T TAXONOMIC STUDIES IN THE TRIBE JUSTICIEAE OF THE FAMILY ACANTHACEAE

by

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PREFACE

The experimental work described in this thesis was carried out in the Deapartment of Botany, University of Natal, Pietermaritzburg, from January 1982 to December 1985, under the supervision of Dr Fiona Getliffe Norris.

These studies represent original work by the author and have not been submitted in any form to another University. Work on *Hypoestes* [Soland. ex] R.Br. was submitted to the University of the Witwatersrand as an honours thesis in 1981 and has subsequently been published (Balkwill & Getliffe Norris, 1985); the work on the inflorescence, however, was done during the research for this thesis. The following was contributed by other people:

All the line drawings - M-J. Cadman

The sections of the ovaries and the drawings in figures 28 and 29
- M-J. Cadman

The sections of the seed coat and the photographs for Plate 28
- Dr Fiona Getliffe Norris

The scanning electron microscopy for plate 8c
- J.C. Manning

Information about the typification of *Peristrophe*
- R.K. Brummitt.

Where other use was made of the work of others it has been duly acknowledged in the text.

TO MY

FAMILY

ABSTRACT

The southern African species of *Dicliptera* Juss. and *Peristrophe* Nees (like those of many other genera of the Acanthaceae) were last revised by C.B. Clarke in 1901. Lindau proposed a classification of the family in 1895 and applied it on a world-wide basis. Bremekamp (1965) made significant changes to Lindau's classification, but did not re-examine some of the southern African genera and based his lists of genera in each tribe on the lists provided by Lindau.

During the course of this revision of the southern African species of *Peristrophe* and *Dicliptera*, habit; morphology of leaves, inflorescences, bracts, flowers and fruits; micromorphology of seeds and pollen; indumentum; flavonoid spot patterns and distribution and phytogeographical affinities of species were examined and in some cases comparisons were made throughout the family. Characters were evaluated, evolutionary trends were considered and a formal revision of the genera *Peristrophe* and *Dicliptera* is presented. Slight modifications to Bremekamp's (1965) classification have been proposed and applied to the southern African species of the Acanthaceae. Lindau's (1895) Diclipter inae has been amended and accepted. Specific and generic limits that are applied to the Acanthaceae and the relationship of *Peristrophe* and *Dicliptera* to each other and to the genus *Hypoestes* [Soland. ex] R. Br. have been considered and evaluated.

Keys to the tribes and genera of the southern African Acanthaceae are presented. Descriptions of *Peristrophe* and *Dicliptera* have been provided, and the subdivision of *Peristrophe* into three sections has been proposed. During the course of this study it has been found that some nomenclatural changes have become necessary and that some names should be placed in synonmy. Some recombinations were necessary and have been made (Getliffe Norris, Manning and Balkwill, 1985) and two new species of *Peristrophe* (Balkwill, Cadman and Getliffe Norris, 1985) and one new species of *Dicliptera* (Balkwill, Manning and Getliffe Norris, 1986) have been described. In this thesis, another new species of *Peristrophe*, with two subspecies and five other new species of *Dicliptera* are proposed.

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ERRATA

The following errors occur in this manuscript:

In the captions of tables 14 - 25 on pages 156 - 167,
Please read occurrence for occurence.

In the caption of table 25 on page 165,
Please read *D. minor* ssp. *1* for *D. minor* ssp. *"white"*.

For quinuncial please read quincuncial.

For discreet please read discrete.

CHAPTER 1
INTRODUCTION

In 1753, Linnaeus included eleven species in the genus *Justicia* L. and it is these that form the basis of the tribe Justicieae *sensu* Bremekamp. Martinus Vahl included 40 species under *Justicia* in his herbarium and since that time, these species have been segregated into various smaller genera in the Justicieae and this tribe has been variously subdidvided. Linnaeus also included the genera *Acanthus* L., *Barleria* L., *Ruellia* L. and *Dianthera* L. in his *Species Plantarum* (1753). In 1789, de Jussieu united these genera with *Justicia* and *Thunbergia* Retz. into a single group he called 'Acanthi' and divided this 'ordo' into two groups on the basis of the number of stamens. This was the first recognition of the family Acanthaceae.

The Acanthaceae is a pantropical family with 2 200 species in 240 genera (Lawrence, 1951). It can be distinguished from other families by its two-locular, dehiscent capsules with a single row of ovules in each locule and funicles elaborated into retinacula. Southern Africa represents the end point in the African distribution of this family and while the Justicieae appear well represented, some tribes, such as Holographideae, Andrographideae, Chroesthideae and Strobilanthideae (all *sensu* Bremekamp) are absent from the southern African flora. There are approximately 39 genera and 340 species of Acanthaceae in southern Africa. These occur mainly in the semi-arid or the summer rainfall areas, with no species occurring in communities of plants belonging to the Cape floral kingdom.

The only comprehensive accounts of the species of the Acanthaceae in southern Africa are those of Burkill & Clarke (1899) and Clarke (1901). Since that time, Meyer (1968) published an account of the Acanthaceae in Namibia. Other work has been done, but only on individual or closely related small groups of genera and a list of these is presented in Table 1. Since the accounts of Burkill & Clarke (*loc. cit.*) and Clarke (*loc. cit.*), a considerable amount of herbarium material has been collected so that reappraisals are necessary.

Table 1 Recent work on the Acanthaceae

Genera	Worker	Date	Publication Details
	Published work on southern African Acanthaceae.		
Barleria	A.A. Obermeijer	1933	Ann. Trans. Mus. 15,2: 123 - 180
Petalidium	A.A. Obermeijer	1936	Ann. Trans. Mus. 18,2: 151 - 162
Ruspolia and Pseuderanthemum	E. Milne-Redhead	1936	Kew Bull. 1936: 255 - 274
Blepharis	A.A. Obermeijer	1937	Ann. Trans. Mus. 19,1: 105 - 139
Angkalanthus	A.D.J. Meeuse	1956	Fl. Pl Africa 31 t. 1277
Sclerochiton	O.M. Hilliard and B.L. Burtt	1970	Notes Roy. Bot. Gard, Edinb. 30: 109 - 113
Metarungia (=Macrorungia)	C. Baden	1981a	Nord. J. Bot. 1: 143 - 153
Anisotes	C. Baden	1981b	Nord. J. Bot. 1: 623 - 664
Thunbergia	E. Retief and Reyneke	1984	Bothalia 15: 107 - 116
Hypoestes	K. Balkwill	1985	S. Afr. J. Bot. 51(2): 133 - 144
Duvernoia and Adhatoda	J. Manning and F. Getliffe Norris	1985	S. Afr. J. Bot. 51(6):
	Completed work, but unpublished.		
Monechma	J. Munday	1980	M.Sc Thesis, Univ. of Witwatersrand
Asystasia (in Natal)	T.J. Edwards	1984	Hons. Thesis, Univ. of Natal
Peristrophe and Dicliptera	K. Balkwill	1985	Ph. D. Thesis, Univ of Natal
Justicia	K. Immelman	1984	Part of Ph. D. Thesis, Univ. of Natal
Pseuderanthemum	M-J. Cadman	1985	Hons Thesis, Univ. of Natal
	Work in Progress.		
Siphonoglossa and Aulojusticia	K. Immelman	1985	Part of Ph. D. Thesis, Univ. of Natal
Asystasia	F. Getliffe Norris & T.J. Edwards		

Apparent discontinuities in the range of variation have occasionally been disproved by the augmented material. It has, for example, been found that there is a cline in the size of flowers and bracts, which links *Peristrophe cernua* Nees and *P. natalensis* T. Anderson. These two forms are conspecific and the latter has been placed in synonomy with the former which has priority. Similarly, *Hypoestes triflora* (Forsskal) Roem. & Schult. was thought to be morphologically distinct from *H. phaylopsoides* S. Moore, but the range of material now available makes it impossible to distinguish between these taxa (Balkwill & Getliffe Norris, 1985).

Some new taxa have been collected since 1900 and have been or must be described. These include a species of *Monechma* Hochst. (Munday, 1984), a species of *Angkalanthus* Balf. f. (Meeuse, 1956), two new species of *Peristrophe* Nees (Balkwill, Cadman & Getliffe Norris, 1985) and four new species of *Dicliptera* Juss., described in this thesis.

Clarification of infraspecific taxa is now possible in some species. Two subspecies of *Justicia petiolaris* (Nees) T. Anders. have been recognised (Immelman, *pers. com.*), two new varieties of *Hypoestes aristata* (Vahl) [Soland. ex] Roem. & Schult. have been described and two forms of *H. forskaolii* (Vahl) [Soland. ex] R. Br. have been recognised (Balkwill & Getliffe Norris, 1985). Two subspecies are recognised in *Dicliptera minor* C.B. Clarke and two varieties (one of which comprises two forms) have been recognised in *D. clinopodia* Nees in this thesis.

When Clarke (1901) described *D. transvaalensis* C.B. Clarke, no fruiting material was available. More recently, however, fruiting material has been collected and it has been necessary to transfer this species to the genus *Peristrophe* (Getliffe Norris, Balkwill & Manning, 1985).

There are still a number of nomenclatural problems in the Acanthaceae. One of the most difficult, and yet most critical, is the typification of the genus *Justicia*. Until a conclusive solution to this problem has been found, the nomenclature of many genera in the Justicieae is slightly unstable.

Having revised *Hypoestes* [Soland. ex] R. Br. in 1981, I became interested in the relationship of *H. triflora* to *Dicliptera zeylanica* Nees, because these species are morphologically very similar and grow in very similar habitats. In order to examine this relationship, I decided to revise *Dicliptera* and its close ally *Peristrophe*. *Dicliptera* is a pantropical genus with approximately 150 species, of which fifteen occur in southern Africa. *Peristrophe* is also a tropical genus, but occurs only in Africa, Asia and the Indian peninsula. Nine species of *Peristrophe* occur in southern Africa. These two genera are closely related and differ only by the nature of the bases of the placentae, which are elastic in *Dicliptera* and inelastic in *Peristrophe*.

I have found that observations made in the field and on living material have been most helpful and, indeed, it was in the course of field work that *P. cliffordii* Balkwill and *D. sp. 4* were discovered. Field work has been augmented by morphological, micromorphological, palynological and chemotaxonomic studies. The taxonomic significance of these characters are discussed in the following chapters and this section culminates in a revision of the southern African species of *Peristrophe* and *Dicliptera*.

In order to assess the relationship of *Hypoestes* to *Dicliptera* and of *Peristrophe* to *Dicliptera*, it was necessary to investigate the position of these genera in the sytems of classification that had been proposed for the family and to investigate the distribution (throughout the family) of the characters that separate them.

Lindau (1895) placed *Peristrophe, Dicliptera* and *Hypoestes* in a group called Diclipteriinae, but also included unrelated genera, e.g. *Rungia* Nees. Burkill & Clarke (1899) placed *Hypoestes* and *Peristrophe* in their Section Hypoestae and *Dicliptera* in their Section Solutae, but I cannot agree that *Dicliptera* is more closely related to *Macrorungia* C.B. Cl. than to *Peristrophe* and

Hypoestes. Bremekamp (1965) has published the most recent comprehensive account of the classification of the family and has placed Lindau's Diclipteriinae within the Justiciinae. He does, however, make the comment 'I will not say that the classification of the Justicieae given above is perfect. On the contrary, I am convinced that it is no more than a tentative effort'. While Bremekamp's placement of *Peristrophe, Dicliptera* and *Hypoestes* shows their affinities with other taxa more accurately than the accounts of Burkill & Clarke (1899) or Lindau (1895), it does not, in my opinion, reflect their close affinity to one another.

Thus it has been necessary to evaluate southern African genera in the light of the classifications of Bremekamp (1965) and Lindau (1895) and to decide on the correct position of *Peristrophe, Dicliptera* and *Hypoestes*. Conclusions are presented in chapter 13, which is followed by keys to tribes and genera and formal revisions of the genera *Peristrophe* and *Dicliptera*.

CHAPTER 2
HABIT AND LEAF MORPHOLOGY

Introduction

Habit is a character that is often overlooked, although it can be useful at generic (Dyer 1975) and specific (Napper, 1970) levels. Unless taxonomists have personally collected or grown material of the group on which they are working, they are dependent on information provided on herbarium labels. Unfortunately, some collectors do not provide information about habit and others have definitions of terms that differ from those most commonly used; thus habit is not used as a character as often as it may. Leaf morphology is a plastic character and varies between plants growing in slightly different habitats, thus it is often treated with suspicion. Dokosi (1979), however, has used leaf morphology in the diagnosis of *Elytraria minor* Dokosi and this character has been used to distinguish a variety of *Hypoestes aristata* (Balkwill & Getliffe Norris, 1985).

Material and Methods

In order to obtain information about the habit and leaf morphology of species of *Hypoestes, Dicliptera* and *Peristrophe*, plants have been observed in the field; plants have been collected and then cultivated and observed in a greenhouse and in a bed in the botanical garden and specimens, and notes on herbarium sheets have been observed. Note has also been taken of the descriptions available in literature (e.g. Dyer, 1975 & Lindau, 1895).

Observations

Habit

Within the Acanthaceae, there is a range of habit, from annuals (e.g. *P. paniculata* (Forsskal) Brummitt) to small trees (e.g. *Mackaya bella* Harv. and *Duvernoia adhatodoides* [E. Mey. ex] Harv.). Within this range, are included forms such as that of *D. zeylanica*, which is a soft-stemmed herb with a prostrate stem that frequently roots at the nodes; that of *D. fruticosa* Balkwill *ined.*, which has an upright stem that is woody at the base and seldom roots at the nodes, and that of

Angkalanthus transvaalensis A. Meeuse, which is an upright, woody shrub that grows to two metres high, with woody terminal branches and does not root at the nodes.

Within *Peristrophe* and *Dicliptera*, the range includes annuals, soft-stemmed herbs and suffrutices that are variously woody. There is also a range in the ability to root at the nodes or to produce stolons. In southern Africa, most species of *Peristrophe* are suffrutices up to 1,5 m high and are quite woody. *P. cernua* has softer stems than the other species; the branches droop and touch the ground and then root from the nodes.

Differences in habit have assisted the identification of *P. kotschyana* Nees. Material of *P. kotschyana* collected in southern Africa has often been misidentified and filed with material of *P. paniculata*. It has, however, been noted that although the stems of *P. paniculata* are often thicker than those of *P. kotschyana*, they are much softer (they frequently split due to the pressure applied to them during drying). *P. kotschyana* develops a woody fibrous root system (plate 1b), while all plants of *P. paniculata* have a small tap root system (plate 1a). Comparison of collection dates has shown that *P. kotschyana* has been collected in flower through most of the year (fig. 1), while *P. paniculata* has only been collected between February and August (fig. 1). A sequence of development can be observed in the plants of *P. paniculata* collected from consecutive months of the same year (plate 2 a - d). Plants cultivated from seed from the gathering *Goldblatt 1929*, have all grown and flowered for a few months, produced seed and died. Specimens of *P. kotschyana* grown under identical conditions to those under which *P. paniculata* was grown, are evergreen and have grown from the same rootstocks for four years.

There is a great range of habit displayed by members of the genus *Dicliptera* in southern Africa. *D. zeylanica* has soft prostrate stems, which produce adventitious roots at the nodes, so that the plants appear to be stoloniferous. When growing under ideal conditions, *D. clinopodia* has stems that are very similar to those of *D. zeylanica*, but the stems are markedly ridged; in drier situations, the bases of the stems become woody, and a few stems are produced from the same rootstock. *D. eenii* S. Moore, which grows under drier conditions

Facing page number 8

Plate 1: Habit of *Peristrophe kotschyana* and *P. paniculata*.

a) Habit of *P. kotschyana* with fibrous root system, *Repton 4765*, X 0,5 and b) habit of *P. paniculata* with a tap root system, *Smith 1293*, X 0,5.

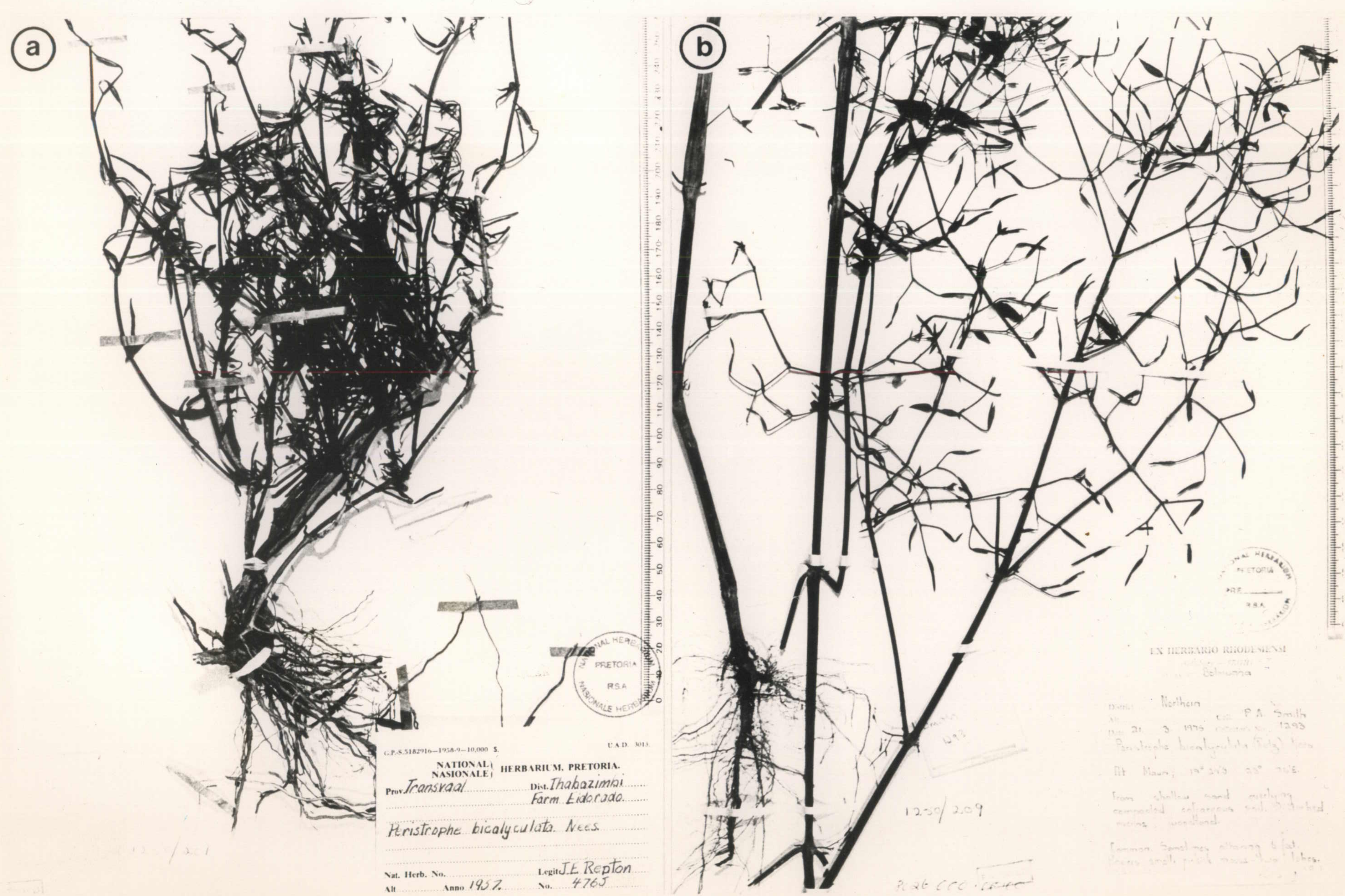
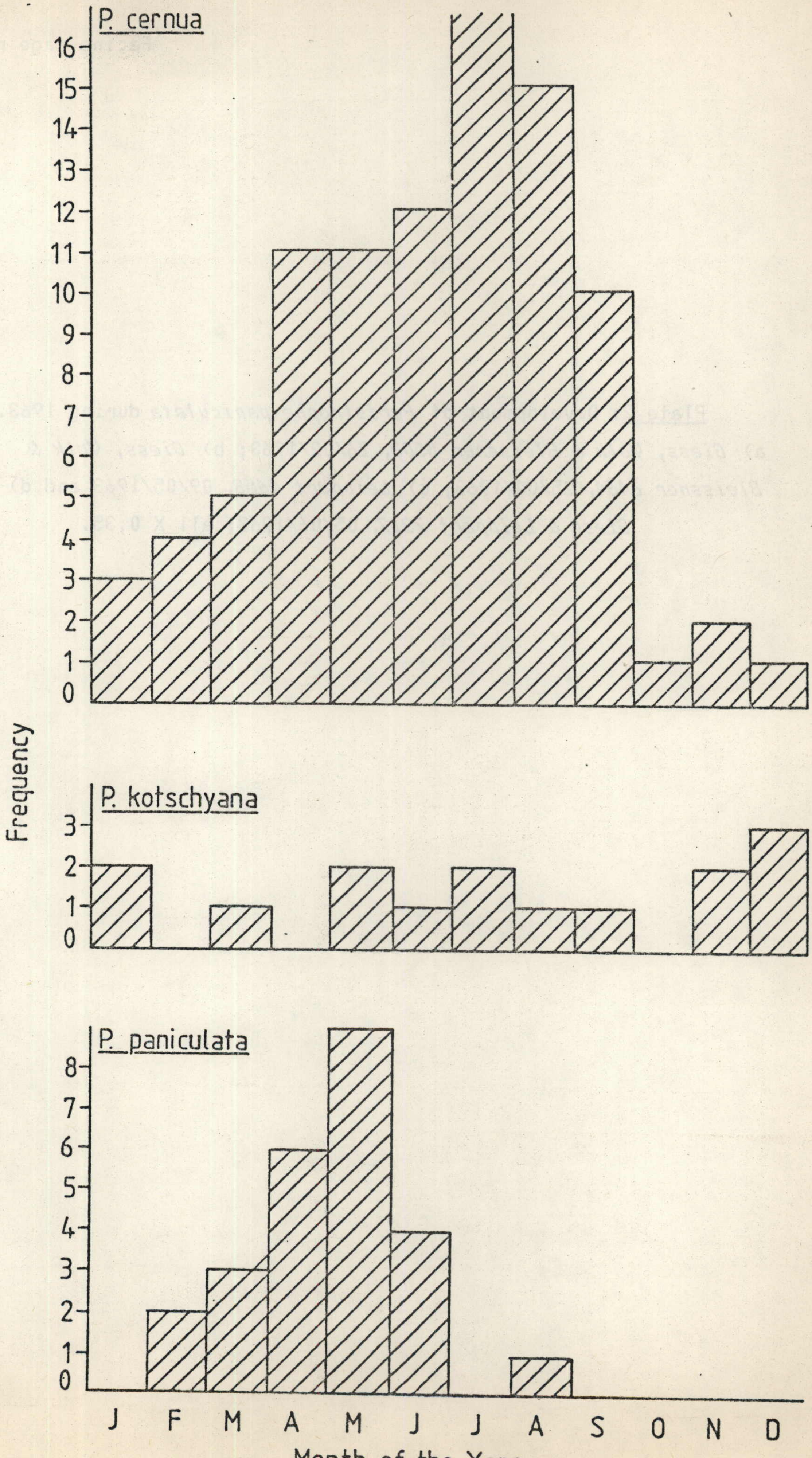

a
b
NATIONAL HERBARIUM PRETORIA RSA NASIONALE HERBARIUM
G.P.-S.5182916—1958-9—10,000 S.
U.A.D. 3013
NATIONAL
NASIONALE HERBARIUM, PRETORIA.
Prov. Transvaal Dist. Thabazimbi
Farm Eldorado
Peristrophe bicalyculata Nees.
Nat. Herb. No. Legit J.E. Repton
Alt Anno 1957 No. 4765
PRETORIA
RSA
EX HERBARIO RHODESIENSI
Botswana
Northern
P.A. Smith
21 3 1975 1293
1250/209

Figure 1: Flowering times of *Peristrophe cernua, P. kotschyana* and *P. paniculata*. Flowering times scored as frequency of collection of flowering specimens.

Flowering Times
(Frequency of Collections of Flowering Material)



HERBARIUM SOUTH WEST AFRICA SUIDWES-AFRIKA
S.W.A. HERBARIUM Nr. WINDHOEK
South West Africa Dist. Bethanien
Peristrophe bicalyculata (Retz.) Nees
a
HERBARIUM SOUTH WEST AFRICA SUIDWES-AFRIKA WINDHOEK
South West Africa Dist. Grootfontein
Peristrophe bicalyculata (Retz.) Nees
Sehr sparrige Staude. Blüten sehr
lang gestielt, klein, rot-violett.
b
3.
HERBARIUM SOUTH WEST AFRICA SUIDWES-AFRIKA
S.W.A. HERBARIUM Nr.
South West Africa. Dist. Rehoboth.
Peristrophe bicalyculata (Retz.) Nees
c
Zitiert in:
PRODROMUS einer Flora von Südwestafrika
130: 49 (1968)
Bearbeitung:
P.G. Meyer
HERBARIUM SOUTH WEST AFRICA SUIDWES-AFRIKA WINDHOEK
South West Africa. Dist. Kaokoveld
Peristrophe bicalyculata (Retz.) Nees
aufrecht bis 1,30 m hoch, dürftig
verzweigt.
in kleinem Rivier. 5.8.1963
S.W.A. HERBARIUM Nr. WINDHOEK
d

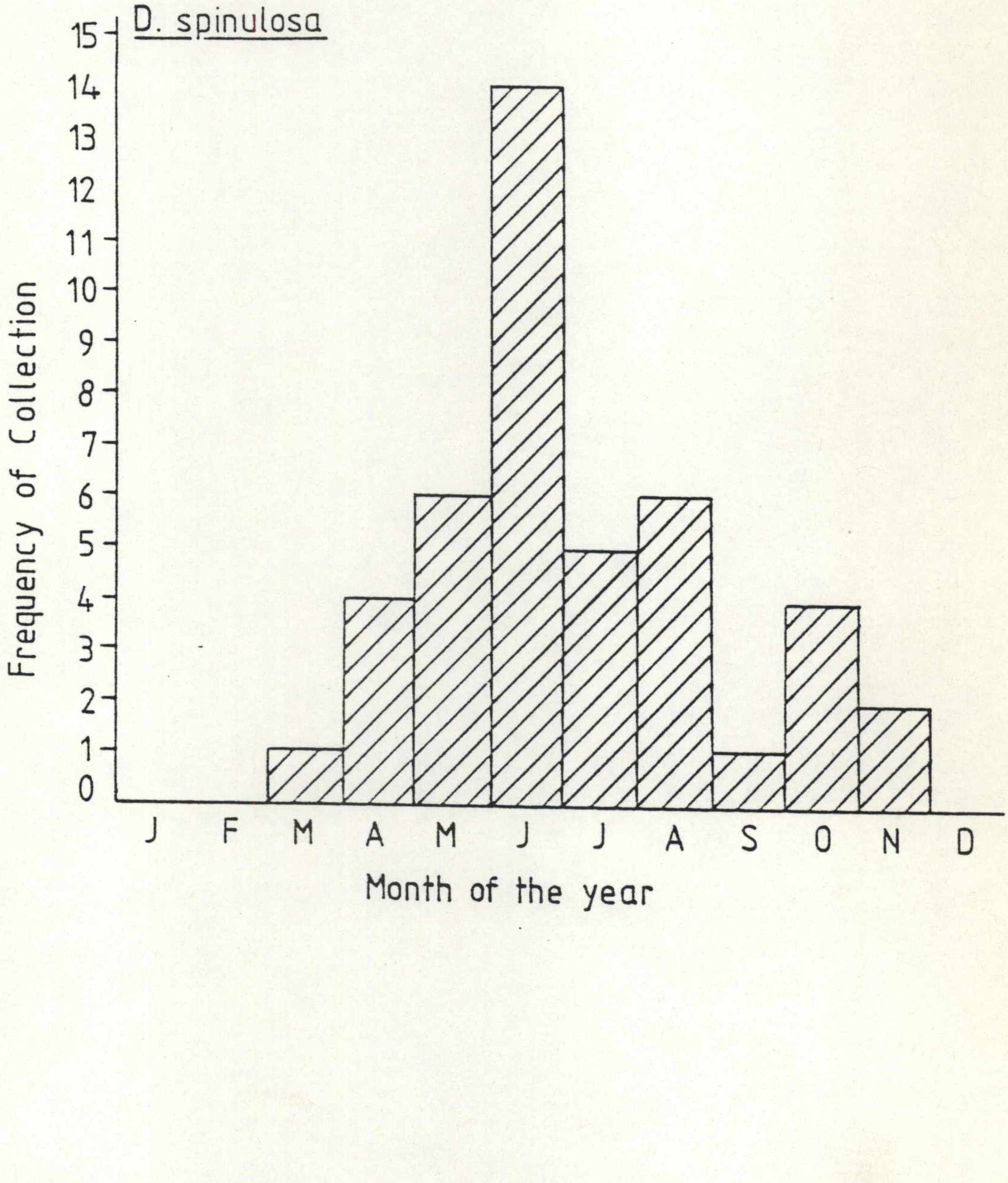
than does *D. clinopodia*, has many more stems from each rootstock. The stems are shorter, thinner and slightly more woody than those of *D. clinopodia*. The tips of branches sometimes touch onto the ground and may then root at the nodes. *D. fruticosa* is a rather larger plant than *D. eenii* with thicker and woodier stems that do not bend over at the tips. I have observed that even when stems are buried during the course of road works, they do not root at the nodes. Plants of this species have a woody base and rootstock. *D. minor* grows in dry areas; its stems are prostrate, frequently root at the nodes and seldom grow higher than 20 cm. It seems that the plants sometimes overwinter as small succulent subterranean sections of stem, from which they grow in response to rain in the new season (pers. obs. in cultivation and in field). *D. sp. 4* has stiff, brittle, upright stems and subterranean stolons, a unique feature amongst southern African members of the Dicliperiinae. *D. spinulosa* Hochst. ex Nees is a small plant that occurs in very dry areas; it has a small rootstock, a single stem from the base, and starts to flower at the first node above the ground. This species has only been collected between March and November (fig. 2), and seems to be an annual.

Leaves

The leaves of *D. zeylanica* and *H. triflora* are soft and thin. Those of many species of *Peristrophe* and *Dicliptera* that grow in drier areas are stiffer and slightly thicker in texture. The leaves of both *P. paniculata* and *D. spinulosa*, two annual species, appear to be quite thin and are caducous. The leaves of *P. grandibracteata* Lindau *sensu lato* appear to be quite thickly textured, while those of *D. minor* are slightly succulent. The leaves of *D. sp. 4* are stiff and slightly leathery, an unusual feature. Within *D. heterostegia* Nees, the leaves show some variation; some plants have herbaceous leaves, while some of those growing at Mkuze Game Reserve and some of those growing on sea-facing dunes have slightly succulent leaves. Within *D. clinopodia*, there is a group of plants that grow on sea-facing slopes in the Transkei and have slightly succulent leaves. This difference in leaf texture is correlated with a difference in the shape and colouration of the tertiary bracts and in the stature of the plants.

P. sp. 1 differs from *P. grandibracteata* and *P. hereroensis* (Schinz) Balkwill by having proportionally broader leaves, while the

Figure 2: Flowering time of *Dicliptera spinulosa*. Flowering times scored as frequency of collection of flowering specimens.


D. spinulosa
Frequency of Collection
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
J F M A M J J A S O N D
Month of the year

narrowly lanceolate leaves of *P. gillilandiorum* Balkwill are unique amongst the species of *Peristrophe* in section *Cernuae* Balkwill *ined.*. The leaves near the base of the stems of *D. minor* are smaller than the leaves in similar positions in any other species of *Dicliptera*. During flowering, the large lower leaves of *D. fruticosa* are shed and very small leaves are produced at the tips of the plant. No other species has mature leaves as small as those produced at the tips of the flowering branches of *D. fruticosa*.

Discussion

Peristrophe montana Nees, *Dicliptera zeylanica* and *Hypoestes triflora* are very similar in many aspects. They have very similar inflorescences, their tertiary bracts are very similar (broadly ovate or obovate with five veins from the base), their flowers are amongst the largest in their respective genera and all three grow in similar habitats. On the basis of these similarities, I hypothesise that these three species are the most primitive in each of these genera and that the other species have in some way evolved from stock similar to these three. As these species share the same habit (i.e. soft prostrate stems that frequently root at the nodes), I believe this is the primitive state in the subtribe Diclipterinae. It is also likely that this is the most primitive habit in the family. Evolution from this putatatively primitive habit must have been in response to the selective pressures that acted as the plants colonised drier habitats. It seems that the habits must have evolved in radiating lines from the primitive form. One line would lead to the annual species (i.e. *P. paniculata* and *D. spinulosa*) that occur in some of the driest habitats in which the genera are found. Another line of evolution would be that which leads through *D. clinopodia* to *D. eenii* and then to *D. fruticosa*, with an offshoot that would lead to the form displayed by *D. sp. 4*. The third line is probably directly from the putatively primitive form to one with succulent subterranean perrenating organs, such as those shown by *D. minor*.

There seems to be a similar pattern of radiation in the evolution of the various leaf types. The first line would lead to the annual species where the leaves are caducous. The second line would lead through the slightly thickened leaves to the slightly succulent leaves and the third line would lead to stiff leathery leaves of *D. sp. 4*. The form of *D. clinopodia* that has succulent leaves has been recognised at the varietal level because of the correlation it shows with other characters. The thick leaves in some plants of *D. heterostegia* show no correlation with other characters and thus are thought to represent infraspecific variation and are not formally recognised.

Habit has been a useful character to distinguish between *D. minor* and other closely related species and between *P. kotschyana* and *P. paniculata*. Leaf texture has been valuable to distinguish between *D. minor* and other species of *Dicliptera*, as between *D. sp. 4* and the other species in the genus. Leaf shape has been useful in diagnosing *P. sp. 1* and *P. gillilandiorum* against the other species in *Peristrophe*. Although leaf size is a highly variable character, and although it is difficult to assess whether dried leaves are mature enough to provide true measurements, size of leaves at the base of stems is useful to distinguish *D. minor* from other species of *Dicliptera* and leaf size on the fertile branches is useful to distinguish *D. fruticosa* from other species of that genus.

Conclusion

Although vegetative morphology is highly variable, and sometimes difficult to assess, character states can be arranged into evolutionary sequences within the genera *Peristrophe* and *Dicliptera*. This provides clues to the phylogeny of these species. Vegetative characters can also be used to distinguish between certain species of *Peristrophe* and *Dicliptera* and so have been worthy of study.

CHAPTER 3
MORPHOLOGY OF INFLORESCENCES

Introduction

The structure of the inflorescence of the Acanthaceae is an important character and has been used taxonomically at generic level (Leonard, 1953), specific level (Heine, 1962 and Balkwill & Getliffe Norris, 1985) and to identify infrageneric groups (Immelman, 1983). The most primitive inflorescence in the Acanthaceae is a dichasial cyme (Baden 1981b) and many inflorescence types have evolved from this either by elaboration and subsequent simplification or possibly by direct reduction from the original cyme. In *Hypoestes*, the inflorescence was a very important character, but had probably been misinterpreted by many workers (Balkwill & Getliffe Norris, 1985). This character has been worthy of study while considering the interrelationships of *Peristrophe, Dicliptera* and *Hypoestes*.

Material and Methods

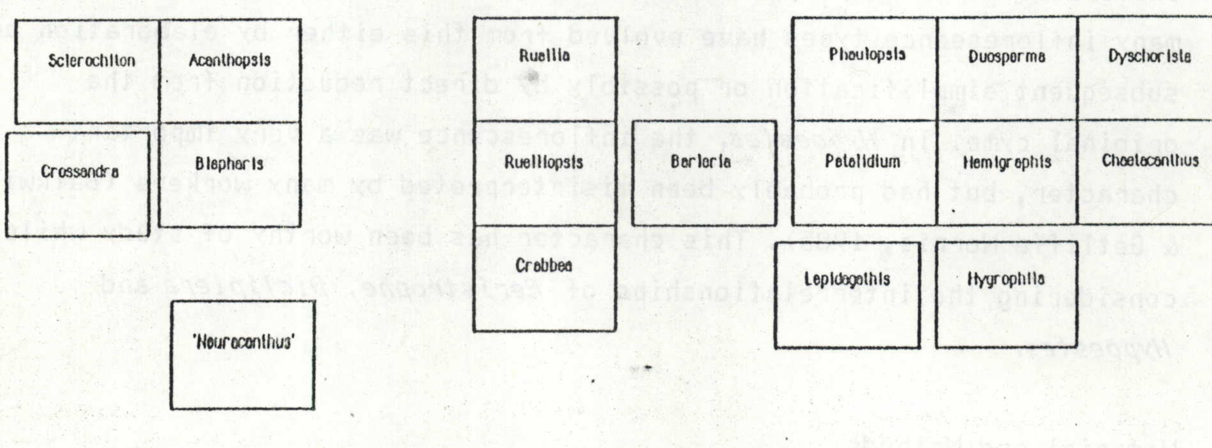
Species of *Hypoestes, Dicliptera, Peristrophe* and some other genera of the Acanthaceae were cultivated in a greenhouse and a garden. Under these conditions the growth of the plants is lush and their inflorescences realise their full potential more frequently than do the inflorescences of wild plants. When cultivated material was not available, herbarium material was boiled and dissected. Five measurements of inflorescence axes and peduncles of each specimen were made. These were averaged for each specimen and the averages were used to calculate means and standard deviations for each species.

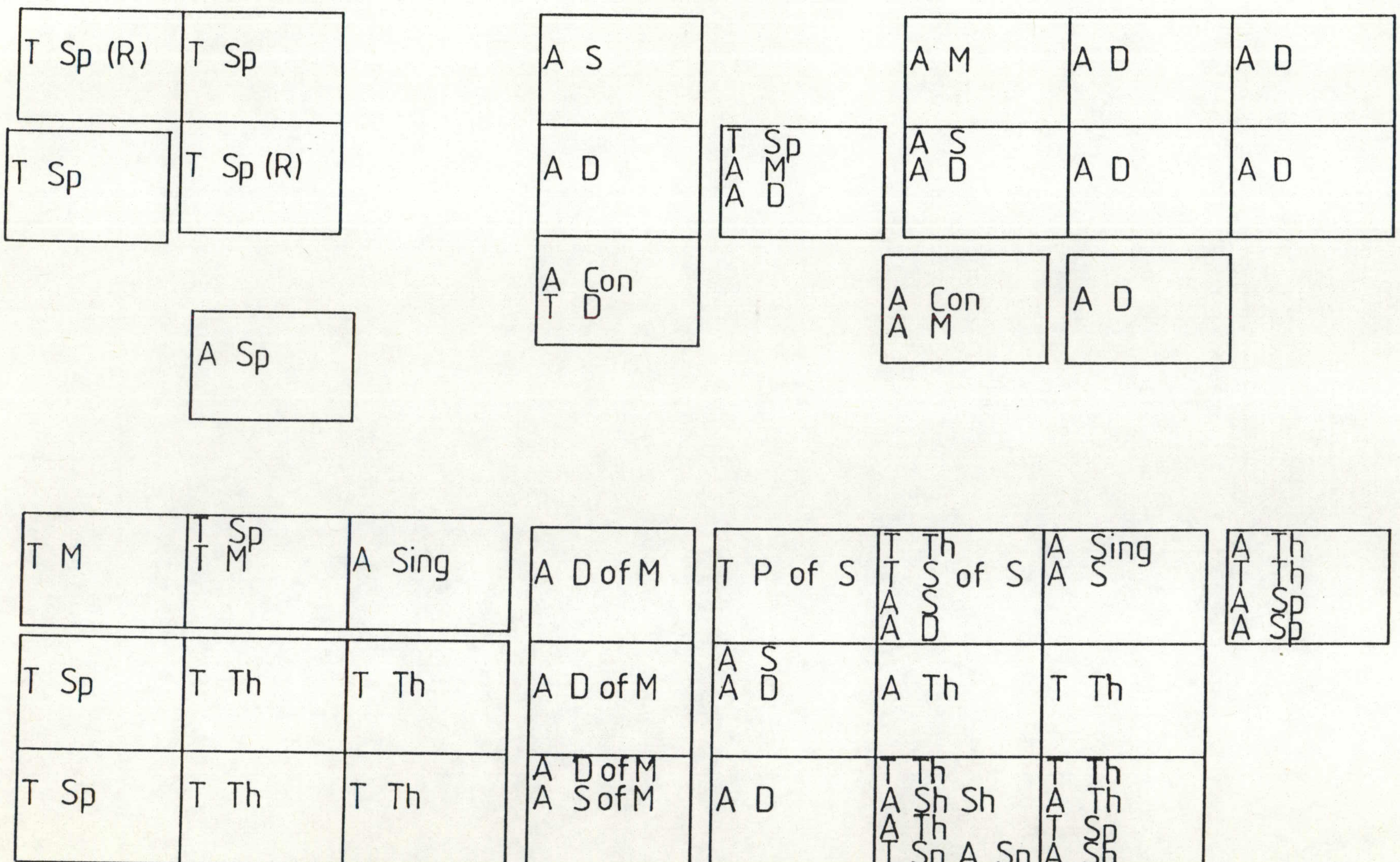
Observations

The results of a survey of inflorescence types in southern African Acanthaceae are presented in Table 2. The most widespread type of inflorescence is a terminal spike and many of the remaining inflorescences are cymose. A terminal thyrse or terminal spike is characteristic of the southern African Acanthoideae and, in the Ruellioideae, is found in almost all members of the subtribe

Table 2: Distribution of types of inflorescences in the southern African Acanthaceae.

Genera arranged as in key below, Types of inflorescence as follows: A = axillary, Con = congested, D = dichasial cyme, M = monochasial cyme, P = panicle, R = reduced, (R) = sometimes reduced, S = scorpioid cyme, ShSh = short shoots, Sing = single flowers, Sp = spike, T = terminal and Th = thyrse.





T Sp (R)
T Sp
T Sp
T Sp (R)
A Sp
A S
A D
A Con
T D
T Sp
A M
A D
A M
A D
A D
A S
A D
A D
A D
A Con
A M
A D
T M
T Sp
T M
A Sing
T Sp
T Th
T Th
T Sp
T Th
T Th
A D of M
A D of M
A D of M
A S of M
T P of S
T Th
T S of S
A S
A D
A Sing
A S
A S
A D
A Th
T Th
A D
T Th
A Sh Sh
A Th
T Sp A Sp
T Th
A Th
T Sp
A Sp
A Th
T Th
A Sp
A Sp

Odontoneminae.

The inflorescences of all species of *Peristrophe* and *Dicliptera* are very similar to one another. All are compound axillary inflorescences, with one or more compound inflorescences ('umbels') in each axil (fig. 3). Each 'umbel' is borne on an inflorescence axis (fig. 3a) and is subtended by a pair of secondary bracts (fig. 3d). Each 'umbel' is usually composed of two to five umbellately arranged inflorescence units, each borne on a peduncle (fig. 3b). Occasionally only one inflorescence unit is present between a pair of secondary bracts and occasionally the 'umbellate' compound inflorescences are in turn compounded (e.g. *Peristrophe bivalvis* (L.) Merr. and *D. spinulosa*). In *Peristrophe, Dicliptera* and *Hypoestes* each inflorescence unit consists of a one-sided cyme (fig. 4), which, in *Hypoestes*, may be complicated by the activity of an accessory bud (*H. triflora* [fig. 4b & g] and *H. forskaolii* [fig. 4d & h]) or variously reduced (*H. forskaolii* [fig. 4e & f] and *H. aristata* [fig. 4j & k]) (Balkwill & Getliffe Norris, 1985). In all the specimens of southern African *Peristrophe* and *Dicliptera* it was found that the inflorescence units were monochasial cymes that were neither complicated by acccessory buds nor reduced (fig. 4c & i). There was some variation in the number of flowers and buds present in each inflorescence unit with as few as two seen in a specimen of *D. minor* ssp. *1*, and as many as five seen in a specimen of *D. capensis* Nees. In one plant of *P. gillilandiorum*, the first bud in each inflorescence unit had been aborted, but this was not found in other plants of the same species, so is not a constant feature. The number of 'umbels' in each axil is characteristic in some species. One, or sometimes two, are present in *D. zeylanica* and two to seven in *D. heterostegia* where the number increases as the flowering season progresses. In *D. clinopodia, D. quintasii* Lindau, D. sp. 2 and *D. sp. 3*, it is common to have many 'umbels' in each axil, while in related species such as *D. divaricata* Compton, *D. minor, D. sp. 4* and *D. eenii*, there are only one or occasionally two inflorescences in each axil.

Variation in the number of inflorescence units in each 'umbel' and the number of 'umbels' that are compounded is shown in fig. 5. No southern African species of *Peristrophe* has five inflorescence units in each 'umbel'. Relatively few species of *Peristrophe* have three

__Figure 3__: Diagram of inflorescence of *Dicliptera zeylanica*. Inflorescence axis (a), peduncle of inflorescence unit (b), leaf or primary bract (c), secondary bract (d), adaxial tertiary bract (e1), abaxial tertiary bract (e2), quaternary bract (f), tertiary bract of (axillary) second flower (h), quaternary bract of second flower (h), first flower of inflorescence unit (i), (axillary) second flower of inflorescence unit (j) and (axillary bud of axillary flower) third flower (k).

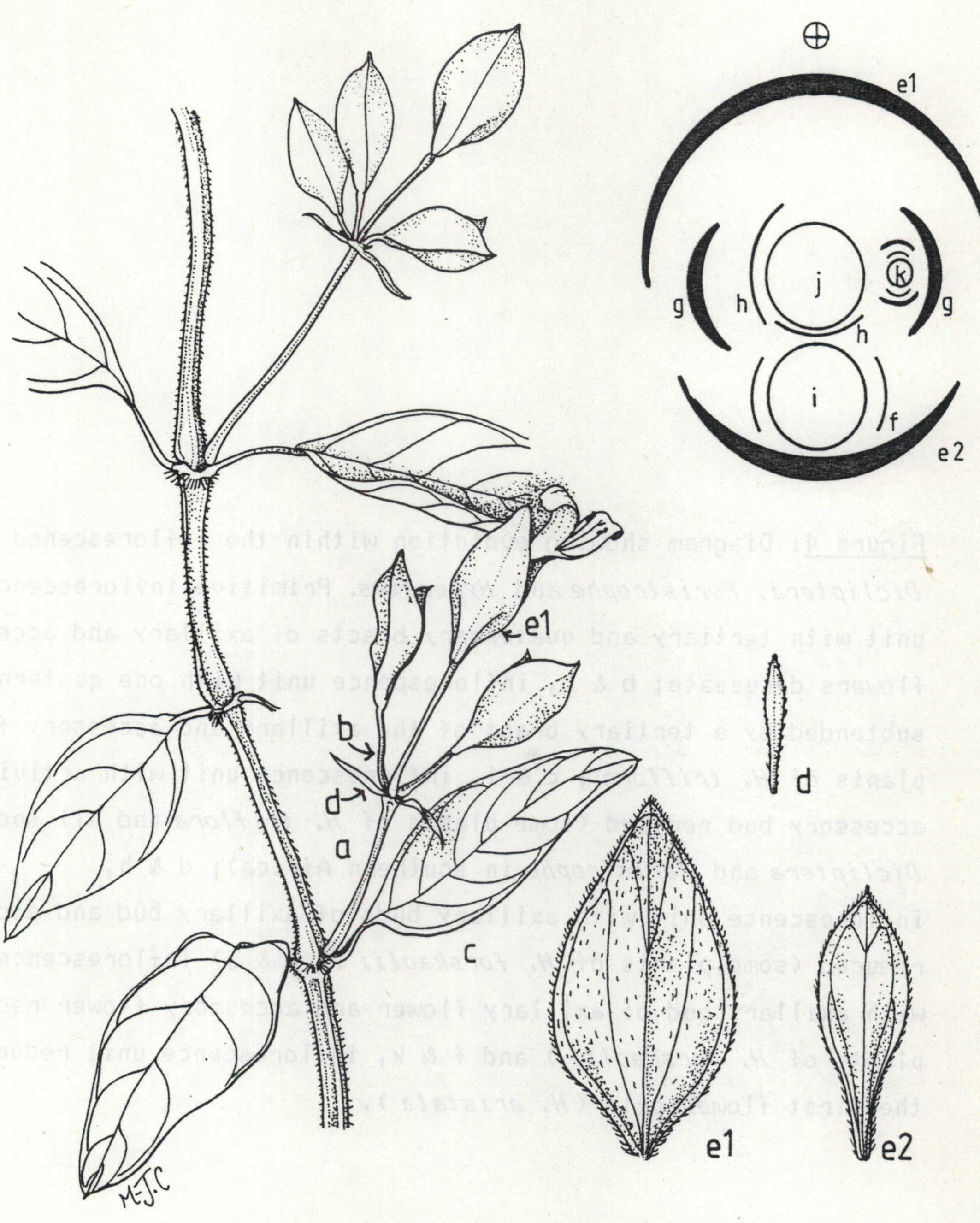

e1
g
h
j
k
h
i
f
e2
b
d
a
c
e1
d
e1
e2
M-J.C

Figure 4: Diagram showing evolution within the inflorescence unit of *Dicliptera, Peristrophe* and *Hypoestes*. Primitive inflorescence unit with tertiary and quaternary bracts of axillary and accessory flowers decussate; b & g, inflorescence unit with one quaternary bract subtended by a tertiary bract of the axillary and accessory flowers (some plants of *H. triflora*); c & i, inflorescence unit with activity of accessory bud reduced (some plants of *H. triflora* and all species of *Dicliptera* and *Peristrophe* in southern Africa); d & h, inflorescence unit with axillary buds of axillary bud and accessory buds reduced (some plants of *H. forskaolii*); e & j) inflorescence unit with axillary bud of axillary flower and accessory flower reduced (some plants of *H. forskaolii*) and f & k, inflorescence unit reduced to the first flower only (*H. aristata*).

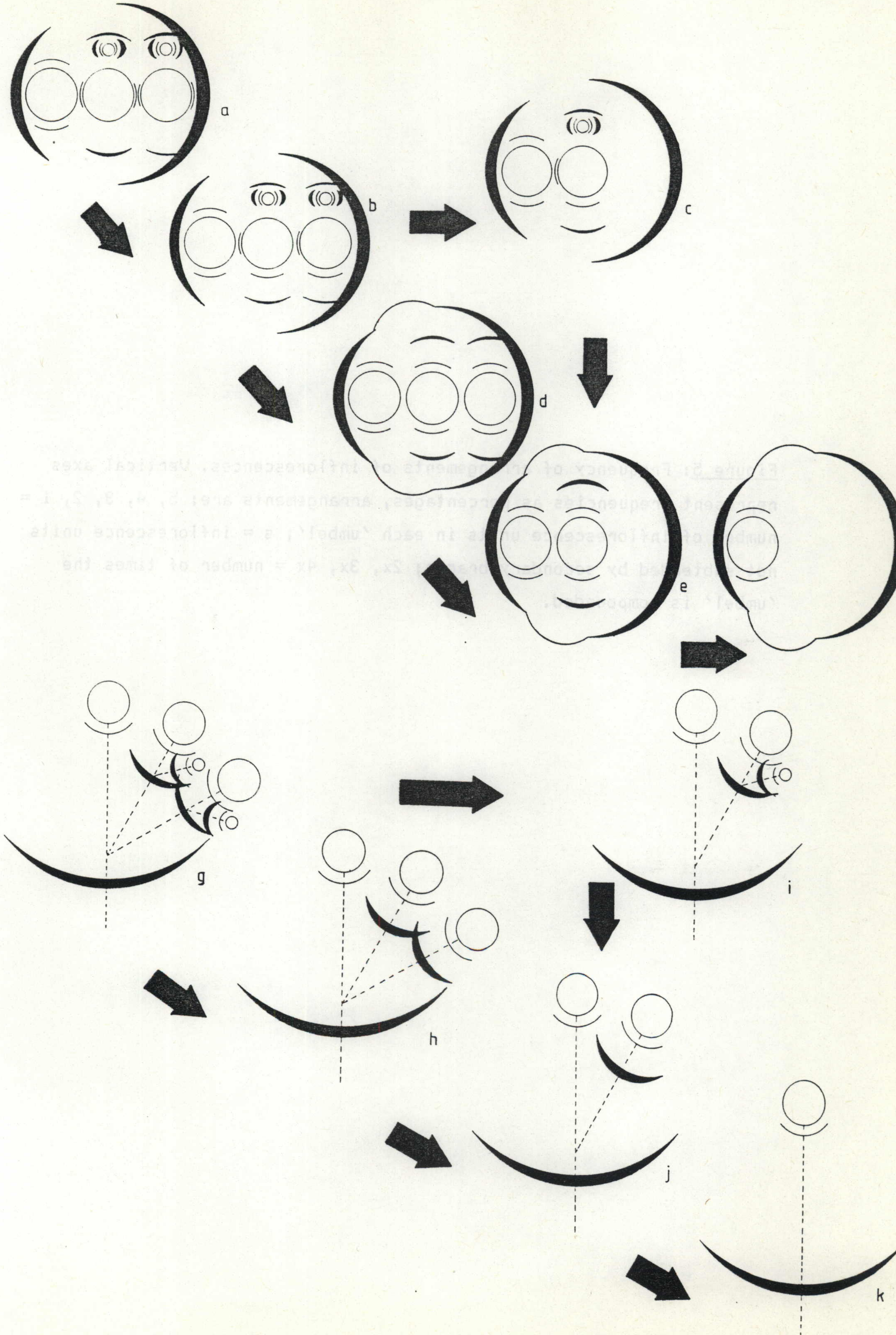
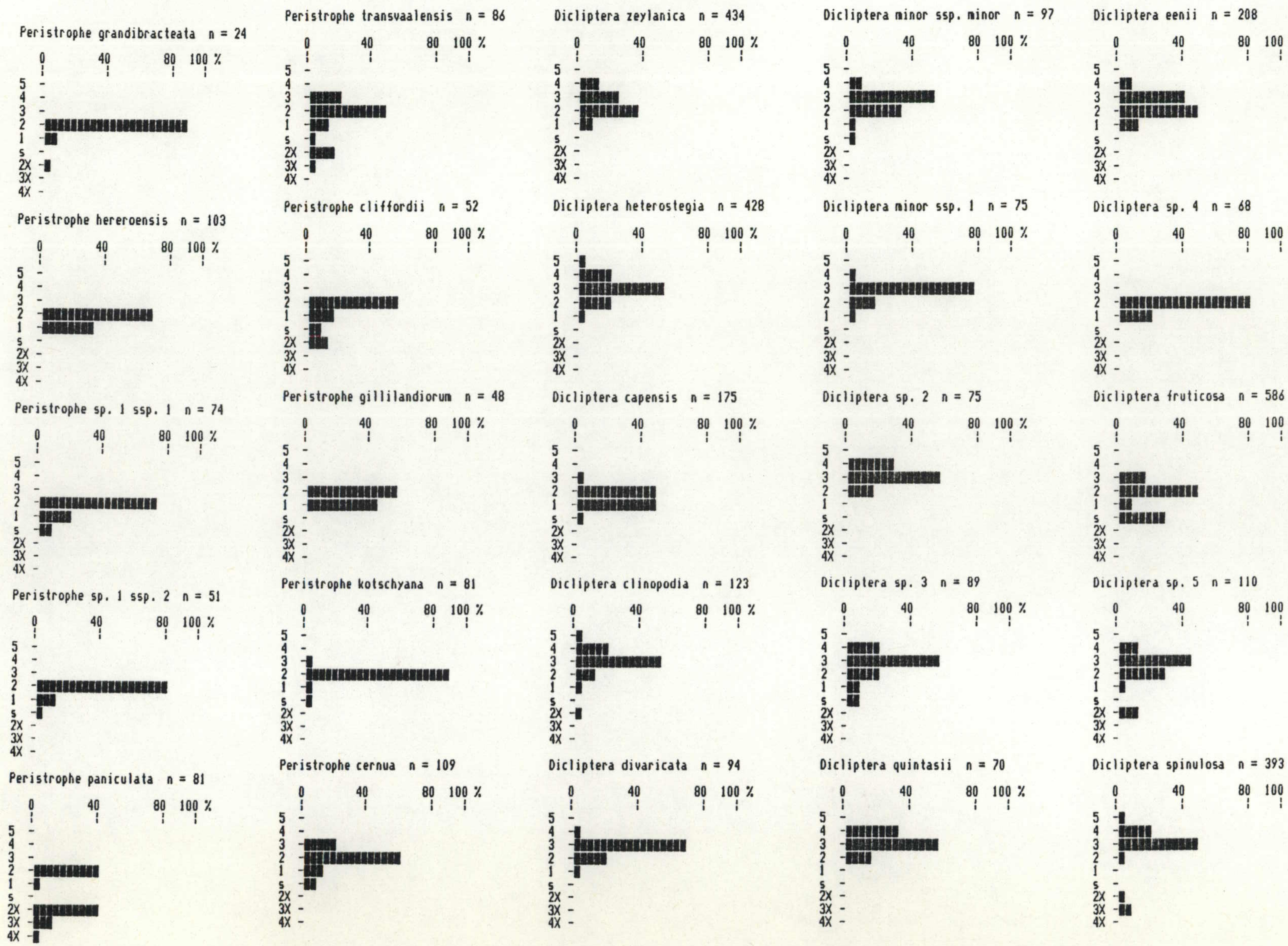

a
b
c
d
e
f
g
h
i
j
k

Figure 5: Frequency of arrangements of inflorescences. Vertical axes represent frequencies as percentages, arrangements are: 5, 4, 3, 2, 1 = number of inflorescence units in each 'umbel'; s = inflorescence units not subtended by secondary bracts; 2x, 3x, 4x = number of times the 'umbel' is compounded.


Peristrophe grandibracteata n = 24
Peristrophe hereroensis n = 103
Peristrophe sp. 1 ssp. 1 n = 74
Peristrophe sp. 1 ssp. 2 n = 51
Peristrophe paniculata n = 81
Peristrophe transvaalensis n = 86
Peristrophe cliffordii n = 52
Peristrophe gillilandiorum n = 48
Peristrophe kotschyana n = 81
Peristrophe cernua n = 109
Dicliptera zeylanica n = 434
Dicliptera heterostegia n = 428
Dicliptera capensis n = 175
Dicliptera clinopodia n = 123
Dicliptera divaricata n = 94
Dicliptera minor ssp. minor n = 97
Dicliptera minor ssp. 1 n = 75
Dicliptera sp. 2 n = 75
Dicliptera sp. 3 n = 89
Dicliptera quintasii n = 70
Dicliptera eenii n = 208
Dicliptera sp. 4 n = 68
Dicliptera fruticosa n = 586
Dicliptera sp. 5 n = 110
Dicliptera spinulosa n = 393
0 40 80 100 %
5 4 3 2 1 s 2X 3X 4X

inflorescence units in each 'umbel'. The most common number of inflorescence units in each 'umbel' is two. Most of the species in the section *Cernuae* have 'umbels' that are twice or thrice compound and *P. paniculata*, the only annual species of *Peristrophe* in southern Africa, has compound 'umbels' as the most common arrangement of inflorescence units.

Some species of *Dicliptera* have as many as five inflorescence units in each 'umbel', many species most commonly have three inflorescence units in each 'umbel' and some species have two inflorescence units in most 'umbels' (fig. 5). Twice and thrice compound 'umbels' are much less common in *Dicliptera* than in *Peristrophe*, although *D. spinulosa*, the only annual species of *Dicliptera* in southern Africa, has these compounded 'umbels' more often than does any other southern African species of *Dicliptera*.

The range of variation in the lengths of the inflorescence axes and peduncles of inflorescence units is shown in figs. 6 & 7. The minimum and maximum values measured, the minimum and maximum means for specimens and a 68% confidence interval for the mean of each species are shown. Figure 8a - c presents the same measurements, but as percentage frequencies of occurrence of measurements. From these figures, it is evident that there is a great deal of overlap between the measurements of certain species, while overlap between some other species is minimal.

Discussion

The family Acanthaceae has opposite leaves and often accessory buds develop so that more than one branch may be produced in any axil. The Thunbergiaceae and the Mendonciaceae are two families that are very closely related to the Acanthaceae *sensu* Bremkamp and they have single axillary flowers. It is likely that this arrangement of flowers is the one from which the acanthaceous inflorescences originally evolved. While it is possible that the modern acanthaceous inflorescences evolved directly from this simple arrangement, both Baden (1981b) and Manning (1983) have suggested that the inflorescences of some Acanthaceae have been derived from dichasial cymes. Figure 9 presents a scheme showing possible routes of evolution of many of the types of inflorescence present among southern African members of the Acanthaceae. Although the

Figure 6: Length of Inflorescence Axes. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ■■■ 68% confidence interval of means for specimens. Taxa as follows: Dicliptera 1, *D. zeylanica*; 2, *D. sp. 1*; 3, *D. heterostegia*; 4, *D. capensis*; 5.1, *D. clinopodia* var. *clinopodia*; 5.2, *D. clinopodia* var. *1*; 6, *D. divaricata*; 7.1, *D. minor* ssp. *minor*; 7.2 *D. minor* ssp. *1*; 8, *D. sp. 2*; 9, *D. sp. 3*; 10, *D. quintasii*; 11, *D. eenii*; 12, *D. sp. 4*; 13, *D. fruticosa*; 14, *D. sp. 5*; 15, *D. spinulosa*; Peristrophe 1, *P. grandibracteata*; 2, *P. hereroensis*; 3, *P. sp. 1*; 4, *P. paniculata*; 5, *P. transvaalensis*; 6, *P. cliffordii* Balkwill; 7, *P. gillilandiorum*; 8, *P. kotschyana* and 9, *P. cernua*.

Character: Inflorescence Axis

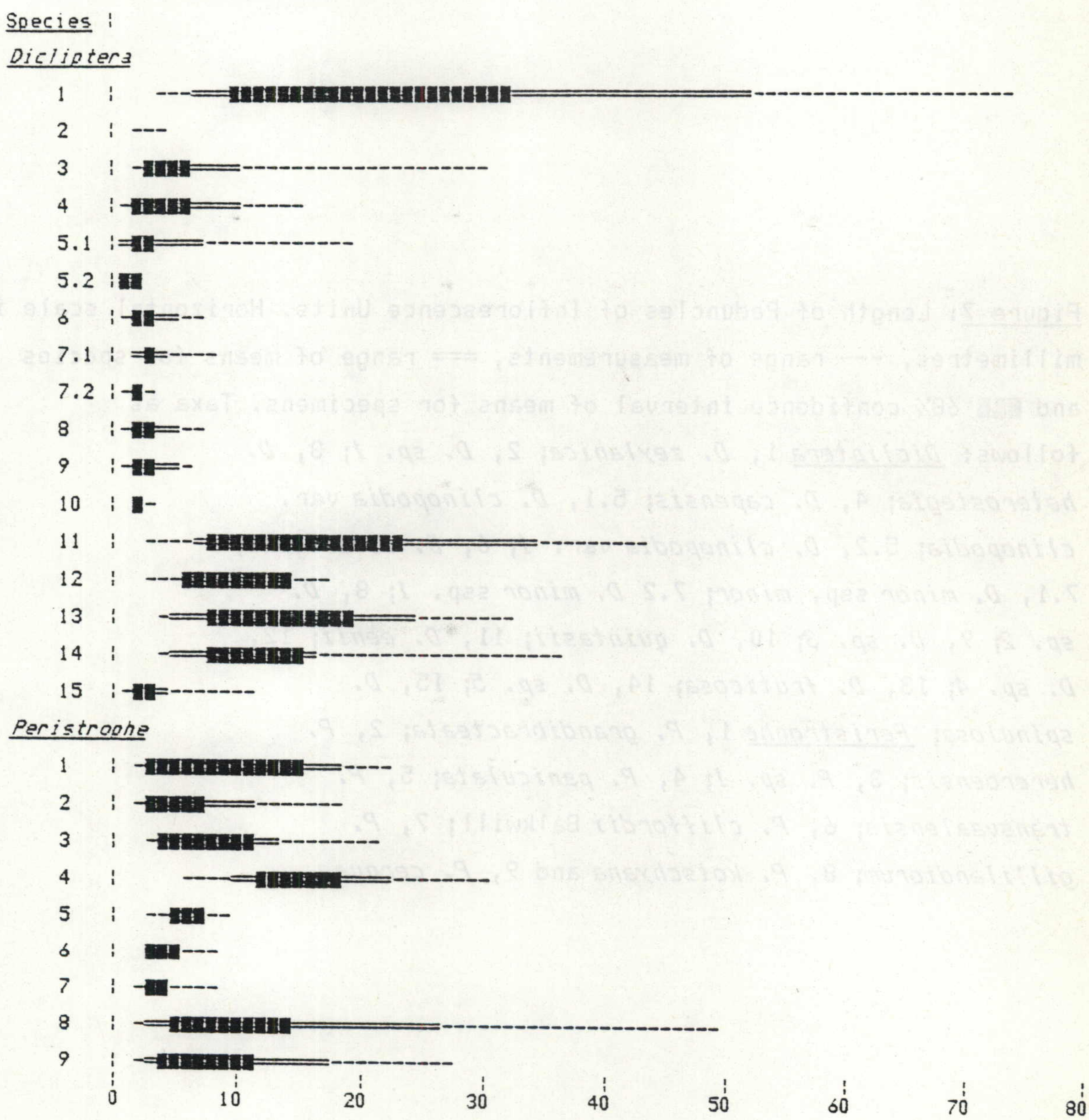


Figure 7: Length of Peduncles of Inflorescence Units. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ▓▓▓ 68% confidence interval of means for specimens. Taxa as follows: Dicliptera 1, *D. zeylanica*; 2, *D. sp. 1*; 3, *D. heterostegia*; 4, *D. capensis*; 5.1, *D. clinopodia* var. *clinopodia*; 5.2, *D. clinopodia* var. *1*; 6, *D. divaricata*; 7.1, *D. minor* ssp. *minor*; 7.2 *D. minor* ssp. *1*; 8, *D. sp. 2*; 9, *D. sp. 3*; 10, *D. quintasii*; 11, *D. eenii*; 12, *D. sp. 4*; 13, *D. fruticosa*; 14, *D. sp. 5*; 15, *D. spinulosa*; Peristrophe 1, *P. grandibracteata*; 2, *P. hereroensis*; 3, *P. sp. 1*; 4, *P. paniculata*; 5, *P. transvaalensis*; 6, *P. cliffordii* Balkwill; 7, *P. gillilandiorum*; 8, *P. kotschyana* and 9, *P. cernua*.

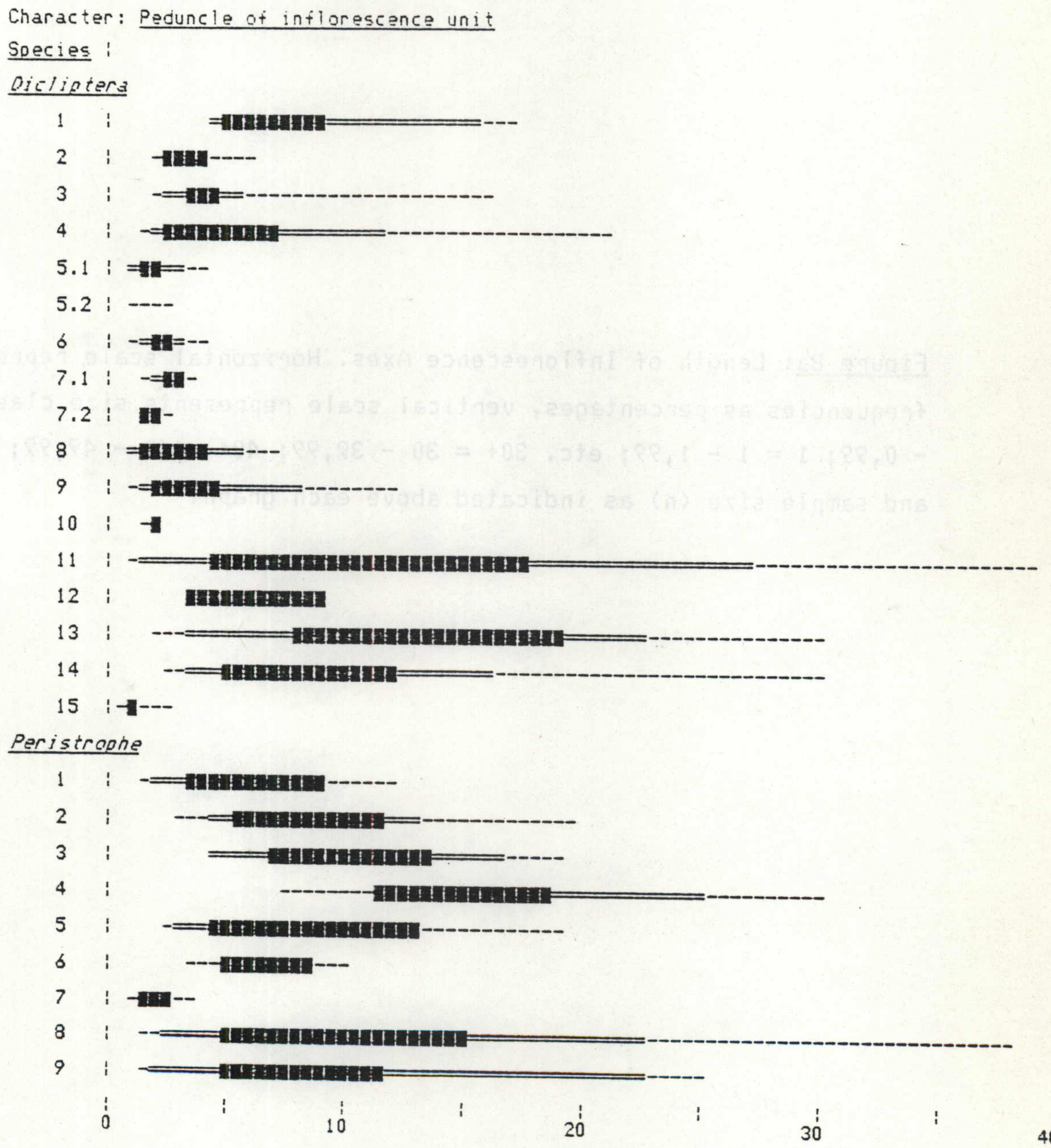
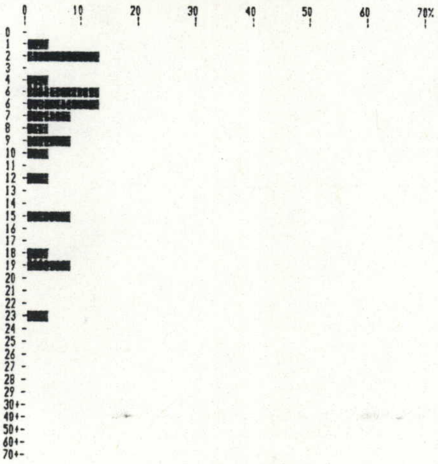
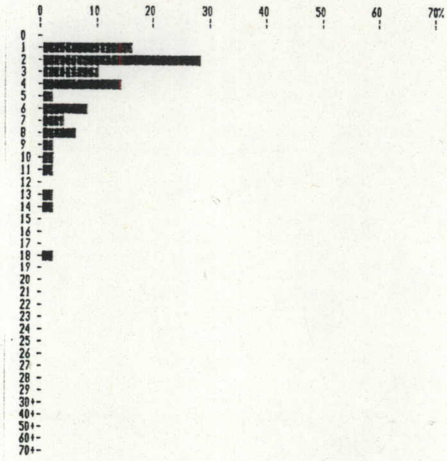

Character: Peduncle of inflorescence unit
Species
Dicliptera
1
2
3
4
5.1
5.2
6
7.1
7.2
8
9
10
11
12
13
14
15
Peristrophe
1
2
3
4
5
6
7
8
9
0
10
20
30
40

Figure 8a: Length of Inflorescence Axes. Horizontal scale representing frequencies as percentages, vertical scale represents size classes, 0 = 0 - 0,99; 1 = 1 - 1,99; etc. 30+ = 30 - 39,99; 40+ = 40 - 49,99; etc. Taxa and sample size (n) as indicated above each graph.

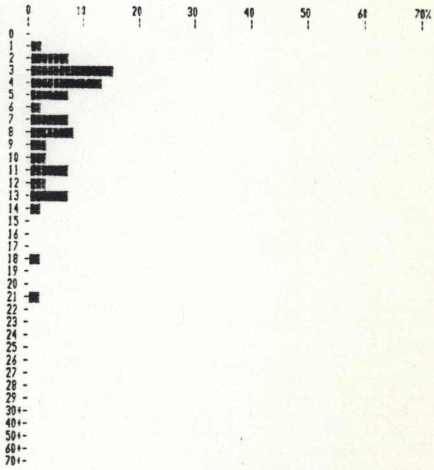
Peristrophe grandibracteata n = 24



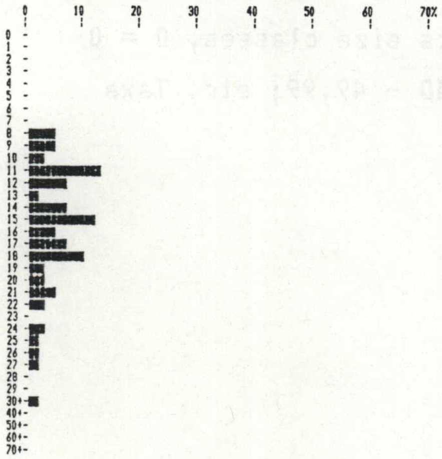
Peristrophe hereroensis n = 50



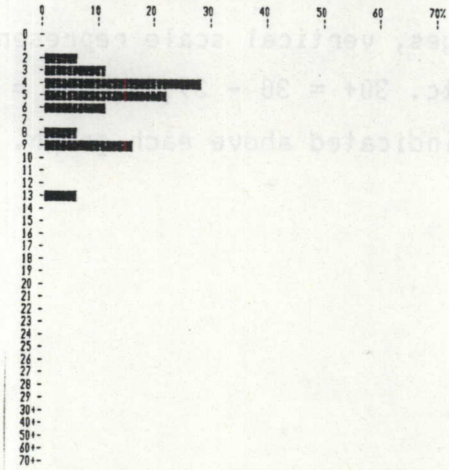
Peristrophe sp. 1 n = 46



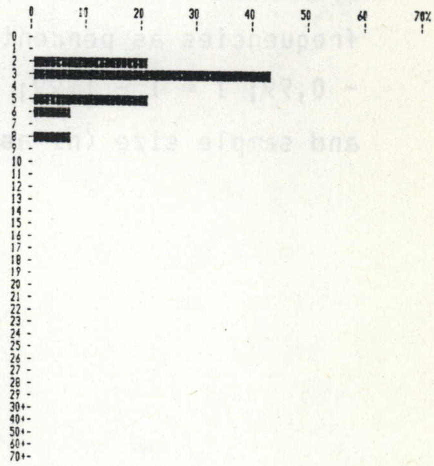
Peristrophe paniculata n = 60



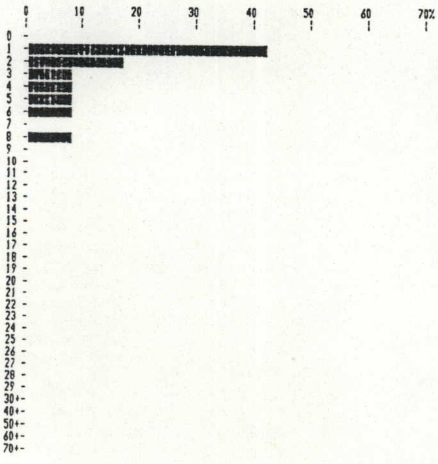
Peristrophe transvaalensis n = 18



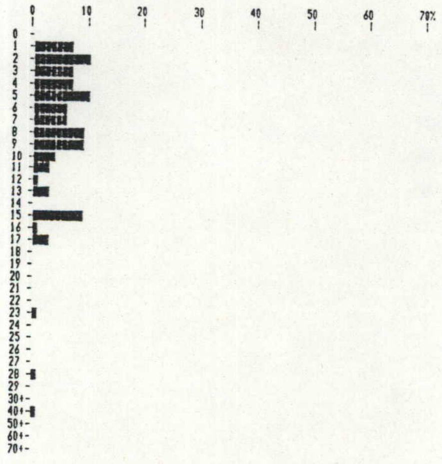
Peristrophe cliffordii n = 14



Peristrophe gillilandiorum n = 12



Peristrophe kotschyana n = 69



Peristrophe cernua n = 341

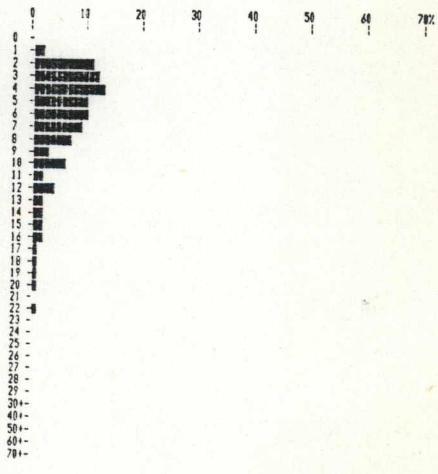


Figure 8b: Length of Inflorescence Axes. Horizontal scale representing frequencies as percentages, vertical scale represents size classes, 0 = 0 - 0,99; 1 = 1 - 1,99; etc. 30+ = 30 - 39,99; 40+ = 40 - 49,99; etc. Taxa and sample size (n) as indicated above each graph.

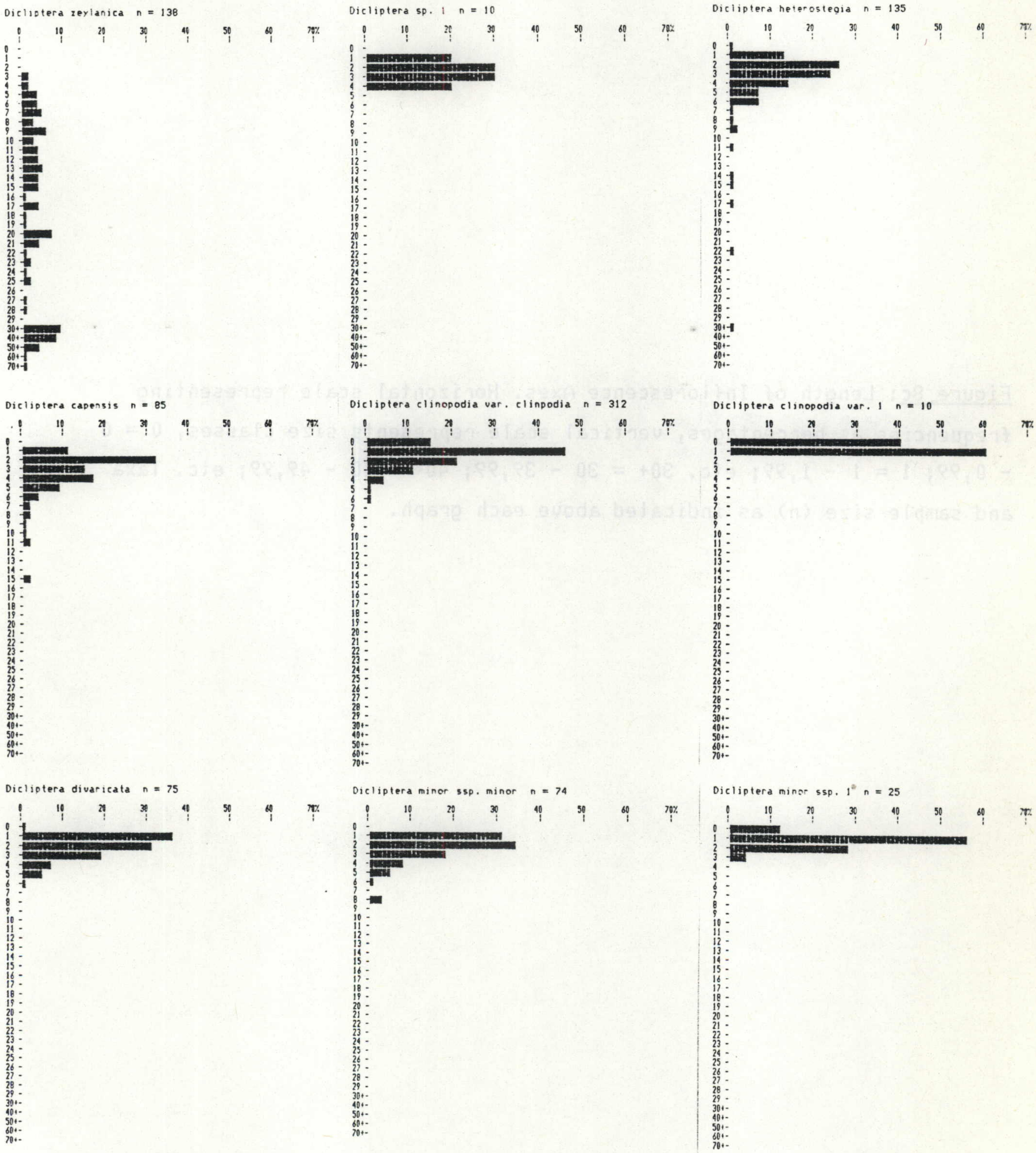


Figure 8c: Length of Inflorescence Axes. Horizontal scale representing frequencies in percentages, vertical scale represents size classes, 0 = 0 - 0,99; 1 = 1 - 1,99; etc. 30+ = 30 - 39,99; 40+ = 40 - 49,99; etc. Taxa and sample size (n) as indicated above each graph.

Figure 8c: Length of Inflorescence Axes. Horizontal scale representing frequencies as percentages, vertical scale represents size classes, 0 = 0 - 0,99; 1 = 1 - 1,99; etc. 30+ = 30 - 39,99; 40+ = 40 - 49,99; etc. Taxa and sample size (n) as indicated above each graph.

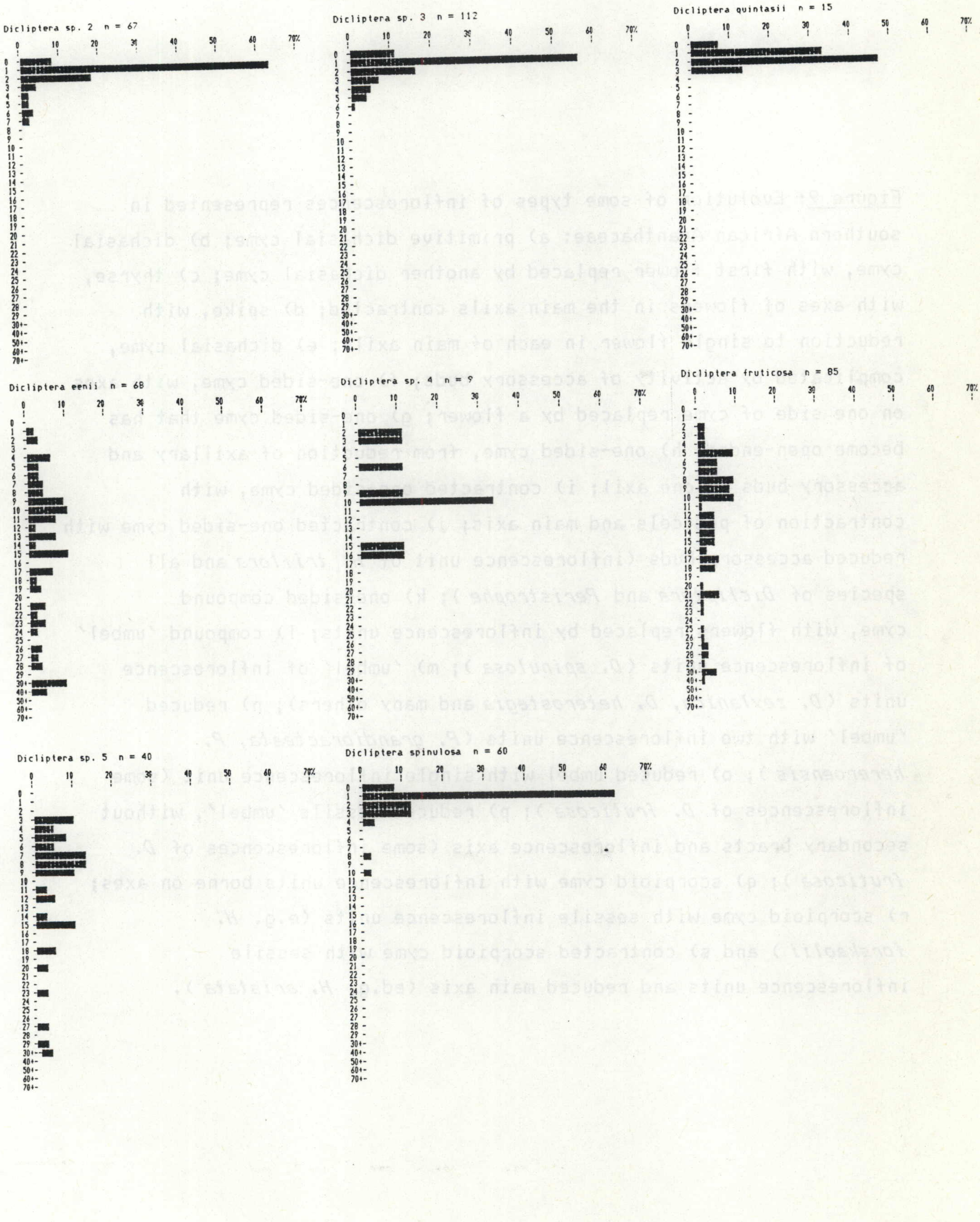
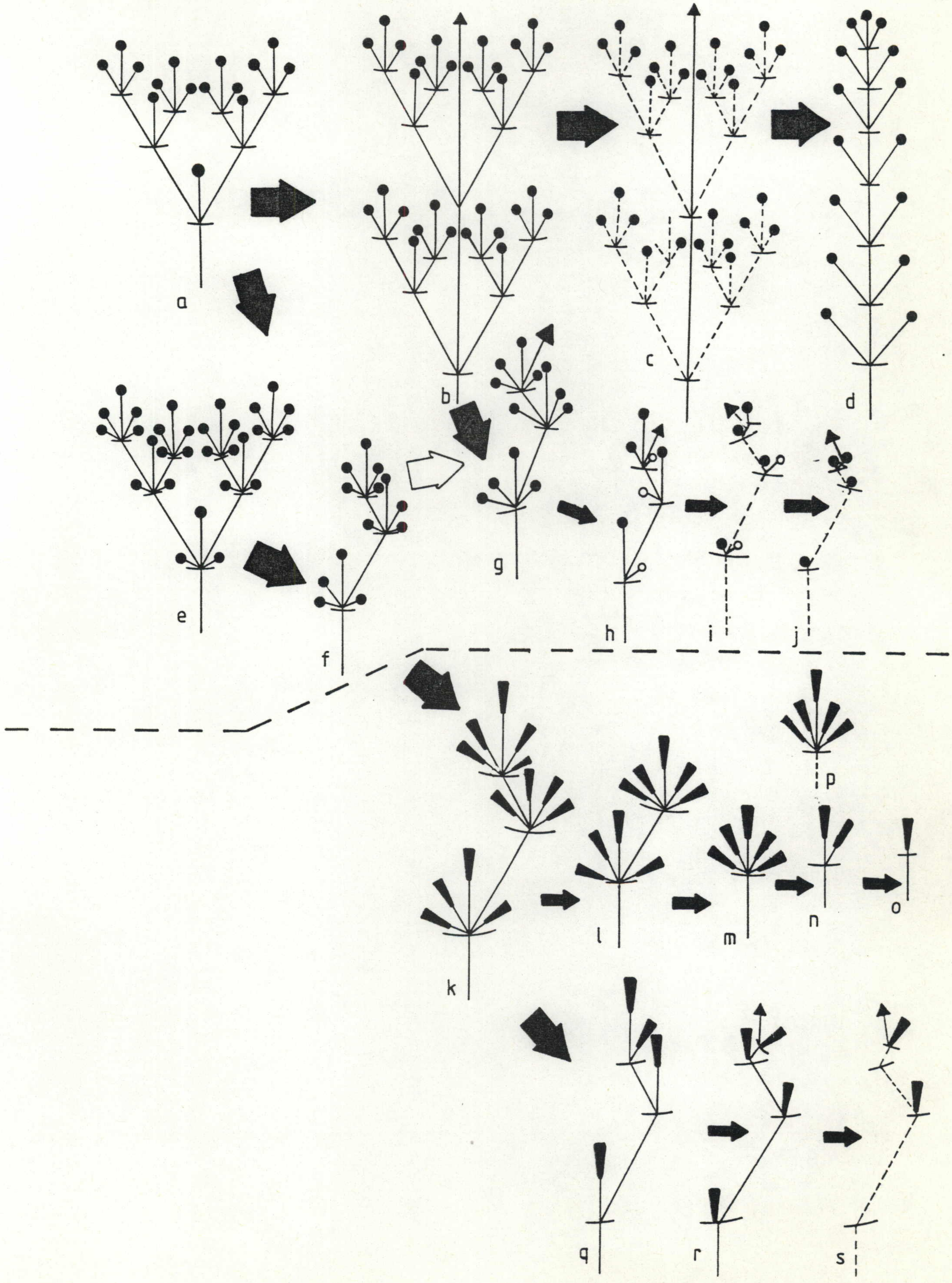

Dicliptera sp. 2 n = 67
Dicliptera sp. 3 n = 112
Dicliptera quintasii n = 15
Dicliptera eenii n = 68
Dicliptera sp. 4 n = 9
Dicliptera fruticosa n = 85
Dicliptera sp. 5 n = 40
Dicliptera spinulosa n = 60
0 10 20 30 40 50 60 70%

Figure 9: Evolution of some types of inflorescences represented in southern African Acanthaceae: a) primitive dichasial cyme; b) dichasial cyme, with first flower replaced by another dichasial cyme; c) thyrse, with axes of flowers in the main axils contracted; d) spike, with reduction to single flower in each of main axils; e) dichasial cyme, complicated by activity of accessory buds; f) one-sided cyme, with axes on one side of cyme replaced by a flower; g) one-sided cyme that has become open-ended; h) one-sided cyme, from reduction of axillary and accessory buds in one axil; i) contracted one-sided cyme, with contraction of pedicels and main axis; j) contracted one-sided cyme with reduced accessory buds (inflorescence unit of *H. triflora* and all species of *Dicliptera* and *Peristrophe*); k) one-sided compound cyme, with flowers replaced by inflorescence units; l) compound 'umbel' of inflorescence units (*D. spinulosa*); m) 'umbel' of inflorescence units (*D. zeylanica, D. heterostegia* and many others); n) reduced 'umbel' with two inflorescence units (*P. grandibracteata, P. hereroensis*); o) reduced umbel with single inflorescence unit (some inflorescences of *D. fruticosa*); p) reduced sessile 'umbel', without secondary bracts and inflorescence axis (some inflorescences of *D. fruticosa*); q) scorpioid cyme with inflorescence units borne on axes; r) scorpioid cyme with sessile inflorescence units (e.g. *H. forskaolii*) and s) contracted scorpioid cyme with sessile inflorescence units and reduced main axis (ed.g. *H. aristata*).



a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s

putative primitive inflorescence types a, b, e, f, g and k have not yet been found in the southern African acanthaceous flora, it is unlikely that so many cymose inflorescences would have arisen from any other primitive type of inflorescence.

The inflorescences of *Dicliptera, Peristrophe* and *Hypoestes* are interesting as they comprise inflorescence units unlike the inflorescences of any other genera in southern Africa. The sequence a, e, f, g, h, i, j in fig. 9 shows the path of evolution of the primitive inflorescence unit (fig. 4a). The path of evolution must have come through the the complicated dichasium (fig. 9e), because the accessory buds are active in some species of *Hypoestes* (Balkwill & Getliffe Norris, 1985). Inflorescence units present in the southern African species of these genera have evolved from the form in fig. 4a (where the tertiary and quaternary bracts of the axillary and accessory flowers are decussate) to the form in fig 4b, where one of the quaternary bracts of each of these flowers has been displaced, so that it is subtended by one of the tertiary bracts of the same flower. Inflorescence units with this form occur in *H. triflora*, although in many specimens it was found that the activity of the accessory bud was lost, so that the type of inflorescence in fig. 4c occurs. This latter form occurs in all species of *Peristrophe* and *Dicliptera* in southern Africa and is relatively primitive, if compared with that in *H. forskaolii* and *H. aristata*. In *H. forskaolii*, the bud in the axils of the axillary and accessory buds is lost (fig. 4d) and, in some cases, the activity of the accessory bud is lost as well (fig. 4e). In *H. aristata* the activity of the axillary and accessory buds is lost (fig. 4f) and this is the most derived inflorescence unit in the southern African Diclipteriinae.

Within *Peristrophe* and *Dicliptera*, the peduncles of the inflorescence units are retained, as are the acccessory buds in the 'umbels' of many species of *Dicliptera*. In *Hypoestes, H. triflora* maintains this arrangement of inflorescence units, but in *H. forskaolii* and *H. aristata* the accessory buds and one of the axillary buds are lost and the inflorescences become open-ended. Thus the inflorescences are one-sided and continuous in these species. The axes between inflorescence units are shortened in *H. forskaolii* (fig. 9r) and totally reduced in *H. aristata* (fig. 9s). Within *Peristrophe*, the accessory buds in the 'umbels' function very rarely, as in some plants of *P. kotschyana* and *P. cernua*. More species of *Peristrophe* have compounded 'umbels' than do species of Dicliptera. There is only one annual species in *Peristrophe* and one in *Dicliptera*. These two annuals have a greater degree of compounding in their inflorescences than any of the other species in these two genera.

Although the lengths of inflorescence axes of many species overlap, it is evident from figs. 6 & 8 that there are statistically significant differences between the range of lengths displayed by some species, so that these values have been used in the key to species of *Dicliptera*. *D. fruticosa, D. sp. 4* and *D. eenii* are separated from *D. sp. 3, D. sp. 2, D. quintasii, D. divaricata, D. minor* and *D. clinopodia*. The validity of this is evident in figs. 6 & 8. The length of the peduncle of the inflorescence unit may be useful to confirm the identification of specimens that are keyed with difficulty.

Conclusion

The inflorescences of *Peristrophe, Dicliptera* and *Hypoestes* are very similar to one another and to the inflorescence of *Periestes* Baill., a Madagascan genus, and all are unlike those of the rest of the Justicieae. This supports the view that these genera belong in a subtribe, Diclipter inae, distinct from the other subtribes in the tribe Justicieae. The inflorescence with its inflorescence units is highly derived, and this suggests that the subtribe Diclipter inae is an advanced one. The arrangement of inflorescence units and of 'umbels' shows variation within the genera, so that the arrangements show characters helpful in distinguishing between species and provides characters that are useful in the key to the species of *Dicliptera*. The lengths of the inflorescence axes and of the peduncles of inflorescence axes show similar patterns of variation and are useful to distinguish between species of *Dicliptera*.

CHAPTER 4
MORPHOLOGY OF BRACTS

Introduction

Bracts have long been used as a taxonomic character in the Acanthaceae (Nees, 1847 & Clarke, 1901). Within the genera *Peristrophe, Dicliptera* and *Hypoestes*, although the bracts have frequently been used as taxonomic characters, there has been no definition of the different kinds of bracts, so that descriptions of these characters are sometimes difficult to understand. The terms primary, secondary, tertiary and quaternary bracts have been adopted throughout this discussion. Illustrations in fig. 3 define these terms.

Materials and Methods

Bracts have been studied on living material, on herbarium sheets and on herbarium material that had been softened by boiling in water. Secondary bracts of *D. clinopodia* var. *clinopodia* were cleared by the method (for difficult material) advocated by O'Brien & von Teichman (1974), mounted on microscope slides in glycerol and used as negatives in a photographic enlarger (du Plessis & van Wyk, 1982). The prints were all made to the same magnification and the drawings in fig. 12 were made from the prints. In order to produce plate 3, inflorescences from herbarium material were boiled in water and photographed in a petri dish of water with a Wild Photomacroscope M400 with a Wild Photoautomat MPS55 Photographic System. Measurements and calculations were made in the same way as described for the inflorescence axes in the previous chapter.

Observations

Primary bracts

The primary bracts are foliage leaves that subtend inflorescence axes, so that the variation in size, shape and texture is the same as that described for the leaves in chapter 2.

Secondary bracts

The length of the secondary bracts of species of *Peristrophe* and

Dicliptera ranges between 1 mm (in *D. fruticosa*) and 25 mm (in *P. hereroensis*) (fig. 10), while the width ranges between 0,2 mm (in many species) and 7,6 mm (in *P. hereroensis*) (fig. 11). Within *Dicliptera* the lengths and breadths of the secondary bracts of different species show few significant differences. *D. sp. 4* does, however, differ conspicuously from *D. eenii* with respect to these characters (figs. 10 & 11). In figs. 10 & 11, it can be seen that there is a great deal of variation in the length and breadth of the secondary bracts of *D. clinopodia* var. *clinopodia*. This variation correlates with geographical distribution, as shown in fig. 12. *D. quintasii*, which occurs in Zululand, where *D. clinopodia* var. *clinopodia* has broad secondary bracts, has narrow secondary bracts. Within *Peristrophe*, the secondary bracts are conspicuously larger in *P. grandibracteata* and *P. hereroensis* than in any other species (figs. 10, 11 & 13) and conspicuously shorter in *P. cliffordii* Balkwill than in any other species (fig. 10).

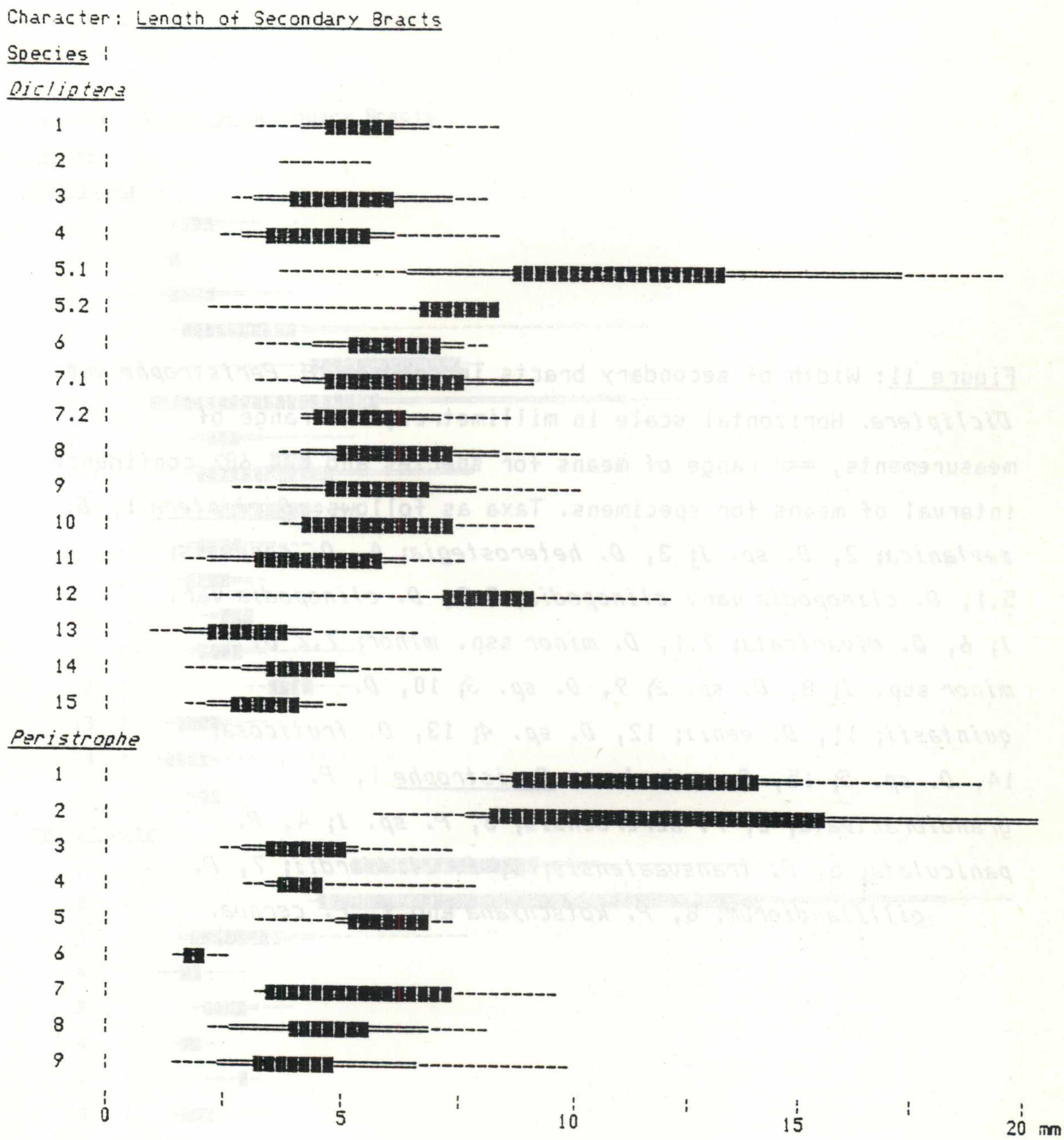
The secondary bracts of most species are green and narrowly lanceolate, but in some plants of *D. clinopodia* var. *clinopodia*, they are bicoloured with white areas ('windows') at their bases and green or purple tips. In *P. grandibracteata* and *P. hereroensis* the secondary bracts are green and ovate (fig. 13b & g) and in *P. sp. 1*, although the secondary bracts are narrowly lanceolate (fig. 13l & q), they are often membranous.

Tertiary bracts

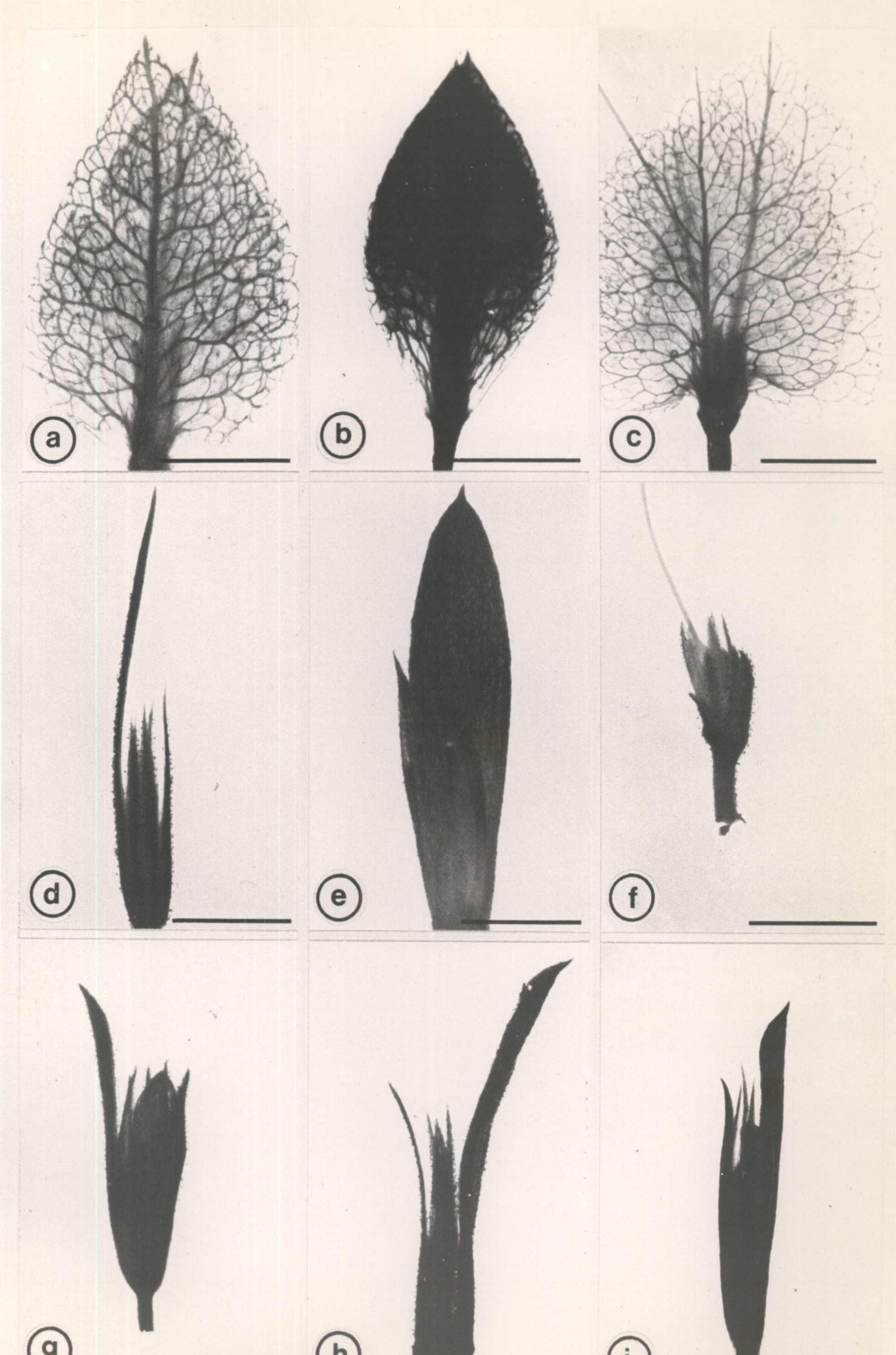
The lengths of the tertiary bracts range between 3 mm (*P. cliffordii*) and 28 mm (*D. clinopodia* var. *clinopodia*) (fig. 14). Within *Dicliptera*, the tertiary bracts of *D. fruticosa* and *D. spinulosa* are conspicuously shorter than those of *D. eenii*. *P. cliffordii* has tertiary bracts conspicuously shorter than those of other species (excepting *D. minor*) and those of *D. sp. 4* are conspicuously longer than those of *D. eenii*. *P. cliffordii* has tertiary bracts conspicuously shorter than those of any other species of *Peristrophe* (fig. 14 & plate 3c) and *P. gillilandiorum* has tertiary bracts conspicuously shorter than most other species (excepting *P. cliffordii*) (fig. 14 & plate 3d).

The widths of the tertiary bracts fall into three categories: 2,25 mm and

<u>Figure 10</u>: Length of secondary bracts in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ███ 68% confidence interval of means for specimens. Taxa as follows: <u>*Dicliptera*</u> 1, *D. zeylanica*; 2, *D. sp. 1*; 3, *D. heterostegia*; 4, *D. capensis*; 5.1, *D. clinopodia* var. *clinopodia*; 5.2, *D. clinopodia* var. *1*; 6, *D. divaricata*; 7.1, *D. minor* ssp. *minor*; 7.2 *D. minor* ssp. *1*; 8, *D. sp. 2*; 9, *D. sp. 3*; 10, *D. quintasii*; 11, *D. eenii*; 12, *D. sp. 4*; 13, *D. fruticosa*; 14, *D. sp. 5*; 15, *D. spinulosa*; <u>*Peristrophe*</u> 1, *P. grandibracteata*; 2, *P. hereroensis*; 3, *P. sp. 1*; 4, *P. paniculata*; 5, *P. transvaalensis*; 6, *P. cliffordii*; 7, *P. gillilandiorum*; 8, *P. kotschyana* and 9, *P. cernua*.


Character: Length of Secondary Bracts
Species
Dicliptera
1
2
3
4
5.1
5.2
6
7.1
7.2
8
9
10
11
12
13
14
15
Peristrophe
1
2
3
4
5
6
7
8
9
0
5
10
15
20 mm

<u>Plate 3</u>: Inflorescences of species of *Peristrophe*, showing the relative size and shape of tertiary bracts. a) *P. grandibracteata, Muller 1311* ; b) *P. hereroensis, de Winter 23560 c) P. sp. 1, de Winter 5828* ; d) *P. paniculata, Goldblatt 1929* ; e) *P. transvaalensis, Balkwill 764* ; f) *P. cliffordii, Balkwill 793* ; g) *P. gillilandiorum, Bruce 58* ; h) *P. cernua, Balkwill 168* and i) *P. kotschyana, Balkwill 801*. Scale line represents 4 mm in all cases.


a
b
c
d
e
f
g
h
i

narrower; 4 mm to 6 mm and over 6 mm (fig. 15). The distribution of the species in these three categories is shown in fig. 15. All species of *Dicliptera* (except *D. fruticosa*) have tertiary bracts with three, five or seven veins from the base (fig. 16), while in southern African species of *Peristrophe* there is a single main vein from the base (plate 3). Within *Peristrophe* the tertiary bracts are lanceolate and green (e.g. *P. paniculata*) or ovate, membranous and transparent (e.g. *P. grandibracteata*). The tertiary bracts of *P. grandibracteata* and *P. hereroensis* have cuneate or broadly cuneate bases (fig. 13c & h & plate 3g & h), while those of *P. sp. 1* have very broadly cuneate, reniform or cordate bases (fig. 13m & r & plate 3i). The tertiary bracts of *P. sp. 1* ssp. *1* are proportionally broader than those of *P. sp 1* ssp. *2* (length to breadth ratio between 1,0 and 1,1 in ssp. *1* and 1,38 and 1,52 in ssp. *2*), while the tertiary bracts of *P. sp 1* ssp. *2* are cordate rather than reniform or very broadly cuneate at the base, as are those of *P. sp. 1* ssp. *1*. In *Dicliptera* the tertiary bracts may be green (usually correlated with the broadly ovate or broadly obovate bracts) as in *D. zeylanica* and *D. heterostegia* (fig 16a & b), or the tertiary bracts may be bicoloured with white or translucent areas ('windows') near the base and green or purple tips as in *D. sp. 5* (fig. 16c). The bicoloured bracts are usually narrower than the green and are narrowly ovate, lanceolate, narrowly obovate or oblanceolate. Some species, however, have narrow bracts that are not bicoloured as *D. sp. 4* and *D. fruticosa*.

Material of *P. cernua* collected in the Cape has smaller tertiary bracts than that collected in Natal (fig. 17). Correlated with this difference, is a difference in corolla length and degree of pubescence of leaves. The material from the Cape has shorter corollas and glabrous leaves, while the Natal material has longer corollas and hairier leaves.

Within *D. heterosregia*, there is variation in size, shape, texture and colour of tertiary bracts. Some plants (e.g. *Balkwill 3028*) have smaller bracts than do most other plants. In this and some other specimens, the bracts are usually dry, stiff and purple at the tips. These features are unusual, but are not always correlated and occur sporadically in the same or different populations as plants with the more usual soft, green bracts and sometimes both forms of bracts occur on the

<u>Figure 15</u>: Width of tertiary bracts in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ▓▓▓ 68% confidence interval of means for specimens. Taxa as follows: <u>*Dicliptera*</u> 1, *D. zeylanica*; 2, *D. sp. 1*; 3, *D. heterostegia*; 4, *D. capensis*; 5.1, *D. clinopodia* var. *clinopodia*; 5.2, *D. clinopodia* var. *1*; 6, *D. divaricata*; 7.1, *D. minor* ssp. *minor*; 7.2 *D. minor* ssp. *1*; 8, *D. sp. 2*; 9, *D. sp. 3*; 10, *D. quintasii*; 11, *D. eenii*; 12, *D. sp. 4*; 13, *D. fruticosa*; 14, *D. sp. 5*; 15, *D. spinulosa*; <u>*Peristrophe*</u> 1, *P. grandibracteata*; 2, *P. hereroensis*; 3, *P. sp. 1*; 4, *P. paniculata*; 5, *P. transvaalensis*; 6, *P. cliffordii*; 7, *P. gillilandiorum*; 8, *P. kotschyana* and 9, *P. cernua*.

Character: <u>Width of Tertiary Bracts</u>

<u>Species</u> :

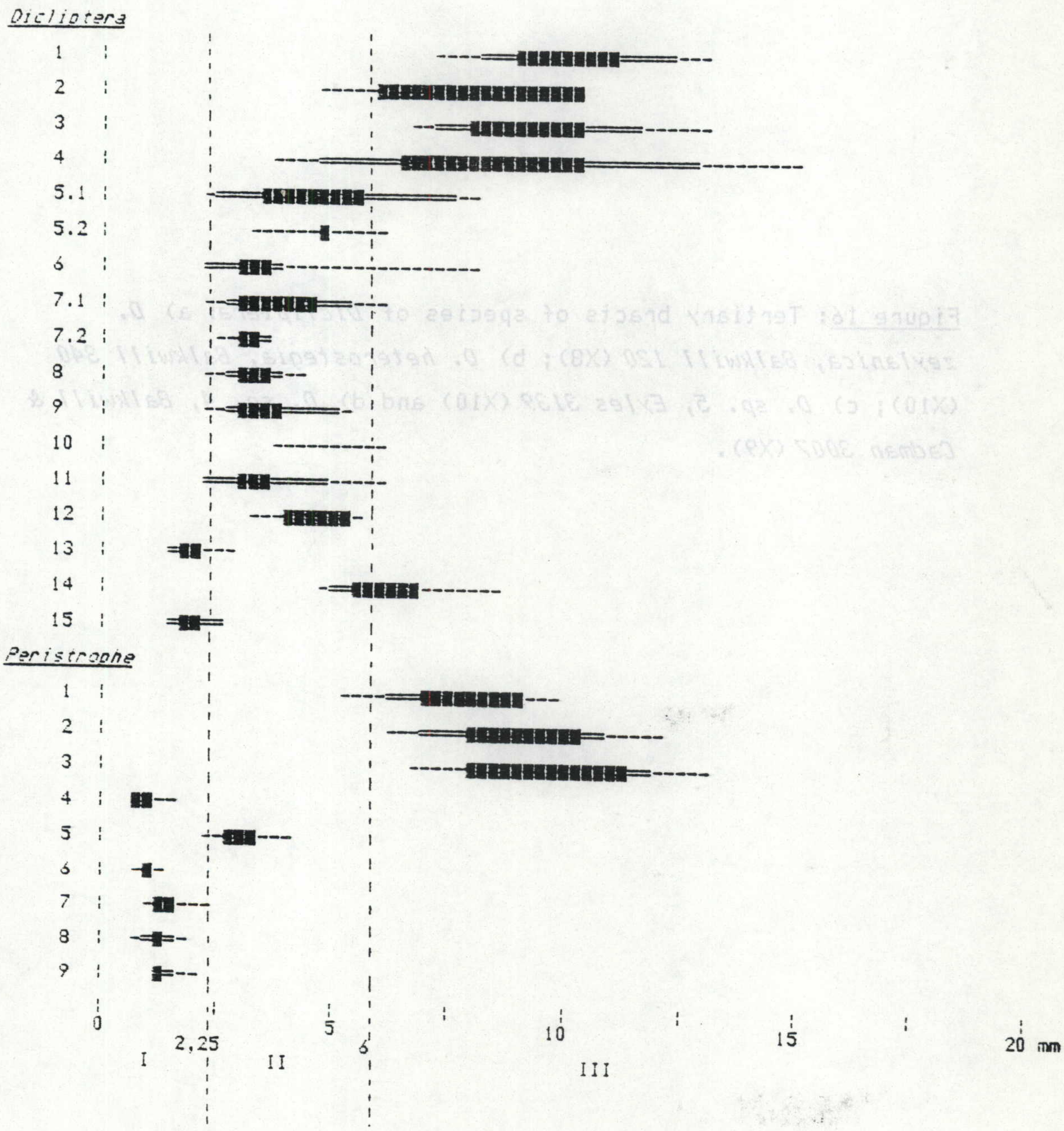


Figure 16: Tertiary bracts of species of *Dicliptera*: a) *D. zeylanica, Balkwill 120* (X8); b) *D. heterostegia, Balkwill 340* (X10); c) *D. sp. 5, Eyles 3139* (X10) and d) *D. sp. 4, Balkwill & Cadman 3007* (X9).

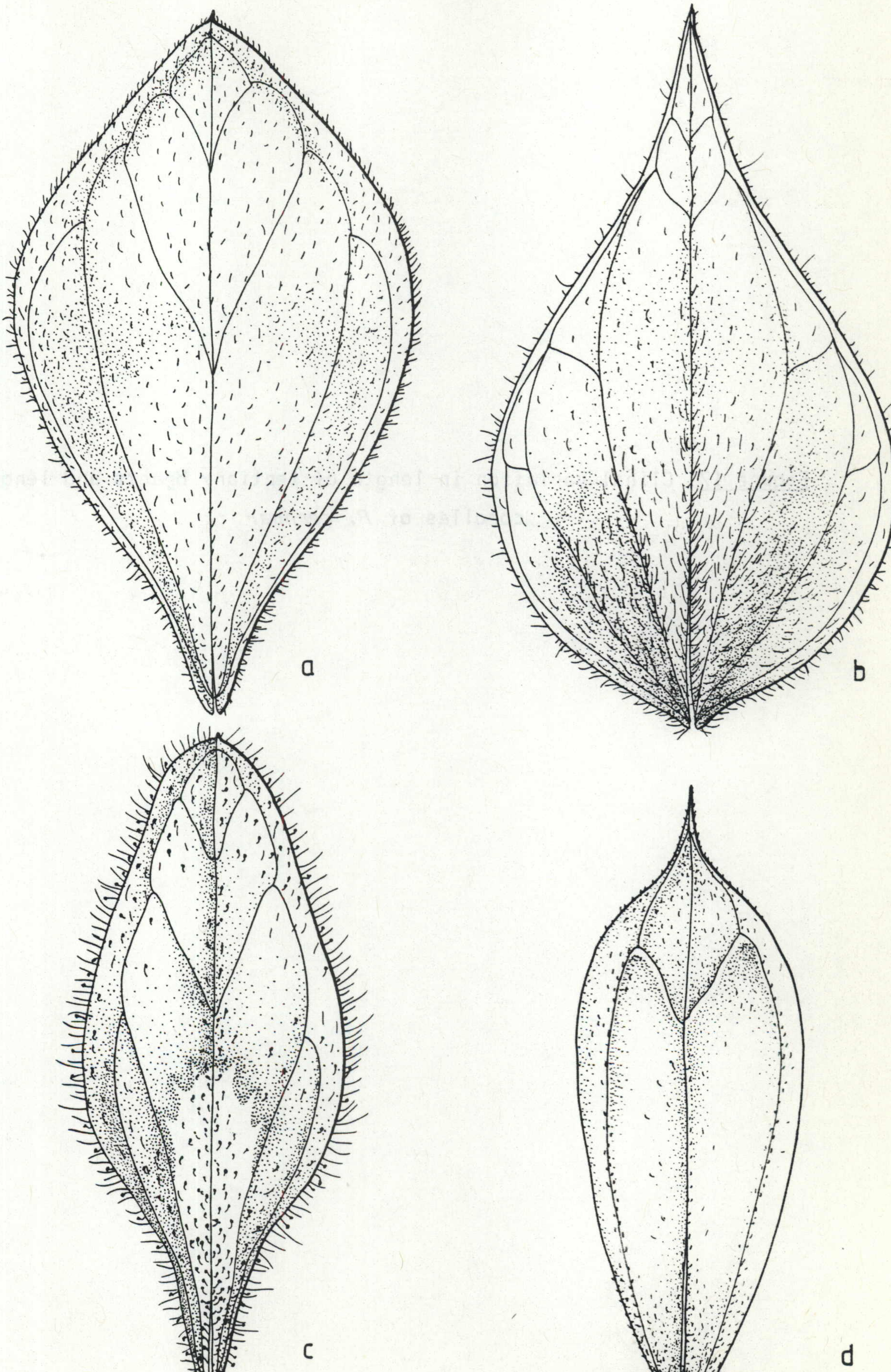

a
b
c
d
M-J.C

Figure 17: Clinal variation in length of tertiary bracts and length of corollas of *P. cernua*.

Clinal Variation in P. cernua

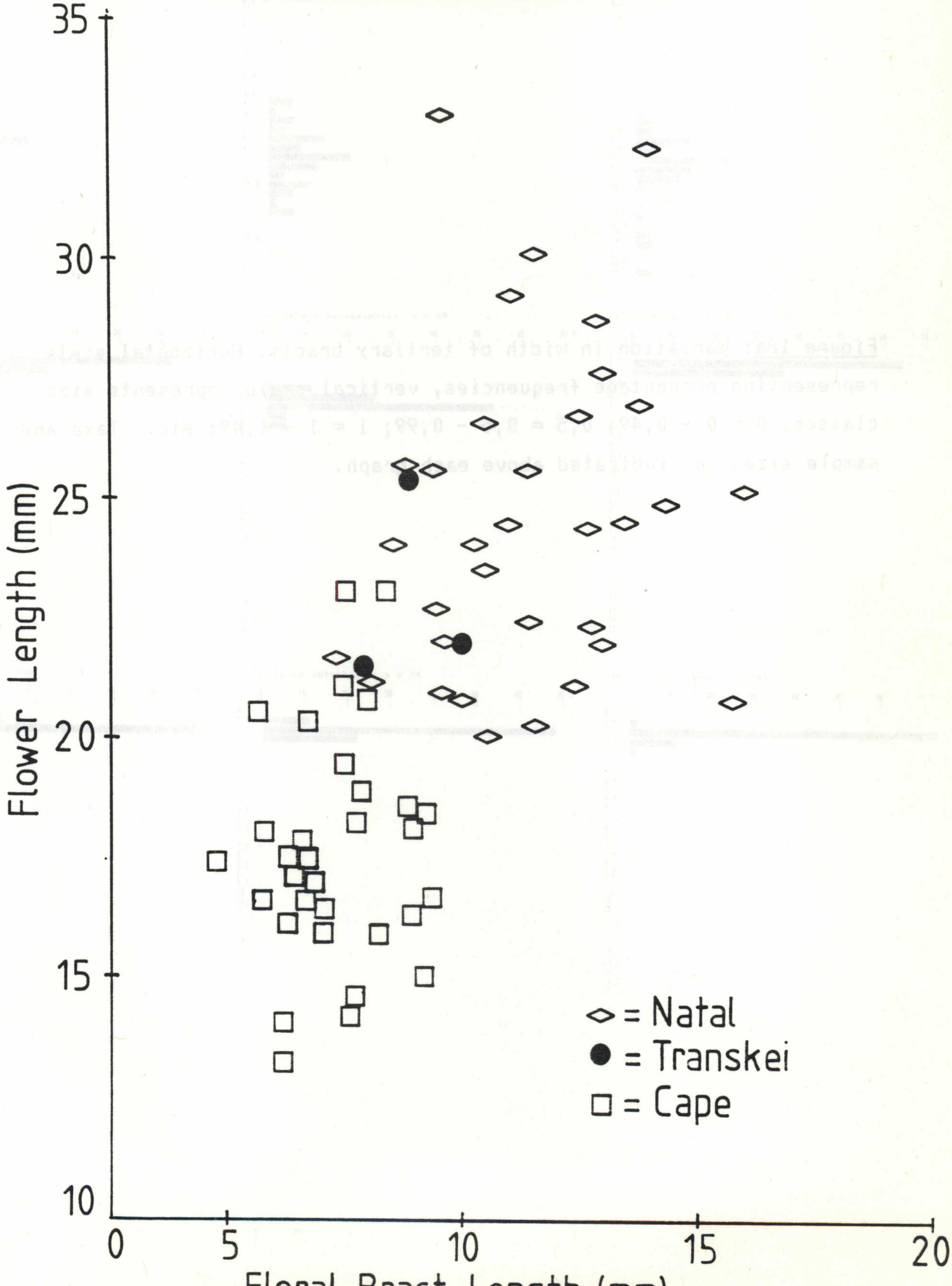
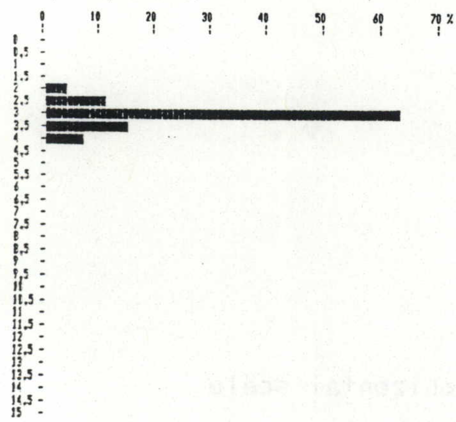
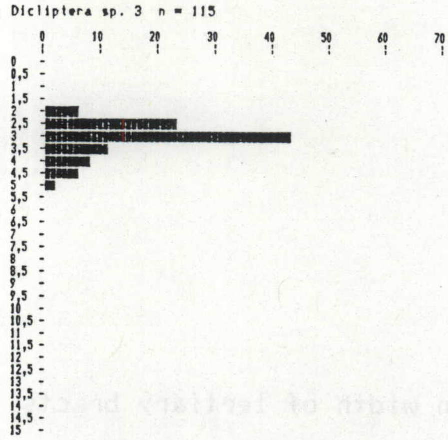


Figure 18c: Variation in width of tertiary bracts. Horizontal scale representing percentage frequencies, vertical scale represents size classes, 0 = 0 - 0,49; 0,5 = 0,5 - 0,99; 1 = 1 - 1,49; etc.. Taxa and sample sizes (n) indicated above each graph.

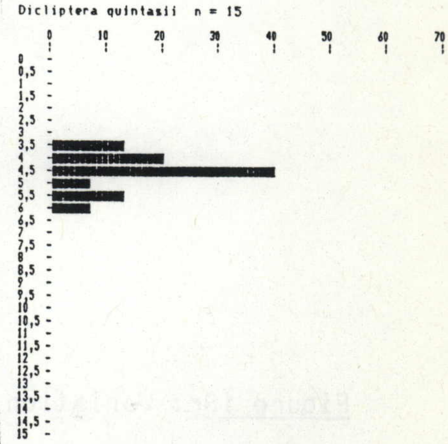
Dicliptera sp. 2 n = 70



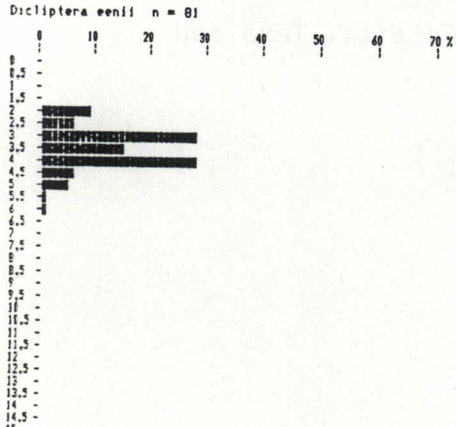
Dicliptera sp. 3 n = 115



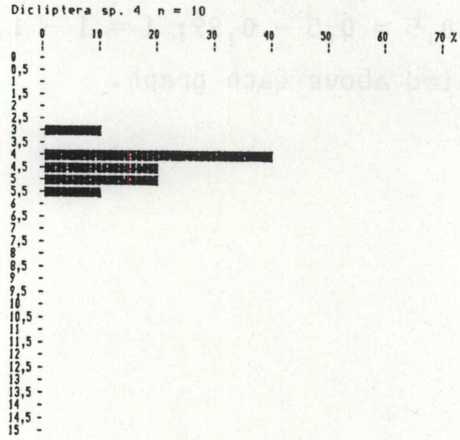
Dicliptera quintasii n = 15



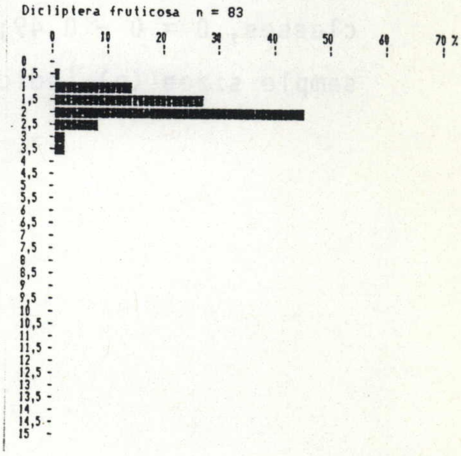
Dicliptera eenii n = 81



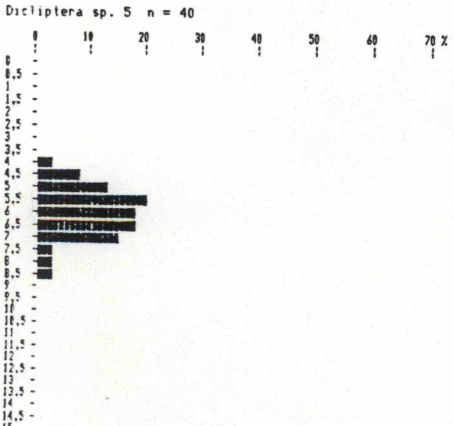
Dicliptera sp. 4 n = 10



Dicliptera fruticosa n = 83



Dicliptera sp. 5 n = 40



Dicliptera spinulosa n = 60

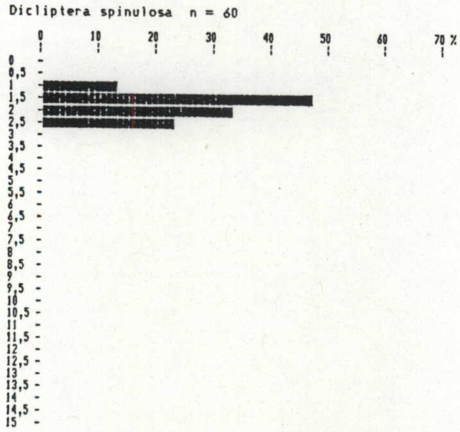


Figure 18c: Variation in width of tertiary bracts. Horizontal scale representing percentage frequencies, vertical scale represents size classes, 0 = 0 - 0,49; 0,5 = 0,5 - 0,99; 1 = 1 - 1,49; etc.. Taxa and sample sizes (n) indicated above each graph.

same plants.

Quaternary bracts

The quaternary bracts of the first flower in an inflorescence unit are similar in size and shape to the tertiary bracts of the axillary flower in most species of *Peristrophe* and *Dicliptera*. In *H. triflora* and *D. zeylanica*, these bracts are similar in length to the smaller of the tertiary bracts of the first flower. In species of *Peristrophe* that have narrow tertiary bracts (e.g. *P. cernua, P. cliffordii* and *P. kotschyana*), the quaternary bracts are similar in size and shape to the tertiary bracts of the first flower. In the species of *Peristrophe* that have broad bracts (e.g. *P. hereroensis*), the tertiary bracts are very much smaller than the tertiary bracts of the first flower, and even smaller than the calyx.

Discussion

Secondary Bracts

The length and breadth of the secondary bracts has been found to be taxonomically useful at the species level. Those of *D. sp. 4* are conspicuously longer than those of *D. eenii*, a species to which it is superficially similar, so that this character can be used to separate these species. *P. hereroensis* and *P. grandibracteata* can be distinguished from *P. sp. 1* (an otherwise very similar species) by means of their larger, broader, green secondary bracts. *P. cliffordii* can be distinguished from any other species of *Peristrophe* by its shorter secondary bracts.

