SYSTEMATIC STUDIES ON THE SUBTRIBE DISINAE

(ORCHIDACEAE)

by

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INDEX

4. Taxonomic studies on the Disinae:

Abstract: Systematic studies on the Disinae.

The subtribe Disinae (Orchidaceae) has been revised over its whole distribution range (Sub-Saharan Africa and including the Yemen, Madagascar and Reunion). One hundred and sixty-five species arranged in 5 genera are recognized. Three new subspecies, 12 new species, 18 new series, 8 new sections and 7 new subgenera are described. Where deemed necessary, the species are grouped into subgenera, sections and series to indicate their interrelationships. Distribution maps were prepared for all the species, and the ecology and nomenclature of every species is discussed, while many are illustrated. The revision is based primarily on morphological data. In complex situations the variation is displayed by scatterdiagrams. Both artificial and natural keys are produced for the large genus Disa.

The grouping of the sections and genera is analysed both by computer-based phenetic analyses, using the BOLAID program, and by Hennigian phylogenetic studies. The eventual classification is based on the phylogenetic scheme. The groupings produced by the two methods are compared and discussed, and the theoretical bases of classifications are briefly discussed.

The phytogeography of the subtribe is analysed in some detail. Centres of endemism are delimited, and their interrelationships are analysed, together with the patterns of species and above-species richness. The history of the subtribe is analysed using the taxonomic rank of the disjunctions between the centres as an indication of the age of the disjunctions. The postulated history is then compared to modern ideas on the recent African palaeoenvironments. On this evidence it is suggested that the Disinae migrated northwards from an early diversification in southern Africa, and that the present patterns have been much influenced by climatic changes in the last 50 000 years.

Phylogeny and Classification of the Disinae (Orchidaceae)

INTRODUCTION

The Disinae (sensu Senghas 1974) form a natural assemblage of 165 species (Linder 1981a, b, c, d, e, f, 1980), readily distinguished from the other Orchidaceae by the more or less reclinate anther, projecting dorsally from the column, the dorsal and usually spurred median sepal and more or less sessile and pulvinate stigma. Although this group of taxa have been placed together since Lindley's (1830-1840) comprehensive treatment, the Satyrium group and occasionally other genera are sometimes included in the Disinae (Bentham & Hooker 1883; Schlechter 1901; Dressler & Dodson 1960). Pfitzer (1889) termed the group the Satyriinae.

There is no consensus in the literature on the number of genera recognized in the group. Lindley (1838, 1842) recognized six genera. Rolfe (1913) increased the number to eight, a treatment followed by Phillips (1926), Schelpe (1966) and Dyer (1976). Bolus (1888, 1893, 1896, 1911, 1913) and Schlechter (1895, 1901, 1915, only recognised three genera, while Bentham & Hooker (1883), Pfitzer (1889) and Senghas (1974) follow an intermediate approach. Although there have been three monographic treatments of the group (Lindley 1830-1840, Kraenzlin 1900, Schlechter 1901) there is at present no generally accepted infrageneric classification of the large genus Disa Berg., and no subgenera have been proposed. Linder (1981a et seq.) recognized five genera (<u>Disa</u> Berg., <u>Schizodium</u> Lindl., <u>Herschelia</u> Lindl., <u>Brownleea</u> Lindl. and <u>Monadenia</u> Lindl.) and subdivided the genus <u>Disa</u> into 15 sections organized into five subgenera.

In this paper the evolutionary base of this classification is discussed. As the order observed in nature, and reflected in biological classifications, is the product of evolutionary processes (Darwin 1859, Simpson 1961) it follows that the optimal classification should be consistent with evolutionary theory. However, the evolution of any group is a complex phenomenon (Gilmour 1961), with three major components (Simpson 1961, Sokal & Camin 1965, Mayr 1965):

(a) the branching pattern in the phylogeny created by speciation events, called 'splitting' by Simpson (1961) but preferably termed cladogenesis (Huxley 1957);

(b) evolution within taxa or clades, or 'any kind of change occurring sequentially in a single line of descent' (Simpson 1961: 201). Simpson called this 'progression', but Huxley's term 'anagenesis' has found more appeal;

(c) the timing of evolutionary events, called chronistics by Sokal & Camin (1965).

From these components the phylogeny of the group may be reconstructed. There are two dimensions of the phylogeny which can be measured and on which a classification may be based (Mayr 1965). These are (a) the cladistic component and (b) the patterns of genetic similarity of the resultant taxa. This includes both a patristic and a homoplastic component (Sokal & Camin 1965) and may be visualized as a time slice through the phyletic tree. The analysis of these two components provides the materials on which the classification of the group are based.

CLADISTIC RELATIONSHIPS

The branching pattern of the phylogeny is determined by grouping taxa into increasingly larger monophyletic groups - that is, groups including all and only the descendents of one ancestor (Hennig 1966, Platnick 1977, but see Ashlock 1974). Monophyletic groups are defined by shared uniquely derived character states (synapomorphies). The theoretical bases and methodology is discussed in detail by Hennig (1966), Kavanaugh (1972), Bremer & Wanntorp (1978) and Funk & Stuessy (1978).

The determination of primitive (plesiomorphic) and derived (apomorphic) character states is critical (see review by Stevens 1980, and Crisci & Stuessy 1980) and consequently the criteria used in every study should be stated explicitly (Crisci 1980). The criteria used in this study are:

(1) Plesiomorphous states are morphologically simple, while apomorphic states show bizarre specializations. These are what Bremer & Wanntorp refer to as 'obviously irreversible steps in the transformation series' (1978 : 319). In the Disinae these are frequently related to the pollination syndromes.

(2) Character distribution is widely used.

The preferable type, out-group comparison, (2a) was found to be particularly helpful with vegetative characters. In-group comparison (2b) has been strongly criticized, and was only used where no other method was available.

(3) Character correlation was used occasionally. If a state occurs rarely, restricted to taxa considered derived by other apomorphic states, it is also considered apomorphic.

The characters used are listed in Table 1. In the majority of the characters there is usually little doubt about the directionality of the change, using the criteria listed above.

Vegetatively, the 'Urtyp' of the Disinae is seen as something similar to the genus Orchis L., with two tubers, a single shoot, green strap-shaped spreading cauline leaves and a spicate inflorescence. The parallel development of sterile shoots in Disa and Satyrium Sw. in the tropical parts of the distribution ranges of these two taxa is interesting. The adaptive value and evolutionary history of this structure is not understood.

Out-group comparison is less helpful in the determination of polarity in the floral structures. For example, the absence of a spur on the dorsal sepal

TABLE 1. List of characters used for cladistic analysis, giving postulated plesiomorphic and apomorphic states. Where several apomorphic states appear to have been derived independently from the same lesiomorphic state, these are indicated by numerical subscripts. Where the same character state is thought to have evolved more than once, this is indicated by an asterisk after the apomorphic state.

Character		Pleisomorphic	Apomorphic	Criterion
Stolons	1	absent	present^{+}	2a
Sterile shoot	2	absent	present^{+}	2a
Basal sheaths	3	smooth	scabrid	2a
Leaves	4	cauline	basal^{+}	2a
	5	lorate	linear^{+}	2a
	6	numerous	- 4	2a
	7	green	hysteranthous	2a
	8	soft	ribbed^{1}	2a
			rigid^{2}	2a
Stems	9	mat	nitid	2a
	10	straight	flexuose	2a
Inflorescence	11	racemose	corymbose^{+}	2a
	12	oblong	capitate	2a
Floral bracts	13	green	dry	2a
Flowers	14	resupinated	not resupinated	2a
	15	numerous	- 5^{+}	2a
Median sepal	16	galeate	flat	2b
Spur	17	= sepal	obsolete^{+1}	2b
			X2 sepal^{+2}	2b

TABLE 1 continued.

Character		Pleisomorphic	Apomorphic	Criterion
Spur	18	horizontal	ascending^{+1}	2b, 3, 1
			pendent^{+2}	2b, 3
	19	cylindrical	massive^{+}	1
Petals	20	erect	reflexed^{1}	1, 2b
			falcate^{2}	1
	21	basal lobe small	large^{+}	1
	22	free	fused to galea^{1}	1
			fused to rostellum^{2}	1
Lip	23	oblong	linear^{1}	1
			spathulate^{2+}	1
			minute^{3}	1
			pandurate^{4}	1
			ovate^{5}	1
			fleshy^{6}	1
	24	entire	lacerate	1
Anther	25	horizontal	erect^{1}	2b
			pendent^{2}	2b
Rostellum	26	oblong, concave	hornlike^{1}	1, 2b
lat. lobes			square^{2}	2b
central lobe	27	small	absent^{1}	2b
			tall^{2}	1, 2b
			V-shaped^{3}	1
total	28	trilobed	Monadenia-type	1

TABLE 1 continued.

Character		Pleisomorphic	Apomorphic	Criterion
Viscidia	29	2	1	2a
Caudicles	30	Longer than pollen-mass	= pollenmass	2a
Tubers	31	present	absent	2a
Petals	32	included in galea	exserted	2b
	33	glabrous	villous	2a
Spur	34	On lip	On dorsal sepal	2a

should be plesiomorphic according to out-group comparison, but the absence of spurs is highly correlated with numerous other derived character states, and only occurs in obviously specialized taxa. Consequently, the spurs are considered to be secondarily lost. It is assumed that the plesiomorphic state for the perianth is the simplest state - the lobes equal, strap-shaped, flat, spreading.
The exception is the petal, where the prevalence of at least traces of a basal anticous lobe suggests that this structure is primitive.

Variation in the gynostegium is complex. The presence of two viscidia is plesiomorphic according to out-group comparison, but the structure of the rostellum is problematic. Again it has been assumed that the original structure was simple, three-lobed with the central lobe small.

Comparative morphological and anatomical studies across the Orchidoideae would be of great value, both testing the above hypotheses and providing the base for a better understanding of the evolution within the group.

The distribution of the character states in the subtribe is given in Table 2, and the resultant cladogram in Figure 1. It is clear that very extensive homoplasy, parallelism and convergence must have occurred, as there are numerous incongruencies.

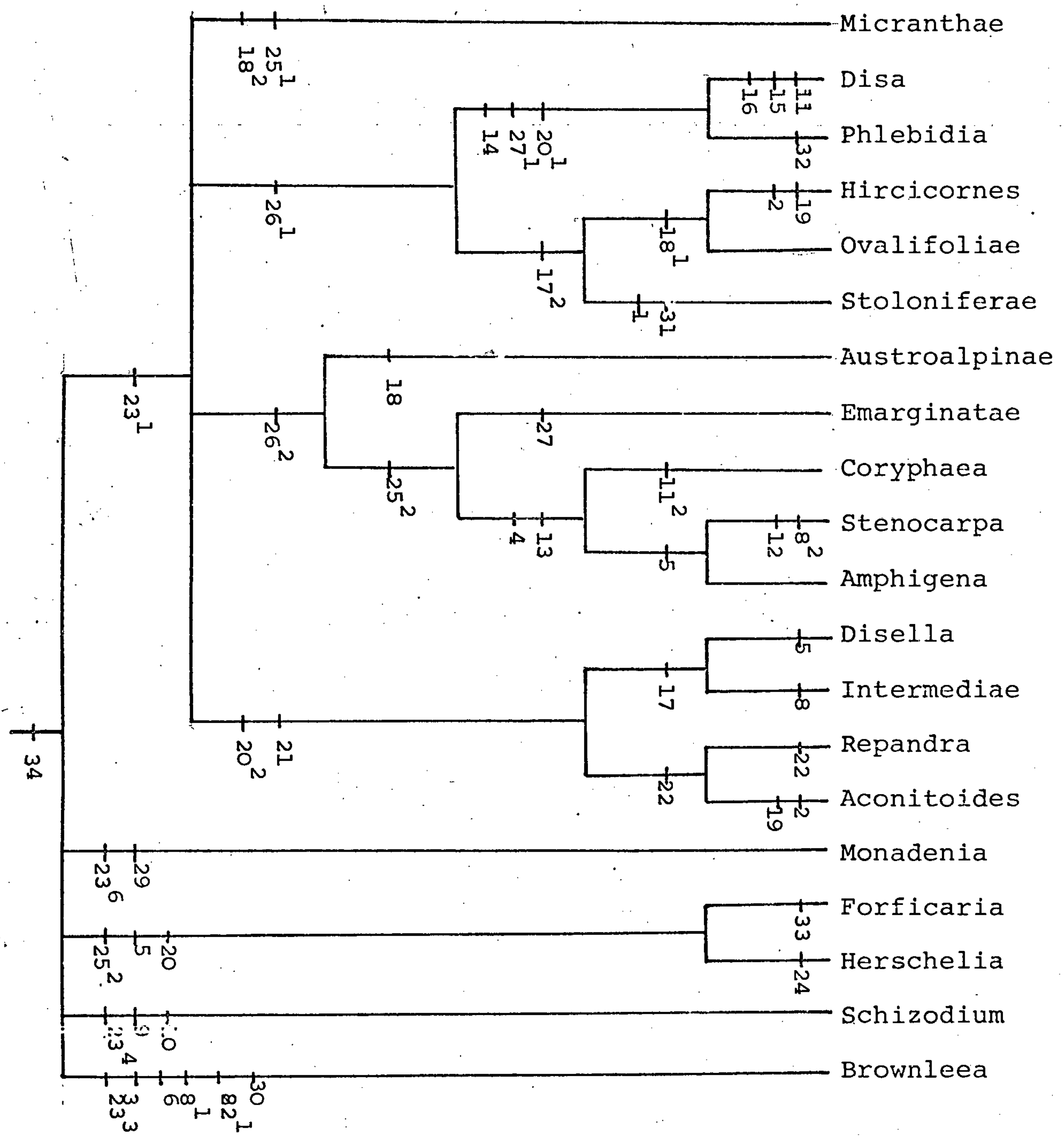
TABLE 2. Distribution of apomorphic character states in the sections of the Disinae. Where only a few species of the taxon possess the character, the character number is followed by a 'v'.

	Micranthae	Disella	Intermediae	Repandra	Aconitoideae	Hircicornes	Ovalifoliae	Amphigena	Coryphaea	Stenocarpa	Emarginatae	Austroalpinae	Stoloniferae	Disa	Phlebidia	Herschelia	Forficaria	Monadenia	Schizodium	Brownleea
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1^{+}													1	1v						
2	1				1	1														
3																				1
4^{+}								1	1v	1v		1		1v	1	1	1		1	
5^{+}		1						1		1v						1	1			
6																				1
7								1	1v	1v						1	1			
8										$1\overset{+}{v}$										1^{1}
9																			1	
10																			1	
11^{+}									1v					1v						
12										1v										
13								1	1v	1v						1	1			
14														1v	1					
15^{+}	1v													1v					1	1v
16	1v													1v						
17^{+}		$1\overset{1}{v}$	$1\overset{1}{v}$			$1\overset{2}{v}$	$1\overset{2}{v}$	$1\overset{1}{v}$	$1\overset{2}{v}$	$1\overset{1}{v}$			$1\overset{2}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	1^{1}	$1\overset{2}{v}$		$1\overset{2}{v}$
18^{+}	1^{2}		$1\overset{1}{v}$			$1\overset{1}{v}$	$1\overset{1}{v}$					$1\overset{1}{v}$						1^{2}		
19^{+}					1v														1v	
20		1^{2}	1^{2}	1^{2}										1^{1}	1^{1}	1^{2}	1^{2}			
21^{+}		1	1	1												1	1			

TABLE 2 continued.

	Micranthae	Disella	Intermediae	Repandra	Aconitoideae	Hircicornes	Ovalifoliae	Amphigena	Coryphaea	Stenocarpa	Emarginatae	Austroalpinae	Stoloniferae	Disa	Phlebidia	Herschelia	Forficaria	Monadenia	Schizodium	Brownleea
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
22				$1\overset{2}{v}$	$1\overset{2}{v}$															1^{1}
23	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	1^{12}	$1\overset{1}{v}$	$1\overset{11}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{1}{v}$	$1\overset{5}{v}$	1^{5}	1^{6}	1^{4}	1^{3}
24																1v				
25	1v								1^{2}	1^{2}	1^{2}							1^{2}		
26						1^{1}	1^{1}	1^{2}	1^{2}	1^{2}	1^{2}	1^{2}	1^{1}	1^{1}	1^{1}					
27											1^{2}			1^{3}	1^{3}	1^{1}	1^{1}	1^{1}		
28																		1		
29								1v										1		
30																				1
31													1							
32															1					
33																	1			
34	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

FIGURE 1. CLADOGRAM OF THE SECTIONS OF DISINAE. APOMORPHIES INDICATED BY CODE NUMBERS GIVEN IN TABLE 1.



Funk & Sruessy (1978) indicate that in analyses involving large numbers of taxa, the number of parallelisms and reversals increase rapidly, leaving very few uniquely derived apomorphic states on which to base the phylogenies. Stuessy (1979) experienced similar problems while working on <u>Melampodium</u>.
If the same apomorphic state has been derived independently in several clades, it could result in false synapomorphies (Bremer & Wannterp 1978).
In this study apomorphic states have been considered as independently derived if (a) they occur in taxa otherwise unrelated by all other apomorphic character states, and (b) they occur as rare phenomena in several taxa. The main phyletic lines are defined by uniquely derived apomorphic states, whilst independently derived apomorphic states are used to group taxa within phyletic lines. Vrba (1979) called these 'conditional synapomorphics', as they are conditional on the synapomorphics defining the major phyletic lines. La Duke & Crawford (1979) effectively used a similar method to utilize independently derived apomorphic characters.

The data are in several instances not adequate to resolve all the nodes to dichotomies. These are left as trichotomies or polychotomies (Bremer & Wanntorp 1978).

The degree of confidence in the monophyly of each group is a factor of our confidence in the character(s) used to delimit the group, and the number of autapomorphous characters of the group. Of course, unique synapomorphies carry more confidence than conditional synapomorphies.

The *Disella-Intermediae-Repandra-Aconitoides* has a rather low level of confidence. Although the group is based on two autapomorphies, both are conditional, and neither occurs in all the taxa included in the group. Similarly, the placing of the *Austroalpinae* into the *Stenocarpa* group is based on a single synapomorphy, namely the rostellum structure, which is minute in this group and difficult to interpret. *Stoloniferae* is also difficult to place, and may be found to be closer to *Stenocarpa*. The genus *Disa* is rather tenuously held together by a single rather broadly defined synapomorphy.

Using sections rather than species as the units in the cladistic analysis creates certain problems, due to the variability of critical characters within the units. Although this variability does give some indicaton of the constancy of characters, it makes a rigorous analysis difficult.

GENETIC RELATIONSHIPS

The genetic relationships among the taxa have to be inferred from the patterns of morphological or phenetic similarities (Gilmour & Turrill 1941, Mayr 1969). These are determined from the overall similarities of homological structures among the taxa, without taking the phylogeny into account (Burtt 1964, Sneath & Sokal 1973, Bock 1974, Davis 1978, McNeill 1979). Consequently this similarity contains both a patristic and a homoplastic component (Sokal & Camin 1965, Sneath & Sokal 1973).

Sneath (1971) noted that many of the misplacings in numerical phenetic studies have been due to the overriding effect of size. Because size is a factor in every dimensional character, it gets recorded many times, and so heavily weighted. Although size may be of some value, it is strongly influenced by environmental factors, and may be very variable in higher taxa (Sneath 1976). Hall (1969a) devised an algorithm for removing the size dimension, but in this study the problem was avoided by recording only shapes and ratios. Flower size is indicated by the lateral sepal length.

The selection of characters may be critical. Earlier studies suggest using at least 60 characters (Sokal & Sneath 1963) to override the effects of uneven sampling and functional homologies. Hall (1969a) suggested the use of deweighting to accomodate the homological characters, while Sneath & Sokal (1973) argue that the careful selection of unit characters may evade the problem. In this study characters were selected to reflect the appearance of each structure to avoid having to deweight.

All characters used were scored over a range, i.e. they are modal. As the items clustered are sections, including from one to 23 species, most characters exhibit a range of variation. Sneath's (1976) suggestion that coding must be chosen to preserve the desired components of phenetic resemblance is important. Where the range of variation is simple, it is represented by two strings of values, giving the extreme values, while for a complex range a third string of values giving the mode is added. Shapes were scored as degree of development, arranged, where possible from simple to complex.

The data were analysed using the BOLAID programme (Hall 1973). No deweightings were used. The degree of space-conservation around items may be selected. For studies where the items form a closed array the minimal amount of space should be conserved, as compared to studies on badly sampled material, where more items may need to be included (Hall 1969c). As the data in this study covered the whole subtribe, but was synthesized to sectional level, the array is almost closed, consequently 20% space conservation was used.

The characters used are listed in Appendix 1.

The resulting phenogram is given in Figure 2.

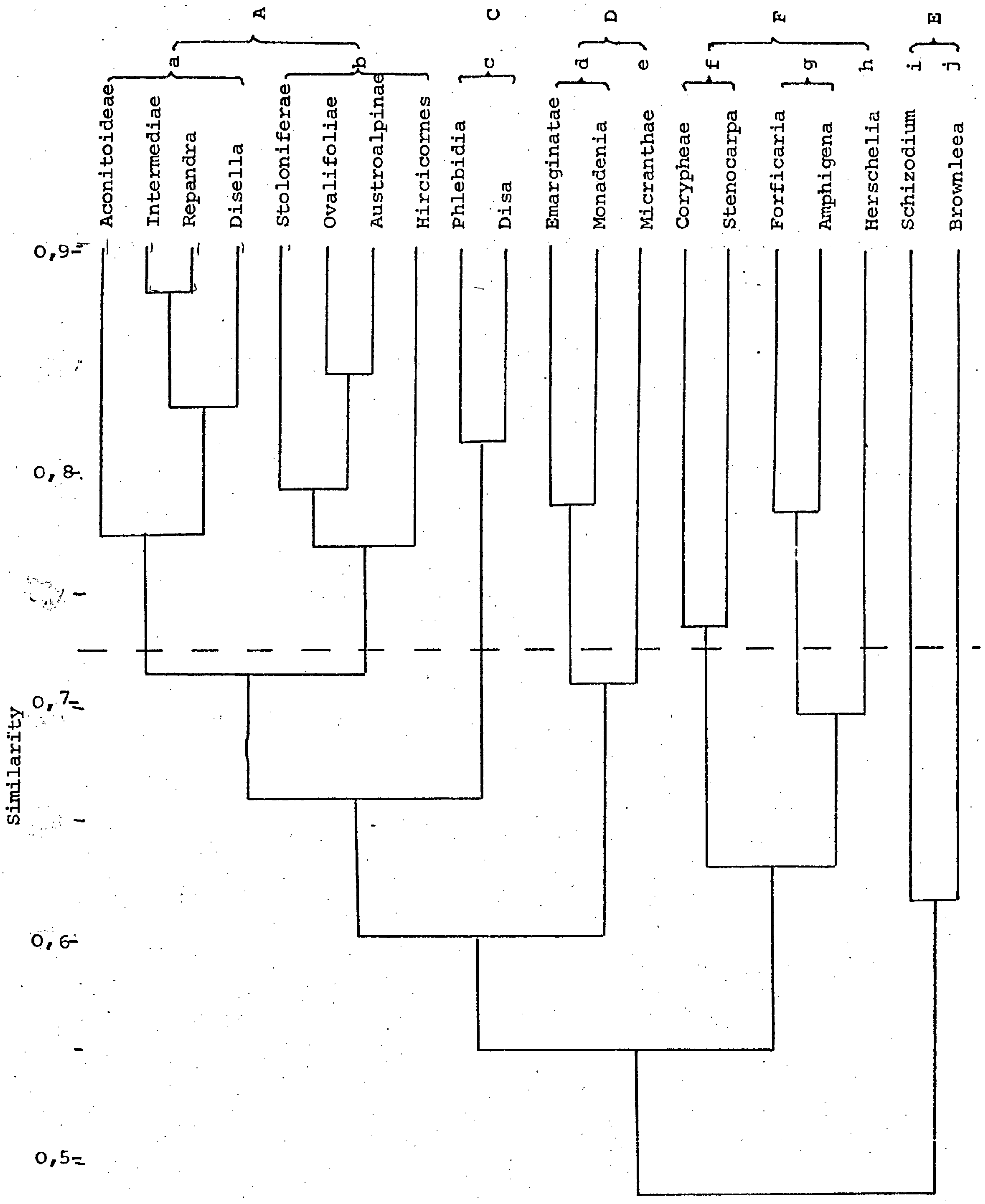


FIGURE 2. Phenogram, showing the phenetic relationships among the taxa. The phenonline is indicated as a broken line. The phenetic groups are indicated by letters above the phenogram.

DISCUSSION

There is substantial agreement between the phenogram and the cladogram. The differences are:

(a) Group F in the phenogram contains elements referable to the Herschelia and Stenocarpa groups in the cladogram. It appears as if the phenetic group is largely based on the shared presence of hysteranthous basal leaves and papery bracts. The substantial differences in flower, and specifically column structure, on which the cladogram is based, appear to have been overridden. Note that in the phenogram Amphigena links very close to Forficaria. Both are small groups, of three and two species respectively, and not very variable vegetatively. This similarity in taxonomic structure and variation range probably also affected the grouping. According to the cladistic analysis, this group F is then based on parallelisms.

(b) The phenetic group D includes three diverse elements, which hold in common green cauline vegetative strap-shaped leaves, with often small flowers in spicate inflorescences and with pendent spurs. In the cladistic analysis they are widely separated by rostellar characters. The leaf and spike characters used in the phenetic grouping are considered to be plesiomorphous, whilst the pendent spurs are the result of parallel evolution.

(c) Although the phenetic group B agrees substantially with <u>Hircicornis</u> of the cladistic analysis, it includes the <u>Austroalpinae</u> at a rather high level of similarity. In the cladistic analysis, <u>Austro-alpinae</u> are placed, with rather low confidence level, with the <u>Stenocarpa</u> group. The phenetic link is probably based on symplesiomorphies in the vegetative and inflorescence structures.

From the comparison of the phenogram and cladogram, the phylogeny of the group may be speculated upon. The major groups in the Disinae are based largely on a combination of the lip, rostellum, column and petal structures. This combination of structures probably controls the pollination syndromes. Although vegetative specialization has occurred in some instances, it cuts across the groups suggested by the floral characters (for example, the occurrence of separate sterile shoots, the presence of hysteranthous basal leaves and of papery bracts). Many of these vegetative specializations are restricted to certain climatic regions, consequently the possibility that they are the result of convergent evolution cannot be excluded. Within the major clades, further diversification appears to affect most structures, but the column - petal - lip pattern remains fairly constant.

This suggests that the evolution of the group may be understood as a series of 'groundplans', with further diversification within this groundplan being strongly canalized (Stebbins 1974, Brundin 1972). This series of groundplans is summarized in the cladogram (Figure 1).

On the basis of this understanding of the genetic, cladistic and phylogenetic patterns within the subtribe, three different types of evolutionary classifications are possible - phenetic, classical and cladistic (Hull 1970, Bock 1974, Mayr 1968). Of these, the first two classify grades, and the latter clades (Huxley 1957, 1958). The core of the disagreement among theoretical and practising taxonomists over the last two decades has been over which classification is optimal (Ashlock 1979, Mayr 1974).

An optimal classification may be defined as that classification which stores the greatest amount of information, is consilient over the greatest range of phenomena (Ruse 1979), allows for the retrieval of the maximal amount of information, and makes sound predictions (Gilmour & Turrill 1941, Gilmour 1951). Whether Linnaean classifications are scientific theories or not (Ruse 1973, 1979, Lovtrup 1973, Cracraft 1974, Mayr 1974), they have certain characteristics which influence their optimal performance:

(a) They are hierarchical. This implies that the classes in the classification are discontinuous. Taxa stored in the classification should ideally be discontinuous (Hull 1979).

(b) They are one-dimensional. Therefore, optimally only one data set can be stored in the classification. If several non-congruent data sets are stored in the same classification, some information must be lost (Wiley 1975).

(c) They are only logical frameworks. For any information to be retrieved from the classification, the principles and rules according to which data was placed in the classifications must be operational and explicit (Hull 1970, Brundin 1972).

Classical evolutionary classifications (Simpson-Mayr school) fare badly when compared to these criteria. In order to maximize the data on which the classification is based, both phenetic and cladistic data are used, and the resultant classification is a compromise, or is eclectic (Bock 1974). Such a classification is likely to be consilient (Ruse 1979), but it probably contains contradictory elements (Brundin 1972). Since there are no rules according to which the compromise between the two data sets is to be effected (Wiley 1975, McNeill 1979) it is not possible to retrieve the data on which it is built (Hull 1979), and it is also confusing (Wiley 1980).

Phenetic classifications have been much attacked by philosophers (Kitts 1977, Ruse 1979), but much of this criticism was directed at the extreme empirical and anti-theoretical stance of pheneticists in the middle 1960's (Sokal et al. 1965, Colless 1967). Logically, they fare much better than classical classifications: they are one-dimensional, and they explicitly classify grades. However, the taxa are not discontinuous (McNeill 1979), Sneath & Sokal 1973), and so information is lost when the groupings are forced into a hierarchical classification. The terminology used for phenetic classifications is vague: of major importance is the meaning of 'similarity'. Phenetic similarity includes many components: symplesiomorphy, synapomorphy, parallelism and convergence. This vagueness in a key concept limits the number of testable deductions that may be made from the classification. In addition, by being strongly empirical, it relies heavily in induction, a form of logic which has long been suspect.
By eschewing the use of the theory of evolution, such classifications cannot be related to or used for work done under the theory.

Cladistic classifications satisfy the three criteria, and therefore give the best fit to Linnaean classifications. Criticisms have been raised both against cladistic methodology and cladistic classifications.

The criticisms against cladistic methodology have by now been mostly rejected, and we are more concerned with criticisms of cladistic classification. The major ones are: (a) that they are information-poor (Sneath & Sokal 1973). This is in comparison with phenetic classifications; (b) that they lead to complex classifications (McNeill 1979).
If the original Hennigian dictum (1966) that every furcation should be given rank were followed, this would indeed be true; but this is no longer applied (i.e. Bremer 1976); (c) some ancient taxa are given high rank, out of proportion of their phenetic isolation. This ranking is information rich, and is therefore valuable.

Overall, cladistic classifications appear to be superior to the competing types of classification, as they clearly state on what evidence the groupings are formed, and what the confidence level of the groupings are. In addition, there is little doubt about what deductions may be made from the classification, and what deductions would be meaningless.

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APPENDIX 1

Characters used for the phenetic analysis.

1. Presence of stolons
2. Presence of sterile shoots
3. Distribution of leaves: cauline, basal or radical
4. Time of production of leaves, relative to flowering time
5. Rigidity of fresh leaves
6. Number of leaves
7. Glossiness of stems
8. Flexuosity of stems
9. Inflorescence shape
10. Number of flowers per inflorescence
11. Dryness of floral bracts or anthesis
12. Shape of median sepal
13. Concavity of galea
14. Length of spur relative to median sepal
15. Clavateness of spur apex
16. Relative thickness of spur
17. Spur at base pendent, horizontal or ascending
18. Spur at apex pendent, horizontal or ascending
19. Lateral sepal length
20. Lateral sepal orientation
21. Petal orientation
22. Petal curvature
23. Relative size of the basal abaxial lobe on petals

24. Shape of petal apex
25. Degree of fusion between petal and rostellum
26. Degree of fusion between petals and median sepal
27. Lip shape
28. Length of lip stalk
29. Degree of serration of lip margin
30. Orientation of lip
31. Angle of the anther
32. Number of viscidia
33. Shape of rostellum lateral lobes
34. Shape of rostellum central lobe
35. Presence of lateral flaps on the rostellum
36. Presence of staminodes
37. Length of stigma pedicel
38. Angle of stigma
39. Degree of development of the lip hypochile, mesochile and epichile.

Synopsis of the generic and infrageneric classification of the Disinae

The Disinae (Orchidaceae) occur widespread in subsaharan Africa. The subtribe has been revised in sections (Chapter 4). The genetic and cladistic relations among the genera and sections in the subtribe are discussed in Chapter 1. The classification, given below, is based on the cladistic relationships in the subtribe.

Disinae Benth. (Excluding the Satyrium alliance sensu Dressler & Dodson, 1960).

- Monadenia Lindl.
- Disa Berg.
  - Subgen. Micranthe (Lindl.) Linder
    - Sect. Micranthae Lindl.
  - Subgen. Falcipetalum Linder
    - Sect. Disella Lindl., Intermediae Linder, Repandra Lindl., Aconitoideae Kraenzl.
  - Subgen. Hircicornu (Kraenzl.) Linder
    - Sect. Hircicornis Kraenzl., Ovalifoliae Linder, Stoloniferae Linder
  - Subgen. Stenocarpa (Lindl.) Linder
    - Sect. Amphigena H. Bol., Coryphaea Lindl., Stenocarpa Lindl., Austroalpinae Linder
  - Subgen. Disa
    - Sect. Disa, Phlebidia Lindl.
- Herschelia Lindl.
  - Subgen. Herschelia
  - Subgen. Forficaria (Lindl.) Linder
- Schizodium Lindl.
- Brownleea Lindl.

Key to the genera of the Disinae:

1. Lip minute, erect in front of the column; petals fused to the galea .... Brownleea

1. Lip not as above, petals free from the galea:

    2. Lip pandurate; stems usually sharply flexuose ... . Schizodium

    2. Lip not as above; stems straight or slightly flexed:

        3. Rostellum with a single viscidium:

            4. Leaves green, cauline .... Monadenia

            4. Leaves dry at flowering time, basal:

                5. Flowers blue; lateral sepals longer than 6 mm .... Herschelia

                5. Flowers white; lateral sepals shorter than 6 mm .... Disa

        3. Rostellum with two viscidia:

            6. Leaves basal, usually hysteranthous:

                7. Flowers blue or white with blue veins; petals with well-developed basal anticous lobes .... Herschelia

                7. Flowers reddish or pure white; basal anticous lobes small or usually absent. .... Disa

            6. Leaves green, spread on the stem. .... Disa

The Phytogeography of the Disinae

(Orchidaceae)

in Africa

INTRODUCTION

In the past two decades our understanding of the phytographical patterns in Africa has been greatly advanced. Nine chorological regions, several of them further subdivided into domains, are generally recognised (White 1965, 1971, 1978, Chapman & White 1970, Wickens 1976, Werger 1978, Brenan 1978). There is still disagreement on the precise boundaries and ranks of the various chorological units. In addition, the historical development of the various chorological units and their constituent taxa in Africa are poorly understood. In this paper the Cape and Afro-montane Regions are investigated in terms of the descriptive and historical phytogeography of the Disinae (Orchidaceae), which are widespread in Subsaharan Africa.

The boundaries and affinities of the Afro-montane Region have not been adequately clarified. The Region consists of several disjunct areas, generally quite crudely indicated on maps. The maps published by Wickens (1976) and White (1971, 1978) disagree in detail, especially on the extent of the Afro-montane Region in Southern Africa. The relationship between the Afro-montane and Sudano-Zambesian Regions is somewhat contentious, with some authors suggesting that the Afro-montane Region is a facies of the chorological unit in which it occurs (Letouzey 1968, Hilliard 1978). Several studies on the historical phytogeography of areas and taxa in the Afro-montane Region (inter alia Wild 1968, Kerfoot 1975, Clayton 1976, Ayodele Cole 1974, Hamilton 1974) have led to a partial understanding of the generalized pattern of historical phytogeography of the Region. However, more studies are needed to test the hypotheses already in existence, and to provide more data, especially on the history of herbaceous plants.

The relationship between the Afro-montane Region and the Cape Region is still controversial, although numerous studies and reviews have documented the interconnections between the floras of the two Regions (inter alia Weimarck 1940, 1941, Levyns 1937, Wild 1968, Oliver & Baker 1967, Rourke 1980, Killick 1963). Some phytogeographers consider the Cape Region to be distinct at the rank of Kingdom, while the remainder of the African floras are included in the separate Palaeotropical Kingeom (Good 1953, Takhtajan 1969, Taylor 1980); others include it as Region in the Palaeotropical Kingdom (Goldblatt 1978). There has been extensive discussion on the origins and affinities of the Cape Flora (Adamson 1948, 1958, Levyns 1958, 1964, Goldblatt 1978 for a review). Although the general consensus is that the Cape flora is ultimately an African flora, with the more primitive taxa occurring to the north, no comprehensive narrative explanation of the origin and history of any Cape taxon has as yet been produced.

A detailed analysis of the Disinae (Orchidaceae) may well cast light on several of these problems. The group has recently been revised (Linder 1981a, b, c, d, e, f). The plants are almost exclusively terrestrial herbs, including about 165 species which are widespread in the Cape and Afro-montane Regions. Groups of species also occur in the Zambezian Domain of the Sudano-Zambezian Region, and in the Madagascan Region.

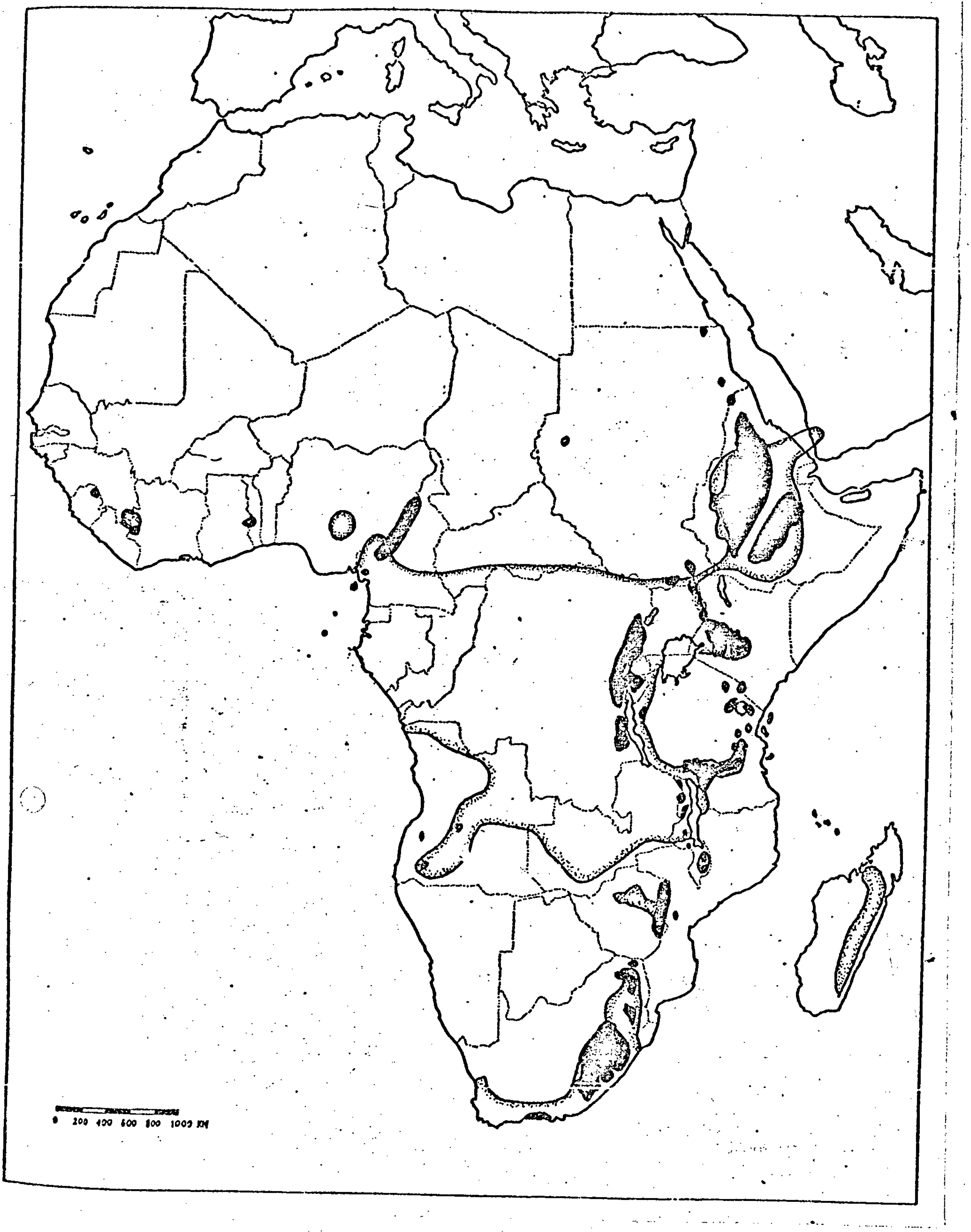

Figure 1. Total distribution of the Disinae in Africa (outline), with the Afro-montane regions (according to White, 1978) indicated in black.

CENTRES OF ENDEMISM

In Africa, 11 more or less isolated geographical areas may be delimited in the Afro-montane and Cape Regions. These are the Western and Southern Cape Province, the Natal Drakensberg and Transvaal Drakensberg in South Africa, the Eastern Highlands in Zimbabwe, the Angolan highlands, the mountains of the southern Rift Valley (southern and western Tanzania, northern Zambia and Malawi), the East African Highlands (Uganda, Kenya and northern Tanzania), the Bamenda Plateau in Cameroon and eastern Nigeria, the highlands of West Africa, the Ethiopian highlands and the mountains of Madagascar.

The centres of endemism for the Disinae in these areas were determined by comparing the species lists for each area. A centre is characterized by a large percentage of endemic taxa (more than 30% of the local species). Subcentres were detected by superposing the distributions of the constituent taxa. Geographic areas that contain few species and very low levels of endemism are regarded as outliers of the centre from which the majority of the species are derived. Between the major centres are areas of change, that may be regarded as overlap zones. These areas contain few endemics, and some of the constituent species link the area to the one centre, while the remainder link it to another centre.

Six centres and one overlap zone have been recognized. (Figure 2).

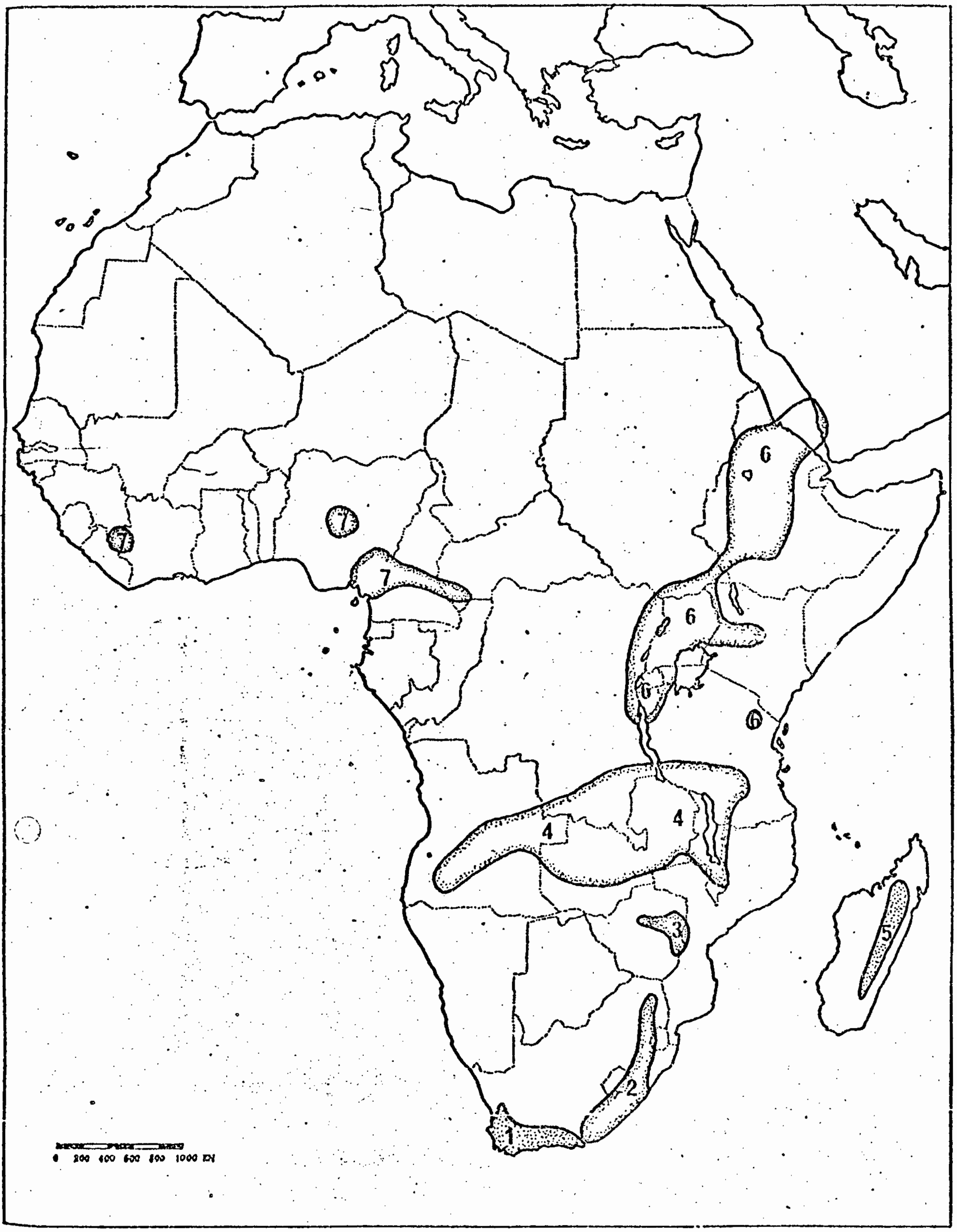

Figure 2. Distribution of centres recognized in Africa: 1, Cape Centre; 2, Natal-Transvaal centre; 3, Zimbabwe overlap region; 4, South-central African centre; 5, Madagascan centre; 6, East African centre; 7, West African outlier. The Reunion centre is not indicated.

Cape Centre

The area encompassed by this centre agrees with the 'Cape Floristic Region' as defined by Goldblatt (1978), but extends eastwards to include Grahamstown. In this area 98 species of Disinae have been recorded, of which 89 (90%) are endemic. The non-endemic species fall into the following groups:

(a) Taxa common in the Natal-Transvaal centre, which only enter the Cape centre at Grahamstown and extend to the coast at Knysna. These taxa, which are regarded as part of the Natal-Transvaal flora, are *Disa polygonoides*, *D. woodii*, *D. chrysostachya*, *D. aconitoides* ssp. *aconitoides*, *Monadenia brevicornis* and *Brownleea recurvata*.

(b) A single species extending from the mountains of the southern Cape through the higher mountains of the eastern Karoo to the western foothills of the Lesotho Drakensberg - *Disa porrecta*.

(c) A single species widespread from the dry sandy coastal flats near Clanwilliam (Western Cape) to the Eastern Highlands in Zimbabwe - *Disa cornuta*.

(d) Typically Cape species that extend up the Transkei coast on outcrops of Table Mountain Sandstone, to southern Natal - *Disa sagittalis* and *D. tripetaloides* ssp. *tripetaloides*. Hilliard (1978) documents some Cape Compositae entering Natal along this route.

To date there have been two attempts at recognizing phytogeographic groups within the Cape flora. The first attempt was Drége & Meyer (1844) on the basis of Drége's extensive collections, while the second was by Weimarck (1941). Monographers have often analysed the phytogeography of their taxa by the groups and centres recognized by Weimarck (Dahlgren 1963, Nordenstam 1969).

In the Disinae it was found that only eight species are ubiquitous in the Cape centre. The remaining 83 species can be grouped into two centres, both of which may be further subdivided. For the lists of species recorded from each centre, see Appendix 1.

The Western Subcentre extends from the Kamiesberg to the Hottentots Holland mountains in the Caledon Division, and inland to the Great Swartberg, but does not include the Langeberg. This group includes 51 taxa. The subcentre may be subdivided into a northern area of 12 taxa, which includes the Cedarberg, Piketberg and the Ceres and Worcester Mountains, and a southern area covering the Cape Peninsula and Caledon Division with some species ranging further afield. Twenty-three taxa have been recorded from this area. However, it is frequently difficult to assign any species definitely to one of these areas, and a large proportion of the species range over the whole Western Subcentre. A certain interdigitation has to be recognized between the areas. The southern area is particularly rich in highly localized taxa; four have been recorded from the Hottentots Holland mountains.

There are three outliers of the Western Subcentre:

(a) Four species have been recorded from the Kamiesberg in Namaqualand, one of which is endemic. Weimarck (1941) recognized the Kamiesberg as a subcentre of the Northwestern Centre.

(b) A single species (Disa draconis) has been recorded from the Roggeveld mountains, along the escarpment of the Great Karoo. Although the existence of 'fynbos' has not been recorded from the Roggeveld mountains (Acocks 1975), Weimarck (1941) listed the locality as an outlier of the Cape flora, on evidence in Diels (1909).

(c) The Swartberg range, between the Little and Great Karoos, is problematic. Eleven species have been recorded from the mountains. Four species are ubiquitous, two group with the southern Subcentre, while five belong to the Western Centre. The area is isolated from the Western Subcentre by the low mountains to the east of the village of Montague, and from the Southern Centre by the plains of the Little Karoo.

The Southern Subcentre extends from the Cape Peninsula and Franschhoek mountains along the coastal mountain ranges (Langeberg, Outeniqua and Tsitsikamma mountains) to Humansdorp. The Disinae occurring on the plateau between the mountains and the sea are also included in this Subcentre. This subcentre includes 29 taxa. The greatest species richness occurs in the Humansdorp area, and several taxa are endemic to the area. In total, 11 species are restricted to the area between Swellendam and Humansdorp, while 17 species extend to the Cape Peninsula.

Williams (1972) showed that the two broad phytogeographic groups recognised in Leucodendron (Proteaceae) correspond to the two major climatic regimes found in the Cape Region: a summer drought regime and an all-year rainfall regime (Weather Bureau 1972). If the all-year regime is extended to include the summits of mountains receiving clouds from the south-easter winds which prevail in the summer months, and which result in extensive cloud condensation (Marloth 1903, Boucher 1978), the Southern Subcentre corresponds with the all-year rainfall system, while the Western Subcentre has a period of summer drought. The systems overlap in the Caledon and Cape Peninsula areas, including the Franschhoek mountains, where the summits and south-facing slopes

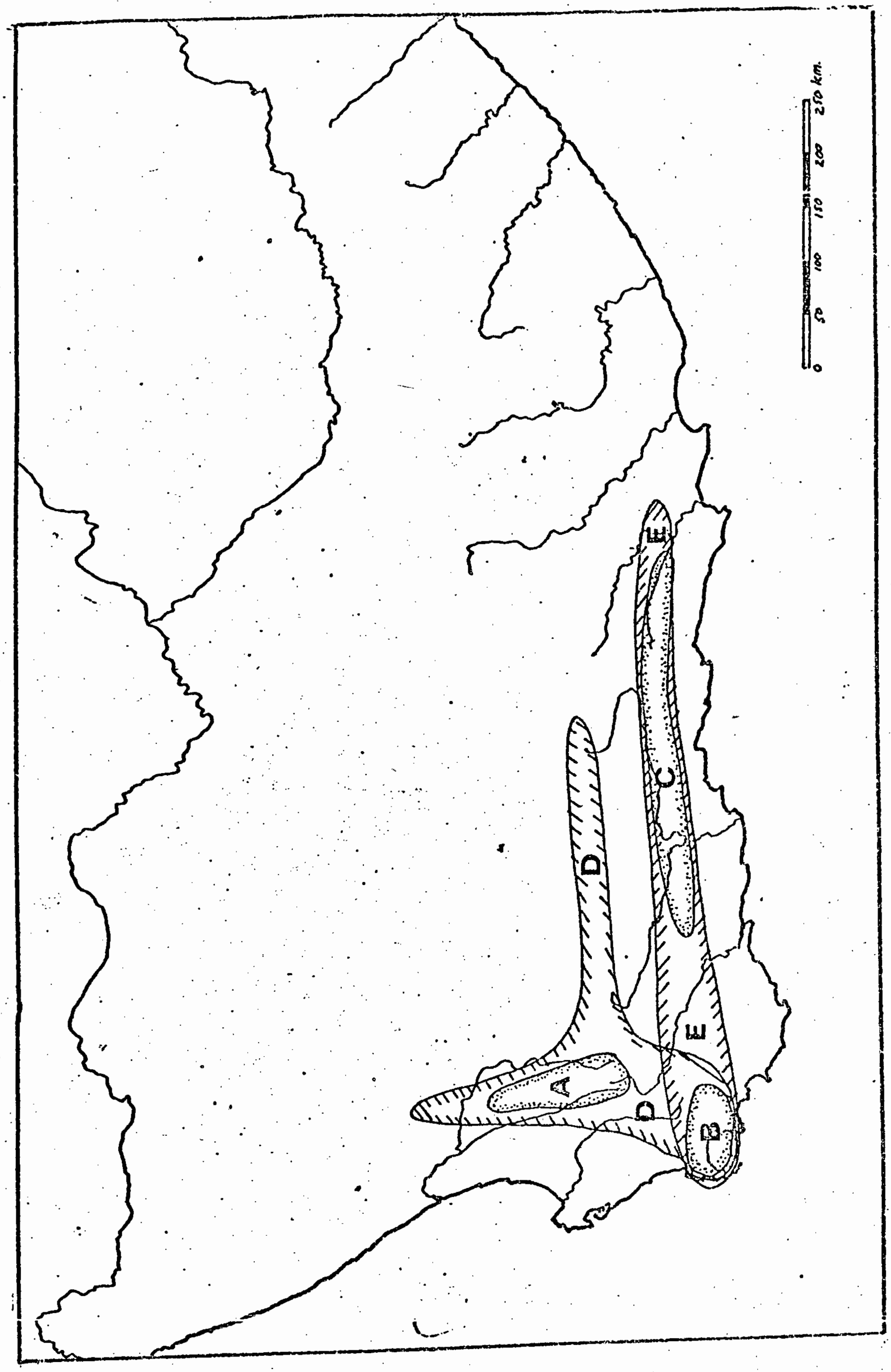

FIGURE 3. Phytogeographical regions recognized within the Cape Centre. D = Western Subcentre, E = Southern Subcentre, A = northern area and B = southern areas of the Western Subcentre, while C = area of endemics to the Southern Subcentre.

receive cloud condensation in the summer months, while the lower slopes and north-facing slopes are dry during the summer months.

If the number of species occurring in each half-degree square are recorded, it is found that the mountainous areas in the Cape centre generally support about 20 species per half-degree square, except in the grids where the southern and western subcentres overlap: here the average figure is 40,5 species. Levyns (1952) remarked that this increase may be considered as a characteristic of the Cape flora. Oliver, Linder & Rourke (in prep.) show that this pattern is widespread.

Natal-Transvaal Centre

This centre includes most of the uplands of Natal and the Transvaal Drakensberg, and extends southwards into the Transkei and the eastern Cape Province, to King Williams Town. Fifty-two species of Disinae have been recorded from this area. Twenty-nine species, or 56%, are endemic. The non-endemic taxa fall into the following groups:

(a) Nine species extend into the Cape centre: these have been discussed above.

(b) Fifteen species are also known from Zimbabwe. Some of these species (i.e. *D. woodii*, *D. rhodantha*, *D. patula* var. *transvaalensis*) are relatively rare in Zimbabwe, and are best regarded as extensions of South African taxa. Other taxa (i.e. *D. cornuta*, *Brownleea galpinii* ssp. *galpinii*) are equally common in both areas. A third group of species are common north of the Limpopo River, but are rare in South Africa (i.e. *D. zimbabweensis*, *D. welwitschii* ssp. *welwitschii*).

(c) Twelve species are widespread in Southern and South-central Africa, and generally reach the Natal-Transvaal centre through Zimbabwe, although one group (*D. similis* and *D. caffra*) is only known from South-central Africa and the Transkei-Natal coast, but is absent from Zimbabwe. The minority of the widespread taxa (i.e. *D. hircicornis*, *D. welwitschii* ssp. *welwitschii*) are rare in the Natal-Transvaal centre, while the majority of the widespread taxa are centered in the Natal-Transvaal centre, but extend far northwards (*Monadenia brevicornis*, *Disa fragrans* ssp. *fragrans*, *D. versicolor*, *D. saxicola*, *Herschelia baurii*, *Brownleea* parviflora).

These figures indicate that a Natal-Transvaal centre can be recognized as being more or less distinct from the South-central African centre. The majority of the endemic species are found in the Natal Drakensberg and the uplands between Kokstad and Bergville. These species are frequently also found in the uplands around Wakkerstroom on the Natal - Transvaal border and the 'highveld' in the Belfast region.

It has been found impossible to recognize subcentres in the Natal - Transvaal centre, although there is some replacement of species along the north-south axis in the Drakensberg. Several outliers can be recognized.

(a) The Amatole Mountains in the King Williams Town area, including the Winterberg near Tarkastad. These mountains have a rich flora including 17 species of Disinae, all belonging to the Natal - Transvaal centre. The area is separated from the nearest outliers of the Transvaal - Natal centre by 130 km, but the flora of the relative nearby Zuurberg (at Grahamstown) groups with the Cape centre.

(b) The mountains of Northern and Western Transvaal: the Waterberg and Soutpansberg. These mountains have a generally impoverished flora of Disinae, with no endemic species. Weimarck (1941) regards the higher mountains in the Lydenburg area

(Mt. Anderson) as an outlier of the Drakensberg flora, but the presence of a very rich flora of Disinae, and several endemic species (Disa alticola, D. amoena, D. aristata) suggests that these mountains are still very much part of the Natal - Transvaal centre.

Hilliard (1978) in a comprehensive analysis of the descriptive phytogeography of the Compositae of Natal, found high levels of endemism in the Drakensberg. Many of the endemics are taxonomically isolated, and Hilliard found that the links to the northern Afro-montane Regions are very tenuous. However, she does not present evidence on the supra-specific distribution tracks. Killick (1963, 1978) presents data to show that the Natal Drakensberg flora is more allied to the flora of the Cape Region than to the flora of the Chimanimani mountains in Zimbabwe.

South-Central African Centre

This centre covers the watershed between the River Zaire and the Zambezi and extends into the highlands between Lake Malawi and Lake Tanganyika, including the Southern Highlands of Tanzania. Thirty-eight species have been recorded from this area, of which 17 (45%) are endemic.

Of the non-endemic species, six are widespread in tropical Africa, while six extend southwards into Zimbabwe and occasionally into South Africa. Only one species extends exclusively northwards. In three polytypic species the northern and southern sub-species meet in northern Zambia and southern Tanzania (D. erubescens, D. aconitoides, D. welwitschii). Two species (D. similis and D. caffra) show a peculiar distribution interval to South Africa; it is discussed above. One species (Disa versicolor) occurs on the Huilla Plateau in Angola, and is then disjunct to Zimbabwe and South Africa.

The majority of the endemic species are widespread in the centre, usually reaching Angola in the west and Tanzania in the east. Previous discussions on the phytogeography of the area separated the centre into the Nyika Plateau and the associated high mountains around the northern margin of Lake Malawi, including the Southern Highlands of Tanzania, and the watershed between the River Zaire and the Zambezi, that is the Mbala - Shaba - Copperbelt area. Goldblatt (1977) in his study on Moraea (Iridaceae) explicitly recognizes these two areas as distinct centres. Exell & Wild (1961) note that in the Mbala - Shaba region 'it seems that in some way conditions are specially favourable for the production of new species'. This most certainly holds for the Disinae. There are six endemic species of Disinae on the Nyika Plateau and the high mountains around Mbeya. This endemism is associated with a remarkably rich orchid flora: Williamson (1979) recorded 148 species of orchids from the Nyika Plateau, an area of only 625 km^2. Hedberg et al. (1980) also noted that the plateau has a remarkably rich flora. Williamson (1979) suggests that the main affinities of the Nyika orchid flora lies with the montane and upland orchid floras of East Africa, but that it also acts as a link between the southern and northern Afro-montane orchid floras.

Despite the obvious heterogeneity of the region as defined here, there are too many endemic species common to both the Nyika upland area and the watershed region to allow the two areas to be profitably separated.

The Disinae of the West African mountains are considered as an outlier of the South-central African centre, while the Zimbabween flora is ecotonal or intermediate between the South-central African and the Natal-Transvaal centres.

West Africa

This area includes Mt. Camaroon the Bamenda Highlands, the highlands in Central Nigeria (Jos Plateau), and the Guinean Highlands. Only eight species have been recorded from this area, one of which is endemic (13% endemism). The affinities of the area are indicated in Table 1.

TABLE 1. The distribution ranges of the Disinae of West Africa

	Guinean Highlands	Jos Plateau, Nigeria	Bamenda Plateau	S - Central Africa	Uganda
Disa ochrostachya			X	X	X
D. welwitschii ssp. *occultans*	X	X	X	X	X
D. erubescens			X	X	X
D. equestris		X	X	X	
D. nigerica			X		
D. hircicornis		X	X	X	X
D. perplexa		X	X	X	X
Brownleea parviflora			X	X	

These data indicate that the Bamenda Plateau is the centre of the region, with outliers extending westwards. The flora has stronger affinities to the south (seven species) than to the east (five species). Morton (1972) recorded 47% endemism on the West African mountains. Eighty-five percent of the endemics are restricted to single mountain complexes. This high degree of endemism is not borne out by the data on the Disinae. Hamilton (1974) summarized data to show that the SE Nigerian highlands have their greatest floristic affinity to East Africa. These findings are supported by a detailed analysis of the phytogeographic patterns of the savanna flora of the Guinean Highlands (Ayodele Cole 1974).

The Zimbabwe Overlap Zone

Although 23 species of Disinae have been recorded from the highlands of Zimbabwe (Chimanimani mountains and escarpment mountains to the Inyanga mountains, and extending along the ridge westwards to Salisbury), only one species (<u>Herschelia</u> <u>chimanimaniensis</u>) is endemic. Wild (1964) reported an endemism level of 4,6% for the flora of the Chimanimani mountains, comparable to the 4,4% here recorded for the Disinae. This remarkably low figure indicates that, although the Eastern Highlands of Zimbabwe are geographically isolated from the South African montane areas by the Limpopo valley, and from the South-central African montane areas by the Zambesi valley, the Disinae have not diversified sufficiently for it to be recognized as an independent centre.

The 22 non-endemic taxa show greater affinity to the north than to the south: eight species are exclusively distributed in Zimbabwe and to the north of Zimbabwe, six exclusively have a southern extension, while eight taxa occur both to the north and to the south of Zimbabwe.

There are two not very clearly differentiated components in the Zimbabween Disinae: a montane component that follows a distribution track along the escarpment mountains, occasionally extending into South Africa (i.e. *Disa saxicola* and *D. zombica*), while the other component is a more or less lowland component, with the plants growing in edaphic grasslands. These taxa follow a generalised track along the ridge between Inyanga and Salisbury, and extend to the River Zaire - Zambezi watershed area, and the *Brachystegia* woodland further to the north (i.e. *Disa aconitoides* ssp. *concinna*, *D. welwitschii* ssp. *welwitschii*, *D. hircicornis* and *D. equestris*).

East-African Centre

This centre extends from Mt. Kilimanjaro northwards to include the Kenyan uplands, the Ruwenzori mountains and the uplands of Uganda, and the highlands of Ethiopia. The area is quite poor in species, including only 13 taxa, of which 4 (31%) are endemic. The non-endemic taxa are all common to the South-central African centre, and it may well be argued that the East African centre is merely an outlier of the South-central African Centre.

Of the endemic taxa, one (D. pulchella) is recorded only from Ethiopia, with a single collection from the Yemen, two occur in the higher regions of the East African mountains, extending via the high peaks in Eastern Uganda (Mt. Poroto and Mt. Napak) to the Ethiopian highlands (Disa scutellifera and D. fragrans ssp. deckenii). One species is restricted to the subalpine zone on all the East African peaks (D. stairsii).

Weimarck (1941) distinguishes three subcentres in this region: the Kenyan subcentre, the Kivu subcentre and the Abyssinian sub-centre. He regards the Rudolf depression as being of some importance, but it appears as if the Disinae relatively easily circumvent the depression along the eastern Ugandan peaks and the Imatong mountains of southern Sudan.

Madagascar Centre

From the island of Madagascar seven species have been recorded, of which three (43%) are endemic. The remaining species are all common to the Natal-Transvaal centre.

Weimarck (1941) considered Madagascar together with Reunion as an independent centre. All the species which he considered were endemic to Madagascar, but the species of Aristea (Iridaceae) (Weimarck 1940) are closely related to taxa found in Natal. Schlechter (1925) in a survey of the known taxa of orchids from Madagascar found an endemism level of 78%. At least some of this high level of endemism is due to a narrower species concept than employed here, as Schlechter (1901, 1925) did not record any species of Disinae common to South Africa and Madagascar. Schlechter recognized the affinities between Africa, specifically South and East Africa, and Madagascar. Wild (1975) listed the known shared species between Madagascar and Africa, showing 12 species are shared with N.E. Africa, compared to the 33 spared with southern Africa. Leroy (1978) reviews copious evidence on African-Madagascan links, and notes that the closest affinities of the Madagascan flora is to Africa.

Reunion Centre

As the single species of Disinae recorded from Reunion (Disa borbonica) is endemic to that island, and is not at all related to the Disinae on Madagascar, Reunion must either be regarded as an independent centre, or as part of the Cape centre. Levyns (1937) also recorded a Cape ally - Stoebe passerinoides (Compositae) - from the island.

Conclusions

The patterns of species richness, endemism and shared taxa are summarized in Table 2. From this it is evident that both species richness and endemism decrease northwards. It is also apparent that diversification, and the resultant high numbers of endemic species, has occurred in some areas (most obviously in the Cape centre, the Natal-Transvaal centre and South-central African centre), while other apparently also suitable areas have not witnessed similar phenomena (i.e. Zimbabwe, the West African highlands and the East African highlands). Genetic diversity, as measured by the number of supra-specific taxa, also decreases northwards.

TABLE 2. Species richness, levels of endemism and affinities among the centres.

	Cape	Natal-Transvaal	Zimbabwe	South-central	E. Africa	W. Africa	Madagascar	Reunion
Cape	99	11	3	0	0	0	1	0
Natal-Transvaal		52	15	9	3	3	3	0
Zimbabwe			23	15	4	5	2	0
South-central				39	9	7	2	0
E. Africa					12	6	1	0
W. Africa						8	0	0
Madagascar							7	0
Reunion								1
No. endemics	89	29	1	17	4	1	3	1
% endemics	90	56	4	45	31	13	43	100
No. sections	11	10	7	7	4	3	3	1
No. subgen.	5	5	4	4	3	3	3	1
No. genera	4	4	4	3	2	2	3	1

CLADISTIC PHYTOGEOGRAPHIC ANALYSIS

In order to reconstruct the history of the migrations of the Disinae in Africa, the cladistic component of the phylogeny of the subtribe is related to the distribution of the centres and intervals recognized in the previous section. The taxonomic rank of the taxon pairs that replace each other across the intervals should be related to the age of the interval. Therefore, by the relative dating of the intervals, the history of the migrations can be inferred.

Supra-specific Groups

The distribution of the supra-specific taxa recognized in the Disinae in the centres of endemism in Africa is given in Table 3.

At the generic level three groups emerge: the genus *Disa* is ubiquitous in the whole distribution area of the subtribe. Centered in the Cape centre are the genera *Monadenia*, *Herschelia* and *Schizodium*, while *Brownleea* is strictly tropical. *Herschelia* and *Monadenia* extend into the Natal - Transvaal and South-central African centres, the latter with one species, while the former has diversified somewhat in the north. *Schizodium* and *Brownleea* do not cross the interval between the Cape and Natal - Transvaal centres (except for some isolated populations

Table 3. Distribution of genera, subgenera and sections of Disinae in Africa. X indicates that several species are present and - that the taxon is rare.

	W. CAPE	E. CAPE	NATAL-TRANSVAAL	SOUTH-CENTRAL	E. AFRICA	MADAGASCAR	REUNION	W. AFRICA
Genera								
Disa	X	X	X	X	X	X	X	X
Monadenia	X	X	-			-		
Herschelia	X	X	-	X				
Schizodium	X	-						
Brownleea			X	X	-	X		-
Subgenera of Disa								
Micranthe		-	X	X	X	X		X
Falcipetalum	X	X	X	X	X			X
Hircicornes	-		X	X	X	X		-
Stenocarpa	X	X	X	-			X	
Disa	X	X	-					
Sections of Disa								
Micranthae		-	X	X	X	X		X
Disella	X	-						
Intermediae			X					
Repandra	X	X	-					
Aconitoideae		-	X	X	X			X

Table 3. Continued

	W. CAPE	E. CAPE	NATAL-TRANSVAAL	SOUTH-CENTRAL	E. AFRICA	MADAGASCAR	REUNION	W. AFRICA
Stoloniferae				-	X			
Amphigena	X							
Coryphaea	X	X	-				X	
Stenocarpa	X	X	X	-				
Emarginatae		-	X	X		X		
Austroalpinae			X	X				
Disa	X	X	-					
Phlebidia	X	-						

of B. recurvata on the Tsitsikamma coast near Knysna). These two genera are highly specialized, but unrelated.

At the subgeneric level the patterns are not that clear. Micranthe and Disa also occur on either one side or the other of the boundary between the Cape and the Natal - Transvaal centres. These are the two most distinct subgenera, and include the highly evolved and large flowered species Disa erubescens and D. uniflora respectively. Disa subgen. Hircicornu occurs predominantly in the Natal - Transvaal and the South-central African centers, while subgen. Stenocarpa has diversified in both the Cape and the Natal - Transvaal centres. Subgen. Falcipetalum occurs widespread in Africa.

The analysis of the distribution of the sections of Disa reveals several striking patterns:

(a) Only one section contains species in the Cape and another centre (Sect. Stenocarpa), and in this section the Cape species belong to series Spirales and Radicales, while the more northern species belong to series Natalenses and Exiles. Within the Cape centre, four sections are either restricted to or concentrated in the Western subcentre, while the sections in the eastern subcentre are all shared with the western subcentre.

This pattern is maintained at generic level by *Schizodium*.

(b) With the exception of sect. *Stoloniferae*, all the sections found in tropical Africa are represented in the Natal - Transvaal centre. However, further analysis shows that the sections that contribute the majority of the taxa in the South-central African and the East African centres (*Micranthae*, *Aconitoideae* and *Hircicornes*) show some differentiation from the Natal - Transvaal centre. The Natal - Transvaal members of sect. *Micranthae* belong to series *Polygonoides*, while the northern centres include series *Welwitschii*, *Englerana* and *Erubescens*, with *Polygonoides* being very weakly represented. Only one subspecies of sect. *Aconitoideae* (*D. aconitoides* ssp. *aconitoides*) penetrates the Natal - Transvaal centre. Sect. *Hircicornis* occurs fairly equally in both the Natal - Transvaal and the South-central African centres, but is absent north of Zambia.

(c) The taxa from the East African centre are heterogeneous. The majority of the species belong to the same sections and series as those in the South-central African centre. Two species comprise the rather peculiar sect. *Stoloniferae* of *Disa*. Although the one species, *D. eminii*, reaches into Zambia, the section is clearly a Rift Valley endemic. In addition, *Disa pulchella*, an endemic of North-eastern Africa and the Yemen, is a rather peculiar and uncomfortable member of sect. *Aconitoideae*.

(d) All the species in the Madagascan centre belong to the sections and series found in the Natal - Transvaal centre, with the exception of *Disa incarnata*, the vicariant of which is *D. scutellifera*, a species from East Africa.

Geographic replacement of species

The analysis of vicariance at the specific level has been much used to elucidate phytogeographic and evolutionary patterns (White 1962, Rourke 1972). A high frequency of ecogeographic replacement between centres also indicates relatively recent diversification, as compared to disjunctions at the supra-specific level.

Within the Cape centre several cases indicate specific replacement between the western and southern subcentres, usually with an overlap zone on the Cape Peninsula. The clearest vicariant pairs are *Monadenia atrorubens* - *ophrydea*, *M. cernua* - *physodes*, *Disa caulescens* - *tripetaloides*, *D. tenuicornis* - *subtenuicornis*, *D. obtusa* ssp. *obtusa* - ssp. *hottentotica* - ssp. *picta*, *D. atricapilla* - *bivalvata*, *Hershelia forficaria* -

newdigatiae and *H.* *spathulata* ssp. *spathulata* - ssp. *tripartita*. This compared to the paucity of geographic replacement within either subcentre supports the hypothesis of only two subcentres within the Cape Centre.

There are only two instances of geographic replacement between the Cape centre and the Natal - Transvaal centre: *Herschelia* *hians* - *baurii* and *Monadenia* *reticulata* - *brevicornis*. That both occur in 'minor' genera indicates a secondary invasion over the disjunction after the evolution of firstly the present infra-tribal structure and secondarily the present phytogeographic groups.

Within the tropical African centres there is some evidence for geographical replacement at the specific and intra-specific levels, but it is contradictory. *Disa* *aconitoides* separates readily into three subspecies: ssp. *aconitoides* in the Natal - Transvaal centre, ssp. *concinna* in Zimbabwe and the South-central African centre and ssp. *goetzeana* in the East African centre. The interval between ssp. *goetzeana* and ssp. *concinna* is actually an overlap zone between Lake Malawi and Lake Tanganyika (the old 'Stevenson Road'). This disagrees with the interface between the South-central African and East African centres, which is further north, and coincides more with the boundary between *D.* *fragrans* ssp. *fragrans* and ssp. *deckenii*, that is between the Southern Highalnds and Mt. Kilimanjaro in Tanzania.

The analysis of species replacement sheds information on the phytogeographical positions of the islands of Madagascar and Reunion: all species not held in common with the African continent have vicariants on the continent. These are summarized in Table 4, and indicate a remarkably close relationship between these insular floras and the Disinae from southern Africa.

TABLE 4. Analysis of the distribution patterns of the Disinae from Madagascar and Reunion.

Reunion:	
Disa borbonica	endemic, *D. vaginata* (Cape centre)
Madagascar:	
Monadenia brevicornis	Cape, Natal-Transvaal, Zimbabwe
Brownleea coerulea	Natal-Transvaal, South-central Africa
B. parviflora	Widespread in tropical Africa
Disa incarnata	Endemic, *D. scutellifera* (East African)
D. caffra	Natal-Transvaal, South-central Africa
D. andringitrana	Endemic, *D. versicolor* (Natal-Transvaal)
D. buchenaviana	Endemic, *D. stachyoides* (Natal-Transvaal)

Conclusions

The history of the Disinae, as inferred from the cladistic analysis, is summarized by Figure 3. This figure presents a superposition of the cladogram of the Disinae over the centres of endemism.
It suggests that the origin of the Disinae was in southern Africa, followed by migration northwards into East and West Africa. The presence of an endemic section in the Rift Valley mountains indicates that it is possible that there were at least two northwards migrations. Madagascar was colonized from both southern and eastern Africa, but predominantly from the south. There has not been sufficient time for diversification on Madagascar and Reunion to sectional level. The Cape Disinae are still diversifying across the western and southern subcentre interval.

BIOLOGY

The distribution of taxa is partially determined by the biology of the taxa. The Disinae are low terrestrial herbs, less than 1m tall, with usually annual supraterranean parts. Consequently the plants cannot compete successfully with dense perennial vegetation. The overriding majority of the species are confined to Cape fynbos, afro-montane grasslands or

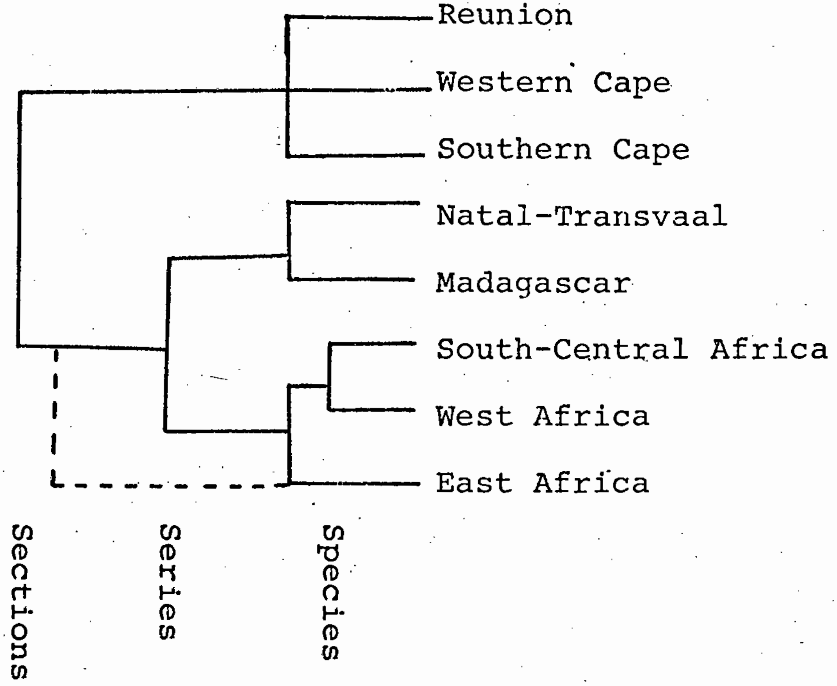

Figure 4: Geographical cladogram, showing the phylogenetic relationships among the Disinae from the various phytogeographic centres. The taxonomic rank of the disjunction is on the vertical axis, and the areas on the horizontal. The broken line connecting East Africa to the ancestral stock is based on the endemic section in East Africa, which probably indicates an earlier wave of immigration.

edaphic grasslands in the Sudano-Zambezian Domain. These are all vegetation types in which fires regularly remove the perennial vegetation (Knapp 1973, Vesey-Fitzgerald 1963, Chapman & White 1970, Kruger 1979, White 1978). Generally the plants are rather soft herbs without obvious xerophytic adaptations. As expected, the distribution of the group as a whole is more or less restricted to the temperate regions; the Mediterranean climate of the SW. and S. Cape, the temperate climates of the montane grasslands and the cool subtropical climates of the Brachystegia woodlands. The rainfall regime under which the plants are found varies from 600 to 2000 mm p.a., usually with a pronounced dry period either in summer or in winter. The majority of the taxa live under a regime of about 1000mm p.a. Very little is known about the biotic environment, which, in the case of orchids, concerns mostly the pollinators. Dispersal of the seed is probably by wind. Each flower produces in excess of 8000 minute seeds, that would be relatively easily distributed by wind. The number of relatively advanced species shared between southern Africa and Madagascar, across a gap of about 1000 km, indicate that long-distance dispersal in the orchids is a feasable mechanism.

Some of the intervals between centres may be related to either hostile environments, or to dramatic changes in one or more of the environmental factors. The Cape centre is environmentally quite unique, the soils are generally very low in nutrients, and there is no period of winter drought. The annual march of the rainfall divides the area into a summer drought area (the western subcentre) and an all-year rainfall area (the eastern subcentre). The tropical centres are all essentially in the same environmental system, but north of the Limpopo there tend to be two summer rainfall maxima separated by a short dry period (Jackson 1961). The mountains in West Africa were separated by tropical forests, while in East Africa they are isolated by hot dry savanna country.

PALAEOCLIMATES

Brenan (1978) holds that the African flora shows 'evidence of gigantic and destructive climatic changes in the past'. Although easy dispersal may override the effects of extensive extinction on the overall distribution range, species richness patterns and cladistic patterns will indicate refugia and migration patterns. However, these can only be understood by comparison with the palaeoclimates.

The climatic changes in central Africa over the last 50 000 years are relatively well substantiated, and the data and conclusions are ably reviewed by Hamilton (1976), Livingstone (1975) and Nicholson & Flohn (1980).

It appears as if the climate was dry and cold between 25 000 and 10 000 years B.P. The Afro-montane forests were restricted to small refugia, with the Afro-montane system replaced by a dry grassy savanna. Ayodele Cole (1974) presents evidence of massive extinction in the Afro-montane element in Western Africa, creating a vacuum subsequently filled by neo-endemics. From 10 000 years B.P. to about 1500 years B.P. the climate was warm and wet. The forests extended their ranges, occupying most of the present range of the Afro-montane system. A brief arid period about 7000 years B.P. does not appear to have strongly affected the vegetation. In the last 2000 years the extent of the forests has been greatly reduced, being replaced by grassland. To some extent, this has been caused by man burning the forests, and using the trees for smelting iron (Chapman & White 1970, Hall & Medler 1975). As the majority of the Disinae occupy afro-montane grasslands in tropical Africa, it is clear that their habitat has undergone some dramatic changes in the recent past.

It is not possible to suggest what happened in the dambo systems of South-central Africa. Paleoclimatic research at Kalambo Falls (Clark & Van Zinderen Bakker 1964) has been criticized (Livingstone 1975) and there do not appear to be any other studies that cast any definite light on the history of the area.

A similar paucity of data exists for the Cape centre. Axelrod & Raven (1978) infer from sea current data that the summer drought climatic regime of the South-western Cape (Weather Bureau 1972) was caused indirectly by the establishment of the Antarctic ice-cap some 4 - 5 m.y. B.P. Evidence from the coastal regions in the Western Cape (Nordhoek and Langebaan) indicate a tropical to subtropical vegetation till some 4 m.y. B.P. (Hendey 1981, Coetzee 1978). Palaeopalynological studies by Martin (1968) at Knysna and Schalke (1973) near Cape Town indicate major extensions of the Knysna forests, with the last major extension occurring some 33 000 years B.P. Circumstantial archaeological evidence indicates a change in vegetation on the coastal flats from a grassland to a more shrubby vegetation about 10 000 years B.P. (Klein 1972, Parkington, 1978). Van Zinderen Bakker (1978) postulated a cyclic climatic change pattern of cold and wet periods replacing warm and dry periods over the last 40 000 years. However, this cycle is largely based on inference and conjecture. Tankard (1976) found further indication of a cyclic change at least in temperature. Deacon (1979) briefly reviewed the existing state of knowledge. A major shortcoming with all palaeoclimatic data in reference to the Disinae available is that it refers to the lowlands, while the majority of the Disinae occur in the mountains. It is quite possible that the climatic changes which might have a major effect on the low-lands, would hardly affect the flora of the mountains, as the topographical diversity could buffer the changes.

Van Zinderen Bakker (1976, 1978) suggests, on the basis of data collected by Van Zinderen Bakker & Werger (1974), that prior to 8000 years B.P. the summit zone of the Drakensberg was very cold and bare of vegetation. Butzer et al. (1973) indicate a rainfall of at least double the present in the western Free State about 16 000 years B.P., while Van Zinderen Bakker (1957) and Coetzee (1967) suggest quite extensive climatic fluctuations in the Holocene. Although it may not be doubted that the climates and vegetation of the Free State high veld underwent dramatic changes, it seems unlikely that the Afro-montane belt in the Drakensberg was ever lost. In fact, recent studies from the Transvaal indicate that fynbos-type vegetation may have been much more widespread (Scott, in press).

SPECIATION PATTERNS

To understand the species richness in the various centres, it is of importance to understand the mechanisms of speciation by which the species richness is generated. At present, models of allopatric speciation have the widest support (Stebbins 1950, Grant 1971). The occurrence of allopatric speciation in the Cape has been suggested by several researchers (Levyns 1954, Rourke 1972, Bremer 1976, Strid 1972, Goldblatt 1978). This mode of speciation implies that taxa should replace each other geographically. Although there is evidence for allopatric speciation in the Disinae, the majority of species in species groups are more readily analysed along ecological gradients, suggesting that differential selection may be more important than geographical isolation. This may be expected in view of the presumed excellent dispersed ability of the Disinae. Various ecological factors appear to be of importance: moisture gradients in the dambos of South-central Africa (Disa sect. Micranthae ser. Welwitschii), altitudinal gradients in Natal (Disa sect. Micranthae ser. Polygonoides), climate and substrate in the Drakensberg (Disa sect. Stenocarpa) and moisture in the Cape mountains (Disa sect. Disa). Linder (1981) discusses numerous suggested speciation scenarios.

Such ecological speciation indicates in situ radiation, as the resultant species are specialized for the highly localized ecological conditions.

It is difficult to envisage, as Axelrod & Raven (1978:113) suggest, that fynbos was displaced northwards from the sandstone fold mountains to the shale mountains of the Karoo, only to be 'largely swept into its present area as the dry climate expanded.'

Extensive radiation or speciation has only occurred in a few places over the distribution range of the Disinae: in South-central Africa, in the Natal - Transvaal centre and in the Western and Southern Cape. This localization of diversification cannot be explained in terms of the present environment, as East Africa is physiographically and climatically more diverse than South-central Africa and possibly than the Natal - Transvaal centre.

CONCLUSIONS

Ball (1976) distinguished two phases in the development of historical biogeographic hypotheses: a narrative and a hypothetico-deductive phase. While the narrative hypotheses account specifically for the history of specific taxa, and only allow for generalization by induction, the hypothetico-deductive hypotheses are more general and have stronger predictive powers.

Narrative Hypotheses

The Disinae probably first diversified in southern Africa, as evidenced by the great genetic diversity across the Cape - Natal interval. From southern Africa the stock migrated northwards along the eastern escarpment up to the Sahara, which acted as a barrier. During the arid period between 25 000 and 10 000 years B.P. the subtribe in West, Central and East Africa was severely depleted, with only a few taxa surviving in refugia in the East African and Ethiopian highlands. During this period extensive radiation occurred in southern Africa, presumably because the high relief buffered the climatic fluctuations, so that there was always adequate suitable habitat available, or possibly due to more favourable climates in the caps/ last glacial period. Radiation also occurred along the watershed between the River Zaire and the Zambezi. Unfortunately the dearth of palaeoclimatic data from that region makes a more accurate interpretation difficult. Over the last few millennia, the ameliorated climate, linked to the man-made destruction of the Afro-montane forests, has led to the extensive formation of Afro-montane grasslands. The Disinae rapidly radiated and spread into these new habitats (for example the six neo-endemics on the Nyika Plateau and the lack of endemism in West Africa). The Eastern Highlands of Zimbabwe were occupied by migration from both the north and the south. Madagascar and Reunion were occupied by long-distance dispersal, mostly from southern Africa. Although there has been sufficient time for some speciation on the islands, none of the taxa have radiated, and there are no supra-specific taxa endemic to the islands.

The general distribution of the Disinae, and the patterns of diversity, agree with those documented for the Coryciinae and Satyriinae (Orchidaceae) (Linder, in press). This indicates the presence of a generalized distribution track from southern Africa northwards through the Afro-montane Region, sometimes extending into Asia.

According to the methods of Croizat, Nelson & Rosen (1974) the data presented can also be interpreted as documenting the generalized track of the Disinae in Africa. According to this model, also known as 'vicariance phytogeography' (Ferris 1980, Rosen 1978), it should be assumed that the Disinae were originally widespread in Africa, and that the present patterns are the result of different palaeoclimatic histories in different parts of Africa. There has been an extensive debate in the literature on the presumed superiority of vicariance phytogeography over dispersal phytogeography (Croizat, Nelson & Rosen 1974, Rosen 1975, Craw 1979, Nelson 1973, McDowall 1978, Platnick 1976, Platnick & Rosen 1978), but the essential point is that biogeographic research should seek general patterns, and avoid accounting for distributions by invoking random long-distance dispersal. But, as Ball (1976) suggests, the formulation of falsifiable generalized statements or hypotheses should transcend the idiosyncracies of individual taxa, and should therefore be seen as distinct from the narrative account.

Generalized Hypotheses

The results of these analyses may be stated as the following hypotheses:

1. Long-distance dispersal is effective in the Disinae.

   Axelrod & Raven (1978), remark that in contrast to the situation in the Americas, there has never been a continuous temperate zone in Africa, implying that the present range of the Disinae in continental Africa could only have been attained by long distance dispersal. Madagascar has been separated from Africa since the end of the Cretaceous (Smith 1976) and Reunion is an oceanic island less than 2 m.y. old (McDougall 1971), and could only have been colonized by long-distance dispersal. This dispersal is not, however, random, as migration tracks can be delimited.
2. The patterns of species-richness in the Afro-montane Region are a product of the climatic fluctuations in the Quaternary.

   During the arid period between 25 000 years B.P. and 10 000 years B.P. the Afro-montane floras were restricted to a few refugia, which may now be identified by endemic species and taxonomically isolated taxa. The two major refuges are the high mountains of Ethiopia and East Africa (also supported by Clayton's (1976) analysis of the Afro-montane grasses, and the Drakensberg in southern Africa (supported by Hilliard's (1978) finding the Drakensberg Compositae to be autochthonous).

3. There is an endemic centre on the watershed between the River Zaire and the Zambezi, reaching into the Mbala area.

   It is not clear whether this is a refuge area or whether for reasons yet unknown, a centre of speciation. As the palaeoclimatic history of the area is unknown, it is still a puzzle.

4. The Cape region is essentially an extension of the Afro-montane Region.

   The floristic diversity of the area may be related to the buffering effects of climatic and topographic diversity, while the uniqueness of the flora is related to the peculiarly poor substrates out of which the mountains are built.

5. The grasslands of the Transkei, Eastern Transvaal and the Natal midlands are, as White (1978) suggests, but contrary to Wickens (1976) part of the Afro-montane Region.

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APPENDIX 1. Distribution of species within the Cape Centre.

1. Ubiquitous species (8)

   Monadenia bracteata, *M. comosa*, *Disa uncinata*, *D. vaginata*, *D. filiformis*, *D. marlothii*, *Schizodium bifidum*, *S. inflexum*.

2. Western Subcentre (51)

   (i) Wides (16)

   Disa ocellata, *D. uniflora*, *D. venosa*, *D. maculata*, *D. telipogonis*, *D. lineata*, *D. atricapilla*, *D. salteri*, *D. draconis*, *D. patens*, *D. elegans*, *Monadenia atrorubens*, *M. physodes*, *M. rufescens*, *Herschelia multifida*, *H. barbata*.

   (ii) Southern area (23)

   Disa tenella ssp. *tenella*, *D. rosea*, *D. oligantha*, *D. fasciata*, *D. longicornis*, *D. tenuicornis*, *D. tenuis*, *D. richardiana*, *D. obtusa* ssp. *obtusa* and ssp. *hottentotica*, *D. brachyceras*, *D. pillansii*, *D. begleyi*, *D. brevipetala*, *Monadenia ecalcarata*, *M. bolusiana*, *D. sabulosa*, *M. pygmaea*, *M. conferta*, *Herschelia forficaria*, *H. purpurascens*, *Schizodium obliquum* ssp. *obliquum* and ssp. *clavigerum*.

(iii) Northern area (11)

Disa minor, D. esterhuyseniae, D.Longifolia, D. triloba, D. ovalifolia, D. tenella ssp. pusilla, D. caluscens, D. neglecta, Monadenia bracteata, Herschelia spathulata, Schizodium longipetalum, S. cornutum.

