The Eocene megafossil flora of Nerriga, New South Wales.

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DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma and, to the best of my knowledge, contains no material previously published or written by any other person except where due reference is made.

Robert S. Hill.

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ABSTRACT.

Numerical taxonomy has had little application in angiosperm palaeobotany. The major reason for this is that angiosperms are usually preserved as individual organs (leaves) which are often fragmentary, and it has therefore been difficult to assemble a large number of characters with proven discriminatory power. Thirty four continuous numeric characters were compiled and their discriminatory power was tested on a set of 100 extant leaves representing 20 species.

The 100 leaves clustered into their species when 31 characters were used; when 17 characters were used (14 most highly correlated characters removed); and when approximately 49% of character scores were removed to simulate missing data. The leaves could not be clustered into their species using only the 14 architectural characters. An interesting feature was that while the characters employed were good at discriminating species, they did not give a true picture of the taxonomic relationships between the species.

Several hundred specimens were curated from Nerriga and 112 were chosen for the initial numerical analyses. These 112 operational taxonomic units (OTUs) were chosen solely on the basis of their state of preservation, although several other factors were considered. Twenty three of the 34 characters available could be scored on all the OTUs and were chosen for the initial analyses. Two extra characters were devloped to bring the number scored to 25.

The fossil OTUs were clustered with several different methods, the most useful being a minimum spanning tree used in conjunction with a nearest neighbour network and error sum of squares dendrogram. Twenty seven different leaf forms (= parataxa) were delimited from the 112 OTUs. Of the

remaining 469 specimens, 445 were assigned to these parataxa. The other 24 specimens could not be assigned to parataxa and were considered to constitute a further 17 parataxa, giving a total of 44. A study of the interrelationships between these parataxa suggested that some represented extreme forms of others, and the true number of parataxa is somewhere in the range of 26 to 34, with some requiring further collections and study to account for their variation.

Four taxa from Nerriga have been identified. The cycads Bowenia papillosa, Pterostoma anastomosans and Lepidozamia foveolata were described as part of this study and the angiosperm Casuarina sp. was identified from vegetative and reproductive structures. A fern frond with possible affinities to the family Gleicheniaceae is discussed.

Based on foliar physiognomy, and the presence or absence of certain types of epiphyllous fungi, the Nerriga flora is believed to represent wet sclerophyll or lowland/lower montane subtropical rainforest vegetation, with rainfall in the range 140 - 180 cm/year. A discussion of the methods of estimating vegetation type and palaeoclimate is presented. The possibility of differential preservation at Nerriga is discussed and possible avenues for future Tertiary angiosperm research in Australia are suggested.

CHAPTER 1

INTRODUCTION.

1.1 HISTORY OF AUSTRALIAN TERTIARY MEGAFOSSIL PALAEOBOTANY:

Interest in the study of Tertiary megafossil floras in Australia was intense prior to the beginning of the twentieth century. The earliest work was that of Johnston (1879,1885a, b,1886a,b,1889,1891,1893), von Mueller (1874,1883) and von Ettingshausen (1883,1886,1888). Their research was valuable both from the historical viewpoint and because of their thoroughness in unearthing new deposits, but it is of little use today. Unfortunately their illustrations were often inadequate and their specimens are generally unavailable or have deteriorated badly. The biggest problem with their work, and that of later researchers of the period (e.g. Deane, 1902a,b,1903,1904,1907,1925) was that generally they insisted on giving the fossils they described names implying extant affinities. This process was a standard procedure at the time and the problems it created have been commented on frequently (e.g. Dilcher, 1971,1974; Dilcher and Mehrotra 1969; Christophel and Blackburn 1978). Duigan (1951) prepared a catalogue of the Australian Tertiary flora, and the large number of extant, and often non-Australasian genera present give an indication of the high priority given to the naming of fossils by early researchers.

After this initial interest, little work was done on Tertiary deposits until the time of Cookson (1947), Cookson and Duigan (1950,1951) and Cookson and Pike (1953a,b,1954). Again the interest was mainly in identification, although their taxonomy was usually more reliable than that mentioned above. However, because of this interest, none of their work was aimed at describing floras, and generally they picked

isolated specimens (usually gymnosperms) which were easily identified.

Therefore, since the turn of the century, no Tertiary floras have been described in Australia, although work is currently underway at the Botany Dept., University of Adelaide, on the Eocene floras of Maslin Bay and Anglesea (D.C. Christophel, pers. comm.) and the Miocene flora of the Yallourn Brown Coal (D.T. Blackburn pers. comm.). In order to gain a true representation of the vegetation of the Australian Tertiary, it is vital to study floras rather than isolated, easily identified specimens. One of the aims of this study is to make a contribution toward the study of the evolution of the Australian flora and vegetation types by describing a complete Tertiary flora.

1.2 AIM OF THE STUDY: There are two major benefits in the study of a Tertiary flora. Firstly, the results can be assessed as a self-contained unit, in which case it is possible to interpret palaeoclimate, describe the parataxa, and, where possible, draw taxonomic conclusions. These are the immediate benefits. Secondly, if the flora has been described in an easily interpretable way, and data collected from it is freely available, then in the long term it may be useful in an evolutionary sense for comparison with other floras, both extant and fossil.

The comparison of fossil floras or even individual taxa within them is an extremely complex problem. The palaeo-botanist is confronted with all the problems facing taxonomists of extant plants. In addition there are problems in having to work with material which is often fragmentary, or at best only represents individual organs. The added variable of time differences between deposits (and thus the

associated evolutionary changes) must also be considered.

The classical taxonomic approach is most often used in palaeobotany, and only recently (Dolph, 1975) has the use of numerical taxonomy been advocated. However with the problems already outlined for comparison between floras, and the vast amount of data now available on both fossil and extant floras (Dolph 1978a), the use of computers in the comparison of fossil material is inevitable. There are advantages and disadvantages in the use of numerical taxonomy in fossil angiosperm taxonomy. The obvious advantage is that many more comparisons can be made quickly between specimens and the approach is more objective and therefore more repeatable. The disadvantages are:

(1) Because angiosperms are usually preserved as individual organs (leaves) the number of characters which can be scored is small;

(2) Many of the leaves which are found in a fossil deposit are incomplete, thus making missing data a major problem;

(3) No character set has been shown to be applicable to the particular requirements of fossil leaves. On the contrary, Dolph (1976a) has shown that the most commonly used descriptive terminology for leaf architecture (that of Hickey (1973)) cannot be adapted to numerical taxonomy.

These problems are not as severe as may be expected. Blackburn (1978a) has shown that 10 continuous numerical leaf characters could efficiently delimit species when applied to a single genus (Saurauia, Actinidiaceae). Therefore it is reasonable to assume that a sufficient number of characters could be defined for use on fossil leaves, particularly since Blackburn's characters were

designed with palaeobotanical application in mind. The problem of missing data is complex and will be considered at length later. Dolph's (1976a) conclusions are not as damaging to the numerical taxonomic approach as they appear. Any classification can only be as good as the character set it is based on. In the case of Dolph's study, he has done a disservice to Hickey's descriptive terminology by even trying to apply it to a numerical taxonomic study. Hickey's terminology does not consist of equally ranked characters. Therefore it is not valid to calculate a distance measure from this data which invalidates the numerical taxonomic approach attempted by Dolph (1976a).

Thus at the present time it has been shown that a set of continuous numerical characters can be successfully applied to a single genus, but a set has never been applied to a heterogenous collection of leaves. This was done as part of this study, since it was apparent that the use of numerical taxonomy on fossil floras could not be undertaken until it had been shown that the method could be successfully applied to extant leaves.

Australia is an ideal testing ground for the application of statistical methods to angiosperm palaeobotany, simply because of the lack of any recent descriptions of floras and because all the work currently being carried out is in one laboratory, making coordination of the program simple.

Because such a project has not been attempted before, it was difficult to plan the steps involved precisely. However, a brief summary of the plan of the study can be given, which outlines the logic of the approach.

(1) Collate character set for use in numerical taxonomy of angiosperm leaves.

(2) Define other characters which may be of use, or modify existing characters for general use.

(3) Collect and score extant leaves to test the character set.

(4) Perform numerical analyses on data from extant leaves and compare the classification produced with the identity of the OTUs (leaves).

*(5) If step (4) is successful, collect and curate specimens from the fossil flora.

(6) Select a subset of fossils for numerical analysis.

(7) If necessary, redefine the character set for application on the fossil leaves (OTUs).

(8) Score OTUs.

(9) Perform numerical analyses and define parataxa from the classifications produced.

(10) Assign remaining fossils to the parataxa defined in (9). If some fossils are found which do not fit into any of the defined parataxa, they must be scored and step (9) repeated.

(11) Describe parataxa.

(12) Study interrelationships between parataxa.

(13) If possible, draw taxonomic conclusions.

(14) Make palaeoclimatic interpretations.

(15) Compare the flora to other Tertiary floras.

* If step (4) is unsuccessful, the character set must be re-examined and if necessary redefined, or a new approach must be attempted.

Initially, this study was intended to be parataxonomic i.e. based purely on morphological similarities, with no attempt to identify the parataxa defined. This is the only approach available in Australia at present, since the

architecture of extant leaves of the Australasian region is poorly understood and will remain so for many years.

The character set used in this study was compiled using the type of preservation found in North American fossil deposits as a guideline for the characters which would be applicable. By the end of the study, a clearer picture had emerged of the type of preservation most commonly found in Australian deposits and some conclusions are drawn on the choice of characters which may be of use for future workers in this field.

CHAPTER 2

SELECTION OF A FOSSIL DEPOSIT.

2.1 LOCATION: The fossil deposit chosen for the study lies about 2 km. north west of Nerriga, New South Wales, and 140 km. east of Canberra by road (fig. 1). The deposit has been exposed by Titringo Creek, a tributary of the Endrick River (fig. 2). Raine (1967) described Titringo Creek siltstone as consisting of laminated purple-brown to gray quartz siltstones and rare fine sandstones. Bedding of the siltstone is horizontal and even. The unit overlies Ordovician rocks at the northern limit of the exposure, the extent of which is shown in figure 2. White clay-bearing sands overlie the unit, and these in turn are overlain by basalt. According to Raine (1967) the altitudinal distribution of Titringo Creek siltstone is about 535 m. (base) to 570 m. (top), making the unit approximately 35 m. thick.

2.2 DEPOSITION: Deposition of the Titringo Creek siltstone probably occurred in a slow moving body of water and appears to have been more or less continuous because of the uniform lithology (Raine 1967). A freshwater lake or slow moving river was probably the site of deposition. The presence of sulphides as a diagenetic component was interpreted by Raine (1967) as being due to the release of H_2S from anaerobic bacterial decay of organic matter. The necessity of an anaerobic environment for initial deposition of sulphides supports the conclusion that the sediments were deposited in a lake.

There may have been a period of erosion between deposition of the Titringo Creek siltstone and the overlying "inter-basaltic" sediments. This is because the Titringo Creek siltstone is horizontally bedded and would thus originally

FIGURE 1. Map of Australia, showing the positions of the Nerriga, Maslin Bay and Anglesea deposits.

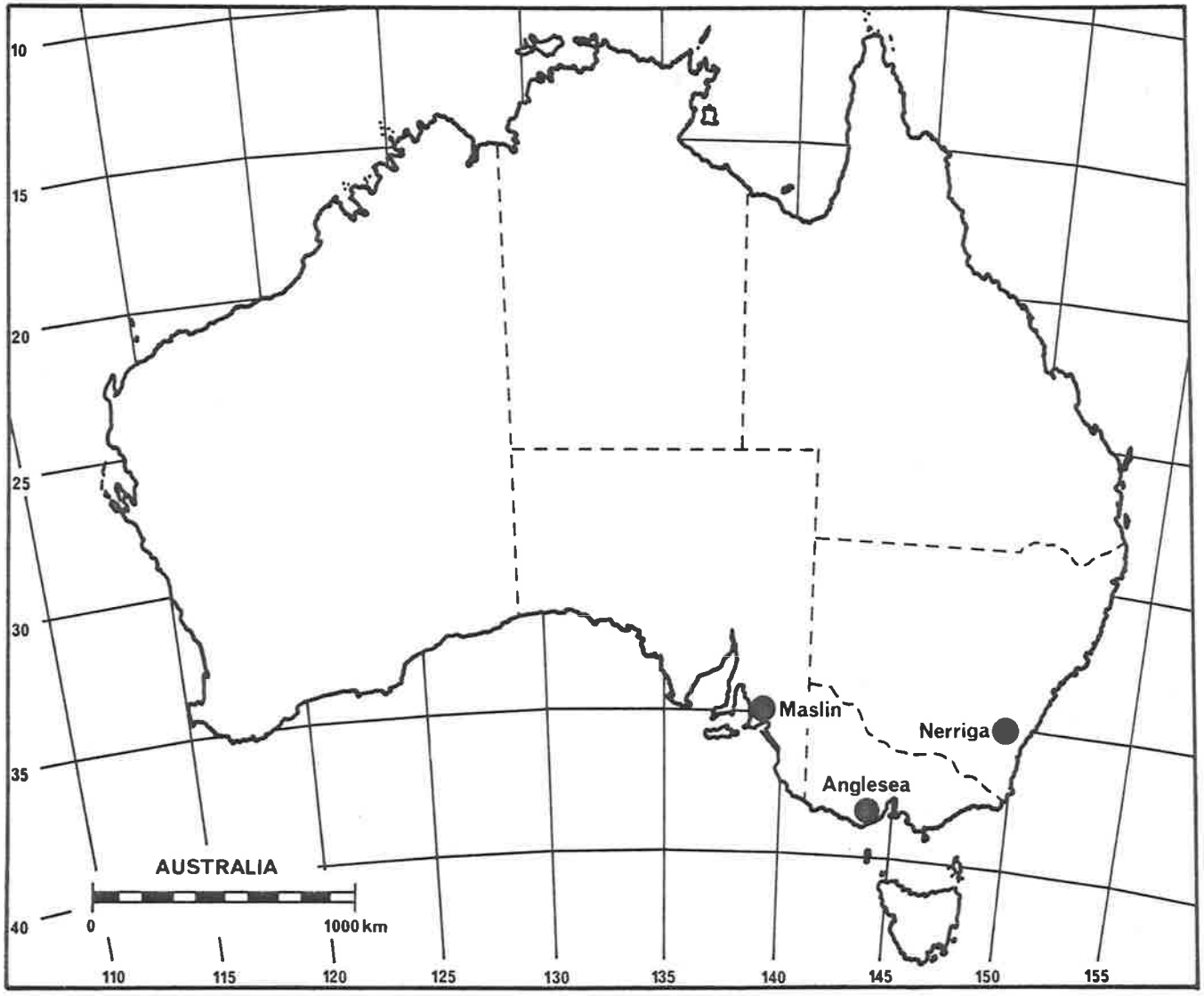
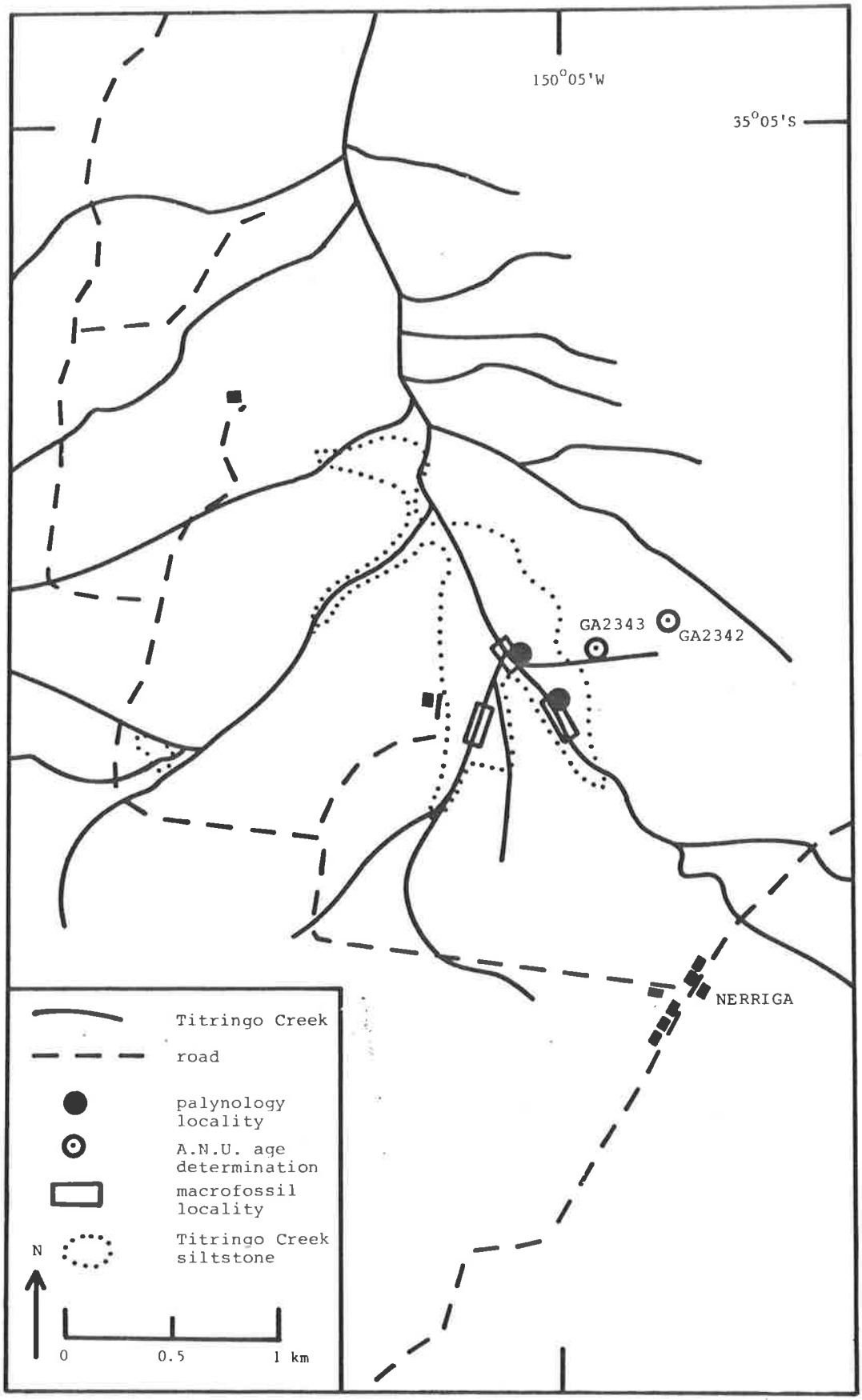

10
15
20
25
30
35
40
110
115
120
125
130
135
140
145
150
155
Maslin
Nerriga
Anglesea
AUSTRALIA
0
1000 km

FIGURE 2. Map of the Nerriga area, showing the macrofossil sampling localities, the palynology sampling localities (Owen 1975) and the K-Ar age determination localities (Wellman and McDougall 1974).


150°05'W
35°05'S
GA2343
GA2342
NERRIGA
Titringo Creek
road
palynology locality
A.N.U. age determination
macrofossil locality
Titringo Creek siltstone
N
0
0.5
1 km

have had a horizontal upper surface, whereas at present it falls to the north (Raine 1967). However, it is equally possible that early basalt flows dammed the drainage further down the valley, causing a lake to form. Later fluvial deposition may have occurred when the barrier was breached and further basalt flows then covered the sequence (J.I. Raine, pers. comm.). It is impossible to choose between these hypotheses without further detailed fieldwork.

2.3 AGE DETERMINATION: A preliminary description of the microfossil flora of the Titringo Creek siltstone was performed by Raine (1967). A complete survey was undertaken by Owen (1975), who found 25 species of spores, 11 species of gymnosperms, 67 species of angiosperms, and three species of uncertain affinities. There was also a great diversity of fungal spores and fructifications, and algae.

The Nerriga microflora could be assigned to the upper Malvacipollis diversus or early Proteacidites asperopolus Zones of Stover and Partridge (1973) and correlation with Harris's (1971) P. confragosus zonule is also indicated by the presence of that species at Nerriga (J.I. Raine, pers. comm.). Owen (1975) concluded that the microflora was most closely allied to the Malvacipollis diversus or Nothofagidites aspersus Zones of Stover and Partridge (1973), giving an early to middle Eocene age.

Odin et. al. (1978) placed the early/middle Eocene boundary at 45 Ma. Wellman and M^{c}Dougall (1974) dated the basalts directly overlying the Titringo Creek siltstone, and their K-Ar ages range from 46 - 40 Ma. Two basalt samples were dated from the area (fig. 2), but their K-Ar ages do not agree with their stratigraphic position. The stratigraphically older rock (GA 2343) gave ages of 40.8 and 41.9 Ma, and

Wellman and M^{c}Dougall suggested that this sample may have undergone argon leakage, making its date unreliable. The stratigraphically younger rock (GA 2342) gave ages of 44.8 and 41.6 Ma. Wellman and M^{c}Dougall (1974) considered it likely that both basalt samples are at least 45 Ma.

To compare the K-Ar dates with the time scale of Odin et. al. (1978), a correction of 2.5% is needed to bring the decay constant differences into line (J.I. Raine, pers. comm.). This makes the ages for GA 2342 45.9 and 42.6 Ma, which is very close to the early/middle Eocene boundary. Therefore current evidence, both palynological and geological, suggests that the Titringo Creek silstone is most close to 45 Ma, at the early/middle Eocene boundary.

2.4 COLLECTIONS: Two collecting trips were made to the Nerriga deposit during the course of this study (1977 and 1978). On the first trip impressions were collected in the field and where it was preserved, cuticle from the specimen was transferred with adhesive tape to an index card for later recovery. On returning to the laboratory, it was found that mummified leaves were often present in the blocks and could be removed by gentle maceration of the block. Therefore, on the second collecting trip, material was selected for laboratory maceration, and where possible, mummified leaves were collected in the field.

Approximately 150 impressions were photographed with a Leitz Aristophot 9 cm. by 12 cm. plate camera, using low angle reflected illumination to emphasise the veins. Blocks were macerated in dilute hydrogen peroxide, which very gently disintegrated the siltstone matrix and liberated the mummified leaves. Approximately 600 mummified leaves were collected in this manner and each was photographed with a

Leitz Aristophot 9 cm. by 12 cm. plate camera, using transmitted light. A piece of the leaf, usually about 1 cm^2., was taken from as near as possible to the position of maximum width of the leaf. These leaf squares, which included the margin, were then placed in hydrofluoric acid to remove all siliceous particles from their surface (usually about one hour). They were then washed and transferred to 20% chromic acid, which dissolved all the organic material with the exception of the cuticle in about five minutes. The cuticles were then neutralised in 3% w/w aqueous ammonia, stained with safranin, and mounted in phenol-glycerine jelly. About 600 cuticles were prepared in this way. The cuticles of the impressions were generally too fragmentary to be prepared, with only a few exceptions. Cuticles were photographed with transmitted light or Nomarski optics with a Reichert UnivaR microscope. Unstained cuticles of some specimens of one parataxon (NER/025) were mounted on aluminium stubs with double sided adhesive tape and coated in a high vacuum evaporative coating unit to a thickness of approximately 200 Å with an 80:20 gold palladium alloy. They were studied with an ETEC Autscan scanning electron microscope operated at 20 KV.

Some specimens are housed in the Botany Department, University of Adelaide, and the others (the 130 specimens used for the numerical analyses) in the South Australian State Herbarium (AD).

CHAPTER 3

NUMERICAL METHODS.

3.1 CHARACTER TYPES: The characters used in this study were restricted to those based on a ratio scale (i.e. continuous numeric characters). This was done for several reasons. Firstly, the amount of information contained in continuous characters is generally higher than in other types of characters. Secondly, more statistical tests and classificatory methods can be applied to continuous characters than to other types. Finally, a set of well documented continuous leaf shape and architectural characters was already in existence (Blackburn 1978a), which eliminated the need to formulate a new set.

3.2 CHARACTER STANDARDISATION: In almost all analyses involving continuous characters, the characters should be standardised before the OTUs are classified. If characters are not standardised, distance coefficients will be biased toward those characters which have the largest variances. This is obviously undesirable, since the characters with the greatest variability often have the lowest discriminatory power.

Character standardisation is not without problems. Characters with small ranges of variability and those with large ranges have equal influence on the distance coefficients after they are standardised. Small variations may be indistinguishable from variation due to other causes, particularly measurement error, and clearly characters with this feature should not be employed (Sneath and Sokal 1973 p. 155). Also, characters that have no variation at all are excluded. Therefore, as the variation of the character decreases, the absolute degree of variation is given more and

more weight, until it is decided there is no variation, and then it is given zero weight by excluding it (Sneath and Sokal 1973 p. 155).

Two methods of standardisation were employed in this study. In the first, characters were standardised to zero mean and unit variance. This was done by computing the mean and standard deviation of each row of the data matrix (the states of each character) and expressing each state as a deviation from the mean in standard deviation units (Sokal 1961). In the second method (Blackburn 1978a) the data for each character are ranked and divided into a number of equal sized states. Each state is assigned an integer value, ranging from one, for the state containing the lowest values, to k for the kth state containing the highest values. The formula for determining the number of states is:

$$k = 1.0 + 3.332 \log n,$$

where k = number of states;

n = number of OTUs (after Sturges (1926)).

The two methods of standardisation have very different effects on the data. Standardising to zero mean and unit variance emphasises the extreme values at the expense of all others. Standardising to states (vide Blackburn 1978a) reduces the effect of extreme values and separates intermediate values. Both methods were employed since it was difficult to estimate which of the two would have the most desirable effect (i.e. produce the least distortion of data).

3.3 CONSTRUCTION OF A SIMILARITY MATRIX: Several coefficients were available, but only two were considered for this study.

(1) Squared Euclidean Distance:

$$d^2_{pq} = \frac{1}{m} \sum_{j=1}^{m} (U_{jp} - U_{jq})^2$$

where d^2_{pq} = squared Euclidean distance,

m = number of characters,

U_{jp} = the mean of character j for the cases comprising cluster p,

U_{jq} = the mean of character j for the cases comprising cluster q.

There are three important features of squared Euclidean distance. Firstly d^2 is used instead of d because it is useful for similarity measures if they are additive over characters, which d^2 is, but d is not (Clifford and Williams 1976). Secondly, d^2 is strictly a dissimilarity measure, which means that it decreases with increasing likeness between OTUs. Thirdly, and most importantly, because of the additive property of d^2, all characters must be either in the same units or they must be standardised. Squared Euclidean distance is one of the most commonly used and simplest of the dissimilarity coefficients.

(2) Coefficient of Shape:

$$C^2_P = d^2_{pq} - C^2_Q$$

where C^2_P = coefficient of shape,

C^2_Q = coefficient of size.

Penrose (1954) suggested dividing d^2_{pq} into two parts; a coefficient of "size" (C^2_Q), defined as the square of the difference between character sizes in OTUs p and q,

$$\text{i.e. } C^2_Q = \frac{1}{m}2\left[\sum_{J=1}^{m} (U_{jp} - U_{jq}) \right]^2$$

and a coefficient of "shape" (C^2_p), defined as the residue

after "size" is removed. C_p^2 represents the variance of differences between the character states of the OTUs being compared (Sneath and Sokal 1973 p. 170).

3.4 CLUSTERING STRATEGIES: (1) Ward's (1963) Error Sum of Squares: This fusion strategy was developed independently by Ward (1963) and Burr (1968, 1970). The error sum of squares (ESS) is defined as the sum of the distances from each individual to the centroid of its parent cluster (Wishart 1978); i.e. $(x - \bar{x})^2$ for the general term x and mean $\bar{x}$. Ward (1963) proposed the hierarchical method which combined those two clusters whose fusion yielded the least increase in ESS.

Williams, Clifford and Lance (1970) have demonstrated that the ESS fusion strategy is space dilating. That is, if a group of m individuals define a single continuous character, with general term x and mean $\bar{x}$, and a second group of n individuals with general term y and mean $\bar{y}$, and the groups are fused to give a new general term z with mean $\bar{z}$, then:

$$D = \Sigma(z - \bar{z})^2 - \Sigma(x - \bar{x})^2 - \Sigma(y - \bar{y})^2$$

where D = increase in ESS.

This can be reduced to:

$$D = \frac{mn}{m + n} (\bar{x} - \bar{y})^2.$$

For the case m = n = 1;

$$D = \tfrac{1}{2} (\bar{x} - \bar{y})^2.$$

(where d = D for the special case of the fusion of two individuals).

For the symmetric case, m = n ≠ 1;

$$D = \frac{n}{n+1} (\bar{x} - \bar{y})^2 = \frac{2n}{n+1} d$$

The multiplier of d is asymptotic - it can never exceed 2.

These calculations lead to two important conclusions.

As groups become larger, it becomes more "difficult" for them to fuse with other large groups, therefore making the strategy intensely clustering. Secondly, because individuals or small groups are relatively easily fused with one another, or with large groups, it is inherently unlikely that non-conformist groups will be produced. (Williams, Clifford and Lance (1970)).

Sneath (1976) suggested that the ESS algorithm behaved similarly to information analysis, in that with increasing numbers of OTUs it is possible for a cluster of numerous very similar OTUs to dominate the picture to such an extent that all other, rarer, OTUs are forced together into one cluster, even though they are extremely different from one another. Sneath illustrated this with an artificial example, which represented an extreme case of several identical OTUs which clustered much more distinctly from the other OTUs with the ESS algorithm than they did with the UPGMA or WPGMA algorithms. However, the demonstration of space dilation by Williams, Clifford and Lance (1970) showed that Sneath's conclusion may not be strictly accurate. While it is true that large numbers of similar OTUs do form very distinct clusters, the rarer individuals are not necessarily forced into nonconformist groups.

Mojena (1976) compared the performance of seven hierarchical grouping methods over 12 randomly generated data sets. He concluded that the ESS algorithm gave "a superior performance across all data sets. Matched t-tests showed very significant differences (<0.001) between.. [ESS] .. and all other methods." The other clustering algorithms he considered were: Nearest neighbour, farthest neighbour, simple average (UPGMA), group (weighted) average (WPGMA),

median, and centroid.

(2) Group Average (UPGMA): Since the ESS algorithm is only valid analytically with distance coefficients, UPGMA was employed on the similarity matrix of coefficients of shape. It is also used in Chapter 4 for comparison with the ESS algorithm.

According to Sneath and Sokal (1973 p. 230) "The UPGMA algorithm computes the average similarity or dissimilarity of a candidate OTU to an extant cluster, weighting each OTU in that cluster equally, regardless of its structural subdivision." The formula used is:

$$U_{L,JK} = \frac{t_J}{t_{(J,K)}} U_{L,J} + \frac{t_K}{t_{(J,K)}} U_{L,K}$$

where $U_{L,JK}$ = the average similarity between clusters L and JK, t_J, t_K and $t_{(J,K)}$ = the number of individuals in clusters J,K and (J,K) respectively, and

$U_{L,J}$ and $U_{L,K}$ = the similarity between cluster L and cluster J and K respectively.

The algorithm is almost space conserving, but has the undesirable feature that distance between groups is dependent on the variance within groups (W.T. Williams pers. comm.). That is, groups appear to be more distant from one another the more heterogeneous they become. UPGMA is a more generally applicable algorithm than ESS, principally because almost any similarity measure is admissible to it, whereas ESS is limited to a Euclidean distance function. This was not a problem in this study, where squared Euclidean distance was used almost exclusively.

(3) Minimum Spanning Tree: Single linkage cluster analysis was proposed by Sneath (1957) as a convenient way of summarising taxonomic relationships in the form of

dendrograms. One of the drawbacks of single linkage cluster analysis is that the dendrograms often contain very elongated clusters ("chaining", Sneath and Sokal (1973 p. 223)). For this reason they are of limited use to taxonomists. Gower and Ross (1969) suggested that chaining can be so severe that individuals belonging to different clusters may be closer together than different members of the same cluster.

Rohlf (1975) has shown that there is a direct relationship between Jardine and Sibson's (1969a,b) B_k cluster analysis (of which single linkage is a special example) and certain types of graphs. If k = 1, then the graph obtained is a minimum spanning tree (MST). The MST has several advantages. Firstly, it can be computed exactly and very efficiently (Farris 1970, Rohlf 1973). Secondly, for every OTU the distance to its nearest neighbour is shown faithfully, which is an advantage over single linkage cluster analysis, where the exact nearest neighbours are usually unknown.

A single linkage cluster analysis was produced for the fossil and extant OTUs used in this study. For the fossil OTUs in particular, the effect of chaining was extreme, making delimitation of clusters impossible. An MST was found to give much more easily interpretable results, and has been presented to the exclusion of the single linkage dendrogram.

(4) Nearest Neighbour Networks: W.T. Williams (pers. comm.) has recently devised a method for determining clusters based on network diagrams. After the similarity matrix has been produced, the nine nearest neighbours of each OTU are located (using the classification program GROUPER, which is held on the permanent library file TAXON in the CSIRO Division of Computing Research in Canberra). Pairs of OTUs are then placed in groups (bond counts) depending on the

following strategy:

Bond count 6: Contains those pairs of OTUs which are mutual nearest neighbours;

Bond count 5: Contains those pairs of OTUs which are first and second nearest neighbours to one another respectively;

Bond count 4: Contains those pairs of OTUs which are mutual second nearest neighbours;

Bond count 3: Contains those pairs of OTUs in which one (A) is the nearest neighbour of the other (B), but B does not have A as either its first or second nearest neighbour;

Bond count 2: Contains those pairs of OTUs in which one (A) is the second nearest neighbour of the other (B), but B does not have A as either its first or second nearest neighbour.

In constructing the nearest neighbour network (NNN), bond counts 6 and 5 are regarded as very strong bonds, bond counts 4 and 3 as strong bonds, and bond count 2 as a weak bond. Firstly, all pairs of OTUs in bond count 6 are linked. Since bond count 5 is also considered to be a very strong bond, those pairs of OTUs are next linked. With the inclusion of the pairs of OTUs in bond count 5, some groups may contain more than two OTUs. The pairs of OTUs in bond count 6 must, by definition, be unique. However, the OTUs in bond count 6 may also occur in bond count 5. For example, if OTUs X and Y are linked in bond count 6, and OTUs Y and Z are linked in bond count 5, the three OTUs should be linked as X=Y=Z. It should be noted that by drawing the network in this way, a relationship can only be inferred between OTUs which are directly

linked. That is, for the above example, it is possible to infer a relationship between OTUs X and Y, and between OTUs Y and Z, but not between OTUs X and Z.

Next the OTUs in bond counts 4 and 3 are added (strong bonds). When this has been done, the OTUs usually fall into several unconnected groups (= clusters). These groups can then be connected using the weak bonds (bond count 2). It is possible that having used bond count 2, some groups may remain unconnected. This suggests that those groups are very isolated. In order to link them, the nearest neighbour lists must be scanned to find the closest link between any of the OTUs in the isolated group(s) with any OTUs in the connected groups.

When the nearest neighbour networks are constructed, no attempt is made to make the distances between OTUs proportional to their similarity coefficients as is done in an MST. The NNN has the advantage of being totally independent of group size.

3.5 ORDINATION: According to Sneath and Sokal (1973 p.245) "Ordination is the placement of t OTUs in an A-space of dimensionality varying from 1 to n or t-1, whichever is less." In this study, the method of ordination used was principal components analysis (PCA).

In PCA, the observed variates (characters) are represented as functions of a smaller number of latent variates. It is particularly useful when no a priori patterns of interrelationship can be suggested or are suspected (Blackith and Reyment 1971 p. 146). In simple terms, if the OTUs are visualised as points plotted in Euclidean hyperspace, with each character representing an axis; a PCA shifts the origin and locates the longest axis through the cluster of

OTUs (which accounts for the maximum possible amount of variation of the OTUs). This axis is the first principal component. Other axes are then defined to account for the maximum amounts of the succeeding residual variation; these axes represent the higher order principal components.

Sneath (1976) concluded that while ordination gave useful maps or models (ordination diagrams), the phenons must be circumscribed by eye, a step that may be unacceptably subjective. This problem is encountered with the ordination diagram drawn for 35 OTUs in Chapter 4. The problem of delimiting clusters in an ordination diagram is often compounded if the number of OTUs is increased. For this reason, the results of the PCAs were not presented as ordination diagrams for the fossil OTUs. However, ordination is a very useful technique in classification. Fordham and Bell (1978) proposed the use of unstandardised principal components as characters in a cluster analysis. This would allow the result of the PCA to be exhibited graphically as a dendrogram. This approach was used in this study. It is important that the PCA scores should not be standardised since this would eliminate differences in the characteristic roots, which is the major advantage of a PCA.

3.6 STOPPING RULE FOR DETERMINING THE NUMBER OF GROUPS IN A DENDROGRAM: Determination of the number of groups in a dendrogram is one of the major problems in numerical taxonomy. Among the earliest approaches was the use of the "phenon line" (Sneath and Sokal 1973 p. 294). This required the drawing of a line across the dendrogram at a particular percentage of similarity and nominating all groups produced by that line as phenons.

There are two objections to this method. Firstly,

without prior knowledge of the taxonomy of the operational taxonomic units (OTUs) there is no way of predicting where the phenon line should be placed. Secondly, Clifford and Williams (1973) and Clifford (1976) showed that, unless the fusion strategy in use is strictly space conserving, the drawing of phenon lines is invalid due to group size dependence. The only completely space conserving strategy which would allow the valid use of phenon lines is centroid (Clifford 1976), which is now rarely used.

To determine the number of groups in a classification, Ratkowsky and Lance (1978) defined a criterion that is applicable to nominal and numeric characters. It depends on the Cramér measure (Cramér 1946 p 443) for the degree of association for nominal characters and a corresponding measure for numeric characters suggested by the analysis of variance.

According to Ratkowsky and Lance (1978), the Cramér measure, applied to the number of individuals in each of the states of the nominal character, after a total of N individuals have been classified in n groups is:

$$C = \left[\frac{\chi^2}{N \min(s-1, n-1)} \right]^{\frac{1}{2}},$$

where χ^2 is the convential chi-square measure of association in a contingency table, and min(s-1,n-1) signifies the smaller of the two quantities s-1 and n-1 (s = the number of states in the character). For numerical characters, a corresponding measure is:

$$S = \left(\frac{B}{T}\right)^{\frac{1}{2}},$$

where B is the between-group sum of squares and T is the total sum of squares (Lance and Williams 1977). Both S and C are constrained between zero and unity and are fully compatible

(Lance and Williams 1977). Ratkowsky and Lance (1978) proposed that the optimum number of groups in a classification is that value of n for which $\overline{C}/n^{\frac{1}{2}}$ has its maximum value ($\overline{C}$ is the average value obtained by applying C to each nominal character and S to each numeric character).

There are two disadvantages to this criterion. A phenon line must be applied to determine the groups for which $\overline{C}$ is calculated. The invalidity of the use of phenon lines has already been discussed. The second disadvantage concerns objectivity. Ratkowsky and Lance (1978 p. 117) found that the criterion should be $\overline{C}/(n-1)^{\frac{1}{2}}$, but "as n was found to work better than n-1 in the examples studied, the final formula is $\overline{C}/n^{\frac{1}{2}}$." They also tried using C^2 rather than C but concluded that "this worked less well for the examples described herein." Although there is nothing invalid in manipulating this quasi-statistical criterion to give the "best" result, it would be preferable to have a more objective approach. A modification of the Ratkowsky and Lance criterion has been devised to overcome these two disadvantages.

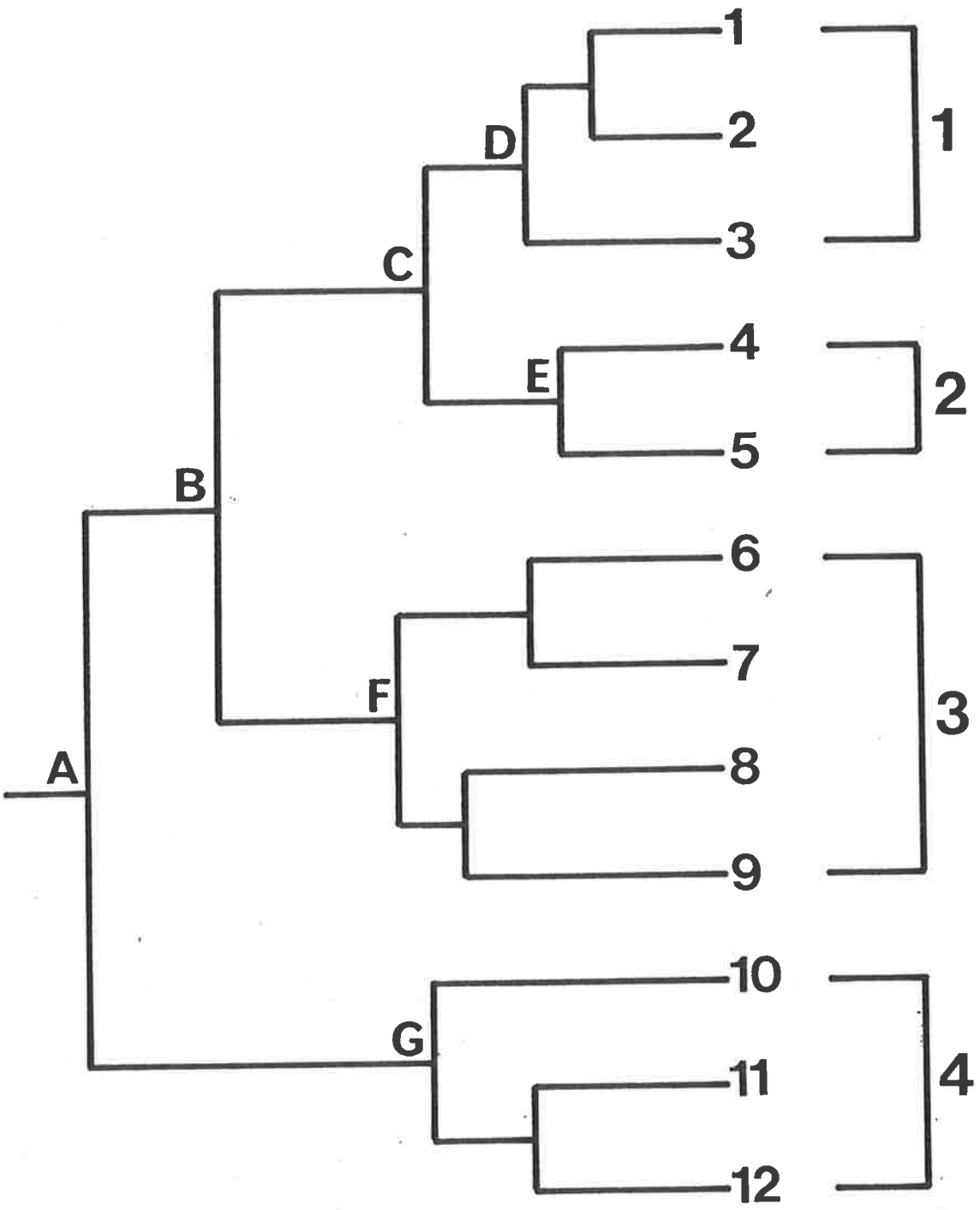
If the value of n is made constant, the Ratkowsky and Lance (1978) criterion can be reduced from $\overline{C}/n^{\frac{1}{2}}$ to $\overline{C}$. The following method restricts n to 2. Fristly, $\overline{C}$ is calculated for the two groups which are linked by the last fusion in the classification. These groups are then considered independently, and for each one, $\overline{C}$ is recalculated for the two groups within it which are linked by the last fusion. This continues for successive pairs of groups until the maximum value of $\overline{C}$ is attained for each group. This modification overcomes the disadvantages of the Ratkowsky and Lance criterion. By making n constant, the criterion can be reduced to $\overline{C}$, which

is independent of n, and by considering successive pairs of groups independent of all other groups, a phenon line is not required.

Lance and Williams (1977) showed that the importance of a character to a classification can be assessed by considering the value of C or S for that character relative to the other characters. Therefore, the modification of the Ratkowsky and Lance criterion suggested in this paper proposes that a group should not be further divided after the maximum average character contribution has been attained i.e. for each group, splitting ceases when $\overline{C}_{max}$ is achieved.

This method is best explained with a small artificial example. The dendrogram (fig. 2.1) contains 12 OTUs. The first furcation of the dendrogram (A in fig. 2.1) splits the OTUs into two groups. One of these groups contains OTUs 1-9 and the other OTUs 10-12. $\overline{C}$ is calculated for these two groups (= $\overline{C}_A$). Each group is then considered independently. The group containing OTUs 1-9 next furcates at B, splitting the OTUs into two groups. One of these groups contains OTUs 1-5 and the other OTUs 6-9. $\overline{C}$ is calculated for these two groups (= $\overline{C}_B$). If $\overline{C}_B < \overline{C}_A$, no further calculation is required, since for this group of OTUs, $\overline{C}_{max}$ (= $\overline{C}_A$) has been attained, and OTUs 1-9 constitute one group. If $\overline{C}_B \geqslant \overline{C}_A$, as is the case in this example, $\overline{C}_{max}$ has not been attained and further calculations are necessary. Each group is again considered independently. The group containing OTUs 1-5 next furcates at C, splitting the OTUs into two groups (OTUs 1-3 and OTUs 4 and 5). $\overline{C}$ is calculated for these two groups (= $\overline{C}_C$), and $\overline{C}_C \geqslant \overline{C}_B \geqslant \overline{C}_A$. Therefore the maximum $\overline{C}$ value has still not been attained. $\overline{C}_D$ is then calculated for the two groups containing OTUs 1 and 2 and OTU 3, and $\overline{C}_D < \overline{C}_C \geqslant \overline{C}_B \geqslant \overline{C}_A$.

FIGURE 2.1. Artificial dendrogram showing 12 OTUs (numbered 1 - 12) on the right hand side falling in four groups (numbered 1 - 4 on the extreme right hand side).


1
2
3
4
5
6
7
8
9
10
11
12
A
B
C
D
E
F
G
1
2
3
4

Therefore $\overline{C}_C$ is the maximum $\overline{C}$ value for this part of the dendrogram, and OTUs 1-3 represent one group (1 in fig. 2.1). For the other OTUs, $\overline{C}_E < \overline{C}_C \geqslant \overline{C}_B \geqslant \overline{C}_A$ gives OTUs 4 and 5 as group 2; $\overline{C}_F < \overline{C}_B \geqslant \overline{C}_A$ gives OTUs 6-9 as group 3; and $\overline{C}_G < \overline{C}_A$ gives OTUs 10-12 as group 4.

The value of any quasi-statistical method can only be assessed by application. In chapter 4 one example will be considered and the method will be applied in chapter 6. At present, a program does not exist to compute the modification of the Ratkowsky and Lance criterion, and its application is therefore restricted due to the large number of calculations required.

(This stopping rule is the subject of a manuscript currently in press to the Botanical Gazette (Hill 1980c). A copy is included in Appendix IV).

CHAPTER 4

NUMERICAL TAXONOMY OF EXTANT LEAVES.

4.1 MATERIALS AND METHODS: Before a fossil flora could be described using a numerical taxonomic approach, it was necessary to test the method on a set of extant leaves. A sampling technique similar to that of Dolph (1976a) was followed. A collection of 100 leaves representing 20 species of trees, shrubs and vines was made from the Adelaide Botanic Garden. Five leaves were taken from an individual of each species. Each of the leaves represents an operational taxonomic unit (OTU). The 20 species are listed in table 1.

TABLE 1. List of the species collected for analysis and the OTU numbers assigned to them.

OTU Numbers	SPECIES	FAMILY
1- 5	Argyrodendron actinophyllum (C. Moore) Edlin	Sterculiaceae
6-10	Elaeocarpus grandis F.vM.	Elaeocarpaceae
11-15	Castanospermum australe A. Cunn & Fraser	Leguminosae
16-20	Tristania conferta R.Br.	Myrtaceae
21-25	Flindersia australis R.Br.	Rutaceae
26-30	Hymenosporum flavum F.vM.	Pittosporaceae
31-35	Brachychiton discolor F.vM.	Sterculiaceae
36-40	Harpullia pendula Planch.	Sapindaceae
41-45	Linociera ramiflora (Roxb.) Wall.	Oleaceae
46-50	Toona australis Harms.	Meliaceae
51-55	Hardenbergia violacea (Schneev.) Stearn	Leguminosae
56-60	Macropiper excelsum Miq.	Piperaceae
61-65	Pittosporum undulatum Vent.	Pittosporaceae
66-70	Rhodosphaera rhodanthema Engl.	Anacardiaceae
71-75	Cinnamomum camphora T. Nees & Eberm	Lauraceae

76-80	Pittosporum rhombifolium A. Cunn.	Pittosporaceae
81-85	Alectryon excelsus Gaert.	Sapindaceae
86-90	Cupaniopsis anacardioides Radlk.	Sapindaceae
91-95	Bauerella australiana Borzi	Rutaceae
96-100	Laurus nobilis L.	Lauraceae

All architectural characters, with the exception of those involving ultimate venation, were measured from photographs. Leaves were photographed shortly after they were collected with high intensity transmitted light. This gave clear detail, at least to tertiary venation. A section including two secondary veins and part of the primary vein was removed from the position of maximum width of the leaves, cleared with the method of Christophel and Blackburn (1975), and stained with the method of Blackburn (1978b). These sections were usually small enough to be mounted on slides and were used to study ultimate venation.

Cuticles were taken from the position of maximum width of the leaves and were prepared using the method of Hill (1978). All materials are housed in the Botany Department, University of Adelaide.

4.2 CHARACTER CHOICE: Many character sets have been proposed for use with angiosperm leaves (e.g. Krussmann 1960/61, Arbeitsgruppe "Cuticulae" 1964, Stace 1965, Mouton 1966,1970,1976, Roselt and Schneider 1969, Ferguson 1971, Mädler and Straus 1971, Walther 1972, Hickey 1973, Dilcher 1974, Mädler 1975, Dolph 1975, Melville 1976, Blackburn 1978a). However, most were developed for descriptive purposes and are unsuitable for numerical taxonomy. For this study, most cuticular characters were taken from Stace (1965) and most

architectural characters from Blackburn (1978a), although some required modification to make them suitable for general use. Because of the confusion often caused by imprecise definition of characters, a list of the characters and an explanation of the method of measurement will be given. For the architectural characters, a strict definition of vein orders is required, and this will be considered first.

4.3 DEFINITION OF VEIN ORDERS: Many of the characters employed on angiosperm leaves will involve the venation pattern. This requires the accurate definition of vein orders. The problem of determining the difference between primary, secondary, and tertiary veins, which is all that was required for this study, does not appear to be difficult. However, as Hickey (1973) found, "In practice the objective designation of vein order is more complex than easily observed differences in thickness, course, and pattern among size classes would seem to indicate." Hickey's definitions are suitable for use with his descriptive terminology, but are unsuitable when precise quantitative characters are to be scored. A literature search proved that few alternative methods have been proposed. A new definition of vein orders was, therefore, formulated using a set of about 200 fossil and extant species. Because of the limited number of species on which this definition was formulated, leaves may be found in which the definition requires modification.

Primary veins: The vein or veins arising from the petiole which, at their base, are the thickest veins of the leaf. The end of a primary vein is defined as the point at which the vein gives rise to a lateral vein of equal thickness to the continuation of the primary vein. Often the primary vein does not end before the apex of the leaf. One problem with

this definition is the presence of what Hickey (1973) called "supra-basal lateral primary veins", i.e. primary veins originating as lateral branches of a primary vein above the base of the leaf. Using the definition given here, these veins would not be considered as primary. Since none of the leaves used in this project fell into the category of possessing "supra-basal lateral primary veins" which could not be adequately considered as secondary veins, the above definition remained unchanged.

Secondary veins: Accurate definition of secondary and intersecondary veins is the most complex problem in the study of vein orders. Hickey (1973) suggested that "the next set of branches of markedly smaller size than their primary source are the secondary veins." This definition is difficult to apply toward the base and apex of most leaves, and usually an arbitary decision as to when a lateral branch from the primary vein is too thin to be a secondary vein is required. Another problem with this definition is that no attempt is made to locate the end of a secondary vein. Identification of intersecondary veins, which are intermediate in length and thickness between secondary and tertiary veins (Hickey 1973), is even more difficult.

It is, therefore, necessary to propose a new definition, which must be reasonably quick to assess and, more importantly, be objective and repeatable. Any attempt to propose a mathematical solution to the problem on the basis of thickness, length, position, or course of veins will fail because of the time required to put such a method into practice. The following definition overcomes this problem without sacrificing too much in accuracy. The only assumption which must be made is that secondary veins may arise only from the primary vein and not from other secondaries.

Note that the set of veins on each side of the primary vein(s) are considered separately.

(1) Locate the lateral vein on each side of the primary vein which at its point of attachment to the primary vein, is the thickest of all the laterals.

(2) Locate the ends of these lateral veins. Although they have not been defined as such, these two veins are treated as secondaries. The end of a secondary vein may be defined in three ways. It is (a) the junction at which the vein divides into two branches of equal thickness, (b) the junction where the vein merges with a vein of greater thickness (as in Hickey's (1973) brochidodromous venation), or (c) in some serrate margined leaves, where the secondary vein runs straight into a tooth without fulfilling either of the first two requirements, the vein ends at the tooth apex.

(3) Locate the thickest vein which arises from these secondaries. Measure the thickness of this vein at its point of attachment to the secondary vein.

(4) Record the length of all lateral veins arising from the primary vein, which at their point of attachment to the primary vein are at least as thick as the vein measured in (3). Only these veins can be secondaries or intersecondaries.

(5) Thickness and length of a vein are generally accepted as being the most important features in separating secondary from intersecondary veins. Therefore, veins are numbered consecutively from the base, and the product of length by thickness (LxT) is calculated for each one.

When determining whether a vein is a secondary or intersecondary, it is best compared to its neighbouring veins rather than to all other veins. This is because secondary veins do not remain constant in length and thickness

along a leaf and a secondary vein near the base or apex of a leaf may have a lower (LxT) than an intersecondary vein near the middle of the leaf.

For definition of secondary and intersecondary veins, most of the usual statistical parameters (mean, variance, standard deviation, etc.) were of no use because they are often more dependent on the variation in secondary veins along the leaf than on the differences between secondary and intersecondary veins. The method finally decided upon will be briefly explained and three examples given.

(6) Determine the range (R) for (LxT)

(7) Sum the absolute differences between succeeding pairs of veins, working apically from the base. That is, for x secondary veins $\sum|A| = |(LxT)_1 - (LxT)_2| + |(LxT)_2 - (LxT)_3| + \ldots\ldots + |(LxT)_{x-1} - (LxT)_x|$.

If no intersecondary veins are present, there will be a gradual transition of (LxT) values, increasing from the base to a maximum value and then decreasing toward the apex. If the leaf was perfectly symmetrical and no intersecondary veins were present, the secondary vein with the greatest (LxT) value would be at the centre of the leaf and $|A| \approx 2R$. However, if the secondary vein with the greatest (LxT) value was close to the base or apex, then $|A| \approx R$. The relative value of R to $|A|$ can be estimated as:

$$\frac{n}{\frac{n}{2} + \left|\frac{(n+1)}{2} - n_x\right|} \times \frac{R}{|A|} \times 100 = P \text{ (as a percentage)}$$

where n = total number of lateral veins on a given side of the primary vein, and

n_x = number of the vein with the maximum (LxT) value, counted from the base.

When no intersecondary veins are present, P will be

approximately 100%, decreasing as the number of inter-secondary veins increase.

(8) When P has been determined, locate the vein with the highest (LxT) value. This vein is not necessarily the same as that in (1) and is defined as a secondary. P of (LxT) is calculated for that vein and subtracted from its (LxT); i.e., (LxT) - (P of (LxT))= M.

(9) The next vein in both the apical and basal direction is now considered. If $M \leqslant$ (LxT) for that vein, it is a secondary; if $M >$ (LxT), it is an intersecondary.

(10) If the vein is a secondary, M is recalculated. If the vein is an intersecondary, N = (LxT) + (P of (LxT)) is calculated. This vein is then compared to the adjacent undefined vein and so on, until all laterals have been defined. Generally if a secondary vein is being compared to another vein, and if (LxT) for the new vein is $>$ M, it is a secondary; otherwise it is an intersecondary. If an inter-secondary vein is being compared to another vein and if (LxT) for the new vein is $\leqslant$ N, it is an intersecondary; otherwise, a secondary.

(11) This pairwise comparison is continued until all veins have been designated as either secondaries or inter-secondaries. An intersecondary vein must have secondary veins on both sides of it (although not necessarily as adjacent veins). Therefore, any "intersecondary" veins beyond the last secondary vein in a basal or apical direction must be classed as nonsecondary.

As examples, three different leaves representing a range from no intersecondary veins through to several are presented. Calculations cover only one side of the primary vein.

EXAMPLE 1: Elaeocarpus grandis (fig. 2.2)

Vein number	(L x T) (cm.mm)		Vein Order
1	0.14	$L \times T > M_2$	Secondary
2	0.43	$L \times T > M_3$; $M_2 = 0.05$	"
3	0.49	$L \times T > M_4$; $M_3 = 0.06$	"
4	1.38	$L \times T > M_5$; $M_4 = 0.17$	"
5	1.26	$L \times T > M_6$; $M_5 = 0.16$	"
6	1.82	$L \times T > M_7$; $M_6 = 0.23$	"
7	2.32*	$M_7 = 0.29$	
8	2.24	$L \times T > M_7$; $M_8 = 0.28$	"
9	2.24	$L \times T > M_8$; $M_9 = 0.28$	"
10	1.38	$L \times T > M_9$; $M_{10} = 0.17$	"
11	0.95	$L \times T > M_{10}$; $M_{11} = 0.08$	"
12	0.56	$L \times T > M_{11}$; $M_{12} = 0.07$	"

* greatest (L x T) value. Therefore, vein 7 is defined as a secondary

$R = 2.32-0.14 = 2.18$

$$|A| = |.14-.43| + |.43-.49| + |.49-1.38| + |1.38-1.26| + |1.26-1.82| + |1.82-2.32| + |2.32-2.24| + |2.24-2.24| + |2.24-1.38| + |1.38-.95| + |.95-.56| + |.56-.27| + |.27-.14| = 4.60$$

$$P = \frac{n}{\frac{n}{2} + \left|\frac{(n+1)}{2} + n_x\right|} \times \frac{R}{|A|} \times 100\%$$

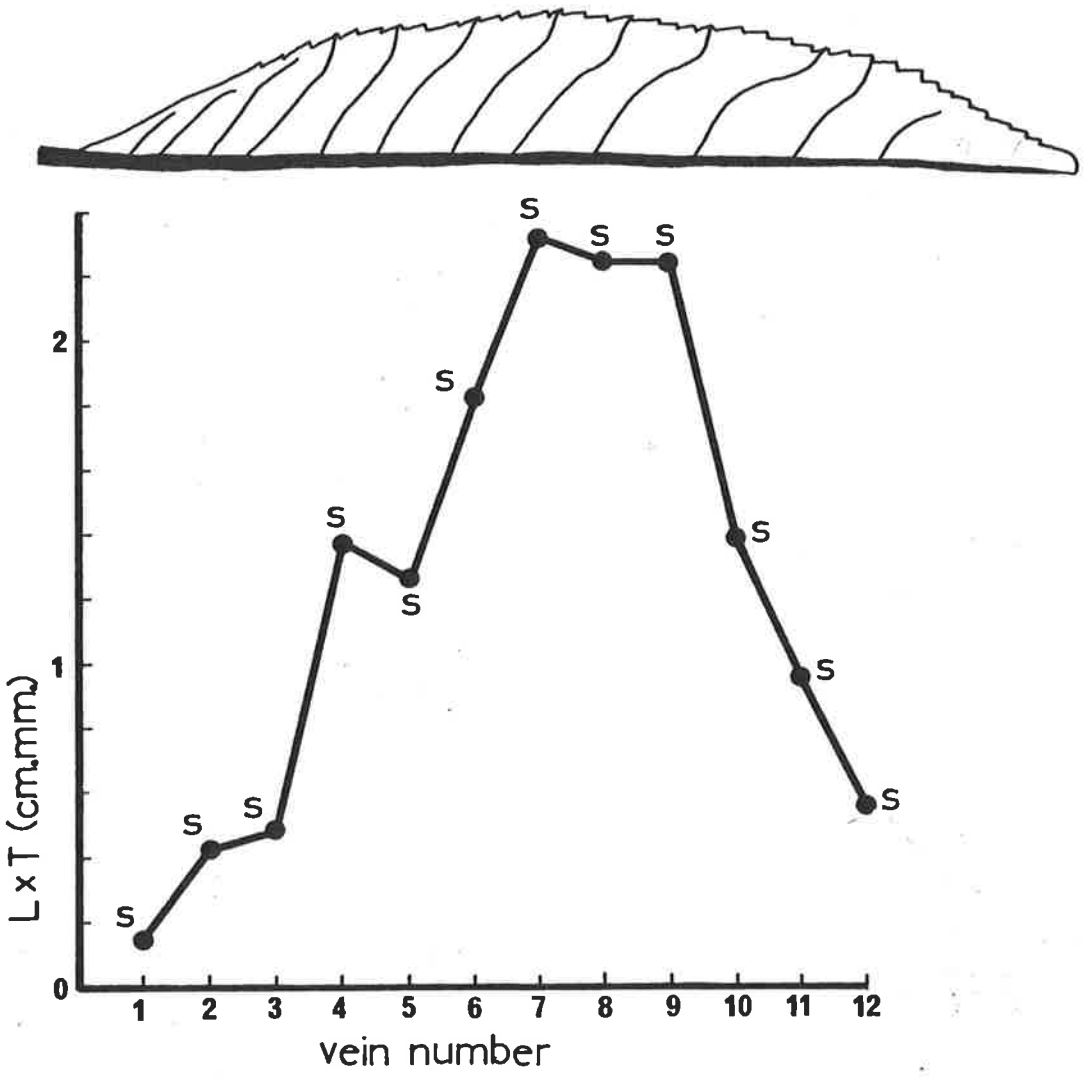
$$= \frac{12}{6+\left|\frac{13}{2} - 7\right|} \times \frac{2.18}{4.6} \times 100\%$$

$$= 87.5\%$$

∴For vein number 7, M = (L x T) - (P of (L x T))

= 2.32-2.03 = 0.29

FIGURE 2.2. Graph of vein number against length x thickness (L x T) for one side of the primary vein of a leaf of Elaeocarpus grandis. A drawing of the leaf showing the veins is also given. (Relative thicknesses of veins are not shown, s = secondary vein).


