SYSTEMATIC STUDIES IN *WACHENDORFIA* (HAEMODORACEAE)

BOTANY HONOURS PROJECT 1990

SUPERVISOR : DR H.P.LINDER

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ABSTRACT

Wachendorfia Burm.(Haemodoraceae) is a small genus endemic to the Cape Floral Region. Two species were originally described by Burman in 1757 and these were followed by numerous other descriptions of what is essentially one very variable species (*W. paniculata* Burm.). This variation is discussed and reasons are given as to why the recognition of formal intraspecific ranks is innapropriate. Formal taxonomic descriptions and distribution maps are given for the four species. Rhizome morphology, leaf anatomy and pollen and seed coat structures were investigated and illustrations are provided. Phenetic analyses (NTSYS and UNITER) were run using these data. The phenograms support the proposed intrageneric classification. A cladogram was inferred and this supports the idea of ecological speciation within the genus. The two species with the most restricted distribution (*W. brachyandra* and *W. parviflora*) are considered to be the most recently evolved. Features of systematic and ecological interest (*e.g* floral enantiomorphy) are discussed and a key differentiating the four species is given.

INTRODUCTION

Wachendorfia Burm. is a small genus of the Haemodoraceae (tribe Haemodoreae), restricted to the Cape Floral Region of southern Africa (*sensu* Bond and Goldblatt 1984).

The presence of arylphenalenone pigments was hypothesized by Simpson (In press) to be the only true synapomorphy uniting the Haemodoraceae. These pigments give the rhizomes, and probably the flowers of *Wachendorfia* and related genera, their red colour. What he found during his study was that there were three other synapomorphies for the family ,viz.1) bifurcate cymes 2) inferior ovary position and 3) discoid or ovoid-globose seeds (Simpson -In press). However, his data do not support his conclusion, as *Barberetta* does not possess a cyme and a number of genera including *Wachendorfia* have superior ovaries. The only consistent synapomorphy does indeed seem to be the presence of arylphenalenones.

The Haemodoraceae is normally divided into two tribes : the Haemodoreae and the Conostyleae (Hutchinson 1973). The Haemodoreae contains all the southern African genera in the family (*Barberetta*, *Dilatris* and *Wachendorfia*) and is united by the presence of two perianth whorls, a short or absent tube and three or six stamens. The Conostyleae is represented by members in Australia and North America and is characterised by one perianth whorl, long, often hairy tubes, and six stamens.

About 80% (63 out of 78) of the species and 70% of the genera (12 out of 17) are confined to Brazil, southern Africa and Australia. The family may thus be interpreted as being essentially Gondwanan, with a secondary invasion of North America having occurred more recently (speculation). There are a limited number of other extant families with an essentially Gondwanan distribution ,*e.g.*Proteaceae and Restionaceae (Goldblatt 1978).

Johannes Burman published the first post-Linnaean description of the genus in his monograph entitled "*Wachendorfia*" (1757). His descriptions were based on specimens collected by Oldenland, and on living material (also collected by Oldenland) from the Amsterdam Botanic Garden. Two of the four species recognised in this review were first described by Burman in 1757.

W.graminifolia was first described by Linnaeus (the younger) in 1781. This description was once again probably based on a single specimen, collected by Thunberg. Thirteen years later Thunberg himself described what was probably the same specimen, giving it the synonym *W.graminea*. These early descriptions are insufficient to distinguish the plant from the variable *W.paniculata* Burm., and this is why I question the reasoning behind recognising it as a distinct species (see Species Descriptions and Appendix 1 for more detail).

Numerous other species were subsequently described, often based on single herbarium specimens, but Baker (1896) relegated these to the ranks of variety and synonym. In 1949 Barker described two distinct new species and these were included in her account of the genus in Adamson and Salter's Flora of the Cape Peninsula (1950). Surprisingly, she also included the dubious species *W.graminifolia* L.f. Barker, in support of her actions, explains that she is merely making a preliminary attempt at separating the species, "until the types can be examined, and the genus revised as a whole".

B.Nilsson began a revision in the mid-eighties, but this was never completed, and a thorough revision of the genus, including several proposed new species (see Barker -

unpublished manuscripts), is long overdue. Ornduff (1979) found the genus to be particularly variable and in need of systematic study.

Wachendorfia species have very attractive yellow flowers, with a striking feature that , along with the flowers of *Barberetta* is unique amongst the angiosperms (Ornduff and Dulberger 1978). This feature is a form of enantiomorphy and manifests itself in the production of both "left" and "right handed" floral forms within a population. Floral enantiomorphy has been interpreted as a mechanism to increase intermorph (and thus interplant) pollinations, ensuring effective outcrossing (Wilson 1887; Ornduff and Dulberger 1978), but there is still much to be learnt concerning the evolutionary and ecological significance of this trait. The fact that this extremely unusual feature is most common in a small, endemic fynbos genus makes the systematic study of this group potentially fascinating. A sound taxonomic base is essential if one wishes to use the genus for exploring some of the intriguing evolutionary questions posed by the group. In this study I hope to a) come to an understanding of species delimitation within the genus, and b) increase our knowledge of the ecology and possible evolutionary history of the species, with a view to highlighting ares of potentially rewarding systematic study.

METHODS

1) Pollen morphology

Pollen was taken from either herbarium specimens or from live material collected in the field. Pollen sources are indicated in Table 1. For both light microscopy and scanning electron microscopy (SEM) pollen was acetolysed according to the method of Erdtman(1960). Anthers were dissected and sieved to remove excess material. The pollen was then transferred to a 10% KOH solution at 50°C for ten minutes, in order to remove and loosen any excess organic material. The pollen solution was then centrifuged (Hermle KG D7209, Gosheim). A sequential list of subsequent treatments follows. Each step was separated by centrifuging

(3 minutes at 2800rpm) and decanting of excess solution.

1) Distilled water
2) Acetolysis mixture (leave for ten minutes in a 70°C water bath)
3) Acetic acid
4) Distilled water
5) Distilled water

The acetolysis mixture consists of nine parts glacial acetic acid and one part sulphuric acid. Acetolysis is designed to remove the contents of the pollen grain, plus any other extraneous material, leaving the exine clearly visible. The pollen grains were picked off the centrifuge tubes with glycerol jelly. Half the pollen was placed on a slide, which was then sealed with wax. The other half was sputter coated with Au/Pd and examined with a Cambridge S200 SEM at 10kV, which proved to be the optimum accelerating voltage for avoiding charging effects and obtaining maximum resolution. Light micrographs using differential interference contrast and oil immersion (at about 1000X) were taken on a Zeiss Axioscop photomicrograph and Ilford FP4 film.

2) Seed morphology

Seeds were taken from herbarium material or from material collected in the field, the sources being indicated in Table 2. Seeds were air dried and sputter coated with Au/Pd and examined with a Cambridge S200 SEM at 5kV. The low kV was necessary to avoid charging effects on the hairy seed surfaces.

Table 1 Species and voucher specimens from which pollen was taken for study

Taxon	Collector	Locality	Herbarium
W.paniculata	Burman 936	Hermanus	BOL
W.paniculata	Esterhuysen 8283	Waaihoek Pk.	BOL
W.paniculata form *ciliata*	Esterhuysen 5244	Mamre	BOL
W.graminifolia	Barker 170	Constantia Nek	BOL
W.thyrsiflora	Fourcade 2436	Humansdorp	BOL
W.brachyandra	Salter 8718	Cape Point	BOL
W.parviflora	Le Roux 2626	Clanwilliam	BOL
Dilatris pillansii	Salter 7902	Cape Point	BOL
D.corymbosa	Pillans 4589	Cape Point	BOL

Table 2 Species and voucher specimens from which seeds were obtained for study

Taxon	Collector	Locality	Herbarium
W.thyrsiflora	NBG	Kirstenbosch	BOL
W.paniculata	Esterhuysen 3236	Pakhuis Pass	BOL
W.paniculata	Helme 7	Kommetjie	BOL
W.paniculata form *laxa*	Leighton 37	Tulbagh	BOL
W.paniculata form *ciliata*	Esterhuysen 5244	Mamre	BOL
W.graminifolia	Leighton 34	Boulders beach	BOL
W.brachyandra	NBG	Kirstenbosch	BOL
W.parviflora	NBG	Kirstenbosch	BOL
Dilatris viscosa	Leighton 40	Tulbagh	BOL
D.ixiodes	Esterhuysen 3165	Pakhuis Pass	BOL

3) Leaf anatomy

Fresh material used for the anatomical study was collected from plants in the field, and preserved in Kew Cocktail (16 parts distilled water, 16 parts EtOH, 1 part formalin, and 1 part glycerine). Fresh material was favoured as cellular constitution is more easily observed and is less likely to show distortion than dried material. Sections were sledge microtomed to a thickness of 25 micrometers, and then stained in Alcian Blue and Safranin (lignin stain and counterstain) for 30 minutes. Sections were then washed in distilled water and dehydrated in an alcohol series (50%, 70%, 90%, 96%, twice in 100%, and finally in Xylene). Permanent slides were made by mounting in DPX.

Small sections of leaf were scraped to reduce their thickness and were then mounted in Hoyer's solution, in order to clear the specimens of excess lignin and cellulose. These slides were then used for the examination of leaf surface features such as stomata, cell shape and hair structure.

4) Plant morphology

This revision is based on specimens seen in the field as well as on extensive material lodged in BOL, PRE, NBG, SAM and STE. Rhizome and flowering stem morphologies were investigated using fresh plants at different stages of development. Thin sections were cut with a scalpel and then stained with iodine in order to check for the presence of starch.

5) Analysis

i) NTSYS

Sixty-one specimens were first sorted into phenetic clusters using the NTSYS computer package (Applied Biostatistics, New York, 1988). Specimens with insufficient information were excluded from the analysis, leaving 28 useful specimens, and size measurements were deweighted according to Hall (1969), so that size would not play a disproportionately large role in clustering the specimens. Properties used are listed in Table 3a and *a priori* specimen groups in Table 3b. An UPGMA analysis was run in favour of an WPGMA, as it produced less distortion of the data. The data were standardized, similarity intervals were computed, and various trees were produced using distance and correlation coefficients.

ii) UNITER

The data were then reformatted for use in the Uniter computer program (Hall- In press). Extra specimens were added to enlarge the data set and thus increase the reliability of the results.

37 specimens and 24 properties were used in the analysis (Tables 3a and 3b). Very few specimens had any missing data which helped increase the reliability of the results.

A whole series of runs were made, incorporating different levels of minimization of group size effect (30-100%), and different deweightings for various properties (Table 3a). Ciliation of the tepals was deweighted to 15% of their original value as it was often difficult to accurately assess whether cilia were present or not, and there was a large error involved in the data collection for this

Table 3a Properties (Uniter and NTSYS) and deweightings (Uniter only) for phenetic cluster analysis

#	Property Description	Deweighted to (%)
1	Max. plant height	100
2	Max. corm length	50
3	Corm depth	50
4	Leaf length	100
5	Max. leaf width	100
6	Leaf shape	100
7	Leaf hairiness	100 (*)
8	Bract texture	100
9	Cilia (presence/absence)	15 (*)
10	Stamen length	100
11	Style length	100
12	Length tepal 1	100
13	Width tepal 1	100
14	Length tepal 2	50
15	Width tepal 2	50
16	Length tepal 3	50
17	Width tepal 3	50
18	Length tepal 4	100
19	Width tepal 4	100
20	Length tepal 5	50
21	Width tepal 5	50
22	Length tepal 6	50
23	Width tepal 6	50
24	Overall size (Uniter)	100

Footnote : * indicates that these properties were the subject of 100% graded deweighting.

Table 3b The specimen numbers grouped according to taxa delimited *a priori*

Specimen #	Taxon
1 - 2	*W. thyrsiflora*
3 - 10	*W. brachyandra*
11 - 15	*W. parviflora*
16 - 25	*W. paniculata*
26 - 27	*W. paniculata* var. *hirsuta* ?
28 - 29	*W. paniculata* form *laxa* ?
30 - 32	*W. paniculata* form *ciliata* ?
33 - 37	*W. graminifolia* ?

Note : ? indicates a hypothetical taxon that is being tested on the phenogram.

property. Deweighting can seldom be justified to an accuracy greater than 10 or 20% (Hall -In press). Numerous other properties were deweighted to 50% of their original values, and these included corm depth and length (repetition), and tepal length and width measurements for four of the six tepals (repetition due to their identical sizes and opposite, corresponding positions in the flower). Two properties that essentially reflected the same structure (*i.e.*isologous structures) were each deweighted 50%, making the overall representation of the property 100% instead of 200%. Leaf hairiness and tepal ciliation were the subjects of 100% graded deweighting, meaning that the common absence of a property was not used to group the specimens (Hall -In press). The system emphasises joint presence, and presence and absence, but gives progressively less weight towards joint absences. This is done by multiplying homogeneity by a correcting factor based on scaled, average property values for the two items (Hall 1968).

Only two specimens of *W.thyrsiflora* were used (Table 3b) due to the surprising lack of suitable pressed flowers in the herbarium, and also due to the fact that the species displays relatively little variation and is very distinct.

Five specimens of *W.parviflora* were used, and eight for *W.brachyandra*.

Deciding on exactly which specimens to use for the analysis of *W.paniculata* proved a little more difficult due to the wide range of variation available. What was done was to take specimens that represented the whole range of variation in previously described (including Barker's unpublished manuscripts) varieties. I tried to include specimens from as wide a geographic range as possible, to cover any variation associated with this. Ten specimens of what I had called the "typical" form of *W.paniculata* were chosen, two specimens of the montane form "laxa", five specimens of what Barker (1950) chose to describe as *W.graminifolia*, three specimens of what appeared to be a ciliated form - "ciliata", and two specimens of the hairy variety designated by Barker (1950) as "hirsuta".

Editor and Factor runs were carried out to extract a joint size factor, which was then used to reduce the specimens to a more even size so that size would not play an overly important role in clustering (Hall- In press). Size may be represented so often that it can damage the accuracy of the group making by simply grouping large specimens together and small specimens together irrespective of other important features.

In order to see how different the two clusters of *W.brachyandra* were, a Homdif program was run, with minimization of group size effect set at 0%. This program simply measures the drop in homogeneity when one group is added to the other, by using a discriminant function (Hall 1968). Two runs were made with samples from the larger group to give balanced contributions to the fusion set (otherwise the larger set would have had a larger influence).

The program also ranked the properties according to ability to distinguish groups within any selected group/cluster. This was done by scoring the average drop in homogeneity for each property when the groups were added together. Thus, the best properties for distinguishing groups are the ones that produce the greatest drop in homogeneity on fusion of the groups.

iii) Cladistics

A cladogram was generated for the four species of *Wachendorfia* and the outgroup - *Dilatris* (Haemodoraceae). Missing or variable characters were coded as 9 or ?. *Dilatris* was chosen as the outgroup because of its similar range and habitat, plus numerous similar morphological features. The only other genus that was considered as a possible outgroup was *Barberetta* (Haemodoraceae), but this monotypic genus was rejected due to its small, isolated range and unusual habitat (forest floors in Transkei and southern Natal). Almost no material of *Barberetta* was available for study and this was another reason for not using it as the outgroup. Ornduff (1979) suggested that, on the basis of chromosome numbers, *Wachendorfia* and *Barberetta* (both with n=15) are more closely related to each other than either is to *Dilatris* (n=ca.19-21). de Vos (1956), however, suggested that *Wachendorfia* and *Dilatris* are closely related, based on embryological studies. She unfortunately did not investigate *Barberetta*, and does not suggest anything regarding its placing. *Barberetta* possess an unusual floral structure (within the family) - having a simple raceme, unlike *Wachendorfia* or *Dilatris* which have helicoid cymes.There is therefore evidence both for and against *Dilatris* being considered as the outgroup for *Wachendorfia*, although there could be a stronger case for choosing *Barberetta* as the outgroup. Simpson (in press) has recently shown that *Barberetta* is in fact the sister taxon to *Wachendorfia*, but this information came too late to be of any real use in the present study.

25 characters were selected for use in the analysis, but only five proved to be useful for cladistic purposes (Table 4a) as these were the ones for which polarity could be determined. A list of character codes is given in Table 4b. The cladogram was generated using Hennig86 and PAUP (phylogenetic analysis using parsimony) (Swofford 1983) was used to give the patristic distances for each species and to show where the characters changed on each branch.

Table 4a The characters, character states, coding and taxa used in the cladistic analysis

#	Character Description	Character state	Code	Taxon/a
1	Plant height	Greater than 1m	0	1
		Less than 1m	1	2,3,4,5
2	Corm length *	Greater than 30mm	0	1,2
		Less than 30mm	1	3,4,5
3	Leaf length	Greater than 50cm	0	1
		Less than 50cm	1	2,3,4,5
4	Leaf width	Greater than 5cm	0	1
		Less than 5cm	1	2,3,4,5
5	Leaf hairiness	Glabrous	0	1,3,5
		Short, dense	1	4
		Variable	?	2
6	Bract texture	Scarious	0	1,2,3,5
		Herbaceous	1	4
7	Max. peduncle length	Greater than 10cm	0	2
		Less than 10cm	1	1,3,5
		Variable	?	4
8	Cilia presence/absence	Present	0	1
		Absent	1	3,4
		Variable	?	2,5
9	Ratio stamen : tepal length	Greater than 0,6	0	1,2,4
		Less than 0,6	1	3
		Variable	?	5
10	Min.tepal width (average)	Greater than/equal 6mm	0	1,2,3
		Less than 6mm	1	4
		Variable	?	5
11	Max.tepal length *	Greater than 20mm	0	1,2
		Less than 20mm	1	3,4,5
12	Palisade width *	Two cells	0	5
		One cell	1	2,3,4
		None	2	1
13	Sclerenchyma cap development	Good	0	2,3,4,5
		Poor/absent	1	1

14	Mucilage canal position	Leaf edge Scattered	0 1	5 1,2,3,4
15	Cuticle	Thick Thin	0 1	5 1,2,3,4
16	Lignification of epidermis	Light Heavy	0 1	1,2,3,5 4
17	Epidermal lip	One lip Two lips	0 1	- 1,2,3,4,5
18	Subsidiary cell shape *	Kidney Rectangular	0 1	1,5 2,3,4,
19	Cortex cells	Unlobed cells Lobed cells	0 1	1,2,3,4 5
20	Sulcus to verrucae distance	Greater than 10um Less than 10um Not applicable	0 1 ?	1 2,3,4 5
21	Exine sculpturing	Verrucae Reticulated	0 1	1,2,3,4 5
22	Seed shape *	Sphere Oval Disc	0 1 2	2,3,4 1 5
23	Seed diameter	Greater than 4mm Less than 4mm	0 1	1 2,3,4,5
24	Epidermal cell shape	Rectangular Irregular	0 1	1,2,3,4 5
25	Colour of pressed flowers	Purple Orange	0 1	2,3,4,5 1

Key to species code :

* indicates a character used in the final analysis

1) *W. thyrsiflora*
2) *W. paniculata*
3) *W. brachyandra*
4) *W. parviflora*
5) *Dilatris*

Table 4b Cladistic character codes for each species

Species	Character codes				
Character #	5	10	15	20	25
Dilatris	11110	01999	10000	01019	12110
W.thyrsiflora	00000	01000	02111	01000	01001
W.paniculata	10119	00900	01011	01101	00100
W.brachyandra	11110	01110	11011	01101	00100
W.parviflora	11111	19101	11011	11101	00100

OBSERVATIONS AND DISCUSSION

1) UNDERGROUND ORGAN

Wachendorfia possesses a distinctive rhizome, containing a red fluid rich in phenalenone pigments. The air dried rhizome varies in diameter from 5mm to 50mm, although the fresh rhizomes may be twice this size. The shape is usually spherical to ovoid, although irregular shapes may occur. An air dried rhizome is usually covered by a papery tunic composed of the dried leaf bases.

An interesting feature is that a new rhizome is produced every year, with the previous years rhizome remaining attached to the present years' rhizome. The old rhizome shrivels, until all that remains is the extensive system of vascular traces. Occasionally one finds up to three old rhizomes attached in sequence to the present rhizome. From between each rhizome sprouts a cluster of thin, short adventitious roots (Plates 1 and 2).

Each rhizome has three nodes, each with its own lateral bud. The lateral buds are arranged in an opposite position. Each lateral bud is capable of producing next year's rhizome, although only one is actually produced. The new rhizome may be produced below or to the side of the parent rhizome. This means that next year's rhizome will be exploring new soil, either deeper or some horizontal distance from the parent. This may be an important function, given the absence of true roots. Each rhizome node produces a single rhizome leaf. A single apical bud is present, giving rise to the single annual flowering shoot and the monopodial (pyramidal) growth form. *W. thyrsiflora* may produce stolon like lateral outgrowths, some of which may ultimately extend several metres. These extended rhizomes are then capable of producing new plants, although all will

Plate 1a *W.paniculata* **rhizome cluster (4 rhizomes visible).** Note the cluster of adventitious roots between each annual rhizome. There is a progression of old, shrivelled rhizomes on the right to the present year's swollen rhizome on the extreme left. Old rhizome leaves sheath the base of the flowering stem.

Plate 1b *W.paniculata* **rhizome with all rhizome leaves removed.** The large node surrounding the middle of the rhizome is node 2 and its lateral bud is visible (large arrow). Node 3 is visible near the base of the stem (small arrow).

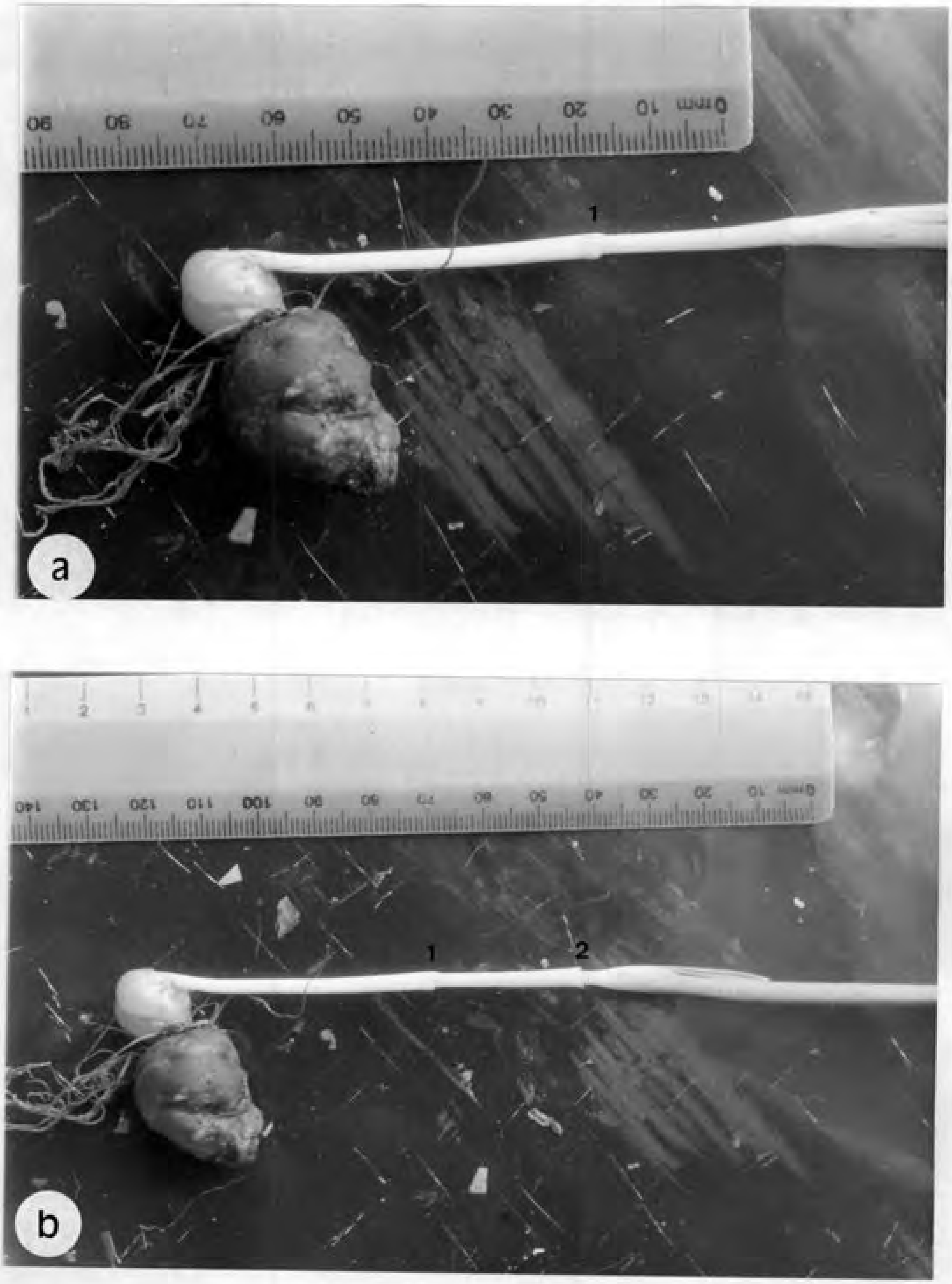


Plate 2i *W.parviflora* rhizome and leaf node morphology.

a) Previous year's rhizome (dark) attached to present year's rhizome, with cluster of adventitious roots between. Stem leaf 1 (amplexicaul, opposite) has been removed to expose stem node 1.

b) Stem leaf 2 (amplexicaul, opposite) removed to reveal stem node 2.