3. Southern Subcentre (29)

(i) Langeberg-Outeniqua endemics (11)

Disa subtenuicornis, D. cardinalis, D. gladioliflora s.l., D. vasselotii, D. schizodioides, D. tripetaloides ssp. aurata, Herschelia hians, H. newdigatiae, H. lugens var. higrescens, H. schlechterana, H. spathulata ssp. tripartita.

(ii) Taxa reaching the western Cape (17)

Disa obtusa ssp. picta, D. tripetaloides ssp. tripetaloides, D. hallackii, D. racemosa, D.micropetala, D. bivalvata, D. cylindrica, D. elegans, D. glandulosa, D. ferruginae, D. bodkinii, Monadenia ophrydea, M. cernua, M. densiflora, M. reticulata, Herschelia graminifolia, H. lugens var. lugens.

(iii) Taxa reaching Natal (2)

Disa sagittalis, D. tripetaloides ssp. tripetaloides.

Taxonomic studies in the Disinae. IV. A revision of _Disa_ Berg. sect. _Micranthae_ Lind.

H.P. Linder*

Abstract

Disa Berg. sect. _Micranthae_ Lindl. (Orchidaceae) is revised. Four series, 22 species and six subspecies are recognized. Each species is fully described, and the nomenclature and ecology of each is discussed. The possible evolutionary and speciation patterns in the section are mentioned.

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Introduction

This paper presents a formal classification of Disa sect. Micranthae. All available data on the ecology and phytogeography of the species are included. The species are defined on morphological characters, but where possible, other information was taken into account for deciding the status of the taxon.

This study is part of a series of papers dealing with the taxonomy of the subtribe Disinae (Ophrydeae) (Linder 1981 a, b, c, d, e). The relationships between Sect. Micranthae and the other sections of the genus Disa will be dealt with elsewhere.

Although the section was recognized by Lindley in 1838, and its delimitation has remained essentially unchanged, no recent comprehensive account of it exists, and the relationships of the species to one another is not clear. There are also some contradictions between the only three recent regional treatments of this section (Summerhayes, 1968, Williamson, 1977, Geerinck, 1974).

Distribution maps will be published in Distr. Pl. Afr.

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Morphological Characters of Taxonomic Importance

This section is morphologically clearly defined by several characters. Among the floral structures, lip, lateral sepal shape and the column are the most consistent. Vegetatively, a sterile shoot is always produced, and the flowering shoot is more or less clothed in cauline leaves.

Inflorescence

Four major inflorescence types may be recognized.

(i) Spike usually slender and often tapering with more than 25, often more than 100, imbricate flowers. The floral bracts tend to be insignificant. Taxa in this group are Ser. *Micranthae*, *D. welwitschii* and *D. roeperocharoides*. The latter taxon provides a transition to the next type.

(ii) Spike usually with 10 - 30 sub-imbricately or laxly arranged flowers. The scape is often visible through the flowers. *D. scutellifera*, *D. incarnata*, *D. englerana*, *D. verdickii*, *D. katangensis*, *D. zombica* and *D. ornithantha* possess this type of inflorescence.

(iii) Spike narrowly cylindrical, the floral bracts prominent and obscuring the flowers. This type appears to be a development from types (i) and (ii). This inflorescence is characteristic of the *D. miniata* group in Series *Welwitschiana*.

(iiii) Inflorescence reduced to a cluster of 1 - 15 flowers at the apex of the scape. The flowers in this group are then also the largest in the Section, with dorsal sepals up to 50 mm long.

Only D. erubescens s.l. and D. katangensis possess this type of inflorescence.

Dorsal sepal

The major variation in this structure is in the claw. In the small-flowered species, possessing inflorescence types (i) and (iii), the claw is either absent, or very reduced, so that the whole structure is ovate or obovate. In the larger-flowered species, often those with inflorescence type (ii), the claw is well developed, but is shorter than or rarely longer than the blade of the dorsal sepal, but it is always straight. The third form of dorsal sepal only occurs in those species with inflorescence type (iiii). Here the claw is longer than the blade, and is curved forwards through almost 90°, so that the axial surface of the blades faces downwards.

Spur

The vast majority of the taxa show the typical spur shape, slender, pendent from near the base of the dorsal sepal. The spur may be clavate (clavate and acute in the D. chrysostachya group, clavate and obtuse in D. miniata), or it may originate above the middle of the dorsal sepal (D. miniata). In D. fragrans the spur is often held at an angle of 45°. In D. erubescens s.l. the spur ascends from its base on the dorsal sepal.

Petals

Taxonomically, the various structural forms displayed by the petals are important. Four basic petal types may be recognized. (i) Petals entire. This form may be primitive, as it closely resembles the petal form common in the rest of the sub-tribe. It is typical of Series Micranthae, associated with inflorescence type (i).

(ii) Petals bilobed, the anterior lobe large, ovate to rounded, the posterior lobe lanceolate to oblong, about as tall as the anterior lobe. This form is found in Series Welwitschiana. D. ochrostachya and D. satyriopsis are intermediate between these two petal types.

(iii) Petal bilobed, the posterior lobe about twice as tall as the anterior lobe, and always straight. This form is associated with a dorsal sepal with a well-developed claw, and is found in Series Englerana. D. englerana and D. ukingensis are intermediate between petal types (ii) and (iii).

(iiii) Petal bilobed, the posterior lobe linear, more than twice as long as the anterior lobe, and with an S-bend, so that the upper parts of the petals flank the entrance to the spur. This form is only found in Series Rubris.

Flower colour

The basic colour in this Section is red, and most of the species show variations in this colour. However, several species have yellow flowers (D. woodii, D. ochrostachya). The occurrence of pure yellow forms of D. chrysostachya is also known. It is therefore considered possible that yellow is a recessive colour.

Summary

It is clear that a strong correlation exists among the characters discussed above. This could be understood as necessary structural changes associated with an increase in flower size: The development of a claw on the dorsal sepal, the elongation of the posterior lobe of the petal, less

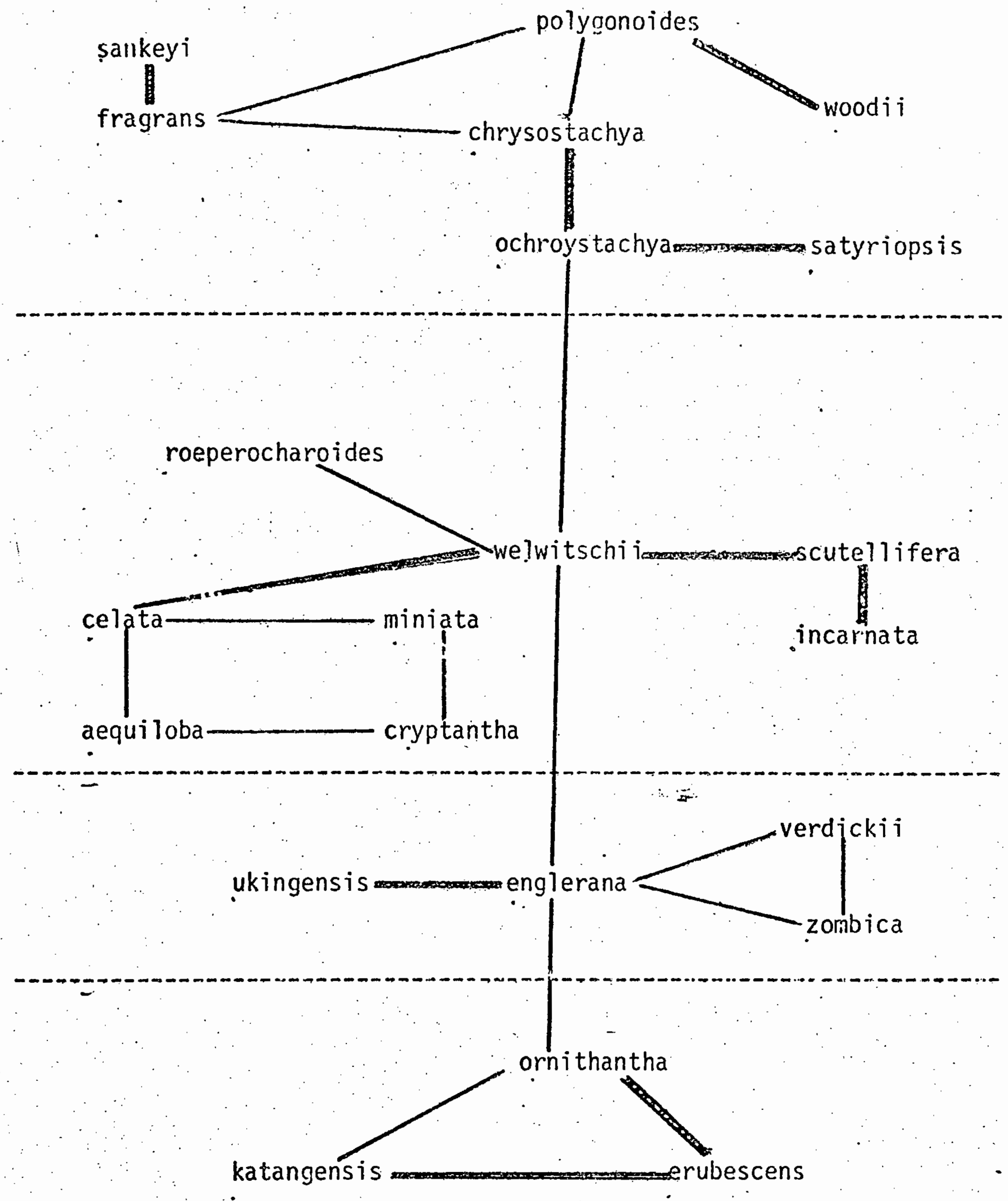


Fig. 1. -- Phenogram, showing graphically the morphological relationships among the taxa in sect. Micranthae. Thick lines show closer relationships than thin lines. Sections are separated by broken horizontal lines.

flowers per inflorescence, the development of a lax inflorescence. This flower size syndrome, which might be functionally related to pollinator groups, provides the basis for the classification of this section, graphically shown in Fig. 1.

Ecology, Phytogeography and Evolution

The series and species groups recognized in this section occupy particular habitats and distribution ranges. At the series category these may be wide, but usually the majority of species in the section fall within a narrow ecological and geographical range. Morphologically closely related taxa (i.e. members of the same species groups) may usually be differentiated ecologically, phytogeographically or eco-geographically. These taxa usually occupy variants of the same habitat type. These variants may be geographical and the relevant taxa may then be regarded as vicariads (Davis & Heywood 1963 : 427). Alternatively, the variants may be sympatric, and the relevant taxa may then be considered to be separated ecologically (Stebbins 1950 : 204). Occasionally, taxa are partially sympatric with usually intermediate forms in the overlap zones.

Theoretically, each higher taxon should reflect an ancient occupation of a habitat type, and the subsequent radiation into the various variants (both geographical and ecological) of that habitat type.

One series occurs in a wide range of habitats in Southern Africa, and the remaining series are centred in South-Central Africa, with taxa extending over the whole of tropical and sub-tropical Africa. It is possible that the series, defined as they are by gross floral and inflorescence morphology, reflect to a large extent pollinator categories, rather than physical habitat categories.

Series *Micranthae*

The three groups in this series each occupy one broad habitat category: The *Polygonoides* group under sub-tropical conditions, the *D. chrysostachya* group montane conditions and the *D. fragrans* group alpine conditions.

D. polygonoides is temporally isolated from *D. woodii*. *D. chrysostachya* is spatially isolated, with an overlap zone between *D. ochrostachya* and *D. satyriopsis*. This overlap might be recent as it is quite possible that *D. satyriopsis* was segregated on the southern Tanzanian highlands, spatially isolated from the rest of *D. ochrostachya*. In the *D. fragrans* group, ssp. *fragrans* is spatially isolated from ssp. *deckenii*, but completely sympatric with *D. sankeyi*. It is not clear what keeps these two taxa distinct.

Series *Welwitschiana*

The *D. scutellifera* group is mostly a grassland group, and occurs in North-east Africa and Madagascar with the two taxa geographically isolated. The other two groups are centred in South-Central Africa, and occur in dambos.

In the *D. welwitschii* group two phenomena appear to be occuring. *D. welwitschii* s.l. consists of numerous forms, over a vast distribution range, between which morphological segregation is still in a very incomplete stage, so that its variation can only be crudely treated at an infra-specific level. However, *D. roeperocharoides* is sympatric with *D. welwitschii* ssp. *welwitschii*, and even occurs in the same dambos. It is not clear what prevents these taxa from interbreeding.

The four species in the *D. miniata* group are sympatric, and all grow in dambos. Their morphological differences are slight, but clearcut. It can only be suggested that they have specialized in response to differences in the available moisture gradient in the dambos.

Series Englerana

The taxa in this series should be placed into three groups. Two of the groups would have a single species each: one in montane grassland (D. zombica), the other in Brachystegia-Uapaca woodland (D. verdickii). The other group contains two species. The common species (D. englerana) appears to be ecologically isolated from the other two species in the series. D. ukingensis is very closely related to D. englerana, but occurs in montane grassland, a habitat in which D. englerana is not found. From this it is clear that the two taxa are separated eco-geographically.

Series Rubris

The four taxa in this series are all closely related. D. katangensis can easily be separated. Although morphologically it is quite similar to D. erubescens s.s., it occurs on dry sand in Brachystegia woodland, while the rest of the series grow in dambos and seepages, mostly in montane grassland. It is not clear what environmental factor isolated D. ornithantha from D. erubescens s.l. The two subspecies of D. erubescens are spatially separated, with intermediate forms occuring in the overlap zone.

Summary of the Ecology and Phytogeography

From the above it is clear that the major isolating mechanism suspected to operate in this group are geographic

(5 pairs), ecological (3 pairs, a complex of 4 species and three isolated taxa), temporal (1 pair) and unknown (2 pairs). Groups and series may be ecologically differentiated (i.e. the groups in series Micranthae) or possibly by having different pollinators (i.e. series Erubescens from the rest of section Micranthae).

Evolution

It would appear as it Series Micranthae is the most primitive in the Section. Evidence of this can be found in the entire petals and unspecialized dorsal sepal. If this is the case, then Series Rubris should be the most highly evolved Series.

Taxonomy

Disa Berg. sect. *Micranthae* Lindl. in Gen. Sp. Orch.:347 (1838).
sect. *Polygonoideae* Kraenzl. in Orch. Gen. Sp. 1:736, 743 (1899).
sect. *Scutelliferae* Kraenzl. in l.c.: 736, 737 (1899).
sect. *Calostachys* Schltr. in Bot. Jahrb. 31:201, 216 (1901).

Lectotype: *D. chrysostachya* Sw. (Summerhayes 1964).

Plants 70 - 1000 mm tall, sterile shoots with 2 - 5 leaves always produced, fertile shoots usually with more or less sheathing cauline leaves. Inflorescence varying from a dense cylindrical tapering spike to a single large flower, bracts generally as tall as the flowers, but frequently taller and sometimes more prominent than the flowers. Dorsal sepal varying from ovate to spathulate, the spathulate forms with a long claw and an ovate blade, the whole up to 50 mm tall, the galea shallow, the margins often incurved. Spur typically pendent from between the middle and the base of the dorsal sepal, slender, occasionally clavate, or ascending, the entrance to the spur always small. Lateral sepals oblong to ovate, a keel or apiculus absent or weakly developed, spreading upwards or sideways. Petals entire or bilobed, erect next to the anther, if bilobed the anterior lobe flanking the anther, the posterior lobe erect inside the galea. Lip generally linear, pendent. Rostellum erect, the lateral lobes canaliculate, usually holding the viscidium to face down, the position of the central lobe obscure. Anther erect, the cells parallel, the connective only prominent in some small-flowered species, pollinia cylindrical, caudicle short, viscidia globular. Stigma sessile or subsessile, tripulvinate. Flower colour basically red, with some yellow forms occurring.

Nomenclatural notes

Lindley (1838) defined sect. Micranthae as having 'anthera erecta', which is still the most important diagnostic character of the section. Kraenzlin (1899) renamed this section 'Polygonoideae' and included numerous species which are not closely related. The larger-flowered members of this section he included in his sect. Scutelliferae. Schlechter (1901) defined the section accurately, stating "Eine recht gut characterisierte Section, welche sich an den aufrechten Antheren ... leicht erkennen laesst". He named it sect. Calostachys. Summerhayes (1964) re-established the correct name, and lecto-typified the section.

Key to the species of *Disa* Sect. *Micranthae*

1. Petals not bilobed:

2. Spur much inflated, subacute, longer than the dorsal sepal . . . . 3. *D. chrysostachya*

2! Spur slender, rarely subclavate, obtuse:

3. Spur shorter than the dorsal sepal:

4. Flowers off-white, inflorescence about as long as the leafy stem . . . . 7. *D. sankeyi*

4! Flowers bright red or yellow, inflorescence usually shorter than the leafy stem:

5. Flowers red; spur 1,5 - 3,3 - 4,5 mm long . . . . 1. *D. polygonoides*

5! Flowers yellow, spur 0,8 - 1,5 - (2,5) mm long . . . . .2. *D. woodii*

3! Spur as long as the dorsal sepal; flowers white to mauve:

6. Petals obtuse; from South Africa to southern Tanzania . . . . 6a. *D. fragrans* ssp. *fragrans*

6! Petals acute; from Kilimanjaro to Ethiopia . . . . 6b. *D. fragrans* ssp. *deckenii*

1! Petals bilobed:

7. Spur reaching to below the base of the dorsal sepal:

8. Spur more or less inflated; flowers in a long dense tapering spike, yellow to orange; dorsal sepal longer than 6 mm:

9. Anterior petal lobe as tall as posterior petal lobe and curved in front of the anther;

lateral sepals 8 - 10 mm long.5. *D. satyriopsis*

9! Anterior petal lobe smaller than the posterior lobe, flanking the anther; lateral sepal 6 - 9 mm long . . . . 4. *D. ochrostachya*

8! Flowers not with the above combination of characters:

10. Petal lobes sub-equal; posterior petal lobe truncate . . . . 13. *D. aequiloba*

10! Petal lobes not sub-equal, if equal in length, then the posterior lobe is not truncate:

11. Posterior petal lobes shorter than anterior petal lobes; bracts prominent:

12. Spur clavate, reaching to the base of the dorsal sepal . . . . 15. *D. miniata*

12! Spur slender, reaching below the base of the dorsal sepal . . . . 14. *D. cryptantha*

11! Posterior petal lobe as long as or longer than the anterior petal lobe:

13. Posterior petal lobe linear, much longer than the anterior petal lobe; from N.E. Africa, Kenya and Madagascar:

14. Flowers pink, plants robust, from N.E. and E. Africa . . . . 9. *D. scutellifera*

14! Flowers red, plants slender, from Madagascar . . . . 8. *D. incarnata*

13! Posterior petal lobe ovate or oblong, up to a 1/3 longer than the anterior lobe:

15. Bracts not prominent and not partially obscuring the flowers:

16. Spur 8 - 13 mm long; dorsal sepal 7,5 - 11,5 mm long; posterior petal lobe truncate, 1/3 taller than the anterior lobe, flowers red . . . . 11. *D. roeperocharoides*

16! Spur 4 - 8 mm long; dorsal sepal 5 - 13 mm long; flowers red or pink; posterior lobe variable.

17. Flowers red or carmine; lateral sepals 5 - 9 mm long; posterior petal lobe generally 1/3 taller than anterior lobe; from South and South-Central Africa . . . . 10a *D. welwitschii* ssp. *welwitschii*

17! Flowers pink; lateral sepals 7 - 12 mm long; posterior petal lobe as tall as or slightly taller than anterior lobe; from East, Central and West Africa . . . . .10b. *D. welwitschii* ssp *occultans*

15! Bracts prominent, partially obscuring the flowers . . . . .12. *D. celata*

7! Spur rarely reaching to the base of the dorsal sepal; usually much shorter than the dorsal sepal:

18. Dorsal sepal shorter than 8 mm . . 15. *D. miniata*

18! Dorsal sepal (12-) 14 - 45 mm long:

19. Posterior petal lobe straight:

20. Claw of the dorsal sepal as long as the blade of the dorsal sepal:

21. Anterior lobe of petal longer than the claw of the dorsal sepal; dorsal sepal 20 mm long or longer . . . . 19. *D. verdickii*

21! Anterior lobe of petal much shorter than the claw of the dorsal sepal; dorsal sepal 20 mm long or less . . . . 18. *D. zombica*

20! Claw of the dorsal sepal about 1/2 as long as, or shorter, than the blade:

22. Petals shorter than 8 mm, inflorescences dense, from Nyika Plateau or Njombe, Tanzania . . . . . 17. *D. ukingensis*

22! Petals longer than 8 mm, inflorescences lax, not from above localities . . . . 16. *D. englerana*

19! Posterior petal lobe twisted through an S-curve:

23. Spur ascending, bracts reaching to the middle of the dorsal sepal or shorter:

24. Dorsal sepal less than 30 mm long, plants usually with 3 - 6 flowers . . . . .22a. *D. erubescens* ssp. *erubescens*

24! Dorsal sepal more than 30 mm long, plants with 1 - 3 (- 12) flowers . . . . 22b. *D. erubescens* ssp. *carsonii*

23! Spur pendent, parallel to the dorsal sepal, bracts usually overtopping the flowers:

25. Anterior petal lobe shorter than the claw of the dorsal sepal; dorsal sepal longer than 30 mm, blade curved forwards . . . . 21. *D. katangensis*

25! Anterior petal lobe as long as the dorsal sepal; dorsal sepal shorter than 30 mm, erect . . . . 20. *D. ornithantha*

Series 1. *Micranthae*

Flowers in dense cylindrical and often tapering spikes; petals generally entire, or if bilobed, the anterior lobe arising from the posterior lobe.

Type: *Disa chrysostachya* Sw.

The majority of species in this series are clearly separated from the rest of the section by their entire petals. However, *D. ochrostachya* is more closely related to *D. chrysostachya* (from which it only differs by the possession of bilobed petals) than to any other species in Sect. *Micranthae*, with the exception of *D. satyriopsis*. *D. satyriopsis* is clearly a vicariant of *D. ochrostachya*. These two taxa therefore have to be included in series *Micranthae*, despite their bilobed petals.

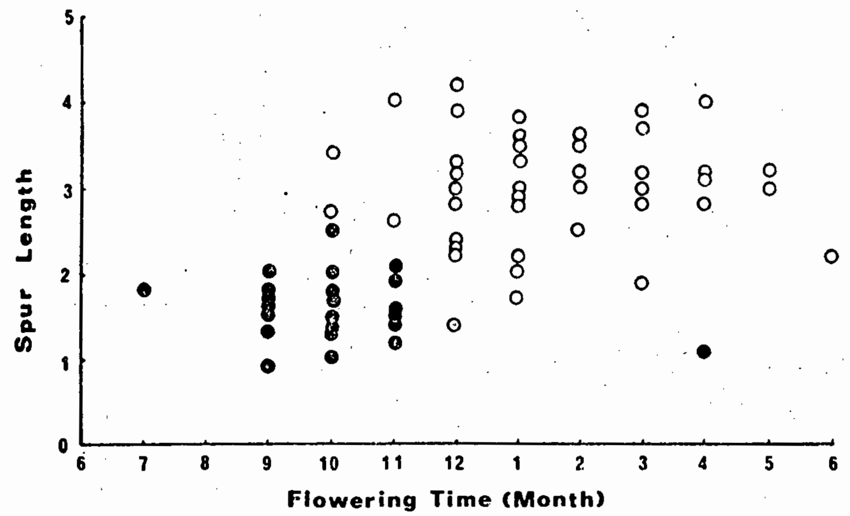
This series is centred in southern Africa, where five of its eight species occur. The species considered to be derived (*D. ochrostachya* and *D. satyriopsis*) occur in South- Central and East Africa.

Three groups can be detected. *D. polygonoides* and *D. woodii* are characterised by a short spur, and an inflorescence shorter than the vegetative parts. These two species occur in the sub-tropical coastal regions of Natal. *D. chrysostachya*, *D. ochrostachya* and *D. satyriopsis* can be recognized by the long inflated spur and the long tapering inflorescences. They occur in the montane zone, in grassland or swamps. *D. fragrans* and *D. sankeyi* have medium-length slender spurs, and the inflorescence is longer than the vegetative parts. These species inhabit the alpine and sub-alpine regions, or in Zimbabwe, the montane zone.

All three groups present taxonomic difficulties.

(a) *D. polygonoides*/*D. woodii* group

Stewart (1973) listed the differences between these two taxa. However, the study of all available herbarium material showed that no single morphological character is sufficient to separate the two species. Field work substantiated the



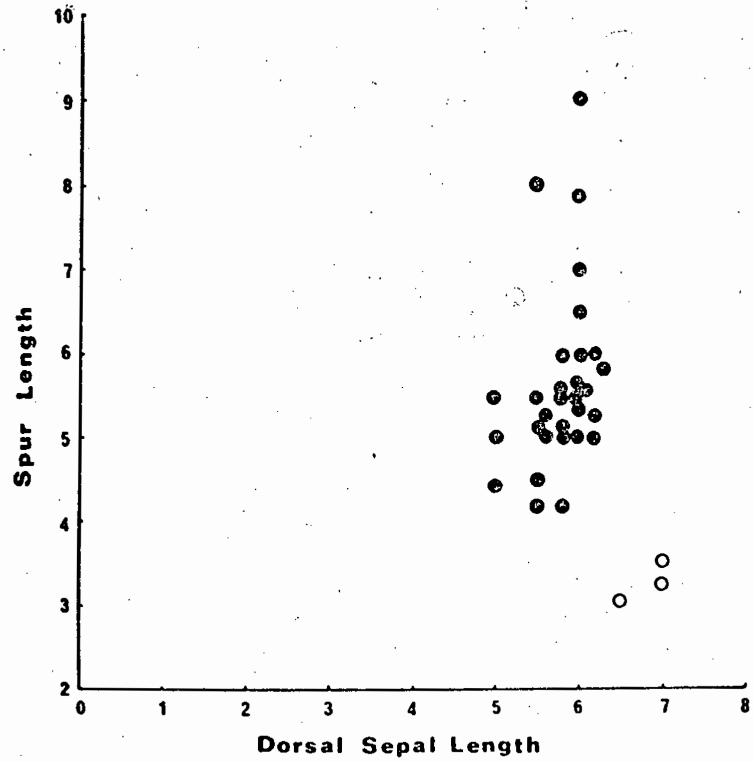


Fig. 2. -- Disa polygonoides group: the closed circles represent the yellow flowered taxon, D. woodii Schltr., and the open circles represent the red flowered taxon, D. polygonoides Lindl.

the different flowering times of the two putative taxa. Furthermore, spur length could be correlated to the flower colour (Fig. 2). An analysis of the habitat notes made by collectors, of the distribution range of the two putative taxa, and of the habitats observed during fieldwork, showed that *D. woodii* occurs in a somewhat drier habitat than *D. polygonoides*. *D. woodii* also occurs as a pioneer on road cuttings and fills, a habitat in which *D. polygonoides* is rare. All specimens seen could satisfactorily be placed in one of the species. These appear to be two biological taxa with a yet little morphological differentiation.

(b) *D. ochrostachya*/*D. satyriopsis* group

The bulk of collections of *D. satyriopsis* can readily be distinguished from *D. ochrostachya* by the larger anterior petal lobe, the shorter and more swollen spur, the more robust plant, and the red base colour of the flowers (Fig. 3). Field studies on the Nyika Plateau showed that no intermediates existed, despite the complete mixing of the populations. All individuals ould readily be referred to one of the taxa. However, a study of the available herbarium material revealed that intermediate forms did appear to exist, especially in Burundi and Rwanda, where the two species also appear to occur mixed (Van der Ben 2421, Verdcourt 3411). The two taxa are partially sympatric. They could therefore be called semi-species (Davis & Heywood, 1963; Grant, 1971). As the evidence from the Nyika Plateau is more reliable than that from Burundi and Rwanda (numerous collections, and personal field studies, see also Williamson, 1977, 1980, as opposed to two herbarium sheets), and this evidence

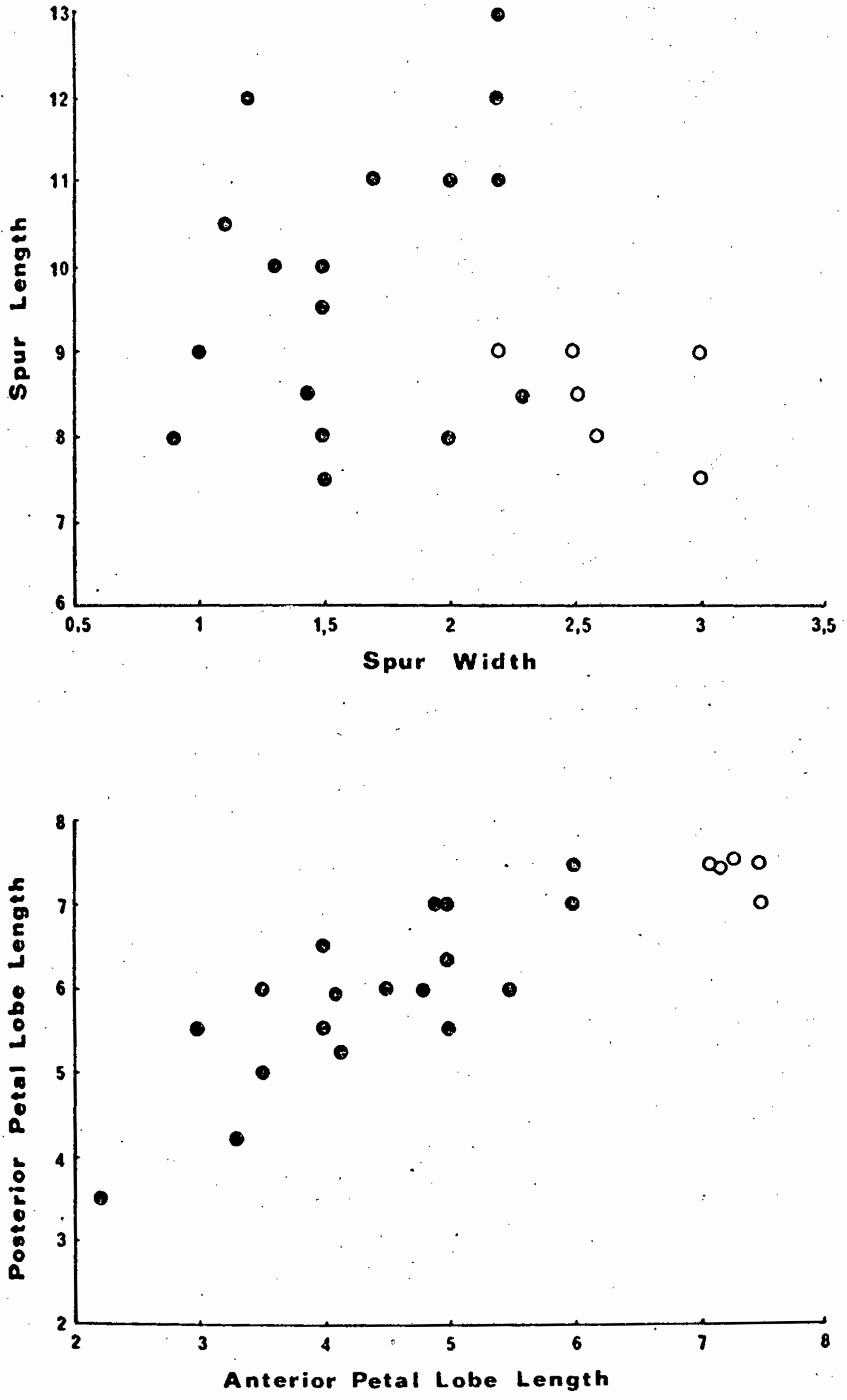


Fig. 3. -- Morphometric differences between *D. ochrostachya* Reichb.f. (closed circles) and *D. satyriopsis* Kraenzl. (open circles).

indicates that the two taxa can occur together without intermediate forms, species status should be awarded.

(c) *D. fragrans*/*D. sankeyi* group

Disa fragrans is a rather variable widespread species, that extends from the Cape Province in South Africa to Ethiopia. Previously three species were recognized in the group: *D. fragrans* in South Africa, *D. leucostachys* in Zimbabwe, Mocambique, and Tanzania, and *D. deckenii* in East Africa.

No morphological or ecological character could be found to separate material referred to *D. fragrans* and *D. leucostachys*. Although the extreme forms (from the summit of the Drakensberg in Natal, South Africa, and the Himalaya Mountains in Zimbabwe) look quite different, collections from areas of intermediate altitudes are intermediate in structure (Eastern Transvaal Drakensberg, Chimanimani mountains in Zimbabwe).

There are several partial differences between material of *D. fragrans* (including *D. leucostachys*) and *D. deckenii*, but only the shape of the petal appears to be constant. A single morphological character associated with allopatric distributions is generally only considered evidence for a subspecific status (Hedberg, 1958; Davis & Heywood, 1963). Population structure and habitat appear to be the same for the two species. *D. fragrans* is strongly scented, whereas there is not a single record of a scent in material referred to *D. deckenii*. As these two taxa are allopatric, and so closely related, they are hereby treated at the subspecific level.

Although *D. fragrans* ssp. *fragrans* and *D. sankeyi* are sympatric, they are morphologically quite distinct. In *D. sankeyi* the flowers are larger, and plants somewhat more robust than in D. fragrans and there are significantly fewer flowers per inflorescence. This is associated with a shorter spur (Fig. 4). Like D. fragrans, D. sankeyi also has a scent. The morphological similarities between the two species, their total sympatry, associated with the general rarity of D. sankeyi and the frequency of D. fragrans are peculiar. There can be no question about the specific status of D. sankeyi.

1. **Disa polygonoides** Lindl., Gen. Sp. Orch. : 349 (1838); Hook.f., Bot. Mag.: t. 6532 (1880); H.Bolus, Journ. Linn. Soc. Lond., Bot. 25 : 198 (1889); Dur. & Schinz, Consp. Fl. Afr. 5 : 106 (1892); Kraenzl., Orch. Gen. Sp. 1 : 747 (1900); Schltr., Bot. Jahrb. 31 : 222 (1901); H.Bolus, Ic. Orch. Austro-Afr. 2 : t.84 (1911); Rolfe, Fl. Cap. 5 (3) : 226 (1913); Ross, Fl. Natal : 143 (1972); Compton, Fl. Swaziland : 157 (1976).
-Type: Transkei, Pondoland, between Omtata and Omsamwubo Rivers, Drège 4572 (K holo-; G, S, W iso-).

D. natalensis Lindl., Journ. Bot. (London) 1 : 16 (1842).
-Type: Rep. S. Afr., Natal, Durban, Harvey s.n. (K holo-).

D. chrysostachya auct. non. Sw.; Batten & Bokelmann, Wild Flowers E. Cape Prov.: pl. 45.2 (red variety) (1966).

Tubers testicular, often sub-cylindrical, up to 50 mm long and 10 mm in diameter, pubescent; sterile shoot rarely produced, ca. 50 mm long; basal sheaths 2 - 3, up to 40 mm long, obtuse, completely sheathing; leaves 3 - 4, semi-erect, acute, linear to

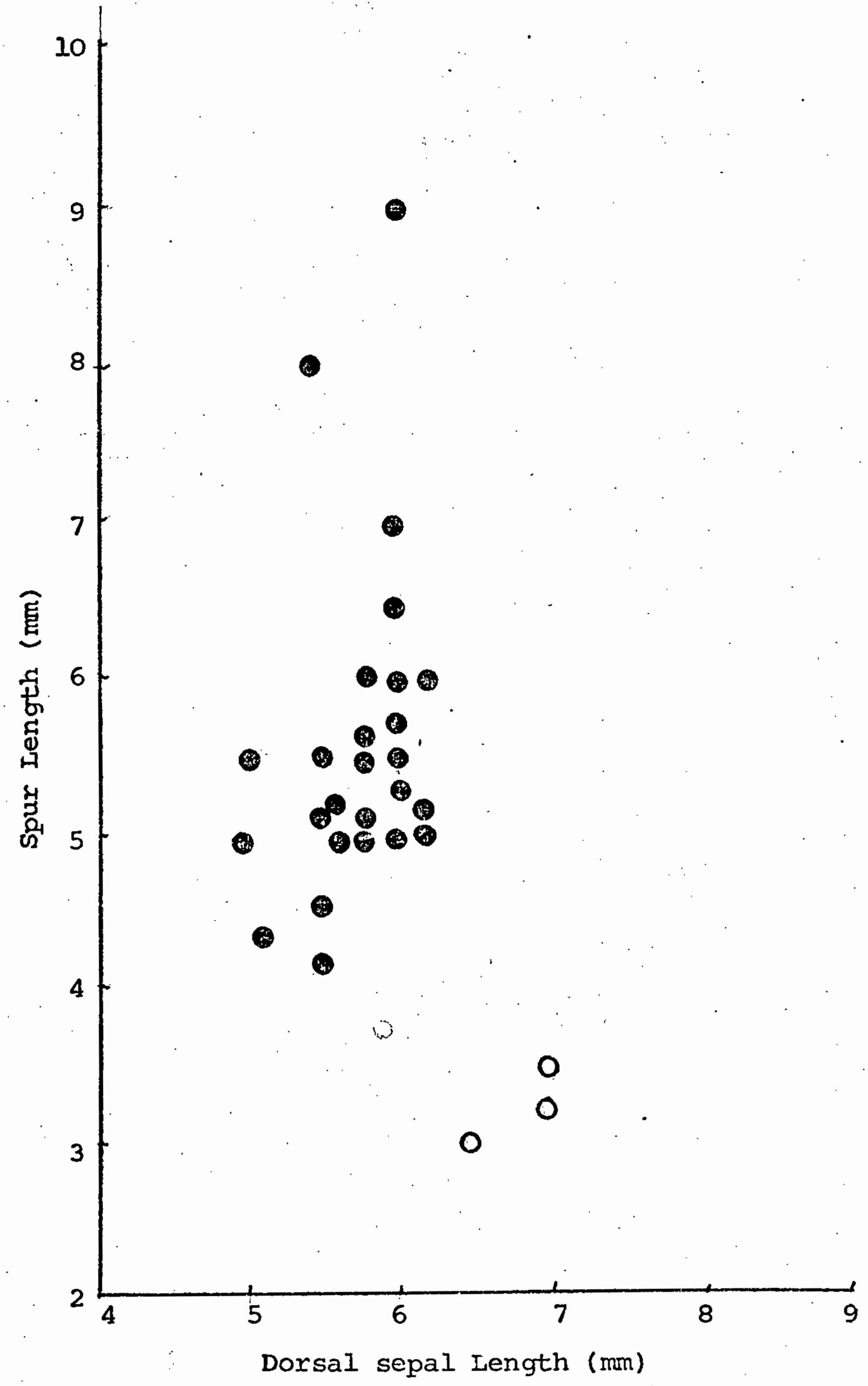


Fig. 4. -- Variation in spur length in D. *fragrans* Schltr. (closed circles) and D. *sankeyi* Rolfe (open circles).

lorate, c. 250 mm long and 30 mm wide; fertile shoot slender to robust, 150 - 300 - 700 mm tall; cauline leaves few if sterile shoots are developed, otherwise numerous, 6 - 25; often clustered near the base of the stem with the largest leaves at the base, linear to narrowly lanceolate, acute, more or less conduplicate, up to 250 mm long and 40 mm wide, sheathing at the base, the upper leaves almost completely sheathing, all leaves imbricate. Inflorescence dense, cylindrical, very rarely somewhat tapering, 30 - 90 - 170 mm long and on average 80 - 100 flowered; bracts as tall as the flowers, narrowly ovate, acute to sub-acuminate, the apex usually reflexed. Flowers small, less than 10 mm in diameter, facing horizontally or rarely down, generally brick-red, often red to red-orange, rarely orange; dorsal sepal erect, elliptical to sub-obovate; galea 5 - 7 mm long, 3 - 4 mm wide and ca. 1 mm deep, obtuse, the upper margin of the galea slightly incurved; spur pendent from shortly above the base of the dorsal sepal, usually reaching to well below the base of the dorsal sepal, cylindrical to more generally dorso-ventrally flattened, sub-clavate, apically obtuse, 1,5 - 3,3 - 4,5 mm long and 1 mm wide; lateral sepals narrowly oblong, acute, 6 - 7 mm long and 2,5 - 3,5 mm wide, spreading forwards, shallowly concave with a rudimentary apiculus; petals narrowly obovate, acute, the apex slightly keeled, 4 - 6 mm long and 2 - 3 mm wide, curving over and behind the anther; lip lorate to linear, rounded, ca. 6 mm long and 1 mm wide, sub-pendent or horizontal, the apex often upcurved; rostellum simple; anther erect, ca. 3,5 mm long, caudicles 0,5 - 1 mm long; ovary 5 - 10 mm long; stigma pulvinate, lateral lobes well developed, 0,5 mm tall.

Note: The concept of <u>D</u>. <u>polygonoides</u> has not been confused in the literature. This could be due to the fact that the type was a

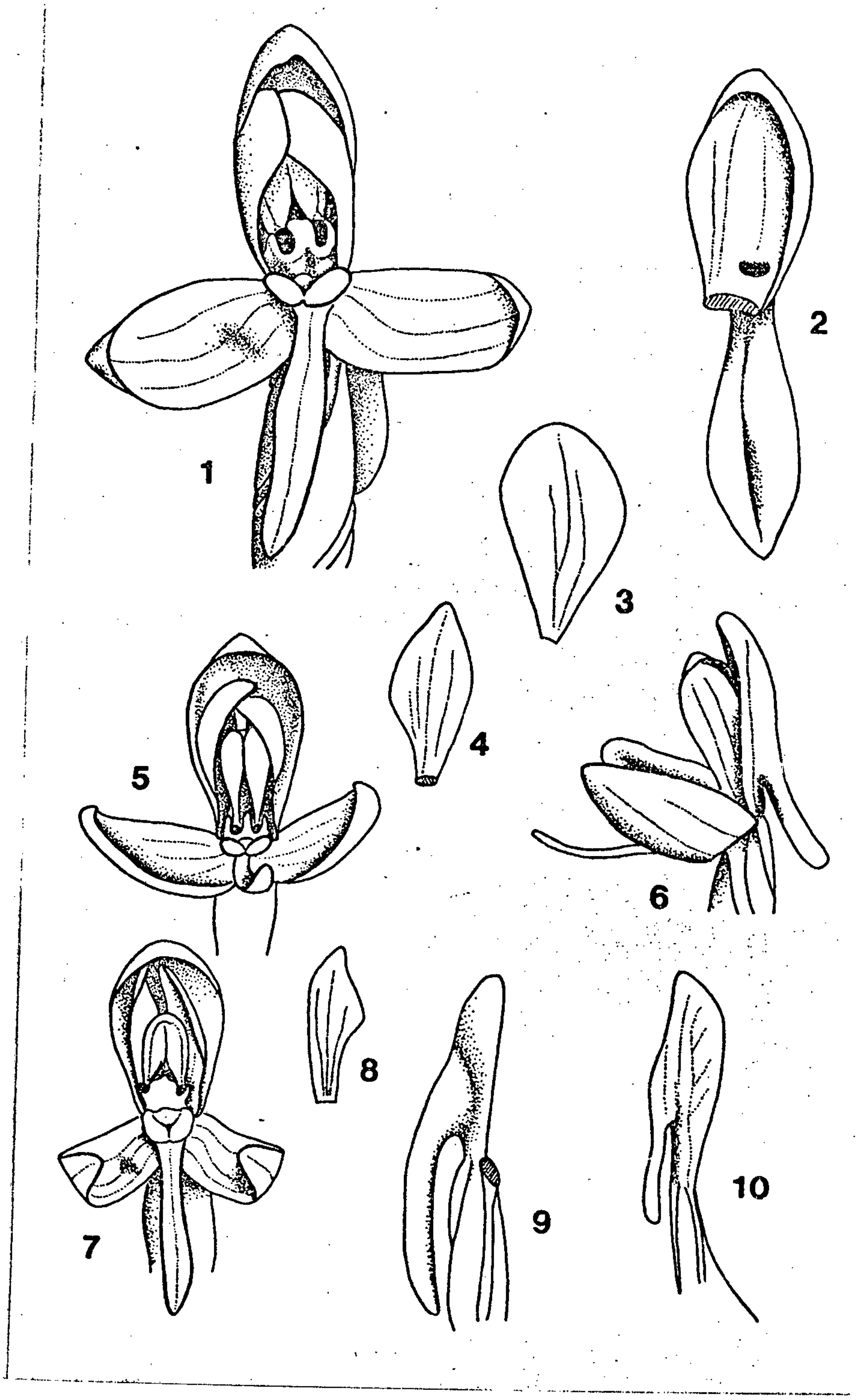


Fig. 5. -- Series *Micranthae* (X4): 1 - 3 *D. chrysostachya* Sw. from Linder 780, 1, frontal view of flower, 2, dorsal sepal showing spur, 3, petal. 4 - 6 *D. polygonoides* Lindl. from Linder 796, 4, petal, 5, frontal view of flower, 6, side view of flower showing spur. 7 - 9 *D. fragrans* Schltr. from Linder 1028, 7, frontal view of flower, 8, petal, 9, side view of dorsal sepal. 10 *D. sankeyi* Rolfe from Sankey 264 (Type), side view of dorsal sepal.

Drège collection, with several duplicates housed in the major herbaria in Europe. The only synonym, D. natalensis, was included in the synonymy of D. polygonoides by Bolus (1889). All subsequent authors followed this approach. However, there has been some confusion among D. chrysostachya, D. polygonoides and D. woodii, resulting in the mis-identification in Batten & Bokelmann (1966).

Distribution and Ecology: D. polygonoides occurs along the eastern coastal areas of southern Africa, from Humansdorp in the south to Inhambane in the north. There is an outlier population in the Magaliesberg between Pretoria and Rustenburg. The altitude range of the species is from sea-level to 1000 m.

Almost all collectors' notes indicate a marshy habitat, with the remainder recorded from grassland. Downing (1966) recorded this species from the Tabamhlope vlei in Natal, where he described the habitat as being a wet-saturated sedge meadow, wet in the dry season and locally flooded to a depth of 10 cm in the wet season. Similar habitat conditions were observed at Ngoya in Kwa-Zulu.

Over most of the distribution range the rainfall is in excess of 1000 mm p.a., but several localities probably do not receive more than 800 mm p.a. In general the bulk of the precipitation occurs in the summer months, with the winter months relatively dry. However, at the southern extreme of the distribution range the rainfall is fairly evenly distributed throughout the year (Jackson, 1961).

Flowering occurs from October to March, with occasional records of specimens collected in flower from the winter months.

The bulk of flowering specimens were collected in the summer months from October to February.

Distribution: Distr. Pl. Afr. 1.

MOCAMBIQUE :

SUL DO SAVE : Zandamela, Stephens s.n. (PRE).

REPUBLIC OF SOUTH AFRICA :

TRANSVAAL : Pretoria, Repton 5746 (PRE); Rustenburg, Venter 412 (PRE).

NATAL : Pinetown, Adams 94 (NU); Ngotsche, E of Louwsburg, Codd 7023 (PRE); Uvongo, Dodds 117 (NU); Beach Terminus, Forssman 310 (PRE); Munster, Gemmell 6009 (PRE); Eshowe, Gerstner 2651 (BOL, PRE); Port Edward, Gibb 7 (NU); Port Shepstone, Oribi Gorge, Glen 271 (NU); Eshowe, Gower 38 (NU); Port Edward, Hampson 5898 (PRE); Mtunsini, Umgoye, Harrison S.N. (BOL); Port Edward, towards Umtawana mouth, Huntley 728 (NU); Uvongo Beach, Lilliecrona 4 (NU); Mtunsini, Ngoya forest, Linder 796 (BOL); Zululand, Marloth 5992 (PRE); South Coast, Vengeli forest, McNeill 53 (NU); Pietermaritzburg, Moll 3031 (PRE); Umlazi, O'Connor 248 (NU); Pietermaritzburg, O'Connor 257 (NU); Mtunzini, O'Connor 346 (NU); Port Edward, O'Connor 357 (NU); Port Shepstone, Pole Evans s.n. (PRE); Port Edward, Poynton 7 (NU); Dumisa, Rudatis 224 (BM, K, PRE, Z); Pietermaritzburg, Killick 233 (PRE); Mtunzini, Rensburg 42 (NU); Natal, Sanderson 480 (BOL); Hlabiza, Schelpe 7261 (BOL); Between Cato Ridge and Inchanga, Stewart 1650 (NU); Mtunzini, Ngoye, Stirton 441 (PRE); Eshowe, Strey 4187 (PRE); Lake St. Lucia, Taylor 174 (NU); Umbumbulu, Venter 168 (PRE); Pietermaritzburg, Venter 187 (PRE); Umdoni Park, Ward 1309 (NU); Uvongo, Whellan 1047 (SRGH); Clairmont, Wood 1094 (PRE); Ngoya, Wood 7600 (BOL); Isipingo, Wood 12587 (NU).

TRANSKEI : Lusikisiki, Bayliss 542 (PRE); Kentani, Chippindal 328 (PRE); Lusikisiki, Crundell s.n. (PRE); Port St. Johns, Galpin 2871 (K, PRE); Mkambati River, Mogg 13609 (K, PRE); Kentani, Pegler 437 (PRE); Port St. Johns, Rutgers 17 (BOL); Port St. Johns, Rutgers 35 (BOL); Port St. Johns, Wagen s.n. (PRE).

CAPE PROVINCE : Gonubie springs, Acocks 10989 (PRE); Grahamstown, Britten s.n. (PRE); Komgha, Codd 6347 (PRE); Kei mouth, Flanagan 528 (BOL, PRE); Kei River, Flanagan 2874 (PRE); Humansdorp, Fourcade 3655 (BOL, K); East London, Gonubie, Leipoldt s.n. (BOL); King Williams Town, Pirie Forest, McLoughlin 440 (BOL); Kei mouth, Schlechter 6205 (PRE, Z); King Williams Town, Widdicombe 32 (BOL); Komgha Morgan Bay, Wilman 1068 (BOL, PRE).

2. **Disa woodii** Schltr., Ann. Transv. Mus. 10 : 247 (1924); Letty, Wild Flowers Trans. : pl. 51 (1962). -Type: Republic of South Africa, Natal, Clairmont, Sept. 1907, Wood 10514 (B syn-; NU lecto-), near Amanzimtote, Sept. 1898, Wood 7280 (B syn-).

Tubers testicular, often sub-cylindrical, up to 50 mm long and 10 mm in diameter, pubescent. Sterile shoot rarely produced, ca. 50 mm long; basal sheaths 2 - 3, up to 40 mm long, obtuse, completely sheathing; leaves 3 - 4, semi-erect, acute, linear to lorate, 250 mm long and 30 mm wide. Fertile shoot slender to robust, 150 - 300 - 700 mm tall; cauline leaves few if sterile shoots are developed, otherwise numerous, 6 - 25; often clustered near the base of the stem with the largest leaves at the base, linear to narrowly lanceolate, acute, more or less conduplicate, up to 250 mm long and 40 mm wide, sheathing at the base, the upper leaves almost completely sheathing, all leaves imbricate. Inflorescence dense, cylindrical, very rarely somewhat tapering, 30 - 90 - 170 mm long and on average 80 - 100 flowered; bracts as tall as the flowers, narrowly ovate, acute to sub-acuminate, the apex usually reflexed. Flowers small, less than 10 mm in diameter, facing horizontally or rarely down, bright yellow, often with the apexes of the parts tinted orange; dorsal sepal erect, elliptical to sub-obovate; galea 5 - 7 mm long, 3 - 4 mm wide and ca. 1 mm deep, obtuse, the upper margin of the galea slightly incurved; spur pendent from shortly above the base of the dorsal sepal, reaching to the base of the dorsal sepal, rarely below, 0,8 - 1,5 (-2,5) mm long; subclavate; lateral sepals narrowly oblong, acute, 6 - 7 mm long and 2,5 - 3,5 mm wide, spreading forwards, shallowly concave with a rudimentary apiculus; petals narrowly obovate, acute, the apex slightly keeled, 4 - 6 mm long and 2 - 3 mm wide, curving over and behind the anther; lip lorate to linear, rounded, ca. 6 mm long and 1 mm wide, sub-pendent or horizontal, the apex often upcurved; rostellum simple; anther erect, ca. 3,5 mm long, caudicles 0,5 - 1 mm long; ovary 5 - 10 mm long; stigma pulvinate, lateral lobes well developed, 0,5 mm tall.

Note: Stewart (1973) indicated the differences between the closely related taxa in this group.

Distribution and Ecology: Like *D. polygonoides*, *D. woodii* also occurs along the east coast of southern Africa, from Port Elizabeth to the Mocambique border. The species is better represented inland, known from scattered localities in the

Transvaal bushveld and highveld, and from Melsetter in Zimbabwe. The altitude range is correspondingly larger, from sea-level in the south to 1500 m in Zimbabwe.

Collectors' notes indicate a habitat range from grassland, often on sand, to damp ground, to occasionally swampy conditions. This species has frequently been recorded from roadsides in Natal, where it acts as a pioneer plant on disturbed road margins (Linder, 1979).

The annual rainfall over the distribution area ranges from well over 1000 mm on the coast in Natal, to between 600 and 800 mm in the Northern Transvaal and Zimbabwe (Jackson, 1961). There does not seem to be a correlation between the habitat type (i.e. dry grassland or swampy) and rainfall. Most of the distribution area receives a summer maximum rainfall, with up to five dry months in winter. Only at the southern extreme of the distribution range is the precipitation evenly distributed over the whole year.

Flowering occurs from September to November, with very few collections from before (to July) or after (till December) the peak period.

Distribution: Distr. Pl. Afr. 2.

ZIMBABWE : Chipinga, Ball 572 (K, SRGH).

REPUBLIC OF SOUTH AFRICA :

TRANSVAAL : Nelspruit, Breyer 17693 (PRE); Nelspruit, Buitendag 710 (PRE); Soutpansberg, Crundell s.n. (PRE); Warmbaths, Dyer & Codd 4703 (BM, PRE, SRGH); Louis Trichard, Entabeni, Grewack s.n. (PRE); Barberton, White River, Holt 31 (PRE); Entabeni, Obermeyer s.n. (PRE); Pretoria, Strey 2896 (PRE); Kransberg, van der Merwe 2023 (PRE).

NATAL : Ingwavuma, Nyanemi Forest, De Winter & Vahrmeijer 8563 (PRE); Pinetown, Edwards 2866 (PRE); Pietermaritzburg, Gordon-Gray 6364 (NU); St. Lucia, Harrison 54 (BOL, PRE); Hlabisa, Harrison 60 (BOL); Lake Sibaya, Hart 6 (NU); Durban, Landsdell s.n. (PRE); Durban Westville, Lawson 192 (NU); St. Lucia, Louw 1953 (PRE); Scottburgh, Mauve 1052 (PRE); Clairmont, Meeboldt 13191 (PRE); Groutville, Moll 2538 (NU, PRE); Umlazi, O'Connor 209 (NU); Richards Bay, Plowes 2204 (PRE, SRGH); Durban, Sanderson 110 (BOL); Umhlabi, Schelpe 008 (NU); Shongweni, Schelpe 82 (NU); Ubombo, Stephen, Graan & Schwabe 1168 (PRE); Ixopo, Stewart 2061 (BOL, NU); Lower Tugela, Compensation, Stirton 1163 (PRE, SRGH); Durban, Strey 4530 (PRE); Durban, Strey 4852 (K, PRE, SRGH); Port Shepstone, Strey 6962 (PRE); Port Shepstone, Hibberdene, Strey 7762 (NU, PRE); Ubombo coastal belt, Tosh 41 (NU); Kosi, Lake Amanzimnayama, Vahrmeijer 1249 (PRE); Ubombo, Mbazwana, Ward 3494 (PRE); Durban, Ward 5184 (NU, PRE); Durban, Wood 6127 (PRE); Clairmont, Wood 11469 (PRE); Berea, Wylie 18 (BR, BOL).

TRANSKEI : Port St. Johns, McLoughlin s.n. (K, PRE, SRGH); Umkwani, Pondoland, Tyson 2610 (BOL, Z); Port St. Johns, Strey 10107 (PRE).

CAPE PROVINCE : Delagoa Bay, Earthy s.n. (BOL); Grahamstown, Read 1815 (K, BOL); Donkerhoek, Schlechter 3717 (BOL).

3. Disa chrysostachya Sw., K. Vet. Handl. 21 : 211 (1800); Willd. Sp. Pl. 4 (1) : 47 (1805); Lindl., Gen. Sp. Orch. : 349 (1838); H. Bolus, Journ. Linn. Soc. Lond., Bot. 25 : 197 (1889); Dur. & Schinz, Consp. Fl. Afr. 5 : 101 (1892); Kraenzl., Orch. Gen. Sp. 1 : 748 (1900); Schltr., Bot. Jahrb. 31 :

221 (1901); H. Bolus, Ic. Orch. Austro-Afr. 2 t. 68, 69 (1913); Rolfe, Fl. Cap. 5 (3) : 226 (1913); Jacot Guillarmod, Fl. Lesotho : 159 (1971); Ross, Fl. Natal : 143 (1972).-Type: Rep. S. Afr., Caput Bonae Spei, Sparrman s.n. (W holo-).

D. gracilis Lindl., Gen. Sp. Orch. : 348 (1838).-Type: Rep. S. Afr., Cape Province, Langekloof, Jan. 1830, Drège 2212 (K holo-; G, P, S, W iso-).

Tubers testicular, up to 100 mm long and 20 mm in diameter, shortly pilose. Sterile shoot rarely produced, up to 100 mm long; basal sheaths 2 - 4, hyaline, acute; leaves 2 - 4, erect, very narrowly elliptical, acute, up to 300 mm long and 50 mm wide. Fertile shoot robust, 250 - 500 - 1100 mm tall; cauline leaves generally 10 - 20, densely imbricate; the lowest 2 - 4 completely sheathing, obtuse, hyaline, c. 20 mm long; the next 5 - 15 leaves with narrowly ovate to narrowly lanceolate free blades from a ca. 40 mm long sheath, the largest leaf 130 - 98 - 60 mm long, the upper leaves grading into the floral bracts. Inflorescence dense, cylindrical, tapering, 90 - 270 - 550 mm long, flowers very numerous; bract narrowly ovate, acute or rarely sub-acuminate, c. 20 mm long, the apex deflexed, brown. Flowers small, c. 8 mm in diameter, orange, rarely yellow; dorsal sepal erect, elliptical, obtuse, galea 6 - 11 mm long, c. 3,5 mm wide and 2,5 mm deep, the upper margin incurved; spur pendent from c. 2 mm above the base of the dorsal sepal, clavate, acute or rarely obtuse, 5 - 11 mm long and 2 - 4 mm wide, dorso-ventrally flattened; lateral sepals oblong, obtuse, 5,5 - 7 - 9 mm long and 2,5 - 4,5 mm wide, shallowly concave, spreading to the sides with the apex usually curved forwards; petals sub-oblique, narrowly ovate, rounded or rarely obtuse, curved over the anther, 4,5 - 6 mm long and 2 - 3,5 mm wide; lip lorate, obtuse, pendent, c. 5 - 7 mm long; rostellum c. 1 mm tall, anther erect, c. 3,5 mm tall; ovary c. 10 mm long; stigma lateral lobes c. 1,5 mm tall; central lobe very small.

Notes: 1. Swartz, after his description, cited a Sparrman collection. The only Sparrman collection of D. chrysostachya that could be located is in Vienna. The hand-writing on the sheet appears to be very similar to that of Swartz. No other sheets of this collection could be located, and it is assumed that this is the holotype. It is generally known that Reichenbach collected parts of type specimens from all the major herbaria in Europe. It is not known where Sparrman collected the type, as he travelled through quite an extensive part of the southern end of the distribution range of the species, from Humansdorp to Somerset East (Forbes, 1945).

2. D. gracilis was described from a specimen collected from the Langkloof. According to Drège (1844), the materal was collected in January, between Welgelegen and Onzer, in a valley, at 1500 - 2000 feet. This locality is in the Langekloof in the Southern Cape Province, near the hamlet of Haarlem. Bolus (1889) included this species in the synonymy of D. chrysostachya, a point of view followed by all subsequent authors.

Distribution and Ecology: D. chrysostachya occurs in the montane regions of southern Africa (sensu White, 1978). In the southern

Cape Province, this species occurs on the coastal flats between Port Elizabeth and Knysna, and inland in the Hogsback Mountains. In the Transkei and Natal, it occurs in the Midlands and Uplands (sensu Ross, 1973). In Transvaal and the Free State this species occurs along the eastern escarpment, in the Drakensberg, from Leribe in Lesotho to Haenertsburg in the north. The altitude range increases from sea-level to 1950 m in the southern Cape Province to 1300 to 2100 m in the Transvaal.

The majority of collections are from marshy habitats, usually along the margins of swamps or in seepages in damp grassland. This species has also (but rarely) been recorded from dry grassland. Downing (1966) recorded *D. chrysostachya* as common in the Tabamhlope vlei in Natal. It occurred in a wet-saturated sedge-meadow, that did not dry out in the winter, and was locally flooded in the rainy season. In the Drakensberg it also occurs on dry rocky ledges at Ramatseliso Gate, and "mountain slopes and plateau" at Leribe (Lesotho) (Phillips, 1917). In the southern Cape Province coastal belt *D. chrysostachya* occurs as a roadside pioneer on damp to fairly dry road-fills (Linder, 1979). Generally fairly large populations are formed, in excess of 20 individuals, and populations may be quite dense.

Two major climatic regimes exist over the distribution range of this species. In the south, on the coastal plateau between Port Elizabeth and Knysna, the climate is equitable, with a precipitation of about 1000 mm p.a., evenly distributed over the whole year. Frost and snow do not occur. To the north of Port Elizabeth the precipitation is seasonal, with the rainfall maxima in the summer months. Most of the populations also occur inland at relatively high altitudes, where frost occurs frequently, and snow occasionally to frequently (Killick, 1963; Story, 1952). The rainfall range over the whole area is from 800 mm to over 1000 mm p.a. (Jackson, 1961).

The majority of populations of this species occur in Acocks' Veldtypes 8 (North-eastern Mountain Sourveld), 44 (Highland sourveld and Dohne Sourveld) and 57 (North-eastern Sandy Highveld) (Acocks, 1975). These are all secondary sour grasslands.

Flowering occurs from November to January.

Variation: Extensive variation in spur length and flower colour occurs. Spur length variation was analysed from six population samples, taken over the whole range of the species (Haenertsburg, 2329DD, Dullstroom, 2530AC, Wakkerstroom, 2730DD, Drakensberg Garden, 2929CC, Gaikas Kop, 3226DB and Humansdorp, 3423BB). Where possible, more than 20 plants were sampled at each station. One or two flowers were collected from each plant, and preserved in liquid for later analysis. The ratio between spur length and dorsal sepal length is given in Fig. 6. This shows that the more northern populations are longspurred compared to the southern populations: this character indicates a topocline.

Flower colour ranges from orange to a bright orange red, but this could not be correlated to a geographical pattern. Occasional pure yellow specimens have been found. These appear to be recessives.

Distribution: Distr. Pl. Afr. 3.

SWAZILAND : Henderson, Forbes concession, Galpin 717 (BOL).

LESOTHO : Leribe plateau, Dieterlen 131 (K, PRE, Z); Leribe Plateau, Dieterlen 6964 (GRA); Sehlabathebe, Jacot Guillarmod,

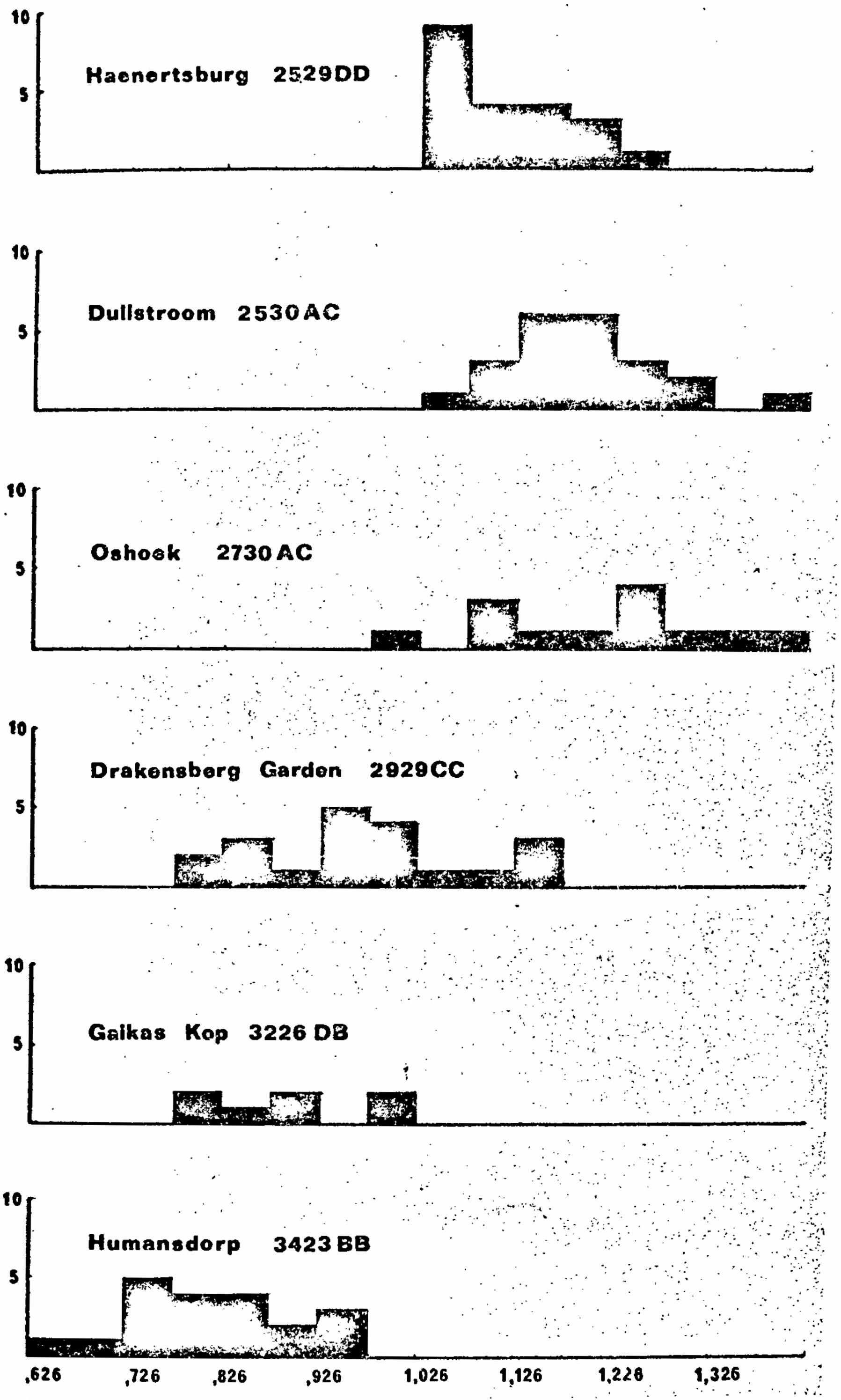


Fig. 6. -- Variation in the ratio of spur length over dorsal sepal length in D. chrysostachya Sw. The data are from six population samples in South Africa. The localities of the samples are given using the Degree Reference System suggested by Edwards and Leistner (1971).

Getliffe & Mzamane 18 (PRE); Blue Mountain Pass, Ruch 4 (PRE); Lesotho, Ruch 2390 (PRE); Lesotho, Staples 288 (PRE).

REPUBLIC OF SOUTH AFRICA :

TRANSVAAL : Ermelo, Burtt-Davy 916 (K, BOL); Carolina, Burtt-Davy 7342 (K); Belfast, Bolus 12326 (BOL); Barberton, Culver 66 (K); Pietersburg, Haenertzburg, Cunliffe s.n. (BOL); Wakkerstroom, Devenish 476 (PRE); Dullstroom, Galpin 13048 (BOL, K, PRE); Wakkerstroom, Galpin s.n. (BOL); Belfast, Hall 842 (BOL); Dullstroom, Hartbeesfontein, Harding s.n. (PRE); Nelspruit, Witklip, Kluge 311 (PRE); Belfast, Leendertz 2860 (K); Pietersburg, Haenertzburg, Murray 3 (PRE); Belfast, Pole-Evans s.n. (PRE); Mavieriestad, Pot 5140 (PRE); Witbank, Botsabelo, Schlechter 3778 (Z); Belfast, Schweickerdt 1018 (PRE, W); Barberton, Lomati Valley, Thorncroft 1100 (PRE); Barberton, Saddleback mts., Thorncroft 1178 (K, PRE); Pietersburg, Haenertzburg, Van der Merwe 274 (K, PRE); Ermelo, Walker s.n. (PRE); Belfast, Worsdell s.n. (K).

ORANGE FREE STATE : Harrismith, Van Reenen, Acutt 9 (NU); Orange Free State, Cooper 979 (K); Harrismith, Besters Vlei, Jacobsz s.n. (PRE); Harrismith, Van Reenen, Van der Zeyde & Jooste s.n. (PRE).

NATAL : Ngome, Acocks 13957 (K, PRE); Durban, Kloof, Ball-Maskey s.n. (BR, PRE); Inchanga, Bates 32 (NU); Dumisa, Bayer 1415 (NU); Richmond, Bell s.n. (BOL); Van Reenen, Bews 859 (NU); East Griqualand, Sussex Downs, Boardman 297 (BOL); Oliviers Hoek, Boyle s.n. (K); Natal, Buchanan s.n. (K); Ixopo, Clark 19 (BM); Estcourt, Broadmoor Vlei, Downing 268 (NU, PRE); Durban, Kloof, Dyke in Marloth

5514 (PRE); Kokstad, Edwards 101 (NU); Hlatikulu, Giants Castle, Edwards 2433 (NU, PRE); Kamberg, Gallways 50 (NU); Underberg, Grice s.n. (NU); Underberg, Hall 781 (BOL); Kamberg Reserve, Hilliard & Burtt 8721 (NU); Belfort, Jacottet 80 (Z); Van Reenen, Jooste s.n. (M); Giants Castle, Luckhoff s.n. (NU); East Griqualand, Swartberg, Marais 1419 (K, PRE); Underberg, farm 'Rainbow', O'Connor 243 (NU); Polela, O'Connor 256 (NU); Pietermaritzburg, Zwartkop, O'Connor 263 (NU); Emtonjaneni, Katazo, Porter s.n. (BOL); Polela, Rennie 299 (NU); Polela, Rennie 500 (NU9; Polela, Rennie 725 (NU); Durban, Rogers 15082 (BM); Rosetta, Rogers 28143 (Z); Dumisa, Rudatis 160 (P); Alexandra, Umgoya, Rudatis 544 (BM, K, P, W, Z); Natal, Sanderson 480 (S); Fields Hill, Sanderson 601 (K); Bergville, Cathedral Peak area, Schelpe 964 (NU); Ixopo, Shirley s.n. (NU); Estcourt, Giants Castle reserve, Stewart 1523 (NU); Pietermaritzburg, Hilton, Stewart 1633 (NU); Umzinto, Umgai, Strey 6207 (BR, PRE); Estcourt, Giants Castle, Symons 298 (PRE); East Griqualand, Clydesdale, Tyson 2904 (BOL, K); Pietermaritzburg, Worlds View, Venter 185 (PRE); Nottingham Rd., Wood 1020a (BM).

TRANSKEI : Ramatseliso Nek, Boardman 16 (PRE); Port St. Johns, Galpin 3418 (PRE); Matatiele, MacAlpine, McLoughlin 168 (BOL); Port St. Johns, McLoughlin s.n. (BOL); Emagusheni, Mt. Enkansweni, Reynolds 3440 (BOL, PRE); Port St. Johns, Rutgers 12 (BOL); Emagusheni, Flagstaff, Schelpe 5066 (BOL); Fort Donald, Tyson 1594 (BOL, GRA, PRE).

CAPE PROVINCE : Plettenberg Bay, Acocks 363 (S); Humansdorp, Stormsriverbridge, Acocks 21763 (K, PRE); Humansdorp, Lottering, Bayliss 6228 (BR, K, Z); Somerset East, Bolus 1815 (BOL); Bathurst, source of Kasinga River, Burchell 4129 (K); Uniondale, Louterwater, Compton 4513 (BOL); Langekloof, Drège 2212 (BOL, K); Port Elizabeth, Emeralds Hill, Drège s.n. (PRE); Humansdorp, Witte Els Bosch flats, Esterhuysen 6831 (BOL); Humansdorp, Fourcade 528 (K); Humansdorp, Witte Els Bosch, Fourcade 964 (K, Z); Humansdorp, Witte Els Bosch, Fourcade 969 (GRA); Knysna, Garside 213 (K); Port Elizabeth, Gordon s.n. (PRE); Port Elizabeth, Walmer, Hallack 949 (BR); Knysna, towards Assegaaibosch, Hill s.n. (K); Humansdorp, Witte Els Bosch, Hutchinson 1391 (BR, K, PRE); Eastern Frontier, Hutton s.n. (BOL, K); Grahamstown, Howiesons Poort, Hutton s.n. (K); Port Elizabeth, Kemsley 1112/178 (Z); Elliot, Ugie, King s.n. (BOL); Knysna, Ratelsbosch, Laughton 80 (BOL); Knysna, near Plettenbergbay, Leipoldt s.n. (BOL, PRE); Port Elizabeth, Bog Farm, Long 1429 (PRE); Port Elizabeth, Walmer, MacOwan s.n. (PRE); Somerset East, Boschberg, MacOwan s.n. (Z); Port Elizabeth, Walmer, MacOwan & Bolus 949 (BM, BOL, K, P, UPS, W); Humansdorp, Coldstream, Marais 576 (GRA, PRE); Port Elizabeth, Paterson s.n. (BOL); Knysna, Blaawkranz, Penther 43 (M. S. W); Knysna, Soutrivier, Penther 52 (M, S, W); Knysna, Keurboomsriver, Penther 84 (W); Knysna, Penther 211 (M, W); Georgetown, Prior s.n. (K); King Williams Town, Hogsback, Rattray 14 (PRE, SRGH); Knysna, Plettenbergbay, Rogers 26697 (BOL); Humansdorp, near Coldstream, Schelpe 4352 (BOL); Knysna, Schlechter 5917 (PRE, Z); Humansdorp, Lottering, Schoenau 302 (BOL); King Williams Town, summit of Elandsberg, Scully 409 (BOL); Knysna, Plettenbergbay, Smart s.n. (PRE); Maclear, Stewart 1869 (NU); Humansdorp, Theron 1835 (K, PRE); Between Plettenbergbay and Humansdorp, Werdermann & Oberdieck 1008 (BR, K, PRE); Port Elizabeth, West 202 (BR, PRE); Knysna, Wettstein s.n. (M).

4. Disa ochrostachya Reichb.f., Flora 48 : 181 (1865); Dur. & Schinz, Consp. Fl. Afr. 5 : 105 (1892); N.E.Br., Fl. Trop. Afr. 7 : 279 (1898); Kraenzl., Orch. Gen. Sp. 1 : 749 (1900); Schltr., Bot. Jahrb. 31 : 217 (1901); Summerh., Fl. W. Trop. Afr. 2 : 414 (1936); Piers, Orchids E. Africa : 61 (1968); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 164 (1968); Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 68 (1974); Agnew, Upland Kenya Wild Flowers : 746 (1974).-Type: Angola, Huilla, Welwitsch 712 (BM holo-; K, W iso-).

D. aurantiaca Reichb.f., Flora 50 : 98 (1867); Dur. & Schinz, Consp. Fl. Afr. 5 : 106 (1892).-Type: Angola, Morro de Lopollo, Welwitsch 713 (BM holo-; W iso-).

D. adolphi-friderici Kraenzl., Bot. Jahrb. 43 : 331 (1901).-Type: Zaire, Kivu volcano, between the Ruhondo and Mwulera lakes, 1800 m, montane meadows, Mildbraed 1806 (B holo-), iconotype: Deutsch. Zentr.-Afr.-Exped. 2 : pl 6 A-C (1911).

Tubers testicular, entire or bifid, up to 60 mm long and 30 mm in diameter. Sterile shoot robust, up to 150 mm long; basal sheaths 3, obtuse to sub-acute; leaves 2 - 3, erect, narrowly elliptical, acute, conduplicate, 150 - 200 mm long and 40 mm wide. Fertile shoot slender to robust, 400 - 900 mm tall; cauline leaves imbricate, the basal leaf completely sheathing, 30 - 40 mm long, the remainder 50 - 90 mm long and 10 - 30 (-40) mm wide, acute or apiculate, rarely with free blades, grading apically into the floral bracts. Inflorescence dense, cylindrical, tapering, 150 - 300 mm long and with 50 - 200 flowers; bract longer than the flower, 15 - 25 mm long,

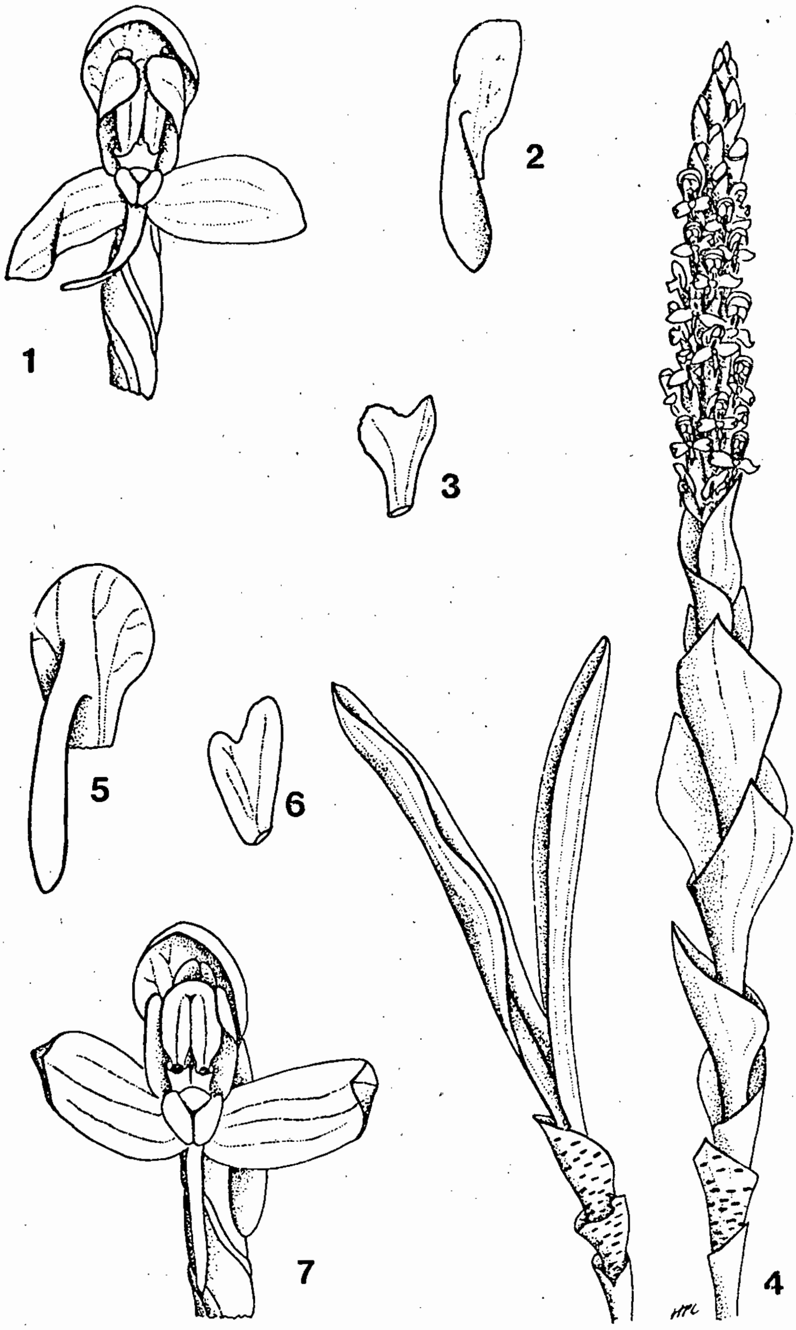


Fig. 7.-- Series Micranthae: 1 - 3 D. satyriopsis Kraenzl. (X 3) from Richards 7703, 1, frontal view of flower, 2, dorsal sepal, 3, petal. 4, D. satyriopsis Kraenzl. (X 0,25) from Linder 2021. 5 - 7 D. ochrostachya Reichb.f. (X 3) from Cribb & Grey-Wilson 10778, 5, dorsal sepal showing spur, 6, petal, 7, frontal view of flower.

acute to acuminate, the apex reflexed. Flowers small, c. 10 mm in diameter, bright yellow or yellow with orange mottling; dorsal sepal obovate, obtuse, galea 6 - 9 mm long, 4 - 7 mm wide and 2 - 3 mm deep, curved to face down; spur pendent from the middle of the dorsal sepal, 7 - 12 mm long, more or less inflated in the lower half, subacute; laterals oblong, obtuse to subacute, 6 - 9 mm long and 3 - 6 mm wide, shallowly concave, spreading sideways, the apex curved forwards; petals bifid, the posterior lobe 5 - 7,5 mm tall, 1 - 2 mm wide, obtuse or subacute, erect behind the anther, anterior lobe 3 - 6 mm tall, narrow and reaching 2/3 up the length of the main petal and flanking the anther, rarely somewhat taller; lip usually linear, sometimes irregularly toothed, pendent, acute, 5 - 9 mm long and 0,5 - 1,5 mm tall; ovary 10 - 15 mm long; stigma 0,5 - 1 mm tall, lateral lobes well developed.

Notes: 1. Reichenbach described both *D. ochrostachya* and *D. aurantiaca* from the Welwitsch collection housed at the British Museum, where Welwitsch took his collection after he left Portugal. Reichenbach studied the material there, as is evidenced by the fact that of *D. aurantiaca* there is a complete specimen at the British Museum, but only a single flower in a capsule in Vienna. Reichenbach (1865) refers to Welwitsch 702 as the type of *D. ochrostachya*, but the sheet that he annotated is in fact Welwitsch 712. N.E. Brown (1898) does not refer to *D. aurantiaca*, but cites Welwitsch 712 and 713. The latter is the type of *D. aurantiaca*. Kränzlin (1900) placed *D. aurantiaca* into his "Species subdubiae mihi non visae". Schlechter (1901) included *D. satyriopsis* and *D. aurantiaca* in the synonymy of *D. ochrostachya*. Summerhayes (1968) did not mention *D. aurantiaca*.

2. The type of *Disa adolphi friderici* has been lost, but an illustration of it survives. From this, and the description, it is clear that this species has to be included in *D. ochrostachya*. Kraenzlin (1909) noted that his new species was very close to *D. ochrostachya*. Schlechter ((1915) included *D. adolphi friderici* in *D. satyriopsis*, which he, contrary to his earlier opinion, separated from *D. ochrostachya*. Summerhayes (1968) included it in the synonymy of *D. ochrostachya*.

3. In 1905 Rendle described a var. *major* for *D. ochrostachya*. This variety was based on a specimen collected by the botanist attached to the Anglo-German Uganda Boundary Commission, Dr. A.G. Bagshawe, from near Lake Karenge in Uganda. The material is housed in the British Museum. It cannot be upheld, as it is well within the variation range of *D. ochrostachya.*

Distribution and Ecology: *D. ochrostachya* is widely distributed in the montane regions of Africa south of the Sudan. The altitude range is from 1500 m to 2600 m above sea level.

Collections have been made from swamps, montane grasslands, grasslands and open savanna woodlands. The majority of collections are from montane grasslands. Rattray & Wild (1961) described these as Themeda or Loudetia grasslands. Vesey-Fitzgerald (1963) described the montane grasslands of southern Tanzania and northern Zambia in some detail. They agree with the Themeda grasslands that Knapp (1973) described from Zimbabwe and Angola, and the Themeda-Andropogon grasslands that he described for the rest of the afro-montane region.

Rainfall over the distribution range is mostly about 1000 mm p.a. (Jackson, 1961), but in mountainous areas it can vary from 740 - 3000 mm p.a. (Phipps & Goodier, 1962; Chapman & White, 1970). The winter months are generally dry, often with mists. Frosts may occur at the higher altitudes.

Populations studied on the Nyika Plateau had low population densities, with the plants occurring scattered over the plateau.

Although flowering occurs in summer, there is some local variation in the exact flowering months. In Tanzania, Zambia and Zimbabwe, almost all flowering specimens were collected in January and February. In Angola flowering occurs from October to December. In the Northern Hemisphere, flowering occurs from June to August. In Uganda flowering occurs from August to December.

Variation: Two distinct geographical forms can be recognized in D. ochrostachya. In the northern half of the distribution range (north of Lake Malawi) the spur is 7,5 to 12 mm long, and the anterior lobe of the petal is almost parallel sided. In the southern half of the distribution range the spur is 9 - 12,5 (-15) mm long, and the anterior lobe of the petal reasonably well developed, so that the petal looks triangular and unequally bifid.

These two morphological forms could not be correlated to flowering time, flower colour or flower size. There is also extensive overlap between the two character states. No extensive population samples were available to measure the range of variation within a population. Clearly this variation cannot be recognized formally.

Distribution: Distr. Pl. Afr. 4.

KENYA :

RIFT VALLEY PROVINCE: Kitale, Cunningham - Van Sonneren

43 (K); Londiani, Geesteranus 5164 (K); Uasin Gishu, Gardner 1415 (K); Londiani, Graham, 3220 (K); West Lembus forest, Graham 3507 (K); Kipkabus, Piers 96 (K); Timboroa, Tweedie 664 (K).

UGANDA :

WESTERN PROVINCE : Near Lake Karenge, Bagshawe s.n. (BM); Karangora, Osmaston 3958 (BR, K); Igua, Purseglove 462 (BR, K); Mt. Ruwenzori, Wollaston s.n. (BM).

CAMEROUN : Mt. Gotel, Letouzey 8614 (BR, K, P); Bamenda, Maitland 1779 (K); Mt. Santa, Saxer 2 (K).

TANZANIA :

SOUTHERN PROVINCE : Songea, Matengo Hills, Milne-Redhead & Taylor 8921 (K).

SOUTHERN HIGHLANDS : Mt. Mtorwi, Cribb & Grey-Wilson 10778 (K); Iringa, Lupembe, Schlieben 1403 (BR, K, S, Z); Ukinga, Ubena, Ward 57 (K).

WESTERN PROVINCE : Buha, Kahinzi, Verdcourt 3411 (BR, K, PRE).

RWANDA : Nyakarambi, Bamps 2775 (BR); Kibungo, Troupin 15626 (BR).

BURUNDI : Bururi, Lewalle 2761 (BR); Kitega, Kuruzi, Van der Ben 2421 (BR, K).

ZAIRE :

SHABA : Kundelungu, Darcis 154 (BR); Kisamba, Kinet 70 (BR); Kundelungu, Schmitz 4308 (BR); Kitu, Urira, Symoens 2025 (BR).

KIVU PROVINCE : Rutschuru, Bequart 1919 (BR, K); Bogora Mboga, Bequart 4981 (BR).

MALAWI :

NORTHERN PROVINCE : Nyika Plateau, Chapman 92 (BM); Nyika Plateau, Lake Kauline, Chapman 379 (BM); Nyika Plateau, Matthews EM 31 (SRGH); Nyika Plateau, Pawek 2119 (K);

Nyika Plateau, Pawek 7931 (K, SRGH); Nyika Plateau, Richards 10449 (K); Nyika Plateau, Robson 645 (K); Nyika Plateau, Sanderson 25 (BM).

ZAMBIA :

NORTHERN PROVINCE : Nyika Plateau, Benson 396 (BR, K); Kawambwa, Mbereshi River, Holmes 288 (K); Kasama, Mungwi, Robinson 4198 (K, M, SRGH); Nyika Plateau, Williamson 146 (K); Nyika Plateau, Williamson 794 (K, SRGH); Kawambwa, Mbereshi - Nchelenga rd., Williamson 1227 (SRGH).

ANGOLA :

MOXICO : Near Vila Luzo, Young 1263 (BM); Vila Luzo, Young 1370 (BM, SRGH).

HUAMBO : Mt. Moco, Huntley, Roberts & Ward 79 (PRE).

HUILLA : Lubango, Barbosa 10370 (SRGH); Huilla, Welwitsch 712 (BM, K); Huilla, Welwitsch 713 (BM).

ZIMBABWE : Inyanga, Beasley 56 (K, SRGH); Rusape, Best 1262 (SRGH); Inyanga, Chase 4362 (BM); Inyanga, Troutbeck, Chase 7289 (SRGH); Inyanga, Chase s.n. (SRGH); Melsetter, Tarka Forest Reserve, Crook 515 (SRGH); Melsetter, Crook 516 (K, SRGH); Rusape, Munch 227 (SRGH); Inyanga, Norlindh & Weimarck 4766 (BM, BR, K); Mt. Inyangani, Norlindh & Weimarck 5085 (K); Chipinga, Percy-Lancaster 89 (SRGH); Inyanga, Bideford Wattle Estate, Plowes 2309 (SRGH); Inyanga, Wild 937 (K, SRGH).

5. **Disa satyriopsis** Kraenzl., Bot. Jahrb. 28 : 177 (1901).

-Type: Tanzania, Southern Highlands, Uhehe, Goetze 577 (B holo-), Zambia, Nyika Plateau, Feb. 1968, Williamson, Ball & Simon 357 (SRGH neo-).

Notes: The type of this species is, unfortunately, lost. From the description it is clearly allied to the *D. ochrostachya* complex, and most botanists (Schlechter, 1901; Summerhayes, 1968) have included it in the synonymy of that species. The spur shape ("calcari . . . clavato v. fusiformi") and petal shape ("petalis dolabratis acutis margine anterior crenulatis") indicate that the name applies to the taxon that Williamson (1977, 1980) recognized as being distinct.

Ecology and Distribution: *Disa satyriopsis* is restricted to the highlands around the northern edge of Lake Malawi and the eastern margins of Lake Tanganyika. It occurs between the altitudes of 1800 and 2500 m above sea level. The rainfall in this area varies from 1000 to 2500 mm p.a. (Jackson, 1961; Chapman & White, 1970). The five winter months tend to be dry but mists often occur in the early part of the dry season. Frosts can be severe.

