

**A SYSTEMATIC STUDY OF *OSCULARIA*
(MESEMBRYANTHEMACEAE)**

BOTANY HONOURS PROJECT 1990

SUPERVISOR : DR H.P.LINDER

SHERAINE HORNE

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.



ABSTRACT

Fifty-nine specimens of *Oscularia* were used in a phenetic study. Various characters were measured to determine the variability of these characters within the genus. The character states were analysed both by univariate and multivariate methods. The univariate analysis (ie. scatter diagrams) showed that there is a continuous variation in the specimens. The data matrix made up of these character states was analysed by two computer systems namely NTSYS and UNITER. These systems used different grouping methods to obtain a cluster diagram of the data. The results obtained by the two systems differed but both indicated that *Oscularia* consists of one species complex and not the three separate species given by previous studies.

A number of *Oscularia* specimens studied did not have dentate leaves. Dentate leaves are a very important distinguishing character for the taxon. It is concluded that these species have been named incorrectly and it is suggested that they are removed from *Oscularia* and be included in various *Lampranthus* species where they seem to fit.

Oscularia is distinct from the genus *Lampranthus* only by its dentate leaves. It is insufficient to define *Oscularia* as a genus based on this character. This study thus supports the proposal to include *Oscularia* in the genus *Lampranthus* as *L. deltoides*.

INTRODUCTION

The family Mesembryanthemaceae is a wide and varied group of botanically and biologically remarkable plants. Most species are succulent and have strange growth forms. These plants are commonly known as ^{only a few genera} 'stone flowers'. Ninety-nine percent of all species within the Mesembryanthemaceae are indigenous to South Africa.

Mesembryanthemaceae is distinct by three major characters: Flowers have numerous showy petaloid staminodes, the ovary is inferior and the fruit which are hygrochastic capsules have a distinct and unique construction (Herre, 1971). ^{Just name?} Various other characters are also used to describe the family: Pollen morphology, chromosome number ($x = 9$), the continuous distribution area and the nectary glands.

Jacobson (1960, in Herre, 1971), indicated that the family consists of 122 genera and 2500 species, but it is felt that the family has been split into too many genera and that reduction of this number is necessary (Herre, 1971). The family Mesembryanthemaceae is renowned ^{at} for its taxonomic problems both at a generic and at a specific level. Generally it seems that there are also too many species that have been delimited within this family and that there is much variability within species. Gibbs Russell & Glen (1984) are of the opinion that because

Mesembryanthemaceae is economically unimportant and restricted to Southern Africa, very little work has been done on the family compared to Poaceae which has a worldwide distribution and is economically important. This explains how the above problems arose.

Mesembryanthemum is the genus into which all the species in the family were originally placed. During the 1920s this large genus was divided into new genera by L. Bolus, G. Schwantes and N.E. Brown on the basis of the morphology of the fruit.

Mesembryanthemaceae has been divided into four subfamilies and so *Mesembryanthemum* is now in a different subfamily to the genus which will be discussed. *Oscularia* belongs to the family Mesembryanthemaceae, subfamily Ruschioideae, tribe Ruschieae and subtribe Lampranthinae. This genus is distinguished from

Mesembryanthemum mainly by the continually open and scented flowers (Schwantes, 1957). These are not properties one can test on herbarium specimens and are consequently not very useful for herbarium taxonomy. For biological classification however, this may be important. The capsule is distinct from *Mesembryanthemum* by the disc which is divided into five parts, but is almost identical to that of *Lampranthus* (Schwantes, 1957). (A further point the author raises is that in cultivation *Oscularia* needs the same treatment as *Lampranthus*.)

Focussing on *Oscularia* we see that the problems mentioned for the family are mirrored at a smaller scale in this group. It is uncertain whether the genus *Oscularia* consists of three species or a species complex. At the generic level there is the unresolved question of whether *Oscularia* is a genus in its own right or whether *Oscularia* should lose its generic status and be reduced to a species within the genus *Lampranthus*.

Oscularia is a native of the South-Western Cape areas. The geographic range in which this shrub is found extends from the Witzenberg to the Caledon Swartberg area (Glen, 1978). (Fig. 1) These plants are found in mountainous areas, usually occurring in rocky places where it forms dense mats covering rock faces. Flowering season is from early spring to summer (Jacobsen, 1954).

Oscularia was first described by Dillenius in Hortus Elthamensis in 1732. There is an illustration of the type specimens which were then named *Mesembryanthemum deltoides* and *M. caulescens* (fig. 2). The only difference shown between these two specimens are the lack of teeth on the keel edge of the leaves in *M. caulescens*. (*M. deltoides* has teeth on all three edges of the leaves.) The herbarium specimens studied correspond precisely to that in Dillenius' diagram. Thus there is no disputing that it is the same species. All subsequent nomenclatural permutations were based on the iconotype in Hort. Eltham. (Dillenius, 1732). The names *Oscularia deltoides* (L.) Schwant. and *O. caulescens* (Mill.) Schwant. were applied to the type specimens mentioned

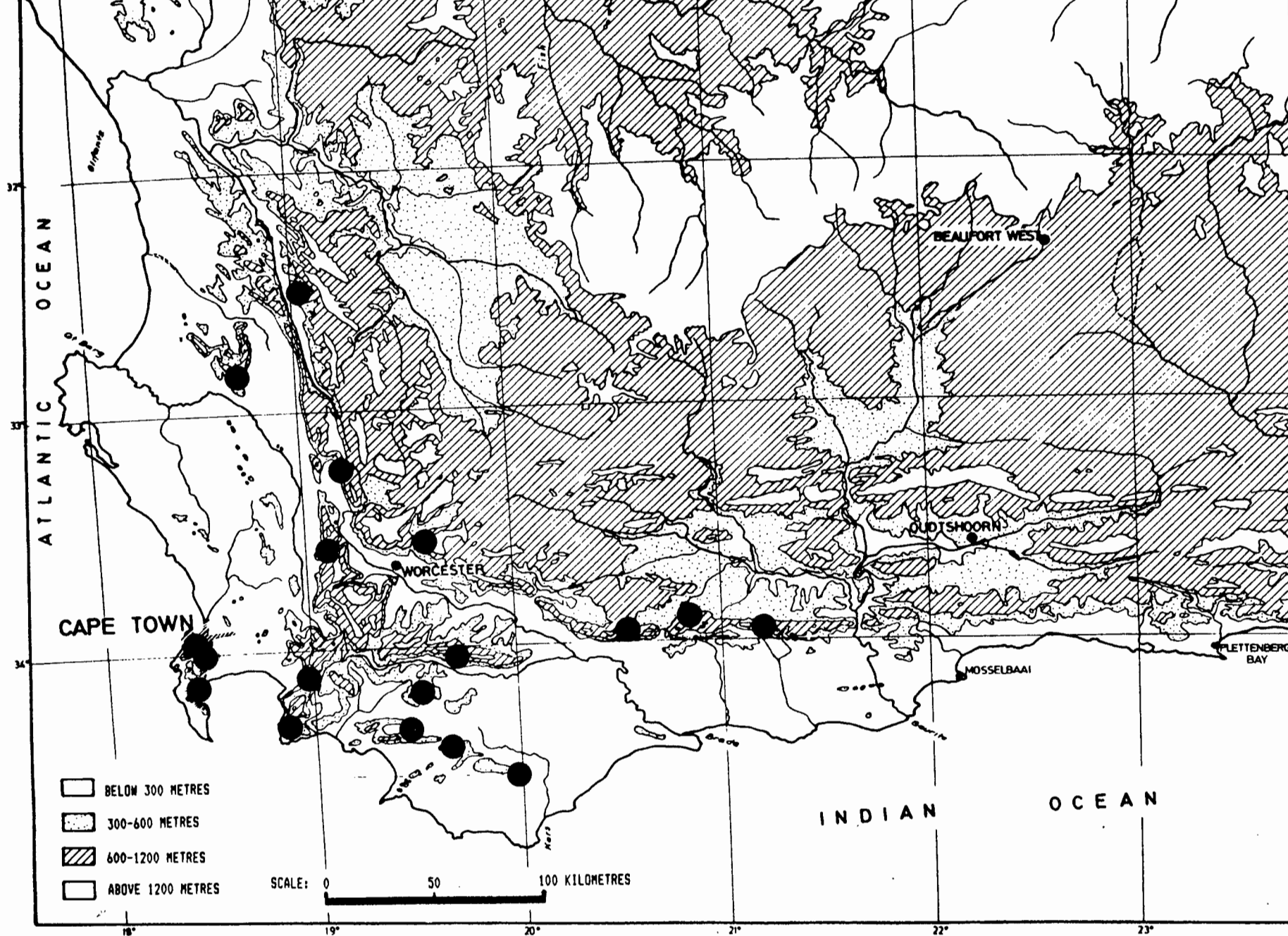


Figure 1: Map showing the distribution of *Oscularia* in the Southern Cape.

Is this based on all the material, or only those with teeth?

above.

illustration,
not type
specimen

For a long time three separate species were recognised in the genus *Oscularia* (Herre 1971, Jacobsen 1970, 1954, 1938, 1935). These species were known as *O. caulescens*, *O. deltoides* and *O. pedunculata*. These species were separated mainly on the basis of the size of the leaves and flowers. The size distinctions of structures for each species are shown in Table 1. *O. caulescens* was discerned from the others by an entire keel edge on the leaves. In all the other species the keel is dentate (Jacobsen 1935, 1938, 1954, 1970). Two varieties were distinguished in the species *O. deltoides*, namely var. *deltoides* and var. *majus* on the basis of flower diameter.

Table 1: Table showing the distinction between *Oscularia* species as described by Jacobsen (1970, 1954).

	<i>O. caulescens</i>	<i>O. pedunculata</i>	<i>O. deltoides</i>	<i>var. deltoides var. majus</i>
Leaf				
-length	20*	10 - 15	6 - 10	6 - 10
-width	10 - 11	8	-	-
Flower				
diameter	12	12	12 - 16	18
Dentate				
leaf keel	NO	YES	YES	YES

*All measurements are in millimetres

Glen (1978) examined *Oscularia* specimens and he concluded that the three species described by Herre (1971) and Jacobsen (1970) are in fact only one species. Glen (1978) maintains that *Oscularia* consists of a series of intermediates that link to the section *Lunati* of the genus *Lampranthus*. A complete range of variation is perceived by Glen (1978) from the typical *O. deltoides* to the typical *L. copiosus* which according to him is



Figure 2: Photograph of the illustrations of *Mesembryanthemum deltoides* in *Hortus Elthamensis* (Dillenius, 1732, p254).

the most closely related species to *O. deltoides*. *O. deltoides* has leaves with many marginal teeth while *L. copiosus* has few or no teeth. (However no teeth were observed on any of the herbarium specimens of *L. copiosus* kept at the Bolus herbarium.)