Within *D. clinopodia* var. *clinopodia*, there is considerable variation in the size and shape of the secondary bracts. On the coastal plain of Mozambique and Natal, the bracts are broad and bicoloured (fig. 12a - m), but in the mountains of the Transvaal and Swaziland, the secondary bracts are much narrower (fig. 12B - H). Although the distinction between these two kinds of bracts is quite clear in these northern areas, the distinction becomes less clear further south, until the two forms are almost indistinguishable in the southern parts of their range. It is on the basis of this variation in the shape of the secondary bracts that the material of *D. clinopodia* var. *clinopodia* has been split into two forms. *D. quintasii*, which occurs in sand forests in Zululand, has narrow secondary bracts, while *D. clinopodia* has broad secondary bracts in that area (fig. 12e, f & g), so that this provides another character with which to distinguish these species.

Tertiary Bracts

The tertiary bracts of the first flower in the inflorescence unit are most likely the bracts to which Nees (1847) and Clarke (1901) referrred in their accounts of *Peristrophe* and *Dicliptera*. It has been assumed by some botanists (Schinz, 1916 & Clarke, 1901) that the width of the tertiary bracts can be used as a generic character to distinguish between *Dicliptera* and *Peristrophe*. From figs. 15 & 18, it can be seen that this is erroneous and this assumption has led to the misclassification of *P. hereroensis* by Schinz (1916) and *P. transvaalensis* by Clarke (1901). For the same reason, material of *D. fruticosa* was misidentified as *P. bicalyculata* (Retz.) Nees (now *P. kotschyana*) in most southern African herbaria and had thus escaped notice until recently. Keys based mainly on the characters of the tertiary bracts, with the aid of some other characters, can separate the southern African members of *Dicliptera* from those of *Peristrophe*. Two such keys are presented at the end of this chapter.

H. triflora, D. zeylanica and *P. montana* have similar tertiary bracts with three, five or seven veins from the base. It seems that in the course of evolution in *Hypoestes*, the tertiary bracts have become narrower and have fused together for some of their length (e.g. *H. forskaolii*). In *Dicliptera*, besides the group with primitive broad tertiary bracts (e.g. *D. zeylanica, D. heterostegia* and *D. sp. 1*) there are two derived groups: one with narrower bicoloured bracts with translucent areas ('windows') near their bases (e.g. *D. clinopodia, D. eenii* and *D. minor*) and one with narrow green bracts (e.g. *D. sp. 4* and *D. fruticosa*). The evolutionary history of *D. sp. 4* is uncertain, so that it is not known from which of the other groups it may have evolved, although it is possible that it may have evolved directly from the putatively primitive group that includes *D. zeylanica*. *D. fruticosa*, on the other hand, is closely related to *D. eenii* and must have evolved from that species or from a common ancestor. During the course of this evolution, the bracts have become much smaller, and in the course of this reduction, the white areas at the base of the bract have been lost. *D. fruticosa* seems then to be a derived species.

Within *Peristrophe*, it seems that the bracts have evolved from forms such as *P. montana* and *P. tinctoria* towards a form such as that of *P. speciosa*, where the bracts are slightly narrower, and the central vein is beginning to dominate over the others that come from the base. From this form, evolution seems to have diverged along two pathways: one with a continued narrowing of the tertiary bracts to produce forms such as *P. cernua* and the other with a secondary widening of the bracts with membranous material, so that a broad membranous bract is formed, with a single vein from the base, such as the bracts of *P. grandibracteata*. These three types of bract are sufficiently different from one another to support recognition of the groups at the sectional level. This is corroborated by the correlation with other characters: the species with broad green bracts with three or five veins from the base have flowers that are much larger than those of the species in the other two groups, while the species with membranous bracts have capsules that are different from those of the species in the other two groups.

Tertiary bracts have also provided characters that could be used in the keys to species of *Peristrophe* and *Dicliptera* and have been helpful in distinguishing between the subspecies of *P. sp. 1*.

The variation in the shape, texture and colouration of the tertiary bracts of *D. heterostegia* can only be due to intraspecific variation, as the different shapes, textures and colours may occur on the same plants or within the same populations. Thus, although Klotzsch (1862 - 1864) distinguished *D. mossambicensis* Klotzsch from *D. heterostegia* on the basis of the texture of the tertiary bracts, it has become necessary to place the former in synonomy with the latter.

Some specimens of *D. capensis* have widely ovate bracts and vertically held inflorescences (e.g. *Balkwill 474* and *Galpin 7750*), while others have ovate bracts and horizontally held inflorescences (e.g. *Balkwill 465*). This variation may be the reason that Nees (1841) described the species *D. propinqua* Nees and was the reason that I originally thought that it may have been possible to subdivide *D. capensis* into two taxa. The nature of the variation in other specimens, however, suggests that the forms integrade into one another, and that it would be erroneous to subdivide *D. capensis*.

The variation in the size of the tertiary bracts and flowers between the Natal and Cape populations of *P. cernua* is no doubt the reason that Anderson (1864) described a species *P. natalensis*. From fig. 17, it is evident that there is no discontinuity in the sizes of the tertiary bracts and the flowers, but rather that there is a cline, with the Transkei material, which is geographically intermediate, being morphologically intermediate. Thus it seems appropriate that *P. natalensis* should be placed in synonomy with *P. cernua*.

Quaternary bracts

Although quaternary bracts have not been used taxonomically, it is apparent that their structure is related to their protective function. The genus *Peristrophe* shows this, as the protective function of the narrow tertiary bracts of species such as *P. cernua* is supplemented by the quaternary bracts that are longer and broader than those of species such as *P. hereroensis*, where the tertiary bracts are large and the quaternary bracts minute.

Conclusion

If the different types of bracts present in the inflorescences of *Peristrophe* and *Dicliptera* are defined, then the secondary and tertiary bracts provide very useful taxonomic characters. The variation in the secondary bracts of *D. clinopodia* var. *clinopodia* and the tertiary bracts of *P. cernua* and *D. heterostegia* is such that it must be attributed to intraspecific variation and does not indicate the existence of different taxa.

Characters of the bracts are valuable for the construcion of artificial keys to the species of *Peristrophe* and *Dicliptera*.

Artificial keys to the genera *Peristrophe* and *Dicliptera* based mainly on characters of the tertiary bracts.

Key 1

1) Tertiary bracts broader than 6 mm 2

1a) Tertiary bracts narrower than 6 mm 3

2) Tertiary bracts with 3, 5 or 7 veins from the base *Dicliptera*

2a) Tertiary bracts with only one vein from the base, bracts membranous *Peristrophe*

3) Tertiary bracts narrower than 2,25 mm 4

3a) Tertiary bracts broader than 2,25 mm 6

4) Tertiary bracts bicoloured (with 'windows' at the base), fringed with white hairs and with 3 - 5 veins from the base *D. spinulosa*

4a) Tertiary bracts uniformly green 5

5) Tertiary bracts shorter than 9 mm and stems glabrous or sparsely pubescent between ridges *D. fruticosa*

5a) Tertiary bracts longer than 9 mm or stems densely pubescent between ridges *Peristrophe*

6) Tertiary bracts narrower than 5 mm, green and with only one vein from the base *P. transvaalensis*

6a) Tertiary bracts broader than 5 mm, or bicoloured or with 3, 5, or 7 veins from the base *Dicliptera*

Key 2

1) Tertiary bracts with 3, 5 or 7 veins from the base *Dicliptera*

1a) Tertiary bracts with a single vein from the base 2

2) Tertiary bracts broader than 5 mm *Peristrophe*

2a) Tertiary bracts narrower than 5 mm 3

3) Flowers shorter than 17 mm, lip in lower position shorter than 10 mm *Peristrophe*

3a) Flowers longer than 17 mm, lip in lower position longer than 10 mm 4

4) Tertiary bracts shorter than 9 mm and stems glabrous or sparsely pubescent between ridges *D. fruticosa*

4a) Tertiary bracts longer than 9 mm or stems densely pubescent between ridges *Peristrophe*

CHAPTER 5
FLORAL MORPHOLOGY

Introduction

The morphology of the flower is a very important taxonomic character in most of the Angiosperms and, in the Acanthaceae, is particularly useful in the subdivision of the family. Both Lindau (1895) and Bremekamp (1965) used floral morphology to distinguish subdivisions of the family.

Material and Methods

Flowers of fresh material, herbarium material and preserved material were studied. To compile the tables showing the distribution of characters through the family, at least one southern African member of each genus was dissected and the information gleaned was compared with available literature. Measurements of the corolla were made on dried material and were computed as described for the inflorescence axes in Chapter 3.

Calyx

Observations and Discussion

Table 3 shows the distribution of characters of the calyx throughout the southern African Acanthaceae. It can be seen that the calyces of *Dicliptera* and *Peristrophe* are undifferentiated from the putatatively primitive form of the calyx, which must have been actinomorphic and with the length of the tube less than the length of the free lobes. Although measurements of the calyx may have provided helpful taxonomic characters to distinguish between species, their use would have been impractical because inflorescences have to be dissected in order to measure the calyces, and too many specimens would have been damaged if a statistically viable number had been dissected.

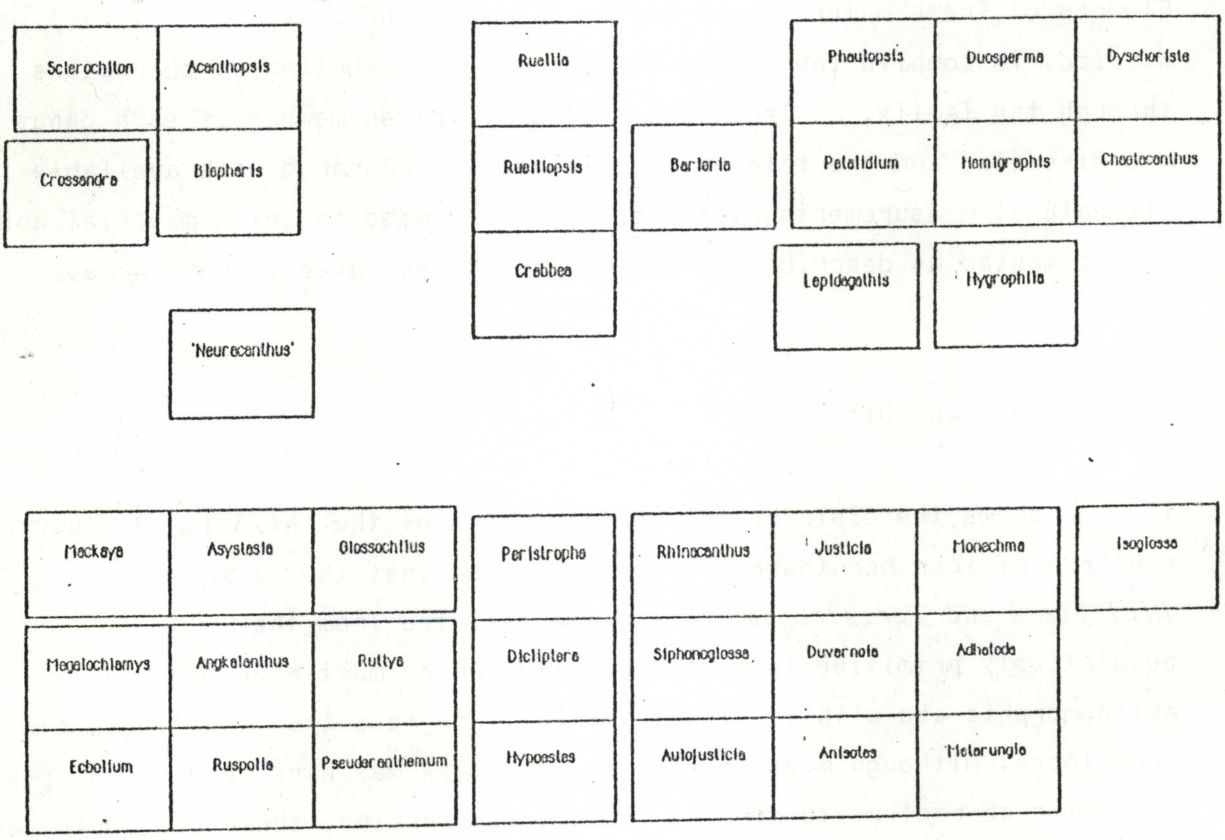
Corolla

Observations

Table 4 shows the distribution of characters of the corolla in the southern African members of the family. Figure 19 shows the distribution

Table 3: Distribution of characters of the calyx in the genera of southern African Acanthaceae.

Genera arranged as in key below, characters as follows: A = actinomorphic, B = bilabiate, IR = irregular, SA = subactinomorphic, SB = sub-bilabiate, SZ = sub-zygomorphic, T = tubular for more than half the length, (T) = sometimes tubular for more than half the length, Z = zygomorphic, 1/4 = one lip with a single lobe - one lip with four lobes, 2/2 = with two lips each of two lobes and numbers on right hand side of blocks = number of lobes.



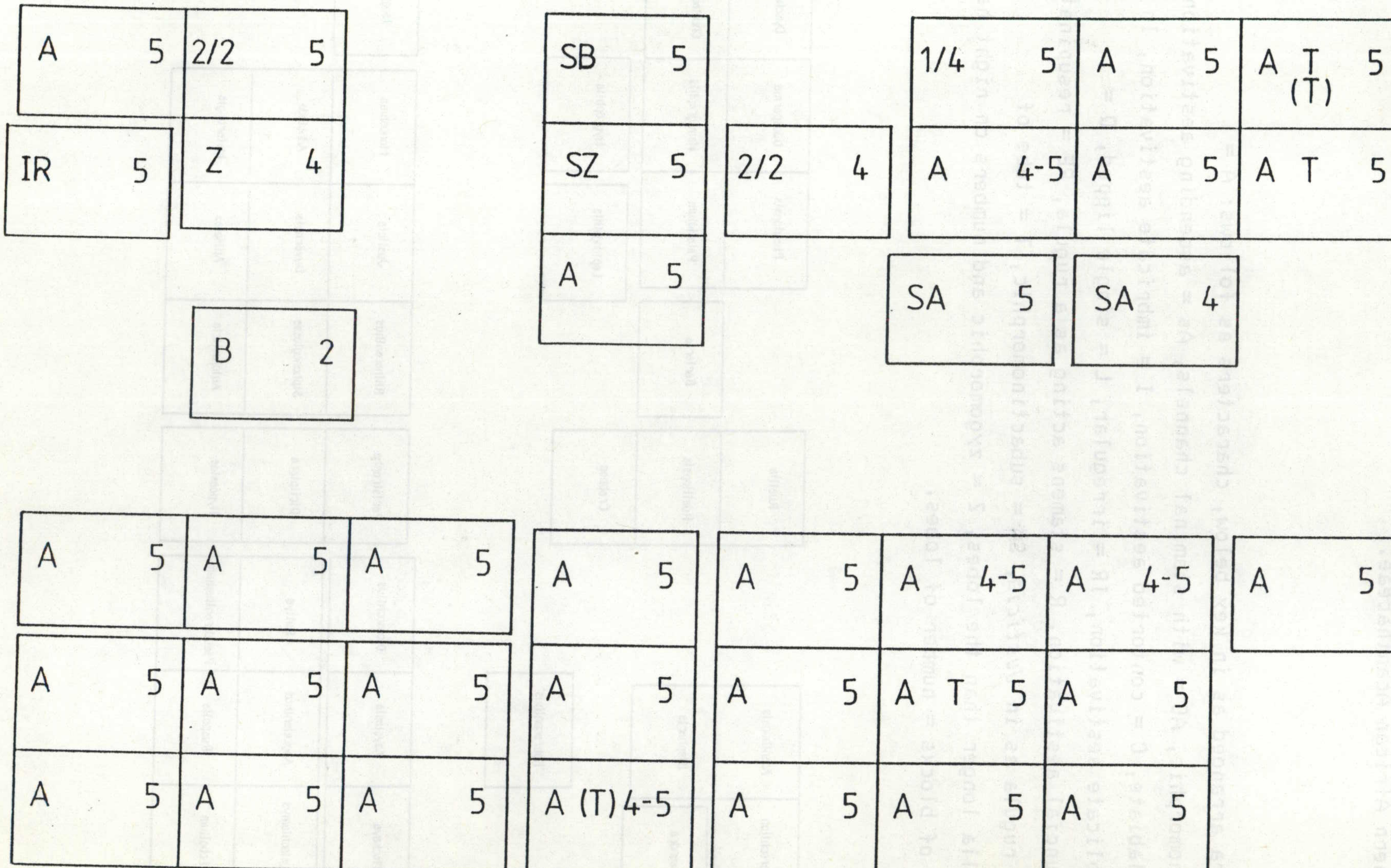
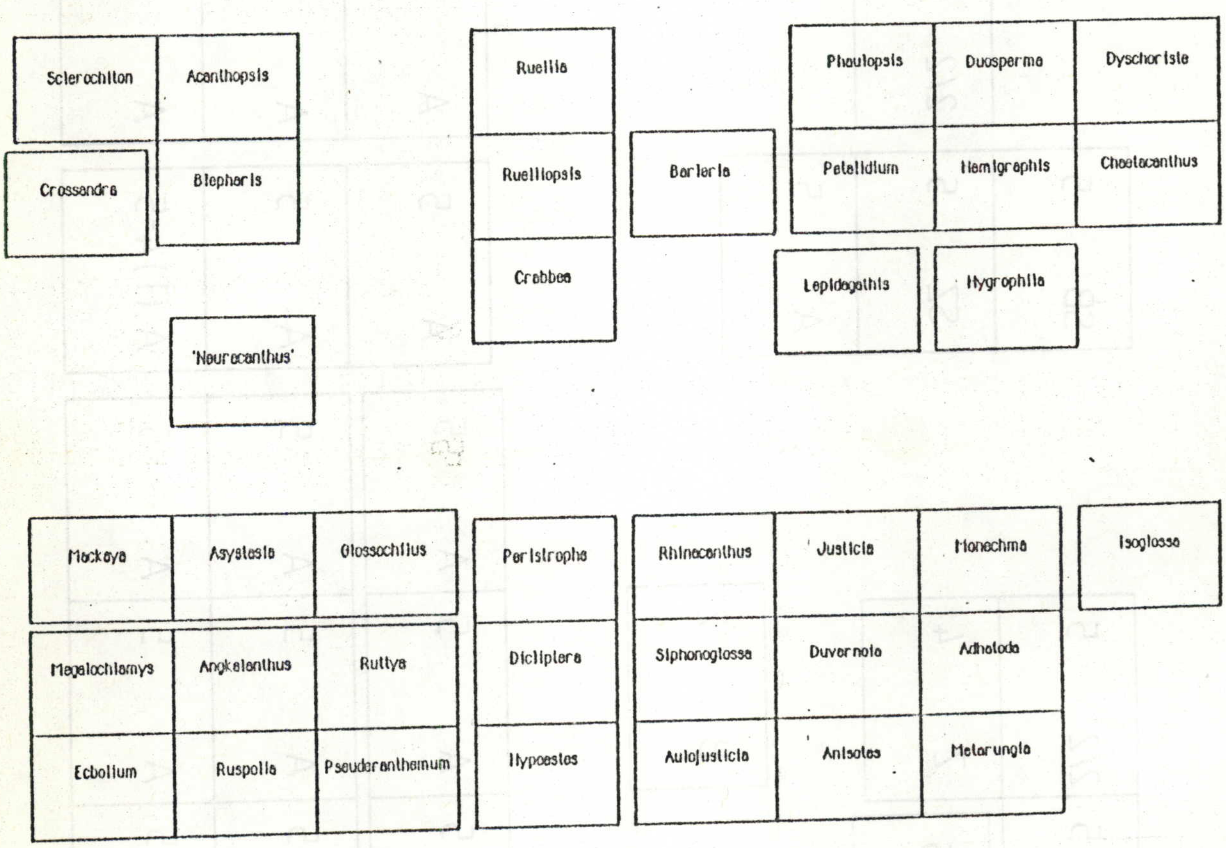

A 5
2/2 5
IR 5
Z 4
B 2
SB 5
SZ 5
A 5
2/2 4
1/4 5
A 5
A T (T) 5
A 4-5
A 5
A T 5
SA 5
SA 4
A 5
A 5
A 5
A 5
A 5
A 5
A 5
A 5
A 5
A 5
A 5
A (T) 4-5
A 5
A 4-5
A 4-5
A 5
A 5
A T 5
A 5
A 5
A 5
A 5

Table 4: Distribution of characters of the corolla in the genera of southern African Acanthaceae.

Genera arranged as in key below, characters as follows: A = actinomorphic, AC = with staminal channels, As = ascending aestivation, B = bilabiate, C = contorted aestivation, I = imbricate aestivation, In = induplicate aestivation, IR = irregular, L = single lipped, Q = quinuncial aestivation, R = stamens acting as a rugula, RE = resupinate, RJ = rugula as in *Justicia*, SA = subactinomorphic, T = tube of corolla longer than the lobes, Z = zygomorphic and numbers on right hand side of blocks = number of lobes.



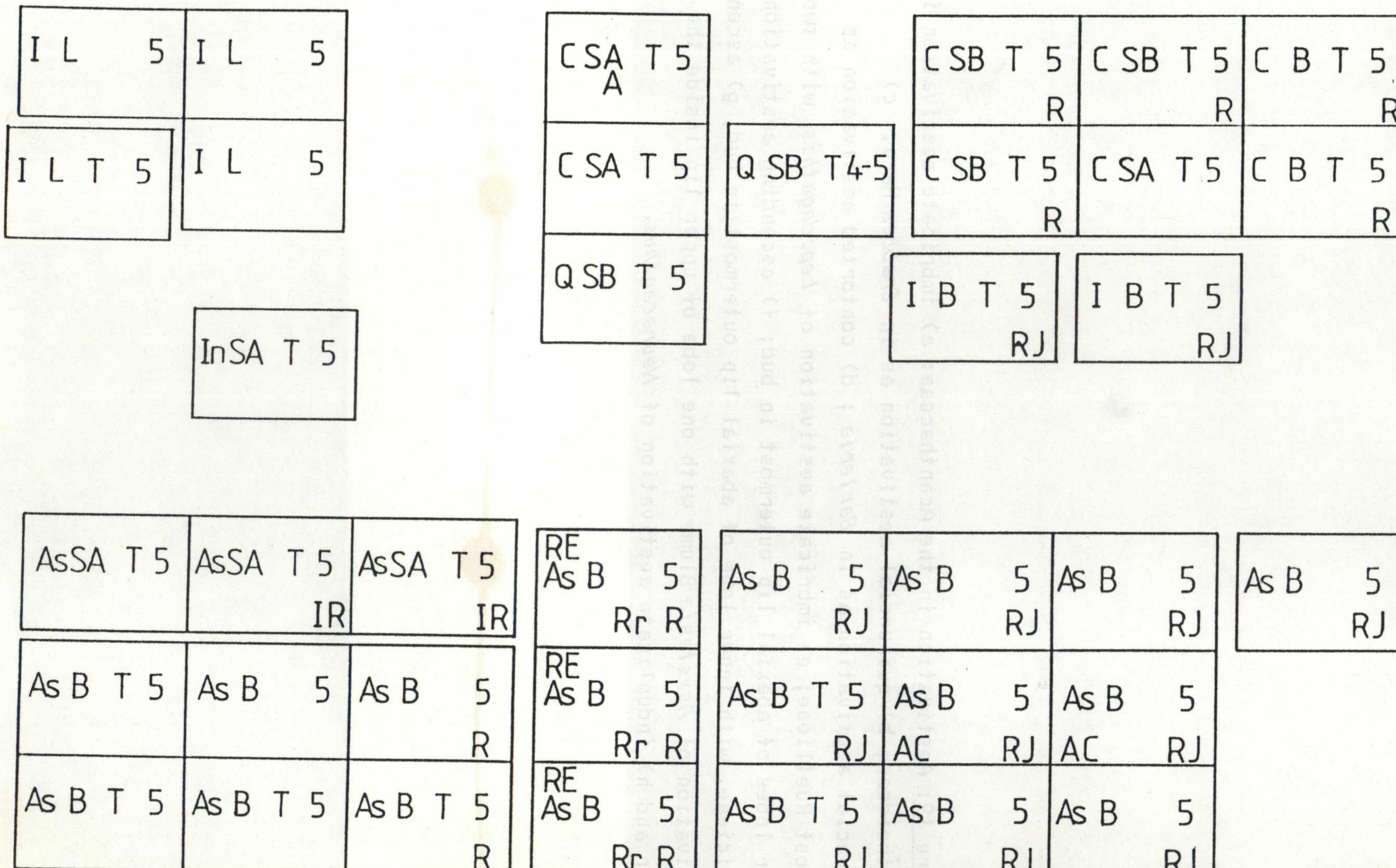
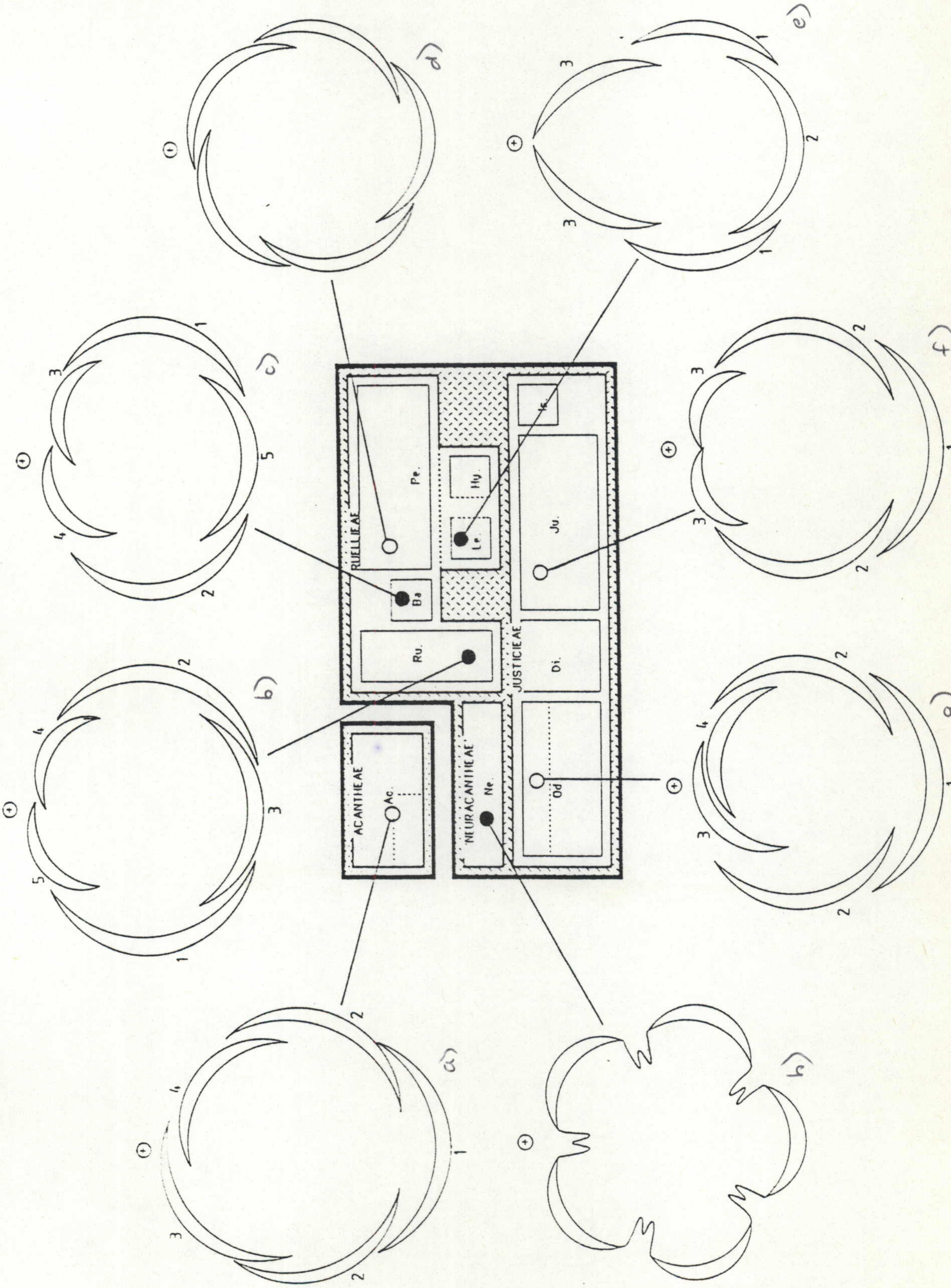

I L 5
I L 5
I L T 5
I L 5
InSA T 5
C SA T 5 A
C SA T 5
Q SB T 5
Q SB T4-5
C SB T 5 R
C SB T 5 R
C B T 5 R
C SB T 5 R
C SA T 5
C B T 5 R
I B T 5 RJ
I B T 5 RJ
AsSA T 5
AsSA T 5 IR
AsSA T 5 IR
As B T 5
As B 5
As B 5 R
As B T 5
As B T 5
As B T 5 R
RE As B 5 Rr R
RE As B 5 Rr R
RE As B 5 Rr R
As B 5 RJ
As B 5 RJ
As B 5 RJ
As B T 5 RJ
As B 5 AC RJ
As B 5 AC RJ
As B T 5 RJ
As B 5 RJ
As B 5 RJ
As B 5 RJ

Figure 19: Aestivation in the Acanthaceae: a) imbricate aestivation in Acanthoideae; b) quinuncial aestivation as in *Crabbea* Harv.; c) quinuncial aestivation as in *Barleria* ; d) contorted aestivation as in most Ruellieae; e) imbricate aestivation of *Lepidagathis*, with two outer lobes of abaxial lip outermost in bud; f) ascending aestivation of Justicieae, with inner lobe of abaxial lip outermost in bud; g) ascending aestivation of *Asystasia* Blume with one lobe of upper lip inside the other and h) induplicate aestivation of *Neuracanthus*.

Ac. = Acanthinae, Ba. = Barleriinae, Di. = Diclipteriinae, Hy. = Hygrophilinae, Is. = Isoglossinae, Ju. = Justiciinae, Le. = Lepidagathidinae, Od. = Odontoneminae, Pe. = Petalidiinae and Ru. = Ruelliinae.


ACANTHEAE
RUELLIEAE
NEURACANTHEAE
JUSTICIEAE
Ac.
Ru.
Ba
Pe.
Le.
Hy.
Ju.
Di.
Od
Ne.
a)
b)
c)
d)
e)
f)
g)
h)

of the types of aestivation in the tribes and subtribes of the Acanthaceae. A particularly interesting feature of these genera is the restricted distribution of a rugula - a fold in the adaxial lip forming a channel in which the style and stigma are held and shielded from self-pollination. A slightly less specialised means of achieving this protection is seen in the genera in which the filaments restrain the style. From table 4, it can be seen that the corollas of *Peristrophe*, *Dicliptera* and *Hypoestes* are unique in the Justicieae, as they are resupinate. They also have a rudimentary rugula, which is clearly visible in the fresh buds of some species (especially *P. cliffordii*), more difficult to detect in older flowers that have undergone resupination and almost impossible to see in herbarium material. The corollas of all species of *Peristrophe* and *Dicliptera* have similar morphology, although they differ in size and in the shape of the lips (figs. 20 - 25). There is variation in the length of the corolla in *P. cernua*, with smaller corollas in the southern areas of its distribution, and larger corollas in the northern regions (fig. 17). *D. spinulosa* has a corolla that is very much smaller than that of other species. Within *Peristrophe*, most species have similarly coloured flowers, i.e. purple with occasional white or pink sports in populations (e.g. *P. cernua* and *P. cliffordii*). *P. cernua* has flowers that are a slightly deeper pink than those of other species and has speckles (honey guides) on the lip in the lower position, an unusual feature in the genus. *P. gillilandiorum* has flowers that are conspicuously lighter than those of other species. Within *Dicliptera*, there are species with white or faint pink or lilac flowers (i.e. *D. zeylanica*, *D. heterostegia* and *D. sp. 4*) and species that usually have purple flowers (e.g. *D. clinopodia* and *D. eenii*). *D. minor* is interesting, as *D. minor* ssp. *minor* has deep magenta flowers and *D. minor* ssp. *1* has white flowers. *D. divaricata*, a species which is morphologically similar to *D. minor*, has light purple flowers and so can be distinguished from both subspecies of *D. minor*. *D. capensis* has similar proportions of white and purple flowers in the same or different populations. White sports of *P. cernua* have been observed in Pietermaritzburg (*Balkwill 445*) and in the Fish River Valley in the Cape (*Brink 327*).

Figure 20: Length of corollas in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ▒▒▒ 68% confidence interval of means for specimens. Taxa as follows: *Dicliptera*: 1, *D. zeylanica* ; 2, *D. sp. 1* ; 3, *D. heterostegia* ; 4, *D. capensis* ; 5.1, *D. clinopodia* var. *clinopodia* ; 5.2, *D. clinopodia* var. *1* ; 6, *D. divaricata* ; 7.1, *D. minor* ssp. *minor* ; 7.2 *D. minor* ssp. *1* ; 8, *D. sp. 2* ; 9, *D. sp. 3* ; 10, *D. quintasii* ; 11, *D. eenii* ; 12, *D. sp. 4* ; 13, *D. fruticosa* ; 14, *D. sp. 5* ; 15, *D. spinulosa* ; *Peristrophe*: 1, *P. grandibracteata* ; 2, *P. hereroensis* ; 3, *P. sp. 1* ; 4, *P. paniculata* ; 5, *P. transvaalensis* ; 6, *P. cliffordii* ; 7, *P. gillilandiorum* ; 8, *P. kotschyana* and 9, *P. cernua*.

Character: Length of Flower

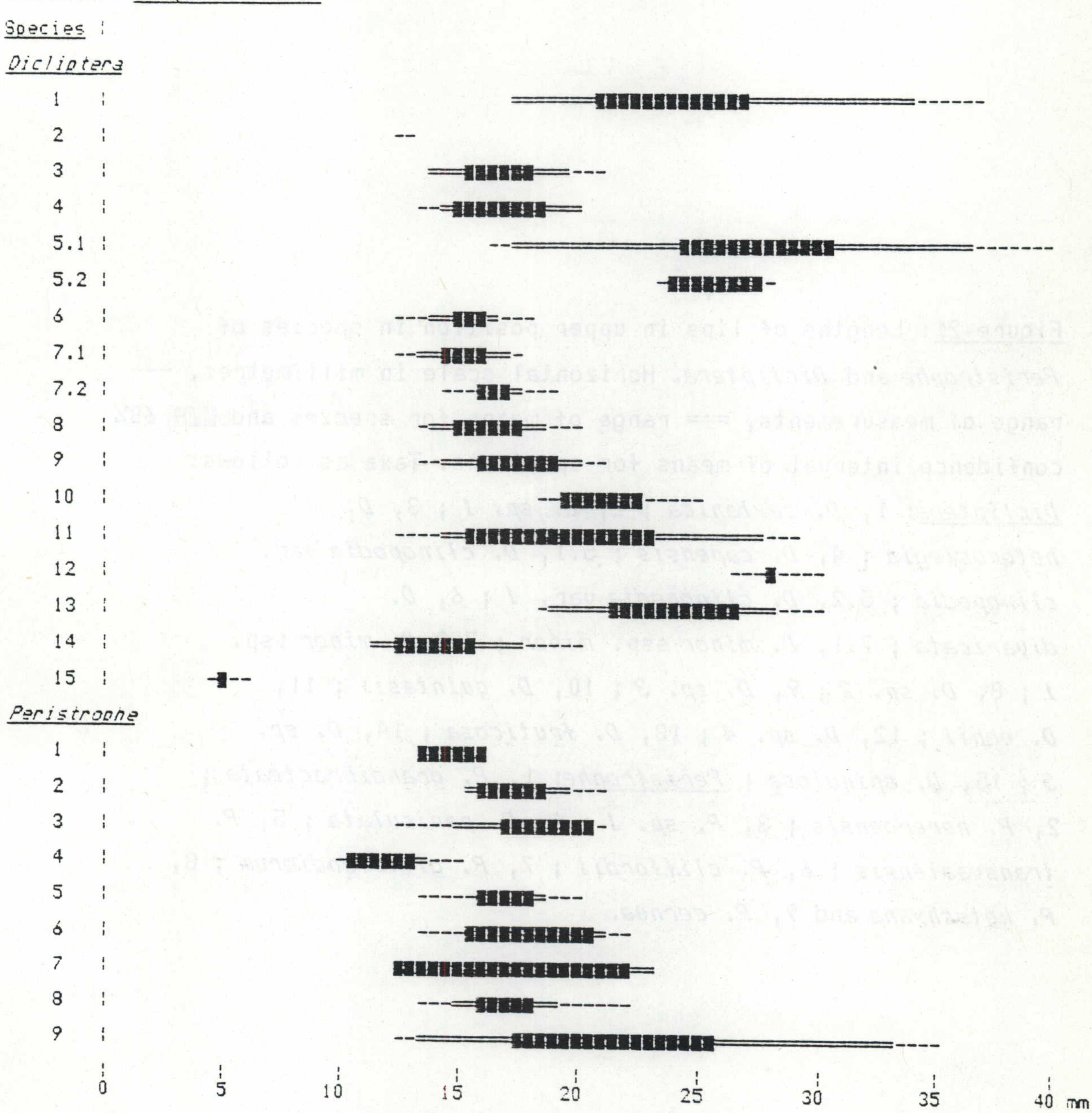


Figure 21: Lengths of lips in upper position in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ▒▒▒ 68% confidence interval of means for specimens. Taxa as follows: Dicliptera: 1, *D. zeylanica* ; 2, *D. sp. 1* ; 3, *D. heterostegia* ; 4, *D. capensis* ; 5.1, *D. clinopodia* var. *clinopodia* ; 5.2, *D. clinopodia* var. *1* ; 6, *D. divaricata* ; 7.1, *D. minor* ssp. *minor* ; 7.2 *D. minor* ssp. *1* ; 8, *D. sp. 2* ; 9, *D. sp. 3* ; 10, *D. quintasii* ; 11, *D. eenii* ; 12, *D. sp. 4* ; 13, *D. fruticosa* ; 14, *D. sp. 5* ; 15, *D. spinulosa* ; Peristrophe: 1, *P. grandibracteata* ; 2, *P. hereroensis* ; 3, *P. sp. 1* ; 4, *P. paniculata* ; 5, *P. transvaalensis* ; 6, *P. cliffordii* ; 7, *P. gillilandiorum* ; 8, *P. kotschyana* and 9, *P. cernua*.

Character: Length of Lip in Upper Position

Species :

Dicliptera

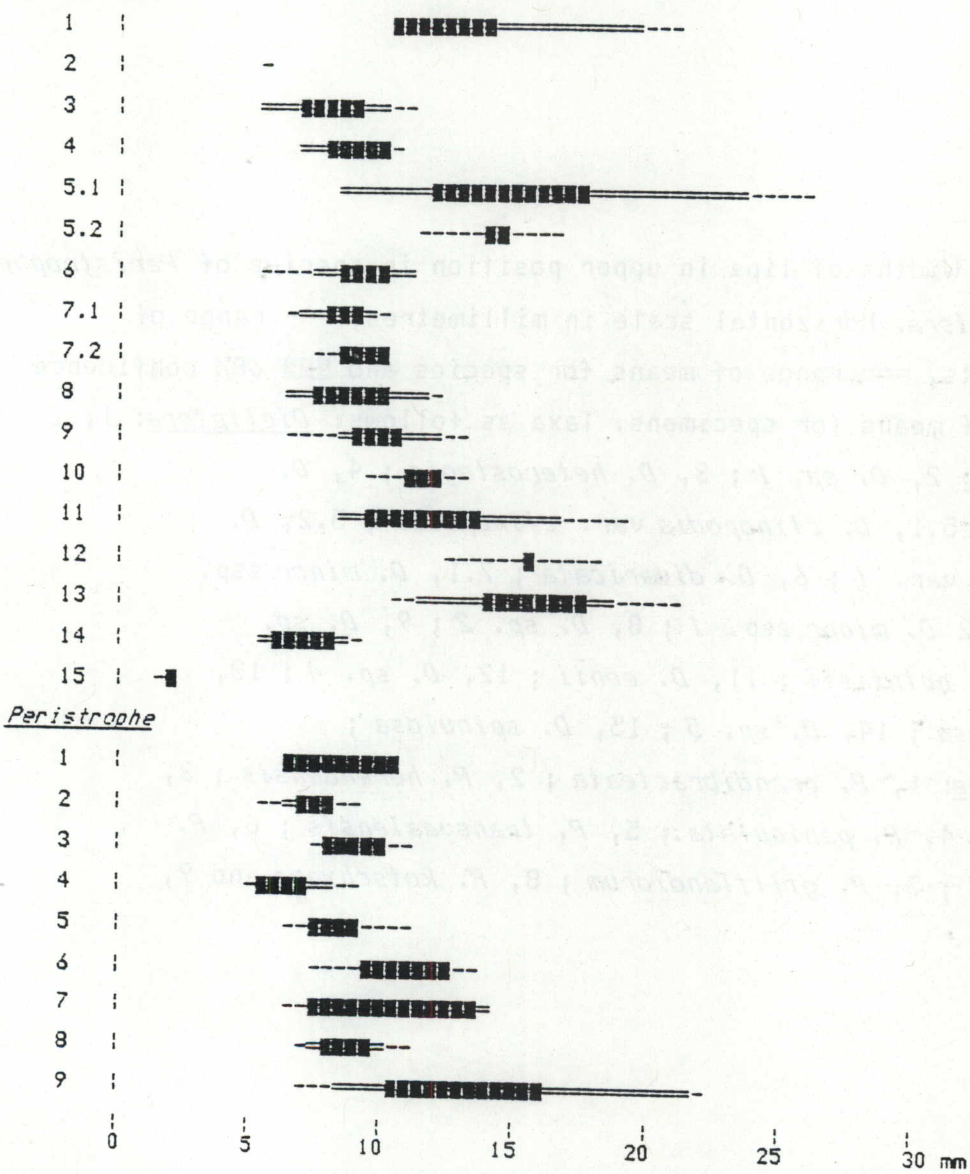


Figure 22: Widths of lips in upper position in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ▓▓▓ 68% confidence interval of means for specimens. Taxa as follows: *Dicliptera*: 1, *D. zeylanica* ; 2, *D. sp. 1* ; 3, *D. heterostegia* ; 4, *D. capensis* ; 5.1, *D. clinopodia* var. *clinopodia* ; 5.2, *D. clinopodia* var. *1* ; 6, *D. divaricata* ; 7.1, *D. minor* ssp. *minor* ; 7.2 *D. minor* ssp. *1* ; 8, *D. sp. 2* ; 9, *D. sp. 3* ; 10, *D. quintasii* ; 11, *D. eenii* ; 12, *D. sp. 4* ; 13, *D. fruticosa* ; 14, *D. sp. 5* ; 15, *D. spinulosa* ; *Peristrophe*: 1, *P. grandibracteata* ; 2, *P. hereroensis* ; 3, *P. sp. 1* ; 4, *P. paniculata* ; 5, *P. transvaalensis* ; 6, *P. cliffordii* ; 7, *P. gillilandiorum* ; 8, *P. kotschyana* and 9, *P. cernua*.

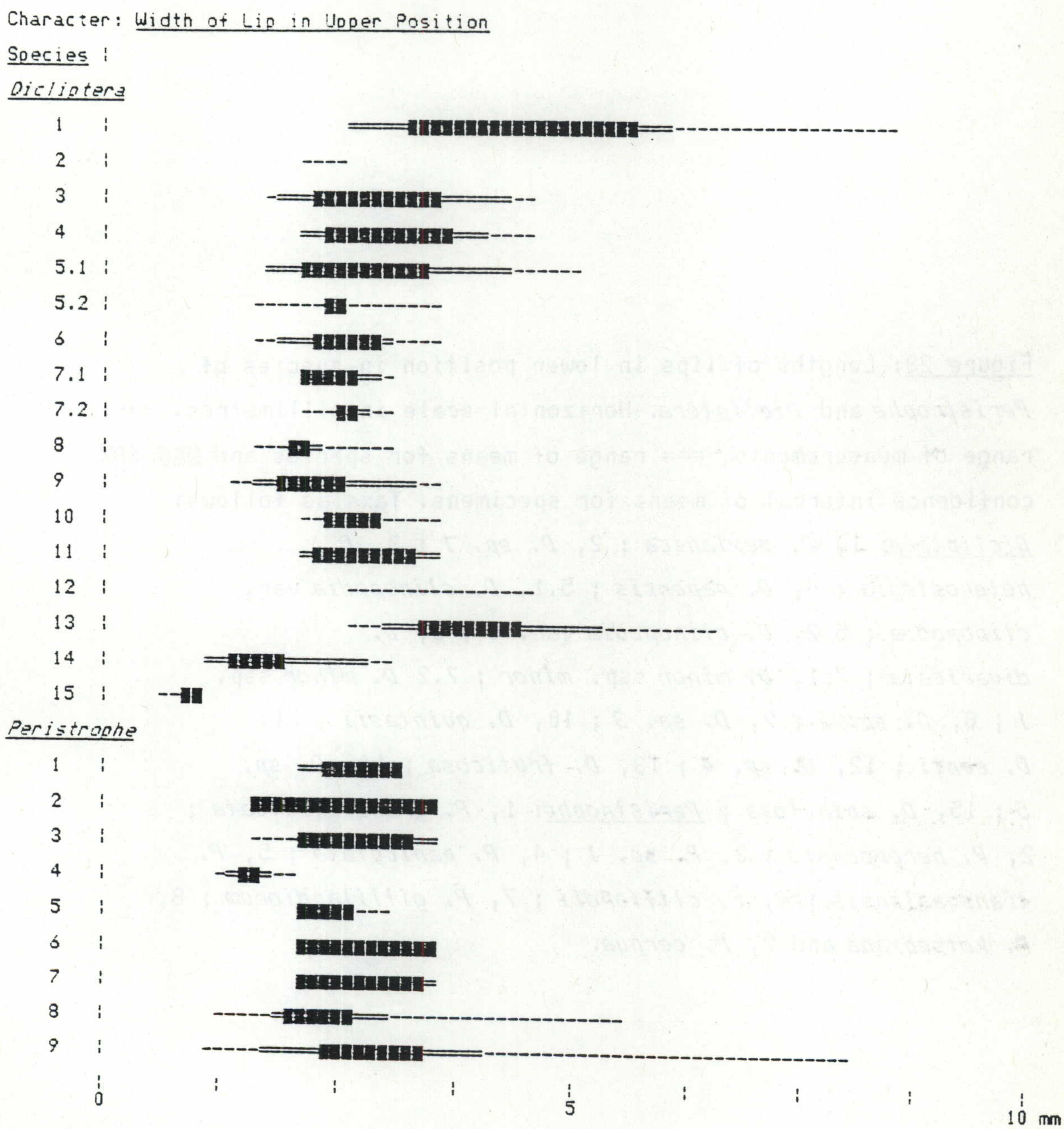

Character: Width of Lip in Upper Position
Species :
Dicliptera
1
2
3
4
5.1
5.2
6
7.1
7.2
8
9
10
11
12
13
14
15
Peristrophe
1
2
3
4
5
6
7
8
9
0
5
10 mm

Figure 23: Lengths of lips in lower position in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ▓▓▓ 68% confidence interval of means for specimens. Taxa as follows: Dicliptera: 1, *D. zeylanica* ; 2, *D. sp. 1* ; 3, *D. heterostegia* ; 4, *D. capensis* ; 5.1, *D. clinopodia* var. *clinopodia* ; 5.2, *D. clinopodia* var. *1* ; 6, *D. divaricata* ; 7.1, *D. minor* ssp. *minor* ; 7.2 *D. minor* ssp. *1* ; 8, *D. sp. 2* ; 9, *D. sp. 3* ; 10, *D. quintasii* ; 11, *D. eenii* ; 12, *D. sp. 4* ; 13, *D. fruticosa* ; 14, *D. sp. 5* ; 15, *D. spinulosa* ; Peristrophe: 1, *P. grandibracteata* ; 2, *P. hereroensis* ; 3, *P. sp. 1* ; 4, *P. paniculata* ; 5, *P. transvaalensis* ; 6, *P. cliffordii* ; 7, *P. gillilandiorum* ; 8, *P. kotschyana* and 9, *P. cernua*.

Character: Length of Lip in Lower Position

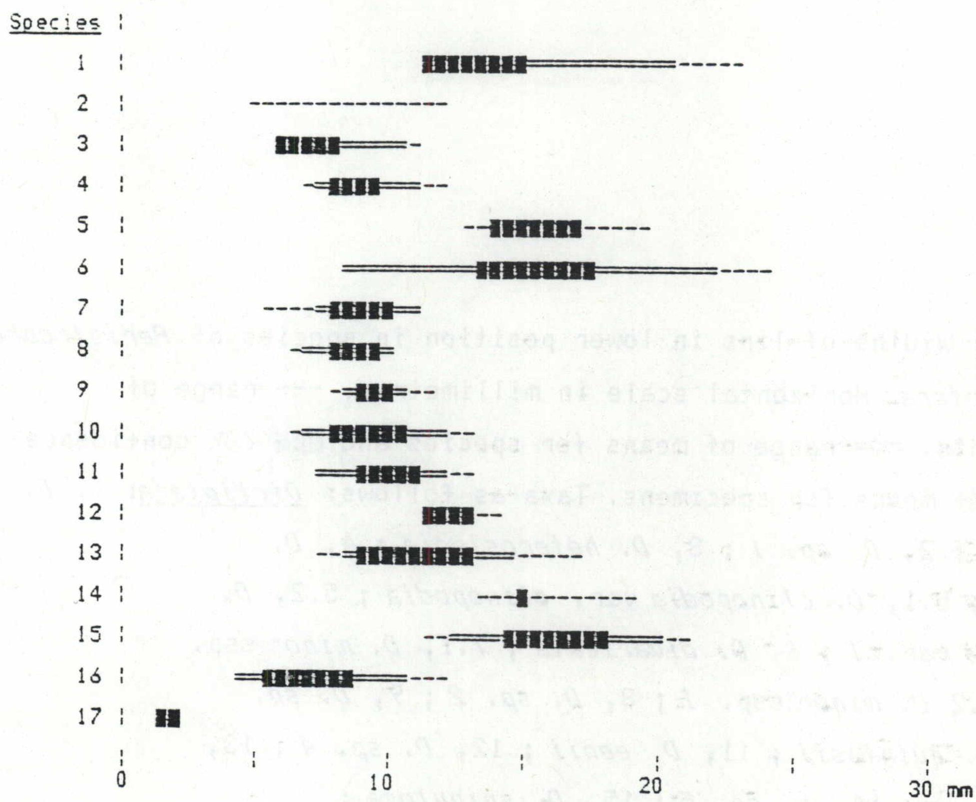


Figure 24: Widths of lips in lower position in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ▩▩▩ 68% confidence interval of means for specimens. Taxa as follows: *Dicliptera*: 1, *D. zeylanica* ; 2, *D. sp. 1* ; 3, *D. heterostegia* ; 4, *D. capensis* ; 5.1, *D. clinopodia* var. *clinopodia* ; 5.2, *D. clinopodia* var. *1* ; 6, *D. divaricata* ; 7.1, *D. minor* ssp. *minor* ; 7.2 *D. minor* ssp. *1* ; 8, *D. sp. 2* ; 9, *D. sp. 3* ; 10, *D. quintasii* ; 11, *D. eenii* ; 12, *D. sp. 4* ; 13, *D. fruticosa* ; 14, *D. sp. 5* ; 15, *D. spinulosa* ; *Peristrophe*: 1, *P. grandibracteata* ; 2, *P. hereroensis* ; 3, *P. sp. 1* ; 4, *P. paniculata* ; 5, *P. transvaalensis* ; 6, *P. cliffordii* ; 7, *P. gillilandiorum* ; 8, *P. kotschyana* and 9, *P. cernua*.

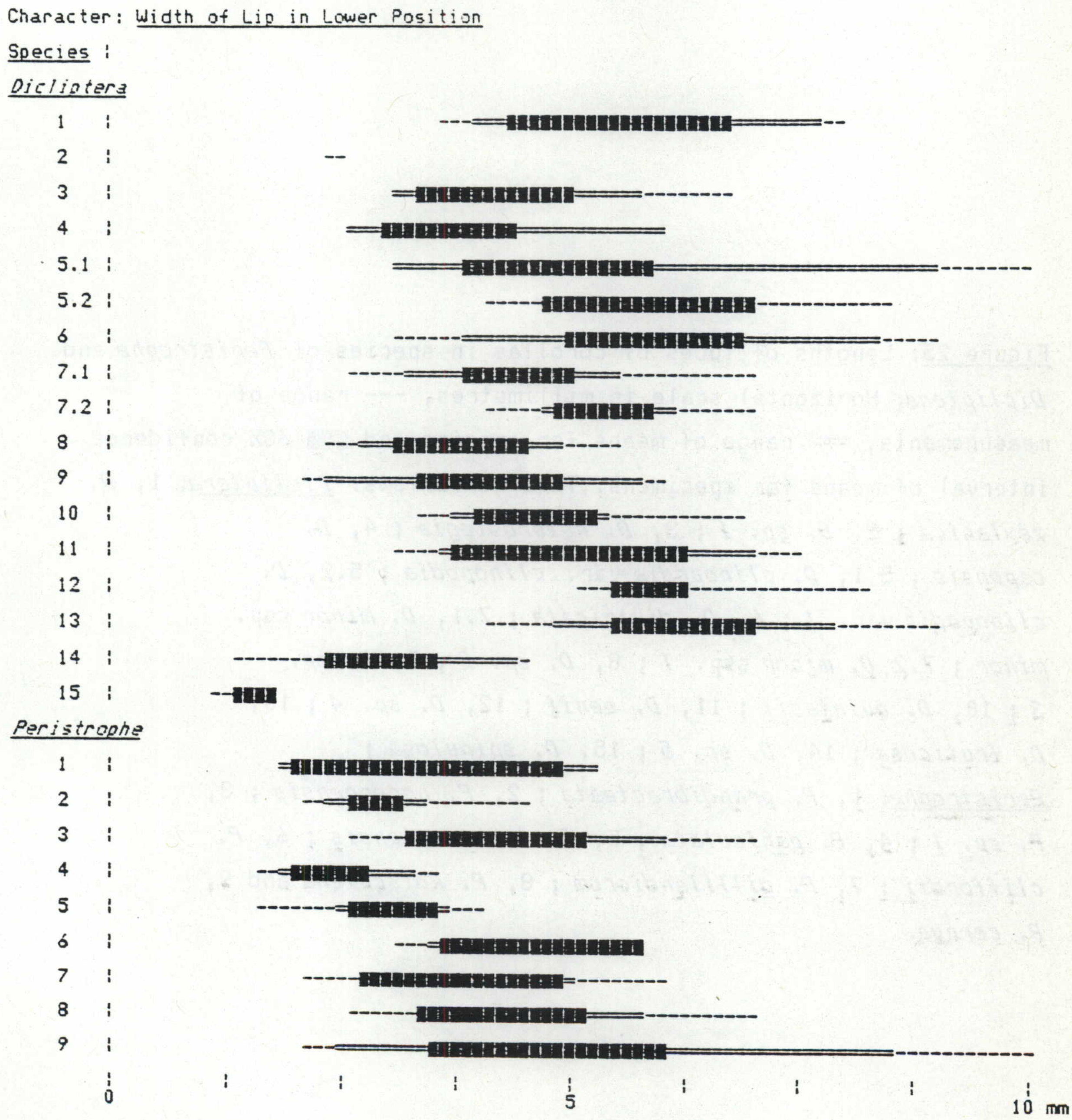
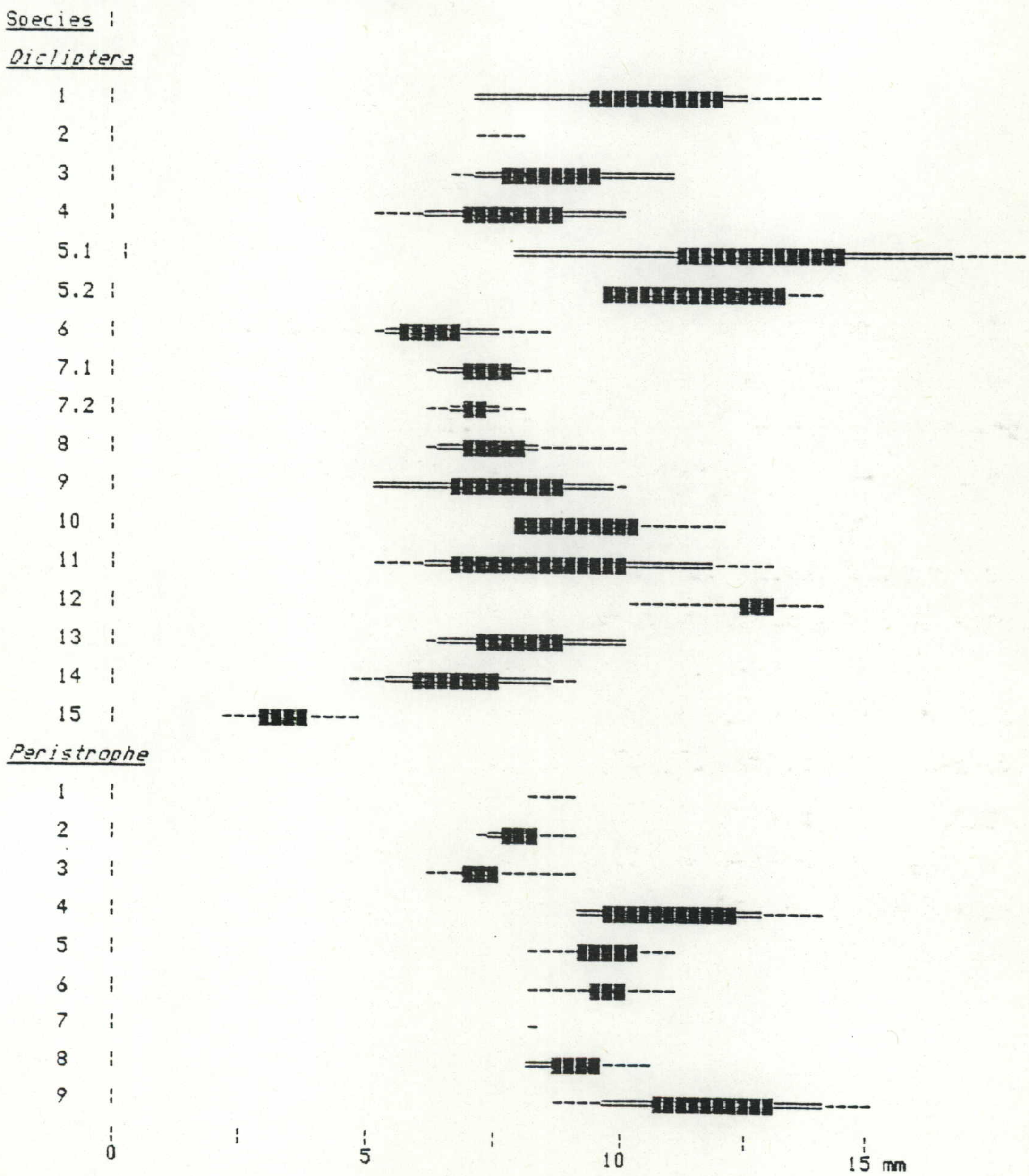

Character: Width of Lip in Lower Position
Species :
Dicliptera
1
2
3
4
5.1
5.2
6
7.1
7.2
8
9
10
11
12
13
14
15
Peristrophe
1
2
3
4
5
6
7
8
9
0
5
10 mm

Figure 25: Lengths of tubes of corollas in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for species and ▓▓▓ 68% confidence interval of means for specimens. Taxa as follows: *Dicliptera*: 1, *D. zeylanica* ; 2, *D. sp. 1* ; 3, *D. heterostegia* ; 4, *D. capensis* ; 5.1, *D. clinopodia* var. *clinopodia* ; 5.2, *D. clinopodia* var. *1* ; 6, *D. divaricata* ; 7.1, *D. minor* ssp. *minor* ; 7.2 *D. minor* ssp. *1* ; 8, *D. sp. 2* ; 9, *D. sp. 3* ; 10, *D. quintasii* ; 11, *D. eenii* ; 12, *D. sp. 4* ; 13, *D. fruticosa* ; 14, *D. sp. 5* ; 15, *D. spinulosa* ; *Peristrophe*: 1, *P. grandibracteata* ; 2, *P. hereroensis* ; 3, *P. sp. 1* ; 4, *P. paniculata* ; 5, *P. transvaalensis* ; 6, *P. cliffordii* ; 7, *P. gillilandiorum* ; 8, *P. kotschyana* and 9, *P. cernua*.

Character: Length of Corolla Tube



Discussion

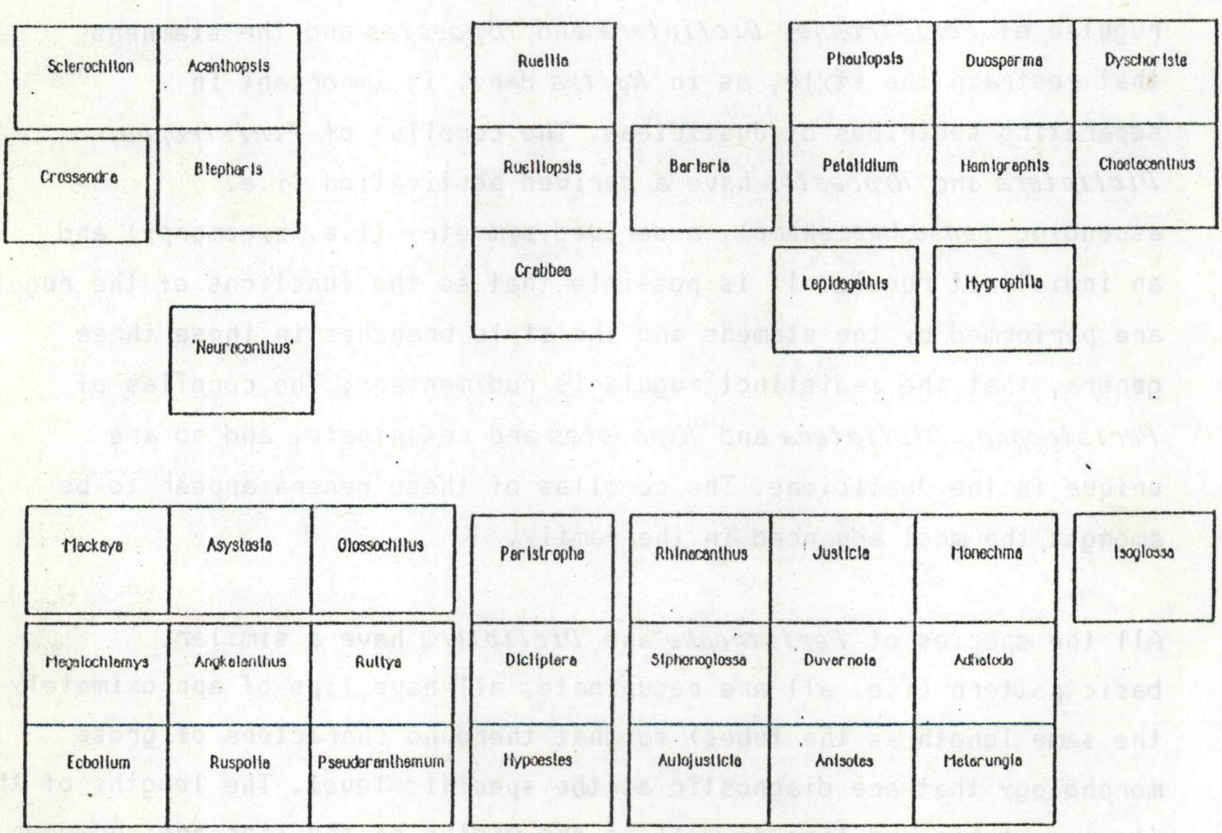
The corolla is an important taxonomic feature in the Acanthaceae. The corollas of the southern African members of the Acanthoideae are slit along the adaxial suture, unlike those of the Ruellioideae. In the Ruellioideae, actinomorphic flowers appear to be ancestral and the bilabiate forms derived. Contorted aestivation is usually correlated with actinomorphy (Table 4), thus suggesting that this too is primitive. In the subtribe Barleriinae, Bremekamp (1965) drew attention to the diagnostic quinuncial aestivation. In the zygomorphic members of the Ruellioideae (including the Justicieae), imbricate aestivation is the norm, but patterns of overlap are also interesting diagnostic features.

The distinction between rugulae as those in *Justicia*, the rudimentary rugulae of *Peristrophe, Dicliptera* and *Hypoestes* and the stamnens that restrain the style, as in *Ruttya* Harv. is important in separating subtribes of Justicieae. The corollas of *Peristrophe, Dicliptera* and *Hypoestes* have a derived aestivation (i.e. ascending *sensu* Bremekamp), a derived symmetry (i.e. zygomorpy) and an indistinct rugula. It is possible that as the functions of the rugula are performed by the stamens and the style branches in these three genera, that the indistinct rugula is rudimentary. The corollas of *Peristrophe, Dicliptera* and *Hypoestes* are resupinate, and so are unique in the Justicieae. The corollas of these genera appear to be amongst the most advanced in the family.

All the species of *Peristrophe* and *Dicliptera* have a similar basic pattern (i.e. all are resupinate, all have lips of approximately the same length as the tubes) so that there no characters of gross morphology that are diagnostic at the specific level. The lengths of the flowers, tubes and lips as well as the widths of the lips are, however, valuable to distinguish between species. *D. spinulosa* can be separated from any other species by its unique small flowers, while the differences between *D. clinopodia* and *D. divaricata, D. minor, D. sp. 2, D. sp. 3* and *D. quintasii* are useful in keying species. This character also helps to distinguish between *D. sp. 4* and *D. eenii*. The variation in the length of the corolla of *P. cernua* seems to be a geographic cline (fig. 17). The flowers from the northern end of the cline are much larger than the flowers of *P. kotschyana*,

Table 5: Distribution of characters of the androecium in the genera of southern African Acanthaceae.

Genera arranged as in key below, characters as follows: C = anthers ciliate, (C) = anthers sometimes ciliate, D = didynamous, FB = filaments bifurcated (fig. 26f), M = anthers muticous, P = thecae parallel, S = anthers spiked or spurred, Sp = thecae superposed, SP = thecae parallel, T = anthers tailed, (T) = anthers minutely tailed, first number = number of stamens, second number = number of staminodes and third number = number of thecae.



4 0 1 MC	4 0 1 MC
4 0 1 M(C)	4 0 1 D MC

4 0 2+1P D FB MC

4 0 2P D M
4 0 2P D S
4 0 2P D M(C)

2 3 4 1 2P 5 0 M

4 0 2P D M/S	4 0 2P D M	4 0 2P D M/S
4 0 2P D S	4 0 2P D M	2 0 2 2 2P D M/S
4 0 2(+1)P D M	4 0 2P D M	

2 2 2P M	4 0 2SP D M/S	4 0 2SP D S
2 0 2P M	2 0 2P M	2 2(+1) 1 M
2 2 2P M/T	2 2 1 M	2 2 2P 2C

2 0 2Sp M
2 0 2Sp M
2 0 1 M

2 0 2Sp M	2 0 2SP T	2 0 2Sp T
2 0 2Sp (T)	2 0 2P (T)	2 0 2SP T/(T)
2 0 2Sp (T)	2 0 2SP (T)T	2 0 2SP T/M

2 0 2Sp M

while those at the southern end of the cline, which are geographically further away from *P. kotschyana*, are of a very similar size to the flowers of the latter.

Colour provides useful information. Most of the species that have broad green bracts have white flowers, while most of those with narrower bicoloured bracts have purple flowers. Colour helps to distinguish between some species (e.g. *D. minor* and *D. quintasii* and *P. gillilandiorum* and *P. cliffordii*) and subspecies (e.g. *D. minor* ssp. *minor* and *D. minor* ssp. *1*). The other infraspecific variation in colour appears to be due to sports (e.g. *P. cliffordii*, *D. zeylanica* and *D. heterostegia*). It seems that hybridisation between a purple flowered species and a white flowered species may lead to a species with white and purple flowers in similar proportions, thus the variation in colour of *D. capensis* may support the view that *D. capensis* is a hybrid between one of the species with broad bracts and one of the species with narrow bicoloured bracts. It was probably a white sport of *P. cernua* that Presl (1844) described as *P. krebsii* Presl, as his description of *P. krebsii* differs from that of *P. cernua* mainly on the basis of colour.

Androecium

Observations and Discussion

Table 5 presents the range of variation in the androecium in southern African Acanthaceae. Many features of the androecium provide important diagnostic features at the tribal, subtribal and generic levels. These include number of stamens, presence of staminodes, relative lengths of filaments, degree of fusion of filaments and morphology of anthers (i.e. the number and disposition of thecae and the number, position and nature of their appendages).

All the Acanthoideae have four stamens, but in the Ruellioideae four, two or even five occur and may or may not be combined with staminodes. In *Barleria* the androecium is a particularly important feature as all permutations of stamens with or without staminodes are recorded and the size of the stamens may vary markedly. Didynamous stamens are common in the Ruellioideae and in several genera the filaments are united into a flap or flange of tissue decurrent on the corolla tube. The distal edge of this tissue bears individual short stamens and staminodes. This peculiar arrangement has been important in assessing the postions of *Chaetacanthus* Nees, *Hygrophila* R. Br. and *Hemigraphis* Nees (see chapter 14). A very peculiar dimorphism in the anthers of *Neuracanthus* Nees and some African *Lepidagathis* Willd. is the existence of both monothecous and bithecous anthers in one flower. The relative position of the thecae appears to be a subtribal feature with parallel thecae (fig. 26c) characterising the Odontoneminae and superposed thecae (fig. 26e) more common in the Justiciinae. Appendages such as tails (fig. 26k), spikes (fig. 26j) or cilia (fig. 26b & i) on anthers are very common.

The androecium of *Peristrophe* and *Dicliptera* is very similar to that of members of the Justiciinae in that there are two stamens, no staminodes and two anther thecae that are superposed. *Hypoestes* differs from *Peristrophe* and *Dicliptera* by having monothecous anthers (fig. 26a), and this is the only character that separates some species of *Hypoestes* from *Peristrophe*. Analysis of the androecium in the family suggests a progressive reduction from an original number of five (still retained in some species of *Barleria*), through intermediate stages with some staminodes (e.g. some species of Chaetacanthus) and ultimately to two stamens without any accompanying staminodes. Although this may not be the only sequence, it is likely that those with only two stamens have been derived from forms similar to those with two (e.g. *Ecbolium* Kurz) and three (e.g. *Ruttya* Harv.) staminodes. The muticous anthers (fig. 26h) of *Peristrophe* and *Dicliptera* are most likely more primitive than those of genera which have tails (e.g. *Justicia* - fig. 26k) or spurs (fig. 26j) (e.g. *Chaetacanthus*). All the species of *Peristrophe* and *Dicliptera* have very similar stamens, so that the androecium does not provide any characters that are taxonomically useful for separating these two genera or for separating the species, subspecies or varieties.

<u>Disc</u>

Observations

The disc is a body of nectariferous tissue situated at the base of the ovary. This disc may be annular (fig. 27a), saucer-shaped (fig. 27b) or cupular (fig. 27c - f). Table 6 shows the distribution of the characters

Figure 26: Range of morphology and appendages of anthers: a) monothecous anther, *Hypoestes aristata, Balkwill 341* ; b) monothecous anther accompanied by a process on the filament, *Blepharis sp, Kerfoot K6333 pro parte* ; c) parallel bithecous anther, *Angkalanthus transvaalensis, Balkwill 1659* ; d) sub-parallel bithecous anther, *Metarungia galpinii, Balkwill 1517* ; e) superposed thecae, *Dicliptera clinopodia, ex hort.*; f) bifurcated filament, *Neuracanthus africanus, Balkwill 1620* ; g) superposed thecae borne at right angles to the filament, *Isoglossa woodii* C.B. Clarke, *Balkwill 182* ; h) muticous thecae, *Dicliptera clinopodia, ex hort.*; i) ciliate thecae, *Crossandra spinescens* Dunkley, *Kerfoot 7370*, j) spiked or spurred thecae, *Ruelliopsis setosa* (Nees) C.B. Clarke, *Balkwill 1656* and k) tailed theca, *Justicia protracta, ex hort.*.

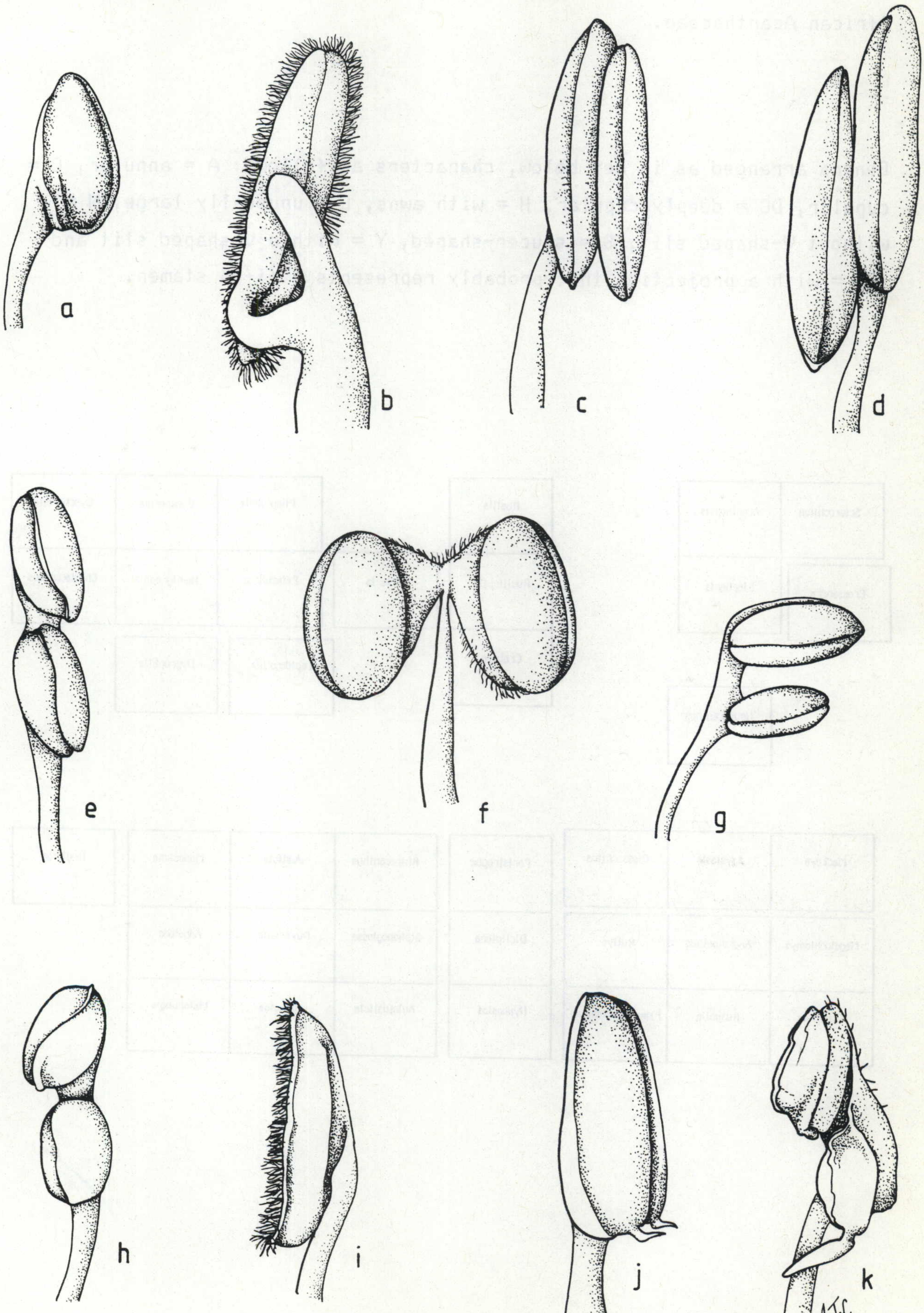
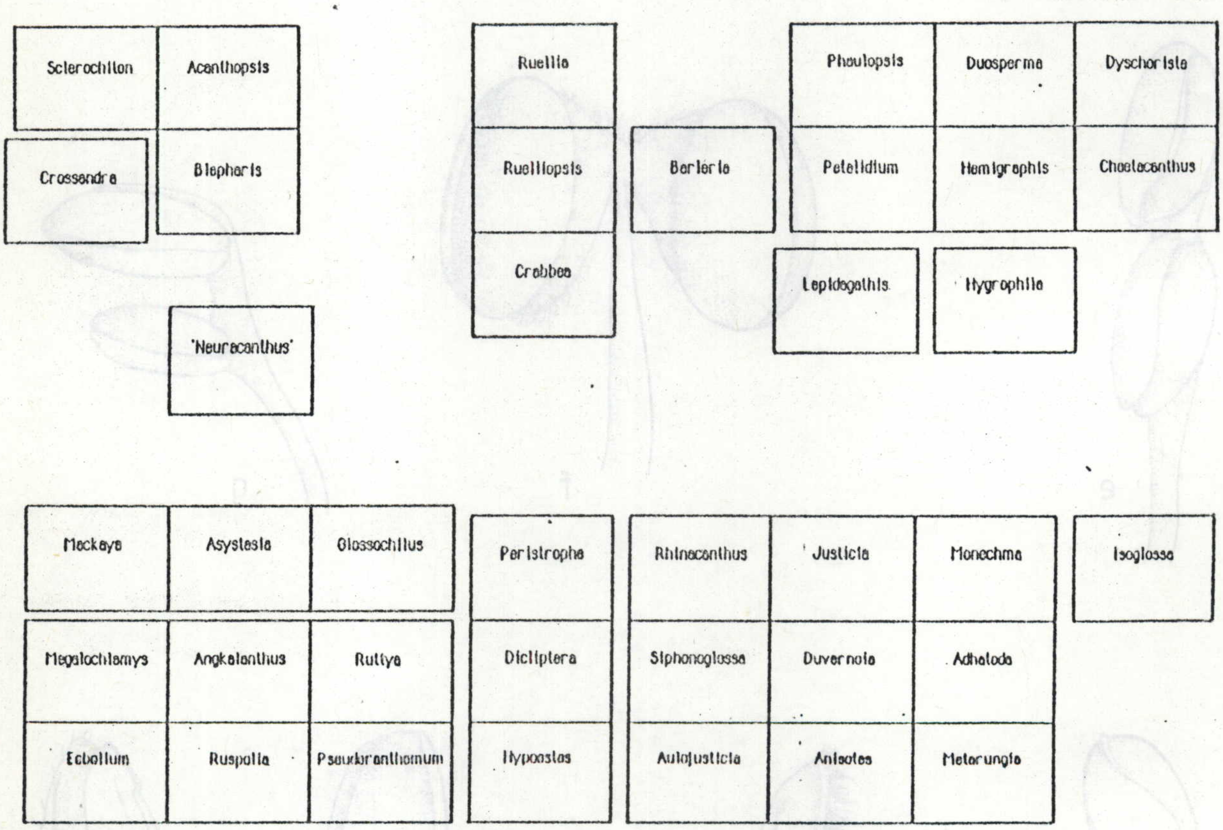
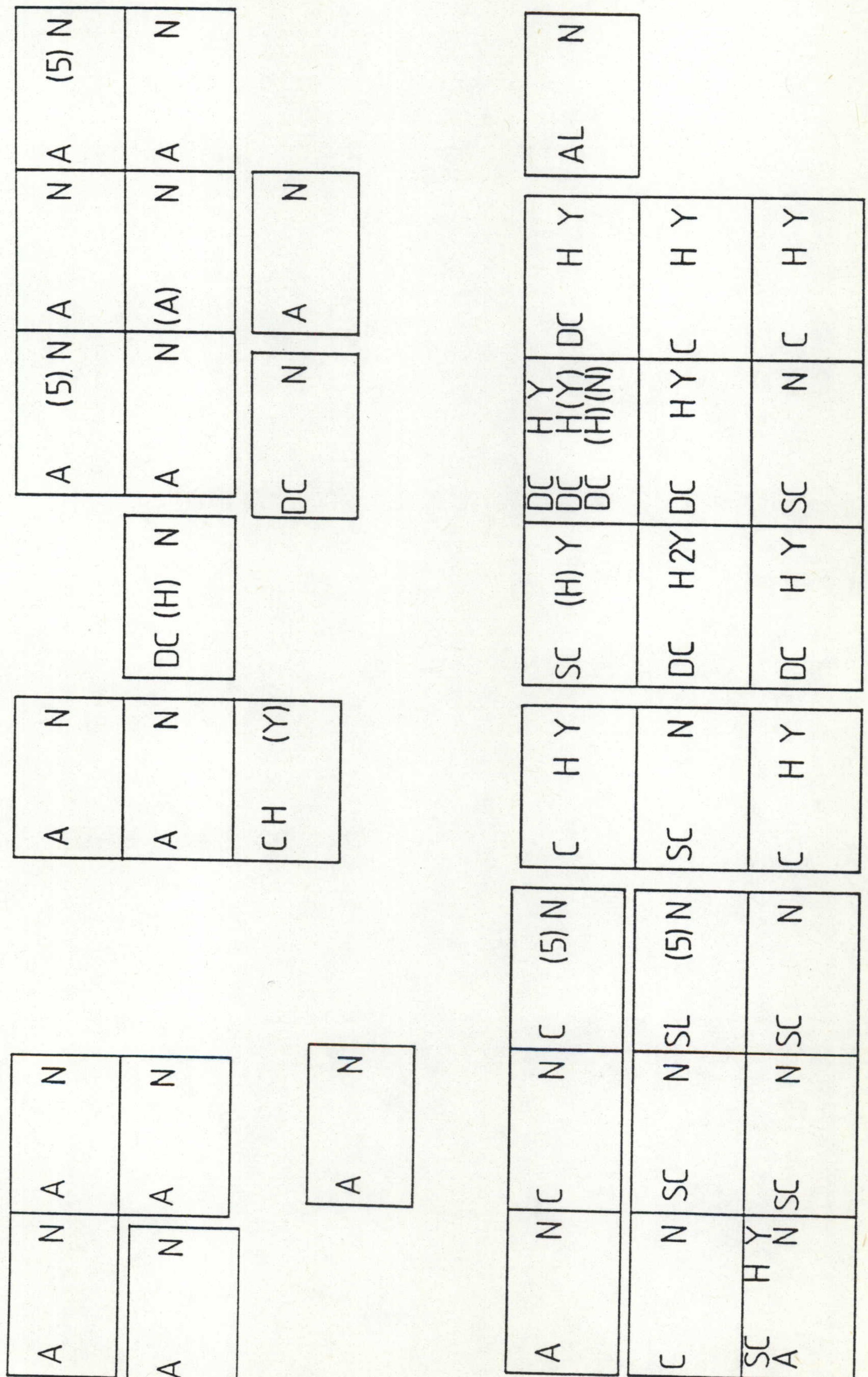

a
b
c
d
e
f
g
h
i
j
k
M.J.C

Table 6: Distribution of characters of the disc in the genera of southern African Acanthaceae.

Genera arranged as in key below, characters as follows: A = annular, C = cupular, DC = deeply cupular, H = with awns, L = unusually large, N = without V-shaped slit, S = saucer-shaped, Y = with a V-shaped slit and (5) = with a projection that probably represents a fifth stamen.




A (5) N
A N
A (5) N
A N
A (A) N
A N
DC N
A N
DC (H) N
A N
A N
C H (Y)
A N
A N
A N
A N
A N
SC (H) Y
DC DC DC H Y H(Y) (H)(N)
DC H Y
DC H2Y
DC H Y
C H Y
DC H Y
SC H Y
N C H Y
AL N
C H Y
SC N
C H Y
A N C
N C
(5) N
C N
SC N
SL (5) N
SC A H Y N
SC N
SC N

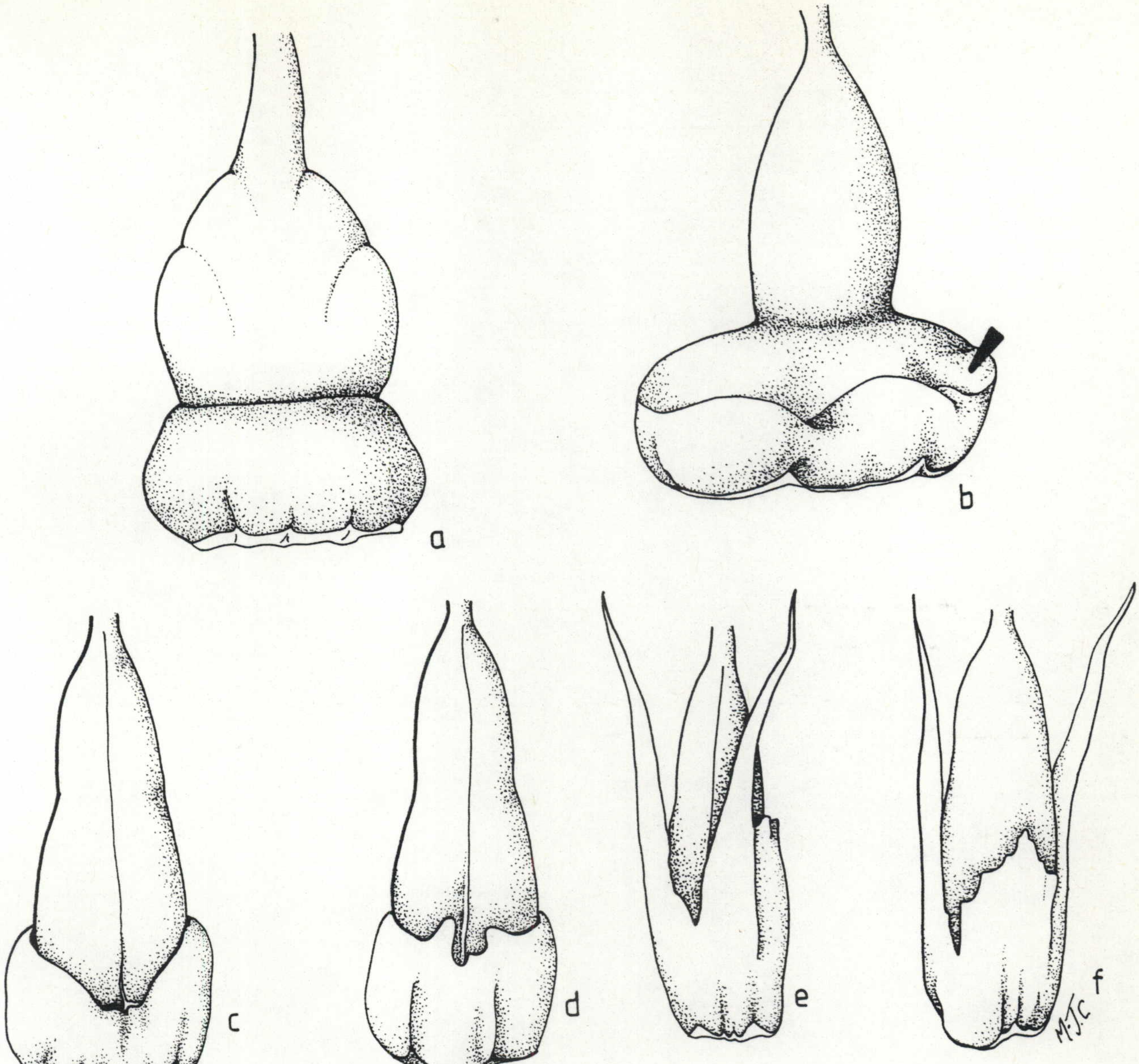
of the disc in southern African Acanthaceae. In the Acanthoideae, the Lepidagathideae and most of the Ruellieae, the disc is annular, while in most members of the Justicieae it is cupular. Most of the discs of the species of the Justiciinae and Diclipteriinae that have been investigated bear awns (fig. 27d). In *Peristrophe, Dicliptera* and *Hypoestes*, the disc is cupular and often has two awns or projections on the upper surface. The discs in most species of *Peristrophe* and *Dicliptera* are similar, although there is a small degree of variation in the shape of the awns. *P. paniculata* is unique in *Peristrophe* as it has a very shallowly cupular disc, while *D. sp. 4* is unique in *Dicliptera* as it has a deeply cupular and thick disc that has no awns. The two subspecies of *D. minor* have slightly different discs, the discs of *D. minor* ssp. *minor* has an irregular surface, while that of *D. minor* ssp. *1* has two minute squared awns on the surface and is slightly deeper. *D. eenii* shows infraspecific variation; some plants have discs with irregular upper surfaces, while others have two awns on the upper surface.

Discussion

A study of vasculature (De, 1967) has shown that in most cases the disc has staminal traces, suggesting that the disc is derived from the bases of the now epipetalous filaments. In some species, there is a protrusion that may represent a fifth stamen (fig. 27b), while many species have awns on the upper surfaces of these discs. In certain populations of *Hypoestes forskaolii* (Vahl) R. Br., the awns look remarkably like staminodes (fig. 27e - f) (pers. obs.).

The disc is a character that is difficult to use for identifications of herbarium material because it requires the dissection of the inflorescence units and so might be destructive. There are some interesting differences, however, and the disc might be useful to distinguish between *P. paniculata* and other species of *Peristrophe* and between *D. sp. 4* and other species of *Dicliptera*. The differences in the discs of the two subspecies of *D. minor* help to confirm that these subspecies are different, while the variation in the discs of *D. eenii* do not correlate with other characters, and so can be no more than infraspecific variation.

Figure 27: Range of morphology of discs: a) annular, *Petalidium oblongifolium* C.B. Clarke, *Balkwill 1573* ; b) saucer-shaped, with bulge that may represent a fifth stamen, *Ruttya ovata* Harv., *Balkwill 1525* ; c & d) cupular disc with small awns, *Dicliptera clinopodia, ex hort.* and e & f) cupular disc with staminode-like awns, *Hypoestes forskaolii, Balkwill 284.*


a
b
c
d
e
f
M.J.C

Gynoecium

Observations

Morphologically the ovaries of the Acanthaceae are very similar throughout the family, and especially so in *Peristrophe, Dicliptera* and *Hypoestes*. There is a slight difference in the shape of the ovaries in one southern African species of each of *Peristrophe* and *Dicliptera*. The ovaries of most species are ovoid, while those of *D. sp. 5* and *P. kotschyana* are ellipsoid and narrowly ellipsoid respectively.

Serial sections revealed that the septum is incomplete in young ovaries of *Peristrophe* and *Dicliptera* (fig. 28 & 29). In sections of *Peristrophe* the ovary is thinwalled and the septum is narrow where it is attached to the ovary wall (fig. 28), whereas in *Dicliptera*, although the walls of the ovary are equally thin, there is a swelling of thickened cells at the point where the septum joins the ovary wall (fig. 29).

Characters of the stigma in various southern African genera of the Acanthaceae are shown in Table 7. In *Peristrophe, Dicliptera* and *Hypoestes*, there are two filiform style branches of similar length.

Discussion

The ovary has few morphological characters that are useful in distinguishing between genera of the Acanthaceae. At the specific level, a single species of *Peristrophe, P. kotschyana* and a single species of *Dicliptera, D. sp. 5*, can each be distinguished from the other species in their respective genera, as they have ellipsoid rather than ovoid ovaries. The anatomy of the young ovaries provides a character by which *Dicliptera* can be separated from *Peristrophe* - a thickened area in the septum that becomes the raphe in the mature fruits of *Dicliptera* and hence contributes to the forces involved in the explosive dehiscence of the capsules. The shape of the style branches of *Peristrophe* and *Dicliptera* is relatively primitive in the family, and does not provide characters that are useful at the generic or the specific level.

Figure 28: Drawing of section through young ovary of *Peristrophe*: a) section of ovary showing ovules and incomplete septum (X90) and b) detailed drawing of one side of septum (X240).

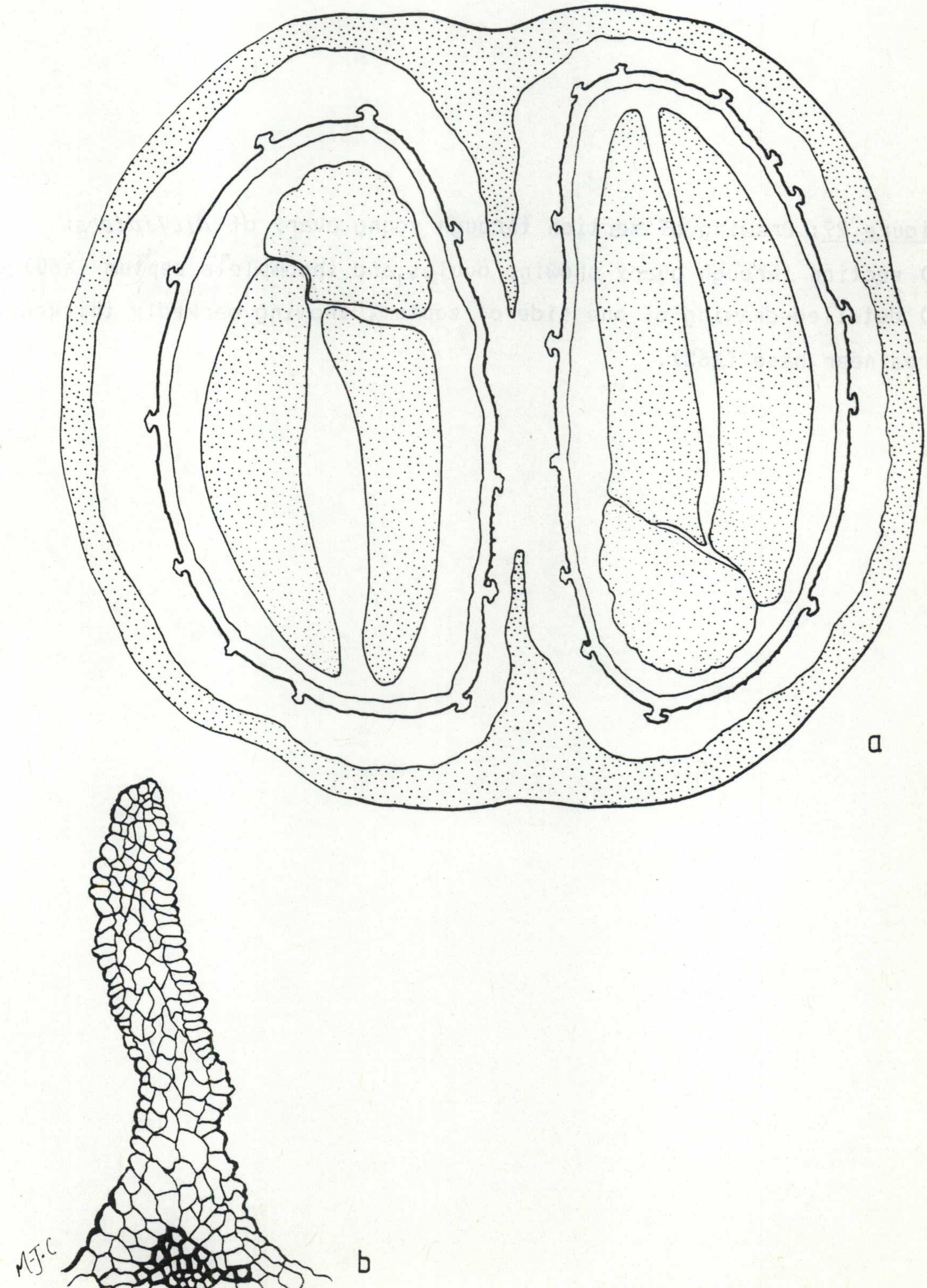

a
b

Figure 29: Drawing of section through young ovary of *Dicliptera*:
a) section through ovary showing ovules and incomplete septum (X60) and
b) detailed drawing of one side of septum, showing markedly thickened
area near base (X65).

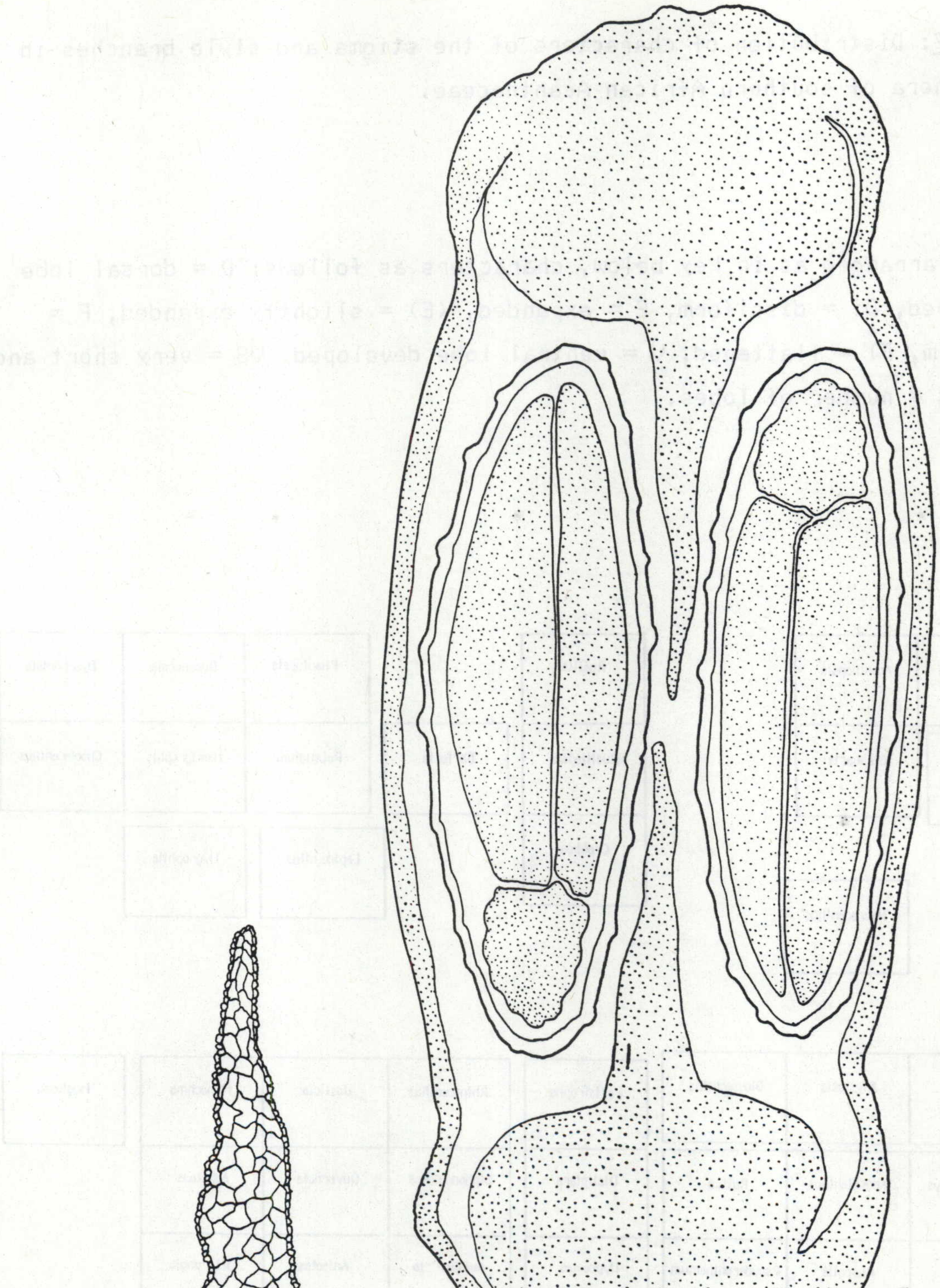
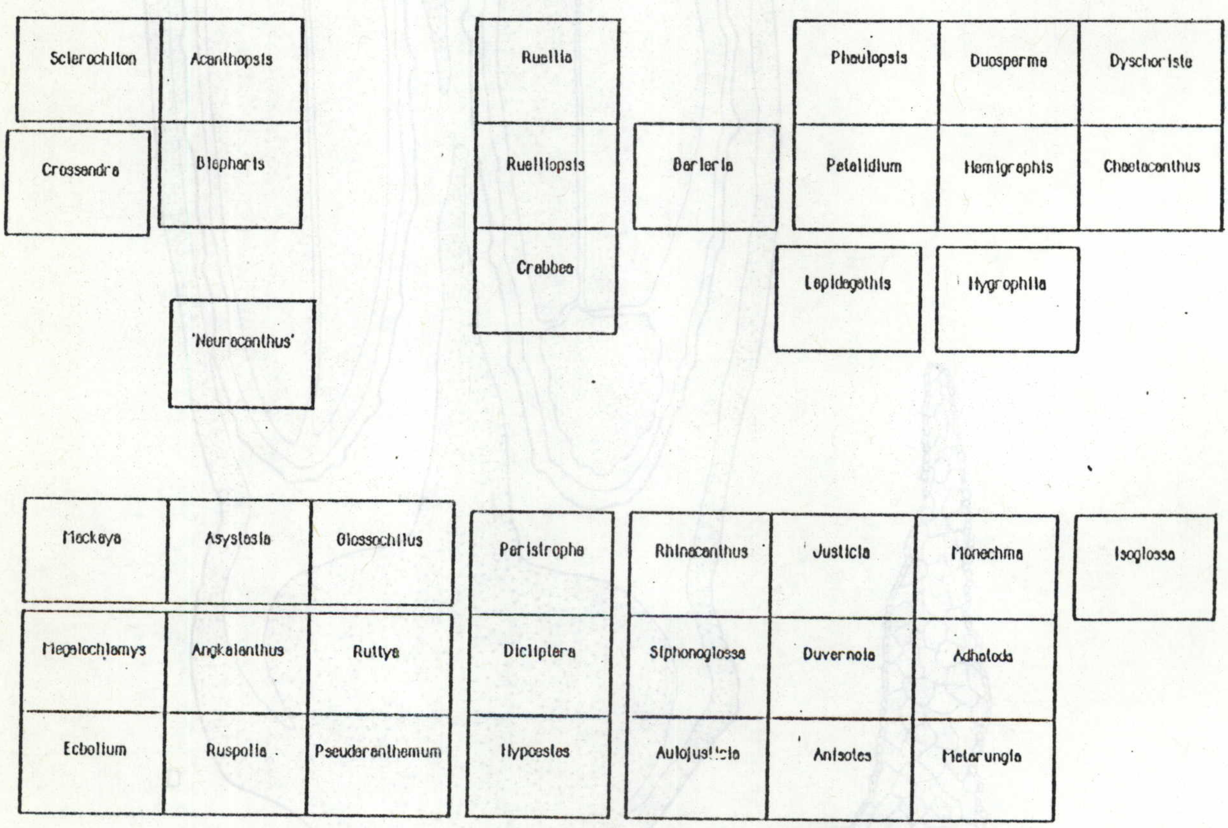
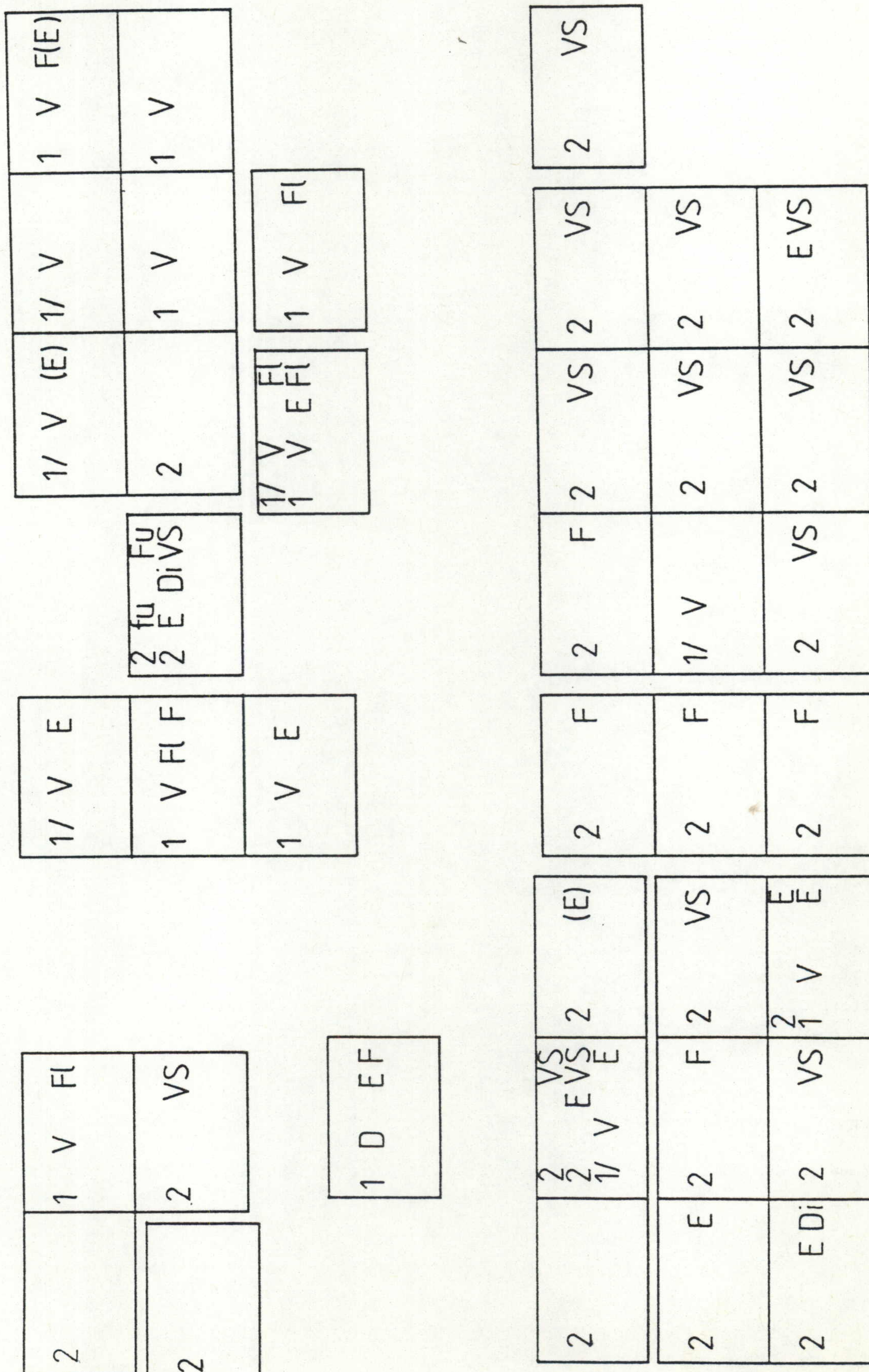

a
b
M.J.C

Table 7: Distribution of characters of the stigma and style branches in the genera of southern African Acanthaceae.

Genera arranged as in key below, characters as follows: D = dorsal lobe developed, Di = disciform, E = expanded, (E) = slightly expanded, F = filiform, Fl = flattened, V = ventral lobe developed, VS = very short and numbers = number of lobes.





Conclusions

Because of the similarity between the flowers of all species of *Peristrophe* and *Dicliptera*, these features provide few characters that are useful at the generic and specific levels. The similarities do, however, indicate the close relationship of these two genera to one another and to *Hypoestes*. The morphology of the corolla of these three genera is regarded as more derived than that of other genera in the Justicieae.

CHAPTER 6
MORPHOLOGY OF FRUITS

Introduction

The fruits of the Acanthaceae have long been used as taxonomic characters (Lindau, 1895), and for the circumscription of the family (Bremekamp, 1965). The nature of the base of the placenta has also been used as a character to distinguish between genera (de Jussieu, 1807). A discussion of capsules is vital to the definition of generic limits between *Peristrophe* and *Dicliptera* and for assessing their relationships within the family.

Materials and Methods

Information about the fruits of southern African genera was obtained by the examination of herbarium material. At least one species of each genus was investigated, and the information was checked against available literature. Measurements of the fruit were obtained in the same way as described for the inflorescence axes, in chapter 3.

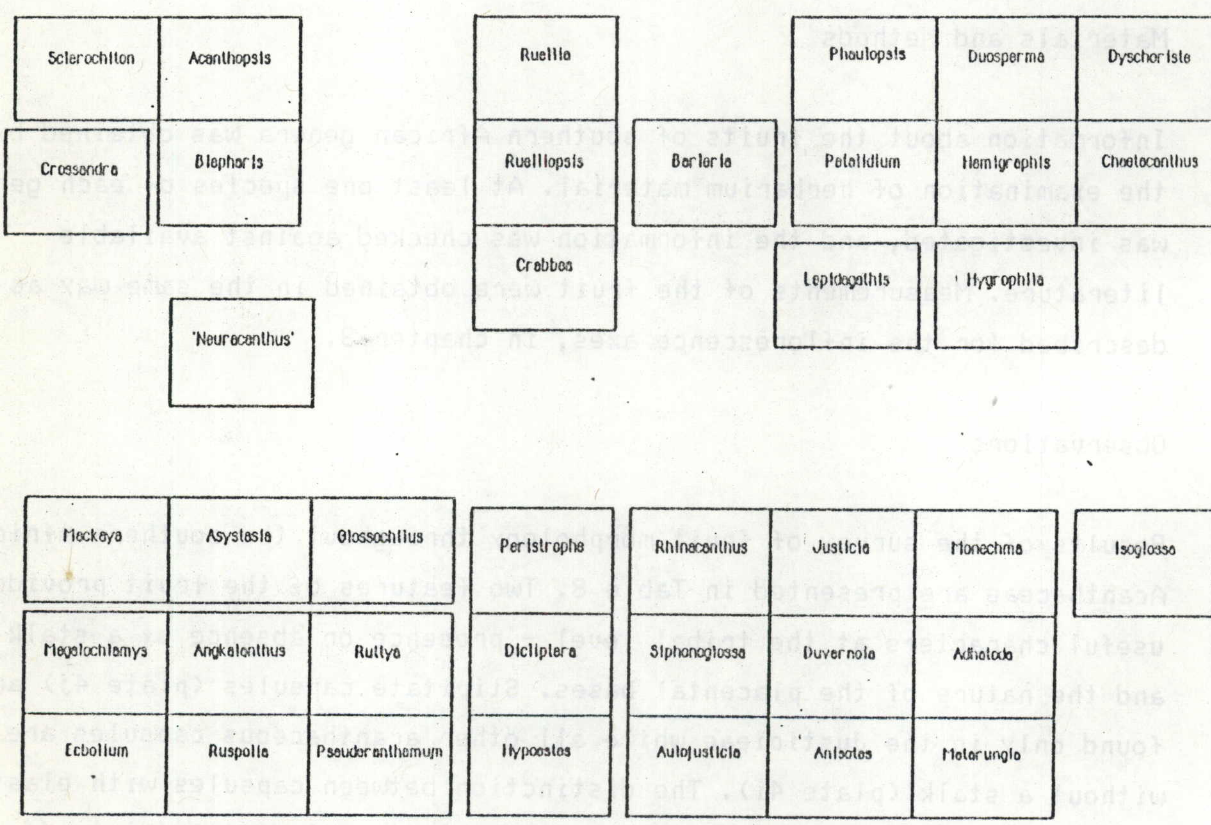
Observations

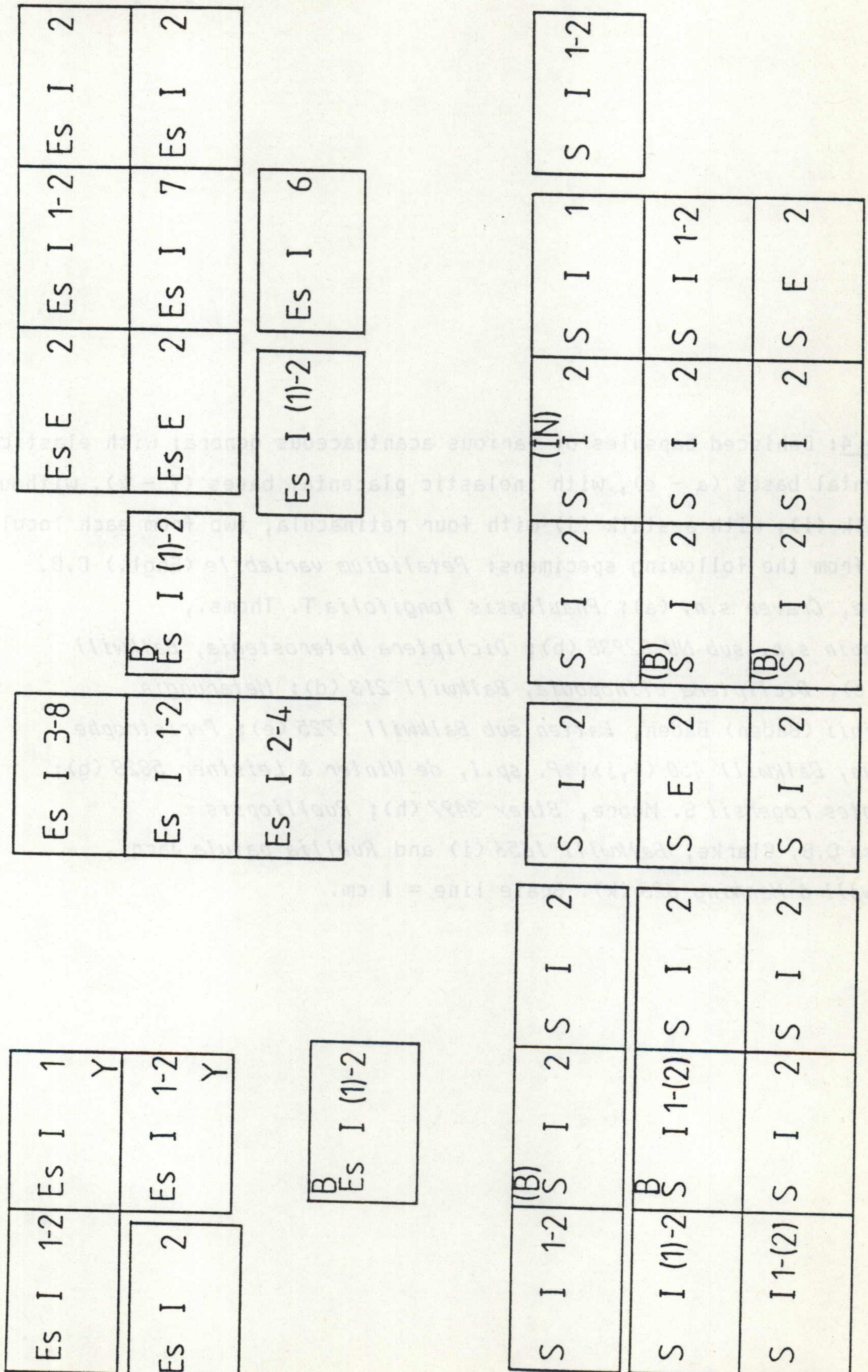
Results of the survey of fruit morphology throughout the southern African Acanthaceae are presented in Table 8. Two features of the fruit provide useful characters at the tribal level - presence or absence of a stalk and the nature of the placental bases. Stipitate capsules (plate 4j) are found only in the Justicieae while all other acanthaceous capsules are without a stalk (plate 4i). The distinction between capsules with elastic placentae (plate 4a - e) and those with inelastic placentae (plate 4f - k) has been used frequently in attempts to explain relationships among genera, especially amongst the subtribes of the Justicieae. The number of seeds in the capsule is a generic marker, especially in the Ruellieae.

Peristrophe and *Dicliptera* have stipitate capsules with two ovules in each locule, as do most other members of the Justicieae. *Dicliptera* differs from *Peristrophe* and *Hypoestes* by having having unusual capsules. In *Dicliptera*, the capsule wall is thinner

Table 8: Distribution of characters of the fruit in the genera of southern African Acanthaceae.

Genera arranged as in key below, characters as follows: B = beaked, (B) = slightly beaked, E = with elastic placental bases, Es = estipitate, I = with inelastic placental bases, (IN) = occasionally indehiscent, Y = with large sessile glands on the ovary and numbers = number of ovules in each locule.





Es I 1-2
Es I 1 Y
Es I 2
Es I 1-2 Y
B Es I (1)-2
S I 1-2
(B) S I 2
S I 2
S I (1)-2
B S I 1-(2)
S I 2
S I 1-(2)
S I 2
S I 2
Es I 3-8
Es I 1-2
Es I 2-4
Es E 2
Es I 1-2
Es I 2
B Es I (1)-2
Es E 2
Es I 7
Es I 2
Es I (1)-2
Es I 6
(B) S I 2
(N) S I 2
S I 1
(B) S E 2
S I 2
S I 1-2
(B) S I 2
S I 2
S E 2
S I 1-2

Plate 4: Dehisced capsules of various acanthaceous genera: with elastic placental bases (a - e), with inelastic placental bases (f - k), without a stalk (i), with a stalk (j) with four retinacula, two from each locule (k); from the following specimens: *Petalidium variabile* (Engl.) C.B. Clarke, *Craven s.n.* (a); *Phaulopsis longifolia* T. Thoms., *Bourquin s.n. sub NU 32938* (b); *Dicliptera heterostegia, Balkwill 174* (c); *Dicliptera clinopodia, Balkwill 213* (d); *Metarungia galpinii* (Baden) Baden, *Batten sub Balkwill 1725* (e); *Peristrophe cernua, Balkwill 450* (f,j); *P. sp.1, de Winter & Leistner 5828* (g); *Anisotes rogersii* S. Moore, *Strey 3497* (h); *Ruelliopsis setosa* C.B. Clarke, *Balkwill 1656* (i) and *Ruellia patula* Jacq., *Balkwill & Manning 628* (k). Scale line = 1 cm.


a
b
c
d
e
f
g
h
i
j
k

than in the other genera and the septum separates into thickened raphes, one at each side of the septum and a pair of placentae (fig. 30 & plate 4c & d). Each placenta bears two retinacula and is joined to a raphe only at its tip. When the capsule dehisces, the raphes move outwards and the placentae upwards. Capsules of this form are described as having elastic placental bases. Elastic placental bases also occur in *Petalidium* Nees and *Phaulopsis* Willd. in the Petalidiinae and in *Metarungia* in the Justiciinae. The walls of the capsules of *Peristrophe* are opaque, while those of *Dicliptera* are slightly translucent (plate 4c & d).

During the survey of fruit morphology, it was noticed that the septum is incomplete in the fruits of many genera (including *Peristrophe* and *Dicliptera*). This character may reward investigation, as it may correlate with other data.

Figures 31 and 32 present the analysis of measurements of the length and width of the capsules of *Peristrophe* and *Dicliptera*. Within *Dicliptera* the fruit of *D. heterostegia* is significantly shorter than that of *D. zeylanica*. *D. clinopodia* and *D. fruticosa* have capsules that are significantly longer than those of *D. divaricata*, *D. minor*, *D. sp. 2* and *D. sp. 3*. The capsules of *D. fruticosa* are also significantly longer and broader than those of *D. eenii*, a very closely related species and significantly longer than those of any other species that has narrow bracts. The fruit of *D. fruticosa* also bulges noticeably when fresh, and this is very unusual in the genus. The capsules of *D. spinulosa* are significantly shorter and significantly narrower than those of any other species of *Dicliptera*.

There are two slightly different forms of capsule in *Dicliptera*. In *D. heterostegia* and *D. chinensis* L. (the type species), the raphes bend far back during dehiscence, so that they form an angle of about 180 degrees with one another (fig. 30a). The walls of the capsule split away from the raphe for more than half their length and the placenta is markedly curved, almost forming a semicircle. The capsules of other species (e.g. *D. clinopodia*), have raphes that bend back until they form an angle of about 120 degrees with each other (fig. 30b). In this form, walls of the capsule split away from the raphe for only the lower third (or slightly less) of their length and the placenta is less

Figure 30: Capsules of *Dicliptera*, with wall removed on one side to show the placenta: a) *D. clinopodia, Moura 47* (X17) and b) *D. heterostegia, Balkwill 340* (X17).

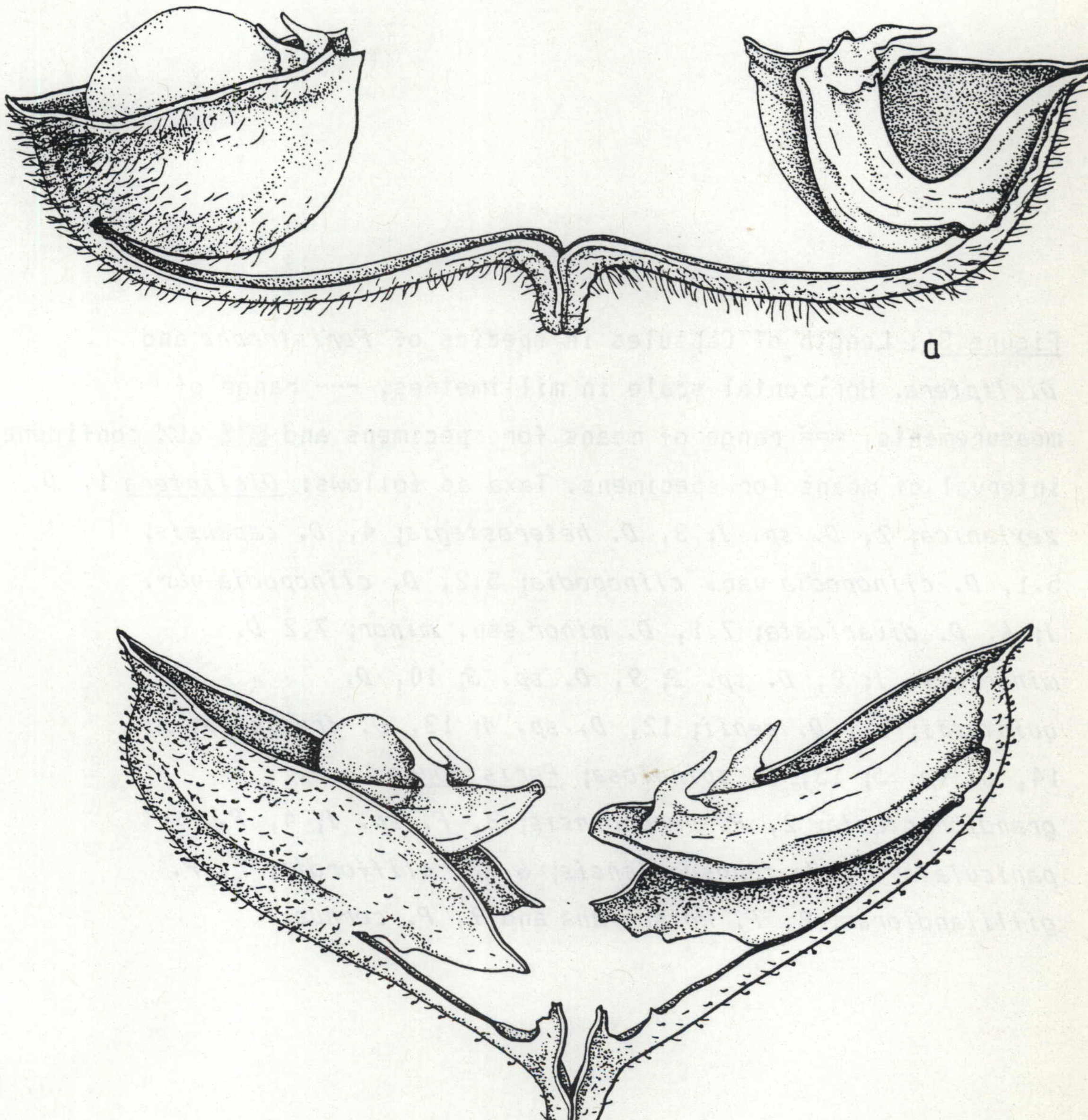

a
b
M.J.C.

Figure 31: Length of Capsules in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for specimens and ▓▓▓ 68% confidence interval of means for specimens. Taxa as follows: *Dicliptera* 1, *D. zeylanica*; 2, *D. sp. 1*; 3, *D. heterostegia*; 4, *D. capensis*; 5.1, *D. clinopodia* var. *clinopodia*; 5.2, *D. clinopodia* var. *1*; 6, *D. divaricata*; 7.1, *D. minor* ssp. *minor*; 7.2 *D. minor* ssp. *1*; 8, *D. sp. 2*; 9, *D. sp. 3*; 10, *D. quintasii*; 11, *D. eenii*; 12, *D. sp. 4*; 13, *D. fruticosa*; 14, *D. sp. 5*; 15, *D. spinulosa*; *Peristrophe* 1, *P. grandibracteata*; 2, *P. hereroensis*; 3, *P. sp. 1*; 4, *P. paniculata*; 5, *P. transvaalensis*; 6, *P. cliffordii*; 7, *P. gillilandiorum*; 8, *P. kotschyana* and 9, *P. cernua*.

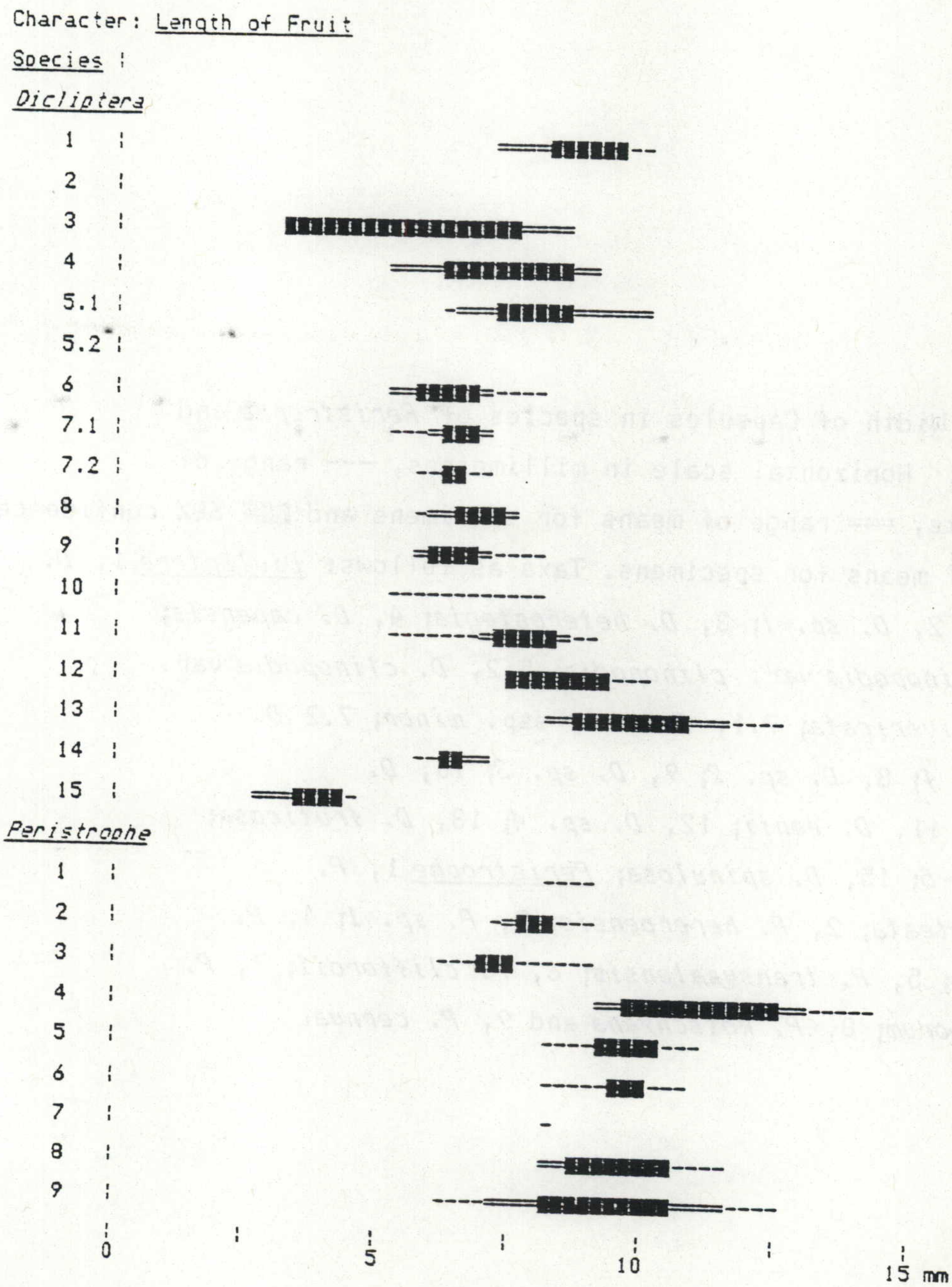
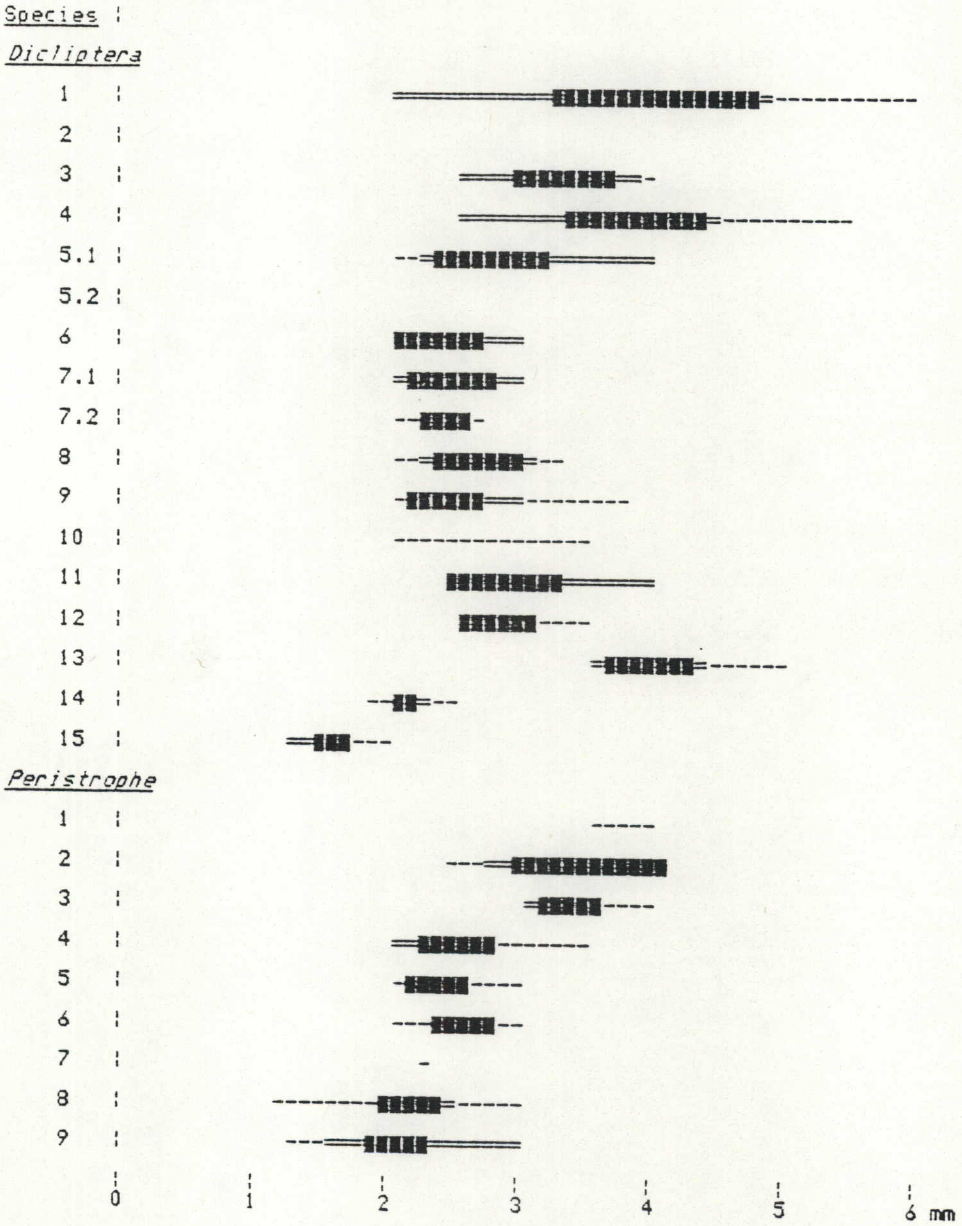

Character: Length of Fruit
Species
Dicliptera
1
2
3
4
5.1
5.2
6
7.1
7.2
8
9
10
11
12
13
14
15
Peristrophe
1
2
3
4
5
6
7
8
9
0
5
10
15 mm

Figure 32: Width of Capsules in species of *Peristrophe* and *Dicliptera*. Horizontal scale in millimetres, --- range of measurements, === range of means for specimens and ▓▓▓ 68% confidence interval of means for specimens. Taxa as follows: *Dicliptera* 1, *D. zeylanica*; 2, *D. sp. 1*; 3, *D. heterostegia*; 4, *D. capensis*; 5.1, *D. clinopodia* var. *clinopodia*; 5.2, *D. clinopodia* var. *1*; 6, *D. divaricata*; 7.1, *D. minor* ssp. *minor*; 7.2 *D. minor* ssp. *1*; 8, *D. sp. 2*; 9, *D. sp. 3*; 10, *D. quintasii*; 11, *D. eenii*; 12, *D. sp. 4*; 13, *D. fruticosa*; 14, *D. sp. 5*; 15, *D. spinulosa*; *Peristrophe* 1, *P. grandibracteata*; 2, *P. hereroensis*; 3, *P. sp. 1*; 4, *P. paniculata*; 5, *P. transvaalensis*; 6, *P. cliffordii*; 7, *P. gillilandiorum*; 8, *P. kotschyana* and 9, *P. cernua*.