L x T (cm.mm)
0
1
2
1
2
3
4
5
6
7
8
9
10
11
12
vein number

All the veins figured on this leaf are secondaries.

EXAMPLE 2: Rhodosphaera rhodanthema (fig. 2.3)

Vein number	(L x T) (cm.mm)		Vein Order
1	0.45	$L \times T < N_2$	Nonsecondary
2	0.54	$L \times T < N_3$; $N_2 = 0.68$	"
3	0.95	$L \times T < M_4$; $N_3 = 1.20$	"
4	1.36	$L \times T > M_5$; $M_4 = 1.01$	Secondary
5	1.40	$L \times T > N_6$; $M_5 = 1.04$	"
6	0.36	$L \times T < M_7$; $N_6 = 0.45$	Intersecondary
7	1.48*	$M_7 = 1.10$	Secondary
8	0.60	$L \times T < M_7$; $N_8 = 0.76$	Intersecondary
9	1.44	$L \times T > N_8$; $M_9 = 1.07$	Secondary
10	0.25	$L \times T < M_9$; $N_{10} = 0.32$	Intersecondary
11	1.24	$L \times T > N_{10}$; $M_{11} = 0.92$	Secondary
12	1.12	$L \times T > M_{11}$; $M_{12} = 0.83$	"
13	0.70	$L \times T < M_{12}$; $N_{13} = 0.88$	Nonsecondary
14	0.60	$L \times T < N_{13}$; $N_{14} = 0.76$	"
15	0.33	$L \times T < N_{14}$; $N_{15} = 0.42$	"
16	0.28	$L \times T < N_{15}$	"

* greatest (L x T) value. Therefore, vein 7 is defined as a secondary

$R = 1.48 - 0.25 = 1.23$

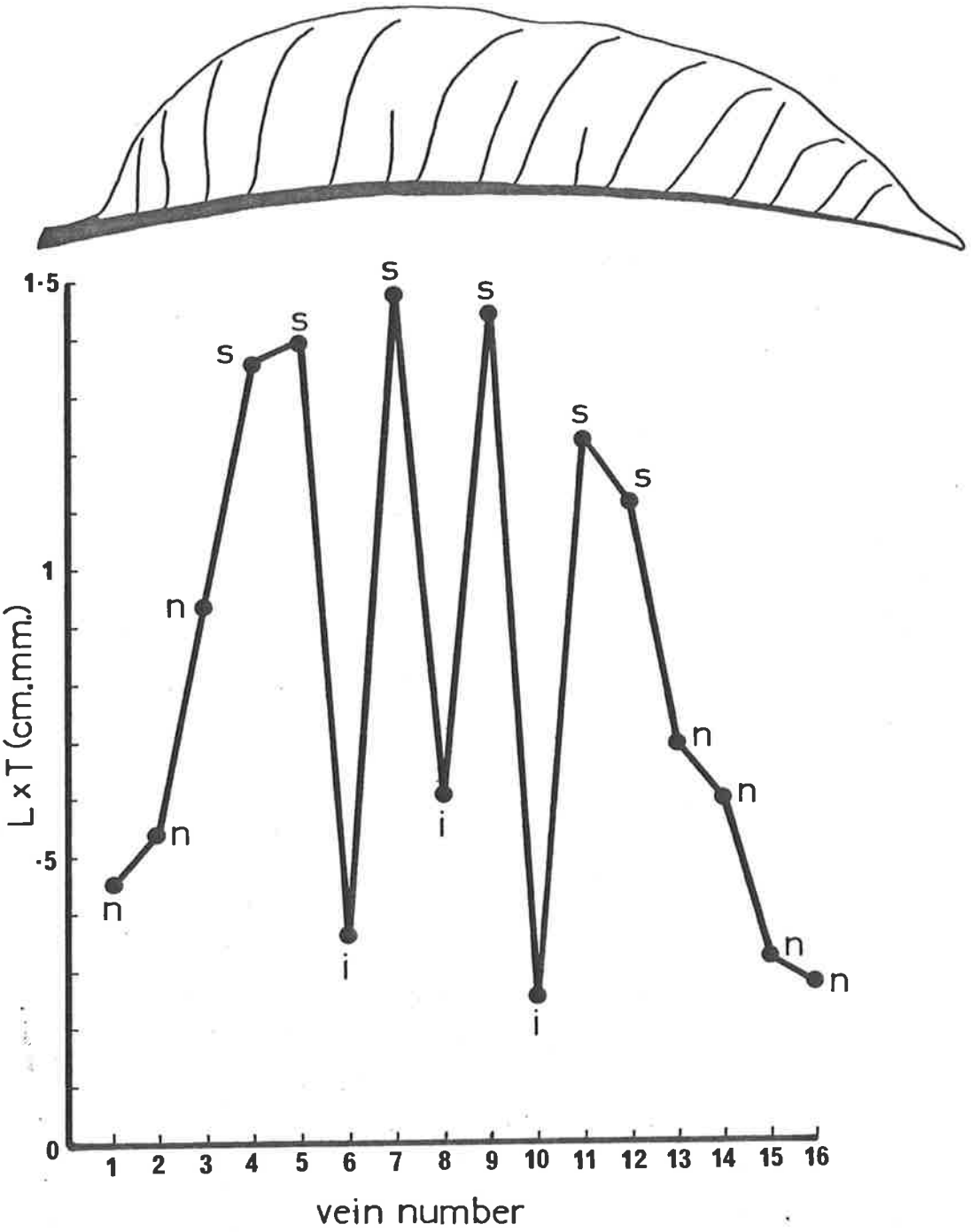
$|A| = 7.97$

$P = \frac{16}{9.5} \times \frac{1.23}{7.97} \times 100\% = 26.0\%$

$\therefore M_7 = 1.48 - 0.38 = 1.10$

Note that vein numbers 1-3 and 13-16 are neither secondary nor intersecondary veins, according to (11).

FIGURE 2.3. Graph of vein number against (L x T) for one side of the primary vein of a leaf of Rhodosphaera rhodanthema. A drawing of the leaf is also given. (Relative thicknesses of veins are not shown, s = secondary vein, i = intersecondary vein, n = nonsecondary vein).

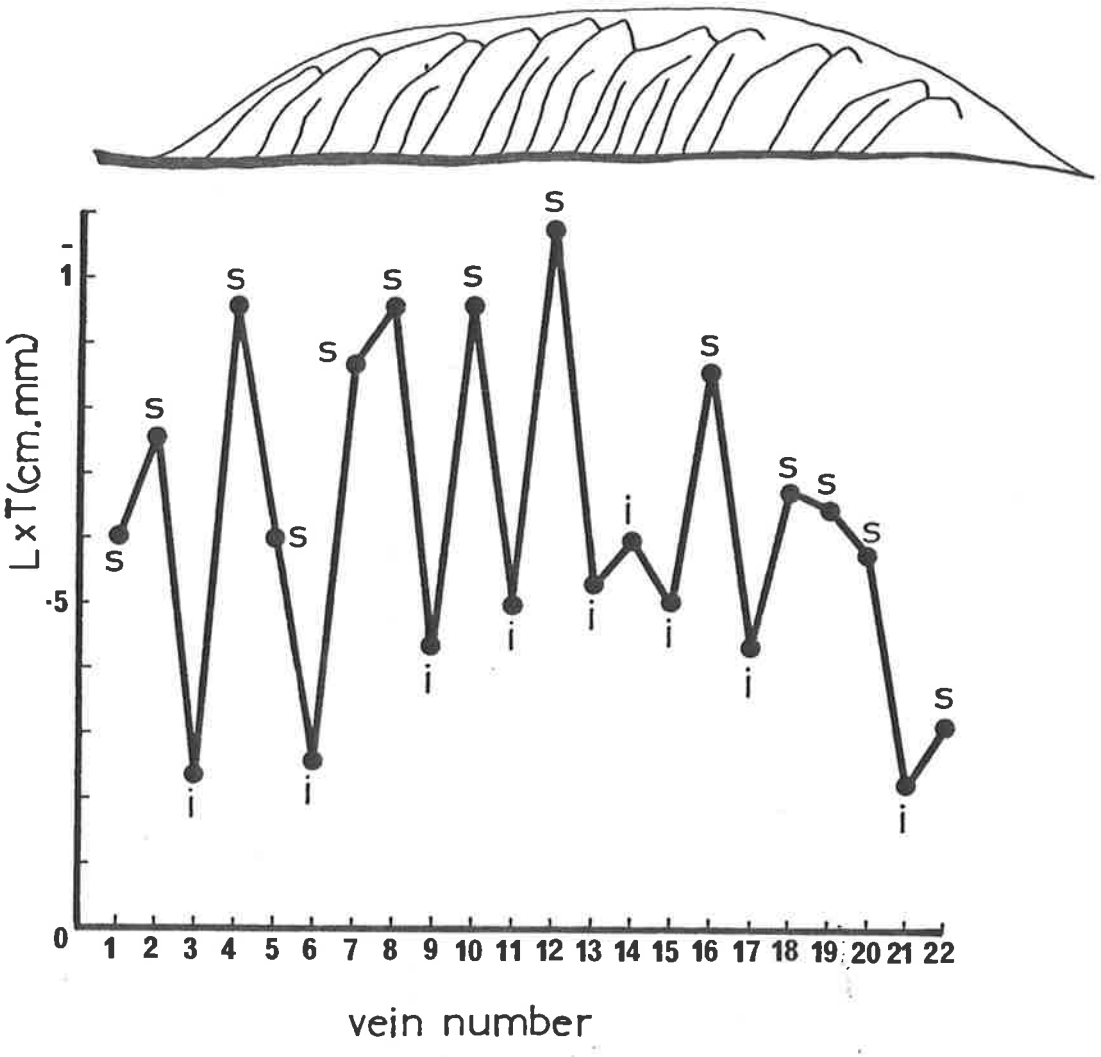

1·5
1
·5
0
L x T (cm.mm.)
n
n
n
s
s
i
s
i
s
i
s
s
n
n
n
n
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
vein number

EXAMPLE 3: Pittosporum undulatum (fig. 2.4)

Vein number	(L x T) (cm.mm)		Vein Order
1	0.60	$L \times T > M_2$	Secondary
2	0.76	$L \times T > N_3$; $M_2 = 0.59$	"
3	0.23	$L \times T < M_4$; $N_3 = 0.28$	Intersecondary
4	0.96	$L \times T > M_5$; $M_4 = 0.74$	Secondary
5	0.60	$L \times T > N_6$; $M_5 = 0.46$	"
6	0.26	$L \times T < M_7$; $N_6 = 0.32$	Intersecondary
7	0.87	$L \times T > M_8$; $M_7 = 0.67$	Secondary
8	0.96	$L \times T > N_9$; $M_8 = 0.74$	"
9	0.43	$L \times T < M_{10}$; $N_9 = 0.53$	Intersecondary
10	0.96	$L \times T > N_{11}$; $M_{10} = 0.74$	Secondary
11	0.50	$L \times T < M_{12}$; $N_{11} = 0.61$	Intersecondary
12	1.08*	$M_{12} = 0.83$	Secondary
13	0.53	$L \times T < M_{12}$; $N_{13} = 0.65$	Intersecondary
14	0.60	$L \times T < N_{13}$; $N_{14} = 0.74$	"
15	0.50	$L \times T < N_{14}$; $N_{15} = 0.61$	"
16	0.87	$L \times T > N_{15}$; $M_{16} = 0.67$	Secondary
17	0.43	$L \times T < M_{16}$; $N_{17} = 0.53$	Intersecondary
18	0.68	$L \times T > N_{17}$; $M_{18} = 0.53$	Secondary
19	0.65	$L \times T > M_{18}$; $M_{19} = 0.50$	"
20	0.58	$L \times T > M_{19}$; $M_{20} = 0.45$	"
21	0.22	$L \times T < M_{20}$; $N_{21} = 0.27$	Intersecondary
22	0.32	$L \times T > N_{21}$	Secondary

* greatest (L x T) value. Therefore, vein 12 is defined as a secondary.

FIGURE 2.4. Graph of vein number against (L x T) for one side of the primary vein of a leaf of Pittosporum undulatum. A drawing of the leaf is also given. (Relative thicknesses of veins are not shown, s = secondary vein, i = intersecondary vein).


L x T (cm. mm)
1
·5
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
vein number

$$R = 1.08-0.22 = 0.86$$

$$|A| = 7.26$$

$$P = \frac{22}{11.5} \times \frac{0.86}{7.26} \times 100\% = 22.7\%$$

$$\therefore M_{12} = 1.08-0.25 = 0.83$$

After some practice this method was found to be easy to apply and consistent in its results. Steps (1) and (2) can be quickly and accurately estimated without making any measurements and the lengths of the veins are required for the character set to be described later. When the thickness of the lateral veins at the point of insertion onto the primary vein are difficult to judge, the thickness should be measured as close as is practical to the primary vein, as long as it is consistent for all lateral veins.

Tertiary veins: For the character set in this study the only tertiary veins measured are those at the position of maximum width. On each side of the primary vein, the vein closest to the point halfway between the primary vein and the margin, which runs between secondary veins (or a secondary and the primary) was arbitrarily chosen as a tertiary vein.

Without using extremely involved definitions, it is impossible to accurately define vein orders higher than secondaries. For many palaeobotanical studies any veins finer than secondaries or intersecondaries are often unreliable. It is therefore proposed that higher vein orders should not be used as primary characters in fossil studies. With extant leaves primary, secondary, and possibly tertiary veins may be studied along with the ultimate venation, but any attempt to define higher vein orders is not recommended.

4.4 CHARACTER SET: *(1) Leaf length: The distance from the leaf apex to the point of insertion of the petiole, measured along the primary vein. This is approximately equal to the

straight line distance ab (fig. 2.5)

*(2) Leaf width: Maximum width of the leaf measured perpendicular to the primary vein, (fig. 2.5, cd).

*(3) Leaf length:width ratio: (fig. 2.5, ab/cd).

(4) Leaf shape index: A method for expressing leaf shape using a standard grid. The average perpendicular distance from the primary vein to the margin is measured as a percentage of the maximum width. A circular grid with lines marked at set angles (fig. 2.7) is placed over the leaf so that the 90^{o}-270^{o} axis lies at the maximum width of the leaf and the origin lies over the primary vein. The perpendicular distance from the primary vein to the intercept of each line with the margin is measured, giving 36 measurements. The shape index is calculated as: Shape index = 200M/W;

where M = mean perpendicular distance from the midrib to the margin and W = maximum width of the leaf.

Since the shape index measures average leaf width as a percentage of maximum leaf width, it is not directly related to leaf size. Width is measured to the primary vein rather than the 0^{o} - 180^{o} axis so that any curvature of the leaf does not influence the result. The angles for this grid were chosen after experimenting on a number of different leaf types. The combination chosen most often gives approximately equal spacing of intercepts around the margin. If a line intercepts the margin in more than one place (e.g. in a lobed leaf), the most meaningful result is obtained by only considering the intercept furthest from the origin, since this intercept best represents the width of the leaf.

*(5) Base angle: The angle between lines joining the intersections with the margin of the axis of 20% maximum width basally and the base (fig. 2.5, the angle between nb

FIGURE 2.5. Drawing of an angiosperm leaf showing primary and secondary venation. The characters measured on this leaf are explained in the text.

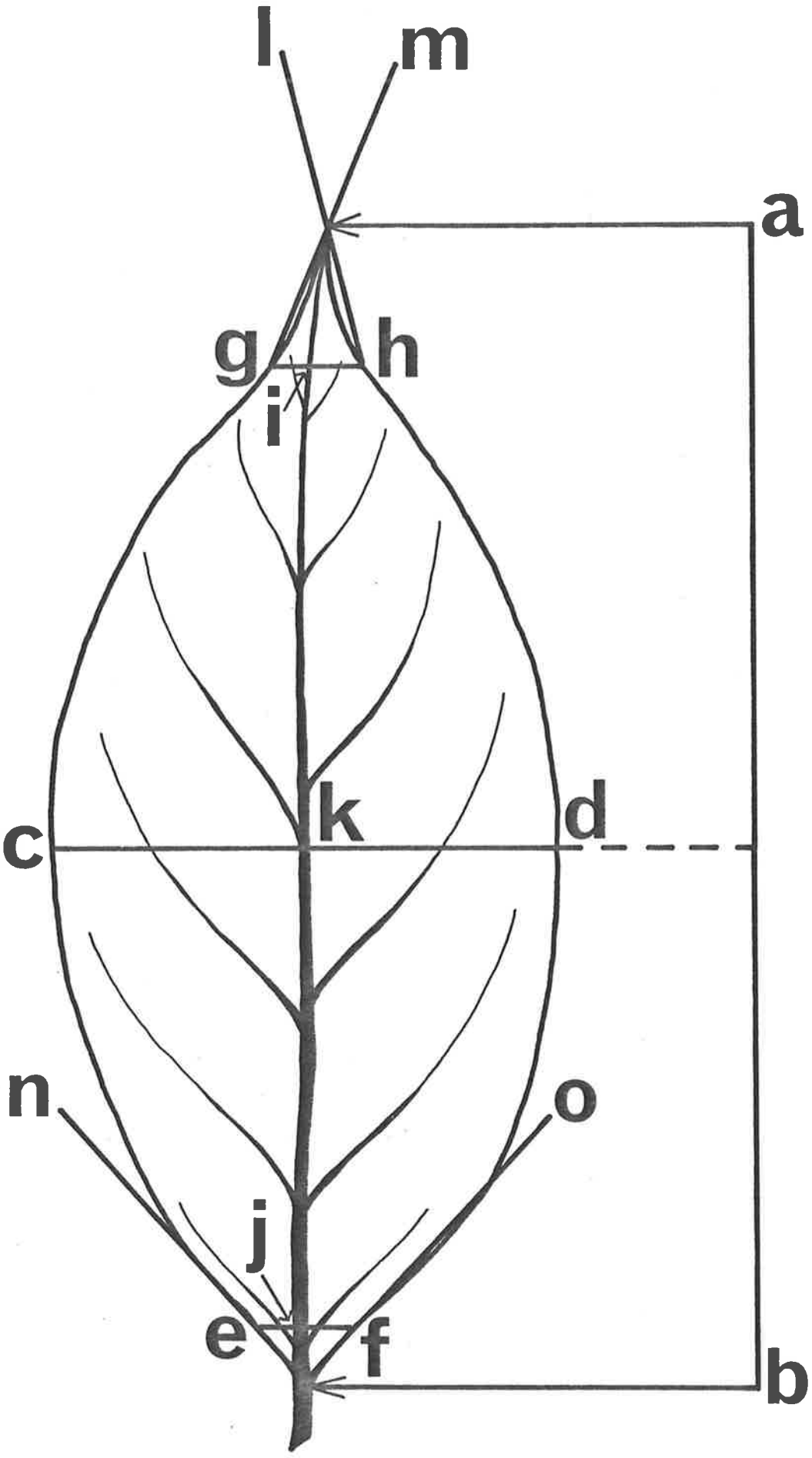

l
m
a
g
h
i
k
c
d
n
o
j
e
f
b

FIGURE 2.6. Section of an angiosperm leaf showing two secondary veins and part of the primary vein. The characters measured on these veins are explained in the text.

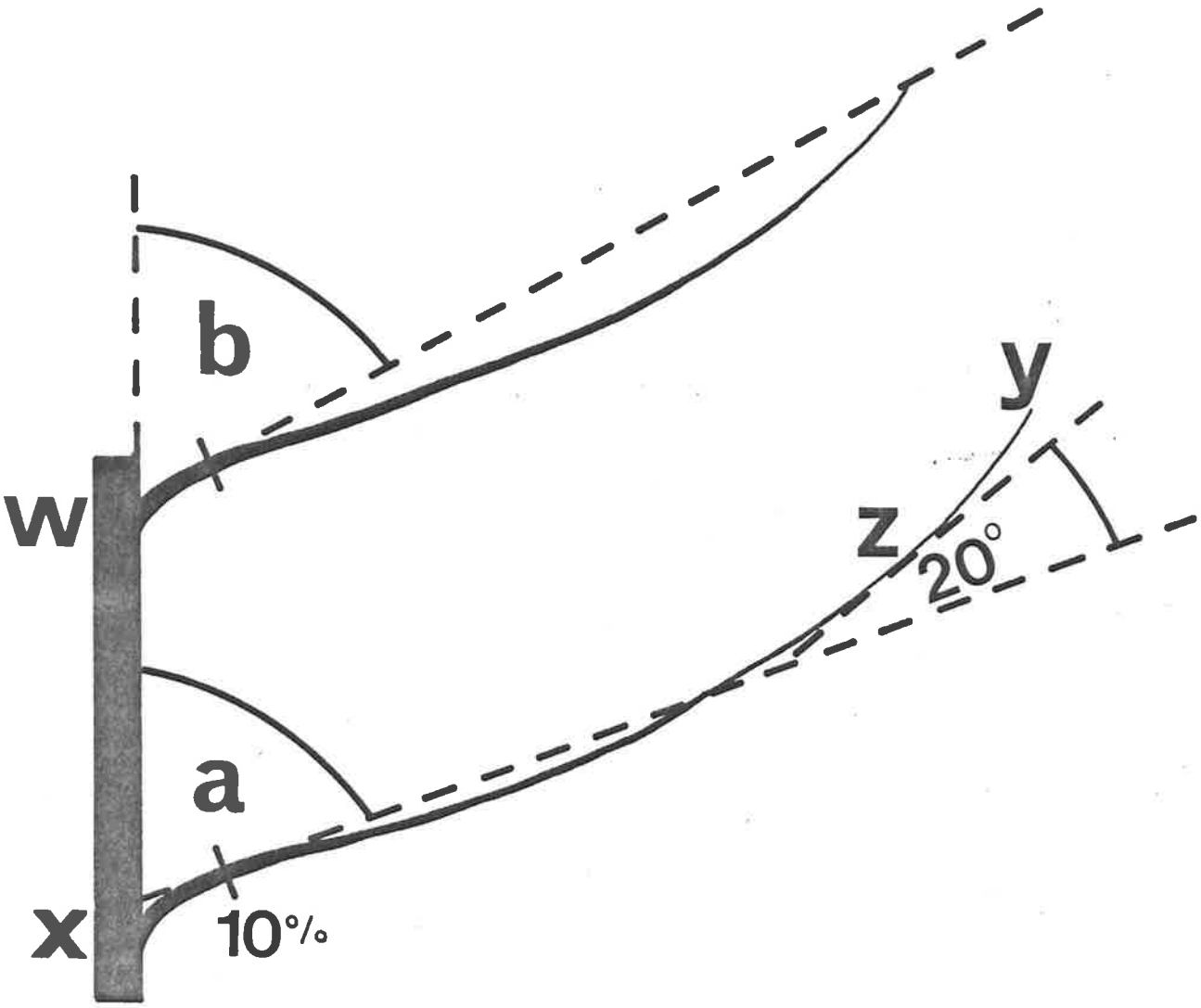
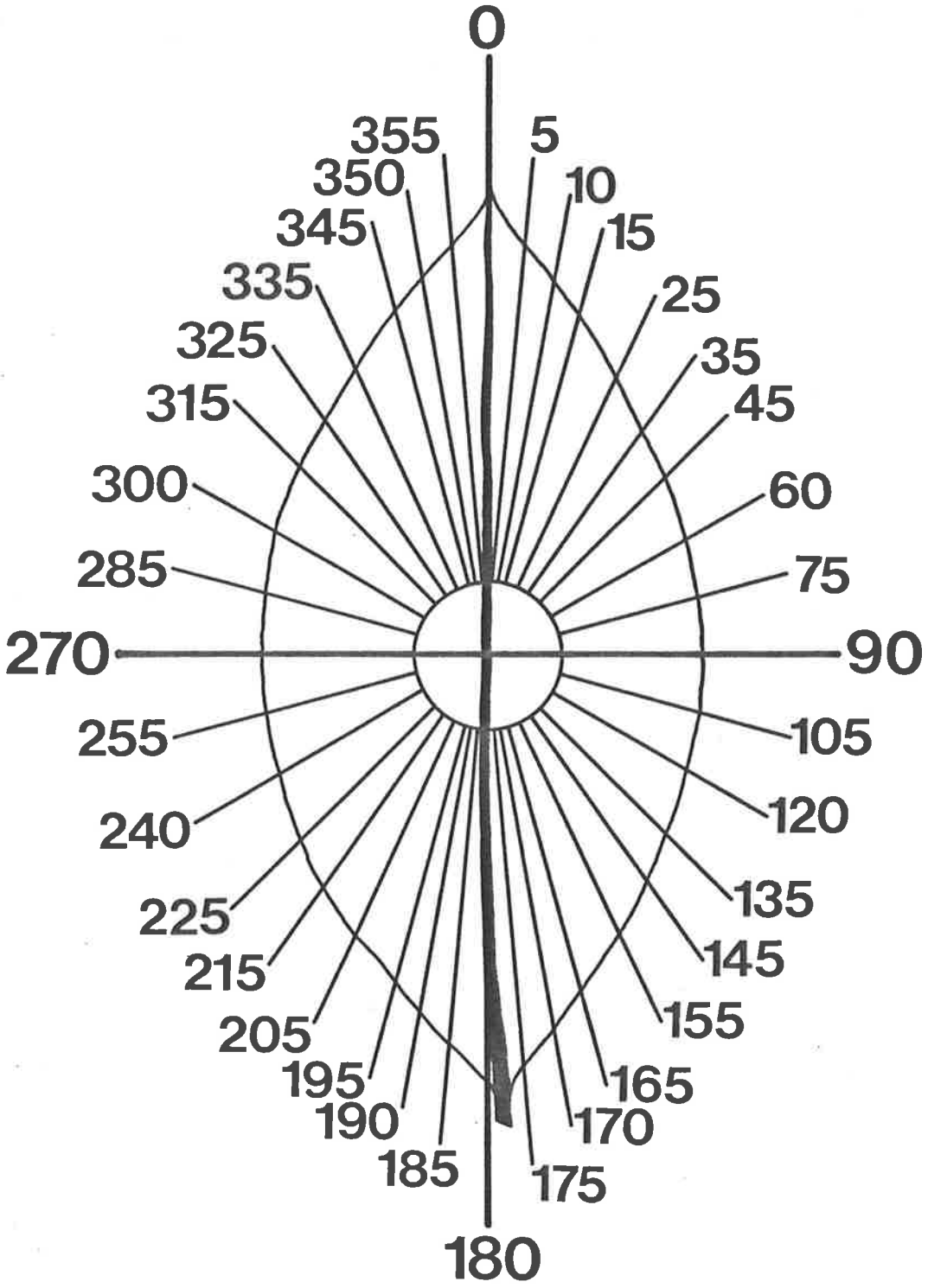

b
w
y
z
20°
a
x
10%

FIGURE 2.7. Drawing of an angiosperm leaf showing the grid used for measuring leaf shape index. The number on each line refers to the angle of that line from the perpendicular to the axis of maximum width in a clockwise direction. See text for an explanation of the measurement of leaf shape index.


0
355
5
350
10
345
15
335
25
325
35
315
45
300
60
285
75
270
90
255
105
240
120
225
135
215
145
205
155
195
165
190
170
185
175
180

and ob where b is the base of the leaf).

*(6) Apex angle: The angle between lines joining the intersections with the margin of the axis of 20% maximum width apically and the apex (fig. 2.5, the angle between la and ma).

*(7) Position of 20% maximum width basally: The distance from the base to the position of 20% maximum width basally expressed as a percentage of leaf length (fig. 2.5, jb/ab x 100).

*(8) Position of 20% maximum width apically: The distance from the apex to the position of 20% maximum width apically expressed as a percentage of leaf length (fig. 2.5, ai/ab x 100).

*(9) Number of secondary veins: Counted for both sides of the primary vein.

*(10) Secondary vein intercostal shape: The ratio of the length of a secondary vein to the distance between secondary veins measured along the primary vein (fig. 2.6, xy/wx).

*(11) Secondary vein angle A: The position of the adaxial 10% length of a secondary vein is located and a tangent to this point is drawn (fig. 2.6). The angle between the tangent and the primary vein is measured (fig. 2.6, angle a) and averaged for all secondary veins. The first 10% of the secondary vein is ignored to remove the effect of locally high curvature which often occurs at the junction of the secondary vein and the primary vein.

(12) Secondary vein angle B: The angle between the primary vein and the line joining the distal end of a secondary vein to the position of the 10% adaxial length (fig. 2.6, angle b). This angle is averaged for all

secondary veins.

(13) Secondary vein straightness index: A measure of the degree of curvature of secondary veins. The point where the tangent to the secondary vein first makes an angle of 20° with the tangent to the position of the adaxial 10% length of the secondary vein is located (fig. 2.6, z). The length of the secondary vein between this point and the midrib is then expressed as a percentage of the total length of the secondary vein and is averaged for all secondary veins. (Some secondary veins that never make an angle of 20° with the tangent will have a straightness index of 100%).

(14) Basal secondary vein angle: Measured as for (11), but only for the basal secondary vein on each side of the midrib. The basal secondary veins often have a makedly different angle to the other secondary veins.

(15) Intersecondary vein percentage: The number of intersecondary veins expressed as a percentage of the number of secondary veins.

(16) Marginal venation index: The number of free-ending veinlets between the areoles and the margin along 1 cm. of a leaf at the point of maximum width expressed as a ratio to the number of areoles ending at the margin in the same length (fig. 2.8, = 6/7).

(17) Tertiary vein angle: The adbasal angle between the projection of the lines joining the ends of a tertiary vein and the primary vein. One tertiary vein is measured on each side of the primary vein at the position of maximum width, halfway between the margin and the primary vein. The average of the two values is taken.

(18) Areole length: An areole is defined as the smallest unit enclosed by veins. The length is measured as

the longest axis of the areole (fig. 2.9, L).

(19) Areole width: The greatest perpendicular distance to areole length (fig. 2.9, W).

(20) Number of veinlets per areole: E.g., in fig. 2.8 there are 7 areoles and ten veinlets within them = 10/7 veinlets per areole.

(21) Number of branches per veinlet: Branches are counted as branching orders (fig. 2.10).

(22) Upper epidermal cell length: The longest axis of an upper epidermal cell, measured to the interface between adjacent cells.

(23) Upper epidermal cell width: The greatest perpendicular distance to upper epidermal cell length.

(24) Lower epidermal cell length: As for (22).

(25) Lower epidermal cell width: As for (23).

(26) Lower epidermal cell length:width ratio.

(27) Subsidiary cell number: Average number of subsidiary cells, measured for stomates on the lower epidermis. A subsidiary cell is defined as an epidermal cell in direct contact with a guard cell. This definition of subsidiary cell number is free of ontogenetic implications. Obviously some information is lost because of this, but it means that stomatal development does not have to be traced. More subtle differences in subsidiary cells such as relative size, shape, and orientation may be introduced as secondary characters.

(28) Stomatal index (SI): Measured for the lower epidermis.

The equation is:

$$SI = \frac{S}{E+S} \times 100.$$

where S = number of stomates in a given area, and

E = number of epidermal cells in the same area.

FIGURE 2.8. The ultimate venation at the margin of an angiosperm leaf. In distance d, seven complete areoles are shown, containing 10 veinlets. Six veinlets occur between the leaf margin and the areoles. See text for an explanation of the characters involving ultimate venation.

FIGURE 2.9. A single areole, showing the length (L) and width (W).

FIGURE 2.10. a - d represent four areoles, each containing one veinlet with different branching orders.

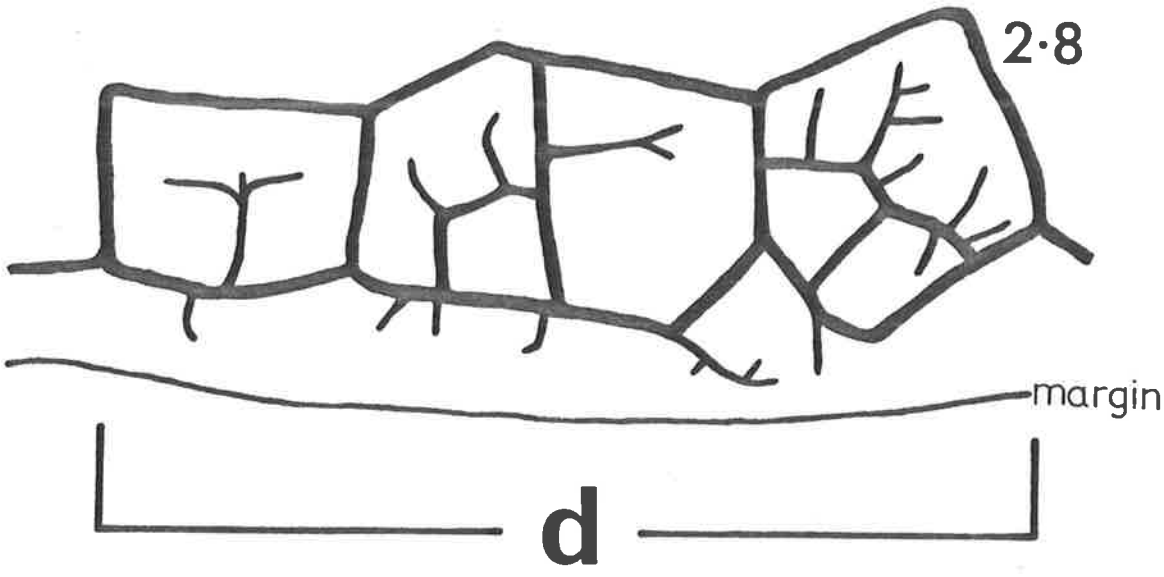
(a) The veinlet has no branches (highest branching order = 0).

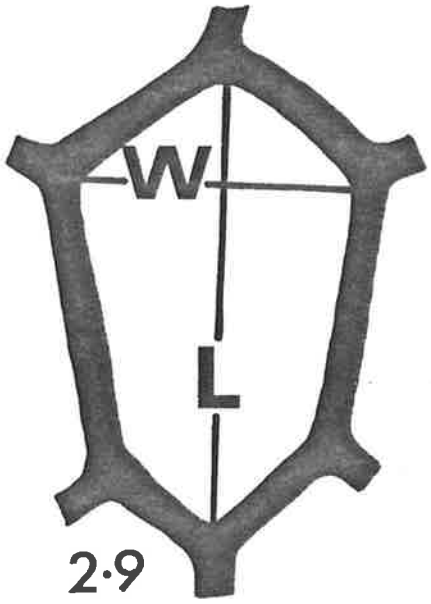
(b) The veinlet has one branch (highest branching order = 1).

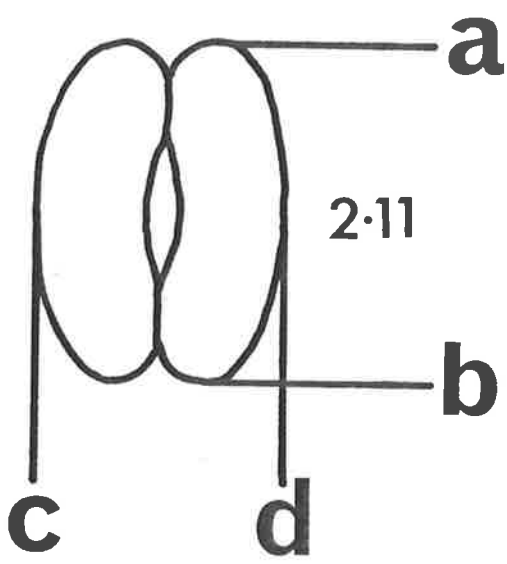
(c) The veinlet has two orders of branching (highest branching order = 2).

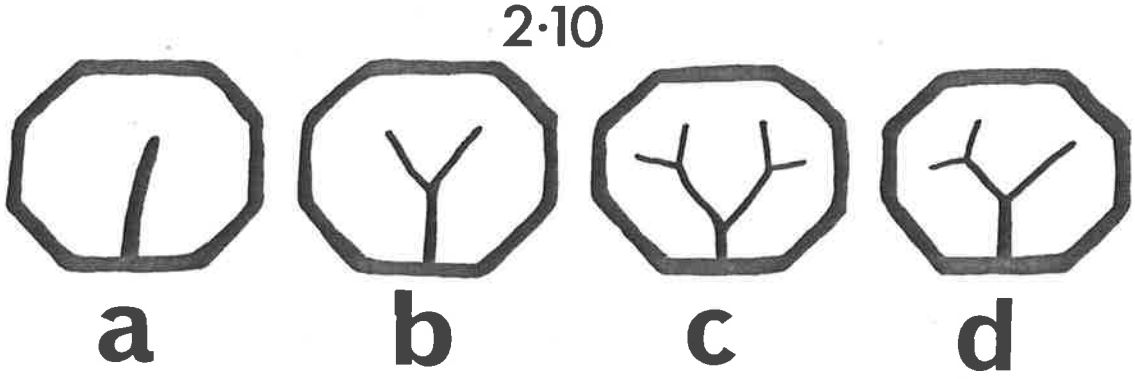
(d) The veinlet has two orders of branching. After the first branch, one of the branchlets remains undivided, but the other undergoes second order branching. The highest branching order is recorded (highest branching order = 2).

FIGURE 2.11. Stomate, showing the length (ab) and width (cd).


2·8
margin
d


W
L
2·9


a
2·11
b
c
d


2·10
a
b
c
d

(29) Stomatal length: The length of the stomate measured along the common wall between the guard cells (fig. 2.11, ab).

(30) Stomatal width: Greatest perpendicular distance to stomatal length (fig. 2.11, cd).

(31) Stomatal length:width ratio: (fig. 2.11, ab/cd).

*(32) Position of maximum width: The distance from the base to the position of maximum width measured along the primary vein expressed as a percentage of the leaf length (fig. 2.5, bk/ab x 100).

(33) Areole length:width ratio: (fig. 2.9, L/W).

(34) Upper epidermal cell length:width ratio.

*(35) Dentition frequency: Number of teeth per cm. counted for 10 cm. around the position of maximum width for both margins. This character was not used in the present study because most of the leaves were not serrate; so most OTU's would have scored 0 teeth/cm., making standardisation of this character impossible. It is listed here because it may be of use in other studies.

* Those characters marked with an asterisk were taken directly or modified from Blackburn (1978a).

Blackburn (1978a) discussed the value of his characters as discriminators and the interrelationship between characters at great length. Although the number of characters he used was relatively low, the amount of unique information in each one made them extremely good for discriminating species of Saurauia, and therefore they have been included in this study.

The cuticular characters are not as completely understood as the architectural characters. It is well documented that epidermal cell size is greatly affected by environment.

However, Stace (1965) indicated that cell size might be of taxonomic value because "polyploids usually have larger cells than diploids, although this is better shown by the stomata than other epidermal cells." Solereder (1908) noted that certain species are characterised by a particularly small- or large-celled epidermis and Stace (1965) substantiated this. For this reason, stomatal and epidermal cell length and width were included in this study.

The shape of epidermal cells is also variable as can be seen by the terminologies available (e.g. Dilcher 1974). An estimate of the shape of cells can be gained by considering the ratio of cell length:width. The use of length:width ratios is valuable for another reason. Stace (1965) noted that cell size usually decreased toward the leaf margin and apex. Although cuticles were normally sampled from the same place in every leaf, this cannot always be guaranteed in fossils due to the fragmentary nature of some specimens. However, Stace (1965) also noted that "Characters such as the comparative sizes of parts of the same leaf are extremely useful as the different parts are equally affected by the external conditions." Therefore these ratio characters should be relatively unaffected by the position on the leaf from which the cuticle was sampled.

Stomatal index has long been acknowledged as the best method of measuring the frequency of stomates. Salisbury (1927) found that of several environmental factors investigated, only humidity affected the value of stomatal index.

The leaves which were used in this study were collected from trees growing in close proximity to one another. Therefore, the environmental conditions under which the trees were growing will be reasonably constant. The same is

probably true of most fossil deposits although it can rarely be estimated how large an area the source vegetation may have covered. However, the environment of leaves on a single tree may change markedly, from those continually exposed at the crown of the tree ("sun" leaves) to those in continual shade beneath the canopy ("shade" leaves). Therefore any characters which are affected greatly by the environment should be applied with caution. F-ratios give a very good estimate of the value of the character as a discriminator, and these will be considered later.

4.5 CHARACTER SAMPLE SIZE: For most architectural characters sample size is determined by the OTU. However, for those characters where sample size is not set, it is desirable to find the minimum number of measurements which need to be taken for each character, so that the estimated value falls within predetermined confidence limits of the true value (i.e., $\bar{x}-h \leqslant x \leqslant \bar{x} + h$, where $\bar{x}$ = true mean, x = estimated mean, and h = maximum tolerated distance of x from $\bar{x}$).

The 95% confidence limits are given by:

$$x \pm t_{.05} SE_{\bar{x}}$$

where $SE_{\bar{x}}$ = standard error of $\bar{x}$,

and $t_{.05}$ can be found in t-distribution tables.

Therefore a sample size, n, must be chosen so that

$$t_{.05} SE_{\bar{x}} \leqslant h$$

i.e., $h \geqslant t_{.05} S/\sqrt{n}$

where S = standard deviation of $\bar{x}$ i.e.,

$$n \geqslant (St_{.05}/h)^2$$

where $t_{.05}$ has n-1 degrees of freedom.

Since $t_{.05}$ depends on n, the minimum value for n ($n=(St_{.05}/h)^2$) cannot be found directly but must be approached by trial and error.

As an example, the following question can be asked for lower epidermal cell length of OTU 1: How many readings should be taken to specify the length within 5% of the mean with 95% confidence? To give an accurate measure of the true mean and standard deviation, 100 readings were taken.

$\bar{x}$ = 24.0 µm S = 1.53 µm

$\therefore h = 1.2$ (5% of $\bar{x}$)

$n = (1.53t/1.2)^2 = 1.626t^2$

if t = 2, n = 6.504

but $t_{.05}$ with 6 d.f. = 2.447

so n = 9.736

but $t_{.05}$ with 9 d.f. = 2.262

so n = 8.320

but $t_{.05}$ with 7 d.f. = 2.365

so n = 9.095

but $t_{.05}$ with 8 d.f. = 2.306

so n = 8.646

which is the same as the previous answer. Therefore, the answer to the question is n = 9.

To specify the length within 2% of the mean with 95% confidence gives n = 41. These values were calculated for several characters over a range of species. Answers ranged between n = 4 (within 5% of the mean) to n = 61 (within 2% of the mean). A value of n = 25 was greater than all values of n within 5% of the mean and well within the range of

values within 2% of the mean. Therefore, when the number of readings was not specified by the character, 25 were made. This method was also used to determine a minimum area of 0.5 mm^2 for measurement of SI.

4.6 CHARACTER VARIATION: The identity of the OTU's was known prior to the analyses, and it was, therefore, possible to calculate F-ratios for each of the characters (table 2).

TABLE 2: F-ratios and their significance levels for the 34 characters scored. The character numbers follow those used in the text.

Character number	F-ratio (19, 4 d.f.)	Significance
1	5.12	$0.05<p<0.1$
2	20.41	$0.001<p<0.01$
3	8.86	$0.01<p<0.05$
4	13.89	$0.01<p<0.05$
5	28.21	$0.001<p<0.01$
6	15.82	$0.001<p<0.01$
7	15.46	$0.001<p<0.01$
8	16.42	$0.001<p<0.01$
9	16.07	$0.001<p<0.01$
10	5.42	$0.05<p<0.1$
11	11.20	$0.01<p<0.05$
12	27.80	$0.001<p<0.01$
13	13.89	$0.01<p<0.05$
14	5.67	$0.05<p<0.1$
15	10.86	$0.01<p<0.05$
16	14.99	$0.001<p<0.01$
17	4.37	$0.05<p<0.1$
18	19.24	$0.001<p<0.01$
19	13.35	$0.01<p<0.05$
20	6.62	$0.01<p<0.05$
21	4.13	$0.05<p<0.1$
22	20.68	$0.001<p<0.01$
23	11.63	$0.01<p<0.05$
24	61.49	$p<0.001$
25	34.74	$0.001<p<0.01$
26	4.11	$0.05<p<0.1$
27	181.75	$p<0.001$
28	10.29	$0.01<p<0.05$
29	59.11	$p<0.001$
30	60.32	$p<0.001$
31	21.81	$0.001<p<0.01$
32	2.25	$0.2<p<0.5$
33	1.89	$0.2<p<0.5$
34	1.64	$0.2<p<0.5$

Characters with $p\leq 0.1$ (10%) were chosen for the study. The normal significance level of 5% was not used because 9 characters would then have been rejected. Since the character

number is low, this was considered unnecessarily strict; so only 3 characters were rejected (nos. 32-34). Many characters proposed consisted of a ratio of two lengths. The validity of using these characters has been questioned (Atchley, Gaskins, and Anderson 1976). In this study characters were screened by means of F-ratios and correlation coefficients, and any ratio characters remaining were utilized.

4.7 RESULTS: The effects of several factors on the numerical analyses were considered. These will be presented in turn with a brief introduction to each section.

A. 100 OTUs with 31 characters: Both the UPGMA and ESS dendrograms (figs. 2.12, 2.13) show that the OTUs clustered into their species. Since both the UPGMA and ESS algorithms are space dilating, the use of phenon lines is invalid due to group size dependence (Clifford and Williams 1973; Clifford 1976). However, clusters are easily delimited without the use of phenon lines. For a positive result to this study, it is important that all members of a species cluster together. That is, it is better to have all members of two or more species in a single group than the members of one species spread throughout the dendrogram, since the latter is more likely to lead to misidentification. The intense clustering of the ESS algorithm makes interpretation of the dendrogram simpler, but both algorithms clustered the OTUs in a satisfactory way. In all future sections, only the ESS dendrogram is presented.

Closely related species do not consistently lie close together in figure 2.13. For example, Pittosporum undulatum (OTUs 61-65) and Hymenosporum flavum (OTUs 26-30) both in Pittosporaceae, lie very close to one another, while

FIGURE 2.12. UPGMA dendrogram for 100 OTUs with 31 characters (r = 0.52).

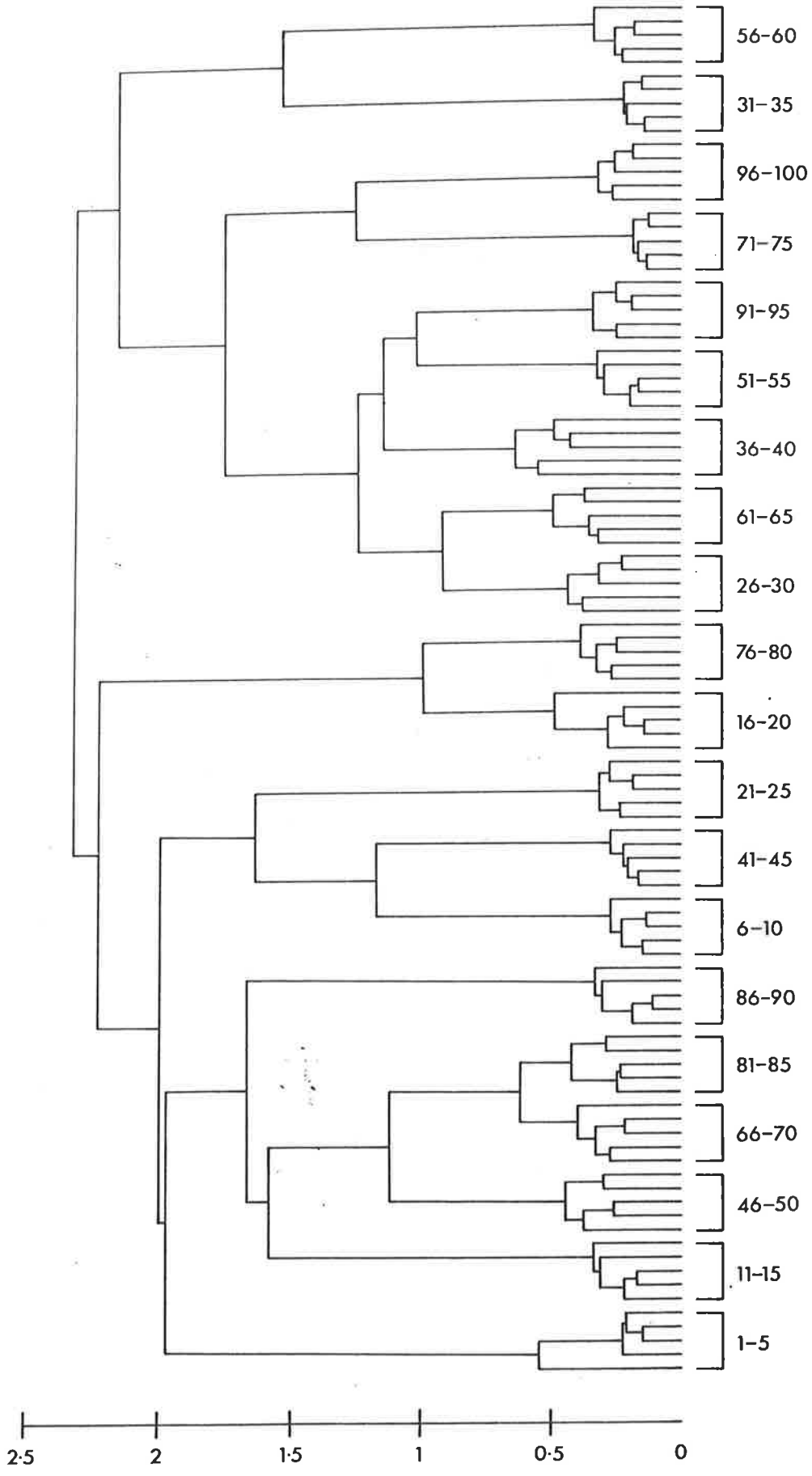
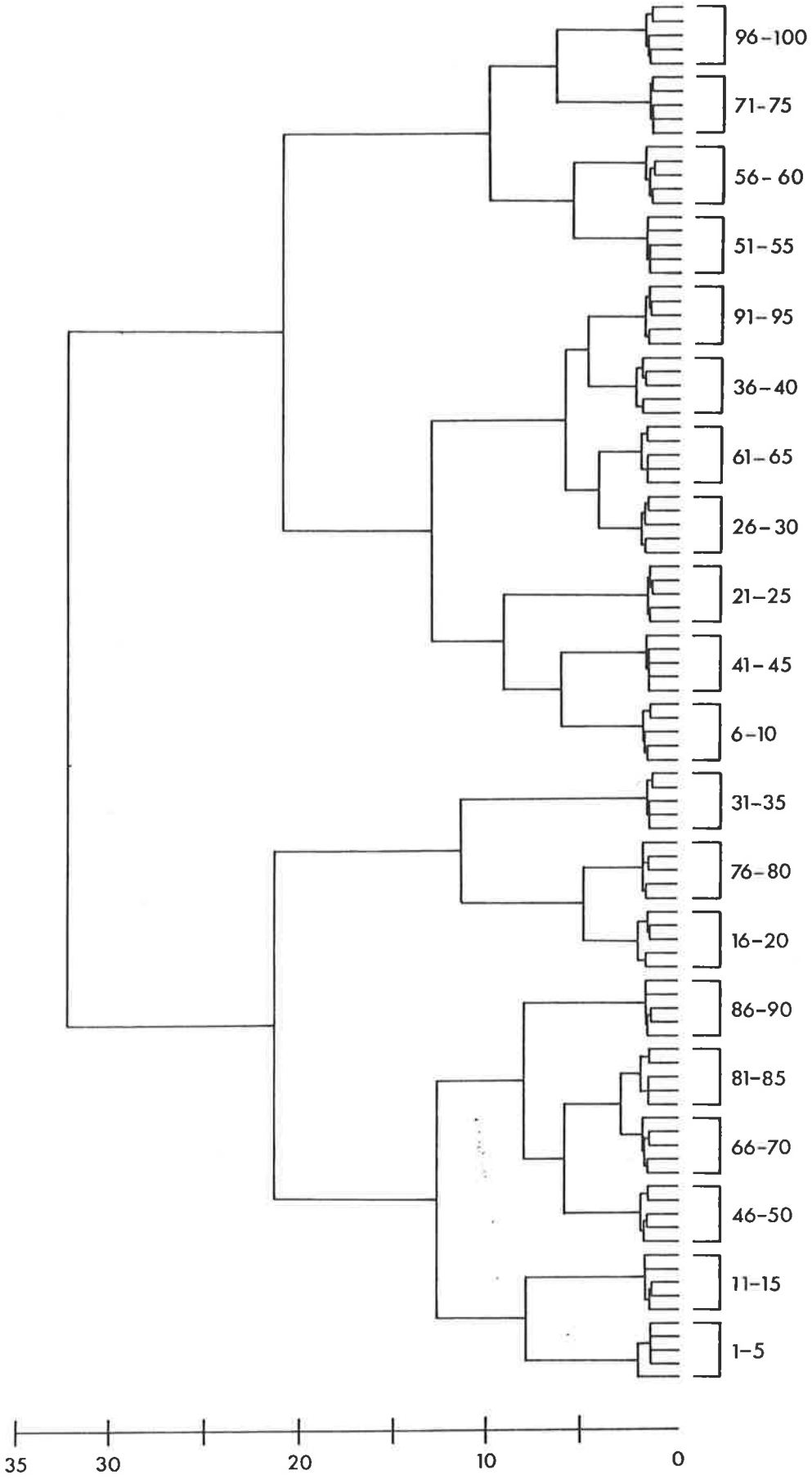

56-60
31-35
96-100
71-75
91-95
51-55
36-40
61-65
26-30
76-80
16-20
21-25
41-45
6-10
86-90
81-85
66-70
46-50
11-15
1-5
2·5
2
1·5
1
0·5
0

FIGURE 2.13. ESS dendrogram for 100 OTUs with 31 characters (r = 0.58).


96-100
71-75
56-60
51-55
91-95
36-40
61-65
26-30
21-25
41-45
6-10
31-35
76-80
16-20
86-90
81-85
66-70
46-50
11-15
1-5
35
30
20
10
0

Pittosporum rhombifolium (OTUs 76-80) is far removed. The character set was designed to cluster members of a single species, not to study relationships between species, genera, or families. Work by Blackburn (1978a) on a single genus (Saurauia) with many species, has shown that relationships between species can be estimated using leaf architecture. However, difficulties may arise when several unrelated genera are included for analysis, as would occur in a fossil deposit. This problem will be reconsidered later.

The stopping rule formulated in chapter 3 for estimating the number of groups in a dendrogram was applied to the ESS dendrogram shown in figure 2.13. Table 3 shows the values for the Ratkowsky and Lance (1978) criterion up to n = 5.

TABLE 3: Values of the Ratkowsky and Lance criterion for increasing values of n. The maximum value occurs at n = 4.

n	$\overline{C}$	$\frac{\overline{C}}{n^{\frac{1}{2}}}$
2	0.307	0.217
3	0.462	0.267
4	0.586	0.293
5	0.637	0.285

In this example all characters were numeric and so $S = \left(\frac{B}{T}\right)^{\frac{1}{2}}$ was used exclusively. According to the Ratkowsky and Lance criterion, the optimum number of groups is four. A phenon line has been drawn at that level in figure 2.14.

The results of calculating $\overline{C}$ for successive pairs of groups are shown in table 4.

FIGURE 2.14. ESS dendrogram from fig. 2.13. The phenon line (a) shows the 4 groups predicted by the Ratkowsky and Lance (1978) criterion. The other line (b) shows the 18 groups, numbered consecutively, predicted by the modification of the Ratkowsky and Lance (1978) criterion.

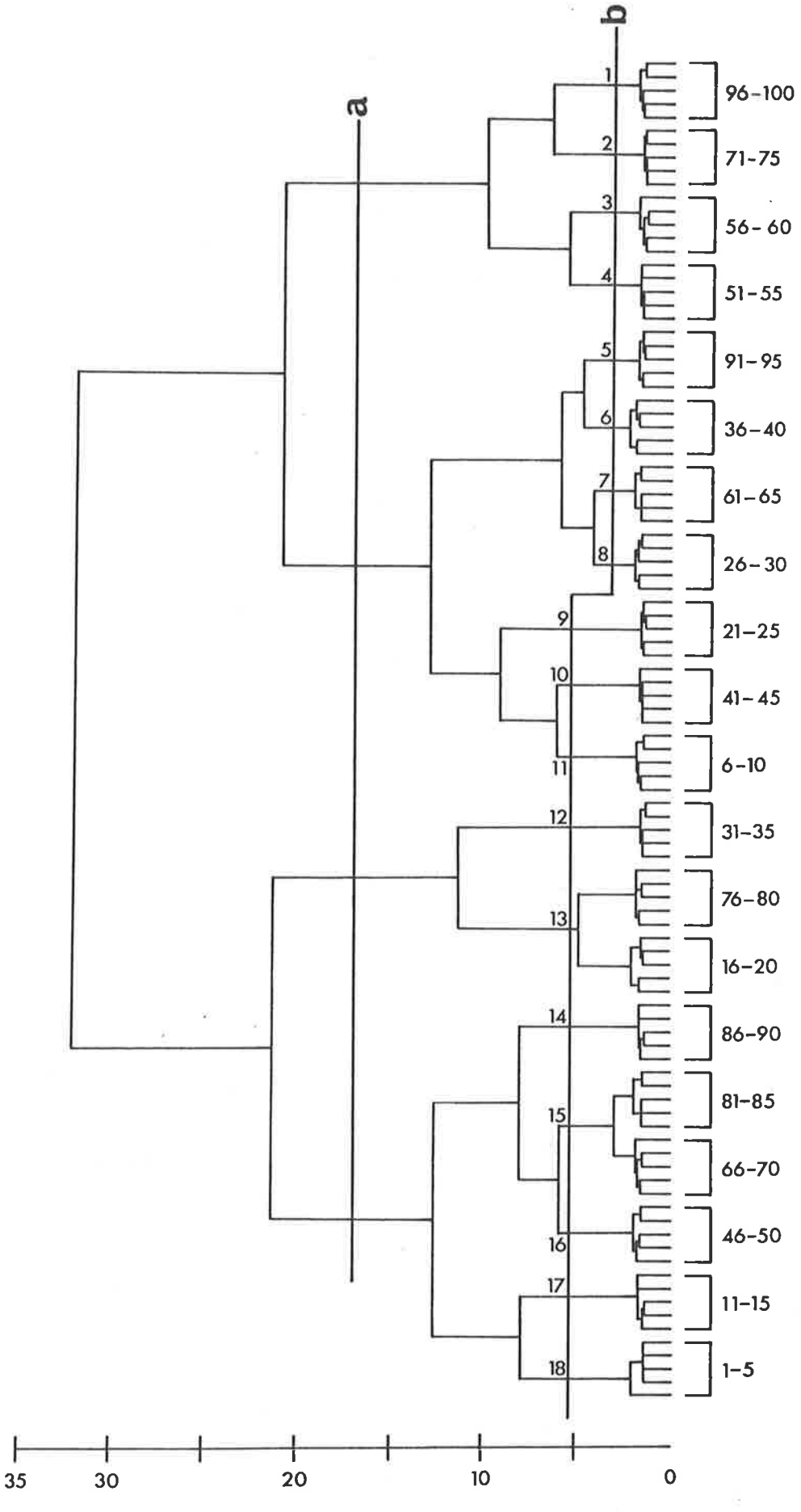

a
b
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
96-100
71-75
56-60
51-55
91-95
36-40
61-65
26-30
21-25
41-45
6-10
31-35
76-80
16-20
86-90
81-85
66-70
46-50
11-15
1-5
35
30
20
10
0

TABLE 4: Values of $\overline{C}$ for each successive pair of clusters, calculated until the maximum value of $\overline{C}$ is passed in each case. The cluster numbers refer to the numbers in fig.2.14(*= maximum value for each cluster).

Group Number	$\overline{C}_1$	$\overline{C}_2$	$\overline{C}_3$	$\overline{C}_4$	$\overline{C}_5$	$\overline{C}_6$
1	0.307	0.422	0.546	0.694*	0.423	
2	0.307	0.422	0.546	0.694*	0.474	
3	0.307	0.422	0.546	0.759*	0.385	
4	0.307	0.422	0.546	0.759*	0.424	
5	0.307	0.422	0.459	0.500	0.656*	0.489
6	0.307	0.422	0.459	0.500	0.656*	0.402
7	0.307	0.422	0.459	0.500	0.553*	0.424
8	0.307	0.422	0.459	0.500	0.553*	0.532
9	0.307	0.422	0.459	0.630*	0.385	
10	0.307	0.422	0.459	0.630	0.669*	0.432
11	0.307	0.422	0.459	0.630	0.669*	0.474
12	0.307	0.385	0.697*	0.328		
13	0.307	0.385	0.697*	0.651		
14	0.307	0.385	0.454	0.494*	0.427	
15	0.307	0.385	0.454	0.494	0.570*	0.495
16	0.307	0.385	0.454	0.494	0.570*	0.527
17	0.307	0.385	0.454	0.632*	0.312	
18	0.307	0.385	0.454	0.632*	0.427	

A total of 18 groups were delimited. These groups are shown in figure 2.14 and it should be noted that it is impossible to draw a phenon line to produce all 18 groups.