All collectors notes indicated that this is a grassland species, which occurs in dry to well-drained grassland (except for Schlieben 1403, recorded from a "moist meadow"). This is likely to be the Themeda-Exotheca grassland described by Knapp (1973). Vesey-Fitzgerald (1963) described it in some detail. Field studies on the Nyika Plateau in Malawi showed that this species tended to form extensive populations on the drier ridges, but the populations were never dense.

Flowering occurs in January and February, with rare records of flowering specimens from December. Copious nectar is produced.

Distribution: Distr. Pl. Afr. 5.

TANZANIA :

SOUTHERN HIGHLANDS : Rungwe mts., Ball 794 (K); Between Isoko and Ibaba, Cribb & Grey-Wilson 10714 (K); Rungwe, Kiwira, Proctor 1628 (K); Njombe, Mtorwi Peak, Richards 7703 (BR, K); Kipengere Mountains, Richards 14009 (K); Kipengere Mountains, Richards 14017 (K); Between Njombe and Mlangala, Richards 14220 (K); Kukuya, Kiwira River, Richards 14241 (K); Kyimbila, Ukinga, Stolz 2450 (BM, BR, C, K, P, S).

WESTERN PROVINCE : Kigoma, Kasulu, Rounce 12 (K).

MALAWI :

NORTHERN PROVINCE : Nyika Plateau, Holmes 201 (K, SRGH); Nyika Plateau, Grosvenor & Renz 1117 (SRGH); Nyika Plateau, Pawek 8093 (K, P).

ZAMBIA :

NORTHERN PROVINCE : Nyika Plateau, Ball 1071 (SRGH); Nyika Plateau, Williamson, Simon & Ball 357 (K, SRGH).

6. *Disa fragrans* Schltr.

Tubers testicular, c. 30 mm long. Sterile shoot up to 70 mm long; basal sheaths 2 - 3; leaves usually 2, narrowly elliptical, acute, semi-erect, conduplicate, 70 - 200 mm long and 10 - 30 mm wide. Fertile shoots generally robust, 70 - 250 - 500 mm tall; cauline leaves imbricate, the lower 2 - 3 reduced to sheaths, the remainder with free narrowly lanceolate to ovate acute blades, 30 - 100 mm long and 15 - 45 mm wide, grading apically into the floral bracts. Inflorescence dense, cylindrical, occasionally even sub-globose, 30 - 100 mm long and with 30 - 150 flowers; bracts narrowly ovate, acute, 10 - 15 mm long, the apexes frequently reflexed. Flowers small, c. 8 mm in diameter, white to pale lilac to rarely crimson, usually mottled darker than the base colour, often with a strong scent; dorsal sepal erect, oblong to elliptic-oblong, obtuse, galea 4,5 - 7 mm long, 2,5 - 4 mm wide and 1 - 2 mm deep, the upper margin incurved; spur originating 1/3 above the base of the dorsal sepal, 4 - 7,5 - 10 mm long, always reaching below the base of the dorsal sepal, slender or apically clavate, frequently sub-acute, pendent at c. 45°; lateral sepals oblong, obtuse to sub-acute, 5 - 6,5 mm long and 2 - 2,5 mm wide, boatshaped, spreading sideways with the apexes curved forwards; petals entire, lanceolate to oblanceolate, acute to obtuse, 3,5 - 6,5 mm long and 1 - 1,8 mm wide, erect with the tips curved over the anther; lip narrowly oblanceolate, 3 - 6 mm long, 0,4 - 1 mm wide, acute to obtuse, semi-pendent; rostellum c. 1 mm tall; anther semi-erect, 2,5 - 3 mm tall; ovary c. 10 mm long; stigma 0,5 - 1 mm tall.

6a. *Disa fragrans* Schltr. ssp. *fragrans*

Disa fragrans Schltr., Bot. Jahrb. 20 Beih. 50 : 40 (1895); Kraenzl., Orch. Gen. Sp. 1 : 748 (1900); Schltr., Bot. Jahrb. 31 : 223 (1901); Rolfe, Fl. Cap. 5 (3) : 225 (1913); Jacot Guillarmod, Fl. Lesotho : 158 (1971); Ross, Fl. Natal : 143 (1972).-Type: Rep. S. Afr., Transvaal, Houtboschberg, in rock cracks near the summit, March 1894, Schlechter 4712 (K lecto-; BOL, Z iso-), Schlechter 4445 (BOL, S syn-).

D. leucostachys Kraenzl., Bot. Jahrb. 30 : 285 (1901); Schltr., Bot. Jahrb. 53 : 540 (1915).-Type: Tanzania, Kinga Mountains, May 1899, Goetze 970 (B holo-; BR iso-).

Monadenia junodiana Kraenzl., Vierteljahrschr. Nat. Ges. Zuerich 74 : 108 (1929).-Type: Rep. S. Afr., Transvaal, summit of Mamotsuiri, Junod 1208 (Z holo-).

Flowers white to pale lilac, usually mottled darker than the base colour, strongly scented; spur on the dorsal sepal (4-) 7,5 - 10 mm long; petals oblanceolate, obtuse, widest above the middle; occurring southwards from Mt. Kilimanjaro.

Notes: 1. Schlechter (1895) described _D. fragrans_ from two collections. Schlechter 4445 was collected from the summit of the Houtboschberg in the Eastern Transvaal as it was starting to flower. From there Schlechter continued his journey northwards, and on his return journey some weeks later, he again visited the mountain, and made another collection, Schlechter 4712. As there are more duplicates of the latter collection, and both originate from the same population, the latter collection is here designed as the lectotype.

2. _D. leucostachys_ was for some time treated as the tropical form of _D. fragrans_. Schlechter (1915) maintained it as a distinct species, but remarked: "The species is very close to _D. fragrans_ Schltr. from Transvaal and Natal, but it has larger flowers and because of that thicker inflorescences". This character has not been found to hold, and Summerhayes (1968) included _D. leucostachys_ in the synonymy of _D. fragrans_.

3. *Monadenia junodiana* was described from Junod 1208, collected from the "summit of Mamotsuiri". This locality is unknown, but Junod is known to have collected in Lesotho and on the Natal and Orange Free State sides of the Drakensberg. This falls in the distribution range of the species. Why Kraenzlin placed this species in *Monadenia* is completely obscure, as inspection of the holotype showed that it is typical of *D. fragrans.*

Distribution and Ecology: Subsp. *fragrans* occurs in the Austro-Afro-Alpine zone (sensu Killick, 1978) in South Africa, and in the upper montane zone (sensu White, 1978) in the Transvaal (South Africa), Zimbabwe and Tanzania. The altitude range varies from area to area, but in general it is between 1800 and 3000 m above sea level. In Tanzania all collections are from between 2100 and 2700 m, in Zimbabwe and Mocambique from 1650 to 2100 m, and in South Africa between 1800 and 2100 m in the Transvaal and between 2000 and 3000 m in the Natal Drakensberg.

This is a grassland species, often forming extensive populations in damp montane grassland. Occasional collections have also been made from rock crevices, but these plants tend to be stunted (Ball 649, Linder 1022).

The climate at these high altitudes has not been extensively documented. Killick (1978c) published some climatic data for the alpine belt in Lesotho, which showed a rainfall of about 1000 mm p.a., but with considerable variation from locality to locality. 77% of the rain falls between October and March. Frost and heavy snowfalls occur in winter. Subsp. *fragrans* occurs mostly in the Merxmuellera-Festuca-Pentaschistis grassland (Killick, 1978; = alpine grassland of Killick, 1978b) on shallow soils derived from basalt. No data are available on the upper montane regions of the Transvaal Drakensberg. In Zimbabwe the rainfall varies from 740 to 3000 mm p.a., depending on the aspect and altitude. Above 1500 m mist occurs frequently, and frost may be severe in the winter (Phipps & Goodier, 1962). In Southern Tanzania the annual rainfall at the altitudes at which ssp. fragrans is found is between 1500 and 2000 mm p.a., mostly concentrated in the summer months (Kerfoot, 1964).

Flowering time tends to be in late summer, but there is some regional variation. In South Africa and Tanzania the vast majority of flowering specimens were collected between January and March. In Zimbabwe flowering appears to occur mostly in April and May, with occasional collections from as early as February, or as late as July.

Variation: Field studies in the Drakensberg revealed extensive variation within populations, particularly with respect to flower colour, spur length and flower size. Similar variation was also found between populations. Some variation, particularly in general plant robustness, is found between the major distribution centres, South Africa, Zimbabwe and Tanzania.

In the Drakensberg flower colour may vary from a fairly deep rose or pink to almost white. The degree of mottling varies from intense to almost invisible. Ball 649 from the Chimanimani Mountains in Zimbabwe is recorded as being 'pure white'. A similar degree of variation is evident from collectors' notes from Tanzania.

Plant robustness depends partially on the habitat. Specimens collected from rock ledges tend to be somewhat stunted. The majority of collections from Zimbabwe are more robust than plants from South Africa. This might be related to the generally less extreme conditions under which the Zimbabwean populations grow.

Distribution: Distr. Pl. Afr. 6.

TANZANIA :

EASTERN PROVINCE : Morogoro District, Semsei 1711 (K).

SOUTHERN HIGHLANDS : Between Poroto and Kitulo, Cribb & Grey-Wilson 10759 (K); Kitulo, Fuller 61 (K); Mbeya Peak, Kerfoot 1766 (K); Elton Plateau, Proctor 1653 (K); Mt. Rungwe, St. Clair - Thompson 867 (K); Ukinga, Stolz 2611 (BM, BOL, K, S, Z).

MOCAMBIQUE :

MANICA E SOFALA : Chimanimani mts., Binga, Dutton 139 (SRGH); Chimanimani mts., Munch 76 (PRE, SRGH); Gorongosa mt., Schelpe 5492 (BM, BOL).

ZIMBABWE : Vumba, Bacon in SRGH 6852 (SRGH); Chimanimani mts., Ball 648 (K, SRGH); Chimanimani mts., Ball 649 (K, SRGH); Mt. Inyangani, Brewer 239 (SRGH); NE of Penhalonga, Chase 2156 (BM, SRGH); Vumba mts., Chase 4065 (SRGH); Inyanga, Rhodes Estate, Chase 4942 (BM, BOL, K, SRGH); Vumba mts., Chase 6016 (BM, K); Melsetter, summit of Mt. Peri, Chase 6393 (SRGH); Chimanimani mts., Chase 7503 (SRGH); Umtali, Zwitambo Mt., Chase s.n. (BOL); Melsetter, Tarka Forest Reserve, Crook 405 (BOL, K, SRGH); Melsetter, Skyline, Crook 463 (K, SRGH); Melsetter, Cooper in Eyles 3515 (BOL, PRE); Inyanga, Mare Dam, Drewe 88 (SRGH); Melsetter, Eyles 3515 (BOL, PRE); Inyanga, Worlds View, Edwards 935 (K, SRGH); Vumba mts., Ferrar 3982 (PRE); Inyanga

Downs, Garley 21 (SRGH); Inyanga Dams, Gilliland 1897 (K); Vumba, Greenfield s.n. (SRGH); Chimanimani mts., Grosvenor 363 (K, SRGH); Melsetter, Grosvenor 366 (K, SRGH); Mt. Inyangani, Grosvenor 831 (BOL, SRGH); Chimanimani mts., Hall 420 (BM, BOL); Inyanga, Hopkins s.n. (K, SRGH); Chimanimani plateau, Leach 9041; Umtali, Stapleford, Martineau 365 (SRGH); Chimanimani mts., McCosh 6 (K, SRGH); Chimanimani mts., Munch 5 (SRGH); Chimanimani mts., Munch 76 (K); Chimanimani mts., Phipps 645 (BR, K); Chimanimani mts., Phipps 681 (K, SRGH); Inyanga, Rushworth 775 (K, SRGH); Zimbabwe, Thompson 39 (PRE, SRGH); Inyanga, Rukotso Range, Whellan 1653 (SRGH); Chimanimani mts., Weiste s.n. (SRGH); Inyanga, Bideford Hill, West 7287 (SRGH); Melsetter, Orange Grove, Ziervogel s.n. (SRGH).

REPUBLIC OF SOUTH AFRICA :

TRANSVAAL : Athole Power Station, Codd & Muller 293 (PRE); Pietersburg, Haenertzburg, Wolkberg, Davidson 3121 (BOL); Middelburg, Kassner 1374 (BR); Lydenburg, Mt. Anderson, Lavranos 4039 (BOL); Lydenburg, Mt. Anderson, Mauve 4634 (PRE); Pietersburg, Haenertzburg, Houtboschberg, Schlechter 4712 (GRA, K).

ORANGE FREE STATE : Witzieshoek, Mopedis Peak, Thode 55 (BOL); Clarens, Golden Gate, Wium 16 (BOL).

NATAL : Underberg, Sani Valley, Brooke 32 (BM); Estcourt, Giants Castle, Bruyns-Haylett 48 (NU); Bergville, Cathedral Peak, Killick 2298 (K, PRE); Bergville, Mt aux Sources, Linder 2060 (BOL); Bulwer, Amarwaga Mt., McClean 229 (PRE); Bergville, Mt aux Sources, McClean 286 (GRA, K); Underberg, farm 'Highlands', Nicholson s.n. (PRE); Bergville, Cleft Peak, Schelpe 516 (NU); Bergville, Mt aux Sources, Schelpe 1314 (NU); Bergville, Organ Pipes Pass, Schelpe 7251 (BOL); Bergville, Witches, Schelpe 7667 (BOL); Estcourt, Giants Castle, Symons 366 (PRE); Bulwer, Amakwa mt., Wood 4565 (BOL, K, Z); Estcourt, Giants Castle, Trauseld 555 (PRE, NU); Estcourt, Giants Castle, Wright 1366 (NU).

TRANSKEI : Matatiele, Ramatseliso Gate, Acocks 22096 (PRE); Matatiele, Quachas Nek, Acocks 22187 (PRE); Matatiele, Ramatseliso Nek, Boardman 38 (PRE); Matatiele, Ramatseliso Nek, Boardman 257 (K); Matatiele, Galpin 14079 (BOL, PRE); Matatiele, Quachas Nek, Mauve 4827 (PRE); Matatiele, Quachas Nek, Mauve 4835 (PRE); Matatiele, Filikemotho Pass, McLoughlin 187 (BOL); Matatiele, Porters Hoek, McLoughlin 215 (BOL); Matatiele, Hobdays mt, McLoughlin 221 (BOL).

CAPE PROVINCE : Maclear, Tsitsa footpath, Galpin 6837 (BOL, GRA, K, PRE); Maclear, Naudes Nek Pass, Linder (BOL).

LESOTHO : Sehlabathebe, Jacottet 60 (Z); Source of Singu, Milford 656 (K).

6b. Disa fragrans Schltr. ssp. deckenii (Reichb.f.) Linder, comb. nov. et stat. nov., basionym: Disa deckenii Reichb.f., Otia Bot. Hamb. (2) : 105 (1881); Dur. & Schinz, Consp. Fl. Afr. 5 : 102 (1892); N.E.Br., Fl. Trop. Afr. 7 : 280 (1898); Kraenzl., Orch. Gen. Sp. 1 : 750 (1900); Schltr., Bot. Jahrb. 31 : 223 (1901); Piers, Orchids E. Africa : 57 (1968); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 165 (1968); Cufodontis, Bull. Jard. Nat. Belg. 42, Suppl.: 1609 (1972); Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 64 (1974); Agnew, Upland Kenya Wild Flowers : 746 (1974).-Type: Tanzania, Kilimanjaro, Kersten s.n. (B holo-).

D. kilimanjarica Rendl., Journ. Linn. Soc. Lond., Bot. 30 : 399 (1895).-Type: Tanzania, Kilimanjaro, Taylor s.n. (BM holo-).

Flowers rose to crimson, apparently without a scent; spur on the dorsal sepal 4 - 6 mm long; petals lanceolate, acute;

occurring northwards from Mt. Kilimanjaro.

Note: Although the type of this species has been lost, there is no confusion about its identity, as it is a fairly common and conspicuous species on the higher mountains of East Africa. D. kilimanjarica of Rendle was reduced to synonymy by Kraenzlin (1900), an approach followed by all subsequent authors.

Ecology and Distribution: Subsp. deckenii occurs in the higher mountains of East Africa and Ethiopia: Kilimanjaro in Tanzania, Kivu in Zaire, the uplands of Kenya, the peaks in the Karamoja District of Uganda, and the Ethiopian highlands. But it is absent from the mountains in the south and west of Uganda.
The altitude range is from 2400 to 3000 m, with several collections occurring down to 2100 and up to 4000 m. Rainfall data for these altitudes are unreliable.

Various collectors have described the habitats as alpine meadows, moorland, alpine shrub or stony hillsides. Jackson (1956) described the summit of Mt. Kinyeti (where this species was collected) as being in the Ericacous zone, among rocks, with Erica arborea growing to two meters tall. According to the treatment of Hedberg (1951), ssp. deckenii would occur in the Moorland zone and the Ericaceous shrub zone in Kenya, with some collections being from the upper limit of the montane forest belt. On Kilimanjaro it occurs in both the Montane Forest Belt and the Ericaceous Belt (Sensu Hedberg, 1951) (i.e. Harvey 89, "clearing in forest, 2200 m", and Richards 23152, "moorland, among grass tussocks, 3000 m").
In Ethiopia this species also occurs in "high altitude grass" (Burger 1790) and in "marshy downlands" (Mooney 7406).

The flowering occurs mostly in December, with occasional collections of flowering specimens from August to May. In Kenya flowering occurs from June to October. In Ethiopia it occurs from June to October.

Distribution: Distr. Pl. Afr. 8.

ETHIOPIA :

ARUZZI PROVINCE : Aruzzi Plateau, Drake-Brockmann 200 (K).

GAMU GOFA PROVINCE : Between Wondo and Adoulo, Burger 1790 (K); 30 km S. of Wondo, Mooney 7406 (K).

SUDAN :

EQUATORIA : Imatong mts, Myers 11636 (K).

KENYA :

CENTRAL PROVINCE : Mt Kenya, Bally 2856 (K); Mt Kenya, Bally 3271 (K); Mt Kenya, McLoughlin s.n. (BOL).

RIFT VALLEY PROVINCE : Oldoroto, Solai, Bally 4573 (K); Cherangani, Dale 3251 (K); Nakuru, E Mau forest, Geesteranus 5979 (BR, K); Cherangani, Geesteranus 6327 (K); Londiani, Graham 3221 (K); Marashoni, Graham 3501 (K); Aberdaire, Honore 1878 (K); Cherangani, Mabberley & McCall 290 (K); Cherangani, Mainwaring 52 (BR,K); Thompsons Falls, Pierce 1460 (K); Aberdaire, Pole-Evans & Erens 1370 (K, PRE); Cherangani, Thulin & Tidigs 205 (K, S); Cherangani, Tweedie 2172 (K).

UGANDA :

NORTHERN PROVINCE : Mt Kadam, Eggeling 5801 (K).

TANZANIA :

NORTHERN PROVINCE : Mt Kilimanjaro, Bally 1235 (K); Mt Kilimanjaro, Chambers s.n. (K); Mt. Kilimanjaro, Bismarck

Hill, Greenway 3905 (K); Bismarck Hill, Grote s.n. (K); Mt Kilimanjaro, Haaren 174 (K); Moshi, above Marangu, Harvey 89 (K); Mt Kilimanjaro, Janssens s.n. (BR); Mt Kilimanjaro, Johnston 5 (K); Mt Kilimanjaro, Revell 289 (K); Mt Kilimanjaro, Richards 23152 (K); Mt Kilimanjaro, Schlieben 4571 (BM, BR, M, PRE, S, Z); Mt Kilimanjaro, Seilinger 4273 (K); Mt Kilimanjaro, Seilinger s.n. (K); Mt Kilimanjaro, Swynnerton 1521 (BM); Mt Kilimanjaro, Taylor s.n. (BM); Marangu, Bismarck, Turrall 95 (K); Mt Kilimanjaro, Bismarck Hut, Verdcourt 1235 (K); Marangu, Volkens 800 (BM, K).

ZAIRE :

KIVU PROVINCE : Kivu, Boutakoff s.n. (BR); Kabare, Lushanja, Christiaensens 254 (BR, K); Kivu, Mt Bisunzu, Christiaensens 1954 (BR); Buzezu, Hendrickx 4972 (BR, K, PRE); Kivu, Mt Muhi, Kinet 112 (BR).

7. **Disa sankeyi** Rolfe, Fl. Cap. 5 (3) : 225 (1913).-Type: Rep. S. Afr., Orange Free State, Harrismith, Sankey 264 (K holo.-).

D. basutorum Kraenzl., Mitt. Bot. Mus. Zuerich 71 : 391 (1915), non Schltr.-Type: Lesotho, Feb. 1912, Jacottet 61 (Z holo-).

Tubers testicular, c. 40 mm long and 10 mm in diameter. Sterile shoot apparently hysteranthus, only a juvenile shoot with 2 - 3 leaves seen. Fertile shoots robust, 100 - 300 mm tall; leaves 6 - 12, the basal 2 - 3 reduced to red or hyaline, 10 - 40 mm long basal sheaths, the remainder imbricate, lanceolate, acute to acuminate, up to 150 mm long and 20 mm wide, semi-erect, sheathing at the bases, grading apically into the floral bracts. Inflorescence dense, cylindrical, 40 - 80 mm long with 30 - 80 flowers; bracts narrowly ovate, acuminate, taller than the flowers, the apex often reflexed. Flowers greenish or white or yellow, with or without purple blotches, fragrant, facing down; dorsal sepal oblong-obovate, rounded, galea 7 - 7,5 mm long, 2,8 - 3 mm wide and 1 - 1,5 mm deep, the upper margin incurved; spur pendent from 1,5 - 2,5 mm above the base of the dorsal sepal, slender or somewhat clavate, 3 - 3,5 mm long; lateral sepals oblong-lanceolate, sub-acute, 6,5 - 7,5 mm long and 3 mm wide, shallowly boatshaped, spreading sideways with the apexes curved forwards; petals erect, obliquely obovate, sub-acute to rounded, 5,7 mm long and 2,6 mm wide, the inner margin of the petals curved behind the anther; lip narrowly oblanceolate, rounded, 7 mm long and c. 1,6 mm wide, pendent, flat, the apex somewhat upcurved; rostellum c. 0,8 mm tall; anther erect, c. 3,6 mm long and caudicles c. 0,3 mm long; ovary c. 10 mm long; stigma flat, vertical.

Note: The existence of this species was for a considerable time not taken seriously. Guillarmod (1971) does not refer to either of the two names. Until very recently, the species was only known from the two type collections. The locality of the type collection of <u>Disa sankeyi</u> is still a mystery. The species has not since been found in the Harrismith area of the Drakensberg. The type of <u>D. basutorum</u> is likely to have been collected from the area around Sehlabathebe, where Mlle. Jacottet did the bulk of her collecting (Guillarmod 1971). In this area several populations of this species have been located recently.

Distribution and Ecology: This rare species is only known from four localities in the Drakensberg. All the collections appear to be from about 2100 m.

This falls in the Sub-alpine Belt, as defined by Killick (1978). The rainfall in this region is probably 2000 mm p.a., and mists occur frequently. In winter heavy snowfalls occur (Killick, 1963). A population studied at the Bushmans Nek Pass (Linder 2089) occurred in well-drained montane grassland in pebbly soils. The population was fairly dense.

Flowering occurs in February and March.

Distribution: Distr. Pl. Afr. 7.

REPUBLIC OF SOUTH AFRICA :

ORANGE FREE STATE : Harrismith, Sankey 264 (K).

NATAL : Underberg, Bamboo mt., Grice s.n. (NU); Underberg, Bushmans Nek, Hilliard & Burtt 7996 (NU); Underberg, Bushmans Nek, Linder 2089 (BOL).

TRANSKEI : Matatiele, Mac Alpine, McLoughlin 204 (BOL).

Series 2. *Welwitchiana* Linder, ser. nov.

Flores in inflorescentis densis, cylindricis, sepalis lateralibus generatim brevissimus, quam 15 mm, petalis bilobis, lobis posticis generatim angustatibus et longioribus quam lobis anticis, calcaribus generatim longioribus quam sepalis dorsalibus.

Flower in dense cylinderical spikes; lateral sepals generally less than 15 mm long; petals bilobed, both lobes arising from the base of the petal, the posterior lobe generally narrower than the anterior lobe, and slightly taller than the anterior lobe; spur generally reaches to below the base of the dorsal sepal.

Type: *D. welwitschii* Reichb.f.

This series is widespread in tropical Africa, from Ethiopia to the Northern Transvaal in South Africa, and from Liberia to Madagascar. It is fairly distinct series, although some forms of *D. welwitschii* approach *D. englerana*. Most of the species are swamp species, and only *D. scutellifera* occurs frequently in grassland.

Three groups can be readily detected in this series. *D. incarnata* and *D. scutellifera* are characterised by an almost filiform posterior petal lobe and large flowers (lateral sepals 7 - 15 mm long). This group occurs in North-east Africa and Madagascar. The *D. welwitschii*/*D. roeperocharoides* group is found over the whole range of the series, and can be distinguished by the slender spur, the narrowly oblong or narrowly ovate posterior petal lobe, and the relatively small floral bracts. The remaining four species form a somewhat heterogeneous group, centred in South-Central Africa, and characterised by small flowers and large floral bracts that partially obscure the flowers. The species in this group are all well defined by clear-cut differences in several characters.

(a) *D. incarnata*/*D. scutellifera* group

D. scutellifera occurs in the high mountains of Ethiopia, the Karamoja District of Uganda and Kenya, while *D. incarnata* is restricted to the northern and north-western parts of Madagascar. Morphologically the two taxa cannot easily be distinguished. *D. incarnata* is more slender, with rather sparse cauline sheaths. The basal leaves are long and slender. Not much good material was available of this species. The floral morphology of the two species is very similar. Habitat notes (of which there are very few) indicate that D. incarnata occurs in a wetter habitat than D. scutellifera. Collectors' notes indicate that D. incarnata is bright red, while D. scutellifera is more or less pink.

There is a need for more detailed habitat data and better herbarium material of especially D. incarnata before the exact relationship between these two taxa can be documented.

(b) D. welwitschii/D. roeperocharoides group

Summerhayes (1964) combined several species into D. welwitschii, stating "D. welwitschii shows considerable segregation in different parts of its range, but nowher do the segregates become sufficiently clear cut to be treated as subspecies". However, a detailed re-evaluation of the available material revealed several clear patterns, by virtue of which formal taxa may be recognized.

Three core groups may be recognized:

i. D. roeperocharoides Krzl. Flowers bright red or orange, dorsal sepal 7,5 - 11,5 mm tall, posterior petal lobe oblanceolate, generally truncate or sub-truncate, 1/3 taller than the anterior lobe, spur 8 - 13 mm long, distributed along the high ground from Lubumbashi to Lusaka.

ii. D. welwitschii ssp. welwitchii. Flowers generally bright brick red, carmine, crimson or magenta, dorsal sepal 4 - 8 mm long; posterior petal lobe oblanceolate, truncate, usually 1/3 taller than the anterior lobe, spur 3,5 - 6,5 mm long, distributed south of 8°S to Transvaal.

iii. D. welwitschii ssp. occultans. Flowers generally pink, occasionally mauve, dorsal sepal 5 - 11 mm long, posterior petal lobe more or less ovate, acute, usually only slightly taller

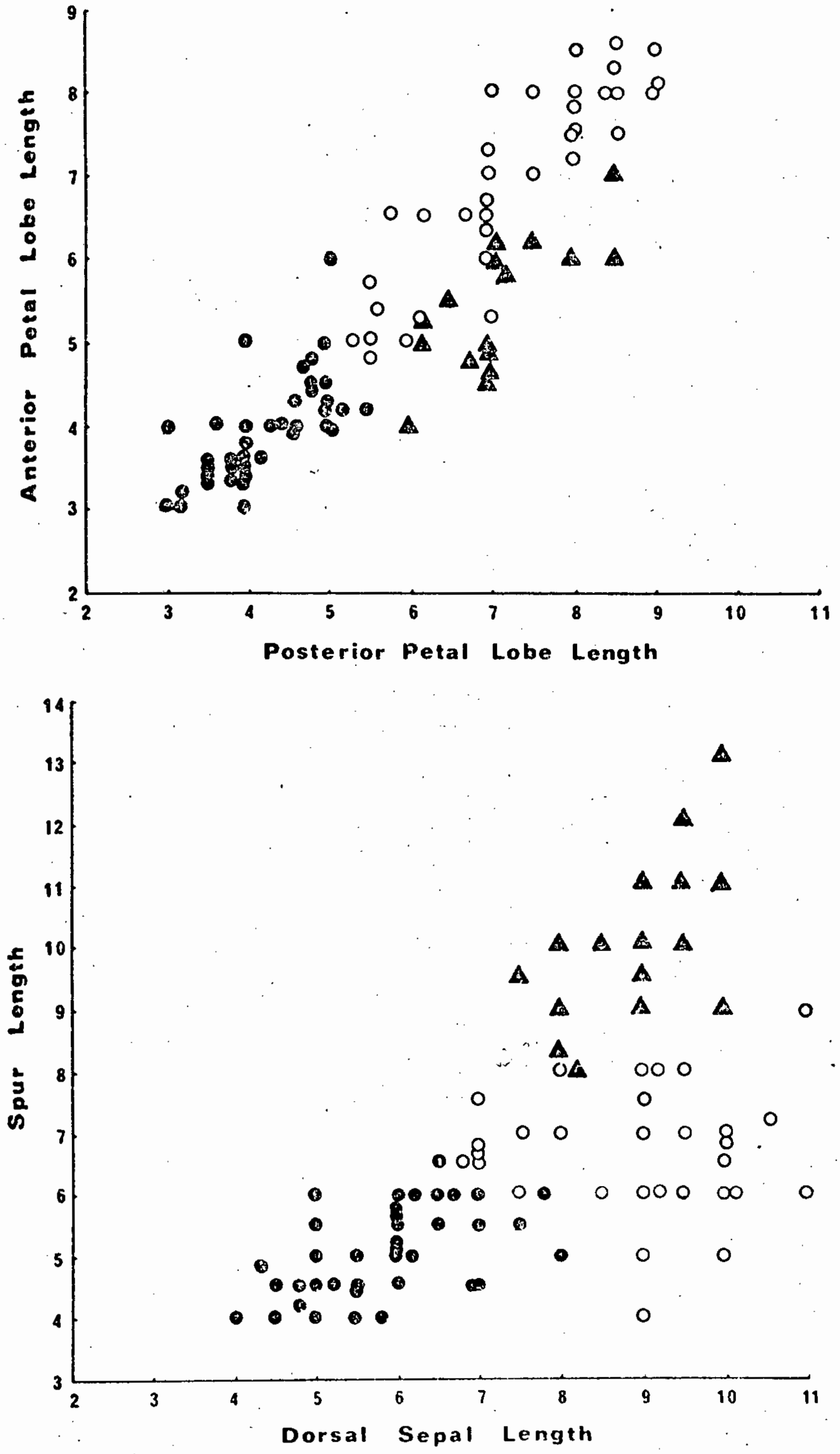


Fig. 8. -- Disa welwitschii - D. roeperocharoides group: variation in flower dimensions. D. welwitschii Reichb.f. ssp. welwitschii is represented by closed circles, ssp. occultans (Schltr.) Linder by open circles and D. roeperocharoides Kraenzl. by triangles. Only material from Zaire (Shaba province) and Zambia is shown.

than the anterior petal lobe, spur 5 - 9 mm long, distributed to the north of 12°S.

Two major overlap areas may be recognized. Zambia and the Shaba Province of Zaire (all three taxa) and the central part of the western Rift Valley (the two subspecies of *D. welwitschii*). The understanding of the behaviour of the putative taxa in the overlap zone is considered to be critical for the understanding of the nature of these putative taxa.

An analysis of the quantified variable characters (spur length, dorsal sepal length, petal lobes length) in the western overlap area (Fig. 8) showed that *D. roeperocharoides* can readily be distinguished from *D. welwitschii* ssp. *welwitschii* by the spur length and the general flower size. The two taxa are partially sympatric, and have been collected together in one dambo (Morze 45). There is more overlap between *D. roeperocharoides* and *D. welwitschii* ssp. *occultans*, as the flowers are approximately the same size. Spur length still separates the bulk of the collections, and petal lobe length about half of the collections. There is also a colour difference between the taxa. Williamson (pers. com.) is of the opinion that the two taxa have slightly different habitats. The two subspecies of *D. welwitschii* are separated mainly on flower size and colour. Here several intermediate collections exist.

In the eastern overlap area the two subspecies of *D. welwitschii* intergrade extensively, and several rather peculiar forms exist (i.e. *D. tanganyikensis* Summerh.) Not many collections from this area are available. It is suggested that collections from this area be treated as intermediates, as it is not clear whether differentiation has not been completed, or whether these specimens are hybrids. Material from the south (Malawi) falls clearly into ssp. welwitschii, and material from Uganda into ssp. occultans.

As all material of D. roeperocharoides can be distinguished from material of D. welwitschii s.l. with which it co-occurs, it should receive specific status (Davis & Heywood, 1963). The other two taxa are contiguous geographically, with occasional intermediate forms along the western contact zone, but with all the collections from the eastern contact zone intermediate. On this evidence, subspecific status may be applied.

8. **Disa incarnata** Lindl., Gen. Sp. Orch. : 348 (1838); Dur. & Schinz, Consp. Fl. Afr. 5 : 1892; Hooker, Bot. Mag. 118 : t. 7243 (1892); Kraenzl., Orch. Gen. Sp. 1 : 750 (1900); Schltr., Bot. Jahrb. 31 : 220 (1901); Schltr., Fedde Repert. Beih. 33 : 99 (1924); Perrier de la Bâthie, Fl. Madagascar 49 : 172 (1939).-Type: Madagascar, Lyall 178 (K holo-).

D. fallax Kraenzl., Bot. Jahrb. 17 : 64 (1893); Kraenzl., Orch. Gen. Sp. 1 : 753 (1900).-Type: Madagascar, North Betsileo, Jan. 1881, Hildebrandt 3874 (B holo-; P, W iso-).

Tubers bifid, almost like swollen roots; sterile shoot slender, c. 50 mm tall; basal sheaths 1 - 2; leaves 2 - 3, linear, up to 180 mm long and 30 mm wide, not well known. Fertile shoots slender, 300 - 500 mm tall; cauline leaves more or less imbricate; the lower 2 - 3 reduced to sheaths, c. 20 mm long; the remainder only sheathing in the lower 1/2 of the leaf, narrowly lanceolate to linear, acute, 60 - 80 mm long and c. 10 mm wide, grading apically into the floral bracts. Inflorescence sub-dense, 80 - 160 mm long and with 10 - 30 flowers; bracts leaf-like, acuminate, as tall as the flowers or the apex overtopping the flowers, 20 - 30 mm long. Flowers bright red; dorsal sepal spathulate, obtuse, erect, 8 - 12 mm long; basal claw 3 - 4 mm long and c. 2 mm wide, usually wider near the apex; blade elliptical or sub-cordate, shallowly galeate, 5 - 9 mm long and 4 - 6 mm wide; spur pendent from near the base of the dorsal sepal blade, slender, obtuse, 6 - 9 mm long, c. 0,5 mm in diameter at the base and c. 1 mm in diameter near the apex; lateral sepals obliquely oblong, obtuse, 9 - 11 mm long and 4 - 6 mm wide, spreading sideways and upwards; petals bilobed, 6 - 10 mm long; anterior lobe ovate, 6 mm long and 4 - 5 mm wide, spreading on both sides of the anther, the upper margin incurved;posterior lobe linear, 6 - 10 mm long and 1 mm wide, obtuse, erect inside the galea; lip linear, acute, 8 - 9 mm long and 0,4 - 0,6 mm wide, pendent; rostellum simple; anther erect, 3 mm long; ovary 10 - 15 mm long; stigma c. 1 mm in diameter.

Note: *D. incarnata* has not been confused with any other species. *D. fallax* was based, according to Kraenzlin (1893), on a specimen which superficially resembles *D. incarnata,* but the three dimensional shape of the galea was said to be different. An analysis of the isotype material does not bear this out, and it is assumed that the specimen that Kraenzlin studied was monstrosity. However, under the nomenclatural rules as amended by the Leningrad Congres of 1975, the name is still valid (Stafleu et al. 1978), and has to be relegated to the synonymy of *D. incarnata*, as was proposed by Schlechter (1901).

Distribution and Ecology: *Disa incarnata* is restricted to Madagascar, where it occurs in the central and north-western parts of the island. Not much information is available on the habitat of the species; most indicate a swampy habitat at an altitude of about 1600 m. This area has a rainfall of 1500 - 2000 mm p.a., and a dry period of 5 - 6 months (Koechlin, 1972).

Flowering occurs mostly from January to March.

Distribution: Distr. pl. Afr. 9.

MADAGASCAR : Manjankambiana, Mozamanga, Alleizette 7031 (P); Amboritre, Mt Anleby, Apperl s.n. (Z); Central Madagascar, Baron 496 (K); Central Madagascar, Baron 2189 (BM, K); North-West Madagascar, Baron 4978 (K); Ankaratra, Bosser 17578 (P); Ankazobe, Decary 7301 (P); Ankazobe, Decary 7440 (P); Tampoketsa, Decary 7597 (P, S); Ambatofinandrahana, Decary 12905 (P); Ambatofinandrahana, Decary 12976 (K, P); Ambatofinandrahana, Decary 13073 (P); Manankazo, Decary 17204 (P); Ambositra, Decary 17307 (P); Ambositra, Decary 17325 (BM, P); Imerina, Fox 9 (K); Anvranatra, Hildebrandt 3874a (K); Madagascar, Lyall 178 (K); Aatrizahe, Perrier de le Bâthie 8107 (K, P); Intrevu, Morat 4192 (P); Arivominanio, Scott-Elliott 1940 (K, P); Madagascar, Waterlot 49 (P).

9. **Disa scutellifera** A. Rich., Ann. Sc. Nat., Ser. 2, 14 : 272 (1840); A. Rich., Tent. Fl. Abyss. : 302 (1847); A. Rich., Tent. Fl. Abyss, Atlas : pl. 94 (1851); Dur. & Schinz, Consp. Fl. Afr. 5 : 107 (1892); N.E. Br., Fl. Trop. Afr. 7 : 278 (1898); Kraenzl., Orch. Gen. Sp. 1 : 739 (1900); Schltr., Bot. Jahrb. 31 : 218 (1901); Summerh., Fl. W. Trop. Afr. 2 : 414 (1936); Piers, Orchids E. Africa : 62 (1968); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 159 (1968);

Cufodontis, Bull. Jard. Bot. Nat. Soc. Belg. 42, Suppl. : 1610 (1972); Agnew, Upland Kenya Wild Flowers : 750 (1974).-Type: Abyssinia, Adowa, Mount Sholoda, Aug. 1839, Quartin Dillon & Petit s.n. (P holo-; BR iso-).

D. schimperi N.E. Br., Fl. Trop. Afr. 7 : 279 (1898).-Type: Ethiopia, Sanka Ber on the Red River, Schimper 1309 (K holo-; PRE iso-).

Tubers testicular, 20 - 30 mm long and c. 10 mm in diameter. Sterile shoot up to 60 mm long; basal sheaths 2 - 3, acute, longer than the shoot; leaves 2 - 4, erect, linear-lanceolate, acute, conduplicate, up to 200 mm long and 20 mm wide. Fertile shoot robust, 250 - 600 (- 900) mm tall; cauline leaves imbricate, the lower 2 - 3 reduced to sheaths, the remainder 60 - 120 mm long and 12 - 25 mm wide, the upper part of the leaf forming a free ovate acute blade, the lower part of each leaf sheathing, leaves grading apically into the floral bracts. Inflorescence dense, 60 - 200 mm long and with 30 - 80 flowers; bracts ovate, acuminate, 20 - 35 mm long, generally overtopping the flowers. Flowers more or less pink, the galea frequently reported to be spotted; dorsal sepal obovate to shortly spathulate, erect; the claw not well developed, at most 3 mm long, but usually (and always in Kenya) not distinct from the blade; blade 7 - 10 mm long, 5 - 9 mm wide, obtuse or apiculate, very shallowly galeate; spur pendent from below the middle of the dorsal sepal, reaching to below the base of the dorsal sepal; 4,5 - 9 (- 14) mm long; generally sub-clavate, obtuse; 0,5 - 1,5 mm in diameter at the base and 1 - 2 mm in diameter at the apex; lateral sepals obliquely oblong, sub-acute, 7 - 11 (- 17) mm long and 3 - 6 (- 10) mm wide, spreading sideways and upwards; petals bilobed, 6 - 11 (- 13) mm long; anterior lobe ovate, 4 - 7 (- 11) mm long and 3 - 5 (- 7) mm wide, spreading on the sides of the anther, the upper margin incurved; the posterior lobe linear, sub-acute, 6 - 11 (- 13) mm long and 0,5 - 1 (- 2) mm wide, erect inside the galea; lip linear, acute, 6 - 10 (- 14) mm long and 0,5 - 1 mm wide, pendent; rostellum simple; anther erect, 3 - 6 mm long; ovary 1/ - 20 mm long; stigma c. 2 - 3 mm in diameter.

Note: There has never been any confusion associated with *D. scutellifera*. N.E. Brown (1898) noted that *D. schimperi* could be distinguished from *D. scutellifera* by its smaller flowers, and by the small teeth at base of the lip. However, the species shows a continuous size gradient which easily includes both type specimens. Irregular teeth on the lip occur frequently in this species, as well as the other species in this section. Kraenzlin (1900) and all subsequent botanists treated *D. schimperi* as a synonym of *D. scutellifera*.

Distribution and Ecology: *D. scutellifera* occurs in the highlands of north-eastern Africa. The distribution forms a curve from the Ethiopian mountains, via the Imatong Mountains in the Sudan, the peaks in the Karamoja District of Uganda, to Mt. Kenya. The altitude range of the species is from 2100 m to 2700 m above sea level, with a few collections from as low as 1800 m. It therefore falls clearly in the montane zone (Hedberg, 1951).

Most specimens have been collected in montane grassland, although several collectors refer to marshy downlands and vlei grassland. Some collectors indicated a grassland with scattered cedars (Juniperus) and Podocarpus. Langdale-Brown et al. (1964) describe the climax vegetation for the relevant altitudes in Karamoja in Uganda as a Juniperus - Podocarpus dry montane forest.

The rainfall over the distribution range is between 1000 and 1500 mm p.a., with 4 - 5 dry months in winter (Jackson, 1961, Langdale-Brown et al., 1964). Flowering occurs mostly in June and July, with occasional flowering specimens collected in May and August.

Distribution: Distr. Pl. Afr. 10.

ETHIOPIA :

GOJJAM PROVINCE : Giga, NW of Debra Marcos, Burger 603 (K).

SIDAMO BORAMA : Sidamo, 30 km S of Wondo, Mooney 7406 (K); Between Wondo and Adola, Ouren 20861 (K).

SUDAN :

EQUATORIA : Imatong mts, Myers 11596 (K).

KENYA :

CENTRAL PROVINCE : Mt Kenya, Dyson 414 (K).

RIFT VALLEY PROVINCE : Londiani, Graham 2818 (K); Londiani, Graham 2881 (K); Maji Mazari, Graham 3499 (K); Tinderet, Mainwaring 1270 (K); Tinderet, Mainwaring 1279 (K); Naivasha, Oleolondo, Piers s.n. (K); Near Lake Solai, Pole-Evans & Erens 1405 (K); Londiani, Smart 15 (K); South Elgon, Tweedie 472 (K); Cherangani, Tweedie 38 (K); Mau Forest, Whittal 58 (K).

UGANDA :

NORTHERN PROVINCE : Mt Morongole, Dale 282 (K);

Mt Napak, Eggeling 5921 (K); Mt Moroto, Philip 791 (K); Mt Napak, Thomas 3627 (K); Mt Moroto, Tweedie 2654 (K); Mt Moroto, Wilson 975 (K).

10. *Disa welwitschii* Reichb.f.

Tubers testicular, 20 - 60 mm long. Sterile shoots slender or robust, up to 150 mm tall; basal sheaths usually 3, often more or less blotched or striped with red; leaves 2 - 4, linear-elliptical, acute or apiculate, sub-erect, conduplicate, 100 - 300 mm long and 10 - 40 mm wide. Fertile shoots robust, rarely slender, 200 - 1000 mm tall; cauline leaves imbricate, the basal 2 usually reduced to short sheaths, blotched with red, the remainder lanceolate, sub-acuminate, 30 - 100 mm long, mostly sheathing, rarely with a large free blade. Inflorescence dense, 30 - 250 mm long and with 20 - 100 flowers; bracts narrowly ovate, acuminate, as long as the ovaries, inconspicuous. Flower small to medium sized, 0,5 - 10 mm in diameter, pink, carmine, brick red, magenta or paler with darker blotches; dorsal sepal sub-rhomboid, galea narrowly oblong to lanceolate, sub-acute, 5 - 13 mm tall and 2,5 - 6 (- 8) mm wide; spur pendent from the middle or below the middle of the dorsal sepal, reaching below the base of the sepal, slender cylindrical to rarely sub-clavate, 4 - 8 mm long; lateral sepals sub-oblique, oblong-ovate, obtuse to rounded, 5 - 13 mm long and 3 - 8 mm wide, shallowly boat-shaped; petals bilobed, the anterior lobe ovate, 3 - 7 (- 8,5) mm long and 2,5 - 6 mm wide, spreading, the upper margin incurved, the posterior lobe as tall as or 1/3 taller than the anterior lobe, lanceolate to oblanceolate, truncate to acute,

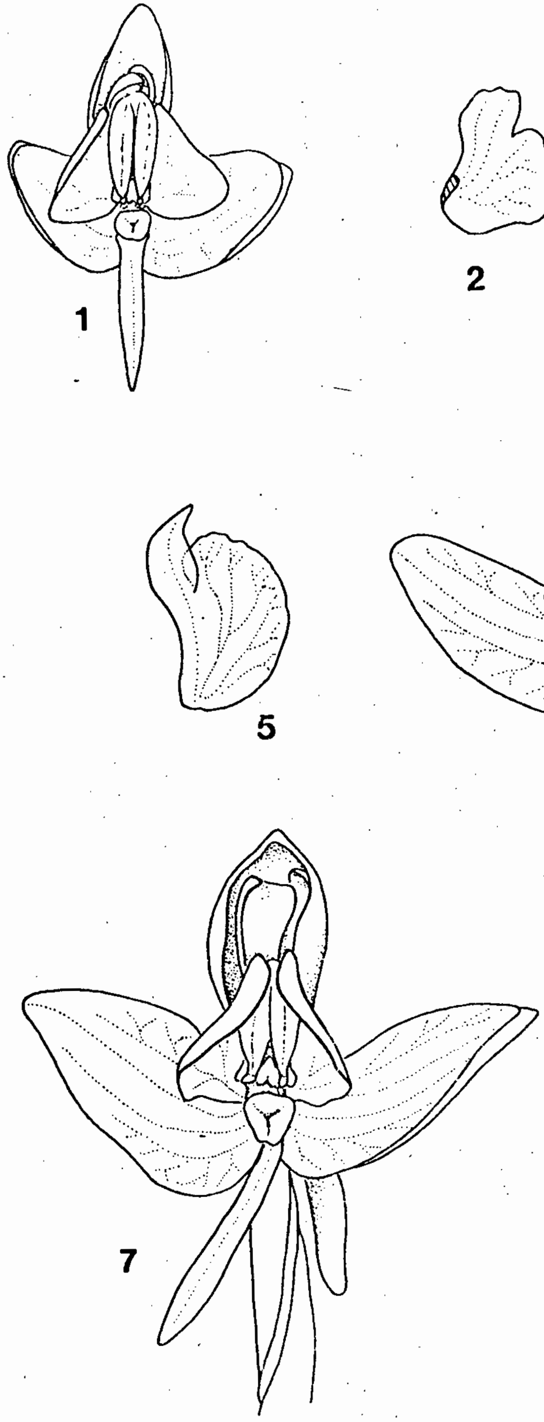


Fig. 10. -- Series *Welwitschiana*, *D*. *welwitschii* - *D*. *roeperocharoides* group: 1 - 3 *D*. *welwitschii* Reichb.f. ssp. *welwitschii* (X 5) from Greatrex s.n., 1. frontal view of flower, 2, petal, 3, dorsal sepal. 4 - 6 *D*. *welwitschii* Reichb.f. ssp. *occultans* (Schltr.) Linder (X 5) from Bogdan in EAH 10191, 4, frontal view of flower, 5, petal, 6, dorsal sepal. 7, *D*. *roeperocharoides* Kraenzl. (X 3) from Lemaire-Elias 157.

4 - 10 mm long and 0,8 - 2,5 mm wide; lip linear, acute, pendent, 4 - 12 mm long; anther 3 - 5 mm long; ovary 10 - 20 mm long; stigma c. 2 mm in diameter, equally three-lobed.

10a. Disa welwitschii Reichb.f. subsp. welwitschii

Disa welwitschii Reichb.f., Flora 48 : 181 (1865); Dur. & Schinz, Consp. Fl. Afr. 5 : 110 (1892); N.E. Br., Fl. Trop. Afr. 7 : 280 (1898); Kraenzl., Orch. Gen. Sp. 1 : 752 (1900); Schltr., Bot. Jahrb. 31 : 219 (1901); Summerh., Kew Bull. 17 : 543 (1964); Piers, Orchids E. Africa : 66 (1968); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 160 (1968); Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 70 (1974); Williamson, Orchids S-Central Africa : pl.54 (1977).-Type: Angola, Huila, Morro de Lopollo, Welwitsch 715 (W holo-; BM, C, K, P iso-).

D. welwitschii Reichb.f. var. buchneri Schltr., Bot. Jahrb. 31 : 219 (1901).-Type: Angola, near the Ohamba River, Buchner 699 (B syn-); Huilla, Antunes s.n. (B syn-).

D. calophylla Kraenzl., Bot.Jahrb. 33 : 58 (1901).-Type: Tanzania, Songea, Busse 834 (B holo-; K iso-).

D. ignea Kraenzl., Bot. Jarhb. 33 : 57 (1902).-Type: Tanzania, Mwasukula, Stolz 12 (B holo-).

D. hyacinthina Kraenzl., Bot. Jahrb. 48 : 390 (1912).-Type: Malawi, Msambia, between Tanzania and Lake Malawi, Fromm-Muenzner 199 (B holo-).

D. breyeri Schltr., Ann. Transv. Mus. 10 : 247 (1924).-Type: Rep. S. Afr., Transvaal, Waterberg, Palala River, Breyer s.n. (B holo-; PRE iso-).

Plants slender to robust, 200 - 470 - 700 mm tall; cauline leaves 30 - 90 mm long; inflorescence 30 - 90 - 140 mm long; dorsal sepal 4,5 - 5,8 - 7,1 mm long, spur 3,5 - 5,1 - 6,4 mm long; lateral sepals 5 - 7 - 9 mm long and 3 - 3,8 - 5 mm wide; petal posterior lobe generally 1/3 longer than the anterior lobe and truncate; flowers bright red or carmine.

Notes: 1. Although there has been extensive confusion in recent years as to the correct delimitation of *D. welwitschii*, this only dates (nomenclaturally) to Summerhayes (1964). Previously the name was only applied to what is here treated as *D. welwitschii* ssp. *welwitschii*, and the East and West African forms were separated off under various other names (now included in *D. welwitschii* ssp. *occultans*).

2. All type material of both *D. ignea* and *D. hyacinthina* were lost in the Second World War. From the descriptions it is clear that these species are closely allied to *D. welwitschii* ssp. *welwitschii*. Schlechter (1915) included these two species in the synonymy of *D. calophylla*, of which an isotype is extant at Kew. As the types of these three species come from the same area, and the descriptions are similar, Schlechter's approach is followed here. Schlechter separated *D. calophylla* from *D. welwitschii* s.s. on the basis of larger flowers and more robust plants. However, he did not see the material from Zambia,

which falls intermediate between these two concepts. These three names are therefore included in the synonymy of subsp. *welwitschii*.

3. Schlechter (1924) allied *D. breyeri* to the *D. ochrostachya* group, and does not seem to have realized that it represented the southern most extension of the *D. welwitschii* group. Close study showed that it could not be separated from the Zimbabwean representatives of this sub-species.

Ecology and Distribution: This subspecies occurs predominantly in southern and south-central Africa: the Northern Transvaal in South Africa, the highlands of Zimbabwe, Zambia and Angola. The altitude range of the subspecies is 900 - 1500 m over the whole distribution range, except for the Nyika Plateau, where it has been collected from between 2000 and 2400 m. Collectors' notes indicate that the taxon grows in dambos or wet vleis or moist grassland over the whole range, except for the South Tanzanian Highlands, where it apparently occurs in montane grassland. There is no record of the habitat in South Africa.

The 'dambos' of South-Central Africa have been described in some detail by Vesey-Fitzgerald (1963). He calls them 'Headwater valley grasslands', and also describes a central 'bog' area, which is perennially wet and spongy, with peaty soils. Several collectors indicated this central bog as the habitat, but Williamson (1977) records it from the dambo margins, in seasonally wet grassland.

The vegetation over the whole distribution range is Brachystegia woodland or open or montane grassland (Rattray & Wild, 1961). In South Africa the subspecies appears to occur in North Eastern mountain sourveld (Acocks, 1975). The rainfall is probably about 1000 mm p.a., falling mostly in the summer months, with 3 - 5 dry months in winter (Jackson, 1961).

Flowering occurs from November to February, with a few records from October.

Distribution: Distr. Pl. Afr. 11.

TANZANIA :

SOUTHERN PROVINCE : Songea, Busse 834 (K); Songea, Ulamboni, Milne-Redhead & Taylor 8157 (K).

SOUTHERN HIGHLANDS : Iringa, Mbosi, Horsbrugh-Porter s.n. (BM); Mbeya, Leedal 3 (K); Mbeya, Mbosi, Richards 13880 (K); Kyimbila, Stolz 136 (BM, K).

WESTERN PROVINCE : Ufipa, Chala-Kisi, Bullock 2252 (BR, K, PRE); Ufipa, Kawimbe, Richards 8053 (K); Ufipa, Lake Kwela, Richards 11146 (K); Kigoma, Kasulu, Rounce 9 (K).

BURUNDI : Bururi, Mashua, Delarge 16 (BR); Bururi, Nyanza-lac, Lewalle 4229 (BR); Luvironza, Michel 4994 (BR); Ruyigi, Michel & Reed 517 (BR).

ZAIRE:

SHABA PROVINCE : Upemba National Park, Bamps 853 (BR); Upemba National Park, Bamps 896 (BR); Katanga, Bredo 5868 (BR); Welgelegen, Corbisier 580 (BR); Takalu, Claessens 1115 (BR); Kaseba, Detilleux 297 (BR); Upemba National Park, De Witte 3254 (BR, K); Upemba National Park, De Witte 4765 (BR); Upemba National Park, De Witte 5105 (BR); Lualaba River, Kassner 3387 (BM); Kundelungu, Malaisse 4861 (BR, K); Potopoto, Malaisse 8776 (BR); Kapanga, Overlaet 470 (BR); Kapanga, Overlaet 479 (BR); Biano Plateau, Russel 86 (K); Plateau de la Manika, Symoens, De Bilde & Schwind 7 (BR); Rukafu, Verdick 393 (BR, K).

MALAWI :

NORTHERN PROVINCE : Mzimba, Benson 1228 (K); Nyika Plateau, Pawek 733 (SRGH); Mzimba, Pawek 10761 (K); Nyika Plateau, Williamson 226 (K, SRGH); Chitipa, Williamson & Drummond 1927 (SRGH).

CENTRAL PROVINCE : Kasungu, Hall-Martin 1628 (K, SRGH); Kasungu, Robson 1163 (K, SRGH).

SOUTHERN PROVINCE : Shire Highlands, Adamson 286 (K); Zomba, Ngokwe, Jackson 1467 (K); Near Blantyre, Last s.n. (K); Zomba, Mainwaring 8 (K); Zomba, Sharpe 196 (K); Mt. Zomba, Whyte s.n. (K).

NO EXACT LOCALITY: Buchanan 177 (BM); Buchanan 288 (BM, K); Buchanan 674 (BM, K, SRGH); Whyte 343 (K).

ZAMBIA :

NORTHERN PROVINCE : Luwingu, Baker 168 (SRGH); Mwero Wantipa, Bredo 5859 (BR); Kasama, on road to Chambesi, Holmes 274 (SRGH); Mbala, Richards 4182 (BR, K); Mporokoso, Lumangwe Falls, Richards 12098 (K, SRGH); Mbala, Chinakila woodland, Richards 19466 (K); Mbala, Saisi Valley, Richards 22899 (K); Mbala, Saisi Valley, Richards 22900 (K); Mbala, Zombe Plain, Richards 22943 (K); 40 km S of Mbala, Robinson 4055 (K); Kasama, Mungwi, Robinson 4125 (K, SRGH); Nyika Plateau, Williamson 226 (K); Mporokoso, Williamson & Simon 682 (K); Between Mbereshi and Nchelenge, Kawambwa, Williamson 1226 (SRGH); Mporokoso, Williamson 1302 (SRGH); 61 km N of Isoka, Williamson & Drummond 1913 (SRGH).

EASTERN PROVINCE : Chipata - Katete, Robson 1116 (K).

CENTRAL PROVINCE : Katuba stream, Kassner 2250 (K); Kabwe, Morze 45 (K); Mulungushe River, Morze 45b (K); Mkushi, Robinson 2704 (K); Kundalila Falls, Williamson 2219 (SRGH);

Kundalila Falls, Williamson & Simon 630 (K, SRGH).

COPPERBELT : Nkana, Brenan 16 (K); Kitwe, Fanshawe 2695 (BR, K); Kitwe, Fanshawe 2696 (K, SRGH); Kitwe, Fanshawe 9910 (K); Kitwe, Fanshawe 10703 (SRGH); Nchanga, Ferrar in SRGH 4811 (SRGH); Kitwe, Ichimpi, Mutimushi 140 (SRGH); Nkana south, Mutimushi 247 (K, SRGH); Kitwe, Mutimushi 1729 (K); Bancroft, Retief 27 (PRE); Nchanga, Terror 4811 (K).

NORTH-WESTERN PROVINCE : Mwinilunga, Dobeka dambo, Brummitt, Chisampa & Polhill 13984 (K); Between Matonchi and Mwinilunga, Drummond & Williamson 9420 (SRGH); Mwinilunga, Holmes 75 (BR, K, SRGH); Zambezi source, Leach & Williamson 13503 (SRGH); Kasempa Road, Linley 54 (SRGH); Mwinilunga, Marks 94 (K); Mwinilunga, River Kasompe, Milne-Redhead 2991 (BR, K, PRE); Mwinilunga, Richards 17243 (K); Mwinilunga, Sinkabolo dambo, Richards 17437 (K, SRGH); Between Mwinilunga and Kalene Hill, Strid 2551 (K); Kasempa, Uys 16/89 (SRGH); 40 km E of Mwinilunga, Williamson & Simon 1783 (K, PRE, SRGH); Mwinilunga, Dobeka River bridge, Williamson & Simon 1808 (SRGH); Kabompo, Williamson & Simon 1837 (SRGH).

SOUTHERN PROVINCE : Mambuva, Gilges 908 (K, SRGH); Choma, Robinson 461 (K); Choma, Robinson 2113 (K, SRGH); Mazabuka, Siamambo Reserve, White 6597 (K, SRGH).

ANGOLA :

LUNDA : Saurimo, Young 1144 (BM, SRGH); Saurimo, Young 1235 (BM, SRGH).

MOXICO : Vila Luzo, Young 1224 (BM); River Luena, Vila Luzo, Young 1373 (BM).

CUBANGO : Cubango, Gossweiler 2368 (K).

HUILLA : Lubango, Barbosa 10381 (SRGH); Humpata, Barbosa & Moreno 10199 (PRE, SRGH); Huilla, Welwitsch 715 (BM, K).

ZIMBABWE : Luxula valley, Allen 482 (K, SRGH); Inyanga, Ball 501 (SRGH); Makoni, Beasley 159 (SRGH); Makoni, Best 1255 (BOL); Domboshawa, Greatrex in SRGH 26783 (K, SRGH); Marandellas, Greatrex in SRGH 228712 (SRGH); Manicaland, Gilliland 1508 (K); Chilimanzi, Mackintosh 5/68 (SRGH); Rusape, Munch 226 (K, PRE, SRGH); Marandellas, Pole-Evans 7255b (K); Stapleford, Wild 940 (K, SRGH).

MOCAMBIQUE :

MANICA E SOFALA : Murrupula, de Calvalho 406 (K).

REPUBLIC OF SOUTH AFRICA :

TRANSVAAL : Pietersburg, Waterberg, Bremekamp & Schweickerdt 5 (PRE); Palala River, Breyer in PRE 17784a (PRE); Pietersburg, Haenertzburg, Woodbush, Schweickerdt s.n. (PRE); Pietersburg, Haenertzburg, Van der Merwe 302 (K); Pietersburg, Woodbush, Water in PRE 23038 (PRE).

10b. *Disa welwitschii* Reichb.f. subsp. *occultans* (Schltr.) Linder, stat. nov. et comb. nov., basionym: Disa occultans Schltr., Notizbl. Bot. Gart. Berlin 8 : 225 (1922).-Type: Kenya, N. Kavirondo District, Kitosh, Lindblom s.n. (S holo-).

D. subaequalis Summerh., Kew Bull. 1936 : 221 (1936); Summerh., Fl. W. trop. Afr. 2 : 414 (1936).-Type: Uganda, Mongo District, Kyagwe, Ntakafumu, Dummer 738 (K holo-; BM iso-).

D. tanganyikensis Summerh., Kew Bull. 17 : 541 (1964); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 161 (1968).-Type: Tanzania, Iringa District, Dabaga highlands, Polhill & Paulo

1447 (K holo-; P, PRE iso-).

Plants slender to robust, 200 - 560 - 950 mm tall; cauline leaves 40 - 120 mm long; inflorescence 60 - 139 - 250 mm long; dorsal sepal 5 - 11 mm long; lateral sepals 7 - 9,2 - 11,5 (- 13) mm long and 4 - 5,2 - 6 (- 8) mm wide; petal posterior lobe generally as tall as or slightly taller than the anterior lobe, more or less ovate lanceolate, acute; flowers pink, and variations on pink; spur 5 - 9 mm long.

Notes: 1. The first name to be proposed for the northern forms of Disa welwitschii s.l. was D. occultans Schltr. Unfortunately this was published in a rather obscure journal, based on a collection with a single sheet, housed in Stockholm. In 1936 Summerhayes proposed the name D. subaequalis apparently unaware of the earlier name of Schlechter, as he does not refer ot it, and cites specimens from Kenya, the area from which the type of D. occultans originates.

2. In 1964, when Summerhayes studied the Disa welwitschii group in some detail, he separated out D. tanganyikensis. The type of this species comes from the overlap zone between the two subspecies. In this area extensive variation and several rather peculiar forms occur. These have been grouped as well as possible into the two subspecies, and D. tanganyikensis shows more similarity to the northern subspecies than to the southern subspecies.

Disa welwitschii, as defined by Summerhayes (1964), and applied by Piers (1968), Summerhayes (1968), and Stewart (1974), includes both subspecies.

Distribution and Ecology: Subspecies occultans is widely distributed in the montane and sub-montane regions north of the equator, and in the Zaire basin. In the different areas in the distribution range it appears to occupy somewhat different habitats. Slight morphological differences can also be detected between these different areas, but not enough material is available for a detailed analysis.

In Kenya this subspecies occurs between Mt. Elgon and Mau Peak, between 1700 and 2000 m above sea level. Most of the records indicate a swampy habitat. A single record (Graham 2883) is from montane grassland at 2300 m, at Londiani.

Almost all collections from Uganda are from Buganda, where this subspecies occurs between 1000 and 1200 m above sea level. All records are from swamps. Langdale-Brown et al. (1964) noted that there are numerous swampy areas in Buganda. The perennial swamps are dominated by papyrus, and the habitat of ssp. occultans is probably in the seasonally inundated parts of the swamps, which are usually dominated by *Miscanthidium*.

On the Bamenda highlands ssp. occultans occurs between 1500 and 1800 (rarely 2400) m above sea level. Most of the habitat notes indicate a grassland habitat, several a stony grassland. Chapman 17, from the Mambila Plateau, is from a marsh. There are only three records from the Bauchi Plateau in Nigeria. All of them are from swamps at about 1200 m. In the West African mountains this subspecies occurs at about 1600 m, in montane grassland. Knapp (1973) records it from *Themeda-Andropogon* submontane dry and fresh grassland, dominated by *Hyparrhenia*, *Andropogon* and *Loudetia*.

Although widespread in Zaire, not much has been recorded about the habitat. The collections from the Kisantu and Kikwit areas are from below 1000 m, where the climax would be evergreen tropical rainforest (Knapp, 1973). More information is available about the habitats in the south of Zaire, in Shaba and along the Zambesi-Zaire watershed. Here most of the collections are from about 1400 m above sea level, from dambos or swamps. The surrounding vegetation would be Brachystegia woodland (Rattray & Wild, 1961) and tall woodland savanna dominated Strychnos, Erythrina and Annona (Knapp, 1973). Although Williamson (1977) records this subspecies only from perennial dambos, several collectors indicated dambo verges as the habitat. Some collections from the highlands of Southern Tanzania and Northern Zambia are from montane grassland.

The rainfall over most of the distribution range is about 1000 - 1400 mm p.a. In West Africa and the lower Zaire basin the rainfall can exceed 2400 mm p.a. (Jackson, 1961; Knapp, 1973). Although most of the rain falls in the summer months, a significant dry winter period of several months is only found in the southern parts of the distribution range, in Zambia and the Shaba Province of Zaire.

Flowering occurs in the summer: in the northern Hemisphere between June and August, and in the southern hemisphere between November and February.

Variation: As can be expected from such a widespread taxon, there is extensive geographical variation, mainly in the general flower size, the relative length of the posterior petal lobe, the length of the spur and the point of attachment of the spur. Two topoclines have been detected: a circular topocline, around the evergreen tropical forest of the Zaire basin, and along the mountains of West Africa.

The West African cline is expressed in the length of the spur relative to the dorsal sepal, and in the length of the posterior petal lobe relative to the anterior petal lobe. Three centres may be recognized: the mountains of Northern Nigeria and the Cameroun (Bamenda Plateau), the Jos Plateau in the centre of Nigeria, and the escarpment mountains to the west of Nigeria (Mt. Loma, Mt. Nimba and the Bintimani mountains).

The circum-Zaire cline is best expressed by the same group of characters. The range of variation in spur length is almost constant over the whole cline, but flower size increases from the east (Uganda, Kenya) to the west (Cameroun, Zaire). The posterior petal lobe becomes relatively longer from the east to the west. This analysis to a large extent also reflects an increase in flower size. Interestingly, the material from the West Coast of Africa is more similar to material from Uganda and Kenya, than to material from the Camerouns.

Distribution: Distr. Pl. Afr. 12.

KENYA :

RIFT VALLEY PROVINCE : Kipkarren, Brodhurst-Hill 70 (K); Kipkarren, Brodhurst-Hill 69 (K); Kitale, Cogdan s.n. (K); Nandi, Dale 3167a (K); Londiani, Graham 2883 (K); Kitale, Lewin 113 (K); Nzoia River near Lugari, Piers 622 (K); Near Lake Solai, Pole-Evans & Erens 1405 (PRE); Trans-Nzoia, Tweedie 35 (K); Trans-Nzoia, Tweedie 40 (K); Kitale, Wiltshire 47 (K).

NYANZA : Kitosh, Lindblom s.n. (K).

UGANDA :

NORTHERN PROVINCE : Lira, Hancock s.n. (K).

EASTERN PROVINCE : Serere, Kamod, Synge 711 (K).

BUGANDA : Kampala, Kings Lake, Chandler-Hancock 127 (K); Ntakafunvu, Duemmer 738 (BM, BOL, K, PRE, NBG); Bunyoro, Eggeling 2080 (K); Bunyoro, Eggeling 3033 (K); Kampala, Kabaka's Lake, Hancock 1950 (BM); Sanyo Bay area, Maitland 911 (K); Busungwe, River Kagera mouth, Norman 65 (K).

CENTRAL AFRICAN REPUBLIC : Upper Kotto River, 85 km S of Wadda, Le Testu 2925 (BM, K); Upper Kotto River, M'batha, Le Testu 3924 (BM, K); near Pudjeyo, SE of Bambari, Tisserant 2557 (BM, K).

CAMEROUN : Bambili, Bauer 84 (K); Adamawa, Mambila Plateau, Chapman 17 (K); Mambila Plateau, Chapman 2852 (K); Bamenda, Daramola in GHI 41178 (K); Mbéré Plateau, Jacques Félix 4376 (K); Bamenda, Johnston 1931 (K); Mt Gotel, Letouzey 8590 (K); Bamenda, Maitland 1545 (K); Bamenda, Maitland 1616 (K); Bamenda, Bum-Nekan, Maitland 1788 (K); Ngaunreke, Mildbraed 10020 (K); Mt Santa, Saxer 3 (K); Bamenda, Bali Ngemba, Ujor in FHI 30324 (K).

NIGERIA :

EASTERN REGION : Obudu, Head 83 (K); Ogoja District, Obudu Plateau, Howard 18b (K).

NORTHERN REGION : Vom, Bauchi Plateau, Dent Young s.n. (K); Heiphang, King 18 (K); Heipan Pnomel, Summerhayes 152 (K).

IVORY COAST : Mt Nimba, Boughey 18047 (BR, K); Mt Nimba, Schnell 1491 (K); Mt Nimba, Schnell 1558 (K); Mt Nimba, Schnell 3372 (K); Mt Nimba, Schnell 3394 (K).

LIBERIA : Loma mts, Bakshi 252 (K); Loma mts, Jaeger 1042 (K); Loma mts, Morton 3553 (K).

GUINEA : Lola, Mt Nimba, Jacques-Félix 7066 (K).

TANZANIA :

SOUTHERN HIGHLANDS : Iringa, Iheme, Dabaga Highlands, Polhill & Paulo 1447 (K); Lupembe, Schlieben 1403 (BM); West-Fwambo, Von Prittwitz - Gaffron 112 (BM).

LAKE PROVINCE : Bukoba, Ngona swamp, Haarer s.n. (K); Bukoba, Mainwaring 6006 (K).

WESTERN PROVINCE : Ufipa, between Sumbawanga and Mbala, Richards 16103 (K).

ZAIRE :

HAUT ZAIRE : Bokoya, Seret 596 (BR).

KIVU : Maniema, Lebrun 6021 (BR, K).

BANDUNDU PROVINCE : Kahemba, Achten 570 (BR, K); Bas-Congo, Allard 105 (BR); Maluku, between Menkao and Kingankati, Breyne 2021 (BR); Bangu, Compere 1147 (BR); Thysville, Delhaye 311 (BR); M'Vuanzi, Devred 5 (BR); M'Vuanzi, Devred 432 (BR); Luvu, Kisantu, Gallens 3802 (BR, K); Luvu, Gallens 3814 (BR, K); Kikwit, Lebrun 66 (BR, K); Maluku, Plateau Bateke, Muambi 16 (BR); Popokabaka, Mt Mbombo, Pauwels 497 (BR); Popokabaka, Kimvula, Pauwels 765 (BR); Popokabaka, Mt Mbombo, Pauwels 1189 (BR); Matimba, Pauwels 3228 (BR); Maluku, Pauwels 5447 (BR); Kisantu, Vanderyst 37478 (BR); Kwilu River, Van Tilborg s.n. (BR).

KASAI : Tshofa, De Giorgi 198 (BR); Route Kabinda - Tshofa, Durant s.n. (BR); Kaka, Vanderyst 3374 (BR).

SHABA PROVINCE : Katanga, Bredo 5856 (BR); Lulua River, Duvlaet 538 (K); Kitimbo, Kassner 2360 (BM); Kantu, Kassner 2370 (BM); Lovoi River, Kassner 3341 (BM); Lovoi River, Kassner 3361 (BM); Luemba, Mayi ya Ndeke, Kinet 1520 (BR); River Luemba, Nboy s.n. (BR); Kapanga, Overlaet 470 (BR); Kapanga, Overlaet 479 (BR); Kapanga, Overlaet 538 (BR); Kapanga Overlaet 539 (BR); Near Lubumbashi, Russell 85 (K).

ZAMBIA :

NORTHERN PROVINCE : Mbala, Nakatali, Bullock 3654 (BR, K); Mborokoso, Holmes 278 (K, SRGH); Fwambo, Nutt s.n. (K); Shiwa Ngandu, Ricardo 120 (BM); Lake Chila, Richards 4324 (K); Mbala, Richards 4476 (K); Mbala, Richards 8110 (K); Mbala, Richards 8227 (K); Mporokoso, Richards 12421 (BR, K, SRGH); Mbala, Richards 14368 (K); Mbala, Lunzua swamp, Richards 15924 (K, SRGH); Kasama, Chambeshi flats, Richards 19333 (K); Mbala, Saisi plain, Sanane 1015 (K); Mbala, Saisi plain, Sanane 1023 (K); 30 km S of Mporokoso, Williamson 345 (K, SRGH).

CENTRAL PROVINCE : Lusaka, Chakwenga headwaters, Robinson 6390 (K).

COPPERBELT : Luanskya, Fanshawe 1778 (BR, K).

NORTH-WESTERN PROVINCE : Mwinilunga, River Kaoomba, Milne-Redhead 3674 (K, PRE); Mwinilunga, Kalene Hill, Robinson 5912 (K); Mwinilunga, Kalenda Plain, Williamson & Simon 1797 (K, PRE, SRGH).

11. *Disa roeperocharoides* Kraenzl., Bot. Jahrb. 51 : 379 (1914); Williamson, Orchids S. Central Africa : 81, pl. 55 (1977).-Type: Zaire, Shaba Province, Kantu, Kassner 2378 (B holo-; BR, K iso-).

D. welwitschii Reichb.f., Summerh., Kew Bull. 17 : 543 (1964), partially; Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 70 (1974), partially.

Tubers testicular, up to 40 mm long and 20 mm in diameter, villous. Sterile shoot slender, up to 80 mm tall; basal sheaths usually 3; leaves linear to narrowly oblanceolate, acuminate, conduplicate, up to 200 mm long and 10 - 25 mm wide. Fertile shoots sub-robust, 300 - 580 - 700 mm tall; cauline leaves imbricate, narrowly lanceolate, acuminate, 50 - 120 mm long, grading into the floral bracts. Inflorescence dense, 70 - 170 mm long and with c. 30 flowers; bracts lanceolate, acuminate, somewhat longer than the ovaries. Flowers c. 15 mm in diam., bright red, the posterior petal lobes and the inside of the galea usually yellow with bright red blotches, the anther purple to yellow; dorsal sepal erect, rhomboid, sub-acute, 7,5 - 8,9 - 11,5 mm long and 5 - 8 mm wide, galea usually narrowly oblong, subacute, c. 2 mm deep; spur pendent, slender cylindrical, 8 - 10 - 13 mm long; lateral sepals sub-oblique, ovate-oblong, obtuse to rarely apiculate, 9 - 10 (- 12) mm long and 4 - 6 mm wide, shallowly concave, facing forwards; petals bilobed, the anterior lobe more or less narrowly ovate rounded, spreading with the upper margin curved over the anther, 4 - 7 mm long and c. 3 mm wide, the posterior lobe erect inside the galea, oblanceolate, truncate, 1/3 taller than the anterior lobe, 7 - 9 mm tall and 1,5 - 2,5 mm wide, the apexes of the posterior lobes overlapping; lip pendent, linear, acute, 9 - 10 mm long; anther erect, c. 4 mm long; ovary 15 - 20 mm long; stigma sessile, equally three-lobed.

Note: Kraenzlin (1914) commented on the similarity between his new species and D. welwitschii. Summerhayes (1964), in the next treatment of the group, included D. roeperocharoides in the synonymy of D. welwitschii. Williamson (1977) separated the species again on the grounds of its larger flowers and distinctive petal shape. The type locality falls well within the distribution range of this species.

Distribution and Ecology: This species is restricted to the high watershed between the River Zaire, the Kafue and the Lunsemfwa (a tributary of the Luangwe). To the south the species extends to Lusaka, to the north to Lubumbashi and Solwezi. The altitude range is about 1200 - 1500 m above sea level, and the dominant vegetation over the whole area is miombo (*Brachystegia* woodland) (Rattray & Wild, 1961; Knapp, 1973). The rainfall varies from 800 - 1400 mm p.a., with usually 5 dry months in winter (Jackson, 1961).

Collectors' notes appear to indicate a range of habitats in the woodland, from 'dry short grassland' (Noak 79) to 'seepage zone in dambo' (Kornas 3107). The majority of collections are from dambos.

Flowering occurs mostly in January and February, with occasional flowering specimens collected in December and March.

Distribution : Distr. Pl. Afr. 13.

ZAIRE :

SHABA PROVINCE : Between Luvua River and Niemba, Ball 761 (K); Kifofo, Darcis 126 (BR); Munama, De Giorgi 441 (BR); Munama, Detilleux 399 (BR); Lubumbashi, Lemair-Elias 157 (BR);

Katuba, Quarré 36 (BR); Karavia, Quarré 1987 (BR); Katuba, Quarré 3764 (BR); Lubumbashi, Schmitz 105 (BR); Lubumbashi, Schmitz 2218 (BR); Lubumbashi, Schmitz 3343; Lubumbashi, Schmitz 5214 (BR); Lubumbashi, Symoens 3095 (BR); Katanga, Von Hirschberg 153 (K).

ZAMBIA :

CENTRAL PROVINCE : Lusaka, Kornás 3107 (K); Lusaka, King 278 (K); Mulungushi River, Morze 45a (K); Lusaka, Noak 79 (K, SRGH); Chakwenga headwaters, Robinson 6390 (SRGH); Lusaka, Leopards Hill, Vetenary Officer in CRS 255 (PRE).

COPPERBELT : Kabwe, Marr-Levin in SRGH 105025 (SRGH); Kitwe, Mutimushi 1729 (SRGH).

NORTH-WESTERN PROVINCE : Solwezi, Kafue - Musaka Forest Reserve, Holmes 316 (K, SRGH).

12. *Disa celata* Summerh., Kew Bull. 17 : 535 (1964); Williamson, Orchids S. Central Africa : 82, pl. 58 (1977).-Type: Angola, Benguela Province, Canjaugen, Stopp B0224 (K holo-).

Tubers testicular, 20 - 40 mm long and c. 10 mm in diameter. Sterile shoot slender, up to 70 mm long; basal sheaths usually 3, sub-acute, the upper sheath almost leaf-like; leaves at least one, linear-elliptical, acute to sub-acuminate, conduplicate, 100 - 200 mm long and up to 10 mm wide. Fertile shoots slender, 300 - 500 mm tall; cauline leaves imbricate, at the base 20 - 40 mm long, obtuse, hyaline or red, the rest 50 - 70 mm long and 8 - 12 mm wide, acute, usually closely sheathing with only the apexes free. Inflorescence dense, 60 - 80 mm long, floral bracts prominent so that it cannot be clearly distinguished from the rest of the stem; bracts narrowly ovate, sub-acuminate, c. 20 mm long and 5 - 10 mm wide, overtopping the flowers and partially obscuring the flowers. Flowers orange to yellow; dorsal sepal obovate, usually obtuse, 5,5 - 7 mm long, galea erect, 3 - 5,5 mm wide, shallow; spur pendent from the middle of the galea, slender, cylindrical, obtuse, 5 - 6,5 mm long and 0,4 - 0,8 mm in diameter; lateral sepals oblong, sub-obtuse or shortly apiculate, 7 - 8 mm long and 3 - 4,5 mm wide, shallowly boat-shaped; petals bilobed, anterior lobe rotund, 3,5 - 5 mm in diameter, spreading, posterior lobe linear, acute, 4,5 - 6 mm long, inside the galea; lip linear, acute, pendent, 5 - 6,5 mm long and 0,4 - 0,6 mm wide; rostellum c. 1,5 mm tall; anther c. 3 mm long; ovary c. 10 mm long; stigma subsessile.

Distribution and Ecology: Disa celata occurs on the high country along the River Zaire-Zambezi watershed: Nova Lisboa in Angola, Mwinilunga, Serenje, Mbala and Nyika in Zambia, and the Southern Highlands in Tanzania. Very few collectors give an indication of the altitude, but it appears to vary from 1400 m to 2200 m above sea level. The climax vegetation over this distribution range varies from Brachystegia woodland (Rattray & Wild, 1961) to submontane grassland (Knapp, 1973) in Angola, to montane grassland in Tanzania. The rainfall is probably in the region of 1000 - 1400 mm p.a. with 5 dry months a year (Jackson, 1961), but it is not clear how much this is effected by higher altitudes.

According to Williamson (1977), this species occurs in "wet boggy upland grassland". All collectors' notes seem to support this. This species could be understood to grow in the centres or wettest parts of the dambos or headwater valley grasslands.

Flowering occurs mostly in December, and only the collection from Angola (Stopp 130224) was collected in flower in February.

This species appears to be very rare.

Distribution : Distr. Pl. Afr. 14.

TANZANIA :

SOUTHERN HIGHLANDS : Njombe, Leedal 4777 (K); Sao Hill, Watermeyer 210 (K).

MALAWI :

NORTHERN PROVINCE : Nyika Plateau, Ball 1214 (SRGH).

ZAMBIA :

NORTHERN PROVINCE : Nyika Plateau, Williamson 232 (K, SRGH); Mbala, Lake Chila, Williamson 675 (K).

CENTRAL PROVINCE : Serenje, Williamson 404 (K, SRGH).

NORTH-WESTERN PROVINCE : Mwinilunga, Sinkabolo dambo, Milne-Redhead 3774 (K); Matonchi, Sinkabolo, Williamson & Simon 1815 (SRGH).

ANGOLA :

HUAMBO : Conjuagen, NW of Nova Lisboa, Stopp 130224 (K).

13. *Disa aequiloba* Summerh., Kew Bull. 1927 : 419 (1927); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 163 (1968); Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 64 (1974); Williamson, Orchids S. Central Africa : 82, pl. 56 (1977).-Type: Zaire, Shaba Province, moist Places, Von Hirschberg 177 (K holo-; BR, PRE iso-).

Tubers testicular, 10 - 20 mm long and c. 10 mm diameter. Sterile shoot slender, up to 40 mm long, with a couple of basal sheaths; leaves linear-lanceolate, erect, apiculate, c. 80 mm long and 8 mm wide. Fertile shoots slender, 200 - 500 mm tall;

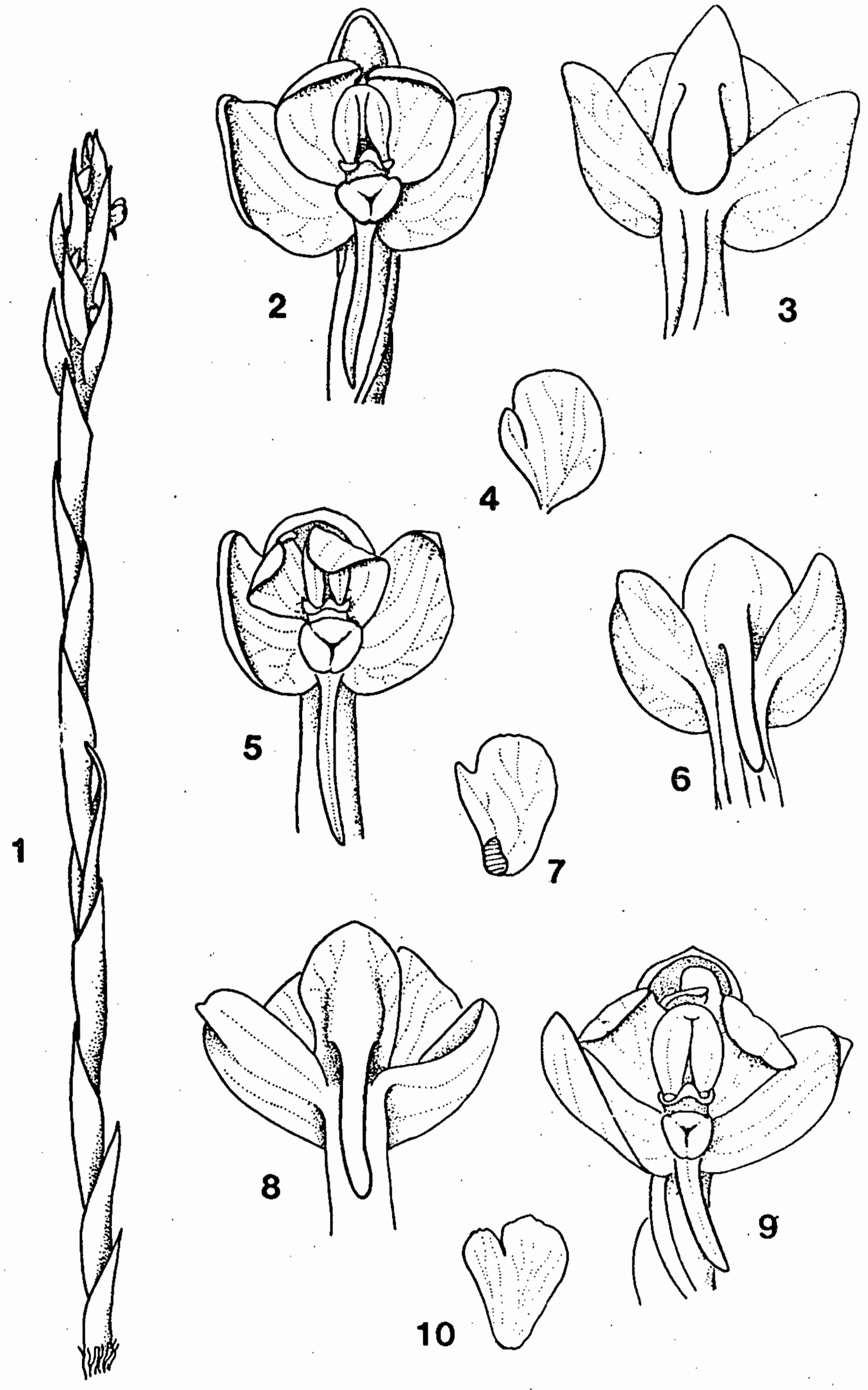


Fig. 11. -- Series *Welwitschiana*. 1, *D. miniata* Summerh. from Linder 2029. 2 - 4, *D. miniata* Summerh. from Wild 3993 : 2, frontal view of flower. 3, rear view of flower, 4, petal. 5 - 7, *D. cryptantha* Summerh. from Milne-Redhead 3585, 5, frontal view of flower, 6, rear view of flower, 7, petal. 8 - 10 , *D. aequiloba* Summerh. from Williamson 641, 8, rear view of flower, 9, frontal view of flower, 10, petal. (1, X 0,5; 2 - 10, X 5).

cauline leaves imbricate, the basal 1 - 2 reduced to c. 30 mm long sheaths, the remainder 30 - 60 mm long, sub-acuminate, the apex free, grading apically into the floral bracts. Inflorescence dense, cylindrical, 30 - 80 mm long and with 10 - 30 flowers; bracts conspicuous, narrowly ovate, acuminate, c. 15 mm long and 5 mm wide, the apexes reaching to the tops of the flowers or overtopping them. Flowers small, white to pale mauve with maroon to purple mottling; dorsal sepal obovate-elliptical, obtuse, 4 - 5 mm tall, galea 2,5 - 4 mm wide and 1,5 - 2 mm deep, the upper margin somewhat incurved; spur pendent from shortly below the middle of the dorsal sepal, 3,5 - 5 mm long, slender cylindrical, 0,5 - 0,8 mm in diameter, rarely tapering somewhat towards the apex, obtuse; lateral sepals oblong-ovate, obtuse, 4 - 5 mm long and 3 - 4 mm wide, shallowly boat-shaped, spreading upwards and curved forwards; petal bilobed, 3,5 - 5 mm tall and 3 - 4,5 mm wide, the lobes sub-equal, the anterior lobe c. 0,2 - 0,5 mm taller and up to twice as wide as the posterior lobe, often longer than the dorsal sepal, the upper margin incurved, hooding the anther, posterior lobes overlapping, inside the galea; lip linear, 3,5 - 4,5 mm long and 0,5 mm wide, pendent, acute; rostellum erect, c. 1,5 mm tall; anther erect, 2 - 2,8 mm long; ovary c. 10 mm long; stigma tripulvinate, 0,3 mm tall, 1 - 2 mm in diameter.

Distribution and Ecology: Disa aequiloba occurs along the high ground along the River Zaire and Zambezi watersheds, from the Huambo highlands in Angola to the Southern Highlands in Tanzania. Most of the collections are from between 1300 and 2200 m above sea level. A single collection (Holmes 0289) is from the Mbereshi dambo, near Kawambwa, in the Northern Province of Zambia, from an altitude of about 1000 m above sea level.

The climax vegetation over this range is mostly Brachystegia woodland (Knapp, 1973) and occasionally sub-montane grassland. Rainfall is between 1000 and 1400 mm p.a., with about 5 dry months in winter (Jackson, 1961).

Williamson (1977) described the habitat as being "Upland perennially wet boggy grassland". For the majority of the collections this is correct. Some collections are from lower altitudes (Holmes 0289). Other collections are from damp meadows or from short grass (Watermeyer 239a, Sanane 1026).

Flowering occurs mostly in December and January. A collection from Angola (Young 1140) was made in October.

Distribution: Distr. Pl. Afr. 15.

TANZANIA :

SOUTHERN HIGHLANDS : Njombe, Richards 7847 (K); Sao Hill, Watermeyer 210a (BR, K); Sao Hill, Watermeyer 239a (K).

ZAIRE :

SHABA : Upemba, Lufira, Bamps 858 (BR); Katanga, Von Hirschberg 177 (K).

ZAMBIA :

NORTHERN PROVINCE : Kawambwa, Mbereshi dambo, Holmes 289 (K, SRGH); Mbala, Saisi Valley, Sanane 1026 (K); Mbala, Kawimbwe, Williamson & Drummond 1962 (SRGH).

CENTRAL PROVINCE : Serenje dambo, Williamson & Simon 641 (K, SRGH).

NORTH-WESTERN PROVINCE : Kucheka valley, Holmes 311 (K, SRGH); Mwinilunga, Kalene Hill, Robinson 5913 (K).

