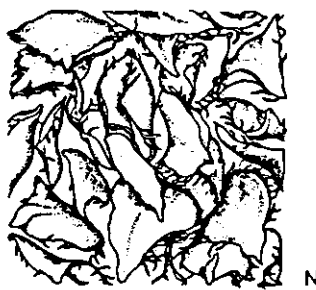
beak or apex, it is always hirsute with papillose hairs. The proboscis is variable and occurs only on some of the sepals and/or petals of some species.

Crown shape is variable but is nonetheless a distinctive feature of some species. Leaf shape in T.S. - both width and thickness - are taken at the mid-point along the length of the leaf. Leaf shape terms (Figure 5.2, A-L) are from the Systematics Association Committee for Descriptive Biological Terminology, chart 1a, (1962). Scape diameter is measured just below the spike, and spike diameter is measured at the surface of the bracts at the widest point of the spike.

The shape of the leaf-base is characteristic in some species but this part of the leaf has been insufficiently collected for reliable descriptions to be provided. Capsule shape is also sometimes characteristic, but it varies during development and must be used with caution. In this treatment the only fruiting character noted is the upward-curved capsule typical of some species.

Particularly variable characters are trunk height, leaf dimensions, and scape and spike length (occasionally also the proportion). Field observation and glasshouse experiments indicate that much of this variation is environmental.

Xanthorrhoeas can rarely be identified on one or two characters alone; usually a combination of many characters is required for critical determination. As most species occur in well-defined regions, locality of collection is often a useful aid to identification. The key below is designed especially for use in the field and with fresh

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material, relying in part on characters such as trunk height, ratio of length of scape to length of flowering spike, and leaf colour. When collecting Xanthorrhoeas for later study these data should be recorded and kept with the specimens.

5.6 Key to species

1 Scape 8 or more times as long as spike;
   flowering spike broad and brush-like from
   the very long erect filaments; stomates in
   linear, subsurface, hair-lined chambers
   (Figure 5.2, S)
     2 Packing-bracts glabrous (eastern
       Australia) .... 1. <u>X. macronema</u>
     2: Packing-bracts hirsute (W.A) .... 2. <u>X. gracilis</u>
1: Scape 5 or less times as long as spike;
   flowering spike ± cylindrical, the
   filaments short and erect or, if longer,
   recurved; stomates at leaf surface or if
   sunken, then each in a pit (Figure 5.2, T)
     3 Spike longer than scape
      4 Packing-bracts subulate, glabrous
       5 Leaves 5-12 mm wide .... 28. <u>X. semiplana</u>
       5: Leaves 1.2-3 mm wide
         6 Spike only slightly longer than
          scape (W.A.) .... 26. <u>X. acanthostachya</u>
         6: Spike usually much longer than
          scape (eastern Australia) .... 27. <u>X. australis</u>
      4: Packing-bracts shortly acute to

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triangular, glabrous to hirsute or

fringed with hairs

7   Cluster-bracts obscure or almost so

 8   Leaves 4-8 mm wide

    9   Trunk to 60 cm long (W.A.) .... 15. X. platyphylla

    9: Trunk usually 2-6 m long

        N.S.W.) .... 24. X. malacophylla

 8: Leaves usually less than 4 mm

    wide

    10   Leaves grey-green, glaucous;

         bracts dark brown; hirsute .... 14. X. drummondii

    10: Leaves green, not glaucous;

         bracts green or dark brown,

         glabrous to moderately hirsute

        11   Spike 2 or more times length

             of scape; bracts green,

             glabrous to subglabrous (W.A.) .... 16. X. preissii

        11: Spike less than 2 times length

             of scape; bracts dark brown,

             glabrous to moderately hirsute

             (eastern mainland Australia) .... 19. X. media

7: Cluster-bracts prominent for at least

   part of spike

   12   Leaves blue-green or grayish,

        glaucous

       13   Cluster-bracts prominent for most

            or all of mature spike length;

            packing-bracts dark-brown (eastern

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Australia) .... 25. <u>X. glauca</u>

13: Cluster-bracts prominent only at

base of mature spike; packing-

bracts light-brown (central

Australia & inland W.A.) .... 22. <u>X. thorntonii</u>

12: Leaves green, not glaucous

14 Scape diam. 20-30 mm; leaves

soft and spongy to the

touch .... 24. <u>X. malacophylla</u>

14: Scape diam. 20 mm or less

leaves tough, hard to the touch

15 Trunk usually none, sometimes

to 30 cm long; crown ±

hemispherical (N.S.W., Hunter

R. to Sydney region) .... 19. <u>X. media</u>

15: Trunk usually longer than 30

cm; crown with young leaves in

spreading upright tuft and old

leaves usually strongly reflexed

over trunk (Qld, & N.S.W. north of

Hunter R.) .... 23. <u>X. almae</u>

3: Spike shorter than or equal to scape

16 Packing-bracts narrowly triangular to

subulate

17 Packing-bracts fringed with hairs to

moderately hirsute .... 12. <u>X. caespitosa</u>

17: Packing-bracts glabrous or subglabrous

18 Plants without trunk; leaves

depressed-obtrullate to depressed

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-cuneate in T.S. (Tas.) .... 9. <u>X. arenaria</u>

18: Plants with trunk; leaves quadrate-

rhombic in T.S. (W.A.) .... 24. <u>X. acanthostachya</u>

16: Packing-bracts obtuse to triangular

19 Packing-bracts densely hirsute on

abaxial surface, appearing velvety

20 Leaves transverse-rhombic in T.S.;

spike dark-brown velvety at

flowering .... 5. <u>X. resinifera</u>

20: Leaves depressed-obtrullate to

concave in T.S.; spike cream to ±

light brown velvety at flowering

21 Leaves very depressed-cuneate to

concave in T.S., 3-6 mm wide, 1.5-

2 mm thick (N.S.W., Sydney & south-

wards) .... 3. <u>X. concava</u>

21: Leaves depressed-obtrullate to

depressed-cuneate in T.S., 1.9-

3.5 mm wide, 1-1.5 mm thick (Qld,

& N.S.W. north of Wyong) .... 4. <u>X. fulva</u>

19: Packing-bracts glabrous to hirsute or

fringed with hairs but not velvety

22 Scape and spike together usually

less than 90 cm long

23 Scape and spike distinctly curved;

spike often at ± 90° to scape

(W.A.) .... 13. <u>X. nana</u>

23: Scape emerging from crown ±

vertically; spike and scape ±

straight

24 Leaves quadrate-rhombic in

T.S. (S.A.) .... 17. <u>X. quadrangulata</u>

24: Leaves ranging from transverse-

rhombic, depressed-obtrullate

to very depressed-cuneate or

transverse-linear in T.S.

25 Cluster-bracts prominent on spike

26 Packing-bracts triangular to

narrowly triangular

(Tas.) .... 11. <u>X. bracteata</u>

26: Packing-bracts shortly acute

to acute

27 Leaves depressed-cuneate in

T.S., often concave, green, not

glaucous; cluster-bracts shortly

acute to triangular (eastern

mainland Australia) .... 10. <u>X. minor</u>

27: Leaves transverse-rhombic or

depressed-obtrullate in T.S.,

rarely depressed-cuneate,

grayish, glaucous; cluster-bracts

narrowly triangular to

subulate .... 8. <u>X. acaulis</u>

25: Cluster-bracts obscure or

restricted to junction of scape

and spike

28 Crown-leaves broadly spreading

or recurved (Qld.) .... 18. <u>X. pumilio</u>

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28: Crown an erect tuft of

    leaves (W.A. & SE Australia)

      29 Scape and spike together

         usually more than 80 cm

         long (W.A.) .... 6. X. brunonis

      29: Scape and spike together

         usually less than 75 cm

         long (eastern mainland

         Australia) .... 10. X. minor

22: Scape and spike together usually 90 cm or

  more long

    30 Cluster-bracts usually prominent at least in

      some part of spike

      31 Leaves usually more than 2.5 mm wide, soft

        and spongy; plant of moist

        habitats .... 24. X. malacophylla

      31: Leaves usually 2.5 mm wide or less, tough

        and hard; plant of dry sclerophyll forest

        and heath .... 23. X.almae

    30: Cluster-bracts obscure or restricted to

      junction of scape and spike

      32 Leaves usually $\pm$ quadrate-rhombic to

        transverse-rhombic in T.S., less than

        3 mm wide

      33 Trunk none or to 30 cm long; crown $\pm$

        hemispherical (N.S.W., Sydney region and

        adjacent areas S of the Hunter R.) ...... 19. X. media

      33: Trunk 10 cm to 5 m long; crown with young

        leaves in spreading upright tuft, old leaves

usually strongly reflexed over trunk (Qld &

N.S.W. north of the Hunter R.) .... 23. X. almae

32: Leaves narrowly transverse-rhombic, depressed

obtrullate, depressed-cuneate to transverse-linear

or concave in T.S., 1.7-10 mm wide

34 Leaves blue-green .... 7. X. brevistyla

34: Leaves green

35 Spike usually greater than 1/2 as

long as scape in length .... 21. X. arborea

35: Spike usually less than 1/2 or as

long as scape

36 Leaves usually more than 4 mm

wide; spike 30-150 cm

long .... 20. X. latifolia

36: Leaves usually less than 4 mm

wide; spike usually 5-40 cm long

37 Spike 20-40 mm diam.; petals

without proboscis

(W.A.) .... 6. X. brunonis

37: Spike 14-23 mm diam; petals

with proboscis (Qld) .... 18. X. pumilio

5.7 Species Descriptions

1. Xanthorrhoea macronema F. Muell. ex Benth., Fl. Austral. 7: 113 (1878).

T: Hastings R., N.S.W., H. Beckler s.n.; lecto: K n.v., fide A.T. Lee Contr. New South Wales Natl Herb. 4: 54 (1966 a); isolecto: MEL.

Trunk none; stem sometimes branched below ground; crowns 1 to many, in a loosely upright or reflexed tuft. Leaves obtrullate, irregularly rounded depressed-cuneate or concave in T.S., usually 2.3-3.5 mm wide, 1.2-1.8 mm thick, light to dark green, not glaucous. Scape 100-160 cm long, 4-5 mm diam. Spike 0.1-0.05 times as long as scape, 5-13 cm long, 14-20 mm diam. Cluster-bracts obscure. Packing-bracts shortly acute to acute, glabrous. Sepals acute, beaked, without proboscis, glabrous. Petals large and prominent, erect, with proboscis, glabrous except for very few hairs at apex.

Occurs in Qld and N.S.W. from Fraser Is. to the Sydney region, on coastal sand and ranges. Flowers July-Jan. Map 1, Figure 5.5.

Qld: Stradbroke Is., Moreton Bay, J.B. Cleland NSW 56765 (NSW). N.S.W.: Mayers Hill, Boolambayte, Myall Lakes, E.F. Constable NSW 23594 (NSW); Tanilba, Port Stephens, H. van Rees 182 (MEL).

A distinctive Xanthorrhoea in its habit, with long thin scape and short brush-like spike, large cream to yellow flowers and staminal filaments (Figure 5.6), long-pointed fruit with persistent styles and rounded glossy seed. Leaves longer (1-2 m) and more flexible than in

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Figure 5.5 Distribution maps:

1. <u>X. macronema</u>

2. <u>X. gracilis</u>

3. <u>X. concava</u>

4. <u>X. fulva</u>

5. <u>X. resinifera</u>

6. <u>X. brunonis</u> subsp. <u>brunonis</u>

1 2 3

4 5 6

Figure 5.6 X. macronema inflorescence. Nullum State Forest, northern
New South Wales, April 1975, D.J. Bedford P75M6, (SYD).
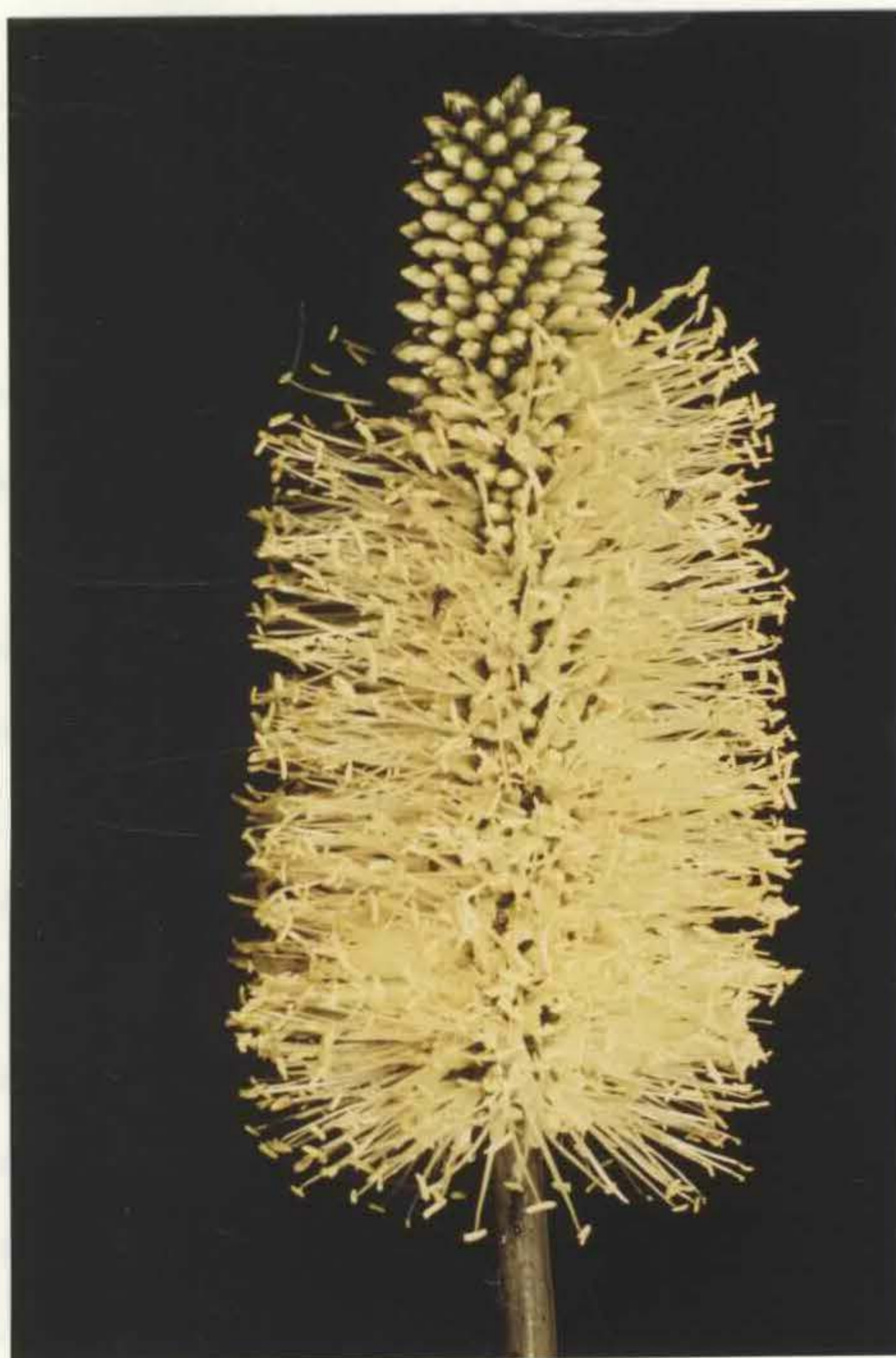
most species, with stomates in subsurface hair-lined chambers rather than singly as all other species except X. gracilis (Figure 5.2, S).

A close relative of X. gracilis from W.A. The name was not validly published by Mueller in Fragm. 4 112 (1864) where alternative ranks were cited.

2. Xanthorrhoea gracilis Endl. in J.G.C. Lehmann, Pl. Preiss 2: 39 (1846).

T: Darling Range, Perth, W.A., 16 Jan. 1840, L. Preiss 1619; lecto: MEL 625759, fide D. Bedford, Fl. Australia 46: 227 (1986).

Trunk none; stems branched underground; crowns 1 to many, each a loosely upright to decumbent tuft. Leaves irregularly rounded depressed-obtrullate to depressed-cuneate in T.S., usually c. 3 mm wide and 1.4-1.6 mm thick, green, not glaucous, hairy at base. Scape c. 150 cm long, c. 5 mm diam., hairy at base, glaucous above. Spike 0.1-0.05 times as long as scape, c. 11 cm long and 13-14 mm diam. Cluster-bracts obscure. Packing-bracts shortly acute, hirsute, dark brown. Sepals shortly acute, with very short beak, without proboscis, hirsute. Petals large and prominent, recurved, with proboscis, glabrous except short hairs at apex.

Occurs in south-western W.A., south of the Avon R. and as far east as Albany, in sandy soil with laterite, often in Jarrah forest. Flowers (Sept.) Oct.-Jan. Map 2, Figure 5.5.

W.A.: Yarloop, between Bunbury and Pinjarra, H. Eichler 16153 (AD); c. 1.6 km N. of North Dandalup, B.G. Briggs NSW 87522 (NSW); East Jarrahdale, D.J. Bedford 2 & T.D. Macfarlane (NSW); Collie, A.R. Fairall 742 (PERTH); Harvey Dam Reserve, T.D. Macfarlane 658 (PERTH).

A close relative of X. macronema from eastern Australia, from which it is distinguished by the long hairs on leaf-bases, proximal portions of leaves and on base of scape, the usually distally glaucous scape, the dark-brown hirsute packing-bracts and sepals, and the dorsiventrally flattened seeds.

3. Xanthorrhoea concava (A. Lee) Bedford, Fl. Australia 46: 226 (1986).

X. resinosa subsp. concava A. Lee, Contr. New South Wales Natl Herb. 4: 45 (1966 a). T: 1 mile [c. 1.6 km] W of Buxton, N.S.W., 5. Dec. 1960, A.T. Lee NSW 61300; holo: NSW.

Illustration: A.T. Lee, Contr. New South Wales Natl. Herb., Fl. Ser. 34: 5 (1966 b) as X. resinosa subsp. concava.

Trunk none; stem branched below ground; crowns 1 to many, each a loosely erect tuft. Leaves very depressed-cuneate to concave in T.S., 3-6 mm wide, 1.5-2 mm thick, blue-green, glaucous. Scape 50-250 cm long, c. 10 mm diam. Spike c. 1/2 as long as scape, 50-90 cm long, 15-30 mm diam. Cluster-bracts obscure, or prominent only at base of spike, shortly acute, densely hirsute. Packing -bracts shortly acute, densely hirsute with pale hairs. Sepals shortly acute, with beak,

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without proboscis, densely hirsute with pale hairs.   Petals reflexed, with proboscis, glabrous except a terminal tuft of short hairs. Figure 5.2, L.

Occurs in N.S.W. from Sydney as far south as Eden on the coast and tablelands, often growing in seasonally waterlogged sites. Flowers Oct.-Dec. Map 3, Figure 5.5.

N.S.W.: Treble Mtn. N. of Cobargo, <u>E.F. Constable 5481</u> (NSW); Mogo State Forest, SSW. of Batemans Bay, 12 Dec. 1961, <u>A.T. Lee</u> (NSW); Windellama, SE of Goulburn, <u>B.G. Briggs NSW 61298</u> (NSW); Mittagong, 30 Nov. 1919, <u>J.B. Cleland</u> (AD).

The spike appears distinctly velvety light brown from the long pale hairs on the packing-bracts and sepals.

4. <u>Xanthorrhoea fulva</u> (A. Lee) Bedford, <u>Fl. Australia</u> 46: 226 (1986).

<u>X. resinosa</u> subsp. <u>fulva</u> A. Lee, <u>Contr. New South Wales Natl. Herb.</u> 4: 45 (1966 a).   T: Coffs Harbour, N.S.W., 17 Oct. 1961, <u>E.F. Constable</u> <u>NSW 61664</u>; holo: NSW.

Illustration: A.T. Lee, <u>Contr. New South Wales Natl. Herb., Fl. Ser.</u> 34: 5 (1966 b) as <u>X. resinosa</u> subsp. <u>fulva</u> (incorrect leaf habit shown).

Trunk none; stem branched below ground; crowns 1 to many, each a stiff erect tuft.   Leaves depressed to very depressed-obtrullate to

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depressed-cuneate in T.S., 1.9-3.5 mm wide, 1-1.5 mm thick, usually ± blue-green, glaucous. Scape 20-160 cm long, 5-20 mm diam. Spike 1/3-1/2 as long as scape, 10-60 cm long, 10-30 mm diam. Cluster-bracts obscure or slightly prominent, shortly acute, densely hirsute. Packing-bracts obtuse, densely hirsute with pale hairs. Sepals shortly acute, without or with very short beak, without proboscis, hirsute. Petals slightly reflexed, with beak at tip, glabrous except for a few hairs near beak. Figures 5.2, A, E, M, 5.3, A-G, 5.7.

Occurs in coastal areas from Rockhampton, Qld, to Wyong, N.S.W.; grows in periodically waterlogged sites in sand. Flowers Aug.-Oct. Map 4, Figure 5.5.

Qld: Cooloola, C. Sandercoe C504 (NSW). N.S.W.: Corindi-Red Rock road, 18 Sept. 1961, E.F. Constable (NSW); Lake Cathie, c. 8 km NNE of Kew, E.F. Constable 4795 (AD, NSW); N of Booti Booti, 13 Oct. 1953, L.A.S. Johnson (NSW); between Grassy Hill and Putty, c. 10.8 km from Singleton, 10 Feb. 1966, A. Lee (NSW).

This species is known to hybridise with X. almae in Qld and with X. glauca in N.S.W., the progeny sometimes resembling X. resinifera. It is usually recognizable in the field by its velvety cream to beige coloured flowering spikes, from the pale hairs on the packing-bracts (Figure 5.7). It exhibits great variability of inflorescence size; in small plants (young or in poor growing conditions) the inflorescences may be only 22 cm tall and very slender, while older plants in good growing conditions may have stout inflorescences 2.5 m tall.

Figure 5.7 <u>X. fulva</u>, close-up of spike, showing the tawny colour from which the species is named. Beerwah Scientific Purposes Area, Queensland, Sept. 1976, <u>D.J. Bedford P76M2</u>, (SYD).
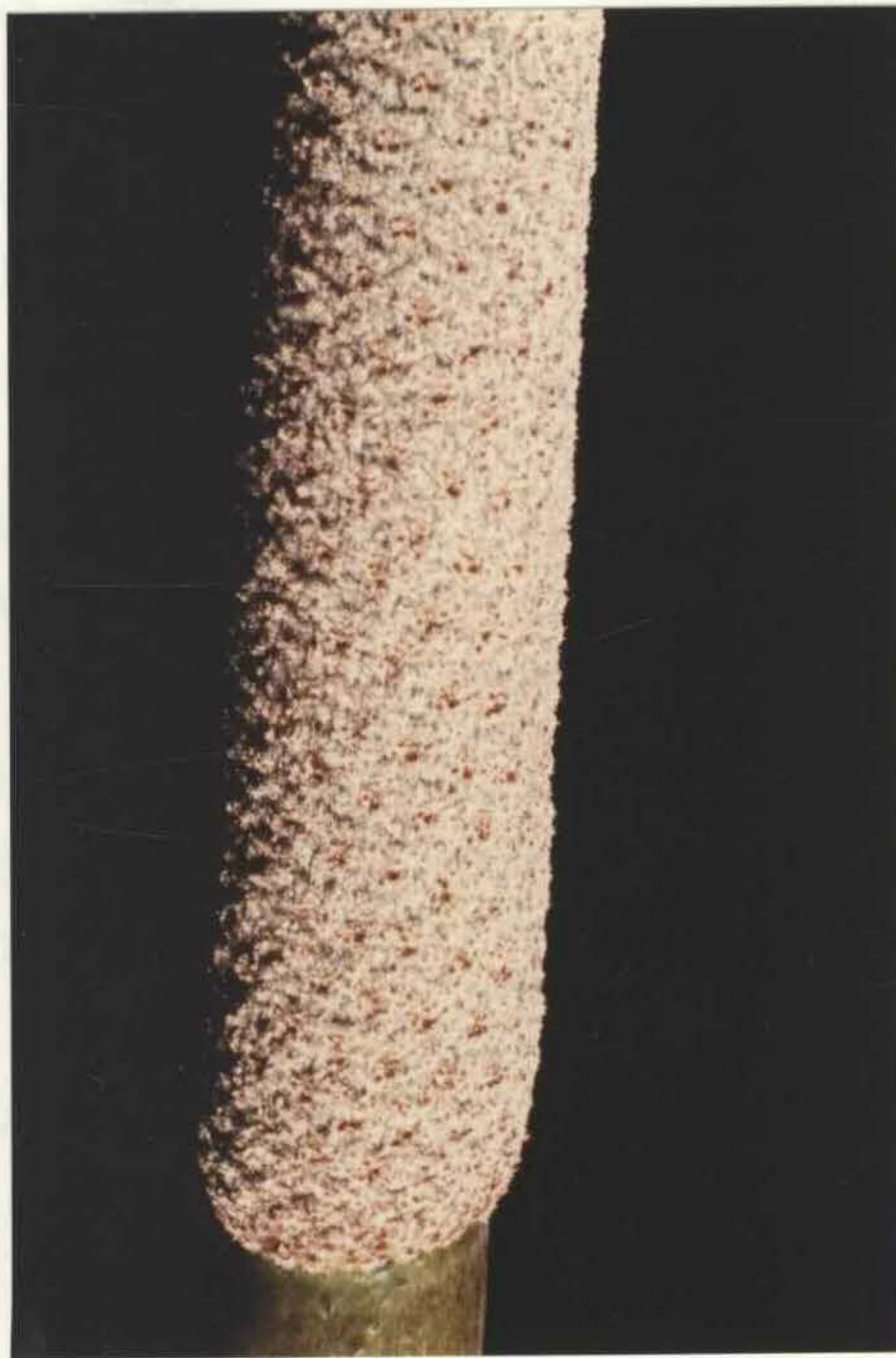
5. Xanthorrhoea resinifera (Kite) Nelson (in press)

basionym: Acoroides resinifera Kite, Essays and observations ... and on the resin of Acoroides resinifera, or yellow gum of Botany Bay 141-210, (1795).

Lectotype described in A. Phillip, The voyage of Governor Phillip to Botany Bay... 60, (1789).

Syn. Xanthorrhoea hastile J.E. Smith ex Dryander, Cat. bibl. Banks, 3: 486, (1797); Dryander, Ann. Bot. 2: 517 (1806); R. Brown, Prodr. : 288, (1810).

X. resinosa auct. Naturalists Pocket Magazine 1, (1798); Persoon, Syn. Pl. 1: 370 (1805).

[X. arborea auct. non R.Br.: C. Moore & E. Betche, Handb. Fl. New South Wales 425 (1895); J.H. Maiden & E. Betche, Census New South Wales Pl. 42 (1916)]

Illustration: A.T.Lee, Contr. New South Wales Natl. Herb. Fl. Ser. 34: 5 (1966 b) (as X. resinosa).

Trunk none or to 60 cm long; stem usually simple; young leaves in a stiff ± erect spreading tuft. Leaves transverse-rhombic in T.S., 2-4 mm wide, 1.5-2.5 mm thick, blue-green, glaucous. Scape 70-150 cm long, rarely to 220 cm, 10-30 mm diam. Spike ± as long as scape, sometimes shorter than scape, 60-120 cm long, 20-45 mm diam. Cluster-bracts obscure or prominent only at base of spike, shortly

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acute, densely hirsute. Packing-bracts shortly acute, densely hirsute, dark brown. Sepals shortly acute, without beak or proboscis, hirsute. Petals erect or slightly reflexed, sometimes with proboscis, at least one petal in each flower abaxially hirsute on mid-vein and apex. Figures 5.3, T, 5.8.

Occurs in the Blue Mountains and coastal areas of N.S.W. from Sydney, to eastern Vic., growing in sandy soils and on sandstone, usually in seasonally wet sites. Flowers Aug.-Oct. Map 5, Figure 5.5.

N.S.W.: Point Perpendicular, L.A.S. Johnson 1031 (NSW); Blackheath Aerodrome, 29 Nov. 1961, E.F. Constable (AD, NSW); La Perouse, Oct. 1897, E. Betche (NSW). Vic: Mallacoota, Wingan, A.C. Beauglehole 31091 (MEL); Cape Everard, 8 Feb. 1961, A. Dyce (NSW).

The spikes are distinctively dark brown and velvety at flowering from the densely hairy, dark brown packing-bracts (Figure 5.8). Typical specimens have the spike about as long as the scape; some southern specimens, which have a more slender spike much shorter than the scape, may be subspecifically distinct.

6. Xanthorrhoea brunonis Endl. in J.G.C. Lehmann, Pl. Preiss. 2: 39 (1846).

T: near the Swan River, W.A., 20 Nov. 1839, L. Preiss 1621; lecto: MEL 625771, fide D. Bedford, Fl. Australia 46: 225 (1986).

Trunk none or up to 10 cm long; stem branched below ground; crowns 1

Figure 5.8 X. resinifera, close-up of spike showing the distinctive velvety-brown appearance prior to flowering.   Kurnell, Sydney, New South Wales, July 1976, D.J. Bedford, P76M12, (SYD).
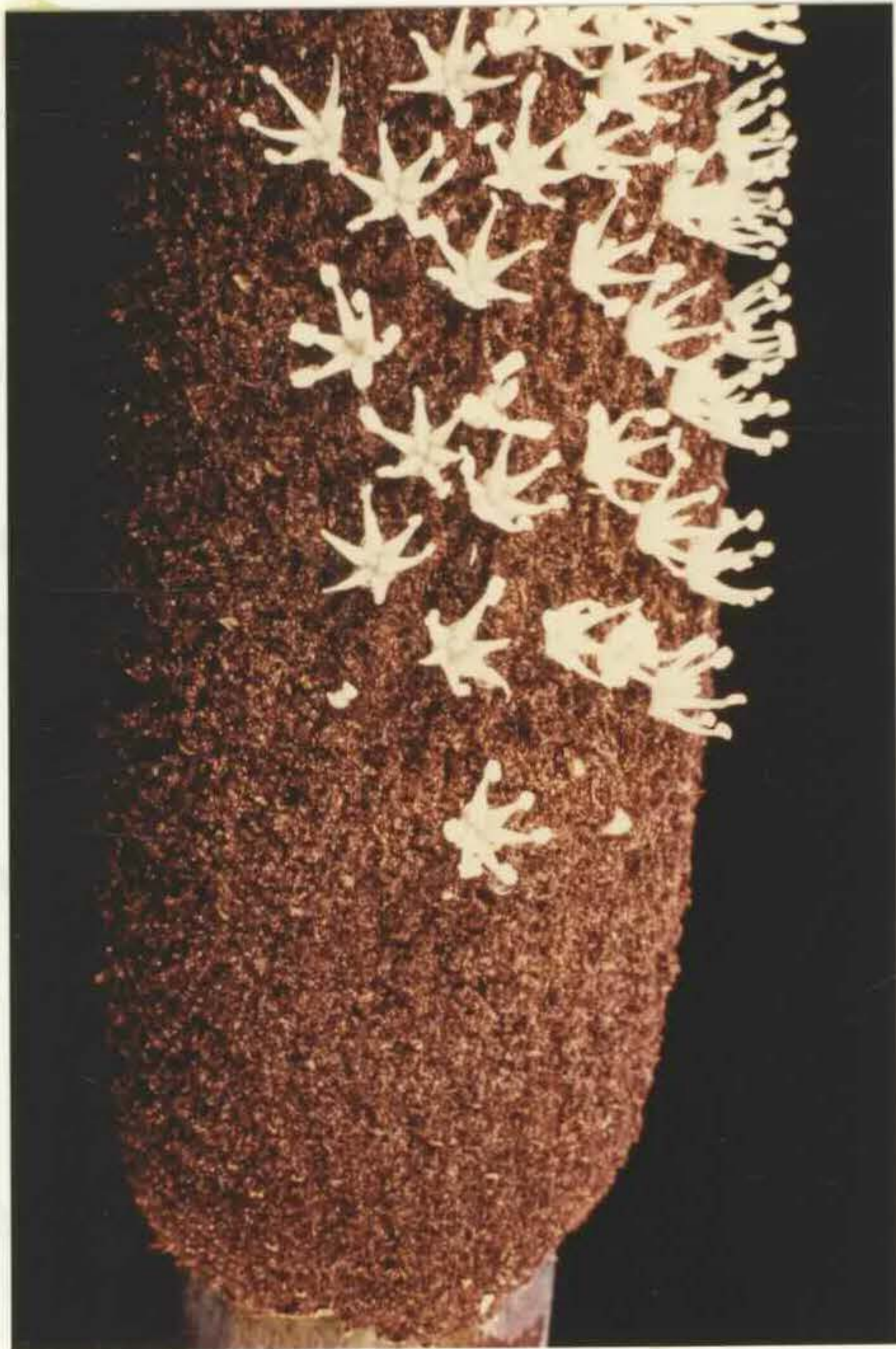
to many, each an erect tuft. Leaves narrowly transverse-rhombic to depressed-cuneate in T.S., 1.7-4 mm wide, 1-2.3 mm thick, green, not glaucous. Scape 35-150 cm long, 5-20 mm diam. Spike 1/3-1/2 as long as scape, 10-30 cm long, 20-40 mm diam. Cluster-bracts obscure or restricted to junction of scape and spike, shortly acute to narrowly triangular, glabrous. Packing-bracts shortly acute to acute, glabrous to fringed with hairs. Sepals acute, beaked, sometimes with distinct abaxial median ridge, without proboscis, glabrous. Petals ± erect to reflexed, without proboscis, glabrous except a tuft of hairs at apex.