Character: Width of Fruit



curved. In this latter form, the ovules are slightly further apart than they are in the former.

The capsules of *P. grandibracteata, P. hereroensis* and *P. sp. 1* are shorter than those of most other species and significantly broader than all other species in *Peristrophe*. The capsules of these three species are obtrullate rather than clavate as are those of the other species (fig. 33). In *P. grandibracteata, P. hereroensis* and *P. sp. 1*, the two ovules in each locule are attached at similar levels to one another, while in the other species the two ovules in the same locule are attached one above the other (fig. 33).

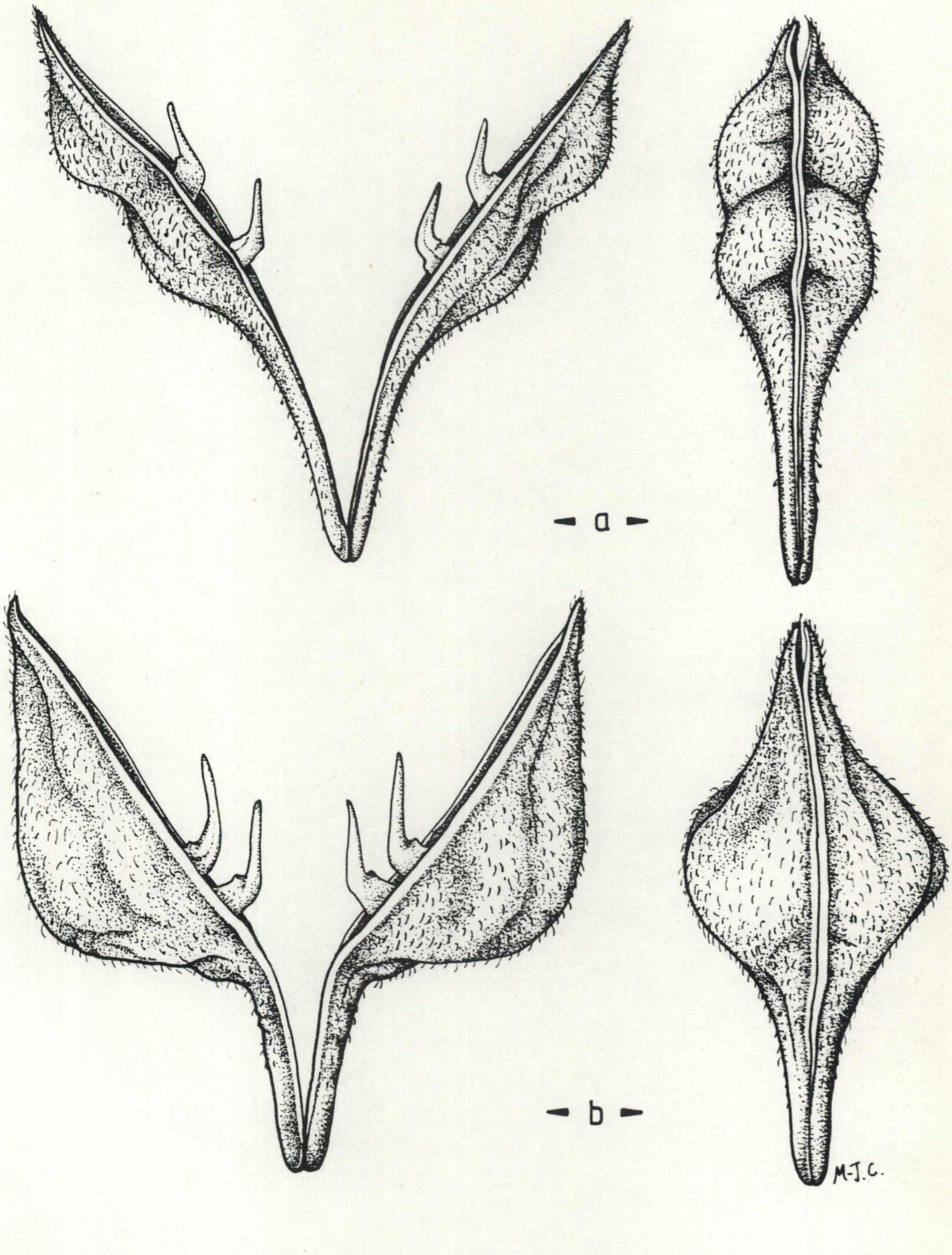
Discussion

The structure of the capsules and the number of ovules in each locule have provided important characters for the subdivision of the family. The relevance of these and of the elastic placental bases to the classification of the various genera in the family is discussed in chapter 14. There has been some debate about the value of the elastic placental base as a generic character (Hansen, pers. comm.). In Table 8, it can be seen that amongst the southern African genera, the phenomenon is uncommon, but that it must have evolved more than once. The only character that reliably separates *Dicliptera* from *Peristrophe* is the elastic placental base (Getliffe Norris, Balkwill & Manning, 1985). While there may be some doubt about the distinction between genera based on single characters, it must be realised that the different types of placental bases are real and are present and that little would be gained by disregarding this character and making a single genus from these two genera.

Although there are two different forms of capsule in *Dicliptera*, their distributions do not correlate with the groups that could be constructed on the basis of morphology of bracts or any other feature. *D. zeylanica*, which is otherwise very similar to *D. heterostegia*, has a capsule more similar to that of *D. clinopodia* (fig. 30b) than to that of *D. heterostegia* (fig. 30a).

Within *Peristrophe*, the two forms of the capsule correlate with the groups into which the southern African species are divided on the basis

<u>Figure 33</u>: Capsules of *Peristrophe*. a) *P. cernua, Balkwill 168* (X7) and b) *P. grandibracteata, Kinges 2446* (X11).


a
b
M-J.C.

of the structure of their bracts. This supports the view that it is possible to subdivide the genus *Peristrophe* into two sections, on the basis of the morphology of bracts and fruits.

The sizes of the capsules differ in different species so that they can be used to distinguish between species and thus are used in the key to the species of *Dicliptera*. The differences in the size of the capsules of *D. fruticosa* confirms the view that it is a species different from *D. eenii*, a species with which it may often be confused.

Conclusion

The structure of the capsules of *Peristrophe* and *Dicliptera* is the only single character that reliably separates the two genera. The shape of the capsule in *Peristrophe* corroborates the view that the genus can be subdivided into sections and measurements of the length and width of capsules help to distinguish between species of both genera. *

CHAPTER 7
PALYNOLOGY

Introduction

Pollen morphology has long been recognised as an important feature of this family. Indeed, Lindau (1895) relied very heavily on this feature in his classification. More comprehensive surveys have, however, often revealed gaps in Lindau's information (Immelman; 1983). Burkill & Clarke (1899) were particularly critical of the absolute reliance on pollen features as generic markers, nevertheless, there appear to be common patterns within tribes against which aberrant genera can be contrasted. Features which are emphasised are the shape of the grain, the nature of the apertures, the texture of the exine and the presence or absence of a margocolpus. Raj (1961) published a comprehensive survey of the pollen of the Acanthaceae using the light microscope. Since that time, Bremekamp (1965) published a revised subdivision of the Acanthaceae and scanning electron microscopes, which have a large depth of field and allow three-dimensional views, have become more readily available. No-one has published a comprehensive survey of Acanthaceous pollen since these two very important events. I have conducted a survey of the pollen morphology of southern African Acanthaceae in order to aid my understanding of the classification of *Peristrophe* and *Dicliptera* in particular and of the family as a whole.

Material and Methods

At first, fresh pollen grains were placed in glacial acetic acid, rinsed twice with distilled water and placed on stubs in a drop of distilled water, which was then allowed to evaporate. Once the water had evaporated, the stub was placed in a desiccator overnight and then coated with gold palladium with a Polaron E5100 sputter-coater. Pollen from herbarium material was boiled briefly in glacial acetic acid, then rinsed in distilled water and prepared in the same way. Results from these methods were sometimes unsatisfactory, so others were tried. Untreated pollen was then placed on stubs in distilled water, the water evaporated and then the material dried and coated as before. In these instances, the volume of the pollen cytoplasm was increased by osmosis and the cytoplasm exuded from the pore and obstructed viewing, so that this method was also abandoned. It was found that the most successful method of preparing the pollen was to place untreated pollen from fresh or herbarium material onto a dry stub or onto double-sided cellotape on a stub and then to dry the pollen in a desiccator overnight before coating and viewing. Measurements of pollen grains were made from the images on electron micrographs.

Observations

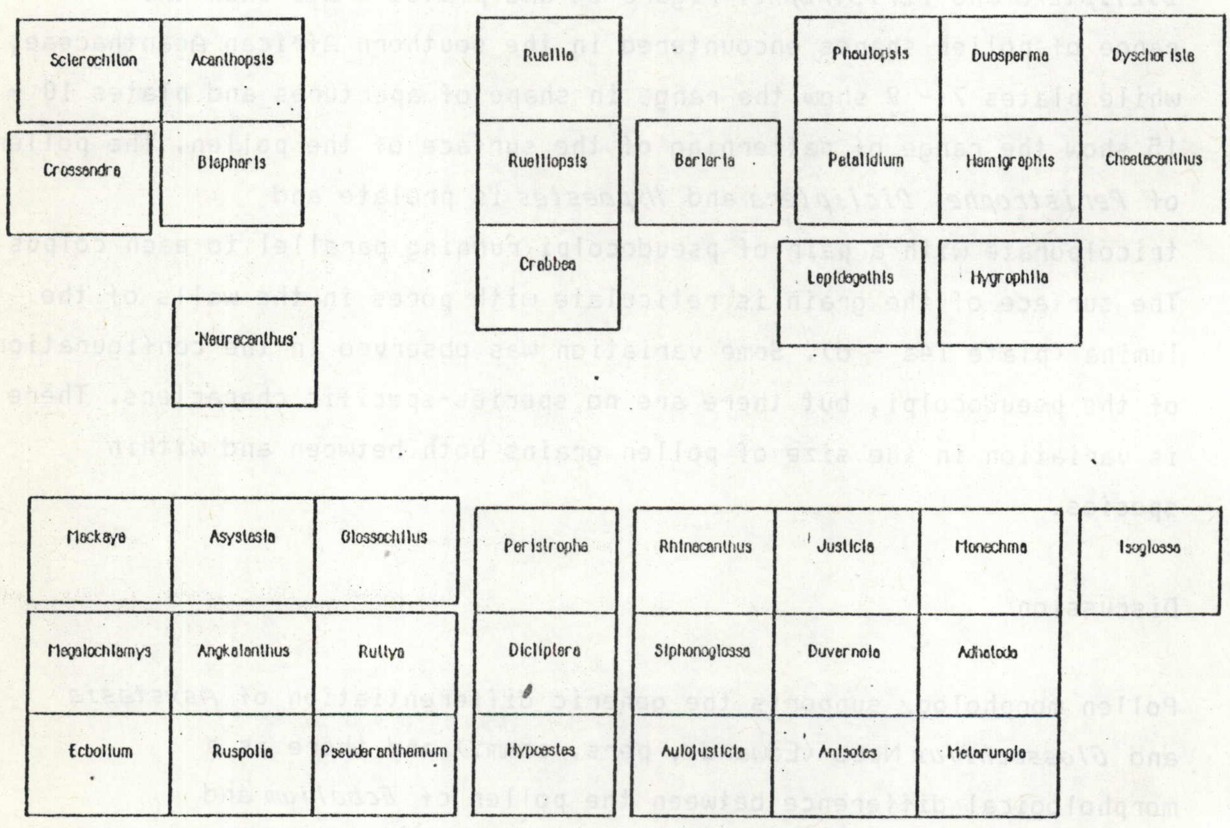
Table 9 provides a summary of the distribution of the features of the pollen throughout the southern African members of the Acanthaceae. Table 10 presents the measurements of the pollen of some species of *Dicliptera* and *Peristrophe*. Figure 34 and plates 5 & 6 show the range of pollen shapes encountered in the southern African Acanthaceae, while plates 7 - 9 show the range in shape of apertures and plates 10 - 15 show the range of patterning of the surface of the pollen. The pollen of *Peristrophe*, *Dicliptera* and *Hypoestes* is prolate and tricolporate with a pair of pseudocolpi running parallel to each colpus. The surface of the grain is reticulate with pores in the walls of the lumina (plate 14a - d). Some variation was observed in the configuration of the pseudocolpi, but there are no species-specific characters. There is variation in the size of pollen grains both between and within species.

Discussion

Pollen morphology supports the generic differentiation of *Asystasia* and *Glossochilus* Nees (Edwards, pers. comm.) and there is a morphological difference between the pollen of *Ecbolium* and *Megalochlamys* Lindau (pers. obs.). Manning (1983) and Immelman (1983) have found that there is some correlation between morphological characters (such as inflorescence morphology and seed surface sculpturing) and morphology of pollen in *Adhatoda* Nees, *Duvernoia* [E. Mey. ex] Nees and *Justicia*. Baden (1981b) found that morphology of the pollen of *Anisotes* Nees not only provided support for the division of the genus into sections, but sufficiently distinctive characters for a key (based on pollen characters) to those sections and to the species. In *Hypoestes*, Balkwill and Getliffe Norris (1985)

Table 9: Distribution of features of pollen of the genera of southern African Acanthaceae.

Genera arranged as in key below, characters as follows: A = areolate, B = banded or with many pseudocolpi, C = colpate, CP = colporate, F = foveolate, L = aperture lipped, LR = with large reticulations, P = prolate, PC = with pseudocolpi, Po = porate, Pu = pusticulate, R = reticulate, S = spheroidal, Sp = spinose, SR = with shallow reticulations and numbers = number of apertures.



3 C P SR	3 C P SR
3 C P F	3 C P SR

3 CP S F

3 Po S LR
3 Po^{L} S R B
3 Po S LR

3 Po S LR

3 Po^{L} P R PC	3 Po^{L} P R PC	3 (CP)^{L} P Pu B
3 Po^{L} P R PC	3 CP P SR B	3 (CP)^{L} P Pu B

3 CP P LR	3 CP P R B

3 CP S R PC	3 CP P R PC	2 CP S R PC
3 CP P R	3 CP S R	3 CP S R PC
3 CP S R PC	3 CP (P) R (PC)	3 CP P R PC

3 CP P R PC
3 CP P R P
3 CP P R PC

3 CP P R PC A	2 CP P R PC A	2 CP P
2 CP P R PC A	2 CP P R PC	2 CP P R PC A
2 CP P R PC A	2 3 CP P 4 R PC A	2 CP P R PC A

2 Po S Pu+Sp

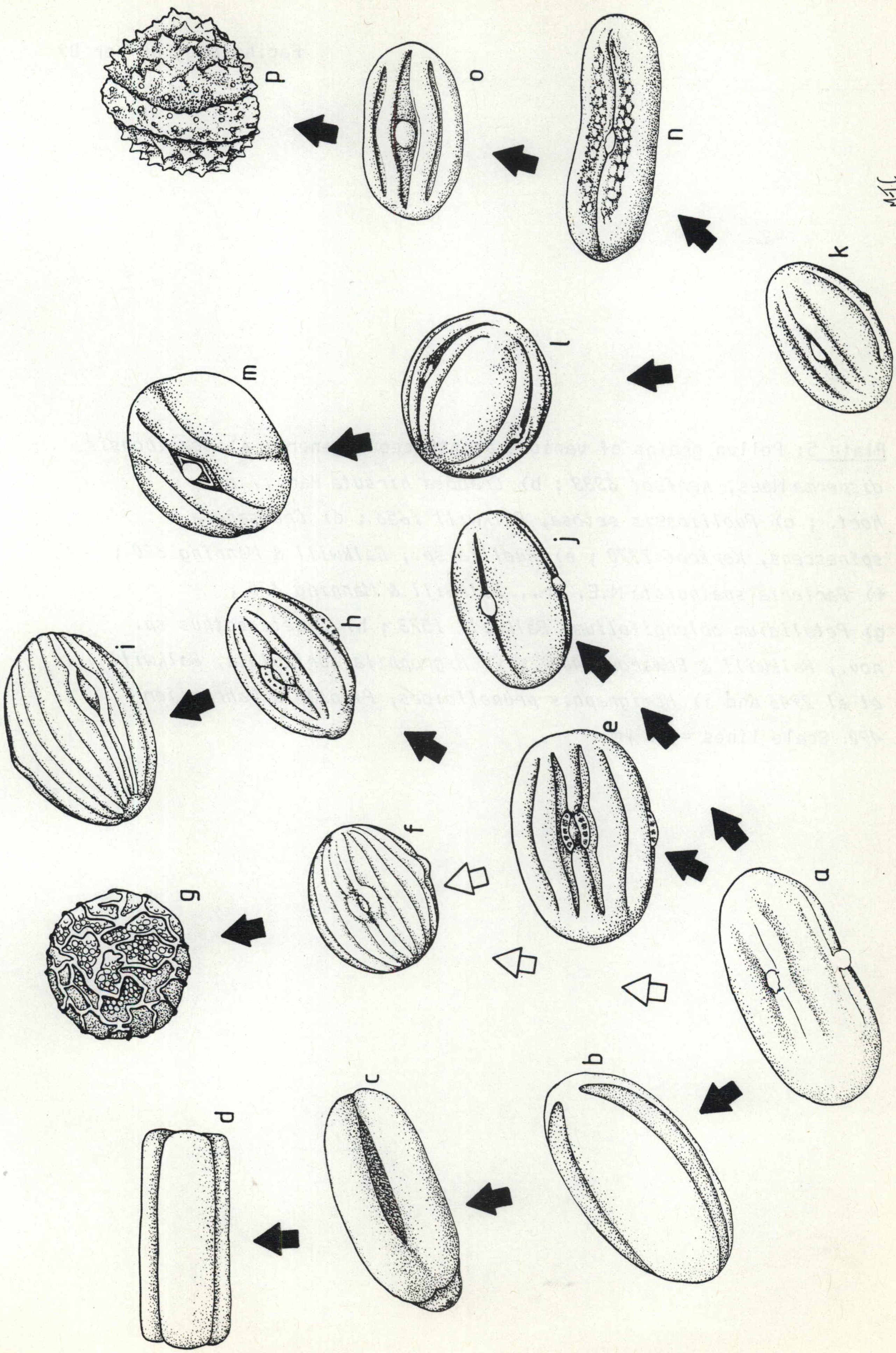
Table 10: Sizes of pollen grains of some species.

Species	Length µm	Breadth µm	Ratio l : b	n	N
Peristrophe					
P. transvaalensis	34,76 ± 0,00	23,81 ± 0,67	1,46 ± 0,041	2	1
P. kotschyana	38,1	21,43	1,778	1	1
P. cernua	35,03 ± 2,89	24,37 ± 1,018	1,44 ± 0,142	6	4
Dicliptera					
D. zeylanica	39,29 ± 5,62	27,74 ± 2,14	1,44 ± 0,170	6	4
D. capensis	32,38 ± 0,67	28,57 ± 0.67	1,13 ± 0,003	2	1
D. clinopodia	50,39 ± 9.50	30,22 ± 4,97	1,66 ± 0,200	10	9
D. divaricata	38,47 ± 5,67	24,66 ± 5,52	1,59 ± 0,206	4	3
D. minor	35,00 ± 4,38	20,24 ± 0,34	1,73 ± 0,188	2	1
D. sp. 3	39,05	22,38	1,745	1	1
D. fruticosa	43,13	27,5	1,568	1	1

n = number of grains measured

N = number of different collections from which grains were measured

Figure 34: Putative course of evolution of shape of pollen grains in the southern African members of the Acanthaceae: a) putative primitive grain, prolate with three apertures; b - d) grains of the Acanthoideae, c & d) fossaperturate, d) with squared ends; e - i) grains of the Ruellieae, e & h) subprolate, f) subglobose, g) globose, i) prolate; j) grain of Lepidagathideae, prolate; k - p) grains of Justicieae, k) prolate, triaperturate, l) subprolate, triaperturate, m) lenticular, biaperturate, n) prolate, biaperturate, o) subprolate, biaperturate and p) globose, biaperturate.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<u>Plate 5</u>: Pollen grains of various acanthaceous genera: a) *Acanthopsis disperma* Nees, *Kerfoot 6333* ; b) *Crabbea hirsuta* Harv., *ex hort.* ; c) *Ruelliopsis setosa, Balkwill 1656* ; d) *Crossandra spinescens, Kerfoot 7370* ; e) *Ruellia sp., Balkwill & Manning 690* ; f) *Barleria spathulata* N.E. Br., *Balkwill & Manning 675* ; g) *Petalidium oblongifolium, Balkwill 1573* ; h) *Chaetacanthus sp. nov., Balkwill & Edwards 1406* ; i) *Hygrophila auriculata, Balkwill et al 2946* and j) *Hemigraphis prunelloides, Pienaar & Vahrmeijer 490.* Scale lines = 10 µm.

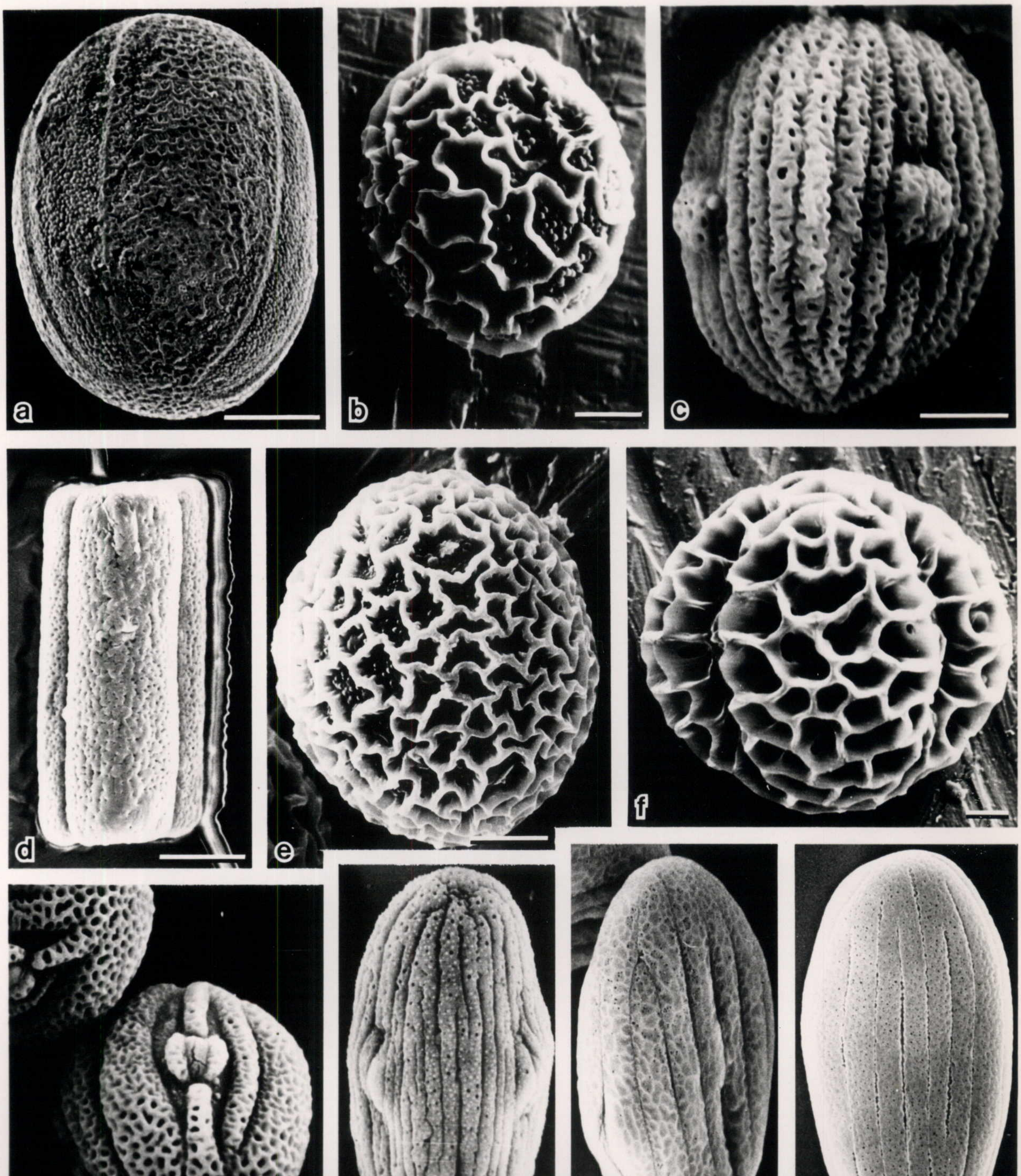
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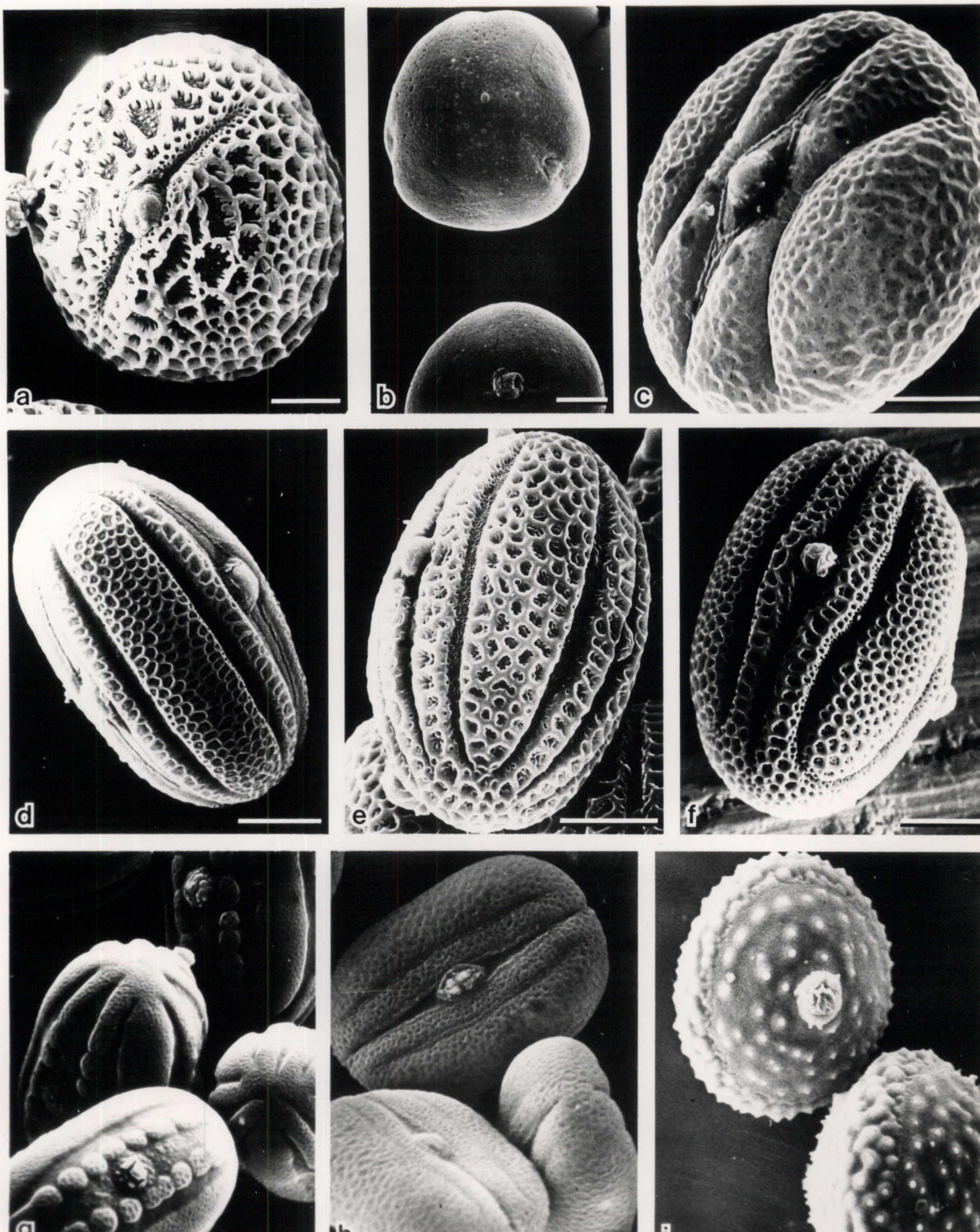
Plate 6: Pollen grains of various acanthaceous genera: a) *Lepidagathis scabra* C.B. Clarke, *Jacobsen 2391* ; b) *Neuracanthus africanus, Balkwill 1620* ; c) *Glossochilus burchellii* C.B. Clarke, *Leistner 1397* ; d) *Dicliptera sp. 4, Balkwill 1574* (e); *Periestes sp., Baron 6138* ; f) *Rhinacanthus gracilis, Balkwill 471* ; g) *Anisotes rogersii, Balkwill 1622* ; h) *Duvernoia aconitiflora* A. Meeuse, *Balkwill 1518* and i) *Isoglossa hypoestiflora, Balkwill 344* .
Scale line = 10 µm.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found that although there was variation in the configuration of the pseudocolpi, this variation was not consistent within or between species and therefore was not a taxonomically useful character. As the pollen morphology of species of *Dicliptera* and *Peristrophe* is almost identical, there are no characters that can be used to differentiate between these genera, between sections in the genera or between species. Although the pollen grains of *D. clinopodia* are significantly larger than those of the other species measured, the samples are too small to decide whether or not this difference is diagnostic.

The morphology of the pollen of all southern African genera of the Acanthaceae has been important in making decisions about the classification of the southern African genera. The Acanthoideae are characterised by colpoid pollen (plate 5a & d), but that of *Crossandra* Salisb. differs in shape (plate 5d). In the Ruellioideae colporate or porate grains are found. Ruelliinae and Barleriinae have spheroidal, porate pollen (plate 5b, e & f). Petalidiinae *sensu* Bremkamp have prolate grains with bordered pores in bands of solid exine (plate 5g & h). The tribe Justicieae is characterised by colporate grains with pseudocolpi (colpoid streaks *sensu* Raj 1961) (plate 6c - h). Within subtribes of the Justicieae, a range of pollen morphs is found. *Isoglossa* Oerst. has spheroidal pollen unlike that of any other southern African genus in the family (plate 6i) with two polar pores, a girdle of pusticulate exine around the equatorial circumference and a spinescent surface.

Although Walker & Doyle (1975) present guidelines for the interpretation of evolutionary trends in pollen characters, it was not easy to determine patterns in the apparently highly derived, eurypalynous Acanthaceae. It was very difficult to visualise a single line of evolution that would lead to the derivation of pollen morphs as different as those of *Crabbea* Harv. (plate 5b) and *Anisotes rogersii* S. Moore (plate 6g). If, however, evolutionary trends are sought within the subfamilies, tribes and in some cases subtribes that are proposed o r accepted in chapter 14, more meaningful trends can be found. Evolutionary trends in three characters were analysed, and are presented in fig. 34 and plates 7 - 15. The most difficult step in formulating these evolutionary trends has been to decide what the primitive Acanthaceous pollen looked, or looks, like.

Within the family, the most commonly occurring shape of grain is prolate with three apertures, some of the exceptions being the spheroidal grains of *Ruellia* and *Isoglossa* and bicolporate grains of *Glossochilus* and *Duvernoia aconitiflora* A. Meeuse. Although Walker & Doyle (*loc. cit.*) generally regard spheroidal grains as less advanced, in the Acanthaceae this shape is most often associated with highly derived features of sculpturing and apertures so that it seems probable that, in the Acanthaceae, prolate grains are basic and spheroidal grains derived. Thus I think the primitive grain would have been prolate with three apertures.

There are colpi, pores and colpori present in the the pollen of the family, with colpori most common in the Justicieae; pores, colpi and colpori present in the Ruellieae and colpi present in the Acanthoideae. The primitive acanthaceous pollen may have been colporate, with shallow colpi like the apertures of *Neuracanthus* (plate 7a). Colporate grains with distinct colpi may have evolved by the deepening of the colpi, those with pores by the loss of the colpi and those with colpi by the loss of the pores.

The primitive pollen grain would probably have had a relatively undissected tectum. The pollen of *Anisotes rogersii* is tectate imperforate (plate 15 a) and probably has the most primitive pollen surface present amongst the southern African members of the family. The pollen of *Neuracanthus africanus* [T. Anders. ex] S. Moore has colpori with relatively indistinct colpi, and has a foveolate surface. Although it is not prolate, I think that, in terms of the surface and the aperture, this pollen morph is one of the most primitive extant in the southern African Acanthaceae.

Figure 34 presents a possible scheme of evolution of pollen shape within southern African members of the Acanthaceae. Within the Acanthoideae, the pollen shape of *Acanthopsis* Harv. (plate 5a) with its prolate grain and three apertures is relatively unspecialised, while the grain of *Sclerochiton* Harv. is derived in terms of its amb type, which is fossaperturate. The fossaperturate grain of *Crossandra*, however, with its squared ends is derived, as is the highly specialised grain of

Crossandra stenostachya Lindau, described by Brummitt *et al* (1980), which is much longer than any other grain reported in the family.

In the Ruellieae, the subprolate grain of *Petalidium* would be the first step in the evolution from the primitive form. From this subprolate shape, a line may lead to the subglobose grain of *Ruellia* and then to the globose grain of *Crabbea*. If one considers the aperture, the dissection of the surface of the pollen as well as the morphology of the corolla and stamens of *Chaetacanthus*, it will be seen that these features are advanced. Thus, it seems possible that the prolate grain of *Chaetacanthus* may be secondarily derived. The evolution of the shape of the pollen in the Petalidiinae would follow from the subprolate grain of *Petalidium*, to the grain of *Phaulopsis* and thence to the prolate grain of *Chaetacanthus*.

Within the Justicieae, there are two lines of evolution of shape. One (in the subtribe Odontoneminae) leads from the triaperturate prolate grains such as those of *Megalochlamys*, to the subglobose triaperturate grains such as those of *Ecbolium* and from there to the lenticular biaperturate grain of *Glossohilus*. Within the subtribes Diclipterinae, Justiciinae and Isoglossinae, there is a line from the primitive prolate, triaperturate grain to the prolate biaperturate grain (e.g. *Aulojusticia sp. nov.*), from this to the shortly prolate biaperturate grain of *Duvernoia aconitiflora* and from that to the globose biaperturate grain of *Isoglossa hypoestiflora* Lindau.

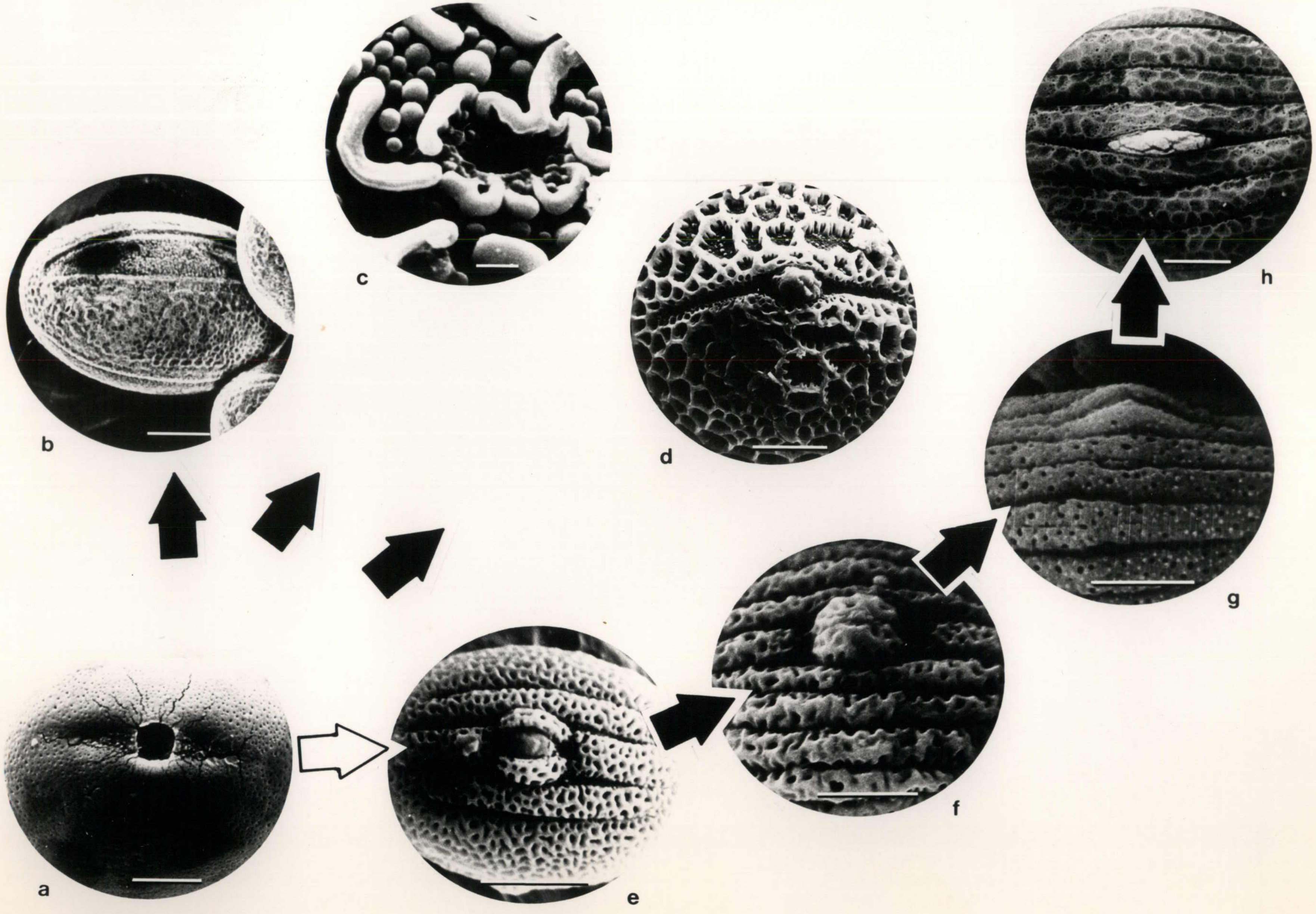
Plates 7 - 9 present a scheme of evolution of the types of apertures found in southern African Acanthaceae. From the putatively primitive colporate aperture of *Neuracanthus africanus*, evolution to a colpus can occur by the specialisation of the colpus and the loss of the pore to produce colpi as are found in the Acanthoideae. The evolution of the pore in pollen morphs such as those of *Crabbea* in the Ruellieae, could be by the loss of the colpus and the specialisation of the pore of the putatatively primitive grain. *Lepidagathis* in the Lepidagathideae has a colporus that may have evolved directly from the primitive aperture by an emphasis of the colpus, to produce a distinctly colporate aperture. The relationship of the Lepidagathideae to the Ruellieae is, however, uncertain. It seems unlikely that such similar, derived surface sculpturing would have arisen independently, yet the derivation of the pore of the Ruellieae and the colpus of Lepidagathideae must be along independent divergent lines.

Within the Petalidiinae and Hygrophillinae, there seems to have been an intial evolution of pseudoapertures, in this case pseudocolpi, before there were any other changes. These pseudocolpi function in a harmomegathic capacity (Walker & Doyle, 1975). As the pores are functional for the emergence of the pollen tube from the colporate grains, it seems that the colpi of these colporate apertures also have a primarily harmomegathic function. I think that pollen such as that of *Phaulopsis* (plate 7e), which has fewer pseudocolpi, is probably more primitive than that of *Chaetacanthus* (plate 7g), which has many pseudocolpi. This has influenced my view of the evolution of the apertures in this group, as circular pores are correlated with fewer pseudocolpi (c.f. plate 7e and plate 7h). The course of evolution in this group would involve an increase in the number of pseudocolpi and an increase in the length of the aperture, from the pore of *Phaulopsis*, via the slightly elongated pore of *Ruelliopsis* C.B. Clarke (plate 7f) and *Chaetacanthus* (plate 7g) to the colporus (with an elongated pore) of *Hygrophila* (plate 7b).

Within the Odontoneminae (plate 8), evolution would proceed from a grain, like that of *Megalochlamys* (plate 8a), which has pores, faint colpi and no pseudocolpi, to a grain like that of *Ecbolium* (plate 8b), which has clearly defined colpori and pseudocolpi that are discreet. From this form, there is a divergence to the form found in *Asystasia gangetica* (L.) T. Anders. *sensu lato* (plate 8c), where the clearly defined colpori and pseudocolpi are confluent at the poles, and to the form found in cleistogamous plants of *Pseuderanthemum subviscosum* (C.B. Clarke) Stapf (plate 8d), which are colpate rather than colporate.

Within the southern African Justiciinae, Diclipterinae and Isoglossinae, it seems that the grain with the most primitive aperture configuration is a grain such as that of *Rhinacanthus* Nees and *Dicliptera* (plate 9a), which is colporate with a pair of pseudocolpi parallel to each colporus. From this there seems to be a bifurcation of the evolutionary trend. The first branch leads to forms such as that of *Anisotes rogersii* (plate 9b), where the margocolpi (ridges between the colpi and

Plate 7: Evolution of apertures in southern African Acanthoideae and Ruellioideae: a) putatatively primitive colporus, *Neuracanthus africanus, Balkwill 1620* ; b) colpus of Acanthoideae, *Acanthopsis disperma, Kerfoot K6333* ; c) pore of Ruelliinae, *Crabbea sp., ex hort.* ; d) colporus of Lepidagathideae, *Lepidagathis scabra* C.B. Clarke, *Jacobsen 2391* ; e - h) apertures of Petalidiinae: e) pore with few pseudocolpi, *Phaulopsis imbricata* (Forsskal) Sweet, *ex hort.* ; f) slightly elongated pore with many pseudocolpi, *Ruelliopsis setosa, Balkwill 1656* ; g) elongated pore with many pseudocolpi, *Chaetacanthus sp. nov., Balkwill and Edwards* 1406 and h) colpus with many pseudocolpi, *Hygrophila auriculata, Balkwill et al 2946.* Scale lines all = 10 µm except c) where scale line = 20 µm.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<u>Plate 8</u>: Evolution of pollen apertures in south African Odontoneminae: a) colporus with indistinct colpus and no pseudocolpi, *Megalochlamys strobilifera, Balkwill 166* ; b) colporus with distinct colpus and pseudocolpi, *Ecbolium flanaganii* C.B. Clarke, *ex hort.* ; c) colpori and pseudocolpi that are continuous at the poles, *Asystasia gangetica sensu lato, ex hort.* and d) colpi and pseudocolpi, *Pseuderanthemum subviscosum, ex hort.*. Scale lines all = 10 µm.

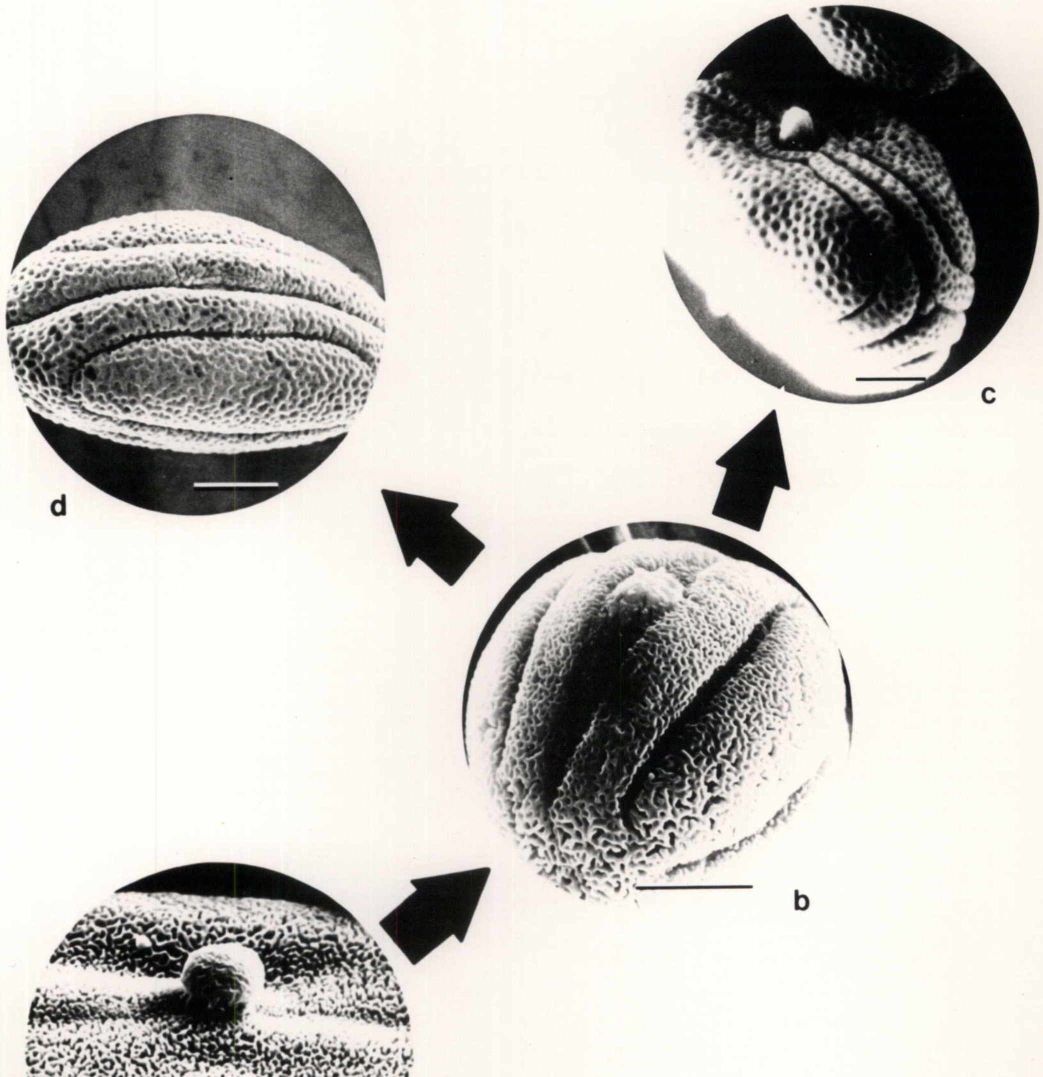
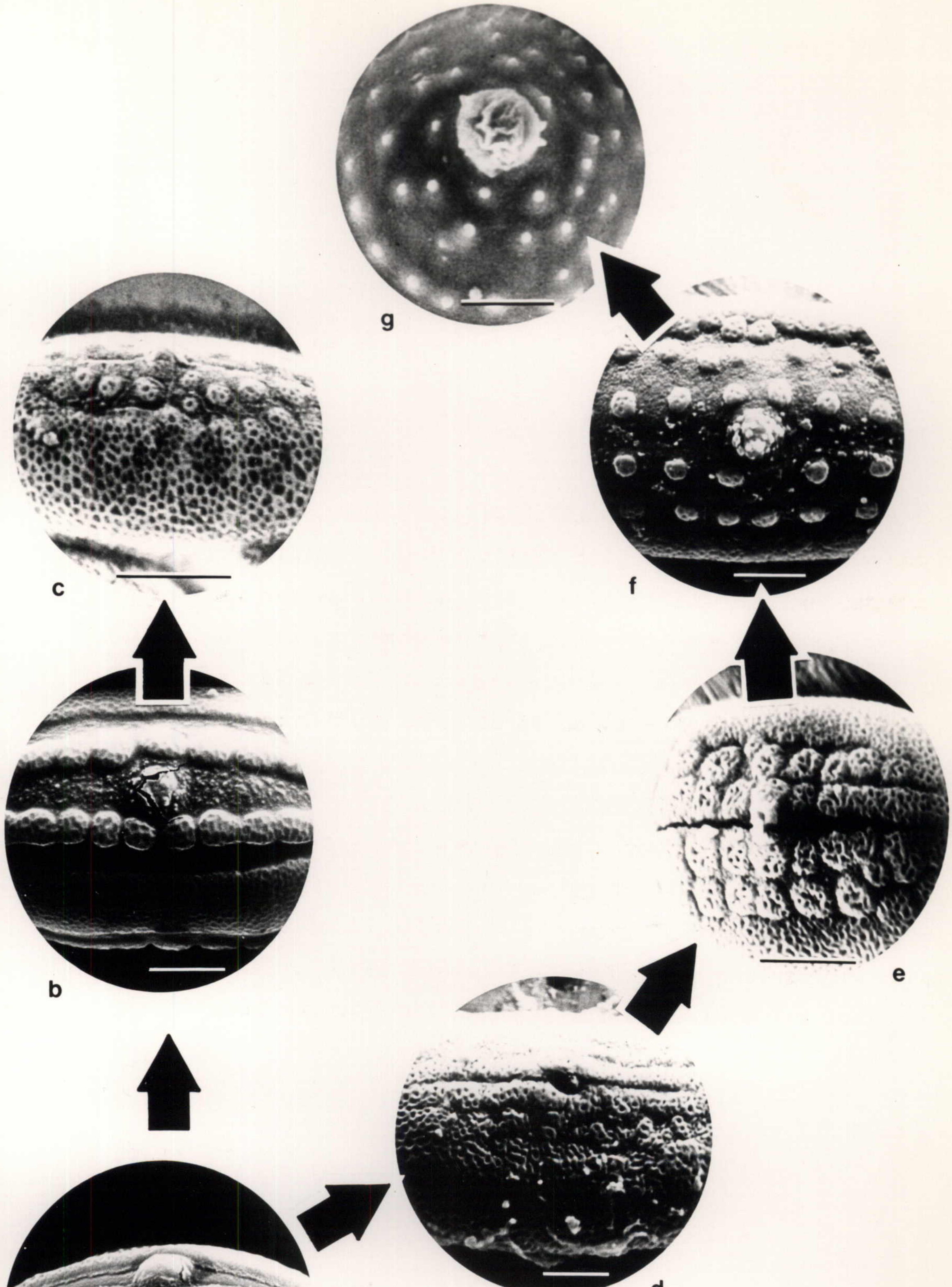


Plate 9: Evolution of apertures in Diclipterinae, Justiciinae and Isoglossinae: a) colporus with continuous margocolpi, *Dicliptera fruticosa, Balkwill 1574* ; b) colporus with dissected margocolpus, *Anisotes rogersii, Balkwill 1622* ; c) colporus bounded by a row of areoli and by pseudocolpi, *Monechma debile* (Forsskal) Nees, *Balkwill & Edwards 1407* ; d) colporus with two pseudocolpi on each side, *Siphonoglossa leptantha* ssp. *lateovata* ; e) colporus with two pseudocolpi, the margocolpi and ridges between pseudocolpi dissected into areoli, *Siphonoglossa leptantha* ssp. *leptantha , ex hort.* ; f) colporus with indistinct colpus and two indistinct pseudocolpi on each side, *Metarungia longistrobus, Balkwill & Manning 666* and g) secondarily derived pore, *Isoglossa hypoestiflora, Balkwill 344.* Scale lines all = 10 µm except c and d) where scale line = 5 µm.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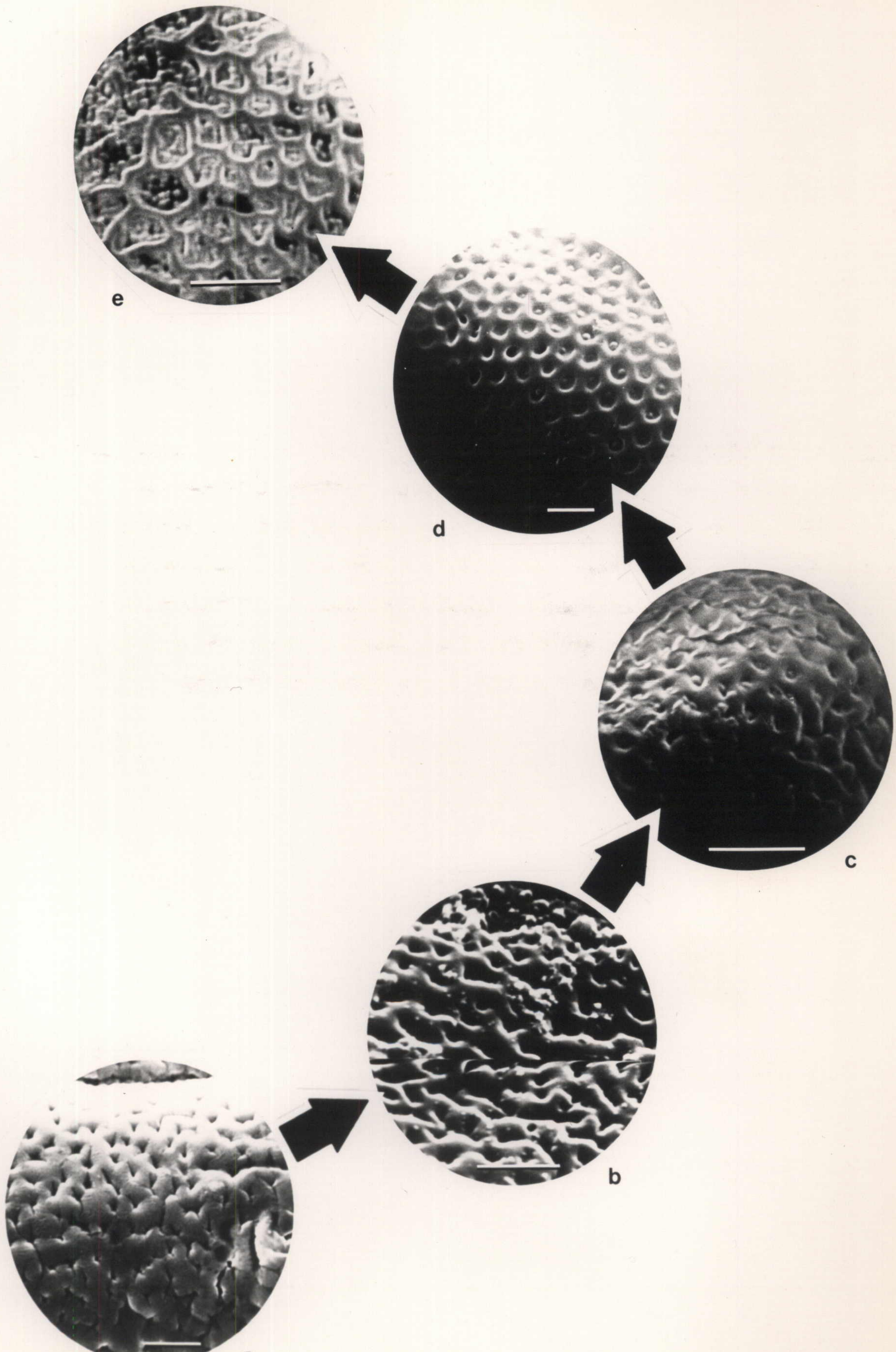
pseudocolpi) begin to become dissected and then to forms such as *Monechma*, where the margocolpi have become broken up into discreet areoli (plate 9c). The other branch leads to forms such as that of *Siphonoglossa leptantha* (Nees) Lindau ssp. *lateovata* Immelman *ined.* where a row of areoli is beginning to develop parallel to the margocolpi (plate 9d) and from this to a form such as that of *Siphonoglossa leptantha* ssp. *leptantha* (plate 9e), where each colporus is flanked by a pair of rows of areoli. With further reduction in the area of reticulation, forms such as the pollen of *Metarungia longistrobus* (C.B. Clarke) Baden (plate 9f) occur, where the areoli have become so small that the colpi of the colporus become indistinct. The final stage in this line leads to forms such as *Isoglossa hypoestiflora* (plate 9g), where the aperture is a secondarily derived pore. This pore has been derived by the reduction of much exine in the region in which there was a colporus, so that it is no longer possible to detect the colpus.

Evolution of the patterns of the exine also seem to have followed different paths in different tribes and subfamilies. From a primitive imperforate surface, a form such as *Neuracanthus africanus* (plate 11a) with small surface perforations would evolve. From this form, the forms found in the southern African Acanthoideae may have evolved. One of the first stages would resemble that of *Crossandra spinescens* Dunkley (plate 10a), where the perforations have become slightly larger. A sequence of increasing size of perforations would lead through a form like that of *Crossandra greenstockii* S. Moore (plate 10b) and *Blepharis natalensis* Obermeyer (plate 10c) to a form like that present in *Blepharis subvolubilis* C.B. Clarke (plate 10d). *Acanthopsis* (plate 10e) has larger perforations than other Acanthoideae, and these form a reticulate pattern of muri and lacunae. The floors of the lacunae have an uneven surface. The pollen of *Acanthopsis* has the most advanced sculpturing present in the southern African Acanthoideae.

Reticulate surface sculpturing, like that of *Petalidium oblongifolium* (plate 11b), could have been derived from that of *Neuracanthus* (plate 11a) by enlargement of the perforations in the tectum. The forms present in *Petalidium oblongifolium* C.B. Clarke (plate 11f) and *Barleria* (plate 11g) would be formed by a further enlarging of the holes in the

<u>Plate 10</u>: Evolution of surface sculpturing in pollen of southern African Acanthoideae: a) small perforations through tectum, *Crossandra spinescens, Kerfoot, K7370* ; b – d) increasing size of reticulations [b) *Crossandra greenstockii, Ward 1601* ; c) *Blepharis natalensis, Edwards 1211* ; d) *Blepharis subvolubilis, Balkwill & Manning 636*] and e) large reticulations with rough surface on floor of lacunae, *Acanthopsis disperma, Kerfoot K6333.* Scale lines all = 2 µm.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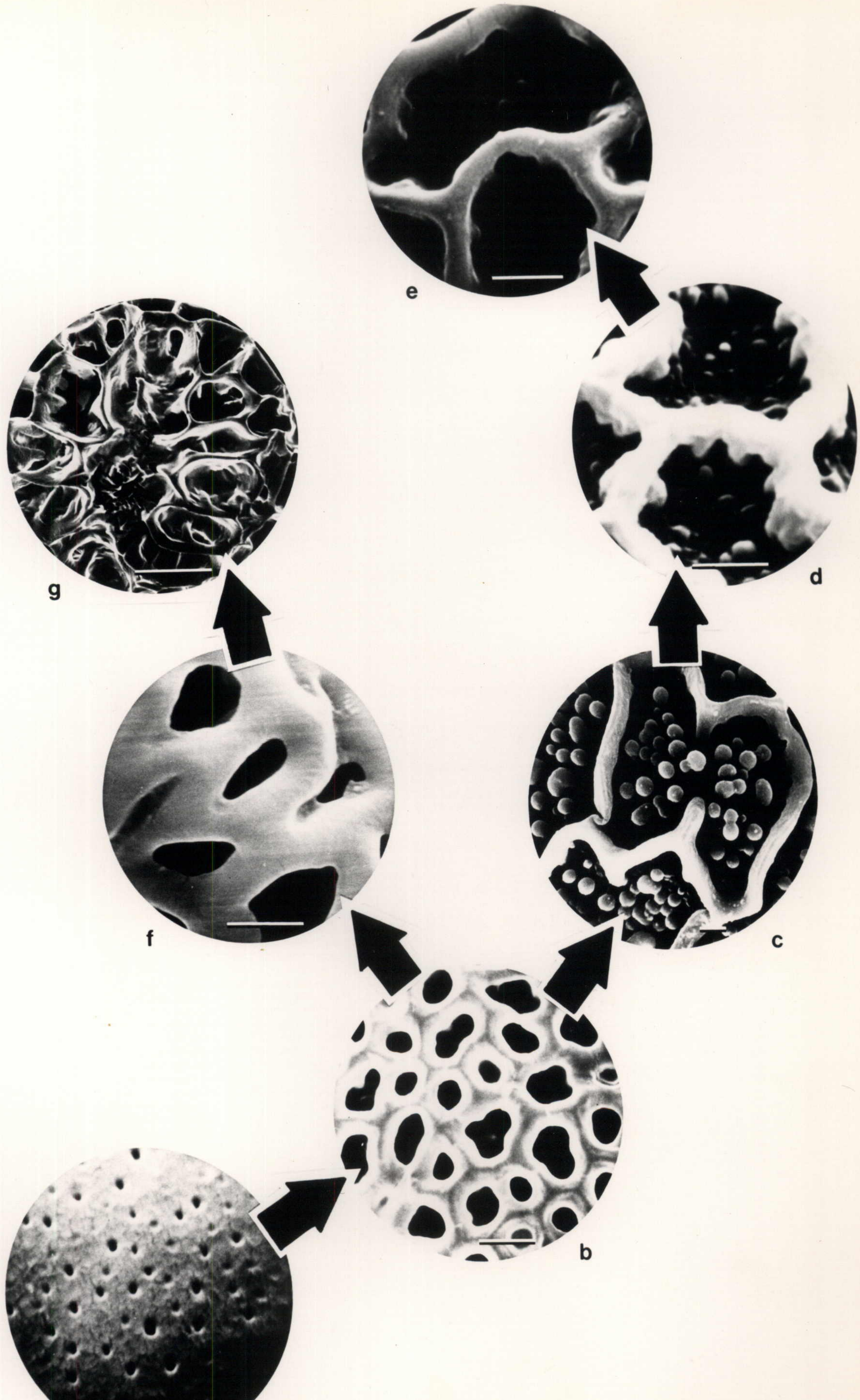
<u>Plate 11</u>: Evolution of surface sculpturing in some Ruellieae: a) foveolate surface with small perforations through tectum, *Neuracanthus africanus, Balkwill 1620* ; b) reticulate surface, *Petalidium oblongifolium, Balkwill 1573* ; c) larger reticulations with columellae between muri, *Crabbea sp. ex hort.*; d) large reticulations, with reduced number of columellae, *Lepidagathis scabra, Jacobsen 2931* ; e) large reticulations with very few columellae, *Ruellia sp., Balkwill & Manning 690* ; f) reticulations, larger and deeper than those of b), *Petalidium oblongifolium, Balkwill & Manning 669* ; and g) very large, very deep reticulations, *Barleria lancifolia, Balkwill 1484*. Scale lines all = 2 µm except g) where scale line = 20 µm.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tectum with a simultaneous heightening of the columellae that support the tectum and loss of the columellae in the lacunae. The step from *Petalidium oblongifolium* to *Crabbea* (plate 11c) involves an increase in the size of the perforations in the tectum, without a simultaneous loss of the columellae in the lacunae. A gradual reduction in the number of columellae would lead first to a surface like that of *Lepidagathis* (plate 11d) and then to that of *Ruellia* (plate 11e).

Plate 12 shows the possible course of evolution in the surface sculpturing of grains that have first been dissected by a large number of pseudocolpi to produce a surface like that of *Hemigraphis prunelloides* S. Moore, where the tectum is broken into many bands and is perforate (plate 12a). From this, evolution could take two courses, both involving the reduction of the area of the tectum. The first course would be by a coalescence of the perforations to form shallow lacunae, as in *Brillantaisia* Beauv. (plate 12b), followed by a deepening of the lacunae to form a surface like that of *Hygrophila auriculata* (Schumach.) Heine (plate 12c). If the lacunae then perforated right through the tectum, a surface like that of *Ruelliopsis setosa* (Nees) C.B. Clarke (plate 12d) would be formed. A complete loss of the tectum and considerable reduction in the number and size of the columellae would yield a surface like that of *Chaetacanthus sp. nov.* (plate 12e); further dissection of the lower surface would lead to the sculpturing seen in *Dyschoriste* Nees (plate 12f). The second evolutionary trend would begin from a form like that of *Strobilanthes isophyllus* T. Anders. (plate 12g) where the perforations are shallow and form only one lacuna across each band of the grain. Further erosion of the tectum might lead to a surface like that of *Sanchezia* Ruiz et Pavon (plate 12h), which may be further eroded to a form like that of *Chaetacanthus* (plate 12e).

The course of evolution in the Odontoneminae would be by a progressive deepening and enlarging of the perforations in the tectum which, from a surface like that of *Glossochilus* (plate 13a), would produce a sequence like that seen in *Ruttya ovata* Harv. (plate 13b), *Ruspolia hypocraterifomis* (Vahl) Milne-Redhead (plate 13c) and *Ecbolium amplexicaule* S. Moore (plate 13d). By a coalescence rather than enlargement of the perforations, evolution may have produced a surface

Plate 12: Evolution of surface sculpturing in some Petalidiinae and some Hygrophillinae: a) bands with small perforations, *Hemigraphis prunelloides* S. Moore, *Pienaar & Vahrmeijer 490* ; b) bands with coalesced perforations and more than one lacuna across a band, *Brillantaisia leonensis* Burkill, *Thompson sub J44010* ; c) band with deeper lacunae, *Hygrophila auriculata, Mogg 35156* ; d) bands with perforations right through tectum, *Ruelliopsis setosa, Balkwill 1656* ; e) bands with tectum reduced to a few small columnellae, *Chaetacanthus setiger* (Pers.) Lindl., Balkwill 721 ; f) bands with a few small columellae and with undersurface being eroded, *Dyschoriste fischeri* Lindau, *Balkwill & Manning 649* ; g) bands with large perforations into tectum, only one lacuna across each band, *Strobilanthes isophylla, Balkwill 1726* ; and h) bands with similar large lacunae that have perforated the tectum, *Sanchezia sp., ex hort.*. Scale lines all = 2 µm.

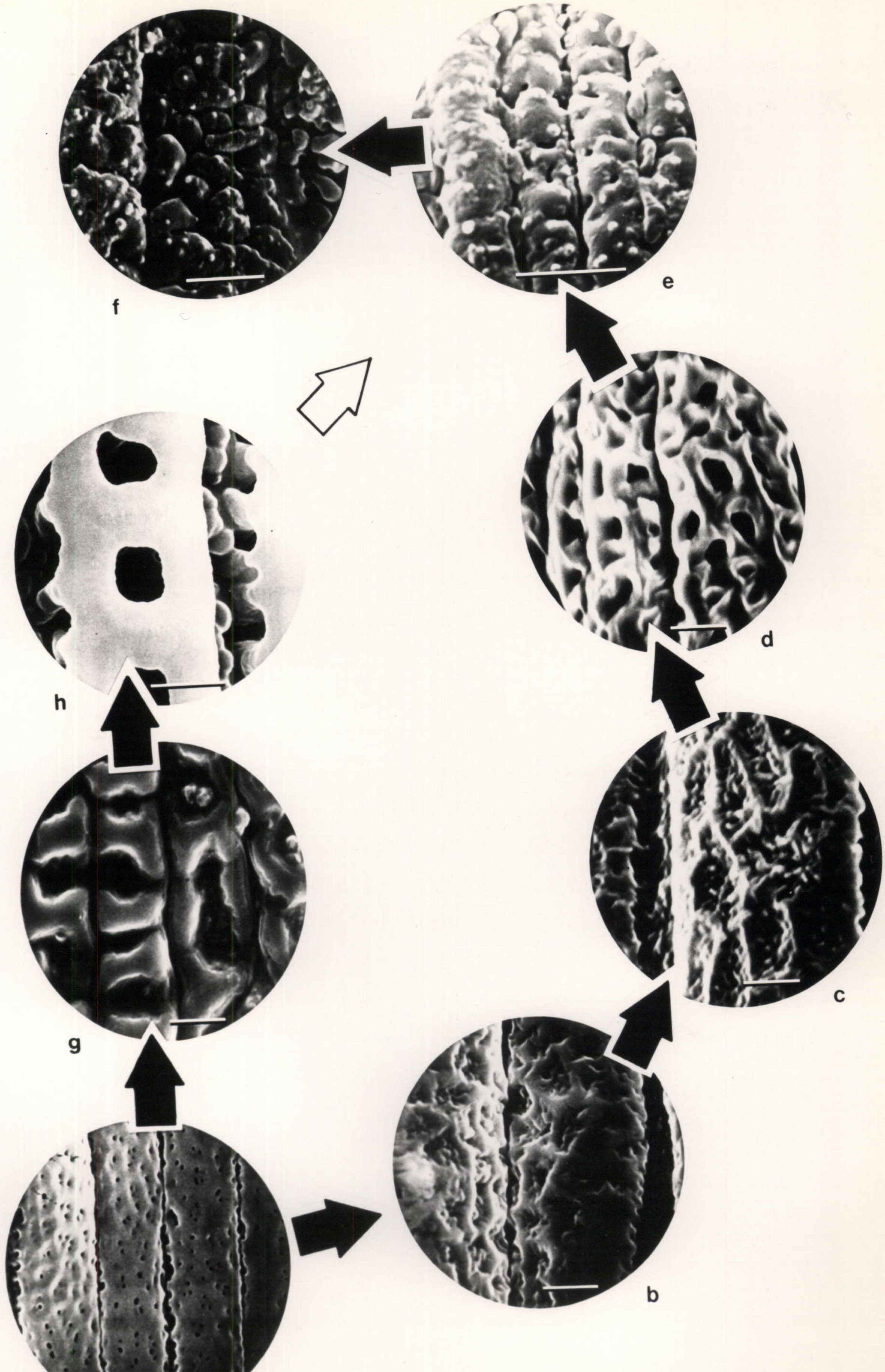
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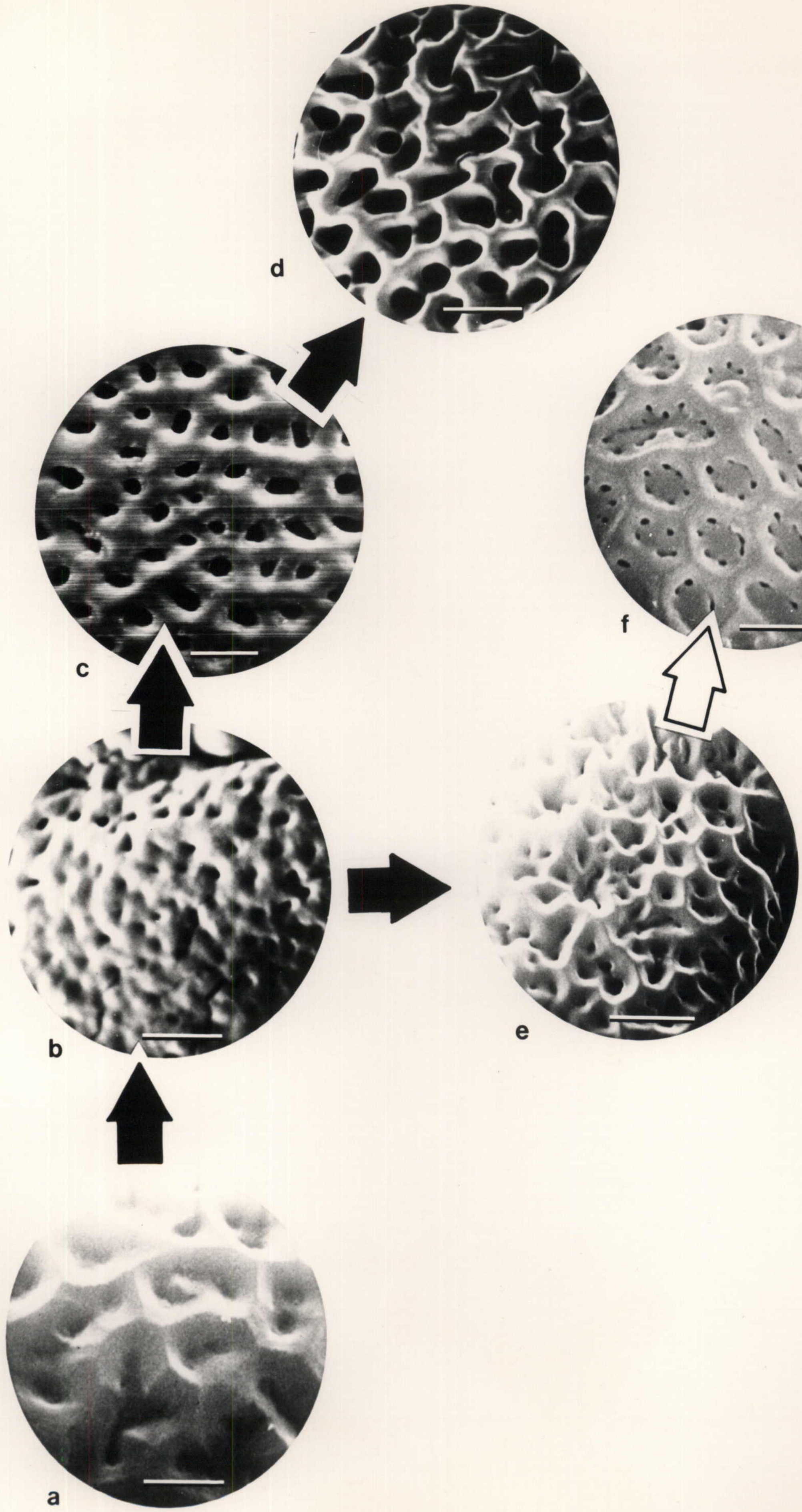
Plate 13: Evolution of surface sculpturing in Odontoneminae and possible link to Diclipterinae: a) surface with shallow imperforate depressions, *Glossochilus burchellii, Leistner 1397*; b) surface with small perforations, *Ruttya ovata, Tinley 701*; c & d) surfaces with slight sequential increase in size of perforations [c) *Ruspolia decurrens, Chase 638* ; d) *Ecbolium amplexicaule, ex hort.*]; e) surface with small perforations beginning to coalesce *Angkalanthus transvaalensis, Codd & Dyer 7741* and f) reticulations with a number of perforations coalesced to form lacunae with perforations in their floors, *Dicliptera zeylanica, Balkwill 120*. Scale lines all = 2 µm.



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like that seen in *Angkalanthus transvaalensis* (plate 13e). It is possible that the surface of the Diclipterinae [e.g. *Dicliptera zeylanica* (plate 13f)] may have been derived by a continuation of this trend.

Plates 14 and 15 show the evolution of the surface of pollen grains in the Diclipterinae, Justiciinae and Isoglossinae. The surface of the pollen of *Anisotes rogersii* (plate 15a) is probably the most primitive surface present in the family in southern Africa. By the perforation of the tectum, a surface like that of *Metarungia longistrobus* (plate 15b) would be formed. Sequential enlarging of the perforations in the tectum may have led to the surfaces of *Aulojusticia linifolia* Lindau (plate 15c) and *Adhatoda sp. nov.* (plate 15d). Coalescence of the perforations might lead to the surface of *Duvernoia aconitiflora* (plate 15e) or *Justicia campylostemon* (Nees) T. Anders. (plate 15f). An almost total reduction of the tectum and columellae would lead to a surface such as that between the girdle and the pores of *Isoglossa hypoestiflora* (plate 15g), while the surface of the girdle (plate 15h) could evolve from the addition of knobs to the exine of a surface like that of *Aulojusticia linifolia* (plate 15c).

Another line of evolution from the surface of *Metarungia longistrobus* (plate 15b) may involve the successive enlargement and coalescence of the perforations in the tectum, until reticulations like those in *Hypoestes sp.* (plate 14a), *Rhinacanthus gracilis* Klotzsch (plate 14b), *Dicliptera heterostegia* (plate 14c), *Dicliptera clinopodia* (plate 14d), *Peristrophe cernua* (plate 14e) and *Periestes sp.* (plate 14f) are formed. These reticulations, with perforations in the floors of the lacunae seem to be more derived than the reticulations of the southern African species of Justiciinae.

The paths of evolution that have been traced are merely possible paths along which the structures described may have been derived. I do not intend to suggest that the organisms cited as examples were derived from one another, and fully realise that in the Acanthaceae many characters have arisen more than once.

<u>Plate 14</u>: Evolution of surface sculpturing in Justiciinae and some Diclipterinae: a) small reticulations with perforations in floor of lacunae, *Hypoestes sp., ex hort.* and b - f) larger reticulations, with perforations in floor of lacunae [b) *Rhinacanthus gracilis* Klotzsch, *Balkwill 471* ; c) *D. heterostegia, Balkwill 244* ; d) *Dicliptera clinopodia, Balkwill 215* ; e) *Peristrophe cernua, Balkwill 402* and f) *Periestes sp., Baron 6138*]. Scale lines all = 2 µm.

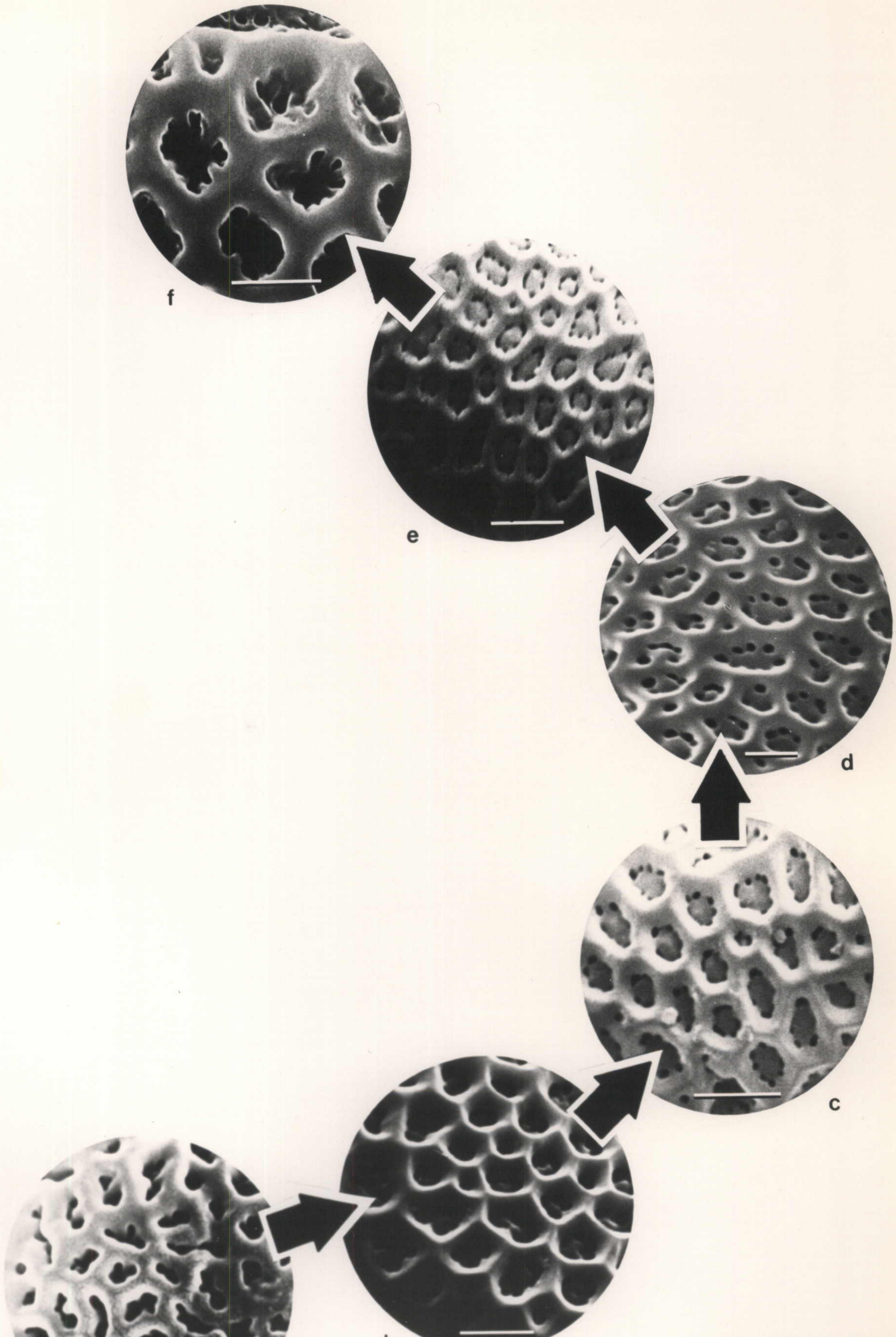

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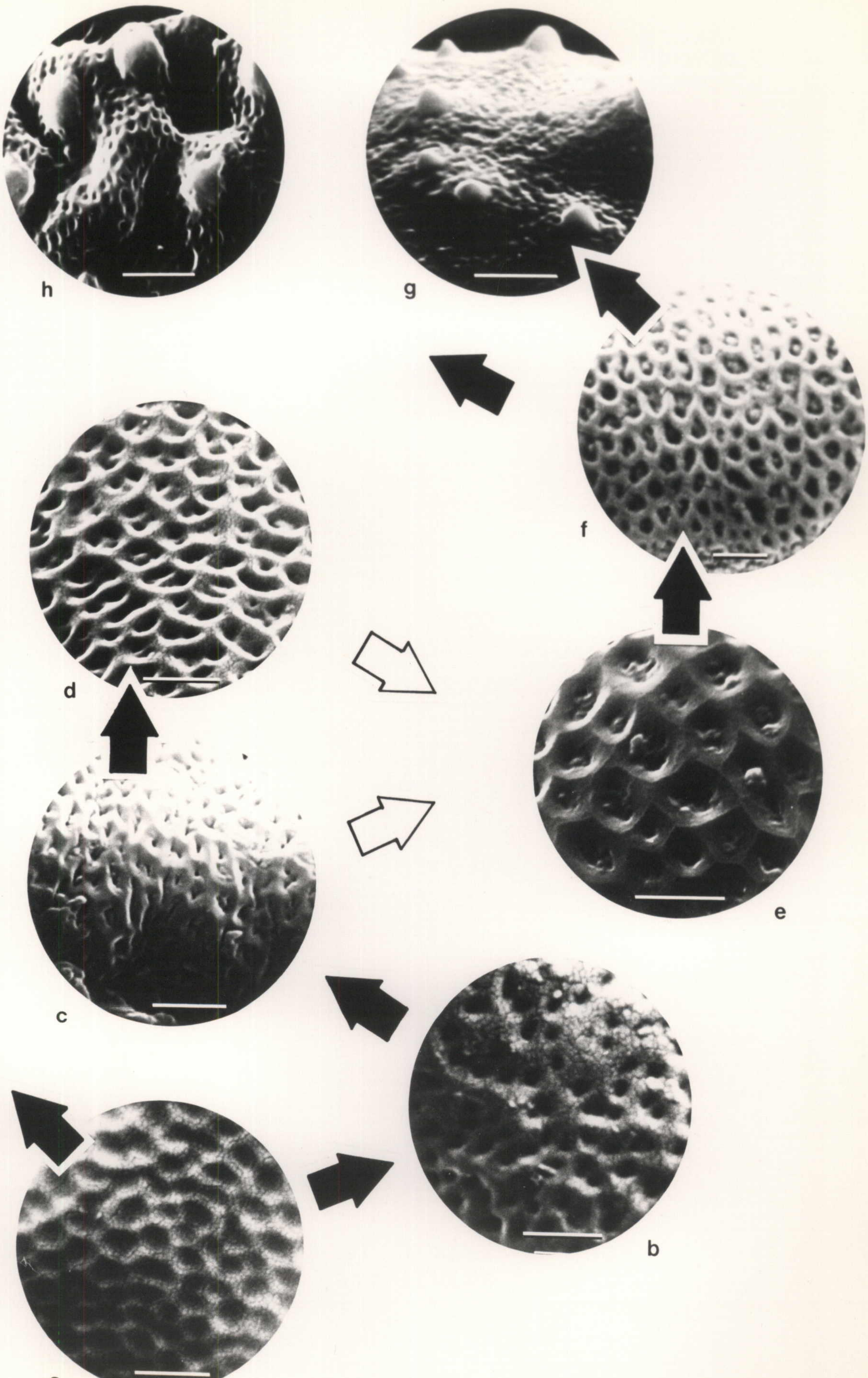
Plate 15: Evolution of pollen surface in Justiciinae and Isoglossinae: a) imperforate surface, *Anisotes rogersii, Balkwill 1622* ; b) surface with small perforations, *Metarungia longistrobus, Balkwill & Manning 666* ; c) surface with small, slightly closer perforations, *Aulojusticia linifolia* Lindau, *Hilliard & Burtt 3670* ; d) surface with small perforations some of which have coalesced, *Adhatoda sp. nov.. Sim 4172* ; e) surface with perforations coalesced in depressions, *Duvernoia aconitiflora, Balkwill 1518* ; f) reticulate surface, but without perforations in the floor of the lacunae, *Justicia campylostemon* (Nees) T. Anders., *Balkwill 1488* ; g) surface with almost total loss of outer layer, except for some knobs (spikes) and h) folded surface with perforations and knobs (spikes) [g & h) *Isoglossa hypoestiflora, Wells & Edwards 89*]. Scale lines all = 2 µm.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Conclusion

Although pollen morphology and shape has provided characters that are specific to some genera, subgenera, sections and species of the Acanthaceae, this is not true for the genera *Peristrophe* and *Dicliptera*, which have pollen that is identical in terms of all the features investigated. The size of the pollen may be diagnostic of *D. clinopodia*, but considerable sampling is required before this can be statistically verified. The pollen of *Peristrophe* and *Dicliptera* is relatively underived in the family as a whole, because it has a primitive shape and surface sculpturing when compared with the pollen of *Crabbea*, for example. The pollen of these two genera has the shape that I think is primitive in the Justicieae, but has a reticulation pattern that is more derived than that of other genera in the tribe, except that of *Isoglossa*.

CHAPTER 8

MICROSCULPTURING OF SEED SURFACE

Introduction

Davis and Heywood (1963) remarked "Seeds frequently receive summary treatment in Floras, and even in detailed taxonomic studies their potential importance in providing characters of value for comparative and interpretive purposes is seldom adequately explored". In response to this challenge, the overall shape and morphology of the seed, the surface sculpturing at the level of scanning electron microscopy and the anatomical basis of testa topography have been examined, as have the taxonomic implications of these features in the genera *Peristrophe* Nees and *Dicliptera* Juss..

From as early as 1799 when Willdenow described the genus *Eriospermum* [Jacq. ex] Willd., seed structure has been used as a taxonomic character, both at different hierarchical ranks as well as in very different groups of plants. Seed characteristics have been used in the dicotyledons at the species level by Brenan (1954) in *Chenopodium* L. (Chenopodiaceae), by Thulin (1978) in *Wahlenbergia* [Schrad. ex] Roth (Campanulaceae) and by Clark & Jernstedt (1978) in *Eschscholzia* A.P. de Candolle (Papavaraceae). At the subsectional and sectional level, Chuang and Heckard (1972) working on seeds of *Cordylanthus* Blume (Scrophulariaceae) found them to be useful, while seeds were found to be generic and sectional characters in *Epilobium* L. and related genera of the Onagraceae (Seavey, Magil & Raven, 1977). In the Melastomataceae, Whiffin & Tomb (1972) found characteristics of seeds useful at the tribal level, as did Lersten (1981) working on the subfamily Papilionoideae (Leguminosae). Corner (1951) and Gunn (1981) used seed surface characters when considering the rank at which the legumes should be subdivided. In the monocotyledons, features of the seed have been used as generic characters by Übermeyer (1962) in *Anthericum* L., *Chlorophytum* Ker-Gawler and *Trachyandra* Kunth (Liliaceae *sensu lato*), at the sectional level by Archibald (1967) in *Dioscorea* L. (Dioscoreaceae), to define groups of species in *Rhodohypoxis* Nel (Hypoxidaceae) by Hilliard & Burtt (1978) and at the species level by Vincent (1982) in *Aristea* Ait. (Iridaceae). The taxonomic importance of seed shape and surface features in the Acanthaceae was recognised by Nees in 1847. Seed shape was used by Bremekamp (1965) as a character useful in the delimitation of the Acanthaceae while characters of the testa were used at the tribal and subtribal levels. Clarke (1901) used seed surface features coupled with number of seeds in the capsule to distinguish the genus *Monechma* from *Justicia*. Henricksen & Hilsenbeck (1979) considered seed characters in their delimitation of subgenera and sections in *Siphonoglossa* Oerst. as did Immelman (1983) for *Justicia*. Milne-Redhead (1936), Heine (1967) and Balkwill & Getliffe Norris (1985) found features of the seed surface to be taxonomically important at the species level.

The anatomy of the seeds of members of the Acanthaceae has been investigated by many workers, as listed by Corner (1976) and Maheshwari & Negi (1955). Some of the work, however, was done on *Elytraria* Michx. (Johri & Singh, 1959) and *Nelsonia* R. Br. (Mohan Ram & Masand, 1977), genera which are not included in the Acanthaceae sensu Bremekamp (1965), and so extrapolation from these works to other acanthaceous genera must be done with caution.

MATERIALS AND METHODS

Seeds of most southern African genera of the Acanthaceae were observed with a light microscope. For plate 16, some seeds were photographed dry and then under water. These photographs were taken with a Pentax LX camera, with a 100 mm macro lens and extension tubes. Seeds of species of *Dicliptera* and *Peristrophe* were collected from wild plants in the field, from plants cultivated in our botanic garden or were taken from herbarium specimens. If possible, more than one seed from each collection, and more than one collection of each species was investigated with the SEM in order to gain an indication of the infraspecific variation. Where material was available, the data base was broadened by checking the structure of features such as the height of tubercles and whether they were hooked or not, with the aid of a dissecting microscope. Unless great care is taken by collectors to save the mature seeds of species of the Acanthaceae, these seeds are lost, because they are small and are expelled from capsules, which dehisce explosively during the pressing and drying of material. Few specimens have mature seeds and thus unfortunate restrictions are imposed upon this interesting field of research. *P. grandibracteata* and *D. sp 1* had to be omitted from the study as no mature seeds were available. Voucher specimens of species studied on the SEM are provided in Appendix 1 (at the end of this chapter).

In order to obtain photographs of whole seeds, untreated seeds were photographed with a Wild Photomacroscope M 400 with a Wild Photoautomat MPS55 photographic system. To investigate embryo orientation and testa ornamentation, seeds were cleared by the method of O'Brien and von Teichman (1974). For electron microscopy, mature seeds were mounted on copper stubs with double-sided adhesive tape, placed in a desiccator for 24 hours, coated with gold palladium (with a Polaron E5100 sputter-coater) and viewed with a Jeol JSM T 200 or Hitachi S570 scanning electron microscope (SEM). A series of capsules of varying ages was fixed in 6% glutaraldehyde and divided into two sets. The first was dehydrated, embedded in resin and stained with Ladd's Multiple stain (Toluidine Blue and Basic Fuchsin). The second set was dehydrated in a tertiary butyl alcohol series and embedded in Tissue Tek Prep Wax (m.p. 65°C) and serial sections were made on a rotary microtome at 10 - 12 µm. Selected slides were stained with iodine in potassium iodide and Sudan IV, but the bulk of the second series was stained in safranin and fast green (Sass 1958). Photomicrographs were taken with an Olympus PM-10AD photomicrographic system.

Observations

External Seed Morphology

Acanthaceous seeds have a range of surface sculpturing (table 11), some may be glabrous, some rough, some tubercled and some have hygroscopic hairs (plate 16). Some genera in the Acanthoideae and all in the Justicieae lack hygroscopic hairs and in the latter, seed coat texture and the presence of tubercles on the seeds provide characters that are diagnostic at the subtribal, generic and specific levels.

The seeds of *Peristrophe* Nees are discoid, notched at the hilum and often have depressions in the regions where they have pressed against the loculicidal suture lines (arrowed in plate 17a). Under the dissecting microscope (50X), the surfaces of the seeds of species of *Peristrophe* and *Dicliptera* appeared variously convoluted, glossy, rough and tuberculate; some tubercles were hooked.

Table 11: Distribution of characters of the seed surface of genera of the southern African Acanthaceae.

Genera as in key below, characters as follows: C = convoluted or rugose, D = dorsiventral, F = with feathery hygroscopic hairs, H = with hygroscopic hairs, P = papillate, R = rough, Ri = rimmed, S = smooth, Sc = with hygroscopic hairs fused to form scales, Sp = speckled and T = tuberculate.

Sclerochiton	Acanthopsis
Crossandra	Blepharis

'Neuracanthus'

Ruellia
Ruelliopsis
Crabbea

Barleria

Phaulopsis	Duosperma	Dyschoriste
Petalidium	Hemigraphis	Chaetacanthus
Lepidagathis	Hygrophila	

Mackaya	Asystasia	Glossochilus
Megalochlamys	Angkalanthus	Ruttya
Ecbolium	Ruspolia	Pseuderanthemum

Peristrophe
Dicliptera
Hypoestes

Rhinacanthus	Justicia	Monechma
Siphonoglossa	Duvernoia	Adhatoda
Aulojusticia	Anisotes	Metarungia

Isoglossa

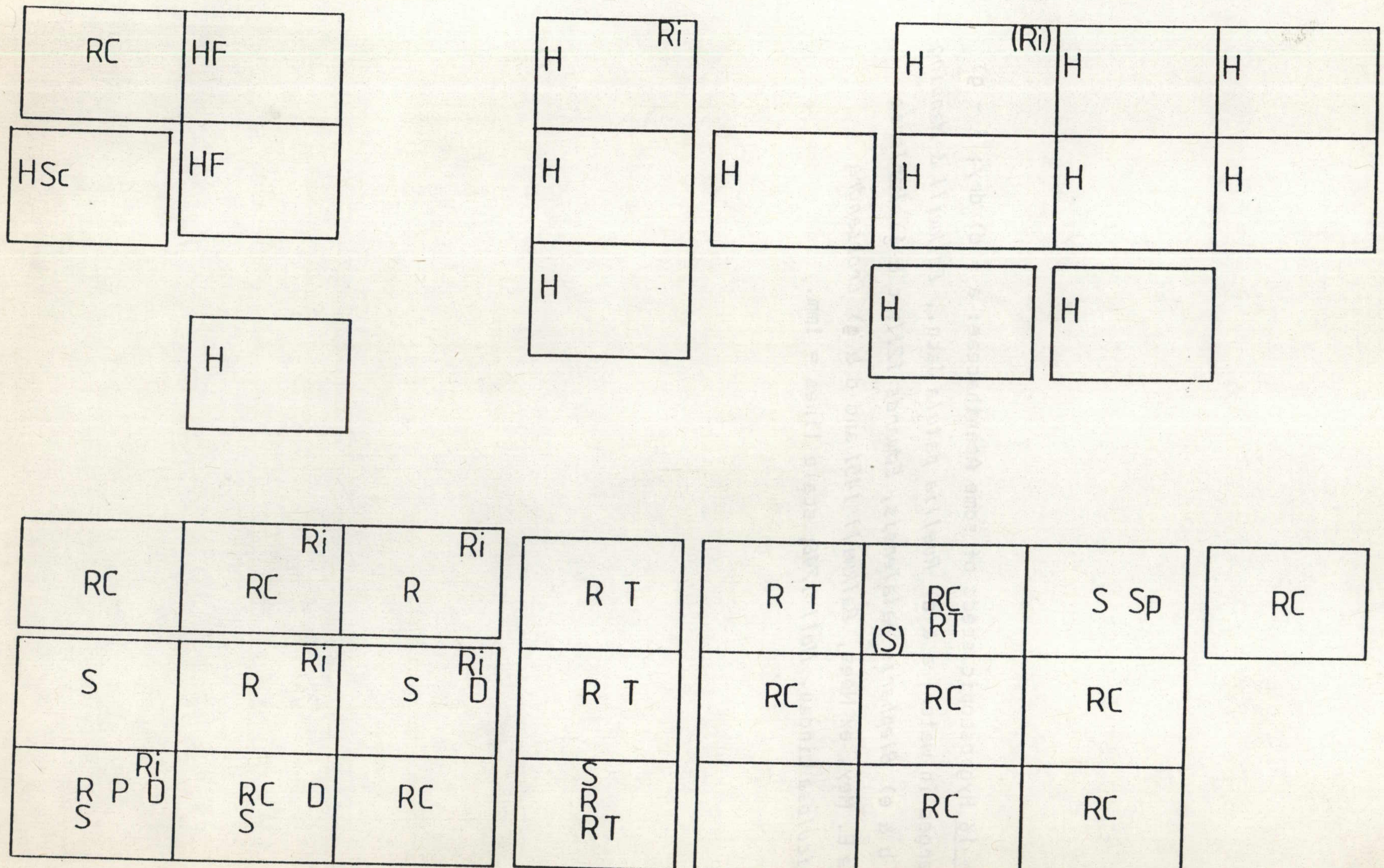
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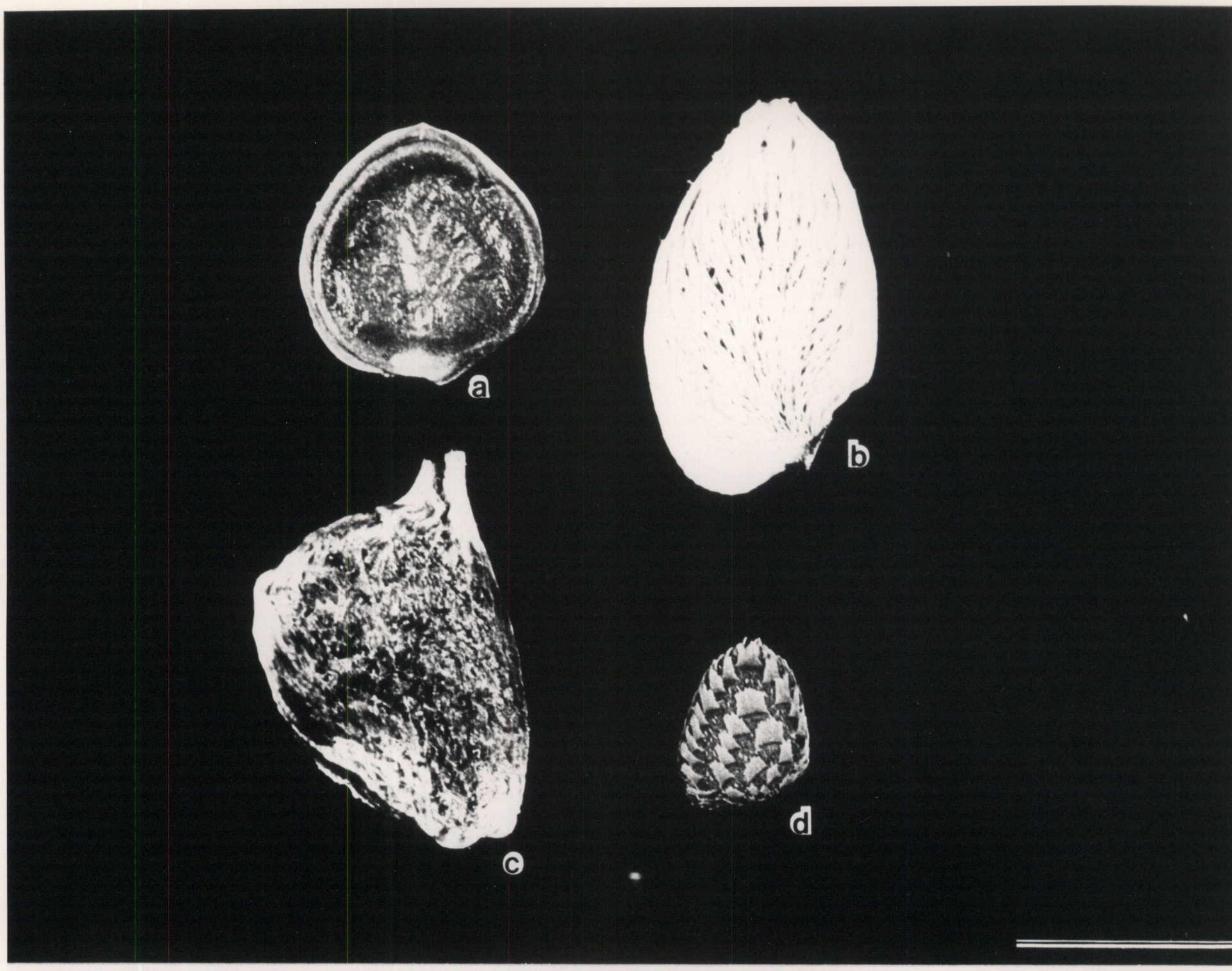
Plate 16 Hygroscopic seeds of some Acanthaceae: a - d) dry; e - h) submerged in water; a & e) *Ruellia patula* Jacq., *Balkwill & Manning 628*; b & f) *Blepharis natalensis, Edwards 1211*; c & g) *Barleria ovata* E. Mey. ex Nees, *Balkwill 1451* and d & h) *Crossandra fruticulosa* Lindau, *Moll 1748*; scale lines = 1mm.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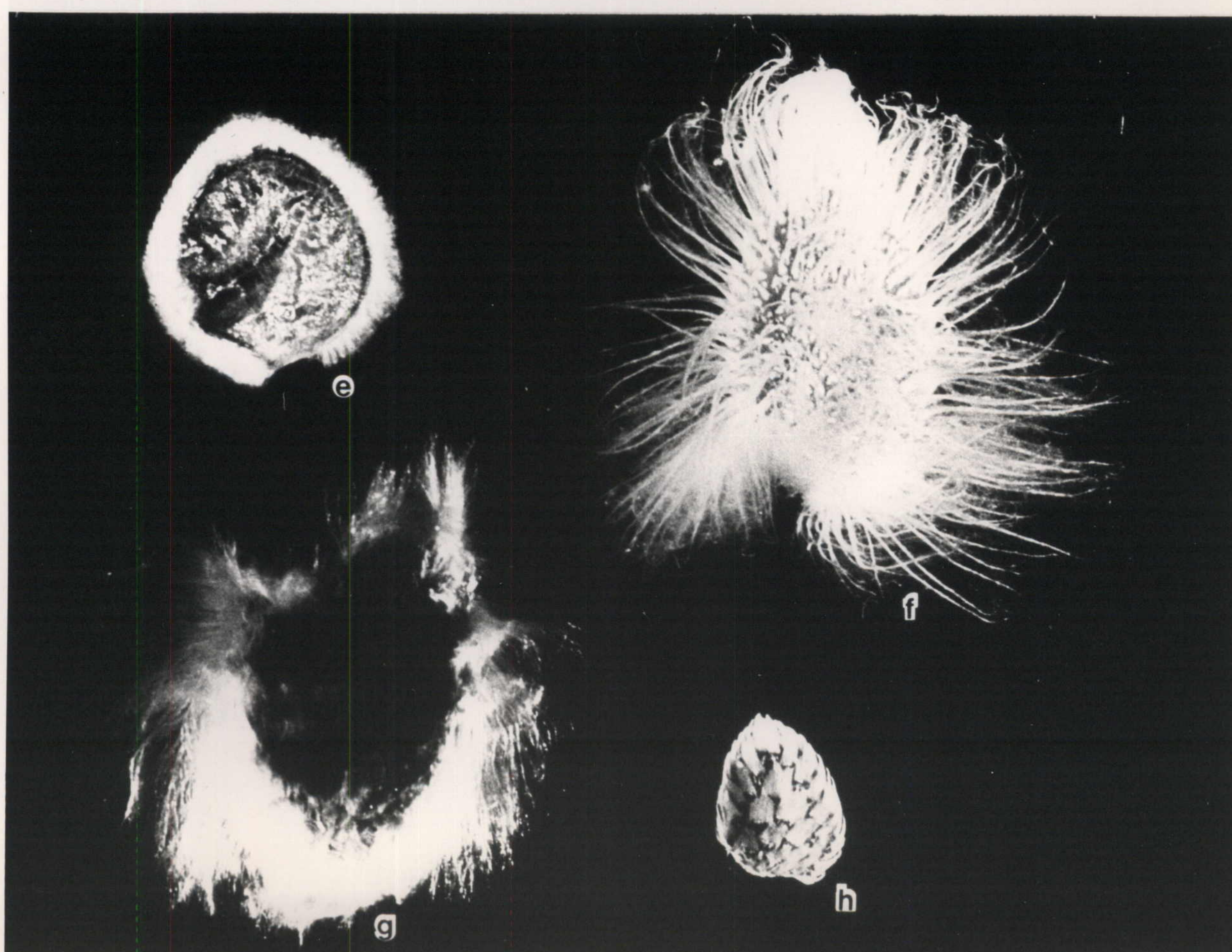
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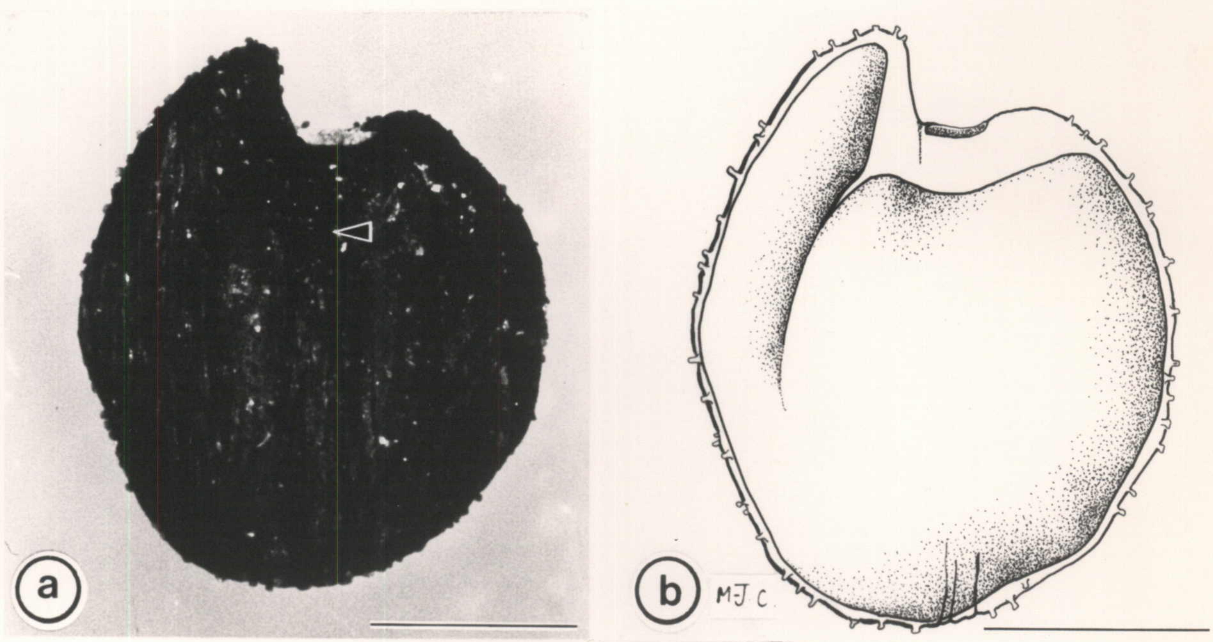
Plate 17 Seeds of *P. cernua; Balkwill 326*: a) Light micrograph of seed, arrow marks depression against which retinaculum pressed, scale line = 1 mm; b) Drawing of cleared seed showing the orientation of the embryo, scale line = 1 mm.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Investigation with the SEM revealed that the surface of the seeds was reticulate, tuberculate, and had small papillae (plate 18b), large papillae (plate 22b & c) or rod-like structures at various densities (plates 22i & 23a). The papillae resemble the structures described by Chuang & Heckard (1972) as "papillose wax deposits" and they also resemble the structures on *Salvinia auriculata* Aubl. described by Barthlott & Wollenweber (1981) as hydrophobic, simple rodcrystalloid sculpturing. The rod-like structures are similar to some that have been described by Barthlott & Wollenweber (1981) as prostrate rods, often brøken off at the base. The reticulate pattern may be indistinct (plate 19f) or clearly defined with deep depressions between ridges (plate 19h & i). Tubercles are produced by all species examined and although they may appear crushed on the flat surfaces (as that arrowed in plate 19e) are better developed around the edges of the seeds. Tubercles may be hooked (plate 18e) or unhooked (plate 18c) and with or without papillae. Hooks on tubercles may be at one level (plate 18e), two levels (plate 20a), three levels (plate 19g) or at a number of ill-defined levels (plate 19d). Tubercles may be without papillae (plate 18e), with occasional papillae (plate 18c) or with papillae common (plate 20g). The hooks too might be papillate (plate 19g) or smooth (plate 20d).

The testa of *P. cernua* has clearly defined reticulations (plate 18b & d) and unhooked tubercles with papillae are present (plate 18a & c). In *Peristrophe paniculata* the reticulations are indistinct (plate 18f & g), and the tubercles have a single row of hooks (plate 18e). The hooks are sharp-pointed, and have a rugose surface; there are no wax papillae on the tubercles. *P. transvaalensis* has clearly defined reticulations (plate 19b & c) and a relatively sparse distribution of wax papillae, and the tubercles have protuberances rather than hooks (plate 19a), giving the tubercles a flattened appearance; there are no wax papillae on the tubercles. In *P. cliffordii*, the surface is alveolate (plate 19e & f) and the tubercles are hooked at different levels (plate 19d). The hooks are broader than those of *P. paniculata*, but their surfaces are similarly rugose. In *P. gillilandiorum* the surface of the seed is distinctly reticulate, with deep depressions (plate 19h & i), and there are hooks on the tubercles at three levels (plate 19g). Wax papillae occur on the lower hooks. *P. kotschyana* has a reticulate surface (plate 20c) and two kinds of tubercles, one with two rows of hooks (plate 20a), and one with the axis of the tubercle shortened so that the hooks

<u>Plate 18</u> a – d) *P. cernua*: a) Tubercle; *Balkwill 445*, scale line = 10 µm; b) Surface of testa showing tubercles and reticulation; *Balkwill 168*, scale line = 100 µm; c) Tubercle; *Balkwill 326*, scale line = 10 µm and d) Reticulation on testa; *Balkwill 326*, scale line = 20 µm.

e – g) *P. paniculata; Seydel 1128*: e) Hooked tubercle, scale line = 10 µm; f) Surface of testa showing tubercles and reticulation, scale line = 100 µm and g) Reticulation on testa, scale line = 20 µm.

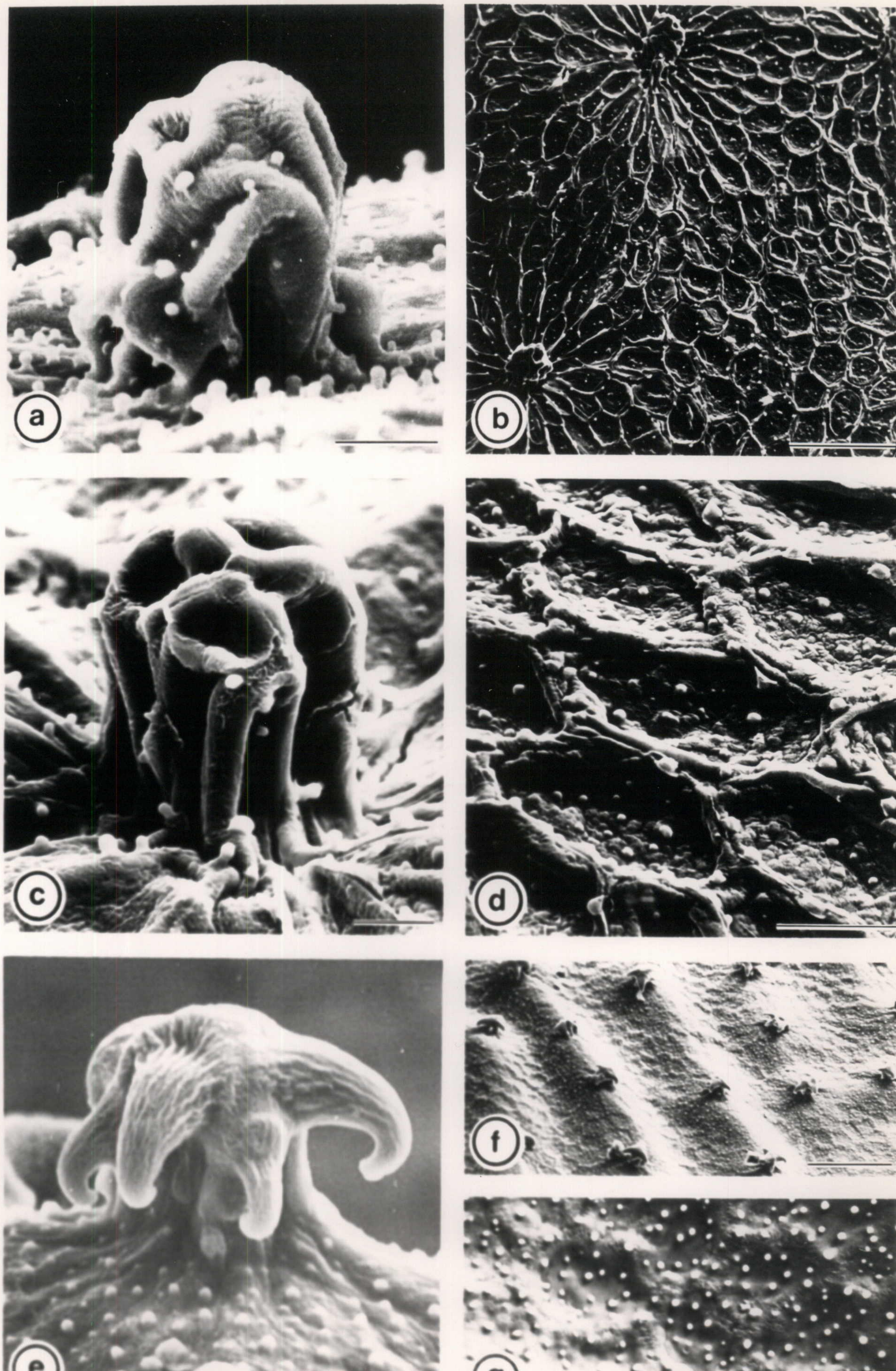
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Plate 19 a - c) *P. transvaalensis; Balkwill 764*: a) Tubercle, scale line = 20 µm; b) Surface of testa showing tubercles and reticulations, scale line = 100 µm and c) Reticulation on testa, scale line = 20 µm.

d - f) *P. cliffordii; Balkwill 793*: d) Tubercle, scale line = 10 µm; e) Surface of testa showing tubercles and reticulation, scale line = 100 µm and f) Reticulation on testa, scale line = 20 µm.

g - i) *P. gillilandiorum; Grosvenor 820*: g) Tubercle, scale line = 20 µm; h) Surface of testa showing tubercles and reticulations, scale line = 100 µm and i) Reticulation on testa, scale line = 20 µm.

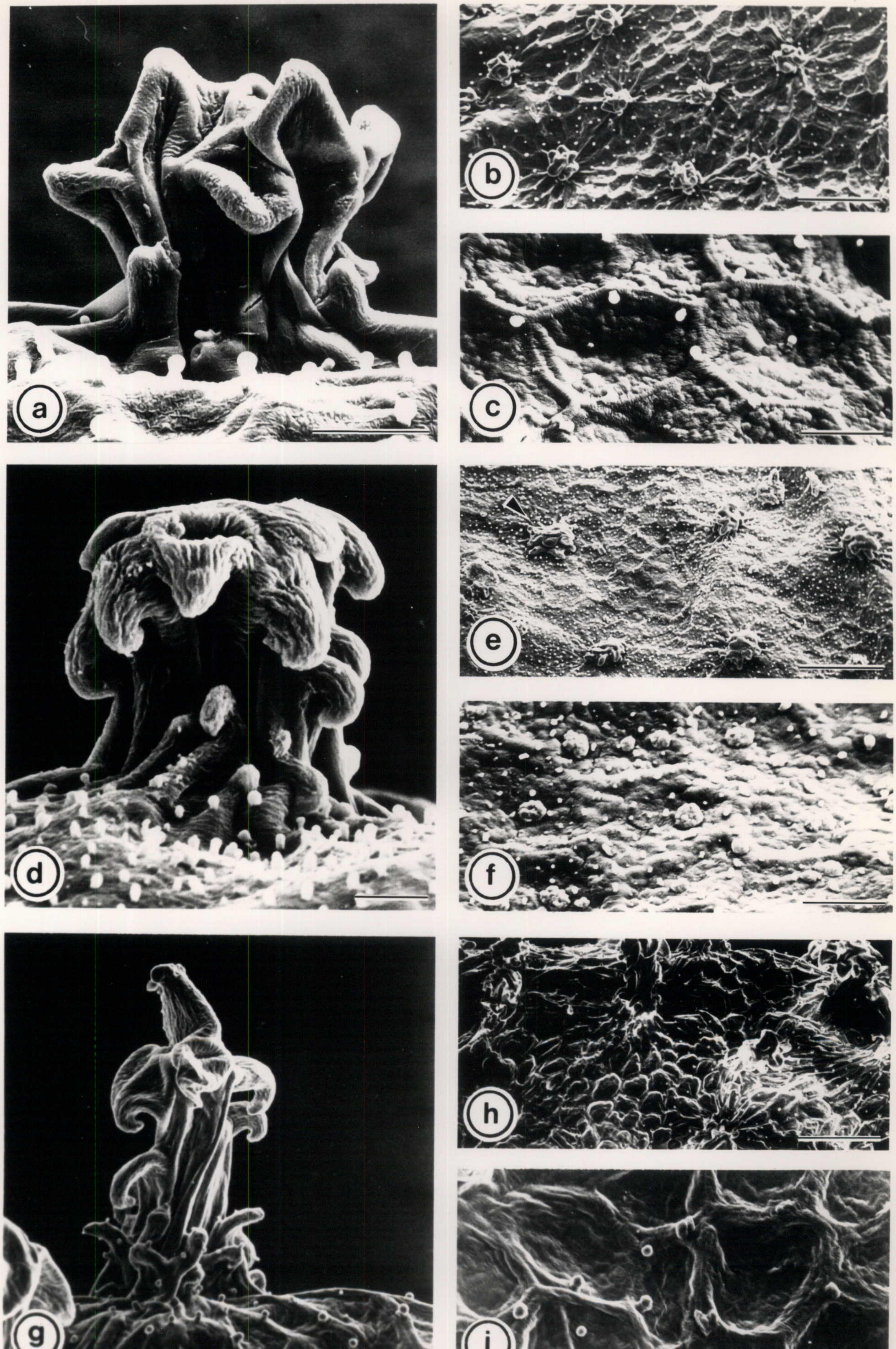
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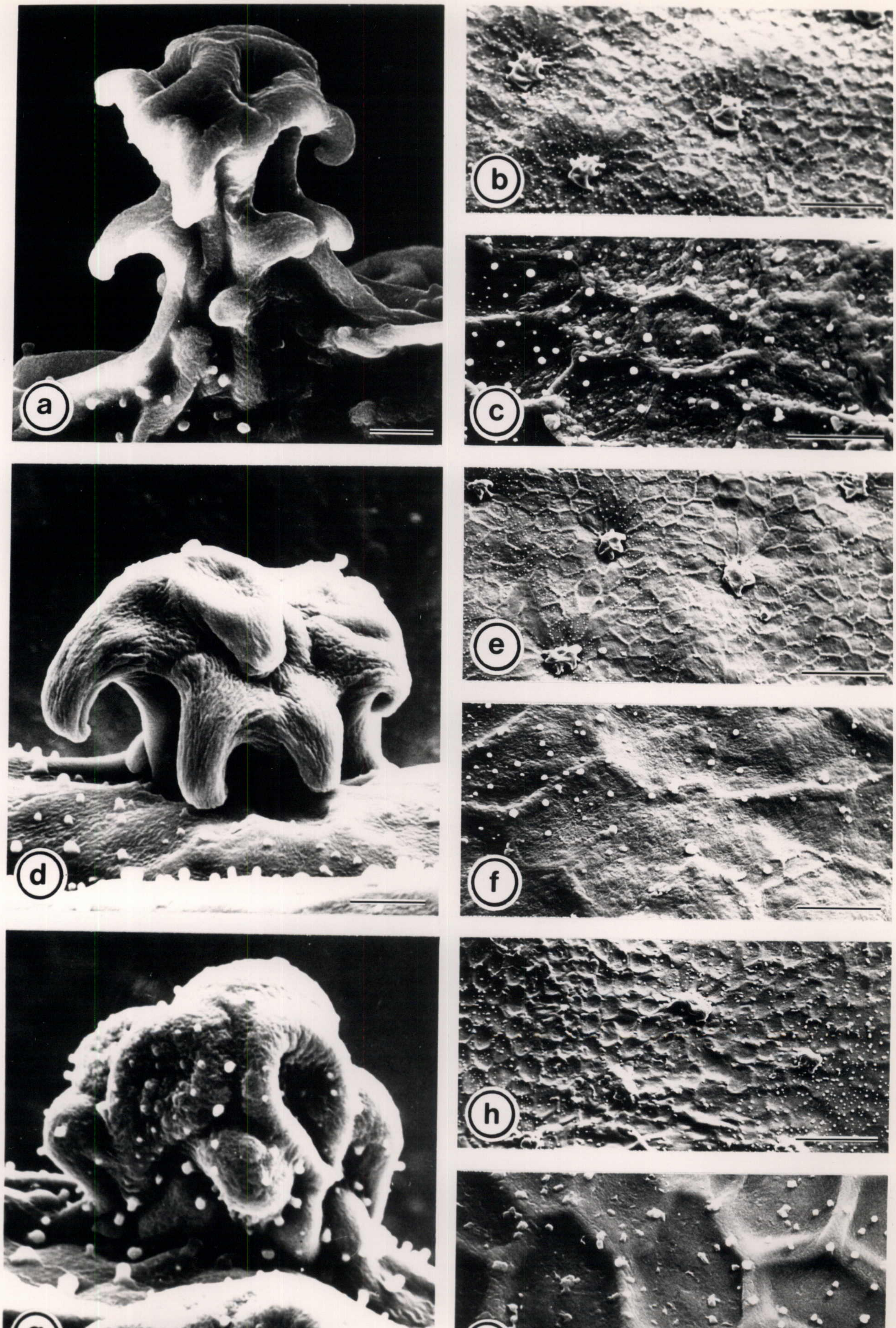
Plate 20 a - c) *P. kotschyana*: a) Tubercle; *Balkwill 760*, scale line = 10 μm; b) Surface of testa showing tubercles and reticulations; *Balkwill 760*, scale line = 100 μm and c) Reticulation on testa; *Balkwill 732*, scale line = 20 μm.

d - f) *P. hereroensis; De Winter 2356*: d) Tubercle, scale line = 10 μm; e) Surface of testa showing tubercles and reticulations, scale line = 100 μm and f) Reticulation on testa, scale line = 20 μm.

g - i) *P. sp. 1*: g) Tubercle; *Craven 1021*, scale line = 10 μm; h) Surface of testa showing tubercles and reticulation; *Craven 1021*, scale line = 100 μm and i) Reticulation on testa; *De Winter & Leistner 1828*, scale line = 20 μm.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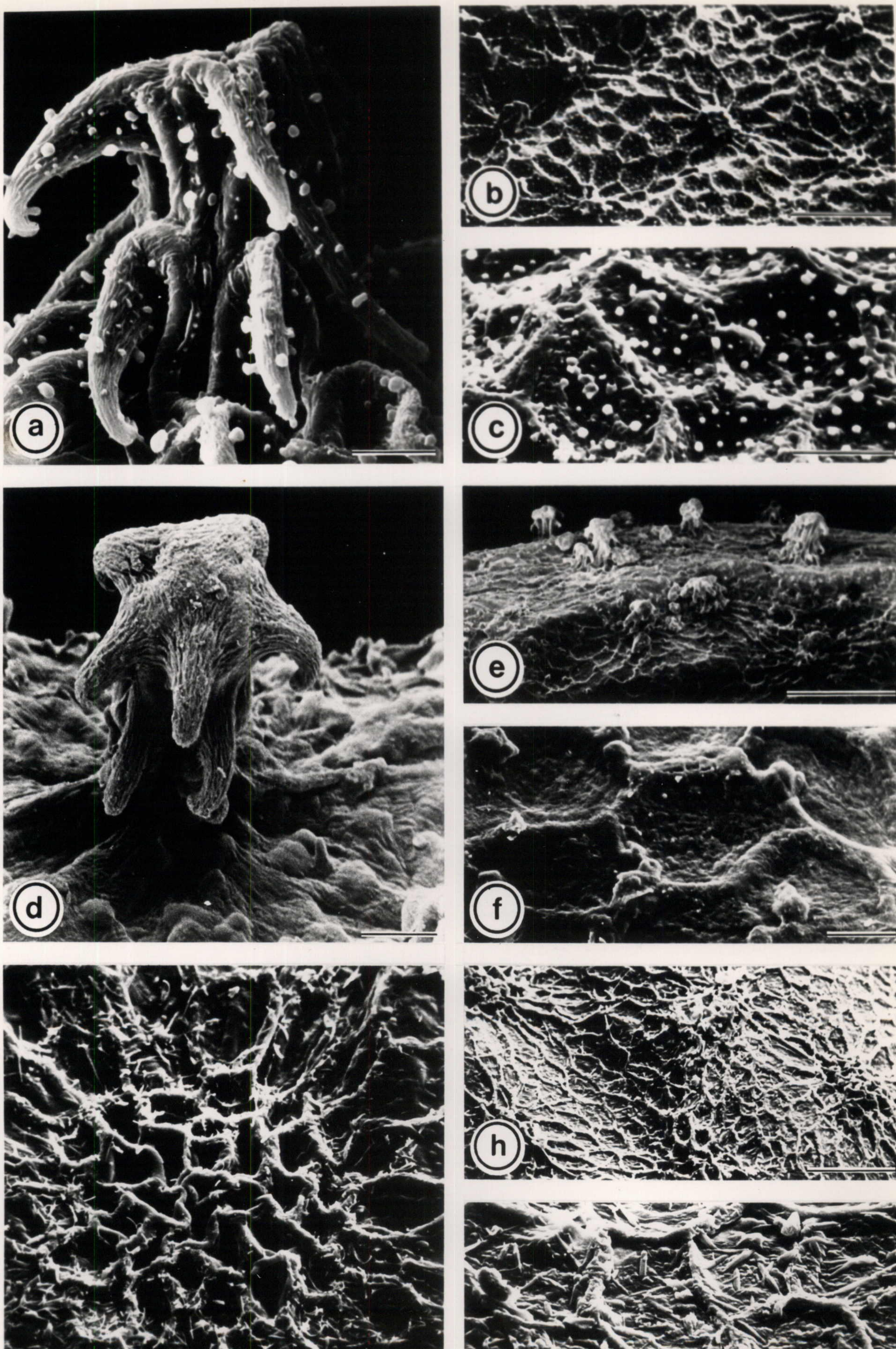
are approximated. The surfaces of the hooks are smooth, and wax papillae are present near the bottom of the tubercles. In *P. hereroensis* the reticulations are less distinct (plate 20e & f)and the tubercles on which papillae are occasional, have one row of hooks (plate 20d). *P. sp. 1* has a distinctly reticulate surface (plate 20h & i) and wax papillae are common on the unhooked tubercles (plate 20g).

D. zeylanica and *D. heterostegia* both have seed surfaces with well defined reticulations (plate 21b & e), although the depressions between the ridges are shallow. Both species have similar tubercles that are hooked and have rough surfaces on the hooks (plate 21a & d). D. zeylanica can be distinguished from *D. heterostegia*: the former has small papillae on the seed surface (plate 21c) and on the tubercles (plate 21a), while *D. heterostegia* has larger papillae on the seed surface (plate 21c) and no papillae on the tubercles at all (plate 21d). *D. capensis* has clearly defined reticulations on the seed surface with shallow depressions between these ridges (plate 21h & i). On the surface there are sparse deposits of short flattened rod-shaped structures (plate 21i). The tubercles of this species are flattened and the outer tangential walls have become invaginated, so that the surface is extremely convoluted (plate 21 g). In both forms of *D. clinopodia* var. *clinopodia*, the seed surface has clearly defined reticulations (plate 22b & e). There are large wax papillae on the surface (plate 22c) as well as rod-shaped structures (plate 22c, d, e, f, g, h & i), which are at different densities, i.e. sparse (plate 22c) or more dense (plate 22h). The rod-shaped structures are shorter and straighter in form A (plate 22c) than in form B (plate 22i). The tubercles of both forms are unhooked and have a convoluted surface (plate 22a, d & g) as in *D. capensis*, but have a slightly higher profile than those of *D. capensis* (plate 21g). The tubercles of *D. clinopodia* may sometimes have rod-like wax structures on their surfaces (plate 22g). In *D. divaricata*, the reticulations on the seed surface are well developed (plate 23b & c). There are large papillae on the surface (plate 23c), but these become covered in rod-like structures in the mature seed coat (plate 23c). The tubercles, which are unhooked and have convoluted surfaces (plate 23a), are similar to those of *D. clinopodia*, but slightly taller. The two subspecies of *D. minor* have clearly defined reticulations on the seed surface (plates 23d & 24a) and have some rod-like structures on the surface (plate 23f). In *D. minor* ssp.