Glen (1978) proposed that the genus *Oscularia* be included in *Lampranthus* section *Lunati* and be named *Lampranthus deltoides* (L.) Glen. He suggests that the name *Lampranthus* be conserved over *Oscularia* (L.) Schwant. to prevent the number of name changes necessary were '*Oscularia*' maintained. Glen's proposal to include *Oscularia* into the genus *Lampranthus* was accepted by Brummitt (1983).

A number of Glen's proposals for changes in the taxonomy of the Mesembryanthemaceae has been rejected. This casts doubt on whether Glen's proposals pertaining to *Oscularia* can be trusted.[?] However, errors in other areas of Glen's work does not imply that his treatment of *Oscularia* is wrong but does necessitate an evaluation of his work.

This project was initially aimed at ^{resolving} diffusing the specific problem using phenetic methods and some suggestions will be made as to the resolving of the generic problem.

METHODS

The Bolus Herbarium, housed at the University of Cape Town, has a total of fifty nine specimens of *Oscularia* which were studied during this study (fig. 3). These specimens cover the whole distribution range of *Oscularia*.

Data on the following

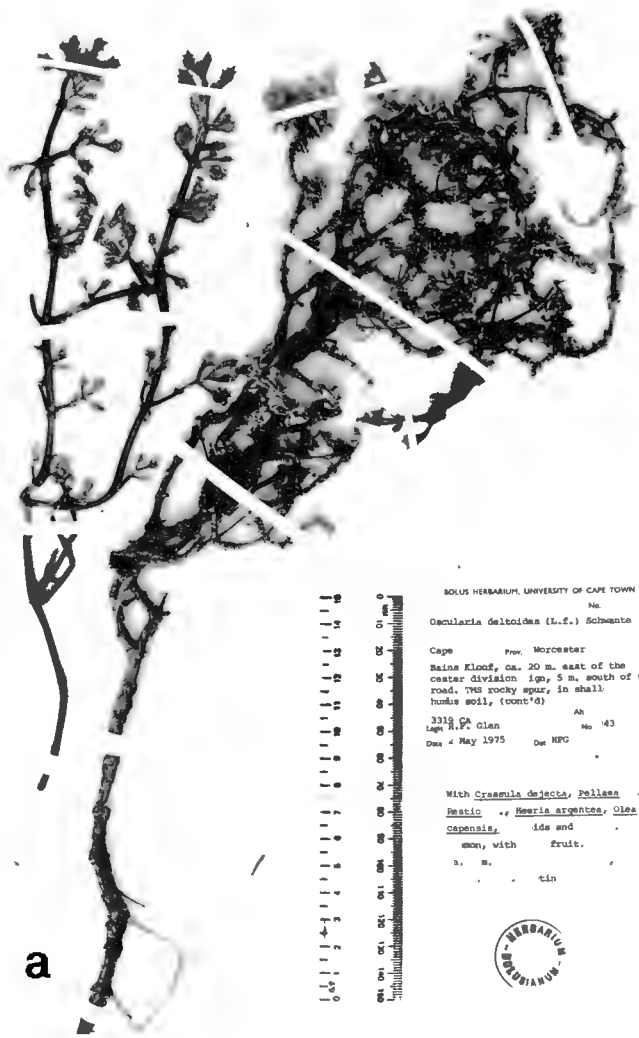
The following characters were collected from the specimens:

The number of teeth on the keel edge of the leaves was observed and noted. The number of teeth on the keel edge of the leaves was coded 0 for no teeth, 1 for one tooth and 2 for two teeth (fig. 4).

The presence of teeth on leaves was coded as presence (=1) or absence (=0) (fig. 5).

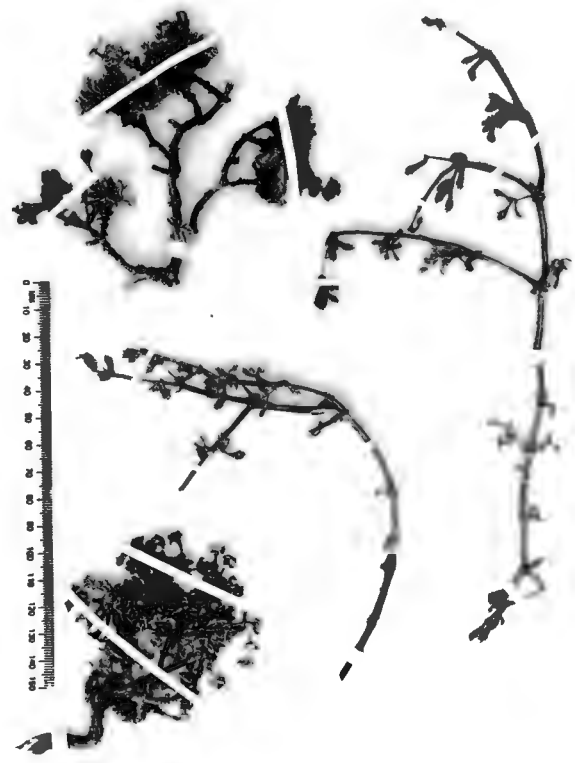
The length of stem from one node to another is considered as the internode length (fig. 6). This character was measured in millimeters with a clear plastic ruler. The 'internode length' incorporates a measure of the compact appearance of the specimen, that is the dense packing of the leaves.

Leaf length and width: Leaf width was measured at the broadest section of the leaf, and leaf length at the longest section (fig. 7). Three readings were made for each character as described for



SOLUS HERBARIUM UNIVERSITY OF CAPE TOWN
 No.
Oscularia deltoides (L.f.) Schwanke
 Cape Prov. Worcester
 Bains Kloof, ca. 20 m. east of the
 center division 100, 5 m. south of E
 road. The rocky spur, in shall-
 humus soil, (cont'd)
 3319 CA AH
 Leg. R.P. Glen No. 43
 Date 4 May 1975 Det MPG

With *Crasula dejecta*, Pallas
Restio .. *Heeria argentea*, Olee
capensis, ide and
 mon, with fruit.
 a. b. tin

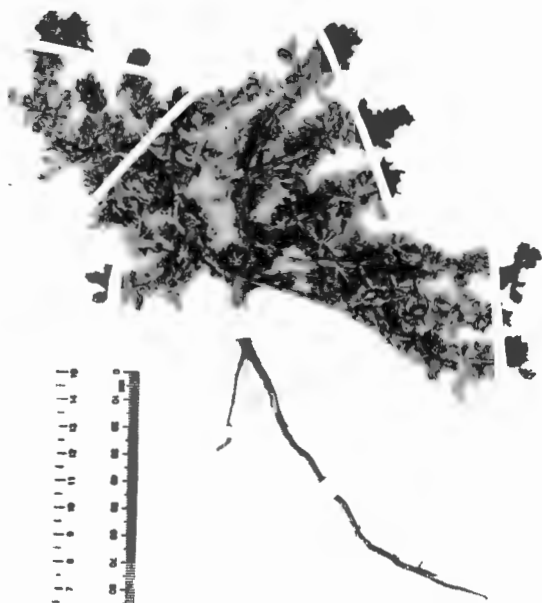


SOLUS HERBARIUM UNIVERSITY OF CAPE TOWN
 3319CC
Oscularia deltoides GC Schwanke
 Mesembryanthemaceae
 MPE LEUBOSCH
 common rocky outcrops 1000s
 on low substrate in or cascading
 over rocks 1 meter wide (flattening)
 11 km NW Franschhoek m.
 in number



b

Figure 3: (a) - (d) Photographs of herbarium specimens showing the typical features of *Oscularia*.



BOLUS HERBARIUM, UNIVERSITY OF CAPE TOWN
 JWN
 2419 AA
Oscularia dolobrichii

The Galy, Romsfontein, Mt. Athol
 above P.O. road to Swartkops, in F.M.S. road
 crosses a short. Tightly spreading caudex with
 long, thin woody stems. Level: 4000'
 P.A. Breen 762
 14.12.1981 H. O.C. Fenton



c



BOLUS HERBARIUM, UNIVERSITY OF CAPE TOWN
 1785
Oscularia muscicola
 Pro: [blank]
 H. Kesteven
 M.
 Lige: [blank]
 Date: 12. 11. 1981 Det. [blank]



d

HERBARIUM AFRICANUM BOUBIARUM
 FLORA

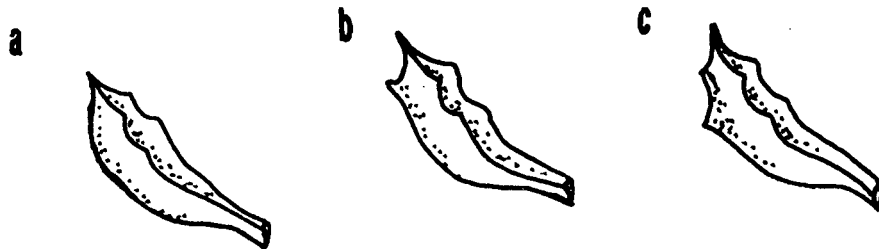


Figure 4: Diagram showing the various character states of the keel edge of the leaves. (a) No teeth, (b) One tooth, (c) Two teeth. (Lifesize)

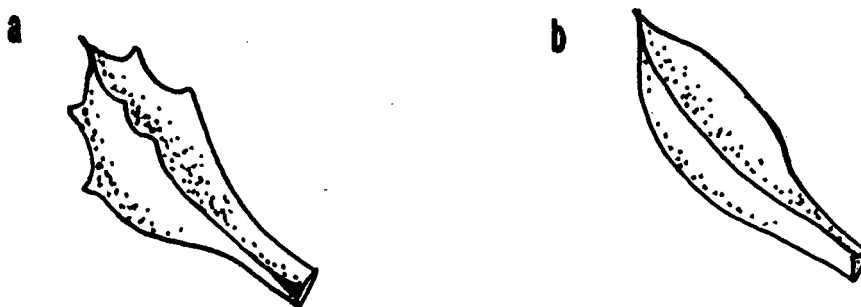


Figure 5: Diagram of a dentate (a) and an entire leaf (b). (Magnification of 1.5X)