Occurs on the coastal plain from Perth region southwards as far as Albany, W.A., in sand. There are 2 subspecies.

Packing-bract apex margin glabrous and abaxial surface glabrous and shiny, so that bracts appear glabrous at spike surface   a. subsp. brunonis

Packing-bract apex margin and abaxial surface fringed with hairs, so that bracts appear hairy at spike surface   b. subsp. semibarbata

6a. Xanthorrhoea brunonis Endl. subsp. brunonis.

Leaves 3-4 mm wide, c. 2 mm thick. Scape 70-90 cm long, 5-20 mm diam. Spike 10-30 cm long, 20-40 mm diam. Packing-bracts shortly acute to acute; margin below apex subglabrous to fringed with hairs, margin and abaxial surface of apex glabrous and shiny.

Common on the coastal plain around Perth and southwards, W.A. Flowers

Oct.-Nov. Map 6, Figure 5.5.

W.A.: Bruce St,(opposite Como High School) South Perth, <u>D.J. Bedford</u> <u>102 & T.D. Macfarlane</u> (NSW, PERTH); Harvey R., <u>F. Mueller</u> (MEL 625782); near Wilson Inlet, Denmark-Albany road, <u>D. Bedford 23 & T.D.</u> <u>Macfarlane</u> (NSW, PERTH).

6b. <u>Xanthorrhoea brunonis</u> subsp. <u>semibarbata</u> Bedford, <u>Fl. Australia</u> 46: 225 (1986).

T: Poad Road, S. of Dardanup, W.A., 24 Nov. 1982, <u>D.J. Bedford & T.D.</u> <u>Macfarlane</u>; holo: NSW: iso: PERTH.

Leaves 1.7-3.5 mm wide, 1-2.3 mm thick. Scape 80-150 cm long, 10-17 mm diam. Spike 30-50 cm long, 25-40 mm diam. Packing-bracts acute, occasionally subglabrous, more often fringed with hairs on apex and margin.

Occurs on coastal sand slightly N and S of Perth as far as Albany, W.A. Flowers Oct.-Dec. Map 1, Figure 5.9.

W.A.: North Dandalup, <u>D.J. Bedford 5 & T.D. Macfarlane</u> (NSW, PERTH); Edgewater Road, Canning R. foreshore, Perth, <u>M.L. Clark 161</u> (PERTH); 1.6 km N. of Boyanup, along South Western Hwy, <u>V. Mann 61 & A.S.</u> <u>George</u> (NSW, PERTH).

Figure 5.9 Species distributions:

1. _X. brunonis_ subsp. _semibarbata_

2. _X. brevistyla_

3. _X. acaulis_

4. _X. arenaria_

5. _X. minor_ subsp. _minor_

6. _X. minor_ subsp. _lutea_

7. <u>Xanthorrhoea</u> <u>brevistyla</u> D. Herbert, <u>J. & Proc. Roy. Soc. W.</u>
<u>Australia</u> 7: 82 (1921).

T: Narrogin State Farm, W.A., 13 Nov. 1920, <u>D.A. Herbert s.n.</u>; lecto:
PERTH, <u>fide</u> D. Bedford, <u>Fl. Australia</u> 46: 225 (1986); isolecto: MEL.

Trunk usually none, rarely to 5 cm long; stem often branched below
ground; crowns 1 to many, each a ± erect tuft. Leaves
depressed-obtrullate to depressed-cuneate in T.S., sometimes concave,
3.2-4.4 mm wide, c. 1.8 mm thick, blue-green, very glaucous. Scape
80-125 cm long, 10-24 mm diam. Spike c. 1/3-1/2 as long as scape,
rarely equal to scape, 24-96 cm long, 22-42 mm diam. Cluster-bracts
obscure or very slightly prominent, acute to triangular, sparsely
hairy. Packing-bracts shortly acute to acute, subglabrous to hirsute.
Sepals triangular, beaked, without proboscis, glabrous. Petals
recurved, with proboscis, glabrous except for short hairs adaxially at
apex. Figure 5.10.

Occurs from Narrogin to Cranbrook, W.A. Flowers Oct.-Dec. Map 2,
Figure 5.9.

W.A.: Narrogin, <u>D. Bedford 51 & T.D. Macfarlane</u> (NSW, PERTH);
Williams-Narrogin area, <u>T.D. Macfarlane 743</u> (PERTH); 21 km E of
Narrogin on road to Toolibin, <u>D. Bedford 49 & T.D. Macfarlane</u> (NSW,
PERTH); 14.6 km S of Woodanilling on Great Southern Hwy, <u>D. Bedford 38</u>
<u>& T.D. Macfarlane</u> (NSW, PERTH).

This species includes considerable variation in bract hairiness, which
may indicate some unresolved taxonomic problems. The specific epithet

Figure 5.10 X. brevistyla, habit. Narrogin, Western Australia Dec. 1982, D.J. Bedford 50 and T.D. Macfarlane, (NSW and PERTH).

is misleading, as style length is neither a distinguishing nor a constant feature.

8. <u>Xanthorrhoea acaulis</u> (A. Lee) Bedford, <u>Fl. Australia</u> 46: 225 (1986).

<u>X. australis</u> subsp. <u>acaulis</u> A. Lee, <u>Contr. New South Wales Natl. Herb.</u> 4: 53 (1966 a). T: 6.5 miles [10.5 km] W of Dubbo on Minore Road, N.S.W., 9 Dec. 1961, <u>E.F. Constable NSW 61344</u>; holo: NSW.

Illustration: A.T. Lee, <u>Contr. New South Wales Natl. Herb., Fl. Ser.</u> 34: 5 (1966 b) as <u>X. australis</u> subsp. <u>acaulis</u>.

Trunk none or rarely up to 30 cm long, branched below ground; crowns 1 to many, each a spreading tuft. Leaves transverse-rhombic or depressed-obtrullate in T.S., rarely depressed-cuneate, c. 1.8 mm wide, c. 1 mm thick, grayish, glaucous. Scape 25-45 cm long, 8-12 mm diam. Spike 0.2-0.75 times as long as scape, 10-25 cm long, 25-34 mm diam. Cluster-bracts prominent, rarely obscure, narrowly triangular to subulate, subglabrous. Packing-bracts acute, subglabrous. Sepals shortly acute, with median abaxial ridge, glabrous; beak usually very short, rarely to 0.9 mm long; proboscis often present. Petals ± erect to recurved, with proboscis, glabrous except hirsute margins and apex.

Occurs in N.S.W. to the west of the Great Divide, in the area bounded by Narrabri and Pilliga in the north and Grenfell in the south. Grows mainly in sandy soils. Flowers Nov.-Jan. Map 3, Figure 5.9.

N.S.W.: Narrabri, Nov. 1899, J.H. Maiden (NSW); Pilliga scrub, Nov. 1979, J. Ford (NSW, SYD); Gunnedah district, W. Forsyth NSW 56719 (NSW); near Coonabarabran, E. Wait NSW 82220 (NSW); 5-6.5 km SSE of Coonabarabran, H. Salasoo 2328 (NSW).

9. Xanthorrhoea arenaria Bedford, Fl. Australia 46: 225 (1986).

T: c. 5 km NW of Coles Bay township, Tas., 26 Jan. 1984, D. Bedford 124; holo: NSW.

Trunk none; stem usually branched below ground; crowns 1 to many, each an upright tuft. Leaves depressed-obtrullate to depressed-cuneate in T.S., 2-3 mm wide, 1-1.7 mm thick, sometimes slightly grayish, glaucous. Scape 20-60 cm long, 5-9 mm diam. Spike shorter than scape, occasionally equal to scape, 7-30 cm long, 18-24 mm diam. Cluster-bracts very prominent, elongated, subulate, glabrous. Packing-bracts subulate, glabrous. Sepals triangular to narrowly triangular, with very long beak, with proboscis, glabrous. Petals erect to slightly recurved, with proboscis, glabrous except papillose hairs at apex and on proboscis.

Occurs on the N and NE coast of Tas., usually in low-lying sandy areas. Flowers June-Jan. Map 4, Figure 5.9.

Tas.: E of Tamar R., M. Cameron (AD, HO); Tam O'Shanter Bay, W of Weymouth, M. Bennett NSW 72129 (NSW); South Croppies Point, Honeysett `B' NSW 77853 (NSW); 5 km from Cape Portland, E. Rodway NSW 61296 (NSW); NE coast of Tas., June 1951, G. Sharman (HO).

A.T. Lee, Contr. New South Wales Natl. Herb. 4: 54 (1966 a), regarded this taxon as representing a hybrid between X. minor and X. australis.

10. Xanthorrhoea minor R.Br., Prodr. 1: 288 (1810).

T: Port Jackson, N.S.W., 1803, R. Brown Iter Australiense 5773; lecto: BM, fide D. Bedford, Fl. Australia 46: 227 (1986).

Illustration: A.T. Lee, Contr. New South Wales Natl. Herb., Fl. Ser. 34: 5 (1966 b).

Trunk none; stem branched below ground; crowns many, each a ± erect tuft. Leaves depressed-cuneate, often concave in T.S., 1.9-3.5 mm wide, 1-1.5 mm thick, green, not glaucous. Scape 30-60 cm long, 3-8 mm diam. Spike 0.2-0.5 times as long as scape, 5-12 cm long, 7-20 mm diam. Cluster-bracts sometimes prominent, shortly acute to triangular, distal, 1/3 glabrous to sparsely fringed with hairs, proximally subglabrous to densely hairy. Packing-bracts shortly acute to acute, subglabrous to hirsute. Sepals shortly acute, beaked, sometimes with proboscis, glabrous to moderately hirsute. Petals recurved, sometimes with proboscis, glabrous except papillose hairs at apex. Figures 5.2, B, D.

Occurs in coast and tableland areas of N.S.W., Vic. and in south-eastern S.A. Depauperate plants of other species (e.g. X. media, X. fulva, X. pumilio) sometimes produce inflorescences with the dimensions of X. minor, and are thus mistaken for it. They are distinguished, however, by their leaf, bracts, and flower characters.

The fruit of X. minor are also often distinctively curved with the apices pointing upwards. There are 2 geographically separate subspecies with some overlap of characters.

Packing-bracts ± shortly acute, subglabrous to
fringed with hairs, abaxial surface glabrous;
petals white to cream (NSW)   a. subsp. minor

Packing-bracts ± acute, medium hairy on margins
and abaxial surface; petals yellow (Vic. & S.A)   b. subsp. lutea

10a. Xanthorrhoea minor R.Br. subsp. minor

Cluster-bracts usually prominent for at least part of spike. Packing-bracts ± shortly acute; margins usually fringed with hairs; abaxial surface usually glabrous. Petals broad, with proboscis, white to cream.

Occurs mainly in the central coast and tableland areas of N.S.W., in the area bounded by Gosford, Lithgow and Campbelltown; possibly also present in north and south coastal areas. Usually grows on poorly drained sites which are seasonally waterlogged, very often in clay soils. Flowers Oct.-Nov. Map 5, Figure 5.9.

N.S.W.: East Hills, H.S. McKee 789 (NSW); Agnes Banks, R. Coveny 8437, D. Benson & H. Bryant (NSW); Gladesville, H. Deane NSW 59870 (NSW); Glenbrook, W. Forsyth NSW 25003 (NSW); between Euroka clearing and Glenbrook, Lower Blue Mountains Natl. Park, D. Bedford 7949 (SYD).

There is some variability within this subspecies. Some plants (including the lectotype at BM) have quite hairy bracts, while other plants (such as a R. Brown collection at K) have less hairy, longer and more acute bracts.

10b. Xanthorrhoea minor subsp. lutea Bedford, Fl. Australia 46: 228 (1986).

T: 3 miles [c. 5 km] SSW of Nowa Nowa, Vic., 29 Oct. 1964, E.F. Constable 5341; holo: NSW.

Cluster-bracts sometimes prominent, often obscure. Packing-bracts ± acute, medium hairy on margins and abaxial surface. Petals very broad, sometimes with proboscis, yellow. Figure 5.11.

Occurs in Vic. from the N.S.W./Vic. border to Naracoorte in south-eastern S.A. Flowers Mar.-Apr. Map 6, Figure 5.9.

Vic.: Kiewa valley, J.R. Grig NSW 75660 (NSW); Park Orchards, North Ringwood, 18 Nov. 1969, O. McHaffie (MEL); Oakleigh, 11 Nov. 1893, A. Morrison (AD); near Bellbrae, c. 11.3 km N. of Anglesea, 31 Jan. 1965, L.A.S. Johnson (NSW).

Figure 5.11 <u>X. minor</u> subsp. <u>lutea</u>, habit. Between Millicent and Kingston, South Australia, Jan. 1985, <u>D.J. Bedford 117</u>, (NSW and AD).

11. <u>Xanthorrhoea bracteata</u> R.Br., <u>Prodr</u>. 288 (1810).

T: probably Port Dalrymple [George Town], Tas, <u>R. Brown Iter Australiense 5772</u>; holo: BM.

Trunk none, stem branched below ground; crowns 1 to many, each a ±
erect tuft.   Leaves ± very depressed-cuneate or very depressed-
-obtrullate in T.S., 2.2-2.8 mm wide, 1-1.5 mm thick; ?green and not
glaucous. Scape 30-50 cm long, 5-8 mm diam. Spike c. 1/3 as long as
scape, 10-18 cm long, 14-22 mm diam. Cluster-bracts prominent,
triangular to narrowly triangular, glabrous to very slightly
subglabrous.   Packing-bracts triangular to narrowly triangular,
glabrous to very slightly subglabrous.   Sepals triangular, beaked,
without proboscis, glabrous.   Petals reflexed, often without
proboscis, glabrous except papillose hairs at apex. Figure 5.3, H-K.

Occurs from Waterhouse in north-eastern Tas. south to Hobart, in
heathlands and low-lying sandy places.   Flowers Jan.-Feb. Map 1,
Figure 5.12.

Tas: near Clarence Point, West Tamar, 19 Mar. 1975, <u>D.I. Morris</u> (HO);
Badger Head Road, <u>D.I. Morris 79154</u> (AD, HO); c. 1 km W of Bridport,
<u>M. Bennett NSW 72396</u> (NSW); Bridport, Jan. 1948, <u>M. Hart</u> (BRI, HO);
Waterhouse, 1 Feb. 1961, <u>W.D. Jackson</u> (HO).

Although Brown stated that the type was collected at Port Jackson, all
later specimens which correspond with the type are from eastern Tas.
This strongly indicates that Brown collected the type from Port
Dalrymple, now George Town.

Figure 5.12 Species distributions:

1. <u>X. bracteata</u>

2. <u>X. caespitosa</u>

3. <u>X. nana</u>

4. <u>X. drummondii</u>

5. <u>X. platyphylla</u>

6. <u>X. preissii</u>

A.T. Lee, Contr. New South Wales Natl. Herb. 4: 46 (1966 a), reduced this taxon to synonymy with X. minor. It is very similar to the latter, but is morphologically and geographically distinct and worthy of specific rank.

12. Xanthorrhoea caespitosa Bedford, Fl. Australia 46: 226 (1986).

T: Meningie, S.A., 13 Nov. 1957, J.B. Cleland s.n.; holo: AD 966081326.

[X. australis auct. non R. Br.: J.M. Black, Fl. S. Australia 3rd edn, 1: 361 (1978)]

Trunk none; stem many-branched below ground; crowns many, each an uneven open tuft. Leaves very depressed-cuneate in T.S., sometimes concave above, 3.2-7 mm wide, 1-2 mm thick, grey, glaucous. Scape 90-120 cm long, 10-17.5 mm diam. Spike c. 1/3-1/2 as long as scape, 45-65 cm long, 22-28 mm diam. Cluster-bracts prominent, narrowly triangular, subglabrous to fringed with hairs. Packing-bracts narrowly triangular to subulate, fringed with hairs to moderately hirsute. Sepals acute, with beak, without proboscis, distal 1/3 subglabrous to fringed with hairs. Petals ± erect to recurved, with large proboscis, distal 1/3 hirsute with short papillose hairs. Figure 5.13.

Occurs in SE and Murray regions of S.A. near or within the triangle bounded by Meningie, Mt Gambier and Bordertown. Flowers Oct.-Dec. Map 2, Figure 5.12.

Figure 5.13 <u>X. caespitosa</u>, habit. Between Salt Creek and Meningie,
South Australia, Dec. 1982, <u>D.J. Bedford 121</u>, (NSW, AD).

S.A.: Dark Island Heath, 14.4. km NE of Keith, R. Specht & R. Rayson 16 (AD); 48.8 km from Salt Creek on road to Meningie, D. Bedford 121 (NSW); Fairview, c. 22 km from Naracoorte and c. 16 km N of Lucindale, J. Cleland AD 98309269 (AD); road from Millicent to Kingston, 16.7 km from Millicent, D. Bedford 118 (NSW).

In the past some specimens of this species have been identified as X. australis in S.A., while others have been ascribed to a putative hybrid swarm between X. australis and X. minor, see A.T.Lee, Contr. New South Wales Natl. Herb. 4: 54 (1966 a). The fruit are sometimes distinctively curved so that the apices point upwards.

13. Xanthorrhoea nana D. Herbert, J. & Proc. Roy. Soc. W. Australia 7: 83 (1921).

T: about 2 miles [c. 3 km] NE of Bruce Rock, W.A., 25 Oct. 1920, D.A. Herbert; lecto: PERTH, fide D. Bedford, Fl. Australia, 46: 228 (1986); isolecto: MEL.

Trunk none or to 50 cm long; stem many-branched; crowns usually 2-6, each a stiff open tuft but together appearing as a single hemispherical crown. Leaves depressed-obtrullate in T.S., c. 3 mm wide, c. 2 mm thick, blue-grey, glaucous. Scape c. 30 cm long, 10-15 mm diam. emerging horizontal then curved upwards. Spike ± equal to scape, 25-35 cm long, 25-50 mm diam. Cluster-bracts obscure or prominent only at base of spike, shortly acute, hirsute at margins. Packing-bracts shortly acute to acute, sparsely to densely hirsute on distal 1/3 mainly at margins. Sepals obtuse, beaked, often with

median abaxial ridge, without proboscis, hirsute along ridge and apex. Petals erect, with proboscis, glabrous. Figures 5.2, U, 5.4, E-F, 5.14.

Occurs in inland south-western W.A. between Lake Grace and Lake Moore, growing in yellow sand and yellow sandy clay in heath and mallee shrubland. Flowers Sept.-Oct. Map 3, Figure 5.12.

W.A.: c. 26 km N of Hyden Track along No. 1 Rabbit Proof Fence, K.M. Allen 815 (PERTH); Wialki-Bonnie Rock district, 11 Sept. 1957, A.R. Main (PERTH); c. 10 km W of Lake King, R.H. Kuchel 1863 (AD); 7.5 km from Bruce Rock towards Merredin, D. Bedford 67 & T.D. Macfarlane (NSW, PERTH); 69.5 km E of Southern Cross towards Coolgardie, D. Bedford 71 & T.D. Macfarlane (NSW, PERTH).

Distinguished by very pungent leaves, and curved scape and spike which emerge from crown ± horizontally then turn at ± 90° (Figure 5.14).

14. Xanthorrhoea drummondii Harvey, Hooker's J. Bot. Kew Gard. Misc. 7: 57 (1855).

T: near Perth and elsewhere, W.A., J. Drummond s.n., apparently lost; Wedin Siding, W.A., 28 Nov. 1982, D.J. Bedford 46 & T.D. Macfarlane; neo: NSW, fide D.J. Bedford, Fl. Australia 46: 226 (1986); isoneo: PERTH.

[X. reflexa auct. non D. Herbert: D.A. Herbert, J. & Proc. Roy. Soc. W. Australia 6: 33 (1920); W.E. Blackall & B.J. Grieve, How to know W. Austral. Wildfl. 70 (1954)]

Figure 5.14 X. nana, habit. 69.5 km E of Southern Cross towards Coolgardie, Nov. 1982, D.J. Bedford 71, and T.D. Macfarlane (NSW, PERTH).

Trunk to 2 m long; stem usually simple; crown usually 1; young leaves in ± stiffly erect tuft; older leaves often strongly reflexed. Leaves quadrate-rhombic in T.S., 1.8-2.5 mm wide, 1.5-2.3 mm thick, grey-green, glaucous. Scape 50-90 cm long, c. 30 mm wide. Spike c. 1.5-2 times as long as scape, 120-180 cm long, 55-65 mm diam. Cluster-bracts obscure. Packing-bracts shortly acute to acute, medium to densely hirsute. Sepals obtuse, with short beak, without proboscis, centre line and beak medium to densely hirsute. Petals ± erect, with proboscis, glabrous except for hairs at apex. Figures 5.2, H, 5.4, A-B, N-O, 5.15.

Occurs in W.A., from Dongara southwards, E of the Darling Range, as far as Wagin. Flowers Sept.-Nov. Map 4, Figure 5.12.

W.A.: Lake Indoon, Dongara, D.J. Bedford 93 & T.D. Macfarlane (NSW< PERTH); near Boyagering Ck, Toodyay, T.D. Macfarlane 1135 (NSW, PERTH); between York and Spencer Brook, D.J. Bedford 59 & T.D. Macfarlane (NSW, PERTH); 4.5 km WSW. of Noman Lake on road between Murdoch Road and Toolibin, D. Bedford 45 & T.D. Macfarlane (NSW, PERTH); Wagin, C.A. Gardner 1231 (PERTH).

The spike is distinctively dark brown at flowering and is hirsute at X10 magnification (Figure 5.4, N-O).

Some populations in the Dongara - Lake Indoon - Jurien region N of Perth resemble this taxon but differ from it by having less glaucous leaves and less hairy bracts. These populations may be an undescribed subspecies of X. drummondii.

Figure 5.15   X. drummondii, habit, Lectotype, Wedin Siding, W.A., 28
Nov. 1982, D.J. Bedford 46 & T.D. Macfarlane.

15. <u>Xanthorrhoea platyphylla</u> Bedford, <u>Fl. Australia</u> 46: 228 (1986).

T: 36.5 km NW. of Esperance on road to Ravensthorpe, W.A., 27 Nov. 1982, <u>D. Bedford 35 & T.D. Macfarlane</u>; holo: NSW; iso: PERTH.

Trunk usually none, rarely to 60 cm long; stem usually simple; crown usually 1, in an erect dense tuft. Leaves depressed-obtrullate to depressed-cuneate in T.S., 4-7.7 mm wide, 1.8-2.5 mm thick, green to slightly blue-green, slightly glaucous. Scape 50-80 cm long, 25-30 mm diam. Spike 2-3 times longer than scape, 95-165 cm long, rarely to 2.65 m, 40-60 mm diam. Cluster-bracts almost obscure, shortly acute to acute, subglabrous. Packing-bracts shortly acute, subglabrous to fringed with hairs. Sepals acute, with very short beak, without proboscis, subglabrous, with a median line of hairs. Petals reflexed, with proboscis, glabrous except for short hairs at apex.

Occurs in southern W.A., from the Stirling Range E beyond Esperance. Flowers June. Map 5, Figure 5.12.

W.A.: 25 km E. of Ravensthorpe, <u>K. Newbey 9734</u> (PERTH); Esperance Airport, <u>A.S. George 9863</u> (NSW, PERTH); c. 65 km E of Esperance, <u>R.H. Kuchel 1650</u> (AD).

Several collections from the geographic range of this species are somewhat similar, but cannot be ascribed to it or in any other described species. Their leaves are very similar to those of this species but the spikes are shorter than the scapes and there are differences in bract shape and hairiness. Such specimens most probably represent one or more undescribed taxa but more collections

and data are needed to resolve this.

16. <u>Xanthorrhoea preissii</u> Endl. in J.G.C. Lehmann, <u>Pl. Preiss</u>. 2: 39 (1846).

T: York [probably near Toodyay, perhaps the present-day Boyagerring Ck which flows to Toodyay from 10 km NE], W.A., 22 Mar. 1840, <u>L. Preiss 1620</u>; lecto: MEL 625774, <u>fide</u> D. Bedford, <u>Fl. Australia</u> 46: 228 (1986).

<u>X. pecoris</u> F. Muell., <u>Fragm.</u> 4: 110 (1864). T: Gordon River, W.A., <u>A. Oldfield 628</u>; holo: MEL 625762.

<u>X. reflexa</u> D. Herbert, <u>J. & Proc. Roy. Soc. W. Australia</u> 6: 33 (1920). T: Blackboy Hill, 15 miles [c. 24 km] from Perth, W.A., Oct. 1919, <u>D.A. Herbert s.n.</u>; holo: MEL 625775.

Trunk to over 3 m long; stem simple or branched; crowns 1 to few, each an uneven hemisphere. Leaves quadrate-rhombic to transverse-rhombic in T.S., 2.2-2.8 mm wide, 2.1-2.4 mm thick, green, not glaucous. Scape 60-100 cm long, 20-30 mm diam. Spike c. 2-3 times longer than scape, 150-250 cm long, rarely to 320 cm, 30-60 mm diam. Cluster-bracts obscure. Packing-bracts shortly acute to triangular, distally glabrous to very slightly subglabrous, the proximal margins and adaxial surface glabrous to hairy. Sepals shortly acute to acute, without beak or proboscis, subglabrous to sparsely hairy. Petals recurved, with proboscis, glabrous except at apex. Figures 5.2, P, 5.4, C-D, 5.16.

Figure 5.16 <u>X. preissii</u>, habit. Near Perth, Western Australia, Nov.
1982, <u>D.J. Bedford 52 and T.D. Macfarlane</u>, (NSW, PERTH).

Widespread in south-western W.A. Flowers Jan.-Nov. Map 6, Figure 5.12.

W.A.: Albany Hwy, SE of Mt Cooke, T.D. Macfarlane 737 (NSW, PERTH); 5.7 km S of Nanson on Yuna to Geraldton Road, D.J. Bedford 86 & T.D. Macfarlane (NSW, PERTH); Cape Leeuwin, D.J. Bedford 14 & T.D. Macfarlane (NSW, PERTH); Blackboy Hill, Swan View, near Perth, D.J. Bedford 53 & T.D. Macfarlane (NSW, PERTH); road to Bannister from Wandering, D.J. Bedford 52 & T.D. Macfarlane (NSW, PERTH).

The bracts on the spike are distinctly green at flowering. There is considerable variation in leaf width and thickness, and a little variation in leaf shape. The type has narrow leaves, quadrate-rhombic in T.S., 1.7 mm wide, 1.5 mm thick, whilst specimens in lateritic or loam soils and in higher rainfall areas have larger leaves, transverse-rhombic in T.S., sometimes tending to be wider than they are thick, to 3.3 mm wide and 2.5 mm thick.

The type of X. reflexa belongs to this taxon, although parts of Herbert's description and his photograph refer to X. drummondii.

17. Xanthorrhoea quadrangulata F. Muell., Fragm. 4: 111 (1864).

T: [St Vincent Gulf], S.A., 3 Feb. 1848, F. Mueller; lecto: MEL 625754, fide D. Bedford, Fl. Australia 46: 228 (1986); isolecto: K, MEL, 625760.

Trunk to 2 m long; stem sometimes branched; crowns usually 1 or 2,

hemispherical. Leaves quadrate-rhombic in T.S., c. 1.8 mm wide, 1-1.5 mm thick, very blue-grey, glaucous. Scape c. 55 cm long, c. 12 mm diam. Spike length usually less than scape, c. 30 cm long, c. 30 mm diam. Cluster-bracts obscure. Packing-bracts shortly acute to acute, subglabrous. Sepals shortly acute, beaked, without proboscis, subglabrous. Petals shortly recurved, sometimes with very small proboscis, glabrous except for tuft of short hairs at apex.

Occurs in S.A. from St Vincent Gulf to the northern Mt Lofty Ranges. Inhabits dry rocky sites, especially ridges, but also heavy clay soils. Flowers Mar.-Aug. Map 1, Figure 5.17.

S.A.: Oraparinna Natl Park, D.E. Symon 7214 (NSW); Mt Griselda, Arakoola, B.G. Briggs 4664 (NSW); Arakoola Sanctuary, R.H. Kuchel 2976 (AD); Black Hill, c. 12 km E of Adelaide, D.J.E. Whibley 914 (AD); Parrabana Springs, 125 km E of Blinman, J. Carrick 2035 (AD).

Bracts are dark brown at flowering.

18. Xanthorrhoea pumilio R.Br., Prodr. 288 (1810).

T: Port Curtis, near Gladstone, Qld, 1802, R. Brown Iter Australiense 5774; holo: BM.

Syn. Xanthorrhoea johnsonii A. Lee, Contr. New South Wales Natl. Herb. 4: 49 (1966 a)

T: between Dimbulah and Petford, W of Mareeba, Qld, 20 May 1962,

Figure 5.17 Species distributions:

1. <u>X. quadrangulata</u>

2. <u>X. pumilio</u>

3. <u>X. media</u>

4. <u>X. latifolia</u> subsp. <u>latifolia</u>

5. <u>X. latifolia</u> subsp. <u>maxima</u>

6. <u>X. arborea</u>

L.A.S. Johnson NSW 61293; holo: NSW.

Trunk none or up to 60 cm long; stem simple or branched; crown 1; leaves broadly spreading or recurved. Leaves transverse-linear to very depressed-obtrullate or very depressed-cuneate in T.S., 1.7-2.3 mm wide, 0.7-1.2 mm thick, green, not glaucous. Scape 50-180 cm long, rarely to 210 cm, 5-11 mm diam. Spike less than 1/4 as long as scape, 5-40 cm long, 14-23 mm diam. Cluster-bracts obscure. Packing-bracts obtuse to shortly acute, glabrous to subglabrous. Sepals shortly acute, without beak or beak very short, sometimes with a short median abaxial ridge, without proboscis, glabrous. Petals recurved, with proboscis, glabrous except hirsute apex.

Occurs in Qld. from Cooktown to Gladstone and W to the Great Dividing Ra. Flowers Apr.-May. Map 2, Figure 5.17.

Qld: Ravenshoe, P. Mesmer NSW 59789 (NSW); 16 km S of Innisfail, D.E. Boyland 550 & J.G. Gillieat (BRI); 41.7 km N of Townsville, D.J. Bedford 7612 (SYD); 35 km S of Bowen, D. Bedford 7609 (SYD); between Lowmead and Agnes Water, D. Bedford 7724 (SYD).

Distal one-third of packing-bracts are dark brown at flowering. This very small species is sometimes hard to distinguish from small plants of X. almae and X. latifolia.

19. Xanthorrhoea media R.Br., Prodr. 288 (1810).

T: Port Jackson, N.S.W., R.Brown; n.v. apparently lost, fide A.T. Lee,

Contr. New South Wales Natl. Herb. 4: 47 (1966 a); Parramatta, N.S.W., Nov. 1897, J.H. Camfield NSW 59863; neo: NSW, fide A.T. Lee, loc. cit.

Trunk none or up to 30 cm long; stem and crown usually 1, ± hemispherical. Leaves transverse-rhombic in T.S., 2-2.8 mm wide, 1.1-1.5 mm thick, mid to dark green, not glaucous. Scape 100-180 cm long, rarely to 210 cm, 7-11 mm diam. Spike less than 1/2, rarely equal to or slightly longer than scape, 35-90 cm long, 20-27 mm diam. Cluster-bracts almost obscure, sometimes at base only, shortly acute to narrowly triangular, abaxially hirsute. Packing-bracts shortly acute to acute, glabrous to moderately hirsute. Sepals shortly acute to acute, with short beak and median abaxial ridge, without proboscis, subglabrous to slightly abaxially hirsute. Petals recurved, sometimes with proboscis, glabrous except hairs at apex. Figure 5.2, I, O.

Occurs from Stony Hill to Hill Top on the central coast of N.S.W. as far north as Sandy Hollow. Grows on sandstone, usually on the drier, more exposed ridges and hillsides. Flowers Aug.-Mar. Map 3, Figure 5.17.

N.S.W.: Hawkesbury R., A.T. Lee NSW 61291 (NSW); Blaxlands Ridge, c. 16 km NE of Kurrajong, E.F. Constable 4208 (NSW); 42 Manor Road, Hornsby, A.T. Lee NSW 81658 (NSW); Warrimoo, E.F. Constable NSW 59862 (NSW); Hill Top, E. Cheel NSW 59844 (NSW).

Some larger plants on the central coast of N.S.W. (Sandy Hollow to Grassy Hill) have prominent cluster-bracts over the entire length of the spike. Further research is necessary to determine the status of these specimens. A.T. Lee, Contr. New South Wales Natl. Herb. 4: 47-48 (1966 a), regarded them as possible hybrids with X. australis

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subsp. _australis_.