<u>Plate 21</u> a - c) *D. zeylanica, Balkwill 448*: a) Tubercle, scale line = 10 μm; b) Surface of testa showing tubercles, reticulations and wax papillae, scale line = 100 μm and c) Reticulation on testa, scale line = 10 μm.

d - f) *D. heterostegia, Balkwill 198*: d) Tubercle, note absence of papillae, scale line = 10 μm; e) Surface of testa showing tubercles and reticulations, scale line = 100 μm and f) Reticulation on testa, scale line = 10 μm.

g - i) *D. capensis, Balkwill 465*: g) Tubercle, scale line = 20 μm; h) Surface of testa showing tubercles, reticulations and wax rods, scale line = 100 μm and i) Reticulations and wax rods, scale line = 20 μm.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<u>Plate 22</u> a - e) *D. clinopodia* var. *clinopodia* form A, *Balkwill 396*: a) Tubercle, scale line = 20 µm; b) Surface of testa showing reticulations and tubercles, scale line = 100 µm; c) Reticulations, scale line = 10 µm; d) Tubercle, *Balkwill 396*, scale line = 10 µm and e) Reticulations, scale line = 10 µm.

f - i) *D. clinopodia* var. *clinopodia* form B: f) Surface of testa showing reticulations and tubercles, scale line = 100 µm; g) Tubercle, *Balkwill 213*, scale line = 10 µm; h) Reticulations with long wax rods, *Balkwill 215*, scale line = 10 µm and i) Reticulations with long wax rods, *Balkwill 287*, scale line = 20 µm.

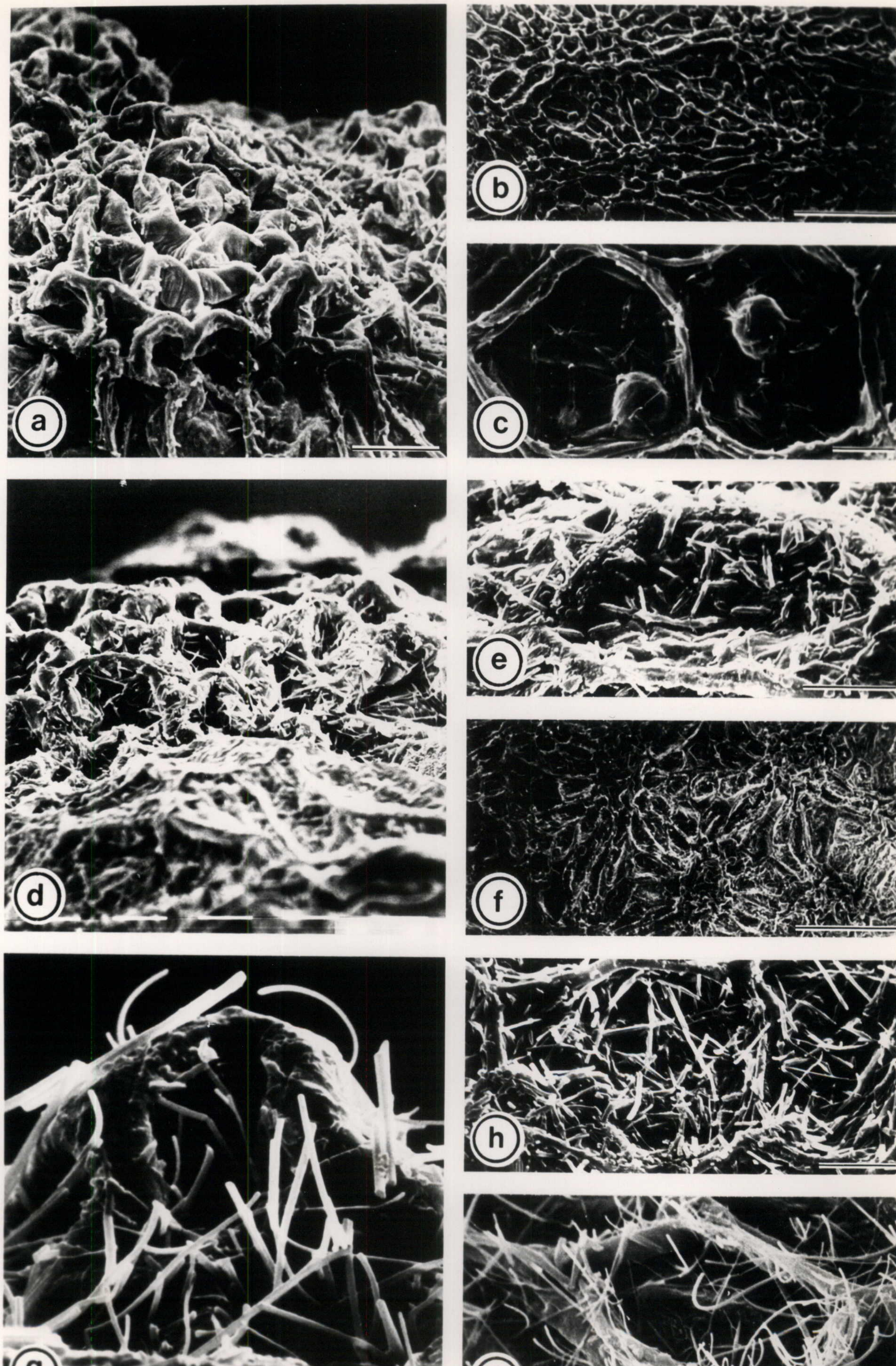
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Plate 23 a - c & e) *D. divaricata*, *Balkwill 175*: a) Tubercle with wax rods, scale line = 10 µm; b) Surface of testa with tubercles, reticulations and wax rods, scale line = 100 µm; c) Reticulations with wax rods, scale line = 20 µm and e) Reticulations with wax rods, scale line = 10 µm.

d & f - h) *D. minor* ssp. *minor*, *Gerstner 5528*: d) Surface of testa with tubercles and reticulations, scale line = 100 µm; f) Reticulations, scale line = 10 µm; g) Tubercle (less frequent), scale line = 10 µm and h) Tubercle (more frequent), scale line = 20 µm.

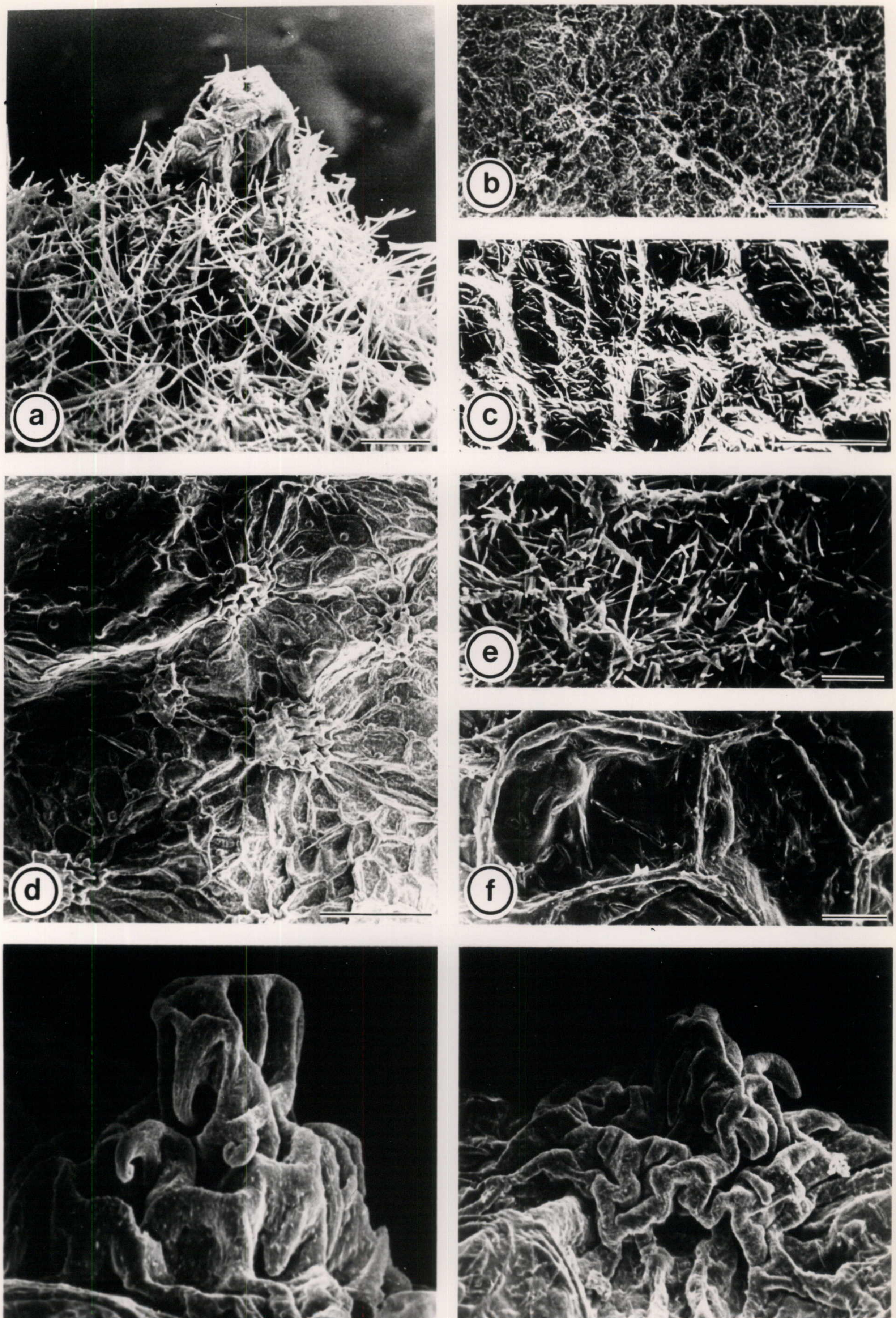
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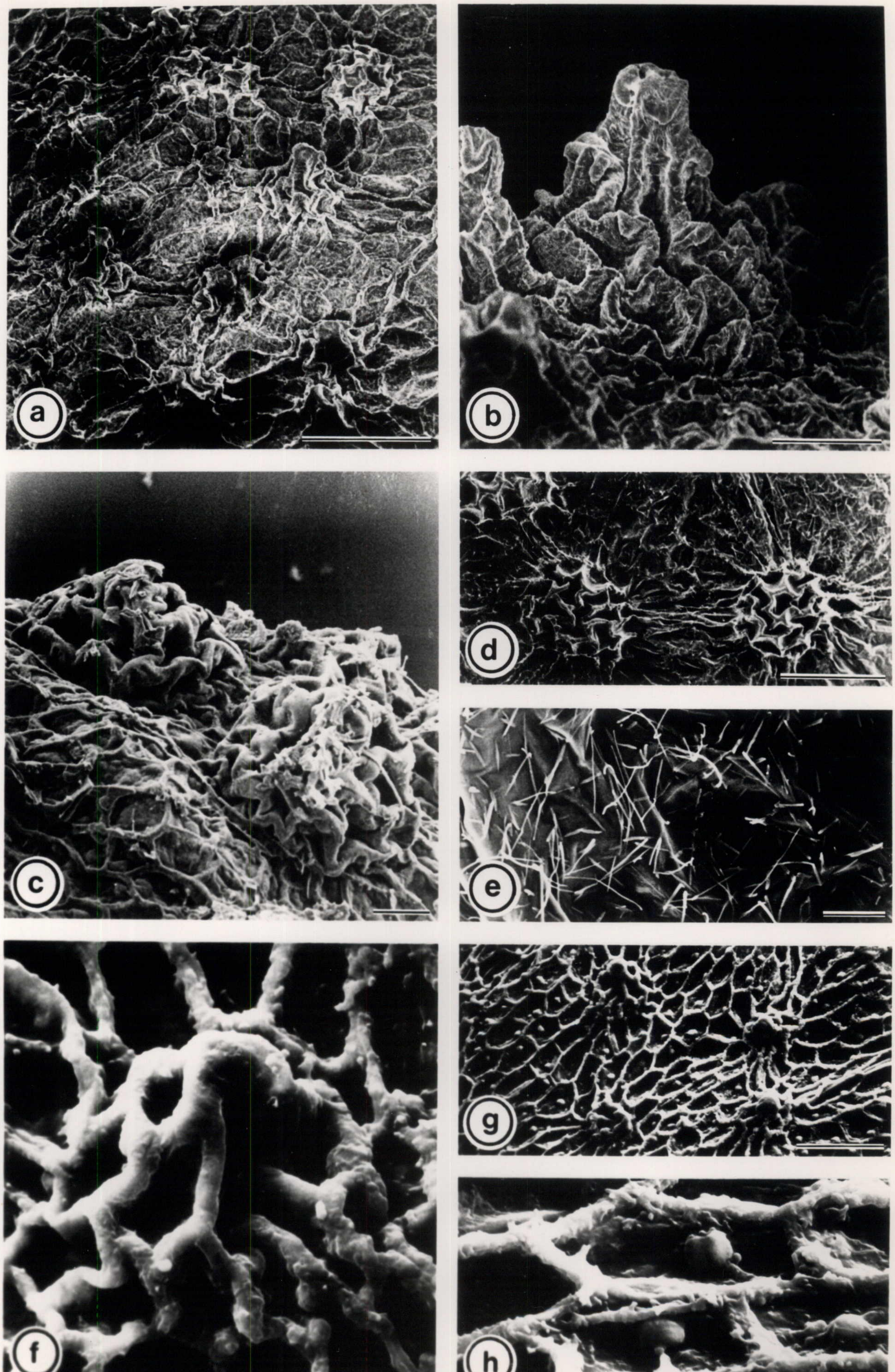
Plate 24 a & b) *D. minor* ssp. *1*, *Balkwill 1598*: a) Surface of testa with reticulations and tubercles, scale line = 100 µm and b) Tubercle, scale line = 20 µm.

c - e) *D. sp. 2, Forbes 427*: c) Tubercle, scale line = 20 µm; d) Surface of seed with reticulations and tubercles, scale line = 100 µm and e) Reticulations, scale line = 10 µm.

f - h) *D. sp. 3, Balkwill 766*: f) Tubercle, scale line = 20 µm; g) Surface of seed with reticulations and tubercles, scale line = 100 µm and h) Reticulations, scale line = 20 µm.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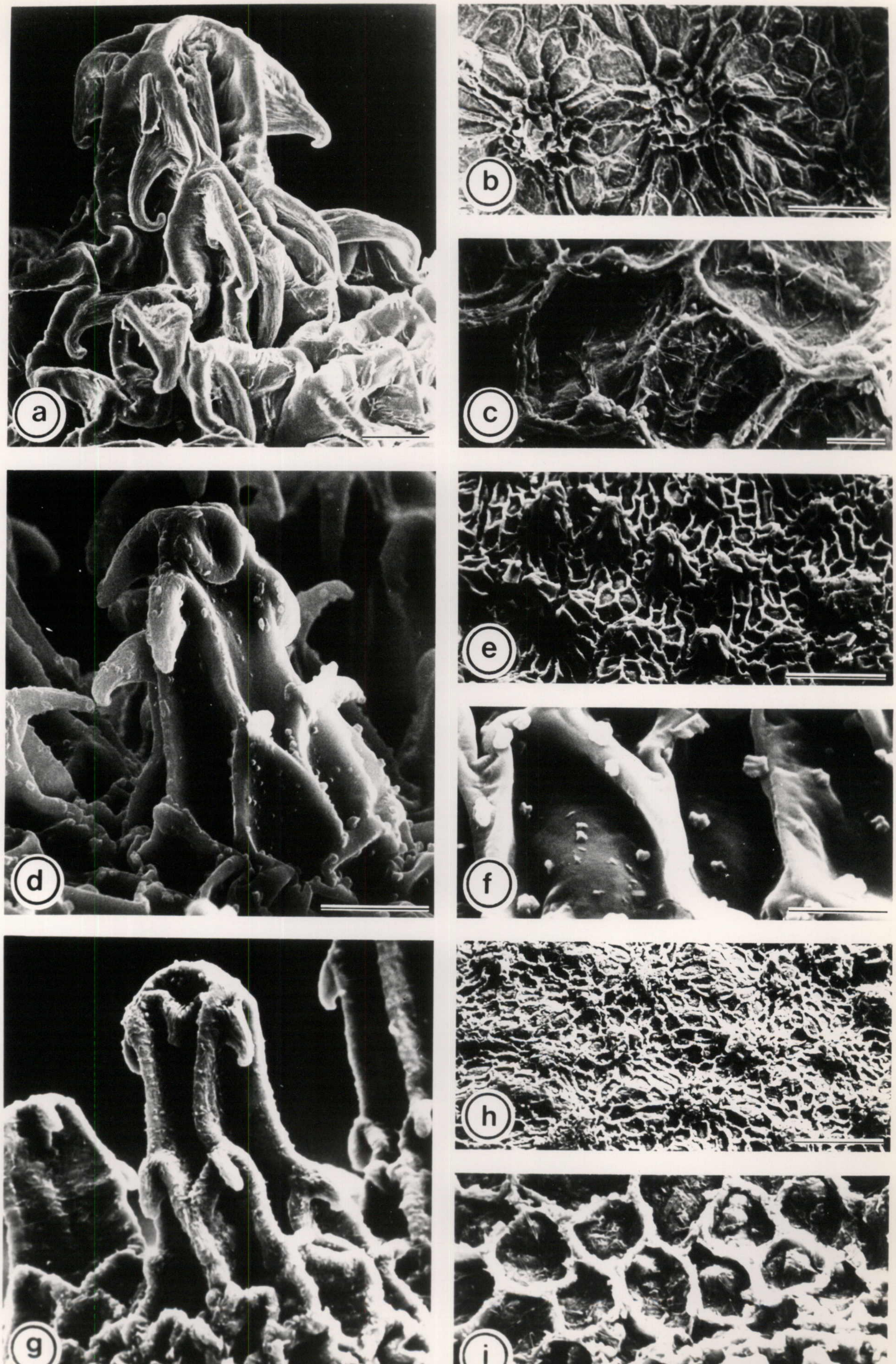
minor there are two forms of tubercle, both forms are hooked and have convoluted surfaces (plate 23g & h), but the form with the lower profile (plate 23h) is more common than the other in this subspecies. In *D. minor* ssp. *1*, the most common form of tubercle on the edge of the seeds (plate 24b) is almost identical to the taller form in *D. minor* ssp. *minor* (plate 23g). *D. sp. 2* has ridges and rod-like structures on the seed surface (plate 24d & e) and the tubercles are low in profile and very convoluted (plate 24c). *D. sp. 3* has clearly defined reticulations, with rough ridges on the seed surface (plate 24g & h). There are large papillae in most cells (plate 24g & h), but no rod-like structures. The tubercles (plate 24f) are unhooked and have very convoluted surfaces. *D. quintasii* has clearly defined ridges on the surface (plate 25b & c). There are large papillae (plate 25c) and crystals in some cells and some rod-shaped structures appear to be forming (plate 25c). The bases of the tubercles are highly convoluted and have hooks amongst these convolutions and a hooked region raised above the convolutions (plate 25a). *D. eenii* has a seed surface with very clearly defined reticulations (plate 25e & h). In Namibian material, the ridges are smooth and small papillae are common on the surface (plate 25f), while in the Transvaal material, the ridges are rough, large papillae are evident and some rod-like wax structures are present (plate 25i). The tubercles from both localities are tall with clearly defined ridges and hooks (plate 25d & g), although the ridges in the Transvaal material are rougher (plate 25g) and the small papillae are more obvious on the tubercles of the Namibian material (plate 25d). In *D. sp. 4*, the reticulations are clearly defined and the depressions between the ridges are quite deep (plate 26b). Some rod-like structures are beginning to develop on the surface (plate 26c). The tubercles are high in profile, have a very convoluted surface and have collapsed hooks (plate 26a). The surface of seeds of *D. fruticosa* is very similar to that of *D. eenii* from the Transvaal, except that the depressions between the ridges appear slightly shallower and small papillae are more common (plate 26e & f). The tubercles of *D. fruticosa* are tall and ridged as in *D. eenii*, but are unhooked (plate 26d). Small papilllae are clearly evident on the tubercles of *D. fruticosa* (plate 26d). The seed surface of *D. sp. 5* is unique, as the ridges are poorly developed or absent (plate 27a & b). There are angled protusions from the surface (plate 27b), which are probably formed by crystals that are under the surface. The most common form of tubercle (plate 27d) is relatively

<u>Plate 25</u> a - c) *D. quintasii, Balkwill, Cadman & Stormanns 3055*: a) Tubercle, scale line = 10 μm; b) Surface of testa with reticulations and tubercles, scale line = 100 μm and c) Reticulations, scale line = 10 μm.

d - f) *D. eenii* from Namibia, *Giess 12376*: d) Tubercle, scale line = 20 μm; e) Surface of testa with reticulations and tubercles, scale line = 100 μm and f) Reticulations, scale line = 10 μm.

g - i) *D. eenii* from the Transvaal, *Balkwill 798*: g) Tubercle, scale line = 20 μm; h) Surface of testa with reticulations and tubercles, scale line = 100 μm and i) Reticulations, scale line = 20 μm.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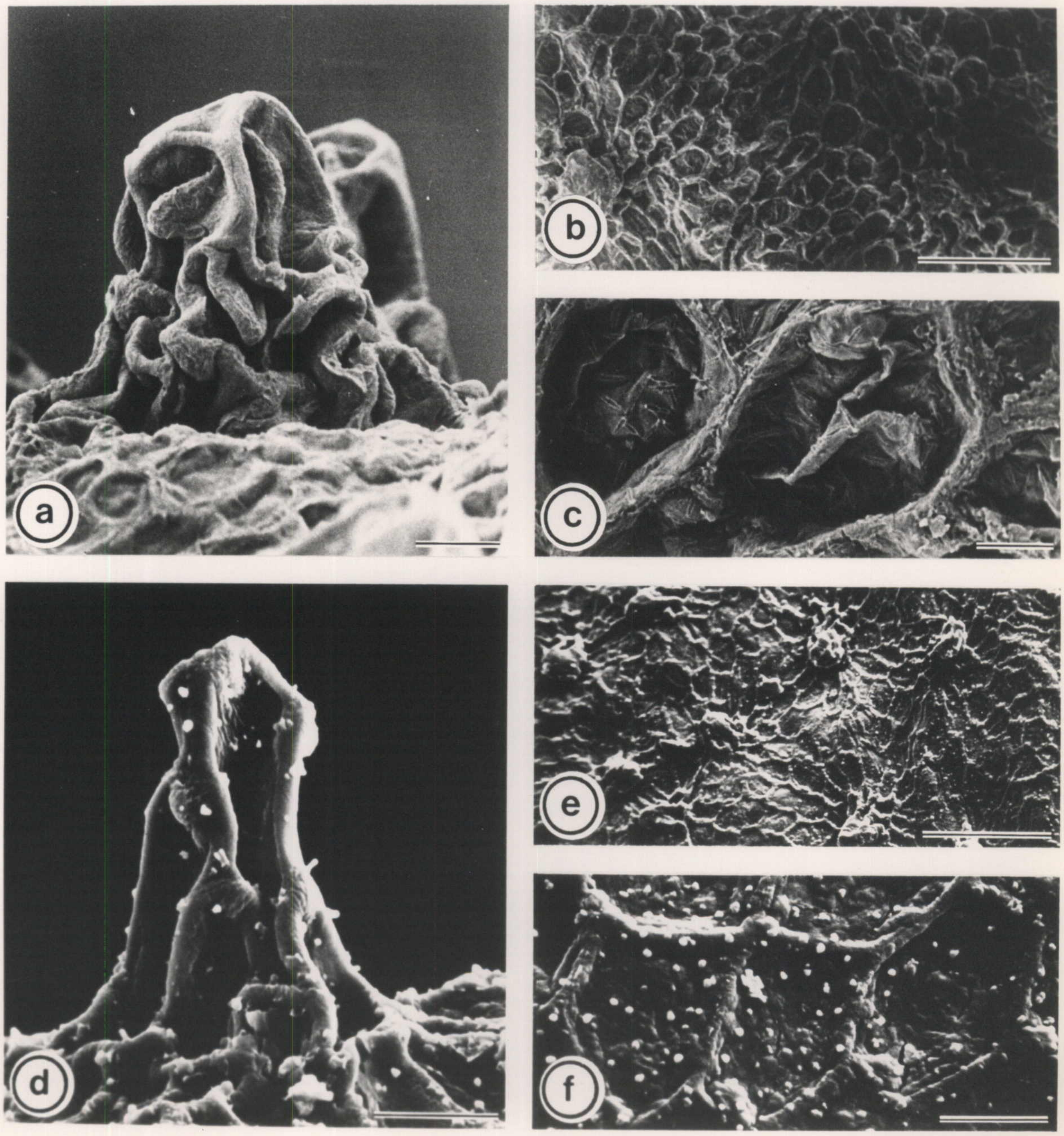
<u>Plate 26</u> a - c) *D. sp. 4, Balkwill 1587*: a) Tubercle, scale line = 10 µm; b) Surface of testa with reticulations and tubercles, scale line = 100 µm and c) Reticulations, scale line = 10 µm.

d - f) *D. fruticosa, Balkwill 777*: d) Surface of testa with reticulations and tubercles, scale line = 100 µm; e) Reticulations, scale line = 20 µm and f) Tubercle, scale line = 20 µm.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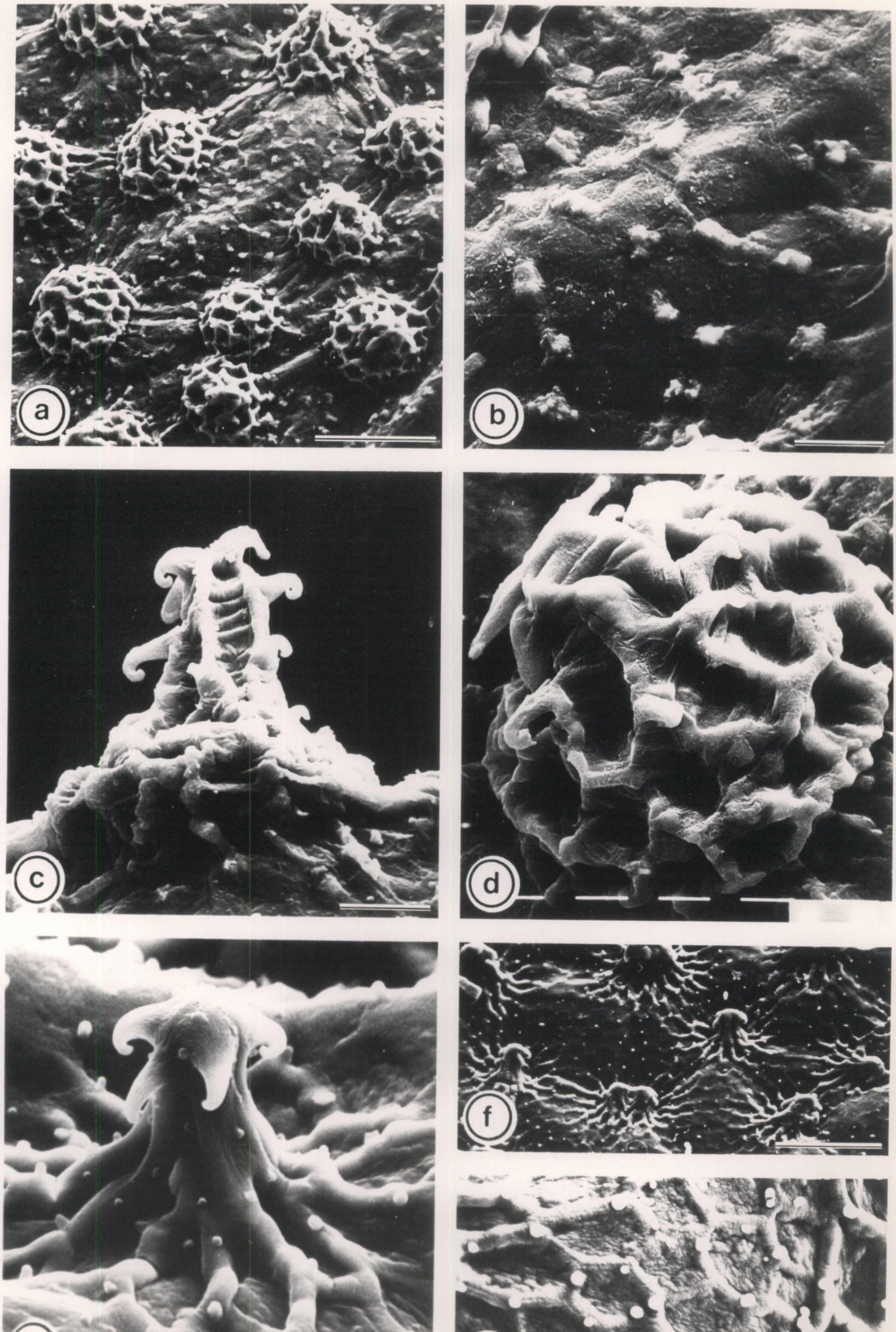
<u>Plate 27</u> a -d) *D. sp. 5*, *Story 4752*: a) Surface of testa with reticulations and tubercles, scale line = 100 µm; b) Reticulations, scale line = 20 µm; c) Tubercle, scale line = 20 µm and d) Tubercle, scale lines = 10 µm.

e - g) *D. spinulosa*, *Biggs M605*: e) Tubercle, scale line = 10 µm; f) Surface of testa with reticulations and tubercles, scale line = 100 µm and g) Reticulations, scale line = 20 µm.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low in profile, is very convoluted and has hooks at the top. Along the edges of the seeds there are occasional tubercles that have a convoluted basal portion out of which extends an upper portion. This extended portion has raised vertical ridges, with rung-like crossbars between them, and hooks (plate 27c). *D. spinulosa* has a surface with clearly and indistinctly defined ridges (plate 27f). The surface has small wax papillae (plate 27g), which also occur on the tubercles (plate 27e). The tubercles are hooked and do not have convoluted surfaces (plate 27e).

Internal Seed Morphology

Cleared preparations indicate that the cotyledons of *Peristrophe* are in the incumbent position (plate 17b).

Ovules of *P. cernua* are unitegmic with a many layered outer integument, which is gradually absorbed as the embryo develops. The testa of the mature seed generally consists of a well-defined epidermis and one to three layers beneath this (plate 28a), except at the chalazal end of the ovule where there may be many layers . The outer epidermal cells of the integument are distinguishable at a very early stage by their dense starchy contents (plate 28a). They appear to have lignified inner tangential and radial walls. The outer tangential wall is less markedly thickened, but clearly cutinised and, on drying, collapses inwards to give the reticulate pattern. The inner layers of the integument are loosely packed thin-walled parenchyma cells (plate 28b). The developing embryo is embedded in a cellular endosperm with a clearly differentiated outer epidermis, which is differentiated by its dense contents that gave positive test for lipids with Sudan IV. The layer immediately beneath this also has densely staining contents. These two layers persist in the mature seed as an epithelium, which, in imbibed seeds, lines the inner surface of the integument, but on drying collapses in convolutions round the embryo.

The tubercles are of epidermal origin (plate 28b). These multicellular structures consist of four to six elongated cells thickened on their radial and inner tangential walls by reticulate or scalariform thickening (fig. 35a & b) and, at the base of the cells, delicate annular rings. Periclinal walls sometimes occur (plate 28b). Cleared material showed that hooks on the tubercles are hollow cellulose extensions of the outer unlignified cell walls. The folds on the tubercles, such as those of *P.*

Plate 28 a - c) *P. cernua, Balkwill 463* : a) Light micrograph of section through part of a seed; outer layer with thick cuticle and dark contents is outer layer of multiseriate integument, thin-walled cells immediately below this are inner layers of the integument, the two dark layers below this are the epithelium formed by the outer layer of the endosperm, the dark tissue in the bottom right hand part of the micrograph represents one of the cotyledons, scale line = 10 µm; b) Light micrograph of section through young tubercle, showing that it is multicellular and that, unlike the tubercle in a), it has cross-walls, scale line = 10 µm and c) section through tubercle showing thickenining on radial walls, scale line = 10 µm.

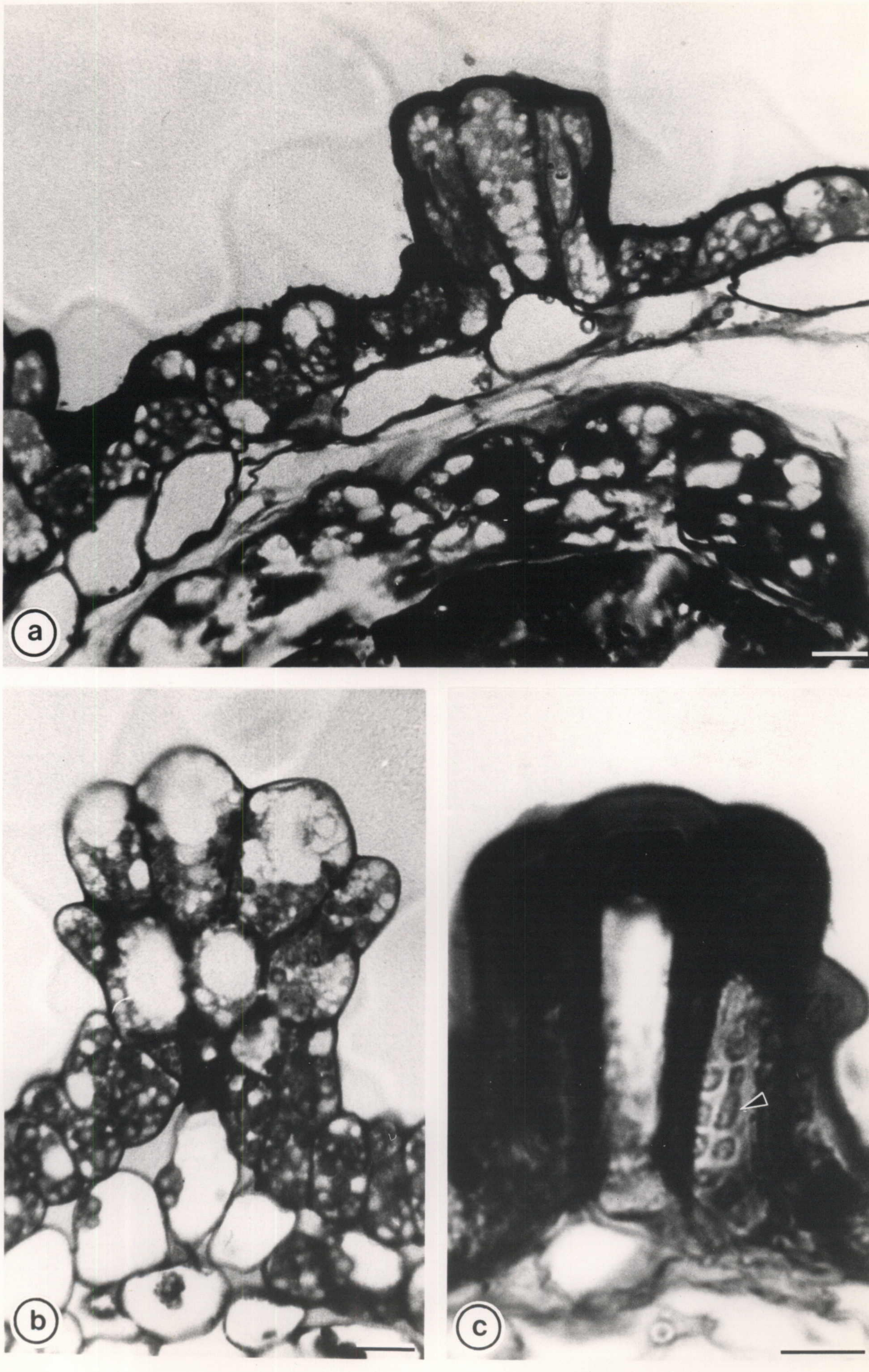
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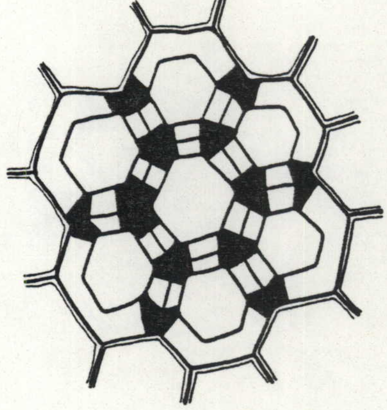
Fig. 35: Details of thickening of tubercles drawn from cleared material of *P. cernua, Balkwill 463*: a) View from top of a tubercle, areas between black areas coincide with pits in thickening [c.f. plate 28c], X400 and b) sideview of tubercle, black blocks represent ends of bars of thickening on touching walls, X400.



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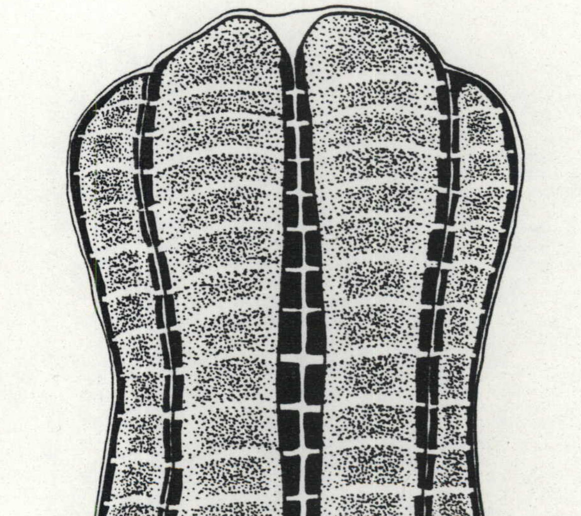

b

cernua (plate 18a & c), are formed as the outer unthickened walls collapse against the framework of thickening. The effect of this in *D. sp. 5* (plate 27c) is a ribbed pattern.

DISCUSSION

In *Dipteracanthus* Nees (Maheshwari & Negi, 1955) and *Nelsonia* (Mohan Ram & Masand, 1977) the relatively thin but hard testa is formed from a single integument, which, in its immature state, consists of many layers of thin-walled cells. The endosperm develops at the expense of the inner layers of integumentary cells leaving a final testa of three to five cell layers. Interpretation of sections of seeds of *Peristrophe* suggests a very similar structure. The thin-walled, crushed cellular tissue beneath the epidermis (plate 28a) between the testa and the embryo represents the remains of the multiseriate integument. An epithelium of two layers similar to that found in *Justicia simplex* Don.. by Mohan Ram & Segal (1958) surrounds the embryo.

An uneven seed surface has been reported in many Acanthaceae (Corner, 1976). This may be caused by the presence of trichomes: rigid or mucilaginous, long or short, like the unicellular hairs developed from the richly cytoplasmic radially elongated epidermis cells of *Dipteracanthus patulus* (Jacq.) Nees (Maheswari & Negi, 1955), or by the presence of small epidermal outgrowths, formed by repeated anticlinal divisions of the epidermis which then breaks away from the underlying testa layers, forming small loops as in *Justicia betonica* L. (Bhatnagar & Puri, 1970).

As far as could be determined tubercles similar to those found on the testa of *Peristrophe* and *Dicliptera* have not been recorded before.

These tubercles may be analogous with the "papillenhare" described by Eckhart (1929, in Uphof, 1962) on which conspicuous protuberances occur. These protuberances were described by Uphof (1962) as evaginations of the young cell wall which narrow until the internal cavity disappears. In *Peristrophe*, the protuberances or hooks proved to be persistently hollow and appear to be simple extensions of an unlignified outer cell wall. They are without the cellulose or cutinised contents which characterise the "papillenhare" of *Coleus* Lour., *Cynoglossum* L., *Verbascum* L. or *Digitalis* L. (Kurer in Uphof, 1962).

The rigid central framework of lignified inner cell walls of the tubercles maintains the shape during preparation for scanning electron micrscopy and the dehydration process preceeding wax embedding. This framework is more clearly defined in the tubercles of *P. cernua* than in *P. paniculata*.

The function of the hygroscopic hairs present on the seeds of some Acanthaceae has been considered by Schnepf & Deichgräber (1983) and Gutterman *et al* (1973) who found that these hairs, and the mucous they produce, played a role in seed dispersal and dormancy. These unicellular hygroscopic hairs are quite different from the tubercles of *Peristrophe*, both morphologically (pers. obs.) and anatomically (Schnepf & Deichgräber, 1983) and thus, it is likely that the functions of these structures may be different. Although the function of the tubercles on the seeds of *Peristrophe* was not specifically investigated during this study and has not been suggested in the availabe literature, it is possible that the pits in the distal wall of the tubercles and the tubercles themselves may act as one-way valves, thus enhancing the uptake of water prior to germination.

Bremekamp (1965) differentiated the Acanthaceae from the Scrophulariaceae, Mendonciaceae and Thunbergiaceae on the basis of the discoid seeds. Seeds of *Peristrophe* and *Dicliptera* have this characteristic shape. In the same publication, Bremekamp used the criterion "seed surfaces not covered with unicellular hairs" as a diagnostic character of the tribe Justicieae. Seeds of *Peristrophe* and *Dicliptera* fulfill this requirement and thus the seed surface confirms the position of the genera in the Justicieae.

From these studies, it is found that there is no character specific to either *Peristrophe* or *Dicliptera*, so that microsculpturing of the seed coat does not provide any generic characters, although it is noteworthy that the rod-like structures (plate 23a) that are common amongst species of *Dicliptera* do not occur in any species of *Peristrophe*.

In *Justicia*, seed surfaces and pollen characters correlate to define infrageneric groups (Immelman, 1983). In *Peristrophe*, however, the characters of the seed surface do not correlate with subdivision of the genus based on morphology of bracts. Topography of the testa has been particularly valuable in confirming the separation of *P. sp. 1* from *P. hereroensis*, despite similarity in gross morphology. In *Dicliptera* the microsculpturing of the seed coat provides information that supports the relationships that are thought to exist between species. The seed surfaces of *D. zeylanica* and *D. heterostegia*, which are very closely related species, differ only by the presence of small papillae in *D. zeylanica* and absence of these structures in *D. heterostegia*. The group of species including *D. clinopodia, D. divaricata, D. minor, D. sp. 2, D. sp. 3* and *D. quintasii* are characterised by having tubercles with highly convoluted surfaces, often without hooks. Most of these species have rod-like structures on the surface and none of them have small papillae. All of these species are thought to be derived from *D. clinopodia* and thus similarity in their seed surfaces might be expected. *D. capensis*, which is thought to have been derived by hybridistaion of one of the members of this group with either *D. heterostegia* or *D. zeylanica*, has gross morphology very similar to the latter two species, but microsculpturing of seed coat very similar to *D. clinopodia* and its allies. This supports the view that *D. capensis* might have arisen by hybridisation of a member from each of these groups. Within *D. clinopodia*, it appears that form A may differ from form B by having shorter straighter rod-like structures on the surface. There is also a difference in the seed coat of the two subspecies of *D. minor*, as taller tubercles are more common in *D. minor* ssp. *1*. *D. sp. 2* and *D. sp. 3* have very similar tubercles, emphasising their close relationship, while the fact that the former has rod-like structures that are absent from the latter confirms that they are different at the specific level. The tubercles of the seeds of *D. quintasii* are unique in the genus, because no other tubercles have as many hooks. This confirms that *D. quintasii* is different from *D. clinopodia*, a species to which it is morphologically very similar. *D. fruticosa* and *. eenii* have similar seed surfaces and tubercles; this supports the view that these species are closely related, while confirming that they are different species. The variation within *D. eenii* is very interesting. The Namibian population has a seed surface slightly different from that of the Transvaal population. It appears that there is a discontinuity in the distribution of these populations of *D. eenii*, although this may be due to under-collection. If, however, it is found that the discontinuity is real, and that there is no link between these populations, it seems that the geographical disjunction and the difference in seed surface may suggest that the two populations should be formally recognised at an infraspecific level. The folds in the surface between the ridges on the surface of seeds of *D. sp. 4* are very unusual, and may further emphasize the uniqueness of this species, although it is possible that the folds are an artefact of preparation. It is not possible to verify this at present, as only one seed of the species is available. *D. sp. 5* has unusual tubercles and crystals are evident on the surface that are not present in other species investigated. This suggests that *D. sp. 5* may not be closely related to other southern African species of *Dicliptera*. While *D. spinulosa* is morphologically similar to *D. clinopodia* and its allies, the microsculpturing of the seed coat is more similar to that of *D. heterostegia*. The tubercles of *D. spinulosa* are very similar to those of *P. paniculata*, which is the only other southern African member of these two genera that is an annual, is geographically widespread and grows in deserts or very dry areas.

CONCLUSIONS

Although observations with a dissecting microscope, at 50X magnification were useful to confirm the classification of *Peristrophe* and *Dicliptera*, these observations did not seem to be diagnostic at the species level. However, micrographs prepared with a SEM, at 500X magnification, provided characters of the seed coat that are diagnostic at the species level and correlated with species concepts which had been formulated on the basis of macromorphological observations. It appears that these characters are not useful to define infrageneric groups in *Peristrophe*, although they provide useful information in *Dicliptera*.

The function of these elaborately thickened tubercles is not as yet known, and is worthy of further investigation. The similarity between the tubercles of *D. spinulosa* and *P. paniculata*, which are both annuals, and which occur in similar habitats, however, suggests that these structures may have some eclogical function.

APPENDIX 1

Peristrophe paniculata (Forssk.) Brummit
Seydel 11 & *Giess & Leippert 7317*

P. transvaalensis (C.B. Clarke) Balkwill
Balkwill 764

P. cliffordii Balkwill
Balkwill 793

P. gillilandiorum Balkwill
Grosvenor 820

P. kotschyana Nees
Balkwill 732

P. cernua Nees
Balklwill 168, 326, 402 & *445*

P. hereroensis (Schinz) Balkwill
de Winter 2356

P. sp. 1
Craven 1021 & *de Winter & Leistner 58*

D. zeylanica
Balkwill 349 & *448*

D. heterostegia
Balkwill 197, 198, 244, 261 & *412*

D. capensis
Balkwill 465

D. clinopodia var. *clinopodia* form A
Balkwill 396 & *790*

D. clinopodia var. *clinopodia* form B
Balkwill 213, 215, 287 & *289*

D. divaricata
Balkwill 175 & *177*

D. minor ssp. *minor*
Balkwill 752 & *Gerstner 5528*

D. minor ssp. *1*
Balkwill 1598

D. sp. 2
Balkwill & Cadman 3024 & *Forbes 427*

D. sp. 3
Balkwill 766

D. quintasii
Balkwill, Cadman & Stormanns 3055

D. eenii Namibian population
Giess 12376

D. eenii Transvaal population
Balkwill 798

D. sp. 4
Balkwill 1587

D. spinulosa
Biggs M603

D. sp. 5
Strey 4752

D. fruticosa
Balkwill 777 & *1570*

CHAPTER 9
INDUMENTUM

Introduction

The indumentum on various parts of species of Acanthaceae has been found to be taxonomically useful at the specific level and, in one instance, has been used at the subtribal level (Bremekamp, 1944). This character has been used in keys to species, in the formal diagnoses of new species and is often mentioned in discussions about the differences between species. In keys, indumentum of the corolla (Wasshausen, 1970), of the stem (Wasshausen, 1966), of the ovary (Baden, 1981a), of the bracts (Baden, 1981a), of the leaves (Daniel, 1982b), of the calyx (Daniel, 1980a) and of the filaments (Balkwill & Getliffe Norris, 1985) has been used. Indumentum of various structures has been used in formal diagnoses of new species; Henrickson & Daniel (1979) used that of the stem and the capsule; Wasshausen (1984a) used that of the stem and Brummitt & Feika (1978) that of the inflorescence. While discussing the differences between species, Wasshausen (1977a) used the indumentum of the calyx; Daniel and Henrickson (1982) that of stems, axes of the inflorescence, pedicels and calyces; MacDade (1982a) that of corollas and Heine (1962) that of styles.

Material and Methods

Indumentum has been studied on fresh material, on dried herbarium material, on herbarium material that had been rehydrated by simmering and on fresh and dried material that had been cleared using the method of O'Brien & von Teichman (1974). Observations have been made at 6, 12, 25 and 50X magnification using a dissecting microscope and at higher magnifications using a compound microscope. A general survey was conducted, investigating only a few specimens of each species and then the constancy of potentially useful characters was established by checking the feature in available specimens of the species concerned.

Observations

Stems

There is a species-specific variation in the indumentum of the stems of *Peristrophe* (plate 29). Of particular note is the stem of *P. grandibracteata* (plate 29a), which is white. This colour is caused by the dense indumentum (fig. 36a) of trichomes with large ornamented terminal cells (fig. 36b - d). *P. hereroensis* has a stem that is green (plate 29b), because of the sparse indumentum (fig. 36e). This indumentum is composed of slightly different trichomes, also with ornamented cells (fig. 36f, g, i & j). *P. sp. 1* (plate 29c) also has green stems with a sparse indumentum (fig. 36k & p), but the cells of the trichomes of this species are not ornamented (fig. 36 l - o & q - u). *P. paniculata*, *P. kotschyana* and *P. cernua* have relatively few hairs on their stems and the hairs are restricted to the ridges (c.f. plate 29d, h & i). *P. transvaalensis* has a relatively denser indumentum on its stem than do the previous three species, but the hairs are concentrated near and on the ridges on the stem (plate 29e). The stems of *P. cliffordii* (plate 29f & fig. 37i) and *P. gillilandiorum* (plate 29g & fig. 38i) are densely pubescent, with the trichomes between the ridges.

The range of types of indumentum on the stems of *Dicliptera* includes stems that are glabrous, except for a few hairs at the nodes (e.g. *D. sp. 3*), stems that are variously pubescent and stems like those of *D. sp. 5*, which have dense white silky trichomes up to 3 mm long, particularly on the lower nodes. The other stems that are of interest are those of *D. sp. 2*, which have trichomes with soft-walled cells that collapse when the specimens are dried and often have a right-angled bend when fresh. *D. clinopodia*, a closely related species, has stems that are glabrous or have short trichomes (up to 0,5 mm long) or have larger thick-walled trichomes that do not collapse when specimens are dried. The indumentum of the stems of *D. eenii* shows more variation than does that of any other species studied. *Giess 12376* and *Rutherford 435* from Namibia and *Obermeijer 30992* and *van Vuuren 150* from the Transvaal, have densely pubescent stems, while *Giess 10165* from Namibia and *Repton 614* from the Transvaal are almost glabrous.

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<u>Plate 29</u>: Trichomes on the stems of species of *Peristrophe*: a) *P. grandibracteata*, b) *P. hereroensis*, c) *P. sp. 1* d) *P. paniculata*, e) *P. transvaalensis*, f) *P. cliffordii*, g) *P. gillilandiorum*, h) *P. kotschyana* and i) *P. cernua*.

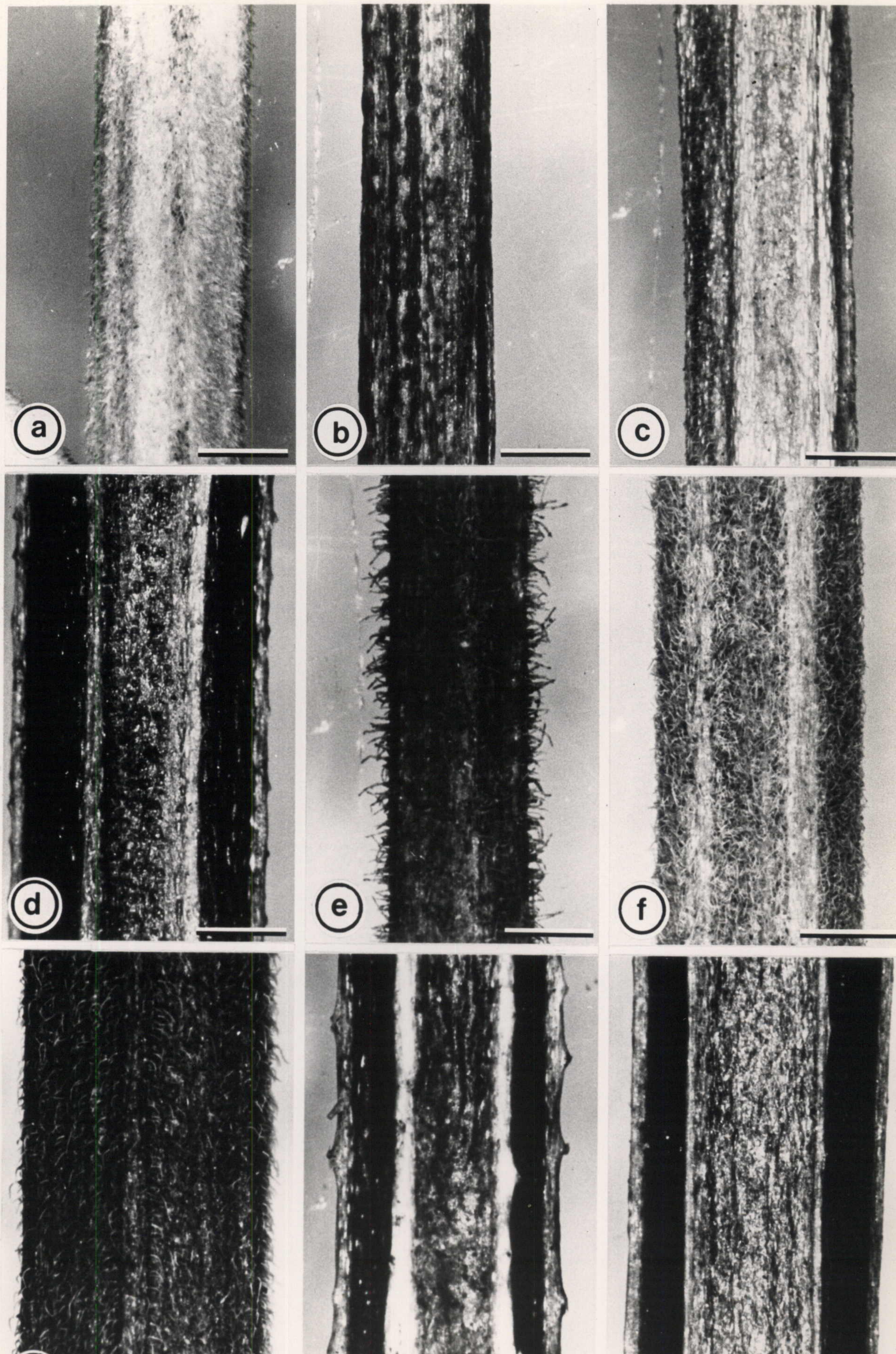
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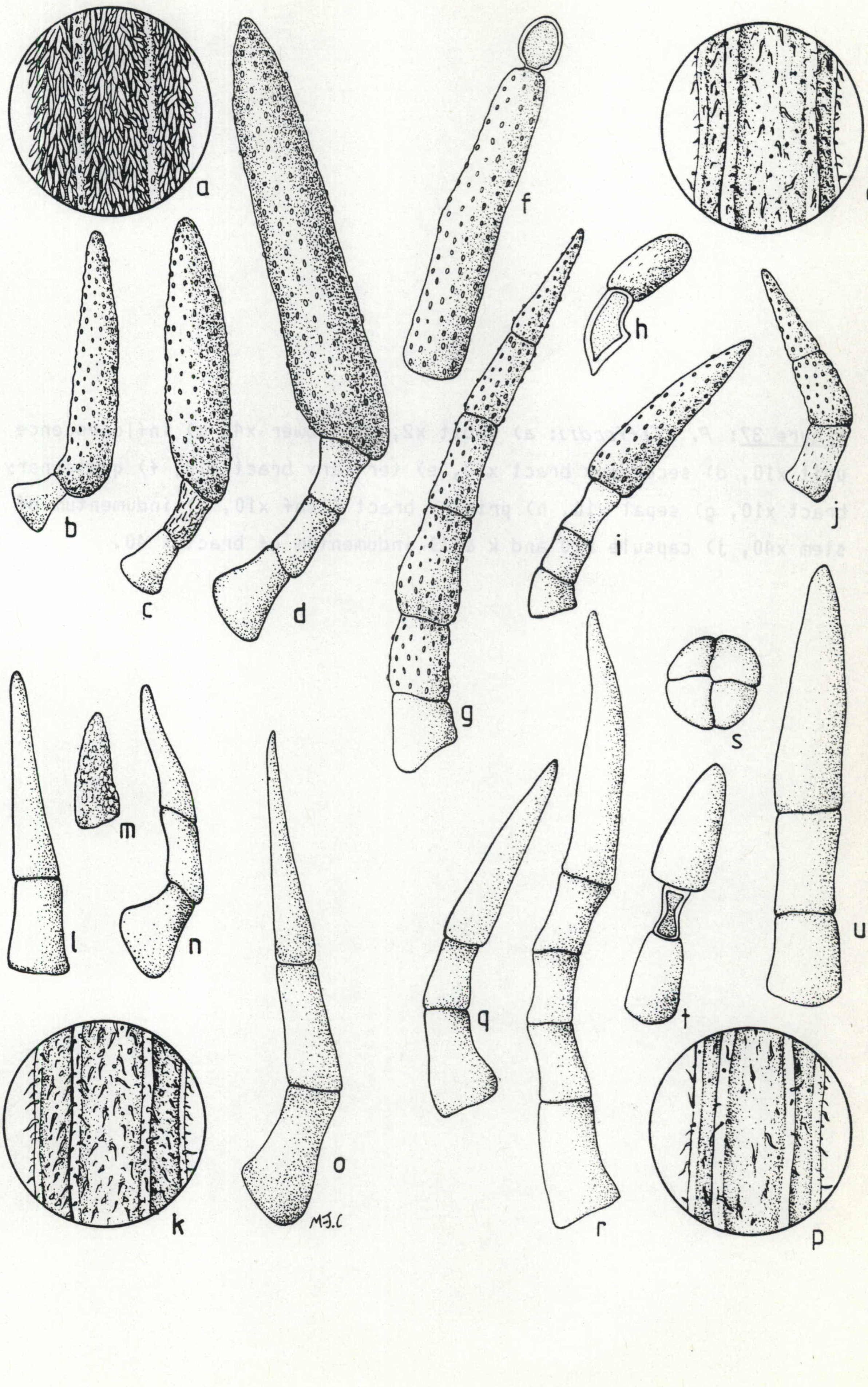
Figure 36: Trichomes on the stem of some species of *Peristrophe*: a - d) *P. grandibracteata*, b - j) *P. hereroensis*, k - o) *P. sp. 1* ssp. *1* and p - u) *P. sp. 1* ssp. *1*; a, e, k & p) indumentum of stems, X 10; all others X 600.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<u>Figure 37</u>: *P. cliffordii*: a) habit x2, b) flower x4, c) inflorescence unit x10, d) secondary bract x10, e) tertiary bract x10, f) quaternary bract x10, g) sepal x10, h) primary bract (leaf x10, i) indumentum of stem x40, j) capsule x10 and k & l) indumentum of bract x 40.

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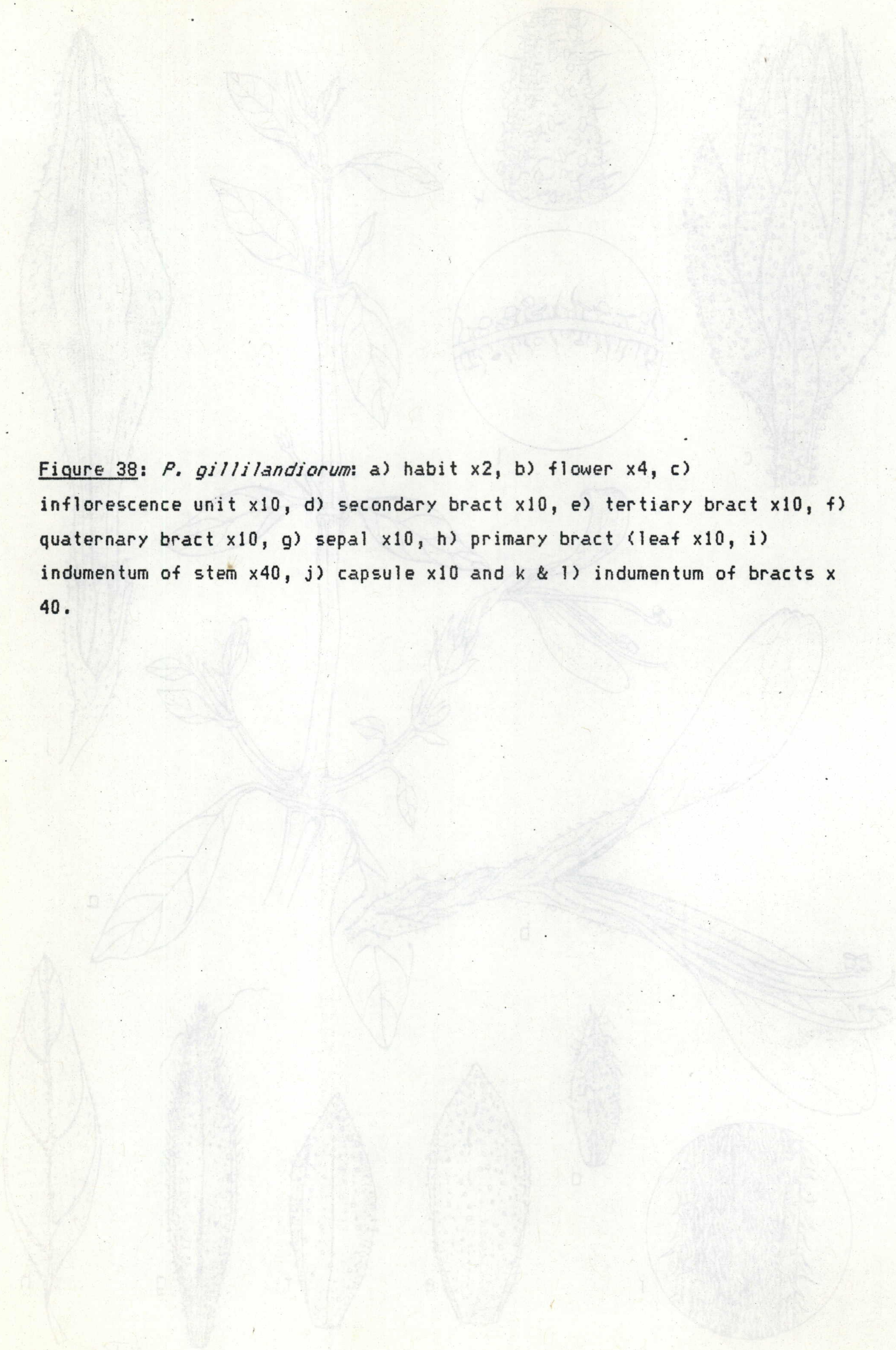

<u>Figure 38</u>: *P. gillilandiorum*: a) habit x2, b) flower x4, c) inflorescence unit x10, d) secondary bract x10, e) tertiary bract x10, f) quaternary bract x10, g) sepal x10, h) primary bract (leaf x10, i) indumentum of stem x40, j) capsule x10 and k & l) indumentum of bracts x 40.


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M.J.C.

Leaves

The indumentum of the leaves of *P. transvaalensis* is more dense than that of other species of *Peristrophe* and the hairs are longer and this imparts an unusual grey-green colour to the leaf. The Cape material of *P. cernua* has glabrous leaves, while the Natal material of the same species has hairy leaves. The leaves of *D. sp. 3* are glabrous, as are the leaves of *D. minor* and *D. divaricata*. *D. sp. 2* and most other species of *Dicliptera* have hairy leaves.

Secondary bracts

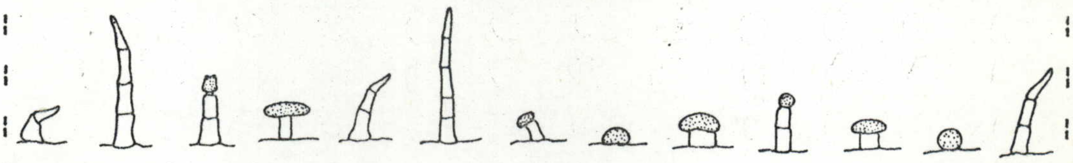
There is a variation in the indumentum of the secondary bracts, but the distribution of the types of indumentum on the secondary bracts is very similar to that of the more obvious tertiary bracts and so is not discussed.

Tertiary bracts

The tertiary bracts *P. grandibracteata* have trichomes with large ornamented terminal cells (fig. 36b - d) on the midrib and occasionally on the lamina, while *P. hereroensis* has trichomes like those in fig. 36f - g on the midrib and occasionally on the lamina. The tertiary bracts of *P. sp. 1* are almost glabrous. The tertiary bracts of *P. paniculata* are sparsely strigose with short-stalked and sessile glands on the surface. *P. transvaalensis* has many long eglandular trichomes on its tertiary bracts, which make them appear grey-green. The tertiary bracts of *P. kotschyana* are strigose on the margins, veins and surface, but have short-stalked glands near the apex. *P. cernua* has multicellular eglandular trichomes and large and small short-stalked glands on the tertiary bracts. *P. cliffordii* is unusual, as the bracts are ciliate on the margins and veins, but densely glandular on the surface (fig. 37e, k & l) and the glands, or their exudate, give the bracts a golden-brown colour. *P. gillilandiorum* has densely glandular-pubescent tertiary bracts (fig. 38e, k & l).

The distribution of types of trichomes on the tertiary bracts of *Dicliptera* is presented in Table 12. Of particular interest are the long hairs fringing the bracts of *D. spinulosa*, the glabrous or near glabrous bracts of *D. sp. 2* and *D. sp. 3* and the bracts of *D. quintasii* and *D. clinopodia* , which have curved and straight eglandular hairs and sessile pin-like and mushroom-like glandular

Table 12: Types and densities of trichomes present on the tertiary bracts of species of *Dicliptera*.



Species	Margins and Veins				Outer Surface						Inner Surface		
1)	s				s.s								
2)	p		p		d			p		p		p	p
3)	p		p		p			p		p			p
4)	s				s								
5.1)	p	p	p		p	s		p	p	p			
5.2)	p	p	p		p	s		p		p			
6)	sp						v.d	v.d	v.d				
7.1)	s								i				
7.2)	s						d		d				
8)	s									i			
9)	s.s								i				
10)	s	p							p				
11)	s								i				
12)					sp		sp						
13)	s										c		p
14)	p	p			p				p				
15)	p	d			p				p				

Terms for presence of trichomes.

i initially present, then lost

s.s sparsely strigose

s strigose

Terms for density of trichomes, in order of increasing density.

sp sparse

p present

c common

d dense

v.d very dense

trichomes.

Calyx

The indumentum of the calyx of most species of *Dicliptera* and *Peristrophe* is very similar. Within the calyx lobes there are small broad-based appressed eglandular hairs and small, erect glandular hairs. The outside of the lobes are densely glandular with small and large-headed glandular trichomes and the margins of the lobes and the veins are variously strigose, ciliate or sparsely strigose with eglandular or a mixture of glandular and eglandular trichomes. Only two taxonomically useful variations were observed. The outer surface of the calyx of *D. quintasii* has eglandular and glandular trichomes in equal proportions and the margins have some long wispy hairs. *P. cliffordii* is also unusual as it has long wispy hairs near the apex of the calyx lobes (fig. 37g).

Corolla

All species of *Peristrophe* and *Dicliptera* have a similar indumentum on the outer surface of the corolla, with many curved and some straight eglandular and some glandular trichomes. Species of *Peristrophe* have slightly more glandular trichomes on their corollas than do species of *Dicliptera*.

Stamens

In *Peristrophe* and *Dicliptera*, trichomes occur on the filaments on the lower and on the inner surfaces and immediately below the anthers. The trichomes in the proximal regions are usually broad-based, appressed and eglandular and are occasionally accompanied by a few short-stalked glandular trichomes. The trichomes immediately below the thecae are very small, short-stalked and glandular. A similar pattern of distribution occurs in all species.

Style

Most species of *Peristrophe* and *Dicliptera* have styles that are sparsely strigose or strigose. Some species (e.g. *P. paniculata, P. kotschyana, D. sp. 2* and *D. spinulosa*), however, have glabrous styles.

Ovary

The indumentum on the ovaries of a plant may change in density and composition as a flower ages so that care must be taken to observe the trichome types on a range of ovaries. In *D. sp. 4*, for instance, the ovary is initially puberulous (with what may be developing glandular trichomes), then it develops some glandular trichomes and later has both glandular and eglandular trichomes. In *Peristrophe*, *P. grandibracteata* and *P. hereroensis* have glandular trichomes on the ovary; *P. paniculata* and *P. cernua* have mixed eglandular and glandular trichomes on the ovary; *P. transvaalensis*, *P. cliffordii* and some specimens of *P. kotschyana* have scattered eglandular trichomes on the ovary and *P. gillilandiorum* and some specimens of *P. kotschyana* have glabrous ovaries. *P. sp. 1* ssp. *1* has dense eglandular trichomes and *P. sp. 1* ssp. *2* has glabrous ovaries.

In *Dicliptera*, ovaries may be glabrous or pubescent with glandular or eglandular trichomes. Species that have glabrous ovaries are *D. heterostegia*, *D. minor* ssp. *minor*, *D. sp. 3*, *D. quintasii*, *D. sp. 5*, *D. spinulosa* and some specimens of *D. eenii*. Those that have only eglandular trichomes may be nearly glabrous with only a few eglandular trichomes near the tip (*D. clinopodia* var. *1* and *D. sp. 3*) or they may be strigose as are some specimens of *D. eenii*. Those with glandular trichomes may have very few glandular trichomes near the tip (*D. clinopodia* var. *clinopodia* and *D. divaricata*), they may have only glandular trichomes (*D. capensis*) or they may have a mixture of glandular and eglandular trichomes (*D. sp. 1*, *D. sp. 4* and *D. fruticosa*).

Fruits

Peristrophe sp. 1 ssp. *2* and some plants of *P. kotschyana* have glabrous fruits. The fruits of *P. sp. 1* ssp. *1*, *P. paniculata*, *P. transvaalensis* and some plants of *P.kotschyana* have eglandular trichomes, while *P. grandibracteata*, *P. hereroensis*, *P. cliffordii* (fig. 37j), *P. gillilandiorum* (fig. 38j) and *P. cernua* have glandular and eglandular trichomes on the fruits.

Dicliptera heterostegia and *D. spinulosa* have only eglandular trichomes on the fruits; *D. zeylanica* and *D. sp. 2* have more eglandular trichomes than glandular ones; *D. clinopodia* var. *1*, *D. sp. 4* and *D. fruticosa* have glandular and eglandular trichomes equally common and *D. capensis*, *D. clinopodia* var. *clinopodia*, *D. divaricata*, *D. minor* ssp. *1*, *D. quintasii* and *D. sp. 5* have more glandular than eglandular trichomes. *D. minor ssp. minor* and *D. sp. 3* have only glandular trichomes and those of *D. sp. 3* are scattered. The fruits of *D. eenii* are initially strigose with short eglandular trichomes, but later develop some longer eglandular trichomes and many stalked, glandular trichomes.

Discussion

There are some difficulties inherent in the study of trichomes.
1) As some structures mature, so the types of trichomes, the density of trichomes and the relative frequency of different types of trichomes may vary, as in the maturing fruit of *D. eenii*.
2) It is difficult to define different types of trichomes because, although different kinds of trichomes are distinguishable, they sometimes intergrade into one another on the same structure, on the same plant and sometimes the trichome type on one species may be intermediate between two discreet types on another. Different developmental stages of the more complex glandular trichomes (Oosthuizen & Coetzee, 1983) may be mistaken for different kinds of trichomes.
3) It is very difficult to find accurate and concise terminology to describe the different types, sizes and shapes of trichomes.
4) It is difficult to find appropriate terminology and a pragmatic method of estimating the relative frequencies of different types of trichomes on the same structure. Most available methods are too subjective, too time-consuming or too impractical to use during the identification of specimens.
5) Similar difficulties exist with the description and estimation of density of trichomes.
6) It is difficult to record the information about indumentum by visual means. When using electron microscopy, it was found that trichomes collapsed during preparation of material, while it was found that there was insufficient depth of field to obtain clear photographs with light microscopy.

In spite of these difficulties, this survey has provided interesting taxonomic data. In *Peristrophe*, the indumentum of the stem has been a particularly important character that drew attention to the differences between *P. grandibracteata* and *P. hereroensis* and to *P. gillilandiorum* and *P. cliffordii*, two hitherto undescribed species. This character is also useful in the key to the species of *Peristrophe*. The indumentum on the stems of species of *Dicliptera* has also been important in the key to species and to differentiate *D. sp. 5* from all other species, or to distinguish between *D. sp. 2* and *D. clinopodia* var. *clinopodia* and between *D. sp. 2* and *D. sp. 3*. There is variation in the degree of pubescence and the length of the trichomes on the stems of *D. eenii* that does not correlate with variation in other characters or with geographical distribution and, thus, can only represent intraspecific variation.

The indumentum on the leaves of different species of *Peristrophe* and *Dicliptera* is very similar, although some species of *Dicliptera* have glabrous leaves. *D. sp. 2* has glabrous leaves, and although this character alone is not sufficient to differentiate *D. sp. 2* from other species, it is correlated with glabrous stems and glabrous surfaces of tertiary bracts. These three characters together with the height of the plant, differentiate *D. sp. 2* from all other species of *Dicliptera*.

The indumentum on the secondary bracts is very similar to that on the tertiary bracts in all southern African species of *Dicliptera* and *Peristrophe*. As the tertiary bracts are more obvious, it is convenient to consider the indumentum on the latter rather than that on the former. Indumentum on the tertiary bracts is important in distinguishing between species, and has been used in the key to separate *D. spinulosa, D. sp. 2, D. quintasii* and *D. divaricata* from other species. This character has also been used in the diagnosis of *D. sp. 3* and in discussion of the differences between the species mentioned above and their congenors. *D. minor* ssp. *1* can be differentiated from most specimens of *D. minor* ssp. *minor*, as the former has dense glandular trichomes on the tertiary bracts and the latter (except for *Gerstner 5528*, collected from an irrigated area) has glabrous or very sparsely glandular tertiary bracts.

The indumentum on the calyx is very similar in species of *Dicliptera* and *Peristrophe*. It will be interesting to compare the distribution of trichomes with those of other genera, particularly those in different subtribes and tribes, to test whether their distribution is taxonomically useful to distinguish between these groups. *D. quintasii* can be separated from other species of *Peristrophe* and *Dicliptera* by its equal density of eglandular and glandular trichomes on the outer surface of the calyx. *P. cliffordii* can be separated from other species of *Peristrophe* because it has a few wispy hairs at the tips of the calyx lobes, as can *D. quintasii* from species of *Dicliptera*.

The only difference between the indumentum on the corollas of all species of *Peristrophe* and *Dicliptera* is a greater frequency of glandular trichomes on the corollas of species of *Peristrophe*. This difference is not sufficiently clear-cut to be used as a generic character.

Although the indumentum on the stamens of the southern African species of *Hypoestes* was found to be species-specific (Balkwill & Getliffe Norris, 1985), this does not appear to be the case in *Dicliptera* and *Peristrophe*.

The styles of some species of *Peristrophe* and *Dicliptera* are glabrous, while most others are strigose and this provides another character with which to distinguish between *D. sp. 2* and *D. sp. 3* and between *D. sp. 2* and *D. clinopodia*.

There is a range in distribution, density and types of hairs present on ovaries of species of *Peristrophe* and *Dicliptera*. The density and relative abundance of types of trichomes on the fruits of these genera are useful. The relative abundance of stalked glandular and of eglandular trichomes on the fruits allows one to distinguish between *D. sp. 2* and *D. clinopodia*, but the changes in the relative abundance of types of trichomes accompanying growth of the capsules of *D. eenii* suggests that comparisons of indumenta should only be made on mature capsules.

Conclusions

Indumentum provides a number of characters useful in keys, but its value is lessened slightly by the possibility that changes may occur with age. These characters must thus be used with care. The indumentum on various structures of the species of *Peristrophe* and *Dicliptera* provides useful characters to distinguish between species and subspecies.

CHAPTER 10
CHEMOTAXONOMY

Introduction

Chemotaxonomy has been a useful taxonomic tool in studies of the Angiosperms as well as of other divisions (e.g. lichens (Culberson, 1969) and Lycophyta (Braekman *et al* 1980)). The long history of chemotaxonomy has been described by Gibbs (1963 & 1974). Many different kinds of substances have been investigated as sources of taxonomic information, and many provide much important information (Smith, 1976). Flavonoids are a group of compounds that are particularly useful (Bate-Smith, 1963 & Smith, 1976). An account of the structure and different kinds of flavonoids is given by Markham (1982), while Hahlbrock & Grisebach (1975) describe the processes of biosynthesis of flavonoids and Stotz *et al* (1984) describe the biosynthesis of flavonoids in flowers of a species of *Verbena*. Flavonoids are compounds that affect flower colour (Goodwin, 1965) and because flowers of different colours might attract different pollinators, the presence of flavonoids may have taxonomic and evolutionary importance. Although much work has been done on the distribution and taxonomic significance of flavonoids in many Angiosperms, relatively little work, other than that listed by Gibbs (1974) and that of Bloom (1976), has been published about the Acanthaceae. This pilot study emphasises that there is great potential in this field of research in the Acanthaceae.

Material and Methods

1) Acquisition and Storage of Material

For extraction of floral flavonoids

a) Field collections

Flowers were collected from plants in the field, placed in jars of 95% ethanol and then stored in a cooler box or a refrigerator, until the termination of the field trip. Jars were then transferred to and stored in a refrigerator until the contents were prepared for extraction. In these collections, flowers were collected from a number of plants in the same population and thus represent population samples.

b) Accumulated collections from cultivated plants

Some species, such as *P. transvaalensis*, flower sporadically so that it was difficult to make sufficiently large collections in the field. In these cases plants were collected and cultivated in the botanical garden of the Department of Botany. Flowers were harvested from plants every two or three days and accumulated in 95% ethanol and stored in jars in a refrigerator. Flowers from plants that flower more prolifically were also accumulated and in these cases the flowers from each plant of each species were kept separately.

c) Direct extracts from cultivated plants

Flowers from some of the more prolifically flowering species were collected in test tubes and extracted immediately.

For extraction of foliar flavonoids

Leaf material was collected from plants in cultivation and extracted directly in 95% ethanol.

2) Extraction of flavonoids from plant material

Flavonoids were extracted using the methods recommended by Harborne (1973). Extraction was in minimal amounts of 95 % ethanol, heated over a waterbath to 90 ° C for 15 minutes. The extracts were cooled to room temperature, poured onto large watchglasses (10 cm in diameter) and concentrated in the draft of a fume hood. During concentration of the extracts, much sticky material was deposited on the watchglasses. If the liquid was evaporated to dryness, or if the extracts were to be re-used after they had dried, they were resuspended by pouring between three and five ml. of 95% ethanol onto the watchglass until the dried deposit was covered. The acohol was then concentrated as described above, and during this process the compounds were resuspended. If 95% ethanol was added and gently heated over a waterbath, it was found that there were more spots on the resultant chromatograms, suggesting that the heating may alter some of the compounds. The sticky material on the watchglasses was also resuspended with heating, and appeared to cause overloading of the chromatograms.

3) Separation of flavonoids

Chromatograms were prepared by descending development on Whatman No. 1 paper (460 X 570 mm). A drawn capillary tube was used to apply small amounts of extract to the paper in a stream of warm dry air. If too much material was spotted onto a paper, the spots on these overloaded chromatograms were elongated and often overlapped in the first dimension. Rf values of these streaks were depressed when compared with those of spots on other chromatograms. Leaf extracts were separated in a single dimension, where the solvent was the upper layer of n-butanol - glacial acetic acid - water (B.A.W.) in the proportions of 4:1:5. Floral extracts and selected foliar extracts were separated in two dimensions, using B.A.W. as the first solvent and 5% aqueous acetic acid as the second. Chromatograms were dried in a ventilated oven at 80 ° C.

4) Characterisation of compounds

Dried chromatograms were viewed under ultra-violet light (wave-length 366 nm). Each spot was circled in pencil and the colour was noted. Chromatograms were fumed with ammonia and changes in colour noted. Relative flow (Rf) values were calculated for each spot in each solvent by the method of Harborne (1973). Spots were characterised on the basis of these four criteria. In species where more than one extract had been prepared, the chromatograms were critically compared under ultra-violet light and by comparison of their colours and relative positions, spots that most likely represented the same compound on the different chromatograms were given the same code number. The Rf values for each spot with the same code number were then averaged, and these averages were used to characterise the spots for these species. Comparison of spots on chromatograms of different species was based on colour and Rf values. A 5% range of variation in Rf value was accepted.

5) Presentation and manipulation of results.

Tables

Table 13 presents the distribution of spots from the one-dimensional foliar chromatograms.

A list of spots that occurred on the two-dimensional chromatograms of the floral extracts from each species was prepared. Presence and absence of these spots in each collection is indicated on Tables 14 - 30. This information was also scored onto a large table, on which all 118 spots recognised were recorded. This was useful for observing patterns of distribution of spots and for preparing similarity coefficients based on

Table 13: Presence and absence of spots in one-dimensional chromatograms of leaf extracts.

Spot	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
1				?	?	?			?		?	?			?	
2																
3			+	+	+	+	+				+	+	+	+	+	+
4								+	+	+						
5																
6	+	+														
7																
8	+	+	+		+						+	+	+			+
9																
10			+		+					?	+	+	+	+	+	+
11																
12																
13																
14																
15																
16	+	+														
17																
18																
19																
20																
21	+	+														
22			+	+	+	+	+	+	+	+	+	+	+	+	+	+
23																

Spot	Q	R	S	T	U	V	W	X	Y	Z	a	b	c	d	e	f	g
1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2																+	+
3	+	+							+	+	+	+		+		+	
4																	
5																	
6																	
7																	
8	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
9											+	+	+	+		+	+
10			+	+	+	+	+	+	+	+					+		
11																	
12									+								
13																	
14																	
15																	
16																	
17			+	+	+	+	+	+	+			+	+	+	+	+	+
18																	
19																	
20																	
21																	
22																	
23																	

Spot	h	i	j	k	l	m	n	o	p	q	r	s	t	u	v	w	x	y	z	1
1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2																				
3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+
4																				
5																				
6																				
7									+	+	+									
8	+	+	+	+	+	+	+	+				+	+			+	+	+	+	+
9																				
10																				
11		+	+	+	+	+	+													
12																				
13																				
14																			+	
15																				
16																				
17																				
18																		+		
19												+	+	+						
20																		+		
21													+	+	+					
22																				
23																		+		

Spot	2	3	4	5	6	7	8	9	0	@	#	$	%	&	*	{	}
1	+	+	+	+	+		+	+		+	+	+	+	+	+		
2																	
3		+		+	+		+				+	+		+	+	+	+
4																	
5						+	+	+		+		+					
6		+		+	+												
7															+		
8						+	+		+	+	+	+	+	+			
9						+	+	+	+	+	+	+	+	+	+	+	+
10																	
11																	
12																	
13		+		+	+												
14						+		+	+		+		+				
15																	
16		+		+	+												
17																	
18																	
19																	
20																	
21	+																
22																	
23																	

Part 1 of Key to Table 13: Colours and Rf values of spots.

Spot Number	Colour in ultra-violet light	Colour in ultra-violet light after fuming with ammonia	Rf Value in B.A.W.
1	pale blue	blue	81,0 - 91,0
2	buff		69,0 - 74,0
3	colourless/blue	blue	62,0 - 79,0
4	very pale		64,0 - 70,0
5	pale	yellow	65,0 - 73,0
6	white	green	63,0 - 70,0
7	blue	blue	53,0 - 60,0
8	dark	yellow	46,0 - 65,0
9	colourless	pale yellow	37,0 - 53,0
10	dark	buff	38,0 - 52,0
11	colourless	buff	39,0 - 43,0
12	blue	blue	45,0 - 46,0
13	white	green	41,0 - 43,0
14	dark blue	dark purple	34,0 - 40,0
15	pale blue	pale blue	32,0 - 34,0
16	colourless	very pale blue	27,0 - 30,0
17	reddish green	green	31,0 - 36,0
18	dark	buff	30,0 - 31,0
19	light blue	light blue	23,0 - 25,0
20	pale	yellow	21,0 - 22,0
21	dark blue	dark blue	18,0 - 19,0
22	colourless	shiny green	16,0 - 25,0
23	colourless	buff	12,0 - 13,0

Part 2 of Key to Table 13: Species and Localities of Voucher specimens.

D. capensis

A	474	Cintsa Mouth
B	s.n.	Markmans Industrial Area

D. heterostegia

C	2	Ngoye Forest
D	171	Mkuze Game Reserve
E	174	Mkuze Game Reserve
F	187	Manzengwenya
G	198	Lake Sibaya
H	201	Lake Sibaya
I	214	Ndumu Game Reserve
J	244	Nongoma
K	249	Hlabisa
L	297	Ngoye
M	314	Ngoye Forest
N	327	Oribi Gorge
O	412	Oribi Gorge
P	472	Gonubie River Mouth

D. zeylanica

Q	120	The Downs
R	126	The Downs
S	134	Duiwelskloof
T	148	Hanglip Forest
U	149	Hanglip Forest
V	154	Entabeni Forest
W	158	Entabeni Forest
X	159	Entabeni Forest
Y	231	Ngome Forest
Z	232	Ngome Forest

D. zeylanica continued

a	233	Ngome Forest
b	242	Ngome Forest
c	338	Oribi Gorge
d	345	Umtamvuna
e	349	Umtamvuna
f	428	Umtamvuna
g	448	Storms River Mouth

D. clinopodia

h	s.n.	Wolkberg
i	103	Makapaansgat Valley
j	108a	Makapaansgat Valley
k	110	Wolkberg
l	111	Wolkberg
m	118	The Downs
n	132	Debengeni Falls
o	140	Bergplaas
p	180	Ubombo
q	213	Ndumu Game Reserve
r	215	Ingwavuma
s	216	Ingwavuma
t	280	Nkandla Forest
u	282	Nkandla Forest
v	287	Nkandla Forest
w	288	Nkandla Forest
x	289	Nkandla Forest
y	396	Umtamvuna
z	405	Horseshoe Dam
1	446	Pietermaritzburg

D. divaricata

2	170	Mkuze Game Reserve
3	175	Mkuze Game Reserve
4	177	Mkuze Game Reserve
5	220	Josini
6	259	Near Hluhluwe

P. cernua

7	168	Bishopstowe
8	444	Pietermaritzburg
9	445	Pietermaritzburg
0	169	Ashburton
@	326	Oribi Gorge
#	401	Horseshoe Dam
$	402	Horseshoe Dam
%	441	Gibraltar Valley
&	450	Baviaanskloof
*	463	Coega
(	464	Committees Drift
)	468	Committees Drift

All collecting numbers are those of Balkwill.

Table 14: Occurence of spots in gatherings of *P. cernua*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B	C	D	E	F	G	H	I
1	ice	green	53,8 ± 3,9	54,8 ± 2,9	+	+	+	+	+	+	+	+	+
2	ice	green	54,0 ± 3,9	74,8 ± 2,1	+	+	+	+	+	+	+	+	
3	dark	yellow	42,3 ± 2,9	56,4 ± 2,8	+	+	+	+	+	+	+	+	+
4	blue/ice	ice/green	78,3 ± 1,5	61,9 ± 3,6	+	+	+	+	+	+	+	+	+
5	ice	ice/green	80,1 ± 1,5	77,0 ± 2,8	+	+	+	+	+	+	+	+	+
6	blue	ice	64,4 ± 1,4	57,3 ± 3,2	+	+		+	+	+	+	+	+
7	ice	ice	66,1 ± 3,7	72,4 ± 9,3	+	+		+	+	+	+	+	+
8	colourless	blue	68,3 ± 3,7	69,7 ± 2,0	+	+		+	+	+	?		
9	colourless	blue	71,3 ± 1,4	81,7 ± 1,4	+	+		+	+	+	?		
10	colourless	blue	87,4 ± 1,5	68,4 ± 4,0	+		+	+	+	+	+	+	+
11	colourless	blue	89,0 ± 1,9	81,1 ± 3,9	+		+	+	+	+	+	+	+
12	blue	ice	84,9 ± 1,6	63,6 ± 4,2	+	+	+	+	+	+	+	+	+
13	blue	ice	85,6 ± 1,6	76,6 ± 3,7	+	?	+	+	+	+	+	+	+
14	dark	yellow	50,6 ± 5,3	32,9 ± 1,5	+	+	+	+	+	+	+	+	
15	dark	yellow	56,4 ± 1,5	45,8 ± 6,2	+	?	+	?	?	+	+	+	+
16	dark	yellow	62,8 ± 1,2	35,4 ± 2,3	+	+	+	+	+	+	+	+	+
17	dark	yellow	68,2 ± 3,5	25,5 ± 2,3	+	+	+	+	+	+			
18	dark	yellow	81,6 ± 3,9	18,0 ± 4,8	+	+	+	+	+	+	+		
19	dark	yellow	52,5 ± 2,1	43,0 ± 2,8					+	+			
20	blue range		82,5 ± 0,7	47,5 ± 3,5	+				?				
21	colourless	ice	81,4 ± 1,4	37,8 ± 2,8	+	+	+	+	+	+	+	+	+
22	colourless	ice	81,4 ± 1,3	27,1 ± 3,4	+	+	+	+	+	+	+		+
23	blue		79,5 ± 3,0	0	+		+	+	+	+	+		
24	dark	yellow	93,3 ± 0,8	0	+	+		?	+	+	+		+
25	dark	yellow	12,3 ± 2,2	74,3 ± 2,1	+	+				+			
26	dark	yellow	29,8 ± 3,3	77,3 ± 1,8	+	+	+	+	+	+	+	+	+
27	dark	yellow	43,6 ± 2,9	17,8 ± 3,4	+			+	+	+			+
28	dark	yellow	55,2 ± 4,0	14,8 ± 1,2	+	+	+	+	+	+			
29	dark	yellow	35,3 ± 2,4	22,8 ± 5,5	+		+	+	+	+			
31	dark	yellow	36,0 ± 3,0	59,2 ± 3,3	?	+	+			+		+	+
32	dark	yellow	28,5 ± 2,1	54,5 ± 3,5	?	+							+
33	dark	yellow	14,0 ± 4,2	55,0 ± 2,8	+	+							
34	(purple anthocyanin)		10,0 ± 2,3	22,9 ± 3,3	+		+	+	+	+	+	+	+
35	(purple anthocyanin)		28,0 ± 1,1	20,8 ± 2,4	+		+	+	+	+		+	

Key

A Balkwill 168 cultivated outside, from Bishopstowe
B Balkwill 772 cultivated outside, from Ashburton
C Balkwill 441 cultivated outside, from Gibraltar
D Balkwill 326 cultivated outside, from Oribi Gorge
E Balkwill 402 cultivated outside, from Horseshoe Dam
F Balkwill s.n. cultivated outside, from Nahoon Dam
G Balkwill 468 cultivated outside, from Committees Drift
H Balkwill 463 cultivated outside, from Coega
I Balkwill 450 cultivated outside, from Baviaanskloof
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 15: Occurence of spots in gatherings of *P. cliffordii*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B
1	blue	ice	52,5 ± 2,1	51,7 ± 1,0	+	+
4	blue	ice	76,0 ± 1,4	61,8 ± 1,2	+	+
5	ice	ice/green	78,5 ± 5,0	76,0 ± 2,8	+	+
6?	ice	ice	60,5 ± 3,5	53,8 ± 1,2	+	+
6?	ice	ice	59,8 ± 3,2	62,5 ± 2,1	+	+
6?	ice	ice	66,0 ± 2,8	58,4 ± 0,8	+	+
10	colourless	blue	86,3 ± 1,1	65,2 ± 3,1	+	+
11	colourless	blue	88,3 ± 1,1	78,6 ± 2,2	+	+
12	blue	ice	83,5 ± 3,5	60,3 ± 1,8	+	+
13	blue	ice	84,0 ± 2,8	73,5 ± 3,5	+	+
14	dark	yellow	49,0 ± 2,1	31,6 ± 0,9	+	+
16	dark	yellow	58,3 ± 3,2	36,2 ± 2,5	+	+
17	dark	yellow	71,8 ± 0,4	20,6 ± 3,6	+	+
21	blue	ice	79,8 ± 2,5	35,7 ± 0,9	+	+
22	blue/ice	ice	80,0 ± 2,8	23,6 ± 0,6	+	+
34	(purple anthocyanin)		9,0	21,75	+	
36	dark	yellow	62,3 ± 1,8	29,6 ± 3,7	+	+
37	yellow	yellow	49,3 ± 1,8	73,7 ± 0,3	+	+
38	bright blue	bright blue	11,8 ± 1,1	87,0 ± 2,9	+	+
39	yellowish	yellowish	22,0	89,1	+	
40	faint	yellow	84,3 ± 1,8	7,4 ± 3,3	+	+
41	colourless	ice	81,0	18,0		+

Key
A Balkwill 793 cultivated inside, from Messina
B Balkwill 1627 cultivated inside, from Messina
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 16: Occurence of spots in gatherings of *P. kotschyana*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B	C	D
1?	ice	ice	55,0	51,0		+		
2?	blue	faint	57,0	75,0		+		
4	ice	green	79,1 ± 2,7	61,1 ± 3,1	+	+	+	+
5	ice	green	81,5 ± 1,9	80,0 ± 6,5	+	+	+	+
6	colourless	ice	63,0	58,0		+		
6?	blue	ice	58,5 ± 4,8	62,7 ± 5,9	+	+	+	
10	colourless	blue	87,0 ± 1,8	67,0 ± 3,9	+	+	+	+
11	colourless	blue	89,8 ± 3,2	78,3 ± 2,9	+	+	+	+
12	blue	ice	84,4 ± 2,5	62,3 ± 4,7	+	+	+	+
13	blue	ice	84,0 ± 1,0	74,5 ± 4,4	+	+	+	+
14	dark	yellow	55,4 ± 3,5	30,9 ± 2,5	+	+	+	+
16	dark	yellow	63,4 ± 2,7	32,8 ± 4,2	+	+	+	+
17?	dark	yellow	72,4 ± 5,7	19,9 ± 2,8	+	+	+	+
21	ice	ice	80,0 ± 1,4	37,8 ± 1,1	+			+
22	ice	ice	81,8 ± 1,8	25,0 ± 1,4	+			+
31	dark	yellow	36,8 ± 1,8	61,0 ± 4,2		+	+	
34	(purple anthocyanin)		9,3 ± 0,3	22,8 ± 2,2	+	+	+	+
38	bluish streak		21,7 ± 4,0	91,3 ± 0,6	+	+	+	+
42	dark	yellow	55,9 ± 7,9	61,9 ± 9,5	+	+	+	+
43	dark	yellow	48,3 ± 5,5	49,0 ± 5,0		+	+	+
?	colourless	ice	56,0	55,0		+		
?	?	?	54,0	63,0		+		

Key
A   Balkwill 3119 cultivated outside, self-sown
B   Balkwill 760 cultivated inside, from Tweekoppies
C   Balkwill 760 cultivated outside, from Tweekoppies
D   Balkwill 732 cultivated outside, from Mohlapietse
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 17: Occurence of spots in gatherings of *P. transvaalensis*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A
7	colourless	blue	63,0	73,0	+
10	colourless	blue	87,5	62,0	+
11	colourless	blue	88,0	75,0	+
12	colourless	blue	81,0	64,0	+
13	colourless	blue	81,0	79,0	+
34	(purple anthocyanin)		14,0	22,0	+
38	bluish streak		23,5	86,0	+
44	colourless	blue	50,5	55,0	+

Key
A Balkwill 764 cultivated inside and outside, from Warmbaths
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 18: Occurence of spots in gatherings of *P. gillilandiorum*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A
4	blue	green	81,0	66,0	+
5	blue	green	79,0	78,0	+
10	colourless	blue	87,0	73,0	+
19	faint	orange	54,0	39,0	+
37	yellow	orange	52,0	79,0	+
45	blue		54,0	60,0	+
46	blue		51,0	68,0	+
60	faint	orange	65,0	49,0	+
61	faint	yellow	37,0	74,0	+
63	faint	orange	43,0	63,0	+
96	pinkish		97,0	0	+
101	faint	orange	33,0	88,0	+
108	faint	orange	42,5	41,0	+
109	faint	orange	33,0	32,0	+
110	dark	colourless	64,0	9,0	+
111	violet	violet	45,0	86,0	+
112	violet	violet	36,0	83,0	+
113	yellowish		71,0	5,0	+
?	whitish blue		51,0	89,0	+

Key
A Balkwill 1626 cultivated inside, from Messina
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 19: Occurence of spots in gatherings of *P. paniculata*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A
3	faint	orange	44,0	57,0	+
4	blue	green	79,0	66,0	+
5	blue	green	79,0	81,0	+
16	dark	orange	57,0	38,0	+
25	colourless	yellow	13,0	67,0	+
26	dark	orange	29,0	78,0	+
31?	faint	orange	38,0	53,0	+
34	(purple anthocyanin)		10,0	27,0	+
39	bluish streak		12,0 - 32,0	85,0	+
42	colourless	yellow	61,0	63,0	+
43?	faint	yellow	49,0	55,0	+
46	blue	blue	54,0	67,0	+
60	dark	yellow	67,0	45,0	+
61	faint	orange	33,0	67,0	+
64?	dark	yellow	78,0	34,0	+
114	dark	yellow	84,0	32,0	+
115	faint	orange	32,0	47,0	+
116	(faint anthocyanin)		26,0	54,0	?
117	faint	colourless	19,0	52,0	+
118	(purple anthocyanin)		28,0	5,0	+

Key
A Balkwill 3059 cultivated outside, seed from Goldblatt 1929
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 20: Occurence of spots in gatherings of *D. zeylanica.*

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B	C	D	E	F	G	H	
1	blue	ice	55,8 ± 6,7	66,4 ± 3,2	+	+	+	+	+	+	+	+	
2	blue	ice	54,8 ± 9,0	77,8 ± 1,9	+	+		+	+	+		+	
4	blue	green	77,1 ± 4,3	65,0 ± 2,3	+	+	+	+	+	+	+	+	
3	dark	yellow	39,9 ± 6,6	63,3 ± 3,7	+	+	+	+	+	+			
5	blue	green	68,6 ± 5,1	79,0 ± 2,4	+	+	+	+	+	+	+	+	
7	bluish		62,4 ± 7,1	76,5 ± 4,4		+		+	+		+	+	
10	colourless	blue	85,3 ± 4,7	71,5 & 3,4	+	+	+	+		+	+	+	
11	colourless	blue	86,8 ± 4,5	81,8 ± 3,1	+	+	+	+	+	+	+	+	
19	dark	yellow	53,0 ± 5,5	45,5 ± 9,8	+	+	+	+	+	+	+	+	
22	blue		77,0	0	+								
25?	dark	yellow	16,6 ± 7,0	82,6 ± 1,9	+	+	+	+	+	+	+	+	
26	dark	yellow	25,3 ± 6,7	79,8 ± 1,6	+	+	+	+	+	+	+	+	
32	dark	yellow	23,6 ± 8,52	55,6 ± 7,2	+	+	+	+	+	+	+		
38	whitish streak		23,9 ± 3,6	89,6 ± 1,9	+	+	+	+	+	+	+	+	
38?	whitish streak		12,4 ± 4,0	88,8 ± 4,2	+	+	+	+	+	+	?		
45	blue		47,2 ± 7,3	60,0 ± 5,6	+	+	+	+	+	+		+	
46	blue		46,3 ± 7,1	68,0 ± 2,5	+	+	+	+	+	+		+	
47	whitish blue		96,4 ± 2,1	82,2 ± 0,5	+	+	+			+	+		
48	dark	yellow	26,3 ± 7,2	65,0 ± 2,9	+	+	+	+	+	+			
49	colourless	bright blue	90,0	90,5	+								
50	faint blue		36,5 ± 13,4	82,5 ± 3,5		+	+						
51	colourless	blue	90,0	23,0	+								
52	dark	yellow	23,9 ± 6,8	29,0 ± 6,8		+		+		+	+	+	
53	bluish		60,0 ± 8,9	70,0 ± 1,0		+		+				+	
54	dark	yellow	11,0	28,0		+							
55	dark	yellow	9,0	68,0		+							
56	colourless	violet	69,0	80,0			+						possibly from tank
57	whitish blue		69,0	85,0			+						

Key

A	Balkwill 134	cultivated outside,	from Duiwelskloof
B	Balkwill 126	cultivated inside,	from The Downs
C	Balkwill 149	cultivated inside,	from Louis Trichardt
D	Balkwill 158 & 159	cultivated inside,	from Entabeni
E	Balkwill 231 & 233	cultivated inside,	from Ngome
F	Balkwill 338	cultivated inside,	from Oribi Gorge
G	Balkwill 349	cultivated inside,	from Umtamvuna
H	Balkwill 428	cultivated inside,	from Umtamvuna

U.V. Colour in ultra-violet light

NH4 Colour in ultra-violet light after fuming with ammonia

B.A.W. Rf value in B.A.W.

A.A Rf value in 5% aqueous acetic acid

(purple anthocyanin) Colour of anthocyanin in visible light

Table 21: Occurence of spots in gatherings of *D. heterostegia.*

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B	C	D	E	F	G	H	I
2		ice	58,3 ± 17,9	76,0 ± 18,3	+		+			+			
4	blue	green	80,0 ± 1,4	64,4 ± 2,0	+	+	+	+	+	+	+	+	+
5	blue	green	80,6 ± 1,3	77,2 ± 1,7	+	+	+	+	+	+	+	+	+
10	colourless	blue	87,9 ± 1,6	73,8 ± 1,9	+	+	+	+	+	+	+	+	+
11	colourless	blue	88,1 ± 1,7	81,9 ± 2,1		+	+	+	+	+	+	+	+
14	faint	yellow	47,0	30,0							+		
17	faint	yellow	66,7 ± 1,5	22,7 ± 1,2			+	+					+
19	dark	yellow	53,2 ± 2,0	39,8 ± 4,0	+	+	+	+	+	+	+	+	+
21?	blue	ice	83,0 ± 1,7	38,3 ± 4,7			+	+			+		
22?	blue	ice	82,3 ± 2,1	28,2 ± 2,8			+	+			+		
23	blue		79,0 ± 1,3	0			+	+	+		+	+	+
31	dark	yellow	32,6 ± 4,3	51,3 ± 6,3		+		+		+	+	+	+
32	dark	yellow	21,3 ± 5,4	56,8 ± 4,5		+		+		+	+	+	
34	(purple anthocyanin)		12,0	24,0	+								
38	whitish streak		25,9 ± 3,3	90,3 ± 3,1	+	+	+	+	+	+	+	+	+
38?	whitish streak		15,7 ± 1,5	90,2 ± 2,4		+	+	+	+	+			+
38?	whitish streak		10,0 ± 2,6	90,0 ± 3,0					+			+	+
42	dark	yellow	52,8 ± 5,3	58,0 ± 3,6		+	+		+	+		+	+
43	dark	yellow	49,0 ± 2,8	49,3 ± 1,8			+					?	
45	blue		53,6 ± 1,3	58,4 ± 3,5		+	+	+	+	+	+	+	+
46	blue		53,8 ± 1,6	66,7 ± 2,3	+	+	+	+	+	+	+	+	+
47	whitish		96,5 ± 1,5	86,0 ± 4,9	+	+		+	+			+	+
48	dark	orange	24,3 ± 2,5	61,8 ± 0,4		+		+					
49	colourless	bright blue	89,3 ± 2,5	88,7 ± 4,5			+	+				+	
58	blue	ice	61,3 ± 1,8	66,3 ± 3,9		+	+	+	+	+	+	+	+
59	blue	ice	61,4 ± 1,7	74,3 ± 2,7	+	+	+	+	+	+	+	+	+
60	dark	yellow	64,6 ± 1,7	42,7 ± 3,2	+	+	+	+	+	+	+	+	+
61	dark	yellow	35,1 ± 3,4	68,7 ± 3,7	+	+	+	+	+	+	+	+	+
62	dark	yellow	30,0	78,0								+	
63	dark	yellow	41,0 ± 1,6	62,1 ± 0,9	+		+	+				+	
64	faint	orange	77,0	27,0				+					
65	colourless	blue	88,0 ± 2,0	0		+		+				+	
66	yellowish		58,5 ± 0,7	2,5 ± 0,7		+						+	
67	yellowish	orange	21,0	86,0								+	
68	colourless	blue	90,0	6,0							+		
69	colourless	blue	90,0	16,0							+		

Key

A	Balkwill 3028	cultivated inside, Barberton
B	Balkwill 171	cultivated outside, Mkuze
C	Balkwill 472	cultivated outside, Gonubie River Mouth
D	Balkwill 346	cultivated outside, Umtamvuna
E	Balkwill 2	cultivated inside, Ngoye Forest
F	Balkwill 298	cultivated outside, Ngoye Forest
G	Balkwill 197 - 199	cultivated inside, Lake Sibaya
H	Balkwill 214	cultivated outside, Ndumu Game Reserve
I	Balkwill 323	cultivated outside, Oribi Gorge

U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 22: Occurence of spots in gatherings of *D. capensis*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B	C
3	dark	yellow	41,0 ± 5,7	55,5 ± 0,7	+	+	
23	whitish		82,3 ± 10,8	0	+	+	+
25?	dark	yellow	13,8 ± 6,2	68,3 ± 3,8	+	+	+
38	whitish streak		9,0 - 43,0	80,0 - 96,0	+	+	+
46	blue		53,7 ± 4,9	68,0 ± 10,2	+	+	+
58	blue white	white ice	65,0 ± 4,4	64,3 ± 3,2	+	+	+
59	blue white	white ice	64,3 ± 7,2	78,0 ± 2,0	+	+	+
60	dark	yellow	60,5	42,0		+	
61	dark	yellow	39,5 ± 5,0	71,0 ± 2,8	+	+	
68	colourless	faint blue	90,0	9,0			+
70	colourless	blue	76,7 ± 7,5	72,0 ± 3,0	+	+	+
71	colourless	blue	78,0 ± 6,1	82,7 ± 1,5	+	+	+
72	colourless	ice	84,0	87,0		+	
73	colourless	ice	85,0	82,0		+	
74	colourless	faint blue	90,0 ± 4,2	74,5 ± 2,1	+		+
75	colourless	faint blue	90,5 ± 3,5	61,8 ± 0,4	+		+
76	colourless	faint blue	89,0 ± 1,4	46,0 ± 1,4	+		+
77	colourless	faint blue	90,0	31,0			+
78	dark	yellow	68,0 ± 0,0	43,5 ± 3,5		+	+
79	dark	yellow	48,0 ± 5,7	69,5 ± 5,0	+	?	
80	(purple anthocyanin)		9,5 ± 0,7	34,0 ± 5,7	+		+
81	bluish		87,0	83,0	+		
82	bluish		86,0	93,0	+		
83	dark	yellow	11,5 ± 2,1	81,0 ± 4,2	+		+

Key

A Balkwill 465 cultivated outside, from Committees Drift (flowers purple)

B Balkwill s.n. cultivated outside, from Markmans Industrial Area (flowers white)

C Balkwill 474 cultivated inside, from Cintsa River Valley (flowers purple)

U.V. Colour in ultra-violet light

NH4 Colour in ultra-violet light after fuming with ammonia

B.A.W. Rf value in B.A.W.

A.A Rf value in 5% aqueous acetic acid

(purple anthocyanin) Colour of anthocyanin in visible light

Table 23: Occurence of spots in gatherings of *D. clinopodia*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B	C	D	E	F	G	H	I	J	K	L	M
3	dark	yellow	44,3 ± 4,0	59,1 ± 4,3	+	+		+	+		+		+	?			
6	white	ice	66,2 ± 2,5	63,4 ± 1,0	+	+	+	+	+	+	+	+	+	+	+	+	+
7	white	ice	78,9 ± 2,9	71,9 ± 2,0	+	+	+	+	+	+	+	+	+	+	+	+	+
26	dark	yellow	29,5 ± 0,7	79,5 ± 2,1			+				+						
38	whitish streak		11,0 ± 3,0	86,4 ± 2,0		+		+	+	+	+		+	+			
38′	whitish streak		17,0 ± 4,0	88,3 ± 3,0	+			+		?	+	+	?				+
38"	whitish streak		21,8 ± 3,6	89,6 ± 3,9		+	+	+		+	+	+	?	+	+	+	
38"′	whitish streak		26,4 ± 1,7	90,1 ± 2,0	+		+			+	+	+	?	+	+	+	
48	dark	pale yellow	27,9 ± 2,7	61,9 ± 4,0	+		+			+	+		+	?	?	+	
55	dark	yellow	11,8 ± 2,1	63,5 ± 1,6	+	+		+	+		?		+	+			
60	dark	yellow	64,8 ± 3,2	42,5 ± 0,9	+	+		+	+	+	+		+	+		+	
61	dark	yellow	35,2 ± 3,0	65,5 ± 1,7	+	+	+	+	+	+	+	+	+	+	+	+	+
62	dark	yellow	29,5 ± 4,4	84,1 ± 2,9	+				+	+		+	+	&	+	+	+
70	colourless	blue	78,9 ± 2,9	71,9 ± 2,2	+	+	+	+	+	+	+	+	+	+	+	+	+
71	colourless	blue	79,2 ± 3,0	82,2 ± 1,6	+	+	+	+	+	+	+	+	+	+	+	+	+
79	dark	yellow	47,8 ± 2,1	74,5 ± 1,9								+	+			+	+
80	(purple anthocyanin)		7,6 ± 2,1	31,9 ± 1,8	+	+		+	+		+		+	+			
80′	(purple anthocyanin)		5,6 ± 0,9	26,0 ± 1,6			+			+		+			+	+	+
80"	(purple anthocyanin)		10,7 ± 1,8	30,3 ± 2,3			+			+		+			+	+	+
83	dark	yellow	11,0 ± 2,4	78,9 ± 3,2		+		+	+		+	?	+	+			
83′	dark	yellow	7,5 ± 0,7	81,5 ± 3,5		+							+				
83"	dark	yellow	22,0 ± 5,1	83,6 ± 2,5									+	+		+	+
83"′	dark	yellow	21,3 ± 5,0	84,8 ± 0,9								+					+
84	colourless	ice	40,9 ± 3,0	72,5 ± 1,4	+	+	+	+	+	+	+	+	+	+	+	+	+
85	colourless	ice	41,6 ± 3,4	81,7 ± 1,6	+	+	+	+	+	+	+	+	+	+	+	+	+
86	faint	colourless	55,6 ± 4,4	37,8 ± 3,7	+	+		+	+	+	+		+	+			
87	dark	yellow	55,8 ± 1,5	75,8 ± 1,3								+	+			+	+
88		clear yellow	17,8 ± 8,9	86,3 ± 8,9		+			+			+	+			+	+
89	ice	yellowish	29,8 ± 2,2	0,3 ± 0,5	+				+		+		+	?	+		
90	yellowish	pink	59,3 ± 3,6	3,0 ± 0,6	?	+	+	+	+	+			+	+			

Key

A Balkwill 132 cultivated outside, from Debengeni Falls
B Balkwill s.n. cultivated outside, fron Island Blue Waterfall (stored)
C Balkwill s.n. cultivated outside, from Island Blue Waterfall (fresh)
D Balkwill 110 cultivated outside, from Wolkberg
E Balkwill 140 cultivated outside, from Bergplaats
F Balkwill 123 cultivated outside, from The Downs
G Balkwill 108a cultivated outside, from Makapaansgat Valley
H Balkwill 213 cultivated outside, from Ndumu
I Balkwill 180 cultivated outside, from Ubombo
J Balkwill 253 cultivated outside, from Hlabisa
K Balkwill 287 - 289 cultivated outside, from Nkandla Forest
L Balkwill 446 cultivated outside, from Pietermaritzburg
M Balkwill 405 cultivated outside, from Horseshoe Dam
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light
& spot clear, but uncertainly the same as the others.

Table 24: Occurence of spots in gatherings of *D. minor* ssp. *minor*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B
3	dark	yellow	43,0	59,0	+	
4?	bluish	ice	80,0	65,0	+	
6	ice	ice	67,0 ± 2,8	62,0 ± 0,0	+	+
7	ice	ice	68,0 ± 4,2	76,0 ± 1,4	+	+
14	dark	yellow	54,5 ± 5,0	32,3 ± 5,3	+	+
21	ice		81,0	43,0	+	
22	ice		83,0	31,0	+	
38	bluish streak		15,0 - 33,0	84,0 - 92,0	+	+
53	faint blue		55,5 ± 2,1	65,0 ± 4,2	+	+
70	colourless	blue	78,3 ± 2,5	68,5 ± 2,1	+	+
71	colourless	blue	78,0 ± 2,8	80,0 ± 2,8	+	+
80	(purple anthocyanin)		11,3 ± 1,1	28,0 ± 1,4	+	+
91	colourless	bluish	85,0	32,0	+	
92	very dark	dark	57,0 - 87,0	100,0	+	+
93	dark	yellow	46,0 ± 2,8	34,0 ± 1,4	+	+
94	whitish		95,5 ± 2,1	0	+	+
95	(purple anthocyanin)		6,0 ± 0,0	26,8 ± 0,4	+	+
96	pinkish		88,0	3,0	+	

Key

A Balkwill 751 collected in field, from Pienaar's River (stored)

B Balkwill 752 cultivated inside, from Naboomspruit (fresh)

Table 25: Occurence of spots in gatherings of *D. minor* ssp. *"white"*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B
6	ice	greenish	63,5 ± 0,7	62,5 ± 3,5	+	+
7	ice	greenish	63,5 ± 0,7	76,0 ± 0,0	+	+
14	dark	yellow	50,8 ± 2,5	34,8 ± 5,3	+	+
38	whitish streak		9,0 - 35,0	91,3 ± 1,1	+	+
53	blue	blue	51,0 ± 1,4	65,8 ± 0,4	+	+
70	colourless	blue	76,0 ± 4,2	71,5 ± 1,4	+	+
71	colourless	blue	75,5 ± 3,5	81,8 ± 1,1	+	+
91	colourless	ice	81,0	25,0	+	
92	very dark	dark	60,0 - 91,0	100,0	+	+
93	dark	yellow	42,0	32,0	+	
94	whitish		92,9 ± 2,8	0	+	+
97	colourless	ice	72,0	73,0	+	
98	colourless	ice	68,7 ± 3,9	85,0 ± 2,8	+	+
99	colourless	ice	38,3 ± 1,8	59,8 ± 1,1	+	+
100	colourless	ice	30,0	58,0	+	

Key

A Balkwill 791 & 792 coolected in field, from Soekmekaar (stored)

B Balkwill 791 & 792 cultivated inside, from Soekmekaar (fresh)

U.V. Colour in ultra-violet light

NH4 Colour in ultra-violet light after fuming with ammonia

B.A.W. Rf value in B.A.W.

A.A Rf value in 5% aqueous acetic acid

(purple anthocyanin) Colour of anthocyanin in visible light

Table 26: Occurence of spots in gatherings of *D. sp. 2.*

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B
6	white	ice	65,3 ± 0,4	63,5 ± 0,7	+	+
7	colourless	blue	65,5 ± 0,7	76,5 ± 0,7	+	+
38	bluish streak		11,0 - 34,0	92,0	+	+
45	blue	blue	51,8 ± 1,8	58,0 ± 1,4	+	+
46	blue	blue	51,5 ± 0,7	68,5 ± 2,1	+	+
47	whitish		97,0	77,0		+
53		green	61,0	68,0	+	
61	dark	faint yellow	36,0	65,0	+	
67	dark	yellow	11,0 - 38,0	84,0 - 88,0	+	+
70	colourless	blue	78,0 ± 1,4	70,5 ± 2,1	+	+
71	colourless	blue	77,0	82,0	+	+
79	dark	yellow	50,0 ± 1,4	74,5 ± 3,5	+	+
80	(purple anthocyanin)		8,5 ± 0,7	32,3 ± 3,2	+	+
101	dark	yellow	35,0 ± 5,7	85,0 ± 1,4	+	+

Key
A Balkwill & Cadman 3024 cultivated inside, from Hekpoort (stored)
B Balkwill & Cadman 3024 cultivated inside, from Hekpoort (fresh)
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 27: Occurence of spots in gatherings of *D. sp. 4.*

Spot No.	U.V.	NH4	B.A.W.	A.A.	A
6?	blue	green	58,0	65,0	+
7?	blue	green	57,0	78,0	+
8	colourless	blue	69,0	73,0	+
9	colourless	blue	69,0	84,0	+
38	bluish streak		7,0 - 21,0	79,0 - 93,0	+
45	faint blue		49,0	58,0	+
46	faint blue		47,0	71,0	+
47	whitish		96,0	86,0	+
55	dark	orange	9,0	77,0	+
63	faint	orange	40,0	67,0	+
83	dark	orange	16,0	84,0	+
102	dark	blue	33,0	94,0	+
103	dark	blue	27,0	93,0	+

Key
A Balkwill 1587 collected in field, from Wolkberg
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 28: Occurence of spots in gatherings of *D. sp. 3.*

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B
6	ice blue	ice	65,5 ± 2,1	65,0 ± 0,0	+	+
7	ice blue	ice	65,6 ± 3,5	79,0 ± 2,8	+	?
8	colourless	blue	67,0	71,0	+	
9	colourless	blue	69,5 ± 3,54	79,0 ± 2,8	+	+
38	bluish streak		8,0 - 32,0	79,0 - 93,0	+	+
45	whitish blue		53,5 ± 2,12	61,0 ± 0,0	+	+
47	whitish		90,5 ± 3,5	0	+	+
60	dark	yellow	62,0	40,0	+	
67	dark	yellow	8,0 - 34,0	77,0 - 91,0	+	+
78?	dark	yellow	70,0	35,0	+	
79	dark	yellow	48,0 ± 2,8	73,8 ± 4,6	+	+
87	dark	yellow	54,0 ± 2,8	73,0 ± 1,4	+	+
92	very dark	dark	62,5 - 92,5	100,0	+	+
93	dark	yellow	52,5	36,0	+	
104	yellow	bright yellow	33,0 ± 0,0	88,0 ± 1,4	+	+

Key

A Balkwill 766 collected in field, from Vaal River Valley (stored)

B Balkwill 766 cultivated inside, from Vaal River Valley (fresh)

U.V. Colour in ultra-violet light

NH4 Colour in ultra-violet light after fuming with ammonia

B.A.W. Rf value in B.A.W.

A.A Rf value in 5% aqueous acetic acid

(purple anthocyanin) Colour of anthocyanin in visible light

Table 29: Occurence of spots in gatherings of *D. eenii.*

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B	C	D	E
3	dark	yellow	35,8 ± 3,3	51,5 ± 2,3	+	+		+	
6	white	ice	64,8 ± 2,4	64,4 ± 2,3	+	+	+	+	+
7	white	ice	65,9 ± 2,3	75,8 ± 5,1	+	+	+	+	+
14	dark	yellow	50,5 ± 3,7	35,8 ± 3,4	+	+	+	+	+
16	dark	yellow	63,9 ± 2,8	33,8 ± 3,0	+	+		+	+
21	colourless	blue	82,0	42,0	+				
25	dark	yellow	12,5 ± 4,02	67,0 ± 1,4	+	+	+	+	
31	dark	yellow	9,5 ± 2,1	76,8 ± 3,9	+			+	
32	dark	yellow	26,5 ± 3,5	58,0 ± 1,4			+		+
34	(purple anthocyanin)		7,3 ± 0,4	26,5 ± 3,5			+		+
34′	(purple anthocyanin)		7,0 ± 0,0	27,0 ± 1,4		+		+	
34"	(purple anthocyanin)		11,8 ± 0,4	28,0 ± 2,8			+		+
38	bluish streak		5,0 - 35,0	81,0 - 96,0	+	+	+	+	+
70	colourless	blue	76,5 ± 1,0	68,6 ± 3,5	+	+		+	+
71	colourless	blue	76,2 ± 1,8	79,0 ± 3,0	+			+	+
91	colourless	blue	82,0	31,0	+				
92	very dark	dark	55,0 - 98,0	100,0	+	+	+	+	+
94	whitish blue		91,5 ± 6,4	0,8 ± 1,5	+	+		+	+
96	pinkish		86,0	3,0	+				
105	colourless	blue	82,3 ± 1,8	66,0 ± 8,5	+				+
106	colourless	ice	18,0	72,0	+				
107	colourless	ice	26,0	75,0	+				

Key
A Balkwill 799 collected in field, from Harnham (stored)
B Bulk of C,D & E
C Balkwill cultivated outside, self sown
D Balkwill 798 cultivated outside, from Harnham
E Balkwill 773 cultivated inside, from Hartebeespoort
U.V. Colour in ultra-violet light
NH4 Colour in ultra-violet light after fuming with ammonia
B.A.W. Rf value in B.A.W.
A.A Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

Table 30: Occurence of spots in gatherings of *D. fruticosa*.

Spot No.	U.V.	NH4	B.A.W.	A.A.	A	B
6	blue	ice	64,5 ± 0,7	65,5 ± 2,1	+	+
7	blue	ice	65,8 ± 1,8	79,3 ± 1,8	+	+
14	dark	yellow	53,5 ± 0,7	35,5 ± 3,5	+	+
16	dark	yellow	59,5 ± 3,5	33,0 ± 4,2	+	+
21	colourless	ice	81,0	42,0	+	
25	dark	yellow	11,0	76,0	+	
26	dark	yellow	29,0	73,0	+	
33	dark	yellow	11,0	52,0	+	+
38	bluish streak		10,5 - 32,5	87,0 0 94,0	+	+
42	dark	yellow	49,0	63,0	+	+
46	blue		53,8 ± 0,4	68,5 ± 2,1	+	+
55	dark	yellow	10,0 ± 0,7	65,5 ± 2,1	+	+
63	dark	yellow	43,0	63,0	+	+
70	colourless	blue	76,5 ± 0,7	71,0 ± 1,4	+	+
71	colourless	blue	77,3 ± 0,4	81,8 ± 1,1	+	+
91	colourless	ice	82,0	30,5	+	
92	very dark	dark	57,0 - 97,0	100,0	+	+
94	whitish		93,5 ± 0,7	0	+	+
96	pinkish		85,0 ± 2,8	5,5 ± 2,1	+	+
101	dark	yellow	37,0	80,0	+	
105	colourless	blue	82,0	61,0	+	
108	dark	yellow	46,5 ± 0,7	40,5 ± 0,7	+	+

Key
A   Balkwill 777   collected in field, from Ohrigstad (stored)
B   Balkwill 1570   collected in field, from Burgersfort (stored)
U.V.   Colour in ultra-violet light
NH4   Colour in ultra-violet light after fuming with ammonia
B.A.W.   Rf value in B.A.W.
A.A   Rf value in 5% aqueous acetic acid
(purple anthocyanin) Colour of anthocyanin in visible light

presence or absence of spots. Tables of frequency of distribution of each spot were prepared for each species (e.g. Table 31). These were used during the calculation of coefficients of similarity based on frequencies.

Similarity coefficients

Coefficients of similarity based on presence or absence of spots were prepared with the Coefficient of Similarity used by Olsson (1967) and Getliffe (1968) i.e. :

$$\frac{m}{m + d}$$

where m is the number of compounds present in both species and d is the number of compounds occurring in only one of the two species being compared. This can be more conveniently calculated with the formula:

$$\frac{C}{Ta + Tb - C}$$

where C is the number of spots in common in species A and B and Ta and Tb are the total number of spots that occur in species A and B respectively. It was assumed that any spot that occurred in at least half of the chromatograms prepared for any species was present in that species, while any spot present in fewer than half the chromatograms was disregarded in this analysis. From these similarity coefficients, fig. 39a - q were prepared. The length of any spoke represents the degree of similarity between the species represented by that spoke and the species with which it is being compared.

It was found that some spots occurred in less than half of the chromatograms of two species that were being compared with one another and that the coefficient of similarity did not take this into account. Thus, a coefficient was designed that compared the frequencies at which the spots occurred in the chromatograms of any species, rather than by comparing presence and absence. The formula used is:

$$\frac{TFc}{TFa + TFb - TFc}$$

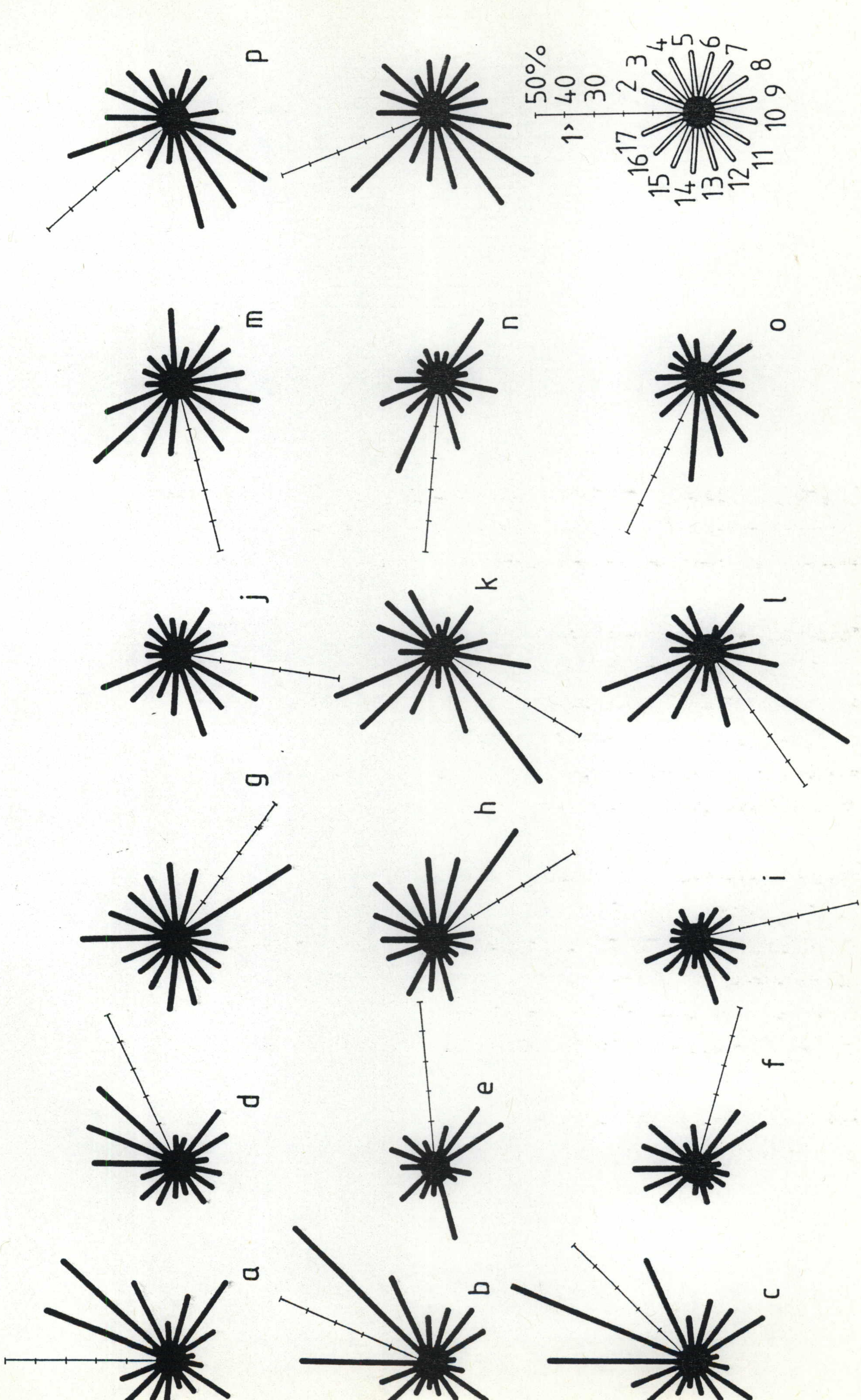
where TFc is the sum of the common frequency of occurrence of each spot in species A and B and TFa and TFb are the total frequencies of occurrence of each spot in species A and B respectively. TFc is calculated by summing the lower frequency of any spot that is present in

<u>Table 31</u>: Frequency of spots on chromatograms of *D. heterostegia* .

1		26		51		76		101	
2	0,3333	27		52		77		102	
3		28		53		78		103	
4	1,0	29		54		79		104	
5	1,0	30		55		80		105	
6		31	0,6667	56		81		106	
7		32	0,5556	57		82		107	
8		33		58	0,8889	83		108	
9		34	0,1111	59	1,0	84		109	
10	1,0	35		60	1,0	85		110	
11	0,8889	36		61	1,0	86		111	
12		37		62	0,1111	87		112	
13		38	1,0	63	0,4444	88		113	
14	0,1111	39		64	0,1111	89		114	
15		40		65	0,3333	90		115	
16		41		66	0,2222	91		116	
17	0,3333	42	0,6667	67	0,1111	92		117	
18		43	0,2222	68	0,1111	93		118	
19	1,0	44		69	0,1111	94			
20		45	0,8889	70		95			
21	0,3333	46	1,0	71		96			
22	0,3333	47	0,6667	72		97			
23	0,6667	48	0,2222	73		98			
24		49	0,3333	74		99			
25		50		75		100			

Total No. of Spots: 34

Total Frequency: 18.7776



a
b
c
d
e
f
g
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i
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k
l
m
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o
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50%
40
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17

both species A and B. A matrix of coefficients was prepared. The group average method of agglomerative polythetic clustering techniques (Clifford & Stephenson, 1975 & Sokal & Michener, 1958) was used to analyse the matrix of similarities in order to construct a dendrogram (fig. 40). From this dendrogram, hypotheses about the relationships of species could be tested.