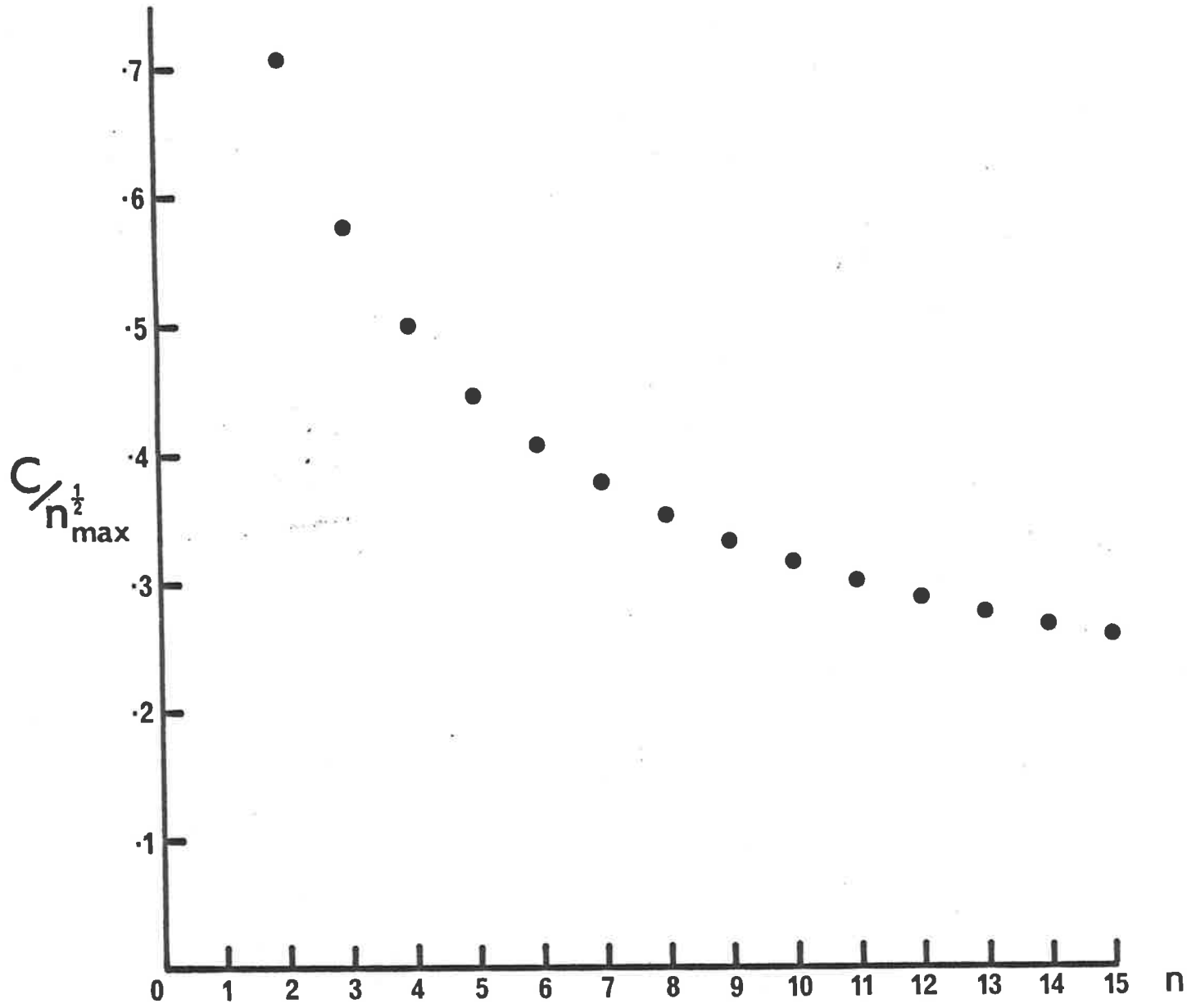
Although all 20 species are easily delimited in figure 2.13, the modified Ratkowsky and Lance criterion has only separated 18 groups. Two of these groups contain two

species (fig. 2.14). However, this result is more satisfactory than the Ratkowsky and Lance (1978) criterion, which delimited only four groups. This illustrates an unusual feature of the Ratkowsky and Lance criterion. Since the values of C and S are bounded by zero and unity, as n increases the maximum possible value of $C/n^{\frac{1}{2}}$ decreases. Figure 2.15 shows a graph of n against $C/n^{\frac{1}{2}}$ max.. The graph asymptotes to the positive X-axis. The decrease in the value of $C/n^{\frac{1}{2}}$ max. over the first few values of n is very marked. For example, from n = 2 to n = 5, $C/n^{\frac{1}{2}}$ max. decreases by 0.26 (0.707 to 0.447), compared with a further decrease of only 0.189 up to n = 15 (0.447 to 0.258). This substantial initial decrease in $C/n^{\frac{1}{2}}$ max. indicates that it is unlikely that $\overline{C}/n^{\frac{1}{2}}$ could reach its maximum value at high values of n because of its relatively low theoretical maximum. In the six examples given by Ratkowsky and Lance (1978), the optimum value of n was 2,3, or 4. The example given above (fig. 2.14) illustrates that a low value for n is not always the optimum result.

The modification to the Ratkowsky and Lance criterion suggested in this study has one drawback. In very small clusters, particularly with a low number of characters, the value of $\overline{C}$ can continue to increase until it has split the cluster into its individual OTUs. This is because small differences between OTUs take on relatively greater importance as group size decreases. This method should be considered as producing the maximum number of groups rather than the optimum number and other criteria may be necessary to fuse groups.

B. <u>100 OTUs with 17 characters</u> (highly correlated characters removed): Whenever a large number of characters are

FIGURE 2.15. Graph of n against $C/n^{\frac{1}{2}}$ max., up to n = 15.

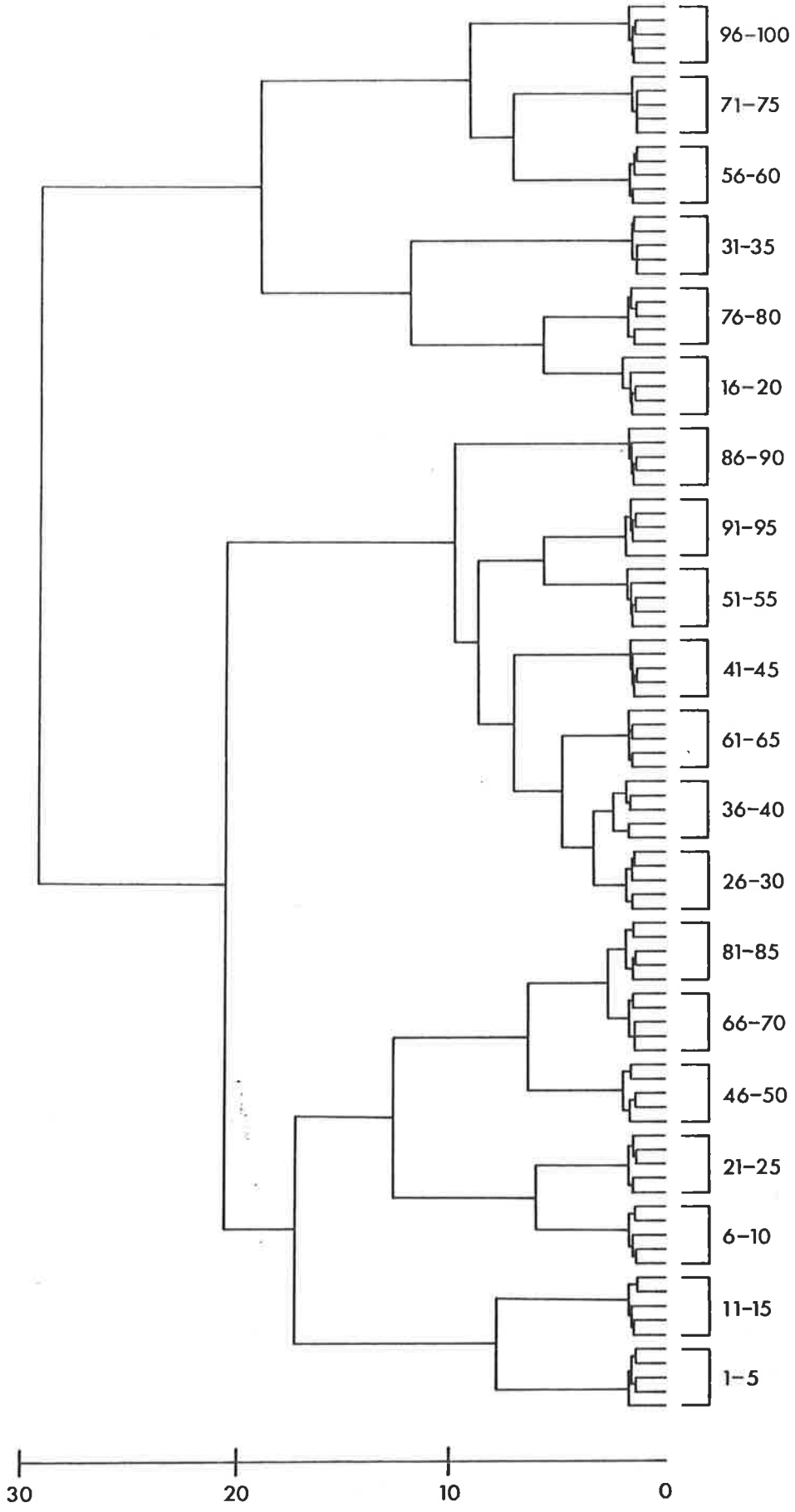

·7
·6
·5
·4
·3
·2
·1
$C/n^{\frac{1}{2}}_{max}$
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
n

measured on a single organ, it is expected that many significant correlations will be found between pairs of characters. The effect of character correlation has been subjected to many interpretations. Dolph (1976b) found that character correlations in Hickey's (1973) characters "limit the usefulness of the characters in taxometrically partitioning fossil leaf collections ..... and in carrying out comparisons between fossil and modern leaf taxa." According to Rohlf (1967), the major effect of using correlated characters was that phenetic clusters became elongated. Sneath and Sokal (1973 p. 106) suggested that even highly correlated characters should be included since they assumed at least some independent sources of variation in any empirical correlation.

To test the effect of correlated characters in this study, the 14 most highly correlated characters were removed. With the Pearson product-moment correlation coefficients for characters 1 to 31, for a 5% level of significance the correlation coefficient is approximately 0.195. If this level of significance has been chosen, all characters would have been deleted (Appendix I). Instead a value of $r>0.6$ was selected, and where a pair of characters had an r value within this range, the character with the lowest F-ratio was deleted. By this method, characters 2,4, 5,9,12,17,19,21-25,28, and 30 were removed.

The ESS dendrogram (fig. 2.16) again shows that the OTUs have grouped into their species. However the dendrogram drawn from all 31 characters (fig. 2.13) gave better definition of the groups. Removal of highly correlated characters did not improve the interpretation of the relationship between species. This suggested that it was

FIGURE 2.16. ESS dendrogram for 100 OTUs with 17 characters (r = 0.51).

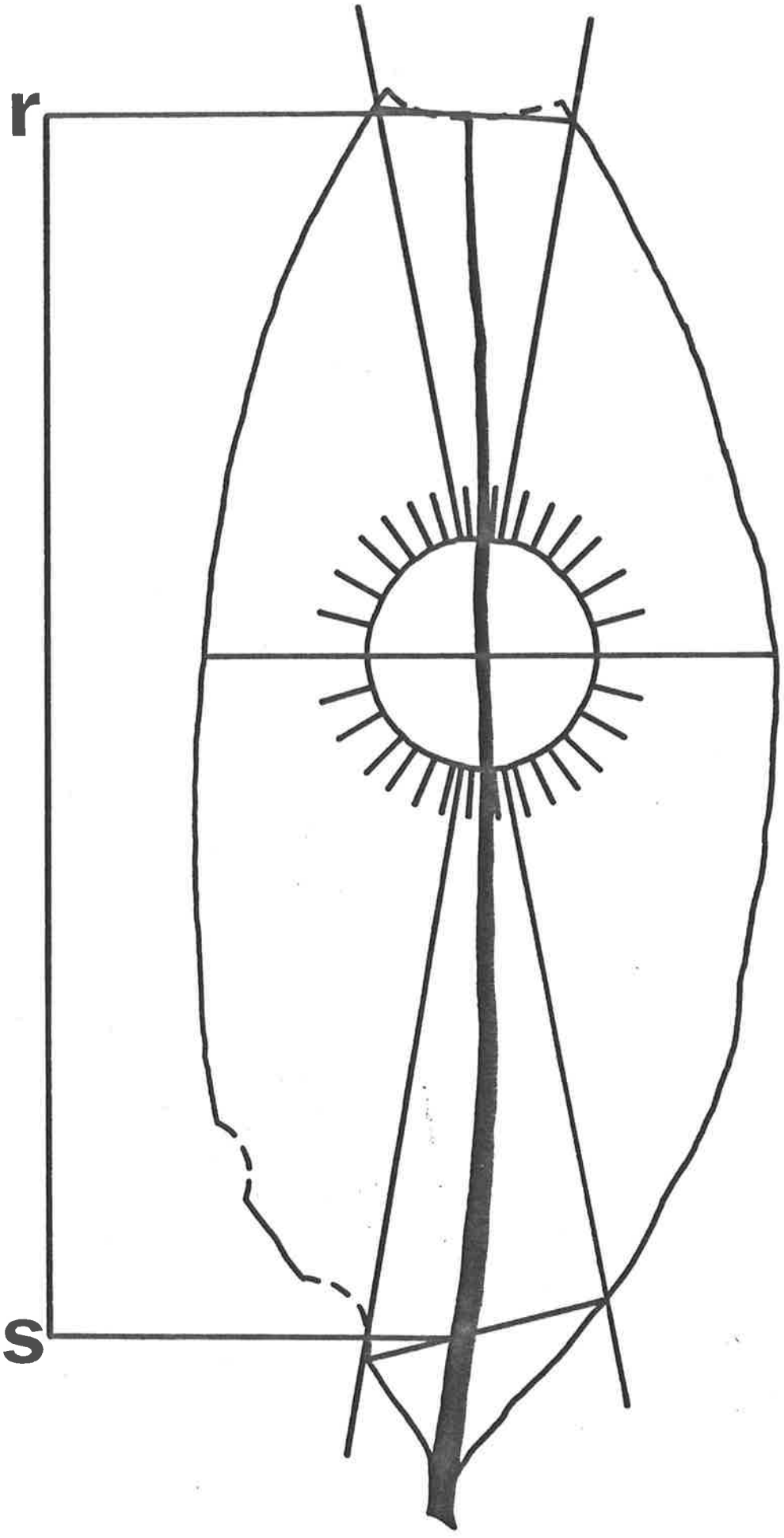

96-100
71-75
56-60
31-35
76-80
16-20
86-90
91-95
51-55
41-45
61-65
36-40
26-30
81-85
66-70
46-50
21-25
6-10
11-15
1-5
30
20
10
0

better to include as many characters as possible. Firstly, the total number of character (31) is low, and by removing 14 characters, the number becomes lower than is usually acceptable in numerical taxonomy. Secondly, the information content in those 14 characters outweighs any deleterious aspects of correlation since the analysis utilising all the characters most clearly separates the OTUs into the expected groups.

C. 100 OTUs with 14 architectural characters: In many fossil deposits cuticles are either poorly preserved or absent. These floras must be classified using architectural characters. Of the 31 characters in this study, 21 are architectural. Five of the architectural characters will be impossible to measure on most fossils due to lack of preservation of ultimate venation patterns (characters 16 and 18 - 21). The base and apex angles of the leaves will be difficult to measure in many cases because of incomplete specimens.

Often the entire length of a leaf is not preserved, and it is difficult to extrapolate the margin accurately to estimate length. Of the 14 remaining architectural characters, seven require the total length of the leaf to be preserved. After experimenting on leaves from three fossil floras, a solution was found which should be applicable in most deposits. If the position of maximum width of the leaf is located, the leaf shape index grid may be placed over the leaf (fig. 2.17). If the intercept of the 10^{o} lines with the leaf margin (i.e. 10^{o}, 170^{o}, 190^{o}, 350^{o}) are connected at the base and apex, a modified length of the leaf can be defined as the distance along the primary vein between the two intercepts (fig. 2.17, rs). This length can then be substituted for total leaf length where required. This definition of

FIGURE 2.17. Fossil angiosperm leaf with the apex missing. The grid for measuring leaf shape index has been placed over this leaf and the 10^{o} lines extrapolated to the margin (i.e., lines with angles of 10^{o}, 170^{o}, 190^{o}, 350^{o}). The modified leaf length is given by rs.


r
s

modified leaf length makes no assumptions about total leaf length and only requires the maximum width of the leaf to be preserved. If the 10^{o} lines do not intercept the margin because too much of the leaf is missing, then generally that leaf is too incomplete for the architectural characters defined in this study to be applied.

The ESS dendrogram produced from the 14 architectural characters (fig. 2.18) did not group all the OTUs into their correct species. Three or more OTUs representing one species in a group are defined as representing the "nucleus" of that species. Using this definition, three OTUs (36, 81 and 85) are misidentified in figure 2.18. However, it is likely that OTUs 36, 82-84, 66-70, 81 and 85 in figure 2.18 would be interpreted as a single group, meaning that only OTU 36 is misidentified.

D. 100 OTUs with 31 characters and missing data: Missing data are a problem which is especially pertinent to palaeobotanists. To test the effect of missing data, a random sample of 100 specimens from the Nerriga deposit was selected; for each one those of the 31 characters which could not be measured was noted (tables 5,6).

TABLE 5: Number of characters with missing data for each of the 100 random specimens from Nerriga.

No. of characters with missing data:	0	1	2	3	4	5	6	7
No. of specimens:	4	0	0	0	0	5	0	2
No. of characters with missing data:	8	9	10	11	12	13	14	15
No. of specimens:	1	0	4	0	5	2	3	4
No. of characters with missing data:	16	17	18	19	20	21		
No. of specimens:	20	8	5	13	13	11		

FIGURE 2.18. ESS dendrogram for 100 OTUs with 14 architectural characters (r = 0.52).

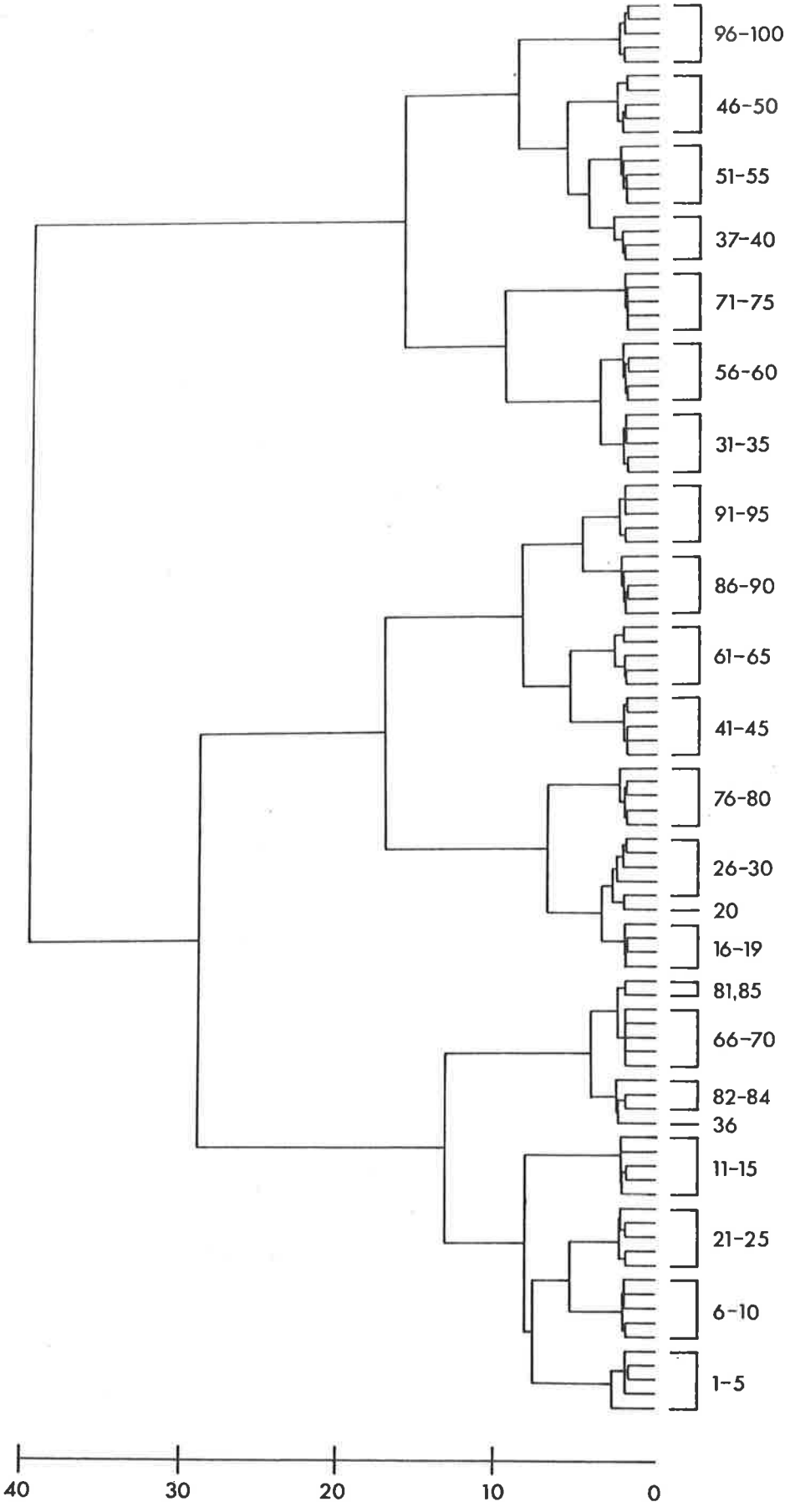

96-100
46-50
51-55
37-40
71-75
56-60
31-35
91-95
86-90
61-65
41-45
76-80
26-30
20
16-19
81,85
66-70
82-84
36
11-15
21-25
6-10
1-5
40
30
20
10
0

TABLE 6: Percentage of specimens with missing data for the 100 specimens from Nerriga.

Character number:	1	2	3	4	5	6	7	8	9	10
% of OTU's with missing data:	89	84	65	79	78	85	86	86	86	70
Character number:	11	12	13	14	15	16	17	18	19	20
% of OTU's with missing data:	85	63	63	63	0	0	0	0	0	0
Character number:	21	22	23	24	25	26	27	28	29	30
% of OTU's with missing data:	48	89	78	86	39	63	63	0	0	0
Character number:	31									
% of OTU's with missing data:	0									

This proportion of missing data was then transferred to the 100 extant OTUs. A coefficient of relevance, R, was calculated for pairs of OTUs, where $R_{j,k} = a_{j,k}/n$ ($a_{j,k}$ is the number of characters applicable in OTU j that are also applicable in OTU k, and n is the number of characters in the study (Sneath and Sokal 1973 p. 278)). The R values for several OTUs with missing data are given in table 7. The amount of missing data is high (1,548 out of 3,100 character scores, or 49.94%).

TABLE 7: Coefficients of relevance for 20 of the 100 OTUs.

OTU No.	1	6	11	16	21	26	31	36
6	0.52							
11	0.52	0.74						
16	0.52	0.74	0.77					
21	0.39	0.39	0.39	0.39				
26	0.39	0.39	0.39	0.39	0.39			
31	0.39	0.39	0.39	0.39	0.39	0.39		
36	0.35	0.35	0.35	0.35	0.35	0.35	0.35	
41	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
46	0.39	0.39	0.39	0.39	0.32	0.32	0.32	0.32
51	0.48	0.32	0.32	0.32	0.32	0.32	0.32	0.32
56	0.39	0.39	0.39	0.39	0.32	0.32	0.32	0.32
61	0.58	0.42	0.35	0.42	0.35	0.35	0.35	0.32
66	0.48	0.32	0.32	0.32	0.32	0.32	0.32	0.32
71	0.48	0.32	0.32	0.32	0.32	0.32	0.32	0.32
76	0.45	0.45	0.45	0.45	0.39	0.39	0.39	0.35
81	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
86	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
91	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
96	0.55	0.39	0.39	0.32	0.32	0.32	0.32	0.32

	41	46	51	56	61	66	71	76
46	0.32							
51	0.32	0.32						
56	0.32	0.39	0.32					
61	0.32	0.35	0.48	0.35				
66	0.32	0.32	0.48	0.32	0.32			
71	0.32	0.32	0.48	0.32	0.32	0.48		
76	0.32	0.35	0.32	0.35	0.32	0.32	0.32	
81	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
86	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
91	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
96	0.32	0.35	0.48	0.39	0.32	0.48	0.48	0.35

	81	86	91
86	0.32		
91	0.32	0.32	
96	0.32	0.32	0.32

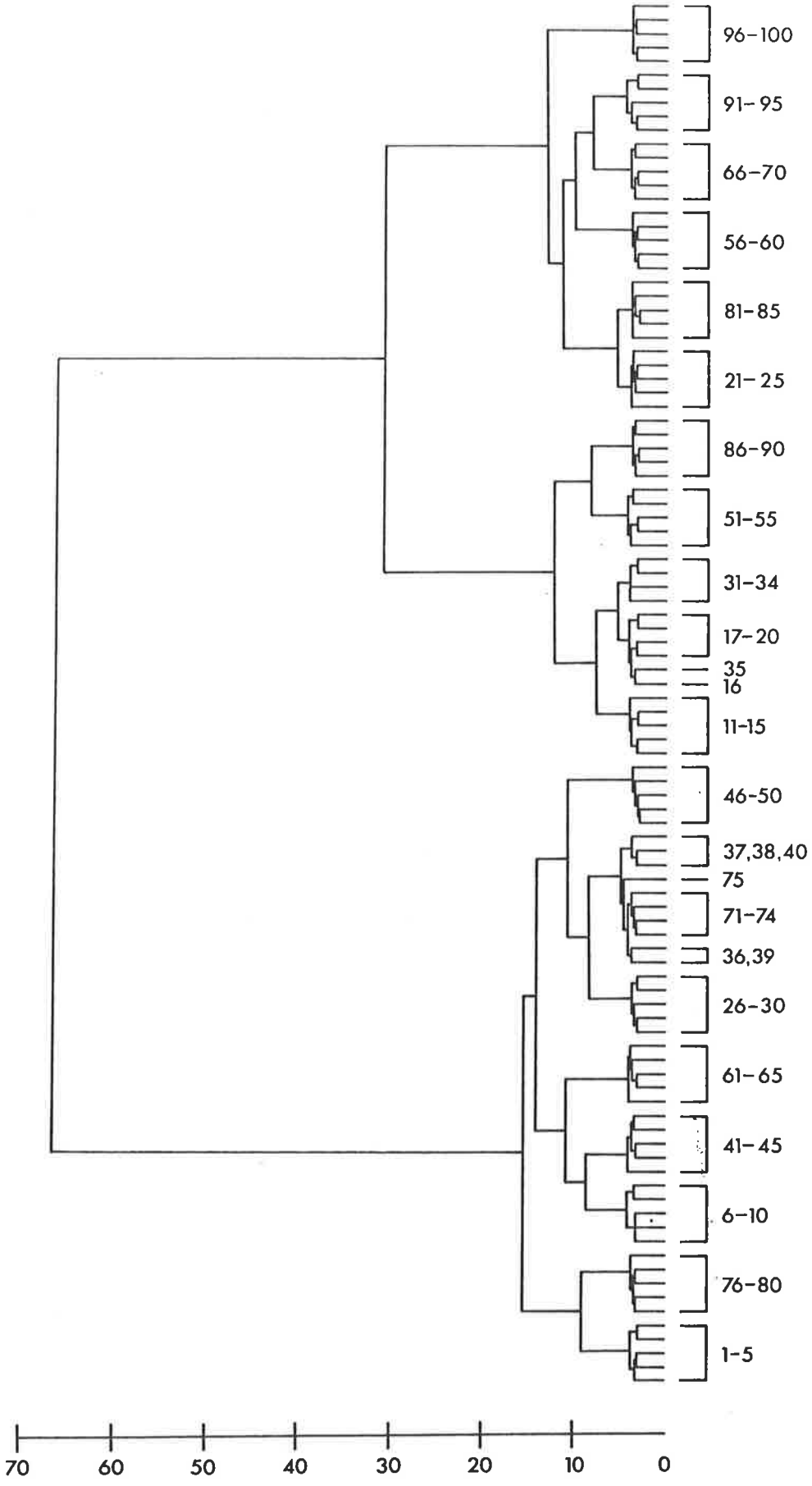
The ESS dendrogram (fig. 2.19) did not misidentify any of the OTUs, although two or three species are sometimes clumped together. This is an unexpectedly good result, since some OTUs were scored for only 10 characters.

E. 35 OTUs with 31 characters: Dolph (1976a) found that increasing the sample size only led to greater confusion in his classification. He concluded that this was due to the lack of discriminatory power in his character set. To test the effect of sample size in this study, 35 OTUs were selected at random from the original 100 OTUs (table 8) and subjected to the same analysis.

TABLE 8: 35 specimens selected at random to test the effect of sample size and the OTU numbers assigned to them.

OTU number	Species
1-3	Argyrodendron actinophyllum
4	Elaeocarpus grandis
5,6	Castanospermum australe
7	Tristania conferta
8-10	Flindersia australis
11,12	Hymenosporum flavum
13,14	Brachychiton discolor
15-17	Harpullia pendula
18.19	Linociera ramiflora
20,21	Hardenbergia violacea
22	Macropiper excelsum
23.24	Pittosporum undulatum
25	Pittosporum rhombifolium
26-29	Alectryon excelsus
30,31	Cupaniopsis anacardioides
32,33	Bauerella australiana
34,35	Laurus nobilis

FIGURE 2.19. ESS dendrogram for 100 OTUs with 31 characters and missing data (r = 0.64).


96-100
91-95
66-70
56-60
81-85
21-25
86-90
51-55
31-34
17-20
35
16
11-15
46-50
37,38,40
75
71-74
36,39
26-30
61-65
41-45
6-10
76-80
1-5
70
60
50
40
30
20
10
0

The ESS dendrogram (fig. 2.20) correctly identified all the OTUs. Figure 2.21 is an ordination diagram of the first three factor scores from a principal components analysis, which account for 49% of the variation. Ordination diagrams require careful interpretation, and in this case 10 clusters were delimited (table 9) which gave no misidentification.

TABLE 9: 10 clusters delimited from the principal components analysis on 35 OTUs with 31 characters.

Cluster number	OTU number
1	1-3
2	4,7, 26-29, 30, 31
3	5,6
4	8-10, 32, 33
5	11, 12, 23, 24, 18, 19
6	13, 14
7	15-17
8	20-22
9	25
10	34, 35

4.8 CONCLUSION: The results of this study were encouraging in that the classification produced using all the characters was good enough to suggest that the method may work on a fossil flora. Some of the other results were also useful. It appears that unlike the result of Dolph (1976a) this analysis does not deteriorate as sample size increases. On the contrary, the classification is clearer when sample size is increased, a result similar to that of Blackburn (1978a). The method also appears to be very tolerant to missing data. Although the classification is not as clear when missing data are included, the result is extremely good considering

FIGURE 2.20. ESS dendrogram for 35 OTUs with 31 characters (r = 0.52).

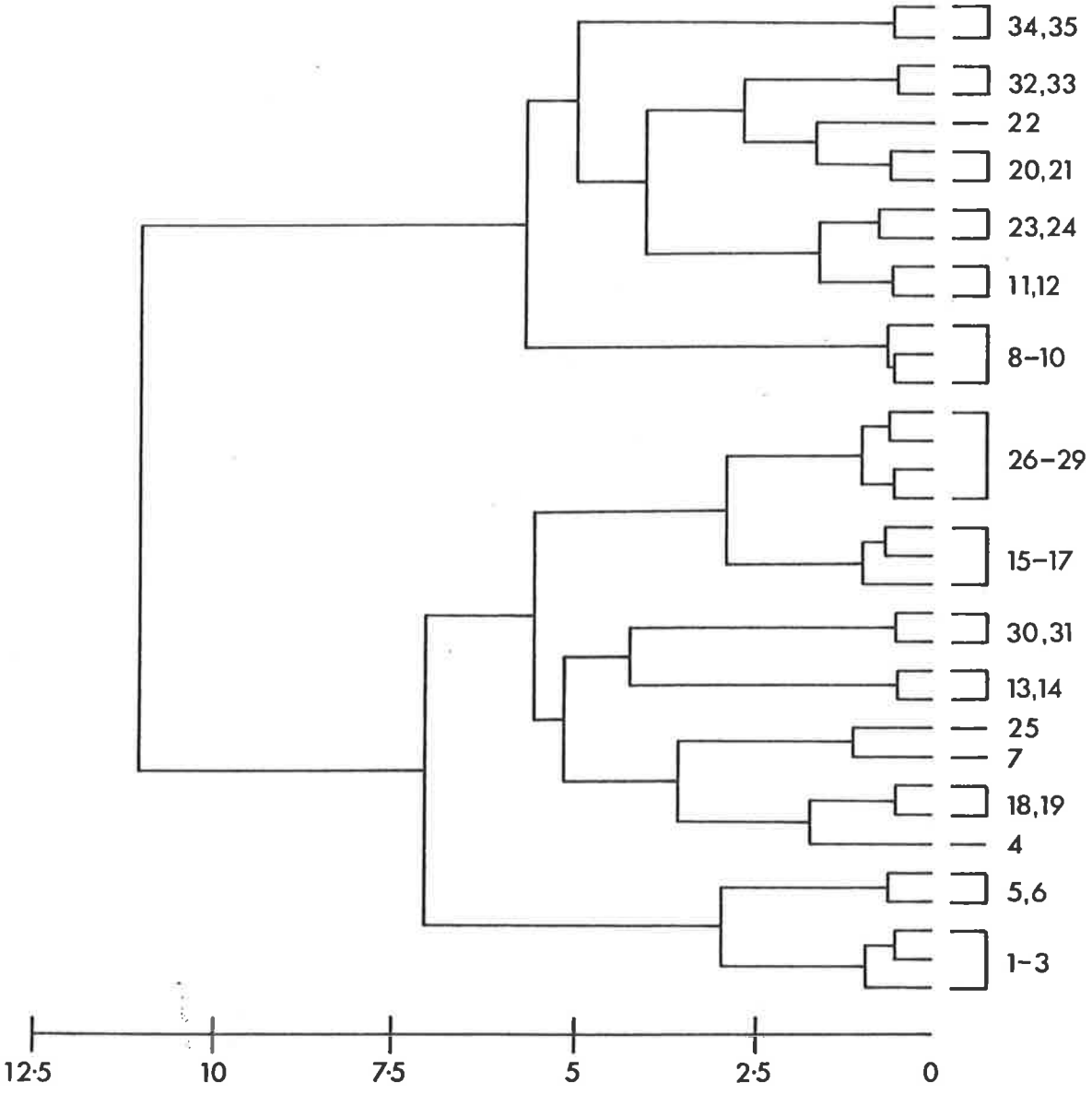
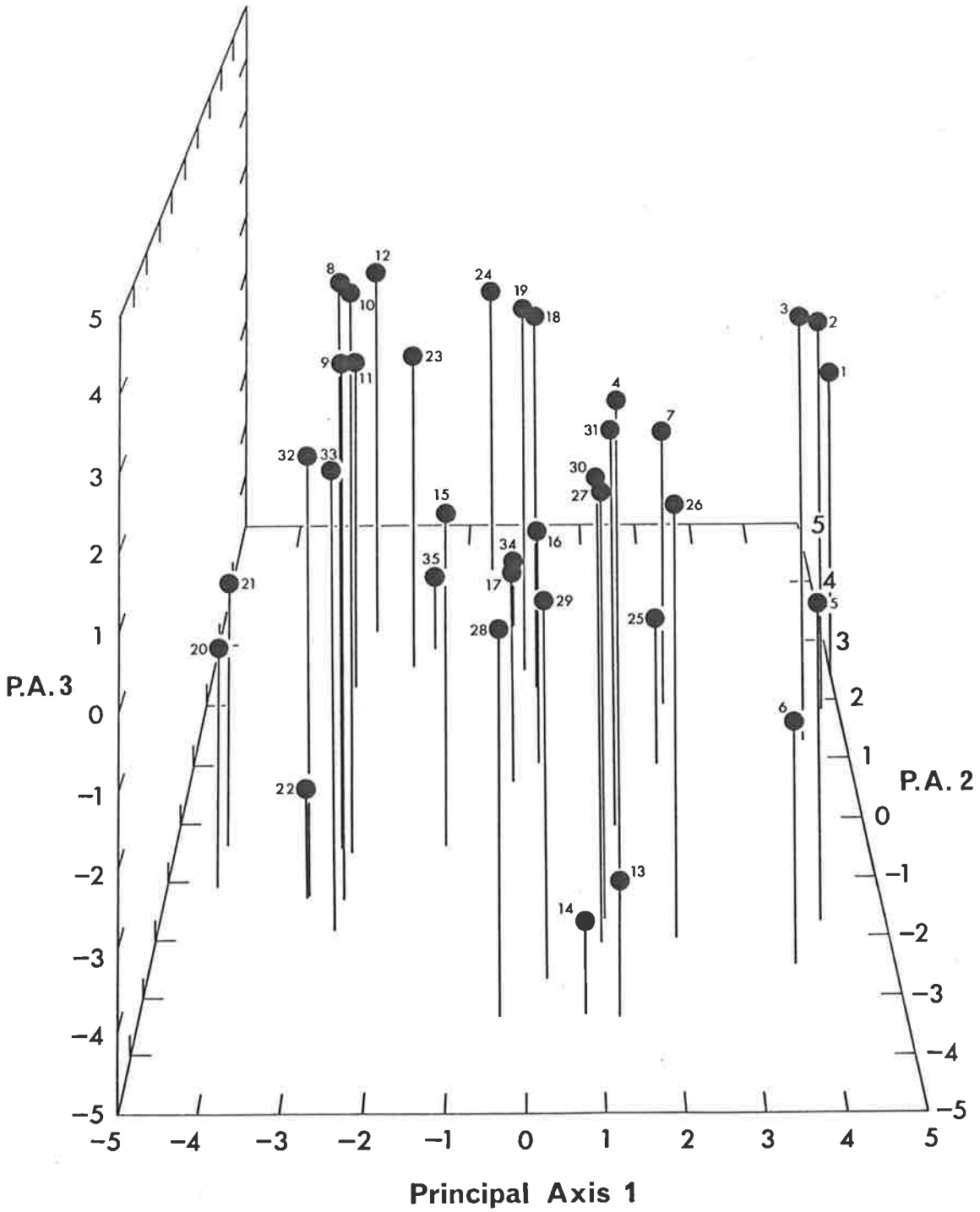

34,35
32,33
22
20,21
23,24
11,12
8–10
26–29
15–17
30,31
13,14
25
7
18,19
4
5,6
1–3
12·5
10
7·5
5
2·5
0

FIGURE 2.21. Ordination diagram of the first three factors of a PCA on 35 OTUs with 31 characters.


P.A. 3
P.A. 2
Principal Axis 1
5
4
3
2
1
0
−1
−2
−3
−4
−5

the amount of missing data. One of the negative aspects of the study was that it is apparent that cuticular characters must be used as well as architectural characters. This involves a great deal more work, since not only must cuticles be prepared for each OTU, but the very time consuming task of scoring the characters must also be performed. Cuticles, if present, add a great deal of information and must at some stage be considered, but it would be useful if they could be used as secondary characters, since the time required to produce the initial classification would then be considerably shorter.

One of the interesting features of this study was the extremely poor result that this character set gave in terms of estimating the relationships between the "taxa" (species). Hickey and Wolfe (1975) have shown that "a number of lower order leaf architectural features, including leaf organisation, configuration of the first three vein orders, and characteristics of the leaf margin are significant systematic indicators within the dicotyledons." The type of characters they worked with would lend themselves more readily to application as binary (presence/absence) characters in numerical analysis, than as continuous characters.

The character set used in this study was designed to match leaves which were most similar in overall morphology. This is not a good character set for estimating relationships between taxa, because overall morphological similarity is not always a good indication of taxonomic relationships. Probably the best type of character set for this purpose would be a set of key binary characters which recorded the presence or absence of a set of features, which alone, or in combination with continuous numeric characters could delimit

higher taxonomic groups (genera, families). A great amount of research needs to be done before such a character set will be available, but if it is possible it would certainly be of value to researchers on both extant and fossil angiosperms.

The cophenetic correlation coefficients were calculated for all the dendrograms produced for this chapter. This coefficient, developed by Sokal and Rohlf (1962) gives an estimate of how well the dendrogram reflects the similarity matrix. According to Sneath and Sokal (1973 p. 278) the value usually varies from 0.6 to 0.95. The values calculated for the dendrograms in this study generally fall below this range. However, it would be interesting to calculate the effect that increasing the number of OTUs has on the coefficient, since in this study they were generally high. One interesting feature was that both the UPGMA and ESS clustering algorithms produced poor correlations. The cophenetic correlation coefficients were calculated by hand since no program was available to compute them. They were not computed for the dendrograms in chapters 6 and 8.

(This chapter is the subject of a manuscript currently in press to the Botanical Gazette (Hill 1980b). A copy is included in Appendix IV).

CHAPTER 5

SELECTION OF FOSSIL OTUs AND CHARACTERS.

5.1 SELECTION OF OTUs: Approximately 750 specimens were collected and curated from Nerriga and were therefore available as Operational Taxonomic Units (OTUs). These specimens could be broadly split into two groups. About 150 consisted of impressions, with generally poor cuticular preservation. A close examination of these specimens showed that the preservation of venation was also relatively poor, with rarely more than primary and secondary vein impressions visible. The rest of the specimens (approximately 600) were mummified leaves. These specimens had excellent cuticular preservation, and the venation detail was generally clear at least to the tertiary level. However, whereas the impressions usually consisted of nearly complete leaves, the mummified leaves were often fragmentary, and only rarely were complete leaves preserved in this way.

In selecting the OTUs from these specimens, five major criteria were taken into account:

(1) The capacity of the computer program: Most available packages have limits on the number of OTUs which can be processed. The capacity of release 2 of CLUSTAN 1C, which was used extensively in this study, is 999 OTUs. Since this is greater than the total number of specimens, it was not a limiting factor.

(2) The preservation of the specimens: There are three features of preservation which need to be considered if the character set compiled in chapter 4 is to be utilised. The leaves must be reasonably complete, venation at least to the tertiary level should be clear, and both upper and lower cuticles should be preserved. The characters proposed in

chapter 4 dealing with ultimate venation will not be useful for these specimens, since ultimate venation is virtually never preserved, even in the mummified leaves. Using these features, 112 of the specimens were selected from the 750 available.

(3) The diversity of the taxa: If possible, all parataxa should have representatives in the OTUs. In practice, this was difficult to ensure, since the parataxa had not been defined at this stage. However, no obviously unusual specimens were not represented in the 112 specimens selected in (2).

(4) The diversity within the taxa: In some deposits, where the parataxa are clearly defined, it may be possible to add more OTUs from a particularly variable parataxon, to better account for its variation. However, since the definition of parataxa was not attempted prior to the numerical analyses for the Nerriga flora and the limits of some parataxa were obviously unclear, no extra OTUs were added for this purpose.

(5) The time factor for scoring of characters: If too many OTUs were used, the time required to score the characters would be prohibitive. Previous experience in character scoring (Chapter 4) had shown that 100 OTUs scored for 34 characters took 300 hours, or about three hours per OTU. Therefore, it was desirable to keep the number of OTUs reasonably low, since the time factor quickly becomes a major obstacle. 112 OTUs was not considered to be an unnecessarily large number.

Therefore, the only factor which was used in selecting the OTUs was the preservation of specimens. The 112 OTUs and the numbers of the specimens they represent are given in appendix II.

5.2 SELECTION OF CHARACTERS: The characters scored follow those defined in chapter 4 for use on extant leaves, with the addition of two cuticular characters:

Upper epidermal cell width: lower epidermal cell width.

Upper epidermal cell length: lower epidermal cell length.

Of the 35 characters defined in chapter 4, 12 could not be applied to the Nerriga fossils. They were:

(5) Base angle

(6) Apex angle

(7) Position of 20% maximum width basally

(8) Position of 20% maximum width apically

(14) Basal secondary vein angle

(16) Marginal venation index

(18) Areole length

(19) Areole width

(20) Number of veinlets per areole

(21) Number of branches per veinlet

(33) Areole length:width ratio

(35) Dentition frequency.

The reason for the non-applicability of these characters was that in a significant number of the OTUs, they would have been impossible to score, because of incompleteness of specimens or lack of preservation of veins. The exception to this was dentition frequency, where most of the OTUs would have scored 0 teeth/cm., making the character impossible to standardise, due to its non-normal distribution. In Chapter 4, the problem of missing data was considered, and it was concluded that while the numeric methods employed were tolerant to large amounts of missing data, it was preferable to avoid missing data whenever possible. Since 25 characters could be measured on the 112 OTUs with no missing data, it

was decided to restrict the initial analyses to those characters, incorporating others at a later stage if required. Another reason for omitting characters with missing data was that the computer package used for the cluster analysis (release 2 of CLUSTAN 1C) could not compute a similarity matrix when missing data was present.

The 25 characters scored on the Nerriga OTUs were:

(1) Modified leaf length

(2) Leaf width

(3) Modified leaf length:width

(4) Position of maximum width

(5) Leaf shape index

(6) Number of secondary veins

(7) Intersecondary vein percentage

(8) Secondary vein angle A

(9) Secondary vein angle B

(10) Secondary vein intercostal shape

(11) Secondary vein straightness index

(12) Tertiary vein angle

(13) Upper epidermal cell length

(14) Upper epidermal cell width

(15) Upper epidermal cell length:width

(16) Lower epidermal cell length

(17) Lower epidermal cell width

(18) Lower epidermal cell length:width

(19) Upper epidermal cell length:lower epidermal cell length

(20) Upper epidermal cell width:lower epidermal cell width

(21) Stomatal length

(22) Stomatal width

(23) Stomatal length:width

(24) Subsidiary cell number

(25) Stomatal index

(A list of the raw data is given in Appendix II)

These characters were measured using the methods described in Chapter 4, with the exception of stomatal index. Stomatal index (SI) is a frequently used character, and often proves to be a very useful discriminator. To get a reliable estimate of SI, a relatively large area must be measured (approximately 0.5 mm^2). This creates problems, firstly because it is difficult to accurately count a large number of epidermal cells under a microscope, and secondly, with fossil cuticles especially, it is often impossible to find large areas of cuticle with suitable preservation to allow the epidermal cells to be accurately counted. Therefore a method for estimating SI was devised.

The number of stomates in an area X is counted ($X=0.5mm^2$ where possible). The average stomatal length (p) and width (q) is calculated, as is the lower epidermal cell length (a) and width (b). These values are required for characters 16,17,21 and 22 above. The area occupied by stomates is calculated as

$$n\left[\frac{p+q}{2}\right]^2$$

assuming that a stomate approximates an ellipse. Therefore, the area taken up by epidermal cells is

$$X-n\pi\left[\frac{p+q}{2}\right]^2,$$

where n = the number of stomates in area X. If the epidermal cells are also assumed to approximate ellipses, then the number of epidermal cells in area X is

$$X - n\pi \frac{\left[\frac{p+q}{2}\right]^2}{\left[\frac{a+b}{2}\right]^2}$$

Therefore SI = $$\frac{S}{\left[\frac{X - n\pi \left[\frac{p+q}{2}\right]^2}{\left[\frac{a+b}{2}\right]^2}\right] + S}$$

This formula gave an estimate of stomatal index which, when tested on the extant cuticles used in Chapter 4, consistently gave results which were within 5% of the value calculated from the original formula. For epidermal cells with extremely sinuous walls, the length and width of the cells must be slightly modified before this estimation can be used because an ellipse is not a good estimate of epidermal cell area when the cells have extremely sinuous walls. A mean length and width must be used. Mean length is the average of the distance between the two "troughs" nearest the "peaks" used to measure maximum length. Mean width is defined in the same way, with the substitution of width for length. Epidermal cell area was estimated by other means (e.g. a rectangle) but an ellipse was found to consistently give the best estimate.

This estimation has two advantages over the normal method for measuring SI. It can be used when epidermal cell outlines are not clear enough to make an accurate count of E possible (since the number of epidermal cells is estimated, not counted) and it is time saving.

It was suggested in Chapter 4 that because of missing bases and/or apices, many fossil leaves could not have their lengths measured without the inaccurate and unsatisfactory

extrapolation of the margins. A modified leaf length was therefore defined and this has been used exclusively on the Nerriga fossils. All characters which require leaf length to be defined have been modified accordingly. The base and apex of the leaf are defined as being at the intercepts of the 10^{o}-350^{o} and 170^{o}-190^{o} lines with the primary vein (see Chapter 4 for a full explanation of modified leaf length).

Leaf shape index was also modified. The 0^{o};5^{o},175^{o},180^{o}, 185^{o}, and 355^{o} intercepts with the margin were not measured and the formula for leaf shape index was modified in that W represented the average of 30 measurements instead of 36. It should be noted that these modified leaf shape index values should not be compared directly to those calculated using the original formula.

For characters involving secondary veins, only the veins which arise from the primary vein(s) inside the modified length were considered.

Two characters were added to the set used in Chapter 4. Solereder (1908) found that in general the upper epidermis was composed of larger cells than the lower, but Stace (1965) found the opposite to be true. Therefore the ratio of upper epidermal cell length to lower epidermal cell length and upper epidermal cell width to lower epidermal cell width were incorporated to measure this possibly variable feature.

The sample sizes used for each character were the same as those calculated in Chapter 4. Approximately 400 hours was required to score the 112 OTUs.

CHAPTER 6.

CLASSIFICATION OF 112 FOSSIL OTUS.

6.1 CHOICE OF METHOD OF ANALYSIS: In chapter 4 it was shown that the ESS algorithm generally clustered the 100 extant leaves into species in a satisfactory way. This algorithm was therefore the logical starting point for the classification of the 112 fossil OTUs. The dendrogram produced for 112 OTUs with 25 characters standardised to zero mean and unit variance is shown in figure 3.

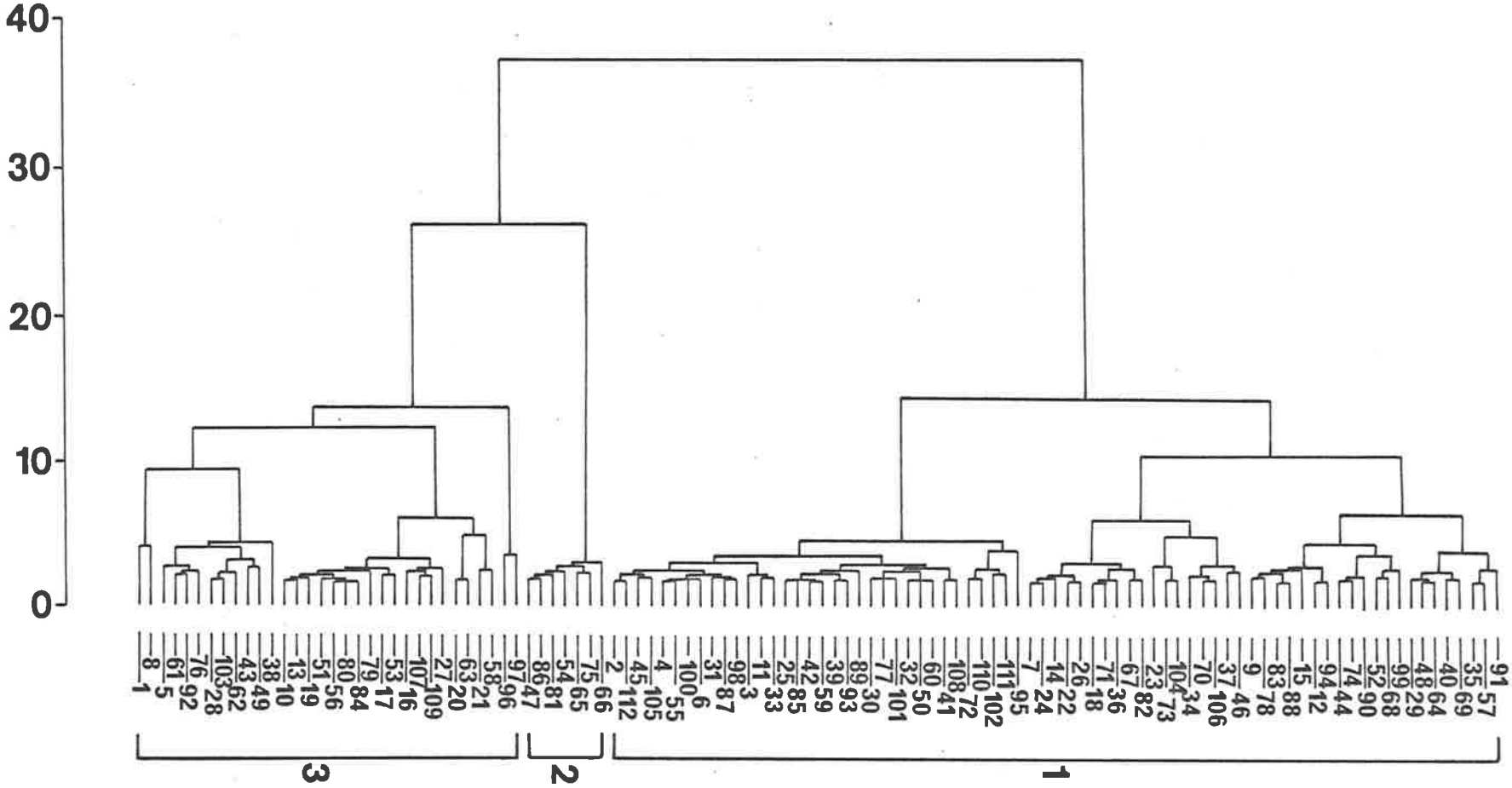
The most obvious feature of this dendrogram is that it is much more difficult to delimit groups from it than it was for any of the dendrograms produced in chapter 4. There are two reasons for this. Firstly, the number of leaf types present among the 112 fossil OTUs is unknown. Therefore, even if the assumption is made that each leaf type is represented by a group in the dendrogram, the number of groups which should be present in the dendrogram is unknown. Secondly, groups were generally very clear in the dendrograms in chapter 4, whereas in figure 3 they are not.

The stopping rule proposed in chapter 3 can be applied to this dendrogram and may give an indication of the number of groups present. The values of $(\frac{B}{T})^{\frac{1}{2}}$ for the dendrogram in figure 3 are given in table 10.

TABLE 10: $(\frac{B}{T})^{\frac{1}{2}}$ data for the dendrogram shown in fig.3 of 112 OTUs with 25 characters standardised to variance. The groups marked on the dendrogram match those in this table as: 1 = 1, 2 = (2+3), 3 = (4+5).

GROUP NUMBER	$(\frac{B}{T})^{\frac{1}{2}}$			
1	0.349	0.339		
2	0.349	0.391	0.430	
3	0.349	0.391	0.430	0.444
4	0.349	0.391	0.400	1.000
5	0.349	0.391	0.400	0.396

FIGURE 3. ESS dendrogram for 112 fossil OTUs with 25 characters standardised to zero mean and unit variance. (Large numbers = groups; small numbers = OTU numbers).


40
30
20
10
0
1 8 5 61 92 76 28 103 62 43 49 38 10 13 19 51 56 80 84 79 17 53 16 107 109 27 20 63 21 58 96 97 47
86 81 54 65 75 66
2 112 45 105 4 55 100 6 31 87 98 3 11 33 25 85 42 59 39 93 89 30 77 101 32 50 60 41 108 72 110 102 111 95 7 24 14 22 26 18 71 36 67 82 23 73 104 34 70 106 37 46 9 78 83 88 15 94 12 74 44 52 90 99 68 48 29 40 64 35 69 57 91
3
2
1

The data in this table must be considered carefully. Group 1 (table 10) contains 73 OTUs. This group has been outlined on the dendrogram (fig.3) as group 1. Group 2 (table 10) contains only OTU 66. It was noted in chapter 4 that the stopping rule gives the maximum number of groups in a dendrogram, not the optimum number. The reason for this is that small groups tend to be divided into individual OTUs, because small differences between OTUs take on relatively greater importance as group size decreases. Therefore the division of small groups should be treated with caution. Because of this OTU 66 has been combined with the six OTUs in group 3 (table 10) to give group 2 in figure 3. It can be seen that this group of seven OTUs is tightly clustered and widely separated from all other OTUs. Splitting this group of OTUs on the basis of their positions in the dendrogram could not be justified.

Similarly group 4 (table 10) which contains two OTUs (96 and 97) has been amalgamated with group 5 (table 10) to give group 3 (fig.3). Therefore according to the stopping rule, three groups are present in this dendrogram. A visual comparison of the OTUs in each of these groups clearly showed that more than one leaf type is present in groups 1 and 3 of figure 3. It was apparent at this stage that other clustering methods would be required to properly classify the OTUs.

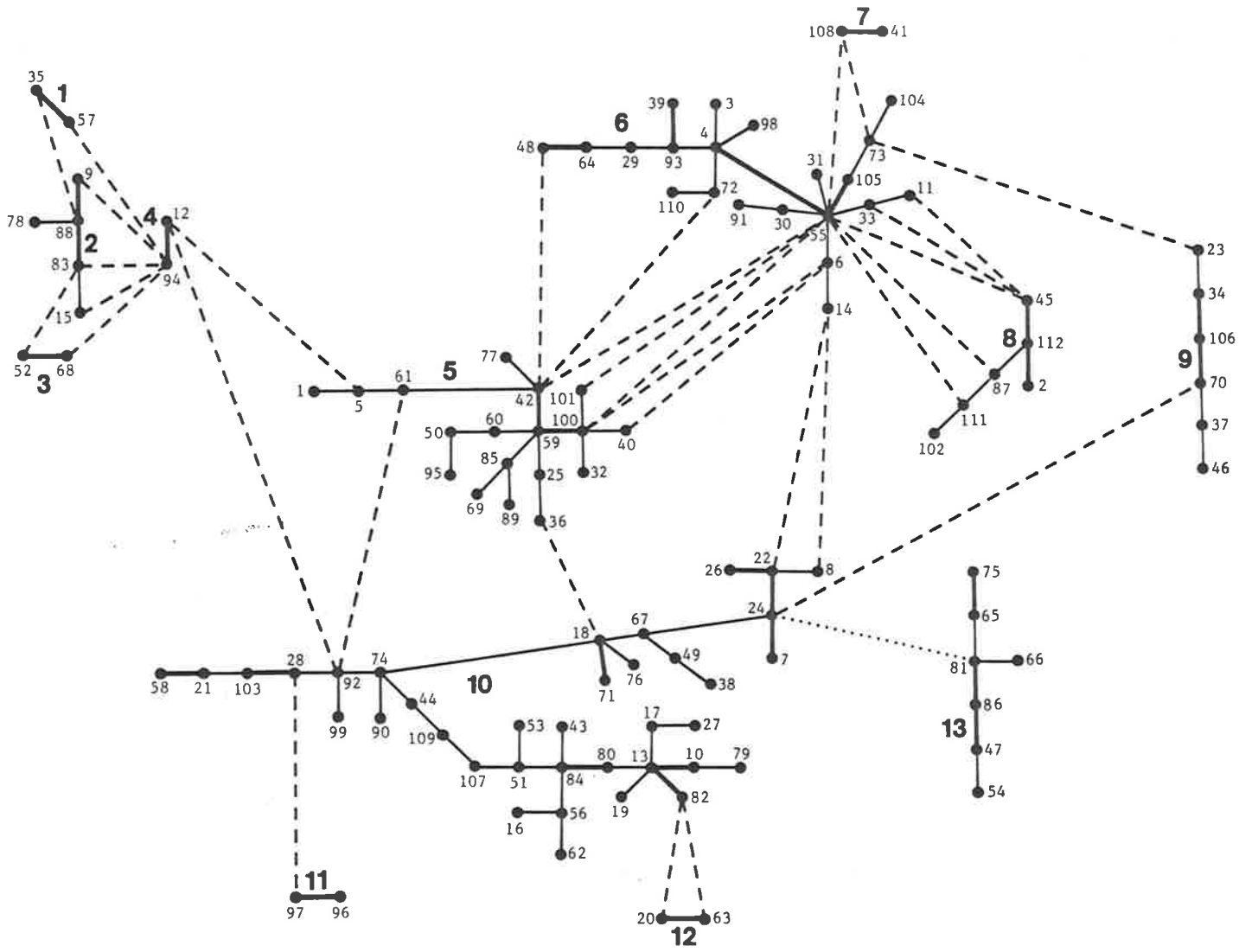
Several methods have been suggested for manipulating the data on which the dendrogram is based. Some of these, including standardisation to states (Blackburn 1978a), deletion of highly correlated characters, and the use of unstandardised principal components as character scores were attempted. The four ESS dendrograms produced were then compared.

Some groups of OTUs consistently clustered closely together and it was possible to delimit some of the leaf types (= parataxa) present. However a few of the OTUs showed no consistent trends and remained unclassified. The ESS dendrograms were therefore unsuccessful at classifying all the OTUs. The possible reasons for this failure will be discussed later.

A nearest neighbour network (NNN) and minimum spanning tree (MST) were then drawn from the similarity matrix produced using 25 characters standardised to zero mean and unit variance (figs 4,5). An MST produces a very useful graphical display of the OTUs since it gives an undistorted indication of the distances of the nearest neighbour of each OTU. One of the disadvantages of an MST is that the only way groups can be delimited is by choosing an arbitrary distance (d), and where OTUs are separated by a distance $>$ d, they are placed in separate groups. This was considered to be unsatisfactory. However an NNN forces the OTUs into groups, and by comparing these groups with the position of the OTUs in the ESS dendrogram produced from the same similarity matrix and the MST it was possible to delimit groups in the MST and classify all the fossil OTUs. This comparison and classification will now be presented followed by a discussion of the placement of the parataxa in the ESS dendrograms.

6.2 COMPARISON OF THE PLACEMENT OF 112 OTUs IN AN MST, NNN AND ESS DENDROGRAM: The NNN (fig.4) contains 13 groups, which are listed, with their component OTUs in table 11.

FIGURE 4. Nearest neighbour network for 112 fossil OTUs. The heavy, unbroken lines represent very strong bonds, the light, unbroken lines represent strong bonds, the broken lines represent weak bonds and the dotted line represents a very weak bond. The large numbers = groups; small numbers = OTU numbers.