20. _Xanthorrhoea latifolia_ (A. Lee) Bedford, _Fl. Australia_ 46: 227 (1986).

X. media subsp. _latifolia_ A. Lee, _Contr. New South Wales Natl. Herb._ 4: 48 (1966 a). T: Beerwah, Qld, May 1962, _E.F. Constable NSW 61667_; holo: NSW; iso: AD.

Trunk none or up to 3.6 m long; stem branched or single; crowns 1 to many, each with spreading mature leaves; young leaves in ± erect tuft. Leaves narrowly transverse-rhombic to very depressed-cuneate in T.S., 2.4-10 mm wide, 0.7-3.5 mm thick, bright-green, not glaucous. Scape 75-210 cm long, 7-20 mm diam. Spike shorter than or almost equal to scape, 30-150 cm long, 18-41 mm diam. Cluster-bracts obscure. Packing-bracts obtuse, shortly acute to acute, glabrous to fringed with hairs, sometimes abaxially hirsute. Sepals shortly acute to acute, without proboscis, with short beak and median abaxial ridge, subglabrous to slightly hirsute. Petals recurved, with proboscis, glabrous except at apex.

Occurs in coastal regions from Wyong, N.S.W., to Cape Cleveland, Qld, usually in sandy or gravelly soil. There are 2 subspecies.

Leaves 2.4-5.7 mm wide, 0.7-1.7 mm thick; spike c. 1/2 as long or almost equal to scape; packing bracts obtuse to shortly acute   a. subsp. latifolia

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Leaves 4.2–10 mm wide, 1–3.5 mm thick; spike less than 1/2

as long as scape; packing-bracts acute   b. subsp. maxima

20a. Xanthorrhoea latifolia (A. Lee) Bedford subsp. latifolia

Trunk none or up to 2 m long; crowns 1–4.   Leaves narrowly
transverse-rhombic to very depressed-cuneate in T.S., 2.4–5.7 mm wide,
0.7–1.7 mm thick, bright green. Scape 100–210 cm long, 10–16 mm diam.
Spike c. 1/2 as long or almost equal to scape, 50–120 cm long, 21–33
mm diam. Packing-bracts obtuse to shortly acute. Figure 5.2, J.

Occurs from Wyong, N.S.W., to Cape Cleveland, Qld.   Usually grows in
sandy or gravelly soil in sclerophyll forest. Flowers Mar.–Oct. Map
4, Figure 5.17.

Qld: Kroombit Tableland, I.R. Telford 5517 (CBG, NSW). N.S.W.: c. 1.6
km of Karuah, E.F. Constable 4788 (NSW); junction of Pacific Hwy and
Lake Munmorah Road, c. 16 km NE of Wyong, E.F. Constable 4303 (NSW).
Some specimens have much narrower leaves than typical plants, such
depauperate specimens are usually found in habitats only marginally
suitable for the species or to be stressed by poor seasons or disease.
They can sometimes appear similar to, and possibly be mistaken for,
small specimens of X. almae or large specimens of X. pumilio. Some
specimens from coastal sand areas between the Hawkesbury and Hunter
Rivers, N.S.W., have prominent cluster-bracts and triangular
packing-bracts.   These specimens are most probably hybrids with X.
glauca subsp. glauca as a hybrid swarm has been observed in such a
situation near Nelson Bay. Similar specimens are sometimes found on

the sandstone ridges near Central Mangrove in New South Wales, and may be subspecifically distinct. Specimens north of the Hunter R. but south of the Queensland border (in New South Wales) are smaller and more slender than the type and may also be subspecifically distinct.

20b. *Xanthorrhoea latifolia* subsp. *maxima* Bedford, *Fl. Australia* 46: 227 (1986).

T: Mt Warning, near Murwillumbah, N.S.W., 2 June 1962, E.F. Constable NSW 61357; holo: NSW.

Trunk none or up to 3.6 m long; crowns usually many. Leaves narrowly transverse-rhombic in T.S., 4.2-10 mm wide, 1-3.5 mm thick, bright green. Scape 75-210 cm long, 12-17 mm diam. Spike less than 1/2 as long as scape, 45-60 cm long, 28-35 mm diam. Packing bracts acute.

Occurs in wet sclerophyll forest on the summit of Mt Warning and at Minyon Falls and Mebbin State Forest, N.S.W. Flowers June-Oct. Map 5, Figure 5.17.

N.S.W.: Minyon Falls, Whian Whian State Forest, E.F. Constable NSW 61360 (NSW); near Minyon Falls, Whian Whian State Forest, L.A.S. Johnson & H.C. Hayes NSW 613581 (NSW).

This subspecies has distinctively large, swollen leaf bases which are sometimes dark red.

21. _Xanthorrhoea arborea_ R.Br., _Prodr._ 288 (1810).

T: Port Jackson, N.S.W., 17 May 1802, _R. Brown_; _n.v._ apparently lost, _fide_ A.T. Lee, _Contr. New South Wales Natl. Herb._ 4: 49 (1966 a); Manly, N.S.W., Jan. 1900, _E. Cheel NSW 56675_; neo: NSW, _fide_ A.T. Lee, _loc. cit._

Trunk usually 1-2 m long; stem simple or branched; crown 1 to many, each an uneven hemisphere or older leaves falling away from new upright tuft. Leaves narrowly transverse-rhombic to transverse-linear or concave in T.S., 5-7 mm wide, 0.8-1.9 mm thick, green or dull green, glaucous. Scape 135-165 cm long, rarely to 210 cm, 12-16 mm diam. Spike 2/3 to as long as scape, 100-150 cm long, 25-28 mm diam. Cluster-bracts obscure. Packing-bracts shortly acute, occasionally acute, fringed to moderately hirsute. Sepals shortly acute, without proboscis, beaked, usually subglabrous to ± abaxially hirsute. Petals recurved, with proboscis, glabrous except a terminal tuft of very short hairs. Figures 5.2, G, K, N, 5.3, L-Q.

Occurs on the central coast and adjacent tablelands of N.S.W., from Rylstone to just S of Sydney. Grows in sand or on sandstone, usually in sheltered sites. Flowers Jan.-Apr. Map 6, Figure 5.17.

N.S.W.: between Mt Coricudgy and Currant Mountain Gap (E of Rylstone), _A. Lee NSW 83579_ (NSW); Grassy Hill, on Windsor-Putty Road, _E.F. Constable 4211_ (NSW); c. 8 km N of Ten Mile Hollow, W of Mangrove Ck, _H.S. McKee 764_ (NSW); c. 5.5. km NE of Mt Irvine, _E.F. Constable 1_ (NSW); Heathcote, _E. Cheel NSW 61370_ (NSW).

Packing-bracts are dark brown at flowering.

22. _Xanthorrhoea thorntonii_ Tate, _Rep. Horn Sci. Exped. Centr. Australia_ 3: 191 (1896).

T: James Range, N.T., June 1894, _R. Tate_; syn: AD, MEL. No specimens from the other localities cited by Tate have been found.

Trunk to 5 m long; stem and crowns 1 or 2; young leaves ± erect; older leaves sometimes strongly reflexed or absent by abscission. Leaves ± quadrate-rhombic in T.S., 2-2.2 mm wide, c. 1.6 mm thick, slightly grey-green, glaucous. Scape 60-80 cm long, 25-35 mm diam. Spike 1.5-2 times as long as scape, 100-150 cm long, 50-60 mm diam. Cluster-bracts obscure, rarely prominent at base of spike, narrowly triangular, glabrous or almost so. Packing-bracts shortly acute to triangular, glabrous to subglabrous, light brown. Sepals shortly acute, with very short beak, without proboscis, glabrous. Petals erect, with proboscis, sometimes with beak, glabrous except hairs at apex. Figure 5.18.

Occurs in scattered localities in central Australia (S.A. & N.T.) and central-eastern W.A. Grows in yellow to red sand, usually on plains with _Triodia_ spp. Flowers Sept.-Dec. Map 1, Figure 5.19.

W.A.: Queen Victoria Spring, _D.J. Bedford 76 & T.D. Macfarlane_ (NSW, PERTH); c. 21 km E of Cosmo Newberry on Warburton road, _A.S. George 8102_ (PERTH); near Docker Ck, Petermann Ra., 29 June 1958, _J.B. Cleland_ (AD). N.T.: Gosse Bluff area, _D.J. Nelson 1359_ (AD, NSW, NT).

Packing-bracts are light brown; the petals are chartaceous rather than ± soft and membranous.

Figure 5.18   X. thorntonii, habit.   Gindalbie Station, Western Australia, Nov. 1982, D.J. Bedford 80 and T.D. Macfarlane, (NSW, PERTH).

Figure 5.19 Species distributions:

1. _X. thorntonii_

2. _X. almae_

3. _X. malacophylla_

4. _X. glauca_ subsp. _glauca_

5. _X. glauca_ subsp. _angustifolia_

6. _X. acanthostachya_

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23. _Xanthorrhoea_ _almae_ sp. nov.

Auct. non _Xanthorrhoea johnsonii_ A. Lee, _Contr. New South Wales Natl._
Herb. 4: 49 (1966 a).

T: Moggill State Forest, May 1977, _D. J. Bedford 7759_; Holo: NSW.

Trunk 10 cm to 5 m long, usually 30 cm to 2 m; stem and crown usually
1; young leaves in spreading upright tuft; old leaves often strongly
reflexed. Leaves ± quadrate-rhombic to transverse-rhombic in T.S.,
1-2.5 mm wide, 0.8-1.8 mm thick, green, not glaucous. Scape 75-190 cm
long, 7-20 mm diam. Spike 0.75-1.25 as long as scape, 20-120 cm long,
rarely to 225 cm, 20-40 mm diam. Cluster-bracts prominent only in
lower portion of spike, acute to narrowly triangular, subglabrous to
moderately hirsute. Packing-bracts shortly acute to acute, the distal
1/3 subglabrous to moderately hirsute. Sepals shortly acute, beak
absent or very short, sometimes with proboscis, often with median
abaxial ridge, glabrous to subglabrous. Petals erect to recurved,
with proboscis, glabrous except some hairs abaxially at apex. Figure
5.2, T.

Widespread in Qld and on the coast, tablelands and western slopes as
far S as Singleton in N.S.W., usually in sclerophyll forest and heath.
Flowers Apr.-Dec. Map 2, Figure 5.19.

Qld: 40 km from Cooktown, W of Annan R. crossing, _D.J. Bedford 7759_
(SYD); W of Mt Garnet (75 km W of Ravenshoe) _D.J. Bedford 76-5_;
Tinaroo Dam, _D.J. Bedford 7764_ (SYD); Chermside Hills, Brisbane, _S.T._
Blake 23562 (BRI). N.S.W.: 56 km from Singleton on Putty Road, _D._

<u>Bedford 201</u> (NSW, SYD).

The most common and widespread species of <u>Xanthorrhoea</u> in Qld., occurring over a wide geographic and environmental range. Extremely variable, showing considerable variation (mostly within the range quoted above) in most characters, including leaf width and thickness, scape length to spike length ratio (which often vary within one population) and bract shape and hairiness (although the more hirsute specimens found almost certainly result from gene flow from <u>X. fulva</u>). Hybridises with <u>X. fulva</u> in coastal south-eastern Qld, the offspring sometimes resembling <u>X. resinifera</u>.

This new species is named after Alma T. Lee (the name means Alma's <u>Xanthorrhoea</u>), both because it was Alma Lee who first alerted me to the possibility that the species might exist, and in recognition of her ground-breaking work on the genus.

No latin description is included here because this description is not valid nor effective publication under the rules of botanical nomenclature. It will be published separately.

24. <u>Xanthorrhoea malacophylla</u> Bedford, <u>Fl. Australia</u> 46: 227 (1986).

T: Camp Ridge Trig., Queens Lake State Forest, 5 miles [8 km] NNE of Kew, N.S.W., 15 May 1964, <u>E.F. Constable 4792</u>; holo: NSW.

Trunk usually 2-6 m long; stem branched, sometimes single; crowns 1-10; new leaves in ± erect tuft; mature leaves spreading, lax. Leaves transverse-rhombic to depressed-obtrullate in T.S., distally

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transverse-linear, 2.5-3.5 mm wide, rarely to 6.7 mm, 1.3-2.4 mm thick, green to bright green. Scape 135-185 cm long, 20-30 mm diam. Spike 0.6-1.6 as long as scape but usually equal to scape, 110-180 cm long, 30-50 mm diam. Cluster-bracts prominent for at least basal 10% of spike length, rarely obscure, narrowly triangular, subglabrous to fringed. Packing bracts acute, subglabrous. Sepals acute to triangular, with beak 0.5 mm long, without proboscis, glabrous to subglabrous. Petals recurved, sometimes without proboscis, glabrous except hairs at apex.

Occurs on coastal ranges of N.S.W. from Wyong north almost to Casino, on steep rocky hillsides, usually in moist or wet sclerophyll forest, or at rainforest margins. Flowers May-Sept. Map 3, Figure 5.19.

N.S.W.: Coramba Mtn, c. 8 km NW. of Coffs Harbour, E.F. Constable 4825 (NSW); Mt Boss State Forest, NW. of Wauchope, J.C. Cousins NSW 56762 (NSW); Camden Haven, J.B. Cleland NSW 56760 (NSW); Alum Mt, Bulahdelah, E.F. Constable 4296 (NSW).

Distinct in having a very tall trunk, and ± bright-green leaves which are unusually spongy and soft compared with most other species. Packing-bracts and sepals are dark brown.

A.T. Lee, Contr. New South Wales Natl. Herb. 4: 52 (1966 a) and Contr. New South Wales Natl. Herb., Fl. Ser. 34: 6-7 (1966 b), considered this species to be a hybrid between X. australis and X. media subsp. latifolia (= X. latifolia).

25. <u>Xanthorrhoea glauca</u> Bedford, <u>Fl. Australia</u> 46: 226 (1986).

T: edge of Levers Plateau, Qld, 4 July 1977, <u>D. Bedford 7776</u>;   holo: NSW.

Trunk 1-5 m long, branched or single; crowns 1 to many, ± spherical. Leaves quadrate-rhombic to narrowly transverse-rhombic in T.S., 1.3-5.2 mm wide, 0.9-2.4 mm thick, blue-green to grayish, glaucous. Scape 50-100 cm long, 18-46 mm diam.   Spike 1.5-4 times as long as scape, rarely equal to scape, 100-200 cm long, rarely to 250 cm, 35-77 mm diam.   Cluster-bracts prominent for most of spike length, ± narrowly triangular, subglabrous. Packing-bracts acute or triangular, subglabrous, rarely glabrous.   Sepals acute to narrowly triangular, beaked, without proboscis, glabrous except hairs in beak. Petals erect to slightly recurved, with proboscis, glabrous except hairs at apex. Figures 5.20, 5.21.

Occurs in N.S.W. and south-eastern Qld. There are 2 subspecies, with some overlap of characters where their distributions abut.

Leaves ± transverse-rhombic to narrowly transverse-
rhombic in T.S., 2.5-5.2 mm wide, blue-green   a. subsp. glauca

Leaves ± quadrate-rhombic to broadly transverse-
rhombic in T.S., 1.3-2.8 mm wide,
grayish   b. subsp. angustifolia

Figure 5.20 X. glauca subsp. glauca.   Queensland edge of Lever's

Plateau, Sept. 1977, D.J. Bedford P77M6, (SYD).

1. Habit.

Figure 5.21. Prominent cluster-bracts at the base of the spike, over.

25a. <u>Xanthorrhoea glauca</u> Bedford subsp. <u>glauca</u>.

Leaves transverse-rhombic to narrowly transverse-rhombic in T.S., distally transverse-linear, 3-4 mm wide, 1-1.6 mm thick. Scape 27-46 mm diam. Spike 100-200 cm long, 40-60 mm diam. Cluster-bracts with hairs only on proximal abaxial surface; margins glabrous. Packing bracts acute or triangular. Sepals triangular to narrowly triangular, with a beak to 1.5 mm long. Figures 5.20, 5.21.

Occurs on the northern coast and tablelands of N.S.W., and in south-eastern Qld, from Newcastle to Gayndah. Grows on steep slopes and ridges mainly in rich basaltic soils and, at some sites in N.S.W., in serpentine soils, and in deep sand on coastal N.S.W. from Newcastle to Byron Bay. Flowers June-Oct. Map 4, Figure 5.19.

Qld: c. 16 km NW of Gayndah, <u>S.L. Everist 7942</u> (NSW); Great Dividing Ra., near Toowoomba on the Warrego Hwy, <u>D. Bedford 7770</u> (NSW, SYD); c. 3 km SW of Rathdowney, 1977, <u>D.J. Bedford</u> (SYD). N.S.W.: Black Cutting, Tomalla Road via Moonan Flat [sic], <u>R.W. Earp NSW 56570</u>.

Populations on the coastal dunes from Byron Bay to Newcastle, N.S.W., hybridise with <u>X. fulva</u> and <u>X. latifolia</u> in distinct short-range hybrid swarms. These populations growing on sand cannot be distinguished morphologically from populations on the more typical rich basaltic soil substrates, although it appears unlikely for the one species of <u>Xanthorrhoea</u> to occupy such different habitats. A.T. Lee, <u>Contr. New South Wales Natl. Herb</u>. 4: 48 (1966 a) regarded this taxon as part of a very large hybrid swarm between <u>X. australis</u> and <u>X. latifolia</u>.

25b. *Xanthorrhoea glauca* subsp. *angustifolia* Bedford, _Fl. Australia_
46: 226 (1986).

T: 5 miles [8 km] NW of Coonabarabran on Bugaldie Road, N.S.W., 13
Dec. 1961, <u>E.F. Constable NSW 61353</u>; holo: NSW.
Leaves quadrate-rhombic to broadly transverse-rhombic in T.S., 1.3-2.8
mm wide, 0.9-1.6 mm thick.   Scape 18-40 mm diam.   Spike 100-160 cm
long, 40-50 mm diam.   Cluster-bracts with hairs mainly at margins.
Packing-bracts acute. Sepals acute, with beak to 0.5 mm long.

Occurs in N.S.W. along the ranges of the Great Divide from the slopes
of the Snowy Mts to Inverell, usually on rocky (limestone, trachyte)
and gravelly slopes. Flowers Sept.-Dec. Map 5, Figure 5.19.

N.S.W.: Mt Nombi, 27 km SW of Mullaley, <u>A.N. Rodd NSW 112483</u> (NSW);
Guneemooroo Stn, 10 km NNE of Tooraweenah, <u>E.F. Constable NSW 61352</u>
(AD, NSW); Winburndale Ck, c. 19 km N. of Bathurst, <u>E.F. Constable NSW
63506</u> (NSW). A.C.T.: Mt McDonald, <u>N.T. Burbidge 6713</u> (CANB, NSW).

A.T. Lee, <u>Contr. New South Wales Natl. Herb.</u> 4: 51 (1966 a) and <u>Contr.
New South Wales Natl. Herb., Fl. Ser.</u> 34: 6-7 (1966 b), regarded this
subspecies as a good example of <u>X. australis</u>, but it differs from the
latter in leaf, bract and floral characters.

S.W.L. Jacobs & J. Pickard, <u>Pl. New South Wales</u> 59 (1981), recorded
subsp. <u>angustifolia</u> as <u>X. australis</u> subsp. <u>australis</u> (western form).

26. Xanthorrhoea acanthostachya Bedford, Nuytsia 5: 317 (1985).

T: Chatfield Road, South Western Highway, c. 16 km N of North Dandalup, W.A., 24 Nov. 1982, D.J. Bedford 4 & T.D. Macfarlane; holo: NSW; iso: PERTH.

Trunk to 1.5 m long; crowns 1 or 2, $\pm$ hemispherical. Leaves quadrate-rhombic in T.S., 2-2.3 mm wide, 1.5-2 mm thick, green to slightly blue-green, slightly glaucous. Scape 40-50 cm long, 7-16 mm diam. Spike $\pm$ equal in length to scape, 40-50 cm long, 20-40 mm diam. Cluster-bracts very prominent, rarely only slightly prominent, very elongated, subulate, glabrous, sometimes subglabrous. Packing-bracts subulate or almost so, often twisted or folded, glabrous to subglabrous. Sepals shortly acute, beaked, without proboscis, glabrous. Petals $\pm$ erect, sometimes beaked, with proboscis, glabrous except hairs in beak. Figures 5.2, Q, 5.4, G-L.

Occurs in the Perth region, W.A., on the coastal plain and slopes of the Darling Scarp. Grows in lateritic soil and in grey sand overlain with lateritic gravel. Flowers Aug.-Nov. Map 6, Figure 5.19.

W.A.: Harvey Dam Reserve, T.D. Macfarlane 659 (PERTH); Keysbrook, Nov. 1900, W.V. Fitzgerald (NSW); c. 8 km E of Mogumber, 25 Aug. 1970, K.M. Allan (PERTH).

A species known from few collections, though field observations suggest it may be reasonably widespread along the coast north of Perth. The only species in W.A. with very prominent cluster-bracts, and a distinctively prickly flowering spike.

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27. _Xanthorrhoea australis_ R.Br., _Prodr_. 288 (1810).

T: Grass Tree Hill, near Risdon Cove, Tas., Feb. 1804, _R. Brown Iter Australiense 5775_; holo: BM.

Trunk to 3 m; stem often branched; crowns 1 to many, each with young leaves in erect tuft, spreading with age; old leaves often reflexed, crown ± spherical. Leaves quadrate-rhombic to transverse-rhombic in T.S., occasionally depressed-obtrullate, 1.2-3 mm wide, 1-2.2 mm thick, blue-grey, glaucous. Scape 30-50 cm long, 18-40 mm diam. Spike 2-6 times as long as scape, 110-180 cm long, rarely to 2.5 m, 50-80 mm diam. Cluster-bracts very prominent, elongated, subulate, glabrous. Packing-bracts elongated, subulate, glabrous. Sepals triangular to narrowly triangular, with long beak, with proboscis, glabrous. Petals erect to slightly recurved, with proboscis, glabrous except papillose hairs at apex. Figures 5.2, R, 5.3, R-S, 5.22.

Occurs in northern and eastern coastal Tas. from Rocky Cape to N. Bruny Is., in south-eastern S.A. west to Lucindale, in Vic. south of Wangaratta, and in N.S.W. south of Nowra. Flowers July-Dec. Map 1, Figure 5.23.

S.A.: road to Glencoe, _D. Bedford 116_ (NSW). N.S.W.: Mt Bumbo Fire Trail, Dampier State Forest, W. of Bodalla, _E.F. Constable 448_ (NSW). Vic.: SE corner of Glenelg Natl. Park, _D. Bedford 115_ (NSW). Tas: Sisters Ck, _D. Martin NSW 67463_ (NSW); road to Sloop Rock and the Gardens, 3 km N of the Binnalong Bay turnoff, _D. Wolfe NSW 66053_ (NSW).

Figure 5.22 <u>X. australis</u>, habit. Near Glencoe, South Australia, Dec.
1982, <u>D.J. Bedford 116</u>, (NSW).

Figure 5.23 Species distributions:

1. <u>X. australis</u>

2. <u>X. semiplana</u> subsp. <u>semiplana</u>

3. <u>X. semiplana</u> subsp. <u>tateana</u>

A.T. Lee, <u>Contr. New South Wales Natl. Herb.</u> 4: 52-53 (1966 a), described two subspecies of <u>X. australis</u>, but the species is here restricted to its typical form. <u>X. australis</u> subsp. <u>acaulis</u> is described above as <u>X. acaulis</u>. The <u>X. australis</u> subsp. <u>australis</u> (western form) of S.W.L. Jacobs & J. Pickard, <u>Pl. New South Wales 59</u> (1981), is described above as <u>X. glauca</u> subsp. <u>angustifolia</u>.

28. <u>Xanthorrhoea semiplana</u> F. Muell., <u>Fragm.</u> 4: 111 (1864).

T: near Gawler, S.A., ? Nov. 1851, <u>F. Mueller</u>; lecto: MEL 625756, <u>fide</u> D.J. Bedford, <u>Fl. Australia</u> 46: 229 (1986).

Trunk to 6 m long; crowns 1 to many, each an even sphere. Leaves narrowly transverse-rhombic to very depressed-cuneate in T.S., 5-12 mm wide, c. 2.5 mm thick, bluish, very glaucous. Scape 80-120 cm long, rarely to 2 m, 20-45 mm diam. Spike 1.5-2 times as long as scape, 150-250 cm long, rarely to 4 m, 30-45 mm diam. Cluster-bracts obscure. Packing-bracts subulate, glabrous. Sepals shortly acute to acute, beaked, without proboscis, glabrous. Petals recurved, with proboscis, glabrous except short hairs at apex. Figures 5.24, 5.25.

Occurs on the Eyre, Yorke and Fleurieu Peninsulas, Kangaroo Island, and south-eastern S.A., and probably in central-western Vic. Flowers Oct.-Nov. There are 2 subspecies.

Spike relatively short and slender, 150-200 cm long,
c. 30 mm diam; trunk to 1 m long   a. subsp. semiplana

Figure 5.24 <u>X. semiplana</u> subsp. <u>semiplana</u>, habit.   45 km   from Kingscote
   towards Flinders Chase, Kangaroo Island, Dec. 1982, <u>D.J. Bedford P82M</u>
   (NSW).

Figure 5.25 <u>X. semiplana</u> subsp. <u>tateana</u>, habit. Near Stun'sail boom
Bridge, Kangaroo Island, Dec. 1982, <u>D.J. Bedford 104</u>, (NSW, AD).

Spike relatively long and stout, 235-265 cm long,

40-45 mm diam; trunk 1-5 m long   b. subsp. tateana

28a.   Xanthorrhoea semiplana F. Muell, subsp. semiplana.

Trunk absent or to 1 m long.   Scape 1-1.2 m long, c. 20 mm diam.
Spike 150-200 cm long, c. 30 mm diam. Figure 5.24.

Occurs on the Fleurieu Peninsula, south-eastern S.A., and probably
western Vic. Map 2, Figure 5.23.

S.A.: c. 3 km SE of Willunga, 4 July 1957, R. Hill (AD); 3 km SSW of
Currency Ck, H. Eichler 15018 (AD); Tooperang, near Mt Compass, Oct.
1951, C.M. Eardley (AD); Mt Lofty Botanic Garden, J.R. Wheeler 121
(AD); 14 km from Strathalbyn on road to Goolwa, D.J. Bedford 122
(NSW).

28b.   Xanthorrhoea semiplana subsp. tateana (F. Muell.) Bedford, Fl.
Australia 46: 229 (1986).

X. tateana F. Muell., Z. Allg. Osterr. Apotheker-Vereines 23: 294
(1885). T: Kangaroo Island, S.A., 1883, Somerville & Wilks; lecto:
MEL 625766, fide D. Bedford, Fl. Australia 46: 229 (1986).

Trunk 1-5 m long. Scape c. 90 cm long, c. 45 mm diam.   Spike 235-265
cm long, 40-45 mm diam. Figures 5.2, F, 5.25.

Occurs on the Eyre, Yorke and Fleurieu Peninsulas and on Kangaroo Is., S.A. Map 3, Figure 5.23.

S.A.: near Pearson Is., off W coast of Eyre Peninsula, May 1959, J.B. Cleland (AD); Marble Ra., Eyre Peninsula, E.N.S. Jackson 3617 (AD); Yacca Flat, Kangaroo Is., H. Eichler 15115 (AD); near Kelly Hill Natl. Park, Kangaroo Is., D.J. Bedford 104 (NSW).

Doubtful name

Xanthorrhoea undulatifolia Riccob. in L.H. Bailey, Stand. Cycl. Hort. 6: 3522 (1917).

T: not designated

Insufficiently described, most probably described from a plant (?in cultivation) showing abnormal undulating foliage, as sometimes found as a result of insect or fire damage.

Chapter 6

CONCLUSIONS

6.1   Summary of the conclusions in Chapters 2-5

Methodological conclusions from the phenetic analyses

In the study of the X. pumilio/latifolia/johnsonii complex in Queensland a number of methodological considerations were discussed.

Primary amongst these was the possibility of statistically testing the results of the classification. A classification produces an hypothesis that there are a number of valid groupings or nested subsets present in the total set of individuals or taxa in the classification. It is desirable to test or corroborate such an hypothesis in some manner.

The possibility of testing the statistical significance of classifications produced by SAHN and similar programs by using one of the available analysis of variance (ANOVA) statistics such as an F test was discussed. It is reported that such an exercise is essentially tautological, and does not provide a test of the significance in such a situation (pers. comm. J. Robinson). It was concluded that there is no test of the statistical significance of a classification in existence, but that it may be possible to corroborate or support a classification, for example, by comparing it with additional characters or samples.

Interpretation of ordination results was also discussed, particularly in reference to the distinctive "horseshoe" curves described by some authors for ecological ordinations, where such a distribution is regarded as an artifact of the method (arch effect of Gauch et. al.,

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1977, or horseshoe effect of Kendall, 1971). The possibility that such a distribution curve in taxonomic data may have some information content about the entities being ordinated is considered.

It is concluded that the curved distribution of entities in a taxonomic ordination most likely reflects that there is not a simple linear relationship between the individuals or groups.

After a comparison of the results of the classifications and ordinations it was concluded that the variation seen in the individuals analysed was discontinuous, not continuous as in a cline, and that therefore the classifications presented the better summary of the information content of the data.

Taxonomic conclusions for <u>Xanthorrhoea pumilio/latifolia/johnsonii</u> complex

All classifications indicate that there are three discrete groups of individuals with more or less equivalent levels of internal euclidean distance dissimilarity in the data set (GP β, GP Ω and GP θ). One of the groups (GP β) is quite variable in all classifications, but subsequent investigation of the internal structure of this group has failed to find any clear cut distinctions within the group.

GP Ω represents <u>X. latifolia</u> (Lee) Bedford as a single distinct taxon, GP β represents a single taxon currently containing two type specimens – <u>X. pumilio</u> R.Br. and <u>X. johnsonii</u> Lee, of which the former name has priority. There is no type that falls within the range of variation of GP θ and therefore this group requires a new name.

It is proposed to name the species represented in the analyses by GP θ as X. almae after Alma T. Lee (Chapter 5).

Conclusions from studies in intergradation between Xanthorrhoea species

Hybridism on the Quaternary sand systems

Examples of the hybrid swarms postulated by Bedford (1986 a) and Lee (1966 a and b) were documented on the Quaternary sand masses along the east coast of Queensland and New South Wales.

Lack of evidence for hybridisation on older soils

Details were given of a study, at Pearl Beach, of the only example found of apparent hybrids or intermediates on sandstone (pre-Quaternary) substrates which had not been resolved by recognition of the "intermediates" as a separate previously undescribed taxon by Bedford (1986 a). It was concluded that the taxa present, X. arborea and X. latifolia subsp. latifolia, did not hybridise or intergrade at this site.

The studies in this chapter therefore support the hypothesis that hybridisation does occur in Xanthorrhoea, but not as extensively as previously reported. The lack of evidence found for hybridism on older soils during the extensive studies throughout Australia conducted for the taxonomic revision of the genus (Chapter 5) supports the hypothesis that hybridism is restricted to habitats on the Quaternary age sand deposits along the east coast of Australia.

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It was also concluded that hybridism is only found where two species meet on a wet-dry ecocline such that there is an intermediate habitat with conditions not preferred by either parent. It appears that the hybrids have habitat drainage preferences intermediate to those of their parents and are therefore able more effectively to colonise the intermediate habitat of the ecocline than are their parents.

The causative factors for such a restricted distribution of hybrids were discussed. It was concluded that the relative youth of the Quaternary sands, or possibly the series of sharp changes (advances and retreats) they have undergone during the Pleistocene might cause such hybridism to occur. These two conditions, relative youth and fluctuating changing environment, are the kind of conditions that are postulated to be the cause of inefficient barriers to gene flow, and thus the increase the formation of intermediates or hybrids.

It was considered that, as X. fulva is restricted in distribution to the Quaternary sands, it has most likely evolved on the sand systems. This was discussed relative to other taxa which are restricted to the deep sand systems in the same way as is X. fulva (e.g. Caustis recurvata and Eucalyptus signata, Carolin, pers. comm.). It was postulated that all these taxa have evolved on these sand systems, which makes them between about 130,000 and 1,000,000 years old.

Cladistic studies

The cladistic analyses support the hypothesis that the Agavaceae are the sister-group to the Xanthorrhoeaceae, and suggest a phylogenetic relationships of species.

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Characters

The paucity of reliable characters found for phenetic studies was paralleled in the cladistic studies. Five characters were found to be reliable evolutionary indicators, six characters were partially reliable, and fifteen were shown as having parallel development or a pattern of change in conflict with the character scoring. That is, only the minority of the characters in the analysis were good or reasonable indicators of the main evolutionary thrust of the genus. Thus many of the apparent similarities in the genus are postulated to be non homologous parallel developments.