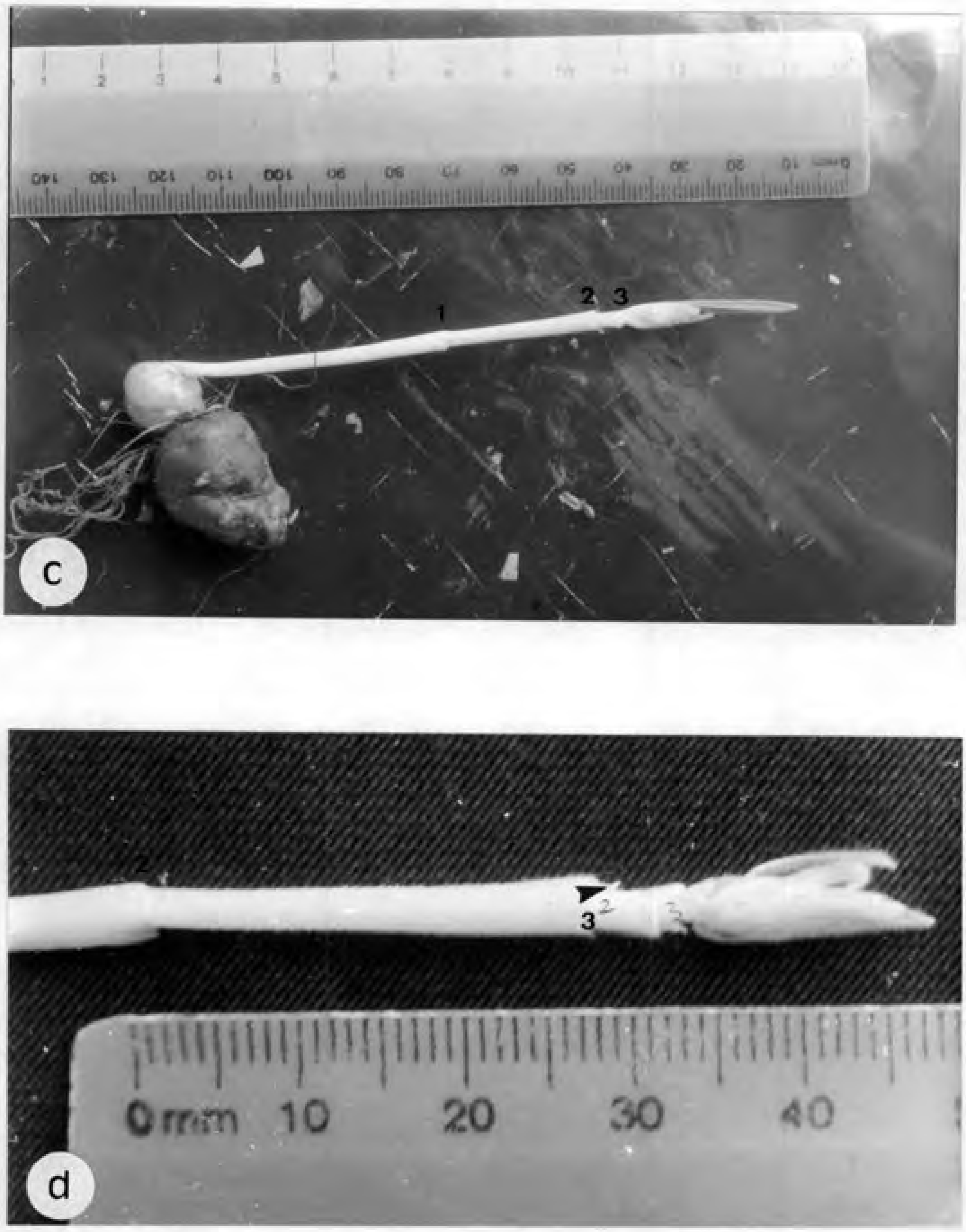


Plate 2ii ***W.parviflora*** **stem leaf morphology.**

c) Stem leaf 3 removed to show stem node 3. This leaf (and all later leaves) is spiral and not amplexicaul.

d) Close up of young plant's growing tip. Nodes 2 and 3 visible, the latter^{2} wih a small sterile bud (arrowed). A further opposite, sterile bud is visible at the next node (#4).

be genetically similar ramets. Vegetative reproduction is common in monocots, and indeed seems to be an important feature of *Wachendorfia*. *W.thyrsiflora* is the only species likely to have above ground parts burnt by fire, as none of the other species are usually present aboveground during the peak fire seasons of summer and autumn. From field observations it would seem that *W.thyrsiflora* is able to resprout vigorously after being burnt. Plants have been seen to flower the first year after losing their leaves to fire. The other species tend to be fire avoiders, although they are often quick to come up in burnt areas, and I suspect that they might also resprout if burnt.

The rhizomes stain positive for starch. However, *W.paniculata* and *W.parviflora* are unusual in that the amyloplasts are concentrated within the vascular stele, with almost none in the more conventional storage site - the cortex. *W.thyrsiflora* appears to possess the more usual arrangement of amyloplasts, these being equally common in the cortex and the stele. The reasons for this variation are unknown, but may have something to do with the fact the rhizome of *W.thyrsiflora* does not shrivel up annually, but continues to form an extremely long underground organ.

The xylem elements have an amphivasal arrangement.

2) LEAVES

i) Morphology

Leaf morphology is exceptionally variable, especially in *W.paniculata*. Colour varies from dark green through to light yellow-green, and is of no real use in species identification as it is not constant within or between the species, often being a function of leaf age.

Shape may vary within a species, some populations of *W. paniculata* having almost needle like leaves, and others having broad, falcate leaves. *W. thyrsiflora* usually has large ensiform leaves, while *W. brachyandra* has lanceolate or falcate leaves. *W. parviflora* is normally characterised by falcate leaves, but may often have lanceolate leaves. *W. thyrsiflora* has distinctly longer and broader leaves than any of the other species (up to 90cm long and 7cm wide). The other three species show much inter-plant variation in leaf size, but are all within approximately the same range (up to 4cm wide and 40cm long). There seems to be some altitudinal variation in leaf size and shape in *W. paniculata*, specimens growing at high altitudes tending to have extremely long, narrow, linear leaves.

Wachendorfia leaves have two main points of origin : the rhizome and the culm. There are usually three large rhizome leaves, each arising from a different node on the rhizome (Plates 1 and 2). These leaves sheath the culm at the base. The culm leaves fall into two major types : the lowest two are amplexicaul and opposite, while those further up the stem are not amplexicaul and are spirally arranged. The lower leaves thus give the distinct impression of being two-ranked. The leaves are always firm in texture, longitudinally plicate, simple and entire. *W. thyrsiflora* and *W. brachyandra* are always glabrous or very nearly so, while *W. parviflora* is distinct in having a dense coating of numerous short hairs. *W. paniculata* leaves vary from being nearly glabrous to being densely hairy with long white hairs. Within- plant variation in leaf hairiness is small, although within- population variation may be great in this species. There appears to be no obvious reason for the difference in leaf hairiness within the species, as it does not seem to follow a gradient of habitat dryness, altitude or any other single factor. It would appear that leaf hairiness is either genetically controlled or is responding to a whole suite of selective pressures, making it difficult to correlate with any habitat variable.

The dense leaf hairs in *W.parviflora* are of two types. Uniseriate, unicellular hairs are by far the most common, outnumbering the pilate, uniseriate, tricellular hairs by about 5:1. Both types seem to be equally common on upper and lower surfaces. Four or occasionally five large epidermal cells support the base of each hair. The unicellular hairs taper to a point and appear to have a hollow base, while the tricellular hairs have a small terminal cap cell that is possibly glandular, the function of which is unknown.

It is perhaps worth noting that both species that are confined to permanently damp habitats (*W.thyrsiflora* and *W.brachyandra*) have glabrous leaves, while the two dryland species usually have hairy leaves. This suggests that the hairs may help to reduce water loss from the leaves. However, this is a little strange as *W.parviflora* has leaves until October at the latest, and this is not yet the start of the dry season. I would not expect the species to suffer from any moisture stress due to its above ground parts being present only in the rainy season, and I suggest that the species may be a "recent" invader of the early flowering niche, its hairy leaves being an evolutionary legacy from the days when it flowered later in the year, deeper into the dry season, a time when it may have derived some benefit from its hairy leaves. Its narrow tepals support the idea of neoteny *i.e.* the ability to flower and reproduce at an abnormally early stage in its development. This idea is entirely speculative and requires experimental and empirical testing.

ii) Leaf Anatomy

The leaf anatomy of *Dilatris pillansii*, *D.corymbosa*, and the four species of *Wachendorfia*, was examined (Table 5).

i) <u>Special features in *Dilatris*</u>

Dilatris has narrow, rigid leaves with a number of special associated features. The palisade layer is two cells wide. Leaf anatomy of two closely related North American genera in the Haemodoraceae was examined by Simpson and Dickison (1981). They found palisade layers to be absent altogether in *Lachnanthes*, while *Lophiola* was found to possess a palisade layer composed of one or two cells. [*Lophiola* has recently been removed from the Haemodoraceae by Simpson (In press)]. A related Australian genus, *Conostylis* (Haemodoraceae), has a palisade layer consisting of two layers of columnar cells (Green 1959). There is thus a wide range of palisade structures within the family. The Cape genera reflect this variation well, with *Dilatris* having a two cell layer, *W. thyrsiflora* without a distinct layer, and the other *Wachendorfia* species with either a one or a two cell layer.

Cortical air spaces are absent in *Dilatris*, so the cortical cells are lobed in order to facilitate the diffusion of gases (Figure 1c). The spaces between the lobes may act as air channels, allowing air to circulate between the stomata and the internal photosynthetic cells.

Dilatris has a single large canal within the leaf (Figure 1b), and this is always located in the side of the leaf closest to the aerial stem. There are a number of other smaller canals scattered throughout the leaf cortex. The function of these canals is unknown, but it is suggested that they transport mucilage.

Figure 1a

Plan of T.S. of *Dilatris pillansii* leaf ×400

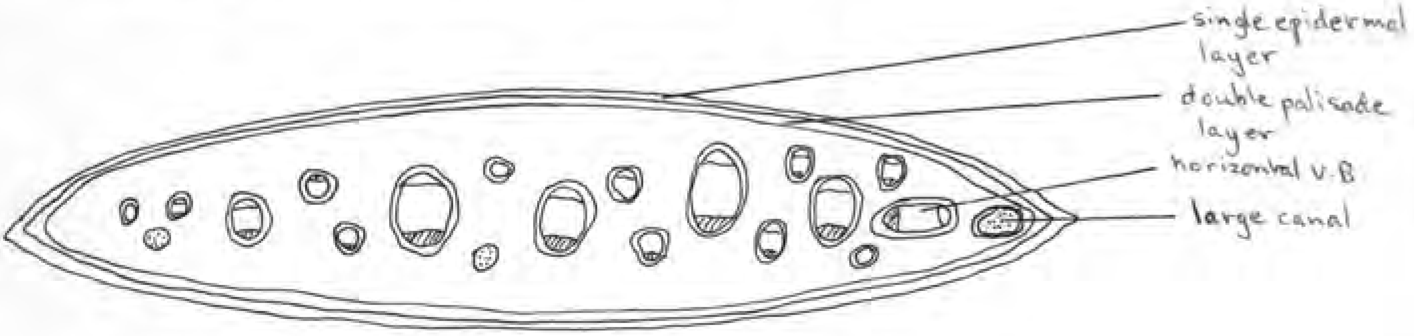


Figure 1b

T.S. of mucilage canal in leaf of *D. pillansii* ×400

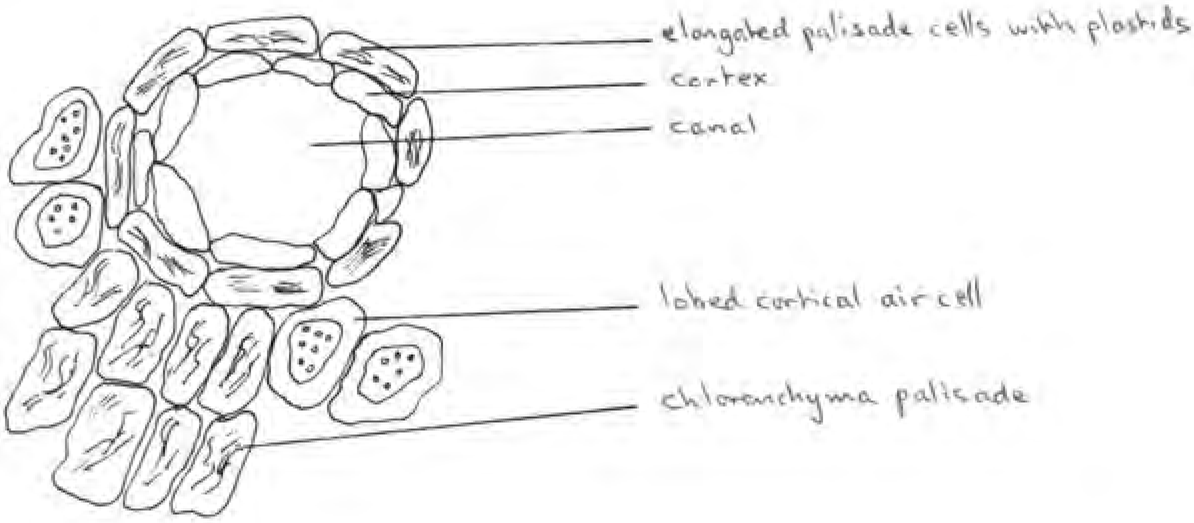


Figure 1c

Leaf anatomy of *D. pillansii* ×400

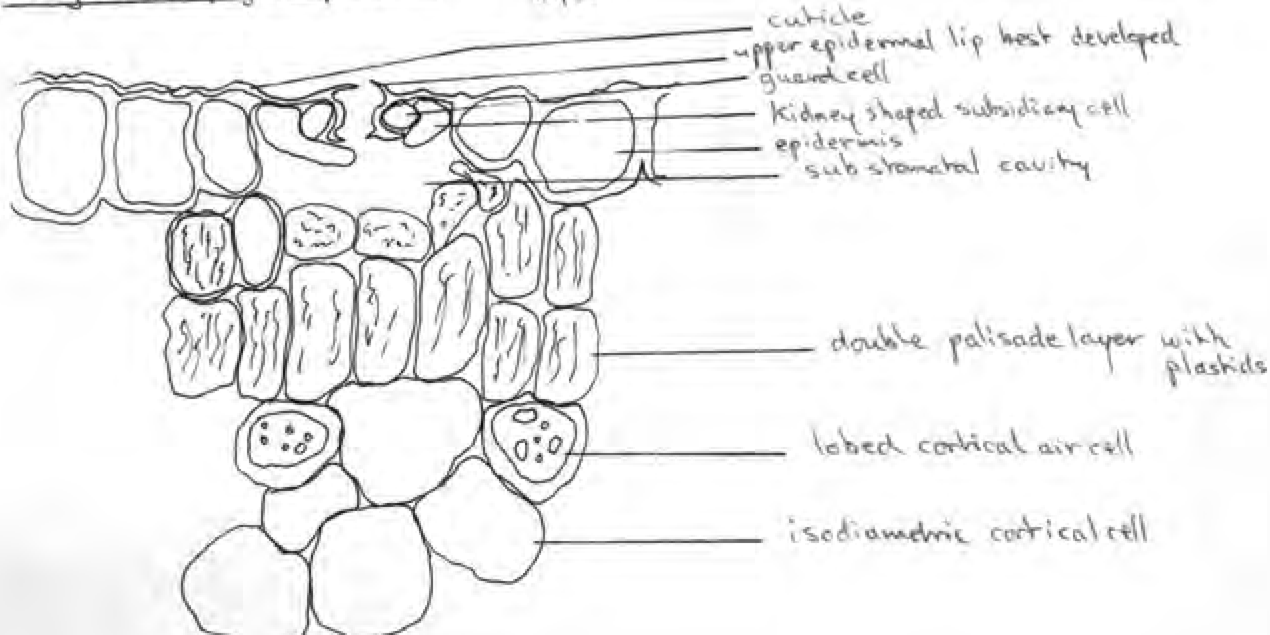


Table 5 Leaf anatomical characters of *Dilatris* and *Wachendorfia*

Character	Dilatris	W.thyrs.	W.parv.	W.brachy.	W.pan.
Width of palisade	Two cells	One	One	One or two	One
Sclerenchyma caps	Large	Small	Large	Variable	Variable
Mucilage canals	Large	Large	Small	Small	Small
Cuticle lignification	Light	Medium	Medium	Light	Medium
Cuticle thickness	Thick	Medium	Thin	Thin	Medium
Epidermal lignification	Light	Light	Medium	Light	Light
Epidermal lip	Two spurs	Two	Two	Two	Two
Subsidiary cell shape	Kidney	Kidney	Rectangle	Rectangle	Rectangle
Cortex cells	Lobed	Unlobed	Unlobed	Unlobed	Unlobed
Position of amyloplasts in rhizome	Unknown	Cortex + stele	Stele	Unknown	Stele

Dilatris has a kidney shaped subsidiary cell (Figure 1c), a feature which it shares with *W. thyrsiflora*. All other *Wachendorfia* species have rectangular subsidiary cells.

ii) Anatomical features uniting *Dilatris* and *Wachendorfia*

Anatomical features which unite *Dilatris* and all *Wachendorfia* species include the structure of the epidermal lip which acts as a closure for the stomata, the presence of raphides (rarer in *Dilatris*), paracytic stomata, and the horizontal vascular bundle on one side of the leaf. The epidermal lip has a well developed upper component, and a lower lip of about half the length of the upper. This double epidermal lip is also recorded in *Lachnanthes* and *Lophiola* (Simpson and Dickison 1981). *Lophiola* was found to be unusual in that there were no subsidiary cells visible. Green (1959) made no mention of these epidermal lips in his study of the Australian genus *Conostylis*, although his drawings show slight spurs on the outer edges of the stomata.

Raphides have been recorded in the leaves of both *Lachnanthes* and *Lophiola* (Simpson and Dickison 1981). Paracytic stomata appear to be found throughout the family (Green 1959; Simpson and Dickison 1981).

The large first order vascular bundle within the extreme edge of the leaf closest to the aerial stem lies horizontally, while all others in the leaf are vertically orientated. This feature is also found in *Conostylis* (Green 1959). I believe this unusual arrangement to be the result of the leaf sheathing around the rhizome and the culm, thus flattening one edge of the leaf and distorting the apparent bundle position.

iii) Features of *Wachendorfia* leaf anatomy

All *Wachendorfia* species have large air spaces between the isodiametric cortical cells (Figures 2-5).

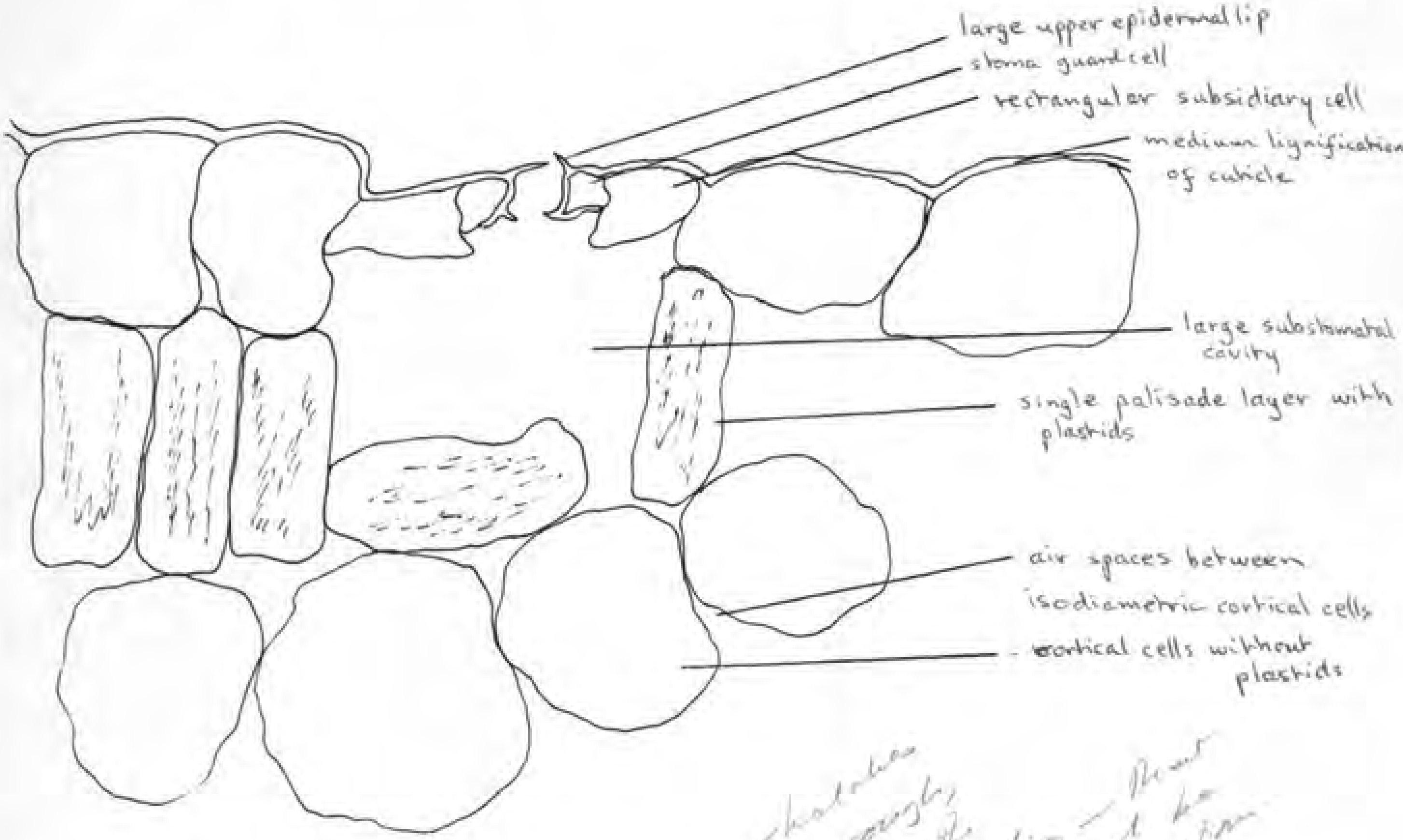
Sclerenchyma cap development in the vascular bundles is very variable. *W. thyrsiflora* has poorly developed caps, while *Dilatris* and *W.parviflora* have well developed sclerenchyma caps. This feature is variable in both *W. brachyandra* and *W. paniculata*, and in the latter the bundles may be exceptionally well developed.

The epidermal cuticle is thick in *Dilatris*, *W. thyrsiflora* and *W. paniculata*, but is noticeably thinner in *W. parviflora* and *W. brachyandra*. Lignification of the epidermal layer is light in all taxa bar *W. parviflora*, in which extensive lignification is evident.

Intervascular connections are evident in most specimens, and it is assumed that this is a regular feature of all taxa. Stomata appear to be equally common on both sides of the leaf, and are very slightly sunken relative to the epidermal layer. Large sub-stomatal cavities are present in all taxa.