1
2
3
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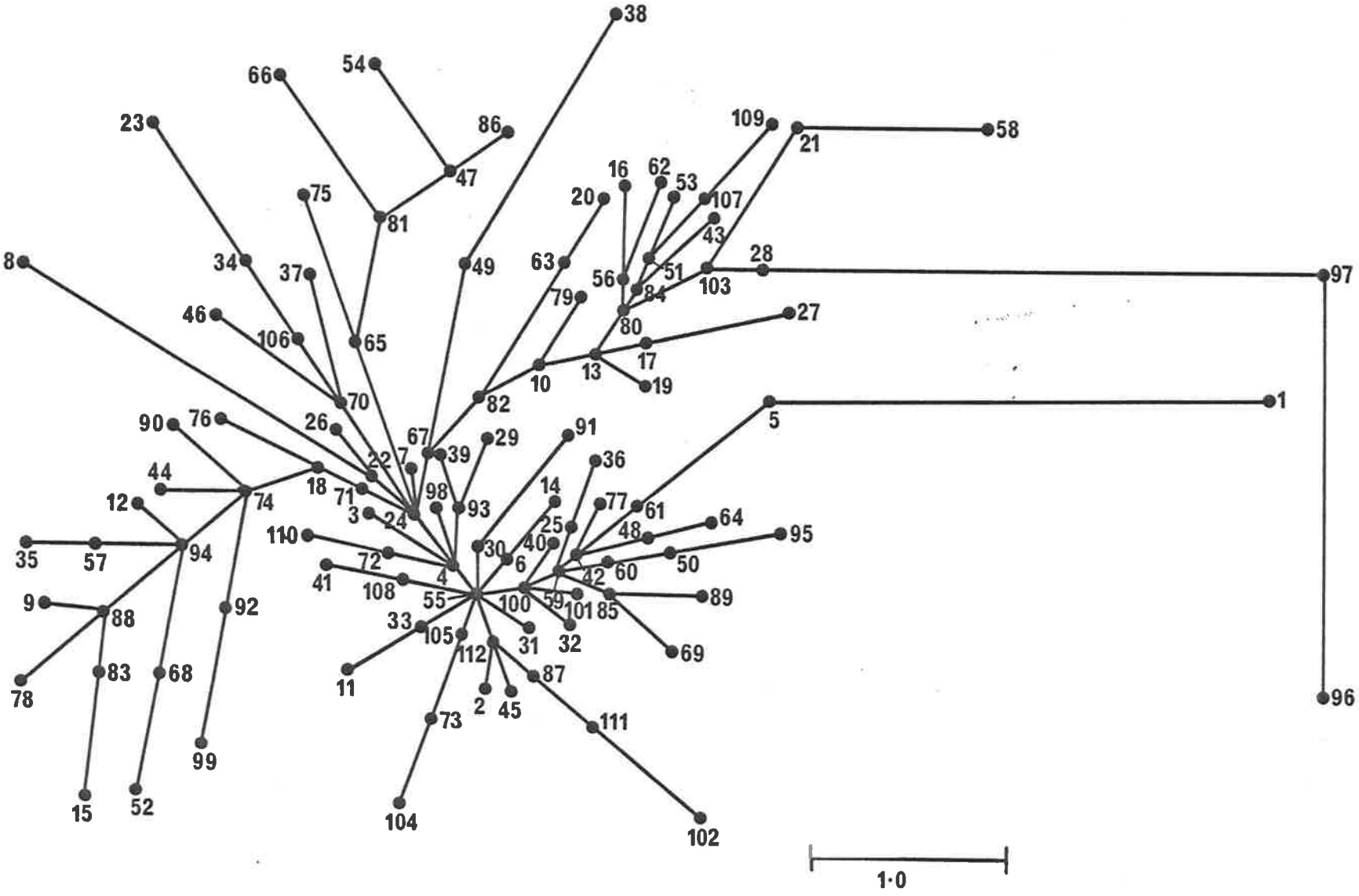
12
13

FIGURE 5. Minimum spanning tree for 112 fossil OTUs, based on a similarity matrix constructed from 25 characters standardised to zero mean and unit variance. (numbers correspond to OTU numbers).


38
54
66
86
23
109
58
21
47
16
62
53
107
75
20
81
43
8
49
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97
34
37
56
51
103
46
79
27
106
65
80
17
10
13
19
70
82
1
90
76
26
67
29
91
5
22
7
39
36
44
18
71
98
14
77
61
64
12
74
3
24
93
25
48
95
110
30
40
6
50
35
57
94
72
4
42
60
41
108
55
100
59
101
85
89
9
88
92
33
105
31
32
69
112
87
78
83
68
11
2
45
73
111
99
52
15
104
102
96
1·0

TABLE 11: List of the OTUs in each group of the NNN.

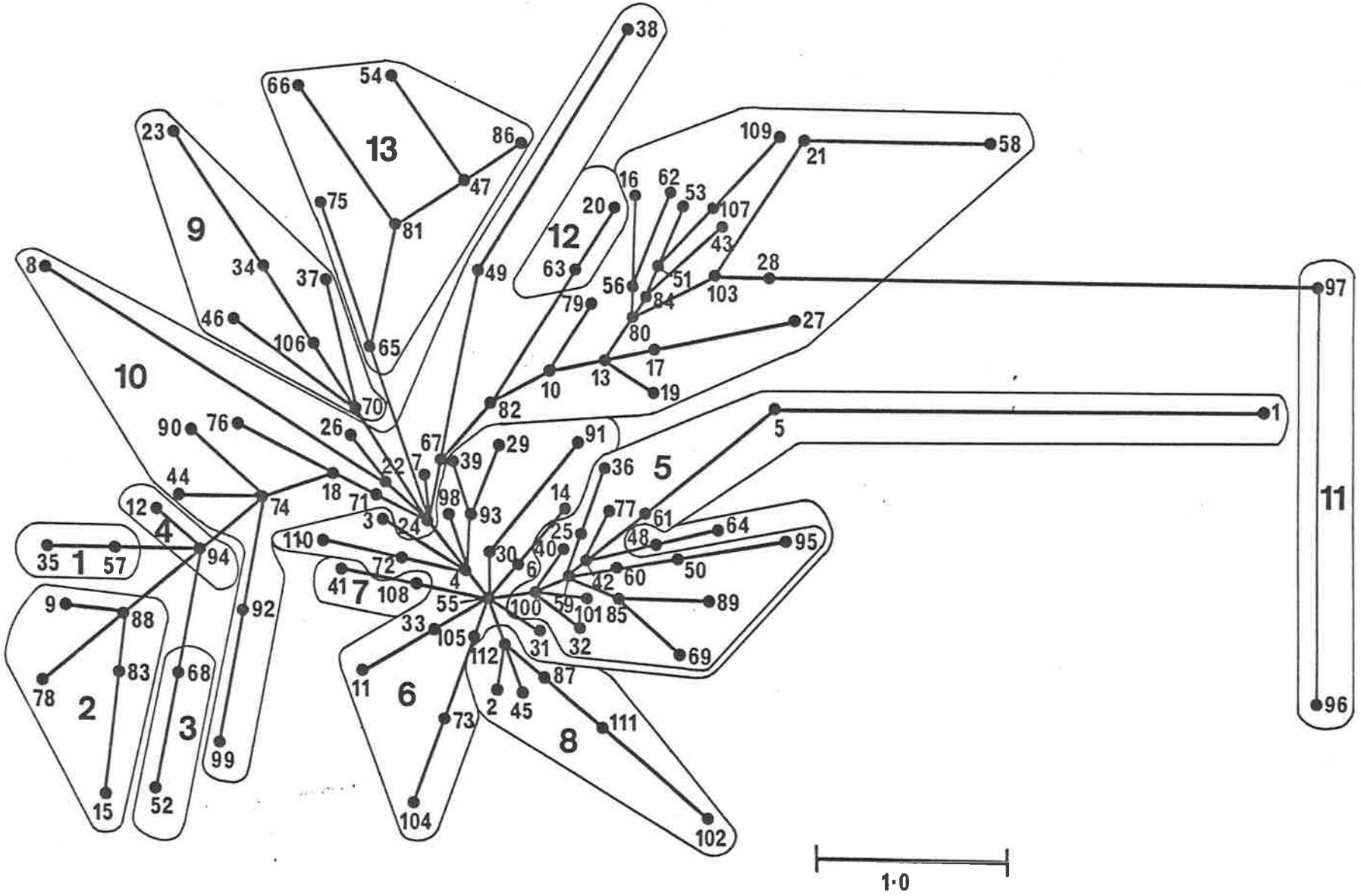
GROUP NUMBER	OTU NUMBERS	NO. OF OTUs PER GROUP
1	35,57	2
2	9,15,78,83,88	5
3	52,68	2
4	12,94	2
5	1,5,25,32,36,40,42,50,59,60, 61,69,77,85,89,95,100,101	18
6	3,4,6,11,14,29,30,31,33,39, 48,55,64,72,73,91,93,98,104, 105,110	21
7	41,108	2
8	2,45,87,102,111,112	6
9	23,34,37,46,70,106	6
10	7,8,10,13,16,17,18,19,21,22, 24,26,27,28,38,43,44,49,51,53, 56,58,62,67,71,74,76,79,80,82, 84,90,92,99,103,107,109	37
11	96,97	2
12	20,63	2
13	47,54,65,66,75,81,86	7

Two factors of an NNN should be noted. Firstly it is impossible for an OTU to be in a group by itself. The smallest group size is two. Therefore if a taxon is represented by only one OTU, that OTU must occur in a group with other taxa. Secondly, if two groups are linked by a relatively large number of weak bonds, it is possible that these groups should be fused and treated as a single group.

The MST (fig.5) is very complex and it would be difficult to objectively delimit groups without the aid of other methods. When the groups delimited from the NNN (fig.4) are outlined on the MST (fig.5.1) some interesting trends are apparent. Groups 1,2,3 and 4 are connected by a large number of weak bonds in figure 4 and judging from their relatively close positions in figure 5.1 they could be considered as a single group. The OTUs in these groups (table 11) occur in close proximity in group 1 of the ESS dendrogram (fig.3).

Groups 5,6,7 and 8 in figure 4 are also connected by a large number of weak bonds, and again their relatively

FIGURE 5.1. The MST drawn in fig. 5, with the groups delimited from the NNN (fig. 4) added. (Small numbers = OTU numbers, large numbers = group numbers).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close positions and overlap in the MST (fig.5.1) supports their amalgamation to form a single group. All the OTUs in these groups occur in group 1 in the dendrogram (fig.3), with the exception of OTUs 1,5 and 61 (group 3). Of these three OTUs, only OTU 1 appears to be far enough removed from the other OTUs in the MST (fig.5.1) to warrant its exclusion, and it will be considered independently.

Group 9 in figures 4 and 5.1 represents a set of OTUs which are well separated from all other OTUs and should be considered as a single group. These six OTUs occur in close proximity in group 1 in figure 3. Group 10 in figure 4 contains 37 OTUs. Of these 37 OTUs, 12 (OTUs 7,18,22,24,26,44, 67,71,74,82,90 and 99) occur in group 1 of the dendrogram (fig.3) and the remainder in group 3. A similar pattern can be seen in the MST (fig.5.1) where the 37 OTUs are split into two approximately equal sized groups. Based on the placement of these OTUs in the MST, this group will be split between OTUs 67 and 82. Two OTUs in group 10 (fig.4) are widely separated from all other OTUs in the MST (OTUs 8 and 38 in fig.5.1) and should be considered independently.

Group 11 in figures 4 and 5.1 contains two OTUs which are widely separated from all other OTUs and from each other. These OTUs (96 and 97) are also widely separated from all others in the dendrogram (fig.3) and should be considered individually. Group 12 contains two OTUs (20 and 63) which are closely related to each other, but are widely separated from all other OTUs in figures 3,4 and 5.1. This group should be retained. Group 13 in the NNN (fig.4) contains seven OTUs which are linked to other OTUs by only a very weak bond. These seven OTUs make up group 2 in the dendro-

gram (fig.3) where they are also widely separated from all other OTUs. These OTUs should be retained as an independent group.

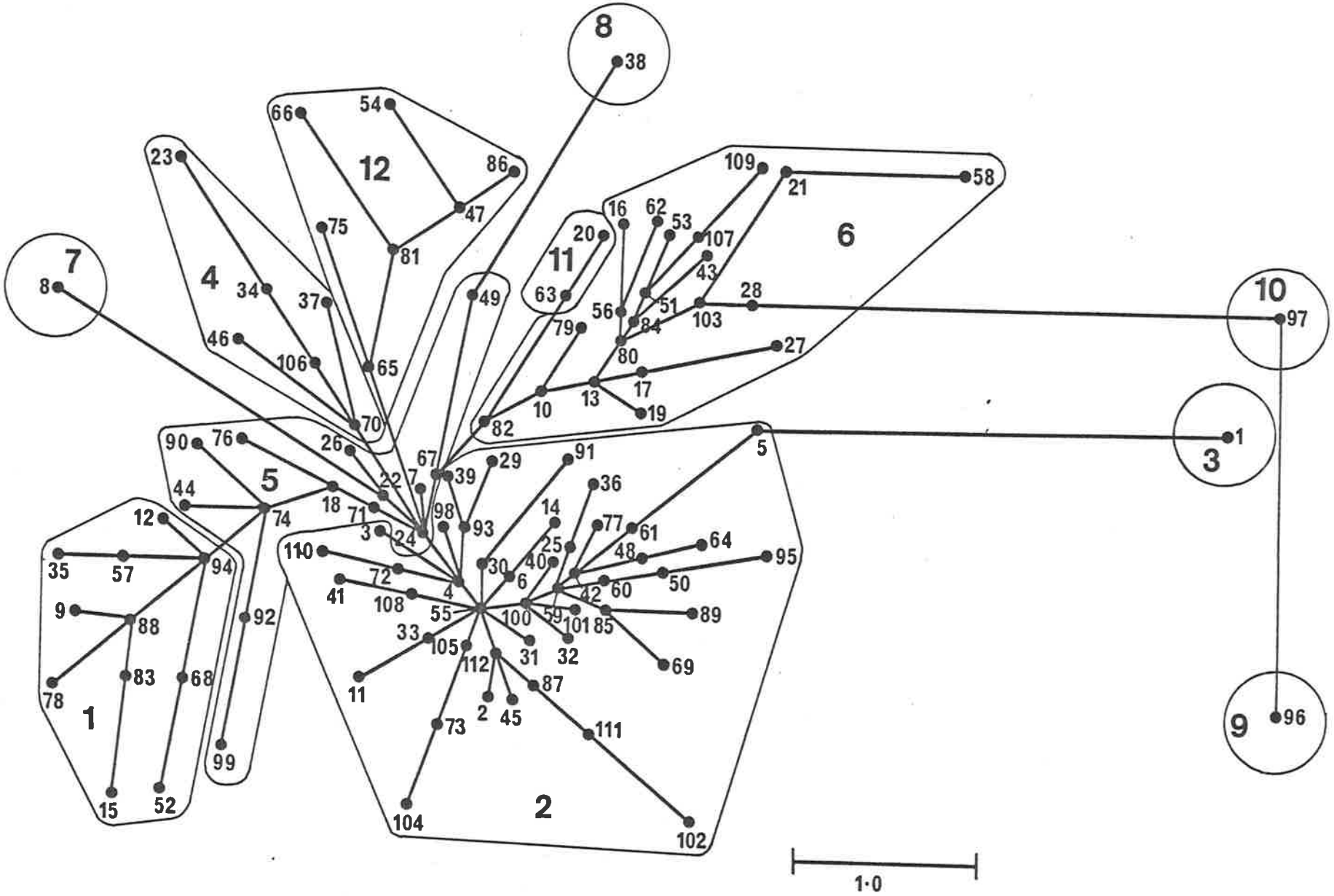
As the result of the comparison between the ESS dendrogram (fig.3), the NNN (fig.4) and the MST (fig.5.1), 12 groups have been delimited. These groups, their component OTUs, and their equivalents in the NNN (fig.4) are shown in table 12. The groups have been plotted on the MST in figure 5.2.

TABLE 12: List of the OTUs in each group derived from a comparison of the MST, NNN and ESS dendrogram.

GROUP NO.	GROUP NO. IN THE NNN	OTU NUMBERS	NO. OF OTUs PER GROUP
1	1,2,3,4	9,12,15,35,52,57,68, 78,83,88,94	11
2	5,6,7,8	2,3,4,5,6,11,14,25, 29,30,31,32,33,36,39, 40,41,42,45,48,50,55, 59,60,61,64,69,72,73, 77,85,87,89,91,93,95, 98,100,101,102,104, 105,108,110,111,112	46
3	5	1	1
4	9	23,34,37,46,70,106	6
5	10	7,18,22,24,26,44,49, 67,71,74,76,90,92,99	14
6	10	10,13,16,17,19,21,27, 28,43,51,53,56,58,62, 79,80,82,84,103,107, 109	21
7	10	8	1
8	10	38	1
9	11	96	1
10	11	97	1
11	12	20,63	2
12	13	47,54,65,66,75,81,86	7

The OTUs in each of the groups in table 12 can now be scanned to ascertain whether they contain morphologically similar leaf types (= parataxa), and whether there is any overlap between groups. In defining parataxa from the 112 OTUs, it must be remembered that only a sample of the

FIGURE 5.2. The MST drawn in fig. 5, with the groups delimited from a comparison of the ESS dendrogram (fig. 3), NNN (Fig. 4) and MST (fig. 5) added. (Small numbers = OTU numbers, large numbers = group numbers).


8
38
12
66
54
86
47
23
75
81
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34
37
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106
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49
11
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63
16
62
53
107
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109
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58
7
8
56
51
103
28
10
97
79
84
80
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17
13
10
19
82
3
1
90
76
26
67
29
91
5
44
5
22
7
39
36
18
71
98
93
14
77
61
64
12
74
3
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25
48
95
110
30
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6
72
60
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57
94
41
108
4
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59
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105
31
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83
68
112
87
78
1
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45
73
111
99
15
52
104
102
9
96
1·0

collection of fossils from Nerriga is being examined. The effect of this will be to underrepresent the variation of some parataxa. For this reason parataxa were very strictly defined from the OTUs. That is, the limits of each parataxon were set and if an OTU fell outside those limits it was placed in a different parataxon. The reason for doing this was that it meant that the maximum number of parataxa would be described from the 112 OTUs. When the remainder of the specimens were assigned to those parataxa, it would be relatively simple to amalgamate parataxa which were found to represent stages in a morphological continuum.

GROUP 1: The 11 OTUs (figs 21-28,30,31,33) share many similarities. These OTUs occur among a group of 21 in group 1 of the dendrogram (fig.3) and the remaining 10 OTUs were scanned for similarities of leaf form. Only one (OTU 91) bore any close resemblance to the 11 OTUs in group 1 of table 12. OTU 91 (fig.29) is in group 2 in the MST (fig.5.2) and is well separated from the OTUs in group 1. However it should be noted that although OTU 91 has OTU 30 as its nearest neighbour (distance = 0.721), OTU 35 (which is in group 1) is its second nearest neighbour (distance = 0.768) and so it is not as widely separated from group 1 as its position in the MST (fig.5.2) suggests.

The 11 OTUs in group 1 along with OTU 91 share enough similarities to allow them to be considered as a single parataxon, but a careful comparison of leaf shape and details of the venation and cuticular patterns suggested that four distinct leaf types were present. Nine OTUs (9,35,57,68,78, 83,88,91,94; figs 23-31) were assigned to parataxon NER/004; one OTU (12; fig.21) was assigned to parataxon NER/002; one

OTU (15; fig.22) was assigned to parataxon NER/003; and the remaining OTU (52; fig.33) was assigned to parataxon NER/005.

GROUP 2: This group contains 46 OTUs of which one (OTU 91) has already been assigned to parataxon NER/004. Of the remaining 45 OTUs, 42 consist of very distinctive serrate margined leaves (figs 81-84,86-89,91-108,110-125). A scan of the remaining 54 OTUs revealed that six others resembled this leaf type. They were OTUs 7 (fig.85), 18 (fig.41), 22 (fig.44), 24 (fig.43), 26 (fig.90) and 71 (fig.109). It should be noted that these six OTUs all occur in group 5 in figure 5.2 and are very closely linked to OTUs in group 2. They are also closely linked in the dendrogram (fig.3). Three of the six OTUs (18,22 and 24) were considered to differ too much in venation detail from the 42 serrate margined leaves in group 2 to be placed in the same parataxon. However, the other three OTUs (7,26 and 71) were included. This group of 45 OTUs (figs 81-125) were assigned to parataxon NER/027.

Three OTUs in group 2 remain undefined (OTUs 5,61 and 95). OTUs 5 and 61 (figs 38,39) represent a unique leaf type, and they were assigned to parataxon NER/011. It should be noted that these two OTUs occur in group 3 in the dendrogram (fig.3) whereas all the other OTUs in group 2 (table 12) occur in group 1 in the dendrogram. OTU 95 (figs 147-149) represents an unusual, deeply lobed leaf, which occurred nowhere else among the OTUs. OTU 95 was assigned to parataxon NER/016. Therefore, after studying groups 1 and 2, seven parataxa have been delimited, which account for 60 OTUs.

GROUP 3: This group consists only of OTU 1 (fig.40). This OTU is very distinct from all others and has been assigned

to parataxon NER/013.

GROUP 4: Five of the six OTUs in this group represent a distinct leaf type (OTUs 34,37,46,70 and 106; figs 53,145,54, 55 and 57). A scan of the remaining 45 OTUs revealed two which appear to belong to this leaf type. They are OTUs 44 (fig.50) and 90 (fig.56), which occur in group 5. OTUs 90 and 44 are closely related (OTU 90 has OTU 44 as its second nearest neighbour at a distance of 0.692), and OTU 46 (in group 4) has OTU 90 (in group 5) as its third nearest neighbour (distance = 0.960). Therefore, although the two groups of OTUs in this leaf type are not as distantly related as the MST suggests, they are still widely separated. The five OTUs in group 4 (table 12) which represent a distinct leaf type cluster closely together in the dendrogram (fig.3), but the other two OTUs belonging to this leaf type, while occurring in the same group (1) are well separated. It can be seen (figs 50,53-57 and 145) that the leaves vary greatly in size and shape.The most important features which identify them as belonging to the same leaf type are the tertiary venation pattern and the type and distribution of trichome bases and stomates. These features are not well represented in the character set. The variability of many of the characters scored for the OTUs belonging to this leaf type probably explains their poor clustering. These seven OTUs (34,37,44, 46,70,90 and 106) were assigned to parataxon NER/024. The remaining OTU in group 4 (23; fig.48) represents a unique leaf type and was assigned to parataxon NER/021.

GROUP 5: Five of the 14 OTUs in this group have already been assigned to parataxa. OTUs 7,26 and 71 belong to parataxon NER/027 and OTUs 44 and 90 belong to parataxon NER/024. Of the remaining nine OTUs, three have already been discussed

for their similarity to NER/027 (OTUs 18,22 and 24; figs 41, 44 and 43). A careful study of the venation pattern of these leaves suggested that they consisted of two leaf types. The first, containing OTUs 18 and 24, was assigned to parataxon NER/014 and the second, containing OTU 22 was assigned to parataxon NER/018.

The remaining six OTUs represent several distinct leaf types. OTU 49 (fig.42) is widely separated from all other OTUs and represents a unique and distinctive leaf type. This OTU was assigned to parataxon NER/015. OTU 99 (fig.32) is well separated from all other OTUs. Its nearest neighbour is OTU 92 (fig.20), which it resembles somewhat in leaf shape and venation, but the cuticular patterns of the two are distinct. OTU 99 represents a unique leaf type and was assigned to parataxon NER/006. OTU 76 (fig.45) represents a distinctive and unique leaf type, although it is closely related to OTU 18 (NER/014). OTU 76 was assigned to parataxon NER/017.

Three OTUs remain undefined in group 5. They are OTUs 67 (fig.18), 74 (fig.19) and 92 (fig.20). OTUs 74 and 92 are directly linked in the MST (fig.5.2) but OTU 67 is widely separated. These OTUs vary greatly in leaf size, which probably accounts for their wide separation in the MST and dendrogram, because their venation pattern is similar and their cuticular pattern is virtually identical. These three OTUs were considered to represent a single leaf type and were assigned to parataxon NER/001.

GROUP 6: Sixteen of the 21 OTUs in group 6 appear to belong to the same leaf type. The leaf form and venation, and particularly the cuticular pattern is very distinctive.

These OTUs are: 10,13,16,17,19,27,43,51,53,56,79,80,82,84, 107 and 109 (figs 65-80), and they form a tight cluster within group 6 (fig.5.2). These 16 OTUs were assigned to parataxon NER/026. The remaining five OTUs represent more than one leaf type. OTU 58 (fig.46) is well separated from all other OTUs. In leaf size and shape it bears some resemblance to OTU 21 (fig.47), to which it is directly linked, but the venation and cuticular patterns differ greatly between the two. OTU 58 was assigned to parataxon NER/019 and OTU 21 was assigned to parataxon NER/020. OTUs 28 and 103 occur very close to one another and are directly linked. They are very similar in all aspects and represent a single leaf type. OTU 103 is linked to OTU 80, which has been assigned to NER/026. OTUs 28 and 103 resemble the OTUs in NER/026 in leaf size and shape but differ greatly in venation and cuticular patterns. These two OTUs (28 and 103) were assigned to parataxon NER/007. OTU 62 (fig.49) is also closely aligned to OTUs in NER/026, but is extremely distinct in its cuticular pattern. This OTU was assigned to parataxon NER/022. At this stage 21 parataxa have been delimited, accounting for 99 OTUs.

GROUP 7: This group consists only of OTU 8 (fig.37). This OTU is distinct from all others and was assigned to parataxon NER/012.

GROUP 8: This group consists only of OTU 38 (fig.36). This OTU is very distinct from all others and has been assigned to parataxon NER/008.

GROUP 9: This group consists only of OTU 96 (figs 150,151). This particularly distinctive and unique lobed leaf has been assigned to parataxon NER/009.

GROUP 10: This group consists only of OTU 97 (figs 152,153). This distinctive and unique lobed leaf has been assigned to parataxon NER/010.

GROUP 11: The two OTUs in this group (OTUs 20 and 63; figs 51,52) represent a single leaf type. The venation pattern of this leaf type is particularly distinctive, with very obvious paired basal secondary veins present. This pattern does not occur in any other OTUs. The very similar cuticular patterns confirm that OTUs 20 and 63 belong to the same leaf type. These two OTUs were assigned to parataxon NER/023.

GROUP 12: The seven OTUs in this group (47,54,65,66,75,81 and 86; figs 58-64) represent probably the most distinctive leaf type in the Nerriga deposit. In leaf shape, venation and cuticular pattern these OTUs are unmistakably unique and have been assigned to parataxon NER/025. Therefore from 12 groups, 27 parataxa have been delimited containing 112 OTUs (table 13).

TABLE 13: Parataxon numbers and the OTUs assigned to each.

PARATAXON NUMBER	OTU NUMBERS
NER/001	67,74,92
NER/002	12
NER/003	15
NER/004	9,35,57,68,78,83,88,91,94
NER/005	52
NER/006	99
NER/007	28,103
NER/008	38
NER/009	96
NER/010	97
NER/011	5,61
NER/012	8
NER/013	1
NER/014	18,24
NER/015	49
NER/016	95
NER/017	76
NER/018	22
NER/019	58
NER/020	21
NER/021	23

TABLE 13 (continued)

PARATAXON NUMBER	OTU NUMBERS
NER/022	62
NER/023	20,63
NER/024	34,37,44,46,70,90,106
NER/025	47,54,65,66,75,81,86
NER/026	10,13,16,17,19,27,43,51,53,56,79,80,82,84,107, 109
NER/027	2,3,4,6,7,11,14,25,26,29,30,31,32,33,36,39,40, 41,42,45,48,50,55,59,60,64,69,71,72,73,77,85,87, 89,93,98,100,101,102,104,105,108,110,111,112

Some comments can be made on the placement of the parataxa within the groups shown in figure 5.2 (table 14).

TABLE 14: Placement of parataxa within the groups delimited in figure 5.2.

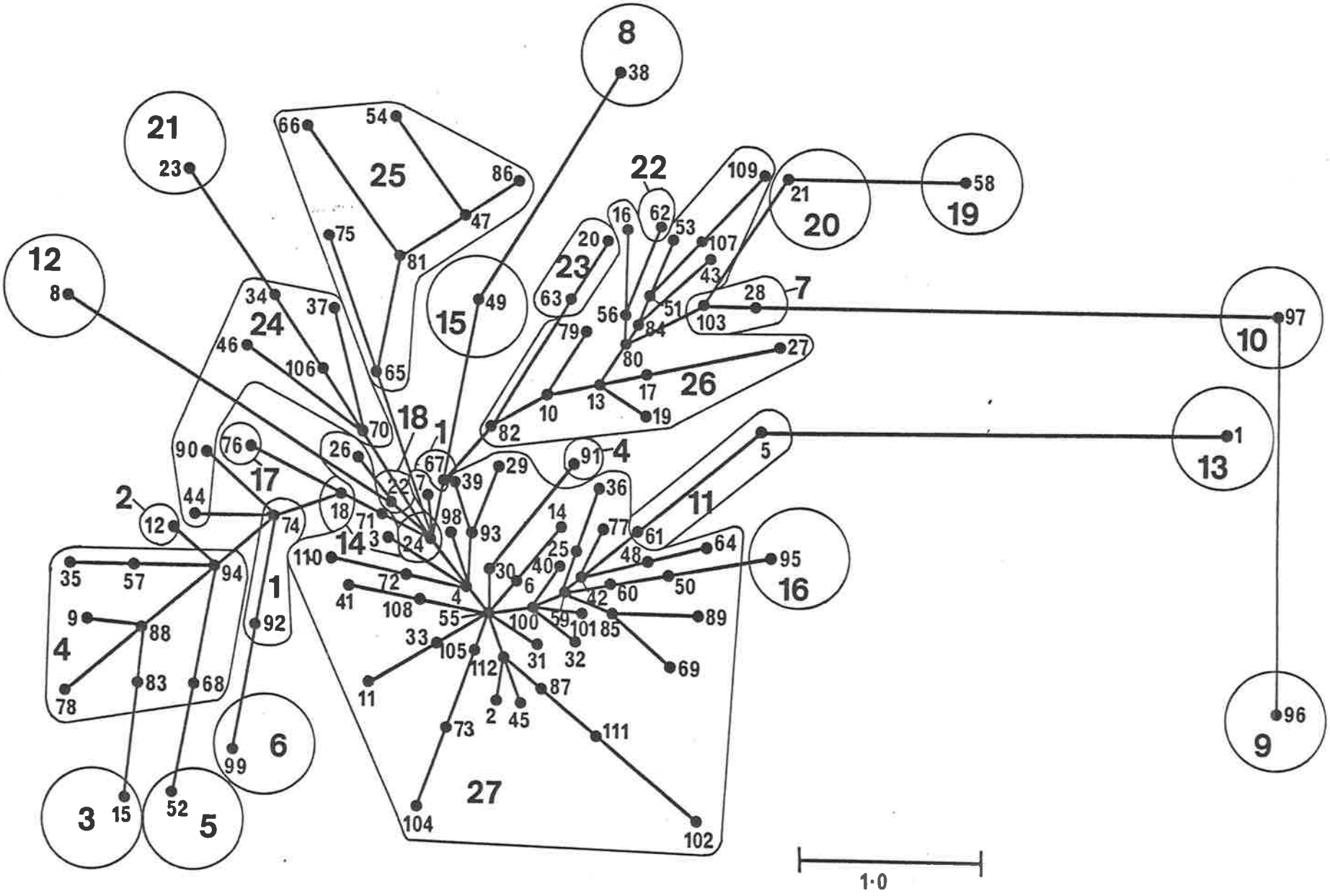
GROUP NO.	PARATAXON NUMBER (including the number of OTUs per parataxon in that group - e.g. 4/5 means that there are 5 OTUs in the parataxon and 4 occur in that group).
1	NER/002 (1/1), NER/003 (1/1), NER/004 (8/9), NER/005 (1/1).
2	NER/004 (1/9), NER/011 (2/2), NER/016 (1/11), NER/027 (42/45).
3	NER/013 (1/1).
4	NER/021 (1/1), NER/024 (5/7).
5	NER/001 (3/3), NER/006 (1/1), NER/014 (2/2), NER/015 (1/1), NER/017 (1/1), NER/018 (1/1), NER/024 (2/7), NER/027 (3/45).
6	NER/007 (2/2), NER/019 (1/1), NER/020 (1/1), NER/022 (1/1), NER/026 (16/16).
7	NER/012 (1/1).
8	NER/008 (1/1).
9	NER/009 (1/1).
10	NER/010 (1/1).
11	NER/023 (2/2).
12	NER/025 (7/7).

6.3 CONCLUSION FROM A COMPARISON OF THE NNN, MST AND ESS DENDROGRAM: Five of the 12 groups considered contained only one OTU, which in each case was the sole representative of a parataxon. These five OTUs were very distinct from all other OTUs, both in their placement in figure 5.2 and their leaf form. Therefore, their classification was relatively simple. The remaining seven groups contained an average of just over

three parataxa each, ranging from one in groups 11 and 12 to eight in group 5 (table 14). The greater the number of parataxa in a group, the more difficult they were to classify. This was particularly the case for groups 5 and 6, which when combined form group 10 in the NNN (fig.4). Another factor which made classification of OTUs difficult was when OTUs belonging to a parataxon occurred in more than one group. This was not a major problem in this study. If all parataxa containing more than one OTU are considered (10 parataxa), then on average 93.7% of the OTUs in each parataxon fell in one cluster (see data in table 14). This appears to be a good result. The parataxa are outlined on the MST in figure 5.3.

Although the parataxa were delimited in a systematic way from the NNN, MST and ESS dendrogram, there is no doubt that many subjective descisions were required when comparing OTUs. However, most of the descisions were required on relatively small numbers of OTUs within groups - there was very little overlap of parataxa between groups. The 12 groups which were considered (table 12) were erected solely on the placement of the OTUs within the NNN, MST and ESS dendrograms. No knowledge of the identity of the OTUs was required. Twenty seven parataxa were then delimited from the 12 groups, and if all parataxa are considered, 98.3% of OTUs in each parataxon on average fell within one group. Although it would have been a better result if the number of groups had been higher, the small overlap of parataxa between groups is very significant. In order to identify OTUs correctly from numerical taxonomic techniques, the most important requirement is that the OTUs in each taxonomic category

FIGURE 5.3. The MST drawn in Fig. 5, with the 27 parataxa outlined. (Small numbers = OTU numbers, large numbers correspond to parataxon numbers; e.g. 2 = NER/002 etc.).


1·0

should occur in the same group. This has certainly been the case with the majority of the 112 OTUs.

One of the most common methods of presenting OTUs graphically is a dendrogram. For this reason, and also because dendrograms were successfully employed in chapter 4, a short discussion of the placement of the OTUs within the four ESS dendrograms will now be presented.

6.4 COMPARISON OF ESS DENDROGRAMS: A: 112 OTUs classified using the ESS clustering algorithm with 25 characters standardised to zero mean and unit variance: The dendrogram (fig. 3) has already been used for comparison with the NNN (fig.4) and MST (fig.5). It has been reproduced (fig.6) with parataxon numbers inserted in place of OTU numbers. The three groups suggested by the stopping rule have been included.

The most obvious feature of the dendrogram is the relatively small number of groups (3) compared to the NNN (fig. 4) which had 13. The seven OTUs in parataxon NER/025 are very clearly separated in group 2. However, delimitation of the other parataxa is generally poor. Group 1 in figure 6 contains representatives of 13 parataxa and group 3 contains representatives of 15 parataxa.

The character contributions to the classification (table 15) show that for the first furcation (splitting group 1 from groups 2 and 3 in figure 6) characters 16 (lower epidermal cell length), 17 (lower epidermal cell width), 21 (stomatal length), 14 (upper epidermal cell width) and 9 (secondary vein angle B) are the five highest contributing characters.

FIGURE 6. ESS dendrogram for 112 fossil OTUs with 25 characters standardised to zero mean and unit variance. (large numbers = groups; small numbers correspond to parataxon numbers, e.g. 4 = parataxon NER/004).

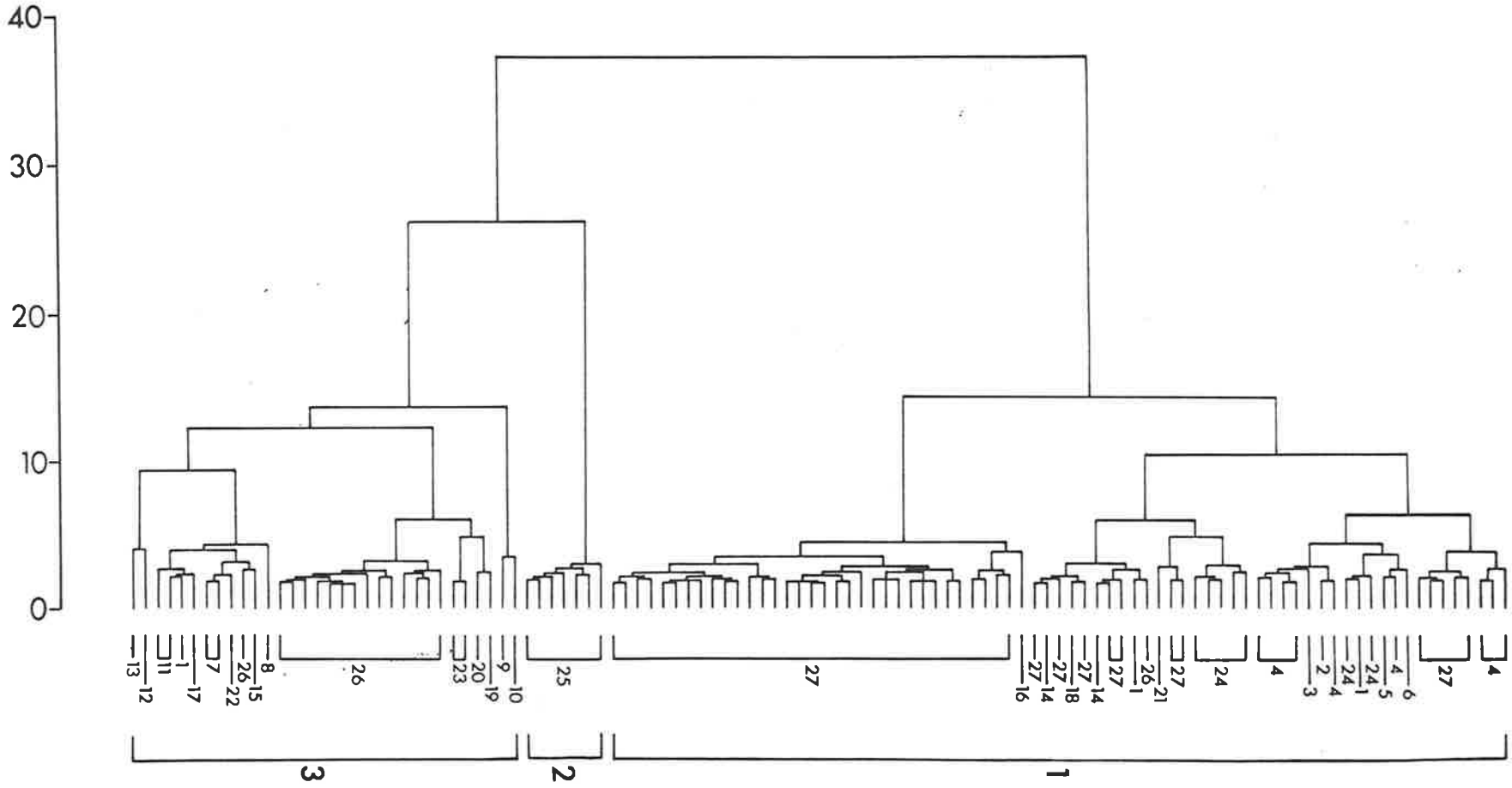

40
30
20
10
0
13 12 11 1 17 7 26 22 15 8
26
23 20 19 9 10
25
27
16 27 14 18 27 14 27 1 26 21 27
24
4
3 2 4 24 1 24 5 4 6
27
4
3
2
1

TABLE 15: Character contributions for the three groups shown in figure 6.

CHARACTER NUMBER	1/2,3	2/3
1	0.147	0.062
2	0.354	0.760
3	0.276	0.720
4	0.085	0.447
5	0.307	0.743
6	0.413	0.043
7	0.043	0.345
8	0.293	0.165
9	0.568	0.024
10	0.526	0.034
11	0.282	0.603
12	0.352	0.323
13	0.567	0.207
14	0.585	0.037
15	0.037	0.331
16	0.730	0.662
17	0.696	0.620
18	0.205	0.177
19	0.198	0.771
20	0.166	0.690
21	0.681	0.192
22	0.514	0.312
23	0.367	0.212
24	0.324	0.656
25	0	0.641

It appears that these characters, the first four of which are cuticular, are good discriminators, since there is little overlap of parataxa between the two groups formed by the first furcation. Similarly, for the furcation which divides group 2 from 3 (fig.6), the five most highly contributing characters are 19 (upper epidermal cell length: lower epidermal cell length), 2 (leaf width), 5 (leaf shape index), 3 (modified leaf length:width) and 20 (upper epidermal cell width:lower epidermal cell width). Except for the size difference between upper and lower epidermal cells, the most important characters are leaf width and shape. This is not unexpected, considering that group 2 (fig.6) contains parataxon NER/025, which is notable for its unusual leaf shape (figs 58-64).

This dendrogram (fig.6) could not be used to classify

all the OTUs, since beyond the three group stage parataxa are not well delimited. There are two obvious ways in which the classification could be improved. Firstly, the method for standardising the characters could be changed and secondly, the highly correlated characters could be removed.

B: 112 OTUs classified using the ESS clustering algorithm with 25 characters standardised to states: The dendrogram is shown in figure 7, and the values for $(\frac{B}{T})^{\frac{1}{2}}$ are given in table 16.

TABLE 16: $(\frac{B}{T})^{\frac{1}{2}}$ data for the dendrogram shown in figure 7 of 112 OTUs with 25 characters standardised to states. The groups marked on the dendrogram match those in this table.

GROUP NUMBER	$(\frac{B}{T})^{\frac{1}{2}}$	
1	0.359	0.314
2	0.359	0.290

Two groups are suggested by these calculations. Only parataxon NER/027 overlaps between these two groups, but generally the clustering of parataxa within the groups is poor.

The character contributions to the classification (table 17) show that for the first furcation (splitting groups 1 and 2) the five most important characters were 13 (upper epidermal cell length), 16 (lower epidermal cell length), 14 (upper epidermal cell width), 17 (lower epidermal cell width) and 3 (modified leaf length:width). As in figure 6, the four most highly contributing characters to the first furcation are cuticular, and three of the four are common to both dendrograms (characters 14,16 and 17). The initial furcation appears to have been relatively unaffected by the method of character standardisation.

FIGURE 7. ESS dendrogram for 112 fossil OTUs with 25 characters standardised to states. (large numbers = groups; small numbers correspond to parataxon numbers).

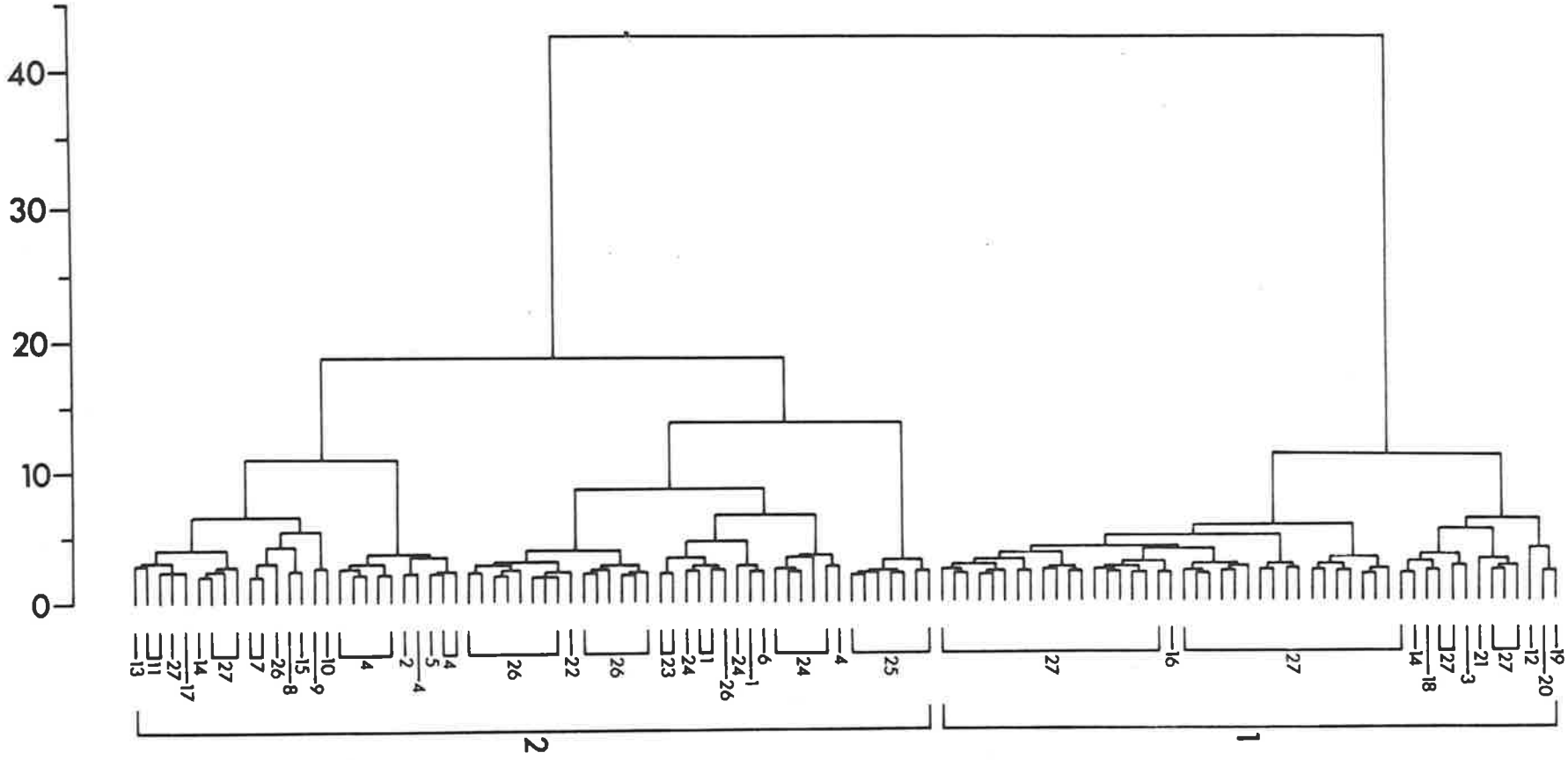

40
30
20
10
0
13
11
27
17
14
27
7
26
8
15
9
10
4
2
4
5
4
26
22
26
23
24
1
26
24
6
1
24
4
25
27
16
27
14
18
27
3
21
27
12
20
19
2
1

TABLE 17: Character contributions for the two groups shown in figure 7.

CHARACTER NUMBER	1/2
1	0.358
2	0.490
3	0.540
4	0
5	0.423
6	0.504
7	0.390
8	0.155
9	0.330
10	0.440
11	0.063
12	0.105
13	0.730
14	0.632
15	0.358
16	0.645
17	0.550
18	0.392
19	0.212
20	0.089
21	0.462
22	0.326
23	0.276
24	0.330
25	0.182

It is interesting to note the position of the seven OTUs in parataxon NER/025. They still occur in a very distinct cluster, but as part of a larger group (2 in fig.7). This is a good illustration of the effect of the different methods of standardisation. The OTUs in parataxon NER/025 have many extreme character values, which are emphasised when the characters are standardised to variance. Therefore, in figure 6 these seven OTUs are very widely separated from all other OTUs. However, in figure 7, where extreme values have not been emphasised, by standardising to states (Blackburn 1978a), these seven OTUs still form a distinct cluster, but they are not widely separated from other OTUs.

Parataxa are not well delimited in this classification (fig.7) and it is evident that for this set of OTUs at least, standardising to variance (fig.6) produced a slightly clearer

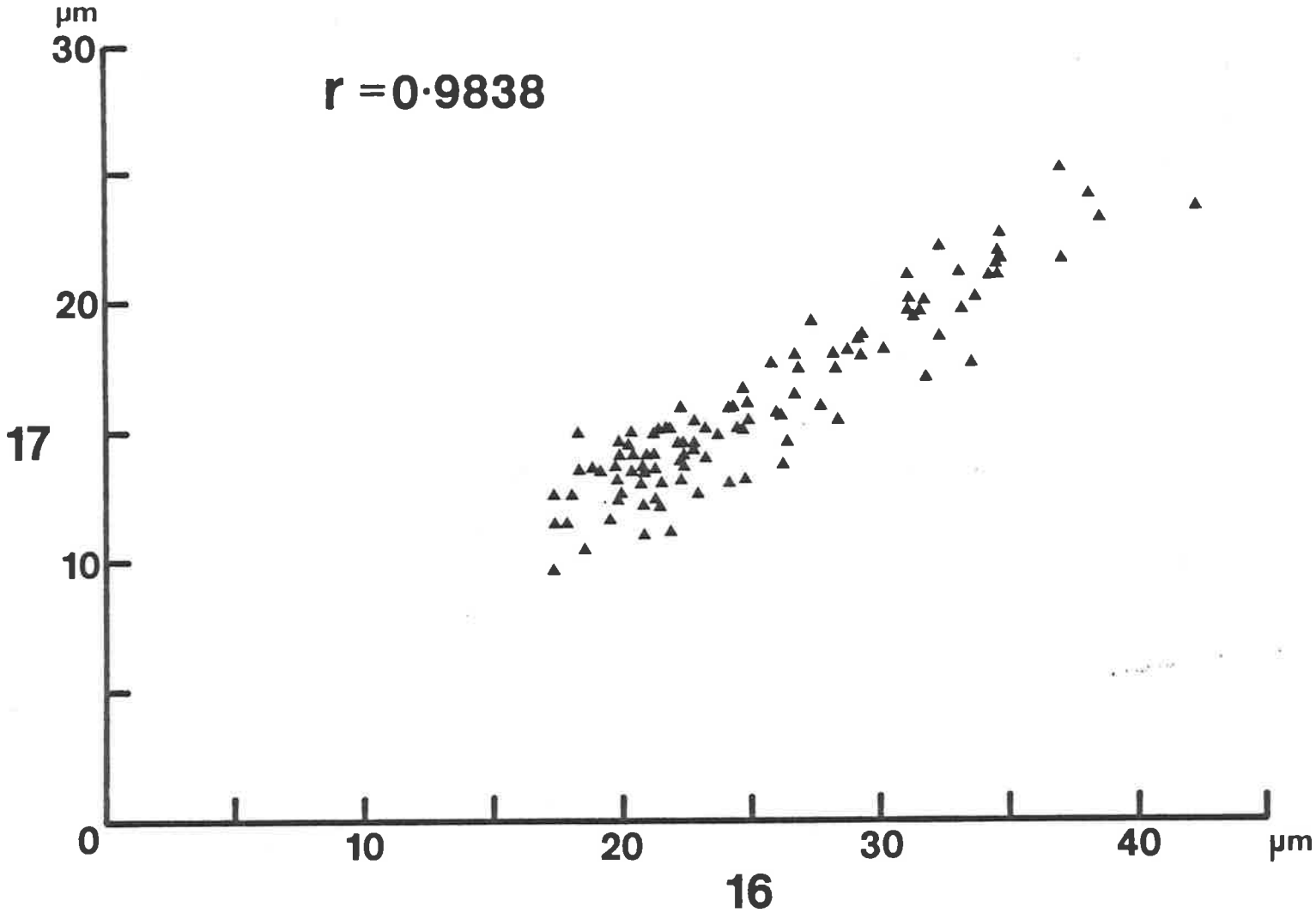
classification than standardising to states (fig.7).

C: 112 OTUs classified using the ESS clustering algorithm with 13 characters standardised to zero mean and unit variance: The effect of highly correlated characters was investigated in chapter 4 on extant leaves. It was concluded that the new information in each character outweighed the deleterious effects of high correlation, and therefore as many characters as possible should be used. However, the example used in chapter 4 represented an extremely artificial situation, where the success or failure of different approaches could be assessed easily. In this study, the effect of different approaches is not as easily guaged, and enough doubt exists over character correlation that it was considered useful to re-classify the OTUs with the more highly correlated characters removed.

The Pearson product-moment correlation coefficients were calculated for the 25 characters over the 112 OTUs (appendix I). If the 5% level of significance was chosen for discarding characters, virtually all characters would be removed from this study. It is instructive to examine graphs of pairs of characters with different correlation coefficients to gain a visual impression of how strongly any two characters are correlated. Figure 8 is a plot of character 16 (lower epidermal cell length) against character 17 (lower epidermal cell width), for which r = 0.9838. This value is much greater than the 0.001 (0.1%) significance level. These two characters are very highly correlated, and it can be seen from the plot (fig.8) that they contain very little unique information.

The 5% significance level with 111 degrees of freedom

FIGURE 8. Graph of character 16 (lower epidermal cell length) against character 17 (lower epidermal cell width) for 112 fossil OTUs.


µm
30
20
17
10
0
r =0·9838
10
20
30
40
µm
16

is approximately 0.185. Figure 9 is a plot of character 6 (number of secondary veins) against character 4 (position of maximum width), for which r = 0.2623. This is still much higher than the 5% significance level, and yet each character obviously contributes a large amount of unique information. It is apparent that when discarding highly correlated characters, some parameter other than the 5% significance level is required. In chapter 4, $|r| = 0.6$ was chosen as an arbitrary significance level, and all pairs of characters with an $|r|$ value greater than this had their F-ratios examined and the character with the lowest F-ratio was discarded. This method could not be used here because the F-ratios cannot be calculated, since the identity of the OTUs is not certain.

A nearest neighbour network was constructed for the 25 characters using the absolute correlation coefficient, $|r|$, as the criterion. In this type of numerical taxonomic approach, the only concern is the absolute empirical correlation, whether it is positive or negative is unimportant. Figure 10 shows the NNN, containing five clusters. The largest cluster contains characters 10,13,14,16,17,21,22,23,24 and 25, which are all cuticular, with the exception of character 10 (secondary vein intercostal shape). The next largest cluster contains characters 4,6,7,8,9 and 12, which are all venation characters,with the exception of character 4 (position of maximum width). The third largest cluster contains characters 1,2,3,5 and 11, which are all characters of leaf size and shape, with the exception of character 11(secondary vein straightness index). The final two clusters contain only two characters each, 19 and 20 (cuticular characters) and 15 and 18 (cuticular characters).

FIGURE 9. Graph of character 6 (number of secondary veins) against character 4 (position of maximum width) for 112 fossil OTUs.

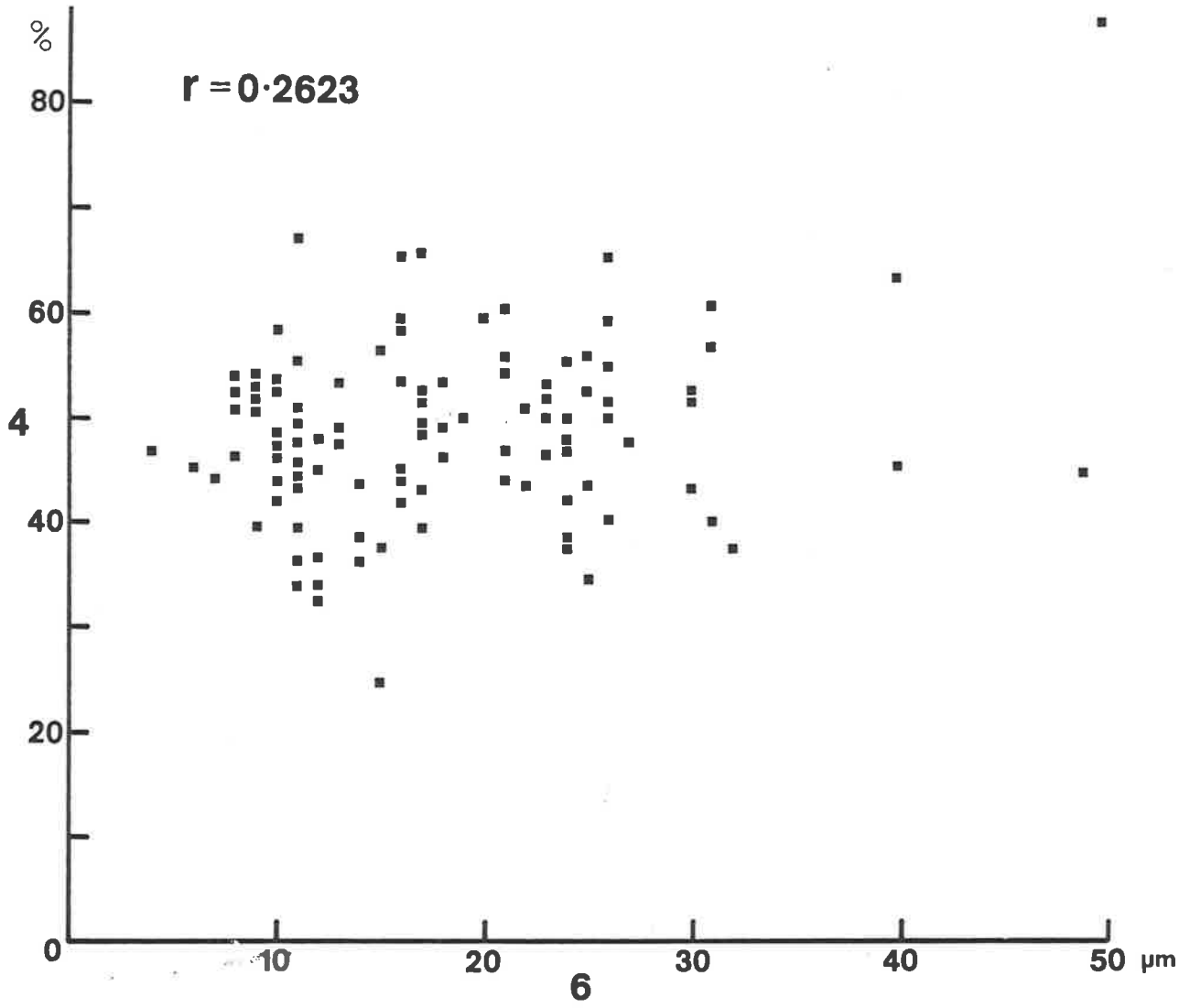
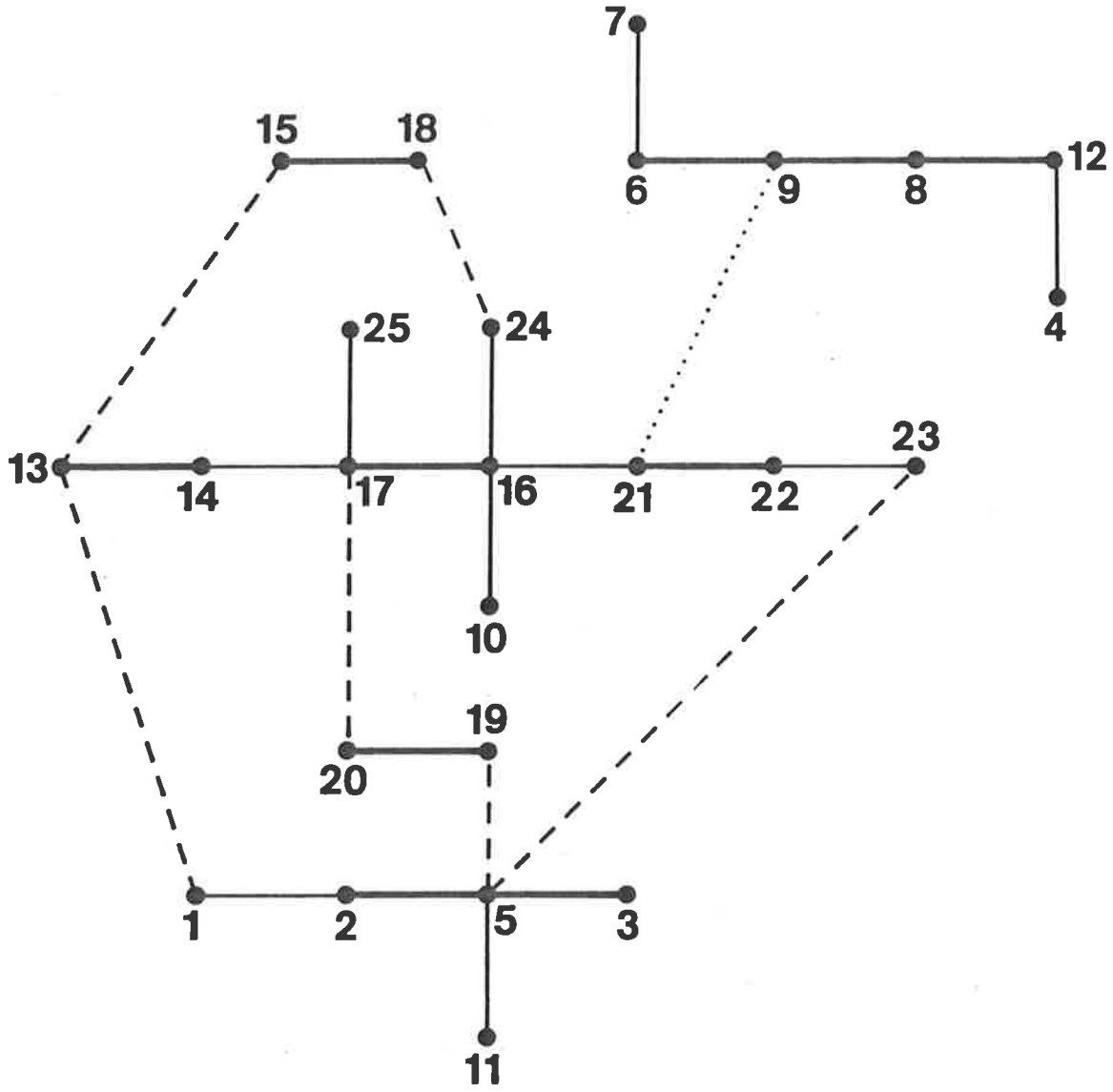

%
r = 0·2623
80
60
40
20
0
4
10
20
30
40
50 µm
6

FIGURE 10. Nearest neighbour network for the 25 characters scored for the 112 fossil OTUs, based on Irl. The heavy, unbroken lines represent very strong bonds, the light, unbroken lines represent strong bonds, the broken lines represent weak bonds and the dotted line represents a very weak bond. The numbers = character numbers.


7
15
18
12
6
9
8
4
25
24
23
13
14
17
16
21
22
10
19
20
1
2
5
3
11

This is an interesting, if somewhat predictable result. The characters used on fossil angiosperm leaves fall into three basic groups: leaf size and shape; venation; and cuticular. Characters within each of these three groups are generally highly correlated to one another, but the correlations between the three groups are usually much lower. Of the 25 characters, five fall into the first category (leaf size and shape), seven in the second (venation), and 13 in the third (cuticular). The large number of cuticular characters is an artifact of the exceptionally good cuticular preservation of the Nerriga fossils.

The strategy chosen for the removal of highly correlated characters was as follows: firstly the modulus of the correlation coefficients for each character with every other character was summed and an average correlation coefficient was calculated ($|\bar{r}|$). The character with the largest $|\bar{r}|$ value was then deleted and $|\bar{r}|$ was recalculated for the remaining 24 characters. This process was repeated until the maximum value of $|\bar{r}|$ fell below the 5% significance level (0.185). At that stage 13 characters remained. They were 1,4,7,8,10,11,12,14,15,18,20,23 and 25. The values for $|\bar{r}|$ are shown in table 18.