Taxonomic implications of the cladogram

The application of Hennigian principles (1966) to Xanthorrhoea makes some significant conceptual changes necessary within the genus. This is mainly seen in the re-arrangement of taxa (Chapter 5) relative to the arrangement in Bedford (1986 a).

The possibility of considering the divisions of the genus into clades (e.g. as shown in Figures 4.2 and 4.3) as formal subgeneric groupings of the species, as is done in many cladistic analyses, was discussed. It was concluded that this classification should not be adopted as a formal subgeneric classification at this stage. Rather it should be regarded as a first approximation, which needs to be tested by comparison with data from other aspects of the group, possibly such as protein or isoenzyme analyses, before it could be regarded as a reliable subgeneric classification.

The biogeographic implications of the preferred cladogram were also discussed. The finding that the closest two branches of the clade are widely geographically separated (eastern Australia and south-west Western Australia respectively) was considered significant for the evolutionary history of the genus. In biological terms this infers that the genus is older than the biological isolation of eastern Australia from western Australia.

The result of component analysis of the full area-cladogram, which yields only one possible resolved cladogram for all the areas in which taxa occur, was discussed. The resulting reduced-area-cladogram specifies a series of historical area relationships which can then be interpreted in biological terms for the evolution of the genus.

The area-cladograms for Xanthorrhoea were also compared with known or presumed events in the geological history of Australia in order to establish hypotheses about possible vicariance events involved in the separation of areas in the area-cladogram.

It is concluded that the vicariance events for Xanthorrhoea hypothesised by the area-cladogram for the genus best corresponds (with some reservations) to a series of climatic and physical vicariance events during the Quaternary. As such, the genus can be presumed to be a relatively young group, with relatively recent evolution, in common with much of the Australian flora (Kemp 1981).

Thus the cladistic results have suggested a new arrangement of some of the taxa and this is reflected in the taxonomic arrangements. They also suggest that the genus is, as a whole, more ancient than the

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floristic division of east and west Australia. This is not unexpected as many other genera show the same feature (e.g. eucalypts, Ladiges and Humphries, 1983; 1986; Ladiges et al., 1987). Also the separation into dryland and wetland species also predates the floristic division. It is possible that this may be due to parallel evolution of similar characters to accommodate similar environments, but evidence for such an hypothesis is lacking.

Taxonomic revision

Many purported hybrids described by Lee (1966 a and b) were found to be well defined, if somewhat cryptic, species. Clear and reliable characters to distinguish them were, in fact, found (Chapter 5).

Most of these results have been published before submission of this thesis (Bedford, 1986 a and b). Here the species are arranged to reflect their relationships following cladistic analysis (chapter 4), and the description of a new taxon discovered as part of the analysis of _Xanthorrhoea_ in Queensland (chapter 2). In addition new nomenclatural discoveries concerning the name _Xanthorrhoea_ were discussed.

6.2 General conclusions

Many aspects of the general conclusions are embodied in the taxonomic revision (Chapter 5). The hypotheses generated from the phenetic analyses result in a particular taxonomic treatment and circumscription of species, and those generated by the cladistic analyses result in the arrangement of the taxa.

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In general one can conclude that the reputation that <u>Xanthorrhoea</u> has as a "critical" genus in the sense that species are difficult to circumscribe, and hybridise widely, is not justified.   Most of the putative hybrids are shown to be definable taxa which are probably not even intermediate between others.   One putative hybrid zone (<u>X.</u> <u>arborea</u> - <u>X. latifolia</u> subsp. <u>latifolia</u>) which was examined in some detail, was shown not to have intermediates (or hybrids) at all.   In only one putative hybrid situation did an analysis show a series of intermediates, i.e., on ecoclines on the Quaternary sands along the east coast of Australia.

Thus many of the difficulties encountered by earlier taxonomists are shown to be partly the result of the inadequate collections available for study, and partly the considerable inherent variability of many <u>Xanthorrhoea</u> species.

It appears that the reasons for the inherent variability of many <u>Xanthorrhoea</u> species are likely to be:

1. The vegetative nature of many of the characters used to distinguish taxa.   Characters such as leaf width, leaf thickness and lengths of the scape and spike are dependant to some extent on the well-being of the plant.   In poor conditions, poor seasons, or in unhealthy plants, these dimensional characters are often reduced in size, and may become outside the range recognised for the taxon, and into the range recognised for another taxon, thus leading to a misidentification;

2. The putative facultative inbreeding and facultative apomixis or other form of seed-producing asexual reproduction suggested above (Chapter 5), which would both act to decrease within population

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variation but increase between population variation.

Both of the latter possibilities have far reaching evolutionary consequences for the genus. Clausen (1954) has described partial apomixis as an equilibrium system of great significance in evolution. He notes that species which achieve a balance in nature between sexual and asexual reproduction have a greater range of potential variability available for natural selection than do obligately sexually reproducing species. This is because facultative apomixis multiplies certain varieties of a genome but does not prevent recombination through sexual reproduction. Baker has discussed the significance of reproductive method to both race formation (1953 a), and to speciation (1960). He notes in relation to race formation that ecotype formation is promoted by self compatibility but not by self in/compatibility, which tends to promote clinal variation. Basically he says that both apomixis and inbreeding promote discontinuous variation whereas outbreeding promotes continuous variation. The situation in Xanthorrhoea, of puzzling between-population variation, agrees well with this description, although such evidence is extremely circumstantial.

In relation to speciation Baker (1960) paints a more complex picture. He says that inbreeding (at least in diploids) tends to promote speciation, partially through promotion of polyploidy, but that apomixis is not necessarily a promoter of speciation because it favours retention of variability. Although, when asexual reproduction predominates in a facultative apomict the situation tends to resemble that for inbreeders. He notes that overall the breeding system is of great importance to the process of speciation, but that the result

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depends on a great number of factors, especially environmental selection pressure. That is, both facultative apomixis and inbreeding promote race formation, and taxonomic difficulty ("provides grist to the mill for splitters"), but not necessarily speciation. Once again this result is circumstantially relevant to Xanthorrhoea, where race formation seems apparent, but speciation is not necessarily taking place.

Role of hybridisation in evolution within Xanthorrhoea

Stebbins (1959) noted that a number of taxonomically difficult groups had achieved evolutionary success due largely to the after effects of natural hybridisation. In this context, coupled with the widespread distribution of Xanthorrhoea and its obvious success in the fire dominated Australian ecosystems, the attribution of the traditional difficulty in identification of the group to putative hybridism by Lee, (1966 a and b), was an apparently reasonable concept.

However, now that it has been demonstrated that hybridisation in the genus is restricted to the Quaternary sands, the question arises as to what role hybridisation may play in evolution within Xanthorrhoea. Stebbins (1959) contended that hybridisation "usually affects profoundly the course of evolution". Although he notes that this depends on the effect hybrids have on the genetic variability of the natural population. Many other authors have commented on the effects of hybridisation on evolution, mostly more or less in agreement with the above (e.g. Levins, 1964; Lewis, 1966), although some believe that hybridisation has a minimal effect on evolution (e.g. Bobrov, 1982).

Levins (1964) discussed the adaptive advantage of gene flow in a changing environment. He noted that stable habitats favour reduced gene flow, whilst changing habitats favour increased gene flow. This appears to be exactly the situation found in Xanthorrhoea.

Hybridisation occurs on the new and fluctuating habitat of the Quaternary sands, but not on the older soils, which are presumably more stable habitats. It is interesting to note that although Bobrov (1982) minimised the role of hybridisation in evolution as noted above, he documented hybridism in Picea which he believed to be connected with the change of climate of "the Quaternary and Holocene periods", a direct parallel with the postulated timing for the onset of hybridisation in Xanthorrhoea.

Lewis (1966) also discusses the evolutionary effects of hybridisation and draws conclusions that seem to be relevant to what is happening in Xanthorrhoea. He discusses the gradual evolution of ecological races, which each have different habitat preferences to their parents, as is postulated in Chapter 2 for the hybrids along the ecoclines in Xanthorrhoea, although the process there appears to be at an early stage of development, without significant disjunctions within the hybrids at this stage.

Stebbins (1959) commented that it is possible that hybrids, because of their differing habitat preferences, may extend the geographical range of their parents. Evidence for this in Xanthorrhoea, is limited, so that it does not appear to have taken place, at least to any large extent. The only evidence for such an occurrence may be in the variability of some characters in some taxa, particularly the character of bract indumentum in populations of X. almae in south-east

Queensland which may indicate some degree of gene flow from X. fulva even at some distance from areas of actual overlap, and could mean that some habitat preference characters have also been transferred.

It appears then that hybridisation in Xanthorrhoea is likely to have an affect on the evolution of the taxa involved, both by extending the range of habitat selection and by the introgressive gene flow increasing the variability of those taxa occurring in the most variable environment, the Quaternary sands.

6.3 Future directions

It is clear from the above that the future direction for Xanthorrhoea taxonomy must, at least to some extent, lie in finding more reliable characters on which to distinguish taxa. It is most likely that such characters will be found closer to the genetic level, as the present author has thoroughly surveyed the available morphological characters, and investigated chromosome and flavonoid characters without finding suitable alternative or additional characters to those used in the present study. The one exception likely to this proviso is the possibility that the resins may prove useful in distinguishing taxa. Duewell (in press) contends that the resins can be used to reliably distinguish taxa, and the present author has found Duewell's identification of taxa useful in distinguishing cryptic species near the mouth of the Hunter River, New South Wales. Joint research by Bedford and Duewell is continuing in this area and offers promise.

The possibility of facultative inbreeding and facultative apomixis in the genus are also worthy of investigation because of the considerable

taxonomic and evolutionary consequences for organisms of such phenomena.

Other areas worthy of study appear to be enzyme/isoenzyme and protein electrophoretic techniques which, although unfamiliar to the present author offer promise of finding characters closer to the genetic level, which may be less variable than the morphological characters presently used.

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APPENDICES

Appendix 2.1 Collection localities for studies in Queensland

(Anal. no. = analysis number; coll. no. = collection number; *

marks specimens which are from localities collected from in two

successive years.)

Anal. no.	Coll. no.	Locality	Latitude	Longitude
1	76-7	20 km N of Proserpine	20 25' S	148 35'E
2	76-10	ditto	"	"
3	76-9	35 km S of Bowen	20 15'	148 28'
4	76-6*	Mt Elliot Natl Park	19 24'	147 00'
5	76-8	33 km N of Townsville	19 08'	146 30'
6	76-13	41.7 km " " "	19 04'	146 27'
7	76-12	ditto	"	"
8	76-14	133 km " " "	18 30'	146 10'
9	76-15	ditto	"	"
10	76-1	just N of Cardwell	18 14'	146 00'
11	76-2	100 km N of Mt Molloy	16 10'	144 45'
12	76-16	30 km S of Cooktown	15 41'	145 11'
13	76-4	just W of Kuranda	16 55'	145 33'
14	76-5*	W of Mt Garnet	17 46'	145 00'
		(75 km W of Ravenshoe)		
15	76-17	Dimbulah – Petford	17 15'	145 00'
16	76-18	ditto	"	"
17	76-19	ditto	"	"
18	76-20	45 km W of Dimbulah	17 22'	144 50'
19	76-21*	5 km W of Petford	17 21'	144 56'
20	77-15	near Maryborough	25 32'	152 13'
21	77-16	near Bundaberg	24 49'	152 13'
22	77-17	ditto	"	"

23	77-18	ditto	"	"
24	77-20	ditto	"	"
25	77-25	near Agnes Waters	24 31'	151 45'
26	77-28	near Rockhampton	23 23'	150 30'
27	77-31	Marlborough	22 54'	149 37'
28	77-32	ditto	"	"
29	77-35	Yaki Pari	21 04'	149 00'
30	77-36	ditto	"	"
31	77-37	N of Bloomsberry	20 30'	148 37'
32	77-40	Burdekin Gorge	20 00	147 15'
33	77-42	ditto	"	"
34	77-43*	Mt Elliot Natl Park	19 24'	147 00'
35	77-44	Mt Spec	18 57'	146 11'
36	77-45	ditto	"	"
37	77-47*	just N of Cardwell	18 14'	146 00'
38	77-48*	near Petford	17 21'	144 56'
39	77-50	ditto	"	"
40	77-52	Stannary Hills	17 19'	145 13'
41	77-53	Atherton - Herberton	17 21'	145 25'
42	77-54	ditto	"	"
43	77-55	Kuranda - Mareeba	16 55'	145 33'
44	77-57	Cairns - Pt Douglas	16 50'	145 42'
45	77-58*	ditto	"	"
46	77-59	Annan River crossing	15 41'	145 11'
47	77-61	Morehead River cross.	15 04'	143 40'
48	77-63	Tinaroo Dam	17 10'	145 35'
49	77-64	ditto	"	"
50	77-66*	W of Mt Garnet	17 46'	145 00'

(75 km W of Ravenshoe)

51	77-67	just W of Nebo	21 41'	148 41'
52	77-69	near Springsure	24 07'	148 05'

NQ 78 Entity analysis individual numbers: (1 - 52 AS ABOVE)

Anal. no.	Coll. no.	Locality	Latitude	Longitude
53	m-20	Beerwah 1975	26 53'	153 00'
54	m-21	"	"	"
55	m-22	"	"	"
56	m-23	"	"	"
57	j-35	"	"	"
58	j-36	"	"	"
59	j-37	"	"	"
60	j-38	"	"	"
61-73	77-108 - 77-120 are Beerwah 1977		"	"
74-78	78-18 - 78-22 are Beerwah 1978		"	"

i.e. 53 - 56 are <u>X. latifolia</u> collected at Beerwah Scientific purposes area during 1975, as part of Honours project.

57 - 60 are <u>X. johnsonii</u> at the same site and same year.

61 - 73 are <u>X. latifolia</u> at the same site collected in 1977.

74 - 78 are <u>X. latifolia</u> at the same site collected in 1978.

[* denotes those specimens which represent collections from the same locality in different years.]

Appendix 2.2 data input file - north and south Queensland data set (78 entities) analyses.

```
NQ78GA,T20.
USER,SNHDBD,XANTO.
CHARGE,SNH,SNHTAX.
CNSOFT,PRRREL.
TAXON.
PARAMS.
ITCOPY,INPUT,DATX.
DATLST.
NSED.
SAHN.
DENDRO.
T=NQ78GA 78 ENT DATA MOD 4 CLASSIFICATION
II=78, IFN=7, IDN=8, APRINT=AUTO, NGREQ=78, SORTSTRAT=UPG
*STATES
4 2 5 3 5 2 3 5
*END
*ANAME
LEAF SHAPE
LEAF COLOUR
CLUSTER BRACTS
JUV. CLUSTER BR.
BRACT COLOUR
SCAPE COLOUR
BRACT SHAPE
BR. INDUMENTUM
LEAF WIDTH
SCAPE LENGTH
SCAPE DIAMETER
SPIKE LENGTH
SPIKE DIAMETER
SP/SC RATIO
TRUNK HEIGHT
*END
*SNAME
QUADRATE-RHOMBIC
NARROWLY-Q-R
OBTRULL>OBTRIANG
CONCAVE
GREEN
GLAUCOUS
ABSENT
SHORTLY ACUTE
BASE OF SPIKE
BASAL 10 CM
100% SPIKE
ABSENT
SHORTLY ACUTE
LINEAR-TRIANG
WHITE TO CREAM
GREEN
BROWN
LT BROWN VELVET
DK BROWN VELVET
GLAUCOUS
GREEN
```

OBTUSE
SHORTLY ACUTE
LINEAR-TRIANGULAR
GLABROUS
SHORT BLACK HAIRS
TOMENTOSE
FRINGED
DENSELY HIRSUTE
*END
$
3,*,1,*,*,*,2,4,   76-7B
    275   191   90   28   22   15   5   76-7A
$
3,*,1,*,*,*,2,4,   76-10B
    275   165   90   16   20   9   0   76-10A
$
3,*,1,*,*,*,2,4,   76-9B
    240   208   110   52   28   25   0   76-9A
$
2,*,1,*,*,*,2,4,   76-6B
    450   285   200   97   37   34   0   76-6A
$
1,*,1,*,*,*,2,4,   76-8B
    160   129   120   67   22   51   40   76-8A
$
1,*,1,*,*,*,2,4,   76-13B
    230   195   110   44   25   22   0   76-13A
$
4,*,1,*,*,*,2,4,   76-12B
    220   59   60   5   17   9   0   76-12A
$
4,*,2,*,*,*,2,4,   76-14B
    180   139   90   32   20   23   2   76-14A
$
1,*,2,1,*,*,2,4,   76-15B
    220   158   110   48   20   30   2   76-15A
$
3,*,2,1,2,*,2,4,   76-1B
    220   173   70   40   *   23   7.5   76-1A
$
1,*,1,*,*,*,2,4,   76-2B
    130   194   130   35   27   18   20   76-2A
$
1,*,2,1,*,*,2,4,   76-16B
    165   173   130   73   20   42   7.5   76-16A
$
1,*,5,2,*,*,2,4,   76-4B
    220   101   200   71   31   70   100   76-4A
$
1,*,4,2,*,*,2,4,   76-5B
    240   90   200   135   35   150   100   76-5A
$
1,*,3,*,*,*,2,4,   76-17B
    175   142   100   56   25   39   20   76-17A
$
1,*,1,1,*,*,2,4,   76-18B
    150   73   80   13   20   18   20   76-18A

```
$
1,*,2,1,*,*,2,4,                                                    76-19B
   215     111      70      24      22      21      10              76-19A
$
1,*,2,1,*,*,2,4,                                                    76-20B
   150      75      70      23      19      30      20              76-20A
$
1,*,2,1,2,*,2,4,                                                    76-21B
   150      93     100      33      22      35      10              76-21A
$
2,1,1,*,2,*,2,4,                                                    77-15
   250     160      60      33      18      20       0              77-15A
$
2,1,3,*,*,*,2,4,                                                    77-16
   180      83     120      54      27      65      10              77-16
$
1,1,3,*,*,*,2,4,                                                    77-17
   190      99     130      84      26      92      60              77-17A
$
2,1,1,2,*,*,2,4,                                                    77-18
   160      77     120      73      26      94      20              77-18A
$
2,1,3,2,2,1,2,4,                                                    77-20
   200     210     100      75      21      35      10              77-20A
$
2,1,1,*,*,*,2,4,                                                    77-25
   330     296     100      66      20      22      15              77-25A
$
2,1,1,*,*,1,2,4,                                                    77-28
   250     164      80      39      16      23       5              77-28A
$
1,1,5,3,*,*,2,4,                                                    77-31
   130      60     120      60      25     100      50              77-31A
$
1,1,4,3,2,*,2,4,                                                    77-32
   130      90     150      55      31      61      80              77-32A
$
2,1,1,*,2,1,2,4,                                                    77-35
   300     165     120      70      27      42     120              77-35A
$
2,1,1,*,*,1,2,4,                                                    77-36
   390     250     170     134      32      53     100              77-36A
$
2,1,1,*,*,1,2,4,                                                    77-37
   350     181     110      47      26      25       0              77-37A
$
1,1,3,2,2,*,2,4,                                                    77-40
   135     179     110      57      25      31      20              77-40A
$
1,1,3,2,2,*,2,4,                                                    77-42
   175     101     120      17      23      16      20              77-42A
$
2,1,1,*,2,1,2,4,                                                    77-43
   330     260     170     133      32      51      80              77-43A
$
2,1,1,*,*,*,2,4,                                                    77-44
   260     100      70      23      17      23       0              77-44A
```

```
$
2,1,1,*,*,1,2,4,                                                    77-45
    200    179    100    47    24    26    0                        77-45A
$
1,1,3,2,2,*,2,4,                                                    77-47
    180    150    100    72    21    48    20                       77-47A
$
1,1,4,3,2,1,2,4,                                                    77-48
    150    110    120    81    24    73    10                       77-48A
$
1,1,4,3,2,1,2,4,                                                    77-50
    185    75     70     21    22    28    0                        77-50A
$
1,1,4,3,*,*,2,4,                                                    77-52
    220    145    150    100   35    68    80                       77-52A
$
2,1,3,2,2,1,2,4,                                                    77-53
    205    190    70     42    20    22    10                       77-53A
$
2,1,1,*,*,1,2,4,                                                    77-54
    230    195    90     51    22    26    10                       77-54A
$
1,1,5,3,2,1,2,4,                                                    77-55B
    200    115    190    140   28    121   100                      77-55A
$
1,1,3,2,*,*,2,4,                                                    77-57
    220    90     90     30    22    33    10                       77-57A
$
1,1,3,*,*,*,2,4,                                                    77-58
    140    60     70     11    22    18    5                        77-58A
$
1,1,3,3,2,*,2,4,                                                    77-59
    190    150    120    25    27    16    10                       77-59A
$
1,1,3,*,*,*,2,4,                                                    77-61
    175    83     120    63    28    75    100                      77-61A
$
1,1,3,2,*,*,*,4,                                                    77-63
    180    190    130    80    28    42    40                       77-63A
$
1,1,3,2,*,1,2,4,                                                    77-64
    135    140    100    31    22    22    40                       77-64A
$
1,1,4,3,2,1,2,4,                                                    77-66B
    170    94     120    88    26    93    100                      77-66A
$
2,1,1,*,*,1,2,4,                                                    77-67
    300    265    110    104   22    39    60                       77-67A
$
1,1,1,*,*,1,2,4,                                                    77-69
    200    129    70     29    20    22    0                        77-69
$
2,1,1,1,3,1,2,4,                                                    LAT20
    415    266    210    108   25    40    22                       LAT20
$
2,1,1,1,3,1,2,4,                                                    LAT21
    310    220    150    88    21    40    20                       LAT21
```

```
$
2,1,1,1,3,1,2,4,                                        LAT22
    406     238    155    103    29    43    18         LAT22
$
2,1,1,1,3,1,2,4,                                        LAT23
    325     167    170     74    30    44    20         LAT23
$
1,1,*,*,2,*,2,4,                                        JOH35
    190      94    155     98    27   104   100         JOH35
$
1,1,*,*,2,*,2,*,                                        JOH36
    170     110    195    140    37   127   100         JOH36
$
1,1,*,*,2,*,2,*,                                        JOH37
    190      66    135     70    30   106   100         JOH37
$
1,1,*,*,2,*,2,*,                                        JOH38
    230      85    167    128    34   150   100         JOH38
$
2,1,1,*,*,*,2,4,                                        77108B
    425     246    120     80    25    32    40         77108A
$
2,1,3,*,*,*,2,4,                                        77109B
    350     218    150    120    27    55    40         77109A
$
2,1,1,*,*,*,2,4,                                        77110B
    275     207    120     92    27    44    40         77110A
$
2,1,1,*,*,*,2,4,                                        77111B
    360     152    120     50    27    33    40         77111A
$
2,1,1,*,*,*,2,4,                                        77112B
    320     168     90     63    21    37    40         77112A
$
2,1,1,*,*,*,2,4,                                        77113B
    420     281    150    128    29    45    40         77113A
$
2,1,1,*,*,*,2,4,                                        77114B
    290     282    110     71    25    25    40         77114A
$
2,1,3,*,*,*,2,4,                                        77115B
    310     200    120     90    27    45    40         77115A
$
2,1,1,*,*,*,2,4,                                        77116B
    330     170    100     73    24    43    40         77116A
$
2,1,1,*,*,*,2,4,                                        77117B
    350     253    130     75    29    29    40         77117A
$
2,1,1,*,*,*,2,4,                                        77118B
    360     180    140     82    24    45    40         77118A
$
2,1,1,*,*,*,2,4,                                        77119B
    360     200    120     82    27    41   100         77119A
$
2,1,1,*,*,*,2,4,                                        77120B
    465     238    140    114    31    47   150         77120A
```

```
$
2,1,1,*,*,*,2,4,                                                          78 18B
     260     282    140     89     27     31    100                       78 18A
$
2,1,1,*,*,*,2,4,                                                          78 19B
     310     208    120     94     29     45     10                       78 19A
$
2,1,1,*,*,*,2,4,                                                          78 20B
     340     252    140     96     31     38     15                       78 20A
$
2,1,1,*,*,*,2,4,                                                          78 21B
     370     205    120     83     26     40     30                       78 21A
$
2,1,1,*,*,*,2,4,                                                          78 22B
     250     250    160    120     27     48     10                       78 22A
$END
```

Appendix 2.3 SAHN dissimilarity levels North Queensland (52 entity) data set (NQ52) UPG Classification

FUSION		GROUP	DISSIMILARITY	D(I)-D(I-1)
20 +	26 =	53	.0228	.0228
36 +	42 =	54	.0232	.0004
1 +	2 =	55	.0248	.0016
15 +	32 =	56	.0395	.0147
30 +	34 =	57	.0426	.0031
18 +	19 =	58	.0569	.0143
35 +	53 =	59	.0574	.0005
37 +	56 =	60	.0582	.0008
33 +	49 =	61	.0629	.0048
24 +	41 =	62	.0671	.0042
9 +	12 =	63	.0732	.0061
17 +	58 =	64	.0790	.0058
16 +	52 =	65	.0922	.0132
44 +	61 =	66	.0940	.0018
22 +	47 =	67	.0962	.0022
48 +	60 =	68	.1221	.0259
45 +	66 =	69	.1279	.0059
6 +	11 =	70	.1370	.0091
54 +	59 =	71	.1523	.0153
25 +	51 =	72	.1612	.0089
28 +	50 =	73	.1617	.0005
3 +	55 =	74	.1844	.0227
63 +	64 =	75	.2072	.0228
40 +	73 =	76	.2244	.0171
68 +	69 =	77	.2317	.0073
5 +	70 =	78	.2336	.0019
31 +	71 =	79	.2601	.0265
38 +	39 =	80	.2745	.0144
21 +	23 =	81	.2902	.0157
46 +	77 =	82	.3028	.0126
65 +	78 =	83	.3083	.0054
27 +	67 =	84	.3447	.0364
62 +	79 =	85	.3525	.0078
10 +	74 =	86	.3554	.0029
29 +	57 =	87	.3966	.0412
8 +	75 =	88	.3966	.0000
76 +	84 =	89	.4048	.0082
72 +	85 =	90	.4421	.0373
82 +	83 =	91	.4695	.0275
80 +	91 =	92	.5526	.0831
13 +	43 =	93	.5671	.0145
88 +	92 =	94	.5787	.0116
89 +	93 =	95	.6161	.0374
86 +	90 =	96	.6266	.0105
81 +	96 =	97	.7864	.1598
94 +	97 =	98	.8059	.0195
4 +	87 =	99	.8086	.0027
7 +	98 =	100	.8884	.0798
14 +	95 =	101	.9302	.0418
100 +	101 =	102	1.3593	.4291
99 +	102 =	103	1.6420	.2827

MOJENA OPTIMAL GROUP DISTANCE - 1.06 (FORMULA 1, K=3)

Appendix 2.4 SAHN dissimilarity levels North Queensland (52 entity) data set (NQ52) ISS Classification

FUSION		GROUP	DISSIMILARITY	D(I)-D(I-1)
20 +	26 =	53	.0228	.0228
36 +	42 =	54	.0232	.0004
1 +	2 =	55	.0248	.0016
15 +	32 =	56	.0395	.0147
30 +	34 =	57	.0426	.0031
18 +	19 =	58	.0569	.0143
33 +	49 =	59	.0629	.0060
37 +	56 =	60	.0644	.0015
24 +	41 =	61	.0671	.0027
35 +	53 =	62	.0689	.0018
9 +	12 =	63	.0732	.0043
17 +	58 =	64	.0864	.0132
16 +	52 =	65	.0922	.0058
22 +	47 =	66	.0962	.0040
44 +	59 =	67	.1044	.0082
6 +	11 =	68	.1370	.0326
45 +	67 =	69	.1501	.0131
48 +	60 =	70	.1571	.0070
25 +	51 =	71	.1612	.0041
28 +	50 =	72	.1617	.0005
31 +	54 =	73	.2301	.0684
3 +	55 =	74	.2376	.0075
40 +	72 =	75	.2452	.0076
5 +	68 =	76	.2657	.0205
38 +	39 =	77	.2745	.0088
21 +	23 =	78	.2902	.0157
63 +	64 =	79	.3961	.1059
8 +	10 =	80	.3996	.0035
46 +	69 =	81	.4172	.0176
27 +	66 =	82	.4275	.0104
62 +	73 =	83	.4468	.0192
29 +	57 =	84	.5145	.0678
65 +	76 =	85	.5234	.0089
13 +	43 =	86	.5671	.0437
70 +	81 =	87	.6237	.0566
14 +	86 =	88	.7016	.0780
7 +	80 =	89	.7381	.0365
75 +	82 =	90	.7490	.0109
61 +	83 =	91	.8091	.0602
71 +	91 =	92	.9520	.1429
77 +	90 =	93	1.0649	.1129
4 +	84 =	94	1.0737	.0088
74 +	89 =	95	1.1316	.0580
79 +	85 =	96	1.3439	.2123
78 +	92 =	97	1.5590	.2151
88 +	93 =	98	2.3653	.8064
95 +	96 =	99	2.3723	.0069
87 +	99 =	100	3.7082	1.3359
94 +	97 =	101	4.7452	1.0371
100 +	101 =	102	8.8490	4.1038
98 +	102 =	103	10.3645	1.5154

MOJENA OPTIMAL GROUP DISTANCE -   4.90   (FORMULA 1, K=3)

Appendix 2.5 PCOA Vector scores, north Queensland (52 entity) data set (NQ52) analysis.