W. thyrsiflora was found to have larger canals within the leaf cortex relative to other species in the genus. Whether this is an allometric feature associated with the overall large size of the species, or the result of purely ecological or phylogenetic factors is unknown, although I would tend to think that it does in fact have some ecological relevance, as the various species' leaf sections

Figure 2 Leaf anatomy of W. paniculata



These sketches are too rough, especially the blue labelling — these should not be in the caption

Figure 3 Leaf anatomy of W. thyrsiflora

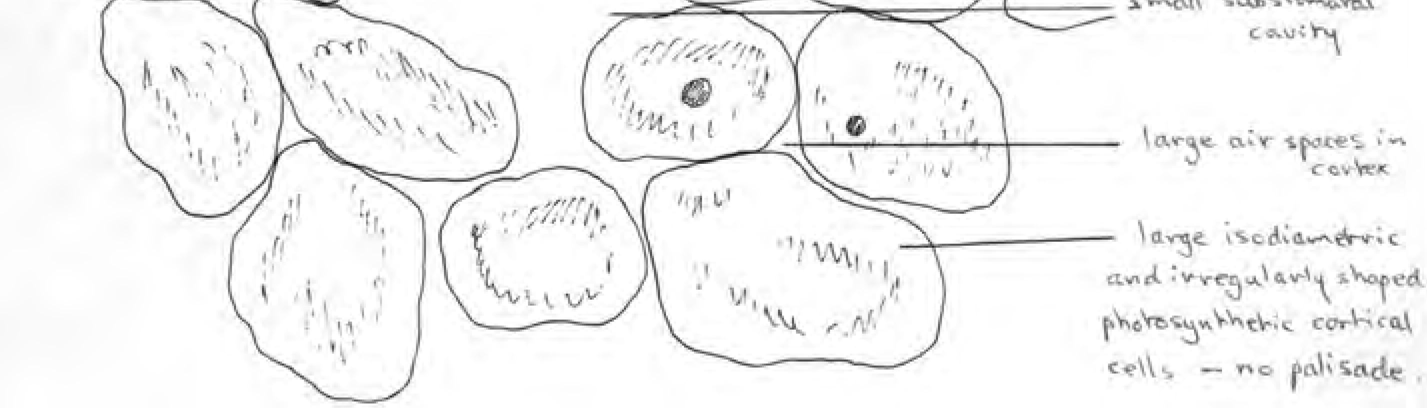


Figure 4 Leaf anatomy of W. parviflora

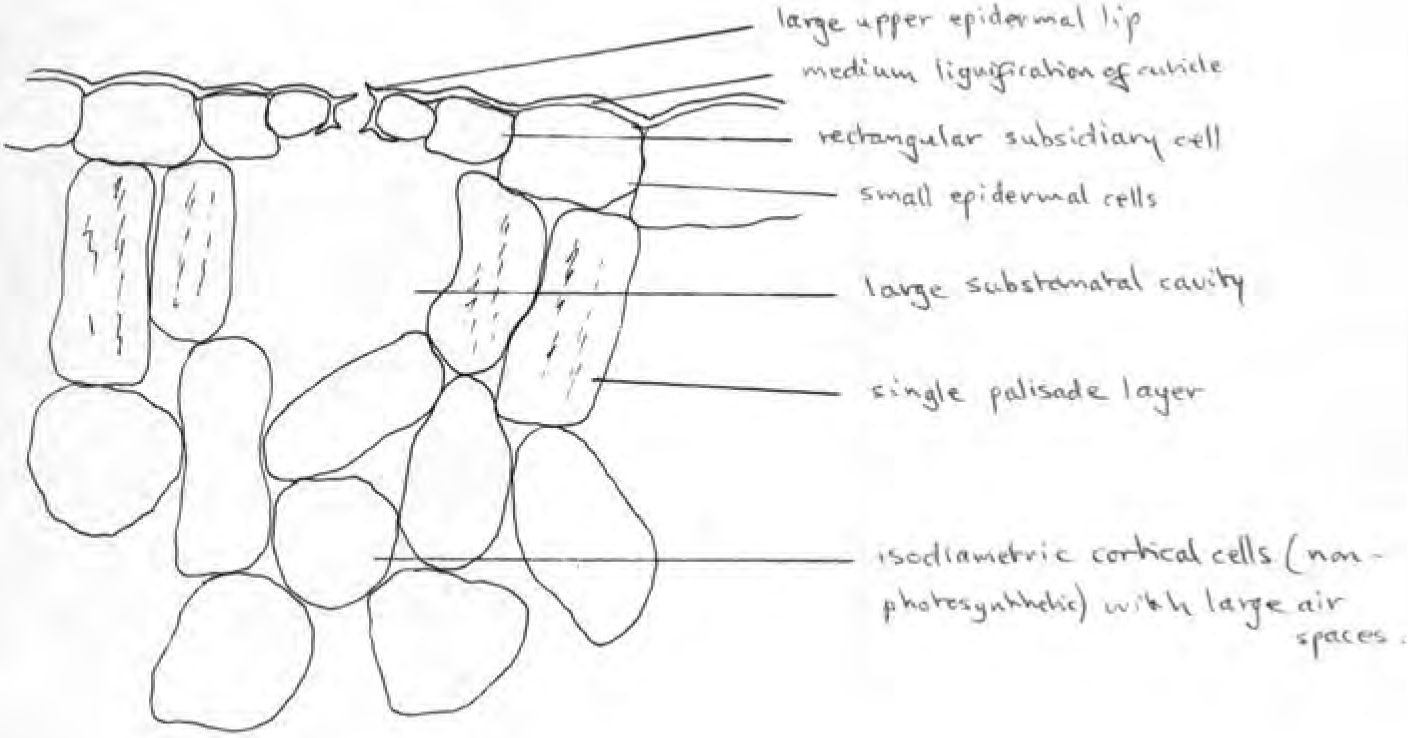
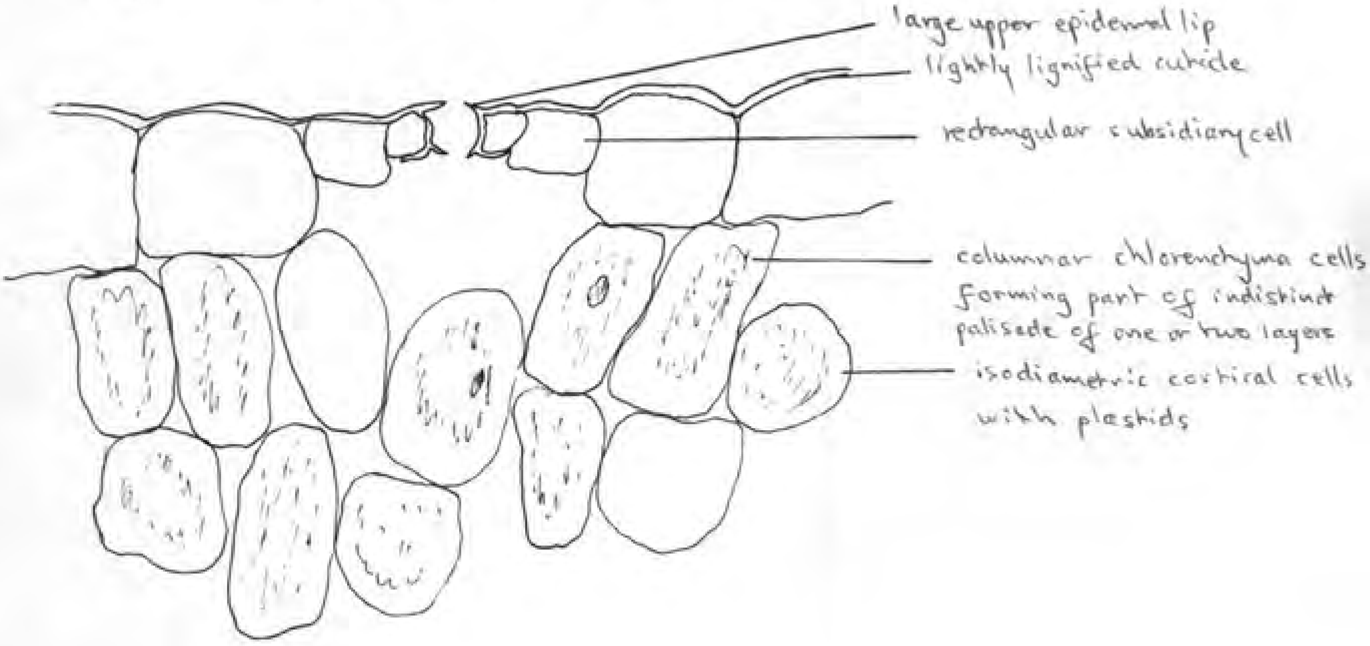


Figure 5 Leaf anatomy of W. brachyandra



were taken from leaves of the same size (reducing any allometric effects), and *W. thyrsiflora* is confined to permanently damp sites. Large quantities of mucilage can be seen in cut sectionc of *W. thyrsiflora* leaves, and most of this appears to come from the large canals in the leaf.

3) FLOWERS

Wachendorfia flowers are enantiomorphic. The flowers of some plants have the style sharply directed to the right, while in other plants it is deflected to the left (Figure 6). In both cases, one of the three stamens is borne close to the style, the other two being deflected in the oposite direction. The few studies that have looked at the evolutionary significance of this trait have suggested that the enantiomorphy is probably a feature which promotes outcrossing, that is, increases the level of intermorph pollination (Wilson 1887; Ornduff and Dulberger 1978). This conclusion is based on the findings that *W. paniculata* has a weakly developed self-incompatibility system, and that intermorph crosses produce more seeds than self-pollinators or intramorph pollinations.

Dilatris (Haemodoraceae) is also enantiomorphic, but differs in that both left and right handed flowers may be found on the same inflorescence. Selection for outcrossing is thus apparently not the driving force behind the evolution of its flower structure. Exactly what the evolutionary history behind such a strange system may be is completely unknown (Ornduff and Dulberger 1978).

Pollination

The upper three tepals in *Wachendorfia* have pale markings surrounded by dark rings which may act as nectar guides.

There is much interplant variation in the contrast, size, and shape of these markings, but whether this is genetically controlled or not is unknown. The genus displays a curious feature related to pollination, this being the presence of large "extrafloral" nectaries (Figure 6). These are formed by the bases of the outer upper and the two adjacent inner tepals, one being present on each side of the flower. These are elongated into spurlike structures and produce significant quantities of nectar, which may persist even after the flower itself has withered. Nectar is also produced long before the flower is open! Sugar concentration in an open flower is about 20% , rising to about 50% in a withered flower (Ornduff and Dulberger 1978). These nectaries open to the outside of the flower and nectar stealing is therefore very easy, as the "thief" doesn't have to get anywhere near the pollen or stigmatic surfaces. Ants are seldom seen on the plants due to the glandular hairs on the stem, so it does not appear to have any function in feeding "ant guards" (see Faegri and Van der Pijl 1966). This seemingly wasteful feature is once again difficult to explain in evolutionary terms, and deserves further study.

The pollinators ~~of the genus~~ are unknown. This would be a rewarding field of study, as the unusual floral morphology is thought by many to reflect interesting evolutionary/ecological interactions. One of the problems with the pollination syndrome is that, in all species except *W. brachyandra*, the stigma and anthers seem too far apart for most insects to touch when visiting the flower. We might predict that seed set would be greater in *W. brachyandra* than in the other species (ease of pollination), but preliminary observations do not support this prediction. There must therefore be some insects which can and do pollinate the other species. These insects would have to be significantly larger than the common honeybee, *Apis mellifera*, as this species is not able to reach the anthers. The carpenter bee, *Xylocopa caffra*, is large enough to do the job, but it is very seldom seen on low growing *Wachendorfia*, as it tends to favour tall shrubs and small trees, *e.g.Virgilia oroboides*. I have seen tabanid flies (family Tabanidae) taking nectar from *W.parviflora* and *W.paniculata*, and in the process the wings of this large-bodied fly touched the anthers. I suggest that this group of flies may be important pollinators of the genus due to their size and anthophilous behaviour. More observations are needed to confirm this view. Other potential pollinators include numerous small beetles that appear to feed on the pollen. These beetles clamber over the anthers and may effect a degree of "mess and soil" pollination.

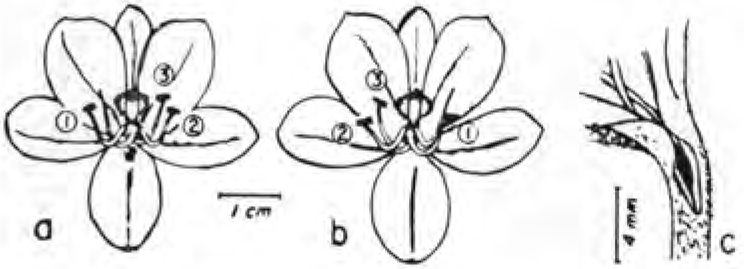


Figure 6 Floral features of *Wachendorfia paniculata*
a) left handed flower b) right handed flower c) detail of perianth aperture (= extrafloral nectary) [*ex* Ornduff and Dulberger 1978].

Variation

Considerable interplant and interpopulation variation occurs in the length of the inflorescence, the number of cymes produced, the number of flowers in a cyme, the size and colour of the flowers, the degree of perianth spreading, and the size of the nectaries.

The genus is essentially spring flowering, although there are some intra- and interspecific differences worth noting. High altitude forms of *W.paniculata* are noted for their late flowering. This is not a particularly surprising phenomenon as it has been found for various other fynbos taxa (Linder - pers.comm.). The species has an extremely long flowering period (Figure 8a), and this may be attributed to the varied habitats in which the species is found, as different selective pressures will be acting on the different populations.

W.thyrsiflora is often found flowering in late summer (Figure 7). This might be a reflection of its moist habitat, as severe moisture stress is unlikely, perhaps allowing this species to flower much later than the other species which favour drier habitats.

W.parviflora is interesting in that it is an early flowerer, with no flowering records for any later than September (Figure 9). It is thus often the only species of the genus in flower in early August, and it may be deriving some benefit from reduced co~~m~~ngeneric competition. As I have mentioned, this feature, along with its hairy leaves and narrow tepals, supports the idea of a neotenous species. Briefly, what this means is that *W.parviflora* is moving into an early flowering niche, its hairy leaves being an evolutionary legacy from a drier, later flowering period. The flower is perhaps genetically more plastic, and has

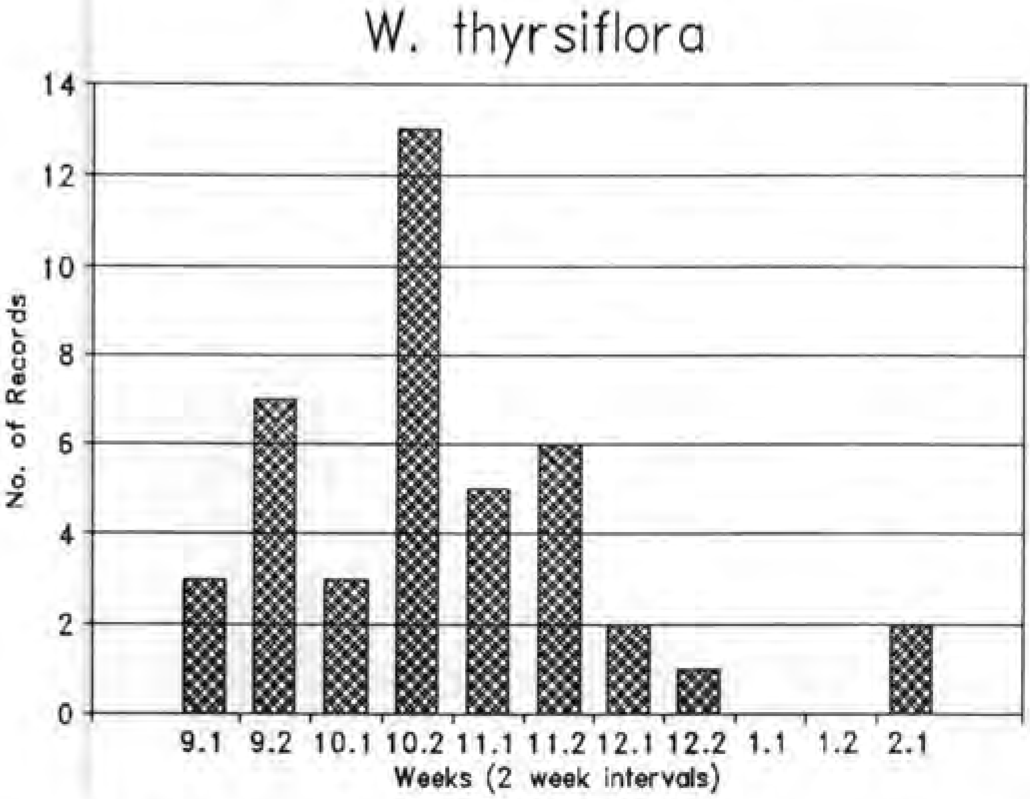


Figure 7 **Graph of the distribution of flowering records for *W. thyrsiflora*.** The figures on the X-axis refer to months of the year, each month being divided into the first two weeks and the second two weeks, *e.g.* 10.1 means the first two weeks in October.

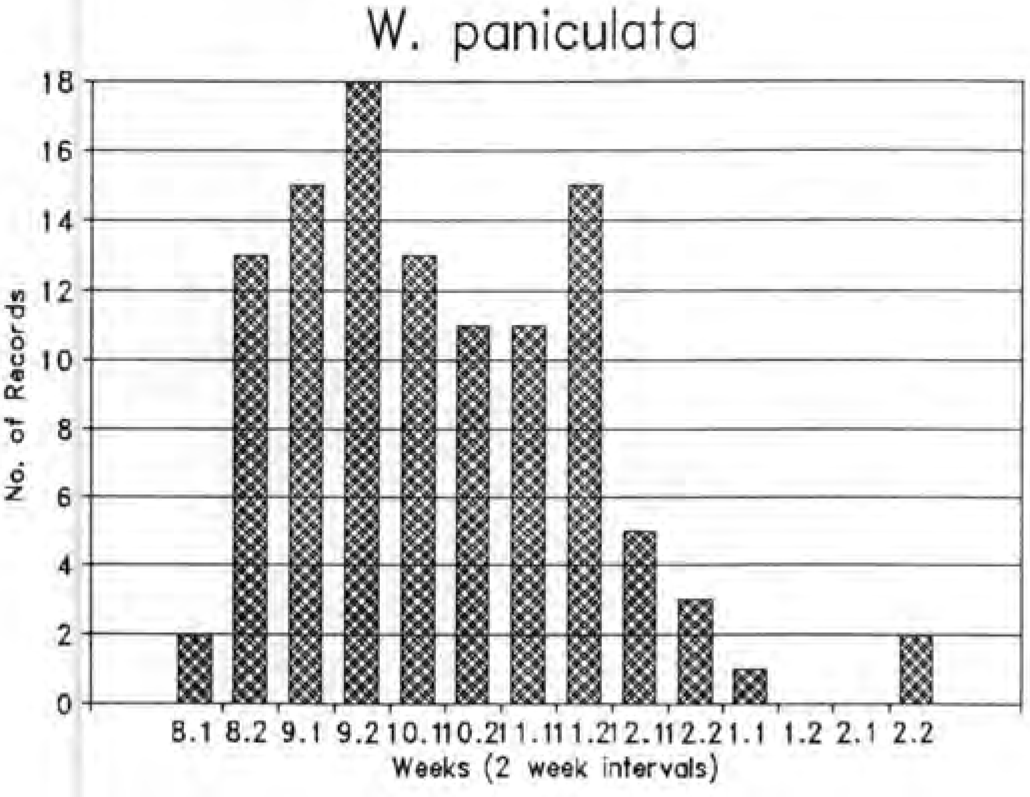


Figure 8a **Graph of the distribution of flowering records for *W. paniculata* (typical form).** The figures on the X-axis refer to months of the year, each month being divided into the first two weeks and the second two weeks, *e.g.* 10.1 means the first two weeks in October.

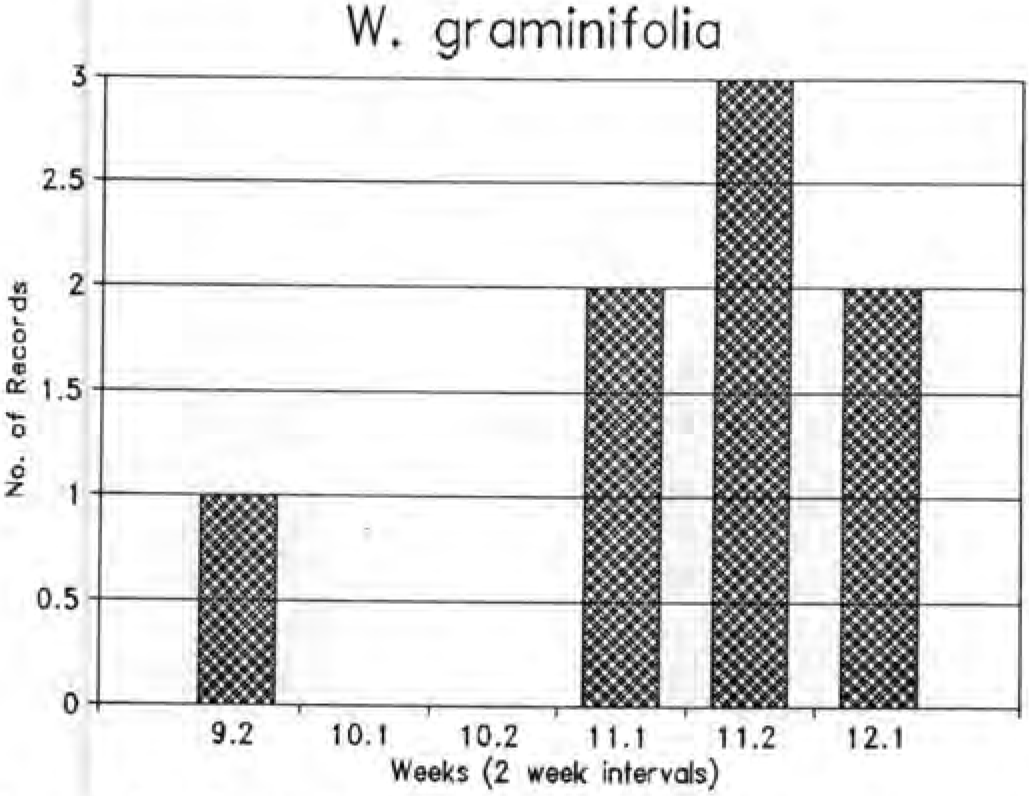


Figure 8b Graph of the distribution of flowering records for *W.graminifolia*. The figures on the X-axis refer to months of the year, each month being divided into the first two weeks and the second two weeks, *e.g.* 10.1 means the first two weeks in October.

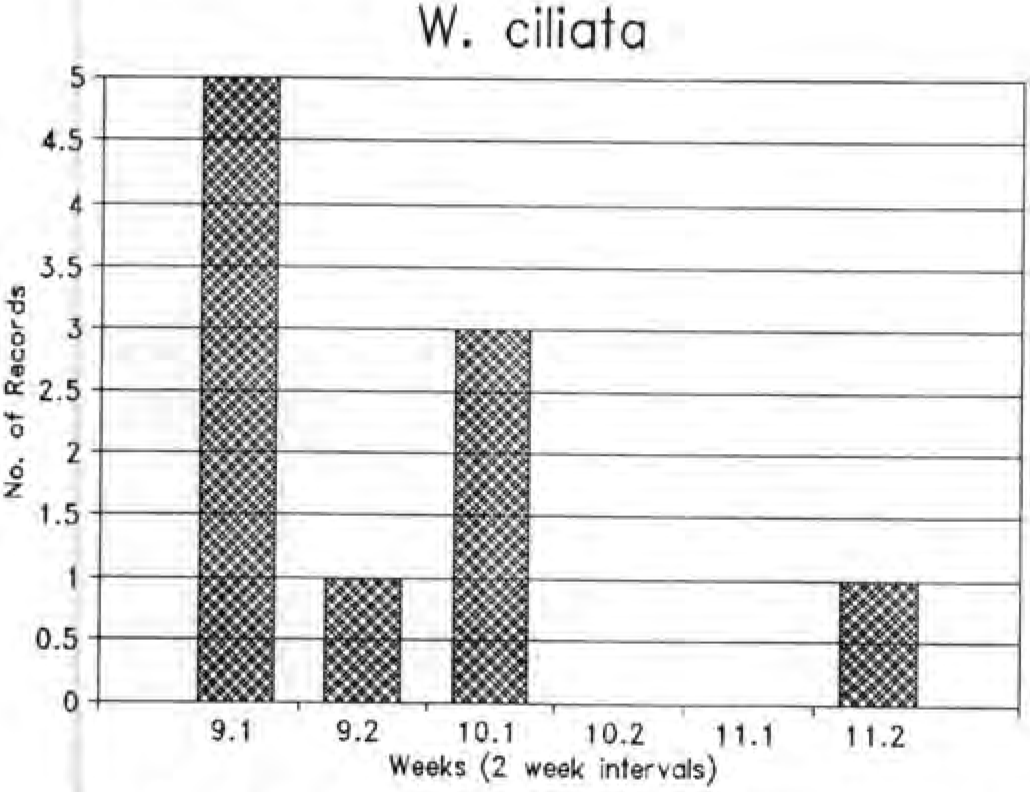


Figure 8c Graph of the distribution of flowering records for *W.paniculata* (form *ciliata*). The figures on the X-axis refer to months of the year, each month being divided into the first two weeks and the second two weeks, *e.g.* 10.1 means the first two weeks in October.