Two of the 13 characters remaining were of leaf size or shape, five were of venation and six cuticular. By referring to figure 10 it can be seen that all five clusters contribute to the 13 characters, but now the largest cluster contains four characters, and the smallest one.

The dendrogram produced using 13 characters standardised to variance is shown in figure 11 and the values for $(\frac{B}{T})^{\frac{1}{2}}$ are given in table 19.

CHARACTER NUMBER	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|
1	3.5781	3.4091	3.1586	3.0223	2.4730	2.4183	2.1769	1.9949	1.9464	1.8094	1.7225	1.5069
2	6.9965	6.8096	6.2760	6.1150M								
3	6.4046	6.1717	5.6743	5.4969	4.7800	4.6578	3.8643	3.7736	3.4215	3.1252M		
4	2.8649	2.8514	2.8024	2.7707	2.6017	2.4039	2.2732	2.1432	1.8809	1.8579	1.6976	1.6259
5	6.6827	6.5139	5.9826	5.8259	4.9633	4.8833M						
6	6.5628	6.1354	5.8041	5.4645	5.3608	4.6582	4.6045	4.3298M				
7	4.9427	4.7737	4.5883	4.4784	4.2033	3.8193	3.5521	3.3920	2.8679	2.8229	2.4632	2.3315
8	5.4849	5.2344	5.1267	4.8732	4.7644	3.9331	3.7968	3.5112	2.9769	2.8032	2.6411	2.3148
9	7.0309	6.5500	6.2596	5.8136	5.7203M							
10	5.8564	5.3645	4.9518	4.5424	4.3166	3.9713	3.7759	3.3248	2.8742	2.7774	2.6298	2.1416
11	4.5632	4.2996	4.1891	3.9479	3.6500	3.3584	3.0475	2.8037	2.5776	2.3541	2.0950	1.8390
12	4.6628	4.4135	4.3404	4.0738	3.9281	3.4001	3.2800	3.0147	2.6491	2.4612	2.3166	2.0838
13	8.3432	7.6506M										
14	7.4906	6.7944	5.8795	5.1558	4.7031	4.4149	3.9387	3.4416	3.2188	3.0204	2,6129	1.9576
15	3.4941	3.3703	3.0299	3.0140	2.7326	2.7109	2.4909	2.4106	2.1257	1.8824	1.5870	1.5577
16	8.9602M											
17	8.0815	7.1432	6.4806M									
18	3.9077	3.5832	3.3628	3.3474	3.2288	3.0576	2.9785	2.8137	2.4735	2.4015	2.1825	1.9865
19	6.1461	5.7335	5.4307	5.0312	4.6001	4.3598	3.9215	3.6438	3.4966M			
20	5.5166	5.1440	4.8936	4.4419	4.0874	3.8772	3.4862	3.2954	3.1936	2.3655	2.0657	2.0074
21	7.4761	6.7736	6.1760	5.4950	5.1928	4.6924	4.3820	3.4924	3.1885	3.0588	2.8486M	
22	7.1225	6.4522	6.0257	5.3737	5.2341	4.8323	4.6991M					
23	3.5956	3.5192	3.2608	3.2029	2.9614	2.7379	2.4557	2.1113	2.0917	1.8992	1.6869	1.5970
24	4.4583	3.9666	3.7696	3.3805	3.2881	3.1995	3.1115	3.0915	3.0542	2.7024	2.6974	2.6284M
25	3.5938	3.2388	3.1321	2.7670	2.6141	2.5772	2.3615	2.2104	2.1743	1.8763	1.7176	1.6921
$\bar{\lvert r \rvert}$	=.3733	=.3326	=.2946	=.2912	=.2860	=.2570	=.2611	=.2547	=.2185	=.2083	=.2035	=.2022

TABLE 18: The sum of r values for each character. In each column the maximum value is marked (= M), and at the bottom of each column $\bar{r}$ is given for that character.

CHARACTER NUMBER	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|	|r|
1	1.4552	1.4049	1.2984	1.2403	1.0503M							
2												
3												
4	1.4820	1.2198	1.1613	1.1291	0.9144	0.8027	0.6708	0.6201M				
5												
6												
7	2.1069	1.5998	1.4465	1.4000M								
8	2.2145M											
9												
10	1.9078	1.8025M										
11	1.6409	1.5149	1.2360	1.1054	0.9108	0.7358	0.6888	0.5876	0.4205	0.2743M		
12	1.9594	1.3429	1.2299	0.9903	0.7103	0.6571	0.5763	0.5225	0.2477	0.1612	0.0660M	
13												
14	1.7761	1.6544	1.2815	1.0233	0.9238	0.7341	0.5160	0.4484	0.4212M			
15	1.4461	1.3982	1.2141	1.1986	0.9886	0.7823	0.6562	0.2467	0.2079	0.1493	0.0644	0.0155
16												
17												
18	1.6318	1.6119	1.2804	1.0844	0.9044	0.7978	0.7077M					
19												
20	1.7072	1.5141	1.4803M									
21												
22												
23	1.3369	1.2481	1.1972	1.0439	1.0141	0.9903M						
24												
25	1.3486	1.2729	1.1520	0.8035	0.8021	0.6181	0.3938	0.3689	0.2567	0.1268	0.0326	0.0155
$\overline{\lvert r \rvert}$	=.1845	=.1639	=.1480	=.1556	=.1313	=.1415	=.1180	=.1240	=.1053	=.0914	=.0330	

TABLE 18: Continued.

FIGURE 11. ESS dendrogram for 112 fossil OTUs with 13 characters standardised to zero mean and unit variance (large numbers = groups; small numbers correspond to parataxon numbers).

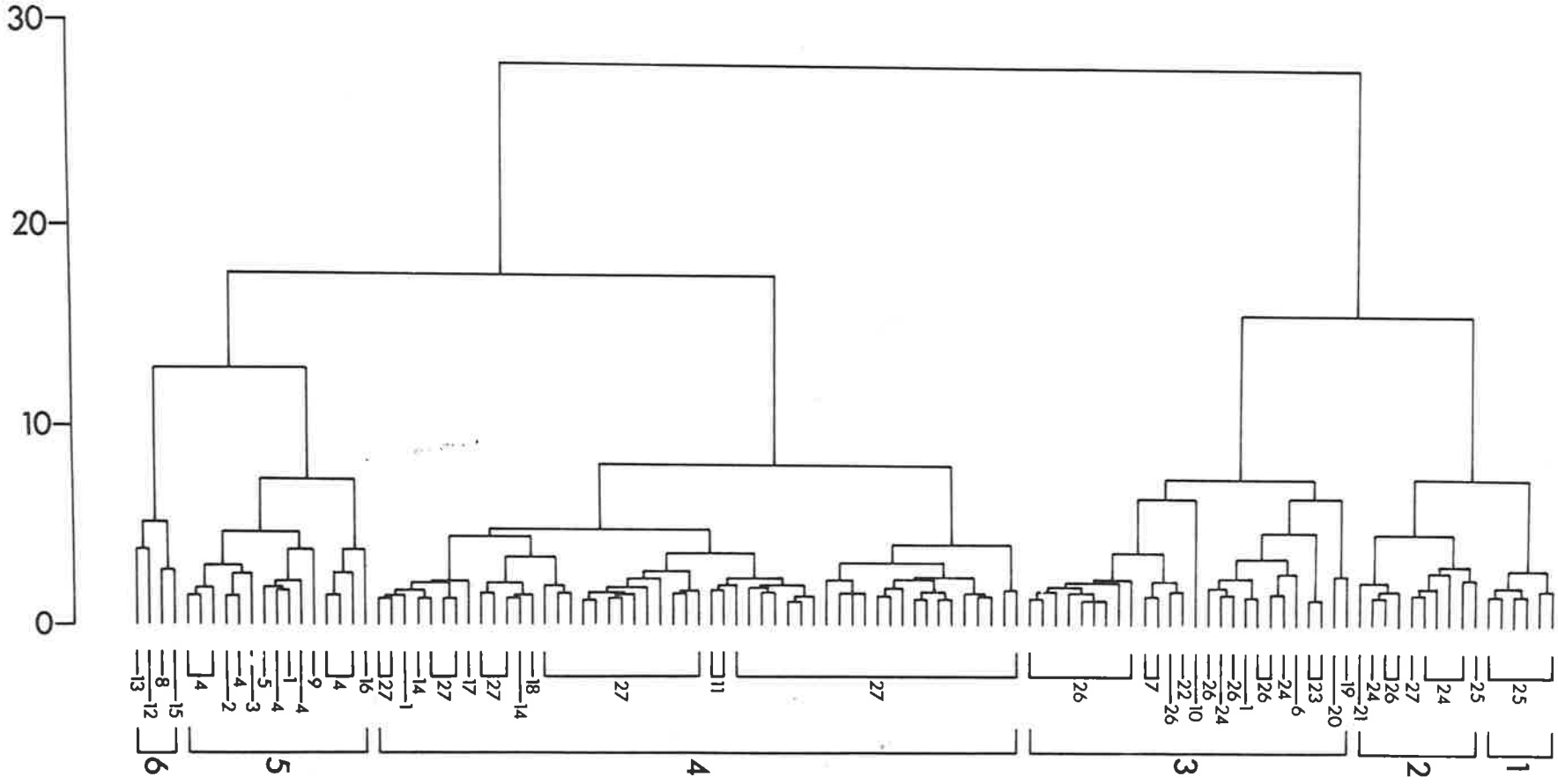

30
20
10
0
13 12 15 8 4 2 3 4 5 4 1 4 9 4 16 1 27 14 27 17 27 18 14 27 11 27 26 7 26 22 10 26 24 1 26 6 24 23 20 19 21 24 26 27 24 25 25
6
5
4
3
2
1

TABLE 19: $(\frac{B}{T})^{\frac{1}{2}}$ data for the dendrogram shown in fig.11 of 112 OTUs with 13 characters standardised to variance. The groups marked on the dendrogram match those in this table.

GROUP NUMBER	$(\frac{B}{T})^{\frac{1}{2}}$			
1	0.284	0.349	0.425	
2	0.284	0.349	0.425	0.411
3	0.284	0.349	0.322	
4	0.284	0.329	0.271	
5	0.284	0.329	0.368	0.356
6	0.284	0.329	0.368	0.588

Six groups are suggested by the calculations in table 19. Group 1 (table 19) does not reach a maximum value for $(\frac{B}{T})^{\frac{1}{2}}$ but it can be seen (fig.11) that this group contains six of the seven OTUs in parataxon NER/025 and it was therefore not further split. Group 2 (table 19, fig.11) is largely a non-conformist group, containing the seventh OTU belonging to parataxon NER/025, one OTU belonging to parataxon NER/027, two OTUs belonging to parataxon NER/024 and the only OTU in parataxon NER/021. Groups 3,4 and 5 (table 19, fig.11) also contain a number of parataxa. Group 6 contains four parataxa, each represented by a single OTU. It can be seen (table 19) that $(\frac{B}{T})^{\frac{1}{2}}$ does not reach a maximum value for this group. The four parataxa could each have been considered as individual groups according to the $(\frac{B}{T})^{\frac{1}{2}}$ values, but they have been amalgamated because of the small group size.

The character contributions to the first furcation (splitting groups 1,2 and 3 from groups 4,5 and 6 in fig.11) are shown in table 20.

TABLE 20: Character contributions for the six groups shown in fig.11.

CHARACTER NUMBER	1,2,3/4,5,6	1,2/3	1/2	4/5,6	5/6
1	0.224	0.084	0.155	0.355	0.696
4	0.341	0.329	0.303	0.420	0.187
7	0.610	0.367	0.504	0.290	0.762
8	0.505	0.463	0.389	0.507	0
10	0	0.738	0.195	0.084	0.470
11	0.336	0.363	0.214	0.095	0.207
12	0.556	0	0.639	0.420	0.032
14	0.470	0.167	0.585	0.239	0.197
15	0.126	0.190	0.202	0.614	0.355
18	0.148	0.352	0.485	0.489	0.182
20	0.114	0.669	0.675	0.089	0.443
23	0.063	0.338	0.318	0.421	0.884
25	0.192	0.473	0.867	0.253	0.367

The five characters contributing most are 7 (intersecondary vein percentage), 12 (tertiary vein angle), 8 (secondary vein angle A), 14 (upper epidermal cell width) and 4 (position of maximum width). It is interesting that the first three characters are venation characters, which rarely figured in the first two dendrograms (tables 15 and 17), and only one character is cuticular. Therefore removal of highly correlated characters has had a significant effect on the type of characters contributing most to the classification.

Character contributions to the other furcations in figure 11 are also given in table 20. Perhaps the most interesting are those contributing to the furcation splitting groups 1 and 2. It was noted earlier that characters of leaf width and shape contributed heavily towards splitting those OTUs in parataxon NER/025 from other OTUs (fig.6, table 15). In this dendrogram (fig.11) the five most highly contributing characters are 25 (stomatal index), 20 (upper epidermal cell width:lower epidermal cell width), 12 (tertiary vein angle), 14 (upper epidermal cell width) and 7 (intersecondary vein percentage). It is apparent that the characters which

emphasised the leaf width and shape of parataxon NER/025 are among those which have been deleted and the OTUs in this parataxon are no longer very widely separated from other OTUs.

A significantly larger number of groups were proposed for this dendrogram in comparison to the previous two (figs 6 and 7). There is some overlap of parataxa between the groups, but the clustering in this dendrogram most closely approaches that in the MST (fig.5.2).

D: 112 OTUs classified using the ESS clustering algorithm with 10 principal components as unstandardised characters:

A different approach can be made to the problem of character correlation through the use of ordination. Ordination takes correlation between characters into account by using the inverse of the dispersion (correlation) matrix. The principal components produced are therefore uncorrelated.

The 25 characters were reduced to 10 principal components which were then substituted for the characters in the cluster analysis. The principal components were unstandardised, for reasons discussed in chapter 3. The eigenvalues, percentage variance and cumulative variance are given in table 21.

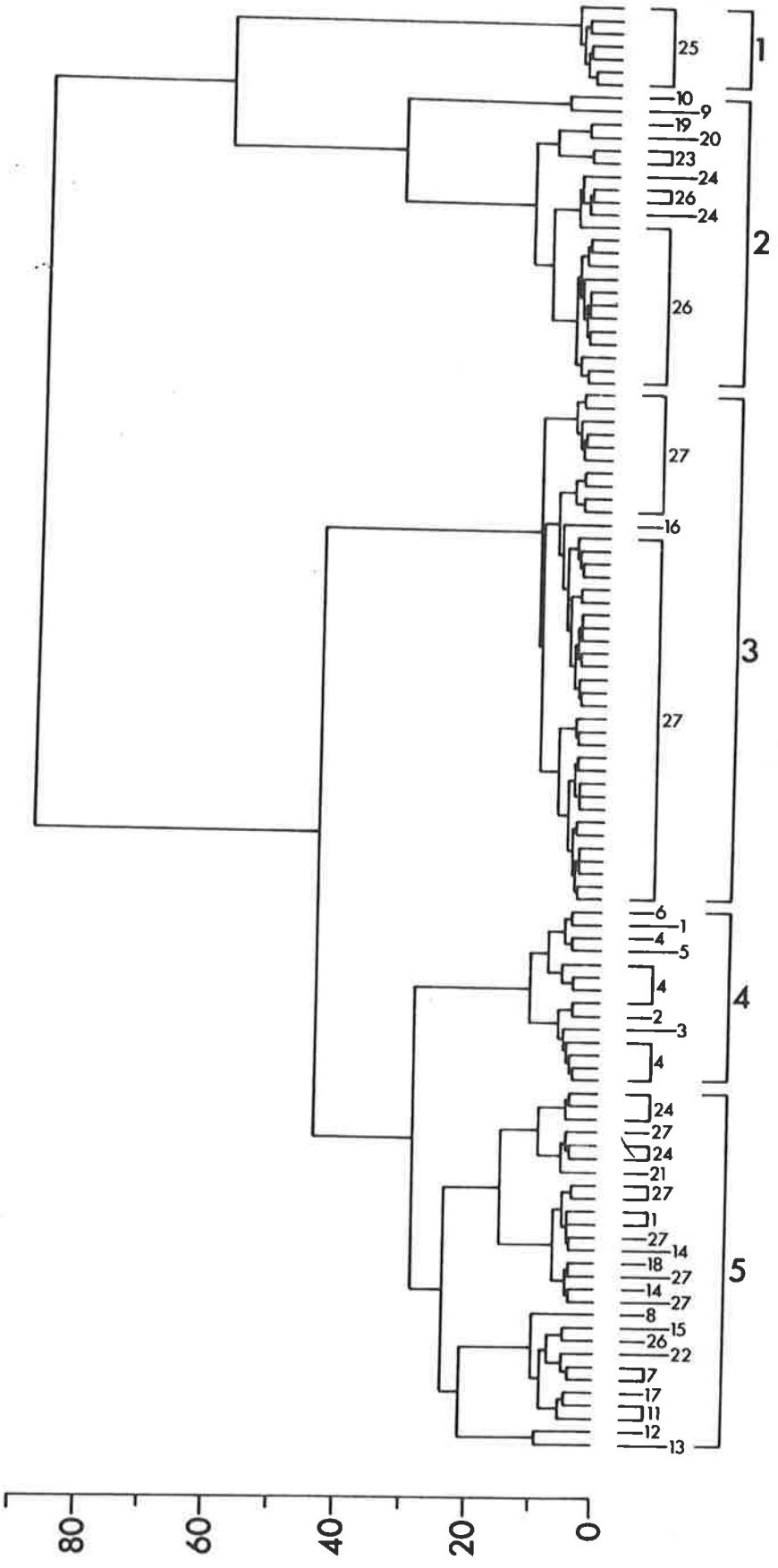
TABLE 21: Eigenvalues, percent variance and cumulative variance from the PCA on 112 OTUs with 25 characters.

EIGENVALUES	% VARIANCE	CUMULATIVE VARIANCE
6.56	26.23	26.23
4.15	16.59	42.82
2.79	11.15	53.79
1.89	7.57	61.54
1.66	6.63	68.16
1.43	5.73	73.89
0.93	3.72	77.60
0.91	3.65	81.26
0.84	3.38	84.64
0.74	2.96	87.60
0.61	2.46	90.05
0.57	2.28	92.33
0.50	2.02	94.35
0.38	1.51	95.86
0.32	1.27	97.13
0.28	1.13	98.27
0.19	0.77	99.03
0.07	0.29	99.33
0.06	0.25	99.57
0.05	0.18	99.76
0.04	0.15	99.91
0.01	0.05	99.96
0.01	0.02	99.98
0.00	0.01	100.00
0.00	0.00	100.00

The dendrogram is shown in figure 12. The number of groups cannot be estimated using the method described in chapter 3, because the characters are unstandardised. The number of clusters in this dendrograms was estimated after comparison with the other dendrograms (figs 6,7 and 11). Five clusters were delimited, as shown in figure 12.

Group 1 in figure 12 contains the seven OTUs in parataxon NER/025. These OTUs are well separated from all other OTUs. Cluster 2 in figure 12 contains 23 OTUs. Fifteen of the 16 OTUs in parataxon NER/026 occur in this group, as do all the OTUs in parataxa NER/009, NER/010, NER/019, NER/020 and NER/023. The remaining two OTUs belong to parataxon NER/024 (the other five OTUs in parataxon NER/024 are in group 5).

FIGURE 12. ESS dendrogram for 112 fossil OTUs with 10 unstandardised principal components as characters. (large numbers = groups; small numbers correspond to parataxon numbers).


25
1
10
9
19
20
23
24
26
24
2
26
27
16
3
27
6
1
4
5
4
2
3
4
4
24
27
24
21
27
1
27
14
18
27
14
27
8
15
26
22
7
17
11
12
13
5
80
60
40
20
0

Group 3 in figure 12 contains 40 OTUs, 39 of which belong to parataxon NER/027. The remaining OTU belongs to parataxon NER/016. The 14 OTUs in group 4 account for all members of parataxa NER/002, NER/003, NER/004 and NER/005. The remaining OTU belongs to parataxon NER/001. Group 5 appears to represent a non-conformist group. Of the 28 OTUs, 14 are accounted for by parataxa with only one or two OTUs (NER/007, NER/008, NER/011, NER/012, NER/013, NER/014, NER/015, NER/017, NER/018, NER/021 and NER/022). The remaining 14 OTUs consist of five of the seven in parataxon NER/024, two of the three in parataxon NER/001, six of the 45 in parataxon NER/027 and one of the 16 in parataxon NER/026. The OTUs cluster into their parataxa well in this dendrogram, except for some in the non-conformist group 5. The use of principal components as characters in the cluster analysis certainly gave a better classification than that produced with the 25 characters (fig.6), and is probably better than any of the other dendrograms.

Many authors have expressed the view that the first principal component may be an indicator of size (e.g. Fordham and Bell 1978). Sneath (1976) noted that size is a particularly serious problem in botanical taxonomy because of the extreme size differences which may be found between closely related taxa. For this reason, and also because it was suspected that leaf size was an extremely variable factor in several parataxa, the cluster analysis was rerun using only the latter nine of the first ten principal components. The result was extremely poor clustering, and very poor concurrence with any of the other classifications. The dendrogram has not been presented. It is of importance that PCA does not always produce size as the first component. In

fact it is totally dependent on the data set and no general rules can be made to apply (Blackburn 1978a).

6.5 CONCLUSION: The four dendrograms presented (figs 6,7,11 and 12) generally gave poorer classifications than the combination of the NNN (fig.4), MST (fig.5) and ESS dendrogram (fig.3). The major reason for this appears to be that the dendrograms are more seriously affected by the variability in the number of OTUs per parataxon than the NNN or MST. This problem will be considered later.

The stopping rule proposed in chapter 3 generally proved to be a very useful aid in interpreting the dendrograms. Its major value appeared to be in not splitting large groups of OTUs in which members of one or more parataxa are dispersed throughout the group (e.g. group 1 in fig.6 and group 1 in fig.7). The UPGMA dendrograms based on squared Euclidean distance and the coefficient of shape have not been presented because they were almost identical and were inferior to the ESS dendrograms in all facets.

6.6 ASSIGNING REMAINING SPECIMENS TO PARATAXA: The next step in the analysis was to assign the remainder of the specimens to the parataxa which have now been defined. Firstly the specimens were examined to select those which were well enough preserved to allow critical comparisons to be made. Many of the impressions were rejected as were some of the mummified leaves, which were too incomplete. When this sorting was completed, 469 specimens remained, giving a total of 581 specimens.

Most of these specimens could be assigned to the parataxa relatively easily, usually with the cuticular patterns being more reliable than the architecture or leaf shape.

The reason for this was twofold. Firstly, most of the mummified leaves were very incomplete, allowing only small parts of the leaves to be compared architecturally. Secondly, the cuticular preservation at Nerriga was extremely good, and for most parataxa, cuticular features could be defined which were unambiguous and easily determined. Of the 469 specimens, 445 were assigned to the existing parataxa. This left 24 specimens which were considered to belong to undefined parataxa.

It was proposed in chapter 1 that if any specimens were found which did not fit into the defined parataxa, they should be scored and added to the original set of OTUs and the analyses repeated. However, at this stage this was not considered to be the best course of action, because most of the new OTUs would score a large amount of missing data, and a program was not readily available to process data with missing scores.

For this reason, the 24 specimens were placed into parataxa without the aid of a numerical classification. The parataxa could then be formally described before determining any relationships between them. There are several advantages to this approach. The parataxa to be described will accomodate all the specimens available for comparison. It is necessary to give formal descriptions of these parataxa, so that it is possible to monitor the differences between the parataxa and the variability within them. The 24 specimens were split into 17 parataxa. A list of the parataxa and the number of specimens in each is given in table 22.

TABLE 22: List of the 44 parataxa at Nerriga and the number of specimens in each. Total number of specimens = 581.

PARATAXON	NO. OF SPECIMENS	PARATAXON	NO. OF SPECIMENS
NER/001	3	NER/023	2
NER/002	1	NER/024	18
NER/003	2	NER/025	71
NER/004	87	NER/026	100
NER/005	1	NER/027	246
NER/006	1	NER/028	2
NER/007	2	NER/029	1
NER/008	2	NER/030	2
NER/009	1	NER/031	1
NER/010	1	NER/032	1
NER/011	4	NER/033	1
NER/012	1	NER/034	1
NER/013	1	NER/035	1
NER/014	2	NER/036	1
NER/015	1	NER/037	1
NER/016	1	NER/038	1
NER/017	4	NER/039	1
NER/018	1	NER/040	1
NER/019	1	NER/041	1
NER/020	1	NER/042	6
NER/021	1	NER/043	1
NER/022	1	NER/044	1

CHAPTER 7

DESCRIPTION OF PARATAXA.

7.1 INTRODUCTION: Mayr (1969 p. 265) noted that the chief aim of a description is to aid subsequent recognition of the taxon involved. He suggested the use of a diagnosis to "distinguish the species (or whatever taxon is involved) from other known similar or closely related ones", and a description to "present a general picture of the described taxon."

It is important, particularly when describing fossils, to make use of as many features as possible, since the material is often fragmentary, or represents only a single organ. This is where the value of descriptive terminology becomes apparent. Three extremely useful terminologies are available for dicotyledonous leaves. Hickey (1973) described the architecture, including both the gross morphology and venation of dicotyledonous leaves; Stace (1965) described the cuticles of dicotyledonous leaves, and Dilcher (1974) reviewed both the architectural and cuticular characters. These three sources were used exclusively for terminology in the following descriptions.

Several important recommendations on the preparation of descriptions were summarised by Mayr (1969 p. 272). The following were considered to be important in the preparation of the parataxonomic descriptions:

(1) The taxonomic characters should be treated in a standardised sequence,

(2) The most easily visible characters should be featured,

(3) The description should provide quantitative data,

(4) The formal description should be followed by an informal discussion of the variable characters.

Each description is accompanied by a discussion and a table. The discussion is more important when there is more than one specimen in the parataxon, since the variability of the parataxon may then be considered. The tables contain 28 quantitative characters, showing the mean, standard deviation, range and number of specimens (where appropriate) on which each character was scored.

The 28 quantitative characters are:

(1) Modified leaf length

(2) Leaf width

(3) Modified leaf length:leaf width

(4) Position of maximum width

(5) Leaf shape index

(6) Dentition frequency

(7) Leaf base angle

(8) Leaf apex angle

(9) Number of secondary veins

(10) Intersecondary vein percentage

(11) Secondary vein angle A

(12) Secondary vein angle B

(13) Secondary vein straightness index

(15) Tertiary vein angle

(16) Upper epidermal cell length

(17) Upper epidermal cell width

(18) Upper epidermal cell length:width

(19) Lower epidermal cell length

(20) Lower epidermal cell width

(21) Lower epidermal cell length:width

(22) Upper epidermal cell length:lower epidermal cell length

(23) Upper epidermal cell width:lower epidermal cell width

(24) Stomatal length

(25) Stomatal width

(26) Stomatal length:width

(27) Subsidiary cell number

(28) Stomatal index

These characters were defined in chapter 4.

Where possible, illustrations have been provided, and for every OTU the specimen and its upper and lower epidermis are figured. Except where otherwise defined, the upper epidermis is taken to be the surface without stomates, and the lower epidermis is taken to be the surface with stomates. Figures showing detailed features of the cuticle were photographed with Nomarski optics. Where trichome bases were present on both epidermises, only those on the lower epidermis were figured unless they were structurally different from those on the upper epidermis.

7.2: DESCRIPTIONS: PARATAXON NER/001. (Table 23).

Lamina: Symmetrical, ovate to elliptical. Leaf narrows into an obtuse base and apex. Base and apex symmetrical. Leaf length 6.5 - 13 cm., width 2 - 3.2 cm. (figs. 18,19,20).

Margin: Crenate or serrate. Crenations or serrations of several orders, somewhat irregularly spaced.

Petiole: Unknown.

Venation: Primary vein straight or slightly curved, stout to massive. Secondary venation pattern semicraspedodromous. 12 - 17 uniformly curved secondary veins arise at an angle of 56-65°. This angle is uniform throughout the leaf. The loop forming branches of the secondary veins join superadjacent secondary veins at 90° or less. Secondary, tertiary and quaternary vein arches well formed. Composite, weakly developed intersecondary veins present to varying degrees. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with variable number of sides and straight to slightly sinuous walls (figs. 155,157,159). Cuticular pegs occur at cell wall junctions and the cuticular flange may extend deeply between adjacent cells. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight to slightly sinuous walls (figs. 156,158,160). Cuticular pegs occur at cell wall junctions and the cuticular flange may extend to a moderate degree between adjacent cells. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Stomata generally confined to areoles, oriented at random. The poral walls of the guard cells are heavily thickened.

Larger stomates occur occasionally over veins. The subsidiary cells are atinocytic and overlie the guard cells. Subsidiary cells of the stomata over the veins heavily striated. Trichome bases with a heavily thickened, circular foot cell and unmodified basal cells occur rarely over the major veins. Trichomes not preserved.

Specimens examined: N 0085 (fig. 18), N 0095 (fig. 19), N 0124 (fig. 20).

Discussion: All specimens consist of nearly complete leaves, although only two complete apices and one base are preserved. The apex of N 0124 (fig. 20) is attenuated, almost into a drip-tip, although according to Hickey's (1973) definition the apex is still strictly obtuse. The apex of N 0085 (fig. 18) is not drawn out, but is more bluntly obtuse. The base of N 0095 (fig. 19) is symmetrical and obtuse as is likely to be the case for N 0124. However, although the base of N 0085 is not preserved, it can be seen that the lamina begins to taper towards the base in a manner not exhibited by the other specimens. The venation pattern is semicraspedodromous, with each secondary vein dividing into two branches of approximately equal thickness, one of which runs directly into a tooth, while the other loops into the superadjacent secondary vein. Below this branch other higher order veins arise from the secondary vein and terminate in teeth. Weakly developed compound intersecondary veins occur in all specimens. Tertiary veins are not well defined.

The teeth in this taxon are extremely variable. In N 0095 (fig. 19) and N 0124 (fig. 20) they are serrations, although different in form. Specimen N 0085 (fig. 18) has crenations, with the veins terminating in the apical notch. Specimen N 0095 and N 0124 are both lacking cuticle at the

tooth apex, suggesting that a gland may have been present. A similar structure has not been conclusively identified in N 0085.

On the upper epidermis of one specimen (N 0085) the cuticular flange extends deeply between adjacent cells and in all specimens a well formed cuticular peg occurs at the junction of three cells. This is easily observable in figures 155 and 159. The cells above the veins are markedly longer and narrower than the non-venous cells.

The cuticular flanges on the lower epidermis are not heavily thickened, but a well formed cuticular peg occurs at the junction between three cells. This is especially noticable in figure 154. The cells above the veins are markedly longer and narrower than the non-venous cells.

Stomates are generally confined to the areoles, but larger stomates occur occasionally over the veins (figs. 166, 167). Stace (1965) noted that abnormally large stomata "are often, if not always, water-stomata, which are supposed to secrete drops of water." However, since the function of these stomates connot be demonstrated in fossils, the term water-stomate, with its implied function, will not be used.

All stomates have atinocytic subsidiary cells which are more heavily cutinised (and therefore more heavily stained) than the epidermal cells. The subsidiary cells overlie the guard cells (figs. 166,167,168), and in the larger stomates they are heavily striated (fig. 167). Trichome bases, with a heavily cutinised, circular foot cell and unmodified basal cells occur rarely over the major veins (fig. 169).

PARATAXON NER/002. (Table 24).

Lamina: Symmetrical, ovate. Leaf narrows into an obtuse base and apex. Base and apex symmetrical. Leaf length approximately 8 cm., width 4.6 cm. (fig. 21).

Margin: Serrate. Serrations of several orders, regularly spaced. Apical side of serration concave, basal side convex.

Petiole: Unknown.

Venation: Primary vein slightly sinuous, moderate. Secondary venation pattern semicraspedodromous. Eleven secondary veins arise at an angle of 69.5°. This angle is uniform throughout the leaf. The loop forming branches of the secondary veins join superadjacent secondary veins at 90° or less. Higher order arches not well formed. Simple and composite intersecondary veins well developed and common. Tertiary veins random reticulate. The apices of the serrations are not cutinised, suggesting the possible presence of glands (fig. 173).

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight to slightly sinuous walls (fig. 161). Fine cuticular pegs occur at cell wall junctions, and the cuticular flange extends deeply between cells. No surface ornamentation. Venous cells smaller than non-venous cells and with a greater length:width ratio. Trichome bases with a small, heavily thickened, irregularly shaped foot cell and unmodified basal cells occur occasionally over the major veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and curved or sinuous walls (fig. 160). Fine cuticular pegs occur at cell wall junctions but cuticular flanges are only lightly thickened. No surface ornamentation. Venous cells longer and narrower than non-venous cells.

TABLE 23: PARATAXON NER/001.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	3	3	3	3	3	3	2	2	3	3	3	3	3	3
M	6.9	2.5	2.7	48.1	79.0	2.94	68	52.5	14.0	28.4	60.7	35.5	1.87	46.4
SD	2.9	0.6	0.4	3.5	4.5	1.28	21.2	27.6	2.6	22.4	4.4	1.5	0.20	4.0
R	5.2	2.0	2.41	44.9	73.9	1.77	53	33	12	16.7	56.4	34.3	1.68	43.9
	10.3	3.2	3.22	51.9	82.1	4.31	83	72	17	52.9	65.1	37.2	2.11	51.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	3	3	3	3	3	3	3	3	3	3	3	3	3	3
M	62.7	32.5	21.7	1.50	28.6	17.4	1.65	1.14	1.25	20.2	19.5	1.04	4.98	10.1
SD	6.5	2.5	1.9	0.09	2.2	1.6	0.05	0.08	0.07	2.4	2.5	0.04	0.38	3.1
R	56.5	30.8	19.8	1.41	26.1	15.6	1.59	1.05	1.18	18.4	17.1	1.00	4.65	6.4
	69.5	35.4	23.6	1.58	30.3	18.5	1.68	1.20	1.31	22.9	22.0	1.08	5.4	11.9

TABLE 24: PARATAXON NER/002.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	6.9	4.6	1.5	44.4	69.5	2.20	100	77	11	81.8	69.5	44.2	2.00	43.7

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	52.5	33	20.9	1.58	26.3	15.5	1.70	1.26	1.35	18.9	16.0	1.18	4.25	11.9

(NS = number of specimens; M = mean; SD = standard deviation; R = range).

Stomata generally confined to areoles, oriented at random. The poral walls of the guard cells are thickened. Larger stomates occur occasionally over the veins. Subsidiary cells actinomorphic and not overlying the guard cells (figs. 170, 171). Trichome bases with a small,thickened, irregularly shaped foot cell and unmodified basal cells occur commonly over veins (fig. 172). Trichomes not preserved.

Specimen examined: N 0013 (fig. 21).

Discussion: The specimen consists of an almost complete leaf with both the base and apex preserved (fig. 21). The venation pattern is semicraspedodromous, with each secondary vein dividing into two branches of approximately equal thickness, one of which runs directly into a tooth while the other loops into the superadjacent secondary vein. Below this branch, several higher order veins branch off from the secondary and terminate in teeth of varying sizes. The serrations are irregularly spaced and of several orders. They have a concave apical side, convex basal side and a rounded sinus (fig. 21).

PARATAXON NER/003. (Table 25).

Lamina: Symmetrical, elliptical. Leaf base acute, cuneate, apex obtuse. Base and apex symmetrical. Leaf length 4.5 cm., width 1.3 cm. (fig. 22).

Margin: Serrate. Serrations of several orders, regularly spaced. Basal side convex.

Petiole: Unknown.

Venation: Primary vein straight, stout. Secondary venation pattern semicraspedodromous. Fifteen secondary veins arise at an angle of 69°. This angle is uniform throughout the leaf. The loop forming branches of the secondary veins

join superadjacent secondary veins at approximately 90°. Higher order arches not well formed. Composite inter-secondary veins uncommon and not well formed. Tertiary veins random reticulate or weakly percurrent. The cuticle is absent from the apex of the serrations, suggesting the presence of a gland.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls (fig, 163). Cuticular pegs occur at cell wall junctions, and the cuticular flange extends deeply between cells. No surface ornamentation. Venous cells not highly modified, but narrower and more heavily cutinised than the non-venous cells. Trichome bases with a small, heavily thickened, circular foot cell and unmodified basal cells common over major veins. Basal cell of trichome long and thinly cutinised. Apical cell(s), if present, unknown.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 162). Cuticular pegs occur at cell wall junctions, but otherwise the cuticular flanges are not heavily thickened. No surface ornamentation. Venous cells longer, narrower, and more regularly arranged than the non-venous cells. Stomata generally confined to areoles, oriented at random. Larger stomates occur occasionally over veins. Subsidiary cells actinomorphic and not overlying the guard cells (figs. 192, 193). The poral walls of the guard cells are heavily thickened. Trichome bases with a heavily thickened, circular foot cell occur commonly over and between veins (fig. 194). Over veins, the basal cells are unmodified, between veins they are radial. Trichomes as for upper epidermis.

Specimen examined: N 0016 (fig. 22).

Discussion: The specimen consists of a complete leaf. The venation pattern is semicraspedodromous, with each secondary vein dividing into two branches of approximately equal thickness. One of these veins runs directly into a serration while the other loops into the superadjacent secondary vein at approximately 90°. Below this branch, one or two other higher order veins branch off from the secondary vein and terminate in serrations of varying sizes. The basal side of a serration is extremely convex, and the apex is acute. Despite the varying orders of serrations, the difference between them is slight and they are regularly arranged.

PARATAXON NER/004. (Table 26).

Lamina: Symmetrical, obovate. Leaf base acute, normal or cuneate; apex obtuse. Leaf length 7 - at least 14.5cm., width 2.4 - 5.3cm. (figs. 23-31).

Margin: Minutely serrate. Serrations of one order, regularly spaced.

Petiole: Unknown.

Venation: Primary vein straight, slightly curved or sinuous, usually moderate. Secondary venation pattern semicraspedodromous. 10-21 uniformly curved secondary veins arise at an angle of 56°- 70°. This angle is uniform throughout the leaf. The loop forming branches of the secondary veins join superadjacent secondary veins at 90° or less. Secondary, tertiary and quaternary arches often well formed. Simple and composite intersecondary veins present. Tertiary veins random reticulate or weakly percurrent. The cuticle is missing at the apex of the serrations, suggesting the

TABLE 25: PARATAXON NER/003.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	3.3	1.3	2.5	49.0	76.9	3.89	46	74	13	15.4	68.6	36.7	1.9	41.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	34.0	23.8	16.0	1.49	17.3	9.6	1.80	1.38	1.67	21.5	19.8	1.09	5.25	9.4

TABLE 26: PARATAXON NER/004.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	9	9	9	9	9	9	4	3	9	9	9	9	9	9
M	8.2	3.9	2.1	56.1	77.1	3.15	71	70.7	16.1	31.8	65.4	43.2	2.15	58.0
SD	2.0	0.9	0.2	4.7	2.8	2.23	14.0	30.9	2.9	17.0	4.3	3.8	0.27	15.8
	5.2	2.4	1.69	49.2	73.7	0	57	35	10	14.3	56.3	39.3	1.75	34.0
R	11.9	5.3	2.46	65.8	82.8	7.82	83	90	21	60.0	70.2	49.8	2.60	84.9

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	9	9	9	9	9	9	9	9	9	9	9	9	9	9
M	55.9	28.0	17.3	1.62	22.6	13.0	1.76	1.24	1.35	19.9	17.9	1.11	4.97	11.03
SD	7.6	3.3	1.5	0.10	2.3	1.8	0.17	0.11	0.18	1.2	1.4	0.04	0.28	2.04
	44.5	24.3	15.8	1.41	19.6	10.9	1.49	0.98	0.96	17.9	16.1	1.07	4.5	7.35
R	68.0	34.4	20.4	1.76	27.3	16.6	2.01	1.38	1.53	21.3	20.0	1.19	5.4	13.84

(NS = number of specimens; M = mean; SD = standard deviation; R = range).

possible presence of a gland.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls (figs. 175,177,179,181,183,185,187,189,191). Small cuticular pegs occur at cell wall junctions, and occasionally the cuticular flange extends deeply between cells. No surface ornamentation. Venous cells smaller, and with a greater length:width ratio than non-venous cells. Trichome bases with a small, circular, heavily thickened foot cell and unmodified basal cells common over and between the veins. Trichomes not preserved.

Lower epidermis: Non-venous cells with a variable number of sides and straight or curved walls (figs. 174,176,178,180, 182,184,186,188,190). Very fine cuticular pegs occur at cell wall junctions, but otherwise the cuticular flange is not heavily thickened. No surface ornamentation. Venous cells much longer and narrower than non-venous cells. Stomata generally confined to areoles, oriented at random. The poral walls of the guard cells are heavily thickened. Larger stomates occur occasionally over the veins. Subsidiary cells actinomorphic and overlying the guard cells. Trichome bases with a small, circular, heavily thickened foot cell occur commonly over and between the veins. Trichome basal cells unmodified over the veins, more or less radial between the veins. Trichomes unicellular, long, thinly cutinised.

Specimens examined: N 0009 (fig. 23), N 0048 (fig. 25), N 0072 (fig. 24), N 0086 (fig. 26), N 0099 (fig. 27), N 0104 (fig. 30), N 0119 (fig. 31), N 0123 (fig. 29), N 0127 (fig. 28).

Discussion: The specimens consist of relatively complete leaves. The base is preserved on four specimens (figs. 23, 28,30,31), and is acute, while the apex, which is preserved

on three specimens (figs. 28,29,30), tends to be obtuse and normal or cuneate. One specimen, (N 0104, fig. 30) has a drip-tip apex. While the absolute size of the specimens varies greatly, they are all very similar in shape, being obovate and having a modified leaf length:width ratio of approximately two. The primary vein is variable, being straight, curved or sinuous. The venation pattern is semicraspedodromous, with each secondary vein dividing into two branches of approximately equal thickness, one of which runs directly into a serration, while the other loops into the superadjacent secondary vein. Below this branch, several other higher order veins branch from the secondary and terminate in serrations. The serrations are extremely small, and are not cutinised at the apex, suggesting the possible possession of a gland (fig. 199). Simple and composite intersecondary veins are present to varying extents and the tertiary veins are not well defined.

At the junction of three cells on the upper epidermis, a small cuticular peg is formed (figs. 175,177,179,181,183, 185,187,189,191), and in some specimens the cuticular flange extends between adjacent cells to a moderate degree. Trichome bases with a small, roughly circular, heavily thickened foot cell and unmodified basal cells are over, and in some specimens, between the veins (figs. 175,177,179,181, 185,191).

At the junction of three cells on the lower epidermis, very fine cuticular pegs are formed, but otherwise the cuticular flange is not heavily thickened. Stomates are generally confined to the areoles (figs. 174,176,178,180,182, 184,186,188,190), but larger stomates occur occasionally over the veins (fig. 195). All stomates have actinomorphic

subsidiary cells which cannot be distinguished from the surrounding epidermal cells (figs. 195,196). The subsidiary cells overly the guard cells and the poral walls of the guard cells are generally heavily thickened (figs. 195,196). Trichome bases with a small, circular, heavily thickened foot cell are common over and between the veins (fig. 197). Over the veins, the trichome basal cells are unmodified, but they are generally radial between the veins. In several specimens the trichomes are preserved, and are unicellular, thinly cutinised, and taper to an acute apex (fig. 198).

PARATAXON NER/005. (Table 27).

Lamina: Symmetrical, slightly obovate. Leaf narrows into an obtuse base and apex. Base and apex symmetrical. Leaf length 11.4cm., width 3.5cm. (fig. 33).

Margin: Weakly serrate. Serrations of several orders, regularly spaced.

Petiole: Unknown.

Venation: Primary vein straight, moderate. Secondary venation pattern semicraspedodromous. 16 uniformly curved secondary veins arise at an angle of 66.5°. This angle is uniform throughout the leaf. The loop forming branches of the secondary veins join superadjacent secondary veins at approximately 90°. Secondary, tertiary and quaternary arches well formed. Poorly formed composite intersecondary veins occasionally present. Tertiary veins weakly percurrent. The cuticle is missing at the apex of the serrations, suggesting the possible presence of a gland.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and curved or sinuous walls (fig. 165). Fine cuticular pegs occur at cell wall junctions, but the cuticular

flange is not heavily thickened. No surface ornamentation. Venous cells smaller, and with a greater length:width ratio than non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and curved or sinuous walls (fig. 164). Extremely fine cuticular pegs occur at cell wall junctions, but the cuticular flange is not heavily thickened. No surface ornamentation. Venous cells longer, narrower, and slightly more heavily thickened than non-venous cells. Stomata generally confined to areoles, oriented at random. The poral walls of the guard cells are heavily thickened. Larger stomates occur occasionally over veins (fig. 206). Subsidiary cells actinomorphic, overlying the guard cells (figs. 206,207). Trichome bases with a small, thickened, circular foot cell and unmodified basal cells occur rarely over the major veins.(fig. 208). Trichomes not preserved.

Specimen examined: N 0067 (fig. 33).

Discussion: The specimen consists of an almost complete leaf. The venation pattern is semicraspedodromous, with each secondary vein dividing into two branches of approximately equal thickness, one of which runs directly into a serration, while the other loops into the superadjacent secondary vein at about 90°. Below this branch, several other higher order veins branch off from the secondary and terminate in serrations of varying sizes. Tertiary veins are well defined at the widest part of the leaf, where they are conspicuously percurrent, but definition becomes poorer towards the base and apex (fig. 33).

PARATAXON NER/006. (Table 28).

Lamina: Symmetrical, elliptical. Leaf base obtuse, apex unknown. Base symmetrical. Leaf length at least 13 cm., width 3.9cm. (fig. 32).

Margin: Finely serrate. Serrations irregularly spaced, but of one order.

Petiole: Unknown.

Venation: Primary vein straight, moderate. Secondary venation pattern semicraspedodromous. Approximately 14 uniformly curved secondary veins arise at an angle of 55^{o}. This angle increases toward the apex. The loop forming branches of the secondary veins join superadjacent secondary veins at approximately 90^{o}. Secondary, tertiary and quaternary arches well formed. Weakly formed, composite intersecondary veins occur occasionally. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and curved or sinuous walls (fig. 201). Cuticular pegs occur at cell wall junctions, but otherwise cuticular flanges are not heavily thickened. No surface ornamentation. Venous cells not highly modified, but longer and narrower than non-venous cells. Trichome bases with a small, approximately circular, thickened foot cell, and basal cells which are smaller than the surrounding epidermal cells, occur rarely over the major veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and curved or sinuous walls (fig. 200). Cuticular flanges not heavily thickened. No surface ornamentation. Venous cells much longer, narrower, and straighter walled than non-venous cells. Stomata generally

confined to areoles, oriented at random.

The poral walls of the guard cells are heavily thickened. Larger stomates occur occasionally over veins. Subsidiary cells actinomorphic, slightly overlying the guard cells (fig. 209). Trichome bases with a small, approximately circular, thickened foot cell and unmodified basal cells occur very rarely over the major veins (fig. 210). Trichomes not preserved.

Specimen examined: N 0146 (fig. 32).

Discussion: The venation pattern is semicraspedodromous, with each secondary vein dividing into two branches of approximately equal thickness, one of which runs directly into a serration, while the other loops into the superadjacent secondary vein at approximately 90°. Below and sometimes above this branch, several other higher order veins branch off from the secondary and terminate in serrations.

PARATAXON NER/007. (Table 29).

Lamina: Slightly asymmetrical, ovate. Leaf base acute, apex unknown. Base symmetrical. Leaf length at least 8 cm., width 2.3 - 2.9cm. (figs. 34,35).

Margin: Entire.

Petiole: Incomplete. Apparently normal.

Venation: Primary vein curved, stout. Secondary venation pattern weakly brochidodromous. 15 - 17 secondary veins arise at an angle of 63° - 64°. This angle is uniform throughout the leaf. Secondary veins uniformly curved except for a sharp upward and inward curve in the distal third, when they loop into the superadjacent secondary vein at 90° or less. Simple and composite intersecondary veins well formed and frequent. Tertiary veins random reticulate.

TABLE 27: PARATAXON NER/005.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	0	1	1	1	1	1	1
M	10.5	3.5	3.0	65.5	80.4	3.03	73		16	6.3	66.5	36.3	1.83	40.6

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	57.5	33.5	22.4	1.50	22.4	13.9	1.61	1.50	1.61	21.8	19.3	1.13	4.95	13.6

TABLE 28: PARATAXON NER/006.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	0	1	1	1	1	1	1
M	10.2	3.9	2.6	53.5	79.9	4.65	86		13	23.1	55.0	32.2	1.80	50.8

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	66.0	34.3	21.5	1.60	26.9	17.8	1.51	1.28	1.21	16.4	14.6	1.12	4.25	21.4

TABLE 29: PARATAXON NER/007.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	2	2	2	2	2	2	2	0	2	2	2	2	2	2
M	7.5	2.6	2.90	40.5	83.3	0	83.5		16	76.5	63.5	31.0	1.94	44.3
R	7.0	2.3	2.76	37.7	82.4	0	83		15	52.9	63.9	26.7	1.9	40.6
	8.0	2.9	3.04	43.2	84.1		84		17	80.0	63.1	35.2	1.98	48.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	2	2	2	2	2	2	2	2	2	2	2	2	2	2
M	69.8	33.5	24.4	1.38	34.2	21.3	1.61	0.98	1.15	25.2	21.0	1.20	4.38	13.2
R	64.5	32.0	22.5	1.33	33.3	21.0	1.59	0.96	1.07	24.8	20.9	1.19	4.20	12.5
	75.0	35.0	26.3	1.42	35.0	21.5	1.63	1.00	1.22	25.6	21.1	1.21	4.55	13.8

Upper epidermis: Non-venous cells 4-5 sided, somewhat irregular, with straight walls (figs. 203,205). The cuticular flange extends deeply between adjacent cells. Venous cells narrower and more regularly arranged than non-venous cells. Trichome bases with a small irregularly shaped and very heavily thickened foot cell and unmodified basal cells occur occasionally over the veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight walls (figs. 202,204). Cuticular flange irregularly thickened, giving a beaded appearance. Venous cells longer, narrower, and more heavily cutinised than non-venous cells. Stomata generally confined to areoles, oriented at random. The poral wall of the guard cells is heavily thickened. Larger stomates occur occasionally over the veins. Subsidiary cells brachyparacytic, not overlying the guard cells (figs. 212,213). Trichome bases with a small, thickened, circular foot cell occur over and between veins (fig. 211). Basal cells are unmodified over the veins and radial between them. Trichomes not preserved.

Specimens examined: N 0036 (fig. 34), N 0232 (fig. 35).

Discussion: The apex is incomplete in both specimens, but in N 0232 (fig. 35) enough is preserved to suggest that a "drip-tip" apex may have been present. The venation pattern is weakly brochidodromous, with secondary veins looping into the superadjacent secondary vein. The venation pattern becomes more conspicuously brochidodromous toward the apex.

PARATAXON NER/008. (Table 30).

Lamina: Symmetrical, elliptical. Leaf base angle approximately 90°, apex obtuse. Base and apex symmetrical, Leaf length

4 cm., width 1.2 cm. (fig. 36).

Margin: Serrate. Serrations irregularly spaced, but of one order.

Petiole: Normal, almost 1/3 of leaf length, narrowing from base to point of insertion of lamina.

Venation: Primary vein slightly sinuous, massive. Secondary venation pattern irregularly semicraspedodromous. 11 uniformly curved secondary veins arise at an angle of approximately 59°. This angle is uniform throughout the leaf. The loop forming branches of the secondary veins join superadjacent secondary veins at less than 90°. Higher order arches not well formed. Intersecondary veins absent. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls (fig. 215). The cuticular flange extends to a small degree between adjacent cells, increasing in extent at the junction of three cells to form a small cuticular peg. No surface ornamentation. Venous cells not highly modified, but smaller and more regularly arranged than the non-venous cells. Trichome bases with a small, irregularly shaped, very heavily thickened foot cell and basal cells which are smaller than the surrounding epidermal cells occur over, and rarely between the veins (fig. 215). Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 214). Cuticular flange not heavily thickened. No surface ornamentation. Venous cells only slightly modified over minor veins, generally elongated over major veins. Stomata confined to areoles, oriented at random. The poral wall of the guard cells is heavily thickened. Subsidiary cells

actinomorphic, not overlying the guard cells (fig. 226). Trichome bases with an irregularly shaped, thickened foot cell and unmodified basal cells occur commonly over and between the veins (fig. 227). Trichomes not preserved.

Specimen examined: N 0051 (fig. 36).

Discussion: Although the specimen is virtually an entire leaf, several large holes are present in the lamina. These holes probably appeared during leaf development, because they have severely affected the course of the adjacent secondary veins. They are possibly the result of insect attack. The venation pattern is best described as semicraspedodromous, although it is very irregular. Particularly toward the base, but also toward the apex, the secondary veins loop into the superadjacent secondary vein without giving rise to branches which teminate in serrations. However, the more central secondary veins do give rise to branches which terminate in serrations. Since the number of branches arising from each secondary vein which terminate in serrations varies from 0 to 3, the spacing of the serrations is highly irregular.

PARATAXON NER/009. (Table 31).

Lamina: Three lobed, symmetrical. Leaf base acute and apex of each lobe acute. Base and apices symmetrical. Leaf length at least 10.5cm., width 6.2cm. (figs. 150,151).

Margin: Lobed, but not toothed.

Petiole: Unknown.

Venation: Three primary veins arise at the base of the leaf and one enters each lobe. The two primary veins going into the lateral lobes make an angle of 25^{o}- 30^{o} to the primary vein entering the central lobe. All primary veins are

slightly curved. Venation pattern actinodromous, perfect, marginal. An estimated 50 secondary veins arise from the three primary veins at an angle of approximately 67^{o} and curve strongly in their distal third to loop into the superadjacent secondary vein. The angle at which the secondary veins arise is constant throughout the leaf. Simple intersecondary veins common. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 217). Cuticular flanges not heavily thickened. No surface ornamentation. Venous cells not highly modified, but narrower and more regularly arranged than the non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 216). Cuticular flanges not heavily thickened. Cuticle above epidermal cells ornamented with numerous small, knob-like papillae (fig. 228). Venous cells not highly modified, but more regularly arranged than non-venous cells. Stomata confined to areoles, oriented at random. Poles of guard cells marked by a T-piece of thickened cuticle. Subsidiary cells cyclocytic, overlying the guard cells (fig. 228). Trichomes absent.

Specimen examined: N 0136 (figs. 150,151).

Discussion: The specimen consists of an almost complete leaf. The base is not fully preserved, but judging from the way it tapers, it is probably very acute.

PARATAXON NER/010. (Table 32).

Lamina: Leaf three lobed, symmetrical. Leaf base obtuse, apex of central lobe acute, other apices unknown. Base and apex of central lobe symmetrical. Leaf length approximately 10 cm., width 8.9 cm. (figs. 152,153).

Margin: Lobed, but not toothed.

Petiole: Unknown.

Venation: Three primary veins arise at the base of the leaf and one enters each lobe. The two primary veins going into the lateral lobes make an angle of 35^{o}- 40^{o} to the primary vein entering the central lobe. The central primary vein is slightly curved, while the other primary veins are sinuous. Venation pattern actinodromous, perfect, marginal. An estimated 40 secondary veins arise from the primary veins at an angle of approximately 69^{o}, and curve strongly in their distal third to loop into the superadjacent secondary vein. The angle at which the secondary veins arise is constant throughout the leaf. Simple intersecondary veins common. Tertiary veins weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls (fig. 219). Epidermal cells large and cuticular flanges extremely thick, but not extending deeply between cells. Surface ornamented with minute ridges in a reticulate pattern. Venous cells not highly modified, but over larger veins they are narrower than the non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and curved walls (fig. 218). Cuticular flanges extremely thick but not extending deeply between cell walls. Surface ornamented with cuticular ridges. Venous cells not highly modified, but over major veins longer,

TABLE 30: PARATAXON NER/008.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	3.3	1.2	2.75	67.2	81.9	2.39	99	121	11	0	58.8	32.2	2.0	34.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	52.0	49.6	31.9	1.55	32.6	22.0	1.48	1.52	1.45	28.5	21.6	1.32	5.5	9.1

TABLE 31: PARATAXON NER/009.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	0	N.A.	1	1	1	1	1	1
M	8.1	6.2	1.31	88.5	49.0	0			50	76	67.3	44.3	1.6	49.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	50	39.4	27.4	1.44	37.3	21.5	1.73	1.06	1.27	30.6	27.0	1.13	3.2	8.57

TABLE 32: PARATAXON NER/010.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	N.A.	1	1	1	1	1	1
M	7.8	8.9	0.88	45.7	47.9	0	151		40	86	69.4	50.6	1.3	65.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	48	43.5	35.1	1.24	37.3	25.0	1.49	1.17	1.40	31.9	26.5	1.20	3.9	16.56

narrower, and more regularly arranged than the non-venous cells. Stomata confined to areoles, oriented at random. Subsidiary cells actinomorphic, overlying the guard cells (fig. 229). Trichomes absent.

Specimen examined: N 0137 (figs. 152,153).

Discussion: The specimen consists of a nearly complete leaf with a base which appears to be obtuse, but which may taper and be acute.

PARATAXON NER/011. (Table 33).

Lamina: Symmetrical, elliptical. Leaf base obtuse, apex unknown. Base slightly asymmetrical. Leaf length at least 6.5 cm., width 1.7 - 2.5 cm. (figs. 38,39).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein slightly curved, stout. Secondary venation pattern brochidodromous. 17 - 21 secondary veins arise at an angle of 61 - 69°. This angle is uniform throughout the leaf. The secondary veins curve sharply upwards about halfway along their length. The loop forming branches of the secondary veins join superadjacent secondary veins at 90° or less. Secondary, tertiary and quaternary vein arches well formed. Strongly developed simple and composite intersecondary veins present. Tertiary veins transverse ramified or random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides, and straight or slightly curved walls (figs. 221,222,224,225). The cuticular flange extends moderately between adjacent cells. No surface ornamentation. Venous cells not highly modified, but over the major veins they are smaller, narrower, and more regularly arranged than the

non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (figs. 220,223). The cuticular flange extends deeply between adjacent cells. No surface ornamentation. Cells over veins markedly narrower than non-venous cells, particularly over the larger veins. Stomata generally confined to areoles, oriented at random. The poral walls of the guard cells are heavily thickened. Larger stomates occur occasionally over veins. Subsidiary cells brachyparacytic or actinomorphic, overlying the guard cells (fig. 230). Trichome bases with a small, heavily cutinised foot cell and radial basal cells occur rarely over veins (fig. 232). Trichomes not preserved.

Specimens examined: N 0005 (fig. 38), N 0076 (fig. 39).

Discussion: The apex is missing in both specimens but the slightly asymmetrical, obtuse base is present in N 0005 (fig. 38).

PARATAXON NER/012. (Table 34).

Lamina: Symmetrical, elliptical. Leaf base and apex absent. Leaf length at least 3 cm., width 0.6 cm. (fig. 37).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein straight, massive. Secondary venation pattern brochidodromous, At least 10 uniformly curved secondary veins arise at an angle of approximately 47^{o}. This angle is uniform throughout the leaf. The loop forming branches of the secondary veins join superadjacent secondary veins at an angle of 90^{o} or more. Higher order vein arches present but not conspicuous. Simple and composite inter-secondary veins conspicuous and common. Tertiary veins transverse ramified or random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 237). Large cuticular pegs occur at cell wall junctions and the cuticular flange extends deeply between cells. No surface ornamentation. Venous cells not highly modified, becoming narrower as veins become larger. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (figs. 234, 235). The cuticular flange extends deeply between cells. No surface ornamentation, but the cuticular flanges are perpendicularly striated (fig. 233). Venous cells not highly modified, becoming narrower as veins become larger (fig. 236). Stomata confined to areoles, oriented at random. The polar walls of the guard cells are heavily thickened. Subsidiary cells actinomorphic, overlying the guard cells (fig. 233). Trichome bases with a small, circular, heavily thickened foot cell and radial basal cells occur occasionally over veins (fig. 246). Trichomes not preserved.

Specimen examined: N 0008 (fig. 37).

Discussion: The apex and base of the specimen have not been preserved. The margin of the leaf runs nearly parallel for the whole of its preserved length.

PARATAXON NER/013. (Table 35).

Lamina: Symmetrical, elliptical. Leaf base and apex acute and symmetrical. Leaf length 3.6 cm., width 1.1 cm. (fig. 40).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein straight, massive. Secondary venation pattern brochidodromous. 19 secondary veins arise at an angle of approximately 56°. This angle is uniform throughout the

TABLE 33:PARATAXON NER/011.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	2	2	2	2	2	2	2	0	2	2	2	2	2	2
M	5.8	2.1	2.85	49.7	84.4	0	97		19	91.7	65.3	34.9	2.58	43.9
R	5.7	1.7	2.28	46.9	79.5	0			17	61.2	29.3	88.2	2.36	38.7
	5.8	2.5	3.41	52.5	89.2				21	69.3	40.4	95.2	2.80	49.1

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	2	2	2	2	2	2	2	2	2	2	2	2	2	2
M	70.0	31.8	21.8	1.46	29.0	17.4	1.67	1.11	1.28	19.2	16.5	1.17	3.5	8.82
R	69.5	30	21.3	1.41	24.6	15.1	1.63	1.00	1.14	19.0	16.4	1.16	3	6.44
	70.5	33.5	22.3	1.50	33.4	19.6	1.70	1.22	1.41	19.4	16.5	1.18	4	11.20

TABLE 34:PARATAXON NER/012.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	0	0	1	1	1	1	1	1
M	2.3	0.6	3.83	46.4	93.8	0			10	90	47.3	15.3	1.3	32.9

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	57	15.6	11.1	1.41	21.6	12.0	1.80	0.72	0.93	18.8	12.8	1.47	3.8	4.29

TABLE 35:PARATAXON NER/013.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	2.7	1.1	2.45	48.7	81.1	0	53	72	17	29.4	55.9	28.8	2.61	48.2

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	56	26.6	18.0	1.48	29.5	17.8	1.66	0.90	1.01	12.6	7.0	1.80	2	12.22

leaf. The secondary veins are uniformly curved until their distal quarter when they curve sharply upwards and inwards and loop into the superadjacent secondary veins at an angle of approximately 90°. Higher order vein arches not conspicuous. Weakly developed simple intersecondary veins occur uncommonly. Tertiary veins weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides, and curved or slightly sinuous walls (fig. 239). Cuticular flange moderately thickened. No surface ornamentation. Venous cells longer, narrower, and with straighter walls than non-venous cells. Trichome bases with a circular, thickened foot cell and unmodified basal cells occur rarely over the veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and sinuous walls (fig. 238). Cuticular flanges slightly thickened. No surface ornamentation. Venous cells not highly modified over minor veins, but over the larger veins they are slightly more elongate and with straighter walls than the non-venous cells. Stomata confined to areoles, oriented at random. The polar walls of the guard cells are thickened. Subsidiary cells generally paracytic (fig. 248). Trichome bases with a small, circular, thickened foot cell occur commonly over the veins and less commonly between them (fig. 247). Over the veins the basal cells are unmodified, but between veins they are radial. Trichomes not preserved.