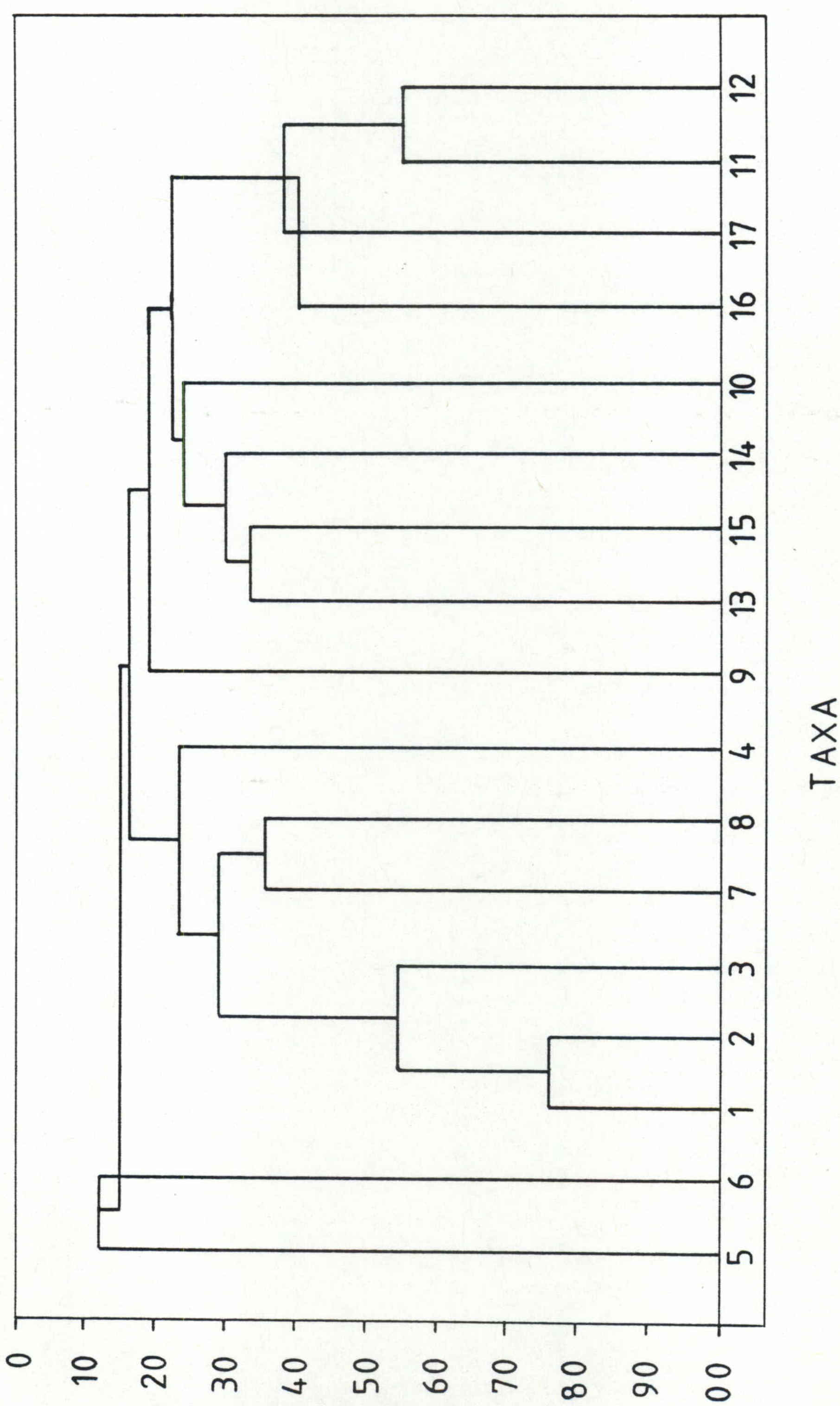
Olsson (1967) also used a Matching Coefficient, which is based on the assumption that spots that are absent in both species are matches and thus they are included in calculations. In the present study, there are 118 spots, of which between 8 and 37 spots occur in each species. If Matching Coefficients were used, species would be compared more on the basis of compounds that are absent, than on the basis of those present. As this was not considered to be sound, it was not attempted.

6) Identification of compounds

Identification of flavonoid compounds is possible by the methods suggested by Markham (1982), Seikel (1962) and Wollenweber (1982), but both isolation of quantities of individual compounds sufficient for identification and identification of compounds is very time consuming. As there are very many spots on the chromatograms prepared, it was beyond the scope of this pilot study to identify all the chemicals. It has been assumed that spots in different species that have similar Rf values and similar colours represent the same compound. In some pairs of species there are spots that have Rf values only slightly more different than the error allowed and which may represent the same compounds, but they have been assumed to be different in this study. Many chromatograms have groups of spots with similar colours and Rf values and other spots that always occur in pairs - it is possible that they represent isomers of the same compound, so that these differences may not be as taxonomically significant as has been assumed in this study. None of these assumptions have been tested by co-chromatography or isolation and identification of compounds.

Results and Discussion

Taxonomic implications of this pilot chemotaxonomic study are based on the premise that spots with similar Rf values and colours represent the


0
10
20
30
40
50
60
70
80
90
100
Degree of Similarity (%)
5
6
1
2
3
7
8
4
9
13
15
14
10
16
17
11
12
TAXA

same compounds. In spite of the possibility that this premise is not true, the results have been analysed to test the potential value of studies of flavonoids in this group of plants.

a) The value of flavonoid spot patterns in the identification of vegetative material.

The one-dimensional chromatograms of extracts from the leaves of 70 different collections, representing five species of *Dicliptera* and one species of *Peristrophe*, showed that although all compounds were not separated into discreet spots, it was clear that spot 22 was unique spot to *D. heterostegia*. This spot had an Rf value between 16% and 25%, was colourless in ultra-violet light and fluoresced bright shiny-green when fumed with ammonia (Table 13). Two-dimensional chromatograms of selected collections from each species confirmed that spot 22 was absent from other species, but also showed that it was split into a number of spots in the second dimension. At least one shiny-green spot was present in all samples of *D. heterostegia*, although the Rf values of the spots in different collections varied (as did many other compounds present in the leaves). This confirms that this species is different from the others investigated, and could provide a useful character if it should ever be important to identify a vegetative specimen of this species.

b) Flavonoid spot patterns as generic markers in *Peristrophe* and *Dicliptera*.

It has been found that there are no spots that occur in all the species of *Peristrophe* and not in any species of *Dicliptera*, nor any that occurs in all the species of *Dicliptera* but not in *Peristrophe*.
It is also of interest that in the dendrogram (fig. 40) some of the species of *Dicliptera* are grouped with some of the species of *Peristrophe*, before they are grouped with the other species of *Dicliptera*. Thus, it appears that in this study, no generic markers have been found to separate these two genera. It is possible, however, that some compounds may be specific to other genera in the Acanthaceae, and so would be generic markers.

c) Spot patterns supporting the subdivision of a genus.

On the basis of morphology and anatomy of bracts, it has been suggested that *Dicliptera* may be subdivisible into two sections. In the dendrogram (fig. 40), all the species of *Dicliptera* with broad bracts without 'windows' are linked to each other before they link to the species that have narrower bracts with 'windows' at their bases. It appears then, that the flavonoid spot patterns would support the subdivision of the genus *Dicliptera*.

d) Predictions about which species are primitive

On the basis of the morphological similarity of *D. zeylanica* and *D. heterostegia* to *P. montana* and *Hypoestes triflora* and on the basis of their geographical distribution, it has been predicted that *D. heterostegia* and *D. zeylanica* are the most primitive of the species of *Dicliptera* represented in southern Africa. *P. kotschyana*, on the basis of its wide geographical distribution and its relationships to other species, is probably the most primitive species of *Peristrophe* in southern Africa. It is interesting that in the dendrogram (fig. 40), *D. heterostegia* and *D. zeylanica* are linked to *P. kotschyana*, before they are linked to the other species of *Dicliptera*. This linkage may indicate that these three species may share primitive chemical compounds. This could be verified by the identification of compounds and an understanding of the biochemical pathways by which these compounds are formed. The average coefficient of similarity of *P. kotschyana* when compared with all the other species of *Peristrophe* is higher than that of any other species. This indicates that *P. kotschyana* has more in common with the other species of *Peristrophe* than does any other species and may imply that *P. kotschyana* has retained more primitive characters than have the other species of *Peristrophe*.

e) Predictions about advanced species

Some of the southern African species of *Peristrophe* and *Dicliptera* are relatively more advanced than other species, and it is interesting to note that the analyses of the flavonoid spot patterns indicate this. Chemically advanced species are likely to have fewer spots in common with other species than would primitive species. In the dendrogram (fig. 40), a species with few spots in common with other species would be linked to the other species much later than a species with many spots in common with other species. *P. paniculata* is the only annual species in this group of genera and so may be regarded as advanced. *P. paniculata* is one of the last species to be grouped with any other in the dendrogram (fig. 40), thus predictions based on spot patterns coincide with those made from the life history of this plant.

P. gillilandiorum has a limited geographical distribution and has leaves with a unique shape (i.e. very narrowly lanceolate); these two facts suggest that this species is derived. In the dendrogram (fig. 40), it can be seen that *P. gillilandiorum* is one of the last species to link to any other species, suggesting that in terms of spot patterns it is derived.

D. sp. 4 is a very unusual species in terms of its morphology, and so far has only been found growing at a single locality, in a specialised habitat (i.e. on dolomite). This degree of advancement is not suggested by the position of this species in the dendrogram (fig. 40). In fig. 39n and in the matrix of similarity values (table 32), however, it can be seen that *D. sp. 4* is relatively unlike most other species of *Dicliptera* in southern Africa. This supports the hypothesis that *D. sp. 4* is derived.

f) Predictions about the derivation of species.

On the basis of morphology and geographical distribution, hypotheses about the derivation of some advanced species have been made. Amongst the southern African species of *Peristrophe*, *P. kotschyana* appears to be the species from which most others have been derived. *P. cernua* may have evolved by the isolation of the southernmost populations of *P. kotschyana*. *P. cliffordii* has become specialised for survival in Kalahari sand and very likely evolved from a population of *P. kotschyana*. In the dendrogram (fig. 40), these two species link to each other, and then to *P. kotschyana*, the species from which they are thought to have diverged. This lends support to the view that *P. kotschyana* may be the species from which *P. cernua* and *P. cliffordii* were derived.

It is, however, also thought that *P. gillilandiorum* and *P. transvaalensis* are derived from *P. kotschyana*. The fact that *D. heterostegia* and *D. zeylanica* link to *P. kotschyana* before the two former species, implies that this relationship is not reflected in the distribution of flavonoids. *P. transvaalensis* flowers sporadically, so that it is difficult to collect sufficient flowers to

Table 32: Matrix of percentage of similarity calaculated from frequency of occurence of spots.

Sp.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
2	75,21															
3	41,96	60,47														
4	20,24	28,57	34,29													
5	7,80	12,12	9,84	8,33												
6	19,12	16,42	17,36	3,70	11,76											
7	25,63	20,00	20,37	21,21	19,15	14,29										
8	19,76	19,30	29,21	17,56	29,30	17,51	35,01									
9	5,68	7,07	6,11	8,96	5,10	7,92	12,36	17,04								
10	6,41	6,06	5,88	9,09	5,24	7,09	7,45	6,18	19,08							
11	13,21	15,25	16,19	9,52	8,2	2,94	14,80	7,23	18,99	26,53						
12	7,59	10,42	10,76	10,64	0	0	7,19	3,65	12,92	21,01	54,44					
13	4,98	6,78	6,67	17,14	12,96	1,56	16,83	14,66	25,36	31,38	30,95	27,78				
14	8,92	6,67	6,54	16,67	10,71	0	15,94	14,40	10,00	17,08	12,00	13,16	2,75			
15	8,03	6,72	6,60	9,21	5,13	1,55	11,74	11,17	8,05	15,53	18,09	18,84	32,89	32,05		
16	19,37	16,91	15,27	9,47	4,05	13,10	8,86	3,35	11,20	22,75	36,95	17,67	8,40	12,06		
17	13,47	15,15	14,05	12,50	13,85	4,00	9,92	9,32	15,85	18,80	38,78	36,48	23,53	13,39	38,26	

Key to Table 32:

1	P. cernua	A	1 + 2
2	P. cliffordii	B	11 + 12
3	P. kotschyana	C	1/2(A) + 3
4	P. transvaalensis	D	11/12(B) + 17
5	P. gillilandiorum	E	11/12/17(E) + 16
6	P. paniculata	F	7 + 8
7	D. zeylanica	G	13 + 15
8	D. heterostegia	H	13/15(G) + 14
9	D. capensis	I	1/2/3(C) + 7/8(F)
10	D. clinopodia	J	13/14/15(H) + 10
11	D. minor ssp. minor	K	1/2/3/7/8(I) + 4
12	D. minor ssp. nova	L	10/13/14/15(J) + 11/12/16/17(E)
13	D. sp. 2	M	10/11/12/13/14/15/16/17(L) + 9
14	D. sp. 4	N	1/2/3/4/7/8(K) + 9/10/11/12/13/14/15/16/17(M)
15	D. sp. 3	O	5 + 6
16	D. eenii		
17	D. fruticosa		

Table 32 continued: Matrix of percentage of similarity calculated from frequency of spot occurence.

Sp.	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
1															
2															
3	54,09	13,51													
4	25,24	10,05	17,48	11,66	10,50	21,51	13,01	9,18	23,01	11,66					
5	10,13	1,59	8,22	7,95	6,01	23,66	8,89	8,83	15,22	7,35	12,36	6,46	10,14	8,96	
6	16,84	1,50	20,62	3,60	7,87	17,21	1,56	0,77	16,81	6,19	11,02	7,03	6,50	8,92	
7	25,32	9,28	22,34	11,41	10,82										
8	20,95	6,04	23,50	10,08	7,00										
9	7,07	16,73	6,53	16,55	15,09	15,23	16,81	14,77	11,05	20,06	10,63	18,27			
10	7,45	23,81	6,36	23,26	20,75	7,55	23,73	23,57	7,69						
11	15,68														
12	9,25														
13	6,04	17,86	6,21	28,15	22,74	16,47									
14	8,21	12,55	7,31	18,40	13,33	14,84	29,75								
15	8,28	18,97	7,37	16,55	14,24	16,40									
16	20,58	37,28	18,01	40,07											
17	16,48	37,66	15.98												
A		12,47													
B			13,32												
C			16,43	18,04	28,37	7,41	7,36								
E					12,88	21,72	19,29	17,28	22,04						
F						15,13	15,97								
H								9,36							
I									11,69		19,61				
K											9,90	15,52			
N															14,86

extract flavonoids at a concentration that is easily detectable on chromatograms. Thus, the apparent dissimilarity of *P. transvaalensis* from *P. kotschyana* may be due to the difficulty experienced in obtaining representative chromatograms, rather than due to an actual dissimilarity in the distribution of flavonoids. From the matrix of similarity values (Table 32), it can be seen that within *Peristrophe*, *P. gillilandiorum* has more spots in common with *P. cliffordii* than with any other species. This is a more accurate reflection of the relationships hypothesised on the basis of morphology and distribution, than are the relationships implied by the dendrogram (fig. 40). It is possible, however, that during the manipulation of the data (i.e. group averaging) to produce the dendrogram, some of the relationships between species were obscured.

D. capensis is thought to have been derived by the hybridisation of either *D. zeylanica* or *D. heterostegia* with one of the species of *Dicliptera* that has narrow bracts and purple flowers. In the dendrogram (fig. 40), *D. capensis* is the last species of *Dicliptera* to be linked with the species with narrow bracts and purple flowers, before these species are linked with the group of species that contains *D. heterostegia* and *D. zeylanica*. This lends support to the hypothesis about the derivation of *D. capensis*.

D. sp. 3 and *D. sp. 2* are grouped with *D. clinopodia* before being grouped with any other species (with the exception of *D. sp. 4*). This is of interest, as it is most likely that these species are closely related to and may have been derived from *D. clinopodia*.

Initially it was thought that *D. minor* was derived from *D. clinopodia*, a species that grows at forest margins, and some other habitats rather damper than those in which *D. minor* grows. It has thus been thought that *D. minor* is more likely to have been derived from *D. eenii*, which occurs in more similar habitats. This latter view is confirmed by the sequence in which *D. minor* is grouped first with *D. eenii* and then with *D. clinopodia* in the dendrogram (fig. 40). The morphology of *D. fruticosa* and *D. eenii* suggests that these species are very closely related, and it is most likely that the former is derived from the latter. The position of *D. eenii* in the dendrogram (fig. 40) is most interesting, as the three taxa that are thought to have been derived from *D. eenii* are grouped with it. They are also linked to *D. eenii* before they are grouped with *D. clinopodia*, the species from which they were originally thought to have been derived.

Initially I thought that *D. sp. 4* was derived from and was closely related to *D. eenii*, but after closer investigation, I have doubted that view. Thus, it is of interest that *D. sp. 4* has not been grouped with *D. eenii* in the dendrogram (fig. 40). It is possible that the parent species, from which *D. sp. 4* has been derived, is not present in southern Africa. This would explain why it does not show a high degree of similarity to any southern African species of *Dicliptera*.

g) Implications about the level at which taxa should be differentiated. *D. sp. 2* and *D. sp. 3* are species that are morphologically similar, and may be considered to be conspecific by some scientists. In the dendrogram (fig. 40), however, they are linked to one another at lower degrees of similarity than are widely accepted species, such as *D. heterostegia* and *D. zeylanica*. This supports the opinion that they are different at the specific level.

The two subspecies of *D. minor* are grouped with each other before being grouped with any other species, which supports the view that these taxa have close affinities. They are linked, however, at a lower coefficient of similarity than are *P. cernua* and *P. cliffordii*. The latter two species are linked to *P. kotschyana* at a lower coefficient of similarity than that at which the subspecies of *D. minor* are linked. This suggests that these taxa may be different at the specific rather than at the subspecific level, but more material is required before this decision can be finalised.

Conclusions

Some limitations are placed on the extent to which conclusions may be drawn from this study, because the compounds that are represented by the spots on chromatograms have not been identified. Nevertheless the analysis of the distribution of these spots (which to some degree must indicate the distribution of flavonoid compounds) has provided considerable support for many of the hypotheses that have been formulated about the relationships of southern African species of *Dicliptera* and *Peristrophe*.

CHAPTER 11

DISTRIBUTION, HABITATS AND PHYTOGEOGRAPHY

Introduction

The Acanthaceae is a pantropical fammily and is well represented in all three southern Continents, as well as in Central America, Asia and India. In Africa, the Acanthaceae reach their southern-most point in the southern Cape, with very few species occurring in the south-western Cape. Migration of the members of this family was probably limited by their mode of seed dispersal, which does not promote long range dispersal. The present pattern of distribution suggests an early Gondwanaland origin and evolution in isolation as tectonic plates migrated. In Africa, the slow move northwards and accompanying geomorphological changes have had profound influences on phytochoria (Axelrod & Raven, 1978) and on the elements constituting the phytochoria.

Materials and Methods

Distributions have been mapped from the information available on herbarium labels (figs. 41 - 66). These maps have been compared with the maps of factors that may affect plant distribution and correlations were noted. Table 33 was compiled from these data. The sources from which the data were compiled include Werger & Coetzee (1978) for occurence of frost; Werger (1978b) for phytochorological subdivisions; Werger (1978a) for altitude; Schulze & McGee (1978) for other climatological characters; Acocks (1975) for veld types; von M Harmse (1978) for soils and Geological Survey (1984) for geology.

Observations

Table 33 presents data about the areas in which the southern African species of *Peristrophe* and *Dicliptera* occur. Figures 41 - 66 present the distributions constructed from available herbarium material. Figures 67 & 68 present the distributions of *Peristrophe* and *Dicliptera* in southern Africa, showing the concentrations of species. Fig. 69 presents the same information for all the southern African

Key to Table 33:

Phyto:	Phytochorological subdivisions (and distribution patterns) Am = Afromontane distribution pattern; CK = Central Kalahari Subdomain; KN = Karoo-Namib Region; SZ = Sudano-Zanmbezian Region; TP = Tongaland-Pondoland Regional Mosaic.
Altitude:	Values represent metres above mean sea level.
Precip:	Mean Annual Precipitation; values represent millilmetres per annum.
Ja me:	January Mean Daily Temperature; values represent °C.
Ju me:	July Mean Daily Temperature; values represent °C.
Ja ma:	January Mean Daily Maximum Temperature; values represent °C.
Ja mi:	July Mean Daily Minimum Temperature; values represent °C.
An me:	Mean Annual Temperature; values represent °C.
An Ra:	Mean Annual Range of Temperature; values represenr °C.
Oc Fr:	Duration of Frostless Period; values represent the duration (in days) of the frostless period; NA = frost less frequently than annually; NO = No frost.
An Wa De:	Average Annual water deficiency, values represent mm per annum.
Köppen Cl:	Köppen's Classification Aw = Equatorial climate, winter dry period; BSh = Arid zone, steppe climate, dry-hot , mean annual temperature over 18 °C; BWh = Arid zone, desert climate, dry-hot, mean annual temperature over 18 °C; BWk = Arid zone, desert climate, dry-hot, mean annual temperature below 18 °C; Cfa = Warm temperate climates, coldest month 18 - 30 °C, sufficient precipitation during all months, warmest month over 22 °C; Cfb = Warm temperate climates, coldest month 18 - 30 °C, sufficient precipitation during all months, warmest month below 22 °C, but at least 4 months above 10 °C; Cwa = Warm temperate climates, coldest month 18 - 30 °C, winter dry season, warmest month over 22 °C; CWb = Warm temperate climates, coldest month 18 - 30 °C, winter dry seasons, warmest month below 22 °C, but at least 4 months above 10 °C.
Th Re:	Thermal Regions, for definitions, see Schulze & McGee (1978)

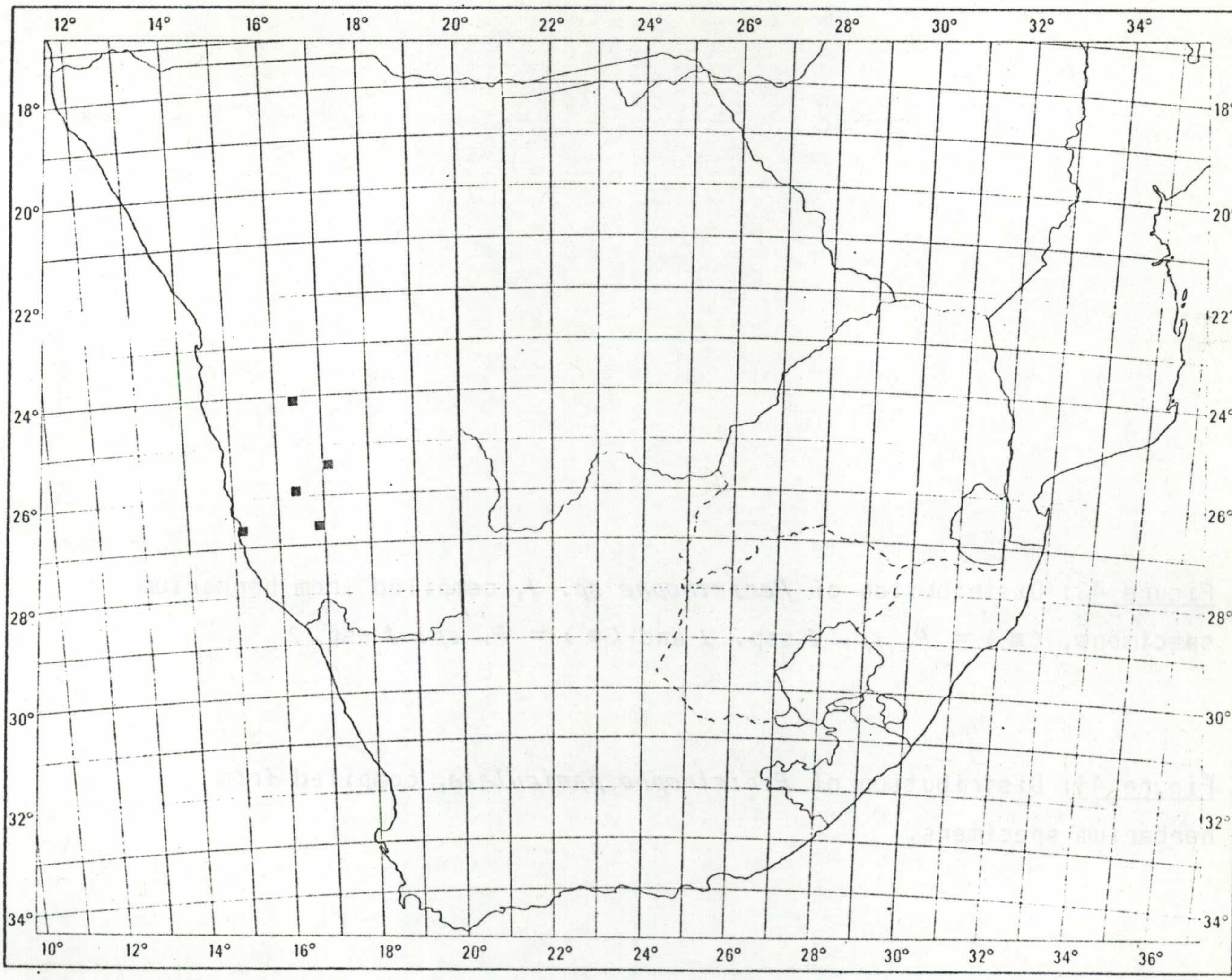
<u>Note</u>: Values that are underlined occur infrequently.

Table 33: Biological, Climatological and Geomorphological Factors that may influence the distribution of species.

Species	Phyto.	Altitude	Precip.	Ja me	Ju me	Ja ma	Ju mi	An Me	An Ra	Oc Fr	An Wa De	Koppen Cl	Th Re
D. zeylanica	Am/SZ/TP	0 -2000	400-1400	20-22	12-18	<30 -32,5	2,5-15	14-24	6-16	180-NO	0-1000	Cwa/Cfb	1-2
D. clinopodia	Am/SZ/TP	0 -1500	600-1400	18-26	10-18	<30 -32,5	2,5-12,5	14-22	10-12	>240	<799	Cwa/BSh/Cfb	1-3
D. heterostegia	SZ/TP	0 -1000	800-1400	>22	>14	22,5-32,5	2,5-10	>17	8-10	>270	0-999	BSh/Aw/Cfa/Cfb	2-5
D. minor	SZ	500-1500	400- 800	22-24	10-14	27,5-30	0 - 2,5	18-20	10-14	NA-NO	200-599	BSh	4-5
D. divaricata	SZ/Am/TP	0 -1000	600- 800	20-25	12-16	27,5-32,5	5-7,5-12,5	16-22	8-10	>240	400-999	Cwb/Cwa/BSh	3-5
P. kotschyana	SZ	500-1500	200- 800	20-26	10-14	27,5-32,5	0 -10	>18	10-14	NA	200-799	BSh	3-5
P. cernua	TP	<500-1000	800-1000	20-24	9-11	27,5-30,5	0- 5	7-16	<10	NA	<100	BSh	1-4
D. sp. 2	Am/SZ	1500-2000	600	20-24	10-12	27,5-30	0-2,5	16-18	10-12	>270-NO	200-399	BSh	3-4
D. sp. 3	SZ	500-1500	400-800	20-22-26	8-10	25 -27,5-30	0-2,5	16	8-10-14	180-270	200-399	BSk	5
P. grandibracteata	KN		0-200	16-26	10-14	20 -35	5-10	14-18	10	>270	600-799	BWh/BWk	5-6
P. hereroensis	SZ/CK	1500-2000	200-600	22-26	12-16	27,5-32,5	2,5-10	16-22	8-14	>270	400-999	BSh	4-5
P. sp. 1 ssp. 1	KN/SZ		100-600	16-26	12-14	22,5-30	7,5-10	14-22	<10	>270	600-999	BWh/BWk	5-6
P. sp. 1 ssp. 2	KN		0-200	16-26	10-14	20 -27,5	7,5-10	14-20	<10	270-NA	600-799	BWh/BWk	5-6
D. eenii	SZ	1000-1500	400-800	20-26	10-16	27,5-32,5	0-7,5	18-22	8-14	270-NA	200-799	BSh	4-5
D. fruticosa	SZ	1000-1500	400-600	20-22	10-12	27,5-30	0-2,5	18-20	10-12	NA	400-599	BSh	3-4
P. transvaalensis	SZ	1000-1500	400-800	20-24	10-12	27,5-30	0-2,5	18-20	10-12	240-270	400-599	BSh	3-4
P. gillilandiorum	SZ	0-500	200-400	26	14-16	32,5->32,5	7,5-10	20	10-12	NA-NO	800-899	BSh	3
P. cliffordii	SZ	0-500	200-400	26	14-16	32,5->32,5	7,5-10	20	10-12	NA-NO	800-899	BSh	3
D. sp. 4	SZ	1000-1500	400-600	22-24	10-12	27,5-30	0-2,5	18	10-12	240-270	600-799	BSh	4
D. quintasii	TP	<500	600-1000	24-26	16-18-20	27,5-32,5	7,5-12,5	20-22-24	<8	NA	100-599	Aw/BSh/Cfa	2

Figure 41: Distribution of *Peristrophe grandibracteata*, compiled from herbarium specimens.

Figure 42: Distribution of *Peristrophe hereroensis*, compiled from herbarium specimens.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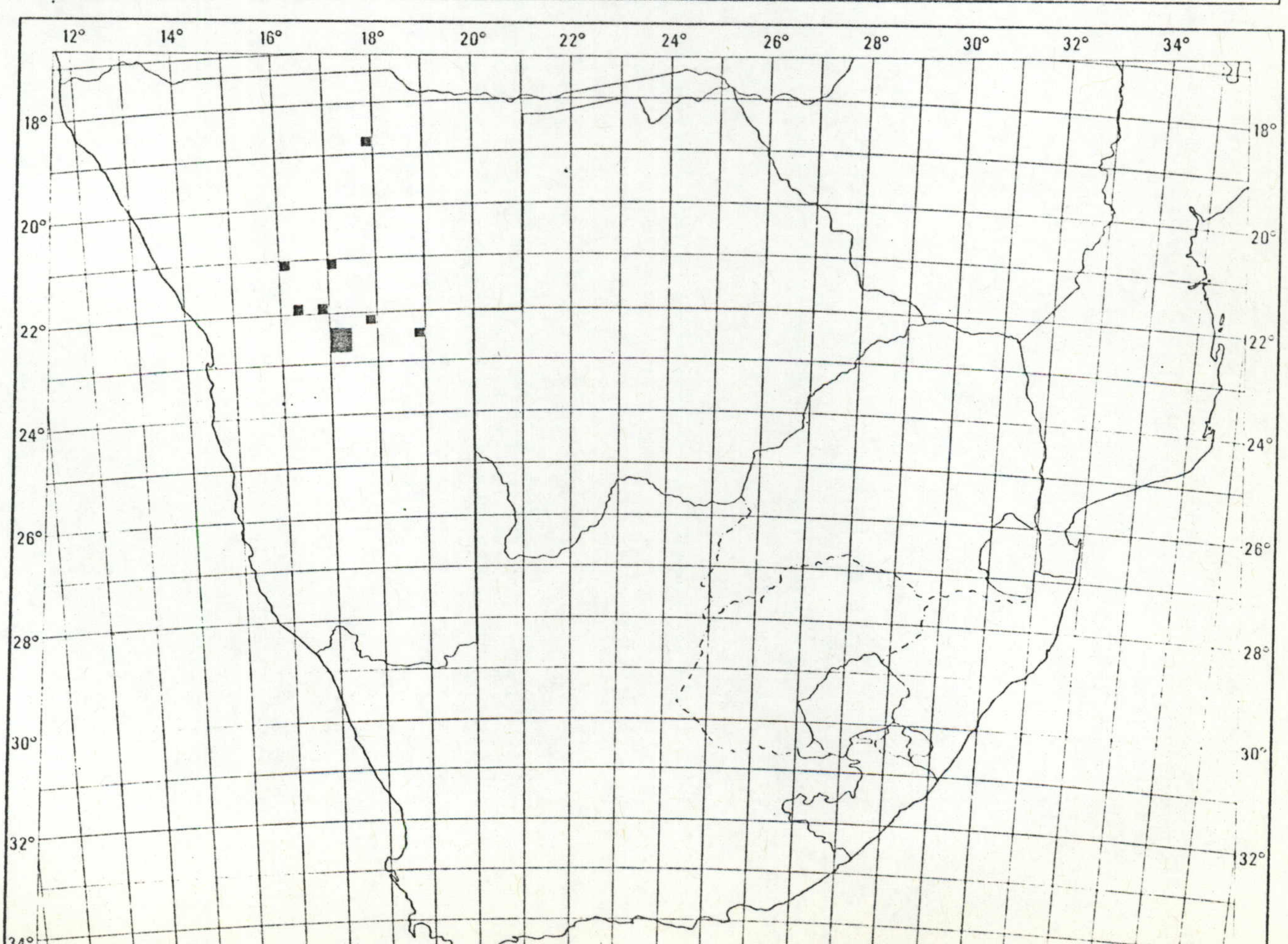
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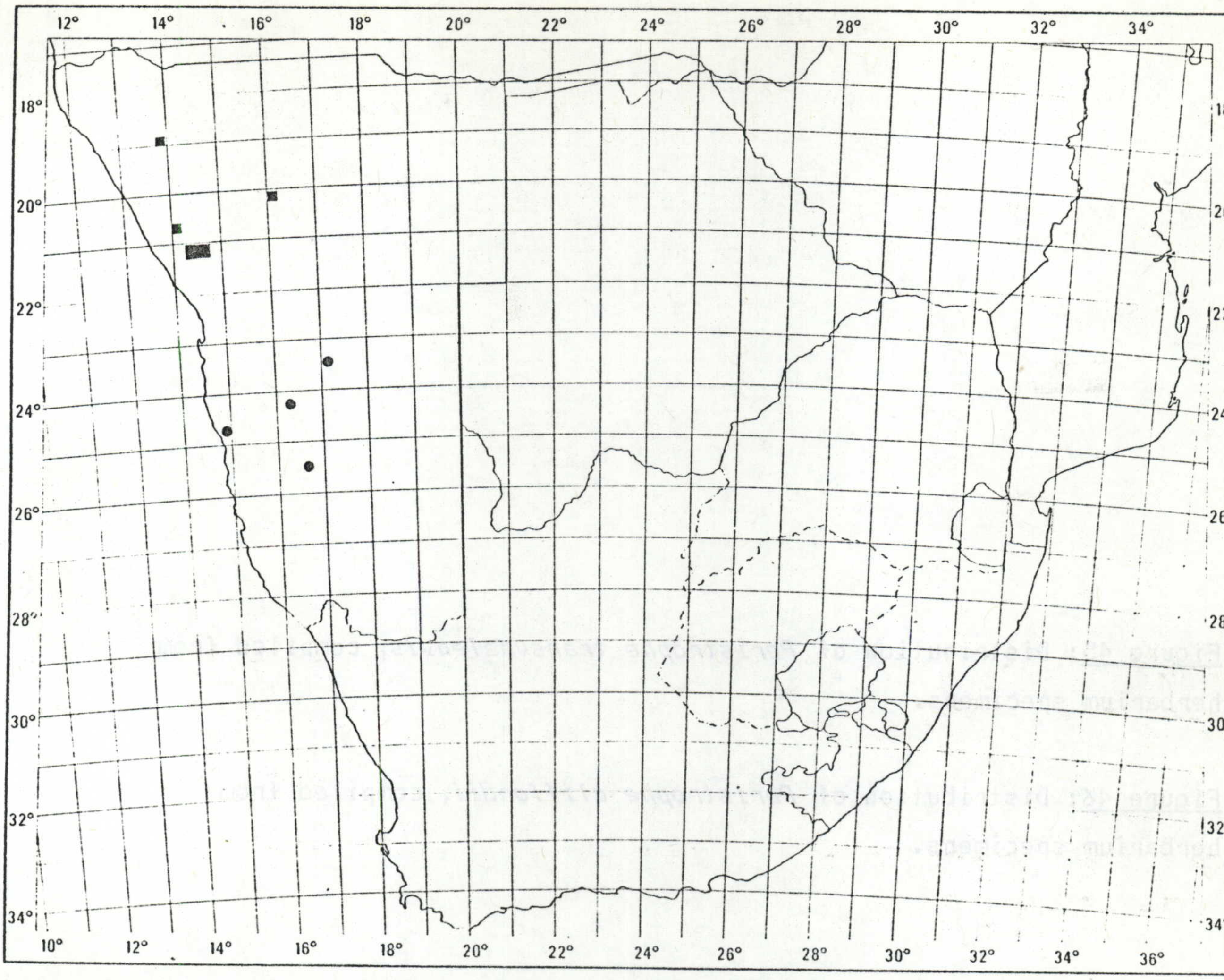
Figure 43: Distribution of *Peristrophe sp. 1*, compiled from herbarium specimens, (■) = *P. sp. 1* ssp. *1* and (●) = *P. sp. 1* ssp. 2

Figure 44: Distribution of *Peristrophe paniculata*, compiled from herbarium specimens.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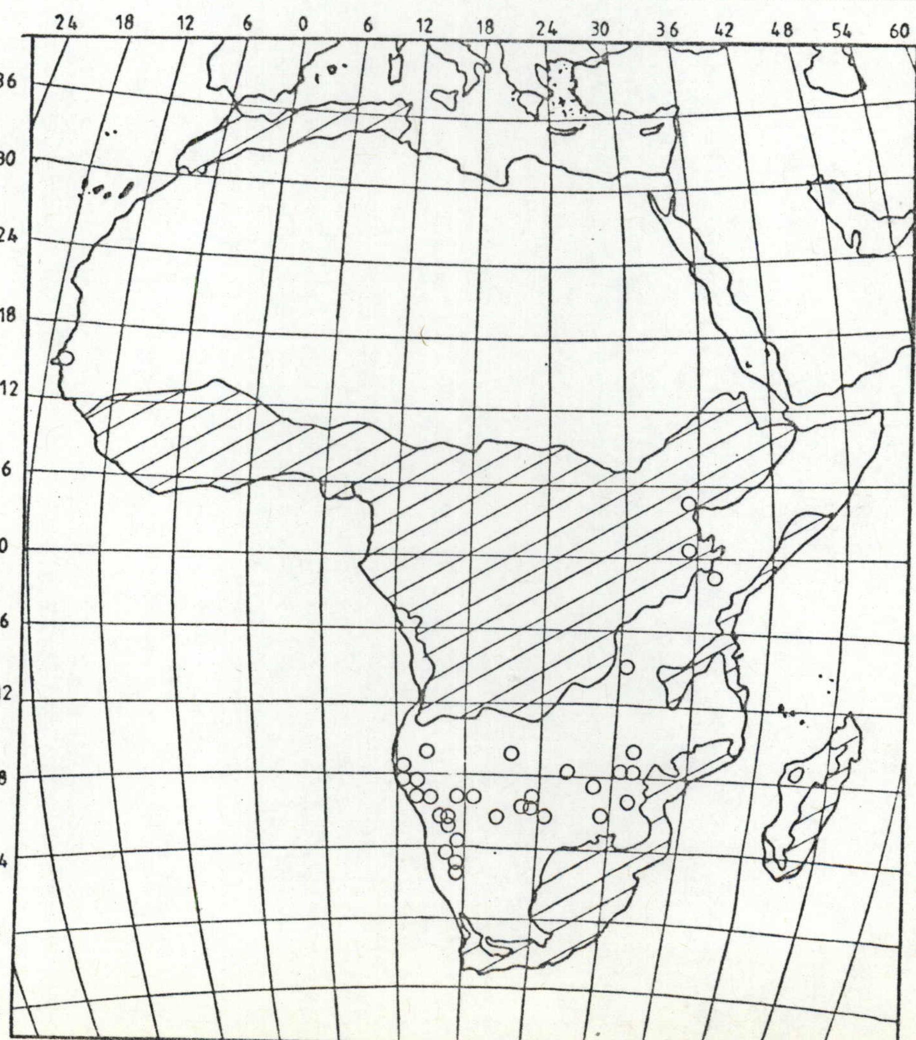
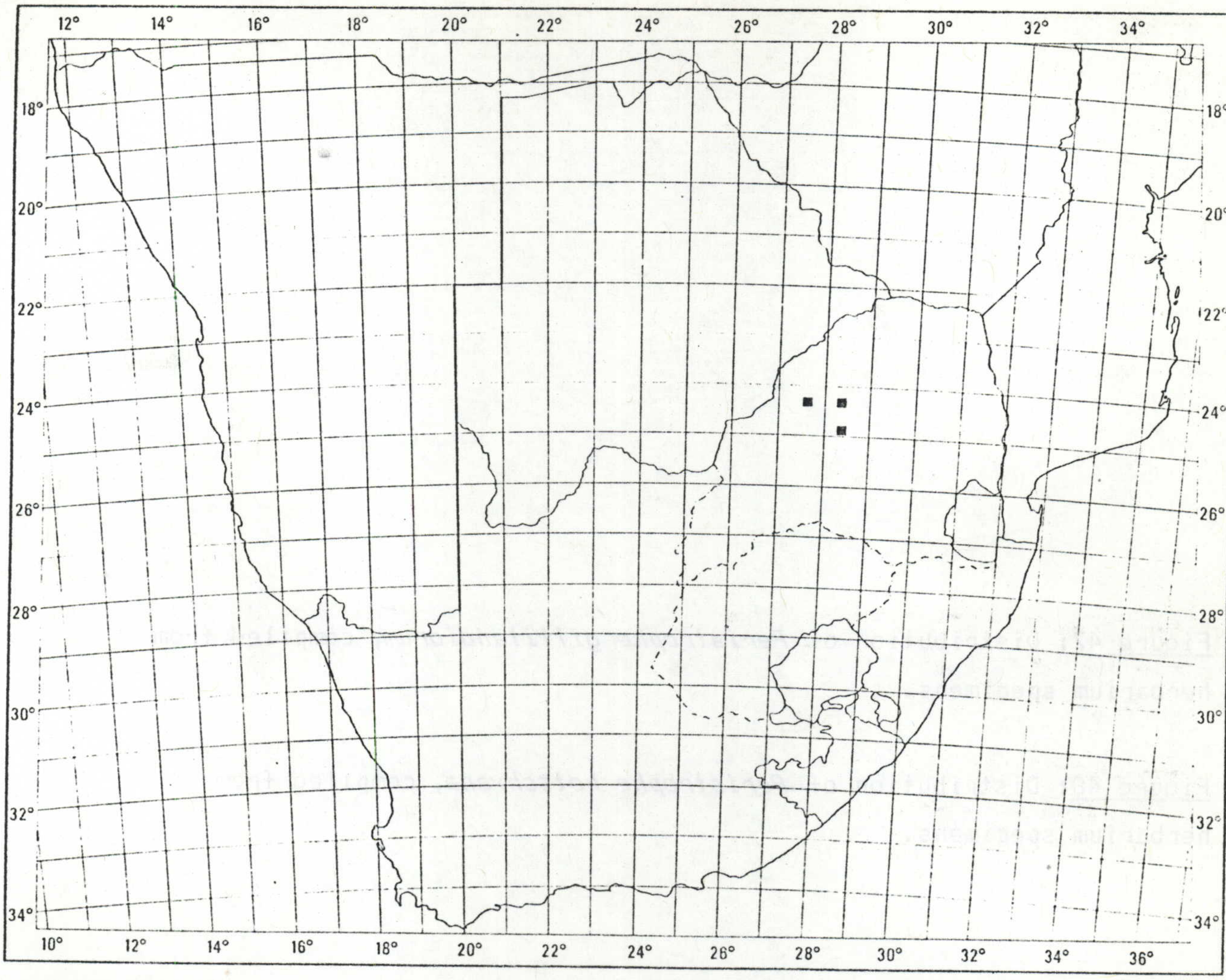

24 18 12 6 0 6 12 18 24 30 36 42 48 54 60
36 30 24 18 12 6 0 6 12 18 24 30 36

Figure 45: Distribution of *Peristrophe transvaalensis*, compiled from herbarium specimens.

Figure 46: Distribution of *Peristrophe cliffordii*, compiled from herbarium specimens.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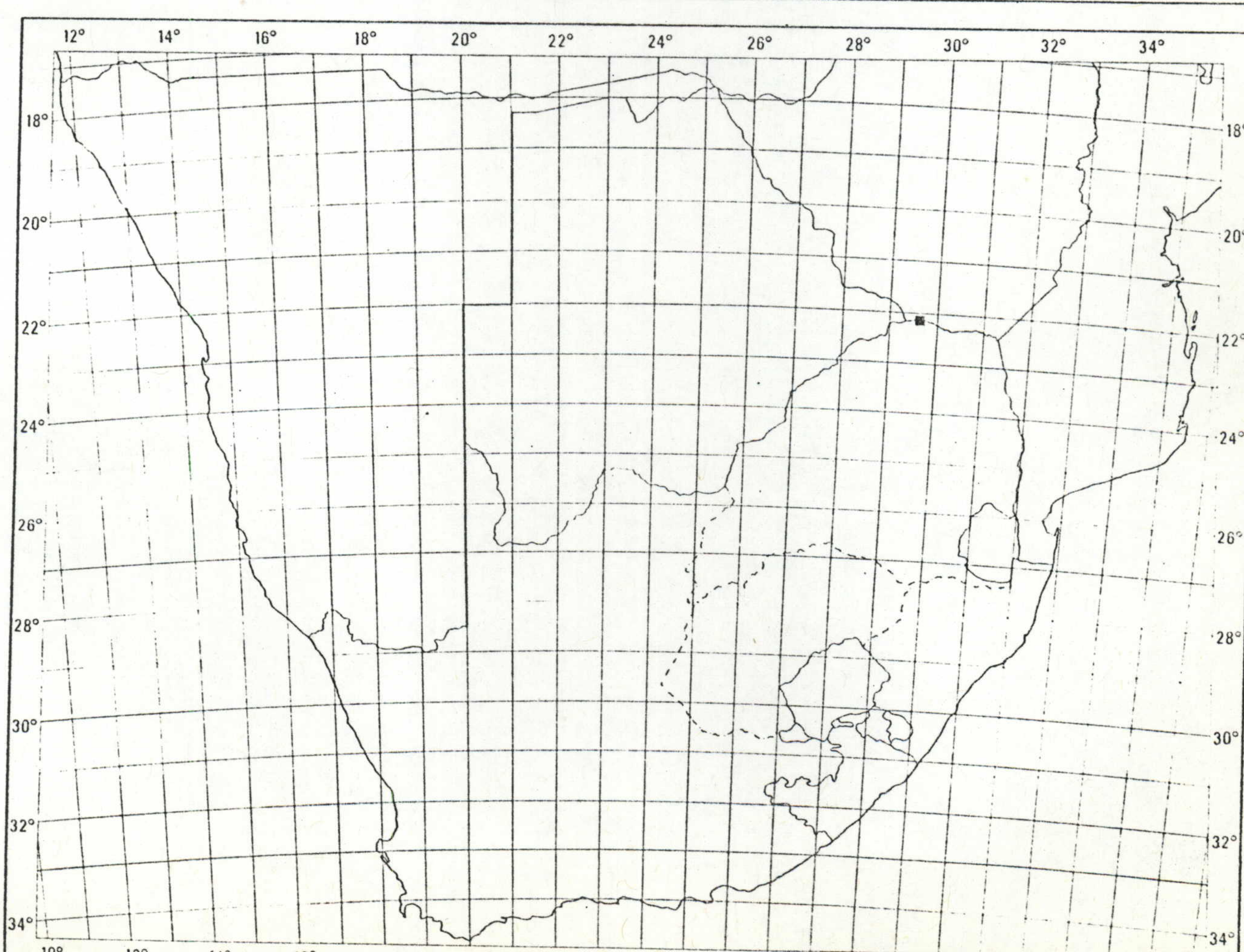
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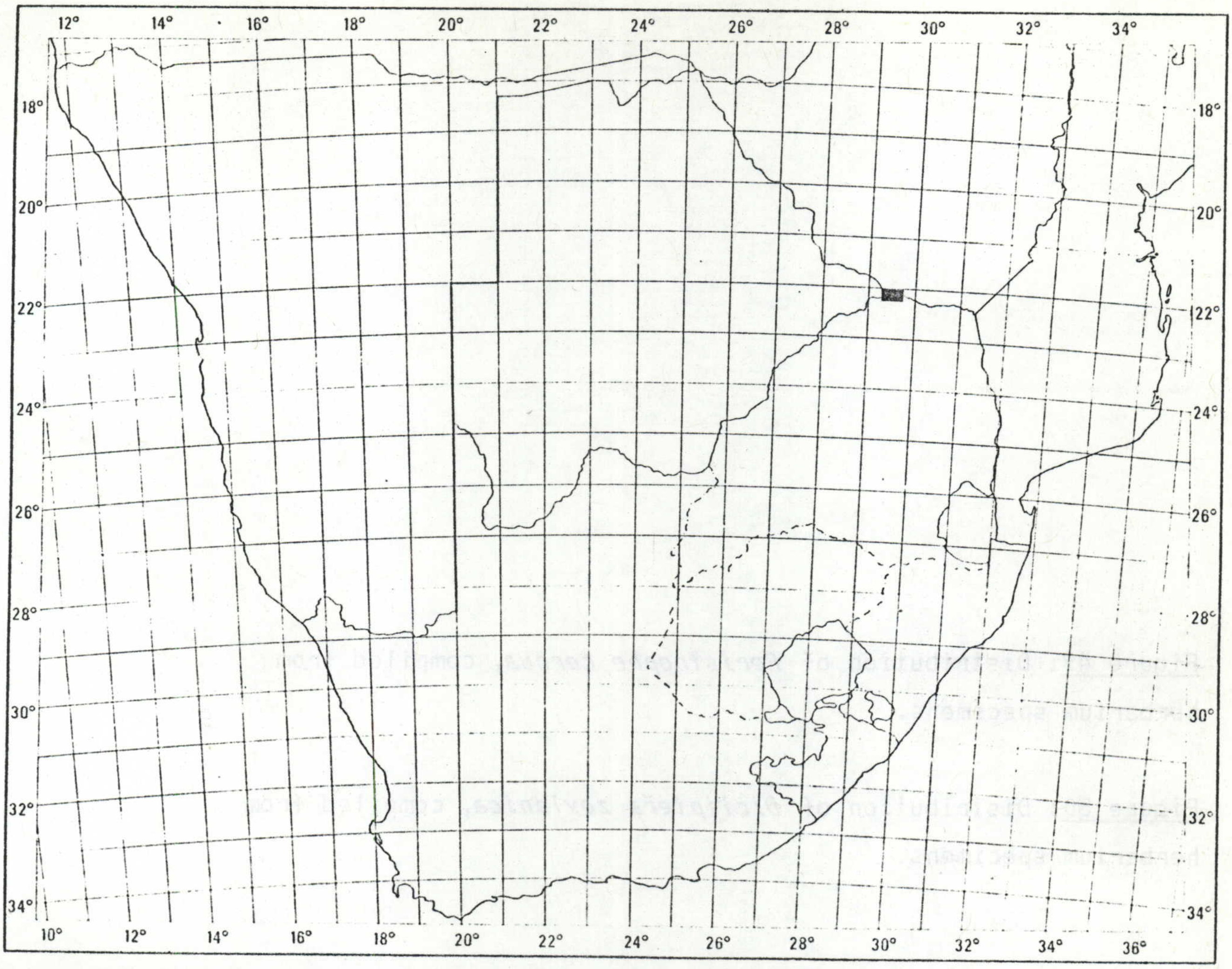
Figure 47: Distribution of *Peristrophe gillilandiorum*, compiled from herbarium specimens.

Figure 48: Distribution of *Peristrophe kotschyana*, compiled from herbarium specimens.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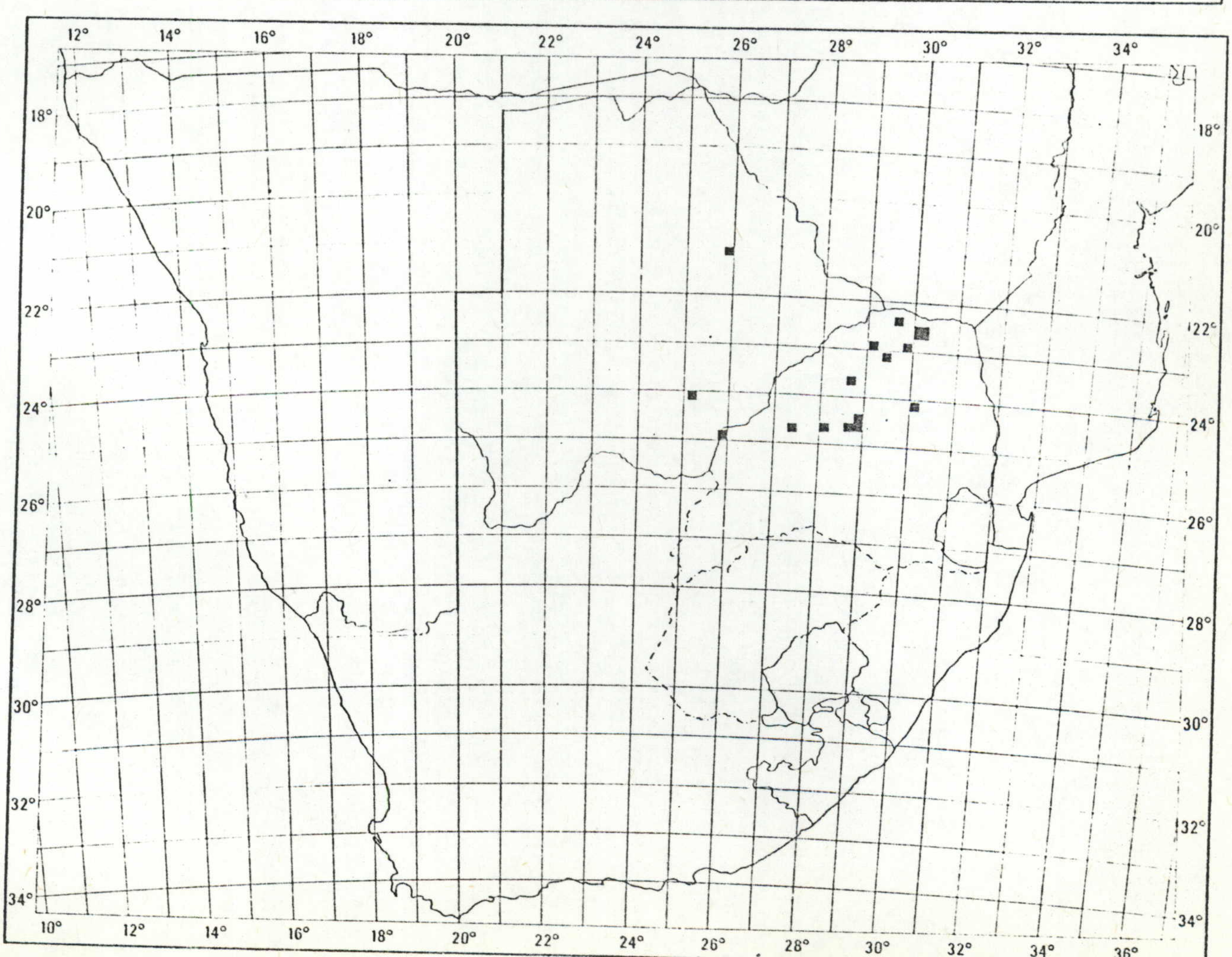
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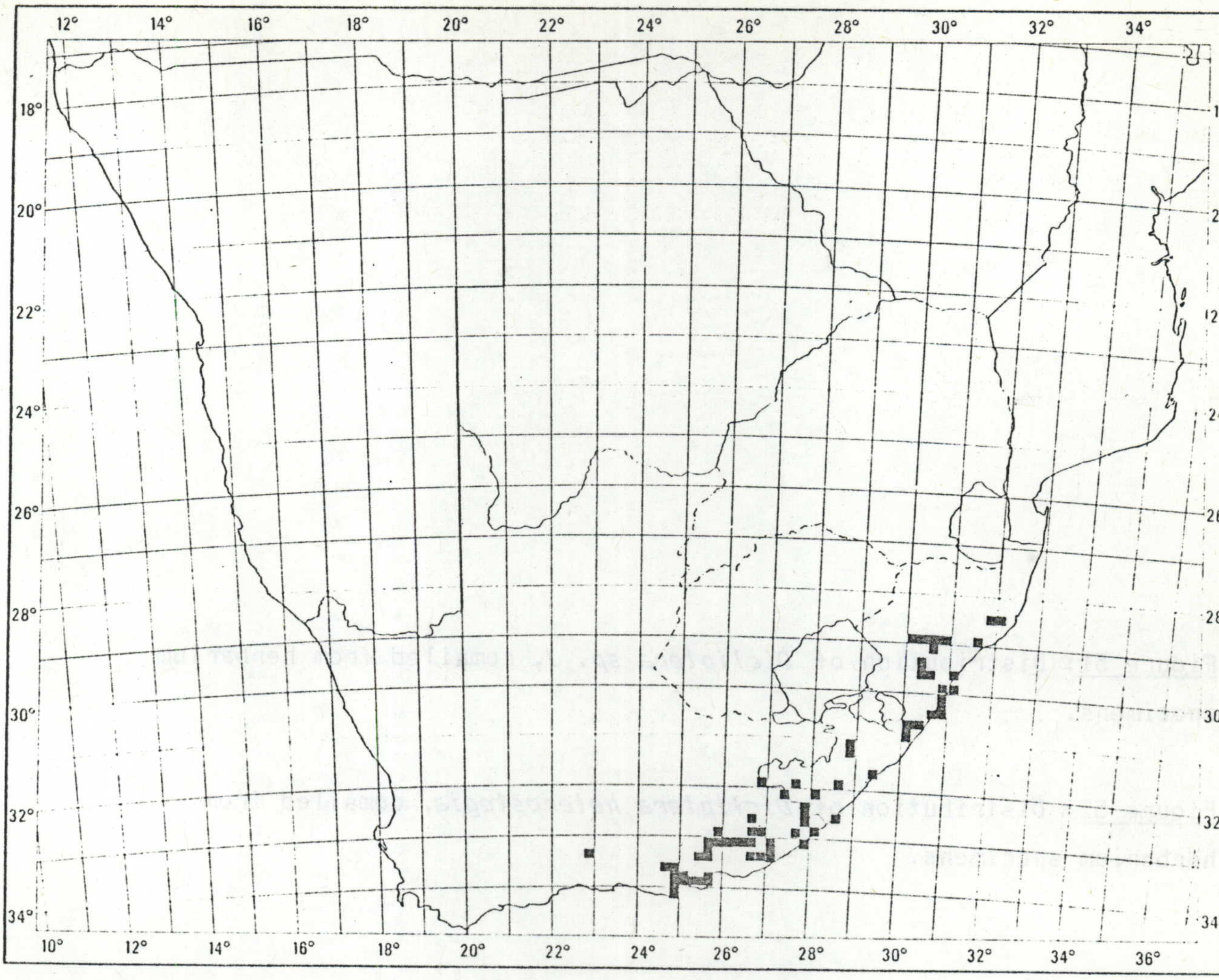
Figure 49: Distribution of *Peristrophe cernua*, compiled from herbarium specimens.

Figure 50: Distribution of *Dicliptera zeylanica*, compiled from herbarium specimens.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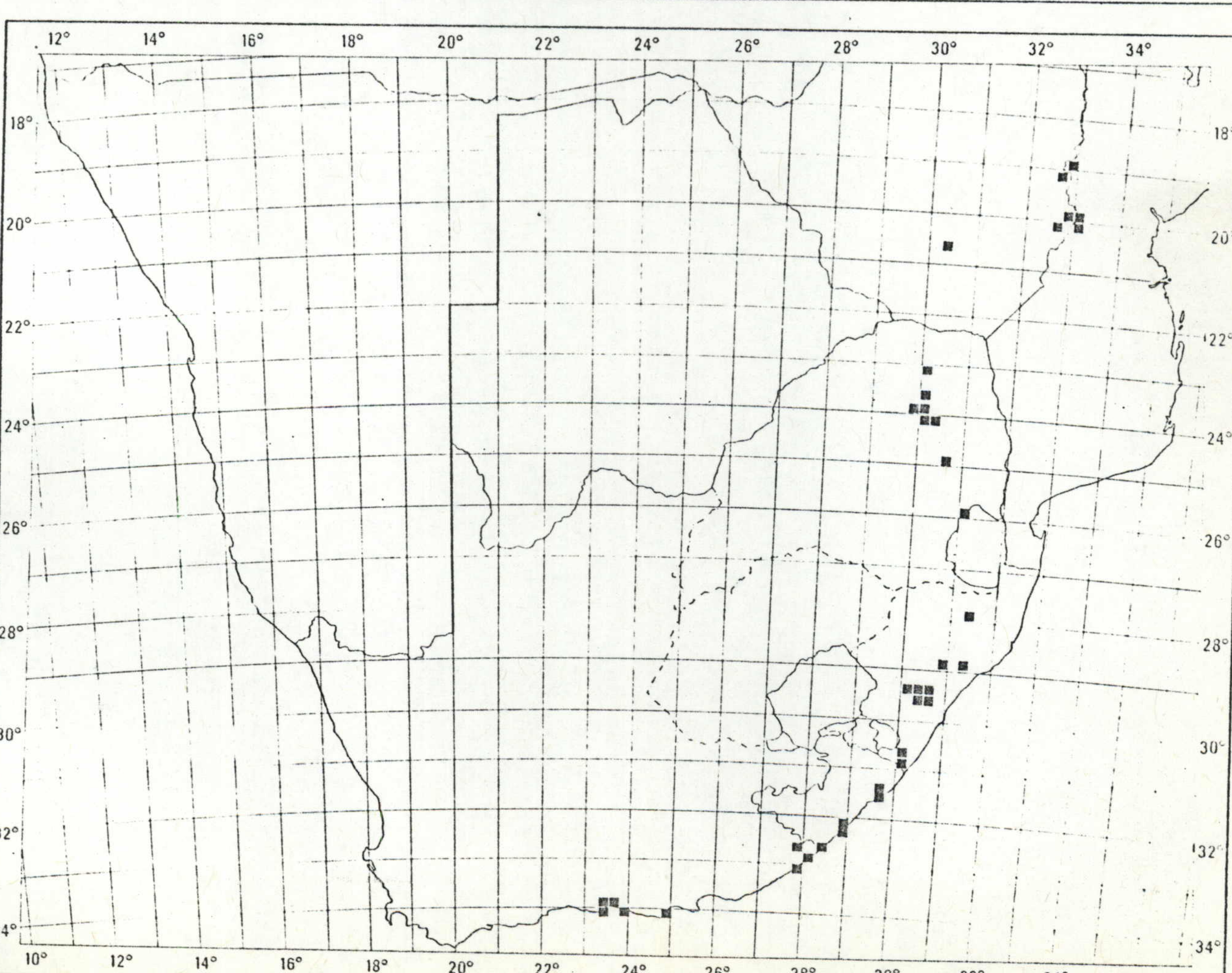
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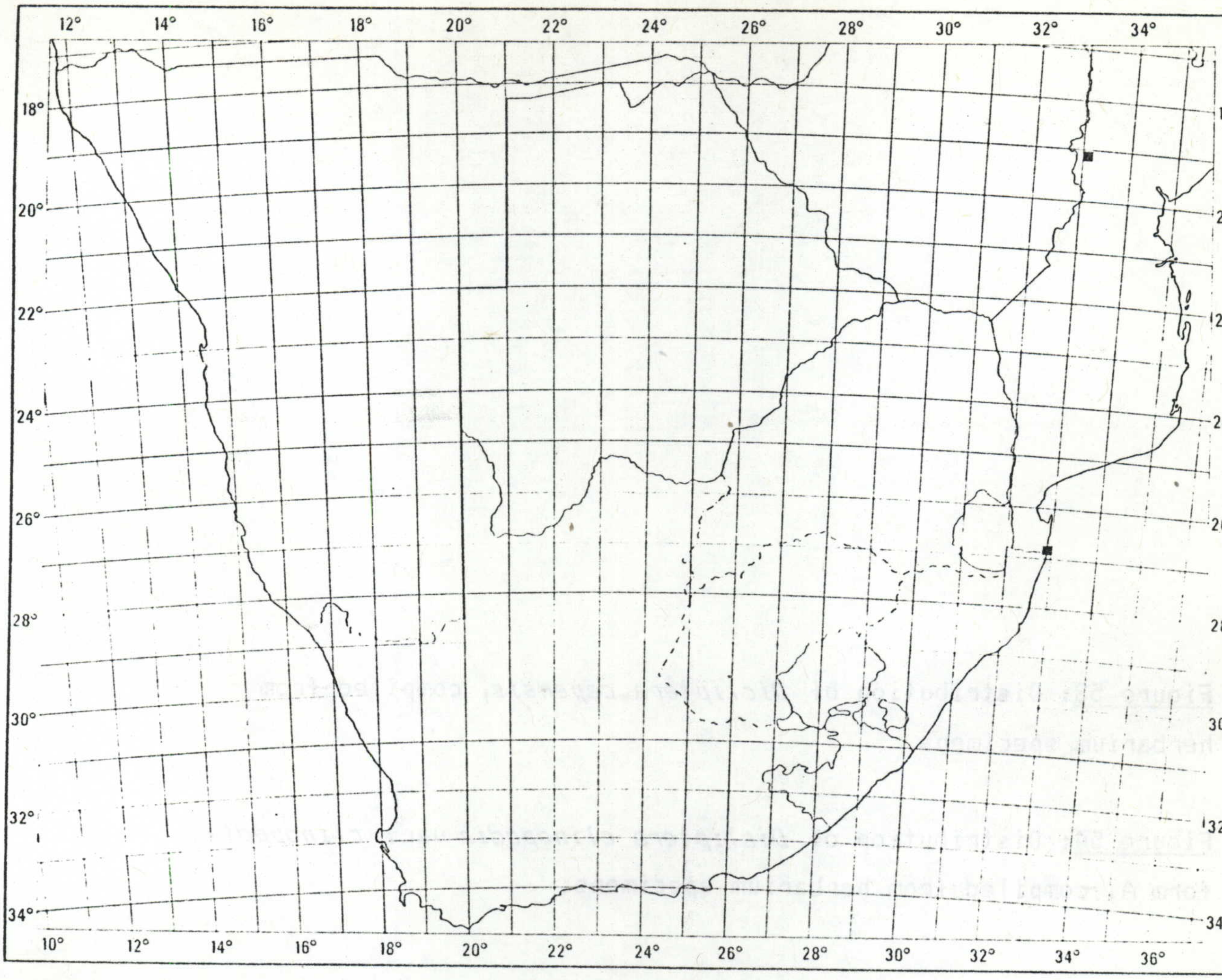
Figure 51: Distribution of *Dicliptera sp. 1*, compiled from herbarium specimens.

Figure 52: Distribution of *Dicliptera heterostegia*, compiled from herbarium specimens.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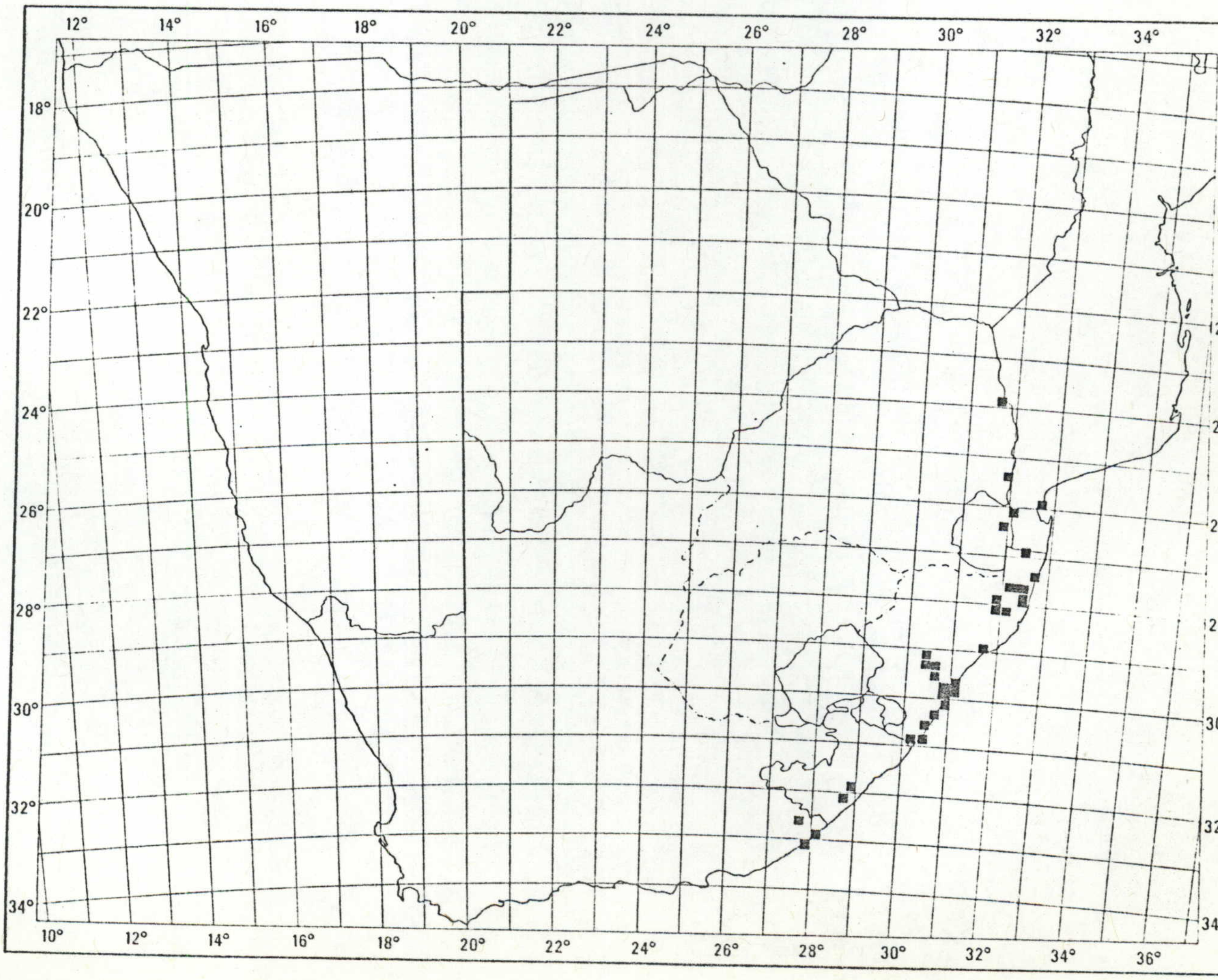
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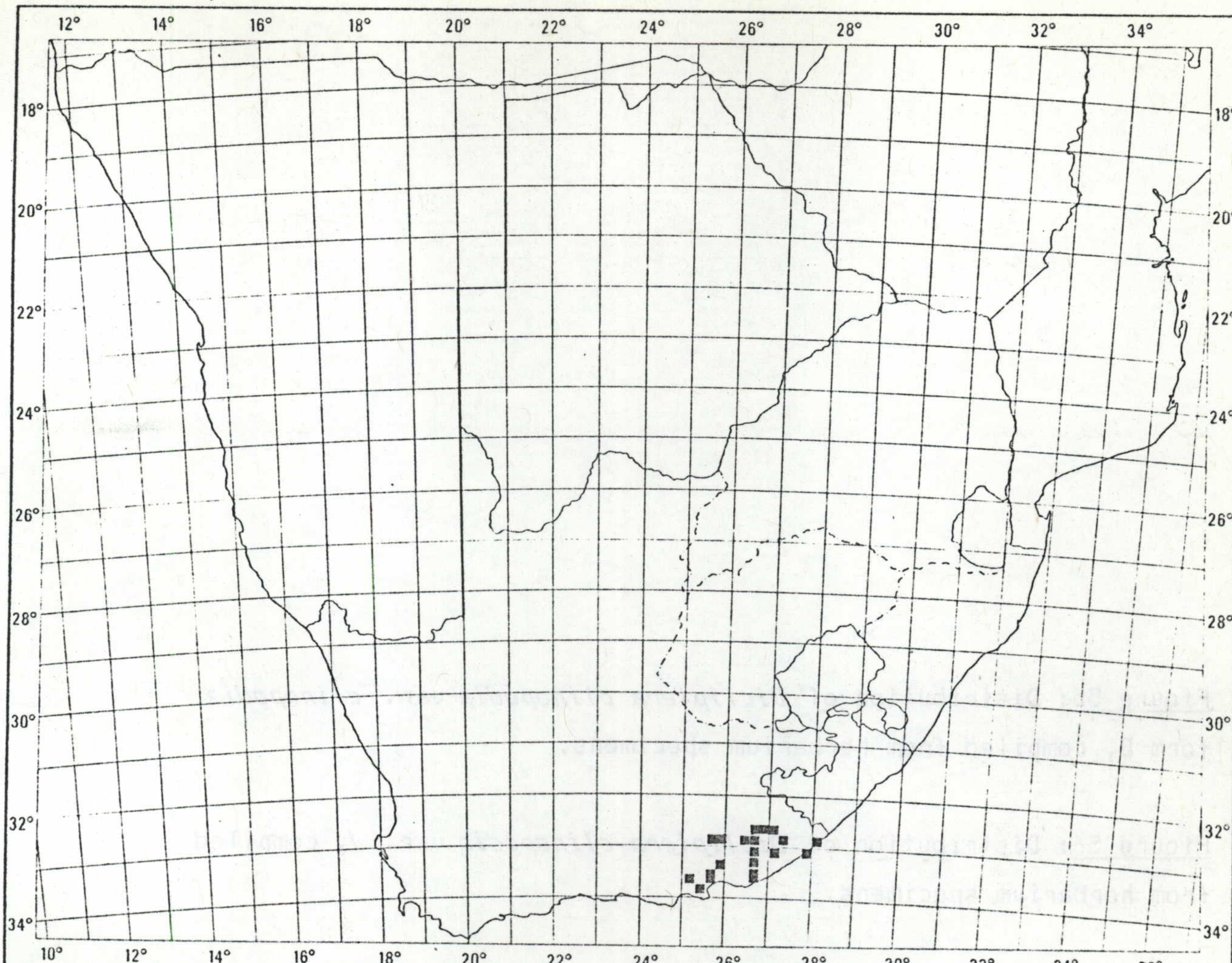
Figure 53: Distribution of *Dicliptera capensis*, compiled from herbarium specimens.

Figure 54: Distribution of *Dicliptera clinopodia* var. *clinopodia* form A, compiled from herbarium specimens.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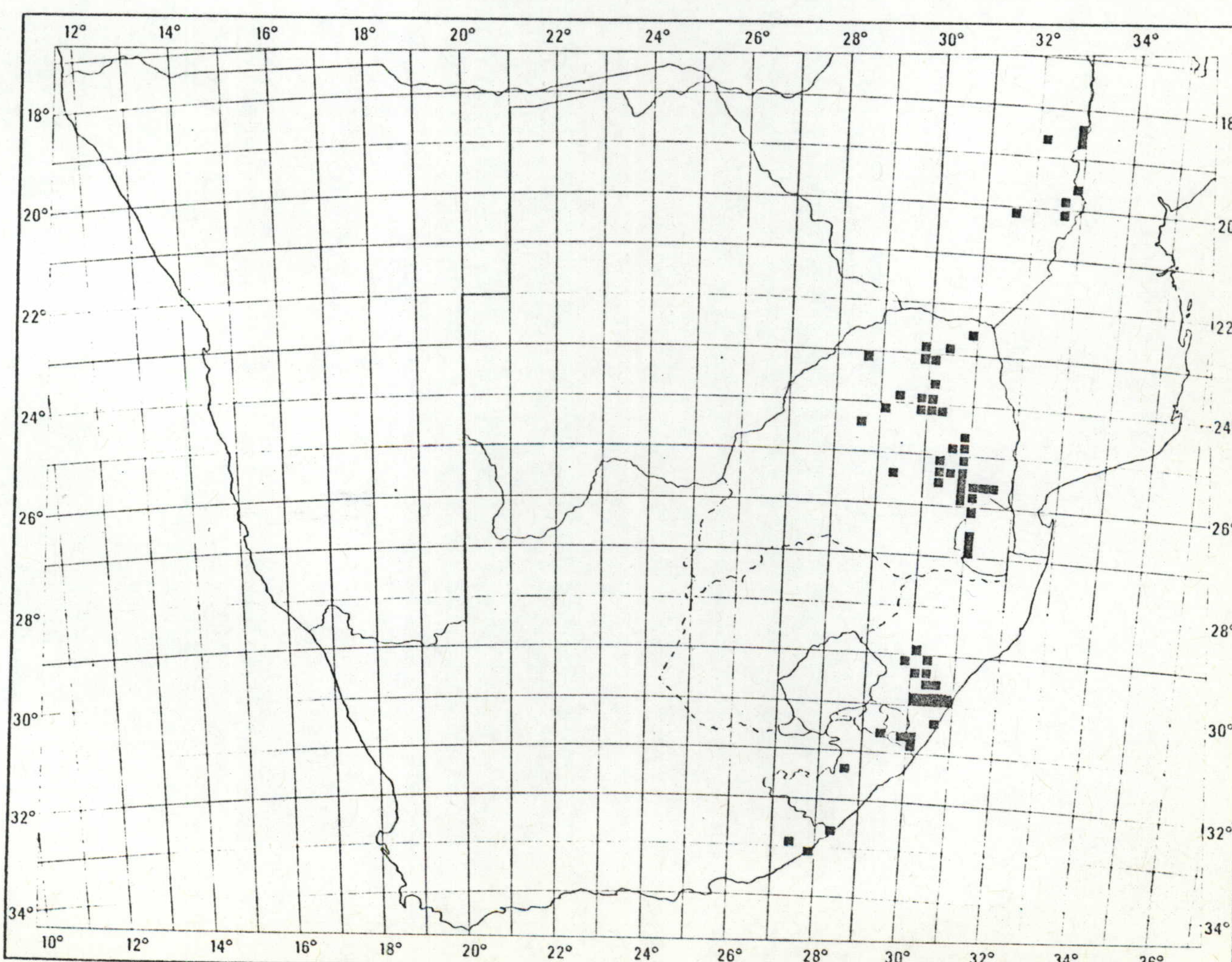
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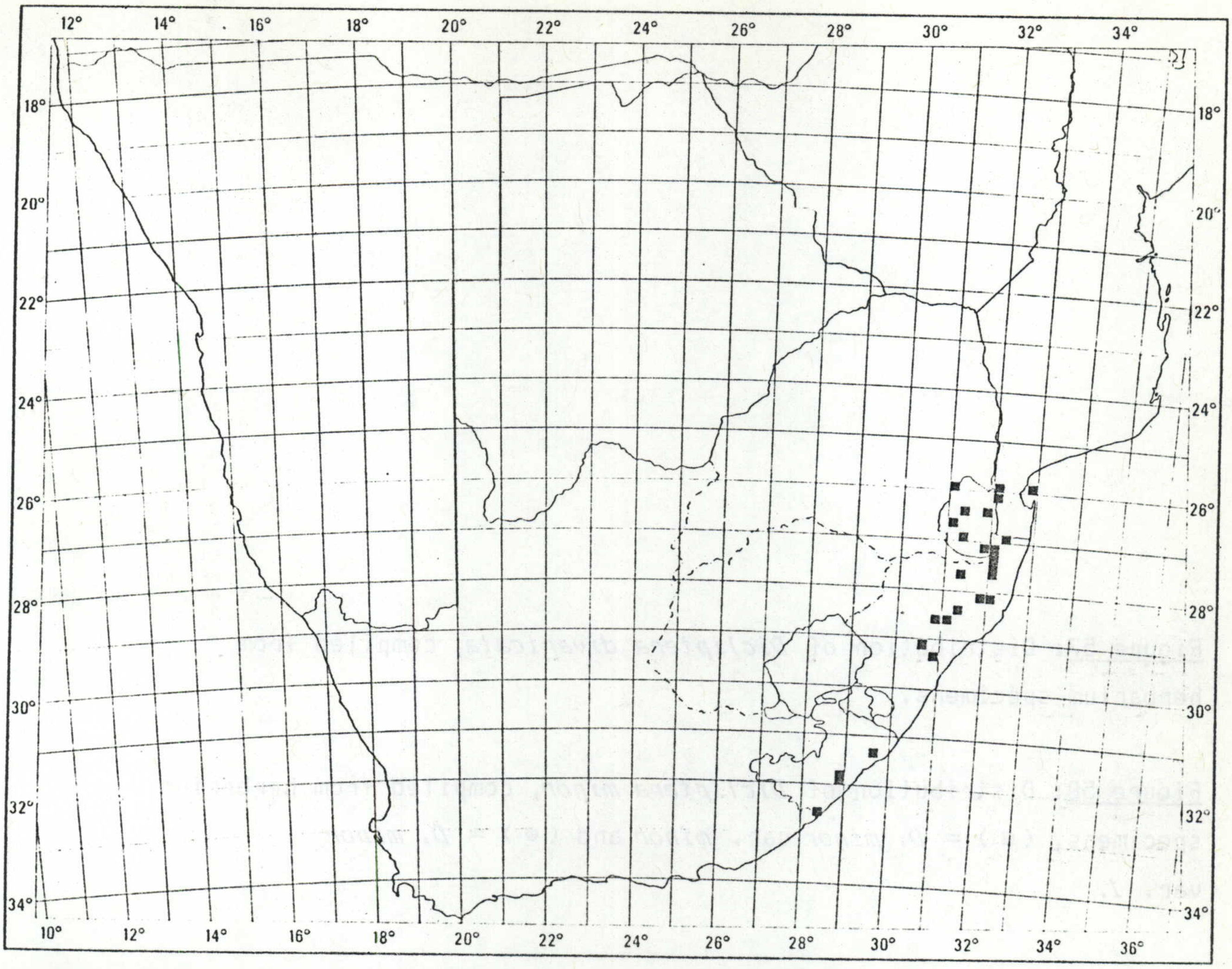
Figure 55: Distribution of *Dicliptera clinopodia* var. *clinopodia* form B, compiled from herbarium specimens.

Figure 56: Distribution of *Dicliptera clinopodia* var. *1*, compiled from herbarium specimens.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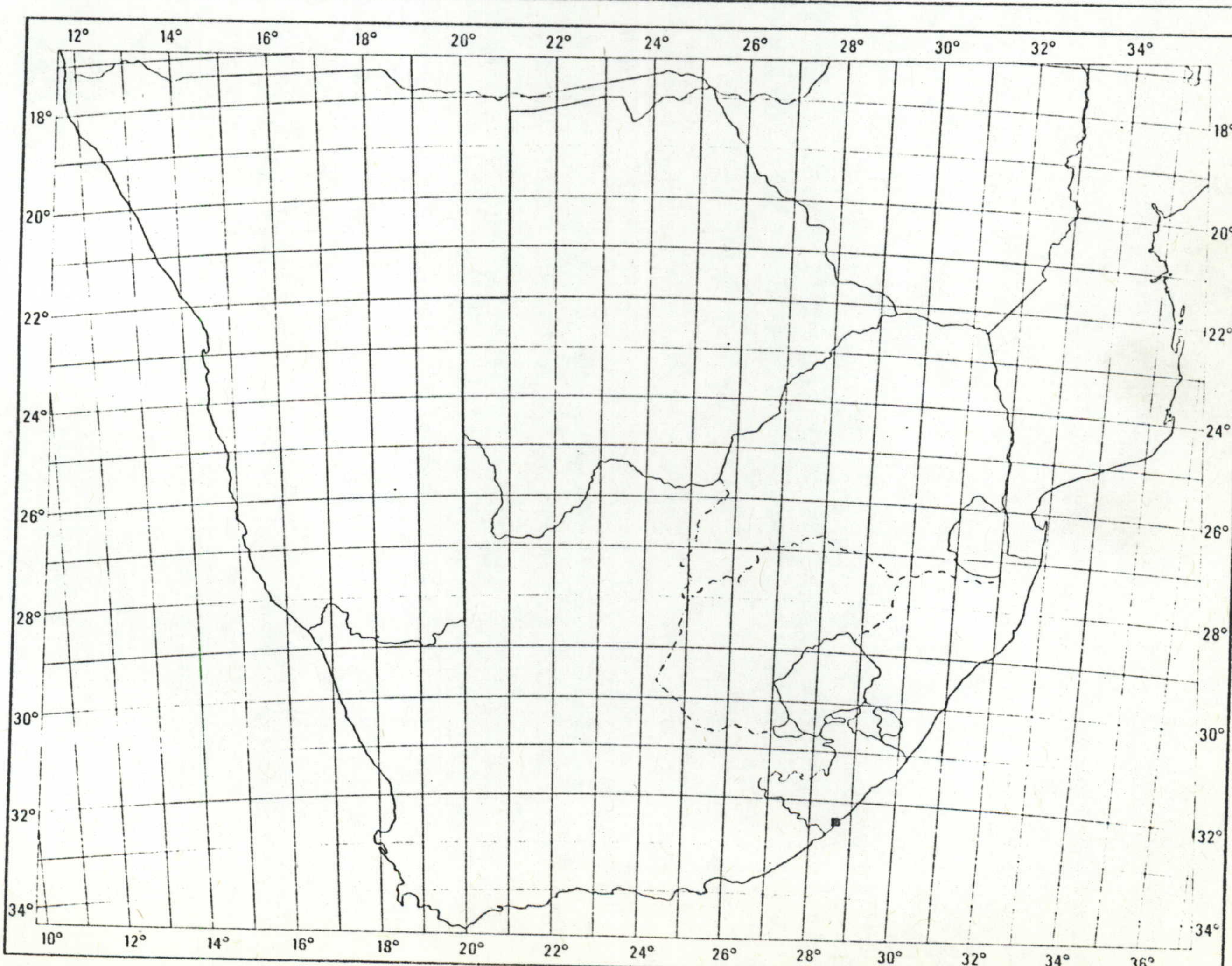
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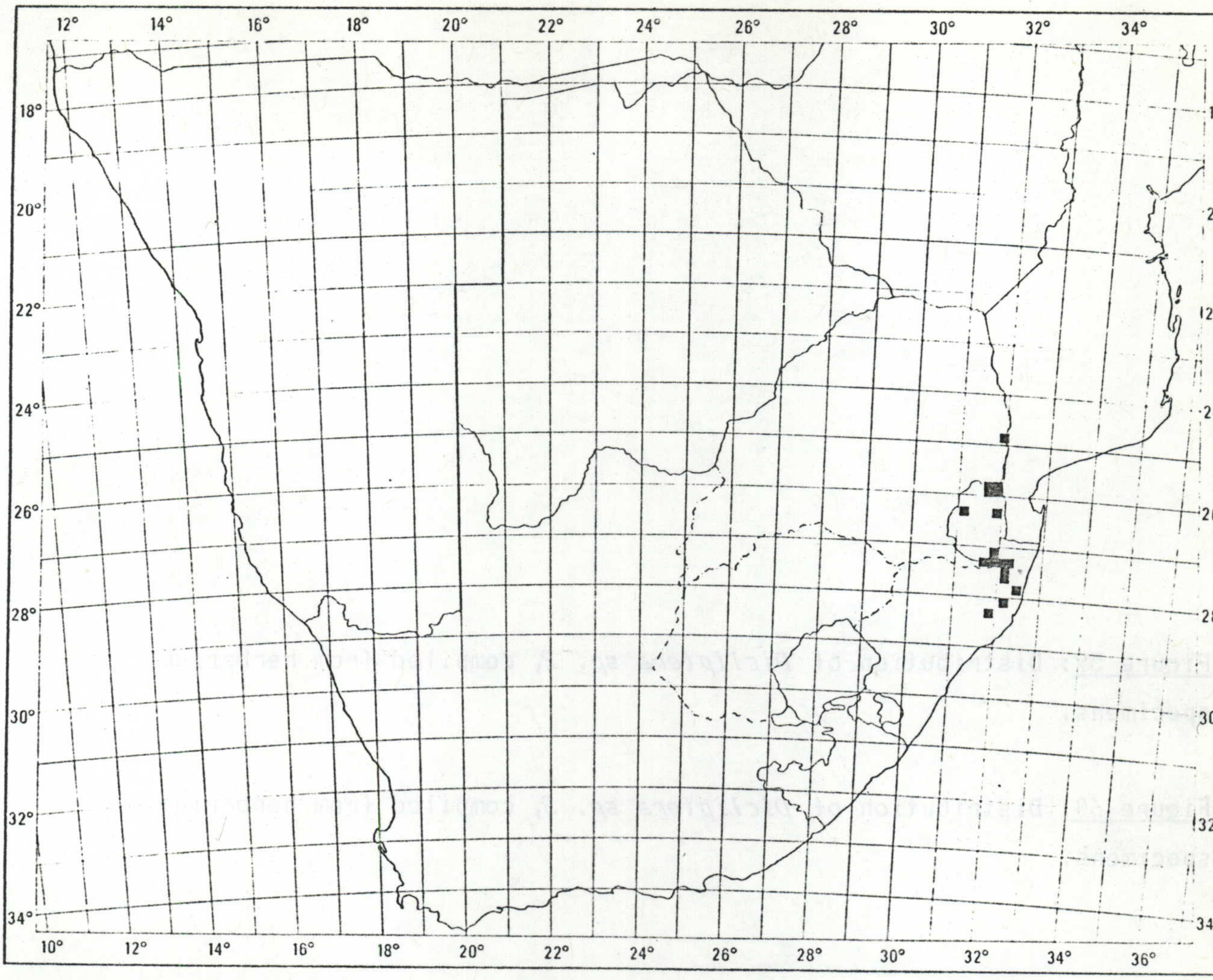
Figure 57: Distribution of *Dicliptera divaricata*, compiled from herbarium specimens.

Figure 58: Distribution of *Dicliptera minor*, compiled from herbarium specimens, (■) = *D. minor* var. *minor* and (●) = *D. minor* var. *1*.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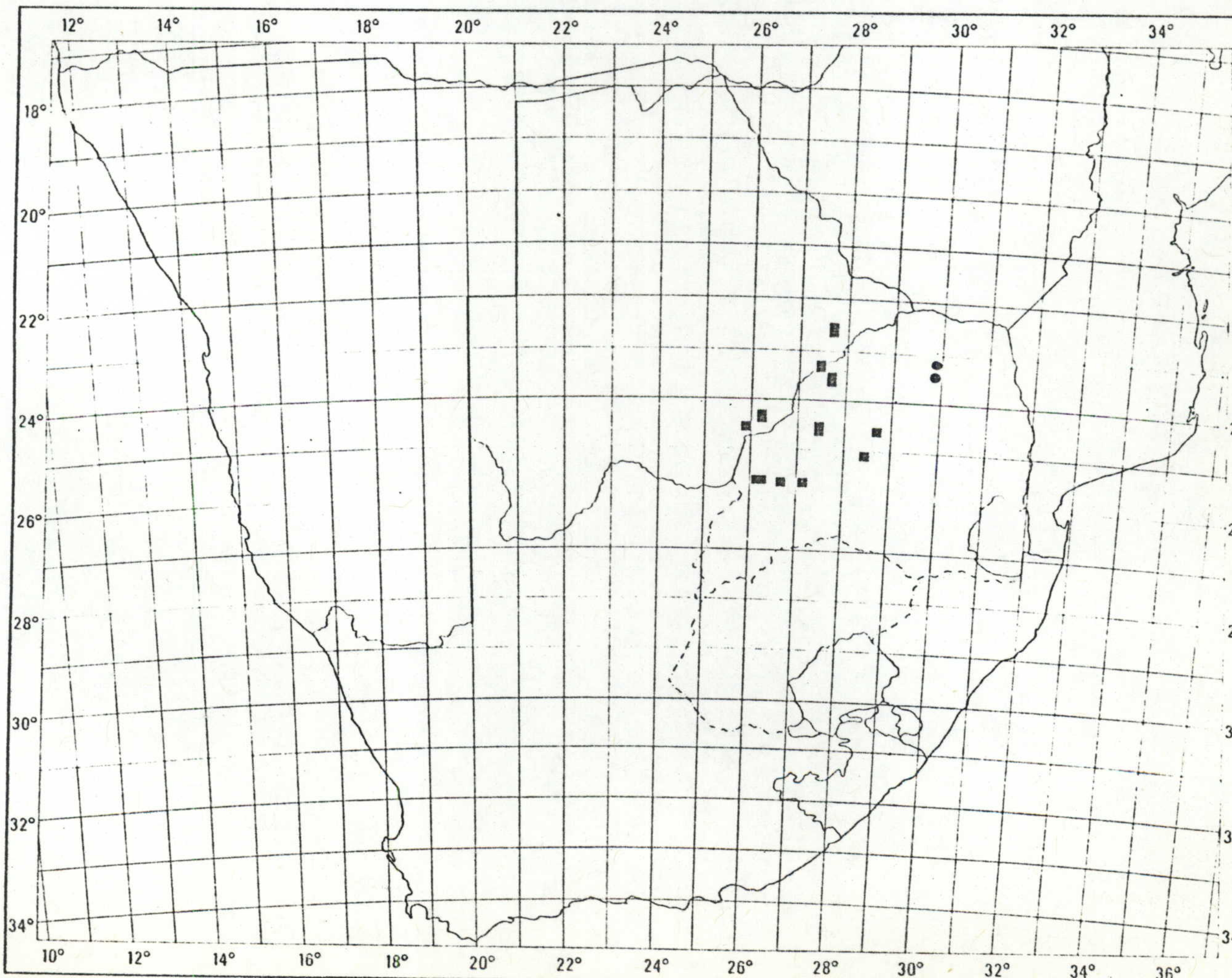
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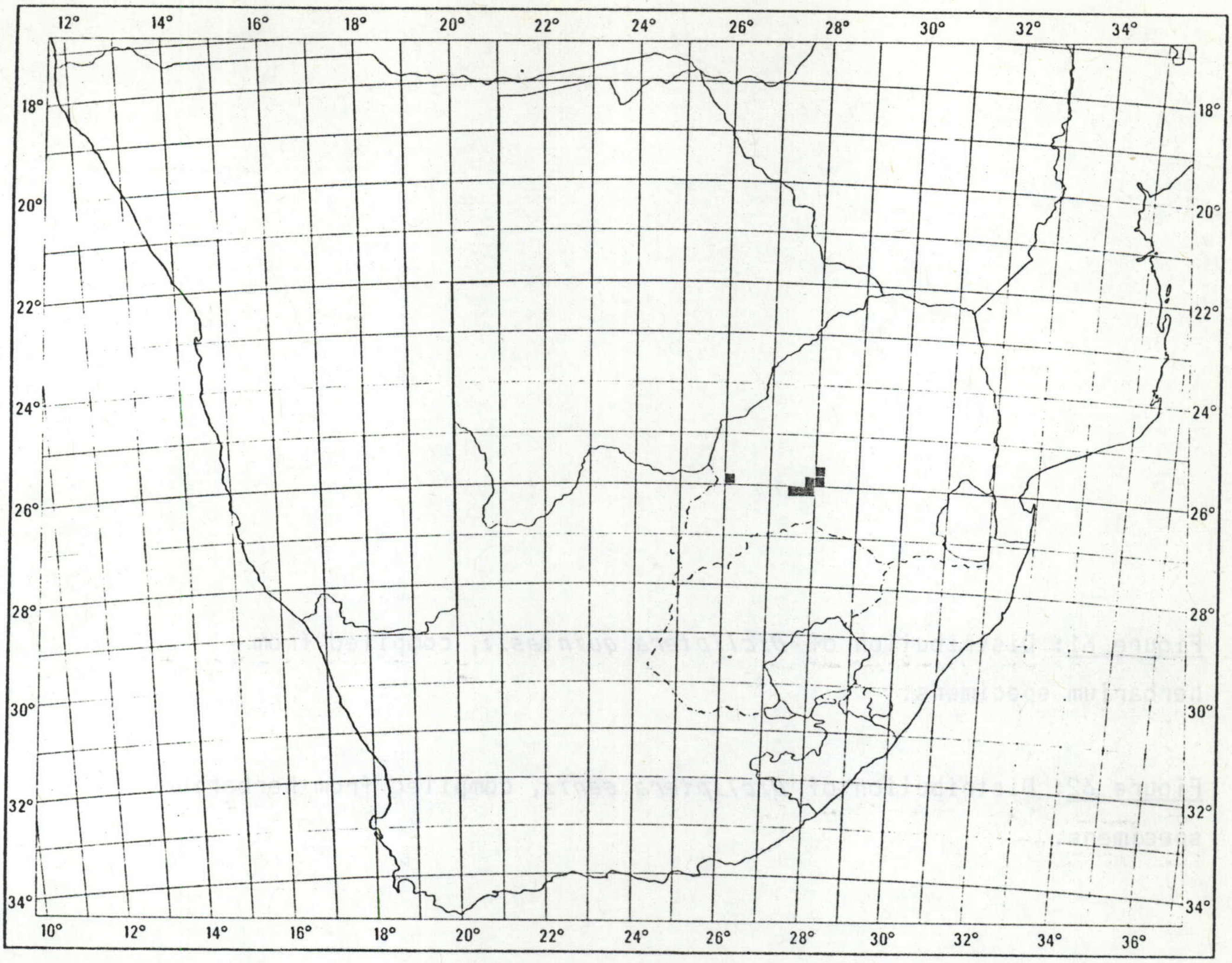
Figure 59: Distribution of *Dicliptera sp. 2*, compiled from herbarium specimens.

Figure 60: Distribution of *Dicliptera sp. 3*, compiled from herbarium specimens.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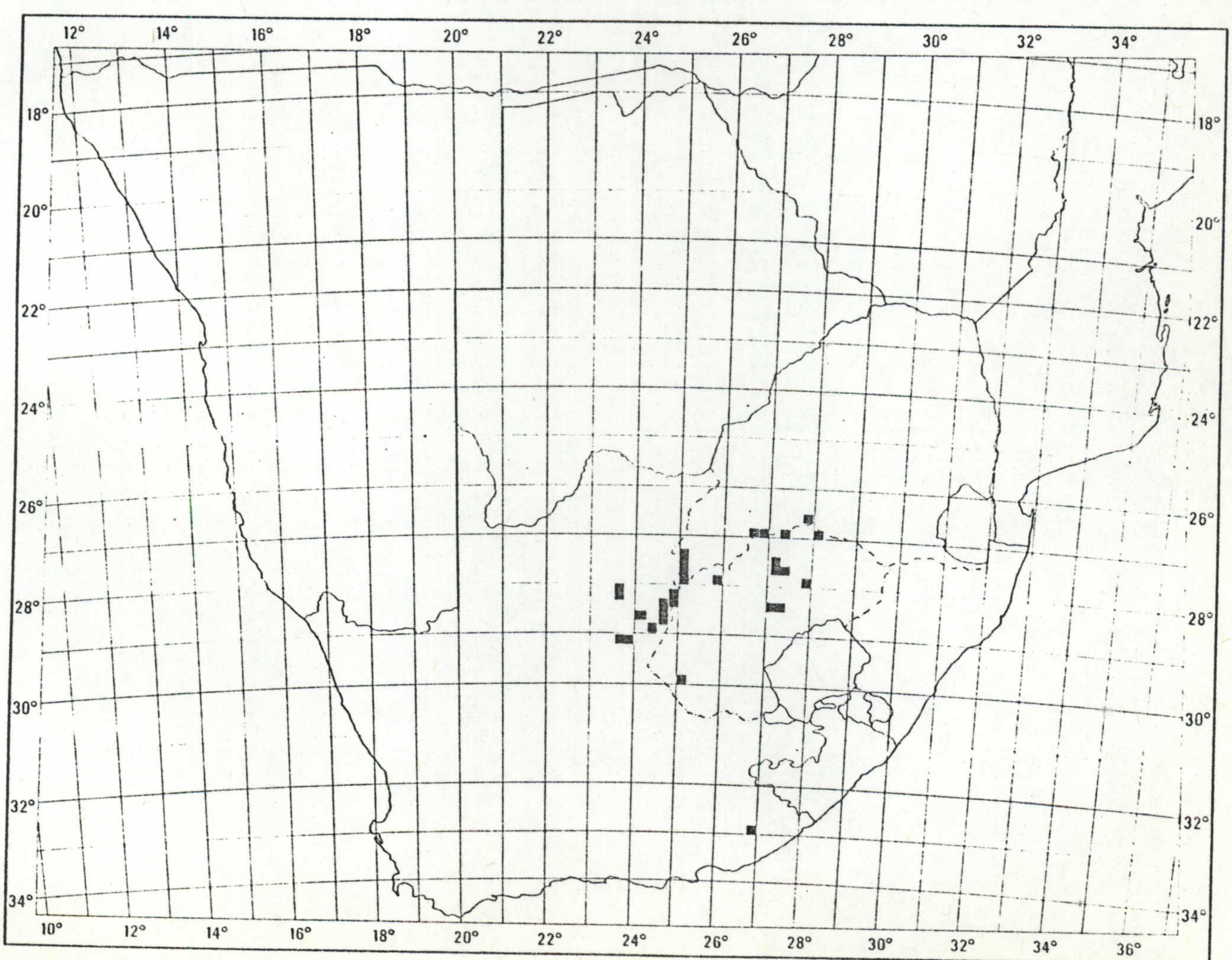
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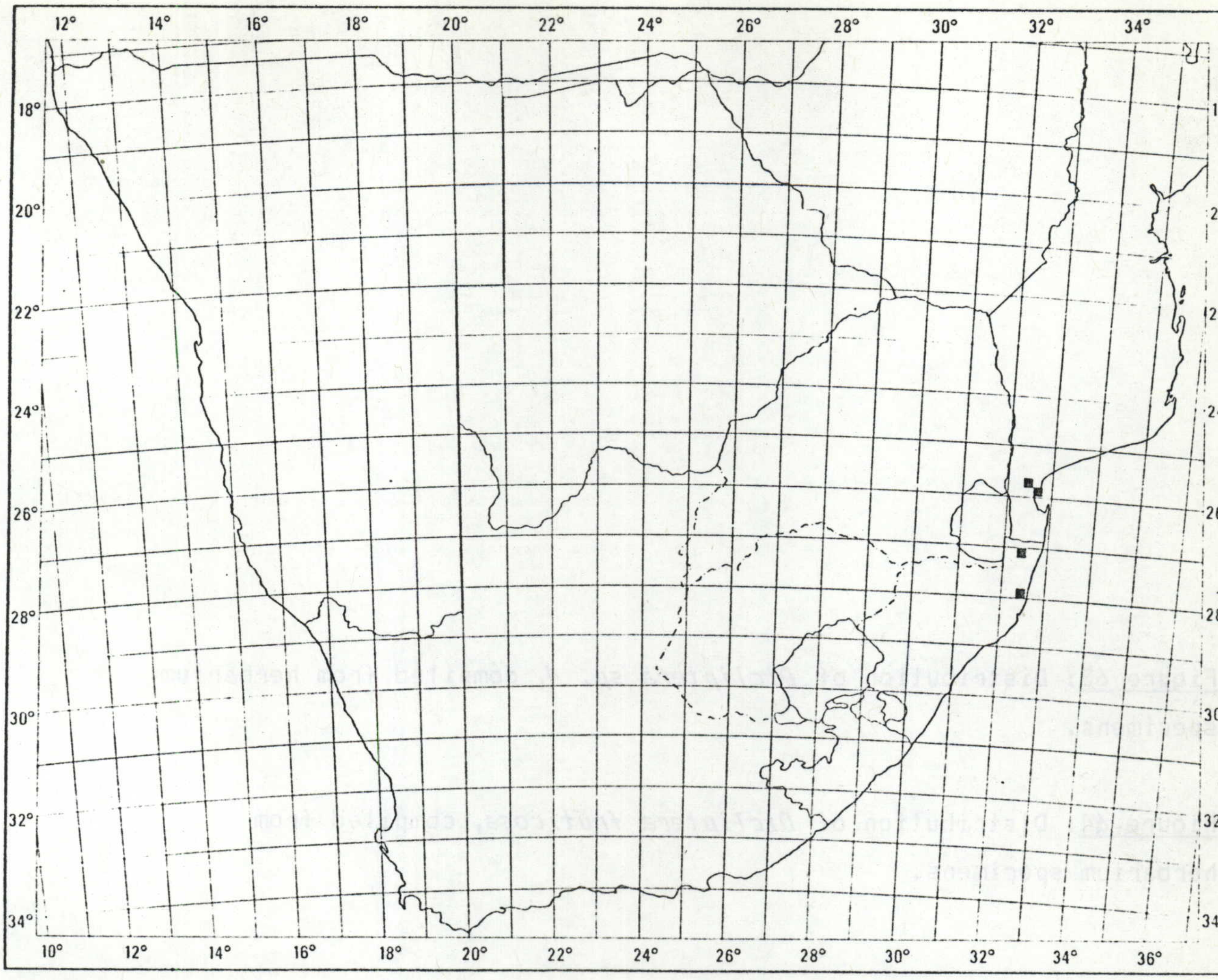
Figure 61: Distribution of *Dicliptera quintasii*, compiled from herbarium specimens.

Figure 62: Distribution of *Dicliptera eenii*, compiled from herbarium specimens.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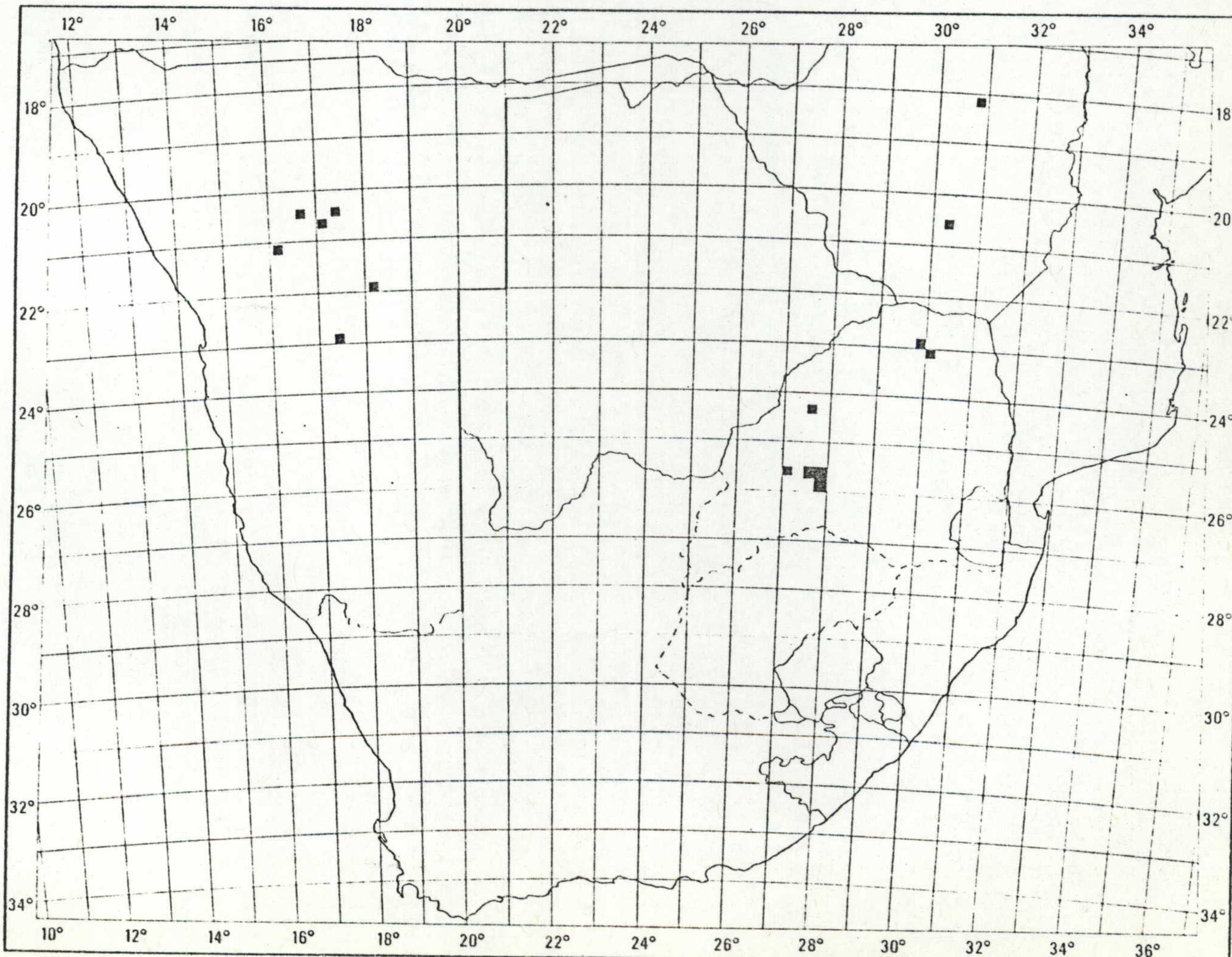
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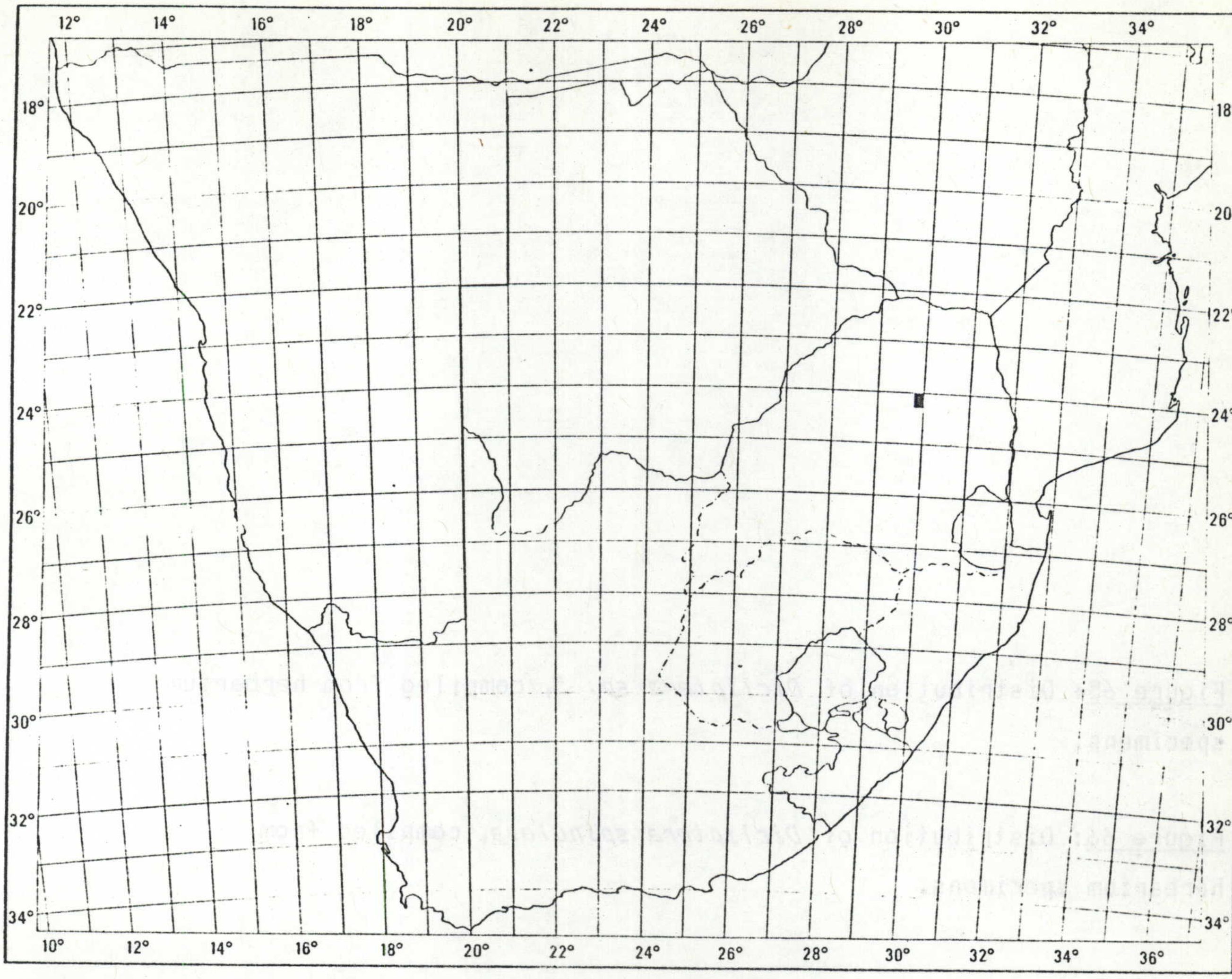
Figure 63: Distribution of *Dicliptera sp. 4*, compiled from herbarium specimens.

Figure 64: Distribution of *Dicliptera fruticosa*, compiled from herbarium specimens.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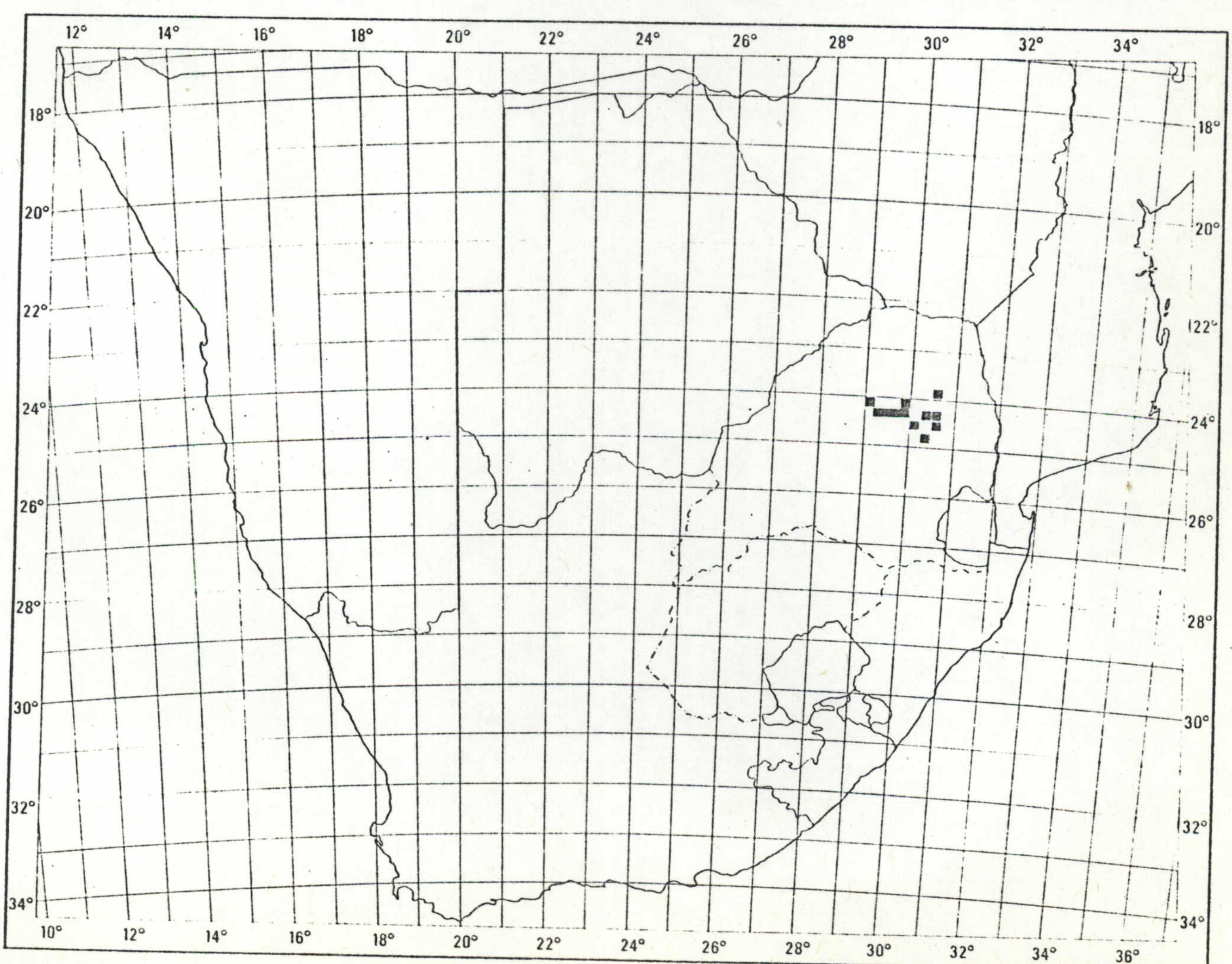
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Figure 65: Distribution of *Dicliptera sp. 5*, compiled from herbarium specimens.

Figure 66: Distribution of *Dicliptera spinulosa*, compiled from herbarium specimens.

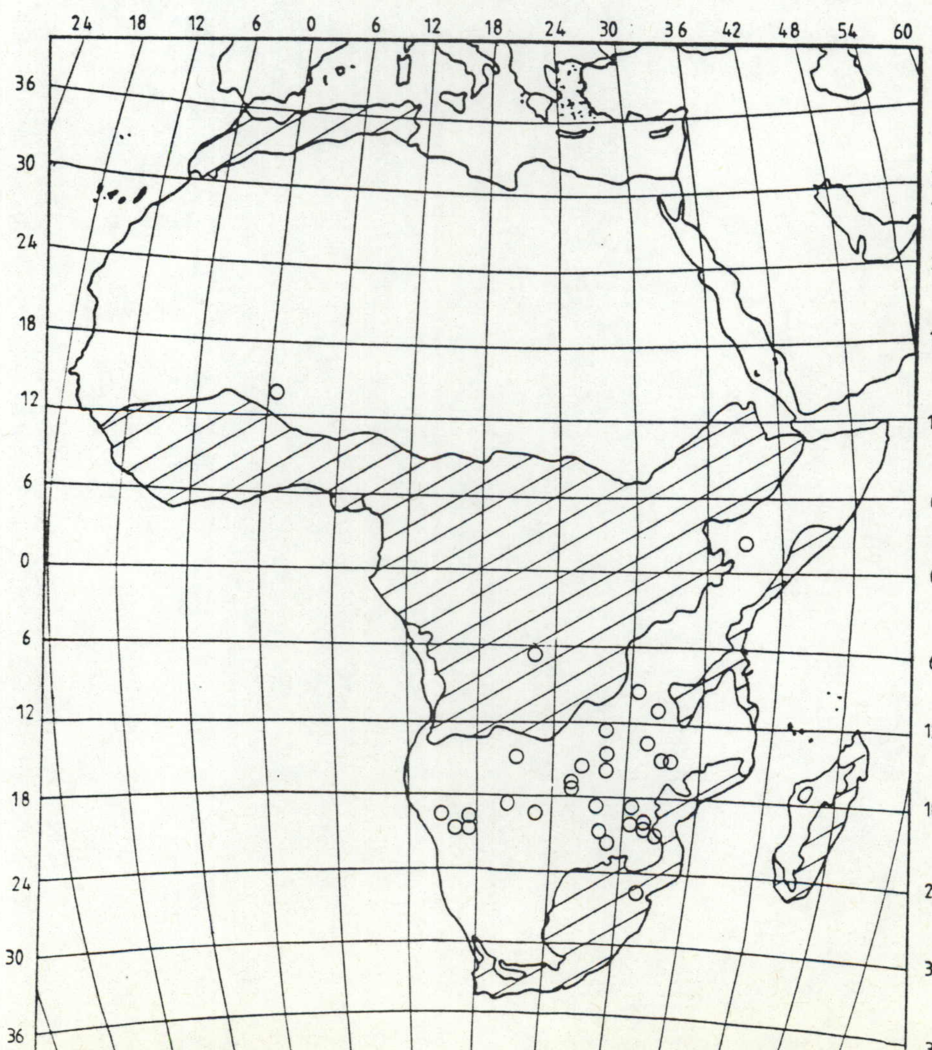
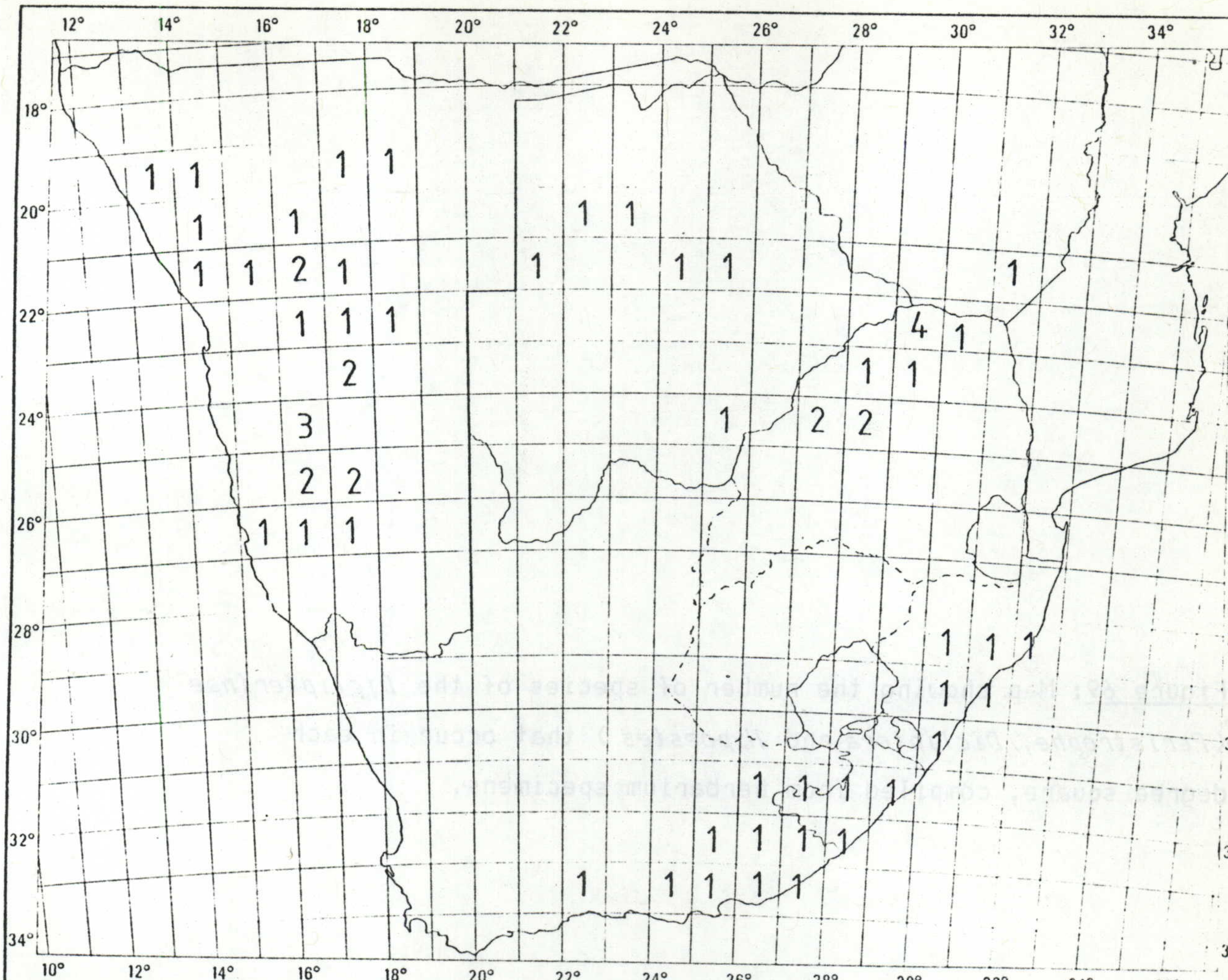


Figure 67: Map showing the number of species of *Peristrophe* that occur in each degree square, compiled from herbarium specimens.

Figure 68: Map showing the number of species of *Dicliptera* that occur in each degree square, compiled from herbarium specimens.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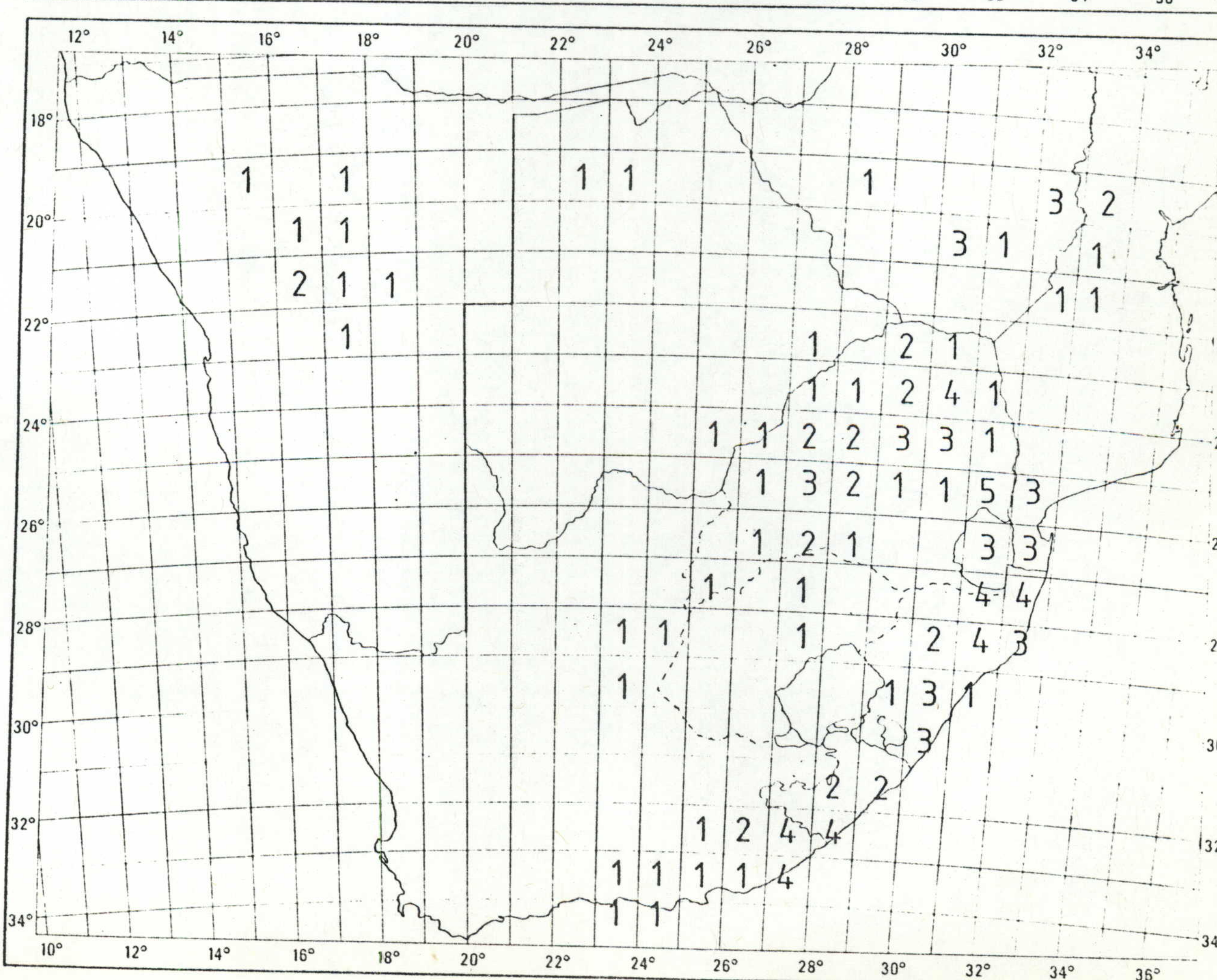
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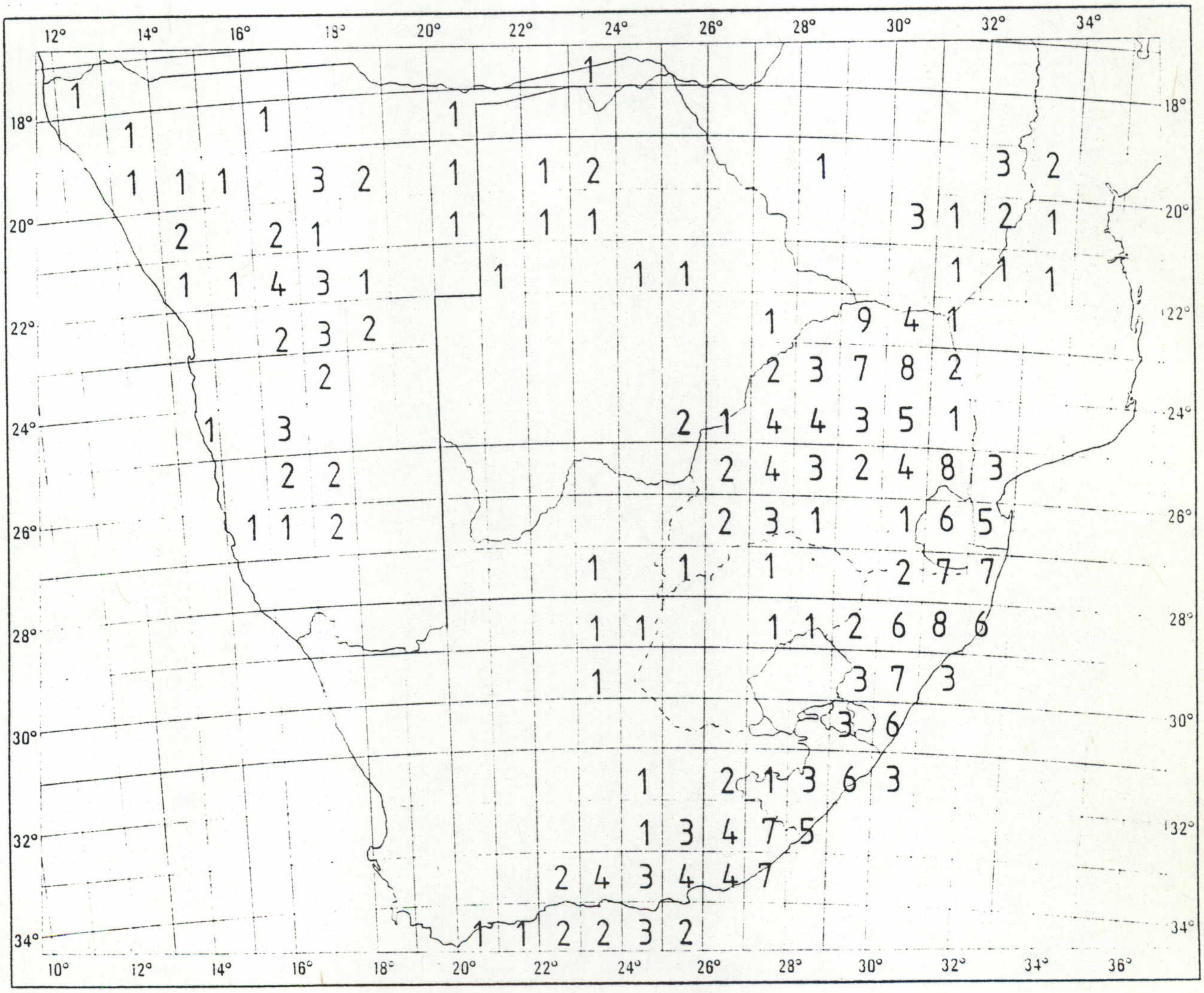
Figure 69: Map showing the number of species of the *Diclipterinae* (*Peristrophe, Dicliptera* and *Hypoestes*) that occur in each degree square, compiled from herbarium specimens.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species of the Diclipterinae. Figures 70 and 71 show inferred distributions for the species of *Peristrophe* and *Dicliptera*, and highlight the vicarious taxa.