ANGOLA :

LUNDA : Saurimo, Young 1140 (BM, SRGH).

14. *Disa cryptantha* Summerh., Kew Bull. 17 : 537 (1964); Summerh., Fl. Trop. E. Afr. Orchid (1) : 163 (1968); Williamson, Orchids S. Central Africa : 82, pl. 57 (1977).-Type: Tanzania, Songea District, Milne-Redhead and Taylor 8142 (K holo-).

Tubers testicular, 15 - 30 mm long and c. 10 mm in diameter. Sterile shoot slender, c. 80 mm long; basal sheaths 3, acute; leaves erect, linear, acute, c. 140 mm long and 6 mm in diameter. Fertile shoots slender, 300 - 600 mm tall; cauline leaves imbricate; basal sheaths c. 20 mm long, apiculate, reddish; the remainder 65 - 75 mm long and c. 10 mm wide, acute to sub-acuminate, only the apical part free and leaflike; grading apically into the floral bracts. Inflorescence dense 70 - 110 mm long and with 15 - 50 flowers; bracts 20 - 30 mm long, prominent, narrowly ovate, overtopping the flowers and partially obscuring them. Flowers brightly flesh-coloured with darker spots; dorsal sepal broadly elliptical, galea 3,5 - 5,5 mm tall, 2,5 - 3,7 mm wide and c. 1,5 mm deep, obtuse or sub-apiculate, erect, the upper margins incurved; spur pendent from near the base of the dorsal sepal, reaching below the base of the dorsal sepal, 3,5 - 5 mm long and 0,6 mm in diameter; lateral sepals obliquely oblong-elliptical, 3,8 - 6,5 mm long and 2,5 - 4 mm wide, boat-shaped, spreading upwards; petals bilobed, anterior lobe ovate, 4 - 5,5 mm long and 1,8 - 3 mm wide, taller than the dorsal sepal, the upper margin incurved, posterior lobe 0,5 - 1 mm shorter than the anterior lobe, acute, 0,5 mm wide; lip linear, acute, pendent, 4 - 6 mm long and 0,5 mm wide; rostellum c. 1 mm tall, anther erect, 2 - 3 mm tall, the connective massive; ovary c. 10 - 15 mm long; stigma 0,5 mm high.

Ecology and Distribution: The distribution of this species is the same as that of the previous two species, except that it has not yet been recorded from Angola. The altitude range is about 1000 - 1800 m above sea level, and the climax vegetation either Brachystegia woodland (in Zambia) or montane grassland (in the Southern Highlands of Tanzania). Rainfall is 1000 - 1400 mm p.a., with about five dry months in winter (Jackson, 1961).

Williamson (1977) records the habitat to be semi-wet seasonally flooded grassland. All collectors refer to dambos (sometimes rather dry dambos, Holmes 0275) or boggy grassland. As Vesey-Fitzgerald (1963) and Fanshawe (1969) both distinguish between 'dambos' or headwater valley grassland and seasonally flooded grasslands, it is not clear which habitat this species occurs in.

Flowering occurs in December and January. This is a rare species, of which only some five collections were available for study.

Distribution : Distr. Pl. Afr. 16.

TANZANIA :

SOUTHERN PROVINCE : Songea, Milne-Redhead & Taylor 8142 (K).

ZAMBIA :

NORTHERN PROVINCE : 40 km S of Chambeshi, Holmes 275 (SRGH); 30 km S of Mporokoso, Williamson 336 (K, SRGH).

CENTRAL PROVINCE : Kundalila Falls, Williamson 725 (K, SRGH).

NORTH-WESTERN PROVINCE : Mwinilunga, Sinkabolo, Milne-Redhead 3585 (K).

15. *Disa miniata* Summerh., Kew Bull. 17 : 539 (1964); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 164 (1968); Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 66 (1974); Williamson, Orchids S. Central Africa : 82 (1977).-Type: Zambia, Mbala district, upper end of Lake Chila, Richards 256 (K holo-).

Tubers testicular, up to 20 mm long. Sterile shoot generally slender, up to 70 mm tall; basal sheaths 2 - 3, obtuse, up to 50 mm long; leaves 2 - 3, oblanceolate-linear, acute, conduplicate, up to 300 mm long and 10 mm wide. Fertile shoots generally slender, 300 - 600 mm tall; cauline leaves imbricate or sub-imbricate; basal sheaths grading into the leaves; leaves 40 - 80 mm long, lanceolate, acute, usually closely sheathing the scape. Inflorescence sub-dense to dense, 40 - 160 mm long and with 5 - 40 flowers; bracts narrowly ovate, acute to acuminate, 20 - 30 mm long, overtopping the flowers. Flowers more or less orange; dorsal sepal ovate-elliptical, subacute, erect or slightly curved forwards, 4,5 - 6,6 mm long and 2,5 - 3,6 mm wide, galea c. 1,5 mm deep; spur pendent from above the middle of the galea, reaching to the base of the dorsal sepal, 3,5 - 4,2 mm long, strongly clavate, at the base 0,5 - 1 mm in diameter, at the apex 1,5 - 2 mm in diameter; lateral sepals ovate, sub-acute, 5,5 - 6,6 mm long and 3,5 - 4,7 mm wide, concave, spreading sideways or upwards; petals bilobed, anterior lobe 3,5 - 5 mm tall and

3 - 4 mm wide, the upper margins incurved, posterior lobe 3 - 4,5 mm tall and 0,5 - 0,7 mm wide; lip linear, acute, pendent, 4 - 6 mm long; rostellum less than 1 mm tall; anther erect, with a massive curved connective; ovary 10 - 20 mm long; stigma massive, up to 3 mm in diameter, vertical.

Ecology and Distribution: This species occurs on high ground (usually well above 1000 m above sea level) in South-Central Africa. Most of the collections are from the Northern Province of Zambia (with outliers on the Nyika Plateau, and at Iringa in the Southern Highlands of Tanzania), and in the Mazoe-Salisbury area in Zimbabwe. A single collection is from Kapanga in the Haut Lomami district of Zaire.

The climax vegetation over the whole range of this species is either Brachystegia woodland or (rarely) montane grassland (Rattray & Wild, 1961; Knapp, 1973). The rainfall varies from about 1000 to 1400 mm p.a., with about five dry months in winter (Jackson, 1961).

Collections have been made both from headwater valley grasslands (dambos) and flood plain grassland (mbugas). Only the collection from Zaire (Overlaet 838) appears to be from fairly dry conditions. Most collectors have indicated that the habitat is very wet to perennially wet. Williamson (1977) described the habitat as being "wet upland grassland".

Flowering occurs in December to January. The collection from Zaire (Overlaet 838) flowered in September, and the collections from Malawi and Tanzania flowered in February. Several populations studied on the Nyika Plateau in Malawi (Linder 2029) consisted of widely scattered individuals, with the total population size probably less than 20 individuals.

Distribution: Distr. Pl. Afr. 17.

TANZANIA :

SOUTHERN HIGHLANDS : Iringa, Dabaga, Polhill & Paulo 1536 (K).

MALAWI :

NORTHERN PROVINCE : Nyika Plateau, Holmes 225 (K, SRGH).

ZAMBIA :

NORTHERN PROVINCE : Mbala, Lake Chila, Bullock 2213 (K); Mbala, Lake Chila, Richards 256 (K); Mbala, Kali dambo, Richards 945 (K); Mbala, Lake Chila, Richards 22803 (K); 30 km S of Mporokoso, Williamson 336 (K); Mpika, Williamson & Simon 652 (K); Mbala, Lake Chila, Williamson & Simon 678 (BOL, K, SRGH).

ZAIRE :

SHABA : Haute Lorraine, Lulua River, Overlaet 838 (BR).

ZIMBABWE : Salisbury, Greatrex in SRGH 228718 (SRGH); Mazoe, Umvukwes, Wild 3993 (K, SRGH).

Series 3. *Englerana* Linder, ser. nov.

Flores sepalis lateralibus 9 - 25 mm longis, inflorescentis densis vel laxis, calcaribus generatim angustatibus quam sepalis dorsalibus, sepalis dorsalibus limbibus brevis vel longis, petalis lobis posticis generatim plus quam 1/3 longioribus quam lobis anticis, semper rectus.

Flowers medium-sized, lateral sepals 9 - 25 mm long, in a dense to lax inflorescence, spur generally not reaching below the base of the dorsal sepal, dorsal sepal with a short or long limb, posterior petal lobe generally more than 1/3 longer than the anterior lobe, always straight.

Type: *D. englerana* Kraenzl.

This series is restricted to South-Central Africa. Most of the species are clearly grassland taxa. *D. englerana* has been recorded from a range of habitats, including dambos. *D. zombica* and *D. verdickii* are morphologically and eco-geographically clearly discrete taxa. *D. englerana* and *D. ukingensis* are very closely related.

Herbarium material of *D. englerana* and *D. ukingensis* is at first sight very similar. However analysis reveals several distinguishing micro-characters: the relative lengths of the petal lobes, the relative length of the petals and dorsal sepal, and plant size (Fig. 12). The taxa are also eco-geographically separated. *D. englerana* is widespread in South-Central Africa, where it has been collected from a range of habitats, but not from upland grassland. The species is also absent from the Nyika Plateau. *D. ukingensis* occurs in upland grassland on the Nyika Plateau and the high mountains of southern Tanzania.

Associated with these easily quantifiable differences, there are several other characters, such as differences in flower colour and inflorescence density.

Disa ukingensis can therefore readily be recognized as being closely related to *D. englerana.*

16. *Disa englerana* Kraenzl., Bot. Jahrb. 33 : 58 (1902); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 159 (1968); Geerinck,

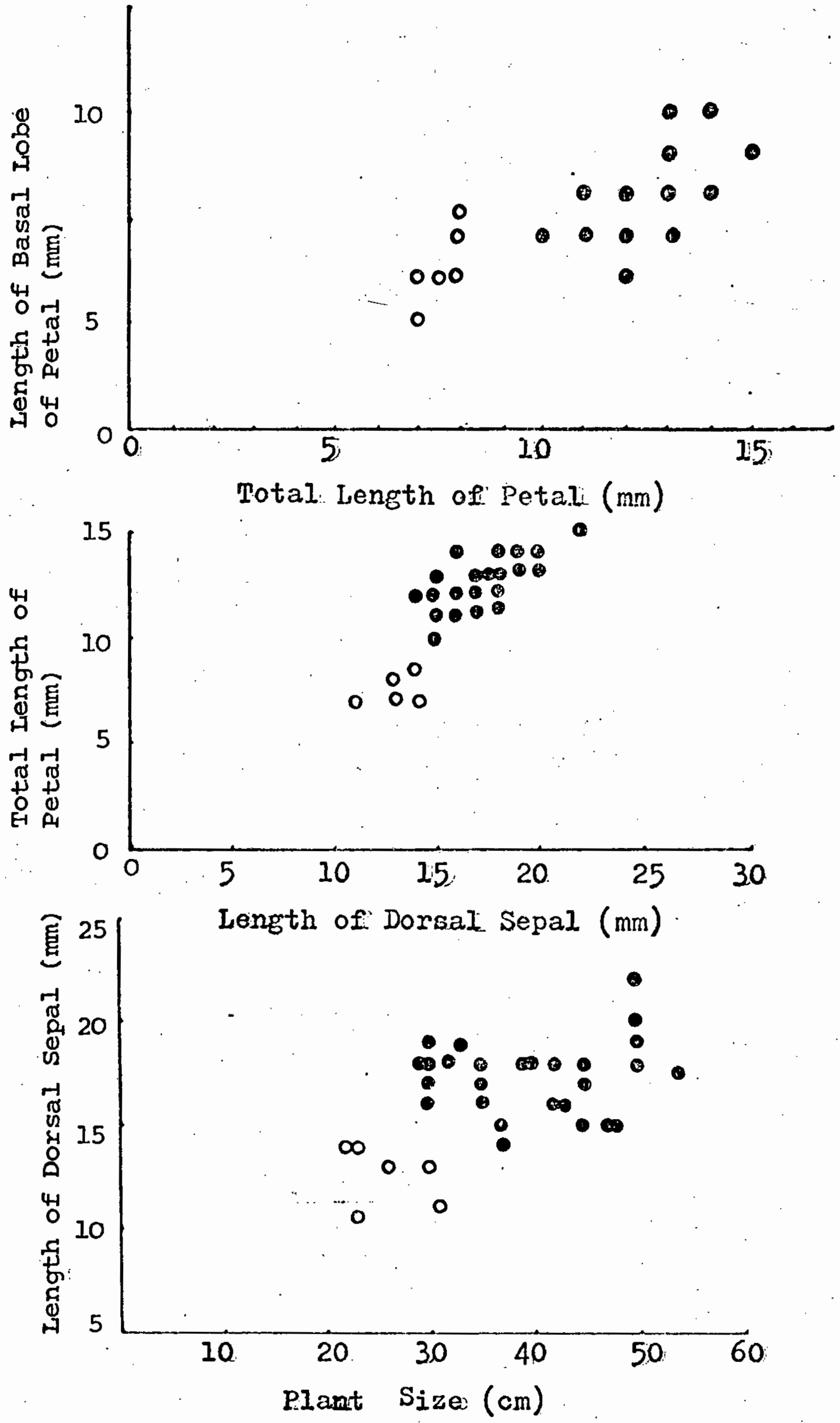


Fig. 12. -- Morphometric differences between *D. englerana* Kraenzl. (closed circles) and *D. ukingensis* Schltr. (open circles).

Bull. Soc. roy. Bot. Belg. 107 : 65 (1974); Williamson, Orchids S. Central Africa : 80, pl. 52 (1977).-Type: Tanzania, Rungwe District, near Bundali, Isoko, Stolz 1 (B holo-), Tanzania, Iringa, Mufindi, Mar. 1969, Polhill & Paulo 1787 (K neo-).

D. subscutellifera Kraenzl., Bot. Jahrb. 48 : 389 (1912).-Type: Tanzania, Rungwe District, Kyimbila, Stolz 141D (B holo-).

Tubers testicular, 20 - 30 mm long and c. 10 mm in diameter. Sterile shoot up to 600 mm tall; basal sheaths 2 - 3, acute, red spotted or striped; leaves 2 - 4, linear-oblanceolate, acute, up to 220 mm long and 20 mm wide. Fertile shoots slender, up to 600 mm tall; cauline leaves imbricate; basal sheaths 25 - 30 mm long; the remainder 40 - 60 mm long, closely sheathing the stem and only rarely with free blades, grading apically into the floral bracts. Inflorescence lax to sub-dense, 60 - 220 mm long and with 3 - 20 flowers; bracts ovate, acuminate, 30 - 50 mm long, usually overtopping the flowers. Flowers facing down, galea recurved to the vertical, flowers pink; dorsal sepal spathulate, claw not always distinct, 3 - 6 mm long, canaliculate, c. 3 - 4 mm broad, blade orbicular, obtuse, c. 14 mm in diameter, bowlshaped and usually curved backwards, the whole sepal 14 - 22 mm long; spur pendent from shortly below the middle of the dorsal sepal, reaching below the base of the dorsal sepal, 5 - 7 mm long, clavate, obtuse, 0,5 - 1,5 mm in diameter at the base and 1,5 - 2,5 mm in diameter at the apex; lateral sepals obliquely oblong, obtuse, 13 - 20 mm long and 6 - 10 mm wide, flat, spreading sideways and up; petals bilobed, 10 - 15 mm long, anterior lobe 7 - 11 mm long and 5 - 8 mm wide, margin entire or rarely serrate, spreading, margins occasionally incurved, posterior lobes 10 - 15 mm long, ovate-spathulate, 3 - 5 mm wide, acute to serrate apically, included in the galea, partially overlapping; lip linear, 14 - 18 mm long and 0,5 - 1,5 mm

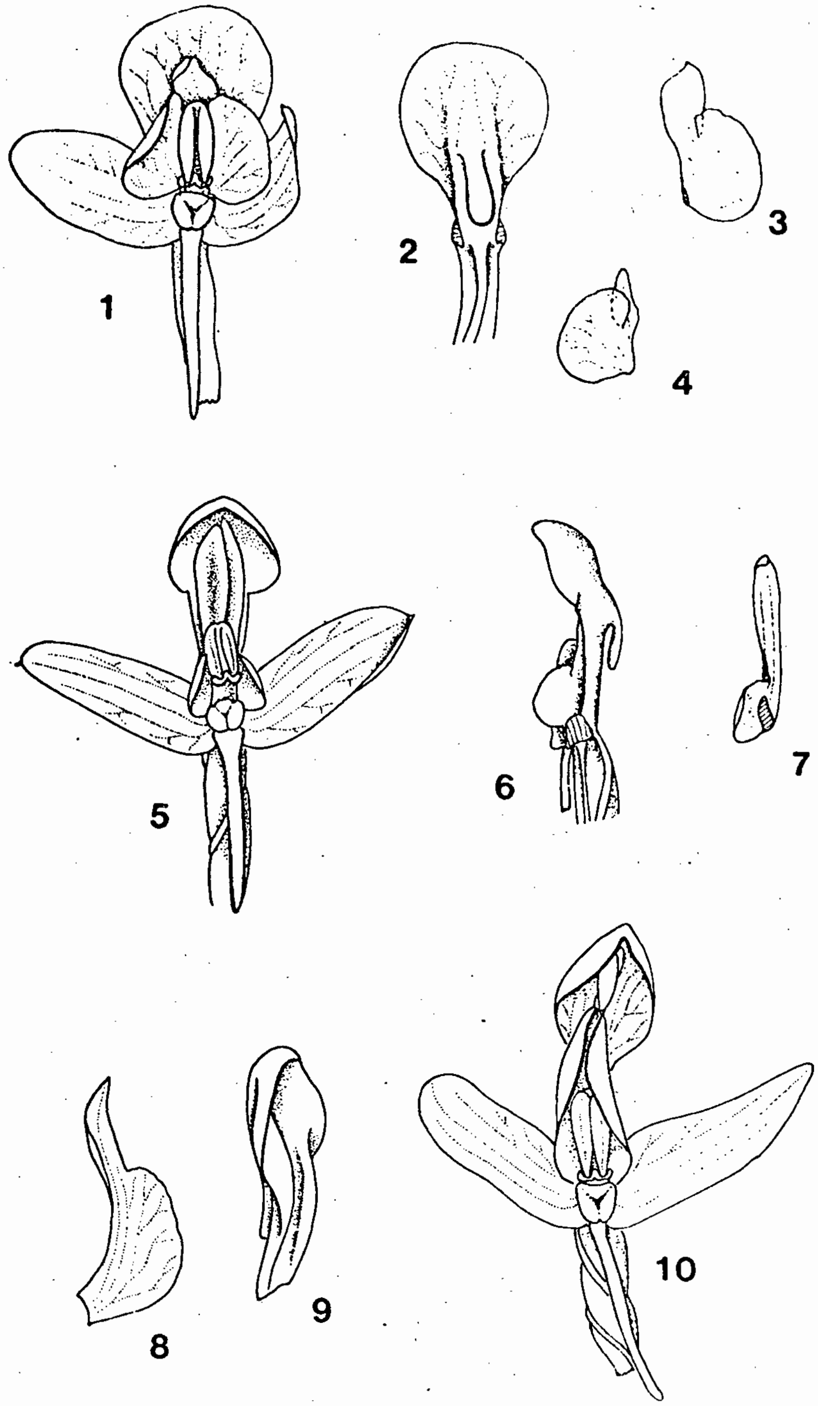


Fig. 13. -- Series *Englerana* (X 1,5). 1 - 3 *D. englerana* Kraenzl. from Holmes 0211, 1, frontal view of flower, 2, rear view of dorsal sepal, 3, petal. 4, *D. ukingensis* Schltr. from Cribb & Grey-Wilson 10767, petal. 5 - 7 *D. zombica* N.E.Br. from Ball in SRGH 74583, 5, frontal view of flower, 6, side view of dorsal sepal, 7, petal. 8 - 10, *D. verdickii* De Wild. from Milne-Redhead 3661, 8, petal, 9, dorsal sepal, 10, frontal view of flower.

wide, acute, pendent; anther erect, 5 - 7 mm long, connective longer than the anther; ovary c. 20 mm long; stigma flat, c. 3 mm in diameter.

Note: The identity of D. subscutellifera is not clear. Kraenzlin (1902) placed the species near D. scutellifera, and Schlechter (1915) stated that it is "a good species, which to some extent can be placed between the D. erubescens type and the D. welwitschii type". Summerhayes (1964, 1968) included the name in the synonymy of D. welwitschii. However, the size range of the flowers and the description of the petals, probably comes closer to the type of D. englerana.

Ecology and Distribution: Disa englerana occurs on the higher areas in South-Central Africa, mainly around Mbala in the Northern Province of Zambia, around Lubumbashi in the Shaba Province of Zaire, and in the Northern Province of Malawi. There is a single collection both from Iringa in the Southern Highlands of Tanzania and from the Luembe River in the northern part of the Shaba Province. The altitude range of the species is from 1000 to 2000 m, with most of the collections from about 1400 m above sea level. The climax over almost the whole distribution range is Brachystegia woodland (Rattray & Wild, 1961; Knapp, 1973). In Mbala and Sumbawanga it is possible that this species might occur in upland grassland. The rainfall over the distribution area is 1000 to 1400 mm p.a., with a dry period of about five months in winter (Jackson, 1961).

This species appears to have a remarkable range of habitats. It has been recorded from dambos, grassland in laterite soils, sandy grassland in Brachystegia woodland, from flat granite rocks, Uapaca-Protea woodland and Brachystegia woodland. There is no clear record of it occurring in upland grassland. Most of the habitat variation occurs in Zambia. All records from Malawi indicate Brachystegia woodland.

Flowering occurs mostly in January and February, but in Malawi the flowering time appears to be later, with most of the collections made in March, and some even in April.

Distribution: Distr. Pl. Afr. 18.

TANZANIA :

SOUTHERN HIGHLANDS : Iringa, Polhill & Paulo 1787 (K).

WESTERN PROVINCE : Ufipa, Leedal 1085 (K).

MALAWI :

NORTHERN PROVINCE : Vipya Plateau, Benson 1455 (BM); Vipya, Chapman 123 (BM); Nyika Plateau, Holmes 211 (K, SRGH); Vipya, Pawek 1864 (K); Nchena Nchena, Pawek 4462 (K); Katoto, Pawek 5078 (K, SRGH); Vipya, Pawek 8510 (K); Nyika, below plateau, Williamson 846 (K, SRGH).

ZAMBIA :

NORTHERN PROVINCE : Mbala, Bullock 2199 (K); Mbala, Bullock 2594 (K); Mbala, Nash 137 (K); Mbala, Lake Chila, Richards 255b (K); Mbala,old Isanya road, Richards 450 (K); Mbala, old Katwe road, Richards 4045 (K); Mbala, Richards 4261 (K); Mbala, Richards 8078 (BR, K); Mbala, escarpment above Lufubu Plains, Richards 8245 (K); Mbala, new road from Kambole to Iyendwe valley, Richards 10812 (K); Mbala Ndundu, Richards 10850 (K, SRGH); Mbala, Itembwe gorge, Richards 12050 (K); Mbala, Ningi Plains, Richards 15941 (K); Mbala, Lunzua road, Richards 15947 (BR, K, P, SRGH); Mbala, N'Muge Pans, Richards 18757 (K); Mbala, Itembwe gap, Richards 18836 (K); Kasama,Misanfu, Robinson 4290 (K, SRGH); 30 km S of Shiwa Ngandu, Robinson 4319 (K, SRGH); Mbala, Vesey-Fitzgerald 1552 (K); Nyika, Danger hill, Williamson 1396 (K); Shiwa Ngandu, Williamson 1447 (BOL); Danger Hill, NW of Mpika, Williamson & Drummond 1892 (SRGH).

COPPERBELT : Kalulushi, Baker 179 (SRGH); Ndola, Draper 21 (K); Mufulira, Fanshawe 2956 (K); Kitwe, Fanshawe 9918 (K, SRGH); Bancroft, Retief 134 (PRE).

ZAIRE :

SHABA : Lubumbashi, Bulaime 616 (BR); Welgelegen, Corbisier 581 (BR); Munama, De Giorgi 458 (BR, K); Keyberg, Detilleux 490 (BR); Luembe valley, Hock s.n. (BR); Lupaka river, Kassner 2453 (BM, K); Kipopo, Lemaire-Elias 185 (BR); Bragrasse, Quarré 1031 (BR); Kipopo, Schmitz 8152 (BR); Lubumbashi, Schmitz 7125 (BR); Katanga, Von Hirschberg 175 (BR, K, PRE).

17. *Disa ukingensis* Schltr., Bot. Jahrb. 53 : 539 (1915).-Type: Tanzania, Njombe District, Tandala, Stolz 2593 (B holo-, BM, BR, P, PRE iso-).

D. englerana Kraenzl., partially, Williamson, Orchids S. Central Africa : pl 53 (1977).

Tubers testicular, 15 mm long and c. 10 mm in diameter. Sterile shoot c. 40 mm tall; basal sheaths 2 - 3, up to 50 mm long, acute, barred or spotted with red; leaves up to 5, linear-lanceolate, erect, acute, conduplicate, 70 - 120 mm long and up to 12 mm wide. Fertile shoots robust, 150 - 300 mm tall; cauline leaves imbricate; basal sheaths 20 - 30 mm long, grading into the leaves; remainder 45 - 55 mm long and c. 13 mm wide, ovate-lanceolate, acute, usually the apical 1/3 free, grading apically into the floral bracts. Inflorescence dense, 60 - 100 mm long and with 7 - 15 flowers; bracts ovate, acute to sub-acuminate, c. 30 mm tall, usually overtopping the flowers. Flowers magenta, the galea paler with darker spots; dorsal sepal spathulate, claw 3 mm long and 3 mm wide, sometimes difficult to distinguish from the blade, blade rotund, obtuse, shallowly galeate, 10 - 13 mm in diameter, the margin incurved; spur pendent from just below the middle of the blade, reaching to the base of the dorsal sepal, 4 -6 mm long, obtuse, clavate, 0,5 - 1 mm in diameter at the base and 1 - 1,5 mm in diameter near the apex; lateral sepals oblong, obtuse to sub-acute, 9 - 13 mm long and 4 - 5 mm wide, flat, spreading sideways and upwards; petals bilobed, anterior lobe 6 - 7 mm tall and 4 - 5 mm wide, flanking the anther and spreading, the margins incurved and sometimes serrate, posterior lobe 7 - 8 mm tall and 2 - 3 mm wide, more or less ovate, acute to obtuse and occasionally serrate, erect inside the galea and somewhat overlapping; lip linear, acute, pendent, 10 - 11 mm long and 0,5 - 1 mm wide; anther erect, 4 - 5 mm long; ovary c. 15 mm long; stigma vertical, sessile, tripulvinate.

Note: Summerhayes (1968) included this species in the synonymy of Disa englerana. Williamson (1977) indicated some of the differences between these taxa by figuring both. This species was only known from the Nyika Plateau, while the type locality is in the Njombe District in Tanzania. However, in 1976 Cribb and Grey-Wilson recollected this beautiful species from near the type locality.

Ecology and Distribution: Disa ukingensis is restricted to the high mountains around the northern end of Lake Malawi. All collections have been made from upland grassland between 2100 m and 2800 m above sea level. The rainfall at this altitude varies from 1000 to 2400 mm p.a., depending on the topography. The winter months are dry, with frequent frost, and often mist (Chapman & White, 1970). The grassland is frequently burnt.

All habitat records indicate that this is a grassland species. Grosvenor & Renz 1116 record a high population density. Flowering occurs in March and April.

This species appears to be an upland vicariant of Disa englerana.

Distribution : Distr. Pl. Afr. 19.

TANZANIA :

SOUTHERN HIGHLANDS : Kitulo, Cribb & Grey-Wilson 10767 (K); Kyimbila, Stolz 2573 (BM, K).

MALAWI :

NORTHERN PROVINCE : Nyika Plateau, Grosvenor & Renz 1116 (BOL, SRGH); Nyika Plateau, Pawek 2058 (K); Nyika Plateau, Pawek 9274 (K); Nyika Plateau, Williamson 281 (K, PRE, SRGH); Nyika Plateau, Williamson 282 (K, SRGH).

18. **Disa zombica** N.E.Br., Fl. Trop. Afr. 7 : 278 (1898); Kraenzl., Orch. Gen. Sp. 1 : 783 (1900); Summerh. Kew Bull. 4 : 432 (1949); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 158 (1968); Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 71 (1974); Williamson, Orchids S. Central Africa : 80 (1977).-Type: Malawi, summit of Mt. Zomba, Buchanan 305 (K holo-).

D. nyassana Schltr., Bot. Jahrb. 53 : 538 (1915).-Type: Tanzania, Rungwe District, Kiwira River, Stolz 2486 (B holo-; BOL, BR, C, K, P, S, Z iso-).

Tubers testicular, up to 40 mm long and 15 mm in diameter. Sterile shoot up to 60 mm long; basal sheaths 2 - 3, c. 30 mm long, sub-acute, red spotted or barred; leaves 2 - 3, linear - elliptical, erect, acute or apiculate, conduplicate, 60 - 200 mm long and 8 - 20 mm wide. Fertile shoots slender to robust, 200 - 600 mm tall; cauline leaves imbricate; basal sheaths 20 - 30 mm long, acute, red spotted or barred, grading into the upper leaves; remaining leaves 40 - 60 (- 130) mm long, ovate-lanceolate, acute, often the apical half of the leaf free; grading apically into the floral bracts. Inflorescence usually dense, rarely lax, 90 - 160 mm long and with 10 - 25 flowers; bracts lanceolate-ovate, acute to acuminate, 35 - 45 mm long, overtopping the flowers. Flowers with gray-green lateral sepals and magenta to purple petals and dorsal sepal; dorsal sepal spathulate, 14 - 21 mm long, claw 7 - 11 mm long and c. 3 mm wide, canaliculate, erect, blade 7 - 11 mm long and 5 - 10 mm wide, ovate, obtuse, galeate, the margins curved in and the blade facing somewhat down; spur pendent from a small hump near the base of the blade, not reaching to the base of the dorsal sepal, 4 - 7 mm long, sub-clavate to clavate, obtuse, 0,5 - 1 mm in diameter at the base and 1 - 2 mm in diameter near the apex; lateral sepals obliquely oblong, sub-acute, 14 - 18 mm long and 5 - 8 mm wide, flat, spreading sidewards and upwards; petals bilobed, anterior lobe 4 - 7 mm long and 3 - 5 mm wide, ovate, flanking the anther and spreading, posterior lobe oblanceolate, acute to sub-acute, 12 - 18 mm long and 2 - 3 mm wide, erect inside the galea, the lobes half over-lapping, apexes incurved; lip linear, acute, pendent, 13 - 17 mm long and 1 - 1,5 (- 2) mm wide; rostellum c. 3 mm tall; anther erect, 4 - 5 mm long and 0,8 - 1 mm wide; ovary c. 10 - 15 mm long; stigma sessile, tripulvinate, c. 2 mm in diameter.

Note: Schlechter (1901) included D. zombica in the synonymy of D. erubescens, and in 1915 he proposed another name for the same species. It is not clear whether Schlechter had seen the type of D. zombica. Summerhayes rectified the situation in 1968 by reducing D. nyassana to the synonymy of D. zombica.

Ecology and Distribution: Disa zombica occurs along the eastern escarpment mountains from Zimbabwe to Tanzania. The absence of this species from the Malawi side of the Nyika Plateau is unexpected. The northernmost collection is from Kasulu, in north-western Tanzania, and about 500 km to the north of the next collection. The absence of this species from the highlands of Sumbawanga, which lie in between, is not expected.

Although the altitude range of the species is only from 1200 to 2200 m, most of the collectors have indicated a grassland (probably upland grassland) habitat. Phipps and Goodier (1962) list the climatic differences between the eastern escarpment in the more inland areas in Zimbabwe; these could well lead to a lowering of the upland grassland border. Rainfall and climate are variable in the escarpment mountains. Phipps and Goodier indicate a rainfall range from 741 to 2997 mm p.a. for the Chimanimani mountains in Zimbabwe, and Chapman & White (1970) give a range of 1062 to 2344 mm p.a. for the Nyika Plateau in Malawi. In both areas the winter months are dry, often with severe frost. Occasionally misty days occur in winter. Grassland fires can be severe.

Although this species has such a large distribution area, it does not appear to be common anywhere along its range, and its ecology is not understood.

Flowering occurs from January to March, with one specimen collected in flower in December.

Distribution: Distr. Pl. Afr. 20.

TANZANIA :

WESTERN PROVINCE : Kigoma, Kasulu, Rounce 6 (K).

SOUTHERN HIGHLANDS : Between Kyela and Isoko, Cribb and Grey-Wilson 10697 (K); Bundali mts, Davies 862 (K); Ilambo, Bundali Hills, Leedal 71 (K); Kyimbila, Stolz 2486 (BM, K); Kyimbila, Stolz 2623 (BM, BOL, BR, K, PRE, Z).

BURUNDI : Kitega, Delarge 28 (BR); Mwaro, Lewalle 293 (BR).

MALAWI :

NORTHERN PROVINCE : Mzimba, Pawek 8024 (K); Mzuzu, Pawek 10857 (SRGH).

SOUTHERN PROVINCE : Shire Highlands, Buchanan 305 (K); Zomba, McLoughlin 125/6 (K, PRE).

ZAMBIA :

NORTHERN PROVINCE : Nyika Plateau, Williamson & Odgers 295 (K, SRGH).

MOCAMBIQUE :

MANICA E SOFALA : Mt Tsetsera, Ball 534 (K, SRGH).

ZIMBABWE : Melsetter, Ball 629 (K, SRGH); Mt Vumba, Ferrar 3985 (PRE).

19. **Disa verdickii** De Wild., Ann. Mus. Congo Bot., Sér. 4 (1) : 26 (1902); Geerinck, Bull. Soc. roy. Belg. 107 : 69 (1974); Williamson, Orchids S. Central Africa : 80, pl. 51 (1977).-Type: Zaire, Lukafu, Verdick 410 (BR holo-).

Tubers testicular, c. 25 mm long and 15 mm in diameter. Sterile shoot slender, up to 50 mm long; basal sheaths 2 - 3, acute or obtuse, up to 40 mm long; leaves up to 5, erect, linear to elliptical, acute, conduplicate, up to 110 mm long and 15 mm wide. Fertile shoots 250 - 500 mm tall; cauline leaves subimbricate, reduced basally to several sub-acute, 30 mm long sheaths, the remainder of the leaves 40 - 70 mm long, acute to sub-acuminate, ovate-lanceolate, with only the apexes free, grading apically into the floral bracts. Inflorescence sub-imbricate, 80 - 200 mm long and with 8 - 25 flowers; bracts ovate-lanceolate, sub-acuminate, 30 - 40 mm long, reaching to the middle or overtopping the flowers. Flowers rosy-mauve to magenta-pink; dorsal sepal spathulate, 20 - 25 mm tall, claw 11 - 12 mm long, erect, deeply canaliculate towards the apex, c. 4 mm wide, blade orbicular, obtuse, c. 12 mm in diameter, galeate, the upper margin incurved, the groove in the claw continued into the blade; spur pendent from below the middle of the dorsal sepal, usually following the curve in the dorsal sepal, 6 - 7 mm long, clavate, 1 - 3 mm in diameter; lateral sepals sub-oblique, oblong, obtuse to sub-acute, 20 - 25 mm long, 7 - 10 mm wide, flat, spreading sidewards; petals bilobed, anterior lobe oblong, 13 - 15 mm long and 6 - 8 mm wide, flanking the anther and spreading, the margins incurved, posterior lobe 20 - 22 mm long and 2 - 3 mm wide, narrowly oblanceolate to linear, sub-acute, included in the galea, partially overlapping; lip linear, acute, pendent, 20 - 23 mm long and 1 mm wide; rostellum c. 3 mm tall; anther erect, 6 - 9 mm tall, connective longer than the anther sacs; ovary c. 20 mm long; stigma flat, tripulvinate, sessile.

Ecology and Distribution: Disa verdickii has an unusual distribution in the eastern part of South-Central Africa. Collections are known from the Upemba National Park and Kasai Province in Zaire, from Mwinilunga in Western Zambia, and from Huambo in Angola.

The habitat of this species is not well known. Williamson (1977) describes it as "wet grassland and open Uapaca woodland on grassland verge". The collections from Kasai probably come from tall moist savanna woodland (Knapp, 1973). Milne-Redhead 3661 was collected from the edge of Cryptosepalum woodland near Mwinilunga. The collections from Angola are from montane grassland and dwarf shrub savanna. No collection notes indicated moist or wet conditions.

The rainfall over the range varies from near 1000 mm p.a. to probably over 1400 mm p.a., with about five dry months in winter (Jackson, 1961). Flowering times varies from October to January, but one flowering specimen has been collected as early as August (Kassner 3245, from Kasai in Zaire).

Distribution: Distr. Pl. Afr. 21.

ZAIRE :

KASAI : Lusambo - Luluaburg, Kassner 3245 (BM); Lankuru River, Kassner 3339 (BM).

SHABA : Upemba National Park, De Witte 5290 (BR, K); Kundelunga, Malaisse 4906 (BR); Lukafu, Verdick 410 (K).

NO EXACT LOCALITY : Quarré 5036b (BR).

ZAMBIA :

NORTH-WESTERN PROVINCE : Mwinilunga, Holmes 105 (K); Mwinilunga, Marks 97 (K); Mwinilunga, Dobeka plain, Milne-Redhead 3661 (BR, K, PRE); Source of the River Zambezi, Robinson 5982 (K, SRGH); 48 km E of Mwinilunga, Williamson & Simon 1774 (K, PRE).

ANGOLA :

HUAMBO : Mt Moco, Huntley, Roberts & Ward 104 (PRE); Mt Moco, Huntley, Roberts & Ward 112 (PRE).

Series 4. **Rubris** Linder, ser. nov.

Flores grandes, sepalis lateralibus 17 - 35 mm longis, inflorescentis laxis, calcaribus angustatibus quam sepalis dorsalibus, petalis lobis posticis multis longioribus quam lobis anticis, S-flexis, limbibus sepalis dorsalibus longis.

Flowers large, lateral sepals 17 - 35 mm long, in a lax inflorescence, spur not reaching to the base of the dorsal sepal, posterior petal lobe much longer than the anterior lobe, with a characteristic S-bend halfway up the length, dorsal sepal with a long limb.

Type: *D. erubescens* Rendl.

The four taxa in this series are all rather closely related. The distribution areas also overlap to some extent. Three of the taxa occur in dambos or seepages in montane grassland, while the fourth taxon (*D. katangensis*) grows in *Brachystegia* woodlands.

This series is centred in South-Central Africa, with one species reaching the Cameroun mountains and Kenya, and another reaching the Eastern Districts of Zimbabwe.

Of the four taxa, *D. katangensis* is the most distinct. Material of *D. ornithantha* can usually be separated from *D. erubescence* s.l. Some difficulty has been experienced in the determination of fresh material. Williamson (pers. com) maintains that hybrids between these two taxa exist on the Nyika Plateau in Malawi.

The remaining two taxa, *D. erubescens* ssp. *erubescens* and ssp. *carsonii*, appear at first glance to be quite distinct. The distribution areas of these two taxa are almost contiguous, with an overlap zone in the highlands of Southern Tanzania and on the Nyika Plateau. A study of the available herbarium material showed that although most of the collections could readily be referred to one of these taxa, there were several collections from the overlap zone that are intermediate (Bjornstad 569, Watermeyer 208, 21, Cribb & Grey-Wilson 10539, Richards 15851 and Bullock 2049). Field studies on the Nyika Plateau in Malawi elucidated several patterns. *D. erubescens* ssp. *carsonii* occurred in somewhat wetter conditions than ssp. *erubescens*. The result is that the two species only rarely grow together. Intermediate forms occurred where an intermediate habitat was available, irrespective of whether only one or both typical forms were present. Population studies on ssp. *carsonii* showed that there is a remarkable degree of inter-population variation, and that this variation often exceeds the variation found between populations of the two subspecies. This is easily substantiated by reference to herbarium material of ssp. *carsonii*.

From this it would appear as if ssp. carsonii has not clearly established a morphological entity, and as though gene flow between the two subspecies still regularly occurs. To give this taxon specific status would obscure the internal variation and the links to D. erubescens s.s.

20. **Disa ornithantha** Schltr., Bot. Jahrb. 53 : 538 (1915); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 158 (1968); Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 68 (1974); Williamson, Orchids S. Central Africa : 79, pl. 50 (1977).-Type: Tanzania, Rungwe District, Kyimbila, Stolz 135 (B holo-; G, K, W, Z iso-).

Tubers testicular. Sterile shoot with 2 basal sheaths; leaves 3 - 4, linear, acute, erect, conduplicate, up to 200 mm long and 10 mm wide. Fertile shoot 190 - 280 - 500 mm tall; cauline leaves imbricate, ovate to lanceolate, acute, 40 - 70 mm long and c. 12 mm wide, with free apexes, grading basally into the basal sheaths and apically into the floral bracts. Inflorescence small, compact, 40 - 90 mm long and with 1 - 5 (- 6) flowers; bracts acuminate, as tall as or overtopping the flowers, often keeled towards the apex. Flowers red, posterior petal lobes white; dorsal sepal spathulate, claw narrowly oblong, 7 - 12 mm long and c. 3 mm wide, erect, blade ovate, acute, 10 - 14 mm long and 9 - 12 mm wide, galea c. 4 mm deep with the margins incurved, blade somewhat reflexed; spur pendent from above the base of the blade, reaching to the base of the dorsal sepal, 9 - 11 mm long, sub-clavate and sub-acute, c. 0,5 mm in diameter at the base and 1 - 2 mm in diameter near the apex; lateral sepals obliquely oblong, obtuse, 17 - 23 mm long and 8 - 10 mm wide, more or less flat, spreading sideways and upwards; petals bilobed,

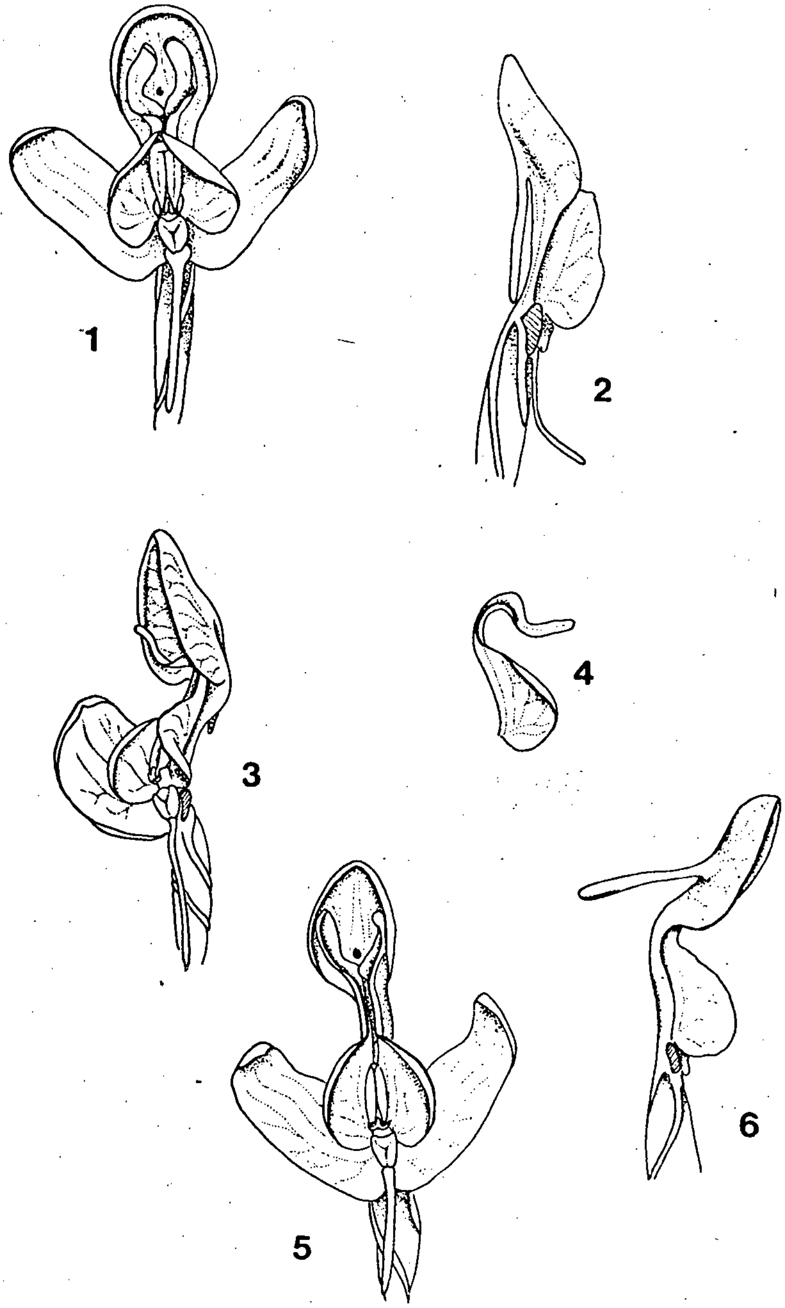


Fig. 14. -- Series *Rubris*. 1, 2, *D. ornithantha* Schltr. (X 1,5) from Brummitt. Chisampa & Polhill 13882. 3, *D. katangensis* De Wild. (X 1) from Milne-Redhead 4321. 4, *D. katangensis* petal (X 1) from Milne-Redhead 4321. 5, *D. erubescens* Rendl. ssp. *carsonii* (N.E.Br.) Linder (X 1) from Brummitt & Polhill 13682. 6, *D. erubescens* ssp. *carsonii* (X 1) from Milne-Redhead & Taylor 8309.

anterior lobe ovate, 9 - 11 mm long and 5 - 6 mm broad, flanking the anther and spreading, the margins incurved, posterior lobe linear, c. 20 mm long and 2 - 3 mm wide, sub-conduplicate, parallel at the base, then diverging by a S-shaped twist, included in the galea; lip linear, acute, pendent, 9 - 14 mm long; rostellum 2 - 3 mm tall; anther erect, 6 - 8 mm long; stigma flat, tripulvinate, 2 - 4 mm in diameter.

Ecology and Distribution: *Disa ornithantha* is widespread in the higher areas in South-Central Africa. From Angola (Moxico) and Tanzania (Southern Highlands) very few collections are known. In Zambia the species is known from the Northern Province and from Mwinilunga in Western Province. In Malawi and Zimbabwe *D. ornithantha* appears to be common on the mountains above 1500 m above sea level.

Most of the collections are from between 1500 and 2000 m above sea level, but a few collections are from about 1000 m (Holmes 0290). The climax vegetation over the distribution range in Zambia is *Brachystegia* woodland, but in Malawi and Zimbabwe this species is recorded only from the montane zone, with upland grassland or montane forest as climax (Rattrey & Wild, 1961). The rainfall over the range is mostly from 1000 to 1400 mm p.a., but in the montane areas of Malawi and Zimbabwe, the rainfall can vary from about 800 mm to 3000 mm p.a. (Phipps & Goodier, 1962; Chapman & White, 1970).

Most of the collections have been made from damp grassland or dambo conditions. In Mwinilunga the species has been collected from dry sand in Uapaca shrubland. A population studied on the Nyika Plateau in Malawi (Linder 2047) occurred in a temporary seepage on the edge of a dambo. Williamson (1977) describes the habitat of this species as "wet upland boggy grassland". Possibly it could more accurately be described as seasonally damp.

Flowering occurs in December and January in Zambia, and from January to March in Malawi and Zimbabwe.

Distribution : Distr. Pl. Afr. 22.

TANZANIA :

SOUTHERN HIGHLANDS : Lupembe, Schlieben 189 (BR); Kyimbila, Stolz 135 (BM, K, M, S); Sao Hill, Watermeyer 208e (K).

MALAWI :

NORTHERN PROVINCE : Nyika Plateau, Grosvenor & Renz 1114 (SRGH); Nyika Plateau, Phillips 1014 (SRGH); Nyika Plateau, Robinson 4487 (K, M, SRGH); Nyika Plateau, Williamson, Simon & Ball 792 (K, SRGH).

SOUTHERN PROVINCE : Zomba Plateau, Banda 386 (SRGH); Zomba Plateau, Benson 1042 (P, PRE); Zomba Plateau, Brummitt 9139 (K); Zomba Plateau, Exell, Mendoza & Wild 715 (BM, SRGH); Zomba Plateau, Exell, Mendoza & Wild 755 (BM, SRGH); Zomba Plateau, Grosvenor & Renz 965 (SRGH); Zomba Plateau, Jones 9 (SRGH); Zomba Plateau, McLoughlin 105 (K, PRE); Mt Zomba, Robson 1318 (K, SRGH); Zomba Plateau, Salubeni 218 (SRGH).

ZAIRE :

SHABA : Kiluba, Luadika, De Witte 3128 (BR); Lovoi River, Kassner 3340 (BM); Potopoto, Malaisse 8786 (BR); Between Kolwezi and Djoni, St. Lisowski, Malaisse & Symoens 7809 (BR); Katena, St. Lisowski, Malaisse & Symoens 13280 (BR); Kasongami, Symoens 6365 (BR).

ZAMBIA :

NORTHERN PROVINCE : Mbala, Lake Chila, Bullock 2205 (K);

Kawambwa, Mbereshi River, Holmes 290 (K, SRGH); Mbala, Lumi River, Richards 4408 (K); Mbala, Richards 22926 (K); Kawambwa, Williamson 1212 (SRGH); Nyika, Williamson 1397 (BOL, K, SRGH).

NORTH-WESTERN PROVINCE : Mwinilunga, Brummitt, Chisumpa & Polhill 13882 (K); Mwinilunga, Marks 95 (K); Mwinilunga, Dobeka Plain, Milne-Redhead 3663 (BR, K, PRE); Mwinilunga, Samahani, Robinson 6087 (K); 48 km E of Mwinilunga, Williamson & Simon 1778 (K, SRGH).

ANGOLA :

MOXICO : River Muchula, Milne-Redhead 4028 (K).

21. *Disa katangensis* De Wild., Ann. Mus. Congo Bot., sér. 4 (1) : 25 (1902); Williamson, Orchids S. Central Africa : 80 (1977).-Type: Zaire, Lukafu, Verdick 418 (BR holo-).

D. erubescens Rendl. var. *katangensis* (De Wild.) Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 66 (1874).

Sterile shoot with 3 basal sheaths, c. 25 mm long, acute, to obtuse, and with 2 - 3 linear, acute, erect leaves, up to 220 mm long and 10 mm wide. Fertile shoots 400 - 600 mm tall; cauline leaves imbricate, c. 50 - 80 mm long and 12 - 18 mm wide, the lower half of the leaf sheathing, leaves grading basally into the basal sheaths and apically into the floral bracts. Inflorescence lax, 80 - 160 mm long and with 2 - 8 flowers; bracts lanceolate, long-acuminate, 50 - 70 mm long, the apical part rolled, overtopping the flowers. Flowers red to pink to scarlet, galea with darker spots; dorsal sepal spathulate, claw 16 - 17 mm long and 3 - 4 mm wide, canaliculate, erect, blade ovate, sub-cordate, obtuse, 13 - 20 mm long and 11 - 18 mm wide, galea c. 8 mm deep, curved forwards; spur pendent from a ridge below the middle of the dorsal sepal, 13 - 16 mm long, filiform to rarely sub-clavate, 0,75 - 1,5 mm in diameter; lateral sepals obliquely oblong, sub-obtuse to acute, 21 - 36 mm long and 8 - 13 mm wide, flat, spreading sideways and upwards; petals bilobed, anterior lobe ovate, 9 - 15 mm tall and 6 - 8 mm wide, flanking the anther and spreading, the margins incurved, posterior lobe linear, 22 - 30 mm long and 3 - 4 mm wide, parallel at the base, then diverging through as S shaped curve; lip linear, acute, pendent, 14 - 22 mm long; rostellum simple; anther erect, 6 - 9 mm tall, the connective longer than the cells; ovary c. 20 mm long; stigma 3 - 4 mm in diameter.

Note: The status of this rather little known species was for some time not clear, and Geerinck (1974) reduced it to a variety of D. erubescens. Williamson (1977), on the basis of extensive field-work, upheld the species.

Ecology and Distribution: Disa katangensis occurs on the watershed between the River Zaire and the Zambezi. The area receives a rainfall of 1000 - 1400 mm p.a., with about five dry months in winter (Jackson, 1961). Theoretically, the climax vegetation over the whole range of D. katangensis should be Brachystegia woodland (Rattrey & Wild, 1961; Fanshawe, 1969). However, most collectors indicated an Uapaca-Monotes woodland. This is an early successional stage to Brachystegia woodland after heavy biotic disturbance (Fanshawe, 1969). Several collectors indicated a sandy substrate.

Williamson (1977) describes the habitat as low Brachystegia woodland in wet sand and in deep shade, and also wet Brachystegia woodland. No other collectors indicated the moisture of the sand, or the shaded conditions.

Flowering occurs in January and February. Quarré 0339 was collected in flower in May, from Lubumbashi in Zaire.

Distribution: Distr. Pl. Afr. 23.

ZAIRE :

SHABA : Lubumbashi, Quarré 339 (PRE); Lukani, Schmitz 4933 (BR); Kalule Sud, Shantz 544 (K); Tumbwe, Symoens 7084a (BR); Star Mine, Von Hirschberg 208 (PRE).

ZAMBIA :

NORTHERN PROVINCE : Mpika, Fanshawe 1940 (K); 40 km N of Nyika Plateau, Williamson 1486 (K); Shiwa Ngandu, Williamson 413 (BOL, K, SRGH).

NORTH-WESTERN PROVINCE : Mwinilunga, Marks 96 (K); Mwinilunga, Milne-Redhead 4321 (BR, K).

ANGOLA :

MOXICO : Near Lusavo Falls, Milne-Redhead 4045 (BM, BR, K, PRE).

22. Disa erubescens Rendl.

Tubers testicular, fleshy. Sterile shoot up to 120 mm long; basal sheaths 2 - 3, red spotted; leaves 2 - 3, linear, acute, erect, conduplicate, up to 300 mm long and 20 mm wide. Fertile shoot 400 - 900 mm tall; cauline leaves imbricate, 30 - 80 mm long and 10 - 15 mm wide, lanceolate, acute, with only the apex free, grading basally into the basal sheaths and apically into the floral bracts. Inflorescence lax, 50 - 130 mm long and with (1 -) 3 - 7 - 12 flowers; bracts lanceolate, acute, c. 30 mm long, reaching up to the flowers. Flowers bright red; dorsal sepal spathulate, claw erect, 11 - 26 mm long and 3 - 7 mm wide, canaliculate, blade ovate-elliptical, acute, 12 - 24 mm long and 8 - 18 mm wide, galea 3 - 5 mm deep; base of the blade curved geniculately to face the blade down; spur ascending from shortly below the middle of the blade, slender, 8 - 16 mm long, 0,5 -4 mm wide; lateral sepals obliquely oblong, sub-acute to acute, 17 - 35 mm long and 6 - 14 mm wide, spreading upwards, twisted forwards or backwards; petals bilobed, anterior lobe ovate, 8 - 15 (- 20) mm long and 5 - 10 mm wide, flanking the anther and spreading, posterior lobe linear, 20 - 41 mm long and 1 - 3 mm wide, ascending inside the galea, parallel in the lower half, then diverging by a S shaped curve; lip linear, acute, pending, 9 - 20 mm long; rostellum simple, c. 2 mm long; anther vertical, 5 - 8 mm long; ovary c. 20 mm long; stigma tripulvinate, 3 - 4 mm in diameter, sessile.

22a. *Disa erubescens* Rendl. subsp. *erubescens*

Disa erubescens Rendl., Journ. Linn. Soc. Lond., Bot. 33 : 297 (1895); N.E. Br., Fl. Trop. Afr. 7 : 277 (1898); Kraenzl., Orch. Gen. Sp. 1 : 738 (1900); Schltr., Bot. Jahrb. 31 : 216 (1901); Schltr., Bot. Jahrb. 53 : 537 (1915); Summerh., Fl. W. Trop. Afr. 2 : 414 (1936); Piers, Orchids E. Africa : 57 (1968); Summerh., Fl. Trop. E. Afr. Orchid. (1) : 157 (1968); Agnew, Upland Kenya Wild Flowers : 746 (1974); Geerinck, Bull. Soc. roy. Bot. Belg. 107 : 65 (1974); Williamson, Orchids S. Central Africa : 78 (1977).-Type: Uganda, Ruwenzori, Scott Elliott 7809 (BM holo-; K iso-).

Fig. 15. -- D. erubescens Rendl. ssp. erubescens (X 0,5) from Linder 2013.

D. erubescens Rendl. var. *leucantha* Schltr., Bot. Jahrb. 53 : 537 (1915).-Type: Tanzania, Rungwe District, Kyimbila, Stolz 141c (B holo-).

Inflorescence (1 -) 3 - 7 - 10 flowered; flowers medium-sized, dorsal sepal less than 30 mm long, ovate to elliptical; plants 400 - 900 mm tall.

Notes: The concept of *D. erubescens* has undergone some fluctuations since the original description of the species. Brown (1898) and Kraenzlin (1900) defined the species narrowly, excluding the larger flowered *D. carsonii*. Schlechter (1901) included not only the larger flowered forms, but also the quite different *D. zombica*. In 1915 Schlechter separated *D. carsonii* as a distinct species, but did not indicate whether he still regarded *D. zombica* as being part of *D. erubescens*. His description of *D. nyassana* in the same publication would indicate that he had mis-identified the nature of *D. zombica*, as there is no difference between the types of these two species.

Summerhayes (1936m,1968) kept *D. erubescens* and *D. carsonii* separate. *Disa leopoldi* was described in 1899 by Kraenzlin from a mixed type, where the inflorescence is from *D. erubescens* and flower from *D. walleri* Reichb.f. According to article 9 of the I.C.B.N., the name must apply to that portion of the mixed collection "which corresponds most nearly with the original description". In this instance, then, the name is applied to *D. walleri* Reichb.f.

Ecology and Distribution: *Disa erubescens* ssp. *erubescens* is widespread in montane areas (between 1800 and 2400 m above sea level) in tropical Africa. It has not been recorded west of the

Bamenda Plateau in Nigeria, or north of the Sudan. The rainfall over this distribution range varies from 1500 mm to over 2500 mm p.a. (Chapman, 1962; Chapman & White, 1970; Jackson, 1961; Jackson, 1956).

The distribution of rainfall varies from unimodal with a dry season of four to five months in winter (most of the distribution range), to bimodal with a dry season of about three months, that is frequently broken by thunderstorms, in the Ruwenzori and Ankole areas of Uganda (Langdale-Brown et al., 1964).

Robyns and Tournay (1955) recorded this subspecies from sclerophyll forest on ancient lava and montane grassland, between 1700 and 2000 m, in the Ruwenzori mountains in Zaire. Lewalle (1970) recorded it from between 1600 and 2400 m above sea level in Burundi. Williamson (1977) described the habitat in South-Central Africa as "Very wet seasonally or perenially boggy upland grassland. Also on rocks in seepage peat mats". This habitat description was verified by field studies in Malawi, on Mt. Mlanje, Zomba Plateau and the Nyika Plateau, where the taxon was found to grow in seepage areas in grassland, as well as the habitats described by Williamson.

Flowering occurs in summer. North of the equator (Kenya, Sudan, Nigeria and Cameroun) this is in June and July, with occasional collections from May. South of the equator it flowers from December to February. In Uganda flowering occurs mainly from October to December. This appears to be transitional.

Distribution: Distr. Pl. Afr. 2 4.

SUDAN :

EQUATORIA : Imatong mts, Andrews 1900 (K); Imatong Mts, Andrews 1976 (K); Imatong mts, Mangalla, Johnston 1430 (K); Torit, Dumuso, Jackson 1573 (K); Imatong mts, Lomuleng, Myers 11574 (K).

KENYA :

RIFT VALLEY PROVINCE : Amala, Molo, Copley 103 (K); Mt Elgon, Dale 3135 (K); Londiani, Davis 19 (BM, K); Masai, Olulunga, Glover, Samuel & Wateridge 3223 (K); Londiani, Graham 2824 (K, PRE); Cherangani, Lucas 161 (K); Kenya, Mainwaring 1281 (K); Kisii, Napier 1890 (K); Kapenguria, Piers 120 (K); Londiani, Smart G8 (K); Cherangani, Symes 613 (K); Elgon, Tweedie 33 (K); Kitale Prison Farm, Tweedie 3658 (K); Mau Forest, Whittal 186 (K); Near Mau summit, Williams in EAH 11086 (BR, K).

UGANDA :

EASTERN PROVINCE : Bulunchebe Mbale, Nusu summit, Maxwell-Forbes 201 (PRE).

WESTERN PROVINCE : Ruchiga, Bagshawe 468 (BM); Near Kisolo, Burtt 2594 (BR, K); Mutanda, Chandler-Hancock 2662 (K); Between Mgahinga and Sabinio, Eggeling 1107 (K); Ankole, Bushenyi, Eggeling 4229 (K); Kigezi, Lake Bungoni, Gardner 276 (BR, K); Kanaba Pass, above Muko, Lind 2342 (K); Kigezi, Bufumbira, Lye 893 (K); Toro, Mbatia & Kafambo 10 (K); Ruwenzori, Osmaston 1340 (K); Karangoro, Osmaston 3955 (K); Ankole, Nyabubale, Purseglove 463 (K); Kigezi, Purseglove 1614 (K); Kigezi, Lake Mutanda, Sandford 4 (K); Ruwenzori, Scott-Elliott 7809 (BM, K); Kigezi, Lake Mutanda, Synge 1234 (BM, K).

CAMEROUN : Mezam, Bambili lakes, Bauer 70 (K); Mezam, Bambili, Bauer 82 (K); Bafut-Ngem 838 (K); Adamawa, Mambila Plateau, Chapman 12 (BR, K); Banada, Basenaka, Chapman 1503 (K); Manenquba mts, Gregory 301 (K); Djutti, Muerillon 1328 (BR, K, P); Mt Santa, Saxer 8 (K); Santa, Saxer 61 (K).

NIGERIA :

EASTERN REGION : Ogoja, Obudu Plateau, Hall 2957 (K).

TANZANIA :

EASTERN PROVINCE : Ulugurus, Lukwangule, Bruce 778 (K, P); Ulugurus, Chenzena, Cribb & Grey-Wilson 10439 (K); Ulugurus, Lukwangule Plateau, Drummond & Hemsley 1561 (K); Ulugurus, Moreau 281 (K, S); Ulugurus, Schlieben 5459 (BM, BR, P, M, S, Z).

SOUTHERN PROVINCE : Songea, Matengo Hills, Milne-Redhead & Taylor 8309 (K).

SOUTHERN HIGHLANDS : Between Iringa and Mbeya, Ball 780 (K); Mt Rungwe, Ball 796 (K); Kigogo, Carmichael 348 (K); 48 km W of Iringa, Cribb & Grey-Wilson 10531 (K); Tukuyu, Davies 814 (K); Rungwe, Davies 823 (K); Iringa, Dabaga highlands, Polhill & Paulo 1418 (BR, K); Mbeya Road, Pollock s.n. (K); Livingstone mts, Rae A10 (BM); Njombe, Elton Plateau, Richards 7694 (K); Njombe, Kipengere Range, Richards 7812 (BR, K); Njombe, Milo Mission, Richards 14059 (K, P); Southern Highlands, Semsei1555 (K); Southern Highlands, Semsei 1604 (K); Sao Hill, Watermeyer 208a, b, c, d (K).

WESTERN PROVINCE : Ufipa, Malonje Plateau, Richards 15851 (PRE).

BURUNDI : Gitega, Delarge 12 (BR); Route Bujumbana - Matana, Delarge 24 (BR); Bujumbara, Lewalle 181 (BR, K); Tora, Lewalle 1441 (BR); Route Bugarama - Rushubi, Petit 2067 (BR); Muramwya, Reekmans 1326 (BR).

RWANDA : Biumba, Bequart 177 (BR).

ZAIRE :

KIVU : Mt Kahuzi, Bamps 2822 (BR); Kaleha, Deube

55/27 (BR); Mt Kahuzi, Hendrickx 3619 (BR); Lushanja, Kabare, Christiaensen 258 (BR, K, PRE, Z); Busogo, Lebrun 8654 (BR); Batambo, Staner 2034 (BR); Kahuzi Saddle, Stauffer 1087 (BR, K, PRE, Z); Uvira, Symoens 2140 (BR); Kabore, Thomas 1450 (BR); Between Kingi and Busogo, Tobrum 8654 (K).

KASAI : Mukishi, Becquet 7 (BR).

SHABA : Lovoi, Kassner 3362 (BM); Luemba, Kinet 1520 (BR); Kabwe - Nyamobwa, Rossignol s.n. (BR).

MALAWI :

NORTHERN PROVINCE : Vipya, Chapman 1554 (K, SRGH); Nyika Plateau, Grosvenor & Renz 1137 (SRGH); Nyika Plateau, Pawek 7849 (K); Vipya Plateau, Pawek 8134 (K); Nyika Plateau, Phillips 864 (SRGH); Nyika Plateau, Richards 14405a (K); Nyika Plateau, Williamson 793 (K); Nyika Plateau, Williamson, Simon & Ball 820 (K).

CENTRAL PROVINCE : Mt Dedza, Grosvenor & Renz 1025 (SRGH).

SOUTHERN PROVINCE : Mt Mlanje, Binns 184 (SRGH); Zomba Plateau, Grosvenor & Renz 985 (SRGH); Mt. Mlanje, Lupton 91 (BM); Mt Zomba, McLoughlin 114 (K, PRE, SRGH); Mt Zomba, Whyte s.n. (K).

ZAMBIA :

CENTRAL PROVINCE : Kundalila Falls, Williamson 2149 (SRGH).

NORTH-WESTERN PROVINCE : Kalene Hill, Robinson 6087 (SRGH).

ZIMBABWE : Chimanimani Mts, Hall 223 (BOL).

22b. *Disa erubescens* Rendl. ssp. *carsonii* (N.E.Br.) Linder, comb. nov. et stat. nov., basionym: Disa carsonii N.E.Br., Fl. Trop. Afr. 7:277 (1898); Kraenzl., Orch. Gen. Sp. 1 : 737 (1900); Schltr., Bot. Jahrb. 53 : 537 (1915); Williamson, Orchids S. Central Africa : 78 (1977).-Type: Zambia, south of Lake Tanzania, Carson 22 (K! holo-).

Disa stolzii Schltr., Bot. Jahrb. 53 : 537 (1915); Summerh., Fl. Trop. E. Afr., Orchid. (1) : 156 (1968); Williamson, Orchids S. Central Afr. : 78, pl. 49 (1977).-Type: Tanzania, Mt. Rungwe, Stolz 2506 (B holo-, BM! K! PRE! iso-).

Plants (140 -) 180 - 350 (- 1000) mm tall; inflorescence with 1 - 4 (- 12) flowers; flowers large, dorsal sepal more than 30 mm long; often sub-acuminate.

Notes: The types of the two taxa look quite different, and it is not surprising that when Schlechter separated D. carsonii from D. erubescens in 1915, he should also recognize D. stolzii as a distinct species. This complex had until now not been critically studied, as much of the important material fell outside the area of the Flora of Tropical East Africa. Williamson (1977) noted that D. carsonii only differed in size from D. stolzii, and that it might not be a distinct species.

Ecology and Distribution: This subspecies is restricted to the highlands around Lake Malawi, to the Northern Province of Zambia and the Kundelungu Plateau in Zaire. The altitude range is about 1500 to 2500 m. The rainfall is about 1000 mm p.a. over most of the range (Jackson, 1961), but in the more mountainous areas it can be as high as 2500 mm p.a. (Chapman & White, 1970). There is usually a dry season of up to five months in winter, during which severe frosts can occur at the higher altitudes.

Williamson (1977) described the habitat as "very wet upland grassland". Most collectors indicated a 'dambo' habitat, the remainder grassland. Field studies in Malawi by the present author (Nyika Plateau), showed that this subspecies occurs under wetter conditions than ssp. erubescens. It was found to form fairly dense populations (c. 1 plant per m²) in the tussocky very wet centres of dambos.

Variation: As mentioned above, there is remarkable variation in this taxon, mainly in flower size and the number of flowers per inflorescence. Field studies in Malawi (Nyika Plateau) revealed inter-population variation in the direction of the curvature of the lateral sepals and the shape of the sepals in general.

Collections from the central part of the Northern Province of Malawi tend to have smallish flowers (dorsal sepal 30 - 40 mm long), with a single flower in each inflorescence. In the higher country (around Mbala in Zambia, and towards the Nyika Plateau) the flowers are larger, with the dorsal sepal up to 50 mm tall, and with inflorescences with up to 15 flowers. This latter form has been named D. carsonii, while the former form is known as D. stolzii. Numerous collections exist that are intermediate between these two extreme forms. On the Nyika Plateau the whole range of forms was found, although the larger flowered form was most common.

In a large dambo studied on the Nyika Plateau, several sub-populations existed. One of these had lateral sepals that were curved forwards, while in the others the lateral sepals were reflexed. The shape of the blade of the dorsal sepal also varied from cordate to decurrent ovate.

Distribution : Distr. Pl. Afr. 25.

TANZANIA :

SOUTHERN PROVINCE : Songea, Milne-Redhead & Taylor 8143 (K); Songea, Milne-Redhead & Taylor 8819 (BR, K).

SOUTHERN HIGHLANDS : Between Iringa and Mbeya, Bjornstad 569 (K); Sao Hill, Brummitt & Polhill 13652 (K); Mbeya, Kitulo Sheep Station, Fuller 37 (K); Mbeya Peak, Kerfoot 1768 (K); Njombe, Lynes 130 (K); Njombe, Lynes 175 (K); Mt Mbeya, MacInnes 235 (BM); Njombe, Elton Plateau, Richards 7694a (K); Mwakete - Njombe road, Richards 7854 (K); Mt Rungwe, Richards 14313 (K); Njombe, Semsei 1644 (K); Mt Rungwe, St. Clair Thompson 845 (K, P, S); Iringa, Iheme, Ward 33 (K, PRE); Njombe, Ward 53 (K); Sao Hill, Watermeyer 208 (K); Kitulo, Williams 27 (K); Kyimbila, Stolz 145 (BM, K, Z); Kyimbila, Stolz 2506 (BM, K, P).

WESTERN PROVINCE : Ufipa, Chapota, Bullock 2049 (K).

MALAWI :

NORTHERN PROVINCE : Nyika Plateau, Ball 1067 (SRGH); Vipya Plateau, Benson 1465 (BM); Nyika Plateau, Chapman 71 (BM); Vipya, Chapman 361 (BM); Nyika Plateau, Holmes 202 (K, SRGH); Nyika Plateau, Irvine 201033 (K, SRGH); Nyika Plateau, Lawton 535 (K); Mzimba, Pawek 3344 (K); Nyika Plateau, Pawek 4849 (SRGH); Mzuzu, Pawek 6327 (SRGH); Nchena Nchena, Pawek 9066 (K, PRE); Nyika Plateau, Phillips 611a (SRGH); Nyika Plateau, Richards 10464 (K, PRE); Nyika Plateau, Williamson 222 (K, SRGH); Nyika Plateau, Williamson, Simon & Ball 793 (K); Nyika Plateau, Williamson, Simon & Ball 800 (K).

SOUTHERN PROVINCE : Zomba mts, Banda 221 (BM, SRGH).

BURUNDI : Luvironza, Michel 4996 (BR); Munini, Reekmans 6727 (BR).

ZAIRE :

SHABA : Upemba, Bamps 852 (BR); Kundelungu Plateau, Malaisse 4860 (BR, K); Kundelungu, St. Lisowski, Malaisse & Symoens 559 (BR).

ZAMBIA :

NORTHERN PROVINCE : Kasama, Anton-Smith 181832 (K, P, SRGH); Kasama, Mungwi Road, Astle 1146 (SRGH); Kasama, Benson 103 (BM, SRGH); Kasama, Benson 120 (BM); Kasama, Benson 123 (BM); Nyika Plateau, Benson 428 (K); Nyika Plateau, Benson 429 (K); Mbala, old Kafue road, Bock 220 (PRE); Mbala, Nakatali, Bullock 3655 (K); Fwambo, Carson 22 (K); Mbala, Saisi valley, Gamwell 1 (BM); Mbala, Kali dambo, Nash 28 (BM); Mbala, Ricardo 530 (BM); Mbala, Lake Chila, Richards 255a (K);Mbala, old Katwe road, Richards 4044 (K); Mbala, Richards 4082 (BR, K); Mbala, old Katwe road, Richards 4713 (K); Nyika Plateau, Richards 10420 (K); Shiwa Ngandu, Richards 10670 (K); Shiwa Ngandu, Richards 10720 (BR, K, SRGH). Nyika Plateau, Richards 14391 (K); Nyika Plateau, Richards 14405 (BR, K); Shiwa Ngandu, Richards 17094 (K); Mbala, Richards 18882 (K); Kasama, Chilweleni road, Richards 19382 (K); Mbala, Ndundu, Richards 19602 (K); Kasama, Robinson 4165 (K); Nyika Plateau, Robson 649 (K); Mbala, Saisi valley, Semane 1022 (K); Mbala, Saisi valley, Semane 1047 (K); Shiwa Ngandu, Trapnell 1699 (K, PRE); Mbala, Van Zinderen Bakker 889 (K); Nyika Plateau, Williamson 222 (K); Mporokoso, Williamson 307 (K); Shiwa Ngandu, Chinsali, Williamson & Simon 658 (K, SRGH); Mbala, Williamson 698 (K); Kawambwa, Williamson 1228 (K, SRGH); Mpika, Danger Hill, Williamson 1404 (K, SRGH); Shiwa Ngandu, Williamson 1444 (SRGH); Mpika, Williamson 1479 (SRGH).

CENTRAL PROVINCE : Mkushi, Marr-Levin 610 (SRGH).

SPECIES NOT SATISFACTORILY KNOWN

1. *Disa helenae* Buscalioni & Schltr., Bot. Jahrb. 49 : 463 (1913).

Type: Aosta 167, Steppe at Broken Hill, Zambia, 26.1.1910 (B holo-). In BR there is a drawing of this collection, but even with the aid of this drawing and the description, the identity of this species is not clear. It possesses characters of both *D. englerana* Kraenzl. and *D. erubescens* Rendl.

SPECIES EXCLUDED

Disa leopoldii Kraenzl. in Bull. Soc. Roy. Bot. Belg. 38 : 218 (1900). Type: Zaire, Mussima, Briart (BR! holo-). The type is a mixed collection, consisting of a badly preserved inflorescence of *D. erubescens* Rendl. (determined as *D. erubescens* by Schlechter, 1901, and as *D. verdickii* De Wild. by Geerinck (in schedule, BR.) and several well-preserved flowers of *Disa walleri* Reichb.f. According to the I.C.B.N. (1979), "the lectotype should be so selected as to preserve current usage unless the element thus selected is discordant with the major elements of the protologue" (Recommendation 7B). Schlechter (1901) included this name in the synonymy of *D. walleri*. This therefore establishes the current usage. There are no elements in the protologue which make this impossible.

PUTATIVE HYBRIDS

1. *D. welwitschii* Reichb.f. ssp. *occultans* (Schltr.) Linder X

D. englerana Kraenzl.

Tweedie 3798, from Kitale, Kenya. Only two specimens were found in a relatively well-collected area. The specimens show some similarity to D. ornithantha, but fall outside the variation range of that taxon, as well as being well outside its distribution range. The majority of the structural characteristics are intermediate to the two putative parents.

2. D. celata Summerh. X D. aequiloba Summerh.

Kornás 3035, from Kabwe, Zambia. The specimens are clearly intermediate to the two parents, both of which occur in the area.

Index

Index to the names referred to in the text. Names printed in italics are upheld in this study.

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APPEMDIX 1.

Dot maps showing the distributions of the species in Africa.

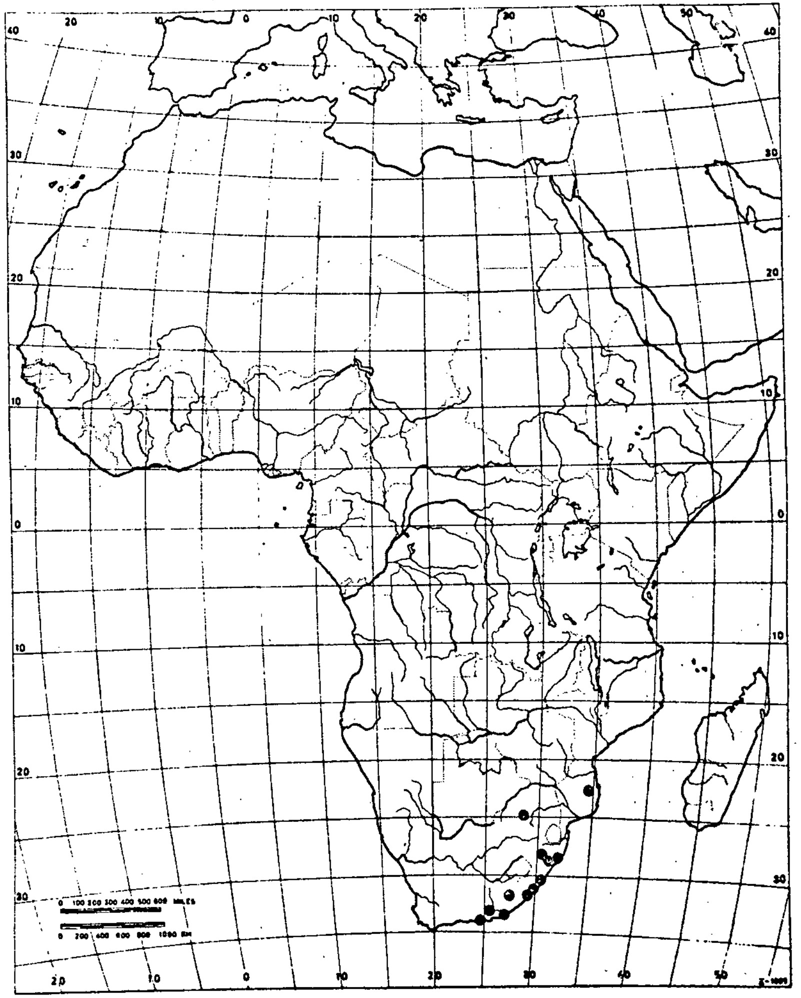

Fig. 1 Disa polygonoides Lindl.

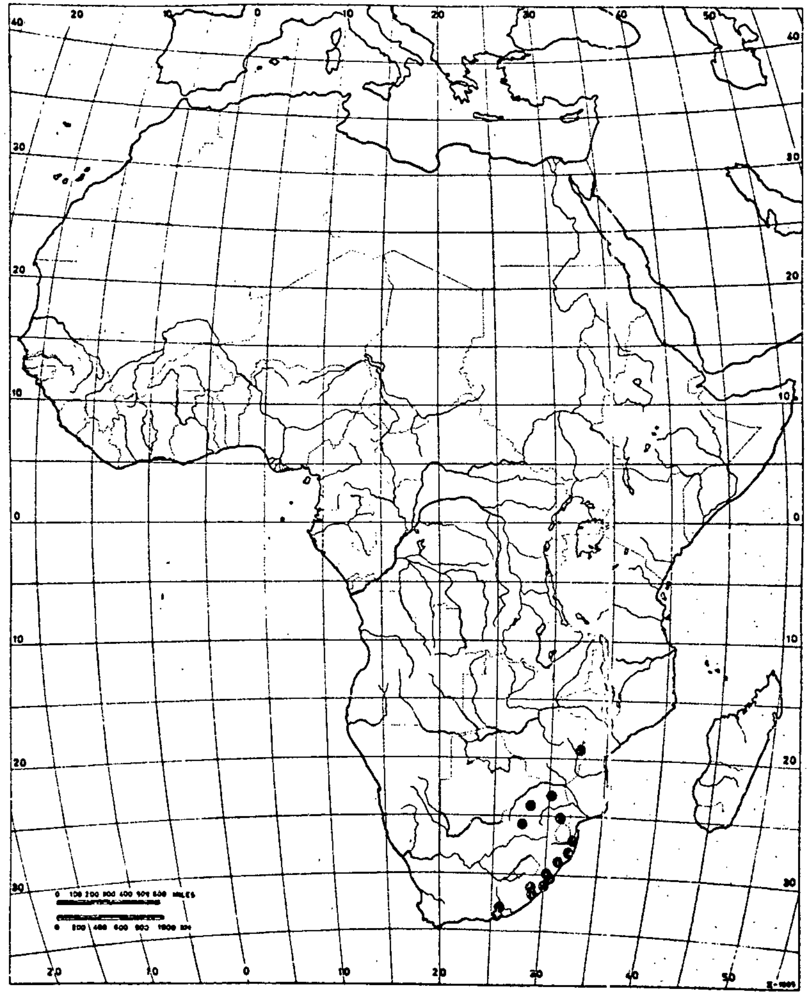

Fig. 2 D. woodii Schltr.

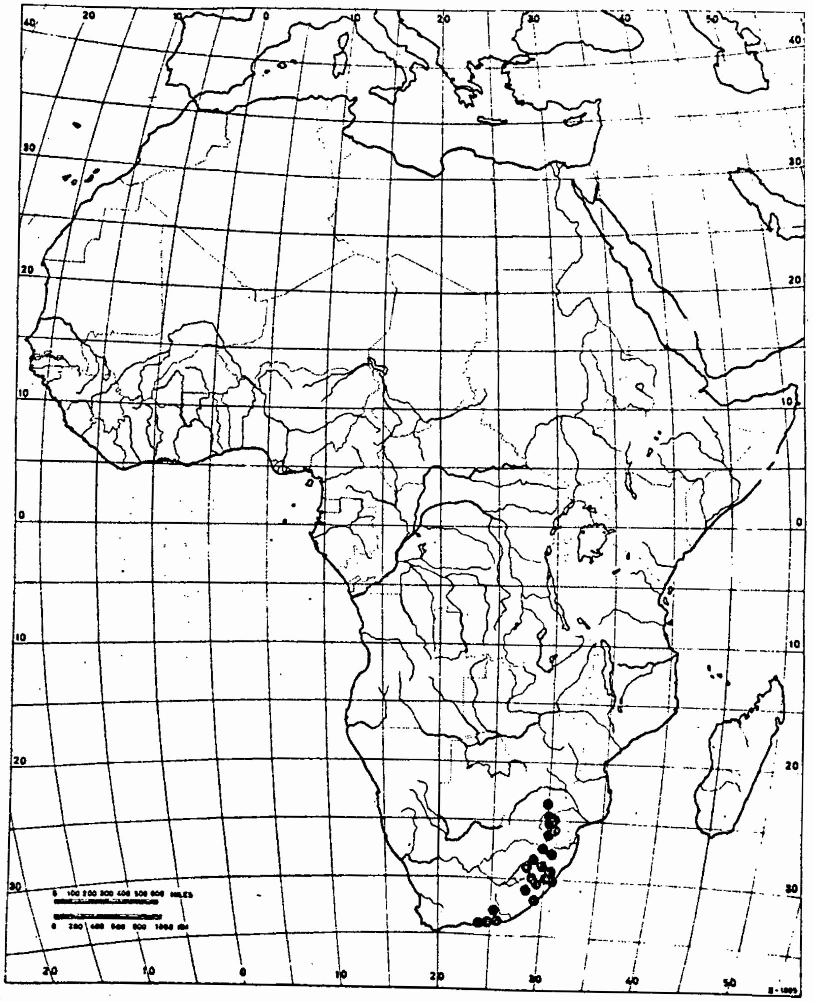

Fig. 3. D. chrysostachya Sw.

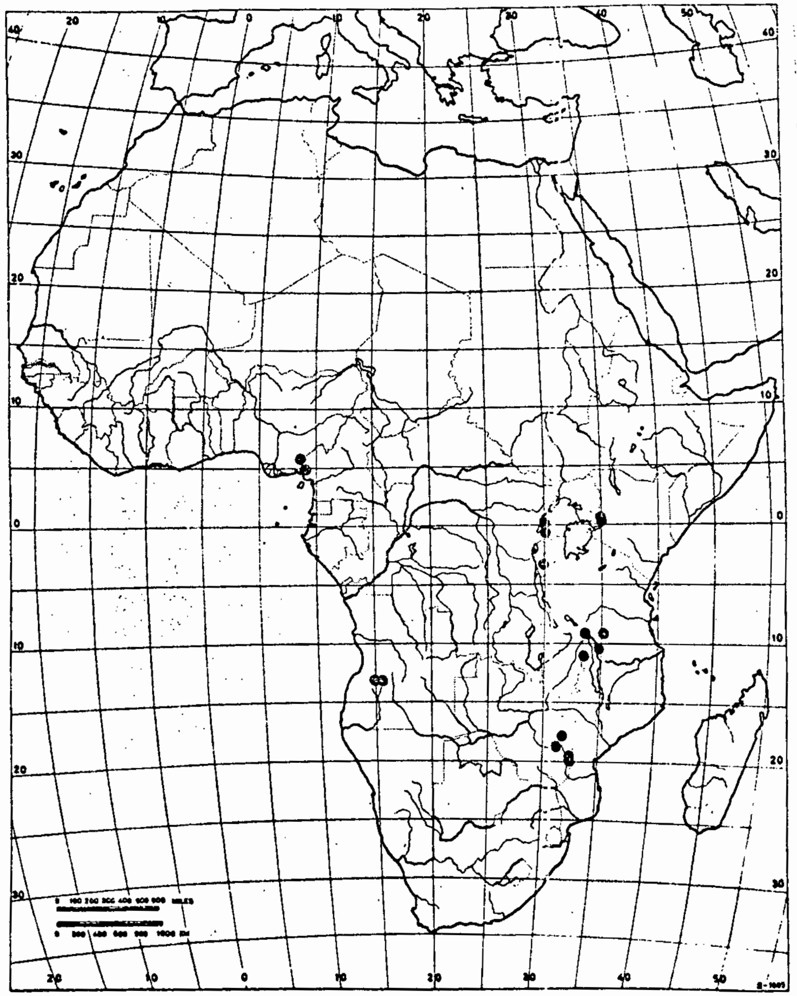

Fig. 4. D. ochrostachya Reichb.f.

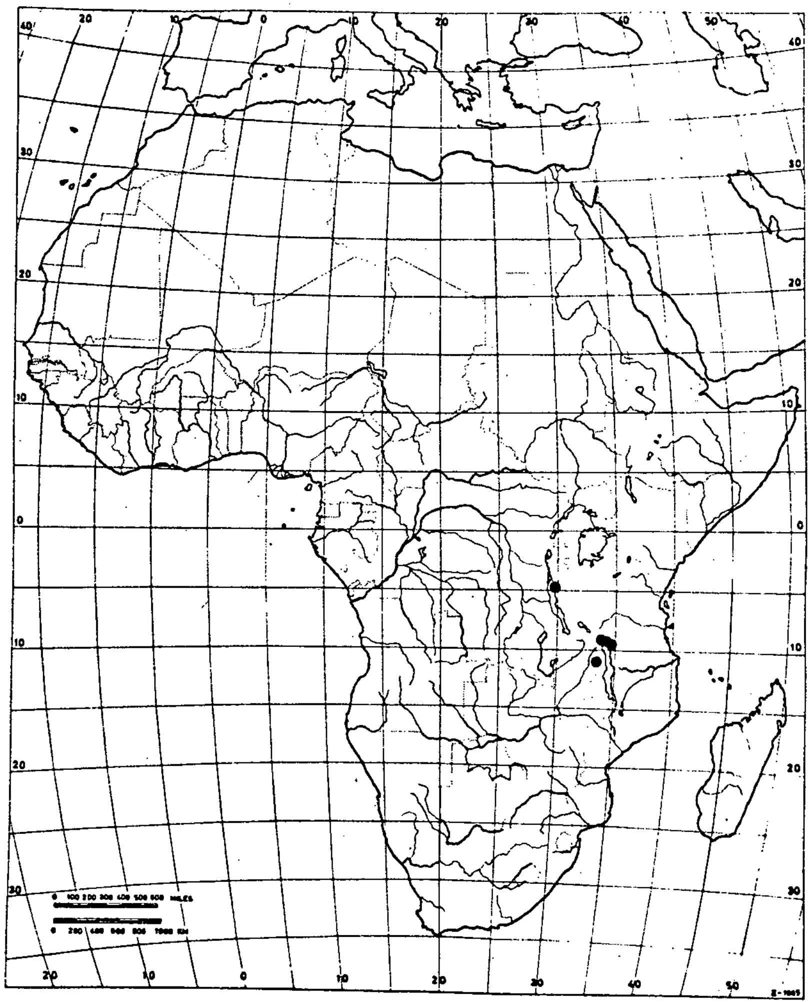

Fig. 5. D. satyriopsis Kraenzl.

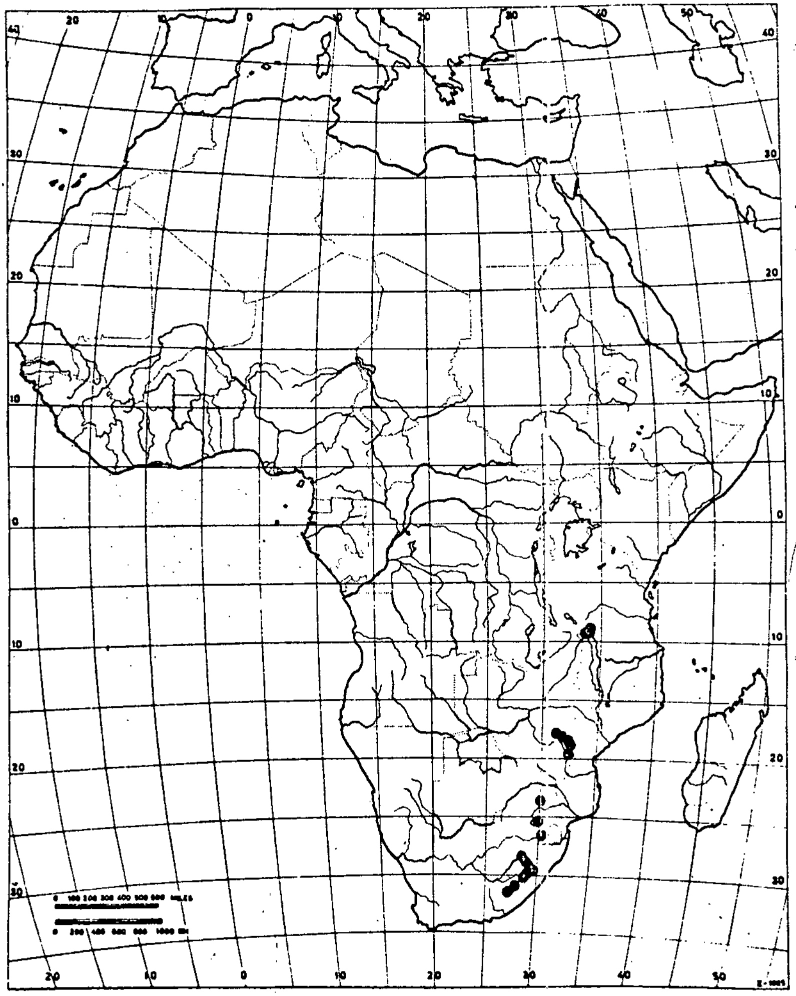

Fig. 6. D. fragrans Schltr.