TRACE=   6.359

EIGENVALUES

2.248	1.726	.546	.478	.301	.270	.226	.175	.167	.117
.110	.102	.069	.041	.037	.028	.017	.016	.009	.006
.002	.000	.000	.000	.000	.000	.000	.000	-.001	-.001
-.001	-.001	-.001	-.002	-.002	-.002	-.003	-.004	-.004	-.004
-.005	-.006	-.009	-.009	-.013	-.015	-.017	-.022	-.031	-.036
-.047	-.095								

VECTORS SCALED BY EIGENVALUE

VECTORS

E.VALUE	2.248	1.726	.546	.478	.301	.270	.226
XTRACE	35%	27%	8%	7%	4%	4%	3%
ACC. %	35%	62%	71%	78%	83%	87%	91%
1	-.188	-.172	-.100	.032	-.079	.075	.042
2	-.244	-.149	-.090	.012	-.081	.094	.045
3	-.063	-.169	-.132	.081	-.087	.076	.069
4	.291	-.496	-.180	.175	-.028	.058	.076
5	.010	.094	-.059	-.027	-.028	.035	-.150
6	-.083	-.042	-.104	.093	-.104	-.006	-.098
7	-.351	.009	-.001	-.129	-.035	.150	.025
8	-.218	.041	-.074	-.009	.124	-.007	.106
9	-.134	.056	-.177	.046	.128	-.076	-.038
10	-.188	-.063	-.196	.017	.102	-.035	.173
11	-.048	.041	-.099	.105	-.130	.004	-.117
12	-.056	.084	-.174	.051	.161	-.100	-.071
13	.343	.136	-.069	.078	.018	.172	-.060
14	.593	.177	-.088	-.010	.105	.146	.033
15	-.034	.150	.032	.142	-.007	-.044	.023
16	-.237	.125	-.088	-.073	-.047	.083	-.127
17	-.212	.109	-.154	.004	.089	-.035	.002
18	-.232	.203	-.119	-.055	.121	-.020	-.022
19	-.145	.174	-.138	-.016	.107	-.040	-.002
20	-.219	-.173	.084	-.116	.005	-.024	-.002
21	.030	.032	.145	-.009	.085	.071	.144
22	.187	.192	.059	.029	.064	.006	-.002
23	.091	-.034	.124	-.122	.080	.215	-.024
24	-.022	-.122	.204	.073	.095	-.053	.045
25	-.059	-.360	.029	.017	.015	-.088	-.059
26	-.190	-.184	.082	-.122	.032	-.024	-.043
27	.139	.250	.005	-.159	-.029	.032	-.008
28	.212	.205	-.043	-.084	-.133	-.032	.077
29	.173	-.195	.051	-.120	-.004	.017	-.032
30	.393	-.369	.004	-.017	.011	-.031	-.039
31	-.033	-.283	.008	-.031	-.035	.031	.030
32	-.008	.105	.104	.176	-.011	-.030	-.020
33	-.087	.143	.109	.132	-.043	.049	.008
34	.352	-.329	.006	.004	.005	-.076	-.003

35	-.239	-.131	.086	-.149	.016	.065	-.001
36	-.090	-.167	.046	-.053	-.014	.005	-.016
37	-.010	.105	.121	.115	.044	-.020	-.030
38	.096	.149	-.010	-.111	-.067	-.100	.045
39	-.125	.148	.012	-.137	-.144	-.094	.081
40	.340	.083	-.098	-.029	-.121	-.063	.088
41	-.128	-.103	.224	.043	.065	-.045	.061
42	-.097	-.198	.053	-.063	.002	-.020	-.032
43	.465	.132	.012	-.129	.038	-.084	-.034
44	-.106	.128	.119	.107	-.008	.071	.012
45	-.216	.232	.101	.047	-.048	-.017	.042
46	-.039	.092	.020	.097	-.154	-.081	.082
47	.182	.222	.067	.016	.019	.023	-.002
48	.116	.076	.096	.227	-.003	-.020	-.042
49	-.071	.138	.137	.119	-.018	-.007	-.054
50	.250	.180	.017	-.177	-.045	-.086	.017
51	.099	-.305	.047	-.047	.048	-.090	-.092
52	-.191	.035	-.011	-.043	-.078	-.033	-.107

Appendix 2.6 SAHN dissimilarity levels North and south Queensland (78 entity) data set (NQ78) UPG Classification

UNWEIGHTED PAIR GROUP OR GROUP-AVERAGE SORTING

FUSION		GROUP	DISSIMILARITY	D(I)-D(I-1)	FUSION		GROUP	DISSIMILARITY	D(I)-D(I-1)
36 +	42 =	79	.0201	.0201	56 +	115 =	118	.1478	.0032
20 +	26 =	80	.0233	.0032	74 +	88 =	119	.1610	.0132
1 +	2 =	81	.0234	.0001	28 +	40 =	120	.1627	.0017
65 +	69 =	82	.0261	.0027	101 +	106 =	121	.1767	.0140
30 +	34 =	83	.0301	.0040	110 +	118 =	122	.1804	.0038
15 +	32 =	84	.0306	.0005	3 +	81 =	123	.1812	.0008
71 +	77 =	85	.0314	.0008	95 +	96 =	124	.1871	.0059
63 +	75 =	86	.0410	.0096	5 +	109 =	125	.2091	.0220
55 +	76 =	87	.0437	.0027	112 +	114 =	126	.2109	.0018
29 +	72 =	88	.0483	.0046	113 +	122 =	127	.2166	.0057
35 +	80 =	89	.0496	.0013	53 +	78 =	128	.2525	.0359
50 +	57 =	90	.0530	.0035	38 +	39 =	129	.2598	.0073
14 +	60 =	91	.0534	.0004	73 +	116 =	130	.2827	.0229
33 +	49 =	92	.0540	.0006	102 +	125 =	131	.2851	.0023
37 +	84 =	93	.0554	.0014	46 +	126 =	132	.2929	.0079
18 +	19 =	94	.0573	.0020	27 +	121 =	133	.3007	.0078
9 +	12 =	95	.0607	.0034	119 +	130 =	134	.3211	.0204
17 +	94 =	96	.0632	.0025	127 +	128 =	135	.3243	.0032
31 +	64 =	97	.0640	.0008	21 +	23 =	136	.3247	.0004
61 +	85 =	98	.0642	.0002	43 +	107 =	137	.3308	.0061
24 +	41 =	99	.0644	.0002	120 +	133 =	138	.3477	.0169
70 +	87 =	100	.0693	.0049	99 +	117 =	139	.3500	.0022
59 +	90 =	101	.0717	.0025	8 +	124 =	140	.3881	.0381
16 +	52 =	102	.0747	.0030	10 +	123 =	141	.3911	.0030
44 +	92 =	103	.0756	.0009	104 +	135 =	142	.4151	.0240
62 +	68 =	104	.0769	.0014	134 +	142 =	143	.4429	.0279
51 +	67 =	105	.0787	.0018	131 +	132 =	144	.4939	.0510
22 +	47 =	106	.0897	.0110	136 +	139 =	145	.5650	.0711
58 +	91 =	107	.0949	.0052	13 +	138 =	146	.5659	.0009
86 +	100 =	108	.0985	.0036	129 +	144 =	147	.5723	.0065
6 +	11 =	109	.0988	.0004	140 +	147 =	148	.6052	.0329
82 +	97 =	110	.1014	.0026	137 +	146 =	149	.6237	.0184
54 +	98 =	111	.1073	.0059	141 +	145 =	150	.6879	.0642
45 +	103 =	112	.1121	.0048	4 +	143 =	151	.7212	.0333
25 +	105 =	113	.1144	.0023	148 +	150 =	152	.7428	.0216
48 +	93 =	114	.1177	.0033	7 +	152 =	153	.8472	.1044
108 +	111 =	115	.1214	.0037	151 +	153 =	154	1.1001	.2529
66 +	83 =	116	.1413	.0199	149 +	154 =	155	1.4489	.3488
79 +	89 =	117	.1446	.0033					

MOJENA OPTIMAL GROUP DISTANCE -   .79

Appendix 2.7 SAHN dissimilarity levels North and south Queensland (78 entity) data set (NQ78) ISS Classification

FUSION	GROUP	DISSIMILARITY	D(I)-D(I-1)	FUSION	GROUP	DISSIMILARITY	D(I)-D(I-1)
36 + 42 =	79	.0201	.0201	74 + 88 =	118	.1986	.0150
20 + 26 =	80	.0233	.0032	3 + 81 =	119	.2338	.0352
1 + 2 =	81	.0234	.0001	53 + 105 =	120	.2424	.0086
65 + 69 =	82	.0261	.0027	5 + 106 =	121	.2459	.0034
30 + 34 =	83	.0301	.0040	38 + 39 =	122	.2598	.0139
15 + 32 =	84	.0306	.0005	73 + 83 =	123	.2869	.0271
71 + 77 =	85	.0314	.0008	89 + 109 =	124	.2918	.0049
63 + 75 =	86	.0410	.0096	115 + 117 =	125	.2988	.0070
55 + 76 =	87	.0437	.0027	79 + 93 =	126	.3023	.0036
29 + 72 =	88	.0483	.0046	21 + 23 =	127	.3247	.0224
50 + 57 =	89	.0530	.0047	94 + 98 =	128	.3636	.0389
14 + 60 =	90	.0534	.0004	8 + 10 =	129	.3901	.0265
33 + 49 =	91	.0540	.0006	4 + 120 =	130	.4070	.0169
18 + 19 =	92	.0573	.0033	46 + 111 =	131	.4098	.0028
35 + 80 =	93	.0583	.0010	27 + 124 =	132	.4114	.0016
9 + 12 =	94	.0607	.0024	43 + 108 =	133	.4557	.0443
37 + 84 =	95	.0636	.0029	100 + 121 =	134	.5015	.0457
31 + 64 =	96	.0640	.0004	114 + 125 =	135	.5175	.0160
24 + 41 =	97	.0644	.0004	110 + 135 =	136	.5339	.0164
17 + 92 =	98	.0652	.0008	113 + 131 =	137	.5731	.0392
61 + 70 =	99	.0662	.0010	118 + 123 =	138	.6128	.0397
16 + 52 =	100	.0747	.0085	116 + 132 =	139	.6837	.0709
47 + 59 =	101	.0756	.0009	128 + 129 =	140	.7325	.0488
62 + 68 =	102	.0769	.0013	97 + 102 =	141	.7555	.0229
51 + 67 =	103	.0787	.0018	13 + 139 =	142	.8064	.0509
44 + 45 =	104	.0798	.0011	7 + 126 =	143	.8461	.0397
66 + 87 =	105	.0960	.0162	127 + 141 =	144	.9524	.1063
6 + 11 =	106	.0988	.0028	122 + 134 =	145	1.1698	.2174
54 + 85 =	107	.1005	.0017	119 + 143 =	146	1.4217	.2519
58 + 90 =	108	.1087	.0082	130 + 136 =	147	1.6471	.2254
22 + 101 =	109	.1181	.0094	137 + 145 =	148	2.0946	.4475
25 + 103 =	110	.1262	.0082	133 + 142 =	149	2.2257	.1311
91 + 104 =	111	.1369	.0107	138 + 147 =	150	2.3657	.1400
78 + 86 =	112	.1520	.0151	144 + 146 =	151	3.2117	.8460
48 + 95 =	113	.1530	.0010	140 + 148 =	152	3.3510	.1394
82 + 96 =	114	.1577	.0047	151 + 152 =	153	4.9827	1.6316
99 + 107 =	115	.1605	.0028	149 + 153 =	154	17.4474	12.4648
28 + 40 =	116	.1627	.0022	150 + 154 =	155	19.6701	2.2227
56 + 112 =	117	.1836	.0209				

MOJENA OPTIMAL GROUP DISTANCE -   6.99

NUMBER OF GROUPS IS   3

Appendix 2.8 PCOA Vector scores, north and south Queensland data set (78 entities) analysis

TRACE=   8.758

EIGENVALUES

3.130	2.934	.638	.545	.403	.335	.290	.258	.231	.157
.128	.123	.107	.076	.054	.045	.028	.024	.016	.012
.006	.001	.000	.000	.000	.000	.000	.000	.000	.000
.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
.000	.000	.000	.000	.000	.000	-.001	-.001	-.001	-.001
-.001	-.001	-.002	-.002	-.002	-.003	-.003	-.003	-.003	-.004
-.004	-.005	-.005	-.006	-.006	-.008	-.009	-.013	-.015	-.018
-.019	-.022	-.029	-.041	-.047	-.076	-.155	-.276		

VECTORS SCALED BY EIGENVALUE

VECTORS

E.VALUE	3.130	2.934	.638	.545	.403	.335	.290
%TRACE	35%	33%	7%	6%	4%	3%	3%
ACC. %	35%	69%	76%	82%	87%	91%	94%
1	.153	-.207	-.059	-.004	-.100	.067	-.009
2	.208	-.224	-.059	-.019	-.077	.074	-.008
3	.048	-.135	-.087	.050	-.142	.073	.053
4	-.384	-.180	-.107	.178	-.141	.032	.082
5	.112	.077	-.099	-.035	.028	.073	-.011
6	.126	-.063	-.100	.063	-.070	.111	.009
7	.358	-.187	-.032	-.120	.059	.066	.009
8	.275	-.074	-.067	.021	-.020	-.142	.003
9	.212	-.009	-.167	.074	-.011	-.145	-.052
10	.217	-.075	-.075	-.010	-.222	-.190	-.018
11	.127	.003	-.110	.071	-.087	.151	.001
12	.158	.048	-.176	.090	-.005	-.172	-.027
13	-.113	.313	-.093	.063	.030	.089	-.097
14	-.284	.482	-.122	.026	.054	-.015	.044
15	.189	.109	.030	.157	.014	.020	-.010
16	.310	-.042	-.135	-.074	.054	.090	-.048
17	.299	-.014	-.148	.023	-.004	-.104	-.079
18	.355	.032	-.144	-.022	.049	-.118	-.074
19	.284	.090	-.109	-.011	-.061	-.133	-.030
20	.172	-.207	.118	-.147	-.040	-.039	.033
21	.060	.055	.101	.062	.127	-.050	.120
22	.032	.263	.020	.071	.109	-.017	-.011
23	-.028	.039	.047	-.097	.143	.022	.141
24	.059	-.059	.241	.068	-.006	-.088	.039
25	-.045	-.277	.052	-.003	-.028	-.032	-.014
26	.136	-.232	.051	-.105	.067	-.030	.028
27	.090	.277	-.060	-.106	.093	.027	.079
28	.026	.300	-.019	-.090	-.116	.075	.033
29	-.138	-.012	.096	-.173	-.051	.017	-.128
30	-.398	-.035	.017	-.021	-.019	.006	-.053
31	-.030	-.201	.009	-.024	-.001	.030	.057
32	.158	.116	.140	.138	-.065	.033	-.019
33	.239	.101	.126	.101	-.019	.078	-.039
34	-.339	-.010	.076	-.033	-.135	-.026	-.005

35	.192	-.218	.046	-.131	.099	-.002	.039
36	.055	-.164	.020	-.040	.013	.020	.084
37	.164	.119	.148	.091	-.007	-.016	-.021
38	.100	.202	-.008	-.078	-.061	-.011	.151
39	.278	.083	.019	-.121	-.072	.046	.094
40	-.138	.276	-.077	-.016	-.097	.058	.036
41	.153	-.102	.258	.031	.000	-.063	.010
42	.051	-.188	.036	-.058	.017	.000	.045
43	-.193	.386	-.005	-.090	.010	-.050	.038
44	.238	.065	.092	.109	.086	.062	-.023
45	.360	.062	.062	.075	.070	.054	-.007
46	.176	.092	.079	.085	-.122	.080	.028
47	.049	.279	.036	.033	.089	.034	-.104
48	.034	.144	.096	.209	.004	.057	-.043
49	.215	.080	.102	.114	.058	.075	-.073
50	-.003	.308	.017	-.165	-.030	-.003	.003
51	-.143	-.155	.053	-.056	.005	-.045	-.042
52	.248	-.067	-.048	-.047	.014	.079	-.001
53	-.304	-.216	-.149	.113	.116	.003	.005
54	-.128	-.223	-.130	.033	.163	-.007	-.005
55	-.255	-.212	-.138	.079	.101	.012	.010
56	-.186	-.150	-.166	.059	.138	.057	.034
57	-.056	.344	-.004	-.064	.009	-.033	-.053
58	-.294	.509	-.005	.009	-.053	-.031	.056
59	-.008	.381	.009	-.098	.008	.008	-.053
60	-.246	.495	.010	-.067	.021	-.058	.041
61	-.169	-.206	.024	-.018	-.013	-.005	-.042
62	-.202	-.015	.113	.142	.053	-.107	.015
63	-.133	-.101	.012	-.032	.004	-.007	.025
64	-.080	-.136	.000	-.060	.022	.043	-.011
65	-.008	-.168	.038	-.103	.055	-.018	-.025
66	-.322	-.148	.008	.040	-.037	-.027	.008
67	-.103	-.197	.038	-.004	-.047	.004	-.029
68	-.096	-.034	.127	.111	.043	-.083	-.004
69	-.066	-.138	.024	-.083	.042	-.010	-.006
70	-.177	-.163	.009	.013	-.052	.026	-.013
71	-.141	-.123	-.002	-.045	.045	-.007	.003
72	-.195	-.088	.031	-.094	.015	.019	-.121
73	-.395	-.056	.045	-.092	-.007	.025	-.214
74	-.215	-.096	.036	-.029	-.040	.022	-.112
75	-.143	-.126	-.001	.005	-.013	-.007	.085
76	-.215	-.143	-.008	.051	-.057	.008	.067
77	-.139	-.155	.009	-.028	.008	-.006	.012
78	-.204	-.100	-.011	.052	-.009	-.028	.113

Appendix 2.9 SAHN (UPG) dissimilarity levels 39 entity subset of the north Queensland
(52 entity) data set UPG GP β Classification Groups

FUSION		GROUP	DISSIMILARITY	D(I)-D(I-1)
1 +	2 =	40	.0531	.0531
27 +	32 =	41	.0618	.0087
17 +	22 =	42	.0647	.0029
12 +	24 =	43	.0661	.0014
26 +	42 =	44	.0854	.0193
28 +	43 =	45	.1320	.0467
14 +	15 =	46	.1522	.0202
8 +	11 =	47	.1618	.0096
20 +	31 =	48	.1642	.0024
16 +	46 =	49	.1731	.0089
25 +	37 =	50	.1815	.0084
33 +	34 =	51	.2096	.0281
13 +	39 =	52	.2197	.0101
45 +	50 =	53	.2927	.0730
23 +	41 =	54	.3225	.0299
5 +	10 =	55	.3267	.0042
49 +	52 =	56	.3940	.0673
51 +	53 =	57	.4031	.0091
35 +	55 =	58	.4077	.0046
3 +	40 =	59	.4231	.0153
18 +	19 =	60	.4283	.0053
7 +	9 =	61	.4299	.0016
44 +	54 =	62	.4472	.0173
48 +	62 =	63	.5118	.0647
30 +	56 =	64	.5536	.0418
4 +	36 =	65	.5915	.0379
21 +	63 =	66	.6053	.0138
47 +	61 =	67	.6066	.0013
57 +	58 =	68	.6291	.0225
64 +	67 =	69	.6402	.0111
59 +	66 =	70	.7176	.0774
65 +	68 =	71	.7362	.0186
29 +	60 =	72	.7369	.0007
69 +	71 =	73	.8885	.1516
70 +	73 =	74	1.0374	.1489
6 +	74 =	75	1.2475	.2101
72 +	75 =	76	1.3381	.0906
38 +	76 =	77	1.8531	.5151

MOJENA OPTIMAL GROUP DISTANCE - 1.33

Appendix 3.1 Myall Lakes data set and UPG Classification results

```
**** T=MYALL HYBRID SITE UPG ANALYSIS 40 ENTITIES
**** II=40, IFN=10, IDN=5, APRINT=AUTO, NGREQ=40, SORTSTRAT=UPG
**** *AMASK
.... 1-5 0
.... 1-7 9 10 0
```

1/	2/	3/	1/	3/								A1M1B
3.70	2.75	34	286	50	70	8.41	75	100	0			A1M1
1/	2/	3/	1/	3/								A2M1B
4.00	2.70	20	*	42	51	*	100	111	0			A2M1
1/	2/1,2/	*/	1/									A3M1B
3.20	2.20	75	230	37	51	3.06	0	21	5.0			A3M1
1/	2/	1/	*/	1/								A4M1B
3.30	2.20	93	240	35	53	2.58	0	21	5.0			A4M1
1/	2/	3/	1/	3/								A5M1B
3.10	2.30	46	286	37	60	6.21	50	40	0			A5M1
1/	2/	1/	2/	1/								A6M1B
3.40	*	129	119	22	34	.92	0	10	5.0			A6M1
1,3/	2/	1/	2/	1/								A7M1B
4.00	*	123	48	16	26	.39	0	4	5.0			A7M1
1,3/	2/	1/	2/	1/								A8M1B
3.50	1.80	133	69	15	26	.52	0	5	5.0			A8M1
3/	2/	1/	2/	2/								A9M1B
3.00	*	100	34	11	20	.34	1	0	5.0			A9M1
1,3/	2/	1/	2/	1/								A10M1B
3.00	*	48	11	8	19	.23	0	0	5.0			A10M1
1,3/	2/	1/	2/	1/								A11M1B
4.00	2.40	81	39	11	21	.48	0	0	5.0			A11M1
1,3/	2/	1/	2/	1/								A12M1B
3.75	*	98	56	12	22	.57	0	0	5.0			A12M1
1,3/	2/	3/	1/	3/								B 1M1B
3.00	2.50	57	240	42	51	4.21	50	40	1.0			B1M1
1,3/	2/	3/	1/	1/								B 2M1B
3.70	2.30	40	210	57	89	5.25	0	85	0			B2M1
1,3/	2/	1/	*/	1/								B 3M1B
3.50	2.00	61	180	30	40	2.95	0	30	5.0			B3M1
1,3/	2/	3/	1/	3/								B4 M1B
2.75	2.20	40	150	35	43	3.75	100	90	0			B4M1
1,3/	2/	1/	*/	2/								B 5M1B
3.00	2.00	67	153	28	42	2.28	10	30	4.0			B5M1
1/	2/2,3/	1/	1/									C 1M1B
3.50	2.40	33	216	40	60	6.54	0	60	1.0			C1M1
1,3/	2/	3/	1/	3/								C 2M1B
5.00	2.60	45	320	55	68	7.10	50	100	0			C2M1
1,3/	2/	3/	1/	3/								C 3M1B
4.00	2.40	62	144	40	53	2.32	50	100	0			C3M1
1,3/	2/2,3/	1/	3/									C 4M1B
4.20	1.70	60	280	39	50	4.66	50	30	.5			C4M1
1,3/	2/	1/	*/	3/								C 5M1B
3.60	2.30	65	262	40	54	4.03	30	50	2.0			C5M1
1,3/	2/	1/2,3/	1/									C 6M1B
4.10	2.70	133	78	17	30	.58	0	0	5.0			C6M1
1,3/	2/	1/	2/	1/								C 7M1B
4.30	2.70	114	100	18	29	.87	00	0	5.0			C7M1
1,3/	2/	1/	2/	1/								C 8M1B

3.00	2.20	106	70	15	25	.66	0	0	5.0	C8M1
1,3/ 2/ 1/ 2/ 1/										C 9M1B
3.50	2.20	109	55	13	27	.50	0	0	5.0	C9M1
*/ */ 3/ */ 3/										D1 M1B
*	*	41	260	47	66	6.34	50	60	0	D1M1
1,3/ 2/ 3/ */ 3/										D 2M1B
3.40	1.75	31	240	38	57	7.74	50	130	.5	D2M1
1,3/ 2/2,3/ */ 3/										D 3M1B
3.50	2.00	36	130	40	58	3.61	15	100	2.0	D3M1
1,3/ 2/2,3/ */ 3/										D 4M1B
3.50	1.90	45	253	52	66	5.62	20	130	.5	D4M1
3/ 2/ 1/ 2/ 2/										D 5M1B
3.75	1.75	92	30	11	23	.33	3	0	5.0	D5M1
3/ 2/1,2/ 2/ 1/										D 6M1B
3.25	2.00	93	39	12	23	.41	00	0	5.0	D6M1
3/ 2/ 1/ 2/ 1/										D 7M1B
4.00	2.00	82	21	11	24	.26	0	0	5.0	D7M1
3/ 2/ 1/ 2/ 1/										D 8M1B
3.00	1.50	100	27	11	27	.27	0	0	4.0	D8M1
1,3/ 2/ 1/ 2/ 1/										E1 M1B
3.00	2.00	108	40	10	21	.37	0	0	5.0	E1M1
1,3/ 2/1,2/ 2/ 2/										E 2M1B
3.10	1.75	99	90	18	36	.91	2	0	5.0	E2M1
1,3/ 2/1,2/ */ 2/										E 3M1B
3.20	2.20	65	147	27	50	2.26	2	5	5.0	E3M1
1,3/ 2/2,3/ */ 2/										E 4M1B
3.00	1.90	72	197	24	42	2.73	1	5	2.0	E4M1
1,3/ 2/ 3/ */ 3/										E 5M1B
3.60	1.80	47	320	40	57	6.80	10	75	2.0	E5M1
1,3/ 2/2,3/ */ 3/										E 6M1B
4.00	2.10	61	220	34	53	3.28	30	50	1.0	E6M1

ATTRIBUTE NUMBERS AFTER MASKING -

    5 DISORDERED MULTISTATES
    9 FREE FORMAT NUMERICS

    14 STATES IN DISORDERED MULTISTATES

-MSED

STANDARDISED EUCLIDEAN METRIC

-SAHN.

UNWEIGHTED PAIR GROUP OR GROUP-AVERAGE SORTING

FUSION			GROUP	DISSIMILARITY
12 +	26	=	41	.0186
25 +	35	=	42	.0236
7 +	24	=	43	.0328
5 +	27	=	44	.0500
11 +	41	=	45	.0549
1 +	2	=	46	.0896
45 +	43	=	47	.0939
9 +	31	=	48	.0989

```
 8 +   42 =    49        .1032
21 +   40 =    50        .1072
 4 +    3 =    51        .1281
39 +   28 =    52        .1308
13 +   16 =    53        .1539
37 +   17 =    54        .1618
30 +   29 =    55        .1626
49 +   47 =    56        .1861
33 +   32 =    57        .1974
54 +   36 =    58        .2175
44 +   46 =    59        .2324
34 +   57 =    60        .2358
56 +   10 =    61        .2755
55 +   52 =    62        .2847
20 +   53 =    63        .3003
51 +    6 =    64        .3199
48 +   60 =    65        .3440
50 +   62 =    66        .3622
23 +   61 =    67        .3634
38 +   58 =    68        .3863
15 +   67 =    69        .3904
22 +   63 =    70        .4109
66 +   70 =    71        .4531
59 +   18 =    72        .4998
69 +   65 =    73        .6046
19 +   14 =    74        .6456
71 +   72 =    75        .6658
75 +   74 =    76        .7105
68 +   73 =    77        .7677
77 +   64 =    78        .8366
76 +   78 =    79       1.7998
```

MOJENA OPTIMAL GROUP DISTANCE -   1.02
   (FORMULA 1, K=3)

421

Appendix 3.2 Myall Lakes, ISS Classification results.

FUSION		GROUP	DISSIMILARITY
12 +	26 =	41	.0186
25 +	35 =	42	.0236
7 +	24 =	43	.0328
5 +	27 =	44	.0500
11 +	41 =	45	.0670
2 +	1 =	46	.0896
31 +	9 =	47	.0989
40 +	21 =	48	.1072
4 +	3 =	49	.1281
8 +	42 =	50	.1297
28 +	39 =	51	.1308
13 +	16 =	52	.1539
17 +	37 =	53	.1618
29 +	30 =	54	.1626
43 +	45 =	55	.1715
32 +	33 =	56	.1974
36 +	53 =	57	.2360
34 +	56 =	58	.2486
10 +	50 =	59	.2867
23 +	55 =	60	.3314
20 +	52 =	61	.3491
6 +	49 =	62	.3839
44 +	46 =	63	.3949
51 +	54 =	64	.4228
15 +	22 =	65	.4370
38 +	57 =	66	.4799
14 +	18 =	67	.5576
47 +	58 =	68	.5878
48 +	64 =	69	.6556
59 +	60 =	70	.7828
19 +	63 =	71	.7997
61 +	69 =	72	.8936
65 +	66 =	73	1.0574
67 +	71 =	74	1.1276
62 +	73 =	75	2.0258
72 +	74 =	76	2.3248
68 +	70 =	77	2.5503
75 +	77 =	78	4.0885
76 +	78 =	79	23.7747

MOJENA OPTIMAL GROUP DISTANCE -   8.85

Appendix 3.3 GOWER Ordination vector scores, Myall Lakes.

ANALYSIS NUMBER	COLL. NUMBER	VECTOR 1	2	3
1	A1	-.510	-.187	-.064
2	A2	-.443	-.179	.031
3	A3	.025	-.200	-.250
4	A4	.050	-.247	-.191
5	A5	-.374	-.074	-.185
6	A6	.263	-.229	-.132
7	A7	.341	-.096	.139
8	A8	.339	-.012	.029
9	A9	.373	.183	-.042
10	A10	.332	.006	-.027
11	A11	.298	-.107	.129
12	A12	.335	-.067	.093
13	B1	-.279	.046	-.023
14	B2	-.364	-.056	.025
15	B3	.099	-.046	-.001
16	B4	-.273	.140	-.043
17	B5	.088	.111	-.100
18	C1	-.307	-.165	-.189
19	C2	-.494	-.094	.274
20	C3	-.290	.022	.159
21	C4	-.288	.128	.066
22	C5	-.140	-.015	.064
23	C6	.293	-.186	.156
24	C7	.268	-.196	.185
25	C8	.312	-.032	-.031
26	C9	.315	-.062	.045
27	D1	-.489	.033	.004
28	D2	-.369	.154	.027
29	D3	-.253	.142	.032
30	D4	-.392	.142	.013
31	D5	.336	.195	.036
32	D6	.349	.100	-.033
33	D7	.340	.032	.114
34	D8	.368	.159	-.053
35	E1	.349	.002	-.033
36	E2	.254	.173	-.119
37	E3	.096	.090	-.112
38	E4	-.025	.203	-.133
39	E5	-.314	.106	.035
40	E6	-.221	.082	.104

Appendix 3.4 Northern New South Wales analyses, Data set and SAHN Classification and PCOA Ordination results, with associated diagnostic program results, (GCON, GSTAT).

LNXHD= Lennox Head; COFFS= Coffs harbour airport; HATHD=Hat Head; RLBCK=Ridge, Limeburners Creek Reserve; OSLMB=Open swamp, Limeburners Creek reserve; PSLMB=Paperbark swamp, Limeburners Creek Reserve;DMDHD=Diamond Head; RDSTH=Road south from Diamond Head.

DATLST

3 (1,2) 1, 2, 1, 3,						LNXHD250
315	166	32	183	43	110	0	LNXHD250
3, 2, 1, 2, (1,2) 3,						LNXHD251
490	150	20	89	29	59	0	LNXHD251
3, (1,2) 1, (2,3) 1, 3,						LNXHD252
340	90	11	26	18	28	0	LNXHD252
3, 2, 1, 2, 1, 3,						LNXHD253
395	129	16	74	27	57	0	LNXHD253
3, 2, 1, 2, 1, 3,						LNXHD254
345	125	13	35	24	28	0	LNXHD254
3, 2, 1, 3, 1, 3,						COFFS257
330	118	17	58	25	49	0	COFFS257
3, 2, 1, 2, 1, 3,						COFFS258
300	75	13	30	22	40	0	COFFS258
3, 2, 1, 2, 1, 3,						COFFS259
295	90	14	41	23	45	0	COFFS259
3, 2, 1, 2, 1, 3,						COFFS260
270	97	12	35	21	36	0	COFFS260
(1,3) 2, 1, 3, 1, 3,						COFFS261
265	127	19	131	32	103	0	COFFS261
(1,3) 2, 1, 3, 1, 3,						HATHD262
1, 2, 1, 2, (1,2) 3,						HATHD263
375	105	28	200	43	190	0	HATHD263
(1,3) 2, 1, 2, (1,2) 3,						HATHD264
370	133	19	92	30	69	10	HATHD264
1, (1,2) 3, *, 3, 1,						HATHD265
330	34	22	160	34	470	10	HATHD265
(1,3) (1,2) 3, *, 3, 1,						HATHD266
345	81	16	89	24	109	5	HATHD266
(1,3) 2, 3, 2, 1, 3,						HATHD267
305	90	22	107	34	118	5	HATHD267
1, 2, 3, 3, 2, 3,						HATHD268
295	105	21	117	35	110	40	HATHD268
1, 2, 5, 1, 3, 1,						RLBCK269
235	67	23	69	36	102	5	RLBCK269
1, 2, 3, 1, 3, 1,						RLBCK270
245	51	33	145	50	284	68	RLBCK270
1, 2, 4, 1, 3, 1,						RLBCK271
225	35	21	126	33	360	25	RLBCK271
1, 2, 5, 1, 3, 1,						RLBCK272
290	30	30	143	45	476	80	RLBCK272
1, 2, 1, 2, 1, (2,3)						RLBCK273
315	72	34	217	48	300	65	RLBCK273

```
          1,  2,   3,  1,   3,  (1,2)                            RLBCK274
             250      51       29      137      45     268     25     RLBCK274
          1,  2,   5,  1,   3,  (1,2)                            RLBCK275
          1,  2,   1,  3,   1,   3,                              OSLMB276
             320     125       19      105      29      84      0     OSLMB276
          1,  2,   1,  2,   1,   3,                              OSLMB277
             280     140       15       62      31      44      0     OSLMB277
         (1,3)  2,  1,  2,   1,   3,                             OSLMB278
             360      88       11       19      21      21      0     OSLMB278
          1,  2,   1,  2,   1,   3,                              PSLMB279
             340     102       17       84      32      82      20    PSLMB279
         (1,3)  2,  1,  (2,3)  1,   3,                           PSLMB280
             320     106       14       80      27      75      10    PSLMB280
          3,  2,   3,  (2,3)  1,   3,                            DMDHD281
             370     124       12       32      23      22      0     DMDHD281
          3,  2,   3,  (2,3)  1,  (2,3)                          DMDHD282
             445     129       16       60      28      46      0     DMDHD282
         (1,3)  2,  3,  (2,3)  1,   3,                           DMDHD283
             410     131       12       30      24      25      0     DMDHD283
         (1,3)  2,  1,  2,   1,   3,                             DMDHD284
             390     150       20       93      32      62      0     DMDHD284
          3,  2,   1,  (2,3)  1,   3,                            DMDHD285
             350      89       12       18      29      20      0     DMDHD285
          3,  2,   1,  2,   1,   3,                              DMDHD286
             420     103       16       51      25      50      0     DMDHD286
          3,  2,   1,  3,  (1,2)  3,                             RDSTH287
             360     128       17       75      28      58      0     RDSTH287
          3,  2,   1,  3,   1,   3,                              RDSTH290
             400     120       13       56      21      47      0     RDSTH290
```

-MSED.

STANDARDISED EUCLIDEAN METRIC

-SAHN.