Discussion

Some of the southern African Acanthaceae have interesting affinities with plants in other areas. *D. zeylanica* has an Afromontane distribution in southern Africa and also occurs on the Indian Penuinsula, Ceylon and Sarawak. *D. heterostegia* is very closely related to or possibly conspecific with *D. burmanni* Nees (from India, China and Timor), *D. ciliaris* Juss. (from Guinea, Brazil, Madagascar and the Comores), *D. glabra* Decaisne (from Timor) and *D. javanica* Nees (from Java). *Justicia hyssopifolia* L. occurs at East London and on the Canary Islands (Immelman, pers. com.). The genus *Dicliptera* occurs in America, Africa, Asia and Australia and *Peristrophe* occurs in Africa, Asia and Australia. These distribution patterns suggest that the genera and possibly even the more primitive species (e.g. *D. zeylanica*) of the Diclipterinae and Justiciinae must have evolved before these land masses were separated by plate tectonics. This separation occurred in the Cretaceous period. The movements of vegetation that have since occurred through Africa have affected the distribution of species, and has possibly lead to speciation of some of the vicarious taxa. Another factor that has been of fundamental importance to the present distribution and migration of the Acanthaceae, is their mode of seed dispersal. The capsules are explosively dehiscent, and may shoot seeds up to 4 m from the plants. While this may be very effective for seed distribution within a population, it is not nearly as effective for long distance dispersal as is dispersal by wind, water and animals.

Species of *Peristrophe* and *Dicliptera* in southern Africa have distributions that can be categorised into a number of groups, under which they are discussed.

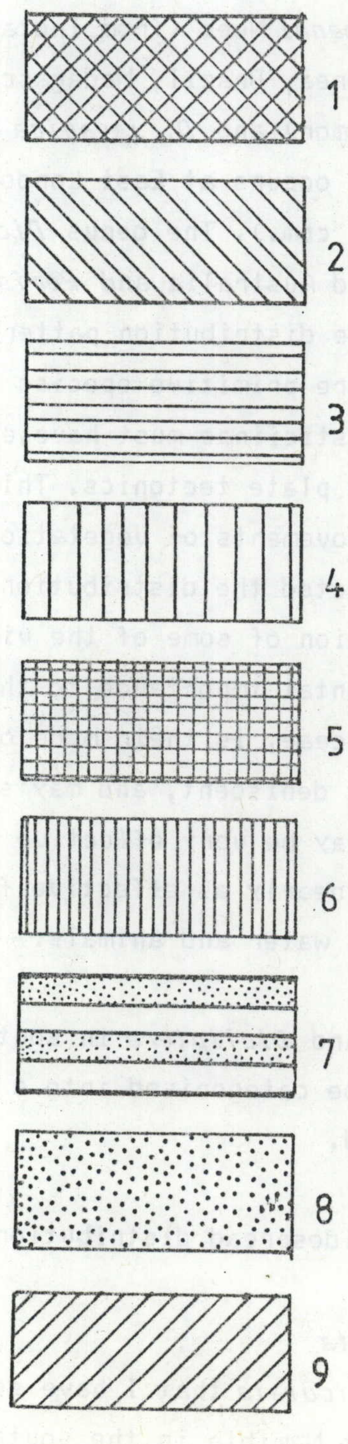
Group 1: Species with widespread distributions

1) The Arid Corridor

a) *Peristrophe paniculata*

The specimens of *P. paniculata* that I have seen, occur in a diagonal band across Africa, from Namibia in the southwest to Kenya in the

Figure 70: Inferred distribution of species of *Peristrophe* that are endemic to southern Africa, compiled from herbarium specimens, Key as below, taxa as follows: 1) *P. sp. 1* ssp. *1*, 2) *P. hereroensis*, 3) *P. grandibracteata*, 4) *P. sp. 1* ssp. *2*, 5) *P. cliffordii*, 6) *P. gillilandiorum*, 7) *P. kotschyana*, 8) *P. transvaalensis* and 9) *P. cernua*.



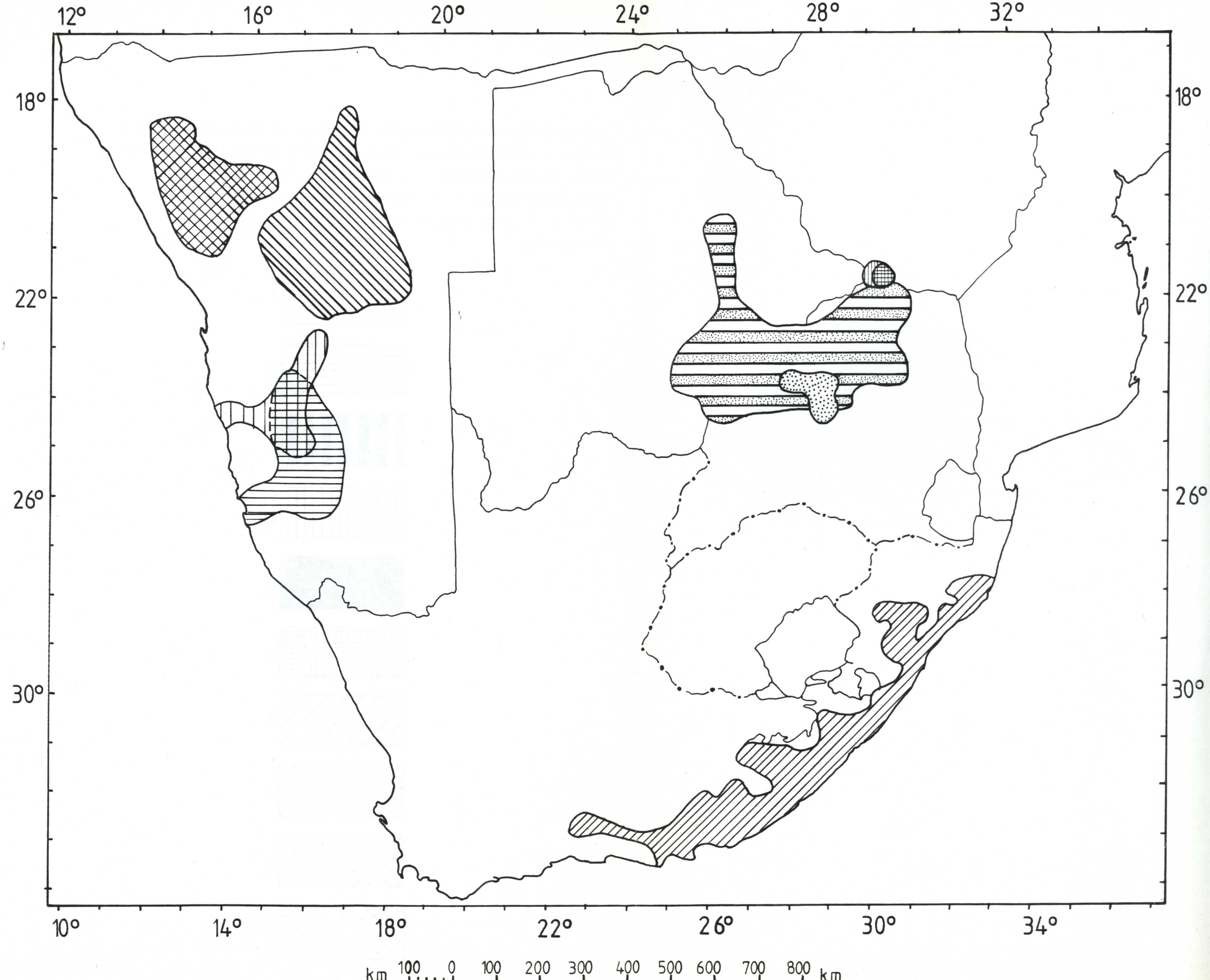

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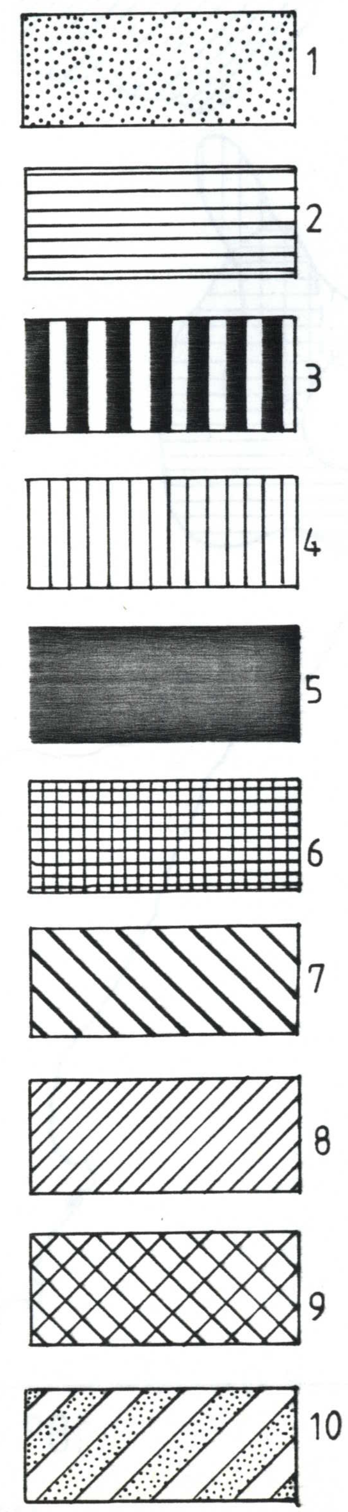
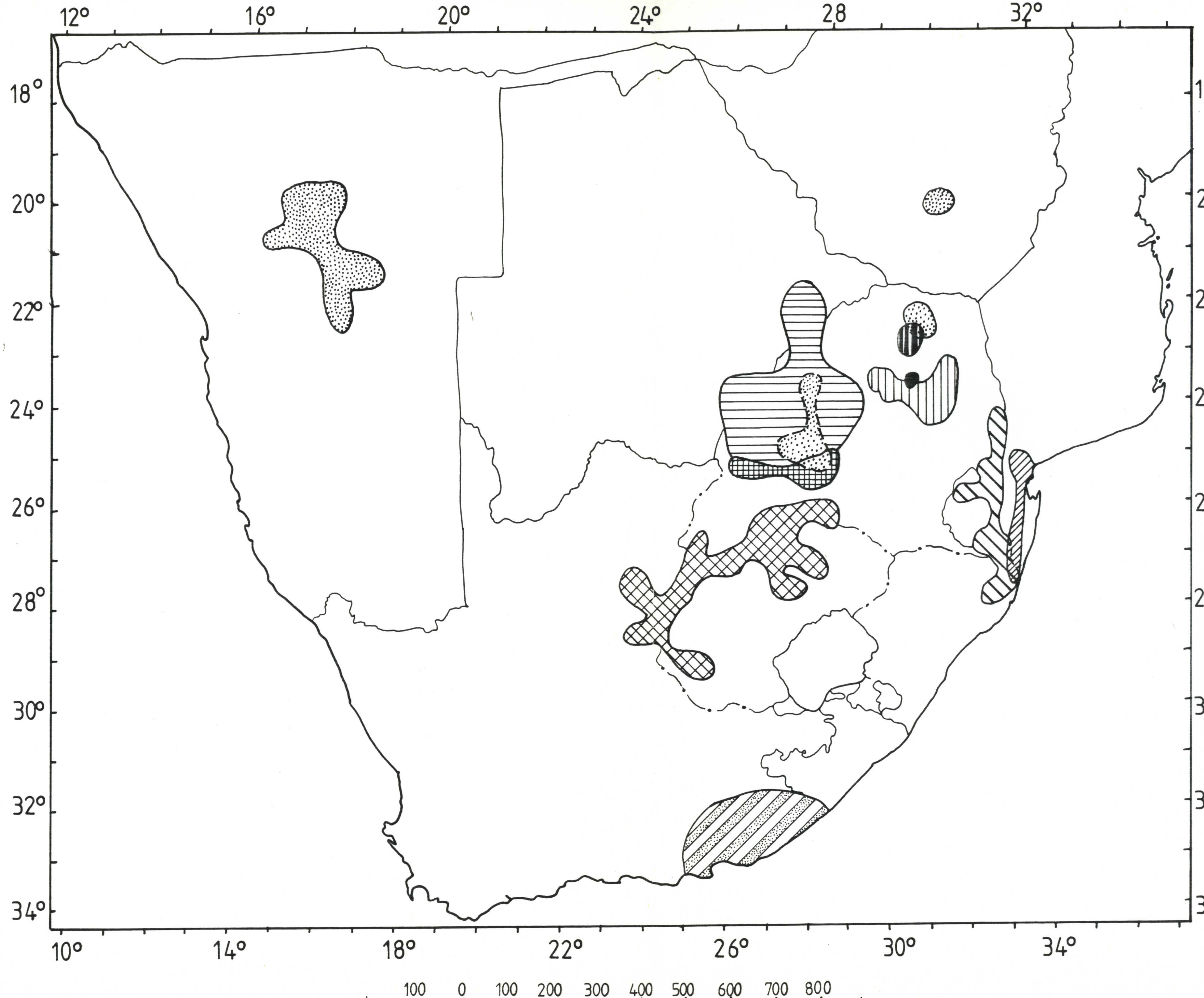
Figure 71: Inferred distribution of species of *Dicliptera* that are endemic to southern Africa, compiled from herbarium specimens, Key as below, taxa as follows: 1) *D. eenii*, 2) *D. minor* ssp. *minor*, 3) *D. minor* ssp. *1*, 4) *D. fruticosa*, 5) *D. sp. 4*, 6) *D. sp. 2*, 7) *D. divaricata*, 8) *D. quintasii*, 9) *D. sp. 3*, 10) *D. capensis*.

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northeast, and a specimen that was collected north of 12 °N. Except for a single specimen, *Codd 7549*, this distribution corresponds to that of the arid corridor (unshaded area in fig. 44). This species is the only annual in the genus *Peristrophe* in southern Africa and the only southern African species of *Peristrophe* that has widespread distribution in arid areas. This correlation suggests that the annual habit in this genus may be an adaptation to this habitat.

b) *Dicliptera spinulosa*

D. spinulosa has a distribution pattern very similar to that of *P. paniculata*, i.e. it occurs in the arid corridor (fig. 66). In this case, however, two collections have been made outside of the arid corridor, and I have seen no collections from the northern portion of this arid area. Like *P. paniculata*, this species is the only annual in its genus in southern Africa, and the only species in its genus that has this distribution. The correlation between habit and habitat may be significant.

c) *Dicliptera sp. 5*

D. sp. 5 is the third species that occurs in the arid corridor (fig. 65). Unlike the other two species, it is not annual but perennial, and unlike them is always associated with damper areas within the arid corridor (Table 34).

2) Afromontane Distributions

White (1978) regards the flora of the lower slopes of the African mountains to be a distinct phytochorion. His hypothesis is, however, based mainly on the forest species. While many forest species have tropical affinities and so have an archipelago-like distribution on the mountain slopes of eastern Africa, Hilliard (1978) has shown that in the Compositae in southern Africa, species on the mountain slopes of Natal have greater affinities with the flora of the surrounding areas than with other Afromontane areas. Thus, on the basis of the evidence of the Compositae, it is inappropriate to consider the Afromontane flora a phytochorion recognised at the level of a region. The Acanthaceae to which I refer in this discussion are forest species, and so occur in the forests of the Afromontane area. I personally do not have sufficient experience to make a decision on this point and thus refer to Afromontane

Table 34: Habitat of *D. sp. 5.*

Collector(s)	Number	Habitat notes
Biegel, Muller & Gibbs Russel	4978	in riverine woodland
Eyles	3139	Hunyani River, in alluvium
Maguire	62	near river banks
Chase	2310	in shade of trees near river
Story	4752	Banks of Okavango
Story	4767	under tall riverine bush
Smith	692	Moshupatsila Island
Jacobsen	3951	Hunyani River
Robinson	2206	shady riverside thicket
Abel	82	riverine woods
Sayer	1228	in river channel
Mutimushi	340	dried up river bank

distributions and not to an Afromontane phytochorion.

a) *Dicliptera zeylanica*

D. zeylanica occurs in Asia as well as in Africa, but in Africa has not been collected north of the Chimanimani Mountains in Zimbabwe. It is striking to see that within southern Africa, *D. zeylanica* follows an almost classic Afromontane distribution pattern (c.f. fig. 50 with fig. 1 in White, 1978). *D. zeylanica* occurs in the transition zones as well as the Afromontane regions, and has not been recorded from the eastern Cape, where there is a disjunction in the Afromontane distribution suggested by White (1978).

b) *Dicliptera clinopodia*

D. clinopodia occurs in two forms in southern Africa (chapter 4). The western form has narrow secondary bracts and follows an Afromontane distribution. Unlike *D. zeylanica*, however, it does not occur in the Knysna forest in the south. Form B of *D. clinopodia* has a more easterly distribution, and appears to be associated with the flora of the Indian Ocean Coastal Belt. Axelrod & Raven (1978) have suggested that the Afromontane vegetation moved southwards between the late Cretaceous or early Paleocene and the present. It seems possible that early on in this migration, a coastal population of *D. clinopodia*, which had migrated to the coast in the Lowland Rainforest of the Oligomiocene, may have become isolated from the population that was migrating southwards along the mountains. The coastal population must have developed the unusually broad secondary bracts (a character unique among the southern African members of the genus) while it was isolated. When the populations moved as far south as the present position of Swaziland, they were able to make contact once more and hybridise. Hybridisation has probably happened more freqently as they moved further south, so that by the time they reached their present southern limit near East London, the two forms were virtually indistinguishable (fig. 12, chapter 4).

3) Indian Ocean Coastal Belt

Dicliptera heterostegia is a species that occurs along the eastern coast in southern Africa and must be part of the phytochorion of the Indian Ocean coastal belt. Further north, in the Transvaal and Zimbabwe, *D. heterostegia* is found further inland, which is unexpected. The following interpretations are possible:

i) *D. heterostegia* was originally associated with the eastern coast of Africa, but during the Oligo-miocene, some plants were able to migrate to the Afromontane areas, and these have since migrated southwards with that flora and are at present located in the Transvaal and in Zimbabwe.
ii) *D. heterostegia* was originally associated with the Afromontane flora and during the Oligo-miocene was able to migrate from this area to the Indian Ocean Coastal Belt. During the southwards migration, *D. heterostegia* has become better adapted to the ecological pressures of the Indian Ocean coastal belt and so has become more successful in that phytochorion and less frequent in the Afromontane areas.
iii) *D. heterostegia* was originally associated with the Indian Ocean coastal belt and the present population has mainly similar associations. Some small satellite populations have, however, migrated inland in lowlying areas, where they now occur.
The distribution in southern Africa supports the latter possibility, as the inland populations of *D. heterostegia* are limited to low-lying areas. As this may not be true of the situation further north, it is impossible to be certain of this interpretation.

Group 2 Species that display vicarianism on an African scale.
1) *Peristrophe cernua*
In southern Africa, *P. cernua* has a coastal distribution and does not occur north of 27 °S. A species of *Peristrophe*, presently known as *Dicliptera hensii* Lindau, is almost identical to *P. cernua* and occurs in the Congo. These two species must be closely related vicariants.

2) *Peristrophe kotschyana*
The type of *P. kotschyana* came from Ethiopia (Abyssinia) and it seems that there are no populations of this species between Ethiopia and Malawi. In Malawi, there is a very closely related species, known as *Dicliptera aculeata* C.B. Clarke. There is another disjunction between this population of *Peristrophe* [= *D. aculeata*] and the southern African material that I refer to by the name *P. kotschyana*. These three populations have discreet distributions, but without examining living material of these three taxa, I would not like to decide whether or not they should be recognised formally, nor at which level they should be recognised. These three populations are none-the-less vicariant, and it seems that the arid corridor may be a barrier to their distribution.

3) *Peristrophe grandibracteata s.l.*

Three species of *Peristrophe* occur in Namibia. They are morphologically so different from the other species, that they are to be proposed as a separate Section of the genus. Other plants that occur in Namibia have vicariant taxa in the northeastern corner of Africa (Werger, 1978). Because of these other arid disjunctions I feel it is likely that there are other species of *Peristrophe* that belong to this section in north-eastern Africa.

Group 3 Taxa that are vicarious in southern Africa

1) *Dicliptera minor* and *Dicliptera divaricata*

D. minor and *D. divaricata* are very similar species, differing only slightly in habit and in the colour of their flowers. *D. minor* occurs in the western Transvaal, south-eastern Botswana and northern Transvaal, while *D. divaricata* occurs along the Lebombo Mountains in the eastern Transvaal, Mozambique, Swaziland and Natal. *D. minor* is associated with Fersialtic sands and loams, with a January mean daily temperature between 22 and 24 °C and with areas that are frosted less frequently than once a year. *D. divaricata*, on the other hand, has a distribution that correlates very strongly with the distribution of Montmorrilionitic clays and rocks of the Josini and Letaba formations of the Lebombo group of rocks.

2) *Peristrophe kotschyana* and *Peristrophe cernua*

Although good species, *P. kotschyana* and *P. cernua* are very similar and closely related. *P. kotschyana* occurs in southwestern Botswana and north and western Transvaal. Its distribution correlates well with areas that are frosted less than once a year and especially with those areas that have a mean annual temperature between 18 and 20 (sometimes 22) °C. *P. cernua* occurs along the eastern coast of southern Africa, from Zululand south to the eastern Cape. This distribution correlates very closely with the distribution of valley bushveld (Acocks, 1975) and with areas that have an average annual water deficiency less than 100 mm and in which frost occurs less often than once a year.

Because the Acanthaceae is a tropical family, it is limited to low and medium altitudes, where temperatures are warmer. Between the Palaeocene and the present, the savannah-woodland (in which *P. cernua, P. kotschyana, D. minor* and *D. divaricata* occur) moved southeastwards (Axelrod & Raven, 1978). In Zimbabwe and the Transvaal, there are gaps in the escarpment in the Limpopo and Crocodile River valleys. During the southeastward migration of the parent populations that have given rise to the two vicariant pairs listed above, a part of the population of each species must have been trapped against the mountains that form the escarpment, while another part of each population passed through one of the gaps in the mountains and down the eastern coast of southern Africa. It seems that the continuing southeastward migration of the climatic conditions that caused the migration of the savannah-woodland has now caused the two populations of each parent species to move southward, so that they have become isolated by the closing of their migration south of the gaps in the mountains. They have since moved further south to their present positions.

3) *Dicliptera sp. 2* and *Dicliptera sp. 3*

D. sp. 2 and *D. sp. 3* are two closely related and morphologically similar species that occur in southern Africa. *D. sp. 2* occurs in the Magaliesberg mountain range, which represents the Magaliesberg extension of the Afromontane distribution (White, 1978). The distribution of this species correlates well with the area in the Transvaal that has at least 270 frost free days a year and a mean annual precipitation of about 600 mm. The distribution also correlates well with that of the Bankenveld and of the Chuniespoort and Pretoria groups of the Transvaal Geological Sequence. *D. sp. 3* occurs to the southwest of *D. sp. 2.* and grows in the southern tail of the Sudano-Zambezian phytochorion and is the only species of the Diclipterinae in southern Africa that occurs in this area (*c.f.* fig. 60 and fig. 69). The distribution of *D. sp. 3* correlates well with areas that have a July mean daily temperature between 8 and 10 °C, a mean annual temperature close to 16 °C, a July mean daily minimum temperature between 0 and 2,5 °C and an annual water deficiency between 200 and 399 mm. Except for the specimen collected from the eastern Cape, the species occurs along the banks of the Orange, Vaal and Harts Rivers and their tributaries. It seems that *D. sp. 2* has been derived by the isolation of the population of *D. clinopodia* that migrated onto the Magaliesberg extension of the Afromontane area. It is possible that some small degree of hybridisation with *D. eenii* may have occurred, because *D. sp. 2* is intermediate between *D. eenii* and *D. clinopodia* in many characters. *D. sp. 3* may have been derived from a population of *D. sp. 2* that has migrated from the Magaliesberg where *D. sp. 2* occurs, down one of the river valleys into the Vaal river valley, from where it has become established in its present habitat. This migration must have occurred when there was a greater canopy cover than there is in these areas at present.

4) The two subspecies of *Dicliptera minor*

The two subspecies of *D. minor* show a disjunct distribution. The distribution of both subspecies of *D. minor* is very strongly correlated with that of mixed bushveld (Acocks, 1975) and apparently not occurring in the adjacent arid sweet bushveld (Acocks, 1975). The area of mixed bushveld that links the areas in which the two subspecies of *D. minor* grow, is in a region with a higher occurrence of frost, and this is very likely the factor that causes the disjunction in distribution and so prevents the interbreeding of the two subspecies.

5) *Peristrophe grandibracteata* and *Peristrophe hereroensis*

P. grandibracteata and *P. hereroensis* are two closely related species that occur in Namibia. From Table 33, it can be seen that the factors affecting the distributions of these species are very similar, except that the conditions under which *P. hereroensis* grows are slightly ameliorated with respect to those under which *P. grandibracteata* grows. *P. grandibracteata* occurs in the Karoo-Namib phytochorion and in a region with a mean annual rainfall less than 200 mm, while *P. hereroensis* occurs in the Sudano-Zambezian phytochorion in areas with a mean annual rainfall between 200 and 600 mm. *P. grandibracteata* is in the area that has no months with a rainfall over 50 mm, while the area in which *P. hereroensis* occurs has more than 50 mm of rain from December or January through to March. *P. grandibracteata* is unique in the genus as it has a dense indumentum of hairs on the stem. It is possible that these hairs provide protection against frost, radiation or heat. It is also possible that they may be some kind of adaptation for intercepting water from fog.

6) The two subspecies of *Peristrophe sp. 1*

P. sp. 1 occurs in Namibia, but has two geographically separated subspecies that are morphologically distinct. The two subspecies appear to be growing under very similar conditions, except that the area in which *P. sp. 1* ssp. *2* has a rather lower annual rainfall, and this may be the factor that separates the two subspecies.

Group 4 Relict Taxa

D. eenii has a scattered disjunct distribution (fig. 62) and the areas in which it occurs are in different phytochoriological regions, have different means of annual rainfall, different degrees of frosting and different annual water deficiencies. In the Oligomiocene, all four areas in which *D. eenii* now occurs were covered by 'savanna-woodland and thorn scrub' (Axelrod & Raven, 1978), but during the late Miocene, and early Pliocene this type of vegetation migrated eastwards, so that it no longer occurs in Namibia. It is possible that the Waterberg (in Namibia) has provided enclaves in which the species has survived as relicts.

Group 5 Endemic Taxa

1) *Dicliptera fruticosa*

The distribution of *D. fruticosa* does not overlap with that of any other species of *Dicliptera* in southern Africa (fig. 71). It grows in areas that do not have frost annually, that have mixed bushveld and have dolomite and magnesite rocks of the Pretoria Group. *D. fruticosa* is closely related to *D. eenii* and it seems that it may have evolved from a population of the latter species that was isolated in areas with the geology described above and have become specialised for growth on those rock types. If this was the case, the daughter species is now more successful than its parent species in this habitat.

2) *Peristrophe transvaalensis*

P. transvaalensis is a rare species that occurs in the central and western Transvaal. It occurs in a range of similar types of bushveld and on the Kransberg and Nylstroom subgroups of the Waterberg group of rocks. It seems that a combination of veld type and geology may determine the distribution of this species.

3) *Peristrophe gillilandiorum*

P. gillilandiorum grows in a very small area in the Limpopo River valley. This area is unique as it has a combinaton of alluvial rocks, Mopani veld, a low frequency of frosting, a high mean annual temperature, a low mean annual rainfall and a high annual water deficiency. Adaptation to this suite of conditions may have resulted in the evolution of this species.

4) *Peristrophe cliffordii*

P. cliffordii grows in the same area as *P. gillilandiorum*, but where *P. gillilandiorum* occurs on clays and sand stone ridges, *P. cliffordii* occurs only on Kalahari sand. *P. cliffordii* has not yet been found north of the Limpopo River, but it is likely to occur there (Drummond, pers. comm.).

5) *Dicliptera sp. 4*

D. sp. 4 occurs on the Wolkberg in the northeastern Transvaal, where it grows amongst dolomite of the Malmai subgroup of the Chunniespoort group of rocks and where it is very localised. This particular area has a higher annual water deficiency than other areas in the northeastern mountain sourveld, and it seems that the combination of these factors has provided the niche in which this species has evolved.

6) *Dicliptera quintasii*

D. quintasii occurs in the Tongaland-Pondoland Regional Mosaic of the Indian Ocean Coastal Belt phytochorion. It occurs in areas that have low altitudes, a low range in mean annual temperature and little frost. *D. quintasii* occurs in sand forests on alluvial rock deposits, which is a very unusual habitat for *D. clinopodia*, the most closely related species.

7) *Dicliptera sp. 1*

D. sp. 1 is a rare species that occurs near Kosi Bay and near Bandula in Mozambique. The present known distribution is disjunct, but the two localities are alike in that they have a January mean daily temperature between 24 and 26 °C, a July mean daily temperature between 18 and 20 °C, a mean annual precipitation between 800 and 1 000 mm, an average annual water deficit between 200 and 399 mm and an annual range in temperature that is less than 8 °C. Both areas experience no frost and are below 500 m in altitude. The two known localities of this species are linked by a narrow band that has the parameters described above and it is likely that other populations of this species occur along this strip.

8) *Dicliptera capensis*

D. capensis occurs in the eastern Cape, in the gap in the Afromontane distribution. This species occurs between the endpoints of distribution of *D. sp.3, D. clinopodia* and *D. heterostegia* as well as in the gap between two populations of *D. zeylanica* (fig. 50). The eastern Cape has a very high species diversity and Gibbs Russell & Robinson (1981) have suggested that this large number of species is not attributable to the eastern Cape being a centre of endemism, but rather to the number of phytochoria that meet in the eastern Cape. Figure 68 shows that there is a relatively large number of species of *Dicliptera* in each degree square near East London and this concentration of species is attributable to the reason suggested by Gibbs Russell & Robinson (1981). Their view is applicable to the Acanthaceae as a whole, as there is a low proportion of endemics in the eastern Cape, but possibly will not apply equally to all the genera. In the eastern Cape, the unusual, dynamic nature of the vegetation (Gibbs Russell & Robinson, 1981) might provide a habitat in which hybrid species could become established. *D. capensis* seems to be of hybrid origin, and may have been derived by the hybridisation of two species from different phytochoria that became sympatric in the eastern Cape. Thus, *D. capensis* may have a different type of origin from that of other species of the Acanthaceae that are endemic to the eastern Cape. There are large disjunctions in the distribution of some genera that have endemic species in the eastern Cape. *Asystasia natalensis* C.B. Clarke, the species to which *Asystasia stenosiphon* C.B. Clarke, is most closely related occurs in Zululand, as does *Ecbolium amplexicaule*, the species of *Ecbolium* that is the nearest neighbour to *Ecbolium flanaganii* C.B. Clarke (of the eastern Cape). *Metarungia longistrobus*, the geographically closest species to *Metarungia galpinii* (Baden) Baden (of the eastern Cape), occurs in northern Swaziland and southeastern Transvaal. Thus, at least these three species are true endemics of the eastern Cape, so that there is a small degree of endemism in the Acanthaceae in the eastern Cape.

9) *Dicliptera clinopodia* var. *1*

D. clinopodia var. *1* occurs on sea-facing grassy slopes in the Transkei. Most plants of the typical variety of *D. clinopodia* grow in water courses or at forest edges, so that the habitat of *D. clinopodia* var. *1* is unusual for the species. This variety represents some of the few plants of the species that grow on soil formed from alluvium and the specialisation for this unusual habitat and soil type may have lead to the differentiation of these plants so that they can be recognised as a separate variety.

Conclusion

The species of *Peristrophe* and *Dicliptera* that occur in southern Africa have distribution patterns that fit into a number of categories. These categories include those that are widely distributed in Africa, those that have vicarious distributions in Africa, those that have vicarious distributions in southern Africa and those that are endemic to southern Africa. Study of the factors affecting the distribution of the species in southern Africa can provide clues to their evolution and relationships.

CHAPTER 12
SOME BIOLOGICAL COMMENTS

Introduction

The morphology and micromorphology of the Acanthaceae must have biological functions in terms of the interrelationships of plants, populations, species and survival. Some very significant work has been done in this area of study, in particular on *Ruellia* by Long (1961, 1964, 1971 & 1975) in America. MacDade (1984) and MacDade and Kinsman (1980) have also contributed significant work on the biology of the genus *Aphelandra*. So far, little work has been published on the biological significance of structures in the southern African Acanthaceae. Meyer (1961) has made a number of pertinent observations about the biology of some of the Namibian Acanthaceae and Bremekamp (1926) has made contributions to the biological relevance of capsule structure and methods of opening. Cadman and Getliffe Norris will shortly publish a significant study on floral polymorphism in *Pseuderanthemum subviscosum*, which will be one of the first of its kind conducted on southern African Acanthaceae.

In this chapter, I make observations and hypothesise about the biological significance of some of the features of the Diclipterinae. Future detailed study of these aspects will be rewarding.

Observations and Discussion

Factors that affect breeding between the Diclipterinae and plants in other tribes and subtribes

1) Shape of corolla

The southern African Diclipterinae are unusual amongst the Acanthaceae, as they have corollas with tubes approximately as long as the lips. The lips of species in this subtribe are relatively narrower than those of plants in other groups. This morphological distinction, I believe, is sufficient to allow pollinators to discriminate between members of the Diclipterinae and those of other groups. Faegri & van der Pijl (1966) designed a system of classification of blossoms and the Diclipterinae have corollas that belong to the trumpet subtype of the tube type of blossoms. Although shared by the genera *Aulojusticia* Lindau, *Siphonoglossa* and *Rhinacanthus*, this type of blossom is unusual amongst the Justicieae, which more commonly have blossoms of the gullet type.

2) Colour of corolla

The corollas of the members of the Diclipterinae are in the white, pink, purple and magenta range. Although these colours are present in the other tribes and subtribes, they do separate members of the Diclipterinae from species such as *Justicia flava* (Vahl) Vahl and *Justicia campylostemon*, which have yellow flowers, and from *Metarungia galpinii* and *Anisotes rogersii*, which have red or reddish brown flowers. In the Diclipterinae, the palate and honey guides are on the lip in the upper position, while in all the other species of the family in southern Africa the palate is on the lip in the lower position. This is another feature of the colouration that distinguishes the Diclipterinae from other groups. The positioning of this obvious patch of colour would allow pollinators to distinguish between members of the Diclipterinae and all other members of the Acanthaceae.

3) Resupination of the corolla

The corollas of all members of the Diclipterinae are resupinate through 180 degrees. This may have three important effects on pollination.

a) Resupination causes the honey guides on the palate of members of the Diclipterinae to be on the lip in the upper position. As described above, this allows pollinators to discriminate between this subtribe and other members of the family.

b) Resupination of the corolla can affect the access to nectar in two possible ways. Firstly, resupination causes a narrowing of the tube and thus prevents insects that have short probosces from having access to nectar. Alternatively, the narrowing of the tube caused by resupination may cause the nectar to move (by capillarity) towards the mouth of the corolla tube, where it is more accessible to insects with shorter probosces. Both of these functions could allow the evolution of specialised interactions with pollinators and hence facilitate the evolution of new species.

c) Resupination has a very fundamental role in separating the Diclipterinae from all the Justicieae as well as from all the other southern African Acanthaceae. In all non-resupinate members of the family, the blossoms are nototribic (i.e. place the pollen on the dorsal surface of pollinators), while in the Diclipterinae, the blossoms are sternotribic. Thus, there is a spatial separation of pollen of the Diclipterinae and pollen of other Acanthaceae on the pollinator. This spatial separation makes hybridisation between these groups highly unlikely and may have been responsible for the evolution of the subtribe, Diclipterinae.

4) Pollen morphology

Within the Acanthaceae there is a range in the morphology of pollen and it is possible that physical parameters might prevent pollen of some groups from germinating on the stigmas of others. The pollen of *Ruellia* and *Barleria* is larger than that of other groups and has very large, deep reticulations. The stigmas of these genera are papillate and thus match the morphology of the pollen. It is possible, then, that the pollen of *Ruellia* and *Barleria* would not germinate on the smoother surfaces of the stigmas of the Diclipterinae, because the stigma would be unable to make contact with the pores of the pollen, which are between the ridges. This would serve to separate these groups.

Factors that affect breeding between plants in different genera of the Diclipterinae.

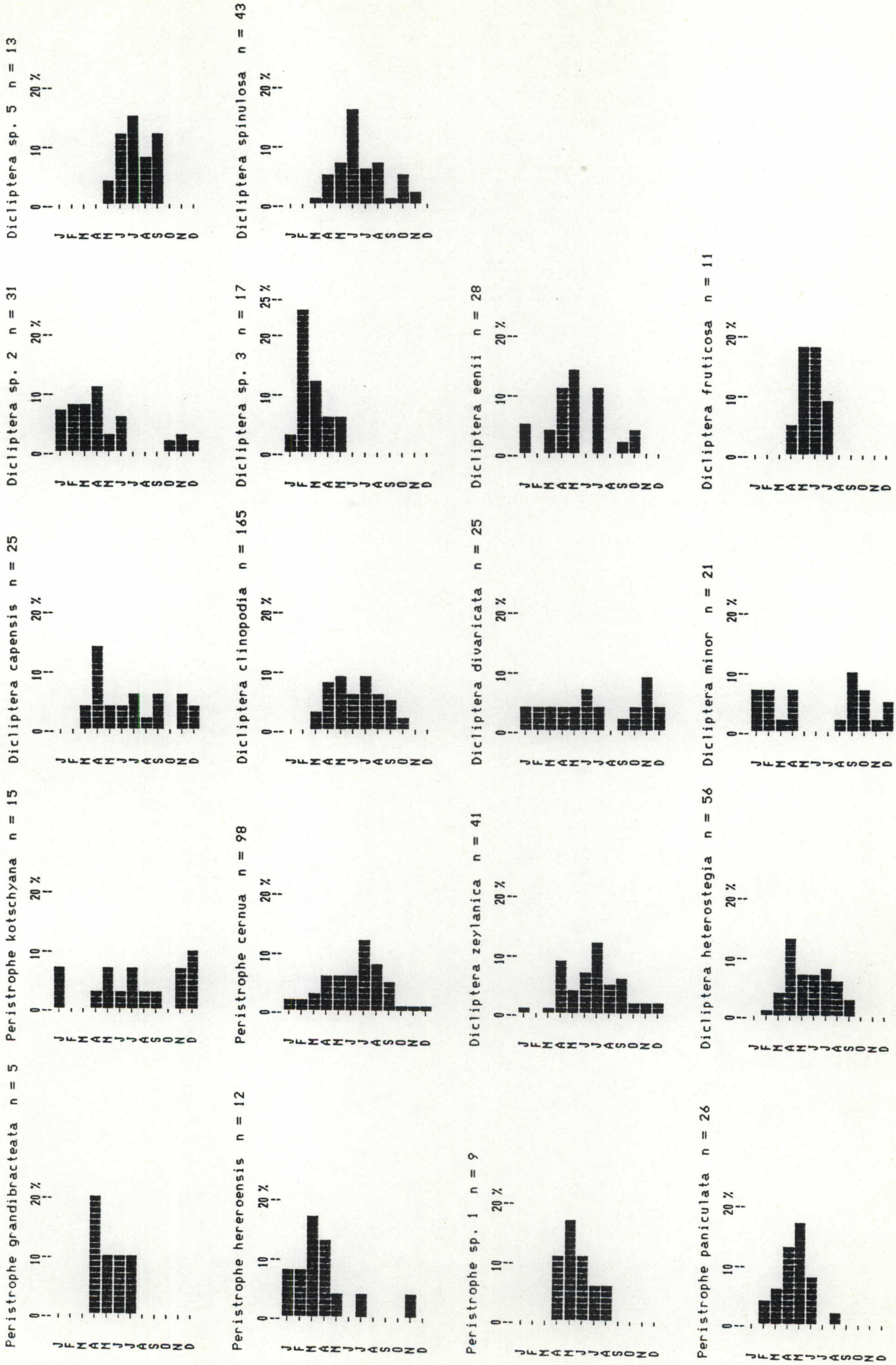
I am not aware of any physical or morphological character that would enable pollinators to distinguish all the species of one genus in the Diclipterinae from all the species of any of the other genera. All three genera have a similar range in colour and size of the corolla and in the colour and size of the tertiary bracts. It is, however, possible for pollinators to distinguish between species of different genera that are sympatric. *Dicliptera zeylanica* and *Hypoestes triflora* grow sympatrically at The Downs and in the Magoebaskloof forests in the Transvaal as well as near The Cascades in Pietermaritzburg, Natal. In all three localities, *H. triflora* has honey guides that are composed of larger darker blotches, which are far more obvious than those of *D. zeylanica*, hence making it possible for pollinators to distinguish between these species. In Natal, *D. clinopodia* and *P. cernua* frequently occur sympatrically, but the former can be readily distinguished by its larger, more obvious tertiary bracts that are often white and purple.

Factors that affect breeding between species.

1) Flowering Time

Figure 72 presents the flowering times of southern African species of *Peristrophe* and *Dicliptera*. The southern African species of *Peristrophe* can be categorised on the basis of their flowering time. Some species flower continuously throughout the year (e.g. *P. kotschyana* and *P. transvaalensis*), some flower in late summer (e.g. *P. hereroensis*), some in autumn (e.g. *P. grandibracteata, P. sp. 1* and *P. paniculata*) and some in winter (e.g. *P. cernua, P. cliffordii* and *P. gillilandiorum*). *P. grandibracteata* has a flowering time different from that of *P. hereroensis*, the species to which it is most closely related. This provides a biological separation of these species. The flowering time of *P. paniculata* is more clearly defined than that of most other species and, as described in chapter 2, provided clues that led to the hypothesis that *P. paniculata* was an annual. The hypothesis was supported by growing plants for three successive generations and finding all to be annual. In cultivation, *P. kotschyana* flowers continuously and *P. cernua* is winter flowering, as these species are in nature.

The southern African species of *Dicliptera* can also be categorised on the basis of flowering periods. *D. capensis* flowers continuously, while *D. eenii* flowers sporadically, although mainly in winter. *D. zeylanica, D. heterostegia, D. clinopodia, D. quintasii, D. fruticosa, D. sp. 4, D. sp. 5* and *D. spinulosa* flower in winter and *D. minor, D. sp. 2* and *D. sp. 3* are summer flowering. *D. spinulosa*, which is an annual species, flowers for a longer period than does *P. paniculata*. *D. eenii* occurs in isolated populations (chapter 11) and appears to flower sporadically. At first I thought there may have been a different flowerng period for each isolated population. This would have resulted in what appears to be the sporadic flowering represented in fig. 72. Although the number of specimens from each locality is small, I compared the flowering times of the different localities and found that each locality had a similarly sporadic flowering period. Although they overlap, the flowering times of *D. clinopodia, D. sp. 2* and *D. sp. 3* have different peaks of flowering. Thus, although the possibility of hybridisation is not totally reduced, the probability of interbreeding is lower than it would be if all three species flowered at the same time.


Dicliptera sp. 5 n = 13
Dicliptera spinulosa n = 43
Dicliptera sp. 2 n = 31
Dicliptera sp. 3 n = 17
Dicliptera eenii n = 28
Dicliptera fruticosa n = 11
Dicliptera capensis n = 25
Dicliptera clinopodia n = 165
Dicliptera divaricata n = 25
Dicliptera minor n = 21
Peristrophe kotschyana n = 15
Peristrophe cernua n = 98
Dicliptera zeylanica n = 41
Dicliptera heterostegia n = 56
Peristrophe grandibracteata n = 5
Peristrophe hereroensis n = 12
Peristrophe sp. 1 n = 9
Peristrophe paniculata n = 26
0
10
20 %
25 %
J F M A M J J A S O N D

This biological separation of the species supports the view that was based on morphological characters.

2) Colour of flower

D. sp. 4 and *D. fruticosa* have flowers that are morphologically similar in size and shape, but *D. sp. 4* has white flowers and *D. fruticosa* has flowers that are cobalt violet. If these species became sympatric, pollinators would be able to distinguish between them on the basis of flower colour.

3) Colour of bracts

D. sp. 2 and *D. clinopodia* are closely related species. *D. clinopodia* has tertiary bracts that have a marked contrast of white 'windows' at their bases and purple apices. The bracts of *D. sp. 2* have 'windows' that are not as noticeable and have green apices. If these species became sympatric, pollinators would probably be able to distinguish between them on the basis of the degree of contrast of the tertiary bracts.

4) Size of flower

D. heterostegia and *D. zeylanica* occur sympatrically between the Umtamvuna River and East London. The flowers of *D. zeylanica* are larger than those of *D. heterostegia* (figs. 20 - 24, chapter 5) and have longer corolla tubes (fig. 25, chapter 5). These differences will separate the species in two ways. Firstly, pollinators will be able to distinguish between the two species because of the differences in size and secondly, the different lengths of the tube will partition the pollinators on the basis of the length of their probosces. Insects with shorter probosces will not be able to obtain nectar from *D. zeylanica*, which has a longer tube, and so will be better rewarded by visiting flowers of *D. heterostegia* more frequently. Pollinators with longer probosces will have less competition for the nectar in the longer tubes of *D. zeylanica* than they would have for the nectar in *D. heterostegia*; if they visit the flowers of *D. zeylanica* more frequently than those of *D. heterostegia*, they will be rewarded by obtaining larger quantities of nectar from each flower. Similar relationships would exist between *H. aristata* and *H. forskaolii*, two species that often grow sympatrically.

Factors that affect breeding relationships within species

1) Geographical isolation

The two subspecies of *P. sp. 1* and the two of *D. minor* are geographically isolated, making interbreeding between members of the two populations impossible. The allopatric subspecies may deviate from one another in certain characters (e.g. *D. minor* ssp. *minor* has magenta flowers and *D. minor* ssp. *1* has white flowers), so that if they become sympatric they will remain separate populations. If, however, the two allopatric subspecies do not differentiate in any way that will affect their pollination, they will become a single population if they once more become sympatric.

2) Habitat preferences

D. clinopodia var. *1* grows in a specialised habitat (chapter 11) in which *D. clinopodia* var. *clinopodia* does not occur. The two varieties are thus spatially separated because they are adapted to separate habitats, and the probability of hybridisation is reduced. The two forms of *Hypoestes forskaolii* that are recognised by Balkwill and Getliffe Norris (1985) occur in different habitats. Form A occurs in arid grasslands and form B in slightly damper and cooler areas, such as in shade in bushveld and in river valleys. Because of habitat separation the incidence of hybridisation between these forms is reduced. Another form of *H. forskaolii* occurs in forests of the northeastern Transvaal. This habitat is unusual for the species and the plants in this habitat have an unusual indumentum on their tertiary bracts. It is possible that this differentiation might eventually lead to speciation.

3) Colour of flowers

The subgroups within some species of the Diclipterinae have different flower colours. *Hypoestes aristata* var. *aristata* has purple flowers, while *H. aristata* var. *alba* Balkwill has white flowers. *D. minor* has one subspecies with magenta flowers and one with white flowers. Presently the two subgroups of these species are allopatric, but if they become sympatric in the future, pollinators would be able to distinguish between the differently coloured flowers.

Factors that affect breeding within populations

1) Flowering time

D. divaricata has a summer flowering time, but it appears that there may be bimodal flowering in at least one population of this species. A flowering specimen was collected from Josini in Zululand in autumn of 1982 and then cultivated in Pietermaritzburg. It flowered again in Autumn of 1983. In spring of 1982, another flowering specimen of this species was collected from the same locality and cultivated. It flowered for a short period, but then stopped flowering until the spring of 1983. In the summer of 1984 - 1985, both plants flowered. This occurrence may have been a stochastic event or may indicate that this population of *D. divaricata* displayed bimodal flowering. It would be interesting to test this, and if it was found to be a real phenomenon, it would be interesting to investigate the effects on the interbreeding of members of that population, and to establish what control mechanisms were operative.

2) Dichogamy

All members of the Diclipterinae are protandrous. This must serve to enhance cross pollination and so will influence breeding between individuals growing in the same population. Interaction of the maturation of stigmas with the morphology of stigmas is another important means by which the sexual parts of the flower are spatially separated. In the Diclipterinae, the style has two filiform branches. The stigmatic surfaces are on the inner surfaces of these branches, so that before the style branches diverge, pollen cannot be deposited onto the stigmatic surfaces. In the Justiciinae, most species have very short style branches, and it seems that they may be receptive on both the inner and outer surfaces of these branches. Thus, the branches of the style cannot shield the stigma in the same way as do those of the Diclipterinae and this function is fulfilled by rugulae in the Justiciinae. The rugula is a channel in the upper lip of the corolla, in which the style is enclosed. Once the anthers have shed their pollen, the style elongates and protrudes from the rugula and so is able to receive pollen. There is an indistinct rugula in the corollas of the Diclipterinae, but it becomes very difficult to see in the corollas that have become resupinate. In the Diclipterinae, the rugula is not functional, as the style is held in position by the stamens, and the stigmatic surfaces are shielded by the style branches. It is difficult to decide whether the indistinct rugula in the Diclipterinae is a relic, or whether its evolution was arrested in this group.

3) Hercogamy

Hercogamy is displayed by many members of the Acanthaceae. In the Diclipterinae, the anthers and stigmas of flowers are separated by the twisting of the filaments, which results in the reflexing of the anthers out of the area in which the receptive stigma is held. In some species of the Diclipterinae, the twisting of the anthers is so effective, that the anthers are eventually held behind the throat.

Factors that affect breeding within individuals

1) Geitonogamy

Although it is known that there are mechanisms that prevent self-pollination in the Acanthaceae, it is not known whether there are mechasnisms that prevent geitonogamy. The probability of the occurrence of geitonogamy could be estimated once it had been established whether self-sterility mechanisms exist in the Acanthaceae.

2) Cleistogamy

Seeds of *P. paniculata* that were ten years old were germinated. Of the ten seeds that were imbibed, two grew and these two plants produced cleistogamous flowers. The plants successfully set seed and the seed was germinated to produce a second generation. The plants of the second generation were germinated in a greenhouse, and began to produce cleistogamous flowers. Some of the plants were planted into a garden, and produced cleistogamous flowers initially, but then began to produce chasmogamous flowers. These plants set and shed seed, and a third generation germinated in the garden; the first flowers produced by this generation were chasmogamous, although the plants produced occasional cleistogamous flowers. An annual that produces cleistogamous flowers after a long delay between generations would have advantages and these observations raise the following interesting questions:

a) Does *P. paniculata* produce two kinds of seeds, one kind that germinates immediately into plants that have chasmogamous flowers and another that has delayed germination and produces plants with cleistogamous flowers ?

b) Do all plants of *P. paniculata* have the facility to produce cleistogamous flowers ?

c) Under what conditions does *P. paniculata* produce cleistogamous flowers ?

d) Were the cleistogamous flowers induced by the conditions in the greenhouse ?

e) Would plants that were germinated and established outside become cleistogamous if they were moved into the greenhouse ?

f) Do cleistogamous flowers occur in wild populations of *P. paniculata* ?

Answers to these questions would provide information relevant to discussion of the breeding within individuals and populations of *P. paniculata*.

Factors that affect the dispersal of populations

1) Seed dispersal

The capsules of the Acanthaceae dehisce explosively and propel the seeds away from the plants. Through personal observations, I estimate that this method of dispersal distributes the seeds up to four metres away from the parent plant. Although this method of dispersal is effective for mixing of the gene pool in small populations, it is ineffective for long distance dispersal, especially if compared with the distance that seeds might be moved if they are dispersed by water, wind or animals. The projectile forces are generated by differential distortion of the cells of the capsule as the capsules dry (Bremekamp, 1926). Similar forces must also be generated in the retinaculum and, in the capsule of *Dicliptera*, in the placenta. Because of the extra forces that can be generated in the capsules of *Dicliptera*, it is expected that capsules of these plants will be able to project their seeds further than will the capsules of other genera. This would be a very interesting aspect to test.

2) Vegetative reproduction

Some species (e.g. *D. zeylanica*) have prostrate stems that grow rapidly and frequently root at the nodes. These stems are effective means of vegetative propagation. This growth habit must also be effective for the increasing the size of populations, as plants can cover quite large distances in this manner.

Factors affecting survival in arid areas

1) Hygrochastic and xerochastic capsules

The capsules of most of the Diclipterinae are xerochastic and so often dehisce when they are dried during the drying of herbarium specimens. Bremekamp (1926) has described the hygrochastic opening of fruits in the Acanthaceae and this method of opening seems predominant in the Ruelliae and the Odontoneminae. Some specimens of *Megalochlamys strobilifera* C.B. Clarke have undehisced capsules amongst bracts that appear to be from the previous season. These capsules are hygrochastic, as those described by Bremekamp (1926), and only dehisce when they are wet. This is an advantage for plants that grow in very arid areas, as the seeds will be protected by the walls of the capsules until there is rain, which will provide suitable conditions for both the dehiscence of capsules and germination of the seeds.

2) Indehiscent capsules

Some species of *Justicia* produce indehiscent capsules (Sell, 1969). These capsules are thick-walled and provide protection for the seeds, until the capsules are broken down. These capsules thus allow the seeds to remain viable for a longer time, during successive seasons of drought. These capsules are winged and may be dispersed by wind - a very unusual mode of dispersal in the Acanthaceae.

3) Cleistogamy

P. paniculata is annual and so the seedbank must be replenished after each generation. The sooner the seedbank is replenished, the sooner is the continued survival of the species assured. Cleistogamy is a phenomenon that may evolve under this selective pressure, as there is guaranteed pollination, and hence guaranteed seed production.

4) Seed viability

Seeds of *P. paniculata* that had been collected and preserved with a herbarium specimen were germinated 10 years later. Thus, it is known that these small seeds can remain viable for up to 10 years in the dry conditions that prevail in semi-deserts where the plants occur. Prolonged viability of seeds would be of great advantage to plants that grow in very dry areas that are prone to long periods of drought.

Other Observations

1) Function of anther appendages

Many members of the Acanthaceae have appendages on the bases of the anthers. These appendages may be tails or in some cases spurs or spikes. The function of these appendages may be to hook onto the body of potential pollinators and hence cause the anthers to be shaken as the visitors move. This shaking would cause pollen to drop out of the anthers onto the bodies of visitors. *P. gillilandiorum*, which does not have any anther appendages, has a different mechanism of exposing the pollen. As the anthers dehisce, some mechanism causes the pollen to exude from the apertures and the pollen is then clearly visible as a yellow mass on the purple anthers.

2) Possible functions of the glandular trichomes

Many parts of the inflorescences of many species of Acanthaceae are covered with glandular trichomes which exude a liquid. There are a few possible functions, one or more of which may be performed by these glandular trichomes:

a) Ants produce chemical substances that adversely affect pollen and hence germination (Beattie *et al* 1984 & 1985). The glandular trichomes may thus act as extrafloral nectaries, and attract the ants away from flowers or they may be acting as osmophores, which produce deterrents that keep the ants away. The former is unlikely, as ants are seldom seen on Acanthaceae, and certainly are not present often enough to be thought to have been attracted to a plant. The second possibility is unlikely, as deterrents that chase ants may also deter potential pollinators.

b) The glandular trichomes may produce pheromones that attract pollinators to the flowers of the Acanthaceae. Although this is possible, it is unlikely for two reasons. Firstly, the glandular trichomes are present on the bracts and not within the flowers.? If they were attracting potential pollinators, they would attract them outside of the flowers, and hence not to the sexual parts of the flower. Secondly, many parts of the inflorescence are glandular when they are young and developing, and not when the flowers are open, and thus it seems unlikely that they would be acting as attractants to pollinators.

c) The glandular trichomes may be providing protection to the reproductive parts of the plant. This speculation is supported by two facts. Firstly, young and developing parts, which are particularly vulnerable to predators are often densely glandular and would then be protected against predation. Secondly, I have tried to taste the exudate of the glandular trichomes, and found that this exudate has anaesthetised my tongue. If insects that ingested or touched the exudate of the glandular trichomes were anaesthetised, it would afford a plant considerable protection against predation.

3) Another function of resupination

As stated above, resupination of the corolla narrows the tube of the corolla and restricts entry into the corolla. Besides the possible consequences with regard to the pollination biology of plants with a narrower tube, the narrower tube would also restrict the entry of predators into the corolla. This would provide protection to the young ovary, and would reduce the incidence of nectar-robbing by insets that were too large to enter the small opening in the tube, but too small to touch the sexual parts when visting the flower.

Conclusion

It is quite evident, that there are many very interesting biological functions of various structures of the Acanthaceae. The design and implementation of experiments to discover, identify and clarify these functions will be rewarding.

CHAPTER 13
DISCUSSION OF TAXONOMIC LIMITS

There appears to be conflict between the type species concepts under which I think I operate and the taxonomic work which I have published. I believe that I operate under a biological species concept and yet my appraisal of *Hypoestes* (Balkwill & Getliffe Norris, 1985) is almost exclusively based on morphological characters. I have also found that my concepts of genera are narrower than those of some other workers. I have thus tried to assess what kinds of characters have been used to distinguish between species and between genera of the Acanthaceae and to evaluate whether these distinctions are purely morphological or whether there are underlying, but unstated, biological differences between taxa.

There is much discussion about theoretical definitions of species (Paterson, 1978; Paterson, 1981; White, 1978; Mayr, 1970 & Dobzhansky 1976). White (1978) has said of speciation that 'It is emphatically not a field that should be encumbered by sterile semantic arguments as to the meaning and definition of terms, as has too often been the case in the past'. Paterson (1981) has countered that 'it is important to provide a clear concept of what a species is and then to apply it consistently'.

The basic arguments in this field revolve around the type of concept that should be used. Historically, morphological species concepts were used, but currently, biological species concepts are finding far more favour. Within the biological species concepts, there is a range of views about the ways in which species evolve. One of the extreme views is that if allopatric populations become sympatric and if hybrids between these populations are less fit than either parent, there will be selection for individuals of each of the parent populations that do not interbreed. In the course of this evolution, one population will cause character displacement in the other, and this will lead to biological separation of the species. Another view is that two populations will experience stochastic changes while in allopatry. These changes, by chance, will isolate the two populations if they become sympatric. The view at the other extreme from the first is that natural selection acts on the processes that precede syngamy so that the probability of syngamy is enhanced. By chance, the changes that may occur in two allopatric populations will biologically separate the two populations if they become sympatric.

The species concept under which each taxonomist operates influences the taxonomic decisions made. Some may base their decisions wholly on morphological data, others may conduct hybridisation experiments to look for processes that isolate species, or others may conduct pollination experiments in order to identify processes that enhance syngamy in one group while incidentally reducing the probability of hybridisation with another. A large problem with botanical work, however, is that it is very difficult to study all species in their natural habitat or to conduct breeding experiments on them. Thus, botanists often face the prospect of deciding on species delimitations with only herbarium material and no living material available. This makes it impossible for some botanists to assess gene flow, isolating mechanisms or processes that enhance syngamy. This appears to necessitate the use of purely morphological species concepts, but this may not be true.

Table 35 summarises the kinds of characters used to distinguish species in the Acanthaceae and the frequency with which they are used. The survey is based on 31 references, in which formal diagnoses, keys to species or discussions about differences between species were included, and includes 165 species. From the table, it is possible to find how frequently characters are used to distinguish between species and approximately how many categories of characters are used to distinguish between a pair of closely related species. An average of 3,8 characters has been used to distinguish between each species, with a range between none (in the case of *Dicliptera dodsonii* Wasshausen and *Siphonoglossa durangensis* Henrickson & Hilsenbeck) and eleven (in the case of *Razisea wilburii* MacDade). Of the 72 categories of characters, 67 were used an average of 9,4 times each. The characters that were most often used are the shape and size of the bracts (58 and 45 times respectively), closely followed by the size of the corolla (44 times). These figures are, however, weighted by records of 29 species of *Dicliptera* (all from Wasshausen, 1966). Wasshausen (loc. cit.) used the size and shape of the bracts more frequently than any other character no doubt because they are large and obvious in *Dicliptera* and thus convenient. Characters that are used only once include shape of stems, 'architecture' of leaves, texture of leaves, venation of calyx, Key to references in Table 35:

1) Dokosi, 1979; 2) Morton, 1979; 3) Morton, 1978; 4) Hilliard & Burtt, 1970; 5) Napper, 1970; 6) Leonard, 1953; 7) Balkwill & Getliffe Norris, 1985; 8) Wasshausen, 1977a; 9) Wasshausen, 1970; 10) Daniel & Henrickson, 1982; 11) Daniel, 1983; 12) Henrickson & Daniel, 1979; 13) Daniel, 1980b; 14) Wasshausen, 1977b; 15) Wasshausen, 1984b; 16) Wasshausen, 1966; 17) Wood, 1980; 18) Brummitt & Feika, 1978; 19) Brummitt & Seyani, 1978; 20) McDade, 1982b; 21) McDade, 1982a; 22) Baden, 1981b; 23) Baden, 1981a; 24) Daniel, 1982b; 25) Sreemadhavan, 1977; 26) Heine, 1962; 27) Daniel, 1980a; 28) Heine, 1967; 29) Henrickson & Hilsenbeck, 1979; 30) Hansen, 1983 and 31) Daniel, 1982.

Key to source in Table 35:

Di = in diagnosis, Ds = in discussion and K = in key.

Table 35: Characters used to distinguish between species of the Acanthaceae.

	Reference	Source	Habit	Stem			Leaf								Inflorescence						Bracts								
				Shape	Size	Indumentum	"Architecture"	Morphology	Shape	Size	Indumentum	Margin	Texture	Spinose	Position	Morphology	Shape	Size	Indumentum	Pedicel length	Arrangement	Shape	Size	Indumentum	Colour	Texture	Extrafloral nectaries	Venation	Spinous
Elytraria minor	1	2D							+	+						+		+							+				
Nelsonia	2	Ds	+								+					+													
Justicia schimperi	3	K																				+	+						
J. striata	3	K																				+	+						
Sclerochiton caeruleus	4	K						+	+														+						
S. ilicifolius	4	K																						+					
S. odoratissimus	4	KD																											
S. harveyanus	4	KD																											
Blepharis tannae	5	Di	+																										+
B. trispina	5	Di						+																					
B. ilicifolia	5	Di	+																										
Crossandra spinosa	5	K																											+
C. mucronata	5	K	+		+																	+							
C. subacaulis	5	K	+		+																	+							
C. niloticus	5	K																				+				+			
C. infundibuliformis	5	K																				+				+			
Dicliptera assurgens	6	K																				+							
D. vahliana	6	K																				+							
D. trianae	6	K														+		+											
D. sciaphila	6	K													+														
D. uribei	6	K																					+	+					
D. bogotensis	6	K																					+	+					
D. pilosis	6	K							+																				
D. caucensis	6	K																				+	+						
D. conformis	6	K																				+	+						
D. orochlamys	6	K																					+		+	+			
D. cuatrecasasii	6	K																				+	+		+	+			
D. killipii	6	K																				+							
D. driophila	6	K																				+							
D. garciae	6	K																				+	+		+				
D. ewanii	6	K									+																		
D. haughtii	6	K																				+							
D. koiei	6	K																				+							
D. danielii	6	K																						+					
D. scandens	6	K													+	+													
D. sarcochroma	6	K								+																			
D. hazenii	6	K																						+					
D. inamoena	6	K																						+					
D. megalochlamys	6	K														+		+											
D. batilliformis	6	K														+		+											
D. santae-martae	6	K																				+				+			
D. rhombochlamys	6	K				+					+																		
D. nanodes	6	K				+					+																		

	Calyx						Corolla						Androecium						Gynoecium					Fruit					Seed			Pollen					Ecology			Floral Biology		Scent	Cystoliths	Staminode vestiture	Root branching
	Morphology	Shape	Size	Indumentum	Texture	Venation	Morphology	Shape	Size	Indumentum	Colour	Texture	Morphology	Length of stamens	Exsertion of stamens	Morphology of thecae	Number of thecae	Size of thecae	Stigma morphology	Style length	Style indumentum	Ovary shape	Ovary pubescence	Morphology	Shape	Size	Indumentum	Colour	Shape	Size	Surface Micromorphology	Morphology	Shape	Size	Pore size	Pore shape	Geographical distribution	Altitude	Habitat	Pollinator	Biology				
Elytraria minor																												+													+				
Nelsonia								+			+																												+						
Justicia schimperi								+	+		+																																		
J. striata								+	+		+																																		
Sclerochiton caeruleus										+																																			
S. ilicifolius				+																																									
S. odoratissimus			+					+	+		+																															+			
S. harveyanus			+					+	+		+																																		
Blepharis tannae																																													
B. trispina																																													
B. ilicifolia									+																																				
Crossandra spinosa																																													
C. mucronata																																													
C. subacaulis																																													
C. niloticus																			+																										
C. infundibuliformis																			+																										
Dicliptera assurgens																																													
D. vahliana																																													
D. trianae																																													
D. sciaphila									+																																				
D. uribei																																													
D. bogotensis																																													
D. pilosis																																													
D. caucensis																																													
D. conformis																																													
D. orochlamys																																													
D. cuatrecasasii																																													
D. killipii																																													
D. driophila																																													
D. garciae																																													
D. ewanii											+																																		
D. haughtii																																													
D. koiei																																													
D. danielii																																										+			
D. scandens																																													
D. sarcochroma																																													
D. hazenii																																													
D. inamoena																																													
D. megalochlamys																																													
D. batilliformis																																													
D. santae-martae																																													
D. rhombochlamys																																													
D. nanodes																																													

Table 35 cont.: Characters used to distinguish between species of the Acanthaceae.

Species	Reference	Source	Habit	Stem: Shape	Stem: Size	Stem: Indumentum	Leaf: "Architecture"	Leaf: Morphology	Leaf: Shape	Leaf: Size	Leaf: Indumentum	Leaf: Margin	Leaf: Texture	Leaf: Spinose	Inflorescence: Position	Inflorescence: Morphology	Inflorescence: Shape	Inflorescence: Size	Inflorescence: Indumentum	Inflorescence: Pedicel length
D. columbiana																				
D. compacta	6	K														+				
Hypoestes triflora	7	K																		
H. aristata	7	K														+				
H. forskaolii	7	K														+				
Dicliptera cundinamarcana	8	Ds						+												
Habracanthus cleefii	8	Ds																		
H. santamartae	8	Ds	+																	
Suessenguthia leucerythra	9	K															+			
S. vargassi	9	K															+			
S. cuscoensis	9	K														+				
S. trichophylla	9	K														+				
Anisacanthus junceus	10	Ds				+			+	+									+	+
A. linearis	10	Ds				+			+	+									+	+
A. wrightii	10	Ds				+			+										+	
Holographis tamaulipica	11	K						+			+				+					
H. virgata	11	K				+														
H. argyrea	11	K				+								+						
H. ilicifolia	11	K							+			+								
H. parayana	11	K				+														
H. anisophylla	11	K																	+	
H. pallida	11	K				+						+				+				
H. pueblensis	11	K																+		
H. ehrenbergia	11	K																+		
Carlowrightia texana	12	Di				+									+					
C. mexicana	12	Di	+																	
C. lesuerii	12	Di				+														
C. macvaughii	13	Ds							+							+		+		
Ruellia riopalenquensis	14	Di																		
Dicliptera dodsonii	14	Di																		
Justicia ianthina	14	Di																		
J. riopalenquensis	14	Di							+											
Habracanthus malacus	15	2D				+			+	+	+		+							
H. latifolius	15	2D				+		+	+	+	+									
Elytraria bromoides	16	K	+																	
E. imbracata	16	K	+																	
Dyschoriste linearis	16	K	+			+			+											
D. decumbens	16	K	+									+								
D. crenulata	16	K	+									+								
Ruellia metziae	16	K				+			+		+									
R. occidentalis	16	K								+								+		
R. davisiorum	16	K								+								+		
R. druschellii	16	K	+			+					+									

Species	Bracts: Arrangement	Bracts: Shape	Bracts: Size	Bracts: Indumentum	Bracts: Colour	Bracts: Texture	Bracts: Extrafloral nectaries	Bracts: Venation	Bracts: Spinous	Calyx: Morphology	Calyx: Shape	Calyx: Size	Calyx: Indumentum	Calyx: Texture	Calyx: Venation	Corolla: Morphology	Corolla: Shape	Corolla: Size	Corolla: Indumentum	Corolla: Colour	Corolla: Texture
D. columbiana																					
D. compacta																					
Hypoestes triflora			+	+													+	+	+		
H. aristata		+								+							+				
H. forskaolii		+								+							+				
Dicliptera cundinamarcana			+															+			
Habracanthus cleefii																	+	+		+	
H. santamartae				+													+	+			
Suessenguthia leucerythra		+																	+		
S. vargassi		+																	+		
S. cuscoensis																		+			
S. trichophylla																		+			
Anisacanthus junceus											+	+	+								
A. linearis											+	+	+								
A. wrightii											+										
Holographis tamaulipica			+	+								+							+		
H. virgata																		+		+	
H. argyrea																		+		+	
H. ilicifolia																					
H. parayana		+		+								+									
H. anisophylla		+	+																		
H. pallida		+																+		+	
H. pueblensis			+									+									
H. ehrenbergia			+									+								+	
Carlowrightia texana		+																			
C. mexicana																		+		+	
C. lesuerii			+															+			
C. macvaughii												+								+	
Ruellia riopalenquensis			+									+						+			
Dicliptera dodsonii																					
Justicia ianthina		+	+															+			
J. riopalenquensis			+							+											
Habracanthus malacus																	+				
H. latifolius												+					+	+		+	
Elytraria bromoides		+																			
E. imbracata		+																			
Dyschoriste linearis																					
D. decumbens																					
D. crenulata																					
Ruellia metziae																				+	
R. occidentalis																					
R. davisiorum																					
R. druschellii																+					

Species	Androecium: Morphology	Androecium: Length of stamens	Androecium: Exsertion of stamens	Androecium: Morphology of thecae	Androecium: Number of thecae	Androecium: Size of thecae	Gynoecium: Stigma morphology	Gynoecium: Style length	Gynoecium: Style indumentum	Gynoecium: Ovary shape	Gynoecium: Ovary pubescence	Fruit: Morphology	Fruit: Shape	Fruit: Size	Fruit: Indumentum	Fruit: Colour	Seed: Shape	Seed: Size	Seed: Surface Micromorphology	Pollen: Morphology	Pollen: Shape	Pollen: Size	Pollen: Pore size	Pollen: Pore shape	Ecology: Geographical distribution	Ecology: Altitude	Ecology: Habitat	Floral Biology: Pollinator	Floral Biology: Biology	Scent	Cystoliths	Staminode vestiture	Root branching
D. columbiana																																	
D. compacta																																	
Hypoestes triflora																			+												+		
H. aristata																			+														
H. forskaolii																			+														
Dicliptera cundinamarcana																																	
Habracanthus cleefii			+																														
H. santamartae																																	
Suessenguthia leucerythra																																	
S. vargassi																																	
S. cuscoensis						+								+																			
S. trichophylla						+								+																			
Anisacanthus junceus																																	
A. linearis																																	
A. wrightii																																	
Holographis tamaulipica																									+								
H. virgata		+																							+								
H. argyrea		+																							+								
H. ilicifolia																																+	
H. parayana								+			+																						
H. anisophylla		+																															
H. pallida																																	
H. pueblensis																																	
H. ehrenbergia																																	
Carlowrightia texana																			+														
C. mexicana																			+														
C. lesuerii														+		+			+														
C. macvaughii																	+		+														
Ruellia riopalenquensis																																	
Dicliptera dodsonii																																	
Justicia ianthina																																	
J. riopalenquensis																																	
Habracanthus malacus																																	
H. latifolius																																	
Elytraria bromoides																																	
E. imbracata																																	
Dyschoriste linearis																																	
D. decumbens																																	
D. crenulata																																	
Ruellia metziae																																	
R. occidentalis																																	
R. davisiorum																																	
R. druschellii																													+				

Table 35 cont.: Characters used to distinguish between species of the Acanthaceae.

	Reference	Source	Habit	Stem			Leaf							
				Shape	Size	Indumentum	"Architecture"	Morphology	Shape	Size	Indumentum	Margin	Texture	Spinose
R. nudiflora	16	K	+			+					+			
R. yucatana	16	K	+						+					
R. corzoi	16	K				+			+		+			
R. runyoni	16	K				+			+		+			
R. pinetorum	16	K						+						
R. pedunculata	16	K						+						
Stenandrium barbatum	16	K	+					+	+	+	+			
S. fascicularis	16	K	+					+	+	+	+			
Carlowrightia parviflora	16	K							+					
C. linearifolia	16	K							+		+			
C. arizonica	16	K						+		+				
C. torreyana	16	K				+					+			
C. serpiphylla	16	K				+					+			
Anisacanthus insignis	16	K												
A. wrightii	16	K												
Tetramerium hispidum	16	K												
T. platystegium	16	K												
Dicliptera brachiata	16	K												
D. vahliana	16	K												
Siphonoglossa greggii	16	K				+								
S. dipteracantha	16	K				+								
Justicia americana	16	K												
J. lanceolata	16	K												
J. runyoni	16	K												
J. warnockii	16	K							+	+				
J. wrightii	16	K							+	+				
Dicliptera suffruticosa	17	Di	+											
Isoglossa pawekiae	18	Di												
I. cataractum	18	Di												
Barleria sunzuana	19	2D	+			+					+			
B. lactiflora	19	2D												
Aphelandra panamensis	20	Ds	+								+			
A. goldfulcensis	20	Ds	+			+					+			
A. leonardii	20	Ds	+											
Justicia sarapiquensis	21	Ds	+											
Razisea wilburii	21	Ds								+				
Anisotes guineensis	22	K												
A. macrophyllus	22	K												
A. madagascariensis	22	K												
A. formosissimus	22	K		+						+				
A. tangensis	22	K												
A. zenkeri	22	K												
A. nyassae	22	K												

	Inflorescence						Bracts								
	Position	Morphology	Shape	Size	Indumentum	Pedicel length	Arrangement	Shape	Size	Indumentum	Colour	Texture	Extrafloral nectaries	Venation	Spinous
R. nudiflora															
R. yucatana															
R. corzoi															
R. runyoni															
R. pinetorum															
R. pedunculata															
Stenandrium barbatum															
S. fascicularis															
Carlowrightia parviflora															
C. linearifolia															
C. arizonica		+		+											
C. torreyana															
C. serpiphylla															
Anisacanthus insignis															
A. wrightii															
Tetramerium hispidum		+		+											
T. platystegium		+		+											
Dicliptera brachiata		+													
D. vahliana		+													
Siphonoglossa greggii															
S. dipteracantha															
Justicia americana		+													
J. lanceolata		+													
J. runyoni		+													
J. warnockii															
J. wrightii															
Dicliptera suffruticosa	+	+													
Isoglossa pawekiae		+			+										
I. cataractum		+					+	+							
Barleria sunzuana		+													
B. lactiflora															
Aphelandra panamensis								+					+		
A. goldfulcensis									+	+	+				
A. leonardii		+						+					+		
Justicia sarapiquensis								+	+		+				
Razisea wilburii		+							+						
Anisotes guineensis		+						+	+						
A. macrophyllus								+	+	+					
A. madagascariensis				+				+	+	+					
A. formosissimus								+	+					+	
A. tangensis						+		+	+						
A. zenkeri								+	+						
A. nyassae							+	+	+						

	Calyx						Corolla					
	Morphology	Shape	Size	Indumentum	Texture	Venation	Morphology	Shape	Size	Indumentum	Colour	Texture
R. nudiflora							+					
R. yucatana							+					
R. corzoi									+			
R. runyoni									+			
R. pinetorum				+								
R. pedunculata				+								
Stenandrium barbatum												
S. fascicularis												
Carlowrightia parviflora												
C. linearifolia												
C. arizonica												
C. torreyana												
C. serpiphylla												
Anisacanthus insignis		+	+						+			
A. wrightii		+	+						+			
Tetramerium hispidum												
T. platystegium												
Dicliptera brachiata												
D. vahliana												
Siphonoglossa greggii												
S. dipteracantha												
Justicia americana												
J. lanceolata												
J. runyoni									+			
J. warnockii												
J. wrightii												
Dicliptera suffruticosa												
Isoglossa pawekiae									+			
I. cataractum									+		+	
Barleria sunzuana		+							+			
B. lactiflora		+		+					+			
Aphelandra panamensis									+			
A. goldfulcensis												
A. leonardii												
Justicia sarapiquensis										+	+	
Razisea wilburii			+						+		+	
Anisotes guineensis			+						+	+	+	
A. macrophyllus										+		
A. madagascariensis			+	+								
A. formosissimus										+		
A. tangensis							+		+	+		
A. zenkeri										+		
A. nyassae							+				+	

	Androecium						Gynoecium				
	Morphology	Length of stamens	Exsertion of stamens	Morphology of thecae	Number of thecae	Size of thecae	Stigma morphology	Style length	Style indumentum	Ovary shape	Ovary pubescence
R. nudiflora											
R. yucatana											
R. corzoi											
R. runyoni											
R. pinetorum											+
R. pedunculata											+
Stenandrium barbatum											
S. fascicularis											
Carlowrightia parviflora											
C. linearifolia											
C. arizonica											
C. torreyana											
C. serpiphylla											
Anisacanthus insignis											
A. wrightii											
Tetramerium hispidum											
T. platystegium											
Dicliptera brachiata											
D. vahliana											
Siphonoglossa greggii											
S. dipteracantha											
Justicia americana											
J. lanceolata											
J. runyoni											
J. warnockii											
J. wrightii											
Dicliptera suffruticosa											
Isoglossa pawekiae											
I. cataractum											
Barleria sunzuana											
B. lactiflora											
Aphelandra panamensis											
A. goldfulcensis											
A. leonardii											
Justicia sarapiquensis											
Razisea wilburii			+					+			
Anisotes guineensis											
A. macrophyllus											+
A. madagascariensis											
A. formosissimus											
A. tangensis											
A. zenkeri											+
A. nyassae											

	Fruit					Seed			Pollen				
	Morphology	Shape	Size	Indumentum	Colour	Shape	Size	Surface Micromorphology	Morphology	Shape	Size	Pore size	Pore shape
R. nudiflora													
R. yucatana													
R. corzoi													
R. runyoni													
R. pinetorum													
R. pedunculata													
Stenandrium barbatum													
S. fascicularis													
Carlowrightia parviflora													
C. linearifolia													
C. arizonica													
C. torreyana													
C. serpiphylla													
Anisacanthus insignis													
A. wrightii													
Tetramerium hispidum													
T. platystegium													
Dicliptera brachiata													
D. vahliana													
Siphonoglossa greggii													
S. dipteracantha													
Justicia americana													
J. lanceolata													
J. runyoni													
J. warnockii													
J. wrightii													
Dicliptera suffruticosa													
Isoglossa pawekiae													
I. cataractum													
Barleria sunzuana													
B. lactiflora													
Aphelandra panamensis			+		+								
A. goldfulcensis				+	+								
A. leonardii	+												
Justicia sarapiquensis						+	+						
Razisea wilburii									+				
Anisotes guineensis													
A. macrophyllus									+		+		
A. madagascariensis											+		
A. formosissimus											+		
A. tangensis											+		
A. zenkeri											+		
A. nyassae											+		

	Ecology			Floral Biology		Scent	Cystoliths	Staminode vestiture	Root branching
	Geographical distribution	Altitude	Habitat	Pollinator	Biology				
R. nudiflora					+				
R. yucatana					+				
R. corzoi									
R. runyoni									
R. pinetorum									
R. pedunculata									
Stenandrium barbatum									
S. fascicularis									
Carlowrightia parviflora									
C. linearifolia									
C. arizonica									
C. torreyana									
C. serpiphylla									
Anisacanthus insignis									
A. wrightii									
Tetramerium hispidum									
T. platystegium									
Dicliptera brachiata									
D. vahliana									
Siphonoglossa greggii									
S. dipteracantha									
Justicia americana									
J. lanceolata									
J. runyoni									+
J. warnockii									
J. wrightii									
Dicliptera suffruticosa									
Isoglossa pawekiae									
I. cataractum									
Barleria sunzuana									
B. lactiflora									
Aphelandra panamensis	+		+	+					
A. goldfulcensis									
A. leonardii									
Justicia sarapiquensis									
Razisea wilburii	+	+							
Anisotes guineensis									
A. macrophyllus									
A. madagascariensis									
A. formosissimus									
A. tangensis									
A. zenkeri									
A. nyassae									

Table 35 cont.: Characters used to distinguish between species of the Acanthaceae.

Species	Reference	Source	Habit	Stem: Shape	Stem: Size	Stem: Indumentum	Stem: "Architecture"	Leaf: Morphology	Leaf: Shape	Leaf: Size	Leaf: Indumentum	Leaf: Margin	Leaf: Texture	Leaf: Spinose
A. bracteatus	22	K	+											
A. umbrosus	22	K	+											
A. involucratus	22	K												
A. trisulcus	22	K												
A. tanensis	22	K												
A. velutinus	22	K												
A. parviflorus	22	K												
A. sessiliflorus	22	K							+	+				
A. rogersii	22	K							+	+				
A. diversifolia	22	K							+					
A. dumosus	22	K												
A. ukambensis	22	K												
Macrorungia pubinervia	23	K												
M. longistrobus	23	K				+		+						
M. galpinii	23	K				+		+						
Mirandea huastecensis	24	K						+				+		
M. grisea	24	K						+				+		
Andrographis rotundifolia	25	Di					+							
Acanthus guineensis	26	Ds												
Adhatoda camerunensis	26	Di				+					+			
A. guineensis	26	Di							+		+			
Asystasia decipiens	26	Di												
Crossandra obanensis	26	Di							+					
Justicia hepperi	26	Di	+								+			
J. coahuilana	27	K												
J. henrickson	27	K							+	+				
J. wrightii	27	K							+	+				
J. warnockii	27	K				+					+			
J. linearis	27	K												
Rungia guineensis	28	K							+					
Siphonoglossa durangensis	29	Ds												
S. linearifolia	29	Ds				+			+	+				
Chroesthes lanceolata	30	K												
C. bracteata	30	K												
C. longifolia	30	K												
Anisacanthus andersonii	31	Di	+											

Species	Inflorescence: Position	Inflorescence: Morphology	Inflorescence: Shape	Inflorescence: Size	Inflorescence: Indumentum	Inflorescence: Pedicel length	Bracts: Arrangement	Bracts: Shape	Bracts: Size	Bracts: Indumentum	Bracts: Colour	Bracts: Texture	Bracts: Extrafloral nectaries	Bracts: Venation	Bracts: Spinous
A. bracteatus															
A. umbrosus															
A. involucratus		+						+	+					+	
A. trisulcus		+						+	+					+	
A. tanensis								+	+					+	
A. velutinus								+	+					+	
A. parviflorus		+						+	+					+	
A. sessiliflorus		+													
A. rogersii		+													
A. diversifolia		+						+	+						
A. dumosus								+	+	+					
A. ukambensis								+	+	+					
Macrorungia pubinervia	+										+				
M. longistrobus	+			+					+	+					
M. galpinii	+			+					+	+					
Mirandea huastecensis								+	+						
M. grisea								+	+						
Andrographis rotundifolia															
Acanthus guineensis								+							
Adhatoda camerunensis		+		+				+		+					
A. guineensis		+		+				+							
Asystasia decipiens															
Crossandra obanensis		+						+							
Justicia hepperi								+							
J. coahuilana									+						
J. henrickson															
J. wrightii															
J. warnockii															
J. linearis															
Rungia guineensis								+			+				
Siphonoglossa durangensis															
S. linearifolia		+						+	+						
Chroesthes lanceolata									+						
C. bracteata								+							
C. longifolia								+							
Anisacanthus andersonii															

Species	Calyx: Morphology	Calyx: Shape	Calyx: Size	Calyx: Indumentum	Calyx: Texture	Calyx: Venation	Corolla: Morphology	Corolla: Shape	Corolla: Size	Corolla: Indumentum	Corolla: Colour	Corolla: Texture
A. bracteatus			+						+			
A. umbrosus			+						+			
A. involucratus												
A. trisulcus												
A. tanensis										+		
A. velutinus										+		
A. parviflorus			+							+		
A. sessiliflorus			+			+						
A. rogersii			+									
A. diversifolia			+						+	+		
A. dumosus	+		+	+								
A. ukambensis	+		+	+								
Macrorungia pubinervia									+		+	
M. longistrobus			+	+								
M. galpinii			+	+								
Mirandea huastecensis											+	
M. grisea											+	
Andrographis rotundifolia												
Acanthus guineensis			+								+	
Adhatoda camerunensis												
A. guineensis												
Asystasia decipiens			+						+			
Crossandra obanensis											+	
Justicia hepperi									+		+	
J. coahuilana	+		+	+					+	+		
J. henrickson									+			
J. wrightii									+			
J. warnockii									+			
J. linearis												
Rungia guineensis												
Siphonoglossa durangensis												
S. linearifolia		+							+		+	
Chroesthes lanceolata												
C. bracteata		+										
C. longifolia		+										
Anisacanthus andersonii												

Species	Androecium: Morphology	Androecium: Length of stamens	Androecium: Exsertion of stamens	Androecium: Morphology of thecae	Androecium: Number of thecae	Androecium: Size of thecae	Gynoecium: Stigma morphology	Gynoecium: Style length	Gynoecium: Style indumentum	Gynoecium: Ovary shape	Gynoecium: Ovary pubescence
A. bracteatus											
A. umbrosus											
A. involucratus											
A. trisulcus											
A. tanensis											
A. velutinus											
A. parviflorus											
A. sessiliflorus											
A. rogersii											
A. diversifolia											
A. dumosus											
A. ukambensis											
Macrorungia pubinervia											
M. longistrobus											
M. galpinii											
Mirandea huastecensis											
M. grisea											
Andrographis rotundifolia											
Acanthus guineensis									+		
Adhatoda camerunensis											
A. guineensis											
Asystasia decipiens											
Crossandra obanensis											
Justicia hepperi											
J. coahuilana											
J. henrickson						+					
J. wrightii						+					
J. warnockii				+		+					
J. linearis				+							+
Rungia guineensis											
Siphonoglossa durangensis											
S. linearifolia											
Chroesthes lanceolata											
C. bracteata											
C. longifolia											
Anisacanthus andersonii											

Species	Fruit: Morphology	Fruit: Shape	Fruit: Size	Fruit: Indumentum	Fruit: Colour	Seed: Shape	Seed: Size	Seed: Surface Micromorphology	Pollen: Morphology	Pollen: Shape	Pollen: Size	Pollen: Pore size	Pollen: Pore shape
A. bracteatus											+		
A. umbrosus											+		
A. involucratus											+		
A. trisulcus									+		+		
A. tanensis									+		+		
A. velutinus													
A. parviflorus											+	+	
A. sessiliflorus											+	+	
A. rogersii											+	+	
A. diversifolia									+				
A. dumosus									+		+		
A. ukambensis									+		+		
Macrorungia pubinervia													
M. longistrobus													
M. galpinii													
Mirandea huastecensis													
M. grisea													
Andrographis rotundifolia													
Acanthus guineensis													
Adhatoda camerunensis													
A. guineensis													
Asystasia decipiens													
Crossandra obanensis													
Justicia hepperi			+				+						
J. coahuilana													
J. henrickson													
J. wrightii													
J. warnockii						+							
J. linearis						+		+					
Rungia guineensis													
Siphonoglossa durangensis													
S. linearifolia													
Chroesthes lanceolata													
C. bracteata													
C. longifolia													
Anisacanthus andersonii													

Species	Ecology: Geographical distribution	Ecology: Altitude	Ecology: Habitat	Floral Biology: Pollinator	Floral Biology: Biology	Scent	Cystoliths	Staminode vestiture	Root branching
A. bracteatus									
A. umbrosus									
A. involucratus									
A. trisulcus									
A. tanensis									
A. velutinus									
A. parviflorus									
A. sessiliflorus									
A. rogersii									
A. diversifolia									
A. dumosus									
A. ukambensis									
Macrorungia pubinervia									
M. longistrobus									
M. galpinii									
Mirandea huastecensis									
M. grisea									
Andrographis rotundifolia									
Acanthus guineensis	+								
Adhatoda camerunensis									
A. guineensis									
Asystasia decipiens									
Crossandra obanensis									
Justicia hepperi									
J. coahuilana									
J. henrickson									
J. wrightii									
J. warnockii									
J. linearis									
Rungia guineensis									
Siphonoglossa durangensis									
S. linearifolia									
Chroesthes lanceolata									
C. bracteata									
C. longifolia									
Anisacanthus andersonii									

morphology of fruit, size of seeds, altitude, pollinator, shape of cystoliths, vestiture of staminodes and branching patterns of roots. None of the authors specifically refers to biological species concepts, but MacDade (1982b) stated that the difference in morphology of the corolla resulted in the species having a different pollinator. This implies she was using a biological species concept.

From the the data in Table 35, it is quite clear that when dealing with formal taxonomy, botanists are using morphological species concepts, as most use exclusively morphological data to differentiate between species. Exceptions include MacDade (1982), who included comments about pollinators and Hilliard & Burtt (1970), who included notes on scent, which is hardly a morphological character. Some others referred to distributions, thus indicating that species are allopatric and so are making biological comments. The reason, no doubt, that botanists who (like myself) think they are using biological concepts and yet are presenting purely morphological concepts, is the nature of formal taxonomy and herbarium material. Formal taxonomy, especially in diagnoses, places emphasis on morphological characters, because most specimens that are identified are dried material, and thus have mainly morphological data available. While this is practical, it may mean that taxonomists are ignoring biological information, that they are not interpreting morphological differences in terms of biological function, or in spite of their doing so, they are not describing the biological information available, nor the interpretations they have made. An analysis of some of the commonly used characters may illustrate these possibilities.

From Table 35, it can be seen that the shape and size of bracts are the most commonly used characters to differentiate between species. In some species and some genera of the Acanthaceae (e.g. *Petalidium oblongifolium*), the bracts are brightly coloured and conspicuous and thus may be involved in the attraction of pollinators. Differences in shape and size of the bracts may be recognisable to pollinators and so attract different pollinators to different species. In *Dicliptera, D. clinopodia* has large tertiary bracts that are massed together and have white areas near their bases and purple areas near their tips. It thus seems highly likely that the tertiary bracts would be involved in the attraction of pollinators. The tertiary bracts of *D. fruticosa* are much smaller and are green and so are probably not involved in the attraction of pollinators. Hence, these morphological characters (i.e. size and shape of bracts) may be indicative of biological differences between species through the attraction of different pollinators.

Size of the corolla is another character that is frequently used in the differentiation between species. Essentially this is a morphological character, but it has biological implications. Lobes and lips of different sizes may enable pollinators to distinguish between species, while tubes of different lengths make nectar available to insects with different lengths of proboscis and tubes of different girth may allow entry of pollinators of different sizes. Thus, although size of corolla appears to be a morphological character, it may have important biological implications.

Although many differences in inflorescences may have only morphological implications, the inflorescence may be acting as the attraction unit. If the difference in morphology of the inflorescence does change the shape of the attraction unit, the inflorescence may attract different pollinators and thus have a biological implication as well as a morphological difference.

Other characters that are very likely involved in the attraction of pollinators (and so are indicative of biological differences between species) include colour of flowers, morphology of corolla, scent, size and shape of calyx lobes (in genera such as *Barleria* which have large conspicuous calyx lobes), colour of bracts and presence and position of extra-floral nectaries. The length of the stamens and style and the degree to which the stamens are exserted determine the position on a pollinator in which pollen is carried and this may biologically separate species. Characters such as size, shape and surface of pollen and surface of stigma may also determine the compatability of pollen from different species and so may have biological implications. Other characters that are available from herbarium labels and may influence biological relationships of species include the geographical distribution, the altitudinal distribution and the habitat in which a plant occurs. Habit, too, may have implications for the breeding of plants; in a forest, for example, plants with a low-growing habit will be pollinated by animals that live on the floor of a forest, while small trees may be pollinated by animals that live in the canopy or subcanopy.

There are some characters that probably have very little relevance to the biological relationships of species and so can be considered as nothing other than morphological characters (e.g. indumentum of stem, size of leaves and shape of stem), but discontinuities in the range of morphological variation may indicate discontinuities in gene flow and so indicate the existence of biological species. Other apparently morphological features may differentiate plants ecologically and so separate them spatially. Spatial separation may lead to biological speciation.

Distribution is an extremely important character that may provide information about the relationships of species. Populations that are allopatric cannot interbreed and if they are morphologically distinguishable, it is an indication that they do not interbreed. It is probably safe to call them species without testing to see what would happen if they became sympatric, because there is no way of knowing whether they will become sympatric during the course of evolution. Often, there is some overlap in morphological characters of two species which have different distributions, but the distributions are for some reason not included in keys (e.g. Codd, 1985).

Many of the theoretical discussions about species concepts seem to be inappropriate to the practice of taxonomy, because they deal with time on a very different scale. Taxonomic accounts are accounts of the *status quo* and are not expected to be valid indefinitely. In the case of most southern African Acanthaceae, the most recent revision is that of Clarke (1901). His account has been valid for 84 years and it is unlikely that a more recent revision will be expected to be accurate for a period that is any longer than this. In *Peristrophe, Dicliptera* and *Hypoestes*, more changes have to be made to Clarke's account because of changes in the amount of available herbarium material, in scientific thought and in scientific techniques than have to be made because of changes in the species themselves. Indeed, the type specimen of *Peristrophe paniculata*, which was collected by Forsskal before 1775 is practically identical morphologically to material that has been collected recently. As *P. paniculata* is an annual species, it is expected that it would vary more rapidly than species that are perennial and thus have longer generation times. Thus, it seems that the time for which a taxonomic account is accurate is negligible in terms of time on an evolutionary scale.

There is far less argument about generic concepts than there is about species concepts. Davis & Heywood (1963) have said that a genus should be a natural group, but this should surely be true of any group at any taxonomic rank. By discussing with colleagues and reading some of the current literature on the Acanthaceae, I have found that once again there is disagreement between 'splitters' and 'lumpers', particularly with reference to the genus *Justicia*.

Table 36 presents some of the characters with which taxonomists differentiate between the genera in the Acanthaceae and indicates the degree of difference that taxonomists expect between genera. The average number of characters that taxonomists have used to distinguish between genera is 2,48 characters. Categories of characters are used an average of 6,2 times each. Characters that are used more frequently than this average number of times, can be thought of as being more important than characters that are used less frequently.

These estimates are, however, based on work that was done on a regional basis and so there may be more differences between genera than there would be in a more cosmopolitan comparison of the same genera. Some of the keys, for example that of Dyer (1975), are not natural, so that in some cases the genera are distinguished from genera in different tribes and this means that characters that appear to be useful at the generic level are in fact the characters that separate the tribes to which the genera belong. Thus, some conclusions drawn from Table 36 may be inaccurate, although helpful as a guide.

The character most frequently used to distinguish between genera is the morphology of the corolla, which was used 26 times. Morphology of the corolla can have very important effects on the pollination of plants, so that limits based on this character have a biological basis. The frequency with which morphology of corolla is used as a character suggests that many generic limits are based on biological differences between groups, and thus are very likely natural. Morphology of the anther thecae was used 24 times, only slightly less often than the

Key to references in Table 36:

1) Dyer, 1975; 2) Long, 1973; 3) Daniel, 1981; 4) Wasshausen, 1984a; 5) Daniel, 1983; 6) Daniel, 1982b; 7) Hansen, 1983; 8) Wasshausen, 1966 and 9) Leonard, 1953.

Key to source in Table 36:

Di = in diagnosis, Ds = in discussion and K = in key.

Table 36: Characters used to distinguish between genera of the Acanthaceae.

	Reference	Source	Habit	Stems	Leaves			Inflorescence			Bracts					Calyx			Corolla					Androecium			Gynoecium		Fruit		Seeds	Pollen					Habitat
					Shape	Colour	Morphology	Position	Morphology	Shape	Arrangement	Shape	Size	Indumentum	Colour	Morphology	Size	Venation	Morphology	Shape	Size	Indumentum	Colour	Morphology	Morphology of thecae	Number of thecae	Stigma morphology	Pits on ovary	Morphology	Size	Surface Micromorphology	Morphology	Shape	Surface	Pore size	Pore shape	
Hygrophila	1	K																	+	+					+												
Hemigraphis	1	K							+											+	+				+												
Ruelliopsis	1	K							+												+				+												
Ruellia	1	K																											+				+		+		
Phaulopsis	1	K										+	+				+																				
Petalidium	1	K											+			+	+																				
Dyschoriste	1	K											+																+								
Duosperma	1	K											+																+								
Chaetacanthus	1	K																						+													
Blepharis	1	K										+														+		+									
Acanthopsis	1	K										+																									
Sclerochiton	1	K														+		+																			
Crossandra	1	K														+		+																			
Crabbea	1	K							+		+								+						+				+								
Glossochilus	1	K							+																												
Lepidagathis	1	K							+																+												
Neuracanthus	1	K																	+						+												
Asystasia	1	K																	+						+				+								
Barleria	1	K														+	+								+												
Ruspolia	1	K	+																				+		+						+						+
Pseuderanthemum	1	K	+																				+		+						+						+
Mackaya	1	K	+																+				+														
Macrorungia	1	K	+													+					+		+														
Dicliptera	1	K	+													+							+														
Peristrophe	1	K																							+												
Hypoestes	1	K																							+												
Ruttya	1	K																	+		+				+												
Siphonoglossa	1	K																				+					+		+								
Aulojusticia	1	K																				+					+										
Justicia	1	K																											+		+						
Monechma	1	K																											+		+						
Rhinacanthus	1	K																	+		+																
Isoglossa	1	K																	+		+																
Adhatoda	1	K	+						+	+																											
Anisotes	1	K							+				+																								
Ecbolium	1	K											+						+																		
Megalochlamys	1	K					+						+																								
Duvernoia	1	K							+				+						+		+																
Ruellia	2	Ds														+			+				+	+			+		+			+					
Mexacanthus	3	Ds											+																								
Pranceacanthus	4	Ds																	+		+		+		+												
Stenandrium	5	K	+																+																		
Aphelandra	5	K																			+		+														

Table 36 cont.: Characters used to distinguish between genera of the Acanthaceae.

Genus	Reference	Source	Habit	Stems	Leaves		Inflorescence			Bracts					Calyx			Corolla					Androecium			Gynoecium		Fruit		Seeds	Pollen					Habitat
				Shape	Colour	Morphology	Position	Morphology	Shape	Arrangement	Shape	Size	Indumentum	Colour	Morphology	Size	Venation	Morphology	Shape	Size	Indumentum	Colour	Morphology	Morphology of thecae	Number of thecae	Stigma morphology	Pits on ovary	Morphology	Size	Surface Micromorphology	Morphology	Shape	Surface	Pore size	Pore shape	
Holographis	5	K																		+		+														
Mirandea	6	K																					+			+										
Anisacanthus	6	K	+																	+		+														
Carlowrightia	6	K	+																	+		+														
Lepidagathis	7	K																						+					+	+						
Chroesthes	7	K																						+					+	+						
Hygrophila	8	K					+											+										+	+							
Dyschoriste	8	K																+		+				+							+					
Ruellia	8	K																+		+				+							+					
Stenandrium	8	K																					+	+							+					
Carlowrightia	8	K						+										+																		
Anisacanthus	8	K						+										+																		
Tetramerium	8	K								+								+																		
Dicliptera	8	K								+								+																		
Siphonoglossa	8	K																+		+											+					
Yeatesia	8	K																+													+					
Justicia	8	K																+						+							+					
Asystasia	9	K																					+													
Pseuderanthemum	9	K																+																		
Odontonema	9	K										+																								
Pachystachys	9	K										+																								
Dicliptera	9	K		+						+																		+								
Fittonia	9	K			+																															
Chaetochlamys	9	K					+		+																											
Siphonoglossa	9	K																	+	+																
Justicia	9	K																						+												
Megaskepasma	9	K										+		+																						
Tetramerium	9	K							+	+	+		+																							
Jacobinia	9	K							+																											
Chaetothylax	9	K																						+												
Pelecostemon	9	K																						+												
Kalbreyeriella	9	K						+											+																	
Habracanthus	9	K						+											+																	
Razisea	9	K						+											+																	
Syringidium	9	K																+																		
Hansteinia	9	K						+											+	+																
Stenostephanus	9	K						+	+										+	+																
Neriacanthus	9	K	+											+																						
Stenandrium	9	K	+											+																						
Cyphacanthus	9	K													+																					
Encephalasphaera	9	K																														+	+			
Aphelandra	9	K																																+	+	
Rhombochlamys	9	K																																+	+	

morphology of the corolla. Thus, this character is also important in the delimitation of genera. The size of the corolla was used 18 times and so is also an important character for distinguishing between genera. As described in chapter 12, the size of the corolla may have important effects on pollination and so may biologically separate genera. The morphology of the inflorescence was used 16 times to distinguish between genera. As discussed in chapter 3, morphology of the inflorescence can be arranged into evolutionary sequences and thus may give clues about relationships and evolutionary trends of genera.

Other characters that were used more often than the average six times each, are the size of the bracts (12 times) as well as the colour of the corolla, the morphology of the capsule and habit (all 11 times each). Some other characters that appear to be important are the morphology of the calyx, the shape of the corolla and the morphology of the pollen. Seed surface microsculpturing and morphology of the androecium (which are very important at the tribal level) are used as often as or slightly less often than average.

There are four genera with resupinate corollas in the Justicieae (i.e. *Peristrophe, Dicliptera, Hypoestes* and *Periestes*). I am familiar with three of these genera, which can be divided on the basis of single characters only (i.e. the morphology of the thecae separates *Hypoestes* and *Peristrophe* and the morphology of the capsule separates *Dicliptera* and *Peristrophe*). I feel that these genera are natural groups and that they are of a reasonable size (i.e. 25 or slightly more species in *Peristrophe* and about 150 each in *Dicliptera* and *Hypoestes*). If these three groups were considered to be congeneric, a single large genus of 325 species would be formed. If one was identifying a member of this enlarged genus, one of the first steps would be to place it into one of the original genera (at whatever rank they were considered to be different) before keying it any further. If these three groups were congeneric, however, there would be more characters separating them from the most closely related genera than presently separate them from one another. On the other hand, if *Peristrophe* was divided into three segregate genera, there would be more differences between each of these segregate genera than there are between *Peristrophe* and *Dicliptera* and between *Hypoestes* and *Peristrophe*. Thus, I do not believe that the number of characters that separate genera are the most important evaluation of the affinity of those genera.

In the Acanthaceae, there is considerable disagreement and confusion about the limits of the genus *Justicia*. Even in its narrow sense, *Justicia* is a large genus with 300 species. A number of genera have been segregated from *Justicia* (e.g. *Monechma, Adhatoda* and *Duvernoia*), but many taxonomists would approve of their reunion with *Justicia*. Personally, I feel that the degree of variation that taxonomists will accept in a genus of the Acanthaceae is influenced by their initial contact with the family. My contact with the family began with *Hypoestes*, which has only a single character that distinguishes it from its closest relative. Within the genus, there is a large degree of similarity between species, so that I now have a generic concept that may be very narrow. Some taxonomists make initial contact with the Acanthaceae by working on *Justicia*, possibly because it is so notoriously difficult and in need of work. Because of the degree of variation that they observe in this genus, they have far broader generic concepts than I have. In some cases, the broad generic concepts that taxonomists hold lead them to have a much broader view of species. I think, though, that some of these taxonomists lose sight of or do not realise the relevance of the history of the genus *Justicia*, which was one of the first genera to be described in the Acanthaceae. Of the eleven species that Linnaeus (1753) listed in his concept of Justicia, seven have been transferred to other genera. Six of these genera are in other subtribes of the Justicieae and one, *Andrographis echioides* (L.) Nees, is in a different tribe, Andrographideae. Vahl's concept of *Justicia* was also very broad so that in his herbarium, he included species from most of the subtribes of the Justicieae in his genus *Justicia*. He also included some species of *Nelsonia* in his concept of *Justicia; Nelsonia* is only very distantly related to *Justicia* and may even be moved out of the family. Many of the genera in the Justicieae have been segregated from the old concept of the genus *Justicia* and so are much more narrowly circumscribed than is *Justicia*. It is, in fact quite likely that *Justicia*, in its present circumscription, still has a residue of forms that are so different that they would be separated into different genera if they were in other subtribes and tribes of the family. Some taxonomists may interpret these forms as the variation within genera in the family and thus have very broad generic concepts. I thus feel that it is unwise to compare the range of variation in morphology in any group with the range in *Justicia*, if one is trying to make decisions about generic limits.

Conclusions

It seems, then, that there is still much disagreement about generic limits in the Acanthaceae. The genera *Peristrophe, Dicliptera* and *Hypoestes* are distinguished from one another by single characters, but I do not think that anything would be gained by placing *Peristrophe* and *Dicliptera* in the same genus and certainly would oppose doing so until a comprehensive study of these genera had been completed. It seems that much of the confusion about generic limits of *Justicia* and other genera in the Justicieae is related to the history of *Justicia*, which was the name applied to the group that we now regard as a tribe. I feel that a wise *modus operandi* may be to sort species into groups within the present genera, to regard these groups as sections or series and to raise them to the appropriate rank when the genera are studied on a worldwide scale.

With regard to species, there is much theoretical discussion about concepts, but some of this is irrelevant to practising taxonomists. Many taxonomists, however, think that they are using biological species concepts, but provide purely morphological accounts of their findings. I would like to make a plea that taxonomists familiarise themselves with the biological implications of the characters they study and provide an account of these in the work they publish.

CHAPTER 14

CLASSIFICATION OF AND EVOLUTION IN THE ACANTHACEAE

Generic revisions cannot be carried out in isolation, but should be done in the context of the super-generic taxa to which the genera belong. *Peristrophe* and *Dicliptera* were compared with the closely related genus *Hypoestes* especially, as well as with the genera *Ecbolium, Angkalanthus, Rhinacanthus* and *Justicia*. It soon became apparent that the subdivision and classification of the family is still not finalised and recent publications, such as those of De (1968) and Bremekamp (1965) present markedly different classifications of the family. Not many schemes of evolution in the family have been proposed or published, but the two I have seen have some significant anomalies.

I have therefore attempted to gain an overview of the family (particularly of the southern African members) by scanning current literature and analysing the features used in keys and in discussions of tribal limits. I have also made observations on herbarium material, on living material and on spirit material gathered on field trips and on the basis of this information have evaluated the present classification of the family.

Since 1789 when de Jussieu divided the Acanthaceae on the basis of two or four stamens, the subdivision of the family has received attention from many authors. One of the most significant treatments of this problem is that of Lindau, published in 1895, as he dealt with the family on a worldwide basis. Lindau recognised 3 subfamilies variously divided into tribes and subtribes. Aestivation was the crucial feature distinguishing the subdivisions of his Acanthoideae and pollen morphology played an important role at lower ranks. Table 37 summarises this classification and southern African genera are placed in their appropriate groups. Burkill & Clarke (1899) and Clarke (1901) contributed information on the classification of the African Acanthaceae. Important characteristics were the number of anthers and number of anther thecae, but pollen characters were not as emphasised as in Lindau's (1895) treatment. Table 38 summarises Burkill and Clarke's (1899) and Clarke's (1901) classifications and places southern African genera in context. In 1965 Bremekamp published a significant work on the reclassification of the

Table 37: Southern African genera of the Acanthaceae in the context of Lindau's (1895) classification.

- **ACANTHACEAE**
  - NELSONIOIDEAE
    - *Hiernia*
    - *Nelsonia*
    - *Elytraria* (as *Tubiflora*)
  - THUNBERGIOIDEAE
    - *Thunbergia*
  - ACANTHOIDEAE
    - CONTORTAE
      - HYGROPHILEAE
        - *Hygrophila*
      - PETALIDIEAE
        - *Petalidium*
        - *Phaulopsis* (as *Micranthus*)
      - STROBILANTHEAE
        - *Dyschoriste*
        - *Chaetacanthus*
      - RUELLIEAE
        - *Ruellia*
      - BARLERIEAE
        - *Barleria*
        - *Lepidagathis*
        - *Crabbea*
        - *Neuracanthus*
    - IMBRICATAE
      - ACANTHEAE
        - *Blepharis*
        - *Acanthopsis*
        - *Crossandra*
        - *Sclerochiton*
      - ASYSTASIEAE
        - *Asystasia*
      - GRAPTOPHYLLEAE
        - *Ruspolia*
      - PSEUDERANTHEMEAE
        - *Pseuderanthemum*
      - ODONTONEMEAE
        - Diclipterinae
          - *Dicliptera*
          - *Peristrophe*
          - *Hypoestes*
        - Odontomeninae
          - *Angkalanthus*
          - *Duvernoia*
          - *Ecbolium*
          - *Mackaya*
          - *Rhinacanthus*
          - *Siphonoglossa*
        - Monotheciinae
          - *Ruttya*
      - JUSTICIEAE
        - *Justicia*
      - ISOGLOSSAE
        - *Isoglossa*

Table 38: Southern African genera of the Acanthaceae in the context of the classification of Burkill & Clarke (1899 & 1901).

ACANTHACEAE

- THUNBERGIEAE
  - *Thunbergia*
- NELSONIEAE
  - *Nelsonia*
  - *Elytraria*
- RUELLIEAE
  - Hygrophileae
    - *Hygrophila*
  - Euruellieae
    - *Ruellia*
    - *Ruelliopsis*
    - *Hemigraphis*
  - Strobilantheae
    - *Chaetacanthus*
    - *Dyschoriste*
    - *Duosperma* (as *Disperma*)
    - *Phaulopsis* (as *Phaylopsis*)
    - *Petalidium*
- ACANTHEAE
  - *Acanthopsis*
  - *Blepharis*
  - *Crossandra*
  - *Sclerochiton*
- JUSTICIEAE
  - Tetrandrae
    - *Crabbea*
    - *Glossochilus*
    - *Lepidagathis*
    - *Asystasia*
    - *Neuracanthus*
  - Eranthemeae
    - *Pseuderanthemum* (as *Eranthemum*)
    - *Ruspolia*
    - *Mackaya*
  - Barlerieae
    - *Barleria*
  - Eujusticieae
    - Monothecieae
      - *Ruttya*
    - Typicae
      - *Justicia*
      - *Monechma*
      - *Siphonoglossa*
      - *Adhatoda*
      - *Rhinacanthus*
      - *Ecbolium*
      - *Isoglossa*
      - *Anisotes*
    - Hypoesteae
      - *Hypoestes*
      - *Peristrophe*
    - Solutae
      - *Dicliptera*
      - *Macrorungia*

family based mainly on his experience of the Asian members. In this he made important modifications by transferring genera previously in the Nelsonioideae *sensu* Lindau (Nelsonieae *sensu* Burkill & Clarke) to the Scrophulariaceae and by elevating the Thunbergioideae *sensu* Lindau (Thunbergieae *sensu* Burkill & Clarke) to the rank of family. The remaining genera placed in Lindau's (1895) Acanthoideae were reassorted into two subfamilies in the narrowly circumscribed Acanthaceae. Extrapolating from Bremekamp's comments, I have inserted southern African genera into a summary of his classification (Table 39), but in so doing, have found some anomalies in the southern African material.

Consideration of tribal limits in the Acanthaceae is based on a concept of the family that excludes both Thunbergioideae and Nelsonioideae *sensu* Lindau. The former was raised to familial rank by Bremekamp (1953, 1965) - a decision that has general acceptance. His recommendation that Nelsonioideae be assigned to the Scrophulariaceae has met with opposition from specialists in Acanthaceae taxonomy (Johri & Singh, 1959; Reddy, Radhakrishnaiah, Narayana & Ghosh, 1980) and from those studying Scrophulariaceae (Burtt, 1965). At least one author has raised Nelsonioideae to familial rank (Sreemadhavan, 1977). I do not feel competent to comment on these decisions without a far more comprehensive knowledge of acanthaceous genera outside southern Africa and of the Scrophulariaceae. Bremekamp (1965) accepted two subfamilies within his narrow view of the Acanthaceae; Acanthoideae and Ruellioideae. This appears to be a logical subdivision, but at the tribal level I find anomalies. Lindau, Burkill & Clarke and Bremekamp all consider that the genera *Blepharis* Juss., *Acanthopsis*, *Sclerochiton* and *Crossandra* Salisb. form a discreet tribe. Lindau (1895), because of his fundamental division on the basis of corolla aestivation, places this tribe in the Imbricatae where it has equivalent status to and relatively close affinity with Justicieae. Bremekamp (1965), however, places it in the tribe Acantheae in the Acanthoideae and the array of characters unique to this tribe supports Bremekamp's decision. These characters are the one-lipped corolla, four monothecous ciliate anthers and colpate pollen. These I believe are far more significant than the aestivation. The inclusion of *Crossandra* with the other southern African genera, however, is debatable as it is distinctly different. *Crossandra* differs from the others as the corolla is in the red and yellow range,

Table 39: Southern African genera of the Acanthaceae in the context of the classification proposed by Bremekamp (1965).

- **ACANTHACEAE**
  - **ACANTHOIDEAE**
    - ACANTHEAE
      - *Acanth opsis*
      - *Blepharis*
      - *Sclerochiton*
      - *Crossandra*
  - **RUELLIOIDEAE**
    - RUELLIEAE
      - Ruelliinae
        - *Ruellia*
      - Barleriinae
        - *Barleria*
        - *Glossochilus*
        - *Crabbea*
      - Petalidiinae
        - *Petalidium*
        - *Dyschoriste*
        - *Chaetacanthus*
        - *Phaulopsis*
        - *Hemigraphis*
      - Hygrophilinae
        - *Hygrophila*
    - LEPIDAGATHIDEAE
      - Lepidagathidinae
        - *Lepidagathis*
        - *Neuracanthus*
    - JUSTICIEAE
      - Odontoneminae
        - *Asystasia*, *Ruspolia*, *Pseuderanthemum*
        - *Peristrophe*, *Dicliptera*, *Hypoestes*
        - *Mackaya*, *Angkalanthus*, *Siphonoglossa*,
        - *Duvernoia*, *Rhinacanthus*, *Ruttya*,
        - *Ecbolium*, *Megalochlamys*.
      - Justiciinae
        - *Justicia*
        - *Monechma*
        - *Adhatoda*
        - *Anisotes*
        - *Metarungia* (as *Macrorungia*)
      - Rhytiglossinae
        - *Isoglossa* (as *Rhytiglossa*)

not in the range of white, blue and purple; the corolla tube is proportionally much longer; the filaments are small and ephemeral, not hard and chitinous; the anthers and stigma are included in the tube and not exserted; the pollen has squared ends, not rounded ones and the surface of the pollen grains is foveolate, not shallowly reticulate (plate 5d & fig. 34). *Crossandra* is therefore anomalous in the Acantheae, but bears closer relationship to this tribe than to any other tribe in the subfamily. Thus I feel that it may be justified to place *Crossandra* in a subtribe of its own within Acantheae.

Ruellieae sensu Bremekamp (1965) is subdivided into three subtribes: Ruelliinae with globose, reticulate pollen with three to seven evenly spaced pores and actinomorphic or subactinomorphic corollas with contorted aestivation; Barleriinae with similar pollen, zygomorphic flowers and quinuncial or opposite aestivation and Petalidiinae with prolate, banded pollen with pores surrounded by lips of margocolpus; bilabiate or subactinomorphic flowers borne in axillary cymes and with didynamous stamens often attached to a flap of tissue decurrent on the corolla tube.

Ruelliopsis C.B. Cl. has pollen that is banded and has lips of margocolpi surrounding the pores (plate 5c), a form which is rather different from that of *Ruellia* (plate 5e), but on the basis of the corolla form and the number of seeds in each locule, I feel it must be retained in the Ruelliinae.

The genus *Crabbea* was placed in Barleriinae by Bremekamp (1965) on the basis of its similar aestivation, but observations reveal that in *Crabbea* the two inner petals are opposed, not adjacent to one another. *Crabbea* also has didynamous stamens (not a feature of other members of the Barleriinae) and pollen almost identical to that of *Ruellia* (*c.f.* plate 5b & e). I therefore propose that *Crabbea* be placed in the Ruellieae. *Glossochilus*, is a second genus in the Barleriinae that appears incorrectly placed. *Glossochilus* has colporate pollen (plate 6c) and didynamous stamens and this does not fit into the definition of Ruellieae at all, but fits more comfortably with the subtribe Odontoneminae where its aestivation and corolla shape suggest close affinity with *Asystasia*. *Glossochilus* is unusual in that subtribe, as it does not possess a terminal thyrse or spike and this may account for its former position in Barleriinae, but this dissimilarity is overridden by the many features it has in common with *Asystasia*.

Removing *Glossochilus* and *Crabbea* from Barleriinae leaves *Barleria*, a genus that shows a great deal of variation in number of stamens and staminodes, number of ovules, shape of fruit and inflorescence type. This degree of variability is far higher than that displayed in many genera, especially those in the Justicieae (pers. obs., Hansen pers. com.) and revision of the genus is evidently necessary.

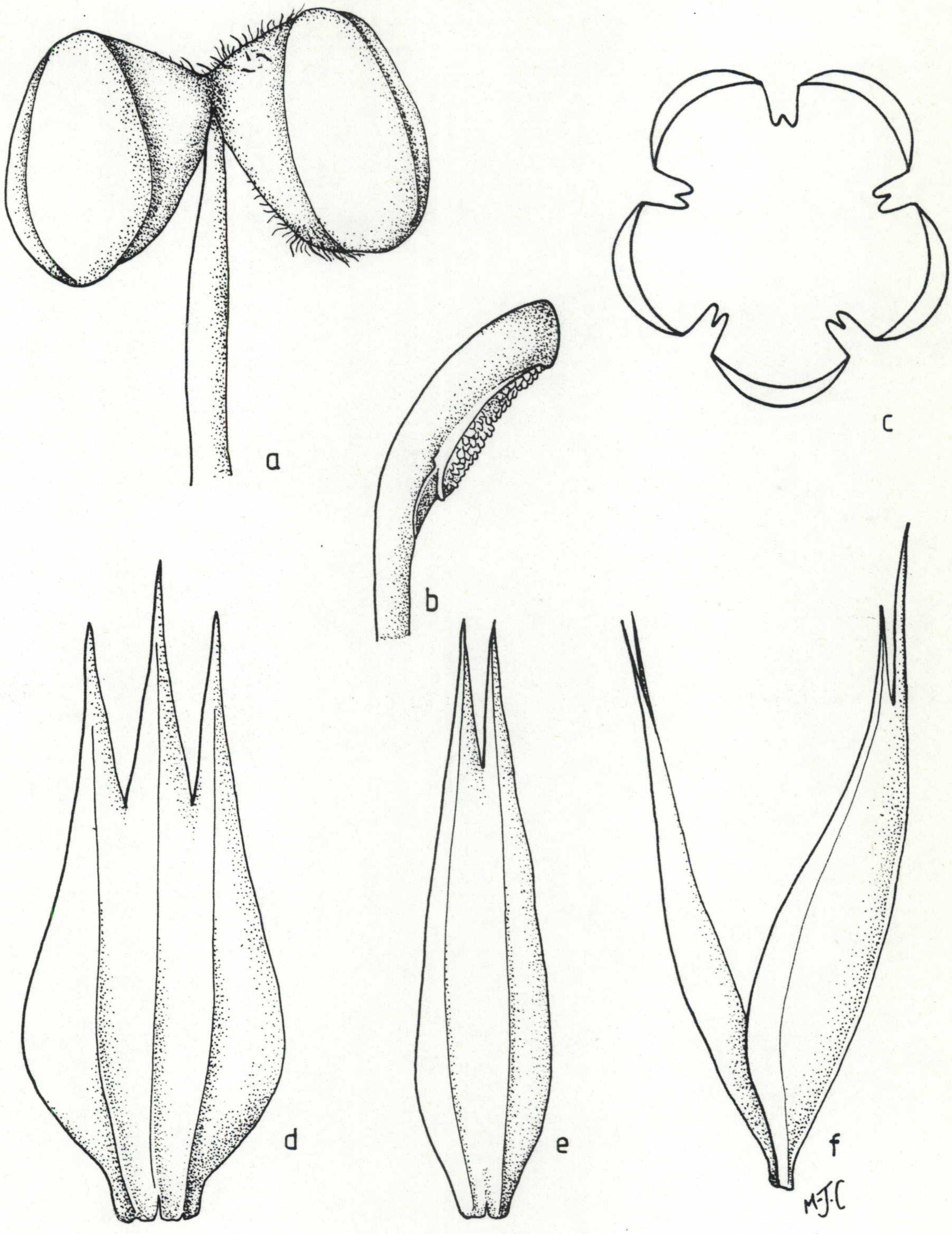
The Petalidiinae, the third subtribe in the Ruellieae, is the largest. *Duosperma* Dayton (which Clarke described as *Disperma* C.B. Cl., in the tribe Strobilantheae *sensu* Lindau) presumably would be placed in the subtribe Petalidiinae by Bremekamp (1965). Similarly *Dyschoriste* and *Chaetacanthus* with axillary cymes have been removed from Strobilantheae to Petalidiinae. These genera share unusual pollen morphology. Their pollen is ellipsoidal, with pusticulate exine divided into narrow longitudinal bands (plate 5h). *Chaetacanthus*, despite its two stamens , fits neatly into this subtribe of the Ruellieae, and appears to be a more derived form.

The genus *Hemigraphis* poses many problems at generic and tribal levels. Nees described two very different species, at the same time as he described the genus. Neither has been designated as a type (Farr, Leussink and Stafleu 1979). Since 1847, a number of other species have been described and Hansen (pers.com.) has indicated that the Asian species in this genus are considered by Terao to be *Strobilanthes* Blume species and that much of the African material has been misidentified. Heine (1971) transferred many of the African species of *Hemigraphis* to *Hygrophila*. During the course of this study, however, it has become evident that southern African material identified as *Hemigraphis prunelloides* cannot be congeneric with southern African species of *Hygrophila*. The former species bears small actinomorphic flowers that lack a rugula, while *Hygrophila auriculata* and *H. gracillima* (Schinz) Burkill, the two southern African species I have seen, have distinctly bilabiate corollas with very distinct rugulae in their upper lips. Pollen morphology (plate 5i & j) and ovule number are, however, very similar. It appears that a very careful revision of *Hygrophila* and *Hemigraphis* including a thorough survey of floral morphology is required. Bremekamp (1965) placed *Hemigraphis* in the subtribe Petalidiinae (together with *Dyschoriste* and *Chaetacanthus*) and segregated *Hygrophila* into its own subtribe, Hygrophilinae. I believe that this overlooks the close relationship between *Hygrophila* and *Hemigraphis* and also the unusual staminal arrangement common to these two genera and to *Dyschoriste, Chaetacanthus* and other genera in the Petalidiinae. In all these genera, stamens (and staminodes in *Chaetacanthus*) are attached to the top of a flange of tissue which is decurrent on the corolla tube in a manner reminiscent of that in *Strobilanthes*. I wonder if it would not be more appropriate to include *Hygrophila* in the subtribe Petalidiinae.

Similarly I have observed that *Lepidagathis scabra* C.B. Clarke resembles *Hygrophila* with respect to shape of the corolla, rugula and colporate pollen (plate 6a). Thus it may not be justified to separate *Lepidagathis*, as Bremekamp (1895) suggested, but to assign it to the subtribe Petalidiinae. Some of the African species of *Lepidagathis* have monothecous posticous anthers and, as the number of thecae in the posticous anthers appears to be the only feature used to separate *Lepidagathis* and *Hulemacanthus* S. Moore, a reappraisal of the generic limits is indicated. If this distinction is valid, then new combinations must be made.

Southern African herbaria include gatherings named *Neuracanthus*. While the Asian species of *Neuracanthus* are bilabiate, as is the type species *N. tetragonostachys* Nees, the African species that are referred to this genus are quite different. The corolla is tubular below, rotate above, the lobes are barely separated and are induplicate in the bud (fig. 73c). Features of this plant that are unique in the southern African Acanthaceae include this morphology of the corolla; the globose, tricolporate pollen with very small pores in the exine (plate 6b); the two-lobed calyx (fig. 73d - f) and the developed dorsal stigma lobe (fig. 73b). Inclusion of the sexual parts in the narrow corolla tube is unique in the Ruellioideae while the axillary thyrse and bifurcated filaments are unique amongst the southern African members of Ruellioideae excluding the Justicieae. Thus it appears that these plants do not belong to the genus *Neuracanthus* and furthermore, it is possible that they do not

Figure 73: Some of the unusual features of *Neuracanthus africanus*: a) stamen with bifurcated filament (X90); b) stigma with dorsal lobe developed and ventral lobe reduced (X120); c) induplicate aestivation and d - f) bilabiate calyx, with lobes of each lip fused for more than half their length (X15).


a
b
c
d
e
f
M.J.C

belong in any of the tribes which have been described in the Acanthaceae. Clearly this deserves further attention.

The tribe Justicieae is clearly distinguished from all other tribes in the subfamily by the lack of hygroscopic hairs on the seed surface. Three subtribes, Odontoneminae, Rhytiglossinae (Bremekamp's name for Isoglossinae) and Justiciinae, are recognised by Bremekamp (1965). The pollen of *Glossochilus burchellii* Nees, the type species, is almost identical to that of *Asystasia stenosiphon*, while the corolla is very similar to that of *Asystasia gangetica s.l.*. The seeds are similar to those of *Asystasia* and, as indicated by C.B. Clarke, the only difference between the genera is in the inflorescence. *Asystasia* has a terminal monochasium, *Glossochilus* has individual flowers in leaf axils. Bremekamp (1933) has described the species *Glossochilus parviflorus* Hutch. as *Asystasia atriplicifolia* Bremekamp, further emphasising the fact that these two genera are very closely related and that their interrelationship must be assessed. The very close relationship between *Glossochilus* and *Asystasia* reinforces the recommendation to move *Glossochilus* into the Odontoneminae. Although the four stamens and campanulate corolla of these genera are very unusual in the subtribe, *Mackaya* Harv., which also has a campanulate corolla, has two stamens and thus provides a link with the other Odontoneminae, as does *A. stenosiphon* with its bilabiate corolla. These links make it impossible to place *Asystasia* and *Glossochilus* into a separate tribe, and suggest that it would be unwise to place them in a separate subtribe. *Angkalanthus* is unusual in Odontoneminae, as it has two stamens and no staminodes, but the parallel anther thecae, the nonresupinate corolla without a rugula and the tricolporate pollen confirm that it belongs in the Odontoneminae.

Peristrophe, Dicliptera and *Hypoestes* are unique in the Justicieae as they have resupinate corollas of a very similar form. They are bilabiate with lips of about the same length as the corolla tube. The lip which is in the upper position is narrowly elliptic, and has three small teeth at the tip, the lip in the lower position is usually lanceolate or ovate and is emarginate at the tip. The pollen of these three genera is extremely similar, the only variation being in the configuration of the pseudocolpi which may be separate (plate 5d) or confluent at the poles. All three genera have compound inflorescences composed of inflorescence units that are monochasia surrounded by a pair of bracts. In *Hypoestes*, these monochasia may be variously reduced (Balkwill & Getliffe Norris 1985). These three genera have no staminodes, and so do not belong in the Odontoneminae. As they have only very indistinct rugulae in their upper lips (held in the lower position), they do not really belong in the Justiciinae. *Periestes*, a genus from Madagascar and the Comores, shares all of these characters, including pollen morphology (plate 6e) and Lindau (1895) placed *Periestes* with *Peristrophe, Dicliptera* and *Hypoestes* in his tribe Diclipterinae. I propose that Diclipterinae be reinstated, but, as Bremekamp (1965) suggested, without *Rungia* Nees which has a clearly defined rugula (*c.f.* Justiciinae) and does not have a resupinate corolla. Burkill & Clarke (1899) separated *Dicliptera* from *Peristrophe* and *Hypoestes*, and hence emphasised the elastic placental bases in *Dicliptera* (plate 4c & d) and *Metarungia* [=*Macrorungia* C.B. Clarke] (plate 4e). Elastic placentae occur in *Rungia* (Justiciinae) and in *Petalidium* Nees (plate 4a) and *Phaulopsis* (plate 4b), two genera of the Petalidiinae. The phenomenon, therefore, appears to have evolved more than once in the family. I believe that differences in other features override the apparent similarity in the dehiscence of the capsules of *Dicliptera* and *Metarungia*. The capsule of *Dicliptera* is thin-walled and has a raphe to which the elastic placental bases are attached (plate 4c & d), while the capsule of *Metarungia* is thick-walled, woody and without a raphe (plate 4e) and has much in common with the woody capsule of *Anisotes* (plate 4h). Thus, Diclipterinae accomodates *Dicliptera, Peristrophe* and *Hypoestes*, and in terms of inflorescence morphology, floral morphology, and size, shape and texture of seeds and appears to be a more natural group in which I accept differences in capsule dehiscence and number of anther thecae as generic characters. Similarly, *Metarungia* and *Anisotes* form a second natural group with bird-pollination and a broad tubular and reddy-brown corolla in common. Thus I consider the form of dehiscence to be important at generic level, but not necessarily indicative of tribal relationships.

Burkill & Clarke (1899) placed *Isoglossa* in the same group as *Justicia*, but Lindau (1895) and Bremekamp (1965) segregate it on the basis of its extraordinary pollen. I support the latter decision.

With the removal of the Diclipterinae and Isoglossinae, the Justiciinae is a more homogenous subtribe characterised by bilabiate corollas with distinct rugulae in their upper lips, two stamens and no staminodes. The upper lip is very often hooded. Generic limits within the subtribe are poorly defined or based on single characters. Intensive study in progress at present includes reassessment of *Justicia* (Immelman, 1983), *Duvernoia* and *Adhatoda* (Manning & Getliffe Norris, 1985) and *Monechma* (Munday, 1980). The relationship of *Aulojusticia* and *Siphonoglossa* will also be investigated by Immelman as Clarke placed *Aulojusticia* in synonomy with *Siphonoglossa*, while Dyer (1975) maintained *Aulojusticia* as a separate genus.