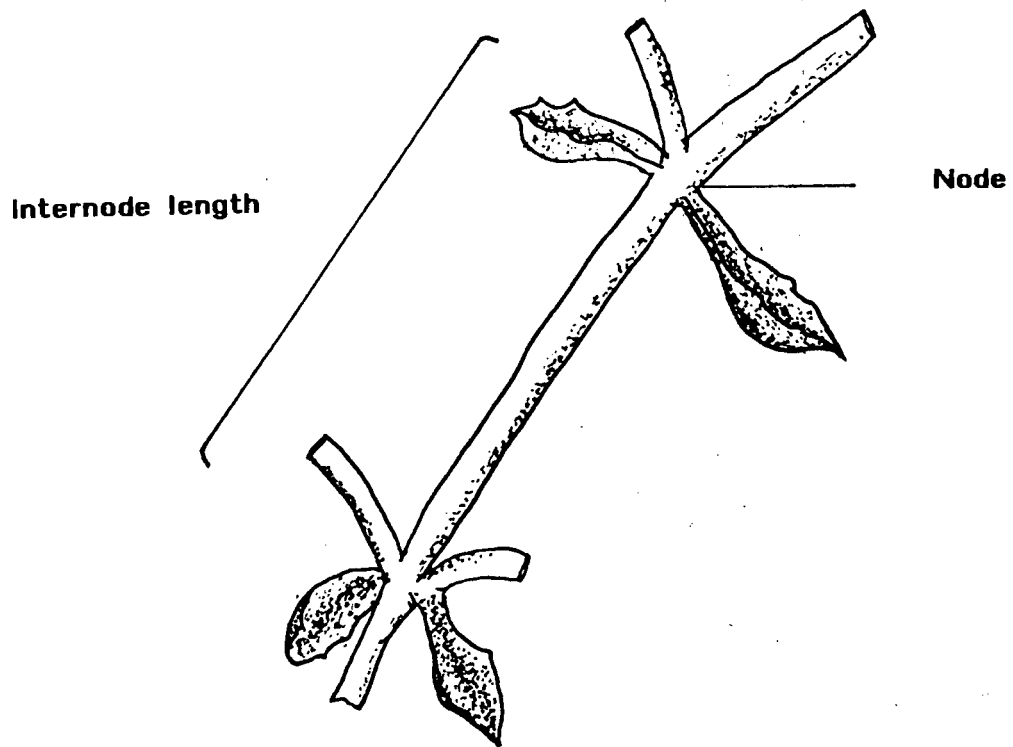


Figure 6: Diagram showing an internode. (Magnification of 1.5X)

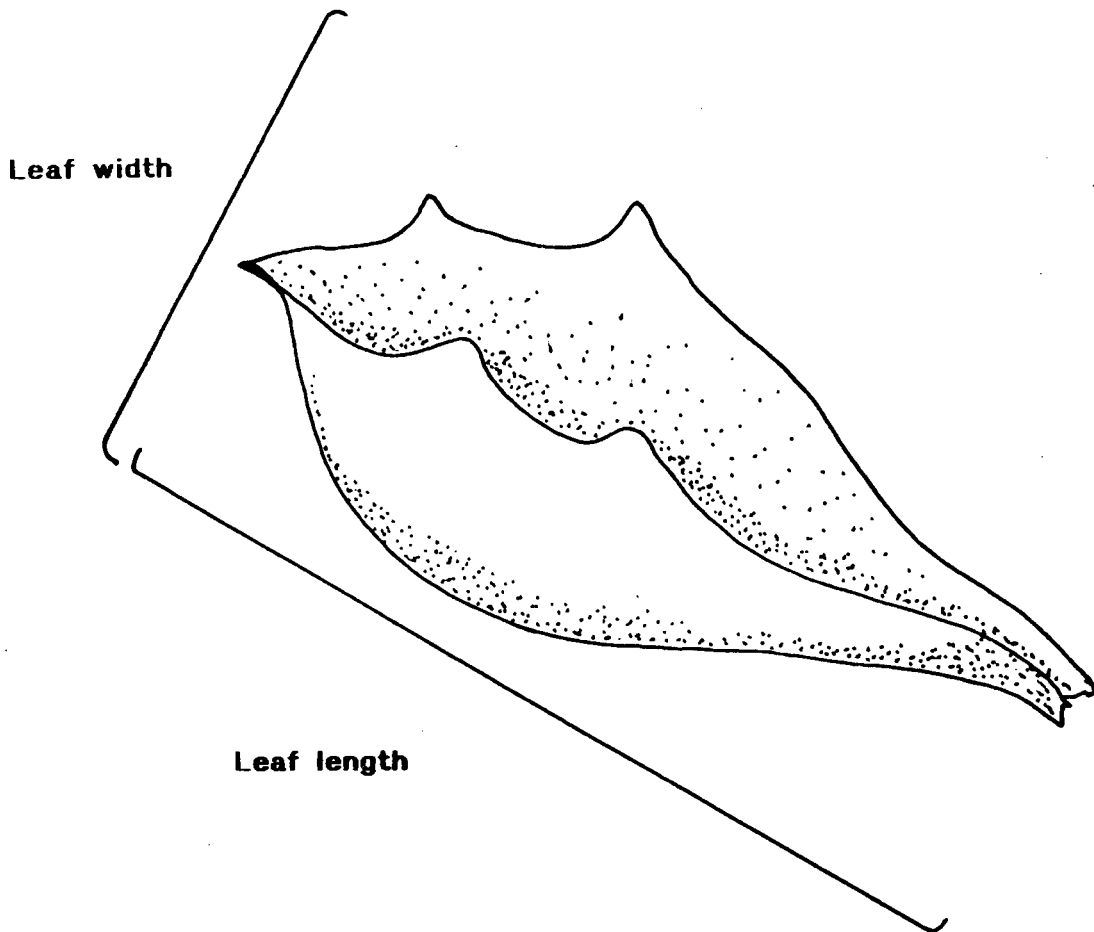


Figure 7: Diagram of the leaf showing where the various measurements were made. (Magnification of 8X)

'internode length' and averaged.

Capsule width: The length of the broadest section of the capsule was measured in millimeters (fig. 8).

Two measurements were made for flower width, one at the widest part of the calyx and another of the broadest section of flower (ie. at the widest expanse of the petaloid staminodes) (fig. 9).

Petaloid staminode width and length: Petaloid staminode dimensions are very crude as these structures are very small (often 0.1 x 1mm in magnitude) (fig. 9).

All frequency measurements (ie. internode length, leaf width and length, capsule width, flower and calyx diameter and petaloid staminode width and length) were made to one decimal point of a millimeter using a transparent plastic ruler. Three measurements were made for each reading. The smallest, largest and an average reading was taken. These measurements were averaged and the resulting value was entered in the data matrix which was used in the various methods of analysis.

Capsule width

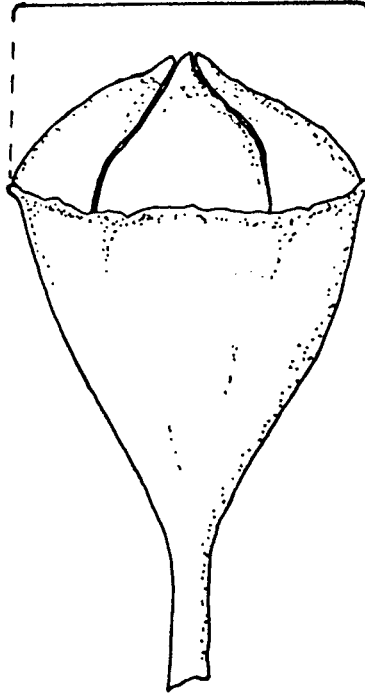


Figure 8: Diagram of a capsule. (Magnification of 7X)

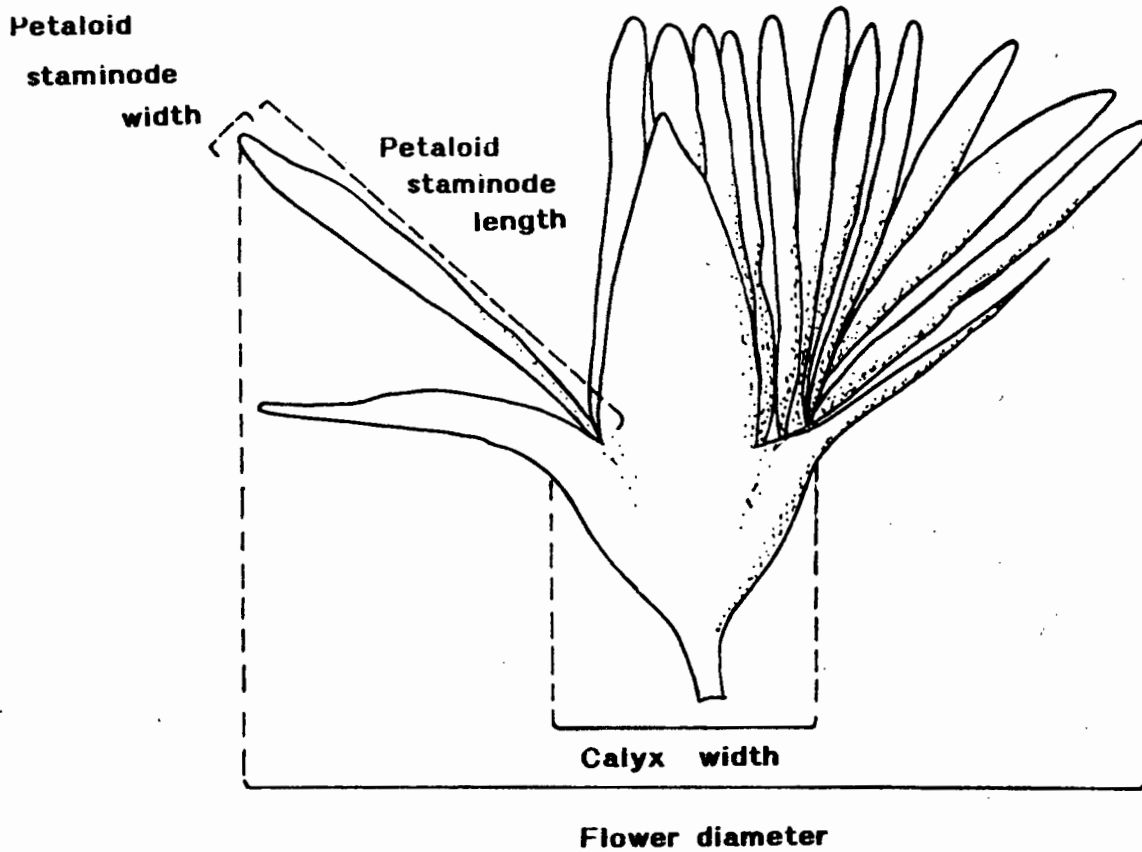


Figure 9: Diagram of a flower showing how calyx and flower diameter and the petaloid staminode dimensions were measured. (Magnification of 6X)

Methods of analysis

Univariate analysis

The range of size measurements was divided into a number of classes and the frequency of data points for each class interval was calculated. Frequency plots were made for each property. Also shown on these graphs is the effect of excluding the specimens which have entire leaf margins.