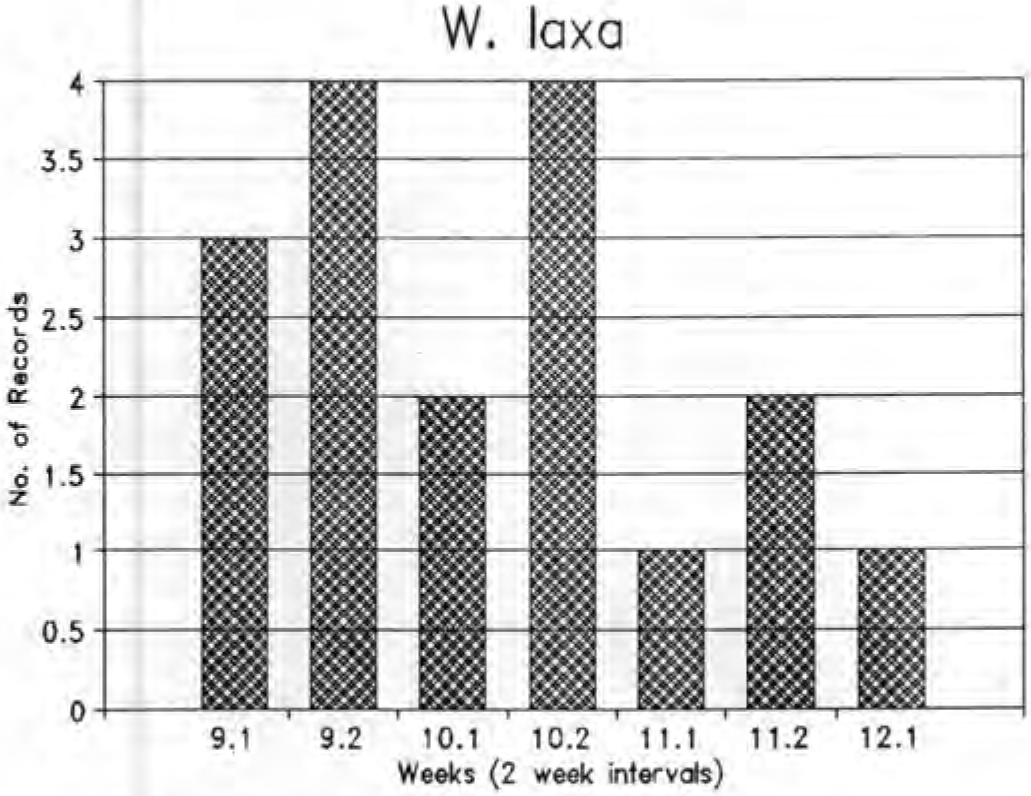


Figure 8d Graph of the distribution of flowering records for *W. paniculata* (form *laxa*). The figures on the X-axis refer to months of the year, each month being divided into the first two weeks and the second two weeks, *e.g.* 10.1 means the first two weeks in October.

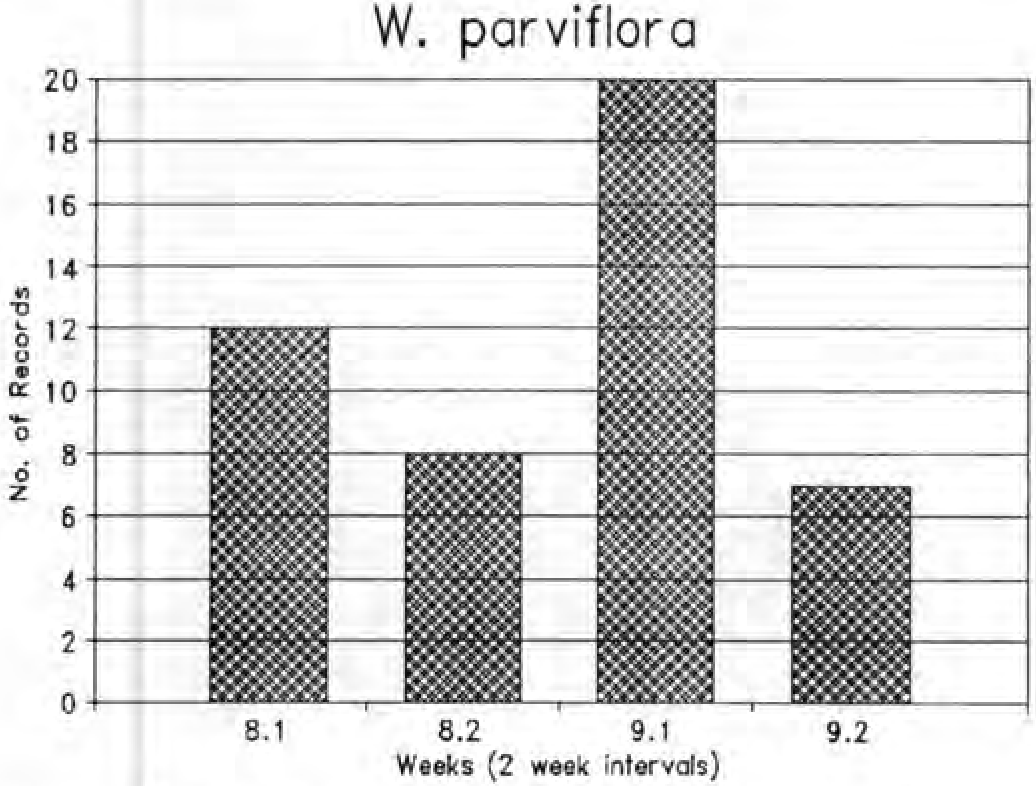


Figure 9 Graph of the distribution of flowering records for *W. parviflora*. The figures on the X-axis refer to months of the year, each month being divided into the first two weeks and the second two weeks, *e.g.* 10.1 means the first two weeks in October.

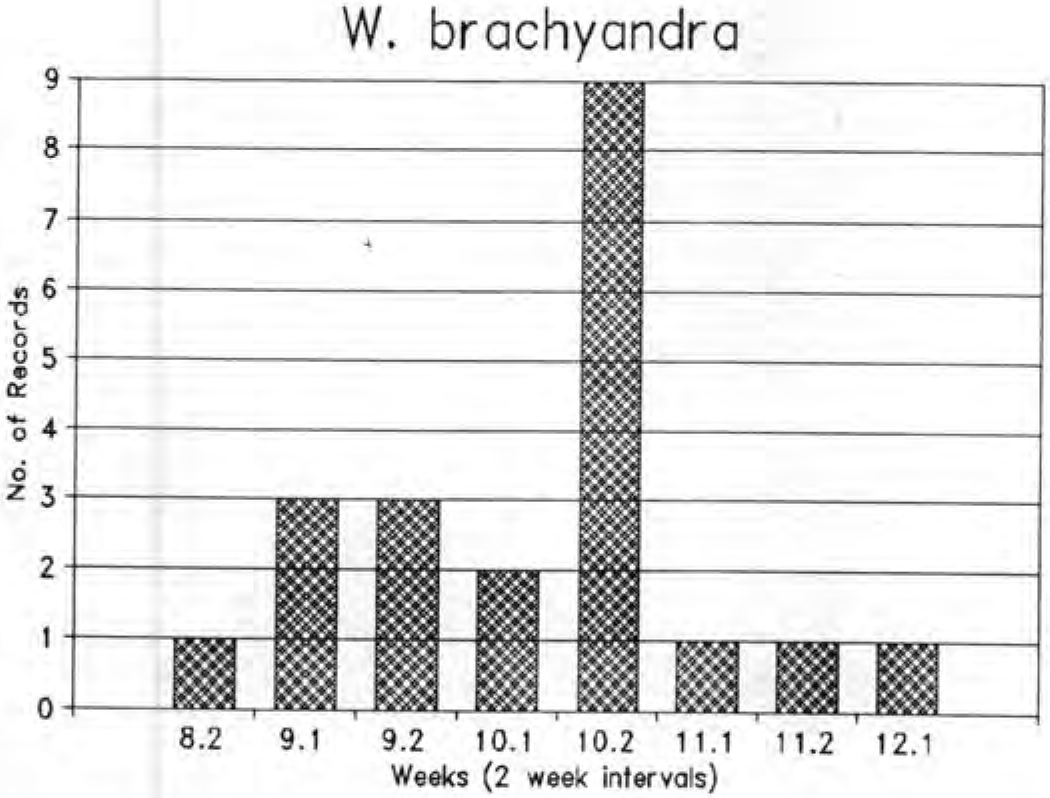


Figure 10 Graph of the distribution of flowering records for *W. brachyandra*. The figures on the X-axis refer to months of the year, each month being divided into the first two weeks and the second two weeks, *e.g.* 10.1 means the first two weeks in October.

already changed its structure, being mature when the tepals are still narrow. The floral structure of *W. brachyandra* supports this idea of floral plasticity, as it also has a rather different flower structure (short, clustered stamens).

4) <u>POLLEN</u>

Erdtman (1966) recognized three pollen types within the Haemodoraceae. Six genera, including both *Dilatris* and *Wachendorfia*, are characterized by monosulcate pollen (20-90um long) with a "usually not very distinct" exine stratification and sexine pattern. *Barberetta* was not studied by Erdtman (1966).

Simpson (1983) studied the family in more detail. He examined, amongst others, two species of *Dilatris*, one species of *Wachendorfia* (*W. thyrsiflora*), and *Barberetta.* His observations provide a useful descriptive base, as the present study was extended to include the other three species of *Wachendorfia*.

Dilatris pillansii and *D. corymbosa* possess very similar pollen grains, being monosulcate and heteropolar, with verrucate to baculate non-apertural sculpturing and gemmate to psilate apertural sculpturing (Plate 4 e and f). Grains are approximately 50um long (polar) and 25um wide (equatorial), with a furrow shape. The exine surface appears quite different from the exine of *Wachendorfia* pollen, as the verrucae (warts) seem to have coalesced to form a more continuous bumpy pattern. *Dilatris* also has a far less obvious micropore-pitted aperture border.

Wachendorfia pollen is monosulcate and heteropolar, with a convex aperture wall consisting of widely separated, two-

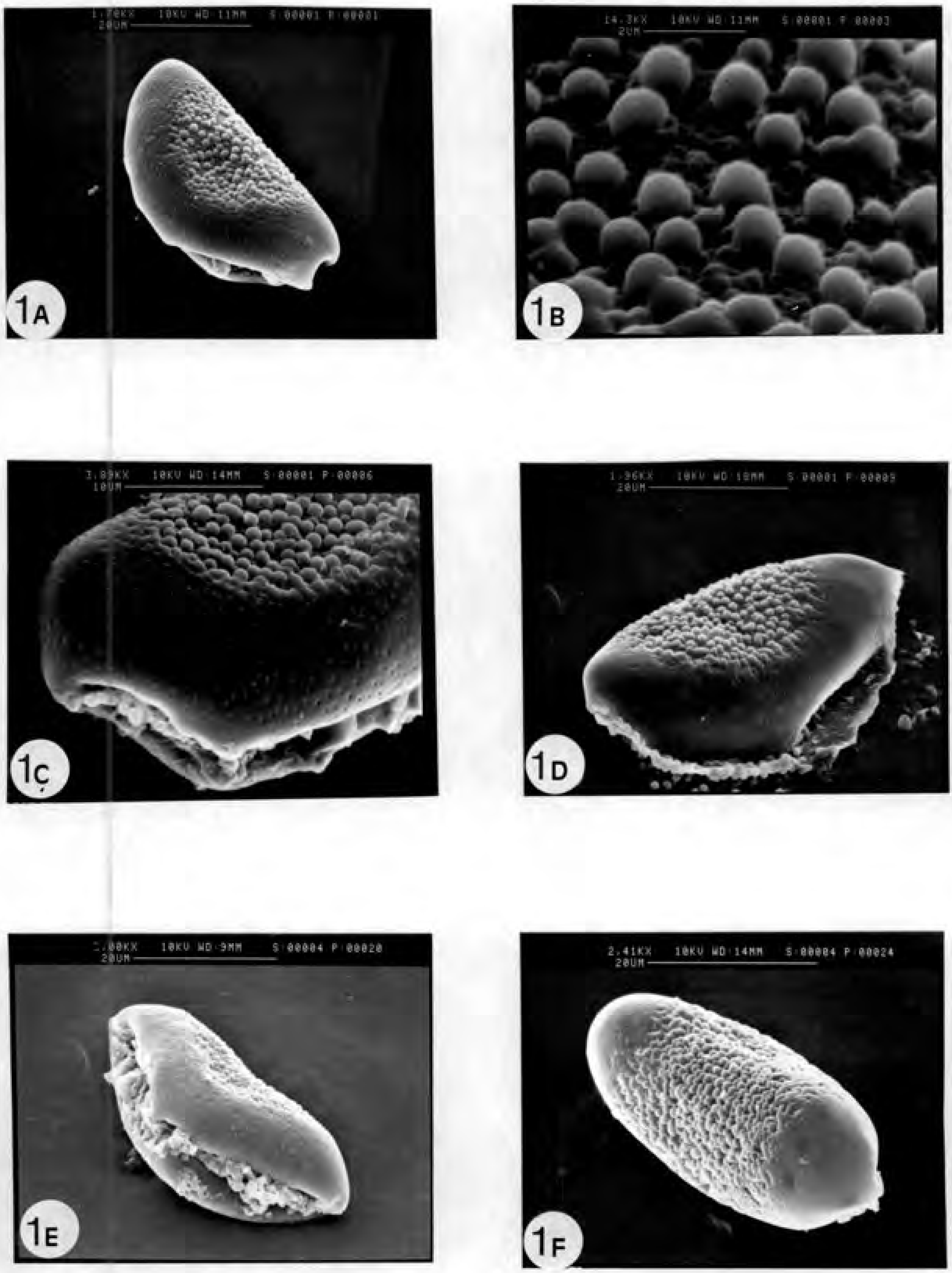


Plate 3 (A–C) *W. paniculata*: A) grain showing shape, and position of verrucae B) exine verrucae and secondary sculpturing beneath C) micropore-pitted aperture border; D) *W. thyrsiflora* grain shape showing width of micropore pitted border; E) *W. brachyandra* grain shape, aperture and micropores; F) *W. graminifolia* verrucae and micropore-pitted border

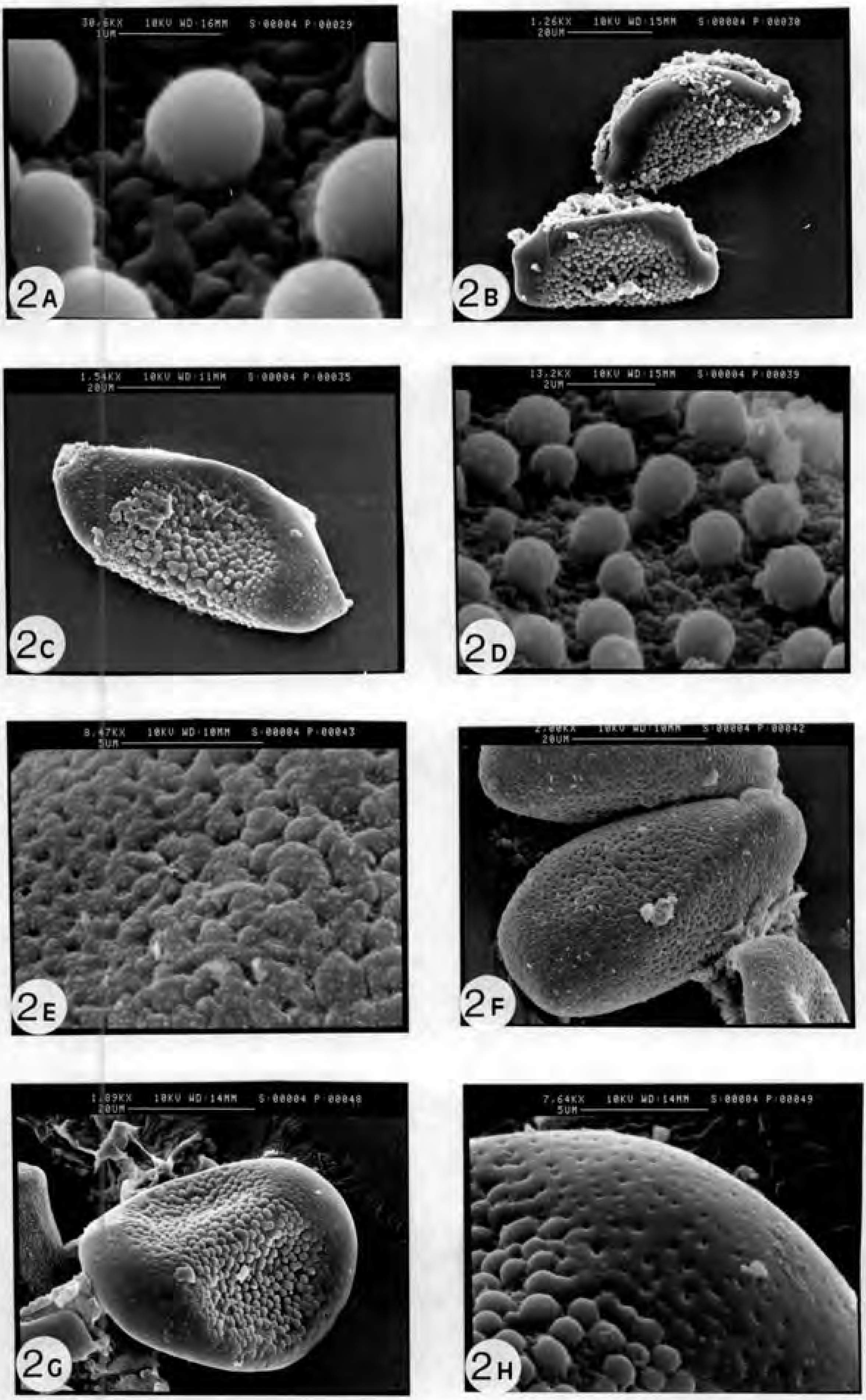


Plate 4 (A–B) *W. paniculata* (high altitude form): A) verrucae and secondary exine sculpturing B) grain shape and verrucae density; (C–D) *W. paniculata* form *ciliata*: C) shape D) verrucae and secondary exine sculpturing; (E–F) *Dilatris corymbosa*: E) exine reticulation F) grain shape and sculpturing - note lack of verrucae; (G–H) *W. parviflora*: G) verrucae pattern H) micropore-pitted aperture border

layered baculate exine elements, over a relatively thick two-layered, fibrillar intine (see Simpson 1983). The concave non-apertural wall is proximally verrucate, with a strange granular appearance between the verrucae (Plates 3 and 4). The verrucae thus appear to "saddle" the pollen grain. The aperture wall is encircled by a smooth border pitted with micropores. The grains are distinctly hemispheric in shape.

In all species the size of the exine verrucae (upper layer of exine) is relatively constant (about 1um in diameter), and all species appear to have the granular substance visible between the verrucae. This granular layer is in fact the lower layer of the two-layer exine.

The only significant difference between any of the species seems to be found in *W.thyrsiflora* (Plate 3 1d), in which the distance between the sulcus and the start of the verrucae,*i.e.*the width of the micropore-pitted border, is twice as great as in the other species. All species have grains between 40 and 50um long, and 20 and 25um wide (Table 7). There is thus no reliable way to identify *Wachendorfia* pollen to species level. This is not an unexpected result, as this is often the case for other monocot taxa (Linder - pers.comm.).

The pollen of *Barberetta* (monotypic) is more similar to the pollen of *Wachendorfia* than it is to the pollen of *Dilatris*, and the pollen of the former two could in fact be mistaken (Plates 5 and 6). This suggests that *Barberetta* is more closely related to *Wachendorfia* than it is to *Dilatris*.

Erdtman's (1966) description of a "coarsely granular, distinctly convex operculum" in *Wachendorfia* is shown to be incorrect. This is not an operculum, but simply an aperture wall with an outer layer of closely spaced exine structural

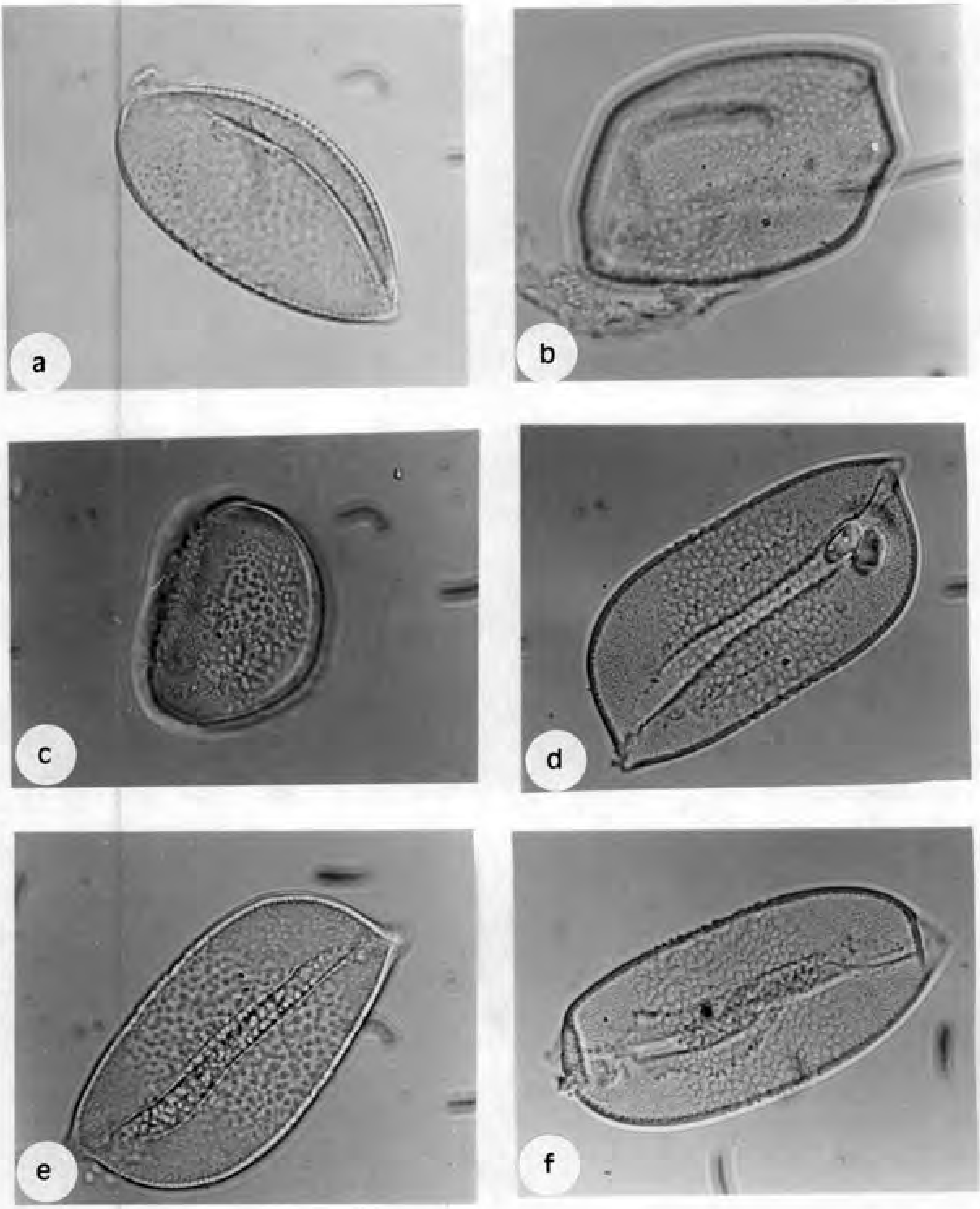
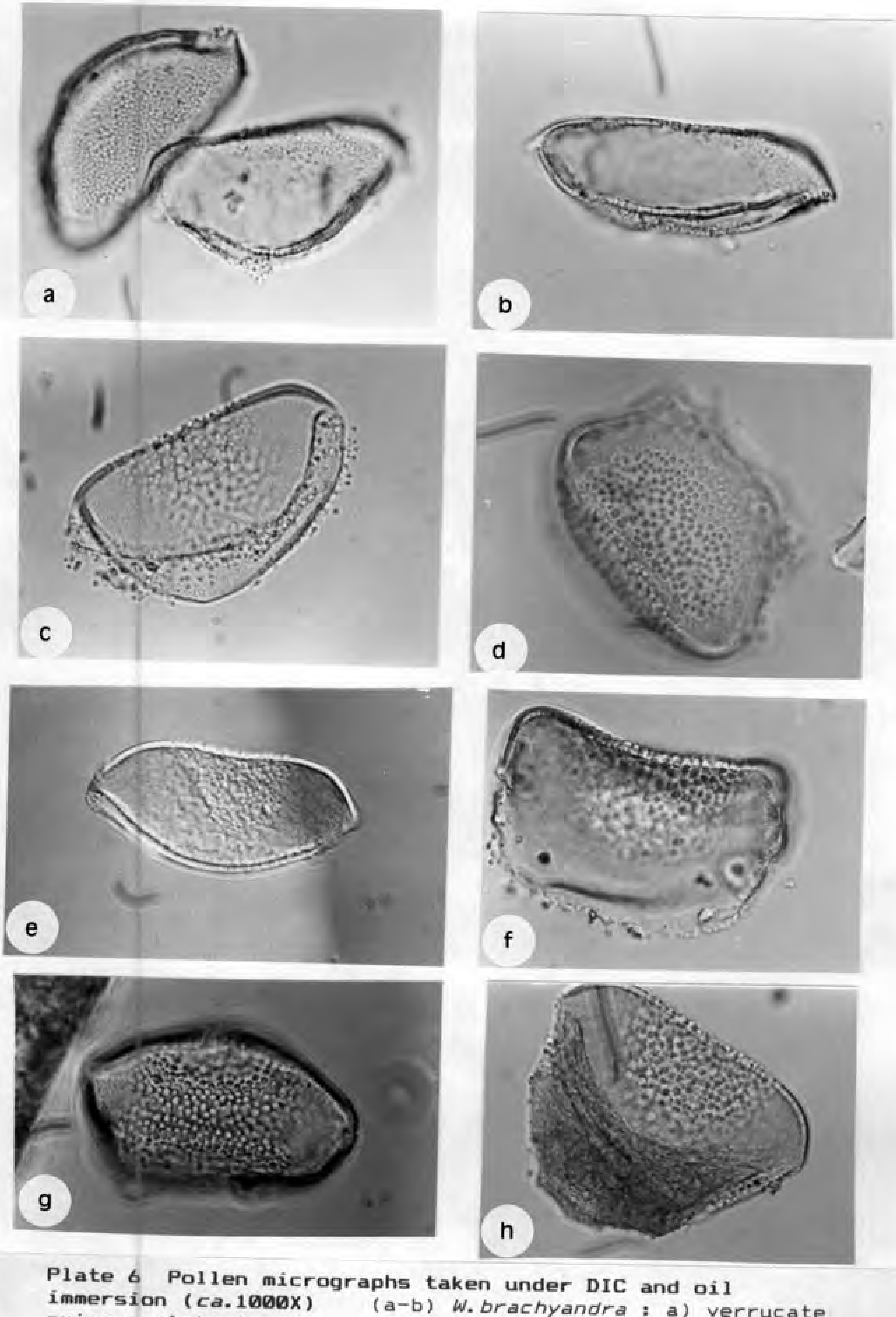


Plate 5 Pollen micrographs taken under DIC and oil immersion (*ca.*1000X).
(a–b) *Dilatris corymbosa* : a) monosulcate pollen grain b) reticulate exine sculpturing; note the lack of verrucae; c) *Barberetta aurea* pollen showing verrucae very similar to *Wachendorfia* pollen; (d–f) *W.parviflora* : d) central sulcus, proximal verrucae and micropore-pitted border e) sulcus f) verrucate exine sculpturing saddling grain.