Specimen examined: N 0001 (fig. 40).

Discussion: The specimen consists of a small, symmetrical, complete leaf with an acute base and apex. The cuticle is very fragmentary and extremely thin, making interpretation of the structures difficult.

PARATAXON NER/014. (Table 36).

Lamina: Symmetrical, ovate to elliptical. Leaf base obtuse, apex unknown. Base highly asymmetrical. Leaf length approximately 3.4 - 5.6 cm., width 1.0 - 1.7 cm. (figs. 41, 43).

Margin: Serrate. Serrations regularly spaced and of one order.

Petiole: Unknown.

Venation: Primary vein straight or slightly curved, massive. Secondary venation pattern mixed craspedodromous. At least 17 uniformly curved secondary veins arise at an angle of 56 - 69°. This angle increases toward the apex. The secondary veins either remain unbranched and terminate in a serration, or branch once, with both branches terminating in serrations. Composite intersecondary veins weakly developed. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls (figs. 241, 243). Long, fine cuticular pegs occur at cell wall junctions and the cuticular flange extends deeply between cells. No surface ornamentation. Venous cells not highly modified, but over the larger veins they are narrower than the non-venous cells. Trichome bases with a small, circular, thickened foot cell and unmodified basal cells occur rarely over veins. Trichomes not preserved. Large multicellular glands occur commonly over veins.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (figs. 240, 242). Very small cuticular pegs occur at cell wall junctions and the cuticular flange is not heavily thickened. No surface ornamentation. Venous cells not highly modified, but longer

and narrower than non-venous cells, particularly over larger veins. Stomates confined to areoles, oriented at random. The polar walls of the guard cells are thickened. Subsidiary cells actinomorphic, overlying the stomates (fig. 249). Trichome bases with a small, circular, thickened foot cell and unmodified basal cells occur over the major veins (fig. 250). Trichomes not preserved. Large multicellular glands occur over the veins (fig. 251).

Specimens examined: N 0019 (fig. 41), N 0025 (fig. 43).

Discussion: The apex is not preserved in either specimen and the base is preserved in only one (N 0019, fig. 41). The base is highly asymmetrical and is reminiscent of that on many sessile leaves, although this is unproven since no attachment is preserved.

The secondary veins either run directly into a tooth or branch once and give rise to two veins which terminate in teeth. Toward the apex the secondary veins begin to loop into the superadjacent secondary vein, and give rise to a branch which terminates in a tooth. For this reason, the venation pattern is mixed craspedodromous.

PARATAXON NER/015.(Table 37).

Lamina: Symmetrical, elliptical. Leaf base angle approximately 90°, apex narrowing into an obtuse "drip-tip". Base and apex symmetrical. Leaf length 6.3 cm., width 1.9 cm. (fig. 42).

Margin: Entire.

Petiole: Incomplete, slightly inflated.

Venation: Primary vein curved, particularly near base and apex, stout. Secondary venation pattern brochidodromous. About 12 secondary veins arise at an angle of 57°. This angle

is uniform throughout the leaf. The secondary veins are uniformly curved for the first three quarters of their length and then curved sharply inwards and loop into the superadjacent secondary vein at an angle of 90^{o} or less. Secondary, tertiary, and quaternary vein arches well formed. Composite intersecondary veins poorly formed and uncommon. Tertiary veins weakly percurrent or random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and highly sinuous walls (fig. 245). Long, fine cuticular pegs occur at cell wall junctions, and the cuticular flange may extend to a small extent between the cells. No surface ornamentation. Venous cells with straighter walls than non-venous cells. Trichome bases with a small, circular, very heavily thickened foot cell and heavily thickened, small basal cells occur over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and sinuous walls (fig. 244). Cuticular flange not heavily thickened. No surface ornamentation. Venous cells longer, narrower, and with straighter walls than non-venous cells. Stomata confined to areoles, oriented at random. The poral walls of the guard cells are moderately thickened. Subsidiary cells actinomorphic, not overlying the guard cells (fig. 252). Trichome bases with a small, irregularly shaped, heavily thickened foot cell and heavily thickened basal cells common over veins (fig. 253). Trichomes not preserved.

Specimen examined: N 0062 (fig. 42).

Discussion: The leaf is almost totally preserved and has a well-developed, "drip-tip" which narrows into an obtuse apex. Part of the petiole is preserved and it appears that it was somewhat expanded.

PARATAXON NER/016. (Table 38).

Lamina: Leaf very deeply three-lobed, asymmetrical. Leaf base unknown. Leaf apex unknown, but probably acute, at least for the central lobe. Leaf length about 19 cm., width unknown (figs. 147,148,149).

Margin: Lobed, but not toothed.

Petiole: Unknown.

Venation: Primary veins straight or curved. Venation pattern actinodromous, perfect, marginal. In the central lobe aproximately 40 secondary veins arise at an angle of 75°. This angle is uniform throughout the lobe. The secondary veins are uniformly curved for the first two thirds of their length and then curve upwards and loop into the superadjacent secondary vein at an angle of 90° or less. Higher order vein arches not well formed. Simple and composite intersecondary veins well formed. Tertiary veins random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls (fig. 255). Cuticulqr pegs occur at cell wall junctions, and the cuticular flange may extend deeply between cells. No surface ornamentation. Venous cells not highly modified, but over the major veins they are square to rectanglular, with straight side walls and straight or oblique end walls. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides, and straight or slightly curved walls (fig. 254). Cuticular flanges heavily thickened and cuticular pegs occur at cell wall junctions. Surface heavily striated (fig. 261). Venous cells longer than non-venous cells. Stomata confined to areoles, oriented at random. The guard cells have slightly thickened poral walls. Subsidiary cells

TABLE 36: PARATAXON NER/014.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	2	2	2	2	2	2	1	0	2	2	2	2	2	2
M	3.8	1.4	2.76	44.3	82.4	3.28	61		17	29.4	62.4	40.1	2.05	49.6
R	2.7	1.0	2.70	39.5	81.6	2.77					55.9	34.7	2.00	45.8
	4.8	1.7	2.82	49.1	83.2	3.78			17	29.4	68.9	45.5	2.10	53.3

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	2	2	2	2	2	2	2	2	2	2	2	2	2	2
M	60.3	29.7	21.0	1.41	26.2	16.1	1.63	1.14	1.32	21.3	19.8	1.08	5.2	9.22
R	54.5	27.6	20.4	1.35	23.8	14.8	1.61	1.12	1.25	20.9	18.9	1.05	5.1	8.12
	66.0	31.8	21.6	1.47	28.5	17.3	1.65	1.16	1.38	21.6	20.6	1.11	5.3	10.32

TABLE 37: PARATAXON NER/015.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	5.0	1.9	2.63	50.8	80.0	0	91	38	11	18.2	57.3	23.4	2.32	33.5

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	56.5	33.8	23.1	1.46	28.5	17.3	1.65	1.19	1.34	27.0	18.4	1.47	5.35	5.36

TABLE 38: PARATAXON NER/016.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	0	0	1	1	1	1	1	1
M	11.6	2.7	4.30	63.8	80.1	0			40	90	75	60.2	2.40	71.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	55.0	21.0	14.9	1.41	19.0	13.6	1.40	1.11	1.10	20.5	18.3	1.12	4.8	5.87

actinomorphic and not overlying the guard cells (fig. 260). Trichomes absent.

Specimen examined: N 0132 (figs. 147,148,149),

Discussion: The specimen consists of an almost complete lobed leaf. The base of the leaf was reinterpreted after the classifications had been produced. It was previously thought to be a compound leaf with at least three leaflets, but the new interpretation suggests that it is a very deeply lobed leaf with at least three lobes. The values in table 38 are those used for the classification and assume that the central lobe is an individual leaflet.

The base of the leaf is unknown, as is the apex of all three lobes, although the central lobe at least can be assumed to have had a long tapering acute apex. The leaf is highly asymmetrical, with one of the side lobes being markedly smaller than the other two lobes (fig. 149). The position of the lobes in relation to one another may be an artifact of preservation. The cuticule was poorly preserved in this specimen.

PARATAXON NER/017.(Table 39).

Lamina: Symmetrical, elliptical. Leaf base acute, symmetrical, apex unknown. Leaf length at least 9.5 cm., width 2.2 cm. (fig. 45).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein straight, stout to massive. Secondary venation pattern brochidodromous. Approximately 20 secondary veins arise at an angle of 71^{o}. The angle increases toward the apex. The secondary veins are relatively straight for about the first half of their length, followed by a sharp

upward curve and toward the end of the vein an inward curve to loop into the superadjacent secondary vein at a variable angle. Secondary, tertiary, and quaternary vein arches well formed. Composite intersecondary veins common. Tertiary veins random reticulate.

Upper epidermis: Non-venous cells irregular, with 4 - 5 sides, and straight walls (fig. 257). The cuticular flange extends deeply between cells. No surface ornamentation. Venous cells unmodified except over larger veins where they are 4 - sided and regularly arranged. Trichome bases with a small, irregularly shaped, heavily thickened foot cell and small basal cells occur occasionally over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls (fig. 256). The cuticular flange extends deeply between cells, but not to the same extent as on the upper epidermis. No surface ornamentation. Venous cells not highly modified over minor veins but over the major veins they are longer and narrower than the non-venous cells. Stomata confined to areoles, oriented at random. The polar walls of the guard cells are heavily thickened. Subsidiary cells usually brachyparacytic, not overlapping the guard cells (fig. 262). Large, very thin cuticular flaps extend into the stomatal cavity (fig. 263). Trichome bases with a small, irregularly shaped, heavily thickened foot cell and unmodified basal cells occur over the veins (fig. 264). Trichomes not preserved.

Specimen examined: N 0097 (fig. 45).

Discussion: The apex of the specimen is missing, but there is evidence of the leaf beginning to extend into a "drip-tip". The base is also partially missing, but there is little doubt

that it was symmetrical and acute.

PARATAXON NER/018. (Table 40).

Lamina: Symmetrical, ovate. Base and apex unknown. Leaf length at least 5 cm., width 1 cm. (fig. 44).

Margin: Serrate. Serrations of one order, regularly spaced.

Petiole: Unknown.

Venation: Primary vein slightly sinuous, massive. Secondary venation pattern mixed craspedodromous. Approximately 20 secondary veins arise at an angle of 49^{o}. The angle increases toward the apex. The secondary veins curve sharply upwards about halfway along their length, particularly in the apical half of the leaf. Composite intersecondary veins poorly formed and uncommon. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and mainly straight walls (fig. 259). Cuticular pegs occur at cell wall junctions and the cuticular flange is slightly thickened. No surface ornamentation. Venous cells not highly modified, but over the larger veins they are smaller than the non-venous cells and have a greater length:width ratio. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls. (fig. 258). Very small cuticular pegs occur at cell wall junctions and the cuticular flange is slightly thickened. No surface ornamentation. Venous cells longer, narrower, and with much larger cuticular pegs than the non-venous cells. Stomata generally confined to areoles, oriented at random. The polar walls of the guard cells are heavily thickened. Subsidiary cells actinomorphic and not overlying the guard

cells (fig. 265). Trichome bases with a small, irregularly shaped, thickened foot cell and unmodified basal cells occur occasionally over the veins (fig. 266). Trichomes not preserved. Large multicellular glands occur over the veins (fig. 267).

Specimen examined: N 0023 (fig. 44).

Discussion: Both the apex and the base of the specimen are missing (fig. 44). The venation pattern is best described as mixed craspedodromous. In the basal half of the leaf, the secondary veins generally branch near the margin, and one branch terminates in a tooth while the other continues to branch and disappears into higher vein orders. However, toward the apex there is an increased tendency for this second branch to loop into the superadjacent secondary vein. Because there is generally only one tooth per secondary vein, the teeth are spread well apart, but occur at relatively regular intervals.

PARATAXON NER/019.(Table 41).

Lamina: Symmetrical, elliptical. Leaf base and apex acute, highly asymmetrical. Leaf length 6.5 cm., width 1 cm. (fig. 46).

Margin: Entire.

Petiole: Slightly winged.

Venation: Primary vein curved, massive. Secondary venation pattern eucamptodromous. Approximately 12 secondary veins arise at an angle of 57.5^{o}. This angle is uniform throughout the leaf. The secondary veins curve sharply inwards near the margin and in the basal half of the leaf merge into an intramarginal vein. Weakly formed composite intersecondary veins common. Tertiary veins weakly percurrent.

TABLE 39: PARATAXON NER/017.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	0	1	1	1	1	1	1
M	6.7	2.2	3.05	52.3	79.7	0	73		17	58.8	70.8	35.2	1.85	44.2

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	34.5	29.5	22.5	1.31	29.6	18.6	1.59	1.00	1.21	20.0	18.5	1.08	4.2	10.90

TABLE 40: PARATAXON NER/018.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	0	0	1	1	1	1	1	1
M	3.5	1.0	3.50	42.0	89.0	3.07			16	31.3	48.6	29.7	2.30	57.6

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	63.0	24.6	18.0	1.37	23.3	13.9	1.68	1.06	1.29	22.1	18.6	1.19	5.25	8.84

TABLE 41: PARATAXON NER/019.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	4.5	1.0	4.50	43.3	88.3	0	40	51	11	81.8	57.5	21.0	1.60	32.4

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	66.0	30.0	16.6	1.81	34.9	21.4	1.63	0.86	0.78	27.9	26.8	1.04	4.55	8.80

Upper epidermis: Non-venous cells irregular, with a variable number of sides and sinuous walls (fig. 269). Cuticular flange with a series of heavily thickened ridges. No surface ornamentation. Venous cells not highly modified, but over the major veins they are more regularly arranged than the non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and sinuous walls (fig. 268). Cuticular flange with a series of thickened ridges, similar to the upper epidermis, but not as well developed. No surface ornamentation. Venous cells not highly modified, but longer and narrower than non-venous cells. Stomata confined to areoles, oriented at random. The poral walls of the guard cells are heavily thickened. Subsidiary cells brachyparacytic, not overlying the guard cells (fig. 280). Trichome bases with a small, circular, thickened foot cell and unmodified basal cells occur rarely over the veins (fig. 281). Trichomes not preserved.

Specimen examined: N 0073 (fig. 46).

Discussion: The specimen, which is an almost complete leaf, has parallel margins for most of its length and is narrow, never exceeding 1 cm. in width. The base is highly asymmetrical, as is the apex, although the apex may be asymmetrical as the result of mechanical damage early in its development. The petiole is not totally preserved, but appears to be slightly winged. However, this could be an artifact of preservation, since it occurs consistently in the mummified leaves.

PARATAXON NER/020. (Table 42).

Lamina: Symmetrical, obovate. Leaf base acute, slightly

asymmetrical, apex unknown. Leaf length at least 3 cm., width 1 cm. (fig. 47).

Margin: Entire.

Petiole: Incomplete, slightly winged.

Venation: Primary vein slightly sinuous, massive. Secondary venation pattern brochidodromous. At least 7 secondary veins arise at an angle of 65°. This angle is uniform throughout the leaf. The secondary veins generally run almost straight to the margin, and curve sharply upwards and run just inside the margin until they loop into the superadjacent secondary vein at an angle of approximately 90°. Well formed simple and composite intersecondary veins occur commonly. Tertiary veins random reticulate.

Upper epidermis: Non-venous cells slightly irregular, with 6 - 8 sides, and straight walls (fig. 271). Cuticular flange very heavily thickened and extending deeply between cells. No surface ornamentation. Venous cells not highly modified, but smaller and more regularly arranged than the non-venous cells, particularly over the larger veins. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with 6 - 8 sides and straight walls (fig. 270). Large, blunt cuticular pegs occur at cell wall junctions and the cuticular flange is very heavily thickened. Surface ornamented with very fine striations and pittings (fig. 282). Venous cells longer and narrower than non-venous cells. Stomata generally confined to areoles, oriented at random. The poles of the guard cells are marked by a T-piece of thickened cutin and the polar walls are heavily thickened. Unmodified stomata occur occasionally over the veins. Subsidiary cells actinomorphic, sometimes overlapping the guard cells to a small extent (fig. 282). Trichome bases with a small, circular, very heavily thickened

foot cell and unmodified basal cells occur rarely over the veins (fig. 283). Trichomes not preserved.

Specimen examined: N 0022 (fig. 47).

Discussion: The apex of the specimen is missing to such an extent that no estimation of its form can be made. The base is highly acute and slightly asymmetrical, ending in a very thick, slightly winged petiole. This winging may be an artifact of preservation.

PARATAXON NER/021. (Table 43).

Lamina: Asymmetrical, obovate. Leaf base acute, slightly asymmetrical, apex unknown. Leaf length at least 7.4 cm., width 1.3 cm. (fig. 48).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein slightly curved, massive. Secondary venation pattern eucamptodromous. Approximately nine uniformly curved secondary veins arise at an angle of approximately 27^{o}. The angle increases toward the apex. Secondary veins unbranched. Intersecondary veins absent. Tertiary veins percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls (fig. 273). Cuticular flange not heavily thickened. Venous cells longer and narrower than non-venous cells. Trichome bases with a small, irregularly shaped, heavily thickened foot cell and small radial basal cells occur over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and generally straight walls (fig. 272). Small, blunt cuticular pegs occur at cell wall junctions,

and the cuticular flange is irregularly thickened, giving a randomly spaced "beaded" appearance. Venous cells longer and narrower than non-venous cells. Stomata generally confined to areoles, oriented at random. The poral walls of the guard cells are heavily thickened. Slightly larger stomata occur occasionally over the veins. Subsidiary cells generally paracytic (fig. 284). Trichome bases with a small, irregularly shaped, thickened foot cell and unmodified basal cells occur commonly over veins (fig. 285). Trichomes not preserved.

Specimen examined: N 0024 (fig. 48).

Discussion: Although the apex of the specimen is not preserved, the leaf probably tapers into a prominent, acute, "drip-tip" apex. The secondary veins in the basal half of the leaf follow an almost straight course, but toward the apex they become more prominently curved. The secondary veins gradually diminish apically inside the margin and the venation pattern is therefore eucamptodromous.

The subsidiary cells vary greatly in size, but are generally paracytic, with the two cells completely enclosing the guard cells and having their long axes parallel to the long axis of the guard cells.

PARATAXON NER/022.(Table 44).

Lamina: Highly asymmetrical, obovate. Leaf base acute, probably symmetrical, apex unknown. Leaf length at least 5.8 cm., width 1.9 cm. (fig. 49).

Margin: Entire.

Petiole: Normal.

Venation: Primary vein highly curved, particularly in basal half, massive. Secondary venation pattern weakly

TABLE 42: PARATAXON NER/020.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	0	1	1	1	1	1	1
M	3.3	1.0	3.30	44.2	88.8	0	51		7	85.7	65.0	22.6	1.30	29.9

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	67.0	25.1	18.6	1.35	31.4	20.0	1.57	0.80	0.93	24.8	23.9	1.04	4.85	10.71

TABLE 43: PARATAXON NER/021.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	1	0	1	1	1	1	1	1
M	5.7	1.3	4.38	54.2	86.9	0	39		8	0	27.3	12.9	1.75	65.4

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	90.0	22.4	16.5	1.36	22.5	14.1	1.60	1.00	1.17	19.1	20.1	0.95	5.30	10.24

TABLE 44: PARATAXON NER/022.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	0	0	1	1	1	1	1	1
M	5.6	1.9	2.95	53.0	77.3	0			10	50.0	50.0	15.6	1.96	36.2

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	86.0	36.3	28.0	1.30	38.5	24.0	1.60	0.94	1.17	23.9	20.5	1.17	4.65	13.98

brochidodromous. Approximately 10 uniformly curved secondary veins arise at an angle of 50°. This angle is uniform throughout the leaf. The loop forming branches of the secondary veins join superadjacent secondary veins at 90° or less. Simple intersecondary veins occur commonly. Tertiary veins weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides, and straight or curved walls (fig. 275). The cuticular flange extends deeply between cells and over the mesophyll cells (figs. 288,289). No surface ornamentation. Venous cells not highly modified but more regularly arranged than non-venous cells. Trichome bases with a small, irregularly shaped, thickened foot cell and radial basal cells occur over the veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or slightly curved walls (fig. 274). No surface ornamentation. Cuticular flanges irregularly "beaded" with heavily thickened regions interspersed with regions having no obvious thickening. The flanges extend deeply between cells and over the mesophyll cells. Venous cells longer and narrower than non-venous cells. Stomata confined to areoles, oriented at random. The polar walls of the guard cells are thickened. Subsidiary cells brachyparacytic, overlying the guard cells (fig. 286). Trichome bases with a small, irregularly shaped, thickened foot cell and radial basal cells occur commonly over and between veins (fig. 287). Trichomes not preserved.

Specimen examined: N 0077 (fig. 49).

Discussion: One side of the specimen appears to have been damaged (perhaps insect attack) early in its development and this probably accounts for the extremely asymmetrical form

of the lamina. The apex is missing and the base is deformed but was probaly acute. The curved, massive primary vein gives rise to about 10 secondary veins which loop weakly into the superadjacent secondary vein. The venation pattern falls somewhere between brochidodromous and eucamptodromous, being closer to brochidodromous.

Stace (1965) noted that some plants "have a heavily cutinised epidermis, the whole of the outer, vertical and inner walls and even the top of the vertical walls of the subepidermal layers being encrusted with cutin. In these cases the preparations have cuticular flanges which are very long and join up at their bases, and in surface view a second, fainter outline, that of the subepidermal layer, may be visible below the epidermal outline." This almost certainly has occurred in this parataxon (figs. 288,289).

PARATAXON NER/023. (Table 45).

Lamina: Symmetrical, ovate. Leaf base acute, symmetrical, apex unknown. Leaf length at least 8.5 cm., width 2 - 2.8 cm. (figs. 51,52).

Margin: Entire.

Petiole: Incomplete, apparently normal.

Venation: Primary vein straight, stout. Secondary venation pattern suprabasal, imperfect, acrodromous. Two strongly developed secondary veins arise from the primary vein just above the leaf base, and run in convergent arches toward the apex. These veins end well below the leaf apex. In total, about 6 uniformly curved secondary veins arise from the primary vein at an angle of 57 - 62°. Apart from the two basal secondary veins, this angle is uniform throughout the leaf. Intersecondary veins absent. Tertiary veins strongly

percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides, and straight walls (figs. 277,279). Fine cuticular pegs may occur at cell wall junctions and the cuticular flange sometimes extends deeply between cells. No surface ornamentation. Venous cells much longer and narrower than non-venous cells. Trichome bases with a small, irregularly shaped, very heavily thickened foot cell and heavily thickened basal cells occur rarely over the veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides, and straight or curved walls (figs. 276,278). Cuticular pegs may occur at cell wall junctions, and the cuticular flange sometimes extends deeply between cells. No surface ornamentation. Venous cells much longer and narrower than non-venous cells. Stomata generally confined to areoles. oriented at random. Larger stomata occur occasionally over veins. The polar walls of the guard cells are thickened. Subsidiary cells are generally brachyparacytic, not overlying guard cells (fig. 290). Trichome bases with a small, circular, thickened foot cell and unmodified basal cells occur over and rarely between veins (fig. 291). Trichomes not preserved.

Specimens examined: N 0021 (fig. 51), N 0078 (fig. 52).

Discussion: Both specimens are incomplete with large parts of the apex missing. The base and part of the petiole of one specimen (N 0078, fig. 52) is present and shows the base to be acute and the petiole normal. The most striking feature of this parataxon is the presence of paired basal secondary veins. These veins arise just above the base and arch upward to what is probably about $\frac{1}{2}$ - 2/3 of the leaf length.

On the upper epidermis fine cuticular pegs are present

at the junction of three cells. The rest of the cuticular flange is only lightly thickened in one specimen (N 0021) while in the other (N 0078) the cuticular flange extends deeply between adjacent cells, but cuticular pegs are absent. Trichome bases occur over the major veins in N 0078 but have not been observed on the fragmentary cuticle of N 0021.

On the lower epidermis cuticular pegs smaller than those on the upper epidermis are present at the junction of three cells in N 0021, while the cuticular flange may extend to a moderate degree between adjacent cells in both specimens.

PARATAXON NER/024. (Table 46).

Lamina: Symmetrical, ovate to elliptical. Base highly variable, symmetrical. Apex acute, symmetrical. Leaf length 5.5 - 11.5 cm., width 1.8 - 5.7 cm. (figs. 50,53,54,55,56,57, 145).

Margin: Entire.

Petiole: Normal.

Venation: Primary vein straight or slightly curved, moderate to stout. Venation pattern eucamptodromous. Approximately 9 - 13 uniformly curved secondary veins arise from the primary vein at an angle of 33 - 51°. This angle is uniform throughout the leaf. The secondary veins diminish apically inside the margin. Simple intersecondary veins very rare or more usually absent. Tertiary veins strongly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or sinuous walls (figs. 297,299, 301,303,305,307,309). Cuticular flange irregularly thickened, giving a slightly beaded appearance. No surface ornamentation. Venous cells longer, narrower and with straighter walls than non-venous cells. Trichome bases with a small, irregularly

TABLE 45: PARATAXON NER/023.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	2	2	2	2	2	2	1	0	2	2	2	2	2	2
M	5.5	2.4	2.31	46.0	78.9	0	81		5	0	59.7	38.2	1.18	54.4
R	5.0	2.0	2.11	45.1	76.6				4		57.3	29.3	1.05	50.0
	5.9	2.8	2.50	46.8	81.2	0	81		6	0	62.0	47.0	1.30	58.7

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	2	2	2	2	2	2	2	2	2	2	2	2	2	2
M	92.5	29.1	19.1	1.52	36.4	21.6	1.69	0.80	0.89	20.2	21.7	0.94	4.4	18.96
R	88.0	27.0	17.6	1.51	34.0	20.0	1.68	0.79	0.88	19.9	20.5	0.90	4.3	17.91
	97.0	31.1	20.6	1.53	38.8	23.1	1.70	0.80	0.89	20.5	22.8	0.97	4.5	20.00

TABLE 46: PARATAXON NER/024.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	7	7	7	7	7	7	5	1	7	7	7	7	7	7
M	6.8	3.5	2.04	42.6	73.7	0	79	44	10.9	4.0	43.1	24.7	2.33	59.3
SD	1.96	1.55	0.51	8.67	5.9	0	23.3		1.1	5.0	7.3	5.1	0.51	11.3
R	3.8	1.8	1.28	32.5	63.9		50		9	0	32.9	17.8	1.69	38.8
	9.0	5.7	2.64	54.3	81.1	0	109	44	12	11.1	50.6	30.0	2.99	72.4

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	7	7	7	7	7	7	7	7	7	7	7	7	7	7
M	70.5	29.9	20.0	1.50	26.5	16.4	1.63	1.12	1.22	19.9	17.5	1.14	4.89	9.51
SD	5.3	3.9	3.3	0.11	2.2	1.8	0.16	0.07	0.10	1.4	1.6	0.07	0.47	3.15
R	61	22.9	15.9	1.30	22.3	14.5	1.45	1.03	1.10	18.6	15.3	1.09	3.95	5.55
	76.5	34.3	26.3	1.64	28.6	19.1	1.87	1.24	1.38	22.1	20.1	1.29	5.25	14.21

shaped, thickened foot cell and unmodified basal cells occur over veins with varying frequency. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides, and straight or slightly sinuous walls (figs. 296,298,300,302,304,306,308). Cuticular flange irregularly thickened, but not as heavily as the upper epidermis, giving a slightly beaded appearance. No surface ornamentation. Venous cells longer, narrower and with straighter walls than non-venous cells. Stomata confined to areoles, oriented at random. The polar walls of the guard cells are heavily thickened. Subsidiary cells brachyparacytic, overlying the guard cells (fig. 292,293). Trichome bases with a small, irregularly shaped, thickened foot cell and unmodified or somewhat radial basal cells occur commonly over and between veins (figs. 294,295). Trichomes long, unicellular, thinly cutinised, and tapering to an acute apex.

Specimens examined: N 0047 (fig. 53), N 0050 (fig. 145), N 0057 (fig. 50), N 0059 (fig. 54), N 0089 (fig. 55), N 0122 (fig. 56), N 0238 (fig. 57).

Discussion: The leaf shape exhibited by the seven specimens is extremely variable, ranging from a long, narrow, elliptical leaf (N 0057, fig. 50), to a very broad, ovate leaf (N 0059, fig. 54). Because of this, the base is also very variable, but the apex, where it is preserved, always elongates into an acute "drip-tip". The venation pattern of all specimens is very similar and intersecondary veins are generally absent.

Despite the extreme variation in size and shape of the leaves, the venation and cuticular patterns are very similar among the seven specimens.

PARATAXON NER/025. (Table 47).

Lamina: Symmetrical, ovate. Leaf base extremely variable, obtuse, symmetrical; apex acute, symmetrical or asymmetrical. Leaf length approximately 5.3 - 11.5 cm., width 4.4 - 10.6 cm. (figs. 58 - 64).

Margin: Entire.

Petiole: Unknown.

Venation: Venation pattern basal actinodromous, with 5 primary veins originating at the base of the leaf. The central primary vein, which is the thickest, runs straight into the apex. The other 4 primary veins gradually curve upwards and continually branch, disappearing just inside the margin. A total of 9 - 15 secondary veins arise from the primary veins at an angle of 41 - 59°. This angle is reasonably uniform throughout the leaf. Weakly developed, composite intersecondary veins may occur rarely. Tertiary veins percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight, curved or sinuous walls (figs. 311,313,315,317,319,321,323). Cuticular flange heavily thickened (fig. 331). No surface ornamentation. Venous cells not highly modified, but over the major veins they are smaller and have thicker walls than non-venous cells. Trichome bases with a large, heavily thickened foot cell and unmodified basal cells occur over veins. Trichomes small, simple, unicellular, and very heavily thickened.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight, curved, or sinuous walls (figs. 310,312,314,316,318,320,322). Cuticular flange not heavily thickened (fig. 328). No surface ornamentation. Venous cells markedly longer and narrower than the non-venous cells. Stomata confined to areoles, oriented at

random. Subsidiary cells actinomorphic, not overlying guard cells (fig. 330). Trichome bases with a large, thickened circular foot cell and radial or unmodified basal cells occur very commonly over and between veins (fig. 329). Trichomes small, simple, unicellular and very heavily cutinised (figs. 326,327).

Specimens examined: N 0060 (fig. 63), N 0069 (fig. 60), N 0082 (fig. 64), N 0084 (fig. 58), N 0096 (fig. 62), N 0102 (fig. 61), N 0112 (fig. 59).

Discussion: Some of the specimens are damaged probably by insects or other mechanical effects, and are not reliable indicators of leaf form. Four specimens (N 0060 (fig. 63), N 0069 (fig. 60), N 0102 (fig. 61), and N 0112 (fig. 59) show that the leaf was large and somewhat heart shaped, generally symmetrical, and tapering into an acute apex. The base is extremely variable, but is generally obtuse and symmetrical. The cuticles are very characteristic, particularly in the presence of very heavily cutinised trichomes (figs. 326,327).

PARATAXON NER/026.(Table 48).

Lamina: Generally symmetrical, ovate to elliptical. Leaf base acute, symmetrical to highly asymmetrical. Leaf apex acute, symmetrical. Leaf length 5 - 16 cm., width 1.7 - 4.9 cm. (figs. 65-80).

Margin: Entire.

Petiole: Normal.

Venation: Primary vein straight or curved, moderate to stout. Venation pattern eucamptodromous. Approximately 8 - 11 uniformly curved secondary veins arise from the primary vein at an angle of 37 - 59°. This angle is uniform throughout the leaf. The secondary veins gradually diminish apically

TABLE 47: PARATAXON NER/025.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	7	7	7	7	7	7	5	1	7	7	7	7	7	7
M	7.1	8.1	0.91	38.4	55.0	0	143	118	12.4	11.7	48.8	26.9	1.91	60.8
SD	1.6	2.5	0.13	8.9	5.6	0	36.3		2.1	6.4	7.0	6.1	0.21	5.9
R	4.9	4.4	0.75	24.7	48.6	0	102		9	6.7	41.1	21.9	1.70	53.4
	9.5	10.6	1.11	52.9	63.7		199		15	25.0	59.0	39.8	2.23	69.1

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	7	7	7	7	7	7	7	7	7	7	7	7	7	7
M	84.7	34.9	22.7	1.54	23.8	14.9	1.60	1.47	1.53	23.1	18.7	1.24	5.96	4.29
SD	3.4	5.6	3.0	0.09	3.4	1.8	0.10	0.11	0.16	1.8	1.5	0.12	0.19	1.18
R	80.0	30.1	18.5	1.45	21.0	12.9	1.44	1.41	1.24	20.6	15.8	1.04	5.60	2.50
	88.0	46.8	28.1	1.67	29.0	18.0	1.75	1.61	1.70	25.8	20.3	1.40	6.15	5.40

TABLE 48: PARATAXON NER/026.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	16	16	16	16	16	16	9	4	16	16	16	16	16	16
M	7.8	3.1	2.56	48.4	79.1	0	69.3	39.5	9.8	16.2	44.7	21.7	1.92	47.3
SD	2.1	0.7	0.54	5.1	1.9	0	13.7	11.8	1.1	16.2	5.1	4.8	0.22	6.1
R	4.0	1.7	1.90	39.5	74.7	0	44	28	8	0	36.7	14.8	1.56	36.0
	13.1	4.9	4.23	58.5	82.2		91	56	11	55.6	59.2	36.6	2.34	61.2

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	16	16	16	16	16	16	16	16	16	16	16	16	16	16
M	76.8	29.2	21.8	1.43	33.2	20.1	1.65	0.96	1.10	27.2	24.7	1.10	4.82	10.98
SD	20.1	8.0	1.7	0.10	3.3	1.8	0.13	0.10	0.10	1.5	1.7	0.06	0.28	2.59
R	65.5	27.4	18.0	1.28	26.0	17.0	1.49	0.85	0.86	24.8	22.4	1.01	4.15	5.14
	91.5	37.0	24.5	1.67	42.6	23.5	1.92	1.25	1.31	29.4	28.1	1.20	5.4	15.03

inside the margin without major branching. Poorly formed composite intersecondary veins occur with varying frequency. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight, curved or sinuous walls (figs. 325,333,335,337,339,341,343,345,347,349,351,353,355, 357,359,361). Cuticular flange heavily thickened, sometimes irregularly so. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Trichome bases with a small, irregularly shaped, heavily thickened foot cell and small, heavily thickened basal cells occur occasionally over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight, curved or sinuous walls (figs. 324,332,334,336,338,340,342,344,346,348,350,352,354, 356,358,360). Cuticular flange sometimes irregular, not as heavily thickened as on the upper epidermis. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Stomata generally confined to areoles. oriented at random. Larger stomata occur occasionally over veins. Subsidiary cells heavily cutinised and covered with perpendicular striations, brachyparacytic, overlying guard cells to varying degrees (figs. 362,363). Trichome bases with a small, irregularly shaped, heavily thickened foot cell and unmodified basal cells common over veins (fig. 364). Trichomes not preserved.

Specimens examined: N 0010 (fig. 65), N 0014 (fig. 66), N 0017 (fig. 67), N 0018 (fig. 69), N 0020 (fig. 68), N 0033 (fig. 70), N 0056 (fig. 72), N 0064 (fig. 71), N 0068 (fig. 73), N 0071 (fig. 74), N 0100 (fig. 77), N 0101 (fig. 76), N 0103 (fig. 79), N 0105 (fig. 78), N 0239 (fig. 75), N 0241 (fig. 80).

Discussion: The specimens consist of generally symmetrical leaves, although occasionally the primary vein is strongly curved and the lamina highly asymmetrical (N 0239, fig. 75). The apex is acute, almost forming a "drip-tip" in some instances. The base is always acute but varies from symmetrical to highly asymmetrical. The venation pattern is consistent throughout the specimens.

The shape of the upper epidermal cells varies considerably, being straight, curved or sinuous (e.g. figs. 325,335). The cuticular flange thickening also varies, from heavy, even thickening on those specimens with straight or slightly curved walls, to irregular, almost beaded thickening on the specimens with sinuous walls.

The shape of the lower epidermal cell walls varies in accordance with the upper epidermis, as does the cuticular flange thickening. The subsidiary cells are heavily cutinised, and are covered in perpendicular striations. The subsidiary cells vary greatly in size (figs. 362,363), and sometimes the wall between the subsidiary cells and the guard cells is difficult to observe (fig. 362).

PARATAXON NER/027. (Table 49).

Lamina: Leaf compound, with at least 5 leaflets (fig. 98). Terminal leaflet present, other leaflets opposite in compound leaf. Lamina of leaflets generally symmetrical, occasionally slightly asymmetrical. Leaflets generally ovate. Base highly variable, symmetrical (probably only for terminal leaflets) or asymmetrical. Apex acute, symmetrical. Leaflet length 3.5 - 12.8 cm., width 1 - 3.1 cm. (figs. 81 - 125).

Margin: Serrate. Serrations generally of one order, regularly spaced.

Petiole: The petiole of the compound leaf is unknown. The terminal leaflet has a long attachment to the compound leaf axis, but the lateral leaflets are sessile.

Venation: Primary vein straight or curved, stout. Secondary venation pattern craspedodromous. 14 - 49 uniformly curved secondary veins arise at an angle of 38 - 72°. This angle is uniform throughout the leaflet. The secondary veins either terminate unbranched in a serration or branch once, with each branch terminating in a serration. Simple or composite inter-secondary veins common. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (figs. 371,373, 375,377,379,381,383,385,387,389,391,393,395,397,399,401,403, 405,407,409,411,413,415,417,419,421,423,425,427,429,431,433, 435,437,439,441,443,445,447,449,451,453,455,457,459). Cuticular pegs occur at cell wall junctions and the cuticular flange may extend deeply between cells. No surface ornamentation. Venous cells longer and narrower than non-venous cells and more regularly arranged. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (figs. 370,372, 374,376,378,380,382,384,386,388,390,392,394,396,398,400,402, 404,406,408,410,412,414,416,418,420,422,424,426,428,430,432, 434,436,438,440,442,444,446,448,450,452,454,456,458). Cuticular pegs occur at cell wall junctions, but the cuticular flange is only lightly thickened. No surface ornamentation. Venous cells longer, narrower, and more regularly arranged than the non-venous cells. Stomata confined to areoles, oriented at random. The polar walls of the guard cells are moderately thickened. Subsidiary cells actinomorphic, not

overlying the guard cells (fig. 365). Trichome bases with a small, irregularly shaped, thickened foot cell and unmodified basal cells occur over the major veins with varying frequency (fig. 366). Trichomes not preserved. Large, multicellular glands occur over the veins with varying frequency. These glands are overlain by very thinly cutinised cells (fig. 367), which are often only partly preserved or completely absent (figs. 368,369).

Specimens examined: N 0002 (fig. 81), N 0003 (fig. 82), N 0004 (fig. 83), N 0006 (fig. 84), N 0007 (fig. 85), N 0011 (fig. 86), N 0015 (fig. 89), N 0026 (fig. 87), N 0027 (fig. 90), N 0037 (fig. 91), N 0038 (fig. 88), N 0041 (fig. 92), N 0044 (fig. 93), N 0045 (fig. 94), N 0049 (fig. 98), N 0052 (fig. 95), N 0053 (fig. 96), N 0054 (fig. 97), N 0055 (fig. 99), N 0058 (fig. 100), N 0061 (fig. 101), N 0063 (fig. 102), N 0070 (fig. 103), N 0074 (fig. 104), N 0075 (fig. 105), N 0079 (fig. 106), N 0088 (fig. 110), N 0090 (fig. 109), N 0092 (fig. 107), N 0094 (fig. 108), N 0098 (fig. 111), N 0109 (fig. 112), N 0118 (fig. 113), N 0120 (fig. 114), N 0125 (fig. 115), N 0144 (fig. 116), N 0149 (fig. 117), N 0156 (fig. 118), N 0159 (fig. 119), N 0234 (fig. 122), N 0236 (fig. 121), N 0240 (fig. 125), N 0262 (fig. 120), N 0503 (fig. 123), N 0555 (fig. 124).

Discussion: One of the 45 specimens, N 0049 (fig. 98), consists of five leaflets, one terminal and the other four as two opposite pairs. The base of this leaf is not preserved, but there is little doubt that it is compound. All other specimens are preserved as individual leaflets. It is very likely that these leaflets all belong to the same parataxon, since despite the extreme variability of some features, the leaflet base, the venation pattern, and

the cuticular pattern are very similar between specimens. The terminal leaflet of the compound leaf is more or less symmetrical, and has a long attachment to the leaf axis. All the lateral leaflets are sessile and extremely asymmetrical . The pair of leaflets closest to the apex in N 0049 (fig. 98) appear to have a short "petiole" attaching them to the compound leaf axis, but close examination of the specimen has shown that this is an artifact of the highly asymmetric base in combination with the lamina being missing from one side of the leaflet (probably lost during preservation). The pair of leaflets furthest from the apex in N 0049 have bases which are not as markedly asymmetrical as the apical pair.

The individual leaflets which have been preserved have bases which vary from symmetrical through stages to highly asymmetrical. The leaflets are also highly variable in size, suggesting that either the leaves varied greatly in size, or that there were a large number of leaflets in the compound leaf which exhibited a large size variation. There is no evidence to support either of these hypotheses. The venation pattern varies little between leaflets.

The cuticular pattern of this parataxon is very characteristic, but some features do vary. The thickening of the cuticular flange of the upper epidermis is one feature which varies greatly. In some specimens it extends deeply between cells, while in others it does not (figs. 373,375). Cuticular pegs at the junction of three cells are common to all specimens. Trichomes are absent from the upper epidermis in all specimens.

The thickening of the cuticular flange of the lower epidermis also varies greatly, but is always markedly less

than that observed on the upper epidermis. Cuticular pegs at the junction of three cells are common to all specimens. Large, thinly cutinised, somewhat elliptical glands occur over the veins on the lower epidermis of all specimens (figs. 367,368,369).

PARATAXON NER/028. (Table 50).

Lamina: Symmetrical. Base and apex unknown. Leaf length unknown, width at least 1.9 cm. (fig. 126).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein straight, stout. Secondary venation pattern eucamptodromous. Tertiary veins weakly percurrent.

Upper epidermis: Non-venous cells 6 - 8 sided, somewhat regular in distribution, with straight walls (fig. 461). The cuticular flange extends deeply between cells and is heavily thickened. No surface ornamentation. Venous cells largely unmodified, but over the major veins they are smaller and more heavily cutinised than the non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 460). The cuticular flange extends very deeply between cells and is heavily thickened. No surface ornamentation. Venous cells largely unmodified, but longer and narrower than the non-venous cells. Stomata generally confined to areoles, oriented at random. Unmodified stomates occur occasionally over veins. The polar walls of the guard cells are heavily thickened. Subsidiary cells brachyparacytic and overlying the guard cells considerably (figs. 472,473). Trichomes absent.

TABLE 49: PARATAXON NER/027.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	45	45	45	45	45	45	24	9	45	45	45	45	45	45
M	5.6	1.8	3.13	48.9	82.1	2.83	58.2	33.2	24.3	47.7	59.1	40.6	2.53	53.4
SD	1.6	0.5	0.71	7.1	3.4	0.79	20.3	22.9	5.8	17.9	6.8	6.5	0.32	7.8
R	2.1	1.0	1.75	34.6	73.1	1.12	28	15	14	7.7	37.6	19.1	1.7	38.7
	8.3	3.1	5.73	65.5	89.3	4.31	101	87	49	80.6	72.4	53.7	3.3	71.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	45	45	45	45	45	45	45	45	45	45	45	45	45	45
M	66.9	23.6	17.0	1.40	20.9	13.7	1.53	1.12	1.24	18.8	17.5	1.07	5.33	9.70
SD	12.0	2.5	1.7	0.08	2.0	1.3	0.12	0.12	0.13	1.5	1.6	0.06	0.38	2.23
R	41.5	19.3	13.4	1.21	17.4	10.3	1.23	0.86	0.89	15.5	13.0	0.96	4.75	4.69
	105	30.0	20.4	1.57	26.8	16.3	1.85	1.46	1.55	21.3	20.5	1.20	6.45	14.54

TABLE 50: PARATAXON NER/028.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	0	0	0	0	1	0	0	0	0	1	1	1	1
M						0					44.3	19.7	1.30	50

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	73.5	23.5	19.0	1.24	23.5	16.4	1.43	1.00	1.16	22.9	20.1	1.14	4.7	8.7

Specimen examined: N 0246 (fig. 126).

Discussion: The specimen consists of probably the apical half of the leaf, so the base is unknown (fig. 126). The apex is also missing but the leaf appears to draw out into a "drip-tip".

PARATAXON NER/029. (Table 51).

Lamina: Base and apex unknown, length unknown, width approximately 1.5 cm. (fig. 127).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein slightly curved, stout. Secondary venation pattern brochidodromous. Secondary veins arise at an angle of 57° and curve uniformly for about 3/4 of their length and then curve sharply inwards to join the superadjacent secondary vein at an angle of less than 90°. Simple well formed intersecondary veins common. Tertiary veins random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or irregularly curved walls (fig. 463). Cuticular flange lightly but irregularly thickened. No surface ornamentation. Venous cells much longer and narrower than the non-venous cells. Trichome bases with a small, irregularly shaped, thickened foot cell and unmodified basal cells occur rarely over the major veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and curved or irregularly sinuous walls (fig. 462). Cuticular flanges very lightly but irregularly thickened. No surface ornamentation. Venous cells longer, narrower, more heavily thickened and with straighter walls

than non-venous cells. Stomata generally confined to areoles, oriented at random. Unmodified stomata occur occasionally over the veins. The polar walls of the guard cells are heavily thickened. Subsidiary cells actinomorphic, not overlying guard cells (fig. 474). Trichome bases with a small, circular, thickened foot cell and unmodified basal cells occur commonly over and between veins (fig. 475). Trichomes not preserved.

Specimen examined: N 0403 (fig. 127).

Discussion: The specimen consists of one side of a leaf with both the base and the apex missing. Three secondary veins are preserved and show the venation pattern to be brochidodromous.

PARATAXON NER/030. (Table 52).

Lamina: Apex and base unknown. Leaf length and width unknown (figs. 128,129).

Margin: Entire.

Petiole: Unknown.

Venation: Secondary venation pattern probably eucamptodromous. Simple intersecondary veins present. Tertiary veins weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and uneven, sinuous walls (figs. 467,469). Cuticular flanges irregularly thickened. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Trichome bases with a small, irregularly shaped, heavily thickened foot cell and unmodified basal cells occur occasionally over and between veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable

number of sides and straight or curved walls (figs. 466,468). Cuticular flange irregularly thickened and extends deeply between cells. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Stomata confined to areoles, oriented at random. The guard cells are heavily thickened. Subsidiary cells actinomorphic, overlying the guard cells (fig. 476). Trichome bases with a small, irregularly shaped, heavily thickened foot cell and unmodified basal cells occur over and between veins with a greater frequency than on the upper epidermis (fig. 477). Trichomes not preserved.

Specimens examined: N 0362 (fig. 129), N 0373 (fig. 128).

Discussion: The two specimens which represent this parataxon appear to be two parts of the same leaf (figs. 128,129). Very little of the leaf is preserved, but some information may be gained from the few secondary veins preserved. It appears as though the secondary venation pattern is eucamptodromous, since two secondary veins can be seen diminishing inside the margin without joining other secondary veins.

PARATAXON NER/031. (Table 53).

Lamina: Base and apex unknown. Leaf length and width unknown (fig. 130).

Margin: Entire.

Petiole: Unknown.

Venation: Secondary venation pattern possibly brochidodromous. Basal secondary veins straight for the first 2/3 of their length and then they curve sharply upward to merge with the superadjacent secondary vein at 90^{o} or less. Simple inter-secondary veins well formed and common. Tertiary veins

TABLE 51: PARATAXON NER/029.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	0	0	0	0	1	0	0	0	1	1	1	1	1
M						0				88	57.0	27.7	2.00	46

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	61.5	32.5	21.6	1.50	26.5	18.6	1.42	1.23	1.16	19.1	17.1	1.12	5.55	6.3

TABLE 52: PARATAXON NER/030.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	0	0	0	0	2	0	0	0	0	0	0	0	0
M						0								
R						0								

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	2	2	2	2	2	2	2	2	2	2	2	2	2
M	72.3	33.7	24.1	1.40	36.3	23.4	1.55	0.93	1.03	26.6	26.4	1.01	4.60	12.7
R		33.4	23.5	1.38	35.6	23.3	1.53	0.92	1.01	25.8	26.0	0.99	4.55	11.6
	72.3	33.9	24.6	1.42	36.9	23.5	1.57	0.94	1.05	27.4	26.8	1.02	4.65	13.7

TABLE 53: PARATAXON NER/031.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	0	0	0	0	1	0	0	0	1	1	1	1	1
M						0				95	59.7	45	2.91	68

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	15	29.6	19.9	1.49	22.6	14.5	1.56	1.31	1.37	22.6	16.9	1.34	5.65	4.3

random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and curved or sinuous walls (fig. 465). Cuticular flange heavily thickened. No surface ornamentation. Venous cells longer, narrower, and with straighter walls than non-venous cells. Trichome bases with a large, heavily thickened foot cell and unmodified basal cells occur over veins. Trichomes small, simple, unicellular and very heavily cutinised.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight walls (fig. 464). Cuticular flange not heavily thickened. No surface ornamentation. Venous cells longer, narrower and more thinly cutinised than non-venous cells. Stomata confined to areoles, oriented at random. Subsidiary cells actinomorphic, not overlapping guard cells (fig. 478). Trichome bases with a large, thickened, circular foot cell and radial or unmodified basal cells occur very commonly over and between veins. Trichomes small, simple unicellular and very heavily cutinised.

Specimen examined: N 0150 (fig. 130).

Discussion: The midrib and the basal part of one side of the leaf is preserved. The base is not preserved and it can be seen that the margin toward the base of the specimen runs almost parallel with the midrib.

PARATAXON NER/032. (Table 54).

Lamina: Symmetrical, elliptical. Leaf base obtuse, symmetrical; apex acute, symmetrical. Leaf length 1.8 cm., width 0.3 cm. (fig. 146).

Margin: Entire.

Petiole: Leaves sessile.

Venation: Primary vein straight or slightly curved, massive. Other venation unknown.

Upper epidermis: Non-venous cells 4 - 5 sided, with straight or slightly curved walls (fig. 470). Cells generally arranged in rows running parallel to the primary vein. The cuticular flange extends to a moderate degree between cells and sometimes cuticular pegs occur at cell wall junctions. No surface ornamentation. Venous cells over the primary vein longer and narrower than non-venous cells. No other cells exhibit any modification. Stomata occur occasionally away from the primary vein and oriented parallel to it. The polar walls of the guard cells are somewhat thickened. Subsidiary cells actinocytic, being much smaller than the surrounding epidermal cells, and overly the sunken guard cells (fig. 479). Trichomes absent.

Lower epidermis: Non-venous cells 4 - sided, with sinuous walls (fig. 471). Cells rectangular and arranged in rows running parallel to the primary vein. Cuticular flange moderately thickened and ridged. No surface ornamentation. Cuticle from above the primary vein not preserved. Stomata similar to those on the upper epidermis, but slightly more common. Trichomes absent.

Specimen examined: N 0083 (fig. 146).

Discussion: The specimen may be either a branch with 27 leaves or part of a compound leaf (fig. 146). Neither the base nor the apex of the branch are preserved and therefore until further evidence becomes available, the specimen will be considered as a branch with alternate, sessile leaves. The leaves are small and linear, with an obtuse base and acute apex. Of the venation, only the massive primary vein is preserved.

The cuticle is fragmentary, and the fragments consist of two types which were designated as upper and lower epidermis on the basis of stomatal frequency. This designation is arbitrary.

PARATAXON NER/033. (Table 55).

Lamina: Symmetrical. Leaf apex acute, slightly asymmetrical; base unknown. Leaf length unknown, width approximately 4.6 cm. (fig. (131).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein slightly curved, moderate. Secondary venation pattern brochidodromous. The secondary veins arise from the primary vein at an angle of 57.5° and run almost straight toward the margin for the first 2/3 of their length. The secondary veins then curve sharply upwards and inwards to join the superadjacent secondary vein at 90° or less. Tertiary vein arches sometimes well formed. Very strongly developed simple intersecondary veins common. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight, curved or sinuous walls (fig. 481). The cuticular flange extends deeply between cells and cuticular pegs occur at cell wall junctions. No surface ornamentation. Venous cells longer and narrower than non-venous cells and somewhat rectangular in shape. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 480). Cuticular pegs occur at cell wall junctions, but otherwise the cuticular flange is only lightly thickened. Venous cells

longer, narrower and more regularly arranged than non-venous cells. Stomata confined to areoles, oriented at random. The polar walls of the guard cells are heavily thickened. Subsidiary cells actinomorphic, overlying the guard cells (fig. 504). Trichomes absent.

Specimen examined: N 0184 (fig. 131).

Discussion: The specimen consists of the apical half of the leaf and therefore the base is unknown.

PARATAXON NER/034. (Table 56).

Lamina: Symmetrical. Base acute, symmetrical, apex unknown. Leaf length unknown, width 0.6 cm. (figs. 132,133).

Margin: Entire.

Petiole: Normal.

Venation: Primary vein slightly sinuous, massive. Secondary venation pattern eucamptodromous. At least 6 uniformly curved secondary veins arise at an angle of 48^{o}. This angle is uniform, at least for the basal part of the leaf. Inter-secondary veins absent and tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells 4 - 5 sided, irregular, with straight or slightly curved walls (fig. 483). The cuticular flange extends unevenly between cells. No surface ornamentation. Venous cells not highly modified, but slightly narrower and more heavily thickened than non-venous cells. Trichome bases with a small, irregularly shaped, heavily thickened foot cell and thickened basal cells occur rarely over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 482). The cuticular flange extends unevenly between cells. No

TABLE 54: PARATAXON NER/032.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	0	0	0	0	0	0	0	0
M	1.2	0.3	4.0	44.4	97	0								

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	0	1	1	1	1	1	1	1	1	1	1	1	1	1
M		63.1	42.3	1.49	46.5	27.6	1.68	1.36	1.53	31.4	22.5	1.40	7.14	5.5

TABLE 55: PARATAXON NER/033.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	1	0	0	0	1	0	1	0	1	1	1	1	1
M		4.6				0		64		86	57.5	29.5	2.71	53

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	66.5	32.3	23.6	1.37	29.6	19.0	1.56	1.09	1.24	19.6	16.8	1.17	4.15	10.4

TABLE 56: PARATAXON NER/034.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	1	0	0	0	1	1	0	0	1	1	1	1	1
M		0.6				0	64			0	48	20.4	1.49	33

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	74.5	28.6	20.0	1.43	26.8	18.1	1.48	1.07	1.10	24.1	29.4	8.82	5.25	9.7

surface ornamentation. Venous cells longer and narrower than non-venous cells. Stomata confined to areoles, oriented at random. Subsidiary cells brachyparacytic, overlying the guard cells (fig. 505). Trichome bases with a small, irregularly shaped, thickened foot cell and unmodified basal cells occur over and sometimes between veins (fig. 506). Trichomes not preserved.

Specimen examined: N 0575 (figs. 132,133).

Discussion: The specimen consists of the basal part of a leaf. The walls between the guard cells on the lower epidermis are difficult to observe, as are the outlines of the guard cells (fig. 505).

PARATAXON NER/035.(Table 57).

Lamina: Symmetrical. Base and apex unknown. Leaf length unknown, width at least 5.7 cm. (fig. 135).

Margin: Unknown.

Petiole: Unknown.

Venation: Primary vein straight. Secondary venation pattern unknown. At least 10 secondary veins present, which follow a relatively straight course for about 3/4 of the way to the margin and then curve upwards. Simple intersecondary veins well formed and common. Tertiary veins weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and curved or slightly sinuous walls (fig. 485). Cuticular flange only lightly thickened. No surface ornamentation. Venous cells smaller, but with a greater length:width ratio than the non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and curved or slightly sinuous walls (fig.

484). Cuticular flange only lightly thickened. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Stomata generally confined to areoles, oriented at random. The polar walls of the guard cells are heavily thickened. Subsidiary cells actinomorphic, not overlying the guard cells (fig. 507). Trichomes absent.

Specimen examined: N 0476 (fig. 135).

Discussion: The specimen consists of the central part of a leaf with both the base and apex missing. Only a small part of the margin is preserved and it is not possible to predict the margin type.

PARATAXON NER/036. (Table 58).

Lamina: Base acute, symmetrical, apex unknown. Leaf length and width unknown (fig. 134).

Margin: Serrate. Serrations of several orders.

Petiole: Unknown.

Venation: Secondary venation pattern possibly semicraspedodromous. Veins of several orders terminate in serrations. Simple intersecondary veins well formed. Tertiary veins random reticulate or weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and curved or sinuous walls (fig. 487). Extremely fine cuticular pegs occur at cell wall junctions but otherwise the cuticular flange is not heavily thickened. No surface ornamentation. Venous cells more regularly arranged and with straighter walls than non-venous cells. Trichome bases with a small, irregularly shaped, thickened foot cell and unmodified basal cells common over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable

number of sides and curved or slightly sinuous walls (fig. 486). Extremely fine cuticular pegs occur at cell wall junctions but otherwise the cuticular flange is not heavily thickened. No surface ornamentation. Venous cells longer, narrower and with straighter walls than non-venous cells. Stomata generally confined to areoles, oriented at random, but occasionally larger stomates occur over veins. The polar walls of the guard cells are heavily thickened. Subsidiary cells cyclocytic, not overlying guard cells (fig. 508). Trichome bases with a circular or elliptical thickened foot cell and unmodified basal cells occur commonly over veins (fig. 509). Trichomes not preserved.

Specimen examined: N 0470 (fig. 134).

Discussion: The specimen consists of the basal part of the leaf. The base is acute and symmetrical, and unusual in that it is convex at the base, becomes concave, and then convex again.

PARATAXON NER/037.(Table 59).

Lamina: Unknown. Base and apex unknown. Leaf length and width unknown (fig. 136).

Margin: Entire.

Petiole: Unknown.

Venation: Secondary venation pattern possibly brochidodromous. Simple intersecondary veins present. Tertiary veins random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 489). Cuticular flange unevenly thickened, giving a beaded appearance. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Trichome bases with a

TABLE 57: PARATAXON NER/035.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	1	0	0	0	0	0	0	0	1	1	1	1	1
M		5.7								75	58.5	47.5	3.34	79
CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	33.5	29	17.8	1.63	21.1	14.4	1.47	1.37	1.24	16.4	15.3	1.07	4.9	8.3

TABLE 58: PARATAXON NER/036.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	0	0	0	0	0	0	0	0	0	1	1	1	1
M											58.5	47.5	3.34	79.0
CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	33.5	24.3	14.9	1.63	20.0	11.4	1.75	1.22	1.31	16.0	13.3	1.20	4.55	14.1

TABLE 59: PARATAXON NER/037.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	0	0	0	0	0	0	0	0	0	1	0	1	0
M											50		1.64	
CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	63.5	34.4	22.8	1.51	35.6	20.0	1.78	0.97	1.14	25.6	28.6	0.90	4.85	7.1

small, irregularly shaped, heavily thickened foot cell and radial basal cells common over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 488). Cuticular flanges unevenly thickened, but not to as great an extent as the upper epidermis. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Stomata generally confined to areoles, oriented at random. Unmodified stomata occur occasionally over veins. Subsidiary cells usually brachyparacytic, sometimes atinocytic (figs. 510,511). The subsidiary cells are covered in perpendicular striations. Trichome bases with a small, irregularly shaped, heavily thickened foot cell and unmodified or radial basal cells occur commonly over and between veins (fig. 512). Trichomes not preserved.

Specimen examined: N 0437 (fig. 136).

Discussion: The specimen consists of the apical part of a leaf. The base and apex of the leaf are missing, but enough of the margin is preserved to show that the leaf is probably entire. Only a few secondary veins are preserved and they loop strongly into the superadjacent secondary vein, suggesting a brochidodromous venation pattern.

Subsidiary cells are brachyparacytic with two cells flanking the guard cells but not enclosing them (fig. 510), but occasionally they are atinocytic, being distinguishable from the surrounding epidermal cells because of their striated surface. The common wall between the guard cells and the subsidiary cells is difficult to observe.

PARATAXON NER/038. (Table 60).

Lamina: Unknown. Base and apex unknown. Leaf length unknown, width at least 0.9 cm. (fig. 137).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein massive. Secondary venation pattern probably brochidodromous. Composite intersecondary veins present. Tertiary veins random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 491). Cuticular flanges heavily thickened and ridged. No surface ornamentation. Venous cells not highly modified, but somewhat rectangular and more regularly arranged than non-venous cells. Trichome bases with a small, irregularly shaped, heavily thickened foot cell and radial, thickened basal cells occur over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 490). Cuticular flanges not heavily thickened, slightly irregular. Small cuticular pegs occur at cell wall junctions. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Stomata generally confined to areoles, oriented at random. Occasionally unmodified stomata occur over veins. Subsidiary cells actinomorphic, overlying the guard cells (fig. 513). Trichome bases with a small, irregularly shaped, heavily thickened foot cell and unmodified basal cells occur over and occasionally between veins (fig. 514). Trichomes not preserved.

Specimen examined: N 0356 (fig. 137).

Discussion: The specimen consists of a small portion of a leaf with parts of both margins preserved. Both the base and

apex are missing.

PARATAXON NER/039. (Table 61).