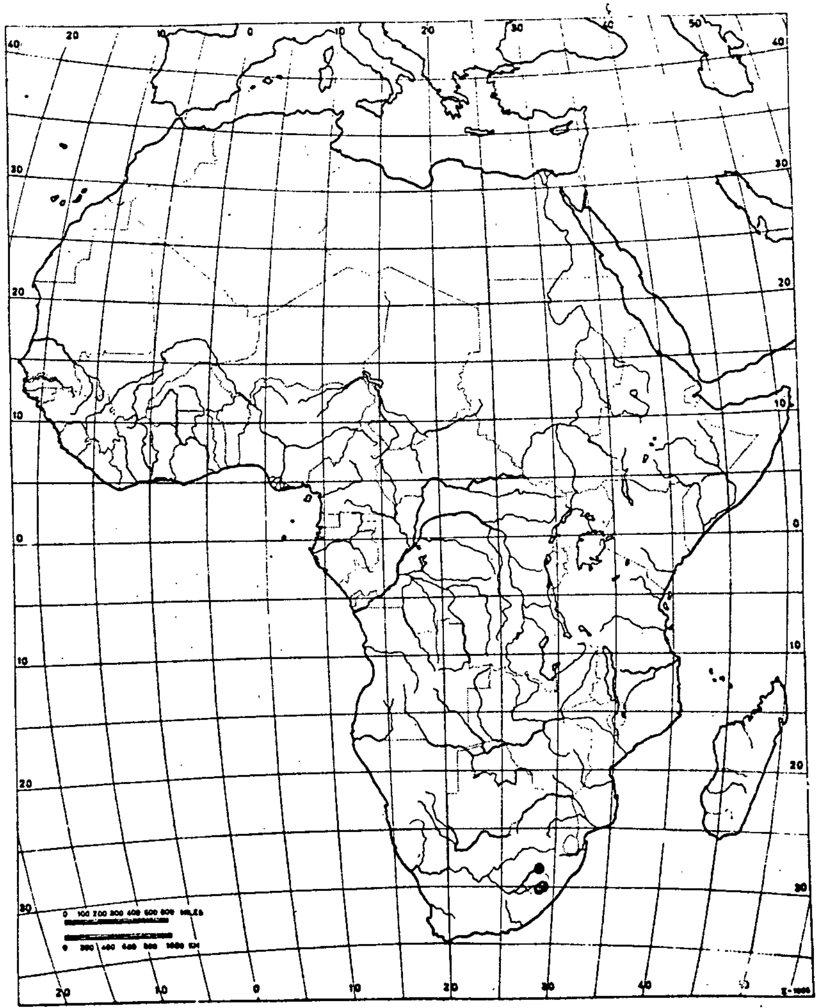

Fig. 7. D. sankeyi Rolfe

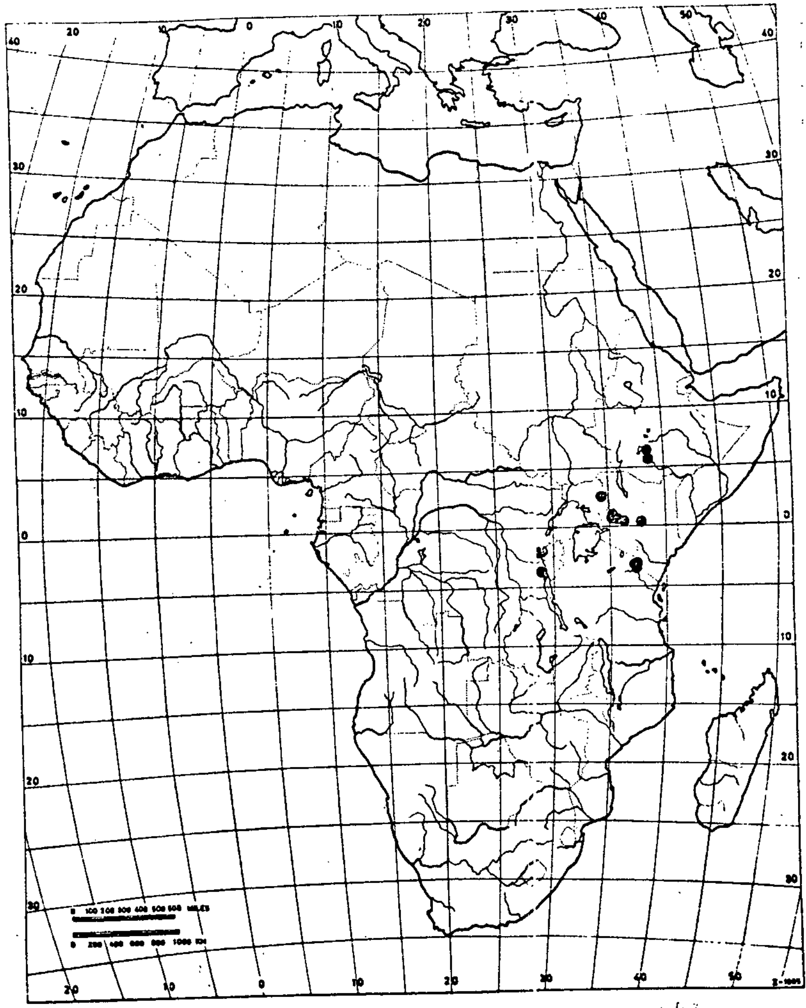

Fig. 8. Disa fragrans Schltr. ssp. deckenii (Reichb.f.) Linder

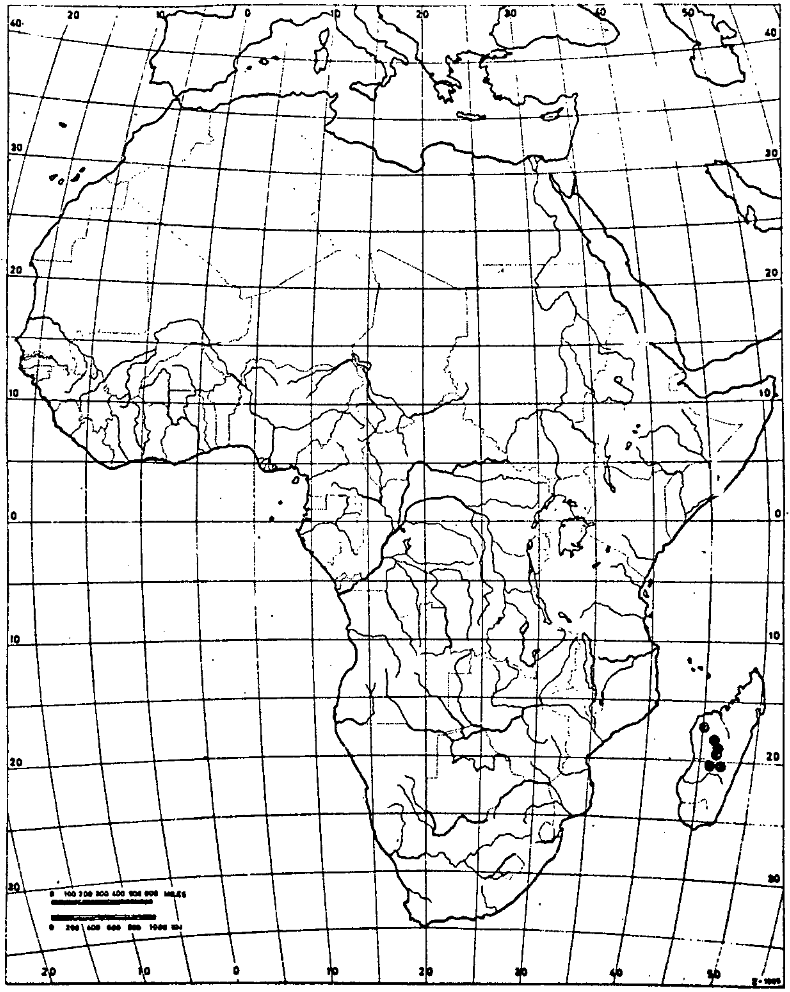

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Fig. 9. D. incarnata Lindl.

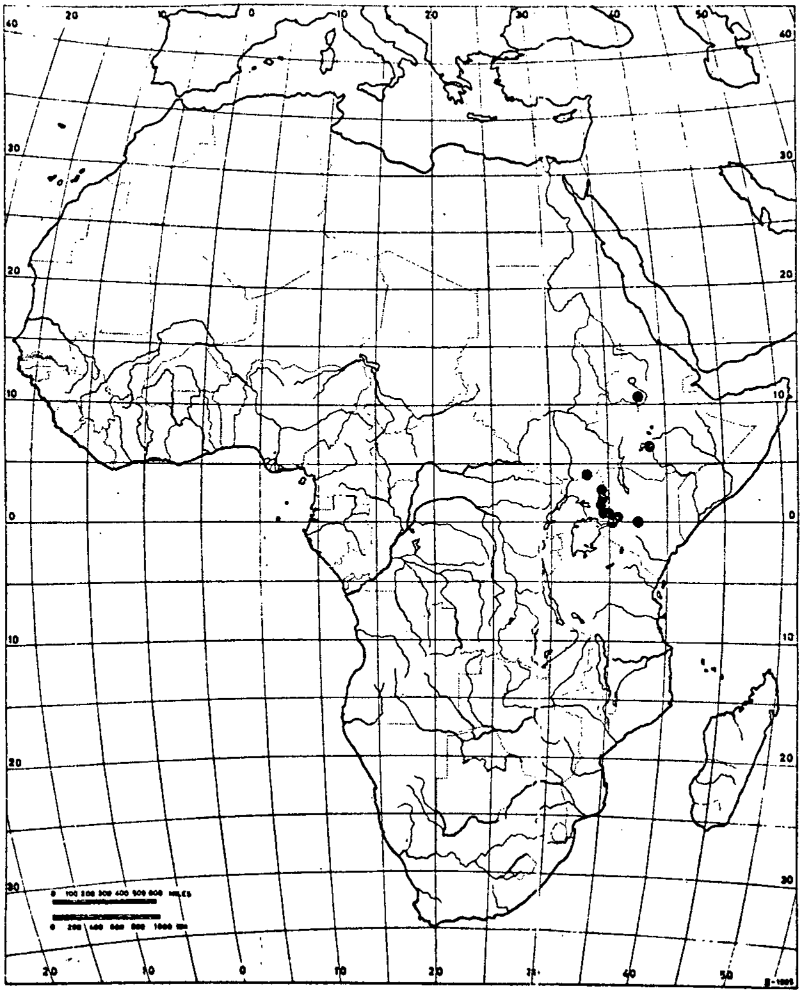

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Fig. 10. D. scutellifera A. Rich.

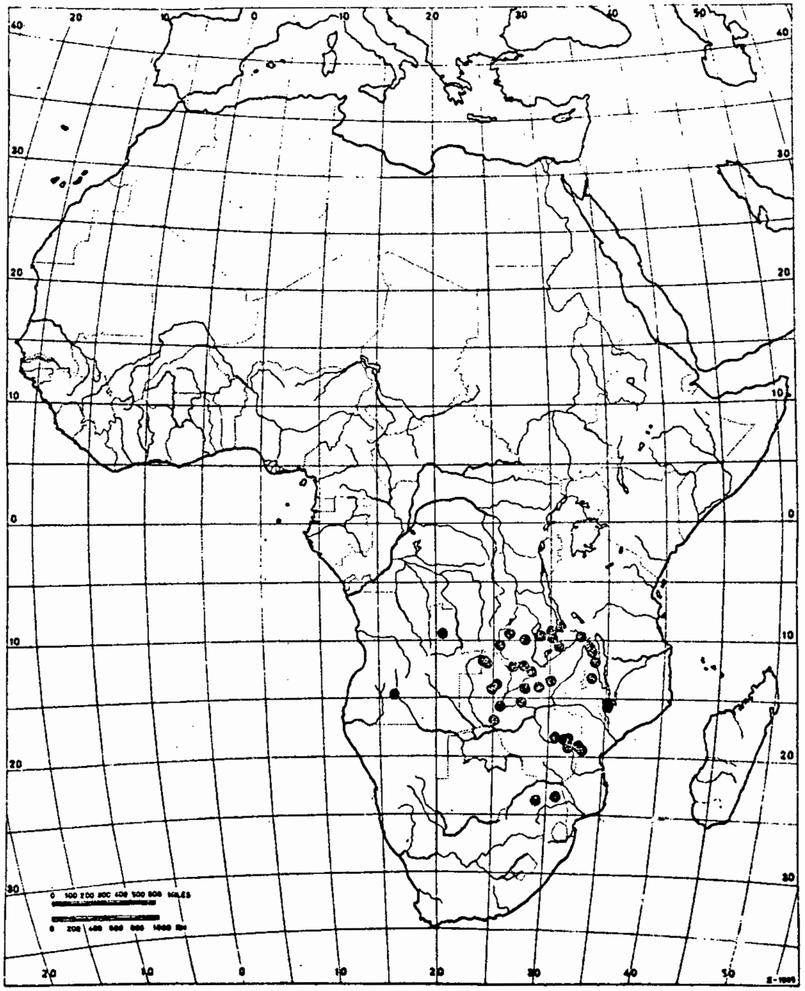

Fig. 11. *D. welwitschii* Reichb.f. ssp. *welwitschii*

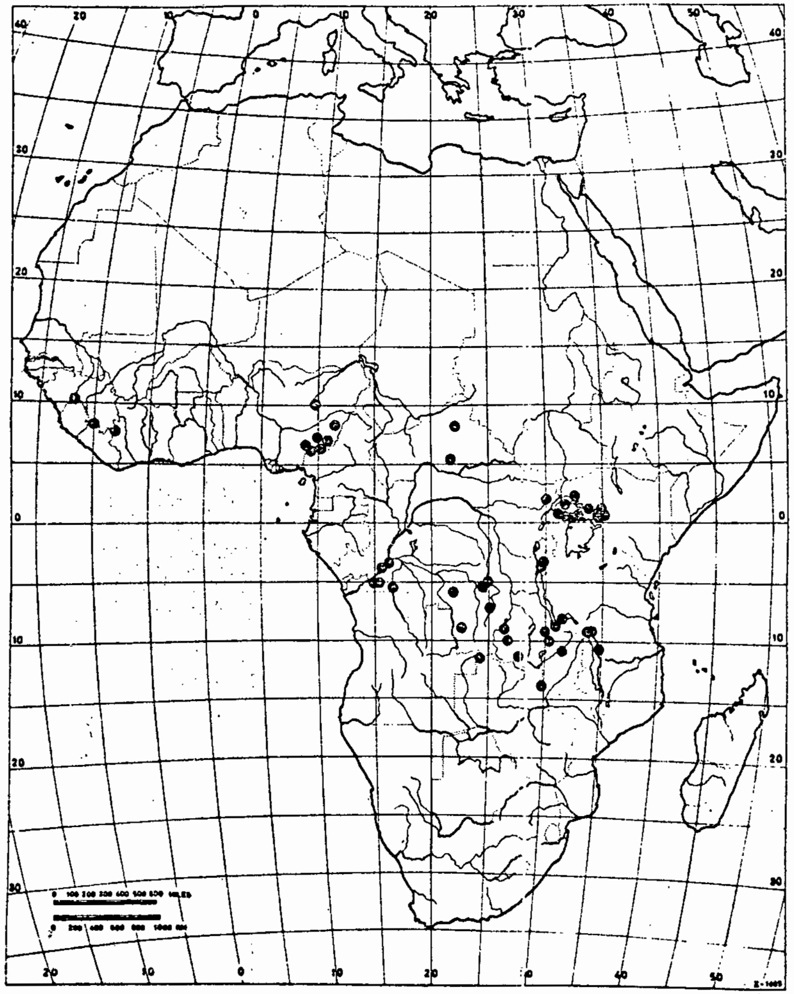

Fig. 12. *D. welwitschii* Reichb.f. ssp. *occultans* (Schltr.) Linder

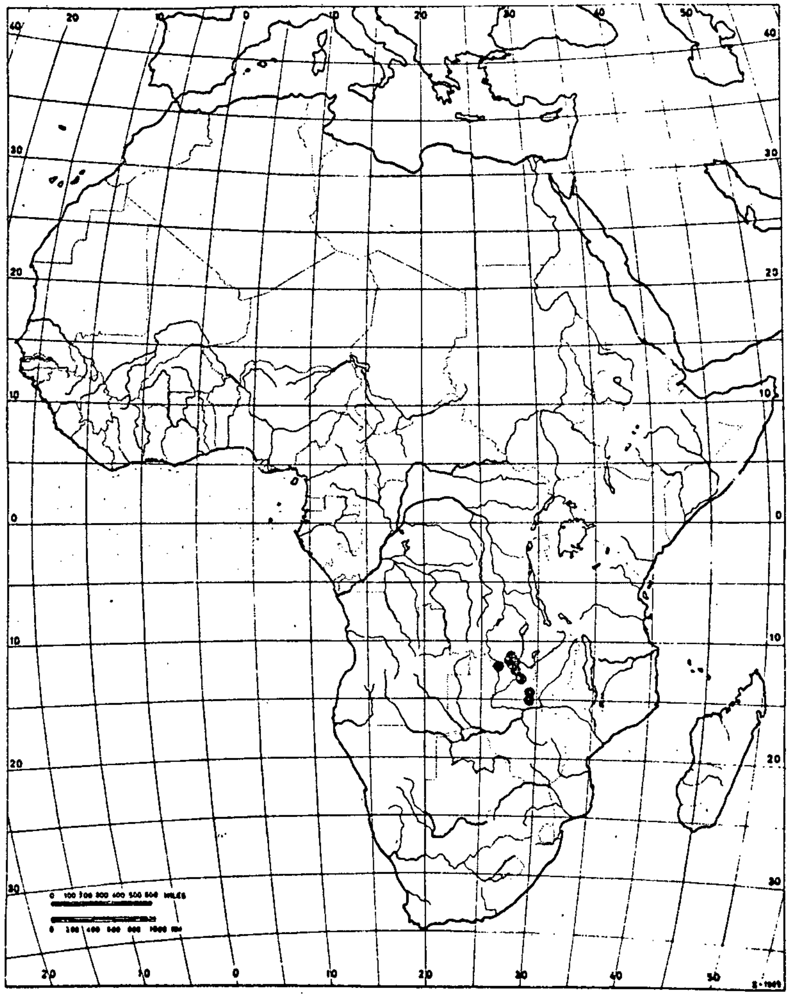

Fig. 13. D. roeperocharoides Kraenzl.

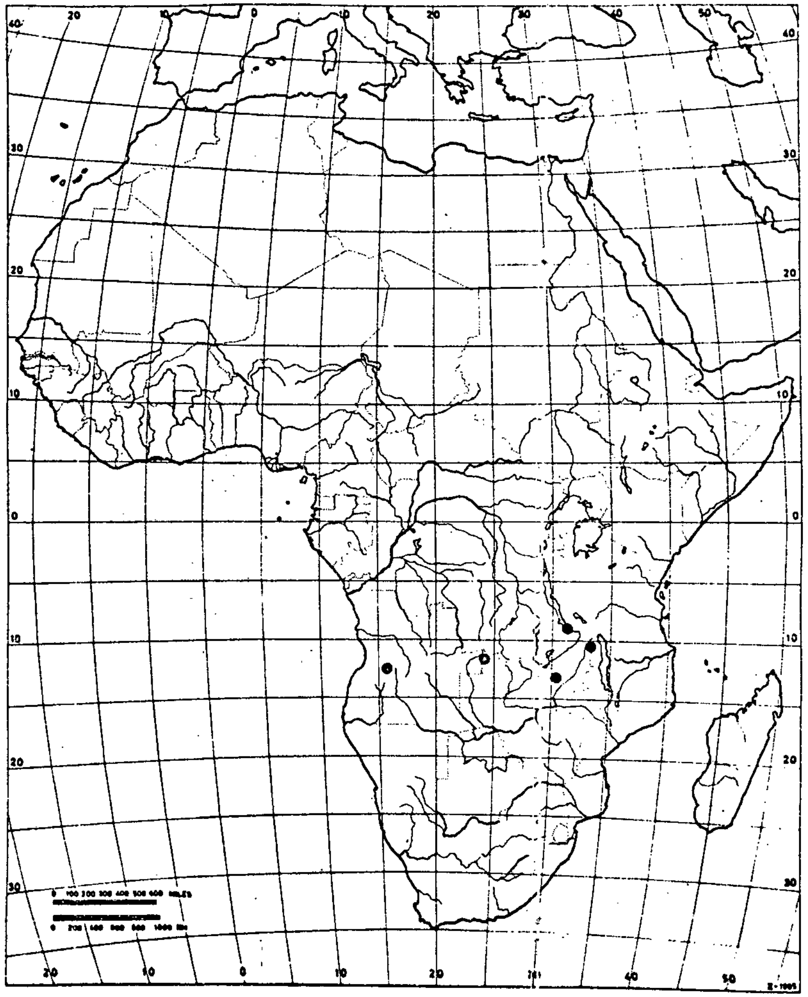

Fig. 14. D. celata Summerh.

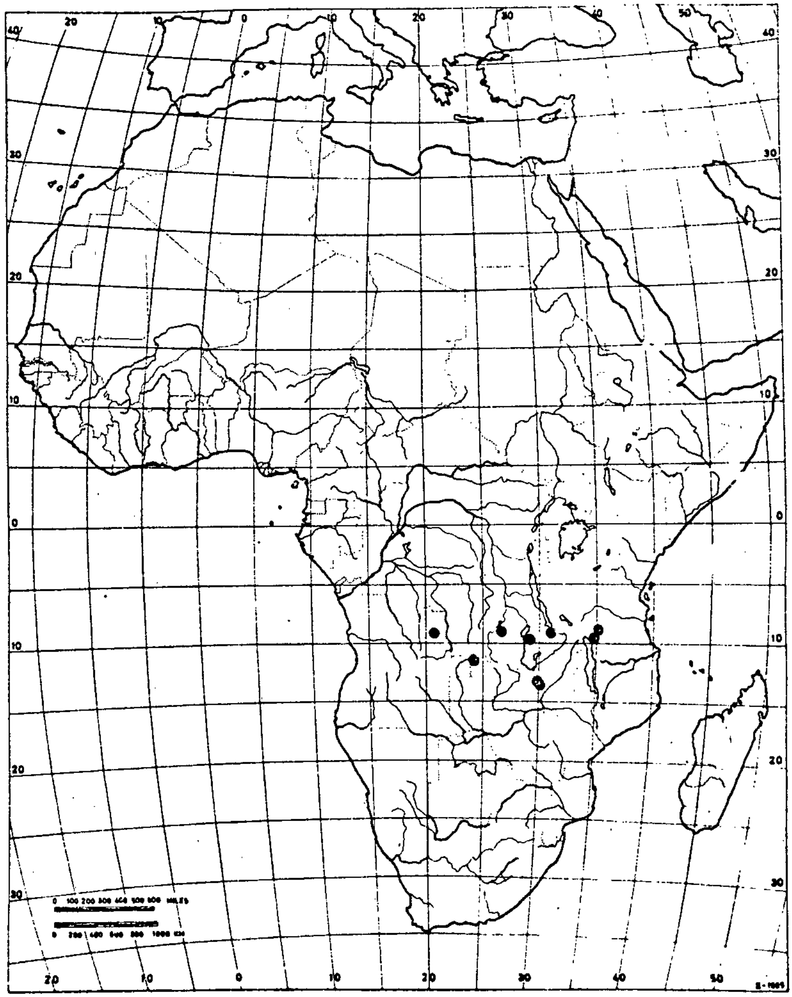

Fig. 15. D. aequiloba Summerh.

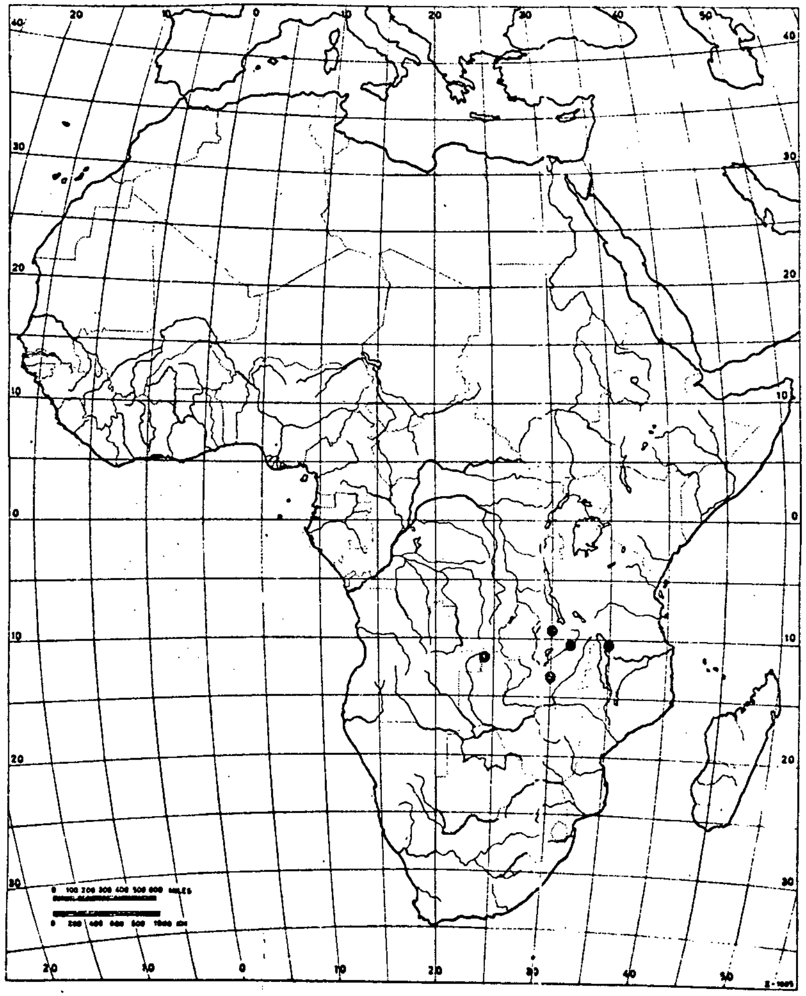

Fig. 16. D. cryptantha Summerh.

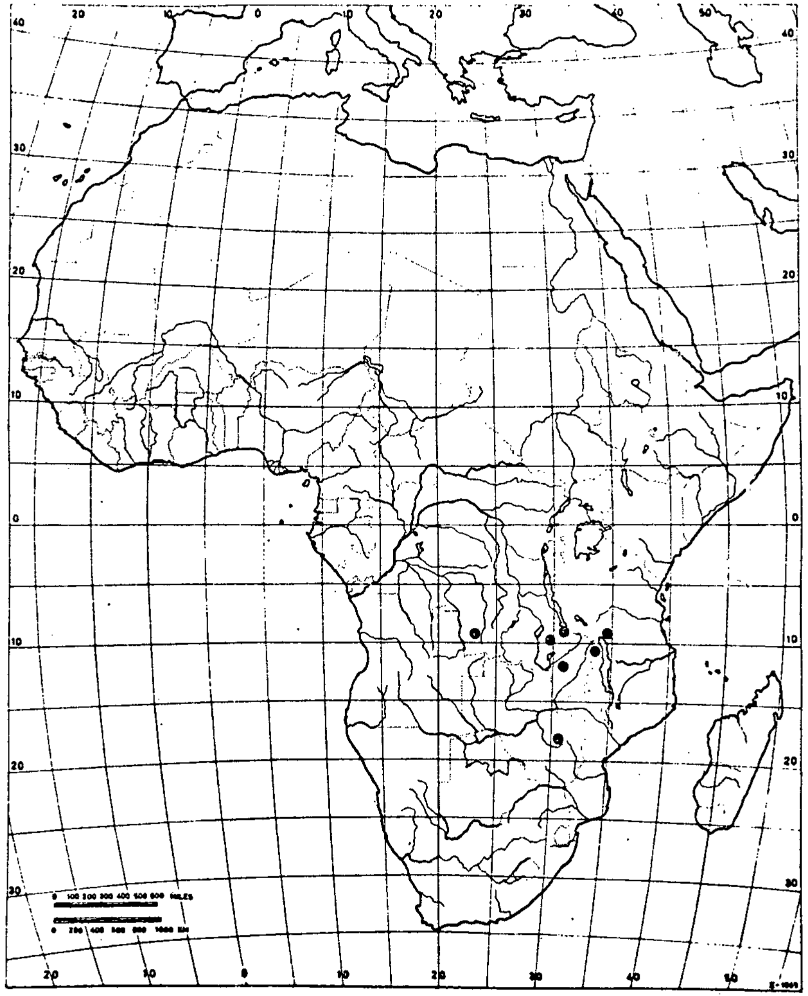

Fig. 17. D. *miniata* Summerh.

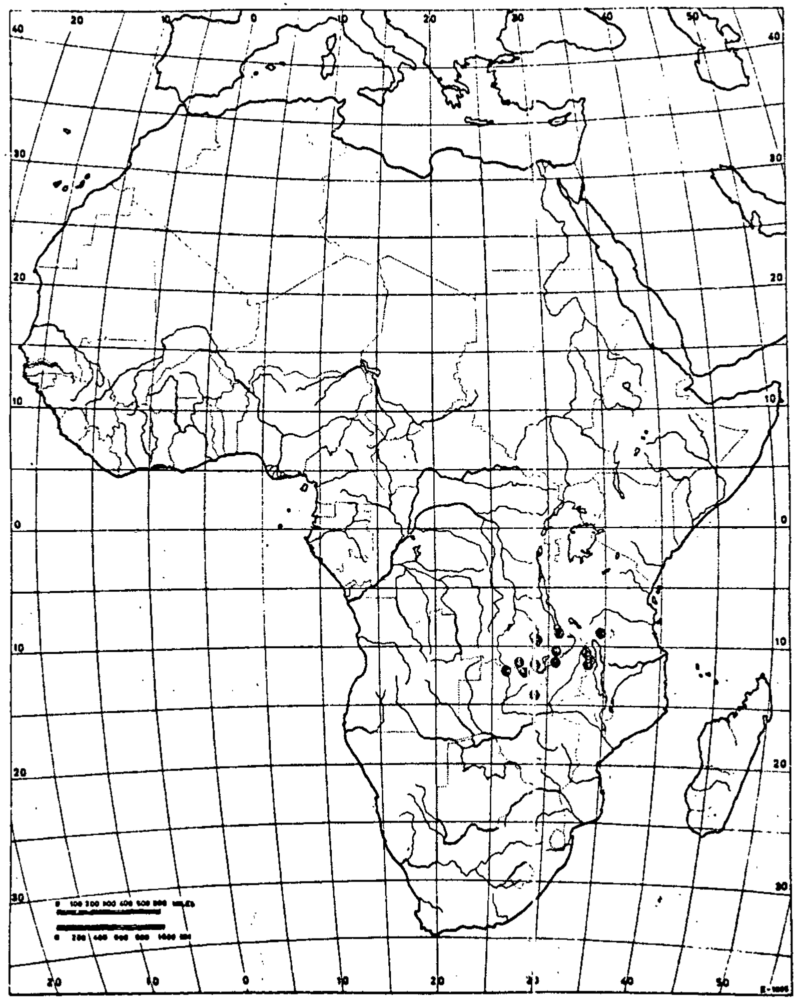

Fig. 18. D. *engleriana* Kraenzl.

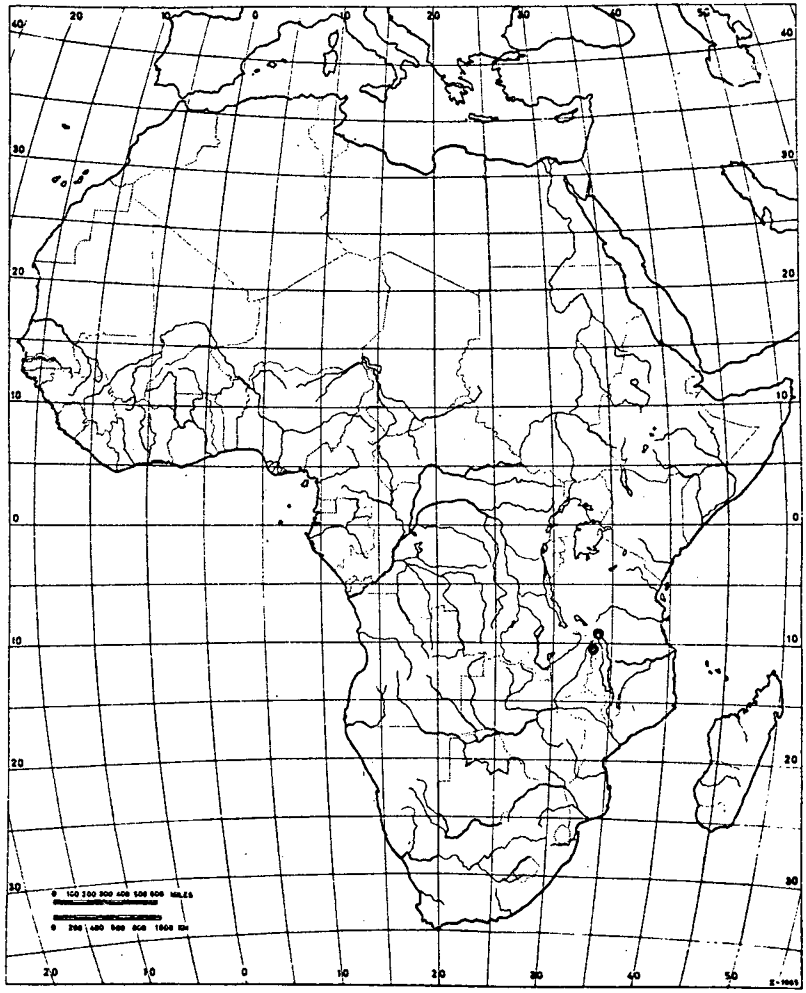

Fig. 19. *D. ukingensis* Schltr.

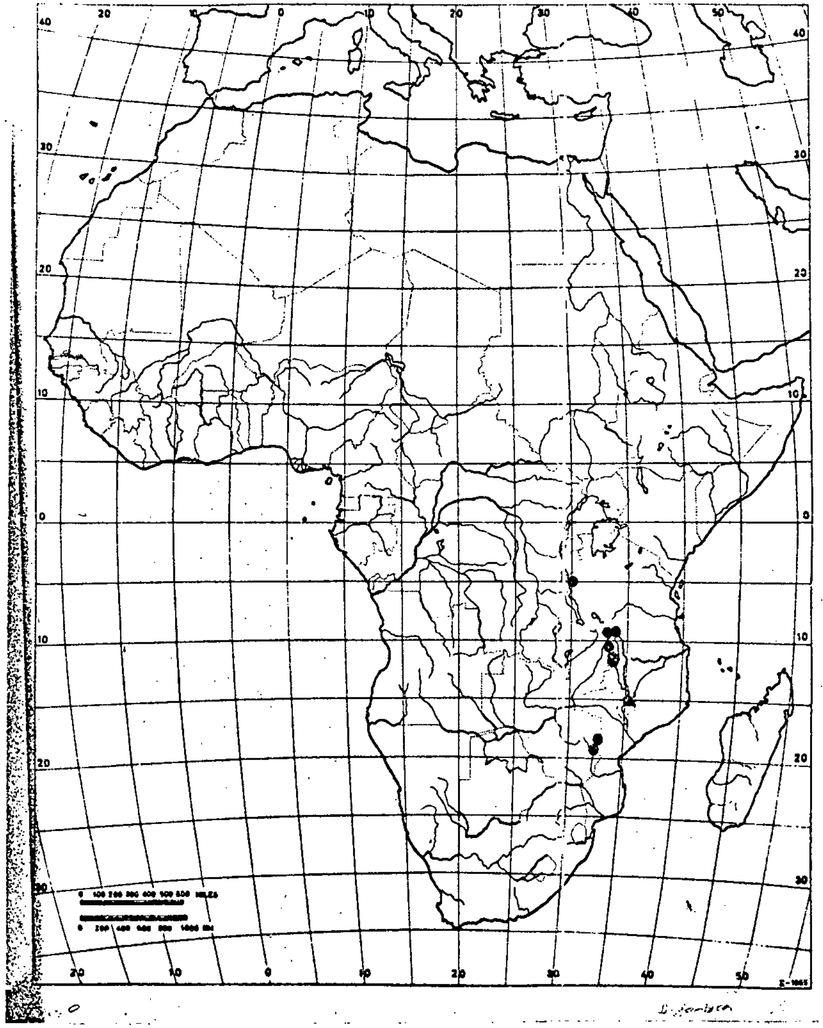

Fig. 20. *D. zombica* N.E.Br.

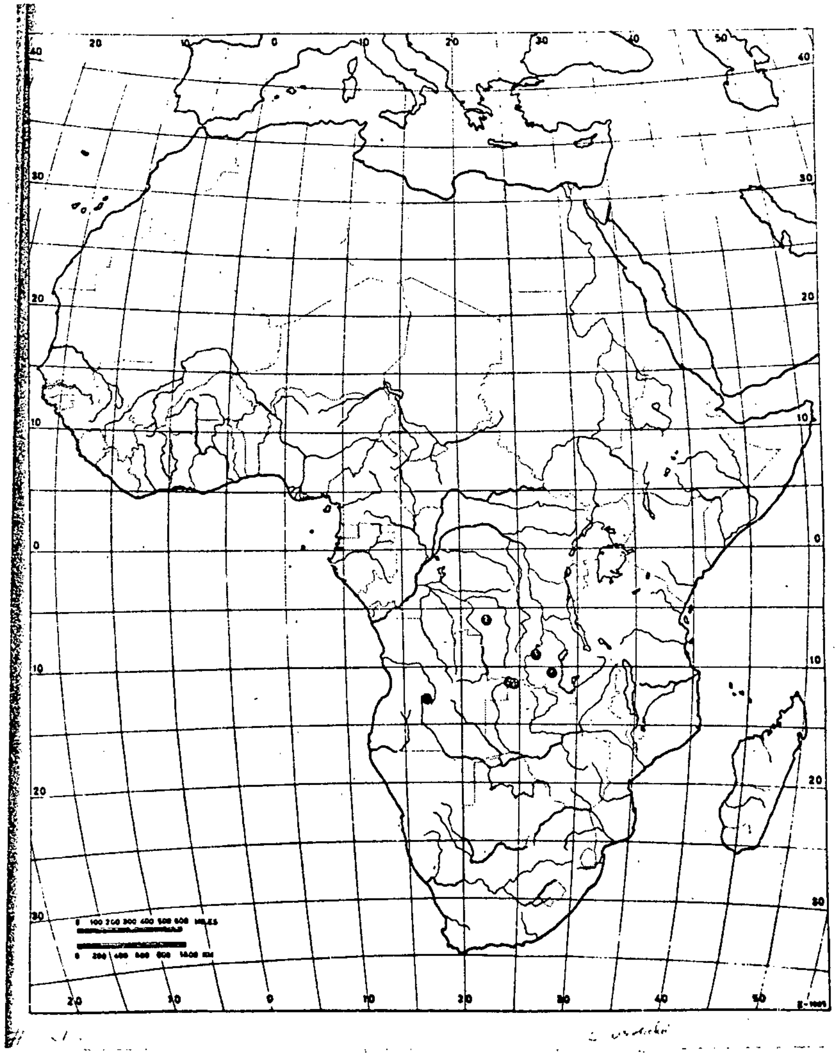

Fig. 21. D. verdickii De Wild.

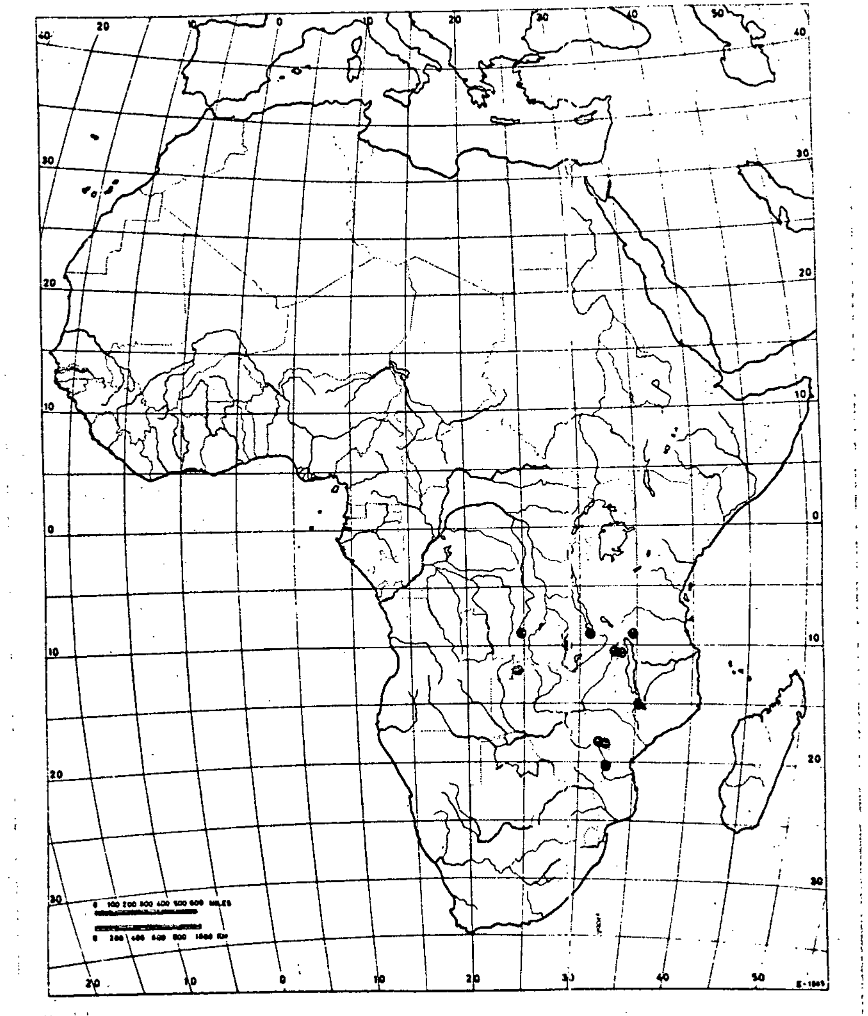

Fig. 22. D. ornithantha Schltr.

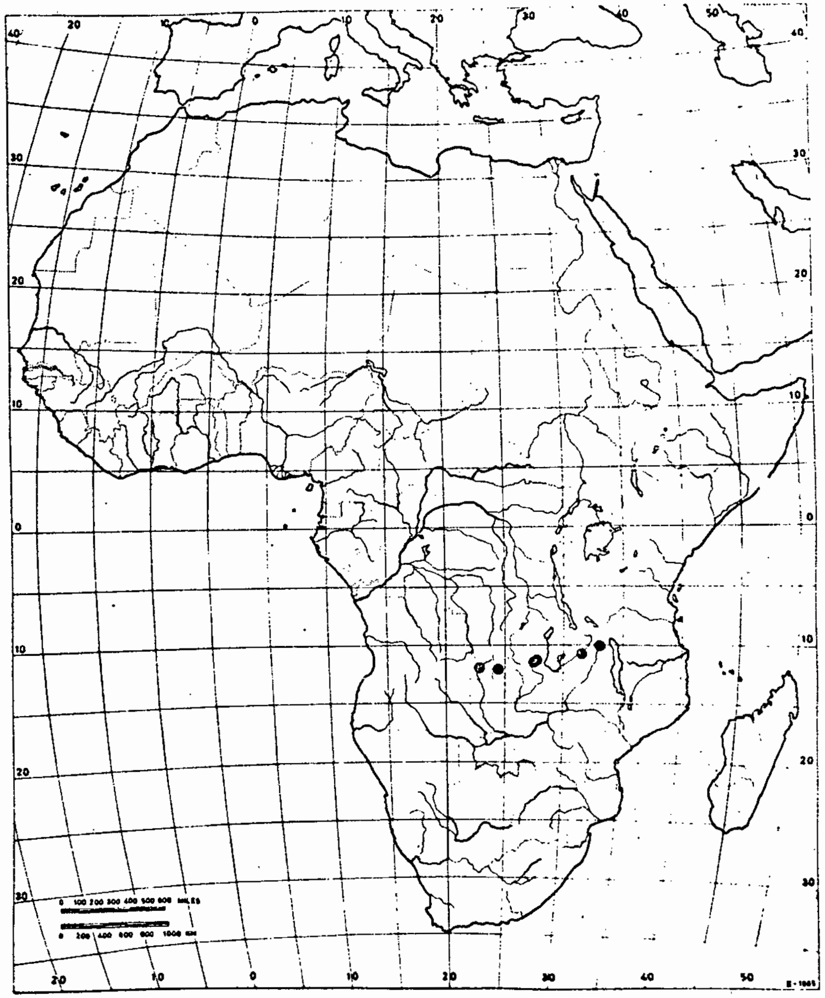

Fig. 23. *D. katangensis* De Wild.

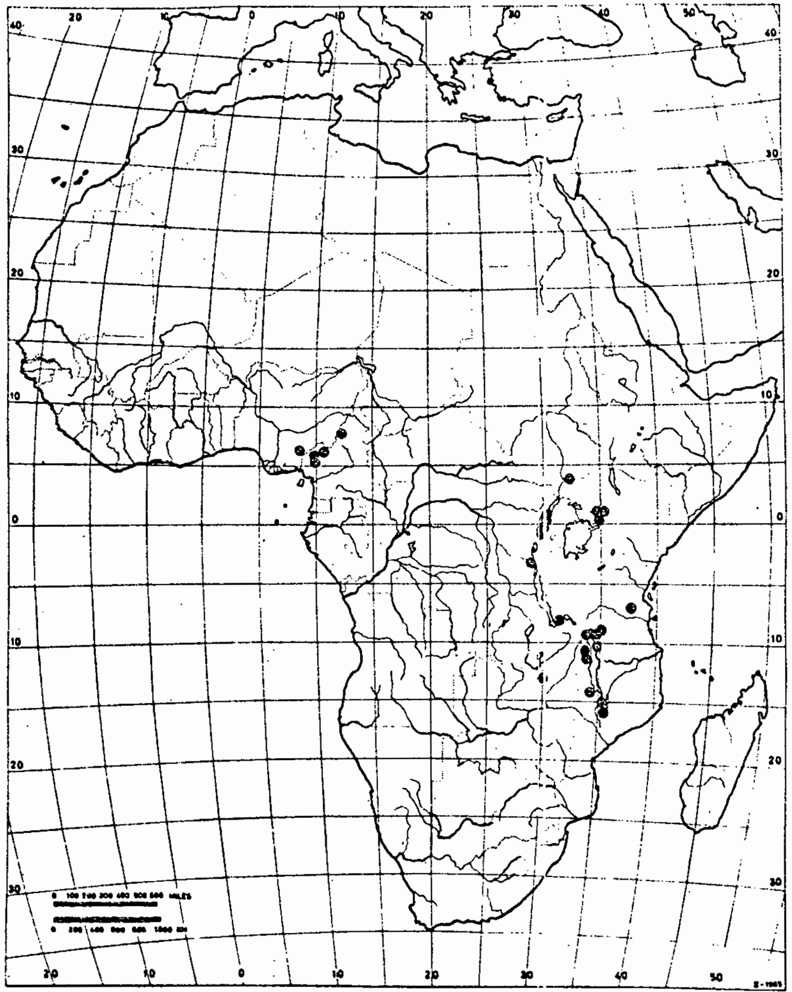

Fig. 24. *D. erubescens* Rendle ssp. *erubescens*

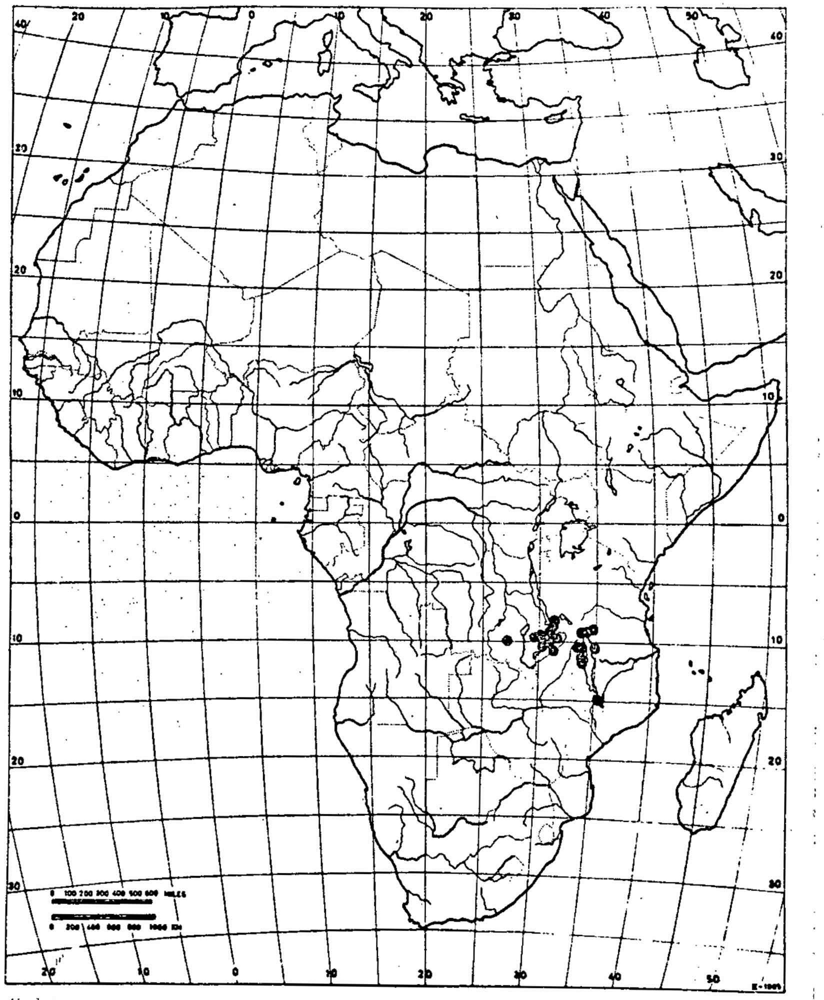

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Fig. 25. D. erubescens Rendle ssp. carsonii (N.E.Br.) Linder

Bothalia 13, 3 & 4: 339–363 (1981)

Taxonomic studies in the Disinae. V. A revision of the genus *Monadenia*

H. P. LINDER*

ABSTRACT

The genus *Monadenia* (Disinae, Orchidaceae) is revised. Sixteen species arranged in four sections are recognized. The distribution of each species is plotted, and 12 species are illustrated. A hypothesis on the phylogenetic relationships of the species is presented.

RÉSUMÉ

ÉTUDES TAXONOMIQUES DES DISINAE. V. UNE RÉVISION DU GENRE MONADENIA

Le genre Monadenia *(Disinae, Orchidaceae) est révisé. Seize espèces arrangées en quatre sections sont reconnues. La distribution de chaque espèce est située, et 12 espèces sont illustrées. Une hypothèse sur les relations phylogénétiques des espèces est présentée.*

INTRODUCTION

Monadenia Lindl. is a small genus of 16 species, which is closely related to *Disa* Berg. (Orchidoideae, Orchidaceae). Fifteen of the 16 species are restricted to the Cape Flora Floral Region (Goldblatt, 1979), whereas the remaining species is rather widespread in the montane grasslands (White, 1978) of southern Africa (Fig. 1). The plants are generally less than 300 mm tall, and have rather inconspicuous green to brownish flowers.

The first species of *Monadenia* were described by Thunberg in 1794 as *Satyrium,* and were transferred to *Disa* by Swartz (1800). The genus *Monadenia* was erected by Lindley in 1838. He included eight species in this genus, of which five were new species. However, he sowed the seeds for later nomenclatural confusion by misapplying *M. rufescens* (Thunb.) Lindl. to another taxon, later to be named *M. comosa* by Reichb. f. (1847). The true *M. rufescens* he named *M. macrocera.* He also gave the new names *M. micrantha* and *M. prasinata* to what should have been *M. bracteata* and *M. cernua,* respectively. Sonder (1847) and Reichenbach (1847) added four new names and one new species to the genus. Our knowledge of the genus was greatly extended by Harry Bolus and Rudolf Schlechter, who described four new and rather rare species in the genus. The last species was added to the genus in 1948 (Lewis, 1948).

To date there have been four taxonomic revisions of the group: Lindley (1838), Kraenzlin (1900), Schlechter (1901) and Rolfe (1913). Lindley only had material of half the presently known species before him. By 1900 the majority of species were known, or at least available in the European herbaria. However, Kraenzlin missed several species, and his work shows that he did not have access to sufficient material. Schlechter's and Rolfe's work differ in approach. Whereas Schlechter employed a broad species concept (combining *M. physodes* with *M. cernua* and *M. reticulata* with *M. macrostachya*), Rolfe raised almost every possible taxon to specific rank. Two species, *M. basutorum* (Schltr.) Rolfe and *M. leydenburgensis* Kraenzl., are here transferred to *Disa,* and have not been discussed above, and are excluded from Table 1.

The rank of the group has been controversial. Lindley (1838) recognized the group as a distinct genus, allied to *Disa.* This treatment was followed by Reichenbach (1847) and Sonder (1847), Bolus (1888, 1889, 1893, 1911, 1913) and Schlechter (1898, 1901) recognized *Monadenia* as a section of *Disa.* However, Rolfe (1913) maintained *Monadenia* as a distinct genus, as did Phillips (1926), Schelpe (1966) and Dyer (1976). The reasons for treating *Monadenia* as a distinct genus in this study will be dealt with in detail in another publication.

MORPHOLOGY

All the species in *Monadenia* may be shown to be rather minor variations on a simple pattern: erect herbs with linear to ovate cauline leaves, inflorescence a spike, dorsal sepal erect or curved forwards and shallowly galeate, oblong to obovate, spur straight, cylindrical, pendent from the base of the galea, lateral sepals somewhat smaller than the dorsal sepal, patent or reflexed, petals erect, obliquely ovate-oblong, retuse or truncate, lip linear to elliptic, pendent, lip and petals fleshy, rostellum simple with a deep central notch for the single large viscidium.

As in the rest of the subtribe Disinae, there are two

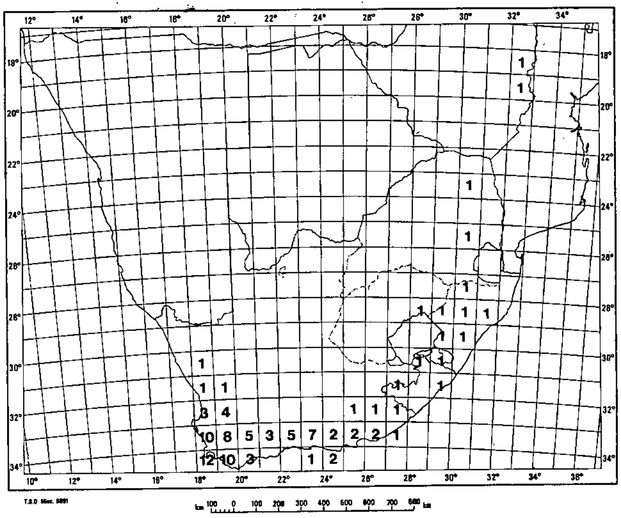

FIG. 1.—Distribution of the genus *Monadenia.* The number of species occurring in each grid square is indicated. The collection from Madagascar is not included.

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*Bolus Herbarium, University of Cape Town, Rondebosch, 7700.

TABLE 1.—Summary of the history of *Monadenia*

	Thunberg	Swartz	Ker	Lindley	Sonder	Reichb. f.	N.E.Br.	Bolus	Kraenzl.	Schltr.	Rolfe	Lewis
M. ecalcarata												x
M. conferta								x	x	x	x	
M. pygmaea								x	x	x	x	
M. sabulosa								x	x	x	x	
M. bracteata		x							x			
M. densiflora				micrantha x	multiflora			auriculata	micrantha x multiflora	micrantha multiflora auriculata	micrantha x multiflora auriculata	
M. macrostachya				x						x	x	
M. reticulata								x	x		x	
M. comosa				rufescens		x	affinis		x	x	x	
M. bolusiana										x	x	
M. atrorubens										x	x	
M. ophrydeae				x					x	x	x	
M. rufescens	x	x		macrocera	lancifolia				x	x	macrocera	
M. physodes		x									x	
M. cernua	x	x	prasinata	prasinata	inflata				x	x	prasinata	
M. brevicornis				x					x	x	x	

Species excluded: M. basutorum (Schltr.) Rolfe = Disa basutorum Schltr.
M. leydenbergensis Kraenzl. = Disa stachyoides Reichb. f.

testicular tubers. There may be some variation in the tuber shape, but this variation is difficult to quantify due to lack of material.

The variation in leaf shape may be used to some extent to subdivide the genus: in sect. *Densiflora* the leaves tend to be linear-lanceolate, as compared to the more lanceolate leaves of the other sections. *M. comosa,* the only species that often occurs in half-shaded conditions, has rather distinctive spreading ovate leaves, sharply differentiated from the upper sheathing cauline leaves.

Inflorescence shape also more or less follows the sectional classification. The small-flowered sect. *Densiflora* has compact cylindrical spikes, the large-flowered sect. *Monadenia* semi-dense cylindrical spikes, and in sect. *Tenuicornes* the inflorescence tends to be lax. *M. sabulosa* and to a lesser extent *M. pygmaea* have an obovate inflorescence. This variation may also be expressed in the angle between the stem and the ovaries: in sect. *Densiflorae* the ovaries spread away from the axis, whereas they are almost erect and adpressed to the axis in sect. *Tenuicornes.* Only in sect. *Tenuicornes* do the floral bracts show any sharp discontinuities: in *M. rufescence* the bracts are almost of a leathery texture, partially obscuring the flowers and imbricate, whereas in *M. reticulata, M. comosa* and *M. bolusiana* they are of a more membranous texture, with the venation clearly visible on dried specimens, and the bracts not imbricate.

There is little variation in the shape of the dorsal sepal. In the majority of taxa the galea is best described as oblong. In some, i.e. *M. sabulosa,* the galea is obovate. There is some variation in the angle at which the galea is held: from vertical to falcately curved forwards, but this is difficult to quantify.

The lateral sepals are almost invariably oblong. In some taxa the sepals are reduced in size relative to the dorsal sepal. This is often associated with being reflexed (e.g. *M. sabulosa*). Generally, the apical parts of the sepals are recurved (e.g. *M. bracteata*). This is considered to be the primitive state. Presumably derived from this state are the sharply reflexed sepals of *M. sabulosa* and *M. atrorubens* or the spreading sepals of *M. ophrydea.*

The petal structure is remarkably uniform throughout the group, and the variation is often rather subtle. This is shown rather clearly by *M. rufescens,* in which the petal shape differs marginally from *M. reticulata,* but the angle and the juxtaposition to the galea is somewhat changed, with a markedly different effect. *M. sabulosa* and *M. pygmaea* are somewhat distinct by virtue of the bifid petals.

Lip shape varies from linear to elliptic in the genus, and the shape is constant for each species. In sect. *Tenuicornes* it may be used as a good differentiating character for the different species.

Rostellum structure is dominated by the small anther, often partially pendent, and the single large viscidium. The rostellum is comparatively simple with a deep notch in which the viscidium is held. The rostellum is often flanked by two erect flanges of tissue, which may also flank the anterior part of the anther. The size of these flanges varies among the species. The origin of these flanges is not known. They may be derived from the staminodes.

The viscidium is generally an almost square structure. However, in *M. rufescens* it is elongated to the back, and has a deep dorsal groove. The two pollen-masses may be as long as or shorter than the caudicles.

The stigma is variable in shape. In general, the two lateral lobes are larger than the posterior lobe. In some cases the stigma is sessile at the base of the rostellum, in others it may be on a tall, often curved, stipe as in sect. *Tenuicornes.*

The spur length and shape provides a very valuable character and has been used as the diagnostic character for the sectional delimitation. In sect. *Tenuicornes* the spur is slender, acute and longer than the dorsal sepal. In sect. *Monadenia* it is much inflated, shorter or longer than the galea, obtuse, rounded or acute. In sect. *Densiflorae* the spur is as long as or shorter than the galea, slender or subclavate, acute to retuse, occasionally constricted at the base.

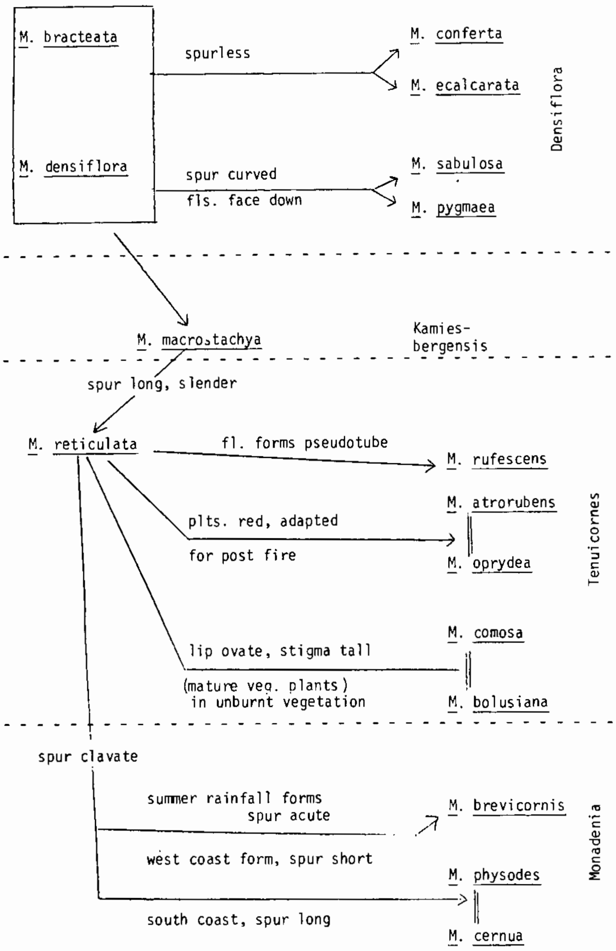

FIG. 2.—Postulated phylogenetic relationships among the species in *Monadenia*.

The morphological relationships in the genus are summarized in the cladogram in Fig. 2. The sectional classification is based on flower size, inflorescence shape and spur shape and length. The first two characters are related to each other, and also to overall plant size. Other characters that vary within the genus (sepal reflexion, stigma size, lip shape and leaf structure) have been found to vary between otherwise obviously closely related taxa (e.g. *M. atrorubens* and *M. ophrydea* for sepal reflexion, lip shape, stigma size, and *M. comosa* and *M. bolusiana* for leaf shape), and are therefore, unlikely to reflect evolutionary tendencies.

PHYLOGENY AND EVOLUTION

The postulated phylogeny of the genus is derived from the relationships among the taxa as indicated by the morphological data. However, to arrange the taxa into a sequence, ancestral and derived character states have to be suggested. The relative age of the extant taxa may be estimated from eco-geographical data.

Ancestral character states are probably those states found in other taxa in the *Disinae*, and also simpler states from which more complex states may be derived. In *Monadenia* the ancestral form was probably a slender herb with narrowly lanceolate, subimbricate cauline leaves, an inflorescence with numerous medium-sized flowers with the sepals about 6 mm long, spreading to slightly reflexed, subequal, the dorsal sepal shallowly galeate with a slender spur as long as or slightly shorter than the sepal, subpendent, petals falcate, erect next to the rostellum, wider towards the base, lip lorate, obtuse, pendent, anther subpendent, rostellum low with a single viscidium, stigma sessile. Such a plant would be comparable to the suggested ancestral forms found in several sections of *Disa* (*Disa polygonoides* Lindl., *D. vaginata* Lindl. and *D. obtusa* Lindl.). In *Monadenia, M. bracteata* has the greatest similarity to this set of character states.

Relatively older species may be expected to be morphologically isolated, often with relic distributions in the form of widely scattered populations over large distribution areas, and possibly with wide ecological amplitudes. Morphologocally isolated species are found in sect. *Densiflorae* (*M. sabulosa, M. pygmaea, M. ecalcarata* and *M. conferta*), whereas in the rest of the genus only *M. rufescens* is morphologically clearly isolated.

Several species in the genus show wide distribution ranges (*M. bracteata, M. densiflora, M. comosa* and *M. reticulata*), but only *M. densiflora* and *M. reticulata* have disjunct distributions. The majority of the species show a restricted distribution range, either on the west coast, or the south coast, or the area bounded by Caledon, Worcester and Cape Town. Two species are only known from very restricted localities: *M. ecalcarata* from a single specimen on the Cape Peninsula and *M. macrostachya* from a single locality in the Kamiesberg.

All the species in sect. *Densiflorae* have at least some morphologically or distributionally primitive features: *M. bracteata* and *M. densiflora* with widespread distributions and being morphologically ancestral, and the remainder of the species in the section being morphologically isolated.

The remaining species in the genus are grouped into interlinking species groups, in which the individual species are often difficult to separate rigorously. They present the aspect of a rapidly evolving group. Sect. *Tenuicornes* has diversified mainly in the mountains of the Cape, with one group adapted for the immediately post-fire temporal niche (*M. ophrydea* and *M. atrorubens*), with suitable cryptic coloration, and the other group adapted for unburnt vegetation, with one species found on rock ledges and the other at high altitudes in high-altitude low heathlands (Taylor, 1978) (*M. comosa* and *M. bolusiana*). One isolated species in the section appears to have become specialized for a particular pollination syndrome (*M. rufescens*). These five species therefore show a certain degree of specialization, and may all be derived from *M. reticulata,* the widespread and presumably simplest member of the section.

Sect. *Monadenia* has a rather specialized spur shape, and is a lowlands group, except in the summer rainfall area. The three species are geographically separated.

The single member of sect *Kamiesbergenses* is best understood as the link between the older sect. *Densiflorae* and the derived remainder of the genus.

These postulated phylogenetic relationships are simplistically displayed in Fig. 2.

MONADENIA

Monadenia *Lindl.,* Gen. Sp. Orch. 356 (1838); Benth. & Hook. f., Gen. Pl. 3: 630 (1883); Pfitzer in

Natürl. PflFam. 2, 6: 98 (1889); Kraenzl., Orch. Gen. Sp. 1: 808 (1900); Rolfe in Fl. Cap. 5, 3: 186 (1913); Senghas in Schltr., Die Orchideen 1: 274 (1972); R. A. Dyer, Gen. 2: 995 (1976). Type species: *Monadenia brevicornis* Lindl., Gen. Sp. Orch. 357 (1838) (lectotype).

Disa Berg. sect. *Monadenia* (Lindl.) H. Bol. in Trans. S. Afr. phil. Soc. 5: 137 (1888); Schltr. in Bot. Jb. 31: 202 (1901).

Monadenia brevicornis is here selected as the lectotype, since it is the only correct name Lindley placed in the genus in 1838.

The generic name refers to the single viscidium and is derived from the greek 'monos' = one and 'adenos' = gland.

Leaves all cauline; dorsal sepal shallowly galeate, spur pendent from the base of the galea; petals obliquely ovate-oblong, subcarnose, partially exserted from the galea; lip linear to elliptic, subcarnose; anther usually semi-pendent, with a single large viscidium.

Plants terrestrial, herbaceous, usually erect, 40-600 mm tall; tubers 2, testicular or cylindrical; basal sheaths hyaline, obtuse; leaves all cauline, usually imbricate, the leaf bases sheathing, the blades elliptic to linear-lanceolate, usually erect, the lowermost the largest, the upper grading into the floral bracts; inflorescence cylindrical to secund, dense to lax; ovaries usually twisted, 5 – 25 mm long; bracts ovate to lanceolate, acute to acuminate, slightly shorter than the ovaries to longer than the flower. *Flowers* resupinate (except *M. ecalcarata* Lewis), purplish, brown or green; dorsal sepal shallowly galeate, usually oblong, obtuse, 2,5 – 15 mm long; spur pendent from the base of the galea, slender or clavate, obsolete or longer than the galea; lateral sepals patent or reflexed, usually oblong, often shorter than the galea; petals generally obliquely narrowly ovate-oblong, acute to bifid, the broad base enclosing the anther and the apex erect in the galea, partially exserted from the galea; lip patent to pendent, linear to elliptic, subfleshy; anther horizontal to semipendent with a single large concrete viscidium and two cells; rostellum simple with a deep notch containing the viscidium and with two often well developed lateral flanges flanking the anterior part of the anther; stigma equally or unequally tripulvinate, shortly stipitate to as tall as the rostellum.

Sect. **Densiflora** *Linder,* sect. nov., calcari sepalo dorsalo plerumque breviore, sepalis 2,5–5 (–7) mm longis, inflorescentia densa dignoscenda.

Spur usually shorter than the dorsal sepal, rarely as long as the dorsal sepal; flowers small, sepal 2,5–5 (–7) mm long; inflorescence dense, cylindrical.

Type species: *Monadenia bracteata* (Swartz) Dur. & Schinz.

This section is linked to the rest of the genus by *M. densiflora*. In the *M. densiflora*/*M. bracteata* group the spur is straight or slightly curved, and about as long as the dorsal sepal. From this group two lines of development may be postulated: a line in which the spur is highly reduced, and flower size is decreased

KEY TO SPECIES

1a Spur as long as or shorter than the dorsal sepal:
2a Spur saccate or obsolete:
3a Inflorescence slender, 10 mm in diameter; lateral sepals 2,5 mm long .... 2. *M. conferta*
3b Inflorescence stout, 15 mm in diameter; lateral sepals 4 mm long .... 1. *M. ecalcarata*
2b Spur well developed, more than 1 mm long:
4a Spur clavate, rounded .... 14. *M. physodes*
4b Spur slender:
5a Spur about as long as the dorsal sepal:
6a Spur with a sharp bend; petals deeply bilobed .... 3. *M. sabulosa*
6b Spur straight or gently curved; petals rounded to obtuse:
7a Lateral sepals c. 7 mm long.. 7. *M. macrostachya*
7b Lateral sepals less than 4 mm long .... 5. *M. bracteata*
5b Spur about ½ as long as the dorsal sepal:
8a Spur constricted at the base and triangular in cross-section .... 6. *M. densiflora*
8b Spur cylindrical; not constricted at the base .... 4. *M. pygmaea*
1b Spur longer than the dorsal sepal:
9a Spur clavate:
10a Spur rounded .... 15. *M. cernua*
10b Spur acute.. 16. *M. brevicornis*
9b Spur slender:
11a Plants suffused beetroot-red when fresh, reddish brown when dry:
12a Lip 8–10 mm long, narrowly elliptic to lorate; lateral sepals spreading .... 12. *M. ophrydea*
12b Lip 5–7 (–8) mm long, oblong to narrowly oblong; lateral sepals reflexed .... 11. *M. atrorubens*
11b Plants green when fresh, pale to dark brown when dry:
13a Bracts leathery, venation not visible; petals purple .... 13. *M. rufescens*
13b Bracts membranous to thin-tissued, venation visible; petals lime-green:
14a Lip lorate; leaves linear-lanceolate .... 8. *M. reticulata*
14b Lip elliptic; leaves elliptic to lanceolate:
15a Lowest 2 (–3) leaves elliptic, spreading, sharply differentiated from the remaining leaves, flowering mostly in October ....10. *M. comosa*
15b Leaves gradually smaller from the base to the apex of the stem; flowering mostly in December and January ....10. *M. bolusiana*

(*M. ecalcarata, M. conferta*), and a line in which the spur becomes sharply curved, the inflorescence becomes relatively massive, and the flowers face downwards (*M. pygmaea, M. sabulosa*).

The *M. bracteata/M. densiflora* group is here considered as being ancestral. These two species are closely related, and may be separated by the shape of the spur and the galea. Both taxa are ecologically diverse and widespread in the Cape Flora. *M. bracteata* is ubiquitous in the area, and *M. densiflora* shows quite a remarkable degree of variation in the floral morphology (see below).

Both *Monadenia ecalcarata* and *M. conferta* are rare *M. ecalcata* is known from a single specimen, whereas the latter taxon is more widespread, but populations are very sparse. As both taxa show specializations not found in the other (the non-resupinate flowers in *M. ecalcarata* and the beetroot-red colouring in *M. conferta*), they cannot be placed in an ancestor-descendant relationship.

Monadenia sabulosa and *M. pygmaea* are restricted to the Cape Peninsula and the Caledon District, showing the False Bay disjunction in their distributions as recorded by Rourke (1972) for *Leucospermum hypophyllocarpodendron* subsp. *hypophyllocarpodendron* and Linder (1981b) for *Herschelia purpurascens*. However, as orchids are rather easily distributed by seed, it is suggested that this distribution pattern is the result of the distribution of available habitats, rather than of geological history, as suggested by Rourke (1972) for *Leucospermum hypophyllocarpodendron*. Although the group is quite distinctive, the species are clearly distinct. Although there is some overlap in the habitats of the species, *M. pygmaea* generally occurs on more rocky and more mountanous localities, whereas *M. sabulosa* is restricted to lowland sandflats. Both taxa are generally recorded as flowering after fire.

1. **Monadenia ecalcarata** *Lewis* in Jl S. Afr. Bot. 14: 31 (1948). Type: Cape Province, Cape Peninsula, on damp rocky northern slopes of Constantiaberg, *Lewis* 1487 (SAM, holo.!).

Icon: Jl S. Afr. Bot. 14: 32, Fig. 2 (1948).

Plant 130 mm tall; tubers testicular, 10 mm in diameter; basal sheaths 2, hyaline, obtuse, up to 20 mm long; leaves linear-lanceolate, acute, erect and curved towards the stem, conduplicate, the longest at the base of the stem, 70 mm long, the upper grading rapidly into the floral bracts, densely imbricate; inflorescence a dense cylinder, 60 mm long and 15 mm in diameter with numerous imbricate flowers; ovaries slender, c. 10 mm long; bracts as tall as the flowers, lanceolate, acuminate. *Flowers* not resupinate, lime-green; dorsal sepal shallowly galeate at the base, narrowly oblong, obtuse, 4 mm long; petals obliquely narrowly oblong, obtuse, fleshy, 3 mm long; lip pendent, lorate, obtuse, 3–4 mm long; anth about 1 mm long; rostellum small, erect; stig a nearly square, pulvinate.

Diagnostic features. Flowers with lateral sepals 4 mm long, spur obsolete, flowers not resupinate.

Flowering time: October.

This species is known from a single collection. It differs in too many characters from its nearest relations, *M. conferta* and *M. micrantha,* to be considered as an aberrant form. It is puzzling that an orchid should be so rare (Fig. 3).

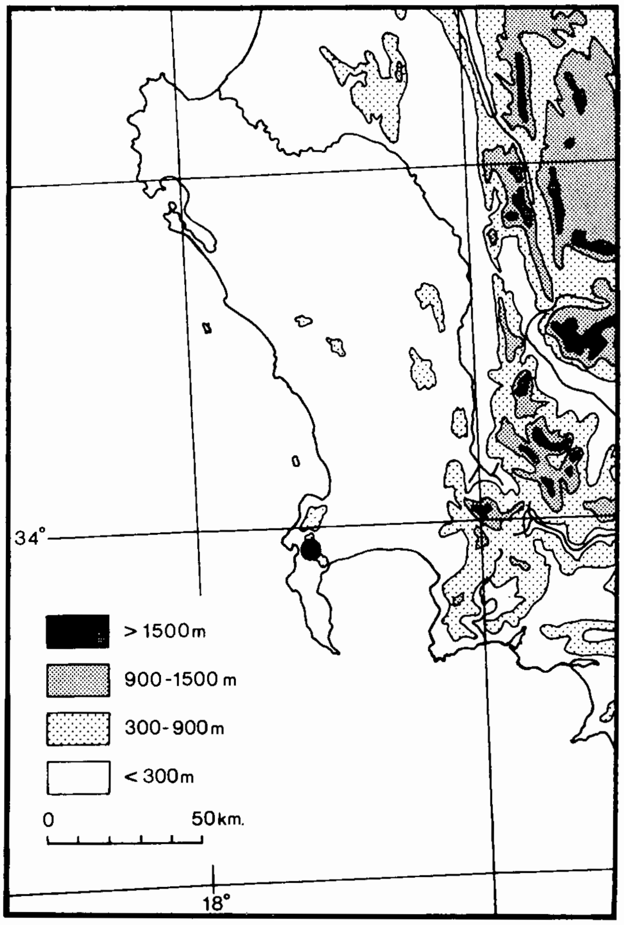

FIG. 3.—Distribution of *Monadenia ecalcarata*.

2. **Monadenia conferta** (*H. Bol.*) *Kraenzl.,* Orch. Gen. Sp. 1: 810 (1900); Rolfe in Fl. Cap. 5,3: 187 (1913). Type: Cape Province, Cape Peninsula, Raapenburg, *Guthrie* 725 (= *Bolus* 7097) (BOL, lecto.!; K!).

Disa conferta H. Bol., Icones Orch. Austro-Afr. 1: t. 28 (1893); Schltr. in Bot. Jb. 31: 212 (1901).

Icon: H. Bol., Icones Orch. Austro-Afr. 1: t. 28 (1893).

Plant slender, suffused with beetroot-red, 80–220 mm tall; tubers c. 10 mm long; leaves linear, acute, numerous, densely imbricate, the largest generally near the base of the stem, up to 70 mm long, erect, conduplicate, grading apically into the floral bracts; inflorescence dense, cylindrical, slender 30–130 mm long and 10 mm in diameter; ovaries 5–10 mm long; bracts as tall as or taller than the flowers, lanceolate, subacuminate, longer towards the base of the inflorescence. *Flowers* lime-green at anthesis, sepals soon turning beetroot-red; dorsal sepal shallowly galeate, rounded to obtuse, oblong, 2,5 mm long; spur saccate, 0,1–0,2 mm long; lateral sepals reflexed, oblong to narrowly oblong, rounded to obtuse, 2 mm long, shallowly concave, erect next to the rostellum; lip pendent, narrowly oblong, obtuse 2–2,5 mm long; another horizontal, 0,5–7 mm long, connective longer than the pollen masses, viscidium minute; rostellum 1 mm tall with large lateral lobes flanking the anther; stigma fused to the base of the rostellum. Fig. 4.

Diagnostic features. Flowers minute, lateral sepal 2,5 mm long; inflorescence dense, slender, cylindrical; spur obsolete.

Flowering time: (September–) October (–December).

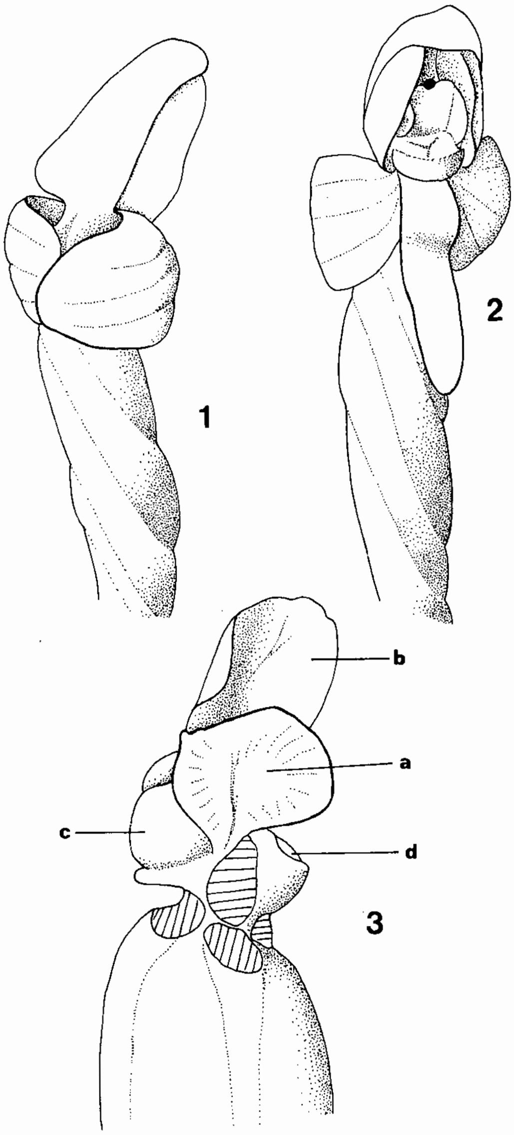

FIG. 4.—*Monadenia conferta*. 1, flower seen from behind, × 10. 2, flower in front view, × 10. 3, dissected flower: a, rostellum; b, petal; c, anther; d, stigma, × 20. All drawn from *Williams* s.n. (BOL).

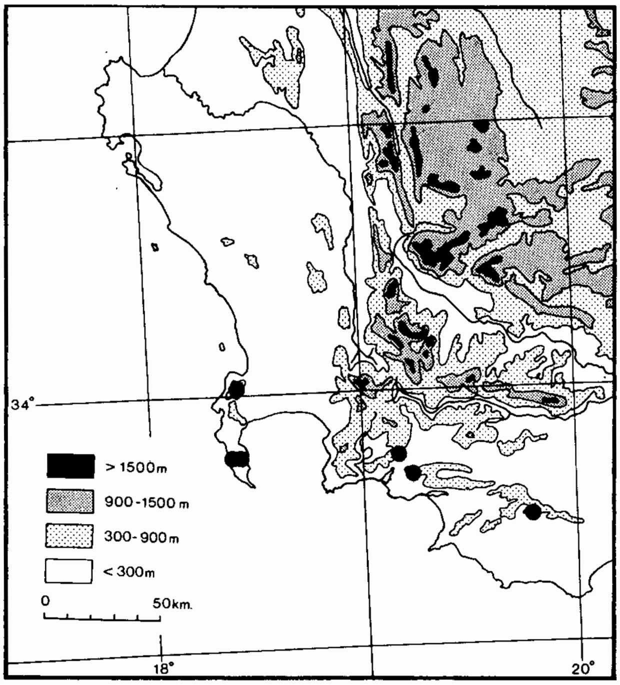

FIG. 5.—Distribution of *Monadenia conferta*.

Locally rare to common in the western Cape Province, occurring on seasonally damp to dry sand, rarely on rocky or gravelly slopes (Fig. 5).

CAPE.*—3419 (Caledon): Koue Rivier Berge near Elim (–AD), Dec. 1896, *Schlechter 9618* (BM; BOL; G; K; P; PRE). 3418 (Simonstown): Buffels River Valley at Hangklip, on a rocky hillside, (–BD), Nov. 1945, *Barker 3925* (NBG); Cape Point Nature Reserve, Olifantsbos (–AD), Oct. 1955, *Lewis 4455* (SAM).

This species may readily be identified by the slender beetroot-red plant with minute spurless flowers.

Only one population has been studied in the field (*Linder* 1528, Caledon District, Babylon's Tower). Occasional to rare individuals occurred on dry scree slopes, flowering one year after a fire. Several collectors noted that the species flowered after fire. The altitude range of the species is from sea level to about 600 m.

Bolus (1893) described *Disa conferta* from two living specimens from different localities. These he cites as *Bodkin* in BOL 6231 from near Houw Hoek and *Guthrie* in BOL 7097 from Raapenburg on the Cape Peninsula. The latter collection is also in BOL under the number *Guthrie* 725. The Guthrie collection is also duplicated in Kew and is here selected as the lectotype.

3. **Monadenia sabulosa** (*H. Bol.*) *Kraenzl.*, Orch. Gen. Sp. 1: 814 (1900); Rolfe in Fl. Cap. 5,3: 195 (1913). Type: Cape Province, Cape Peninsula, Kenilworth, *Bolus* 1374 (= 7104) (BOL, holo.!; BM!; G!; K!; P!; SAM!; UPS!; W!; ZT!).

Disa sabulosa H. Bol. in Icones Orch. Austro-Afr. 1 t. 27 (1893); Schltr. in Bot. Jb. 31: 207 (1901).

Icon: H. Bol., Icones Orch. Austro-Afr. 1: t. 27 (1893).

Plants 80–200 mm tall; leaves lanceolate, acute, sheathing at the base, semi-erect, the margins undulate, imbricate, the largest leaves near the base of the stem, up to 50 mm long, the apical leaves grading into the inflorescence; inflorescence dense, obovate, 30–70 mm long and up to 40 mm in diameter; ovaries c. 15 mm long; bracts as tall as the flowers, lanceolate, acute, green. *Flowers* with lime-green sepals and yellow petals and with a faint scent; dorsal sepal subspathulate to broadly obovate, falcate in sideview, the upper half shallowly galeate, obtuse, 10–15 mm long; spur pendent, flexuose near the base, slender, acute to retuse, 10–15 mm long; lateral sepals reflexed, oblong, rounded, 7–9 mm long, veins prominent; petals subobliquely oblong, the apex deeply and equally bifid, the lobes 2 mm long, petal 7–8 mm long, erect, twisted to face forwards; lip oblanceolate, obtuse, pendent, subfleshy, c. 6 mm long; anther pendent, 2 mm long, viscidium large, square, caudicles 1,5–2 mm long; rostellum lateral lobes partially flanking the anther, c. 2 mm tall; stigma flat, horizontal, 1 mm tall. Fig. 6.

Diagnostic features. Dorsal sepal subspathulate, facing downwards; spur geniculate; petals deeply bifid.

Flowering time: October (–November).

A rare, stout, greenish orchid, occurring on damp to dry sand, usually flowering after fires, in the western Cape Province (Fig. 7).

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*In the treatment of each taxon only representative specimens have been cited. A full list of all specimens studied is given in the Appendix, pp. 361–363.

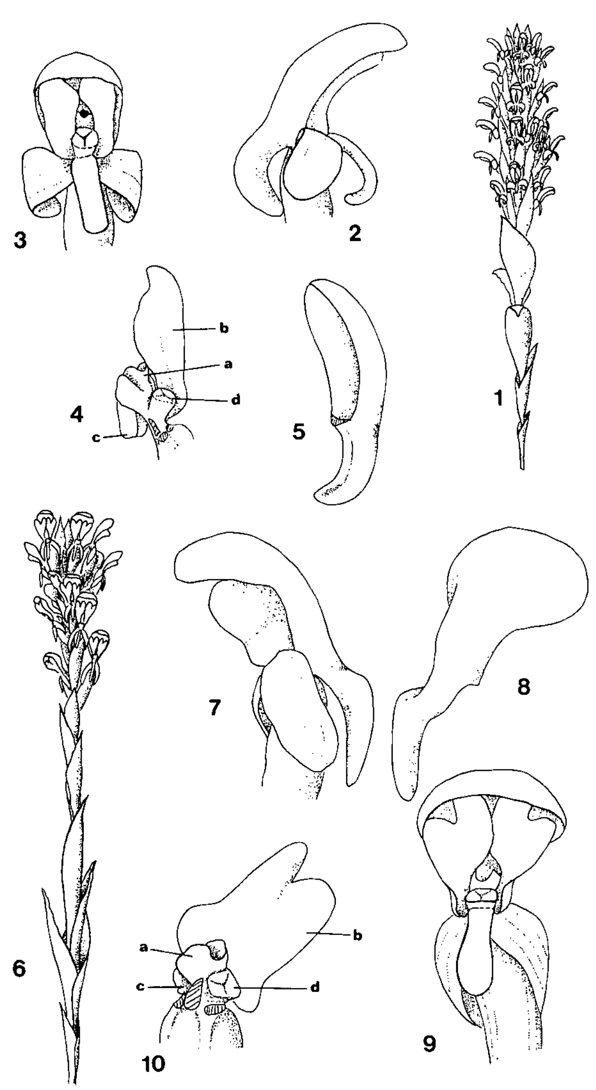

Fig. 6.—*Monadenia pygmaea* (1–5) and *M. sabulosa* (6–10). 1, plant of *M. pygmaea,* × 1, from *Stokoe* s.n. (BOL). 2, flower in side view. 3, flower in front view. 4, dissection of flower. 5, dorsal sepal, (2–5 all drawn from *Linder* 1507, × 6.) 6, plant of *M. sabulosa,* × 0,5, from *Guthrie* 1080. 7, flower in side view. 8, dorsal sepal in rear view. 9, flower in front view. 10, dissection of flower: a, rostellum; b, petal; c, anther; d, stigma. (7–10 from *Linder* 1508; 7–9 × 3 and 10 × 5.)

Cape.—3318 (Cape Town): sandflats at Kenilworth near Wynberg (–CD), Oct. 1891, *MacOwan & Bolus 1374* (BOL; SAM). 3418 (Simonstown): near Hangklip on road to Betty's Bay, on burnt ground (–BD), Oct. 1961, *Thomas in NBG 56374* (NBG).

The type collection of this species was distributed under two different numbers — as *A. Bolus* in BOL 7104 (selected as lectotype) and as *A. Bolus* sub *MacOwan & Bolus* 1374.

Monadenia sabulosa may readily be distinguished from its allies by the deeply bifid petals, and from all the species in the genus by the sharp knee-bend in the spur and the subspathulate dorsal sepal.

A population studied at Betty's Bay (*Linder* 1508) occurred in sand among boulders on the lower slopes of the mountains, in a fire-break. Individuals occurred frequently, mostly in seasonally damp sand. Collectors' notes indicate that this species is most frequently collected after the climax vegetation has been removed (i.e. by fire or mechanical means) from sandy areas. The species ranges from near sea level to about 1 200 m altitude.

The conservation status of the species of the Cape Peninsula is not clear. The majority of collections are from areas now heavily disturbed or built over. However, the status in the Betty's Bay area appears to be satisfactory. It must be noted that the species is restricted to the lower slopes of the mountains and the coastal flats, which are prone to invasion by various introduced *Acacia* species. In the long term, these localities will require active conservation.