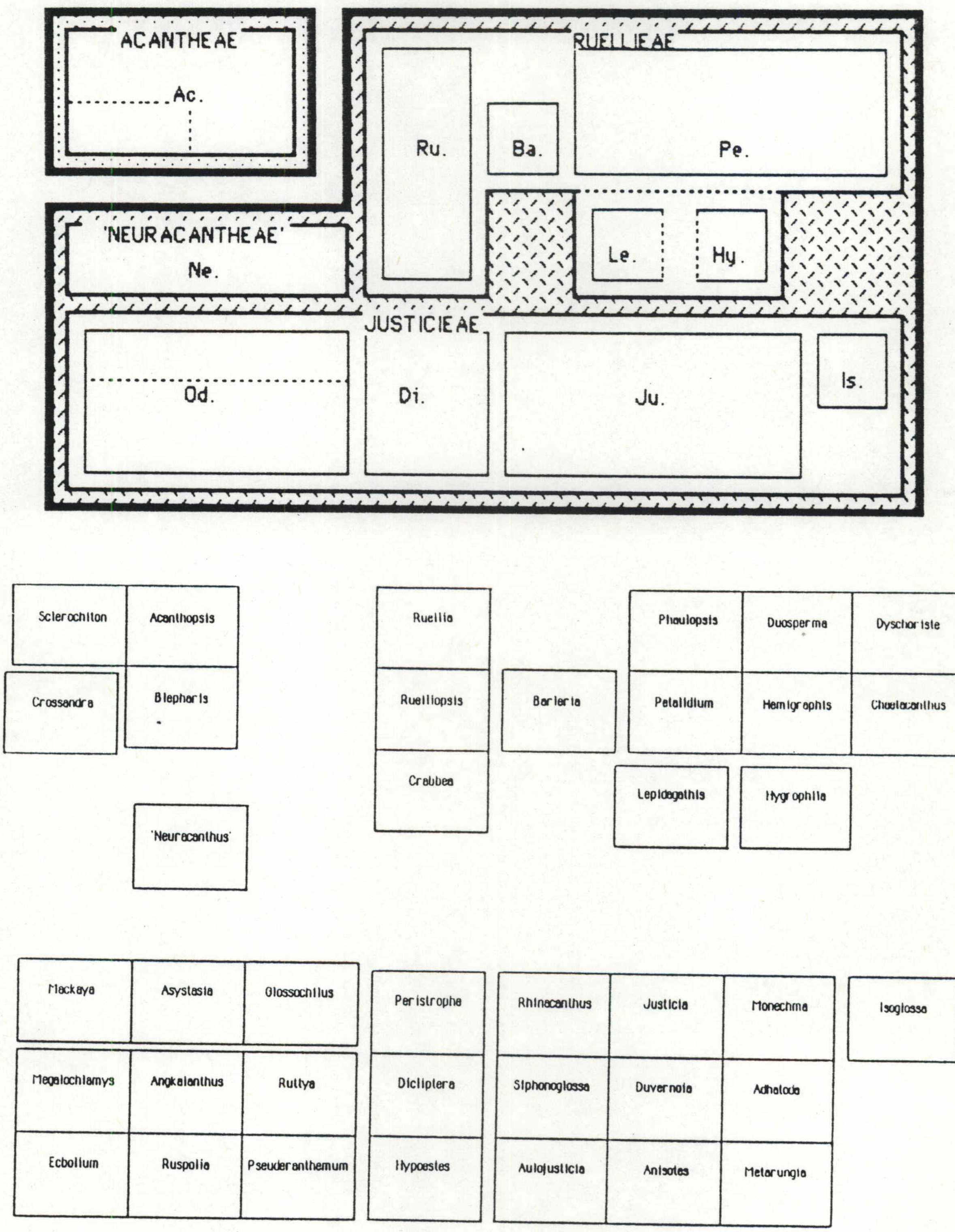
The classification of the Acanthaceae is still fluid, but I believe that Bremekamp has made significant contributions by proposing his scheme of classification (1965). In the course of my appraisal of the classification, I have endeavoured to place the southern African genera in appropriate groups in the Justicieae. I am, however, uncertain that groups have been distinguished at appropriate levels as it appears that the Justicieae are as different from the remainder of the Ruellioideae as are the Acanthoideae from the Ruellioideae. I feel that a more appropriate classification of southern African Acanthaceae may regard the Justicieae as a subfamily with two tribes, representing the present Odontoneminae and Justiciinae. The new Odontonemae would comprise at least two subtribes, namely the Odontoneminae and another including *Angkalanthus* from Africa and *Carlowrightia* A. Gray, *Mexacanthus* T.F. Daniel, *Anisacanthus* Presl, *Mirandea* Rzedowski, *Tetramerium* Nees and *Henrya* Nees from America. Daniel *et al* (1984) have suggested that these American genera should be recognised at suprageneric level, as they all have a chromosome number of 18 and all have no staminodes and in these features are different from other Odontoneminae *sensu* Bremekamp. I endorse their views on the basis of my observations on *Angkalanthus transvaalensis*. The new Justicieae would comprise three subtribes in southern Africa, Diclipterinae (which in many respects is advanced) Isoglossinae and Justiciinae. If there are other close relatives to *Anisotes* and *Metarungia*, their suprageneric affinity may be worthy of recognition.

Conservatively, however, I consider that the southern Afican Acanthaceae belong to two subfamilies, the Acanthoideae and Ruellioideae *sensu* Bremekamp. I find that all the southern African Acanthoideae belong to the tribe Acantheae, but suggest that *Crossandra* may deserve to be placed in its own subtribe. The Ruellioideae in southern Africa represent at least two, if not three, tribes. These are the Ruellieae, the Justicieae, and a tribe, as yet undescribed, which will include the African species that have mistakenly been identified as *Neuracanthus*. The Ruellieae comprise at least three subtribes, the Ruelliinae, the Barleriinae and the Petalidiinae. *Hygrophila* and *Lepidagathis* may represent another two subtribes in the Ruellioideae. Within the Justiciinae there are four tribes represented in southern Africa including the Diclipterinae originally described by Lindau (1895), which I suggest must be ammended and reinstated. My views on the subdivision of the family and classification of the southern African genera are presented in Figure 74.

Having considered the classification of southern African genera in the family, I became interested in the evolution of these groups. I am aware of only two accounts of evolution in the Acanthaceae; that of Willis (1949) and that of De (1968). Willis (*loc. cit.*) did not set out to provide an evolutionary scheme of the Acanthaceae, but has made comments about evolution in his account of the dispersal of the family. He states 'The change from *Justicia* to *Ruellia* could only have been a sudden mutation, and as advantage was not in any way involved, there seems no reason why it should not be repeated, or even reversed, and there is reason to suppose that both these phenomena may be frequent .....As yet, one is very handicapped in work of this kind by complete lack of knowledge of the laws of incidence of character'.

While I cannot claim a full knowledge of the incidence of characters in the Acanthaceae as a whole, I have an inventory of characters in the southern African genera (Tables 2 - 9 & 11) and find that my views differ from those of Willis. I do not think that there was sudden mutation from *Justicia* to *Ruellia* nor do I think that there was no advantage involved. I feel rather that the evolution was from *Ruellia* to *Justicia* through intermediate steps of forms similar to *Asystasia* and *Mackaya*. The selective pressure has been adaptation to bee pollination and *Justicia* appears to be far more specialised for this type of pollination, than does *Ruellia*.

Figure 74: Proposed scheme of classification of southern African Acanthaceae. Thick lines represent boundaries of subfamilies, medium lines of tribes, thin lines of subtribes and dotted lines represent uncertain boundaries. Genera positioned as in key below and subtribes abbreviated as follows: Ac. = Acanthinae, Ba. = Barleriinae, Di. = Diclipteriinae, Hy. = Hygrophilinae, Is. = Isoglossinae, Ju. = Justiciinae, Le. = Lepidagathidinae, Od. = Odontoneminae, Pe. = Petalidiinae and Ru. = Ruelliinae.



ACANTHEAE
Ac.
RUELLIEAE
Ru.
Ba.
Pe.
Le.
Hy.
'NEURACANTHEAE'
Ne.
JUSTICIEAE
Od.
Di.
Ju.
Is.
Sclerochiton
Acanthopsis
Crossandra
Blepharis
'Neuracanthus'
Ruellia
Ruelliopsis
Crabbea
Barleria
Phaulopsis
Duosperma
Dyschoriste
Petalidium
Hemigraphis
Chaetacanthus
Lepidagathis
Hygrophila
Mackaya
Asystasia
Glossochilus
Megalochlamys
Angkalanthus
Ruttya
Ecbolium
Ruspolia
Pseuderanthemum
Peristrophe
Dicliptera
Hypoestes
Rhinacanthus
Justicia
Monechma
Siphonoglossa
Duvernoia
Adhatoda
Aulojusticia
Anisotes
Metarungia
Isoglossa

De (1968) provides a hypothetical family tree, but in this family tree there are some anomalies. *Barleria* and *Ruellia*, which are very similar in many important characters are in the two different sub-orders into which De has divided the family. *Acanthus* L. and *Crossandra*, which I and many authors consider to belong to the Acanthae, De has placed in different sub-orders. *Odontonema* Nees and *Asystasia*, which I consider to belong to the same subtribe as each other have been placed in different suborders by De and the genera that De has placed in her 'Dicliptereae' bear very little resemblance to *Dicliptera*. Some of the genera that De has put into the same suborders are often unrelated. Neither of these schemes, therefore, is satisfactory.

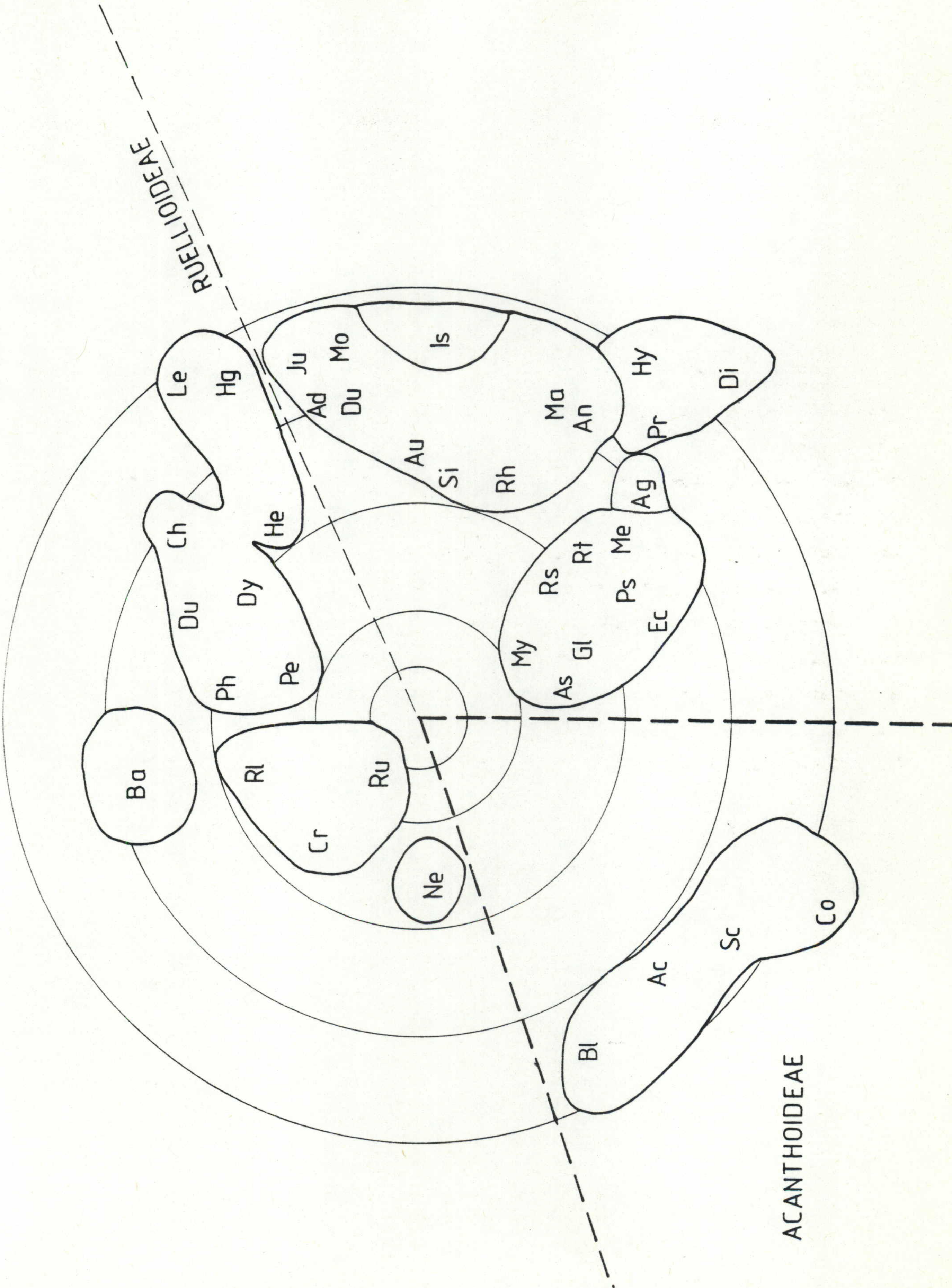
I have designed a scheme of evolution (fig. 75), which I believe reflects evolution in the southern African Acanthaceae more accurately. This scheme, is in no way final, and is a hypothesis with which other workers can compare their results. Indeed, I acknowledge that it was only when I read the hypotheses of Willis and De that I was able to formulate my own hypothesis. The genera have been grouped on the basis of the characters described in the discussion on classification. The level of advancement of each genus has been assessed mainly from the degree of specialisation of the corolla, which is the primary organ involved in the attraction of pollinators. In this scheme, I assume that forms such as *Hygrophila* and *Justicia* have been derived by convergent evolution.

Conclusion

Bremekamp's (1965) classification of the Acanthaceae is appropriate to most of the southern African Acanthaceae, although, as he himself indicated, it is not to be considered as the final classification of the Justicieae. Lindau's (1895) classification, although often criticised, has many positive aspects, and with the reassortment of some genera amongst tribes and subtribes, should to some extent be superimposed on the classification of Bremekamp. Further consideration of the classification and evolution of the Acanthaceae is an interesting, challenging and exciting area that is worthy of much more research.

Figure 75: Proposed scheme of evolution in the Acanthaceae, based on information from southern African material. Circles show degree of advancement, Thick broken lines represent borders between the subfamilies, thinner broken line represents border between the Justicieae and the other tribes of the Ruellioideae, genera as listed :

Ac = Acanthopsis, Ad = Adhatoda, Ag = Angkalanthus, As = Asystasia,
Au = Aulojusticia, Ba = Barleria, Bl = Blepharis, Ch = Chaetacanthus,
Co = Crossandra, Cr = Crabbea, Di = Dicliptera, Du = Duosperma,
Dv = Duvernoia, Dy = Dyschoriste, Ec = Ecbolium, Gl = Glossochilus,
He = Hemigraphis, Hg = Hygrophila, Hy = Hypoestes, Is = Isoglossa,
Ju = Justicia, Le = Lepidagathis, Ma = Macrorungia, Me = Megalochlamys,
Mo = Monechma, My = Mackaya, Ne = Neuracanthus, Pe = Petalidium,
Ph = Phaulopsis, Pr = Peristrophe, Ps = Pseuderanthemum,
Rh = Rhinacanthus, Rl = Ruelliopsis, Rs = Ruspolia, Rt = Ruttya,
Ru = Ruellia, Sc = Sclerochiton and Si = Siphonoglossa.


RUELLIOIDEAE
ACANTHOIDEAE
Le
Hg
Ju
Mo
Is
Ad
Du
Hy
Di
Ma
An
Pr
Au
Si
Rh
Ag
Ch
He
Me
Rt
Rs
Dy
Ps
Du
Ec
My
Gl
Ph
Pe
As
Ba
Rl
Ru
Cr
Ne
Co
Sc
Ac
Bl

FORMAL TAXONOMY

Key to subfamilies, tribes and subtribes of Acanthaceae in southern Africa.

1) Corolla one-lipped, with the adaxial suture slit; stamens 4, all monothecous: Subfamily Acanthoideae 2

1a) Corolla actinomorphic, subactinomorphic or two-lipped, the adaxial suture not slit; if 4 stamens present, then at least two with bithecous anthers: Subfamily Ruellioideae 3

2) Stamens exserted beyond corolla throat, filaments epipetalous for up to half of their length, stout; corolla white, blue, purple or various combinations: Tribe Acantheae, Subtribe Acanthinae

2a) Stamens included in corolla tube; filaments epipetalous for most of their length, slender; corolla yellow, orange or red: Tribe Acantheae, Subtribe 1

3) Calyx markedly bilabiate, lobes of two- and three-fid lips joined for most of their length; corolla tubular below, rotate above, with induplicate aestivation; stamens included in narrow part of tube and filaments bifurcated between the thecae: Tribe 'Neuracantheae'

3a) Calyx not bilabiate or only obscurely so, in which case the lobes are free for at least half of their length; corolla not rotate above, corolla aestivation not induplicate; stamens not included in narrow part of the tube (except in *Hemigraphis*), filaments not bifurcated 4

4) Seeds with hygroscopic hairs on surface; corolla usually with contorted aestivation, but if imbricate, then not ascending; flowers with 4 stamens (except *Chaetacanthus* which has 2 stamens and banded pollen and some species of *Barleria* which have 2 stamens and globose pollen with deep reticulations and porate apertures): Tribe Ruellieae 5

4a) Seeds without hygroscopic hairs; corolla with ascending aestivation; flowers with two stamens (except *Asystasia* and *Glossochilus*, both of which have 4 stamens and colporate pollen with shallow reticulations), sometimes with two, rarely three staminodes: Tribe Justicieae 9

5) Stamens never didynamous, never attached to a flange of tissue; calyx of 4 lobes, two large lobes outside of the two lateral smaller narrower lobes: Subtribe Barleriinae

5a) Stamens didynamous, often attached to a flange of tissue decurrent on the corolla tube; calyx usually of 5 lobes, but if of 4, then not of two large and two small lobes; fruit sometimes with elastic placental bases, sometimes with more than two ovules in each locule 6

6) Flowers distinctly bilabiate, with rugula in upper lip, and either with two yellow bosses on lower lip or with 3 or more seeds in each locule 7

6a) Flowers actinomorphic, subactinomorphic or bilabiate, but if bilabiate, then without a rugula in the upper lip, without yellow bosses on the lower lip or with 2 or less seeds in each locule 8

7) Corolla without bosses in lower lip, the two outer lobes of the lower lip outermost in bud, two seeds in each locule: Subtribe Lepidagathidinae

7a) Corolla with two yellow bosses on lower lip, corolla contorted in the bud, two ovules in each locule: Subtribe Hygrophilinae

8) Flowers actinomorphic, subactinomorphic or subbilabiate and fruits either with inelastic placental bases or fruits with two ovules in each locule; stamens didynamous, but never joined to a flap of tissue: Subtribe Ruelliinae

8a) Either flowers distinctly bilabiate or fruits with elastic placental bases or fruits with with more than two ovules in each locule; stamens sometimes attached to a flange of tissue that is decurrent on the inside of the corolla: Subtribe Petalidiinae

9) Corolla with a distinct rugula in upper lip 10

9a) Corolla without a rugula in upper lip 11

10) Pollen prolate, bi- or tricolporate, without spines: Subtribe Justiciinae

10a) Pollen spheroidal, biporate, with one pore at each pole, a pusticulate ring around the equatorial circumference and spines on the rest of the surface: Subtribe Isoglossinae

11) Corolla not resupinate; seeds usually larger than 3 mm in diameter; with four stamens or two stamens and two or sometimes three staminodes (except *Angkalanthus*, which has two stamens and no staminodes, but the anther thecae are parallel); inflorescence a terminal thyrse, terminal monochasium or of single flowers in the axils of leaves: Subtribe Odontoneminae

11a) Corolla resupinate; seeds seldom larger than 3 mm in diameter; with two stamens and no staminodes, anther thecae superposed (except *Hypoestes* where the anthers are monothecous); inflorescences compound, of monochasia surrounded by a pair of bracts: Subtribe Diclipterinae

Key to genera of Acanthaceae in southern Africa

Acantheae

Acanthinae

1) Calyx with 5 lobes, seed surface convoluted, without hygroscopic hairs 7978 *Sclerochiton*

1a) Calyx with 4 lobes, seed surface with feathery hygroscopic hairs 2

2) Anticous (outer) filaments branched at tip, so that they have a process; ovary with two glands at tip; stigma with two subequal, short lobes 7980 *Blepharis*

2a) Anticous (outer) filaments without a process at tip; ovary without two glands at the tip; stigma lobes unequal, anticous lobe enlarged and flattened, posticous lobe minute 7982 *Acanthopsis*

Subtribe 1

Only one genus in southern Africa 7985 *Crossandra*

'Neuracantheae'

Only one genus in southern Africa 7977 *Neuracanthus*

Ruellieae

Ruelliinae

1) Corolla contorted in bud; disc cupular 7972 *Crabbea*

1a) Corolla quinuncial, not contorted in the bud; disc annular 2

2) Anthers spurred; upper lobe of stigma absent; capsules estipitate; seeds with hygroscopic hairs over the entire surface; pollen banded, pores with a lip on each side 7946 *Ruelliopsis*

2a) Anthers muticous; upper lobe of stigma present although smaller than the lower; capsules stipitate; seeds glabrous in centre, rimmed with hygroscopic hairs; pollen with large reticulations, pores not lipped 7965 *Ruellia*

Barleriinae

Only one genus in southern Africa 7973 *Barleria*

Petalidiinae

1) Fruit with more than two ovules in each locule 7945 *Hemigraphis*

1a) Fruit with one or two ovules in each locule 2

2) Fruit with elastic placenta bases; corolla obscurely bilabiate 3

2a) Fruit with inelastic placenta bases, corolla clearly bilabiate 4

3) Calyx zygomorphic, the anticous lobe much bigger than the other four lobes; posticous stigma lobe smaller than anticous lobe; corolla shorter than 1,5 mm and white 7932 *Phaulopsis*

3a) Calyx actinomorphic; stigma lobes equal in size; corollas often longer than 15mm and showy 7934 *Petalidium*

4) Stamens two, with or without two staminodes 7941 *Chaetacanthus*

4a) Stamens four 5

5) Capsule with one seed in each locule 7940 *Duosperma*

5a) Capsule with two seeds in each locule 7939 *Dyschoriste*

Hygrophilinae

Only one genus in southern Africa 7926 *Hygrophila*

Lepidagathidinae

Only one genus in southern Africa 7971 *Lepidagathis*

Justicieae

Odontoneminae

1) Stamens four 2

1a) Stamens two 3

2) Flowers produced singly in the axils 7970 *Glossochilus*

2a) Flowers produced in monochasia (usually terminally) or in lax terminal thyrses 8007 *Asystasia*

3) Anthers monothecous in chasmogamous flowers 4

3a) Anthers bithecous in chasmogamous flowers 5

4) Corolla tube considerably longer than upper lip; disc shallowly cupular 8022 *Ruspolia*

4a) Corolla tube shorter than or as long as upper lip; disc large, saucer-shaped and with a projection on posticous side 8063 *Ruttya*

5) Inflorescence with small bracts, calyx easily visible 6

5a) Inflorescence with large bracts obscuring the calyx 7

6) Flowers subactinomorphic, campanulate 8039 *Mackaya*

6a) Flowers bilabiate, tubular below 8024 *Pseuderanthemum*

7) Corolla thinly-textured, purplish blue; without staminodes; pollen prolate, without pseudocolpi, yellow when fresh
8061 *Megalochlamys*

7a) Corolla thickly-textured, light blue, pale lilac or white; with two staminodes; pollen almost spheroidal, with pseudocolpi, white or pink when fresh 8048 *Ecbolium*

Diclipteriinae

1) Anthers monothecous 8032 *Hypoestes*

1a) Anthers bithecous 2

2) Capsules with placentae that are inelastic at the bases
8029 *Peristrophe*

2a) Capsules with placentae that are elastic at the bases
8031 *Dicliptera*

Justiciinae

1) Corolla orange, red or yellowy-brown, lower lip longer than 25 mm, but narrower than 10 mm 2

1a) Corolla white, pink, lilac, purple or blue (not orange, red or yellowy-brown), lower lip shorter than 25 mm or, if longer than 25 mm then broader than 10 mm 3

2) Capsules with placentae that are elastic at the bases
8030 *Metarungia*

2a) Capsules with placentae that are inelastic at the bases
8096 Anisotes

3) Corolla tube longer than the lips 4

3a) Corolla tube shorter than the lips 6

4) Stigma with filiform lobes, flowers in terminal inflorescences
8054 *Rhinacanthus*

4a) Stigma with very short lobes, flowers in axillary inflorescences
..........5

5) Upper lip of corolla rectangular, two-lobed, tube glabrous or hairy 8049 *Siphonoglossa*

5a) Upper lip of corolla, triangular, minutely emarginate, tube with glandular trichomes common 8099 *Aulojusticia*

6) One seed in each locule; seed smooth and shiny 8094a *Monechma*

6a) Two seeds in each locule, seeds rough and often tuberculate or seeds borne in an indehiscent capsule, in which case there is only one seed in each capsule and the seed may be shiny 7

7) Calyx lobes shorter than the tube; posticous hooded lip of corolla with staminal channels at least half as long as the lip

8055 *Duvernoia*

7a) Calyx lobes longer than the tube; posticous lip of corolla with staminal channels shorter than half the length of the lip..........8

8) Inflorescences pedunculate and diffuse, anticous lip deeply divided; palate of two smooth tumuli 8094 *Justicia*

8a) Inflorescence sessile, or if pedunculate then strobilate; palate rugose 9

9) Lower anther thecae rounded at the base, or shortly tailed; length of lips of corola nearly equal, the upper lip deeply hooded

8094b *Adhatoda*

9a) Lower anther thecae short- or long-tailed; posticous lip of corolla shorter than anticous lip, posticous lip shallowly hooded

8094 *Justicia*

(Steps 7 to 9 adapted from Manning 1983.)

Isoglossinae

Only one genus in southern Africa 8079 *Isoglossa*

List of southern African genera of the Acanthaceae
placed in the groups according to my revised system of
Bremekamp's (1965) classification

First number after each genus is the number of southern African species in each genus, the number in brackets is the total number of species in the genus (based on Dyer, 1975).

Genera that Bremekamp recommended should be transferred to the
SCROPHULARIACEAE

7909 Nelsonia 1 (1)
7908 Elytraria 1 (7)

THUNBERGIACEAE

7914 Thunbergia 11 (200)

ACANTHACEAE

ACANTHOIDEAE

Acantheae

7978 Sclerochiton 5 (12)
7980 Blepharis 50 (80)
7982 Acanthopsis 7 (7)
7985 Crossandra 3 (7) (should probably be in its own subtribe)

RUELLIODEAE

Lepidagathideae

Lepidagathidineae

7971 Lepidagathis 2 (100)

7977 Neuracanthus 1 (20) (should probably be in its own tribe)

	Ruellieae	
	Hygrophylinae	
7926	Hygrophila	4 (80)
	Petalidiinae	
7932	Phaulopsis	2 (20)
7934	Petalidium	25 (40)
7939	Dyschoriste	10 (100)
7940	Duosperma	1 (several)
7941	Chaetacanthus	4 (4)
7945	Hemigraphis	0 (90)
	Ruelliinae	
7946	Ruelliopsis	2 (3)
7965	Ruellia	9 (150)
7972	Crabbea	8 (12)
	Barleriinae	
7973	Barleria	60 (250)
	Justicieae	
	Odontoneminae	
7970	Glossochilus	2 (2)
8007	Asystasia	7 (70)
8039	Mackaya	1 (1)
8063	Ruttya	1 (3)
8022	Ruspolia	1 (4)
8024	Pseuderanthemum	1 (120)
8048	Ecbolium	3 (17)
8061	Megalochlamys	2 (3)
8044	Angkalanthus	1 (2)
	Diclipterinae	
8031	Dicliptera	16 (150)
8026	Peristrophe	9 (25)
8032	Hypoestes	3 (150)
	Isoglossineae	
8079	Isoglossa	15 (50)

	Justiciinae	
8054	Rhinacanthus	3 (15)
8049	Siphonoglossa	3 (15)
8099	Aulojusticia	2 (2)
8094	Justicia	40 (300)
8094a	Monechma	23 (60)
8094b	Adhatoda	2 (20)
8055	Duvernoia	2 (several)
8030	Macrorungia	3 (7)
8096	Anisotes	2 (15)

PERISTROPHE Nees in Wallich, Plantae Asiaticae Rariores 3: 112 (1832); Endlicher, Genera Plantarum 9: 707 (1839); Meisner, Plantarum vascularium genera 9: 297 (1840); Nees in Linnaea 15: 374 (1841); Nees in DC., Prod. 11: 492 (1847); Harvey, The Genera of South African Plants 286 (1868); Bentham and Hooker, Genera Plantarum 1071 (1876); Clarke in Hooker, Flora of British India 4: 554 (1885); Lindau in Engl. and Prantl, Pflanzenfam. 4(3b): 331 (1897); Clarke in Thiselton-Dyer, Fl. Trop. Afr. 5: 242 (1900); Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 84 (1901); Hutchinson and Dalziel, Flora of West Trop. Afr., ed. 1, 2: 264 (1936); Heine in Hepper, Flora of West Trp. Afr. ed. 2, 2: 424 (1963); Agnew, Upland Kenya Wild Flowers 609 (1974); Dyer, The Genera of South African Flowering Plants 1: 593 (1975). Type Species: *Peristrophe baphica* (Spreng.) Bremekamp in Nova Guinea n.s., 8: 149 (1957) [= *P. tinctoria* (Roxburgh) Nees *comb. illeg.*].

Suffruticose annuals or evergreen perennials up to 2 m high. *Leaves* simple, opposite, widely ovate to lanceolate, acuminate to acute, entire, attenuate at base, herbaceous, usually with eglandular trichomes, especially on midrib; petiolate. *Inflorescence* of monochasial cymes (inflorescence units) enclosed by a pair of tertiary bracts, with (1) - 2 - 3 - (4) inflorescence units umbellately arranged, often compounded. *Bracts*: secondary bracts 2, free, narrowly triangular to lanceolate, sessile or leaflike; tertiary bracts lanceolate to broadly ovate, acuminate. *Flowers* perfect, zygomorphic, occasionally cleistogamous. *Calyx* with short tube and lanceolate lobes, margins usually membranous, inner surface pubescent, trichomes appressed and eglandular. *Corolla* bilabiate, resupinate; tube narrowly cylindric below, subcampanulate above, with 2 pairs of longitudinal hairy ridges within, with eglandular and sometimes glandular trichomes without; lip in lower position elliptic or ovate, minutely emarginate; lip in upper position narrowly elliptic, 3-fid, flower lilac to purple, occasionally white, with dark purple honey guides on white background on lip in upper position. *Stamens* 2, exserted, filaments epipetalous, linear, usually white or yellow; anthers bithecous, thecae superposed and separated, approximated or slightly overlapping, introrse, purple. *Disc* shallowly cupular, with two small awns, nectariferous. *Gynoecium* bicarpellate; stigma bilobed; style exserted, filiform, glabrous to sparsely strigose; ovary superior, with septum in median longitudinal axis, ovoid or ellipsoid, bilocular, with two ovules in each locule. *Fruit* a stipitate capsule, clavate or obtrullate, placentae inelastic at the bases and bearing retinacula, dehiscing loculicidally. *Seeds* discoid, usually 2 in each locule, rough and tuberculate.

The genus Peristrophe occurs in Africa and the East Indies and comprises about 25 species, of which 9 occur in southern Africa. *Peristrophe* is very closely related to *Dicliptera* and differs only in the nature of the placental bases, which are inelastic in *Peristrophe* and elastic in *Dicliptera*. Some workers have tried to apply other characters (e.g. width of the tertiary bracts) as generic characters, and this has led to the incorrect classification of species such as *P. angolensis*, *P. transvaalensis* and *P. hereroensis*, all of which were described in the genus *Dicliptera*. Another species that has been confused with *Dicliptera* is *P. bivalvis* (L.) Merr., which has been confused with *Dicliptera foetida* (Forssk.) Blatter (Wood, Hillcoat & Brummitt, (1983). In southern Africa, the shape and venation of the tertiary bracts, if used simultaneously, can act as a guide to the genera. The tertiary bracts of the southern African species of *Peristrophe* are either narrow and single-veined, or if broad, then the veins are pinnate and the secondary veins are reticulate near the margins (plate 3), while the bracts of *Dicliptera* are 3-, 5- or even 7-veined from the base and the secondary veins do not form conspicuous reticulations near the margins (fig. 16).

Nees, in 1832 and 1847, recognised two sections in *Peristrophe* and subdivided the first of these into two subsections, but did not name the sections or subsections. Since that time, three species of *Peristrophe* have been described from Namibia and these, I believe, belong to a group not described by Nees. Thus, I suggest that Nees's (1847) first section comprises three groups and feel that these three groups are sufficiently different to be recognised at the rank of section. In southern Africa, the species of *Peristrophe* form two groups, corresponding to two of these proposed sections, one described by Nees and the other not seen by him.

Typical Section

Type species: *Peristrophe baphica.*

Inflorescence of two to seven monochasial cymes (inflorescence units) umbellately arranged, 'umbels' sometimes compounded. *Tertiary bracts* spathulate, ovate to obovate, with three, five or seven veins from the base, remaining green when mature. *Capsule* clavate.

Included species: *P. montana and P. speciosa.*

Section 1 differs from the typical section by having only two inflorescence units in each 'umbel', by having a single primary vein from the base of the tertiary bracts, by having tertiary bracts that have conspicuous secondary veins and become membranous when mature and by having capsules that are obtrullate in profile. Type species: *P. grandibracteata.*

Inflorescence of monochasial cymes (inflorescence units), usually two umbellately arranged. *Tertiary bracts* ovate to widely ovate, 9,1 - 14,4 X 6,1 - 13,8 mm, with a single vein from the base and becoming membranous when mature. *Fruit* obtrullate in profile.

Included species: *P. hereroensis* and *P. sp. 1.*.

Section 2 differs from the typical section and from Section 1 by the narrower, less conspicuous tertiary bracts, which are lanceolate to oblanceolate (not ovate to broadly ovate) and narrower than 4 mm and from Section 1 by the tertiary bracts that are green (not membranous and conspicuously veined) at maturity and by having clavate (not obtrullate) capsules. Type Species: *Peristrophe cernua.*

Inflorescence of monochasial cymes (inflorescence units), usually 3 - 4 umbellately arranged, often compounded. *Bracts*: tertiary bracts lanceolate to oblanceolate, 3,0 - 18,0 X 0,4 - 3,2 mm, green. *Fruit* clavate.

Included species: *P. paniculata, P. transvaalensis, P.cliffordii,* *P. gillilandiorum* and *P. kotschyana*.

Key to the southern African species of the genus *Peristrophe*

1) Tertiary bracts broader than 5 mm, veins pinnate, secondary veins forming reticulation at bract edges, capsules obtrullate in profile Section 1) ....2)

1a) Tertiary bracts narrower than 4 mm, with a midrib only, or if more veins present, then not forming reticulation at edges of bract, capsules clavate Section 2) ....5)

2) Secondary bracts leaflike, longer than 7 mm; tertiary bracts widely cuneate at base; leaves lanceolate, length : breadth ratio more than 2,4:1 ....3)

2a) Secondary bracts not leaflike, shorter than 7 mm; tertiary bracts reniform or cordate at base, leaves ovate to widely ovate, length : breadth ratio smaller than 2,4:1 ....4)

3) Young stems appearing white, densely pubescent with eglandular trichomes with enlarged, ornamented terminal cells *1) P. grandibracteata*

3a) Young stems appearing green, not densely pubescent, trichomes without enlarged terminal cells *2) P. hereroensis*

4) Leaf length : width ratio less than 1,75:1; tertiary bract length : breadth ratio less than 1,25:1; capsules pubescent *3.1) P. sp. 1* ssp. *1*

4a) Leaf length : width ratio greater than 1,75:1; tertiary bract length : breadth ratio greater than 1,25:1; capsules glabrous *3.2) P. sp. 1* ssp. 2

5) Corolla 6 - 14 mm long; plant annual, up to 2 m high, rootstock not woody and seldom branched *4) P. paniculata*

5a) Corolla longer than 14 mm; plant suffruticose perennial, up to 1,2 m high; with woody rootstock which is often branched ....6)

6) Tertiary bracts longer than 14 mm and length : breadth ratio less than 6,2:1 *5) P. transvaalensis*

6a) Tertiary bracts shorter than 13 mm, but if longer, then length : breadth ratio greater than 6,2:1 ....7)

7) Mature stems densely pubescent between ridges and found in the Limpopo River Valley ....8)

7a) Mature stems glabrous or sparsely pubescent between ridges or not found in the Limpopo River Valley

..........9)

8) Tertiary bracts up to 5 mm long, length : breadth ratio less than 6:1 *6) P. cliffordii*

8a) Tertiary bracts longer than 7 mm, length : breadth ratio greater than 7:1 *7) P. gillilandiorum*

9) Lip in lower position (6,5) - 7,5 - 9,2 - (10,2) mm long; occurring in Zimbabwe, Botswana and the Transvaal *8) P. kotschyana*

9a) Lip in lower position (7,2) - 9,8 - 16,5 - (22,3) mm long; occuring in Natal, Transkei, Ciskei and Cape *9) P. cernua*

Section 1

1) P. grandibracteata Lindau in Engl., Bot. Jahrb. 49: 404 (1913); P.G. Meyer in Merxmüller, Prod. Fl. Südwestafrika 130: 49 (1968), *pro parte excl. syn. et De Winter 2356, Dinter 858, Dinter 459, Fleck 486, Merxmüller & Giess 1232, Seydel 3997, van Vuuren 573, Volk 11908 & Volk 12705*. Type: NAMIBIA 2616 (Aus): Kuibis (-DB), *Range 613* (SAM, lecto.!; BOL, isolecto.!).

Evergreen suffruticose perennial up to 0,5 m high, with woody stem bases and rootstock. *Leaves* lanceolate, acuminate, entire, attenuate at base (10,8) - 12,0 - 19,7 - (21,1) X (2,8) - 3,3 - 6,4 - (6,8) mm, mature leaves glabrous except along midrib,; petiole 1,6 - 3,7 - (4,4) mm. *Inflorescence* of monochasial cymes (inflorescence unit), (1) - 2 - (3) umbellately arranged; inflorescence axis (1,8) - 2,3 - 15,1 - (18,8) mm; longest axis of inflorescence units (1,3) - 2,9 - 9,1 mm. *Bracts* secondary bracts lanceolate to narrowly elliptic, (8,3) - 8,6 - 13,9 - (15,0) X 1,8 - 3,5 - (4,0) mm, with white eglandular trichomes common on midrib, and occasional on lamina, lamina sometimes glabrous, shortly petioled; tertiary bracts ovate to widely ovate, acuminate, base broadly cuneate, 11,4 - 13,3 - (14,0) X (6,1) - 6,9 - 9,0 mm, with white eglandular trichomes present on midrib, occasional on lamina, cystoliths present. *Calyx* tube 1,5 mm, lobes lanceolate, 3,5 mm, margins membranous and strigose, outer surface dense with small glandular trichomes, inner surface strigose with appressed eglandular trichomes and occasional short-stalked glandular trichomes. *Corolla* tube 9,8 - 11,7 - (12,0) mm with appressed, eglandular trichomes and stalked glandular trichomes; lip in upper position 7,7 - 8.9 - (9,3) X (3,0) - 3,1 - 6,1 - (6,5) mm, lip in lower position narrowly elliptic (6,0) - 6,1 - 10,4 - (10,5) X (2,0) - 2,2 - 3,2 mm; flowers mauve. *Stamens*: filaments with broad-based appressed eglandular trichomes and occasional short-stalked glandular trichomes, white; anther thecae superposed, touching, purple. *Disc* shallow cupular, upper edge smooth with 2 small broad jagged awns. *Gynoecium*: stigma bilobed, slightly uneven; style scarcely strigose; ovary ovoid, with glandular trichomes. *Fruit* a short-stalked capsule, obtrullate in profile, 8,4 X 3,6 mm, with frequent eglandular trichomes and some glandular trichomes.

CITATIONS

NAMIBIA

2416 (Maltahohë): Bullsportie (-AB), *Dinter 2148* (SAM).

2516 (Helmeringhausen): West of Helmeringhausen, Naus (-CD), *Olive, Muller & Steenkamp 6496* (PRE).

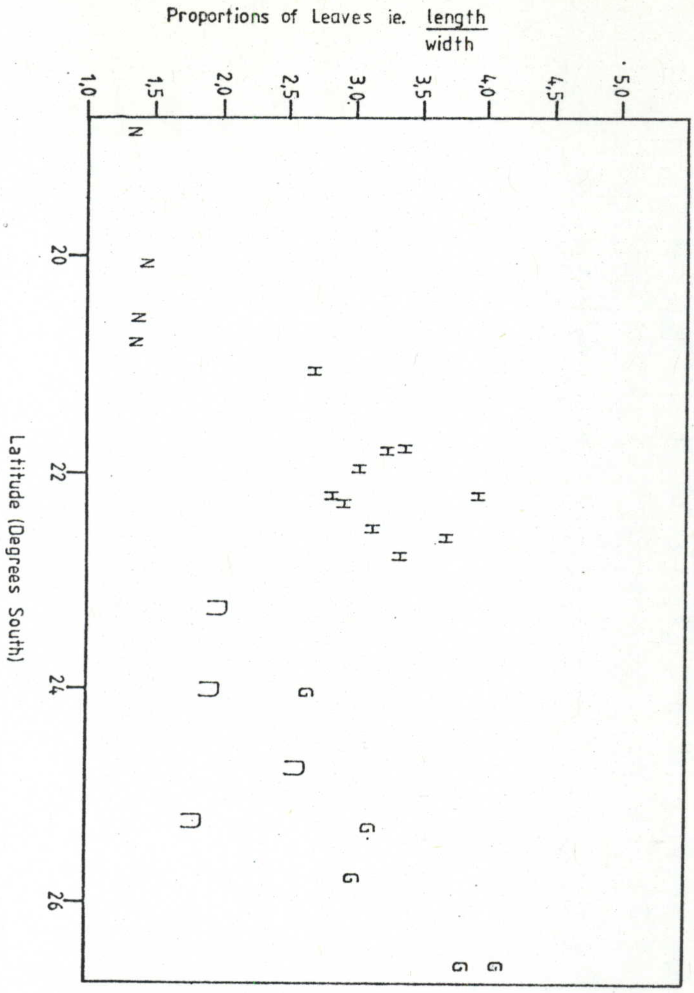
2517 (Gibeon): Farm Rosstrappe MAL 57 (-AC), *Möller 1311* (PRE, WIND).

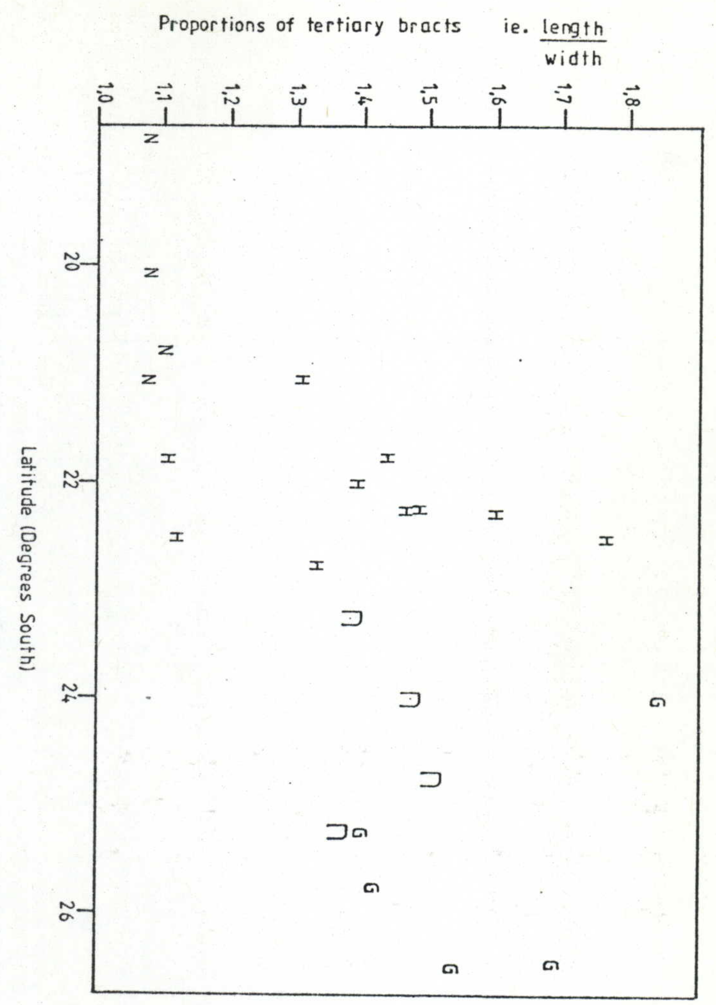
2615 (Luderitz): Rietrivier, Farm Weifsenborn LU 45 (-CA), *Kinges 2446* (PRE, WIND).

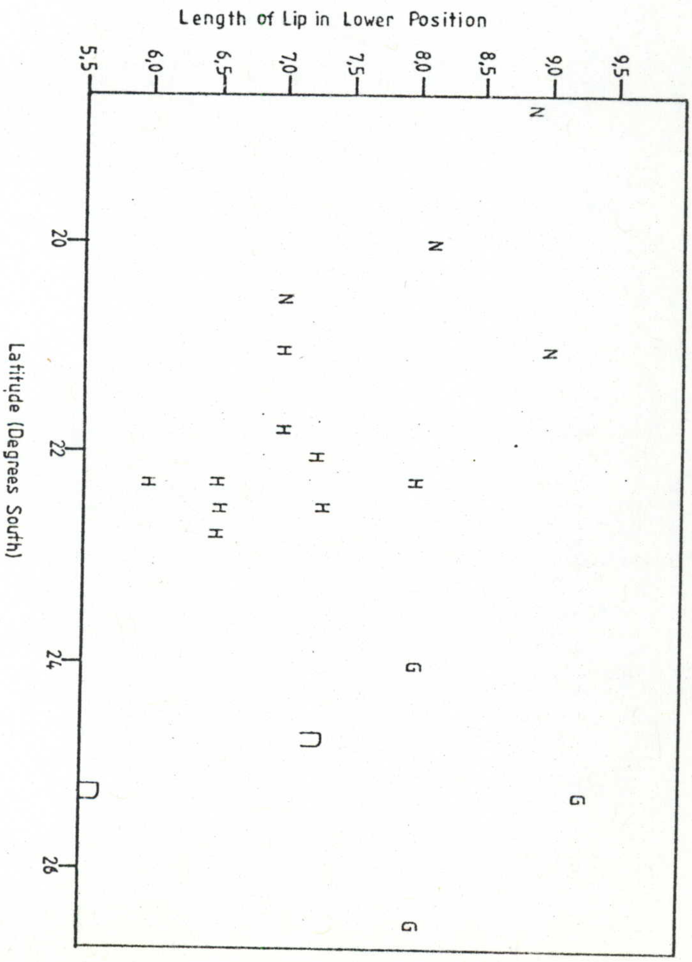
In his account of *P. grandibraceata* in Merxmuller's Prodromus, Meyer (1968) recognised the close relationship of *Dicliptera hereroensis* to *P. grandibracteata* by placing the former in synonomy with the latter. I find, however, that *P. grandibracteata* sensu Meyer represents three closely related species, and *P. grandibracteata s. s.* can be distinguished from the others by means of the dense vestiture of ornamented eglandular trichomes with enlarged terminal cells (fig. 36) present on stems of *P. grandibracteata s. s.*. These trichomes give the stems a conspicuous white colour (plate 29a). *P. grandibracteata s. s.* has a more southerly distribution (fig. 41) than the other species so that it was possible that the variation observed in the size of various structures was due to a clinal variation. Analysis of the variation, however, shows that the variation in the length of tertiary bracts, the length of secondary bracts, the leaf proportions and the length of the lip in the upper position is not distributed over a cline from north to south (fig. 76). *P. grandibracteata s.s.* has been collected in flower between April and June (fig. 72).

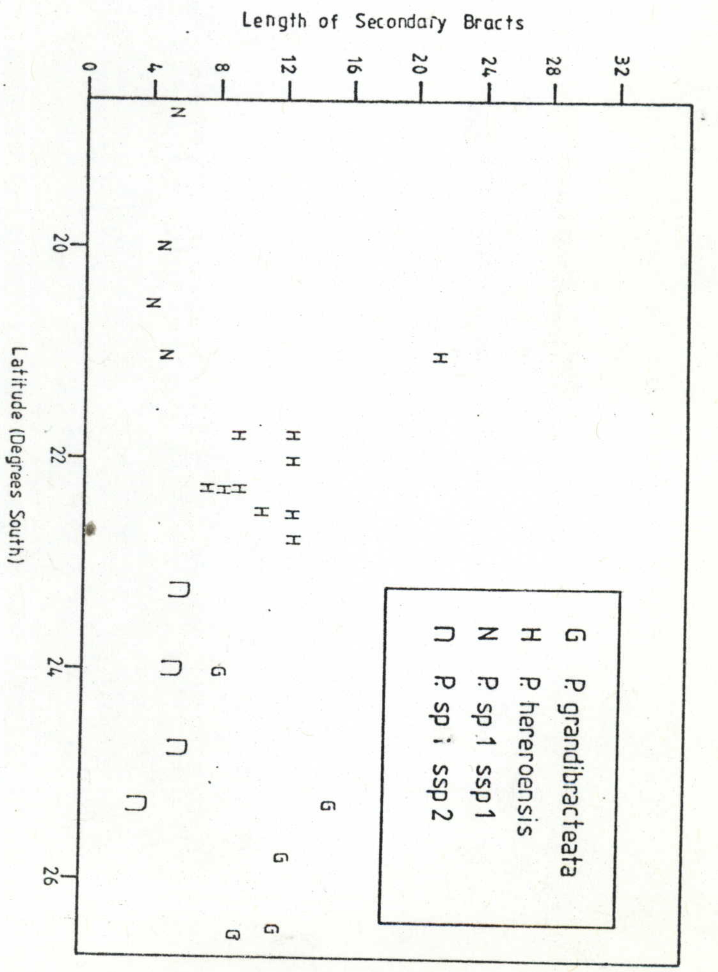
2) P. hereroensis (Schinz) Balkwill in S. Afr. J. Bot. 51(6): 489 (1985). Type: NAMIBIA 2217 (Windhoek): Otjihua (-BB), *Dinter 459* (Z, lecto.!, 2 sheets; GRA, K, SAM, isolecto.!).
Dicliptera hereroensis Schinz in Viert. Nat. Ges. Zurich 61: 438 (1916). Type: as for *P. hereroensis*.

Evergreen suffruticose perennial, up to 0,5m high, with woody stem bases and rootstock. *Leaves* lanceolate, acuminate, attenuate at base (14,3) - 15,7 - 23,2 - (26,0) X (3,9) - 4,5 - 8,0 - (9,6) mm, mature leaves sparsely pubescent, midrib pubescent, cystoliths present; petiole (1,0) - 1,1 - 2,2 - (2,9) mm. *Inflorescence* of monochasial cymes (inflorescence units), occasionally singly or more usually 2 umbellately arranged, inflorescence axis (1,7) - 2,0 - 7,1 - (10,6) mm; longest peduncle of monochasial cymes (4,1) - 4,7 - 11,3 - (13,1) mm. *Bracts*: secondary bracts leaflike, lanceolate to narrowly elliptic, (7,5) - 7,9 - 15,6 - (21,3) X 1,7 - 5,4 - (7,6) mm, with eglandular hairs common on midrib and occasional on lamina, shortly petioled; tertiary bracts ovate to widely ovate, acuminate, base broadly cuneate, (11,1) - 11,6 - 13,3 - (13,5) X (6,7) - 7,6 - 10,4 - (10,8) mm, with eglandular trichomes more common on midrib than lamina, cystoliths present. *Calyx* tube 1,5 mm; lobes lanceolate, 3,5 mm; margins membranous and strigose, outer surface dense with small glandular trichomes, inner surface strigose with appressed eglandular trichomes, and occasional short-stalked glandular trichomes. *Corolla* tube (8,0) - 8,9 - 11,4 - (12,4) mm, with appressed eglandular and short-stalked glandular trichomes; lip in lower position (5,8) - 6,3 - 7,9 - (8,2) X 1,5 - 3,5 - (5,0) mm, lip in upper position narrowly elliptic, 6,3 - 7,5 - (8,0) X (2,3) - 2,5 - 3,1 - (3,4) mm; flowers mauve. *Stamens*: filaments with short appressed


Proportions of Leaves ie. length/width
1,0
1,5
2,0
2,5
3,0
3,5
4,0
4,5
5,0
20
22
24
26
Latitude (Degrees South)


Proportions of tertiary bracts ie. length/width
1,0
1,1
1,2
1,3
1,4
1,5
1,6
1,7
1,8
20
22
24
26
Latitude (Degrees South)


Length of Lip in Lower Position
5,5
6,0
6,5
7,0
7,5
8,0
8,5
9,0
9,5
20
22
24
26
Latitude (Degrees South)


Length of Secondary Bracts
0
4
8
12
16
20
24
28
32
20
22
24
26
Latitude (Degrees South)
G P. grandibracteata
H P. hereroensis
N P. sp.1 ssp 1
⊓ P. sp i ssp 2

broad-based eglandular trichomes, white; anther thecae superposed, just touching, purple. *Disc* shallowly cupular, upper edge smooth, with 2 small triangular awns. *Gynoecium*: stigma bilobed, slightly uneven; style scarcely strigose; ovary ovoid, with glandular trichomes. *Fruit* a short-stalked capsule obtrullate in profile, (7,3) - 7,5 - 8,3 X (2,7) - 2,9 - 4,1 mm, with frequent glandular and eglandular trichomes. *Seeds* 2,1 - 2,6 X 2,1 - 2,5 mm, rough and tuberculate.

CITATIONS

NAMIBIA

1817 (Tsintsabis): Tsintsabis (-DB/DD), *Boss A58* (PRE).

2116 (Okahandja): Between Omaruru and Kalkfeld, Farm Okasongoro (-AA), *Germishuizen 2535* (PRE); Wilhelmstad, Waldhausen (-CD), *Schwudtfyer 4032* (WIND); Wilhelmstal, Farm Erichsfelde OK, Zwischen Spitzkoppe (-CD), *Volk 11908* (WIND); Okahandja (-DD), *Dinter 459* (SAM).

2117 (Otjosondu): Waterberg, Quickborn (-AA), *Bradfield 206* (PRE).

2217 (Windhoek): Beside Windhoek - Goreangab dam road, 500 m from Windhoek - Okahandja road (-AC), *Wanntorp & Wanntorp 363* (PRE); Neudam Exp(erimental) Farm (-AD), *van Vuuren 573* (WIND); Between Windhoek and Gobabis, Otjiwero (-BD), *Gillman 142* (SAM); 10 miles east of Windhoek on road to Neudam (-CA), *de Winter 2356* (PRE, WIND); East of Windhoek (-CA), *Dinter 858* (Z); Windhoek, Avis (-CA), *Seydel 3997* (COI, WIND); 5 miles NW of Windhoek (-CA), *Steyn 95* (NBG); Windhoek, Farm Voigtland (-CA), *Walter & Walter 110* (WIND); Windhoek, Immental (-CA), *von Koenen 560 & 563* (WIND); Windhoek (-CA), *Mücke 38* (PRE); Windhoek, Farm Rietfontein-Binsenheim WIN 85 (-CA), *Leippert 4570* (WIN); Finkenstein (-CB), *Seydel 4243* (SRGH).

2218 (Gobabis): Gobabis, Farm Grünental (-BD), *Merxmüller & Giess 1232* (PRE, WIND).

Hereroland, Churumanas, *Fleck 486* (Z).

Schinz (1916) cited three specimens with the original description of this species so that the name had to be lectotypified. *Dinter 459* was chosen as it was the most widely distributed specimen. Since then, it has been found that Dinter specimens from two localities are numbered 459. The type is that from Otjihua and the sheets of the specimens from Okahandja are not part of the type gathering. Dinter started a second series of numbers between 1903 and 1908 (Gunn & Codd, 1981). This, however, is unlikely to be the reason for trhe duplication in this instance as one sheet was collected on 29 March 1907 and the other in April of the same year. Meyer (1968) considered *D. hereroensis* to be synonomous with *P. grandibracteata*, thus indicating the close relationship of these species. *P. grandibracteata s. s.*, which has white stems that are densely covered with ornamented eglandular trichomes, can easily be distinguished from *P. hereroensis*, which has green stems with sparse eglandular trichomes (plate 29b). *P. hereroensis* has longer secondary bracts than *P. sp. 1* (over 7 mm in *P. hereroensis* and under 6 mm in *P. sp. 1*), and the tertiary bracts of *P. hereroensis* are widely cuneate at the base, while those of *P. sp. 1* are reniform or cordate at the base (plate 3). The length to breadth ratio of the leaves of *P. sp. 1.* is less than 2,4:1, but is greater than 2,4:1 in *P. hereroensis* and this also helps to separate the species. *P. hereroensis* has a more northerly distribution (fig. 42) than *P. grandibracteata s .s.* (fig. 41), while *P. sp.1* has a more coastal distribution (fig. 43) than *P. hereroensis*. P. hereroensis commences flowering in midsummer, with a peak in March and April, and appears to finish flowering in September (fig. 72).

3) P. sp. 1 *species nova* akin to *P. grandibracteata* and *P. hereroensis*, but differs from the former by the absence of dense ornamented trichomes on the stem and from both the former and the latter, as the secondary bracts are not leaflike and are shorter than 7 mm and the tertiary bracts are cordate or reniform rather than widely cuneate at the base.

Evergreen suffruticose perennial up to 1 m high, with woody stem bases and rootstock. *Leaves* broadly ovate to rounded, acuminate, cuneate to attenuate at base, (9,6) - 10,8 - 16,4 - (19,2) X (5,3) - 6,2 - 10,2 - (10,5) mm, mature leaves nearly glabrous above, eglandular trichomes frequent below, cystoliths dense; petiole (1,0) - 1,4 - 3,4 - (4,3) mm. *Inflorescence* of monochasial cymes (inflorescence units), usually 2 umbelllately arranged, occasionally singly in axils; inflorescence axis (2,7) - 3,2 - 11,4 - (13,4) mm; longest peduncle of inflorescence units (4,2) - 6,3 - 13,7 - (16,4). *Bracts*: secondary bracts lanceolate, (3,6) - 4,1 - 5,7, - (6,0) X (0,5) - 0,6 - 1,4 - (1,7) mm, glabrous above, with occasional eglandular trichomes on lower surface, lower midrib and margin; tertiary bracts ovate to widely ovate, acuminate, reniform to cordate at the base, (9,1) - 9,7 - 13,4 - (14,4) X 7,8 - 11,3 - (13,8) mm, glabrous, cystoliths present. *Calyx* tube 0,8 - 1,3 - (1,5) mm, lobes lanceolate, (1,5) - 1,7 - 2,5 mm, margins membranous and strigose, outer surface dense with small glandular trichomes or with both. *Corolla* tube (8,5) - 8,7 - 11,9 - (12,2) mm, with appressed eglandular trichomes and occasional short-stalked glandular trichomes; lip in lower position widely ovate (5,5) - 6,5 - 9,1 X 3,1 - 5,1 - (6,0) mm; lip in upper position narrowly elliptic (7,5) - 7,7 - 9,8 - (10,0) X 2,0 - 3,3 - (3,5) mm; flowers purple or pale magenta with white areas speckled with purple at the base of the lip in the upper position. *Stamens*: filaments with broad-based appressed eglandular trichomes and occasional short-stalked glandular trichomes; anther thecae superposed, sometimes overlapping, sometimes separated. *Disc* very shallowly cupular, with two triangular awns. *Gynoecium*: stigma bilobed, slightly uneven; style very sparsely strigose to strigose; ovary ovoid, glabrous to dense with eglandular trichomes. *Fruit* a short-stalked capsule, obtrullate in profile, 6,8 - 7,5 X (3,0) - 3,1 - 3,6 mm, glabrous or densely pubescent with eglandular trichomes. *Seeds* discoid, 2,3 - 2,8 X 2,6 mm, rough and tuberculate.

The few specimens of this species that have been collected have been identified as *P. grandibracteata*, but I feel that this species differs from both *P. grandibracteata* and *P. hereroensis* by the much smaller secondary bracts (figs. 10 & 11) that are not leaflike and by the shorter, broader leaves. I am grateful to P. Craven (pers. comm.) who drew my attention to the folllowing comment by Nordenstam in his account of the Flora of the Brandberg (1974): 'The Brandberg population seems to deviate in several respects from typical *P. grandibracteata*, e.g. in the unusually broad, ovate leaves' as this comment suppoerts my view that *P. sp. 1* is different from *P. grandibracteata sensu stricta*. *P. sp. 1* can easily be separated from *P. grandibracteata s.s.* as it lacks the dense white ornamented trichomes which are present on the stems of the latter species and make the stems of that species white (plate 29a & c). *P. sp. 1* can be separated from *P. hereroensis* by the its shorter secondary bracts (shorter than 6 mm in

P. sp. 1 and longer than 7,5 mm in *P. hereroensis*); by the shape of the base of the tertiary bracts (reniform or cordate in *P. sp. 1* and cuneate to broadly cuneate in *P. hereroensis*) and by the shape of the leaves (ovate in *P. hereroensis*, with a length to breadth ratio greater than 2,4:1 and broadly ovate to elliptic in *P. sp. 1*, with a length to breadth ratio smaller than 2,4:1). *P. sp. 1* has been collected in flower between April and August (fig. 72).

In *P. sp. 1*, there is a disjunction in geographical distribution and in variation in the width of the leaves, the shape of the base of the tertiary bracts and the pubescence of the calyx and the capsules, so that two subspecies are recognised.

Key to subspecies:

Length to width ratio of leaves less than 1,75:1; length : breadth ratio of tertiary bracts less than 1,25:1; capsules pubescent
3.1) ssp. 1

Length : width ratio of leaves greater than 1,75:1; length : breadth ratio of tertiary bracts greater than 1,25:1; capsules glabrous
3.2) ssp. 2

3.1) ssp. 1 *subspecies nova* Type: NAMIBIA 2016 (Otjiwarongo): Outjo Farm OU 516 Sandsteinruecken (-AA), *Giess & Barnard 7921* (WIND, holo.; NBG, PRE, iso.).

Leaves broadly ovate, (11,2) - 11,5 - 14,9 X (7,8) - 8,1 - 10,5 mm. *Bracts*: secondary bracts (4,1) - 4,2 - 5,1 - (5,3) X (0,5) - 0,6 - 0,9 mm; tertiary bracts widely ovate, broadly cuneate to reniform at base, 8,9 - 12,5 - (13,7) X 8,0 - 12,3 - (13,8) mm. *Calyx* glandular and pubescent or very pubescent. *Corolla* lip in lower position (7,0) - 7,5 - 9,3 X 3,0 - 5,2 - (6,0) mm; lip in upper position (7,5) - 8,1 - 10,2 X (2,0) - 2,2 - 3,5 mm. *Fruit* densely pubescent.

CITATIONS

1813 (Ohopoho): Kaokoveld, 19,5 miles from Warmbad on road to Ombombo, Entrance to ravine leading to Sesfontein, Ohopoho side (-DD), *de Winter & Leistner 5828* (PRE, WIND).

2014 (Welwitschia): Farm Mickberg: Damaraland 274, southern boundary

(-CA), *Craven 1021* (WIND); Damaraland, just south of Twyfelfontein (-CA), *Craven 1021a* (WIND).
2114 (Uis): Brandberg - Inner Baswald Rinne (-AB), *Craven & Craven 489* (WIND), Brandberg, Namasschlucht, Am Berg, OM Nb (-AB), *Giess 3631* (WIND); Brandberg, Sonsuib, below Boschmanskopf (-BA), *Craven 2296* (E, NU); Brandberg, Base of Tsisabspitze (-BA), *Craven 2330* (E, NU); Brandberg, Basswaldrinne (-BA), *Craven 2328* (E, NU).

P. sp. 1 ssp. *1* has a more northerly distribution than *P. sp. 1* ssp. *2* (fig. 43). Morphologically the former differs from the latter by having narrower secondary bracts, proportionally broader tertiary bracts and densely pubescent capsules.

3.2) ssp. 2 *subspecies nova* differs from ssp. *1* by its glabrous rather than pubescent capsules, its narrower leaves (length to breadth ratio greater than 1,75:1) and narrower tertiary bracts (length to breadth ratio greater than 1,25:1). Type: NAMIBIA 2317 (Rehoboth): Farm Blässkranz (REH 7), Berghang (-AC), *Merxmüller & Giess 28127* (PRE, holo.; WIND, iso.).

Leaves ovate, (9,6) - 10,2 - 18,1 - (19,2) X 4,7 - 8,9 - (9,9) mm. Bracts: secondary bracts (3,6) - 4,1 - 6,4 X 1,0 - 1,6 - (1,74) mm; tertiary bracts ovate, cordate at base, (11,2) - 11,4 - 14,0 X (14,4) - 7,8 - 9,9 - (10,4) mm. *Calyx* very glandular to glandular with some eglandular trichomes. *Corolla*: lip in lower position 5,1 - 7,7 X 2,0 - 2,2 mm. *Fruit* glabrous.

CITATIONS
2414 (Fischersbrunn): 150 miles west of Maltahöhe, *Louw 279* (PRE).
2416 (Maltahohe): Noukluft, Swarthoogte (-AA/AB), *Meyer 468/1364* (WIND); Plaas Nüdaüs MAL 17, *du Preez & Kotze s.n.* (WIND).
2516 (Helmeringhausen): Farm Naudaus/Duwisib MAL 76/84 (-BC), *Volk 12705* (WIND).

P. sp. 1 ssp. *2* has been collected south of 24 degrees South, and so has a more southerly distribution than ssp. *1*. The former also differs from the latter by having broader secondary bracts, prportionally narrower tertiary bracts and glabrous capsules.

Section 2

4) Peristrophe paniculata (Forsskal) Brummit in Kew Bull. 38: 451 (1983). Type: ARABICA Medhaesaa, Toaejm, Surdud, *Forsskal 385* (C, lecto.!).

Dianthera paniculata Forsskal in Fl. Aegypt.-Arab. 7 (June, 1775). Type: as for *P. paniculata*.
Dianthera bicalyculata Retzius in Vet. Acad. Handl. (Acta Holm.) 36: 297 (279 *fide* Wood, Hillcoat & Brummitt, 1983) (dated October to December 1775, probably published early in 1776, *fide* Wood *et al*, 1983); Retzius in Obs. Bot. 1: 10 (1779); Vahl in Symb. Bot. 1: 6 (1790). Type: ? *Koenig* (on microfiche of Linnean Herbarium). (*fide* Brummit, 1983).
Justicia bicalyculata (Retzius) Vahl in Symb. Bot. 2: 13 (1791); Willdenow, Sp. Pl. 1: 81 (1797); Vahl, En. Plant. 1: 113 (1804); Roem. et Schult., Syst. Veg. 1: 143 (1817); Roxb. in Carey, Fl. Ind. ed. 1, 1: 127 (1820); Roem. et Schult., Mantissa 1: 130 (1822); Wallich, Cat. 2457, a - g (1830); Roxb. in Carey, Fl. Ind. ed. 2, 1: 126 (1832).
Peristrophe bicalyculata (Retzius) Nees in Wallich, Pl. As. Rar. 3: 113 (1832); Nees in DC, Prod. 11: 496 (1847); Richard, Tent. Fl. Abyss. 2: 160 (1847 - 51); Bentham in Hooker, Niger Flora 484 (1849); Dalzell & Gibson, The Bombay Flora 197 (1861); T. Anders. in J. Linn. Soc., Bot. 7: 47 (1864); T. Anders. in J. Linn. Soc., Bot. 9: 521 (1867); Clarke in Hook., Fl. Brit. Ind. 4: 554 (1885); Lindau in Engl., Die Pflnwelt Ost Afrikas und der Nachbaargebiede C: 371 (1895); Lindau in Ann. Istit. Bot. Roma 6: 80 (1896); Lindau in Engl. & Prantl, Pflanzenfam. 4(3b): 331 (1897); Clarke in Thiselton-Dyer, Fl. Trop. Africa 5:242 & 514 (1900); Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 85 (1901); Chevalier, Exploration Botanique de l'Afrique Occidentale Francaise 501 (1920); Schnell in Icones Plantarum Africanum 1: 20 (1953); Dandy in Milne-Redhead, Mem. N.Y. Bot. Gard. 9: 28 (1954); Andrews, The Flowering Plants of the Sudan 185 (1956); Letty, Wild Flowers of the Transvaal 317 & plt. 159: 3 (1962); Heine in Hepper, Fl. of West Trop. Africa ed. 2, 2: 424 (1963); Cufodontis, En. Pl. Aeth. Spermatophyta 959 (1964); Meyer in Merxmüller, Prod. Südwestafrika 130: 49 (1968); Agnew, Upland Kenya Wild Flowers 609 (1974); Solms-Laub in Schweinfurth, Beitr. Fl. Aethiop.

113 & 244 (1867). Type as for *Dianthera bicalyculata*.
Dianthera malabarica Linn. f., Suppl. Pl. 85 (1781), nom. illeg..
Type: as for *Dianthera bicalyculata* Retz..
Justicia malabarica Aiton, Hortus Kewensis 1: 27 (1789); Lamarck, Tableau Encycl. et Meth. 1: 40 & plate 12 fig. 2 (1791); Cavanilles, Icones et Descrip. Pl. 1(2): ?? & plate 71 (1791); Lamarck, Encycl. Meth. Supp. 2: 95 (1811), *nom. illeg.* based on *Dianthera malabarica* Linn. f..
Justicia ligulata Lamarck, Enc. Meth. Bot. 1: 632 (1785), *nom. illeg.*. Type: as for *Dianthera paniculata* Forssk..

Suffruticose annual up to 2 m high with relatively small tap root system. *Leaves* ovate to lanceolate, acuminate to acute, sometimes rounded, attenuate at base, (12,0) - 17,3 - 46,4 - (12,8) X 3,0 - 13,7 - (38,0) mm, very thin, slightly scabrid above, soft below, with simple hairs and cystoliths; petiole 0,9 - 3,9 - (36,0) mm. *Inflorescence* of monochasial cymes (inflorescence units), (1) - 2 - 3 - (4) umbellately arranged, usually compounded; inflorescence axis (8,0) - 11,8 - 19,4 - (31,0) mm; longest peduncle of inflorescence units (7,0) - 10,9 - 18,6 - (30,0) mm. *Bracts* secondary bracts lanceolate, (2,5) - 3,5 - 4,6 - (7,8) X (0,2) - 0,4 - 0,6 - (1,0) mm, with short broad-based eglandular trichomes; tertiary bracts lanceolate, acuminate, larger (7,0) - 9,2 - 14,9 - (18,0) X (0,4) - 0,6 - 1,1 - (1,5) mm, sparsely strigose, with short-stalked and sessile glandular trichomes on surface. *Calyx* tube 1 mm; lobes lanceolate, 3 mm, margins membranous at base, and strigose, with glandular trichomes more common towards base, outer surface sparsely strigose, with sessile glandular trichomes, inner surface sparsely strigose, with appressed eglandular trichomes. *Corolla* tube (5,0) - 5,2 - 6,6 - (7,0) mm, with medium, straight and curved eglandular trichomes; lip in lower position elliptic, 3,5 - 7,2 - (7,3) X (1,8) - 1,9 - 2,7 - (3,2) mm; lip in upper position narrowly elliptic, (5,0) - 5,2 - 6,9 - (8,0) X (1,2) - 1,3 - 1,7 - (1,8) mm; flower lilac, purple or deep purple. *Stamens* filaments with short, curved, ornamented eglandular trichomes, white; anther thecae superposed, not touching, purple. *Disc* very shallow cupular, upper edge crenate with 2 small triangular awns. *Gynoecium*: stigma bilobed; style glabrous; ovary ovoid, very hairy and glandular. *Fruit* (9,0) - 9,4 - 12,3 - (14,0) X (2,0) - 2,2 - 2,8 - (3,5) mm, hairy. *Seeds* discoid, 2,2 - 2,4 - (2,5) mm, rough and tuberculate.

SELECTED CITATIONS

North-western Hemisphere

SENEGAL

1417: Rufisque, Lac Tanma (-BC), *ADAM 728* (PRE).

North-eastern Hemisphere

SUDAN

0535: Kibish Wells, *Padwa 279* (PRE, SRGH).

KENYA

0135: Rift Valley, Karapokot, Nakuijit, *Tweedie 3854* (SRGH)

South-eastern Hemisphere

KENYA

0237: Kenya, Athi River, near Kibwezi (-BD), *Napper 1254* (PRE))

ANGOLA

1614 (Humbe): Between Cahama and Tchepelongu (-AD), *Pearson 2550* (BOL).

1621 (Amatui): Northern Riquinha, Mashi River bank, Near Santa Cruz Mission (-BB) *Codd 7549* (PRE, SRGH).

ZAMBIA

0830: Sumbu, close to Lake Tanganyika (-DA), *Vesey-FitzGerald 1209* (SRGH).

1724 (Katima Mulilo): Masese (-AC), *Fanshawe 6829* (SRGH).

1725 (Livingstone): Livingstone (-DD), *Borle 314* (NBG, PRE, SRGH).

ZIMBABWE

1631 (Mt. Darwin): Mkumvura (-BA), *Chase 2602* (SRGH).

1726 (Kalomo): Victoria Falls (-DD), *Rogers 13179* (BOL, NH, PRE).

1828 (Gokwe): Sengwa Research Station, between Sengwa and Umgaraga Rivers, *Jacobsen 4086 (673)* (PRE).

1832 (Umtali): Wankie National Park, Robin's Camp (-CA), *Gonde 92/74* (PRE, SRGH).

2131 (Triangle): Nuanetsi, North West Mateke Hills (-BB), *Drummond 5560* (PRE, SRGH).

2229 (Waterpoort): Beitbridge, Umzingwane River Bridge on road to Limpopo ranches (-BB), *Drummond 6035* (PRE).

BOTSWANA

Without precise locality: Northern Botswana, *Drummond & Seagrief 5177 (PRE); Mutsoi, in forest island, Lambrecht 125* (PRE).

1923 (Maun): At Maun (-AD), *Smith 1293* (PRE); Boro Floodplain, Island (-CA), *Biggs M620* (PRE).

2022 (Lake Ngami): 6 km SE of Tsau (-AD), *Wild & Drummond 7129* (PRE).

2023 (Kwebe Hills): Between Ngami and Toteni (-AC), *van Son sub Tvl Museum 28678* (PRE).

2121 (Ghanzi): Ghanzi pan, Farm 59 (-DB), *Brown 8801* (PRE).

2124 (Rakops): Peterhouse, North-east of Mopipi, Boteti Delta Area (-BB), *Thornton 644* (PRE, SRGH); Botletle Riverine Thicket (-BB), *Kunhardt 9* (SRGH).

NAMIBIA

1712 (Posto Velho): West of Kunene River, Just east of Marion Fluss Mouth, On Kunene banks and islands (-AA), *Craven 956* (WIND).

1812 (Sanitatas): Kaokoveld, Orupembe (-BA), *Compton 326* (NBG).

1813 (Ohopoho): Kaokoveld, Banks of river at Otjihu (-AD), *de Winter & Leistner 5652* (PRE, WIND).

1913 (Sesfontein): Zesfontein (-BA), *Thorne sub Herb Musei Austr.- Afr. 35709* (SAM).

1914 (Kamanjab): Kaokoveld, Otjowasandu (-AB), *Giess & Leippert 7317* (NBG, WIND).

1917 (Tsumeb): Etosha National Park East Boundary, opposite Nadubib (-AA), *Le Roux 1045* (WIND); Tsumeb (-BA) *Dinter 3004* (PRE, SAM); Tsumeb (-BA), *Dinter 2909* (SAM); Tsumeb Campsite (-BA), *Goldblatt 1929* (NBG, PRE, WIND); Farm Elandshoek GR 771 (-BC), *Giess 15125* (WIND); Farm Danevis-Sud GR/TS49, *Giess 10377* (PRE, WIND).

1918 (Grootfontein): Grootfontein, Farm Bergen GR 668 (-CA), *Giess, Volk & Bleissner 6464* (WIND).

2115 (Karibib): N-Karibib-Omaruru road (-DB), *Seydel 1128* (PRE).

2116 (Okahandja): Okahandja (-DD), *Dinter 39* (SAM).

2216 (Otjimbingwe): Otjimbingwe, Ustakus (-AC), *Marloth 1312* (PRE, STE).

2317 (Rehoboth): Farm Gravenstein REH 65 (-AC), *Leippert 4653* (WIND).

2416 (Maltahohe): Bergzebra Park, Naukluft: Mal 9 (-AB), *Giess 10480* (WIND).

2517 (Gibeon): Ben Gibeon (-BB), *Range 1358* (SAM).

2617 (Bethanie): Bethanien, Farm Mooifontein BET 50 (-CA), *Giess, Volk & Bleissner 5503* (PRE, WIND).

The names *P. paniculata* and *P. bicalyculata* were both validly published in publications bearing the date 1775. They are taxonomic synonyms but *P. paniculata* has priority (Wood, Hillcoat & Brummitt, 1983). *Peristrophe paniculata* is a widely distibuted species and ranges as far east as India, and as far west and south as Namibia. In southern Africa, it is found in the semi-arid tree savanna and the semi-desert areas. The species has only been collected between February and August, and most often in May in southern Africa (fig. 1). The specimens collected in the earlier months are of younger and smaller plants than those collected in the later months. This is particularly noticeable in the series collected in 1963: *Giess, Volk & Blessner 5503* (26/05/1963); *Giess, Volk & Blessner 6464* (25/04/1963); *Leippert 4653* (09/05/1963); *Giess & Leippert 7317* (05/06/1963) (plate 2). This suggests that the species is an annual, even although it has been said to reach 2 m in height (*fide notes* on *Smith 1293*).
The smaller flowers, which are less than 13,7 mm long (fig. 20), the very shallow disc and the small simple tap root system (plate 1) serve to separate *P. paniculata* from all other southern African species of *Peristrophe*. It has often been confused with *Peristrophe kotschyana* and can be separated from the latter species by means of the mature bark, which is smooth and black in *P. paniculata* and white and peeling in *P. kotschyana*; by means of the ratio of the length of the larger tertiary bract to that of the shorter, which is (1,4) - 1,6 - 2,2 - (2,6) : 1 in *P. paniculata* and 1,2 - 1,4 - (1,6) : 1 in *P. kotschyana* and on the basis of distibution: *P. paniculata* grows in Namibia and in north-western Botswana (fig. 44), *P. kotschyana* in eastern Botswana and in the Transvaal (fig. 48). The fruits of *P. paniculata* are more densely sericeous than those of any other species in southern Africa, but the small flowers (fig. 20) are the most reliable character with which to distinguish *P. paniculata*.

5) Peristrophe transvaalensis (C.B.Clarke) Balkwill in S. Afr. J. Bot. 51(6): 489 (1985). Type: TRANSVAAL, without precise locality, *Holub s.n.* (K, holo.!).
Dicliptera transvaalensis C.B.Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 92 (1901). Type: as for *P. transvaalensis*.

Evergreen suffruticose perennial up to 1 m high. *Leaves* ovate to narrowly elliptic, acuminate, attenuate at base, 25,5 - 40,9 - (42,4) X 7,7 - 12,7 - (13,5) mm, with many multicellular eglandular trichomes and cystoliths; petiole (1,7) - 2,0 - 4,3 - (4,6) mm. *Inflorescence* of monochasial cymes (inflorescence units), (1 - 2) - 3 - (4) umbellately arranged, sometimes compounded; inflorescence axis (4,0) - 4,2 - 7,0 - (7,4) mm long; longest peduncle of inflorescence units (2,4) - 4,1 - 12,9 mm. *Bracts*: secondary bracts 2, free, lanceolate, (4,68) - 5.1 - 6,6 X 0,6 - 1,0 - (1,1) mm, pubescent, sessile; tertiary bracts oblanceolate, unequal, larger (13,6) -13,8 - 16,1 - (16,4) mm, almost tomentose, trichomes multicellular and eglandular. *Calyx* tubes 1,5 mm, lanceolate, 5,5 mm, margins membranous and ciliate, with small glandular trichomes on outer surface. *Corolla* tube (7,3) - 7,5 - 9,0 mm long, sericeous to tomentose; lip in lower position ovate 7,1 - 8,8 - (9,0) X 2,0 - 2,7 mm; lip in upper position narrowly elliptic 7,0 - 8,4 - (8,8) X (2,4) - 2,5 - 3,5 - (3,6) mm; flowers light purple with dark purple honey-guides on white background on lip in upper position. *Stamens*: filaments with short and long multicellular eglandular trichomes, white; anther thecae superposed, purple. *Disc* shallowly cupular with crenate top and 2 short stubby awns. *Gynoecium*: stigma shortly bilobed; style sparsely strigose; ovary ovoid, sparsely pubescent. *Fruit* pubescent, 9,0 - 10,2 X 2,1 - 2,6 mm. *Seeds* 2,0 - 2,2 X 1,8 - 2,0 mm, rough and tuberculate.

CITATIONS:
TRANSVAAL
2427 (Thabazimbi): Kransberg, Geelhoutbos farm (-BC), *Germishuizen 811* (PRE).
2428 (Nylstroom): Geelhoutkop (-AD), *Germishuizen 775* (PRE); Warmbaths, In graminosis, in terra "Bushveld" dicta prope Warmbaths, alt. 3600 ped. (-CD), *Bolus 12219* (BOL); Near Warmbaths Dam, Hillsides and undergrowth (-CD), *Meuse 9644* (PRE); On farm "Little Kariba", in

valley near campsite (-CD), *Balkwill 764, 803* (E, NU); Rocky places north of Warmbaths (-CD), *Gillett 3804* (STE).

It has been necessary to transfer *P. transvaalensis* from the genus *Dicliptera* as the placentae are inelastic at the base. The same is true of *P. angolensis*, a very closely related species. *Peristrophe transvaalensis* is not a common species and is endemic to the central Transvaal (fig. 45), where it grows at the interface of Sourish Mixed Bushveld and Sour Bushveld. In the field the plants were beginning to flower in January, and were flowering profusely when revisited in May, while the plants in cultivation were still in flower in August of the same year. It appears that the species flowers throughout the year, but flowers more profusely in winter. The closest ally to *P. transvaalensis* is *P. angolensis* (S. Moore) Balkwill, which has a characteristic inflorescence structure with many inflorescence units contracted into an axil, and an occasional inflorescence unit with a very long peduncle. In contrast, the inflorescence units of *P. transvaalensis* are not contracted into the leaf axils. The broader tertiary bracts of these two species serve to separate them from the other species of *Peristrophe* in southern Africa. *P. transvaalensis* has a marked vestiture of multicellular uniseriate eglandular trichomes, which imparts a grey-green colour to the leaves of living plants; this feature is very unusual in this section of the genus.

6) Peristrophe cliffordii Balkwill in S. Afr. J. Bot. 51(6): 485 (1985). Type: TRANSVAAL 2229 (Waterpoort): East of Messina, on road to Weipe, 2,8 km from Messina-Pontdrift road (-BA), *Balkwill 793* (NU, holo.!; PRE, iso.!).

Evergreen suffruticose perennial up to 1 m high. *Leaves* ovate to elliptic, acuminate, attenuate at base, 2,8 - 25,7 x 7,5 - 9,0 mm; slightly scabrid, with fine hairs and cystoliths; petiole 2,7 - 4,8 mm. *Inflorescence* of monochasial cymes (inflorescence units) subtended by tertiary bracts, 2 - 3 inflorescence units umbellately arranged, occasionally compounded; inflorescence axis 2,5 - 5,1 - (5,3) mm; longest peduncle of inflorescence units (4,4) - 4,5 - 8,4 mm. *Bracts*:

secondary bracts lanceolate, 1,5 - 1,9 X 0,4 - 0,5 mm, densely glandular-pubescent; tertiary bracts triangular, acuminate, 3,3 - 4,3 X 0,7 - 1,0 mm, ciliate on margins and veins, densely glandular, sessile. *Calyx* tube 1 mm; lobes lanceolate 2,5 mm, margins membranous and ciliate, densely glandular on outer surface. *Corolla* tube 6,6 - 8,8 - (9,0) mm, sericeous, with abundant glandular trichomes; lip in lower position narrowly ovate, 8,0 - 13,3 X 3,1 - 5,3 mm; lip in upper position narrowly elliptic 9,2 - 11,9 X 2,0 - 3,5 mm; flowers purple, rarely pink or white, with dark purple honey guides on white background on lip in upper position. *Stamens*: filaments with curved eglandular and minute glandular trichomes, white; anther thecae superposed, not touching, purple. *Disc* shallowly cupular, top entire to slightly lobed with 2 very short stubby awns. *Gynoecium*: stigma shortly bilobed; style sparsely strigose; ovary ovoid, scarcely pubescent. *Fruit* minutely pubescent and glandular, 9,3 - 10,1 X 2,3 - 2,7 mm. *Seeds* 2,1 - 2,8 X 2,2 - 2,5 mm, rough and tuberculate.

CITATIONS

TRANSVAAL

2229 (Waterpoort): East of Messina, on road to Weipe, 2,8 km from Messina-Pontdrift road (-BA), *Balkwill 795 & 1627* (NU, PRE); Farm Overvlakte, just below watchtower, *Bruce 132* (PRE).

P. cliffordii is named in memory and recognition of Clifford George Balkwill and is known only from the specimens cited. It appears to be restricted to the sandflats of the Mopani veld between the Soutpansberg mountains and the Limpopo River in the northern Transvaal, but examination of tropical material may extend this range. *P. cliffordii* can be distinguished from *P. grandibracteata, P. hereroensis* and *P. sp. 1* by its much smaller, narrower tertiary bracts (plate 3). It can be distinguished from *P. gillilandiorum* by the shorter tertiary bracts, which are rusty brown and by the broader, shorter leaves (c.f. fig. 37h & 38h). The dense trichomes between the ridges of the stem and the short and rusty-brown tertiary bracts (fig. 37i & plate 29) separate *P. cliffordii* from *P. paniculata, P. kotschyana* and *P. cernua*. Occasionally the calyx lobes of *P. cliffordii* have wispy hairs on their tips, another unique feature. The flowering time is in autumn and winter.

7) **Peristrophe gillilandiorum** Balkwill in S. Afr. J. Bot. 51(6): 488 (1985). Type: TRANSVAAL 2229 (Waterpoort): Dongola, Schroda (-AB), *Bruce 58* (PRE, holo.!; K, iso.).

Evergreen suffruticose perennial, up to 0,8 m high. *Leaves* lanceolate, acuminate, attenuate at base, 25,9 - 60,9 X 3,3 - 5,6 mm, young leaves soft and finely pubescent, older leaves slightly scabrid with occasional trichomes and many cystoliths; petiole 0,4 - 4,6 mm. *Inflorescence* of monochasial cymes (inflorescence units) subtended by tertiary bracts, 2 - 3 inflorescence units umbellately arranged, inflorescence axis (2,4) - 2,5 - 3,7 mm, longest peduncle of monochasial cymes (0,9) - 1,0 - 2,8 mm. *Bracts*: secondary bracts lanceolate, glandular-pubescent, 3,2 - 7,3 X 0,8 - 0,9 mm, tertiary bracts lanceolate, acuminate, (5,3) - 5,6 - 9,2 X 1,0 - 1,1 - (1,2) mm, glandular-pubescent. *Calyx* tube 1,5 mm; lobes lanceolate, 3,0 mm, margins ciliate, surface glandular. *Corolla* tube 5,8 - 11,0 mm, densely glandular-pubescent; lip in lower position narrowly elliptic, 7,5 - 12,6 - (13,0) X 2,6 - 4,9 - (5,0) mm; lip in upper position narrowly oblong, 7,0 - 13,5 - (14,0) X 2,0 - 3,4 - (3,5) mm; flower pale mauve with purple honey-guides on white background on lip in lower position. *Stamens*: anther thecae superposed. *Disc* shallowly cupular. *Gynoecium*: stigma shortly bilobed; style sparsely strigose; ovary ovoid, glabrous. *Fruit* glandular-pubescent, 8,0 X 2,2 mm. *Seeds* rough and tuberculate.

CITATIONS

ZIMBABWE

2229 (Waterpoort): 4 miles NE of Pazhi-Limpopo confluence, Sentinel Ranch (-BA), *Drummond 5973* (K, PRE); West of Beit Bridge, Sentinel Ranch (-BA), *Grosvenor 820* (SRGH).

TRANSVAAL

2229 (Waterpoort): Dongola, Schroda (-AB), *Pole Evans 4484* (PRE); ibidem, in *Hyphaene natalensis* community, on banks of Limpopo (-AB), *Balkwill 1626* (E, K, NU, PRE).

P. gillilandiorum is named in honour of H.B. Gilliland (a botanist who collected in the Transvaal and southern Zimbabwe) and his wife. *P. gillilandiorum* can be differentiated from *P. grandibracteata, P. hereroensis* and *P. sp. 1* by its smaller tertiary bracts (plate 3). The areas between the ridges on the stem of this species are densely covered with hairs, unlike those of the other southern African species (excluding *P. grandibracteata* and *P. cliffordii*) (plate 29). *P. gillilandiorum* has tertiary bracts longer than its calyx lobes and this distinguishes it from *P. cliffordii*. The leaves of *P. gillilandiorum* are unusually narrow (fig. 38a & h). *P. gillilandiorum* is not very common and is localised in the Limpopo River Valley (fig. 47), where it grows on rocky hillsides (*Grosvenor 820*), sandstone hills (*Drummond 5973*) and in deep clay amongst plants of *Hyphaene natalensis* Kuntze (*Balkwill 1626*). The only other species of *Peristrophe* that occurs in the Limpopo River Valley is *P. kotschyana* (fig. 48), which has not been found as close to the river as have *P. cliffordii* and *P. gillilandiorum*. Besides the differences in stem indumentum that are described above, *P. gillilandiorum* can be distinguished from other species in Section 2 by its lanceolate leaves. *P. gillilandiorum* begins flowering in March and is winter-flowering.

8) **P. kotschyana** Nees in DC., Prod. 11: 497 (1847) ; A. Richard, Tent. Fl. Abyss. 2: 160 (1850). Type: Ad montem Cordofanum Arash-Cool inter saxa et in umbra Mimosarum, Octobri, *Kotschy* (holo., not seen).
P. schimperiana Hochst. ex Nees in DC., Prod. 11: 497 (1847). Type: Abyssinia, districtus Haramat, prope Geraz, in vallibus, Decembri, *Schimper* (G-DC, holo. seen on microfiche).
P. bicalyculata (Retzius) Nees var. *kotschyana* (Nees) Fiori (1911) (*fide* Cufodontis, En. Pl. Aeth. Spermatophyta 959 (1964).

Evergreen suffruticose perennial up to 1 m high, with woody rootstock. *Leaves* ovate, elliptic or lanceolate, acute, acuminate or occasionally minutely apiculate, attenuate, (11,0) - 19,3 - 37,3 - (59,0) X (2,5) - 5,3 - 8,8 - (14,0) mm, herbaceous, slightly scabrid above, but sometimes soft below, with multicellular eglandular hairs and cystoliths; petiole (1,0) - 1,4 - 3,4 - (6,5) mm. *Inflorescence* of monochasial cymes (inflorescence units), 2 - 3 umbellately arranged, sometimes compounded; inflorescence axis (1,0) - 1,9 - 14,5 - (49,0) mm; longest peduncle of monochasial cymes (1,0) - 4,5 - 14,8 - (38,0) mm. *Bracts*: secondary bracts lanceolate (2,1) - 3,7 - 5,5 - (9,0) X (0,3) - 0,4 - 0,7 - (1,2) mm; with eglandular trichomes; tertiary bracts lanceolate, acuminate, unequal, larger (7,5) - 9,3 - 12,9 - (17,0) X (0,6) - 0,9 - 1,3 - (1,5) mm, strigose on margins, veins and surface, short-stalked glandular trichomes becoming common towards apex. *Calyx* tube 1 mm; lobes lanceolate, 5,5 mm, margins membranous and ciliate with glandular and eglandular trichomes, glandular more common at the base, outer surface glabrous, inner surface with closely appressed glandular and eglandular trichomes. *Corolla* tube (5,0) - 7,2 - 8,4 - (11,0) mm, with straight and curved eglandular trichomes; lip in lower position widely ovate, (6,5) - 7,5 - 9,2 - (10,2) X (2,8) - 3,3 - 5,1 - (5,75) mm; lip in upper position narrowly elliptic, (7,0) - 7,7 - 9,7 - (10,2) X (1,7) - 1,9 - 2,6 - (3,8) mm; flowers light purple, with dark purple honey guides on white background on lip in upper position. *Stamens*: filaments with some curved eglandular trichomes near the base, and some short-stalked glandular trichomes, white; anther thecae superposed, touching, thecae red-purple. *Disc* cupular, upper edge entire with two short stubby erose awns. *Gynoecium*: stigma shortly bilobed; style exserted, glabrous or very sparsely glabrate; ovary narrowly ellipsoid, glabrous, occasionally sparsely hairy. *Fruit* a short-stalked clavate capsule, usually glabrous, occasionally hairy, (8,0) - 8,5 - 10,5 - (11,5) X (1,1) - 1,9 - 2,4 - (3,0) mm. *Seeds* (1,5) - 1,7 - 2,4 X (1,4) - 1,5 - 2,1 mm, rough and tuberculate.

SELECTED CITATIONS

ZIMBABWE

2129 (West Nicholson): Gwanda, Dye River Bridge, *Davies 2342* (PRE).

2131 (Triangle): Nuanetsi River, *Breijer 16068* (PRE).

BOTSWANA

2125 (Lothekane): Near Musu Village, South of Makadikadi Pans (-BB), *Allen X408* (PRE).

2425 (Gaberone): 4 mile W of Letlhakeng in Letlhakeng Valley (-AA), *de Winter 7313* (PRE).

TRANSVAAL

2229 (Waterpoort): Zoutpansberg, On banks of Galumpies River, Farm Little Muck 26, (-BC), *Codd 4330* (PRE); Langjan Nature Reserve, Brak River

(-CC), *Zwanziger 273* (PRE); *ibidem, Huntley 1855* (PRE); Wyllies Poort, Hill and Valley (-DD), *Smuts 2074* (PRE); At junction of N1 with road to Andover (-DD), *Balkwill 802* (E, NU); On the farm Davenham (-DD), *Balkwill 800* (NU).

2230 (Messina): Chipise (-CA), *Lam & Meeuse 4947* (PRE).

2328 (Baltimore): Magoebasnek, 53 miles northwest of Potgietersrus, Farm Skrikfontein (-DA), *Maguire 1461* (BOL, NBG).

2329 (Pietersburg): Near Mara (-AB), *Schlieben & Strey 8282* (PRE, SRGH); V.B. Mara Navorsingstasie, Langs lope en riviere (-AB), *V.B. Mara Navorsingstasie 555* (PRE).

2425 (Gaborone): Marico, Lekkerlach (-DD), *Louw 752* (PRE).

2427 (Thabazimbi): Thabazimbi, Farm Eldorado (-CB), *Repton 4765* (PRE).

2428 (Nylstroom): Potgietersus, about 1/2 mile on road to Roedtan, Farm Doornpoort (-BD), *Meeuse 9457* (COI, PRE); Zandrivier, Farm BadenBaden (-CA), *Breijer 21609* (PRE); Naboomspruit, Mosdene (-DA), *Galpin M597 & M277* (PRE); Near Crecy, On Naboomspruit road, Tweekoppies Station (-DB), *Meeuse 9444* (PRE); *ibidem, Balkwill 760 & 802* (NU); Tuinplaats-Groblersdal road, *Meeuse 9505 & 9505a* (PRE).

2430 (Pilgrim's Rest): Wolkberg, Mohlapietse Wilderness Area, Beside Mohlapietse River (-AA), *Balkwill 732* (NU).

In southern Africa, *P. kotschyana* has been confused with *P. paniculata*, but can be distinguished by means of its larger flowers (14,7) - 15,3 - 17,8 - (19,0) mm as compared with (6,6) - 10,1 - 12,4 - (13,7) mm (fig. 20), its perennial habit, including a woody stem base and root system (plate 1), by its white peeling (not black) bark and in southern Africa, by means of its more easterly distribution (c.f. fig. 44 & 48). *P. kotschyana* may be distinguished from *P. transvaalensis* by its narrower tertiary bracts (plate 3) and its green leaves, which lack the grey-green leaf colour imparted to the stems of *P. transvaalensis* by a vestiture of eglandular trichomes and from *P. cliffordii* and *P. gillilandiorum* by the lack of a dense vestiture of eglandular trichomes between the ridges on the stem (plate 3). The closest relative to *P. kotschyana* is *P. cernua*. These two species have very different distributions, but their tertiary bracts, stem vestiture and inflorescence are very similar. *P. cernua* shows clinal variation in the sizes of the tertiary bracts and flower size (fig. 17).

P. kotschyana is very similar to *P. cernua* in the Cape Province in terms of the size of tertiary bracts and flowers, but is considerably different from *P. cernua* in Natal where the tertiary bracts and flowers are considerably larger. These taxa display vicariant distributions (figs. 48, 49 & 70). *P. kotschyana* can best be separated from *P. cernua* on the basis of distribution, the size of the tertiary bracts (figs. 14 & 15) and the size of the flowers (figs. 20 - 25), while *P. cernua* has honey-guides under the filaments that are not present in *P. kotschyana*. Most specimens of *P. kotschyana* have glabrous fruits, but a few specimens have some eglandular trichomes on the surface of the fruits. *P. kotschyana* has a scattered distribution from north-eastern Africa southwards to Botswana and the Transvaal, where it is found in arid sweet bushveld, mixed bushveld and sourish mixed bushveld. The scattered populations in Africa may represent vicarious species, in which case the southern African material must be renamed. Plants have been collected in flower throughout the year (fig. 72) and in cultivation, plants flower sporadically in all seasons, although they produce more flowers in autumn and early winter.

9) P. cernua Nees in Schlechtend., Linnaea 15: 374 (1841); Hooker in J. Bot. 2 (11): 126 (1840), *nom. nud. as Peritrophe cernua*; Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 85 (1901). Type: CAPE 3325 (Port Elizabeth): 'Inter frutices ad flumen Zwartkopsrivier, Octobre' [= Inter frutices in campis ad flumen "Zwartkopsrivier" prope praedium Pauli Mare, alt. I (Uitenhage), cum *Rhytiglossa ciliata*, Floret Octobri -in original description] (-CD), *Ecklon Un. It. 556* (GZU, holo.!, 2 sheets, STE, iso.!).

Justicia caulopsila E. Mey. in Drège, Pflanzengeogr. Doc. 137, 195 (1843), nom. nud..

Peristrophe krebsii Presl, Botanische Bemerkungen 94 (1844); Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 86 (1901). Type: CAPE without precise locality, *Krebs pl. cap. exs. n 251* (not located).

P. caulopsila E. Mey. ex Nees in DC, Prod. 11: 498 (1847); Presl, Botanische Bemerkungen 95 (1844), nom. nud.; T. Anders. in J. Lin. Soc., Bot. 7: 48 (1864); Lindau in Engl. and Prantl, Pflanzenfam. 4(3b): 331 (1897); Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 84 (1901). Type: CAPE 3325 (Port Elizabeth): Somerset Division, between Zuurberg Range and

Kleinbruintjieshoogte, 2000 - 2500 ft (-AD), Drege (K, lecto.!; G-DC, isolecto., seen on microfiche).
P. natalensis T. Anders. in J. Linn. Soc., Bot. 7: 48 (1864); Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 85 (1901). Type: NATAL 2931 (Stanger): Port Natal (-CC), *Gueinzius* (K, lecto.!).
Non *P. cernua sensu* Compton, Fl. Swaziland 557 (1976).

Evergreen suffruticose perennial up to 1m high. *Leaves* ovate, acuminate, reniform to cuneate and attenuate at base, (11,0) - 18,0 - 37,4 - (49,6) X (4,7) - 7,9 - 15,5 - (22,6) mm, with multicellular eglandular and short-stalked glandular trichomes: petiole (1,0) - 1,2 - 5,5 - (14,6) mm. *Inflorescence* of monochasial cymes (inflorescence units), (1) - 2 - 3 - (4) umbellately arranged, often compounded; inflorescence axis (1,6) - 3,3 - 10,8 - (16,0) mm; longest peduncle of scorpioid cymes (1,7) - 4,5 - 11,6 - (22,7). *Bracts*: secondary bracts lanceolate, (2,2) - 2,6 - 4,5 - (6,2) X (0,2) - 0,3 - 0,5 - (0,6) mm, pubescent; tertiary bracts lanceolate, unequal, larger (4,7) - 6,7 - 12,0 - (16,0) X 1,0 - 1,3 - (1,6) mm, with multicellular eglandular and large and small short-stalked glandular trichomes. *Calyx* tube 1 mm; lobes 3,5 mm, margins membranous and ciliate, with large and small glandular trichomes. *Corolla* tube (5,5) - 8,0 - 9,8 - (12,0) mm, sericeous, with medium-headed glandular trichomes; lip in lower position ovate, (7,2) - 9,8 - 16,5 - (22,3) X (2,4) - 2,9 - 5,6 - (8,6) mm; lip in upper position narrowly elliptic, (8,0) - 10,0 - 16,2 - (21,3) X (1,6) - 2,2 - 3,4 - (4,0) mm; flowers purple with dark purple honey guides below filaments on lip in lower position, and on white background on lip in upper position. *Stamens*: filaments with short and long, straight and curved, multicellular, eglandular trichomes, white; anther thecae superposed, separated, purple. *Disc* cupular with crenate top and 2 short stubby awns. *Gynoecium*: stigma bilobed; style exserted, sparsely strigose; ovary ovoid, with curved multicellular eglandular trichomes and stalked glandular trichomes. *Fruit* a short-stalked clavate capsule, with glandular and eglandular trichomes, (9,4) - 10,4 - 13,1 - (14,0) X (1,5) - 1,8 - 2,3 - (3,0) mm. *Seeds* (2,0) - 2,2 - 2,7 - (2,9) X (1,5) - 1,8 - 2,2 - (2,3) mm, rough and tuberculate.

SELECTED CITATIONS

NATAL

2829 (Harrismith): Estcourt (-DD), *Green 188* (NH).

2830 (Dundee): Weenen county, Flats below Umhlumba Mt. (-CC), *Acocks 10164* (PRE); Near Weenen Nature Reserve (-CC), *Edwards 785* (NU); Road to Muden (-CD), *West 1238* (PRE); Muden (-CD), *Compton 19744* (NBG); Keate's Drift, Mpunzi River, Natal (-DC), *Galpin 14806* (BOL, PRE); 2 miles from Jamesons Drift on road from Kranskop (-DD), *Dyer 4374* (PRE).

2831 (Nkandla): Lower Umfolozi District, Umfolozi Game Reserve (-BD), *Phelan 636* (NU); Umhlatuzi River banks, Umhlatuzana Hills (-DC), *Venter 3821* (PRE).

2832 (Mtubatuba): Umfolozi River (-AC), *Wager sub Tvl Mus. 22382* (PRE).

2930 (Pietermaritzburg): In Valley bushveld, near the Mooi River Falls (-AB), *Balkwill & Manning* 918a (E, NU); Albert Falls, Umgeni River (-AD), *Comins 359* (NU); 16 km from Greytown on Weenen road (-BA), *du Toit 2393* (PRE); Maritzburg (-CB), *Fisher 36* (NU); Dusi River Valley, beside road from Bishopstowe to Ashburton (-CB), *Balkwill 168* (E, NU); Near Ashburton Station (-CB), *Balkwill 169 & 772* (E, NU); bushveld opposite Oribi Airport (-CB), *Balkwill 445* (E, NU); 'Craiglea', Cato Ridge Native Reserve (-DA), *Jacobsen 51* (NU); Farm in Table Mountain area, on banks of Umgeni River (-DA), *Garrett 20* (NU); 10 miles east of Pietermaritzburg (-DA), *Obermeyer sub Herb. Tvl Mus. 33568* (PRE); Camperdown, Nagle Dam (-DA), *Wells 1340* (NU, PRE); Umgeni Dam (-DA), *Moll 1713* (NU, PRE); Near Isipingo (-DD), *Schlechter 2999* (COI); Isipingo (-DD), *Thoday sub Her. Mus. Austr.-Afr. 25204* (SAM); Reservoir Hills (-DD), *Naidoo 11* (INCOL); Springfield (-DD), *Gajadhur 39* (INCOL); Pinetown, Hillcrest, Crestholme (-DD), *Grice s.n.* (NU).

2931 (Stanger): matikulu Nature Reserve (-BA), *Ward 741* (NH); Umhlanga (-CA), *Wood 609* (BOL, K); Everest Heights (-CA), *Gayapersad 34* (INCOL); Phoenix, about 10 miles east of Durban (-CA), *Bolus 13888* (BOL); Durban, hillside (-CC), *Benson sub Moss 15705* (J); Bluff (-CC), *Marriott NH 26839* (NH); Puntan's Hill (-CC), *Khan 13* (INCOL); Mayville (-CC), *Thakersee 5* (INCOL); Near Durban (-CC), *Wood 11881* (BOL, SAM); Burman Bush (-CC), *Huntley 2* (NU, PRE), *ibidem, Bourquin 144* (NU); N.E. end of Berea (-CC), *Pillans 16571*

(BOL); Greenwood Park (-CC), *Govender 4* (INCOL).

3030 (Port Shepstone): Isipingo Beach (-BB), *Ward 4974* (INCOL, NU, PRE); Umkomaas (-BB), *Keerath 2* (INCOL); Park Rynie (-BC), *Thode 2749* (STE); Scottburgh (-BD), *Cooper 1618* (RUH); Umzimkulwana River valley, Horseshoe Dam (-CA), *Balkwill 402* (E, NU); Oribi Gorge Nature Reserve (-CB), *Balkwill 326 & 335* (E, NU); Umzimkulu River, Gibraltar Rock Area (-CB), *Nicholson 1760* (PRE), *ibidem, Balkwill 441* (E, NU); Umtamvuna Nature Reserve, Crocodile (-CC), *Abbott 1144* (PRU).

TRANSKEI

3030 (Port Shepstone): Umtamvunarivier Vallei, Mpunzidrif (-CC), *van Wyk 1650* (PRE).

3127 (Lady Frere): Cofimvaba, Qamata Poort (-DC), *Lewis 4565* (SAM).

3128 (Umtata): south of Umtata (-BB), *Gillett 1293* (STE); Between Umtata and Idutywa (-DC), *Lewis 4566* (PRE, SAM).

3129 (Port St John's): 4 miles S.W. of Tombo Post Office (-CB), *Codd 9290* (GRA, NBG, PRE).

3227 (Stutterheim): Kei River Valley, beside main Cape-Natal road (-BD), *Ward 6925* (INCOL).

3228 (Butterworth): Blythswood Mission (-AA), *Taylor 3516* (NBG); Xabo Valley (-DA), *Van Breda 866* (PRE).

British Caffraria, *Cooper 161* (K).

CAPE

3126 (Queenstown): Gwatyn, 2900 ft (-DD), *Galpin 2044* (BOL); Bradford Drift (-DD), *Galpin 7805* (PRE).

3225 (Somerset East): Stockenstroom, Fort Armstrong (-DD), *Barker 157* (NBG).

3226 (Fort Beaufort): Braeside, 10 miles N. of Ft Beaufort (-DA), *Story 2227* (GRA, PRE); Ft Beaufort (-DC), *Taylor s.n.* (GRA), *ibidem, Sister Frances sub BOL 15707* (BOL); Adelaide, Banks of Koonap River (-DC), *Galpin sub BOL 32312, sub PRE 11553* (BOL, PRE); Koonap (-DC), *Blackbeard NBF 869/14* (BOL); SW of Alice, Garfield (-DD), *Acocks 15970* (PRE).

3227 (Stutterheim): 38 miles S.E. by E. of Queenstown, Stratheric (-AB), *Acocks 17940* (PRE); Kabousie River valley (-DA), *Comins 1561* (PRE); Near Komga, amongst shrubs (-DB), *Flanagan 721* (BOL, NH, PRE, SAM); 5 miles east of East London, Nahoon River (-DC), *Lewis 4564* (SAM).

3228 (Butterworth): Gonubie River Mouth (-CC), *Galpin 7749* (PRE).

3322 (Oudtshoorn): Near Olifants River (-BD), *Taylor 491* (PRE).
3324 (Steytlerville): Baviaanskloof, Gamtoos River Valley (-DA), *Balkwill 450* (E, NU), *ibidem, Bayliss 7984* (PRE); Groot River Poort (-DA), *Fourcade 2746* (STE); Perseverance, Zwartkops (-DB), *Long 685* (PRE); Between Gamtoos River Valley and Hankey (-DD), *Fourcade 5755* (NBG, STE).
3325 (Port Elizabeth): Little Fish River, near Somerset East (-BA), *Bolus 1652* (BOL); Otter Station (-BB), *Burchell 3263; Addo Park (-BC), Liebenberg 7754* (PRE); Enon (-BC), *Thode A2736* (PRE); Prope Uitenhage (-CD), *Bolus 32311* (BOL); SKF (Ball-bearing Company) lands at Uitenhage (-CD), *Dahlstrand 535* (GRA, J); Zwartkops River (-CD), *Harvey 3597* (BOL); Near Uitenhage (-CD), *Schlechter 2545* (COI, PRE); On fields near the Zwartkop River, in the first altitude, Distr. Uitenhage, Fl. December (-DC), *Ecklon & Zeyher 40* (BOL, K, SAM); *ibidem*, Jan. & Februar., *Ecklon & Zeyher 40* (SAM); *ibidem*, Januar - Martio, *Zeyher 40* (SAM); Just E.N.E. of Coega, on Colchester road (-DC), *Balkwill 463* (E, NU); Redhouse (-DC), *Paterson 2093* (BOL), *ibidem, Bayliss 4825* (RUH); Perseverance, Zwartkops River (-DC), *Long 685* (GRA, MPE), *ibidem, Rodin 1069* (BOL, PRE).
3326 (Grahamstown): 26,5 miles from Grahamstown, Carlisle Bridge on Cradock Road (-AA), *Brink 327 & 328* (GRA, PRE); Piggot's Bridge (-AB), *Adamson D303* (PRE); Between Grahamstown and Fort Beaufort, Beside Committees Drift road (-BA), *Balkwill 464, 466 & 468* (E, NU); Beside Kransdrift road (-BA), *Balkwill 469* (E, NU); Grahamstown - Ft Beaufort road beyond Ecca Pass (-BA), *Brink 240* (GRA); Hunt's Hoek (-BC), *Forward sub GRA A1611* (GRA); Grahamstown, Hill Kaif (-BC), *Hurter sub RUH 3283* (RUH); On the farm "Glen Boyd" (-BC), *Lindstedt 12* (PRE), Coombes Valley (-BD), *Bayliss BRI. B. 307* (PRE).
3327 (Peddie): Kingwilliamstown, Line Drift (-AA), *Leighton sub NBG 48702* (NBG); Valley of Umtana River, Peddie - Kaffir Drift road (-AD), *Story 1284* (GRA, PRE); East London (-BB), *Thode sub STE 7964* (STE).
3424 (Humansdorp): Humansdorp, Miskraal (-BB), *Barker 24068* (NBG).

Identification of the type of *P. cernua* has been confused by the complexities of Ecklon and Zeyher's collections and numbering system. Gunn and Codd's (1981) 'Botanical Exploration of southern Africa' has provided much helpful information. Zeyher collected and distributed material from the Uitenhage area before his collecting pact with Ecklon began. Up until the time the pact was initiated, Ecklon had not collected near Uitenhage and had distributed his specimens through a botanical exchange called, Unio Itineraria. Shortly after their pact was initiated, Ecklon collected at Uitenhage and wrote up his 'A list of plants found in the district of Uitenhage between the months of July 1829 and February 1830' in the South African Quarterly Journal (1830). In this list of species, in Family 40, *Justicia capensis* is listed. Later they collected in the area together and distributed specimens with either or both their names on the sheets. After their collecting pact had lapsed, Zeyher collected from the area on his own. Their numbering system was not one with consecutive numbers for consecutive gatherings, but one in which the localities were coded in numbers, and these codes were recorded on the labels of specimens. Because of the coding system, inconsistencies occurred during the preparation of material for distribution, so that specimens from the same gathering may have different data on the labels, while specimens with the same number, locality and collecting data may be from different gatherings (Gunn & Codd, 1981). Some specimens were distributed with personal numbers, some with combined numbers and some with locality numbers. A sheet in SAM bears the numbers 2.2. and 40 in Zeyher's hand, 2.2. being the code for a specimen collected in February from locality 2 (the type locality of *P. cernua*, but the wrong month). It seems that the number 40 is applied to any sheet of *P. cernua* collected from locality 2. Nees does not cite a herbarium for the type of *P. cernua* (and cites his own herbarium as well as others in 1847). The type was in his own herbarium and has been distributed GZU, where it is now housed. One or both of the sheets presently housed at Kew, must represent the gathering(s) to which Hooker referred when offering Zeyher's material for sale. Hooker's listing of the species antedates Nees's description, but as it was not accompanied by a description, diagnosis or precise locality it is a *nomen nudum*. It is uncharacteristic of Nees not to quote previous references when they existed, and unlikely that both Nees and Hooker would have independently decided on the same name for the same species, so that it appears that Hooker must have seen Nees's manuscript before it was published, or that Ecklon and/or Zeyher may have circulated the specimens with a name on them, and Nees took up this name. Once again, it would have been uncharacteristic of Nees not to have cited the source of the name, even if he had taken up the name from a label and the label of the type bears the name *Justicia capensis*. One of the sheets at Kew bears the name *Justicia capensis* and a locality in Ecklon's hand, while those at SAM (the herbarium where much of Zeyher's personal herbarium is housed) bear the name *P. cernua*, one with Nees as author of the name, and one without an authority, suggesting it was a name used by Zeyher, possibly before Nees published the name. The specimen to which Nees referred was an Ecklon specimen, distributed through the Unio Itineraria, and it seems was part of a mixed gathering labelled *Justicia capensis*, and as mentioned above is at GZU. A sheet has been found at STE, bearing the number 556 (now crossed out), the name *Justicia capensis*, and an English version of the locality on the type, and this sheet is most likely an isotype. The sheets at Kew bearing the number 40 are undoubtedly those to which Hooker (1840) referred, most likely those to which Nees referred in 1847, but not that to which he referred in 1841. The data on the labels of these sheets does not agree with that of locality 40, but rather to that of locality 2, so that the number on these sheets cannot be a locality number. It is an interesting coincidence that in Ecklon's 1830 publication the Acanthaceae had the family number 40 and that the Kew sheets with this number bear the name *Justicia capensis* and this coincidence may indicate that these sheets were amongst those to which Ecklon referred for his publication. It is possible, too, that the material at Kew is part of the type gathering (although it has the wrong month of the year on the label), but it would be very difficult if not impossible to prove or disprove this.

P. cernua is closely allied to *P. kotschyana* as discussed under the latter. The sizes of the tertiary bracts and flowers of this species display clinal variation. Figure 17, which presents the variation in lengths of tertiary bracts and flowers of *P. cernua*, shows that the smaller structures are present in material collected in the Cape and the larger in Natal. It is likely that this cline accounts for the number of synonyms of *P. cernua*. This species sometimes produces white individuals (*Balkwill 445*) and white populations (*Brink 327*). As the description of *P. krebsii* differs from *P. cernua* mainly by the white corolla, it is possible that this name was applied to a white colour form of *P. cernua*.

P. cernua can be separated from *P. paniculata* by the larger flowers (fig. 20); from *P. transvaalensis* by the shorter narrower tertiary bracts (plate 3), and from *P. cliffordii* and *P. gillilandiorum* by the lack of curved eglandular trichomes between the ridges on the stem (plate 29). *P. cernua* is usually found in valley bushveld, and the few specimens that are found out of this veld type are found in coastal forest and thornveld communities (fig. 49). Plants have been collected in flower throughout the year, but there is a very marked peak in collections in July and August (fig. 72).

DICLIPTERA Juss. in Ann. Mus. Natl. Hist. Nat. 9: 267 (1807). Type Species (conserved): *Dicliptera chinensis* (Linn.) Juss. in Ann. Mus. Natl. Hist. Nat. 9: 268 (1807). Type specimen is type of *Justicia chinensis* L.

Conserved over *Diapedium* C. König in Ann. Bot. (König & Sims) 2: 189 (1805, '1806'); Koen. ex Steud. Nom. ed. 2, 1: 501 & 504 (1840). Type Species: *Justicia chinensis* L., Sp. pl. ed. 1, 16 (1753). Type: CHINA *Savage Catalogue 28.19* (LINN, seen on microfiche).

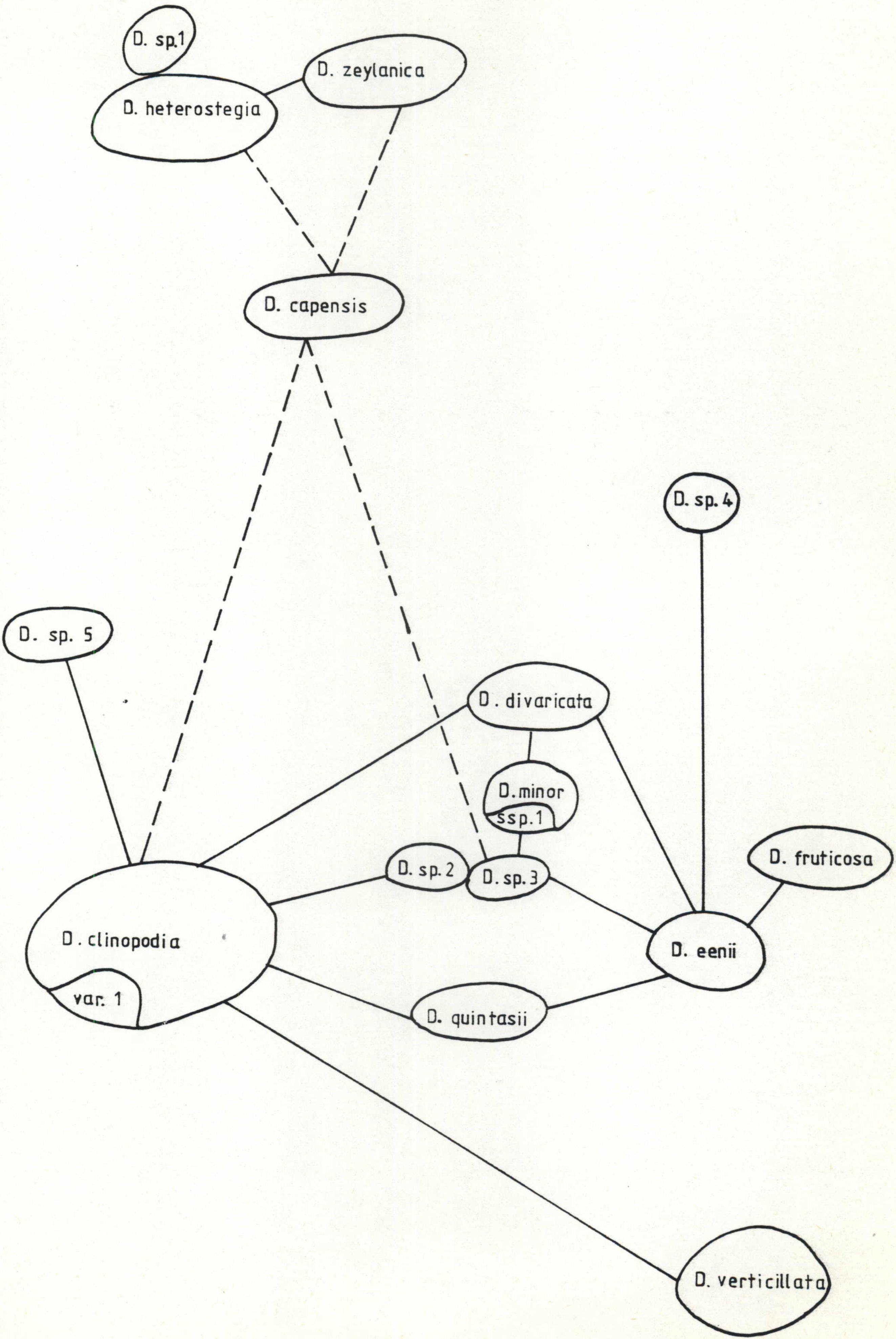
Evergreen herbs or suffruticose perennials up to 2 m high. *Leaves* simple, opposite, widely ovate to lanceolate, entire, herbaceous with simple eglandular multicellular trichomes and cystoliths; petiolate. *Inflorescence* of monochasial cymes (infloresence units) subtended by a pair of bracts, (1 - 2) - 3 - (4) umbellately arranged, rarely compounded, 1 to many 'umbels' in each axil; peduncles sometimes swelling with age. *Bracts*: secondary bracts 2, free, narrowly triangular to lanceolate; tertiary bracts lanceolate to broadly ovate or obovate, acute to apiculate, entire, cuneate to very widely cuneate at the base. *Flowers* perfect, zygomorphic. *Calyx* shortly tubular with lanceolate lobes. *Corolla* bilabiate, resupinate; tube narrowly cylindric below, subcampanulate above, with 2 pairs of longitudinal hairy ridges within, lip in lower position minutely emarginate; lip in upper position narrowly oblong, 3-fid. *Stamens* 2, exserted; filaments epipetalous, linear; anthers 2-thecous, thecae superposed, introrse. *Disc* cupular, nectariferous. *Gynoecium*: stigma bilobed; style exserted, filiform; ovary superior with septum in median longitudinal axis, 2 ovules in each locule. *Fruit* a short-stalked, capitate capsule, markedly laterally compressed, with a raphe, to which the elastic placentae are attached, on each side, placentae bearing retinacula. *Seeds* discoid, usually 4 in each capsule, rough and tuberculate.

In Index Kewensis (Jackson, 1895), only the 1840 reference for *Diapedium* is quoted, so that it appears that the name *Dicliptera* was in wide usage before the 1805 reference was found and in order to promote nomenclatural stability, *Dicliptera* and its type *D. chinensis* were conserved over the genus *Diapedium*.

Confusion exists about the limits of the genus *Dicliptera* and many workers accepted that elastic placental bases and paired bracts subtending the calyx were sufficient to circumscribe the genus. Thus, species with corollas that are not resupinate and with anthers that have parallel thecae have been included in *Dicliptera*. I held a rather narrower view of *Dicliptera*, with resupinate corollas and superposed anther thecae as additional characters. Professor Hilliard was kind enough to examine specimens of *D. chinensis* at Kew, and has established that the type species fits into this narrower concept of the genus. The only reliable character that distinguishes *Dicliptera* from *Peristrophe* is the nature of the bases of the placentae, which are inelastic in *Peristrophe* and elastic in *Dicliptera*.

Species of *Dicliptera* appear to be very closely related to one another and are often very difficult to distinguish from one another. Indeed, the floral morphology of the three southern African genera in the Diclipteriinae is extremely similar, so that one has to rely on other features to delimit species. In *Dicliptera* the tertiary bracts show a great deal of variation, and provide useful characters, as do the morphology of the inflorescences, the length of the inflorescence axes, the length of the peduncles of the inflorescence units and the range in habit that is exhibited by species in the genus. While suites of characters may distinguish some species, some of the same caharacters may overlap in other species of the genus. Some of the characters within a suite may not discriminate between species as effectively as others, although some of the characters will correlate and will distinguish the species. The construction of keys is thus very difficult. Fig. 77 represents the relationships between species of *Dicliptera*. After a specimen has been keyed, it should be compared with the closely related species as well as with the species to which it has been keyed.

It is possible that *Dicliptera* may be divisible into sections. Those species with ovate, obovate or broadly elliptic tertiary bracts without 'windows' would comprise the typical section, while those with oblanceolate, lanceolate or narrowly ovate bracts with 'windows' between the veins at their bases would comprise the other. Southern Africa is the end-point in the African distribution of the family Acanthaceae so that


D. sp.1
D. zeylanica
D. heterostegia
D. capensis
D. sp. 4
D. sp. 5
D. divaricata
D. minor
ssp. 1
D. fruticosa
D. sp. 2
D. sp. 3
D. clinopodia
var. 1
D. eenii
D. quintasii
D. verticillata

it is possible that only a small degree of the worldwide variation in characters is represented in this area. Thus, until I have had opportunity to deal with the genus on a much wider scale, I cannot assess the validity of subdividing it in the manner suggested above.

The genus *Dicliptera* is pantropical and has a total of about 150 species, of which 15 occur in southern Africa.

Key to species of the genus *Dicliptera*

1) Tertiary bracts broader than 6 mm, ovate, elliptic or obovate, always without white "windows" (areas of sclereids) between the veins at their bases ....2)

1a) Tertiary bracts narrower than 6 mm or with white "windows" between the veins at their bases ....5)

2) Only one "umbel" borne in each axil; occurring only in the valley bushveld of the eastern Cape; corolla shorter than 20 mm, flowers purple, lilac or white *4) D. capensis*

2a) Often more than one "umbel" in each axil; not occurring in the valley bushveld of the eastern Cape; flowers lilac or white, or flowers longer than 20 mm ....3)

3) Tertiary bracts elliptic or obovate; corolla tube longer than 7 mm and lip in lower position longer than 11 mm; with up to 2 'umbels' in each axil; occurring in deep shade in forests *1) D. zeylanica*

3a) Tertiary bracts ovate; corolla tube shorter than 7 mm and lip in lower position shorter than 10 mm; occurring in dune and sand forests, at forest edges and in valley bushveld ....4)

4) Leaves linear, narrower than 10 mm *2) D. sp. 1*

4a) Leaves ovate, broader than 10 mm *3) D. heterostegia*

5) Plants annual; flowers shorter than 8 mm; capsules shorter than 5 mm; tertiary bracts narrower than 3 mm and fringed with white hairs; inflorescences often produced at first or second node, often compounded *15) D. spinulosa*

5a) Plants perennial; flowers longer than 8 mm; fruits longer than 5 mm; tertiary bracts usually broader than 3 mm, but if narrower than 3 mm, then not fringed with white hairs; inflorescences never produced at first or second nodes, seldom compounded ....6)

6) Some stems dense with straight, soft, silky hairs, 2 - 3 mm long; occurring in Botswana and Zimbabwe *14) D. sp. 5*

6a) Stems glabrous or variously pubescent, but not as *D. sp. 5* ....7)

7) Inflorescence axes (those bearing 'umbels') longer than 5 mm, so that the inflorescences do not appear to be contracted into the axils ....8)

7a) Inflorescence axes shorter than 5 mm, so that inflorescences appear contracted into the axils * ....10)

8) Tertiary bracts 2,5 mm or narrower; plants bushy and much branched, often taller than 0,6 m and stems woody and thicker than 5 mm at the base *13) D. fruticosa*

8a) Tertiary bracts broader than 2,5 m; plants up to 0,6 m tall; vertical stems less than 5 mm in diameter and plants with decumbent branches frequently rooting at nodes or with subterranean stolons; if bracts 2,5 mm or narrower, then plants never with stem bases thicker than 5 mm ....9)

9) Flowers longer than 25 mm, tube longer than 14 mm, off-white with pale speckles on lip in upper position; leaves stiff and almost elliptic; plants with subterranean stolons *12) D. sp. 4*

9a) Flowers shorter than 25 mm, tube shorter than 14 mm, purple, with dark purple speckles on lip in upper position; leaves thinly textured, often with a very acute tip; if stolons present, then not subterranean *11) D. eenii*

10) Stems, leaves and tertiary bracts with a smooth, green appearence; occurring in the Orange, Vaal and Hartz River Catchments, in the south western Transvaal, the Orange Free State, the north-eastern Cape and at Lovedale in the Eastern Cape *9) D. sp. 3*

10a) Stems and/or leaves and/or bracts glandular, pubescent or glandular-pubescent, with a rough appearance; occurring in Botswana, Transvaal (but not south of ther Magaliesberg mountains), Swaziland or Zululand ....11)

11) Corolla tube shorter than 10 mm, lip in lower position shorter than 15 mm ....12)

11a) Corolla tube longer than 10 mm, lip in lower position longer than 15 mm ....16)

12) Stems conspicuously pubescent with bent eglandular trichomes that

collapse on drying and are 1 - 2 mm long; occurring in the Magaliesberg mountains *8) D. sp. 2*

12a) Stems, if pubescent, with straight trichomes, or bent trichomes that do not collapse on drying; plants not occurring in the Magaliesberg mountains ....13)

13) Plants usually upright, occasionally some branches decumbent; tertiary bracts thin, sparsely glandular-pubescent, narrowly obovate and apiculate; occurring in sand forests in Mozambique and Zululand *10) D. quintasii*

13a) Plants with most stems deflexed above or decumbent; tertiary bracts not thin, glandular and acute; not occurring in sand forests of Mozambique and Zululand ....14)

14) Corolla pale purple; lip in lower position wider at proximal end; mature tertiary bracts very densely glandular; plants often taller than 30 cm; stems deflexed above, infrequently rooting at the nodes; occurring on clay soils in Swaziland, Zululand and the Kruger National Park *6) D. divaricata*

14a) Corolla deep purple (magenta) or white; lip in lower position broadest in centre; if flowers purple, then mature tertiary bracts glabrous, if white then mature tertiary bracts with common glandular trichomes; plants less than 30 cm high; stems markedly decumbent, commonly rooting at the nodes; occurring in Botswana and Transvaal ....15)

15) Flowers deep purple (magenta); mature tertiary bracts glabrous, most tubercles on seeds squat and with many minute hooks (observation at 50 X) *7.1) D. minor* ssp. *minor*

15a) Flowers white; mature tertiary bracts with common glandular trichomes; most tubercles on edges of seeds taller than broad, with few minute hooks (observation at 50 X)

7.2) D. minor ssp. *1*

16) Plants restricted to the Transkei, in grasslands facing the sea; leaves semi-succulent *5.2) D. clinopodia* var. *1*

16a) Plants widespread, usually occurring at forest edge and in bushveld; leaves not semisucculent

5.1) D. clinopodia var. *clinopodia*

* Some plants of *D. eenii* have short inflorescence axes and will

thus follow the wrong arm of the key. These specimens follow the key until couplet 14, where they will key to neither *D. divaricata* nor to *D. minor*. They can be separated from *D. divaricta* on the basis of distribution: *D. eenii* occurs in Namibia, and near Louis Trichardt, Thabazimbi and Rustenburg in the Transvaal, while *D. divaricata* occurs on clay soils in the Kruger National Park, Mozambique, Swaziland and Zululand. *D. eenii* can be separated from *D. minor* on the basis of habit, leaf texture and leaf shape: in *D. eenii* the stems are upright at the base and bend over at the tips; the leaves are thinly textured and acuminate to narrowly acute, while in *D. minor* the stems are deflexed near the base or decumbent; the leaves are thick in texture and acute to obtuse at the tips).