UNWEIGHTED PAIR GROUP OR GROUP-AVERAGE SORTING

FUSION	GROUP	DISSIMILARITY	D(I)-D(I-1)
7 + 8 =	38	.0098	.0098
9 + 38 =	39	.0198	.0100
4 + 35 =	40	.0355	.0158
6 + 37 =	41	..0739	.0384
5 + 40 =	42	.0747	.0008
26 + 28 =	43	.1168	.0422
39 + 42 =	44	.1730	.0562
30 + 32 =	45	.1789	.0059
13 + 33 =	46	.1801	.0012

```
36 +  41 =   47      .1999    .0198
10 +  25 =   48      .2068    .0069
34 +  44 =   49      .2073    .0005
27 +  29 =   50      .2365    .0292
19 +  23 =   51      .2996    .0631
49 +  50 =   52      .3007    .0011
31 +  45 =   53      .3246    .0238
43 +  46 =   54      .3555    .0310
47 +  52 =   55      .3974    .0419
21 +  24 =   56      .3995    .0021
48 +  54 =   57      .4687    .0692
55 +  57 =   58      .5281    .0595
18 +  20 =   59      .5644    .0363
16 +  53 =   60      .6413    .0769
51 +  56 =   61      .6935    .0522
 2 +  58 =   62      .6960    .0026
12 +  22 =   63      .7083    .0123
60 +  62 =   64      .7321    .0238
14 +  15 =   65      .7605    .0284
59 +  61 =   66      .8500    .0895
11 +  63 =   67      .8983    .0483
 3 +  64 =   68     1.2143    .3160
17 +  67 =   69     1.2276    .0133
68 +  69 =   70     1.4113    .1837
 1 +  70 =   71     1.7241    .3128
65 +  66 =   72     1.8776    .1535
71 +  72 =   73     2.5449    .6672
```

MOJENA OPTIMAL GROUP DISTANCE -   1.79
   (FORMULA 1, K=3)

NUMBER OF GROUPS IS   5

NO.   1 (GP   1) WITH   1 MEMBERS - 1

NO.   2 (GP   68) WITH   24 MEMBERS - 2 -10 13 16 25 -37

NO.   3 (GP   69) WITH   4 MEMBERS - 11 -12 17 22

NO.   4 (GP   65) WITH   2 MEMBERS - 14 -15

NO.   5 (GP   66) WITH   6 MEMBERS - 18 -21 23 -24

 -PCOA. TRACE=   6.150

EIGENVALUES

2.758	.868	.625	.398	.315	.270	.197	.163	.144	.104
.095	.067	.047	.036	.028	.017	.012	.007	.004	.001
.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
.000	.000	.000	.000	.000	-.003	-.004			

VECTORS SCALED BY EIGENVALUE

E.VALUE	2.758	.868	.625	.398	.315	.270	.197
%TRACE	44%	14%	10%	6%	5%	4%	3%
ACC. %	44%	58%	69%	75%	80%	85%	88%
1	-.043	-.084	-.475	-.119	.039	.039	.045
2	-.242	.096	-.083	.053	.173	-.007	-.209
3	-.232	-.352	-.158	-.095	.014	.094	.064
4	-.220	.026	.003	-.047	.101	-.012	-.026
5	-.244	-.015	.072	-.084	.061	-.014	.001
6	-.190	-.004	.059	.008	-.041	.168	.032
7	-.201	-.045	.122	-.140	.039	-.021	.049
8	-.198	-.029	.098	-.134	.030	-.019	.047
9	-.213	-.043	.119	-.148	.002	-.019	.055
10	-.070	.082	-.026	.001	-.196	.101	.054
11	.033	.256	-.186	.122	-.031	.161	.049
12	.052	.245	-.195	-.024	-.040	-.107	-.137
13	-.142	.113	-.053	-.005	-.007	-.073	-.143
14	.474	-.371	-.215	.009	-.032	-.053	-.024
15	.202	-.484	-.111	.067	-.015	-.026	-.066
16	.003	.015	.001	.081	-.038	-.184	.078
17	.139	.064	.015	.222	-.173	.004	-.052
18	.358	-.073	.207	-.097	-.057	.026	-.094
19	.564	.048	.044	.040	-.010	-.011	.035
20	.454	-.063	.165	-.124	-.085	.012	-.046
21	.599	.076	.075	-.064	.089	.086	-.024
22	.238	.327	-.200	-.056	.062	-.065	.173
23	.506	-.005	.079	.054	.007	-.059	.055
24	.564	.113	.096	.030	.247	.093	.017
25	-.056	.091	-.003	.013	-.186	.071	.003
26	-.103	.080	.030	-.107	-.128	-.110	.005
27	-.204	-.025	.113	-.077	-.005	-.091	-.015
28	-.049	.106	.005	-.082	-.046	-.099	.006
29	-.148	.024	.029	-.005	-.091	.002	.052
30	-.217	-.117	.106	.182	.029	-.038	.060
31	-.181	-.048	.033	.265	.158	-.046	.089
32	-.188	-.083	.084	.231	-.026	-.107	.013
33	-.156	.098	-.059	-.014	.007	-.076	-.047
34	-.233	-.041	.097	-.020	.033	.062	.056
35	-.225	.003	.037	-.048	.136	-.015	-.031
36	-.194	.044	.006	.063	-.028	.168	-.110
37	-.238	-.025	.068	.048	.009	.166	-.017

Appendix 3.5 Beervah Analyses, Data set, SAHN Classification and PCOA Ordination results, with associated diagnostic programs, (BACRIV).

**** II=44, IFN=10, IDN=4, NGREQ=44, SORTSTRAT=UPG

(1,3)	1,	2,	1,								77107B
2.20	1.40	120	110	17	33	.91	0	81	2.0		77107A
1,	1,	1,	2,								7780B
2.00	1.30	132	100	16	24	.75	1	15	5.0		7780A
3,	2,	1,	2,								7781B
3.20	1.85	100	21	10	22	.21	00	0	5.0		7781A
3,	1,	2,	1,								7782B
2.20	1.40	134	77	17	31	.57	1	20	3.0		7782A
3,	(1,2)	1,	2,								7783B
3.00	1.80	102	18	10	19	.17	0	5	5.0		7783A
3,	(1,2)	1,	3,								7784B
2.50	1.75	115	20	10	20	.17	0	0	5.0		7784A
3,	2,	(1,2)	3,								7785B
2.40	1.70	118	24	11	22	.20	0	0	5.0		7785A
3,	2,	1,	2,								7786B
3.10	2.00	115	47	12	20	.40	0	0	5.0		7786A
3,	1,	(1,2)	1,								7787B
2.20	1.50	95	150	23	39	1.57	5	70	2.0		7787A
3,	1,	2,	1,								7788B
2.60	1.60	126	40	12	21	.31	5	0	4.0		7788A
3,	1,	(1,2)	2,								7789B
2.30	1.60	110	49	13	20	.44	5	4	4.5		7789A
1,	1,	2,	1,								7790B
2.10	1.30	77	70	15	28	.90	5	40	2.0		7790A
3,	1,	(1,2)	(1,2)								7791B
1.80	1.20	79	92	16	28	1.16	5	50	3.0		7791A
(1,3)	1,	1,	1,								7792B
1.90	1.20	136	68	17	27	.50	0	30	5.0		7792A
3,	1,	1,	2,								7793B
2.00	1.40	85	22	10	18	.25	5	15	5.0		7793A
3,	1,	(1,2)	1,								7794B
1.80	1.35	115	76	13	26	.66	5	40	5.0		7794A
(1,3)	1,	1,	2,								7795B
2.50	1.70	105	49	12	19	.46	5	0	4.0		7795A
3,	1,	(2,3)	1,								7796B
2.05	1.35	144	27	12	21	.20	5	5	1.0		7796A
3,	1,	(1,2)	2,								7797B
2.20	1.40	121	61	14	26	.50	5	10	5.0		7797A
3,	(1,2)	(1,2)	1,								7798B
2.25	1.60	73	133	22	33	1.82	5	12	5.0		7798A
(1,3)	1,	(1,2)	2,								7799B
2.30	1.50	118	72	15	26	.61	1	10	3.0		7799A
3,	2,	(1,2)	2,								77100B
2.00	1.40	98	45	12	23	.45	1	0	5.0		77100A
3,	1,	(2,3)	1,								77101B
3,	1,	(1,2)	1,								77102B
2.00	1.60	128	110	21	34	.85	5	100	4.0		77102A
3,	1,	(2,3)	1,								77103B
2.00	1.20	97	65	12	27	.67	5	70	1.0		77103A
(1,3)	1,	*,	1,								77104B
2.10	1.30	118	37	12	21	.31	*	15	*		77104A
3,	1,	(2,3)	1,								77105B
2.00	1.50	83	86	18	31	1.03	1	43	3.0		77105A

```
              3,  1,  1,  2,                                                    77106B
                1.90  1.20   121    78    16    26    .64     0    22   5.0     77106A
                                                                               BHB1B
              3,  *  (1,2)  *,
                2.30      *    100    55    13    22    .54     0    10   4.0     BHB1A
                                                                               BHB2B
              3,  2,  2,  1,
                1.80  *      104    35    11    23    .33     0    30   3.0     BHB2A
                                                                               BHB3B
             (1,3)  2,  1,  2,
                2.70  *       90    29     8    15    .32     1     0   5.0     BHB3A
                                                                               BHB4B
              3,  2,  1,  2,
                2.75  *       98    27     8    18    .27     0     0   5.0     BHB4A
                                                                               BHB5B
              3,  2,  1,  2,
                2.50  *      120    20    10    20    .16     1     0   5.0     BHB5A
                                                                               BHB6B
              3,  2,  1,  2,
                2.30  *      140    45    13    23    .32     1     0   5.0     BHB6A
                                                                               BHB7B
              1,  1,  (2,3)  1,
                1.95  *       85    44    11    24    .51     0    32   3.0     BHB7A
                                                                               BHB8B
              1,  1,  (1,2)  2,
                1.80  *      132    81    15    27    .61     1    24   5.0     BHB8A
                                                                               BHB9B
              1,  1,  (1,2)  *,
                1.95  *       93   115    19    33   1.23     *    50   3.0     BHB9A
                                                                               BHB10B
              1,  1,  (1,2)  *,
                1.75  *       97    73    12    25    .75     1    30   4.0     BHB10A
                                                                               BR1B
              3,  2,  1,  2,
                2.60  *       97    17     9    19    .17     0     0   5.0     BR1A
                                                                               BR2B
             (1,3)  2,  1,  2,
                2.60  *      100    24    10    20    .24     0     0   5.0     BR2A
                                                                               BR3B
              3,  2,  1,  2,
                2.30  *      115    37    10    23    .32     0     0   5.0     BR3A
                                                                               BR4B
              3,  2,  1,  2,
                2.80  *      150    17    10    19    .11     0     0   5.0     BR4A
                                                                               BR5B
              3,  2,  1,  2,
                2.65  *      115    42    12    23    .36     0     0   5.0     BR5A
                                                                               BR7B
              3,  2,  1,  2,
                3.00  *       98    10     7    17    .10     0     0   5.0     BR7A
```

STANDARDISED EUCLIDEAN METRIC

UNWEIGHTED PAIR GROUP OR GROUP-AVERAGE SORTING

FUSION	GROUP	DISSIMILARITY	D(I)-D(I-1)
32 + 39 =	45	.0160	.0160
41 + 43 =	46	.0446	.0286
44 + 45 =	47	.0495	.0049
33 + 46 =	48	.0572	.0077
31 + 40 =	49	.0681	.0109
22 + 29 =	50	.0827	.0146
3 + 8 =	51	.0845	.0018
34 + 48 =	52	.1027	.0182
11 + 19 =	53	.1065	.0038
47 + 51 =	54	.1252	.0187
42 + 52 =	55	.1756	.0504
2 + 36 =	56	.1898	.0142
5 + 54 =	57	.2048	.0150
55 + 57 =	58	.2398	.0350
14 + 26 =	59	.2643	.0245
6 + 7 =	60	.2941	.0298

```
23 +   25 =   61        .3025      .0084
38 +   56 =   62        .3026      .0000
15 +   53 =   63        .3767      .0742
49 +   58 =   64        .3846      .0079
27 +   61 =   65        .4142      .0295
17 +   21 =   66        .4364      .0223
50 +   60 =   67        .4388      .0024
12 +   37 =   68        .4431      .0043
13 +   16 =   69        .4450      .0019
 9 +   24 =   70        .4569      .0119
 4 +   10 =   71        .4847      .0278
64 +   67 =   72        .5312      .0465
63 +   66 =   73        .5386      .0074
18 +   71 =   74        .5738      .0352
28 +   73 =   75        .6172      .0434
 1 +   68 =   76        .7120      .0948
65 +   69 =   77        .7230      .0110
59 +   62 =   78        .7360      .0130
75 +   78 =   79        .8015      .0656
30 +   74 =   80        .8305      .0290
35 +   76 =   81        .8744      .0439
20 +   70 =   82        .8749      .0004
77 +   81 =   83        .9609      .0860
79 +   80 =   84       1.1131      .1522
72 +   84 =   85       1.1865      .0734
82 +   83 =   86       1.2100      .0235
85 +   86 =   87       1.8514      .6415
```

MOJENA OPTIMAL GROUP DISTANCE -   1.33
    (FORMULA 1, K=3)

NUMBER OF GROUPS IS   5

NO.   1 (GP   72) WITH   17 MEMBERS -   3 5 -8 22 29 31 -34 39 -44

NO.   2 (GP   79) WITH   11 MEMBERS -   2 11 14 -15 17 19 21 26 28 36 38

NO.   3 (GP   80) WITH   4 MEMBERS -   4 10 18 30

NO.   4 (GP   82) WITH   3 MEMBERS -   9 20 24

NO.   5 (GP   83) WITH   9 MEMBERS -   1 12 -13 16 23 25 27 35 37

GSTAT and GCOM are given in tables 3.8 and 3.9 in the text.

PCOA Ordination vectors.

TRACE=   6.633

EIGENVALUES

3.205	.777	.729	.459	.396	.269	.222	.163	.128	.117
.106	.073	.056	.039	.034	.028	.019	.016	.010	.005
.004	.003	.001	.000	.000	.000	.000	.000	.000	.000
.000	.000	.000	.000	-.001	-.001	-.003	-.004	-.007	-.008
-.020	-.034	-.056	-.092						

VECTORS SCALED BY EIGENVALUE

VECTORS

E.VALUE	3.205	.777	.729	.459	.396	.269	.222
%TRACE	48%	11%	10%	6%	5%	4%	3%
ACC. %	48%	60%	71%	77%	83%	87%	91%
1	-.378	.033	-.039	.011	-.207	.075	.129
2	-.068	.339	-.046	-.071	.007	-.007	.037
3	.358	-.055	.105	.105	-.033	.101	.037
4	-.214	-.099	-.003	-.138	-.144	.034	-.006
5	.307	-.038	.050	.046	.033	.122	.011
6	.236	-.059	.004	-.021	-.056	.087	-.126
7	.209	-.086	.035	-.002	-.128	.000	-.202
8	.338	-.009	.143	.085	-.082	.113	.014
9	-.521	-.030	.315	.013	-.020	.069	.073
10	-.039	-.185	-.087	-.119	.038	.160	-.085
11	.031	-.016	.031	-.092	.191	.053	-.089
12	-.351	.041	-.160	.175	.040	.043	-.022
13	-.298	-.018	.108	.038	.156	-.153	.042
14	-.123	.158	-.083	-.149	-.125	-.032	.101
15	.101	-.025	-.042	-.045	.277	-.056	.016
16	-.193	-.051	.025	-.130	.063	-.066	-.076
17	.079	.115	-.065	.003	.187	.179	.052
18	-.137	-.266	-.242	-.185	.019	.060	.010
19	-.032	.025	.065	-.156	.149	-.007	-.056
20	-.315	-.018	.373	.123	.037	.049	-.080
21	-.070	.152	-.035	-.029	.016	.079	.018
22	.141	-.020	.074	.027	.017	-.167	-.070
23	-.408	-.240	-.018	.187	.109	-.033	.063
24	-.386	-.023	.210	-.145	-.066	.053	.020
25	-.324	-.241	-.134	.019	.036	-.063	.099
26	-.086	-.022	-.304	-.091	.016	.014	.034
27	-.327	-.143	.036	.084	-.063	-.017	.011
28	-.019	.119	.070	-.142	.020	-.144	.088
29	.073	-.054	.025	.004	-.032	-.068	-.103
30	.003	-.204	-.088	.066	-.178	-.140	-.052
31	.332	.084	-.085	.154	.056	.025	.070
32	.357	-.038	.025	.076	.021	-.040	.035
33	.329	-.024	.021	-.035	-.005	-.047	.026
34	.252	.028	.081	-.116	-.069	-.056	.036
35	-.191	.022	-.309	.191	-.076	.003	-.056
36	-.101	.323	-.069	-.065	-.029	-.018	-.094
37	-.411	.283	.056	.125	-.034	.001	-.042

38	-.159	.230	-.142	.085	.003	-.045	-.132
39	.349	-.038	.016	.064	.018	-.062	.026
40	.304	.111	-.067	.108	-.020	.011	.075
41	.279	.007	.053	-.008	-.037	-.094	.024
42	.381	-.014	.009	-.131	-.086	.020	.052
43	.280	.009	.093	.003	-.050	-.035	.049
44	.414	-.067	-.004	.078	.029	-.001	.043

-BACRIV.

NOTE: CORRELATIONS PRINTED ARE THE CORRELATIONS OF THE ATTRIBUTE VALUES WITH THE SCORES FOR THE VECTOR

CORRELATIONS FOR VECTOR 1

| ATTRIBUTE | | CORREL. | NO. | STATE | |
NAME	TYPE	COEFF.	PRESENT	NO	NAME
SPIKE DIAMETER	FNUM 6	-.8556	44		
SPIKE LENGTH	FNUM 4	-.8373	44		
TRUNK HEIGHT	FNUM 9	-.8296	44		
BRACT COLOUR	DMUL 4	-.8227	41	1	
SP,SC RATIO	FNUM 7	-.8217	44		
SCAPE DIAMETER	FNUM 5	-.8153	44		
LEAF COLOUR	DMUL 2	.7921	43	2	
LEAF COLOUR	DMUL 2	-.7782	43	1	
BRACT SHAPE	DMUL 3	-.7635	43	2	
LEAF WIDTH	FNUM 1	.7427	44		
BRACT INDUMENTUM	FNUM 10	.7173	43		
BRACT COLOUR	DMUL 4	.6839	41	2	
LEAF THICKNESS	FNUM 2	.5979	28		
PCB'S	FNUM 8	-.5906	42		

  8 ITEMS NOT PRINTED

CORRELATIONS FOR VECTOR 2

| ATTRIBUTE | | CORREL. | NO. | STATE | |
NAME	TYPE	COEFF.	PRESENT	NO	NAME
LEAF SHAPE	DMUL 1	.7005	44	1	
LEAF SHAPE	DMUL 1	-.6167	44	3	
BRACT SHAPE	DMUL 3	.5273	43	1	
BRACT COLOUR	DMUL 4	.4772	41	2	
BRACT SHAPE	DMUL 3	-.4700	43	3	
BRACT COLOUR	DMUL 4	-.4348	41	1	
BRACT INDUMENTUM	FNUM 10	.3817	43		
SPIKE LENGTH	FNUM 4	.2944	44		
PCB'S	FNUM 8	-.2735	42		

13 ITEMS NOT PRINTED

CORRELATIONS FOR VECTOR 3

ATTRIBUTE NAME	TYPE	CORREL. COEFF.	NO. PRESENT	STATE NO	NAME
LEAF SHAPE	DMUL 1	-.5214	44	1	
BRACT SHAPE	DMUL 3	.5049	43	1	
SCAPE DIAMETER	FNUM 5	.4503	44		
SP,SC RATIO	FNUM 7	.4237	44		
BRACT SHAPE	DMUL 3	-.4192	43	3	
SPIKE LENGTH	FNUM 4	.4103	44		
LEAF THICKNESS	FNUM 2	.3869	28		
SPIKE DIAMETER	FNUM 6	.3818	44		
LEAF SHAPE	DMUL 1	.3447	44	3	
LEAF COLOUR	DMUL 2	.3065	43	2	
BRACT INDUMENTUM	FNUM 10	.3036	43		

11 ITEMS NOT PRINTED

Appendix 3.6 Pearl Beach, Data set and UPG Classification results.

(Sixteen characters are shown below as two characters were originally scored both as multistate and numeric characters but these alternatives were later masked- out when it was found that they produced the same results.)

```
     2,  1,  2,  *,  1,  *,                                              WARRAH 1
     3.50  1.50  225   115    17   35   .51    0    50   1.0            WARRAH 1
    (1,2)  1,  2,  *,  3,  2,                                           WARRAH 2
     3.50  1.75  225   115    19   41   .49    1    60   1.0            WARRAH 2
     4,  2,  2,  *,  3,  3,                                             WARRAH 3
     9.00  2.25  250   150    32   45   .60    0   100   .5             WARRAH 3
    (1,2)  1,  2,  1,  *,  *,                                           WARRAH 4
     3.20  1.60  210    *     17   36   *      0    20   .5             WARRAH 4
    (1,2)  1,  2,  2,  *,  *,                                           WARRAH 5
     3.40  1.90  220    *     15   30   *      1    10   1.0            WARRAH 5
     4,  2,  2,  1,  3,  3,                                             WARRAH 6
     8.00  2.30  275   210    38   45   .76    0   100   1.0            WARRAH 6
     4,  2,  2,  1,  3,  3,                                             WARRAH 7
     7.00  1.80  250   150    27   38   .60    1    60   1.0            WARRAH 7
     4,  2,  2,  1,  3,  3,                                             WARRAH 8
     6.50  2.00  225   150    29   35   .66    0   150   2.0            WARRAH 8
     4,  2,  2,  *,  2,  2,                                             WARRAH 9
     6.50  1.50  180    80    22   29   .44    0   120   1.0            WARRAH 9
     4,  2,  2,  1,  3,  3,                                             WARRAH10
     7.75  2.25  215   165    29   38   .77    0   200   .5             WARRAH10
    (1,2)  1,  2,  1,  1,  *,                                           WARRAH11
     3.10  1.25  150    54    13   26   .36    1    30   2.0            WARRAH11
     1,  1,  2,  2,  1,  *,                                             WARRAH12
     3.20  2.00  242   107    24   41   .44    0    20   .1             WARRAH12
     1,  1,  2,  1,  3,  1,                                             WARRAH13
     3.20  2.00  166   100    26   43   .60    1    40   1.0            WARRAH13
     1,  1,  2,  1,  2,  *,                                             WARRAH14
     2.75  1.60  224    60    24   38   .27    0    40   1.0            WARRAH14
     1,  1,  2,  *,  2,  *,                                             WARRAH15
     3.35  2.25   80    80    23   34  1.00    0    70    0             WARRAH15
     4,  2,  2,  *,  3,  *,                                             WARRAH16
     6.30  1.50  197   110    24   31   .56    0   100   1.0            WARRAH16
     4,  2,  2,  *,  3,  *,                                             WARRAH17
     4.80  1.80  130    84    15   33   .65    0   150   2.0            WARRAH17
     4,  2,  2,  *,  *,  3,                                             WARRAH18
    11.00  2.00  238   227    30   50   .95    0   120   .5             WARRAH18
     4,  2,  2,  *,  2,  3,                                             WARRAH19
     7.50  2.50  170   138    25   33   .81    0   160   3.0            WARRAH19
     4,  2,  2,  *,  1,  *,                                             WARRAH20
     7.50  2.00  210   129    23   34   .61   .5    60   2.0            WARRAH20
     4,  2,  2,  *,  *,  3,                                             WARRAH21
     6.25  2.00  180   130    22   32   .72    0   100   1.00           WARRAH21
```

-MSED. STANDARDISED EUCLIDEAN METRIC

-SAHN. UNWEIGHTED PAIR GROUP OR GROUP-AVERAGE SORTING

FUSION			GROUP	DISSIMILARITY	D(I)-D(I-1)
16 +	21	=	22	.1386	.1386
3 +	6	=	23	.1451	.0065
1 +	4	=	24	.1783	.0332
8 +	10	=	25	.2119	.0336
2 +	5	=	26	.2240	.0121
18 +	23	=	27	.2837	.0597
17 +	22	=	28	.2989	.0152
25 +	27	=	29	.4010	.1021
14 +	24	=	30	.4038	.0028
7 +	20	=	31	.4163	.0125
9 +	28	=	32	.4308	.0145
31 +	32	=	33	.5678	.1370
12 +	26	=	34	.6431	.0752
30 +	34	=	35	.6529	.0098
13 +	35	=	36	.7694	.1165
29 +	33	=	37	.8140	.0446
19 +	37	=	38	.8447	.0307
11 +	36	=	39	.9297	.0851
15 +	39	=	40	1.1977	.2680
38 +	40	=	41	1.5800	.3823

MOJENA OPTIMAL GROUP DISTANCE -   1.41
   (FORMULA 1, K=3)

NUMBER OF GROUPS IS   3

NO.   1 (GP   38) WITH   12 MEMBERS - 3 6 -10 16 -21

NO.   2 (GP   15) WITH   1 MEMBERS - 15

NO.   3 (GP   39) WITH   8 MEMBERS - 1 -2 4 -5 11 -14

GCOM and GSTAT are in tables 3.10 and 3.11 in the body of the text.

Appendix 3.7 Pearl Beach, ISS Classification results, with GSTAT AND GCOM.

**** T=MEDIA+ARBOREA WARRAH3 ISS 3GROUP ANALYSIS
**** II=21, IFN=10, IDN=6, NGREQ=3, SORTSTRAT=ISS

-MSED.

STANDARDISED EUCLIDEAN METRIC

-SAHN.

BURR'S STRATEGY OR INCREMENTAL SUM OF SQUARES WITH SED

FUSION	GROUP	DISSIMILARITY	D(I)-D(I-1)
16 + 21 =	22	.1386	.1386
3 + 6 =	23	.1451	.0065
1 + 4 =	24	.1783	.0332
8 + 10 =	25	.2119	.0336
2 + 5 =	26	.2240	.0121
18 + 23 =	27	.3299	.1059
17 + 22 =	28	.3523	.0224
7 + 20 =	29	.4163	.0640
14 + 24 =	30	.4790	.0627
9 + 28 =	31	.5235	.0445
25 + 27 =	32	.6453	.1218
12 + 26 =	33	.7827	.1374
13 + 15 =	34	.8944	.1117
29 + 31 =	35	.8985	.0041
11 + 30 =	36	.9515	.0530
19 + 35 =	37	1.0722	.1207
33 + 36 =	38	1.3348	.2626
34 + 38 =	39	1.6173	.2825
32 + 37 =	40	2.6048	.9875
39 + 40 =	41	9.4137	6.8089

MOJENA OPTIMAL GROUP DISTANCE -   5.07
   (FORMULA 1, K=3)

NUMBER OF GROUPS IS   3

NO.   1 (GP   39) WITH   9 MEMBERS - 1 -2 4 -5 11 -15

NO.   2 (GP   32) WITH   5 MEMBERS - 3 6 8 10 18

NO.   3 (GP   37) WITH   7 MEMBERS - 7 9 16 -17 19 -21

-GCOM.

**** COMPARISON NO. 1
**** GROUP A = GP   39
**** GROUP B = GP   32 + GP   37

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 8.5048

		GROUP A 9 MEMBERS		GROUP B 12 MEMBERS		CONTRIBUTION			
ATTRIBUTE (STATE)	NAME	ATTRIBUTE NO. MEAN	PRESENT	ATTRIBUTE NO. MEAN	PRESENT	%	% (CUM)	ACTUAL VALUE	
DMUL 2	LEAF COLOUR		9		12	29	29	2.50	
ST. 1		1.000		.000					
ST. 2		.000		1.000					
DMUL 1	LEAF SHAPE		9		12	23	52	1.94	
ST. 1		.889		.000					
ST. 2		.556		.000					
ST. 4		.000		1.000					

1 ATTRIBUTES MADE NO CONTRIBUTION.

‡‡‡‡   COMPARISON NO. 2
‡‡‡‡   GROUP A = GP   32
‡‡‡‡   GROUP B = GP   37

TOTAL CONTRIBUTION TOWARDS THE FUSION OF GROUP A WITH GROUP B = 2.2945

		GROUP A 5 MEMBERS		GROUP B 7 MEMBERS		CONTRIBUTION			
ATTRIBUTE (STATE)	NAME	ATTRIBUTE NO. MEAN	PRESENT	ATTRIBUTE NO. MEAN	PRESENT	%	% (CUM)	ACTUAL VALUE	
FNUM 6	SPIKE DIAMETER	42.600	5	32.857	7	21	21	.483	
FNUM 5	SCAPE DIAMETER	31.600	5	22.571	7	17	38	.385	
FNUM 4	SPIKE LENGTH	180.400	5	117.286	7	15	53	.347	

4 ATTRIBUTES MADE NO CONTRIBUTION.
-GSTAT.

                    INDIVIDUAL GROUP NO. 1 (GP   39) WITH 9 MEMBERS
                    ****

DISORDERED MULTISTATES NO.   NO. IN STATE
                        MIS   1   2   3   4

    1 LEAF SHAPE   0   8   5   0   0

	NO. MIS	1	2	3	4
2 LEAF COLOUR	0	9	0		
3 BRACT SHAPE	0	0	9		
4 BRACT COLOUR	3	4	2		
5 CLUSTER BRACTS	2	3	2	2	
6 JUV. CLUSTER BR.	7	1	1	0	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S
1 LEAF WIDTH	0	0	9	2.750	2.750	3.500	3.244	3.244	
2 LEAF THICKNESS	0	0	9	1.250	1.250	2.250	1.761	1.761	
3 SCAPE LENGTH	0	0	9	80.00	80.00	242.0	193.6	193.6	
4 SPIKE LENGTH	2	0	7	54.00	54.00	115.0	90.14	90.14	
5 SCAPE DIAMETER	0	0	9	13.00	13.00	26.00	19.78	19.78	
6 SPIKE DIAMETER	0	0	9	26.00	26.00	43.00	36.00	36.00	
7 SP/SC RATIO	2	0	7	.2700	.2700	1.000	.5243	.5243	
8 PCB'S	0	5	4	0.	1.000	1.000	.4444	1.000	
9 TRUNK HEIGHT	0	0	9	10.00	10.00	70.00	37.78	37.78	
10 BRACT INDUMENTUM	0	1	8	0.	.1000E+00	2.000	.8444	.9500	

INDIVIDUAL GROUP NO. 2 (GP 32) WITH 5 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	1	2	3	4
1 LEAF SHAPE	0	0	0	0	5
2 LEAF COLOUR	0	0	5		
3 BRACT SHAPE	0	0	5		
4 BRACT COLOUR	2	3	0		
5 CLUSTER BRACTS	1	0	0	4	
6 JUV. CLUSTER BR.	0	0	0	5	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.D
1 LEAF WIDTH	0	0	5	6.500	6.500	11.00	8.450	8.450	1.6
2 LEAF THICKNESS	0	0	5	2.000	2.000	2.300	2.160	2.160	.14
3 SCAPE LENGTH	0	0	5	215.0	215.0	275.0	240.6	240.6	23.
4 SPIKE LENGTH	0	0	5	150.0	150.0	227.0	180.4	180.4	35
5 SCAPE DIAMETER	0	0	5	29.00	29.00	38.00	31.60	31.60	3.
6 SPIKE DIAMETER	0	0	5	35.00	35.00	50.00	42.60	42.60	6.
7 SP/SC RATIO	0	0	5	.6000	.6000	.9500	.7480	.7480	.1
9 TRUNK HEIGHT	0	0	5	100.0	100.0	200.0	134.0	134.0	42
10 BRACT INDUMENTUM	0	0	5	.5000	.5000	2.000	.9000	.9000	.6

INDIVIDUAL GROUP NO. 3 (GP 37) WITH 7 MEMBERS
****

DISORDERED MULTISTATES	NO. MIS	NO. IN STATE 1	2	3	4
1 LEAF SHAPE	0	0	0	0	7
2 LEAF COLOUR	0	0	7		
3 BRACT SHAPE	0	0	7		
4 BRACT COLOUR	6	1	0		
5 CLUSTER BRACTS	1	1	2	3	
6 JUV. CLUSTER BR.	3	0	1	3	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.
1 LEAF WIDTH	0	0	7	4.800	4.800	7.500	6.550	6.550	.
2 LEAF THICKNESS	0	0	7	1.500	1.500	2.500	1.871	1.871	.
3 SCAPE LENGTH	0	0	7	130.0	130.0	250.0	188.1	188.1	3
4 SPIKE LENGTH	0	0	7	80.00	80.00	150.0	117.3	117.3	2
5 SCAPE DIAMETER	0	0	7	15.00	15.00	27.00	22.57	22.57	3
6 SPIKE DIAMETER	0	0	7	29.00	29.00	38.00	32.86	32.86	2
7 SP/SC RATIO	0	0	7	.4400	.4400	.8100	.6271	.6271	.
8 PCB'S	0	5	2	0.	.5000	1.000	.2143	.7500	.
9 TRUNK HEIGHT	0	0	7	60.00	60.00	160.0	107.1	107.1	3
10 BRACT INDUMENTUM	0	0	7	1.000	1.000	3.000	1.571	1.571	.

STATISTICS FOR ENTIRE DATA
****

| DISORDERED MULTISTATES | NO. | | NO. IN STATE | | |
	MIS	1	2	3	4
1 LEAF SHAPE	0	8	5	0	12
2 LEAF COLOUR	0	9	12		
3 BRACT SHAPE	0	0	21		
4 BRACT COLOUR	11	8	2		
5 CLUSTER BRACTS	4	4	4	9	
6 JUV. CLUSTER BR.	10	1	2	8	

NUMERIC ATTRIBUTES (FNUM)	NO. MIS	NO =0	NO. NOT 0	MIN.	MIN. NOT 0	MAX.	MEAN	MEAN NOT 0	S.I
1 LEAF WIDTH	0	0	21	2.750	2.750	11.00	5.586	5.586	2.:
2 LEAF THICKNESS	0	0	21	1.250	1.250	2.500	1.893	1.893	.3:
3 SCAPE LENGTH	0	0	21	80.00	80.00	275.0	203.0	203.0	45.
4 SPIKE LENGTH	2	0	19	54.00	54.00	227.0	123.9	123.9	45.
5 SCAPE DIAMETER	0	0	21	13.00	13.00	38.00	23.52	23.52	6.:
6 SPIKE DIAMETER	0	0	21	26.00	26.00	50.00	36.52	36.52	5.!
7 SP/SC RATIO	2	0	19	.2700	.2700	1.000	.6211	.6211	.1!
8 PCB'S	0	15	6	0.	.5000	1.000	.2619	.9167	.4:
9 TRUNK HEIGHT	0	0	21	10.00	10.00	200.0	83.81	83.81	52
10 BRACT INDUMENTUM	0	1	20	0.	.1000E+00	3.000	1.100	1.155	.7:

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Appendix 3.8 Pearl Beach, PCOA Ordination vector scores.