Lamina: Symmetrical, ovate or elliptical. Leaf base probably acute, somewhat asymmetrical, apex unknown. Leaf length at least 8 cm., width about 2.5 cm. (fig. 138).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein straight, stout, Secondary venation pattern eucamptodromous. At least 10 uniformly curved secondary veins arise from the primary vein at an angle of 39°. This angle is uniform throughout the leaf. The secondary veins gradually diminish apically inside the margin. Well formed simple intersecondary veins occur rarely. Tertiary veins weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight walls (fig. 493). Cuticular flange heavily thickened and extending deeply between cells and over mesophyll cells. No surface ornamentation. Venous cells smaller than non-venous cells and rectangular, with straight side and end walls. Trichome bases with a small, irregularly shaped, very heavily thickened foot cell and unmodified basal cells occur uncommonly over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight or curved walls (fig. 492). Cuticular flange heavily thickened and extending deeply between cells and over mesophyll cells. No surface ornamentation. Venous cells smaller, more often four sided, and with a greater length:width ratio than non-venous cells. Stomata generally confined to areoles, oriented at random.

Larger stomates occur occasionally over veins. The polar walls of the guard cells are heavily thickened. Subsidiary cells brachyparacytic, overlying the sunken stomata (fig. 515). Trichome bases with a small, irregularly shaped, heavily thickened foot cell and unmodified or radial basal cells common over and between veins (fig. 516). Trichomes not preserved.

Specimen examined: N 0029 (fig. 138).

Discussion: The single specimen consists of two parts of a leaf, with the apex and part of the base missing. The two parts were connected when they were collected, but were separated in lifting them from the block.

PARATAXON NER/040. (Table 62).

Lamina: Symmetrical, ovate or elliptical. Base and apex unknown. Leaf length at least 7 cm., width 1.5 cm. (fig. 139).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein curved, massive. Secondary venation pattern a mixture of brochidodromous and eucamptodromous. At least 20 secondary veins arise from the primary vein at an angle of 63°. The angle increases slightly toward the apex. The secondary veins either loop into the superadjacent secondary vein at approximately 90° or diminish apically inside the margin. Composite intersecondary veins poorly formed and uncommon. Tertiary veins weakly percurrent.

Upper epidermis: Non-venous cells 6 - 8 sided, somewhat regular, with straight or slightly curved walls (fig. 495). Cuticular flange heavily thickened, and extending deeply between cells and over the mesophyll cells. No surface

TABLE 60: PARATAXON NER/038.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	0	0	0	0	1	0	0	0	0	1	1	1	1
M						0					61	39	1.80	43.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	58.5	21.9	15.1	1.45	26.8	17.6	1.52	0.82	0.86	22.4	21.4	1.05	4.95	10.1

TABLE 61: PARATAXON NER/039.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	0	1	0	0	1	1	1	1	1	1
M	6.3	2.5	2.52	47.4		0			10	57	39.3	19.8	2.19	59.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	88.0	24.8	18.3	1.36	25.9	17.4	1.49	0.96	1.05	20.8	13.5	1.54	4.15	13.3

TABLE 62: PARATAXON NER/040.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	1	1	0	0	1	1	1	1	1	1
M	5.7	1.5	3.80	36.7	82.5	0			19	73	62.9	30.4	1.97	34.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	62.0	29.0	22.8	1.27	27.3	19.6	1.39	1.06	1.16	22.5	19.9	1.13	5.0	11.1

ornamentation. Venous cells largely unmodified, but over the major veins they are smaller and more often 4 - sided than the non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight walls (fig. 494). Cuticular flange not heavily thickened, but fine cuticular pegs occur at cell wall junctions. No surface ornamentation. Venous cells largely unmodified, but over the major veins they are smaller and more often 4 - sided than non-venous cells. Stomata confined to areoles, oriented at random. The poral walls of the guard cells are heavily thickened. Subsidiary cells brachyparacytic, overlying the guard cells (fig. 517). Trichome bases with a small, irregularly shaped, very heavily thickened foot cell and unmodified basal cells occur rarely over veins (fig. 518). Trichomes not preserved.

Specimen examined: N 0066 (fig. 139).

Discussion: The specimen consists of an almost complete leaf, but with the base and apex missing. The secondary venation pattern is very erratic, since some secondary veins loop strongly into the superadjacent secondary vein in typical brochidodromous arrangement, while others diminish apically inside the margin in typical eucamptodromous arrangement.

PARATAXON NER/041. (Table 63).

Lamina: Symmetrical, probably obovate. Leaf base symmetrical, acute, apex unknown. Leaf length at least 10 cm., width 4.5 cm. (fig. 140).

Margin: Serrate. Serrations regularly spaced and of one order.

Petiole: Unknown.

Venation: Primary vein straight, Secondary venation pattern

semicraspedodromous. At least 11 secondary veins arise at an angle of 65°. This angle is uniform throughout the leaf. The secondary veins loop into the superadjacent secondary vein at an angle of less than 90°, and at least two branches arise from each secondary vein and terminate in serrations. Secondary, tertiary and quaternary vein arches are well formed. Composite intersecondary veins are weakly developed and rare. Tertiary veins weakly percurrent or random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and unevenly sinuous walls (fig. 497). The cuticular flange is only lightly thickened. No surface ornamentation. Venous cells longer, narrower and with straighter side walls than the non-venous cells. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and highly sinuous walls (fig. 496). The cuticular flange is very lightly thickened. No surface ornamentation. Venous cells longer, narrower and with straighter walls than the non-venous cells. Stomata confined to areoles, oriented at random, unthickened. Subsidiary cells actinomorphic, not overlying guard cells (fig. 519). Trichome bases with an irregularly shaped, thickened foot cell and unmodified basal cells occur over veins (fig. 520). Trichomes not preserved.

Specimen examined: N 0121 (fig. 140).

Discussion: The specimen consists of about the basal 2/3 of one side of a leaf and a small part of the other side. The apex is missing, but the base is symmetrical and acute.

PARATAXON NER/042. (Table 64).

Lamina: Symmetrical, at least in the basal half. Leaf base acute, symmetrical, apex unknown. Leaf length unknown, width at least 3.3 cm. (fig. 141).

Margin: Serrate. Serrations regularly spaced and of one order.

Petiole: Unknown.

Venation: Primary vein straight. Secondary venation pattern undefined. Secondary veins upturned and diminishing apically inside the margin. Each secondary vein gives rise to several minor veins which terminate in serrations. At least 9 secondary veins present. Composite intersecondary veins weakly formed and rare. Tertiary veins weakly percurrent.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight walls (fig. 499). The cuticular flange extends unevenly between adjacent cells and cuticular pegs occur at cell wall junctions. No surface ornamentation. Venous cells not highly modified, but over the major veins they are more regularly arranged, smaller, and more heavily thickened than the non-venous cells. Trichome bases with a small, circular, very heavily thickened foot cell and radial, heavily thickened basal cells occur rarely over veins. Trichomes not preserved.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and sinuous walls (fig. 498). The cuticular flange is only lightly thickened but cuticular pegs occur at cell wall junctions. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Stomata generally confined to areoles, oriented at random. Extremely large stomata occur regularly over the veins. The polar walls of the guard cells are thickened. Subsidiary cells cyclocytic,

overlying guard cells (fig. 521). Trichome bases with a small, circular, very heavily thickened foot cell and radial, heavily thickened basal cells occur rarely over veins (fig. 522). Trichomes not preserved.

Specimen examined: N 0495 (fig. 141).

Discussion: The specimen consists of the basal half of a leaf. The base is symmetrical and acute, and the apex is unknown. The apparently straight primary vein gives rise to at least 9 secondary veins which form a pattern which does not fit into Hickey's (1973) classification. Each secondary vein diminishes apically inside the margin. However, each secondary vein also branches several times into roughly equal sized veins, one of which terminates in a serration. In this way, each secondary vein is associated with about 4 or 5 serrations. The serrations are very regular, both in size and spacing.

PARATAXON NER/043. (Table 65).

Lamina: Symmetrical. Base acute, symmetrical, apex unknown. Leaf length unknown, width at least 0.4 cm. (figs. 142, 143).

Margin: Serrate.

Petiole: Normal.

Venation: Primary vein straight, massive. At least 7 secondary veins arise from the primary vein. The secondary venation pattern is eucamptodromous. Composite intersecondary veins present. Tertiary veins weakly percurrent or random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight walls (fig. 501). The cuticular flange extends deeply between adjacent cells and long cuticular pegs occur at cell wall junctions. No surface

TABLE 63: PARATAXON NER/041.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	1	1	1	1	0	1	1	0	1	1	1	1	1	1
M	9.5	4.5	2.11	56.0		2.22	69.0		12	14.0	64.8	45.4	1.90	50.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	47.0	32.0	21.0	1.52	28.3	17.8	1.59	1.13	1.18	19.5	16.3	1.20	5.0	9.9

TABLE 64: PARATAXON NER/042.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	0	0	0	0	1	0	0	0	1	1	1	1	1
M						4.75				0	64.5	41.3	2.19	51.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	56.0	30.5	18.3	1.67	27.6	16.0	1.73	1.11	1.14	24.3	23.8	1.02	5.2	8.9

TABLE 65: PARATAXON NER/043.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	1	0	0	0	1	1	0	0	1	1	1	1	1
M		0.4				1.11	43.0			29.0	27.9	17.3	2.29	55.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	70.5	24.5	17.9	1.37	24.3	16.0	1.52	1.01	1.12	24.9	22.0	1.13	5.6	10.4

ornamentation. Venous cells not highly modified, but over the major veins they are longer and narrower than the non-venous cells. Stomata similar to those on the lower epidermis occur rarely near the primary vein. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight walls (fig. 500). The cuticular flange extends deeply between adjacent cells and long cuticular pegs occur at cell wall junctions. No surface ornamentation. Venous cells not highly modified, but over the major veins they are longer and narrower than the non-venous cells. Stomata confined to areas between major veins, oriented at random. The polar walls of the guard cells are thickened. Subsidiary cells actinomorphic, not overlying the guard cells (fig. 523). Trichome bases with a small, irregularly shaped, thickened foot cell and unmodified basal cells occur over the major veins (fig. 524). Trichomes not preserved. Large elliptical glands covered by thinly cutinised cells occur over the veins (fig. 525).

Specimen examined: N 0263 (figs. 142,143).

Discussion: The specimen consists of the basal part of a leaf. The base is acute and symmetrical, but the apex is unknown. The venation pattern appears to be eucamptodromous, but there are two unusual features. Firstly there are two large serrations, one on each side of the lamina, near the base of the leaf (fig. 143). These serrations are not associated with veins and there is no sign of any serrations further up the margin. Secondly just before the top of the specimen the primary vein appears to divide into two unequal halves. The effect that this would have on the venation pattern of the leaf is impossible to forecast. Because of these features, the venation will not be considered

in detail until further specimens are collected.

PARATAXON NER/044. (Table 66).

Lamina: Symmetrical. Leaf base unknown, apex probably acute, symmetrical. Leaf length unknown, width at least 2 cm. (fig. 144).

Margin: Entire.

Petiole: Unknown.

Venation: Primary vein straight. Secondary venation pattern brochidodromous. At least 7 secondary veins present, which loop into the superadjacent secondary vein at 90° or less. Simple intersecondary veins well formed and common. Tertiary veins random reticulate.

Upper epidermis: Non-venous cells irregular, with a variable number of sides and straight walls (fig. 503). The cuticular flange is heavily thickened. Surface covered in fine pitting (fig. 503). Venous cells unknown. Trichomes absent.

Lower epidermis: Non-venous cells irregular, with a variable number of sides and straight walls (fig. 502). The cuticular flange is thickened, but not to the extent exhibited on the upper epidermis. No surface ornamentation. Venous cells longer and narrower than non-venous cells. Stomata confined to areoles, oriented at random. The polar walls of the guard cells are thickened. Subsidiary cells brachyparacytic, overlying the guard cells (fig. 526). Trichome bases with a small, irregularly shaped, heavily thickened foot cell and unmodified basal cells occur occasionally over the veins (fig. 527). Trichomes bicellular, with a large, blunt foot cell, and a long, tapering apical cell. Trichomes very thinly cutinised.

Specimen examined: N 0283 (fig. 144).

TABLE 66: PARATAXON NER/044.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NS	0	0	0	0	0	1	0	0	0	0	1	1	1	1
M						0					61.2	22.6	1.81	41.0

CHARACTER	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M	51.5	29.4	21.3	1.38	34.3	24.6	1.39	0.86	0.87	26.8	23.8	1.13	4.55	14.5

Discussion: The specimen consists of the apical half of a leaf. Part of the apex is missing (fig. 144), but it is probably acute. The trichomes are preserved in this specimen, which is rare among the Nerriga specimens, but they are generally so fragmentary and deformed that it was impossible to adequately illustrate them. However, it was possible to determine that they are bicellular, and taper into an acute apex.

7.3 FIELD KEY TO THE NERRIGA PARATAXA: A key to the parataxa is of limited usefulness, since it is unlikely that any future collectors would be able to easily use a key in the field at Nerriga, and also, because only architectural characters were used, it was difficult to produce an unambiguous key. Only 31 of the 44 parataxa described from Nerriga have been included in the key. Parataxa NER/028, NER/029, NER/030, NER/031, NER/033, NER/034, NER/035, NER/036, NER/037, NER/038, NER/042, NER/043 and NER/044 were not well enough preserved in gross morphology to warrant inclusion. Three features of the key should be noted. Because it is designed for primary "sorting" of specimens in the field, only gross morphological and venation characters are used. Secondly, due to the variability of some of the parataxa, they may appear more than once in the key, and thirdly, because they cannot be easily separated on gross morphology or venation, three parataxa (NER/039, NER/022 and NER/026) occur together in the key. Because of their easy identification, the three cycad species, the fern and the Casuarina species are not included.

1. Leaves entire ..... 2.
   Leaves not entire (lobed or toothed) ..... 19.
2. Venation pattern brochidodromous ..... 3.
   Venation pattern not brochidodromous ..... 13.
3. Leaf width $\leqslant$ 1.5 cm. ..... 4.
   Leaf width $>$ 1.5 cm. ..... 10.
4. $<$ 15 secondary veins ..... 5.
   $\geqslant$ 15 secondary veins ..... 7.
5. Secondary veins arise from the primary vein at $<50^{o}$ ..... NER/012.
   Secondary veins arise from the primary vein at $\geqslant 50^{o}$ ..... 6.

6. Leaf base symmetrical ..... NER/020.

   Leaf base highly asymmetrical ..... NER/019.

7. Secondary veins loop well inside the margin ...8.

   Secondary veins loop very close to the margin NER/020.

8. Intersecondary veins usually terminate at more than 2/3 of the length of the adjacent secondary veins ..... NER/011.

   Intersecondary veins rarely terminate at more than 2/3 of the length of the adjacent secondary veins ..... 9.

9. Venation pattern strictly brochidodromous .... NER/013.

   Venation pattern intermediate between brochidodromous and eucamptodromous ..... NER/040.

10. <15 secondary veins ..... NER/015.

    $\geqslant 15$ secondary veins ..... 11.

11. Secondary vein angle increases toward the apex NER/017.

    Secondary vein angle uniform throughout the leaf ..... 12.

12. Intersecondary veins usually terminate at more than 2/3 of the length of the adjacent secondary veins ..... NER/011.

    Intersecondary veins rarely terminate at more than 2/3 of the length of the adjacent secondary veins ..... NER/007.

13. More than one primary vein ..... NER/025.

    One primary vein ..... 14.

14. Secondary veins not obvious NER/032,

    Secondary veins obvious ..... 15.

15. Intersecondary veins absent ..... 16.

    Intersecondary veins present ..... 18.

16. Venation pattern acrodromous ..... NER/023.

    Venation pattern not acrodromous ..... 17.

17. Leaf width $<$ 1.5 cm., tertiary veins not obvious ..... NER/021.

Leaf width $\geqslant$ 1.5 cm., tertiary veins obvious . NER/024.

18. Venation pattern strictly eucamptodromous ... NER/022, NER/026, NER/039.

Venation pattern not strictly eucamptodromous ..... NER/040.

19. Leaves lobed ..... 20.

Leaves toothed ..... 22.

20. Lobes of approximately equal length ..... NER/009.

Lobes of markedly different length ..... 21.

21. Leaf $\leqslant$ 15 cm. long, 3 lobed, symmetrical ..... NER/010.

Leaf $>$ 15 cm. long, asymmetrical or with more than 3 lobes ..... NER/016.

22. Leaf length $\leqslant$ 7 cm. ..... 23.

Leaf length $>$ 7 cm. ..... 30.

23. $<$ 2 teeth per secondary vein on average ..... 24.

$\geqslant$ 2 teeth per secondary vein on average ..... 27.

24. Intersecondary veins present ..... 25.

Intersecondary veins absent ..... NER/008.

25. Venation pattern strongly craspedodromous ... NER/027.

Venation pattern mixed craspedodromous ..... 26.

26. Teeth formed by indentation of the margin ... NER/018.

Teeth protruding from margin ..... NER/014.

27. Leaf width $<$ 2 cm. ..... NER/003.

Leaf width $\geqslant$ 2 cm. ..... 28.

28. Leaf strongly obovate ..... NER/008.

Leaf ovate or elliptical ..... 29.

29. Intersecondary veins well formed and common . NER/002.

Intersecondary veins not well formed and common ..... NER/001.

30. Venation pattern strongly craspedodromous,
< 2 teeth per vein on average ..... NER/027.
Venation pattern not craspedodromous,
⩾2 teeth per vein on average ..... 31.

31. Leaf stongly obovate ..... 32.
Leaf ovate or elliptical ..... 34.

32. Intersecondary veins generally well formed
and common ..... NER/004.
Intersecondary veins poorly formed and rare,
or absent ..... 33.

33. Venation pattern strongly semicraspedodromous,
tertiary veins well formed in the middle of the
leaf ..... NER/005.
Venation pattern weakly semicraspedodromous,
tertiary veins not well formed ..... NER/041.

34. Intersecondary veins well formed and common ... 35.
Intersecondary veins poorly formed and rare,
or absent ..... 36.

35, Leaf length:width ratio < 2 ..... NER/002.
Leaf length:width ratio ⩾ 2 ..... NER/001.

36. Teeth conspicuous ..... 37.
Teeth inconspicuous ..... 38.

37, Teeth extremely variable in size ..... NER/005.
Teeth regular in size ..... NER/001.

38. Venation pattern strongly semicraspedodromous . NER/006.
Venation pattern weakly semicraspedodromous ... NER/041.

CHAPTER 8

RELATIONSHIPS BETWEEN PARATAXA.

8.1 INTRODUCTION: As was mentioned in chapter 6, the parataxa which have been described represent the maximum number of morphological forms present. It is therefore possible that some of the parataxa represent extreme forms of a morphological continuum. The purpose of this chapter will be to examine the relationships between the parataxa and if necessary suggest where parataxa are closely related and could perhaps be combined.

There are two approaches to this problem - qualitative and quantitative. While the qualitative approach has been avoided for most of this study for reasons already mentioned, it is useful to apply it at this point. This is because it was shown in chapter 4 that the character set used in this study is not necessarily very good for estimating the relationships between taxa. Therefore the qualitative approach acts as a control, against which the quantitative results can be judged. It is also much easier to apply a qualitative approach here, since it requires comparisons to be made among only 44 parataxa, not between several hundred specimens.

8.2 QUALITATIVE ESTIMATION OF RELATIONSHIPS: After careful comparison of the architecture and cuticles of all representatives of the parataxa, it appeared as though 18 parataxa were very distinctive and bore no obvious resemblance to other parataxa. They were NER/007, NER/008, NER/009, NER/010, NER/013, NER/015, NER/016, NER/019, NER/020, NER/021, NER/023, NER/024, NER/029, NER/030, NER/032, NER/033, NER/035 and NER/042. The remaining parataxa fall into six groups, listed in table 67.

TABLE 67: Groups of morphologically similar parataxa, estimated from a visual inspection.

GROUP NUMBER	PARATAXA
I	NER/025, NER/031
II	NER/014, NER/018, NER/027, NER/043
III	NER/026, NER/034, NER/037, NER/038
IV	NER/022, NER/028, NER/039
V	NER/011, NER/012, NER/017, NER/040, NER/044
VI	NER/001, NER/002, NER/003, NER/004, NER/005, NER/006, NER/036, NER/041.

Group I: NER/025 is probably the most distinctive parataxon in the Nerriga flora (figs. 58-64). The unique architectural and cuticular characters of this parataxon have already been described and will not be repeated here. However, the cuticle of NER/031 (figs. 464,465) is indistinguishable from that of NER/025 (figs. 310-323). If the so-called primary vein of NER/031 is one of the outer primary veins of NER/025 then the almost parallel margin and the basal curve of the primary vein could easily be explained. The minor venation of NER/031 differs considerably from that of NER/025 and also, if the primary vein were only a lateral primary, the whole leaf would be about 20 cm. wide, which is almost twice the width of any specimen of NER/025.. The cuticle of NER/025 is particularly distinctive however, and because of the close similarity of the cuticle of NER/031, these two parataxa could be combined.

Group II: NER/027 is the dominant parataxon in the deposit. Of the original 112 OTUs, 45 belong to this parataxon. It is distinguished by several features. Firstly, it is a compound leaf, although only one specimen is well enough preserved to show this (fig. 98). Secondly, the leaflets

have a craspedodromous venation pattern and a serrate margin. Thirdly, the lower epidermis contains large and very characteristic glands scattered over the veins (figs. 367-369). Despite the extreme variability in leaflet size and shape, the above group of features are invariant throughout the parataxon.

Three other parataxa have some or all of these features. NER/014 (figs. 41,43) has mixed craspedodromous venation which could be considered as an extreme of the NER/027 venation type. It also has a serrate margin and the glands described for NER/027 over the veins on the lower epidermis (fig. 251). Only one of the two specimens in NER/014 has its base preserved and it is highly asymmetrical, reminiscent of the base of the lateral leaflets of NER/027.

NER/018 (fig. 44) has mixed craspedodromous venation which again could be considered as an extreme of the NER/027 venation type, although it has some marked differences from that type. It also has a serrate margin and the glands described for NER/027 over the veins on the lower epidermis (fig. 267). The base of the only specimen in this parataxon is not preserved.

NER/043 (figs. 142,143) has an unusual venation type and a symmetrical base. However, the glands described for NER/027 also occur over the veins in NER/043 (fig. 525) and it may be that the single specimen in NER/043 represents a juvenile or mechanically damaged form of NER/027. Therefore it is possible that these four parataxa, NER/014, NER/018, NER/027 and NER/043 could represent extreme forms of the same biological group of plants and could be considered as a single parataxon.

Group III: NER/026 (figs. 65-80) is one of the dominant

parataxa in the Nerriga flora. The venation pattern is not particularly distinctive, being eucamptodromous, with a variable number of intersecondary veins. However, the subsidiary cell thickening is particularly distinctive. The subsidiary cells are more heavily thickened than the epidermal cells and are covered in fine striations which run perpendicular to the long axis of the stomate (figs. 362,363). Three other parataxa resemble NER/026.

NER/038 (fig. 137) probably has eucamptodromous venation. It also has the thickened and striated brachyparacytic subsidiary cells found in NER/026 (fig. 513). NER/034 (figs. 132,133) is much smaller than any specimen of NER/026, but has eucamptodromous venation and thickened and striated brachyparacytic subsidiary cells (fig. 505). NER/037 (fig. 136) has apparently brochidodromous venation, although it consists of only one specimen, which is the apical part of a leaf. Many specimens of NER/026 become somewhat brochidodromous toward the apex, although their overall venation pattern is unquestionably eucamptodromous. The same may be true for NER/037. The brachyparacytic subsidiary cells of NER/037 are thickened and striated. Sometimes the subsidiary cells are atinocytic, but this is rare (figs. 510,511). It is therefore quite possible that these four parataxa, NER/026, NER/034, NER/037 and NER/038 all belong to the same biological group of plants and could represent a single parataxon.

Group IV: Three parataxa, NER/022 (fig. 49), NER/028 (fig. 126), and NER/039 (fig. 138) are each represented by a single specimen. NER/022 is a highly asymmetrical leaf, probably the result of mechanical damage early in its development. The venation pattern is weakly brochidodromous and intersecondary veins occur commonly. One of the striking features

of this cuticle is that the cuticular flange not only extends between adjacent cells, but also extends over the subepidermal layer of cells, leaving a second, fainter outline of the mesophyll cells (figs. 288,289). This occurs on both epidermises.

NER/039 has a very similar venation pattern to NER/022, except that it is symmetrical. The cuticles of the two parataxa also share several features, the most distinctive of which is the extreme development of the cuticular flange. NER/028 consists of only one incomplete specimen, Although only the apical half of the leaf is preserved, the venation pattern shows no major differences from NER/022 or NER/039. The cuticle of NER/028 is also similar to that of the other two parataxa, although it lacks trichome bases on the lower epidermis. It is likely that these three parataxa, NER/022, NER/028 and NER/039 all belong to the same biological group of plants and represent a single parataxon.

Group V: Five parataxa, NER/011, (figs. 38,39), NER/012 (fig. 37), NER/017 (fig. 45), NER/040 (fig. 139), and NER/044 (fig. 144) all have a very similar brochidodromous venation pattern, although in NER/040 it appears to be somewhat more loosely defined. A very distinctive feature of the lower epidermis in all parataxa except NER/012 is the presence of cuticle covering the stomatal cavity (figs. 231, 263). NER/012 consists of only one specimen with very fragmentary cuticle and such a covering, if it was present, has not been preserved. The whole stomatal complex of all five parataxa is very similar and it is possible that the six specimens which make up the five parataxa may simply represent extremes of form within a single biological group of plants and could therefore be considered as a single

parataxon.

Group VI: The final group of eight parataxa show more complex interrelationships. There are some very obvious similarities between NER/002 (fig. 21), NER/003 (fig. 22), NER/004 (figs. 23-31) and, to a lesser extent NER/001 (figs. 18-20), NER/005 (fig. 33), NER/006 (fig. 32), NER/036 (fig. 134), and NER/041 (fig. 140). They all have a similar form of semicraspedodromous venation and they all possess toothed margins, although the size and form of the teeth is extremely variable. Intersecondary vein frequency varies considerably, as does leaf shape.

It is the cuticle which exhibits the closeness of the relationship between these parataxa. The lower epidermis of NER/004 (figs. 174,176,178,180,182,184,186,188,190), which is by far the most highly represented of this group of parataxa, has epidermal cells with straight or curved walls, fine cuticular pegs at cell wall junctions, stomata with actinomorphic subsidiary cells and numerous trichome bases. NER/002 (figs. 160,161) is very similar to NER/004 except that the epidermal cell walls may be sinuous. NER/002 is separated from NER/004 on the basis of the size and shape of the lamina and on the fact that only about two teeth per secondary vein are present, as opposed to more than two for NER/004. NER/003 (figs. 22,162,163) is similar to both NER/002 and NER/004 and is separated on its leaf shape and the frequency of intersecondary veins. NER/002 and NER/003 could easily represent extreme forms of NER/004.

NER/001 (figs. 18-20, 154-159) consists of three specimens which share some distinctive features. All three specimens have atinocytic subsidiary cells which would appear to separate this parataxon from NER/004, despite the architectural similarities.

The other four parataxa, NER/005 (figs. 33,164,165), NER/006 (figs. 32,200,201), NER/036 (figs. 134,486,487), and NER/041 (figs. 140,496,497) differ from NER/004 in having only a few trichome bases over the major veins. However, they are similar to one another, both architecturally and in their cuticular pattern. Therefore, this group of eight parataxa, despite their architectural similarities, could possibly fall into three biological groups. NER/002, NER/003 and NER/004 form one group, NER/001 another, and NER/005, NER/006, NER/036 and NER/041 form the third. It is possible that the first and third groups may belong together as one parataxon, but the subsidiary cell arrangement of NER/001 clearly separates it.

On the basis of this qualitative comparison the number of parataxa in the Nerriga flora could be as low as 26, rather than the 44 described in chapter 7. A quantitative assessment of the relationships between the 44 parataxa may now be made to compare with the results of the qualitative review.

8.3 QUANTITATIVE ESTIMATION OF RELATIONSHIPS: Since 17 of the 44 parataxa had missing values for at least some of the characters, missing data had to be accounted for when calculating the similarity matrix. This was achieved in two ways.

(a) CLUSTAN 1C cannot calculate a similarity matrix if missing data occurs, therefore a mean value calculated from all other parataxa was inserted for missing data where-ever it occurred. This method of handling missing data, while commonly used, is not desirable, especially when the amount of missing data is large.

(b) Using a program developed by Blackburn (1978a), a

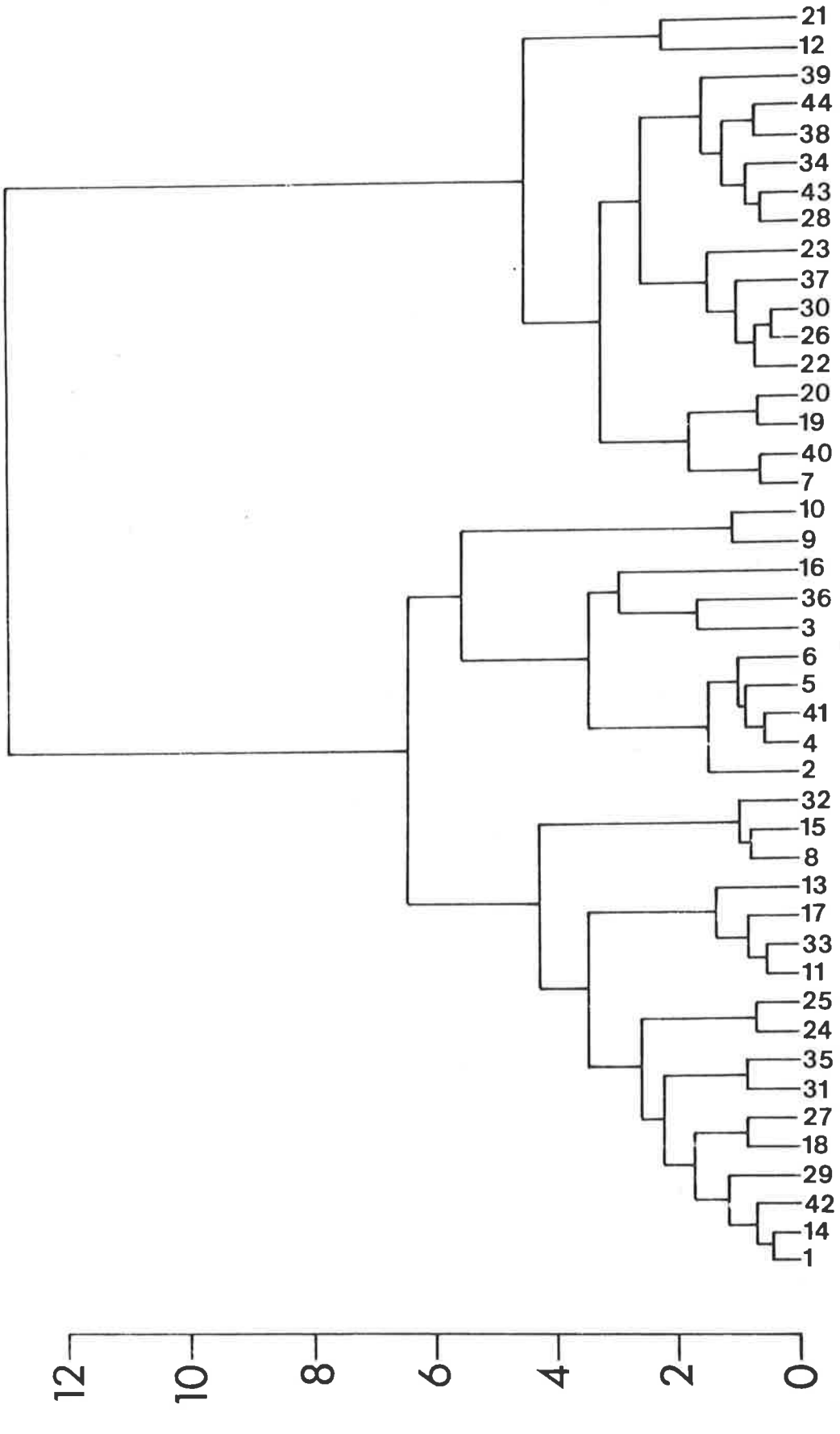
similarity matrix of Euclidean distances can be calculated if missing data is present. When calculating a distance measure between a pair of OTUs, if one or both of the OTUs has missing data for a particular character, that character is deleted from the calculation. The similarity matrix produced could then be input into CLUSTAN 1C. This method for handling missing data is superior to the use of a mean value, since it makes no assumptions about the character value.

A second feature of this program is that it standardises characters to states rather than to variance (see 3.2). Because of this, it is possible for each OTU to score more than once for each character. For example, if, as in this case, each OTU may consist of several individuals, the range of values can be considered rather than the mean. Therefore, if six states were available, one OTU may score in states 2-4 for example. Theoretically, this is a big advantage over using a mean value for each character, since it allows the variability of the OTU for a particular character to be expressed.

Two similarity matrices were therefore available for clustering, one produced by standardising characters to variance and substituting mean values for missing data; and the other produced by standardising multiple scores for characters to states and deleting missing data from the calculations. These two similarity matrices were clustered in four different ways.

8.3.1 RESULTS: A:<u>44 parataxa with 25 characters standardised to zero mean and unit variance, using mean values in place of missing data, clustered using the ESS algorithm</u>: Figure 13 shows the dendrogram produced. The qualitative results suggested that six groups could be closely related (table 67).

FIGURE 13. ESS dendrogram for the 44 parataxa with 25 characters standardised to zero mean and unit variance. The numbers correspond to parataxon numbers, i.e. 1 = NER/001 etc.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These groups will be considered in turn.

GROUP I: The two parataxa occur in a group of 10, but are not closely linked. This is to be expected, since many of the extreme character values in NER/025 (e.g. leaf width and shape) were scored as missing data in NER/031.

GROUP II: Three of the four OTUs occur in the group of 10 parataxa containing the OTUs in group I. The fourth (NER/043) is widely separated from them, possibly because of its extremely small lamina size in comparison to the other three.

GROUP III: The four parataxa in this group occur among a group of 11 parataxa, but they are spread throughout it, with none being particularly closely related.

GROUP IV: The three parataxa in this group occur in the group of 11 parataxa containing the parataxa in group III, but again they are widely separated.

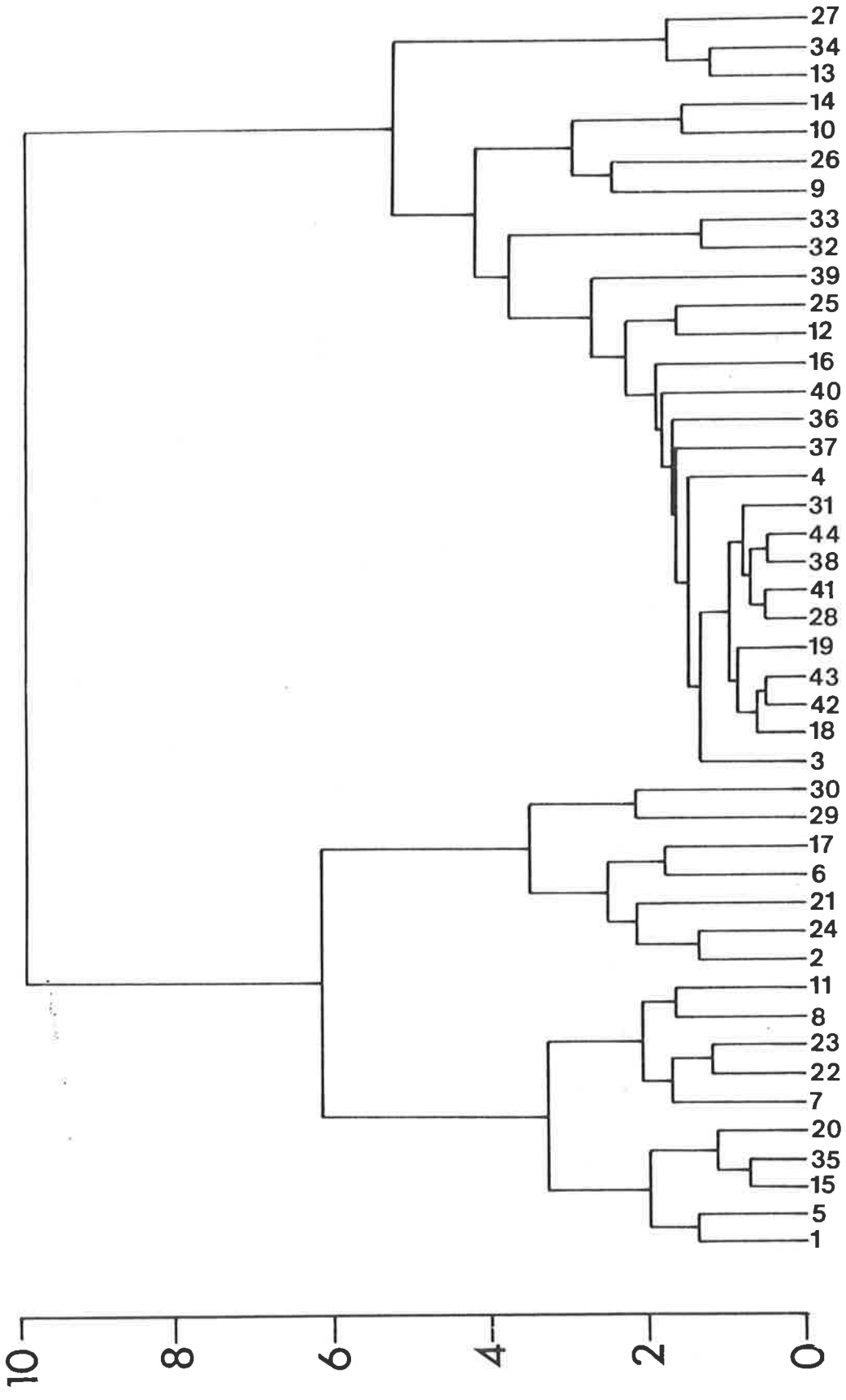
GROUP V: The five parataxa are spread throughout the dendrogram, and none are closely related.

GROUP VI: Seven of the eight parataxa are clustered very closely, occurring in a group of eight parataxa (the eighth being NER/016). The remaining parataxon (NER/001) is not closely related to the others, as predicted in 8.2.

An inspection of fig. 13 suggests that only two clusters could be delimited. In general, the position of the parataxa within the groups lends some support to the qualitative conclusions, but it is unlikely that any of the parataxa would have been selected as possibly being closely related on the basis of this dendrogram.

B: 44 parataxa with 25 characters standardised to states, with missing data deleted and using multiple scores for characters, clustered using the ESS algorithm: Figure 14 shows the dendrogram produced. None of the parataxa in any

FIGURE 14. ESS dendrogram for the 44 parataxa with 25 characters standardised to states. The numbers correspond to parataxon numbers.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of the groups are closely related in the dendrogram. The clustering in this dendrogram (fig. 14) is extremely poorly correlated with the qualitative result and compares very unfavourably with the first dendrogram (fig. 13). The discrepancy probably lies in the use of multiple scores for characters, rather than in the method adopted for handling missing data. Ideally, before multiple scores are used it should be ensured that each OTU contains an equal number of specimens. This was not the case in this study. The effect of using different numbers of specimens per OTU is to bias the range of the characters. This is obviously an undesirable feature and it is evident that Blackburn's (1978a) method should be used with this shortcoming in mind.

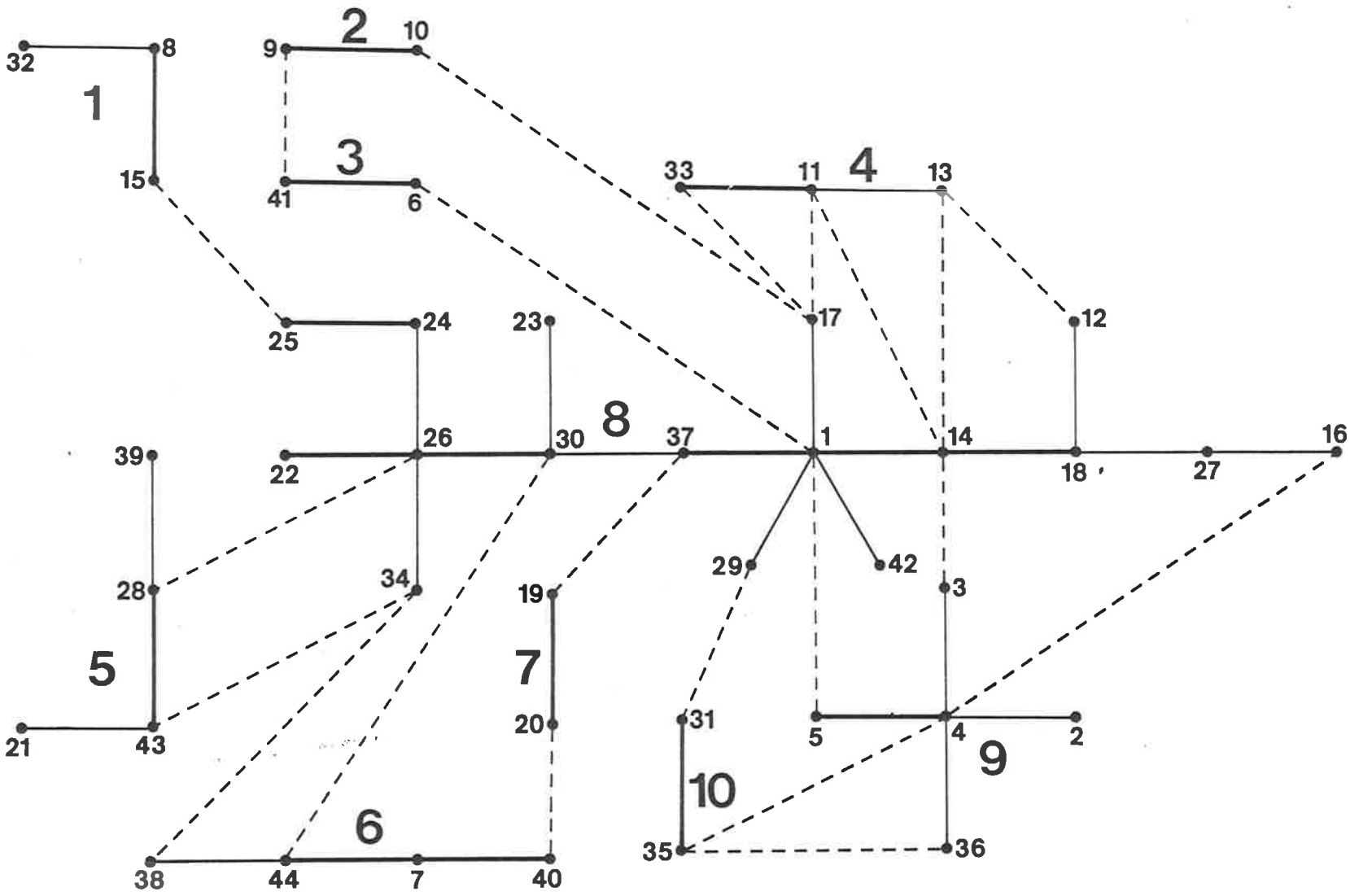
C: 44 parataxa with 25 characters standardised to zero mean and unit variance, using mean values in place of missing data, clustered with an NNN: The NNN (fig. 15) contains 10 groups. The parataxa in each cluster are listed in table 68.

TABLE 68: Parataxa in each of the groups of the NNN (fig. 15).

GROUP	PARATAXA	TOTAL NUMBER OF PARATAXA
1	NER/008,NER/015,NER/032	3
2	NER/009,NER/010	2
3	NER/006,NER/041	2
4	NER/011,NER/013,NER/033	3
5	NER/028,NER/028,NER/039,NER/043	4
6	NER/007,NER/038,NER/040,NER/044	4
7	NER/019,NER/020	2
8	NER/001,NER/012,NER/014,NER/016,NER/017, NER/018,NER/022,NER/023,NER/024,NER/025, NER/026,NER/027,NER/029,NER/030,NER/034, NER/037,NER/042	17
9	NER/002,NER/003,NER/004,NER/005,NER/036	5
10	NER/031,NER/035	2

The six groups of closely related parataxa (table 67) are

FIGURE 15. Nearest neighbour network for the 44 parataxa. The heavy, unbroken lines represent very strong bonds, the light, unbroken lines represent strong bonds and the broken lines represent weak bonds. The small numbers correspond to parataxon numbers, and the large numbers delimit groups.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spread throughout the NNN in the following way:

GROUP I: One parataxon (NER/025) in group 8 and the other (NER/031) in group 10.

GROUP II: Three parataxa among the 17 in group 8 and one (NER/043) in group 5.

GROUP III: Three parataxa among the 17 in group 8 and one (NER/038) in group 6.

GROUP IV: One parataxon (NER/022) among the 17 in group 8 and the other two in group 5.

GROUP V: The five parataxa are spread between groups 4 (NER/011), 6 (NER/040 and NER/044) and 8 (NER/012 and NER/017).

GROUP VI: Five of the parataxa occur in group 9, and two in group 3. They are the only parataxa in these groups. NER/001 occurs among the 17 parataxa in group 8.

The NNN substantiates the qualitative results to some extent, but is certainly not a great improvement on the dendrogram produced from the same similarity matrix (fig. 13).

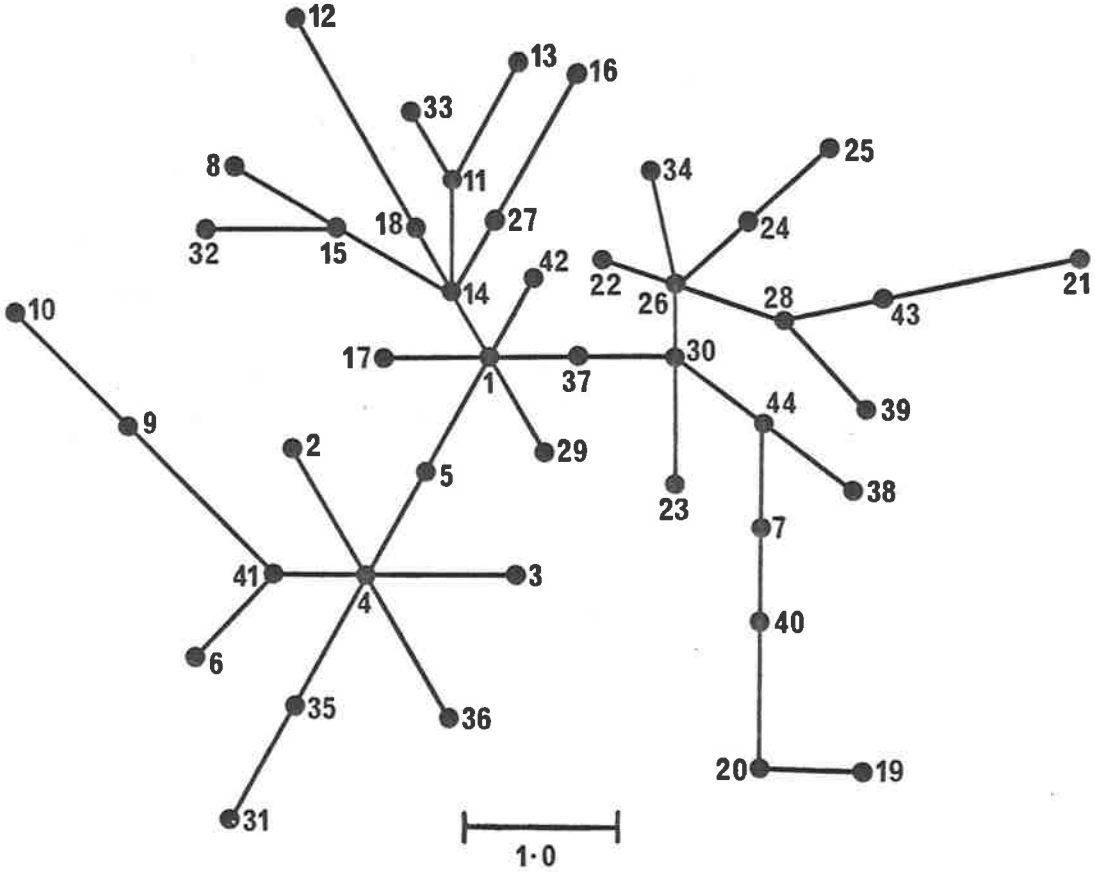
D: 44 parataxa with 25 characters standardised to zero mean and unit variance, and using mean values in place of missing data, clustered using an MST: The MST (fig. 16) can also be scanned for relationships between parataxa. If the six groups suggested from the qualitative analysis (table 67) are again considered, the following can be seen:

GROUP I: The two parataxa (table 67) are widely separated in the MST.

GROUP II: Three of the four parataxa (NER/014,NER/018,and NER/027) are closely related, but NER/043 is widely separated.

GROUP III: Three of the parataxa (NER/026, NER/034 and NER/037) occur in close proximity in the MST, but the fourth

FIGURE 16. Minimum spanning tree for the 44 parataxa described in chapter 7, based on a similarity matrix constructed from 25 characters standardised to zero mean and unit variance, with mean values substitued for missing data. (Numbers correspond to parataxon numbers).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(NER/038) is widely separated.

GROUP IV: The three parataxa (table 67) occur in close proximity in the MST.

GROUP V: The five parataxa (table 67) are widely spread throughout the MST.

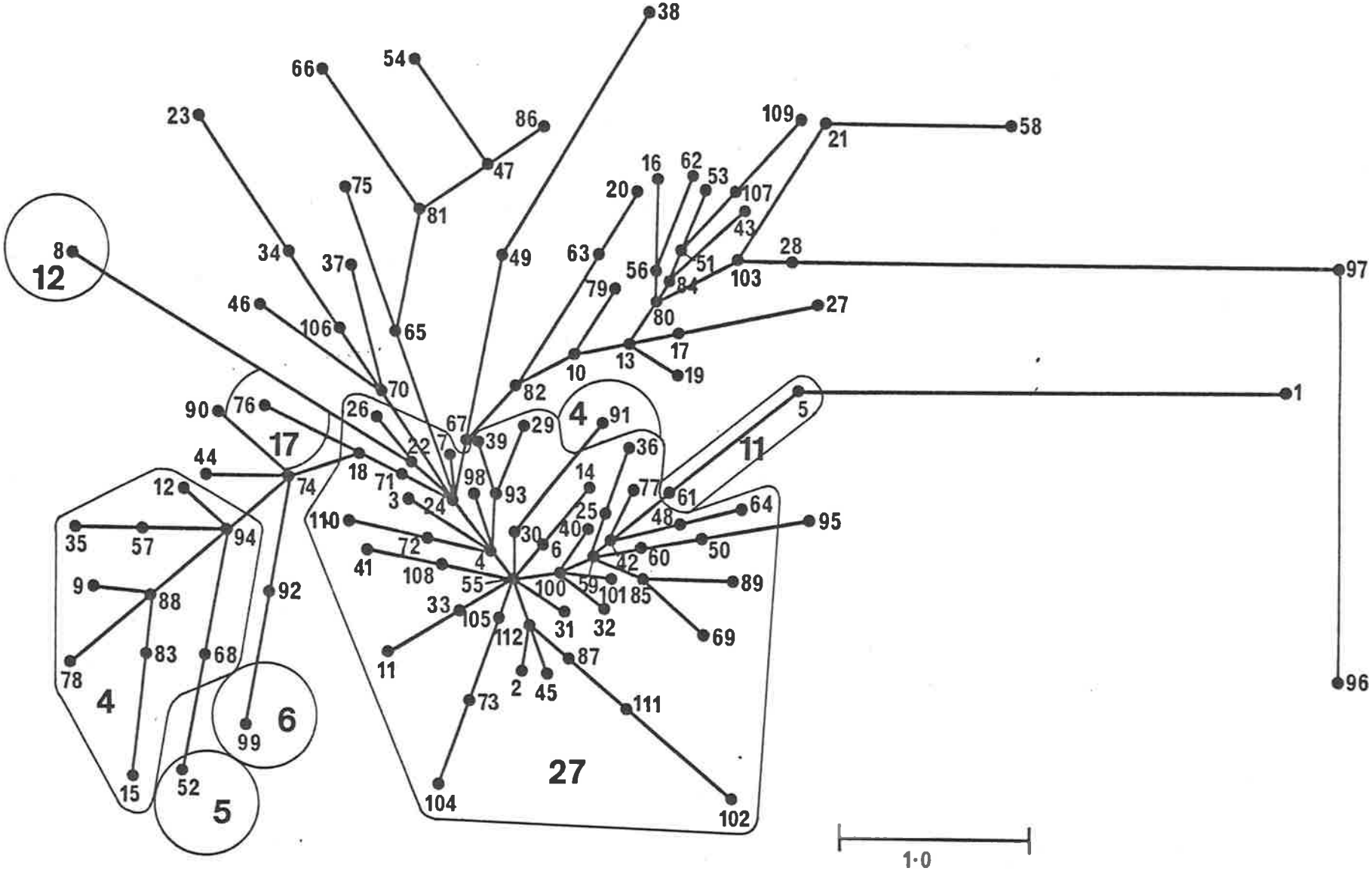
GROUP VI: The eight parataxa (table 67) are directly linked to one another.

The MST shows that the parataxa in groups II, III, IV and VI are more or less closely related, as suggested by the qualitative results, but those in groups I and V are not. In general, the results of the quantitative analyses suggest that providing the qualitative results are accurate, the character set has some weaknesses in estimating relationships between parataxa, as was predicted in chapter 4.

In chapter 6, 27 parataxa were delimited from 112 OTUs. If the qualitative results in this chapter are correct, this number should actually have been 20. There are two possible sources of error for the over-estimation of the number of parataxa in chapter 6. Either the character set may have been inadequate and the OTUs in a parataxon were very widely separated, or the visual comparisons may have been inaccurate in some cases. The MST of the 112 OTUs given in chapter 6 has been reproduced (fig. 17) showing the positions of the OTUs in question. Those parataxa which should be amalgamated are: NER/014 with NER/018 and NER/027; NER/011 with NER/012 and NER/017; NER/002 with NER/003 and NER/004; and NER/005 with NER/006.

It can be seen that the OTUs in parataxa NER/014, NER/018 and NER/027 are very closely linked in the MST (fig. 17) and their amalgamation reduces the complexity of the original interpretation (fig. 5) considerably. The close

FIGURE 17. The MST drawn in fig. 5 (chapter 6). (Small numbers = OTU numbers, large numbers correspond to parataxon numbers). The OTUs in parataxa NER/002 (OTU 12) and NER/003 (OTU 15) have been combined with the OTUs in NER/004. The OTUs in parataxa NER/014 (OTUs 18 and 24) and NER/018 (OTU 22) have been combined with the OTUs in NER/027.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relationship of these parataxa was commented on in chapter 6. The OTUs in parataxa NER/011, NER/012 and NER/017 are widely separated in the MST (fig. 17) and obviously the character set does not reflect the true relationship between the OTUs. The OTUs in parataxa NER/002, NER/003 and NER/004 are very closely related (fig. 5), and again this was commented on in chapter 6. The OTUs in parataxa NER/005 and NER/006 are well separated in the MST and the character set does not reflect the true relationship between them. Therefore, although the character set was sometimes inadequate for depicting the relationships between OTUs, it was also often the case that the visual estimation of relationships was inaccurate. This visual estimation was greatly improved when all the specimens had been studied and the variability of the parataxa was more fully understood. This shows the importance of the taxonomist being familiar with the material being studied, even if numerical methods are being employed.

8.4 CONCLUSION: The 44 parataxa described in chapter 7 were delimited from 130 specimens in chapter 6. It was obvious at that stage that the limits of some of the parataxa were unclear and that further investigation would be required.

After studying all the specimens available (581) relationships between parataxa could be inferred. The results of this study led to some interesting conclusions. Of the 44 parataxa, 18 were acknowledged as being very distinctive and remained unchanged. Of these 18 parataxa, 13 were represented by only one specimen, three by two specimens, one by six specimens and one by 18 specimens (table 22). That is, the 41% of parataxa which are "unrelated" to other parataxa account for only 7.4% of the specimens. The obvious conclusion is that when a large

number of specimens are available for a parataxon it becomes more difficult to define the limits of that parataxon and more likely that the range of form will overlap other parataxa.

The remaining 26 parataxa were interrelated in six groups. A close study of the specimens involved led to the following conclusions:

(1) NER/025, which contains 71 specimens, should include the single specimen of NER/031, which probably represents a fragment of an extremely large leaf.

(2) NER/027, which contains 246 specimens, probably encompasses a large enough range of form to allow it to include NER/014 (two specimens), NER/018 (one specimen) and NER/043 (one specimen).

(3) NER/026, which contains 100 specimens, should probably include NER/034 (one specimen), NER/037 (one specimen) and NER/038 (one specimen) because they have several features which are common to all specimens of NER/026.

(4) NER/022, NER/028 and NER/039 share many similarities and are probably closely related. However these three parataxa contain only four specimens and more material is required to adequately guage the variation of this particular leaf type.

(5) NER/011, NER/012, NER/017, NER/040 and NER/044 share many similarities and are probably closely related. However these parataxa are represented by only 11 mostly fragmentary specimens, and again the variation of this leaf type is not well understood.

(6) The relationship between parataxa NER/002, NER/003, NER/004, NER/005, NER/006, NER/036 and NER/041 is very complex. NER/004, with 87 specimens is by far the most

highly represented of these parataxa. It is possible that NER/002 (one specimen) and NER/003 (two specimens) could be included in the range of form exhibited by NER/004. However NER/005, NER/006, NER/036 and NER/041 which contain only one specimen each probably constitute a separate leaf type, although more specimens are required to test this hypothesis.

Therefore the number of parataxa present among the 581 specimens is somewhere in the range of 26 to 34, depending upon the relationships between some of the poorly represented leaf forms. It is apparent that further collections of some of the rarer parataxa are required to ascertain their variation. For the remainder of this study, the 44 parataxa described in chapter 7 will be referred to unless otherwise indicated.

CHAPTER 9

TAXONOMY.

9.1 TRADITIONAL APPROACHES TO IDENTIFICATION: There are two major problems in identifying fossil angiosperm leaves in Australia, one of which is the consequence of the other. Firstly the leaf architecture of extant Australasian angiosperms is virtually unknown. A cleared leaf collection has been commenced at the Botany Dept., University of Adelaide (D.C. Christophel pers. comm.) but it will be many years before it is large enough and well enough studied to be of significant use for the identification of Tertiary fossils. Secondly, little is known about the evolutionary rates of Australasian angiosperms. That is, many Tertiary angiosperms may be extinct at the specific, generic, or possibly even the family level, but at present there is no way of detecting this.

At present, the only method available for the identification of fossil angiosperm leaves is the much maligned "picture matching" technique. It is worth considering the technique of picture matching in some detail. There is no doubt that the human brain is well equipped for pattern recognition. Subtle differences in venation pattern, leaf shape and cuticular pattern are readily recognised by visual inspection but cannot always be simply put into words or, alternatively, coded as character states for computer data banking. It was for this reason that it was considered necessary to illustrate all the OTUs used in this study, therefore making them available for other researchers to compare visually.

Two serious deficiencies are apparent in the picture matching technique. Firstly, it relies heavily on the

experience and objectivity of the user. Many unrelated leaf types have very similar venation patterns and to the inexperienced or casual researcher they may easily be mistaken as being closely related. It should be noted, however, that this similarity rarely extends over all leaf features (i.e. including cuticular patterns). Secondly, due to the time required for comparison, many leaf types will often not be examined before an identification is made. Lange (1978b) pointed out that the onus is on the palaeobotanist not to ascribe the fossil to the first match detected, but to explore as many alternatives as possible. Australian palaeobotanists have often been guilty of ignoring this advice.

The historical fact is that picture matching has left angiosperm palaeobotany with a huge legacy of misidentifications. Those researchers who still use the method are much less likely to misidentify leaves than earlier researchers were. This is because modern researchers have learnt from the past and no longer feel obliged to indentify virtually every leaf they find, and therefore they tend to be much more critical in their comparisons before they make an identification.

During the course of this study, it is estimated that several thousand species of Australian angiosperms have been observed in herbariums, in the field, and in the cleared leaf collection at Adelaide University. Although many leaves have been collected for critical comparison, no firm identifications of the angiosperm leaves at Nerriga (apart from Casuarina (Christophel 1980 in press) which is extremely distinctive and is accompanied by reproductive material) have been made.

The failure of these comparisons to produce even one

close match and the difficulty being experienced in identifying angiosperm leaves from the Maslin Bay and Anglesea floras (Christophel and Blackburn 1978; D.C. Christophel pers. comm.), indirectly indicates that perhaps many of the species in Australian Eocene deposits are extinct. This possibility has been recognised world wide. For example, Wolfe (1977) suggested that diversification of many families of Sympetalae was largely post-Eocene, judging by the number of extinct forms in the Alaskan fossils he studied.

9.2 DATA BANKING OF ANGIOSPERM LEAF INFORMATION: Dolph (1978a) proposed the initiation of a computer based data bank of fossil and extant leaf information. He gave three major reasons for the need for such a system: "(1) the ever increasing amount of information available on modern and fossil leaves; (2) the difficulty in carrying out an effective literature search to obtain references on leaf material; and (3) the ability to carry out statistical tests based on the information in the data bank."

Dolph suggested that ideally both label data and character data should be entered into the data bank for each specimen. The type of characters which should be entered into the data bank has been commented upon by Dolph (1978a) and Hill (1980b in press). This will be considered again in the conclusion. It is obvious that data banking would be a great advantage to the researcher trying to identify fossils. Undoubtedly the biggest problem in trying to identify a fossil angiosperm leaf is the number of comparisons which must be made. A data bank of leaf information has the potential to significantly reduce this problem by eliminating species which do not need to be compared (because they are obviously different).