Size extraction algorithm

A method to extract overall size variation from a set of measurement characters that are related was proposed by Hall (1969). These characters may be homologically indistinct and it is essential to reduce the contribution of each of these properties to the overall similarity measure. For example, leaf width and length are related, but leaf length varies more than leaf width. The multivariate methods of analysis have a tendency to over-emphasise this variation. To eliminate this undesirable effect the size extraction algorithm is applied to the data.

If two or more properties are related (eg. leaf length and width) the set of measurements are standardised by dividing each data point by the largest measurement in the set. The values now range between zero and one. This is done for both properties. The total of the scaled values is then found for each item. The totals are averaged over all the items. This average is the

numerator of a factor for adjusting the scaled measurements. After applying these factors we get the adjusted size values.

It was necessary to do a size extraction analysis on various characters in this study. Leaf length and leaf width were treated in this manner and calyx width, flower diameter and petaloid staminode length and width were also altered.

Computerised methods of data analyses

A phenetic study is based on numerous precisely delimited characters. As many characters as possible are used. Pheneticists try to maintain a high level of objectivity and all procedures used in a taxonomic study are constructed with this in mind. Computerised methods are used to minimise bias. Numerical methods group taxonomic units into taxa on the basis of their character states (Sokal & Sneath, 1973). Comparison of the characters is made by an explicit method of grouping to obtain a measure of overall similarity. A dendrogram is constructed using the similarity measures.

Two clustering systems were used to analyse the data: NTSYS and UNITER. The different algorithms these methods use ^{are} ~~will~~ be given in table 2.

Table 2: Comparison of the algorithms coefficients used by the different computer clustering methods.

SYSTEM	STANDARD. DATA	SIMILARITY COEFF.	GROUPING	COPHENETIC ANALYSIS	STATSTICAL ANALYSIS
NTSYS	STAND	DIST	UPGMA	0.5	-
		CORR		0.7	-
UNITER	FACTOR REACTS	HOMOGENEITY	GROUPS	-	TRENDS HOMDIF

a) The data was processed using a computer program package called Numerical Taxonomy System (NTSYS) (Rohlf, 1988). This system uses clustering methods to analyse taxonomic data and arrives at one or more partitions within the set of Operational Taxonomic Units (OTUs) with each partition having different properties. The program clusters items on the basis of similarity.

For this study only a few of the available program modules were used. A description of the function of these programs will follow^s.

Before clustering methods can be applied to the data set, the data must be standardised to reduce the effects of different scales of measurement in the different characters. For example, the mean value for each character is subtracted from each variable (Rohlf, 1988). The program module STAND was used for this purpose.

The similarity coefficients for interval measure data are computed by the program module SIMINT. For this study the formula used was the default setting of the system called the average taxonomic distance (DIST). DIST is calculated using the following formula:

$$d_{ij} = \left[\frac{1}{n} \sum_k^n (x_{ki} - x_{kj})^2 \right]^{0.5}$$

SAHN (=Sequential, Agglomerative, Hierarchic, Non-overlapping clustering methods), is the program module by which the clustering of the OTUs is done. This analysis used the UPGMA (=unweighted pair-group arithmetic average cluster) clustering method. The input matrix is searched for the pair of objects that are most similar (or dissimilar). These two objects are merged into a cluster. The individual objects are removed from the data matrix and the new cluster is inserted into the matrix as a single object. This procedure is repeated until only one 'object' remains in the data matrix. Single-link and complete-link clustering methods were also tried but no better results

were obtained. The single-link method uses the 'nearest-neighbour' distance to cluster groups ie. the distance between two groups is determined by the distance between their closest members. The complete linkage cluster method is associated with the 'furthest-neighbour' distance ie. the distance between groups is found by the distance between the most remote pair of individuals from each group.

SAHN will always cluster data whether or not there are clusters present in the data set (Rohlf, 1988). For this reason the cophenetic test is essential to perform on the resulting tree.

The cophenetic values (COPH) program constructs a similarity matrix from the tree produced by the SAHN clustering program. The cophenetic value matrix is compared to the original similarity matrix. The product-moment correlation coefficient r , is calculated. This determines the agreement between the similarity values implied by the phenogram and those of the original similarity matrix (Sokal & Sneath, 1973). This measure r , usually varies between 0.6 and 0.95. The NTSYS user manual recommends that r should be greater than 0.7 to indicate a reasonably good fit. So the reliability of the dendrogram is measured by the cophenetic analysis.

SAHN was executed on the data matrix using the default setting for dissimilarity measure, DIST. This coefficient produced a tree that when analysed cophenetically gave a correlation coefficient (r) of 0.57 which is very low. The dendrogram is rejected on the basis of the great distortion when fitting the data matrix to the dendrogram. All other options of dissimilarity measures within NTSYS gave similarly poor results with r ranging from 0.55 to 0.59. An analysis was then performed using a correlation coefficient for which the cophenetic result was $r = 0.70$ which suggests a fair correlation. The correlation coefficient is based on the idea that 'size' corresponds to the distance of a point from the origin and that 'shape' is the angular difference between the vectors.

b) A system called UNITER was also used to analyse the data set. Once again there are various program modules within the system which is controlled by a main program called AIDORG (Hall, 1973). The EDITOR subroutine edits and inputs the data. FACTOR extracts common factors from the characters and REACTS gathers the data on values and weightings from the inter-item reaction tests. The program automatically deweights data according to the desired deweighting factor given by the user. UNITER operates by calculating the homogeneity of a group. This is a ratio relating the dispersion of the data in a group to that of a dummy set which is maximally heterogeneous. GROUPS then does a joint cladistic and phenetic grouping on the data. In this study the

what is the result of the analysis?

group size effect was minimised at a 70% level. This prevents small clusters from sinking into large groups. TRENDS gives a list of peculiarity indices between the reacting items and groups which is used to sequence the specimens for the dendrogram. A list of homogeneity values between the reacting specimens is given and a dendrogram is drawn from this list. HOMDIF has the ability of finding the internal homogeneity of a particular group and the importance of characters for characterising that groups. HOMDIF also gives the best characters for separating two groups.

All characters were used in the UNITER analysis except 'capsule width' as it was thought to be equivalent to the widest expanse of the calyx.

Both Sokal & Sneath (1963) and Stuessy (1990) strongly advocate against deweighting of characters. They maintain that equally weighted characters eliminate any *a priori* subjectivity. However Stuessy (1990) does state that objective methods of *a posteriori* weighting of characters can have great importance.

The NTSYS analysis of the data was done on an unweighted data. UNITER used a variously deweighted data set. The UNITER analysis using the deweighted data set gave a more instinctively satisfying result than the result using unweighted data.

All weighting of the data set for analysis by UNITER was done after the data were collected and the NTSYS cluster analysis was obtained. Deweighting was based mostly on the accuracy with which the characters were measured, the nature of the character states or according to the portion of missing data. The reasons for deweighting ^{are} ~~is~~ perfectly feasible although the deweighting factors were subjectively chosen (Table 3). It must be appreciated that the collector of the data does have a perception of the accuracy of the measurements and can therefore set acceptable deweighting factors.

Table 3: Characters and the factors to which they were deweighted.

Character No	Character	Deweighted to...%%
1	Internode length	20
2	Leaf length	60
3	Leaf width	60
4	Calyx width	50
5	Flower diameter	50
6	Petaloid staminode - width	10
7	- length	70
8	Teeth on keel of leaves	50
9	Dentate leaves	15

Rationale behind dewaterings - 'Number of teeth on keel edge of leaves' was dewatered to a factor of 50% due to measurement difficulties and the meristic nature of the data for example, the number of repetition of a part like teeth on keel edge of leaves. Where the number of repeated parts is small the value is only a crude estimate of the intensity of the part-making system which may have to reach a threshold before each extra part appears.

'Presence of teeth on leaves' was dewatered to a factor of 15% because of the inaccuracy of 2-state non-sequential data and its tendency to carry more importance than it should. Internode length varies so much within an individual and a population in response to the environment that its reliability as a measure of genetic difference is dubious. It was thus dewatered to 20% when the UNITER program was used. Due to the variable nature of the data, leaf length and width were both dewatered to 60%. UNITER was instructed to deweight 'calyx width' and 'flower diameter' to 50% to allow for the measurement difficulties encountered. The 'petaloid staminode width' was dewatered to a factor of 10% by UNITER to allow for sampling inaccuracy in measuring the extremely small structures. Petaloid staminode length was dewatered to 70% due to the shrivelling of the structures.

RESULTS AND DISCUSSION

Observations

Internode length varies from 4.7 to 30.7mm both within a population as well as within an individual according to the conditions within which the plant grows (pers. obs.). When growing in rock crevices the plant has very short internodes and relatively short, fat leaves. At greater soil depths internode length is greater and the leaves are longer. Internodes are usually long at the base of the specimen decreasing markedly at the tips of branches. It is also observed that internodes in the vegetative part of the plant are often long compared to the reproductive parts where the internodes become very short (fig. 10). Schwantes (1957) gives advice on cultivating *Oscularia* and he suggests that the plant should be 'starved' of water and kept in a small pot in an area which receives much sun to maintain the attractive, compact growth form. He mentions that a plant given ample water looks 'straggly' with long 'bolting' stems and long, bare internodes. If Schwantes could manipulate the appearance of the shrub in this way, then internode length is not a distinct taxonomic character.