TRACE= 3.184

EIGENVALUES

1.427	.498	.364	.265	.207	.154	.142	.091	.082	.046
.027	.017	.009	.003	.000	-.001	-.003	-.016	-.018	-.042
-.067									

VECTORS SCALED BY EIGENVALUE

VECTORS

E.VALUE	1.427	.498	.364	.265	.207	.154	.142
%TRACE	44%	15%	11%	8%	6%	4%	4%
ACC. %	44%	60%	71%	80%	86%	91%	96%
1	-.282	-.047	.092	.088	-.065	-.114	-.054
2	-.267	-.106	.147	.010	.091	.026	.118
3	.311	-.155	.041	.014	-.047	.083	.015
4	-.282	-.107	.037	-.090	-.080	-.208	.023
5	-.352	-.046	.043	.245	.138	-.001	.064
6	.382	-.193	.076	-.071	.013	-.029	-.053
7	.157	-.027	.184	-.073	.064	.042	.012
8	.256	.098	.055	-.090	.011	-.025	-.037
9	-.031	.235	-.033	.050	-.225	.034	.060
10	.332	-.011	-.031	-.083	.003	-.065	.074
11	-.436	.215	.160	-.076	.079	-.057	-.081
12	-.203	-.229	-.090	.173	-.114	.160	-.061
13	-.187	-.145	-.068	-.230	.159	.144	-.004
14	-.256	-.058	-.057	-.175	-.182	.044	-.131
15	-.171	-.057	-.448	-.028	.067	-.063	.061
16	.082	.128	.066	-.020	-.100	.067	.130
17	.057	.284	-.050	-.033	.036	.054	.127
18	.403	-.221	.008	.116	.002	-.109	.025
19	.264	.218	-.158	.076	.120	-.032	-.166
20	.082	.109	.084	.121	.054	.072	-.120
21	.140	.115	-.059	.076	-.024	-.023	-.001

Appendix 4.1 Asparagales analysis 1: Data file and complete results of

cladistic analysis of the Asparagales. (Abbreviations as per Appendix 4.8).

!FILE=ASPARAGS.PAU
!
!CLADISTIC ANALYSIS OF WOODY MONOCOTYLEDONOUS PLANT FAMILIES WITH DRACAENOID
!SECONDARY THICKENING
!
!CODING FROM DAHLGREN & CLIFFORD (1983), DAHLGREN, CLIFFORD & YEO (1985) AND
!DAHLGREN & RASMUSSEN (1983)
!
PARAM NOTU=6 NCHAR=14 MISSING=9 ECHO;

LABELS 1HERBACE 2ROOT-VE 3STEM-VE 4LEAF-VE 5DISTYCH 6BROAD-L 7SPINES 8STOMTYP
9STOMPOS 10INFLOR 11FLOWER 12CAPSUL 13PHYTOM 14RAPHID;

DATA (A6,A1,2X,14I2)
OUTGP   0 0 0 0 0 0 0 0 0 0 0 0 0 0
DRACAE   9 0 1 1 1 0 0 0 9 0 0 0 0 1
AGAVAC   9 0 0 9 1 0 1 0 1 1 0 1 1 0
ASTELI   9 1 1 0 0 0 0 1 9 9 0 1 1 9
NOLINA   0 9 1 1 1 1 1 9 3 9 0 0 0 0
XANTHO   1 0 0 2 1 1 1 1 2 1 1 1 1 1
interact;

define outgroup=outgp;
go/root=outgroup alltrees chglist apolist blrange cspos;
interact;

RESULTS

  Option settings:

            NOTU   6
            NCHAR   14
            User-tree(s) ....   NO
            HYPANC   1
            ADDSEQ ....   N/A
            HOLD ....   N/A
            SWAP ....   N/A
            MULPARS ....   N/A
            OPT ....   FARRIS
            ROOT .... OUTGROUP
            Weights applied ....   NO
            OUTWIDTH   80
            Missing data code   9
            MAXTREE ....   N/A

  Exhaustive search of all possible topologies performed.

Branch lengths and linkages for unrooted tree no. 1

Node	Connected to node	Branch length	Minimum possible length	Maximum possible length
DRACAE (2)	9	1.000	1.000	1.000
AGAVAC (3)	7	2.000	0.000	2.000
ASTELI (4)	10	4.000	4.000	4.000
NOLINA (5)	8	1.000	1.000	3.000
XANTHO (6)	7	3.000	3.000	7.000
7	8	5.000	3.000	6.000
8	9	3.000	1.000	5.000
9	10	2.000	2.000	4.000
10	OUTGP (1)	3.000	1.000	3.000

* Designated outgroup taxa

Possible HTU character-state assignments

```
              1  2  3  4  5  6     8  9  1  1  1  1  1
              H  R  S  L  D  B  7  S  S  0  1  2  3  4
              E  O  T  E  I  R  S  T  T  I  F  C  P  R
              R  O  E  A  S  O  P  O  O  N  L  A  H  A
              B  T  M  F  T  A  I  M  M  F  O  P  Y  P
              A  -  -  -  Y  D  N  T  P  L  W  S  T  H
              C  V  V  V  C  -  E  Y  O  O  E  U  O  I
  Node        E  E  E  E  H  L  S  P  S  R  R  L  M  D

  7           0  0  0  1  1  0  1  0  1  1  0  1  1  0
              1        2  1           2

  8           0  0  1  1  1  0  1  0  1  0  0  0  0  0
                          1           2  1

  9           0  0  1  1  1  0  0  0  0  0  0  0  0  0
                                      1
                                      2

  10          0  0  1  0  0  0  0  0  0  0  0  0  0  0
                                      1
                                      2
```

Statistics for tree no. 1

    Length =   24.000
    Consistency index = 0.708

Tree no. 1 rooted using designated outgroup

```
*********** OUTGP    1
*
*          ****** DRACAE    2
*          *
*  *********9                              ********** AGAVAC    3
*  *       *            *************************7
*  *       *************8                ************** XANTHO    6
**10                    *
   *             ****** NOLINA    5
   *
   ******************** ASTELI    4
```

Change lists

Character	Changed From	To	Along branch	Consistency
1HERBACE				
	0	1	8 ---> 7	
				1.000
2ROOT-VE				
	0	1	10 ---> ASTELI	
				1.000
3STEM-VE				
	1	0	10 <--> OUTGP	
	1	0	8 ---> 7	
				0.500
4LEAF-VE				
	0	1	10 ---> 9	
	1	2	8 ---> 7	
				1.000
5DISTYCH				
	0	1	10 ---> 9	
				1.000
6BROAD-L				
	0	1	9 ---> 8	
	1	0	7 ---> AGAVAC	
				0.500
7SPINES				
	0	1	9 ---> 8	
				1.000
8STOMTYP				
	0	1	7 ---> XANTHO	
	0	1	10 ---> ASTELI	
				0.500

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9STOMPOS

2	0	10 <--> OUTGP	
2	3	8 ---> NOLINA	
2	1	7 ---> AGAVAC	
			0.750

10INFLOR

0	1	9 ---> 8	
			1.000

11FLOWER

0	1	7 ---> XANTHO	
			1.000

12CAPSUL

0	1	8 ---> 7	
0	1	10 ---> ASTELI	
			0.500

13PHYTOM

0	1	8 ---> 7	
0	1	10 ---> ASTELI	
			0.500

14RAPHID

0	1	7 ---> XANTHO	
0	1	9 ---> DRACAE	
			0.500

Apomorphy lists

Node	Ancestor	Character	Ancestral state	Derived state	Length added
DRACAE	9				
		14RAPHID	0	1	1.000
AGAVAC	7				
		6BROAD-L	1	0	1.000
		9STOMPOS	2	1	1.000
ASTELI	10				
		2ROOT-VE	0	1	1.000
		8STOMTYP	0	1	1.000
		12CAPSUL	0	1	1.000
		13PHYTOM	0	1	1.000
NOLINA	8				
		9STOMPOS	2	3	1.000
XANTHO	7				
		8STOMTYP	0	1	1.000
		11FLOWER	0	1	1.000
		14RAPHID	0	1	1.000

7	8				
		1HERBACE	0	1	1.000
		3STEM-VE	1	0	1.000
		4LEAF-VE	1	2	1.000
		12CAPSUL	0	1	1.000
		13PHYTOM	0	1	1.000
8	9				
		6BROAD-L	0	1	1.000
		7SPINES	0	1	1.000
		10INFLOR	0	1	1.000
9	10				
		4LEAF-VE	0	1	1.000
		5DISTYCH	0	1	1.000

Changes between nodes OUTGP   and 10   cannot be polarized.
These changes follow:

Character	------States------		Length
	OUTGP	10	added
3STEM-VE	0	1	1.000
9STOMPOS	0	2	2.000

Appendix 4.2 - Asparagales analysis 2. (Abbreviations as per Appendix 4.8).

AXILLARY INFLORESCENCES AS SYNAPOMORPHIC.

Exhaustive search of all possible topologies performed.

2 trees were found.

Branch lengths and linkages for unrooted tree no. 1

Node	Connected to node	Branch length
DRACAE (2)	7	2.000
AGAVAC (3)	9	0.000
ASTELI (4)	10	3.000
NOLINA (5)	7	1.000
XANTHO (6)	8	4.000
7	8	5.000
8	9	3.000
9	10	3.000
10	OUTGP (1)	3.000

* Designated outgroup taxa

Statistics for tree no. 1

    Length =   24.000
    Consistency index = 0.708

Tree no. 1 rooted using designated outgroup

```
*********** OUTGP   1
*
*                                           ********* DRACAE   2
*                             ********************7
*             *************8                 ***** NOLINA   5
*             *             *
* ************9             ****************** XANTHO   6
* *           *
**10          * AGAVAC   3
   *
   ************* ASTELI   4
```

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Branch lengths and linkages for unrooted tree no. 2

Node	Connected to node	Branch length
DRACAE (2)	9	2.000
AGAVAC (3)	7	2.000
ASTELI (4)	10	4.000
NOLINA (5)	8	1.000
XANTHO (6)	7	3.000
7	8	5.000
8	9	2.000
9	10	2.000
10	OUTGP (1)	3.000

* Designated outgroup taxa

Statistics for tree no. 2

    Length =   24.000
    Consistency index = 0.708

Tree no. 2 rooted using designated outgroup

```
************* OUTGP   1
*
*            ********** DRACAE   2
*            *
*  *********9                                   ********** AGAVAC    3
*  *        *        ***********************7
*  *        **********8                         *************** XANTHO    6
**10                 *
   *            ****** NOLINA   5
   *
   ******************** ASTELI   4
```

Appendix 4.3 - Asparagales analysis 3. (Abbreviations as per Appendix 4.8).

WITH INFLORESCENCE CHARACTER (10) DELETED

Exhaustive search of all possible topologies performed.

2 trees were found.

Branch lengths and linkages for unrooted tree no. 1

Node	Connected to node	Branch length
DRACAE (2)	7	2.000
AGAVAC (3)	9	0.000
ASTELI (4)	10	3.000
NOLINA (5)	7	1.000
XANTHO (6)	8	4.000
7	8	4.000
8	9	3.000
9	10	3.000
10	OUTGP (1)	3.000

* Designated outgroup taxa

Statistics for tree no. 1

Length = 23.000
Consistency index = 0.696

Tree no. 1 rooted using designated outgroup

```
************* OUTGP   1
*
*                                              ********** DRACAE   2
*                                  *****************7
*                 ***************8             ****** NOLINA   5
*                 *             *
* **************9              ****************** XANTHO   6
* *               *
**10             * AGAVAC   3
   *
   *************** ASTELI   4
```

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Branch lengths and linkages for unrooted tree no. 2

Node	Connected to node	Branch length
DRACAE (2)	9	1.000
AGAVAC (3)	7	2.000
ASTELI (4)	10	4.000
NOLINA (5)	8	1.000
XANTHO (6)	7	3.000
7	8	5.000
8	9	2.000
9	10	2.000
10	OUTGP (1)	3.000

* Designated outgroup taxa

Statistics for tree no. 2

    Length =   23.000
    Consistency index = 0.696

Tree no. 2 rooted using designated outgroup

```
************* OUTGP   1
*
*             ****** DRACAE   2
*             *
* *********9                                    ********** AGAVAC   3
* *         *         ************************7
* *         **********8                         *************** XANTHO   6
**10                  *
   *              ****** NOLINA   5
   *
   ******************** ASTELI   4
```

Appendix 4.4 - Asparagales analysis 4. (Abbreviations as per Appendix 4.8).

ANALYSIS WITH INFLORESCENCE CHAR (10) NOT POLARISED

Exhaustive search of all possible topologies performed.

    2 trees were found.

Branch lengths and linkages for unrooted tree no. 1

		Connected to node	Branch length
DRACAE (	2)	7	2.000
AGAVAC (	3)	9	0.000
ASTELI (	4)	10	3.000
NOLINA (	5)	7	1.000
XANTHO (	6)	8	4.000
7		8	5.000
8		9	3.000
9		10	3.000
10		OUTGP (1)	3.000

* Designated outgroup taxa

Statistics for tree no. 1

    Length =   24.000
    Consistency index = 0.708

Tree no. 1 rooted using designated outgroup

```
*********** OUTGP   1
*
*                                              ********* DRACAE   2
*                             ********************7
*              *************8                 ***** NOLINA   5
*              *            *
*  *************9           ****************** XANTHO   6
*  *           *
**10          * AGAVAC   3
   *
   ************* ASTELI   4
```

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Branch lengths and linkages for unrooted tree no. 2

Node	Connected to node	Branch length
DRACAE (2)	9	2.000
AGAVAC (3)	7	2.000
ASTELI (4)	10	4.000
MOLINA (5)	8	1.000
XANTHO (6)	7	3.000
7	8	5.000
8	9	2.000
9	10	2.000
10	OUTGP (1)	3.000

* Designated outgroup taxa

Statistics for tree no. 2

    Length =   24.000
    Consistency index = 0.708

 Tree no. 2 rooted using designated outgroup

```
************* OUTGP   1
*
*            ********** DRACAE   2
*            *
*  **********9                                    ********** AGAVAC   3
*  *         *         *************************7
*  *         **********8                          **************** XANTHO   6
**10                   *
   *                   ****** MOLINA   5
   *
   ******************** ASTELI   4
```

Appendix 4.5 Asparagales analysis 5. (Abbreviations as per Appendix 4.8).

CAPSULES AS PRIMITIVE FRUIT TYPE - DRUPES ETC. AS ADVANCED

Exhaustive search of all possible topologies performed.

    4 trees were found.

Branch lengths and linkages for unrooted tree no. 1

Node	Connected to node	Branch length
DRACAE (2)	7	2.000
AGAVAC (3)	9	0.000
ASTELI (4)	10	3.000
NOLINA (5)	7	1.000
XANTHO (6)	8	4.000
7	8	5.000
8	9	3.000
9	10	3.000
10	OUTGP (1)	3.000

* Designated outgroup taxa

Statistics for tree no. 1

    Length =   24.000
    Consistency index = 0.708

Tree no. 1 rooted using designated outgroup

```
************ OUTGP    1
*
*                                             ********** DRACAE   2
*                          *********************7
*            **************8              ***** NOLINA    5
*            *             *
* *************9           ******************* XANTHO   6
* *           *
**10          * AGAVAC    3
   *
   ************** ASTELI   4
```

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Branch lengths and linkages for unrooted tree no. 2

Node	Connected to node	Branch length
DRACAE (2)	7	2.000
AGAVAC (3)	8	1.000
ASTELI (4)	10	2.000
NOLINA (5)	7	1.000
XANTHO (6)	8	4.000
7	9	3.000
8	9	4.000
9	10	3.000
10	OUTGP (1)	4.000

* Designated outgroup taxa

Statistics for tree no. 2

    Length =   24.000
    Consistency index = 0.708

Tree no. 2 rooted using designated outgroup

```
***************** OUTGP    1
*
*                                ************ DRACAE    2
*                ***************7
*                *               ****** NOLINA    5
*     ****************9
*  *                 *           ******* AGAVAC    3
***10                ********************8
   *                              ***************************** XANTHO    6
   *
   *
   ************ ASTELI    4
```

Branch lengths and linkages for unrooted tree no. 3

Node	Connected to node	Branch length
DRACAE (2)	9	1.000
AGAVAC (3)	7	2.000
ASTELI (4)	10	3.000
NOLINA (5)	8	1.000
XANTHO (6)	7	3.000
7	8	5.000
8	9	3.000
9	10	3.000
10	OUTGP (1)	3.000

* Designated outgroup taxa

Statistics for tree no. 3
    Length =   24.000
    Consistency index = 0.708

Tree no. 3 rooted using designated outgroup

```
*********** OUTGP    1
*
*              ***** DRACAE    2
*              *
*  *************9                              ********** AGAVAC    3
*  *           *              ********************7
*  *           *************8              ************* XANTHO    6
**10                        *
   *              ***** MOLINA    5
   *
   *
   ************* ASTELI    4
```

Branch lengths and linkages for unrooted tree no. 4

	Connected	Branch
Node	to node	length
DRACAE (2)	9	3.000
AGAVAC (3)	8	0.000
ASTELI (4)	10	2.000
MOLINA (5)	7	4.000
XANTHO (6)	7	4.000
7	8	3.000
8	9	3.000
9	10	2.000
10	OUTGP (1)	3.000

* Designated outgroup taxa

Statistics for tree no. 4
    Length =   24.000
    Consistency index = 0.708

Tree no. 4 rooted using designated outgroup

```
************* OUTGP    1
*
*            *************** DRACAE    2
*  **********9
*  *         *              * AGAVAC    3
*  *         ***************8
**10                        *              ******************** MOLINA    5
   *              ****************7
   *                          ******************** XANTHO    6
   *
   *
   ********** ASTELI    4
```

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Appendix 4.6 Data file for cladistic analysis of _Xanthorrhoea_.

(Abbreviations as per Appendix 4.8)

CHARACTERS 2 7 9 10 11 12 13 17 18 UN-POLARISED (CODED MISSING IN OUTGROUP)
PARAM NOTU=34 NCHAR=26 MISSING=9 ECHO OUTWIDTH=132 NORELBASE;

LABELS 1_TRK_HT 2_BRNCHS 3_CROWNS 4_LF_SHA 5_LF_WTH 6_LF_THK 7_LF_COL 8_STOMS
9_SC_L 10_SC_D 11_RATIO 12_SP_L 13_SP_D 14_PCBS 15_PCB_S 16_PCB_H 17_PCKBS
18_PCKBH 19_PCKBC 20_SP_BK 21_SP_PB 22_SP_HR 23_PETSZ 24_PETSH 25_PETPB 26_PETHR;
DATA (A8,A1,1X,26I2);

```
MACRONEM  2 1 2 3 1 1 1 1 1 5 2 1 3 9 9 3 0 0 0 1 0 0 0 0 0
GRACILIS  2 1 2 3 1 1 1 1 1 5 2 1 3 9 9 3 3 9 0 1 3 0 2 0 0
CONCAVA   2 1 2 0 0 1 0 0 0 1 4 2 0 3 9 9 3 4 9 0 1 3 1 2 0 0
FULVA     2 1 2 0 1 2 0 0 1 0 4 2 0 3 9 9 4 4 9 0 1 3 1 1 9 0
RESINOSA  1 9 0 1 1 1 0 0 1 0 2 2 0 3 9 9 3 4 9 1 1 3 1 1 0 1
BRUNBRUN  1 1 2 0 1 1 1 0 0 0 4 2 0 3 9 9 2 0 9 0 1 0 1 1 1 0
BRUNSEMI  1 1 2 0 1 1 1 0 0 0 4 2 0 3 9 9 2 1 9 0 1 0 1 1 1 0
BREVISTY  1 1 2 0 0 1 0 0 1 0 4 2 0 3 9 9 2 1 9 0 1 0 1 2 0 0
PLATYPHY  1 9 0 0 0 1 0 0 0 0 1 0 2 3 1 3 1 9 0 1 1 1 2 0 0
PREISSII  0 0 1 1 1 1 1 0 0 0 0 0 3 9 9 2 0 0 1 1 1 1 2 0 0
DRUMMOND  0 9 0 2 1 1 0 0 0 0 1 1 0 3 9 9 2 3 9 0 1 3 1 1 0 0
QUADRANG  0 0 1 2 2 2 0 0 0 0 3 2 0 3 9 9 2 1 1 0 1 1 1 2 0 0
THORNTON  0 0 1 2 1 1 0 0 0 0 1 1 0 3 9 9 1 1 9 0 1 0 1 0 0 0
NANA      1 0 2 0 1 1 0 0 0 0 2 2 0 3 9 9 2 2 9 0 1 2 1 0 0 0
PUMILIO   1 9 0 0 1 2 1 0 1 1 4 2 1 3 9 9 4 0 1 1 1 0 1 2 0 0
MEDIA     1 9 0 1 1 2 1 0 1 1 4 2 0 2 2 3 2 0 9 0 1 1 1 2 0 0
ALMAE     0 0 0 1 1 1 1 0 1 0 2 1 0 1 2 1 2 1 0 1 1 0 1 1 0 0
LAT LAT   0 0 1 1 0 2 1 0 2 0 3 1 0 3 9 9 3 2 1 0 1 1 1 2 0 0
LAT MAX   0 0 2 1 0 2 1 0 2 0 4 1 0 3 9 9 2 2 1 0 1 1 1 2 0 0
ARBOREA   0 0 0 0 0 1 1 0 1 0 3 1 0 3 9 9 3 2 1 0 1 1 1 2 0 0
MALACOPH  0 0 2 0 1 1 1 0 1 0 2 1 0 1 1 1 2 1 1 0 1 0 1 2 0 0
GLAUCA G  0 0 2 1 1 2 0 0 0 0 0 1 0 0 1 1 2 1 9 0 1 0 1 1 0 0
GLAUCANG  0 0 2 1 1 2 0 0 0 0 0 1 0 0 1 1 2 1 9 0 1 0 1 1 0 0
ACAULIS   1 1 2 0 2 2 0 0 0 1 3 2 0 0 0 1 2 1 9 0 0 0 1 1 0 0
MINOR MI  2 1 2 0 1 2 1 0 0 1 4 2 1 1 1 1 3 2 9 0 1 0 0 2 0 0
MINORLUT  2 1 2 0 1 2 1 0 0 1 4 2 1 2 1 1 2 2 9 0 1 0 0 2 0 0
BRACTEAT  2 1 2 0 1 2 1 0 0 1 4 2 1 0 1 0 1 0 9 0 1 0 1 2 1 0
CAESPITO  2 1 2 0 0 1 0 0 1 0 4 2 0 0 1 1 0 2 9 0 1 1 1 1 1 0
ARENARIA  2 1 2 0 1 2 0 0 0 1 3 2 0 0 0 0 0 9 0 0 0 1 1 0 0
SEMIPLAN  0 0 1 0 0 0 0 1 0 1 1 0 9 9 9 0 0 9 0 1 0 1 2 0 0
SEMI TAT  0 0 1 0 0 0 0 0 0 1 0 0 9 9 9 0 0 9 0 1 0 1 2 0 0
ACANTHOS  0 0 1 1 1 1 0 0 0 0 2 2 0 0 0 0 0 0 9 0 1 0 1 1 0 0
AUSTRALI  0 0 1 1 1 1 0 0 0 0 1 0 0 0 0 0 0 9 0 0 0 1 1 0 0
AGAVALES  0 9 0 0 0 0 9 9 9 9 9 9 0 0 0 0 9 9 0 0 0 0 0 0 0 0
```

INTERACT;
DEFINE OUTGROUP 34;
GO/ SWAP=GLOBAL MULPARS MAXTREE=100 HOLD=25 ADDSEQ=CLOSEST
ROOT=OUTGROUP;

Option settings:

```
        NOTU .................... 34
        NCHAR ................... 26
        User-tree(s) ........... NO
        HYPANC .................. 1
        ADDSEQ .................. CLOSEST
        HOLD .................... 25
        SWAP .................... GLOBAL
        MULPARS ................. YES
        OPT ..................... FARRIS
        ROOT .................... OUTGROUP
        Weights applied ........ NO
        OUTWIDTH ............... 132
        Missing data code ...... 9
        MAXTREE ................ 100
```

18 trees were found.

Statistics for trees

Length = 181.000
Consistency index = 0.293

```
(((((((((((((((((((1,2)3)4)5)(((6,7)8)(((24,29)((25,26)27))28)))14)11)((9,10
)(12((15,16)((18,20)19)))))13)(17,21))(22,23))33)32)(30,31))34);
(((((((((((((((((((1,2)3)4)5)((6,7)(8(((24,29)((25,26)27))28))))14)11)((9,10
)(12((15,16)((18,20)19)))))13)(17,21))(22,23))33)32)(30,31))34);
(((((((((((((((((((1,2)3)4)5)(((6,7)(((24,29)((25,26)27))28))8))14)11)((9,10
)(12((15,16)((18,20)19)))))13)(17,21))(22,23))33)32)(30,31))34);
((((((((((((((((((((1,2)3)4)5)(((6,7)8)(((24,29)((25,26)27))28)))14)11)((9,10)
(12((15,16)((18,20)19)))))13)(17,21))(22,23))(32,33))(30,31))34);
(((((((((((((((((((1,2)3)4)5)(((6,7)8)(((24,29)((25,26)27))28)))14)11)((9,10
)(12((15,16)((18,20)19)))))13)(17,21))(22,23))32)33)(30,31))34);
((((((((((((((((((((1,2)3)4)5)(((6,7)8)(((24,29)((25,26)27))28)))14)11)((9,10
)(12((15,16)((18,19)20)))))13)(17,21))(22,23))33)32)(30,31))34);
((((((((((((((((((1,2)3)4)5)((6,7)(8(((24,29)((25,26)27))28))))14)11)((9,10)
(12((15,16)((18,20)19)))))13)(17,21))(22,23))(32,33))(30,31))34);
((((((((((((((((((((1,2)3)4)5)((6,7)(8(((24,29)((25,26)27))28))))14)11)((9,10
)(12((15,16)((18,20)19)))))13)(17,21))(22,23))32)33)(30,31))34);
((((((((((((((((((((1,2)3)4)5)((6,7)(8(((24,29)((25,26)27))28))))14)11)((9,10
)(12((15,16)((18,19)20)))))13)(17,21))(22,23))33)32)(30,31))34);
(((((((((((((((((((1,2)3)4)5)(((6,7)(((24,29)((25,26)27))28))8))14)11)((9,10)
(12((15,16)((18,20)19)))))13)(17,21))(22,23))(32,33))(30,31))34);
(((((((((((((((((((1,2)3)4)5)(((6,7)(((24,29)((25,26)27))28))8))14)11)((9,10
)(12((15,16)((18,20)19)))))13)(17,21))(22,23))32)33)(30,31))34);
(((((((((((((((((((1,2)3)4)5)(((6,7)(((24,29)((25,26)27))28))8))14)11)((9,10
)(12((15,16)((18,19)20)))))13)(17,21))(22,23))33)32)(30,31))34);
(((((((((((((((((((1,2)3)4)5)(((6,7)8)(((24,29)((25,26)27))28)))14)11)((9,10)
(12((15,16)((18,19)20)))))13)(17,21))(22,23))(32,33))(30,31))34);
(((((((((((((((((((1,2)3)4)5)(((6,7)8)(((24,29)((25,26)27))28)))14)11)((9,10
)(12((15,16)((18,19)20)))))13)(17,21))(22,23))32)33)(30,31))34);
((((((((((((((((((1,2)3)4)5)((6,7)(8(((24,29)((25,26)27))28))))14)11)((9,10)
(12((15,16)((18,19)20)))))13)(17,21))(22,23))(32,33))(30,31))34);
((((((((((((((((((1,2)3)4)5)((6,7)(8(((24,29)((25,26)27))28))))14)11)((9,10
```

}(12((15,16)((18,19)20)))))13}(17,21))(22,23))32)33)(30,31))34);
((((((((((((((1,2)3)4)5)(((6,7)(((24,29)((25,26)27))28))8))14)11)((9,10)
(12((15,16)((18,19)20)))))13)(17,21))(22,23))(32,33))(30,31))34);
((((((((((((((((1,2)3)4)5)(((6,7)(((24,29)((25,26)27))28))8))14)11)((9,10
}(12((15,16)((18,19)20)))))13}(17,21))(22,23))32)33)(30,31))34);

Statistics derived from consensus tree
****

Consensus fork index (component count) =   29
CF (normalized) = 0.906
Term information =260
Total information =289
Mickevich's consensus information (CI) = 0.485
Weighted consensus fork = 0.516
Levels sum = 2790
Rohlf's CI(1) = 0.875
Rohlf's -log CI(2) =0.10231E+03

Appendix 4.7 Chronology of vicariance events in Australia.

I. PHYSICAL CHANGES (Galloway and Kemp, 1981, except as marked)
Mesozoic and Tertiary
East-west physiographic division of the Australian land mass
through uplift of the Australian Eastern Highlands from Cape York
to Tasmania (broadly coincident with the break up of Gondwanaland
and the rifting and separation of Australia and Antarctica) (Nix,
1981).

Late Cretaceous-early Paleocene (80-60 m.y. B.P.)
Eastern part of the Australian/Antarctic segment of Gondwanaland
broke up leading to the separation of New Zealand and New
Caledonia from Australia (Crock, 1981).

Late Paleocene (60-53 m.y. B.P.)
Separation of Australia from Antarctica, and from the Papua New
Guinea mobile belt.

Eocene (Mid at 45 m.y. B.P.)
A time of major marine transgression across southern Australia,
by the late Eocene shallow seas extended across much of the
southern continent (Kemp, 1981).

Miocene (Mid at 15 m.y. B.P.)
The early Miocene showed continuing extensive marine
transgression in the south, but by the late Miocene (7 m.y. B.P.)
there had been a considerable lowering of temperature and
rainfall, accompanied by large expansion of the Antarctic ice
sheet. (Miocene aridity)

Pleistocene
Sea levels fluctuated repeatedly during the pleistocene, within
the range -200m to +43m (due to changes in the temperature
affecting the ice sheets in Antarctica). In the lows, Tasmania,
Australia and New Guinea formed a single land mass.

Holocene
The last severing of the land bridge between the mainland and
Tasmania was only about 12,000-13,500 years ago

II. CLIMATIC CHANGES (Galloway and Kemp 1981, except as marked)
Early Tertiary to middle Eocene
Palaeo-botanical evidence of humid and relatively warm climate
with a tropical flora (Kemp, 1981).

Mid-Tertiary - late Eocene
Climatic changes with development of a north-south disjunction,
tropical pollen largely disappears in south-eastern Australia due
to temperature decrease. However there are some indications that
warm conditions persisted for longer in the south of Western
Australia, with tropical or subtropical conditions (Hos, 1975).
Mid-Oligocene
As Australia moved north the South Tasman Rise cleared Antarctica
(Crock, 1981) and circumpolar circulation is considered to have
reduced temperatures. Reduction in floristic diversity observed
in fossil record for southern parts of Australia (Kemp, 1981).

Miocene
Early warm wet conditions followed by development of cooler
temperatures and probable sudden decrease in rainfall and period
of relative aridity at the end of the period.

Pliocene
Limited information suggests widespread climatic changes. Marked
warming 3.9-4.3 m.y. B.P. likely to have been associated with
increased precipitation, followed by a renewed cooling and
dryness at the end of the Pliocene.

Pleistocene
Predominantly dry, with temperatures similar to the present. sand
dune areas of the continent showed mobile dunes throughout the
period.

Late Pleistocene and Holocene climates
123,000-80,000 years B.P.
Tropical conditions, rainfall at least as high as at present.

80,000-40,000 years B.P.
Reduction in precipitation to about half its present levels.
Glacial activity in Tasmania.

40,000-30,000 years B.P.
Northeast Queensland became drier and cooler, southeastern
Australia showed increasing humidity. Decreasing temperatures at
the end of the period lead to periglacial activity in the
southeast.

30,000-26,000 years B.P.
Dry conditions persisted in the north, glaciers formed in the
Snowy Mountains possibly due to a cold dry windy climate. Some
conflicting evidence for warm conditions in western N.S.W. and
high sea levels points to the possibility there were a variety of
successive climates.

26,000-16,000 years B.P.
Increasing aridity with "peak" achieved 16,000-17,500 B.P. Cold
dry climate with strong winds probable.

16,000-10,000 years B.P.
Dry conditions persisting, but with a gradual warming leading to
increased precipitation.