This plate is sadly made

Plate 6 Pollen micrographs taken under DIC and oil immersion (*ca.*1000X) (a-b) *W. brachyandra* : a) verrucate exine sculpturing b) sulcus; (c-d) *W. paniculata* (typical form) : c) verrucate saddle surrounded by micropore-pitted border, sulcus d) verrucae; e) *W. graminifolia* sulcus and verrucate saddle visible; f) *W. paniculata* (high altitude form) profile of verrucate, concave, non-apertural surface; (g-h) *W. paniculata* form *ciliata* - examples of non-apertural verrucation.

Table 7 Pollen measurements for selected taxa (in µm)

	A	B	C	D	E	F	G	H	I	J
Polar	56.1	51.0	51.0	51.0	51.0	45.9	63.8	56.1	51.0	51.0
	48.5	51.0	58.7	48.5	48.5	51.0	58.7	51.0	51.0	56.1
	53.6	56.1	58.7	45.9	56.1	56.1	45.9	63.8	51.0	45.9
	51.0	53.6	63.8	51.0	48.5	53.6	53.6	61.2	53.6	58.7
	51.0	48.5	56.1	43.4	51.0	48.5	56.1	56.1	51.0	48.5
	48.5	58.7	58.7	48.5	48.5	51.0	53.6	51.0	56.1	56.1
	48.5	53.6	58.7	51.0	51.0	53.6	66.3	53.6	56.1	53.6
	51.0	58.7	56.1	48.5	53.6	48.5	61.2	56.1	53.6	56.1
	51.0	48.5	48.5	40.8	53.6	51.0	56.1	63.8	53.6	53.6
	56.1	58.7	53.6	43.4	56.1	56.1	61.2	58.7	56.1	53.6
Average	51.5	53.8	56.4	47.2	51.8	51.5	57.7	57.1	53.3	53.3
Std.dev.	2.7	3.9	4.2	3.5	2.8	3.2	5.6	4.4	2.1	3.0
Equatorial	30.6	25.5	28.1	23.0	23.0	25.5	33.2	30.6	28.1	28.1
	25.5	38.3	30.6	25.5	25.5	30.6	30.6	25.5	30.6	33.2
	28.1	33.2	33.2	25.5	23.0	30.6	25.5	30.6	25.5	30.6
	33.2	35.7	25.5	20.4	23.0	33.2	25.5	23.0	23.0	33.2
	30.6	30.6	25.5	20.4	25.5	25.5	35.7	28.1	25.5	30.6
	25.5	25.5	33.2	23.0	28.1	25.5	28.1	28.1	30.6	28.1
	33.2	35.7	28.1	23.0	30.6	30.6	25.5	28.1	25.5	28.1
	30.6	30.6	28.1	25.5	28.1	28.1	25.5	30.6	28.1	25.5
	25.5	33.2	25.5	23.0	23.0	23.0	28.1	30.6	25.5	38.3
	28.1	25.5	28.1	23.0	25.5	25.5	28.1	30.6	25.5	28.1
Average	29.1	31.4	28.6	23.2	25.5	27.8	28.6	28.6	26.8	30.4
Std.dev.	2.8	4.4	2.7	1.8	2.6	3.1	3.4	2.5	2.4	3.5

Specimen Key:

A : W.paniculata
B : W.paniculata
C : W.thyrsiflora
D : W.thyrsiflora
E : W.graminifolia
F : W.brachyandra
G : W.parviflora
H : W.decurrens
I : W.ciliata
J : Dilatris corymbosa

elements, a point noted by Simpson (1983). These apertures often disintegrate during acetolysis, probably because of the lack of continuous exine material between the elements.

The generic differences in pollen grain structure are thus well defined in the taxa studied, but there are few significant intrageneric differences, thus supporting the generic delimitations, which are based on plant morphological features. Pollen studies are unfortunately of little use in species delimitations within *Wachendorfia*.

5) <u>SEEDS</u>

The seeds of *Wachendorfia* are all ovoid or spherical, about 2mm in diameter, and covered in numerous short hairs (Plates 8-10). There is not much interspecific variation, and they can not reliably be used for species identification. Hair length and width is very constant with very little variation. All the species have curious nodules on the hairs (see SEM micrographs), and their function and origin is not known.

W. thyrsiflora probably has the most distinctive seed, as it is large and somewhat kidney shaped (Plate 8 f). When viewed under a SEM, the hairs on the seed also have a greater density of nodules than the hairs of other species.

I have seen the seeds of *W. thyrsiflora* floating on the surface of a stream, and I suggest that this is probably their major method of downstream dispersal. The hairs undoubtedly help the seeds to float. However, this does not answer the question of how seeds disperse upstream, as the seeds are unlikely to be animal dispersed (no fleshy pericarp for birds or mammals, no elaiosome for ants). Wind

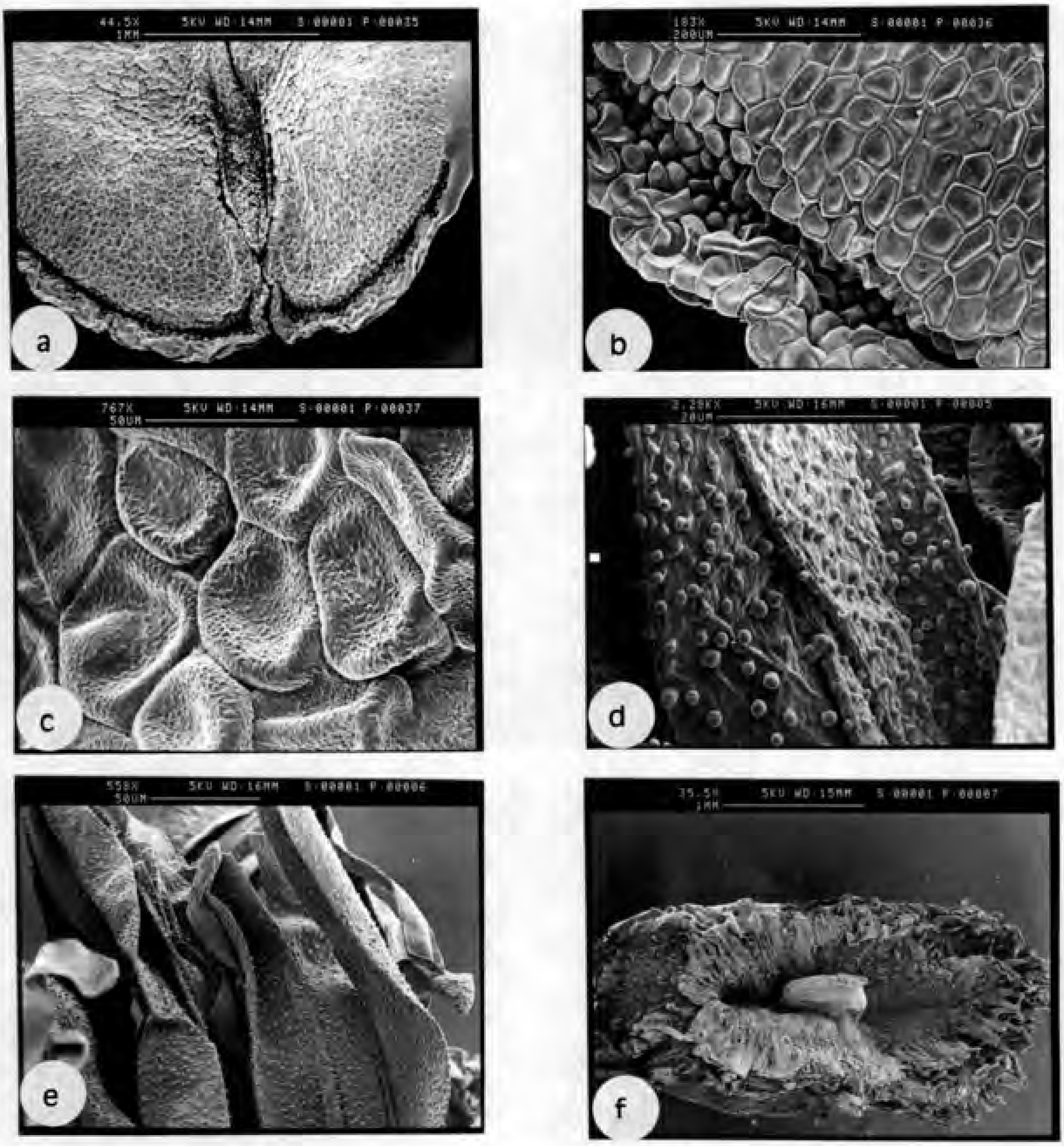


Plate 8 (a-c) *Dilatris viscosa*: a) disc seed b) close up of seed edge c) surface pattern (= warts on *Wachendorfia* seed hairs?) (d-f) *W. thyrsiflora*: d) close up of dense warts on seed hairs e) hair shape f) seed shape showing funicle position

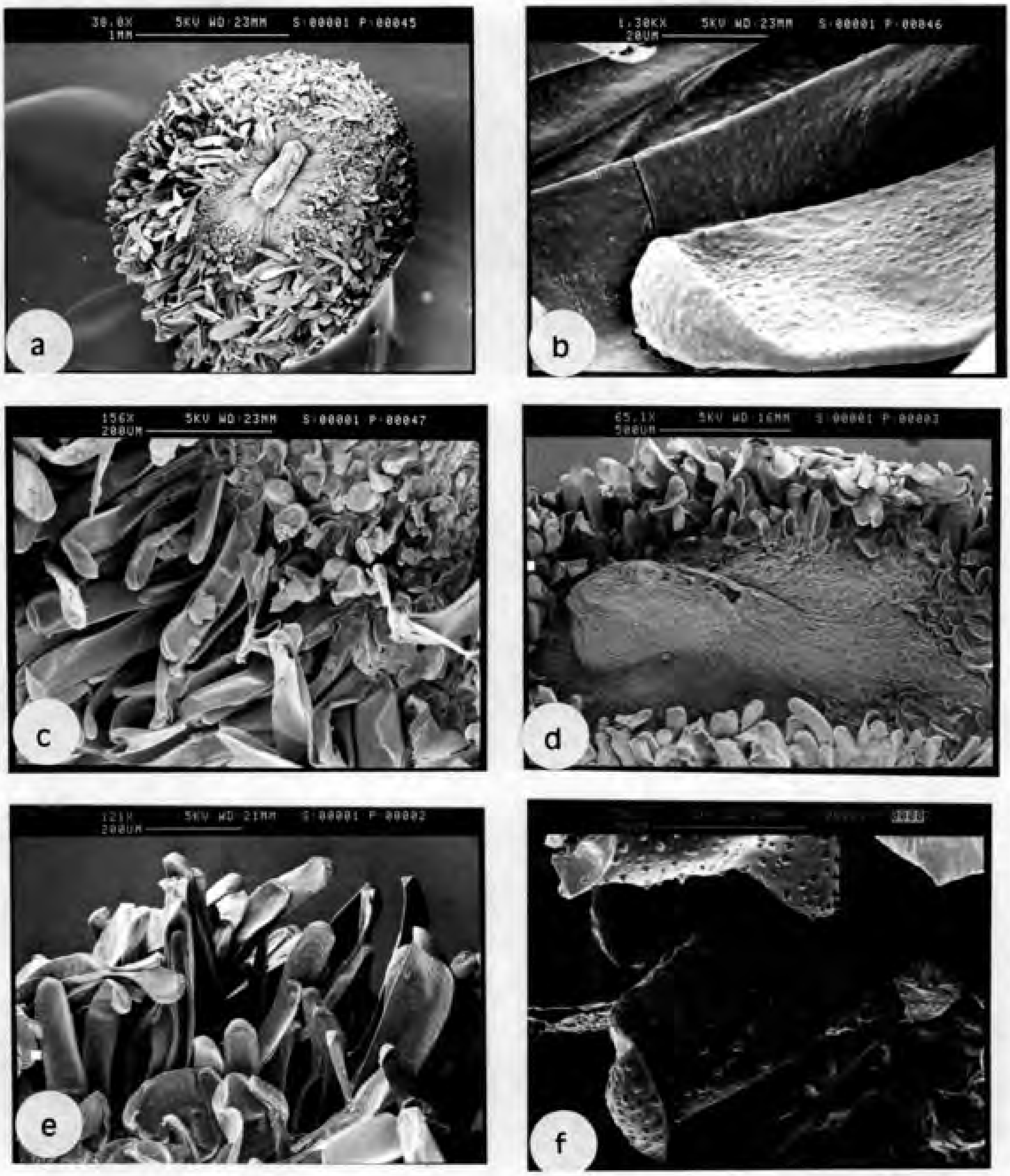


Plate 9 (a–c) *W.brachyandra*: a) seed shape and funicle b) close up of hair c) hair shape and density; (d–f) *W.parviflora*: d) funicle e) seed hair shape f) hair surface with warts

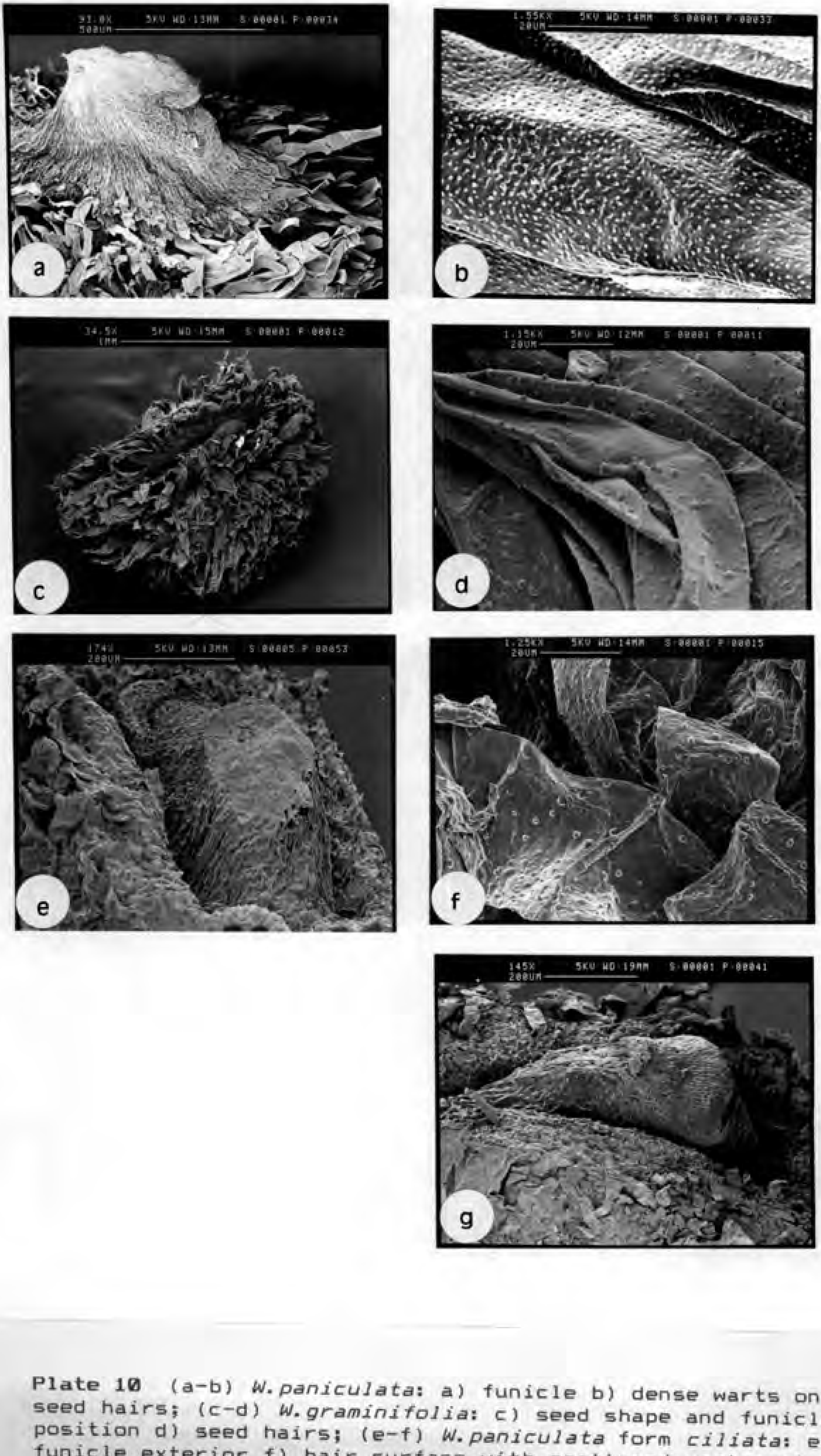


Plate 10 (a–b) *W.paniculata*: a) funicle b) dense warts on seed hairs; (c–d) *W.graminifolia*: c) seed shape and funicle position d) seed hairs; (e–f) *W.paniculata* form *ciliata*: e) funicle exterior f) hair surface with scattered warts; g) *W.paniculata* form *laxa*: funicle structure

is thus perhaps their other major dispersal vector, the short hairs helping to catch the wind. Dispersal is probably very poor in most of the other species, especially if they are growing in dense vegetation where seeds can't roll. These other species seldom grow near flowing water, so this is not likely to be an important dispersal mode for them. I therefore suspect that dispersal is largely restricted to immediate post-fire environments, when ground cover is sparse and the spherical seeds can blow across the sand, in the manner of *Protea* "tumbleseeds" (Bond 1988).

PHENETIC CLUSTERS

a) NTSYS

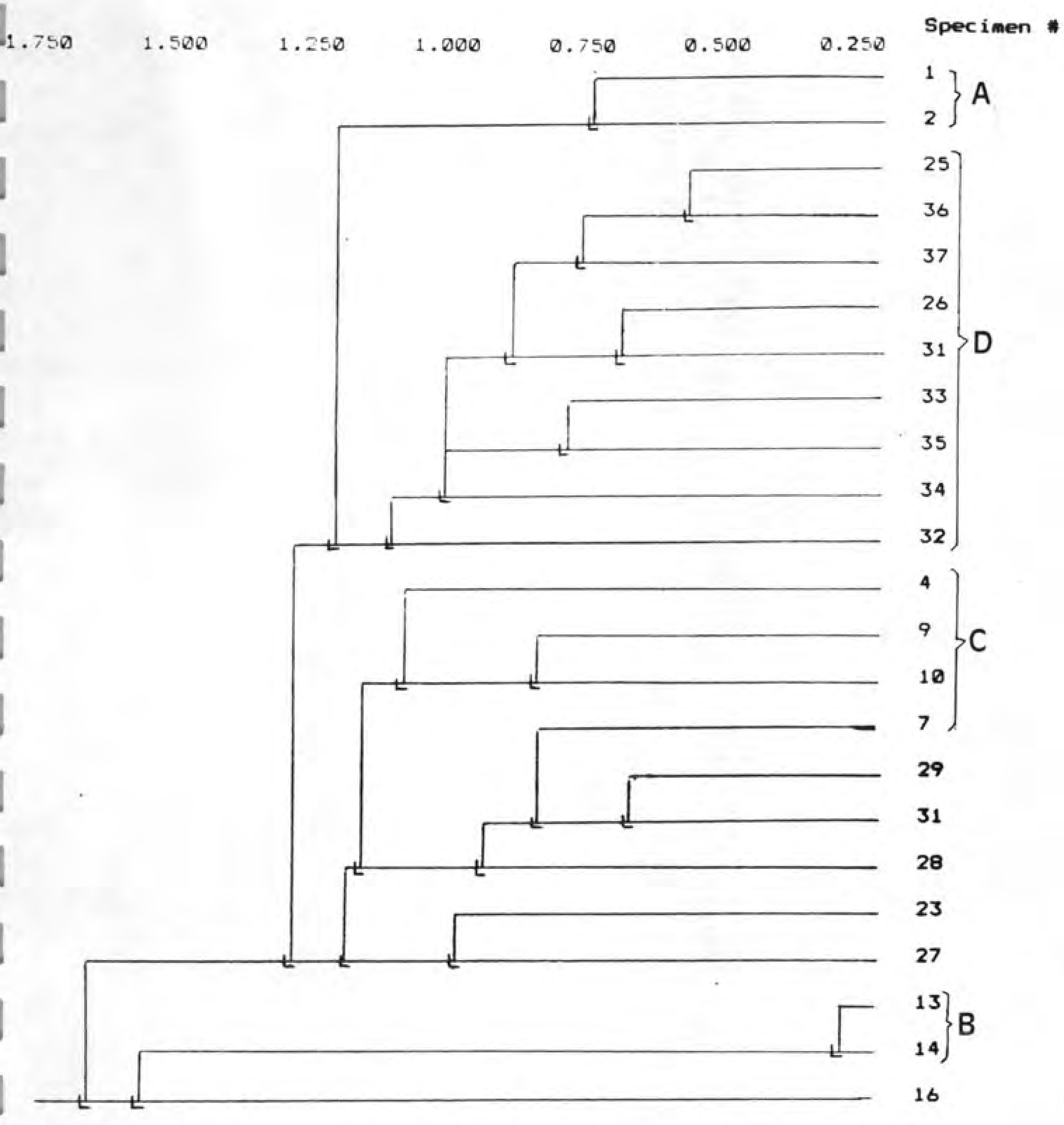
W. thyrsiflora clustered as a distinct group (Figure 11 group A). A large group of various *W. paniculata* forms clustered closest to this species, based on the increased height of many of these specimens.

W. parviflora was unfortunately represented by rather few specimens, but the program still managed to produce quite a discrete cluster (B). A single specimen of *W. paniculata* formed an insignificant outlier quite close to the cluster.

W. brachyandra specimens grouped rather poorly, with three different stems for four specimens (C). NTSYS did not do a very good job of indicating the distinctness of this species, probably as a result of the program being insufficiently detailed to deal with the subtle defining character of the species - the length of the style and filaments.