4. **Monadenia pygmaea** (*H. Bol.*) *Dur. & Schinz,* Consp. Fl. Afr. 5: 111 (1894); Kraenzl. in Orch. Gen. SP. 1: 813 (1900); Rolfe in Fl. Cap. 5,3: 190 (1913). Type: Cape Province, Cape Peninsula, Muizenberg Mountain, *Bodkin* in BOL 4970 (BOL, holo.!; G!; K!; SAM!).

Disa pygmaea H. Bol. in J. Linn. Soc., Bot. 20: 72 (1885); Schltr. in Bot. Jb. 31: 213 (1901).

Icon: H. Bol., Icones Orch. Austro-Afr. 3: t 37 (1913).

Plants 45–150 mm tall; leaves narrowly ovate, acute, imbricate, semi-erect, all equal in size, 15–20 mm long; inflorescence cylindrical, dense, 15–100 mm long, longer than the leafy part of the stem; ovaries c. 5 mm long; bracts taller than the flowers, lanceolate, acute, green. *Flowers* with lime-green lip and petals, green lateral sepals and rusty brown dorsal sepal and spur; dorsal sepal shallowly galeate, oblong, obtuse, 5–6 mm long and up to 2 mm deep; spur c. 2,5 mm long, cylindrical, retuse, falcately curved towards the ovary; lateral sepals patent with the apices reflexed, oblong, obtuse, 4 mm long; petals obliquely narrowly oblong with a small tooth to the rear, the apex shortly and acutely bifid, erect, twisted to face partially forwards, 4 mm long; lip subpendent, the apex reflexed, lorate, 3–4 mm long; anther pendent, 1 mm long; viscidium elongated with a dorsal groove; rostellum with small side lobes, 1 mm tall; stigma 0,3 mm tall, somewhat angled forwards. Fig. 6

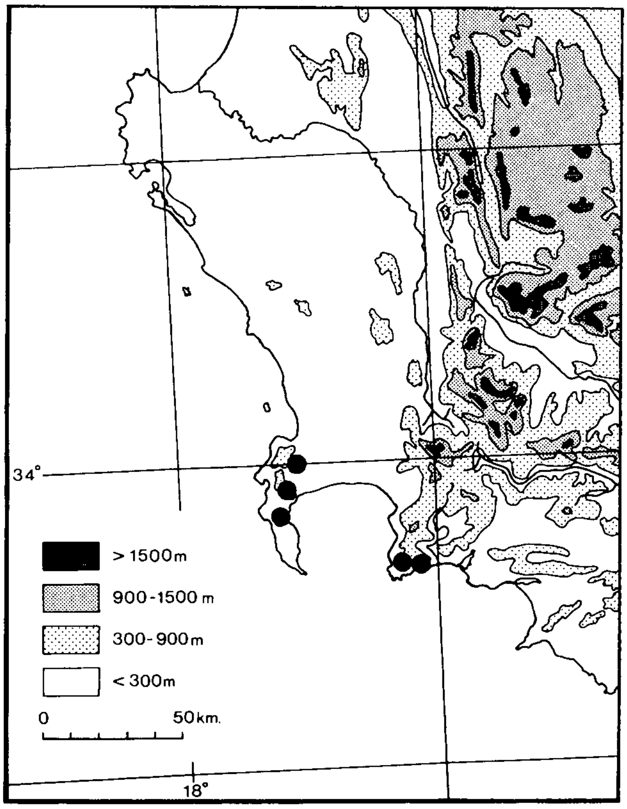

Fig. 7.—Distribution of *Monadenia sabulosa.*

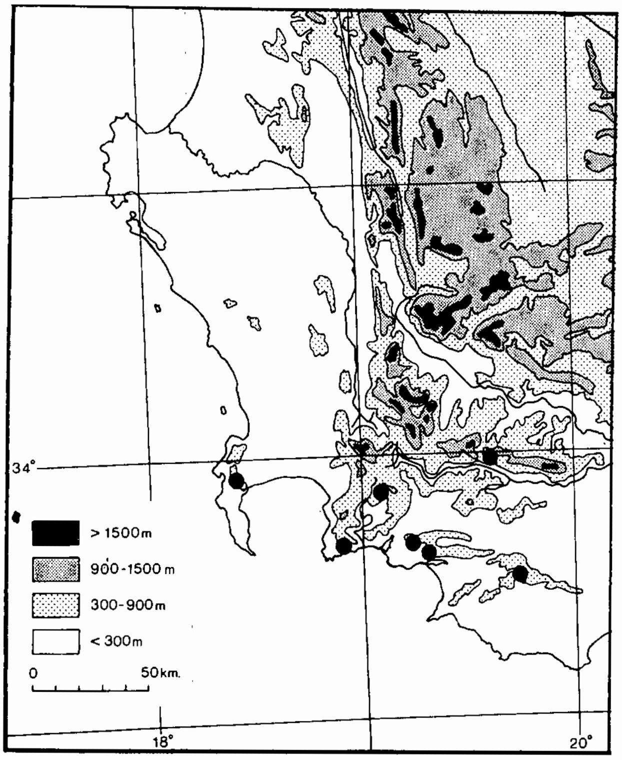

FIG. 8.—Distribution of *Monadenia pygmaea*.

Diagnostic features. Flowers small, lateral sepals 4 mm long; plants less than 150 mm tall, inflorescence longer than the leafy stem.

Flowering time: October and November.

Monadenia pygmaea occurs occasionally in small populations in sandy areas, often flowering after fire (Fig. 8).

CAPE.—3418 (Simonstown): Steenberg Plateau, burnt sandy slope near reservoir (–AB), Oct. 1945, *Lewis 1095* (SAM). 3419 (Caledon): Klein Riversbergen near Onrust (–AC), Nov. 1896, *Schlechter 9501* (BOL).

This species is allied to *M. sabulosa* by the bifid petals and the slight knee-bend in the spur, but may be distinguished from that species by the much smaller flowers and plants (sepals about 4 mm long). From the rest of the genus it may be separated on the inflorescence that is always longer than the leafy stem, the flowers that face downwards, and the short spur.

A population studied near Betty's Bay (*Linder* 1507) was found near *M. sabulosa* in sand in a recently cleared fire-break at the base of the mountain. Individuals occurred frequently in seasonally damp sandy areas. Other collectors also generally indicate a sandy substrate, except two collections from the Lebanon Forest Reserve, which are from dry rocky slopes, one with loose rocky sand. Several collections were made after fire. The altitude range of the species is from sea level to almost 1 000 m. The rainfall ranges from about 800 mm to over 1 500 mm in some localities, mostly restricted to the winter.

Although the majority of collections are from localities suffering from severe disturbance, the species has also been recorded from localities likely to have some long-term protection, such as the Lebanon Forest Reserve.

5. **Monadenia bracteata** (*Swartz*) *Dur. & Schinz,* Consp. Fl. Afr. 5: 111 (1894). Type: Cape of Good Hope, *Sparrman* s.n. (W, holo.!).

Disa bracteata Swartz in Vet. Acad. Handl. 21: 211 (1800).

Monadenia micrantha Lindl., Gen. Sp. Orch. 357 (1838); Kraenzl., Orch. Gen. Sp. 1: 818 (1900); Rolfe in Fl. Cap. 5, 3: 190 (1913). *Disa micrantha* (Lindl.) H. Bol. in Trans. S. Afr. phil. Soc. 5: 142 (1888); Schltr. in Bot. Jb. 31: 213 (1901). Type: Knysna, Ruigtevallei *Drège* 1261 (K, holo.!; G!; P!; W!).

Disa praetermissa Schltr. in Ann. Transv. Mus. 10: 246 (1924). Type: Humansdorp, sandy grassland near Stormsrivier, *Schlechter* s.n. (B, holo.!).

Monadenia australiensis Rupp in Austr. Orch. Rev. 11: 70 (1946). Type: West Australia, Stirling Range, Youngs Siding, *Southerland* s.n. (PERTH, holo.).

Plants up to 300 (–500) mm tall; leaves linear-lanceolate, acute, imbricate, numerous, erect and usually curved inwards, the largest near the base, 40–120 mm long, grading apically into the floral bracts; basal sheaths hyaline, obtuse, 10–20 mm long; inflorescence cylindrical, imbricate, flowers numerous, 20–120 mm long; ovaries erect, 6–10 mm long; bracts shortly overtopping the flowers, rarely much taller than the flowers, narrowly ovate, acuminate. *Flowers* green with the sepals usually tinted maroon; dorsal sepal shallowly galeate, broadly oblong, obtuse to acute, 3–4 mm long and c. 1 mm deep, falcate in side view; spur shallowly triangular, pendent from the base of the galea, rounded to truncate, 3–4,5 mm long; lateral sepals patent with the apices usually reflexed, oblong, obliquely acute, 2,5–3,5 mm long; petals erect, partially included in the galea, broadly obtriangulate in outline, obliquely acute, 2–2,5 mm long, concave, venation strongly falcate; lip pendent narrowly oblong to lorate, often oblanceolate, 2–2,5 mm long; anther pendent, c. 1 mm long; rostellum with a large central notch, staminodes of variable size; stigma pulvinate. Fig. 10.

Diagnostic features. Flowers small, lateral sepals 2,5–3,5 mm long, spur pendent, 3–4,5 mm long, slender, rounded or truncate, inflorescence dense, cylindrical.

Flowering time: September–November.

Monadenia bracteata is a widespread and common little orchid (Fig. 9), that occurs frequently in wasteland areas, especially in areas of mild disturbance. In undisturbed vegetation it is widespread, but somewhat rarer. In Australia it has been recorded as a roadside weed.

CAPE.—3318 (Cape Town): Rondebosch, University of Cape Town football field (–CD), Sept. 1946, *Leighton 2079* (BOL). 3418 (Simonstown): Fish Hoek mountain, in shade under trees (–AB), Nov. 1944, *Lewis 823* (SAM). 3322 (Oudtshoorn): Saasveld, near George, in grassland at the forest edge (–DC), Oct. 1965, *Morze 2026* (BOL). 3323 (Willowmore): near Stormsriver mouth (–DD), Nov. 1894, *Schlechter 5965* (BM; G; K; W; Z).

The identity of *Disa bracteata* has led to much confusion. N. E. Brown applied the name to an illustration of what is clearly *Monadenia multiflora.* Lindley (1838) cited a plate of Brown (1818) as being *Disa bracteata.* Bolus (1888) discussed the problem of the identity of *D. bracteata,* indicating that it could not be confused with *Disa cylindrica* and that it is likely to be a *Monadenia.* He could not, however, trace a type specimen either in the Swartz or Thunberg herbarium. Rolfe (1913) was of the opinion that *D. bracteata* is *M. multiflora,* as 'It does not describe the cylindrical spur and linear lip of *M. micrantha* Lindl'. In Vienna I located a capsule containing several flowers and an inflorescence of *Monadenia micrantha.* The capsule was annotated *'Disa bracteata* Swartz scripsit'. The words 'Disa' and 'Swartz scripsit' were in a hand that I do not know, but *'bracteata'* is written in a hand closely resembling

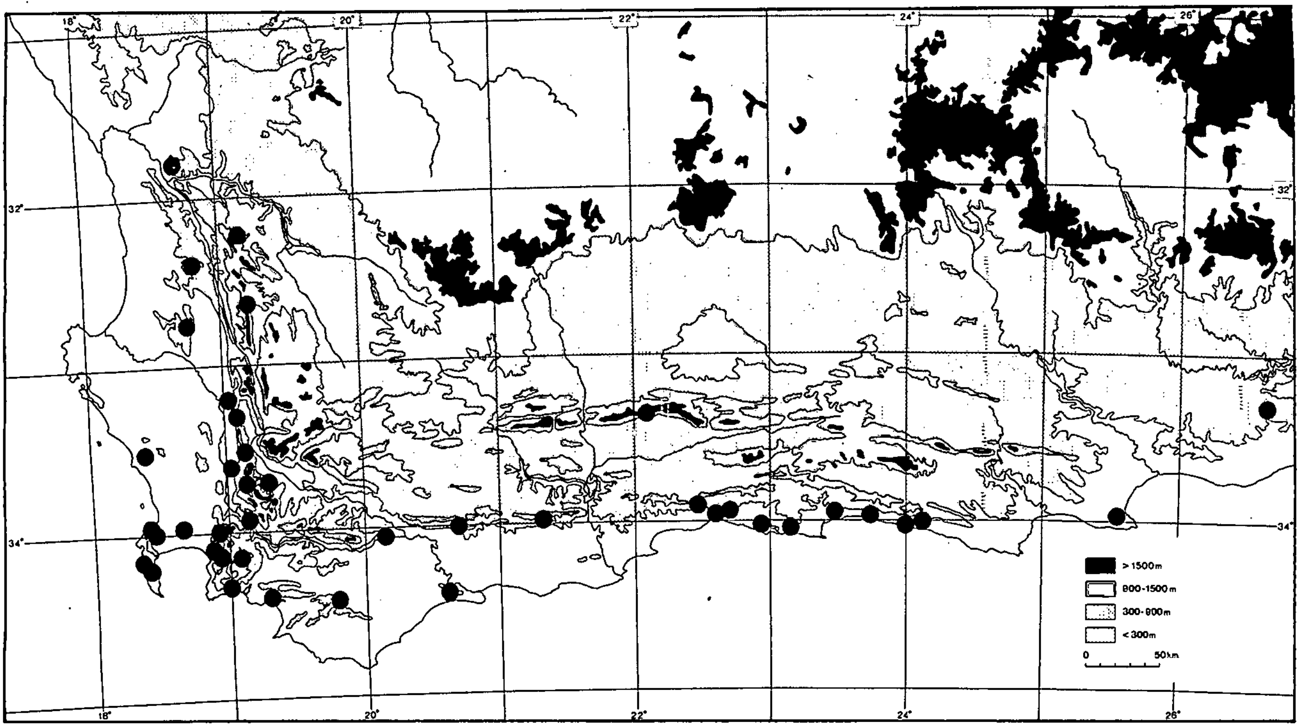

FIG. 9.—Distribution of *Monadenia bracteata.*

that of Olof Swartz (*vide* Burdet, 1978). As there are several sheets of Swartz types at Vienna (Linder, 1981a), this is not exceptional, and might well be the type of *Disa bracteata.*

The type of *Disa praetermissa* has unfortunately been lost. However, from the protologue this name has to be included in the synonymy here, as the distinguishing characters mentioned by Schlechter (1924) (Spur length and leaf shape) are quite variable in *M. bracteata.*

Monadenia bracteata is closely allied to *M. densiflora,* but may be distinguished from this species by the terete spur, which is generally as long as the dorsal sepal. In *M. densiflora,* the galea is often obovate, a state that never occurs in *M. bracteata.* From the rest of the genus these two species are separated by the small flowers (sepals less than 8 mm long) and spur as long as or shorter than the dorsal sepal.

This is by far the most common species of *Monadenia,* and occurs in a wide range of habitats, from dry sandy areas to gravelly mountain slopes, on damp clayey soils and in black turf sand. The altitude range of the species is from sea level to 1 500 m, and specimens have been collected in full sunlight and in shade. The rainfall regime over the distribution range varies from less than 800 mm p.a. to well over 1 600 mm, and from an all-year rainfall in the Knysna-Humansdorp area to several months of summer drought in the Clanwilliam area.

In undisturbed vegetation populations have a low density and individuals occur scattered over a large area. In disturbed conditions (road-cuttings) and fills, old fields, gravel pits, sport fields, etc.) large populations may be found. Over its whole distribution range, this species is well established as a pioneer.

M. bracteata has also been recorded from Australia, initially under the name *M. australiensis,* as it was thought to be indigenous to Australia (Rupp, 1946). Erickson (1965) noted that 'It was found to be most common on the roadsides, the usual lodging place for immigrant plants ...' Pocock (1972) recorded this species only from the south-west of Australia, flowering in November. It was probably introduced accidentally to that continent.

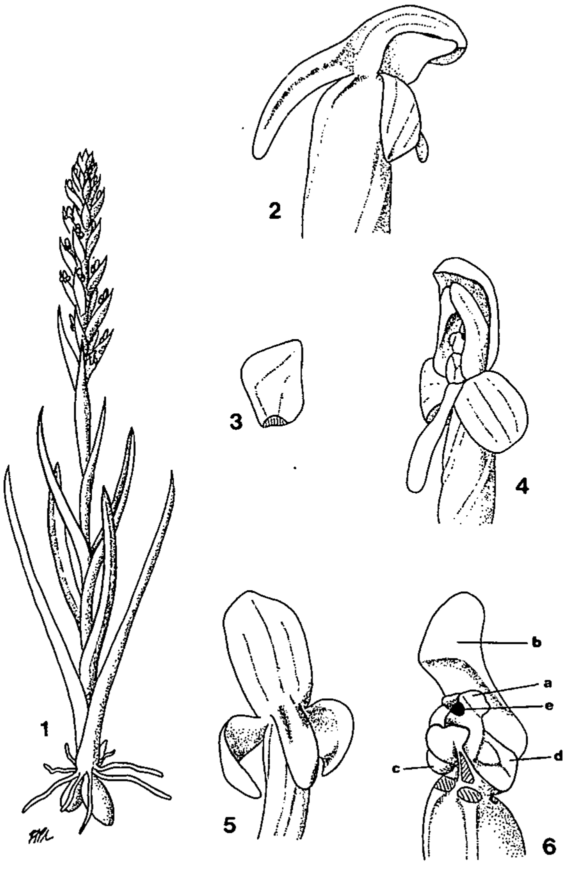

FIG. 10.—*Monadenia bracteata* (1–3) and *M. densiflora* (4–6). 1, plant of M. bracteata, × 0,5, from *Esterhuysen* 12074. 2, flower in side view. 3 petal. (2–3 from *Walters* 508, × 5.) 4, flower of *M. densiflora* in front view. 5, flower in rear view, showing the spur. 6, dissection of flower: a rostellum; b, petal; c, anther; d, stigma. (4–6 from *Linder* 1513, × 5.)

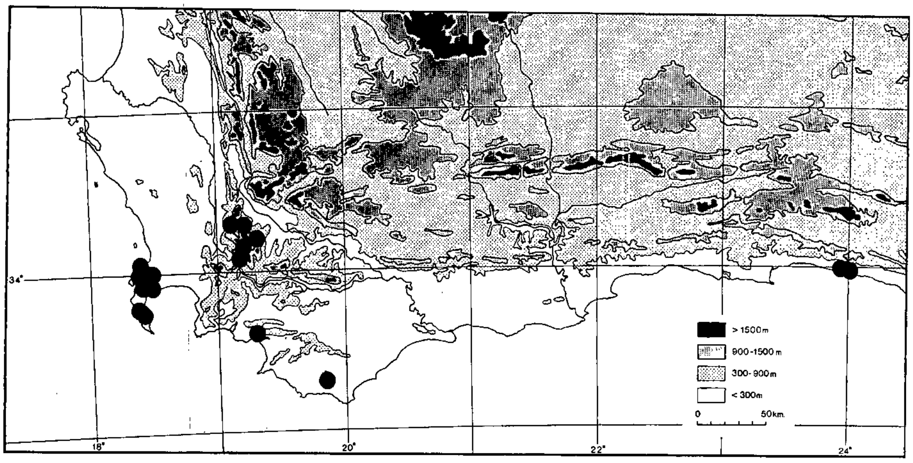

FIG. 11.—Distribution of *Monadenia densiflora*.

6. **Monadenia densiflora** *Lindl.*, Gen. Sp. Orch. 357 (1838); Kraenzl., Orch. Gen. Sp. 1: 814 (1900). Lectotype: Cape of Good Hope, *Thom* s.n. (K, lecto.!).

Disa densiflora (Lindl.) H. Bol. in J. Linn. Soc., Bot 25: 197 (1889).

Monadenia multiflora Sond. in Linnaea 19: 101 (1847); Kraenzl., Orch. Gen. Sp. 1: 811 (1900); Rolfe in Fl. Cap. 5, 3: 188 (1913). *Disa multiflora* (Sond.) H. Bol in Trans. S. Afr. phil. Soc. 5: 140 (1888); Schltr. in Bot. Jb. 31: 215 (1901). Type: Cape Province, Cape Peninsula, Doornhoogte, *Ecklon & Zeyher* s.n. (S, holo.!; K!; P!; W!).

Disa auriculata H. Bol., Icones Orch. Austro-Afr. 1: t. 77 (1896); Schltr. in Bot. Jb. 31: 214 (1901). *Monadenia auriculata* (H. Bol.) Rolfe in Fl. Cap. 5, 3: 189 (1913). Syntypes: Cape Province, Cape Peninsula, *Guthrie* s.n. (BOL!); Humansdorp, near Storms River, *Schlechter* 5958 (BOL!; BM!; G!; W!; Z!).

Icones: H. Bol., Icones Orch. Austro-Afr. 1: t. 77 (1896), as *Disa auriculata:* 3: t. 39 (1913), as *D. multiflora*.

Plants slender to robust, 75–195–350 mm tall; tubers up to 20 mm long; basal sheaths hyaline, obtuse to apiculate, 2–3, up to 40 mm long; leaves linear-lanceolate, acute, conduplicate, numerous, imbricate, 50–90–140 (–220) mm long, generally reaching to the base of the inflorescence and grading apically into the floral bracts; inflorescence slender cylindrical, 25–95–180 mm long, usually longer than the leafy shoot, flowers numerous, imbricate; ovaries 5–10 mm long, twisted; bracts as tall as or overtopping the flowers, generally longer towards the base of the inflorescence, narrowly ovate, acuminate. *Flowers* with dull green petals and lip, and rusty red to green sepals; dorsal sepal shallowly galeate, oblong, obtuse, erect or falcately curved forwards, 3–5 (–7) mm long and 0,5–1 mm deep; spur pendent from the base of the galea, triangular in cross-section, constricted at the base, apex obtuse to retuse, (1–) 2–3 (–4) mm long, shorter than the galea; lateral sepals oblong-ovate, sub-obtuse to rounded, spreading, apices reflexed, 3–5 (–7) mm long; petals erect, narrowly oblong, subfalcate, 2,5–5 (–7) mm long, rounded to rarely acute, the apical 1/3 fleshy; lip pendent, narrowly oblong to oblanceolate, rounded, 2,5–5 (–7) mm long, apex fleshy; anther pendent, c. 0,8 mm long; rostellum with a deep notch for the single viscidium, viscidium flanked by two flat projections; stigma horizontal, unequally three-lobed. Fig. 10.

Diagnostic features. Flowers small, lateral sepals 3–5 (–7) mm long, spur shorter than the galea, 2–4 mm long, triangular in cross-section, somewhat constricted at the base; plants 75–350 mm tall.

Flowering time: (September–) October (–December).

Monadenia densiflora is a widespread, but usually not common, species, occurring usually in sandy places, but also in a wide range of other habitats (Fig. 11).

CAPE.—3318 (Cape Town): Table Mountain, Groene Kloof, 600 m (–CD), Nov. 1897, *Galpin 4612* (PRE), 3418 (Simonstown): Constantiaberg, slopes above Baviaans Kloof (–AB), Oct. 1947, *Lewis 1833* (SAM); Krom River (–AB), Oct. 1945, *Compton 17486* (NBG). 3319 (Worcester): Wemmershoek Peak, 1 650 m (–CC), Dec. 1944, *Lewis 850* (SAM). 3323 (Willowmore): at Stormsriver Mouth (–DD), Nov. 1978, *Linder 1903* (BOL).

Monadenia densiflora Lindl. was based on two syntypes at Kew, namely *Thom s.n and Drège* 8288. According to Article 9.2 of the I.C.B.N. (1978), the element most closely resembling the protologue has to be selected as the lectotype. *Thom* s.n. most closely resembles the protologue. 'Calcare pendulo filiforme antice alato' and 'labello lineari-spathulato carnoso' can only refer to this element, whereas 'petalis ...... galea duplo brevioribus' refers to *Drège* 8288. N. E. Brown in a note on *Thom s.n.* wrote that the description of *M. densiflora* was based on this specimen, but Rolfe (1913) effectively lectotypified the name *M. densiflora* by attaching the *Thom* specimen ('*Thom* 732') to that species and referring *Drège* 8288 to *M. physodes. This lectotypification* should be followed.

This highly variable species has small flowers (sepals 3–5 (–7) mm long) with a spur shorter than the galea. It may be separated from the closely related *M. bracteata* by the relatively short spur which is triangular and constricted at the base.

This species has a peculiarly disjunct distribution, with the vast bulk of the collections known from the western Cape Province, and a few rare collections from the Tsitsikamma coastline between Humansdorp and Knysna. As discussed above, there is some morphological differentiation between these two centres.

In the western Cape, this species occupies a wide range of habitats. It has been recorded from sand near sea level, at Olifantsbos in the Cape Point Nature Reserve, from the summit of Table Mountain, and from rock ledges in the Wemmershoek Mountains. The altitude range of the species is from sea level to over 1 600 m. In general, it appears to be restricted to slightly damp areas, and has often been collected after fires. It does not appear to be common in any of these habitats. The macro-climatic conditions vary from all year rainfall in the Knysna area, to summer drought conditions on the Cape Flats. In the mountains of the western Cape, it often occurs in the south-eastern cloud zone.

Monadenia multiflora has generally been recognized as a distinct species. Sonder (1847) clearly distinguished it from *M. bracteata* by the larger flowers and shorter spur. However, *M. auriculata* has never been satisfactorily separated from *M. multiflora.* Bolus (1896) stated 'It comes near to *D. multiflora, mihi,* in its flowers, but the spike is always slenderer, and the inflorescence usually less dense'. Schlechter (1901) claimed that *D. auriculata* may easily be recognized by 'the more slender habit, smaller flowers, more helm-shaped dorsal sepal and the rostellum'. Rolfe (1913) used the relative lengths of the spike and the leafy shoot to separate the two putative taxa. Lewis (1950) separated the taxa on the width of the spike and the shape of the spur. A careful analysis of all the available material, as well as field studies in the various localities where the types were collected, showed that the two taxa could not be maintained as distinct from each other and *M. densiflora.*

Monadenia densiflora is rather variable with respect to flower size, and the shapes of the petals and the spur. Although the inflorescence is generally longer than the leafy shoot, the ratio is often reversed. Spur length varies from 1 mm (*Barker* 3893) to 4 mm (*Page* in BOL 16232) and spur shape from a rounded apex to an emarginate apex. There is some geographical pattern to flower size. Collections from the Tsitsikamma coastal flats have the smallest flowers (lateral sepal c. 3 mm long, *Linder* 1903), whereas collections from the summit of Table Mountain on the Cape Peninsula show the largest flowers (*Lewis* 1107). One of the syntypes of *D. auriculata* (*Schlechter* 5958) is representative of the small-flowered Tsitsikamma form, whereas the lectotype of *M. densiflora* is typical of the large-flowered form from Table Mountain. The type of *M. multiflora, Ecklon & Zeyher* s.n., is from the more common intermediate size range (lateral sepals c. 3,4 mm long).

Sect. **Kamiesbergenses** *Linder,* sect. nov., calcari sepalo dorsalo aequanti, sepalis c. 7 mm longis, inflorescentia laxa dignoscenda.

Spur about as long as the dorsal sepal; flowers medium sized, sepals about 7 mm long; inflorescence lax.

Type species: *Monadenia macrostachya* Lindl.

The sole species in this section, *M. macrostachya,* could be placed into any of the other three sections, as it is closely related to *M. densiflora, M. reticulata* and *M. brevicornis.* However, in the cladistic analysis followed here, it would appear to be best placed in a position linking the other groups, and possibly ancestral to them. If the other three groups were to be recognized as being distinct sections, this species would also have to be placed into a section by itself.

This analysis would imply that the present distribution of *M. macrostachya* is only a relic of a more extensive older distribution. If this is correct, it is certainly interesting that the relic should be in an outlier of the Cape Flora, where the species richness is relatively low.

7. **Monadenia macrostachya** *Lindl.,* Gen. Sp. Orch. 357 (1838); Kraenzl., Orch. Gen. Sp. 1: 812 (1900), excl. syn.; Rolfe in Fl. Cap . 5, 3: 189 (1913). Type: Cape Province, Namaqualand, Rooiberg. *Drège* 8289 (K, holo.!; G!; K!).

Disa macrostachya (Lindl.) H. Bol. in J. Linn. Soc., Bot 25: 197 (1889); Schltr. in Bot. Jb. 31: 209 (1901), excl. syn.

Plant slender, 300 mm tall; leaves imbricate, the lower 4–8 lorate, acute, erect, conduplicate, up to 130 mm long and 20 mm wide, remaining leaves mostly sheathing, grading into the floral bracts; inflorescence lax with several flowers, up to 200 mm long; ovaries c. 10 mm long; bracts as tall as the flowers, ovate, acuminate, probably dry. *Dorsal sepal* erect, narrowly oblong, acute, 8 mm tall and galea 1,5 mm deep; spur pendent from the base of the galea, somewhat inflated, obtuse to retuse, 6–8 mm long and about 2 mm in diameter, straight; lateral sepals reflexed, oblong, obtuse, c. 7 mm long; petals obliquely narrowly ovate, very acute, 6 mm long, erect; lip pendent, lorate, obtuse, 6 mm long; anther semipendent, 1,5 mm long; rostellum erect, tall; stigma on a 2 mm tall pedicel.

Diagnostic features. Dorsal sepal 8 mm long, spur subclavate, retuse, as long as the dorsal sepal, bracts dry, basal leaves lorate, erect, acute, cauline leaves mostly sheathing.

Flowering time: ? September.

This species is only known from two collections: the type collection probably made in about 1835 by Drège; and from a plant past flowering, collected by me in 1977 (Fig. 12). The above description was prepared from the meagre material available, and upon receipt of further material may well be found to be wanting.

Although *M. macrostachya* is clearly distinct, it is related to several of the major groups in *Monadenia,* and may be regarded phylogenetically as a relic that links these three groups together (Fig. 2).

Following Bolus (1911) and Schlechter (1901) in most herbaria *Monadenia macrostachya* and *M. reticulata* are regarded as synonymous. In this treatment *M. reticulata* is regarded as a distinct species.

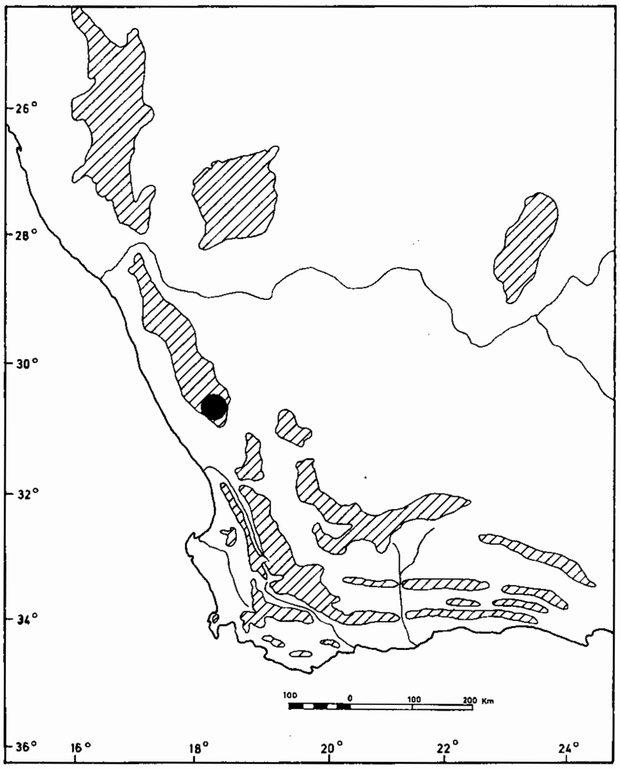

FIG. 12.—Distribution of *Monadenia macrostachya.*

A single small popolution of this species was located by the author in the Kamiesberg on the Rooiberg. The plants occurred in dry stony soil near a stream, and had been heavily grazed by sheep. There might well be more populations, as the mountains have not been properly explored.

Sect. **Tenuicornes** *Linder,* sect. nov., calcari tenui, sepalis dorsalibus longiore, sepalis 6–10 mm longis, inflorescentia laxa dignoscenda.

Spur slender, longer than the dorsal sepal; flowers medium sized, sepal 6 – 10 mm long; inflorescence lax.

Type species: *Monadenia ophrydea* Lindl.

This rather distinct section includes six species: *M. reticulata,* which is closely related to *M. macrostachya,* in which it has been included by some botanists; *M. rufescens,* with a relatively short spur and an elongated viscidium; *M. bolusiana* and *M. comosa,* with green petals and the stigma on a tall stipe; and *M. ophrydea* and *M. atrorubens* in which the plants are suffused with beetroot-red. The section may be distinguished from sect. *Densiflorae* and sect. *Kamiesbergenses* by the spur always being longer than the dorsal sepal, and from sect. *Monadenia* by the slender spur.

Both the *M. comosa* and the *M. ophrydea* groups may be derived from *M. reticulata.* Consequently, this species is treated as being ancestral in the section. Other evidence in favour of the ancestral position of this species is its wide distribution and large range of habitats. It is also closely related to *M. macrostachya.*

M. rufescens is clearly related to *M. reticulata* by the slender spur and the shape of the petals, but may readily be distinguished by the three-dimensional shape of the flowers, the dense tissue of the bracts which do not show the venation, and the elongated viscidium. It appears as if this species may have evolved a peculiar pollination syndrome. Although *M. rufescens* is essentially restricted to the western Cape Province, it has been collected from a wide range of habitats.

Within the *M. comosa* complex three groups might conveniently be recognized. The differences between these groups are given in Table 2. The characters listed in the table are approximations, as several are rather difficult to quantify e.g. variation in leaf shape and the habitats. No difference in the floral structures among the groups has been detected.

The three groups behave like ecotypes. Group one occurs almost invariably in rock crevices, usually in shady places. Group three generally grows in full sunlight, usually on the upper ridges of mountains. Various populations occur in a wide range of habitats: deep sand (*Ebersohn* 151), footpaths (*Linder* 1672) and in rock crevices and ledges (*Linder* 1748). These two groups occur in the Langeberg and in the mountains between Caledon and Clanwilliam. Group two occurs on the summit of the Swartberg near Oudtshoorn, at a high altitude, in a zone receiving the bulk of the rain in the summer months. It grows in a habitat similar to that of Group three.

Groups one and three behave like distinct species. The ranges of these two groups are sympatric but, although populations of the two groups occur on the same mountain, the plants occupy different habitats, and interbreeding is prevented by allochronic flowering. Morphologically, individuals can be placed into these two groups on the basis of the leaf structure and the colour of the vegetative parts of the plants, both in the fresh and dried state.

Group two does not occur sympatrically with groups two and three, and its biological role can therefore not be determined on the basis of its interaction with closely related populations. Morphologically, the populations are quite variable, with the majority of individuals rather similar to group one, but with the variation ranging almost to that typical of group three.

Taxonomically the *M. comosa* complex may be treated in several ways:

1. As a variable species with three infraspecific taxa. However, groups one and three behave as distinct species.

2. As two distinct species, with group two recognized at infraspecific level in either of the two species. However, group two is intermediate between the two species, and such a treatment implies that either group two arose by secondary convergent evolution, or that group one arose by secondary divergence from group two.

3. As two distinct species, with group two recognized as an ancient hybrid complex between the two species. This would account for the extraordinary range of variation in the populations assigned to group two. Hybridization on the Swartberg could be accounted for by the delay of flowering of group one, leading to synchronous flowering. This would lead to the present situation, where parents, hybrids and the results of introgression can no longer be separated. This interpretation of group two would also strengthen the notion that groups one and three represent biological species.

TABLE 2.—Groups recognized within *M. comosa* s.l.

Character	Group one	Group two	Group three
Leaves	Basal two leaves spreading, distinct from rest	Leaves variable, basal leaves generally larger	Basal leaves grading gradually into upper leaves
Flowering (months)	(9–) 10 (–11)	12	(10–) 12–1
Habitat	Shady ledges	Full sun in rocks	Full sun on mountain summits

The third treatment is followed in this study.

Although the *M. comosa* complex is closely related to *M. reticulata,* it may be separated from this species by the higher stigma and somewhat longer spur. Both species of the group are best regarded as specialized derivatives from *M. reticulata.*

Monadenia ophrydea and *M. atrorubens* are also very closely allied and have frequently been confused. There are numerous small differences between the species, most of which are rather difficult to observe on dried material and have at least some exceptions. Only the rostellum height/stigma height ratio appears to be a constant differential character. The differences between the two species are listed in Table 3.

TABLE 3.—Morphological differences between *M. atrorubens* and *M. ophrydea* (note that few collections have all these characters)

M. atrorubens	*M. ophrydea*
Rostellum as tall as stigma	Rostellum twice as tall as stigma
Lateral sepals completely reflexed	Lateral sepals not or barely reflexed
Dorsal sepal narrowly oblong	Dorsal sepal oblong-obovate
Lateral sepals deep purple	Lateral sepals almost white
Caudicles shorter than the pollinarium	Caudicles longer than the pollinarium
Lip oblong to narrowly oblong	Lip narrowly elliptical to lorate
Lip 5–7 (–8) mm long	Lip 8 – 10 mm long

The morphological differences between the species are correlated with ecogeographical differences. *M. atrorubens* occurs on the west coast of the western Cape Province, and extends southwards to Houw Hoek in the Caledon District, whereas *M. ophrydea* extends from Table Mountain on the Cape Peninsula eastwards to Humansdorp. *M. atrorubens* grows mainly on deep sand, in areas in which there is almost no precipitation in the summer months, whereas *M. ophrydea* is generally found on mountain slopes in shallower stony sand, in areas where there is at least some rainfall in the summer months. Flowering in *M. atrorubens* peaks in September, while in *M. ophrydea* it peaks in October.

This group appears to be derived from *M. reticulata,* and is morphologically very similar to it. The beetroot-red colour of the plants appear to be a single-gene factor, as several individuals have been collected in which the red coloration is absent. Such individuals are difficult to distinguish from *M. reticulata* when they are dried.

8. **Monadenia reticulata** (*H. Bol.*) *Dur. & Schinz,* Consp. Fl. Afr. 5,3: 111 (1894); Kraenzl., Orch. Gen. Sp. 1: 816 (1900); Rolfe in Fl. Cap 5,3: 193 (1913). Type: Cape Province, Cape Peninsula, Constantiaberg, *Bodkin* in BOL 4988 (BOL, holo.!; K!).

Disa reticulata H. Bol. in J. Linn. Soc., Bot. 22: 75 (1885); Schltr. in Bot. Jb. 31: 209 (1901), excl. syn.

Icones: H. Bol., Icones Orch. Austro-Afr. 2: t. 88 (1911); 3: t. 41 (1913), as *Disa macrostachya.*

Plants 80–400 mm tall; leaves generally linear-lanceolate, rarely narrowly oblong, acute, imbricate, erect, the lower the longest, up to 150 mm long, gradually grading into the upper leaves that are almost completely sheathing, grading into the floral bracts; inflorescence cylindrical, generally dense with numerous flowers, 30–150 mm long; ovaries c. 10 mm long; bracts reaching to the top of the flowers, narrowly ovate, acuminate, the reticulate venation clearly visible on dried material. *Flowers* lime-green, occasionally with some maroon tinting or mottling on the petals or sepals, scent strong, soapy; dorsal sepal shallowly galeate, oblong, obtuse, somewhat curved forwards, 7–8 mm long; spur pendent from the base of the galea, slender, acute, longer than the galea, 10–20 mm long and c. 1 mm in diameter; lateral sepals oblong, rounded, 6–7 mm long; petals obliquely narrowly ovate to rarely narrowly oblong, apically obliquely retuse to rounded, the broad base of the petals enclosing the anther, the apex twisted to face forwards, 5–6 mm long; lip pendent, lorate to rarely narrowly oblanceolate, acute to rarely rounded, 4–6,5 mm long; anther semipendent, 1,5 mm long; rostellum simple, 1 mm tall; stigma simple, not as tall as the rostellum.

Diagnostic features. Flowers with the lateral sepals 6–7 mm long; spur 10 – 20 mm long, slender, acute; lip lorate; bracts with an obvious reticulate venation; leaves generally linear-lanceolate, erect, about 8.

Flowering time: November and December.

Monadenia reticulata occurs occasionally in seasonally damp places in the western Cape Province, often after fire, between sea level and 1 700 m. It also extends eastwards along the mountains to George (Fig. 13).

CAPE.—3318 (Cape Town): Table Mountain, 700 m (–CD), Dec. 1879, *Bolus 4542* (BOL). 3320 (Montagu): Grootvadersbosch, Heidelberg (–DD), Dec. 1958, *Barker 8838* (NBG). 3322 (Oudtshoorn): Montagu Pass, 600 m (–CD), Nov. 1894, *Schlechter 5791* (BOL; Z).

This species has for some time been confused with *M. macrostachya* (Schlechter, 1901; Bolus, 1913), but it may be separated by the spur which is longer than the dorsal sepal, the laxer inflorescence and the narrower leaves. From the rest of the *Monadenia* species with slender spurs it is distinct by the papery bracts, which clearly display the venation in the dried state, the greenish flowers and the erect linear-lanceolate leaves.

The collections all appear to be from sandy soil derived from Table Mountain Sandstone. Most of the collections are from areas where at least some precipitation occurs in the summer months, even if only from cloud derived from south-east winds.

9. **Monadenia comosa** *Reichb. f.* in Linnaea 20: 687 (1847); Kraenzl., Orch. Gen. Sp. 1: 813 (1900); Rolfe in Fl. Cap. 5, 3: 194 (1913). Type: Cape of Good Hope, *Gueinzius* s.n. (W, holo.!).

Disa comosa (Reichb. f.) Schltr. in Bot. Jb. 31: 206 (1901); H. Bol., Icones Orch. Austro-Afr. 3: t. 43 (1913).

Monadenia rufescens Lindl., Gen. Sp. Orch. 356 (1838), non Thunb. *Disa affinis* N. E. Br. in Gdnrs' Chron. 24: 402 (1835), nom. nov. Lectotype: Cape Province, near Genadendal, *Drège* 1252 (K, holo.!).

Icon: H. Bol., Icones Orch. Austro-Afr. 3: t. 43 (1913), as *Disa comosa.*

Plants erect or subflexuose, 80–300 (–600 mm tall; tubers slender cylindrical, up to 50 mm long, basal sheaths hyaline, obtuse, 1–2; leaves variable the basal 2 (–3) elliptic to rarely narrowly elliptic, ob-

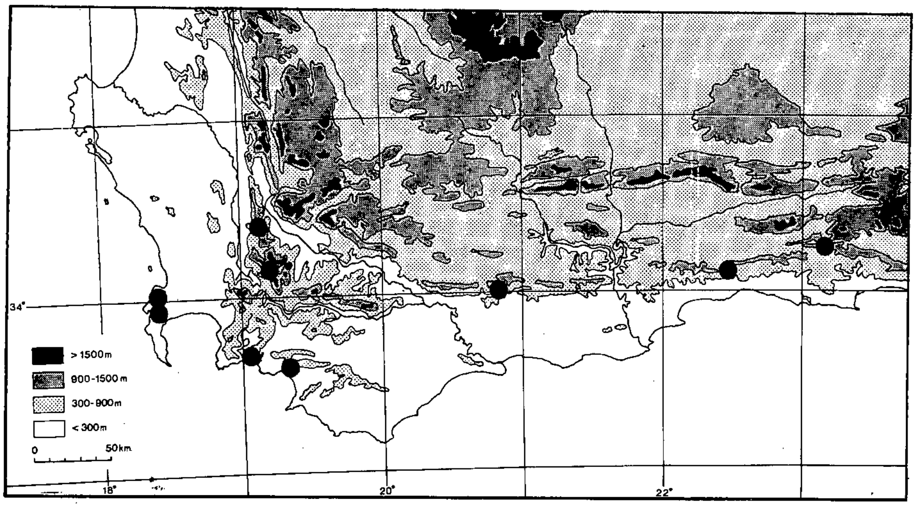

FIG. 13.—Distribution of *Monadenia reticulata.*

tuse, semi-erect, 30–70–120 (–170) mm long, the remaining leaves closely sheathing the stem, acute, lax to imbricate, similar to the floral bracts; inflorescence slender, usually lax, 40–150 mm long, with 1–20 flowers; ovaries erect, 15–20 mm long; bracts slightly shorter than the ovaries, narrowly ovate to rarely ovate, acute to acuminate, venation reticulate and visible. *Flowers* lime-green, occasionally tinted red; dorsal sepal erect to somewhat curved forwards, shallowly galeate, oblong, obtuse to rounded, 9–11 mm tall and c. 1 mm deep; spur pendent from the base of the galea, slender cylindrical, acute, adpressed to the ovary, 17–24 mm long and c. 1,5 mm in diameter; lateral sepals patent to reflexed, obliquely oblong-ovate, obtuse, 6–7 mm long; petals obliquely ovate-narrowly oblong, obliquely retuse to emarginate, 6–8 mm long, the broad basal part enclosing the anther and the narrower apical part curved forwards; lip elliptic, decurved, obtuse to acute, subfleshy, 6–8 mm long; anther semipendent, 2 mm long; rostellum simple, 2 mm tall; stigma as tall as the rostellum. Fig. 14.

Diagnostic features. Spur slender, acute, 17–24 mm long: bracts with the venation visible; stigma as tall as the rostellum; petals lime-green; basal two leaves spreading, the remaining leves closely sheathing the stem.

Flowering time: (September–) October (–November).

A widespread and often common green flowered orchid in rock crevices and on ledges (Fig. 15).

CAPE.—3319 (Worcester): Slab Peak, Michell's Pass (–BA), Oct. 1941, *Compton 11955* (NBG). 3318 (Cape Town): rock crevices on Table Mountain (–CD), Oct 1883, *MacOwan & Bolus 170* (BM: BOL; G; K; P; W; ZT). 3419 (Caledon): Kanonkop, above Greyton, 1500 m (–BA), Jan. 1964), *Oliver* s.n. (BOL). 3322 (Oudtshoorn): summit of Swartbergpas (–AC), Dec. 1977, *Linder 1740* (BOL).

Reichenbach described *M. comosa* from a Gueinzius collection. In the Reichenbach collection at Vienna there is a single specimen of *M. comosa* collected by Gueinzius, but it is labelled *'Monadenia rufescens'*. However, this annotation is not in Reichenbach's hand, and *M. rufescens* is the name that Lindley (1838) applied to this taxon. This sheet is likely to be the holotype.

Lindley mistook the identity of Thunberg's *Satyrium rufescens,* and described it as being: 'foliis radicalibus binis oblongis, caule vaginato', a character unique to *M. comosa*. Of the two collections cited by Lindley, one, *Drège* 1252, fits his description, and the other is referable to *Monadenia rufescens* (Thunb.) Lindl. in the correct sense.

Reichenbach proposed the name *M. comosa* for the species, but he did not refer to Lindley's work. The name is therefore not a *nomen novum,* and the type is the Gueinzius collection. In 1885 N. E. Brown proposed *Disa affinis* as a *nomen novum* for *M. rufescens* Lindl. non Thunb., apparently unaware of the identity of *M. comosa* Reichb. f. This confusion was resolved by Durand & Schinz (1894).

Monadenia comosa belongs to the group of species in *Monadenia* with long slender spurs. It may be separated from the other species in this group by the two or three large spreading narrowly ovate basal leaves, the dry papery floral bracts and the pale green flowers.

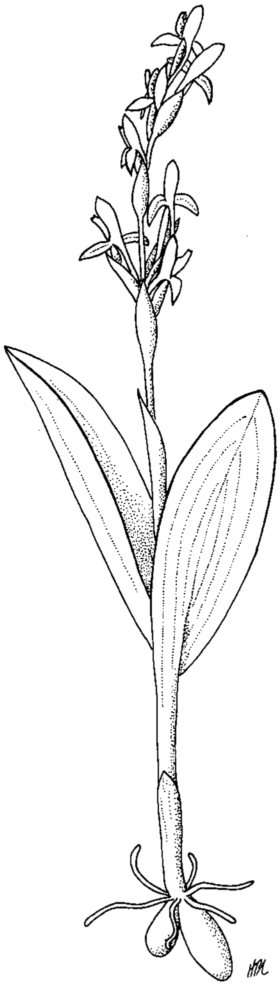

FIG. 14.—*Monadenia comosa,* from *Esterhuysen* 16200, × 0, 5.

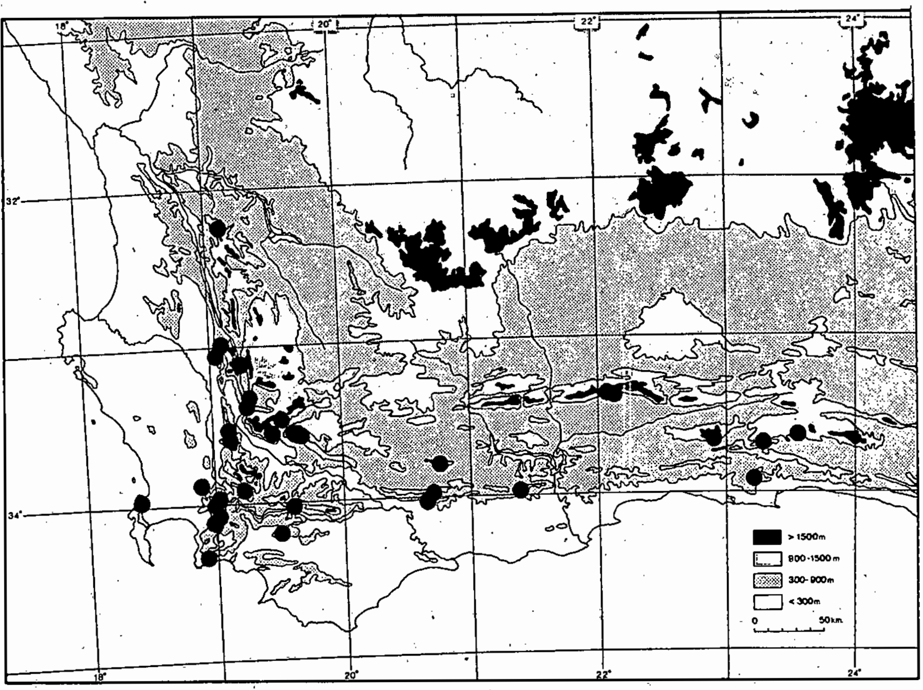

FIG. 15.—Distribution of *Monadenia comosa*

This species is widespread in the mountains of the western and southern Cape Province, where it occurs almost exclusively in crevices and on ledges on rocks and cliffs, often in half-shade. A few collections are from talus slopes e.g. *Linder* 1601. In general, populations consist of numerous individuals, often forming almost monospecific associations on rock ledges. On the summit of the Swartberg at Oudtshoorn, plants occur in gravelly soil (*Linder* 1740).

The altitude range of the species is from near sea level to 1 600 m, although the majority of the collections are from below 1 000 m. Rainfall over the distribution range varies considerably from an all-the-year rainfall in the Knysna area, to summer drought conditions in the western Cape area.

10. **Monadenia bolusiana** (*Schltr.*) *Rolfe* in Fl. Cap. 5,3: 194 (1913). Type: Cape Province, Cape Peninsula, Table Mountain, *Bodkin* in BOL 4903 (BOL, lecto.!; K!).

Disa bolusiana Schltr. in Bot. Jb. 24: 426 (1898); Schltr. in Bot. Jb. 31: 207 (1901).

Icon: H. Bol., Icones Orch. Austro-Afr. 2: t. 90 (1911).

Plants erect, (100–) 200–300 mm tall; basal sheaths hyaline, obtuse; leaves imbricate, the lower 2–5 narrowly oblong, acute, semi-erect, flat, the largest 50 (–70) mm long, grading gradually into the sheathing, narrowly ovate, acute upper leaves; inflorescence subimbricate, occasionally secund, 30–130 mm long and with 2–25 flowers; ovaries 15–20 mm long, erect; bracts about as long as the ovaries, narrowly ovate, acute, the reticulate venation usually visible. *Flowers* lime-green, occasionally tinted red; dorsal sepal erect, curved forwards, shallowly galeate, oblong, obtuse to rounded, 8–11 mm long and c. 1 mm deep; spur pendent from the base of the galea, slender, acute, 16–22 mm long and about 1 mm in diameter; lateral sepals reflexed, oblong, rounded, 6–8 mm long; petals obliquely ovate-narrowly oblong, obliquely emarginate, 6–8 mm long, the broad basal part enclosing the anther, the narrower apical part erect; lip patent or recurved, elliptic, obtuse to acute, subfleshy, 5–7 mm long; anther semipendent, 1,5–2 mm long; rostellum erect, 1,5 mm tall; stigma as tall as rostellum. Fig. 16.

Diagnostic features. Spur slender, acute, 16–22 mm long; petals lime-green, stigma as tall as the rostellum; lower cauline leaves larger than the upper, but gradually grading into them; plants flowering in December and January.

Flowering time: (October–) December–January.

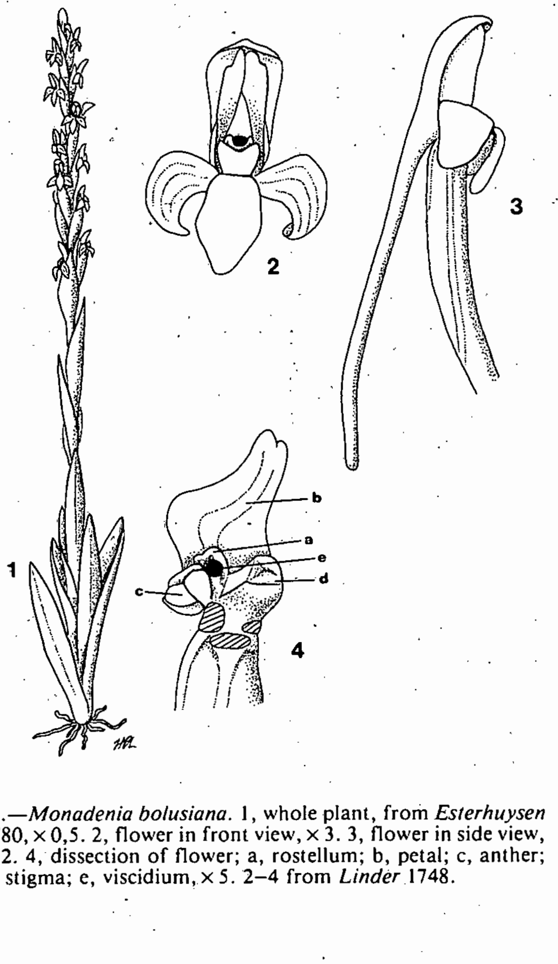

FIG. 16.—*Monadenia bolusiana*. 1, whole plant, from *Esterhuysen* 9780, × 0,5. 2, flower in front view, × 3. 3, flower in side view, × 2. 4, dissection of flower; a, rostellum; b, petal; c, anther; d, stigma; e, viscidium, × 5. 2–4 from *Linder* 1748.

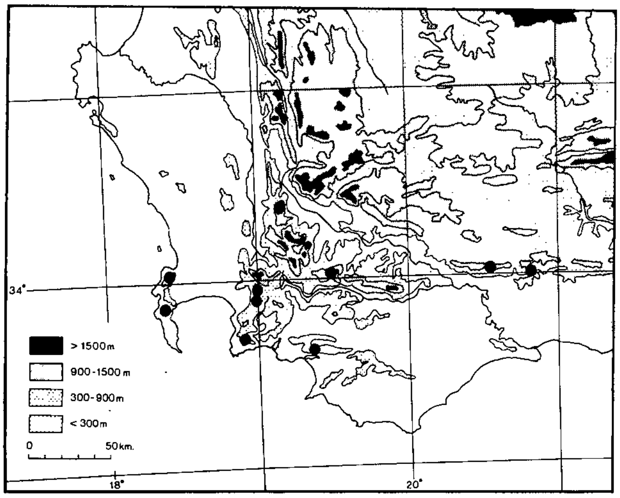

FIG. 17.—Distribution of *Monadenia bolusiana.*

Monadenia bolusiana is a small dark green to even purplish herb that occurs occasionally to frequently in exposed gravelly soil on the summit of the mountains in the western Cape Province (Fig. 17).

CAPE. — 3419 (Caledon). Betty's Bay, Harold Porter Nature Reserve, east slope of Voorberg, 200 m (–BD), Nov. 1970, *Ebersohn 151* (NBG). 3320 (Montague): Strawberry Hill (–DD), Dec. 1957, *Stokoe in CH 9904* (NBG).

Schlechter (1898) cites three collections after his description of *Disa bolusiana: Zeyher* 1570 and *Bolus* 4903 from Maclear's Beacon on Table Mountain and *Schlechter* s.n. from the Langeberg above Zuurbraak near Swellendam. It is likely that these collections were in Schlechter's herbarium in Berlin that was destroyed in World War II. In BOL there is an excellent duplicate of *Bolus* 4903, and that is selected here as the lectotype. However, there are two collections under that number. The first one is a *Bodkin* collection, made in January 1883, while the second is a Scully collection, made in January 1884. The illustration for the Icones was made from the second collection, while Schlechter specified the first collection as the type ('Bolus n. 4903, bluehend im Januar 1883').

This species is closely allied to *Monadenia comosa* by virtue of the long slender spur, green flowers and papery bracts. It may be separated from this species by the numerous cauline leaves, the purplish colour of the plants and the flowering season (November to January).

Monadenia bolusiana occurs mostly in the full sunlight on the summit ridges of mountains, in shallow gravelly soils, often in footpaths and other disturbed areas. At present there are rather few herbarium records of this species, but this might be due to undercollecting in these more or less inaccessible localities. Fieldwork has revealed it to occur at least occasionally, and possibly even frequently and widespread, in the summit zones of the ridges. The altitudinal range of the species is from 200 m in the Betty's Bay area to over 1 200 m in the Langeberg and Hottentots Holland Mountains. Over the whole range there is a certain amount of moisture available in the summer months from condensation from the 'south-easter' clouds.

11. **Monadenia atrorubens** (*Schltr.*) *Rolfe* in Fl. Cap. 5, 3: 196 (1913). Type: Cape Province, Clanwilliam, Zwartboschkraal, *Schlechter* 5167 (B, holo. †; BOL!; Z!).

Disa atrorubens Schltr. in Bot. Jb. 24: 427 (1898); Schltr. in Bot. Jb. 31: 205 (1901).

Monadenia ophrydea Lindl. sensu Kraenzl., Orch. Gen. Sp. 1: 817 (1900), pro parte.

Plants 100–400 mm tall, suffused with beetroot-red; tubers 15 – 20 mm long, acute; basal sheaths hyaline, acute or obtuse, about 20 mm long, occasionally much longer; cauline leaves green, narrowly lanceolate to lanceolate, acute, the longest at the base, up to 90 mm long, semi-erect and sheathing at the base, upper leaves grading into the floral bracts, imbricate to subimbricate, acute; inflorescence slender, lax, (40–) 80–150 (–250) mm long and with (3–) 10–180 (–250) flowers; bracts green, lanceolate to narrowly ovate, acute, reaching the flowers or overtopping them; ovary slender, 15–20 mm long. *Flowers* horizontal, sepals and spur beetroot-red, lip and petals almost black; dorsal sepal narrowly oblong, obtuse, shallowly concave, 7–10 mm long, 3–4 mm wide and c. 1,5 mm deep; spur pendent from the base of the sepal, cylindrical, tapering to an acute apex, parallel to the ovary, 15–30 mm long; lateral sepals reflexed at anthesis, narrowly oblong, obtuse, 6–8 mm long; petals erect inside the galea, obliquely ovate, subacute, often shallow bidentate, fleshy apically and along the margins with papillae on the inside margin surface, 5–7 mm long and 3–5 mm wide; lip oblong to narrowly oblong, rounded, fleshy, horizontal basally but soon decurved, 5–7 (–8) mm long and 2–4 mm wide; rostellum erect, c. 1,5 mm tall with short lateral lobes flanking the caudicles; anther semipendent, 1–1,5 mm long, the single viscidium a large disc; stigma c. 2 mm in diameter, on a pedicel as tall as the rostellum and angled forwards. Fig. 18

Diagnostic features. Plants suffused with beetroot-red in fresh state, reddish brown when dry, spur slender, up to 30 mm long, lip oblong to narrowly oblong, lateral sepals purple to beetroot-red, reflexed.

Flowering time: August–October.

The plants, suffused with beetroot-red, form small populations in sandy areas, where they may be seen in flower the first year after a fire. (Fig. 19).

CAPE.–3119 (Calvinia): between Oorlogs Kloof and Papkuilsfontein. (–AC), Sept. 1939, *Leipoldt 3236* (BOL). 3318 (Cape Town): Pella Mission, common on sandflats after fire (–DA), Sept. 1977, *Linder 1140* (BOL).

This species appears to be restricted to sandy areas in the western Cape Province between Houw Hoek and Calvinia, from near sea level to about 1 000 m in the northern end of the distribution area. Two populations were studied in the field (*Linder* 1140 & 1129). Both flowered the first year after the fire, and occurred on slightly seasonally damp deep sand. The populations were clearly defined, and within the area the species occurred frequently. Among the burnt twigs and branches the purplish red plants were scarcely visible. Despite extensive field work in the western Cape, no plants were found in unburnt vegetation.

Over the whole distribution range the summers are dry, and in the winter 500–800 mm rain falls.

The differences between this species and *M. ophrydea* are discussed above.

12. **Monadenia ophrydea** *Lindl.,* Gen. Sp. Orch. 358 (1838); Kraenzl. Orch. Gen. Sp. 1: 817 (1900); Rolfe in Fl. Cap. 5, 3: 195 (1913). Type: Cape Province, Paarl, Drakenstein Mountains, *Drège* 8290 (K, holo.!).

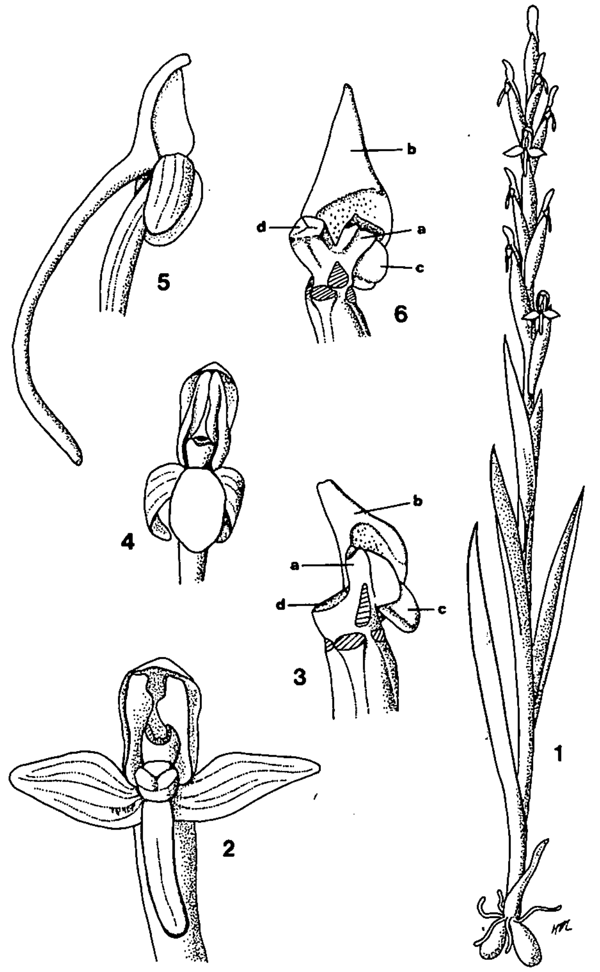

FIG. 18.—*Monadenia ophrydea* (1–3) and *M. atrorubens* (4–6). 1, plant of *M. ophrydea*, from *Esterhuysen* 10573, ×0, 5. 2, front view of flower, ×3. 3, dissection of flower, ×5. (2–3 from *Linder* 1596.) 4, front view of flower of *M. atrorubens*, ×3. 5, side view of flower, ×3. 6, dissection of flower, ×5: a, rostellum; b, petal; c, anther; d, stigma. (4–6 from *Linder* 1129.)

Disa ophrydea (Lindl.) H. Bol. in Trans. S. Afr. phil. Soc. 5: 142 (1888); Schltr. in Bot. Jb. 31: 204 (1901).

Brownleea pentheriana Kraenzl. ex Zahlbr. in Ann. Nat. Hofmus. Wien 20: 6 (1905). Type: Cape Province, Montagu Pass, *Penther* 189 (W, holo.!).

Plants slender, up to 400 mm tall, suffused with beetroot-red tubers 10–20 mm long; basal sheaths 1–2, hyaline, obtuse or acute, 1 (–3) mm long; leaves green, narrowly lanceolate, acute, rarely obtuse, the largest near the base of the stem, up to 100 mm long and 20 mm wide, usually imbricate; inflorescence lax, up to 300 mm long with (1–) 5–15 (–30) flowers; bracts purplish-green, ovate to shortly acuminate, 20–40 mm long and 15–25 mm wide, generally as tall as the flowers; ovaries 20–25 mm long. *Flowers* horizontal, purple-red, the lateral sepals paler and often white; dorsal sepal oblong-obovate, shallowly galeate, rounded, 9–11 mm long, 5–7 mm wide and 1–2 mm deep; spur pendent from the base of the dorsal sepal, slender, tapering to an acute apex, slightly curved towards the ovary, 20–24 mm long; lateral sepals spreading, narrowly ovate, acute, rarely somewhat reflexed, much paler than the rest of the flower, 8–10 mm long; petals erect inside the galea, very obliquely ovate, acute with a shallowly emarginate apex, falcate in side view, somewhat curved around the rear of the anther, the apex and anterior margins fleshy; lip narrowly elliptical to almost lorate, subacute to acute, fleshy, pendent, 8–10 mm long; rostellum simple, flanking the caudicles, c. 3 mm tall; anther semipendent, c. 4 mm long, pollen-masses almost globular, viscidium almost globular, 0,8 mm in diameter; stigma equally tripulvinate, c. 1, 5 mm in diameter, about ½ as tall as the rostellum. Fig. 18.

Diagnostic features. Plant suffused with a beetroot-red when fresh, reddish brown when dry, spur slender, up to 24 mm long, lateral sepals reddish and white, spreading, lip narrowly elliptical to lorate.

Flowering time: October and November.

A slender herb, suffused with beetroot-red, occurring usually in extensive populations in recently burnt veld on mountain sides, in damp conditions, in the western and southern Cape Province (Fig. 19).

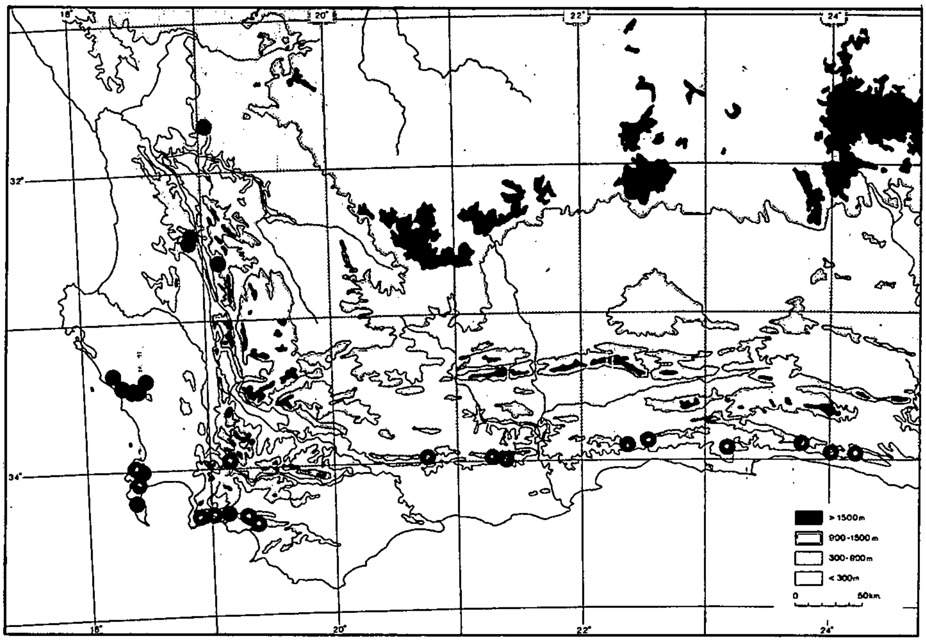

FIG. 19.—Distribution of *Monadenia atrorubens* (solid circles) and *Monadenia ophrydea* (open circles).

CAPE.–3318 (Cape Town): damp grassland on Table Mountain, 700 m (–CD), Oct. 1879, *Bolus 4538* (BOL). 3323 (Willowmore): Outeniqua Mountains near Joubertina (–DD), Dec. 1946, *Esterhuysen in BOL 23635* (BOL).

Several populations of this distinct species have been studied over the length of the distribution range. Generally the populations are extensive with numerous individuals, occurring on damp peaty mountain slopes facing the coast and consequently the rain-bearing winds. This species, as in *M. atrorubens,* appears to flower only after fire, when the beetroot-red plant colour is cryptic in the burnt-out vegetation. The altitude range is from near sea level in the Betty's Bay (Caledon) area to more commonly 300 – 1 000 m in the Langeberg and eastwards to Humansdorp. Over the whole distribution range, the species receives some precipitation throughout the year: in the east from the all-the-year rains and in the west from condensation or occasionally rain from the 'south-easter' clouds.

For the differences from *M. atrorubens,* see above.

13. **Monadenia rufescens** (*Thunb.) Lindl.,* Gen. Sp. Orch. 356 (1838); Kraenzl., Orch. Gen. Sp. 1: 818 (1900). Type: Cape of Good Hope, *Thunberg* in herb. Thunberg 21456 (UPS; holo.!; W!).

Satyrium rufescens Thunb., Prod. 5 (1794). *Disa rufescens* (Thunb.) Swartz in Vet. Acad. Handl. 21: 210 (1800); Schltr. in Bot. Jb. 31: 209 (1901). *Monadenia lancifolia* Sond. in Linnaea 19: 100 (1847), nom. nov.

Monadenia macrocera Lindl., Gen. Sp. Orch. 358 (1838); Rolfe in Fl. Cap. 5, 3: 193 (1913). Type: Cape of Good Hope, *Thom* s.n. (K, holo.!).

Monadenia leptostachya Sond. in Linnaea 19: 101 (1847). Type: Cape Province, Cape Peninsula near Wynberg, *Ecklon & Zeyher* s.n. (S, holo.!; P!; W!).

Icon: H. Bol., Icones Orch. Austro-Afr. 2: t. 89 (1911).

Plants erect, 140–235–400 mm tall; tubers testicular, 20 mm in diameter; base of the stem often with the remnants of old leaf fibres; basal sheaths hyaline, grading into the leaves; leaves imbricate, the largest leaves near the base of the stem, narrowly lanceolate, to linear, acute, 50–70 mm long, conduplicate, gradually smaller and more sheathing towards the apex of the stem, grading into the floral bracts; inflorescence a slender spike, 30–150 mm long and 15 mm in diameter, with 2–25 flowers; ovaries 10–15 mm long; bracts usually slightly longer than the ovaries, narrowly ovate, acuminate, dark green, imbricate and partially obscuring the flowers. *Flowers* lime-green with dark purple petals and lip; dorsal sepal angled forwards, shallowly galeate, oblong, obtuse to rounded, 9–11 mm long and c. 1 mm deep; spur pendent from the base of the galea, slender cylindrical, acute, 10–16 mm long; lateral sepals erect or patent, oblong, obtuse, 6–8 mm long; petals obliquely narrowly oblong, obliquely truncate, wider at the base, subfleshy, concave, 6–7 mm long, the broad basal part enclosing the anther, the narrowly oblong apical part forming a tube with the dorsal sepal; lip decurved, narrowly oblong, obtuse, 6–7 mm long; anther semipendent, 1,5 mm long, viscidium elongated backwards with a longitudinal dorsal groove; rostellum c. 1 mm tall; stigma pedicellate, not as tall as the rostellum. Fig. 20.

Diagnostic features. Flowers with the lateral sepals 6–8 mm long, spur slender acute, 10–16 mm long; floral bracts prominent, green; leaves gradually grading from large at the base to sheathing at the apex; stigma lower than the rostellum.

Flowering time: (September–) October (–November).

Monadenia rufescens is a slender herb that occurs occasionally in seasonally damp localities in the western Cape Province, between sea level and 1 000 m (Fig. 21).

CAPE.–3318 (Cape Town): Lower Plateau of Table Mountain, 750 mm (–CD), Oct. 1884, *Bolus 4969* (BOL). 3418 (Simonstown): Vlakkenberg vlei, 600 m (–AB), Oct. 1947, *Compton 20180* (NBG). 3419 (Caledon): flats east of Viljoenspass (–AA), Sept. 1949, *Stokoe in SAM 61250* (SAM).

The nomenclatural history of this species is complex. The type of *Satyrium rufescens,* although not in a good condition, is clearly recognizable. However, Lindley (1838) misidentified *Satyrium rufescens* Thunb. ('I know no plant to which the definitions of Swartz and Thunberg exactly apply'). His description of *Monadenia rufescens* (Thunb.) Lindl. applies to *Drège* 1252, and must be referred to *M. comosa* Reichb. f. However, the combination *Monadenia rufescens* (Thunb.) Lindl. is valid, and has to be used for *M. rufescens* sensu Thunb. Ironically, the other

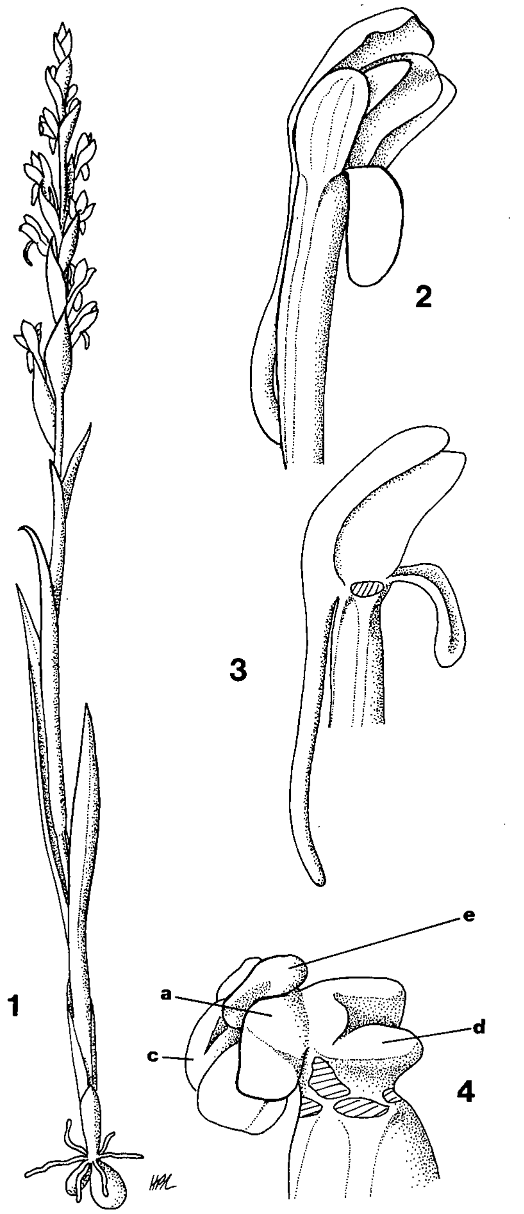

FIG. 20.—*Monadenia rufescens.* 1, whole plant, from *Salter* 8479, ×0,5. 2, flower in angled front view, ×3. 3, flower in side view with the lateral sepal removed, ×3. 4, column, ×10: a, rostellum; c, anther; d, stigma; e, viscidium. (2–4 from *Linder* 1610.)

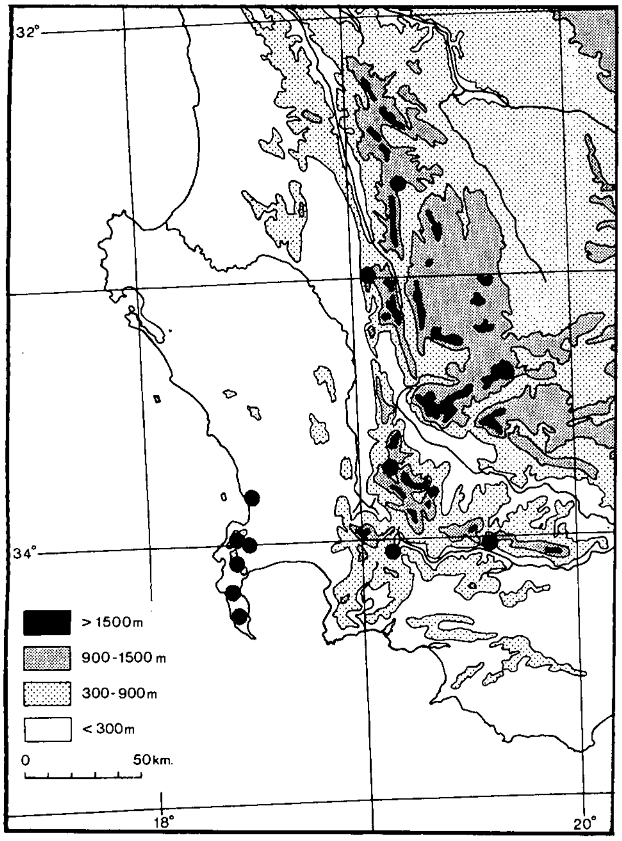

FIG. 21.—Distribution of *Monadenia rufescens*.

collection cited by Lindley is clearly *Satyrium rufescens* Thunb. Sonder (1847) noted that *Monadenia rufescens* Lindl. is not the same as *Disa rufescens* (Thunb.) Swartz. He upheld the former, and proposed *Monadenia lancifolia* as a *nomen novum* for the latter. Lindley (1838) had also received a specimen of the true *Satyrium rufescens* Thunb., and named it *Monadenia macrocera* (1838). This name was used by Rolfe (1913), who followed the 'Kew Rule'. Sonder (1847) also proposed another name, *Monadenia leptostachya* for the species which he separated from *M. lancifolia* on several characters. Examination of the types indicated that these names all apply to the same taxon.

Monadenia rufescens is systematically relatively isolated within the group of slender long-spurred species of *Monadenia*. The dorsal sepal and petals are angled forwards and are applied to each other to form a tube leading over the rostellum into the spur. The rostellum is higher than the stigma and the single large viscidium is elongated backwards. Consequently it has a large surface exposed to the proboscis of an insect probing into the spur. The viscidium also has a longitudinal dorsal groove, which may also be related to this pollination syndrome. Further the species may be distinguished by the leathery bracts and the purple petals and lip.

Although *M. rufescens* is relatively widespread in the western Cape Province, it does not appear to be common at any locality and plants frequently appear to occur singly. The majority of collections are from slightly damp localities in a variety of habitats, ranging from dunes to rocky mountain sides at about 1 000 m. Although the distribution range covers an area of summer drought, many of the sampled localities must receive at least some moisture condensed from the 'south-easter' clouds.

This species is not well known, and more field data could cast some light on its ecological requirements.

Sect. **Monadenia**

Spur longer or shorter than the dorsal sepal, clavate; flowers relatively large, sepals 7 – 14 mm long; inflorescence generally dense.

Type species: *Monadenia brevicornis* Lindl.

This section of three species is clearly defined by the swollen or clavate spurs, the larger flowers and the more robust plants. Only *M. brevicornis* approaches *M. reticulata* in some populations.

The three species replace each other geographically, with narrow overlap zones. M. physodes occurs between the Kamiesberg in Namaqualand and the Cape Peninsula. *M. cernua* extends from the Cape Peninsula to Humansdorp, whereas *M. brevicornis* is widespread in montane grasslands in southern Africa, reaching as far south-west as Knysna. Although the vast majority of the collections are readily distinguished on morphological features, there are some intermediate collections between *M. physodes* and *M. cernua* and between *M. brevicornis* and *M. reticulata.*

M. physodes and *M. cernua* are readily distinguished by the relative spur length (Fig. 22). However, some of the collections from the overlap zone on the Cape Peninsula are rather difficult to assign to one of the two species, whereas others do not present any difficulty (i.e. *Le Sueur in BOL* 4973). One of the intermediate collections is the type collection of *M. inflata* Sond. An analysis of several flowers from this collections indicated that it is best placed under *M. cernua.*

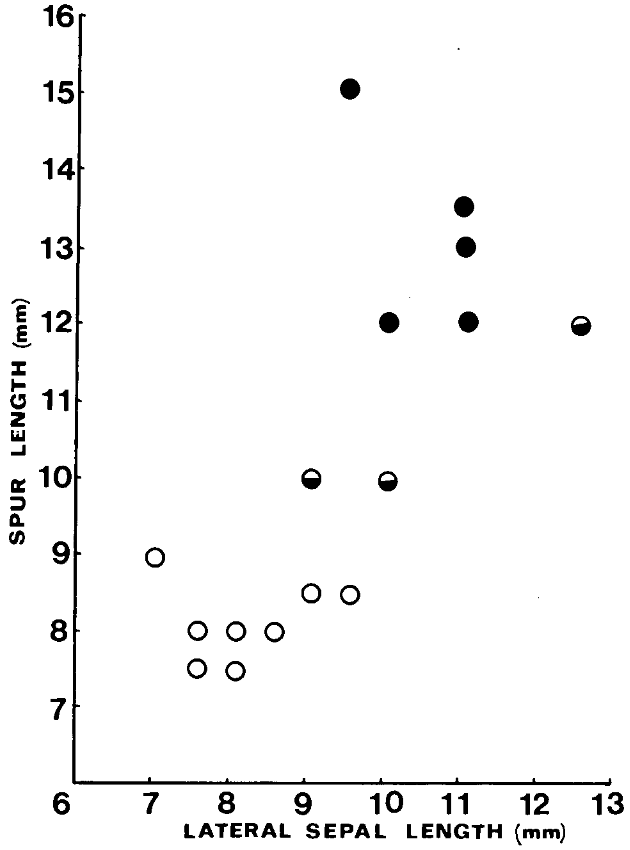

FIG. 22.—Variation in the relative spur length in *Monadenia physodes* and *M. cernua*. The solid circles represent *M. cernua* and the open circles *M. physodes*. The half-solid circles represent two collections from the Cape Peninsula that are intermediate between the two taxa, one of which is the type collection of *Monadenia inflata*.

There are no intermediate forms in the overlap zone between *M. cernua* and *M. brevicornis* — as though the morphological differences between the two taxa are accentuated in this area, with collections of *M. cernua* with longer spurs than is usually found in this species.

However, the southernmost populations of *M. brevicornis* approach *M. reticulata*. Generally these two taxa are separated by the wider and more robust cauline leaves and more inflated spurs of *M. brevicornis*. In collections from the Uniondale area (*Esterhuysen* 10692) the leaves are narrower, more clustered towards the base of the stem, and the spurs are more slender. A possible explanation is hybridization between these two taxa, with introgression into *M. brevicornis*.

14. **Monadenia physodes** (*Swartz*) *Reichb. f.* in Flora 66: 461 (1883); Rolfe in Fl. Cap. 5, 3: 191 (1913). Type: Cape of Good Hope, *Thunberg* in herb Thunberg 21455 (UPS, holo.!).

Disa physodes Swartz in Vet. Acad. Handl. 21: 211 (1800); Thunb., Fl. Cap. 12 (1823); Lindl., Gen. Sp. Orch. 356 (1838); Kraenzl., Orch. Gen. Sp. 1: 788 (1900).

D. cernua (Thunb.) Swartz, Schltr. in Bot. Jb. 31: 210 (1901), pro parte.

Plants robust, 250–600 mm tall; tubers up to 40 mm long; basal sheaths hyaline, obtuse, 1–2; leaves linear-lanceolate, acute, conduplicate, falcately erect, the longest at the base, 140–200 mm long and c. 20 mm wide, grading apically into the foral bracts; inflorescence cylindrical, 50–300 mm long and 30–40 mm in diameter, flowers subimbricate; ovaries c. 15 mm long; bracts as long as the flowers, narrowly ovate, acuminate. *Flowers* with lime-green sepals, often mottled or suffused maroon, petals lime-green; dorsal sepal shallowly galeate, oblong, obtuse erect, 9–11 mm tall and c. 1 mm deep; spur pendent from the base of the galea, clavate, rounded, 7–9 mm long and 3–6 mm wide, adpressed to the ovary; lateral sepals reflexed, oblong, obtuse to rarely acute, 7–10 mm long; petals obliquely narrowly ovate-oblong, bluntly acuminate or obliquely retuse, 7–9 mm long, the broad basal part enclosing the anther and the narrower apical part twisted to face out of the galea; lip pendent, lorate to narrowly oblanceolate, rounded, 7–10 mm long; anther semipendent, 2 mm long; rostellum lateral lobes large, flanking the anther, 2 mm tall, stigma on a 1 mm tall pedicel, horizontal, lateral lobes much larger than the central lobe.

Diagnostic features. Flowers with the lateral sepals 7–10 mm long; spur clavate, rounded, 7–9 mm long, rostellum up to 2 mm tall.

Flowering time: September–October.

This robust herb occurs in the western Cape Province, mostly in swampy localities, but at least one record is from a dry slope after a fire (Fig. 23).

Cape.—3018 (Kamiesberg): Leliefontein, Little Namaqualand (–AB), Oct. 1940, *Leipoldt 3809* (BOL). 3318 (Cape Town): about 6 km north of Malmesbury (–BC), Oct. 1964, *Rabinowitz in NBG 77143* (NBG); lower slopes of Lions Head near Sea Point, 80 m (–CD), Sept. 1884, *Le Sueur in BOL 4973* (BOL).

Thunberg (1794) regarded this species as synonymous with *M. cernua*, as he cites both in his protologue. *M. physodes* was only separated by Swartz in 1800. In general, the distinction between the two taxa has been recognized, except for Schlechter (1901), who regarded *M. physodes* merely as a smaller form of *M. cernua*.

This species is unique because of its strongly clavate spur which is shorter than the dorsal sepal. It is clearly allied to *M. cernua*, but may readily be distinguished by the relatively short spur and the peculiar rostellum with massive lateral lobes flanking the anther.

I have not seen any populations of this peculiar species in the wild, and collectors notes do not indicate the habitat. Oliver (*Oliver* 4761) reports that near Ceres the species flowered in sandy stony flats after a fire.

The altitude range of the species is from near sea level at Sea Point, to over 1 000 m in some inland localities. Many of the localities of herbarium collections are now disturbed, and the number of populations of the species must be much reduced from that of a century ago. The distribution range of the species falls in an area of summer drought and total rainfall values of 500–800 mm p.a.

There are two records of an unpleasant mouse-like scent.

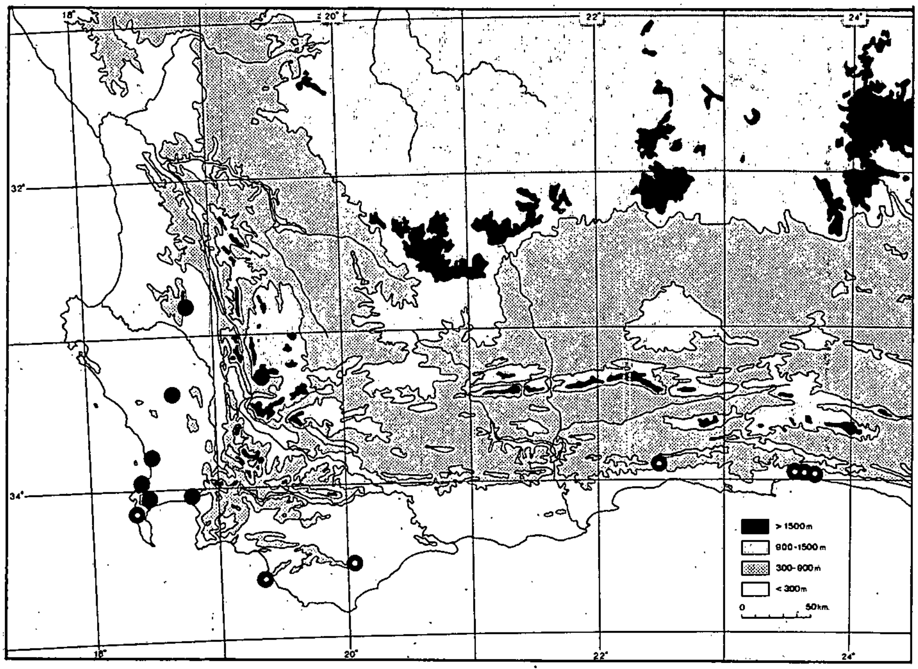

Fig. 23.—Distribution of *Monadenia physodes* (solid circles) *Monadenia cernua* (open circles).

15. **Monadenia cernua** (*Thunb.*) *Dur & Schinz,* Consp. Fl. Afr. 5: 111 (1894); Kraenzl., Orch. Gen. Sp. 1: 815 (1900); Rolfe in Fl. Cap. 5, 3: 192 (1913). Type: Cape of Good Hope, *Thunberg* in herb. Thunberg 21431, 21432 (lecto.), 21433 (all UPS!).

Satyrium cernuum Thunb., Prodr. Pl. Cap. 5 (1794). *Disa cernua* (Thunb.) Swartz in Vet. Acad. Handl. 21: 211 (1800); Thunb., Fl. Cap. 12 (1823); Lindl., Gen. Sp. Orch. 356 (1838); Schltr. in Bot Jb. 31: 210 (1901), excl. *M. physodes.*

Disa prasinata Ker-Gawl. in Edwards's bot. Reg. t. 210 (1817). *Monadenia prasinata* (Ker-Gawl.) Lindl., Gen. Sp. Orch. 358 (1838). Type: Edwards's bot. Reg. t. 210 (1817), iconotype.

Monadenia inflata Sond. in Linnaea 19: 102 (1847). Type: Cape Province, Cape Peninsula near Wynberg, *Ecklon & Zeyher* s.n. (S, holo.!; BOL!; K!; P!; SAM!; W!; Z!).