10,000 years B.P. to the present
Rise in temperature and precipitation leading to the return of
tropical rainforest to north Queensland, followed by decline to
essentially the same conditions as today for the last 2,000 yrs.

Appendix 4.8 Abbreviations used.
A number of abbreviations have been used in the appendices for
chapter 4. Some are as defined in the PAUP manuals, (Swofford
1986) but others have been used to fit plant names into the
constraints of program and data readability, and these are
defined below.

Abbreviations of plant names used in the analysis of the
Asparagales:

AGAVAC = AGAVACEAE
ASTELI = ASTELIACEAE
DRACAE = DRACAENACEAE
NOLINA = NOLINACEAE
OUTGP = OUTGROUP
XANTHO = XANTHORRHOEACEAE

Character labels used in the analysis of the Asparagales:

1HERBACE = herbaceous habit
2ROOT-VE = type of vessels present in the root
3STEM-VE = "   "   "   "   "   " stem
4LEAF-VE = "   "   "   "   "   " leaf
5DISTYCH = distichous phyllotaxy present
6BROAD-L = broad leaves present
7SPINES = spines to leaf margins
8STOMTYP = type of stomates
9STOMPOS = position of stomate relative to leaf surface
10INFLOR = inflorescence position: terminal or axillary
11FLOWER = flowers articulated or sessile
12CAPSUL = capsular fruit present
13PHYTOM = phytomelan in seed coats
14RAPHID; raphides present in leaves

Abbreviations of plant names used in the Xanthorrhoea analyses:

MACRONEM = Xanthorrhoea macronema
GRACILIS = X. gracilis
CONCAVA   = X. concava
FULVA   = X. fulva
RESINOSA = X. resinosa
BRUNBRUN = X. brunonis subsp. brunonis
BRUNSEMI = X. brunonis subsp. semibarbata
BREVISTY = X. brevistyla
PLATYPHY = X. platyphylla
PREISSII = X. preissii
DRUMMOND = X. drummondii
QUADRANG = X. quadrangulata
THORNTON = X. thorntonii
NANA   = X. nana
PUMILIO   = X. pumilio
MEDIA   = X. media
ALMAE   = X. almae
LAT LAT   = X. latifolia subsp. latifolia
LAT MAX   = X. latifolia subsp. maxima
ARBOREA   = X. arborea
MALACOPH = X. malacophylla

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```
GLAUCA G   = X. glauca subsp. glauca
GLAUCANG   = X. glauca subsp. angustifolia
ACAULIS    = X. acaulis
MINOR MI   = X. minor subsp. minor
MINORLUT   = X. minor subsp. lutea
BRACTEAT   = X. bracteata
CAESPITO   = X. caespitosa
ARENARIA   = X. arenaria
SEMIPLAN   = X. semiplana subsp semiplana
SEMI TAT   = X. semiplana subsp. tateana
ACANTHOS   = X. acanthostachya
AUSTRALI   = X. australis
```

Labels used in the Xanthorrhoea analyses:

```
1_TRK_HT = Trunk height
2_BRNCHS = Stem branching position
3_CROWNS = Number of crowns
4_LF_SHA = Leaf shape
5_LF_WTH = Leaf width
6_LF_THK = Leaf thickness
7_LF_COL = Leaf colour
8_STOMS = Leaf stomatal arrangement
9_SC_L = Scape length
10_SC_D = Scape diameter
11_RATIO = Ratio - spike length divided by scape length
12_SP_L = Spike length
13_SP_D = Spike diameter
14_PCBS = Cluster bracts - prominence
15_PCB_S = Cluster bracts - shape
16_PCB_H = Cluster bracts - indumentum
17_PCKBS = Packing bracts - shape
18_PCKBH = Packing bracts - indumentum
19_PCKBC = Packing bracts - colour
20_SP_BK = Sepals - beak
21_SP_PB = Sepals - proboscis
22_SP_HR = Sepals - indumentum
23_PETSZ = Petals - size
24_PETSH = Petals - shape
25_PETPB = Petals - proboscis
26_PETHR = Petals - indumentum
```

Appendix 5.1

ASSOCIATED PUBLICATION -

REPRINTED FROM:

BEDFORD, D.J., (1986 b). <u>Xanthorrhoea</u>, <u>IN</u> A.S. George, (Ed),

<u>FLORA OF AUSTRALIA: APPENDIX: New taxa, combinations and</u>
<u>lectotypifications</u> 46: 225-229

Xanthorrhoea gracilis Endl. in J.G.C. Lehmann, Pl. Preiss. 2: 39 (1845).

T: Darling Range, Perth, W.A., 16 Jan. 1840, L. Preiss 1619; lecto (here chosen): MEL 625759

The only extant syntypes of Preiss's collections appear to be at MEL, since Endlicher's specimens of Xanthorrhoea at W were destroyed during World War II and other herbaria holding Preiss collections, including LD, have no Xanthorrhoea duplicates. MEL 625759 is the better specimen of the two syntypes at MEL.

Xanthorrhoea concava (A. Lee) Bedford, stat. nov.

X. resinosa subsp. concava A. Lee, Contr. New South Wales Natl Herb. 4: 45 (1966). T: 1 mile [c. 1.6 km] W of Buxton, N.S.W., 5 Dec. 1960, A.T. Lee NSW 61300; holo: NSW.

This taxon is distinct from X. resinosa Pers. in habit, in the much longer and more flexible leaves, in leaf shape and dimensions, and in inflorescence, bract and petal characters. Although partially sympatric with X. resinosa it maintains its distinctness.

Xanthorrhoea fulva (A. Lee) Bedford, stat. nov.

X. resinosa subsp. fulva A. Lee, Contr. New South Wales Natl Herb. 4: 45 (1966). T: Coffs Harbour, N.S.W., 17 Oct. 1961, E.F. Constable NSW 61664; holo: NSW.

This taxon is distinct from X. resinosa Pers. in leaf shape and dimensions, inflorescence dimensions and colour, bract shape and in petal characters. It is allopatric with X. resinosa and occupies a different habitat.

Xanthorrhoea brunonis Endl. in J.G.C. Lehmann, Pl. Preiss. 2: 39 (1845)

T: near Swan River, W.A., 20 Nov. 1839, L. Preiss 1621; lecto (here chosen): MEL 625771.

The specimen of X. brunonis at MEL with the collecting label, in Preiss's hand, '1621 Xanthorrhoea...Acaulis...In arenosis ad. fl. Cygnorum.. Sem. num. 333... Novbr. 20.39. L. Preiss legit' is the only known extant material of this taxon collected by Preiss. As there may be duplicate specimens deposited elsewhere the material at MEL is chosen as lectotype to ensure nomenclatural stability.

Xanthorrhoea brunonis subsp. semibarbata Bedford, subsp. nov.

Ab X. brunonis Endl. subsp. brunonis apicibus bractearum floralarum stipantium fimbriatis differt.

T: Poad Road, S of Dardanup, W.A., 24 Nov. 1982, D.J. Bedford 8 & T.D. Macfarlane; holo: NSW; iso: PERTH.

The name is derived from the Latin semi (half) and barbatus (bearded), in reference to the hairs fringing the bracts.

Xanthorrhoea brevistyla D. Herbert, J. Roy. Soc. W. Australia 7: 82 (1921).

T: Narrogin State Farm, W.A., 13 Nov. 1920, D.A. Herbert s.n.; lecto (here chosen): PERTH; isolecto: MEL.

Two syntypes of X. brevistyla are in existence. The specimen at PERTH is chosen as lectotype because it is the more complete and conforms better with the protologue.

Xanthorrhoea acaulis (A. Lee) Bedford, stat. nov.

X. australis subsp. acaulis A. Lee, Contr. New South Wales Natl Herb. 4: 53 (1966). T: 6.5 miles [10.5 km] W of Dubbo on Minore Road, 9 Dec. 1961, E.F. Constable NSW 61344; holo: NSW.

This species is clearly distinct from X. australis R.Br. s. str. in

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trunk and leaf characters, in scape to spike ratio and dimensions, in
bract shape, hairiness and colour and in sepal shape. It also occurs
in a different habitat and geographic area and is sufficiently
distinct to warrant specific status.

Xanthorrhoea arenaria Bedford, sp. nov.

Ab X. minori R. Br. et X. bracteata R. Br. bracteis stipantibus
subulatis et bracteis fasciculorum subulatis prominentioribus et multo
longioribus, differt. Ab X. australi R.Br. caudice nullo et spica quam
scapo breviore vel aequanti, differt; et ab X. caespitosa Bedford
habitu minore, sepalorum rostro longiore, et foliis angustioribus,
differt.

T: c. 0.5 km NW of Coles Bay township, Tas., 26 Jan. 1984, D. Bedford
124; holo: NSW.

The name is derived from the Latin arenarius (growing in sand) in
reference to the most common habitat of the species.

Xanthorrhoea minor R.Br.

T: Port Jackson, N.S.W., 1803, R. Brown Iter Australiense 5773; lecto
(here chosen): BM (photo N/740).

There are three known specimens labelled X. minor by R. Brown, two at

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BM and one at K. At BM, besides the lectotype, is a specimen with two labels bearing conflicting locality details, both in Brown's hand. One reads Port Dalrymple Jan. 1804, the other Port Jackson (localities in Tasmania and N.S.W. respectively). A typed label, added later, reads `Paratype specimen of X. minor R.Br.'. This specimen is not X. minor but appears to be X. bracteata R.Br. The specimen at K is labelled `5 Xanthorrhoea minor Port Jackson, vicinity of Sydney' in R. Brown's writing and has fewer hairs on the bracts than does the specimen at BM designated (above) as lectotype.

A.T. Lee, Contr. New South Wales Natl Herb. 4: 46 (1966), referred to the lectotype specimen as a holotype, unaware of the other labelled specimens. The choice of lectotype, above, therefore maintains existing usage, although the specimen at K has since been incorrectly labelled, in an unknown hand, as the cited specimen.

Xanthorrhoea minor subsp. lutea Bedford, subsp. nov.

Ab X. minori R.Br. subsp. minori bracteis stipantibus acutis hirsutis, et petalis majoribus flavis, differt.

T: 3 miles [c. 5 km] SSW of Nowa Nowa, Vic., 29 Oct. 1964, E.F. Constable 5341; holo: NSW.

Named from the Latin luteus (yellow), in reference to the petals.

<u>Xanthorrhoea caespitosa</u> Bedford, sp. nov.

Ab <u>X. minori</u> R. Br. foliis latioribus glaucisque, inflorescentia plerumque altiori et bracteis stipantibus lineari-triangularibus ad subulatis, differt. Ab <u>X. semiplana</u> F. Muell. absentia caudicis et foliis in T.S. obtriangularibus ad concavis, differt.

T: Meningie, S.A., 13 Nov. 1957, <u>J.B. Cleland s.n.</u>; holo: AD 966081326.

Named from the Latin <u>caespitosus</u> (growing in tufts or clumps) to describe the habit of this species.

This taxon probably corresponds with most of the reported populations of <u>X. minor</u> in S.A. (J.B. Cleland, <u>S. Austral. Naturalist</u> 40: 27, 1965) and with the purported hybrid swarm mentioned by A.T. Lee, <u>Contr. New South Wales Natl Herb</u>. 4: 54 (1966).

<u>Xanthorrhoea nana</u> D. Herbert, <u>J. Roy. Soc. W. Australia</u> 7: 83 (1921).

T: about 2 miles [c. 3 km] NE of Bruce Rock, W.A., 25 Oct. 1920 <u>D.A. Herbert</u>; lecto (here chosen): PERTH; isolecto: MEL.

The PERTH specimen is chosen as lectotype because it is the more complete. The specimen at MEL, which has Herbert's handwritten label, is the same taxon but is a poor specimen. Neither specimen has leaves. A specimen collected at the type locality by D.J. Bedford 76 & T.D. Macfarlane in 1982 (NSW, PERTH), consisting of leaves and

infructescence, serves to confirm Herbert's leaf description.

Xanthorrhoea drummondii Harvey, *Hooker's J. Bot. Kew Gard. Misc*. 7: 57 (1855).

T: near Perth and elsewhere, W.A., *J.L. Drummond s.n*.; *n.v*.; Wedin siding, W.A., 28 Nov. 1982, *D.J. Bedford 46 & T.D. Macfarlane*; neo (here chosen): NSW; isoneo: PERTH.

No sheet of the Drummond collection has been located. The specimen selected as neotype conforms to the protologue; it is complete and well-documented.

Xanthorrhoea platyphylla Bedford, sp. nov.

Ab *X. preissii* Endl. foliis latioribus in T.S. obtrullatis ad obtriangularibus, et absentia caudicis, differt. Ab *X. brevistyla* D. Herbert foliis multo crassioribus et latioribus, spica quam scapo longiori, et bracteis stipantibus minus hirsutis, differt.

T: 36.5 km W of Esperance on road to Ravensthorpe, W.A. 27 Nov. 1982, *D. Bedford 35 & T.D. Macfarlane*; holo: NSW; iso: PERTH.

Named from the Greek *platys* (wide) and *phyllon* (leaf), in reference to the broad leaves which distinguish it from its nearest relatives.

Xanthorrhoea preissii Endl. in J.G.C. Lehmann, <u>Pl. Preiss</u>. 2: 39 (1846).

T: York [vicinity of Toodyay, perhaps the present-day Boyagerring Ck which flows to Toodyay from 10 km NE], W.A., 22 Mar. 1840, <u>L. Preiss 1620</u>; lecto (here chosen): MEL 625774.

There are no Preiss collections of <u>Xanthorrhoea</u> at LD or W. The sheet MEL 625774, which has Preiss's collecting label, is the only specimen found of the type collection of this species. Since it is unlikely to be the holotype, as Preiss usually collected and distributed duplicates, it is best to designate this specimen as lectotype to ensure nomenclatural stability.

Xanthorrhoea quadrangulata F. Muell., <u>Fragm</u>. 4: 111 (1864)

T: [near St Vincent Gulf], S.A., 3 Feb. 1848, <u>F. Mueller</u>; lecto (here chosen): MEL 625754; isolecto: K, MEL 625760.

Three known specimens represent material collected by Mueller and cited in his protologue. Two are at MEL (MEL 625754, MEL 625760) and one at K. One (MEL 625754) consists of part of the scape and spike and 3 pieces of leaf; it is signed `Dr. M' and dated `Feb. 3 1848' and has a vague locality (`non procul a cataracta'). Other specimens collected around this date by Mueller are labelled `Gawler, Torrens, Holdfast Bay [now Glenelg] and St Vincents Gulf' which provides a fairly accurate location for the collection as being `not far from St Vincents Gulf' in the terms Mueller used in his original description.

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The other sheet (MEL 625760) bears two pieces of spike and two pieces of leaf. It is not signed or dated but is labelled in Mueller's early hand `Xanthorrhoea quadrangulata F.M. Mount Lofty Range'. The sheet at K bears part of a spike and two pieces of leaf; it is not dated but is signed and labelled `Xanthorrhoea quadrangulata Ferd. Mll. Lofty-ranges Dr M` in Mueller's hand. The sheet MEL 625754 is chosen as lectotype primarily because it is the most complete both in the specimen and in the date.

Xanthorrhoea latifolia (A. Lee) Bedford stat. et. comb. nov.

X. media subsp. latifolia A. Lee Contr. New South Wales Natl Herb. 4: 48 (1966). T: Beerwah, Qld May 1962 E.F. Constable NSW 61667 holo: NSW.

This taxon is distinct from X. media in its broader more transversely rhombic leaves, longer inflorescence and longer trunk. It is allopatric with X. media and often occupies wetter or more sheltered habitats. It is sufficiently distinct to warrant specific status.

Xanthorrhoea latifolia subsp. maxima Bedford, subsp. nov.

Ab X. latifolia subsp. latifolia caudice altiori, foliis plerumque multo latioribus, spica quam scapo multo breviori, et bracteis stipantibus acutis, differt.

T: Mt Warning, near Murwillumbah, N.S.W., 2 June 1962, E.F. Constable NSW 61357; holo; NSW.

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Names from the Latin _maximus_ (very large), in reference to the width of the leaves.

Xanthorrhoea malacophylla Bedford, sp. nov.

Planta cum caudice altissimo et foliis spongiosis mollibus viridibus. Ab _X. australi_ R. Br. bracteis stipantibus acutis et sepalis brevioribus sine proboscide, et ab illa et _X. glauca_ Bedford foliis mollibus viridibus, scapo spicam fere aequanti, et bracteis fasciculorum minus prominentibus, differt.

T: Camp Ridge Trig., Queens Lake State Forest, 5 miles [8 km] NNE of Kew, N.S.W., 15 May 1964, _E.F. Constable 4792_; holo: NSW.

Names from the Greek _malacos_ (soft to the touch) and _phyllon_ (leaf), in reference to the spongy soft leaves.

Xanthorrhoea glauca Bedford, sp. nov.

Ab _X. australi_ R.Br. bracteis fasciculorum et bracteis stipantibus subglabris, his cum lamina gracili, capitulo lato fusco et apice triangulari vel acuto, differt. Ab _X. johnsonii_ A. Lee bracteis fasciculorum longioribus et multo prominentioribus, foliis glaucis, et spicis grossis quam scapis multo longioribus, differt.

T: edge of Levers Plateau, Qld, 4 July 1977, _D. Bedford 7776_; holo: NSW.

Names from the Latin glaucus (covered with a fine bloom), in reference to the distinctly glaucous fresh leaves.

Xanthorrhoea glauca subsp. angustifolia Bedford, subsp. nov.

Ab X. glauca Bedford subsp. glauca foliis angustioribus quad-rato-rhombeis cineraceis, et scapis spicisque parum gracilioribus, differt.

T: 5 miles [8 km] NW of Coonabarabran on Bugaldie Road, N.S.W., 13 Dec. 1961, E.F. Constable NSW 61353; holo: NSW.

Named from the Latin angustus (narrow) and folium (leaf), in reference to the narrow leaves.

Xanthorrhoea semiplana F. Muell., Fragm. 4: 111 (1864).

T: near Gawler town, S.A., F. Muell., lecto (here chosen): MEL 625756.

Three specimens at MEL (MEL 625755, 625756, 625757), collected by Mueller from localities cited in his protologue, represent the only known syntypes. One (625755) has an early draft of Mueller's description but consists of leaf pieces only; another (625757) is dated (Nov [18]51) and consists of slivers of spike only; the third (625756) is the most complete specimen as it consists of pieces of spike, scape and leaf. Although this last specimen is not dated, its

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label in Mueller's hand 'Xanthorrhoea semiplana mihi', is clearly proof that Mueller regarded it as belonging to this taxon. Additionally, as the locality is the same as MEL 625757 it is most likely that it was collected at the same time as that specimen.

Xanthorrhoea semiplana subsp. tateana (F. Muell.) Bedford, stat. et comb. nov.

X. tateana F. Muell., Z. Allg. Osterr. Apotheker-Vereines 23(19): 293-295 (1885). T: Kangaroo Island, S.A., 1883, Somerville & Wilks; lecto (here chosen): MEL 625766.

The status of X. tateana has long been in doubt. J.M. Black, Fl. S. Australia (1943), noted that 'on the mainland this species tends to run into X. semiplana, to which it is closely related'. J.B. Cleland, S. Austral. Naturalist 39: 61 (1965), treated X. tateana as a form of X. semiplana. A study of specimens and of plants in the field, indicates that the only differences between the two species are inflorescence dimensions and geographical distribution, with considerable overlap in both. It is thus more appropriate that X. tateana be regarded as a subspecies of X. semiplana.

Mueller's protologue left some doubt as to the source of his material and information. Mueller mentions information from Tate, but no suitable specimen collected by Tate has so far been located. However, as he mentions Somerville & Wilks as providing resin material of the taxon, and the only known specimen collected before 1885 was that of Somerville & Wilks, it seems certain that this collection was used by Mueller for his description and it is therefore chosen as lectotype.

Appendix 5.2

ASSOCIATED PUBLICATION -

REPRINTED FROM:

BEDFORD, D.J., (1985). <u>Xanthorrhoea acanthostachya</u> (Xanthorrhoeaceae),
a new species of the Perth Region, Western Australia. <u>Nuytsia</u> 5: 317-
321.

This reprint is enclosed in the pocket attached to the back cover of
this thesis.

Xanthorrhoea acanthostachya (Xanthorrhoeaceae), a new species of the Perth Region, Western Australia

D. J. Bedford

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Abstract

Bedford D. J. *Xanthorrhoea acanthostachya* (Xanthorrhoeaceae), a new species of the Perth Region, Western Australia. Nuytsia 5(2): 317-321 (1984). *Xanthorrhoea acanthostachya* is described and illustrated. It is distinguished from other *Xanthorrhoea* species in Western Australia by the combination of very elongated, prominent cluster bracts and subulate floral bracts and from *X. australis*, its nearest relative, by its scape length to spike length ratio and leaf colour. Very few examples of the species are known.

Xanthorrhoea acanthostachya Bedford, sp. nov. (Figures 1-3)

X. australi similis, sed scapo plus minusve spicam aequanti et foliis viridibus vel minus glaucis differt. A speciebus Australiae Occidentalis bracteis fasciculorum conspicuis elongatissimus ad maturitatem et bracteis floralibus subulatis distinquenda.

Typus: Chatfield Rd, South Western Highway, Western Australia, 24 Nov. 1982, *D. J. Bedford* 4 and *T. D. Macfarlane* (holo: NSW; iso:PERTH).

Trunk short to 1.5 m tall, crowns 1 to 2. *Leaves* (terminal) in more or less hemispherical crowns, 60-70 cm long, quadrate-rhombic in transverse section, 2-2.25 mm wide and 1.5-2 mm thick, green to slightly glaucous. *Leaf-base* swollen and rigid at the junction with the leaf. *Scape* 40-50 cm long, 7-16 mm diam. *Spike* usually more or less equal in length to scape, (20)40-50(90) cm long and 20-40 mm diam., prickly in appearance. *Cluster-bracts* very elongated, subulate in shape, dilated at the base, usually very prominent (occasionally slightly prominent), glabrous, rarely subglabrous. *Packing-bracts* (floral bracts) subulate in shape, often twisted or folded, subglabrous to glabrous (except for occasional large bracts, which have a line of hairs along the centre of the back and hairs at the margins below the tip). *Sepals* short, acute, with short beak at the tip, glabrous except for a tuft of hairs in the beak. *Petals* more or less erect at anthesis, sometimes beaked, with an adaxial proboscis, soft and membranous, glabrous except for short hairs in and around the tip, and hairs covering the proboscis. *Fruit* acute at the tip with a persistent long style-base-point, dark brown at maturity. *Seeds* dorsi-ventrally flattened, narrow ovate to ovate (Systematics Association (1962) figures 37-38), triangular in median transverse section, semi-matt black, 11-12 mm long by 4.5-5.5 mm wide, when fully mature. (Terminology as per Lee (1966a and b) and Systematics Association (1962)).

Other specimens examined. WESTERN AUSTRALIA: Harvey Dam Reserve, 13 Nov. 1981, *T.D. Macfarlane* 659 (PERTH); Keysbrook, Nov. 1900, *W.V. Fitzgerald* NSW 154569 (NSW); 5 miles E of Mogumber, 25 Aug. 1970, *K.M. Allan* s.n. (spirit collection only) (PERTH).

Distribution. At present *X. acanthostachya* is known only from four sites in the Perth Region of W.A. as defined by Marchant and Perry (1981).

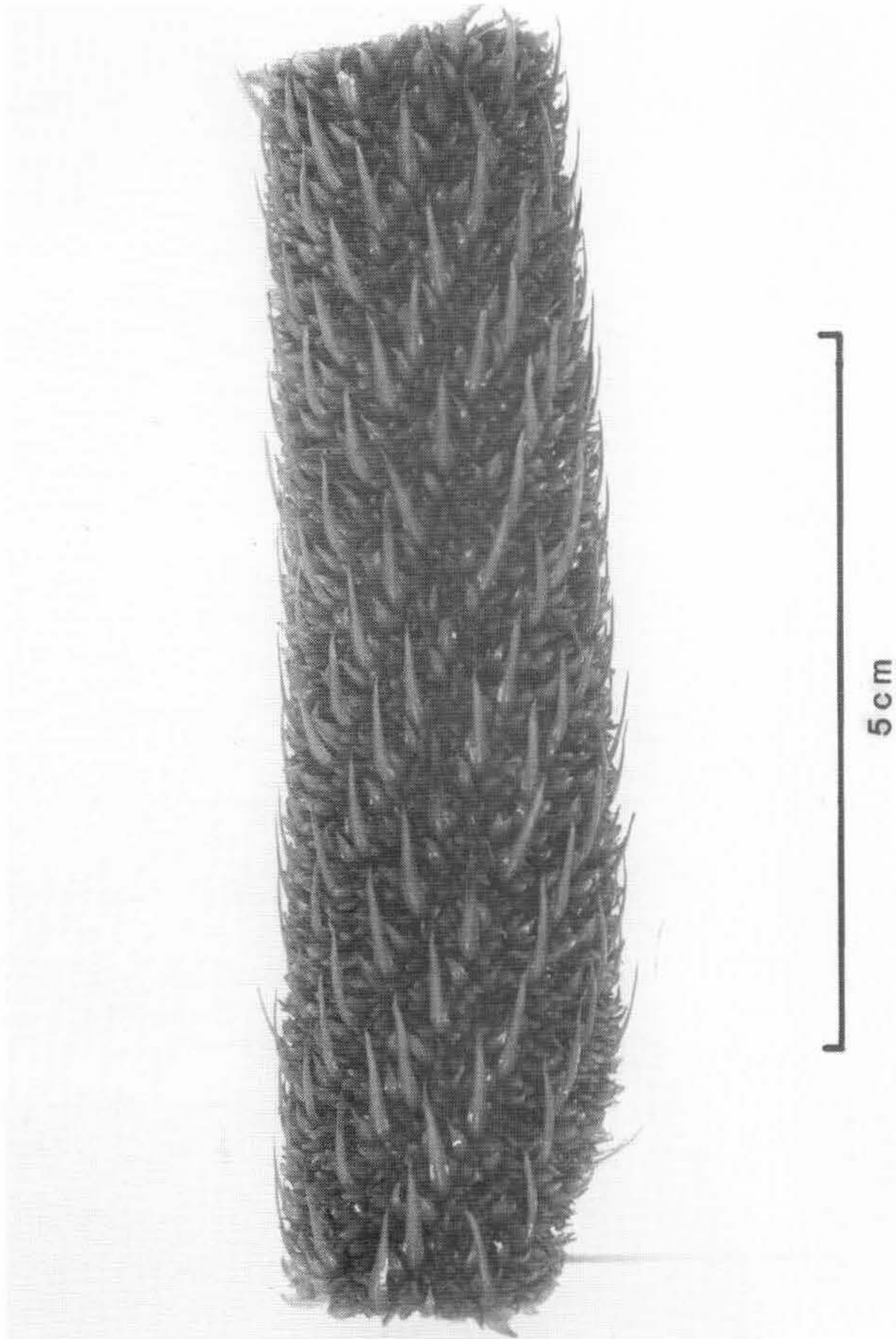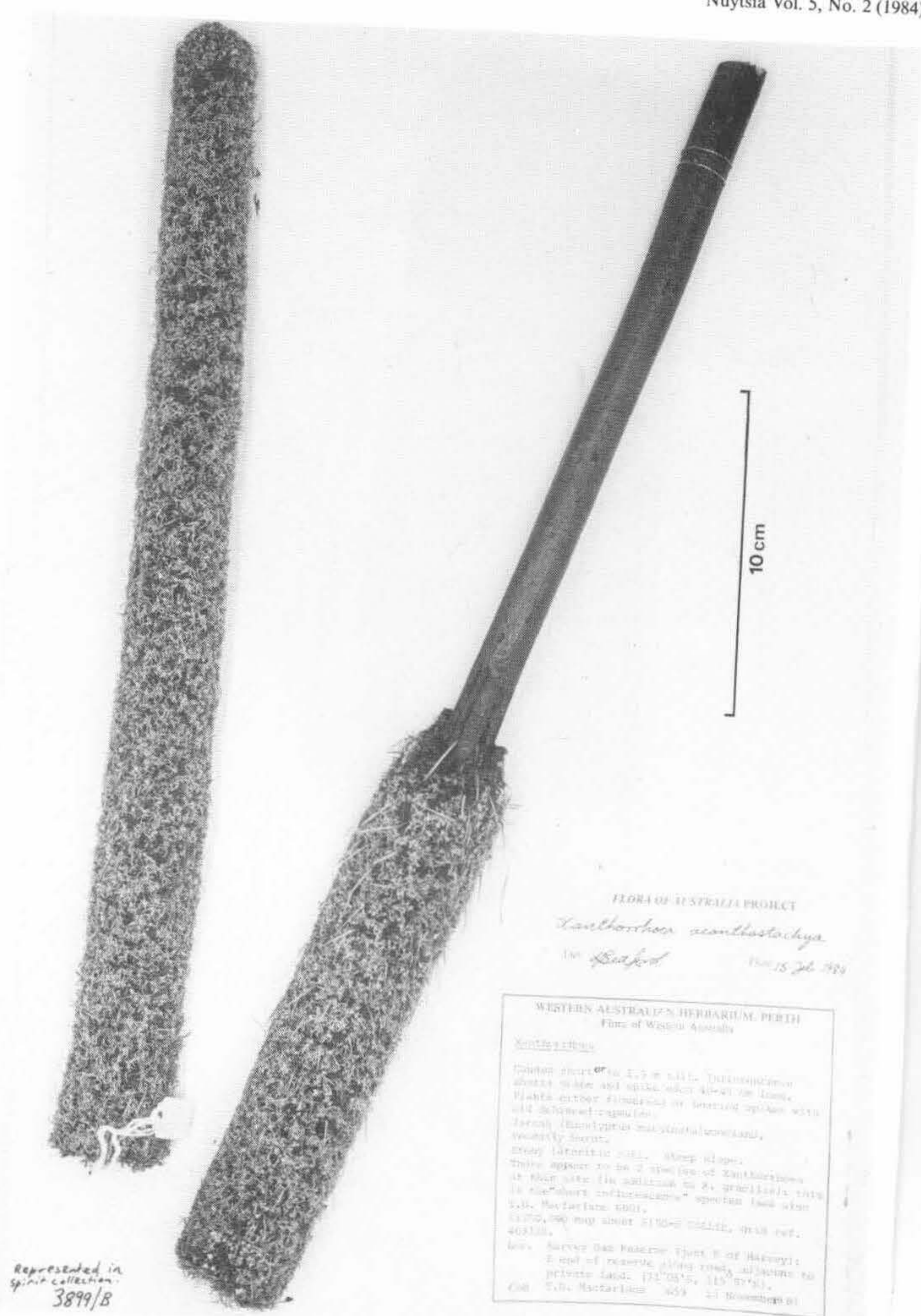Figure 1. *Xanthorrhoea acanthostachya*, holotype specimen in herb. NSW.

Figure 2. *Xanthorrhoea acanthostachya*, close-up view of immature spike, showing very prominent cluster-bracts. *K. M. Allan* s.n., 5 miles E of Mogumber, W. Austral., 25 Aug. 1970.

Ecology. The species occurs on the coastal plain in grey sand overlain by lateritic gravel, often with *Dasypogon bromeliifolius* and *Kingia australis*, and on steep slopes in stony lateritic soil in Jarrah (*Eucalyptus marginata*) woodland.

Figure 3. *Xanthorrhoea acanthostachya*, mature flowering spike showing exceptionally long prominent cluster-bracts. *T. D. Macfarlane* 659, sheet 1.

Flowering period. Young flowering spikes have been collected in August and flowering and recently fruiting spikes have been collected in November.

Affinities. There are no obvious allies of *Xanthorrhoea acanthostachya* in Western Australia, although its leaves are at least superficially similar to those of *X. preissii. X. australis* of eastern Australia has similarly shaped bracts and leaf cross-sectional shape, and is therefore probably the most closely allied species. *X. semiplana* of South Australia has similarly shaped floral bracts to *X. acanthostachya* but is a much more massive plant with large broad transverse-rhombic median transverse section leaves.

Xanthorrhoea acanthostachya differs from *X. australis* in (a) scape length to spike length ratio; *X. acanthostachya* has scape length more or less equal to spike length, *X. australis* always has a much shorter scape than spike (less than ½ the length), (b) leaf colour; *X. acanthostachya* has green to slightly glaucous leaves, *X. australis* has very glaucous leaves, (c) sepals; *X. acanthostachya* has short, acute sepals, with a short beak at the tip, without a proboscis in the beak, *X. australis* has subulate shaped sepals with a long narrow beak at the tip, often with a proboscis in the beak, (d) petals; *X. acanthostachya* petals sometimes have a beak, *X. australis* petals never have a beak.

Etymology. The specific epithet is from the Greek *akantha*, meaning a thorn or prickle, and *stakhys*, an ear of grain or a spike, in reference to the distinctly thorny or prickly appearance of the spike due to the prominent cluster-bracts.

Acknowledgements

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