Herre's (1971) publication implies that dentate leaf margins is the property that separates *Oscularia* from *Lampranthus*. However there are some specimens (18.6% of the herbarium specimens studied) that have been named as *Oscularia* which have no teeth on



Isularia
Kirstenbosch
1184
10 2.55



Figure 10: Photograph illustrating the variability of internode length.

the leaves at all (table 4). Glen (1978) has used this occurrence to support his argument that *Oscularia* is too closely related to *Lampranthus* to be distinguished as a separate genus. It is therefore important to know the extent of dentate leaf margins in Lampranthus. If this character is rare in *Lampranthus*, the implication is that the specimens above have been incorrectly identified and should be removed from *Oscularia* and placed within *Lampranthus*. If however, dentate leaf margins are common in *Lampranthus*, then *Oscularia* cannot be distinguished from *Lampranthus*. However, dentate leaf margins may legitimately occur in both genera in which case it cannot be used as a distinguishing character for *Oscularia*, but only as an indicator that a specimen may belong to *Oscularia*.

While perusing the section *Lunati* of *Lampranthus* (which is most closely related to *Oscularia* according to Glen (1978)), no teeth were seen on the leaves at all. Various species were seen that are very similar to *Oscularia* for example, *L. albus*, *L. copiosus*, *L. piquetbergensis*, *L. primivernus* and *L. thermarum*. The 'toothless' specimens could easily fit into some of the species mentioned. It would seem that *Oscularia* is distinct from the *Lampranthus* species in the section *Lunati* with respect to dentate leaf margins. The effect of removing the 'toothless' specimens from the group will be shown.

Table 4: List of specimens with entire leaf margins and the suggested *Lampranthus* species to which these specimens should be transferred.

Specimen Code	Location	Suggested Species
W	Kirstenbosch Gardens (N.B.G.)	<i>L. albus</i>
I	N.B.G.	<i>L. albus</i>
E	Sir Lowry's Pass	<i>L. albus</i>
JJ	(No information given)	<i>L. piquetbergensis</i>
WW	N.B.G.	<i>L. piquetbergensis</i>
AAA	Kriedouw, Clanwilliam	<i>L. thermarum</i>
Y	N.B.G.	<i>L. thermarum</i>
D	Rooiels	?undecided
R	Piquetberg	?undecided

Leaves are light grey, with powdery film. Leaf length varies between 5 and 46 mm and width ranges from 1.8 to 5.4 mm. The leaves are triangular, opposite and succulent ending with a point at the apex. The leaf margins are usually all dentate. The keel edge is sometimes entire. The margins and teeth are light red. The dried leaves are very shrivelled and did not reconstruct to the original dimensions upon boiling. Thus leaf length and width

measurements are not really a true reflection of leaf dimensions on a live specimen however, since the measurements were consistently made and because it is assumed that drying occurs to the same extent in all specimens, it is acceptable to use this character as it is in the analysis of the group.

The number of teeth on the keel edge of leaves was difficult to record as the specimens were often pressed so that the keel edge could not be seen or was indistinguishable from the other two edges.

Woody five-locular capsules range from 4 to 8.5 mm in diameter and are about 5mm deep. Capsule width is not a 'good' character as many specimens did not have capsules thus there is the problem of missing information.

The flowers are either solitary or in groups of three varying between 2.8 and 32 mm in diameter. A series of 30-40 petaloid staminodes is present. These petaloid staminodes are linear, short and free and are approximately 6mm long and 1mm wide. These structures are often shrivelled and folded and therefore the length and width measurements are equally inaccurate and not very reliable as are the flower diameter measurements. However, since flower diameter has been used previously to delimit taxa, it can hardly be ignored now.

The character of dentate keel leaf margins revealed surprising results. Most specimens had two teeth on the keel, very few (5%) had only 1 tooth, while a number (6.8%) had entire keels. At the time of the first descriptions two ^{species} (specimens) were recognised on the basis of entire or dentate keels of leaves. Some of the herbarium specimens seen had predominantly entire keels, yet dentate keels could still be detected on a few of the small, young leaves. This was the case for a number of specimens. The implication is that an entire leaf keel is not a sufficiently distinct character to separate the taxa into two species.

Scatter diagrams

Internode length (fig. 11a)

The scatter diagram for internode length shows a slight bimodal distribution. This indicates that in the sample studied, two marginally different types of specimens are encountered in terms of internode length. It is strongly suspected that this bimodality is due to the small sample size because the entire range of variation for internode length can be found in a single specimen.

The effect of removing the entire leafed specimens is shown by the shaded bars. The range of the scatter diagram has been reduced which is what one would expect if these specimens are indeed different to the typical dentate leafed specimens of

Oscularia. However, a reduction in the frequency of typical internode lengths is also experienced. This suggests that the toothless leafed specimens display the typical internode length found in *Oscularia*. The scatter diagram for internode length is unrevealing concerning the exclusion of toothless leafed specimens.

Leaf width (fig. 11b) and length (fig. 11c)

The scatter diagrams for both leaf width and leaf length approximate a unimodal distribution. When removing the entire leafed specimens there is a reduction in frequency at the lower extreme and at the peak of the leaf width distribution. As before this character is of no help in resolving the question of whether or not to include the entire leafed specimens in the taxa.

Capsule width (fig. 11d)

The scatter diagram for capsule width shows a distinctly unimodal distribution. Removing the entire leafed specimens from the data set the upper extreme of the frequency diagram is shortened quite markedly. As capsules are important generic markers, this result is critical. It indicates that the entire leafed specimens do not fit into *Oscularia* and should be removed.

Diameter of calyx (fig. 11e) and *flower diameter* (fig. 11f)

The scatter diagrams for these two characters display a unimodular dispersal. The greatest frequencies are dampened when the entire leafed specimens are excluded. This means that removal of these specimens is unsubstantiated by these characters.

Petaloid staminode width (fig. 11g) and *length* (fig. 11h)

The unimodular distributions of these characters are shortened and dampened by the removal of the entire leafed specimens. This does not give an indication of how to treat the set of 'problem' specimens.

These frequency diagrams for the various characters is evidence for the presence of a species complex. If the scatter diagrams showed a bimodal or trimodal distribution, it can be deduced that two or more distinct groups are present in the whole taxa. As this is not the case, the hypothesis that there are three species in *Oscularia* is opposed.

The overall impression is that removal of the toothless leafed specimens will lead to the removal of extreme frequency points in the scatter diagrams of the characters. This supports the argument for removal of these specimens from *Oscularia*. However, the greatest frequencies are reduced too. This implies that these unusual specimens fit the typical character states for