W. paniculata specimens are shown to possess a wide range of variation, and two major groups are visible, with a number

Figure 11 *Wachendorfia* phenogram generated by NTSYS



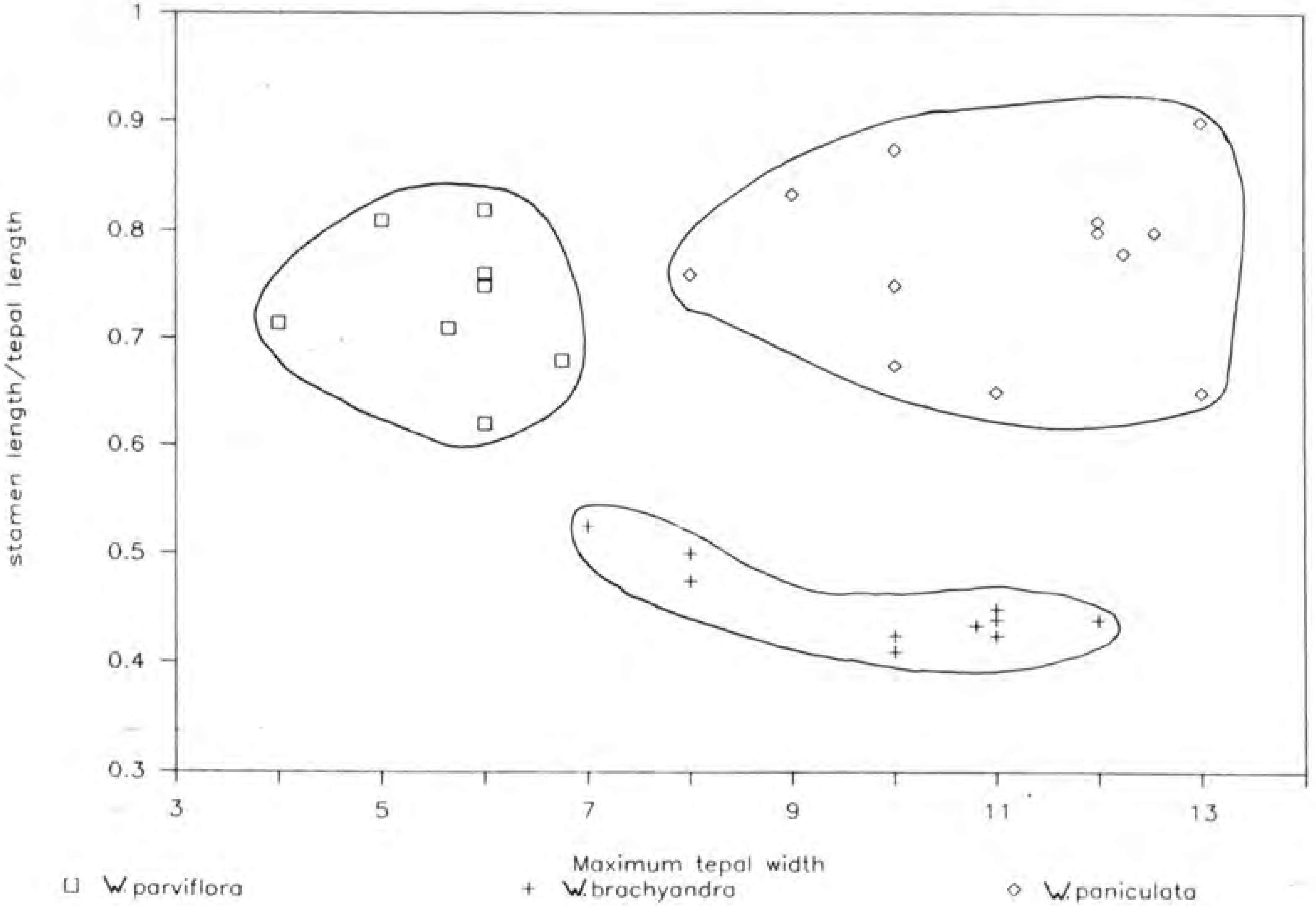


Figure 13 Scatter plot showing that these three species can be effectively differentiated using only two floral characters (and three measurements).

of other less distinct clusters inbetween. The larger cluster (D) essentially consists of the larger more robust specimens of *W.paniculata*, and in no way supports the delimitation of any formal infraspecific ranks, as the specimens show too wide a range of morphological variation. There is no geographical separation of specimens as grouped in the clusters.

This system produced disapointing results for a number of reasons. The specimen data were not ideal, consisting of 23 characters, 14 of which were floral measurements (Table 3a). A number of characters should have been deweighted more heavily, but this is not easily possible with the program. Size effects were largely eliminated using a standardization formula, but unfortunately this did not make much of a difference to the groupings.

Various coefficients were tried, and the distance coefficient proved to be the best.

Out of the 61 specimens sampled, 28 were used in the analysis, as the others were defective in some way, usually as a result of missing data points.

Lastly, but perhaps most importantly, it is easy to separate the three dryland species based entirely on flower structure. *W.thyrsiflora* is a very distinct species in many different ways (habitat, size, anatomy), and for this reason is not included in this analysis.

Figure 13 is a scatter diagram for the three species : *W.parviflora*, *W.brachyandra*, and *W.paniculata*, and uses three floral measurements on its two axes. The y-axis is a ratio of stamen (or style) length over maximum tepal length for each flower. This ratio was chosen to demonstrate the distinctness of *W.brachyandra*.

The x-axis is the maximum tepal width recorded for each flower, and this measurement was chosen to demonstrate the distinctness of *W.parviflora.*

The figure thus clearly illustrates the existence of three distinct taxa, with no overlap of chararacters.

b) <u>UNITER</u>

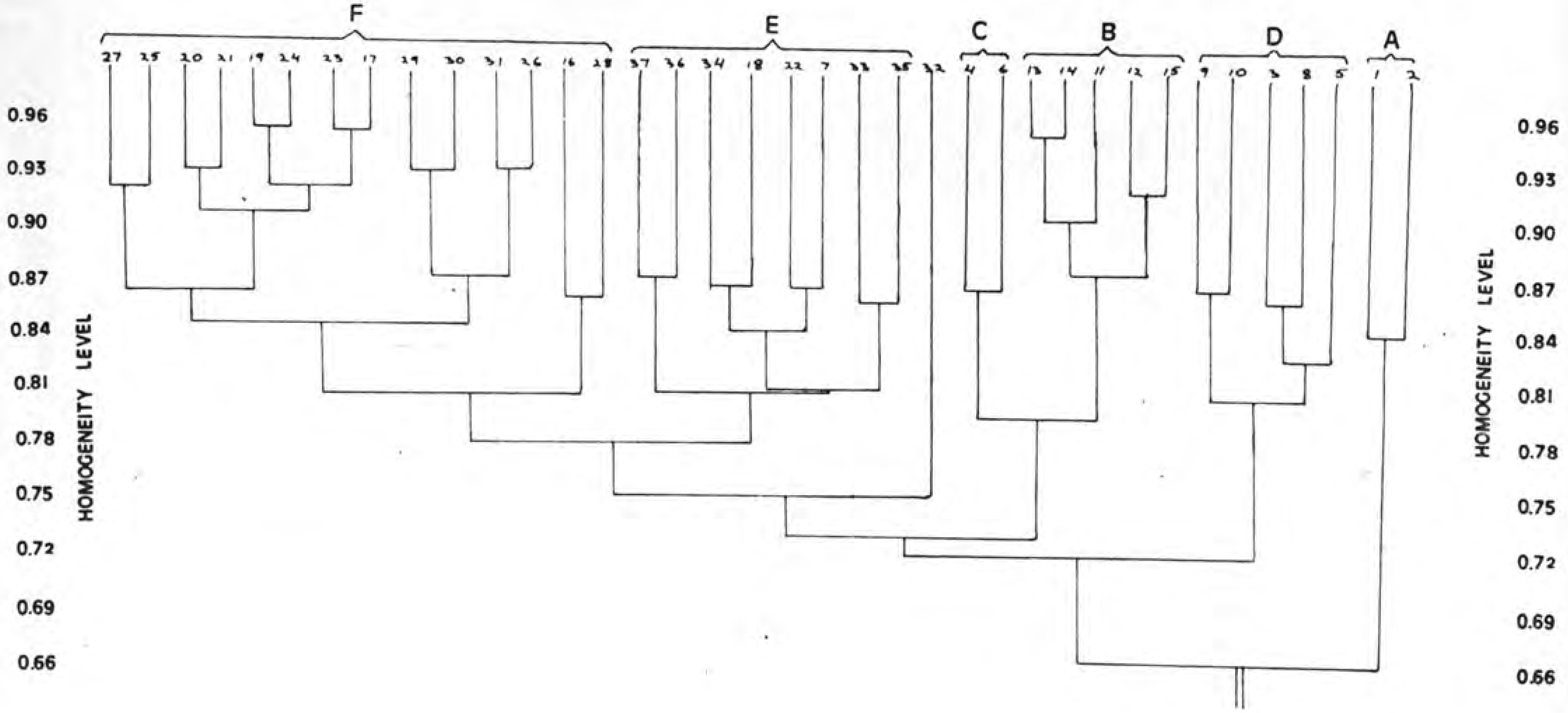
Uniter is a new program developed by Assoc.Prof. Hall for use in group- making. It is extremely advanced and includes numerous important features which make the method useful for identifying polythetic groups. The method takes into account the contexts of items, so important minority groups are not lost, and it can deweight repetitive or unreliable properties, and joint factors can be extracted (*e.g.*size).

The best results were achieved with minimization of group size effect set at 30%, although 60% was only slightly different. The group size effect would thus appear not to have had a major influence on clustering of these specimens. The most important effect of a larger group size effect reduction (60% vs. 30%) is the reduction in peculiarity of the groups, *i.e.*they become less distinct.

The results once again showed *W.thyrsiflora* to be a very distinct group Figure 12 (A) which has only 67% similarity (peculiarity) with the other groups.

W.parviflora formed a very well defined group (B), most closely linked with *W.brachyandra* (links at the 80% similarity level).

Figure 12 Wachendorfia phenogram generated by UNITER



W.brachyandra was revealed to be a somewhat heterogeneous group, with two of the specimens (C) grouping closer to *W.parviflora* than their conspecifics (D), and there was a further outlying specimen. On fusion of the two sub-groups (C and D) the drop in homogeneity, as revealed by the Homdif program, was only about 10%, indicating that the two sub-groups are in fact very similar (this excludes the outlying specimen). This means that the different stems for the two groups are not a particularly significant reflection of phenetic relationships. The two groups are very nearly one, and may be treated as such.

W.paniculata displays a wide range of variation, with no strong evidence for any subspecies. There is one major outlier ("ciliata" form), but I think that this is unimportant as it is just a specimen which possesses a slightly different combination of characters from the other *W.paniculata* specimens, and has thus been grouped separately. On inspection, the specimen is clearly not significantly different from the other *W.paniculata* specimens.

A closer look will reveal two large groups : one composed largely of *W.graminifolia* specimens (E), and the other a real mixture of specimens (F). The former contains the outlier of *W.brachyandra*, and its placement here is puzzling. There are no obvious reasons why it should sit in the middle of this cluster, But I do not think that it is very important, as once again, the specimen is clearly *W.brachyandra* on inspection.

The two "typical" *paniculata* specimens are part of what looks very much like a *graminifolia* sub-group (E). Is it possible that these two specimens are actually *graminifolia*, and should *graminifolia* be accorded a formal rank (either specific or subspecific)?

The two *paniculata* specimens are quite different with respect to tepal length, one of the important features of the species according to Barker (1950). She said that all *W.graminifolia* L.f. specimens should possess tepals between 25 and 30mm long, have glabrous,broad (up to 4cm wide) leaves and be large, robust plants. Specimen 22 has tepals large enough to fit this description, but specimen 18 does not. Both have suitably glabrous leaves, but these are much too narrow to fit the *graminifolia* description. We thus have the usual situation (for species complexes) in which some of the necessary characters are present and others are not. Specimen 22 is closest to the described condition. However, this means very little when one considers that only <u>one</u> of the five supposedly authentic *graminifolia* specimens (named herbarium specimens - *sensu* Barker) in fact fits the description given by Barker (1950). This suggests to me that *W.graminifolia* L.f. is simply a form (genetic subgroup with no formal rank) of *W.paniculata* Burm., as there is far too much continuous variation for one to be able to accurately define two species where only one "superspecies" actually exists (see Figure 14) [for further discussion see under *W.paniculata* in Taxonomy section].

I thus suggest that we can view the two taxa as essentially the same thing, and this of course means that there is nothing exceptional about the cluster containing both *graminifolia* and *paniculata* forms. These two forms (see Taxonomy for definition of "form") are thus very similar in a morphological sense. No anatomical data were available for the different forms, so possible differences in this respect remain unknown.

The other major cluster (F) consists of specimens that are clearly just variants (forms) of *W.paniculata*. The form *hirsuta* is indistinguishable from the typical form apart

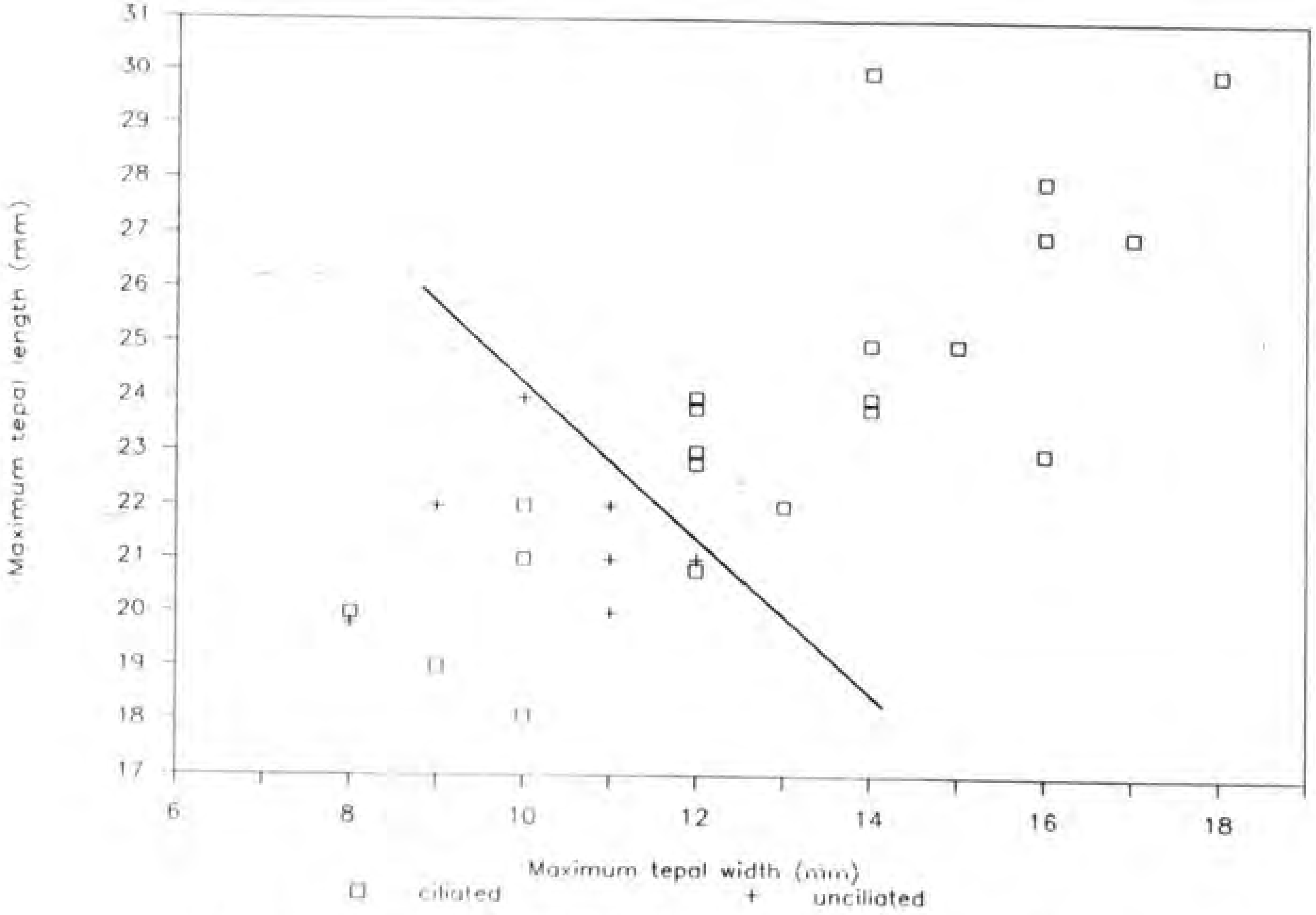


Figure 14 Scatter plot showing that *W.paniculata* specimens with ciliated tepals usually also have broader tepals (above the line). This is not regarded as strong enough evidence for the recognition of a formal intraspecific rank, as there are too many continuous variables involved (note the presence of some small, ciliated tepals below the line) [see Uniter discussion]

Table 8 The best characters for distinguishing groups within *W. brachyandra*, according to the Homdif program in Uniter. Ranked in descending order of importance.

Property #	Description	Drop in homogeneity on fusion of the two groups
19	Width tepal 4	216
8	Texture of bracts	204
10	Stamen length	61
18	Length of tepal 4	59
23	Width of tepal 6	43
11	Style length	41
1	Max. plant height	33
7	Leaf hairiness	31
13	Width of tepal 1	29
15	Width of tepal 2	23
14	Length of tepal 2	21
5	Max. leaf width	20
22	Length of tepal 6	17
4	Max. leaf length	14
20	Length of tepal 5	7
16	Length of tepal 3	4
12	Length of tepal 1	2
6	Leaf shape	0
2	Corm length	-1
3	Corm depth	-2
21	Width of tepal 5	-5
17	Width of tepal 3	-11

from the leaves being very hairy; the form *ciliata* merely has larger (although not always), ciliated tepals; and the form *laxa* differs only in its extremely lax inflorescence, which is often a function of high altitude.

W.paniculata (*sensu lato*) is thus an extremely variable species with about five different forms distinguishable, and this may make identification confusing for those unfamiliar with the genus. However, the other three species are very well defined, and it should be possible to arrive at a correct identification, if only by a process of elimination. I feel that Uniter has reflected this variation well, as it had to cope with a data set with few characters, and often subtle intraspecific differences.

The list of properties arranged in order of ability to distinguish groups within *W.brachyandra* (Table 8) corresponds very closely with my own instinctive feelings about character strength, which is somewhat reassuring! I believe that this list of properties would remain in essentially the same rank order for all species and clusters, and is in fact a good reflection of overall distinguishing ability within the genus.

c) Cladistic analysis

25 properties were selected for use in the cladistic analysis (see Table 4), although only five were of any real use, as all the others indicated nothing about character polarity. The five properties used consisted of three plant morphological, and two leaf anatomical properties (Table 4).

W.thyrsiflora appears closest to the outgroup, and has far more autapomorphies than any of the other species (Figures 16 and 15). This may indicate some form of ecological speciation and specialisation, as this species occurs in the

Figure 16 Most parsimonious cladogram for *Wachendorfia*, using *Dilatris* as the outgroup.

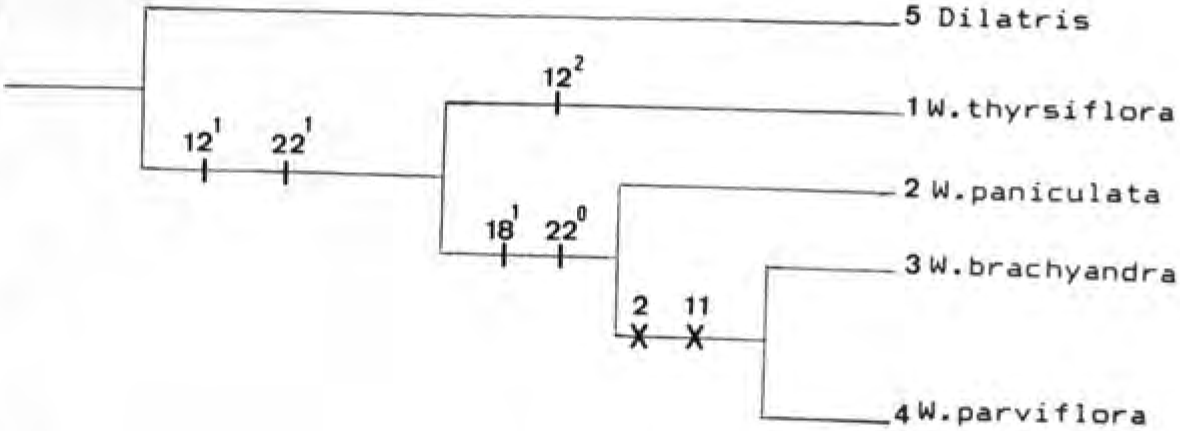
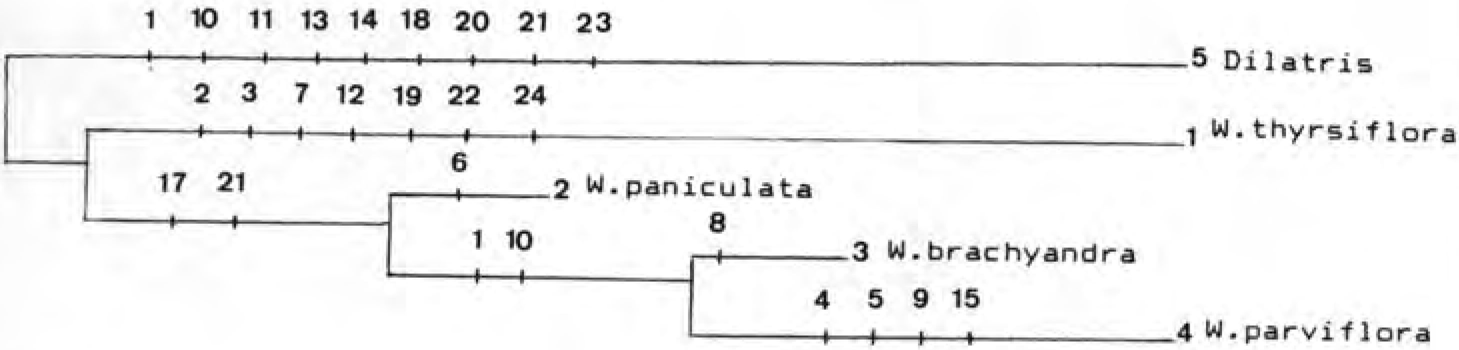


Figure 15 Diagram of patristic distances and indicating the branches along which each character changes its code.



same region as *W.paniculata* but in a more restricted habitat.

W.paniculata is the most widespread species and appears to have come from the same stock as the other two quite similar species. I suspect that *W.brachyandra* is a recent species, as it is confined to a small area in the extreme south western Cape, and has only one derived trait (Figure 15). I suggest that it has speciated on ecological grounds, as it prefers moist areas, often in shade , while *W.paniculata* is more catholic in its habitat requirements, although the latter tends to avoid the moist areas favoured by *W.brachyandra.*

W.parviflora has a number of important derived traits, which may have some ecological significance, particularly in the form of a "neotenous niche" (see Observations). I feel that the cladogram accurately represents its recent split from the parent species - *W.paniculata.* It is interesting that *W.parviflora* is strictly a western Cape species; perhaps a neotenous phenology is not favoured further east. However, a more parsimonious explanation is that the species arose in the west quite recently, and has not yet had time to invade the southern and eastern Cape. The fact that both supposedly recently derived species have the most restricted distributions supports the idea of a "younger" species.

The few autapomorphies present in *W.paniculata* suggest that it may indeed be the ancestral species. Its wide distribution supports this idea (Figure 19). The many derived traits in *W.thyrsiflora* support the idea of a dryland species being the ancestral stock, as the moist habitat in which the former grows has neccessitated the development of numerous new traits. The other two derived species have few autapomorphies as their habitat is not so far removed from the ancestral dryland habitat.

CONCLUSION

Wachendorfia consists of three well defined species and a fourth extremely variable species. This latter species, *W.paniculata*, has been the cause of much confusion in the past, with at least seven specific names having been given to the various forms. This variation was examined and was found to be continuous, making the separation of intraspecific ranks totally arbitrary. There is never any real geographic separation of these forms, so the use of subspecific or varietal rank would be innapropriate (Stuessy 1990). However, there is a form that shows a type of geographical separation along with a distinctively lax morphology (*W.paniculata* form *laxa*). Although this form is confined to the mountains between Ceres and Pakhuis Pass, it is not the only form in the area, so subspecific rank would not be appropriate (no allopatry).

When dealing with a single species complex like this, one must be aware of the possibility of interform hybrids, particularly if the forms are not yet sufficiently well genetically isolated to resist the mixing effects of hybridisation. A relative of *Wachendorfia* is the Australian genus *Anigozanthos* (Haemodoraceae) (Simpson 1983). Interpopulational crosses in *A.humilis* were found to be very common, while in *A.bicolor* they were uncorrelated with interpopulation distances or morphological divergence, and in *A.manglesii* they were consistently associated with morphological differences (Hopper 1980). There are thus numerous potential hybridisation levels within *Anigizanthos* and this is likely to hold true for *Wachendorfia*. The confusing taxonomic structure of *W.paniculata* may in part be due to crosses between morphologically dissimilar populations, thus retarding the rate at which speciation is occurring.

One must also be aware of the dangers in delimiting species using only macro-morphological features, although this may be the only practical method given limited time and money. In this regard, Linder (1990) concluded that " using only macro-morphological structures at specific level in the Restionaceae only reflects a portion of the available information and reliance on such a small portion of the available data set may lead to mistakes when assessing the relationships among species". I support this view and feel that the reliance on macro-morphological features is often the reason for inadequate, confusing species delimitations. This study assessed not only macro-morphological variation within *Wachendorfia*, but also pollen and seed coat features, rhizome storage products, and basic features of leaf anatomy. It is hoped that this broader data base strengthens the proposed classification of *Wachendorfia* (see Taxonomy). Much of this additional information was unfortunately not in the form of specimen data and I was thus unable to use it in the phenetic analyses. Future workers should attempt to use these extra properties in a detailed phenetic analysis, in which case the clusters would be more realistic and reliable.

The cladistic analysis also suffered from a lack of characters and the resulting cladogram should be interpreted with caution. However, the diagram of patristic distances (Figure 15) is interesting in that it illustrates the difference between the habitat specialist (*W. thyrsiflora*) and the habitat generalists, the former having many more derived traits, suggesting that ecological speciation has occurred. *W. parviflora* is notable for the number of derived characters that support the idea of it being a neotenous species.