Icones: Edwards's bot. Reg. t. 210 (1817); H. Bol., Icones Orch. Austro-Afr. 2: t. 91 (1911), as *Disa cernua.*

Plants robust, 200–600 mm tall; basal sheaths hyaline, obtuse, 1–2; leaves linear-lanceolate, acute, conduplicate, imbricate, the largest at the base, (100–) 140–200 mm long and 15–20 mm wide, grading apically into the floral bracts; inflorescence 100–250 mm long and 30–40 mm in diameter, flowers subimbricate; ovaries c. 15 mm long; bracts as tall as the flowers, narrowly ovate, subacuminate. *Flowers* with cream-green sepals, mottled maroon, and lime-green petals and lip; dorsal sepal shallowly galeate, slightly angled forwards, oblong, obtuse, 10–14 mm long and c. 1 mm deep; spur pendent from the base of the galea, clavate, rounded, 11–17 mm long and 3–5 mm wide, adpressed to the ovary; lateral sepals reflexed, narrowly oblong to oblong, acute to obtuse, 9–13 mm long; petals subobliquely narrowly ovate–oblong, bluntly acuminate to obliquely retuse, 7–10 mm long, the broad basal part flanking the anther and the narrow apical part twisted to face out of the galea; lip pendent lorate, rounded, subfleshy, 8–12 mm long; anther subhorizontal, 3 mm long; rostellum with 2–3 mm tall lateral lobes flanking the anterior part of the anther; stigma on a 1 mm tall pedicel, slightly angled forwards, flat, lateral lobes larger than the posterior lobe. Fig. 24.

Diagnostic features. Flowers with the lateral sepals 9–13 mm long; spur clavate, rounded, 11–17 mm long; rostellum with 2–3 mm tall side lobes.

Flowering time: (September–) October (–November).

Monadenia cernua is a tall robust herb that occurs in damp to swampy habitats in the western and southern Cape Province, (Fig. 23) on the flats between the mountains and the sea, from the Cape Peninsula to Humansdorp.

CAPE.—3318 (Cape Town): Rietvalley (–DC), Oct. *Zeyher 1569* (SAM). 3322 (Oudtshoorn): Montagu Pass, George, 400 m (–CD), Oct. 1880, *Young in BOL 5534* (BOL). 3323 (Willowmore): between Keurbooms River and Storms River (–CD), Oct. 1938, *Gillett 4565* (BOL).

Satyrium cernuum Thunb. was based on a mixed type; The discordant element was removed by Swartz and described as *Disa physodes* (1800).

In 1817 Ker-Gawler described *Disa prasinata* from a plant imported from South Africa by a Mr Griffin, who successfully flowered it. The plate in Edwards's Botanical Register has to serve as an iconotype, as no other type material is available. From the illustration it is difficult to decide whether the plant belongs to *M. physodes* or *M. cernua,* but the spur appears to be slightly longer than the dorsal sepal, a character also found in a *Ecklon & Zeyher* collection from Rietvlei near Cape Town. This collection is grouped with *M. cernua. Disa prasinata* is therefore regarded as a synonym of *M. cernua.* The type of *Monadenia inflata* Sond. agrees in all characters with *M. cernua.*

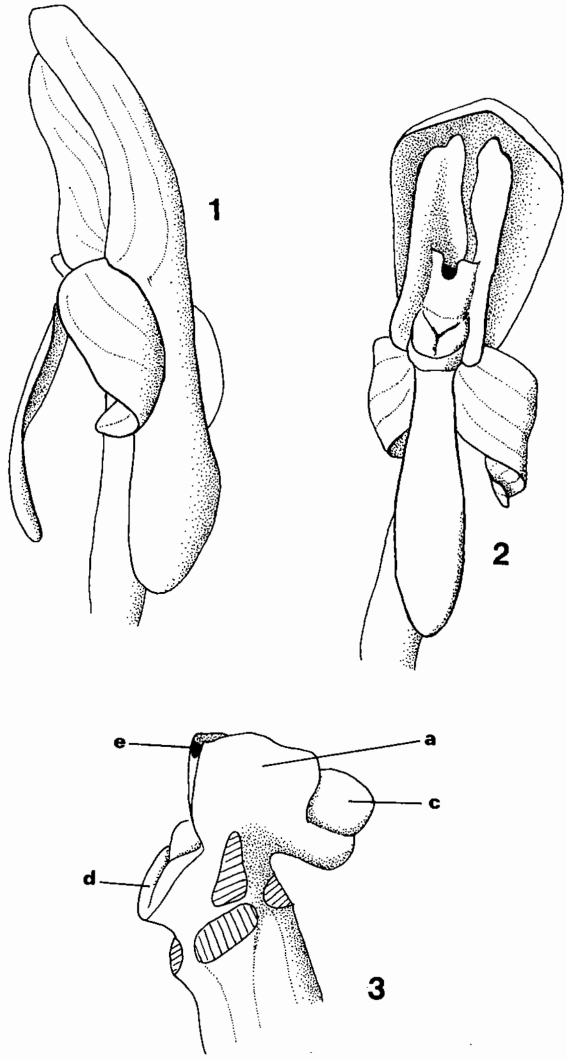

FIG. 24.—*Monadenia cernua.* 1, flower in side view, × 3. 2, flower in front view, × 3. 3, column in side view, × 6: a rostellum; c, anther; d, stigma; e, viscidium. All from *Walters* 536.

This species is closely related to both *M. brevicornis* and *M. physodes,* and to some extent present a morphocline between these two taxa. It may be distinguished from the former by the rounded to obtuse spur, which is straight and not curved towards the ovary, and from the latter by the spur which is longer than the lateral sepal (Fig. 22).

The single population of this species which I studied in the field occurred on the Tsitsikamma coast, in a marshy area along the National Road. In this part of the country there are very few natural habitats still extant. Collectors' notes from the Bredasdorp area indicate that *M. cernua* occurs in damp sandy habitats. No further habitat data are available. One collection from Tsitsikamma (*Bower* 600) was found after fire.

The altitude range of the species is from near sea level at Cape Town, to more commonly between 100 and 300 m above sea level on the coastal flats. The majority of the populations must have been destroyed, as most of the area is under fairly intense cultivation, and in the Knysna area, afforested. Over the whole distribution range at least some summer rainfall occurs. The total rainfall varies from about 600 mm to over 1 000 mm p.a.

16. **Monadenia brevicornis** *Lindl.*, Gen. Sp. Orch. 357 (1838); Kraenzl., Orch Gen. Sp. 1: 816 (1900); Rolfe in Fl. Cap 5, 3: 192 (1913). Type: Cape of Good Hope, *Mund* s.n. (K, holo.!).

Disa brevicornis (Lindl.) H. Bol. in J. Linn. Soc., Bot. 25: 196 (1889); Schltr. in Bot. Jb. 31: 211 (1901).

Icon: H. Bol., Icones Orch. Austro-Afr. 3: t. 40b (1911).

Plants 200–500 mm tall; tubers up to 50 mm long; leaves narrowly lanceolate to rarely narrowly ovate, acute, numerous, imbricate, the largest near the base, up to 150 mm long and grading apically into the floral bracts; inflorescence a lax or cylindrical spike, 40–300 mm tall; ovaries 10–15 mm long, more or less erect; bracts as tall as or overtopping the flowers, narrowly ovate to ovate, acuminate. *Flowers* with lime-green petals and lip, lip with a maroon base, lateral sepals green, dorsal sepal rust-coloured to maroon; dorsal sepal erect, shallowly galeate, obtuse to rounded, apiculate, narrowly obovate to oblong, 7–10 mm tall and c. 1 mm deep; spur pendent with the apex curved towards the ovary, cylindrical, 2–3 mm in diameter and 7–11 mm long; lateral sepals reflexed, oblong, obtuse, apiculate, 5–9 mm long; petals obliquely narrowly ovate to oblong, obliquely retuse, erect and twisted to face forwards, 5–9 mm tall; lip pendent, narrowly oblong, obtuse, 6–8 mm long; anther semipendent, 1,5–2 mm long; rostellum partially flanking the anther with a deep notch to the front containing the viscidium, 1–2 mm tall; stigma with the rear lobe smaller than the lateral lobes shortly pedicellate, horizontal. Fig. 25.

Diagnostic features. Flowers large, lateral sepals 5–9 mm long; spur cylindrical, acute, the apex curved towards the ovary, 7–11 mm long and 2–3 mm in diameter.

Flowering time: November–February.

Monadenia brevicornis is a slender herbaceous orchid, that occurs frequently in montane grassland from the southern Cape Province to southern Malawi and Madagascar (Fig. 26).

CAPE.—3423 (Kynsna): The Crags, Knysna (–AA), Nov. 1949, *Compton 21729* (NBG).

TRANSKEI.—3129 (Port St Johns): Port St Johns (–DA), Oct. 1939, *McLoughlin 403* (BOL).

NATAL.—2930 (Pietermaritzburg): escarpment above the Byrne valley (–CC), Nov. 1975, *Hilliard 5583* (NU).

ZIMBABWE.—Inyanga, Bidford Estate, 1 800 m, March 1958, *Beasley 64* (K; SRGH).

This species is closely allied to *M. cernua,* from which it may be distinguished by the acute spur. From the rest of the genus, the species is distinct, because of its inflated spur, longer than the dorsal sepal, and its distribution in the summer rainfall/winter drought region.

M. brevicornis occurs very widespread in the montane grassland regions of southern Africa. Generally plants are found in slightly damp areas in the grassland. The altitudinal range varies from near the coast in the southern Cape Province (where some populations occur in Cape 'Fynbos' in the Humansdorp, Grahamstown and King William's Town areas), to between 1 300 and 2 700 m in Natal and northwards to Malawi. In this region the rainfall of about 800–1 200 mm p.a. occurs almost totally in the summer months, whereas the higher altitudes receive snow in the winter months (White, 1978). Populations tend to be extensive and sparse.

Although the species appears to be relatively common in South Africa and Zimbabwe, there is only a single collection known from Malawi (Mt Mlanje) and from Madagascar.

As at least Mt Mlanje in Malawi has been floristically well investigated by various botanists, the species has to be accepted as being rare in that country.

A sweet scent has occasionally been recorded.

PUTATIVE HYBRIDS

Monadenia atrorubens × sabulosa

Linder 1510 consists of a single plant found at Betty's Bay in the western Cape, growing between populations of both putative parents. The specimen is intermediate for all characters between the two parents.

EXCLUDED SPECIES

Monadenia leydenburgensis Kraenzl., Orch. Gen. Sp. 1: 811 (1900); Rolfe in Fl. Cap. 5, 3: 189 (1913). Type: Transvaal, Lydenburg, along the Crocodile

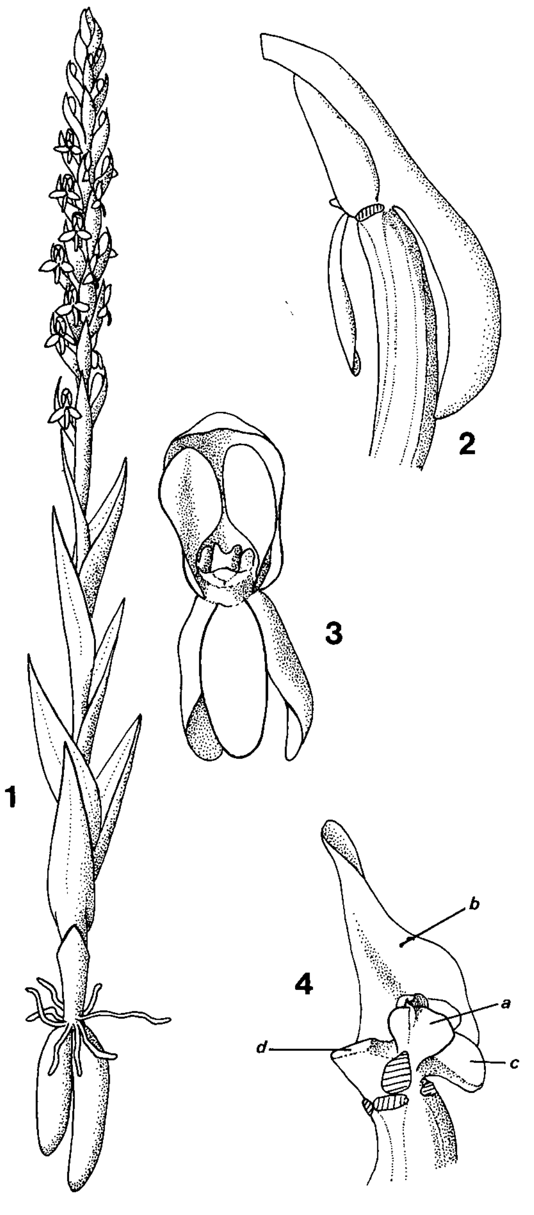

FIG. 25.—*Monadenia brevicornis*. 1, whole plant, ×0,5. 2, flower in side view with one sepal removed, ×3. 3, flower in front view, ×3. 4, dissection of flower, ×6: a, rostellum; b, petal; c, anther; d, stigma. All from *McLoughlin* 42.

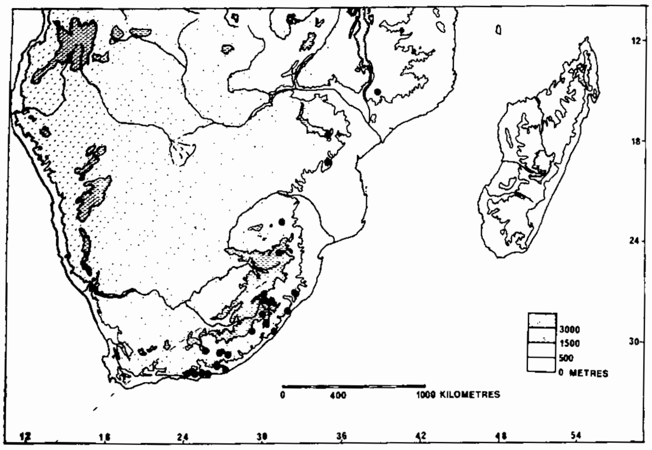

FIG. 26.—Distribution of *Monadenia brevicornis*.

River, *Wilms* 1864 (Z, holo.!; BM!; K!) = **Disa stachyoides** Reichb. f. in Flora 64: 328 (1881).

Monadenia basutorum (Schltr.) Rolfe in Fl. Cap 5, 3: 196 (1913), based on *Disa basutorum* Schltr. in Bot. Jb. 20, 50: 17 (1895). Type: Natal, Drakensberg summit, *Thode* s.n. (K, iso.!) = **Disa basutorum** Schltr.

Monadenia junodiana Kraenzl. in Vierteljahrschr. Nat. Ges. Zürich 74: 108 (1929). Type: Transvaal, Mamotsuri, *Junod* 1208 (Z, holo.!) = **Disa fragrans** Schltr. in Bot. Jb. 20, 50: 40 (1895).

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UITTREKSEL

Die genus Monadenia *(Disinae, Orchidaceae) word hersien. Sestien spesies, in vier seksies verdeel, word erken. Die verspreiding van elke spesie word afgebaken en twee spesies word geïllustreer. 'n Hipotese oor die filogenetiese verwantskappe van die spesies word aangebied.*

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APPENDIX: SPECIMENS STUDIED

The specimens are listed alphabetically according to the name of the collector. The figures in brackets refer to the number of the taxon in the text. Herbaria from which each collection has been studied are indicated by the letter codes of Holmgren & Keuken (1974). Two taxon numbers connected by a dash, e.g. (3–4), indicates that the collection is a hybrid between the two species.

Acocks 1030 (5) S; 5318 (5) S; 19866 (5) PRE; 22797 (15) PRE; 23499 (5) PRE. *Adamson* 438 (16) K; in SAM 52937 (12) SAM. *Alexander* s.n. (5) K. *Andreae* 27 (6) PRE; *sub Marloth* 645 (9) PRE. *Atherstone* 25 (16) K.

Ball 550 (16) K; 568 (16) K. *Barber* 445 (16) K. *Barker* 328 (14) NBG; 1622 (5) NBG; 3398 (13) NBG; 3892 (5) NBG; 3893 (6) NBG; 3925 (2) NBG; 4172 (5) NBG; 8838 (8) NBG. *Beasley* 64 (16) K. *Begley* 8 (10) SAM. *Boardman* 49 (16) BOL; 262 (16) PRE. *Bodkin* in BOL 4903 (10) BOL; 4970 (4) BOL, G. PRE, SAM, Z; 4988 (8) BOL, K; 6231 (2) BOL. *Bohnen* 1066 (5) PRE. *Bolus* 3859 (5) BM, BOL, K, Z; 4336 (14) K; 4538 (12) BM, BOL, K, Z; 4542 (8) BOL; 4551 (13) BM, BOL, K, PRE, Z; 4555 (9) BM, BOL, K, SAM, Z; 4885 (6) BOL, K, PRE, Z; 4897 (8) BOL, K; 4969 (13)

BOL, K, Z; 4973 (14) PRE; 6862 (6) Z; 7104 (3) BOL, SAM; 7317 (16) BOL, G, Z; 9938 (11) BOL; 11646 (9) BOL; 13504 (4) BOL; 13505 (6) BOL; *sub Guthrie* 1080 (3) BOL; s.n. (5) BOL; s.n. (5) BOL; s.n. (8) BOL; s.n. (9) BOL; s.n. (11) BOL; s.n. (13) BOL. *Bond* 115 (9) NBG; 1206 (9) NBG. *Boucher* 699 (5) STE; 829 (12) STE; 1642 (12) STE; 1946 (9) STE; 2422 (5) PRE, STE. *Bower* 600 (15) PRE. *Boyle* 25 (16) K. *Buchanan* s.n. (16) K, W. *Burchell* 4015 (5) K; 6139 (5) K; 7321 (9) K.

Calder in SRGH 46276 (16) K. *Cassidy* 22 (5) NBG. *Cloete* in CH 66620 (13) NBG. *Codd* 2716 (16) K, PRE. *Coleman* 521 (16) PRE. *Compton* 4154 (9) BOL, NBG; 4507 (12) BOL, NBG; 4700 (13) BOL; 9756 (9) NBG; 9759 (9) NBG; 11928 (5) NBG; 11955 (9) NBG; 11993 (5) NBG; 16244 (9) NBG; 16446 (12) NBG; 17486 (6) NBG; 17496 (9) NBG; 18545 (9) NBG; 18609 (9) NBG; 18572 (5) NBG; 19411 (6) NBG; 20090 (5) NBG; 20180 (13) NBG; 20221 (5) NBG; 21729 (16) BOL, NBG; 23670 (5) NBG. *Cutting* s.n. (5) BOL.

Davis & Stokoe in SAM 49539 (9) PRE. *Daly* s.n. (5) PRE. *Dekenal* in CH 57315 (12) NBG. *Devenish* 813 (16) PRE; 1376 (16) PRE. *De Villiers* in NBG 1910/30 (12) BOL; s.n. (5) STE. *Doidge* 4802 (16) K. *Drège* 1252a (9) BM, G. K, P, S; 1252b (9) BM, K, P; 1261b (5) BM, G, K, P, W; 8290 (12) K; in SAM 21998 (13) SAM. *Drège* 94 (5) Z. *Dümmer* 547 (13) BM; 554a (6) BM; 934 (9) BM; s.n. (5) BM.

Ebersohn 151 (10) NBG; 152 (12) NBG. *Ecklon* 247 (5) M. *Emdon* 30 (12) STE. *Esterhuysen* 400 (5) NBG; 493 (5) NBG; 6175 (9) BOL, PRE; 6396 (9) BOL, PRE; 6543 (9) BOL; 6882 (16) BOL; 7086 (16) BOL; 8206 (9) BOL; 9025 (5) BOL; 9780 (10) BOL; 10573 (12) BOL; 10692 (16) BOL, PRE; 10712 (9) BOL; 10999 (9) BOL; 11194 (6) BOL; 11693 (5) NBG; 12074 (5) BOL; 12200 (9) BOL, PRE; 13313 (16) BOL; 16200 (9) BOL; 18979a (15) BOL; 21978 (5) BOL; 23635 (12) BOL; 31166 (9) BOL; in SAM 54324 (2) SAM.

Fannin 33 (16) K. *Farnham* s.n. (5) BOL. *Flanagan* 1687 (16) BOL, PRE; 1807 (16) BOL, PRE, SAM. *Fourcade* 519a (6) K; 1458 (15) K, STE; 1626 (9) BOL; 2840 (12) K, STE; 2848 (16) K; 3446 (5) K, STE, *Franklin* 40 (16) NU. *Frowien* in PRE 15649 (5) PRE. *Fry sub Galpin* 2719 (16) PRE.

Galpin 308 (16) PRE; 2719 (16) PRE; 4605 (9) GRA, K, PRE; 4606 (5) K, PRE; 4607 (5) K, PRE; 4608 (12) PRE; 4609 (9) BOL, K; 4610 (12) BOL, PRE; 4612 (6) PRE. *Garside* 210 (9) K; 1058 (5) K; 1696 (5) K. *Gillett* 982 (12) STE; 1352 (5) STE; 1783 (9) STE; 1842 (6) STE; 1856 (5) STE; 2091 (5) STE; 2094 (12) STE; 4565 (15) BOL; 4573 (5) BOL. *Glass* 617 (16) Z. *Goatcher* in BOL 6862 (6) Z. *Goldblatt* 324 (11) BOL. *Gordon* s.n. (16) PRE. *Gueinzius* 264 (16) P. *Guthrie* 725 (2) BOL; 1082 (9) NBG; 2729 (14) BOL; in BOL 7096 (6) BOL; in BOL 7097 (2) BOL, K.

Häfstrom & Acocks 2089 (9) PRE. *Hall* 419 (16) BOL; 736 (5) BOL; 737 (5) BOL; 1068 (5) BOL; 1073 (5) BOL; 1081 (5) BOL; 1104 (16) BOL; 1116 (16) BOL; 1122 (5) BOL; 1194 (9) BOL. *Hallack* in BOL 6093 (16) BOL, K. *Hanekom* 1264 (9) PRE; 2176 (13) PRE. *Harvey* 141 (5) K. *Haygarth* in PRE 22340 (16) K, PRE, Z. *Haynes Palmer* in CH 57305 (4) NBG. *Hilliard* 1695 (16) NU; 5583 (16) NU. *Hilliard & Burtt* 8028 (16) NU. *Holland* 3739 (16) BOL. *Horrocks* 28 (5) NBG. *Humbert* 13642 (16) P. *Hutchinson* 575 (9) BM, K, PRE; 672 (6) K; 1225 (5) K; 1412a (15) K; 1432 (16) BOL, K.

Jackson in CH 85840 (12) NBG; in CH 86427 (3) NBG. *Jacobsen* 3720 (16) PRE; 3815 (16) K, PRE. *Jacobsz* 109a (16) PRE; 2/62 (16) PRE. *Jacot Guillarmod, Getliffe and Mzamane* 184 (16) K, PRE. *Jeppe* in PRE 33400 (6) PRE; 33401 (15) PRE; 33402 (16) PRE; 33403 (5) PRE; 33404 (12). PRE. *Jordaan (5) STE.*

Kassner 1374 (16) P; 1479 (5) P. *Keet* 1024 (12) PRE. *Kellerman* 26 (13) STE. *Kies* in CH 57316 (10) NBG. *Killick* 3858 (16) PRE; 3873 (16) PRE. *Killick & Vahrmeijer* 3631 (16) PRE. *Krige* in BOL 13491 (6) BOL. *Kruger* 29 (5) STE; 508 (4) STE; 556 (5) STE; 1001 (9) STE; 1072 (12) STE.

Lamb s.n. (13) BOL. *Laughton* 77 (5) BOL; 79 (5) BOL. *Lavranos* 9380 (16) PRE; 15232 (16) PRE. *Leighton* 840 (8) SAM; 1344 (9) BOL, PRE; 1441 (6) BOL; 1499 (5) BOL; 2079 (5) BOL; 2151 (9) BOL; 3146 (11) BOL. *Leipoldt* 3236 (11) BOL; 3237 (5) BOL; 3809 (14) BOL, K; s.n. (5) BOL. *Le Sueur* in BOL 4973 (14) BOL. *Lewis* 93 (5) SAM; 648 (5) SAM; 721 (13) SAM; 722 (12) SAM; 787 (5) SAM; 788 (13) SAM; 816 (5) SAM; 823 (5) SAM; 850 (6) SAM; 851 (8) SAM; 1094 (13) SAM; 1095 (4) SAM; 1096 (5) SAM; 1097 (5) SAM; 1098 (6) SAM; 1099 (6) SAM; 1100 (6) SAM; 1101 (11) SAM; 1107 (6) SAM; 1108 (2) SAM; 1487 (1) SAM; 1490 (8) SAM; 1832 (13) SAM; 1833 (6) SAM; 2403 (14) SAM; 3546 (6) SAM; 3547 (5) SAM; 3548 (6) SAM; 3549 (13) SAM; 4389 (5) SAM; 4455 (2) SAM; 4756 (5) SAM; 4757 (8) SAM; 4758 (10) SAM; 4759 (6) SAM; 4760 (5) SAM; 5020 (9) SAM; 5542 (11) NBG; 5645 (9) NBG; 6161 (5) NBG; s.n. (11) BOL. *Linder* 752 (8) BOL; 763 (5) BOL; 811 (16) BOL; 831 (16) BOL; 841 (16) BOL; 934 (16) BR, BOL; 943 (16) BOL; 973 (16) BOL; 996 (16) BR; 1000 (16) BOL; 1129 (11) BOL; 1140 (11) BOL; 1149 (9) BOL; 1243 (5) BOL; 1479 (9) BOL; 1507 (4) BOL; 1508 (3) BOL; 1509 (11) BOL; 1510 (3 – 11) BOL; 1512 (11) BOL; 1513 (6) BOL; 1519 (5) BOL; 1524 (12) BOL; 1528 (2) BOL; 1536 (6) BOL; 1537 (5) BOL; 1551 (5) BOL; 1552 (16) BOL; 1563 (5) BOL; 1564 (15) BOL; 1570 (16) BOL; 1571 (12) BOL; 1578 (12) BOL; 1580 (5) BOL; 1583 (5) BOL; 1596 (12) BOL; 1599 (5) BOL; 1601 (9) BR, BOL; 1608 (12) BOL; 1610 (13) BOL; 1617 (7) BOL; 1694 (10) BOL; 1706 (12) BOL; 1742 (9) BR, BOL; 1745 (5) BOL; 1748 (10) BOL; 1807 (2) BOL; 1988 (16) BOL; 2078 (16) BOL. *Linley* in SAM 49536 (12) PRE, SAM; in SAM 49537 (9) SAM; 49538 (9) SAM; in SAM 49541 (9) SAM; in SAM 56094 (8) SAM; in SAM 56898 (13) SAM; in SAM 56902 (5) SAM; in SAM 56903 (5) SAM; in SAM 56904 (6) SAM; in SAM 56908 (6) SAM; in SAM 61249 (10) SAM. *Liversidge* 232 (16) NBG. *Long* 163 (5) K; 164 (5) K; 827 (5) K, PRE; 835 (16) K, PRE.

MacOwan 381 (5) K, SAM; 679 (16) BM, K, SAM, W, Z, ZT. *MacOwan & Bolus* 170 (9) BM, BOL, G, K, P, SAM, W, ZT; 171 (12) BM, BOL, G, K, P, W, ZT; 1374 (3) BOL, SAM. *Mann* 55 (5) K. *Manning* in CH 87243 (12) NBG. *Marais* 55 (16) PRE. *Marloth* 61 (9) PRE; 230 (12) PRE; 664 (9) PRE; 1768 (12) PRE; 1854 (11) PRE; 1864 (9) PRE; 4972 (6) BOL; 8916 (5) PRE. *Matheson* in SAM 59669 (16) SAM. *Mauve* 4761 (12) PRE. *McLoughlin* 12 (16) BOL; 42 (16) BOL; 164 (16) BOL; 403 (16) BOL; 488 (16) BOL; in PRE 26260 (16) BOL, K. PRE. *Meebold* 11895 (5) M. *Minicki* in SAM 59671 (2) SAM. *Moll* 2218 (16) PRE. *Moore* s.n. (16) BOL. *Morze* 2026 (5) BOL; 2027 (5) BOL. *Moss* 4141 (5) K; 19257 (5) K. *Muir* 664 (12) PRE; 746 (5) PRE; 748 (5) PRE; 1124 (12) PRE; 1125 (9) PRE; 1795 (6) PRE; 2330 (9) PRE; 2331 (9) PRE; 2332 (9) PRE.

O'Brien s.n. (16) K. *O'Connor* 213 (16) NU; 214 (16) NU; 296 (16) NU; 334 (16) NU. *Oliver* 3942 (9) STE; 4202 (5) STE; 4761 (14) K, PRE, STE; 5088 (9) STE; 5370 (9) PRE, STE; 5438 (5) STE; 5447 (9) PRE, STE; 5591 (9) STE; 6044 (9) STE; s.n. (5) BOL; s.n. (9) BOL.

Page in BOL. 16232 (6) BOL. *Pappe* in SAM 21989 (5) SAM; in SAM 21990 (5) K, SAM; in SAM 21985 (6) SAM; in SAM 21993 (14) SAM; s.n. (12) K. *Paterson* s.n. (5) BOL, PRE. *Penfold* 163 (5) NBG; in CH 57311 (11) NBG. *Penther* 46 (5) M; 53 (16) W; 57 (16) W; 60 (12) W; 65 (16) S, W; 81 (16) W; 99 (12) W; 104 (5) M; 179 (12) W; 186 (8) W; 215 (16) W; 236 (5) W; 277 (5) W; 329 (5) W. *Phillips* 1335 (5) SAM; 1337 (9) SAM; 1341 (12) SAM; 1852 (5) SAM. *Phillipson* s.n. (5) BOL. *Phipps 666 (16) K. Pillans* 2748 (5) PRE; 2748b (6) PRE; 8483 (5) BOL; 9176 (5) BOL; 9324 (5) BOL. *Pocock* 503 (9) STE. *Porter* in CH 57313 (12) NBG. *Prentice* in SAM 10789 (14) SAM; in SAM 10790 (9) SAM; in SAM 10791 (9) SAM. *Primos sub Marloth* 11705 (9) PRE. *Purcell* 424 (9) STE; in SAM 91219 (5) SAM; in SAM 91220 (5) SAM.

Rabinowitz in CH 57307 (14) NBG; in CH 77143 (14) NBG. *Rattray* in BOL 15784 (16) BOL. *Rehmann* 581 (8) Z; 582 (5) Z; 1950 (9) M. *Rogers* 2824 (16) Z; 17735 (5) Z; 23633 (5) PRE; 26494 (5) Z; 26569 (5) Z; 27166 (5) G; 27970 (16) Z; 29057 (8) K; s.n. (13) K. *Rudatis* 565 (16) STE; 784 (16) BM, K.

Salter 8290 (12) K; 8473 (12) BOL; 8479 (13) BOL; 8554 (3) SAM; 9374 (5) BM; 322/15 (6) BM; 322/17 (2) BM; 323/2 (12) BM; 323/5 (13) BM; in SAM 55850 (5) SAM. *Sanderson* 894 (16) BOL; 938 (5) K; s.n. (16) K. *Saunders* s.n. (16) BOL. *Schelpe* 132 (16) NU; 4227 (5) BM; 4882 (11) BOL; 4895 (5) BOL; 4979 (5) BOL; 6328 (16) BOL, K; 7114 (16) BOL; 7118 (5) BOL; 7155 (16) BOL; 7162 (16) BOL. *Schlechter* 1479 (6) G, K, M, P, W, Z; 1550 (13) BM, G, GRA, K, S, W, Z; 4713 (16) BOL, K, P, PRE, W, Z; 5167 (11) BOL; 5791 (8) BOL, Z; 5958 (6) BOL, K, PRE; 5965 (5) BM, G, K, P, PRE, W, Z; 5974 (16) BM, K, Z; 9501 (4) BOL; 9502 (8) BOL; 9618 (2) BM, BOL, G, K, P, PRE, Z. *Schmidt* 606 (5) M; 607 (5) M. *Schonland* 610 (5) PRE. *Schur* in CH 57290 (6) NBG. *Scully* in BOL 4903 (10) BOL. *Seltzer* in CH 57304 (5) NBG. *Sim* 856 (16) NU; 864 (16) NU. *Smith* 4871 (5) PRE. *South* 617 (16) PRE. *Stokoe* 241 (12) PRE; 1151 (9) PRE; 6764 (9) BOL; 7382 (15) BOL; 9065 (9) BOL; in BOL 16649 (12) BOL; in BOL 17531 (4) BOL; in BOL 18388 (9) BOL; in CH 9904 (10) NBG; in SAM 36760 (13) SAM; in SAM 49534 (5) SAM; in SAM 49539 (9) SAM; in SAM 49540 (9) SAM; in SAM 55884 (9) SAM, in SAM 57747 (12) SAM; in SAM 57748 (9) SAM; in SAM 57749 (9) SAM; in SAM 57750 (5) SAM; in SAM 59668 (3) SAM; in SAM 61248 (5) SAM; in SAM 61250 (13) SAM; in SAM 63158 (5) SAM; in SAM 63159 (9) SAM; in SAM 63759 (12) SAM; in SAM 65620 (5) SAM; in SAM 68251 (9) SAM; *sub Marloth* 10569 (9) PRE; s.n. (4); s.n. (9) BOL; s.n. (9) BOL; s.n. (10) BOL; s.n. (10) BOL. *Strauss* 33 (11) NBG.

Taylor 247 (6) BOL; 252 (10) BOL; 258 (12) BOL; 6462 (9) STE. *Thode* A1021 (5) PRE; A2285 (5) PRE; in STE 3836 (16) STE; in STE 5427 (5) STE; in STE 6108 (5) STE; in STE 6110 (12) STE; in STE 8138 (16) STE. *Thomas* in CH 56374 (3) NBG. *Thoms* s.n. (5)

M. *Thompson* 3220 (5) STE. *Trauseld* 569 (16) PRE; 983 (16) PRE. *Trimen* s.n. (13) BM. *Truter* s.n. (13) STE.

Vahrmeijer 1062 (16) PRE. *Van Niekerk* 191 (5) BOL. *Verreaux* s.n. (5) G.

Wall 2228 (8) S; s.n. (5) S; s.n. (16) S. *Walters* 508 (5) BOL; 534 (8) BOL; 536 (15) BOL. *Wasserfall* 972 (5) K, PRE. *Werdermann & Oberdieck* 139 (5) PRE. *Wild* 938 (16) K. *Wilson* in SAM 21999 (13) SAM. *Winkler* 30 (5) NBG; 5049 (5) NBG. *White* 610 (5) Z. *Wolley-Dod* 394 (5) BM, BOL; 1788 (9) K; 1845 (5) K; 1846 (13) BM; 2179 (8) BOL; 2992 (12) BOL, K; 3066 (13) BM, BOL; 3067 (12) BM, BOL, K; 3212 (6) K; 3506 (9) BOL; 3587 (6) BOL, K; 3601 (6) BM; 3602 (5) BM; 3635 (15) BOL, K; 5636 (4) BM, BOL. *Wood* 12254 (16) PRE; 12257 (16) SAM, Z. *Worsdell* 54b (5) K. *Wright* 135 (5) K; 2377 (16) NU. *Wurts* 436 (5) NBG; 2039 (5) NBG.

Zeyher 242 (12) K; 1564 (6) G, K, PRE, SAM, W; 1569 (15) BOL, K, SAM; 1570 (13) BOL, G, K, SAM, W; 3924 (12) BM, K, P, SAM, W; 3925 (9) BM, K, S, SAM, W; 4680 BOL, K, P, PRE, SAM.

INDEX

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Taxonomic studies in the Disinae. VI. A revision of the genus *Herschelia*

H. P. LINDER*

ABSTRACT

The genus *Herschelia* (Disinae, Orchidaceae) is revised. Sixteen species, one subspecies and one variety are recognized. Two new species from tropical Africa (*H.* **chimanimaniensis** Linder and *H.* **praecox** Linder) and a new variety from the Cape Province *H. lugens* (H. Bol.) Kraenzl. var. **nigrescens** Linder are described. Three new combinations are made by transferring the two species of *Forficaria* and *Disa* sect. *Microperistera* (one species) to *Herschelia.* Thirteen species are illustrated, and the nomenclature and the available information about the habitats of the taxa are discussed. The species are grouped into two subgenera, one of which is further divided into two sections and four series. This classification is based on the putative phylogeny, as determined by the method devised by Wagner (1962).

RÉSUMÉ

ÉTUDES TAXONOMIQUES DES DISINAE. VI. UNE RÉVISION DU GENRE HERSCHELIA

Le genre Herschelia *(Disinae, Orchidaceae) est révisé. Seize espèces, une sous-espèce et une variété sont reconnues. Deux nouvelles espèces d'Afrique tropicale* (H. **chimanimaniensis** *Linder et* H. **praecox** *Linder) et une nouvelle variété originaire de la province du Cap,* H. lugens, *(H. Bol.) Kraenzl. var.* **nigrescens** *Linder sont décrites. Trois nouvelles combinaisons sont faites en transférant les deux espèces de* Forficaria *et* Disa *sect.* Microperistera *(une espèce) à* Herschelia. *Treize espèces sont illustrées, et la nomenclature ainsi que l'information disponible quant à leurs habitats et taxa sont discutées. Les espèces sont groupées en deux sous-genres, une desquelles est de plus divisée en deux sections et quatre séries. Cette classification est basée sur la phylogénie putative, déterminée selon la méthode décrite par Wagner (1962).*

INTRODUCTION AND HISTORICAL OVERVIEW

Herschelia is one of the 'minor' genera in the subtribe Disinae (Orchidoideae, Orchidaceae). The genus is centred in the Cape Floral Region (Goldblatt, 1978), where 12 of the 16 species occur. The remaining four species occur in the montane grasslands (White, 1978) of southern and south-central Africa, extending marginally into East Africa (Robyns & Tournay, 1955).

There has been a conspicuous lack of consensus about the delimitation of the genus and the species. Lindley, who describe the genus in 1838, included only *H. graminifolia* in it, and placed the other known species into *Disa* sect. *Trichochila.* This treatment was followed by Bentham & Hooker (1883) and Pfitzer (1889). Harry Bolus transferred all the then known species to *Herschelia,* which he treated as a section of *Disa.* Schlechter (1901) followed a similar approach. Bolus provided descriptions and illustrations for the majority of the species, and did excellent work on the nomenclature and morphology of various species in the group (1882, 1889, 1893, et seq.). Although Rolfe (1913), Schelpe (1966) and Dyer (1976) essentially follow the generic delimitations of Bolus and Schlechter, they treat *Herschelia* as a genus. *Forficaria* has generally been regarded as allied to *Herschelia* (or to *Disa* sect. *Trichochila),* but has never been included in the same group. Kraenzlin (1900) produced a rather artificial treatment, where *H. spathulata* s.l., and *Disa lacera* are removed from *Herschelia,* and grouped with *Disa cooperi, D. scullyi* and *D. thodei* in *Disa* sect. *Spathulatae.*

Several species of this genus have from time to time been introduced into cultivation in Europe, but there is little evidence that the plants lasted more than a few seasons. According to Hooker (1886, 1889), *H. hians* and *H. spathulata* subsp. *spathulata* flowered at Kew. In 1905 it was noted that *H. graminifolia, H. spathulata* and an unknown species of *Herschelia* were in cultivation (Anon., 1905). In 1912 Rolfe remarked: 'Though the species (*H. lugens*) has been repeatedly introduced to cultivation in this country, it is by no means easy to maintain in good condition, owing to its tendency to dwindle away after flowering'. In 1955 Dyer remarked that attempts to introduce *H. graminifolia* were still unsuccessful and that all tuberous orchids fared badly in cultivation. At present several species (*H. spathulata* subsp. *spathulata, H. lugens, H. purpurascens, H. barbata* and *H. graminifolia*) are in cultivation in South Africa. It is to be hoped that methods of propagating these species may soon be perfected, as several of the more striking species are already rare in nature, and may soon, if present trends continue, become extinct.

MORPHOLOGY

In general, the habit of all the species of *Herschelia* is grass-like with a radical tuft of linear, usually rolled, erect leaves, and a slender erect stem. The vegetative structures in this genus appear to be well adapted to the various ecological preferences and phenology of the species, within the framework of the general grass-like structure.

The tubers are rather variable in size and are often remarkably large for the size of the plants. Large tubers are often found on plants collected from well-drained sandy areas.

The radical leaves display three patterns:

(a) In the winter-rainfall and all-the-year rainfall regions, the majority of the species have linear, rolled, erect leaves that are produced before the flowers, and that may be dry or green at anthesis. The leaves do not reach above the base of the inflorescence, presumably as this would obscure the lower flowers from any pollinators.

(b) In the winter-rainfall region, the *H. spathulata* group has flat leaves. The plant is early flowering, before the summer drought starts, and the flat leaves may reflect the absence of xeric adaptations.

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*Bolus Herbarium, University of Cape Town, Rondebosch, 7700.

(c) In the summer rainfall regions the plants appear shortly after the start of the summer rains. This could be a mechanism to avoid competition with the grasses, which are usually burnt in the winter months. The leaves are produced after the flowers and are often up to three times as long as the inflorescence.

Where fires frequently occur, a sheath of old leaf fibres often accumulates around the base of the stem. This indicates that individual tubers must reach a considerable age, as only 5–15 leaves are produced each season. It is also evidence of their remarkable fire resistance.

The inflorescences do not show any exceptional variation. There is a reduction in the number of flowers with increase in flower size — perhaps an index of the degree of advancement of the species. The floral bracts are of little taxonomic value. In the majority of cases the flowers are resupinate. Only in subgen. *Forficaria* is the lip upper-most, in the one species due to the flowers being twisted through 360°, in the other due to a lack of resupination. In the majority of taxa the flowers are of various shades of blue. In sect. *Microperistera* the flowers are white, whereas they are more or less maroon in subgen. *Forficaria.* In all cases, the flowers are the only brightly coloured element on the plants.

The sepals are strongly differentiated into the patent, shallowly concave, lanceolate to ovate lateral sepals and the galeate or deeply concave dorsal sepal. The latter varies from orbicular to ovate, and in some taxa may be shortly spathulate: probably an advanced character. The galea is usually deep, but it may also be very shallow. Generally, the galea bears a spur, but this is absent in three species. The spur is horizontal at the base, cylindrical, usually obtuse, and only in one case longer than the dorsal sepal. In the bulk of the species the spur is a small conical or cylindrical appendage on the back of the galea. It is not clear whether the absence of a spur should be considered primitive or a derived characteristic, or both, but it clearly arose twice. The presence of a long spur, found only in *H. schlechterana,* is almost certainly a derived state, within the genus.

The inner perianth whorl in *Herschelia* is highly specialized. The petals generally show a very distinct structure, consisting of a basal anticous lobe flanking the stigma, with the basal part of the limb reflexed parallel to the anther, and the apex curved upwards. In subgen. *Forficaria* this structure is peculiar; the basal anticous lobe is rudimentary, the apical half of the petals is villous. Among the remaining taxa, variation is restricted to the width of the limb of the petal, the angle of the upward curvature and the shape of the apex. A lanceolate apex is considered primitive and a bifid or flabellate expanded apex derived.

Three basic types of lip structure occur in the genus:

(1) a patent, reniform lip (subgen. *Forficaria*)
(2) an ovate, acute lip with entire margins (sect. *Microperistera*)
(3) an ovate lip, variously modified or dissected (sect. *Herschelia*)

It is probable that an ovate, entire lip is primitive, as it approaches the undifferentiated form of the organ. The reniform lip structure of subgen. *Forficaria* is unique in the subtribe. With sect. *Herschelia* extensive variation in lip shape occurs. Occasional specimens of *H. hians* have entire lips, and the whole range of variation from them to deeply lacerate lips may be found in the one species. From this basic form both the ovate lips with crisped margins, characteristic of ser. *Herschelia,* and the beard-like lips characteristic of the more advanced members of ser. *Lacerae* may be derived. This bearded state appears to have evolved twice (in *H. lugens* and in *H. multi-*

TABLE 1.–Occurrence of taxonomically useful characters in the genus

	forficaria	newdigateae	schlechterana	spathulata	graminifolia	purpurascens	barbata	venusta	lugens	multifida	hians	forcipata	praecox	bauri	chimanimaniensis	goetzeana
Spur absent	X	X														X
short				X	X	X	X	X	X	X	X	X	X	X	X	
long			X													
Sepals blue				X	X	X		X	X	X	X		X	X	X	X
white			X				X									
red	X	X														
Petals acute			X								X	X				X
bifid													X	X	X	
lacerate									X	X						
expanded apex		X		X	X	X	X	X								
aciculate	X															
Lip sessile	X	X	X		X	X	X	X	X		X	X	X	X	X	X
stalked				X						X						
entire	X	X	X		X	X						X				
crenulate											X					
bearded							X	X	X	X		X	X	X	X	
trilobed				X												
ovate			X	X	X	X	X	X	X	X	X	X	X	X	X	X
reniform	X	X														
Rostellum																
lateral lobes	X	X	X	X				X	X	X	X	X	X	X	X	X
three horns					X	X	X									
Flowers resupinate			X	X	X	X	X	X	X	X	X	X	X	X	X	X
not	X	X														

fida). Spathulate lips also evolved twice: in *H. multifida* and in ser. *Spathulatae*.

The column in *Herschelia* is, to a certain extent, characteristic of the genus. Typically the anther is horizontal, usually with two large viscidia (these may, however, be fused), the rostellum erect, with three equal lanceolate, acute lobes, holding the viscidia between them (Bolus, 1882) and a horizontal, shortly pedicellate stigma with three lobes, the rear or odd lobe much smaller than the lateral lobes. The rostellum and stigma structures are variable, but unfortunately it is rather difficult to get a clear picture of these structures from dried material. Frequently the rostellum consists of two lateral horns, which are canaliculate and hold the viscidia at their apices. The central lobe appears to be highly reduced or lost. It is possible that the central lobe could be formed by the fusion of the inner walls of the canaliculate lateral rostellum horns. This suggestion is made more likely by the fact that the inner rostellum lobe is frequently bilobed or bifid. This would indicate that the trilobed rostellum is derived from the bilobed canaliculate rostellum. Variation in the stigma structure affects the size of the odd lobe, which varies from large as the lateral lobes to much smaller.

The occurrence of taxonomically important characters in the genus is indicated in Table 1.

PHYLOGENY

The construction of a putative phylogeny for the genus is basic to the production of a phylogenetic classification of the species (Funk & Stuessy, 1978). Objective methods for the construction of phylogenies have been proposed by Hennig (1966), Wagner (1962) and several others, and are ably reviewed by Fund & Stuessy (1978) and Bremer & Wanntrop (1978). Essentially, the derived and generalized character states for the taxonomically important characters are postulated, and groups of species are formed on the number of shared derived character states. By using the Wagner method (Wagner, 1962) the more specialized taxa in the genus may be identified.

The determination of derived character states is based on two processes (Bremer & Wanntrop, 1978): detection of transformation series in a structure and determining the distribution of the character state in related groups. Generalized character states are likely to be wide-spread in related groups (Judd, 1979). This analysis was applied to the variation in the lip shape, petal apex shape, spur shape and flower colour. In lip and petal apex shape there are clear transformation series from simple entire structures to variously specialized structures. The simple entire structures, especially in the lip shape, are also widespread within the Disinae. The spur shape is more difficult to rank. It is likely that a short semipendent spur is typical for the subtribe, but there is no such structure in *Herschelia*. Consequently, the spurless state is considered to be primitive or generalized. However, this implies that there must have been a reversal in the evolutionary sequence for this structure, as two clearly unrelated taxa (subgen. *Forficaria* and *H. goetzeana)* are spurless. In the flower colour, blue is assumed to be the generalized state. This implies that white flowers evolved twice: in *H. barbata* and *H. schlechterana*. As these two taxa are not closely related, this is thought to be likely. The characters used for the analysis are listed in Table 2. Generalized characters are scored zero, specialized characters one, and intermediate states are scored 0,5. For several characters there are several specialized states.

TABLE 2.—Characters used for the phylogenetic analysis

Character	Generalized state	Specialized state
Spur	absent	short (0,5) or long
sepals	blue	white or red
petals	acute	bifid, lacerate, expanded or aciculate
lip	sessile	stalked
	entire	crenulate (0,5), bearded or trilobed
	ovate	reniform
rostellum	lateral lobes	three horns
flowers	resuplinate	not resupinate

The summed values for each taxon are used to place the taxon on the 'Wagner Tree'. Species sharing the largest number of derived or specialized character states are linked first, whereas species sharing no specialized characters are linked to the putative ancestor.

The Wagner Tree (Fig. 1) clearly demonstrates the major groups among the species:

(a) the *H. forficaria* group is highly specialized and quite isolated. The basic structure of the petal and the specialization of the lip, as well as the vegetative characters, indicate that it has to be included in *Herschelia*.

(b) *H. schlechterana* also shares the vegetative and petal structures typical of the genus, but has a

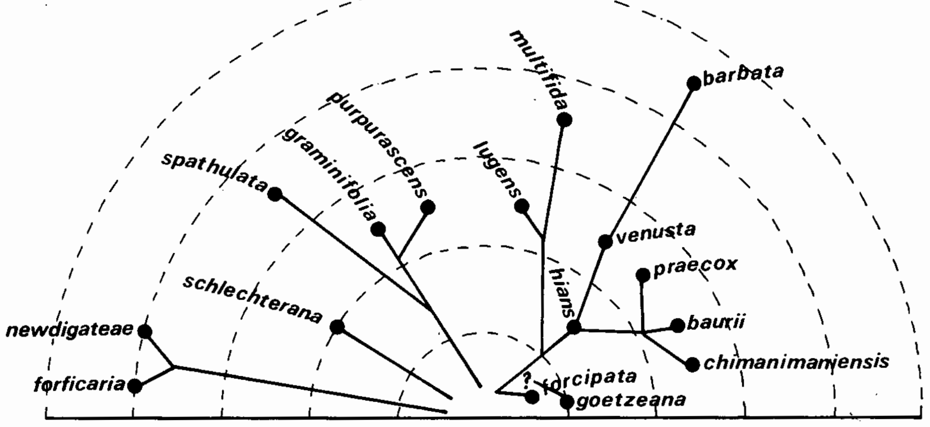

FIG. 1.—Wagner Tree for *Herschelia*. The circles indicate the degree of divergence.

unique spur, white flowers and an entire lip. It may also be derived directly from the ancestral stock of the genus.

(c) The remainder of the genus may be divided into two groups, mainly on the lip and petal apex shapes. *H. spathulata* has a spathulate three-lobed lip, whereas in *H. graminifolia* and *H. purpurascens* the lip is sessile and the lip margins undulate. Both these groups are restricted to the Cape Floral Region (*sensu* Goldblatt, 1978), and show signs of recent, if not ongoing, speciation. The *H. hians* group is characterized by bearded lips. Within the group various lines of development have used different petal shapes. The group may be understood to form a remarkable sequence of geographical and ecologically replacing species. The position of *H. forcipata* is not clear, the species is known only from a single collection. The available data indicate that the taxon may well be ancestral to the group. *H. goetzeana* emerges on the 'Wagner Tree' as being rather primitive. However, it may well be highly specialized, as a reduced form derived from *H. baurii*. At present it is an enigma and is known from a single collection from the summit of Mt Mbeya in southern Tanzania.

HERSCHELIA

Herschelia *Lindl.,* Gen. Sp. Orch. 362 (1838); Benth. & Hook. f., Gen. Pl. 3: 630 (1883); Pfitzer in Natürl. Pflfam. 2,6: 98 (1889); Kraenzl., Orch. Gen. Sp. 1: 801 (1900); Rolfe in Fl. Cap. 5,3: 199 (1913); Senghas in Schltr., Die Orchideen 1: 275 (1973), excl. syn.; Dyer, R.A. Gen. 2: 995 (1976). Type species: *Herschelia coelestis* Lindl. [=*H. graminifolia* (Spreng.) Dur. & Schinz]

Disa Berg. sect. *Herschelia* (Lindl.) H. Bol. in Trans S. Afr. phil. Soc. 5: 168 (1888); Schltr. in Bot. Jb. 31: 282 (1901), excl. *Disa* sect. *Amphigena* in synonymy; Summerh. in Fl. Trop. E. Afr. 156: 154 (1968).

Disa Berg. sect. *Trichochila* Lindl., Gen. Sp. Orch. 353 (1838); Pfitzer in Natürl. PflFam. 2,6: 98 (1889). Type species: *Disa barbata (*L. f.) Swartz. [=*H. barbata* (L. f.) H. Bol.], lectotype.

Forficaria Lindl., Gen. Sp. Orch. 362 (1838); Benth. & Hook. f., Gen. Pl. 3: 631 (1883), Pfitzer in Natürl. PflFam. 2,6:97 (1889); Kraenzl., Orch. Gen. Sp. 1: 722 (1900); Rolfe in Fl. Cap. 5,3: 207 (1913); Senghas in Schltr. Die Orchideen, 1: 271 (1973); R. A. Dyer, Gen. 2: 995 (1976). Type species: *Forficaria graminifolia* Lindl. [=*Herschelia forficaria* (H. Bol.) Linder].

Disa Berg. sect. *Forficaria* (Lindl.) Schltr. in Bot. Jb. 31: 297 (1901).

Disa Berg. sect. *Spathulatae* Kraenzl., Orch. Gen. Sp. 1: 793 (1900). Type species: *Disa spathulata* (L. f.) Swartz [*Herschelia spathulata* (L. f.) Rolfe], lectotype.

Disa Berg. sect. *Microperistera* H. Bol. in Trans. S. Afr. phil. Soc. 16: 149 (1907). Type species: *Disa schlechterana H. Bol.* [=*Herschelia schlechterana* H. Bol.) Linder].

Herschelia is named after Sir John F. W. Herschel (1792–1871), an astronomer who spent some years at the Cape.

Characteristic of this genus are the radical, linear, subsclerophyllous leaves, dry floral bracts, lax inflorescences, the rarely entire lip, usually variously dissected or stalked, petals with a basal anticous lobe, and the limb initially horizontally reflexed, soon falcately or geniculately curved upwards behind the anther, anther horizontal with one or two viscidia, rostellum generally with three equal erect, lanceolate lobes, stigma horizontal, the odd lobe smaller than the lateral lobes.

Plants slender, grass-like, erect 100–1 000 mm tall; tubers testicular, rarely three present, very variable in size, from 10–60 mm long, hirsute; roots unbranched, thick; base of the stem usually with a sheath of old leaf fibres; radical leaves 5–20, linear, flat or rolled, subsclerophyllous, shorter than or longer than the base of the inflorescence, produced during, before or after flowering; cauline leaves lax or imbricate, brown, acuminate, usually longer and overlapping to the base of the stem; inflorescence lax with 1–30 flowers; bracts usually broadly ovate, acuminate to setaceous, dry, varying from half as long as to slightly longer than the ovary; ovaries usually spreading from the stem, slender, 10–30 mm *long*. *Flowers* resupinate, usually blue or shades of blue, to white with pale blue veins, rarely purplish red or with green parts; dorsal sepal erect or angled forwards, generally galeate, rounded to acuminate, usually ovate in front view with the galea about half as deep as tall; spur horizontal from the base of the galea, at length straight, decurved or curved upwards, rarely longer than the sepals, cylindrical or conical; lateral sepals usually patent, lanceolate to ovate, obtuse to acute, 6–30 mm long; petals with a basal anticous lobe flanking the stigma, oblong to ovate, and a limb which is linear or lorate, the basal part of which is reflexed to the horizontal, flanking the anther, the apical part of which is curved falcately or geniculately upwards behind or near the apex of the anther, the apex of which may be lanceolate, expanded fan-like or more or less bifid; lip generally more or less dissected, rarely entire, usually ovate in outline, rarely spathulate, always specialized in some way; anther horizontal or somewhat pendent, the two cells parallel, with two viscidia which may be separate or fused; rostellum generally with the three lobes equal, erect, lanceolate, acute, rarely with the lateral lobes canaliculate and the central lobe not present; stigma horizontal, shortly pedicellate, the odd lobe smaller than the lateral lobes, the whole structure usually wider than the rostellum.

Subgen. **Forficaria** (*Lindl.*) *Linder,* stat. nov.

Forficaria Lindl., Gen. Sp. Orch. 362 (1838). Type species: *Forficaria graminifolia* Lindl.

Flowers with the lip facing towards the axis, dorsal sepal without a spur, lip reniform.

This subgenus contains two closely related species: *H. forficaria and H. newdigateae,* that appear to be vicariants as defined by Davis & Heywood (1963).

KEY TO THE SPECIES

1a Lip entire:
2a Lip kidney-shaped; petals ciliate:
3a Petals obscurely bilobed, flattened; from the southern Cape Province .... 2. *H. newdigateae*
3b Petals aciculate; from the western Cape Province .... 1. *H. forficaria*
2b Lip ovate to lanceolate; petals glabrous:
4a Spur 30 – 35 mm long .... 3. *H. schlechterana*
4b Spur less than 15 mm long:
5a Apex of the petals obtriangulate, flabellate, truncate:
6a Spur conical, tapering; lip margins curved upwards .... 6. *H. purpurascens*
6b Spur subclavate; lip margins curved downwards .... 5. *H. graminifolia*
5b Apex of the petals acute, entire or bifid:
7a Spur bifid .... 12. *H. forcipata*
7b Spur obtuse .... 11. *H. hians*
1b Lip more or less lacerate or bearded:
8a Lip stalked:
9a Lip blade deeply lacerate .... 10. *H. multifida*
9b Lip blade entire, 3-lobed or ovate:
10a Central lobe of lip (12–) 16–22 mm long; from east of Swellendam .... 4b. *H. spathulata* subsp. *tripartita*
10b Centra lobe of lip less than 14 mm long; from west of Swellendam .... 4a. *H. spathulata* subsp. *spathulata*
8b Lip sessile:
11a Petals deeply bilobed; from north of the Limpopo River:
12a Lateral sepals 6–8 mm long; from the Chimanimani Mountains in Zimbabwe ... 15. *H. chimanimaniensis*
12b Lateral sepals 8–25 mm long;
13a Petals as long as the galea; lip almost entire; from the Nyika Plateau in Malawi .... 13. *H. praecox*
13b Petals about ½ as long as the galea; lip deeply lacerate:
14a Spur present .... 14. *H. baurii*
14b Spur absent .... 16. *H. goetzeana*
11b Petals obtriangulate or obscurely bilobed; from south of the Limpopo River:
15a Lip longer than the lateral sepals, green or almost black:
16a Flower blue to green .... 9a. *H. lugens* var. *lugens*
16b Flower almost black .... 9b. *H. lugens* var. *nigrescens*
15a Lip shorter than the lateral sepals, more or less blue:
17a Lateral sepals longer than 15 mm; galea acuminate .... 7. *H. barbata*
17b Lateral sepals less than 16 mm long; galea rarely acuminate:
18a Limb of the petal linear, apex somewhat expanded; lateral sepals 12–16 mm long ...... 8. *H. venusta*
18b Limb of the petals lorate, apex lanceolate or obtriangulate; lateral sepals less than 13 mm long:
19a Petals lanceolate; lip shallowly dissected; from west of Grahamstown .... 11. *H. hians*
19b Petals obtriangulate; lip deeply dissected; from east of Grahamstown .... 14. *H. baurii*

1. **Herschelia forficaria** (*H. Bol.*) *Linder*, comb. nov.

Forficaria graminifolia Lindl., Gen. Sp. Orch. 362 (1838); Kraenzl., Orch. Gen. Sp. 1: 723 (1900); Rolfe in Fl. Cap. 5, 3: 207 (1913). *Disa forficaria* H. Bol., Icones Orch. Austro-Afr. 1: t. 87 (1896), nom. nov. Type: Cape Province, Paarl Division, Du Toit's Kloof, *Drège* 2211b (K, holo.!).

Icon: Flower. Pl. Afr. 11: t. 415 (1931)

Plants up to 500 mm tall; tubers c. 50 mm long; stems often with a sheath of old leaf fibres around the base; radical leaves linear, erect, reaching to the base of the inflorescence, acute; cauline leaves lax, narrowly ovate, acuminate, 20–40 mm long; inflorescence lax, c. 100 mm long; bracts shorter than the ovaries, ovate, acuminate, dry; ovaries c. 15 mm long. *Flowers* twisted through 360°, sepals greenish red, petals and lip deep maroon; dorsal sepal erect to reflexed at anthesis, deeply concave, orbicular, apiculate, 8–12 mm in diameter; lateral sepals patent narrowly ovate, acute to shortly acuminate, shallowly concave, 8–12 mm long; petals with the basal half lorate, reflexed parallel to the anther, 4–6 mm long, the apical half aciculate, geniculately bent forwards, terete, acute, tomentose; lip reniform, patent, 4–5 mm long and c. 6 mm wide, the distant margin somewhat swollen and shortly villose; anther horizontal, 4–5 mm long, caudicles short; rostellum small with well-developed staminodes; stigma pedicellate, almost equally trilobed. Fig. 2.

Diagnostic features. Dorsal sepal spurless, lip reniform, petal apex almost setaceous and tomentose, flowers twisted through 360°.

Flowering time: January and February.

A rare reed-like plant that occurs on well-drained gravelly slopes in the Caledon and Cape Peninsula Division (Fig. 3).

CAPE.*—3418 (Simonstown): Klaver Valley (–AB), Jan. 1922, *Pillans 4125* (BOL). 3419 (Caledon): Viljoenspass (–AA), Feb. 1933, *McGillett 718* (BOL).

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*In the treatment of each taxon only representative specimens have been cited. A full list of all specimens studied is given in the Appendix, pp. 387–388.

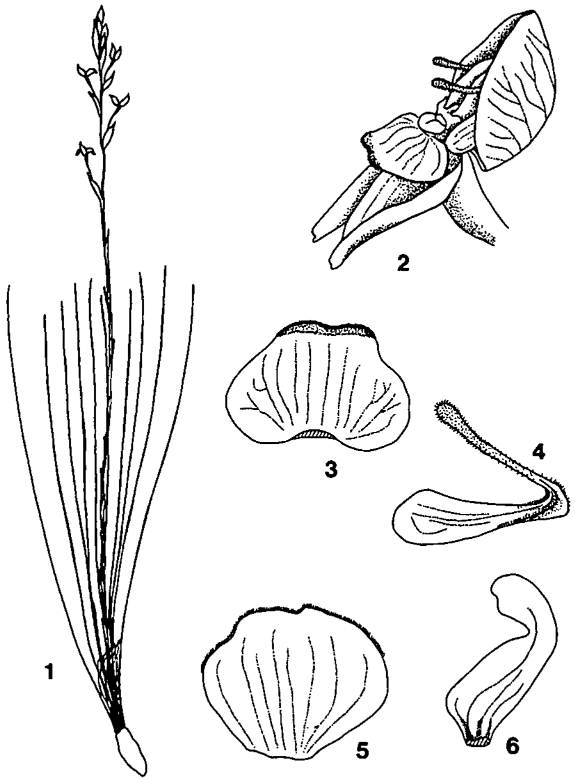

FIG. 2.—*Herscnelia forficaria* (1–4) and *H. newdigateae* (5–6). 1, habit, ×0,25, from *Gillett* 718. 2, flower, ×3. 3, lip, ×5. 4, petal, ×5 (2–5 from *Rosenbruck* s.n.) 5, lip of *H. newdigateae*, ×5. 6, petal, ×5. (5 & 6 from *Bolus* 6327.)

Very little is known about this rather peculiar species. It appears to grow on well-drained gravelly mountain slopes, but I have not succeeded in finding any populations in the field. Several collections were made shortly after veld fires, but this may be due merely to the greater ease of finding these rather cryptic plants in the restioid vegetation that dominates the habitat. The plants occur singly and widely scattered. The altitude range of the species is from about 100 m to 600 m. Rainfall is concentrated in the winter months, and totals about 800 mm p.a. (Jackson, 1961).

The specific epithet '*graminifolia*', under which the species is commonly known, cannot be transferred to *Disa* nor to *Herschelia*, as Sprengel described a *Disa graminifolia* in 1826, which Durand and Schinz transferred to *Herschelia* (1894). When Bolus (1896) transferred *Forficaria graminifolia* to *Disa*, he proposed *D. forficaria* as a *nomen novum*. This epithet is here transferred to *Herschelia*.

2. **Herschelia newdigateae** (*L. Bol.*) *Linder*, comb. nov.

Disa newdigateae L. Bol. in Flower. Pl. Afr. 11: t. 415 (1931). Type: Cape Province, Knysna, Forest Hall, *Newdigate* in BOL 6327 (BOL, holo.!).

Icon: H. Bol., Icones Orch. Austro-Afr. 1: t. 87 (1896), as *Disa forficaria*.

Plants up to 500 mm tall, radical leaves linear, acute up to 300 mm long; cauline leaves lax to subimbricate, acuminate, 30–50 mm long, completely sheathing; inflorescence lax, c. 100 mm long; bracts about as long as the ovaries, acuminate, narrowly ovate; ovaries c. 15 mm long. *Flowers* not resupinate; sepals greenish red, petals and lip deep maroon; dorsal sepal somewhat spathulate with a very short limb, the blade deeply concave, orbicular, apiculate, c. 8 mm in diameter, the margin somewhat dentate; lateral sepals ovate, acute, concave, c. 8 mm long; petals with the basal 4 mm narrowly ovate, parallel to the anther, the apical ⅓ curved up behind the anther, somewhat expanded apically and shallowly bilobed, tomentose; lip reniform, 4 mm long and 6 mm wide with the front margin ciliate; anther horizontal, c. 2 mm long; rostellum with the lateral lobes canaliculate, very small, central lobe apparently obsolete, viscidia big; stigma horizontal, flat. Fig. 2.

Diagnostic features. Dorsal sepal spurless, lip reniform, petal apex somewhat flattened and shallowly bilobed, tomentose, ovary not twisted.

Flowering time: March–April.

Very rare in the area between Nature's Valley and Plettenberg Bay (Fig. 3), from where it is only known from two collections. It grows on dry slopes in short macchia vegetation facing the sea. Superficially this species resembles *H. forficaria*, but a study of the flower soon reveals several distinguishing characters (shape of petal and galea, apex of lip and relative length of anther. Fig. 2). These two taxa are clearly eco-geographic vicariants.

The differences between the two taxa were not observed by the several taxonomists, who had studied the available material. Bolus (1896) published an illustration of *H. newdigateae* under the name *H. forficaria*. It was only when more fresh material of *H. forficaria* became available that the differences between the taxa were detected.

Subgen. **Herschelia**

Flowers resupinate, dorsal sepals (with one exception) spurred, lip more or less ovate and generally lacerate.

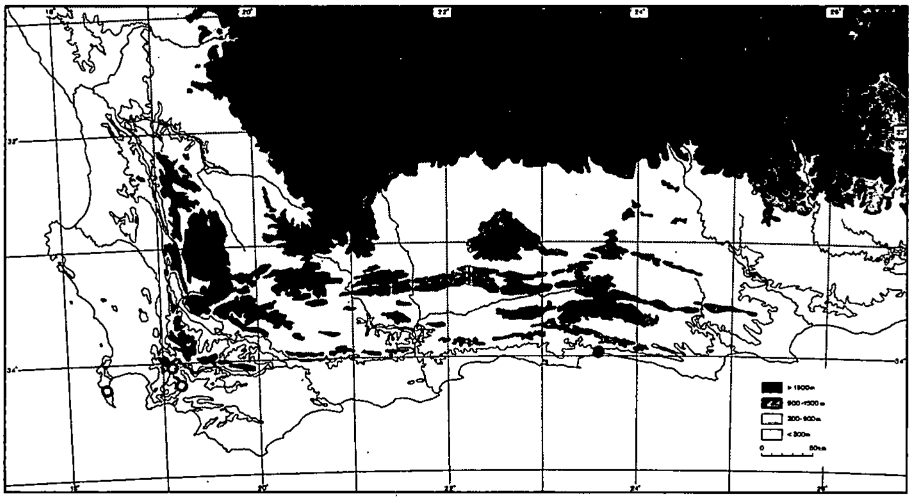

FIG. 3.—Distribution of *H. forficaria* (open circles) and *H. newdigateae* (closed circles).

Type species: *H. graminifolia* (Spreng.) Dur. & Schinz.

This subgenus contains those species which have traditionally been placed in *Herschelia* and which are often popularly known as 'Blue Disas'. The group contains a wide range of forms and is here further subdivided.

Sect. **Microperistera** *H. Bol.* in Trans. S. Afr. phil. Soc. 16: 149 (1907).

Type species: *Herschelia schlechterana* (H. Bol.) Linder.

Lip entire, sessile, ovate, spur longer than sepals.

3. **Herschelia schlechterana** (*H. Bol.*) *Linder*, comb. nov.

Disa schlechterana H. Bol. in Trans. S. Afr. phil. Soc. 16: 149 (1907); Rolfe in Fl. Cap. 5,3: 250 (1913). Type: Cape Province, Riversdale District, Garcias Pass *Luyt* in BOL 10571 (BOL, holo.!; BM!; BR!; K!; W!).

Icon: H. Bolus, Icones Orch. Austro-Afr. 2: t. 75 (1911).

Plants about 600 mm tall; tubers c. 4 mm long and 15 mm in diameter; base of the stem often with the fibrous remains of old leaves; radical leaves about 10, 300–400 mm long and about 2 mm wide, sulcate, the inner leaf surface smooth and the outer ridged longitudinally; cauline leaves about 9, lax or subimbricate, completely sheathing, dry, acute, 30–50 mm long; inflorescence lax, 100–200 mm long and with 3–12 flowers; bracts about ⅔ as long as the ovaries, lanceolate, acuminate, dry; ovaries about 30 mm long at anthesis, slightly curved. *Flowers* cream with mauve veins; dorsal sepal erect, galea obtuse, 22–25 mm tall, c. 16 mm wide and 8 mm deep, the margins curved outwards; spur from a shortly conical base, horizontal at the base and at length gradually decurved, slender cylindrical, subacute, 30–50 mm long; lateral sepals patent, lanceolate to narrowly oblong, suboblique acute 20–25 mm long, aciculus 0,5–1 mm long; petals with the basal anticous lobe orbicular, c. 3 mm in diameter, decurrent with the limb of the petal, limb lorate, 14 mm long, the basal part horizontal, soon geniculately curved through 135° to face forwards, the apex lanceolate, acute; lip patent, flat, narrowly oblong to lorate, acute, 15–20 mm long; anther somewhat pendent, 4,5 mm long with two globular viscidia; rostellum equally 3-lobed, 4 mm tall; stigma unequally 3-lobed, the odd lobe smaller than the lateral lobes, horizontal and c. 3 mm in diameter.

Diagnostic features. Flowers large, lateral sepals 20–25 mm long, spur 30–35 mm long; lip entire, narrowly oblong to lorate.

Flowering time: December.

This striking species has only been recorded from the dry north-facing slopes of the Langeberg (Fig. 4) in the vicinity of Riversdale, where it appears to grow amongst the sclerophyll bush in moister places.

CAPE.—3321 (Ladismith): Garcias Pass (–CC), Dec. 1930, *Ferguson s.n.* (BOL).

Sect. **Herschelia**

Lip sessile or stalked, usually lacerate, spur shorter than the sepals.

Type species: *H. graminifolia* (Spreng.) Dur. & Schinz.

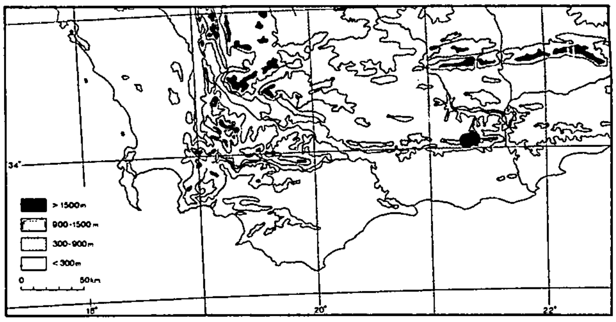

FIG. 4.—Distribution of *H. schlechterana*.

Within this section four clear groups may be recognized, mainly on the basis of petal and lip morphology, and secondarily on the shape of the spur. The exact relationships among these series is not clear, but it is likely that ser. *Spathulatae* and ser. *Herschelia* are closely related rather than to ser. *Hians* and ser. *Ecalcaratae*. The former two series both occur in the western Cape Province and have expanded apical petal lobes and non-lacerate lips, whereas the latter two sections have lacerated lips and extend into East Africa.

Ser. **Spathulatae** (*Kraenzl.*) *Linder*, stat. nov.

Disa sect. *Spathulatae* Kraenzl., Gen. Sp. Orch. 1: 793 (1900).

Type species: *H. spathulata* (L. f.) Rolfe, lectotype.

Lip spathulate, with a short or long stalk and the apical lobe obtusely trilobed to deeply trifid, petals expanded apically.

This series contains a single species complex and is restricted to the western and southern Cape Province.

4. **Herschelia spathulata** (*L. f.*) *Rolfe* in Fl. Cap. 5,3: 205 (1913). Type: Cape of Good Hope, *Thunberg* s.n. (LINN, holo.!; UPS!; W!).

Plants 120–300 mm tall, tubers 15–30 mm long; base of the stems often with a sheath of fibrous leaf remains; basal sheaths 2–3, hyaline, acute radical leaves 5–20, linear, 50–150 mm long and 2–4 mm wide, narrower towards the base, semi-erect, curved falcately; cauline leaves (2–) 3, dry, 20–30 mm long, completely sheathing, acuminate, grading to the floral bracts; inflorescence laxly 1–5-flowered, up to 100 mm long; bracts varying from half as long as the ovary to longer than the ovary, broadly ovate, acuminate to setaceous, dry; ovaries straight or slightly curved, 15–30 mm long. *Flowers* variable in colour from maroon to pale lime or green and blue; dorsal sepal erect, subspathulate, the limb horizontal, 1–3 mm long, the blade usually galeate, rarely flat, erect, 9–17–20 mm long, broadly ovate, obtuse, usually 5 mm deep; spur usually clavate, rarely cylindrical, obtuse, straight or strongly curved downwards, 1,5–3 mm long; lateral sepals patent or curved up in front of the flowers, narrowly ovate to ovate, oblique, acute the apical part conduplicate, 6–16 mm long; petals with the basal anticous lobe oblong, 3 mm long, decurrent with the limb; petal limb linear to lorate, 7–12 mm long, the basal part parallel to the anther, the apical part curved upwards behind the anther, the apex dilated, unequally bilobed, up to 4 mm wide; lip spathulate, the claw linear, 5–35 mm long and 1–2 mm wide, the blade obscurely trilobed to deeply trifid, the margins generally undulate, the central lobe usually longer than the lateral lobes, lip may be held horizontally with the blade pendent, or the whole structure may be pendent; anther more or less horizontal, 1–3 mm long, viscidia separate; rostellum equally trifid, erect, the lobes acute, 1–2 mm tall; stigma with the lateral lobes much larger than the odd lobe, horizontal, 2–3 mm wide and 1 mm tall.

Diagnostic features. Petal spathulate, claw linear, 5–35 mm long, bladé obscure trilobed to deeply tripartite; leaves linear, flat, green at anthesis.

Two subspecies are recognized in this species. There are no absolute differentiating characters between the two postulated taxa, but the overlap in variation is minimal (see Fig. 5). The taxa are allopatric, with about 500 km between the two distribution areas. They may therefore be recognized as geographical subspecies.

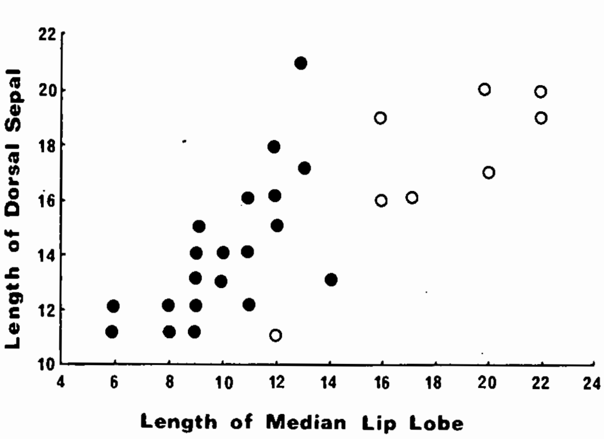

FIG. 5.—Variation in flower size (measured by the length of the dorsal sepal) and lip shape (measured by the length of the median lip lobe) in *H. spathulata*.

(a) subsp. **spathulata**

Orchis spathulata L. f., Suppl. Pl. 398 (1781). *Satyrium spathulatum* (L. f.) Thunb., Prod. 5 (1794). *Disa spathulata* (L. f.) Swartz in Vet. Acad. Handl. 21: 213 (1800); Lindl., Gen. Sp. Orch.353 (1838); Kraenzl., Orch. Gen. Sp. 1: 794 (1900); Schltr. in Bot. Jb. 31: 283 (1901), pro parte. *Herschelia spathulata* (L. f.) Rolfe in Fl. Cap. 5, 3: 205 (1913). Type: Cape of Good Hope, *Thunberg* s.n. (LINN, holo.!; UPS!; W.!).

Disa propinqua Sond. in Linnaea 19: 95 (1847). Type: Cape Province, Clanwilliam Division, Brakfontein, *Ecklon & Zeyher* s.n. (S, holo.!; K!; W!).

D. propinqua Sond. var. *trifida* Sond. in Linnaea 19; 96 (1847). Type: not seen.

D. atropurpurea Sond. in Linnaea 19: 96 (1847); Kraenzl., Orch. Gen. Sp. 1: 794 (1900). *D. spathulata* var *atropurpurea* (Sond.) Schltr. Bot. Jb. 31: 284 (1901). *Herschelia atropurpurea* (Sond.) Rolfe in Fl. Cap. 5, 3: 205 (1913). Type: Cape Province, Tulbagh District, Tulbagh Waterfall, *Ecklon & Zeyher* s.n. (S, holo.!; K!).

Icones: Curtis's bot Mag. t. 6891 (1886), as *Disa atropurpurea;* H. Bol., Icones Orch. Austro-Afr. 3: t. 53 (1913), as *D. spathulata;* 3: t. 54, as *D. spathulata* var. *atropurpurea;* Rice, Wild. Flow. Cape G. H. 163.2 (1950).

Central lobe of lip 5–14 mm long, inflorescence with 1 – 5 flowers (Fig. 6). Distributed in the western Cape Province from Caledon to Nieuwoudtville. Flowering time: September and October.

Widespread in the western Cape Province (Fig. 7) on both sandstone and shale, in a range of habitats, usually occurring in small populations.

CAPE.—3119 (Calvinia): in mountains near Twakfontein, Nieuwoudtville (–AC), *Leipoldt 601* (BOL). 3218 (Clanwilliam): in sand near Swartboschkraal (–BC), Sept. 1894, *Schlechter 5165* (BOL; P; PRE; W; Z). 3319 (Worcester): Tulbagh (–AC), Oct., *Pappe* s.n. (BOL; SAM). 3419 (Caledon): Boontjieskraal (–AA), Sept. 1977, *Linder 1458, 1459* (BOL).

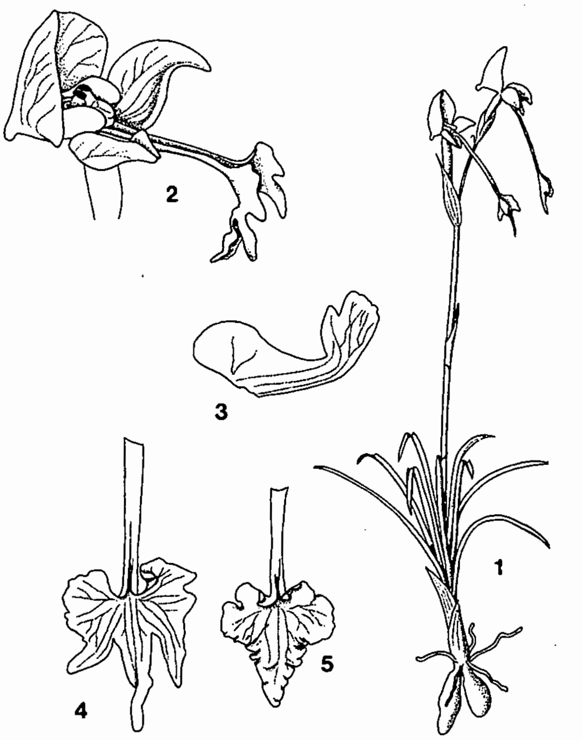

FIG. 6.—*Herschelia spathulata* subsp. *spathulata*. 1, habit, ×0,5, from *Linder* 1244. 2, flower, ×1,5, from *Linder* 1453. 3, petal, ×3, from *Linder* 1453. 4, lip, ×1,5, from *Linder* s.n. 5, lip, ×1,5, from *Linder* 1245.

The altitude range of this species is from 150 to 1 000 m and the precipitation ranges from 200 to 800 mm p.a., mostly occurring in the winter months. The species has been recorded from both gravelly and deep alluvial sands derived from Table Mountain Sandstone, as well as clayey soils derived from Malmesbury shales. Populations growing on shales occurred most frequently on the cooler south-facing slopes, whereas those located on sandstone derived soils ranged from well-drained sites to the margins of temporary vleis.

The variation patterns in this subspecies are complex, with four characters varying extensively (flower size, lip lobe shape, flower colour and the three-dimensional position of the lateral sepals). The characters are to some extent correlated and a small-flowered form (probably *Disa atropurpurea)* and a large-flowered form may be recognized. The small-flowered form has dark red flowers, the lip lobe is more or less ovate and the lateral sepals appear to close at night, whereas the large-flowered form has pale lime or green or pale red flowers, the lip lobe is deeply three-lobed, and the lateral sepals are always spreading. Both forms may be found over the whole distribution range of the subspecies. However, a survey of the available herbarium material indicated that the variation range of each character is continuous, and the characters are not perfectly correlated. No formal taxa are therefore recognized.

The subspecies was studied in the field in several localities. Only at two localities, Wolseley and Caledon, did both forms occur together. At Wolseley (near Worcester) the small-flowered form occurred on a well-drained slope, whereas the large-flowered form occurred about 3 km distant on the margin of a temporary vlei (*Linder* 1244, 1245). At Caledon both forms occurred on the same slope, and the individuals of the two forms occurred intermixed. The

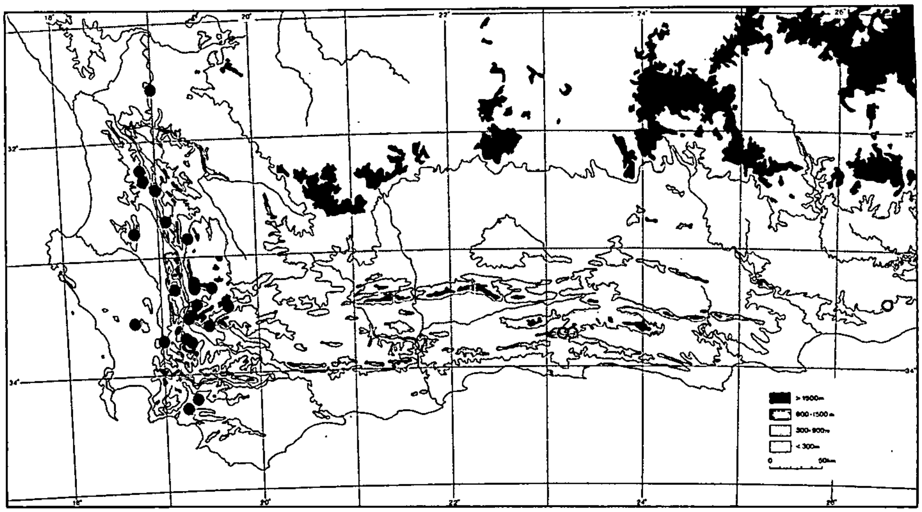

FIG. 7.—Distribution of *H. spathulata* subsp. *spathulata* (solid circles) and subsp. *tripartita* (open circles).

small-flowered form was much rarer than the large-flowered form. An analysis of this population for two characters (flower size and the lip shape) (Fig. 8) clearly shows a bimodal distribution, with a few rare intermediate forms.

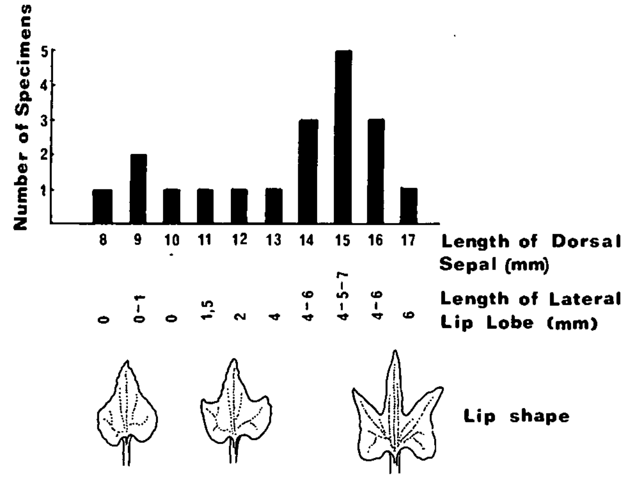

FIG. 8.—Variation in the lip shape, length of the lateral lip lobe and flower size in one population of *H. spathulata* subsp. *spathulata*.

The treatment here is provisional. A detailed study is required to elucidate the mechanism by which this complex polymorphism is maintained. Could this be a case of incipient sympatric speciation?

Sonder (1847) distinguished his *Disa propinqua* from *H. spathulata* by its generally more robust nature. I have studied the type specimen: it is not much different from the type of *H. spathulata* and is clearly included in the range of variation of the latter taxon. *Disa atropurpurea* was distinguished from its congeners by the shorter lip claw and the maroon colour of the flowers (Bolus, 1913; Rolfe, 1913). Lip claw length varies continuously in *H. spathulata* from shorter than that of the type of *D. atropurpurea* to 35 mm. Flower colour and the lip shape indicate, however, that it may well belong to the cryptic small-flowered form discussed above. It appears as if Hooker (1886) and subsequent botanists have misunderstood the complex nature of the so-called *H. atropurpurea*.

(b) subsp. **tripartita** (*Lindl.*) *Linder,* stat. et comb. nov.

Disa tripartita Lindl., Gen. Sp. Orch. 353 (1838); Kraenzl., Orch. Gen. Sp. 1: 797 (1900). Type: Eastern Cape Province, Albany, Geelhoutboom, *Drège* 3577a (K, holo.!; P!; S!).

D. spathulata (L. f.) Swartz, Schltr. in Bot. Jb. 31: 284 (1901), pro parte.

Herschelia tripartita (Lindl.) Rolfe in Fl. Cap. 5, 3: 204 (1913).

Central lobe of the lip (12–) 16–22 mm long, inflorescence with 1–2 flowers. Recorded from the Uniondale area in the Langkloof.

Flowering time: October.

Distribution: Fig. 7.

CAPE.—3323 (Willowmore): Haarlem (–CB), Oct. 1930, *Fourcade 4344* (BOL); Louterwater (–DC), Sept. 1969, *Marsh 1408* (PRE).

This subspecies is rather local in the renosterbosveld near the summit of the Langkloof, near Uniondale. The rainfall in the area is about 600 mm p.a. which is distributed over the whole year.

The type locality for this subspecies is on the Bushmans River, near Grahamstown. This is about 250 km to the east of other known distribution records. It is difficult to decide whether Drège's locality is incorrect, or whether this species is more widely distributed than the present records indicate.

Ser. **Herschelia**

Lip sessile, narrowly elliptical to elliptical, margins crenulate, petals with apices expanded into flabellate structures.

Type species: *H. graminifolia* (Spreng.) Dur. & Schinz.

Two closely related species are included in this series: *H. graminifolia* and *H. purpurascens*. The former species is widespread from the Cape Peninsula to Port Elizabeth, and the latter is restricted to the southern Cape Peninsula and the coastal areas of the Caledon Division. The habitat differences between the two taxa are summarized in Table 3. Although populations of the two species occur within a few kilometres of each other, it is clear that the species occupy quite different habitats. These differences are maintained by the prevention of gene flow between the two species by allochronic flowering (Table 4). The earlier flowering of *H. purpurascens* might be the result of this species occupying a drier habitat but, as the flowering time remains the same under cultivation, it appears to be genetically fixed.

TABLE 3.—A comparison of the habitats of *H. graminifolia* and *H. purpurascens* in the western Cape

Environmental factor	*H. graminifolia*	*H. purpurascens*
Altitude	50 – 1 350 m	0 – 100 m
Rainfall annual*	1 500 – 2 500 mm	800 – 1 200 mm
Rainfall in January*	30 – 80 mm	15 – 25 mm
Fog in summer	Frequent	Never
Snow in winter	Occasional	Never

*Measured at Simonstown and Kleinmond for *H. purpurascens,* and at Table Mountain (Maclears Beacon) and Steenbras Dam (Caledon Division) for *H. graminifolia.*

TABLE 4.—Flowering times of *H. graminifolia* and *H. purpurascens*

Month	*H. graminifolia*	*H. purpurascens*
October	26%	–
November	70%	–
December	4%	12%
January	–	24%
February	–	41%
March	–	22%
Number of collections	27	49

5. **Herschelia graminifolia** (*Spreng.*) *Dur. & Schinz,* Consp. Fl. Afr. 5: 111 (1894); Kraenzl., Orch. Gen. Sp. 1: 802 (1900).

Disa graminifolia Ker-Gawl. ex Spreng. in Linn. Syst. Veg. 3: 699 (1828); Schltr. in Bot. Jb. 31: 290 (1901). Type: Cape of Good Hope, *Masson* s.n. (BM, holo.).

Herschelia coelestis Lindl., Gen. Sp. Orch. 363 (1838); Rolfe in Fl. Cap. 5,3: 201 (1913). Type: Cape of Good Hope, *Burchell* 7801 (K, holo.!).

Icones: Ker-Gawler in Q. Jl Sci. Arts t. 1, fig. 2 (1819); H.Bol. Icones Orch. Austro-Afr. 1: t. 37 (1893); Rice, Wild Flow. Cape G. H. 167.2 (1950); Flower Pl. Afr. 30: t. 1172 (1955).

Plants 500–1 000 mm tall; the base of the stem often with a sheath of old leaf fibres; radical leaves usually 5, 200–500 mm long and up to 5 mm wide, frequently rolled acute, semi-erect; cauline leaves lax, 6–9, 20–40 mm long, acuminate, closely sheathing; inflorescence lax, 40–120 mm long and with 2–6 flowers; bracts about ⅔ as long as the ovaries, dry, broadly ovate, acuminate to setaceous; ovaries 15–25 mm long, straight or slightly curved. *Flowers* blue to violet-purple, apices of the petals green and the lip more purple than the sepals; dorsal sepal erect, galea obtuse, 15–20 mm tall and 5–10 mm deep; spur from the base of the galea, usually straight, 2–4 mm long, clavate, rounded rarely cylindrical and obtuse; lateral sepals narrowly oblong to oblong, obtuse, apiculate, patent, 13–18 mm long and 6–10 mm wide; petals with the basal anticous lobe orbicular to rarely oblong, margins usually entire, 3–4 mm in diameter, limb of the petal lorate, 11–16 mm long, geniculately upcurved through 90° about ⅓ down the length, the apex expanded into a flabellate structure with entire or dentate margins and a diameter of 4–6 mm, twisted to stand erect behind the anther; lip narrowly elliptical to elliptical, margins usually denticulate and down-curved, obtuse, patent, 11–16 mm long; anther c. 5 mm long, viscidia separate or fused; rostellum with three equal lanceolate lobes; stigma flat, unequally three-lobed. Fig. 10.