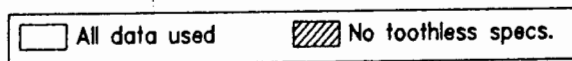
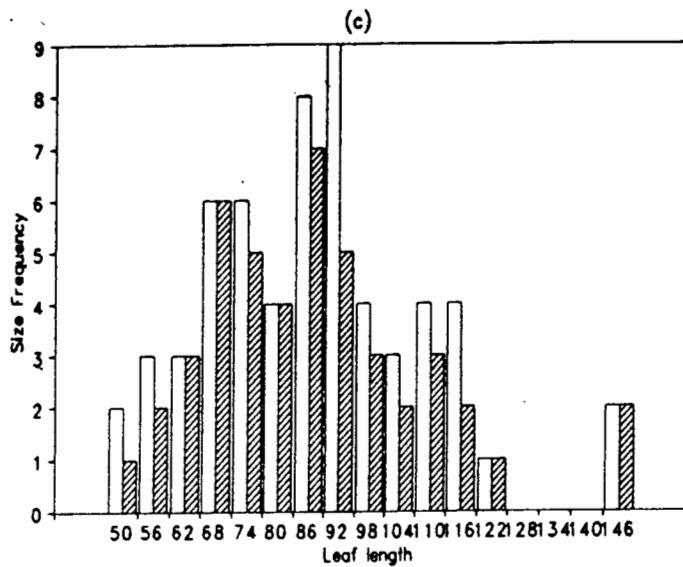
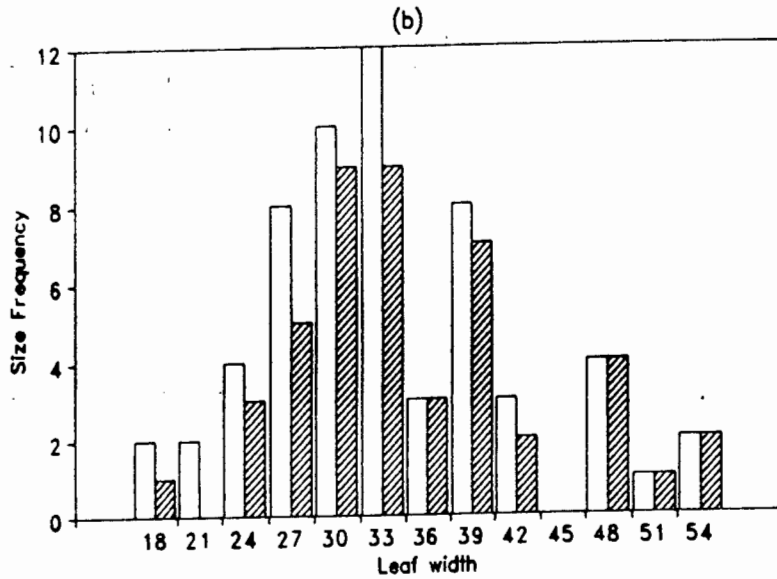
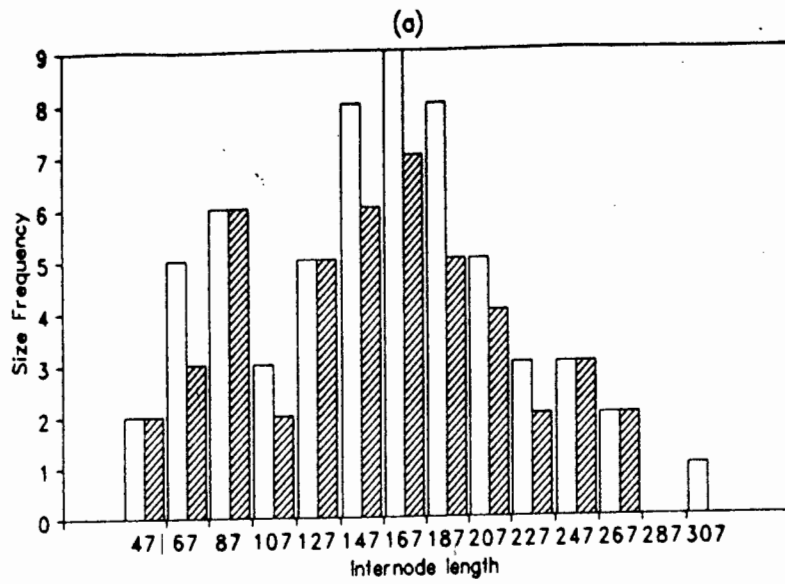
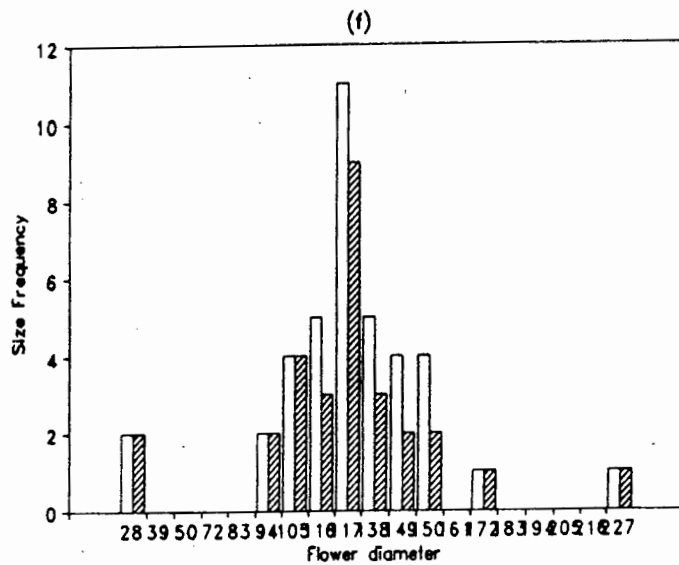
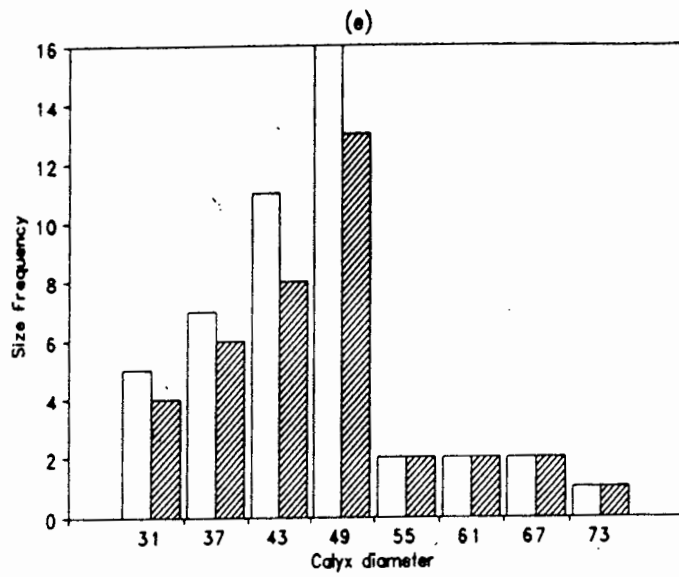
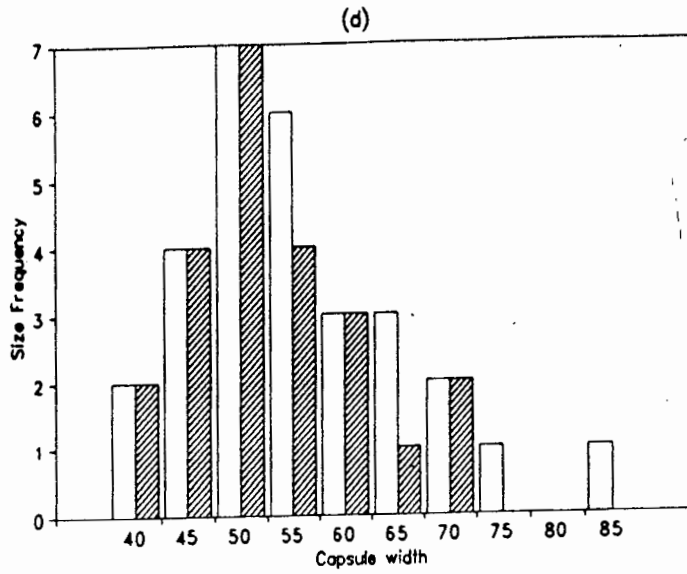
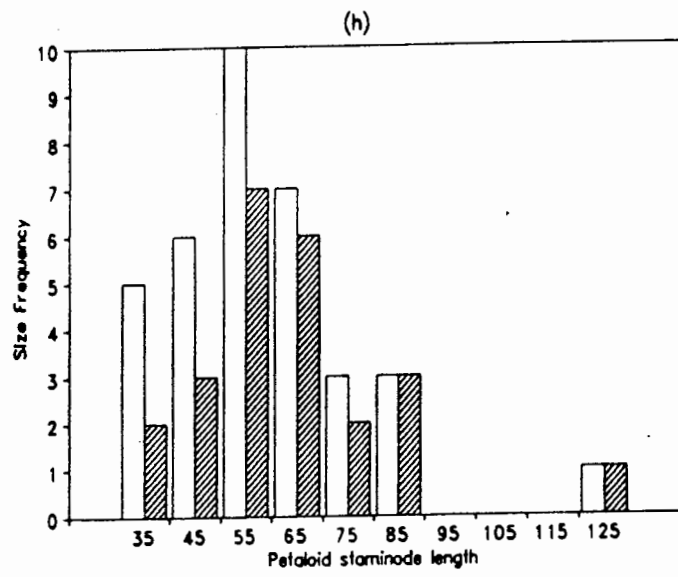
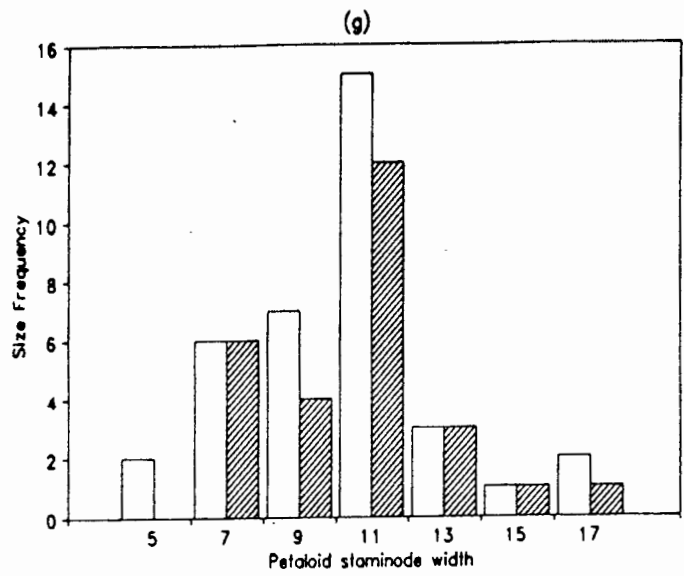


Figure 11 (a) - (h): Scatter diagrams of the characters measured. (a) Internode, (b) Leaf width, (c) Leaf length, (d) Capsule width (e) Calyx diameter (f) Flower diameter, (g) Petaloid staminoid width (h) Petaloid staminode length.



All data used
 No toothless specs.



All data used
 No toothless specs.

Oscularia in these instances. However, any particular entire leafed specimen may fit the typical *Oscularia* description for some characters but not for others. What this combination is in each case has not been investigated. It is reasonable to assume that for every specimen there is some evidence supporting its removal.

NTSYS analysis

The cophenetic tests gave very low values for r when DIST was used which implies that there are no clear taxonomic distinctions within the data set. This means that *Oscularia* consists of a species complex rather than three species.

poor phrasing

When NTSYS used the correlation coefficient to determine the cluster diagram, the cophenetic analysis produced a value of 0.7 for r . This suggests that this measure gives a more reliable indication of the grouping structure within the taxa. The cluster diagram produced superficially shows a grouping of three main clusters (fig. 12). Typical polythetic groups were obtained. When matching the herbarium specimens to the clustering shown in the dendrogram the groups do not make much sense. Within a group specimens are at times very different or resembles a specimen in another group more closely than the one within which it is placed. The clusters seemed to be loosely related to internode length yet this is neither consistent

```

----- SANN ----- 8/13/98 14:57 -----
input aatrix:sher.cor
'Sheraines Ocularia data, for reanalysis'
* STAND: input=sher.prn, divide=STD, sub=YBAM, direction=C
* SIMINT: input=sher.std, coeff=CORR, direction=R
type= 3, size= 59 by 59

```

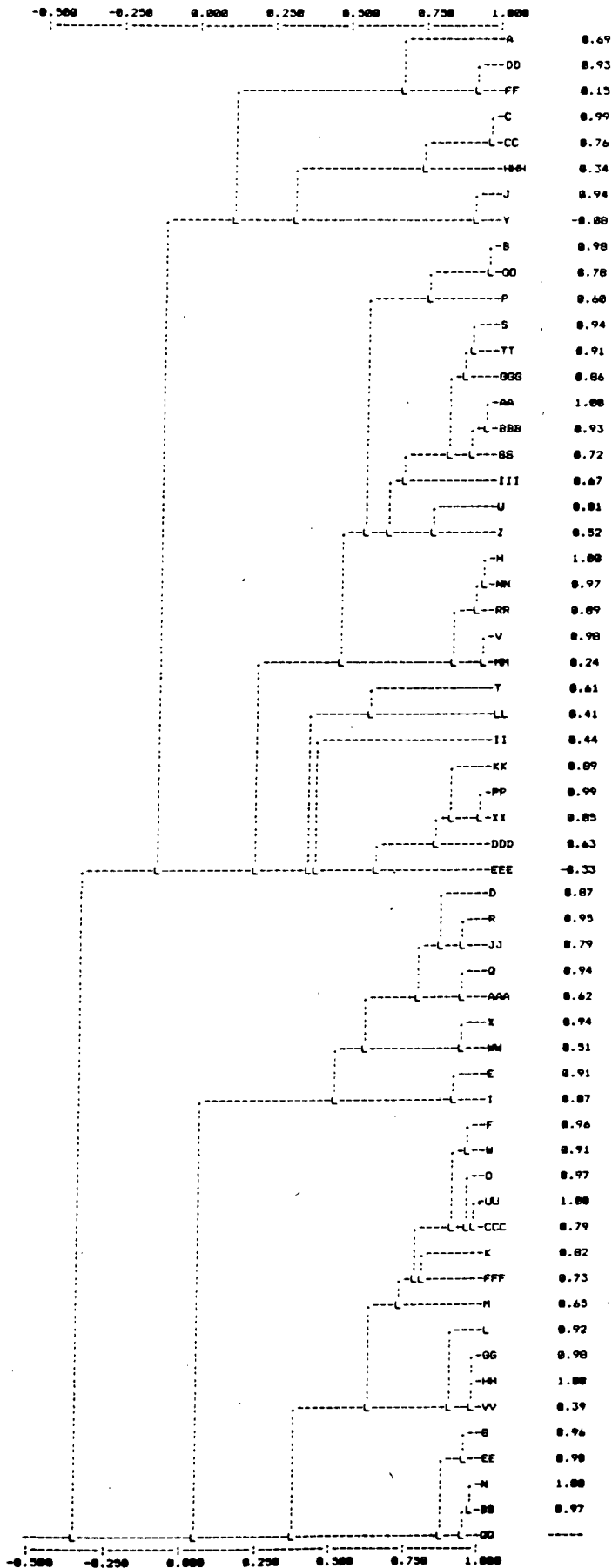


Figure 12: Dendrogram obtained from the NTSYS analysis using the correlation coefficient.

throughout the dendrogram nor, within a cluster. Interestingly all the entire leafed specimens with the exception of one, are grouped together.