Even with an efficiently running data bank there is no doubt that the major problem would still be the number of comparisons which ideally should be made. There is another approach to the problem of reducing the number of required comparisons. If it were possible to place a fossil leaf into a family or even limit it to a group of families the number of comparisons would be greatly reduced. In the picture matching technique comparisons are usually made at the species level, and rarely, if ever are family characteristics considered. With the aid of a great deal of properly directed research it may be possible to delimit families on the basis of a combination of several key features of leaf architecture and/or cuticular pattern. Some work has already been done in this direction. Hickey and Wolfe (1975) proved that this may be possible by producing a key to the dicotyledonous subclasses based on leaf morphology. Lange (1978b) noted that a particular type of complex hair base occurs in Proteaceae, although it is also found in Araliaceae and Platanus, and a particular type of papillae may be restricted to Proteaceae and Barringtoniaceae. There are many other obvious examples: the presence of oil glands and an intramarginal vein in Myrtaceae, oil glands in Rutaceae etc., Research into this area would be invaluable for the future of palaeobotanical angiosperm taxonomy. This type of key leaf character could be easily adapted to computer data banking, and in fact comprehensive literature searches may prove that much of the data is already available. Until such a system is operational little headway will be made in the identification of Australian Tertiary angiosperm leaves.

9.3 TAXONOMIC DETERMINATIONS: The only angiosperm which has been identified from Nerriga is Casuarina, which is represented

by one female cone and 12 isolated twigs (Christophel 1980 in press). The cone and all the twigs are four parted, and this, along with other diagnostic features, prompted Christophel to place them in division Gymnostomae, which will be elevated to generic status by L.A.S. Johnson in his forthcoming revision of the Casuarinaceae. The specific determination of the Nerriga Casuarina has yet to be made.

In comparison to other Tertiary deposits in Australia, Nerriga is somewhat depauperate in non-angiospermous fossils. In fact, out of a total of about 750 specimens only four are non-angiospermous. Three of these four specimens are cycads. They are Bowenia papillosa (Hill 1978), Lepidozamia foveolata (Hill 1980a) and Pterostoma anastomosans (Hill 1980a). Reprints of the papers describing these species are in Appendix IV.

The fourth specimen is an impression of a fern (fig. 560). No cuticle was preserved on the specimen, and epifluorescence microscopy failed to give any details of the epidermis. The specimen consists of an incomplete frond (pinna?) which branches, apparently dichotomously. Each branch contains a large number of pinnules (?), each of which has a midrib which runs the length of the pinnule and gives rise to lateral veins which are not well preserved. The pinnules also occur below the branch.

It is likely that the specimen belongs to the family Gleicheniaceae, because of the presence of the pseudodichotomous branch of the frond (Bower 1963 p. 13). There are six genera in Gleicheniaceae (Copeland 1947 p. 26), four of which would not preclude the fossil (Sticherus Presl, Gleichenia Smith, Dicranopteris Bernhardi and Hicriopteris Presl). Only one of these genera (Sticherus) has been

observed, and the specimen shown in figure 561 (S. flabellatus (RBr.) St. John) exhibits an obvious similarity to the fossil. However, before a definite identification of the fossil could be made, more material would have to be collected, preferably containing sporangia, so that the affinity with Gleicheniaceae could be confirmed.

Therefore, at the present time, one angiosperm and three cycads have been identified from the Nerriga deposit. There is little prospect that this number will be increased significantly in the near future for the reasons outlined in 9.1.

CHAPTER 10

COMPARISON WITH OTHER DEPOSITS.

10.1 EOCENE DEPOSITS: Three Eocene megafossil floras are currently being studied in Australia. Apart from the Nerriga deposit, they are at Anglesea and Maslin Bay (figure 1). The Maslin Bay megafossil flora has been the subject of several research projects (e.g. Lange 1970,1978b; Blackburn 1973; Harvey 1974; Christophel and Blackburn 1978; Christophel 1980 in press), but the bulk of the flora remains undescribed. The Anglesea flora has also been reported in many publications (e.g. Douglas 1977,1978; Lange 1978b; Hill 1978,1980a; Christophel 1980 in press), and is currently being researched by D.C. Christophel and M.D. Peters (Botany Dept., University of Adelaide).

Christophel (1979 in press) concluded that there is not a single leaf species in common between these three floras, and at the generic level there is only one taxon definitely found in all three, that being Casuarina. Since that time, Bowenia and Pterostoma have both been reported from the Anglesea and Nerriga deposits (Hill 1978,1980a).

A survey of specimens from the three deposits suggests that they differ markedly from one another in floristic content. However, since so few taxonomic determinations have been made, it is too early to comment specifically on this. The task will certainly be made easier when parataxonomic studies of the three floras are complete.

Lange (1978b) described some proteaceous cuticles from the Lake Lefroy (Western Australia) deposit. However, since no proteaceous cuticles have been recognised from the Nerriga deposit, no comparison can be made. Therefore, from the limited comparisons which can be made with other Eocene

deposits in Australia, it appears as though the Nerriga flora is so far largely unique in its floristic composition.

10.2 OTHER TERTIARY DEPOSITS: D.T. Blackburn (Botany Dept., University of Adelaide) is currently studying the Miocene flora of the Yallourn brown coal mine. This flora, which has also been studied by Duigan (1966) has been preserved mostly as dispersed cuticle and shows no obvious similarities to the Nerriga flora. The only direct comparison which can be made with Tertiary, non-Eocene floras is at the generic level. Cookson (1953) described Lepidozamia hopeites (Cookson) L. Johnson from the Oligocene of Bacchus Marsh, Victoria. The genus Lepidozamia is also present at Nerriga.

10.3 PALYNOLOGICAL DATA: By far the greatest contribution to the Tertiary floras of Australia is in the form of palynological data. However, it is difficult to make comparisons with megafossil floras because of the paucity of taxonomic determinations of megafossils. Some interesting comparisons can be made between the Nerriga megafossils and the microfossils reported by Owen (1975). Table 69 lists the relative percentages of the major component groups at Nerriga (after Owen (1975)). The first feature of interest is the high percentage of spores (15.5 - 37.5%). A large percentage of the spores were contributed by Cyathidites spp. and Trilites tuberculiformis. The former is definitely a tree fern, and the latter may also be. This tree fern element forms at least 7% of the assemblage (Owen 1975). Tree fern remains are absent from the mega-fossils. There are two possible reasons for this. Firstly, extant Cyathea species do not shed their fronds, which generally decay on the plant and are therefore not likely to be introduced into a deposition site. Secondly, extant

Cyathea species produce enormous numbers of spores, and therefore the 7% of the total spore and pollen component may have been contributed by a relatively rare element of the vegetation.

TABLE 69. Relative Percentages of Major Component Groups, Nerriga (after Owen 1975).
All figures are in percentages of total grain count

Sample No.	Spores	Gymno.	Total Ang.	Notho. (m,f)	Myrt.	Cup.	Prot.	Cas.
147	19.5	2.5	75	8.5 (1,-)	7.5	11	15	2.5
150	15.5	2	82.5	10.5 (1,1)	5.5	11	19.5	3.5
153	25	3.5	71	7.5 (-,2.5)	2	6.5	23	5
155	37.5	3.5	58	2.5 (1,-)	2.5	6	23.5	2.5
158	17	4.5	78.5	10.5 (-, 1)	2	9	18	3.5
161	22	5.5	72	6.5 (-, 1)	6.5	6	23	3

Gymnosperm component: Includes Araucariacites australis, Dilwynites spp., Ephedripites notensis, as well as Podocarpidites spp., Lygistepollenites florinii, Parvisaccites catastus, Microcachryidites antarcticus, and Phyllocladus palaeogenious.

Nothofagidites component: Total of all three groups, brassi+menziesii+fusca; separate values for menziesii and fusca types given in parentheses.

Myrtaceae-type component: Myrtaceidites spp.

Cupanieidites major/orthoteichus component: Cupanieidites major/orthoteichus.

Proteaceae-type component: Proteacidites spp. + Banksieaeidites spp.

Casuarina-type component: Haloragacidites harrisii + H. trioratus.

The second interesting feature is the very small gymnosperm component (2 - 5.5%). This is substantiated by the extremely rare gynosperm megafossils (approximately 0.5%). The angiosperm component of the microflora, which dominates the assemblage, is divided into five components by Owen (1975). The Casuarina-type component accounts for 2.5 - 5% of the assemblage, and correlates well with the occurrence of Casuarina twigs and a female cone (Christophel 1980 in press). The Proteaceae-type component is large (15 - 23.5%), but cannot be correlated to any known proteaceous megafossils, even though they should be relatively easily identified on the basis of cuticular features (Lange 1978). The same is true for the Myrtaceae-type component (2 - 7.5%) which should be easily identified among the megafossils, but is apparently absent. The Cupanieidites major/orthoteichus component (6 - 11%) cannot be easily correlated with any megafossils at present as diagnostic features in the megafossils are not documented. The last component is Nothofagidites, which at 2.5 - 10.5% is small compared to many other localities (Owen 1975, Kemp 1978), but is still significant. The venation pattern and cuticle of extant Nothofagus is well known, and no specimens from Nerriga resemble this genus. This lack of Nothofagus leaves in deposits with a high component of Nothofagidites pollen has been commented upon by Christophel and Blackburn (1978) and Christophel (1979 in press).

Therefore, apart from the general agreement in the proportion of representation of gymnosperms and the presence of Casuarina, there is virtually no taxonomic correlation between the microflora and megaflora. Several reasons have

been advanced for discrepancies such as this, the most common of which are that different species can contribute widely differing amounts of pollen per individual and the dispersal range of pollen differs greatly between species. However, even taking these factors into account, some correlation between the microflora and megaflora should still occur, since the plants growing around the site could reasonably be expected to contribute a significant amount of pollen or spores to the assemblage.

One factor which could be contributing to this problem is the accuracy of the taxonomic determinations of fossil pollen. Potonié (1956,1958) suggested that Tertiary pollen should not be given names based on modern plants if the holotypes are in the form of dispersed fossil material. He believed that placing a spore with only a few characters in a recent genus can cause difficulties in nomenclature and taxonomy. Boulter (1979) concluded that "there is some good palaeobotanical evidence that some modern genera did exist prior to the Quaternary, but as comparitive studies progress an increasing number of major morphological differences become evident for many genera, particularly in the Paleogene. This suggests that rates of evolution were sufficiently fast during parts of the Tertiary to have altered the character of many plants." He also made the important assertion that "the majority of taxonomic problems in palynology can be resolved by reference to the whole megafossil record."

There is no reason to suppose that the evolution of pollen and leaves have occurred at the same rate. If Owen's taxonomic determinations are assumed to be correct, the conclusion must be that many of the leaf features characteristic of some families today (e.g. intramarginal

veins and oil glands in Myrtaceae) must have evolved in the post-Eocene, even though the families may have been well-defined in the Eocene. It is equally plausable, and more conservative, to assume that some of the taxonomic determinations of pollen and spores of the Australian Tertiary must be incorrect, since they cannot be validated by megafossil evidence. The conservative view appears to be the more reasonable to adopt until the taxonomic affinities of Australian Tertiary megafossils are more fully understood.

Therefore it is not possible to make useful comparisons between microfossil and megafossil floras at present. A more complete understanding of the taxonomy of Tertiary megafossils in Australia may greatly alter many of the conclusions reached on the basis of microfossil taxonomy.

CHAPTER 11

DIFFERENTIAL PRESERVATION AND ESTIMATING THE DIVERSITY OF THE FLORA.

11.1 DIFFERENTIAL PRESERVATION: The problem of differential preservation of species in a fossil deposit has been the subject of a great deal of speculation and research. The most notable contribution was by Spicer (1975), who suggested that leaves of different sizes may be differentially selected in the process of transport and preservation. He also concluded that different chemical properties of leaves of different species, or differences in other physical factors such as lamina thickness may also affect preservation. The hypothesis that leaves of different species may be differentially preserved could be tested in two ways for the Nerriga fossils.

One hundred and twelve of the 581 specimens were chosen as OTUs solely on the basis that they were the best preserved (i.e. most complete) leaves. Once the 581 specimens had been divided into parataxa it was possible to compare the number of specimens per parataxon in the remaining, less complete specimens. If the parataxa were not differentially preserved, it would be expected that the proportion of specimens per parataxon would be approximately the same for both sets of specimens.

The Nerriga specimens can also be separated into two groups in another way; those which are preserved as mummified leaves and those which are preserved as impressions with little or no organic preservation. These two forms of preservation are quite distinct, and again if the specimens are split into parataxa, then a comparison of the proportion of specimens per parataxon for mummified leaves and impressions

will give an indication of the extent of differential preservation.

A: Comparison of number of specimens per parataxon for "complete" and "incomplete" leaves: The total of 581 specimens contain 44 parataxa, many of which are represented by only one or two specimens. In fact, four parataxa account for 504 of the 581 specimens (86.7%). Since a χ^2 test is to be used, one of the criteria to be met is that all expected values must be > 5. This was true only if the number of parataxa was reduced to the four mentioned above. This should not greatly effect the analysis, since these four parataxa account for such a large percentage of the specimens. Note that if the number of parataxa is reduced from 44 to 26, as suggested in chapter 8, the number of specimens in each of these four parataxa (NER/004, NER/025, NER/026 and NER/027) is not significantly affected.

H_o: That the percentage of specimens in each parataxon does not differ significantly for "complete" and "incomplete" specimens.

NUMBER OF SPECIMENS PER PARATAXON

PARATAXON	"COMPLETE" SPECIMENS		"INCOMPLETE" SPECIMENS		
NUMBER	O	E	O	E	TOTAL
NER/004	9	13.3	78	73.7	87
NER/025	7	10.8	64	60.2	71
NER/026	16	15.3	84	84.7	100
NER/027	45	37.6	201	208.4	246
TOTAL	77	77	427	427	504

$$\chi^2 = \sum \frac{(O-E)^2}{E} = \frac{(9-13.3)^2}{13.3} + \frac{(7-10.8)^2}{10.8} + \frac{(16-15.3)^2}{15.3} + \frac{(45-37.6)^2}{37.6}$$
$$+ \frac{(78-73.7)^2}{73.7} + \frac{(64-60.2)^2}{60.2} + \frac{(84-84.7)^2}{84.7}$$
$$+ \frac{(201-208.4)^2}{208.4}$$

= 1.39 + 1.34 + 0.03 + 1.46 + 0.25 + 0.24 + 0.01 + 0.26

= 4.98 with (4-1)x(2-1) = 3 df

Therefore $0.25 > p > 0.1$.

Therefore accept H_o, the percentage of specimens in each parataxon does not differ significantly for "complete" or "incomplete" specimens. This suggests that there is no statistically significant differential preservation of specimens at Nerriga. The average size of the specimens in each of the four parataxa are given in table 70.

TABLE 70: Average lengths and widths of the four most common parataxa at Nerriga. Units in cm., standard deviations given in parentheses.

PARATAXON NO.	AVERAGE LEAF LENGTH	AVERAGE LEAF WIDTH
NER/004	10.8 (2.7)	3.9 (0.9)
NER/025	9.5 (2.1)	8.1 (2.5)
NER/026	10.4 (2.9)	3.1 (0.7)
NER/027	8.3 (2.3)	1.8 (0.5)

Although the lengths are similar, the widths vary greatly, and therefore so does the area. It can be concluded that, based on the mummified leaves, neither the size of the leaf nor the parataxon to which it belongs affects its preservation. One feature which cannot be tested is whether the leaves within a parataxon are preserved differentially, i.e. within a parataxon, are the larger specimens less likely to be preserved complete than the smaller specimens? This cannot be tested directly, since the size of the more fragmentary specimens are impossible to estimate.

B: Comparison between number of specimens per parataxon for mummified leaves and impressions: Sixty three impressions were studied and an attempt was made to assign them to

parataxa. Three important conclusions could be drawn from this attempt:

(1) Many of the impressions could not confidently be placed into parataxa due to poor preservation;

(2) At least eight impressions appear to belong to parataxa not previously recognised;

(3) Fourteen of the 63 impressions appeared to belong to NER/023. Of the 581 mummified leaves, only two belong to that parataxon.

The initial reaction to these conclusions is that there is a great deal of differential preservation between parataxa at Nerriga. However, the data gained from impressions may be misleading. Thousands of impressions were available for collection at Nerriga. No attempt was made to collect at random, and in fact some concious bias was used, especially during the second collecting trip. This bias took the form of collecting "new" or particularly interesting leaf forms. It is therefore not surprising that the 63 impressions contain a relatively great diversity of leaf types, and a large number of specimens belonging to NER/023. This particular parataxon is distinctive because it is the only one so far found with paired basal secondary veins. These veins are conspicuous, even when the impression is poor. It is also a parataxon of particular interest historically, since Tertiary leaves with paired basal secondary veins were the basis of the early description of the "Cinnamomum" floras of Australia (e.g. von Ettingshausen 1888, Chapman 1921). It was therefore to be expected that a collecting bias toward this distinctive and important parataxon existed. While the possibility of differential preservation of some parataxa cannot be ruled out, the results based on the mummified leaves

are likely to be much more reliable than those based on the impressions.

Very few of the mummified leaves were specifically collected in the field. Most were recovered from laboratory maceration. Since all specimens recovered from the macerations were used in the analyses, no collecting bias occurred. For this reason, statistical conclusions based on the mummifications are likely to have more meaning than those based on impressions.

The fact that there appears to be no differential preservation at Nerriga supports the theory of J.I. Raine (pers. comm.) that deposition took place in either a lake or a very slow moving river. Any fast moving body of water would be likely to break up the larger leaves. Christophel and Blackburn (1978) noted that because of their relatively delicate nature, leaves, flowers and fruits can be transported only limited distances before decay, mechanical disruption and hydrodynamic sorting have significant effects. In general, the preservation of specimens at Nerriga is exceptionally good, suggesting that the site where they grew was close to the deposition site. Some specimens are poorly preserved, being found only as impressions. Although there is no supporting data, this poor preservation may logically have been a post-depositional effect.

The impressions and mummified leaves are generally found in distinct bands, with little overlap. The siltstone containing the impressions is often much drier than that containing the mummified leaves. The impressions also usually represent reasonably complete leaves, which suggests that they did not travel far before deposition. Therefore it is possible that there is a gradual change taking place,

with the mummified leaves being converted to impressions with no organic remains. This may occur as the siltstone dries out, changing the chemical environment of the fossils or physically degrading them. This drying process may occur over a very long period of time.

11.2 ESTIMATION OF THE DIVERSITY AT NERRIGA: If the diversity of a subsample collected at random from a population is known, it is sometimes possible to estimate the total diversity in the population. Since the mummified leaves from Nerriga represents a random sample, an estimate of the total diversity at Nerriga may be possible. Efron and Thisted (1976) summarised several methods for estimating the total diversity in a population. All the methods assume that the number of specimens per parataxon follow a Poisson distribution. Table 71 shows the number of specimens per parataxon and the following calculation determines whether they follow a Poisson distribution.

TABLE 71: The number of specimens per parataxon for the Nerriga flora.

NUMBER OF SPECIMENS	1	2	3	4	6	18	71	87	100	246
NUMBER OF PARATAXA	28	7	1	2	1	1	1	1	1	1

H_o: That the number of specimens per parataxon conforms to a Poisson distribution.

The expected frequency (E) is calculated using the formula:

$$E = \frac{(e^{-m} m^r)}{r} \times f$$

where m = mean number of specimens per parataxon,

= 581/44 = 13.20;

r = number of specimens per parataxon;

f = 44; and

$$e^{-m} = e^{-13.2} = 0.0000019$$

298.

NUMBER OF SPECIMENS PER PARATAXON	OBSERVED	EXPECTED
$\leqslant 9$	39	6.91
10,11	0	8.14
12,13	0	9.84
14,15	0	8.79
$\geqslant 16$	5	10.35

(note that χ^2 tests can only be employed if all expected values are >5. Therefore some categories have been pooled).

$$\chi^2 = \frac{(O-E)^2}{E} = \frac{(39-6.91)^2}{6.91} + \frac{(0-8.14)^2}{8.14} + \frac{(0-9.84)^2}{9.84} + \frac{(0-8.79)^2}{8.79} + \frac{(5-10.35)^2}{10.35}$$

$$= 149.03 + 8.14 + 9.84 + 8.79 + 2.77 = 178.57 \text{ with } 3 \text{ df}$$

Therefore $p < 0.001$.

Therefore, reject H_o; the number of specimens per parataxon does not conform to a Poisson distribution.

This result means that none of the methods for estimating the total diversity of the deposit can be applied. It is apparent from the statistics in table 71 that there are four or five parataxa which dominate the flora. It is probably the effect of these parataxa which contributes most to the non-Poisson distribution.

CHAPTER 12

THE CLIMATE AND VEGETATION TYPE OF THE NERRIGA DEPOSIT AS INTERPRETED FROM THE FOSSILS.

12.1 INTRODUCTION: Three types of fossils have been preserved in the Titringo Creek siltstone, and each may be used independently to determine the palaeoclimate or vegetation type. They are pollen and spores, epiphyllous fungi and megafossils (angiosperm and gymnosperm leaves). Each of these groups of fossils will be considered separately and then the evidence will be compiled and any consistent trends will be discussed.

12.2 MEGAFOSSIL DATA: Dilcher (1973) summarised three approaches to estimating palaeoclimate from megafossils. They were: (1) Identify individual fossils to their nearest living similar forms and base palaeoclimatic interpretations on the climatic range of these modern forms; (2) identify fossils to similar living forms and analyse the climate of the communities in which these living similar forms are found today; and (3) use the form of the fossil vegetation, its foliar physiognomy and relate this to modern climates where vegetation with a similar foliar physiognomy is found. These three approaches will be considered in two sections, the first covering approaches (1) and (2) and the second covering approach (3).

12.3 IDENTIFYING FOSSILS TO SIMILAR LIVING FORMS: Many Eocene fossils have not been identified, and one of the major reasons may be that a large number represent extinct forms (see chapters 9 and 10). Even when fossils have suggested extant affinities, history has shown that there is a high probability that misidentification has taken place. For example, Dilcher (1973) concluded that of the taxonomic

relationships of fossil forms to modern families and genera published by Berry (1916) for the lower Eocene floras of southeastern North America, at least 60% were incorrect.

Wolfe (1971) cited the case of Axelrod (1964 p. 122) who considered that the presence of Persea in the conifer dominated Miocene Trapper Creek flora of Idaho could be correlated with a high degree of temperateness (equitability). However, Wolfe believed that the illustrated specimen was closer to Alnus than Persea, thus making Axelrod's conclusion invalid. Wolfe also suggested that Axelrod's approach (essentially (1) above) was suspect not only because of the high probability of misidentification, but also because it makes the unfounded assumption that the thermal requirements of most genera have remained unchanged during the Tertiary.

In Australia, the chance of finding extant equivalents of Tertiary fossils is extremely low. Christophel and Blackburn (1978) drew attention to the taxonomic inadequacies of early Australian palaeobotanists work, and illustrated the difficulty in finding extant equivalents for angiosperm fossils. Because the leaf architecture of most of the Australasian flora is not documented, it is virtually impossible to make any critical comparisons between fossil and extant forms. The result is that in their studies of the Maslin Bay flora, out of a minimum of 57 taxa, the relationships of only four have been established and at Nerriga the result is four out of a minimum of 31. Only two of these eight taxa are angiosperms.

For the reasons discussed above, the first two approaches outlined by Dilcher (1973) must be employed with caution. However, if they are used in conjunction with other

approaches they may make a useful comparison.

All the fossils which have been identified from Nerriga, with the exception of the unquestionable Casuarina remains (Christophel 1980 in press), are non-angiospermous. They are the cycads Bowenia papillosa (Hill 1978), Pterostoma anastomosans (Hill 1980a) and Lepidozamia foveolata (Hill 1980a).

Cycads may have an advantage over angiosperms in palaeoclimatic analysis. Firstly, there is a much lower chance that the fossils have been misidentified, due to the smaller number of comparisons required. Secondly, the more conservative evolutionary nature of gymnosperms may make the assumption of unchanging thermal requirements through the Tertiary less tenuous.

Of the four fossils described from Nerriga, one (Pterostoma anastomosans) represents an extinct genus and is of no value in palaeoclimatic analysis. The extant distributions of the other genera will be considered in turn.

Casuarina (Div. Gymnostomae) is now found at only one locality in Australia, in tropical north Queensland (L.A.S. Johnson, pers. comm.). In New Guinea and sometimes in New Caledonia it is a true rainforest plant. The palaeoclimatic value of this distribution is questionable for two reasons. Firstly, it appears as though the members of Casuarinaceae are evolving quickly and therefore may not be reliable as climatic indicators (vide Wolfe, 1971). Secondly, the remains of Casuarina at Nerriga are rare and fragmentary, suggesting that they may have been transported a large distance and perhaps from a different vegetation type, or that Casuarina was present only rarely in the surrounding vegetation.

Bowenia, a genus with two extant species, is now restricted to north east Queensland (Johnson 1959). Bowenia serrulata generally forms a dense understorey in eucalypt (dry sclerophyll) forests, while B.spectabilis is found in and around rainforest (Johnson 1959). Hill (1978) concluded that B.papillosa was distinct from both extant species. Extant Bowenia is a shrub-like plant, with no above ground trunk. The fronds are extremely leathery and persistent. It therefore follows that to become fossilised the plant would need to grow close to the site of deposition. If the assumption is made that B.papillosa had a similar habitat to either B.serrulata or B.spectabilis, then it probably grew along a river or lake shore near dry sclerophyll vegetation or on the margin of a rainforest.

Lepidozamia also has two extant species which are restricted to eastern Australia. L.hopei is found in north east Queensland in hilly country or within rainforest, and L.peroffskyana is found in subtropical eastern Queensland and north coast New South Wales in hilly country in wet sclerophyll forest sometimes bordering on rainforest (Johnson 1959). The presence of L.foveolata in the Nerriga deposit therefore suggests a wet sclerophyll to rainforest vegetation.

The only vegetation type in which all three genera described from Nerriga occur today is tropical rainforest in north Queensland. If the only angiosperm (Casuarina) is ignored the possible vegetation type ranges from wet sclerophyll to tropical rainforest.

12.4 FOLIAR PHYSIOGNOMY: Bailey and Sinnott (1916) concluded that "there is a very clearly marked correlation between leaf-margin and environment in the distribution of

Dicotyledons in the various regions of the earth." Their research was the basis upon which modern physiognomic analyses have been constructed. Richards (1952 p. 154) believed that conclusions on Tertiary climates had more substance when based upon physiognomy than on taxonomic affinities. Wolfe (1971) concluded that there was some adaptive significance between the type of leaf margin and climate, although the exact physiological relationships were not known. Later, Wolfe (1978) was able to show a strong positive correlation between the percentage of species with entire leaf margins and mean annual temperature for woody vegetation in the humid to mesic (moderately humid) forests of eastern Asia. However, Wolfe did not record his method of data collection, which reduces the utility of his correlation.

Dilcher (1973) suggested that rainfall probably also plays an important role in determining the percentage of entire margined leaves. He found that percent entire margined leaves decreased in the cooler and/or drier climates. Wolfe (1978) considered that leaf size changes could be related to precipitation and soils as well as temperature.

There are several problems in comparing fossil physiognomic data to data for extant vegetation types. Leaves of different sizes may be differentially selected in the process of transport and preservation (Spicer 1975), a fact which persuaded Wolfe (1971,1978) not to use leaf size in his analyses, which are based solely on margin type.

Another factor is that a fossil flora may often have an over-representation of stream side plants (Macginitie 1953 p. 46). Wolfe (1971) suggested that this may lead to an over-representation of small size classes, but Dilcher (1973)

pointed out that no critical studies had been made of leaf size classes of modern stream side vegetation which supported that assumption. On the contrary, Gentry (1969) found fewer small sized leaves in the gallery forest than those areas removed from stream sides in the tropical dry forest areas of Costa Rica. Dilcher (1973) suggested that "the best analysis must result when both leaf size and leaf margin are considered." Wolfe (1971) admitted that leaf margin analysis "cannot, of course, be the sole criterion for determination of past climates." He suggested leaf size and the presence or absence of "drip-tips" as being useful supplementary characteristics.

Sample size is another important factor in fossil physiognomic studies. Wolfe (1971) found that an assemblage of at least 30 species appeared to be a highly reliable statistical base. That is, the leaf margin percentage can be reproduced to within a few percent despite the collection of representatives of new species or the revision of the original species. He further concluded that the number of species is the important factor, not the number of specimens.

Some recent publications have thrown considerable doubt on the entire philosophy of physiognomic analyses. Dolph (1979) reasoned that although the theory of foliar physiognomy was based on a correlation between the generalised climates for large land areas and the leaf margin percentage for the broad or regional floras inhabiting them, most fossil leaf floras are the result of local deposition, or at least contain an over-representation of stream or lakeside plants.

Dolph's (1979) research in Costa Rica showed that even at sites located within a few metres of each other, the leaf

margin percentages are not similar. He found no significant correlation between leaf margin percentages and mean biotemperature, mean annual precipitation or potential evapotranspiration ratio. In the tropical basal and premontane altitudinal belts of Costa Rica, the percentage of species having leaves with entire margins ranged from 48% to 100%. This range includes all the vegetation types defined by other palaeobotanists. However Dolph's percentages are based on localised sample sites, whereas most vegetation types are based on regionally defined vegetations. Two important points are made in this and an earlier publication (Dolph 1978b) based on leaf size. Firstly, if plants from several habitats are represented at a fossil locality, foliar physiognomy should not be used to estimate palaeoclimate. Secondly, it is unwise to place too much emphasis on results gained from a single characteristic - the percentage of entire margined leaves.

The work of Roth and Dilcher (1978) is more fundamentally important. It has long been known that a fossil deposit may not accurately reflect the living community which contributed to it. There are several reasons for this, including over-representation of stream or lakeside plants and differential preservation, both of which have already been discussed. Other reasons, cited in Roth and Dilcher (1978), are that sun leaves, which are smaller and thicker than shade leaves, may be over-represented in a fossil deposit (Spicer, 1975) and seasonality of leaf fall may lead to an over-representation of evergreen species in a fossil deposit (Chaney 1924, Ferguson 1971, Spicer 1975).

Roth and Dilcher (1978) sampled recent sediments in a small lake. They noted a strong negative correlation between

leaf size and distance from the shore, even though their transects extended only 10 m. from the shore. Also, fewer than half of the living species of woody plants found in the neighbouring forest were present in the 534 leaves collected. Little weight should be placed on this last observation, since no indication of the relative abundance of the 27 living species is given. The result of this research was that a foliar physiognomic analysis of the recent sediments yielded a colder or drier climatic interpretation than actually existed in the area. Their general conclusion was that the foliar physiognomy of fossil deposits cannot be compared directly to the foliar physiognomy of living plant communities until the relationship between living plant communities and the leaf deposits derived from them is understood.

Three general conclusions can be drawn from the work carried out in north America on palaeoclimatology. Firstly, of the three methods outlined by Dilcher (1973) to estimate palaeoclimate, foliar physiognomy appears to be the method which will come into general use. Secondly, foliar physiognomy will be limited in its usefulness until a better understanding of the factors affecting representation in fossil deposits is reached. Lastly, it seems that the whole philosophy of foliar physiognomy needs to be reappraised. Many palaeobotanists have expressed the view that as many characters as possible should be evaluated before taxonomic identifications of fossils are made. However, these same palaeobotanists have been content to presume that one or two characters (leaf margin type and leaf size) are sufficient to estimate palaeoclimate. Even in the most recent research (Dolph and Dilcher 1979) only a few characters are considered in detail. Dolph (1979) stessed that several ecological

features, and not just the obvious parameters such as rainfall, altitude, humidity etc. may be affecting physiognomy. Research is urgently required at a large number of localised sites to study the correlation between several leaf characters, both architectural and cuticular, and major environmental parameters. A multivariate approach is needed, to compare several leaf features simultaneously with several environmental parameters. This will increase the computational load significantly, but it is much more likely to give a realistic indication of any correlations which exist. Until the physiognomic relationships of extant vegetation types are well understood at the localised level, palaeoclimate must be interpreted cautiously from physiognomic data.

In the Australian situation, the physiognomy of extant vegetation types was well documented on a regional scale by Webb (1959), who classified the vegetation using leaf size, margin type, and percentage of compound leaves. It is interesting to note the large overlap of percentage of entire margins in Webb's rainforest subformations. It appears that the opinion expressed by Dolph (1979) on the danger of the use of leaf margin type alone for physiognomic analysis is especially pertinent to the Australian situation.

Webb's (1959) classification is for vegetation types and later work (Webb 1967) has shown that the relationship of these vegetation types to environmental parameters (e.g. temperature, altitude, latitude, soil type etc.) is complex and therefore no conclusions on palaeoclimate can be drawn from his approach.

With the general exception of percentage of compound leaves, Webb's characters can readily by applied to a fossil

flora. However, there are some difficulties in the application of this method. Webb has given seven rules for determining common leaf size, three of which are impossible to guarantee with fossils. They are:

(1) Consider only tree layers (upper, middle or lower). Understorey shrubs and low growing plants such as ferns, or species with very deeply divided leaves such as palms, are ignored;

(2) Consider only mature exposed ("sun") leaves of evergreen (not deciduous) species;

(3) Avoid "shade" leaves and secondary growth.

It is impossible to determine what type of plant (tree, shrub, herb etc.) a leaf came from in most fossil floras. The presence of the genus Bowenia (Hill 1978) at Nerriga whose extant species are understorey shrubs, shows that such plants are present in the flora.

Despite these limitations, some interesting comparisons can be made with Webb's scheme. Table 72 contains the results for the Nerriga, Maslin Bay, and Anglesea floras. For the Nerriga data, 130 specimens representing 43 "species" (parataxa) were measured. Non-angiosperm leaves and the Casuarina sp. (Christophel 1980 in press) were not considered.

It is known that the most common parataxon (NER/027) is a compound leaf. However, since almost all specimens were preserved as leaflets, the data may be biased significantly by their presence. Therefore a second set of percentages were calculated (also shown in table 72), reducing the effect of the leaflets by dividing their number by 5 (using the assumption that there were 5 leaflets per compound leaf).

Christophel (1979 in press) published a preliminary

	MESOPHYLL		NOTOPHYLL		MICROPHYLL		COMPOUND LEAVES		ENTIRE MARGINS	
	SPEC	INDV	SPEC	INDV	SPEC	INDV	SPEC	INDV	SPEC	INDV
MASLIN BAY	28	21	47	54	25	25	-	-	79	84
ANGLESEA	27	22	50	46	23	32	-	-	78	73
*NERRIGA	3	4	42	50	55	46	3	39	67	46
**NERRIGA	3	6	42	50	55	44	3	11	67	74
NERRIGA	30	21	45	55	25	24	-	-	66	66
SNVF	0-30	0-20	55-75 +x	25-95	0-40 +x	10-70	10-25	0-20 x	40-70	10-70 +
AVW	0-15	0-20	45-60 +x	30-45 +x	40-45 +x	25-65	30-35	15-25 x	65-80	c.85 +x
MVW	0-10	0-20	30-50	30-45 +x	50-60	25-65	c.25	15-25 x	70-90 +x	c.80 x
SEVT	0-10		20-55		40-80		20-30		65-75	

TABLE 72: Comparison of leaf form data from Australian rainforest (Webb 1959) with three Eocene floras. The Maslin Bay, Anglesea and Nerriga data are taken from Christophel (1979 in press). *Nerriga data is based on the results of this study using 43 parataxa and 130 individuals. **Nerriga data is based on the results of this study, but reducing the effect of the leaflets of the compound leaf.
+ = mismatch with **Nerriga, and x = mismatch with *Nerriga

physiognomic analysis of the Nerriga flora, which is also shown in table 72. He used leaves representing 38 "taxa" (parataxa). Many of these specimens were those prepared for the present study, although he also measured many impressions which have not been considered here. Christophel's results differ significantly from those presented in this study. There are two possible reasons for this. Firstly, Christophel divided his 130 specimens into taxa only on the basis of architecture. This led to some erroneous identifications. Secondly, he used several impressions which have not been used in this study. Earlier (Chapter 11), it was suggested that at least some impressions were selectively collected in the field and that because of this statistical conclusions could not be based on them. It was noted that particularly distinctive specimens were collected as impressions. Judging from Christophel's (1979 in press) results, large leaves were also selected. More work is required to discover the exact relationship between mummified leaves and impressions at Nerriga.

The four vegetation types defined by Webb (1959) which most closely match the Nerriga data are also shown in table 72. The two closest vegetation types are Microphyll Vine Woodland (MVW) and Semi-evergreen Vine Thicket (SEVT). Both vegetation types have some features in common i.e.: Microphylls and smaller leaf sizes most common. Mossy and vascular epiphytes inconspicuous in top tree layers; robust lianes generally prominent; plank buttresses absent; prickly and thorny species in usually dense understorey; ground layer sparse; compound leaves and entire leaf margins common.

The features which separate the two vegetation types are:

MVW: Canopy level uneven, av. 6-21m, with mixed evergreen

and semi-evergreen emergent and upper tree layer species; coniferous and deciduous elements are rare or absent.

SEVT: Canopy level uneven, av. 4.5-9m, with mixed evergreen, semi-evergreen and deciduous emergents to av. 9-18m; swollen stems ('Bottle trees') common.

Both these vegetation types are found presently in lowland and lower montane subtropical rainforest in Australia, in the latitude range of 23^{o} to 30^{o}. The rainfall in areas supporting these two vegetation types is generally below 150 cm/year (Webb 1967).

12.5 PALYNOLOGICAL DATA: Christophel and Blackburn (1978) listed three major problems in interpreting vegetation types from palynological data:

(1) It is difficult to judge the geographical relationships between depositional sites and source area of a pollen flora (vide Potter 1976).

(2) Because they have a relatively simple structure, the exact taxonomic affinities of pollen grains are often difficult to determine.

(3) Physiognomic analyses, independent of taxonomy, cannot be carried out on palynological data.

It is the first of these points which makes palynological data so useful in biostratigraphy and at the same time dangerous for the interpretation of palaeoclimate. It is well recorded that some pollen types can be dispersed over large distances, whereas others are extremely limited. Therefore a pollen flora does not necessarily reflect the vegetation of the area around the deposit. Particularly pertinent in Australia is the genus Nothofagus. Nothofagus produces large amounts of pollen with very high dispersal distances (in excess of 700 km., according to Dodson (1976)).

This has led some palynologists into a biased view of Tertiary vegetation. For example, Beard (1977), based on the data of Hos (1975) concluded that the south coastal area of Western Australia had "a warm and humid Eocene climate, supporting a tropical to subtropical rain forest, in which the southern beeches (Nothofagus) were dominants, with Proteaceae and Casuarina as subdominants." Megafossil floras, which are more likely to represent localised vegetations, have not yielded a single specimen which resembles Nothofagus in Australia, despite the dominance of Nothofagidites pollen from the same deposits. This shows the danger of extrapolating palynological data to estimate vegetation types, and also highlights the questionable practice of suggesting extant affinities for dispersed fossil pollen.

Owen (1975) described the pollen and spore flora at Nerriga. She commented at length on the palaeoclimatic implications of her data. A summary of her conclusions will be presented for comparison with the conclusions from the other methods. Owen considered that three main elements were present at Nerriga:

(1) Antarctic Element: Includes Nothofagidites spp. with pollen types assigned to all three groups of Nothofagus now living. Also included is the minor gymnosperm component which contains members of Podocarpaceae and Araucariaceae. Owen believed that the Antarctic element indicated a rain-forest vegetation, probably on higher areas, with moderate temperatures and a high rainfall of at least 140 - 180 cm./ year. However, this conclusion was based mainly on the distribution of extant Nothofagus.

(2) Tropical Element: Includes the Cupanieidites major/ orthoteichus species group which has been related to the

tribe Cupanieae of the Sapindaceae (now found in tropical rainforest communities of northeastern Australia). Anacolsidites acutullus and A. luteoides which have been related to the Olacaceae, a family with predominantly tropical distribution and Santalumidites cainozoicus, which has been compared to Santalum, a genus restricted to warmer rainforest communities in Australia and the Indo-pacific region, have also been recorded at Nerriga. Pteridophyte spores were also uncertainly placed in this group by Owen. The varied nature and abundance of spore taxa also implied a high humidity/abundant rainfall.

(3) Australian Element: Proteacidites comprises 23% of the assemblage but many of the species could not be related to extant taxa. Although many living species of Proteaceae are sclerophyllous, the family probably originated in rainforest environments in eastern Australia and the southwestern Pacific region in the late Cretaceous, and the diversity represented at Nerriga also appears to indicate a rainforest environment (Owen 1976). Myrtaceidites spp. has been related to Myrtaceae with species which may have rainforest associations, but they may be sclerophyllous as well. Haloragacidites harrisii and H. trioratus are also found consistently in low frequencies. These two species are considered to be related to Casuarina, which at present are trees and shrubs found in a wide range of environments.

Owen concluded that in general the Nerriga assemblage represented a rainforest vegetation, with abundant rainfall (140 - 180 cm./year), and in some cases a slightly warmer climate than that found in the area at present. Most elements, except for the possible sclerophyllous groups and Ephedra, require moist conditions in their present

environments. She suggested that the tropical elements and the predominance of Nothofagidites of brassi type over the other two types could favour moderate, and possibly slightly warmer temperatures.

12.6 EPIPHYLLOUS FUNGI: Dilcher (1965) correctly concluded that "it would be unwise to base any generalised ecological conclusions upon the frequent isolated reports of one or two fragments of fossil epiphyllous fungi described from widely separated areas of the world." However, the knowledge of fossil epiphyllous fungi in Australia has expanded greatly in the last decade (e.g. Selkirk 1972, 1975; Lange 1969, 1976, 1978a; Lange and Smith 1971, 1975a,b).

Lange (1976, 1978a) suggested a new method for estimating palaeohabitat from epiphyllous fungi. In the earlier publication, Lange (1976) suggested that "germlings", a term coined by Dilcher (1965), may be of use simply by noting the presence or absence of various forms ("grades"). Although the taxonomy of germlings is unclear, Lange's approach is independent of taxonomy. Lange was able to show that some direct indicator value for the Australasian area could be demonstrated on the basis of precipitation and vegetation type.

In his later work, Lange (1978a) included several other easily identified epiphyllous fungi along with the germlings in his original scheme. Lange's conclusions were still tentative, but with the proviso that the fossil epiphyllous fungi occupied similar habitats to their extant equivalents, then for the Australasian region "as sampling of a Tertiary flora discloses cumulatively (a) grade 5 'germlings', (b) form 1 manginuloid hyphae, (c) rangiferoid setae, (d) .... germinated melioloid spores..... (e) callimothalloid shields,

and (f) cribritoid shields, then the inferred palaeohabitat is progressively restricted towards conditions of present-day wet tropical vegetations." He gave two examples to illustrate the method.

Lange's approach has the advantage of simplicity, since the forms he used are easy to identify, and it can be quickly assessed. It is also useful in a wide range of deposits, since it requires only dispersed cuticle, not complete leaves.

Epiphyllous fungi are common in the Nerriga deposit, with all grades of germlings described by Lange (1976) being present (figs. 528-551). However, despite a careful scan of several hundred cuticles, none of the other epiphyllous fungi suggested as indicators by Lange (1978a) were found. Some of the other epiphyllous fungi present are shown in figures 552-559.

The presence of grade 5 germlings at Nerriga suggests a rainfall of at least 140 cm./year and a wet sclerophyll or rainforest vegetation (Lange 1976). The absence of the other forms described by Lange (1978a) suggests that a rainforest vegetation with monsoonal rainfall was unlikely at Nerriga. The most likely vegetation type is wet sclerophyll, with an even rainfall of approximately 140 cm./year.

12.7 CONCLUSION: Four separate approaches have been made in an attempt to estimate the Nerriga palaeoclimate (foliar physiognomy, comparison of the distribution of living equivalents, palynology, and epiphyllous fungi). On the basis of the overall results, a consistent picture of the palaeoclimate and vegetation type at Nerriga has begun to emerge. The major conclusions are as follows:

(1) Rainfall was in the range of 140 - 180 cm./year: On the basis of foliar physiognomy, a rainfall of below 150 cm./year was predicted, the palynological results suggested 140 - 180 cm./year and the epiphyllous fungi approximately 140 cm./year. The palynological data is somewhat unreliable, as discussed earlier, due to the heavy reliance on the presence of Nothofagidites pollen, and therefore the rainfall was probably closest to the bottom of the range.

(2) The most likely vegetation type was wet sclerophyll or low-land/lower montane subtropical rainforest: This conclusion is supported mainly by the epiphyllous fungi and foliar physiognomy.

(3) At least some of the vegetation represents a river or lakeside flora: This is the most important conclusion to be drawn from the study of the distribution of the extant species of the genera described from Nerriga (especially Bowenia). Since no data is available on the physiognomy of riverside floras in Australia, the effect of this component on the previous conclusions is unknown.

Some general conclusions may also be drawn on the merits of the various approaches to estimating palaeoclimate. Probably the least reliable of all methods is the interpretation of palynological data. The three major reasons for this are the potentially large source area for pollen rain, the doubtful taxonomic affinities of many fossil pollen taxa and the unfounded assumption that the thermal requirements of most genera have remained unchanged during the Tertiary.

The study of the distribution of the extant species of genera described from fossil deposits is also of very limited

use, both because of the assumption of unchanged thermal requirements and the high probability of misidentification of fossils. In Australia this approach is even more restricted because of the paucity of work on extant leaf architecture and the consequent difficulty in identifying fossil angiosperm leaves.

Foliar physiognomy is the approach which is currently receiving most attention. One of the disturbing features of recent research is that the more detailed the experimentation becomes, the more problems are encountered. The problem with foliar physiognomy is that it is deceptively simple. It is very easy to measure leaf size or margin type for a fossil assemblage. However, there are many factors which may be affecting these leaf features. These include environmental parameters, such as precipitation, evapotranspiration, soil type, altitude, latitude etc., physical factors, such as position of the leaf on the tree, position of the tree (e.g. river-side or otherwise), and depositional factors, such as smaller leaves being more easily preserved than larger leaves, more than one vegetation type being represented in the deposit etc.

Some of these factors may be easily accounted for, others will always be impossible or at best very difficult to check. Foliar physiognomy is extremely complex. It is unlikely that a single satisfactory method which allows easy determination of palaeoclimate will ever be forthcoming using this approach.

The most promising of all the approaches used in this study is the interpretation of epiphyllous fungi. There are several advantages to the method described by Lange (1976, 1978a). Firstly it is quick and simple to apply, assuming

that cuticles have already been prepared. Secondly, because the criteria is presence or absence of particular fungal forms it requires little expertise. Thirdly, although more research is required, it appears that the presence of certain epiphyllous fungi may be more easily correlated with environmental parameters than is foliar physiognomic data. There is one major disadvantage to the method - it requires cuticles to be preserved, which is generally the case in Australian fossil deposits, but is often not the case in other parts of the world. The use of epiphyllous fungi in combination with foliar physiognomy may eventually lead to the most reliable estimation of palaeoclimate.

The study of epiphyllous fungi may have another benefit in palaeobotany. It became apparent while scanning the cuticles for epiphyllous fungi that certain types of fungal structures were restricted to particular parataxa. Recently, Saville (1979) has reviewed the use of parasitic fungi in higher plant classification and judging from some of the excellent correlations he presented this appears to be a most promising field. Therefore when more research has been carried out on extant angiosperms and epiphyllous fungi, combinations may become apparent which could be extrapolated to the fossils and used as an aid in identifying the fossil angiosperm leaves. The presence of certain distinct types of epiphyllous fungi may also prove useful in delimiting parataxa, although this would require careful application.

CHAPTER 13

CONCLUSION.

13.1 MEGAFOSSIL PALAEOBOTANY IN AUSTRALIA: Megafossil palaeobotany has several important roles to play in Australia. One of the most obvious is in the interpretation of the evolution of the Australian flora. In the past, fossil evidence has been virtually ignored by researchers on extant Australian plants. For example, Carr and Carr (1969) described the literature on fossil Eucalyptus as "utterly inadequate" and Johnson and Briggs (1975) found the fossil record of Proteaceae to be useless. In part this has been the fault of the researchers concerned for not covering the available literature adequately, but a large part of the blame must fall on palaeobotanists.

It is difficult enough for specialist palaeobotanists to discriminate between the carefully researched and accurate taxonomic work of early palaeobotanists and the multitude of papers suggesting extant affinities for many very poorly preserved specimens. Anybody with a passing interest in Australian palaeobotanical history is quite likely to dismiss it as inadequate. However, the latter part of this century has seen a change in research aims and methods. Most of the taxonomy of Tertiary fossils accomplished in the last 30 years is apparently very sound. Most of the specimens which have been discribed in that time have been gymnosperms, which is not unusual considering their ease of identification compared to angiosperms, but recent work by Christophel (1980 in press) and D.T. Blackburn (pers. comm.) suggests that at least some progress is being made in identifying angiosperm megafossils.

There is no doubt that most angiosperm megafossils will

remain unidentified for many years in Australia. There are a number of reasons for this: the lack of researchers in megafossil palaeobotany in Australia; the lack of knowledge of extant leaf architecture and cuticles; the possibility that many of the fossils are extinct at the specific or generic level, and the lack of research on deposits younger than Eocene. This last point is particularly important. Work by D.T. Blackburn (pers. comm.) on the flora of the Miocene Brown Coal Mine at Yallourn is showing that extant matches are much more readily available than in any of the Eocene deposits. If a range of younger Tertiary deposits could be studied, many of the problems now apparent in identifying Eocene megafossils may disappear. There is no doubt that the fossil record will provide many answers on the evolution of the Australian flora if future research reflects the progress of the last 30 years.

Megafossil palaeobotany has other roles to play. One of the most important and perhaps neglected roles is as an aid in the taxonomy of fossil pollen and spores. Potonié (1956,1958) reflected the views of the European school of palynologists when he suggested that Tertiary pollen should not be given names based on modern plants if the holotypes are in the form of dispersed fossil material. Australian palynologists still appear to be willing to use modern genera to name Tertiary pollen and frequently draw major conclusions on palaeoclimates and vegetation types on the basis of the distribution of these modern genera. Megafossil palaeobotany has aided palynological taxonomy to only a very limited extent in the past, but this is probably the result of the taxonomic problems with the megafossils. As the megafossils become better understood, they are certain to

provide important evidence for palynological determinations. As evidence to this, Christophel (1980 in press) recently reported pollen grains in the anthers of fossil Casuarina male inflorescences from Anglesea, and D.T. Blackburn (pers. comm.) has discovered a composite anther containing a pollen grain from Yallourn. Another major role of angiosperm megafossil palaeobotany is in palaeoclimatic analysis and determination of vegetation types. This will be discussed at more length later.

13.2 TAXONOMIC CONCLUSIONS: In the course of this study three specimens were identified. They were Bowenia papillosa (Hill 1978), Lepidozamia foveolata (Hill 1980a) and Pterostoma anastomosans (Hill 1980a). All these species are cycads and represent a significant increase in our knowledge of Tertiary Australian cycads. A fourth specimen has tentatively been assigned to the fern family Gleicheniaceae, but more material is required to verify this identification. Apart from this, Christophel (1980 in press) has reported Casuarina megafossils from Nerriga, but has not yet formally described them.

Therefore all the angiosperms at Nerriga (at least 26 parataxa) remain unidentified except for the extremely characteristic Casuarina (which is preserved as both vegetative and reproductive material). The reasons for the lack of determinations of Australian angiosperm megafossils have been commented upon at length in chapter 9. Rather than repeating those reasons here, it is probably more pertinent to suggest where future research could be concentrated to improve the accuracy and frequency of fossil angiosperm leaf identifications.

Wolfe (1977) has suggested that cleared leaves were

essential for comparitive studies with his Alaskan fossils, since fine detail generally could not be gained from a herbarium specimen, particularly of rainforest species. This has not proved to be the case in Australia. Because the matrix in which Tertiary leaves are most often found in Australia is siltstone, fine venation of the leaves is rarely preserved. This is even the case with mummified leaves, where the fine venation is often unclear. Therefore comparisons with Australian megafossils will generally be on venation pattern (primary, secondary and tertiary veins) and cuticular patterns. The time consuming and expensive task of compiling a cleared leaf collection may not, therefore, be justified at the present time. Instead a collection of herbarium specimens (which invariably have a clear venation pattern at least to the tertiary level), with cuticle slides for each one would be the best method for compiling a large reference collection quickly and cheaply. The time and money normally spent on clearing leaves would be better spent on compiling information for computer banking.

The collection of this type of reference material, along with the study of younger deposits, as already mentioned, is the most likely method of increasing the number of taxonomic determinations.

13.3 PALAEOCLIMATE AND VEGETATION TYPE: On the basis of the four methods which were employed, three general conclusions were made:

(1) Rainfall was in the range of 140 - 180 cm/year;

(2) The most likely vegetation type was wet sclerophyll or lowland/lower montane subtropical rainforest; and

(3) At least some of the vegetation represented a river or lakeside flora.

A review of the literature on each of the four methods showed that none of them are as yet totally satisfactory. The most promising approaches appear to be foliar physiognomy and the study of epiphyllous fungi. Foliar physiognomy currently has major problems, most of which appear to stem from the fact that there is an extremely complex interaction between leaf form and environmental parameters. Whether this interaction can ever be satisfactorily quantified remains to be seen, but it does appear that the method will never be satisfactory when used in isolation of the other methods.

The study of epiphyllous fungi has shown some promising results in estimating palaeoclimate, but requires a great deal more research before it can be confidently applied. It may be that this method, used in conjunction with foliar physiognomy, will eventually give the best estimates of palaeoclimate and vegetation type.

13.4 NUMERICAL TAXONOMY OF ANGIOSPERM LEAVES: Numerical taxonomy has not had the widespread and successful application in botany that it has enjoyed in other fields (notably zoology). This is especially the case in mega-fossil palaeobotany. There are a variety of possible reasons for this, but one of the most important is the choice of characters.

A survey of numerical taxonomic research in zoology reveals a marked dependence on characters of size. The same is true in botany. However, as Sneath (1976) noted, although in most organisms the variation in size between individuals is usually not very great below the species level, there are some notable exceptions among plants. In general, it would appear that the size characters used

in plant taxonomy may have an inferior discriminatory power at the species level than those used in animal taxonomy. Although it is an oversimplification to presume that all the problems in the numerical taxonomy of plants stem from the characters employed, there is no doubt that it is a very important contributing factor.

Since many of the characters used in this study involved size, and also because of the failure of a previous attempt to classify a set of extant leaves (Dolph 1976), it was decided at the outset to test the discriminatory power of the characters on extant leaves before they were scored on the fossils. This part of the study generally gave very clear clustering of leaves into species, although it was shown that architectural characters alone could not classify the leaves correctly.

Although both the UPGMA and ESS dendrograms were able to satisfactorily cluster the extant leaves into species, neither produced a good classification of the fossil OTUs. There are three major reasons for the failure of these algorithms when applied to the fossils in comparison to the extant leaves. Firstly, because the leaves of the extant species were selected from a single tree, intraspecific variation was not adequately tested. However, some of the fossil parataxa exhibit extreme variation over paticular characters. A good example of this is parataxon NER/027, which was usually preserved as single leaflets from a compound leaf. The leaflets of a compound leaf can vary greatly in size and shape and this was the case for NER/027.

Secondly, because five leaves were chosen for each extant species, the problem of different number of OTUs per species was not considered. The fossil OTUs were

extremely unevenly distributed among parataxa. The exact effect of this on the dendrograms is unknown, but certainly non-conformist groups containing a number of parataxa represented by only one or two OTUs were a problem. These first two reasons for the inadequacy of the classifications produced by the dendrograms represent common biological events, and for a classification to be worthwhile it must be able to cope with them. The third possible reason is that the character set may have had poor discriminatory power.

A comparison of a minimum spanning tree, nearest neighbour network and ESS dendrogram gave a good classification of the OTUs. Using these methods, together with a visual comparison of the OTUs, a minimum of 27 angiosperm parataxa were delimited from 581 specimens examined. The success of this classification suggests that the character set employed did have adequate discriminatory power, although lumping of parataxa in groups caused some problems in interpretation.

13.5 FUTURE APPROACHES TO ANGIOSPERM PALAEOBOTANY: There is a pressing need for research on Australian Tertiary deposits. Although two Eocene deposits (Nerriga and Anglesea) and one Miocene deposit (Yallourn) are currently being researched, many other deposits remain to be collected and a vast number of early collections require revision.

However, because of the lack of recent research on Tertiary deposits in Australia, the potential exists for a coordinated approach for current and future projects. This study has given rise to several guidelines for the direction such a coordinated study should take.

When this study was begun, the Australian Tertiary floras were virtually unknown, with the exception of the

Maslin Bay flora, which was being actively curated and researched. It was therefore necessary to base the initial approach to this study on the results of research on the Maslin Bay flora and Tertiary floras in other parts of the world. In North America, the majority of research has concentrated on leaf architecture rather than cuticular patterns. This was also the case with the Maslin Bay flora. The reason for this is that cuticles are often very poorly preserved or absent in North American deposits (and the Maslin Bay flora), whereas the venation detail is often exceptionally good.

Therefore, when characters were selected for this study, emphasis was placed on selecting those involving leaf shape and architecture. When the Nerriga flora had been collected and curated it was found that the majority of specimens consisted of mummified fragments of leaves with excellent cuticular preservation, but which were too incomplete to allow many of the leaf shape and architecture characters to be scored. However, apart from the addition of several cuticular characters, the character set was not altered because enough specimens were collected on which all the characters could be measured, and these specimens appeared to be representative of the flora. Another reason for not altering the character set was that one of the major aims behind scoring of the characters was to eventually allow large scale evolutionary and biostratigraphical projects to be carried out incorporating the Nerriga flora. Therefore the character set had to be applicable to other Australian Tertiary deposits. Because of the preservation normally found at Maslin Bay and in early collections made at Anglesea (which closely resembled the preservation found at

Maslin Bay), as well as that recorded in most published reports of Australian Tertiary fossils, it was considered necessary to include all the leaf shape and architecture characters, since cuticles rarely appeared to be well preserved.

Recent research on other deposits has shown preservation similar to that at Nerriga. The Anglesea flora is now yielding a large number of mummified leaves, most of which are incomplete. D.T. Blackburn (pers. comm.) has perfected a technique which allows well preserved dispersed cuticle to be retrieved from the brown coal at Yallourn. Lange (1978b) has reported good dispersed cuticle from the Lake Lefroy and Maslin Bay deposits, and he has commented on the potentially vast number of sites available for the study of dispersed cuticles in the form of drill cores. Therefore, it appears as though the majority of specimens available from Tertiary deposits in Australia consist of small fragments of leaves with good cuticular preservation.

The predominance of dispersed cuticle in Australian deposits requires an alteration to the approach used in this study. Many more comparisons could be made if the character set was restricted to features of the cuticle. This would require further research on useful and discriminatory cuticular characters.

Future research will determine whether continuous or binary characters are preferable, but some suggestions can already be made as to their relative utility. Continuous characters were used in this study because they potentially contain much more information than binary characters and their interrelationships and discriminatory power were well understood. The biggest disadvantage in the use of continuous

characters is the amount of time required for scoring. With a large number of specimens this time factor would quickly become prohibitive. A large number of binary characters could be scored in a relatively short time by comparison, and the large number may overcome the relatively poor discriminatory power that each binary character has. Binary characters may prove to have the greatest utility, particularly in large scale projects. Before the Nerriga flora is published, the OTUs will be reclassified on a set of binary cuticular characters for comparison with the classification based on continuous characters.

This study required a large number of comparisons between specimens, considering leaf shape, architecture and cuticular pattern. Invariably it proved easier to recognise a particular parataxon on the basis of its cuticular pattern than on either leaf shape or architecture. This suggests that the cuticular pattern may be less variable within parataxa than the other features.

A concentration on dispersed cuticle studies could be complemented by an increase in research on epiphyllous fungi. At the present time a great deal more research is required on the distribution of various epiphyllous fungi on extant vegetation. A thorough understanding of extant epiphyllous fungi would be of great assistance in estimating vegetation types and palaeoclimates from dispersed cuticle. One largely unexplored field is the potential of epiphyllous fungi as taxonomic indicators, i.e. are certain types of epiphyllous fungi restricted to particular species, genera or families of angiosperms? An answer to this question may be of great assistance in the identification of megafossils.

It is also possible that careful research on cuticular

characters may show that some are good climatic indicators. An approach similar to that used in foliar physiognomy may show some specific correlations between certain cuticular features and environmental parameters. Many authors (e.g. Odell 1932, Wylie 1949) have commented at length on the extreme variation exhibited by cuticular characters in differing environments. Only one (Dilcher 1974) has noted the positive aspect of this variation - that cuticular characters could be used to estimate the environment. Research in this area may prove rewarding, particularly if used in conjunction with the occurrence of epiphyllous fungi.

One of the major aims of megafossil palaeobotany is an understanding of the evolution of plants. In the past significant contributions have been made by palaeobotanists working on non-angiospermous plants, but in Australia in particular, the contribution toward the evolution of angiosperms has been minimal in comparison. It has been mentioned in other places in this study that the major contributing factor toward this is our lack of knowledge of the leaf architecture and cuticular pattern of extant Australasian angiosperms.

Two possible fields of future research arise from this lack of knowledge of extant Australasian leaf types. Firstly, the leaves must be collected and described, although this is largely technical work. Secondly, if the information collected from these leaves is to be of value it must be stored in a computer in a form which allows ready access for comparison with other leaves. This will not be a simple task. One of the best methods of data banking may be to store two types of information - general descriptions or character scores from the type of characters used in this

study and a small set of key characters, which could be scanned by means of a simple program for matches with leaves which the researcher wants to compare.

These key characters would need to be based at the generic or family level, or preferably both. This will require a great deal of research on extant genera and families and may require the use of cleared leaves, but is probably the only way a data bank could be made to work successfully. The following example shows how such a data bank would be set up.

If a researcher was trying to identify a fossil angiosperm leaf by means of a computer data bank, the first step would be to enter information aimed at deciding on possible family affinities. This would be in the form of a series of questions;

e.g. (1) Intramarginal vein present? : (type 0,1 or 2, where 0 = yes, 1 = no, 2 = unknown).

(2) Subsidiary cell arrangement brachyparacytic? (type 0,1 or 2) etc.

At the end of these questions, a list of possible families would be provided by the computer. Then for each family, a similar set of questions could determine possible generic matches. It would be essential to provide a list of all extant families and genera not entered in the data bank which may be relevant.

Within each genus it may be possible to list all the species, and for each one the following information:

(1) Distribution

(2) Ecological and habit notes (with sources)

(3) Pertinent publications

(4) Institutions holding material

(5) Leaf description

(6) Character scores

The information may be slightly different for a fossil species. This data bank would require a competent computer programmer to write the relevant programs and alter them as new information becomes available, but it would allow easy access for anyone not experienced in computing. If a data bank could be established, and if palaeobotanists are willing to contribute to it, the whole process of identification of fossil angiosperm leaves could be revolutionised.

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