The only way to gain an understanding of the phylogenetic history behind the development of floral enantiomorphy in

Wachendorfia is to produce a reliable cladogram of the family as a whole. *Dilatris*, *Barberetta* and *Wachendorfia* are obviously closely related (de Vos 1956; Simpson 1983), but their slightly different forms of enantiomorphy would prove to be an interesting phylogenetic/ecological exploration, especially as many other genera in the family do not possess enantiomorphic flowers. Why are the southern African representatives so unusual?

Wachendorfia and its related genera would certainly repay further study and may provide valuable information concerning the processes of evolution. Further taxonomic study of *Wachendorfia* may also prove rewarding, especially if hybridisation can be demonstrated.

FORMAL TAXONOMY

Historical background

The earliest description of a *Wachendorfia* was by Breyne in 1678. This form was subsequently described (but not published) by Solander, and in 1809 an illustration of this form was published by Ker Gawl, along with a name (*W.brevifolia*) and a description. At about the same time (1796) Salisbury published his own versions of two previously described species, changing *W.thyrsiflora* to *W.elata*, and *W.paniculata* to *W.humilis*. Salisbury also gave two short descriptions of what he chose to call new species - *W.pallida* and *W.lugubris*. These descriptions were based on plants that he had in cultivation in his chapel garden, and I have not been able to trace the type specimens, if indeed there were any preserved. Exactly why he chose to give accepted species new names I do not know, but this seems to have been common practice in horticultural circles at the time. In 1826 Sweet published his description of *W.herbertii*. These latter three names all refer to various forms of what is now regarded as *W.paniculata (sensu lato)*.

Hendrik Oldenland was the Superintendent of Simon Van Der Stel's Company Garden in Cape Town during the period 1691-1699. He collected numerous plants which he intended to send to the Netherlands, and he was preparing a Latin catalogue of his plants when he died. His collection of notes and plants was forgotten about for many years, and in 1770 it was found to be in the possession of Professor Burman, son of Johannes. Johannes Burman published the first post-Linnean (1753) descriptions of *Wachendorfia* in his monograph entitled "*Wachendorfia*", published in 1757.

Prior to Linnaeus, Plukenett (1700) and Breyne (1739) had illustrated and described various *Wachendorfia* specimens, although this was not the name that they used. These works included illustrations, which clearly show the features of the genus.

Thunberg visited the Cape between 1772 and 1775, and made extensive collections, which included specimens of *Wachendorfia.* Some of his specimens were evidently sent back to Europe while he continued on his travels to Japan and the Far East. These specimens were seen by Linnaeus (the younger), who described an apparently new species of *Wachendorfia* in his "Species Plantarum" (1781). He named this *W.graminifolia.* Thunberg returned to Europe in 1779, where he wrote up his preliminary descriptions in his "Prodromus" (1794), describing three more species of *Wachendorfia* (*W.graminea*, *W.tenella*, and *W.hirsuta*). These were thoroughly described in his "Flora Capensis" (1807) thirteen years later.

Generic description

Wachendorfia Burm. 1757 in "*Wachendorfia*" monograph;
Linn. Syst. ed.X, p864 (1759).
No type specimen named, although the material is probably all still in the Geneva Herbarium.

Synonyms: *Pedilonia* Presl, Pedil.Nov.Pl.Gen.(1829); and in Flora 12 (1829) p568.

Wacchendorfia N.L.Burman, Fl.Cap.Prodr.(Fl.Ind.) (1768). A spelling variant.

Wachendorfa Cothenius, Disp.3 (1790). Another spelling variant.

Pre-Linnaean names:

Erythrobulbus Plukenett *Mantissa* (1700)
Asphodelus Breyne. *Prodromus3* (1739)

Perennial rhizomatous herbs, 0,1-2,5m tall, leaves usually annual (one species perennial), annual aerial stems develop from a rhizome, monoecious.

Underground organs : Fleshy, irregular to ovoid, bright red rhizome. Three opposite nodes, each with a lateral bud. Single apical bud produces aerial stem. New rhizome produced annually, 1-3 old ones remaining attached; one species with a perennial rhizome. Cluster of thin adventitious roots sprouts from node between rhizomes. Old rhizome leaf bases form a tunic around rhizome. Ramets often formed.

Leaves : Usually annual, one species perennial. Erect or spreading, linear, lanceolate, or falcate, lower leaves sheathing at the base of flowering stem. Lowest two stem leaves amplexicaul and opposite, leaves above that are spirally arranged and not amplexicaul. Firm in texture, always longitudinally plicate. Simple and entire, glabrous to hirsute, green to yellow-green, 0,1-0,9m long. Three rhizome leaves, plus a variable number of stem leaves.

Branches : Annual. Peduncles herbaceous, terete to angular, very short to quite long (up to 25cm), near vertical, or spreading. Main axis covered in short hairs, pilose at the base, glandular nearer the apex.

Bracts : Erect or recurved, herbaceous or scarious, acute, usually hairy. Older scarious bracts often recurved.

Inflorescence : Lax deltoid, to dense cylindrical panicle.

i) **Tepals** : Subequal, spreading, oblong. Lower three free, upper three united at the base, the latter with small dark and light markings near the base. Open spur-like nectaries produced from origin of outer upper tepal and the two adjacent inner tepals (one each side). Outer segments hairy on outside, especially the central upper tepal. Yellow to pale apricot.

ii) **Stamens** : Three, opposite the inner tepals. Filaments free, filiform, declinate - the upper two pendulous, the lowest turning sideways opposite the style. Anthers ovate-sagittate, two - celled, dehiscing longitudinally, introrse, usually included. Pollen boat shaped, monosulcate, heteropolar, with a verrucate, two-layered exine.

iii) **Gynoecium** : Superior, pubescent, three-locular, one ovule per locule, axile placentation. Style filiform, bent sideways (left or right in any one plant), in same direction as one of the stamens. Stigma minute, capitate.

Fruit : A capsule, acutely three-lobed, dehiscing loculicidally, usually glandular pubescent.

Seeds : One per locule, spherical to ovoid, densely hairy.

Key features of the genus

Perennial herb, three of the four species with annual leaves. Annual flowering stems. Annual (perennial in one species) rhizome with red sap. Leaves lanceolate, linear or falcate, simple, longitudinally plicate, entire. Inflorescence a panicle. Flowers yellow, with right and left-handed forms. Locules uni-ovular. Confined to the fynbos biome.

Key to the species of Wachendorfia

1) Perianth segments narrow, 3-6 mm broad; bracts herbaceous, all erect; leaves usually as long or longer than the flowering stem; plants usually short (less than 25cm tall). .... IV) *W. parviflora*

1) Perianth segments broad, 5-18 mm wide; bracts scarious or submembranous, the upper usually recurved; leaves usually shorter than the flowering stem; plants usually tall (greater than 25cm tall). .... 2)

  2) Stamens and style about half the length of the tepals, clustered. ....III) *W.brachyandra*

  2) Stamens and style from two-thirds to nearly as long as the tepals, spreading. ....3)

    3) Plant tall (over 0,6m); inflorescence dense, cylindrical; leaves broad (greater than 1,5cm wide), glabrous, perennial. ....I) *W.thyrsiflora*

3) Plant short (usually below 0,6m); inflorescence variable, lax to very dense panicle; leaves narrow (usually less than 2cm broad), glabrous to hairy, annual. ....II) *W.paniculata*

SPECIES DESCRIPTIONS

I) *Wachendorfia thyrsiflora* Burm. in "Wachendorfia" (1757).

Synonym: *W.elata* Salisb. Prodr.45 (1796).

Pre-Linnaean synonym : *Asphodelus latifolius* Breyne. Prodr.3.p22.t. (1739).

Rhizomatous perennial herb; 0,6-2,5m tall.

Rhizome : Irregular, usually cylindrical, up to 15cm long, composed of numerous extensions, all of which seem to be perennial. Overlapping leaf bases sheath rhizome, roots sprout from nodes. Numerous root hairs present. Lateral buds produce new rhizome (ramets).

Leaves : Perennial, erect, lorate to lanceolate, deeply plicate, firm, glabrous, usually shorter than the flowering stem, up to 90cm long and 8cm broad. Younger plants with leaves less than 5cm broad.

Leaf anatomy : No distinct palisade layer; intermediate lignification of cuticle; poorly developed sclerenchyma caps on vascular bundles; kidney-shaped subsidiary cells; large mucilage canals.

Stem and branches: Annual flowering stem up to 2,5m tall, stout (up to 1,5cm diameter near base), erect, densely pilose at the base (hairs up to 4mm long) running into short (1mm long) glandular hairs near apex. Peduncles many, short (up to 10cm), regularly spaced on distal half of axis. Younger plants often more laxly branched. Seldom more than 7 pedicels per peduncle. No second degree peduncles.

Bracts: Lanceolate, scarious, recurved, persistent, 1-4cm long.

Inflorescence: Dense cylindrical panicle, up to 60cm long and 20cm wide.

1) <u>Tepals</u>: Bright yellow, nectar guides on base of upper three tepals light to dark. All slightly spoon shaped. Outside uppermost tepal narrower and shorter than the rest, slightly recurved. Measurements variable, tepal lengths from 12mm to 28mm, widths from 8mm to 14mm. Upper five tepals ovelapping, leaving lower somewhat isolated. Tepals may or may not be fringed with orange cilia.

2) <u>Stamens</u>: Filament long, three-quarters of tepal length, from 15mm to 20mm long, spreading. Anthers nearly protruding, 2mm long and 1mm wide, dehiscing longitudinally.

3) <u>Gynoecium</u>: Ovary yellowish, 2-3mm long, 1-2mm wide. Style 13-18mm long.

Fruit: A typical 3-angled capsule; 10mm long, 10mm deep, 7mm wide.

Seed: Large, up to 5mm long, oval or kidney shaped. Dense microscopic blisters (1,5um) on seed hairs.

Flowering time: Beginning of September to end of November, occassionally to mid-January, with a peak in September and October.

Chromosome number: n=15 (Ornduff 1979).

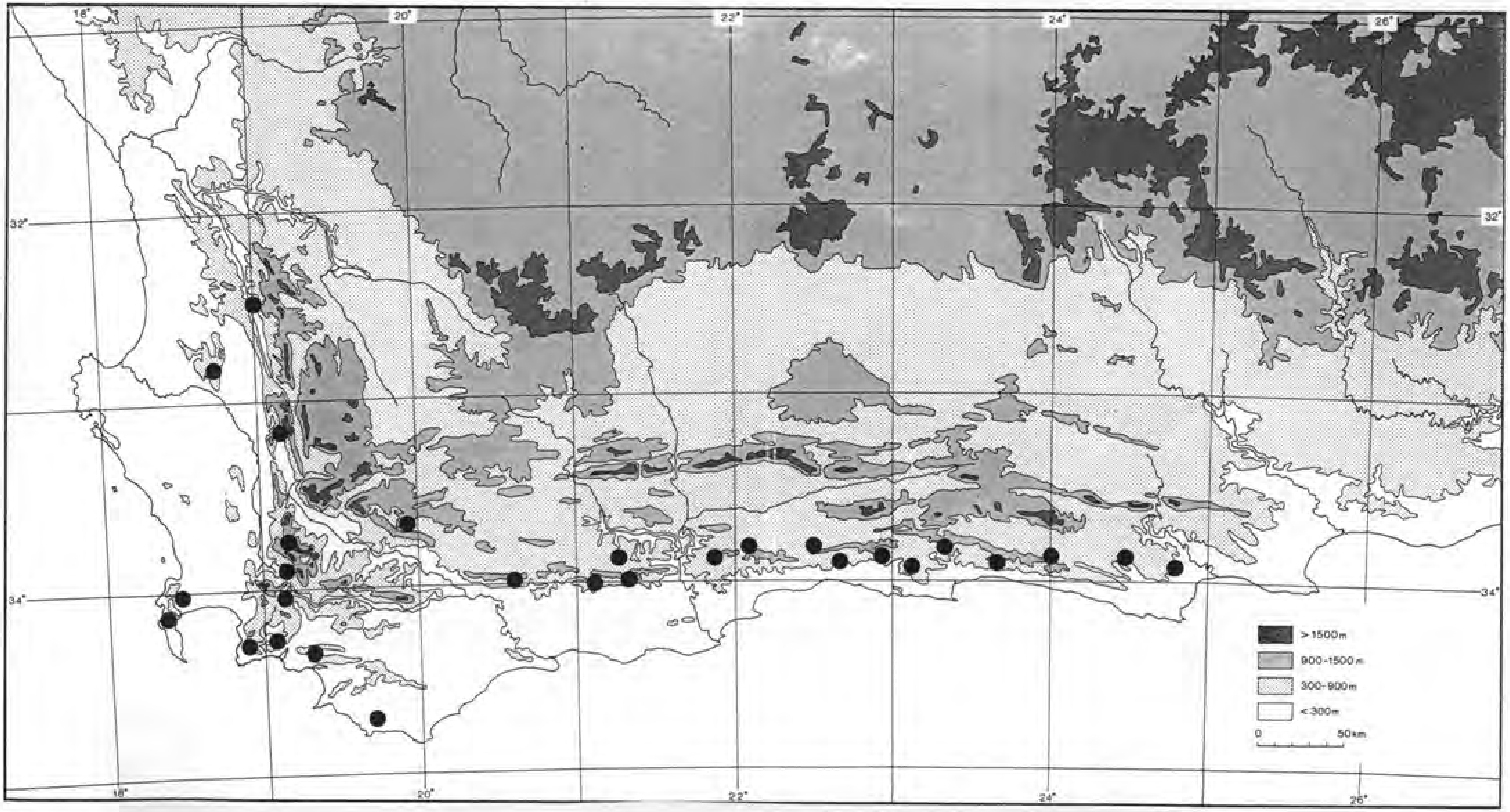
Distinguishing Features: Large size, habitat, large yellow flowers with long spreading stamens, inflorescence a dense, cylindrical panicle, peduncles short.

Distribution and Habitat: *W. thyrsiflora* is a widespread species, occurring from as far north as the Olifants River valley between Citrusdal and Clanwilliam, south to the Cape Peninsula, inland to the Franschoek mountains, and along the south coast and associated mountain ranges as far east as Humansdorp (Figure 17). This species is more of a habitat specialist than any of the other species, and is confined to permanently moist sites, especially along streams and in seepages. The species has a wide altitudinal range, varying from about 50m a.s.l. to about 1200m a.s.sl.

Status: Locally common, but some populations are very small and may be declining due to afforestation of mountain fynbos streams. Wetlands are vulnerable to alien invasion, and *Acacia longifolia*, *A. mearnsii*, *A. melanoxylon* and *Phragmites* spp. are commonly found invading suitable streamside habitat, often to the exclusion of *W. thyrsiflora*. The populations in mountain fynbos are generally stable, as these areas suffer less from the negative influences of man.

Sample specimens examined:

- **3218** (Clanwilliam): Piketberg, *Pillans 8086* (BOL).



G.P.S (L).

Figure 17 Distribution records for *W. thyrsiflora*

- **3319** (Worcester): Bainskloof, *Leighton 1353* (BOL); Elgin, *Levyns 3368* (BOL).
- **3423** (Knysna): Between Knysna and Oudtshoorn, *Liebenberg 7923* (PRE).
- **3424** (Humansdorp): Humansdorp, *Liebenberg 7923* (PRE).

II) *Wachendorfia paniculata* Burm. in "Wachendorfia" (1757).

Type : No holotype named, but an illustration (!) was included so this may be designated the iconotype. This description was probably based on material collected by Oldenland, which is now in the Geneva Herbarium.

Synonyms : *W.graminifolia* L.f. (1781). Type : Near river at Drakenstein. *Thunberg*. (Thunberg Herbarium, Uppsala. Microfiche #1242 !(BOL)).

W.graminea Thunberg. (1807). This is an illegitimate name, as it describes the same specimen as was used by L.f. when describing *W.graminifolia*.

W.hirsuta Thunberg. (1807). Type : Sandfields between Swartland and Saldanha Bay. *Thunberg*. (Thunberg Herbarium, Uppsala. Microfiche #1243 !(BOL))

W.tenella Thunberg. (1807). Type : Between Langevlei and Heerenlogenment. *Thunberg*. (Thunberg Herbarium, Uppsala. Microfiche #1246 !(BOL))

W. brevifolia Solander in Ker Gawl (Bot.Mag.t.1166)(1809). Type : In the Banksian Herbarium (BM). There is an illustration (!)with the description which may be designated an iconotype.

W. herbertii Sweet. (1826). Hort.Brit.ed.3.p400. I was unable to trace this publication and I am thus unsure about whether a type was designated.

A rhizomatous perennial herb, 10 - 90cm tall, very variable.

Rhizome : Ovoid, up to 5cm in diameter, appears tunicate when dry.

Leaves : Annual, variable morphology; narrowly lanceolate or linear to broadly falcate, erect or spreading, dull green to yellow-green, glabrescent to hairy, three-nerved, up to 70cm long (some forms only 10cm long, 0,5cm wide), up to 3,5cm broad (usually less than 2cm broad).

Leaf anatomy : Palisade layer one cell thick; intermediate lignification of cuticle; very variable sclerenchyma cap development; rectangular subsidiary cells; small mucilage canals.

Stem and branches : Variable, stem occasionally up to 1m tall, slender to robust (3-15mm diameter), erect, covered with short, dense simple hairs. Peduncles variable in number and length, longer at the base (may be branched again to form a second degree peduncle), up to 40cm lomg, slender to robust. Pedicels short (less than 10cm).

Bracts : Scarious (often submembranous when fresh), often recurved, especially when old, 0,5 - 5cm long, veined, long-acuminate, pilose, partly sheathing.

Inflorescence : Variable; lax to dense racemose panicle, composed of 5 - 20 scorpid cymes; each cyme bears 1 - 7 flowers. (See Figure 18).

i) **Tepals** : Variable; apricot, yellow, or orange, slightly scented. Lower inner tepal often slightly broader than the rest. Upper outer tepal shorter, narrower, recurved. Margins may or may not be fringed with short cilia. Measurements : (4,0-) 10,0 (-16,0)mm wide; (13,0-) 21,0 (-31,0)mm long.

ii) **Stamens** : From two-thirds to three-quarters the tepal length, spreading. Anthers 2mm by 1mm.

iii) **Gynoecium** : Style 15 - 22mm long, as long as shortest tepal.

Fruit : Acutely three-lobed capsule; 10 by 10 by 5mm.

Seed : Spherical, coarsely pilose, brown, 2mm in diameter.

Flowering time : August to December, very rarely to early February (high altitude), with a broad peak extending through September, October and November.

Chromosome number : n=15 (Ornduff 1979)

Common name : Rooikanol or Spinnekopblom

Figure 18 Floral morphology and rhizome mor¯phology of *W.paniculata* : 1) ciliated tepal 2) filament and dehiscent anther 3) curved style and pubescent ovary. (Taken from a painting by Gower in BOL)

Distinguishing features : Plants from 15-80cm tall; bracts scarious when mature; stamens and style spreading, from two-thirds to three-quarters the length of the tepals; tepals broad; leaves usually shorter than the flowering stem.

Distribution and habitat : This is the most widespread species, found as far north as the Nieuwoudtville region, throughout the mountains of the south - western Cape, as far south as Agulhas and Cape Point, inland as far as Worcester, and as far east as Port Elizabeth. It appears to be entirely confined to the fynbos biome, and is found mainly on soils derived from Table Mountain Sandstones, although it has also been recorded from areas with granitic soils, alluvial sands, and clayey soils derived from Malmesbury shales. The species is found from sea level right up to about 1700m.

Surrounding vegetation types may include mesic and dry mountain fynbos, lowland fynbos on acid or alkaline soils, renosterveld, and strandveld. It is most common in younger vegetation (less than 10 years since last fire), probably because it favours less dense vegetation. The species does not have a requirement for permanent moisture, and can be found in areas ranging from seasonally dry sands to permanently moist shales. This ability to tolerate most environments is certain to be one of the major reasons for the success of the species.

Status : Locally abundant, but usually varies from sparse to common. This species is unlikely to become endangered in the near future due to its cosmopolitan range, varied habitats, and ability to thrive in disturbed (even ploughed) sites.

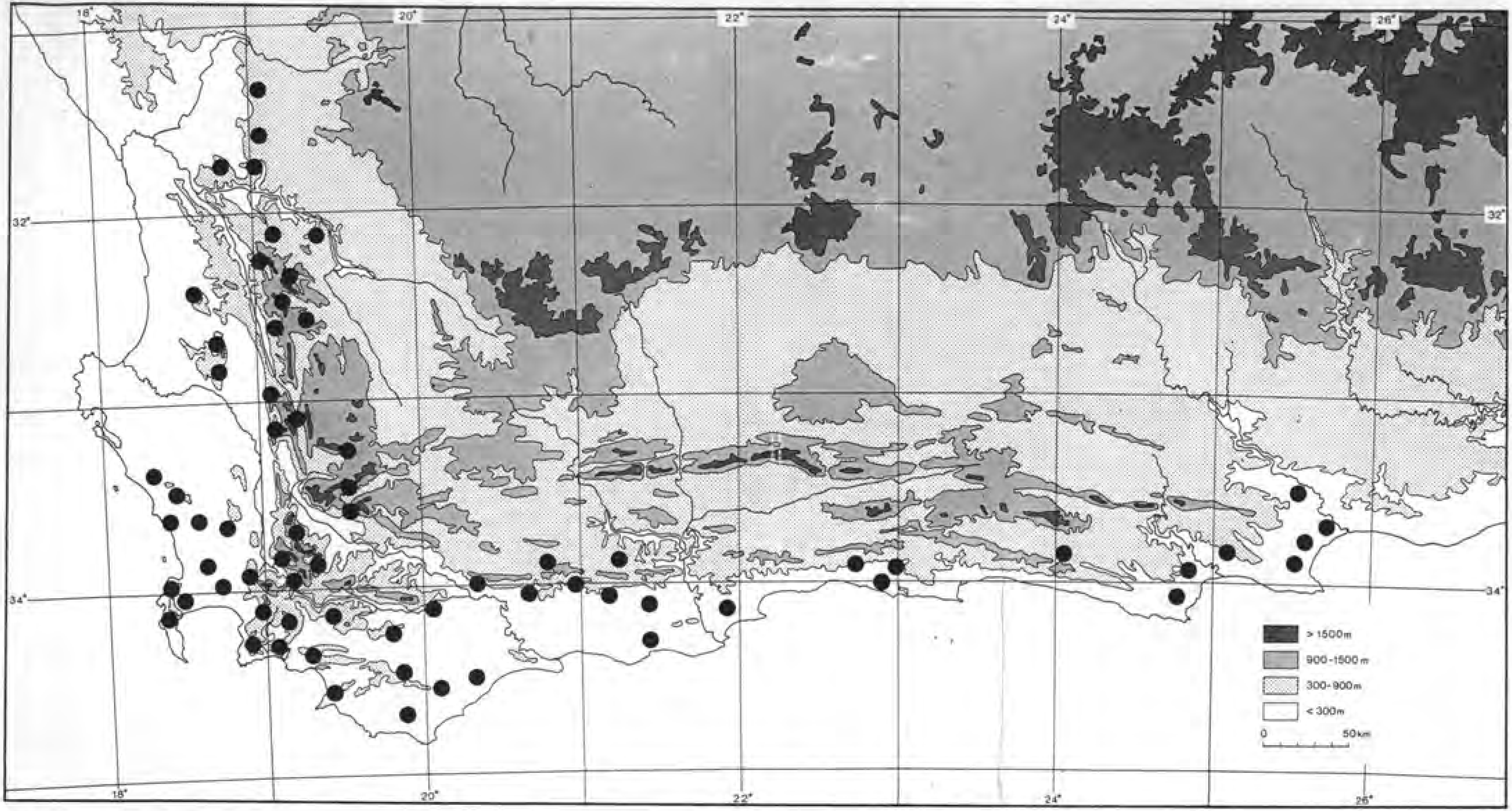


Figure 19 Distribution records for *W.paniculata* (typical form)

Variation within the species

W. paniculata is exceptionally variable with respect to plant size, leaf hairiness and shape, and flower size and structure.

Barker (1950) chose to ressurect *W. graminifolia* L.f as a distinct species, prior to examining all the specimens. The criteria that she used to distinguish this taxon from *W. paniculata* are unfortunately not discrete, *i.e.* they are continuously variable. There is a continuum of variation in all traits mentioned by Barker as reliable discriminators, for example, perianth length, plant robustness, leaf hairiness and width. Many plants show combinations of characters which make the separation of these two species, based on these characters, futile, *e.g.* a plant may be robust and have tepals 2,5 - 3cm long (both *W. graminifolia* characteristics), as well as narrow, hairy leaves (both *W. paniculata* characteristics). The various combinations are endless. For these reasons, plus others described under Observations, I view *W. graminifolia* L.f. as synonymous with *W. paniculata* Burm.