Analysis of UNITER results

The analysis resulted primarily in a cluster diagram (fig. 13) and secondarily in some clustering statistics (table 5). (Groups have been numbered to facilitate the discussion of the dendrogram (fig. 13)). The clustering diagram produced by UNITER differs from that of the correlation analysis of NTSYS. As can be seen on the dendrogram there is a core group consisting of groups 3 to 7 (fig. 13). This group is made up of what is perceived as typical *Oscularia* specimens. According to UNITER the most important distinguishing characters for this core group are 'teeth on keel edge' and 'dentate leaf margins' (ie. characters 9 and 10 in table 5). All specimens in this group clearly display both these characters.

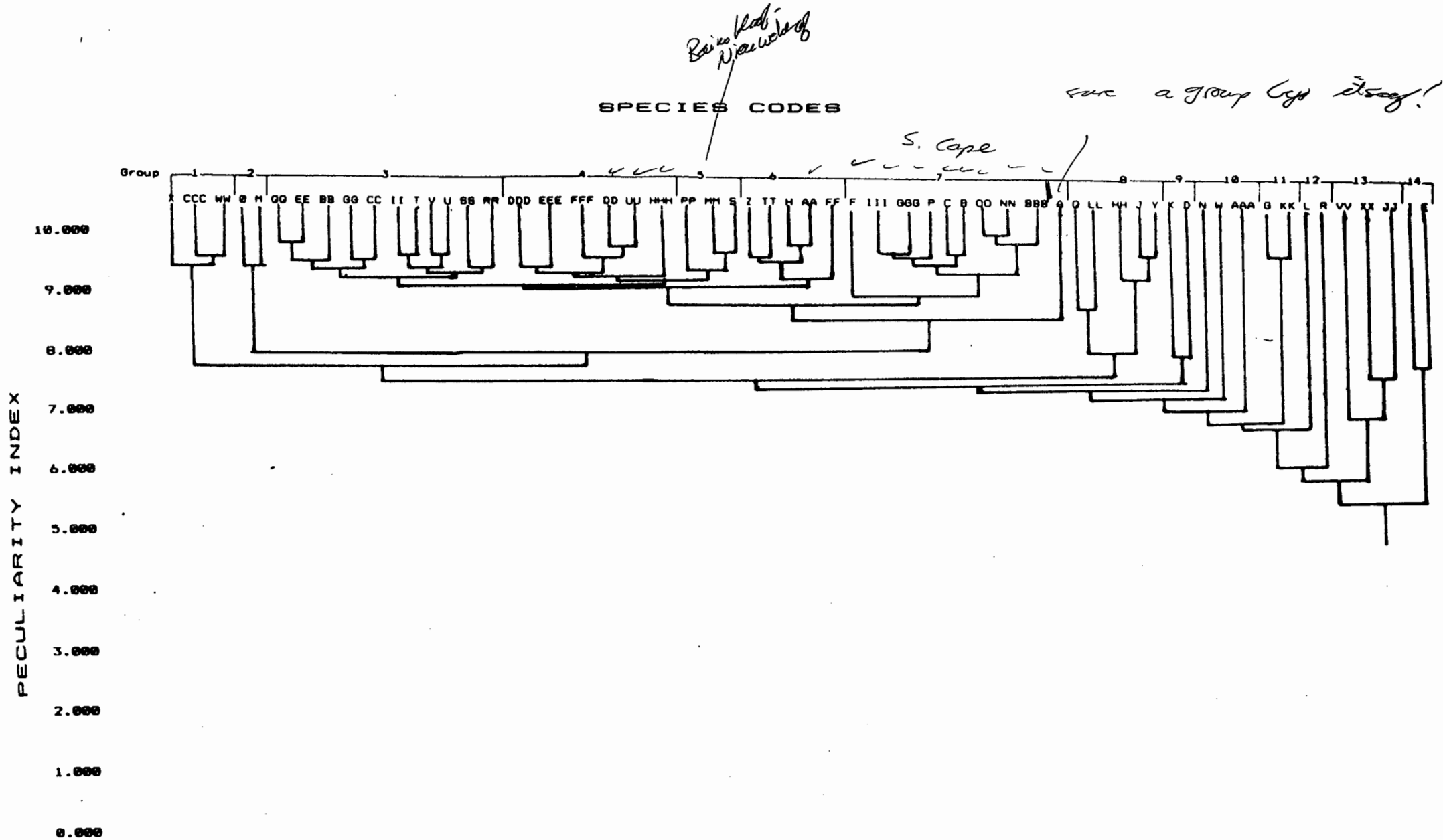


Figure 13: Dendrogram resulting from the UNITER analysis.

Table 5: List of groups identified by UNITER with a measure of the internal cohesion of the group and the most homogeneous characters of the group.

Group	Internal Homogeneity (ratio of 1)	Most homogeneous characters of group.* (%)								
		Char.1	2	3	4	5	6	7	8	9
1	0.933	93	96	96	0	85	94	94	0	0
2	0.937	98	92	88	0	98	94	95	0	0
3	0.890	68	90	86	87	81	80	94	100	100
4	0.896	64	97	75	91	89	92	93	100	100
5	0.927	64	95	96	0	95	88	88	100	100
6	0.901	74	85	89	86	79	94	100	100	100
7	0.862	79	83	88	85	82	78	82	100	100
8	0.705	62	83	77	87	77	68	87	57	13
9	0.793	98	91	100	89	97	100	98	100	0
10	0.636	29	66	93	0	98	100	75	100	0
11	0.920	93	86	90	0	0	0	0	100	100
12	0.556	100	91	66	0	0	0	0	100	0
13	0.676	84	83	83	93	0	0	0	100	0
14	0.770	94	93	97	0	93	94	99	100	0

* The importance of the character in the grouping procedure is given as a percentage.

UNITER places the most peculiar specimens to the right of the main cluster. From group 8 to 14, the grouping of specimens is unstructured and hazy. For example, the two smaller groups (ie. 1 & 2) to the left of the large central cluster with homogeneity of 0.75 when fused. The group is distinguished most by characters 4 and 8 that is, 'calyx width' and 'teeth on keel edge'. This information is conspicuous because it is missing for both these groups.

Group 8 is characterised by petaloid staminode length and calyx width. Groups 9, 10 and 11 are distinguished mostly by petaloid staminode width and flower diameter. The most important characters for groups 12, 13 and 14 are internode length and calyx width and petaloid staminode length respectively. 'Teeth on keel edge of leaves' was instrumental both in the formation of these groups as well as for the others.

There was no geographical correlation found for the placement of specimens in the groups. For example, specimens in group 7 were collected from Caledon, the Langeberg Mountains, Villiersdorp, Tradouw Pass, Bredasdorp and Lemoenshoek.

Interestingly all the specimens with no teeth on the leaves are placed in the 'hazy' area of the dendrogram on the right of the main cluster. This emphasises the peculiarity of these

specimens.

The grouping pattern produced by UNITER resolves the question of whether *Oscularia* is one species or three. It is clear that the group is a species complex with a reasonably large amount of variation within the group. It also shows that the 'toothless' leafed specimens are peculiar (to) the rest of the group and this supports the removal of these specimens.

Treatment of specimens collected at the same location.

There are three cases where more than one specimen has been collected at the same location. There is variation between these specimens but the placement of specimens by the clustering programs is revealing. In some cases specimens collected from the same population have been grouped into widely different groups other times the specimens occur in the same group.

Table 6: The grouping of single locality specimens by the different methods of analysis.

SPECIMENS	PLACEMENT BY:	
	NTSYS	UNITER
Riviersonderend:		
BB	3*	3
CC	1	3
Potteberg:		
DDD	2	4
EEE	2	4
FFF	3	4
Piquetberg:		
GG	3	3
HH	3	8
II	2	3

*Group number in dendrogram

UNITER groups 87.5% of these specimens together while NTSYS only keeps 42.9% together. This constitutes a biological test rather than a numerical (eg. cophenetic analysis) test of the method of analysis used. UNITER is the ~~approach~~ approach which is favoured.

The separation of these specimens is justified however, in the case where the specimens are clearly dissimilar (for example, GG, HH, II). This demonstrates the range of variation that is seen within this population and substantiates the existence of a species complex as the entire variation within the taxa is found within one population. — *but does anyone would agree that* ✓

CONCLUSION

It is generally known that absolute size should be avoided as a taxonomic indicator. For example, leaf length was used previously to distinguish the different species in *Oscularia* from each other. Great variation was found in leaf length for all specimens which makes it absurd to use this character to distinguish different taxa within the group.

Leaf length and flower diameter are the characters that were previously used to delimit the three species thought to be present in the taxa. There is no definite interval in the frequencies of these measurements. Thus the univariate analysis reflects a continuum in the characters which refutes the old taxonomic treatment of *Oscularia* and supports the proposal for a species complex rather than three distinct species.

The results obtained from the computer clustering programs demonstrate that the whole taxonomic group shows a large amount

of variability. This implies that *Oscularia* consists of a species complex.