1) D. zeylanica Nees in DC., Prod. 11: 474 (1847); Clarke in Hooker, Fl. of British India 4: 452 (1885); Lindau in Engl. and Prantl, Pflanzenfam. 4(3b): 332 (1897); Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 91 (1901); Gledhill, Eastern Cape Wildflowers 213 (1969). Type: In Ceylon, *Walker* (K, n.v.).

D. bivalvis (L.) Juss. in Ann. Mus. Natl. Hist. Nat. 9: 268 (1807), *pro parte*.

D. bivalvis sensu Wight, Ill. Nat. Ord. Pl. (Ill. of Indian Botany) 2: 191 & plate 164-b, fig 10 (1850); Nees in DC., Prod. 11: 475 (1847); Wight in Cramer and Swann, Icones Plantarum Indiae Orientalis 1: 7 & 3: plate 1551 (1850); Dalzell and Gibson, The Bombay Flora 196 (1861); T. Anderson in Thwaites, Enumerato Plantarum Zeylaniae 235 (1864); T. Anderson in J. Linn. Soc., Bot. 9: 519 (1867); Christenson in Dansk. Bot. Arkiv. 4(3): 10 (1922), *nomen confusum*.

D. foetida (Forssk.) Blatter *sensu* Wood, Hillcoat and Brummit in Kew Bull. 38(3): 429 - 456 (1983), *pro parte*.

Non *D. foetida* (Forssk.) Blatter in Rec. Bot. Surv. India 8: 361 (1921). Lectotype: (Yemen), Forsskal 382 (C, lecto.!; K, presumed isolecto.).

Non *Justicia bivalvis* L. in Sp. Pl. ed. 2., 23 (1762).

Non *Peristrophe bivalvis* (L.) Merril, Rumph. Herb. Amboin 476 (1917).

Herb up to 0,5 m high, readily stoloniferous. *Leaves* ovate, acute, attenuate, cuneate to broadly cuneate at base, (23,3) - 49,2 - 83,6 -

(98,6) x (8,5) - 20,3 - 38,7 - (44,0) mm; petiole (3,3) - 10,1 - 28,0 - (31,4) mm. *Inflorescence* of (1 - 2) - 3 - 4 - (5) inflorescence units umbellately arranged, very rarely compounded, 1 - 2 umbels in each axil; inflorescence axis (5,5) - 8,6 - 33,4 - (53,0) mm; longest peduncle of inflorescence units (4,2) - 4,8 - 9,1 - (15,7) mm. *Bracts*: secondary bracts lanceolate, occassionally elliptic, rarely leaflike, (4,0) - 4,6 - 6,1 - (6,7) x (0,4) - 0,5 - 0,8 - (0,9) mm, sparsely strigose on margins and veins, trichomes multicellular and eglandular; tertiary bracts obovate or elliptic to widely obovate or elliptic, acuminate to acute, larger (14,2) - 15,1 - 18,8 - (21,0) x (7,9) - 8,7 - 10,9 - (12,3) mm, sericeous on margins and veins, sparsely sericeous on surface, trichomes multicellular and eglandular. *Calyx* tube 1,5 mm; lobes 6,0 mm, inner surface with broad-based appressed eglandular trichomes, outer surface with small and large glandular trichomes, margins with upward pointing eglandular trichomes and with occasional long-stalked spreading glandular trichomes. *Corolla* tube (7,0) - 9,2 - 11,9 - (12,5) mm, with curved eglandular trichomes, and very rare straight glandular trichomes; lip in lower position elliptic, (11,0) - 11,2 - 15,1 - (20,3) x (3,9) - 4,2 - 6,8 - (7,8) mm; lip in upper position narrowly elliptic, 9,8 - 14,2 - (19,3) x (2,5) - 3,1 - 5,6 - (7,3) mm, with feint purple honey guides; flowers white or light lilac. *Stamens*: filaments with curved ornamented eglandular and occasional glandular trichomes on lower surface and minute glandular trichomes close to thecae; anther thecae superposed. *Disc* shallowly cupular, with 2 triangular awns. *Gynoecium*: stigma bilobed, slightly unequal; style sparsely strigose; ovary ovoid, nearly glabrous. *Fruit* (7,0) - 8,0 - 9,5 X (2,0) - 3,2 - 4,8 - (4,9) mm, with some glandular and many eglandular multicellular trichomes. *Seeds* (2,5) - 2,7 - 3,4 - (3,5) x (2,2) - 2,4 - 3,0 - (3,2) mm, rough and tuberculate, tubercles hooked.

SELECTED CITATIONS

MOZAMBIQUE

1832 (Umtali): Manicaland Province, Penhalonga Forest (-DD), *Chase 2910* (SRGH).

ZIMBABWE

1932 (Melsetter): Umtali (-BA), *Eyles 1691* (PRE, SAM); Melsetter (-DD), *Williams 162* (SRGH); On east slopes of Vumba Mountains, *Chase 8614* (PRE); S.W. Vumba, *Chase 5791* (PRE); Tshakwe Mt

Burma Farm, *Chase 5724* (PRE).

1933 (Vila Pery): Chimanimani Mountains (-CC), *Bisset CH8* (SRGH).

2030 (Fort Victoria): Belingwe, Mt. Buhwa (-CB), *West 6636* (PRE); Northern aspect of Mt. Buhwa (-CB), *Simon, Pope & Biegel 2411* (PRE, SRGH).

2032 (Chipinga): Chirinda Forest, *Goldsmith 92/67* (PRE).

2033 (Chibavava): Melsetter, Near Haroni-Makurupini junction (-AA), *Müller 2748* (SRGH).

TRANSVAAL

2329 (Pietersburg): Haenertsburg, Bellarive Estates (-DD), *Balkwill 1583* (E, NU).

2330 (Tzaneen): Louis Trichardt District, Entabeni State Forest (-AA), *Balkwill 159* (NU); Letaba District, Duiwelskloof Waterfall (-CA), *Balkwill 134* (E, NU); Pietersburg District, Woodbush (-CC), *Moss 15540* (J); *ibidem, Edwards sub BOL 32309* (BOL).

2430 (Pilgrim's Rest): Letaba District, The Downs (-AA), *Balkwill 120, 122 & 126* (E, NU); Harmony Block, Farm Balloon (-AB), *Breijer 17568* (PRE); Mount Sheba Nature Reserve (-DC), *Kerfoot K8480* (J).

2531 (Komatipoort): Barberton, Twello Forestry, Highlands Estate (-CC), *Balkwill 1506* (E, NU).

SWAZILAND

2531 (Komati Poort): Pigg's Peak, Havelock Valley bottom (-CC), *Compton 31561* (NBG, PRE); Mtutusi River, Havelock (-CC), *Compton 29132* (NBG, PRE).

NATAL

2731 (Louwsburg): Ngotshe District, Ngome State Forest, Near Inspection Quarters (-CD), *Balkwill 242* (E, NU); Ngome State Forest, Ntendeka Wilderness Area (-CD), *Balkwill 232 & 233* (E, NU).

2830 (Dundee): Kranskop District, Forest patch on Kranskop-Middledrift road (-DD), *Edwards 2104* (NU, PRE).

2831 (Nkandla): Eshowe, Margin of forest (-CD), *Galpin s.n.* (BOL).

2930 (Pietermaritzburg): Near Curry's Post (-AC), *Acocks 11582* (NH, PRE); New Hanover District, 6 miles N.W. of York (-AD), *Acocks 12732* (PRE); 9 miles N.W. of New Hanover (-BC), *Codd 1435* (PRE); Maritzburg (-CB), *Verdoorn sub PRE 40538* (PRE); World's View (-CB), *McGillivray 3647* (RUH); *Town Bush Valley (-CB), Canham 32* (NU); Sweetwaters (-CB), *Phillips s.n.* (NU): Camperdown District, Drummond (-DA), *Tinley 637* (NU).

3030 (Port Shepstone): Oribi Gorge Nature Reserve, Hoepoe Falls Trail (-CA), *Balkwill 338* (E, NU); Umtamvuna Nature Reserve, Beside River Trail from the Pont (-CC), *Balkwill 345 & 349* (E, NU); Umtamvuna Nature Reserve, Smedmore Forest (-CC), *Balkwill 423 & 428* (E, NU); *ibidem, van Wyk 6076* (PRE, PRU).

TRANSKEI

3129 (Port St John's): Near Lusikisiki (-BC), *Johnson 16* (NBG); Port St John's, Agate Terrace (-DA), *Balkwill et al 1900* (E, NU).

3228 (Butterworth): Elliotdale District, The Haven (-BB), *Gordon-Gray 432* (NU); Dwessa Forest Nature Reserve (-BD), *van Jaarsveld 3805* (NBG); Kentani (-CB), *Pegler 1515* (PRE); *ibidem, Pegler 912* (BOL, PRE).

CAPE

3227 (Stutterheim): Near Komgha (-DB), *Flanagan 801* (GRA, PRE, SAM).

3228 (Butterworth): Near Kei Mouth (-CB), *Flanagan 801* (BOL); East London, Gonubie Mouth (-CC), sine legit 20 (NU).

3323 (Willowmore): Knysna, Groot River Valley (-CD), *Gillett 1481* (BOL, PRE); *ibidem, Taylor 660* (NBG, SAAS); Nature's Valley (-DC), *Acocks 21163* (NBG, PRE, SRGH).

3327 (Peddie): East London District, *Rattray 142* (GRA); Fort Grey (-BB), *Galpin 7820* (PRE).

3423 (Knysna): Knysna Plettenberg Bay (-AB), *Rogers 26850* (PRE); Storm's River Mouth (-BB), *Balkwill 448* (E, NU).

3424 (Humansdorp): Humansdorp, Blaauwkrantz (-BB), *Maguire 743* (NBG).

Dicliptera zeylanica was considered to "hardly differ specifically from *D. heterostegia*" by C. B. Clarke in Flora Capensis (1901). This opinion is to some extent justified, as some specimens of these two species are difficult to distinguish from each other. The shape of tertiary bracts and the indumentum on these bracts are usually different, but the variation in these characters may intergrade from the one species to the other. However, these species differ with regard to the number of umbels produced in each axil, the length of inflorescence axes (figs. 6 & 7), the size of flowers (figs. 20 - 25) and the habitat. In addition, scanning electron microscopy has shown that wax bodies are dense on the seed surface and present on the tubercles of *D. zeylanica* and less dense on the testa surface and absent from the tubercles of *D.*

heterostegia (plate 21). Paper chromotography has shown that *D. heterostegia* has a flavonoid compound in the leaves that is different from any compound found in the leaves of any other species in the genus (table 13). On the basis of this evidence, I believe that *D. zeylanica* is specifically different from *D. heterostegia.*

The name *Dicliptera zeylanica* has been applied to southern Africa material since it was used by C.B. Clarke (1901), but confusion exists about the application of this name. Wood *et al* (1983) have examined the problem, and have concluded that the southern African material is conspecific with material from the Yemen and from northern Africa and that the southern African material should then be called *Dicliptera foetida* (Forsskal) Blatter. I, however, do not agree with this and provide my reasons below. Four epithets, of which the basionyms are *Justicia foetida* Forsskal, *Justicia bivalvis* Linnaeus, *Justicia sexangularis* Linnaeus and *Dicliptera zeylanica* Nees are involved.

Wood *et al* (1983) conclude that *J. bivalvis* L. refers to a species of the genus *Peristrophe*, that *Dicliptera bivalvis sensu* Juss. *pro parte et sensu* Nees and others is based on the same type and taxon as *J. bivalvis* L., and that this taxon is a species of the genus *Peristrophe. J. bivalvis* does not appear in Forsskal's (1775) account, and must have been written on the sheet by Vahl (Friis, 1983) after he had decided that *J. foetida* Forssk. was synonomous with *J. bivalvis.* I agree that *J. bivalvis* is a species of *Peristrophe* and so dismiss this epithet from the discussion about the appropriate name for southern African *Dicliptera zeylanica.*

Wood *et al* (1983) selected a lectotype for *J. foetida* Forssk. and reported that the specimen has *Justicia sexangularis* Forssk. written on it. The epithet *sexangularis* has been crossed out and they state that '*pallida*' and then *Justicia bivalvis* have been written above *sexangularis.* However, the word that they think is '*pallida*' is in fact *foetida*, with the 'oe' run together, as was customary; thus the epithet *foetida* does appear on the specimen. I agree with the selection of the lectotype.

J. sexangularis, as indicated by Wood *et al* (1983), was probably not intended as a new publication by Forsskal, but referred to *J. sexangularis* Linnaeus. Forsskal's description of *J. sexangularis* clearly states 'antherae solitariae', indicating that the plant to which he referred is more likely a species of *Hypoestes* than of *Dicliptera*. Thus Vahl must have originally written *J. sexangularis* onto the sheet in error and *J. sexangularis* can be dismissed from the present discussion.

Wood *et al* further conclude that *J. foetida* and *D. zeylanica* are synonomous and have referred the taxon to the combination *D. foetida* (Forssk.) Blatter. Their concept of *D. foetida* is of a widespread species that occurs in three areas (i.e. southern Africa, northeastern Africa and India), which are separated by two major disjunctions. They regard 'the description [of *J. foetida*] as being extremely vague, and so could apply to a wide range of Acanthaceae'. While Forsskal's description is vague, it states that the flowers are green or blue. The flowers of *D. zeylanica* in southern Africa are white (rarely pale lilac) and may or may not have purple honey guides. Thus I am uncertain that Forsskal's description of *J. foetida* could apply to *D. zeylanica* in southern Africa. Of the relationship of African and Asian material of *D. zeylanica* to *D. foetida*, Wood *et al* say 'the distinction from the Forsskal Arabian specimens may be rather tenuous'. If *D. foetida* is conspecific with *D. zeylanica* as they suggest, then I find the discontinuities in distribution between southern Africa and the Yemen and the Yemen and the Indian Peninsula to be surprising. The geographical distribution of variation in *D. foetida sensu* Wood *et al* is also very unusual as the plants that grow in the widely separated areas are more similar to one another than they are to the plants that are geographically intermediate. Wood *et al* (1983) say of the peduncle (which I term the inflorescence axis) of *D. zeylanica*: 'those in the upper part of the plant are sometimes very short'. While this is true, it is very unusual (figure 8) and *Forsskal 382* has these short peduncles near the base of the plant as well as at the tips. *Dicliptera zeylanica* in southern Africa, and presumably in India, is a plant that grows in dense shade in forests, thus the drier areas of north-eastern Africa and south-western Asia represent a considerable barrier to the distribution of this plant. Thus, while it is possible that *D. foetida* is a relict population that was part of a connection between southern Africa and India, it is surprising that it is morphologically different from the plants at each extremity of distribution. I think that *D. foetida* more likely represents an arid land species, which is closely related to *D. zeylanica*, but not conspecific. I thus agree with Blatter who considered *D. foetida* to be a species different from *D. zeylanica* and endemic to the Yemen. Wood *et al* (1983) say that *Mooney 6857* from Ethiopa is conspecific with *D. foetida*, and as Ethiopia is ecologically similar to the Yemen, I would support this.

Peristrophe paniculata (Forssk.) Brummitt, another member of the Acanthaceae that occurs in the Yemen, grows in much drier areas than does *D. zeylanica* and in southern Africa this species occurs to the north-west of the distribution of *D. zeylanica*. Because of its ability to grow in drier areas (such as the arid corridor, fig. 44), *P. paniculata* has a continuous distribution from south-western Africa through Ethiopia and Arabia to Asia.

The breadth of the tertiary bracts and the lack of anastomosing sclereids in the bracts of *D. zeylanica* distinguish it from *D. clinopodia, D. divaricata, D. minor, D. sp. 2, D. sp. 3, D. quintasii, D. eenii, D. sp. 4, D. fruticosa and D. sp. 5. Dicliptera zeylanica* differs from *D. capensis* by having larger flowers, by its habitat (in deep shade in damp forests) and the inflorescence axis in *D. zeylanica* is considerably longer than that in most specimens of *D. capensis. D. zeylanica* produces one or more often two umbels in each axil, while *D. heterostegia* produces up to five. In *D. heterostegia*, each successive inflorescence axis is shorter than that of the umbel previously produced, but the first inflorescence axis produced in each axil of *D. heterostegia* is usually shorter than that produced by *D. zeylanica*. Late in any flowering season, it is easy to tell these species apart by the number of umbels in each axil, but in the earlier part of the season one must rely on the relatively longer inflorescence axis, the larger flowers and the damper, more shady habitat of *D. zeylanica*. The floral bracts of *D. zeylanica* are usually elliptic or obovate and those of *D. heterostegia* are usually ovate, but this character sometimes intergrades. The indumentum on the tertiary bracts of *D. heterostegia* is usually more dense, consists of longer trichomes and occasionally includes stalked glandular trichomes, which I have not observed in any of the material of *D. zeylanica*. *D. zeylanica* is superficially very similar to *Hypoestes triflora*, but differs by having bithecous, not monothecous, anthers and capsules with elastic, not inelastic, placental bases.

D. zeylanica grows on forest floors in relatively damp forests, and so is associated with the Soutpansberg in the northern Transvaal, the escarpment in Zimbabwe, Mozambique and the eastern Transvaal and Swaziland, the foothills of the Drakensberg in Natal, as well as the coastal forests of southern Natal, the Transkei, the eastern Cape and the southern Cape in the region of Knysna (fig. 50). Although plants have been collected in flower in all months of the year except February and December, the significant flowering period is between April and September, with a peak in July (fig. 72). This corresponds with the occurrence of flowering observed in the plants that I have in cultivation.

2) D. sp. 1 *sp. nov.* akin to *D. heterostegia*, but differs from that species by having mature leaves narrower than 10 mm and linear in shape, as well as flowers that are slightly smaller (12,0 - 13,0 mm in *D. sp. 1* and 13,5 - 18,1 mm in *D. heterostegia*). Type: MOZAMBIQUE 1933 (Vila Pery): Bandula, Forest Floor, *Chase 6190* (SRGH, holo.).

Herb up to 1 m high. *Leaves* very narrowly lanceolate to linear, acute to obtuse, base cuneate and attenuate, 22,0 - 86,0 X 4,0 - 8,0 mm; petiole 4,0 - 13,0 mm. *Inflorescence* of 3 - 5 inflorescence units umbellately arranged, with up to 5 'umbels' in each axil, inflorescence axis 1,5 - 4,0 mm, longest peduncle of inflorescence units 1,5 - 6,0 mm. *Bracts*: secondary bracts lanceolate, 3,5 - 5,5 X 0,3 - 0,5 mm, with multicellular eglandular trichomes; tertiary bracts ovate to broadly ovate, abaxial bract slightly smaller, both bracts apiculate, adaxial bract 7,5 - 17,5 X 4,5 - 10,0 mm, with 5 - 7 veins from the base, sometimes papery, pubescent with multicellular eglandular trichomes and glandular trichomes with stalks up to half the length of the eglandular trichomes on the outer surfaces, densely pubescent with silky eglandular hairs and many stalked and sessile glandular trichomes on the inner surfaces. *Calyx* tube 1,0 mm, lobes 3,0 mm, with appressed eglandular and glandular trichomes within, glandular trichomes with small and large heads without, some eglandular trichomes on the margins. *Corolla* tube 7,0 - 8,0 mm, glabrous below, with backward-facing eglandular trichomes above; lip in lower position elliptic, 4,5 - 6,0 X 2,3 - 2,5 mm; lip in upper position narrowly elliptic, 5,0 X 2,0 - 2,5 mm; flowers light pink. *Stamens*: filaments with bent eglandular trichomes; thecae superposed and approximated. *Disc* shallowly cupular, with 2 triangular awns. *Gynoecium*: stigma bilobed, subequal; style very sparsely strigose; ovary ovoid, densely pubescent with some eglandular and glandular trichomes. *Fruit* and *seeds* not seen.

CITATIONS

NATAL

2632 (Bela Vista): Sihadla River Crossing (-DD), *Strey & Moll 3895* (NH, PRE).

This species is very closely allied to *D. heterostegia*, differing mainly by the narrower leaves (10,5 - 41,6 mm in *D. heterostegia* and 5,5 - 7,6 mm in *D. sp. 1*) and the smaller flowers (13,5 - 18,1 mm in *D. heterostegia* and 12,0 - 13,0 in *D. sp. 1*). Although other species in the genus occasionally have leaves as narrow as this species, the linear shape is unique, so that this character distinguishes this species from all others. *D. sp. 1* is extremely rare in southern Africa, being represented by only two gatherings, one from central Mozambique, the other from Kosi Bay in northern Zululand. The type specimen was collected in September, and has flowers, while *Strey & Moll 3895*, which was collected in November, appears to have finished flowering.

3) Dicliptera heterostegia Nees in DC. Prod. 11: 478 (1847); Presl, Botanische Bemerkungen 95 (1845), nom. nud.; T. Anderson in J. Linn. Soc. Bot. 7: 48 (1864); Clarke in Thiselton-Dyer, Fl. Cap. 5, 1: 90 (1901); Wood, Natal Plants 3: 6 & Pl. 254 (1902); Chevalier, Exploration Botanique de l'Afrique Occidentale Francaise 2: 501 (1920); Compton, Fl. Swaziland 559 (1976). Type: TRANSKEI 3129 (Port St John's): Between Umzimvubu (Omsamwubo) and Umsikaba (Omsamcaba), *Drège a.* (in the year) 1837 (G-DC, iso. seen on microfiche; K, iso.!).

Justicia heterostegia E. Mey in Drege, Cat. pl. Afr. austral. 1: 3 (1837); E. Mey. in Drege, Zwei Pflanzengeogr. Doc. 152, 159 & 195 (1843), nom. nud..

Dicliptera mossambicensis Klotzsch in Peters, Reise Mossamb. Bot. 220 (1862 - 1864); Lindau in Engler, Pflanzenw. Ost-Afrikas 371 (1895); Clarke in Thiselton-Dyer, Fl. Trop. Afr. 5: 258 (1900); Compton, Fl. Swaziland 559 (1976). Type: not designated.

Herb up to 0,5 m high. *Leaves* ovate, occasionally elliptic, acute, base cuneate and attenuate, (19,0) - 29,0 - 62,7 - (94,5) X (10,5) - 15,2 - 30,6 - (41,6) mm; petiole (4,0) - 8,33 - 27,33 - (44,0) mm. *Inflorescence* of (2) - 3 - 5 inflorescence units umbellately arranged, the number of 'umbels' in each axil increasing through the season, reaching up to 5; inflorescence axis (1,6) - 2,1 - 5,9 - (9,8) mm; longest peduncle of inflorescence units (1,9) - 2,6 - 4,5 - (5,7) mm. *Bracts*: secondary bracts lanceolate, (3,1) - 3,9 - 5,9 - (7,2) X (0,3) - 0,4 - 0,8 - (1,1) mm, sparsely pubescent, trichomes silky, some sessile glandular trichomes also present; tertiary bracts ovate to widely ovate, abaxial smaller and rounder, adaxial larger and acuminate to apiculate, larger (10,4) - 12,3 - 16,8 - (19,2) X (6,9) - 7,8 - 10,3 - (11,5) mm, with 5 - 7 veins from the base, often papery, pubescent, with eglandular trichomes, stalked glandular trichomes with stalks up to half the length of the eglandular trichomes, and with sessile glandular trichomes. *Calyx* tube 1 mm long, lobes 2,5 - 3,5 mm, inner surface with appressed eglandular and small upright glandular trichomes, outer surface with long-stalked, short-stalked and sessile glandular trichomes, and occassional eglandular trichomes near the apex. *Corolla* tube (7,0) - 7,6 - 9,6 - (11,0) mm, with bent eglandular trichomes; lip in lower position broadly elliptic, (5,8) - 6,9 - 9,1 - (10,5) X (3,0) - 3,2 - 5,1 - (5,8) mm; lip in upper position narrowly elliptic, (13,5) - 14,9 - 18,1 - (19,6) X (5,0) - 6,4 - 8.9 - (10,1) mm; flowers white or light lilac. *Stamens*: filaments with few bent ornamented eglandular trichomes; anther thecae superposed, but touching. *Disc* shallowly cupular with 2 triangular awns. *Gynoecium*: stigma bilobed, slightly unequal; style very sparsely strigose; ovary ovoid and glabrous. *Fruit* pubescent with long eglandular trichomes, (5,5) - 5,9 - 7,6 -

(8.5) X (2,5) - 2,9 - 3,7 - (3,9) mm. *Seeds* (2,0) - 2,2 - 2,7 - (3,0) X (1,7) - 2,0 - 2,6 - (3,0) mm, rough and tuberculate, tubercles hooked.

SELECTED CITATIONS

MOZAMBIQUE

1440 (Nacala): Maputo (-DC), *Hornby 2641* (PRE, SRGH).

1736 (Quelimane): Quelimane (-DD), *Sim 20734* (PRE).

2532 (Lourenco Marques): Lourenco Marques (-DC), *Borle 1102* (PRE).

2632 (Bela Vista): Maputaland, *ex Maputaland Expedition 14369* (PRE).

TRANSVAAL

2331 (Phalaborwa): Letaba, Kruger National Park (-DC), *van der Schijff 3885* (PRE).

2531 (Komatipoort): about 25 km south of Komatipoort, on banks of Komati River (-BD), *Balkwill 3028* (E, NU).

SWAZILAND

2631 (Mbabane): Border Gate, Stegi (-BD), *Compton 27021* (PRE, NBG).

2632 (Bela Vista): Black Umbuluzi River Gorge, Blue Jay Ranch (-AA), *Culverwell 897* (PRE)

NATAL

2632 (Bela Vista): Ndumu Game Reserve, Usutu River Bank (-CD), *Pooley 494* (NH); *ibidem, Balkwill 214* (E, NU).

2731 (Louwsberg): Ngome State Forest (-DD), *Balkwill 243 & 244* (E, NU).

2732 (Ubombo): Around Lake Sibaya (-BC), *Vahrmeijer &Tölken 868* (PRE); *ibidem, Balkwill 197, 198, 200 & 202* (E, NU); Mkuzi Game Reserve (-CA), *Goodman 1066* (NU); *ibidem, Balkwill 171, 172 & 174* (E, NU); Mkuzi Game Reserve (-CB), *Goodman 1085* (NU); Bed of Munywane Spruit (-CD), *Aitken & Gale 14* (NU, PRE); St Lucia Lake Area, Nibela Peninsula (-CD), *Ward 8027* (PRE).

2831 (Nkandla): Beside road between Nongoma and Hlabisa (-BB), *Balkwill 249*; Ngoye Forest (-DC), *Balkwill 294, 297 & 314* (E, NU).

2832 (Mtubatuba): Hluhluwe Game Reserve, Bongweni Valley (-AA), *Balkwill et al 1701* (E, NU).

2930 (Pietermaritzburg): In the valley below the Mooi River Falls (-AB), *Balkwill 899* (E, NU); Albert Falls (-AD), *Comins 201* (NU); Wartburg road (-BC), *Scott sub NU 58773* (NU); Nagle Dam (-DA), *Wells 1490* (NU); Isipingo North (-DD), *Ward 4906* (INCOL, NH, NU);

Clairmont (-DD), *Wood 1309* (BOL, SAM).
2931 (Stanger): Hawaan Forest, south bank of Umhlanga River (-CA), *Ross 2384* (SRGH); Durban (-CC), *Schlechter 2792* (BOL, COI, J, PRE).
3030 (Port Shepstone): Amanzimtoti (-BB), *Wilson 7* (NU); Umdoni Park (-BC), *Balkwill 351 & 352* (E, NU); Izotsha River Forest (-CB) *Strey 7431* (PRE); Umzimkulwana Valley, Oribi Gorge Nature Reserve (-CB) *Balkwill 322 & 323* (E, NU); Umtamvuna River Valley, Umtamvuna Nature Reserve (-CC), *Balkwill 340 & 346* (E, NU); Palm Beach (-CD), *Balkwill 354* (E, NU).
TRANSKEI
3128 (Umtata): Xora Basin (-DD), *Williams 46* (GRA).
3228 (Butterworth): Bashee River Mouth (-BA), *Sidey 686* (PRE).
CAPE
3227 (Stutterheim): Gonubie River Mouth (-DA) *Galpin 7750* (GRA); *ibidem, Balkwill 472 & 473* (E, NU).
3228 (Butterworth): Cintsa River Mouth (-CC), *Balkwill 475* (E, NU).
3327 (Peddie): Bulura Mouth, East London (-BB), *Acocks 15770* (PRE).

The epithet, '*heterostegia*', was first used by E. Meyer in 1837, and transferrred to *Dicliptera* by Presl in 1845, but the original citation was not accompanied by a description, so that the name was validated by Nees in 1847. Although Nees did not designate a type, he quotes only one specimen, stating that he had seen sheets in his herbarium and in that of Drège. The sheet in de Candolle's herbarium is most likely of the same collection as it is from the same locality as that cited by Nees. The epithet is descriptive as it refers to the difference in the size and shape of the abaxial and adaxial tertiary bracts, but may unfortunately fall into disuse. Other species such as *D. burmannii* Nees (from India, China and Timor), *D. ciliaris* Juss (from Guinea, Brazil, Madagascar and Comores), *D. glabra* Decaisne (from Timor) and *D. javonica* Nees (from Java) are all extremely similar to *D. heterostegia*, and a worldwide account of this group may reveal that they are conspecific. The tropical African species, *D. insignis* Mildbr. and *D. silvicola* Lindau, are also closely related and may be conspecific. In southern Africa, *D. heterostegia* occurs along the Mozambique coastal plain, growing in dune forest, forest edge and bushveld. The collection at Mooiriver is further inland than most of the collections made in Natal, but in Mozambique, the Transvaal and

Zimbabwe, the species occurs even further inland. The plants near Lake Sibaya in Zululand are unusual, as there are fewer inflorescences borne in each axil, and the bracts are smaller, so that in these aspects, they are intermediate between *D. heterostegia* and *D. sp 1*, the ovate leaves, however, make it easy to distinguish these plants from *D. sp. 1*. The tertiary bracts are often papery, and it is on the basis of this character that Klotzsch described *D. mossambicensis*, but this feature is variable, as is the degree of pubescence on the stem, one of the characters that apparently would distinguish *D. insignis* from *D. heterostegia*. *D. heterostegia* is closely allied to *D. zeylanica*, but can be distinguished by means of the different habitat (*D. zeylanica* grows in deep shade on forest floors), the ovate acuminate tertiary bracts (*D. zeylanica* has obovate or elliptic bracts that are not acuminate) and the number of inflorescences borne in each axil (*D. zeylanica* has up to two 'umbels' in each axil, while *D. heterostegia* may have up to five or six). *D. capensis* the fourth southern African species that has broad bracts, occurs further south than *D. heterostegia*, their distributions only overlapping near East London (figs. 52 & 53). *D. capensis* can also be distinguished from *D. heterostegia* by having only one 'umbel' in each axil. The other species in the genus *Dicliptera* can be distinguished from *D. heterostegia* as they have narrower tertiary bracts (fig. 15) that often have clear areas between the veins at the bases of these bracts. *D. heterostegia* is a variable species, with a great range of variation in shape of leaves, especially leaf bases, and in the size and texture of the tertiary bracts, which may become papery. At the beginning of a season, there may be only one 'umbel' in the axil of each primary bract, but as the season progresses, more 'umbels' are produced in each axil. The inflorescence axis of each successive 'umbel' is shorter than that of the umbel produced before it, so that often the last 'umbel' produced is sessile. Remarks about chemotaxonomy and seed surface of *D. heterostegia* appear under *D. zeylanica*.

D. clinopodia one of the species in the group with narrow bracts, appears to have hybridised with *D. heterostegia* near Durban, *Ward 5442*, a specimen collected near Durban, must be a hybrid between *D. clinopodia* and *D. heterostegia*. *D. heterostegia* has been collectecd in flower between February and September, with a slight peak in April (fig. 72).

4) **Dicliptera capensis** Nees in Linnaea 15: 373 (1841); Nees in DC., Prod. 11: 477 (1847); T. Anderson in J. Linn. Soc., Bot. 7: 47 (1864); Lindau in Engl. & Prantl, Pflanzenfam 4(3b): 333 (1897); Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 91. Type: CAPE 3325 (Port Elizabeth): Uitenhage District, `circa flumen Zwartkopsrivier ad praedium Pauli Mare. Martio cum floribus fructuque maturo` (-CD), *Ecklon* (not yet located).

D. propinqua Nees in Schldl., Linnaea 15: 373 (1841); Nees in DC., Prod. 11: 477 (1847). Type: CAPE 3325 (Port Elizabeth): 'Ad Coega et trans montes "Winterhoeksbergen" in Karro (Uitenhage)' (-CA), *sine leg.* (not yet located).

Herb up to 0,5 m high, frequently stoloniferous. Leaves ovate to widely-ovate, acute to obtuse, broadly cuneate at base, (7,3) - 10,1 - 18,3 - (23,2) x (5,3) - 7,4 - 13,3 - (17,2) mm, with eglandular trichomes and cystoliths; petiole (2,0) - 3,1 - 7,3 - (9,8) mm long. *Inflorescence* (1) - 2 - (3) monochasial cymes (inflorescence units), umbellately arranged, with 1 `umbel` in each axil, inflorescence axis (1,3) - 1,6 - 6,1 - (9,6) mm, longest peduncle of inflorescence units (1,4) - 1,9 - 7,0 - (11,7) mm. *Bracts*: secondary bracts lanceolate, occasionally elliptic, (2,8) - 3,3 - 5,2 - (5,8) x 0,4 - 1,5 - (12,7) mm, sparsely strigose on margins and veins, trichomes multicellular and eglandular; tertiary bracts widely obovate, widely elliptic to very widely ovate, acuminate to acute, larger (7,2) - 8,9 - 12,2 - (14,0) x (4,5) - 6,3 - 10,1 - (12,7) mm, strigose on margin, sparsely strigose on veins and outer surface, glabrous on inner surface, trichomes multicellular and eglandular. *Calyx* tube 1,5 mm; lobes 3,5 mm; inner surface with broad-based appressed eglandular trichomes, outer surface with glandular trichomes, margins with eglandular trichomes and with glandular trichomes and spreading eglandular trichomes near the base. *Corolla* on short stalk within the calyx, stalk 0,8 mm long; tube (6,0) - 6,8 - 8,7 - (10,0) mm, with curved eglandular trichomes, and straight glandular trichomes; lip in upper position trifid, narrowly elliptic, (6,5) - 7,5 - 9,9 - (10,2) x (2,0) - 2,3 - 3,7 - (4,0) mm, with dark purple honey guides; lip in lower position bifid, narrowly elliptic, (6,8) - 7,4 - 9,7 - (11,0) x (2,5) - 2,9 - 4,4 - (6,0) mm; flower purple, pink or white. *Stamens*: filaments with curved ornamented eglandular trichomes; anther thecae, superposed, approximated. *Disc* very shallowly cupular, with 2 small triangular awns. *Gynoecium*: stigma bilobed; style sparsely strigose; ovary ovoid with glandular trichomes. *Fruit* (5,0) - 6,1 - 8,5 - (9,0) x (2,5) - 3,2 - 4,4 - (4,5) mm, with many glandular and some eglandular trichomes. *Seeds* 2,3 - 2,7 x 2,3 - 2,6 mm, rough and with squat tubercles.

SELECTED CITATIONS

CAPE

3225 (Somerset East): Boschberg (-DC), *MacOwan sub Herb. Mus. Austro-Afr. 42943* (SAM); Middleton (-DD), *Acocks 21683* (PRE).

3226 (Ft Beaufort): Adelaide, Mungo Mountain (-CD), *Galpin sub PRE 11533* (BOL); Stockenstroom, 2m NE of Gonzana Siding (-DA), *Acocks 20084*(PRE); Alice, Woburn (-DB), *Sidey 599* (PRE); Near top of Koonap Heights (-DC), *Schonland 3708* (GRA).

3227 (Stutterheim): King Williamstown, Keiskamma Hoek (-CA), *Goulimis sub Bol 22986* (BOL); Tamacha (-CD), *Sim 4163* (PRE); King William's Town, Bolasse (-CD), *Sim 4137* (GRA, NU); King William's Town (-CD), *Tyson 1013* (BOL, PRE, SAM).

3228 (Butterworth): Cintsa Mouth West, in woodland (-CC), *Balkwill 474* (NU); Near Gonubie River Mouth (-CC), *Galpin 7750* (PRE).

3325 (Port Elizabeth): Alexandria, 3 m N of Sandflats (-BD), *Acocks 13637* (PRE); 10 m NE of Port Elizabeth (-DA), *Dahlstrand 271* (GRA).

3326 (Grahamstown): Beside the Committees Drift road which turns off from the Grahamstown - Ft Beaufort road (-BA), *Balkwill 465* (NU, PRE); Grahamstown (-BC), *Ecklon & Zeyher (Pappe on sheet) sub Her. Mus. Austro-Afr. 42941* (SAM); Grahamstown (-BC), *Mc Gillivray sub RUH 2646* (RUH); Belmont Valley, Near Kowie Ditch (-BC), *Mc Gillivray 3642* (RUH); Grahamstown (-BC), *Schlechter 2603* (BOL, COI, NBG, PRE, STE); *ibidem, Rogers 3139* (BOL); Bathurst, Kenton-on-sea (-DA), *Acocks 18320* (PRE).

3327 (Peddie): Keiskamma (-AA), *Zeyher sub Herb. Mus. Austr-Afr. 42938* (SAM); East London (-BB), *Mottley 2514* (J).

D. capensis is endemic to the eastern Cape and grows mainly in addo bush and other kinds of bushveld. *D. capensis* does not appear to have a specific flowering time and has been collected in flower from March to December, with no significant peak in any of these months. In our Botanic Garden at the University of Natal, where the species is grown as a ground cover, it appears to flower all year round. The eastern Cape is the southernmost point in the African distribution of the genus *Dicliptera* and in fact of most species in the Acanthaceae. As *D. capensis* is an endemic of this area, and has such a limited distribution, it must be a derived species. The other species of *Dicliptera* which occur in this area are *D. clinopodia* Nees, *D. heterostegia* Nees and *D. zeylanica* Nees. *D. capensis* has tubercles on the seed surface very similar to those of *D. clinopodia* and grows in similar habitats and often has purple flowers as does *D. clinopodia*. The flowers of *D. capensis* are, however, smaller than those of *D. clinopodia* and the secondary bracts are broader and lack windows (translucent areas). These features distinguish *D. capensis* from *D. clinopodia*. The indumentum of the bracts, the flower size and the habitat of *D. heterostegia* are similar to those of *D. capensis*, but, as *D. capensis* has secondary bracts that are seldom ovate or aristate and as its 'umbels' are borne singly in the axils, it can be distinguished from *D. heterostegia*, which has ovate, aristate bracts and, usually, more than one 'umbel' in each axil. Also, the flowers of *D. heterostegia* are usually white, sometimes lilac, while those of *D. capensis* are usually purple. *D. zeylanica* and *D. capensis* both have only one 'umbel' in each axil and have a similar indumentum on their bracts. *D. zeylanica* differs by having larger flowers that are white, unlike those of *D. capensis* which are smaller and often purple or pink. *D. zeylanica* grows in deep shade in damp forests, a habitat different from that of *D. capensis*. The inflorescence axis (fig 1b) is between 1,3 and 9,6 mm in *D. capensis*, while in *D. zeylanica* it is conspicuously longer (between 5,5 and 53 mm). On the basis of the tubercles on the seed coat; the shape, structure and indumentum of the tertiary bracts; the size and colour of the flowers and the habitat, I think that *D. capensis* may have originated by the hybridisation of *D. clinopodia* with *D. heterostegia*. However, if one also considers the structure of the inflorescence, it would be equally likely that *D. capensis* may have arisen by the hybridisation of *D. zeylanica* with *D. clinopodia*. These hypotheses suggest an interesting area for future research, when these species could be hybridised and compared with *D. capensis*. *D. propinqua* was described by Nees at the same time as he described *D. capensis* and the former was reduced to synonomy by T. Anderson in 1864. I have not seen the types of either of these names, nor have I seen any material from the type localities. I have noticed that there are some variations in the shape of the bracts of this species, and an extreme example is *Balkwill 474*, which has markedly widely-ovate bracts. In this specimen, the inflorescences are held vertically, while in others, e.g. *Balkwill 465*, they are held horizontally. *Galpin 7750* is very similar to *Balkwill 474*, especially with respect to size and shape of secondary bracts and length of inflorescence axes and peduncles. At first I thought that these differences may have justified the description of separate varieties (probably corresponding to *D. capensis and D. propinqua*). The diagnoses given by Nees and the range of variation within this species, however, indicates that I must agree with Anderson and with Clarke's reappraisal in Flora Capensis in 1901 and retain *D. propinqua* as a synonym of *D. capensis*.

5) D. clinopodia Nees in DC. Prod. 11: 483 (1847); T. Anderson in J. Linn. Soc. Bot. 7: 47 (1864); Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 91 (1901); Compton, Fl. Swaziland 558 (1976). Type: 'In Promont. Bonae Spei' NATAL (Pietermaritzburg): 'In der Valei am Fluss Omblas, März, April (In the valley of the Umlazi River, March, April) (-CD/DC/DD), *Drège* (K, holo.!).

Justicia clinopodia E. Mey. in Drège, Zwei Pflanzengeogr. Docum. 158 & 195. Type: as for *D. clinopodia*.

Dicliptera clinopodia occurs in the more easterly areas of southern Africa, being especially associated with the Soutpansberg mountains, the eastern escarpment and the Mozambique coastal plain. The infloresences of *D. clinopodia* are similar to those of members of the genus *Clinopodium* L., from which *D. clinopodia* takes its epithet. The specimen *Ward 5442* represents a hybrid between *D. clinopodia* and *D. heterostegia*, and it is possible that hybridisation between these species or between *D. clinopodia* and *D. zeylanica* may have given rise to *D. capensis* in the eastern Cape. *D. clinopodia* has close relationships with some tropical African species, especially *D. leonotis* Dalz. ex C.B. Clarke, which differs mainly by having narrower leaves and abaxial tertiary bracts with a larger proportion of white. It is important that species such as *D. clinopodia, D. leonotis, D. carvalhoi* Lindau, *D. olitoria* Mildbr. and *D. umbellata* Juss. should be revised simultaneously, so that their relationships can be assessed. *D. clinopodia var. clinopodia* is a very variable taxon, showing a range in size of flowers, in degree and type of indumentum on the stem and in colouration of the tertiary bracts. These features are important in distinguishing *D. clinpodia* from other closely related species such as *D. divaricata, D. minor, D. sp. 2, D. sp. 3, D. quintasii, D. eenii, D. sp. 4, D. fruiticosa, D. sp. 5* and *D. spinulosa*, so that *D. clinopodia* is distinguished on the basis of a suite of characters and on the basis of distribution, rather than on the basis of any single character. *D. clinopodia* is distinguished from *D. zeylanica, D. sp. 1, D. heterostegia* and *D. capensis* on the basis of the 'windows' or clear areas present between the veins of *D. clinopodia* and its narrower oblanceolate, sometimes narrowly obovate tertiary bracts. *D. divaricata, D. minor, D. sp 2* and *D. sp. 3* all have shorter flowers and shorter lower lips than those of *D. clinopodia*. *D. quintasii* has shorter flowers, shorter corolla tubes, and has bracts which have a much thinner texture than does *D. clinopodia*. *D. eenii, D. sp. 4, D. fruticosa* and *D. maculata* all have longer inflorescence axes and peduncles than does *D. clinopodia*. Other characters that distinguish *D. clinopodia* from the species that are most likely to be confused with it, are discussed under those species. *D. clinopodia* is a widespread, variable species and in southern Africa some plants have succulent leaves and thus have been placed in a separate variety.

Key to Varieties

1) Plants widespread, occurring at forest edges and in bushveld; leaves not semisucculent

5.1) D. clinopodia var. *clinopodia*

1a) Plants occurring in the Transkei, in grasslands facing the sea; leaves semi-succulent

5.2) D. clinopodia var. *1*

5.1) var. clinopodia

Herb or suffrutex, sometimes scandent, stems usually soft and up to 1,2 m. *Leaves* ovate to narrowly-ovate or elliptic, acute, base cuneate and attenuate, (20,0) - 34,25 - 65,49 - (107,0) X (11,5) - 14,6 - 30,5 - (48,6) mm; petiole (3,5) - 6,2 - 23,3 - (43,8) mm. *Inflorescence* of 3 - 5 inflorescence units umbellately arranged, sometimes 1, usually 2 or more 'umbels' in each axil; inflorescence axis 0,7 - 2,78 - (6,7) mm, longest peduncle of inflorescence units (0,7) - 1,0 - 2,0 - (2,9) mm. *Bracts*: secondary bracts obovate or very narrowly lanceolate, sometimes markedly apiculate, (4,8) - 6,9 - 11,7 - (15,8) X 0,2 - 3,2 - (5,4) mm, with straight multicellular eglandular trichomes up to 2 mm and some shorter bent eglandular trichomes on the edges and veins on the bracts, with some sessile glandular trichomes on the surface, often with clear areas or 'windows' between the veins; tertiary bracts obovate, the abaxial bract shorter, apiculate, cuneate at the base, (8,5) - 12,3 - 19,0 - (26,4) X (2,3) - 3,2 - 5,5 - (7,6) mm, with 3 veins from the base, with silky straight eglandular trichomes up to 1 mm long, and shorter bent eglandular trichomes, as well as stalked and sessile glandular trichomes, with clear areas or 'windows' between the veins, the upper portion of the bract often becoming purple. *Calyx* tube 1,3 mm, lobes 3,7 - 7,5 mm, inner surface with appressed eglandular trichomes, and few glandular trichomes, outer surface with many glandular trichomes, and occasional eglandular trichomes on the edges of the lobes. *Corolla* tube (7,5) - 10,8 - 14,4 - (16,5) mm, with straight and some bent eglandular trichomes; lip in lower position elliptic, (8,0) - 13,0 - 17,6 - (22,0) X (3,0) - 3,8 - 5,9 - (9,0) mm; lip in upper position narrowly elliptic, (8,0) - 11,6 - 17,6 - (23,6) X (1,6) - 2,1 - 3,4 - (4,3) mm; flowers purple. *Stamens* with bent trichomes on the proximal half of the filaments on the surfaces facing each other and small glandular trichomes on the lower surfaces of the filaments, especially in the distal half of the filaments; anther thecae superposed, but touching. *Disc* cupular, with 2 small triangular awns. *Gynoecium*: stigma bilobed, shortly filiform; style sparsely strigose; ovary ovoid, with very few glandular trichomes near the tip. *Fruit* with stalked glandular trichomes, and a very few eglandular trichomes, (6,3) - 7,0 - 8,5 - (10,0) X (2,2) - 2,3 - 3,2 - (4,0) mm. *Seeds* (1,7) - 1,9 - 2,4 - (2,9) X (1,5) - 1,7 - 2,2 - (2,5) mm, rough and with squat, unhooked tubercles.

Within *D. clinopodia* var. *clinopodia* there are some specimens markedly different from others in that the secondary bracts are broad and ovate instead of very narrowly lanceolate (fig. 12). Near Pietermaritzburg, however, it becomes extremely difficult to distinguish between these forms (fig. 12), so that I feel it would be unwise to formally recognise these two groups. The citations have been given under two forms. Form A has very narrowly lanceolate secondary bracts, which have many stalked glandular trichomes and this form also has longer calyx lobes, while Form B has obovate, markedly apiculate secondary bracts, with few stalked glandular trichomes, and shorter calyx lobes.

SELECTED CITATIONS

FORM A

Northern Hemisphere

KENYA

0238: Marsabit (-CA), *Verdcourt 1809* (PRE).

Southern Hemisphere

ZAMBIA

1428 (Broken Hill): Broken Hill (-AD), *van Hoepen 1390* (PRE).

ZIMBABWE

1832 (Umtali): Inyanga (-BD), *Booysen 1108* (NBG); Pungwe River, Honde Valley (-CA), *Loveridge 1103* (PRE); Imbeza Valley Road (-DB), *Abbot 12* (NU); Mapoff Estate, NE Vumba Mountains (-DC), *Chase 8300* (PRE).

1932 (Melsetter): Thornton Farm, Chipinga Road (-DB), *Crook M50* (PRE).

2031 (Bikita): 8 km SE of Silveira Mission (-BA), *Biegel 3048* (PRE, SRGH).

2032 (Chipinga): Gungunyana Forest Reserve (-BA), *Goldsmith 56/61* (PRE, SRGH).

TRANSVAAL

2229 (Waterpoort): Zoutpansberg Pass (-DD), *Galpin 14870* (PRE), Wylies Poort (-DD), *Hardy 949* (PRE); Picnic Site on southern slope of Wylie's Poort Pass (-DD), *Balkwill 163* (E, NU); Hanglip State Forest (-DD), *Balkwill 150* (E, NU).

2230 (Messina): Maname (-CD), *Van Wyk & Theron 4793* (PRU); Tate Vondo and Tshamanyatsha Forest Reserve, 22°51'34"/30°18'51" (-CD), *Hemm 142* (J, PRU); Thononda (-CD), *van Wyk & Theron 4541* (PRU); Tshidsini (Tshamutshedsi) (-DB), *van Wyk 3665* (PRU).

2328 (Baltimore): Blaauwberg, Near Malabosh's Kraal (-BA), *van der Schijff 5352A* (PRE).

2329 (Pietersburg): Louis Trichardt (-BB), *Moss 14521 & 14523* (J); Pietersburg (-CD), *Rousseau sub Uniw. Stellenbosiensis 17163* (STE); Foot of Wolkberg (-DD), *Meeuse 9882* (PRE); Haenertsburg, Cheerio Halt (-DD), *Balkwill 790* (E,NU).

2330 (Tzaneen): Klein Australe, Zoutpansberg (-AA), *Hutchinson & Gillett 4189* (SRGH); Duiwelskloof Waterfall (-CA), *Balkwill 135* (E, NU); Magoebaskloof, Franschhoek (-CC), *Hanekom 2325* (PRE); Woodbush Forestry Reserve, Debengeni Falls (-CC), *Balkwill 132* (E, NU).

2428 (Nylstroom): Palala Heights, Bokpoort (-BC), *Meeuse 9351* (COI, PRE).

2429 (Zebediela): Makapaan Valley (-AA), *Balkwill 104, 105 & 108a* (E, NU); Wolkberg, beside road to wilderness area (-BB), *Balkwill 109, 110 & 111* (E, NU).

2430 (Pilgrim's Rest): The Downs (-AA), *Rogers 20359* (J); *ibidem, Balkwill 118, 123, 124 & 127* (E, NU); Trichardtsdal, Makoetsi Kloof (-AB), *Hall 4557* (NBG); Blyderivier (-DB), *van der Schijff 5491* (PRE, PRU); Morgenzon Forest Reserve (-DC), *Mohle 346* (PRE); Clewer Falls (-DD), *Moss 18837* (J).

2529 (Witbank): Loskop Dam Nature Reserve (-AD), *Mogg 30549* (J, PRE).

2530 (Lydenburg): Between Lydenburg and Ohrigstad, Spekboom River Bridge (-AB), *van der Schijff 6730 (PRU); Schoemanskloof (-AD), Smuts 64*

(-PRE); Frankfort Forestry Station (-BB), *Louw 2191* (STE); Uitsoek State Forest (BC), *Kluge 935* (PRE); Lowveld Botanic Garden (-BD), *Buitendag 521* (NBG, PRE); Crocodile River Falls (-BD), *Quintas 226* (COI); Waterval Onder (-CB), *Harvey 3650* (RUH); Kloof below Waterval Boven (-CB), *Acocks 12749* (PRE, SRGH); 30 km north of Barberton (-DB), *Balkwill 1516* (E, NU); Queen's River Valley (-DD), *Balkwill 1427* (E, NU); Near Montrose (-DD), *Compton 19806* (BOL, NBG).

2531 (Komatipoort): Crocodile River Valley, Near Louw's Creek (-CA), *Bolus 1339* (SAM): Kaapmuiden (-CB), *Moss 13843* (J); Barberton, Rimer's Creek (-CC), *Galpin 449* (BOL, GRA, PRE).

SWAZILAND

2531 (Komatipoort): Pigg's Peak, Lomati River (-DA), *Compton 28975* (NBG, PRE).

2631 (Mbabane): Komati Bridge (-AA), *Compton 26830* (NBG,PRE); Usutu (Malkerus) Canal (-CA), *Compton 27754* (NBG); Mankaiana (-CC), *Compton 27718* (NBG, PRE).

NATAL

2830 (Dundee): Scottspoort, (near Weenen) (-CC), *Thode 2721* (STE).

2929 (Underberg): Estcourt, Dalton Bridge (-BB), *West 776* (COI, PRE).

2930 (Pietermritzburg): In valley below Mooi River Falls (-AB), *Balkwill & Manning 900* (E, NU); Howick Falls (-AC), *Hillary 25* (NU); Albert Falls (-AD), *Comins 202* (NU); Pietermaritzburg, Chase Valley (-CB), *Geekie 18* (NU); Mkomazi Valley below Hella-Hella (-CC), *Ward 8014* (NU); Richmond, Salt Pans Valley (-CD), *Sewnandan 7* (INCOL); Inchanga (-DA), *Hoal 16* (NU); Botha's Hill (-DC), *McClean 139* (PRE); Pinetown (-DD), *Impson 8* (NU).

3029 (Kokstad): Kokstad (-CB), *Tyson 1328* (SAM); Near Harding, 'Rooivaal' (-DB), *Hilliard 1276* (NU).

3030 (Port Shepstone): Umzinto, Hazlewood (-BC), *Baijnath 404* (INCOL, NU); Umzimkulwana River Valley, Near Horseshoe Dam (-CA), *Balkwill 405* (E, NU); Umtamvuna Nature Reserve (-CC), *Balkwill 396* (E, NU).

TRANSKEI

3128 (Umtata): St Cuthbert's (-BC), *Kelly sub NBG 48774* (NBG).

3228 (Butterworth): Kentani (-CB), *Pegler 822* (BOL, GRA, PRE).

CAPE

3327 (Peddie): East London (-BB), *Rattray 137* (GRA).

Form B

MOZAMBIQUE

2532 (Lourenzo Marques): Namaacha (-CC), *Moura 47* (COI); *ibidem, de Koning 7086* (SRGH); Lorenzo Marques (-DD), *Borle 1107* (PRE).

2632 (Bela Vista): Goba Fronteira (-AA), *Balsinhas 491* (PRE).

TRANSVAAL

2531 (Komatipoort): 2,5 miles SE of Kobinja (-CC), *Codd 7797* (PRE, SRGH).

SWAZILAND

2631 (Mbabane): Manzini, Mbisi Swamp (-AD), *Compton 31586* (NBG); Stegi, Namahasha Road (-BD), *Compton 28853* (NBG, PRE, SRGH); Ntondozi (-CA), *Compton 26897* (NBG, PRE); Mamiti River (-CD), *Compton 27951* (NBG, PRE).

2731 (Louwsburg): Nsoko, Uhlalwane (-BB), *Lindahl 24* (NH).

NATAL

2632 (Bela Vista): Ndumu Game Reserve (-CD), *Pooley 503* (NH, NU); *ibidem, Balkwill 213* (E, NU); *ibidem, Oatley D3* (PRE).

2731 (Louwsburg): Itala Nature Reserve, Langverwacht Section (-CB), *Porter & Ward 126* (NH).

2732 (Ubombo): About 2 km east of Ingwavuma Village (-AA), *Balkwill 215 & 216* (E, NU); Gwalaweni Forest (-AC), *Strey 8157* (PRE); Ubombo Police Station (-CA), *Stephen, van Graan & Schwabe 999* (PRE); On the outskirts of Ubombo (-CA), *Balkwill 180* (E, NU).

2830 (Dundee): Nkandla, Qudeni (-DB), *Lewis 101* (NU); *ibidem, Gerstner 654* (PRE).

2831 (Nkandla): Hlopekulu Mission Station (-AD), *Markotter sub Uniw. Stellenbosiensis 8658* (STE); Hlabisa (-BB), *Aitken & Gale 25* (NH); Between Nongoma and Hlabisa (-BB), *Balkwill 253* (E, NU); Nkandla Forest (-CA), *Balkwill 280, 282, 287, 288 & 289* (E, NU).

2832 (Mtubatuba): Hluhluwe Game Reserve (-AA), *Ward 3434* (NH, NU, PRE); *ibidem, Balkwill et al 1661* (E, NU).

2930 (Pietermaritzburg): Greytown (-BA), *Wylie sub NH 20523* (NH); Great Noodsberg (-BD), *Medley Wood 4280* (BOL, NH, SAM); Mkomazi Valley below Hella-Hella, Game Valley Estates (-CC), *Ward 8014*

(INCOL).

TRANSKEI

3128 (Umtata): Between Mganduli and Coffee Bay, Near Kwaaiman Post Office (-DD), *Lewis 2866* (PRE, SAM).

3129 (Port St John's): Port St John's (-DA), *Leipoldt 3425* (BOL); Mount Thesiger (-DA), *Balkwill et al 1766* (E, NU).

3227 (Stutterheim): King Williams Town (-CD), *Sim 163* (GRA).

3228 (Butterworth): Elliotdale, The Haven (-BB), *Gordon-Gray 214* (NU); Kentani (-CB), *Pegler 2895* (PRE); ibidem (-CB), *Gordon Gray 214* (NU).

This variety is most often found growing at the edges of forests, although it does sometimes grow in bushveld. *D. clinopodia* var. *clinopodia* is quite common in the areas in which it occurs and has often been collected as it is quite striking when in flower. Although flowering specimens have been collected throughout the year, there is a marked increase in the occurrence of flowering between March and August, with a peak in July (fig. 72). In our botanical garden *D. clinopodia* var. *clinopodia* begins flowering in April, and continues to do so until September. Some collections, such as one collected in Pietermaritzburg itself, begin and finish flowering before plants that were collected from other localities, especially those from the Transvaal. *D. clinopodia* var. *clinopodia* is one of the most attractive members of this genus, as many attractively coloured flowers are borne in congested inflorescences in the leaf axils.

D. clinopodia var. *1* can be distinguished from var. *clinopodia* by its succulent leaves and unusual maritime habitat. The two forms of *D. clinopodia* var. *clinopodia* can be distinguished on the basis of the shape of the secondary bracts, which are narrowly lanceolate in form A, and obovate in form B. Form B appears most closely related to the material named *D. umbellata*, while the species (such as *D. divaricata, D. minor, D. sp. 2* and *D. sp. 3*) that have probably been derived from *D. clinopodia* were most likely derived from form A.

5.2) D. clinopodia Nees var.1 *var. nova* differs from var. *clinopodia* by its smaller succulent leaves and unusual habitat (on sea-facing grassy slopes in the Transkei). Type: TRANSKEI 3228 (Butterworth): Quora Mouth (-BC), *Meeuse 9685* (PRE, holo., GRA).

Herb up to 0,6 m. *Leaves* ovate to elliptic, obtuse to acute, base cuneate, 17,1 - 29,4 X 7,9 - 21,4 mm, under surface with many cystoliths, causing it to dry white, succulent; petiole 17,1 - 29,4 mm. *Inflorescence* of 2 - 4 inflorescence units umbellately arranged, the number of 'umbels' in each axil between 1 and 3; inflorescence axis 0,6 - 1,4 mm; longest peduncle of inflorescence units 1,4 - 1,6 mm. *Bracts*: secondary bracts narrowly oblanceolate, apiculate, 6,7 - 8,2 X 1,5 - 2,8 mm, with clear areas between the veins, and multicellular eglandular trichomes 0,7 mm and others ranging up to 0,35 mm long; tertiary bracts oblanceolate, apiculate, larger 10,9 - 13,6 X 4,4 - 4,9 mm, with 3 veins from the base, fringed with wispy eglandular trichomes up to 1,2 mm long, the edges and outer surface with glandular trichomes with stalks up to 0,6 mm. *Calyx* tube 1mm, lobes 4mm, inner surface sparse with thick-based upward pointing eglandular hairs, and few glandular hairs, outer surface with many short-stalked glandular trichomes, and some much longer eglandular trichomes and and long-stalked small-headed glandular trichomes. *Corolla* tube 9,4 - 13,3 mm, with bent eglandular trichomes; lip in lower position broadly elliptic, 13,5 - 17,0 X 4,7 - 7,0 mm; lip in upper position narrowly elliptic, 13,4 - 14,4 X 2,3 - 2,5 mm; flowers purple. *Stamens*: filaments with a few small eglandular backward-pointing trichomes near the centre; anther thecae superposed, but slightly overlapping. *Disc* shallowly cupular, with two squared awns, closely approximated. *Gynoecium*: stigma shortly-bilobed, lobes equal; style strigose; ovary ovoid, with multicellular eglandular trichomes near the apex. *Fruit* sparsely pubescent with multicellular eglandular and stalked glandular trichomes, 6,0 X 3,0 mm. *Seeds* not seen.

CITATIONS

TRANSKEI

3228 (Butterworth): Mazeppa Bay (-BC), *Wisura 2654* (NBG).

D. clinopodia var. *1* occurs near the end point in the distributional range of *D. clinopodia*. This variety is very closely related to *D. clinopodia var. clinopodia*, but differs in terms of its very unusual habitat, and especially in terms of its succulent leaves. The secondary bracts have more wispy hairs than are common in *D. clinopodia* var. *clinopodia*, and are rather more markedly bicoloured than are the secondary bracts of specimens of *D. clinopodia* var. *clinopodia* that occur in the Transkei. The type specimen differs from *Wisura 2654* and from others in *D. clinopodia* by having much longer petioles, while the tertiary bracts of *Wisura 2654* are rather hairier than those of other specimens of the species. This variety is very limited in distribution, being restricted to grassy sea-facing slopes on the Transkei coastline.

6) **D. divaricata** Compton in J. S. Afr. Bot. 41(1): 49 (1975); Compton, Fl. Swaziland 558 (1976). Type: SWAZILAND 2731 (Louwsburg): Ingwavuma Poort, 100m alt. (-BB), *Compton 28614* (NBG, holo.!; PRE, iso.!).

Peristrophe cernua sensu Compton, Fl. Swaziland 557 (1976).

Herb or suffruticose, up to 0,4 m high, with drooping stems, rooting at nodes that touch the ground. *Leaves* ovate, acute to acuminate, base cuneate and attenuate, (13,0) - 15,5 - 31,7 - (40,3) X (4,5) - 5,8 - 12,4 - (15,8) mm, thickly textured; petiole (1,2) - 1,8 - 5,4 - (7,0) mm. *Inflorescence* of 3 - 4 inflorescence units umbellately arranged, 1 'umbel' in each axil; inflorescence axis (1,0) - 1,3 - 3,4 - (4,6) mm, longest peduncle of inflorescence units (0,8) - 1,4 - 2,5 - (3,1) mm. *Bracts*: secondary bracts narrowly triangular, (4,2) - 4,9 - 6,9 - (7,4) X (0,6) - 0,7 - 1,0 - (1,2) mm, sparsely strigose on veins, ciliate on margins, with some large-headed glands on the outer surface; tertiary bracts obovate to narrowly elliptic, larger (8,9) - 9,0 - 10,2 - (10,8) X (2,1) - 2,7 - 3,6 mm, with three veins from the base, very sparsely strigose on the margins and the veins, otherwise very densely glandular, with small- and large-headed, stalked and sessile glandular trichomes, often with small 'windows' between the veins near the base. *Calyx* tube 0,8 - 1 mm, lobes 2,5 - 3,0 mm, inner surface with some appressed eglandular and a few small glandular trichomes, outer surface with small- and large-headed stalked glandular trichomes and strigose margins and veins. *Corolla* on a short stalk within the calyx; tube (5,2) - 5,6 -

6,7 - (7,4) mm, with bent eglandular trichomes; lip in lower position broadly ovate, (7,3) - 7,7 - 10,3 - (11,0) X (3,8) - 4,9 - 6,9 - (8,4) mm; lip in upper position narrowly oblong, (7,1) - 8,0 - 10,0 - (11,0) X (1,8) - 2,2 - 2,9 - (3,0) mm; flowers lilac. *Stamens*: filaments with some bent trichomes on the lower surface; anther thecae superposed, but slightly overlapping. *Disc* cupular with 3 irregular awns.
Gynoecium: stigma equally bilobed, shortly filiform; style very sparsely strigose; ovary ovoid, with a few glandular trichomes near the tip. *Fruit* pubescent with stalked glandular trichomes and with few eglandular trichomes, (5,0) - 5,44 - 6,7 - (7,1) X 2,0 - 2,7 - (3,0) mm. *Seeds* (1,6) - 1,7 - 2,0 - (2,4) X 1,5 - 1,8 - (1,9), rough and with unhooked tubercles.

SELECTED CITATIONS

MOZAMBIQUE

2531 (Komatipoort): Ressano Garcia (-DD), *Schlechter 11910* (COI, PRE).

TRANSVAAL

2431 (Acornhoek): Kruger National Park (-DD), *Nel 5200* (PRE).

SWAZILAND

2531 (Komatipoort): Tshaneni (-DC), *Barrett 46* (PRE).

2631 (Mbabane): Hlane Wildlife Centre (-AC), *Stephen 1454* (PRE); Stegi (-BD), *Compton 31223* (NBG, PRE).

2731 (Louwsburg): Gollel (-BD), *Rodin 4204* (PRE).

NATAL

2731 (Louwsburg): 12 km from Magudu on road to Pongola (-BC), *Immelman 171* (NH, PRE).

2732 (Ubombo): Beside road below Jozini Dam Wall (-AC), *Balkwill 219 & 220* (NU); Mkuze Game Reserve (-CA), *Balkwill 175 & 177* (E, NU); *ibidem, Goodman 363 & 649* (NU); North of Munywane River (-CD), *Aitken & Gale 19* (NU).

2831 (Nkandla): Umfolozi Game Reserve (-BD), *Bourquin 451* (NH, NU, PRE).

2832 (Mtubatuba): Hluhluwe Game Reserve (-AA), *Ward 1886* (NH, NU, PRE); *ibidem, Balkwill et al 1671 & 1677* (E, NU); 9,6 km from Hluhluwe Game Reserve Gate, on road to Hluhluwe Village (-AA), *Wells 2119* (NH, PRE); *ibidem, Balkwill 259* (E, NU).

D. divaricata is most likely a recently derived species, and probably evolved from *D. clinopodia*. *D. divaricata* grows in habitats similar to those in which *D. minor* grows, but on the eastern side of the escarpment (fig. 71). *D. minor* is very similar to *D. divaricata*, but both subspecies of the former can easily be distinguished. The flowers of *D. divaricata* are pink, while *D. minor* ssp. *minor* has dark reddish purple flowers, and *D. minor* ssp. *1* has white flowers. The lip in the lower position in *D. divaricata* is widest in the lower third, while in *D. minor*, this lip is widest in the middle third. In *D. divaricata*, this lip is ruffled along its edges in the bud, and this ruffling does not occur in any other species of *Dicliptera* in southern Africa. The tertiary bracts of *D. divaricata* are densely glandular, a feature which is unusual in the genus, although *D. clinopodia* from Nkandla forest is also very glandular, but here the upper portions of the bracts are purple, and there is more than 1 'umbel' in each axil. The epithet, *divaricata*, refers to the manner in which the stems diverge from the base of the plant. *D. divaricata* has been collected in flower in all months except July, but there are peaks in June and November (fig. 72). Visits to a population of this species near Josini have revealed the following information. In early June of 1982, most plants were coming to the end of their flowering period. A plant collected at this time and then cultivated, began to flower in the following April. In September 1982, a plant from the same population that was beginning to flower was collected and cultivated. This plant commenced flowering in September of the following year, so that it is possible that this population has a bimodal flowering time. Further work on this interesting possibility and its effect on gene flow may be rewarding.

7) D. minor C.B. Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 92. Type: BOTSWANA 2326 (Mahalapye): Bakwena Territory, 3500 ft, *Holub s.n.* (K, lecto.!).

1) Flowers deep purple (magenta); tertiary bracts glabrous when mature, tubercles on seeds squat and with many minute hooks (observation at 50 X) *7.1) D. minor* ssp. *minor*

1a) Flowers white; tertiary bracts with common glandular trichomes; tubercles on edges of seeds taller than broad, with some minute hooks (Observation at 50X) *7.2) D. minor* ssp. *1*

7.1) ssp. minor

Procumbent herb, seldom higher than 20 cm. *Leaves* ovate, tips rounded, acute or acuminate, base cuneate and attenuate, (11,5) - 12,1 - 19.1 - (21,3) X 4,3 - 10,4 (12,1) mm, thickly textured to slightly succulent; petiole (1,3) - 1,7 - 3,2 - (4,0) mm. *Inflorescence* of 3 inflorescence units umbellately arranged, usually with 1 'umbel' in each axil; inflorescence axis (1,3) - 1,6 - 3,4 - (4,0) mm; longest peduncle of inflorescence unit (1,4) - 1,8 - 3,0 - (3,1) mm. *Bracts*: secondary bracts lanceolate, occasionally leaflike, (4,1) - 4,6 - 7,5 - (9,0) X 0,6 - 1,8 - (3,0) mm, very sparsely strigose with ornamented eglandular trichomes, and a few stalked glandular trichomes; tertiary bracts elliptic to obovate, acute to apiculate, (8,0) - 8,4 - 10,8 - (12,0) X (2,5) - 2,9 - 4,5 - (5,3) mm, glabrescent on surface, margins strigose with curved eglandular, and some stalked glandular trichomes, quaternary bracts with many stalked glandular trichomes. *Calyx* tube 1,0 - 1,2 mm, lobes 3,0 - 3,5 mm, inner surface with appressed eglandular trichomes, and some small glandular trichomes, outer surface densely glandular with stalked small- and large-headed glandular trichomes, margins strigose. *Corolla* tube (6,3) - 6,7 - 7,8 - (8,0) mm, with bent eglandular trichomes; lip in lower position ovate, (6,5) - 7,8 - 9,6 - (9,9) X (3,2) - 3,8 - 5,0 - (5,5) mm; lip in upper position narrowly oblong, (6,4) - 7,7 - 9,2 - (9,5) X 2,0 - 2,2 - (2,9) mm; flowers dark reddish purple. *Stamens*: filaments with sparse bent eglandular trichomes on the lower surface; anther thecae superposed, but slightly overlapping. *Disc* cupular, with irregular upper surface.
Gynoecium: stigma shortly bilobed, slightly unequal; style sparsely strigose; ovary ovoid, glabrous. *Fruit* pubescent with stalked glandular trichomes, (5,7) - 5,9 - 6,8 - (7,0) X (2,0) - 2,1 - 2,8 - (3,0) mm. *Seeds* 1,9 - 2,1 X 1,9 - 2,0 mm, rough and with squat, minutely hooked tubercles.

SELECTED CITATIONS

BOTSWANA

2227 (Palapye): Palapye - Potgietersrus Road, Martin's Drift, *Story 4611* (PRE).

2425 (Mochudi): Between Gaborone and Kopfonteinhek (-DB), *Hansen 3431* (PRE, SRGH).

2426 (Mochudi): Near Mochudi Station (-AC), *Harbor 12* (BOL, KMG).

TRANSVAAL

2327 (Ellisras): Limpopo, Stockpoort (AD), *Mogg 37047* (PRE); Waterberg, 3,5 miles north of Ons Hoop Post Office (-DA), *Codd 8466* (PRE).

2328 (Maasstroom): Rooikop, *Gillett sub BOL 18510* (BOL).

2427 (Thabazimbi): Thabazimbi, Farm Vaalpenskraal (-CB), *Theron & Marsh 236* (PRE, PRU); Rustenburg, Grootkuil, *Nouhuys 14* (PRE); Rustenberg, Klipvoordam, *Balsinhas 3612* (PRE).

2428 (Nylstroom): Nyl River Valley, Beside the road from Naboomspruit to Crecy (-DA), *Meeuse 9434* (PRE); *ibidem, Balkwill 752* (E, NU); Mosdene (-DA), *Galpin 277* (BOL); Nylsvlei Nature Reserve (-DA), *Milton 263* (E, NU).

2526 (Zeerust): Zeerust, road to Linokana (-CA): *Thode A1479* (NH, PRE); Zwartruggens (-DA), *Sutton 835* (PRE); *ibidem, van Hoepen 1752* (PRE); Border between Marico and Rustenburg Districts, Wonderfontein, *Gray 4138* (PRE).

2527 (Rustenburg): Rustenburg (-CA), *Moss 11229* (J).

2528 (Pretoria): Rust der Winter, near Pienaars River Station (-AB), *Gerstner 5528* (PRE); Pienaars River, on banks, where the old national road crosses the river (-AB); *Balkwill 751 & 765* (E, NU); Roodeplaat Experimental Station, *Merxmüller 29* (PRE).

Without precise locality, *Holub s.n.* (K, syn.!).

The epithet, *minor*, no doubt refers to the small size and prostrate habit of *D. minor* and these features distinguish this species from most others in southern Africa. *D. minor* is probably a recently derived species that has evolved from populations of *D. clinopodia*, as has *D. divaricata*, a very closely related species. The syntypes cited by Clarke include *Burchell 2147*, a sterile specimen collected by him in Botswana and although the leaves are almost identical to those of the other syntypes, the habit is unlike that of the two Holub specimens. Thus *Burchell 2147* must be rejected as a type. The other two specimens cited by Clarke are very similar to one another, and the Botswana specimen, which has a fruit in the paper capsule, has been chosen as the lectotype. The type of placental base of the mature fruits is the only reliable character that separates the genus *Dicliptera* from *Peristrophe*, so that it is important that this feature should be represented on the type. *D. minor* ssp. *minor* occurs in mixed bushveld (Acocks, 1975) in the western Transvaal and Botswana. This species has been collected in flower between August and April, with peaks in September and February. *Balkwill 752* was collected on 14/01/83 when the population at that locality was in full flower, but in early May of the same year, the plants had been overshadowed by grass and had died back to the ground. *Balkwill 751* was collected on 12th January 1983 after a dry period, when very few flowers were present and the plants were flaccid and looked quite shrivelled. For the duration of the 15th to the 17th of January, it rained hard in the area. The same locality was revisited on 22nd January, when *Balkwill 765* was collected. By this time the plants had revived and were floribundant, thus suggesting that the flowering of *D. minor* is regulated by access to light and by the availability of moisture. The tertiary bracts are initially glandular, but soon become glabrescent, while those of *D. divaricata* remain densely glandular as they age. This character as well as the smaller, dark reddish purple flowers distinguish *D. minor from D. divaricata*, which has larger, pale lilac flowers. *D. minor* ssp. *1* can be distinguished from *D. minor* ssp. *minor* as it has white flowers, a more easterly distribution and flowers that are slightly larger than those of the latter.

7.2) ssp. 1 *subspecies nova* differs from ssp. *minor* by its white flowers, by the swollen-tipped tubercles on the seed surface, by having fewer glandular trichomes on the secondary bracts and many glandular trichomes on the tertiary bracts and by its more easterly distribution. Type: TRANSVAAL 2329 (Pietersburg): Beside road between Soekmekaar and Bandelierskop, 1,4 km southeast of the western turning to Dawiesville (-BD), *Balkwill 1598* (NU, holo.; E, iso.).

Procumbent herb, up to 20 cm tall. *Leaves* ovate, tips acute or acuminate, base cuneate and attenuate, 15,6 - 19,1 - (20,2) X (6,0) - 6,3 - 8,3 - (8,6) mm, thickly textured to slightly succulent; petiole (1,5) - 1,6 - 2,1 mm. *Inflorescence* of 3 - 4 inflorescence units umbellately arranged, usually with 1 'umbel' in each axil; inflorescence axis (0,8) - 1,0 - 2,0 - (2,2) mm; longest peduncle of scorpioid cyme 1,1 - 2,1 - (2,2) mm. *Bracts*: secondary bracts lanceolate (4,0) - 4,1 - 6,4 - (6,9) X (0,7) - 0,8 - 1,6 -(1,7) mm, strigose on the margins and the midrib, surface glabrous, with very few glandular trichomes; tertiary bracts ovate, elliptic or obovate, acute to apiculate, (7,7) - 9,0 X 2,7 - 3,2 - (3,4) mm, veins strigose, the rest of the surface densely glandular, with small- and large-headed trichomes. *Calyx* tube 0,8 - 1 mm, lobes 3,5 - 5 mm; inner surface with appressed eglandular trichomes and some small glandular trichomes; outer surface dense with small- and large-headed glandular trichomes; margins strigose. *Corolla* tube (6,6) - 6,7 - 7,24 - (7,6) mm, with straight and curved eglandular trichomes interspersed with a few small glandular trichomes; lip in lower position broadly ovate to elliptic, (8,2) - 8,5 - 10,0 - (10,3) X (4,7) - 4,8 - 5,9 - (6,1) mm; lip in upper position narrowly oblong, (7,9) - 8,2 - 9,8 X 2,4 - 2,7 mm; flowers white to very pale pink. *Stamens*: filaments with short curved eglandular and short-stalked glandular trichomes on the lower surface; anther thecae superposed, but slightly overlapping. *Disc* deeply cupular, with two minute squared awns. *Gynoecium*: stigma shortly bilobed; style sparsely strigose; ovary ovoid, with a few glandular trichomes. *Fruit* pubescent with stalked glandular trichomes and some eglandular trichomes, 6,0 - 6,6 X 2,2 - 2,6 mm. *Seeds* 1,6 - 2,0 X 1,6 - 2,0 mm, rough and with tubercles with slightly swollen tips.

CITATIONS

2329 (Pietersburg): Louis Trichardt (-BB), *Breyer sub Tvl Museum 20935* (PRE); Beside the road between Soekmekaar and Bandelierskop (-BD), *Balkwill 791, 792 & 1600* (E, NU).

D. minor ssp. *1* has similar habitat, habit and morphology to those of *D. minor* ssp. *minor*, but the flowers of the former are white or very light pink, rather than dark reddish purple. In other species in the subtribe Diclipteriinae, such as *Peristrophe cernua*, *Dicliptera capensis* and *D. fruticosa*, white sports do occur, but these sports occur in the same populations as plants of the more usual colour and often there are intermediates in the populations. No reports of sports in purple populations of *D. minor* have been made. In May 1984, the white population near Mannamead in the north-eastern Transvaal was visited, and plants were examined every few hundred metres over a distance of 7 kilometres. No purple flowered plants, nor intermediates were observed. This white population also shows a difference in the morphology of the tubercles on the seed (which have swollen tips) as well as in the density of the glands on the bracts (there are fewer glands on the secondary bracts of ssp. *1* than on those of ssp. *minor* and many more glandular trichomes on the tertiary bracts of ssp. than on those of ssp. *minor*). These differences suggest that this population represents a different species, but, in view of the small number of specimens that have been collected, and the similarity to *D. minor* ssp. *minor*, I prefer to be cautious and describe it as a subspecies until further collections have been made. *D. minor* ssp. *1* has been collected in flower in January and April, but in the botanical garden has flowered sporadically between December and mid-June.

8) D. sp. 2 *species nova* akin to *D. clinopodia*, but differs by having smaller flowers, tertiary bracts that remain green and do not turn purple, and by having curly eglandular trichomes on the stem. It is endemic to the Magaliesberg and is summer flowering. Type: TRANSVAAL 2527 (Rustenburg): Crocodile River, *Leendertz 8617* (PRE, holo.; SAM, iso.).

Bushy herb, 0,5 m. *Leaves* ovate, acute to acuminate, base cuneate and attenuate, (26,7) - 30,4 - 46,5 - (53,3) X (9,0) - 11,4 - 18,4 - (20,2) mm with eglandular trichomes; petiole (4,7) - 5,1 - 10,4 - (13,6) mm. Inflorescence of 3 - 5 inflorescence units umbellately arranged, with up to 4 'umbels in each axil, occasionally axillary branches are terminated by an inflorescence unit, in which case it has an unusually long peduncle; inflorescence axis 0,6 - 2,8 - (5,2) mm, longest peduncle of inflorescence units (0,7) - 0,9 - 4,0- (5,3) mm. *Bracts*: secondary bracts narrowly triangular or lanceolate, apiculate, (4,1) - 4,8 - 7,3 -

(8,2) X (0,5) - 0,6 - 1,0 - (1,3) mm, strigose on margins and veins; tertiary bracts narrowly elliptic to narrowly ovate, (9,6) - 10,2 - 13,2 - (14,1) X (2,4) - 2,8 - 3,5 - (3,6) mm, with three veins from the base, initially with long-stalked glandular trichomes, but soon becoming glabrous, except for the veins and margins which are strigose, tips remaining green. *Calyx* tube 1 - 1,5 mm, lobes 3,8 - 4,0 mm, inner surface with appressed eglandular, and some small glandular trichomes, outer surface dense with small- and large-headed stalked glandular trichomes, margin and veins sparsely strigose. *Corolla* tube (6,3) - 6,7 - 8,1 - (8,3) mm, with straight and bent eglandular trichomes; lip in lower position elliptic, (6,5) - 7,5 - 10,3 - (11,8) X (2,6) - 3,0 - 4,5 - (4,9) mm; lip in upper position narrowly oblong, (6,0) - 7,2 - 10,1 - (11,3) X 1,8 - 2,2 - (2,3) mm; flowers purple. *Stamens* with bent eglandular trichomes on the facing surfaces, and minute glandular trichomes near the anthers; anther thecae superposed, but approximated. *Disc* cupular, with two awns. *Gynoecium*: stigma bilobed, shortly filiform, slightly unequal; style glabrous; ovary ovoid almost glabrous. *Fruit* with eglandular trichomes and some stalked glandular trichomes, (5,8) - 6,2 - 7,3 - (7,5) X (2,2) - 2,3 - 2,7 - (2,8) mm. *Seeds* rough with squat, unhooked tubercles.

CITATIONS

TRANSVAAL

2526 (Zeerust): Malopo's Eye (-CC), *Moss 18211* (J).

2527 (Rustenburg): Magalies River Valley, Near Hekpoort (-DC), *Balkwill & Cadman 3024* (E, NU); Near Pretoria, Hennop's River (-DD), *Moss 16268* (J); Magaliesberg, Cramond, *Philips 21906* (J).

2528 (Pretoria): Near Onderstepoort (-CA), *Smith 6047* (PRE); Pretoria, Groenkloof (-CA), *Mogg 10020* (PRE); Wierda Bridge, Six Mile Spruit (-CC), *Munro sub PRE 40544* (PRE); Fountains Valley (-CC), *Repton 235* (PRE); *ibidem, Forbes 427* (NH); *ibidem, Verdoorn 716 & 751* (PRE); Road to Fountain Grove (-CC), *Leendertz 112* (BOL, PRE); Irene (-CC), *Murray 217* (PRE); *ibidem, Rogers 23815* (J).

2627 (Potchefstroom): Near Sterkfontein Caves, Isaac Stegman Nature Reserve (-BA), *Mogg 35366* (J); Witpoortjie Waterfall (-BB), *Moss 10978* (J).

D. sp. 2 is closely related to, and most likely derived from *D. clinopodia*, from which it is geographically isolated. In *D. sp. 2* the tips of the tertiary bracts are green, not purple as in *D. clinopodia*. Although some specimens of *D. clinopodia* have hairs on the stem similar to the curly eglandular trichomes borne on the stems of *D. sp. 2*, they are seldom as dense in the former species, they do not collapse on drying as they do in the former species and they are certainly not constant. While the mature tertiary bracts of *D. clinopodia* retain glandular trichomes at maturity, these trichomes are lost in *D. sp. 2* so that the tertiary bracts are strigose only on the veins and margins. Other characters that help to differentiate between *D. sp. 2* and *D. clinopodia* are the glabrous style (rather than sparsely strigose) and the fruit with eglandular (rather than glandular) trichomes being more common. While *D. clinopodia* is a winter-flowering plant, *D. sp. 2* begins to flower in January, peaks in February and finishes flowering in May (fig. 72). This new species is endemic to the Magaliesberg in the Transvaal (fig. 59), and the parent stock probably migrated westwards from the escarpment along the Elands or Wilge River. *Leendertz 8617* has been chosen as the type because it is one of the earliest collections of this species and it bears a fruit.

9) D. sp. 3 *species nova* akin to *D. clinopodia* and *D. eenii*, but differs from the former by stems, leaves and tertiary bracts that are almost glabrous, by the tertiary bracts that remain green and do not turn purple, by the smaller flowers and by the relatively delicate habitat and differs from *D. eenii* by the shorter inflorescence axes (i.e. shorter than 6 mm). Type: ORANGE FREE STATE 2827 (Senekal): Winburg, Willem Pretorius Game Reserve (-AC), *Leistner 3023* (KMG, holo.; PRE, iso.; SRGH, iso.).

D. clinopodia sensu Wilman, Preliminary checklist of the plants & ferns of Griqualand West 225 (1946).

Herb up to 0,9 m. *Leaves* ovate, acute to acuminate, base cuneate, attenuate, usually oblique, (17,1) - 22,4 - 47,1 - (54,0) X (7,0) - 9,3 - 19,3 - (21,8) mm, glabrous; petioles (2,4) - 2,9 - 12,6 - (18,4) mm. *Inflorescence* 2 - 4 inflorescence units umbellately arranged, with up to 2 'umbels' in each axil, often axillary branches are terminated by an 'umbel', in which case the terminal inflorescence unit has an unusualy long peduncle; inflorescence axis 0,7 - 2,8 - (4,8) mm, longest peduncle of inflorescence units (0,7) - 0,9 - 4,0 - (5,3) mm. *Bracts*: secondary bracts narrowly triangular or lanceolate, apiculate, (3,5) - 4,5 - 6,8 - (7,7) X 0,5 - 0,9 - (1,1) mm, glabrous; tertiary bracts narrowly elliptic to narrowly ovate, (9,9) - 10,6 - 12,2 - (13,2) X (2,5) - 2,7 - 3,7 - (4,9) mm, margins sparsely strigose with short trichomes, surface with some stalked glandular trichomes near the edges, tips remaining green. *Calyx* tube 1,0 mm, lobes 3,5 mm, margin strigose, outer surface dense with stalked glandular trichomes, inner surface with appressed eglandular and some small glandular trichomes. *Corolla* tube (5,0) - 6,5 - 8,8 - (9,7) mm, with bent egandular trichomes; lip in lower position elliptic (7,1) - 8,5 - 11,0 - (12,0) X (2,3) - 3,2 - 4,9 - (5,8) mm; lip in upper position narrowly oblong (7,9) - 8,5 - 10,6 - (12,0) X (1,6) - 1,8 - 2,5 - (3,3) mm; flowers light purple. *Stamens* with bent eglandular trichomes on the facing surfaces, and minute glandular trichomes near the anthers; anther thecae superposed. *Disc* deeply cupular, with two approximated triangular awns and two broader, squatter awns. *Gynoecium*: stigma with two equal, shortly filiform lobes; style sparsely strigose; ovary ovoid, with a few eglandular trichomes near the apex. *Fruit* sparsely glandular with stalked glandular trichomes, (5,5) - 5,9 - 6,8 - (7,1) X (2,0) - 2,1 - 2,6 - (3,0) mm. *Seeds* (1,2) - 1,3 - 1,7 - (1,9) X (1,2) - 1,3 - 1,6 - (1,7) mm, rough with conical, squat, unhooked tubercles.

CITATIONS

TRANSVAAL

2626 (Brandfort): Klerksdorp, Vaal River (-DC), *Repton 7182* (PRE); Near the river, near Orkney (-DC), *Erasmus 2* (PRU).

2627 (Potchefstroom): Venterskroon, Jandorn (-CD), *Louw 1482* (PRE); Venterskroon (-CD), *van Dam 16920* (PRE); Vereeniging (-DB), *M.A. P. 8309* (J).

2628 (Johannesburg): Just below Vaaldam (-CC), *Acocks 21033* (PRE); *ibidem*, *Balkwill 766* (E, NU).

2725 (Bloemhof): Christiana (-CC), *Burtt-Davy 11710* (PRE).

ORANGE FREE STATE

2626 (Brandfort): Samevloei van Renoster- en Vaalrivier (-DD), *van Wyk 938* (PRE).

2725 (Bloemhof): Kroonstad, Vals River (-AC), *Pont 410* (PRE); Kroonstad, East hill (-CA), *J.C. Class 3, 4 & 5* (PRE); Vals River (-CB), *Chennell 17* (NBG); Lindley (-DD), *de Feitjer 149* (PRE).

2827 (Senekal): Willem Pretorius Game Reserve (-AD), *Muller 1862* (PRE).

2925 (Jagersfontein): Parys (-CC), *B.M. 21* (J).

CAPE

2823 (Griekwastad): Barkly West, Daniel's Kuil (-BA), *Esterhuysen 1009* (BOL).

2824 (Kimberley): Warrenton (-BB), *Wilman 5293* (KMG); Kimberley, Soutpan (-BC), *Brueckner 999* (KMG, PRE); Riverton (-BD), *Wilman s.n.* (NBG); *ibidem, Moran sub BOL 32307* (BOL, PRE); Schmidtsdrif (-CA), *Wilman 3297* (KMG, SAM); Riet River (-CD), *Marloth 895* (PRE); Barkly West, Caerwining (-DA), *Paton 5977* (KMG); Nooitgedacht (-DA), *Henderson 75* (KMG).

2923 (Douglas): Bucklands (-BA), *Anderson 753* (GRA); Douglas, St Clair (-BB), *Orpen 1937* (BOL, SAM); *ibidem, Orpen 77* (NBG).

3226 (Fort Beaufort): Lovedale (-DD), *Bennie 730.*

D. sp. 3 shows very close affinity to *D. sp. 2, D. eenii* and *D. clinopodia* so that it is not easy to suggest which is most likely to be the parent species. *D. sp. 3* occurs in the south-western Transvaal, the Orange Free state and the north-eastern Cape and is always associated with the banks of the Orange, Vaal or Harts Rivers or their tributaries. This area is not inhabited by *Hypoestes forskaolii* (Vahl) R. Br. (Balkwill & Getliffe Norris, 1985), which is probably the most ubiquitous species amongst the southern African Diclipterinae, nor by any other species of *Dicliptera* or *Peristrophe* and so is an unusual habitat for the Diclipterinae. *Bennie 730* (collected from Lovedale in the eastern Cape) is definitely a specimen of *D. sp. 3* but shows a rather disjunct distribution (fig. 60). The locality is in a very different veld type and a different river system. Attempts to re-collect from the locality of this specimen will provide useful information. *D. sp. 3* differs from *D. sp. 2* by having glabrous stems and leaves, fewer 'umbels' in each axil and strigose styles and from *D. eenii* by having shorter inflorescence axes and shorter peduncles. *D. sp. 3* differs from *D. clinopodia* by having almost glabrous stems, leaves and tertiary bracts; narrower tertiary bracts that do not turn purple; smaller flowers and a rather less robust habit. *D. sp. 3* has been collected in flower between October and June. Although there is no significant peak in flowering in any month, *D. sp. 3* appears to be a summer flowering species (fig. 72).

10) D. quintasii Lindau in Engl. Bot. Jahrb. 22: 121 (1897); Schinz in Mem. Herb. Boiss. Ser 1, 8 (10): 64 (1900); Clarke in Thiselton-Dyer, Fl. Cap. 5(1): 92 (1901). Type: MOZAMBIQUE 2532 (Lourenco Marques): Pessene (-CB), *Quintas 85* (COI, iso.! 2 sheets).

Herb up to 0,6 m. *Leaves* ovate, tips rounded and apiculate, base broadly cuneate and attenuate, (31,1) - 34,0 - 72,2 - (65,6) X (20,0) - 21,3 - 38,8 - (25,4) mm, almost membranous when dry; petiole (11,7) - 12,5 - 25,2 - (23,8) mm. *Inflorescence* of 3 inflorescence units umbellately arranged, with up to 3 'umbels' in each axil; inflorescence axis (1,3) - 1,4 - 2,2 mm; longest peduncle of inflorescence units 1,4 - 1,9 mm. *Bracts*: secondary bracts narrowly triangular to narrowly lanceolate, apiculate, (4,0) - 4,1 - 7,2 X (0,7) - 0,8 - 1,0 - (1,1) mm, margins and veins strigose and with many long wispy hairs; tertiary bracts narrowly oblong to obovate, markedly apiculate, thinly-textured, tips green, (9,7) - 10,1 - 14,9 X 4,5 - 4,6 mm, with three distinct and two indistinct veins from the base, the indistinct veins later edging the bract, strigose and with wispy hairs up to 1,6 mm long on margins and veins, the rest of the surface with glandular trichomes with stalks up to 0,6 mm long. *Calyx* tube 1,0 mm, lobes 5,0 mm, inner surface with appressed eglandular and some small glandular trichomes, outer surface with eglanduar trichomes and small-headed glandular trichomes equally common, margins and veins strigose and with long wispy hairs. *Corolla* tube 7,9 - 10,2 - (10,3) mm, with bent eglandular trichomes; lip in lower position narrowly elliptic, (11,0) - 11,1 - 12,6 X 3,5 - 4,9 - (5,0) mm; lip in upper position narrowly oblong, 10,6 - 11,8 X 2,6 - 2,8 mm; flowers purple. *Stamens*: filaments with small eglandular trichomes on the facing and lower surfaces, and minute glandular trichomes on the lower surface near the anthers; anther thecae superposed and approximated. *Disc* cupular with two awns. *Gynoecium*: stigma shortly bilobed; style sparsely strigose; ovary ovoid, glabrous. *Fruit* with stalked glandular trichomes and occasional eglandular trichomes, 6,5 - 8 X 2 - 3,5 mm. *Seeds* with squat, unhooked tubercles.

CITATIONS

MOZAMBIQUE

2532 (Lourenco Marques): Pessene (-CB), *Quintas 94* (COI); Rikatla (Ricatla) (-DC), *Junod 270* (PRE).

NATAL

2732 (Ubombo): Tembe Elephant Reserve (-AB), *Ward 757* (NH); Ubombo District, Mtante 13813 (-CD), *Ward 153* (NH); *ibidem, Balkwill et al 3055* (E, NU).

D. quintasii occurs in sand forest in southern Mozambique and in Zululand (fig. 61). *D. quintasii* is closely related to *D. clinopodia* but, is distinguished from the latter by its habitat (it grows in sand forest) and its thin tertiary bracts, which remain green. *D. divaricata*, which also occurs in Mozambique and Zululand (fig. 57), differs from *D. quintasii* by having thick tertiary bracts with dense short-stalked glandular trichomes, while *D. quintasii* has thin tertiary bracts with less dense, long-stalked glandular trichomes. *D. quintasii* displays some features that are unusual in the genus: the outside of the calyx lobes are covered in equal numbers of glandular and eglandular trichomes, rather than having glandular trichomes only and the leaves of *D. quintasii* tend to be proportionally broader, with proportionally longer petioles. Duplicates of Quintas's collections were usually sent to Berlin, where Lindau worked, and although Lindau has not indicated so, it is very likely that he saw the Berlin sheet of *Quintas 85* when he described the species. As attempts to locate the Berlin sheet of *Quintas 85* have been unsuccessful, it appears that the holotype was destroyed. Material of *D. quintasii* has been collected in flower in May and June, indicating that the species is probably winter-flowering.

11) D. eenii S. Moore, J. Bot. 46: 75 (1908); Meyer in Merxm., Prod. Fl. S. W. Afr. 130: 27 (1968). Type: NAMIBIA 2118 (Steinhausen): Damaraland (-CC), *Een s.n.* (BM, holo.!).

Herb up to 0,6 m high. *Leaves* ovate, acute to acuminate, base cuneate, attenuate (14,0) - 14,7 - 40,6 - (56,8) X (4,5) - 5,7 - 15,3 - (24,2) mm; petiole 0,9 - 9,4 - (18,2) mm. *Inflorescence* 2 - 3 inflorescence units umbellately arranged, 1 'umbel' in each axil; inflorescence axis (6,3) - 7,1 - 22,8 - (33,6) mm; longest peduncle of inflorescence units (0,8) - 4,0 - 17,6 - (27,3) mm. *Bracts*: secondary bracts narrowly triangular to narrowly lanceolate, sharply acute, (2,0) - 2,9 - 4,7 - (5,3) X (0,5) - 0,6 - 1,0 - (1,2) mm, strigose, slightly denser on margins and veins; tertiary bracts ovate to elliptic, cuneate at the base, (7,6) - 9,3 - 11,8 - (12,4) X (2,1) - 2,8 - 4,2 - (4,7) mm, with midrib prominent, and two other veins from the base, initially strigose and with stalked glandular trichomes, but later the glandular trichomes are lost, 'windows' not clearly differentiated, tips often turning purple. *Calyx* tube 1,0 - 1,5 mm, lobes 3,5 - 5,0 mm, inner surface with appressed eglandular trichomes and small glandular trichomes, outer surface dense with small- and large-headed glandular trichomes, margins and veins strigose. *Corolla* tube (5,9) - 6,6 - 9,9 - (11,8) mm, with bent eglandular trichomes and occasional glandular trichomes amongst them; lip in lower position ovate or elliptic, (7,8) - 8,5 - 13,2 - (16,3) mm; lip in upper position oblong, (8,0) - 9,0 - 13,7 - (16,4) X (2,0) - 2,2 - 3,2 - (3,5) mm; flowers deep purple. *Stamens*: filaments with a few bent eglandular trichomes proximally, and a few glandular trichomes distally; anther thecae superposed, approximated. *Disc* cupular, with an irregular upper surface or with two awns. *Gynoecium*: stigma shortly bilobed; style sparsely strigose; ovary ovoid, glabrous to strigose. *Fruit* initially strigose, then with some eglandular and many stalked glandular trichomes, (6,8) - 7,1 - 8,2 - (8,4) X 2,4 - 3,3 - (4,0) mm. *Seeds* 1,9 - 2,8 - (2,9) X 1,6 - 2,8 - (2,9) mm, rough with tall, broadly hooked tubercles.

SELECTED CITATIONS

ZIMBABWE

1830 (Hartley): Zimbabwe Ruins (-BB), *Smuts s.n.* (NBG, PRE).

2030 (Bikita): Belingwe, Mount Buhwa (-CB), *Biegel, Pope & Simon 4281* (SRGH).

Matobo District, 'Besna Kobila', *Miller 44654* (SRGH).

NAMIBIA

2016 (Otjiwarongo): Waterberg, Farm Hohensee (-BC), *Meyer 1182* (PRE).

2017 (Waterberg): Waterberg Plateau (-AD), *Rutherford A 27* (PRE); Waterberg Plateau, Farm Kurland OTJ 457 (-AD), *Giess 10165* (PRE); Okarakowisa nórdlich, Farm Bergtuine OTJ 455 (-AD), *Giess 12376* (PRE, WIND); Waterberg, 'Quellgebiet oberhalb alter Polizeistation' (-CA), *Giess 12346* (WIND); Omuverume Plateau, On sand summit plateau (-CA), *Rutherford 435* (WIND).

2116 (Okahandja): Omaruru, 'Omburo N/O' (-AA), *von Koenen 615* (WIND).

2217 (Windhoek): Farm Rietfontein WIN 85 (-CD), *Giess 9603* (PRE, WIND).

TRANSVAAL

2229 (Waterpoort): Masekwa's Poort (-DD), *Balkwill 1617* (E, NU); North-facing slope of the Soutpansberg, Farm Davenham (-DD), *Balkwill 797 & 798* (E, NU); Wyllie's Poort (-DD), *Rogers 21684* (PRE).

2330 (Tzaneen): Ben Lavin Nature Reserve (-AA), *Ben Lavin Group 4, 5 & 12* (PRE).

2427 (Tabazimbi): Kransberg, Matlabas zyn Kloof (-BC), *Germishuizen 817* (PRE).

2527 (Rustenburg): Rustenburg Nature Reserve (-CA), *Jacobsen 964* (PRE); Magaliesberg, Jacksonstuin (-DA), *Obermeijer 30992* (PRE); *ibidem, van Vuuren 150* (PRE); Near Hartebeespoort Dam (-DB), *Balkwill 773* (E, NU); *Repton 614* (PRE); *ibidem, Obermeijer 417* (PRE); Jack Scott Nature Reserve (-DD), *Coetzee V-790* (PRE).

D. eenii is closely related to *D. clinopodia*, *D. minor* and *D. fruticosa*, but differs from *D. clinopodia* by having longer inflorescence axes (fig. 6) and only 1 'umbel' in each axil; from *D. minor* by having longer inflorescence axes (fig. 6) and by having an upright rather than procumbent habit and from *D. fruticosa* by having a shorter habit and smaller flowers (fig. 20). The known distribution of *D. eenii* appears to be very disjunct, with populations in Namibia, central Zimbabwe, southern Zimbabwe, northern Transvaal and western Transvaal (fig. 62). While it is possible that these disjunctions are due simply to lack of collection, it is also possible that there are barriers to the distribution of this species. The sands of the Kalahari may represent a barrier between the populations in the Transvaal and those in Zimbabwe as it appears that *D. eenii* grows mainly on rocky hillsides. The present populations of *D. eenii* may be relicts of the original distribution of the species (chapter 11). The disjunctions within the Transvaal appear to parallel the disjunctions in sour bushveld (Acocks, 1975), suggesting that the factors that affect the distribution of the veld type, may be affecting the distribution of *D.eenii*. *D. eenii* shows a great deal of variation in some characters. The tips of the tertiary bracts of *Balkwill 773* turn purple, while those of *Balkwill 797* remain green, even when cultivated under exactly the same conditions. Some specimens (such as *Giess 12376* and *Rutherford 435* from Namibia and *Obermeijer 30992* and *van Vuuren 150* from the Transvaal) have very pubescent stems, while the stems of others (such as *Giess 10165* from Namibia and *Repton 614* from the Transvaal) are almost glabrous. Were this variation geographically correlated, it would suggest that it might be appropriate to recognise these variants as separate taxa at varietal or subspecific level, but, as this variation occurs in plants collected from localities that are close together, it suggests that this variation has little taxonomic significance. The indumentum on the ovary and fruit also shows variation. The ovaries are initially glabrous, then become strigose, and then, as the fruits mature, the number of stalked glandular trichomes increases until they outnumber the eglandular trichomes. Some of the specimens collected in the Transvaal (such as *Ben Lavin Group 4, 5 & 12* and *Repton 614*) are unusual as they have rather shorter inflorescence axes, and in fact in this respect closely resemble *D. minor*, but their taller, upright, brittle stems distinguish them from *D. minor* with its prostrate, soft stems. *D. eenii* has been collected in flower throughout the year, and occurence of flowering appears to show no correlation with any season of the year (fig. 72).

12) D. sp. 4 *species nova* akin to *D. eenii*, but differs from that species by having larger flowers, with a larger corolla tube and longer, broader lower lip and by having white flowers. *D. sp. 4* is unusual in the genus, as it has stiff leaves and produces subterranean stolons. Type: TRANSVAAL 2429 (Zebediela): Wolkberg, Farm Mimosa 218 KS (-BB), *Balkwill 1587* (NU, holo.; E, iso.).

Herb up to 0,3 m high, with subterranean stolons. *Leaves* ovate, acute and apiculate, cuneate and attenuate at the base, 19,6 - 25,6 X 7,1 - 11,8 mm, stiff, almost succulent; petiole 2,3 - 2,4 mm. *Inflorescence* of (1) - 2 - (3) inflorescence units umbellately arranged, with 1 'umbel' in each axil; inflorescence axis 4,7 - 13,9 mm, longest peduncle of inflorescence unit 2,8 - 9,1 mm. *Bracts*: secondary bracts narrowly triangular to narrowly lanceolate, tips narrowly acute, 7,0 - 9,0 X 1,2 - 1,6 mm, rapidly deciduous, very sparsely strigose on margins and veins, surface with sessile glands when young; tertiary bracts elliptic, tips acuminate to apiculate, base cuneate, 12,3 - 16,4 X 3,7 - 5,2 mm, with three veins from the base, appearing glabrous to the naked eye, but with small eglandular trichomes and short-stalked glandular trichomes. *Calyx* tube 1,0 mm, lobes 6,0 mm, inner surface with appressed eglandular trichomes and some small glandular trichomes, outer surface dense with eglandular and stalked glandular trichomes, margins and veins sparsely strigose. *Corolla* tube 27,3 - 27,8 mm, with straight and curved eglandular and stalked glandular trichomes; lip in lower position broadly elliptic, 14,5 - 15,2 X 6,7 - 7,5 mm; lip in upper position oblong, 14,9 - 15,5 X 3,2 - 3,3 mm; corolla white, sometimes flushed very pale pink. *Stamens* with bent eglandular and small stalked glandular trichomes on the lower and facing surfaces proximally and a few small glandular trichomes distally; anther thecae superposed. *Disc* deeply cupular, thick, not awned. *Gynoecium*: stigma bilobed; style sparsely strigose; ovary ovoid, first puberulous and with some glandular trichomes, then with eglandular trichomes as well. *Fruit* with eglandular and stalked glandular trichomes, 7,2 - 9,2 X 2,5 - 3,1 mm. *Seeds* 3,0 X 2,5mm, rough with tall, minutely hooked tubercles.

CITATION

TRANSVAAL

2429 (Zebediela): Wolkberg, Farm Mimosa 218 KS (-BB), *Balkwill, Cadman & McCullam 3007* (E, NU).

D. sp. 4 is known from only one locality in the Wolkberg in the north-eastern Transvaal (fig. 63). It grows amongst rocks near the top of a hill of dolomite. Attempts to find this plant at The Downs have been unsuccessful and this was surprising as similar dolomite areas occur here, only 35 km from the Wolkberg and only 100 m lower in altitude. Other species such as *Aloe dolomitica* Groenewald, *Seemanneralia gerrardii* (Seem.) Harms and *Rhus gracillima* Engl., which occur with *D. sp. 4* in the Wolkberg, are also absent from the area that was investigated at The Downs, so that there is most likely a factor affecting the distribution of these species. It may be the difference in altitude, or a possible difference in rainfall. It is possible that new localities of *D. sp. 4* may be found if the other localities of the rare species *Rhus gracillima* were visited. The tertiary bracts of *D. sp. 4* are very similar to those of *D. eenii* but the flowers are larger, the corolla tube longer, the lip in the lower position broader and the flowers are white, not purple. The stiff leaves of *D. sp. 4* are unusual in the genus, and the subterranean stolons are unique amongst the southern African species of the Dioclipterinae. *D. sp. 4* has been collected in flower in early April and early May; in cultivation *D. sp. 4* started flowering in April and is still in flower in late July, suggesting that this species is winter-flowering.

13) **Dicliptera fruticosa** Balkwill ined. in Flowering Plants of Africa 49 (1 & 2) (1986). Type: TRANSVAAL 2430 (Pilgrim's Rest): Ohrigstad, 500 m north of the turning to Burgersfort on the road to Hoedspruit (-DA), *Balkwill 777* (NU, holo.!; E, iso.!; K, iso.!; PRE, iso.!).

Very bushy suffrutex up to 1,5 m high, sometimes scandent to 2 m, stem woody at the base, seldom stoloniferous. *Leaves* ovate, acute, cuneate, often decurrent at the base, (9,3) - 13,0 - 38,0 - (57,0) X (2,2) - 4,0 - 11,5 - (16,6) mm; petiole 0,6 - 4,2 - (7,2) mm. *Inflorescence* of single or 2 - 3 inflorescence units umbellately arranged, often compounded, inflorescence axis (4,1) - 7,0 - 19,4 - (23,8) mm, longest peduncle inflorescence units (2,9) - 7,5 - 19,0 - (22,4) mm. *Bracts*: secondary bracts lanceolate, (1,4) - 2,1 - 3,7 - (4,3) X 0,4 - 0,8 - (0,9) mm, strigose on margins and midribs, trichomes multicellular and eglandular; tertiary bracts lanceolate to ovate, acuminate, cuneate at base, (4,0) - 5,4 - 8,4 - (9,1) mm, outer surface strigose on margins and veins, otherwise glabrous, inner surface with many glandular trichomes and few multicellular eglandular trichomes. *Calyx* tube 1,5 mm, lobes 7,0 mm, outer surface dense with multicellular glandular trichomes, inner surface with glandular and eglandular trichomes. *Corolla* cobalt violet, tube cylindric below, subcampanulate above, resupinate, (6,2) - 7,0 - 8,8 - (10,0) mm, with glandular and curved eglandular trichomes; lip in lower position elliptic, (12,0) - 14,1 - 17,8 - (20,1) X (4,8) - 5,3 - 7,0 - (7,9) mm; lip in upper position narrowly elliptic, (11,0) - 13,7 - 17,4 - (18,6) X (2,8) - 3,3 - 4,4 - (5,3) mm, with dark honey guides. *Stamens*: filaments with ornamented, eglandular and small glandular trichomes; anther thecae superposed, but touching. *Disc* cupular, with two short, broad, hooked awns. *Gynoecium*: stigma bilobed; style strigose; ovary ovoid, dense with small glandular trichomes and with a few multicellular eglandular trichomes near the apex. *Fruit* (8,0) - 8,6 - 10,7 - (11,4) X (3,5) - 3,6 - 4,3 - (4,4) mm, densely glandular and eglandular pubescent. *Seeds* 2,3 - 3,2 - (3,7) X 2,2 - 2,7 - (3,0) mm, rough and tuberculate.

SELECTED CITATIONS

TRANSVAAL

2330 (Tzaneen): Gravelotte, on hill (-DC), *Nel 92* (STE).

2429 (Zebediela): about 3 miles east of Potgietersrus, Hill range (-AA), *Maguire 2527* (NBG); ibidem, *Maguire 2529* (NBG); Potgietersrust, On the farm Planknek (-AA), *Mogg 20859* (JU); Between Olifants River and Zebediela (-AD), *Maguire 22027* (J); Pietersburg District, Bewaarkloof area, beside the road to The Downs (-BB), *Balkwill 1575* (NU, PRE); Beside the road between Pietersburg and Burgersfort, 64,4 km from Pietersburg (-BB), *Balkwill 1577* (NU, PRE); Chuniespoort, about 38 km east of Pietersburg (-BC), *Balkwill 1578* (NU, PRE); Potlake Nature Reserve, farm Winterveld (-BD), *Matthée 155 , 255 & 677*

(PRU).
2430 (Pilgrim's Rest): About 20 miles north of Burgersfort on road to Penge Mine (-AD), *Meeuse 9314* (COI, PRE); About 5 km north of Burgersfort on road to Penge Mine (-BC), *Balkwill 788* (NU); ibidem, *Balkwill 789* (NU); Sekukuniland, Farm Ironstone (-CA), *Barnard 347B* (PRE); About 2 km from Steelpoort on the Pietersburg road (-CA), *Balkwill 1574* (NU, PRE); Near Burgersfort (-CA), *Meeuse 9290* (PRE); On the southern outskirts of the town of Burgersfort (-CA), *Balkwill 786* (NU); On the northern outskirts of the town of Burgersfort (-CA), *Balkwill 787* (NU, PRE); ibidem, *Balkwill 1570* (NU, PRE); Near Buffelsvlei (-CD), *Leach & Bayliss 11689* (PRE, SRGH); About 12 miles south of the Strydom Tunnel on the road to Lydenburg (-DA), *Werger 997* (PRE); Erasmus Pass, Farm Nooitgedacht (-DA), *Strey 3810* (PRE, SRGH); At the southern end of Abel Erasmus Pass (-DA), *Balkwill 781* (NU, PRE); Abel Erasmus Pass, with white flowers (-DA), *Balkwill 783* (NU, PRE); At highest point on Abel Erasmus Pass, Scandent in tree to 2 m high (-DA), *Balkwill 785* (NU, PRE); ibidem, *Balkwill 1556* (NU); Near Ohrigstad, At Echo Caves (-DA), *Balkwill 1569* (NU, PRE).

Material now identified as *D. fruticosa* has been collected sporadically since 1931 (Barnard 347B), but few of the specimens bore dehisced capsules, so were misidentified as *Peristrophe bicalyculata* (Retzius) Nees. However, the elastic placental bases observed in dehisced capsules clearly indicated that these specimens belong to the genus *Dicliptera*, but to an undescribed species. *Dicliptera fruticosa* resembles *D. eenii* in its cobalt violet flowers and deep cobalt violet styles, but differs from that species by its suffruticose habit, smaller leaves subtending flowering branches (primary bracts), smaller bracts and its exserted capsules. As the plants are large, bushy, locally common and flower prolifically, they are very attractive and noticeable between April and July when in flower (fig. 72). The species occurs in the eastern Transvaal in mixed bushveld and has been found growing on magnesite and dolomite, two rock types which decompose to produce alkaline soils. The surface of the soil where the species has been found is usually rocky or stony. *D. fruticosa* is unusual in its growth form, which is more bushy and more woody at the base than that of any other species of *Dicliptera* in southern Africa. Another unusual feature is that the large lower leaves are deciduous during flowering, and the many new leaves (primary bracts), which are formed on the upper flowering branches, are very small. The capsules bulge conspicuously, and protrude beyond the bracts; these too are features unusual in the genus. *D. eenii*, which has similarly coloured flowers does not share the other unusual features of *D. fruticosa* and is much more widely distributed, having been recorded in Namibia and Zimbabwe (c.f. figs. 62 & 64). In the Transvaal, however, *D. eenii* has to date been recorded from Wylliespoort, Thabazimbi and from the Magaliesberg only.

14) D. sp. 5 *species nova* akin to *D. maculata* Nees, but differs by having abaxial tertiary bracts that are much smaller than the adaxial tertiary bracts (i.e. one half to one third of the size) and by having dense white silky trichomes, which are up to 3 mm long on the stem. Type: ZIMBABWE 1831 (Marandellas): Lomagundi, Hunyani River (-AB), *Eyles 3139* (SRGH, holo.; BOL, iso.; PRE, iso.; SAM, iso.).

D. maculata sensu C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. 5: 257 (1900).

Lax herb up to 0,6 m. *Stems* often with dense white silky trichomes up to 3 mm long. *Leaves* ovate, tip acute, almost caudate, base cuneate and attenuate, (27,7) - 28,2 - 44,1 - (51,0) X (10,7) - 10,8 - 22,8 - (28,0) mm; petiole (4,3) - 4,7 - 16,3 - (21,0) mm. *Inflorescence* of 2 - 4 inflorescence units umbellately arranged, with 1 or 2 'umbels' in each axil; inflorescence axis (4,4) - 6,9 - 15,0 - (15,4) mm, longest peduncle of inflorescence unit (3,2) - 4,5 - 12,0 - (16,2) mm. *Bracts*: secondary bracts narrowly triangular to narrowly lanceolate, acuminate, (2,8) - 3,3 - 4,8 - (5,2) X 0,3 - 0,7 - (0,8) mm, strigose on margin and veins, with occasional stalked glands on surface or with long wispy hairs, shorter eglandular trichomes and stalked glandular trichomes; tertiary bracts markedly different in size, the adaxial nearly twice as large as the abaxial, adaxial ovate to obovate, (11,4) - 11,6 - 13,8 - (14,2) X (4,8) - 5,2 - 6,8 mm, wispy hairs up to 1,5 mm long on margins and veins, and stalked glandular trichomes on surface, with obvious 'windows' between the bases of the veins. *Calyx* tube 0,7 -

0,8 mm, lobes 3,5 - 4,5 mm, inner surface with few appressed eglandular trichomes and small stalked glandular trichomes near the margins, outer surface with small- and large-headed glandular trichomes, margins and veins with eglandular trichomes, occasional long-stalked glandular trichomes and occasional wispy trichomes near the tips of the lobes. *Corolla* on short stalk within calyx; tube (5,3) - 5,7 - 7,6 - (8,4) mm, sparse with curved eglandular trichomes and occasional stalked glandular trichomes; lip in lower position elliptic (4,2) - 4,9 - 8,6 - (10,7) X 2,3 - 3,5 - (4,3) mm; lip in upper position oblong, (5,0) - 5,4 - 7,8 - (8,7) mm; flowers purple. *Stamens*: filaments with very sparse small curved eglandular trichomes proximally on the facing and lower surfaces and minute glandular trichomes near the anthers; anther thecae supeposed, but approximated. *Disc* shallowly cupular, with two approximated triangular awns. *Gynoecium*: stigma bilobed; style sparsely strigose; ovary ellipsoid, glabrous. *Fruit* with stalked glandular trichomes and some eglandular trichomes, 6,0 - 6,6 - (6,9) X 2,0 - 2,2 - (2,3) mm. *Seeds* 1,5 - 1,7 X (1,2) - 1,3 - 1,6 mm, with squat, hooked tubercles.

SELECTED CITATIONS

ZAMBIA

1228 (Ndola): Kitwe (CC), *Mutimushi 340* (SRGH).

1232 (Mbazo Pool): Lundazi, Lukusuzi National Park, Near Kalindi, *Sayer 1228* (SRGH).

1332 (Fort Jameson): Chipata, 20 miles south of Mfuwe, Lungwa East Bank (-DA), *Abel 82* (SRGH).

1626 (Choma): Mazabuka, Mapanza (-BD), *Robinson 2206* (SRGH).

MOZAMBIQUE

1435 (Fort Johnston): Niassa, Mandimba (-BB), *Torre 483* (COI).

ZIMBABWE

1630 (Sipolilo): Lomagundi, Between Mangula and Raffingora, Hunyani River (-CD), *Jacobsen 3951* (PRE).

2132 (Massangena): Ndanga, Sabi River - Lundi Area (-AD), *Maguire 62* (NBG); Sabi River, Chitsa's Kraal (-AD): *Chase 2310* (SRGH).

BOTSWANA

1821 (Andara): 14 km south of Shakawe, Samocima (-BD), *Biegel, Muller & Gibbs Russel 4978* (SRGH).

922 (Nokoneng): Banks of Okovango (-AB), *Story 4752 & 4767* (PRE); Moshapatsila Island (-BA); *Smith 692* (SRGH).

D. sp. 5 is unusual in the genus, as the tertiary bracts are of very different sizes, the adaxial bract being nearly twice as long and as broad as the abaxial and the stems have dense wispy hairs up to 3 mm long. This hairiness agrees with C.B. Clarkes' (1899) description of *D. maculata* Nees, but not with *Schimper 2: 701*, the type specimen of *D. maculata Nees var. panicularis* Nees, which is based on *Peristrophe maculata* Hochst. (seemingly a manuscript name). This type is in fact more similar to Clarke's *D. lingulata* than to the material Clarke called *D. maculata*. Thus, it appears that *D. lingulata* is a synonym of *D. maculata* Nees and that *D. maculata sensu* Clarke is unnamed. *D. sp. 5* has been collected in riverine forests and woodland (table 34), and apparently forms quite large stands. The species has been collected in flower between May and September, and so must be winter-flowering (fig. 72). *Torre 483* (collected in Mozambique) is unusual, because although the lower stems are pilose, as are those of the other specimens, the upper stems have a close glandular indumentum. This specimen is also unusual because long wispy hairs are very scarce on the tertiary bracts and are absent from the peduncles; also, many of the tertiary bracts are rather narrower than those of the other specimens of this species. As the upper and lower parts of the specimen are not joined, it is possible that this specimen is a mixed gathering.

15) D. spinulosa Hochst. ex Nees in DC., Prod. 11: 484 (1847). Type: SUDAN: Nubia, in the district of 'Cordofanum Milbeo', *Kotschy it. nub. 277* (G-DC, seen on microfiche 1871, row 2, column 2).

Annual herb up to 60 cm. *Leaves* ovate, acuminate, base cuneate and attenuate, (30,7) - 35,4 - 55,5 - (58,7) X (15,0) - 18,2 - 26,9 - (27,7) mm, rapidly decicuous, plants eventually flowering while leafless; petiole (7,7) - 9,3 - 15,6 - (17,0) mm. *Inflorescence* of 3 - 5 inflorescence units umbellately arranged, often compounded, with many 'umbels' in each axil, produced from as low as the first node; inflorescence axis 0,9 - 2,9 - (4,1) mm; longest peduncle of inflorescence units (0,3) - 0,4 - 0,8 - (1,2) mm. *Bracts*: secondary bracts very narrowly lanceolate, (3,5) - 3,8 - 5,6 - (6,0) X (0,5) - 0,6 -

- 0,8 mm, with bent eglandular trichomes and long wispy trichomes on margins and veins; tertiary bracts oblanceolate, apiculate to cuspidate at tip, (6,0) - 6,7 - 9,2 - (10,8) X (1,3) - 1,5 - 2,1 - (2,4) mm, with eglandular curved trichomes and long wispy hairs on the margins and veins, surface with stalked glandular trichomes, base of bract with a clear area on each side at the base and no 'windows' between the veins. *Calyx* tube 0,5 mm, lobes 3,0 mm; inner surface with appressed eglandular and small glandular trichomes, outer surface with short- and long-stalked glandular trichomes, margins and veins with curved eglandular trichomes, long wispy hairs and long-stalked glandular trichomes. *Corolla* tube 2,8 - 3,7 mm, with straight and curved eglandular trichomes; lip in lower position widely obtrullate, 1,0 - 1,8 - (2,0) X 1,3 - 1,7 - (1,8) mm; lip in upper position widely oblong, 1,3 - 1,9 - (2,0) X 0,7 - 1,0 mm; flower lilac. *Stamens* with eglandular trichomes proximally and minute glandular trichomes distally; anther thecae superposed. *Disc* cupular, with two triangular awns. *Gynoecium*: stigma shortly bilobed; style glabrous, turned downward at tip; ovary ovoid, glabrous. *Fruit* with eglandular trichomes, (2,5) - 3,3 - 4,2 X (1,2) - 1,4 - 1,7 mm. *Seeds* (0,8) - 0,9 - 1,2 - (1,3) X (0,8) - 0,9 - 1,1 - (1,3) mm, rough and with tall, hooked tubercles.

SELECTED CITATIONS

Northwestern Hemisphere

UPPER VOLTA

1400: Dori (-DD), *Adam 26925* (PRE).

Northeastern Hemisphere

ETHIOPIA

0339: Moyale (-BA), *Gillett 13763* (PRE).

TANZANIA

Without precise locality, *Swynnerton 1274* (SAM).

Southeastern Hemisphere

ZAÏRE

0623: Gandajika-Kasai (-DB), *Liben 3275* (PRE).

ANGOLA

1421 (Vila Gago Coutinho): Huila, Mulonda (-DB), *Henriques 524* (SRGH).

ZAMBIA

0930: Great East Road, Luangwa Bridge (-DA), *Robson 6* (PRE); Mporokoso District, Kengele River, Near track between Nsama and Lake Chisi, *Tyrer 51* (SRGH).

1228 (Ndola): Kitwe (-CC), *Mutimushi sub NDO 3806* (SRGH); 12 miles south of Lusaka, Mt Makulu Research Station (-CD), *Angus 1349* (SRGH).

1331 (Msoro): Chipala (-BB), *Abel 163* (SRGH).

1428 (Broken Hill): Broken Hill (-AD), *Rogers 26086* (PRE).

1526 (Namwala): Lochinwar National Park, Along Chunga road, *van Lavieren, Sayer & Rees 882* (SRGH).

1528 (Lusaka): Lusaka (-AD), *Best 102* (PRE).

1725 (Katima Mulilo): Masese (-BC), *Fanshawe 6884* (SRGH).

MALAWI

1133: 7 km west of Rumpi on road to Katumbi, Runyina River Bridge (-BB), *Brummitt 10935* (PRE, SRGH).

1433 (Furancungo): Lilongwe, Likuni (-BA), *Pawek 11526* (PRE, SRGH).

1434 (Dedza): Ncheu, Sharpe Vale (-DD), *Jackson 2235* (PRE, SRGH).

MOZAMBIQUE

2133 (Cevano): Maringa, Sabi River (-BC), *Chase 2581* (SRGH).

ZIMBABWE

1827 (Lupani): Binga, Kapari River, Lusulu Veterinary Ranch (-BB), *Bingham 821* (SRGH); Matobola Flats (-BB), *Vincent 46* (SRGH).

1830 (Hartley): Hartley, Poole Farm (-AA): *Hornby 3331* (PRE, SRGH).

1928 (Nyamandhlovu): Nyamandhlovu (-CD), *Hopkins sub PRE 13288, sub SRGH 13394* (PRE, SRGH).

1932 (Melsetter): Umtali Commonage (-BA), *Chase 4574* (PRE); Umtali, near east end of Victory Avenue (-BA): *Chase 8034* (SRGH).

2030 (Fort Victoria): Chitsa's Kraal (-CB), *Wild 3382* (PRE).

2032 (Chipinga): Chipinga, Sabi Valley Experimental Station. *Soane 303* (PRE, SRGH).

2130 (Nuanetsi): Bubye River, near Bubye Ranch Homestead, *Drummond 5694* (SRGH).

2229 (Waterpoort): Sentinel Ranch (-BA), *Symes 67/M/10* (PRE).

NAMIBIA

1821 (Andara): Andara, 'nähere Umgebung Rest Camps (-AB), *Merxmüller & Giess 2049* (PRE).

1915 (Okaukuejo): Kaokoveld, 'Otjitambi am

3156 (PRE, WIND).

1917 (Tsumeb): Farm Kumkauas GR 552 (-CA): *Giess 10988* (PRE, WIND).

2116 (Okahandja): Otjiwarongo - Okahandja road, Omuramba omatoko, not far from Sukses (-BB), *Kers 1377* (WIND).

2117 (Otjosundu): Waterberg, Quickborn (-AA), *Bradfield 421* (PRE).

BOTSWANA

1725 (Livingstone): Ghobe, Serondala (CC), *Miller B/1339* (PRE); 65 miles west of Livingstone, Kasane (-CC), *Story 4814* (PRE); Road to Kasane (-CC), *Lambrecht 277* (PRE); Chobe National Park, Kasane (-CC), *Mavi 1128* (SRGH).

1923 (Maun): Island on Boro Floodplain (-CA), *Biggs 603* (PRE, SRGH).

2027 (Plumtree): 75 miles WNW of Francistown on Maun Road, Tributary of Marsupe River (-AA), *Drummond 5299* (SRGH).

TRANSVAAL

2531 (Komatipoort): Louw's Creek (-CA), *Wager 22418* (PRE).

D. spinulosa is unique in southern Africa as it has minute flowers (figs. 20 - 25); very small, markedly ciliate tertiary bracts (fig. 14) and the plants start to flower from the first node of the stem. The minute flowers probably distinguish this species from any other in tropical Africa where *D. spinulosa* is widespread. Because of their small size, the flowers are hidden between the bracts, so that they can easily be overlooked. *D. spinulosa* may thus appear very similar to sterile material of other species, with which the material may be mixed.

There has been much confusion about which name should be used for the species described above. It seems that three different entities are involved. The first entity has small green bracts that are densely hairy and produces flowers that are between 4 and 6 mm in length (e.g. *Kotschy 513* and *Edgeworth 184*). The second entity, which has similar bracts and similar indumentum, has corollas between 12 and 14 mm long (e.g. *Robyns 4403* (PRE) and *Leeuwenberg 7802* PRE)). The third has bracts that are larger, broader and less ciliate than those of the other entities. There are also fewer inflorescences in each axil than there are in the other two (e.g. *Forsskal 393*). Of these entities, the second is not relevant to discussion of southern African members, but it probably matches Clarke's (1899) concept.

Most of the material of the first entity that is housed in southern African herbaria has been determined as *D. micranthes* Nees. Wood, Hillcoat and Brummitt (1983) have lectotypified *D. micranthes* Nees, and because the lectotype is conspecific with the lectotype of the older name, *D. verticillata* (Forssk.) C. Chr., they have naturally placed *D. micranthes* in synonomy with this name, but these lectotypes match the third entity listed above, and not the first. This lectotypification of *Dicliptera micranthes* Nees is nomenclaturally correct, but I am a little uneasy about the selection of the lectotype. Forsskal included a description of *Justicia sexangularis* in his Flora Aegyptica-Arabica (1775), which Vahl placed in synonomy with *Justicia chinensis* Linnaeus. Nees placed *Justicia chinensis sensu* Vahl in synonomy with *Dicliptera micranthes* when he described the latter. If Forsskal intended a new species by his description of *Justicia sexangularis*, the description must be based on his own observations. If Forsskal intended to cite Linnaeus' *Justicia sexangularis*, however, his description must still be partly based on his own observations, because his description is amplified when compared with any of the Linnean descriptions of *Justicia sexangularis*. In his description, Forsskal states that the lower lip is three-toothed, which suggests that the flower is not resupinate. Forsskal also describes the anthers as solitary, which suggests that they are monothecous. If Forsskal did not make errors in his observations, it is possible that the plant he identified as *Justicia sexangularis* was not a *Dicliptera*, but belonged to another genus and so is not the specimen selected as the lectotype. I am also not certain that Forsskal provided a specimen for every name he used in his Flora Aegypytica-Arabica. Forsskal died on the trip to Arabia, and Vahl worked through the material that he collected on the trip (Friis, 1983); one cannot be certain that the specimen Vahl thought was *Justicia sexangularis* Forsskal was indeed that species, but there is no way of knowing for certain.

The application of the name *D. micranthes* is also problematical, and it seems that what Nees intended by this name, may not be the same as what the nomenclaturally correct application of the name suggests. In his original description, Nees cites *Justicis chinensis* Vahl (which is presumably based on the type of *J. sexangularis* Forsskal) and a specimen 'Wallich Catalogue n. 2466'. Wood *et al (loc. cit.)* have been unable to locate a *Wallich 2466* specimen that could be one of the three entities listed above, and as it appears that Nees did not see any Forsskal specimens, it is difficult to know what species he was describing in 1832. In 1847, however, Nees quoted a number of specimens under *D. micranthes* and it is most likely that these are of the same species that he intended in the original description. Of those he listed, Wallich 2466 has not been located, but the others are all at Kew or on the microfiche of de Candolle's herbarium. All of these specimens agree very closely with the first entity that I have described above, so that it seems that this is the species that Nees intended to name *D. micranthes*. Although he quoted the Vahl names in synonomy, it seems unlikely that Nees saw any of the specimens on which Vahl's names were based, and so he may have been assuming the then current usage of the names was correct and made his decisions on that basis.

There are then two names that may be applied to the species described above. *Dicliptera micranthes* was widely applied to this species before it was shown that nomenclaturally it is synonymous with *D. verticillata*. There may be some justification for conserving the name *D. micranthes* and lectotypifying it with one of the specimens quoted by Nees in 1847, but this may lead to considerable confusion as *D. micranthes* has been placed in synonomy with *D. verticillata*. When Nees dealt with *Dicliptera micranthes* in de Candolle's Prodromus (1847), he included *Dicliptera spinulosa* Hochstetter as a synonym, and by doing so has validated this name. Thus, the combination *Dicliptera spinulosa* Hochstetter ex Nees is available for this taxon, and should probably be applied to it. I am grateful to Dr R.K. Brummitt, who has confirmed that *D. spinulosa* is the best name to apply to this taxon (pers. comm.).

D. spinulosa has been collected in the arid corridor (fig. 66) between March and November, with a peak in July (fig. 72), and appears to be an annual.

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