An extensive review of all available herbarium specimens shows that there is no temporal separation of flowering between the "varieties", nor is there any real geographic separation of the "varieties" . In addition, there is chromosomal evidence supporting the idea that all *W. paniculata* lookalikes are a single species, as chromosome number is constant for specimens from a wide geographical range, and exhibiting a wide range of morphological variation (Ornduff 1979). Further support for this idea is provide by a scatter plot of maximum tepal lengths for two putatively different species - *W. graminifolia* L.f. and *W. ciliata* Barker ms. (Figure 14). There is no clear cut distinction between the two groups, and it is in fact difficult to discern the presence of two separate groups within the diagram. This continuous variation is not indicative of two separate, formal species. The past splitting of *W.paniculata* into "varieties" (*e.g.*Baker 1896; Barker 1950) is thus not based on consistent, discrete traits, making it a redundant, non-predictive classification.

Stuessy (1990) defines "form" as "specimens with small genetic variations, not geographically correlated, and often growing with more 'typical' plants". Subspecies and varieties apply only to allopatric taxa, and the variation within *W.paniculata* should thus be described as forms. Stuessy (1990) also says that "form" should not be used in a formal sense , except for species of economic importance,*e.g.* crops. As *Wachendorfia* clearly does not fit into this category there is no sense in officially naming new forms, as it only adds to the taxonomic "jungle". However, in order to complete the picture, I would like to mention some of the apparent forms making up the "superspecies" *W.paniculata.* But before I do this I think I should mention this particularly trenchant quote from Rosendahl (1949), concerning the dangers of infraspecific taxonomy : "..., some authors when dealing with highly polymorphous groups seem to feel that it is necessary to take account of all variants that can be distinguished and fit them into a formal scheme. The trouble with this procedure is that in attempts to set up a series of units of descending rank, a point of diminishing returns is soon reached, beyond which confusion rather than clarification results. Such schemes may have something to commend them in theory but not in practice".

A fairly recognisable form may be something that we can call *W.paniculata* form *ciliata.* This form has been recorded from Kleinmond in the east, north to Mamre, and south to the Cape

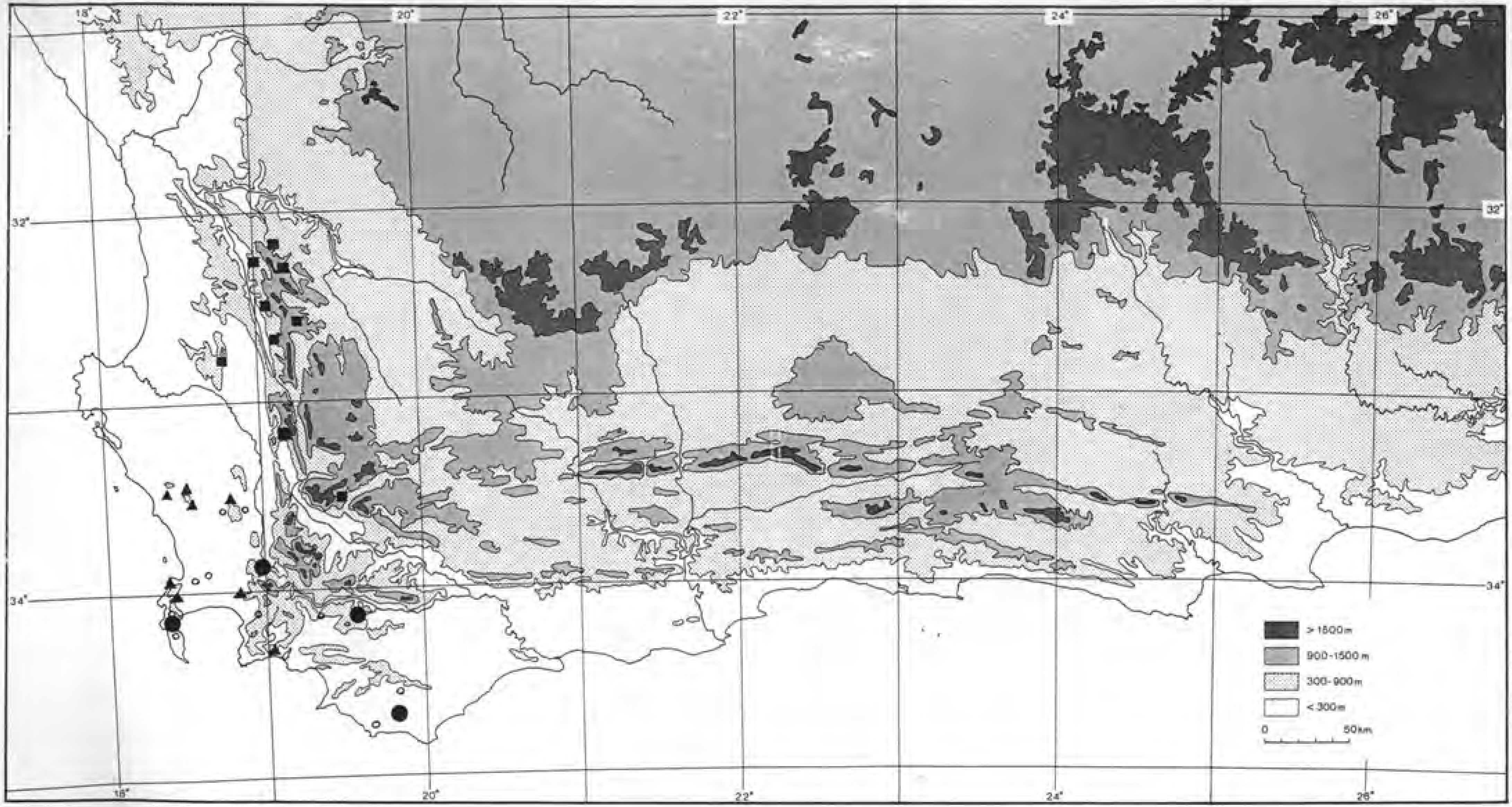


Figure 20 Distribution records for *W.paniculata* form *laxa* ■
W.paniculata form *ciliata* ▲
W.graminifolia ●

Peninsula (Figure 20), and is characterised by large tepals fringed with dark cilia. This feature could well be genetically controlled as these specimens are often found growing next to specimens without any tepal cilia. However, as I have noted, there is continuous variation for this and other characters in the plants, and the distinctness of the morph as a whole is doubted.

Specimens from the mountains between Ceres and Pakhuis Pass are frequently very tall, with extremely lax panicles and long, thin leaves. This is a high altitude area and is exposed to extreme climatic conditions, with cold winters and hot, dry summers, and this may somehow have produced the growth form. I suggest that this form be known as *W.paniculata* form *laxa*, although it does have a degree of environmental and geographical correlation, which suggests that this might be viewed as a subspecies (allopatric, genetically similar). However, the form is not strictly allopatric as the typical form of W.*paniculata* is known to occur in the area (Figure 19) and for this reason I would not recommend the use of a formal subspecific rank for this taxon. Genetic studies of the species are needed to sort out the confusing intraspecific relationships.

Many high altitude specimens flower very late, presumably as a result of spring coming later to the cooler areas. Specimens from the high plateaus of the Hex river mountains (*ca.* 1500m a.s.l.) are often dwarfed, with extremely short leaves, and have been recorded flowering as late as mid February.

A population along the Biedouw river (3219AB) was found to contain extremely tall, robust plants (about 1m tall). This could possibly be attributed to the fact that they were living in a dry area, where the only reliable water source was along the river, and their growth form was responding to the increased water supply.

Dwarf specimens with very narrow, hairy leaves can often be found growing together with more "typical" forms, for example in the hills above Glencairn, and I suspect that there may be some genetic base for this difference, making this yet another form. Some populations appear not to flower every year, and this phenomenon needs attention, as it seems strange to produce leaves but no flowers. Perhaps the rhizome is just recharging its photosynthate reserves, and waiting for some special cue for it to begin flowering. This cue does not seem to be adequate rainfall, as plants living in normally dry areas that experienced very good winter rains were recorded as producing leaves but no flowers.

SAMPLE SPECIMENS EXAMINED :

-3118 (Vanrhynsdorp) : Vanrhynsdorp area, *Rood 2605* (PRE)
-3119 (Nieuwoudtville) : Keyserfontein, south of Nieuwoudtville, *Goldblatt 7065* (PRE)
-3218 (Clanwilliam) : Clanwilliam, *Barker 1097* (NBG); Clanwilliam, *Le Roux 2623* (BOL); Clanwilliam, *Barker 5741* (NBG); Grays Pass, *Compton 2722* (NBG)
-3219 (Wupperthal) : Heuningvlei, *Esterhuysen 12073* (PRE); Pakhuis Pass, *Compton 9575* (NBG); Niewoudt Pass, *Hafstrom and Acocks 290* (PRE)
-3318 (Cape Towm) : Slopes above Clifton, *Levyns 10016* (BOL); Kirstenbosch, *Barker 169* (BOL); Mamre, *Barker 1769* (NBG); Ex hort.Kirstenbosch, *Barker 12/9/1938* (NBG); Kirstenbosch, *Compton 15377* (NBG); Mamre, *Esterhuysen 5244* (BOL); Mamre, *Levyns 2/10/1931* (BOL); Stellenbosch, *Bos 662* (PRE); Bothasig, *Malan 141* (NBG); Riebeek Kasteel, *Barker*

1105 (NBG); Mamre, *Lewis 9/9/1953* (SAM); Bakoven, *Barker 3236* (NBG); Camps Bay, *Barker 3864* (NBG)

-3319 (Worcester) : Mitchell's Pass, *Compton 11968* (NBG); Tulbagh, *Leighton 37* (BOL); Zachariashoek, *Haynes 711* (PRE); Tulbagh, *Esterhuysen 6076* (PRE); Tulbagh, *Theron 2025* (PRE); Wemmershoek Peak, *Esterhuysen 11269* (BOL); Waaihoek mountain, *Esterhuysen 8283* (BOL)

-3320 (Montagu) : Grootvadersbos, *McDonald 1506* (PRE); Swellendam, *Grobler 484* (PRE); Tradouwsberg, *Taylor 241* (BOL)

-3321 (Ladismith) : Garcia's Pass, *Galpin 4636* (PRE)

-3325 (Port Elizabeth) : Port Elizabeth, *Dahlstrand 2531* (PRE)

-3418 (Simonstown) : Vlakkenberg, *Compton 12648* (NBG); Chapmans Peak, *Barker 2709* (NBG); Schusterskraal, *Barker 3887* (NBG); Constantia Nek, *Barker 170* (BOL); Little Lions Head, *Barker 1741/36* (NBG); Boulders, *Leighton 34* (BOL); Cape Point, *Barker 4312* (NBG); Constantia Nek, *Barker 4283* (NBG); Claremont, *Barker 282* (NBG); Palmiet river mouth, *Boucher 701* (STE); Buffels Bay, *Hutchinson 671* (BOL)

-3419 (Caledon) : Greyton, *Rycroft 3368* (NBG); Hermanus, *Leighton 367* (BOL); Zoetendalsvlei, *Esterhuysen 5250* (BOL); Hagelkraal, *Fellingham 78* (PRE); Elim, *Frowein 16118* (PRE)

III) *Wachendorfia brachyandra* Barker in *Jl.S.Afr.Bot.*15: 41 (1949)

Type: Kirstenbosch, *Barker 1096* (NBG!)

A rhizomatous perennial herb, 10-65cm tall.

Rhizome : Small, globose to ovate-oblong, 5-20mm diameter.

Leaves : Annual; erect or spreading; linear to lanceolate, often falcate; glabrous; dark green to yellow green; up to 70cm long and 3,5cm broad.

Leaf anatomy : Poorly defined palisade layer consisting of one or two cells; light lignification of cuticle; variable sclerenchyma cap development; rectangular subsidiary cells; small mucilage canals.

Stem and branches : Stem, peduncles and pedicels slender (stem about 3mm in diameter), covered in short glandular hairs, seldom branches to form second degree peduncles. Flowering shoot usually less than 40cm long. Peduncles short near tip of axis, a few much longer at the bottom (up to 20 cm long).

Bracts : Mature bracts scarious; oblong ovate acuminate, almost sheathing, not recurved lower down; up to 8cm long; densely pilose.

Inflorescence : A lax panicle, from 6-17 pedicels per peduncle.

i) **Tepals** : Light apricot yellow, the markings dark; 12-20mm long, 4-14mm wide. Upper outer tepal smaller than the others, only slightly recurved. Cilia seldom present on tepal edges.

ii) **Stamens** : Clustered, not spreading; only half as long as tepals, 6-14mm long; anthers 2mm by 1mm.

iii) **Gynoecium** : Style short, not curving sideways very much, 7-12mm long.

Fruit : Dry capsule broader than long, three lobed, carpels obtuse.

Seeds : Spherical, coarsely hairy, 2mm diameter.

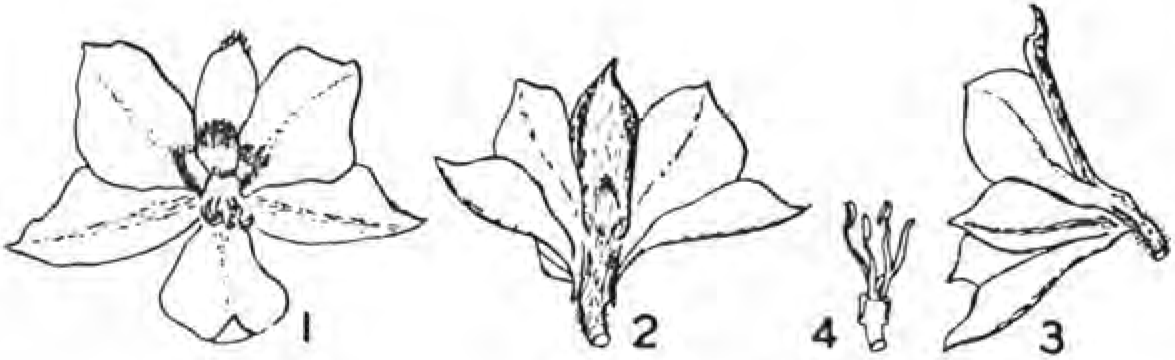
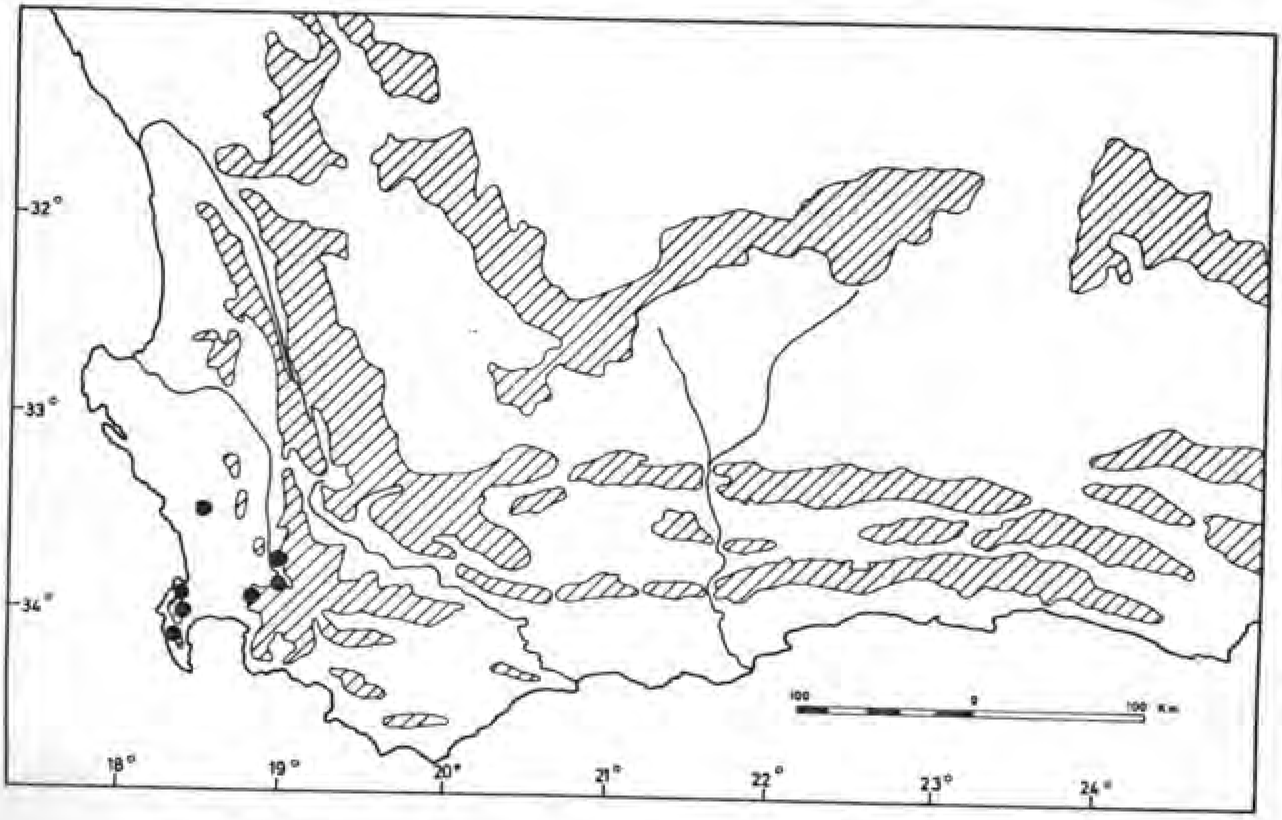


Figure 21 *W. brachyandra* 1) Flower, front view 2) Flower, back view 3) Flower, side view 4) Gynoecium, natural size

Figure 22 Distribution records for *W. brachyandra*



Flowering time : Late August to early December, with a peak in September and October.

Distinguishing features : Stamens and style short, half the length of the tepals, clustered; inflorescence lax; tepals pale yellow-apricot.

Distribution and habitat : This species has the most restricted range of all the species, and is confined to the extreme south western Cape, where it is found in the area between Mamre, Cape Point, and Stellenbosch. It is undoubtedly undercollected, and is so far known from altitudes ranging from 50m a.s.l. to about 600m, on either sandy or granitic soils. The species seems to favour damp sites, often growing in partial shade in forest margins, or in seeps and drainage lines in fynbos. The species also seems to be more common in recently burnt fynbos areas, but will persist for many years in a more open habitat (*e.g.*herbaceous margins of forests).

Status : Locally common, but with a sparse, scattered distribution. Due to the nature of its habitat, *W.brachyandra* may well become endangered, as swampy, moist areas are frequently drained for agriculture, buiding,etc.

SAMPLE SPECIMENS EXAMINED :

-3318 (Cape Town) : Kirstenbosch, *Barker 1096* (NBG)
-3418 (Simonstown) : Karbonkelberg, *Compton 16359* (NBG); Modderdam, *Salter 8718* (NBG); Constantia, *Purcell 90850* (SAM); Liesbeek river,*Salter 9046* (BOL)

IV) *Wachendorfia parviflora* Barker in *J. of S.A.Bot.* 15: 39 (1949)

Type: Camps Bay, *Salter 7457* (NBG!)

A rhizomatous perennial herb, 10-40cm tall, usually dwarf 10-20cm.

Rhizome : Annual, small globose-ovate oblong, 5-25mm in diameter.

Leaves : Annual; erect or spreading; linear to lanceolate, usually falcate and longer than the inflorescence; blue-green; softly hairy; up to 36cm long and 2,5cm broad.

Leaf anatomy : Palisade layer one cell thick; intermediate lignification of cuticle; well developed sclerenchyma caps; rectangular subsidiary cells; small mucilage canals.

Stem and branches : Stem short (usually less than 20cm); stem, peduncles and pedicels covered in short glandular hairs. Peduncles very short, densely clustered on axis.

Bracts : Herbaceous; green; always erect; often produced beyond the flowers.

Inflorescence : A very short, dense panicle.

i) **Tepals** : Dull yellow, fading brownish purple; segments narrow; 15-25mm long and 3-6mm broad. the upper segments usually broader than the rest; lowermost tepal very isolated.

Figure 24 Distribution records for *W.parviflora*

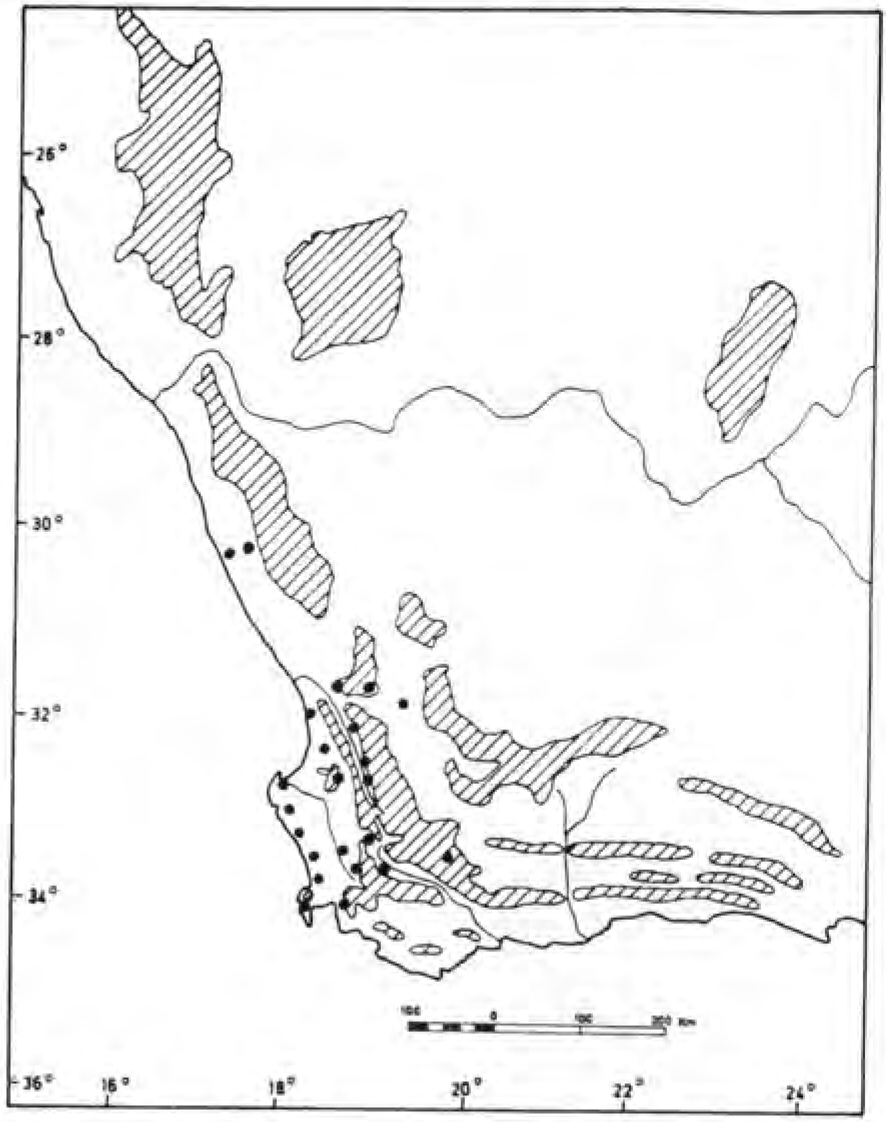


Figure 23 *W.parviflora* 1) Flower, front view 2) Flower, side view 3) Flower, back view

ii) **Stamens** : Two thirds the length of the tepals.
iii) **Gynoecium** : Two-thirds the length of the tepals.

Fruit : Capsule dry, broader than long; carpels obtuse, covered in glandular hairs.

Seeds : Globose, coarsely hairy, 2-4mm in diameter.

Flowering time : Early August to late September, with a peak in early September.

Distinguishing features : Dwarf habit, erect herbaceous bracts, tepals very narrow.

Distribution and habitat : *W.parviflora* is essentially a species of the western Cape, with records from Nieuwoudtville in the north, as far south as the Cape Peninsula, and as far east as McGregor. There is a record for near Soebatsfontein and another for 15km east of Hondeklipbaai (3017BB), which suggests that this species probably occurs all the way up the west coast as least as far north as Hondeklipbaai. This area is seriously undercollected and it is suspected that the species may also occur in the Kamiesberg.

W.parviflora grows on both sandstone and granite derived soils, and there are a few records from shale areas. The species is found at altitudes ranging from 50m a.s.l. to about 500m, in habitats ranging from dry, sandy hollows in coastal fynbos to moist, rocky ledges in thick mountain fynbos. It is often found in association with *W.paniculata* and does not have a requirement for damp sites.

Status : Uncertain, probably uncommon and sparse throughout its range. Appears to be replaced by *W.paniculata* in many seemingly suitable areas.

SAMPLE SPECIMENS EXAMINED :

-**3118** (Vanrhynsdorp) : Nardouw, *Johnson 236* (NBG)
-**3219** (Wupperthal) : Citrusdal, *Hanekom 1168* (PRE)
-**3318** (Cape Town) : Darling, *Barker 4600* (NBG); Kirstenbosch, *Barker 9/8/1935 (BOL)*; Camps Bay, *Salter 7457* (NBG)

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