Dentate leaves are rare in Lampranthus and a distinguishing character in Oscularia. The group of specimens in Oscularia that have no teeth on their leaves should be transferred to the appropriate Lampranthus species.

A study of *Lampranthus* was not done, yet after a perusal of the herbarium specimens of the section *Lunati*, it is felt that *Oscularia* is too similar in general appearance to a number of the *Lampranthus* species to be considered as a separate genus. It seems that dentate leaf margins is the only character that separates *Oscularia* from *Lampranthus* which is an insufficient basis for giving *Oscularia* generic status. It is therefore suggested that *Oscularia* be included in the genus *Lampranthus*.

ACKNOWLEDGEMENTS

Many thanks to Prof. A.V. Hall for help with the analysis of the data through the UNITER system. To my supervisor Dr. H.P.Linder for much help, advice and encouragement, thank you.

TAXONOMY

Genus: *Oscularia* should be included in *Lampranthus*. Glen proposed that the nomenclature be *L. deltoides* (L.) Glen which is supported. Refer to Glen (1978) for the generic nomenclature.

Species nomenclature: refer to Glen (1978).

Species description:

Small, succulent shrub, spreading growth form. Branches erect or spreading, a reddish-brown colour. Internodes ca. 166mm long, 2-3mm wide. Leaves light grey, with powdery film. Leaves bent inwards, narrowing towards base. Leaves triangular, opposite and succulent, expanded at apex, ending with a point. Margins usually all dentate. Keel edge sometimes entire. Leaf margins and teeth light red. Inflorescences cymose. Pedicels 1-1.8mm long, ca. 1mm wide. Flowers white to pink coloured, distinctly almond scented, solitary or 3-nate, diameter ca. 120mm. Bracts up to 10mm long, 3mm wide. Five free sepals present, ca. 7mm long up to 4mm wide, inner three with membranous margins. One series of 30-40 petaloid staminodes, ca. 6mm long, 1mm wide, linear, short and free. Stamens arranged in a column or conically collected, 10-80 filaments, filaments ca. 1-1.5mm long. Dark-green glands with five distant parts. Placentas parietal, five stigmas, 1-5mm long. Woody capsule, five-locular as a rule, rarely occurs with four, six or seven locules, ca. 6mm in

diameter, 5mm deep. Keels expand diverging from base. Keels more than half as long as the valves. Valve-wings ca. 2.5mm long, 1mm wide, separate from valve for most of length. Loculi-roofs present but no tubercle or covering membranes found. Seeds are black. Chromosome number is 18 (ie. 2n) (Propach 1934, Suguira 1938 & 1940b, in Glen 1978).

LIST OF SPECIMENS EXAMINED

The codes used for the specimens in the dendrograms are given in parentheses after the citing.

- 3420 BC Bredasdorp, Potberg, middle of south facing slope, *Pillans 9322* (BOL). (A)
- 3319 AC Villiersdorp, Caledon Division, *De Villiers 54/30* (BOL). (LL)
- 3319 AC Hottentot Rock, Piquetberg Road Station, on Frances Valk's Nieuwekloof, *MacOwen 1874(I-III)* (BOL). (GG,HH,II)
- 3418 BB Sir Lowry's Pass, *Guthrie 17173* (BOL). (J)
- 3419 BD Steenbras, Caledon Division, *Bartlett 1965/22 (I-IV)* (BOL). (K,L,M,N)
- 3419 BD Rooiels, Stellenbosch Division, False Bay, between Gordon's Bay and Hangklip, *Esterhuysen* (BOL). (D)
- 3218 BD Kriedouw, Clanwilliam, rock crevices on Table Mountain Sandstone (TMS) koppie, *Levins 1319* (BOL). (AAA)
- 3319 CA Bainskloof, 20m east of the 'Worcester Division' sign, 5m south of the road on a TMS rocky spur, shallow high humus soil, *Glen 943* (BOL). (G,H)
- 3319 CC Wemmershoek, *Smuts 3117* (BOL). (KK)
- 3418 BB Sir Lowry's Pass, Stellenbosch Division *1892* (BOL). (E)
- 3319 DA Blaauwkop, near Keeromsberg, along ledges on south aspect, 4000ft, *Esterhuysen 19667* (BOL). (CCC)
- 3319 AC Tulbagh, 800ft *5054* (BOL). (QQ)
- 3319 CB Audensberg Peak, Hex River Valley, Worcester Division,

Wilman (BOL). (EE)

-3319 CC Zachariashoek (Platberg), 11km NW of Franschoek, Stellenbosch Division, locally common in rocky outcrops, pink flowers, low shrub 1dm tall or cascading over rocks to 1 meter, 1700m, *Koutnik 1015* (BOL). (BB,CC)

-3319 CD Stettynsberg, lower slopes, on rocks forming compact mass *Esterhuysen 11041* (BOL). (SS)

-3419 AA Houw Hoek, 3000ft 9872 (BOL). (RR)

-3420 BC Potteberg, on cliffs and rocks, 500-1000ft, *Esterhuysen 23156(I-III)* (BOL). (DDD,EEE,FFF)

-3419 BB Riviersonderend, Robertson Division, *Neetling 605/31(I-II)* (BOL). (DD)

-3419 DA Amongst rocks on Elim mountains, *Bolus 28035* (BOL). (HHH)

X -3421 AB Riversdale, *Bolus 28037* (BOL). (UU)

-3419 BA Die Galg, Riviersonderend Mountains, (-BA) north slope, above post office road to summit in TMS rock crevices and sheets, tufted spreading cushion with low bare woody stems, 4000ft, *Bean 762* (BOL). (AA)

-3419 AB Caledon, 1300ft, *Bolus 28036* (BOL). (TT)

S -3319 CA Bains Kloof, Worcester Division, *Moll 3319* (BOL). (MM)

L -3319 AC Nieuwekloof, Saxosis, 700ft, *Schlechter 9045* (BOL). (PP)

-3319 AC North of Ontangskop, Tulbagh, rocky outcrops, *Cameron & Manchip 64* (BOL). (Z)

-3319 CB Audensberg Ridge, Worcester Division, in shelter of

- rocks on hot dry north slope, 5000ft, *Esterhuysen 16665* (BOL).
(FF)
- 3320 DD Langebergen, Lemoenshoek, *Esterhuysen* (BOL). (F)
- 3419 DB Bredasdorp mountain, amongst rocks surrounding beacon on summit of mountain, eastern shoulder of Beacon Peak, *Galpin* (BOL). (C)
- 3420 CA Bredasdorp Division, Fairfield Farm, *Oliver 3419* (BOL).
(B)
- 3320 DC Tradouw Pass, roadside, 1300ft, *Levins 695* (BOL). (BBB)
- 3320 DD Summit of Langeberg (BOL). (GGG)
- 3419 AB Caledon, Swartberg, on rocks along ridge, 2500-3000ft, *Esterhuysen 18959* (BOL). (III)
- 3319 CD Villiersdorp, flowers in August, *Bolus 417/33* (BOL).
(OO)
- 3319 CD Between Villiersdorp and Caledon growing in a thickly matted or congested 'dome' at the top of Ezelgacht, *Salter 28038* (BOL). (NN)

Garden specimens:

- garden of Mrs. Van Zyl (BOL). (Q)
- 3318 CD Kirstenbosch. (JJ)
- 3318 CD Kirstenbosch mesembryanthemum bank, *Fenton* (BOL). (W)
- 3318 CD Kirstenbosch 13(I-III) (BOL). (VV, WW, XX)
- 3318 CD on Mesembryanthemum bank, Kirstenbosch (BOL). (I)
- 3418 AB Mr. Eastman's garden at Muizenberg, *Eastman* (BOL). (X)

- 3318 CD University Gardens, *Herre 11829* (BOL). (O)
- 3318 CD Kirstenbosch, *Lewis 2526/16(I-IV)* (BOL). (S,T,U,V)
- Sauer (BOL). (P)
- 3218 DC Piquetberg, *Immelman* (BOL). (R)

REFERENCES

- ✓ DILLENIIUS J.J., 1732. *Hortus Elthamensis*. Londini, sumptibus auctoris.
- ✓ GIBBS RUSSELL G.E. & GLEN 1984. Register of names and types: a comparison between Mesembryanthemaceae and Poaceae. *Bothalia* 15:125-129.
- GLEN H.F., 1986. MESEMBRYANTHEMACEAE. A new combination in Lampranthus. *Bothalia* 16(1):55.
- ✓ GLEN H.F., 1978. A taxonomic monograph of Lampranthus and allied genera (Mesembryanthemaceae). A dissertation towards a doctoral degree. University of Cape Town. ^aCape Town.
- ✓ HALL A.V., 1969. Automatic grouping programs: the treatment of certain kinds of properties. *Biol. J. Linn. Soc.* 1:321-325.
- ✓ HALL A.V., 1973. The use of a computer-based system of aids for classification. *Contrib. Bol. Herb. No. 6*. Bolus Herbarium, University of Cape Town. Cape Town.
- HERRE H., 1971. *The Genera of the Mesembryanthemaceae*. Tafelberg-Uitgewers Beperk, Cape Town.
- JACOBSEN H., 1970. *Das sukkelenten lexikon*. Gustav Fisher Verlag, Jena.
- JACOBSEN H., 1954. *A handbook of succulent plants*. Vol 3:1337-1339. Blandford Press, London.

- JACOBSEN H., 1938. *Verzeichnis der Arten Gattung, Mesembryanthemum L.. Deutschen Kakteen Gesellschaft. Dahlem, Berlin.*
- ✓ JACOBSEN H., 1935. *Succulent Plants. Williams and Norgate, London.*
- ✓ ROHLF F.J., 1988. NTSYS-pc. *Numerical Taxonomy and Multivariate Analysis system. Ver. 1.4. User manual for the systems for the IBM PC microcomputer. Exeter Publishing, Ltd. New York.*
- ✓ SCHWANTES G., 1957. *Flowering stones and midday flowers. Ernest Benn, London.*
- ✓ SNEATH P.H. & SOKAL R.R. 1973. *Numerical taxonomy. W.H. Freeman & Co. San Francisco, California.*
- ✓ SOKAL R.R. & SNEATH P.H. 1963. *Principles of numerical taxonomy. W.H. Freeman & Co. San Francisco, California.*
- ✓ STUESSY T. 1990. *Plant taxonomy. Columbia University Press. Columbia.*