Diagnostic features. Lip entire, spur 2–4 mm long, clavate, lip flat or the margins somewhat down-curved.

Flowering time: (December–) January to March.

Widespread and local along the coastal mountains from the Cape Peninsula to Port Elizabeth on soils derived from Table Mountain Sandstone, usually in well-drained stony habitats (Fig. 9).

CAPE.—3319 (Worcester): Slanghoek Ridge Peak, 1 350 m (–CA), March 1952, *Esterhuysen* 19990 (BOL). 3318 (Cape Town): Table Mountain, 750 m (–CD), February 1884, *MacOwan & Bolus* 167 (BOL; BM; K; P; SAM; W; ZT). 3320 (Montague): Langeberg near Swellendam (–CD), January 1893, *Schlechter 2061* (BOL; Z). 3323 (Willowmore): Louterwater (–DC), January 1941, *Compton 10499* (NBG).

Although this species is widespread, there appear to be sizeable gaps in the distribution range. This could reflect the lack of botanical exploration of the Langerberg. Distinct populations may be readily recognized, although individuals are quite far apart. There appears to be rather little variation among the populations. Occasional, presumably recessive, white-flowered plants have been found.

The altitude range of the species is from 300 m to 1 500 m, and the majority of collections are from areas receiving in rainfall, an excess of 1 000 mm p.a., usually with no long dry season.

The species was first referred to in the literature by Ker-Gawler, who published a plate of it in 1819. The

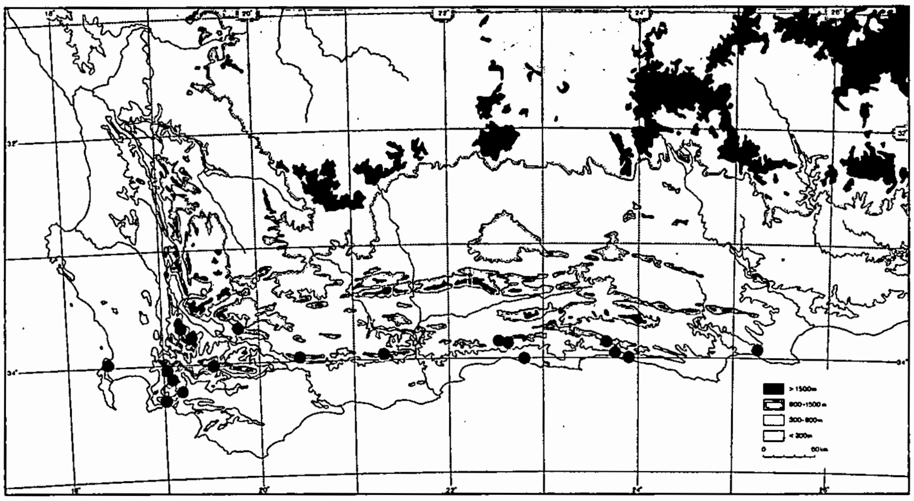

FIG. 9.—Distribution of *Herschelia graminifolia.*

plate was prepared by a 'Dutch' soldier, 'an artist of great skill as a designer of the objects of natural history', whom Francis Masson met at the Cape. Although Ker-Gawler annotated the plate as '*Disa graminifolia'*, he provided neither a description nor a diagnosis. According to Article 32.1 (c) of the I.C.B.N. (1978), the name has to be regarded as a *nomen nudum*. In 1828 Sprengler lists *Disa graminifolia,* providing it with a Latin description and refers to the Masson collection. Sprengler therefore validly published the name.

Lindley (1838) refers the name *Disa graminifolia* to the synonymy of his *Herschelia coelestis.* Rolfe (1913), following the Kew Rule, upheld *Herschelia coelestis* in preference to *H. graminifolia. H. graminifolia,* as the oldest available name, has to be upheld as correct.

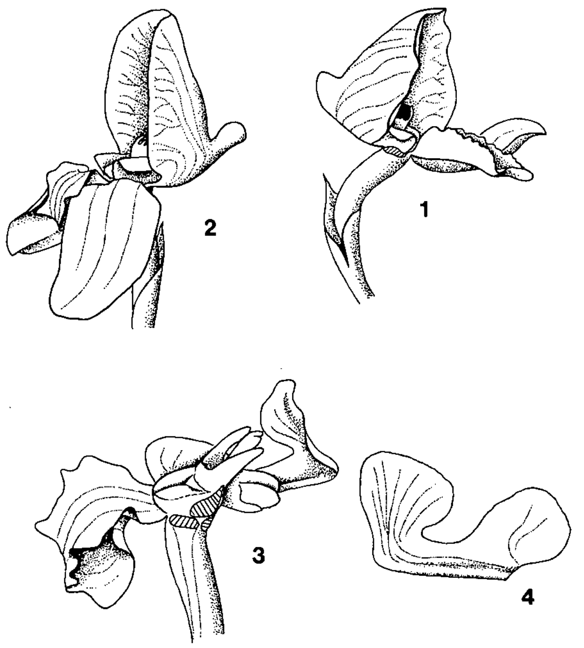

FIG. 10.—*Herschelia purpurascens* (1) and *H. graminifolia* (2–4). 1, flower of *H. purpurascens* with one lateral sepal removed, × 1,5, from *Linder* 759. 2, flower of *H. graminifolia,* × 1,5. 3, lip, column and petal of *H. graminifolia,* × 1,5. 4, petal, × 3. (2–4 from *Linder* 1763.)

6. **Herschelia purpurascens** (*H. Bol.*) *Kraenzl.*, Orch. Gen. Sp. 1: 803 (1900); Rolfe in Fl. Cap. 5,3: 200 (1913). Type: Cape Province, Cape Peninsula, Muizenberg Mountain, *Bolus* 4893 (BOL, holo.!; K!).

Disa purpurascens H. Bol. in J. Linn. Soc., Bot. 20: 482 (1884); Schltr. in Bot. Jb. 31: 291 (1901).

Icones: H. Bol., Icones Orch. Austro-Afr. 1: t. 86 (1896); Rice, Wild Flow. Cape G. H. 146.3 (1950).

Plants 250–500 mm tall; tubers c. 30 mm long and 10 mm in diameter; base of the stem frequently with a sheath of old leaf fibres; radical leaves about 10, from half as long as the stem to as long, up to 1 mm wide, rigid and erect, the midrib sclerenchymatous and prominent; cauline leaves completely sheathing, 5–7, acuminate, dry, 20–40 mm long, grading apically into the floral bracts; inflorescence lax, up to 15 mm long and with 1–2–7 flowers; bracts ½ to ⅔ as long as the ovaries broadly ovate, acuminate to setaceous, dry; ovaries 15–20 mm long, straight or slightly curved. *Flowers* blue, the lip more purplish than the sepals, the rear lobes of the petals yellow or green; dorsal sepal erect, galea subacuminate, 15–25 mm tall and 10–15 mm deep, ovate; spur from the base of the galea, horizontal or slightly curved upwards, conical obtuse, 1–4 mm long; lateral sepals oblong, acute, patent, 15–18 mm long; petals with the basal anticous lobe oblong to semicircular, 3–4 mm in diameter, the margin entire or crenulate, the limb of the petal lorate, 8–10 mm long, falcately curved upwards inside the galea, the apex expanded into a 4–5 mm wide fan with a crenulate margin; lip broadly ovate, obtuse, with a short limb, margins crisped and curved upwards, 12–18 mm long; anther horizontal, 3 mm long, with two viscidia that may be partially fused; rostellum equally 3-lobed, 2,5 mm tall; stigma sub-equally 3-lobed, horizontal, 4 mm in diameter. Fig. 10

Diagnostic features. Lip margin undulate, curved upwards; spur conical, tapering to an obtuse point, lateral sepals 15 – 18 mm long.

Flowering time: October and November.

Local near the coast at low altitudes in the southern Cape Peninsula and the Caledon Division, (Fig. 11), growing in well-drained localities.

CAPE.—3418 (Simonstown): Simonstown (–AB), November 1892, *Fair in BOL 7992* (BOL); Cape Point (–AD), November 1947, *Compton 20236* (NBG). 3419 (Caledon): Betty's Bay (–BD), November 1977, *Linder 759* (BOL).

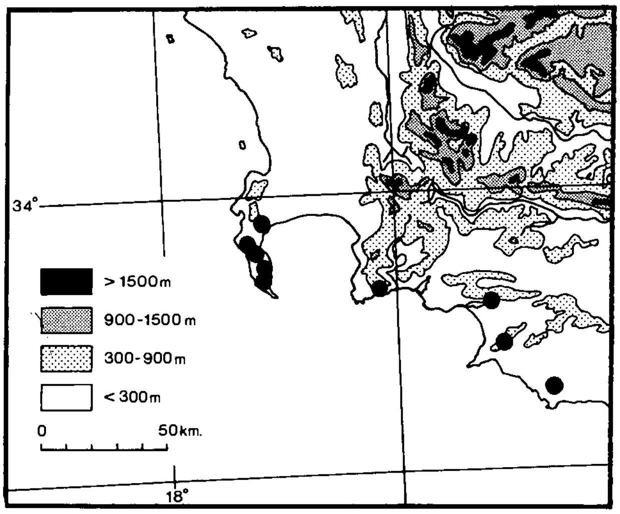

FIG. 11.—Distribution of *Herschelia purpurascens.*

This species has a rather restricted distribution along the coast line along the southern Cape Peninsula and between Cape Hangklip and Cape Agulhas. The altitude range of the species is from sea level to about 100 m. The summers tend to be dry, with only occasional rain. The rainfall in this region varies from 800 to 1 200 mm p.a. Although this species is not common, populations are not as scattered as in *H. graminifolia.* There is not much variation in the species, but occasional plants with white flowers have been recorded (possibly the recessive condition).

H. purpurascens is very close to *H. graminifolia,* from which it may be distinguished by the conical spur, the upcurved lip margins and the much earlier flowering time.

Ser. **Lacerae** *Linder,* ser. nov., labello crenato vel lacero, petalis bidentatis laceris vel acutis. dignoscenda.

Type species: *H. lugens* (H. Bol.) Kraenzl.

Lip sessile or spathulate, the apical blade generally lacerate, rarely entire, petals bidentate, lacerate or acute.

This series contains nine species, all closely related. If a species such as *H. forcipata* or *H. hians* is selected as the starting point, several clear lines of development of the petal and lip structures may be detected. The lines all lead from an entire to a bearded lip, and from a simple acute petal to a lacerate or bifid petal apex. These postulated relationships are graphically shown in Fig. 12.

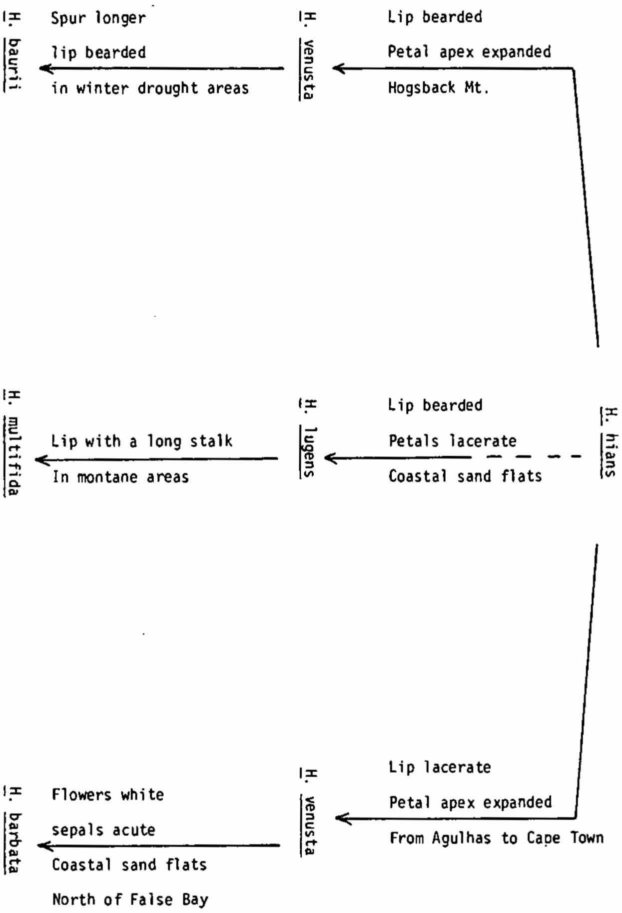

FIG. 12.—Relationships and putative evolution of *Herschelia* ser. *Lacerae*.

The relationships of *H. hians, H. venusta* and *H. forcipata* are not clear, and Hall (1973b) included the former two in the same species. *H. hians* is well established in the southern Cape Province, and the majority of the collections do not show much variation; however, in some populations the lip margins may vary from almost entire to deeply lacerate, as opposed to the normal crenulate condition. *H. forcipata* is clearly very closely related to *H. hians,* but differs in the shallowly bidentate spur and the long floral bracts. It is quite possible that further fieldwork may show that these forms also lie within the range of variation of *H. hians*. The position of *H. venusta* is somewhat clearer. The lip is irregularly lacerated, and the petal somewhat expanded towards the apex (Fig. 14). The distribution of this species is puzzling, with records from the Caledon and Cape Peninsula Divisions, and the Hogsback Mountains near King William's Town. Either the species has had a polytopic origin, or it is merely an extreme form of *H. hians*.

From this postulated basal group three lines of development may be suggested:

(a) to *H. barbata*. This species is quite closely related to *H. venusta,* especially to the forms of that species occurring on the Cape Peninsula. Compared to *H. venusta, H. barbata* shows many of the characteristics of a more recently derived species: an almost unique flower colour (white) in the genus, an inflorescence with few large flowers (cf. Linder, 1981), and a small, probably neo-endemic distribution range. Until a few decades ago, the two species overlapped on the Cape Peninsula, but with the extinction of the Cape Peninsula populations of *H. barbata,* the interaction between the two taxa in the overlap zone can no longer be investigated.

(b) to *H. multifida. H. lugens* and *H. multifida* are closely related, sharing several peculiar characters: lacerate petals, green bearded lips, a shortish conical spur. Morphologically they can only be separated by the length of the lip stalk. Within *H. multifida* there is extensive variation in the length of the lip stalk, but the great majority of the populations possess a lip stalk, longer than 20 mm, whereas only a few populations on the fringes of the distribution range of the species have shorter lip stalks. One collection from the Cape flats, *Schelpe* 6313, possesses some flowers typical of *H. lugens* (Fig. 14); others have a lip stalk up to 10 mm long, approaching the type collection of *H. multifida*. With the exception of the populations around Grahamstown, *H. lugens* occurs on coastal sandy flats, and *H. multifida* occurs in the montane areas. *H. lugens* occasionally grows mixed with *H. hians* (*Hall* 664), but the relationship to this species is not clear.

(c) to *H. baurii. H. baurii* is linked to *H. hians* via *H. venusta,* and again the differences between the species are not very clearcut. Morphologically the South African populations of *H. baurii* may be separated from *H. venusta* by the longer spur and the more deeply dissected lip, whereas the northern populations of *H. baurii* are distinguished by the equally bidentate petals. Ecologically, *H. baurii* is the tropical extension of a Cape genus, and it occurs in areas of winter drought. *H. baurii* shows extensive geographical variation, but in only two places does this result in speciation: in the Chimanimani Mountains (*H. chimanimaniensis*) and the Nyika Plateau (*H. praecox*). Detailed analysis of populations may result in the recognition of geographical subspecies within the species, but at present the data for this are inadequate.

7. **Herschelia barbata** (*L. f.*) *H. Bol.* in J. Linn. Soc., Bot. 19: 236 (1882); Kraenzl. in Orch. Gen. Sp. 1: 804 (1900); Rolfe in Fl. Cap. 5,3: 201 (1913). Type: Cape of Good Hope, *Sparrman* s.n. (LINN, holo.!; S!).

Orchis barbata L. f., Suppl. Pl. 399 (1781). *Satyrium barbatum* (L. f.) Thunb., Prod. 5 (1794). *Disa barbata* (L. f.) Swartz in Vet. Acad. Handl. 21: 212 (1800); Lindl., Gen. Sp. Orch. 354 (1838); Schltr. in Bot. Jb. 31: 286 (1901).

Icones: H. Bol. Icones Orch, Austro-Afr. 3: t. 51 (1913), as *Disa barbata;* Mason, Western Cape Sandveld flowers, Pl. 34.2 (1972).

Plants 250–500 mm tall, the base of the stem often with a sheath of fibrous leaf remains; tubers oval to cylindrical, 20–40 mm long; radical leaves often reaching the base of the inflorescence but never overtopping the flowers, c. 1 mm wide, the base expanded to clasp the stem, conduplicate, 4–7, sclerenchymatous; cauline leaves completely sheathing, lanceolate, acuminate, 20–40 mm long, dry, grading into the floral bracts; inflorescence lax, about 60 mm long and with 2–6 flowers; bracts dry, half as long to as long as the ovary, lanceolate, acuminate; ovaries 15–20 mm long, straight or slightly curved. *Flowers* white to very pale blue, veins and lip more or less blue, spur often green, no scent detected; dorsal sepal angled forwards, galea acuminate, 15–25 mm long, 13–18 mm wide and 8–12 mm deep, ovate; spur conical, not clearly distinct from the galea, usually obtuse to shallowly bifid, rarely acute, straight or rarely upcurved, 1–5 mm long; lateral sepals patent, narrowly oblong, acute, suboblique, 15–25 mm long; petals with the basal anticous lobe oblong, c. 2 mm in diameter, flanking the stigma, usually decurrent with the rest of the petal, the limb linear, straight or subfalcate, 5–6 mm long, apex obtriangular, incised to bifid, 3–4 mm long and c. 3 mm wide; lip horizontal at the base and soon decurved, ovate, deeply lacerate, c. 15 mm long, the entire central part lanceolate, c. 3 mm wide; anther 3 mm long with 2 distinct viscidia, often only partially separated, elliptical to ovate, taller than wide; rostellum almost equally trilobed, lobes awn-shaped, 1,5 mm long, erect; stigma unequally tripulvinate, the odd lobe much smaller than the lateral lobes, horizontal, fused to the base of the rostellum. Fig. 14.

Diagnostic features. Lip deeply lacerated or bearded; flowers white to pale blue with pale blue veins; inflorescence with 2–6 flowers; dorsal sepal acuminate, 15–25 mm long.

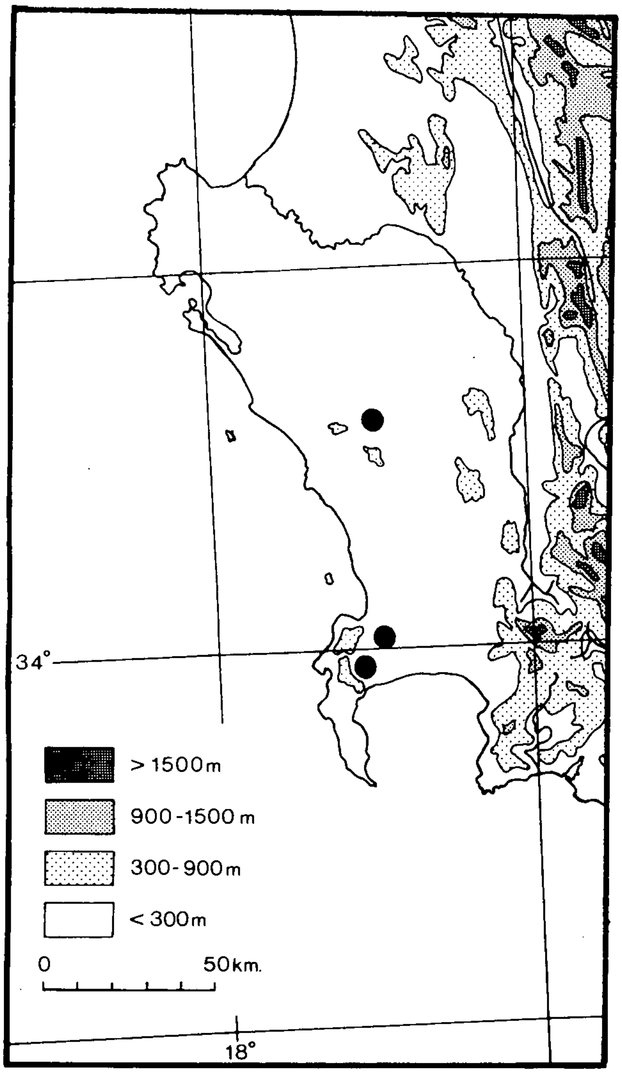

FIG. 13.—Distribution of *Herschelia barbata.*

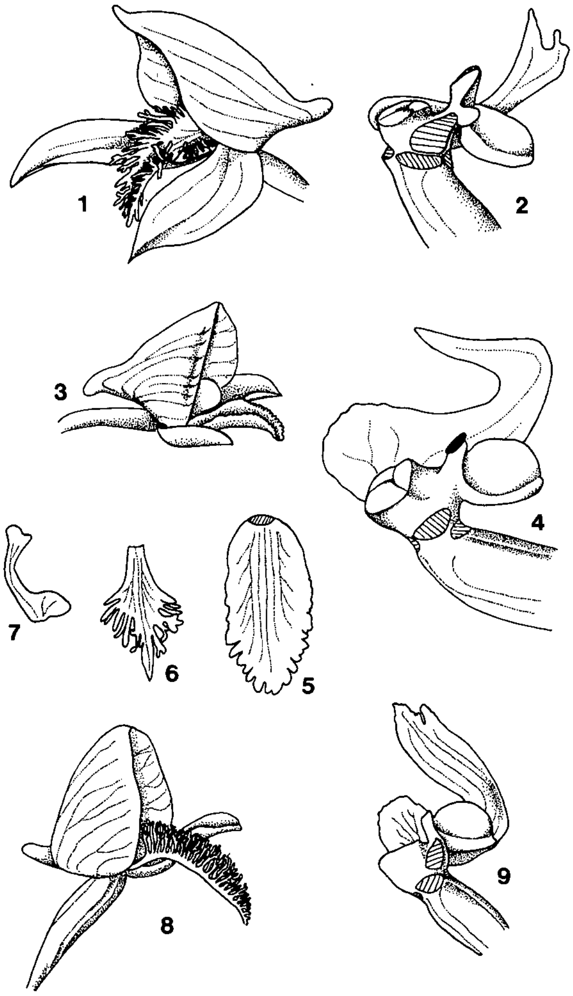

FIG. 14.—*Herschelia barbata* (from *Linder* 1806): 1, flower, × 1,5; 2, column and petal, × 5. *Herschelia hians* (from *Linder* 1731): 3, flower, × 1,5; 4, column and petal, × 6; 5, lip, × 3. *Herschelia venusta* (from *Bolus* 17494): 6, lip, × 3; 7, petal, × 3. *Herschelia lugens:* 8, flower with one lateral sepal removed, × 1,5, from *Schelpe* 6313; 9, column and petal, × 3, from *Jacot-Guillarmod* s.n.

Flowering time: October and November.

Very local and rare in damp sandy localities on the Cape Flats and sandy coastal flats to the north of the Cape Peninsula, mostly extinct (Fig. 13).

CAPE.—3318 (Cape Town): Mamre Road, 150 mm (–BC), November 1978, *Linder 1806* (BOL); sand dunes on the Cape Peninsula, 30 m, (–CD), October 1883, *MacOwan & Bolus* 166 (BM; BOL; K; P; W; ZT).

This species is at present known from a single locality near Darling. Formerly it appears to have been relatively common on the Cape Flats, where it was frequently collected: the populations in these localities now all appear to be extinct. It occurs in damp to wet areas on Recent Sand, near sea level. The rainfall in these areas occurs almost wholly in the winter months, and is approximately 400–600 mm p.a.

This species is closely related to *H. venusta,* from which it may be distinguished by the more acuminate sepals and the white flowers. Formerly the two taxa overlapped on the Cape Peninsula, and both were recorded from the Kenilworth Race Course. Due to human activities during the last decades, the taxa are now allopatric.

8. **Herschelia venusta** (*H. Bol.*) *Kraenzl.*, Orch. Gen. Sp. 1: 805 (1900); Rolfe in Fl. Cap. 5,3: 202 (1913), excl. syn. Type: Cape Province, Cape Flats, *Bolus* 4556 (BOL, lecto.!; K!; PRE!).

Disa venusta H. Bol. in J. Linn. Soc., Bot. 20: 482 (1884).

D. lacera Swartz, Schltr. in Bot. Jb. 31: 287 (1901), pro parte.

Icones: H. Bol., Icones Orch. Austro-Afr. 3: t. 52 (1913), as *D. lacera;* Flower. Pl. Afr. 6: t. 234 (1926), as *D. lacera.*

Plants 300–600 mm tall; tubers up to 40 mm long; base of the stems often with a sheath of old leaf fibres; radical leaves 6–12, reaching to the base of the inflorescence or shorter, less than 2 mm wide, sclerophyllous with the veins prominent, rigid-erect; cauline leaves lax, acuminate, 15–40 mm long, brown; inflorescence lax with 2–5–12 flowers; bracts dry, as long as the ovary or half as long as the ovary, ovate, acuminate; ovaries 15–20 mm long, straight or curved. *Flowers* blue; dorsal sepal erect, acuminate, galea 10–18 mm tall and 4–8 mm deep; spur horizontal from the base of the galea, conical, acute, 1,5–3 mm long; lateral sepals patent, oblong to narrowly oblong, obtuse to acute, 12–16 mm long; petals with small basal anticous lobes, oblong, 1,5 mm long, the limb linear, falcate, 6 mm long, apically expanded to form a fan up to 3 mm wide or unequally and often obliquely bilobed; lip more or less ovate in outline, variably lacerate, shorter than the lateral sepals, curved downwards, 7–12 mm long; anther horizontal, 2 mm long, possibly with the two viscidia fused; rostellum with 3 equal narrowly lanceolate lobes, 1 mm tall; stigma unequally 3-lobed, 2 mm wide and 1 mm tall, horizontal. Fig. 14.

Diagnostic features. Flowers with the lateral sepals 12 – 16 mm long; spur 1,5 – 3 mm long; lip variably lacerate; petals with the basal anticous lobe less than 2 mm long, the limb linear, falcate with an expanded apex or strongly unequally bifid.

Flowering time: October—January.

Local along the coast of the Cape Peninsula and the Caledon Divisions, growing probably in sandy or damp localities, rare in the Hogsback Mountains near King William's Town (Fig. 15).

CAPE.—318 (Cape Town): Kenilworth, 30 m (–CD), *Bolus* s.n. (BOL). 3419 (Caledon): Hermanus Flower Show exhibit (–AD), *Specimen in BOL 17494* (BOL); Vogelgat (–AD), *Schlechter 9544* (BOL; BR; PRE). 3227 (Stutterheim): Hogsback Mountain (–CA), *Rattray in BOL 15770* (BOL).

I have not seen this species in the wild. It occurs from the Cape Peninsula to Hermanus on the Caledon Coast, and near King William's Town. Collector's notes indicate damp habitats, generally under sandy conditions. The taxon is possibly extinct on the Cape Peninsula, where it has only been recorded from the Kenilworth Race Course and from Steenberg. However, it appears to be locally common in the Betty's Bay and Hermanus areas, only flowering after fire.

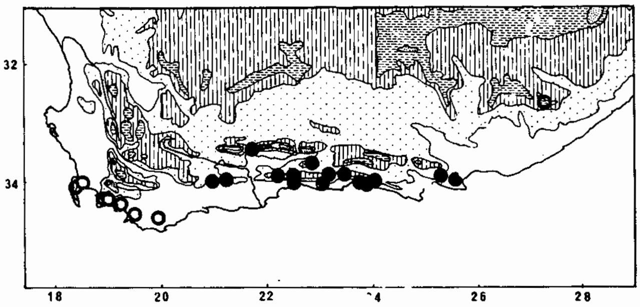

FIG. 15.—Distribution of *Herschelia venusta* (open circles) and *H. hians* (closed circles).

There are two collections from the Hogsback Mountains near King William's Town which have to be referred to this species. However, there are numerous slight differences, difficult to quantify, which raise the possibility that the Hogsback population may have been derived independently from *H. hians.*

This species has previously been included in *H. hians,* as the lip shape was used as the sole differentiating character. Although the lip shape in *H. venusta* is somewhat different from that in *H. hians,* the extensive variation that may be found in a single population in both species is convincing evidence that this character may not be sufficiently reliable for specific delimitation. *H. venusta* may also be differentiated from *H. hians* by the shorter spur, the much more slender petal with a more slender limb, a smaller basal anticous lobe and the enlarged bifid apex, and by the shallower galea. On this evidence, it is here regarded as distinct.

Bolus (1884) cited two syntypes. *Bolus* 4566 occurs in three herbaria, and the material is in better condition, than *Harvey* 140. The former was therefore selected as lectotype.

9. **Herschelia lugens** (*H. Bol.*) *Kraenzl.*, Orch. Gen. Sp. 1; 806 (1900); Rolfe in Fl. Cap. 5,3: 203 (1913). Types: Cape Province, near Cape Town, *Bolus* 3810 (BOL, lecto.!; K!); near Kuils River, *Pappe* 377 (BOL!; SAM!), *Pappe* 39 (BOL!; K!; SAM!), *Ecklon* 1566 (G!; S!; SAM!; W!).

Icones: H. Bol., Icones Orch. Austro-Afr. 2: t. 76 (1911); Curtis's bot. Mag. t. 8415 (1912); Rice, Wild Flow. Cape G. H. 148.2 (1950).

Plants 450–1000 mm tall; tubers 2–3, c. 50 mm long and 20 mm wide: base of the stem often with a sheath of old leaf fibres; radical leaves 8–15, from ½ to ⅔ as long as the shoot, never overtopping the lowest flower in the spike, c. 2 mm wide, rigid erect, the veins sclerified and prominent; cauline leaves lax, acuminate, 60–20 mm long with the longest at the base of the stem, dry, grading into the floral bracts; inflorescence lax, 70–150–400 mm long and with 5–10–25 flowers; bracts about half as long as the ovaries broadly ovate, acuminate to setaceous, dry; ovaries slender, slightly curved, 15–25 mm long. *Flowers* with a cream-green galea, mauve lateral sepals, a green to grey-green lip and white petals, but with some variation in the colour rarely almost black; dorsal sepal erect, galea obtuse, 12–16 mm tall and about 10 mm deep, narrowly ovate; spur from the base of the galea, generally slender, cylindrical, straight or curved upwards, 1–5 mm long, sometimes conical; lateral sepals patent, narrowly oblong, obtuse or acute, 8–13 mm long, subconduplicate in the apical half; petals with the basal anticous lobe oblong, c. 4 mm long, parallel to the stigma; limb linear, 10–15 mm long, with a geniculate bend through c. 90° near the middle, the distal half of the petal varying from obliquely obtriangulate to lorate, acute or deeply lacerate; lip ovate, c. 13–19 mm long, deeply dissected and beard-like, horizontal at the base but soon decurved, longer than the lateral sepals; anther horizontal or semi-pendent, 3 mm long, viscidia separate; rostellum equally 3-lobed, c. 1,5 mm tall; stigma unequally 3-lobed with the odd lobe smaller than the lateral lobes, horizontal, 3 mm in diameter. Fig. 14.

Diagnostic features. Flowers medium-sized, lateral sepals 8–13 mm long; lip bearded, longer than the lateral sepals, greenish or almost black.

Flowering time: October to November (–March).

This species occurs locally along the coastal flats between the Cape Peninsula and Port Elizabeth, usually in sandy well-drained conditions, and around Grahamstown in macchia on sandstone derived soils (Fig. 16).

(a) var. **lugens**

Disa lugens H. Bol. in J. Linn. Soc. 20: 483 (1884); Schltr. in Bot. Jb. 31: 288 (1901).

Flowers cream-green, lip usually much longer than the lateral sepals, widespread from the Cape Peninsula to Grahamstown.

CAPE.—3318 (Cape Town): sand dunes near Cape Town, 30 m (–CD), Nov. 1886, *MacOwan & Bolus 494* (BOL; P; Z; ZT). 3421 (Riversdale): Yzervarkfontein (–BC), May 1913, *Muir 908* (BOL; PRE). 3325 (Port Elizabeth): marshy flats near Van Staadens Railway Station, 300 m (–CC), Oct. 1958, *Hall 664* (BOL). 3326 (Grahamstown): mountains near Grahamstown (–BC), *MacOwan 700* (GRA; SAM).

This variety has a wide distribution, occurring rather locally on the coastal flats. The only inland locality is in macchia on the hills surrounding Grahamstown. In most localities and all localities south-west of Knysna, it occurs on deep sand, and usually grows inside restioid tussocks. A population studied near Grahamstown occurred on soils derived from quartzite. The majority of the populations occur in well-drained conditions, under a rainfall regime that varies from 500 to 1 000 mm p.a., in some areas evenly distributed over the whole year, and in others with a period of summer drought.

The association between plants of this species and restioid tussocks might be a result of predation, as plants under cultivation do not require restioid tussocks for normal growth.

This variety is becoming rare in the western Cape, owing to the spread of urban development in the coastal areas, and the spread of alien vegetation into the remaining habitats. It may already be extinct on the Cape Flats.

It was for some time confused with *Herschelia barbata,* because of the superficial similarity of the two taxa, especially when the plants are dried. Bolus (1884) cited several syntypes in his protologue, indicating that the material was known for some time without being recognized.

(b) var. **nigrescens** *Linder,* var. nov., a var. *lugenti* floribus nigrescentibus differt.

Flowers purplish black, recorded only from the coast at Cape St Francis, near Humansdorp.

TYPE.—Cape, 3424 (Humansdorp): near Oyster Bay in the vicinity of White Point (–BA), *Muller s.n.* (NBG, holo.!).

This almost black variety of *H. lugens* was only discovered in 1979 in the Humansdorp area, and as yet not much information is available about it. It appears to grow in the vicinity of the common *H. lugens var. lugens,* but may be distinguished by the almost black flowers, which also appear to be somewhat larger than is common for the typical variety. It is desirable to recognize this form formally, to prevent any confusion should the taxon be introduced into cultivation.

Information on the genetic status of the variety would doubtlessly give greater certainty about the rank of this taxon.

The two varieties grow sympatrically. Leaves and underground parts of the new variety were not seen.

10. **Herschelia multifida** (*Lindl.*) *Rolfe* in Fl. Cap. 5, 3: 206 (1913). Type: Cape Province, Clanwilliam District, Blouberg, *Drège* 3577b (K, holo.).

Disa multifida Lindl., Gen. Sp. Orch. 353 (1838); Schltr. in Bot. Jb. 31: 285 (1901).

D. charpentieriana Reichb. f. in Linnaea 20: 668 (1847); Schltr. in Bot. Jb. 31: 285 (1901). *Herschelia charpentieriana* (Reichb. f.) Kraenzl., Orch. Gen. Sp. 1: 807 (1900); Rolfe in Fl. Cap. 5, 3: 206 (1913); Hall in Flower. Pl. Afr. 42: t. 1673 (1973). Type: Cape of Good Hope, *Gueinzius* s.n. (W, holo.!).

D. macroglottis Sond. ex Drège in Linnaea 20: 219 (1847), nom. nud.

Icones: H. Bol., Icones Orch. Austro-Afr. 2: t. 77 (1911), as *Disa charpentieriana;* Rice, Wild Flow. Cape G. H. 1771 (1950), as *Herschelia charpentieriana;* Flower. Pl. Afr. 42: t. 1673 (1973), as *H. charpentieriana.*

Plants 400–600 mm tall; tubers up to 40 mm long; base of the stem often with a sheath of old leaf fibres; radical leaves 10–20, usually about half as long as the stem and rarely reaching to the base of the inflorescence, c. 1 mm wide, rigid with sclerenchymatous veins; cauline leaves completely sheathing, 20–50 mm long, lanceolate, acuminate, lax, grading into the floral bracts; inflorescence lax, 40–100 mm long and with 3–8 flowers; bracts

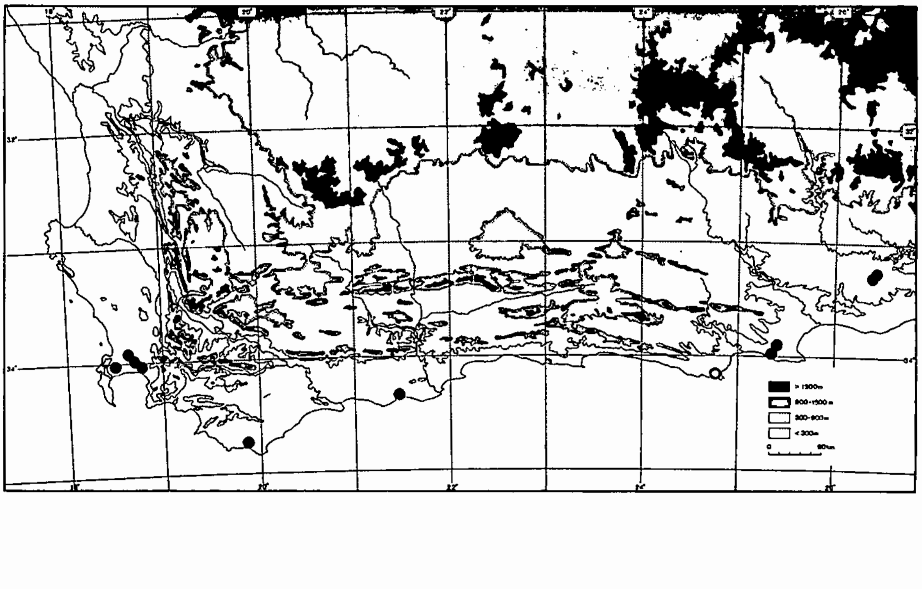

FIG. 16.—Distribution of *Herschelia lugens* var. *lugens* (closed circles) and var. *nigrescens* (open circle).

usually ¾ as long as the ovaries, broadly ovate, very acuminate to setaceous, dry; ovaries 15–20 mm long; straight or slightly curved. *Flowers* blue; with a green lip, often with greenish veins and a brownish spur; dorsal sepal erect, galea ovate, acuminate, 10–20 mm tall and c. 6 mm deep; spur conical, subacute, rarely cylindrical, obtuse or almost absent, generally curved downwards, 1–4–6 mm long; lateral sepals patent, lanceolate to narrowly ovate, acute, 10–15 mm long, the apical halves deeply concave; petals with the basal anticous lobe oblong, 3–4 mm long, the margins entire or crenulate, rarely decurrent with the limb, the limb falcate or rarely geniculate, linear, 7–10 mm long, the apex acute or narrowly obtriangular, occasionally lacerate; lip with a linear (10–) 30–65–100 mm long limb, the blade narrowly ovate, deeply lacerate; anther 3–4 mm long, viscidia narrowly ovate, c. 1 mm long; rostellum equally 3-lobed, lobes lanceolate, 1 mm long; stigma with the lateral lobes better developed than the odd lobe, on a 1 mm tall pedicel, 3,5 mm in diameter. Fig. 17.

Diagnostic features. Lip dissected, with a claw at least twice as long as the dissected blade and usually much longer.

Flowering time: November and December.

Herschelia multifida is a very distinct species that may always be recognized by its peculiar lip with a long claw. It is rather widespread in the mountains of the Cape Floral Region, from Prince Albert in the south-east to the Vanrynsdorp Bokkeveld in the north-west (Fig. 18).

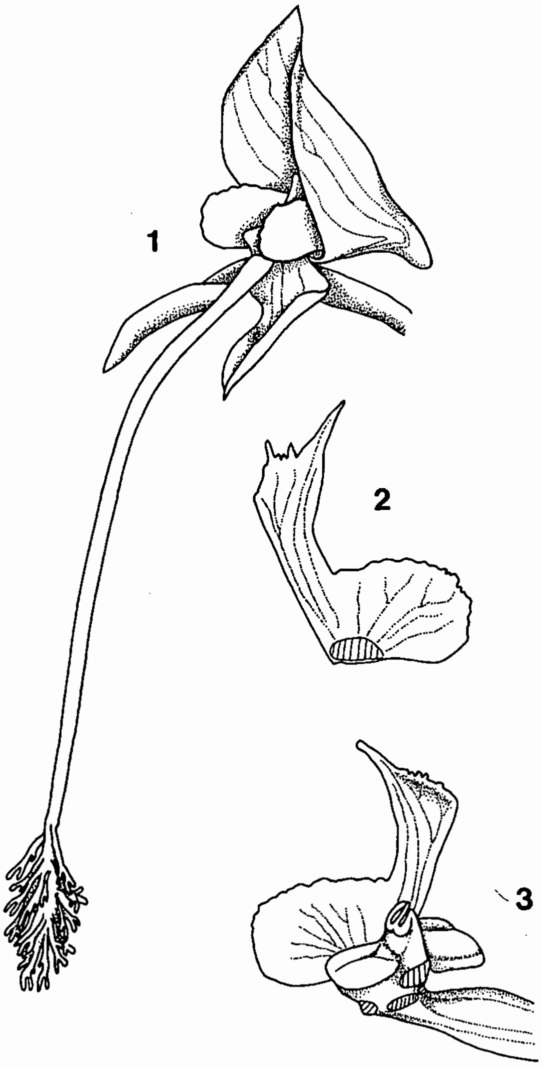

FIG. 17.—*Herschelia multifida*, from *Linder* 1642. 1, flower, ×1,5. 2, petal, ×3. 3, column, ×3.

CAPE.—3219 (Wuppertal): Cedarberg, Nov. 1913, *Pattison in BOL 14455* (BOL). 3319 (Worcester): Agterwitzenberg Vlakte (–AA), Nov. 1967, *Powrie 168* (BOL); Darling Bridge (–CA), Nov. 1940, *Esterhuysen 3802* (BOL). 3419 (Caledon): base of mountains at Highlands Forest, Elgin (–AA), Nov. 1965, *Oliver in STE 29974* (PRE; STE). 3322 (Oudtshoorn): Swartberg Pass, slopes of Krevasberg, 1 200 m (–AC), Dec. 1942, *Stokoe 8679* (BOL).

This species occurs on slightly damp mountain sides: 'swampy slope' (Esterhuysen 20907) on the Roodeberg near Ceres; well-drained soil near a stream on the Piketberg (*Linder* 1642), a slight seepage on a mountain side in the Skurfteberge near Ceres (*Linder* 1656) and a dry, well-drained stony mountain side, in the mist belt, on the Swartberg at Prince Albert (*Linder* 1743). Many of the populations receive snow almost every winter. Rainfall is also concentrated in the winter months, and is about 1 000 mm p.a. The altitude range of the species is from 300 to 1 500 m.

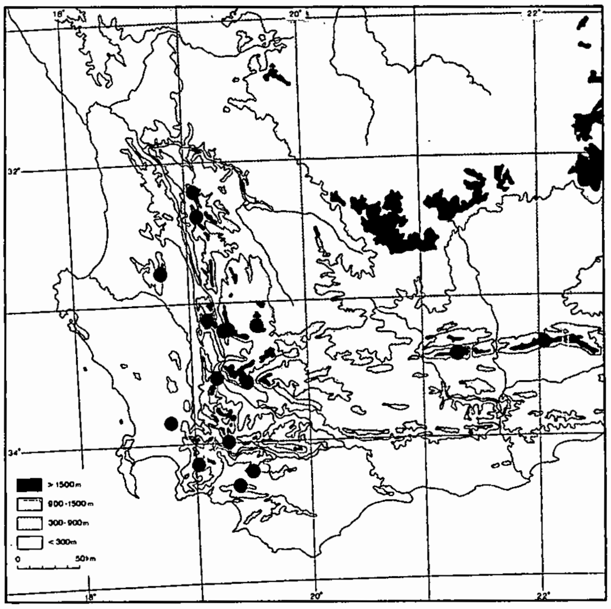

FIG. 18.—Distribution of *Herschelia multifida*.

There is considerable variation in the lip length in this species: this is the basis on which *H. charpentieriana* and *H. multifida* had been separated (Schlechter, 1901; Rolfe, 1913). An analysis of the distribution of the short-spurred forms indicated that these collections all exist at the margin of the distribution area of the species as defined here, i.e. on the Swartberg above Prince Albert and in the Cedarberg and northwards to the Vanrhynsdorp Bokkeveld. It is suggested that the short-spurred form is a variation that occurs in the marginal areas of the species and cannot be formally separated.

Although the type collection of *H. multifida* should be at Kew, I have not seen it. There is a photograph of the type at the Bolus Herbarium and from this the nature of Lindley's *Disa multifida* is clear. There is some uncertainty about the type locality, which Drège indicates as 'Blaauwberg'. It appears to be between Boskloof and Heuningvlei, near Clanwilliam in the northern Cedarberg.

Disa macroglottis Sond. ex Drège has to be treated as a *nomen nudum,* as the name, listed with a reference to an *Ecklon & Zeyher* collection, was published without a description.

11. **Herschelia hians** (*L. f.*) *Hall* in Flower. Pl. Afr. 42: t. 1674 (1973). Type: Cape of Good Hope, *Thunberg* s.n. (LINN, holo.!; UPS!).

Satyrium hians L. f., Suppl. Pl. 401 (1781). *Limodorum hians* (L. f.) Thunb., Prod. 3 (1793). *Disa hians* (L. f.) Spreng., Linn. Syst. Veg. 3: 698 (1826). *Eulophia hians* (L. f.) Spreng., Linn. Syst. Veg. 3: 720 (1826); Rolfe in Fl. Cap. 5,3: 32 (1912).

Disa excelsa sensu Lindl., Gen. Sp. Orch. 356 (1838), non (Thunb.) Swartz; H. Bol. in J. Linn. Soc., Bot. 25: 203 (1889); Schltr. in Bot. Jb. 31: 292 (1901). *Herschelia excelsa* sensu Rolfe, in Fl. Cap. 5,3: 200 (1913), non (Thunb.) Rolfe.

Disa lacera Swartz in Vet. Acad. Handl. 31: 212 (1800); Lindl., Gen. Sp. Orch.: 354 (1838); H. Bolus in J. Linn. Soc., Bot 25: 202 (1889); Kraenzl., Orch. Gen. Sp. 1: 797 (1900); Schltr. in Bot. Jb. 31: 287 (1901). *Herschelia lacera* (Swartz) Fourc. in Trans. R. Soc. S. Afr. 21: 81 (1932). Type: Cape of Good Hope, *Sparrman* s.n. (W, holo.!).

Disa outeniquensis Schltr. in Ann. Transv. Mus. 10: 246 (1924). Type: Cape Province, Mossel Bay District, Robinson Pass, *Bolus* 12327 (BOL, lecto.!).

D. lacera Swartz var. *multifida* N. E. Br. in Gdnrs' Chron. 1888 2: 664 (1888). Iconotype: Gdnrs' Chron. 1888, 2, fig. 93 (1888).

Icones: Curtis's bot. Mag. 115: t. 7066 (1889); Flower. Pl. Afr. 42: t. 1674 (1973).

Plants 400–600 mm tall; tubers up to 20 mm long; base of the stem often with a sheath of old leaf fibres; radical leaves 8–13, often hysteranthous, reaching up to the base of the inflorescence or shorter, less than 2 mm wide, sclerophyllous with prominent veins, semi-rigid erect; cauline leaves completely sheathing, lax, acuminate, brown, 20–40 mm long; inflorescence lax, up to 200 mm long and with 3–16 flowers; bracts from half as long to as long as the ovaries, ovate to broadly ovate, acuminate to setaceous, dry; ovaries 15–20 mm long, slender, usually curved. *Flowers* varying in colour from very pale blue to purplish blue, the lip frequently darker coloured than the sepals; dorsal sepal erect, obtuse to more commonly acute, galea 10–15 mm long and 8–10 mm deep, ovate to broadly ovate; spur horizontally from the base of the galea, at length decurved, conical, tapering to a subacute apex, 4–6 mm long; lateral sepals patent, oblong-narrowly ovate to rarely narrowly oblong, usually rounded, rarely acute, the apical part subconduplicate, 8–12 mm long; petals with the basal anticous lobe broadly oblong, rounded or truncate, the margins entire or shallowly serrulate, subdecurrent with the limb, 3–4 mm long, the limb lorate, 7–10 mm long, the apex acute or rarely with the small tooth to the rear, curved falcately or geniculately upwards behind the anther; lip patent with the margins curved upwards, narrowly oblong, oblong or broadly elliptical, rarely broadly auriculate at the base, the margins rarely entire, the distal margin usually more or less crenulate to rarely lacerate, 7–12 long; anther horizontal, 2–3 mm long, viscidia separate; rostellum with 3 equal narrowly lanceolate lobes, 1 mm tall; stigma unequally 3 lobed with the odd lobe smaller than the lateral lobes, horizontal, 2–2,5 mm in diameter and on a 1 mm tall pedicel. Fig. 14.

Diagnostic features. Flowers with the lateral sepals 8–12 mm long; lip narrowly oblong to broadly elliptical, the margins entire or more commonly with the distal margin crenulate; petals with the limb lorate, the apex acute; spur 4–6 mm long.

Flowering time: December to January (–February).

Widespread and fairly common in the southern Cape Province on the coastal flats and the first range of mountains, occurring mostly on well-drained and often stony sandstone mountain slopes and flats (Fig. 15).

CAPE.—3419 (Caledon): Hermanus (–AC), Jan. 1920, *Burtt Davy 18483* (BOL). 3321 (Ladismith): Garcias Pass (–CC), Dec. 1977, *Linder 1714* (BOL). 3322 (Oudtshoorn): mountains near George (–CD), Jan. 1897, *Bolus 13514* (BOL). 3422 (Mosselbay): near Sedgefield, near Knysna, 30 m (–BB), Oct. 1963, *Chater* s.n. (BOL; PRE; STE). 3323 (Willowmore): Outeniqua mountains near Joubertina (–DD), Jan. 1947, *Esterhuysen 13599* (BOL; K; PRE). 3325 (Port Elizabeth): Port Elizabeth (–DC), Feb. 1889, *Galpin 391* (PRE).

This species forms open scattered populations throughout the southern Cape Province, generally on well-drained and often stony soils. The rainfall in the area is almost evenly distributed over the whole year, and the total rainfall ranges from 600 to over 1 000 mm p.a. The altitude range of the species if from 80 m to over 1 000 m.

Extensive variation in flower colour and lip laceration occurs. The majority of populations investigated showed extraordinary colour variation, from pale sky-blue to deep purple-blue flowers. Colour variation commonly occurs within populations, but lip variation tends to be rather between populations. In the Knysna area the lip is occasionally entire. Despite extensive searching, I have failed to locate any such populations, but occasional herbarium specimens with entire lips are known from the Knysna area. Over the rest of the range the distal margin of the lip tends to be shallowly crenulate. In the Langeberg near Riversdale the lip frequently shows two broad auricles at the base, and the apex is variably shallowly lancerate (type of *D. lacera* Swartz agrees with this lip shape) (*Linder* 1714). Some collections from near Port Elizabeth also show lips that are variably lacerate (e.g. *Hall* 1160).

Hall (1973b) partially resolved the nomenclatural confusion surrounding the correct name for this taxon. *Satyrium hians* L. f. [= *Limodorum hians* (L. f.) Thunb.] was transferred to *Eulophia* by Sprengel and was mistaken for *Eulophia clavicornis* by subsequent botanists (Lindley, 1838; Bolus, 1889; Rolfe, 1912). Sprengel cited Thunberg's *Limodorum hians* as basionym. However, Sprengel had also transferred the epithet to *Disa,* citing *Satyrium hians* L. f. as basionym.

Thunberg (1794) proposed *Satyrium excelsum* as a *nomen novum* for *Orchis tripetaloides* L. f. As *Orchis tripetaloides* is a perfectly good name, *S. excelsum* has to be regarded as a superfluous name. Swartz (1800) transferred the epithet to *Disa.* Lindley (1838) noted that Thunberg's descriptions of *D. excelsa* (Thunb.) Swartz did not agree with the type of *O. tripetaloides* and maintained it as a distinct species. However, since the name is derived from a superfluous name, *Disa excelsa* sensu Lindley has to be regarded as a illegitimate name. The same then applies to *Herschelia excelsa* (Thunb.) Rolfe.

Disa lacera has generally been regarded as the same species as *D. venusta.* However, a study of the type found in Vienna showed that *D. lacera* agrees more with the form of *H. hians* found in the Langeberg at Riversdale than with *D. venusta.* Swartz's protologue, describing the lip as oblong, substantiates this finding, and *D. lacera* is included as a synonym under *H. hians.* The var. *multifida* which N. E. Brown described appears to be a more lacerate version of *D. hians,* of which a few collections from the Knysna area had been recorded. It does not show the characters of *H. venusta.*

Disa outeniquensis of Schlechter agrees in all characters with the most common form of *H. hians.*

12. **Herschelia forcipata** (*Schltr.*) *Kraenzl.*, Orch. Gen. Sp. 1: 807 (1900); Rolfe in Fl. Cap. 5, 3: 200 (1913). Type: Cape, *Trimen* s.n. (BM, holo.!).

Disa forcipata Schltr. in Bot. Jb. 24: 428 (1897); in Bot. Jb. 31: 292 (1901).

Plant 600 mm tall; radical leaves and tubers not known; cauline leaves closely sheathing, acuminate, subimbricate, 40–50 mm long, dry; inflorescence laxly 25-flowered, 200 mm tall, cylindrical; bracts as long as the ovaries, lanceolate, acuminate, dry; ovaries slender, generally straight, c. 20 mm long. *Flowers* greenish yellow; dorsal sepal acute, galea broadly ovate, c. 13 mm long and 6 mm deep; spur horizontal from the base of the galea, slender cylindrical, straight, 3–4 mm long, the apex bifid; petals with a smaller orbicular basal anticous lobe, decurrent with the limb, 2 mm in diameter, the limb lorate, geniculately curved up through 90° behind the anther, c. 10 mm long, the apex unequally bifid, the lobes acute, the anterior lobe longer than the posterior lobe; lip lanceolate, acute, the margins entire, c. 10 mm long; anther reflexed width the connective shorter than the cells; rostellum erect, trifid, the lobes acute; stigma pulvinate.

Diagnostic features. Lip lanceolate, acute, entire; petals with the apices bilobed, spur horizontal, slender, bifid.

This species is known from the single plant in Trimen's collection, made somewhere in the Cape in 1870, probably in the Knysna area (Schelpe pers. com). It is a very distinct taxon by virtue of the bilobed petals, the entire lip, the peculiar spur and rather dense inflorescence. It appears to be related to *H. hians,* rather than to the *H. graminifolia* group, as Schlechter (1897, 1901) and Rolfe (1913) suggested. The greenish yellow colour indicated by the collector, however, is reminiscent of *H. lugens.*

13. **Herschelia praecox** *Linder,* sp. nov., a *H. baurii* (H. Bol.) Kraenzl. labello fere integro, petalis pro ratione majoribus differt. Crescit in graminosis montis Nyikae Malaworum.

Type.—Zambia, Northern Province, Nyika Plateau, Sept. 1967, *Williamson* 312 (K, holo.!).

Plants 200–400 mm tall; tubers ovate, about 30 mm long; stems usually with a basal sheath of fibrous leaf remains; radical leaves produced after flowering, about 6, c. 300 mm long and 1–2 mm wide, semi-erect, subsclerophyllous; cauline leaves lax, acuminate, completely sheathing, c. 20 mm long; inflorescence laxly 2–10 flowered and 40–130 mm long; bracts ovate, acuminate, dry, about 10 mm long; ovaries 10–15 mm long, usually curved. *Flowers* white to blue or dark mauve, occasionally the apices of the petals green; dorsal sepal erect, galea acuminate with the apex reflexed, ovate, 10–12 mm tall, c. 8 mm wide and 4–6 mm deep; spur horizontal from the base of the galea, often gradually ascending, cylindrical to laterally flattened, rounded, c. 2 mm in diameter and 3–5 mm long; lateral sepals patent, narrowly ovate to lanceolate, subacuminate, 10–12 mm long, shallowly concave; petals with an ovate basal anticous lobe, c. 2 mm in diameter, the limb lorate, falcately curved up next to the anther inside the galea, c. 12 mm long and 1,5–2 mm wide, the apex widened and unequally acutely bilobed with the anterior lobe longer than the posterior lobe; lip narrowly ovate to lanceolate, 11–13 mm long, margins varying from almost entire to shallowly fimbriate, curved upwards; anther horizontal, c. 3 mm long, the connective longer than the anther; rostellum with 1,5 mm tall canaliculate erect lateral lobes; stigma subsessile, somewhat angled forwards. Fig. 20.

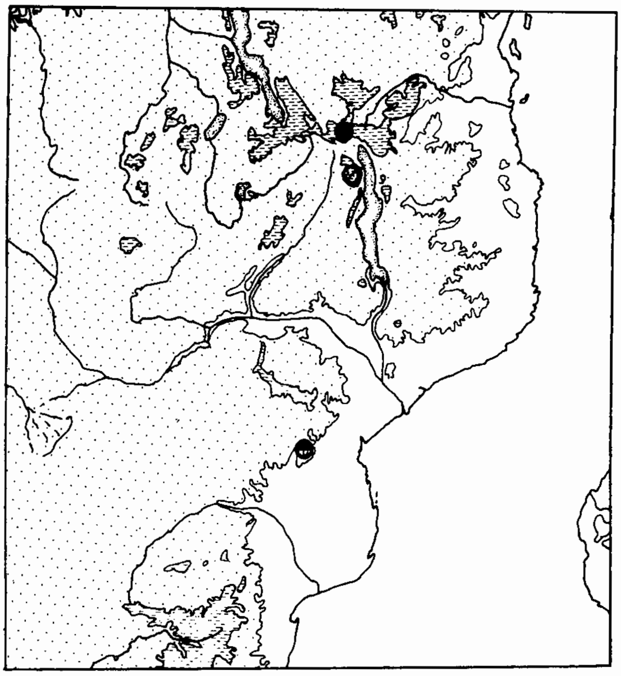

FIG. 19.—Distribution of *Herschelia praecox* (open circle), *H. goetzeana* (solid circle) and *H. chimanimaniensis* (half-solid circle).

Diagnostic features. A short plant, flowering in September, shortly after the winter grass fires, re-

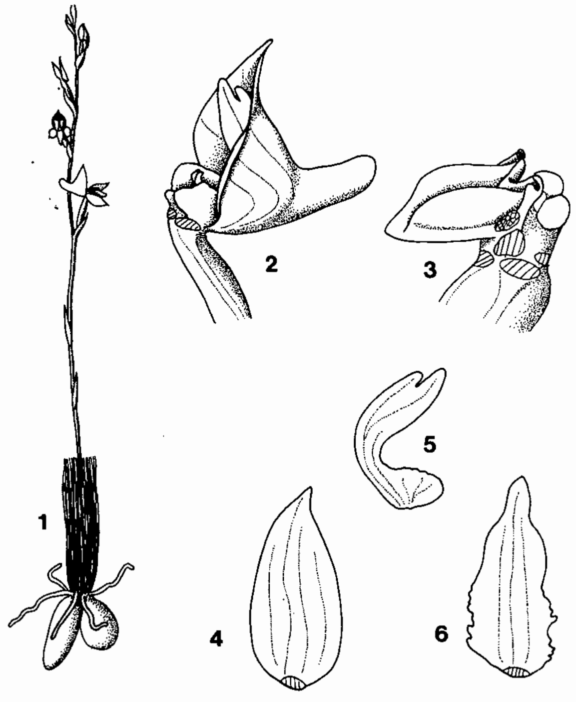

FIG. 20.—*Herschelia praecox.* 1, habit, ×0,5. 2, flower with the lateral sepals and the lip removed, ×6. 3, column, ×8. 4, lateral sepal, ×6. 5, petal, ×6. 6, lip, ×6. 1 from *Tyrer* 726, 2–6 from *Williamson* 312.

stricted to the montane grasslands on the Nyika Plateau, Malawi and Zambia.

MALAWI.—Northern Province, Rumphi District, Nyika Plateau, September 1962, *Tyrer* 966 (BM; SRGH).

ZAMBIA.—Northern Province, Lundazi District, Nyika Plateau, September 1964, *Robinson 6259;* September 1968, *Williamson 1023* (K; SRGH).

The epithet *'praecox'* refers to the early flowering time, shortly after the winter fires.

H. praecox is very similar to *H. baurii,* and if it were compared with all the variations of the latter taxon over its whole range, it might be found difficult to maintain as a distinct taxon. The entire distribution area of *H. praecox* is included in that of *H. baurii.* In the overlap region, on the Nyika Plateau, the flowers of *H. baurii* are larger than anywhere in the rest of its range (Fig. 22), therefore creating a size differential from *H. praecox.* There is also a shift in flowering time: on the plateau, *H. baurii* flowers in October and November, whereas *H. praecox* flowers in September. This difference was also noted by Williamson (1977). Morphologically, the lack of deep dissection of the lip and the large petals provide substantiation for what is clearly a biological micro-species.

H. praecox grows in well-drained short montane grassland on the Nyika Plateau (Vesey-Fitsgerald, 1963; Chapman & White, 1970), under a rainfall regime of 1 000 – 2 000 mm p.a., mostly concentrated during the summer months. The winter months are dry, with occasional frost and frequent grass fires. *H. praecox* appears to flower after the fires, possibly before the first rains and before the grasses grow tall, therefore the flower spikes do not have to compete with the grasses and are consequently short. Leaves are only produced when flowering is completed, possibly after the rains start. As such, this species occupies the temporal niche before that of *H. baurii.*

14. **Herschelia baurii** (*H. Bol.*) *Kraenzl.,* Orch. Gen. Sp. 1: 804 (1900); Rolfe in Fl. Cap. 5, 3: 204 (1913. Type: Mt Baziya, *Baur* 814 (K, holo.!).

Disa baurii H. Bol. in J. Linn. Soc., Bot. 25: 174 (1889); Schltr. in Bot. Jb. 31: 289 (1901).

D. hamatopetala Rendle in Trans. Linn. Soc., 2, 4: 47 (1894); N. E. Br. in Fl. Trop. Afr. 7: 286 (1898); Summerh. in Fl. Trop. E. Afr. 156: 177 (1968). *Herschelia hamatopetala* (Rendle) Kraenzl., Orch. Gen. Sp. 1: 803 (1900). Type: Malawi, Mt Mlanje, *Whyte* s.n. (K, lecto.!).

Herschelia bachmanniana Kraenzl., Orch. Gen. Sp. 1: 805 (1900). Type: Transkei, East Pondoland, *Bachmann* 414 (?B†).

Disa longilabris Schltr. in Bot. Jb. 38: 150 (1907). *Herschelia longilabris* (Schltr.) Rolfe in Orch. Rev. 27: 9 (1919). Type: Tanzania, Kinga Mountains, slopes of Mt Buongwe, *Goetze* 1222, 1226 (B, holo. †; Z!).

Icones: H. M. L. Bol. in Ann. Bolus Herb. 4: Pl. 11 (1926); Williamson, The orchids of south-central Africa, Pl. 71 (1977).

Plants 200–400 mm tall; tubers 20–30 mm long; base of the stem frequently with a thick sheath of old leaf fibres; radical leaves 5–10, produced after flowering, frequently overtopping the spike, up to 300 mm long and less than 2 mm wide, semirigid and subsclerophyllous; cauline leaves lax, completely sheathing, acuminate, 15–25 mm long, larger towards the base of the stem; inflorescence lax, rarely subsecund, with 2–14 flowers; bracts usually about ½ as long as the ovaries, rarely as long as the ovaries, ovate, acuminate, dry; ovaries straight or curved, 10–15 mm long. *Flowers* varying from pale sky-blue to deep purple-blue, the lip frequently a darker blue than the sepals; dorsal sepal erect, galea ovate, acute, (8–) 10–20 mm tall, 6–12 mm wide and 5–10 mm deep; spur horizontal from the base of the galea, often somewhat ascending, cylindrical, rounded, 4–6 mm long; lateral sepals patent, oblong to rarely lanceolate, acute to rounded, (8–) 10–18 mm long, shallowly concave; petals with the basal anticous lobe oblong to ovate, 1–2,5 mm in diameter, rounded, the margin rarely crenulate, limb linear, 8–13 mm long, the apex variously expanded, deeply bifid to lacerate to acute; lip horizontal, at least at the base, broadly to narrowly ovate, 10–25 mm long, more or less deeply dissected; anther horizontal, 2–5 mm long, viscidia separate, ovate; rostellum erect, 2–3 mm tall, equally 3-lobed; stigma horizontal, 1 mm tall and 1,5–2,5 mm in diameter. Fig. 22.

Diagnostic features. Flowers with the lateral sepals 10–18 mm long; lip deeply and unevenly lacerate, generally longer than the lateral sepals; petals with usually a bilobed apex; spur generally cylindrical and obtuse,

Flowering time: mostly September and October, but with occasional collections from almost every month of the year.

A variable plant with hysteranthous leaves which occurs widespread in the montane grassland in southern and south-central Africa (Fig. 21), flowering at the beginning of the rainy season.

TRANSKEI.—3129 (Port St Johns): Msimkaba River mouth (–BA), Aug. 1976, *Venter & Vorster 195* (PRE).

NATAL.—2929 (Underberg): Kamberg (–BD), Oct. 1941, *Schelpe 013* (NU).

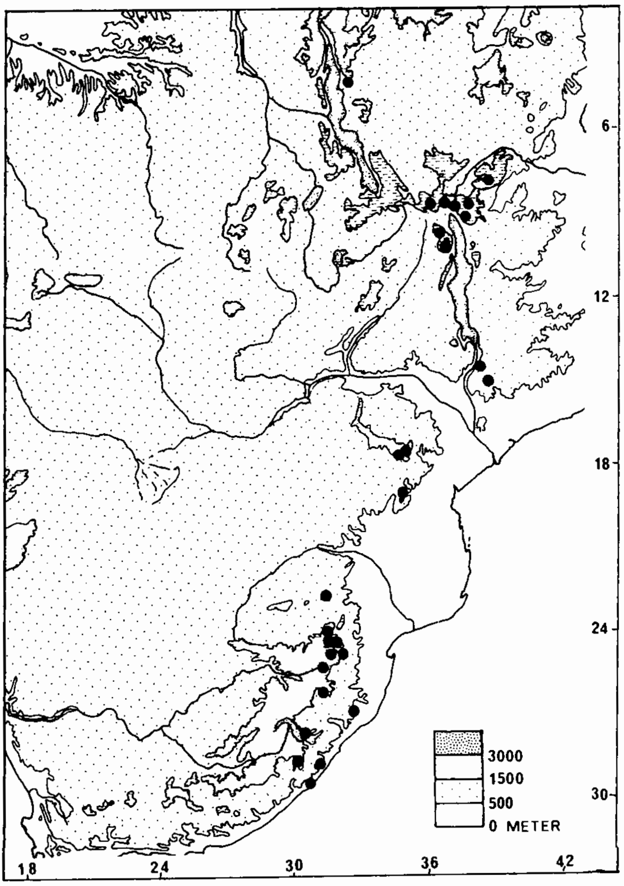

FIG. 21.—Distribution of *Herschelia baurii.*

SWAZILAND.—Sept. 1910, *Steward 8875* (PRE).

TRANSVAAL.—2630 (Carolina): Brereton P.S. (–CD), Sept. 1945, *Acocks 11731* (PRE). 2531 (Komatipoort): Saddleback Mountains, Barberton (–CC), Sept. 1889, *Galpin 427* (BOL, PRE). 2330 (Tzaneen): Woodbush Mountains (–CC), Sept. 1927, *Moss 15432* (PRE).

ZIMBABWE.—Melsetter District, Mt Musapa, 2100 m, *Wild 3556* (K; SRGH). Inyanga District, World's View, Sept. 1956, *Davies 2120* (K; SRGH). Inyanga District, head on Nyamaziwa River, 1800 m Sept. 1965, *Biegel 257* (SRGH).

MALAWI.—Southern Province, Mulanje District, Mt Mlanje, 2 000 m, Oct. 1941, *Greenway 6318* (K). Northern Province, Rumphi District, Nyika Plateau, Oct. 1958, *Robson 297* (K).

TANZANIA.—Southern Highlands, Njombe District, Elton Plateau, Nov. 1963, *Richards 18500* (K); Mbeya District, summit of Mt Mbeya, Oct. 1957, *Watermeyer 167* (K).

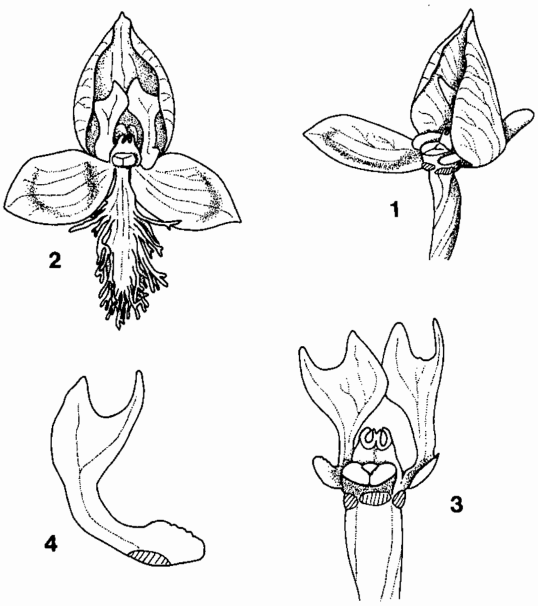

FIG. 22.—*Herschelia baurii,* from *Williamson* 119. 1, flower with the lateral sepal and the lip removed, ×1,5. 2, front view of flower, ×1,5. 3, front view of column and petals, ×3. 4, petal, ×3.

This species occurs in the grasslands of the Montane Region (White, 1978), between Grahamstown in the eastern Cape Province and Kigoma in western Tanzania. Robyns & Tournay (1955) also recorded this species from the Ruwenzori Mountains in Zaire. In general, the altitude range of these grasslands is from 1 000 to 2 400 m, and they receive approximately 1 000 to 1 500 m rainfall p.a., concentrated in the summer months, usually with about four dry months in winter (Jackson, 1961; Phipps & Goodier, 1962; Chapman & White, 1970). Vesey-Fitzgerald (1963) notes that the grasslands are generally burnt in the winter months, after which the geophytes flower. During the rainy season the grasses grow rapidly, to flower at the end of the rainy season. *H. baurii* exploits the temporal niche at the beginning of the rainy season, before the grasses grow tall. This lack of height competition is manifested by the rather short flowering spikes. The leaves are produced after flowering is completed.

As might be expected from such a wide-ranging species, there is extensive geographical variation. Plants from Malawi tend to have much larger flowers, and relatively shorter spurs, than plants from Zimbabwe or South Africa (Fig. 23). In South Africa the petals usually do not have deeply bifid apices, but are narrowly obtriangulate towards the apex, often obliquely bifid or lacerate, whilst over the rest of the range the petals are deeply bifid. The geographical variation in flower size is shown in Fig. 23. This variation has been used to maintain separate taxa for South Africa and the areas north of South Africa (Summerhayes, 1968). However, a detailed study has shown that there is extensive overlap for all characters, with collections from Zimbabwe frequently intermediate between those from South Africa and those from Malawi.

In south Tanzania a smaller-flowered form occurs, which has been kept distinct as *Disa longilabris* by Summerhayes (1968). However, it only appears to be smaller in all its parts than *H. baurii,* and the characters mentioned by Summerhayes (1968) were found to be variable. However, there is little material of *D. longilabris* and the available evidence indicates that it is best treated as a depauperate form of *H. baurii.*

The type material of *H. bachmanniana* could not be traced. Kraenzlin (1900) notes that it is very similar to *H. baurii,* but that it possesses a much shorter spur, rounded sepals, dissected petals and flattened lip fimbriae. However, the type specimen of *D. baurii* is peculiar in that the spur is about twice as long as is typical for the species and this probably confused Kraenzlin. The other characters mentioned by Kraenzlin occur in *H. baurii.*

15. **Herschelia chimanimaniensis** *Linder,* sp. nov., a *H. baurii* (H. Bol.) Kraenzl. floribus minoribus, sepalis lateralibus 6 – 8 mm longis differt.

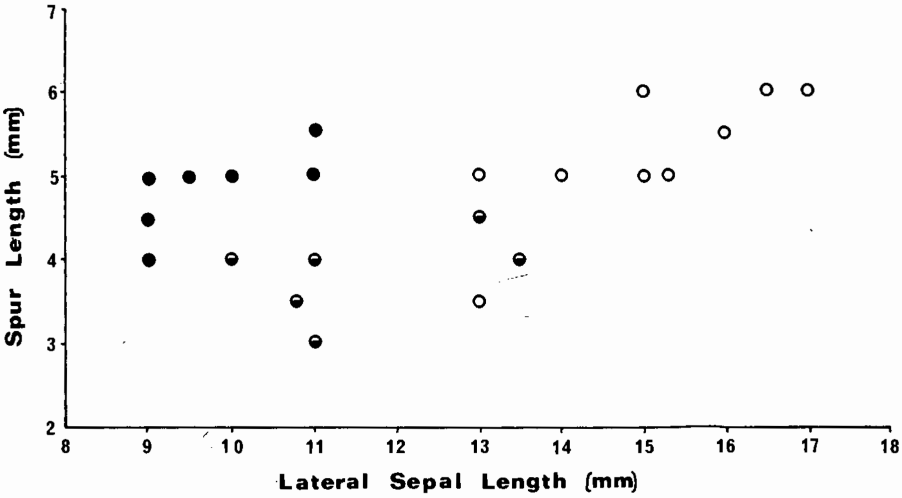

FIG. 23.—Geographical variation in flower size and spur length in *Herschelia baurii.* Material from South Africa plotted in solid circles, from Zimbabwe in half-solid circles and from Malawi and Tanzania in open circles.

Crescit in montibus Chimanimanorum Zimbabwe.

TYPE.—Zimbabwe, Chimanimani, *Ball* 577 (K, holo.!; SRGH!).

Plants slender, 200–400 mm tall; base of the stem occasionally with a sheath of the fibrous leaf remains; radical leaves apparently produced after flowering, 3–6, 150–200 mm long and 1–2 mm wide, subsclerophyllous; cauline leaves closely sheathing, 4–8, 15–20 mm long, acuminate, the lower 2–3 much larger and imbricate; inflorescence laxly 2–8-flowered, 30–80 mm long; bracts ovate, acuminate, about half as long as the ovary, dry; ovaries 5–15 mm long. *Flowers* pink-mauve to white, rarely blue; dorsal sepal erect, galea ovate, acute, 5–7 mm tall, 4 mm wide and 4 mm deep; spur horizontal from the base of the galea, often gradually ascending, straight, cylindrical or somewhat laterally flattened, rounded, 3–4 mm long; lateral sepals patent, narrowly oblong – ovate, acute, 6–8 mm long, shallowly concave; petals with the basal anticous lobe ovate, 1–1,5 mm in diameter, the limb lorate, falcately curved up next to the anther, included in the galea, c. 5,5 mm long and 1 mm wide, the apex acutely bifid; lip ovate, 8–10 mm long, deeply dissected, the margins curved upwards; anther horizontal, c. 1,5 mm long; rostellum lateral lobes canaliculate, erect, 1–1,5 mm tall; stigma horizontal, c. 0,6 mm tall, flat, c. 1 mm in diameter. Fig. 24.

Diagnostic features. Plants slender, flowers small with the lateral sepals 6–8 mm long. Occurs in the Chimanimani Mountains of Zimbabwe.

Flowering time: September and October.

A small-flowered and very slender plant which occurs between about 1 500 and 1 800 m in the Chimanimani Mountains in eastern Zimbabwe and the neighbouring areas in Mozambique (Fig. 19).

ZIMBABWE.—Melsetter District, Chimanimani Mountains, Oct. 1950, *Munch 327* (K; SRGH); *Grosvenor 178* (K; SRGH).

MOZAMBIQUE.—Manica e Sofala District, Chimanimani Mountains, August 1964, *Whellan 2145* (SRGH).

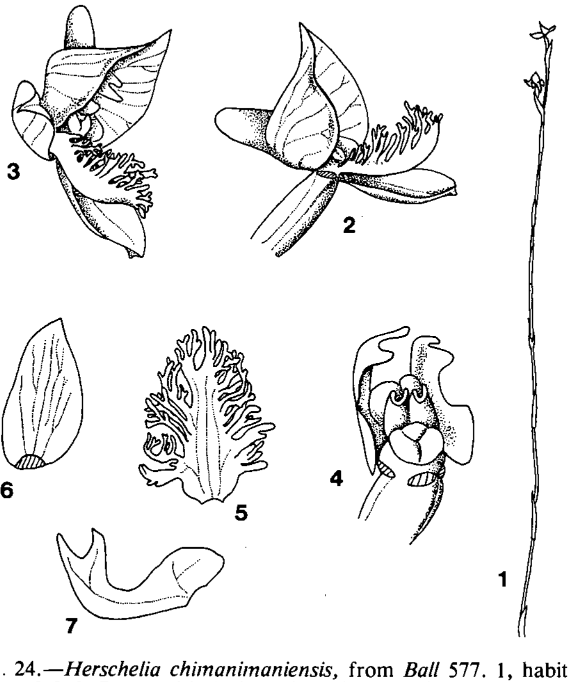

FIG. 24.—*Herschelia chimanimaniensis*, from *Ball* 577. 1, habit, ×0,5. 2, flower with the lateral sepal removed, ×4. 3, flower, ×4. 4, front view of column and petals, ×8. 5, lip, ×4. 6, lateral sepal, ×4, petal, ×4.

From collectors' notes it appears as if the species has a wide ecological range, as it has been recorded from montane grassland, cliff faces, rocky ground, seasonally damp ground and bogs. Phipps & Goodier (1962) describe the climate as cool, with frequent mist in the summer and frequent frost in the winter months. Available records indicate that rainfall is highly dependent on local topography and varies from 800 to 3 000 mm p.a.

This new species is clearly closely related to *H. baurii*. The ecological relationships of the two taxa in the Chimanimani Mountains are not clear. The majority of collectors recognized the two taxa as being distinct and collected them under different numbers. It also appears as if *H. baurii* occurs at higher altitudes than *H. chimanimaniensis,* but no explicit data are available. *H. chimanimaniensis* may be distinguished by the smaller flowers and more slender habit.

Ser. **Ecalcaratae** *Linder,* ser. nov., labello lacero, calcari obsoleto dignoscenda. Flowers with a bearded lip, spur obsolete.

Type species: *H. goetzeana* Kraenzl.

The single species in this series is most peculiar. Although it is clearly related to ser. *Lacerae* in the bearded lip and petal shape, it differs from *H. baurii* in the absence of a spur and the acute entire petal. It is difficult to explain the origin of this species. If it cannot be derived from *H. baurii,* it must be seen as a relic of a previous expansion of *Herschelia* from the south.

16. **Herschelia goetzeana** *Kraenzl.* in Bot. Jb. 30: 286 (1901). Type: Tanzania, Njombe District, Bulongwa, *Goetze* 925 (B, holo. †).

Disa goetzeana (Kraenzl.) Schltr. in Bot. Jb. 38: 150 (1906), in obs. non Kraenzl. (1900), nom. illegit. *D. walteri* Schltr. in Bot. Jb. 53: 544 (1915), nom. nov.; Summerh. in Fl. Trop. E. Afr. 156: 176 (1968).

Plants 200–600 mm tall; tubers about 20 mm long; base of the stem with a sheath of old leaf remains; radical leaves 5–10, 150–250 mm long and 1–3 mm wide, suberect, veins prominent, subsclerophyllous; cauline leaves lax, acuminate, about 25 mm long, completely sheathing; inflorescence closely 1–9-flowered; bracts ovate, acuminate, as long as the ovary, dry; ovaries about 10 mm long. *Flowers* foam-pink to crimson–cherry-coloured; dorsal sepal erect, galea hemispherical, almost orbicular from the front, 8–14 mm tall and 10–16 mm wide; spur obsolete; lateral sepal oblong, obtuse, spreading downwards, 10 mm long; petals with the basal anticous lobe oblong, 2 mm long, limb narrowly oblong to lorate, falcate, subacute, c. 7 mm long; lip patent, 20–25 mm long and up to 12 mm wide, entire at the base, obscurely 3-lobed, deeply and finely lacerate; anther horizontal, 7,5 mm long and with two distinct viscidia; rostellum with 3 linear erect lobes; stigma pulvinate, c. 2,5 mm in diameter.

Diagnostic features. Flowers with the lateral sepals c. 11 mm long; lip pectinate or lacerate; spur obsolete.

Flowering time: March.

Known from a single collection from southern Tanzania (Fig. 18), where it is said to be restricted to rock crevices on Mt Mbeya between 2 700 m and 2 900 m.

TANZANIA.—Southern Highlands, Mbeya District, Mbeya Peak, 2 700 m, March 1960, *Kerfoot 1632* (K).

Kerfoot (1964) describes the vegetation of the Mbeya Range, and notes for the high-altitude lithophytic communities that cloud and mist occur frequently. Growth is highly seasonal, with flowering occurring between February and April, and the flora is dominated by Orchidaceae.

Morphologically, this species is quite distinct, but clearly related to the species in Ser. *Lacerae* It is therefore, other than *H. praecox* and *H. chimanimaniensis,* unlikely to be a neo-endemic. It is difficult to understand where this species fits in with the rest of the genus and in the classification proposed here it is anomalous. It would be most interesting to see more material of this species and to confirm its limited distribution.

The type collection has been lost, but from the description there cannot be any doubt about the identity of the species. The name 'goetzeana' cannot be transferred to *Disa,* as there is already a *Disa goetzeana* Kraenzl. Schlechter (1915) proposed *D. walteri* as a *nomen novum* for the species. The name is derived from Walter Goetze, the original collector of the species.

ACKNOWLEDGEMENTS

I am indebted to the various people with whom I have discussed this genus, and who criticized some of my ideas. I would especially like to thank my supervisor, Prof. E. A. Schelpe, for numerous comments and much patience. I am grateful to the Directors and Curators of the various herbaria where I was provided with working facilities, or who loaned material for study purposes. This research was done while holding a Smuts Fellowship and a CSIR Postgraduate bursary.

UITTREKSEL

Die genus Herschelia (Disinae, *Orchidaceae*) *is hersien. Sestien spesies, een subspesie en een variëteit word erken. Twee nuwe spesies uit tropiese Afrika* (H. **chimanimaniensis** *Linder en* H. **praecox** *Linder sowel as 'n nuwe variëteit ui die Kaap* [H. lugens (*H. Bolus*) *Kraenzl var.* **nigrescens** *Linder*] *word hier beskryf. Drie nuwe kombinasies word gemaak deur die oorplasing van die twee spesies van* Forficaria *en* Disa *seksie* Microperistera (*een spesie*) *na* Herschelia. *Dertien spesies word geïllustreer en die nomenklatuur en die beskikbare gegewens in verband met die groeiplekke van die taksons word bespreek. Die spesies is in twee subgenera gegroepeer waarvan een in twee verdere seksies en vier series verdeel is. Hierdie klassifikasie is gebaseer op die veronderstelde filogenie soos bepaal deur die metode opgestel deur Wagner (1962).*

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APPENDIX: SPECIMENS STUDIED

The specimens are listed alphabetically according to the name of the collector. The figures in brackets refer to the number of the taxon in the text. Herbaria from which each collection has been studied are indicated by the letter codes of Holmgren and Keuken (1974).

Acocks 2087 (6) S; 3678 (10) S; 11731 (14) PRE. *Alchenck* 549 (5) Z. *Andraea* 278 (5) STE. *Atherstone* 29 (9a) K.

Baker 37 (6) K. *Ball* 577 (15) K, SRGH. *Balsinhas-Kersberg* 2054 (14) PRE. *Barker* 56 (4a) NBG; 620 (11) NBG; 625 (11) NBG; 3042 (4a) NBG; 444 (6) NBG; 4785 (4a) NBG; 5760 (4a) NBG; 6043 (11) (NBG; 8476 (6) NBG; 8828 (11) NBG. *Barkley* in BOL 4884 (5) BOL. *Bayliss* 3067 (11) NBG; 4162 (11) NBG. *Benson* 149 (13) BM; 189 (13) BM. *Bergius* s.n. (5) P. *Biegel* 257 (14) BOL, SRGH. *Bodkin* 494 (9a) BOL, K, SAM. *Bolus* 494 (9a) BOL, K, SAM; 1552 (11) BOL; 3810 (9a) BM, BOL, GRA, PRE, Z; 4393 (4a) PRE; 4566 (8) BM, BOL, K, PRE; 4566b (7) BM; 4857 (7) BOL, GRA, K; 4893 (6) BOL, GRA, K; 5278 (10) BOL, K; 7992 (6) Z; 9788 (14) BOL, K; 11379 (5) GRA; 11645 (10) BOL, PRE; 12327 (11) BOL, BR; 13514 (11) BOL; 17494 (8) BOL; s.n. (46) BOL; s.n. (5) BOL; (6) SAM; s.n. (8) BOL; s.n. (11) BOL. *Bond* 878 (11) NBG. *Bowie* 12 (5) BM; 13 (4a) BM; s.n. (11) BM. *Breach* s.n. (10) BOL. *Britten* 1058 (11) GRA, PRE; 6575 (9a) GRA. *Brook* s.n. (4a) PRE. *Buchanan* 1016 (14) K. *Buchholz* s.n. (5) STE. *Buhr* 5 (11) BOL. *Burchell* 747 (11) K; 808a (5) K; 7001 (5) K; 7801 (5) K; 4572 (11) K; 4592 (11) K; 7182 (11) K; 7372 (5) W. *Burtt Davy* 1915 (14) K; 4245 (5) PRE; 12004 (11) PRE; 18483 (11) BOL; 22070 (14) K; s.n. (14) BOL.

Carter & Barres s.n. (4a) BOL. *Chapman* 148 (14) BM; 330 (14) BM, SRGH. *Chase* 2949 (14) BM, BOL, K; 4059 (14) SRGH. *Chater* s.n. (11) BOL, PRE. *Clarke* in NBG 2184/31 (9a) BOL. *Codd* 523 (14) BM, PRE; 9714 (14) GRA, K, PRE, UPS. *Collins* 1538 (4a) K. *Compton* 4150 (4a) BOL, NBG; 4515 (11) BOL, NBG; 10499 (5) NBG; 12322 (6) NBG; 16644 (8) NBG; 20236 (6) NBG; 24487 (14) NBG; 25150 (14) NBG; s.n. (5) BOL. *Cookson* 3 (14) PRE, SRGH. *Cooper* 1464 (11) BM, K, W; *sub Eyles* 2743 (14) PRE, SRGH. *Cresswell* s.n. (9a) SAM. *Crook* 136 (14) SRGH; 409 (14) K, SRGH. *Crundall* s.n. (14) PRE Culver 20 (14) BM, BOL, BR, K. *Cuthbert* 5 (14) K. *Cutting s.n.* (9a) BOL; s.n. (11) BOL.

Dahlstrand 2586 (11) GRA. *Daly & Sole* 527 (9a) GRA. *Davidson* s.n. (4a) SAM. *Davies* 2120 (14) PRE, SRGH; s.n. (4a) SAM. *Dart* s.n. (9a) BOL, STE. *Delhaye* s.n. (14) K. *Denman* 237 (11) GRA. *De Villiers* s.n. (11) STE. *De Vos* 738 (8) PRE. *Doe* s.n. (8) BOL. *Drège* 1234 (4a) K, P; 2211a (11) K, W; s.n. (5) SAM; 63 (11) GRA. *Drummond* 8956 (14) SRGH; 8981 (14) SRGH; 8982 (15) SRGH. *Dümmer* 756 (9a) BM; 1502 (14) BM. *Duthie* 1027 (11) STE. *Du Toit* s.n. (9a) BOL. *Dyer* 229 (9a) PRE.

Ecklon 1565 (9a) W. *Edwards* 2157 (14) NU; s.n. (14) BOL. *Esterhuysen* 3802 (10) BOL; 4628 (11) BOL; 7298 (10) BOL; 8207 (4a) BOL; 13599 (11) BOL, K, PRE; 13664 (5) BOL; 15154 (5) K, PRE; 17441 (4a) BOL, PRE; 19990 (5) BOL; 20353 (4a) BOL; 20907 (10) BOL; 22712 (5) BOL, K. *Eyles* 2743 (14) PRE, SRGH.

Fair in BOL 3810 (9a) PRE; in BOL 7992 (6) BOL, GRA, PRE. *Ferguson* s.n. (3) BOL; s.n. (11) BOL. *Flugge-De Smit* s.n. (5) BOL. *Fourcade* 542 (11) GRA; 548 (5) BOL, GRA; 3167 (9a) K; 4309 (11) K, STE; 4344 (4b) BOL; 6443 (4b) PRE. *Franks* 9810 (14) PRE. *Froemling* s.n. (9a) NBG. *Frowein* 16131 (8) PRE.

Galpin 294 (9a) PRE; 427 (14) BOL, GRA, K, PRE, SAM; 428 (14) GRA; 4917 (5) PRE; 12545 (5) PRE. *Garley* 167 (14) SRGH. *Garside* 46 (9a) K, PRE. *Gemmell* 5037 (11) PRE. *Gerloin* 249 (11) GRA. *Germain* 1563 (14) BR. *Gillett* 326 (11) K; 718 (1) BOL; 1602 (4b) BOL; 17648 (14) K, PRE; 17799 (14) K; s.n. (5) STE; s.n. (9a) K; s.n. (11) BOL. *Gillett & Bolus* in BOL 18506 (11) BOL. *Gillies* 107 (14) NU. *Glass* s.n. (9a) GRA, PRE. *Goatcher* s.n. (4a) BOL. *Goetze* 1222 (14) BM. *Grant* 2464 (4a) BR, M, PRE; s.n. (14) BM. *Greenway* 6318 (14) K, PRE. *Grice* s.n. (14) NU. *Grosvenor* 178 (15) K, SRGH; 257 (14) K, SRGH. *Gueinzius* s.n. (10) W. *Guthrie* 871 (4a) BOL; 4383 (11) NBG; 8384 (11) NBG; in BOL 6861 (10) GRA.

Hafström & Acocks 2087 (6) PRE, Z, S. *Hall* 664 (9a) BOL; 1043 (4a) BOL; 1160 (11) BOL. *Hallack* in BOL 6210 (11) BOL, GRA. *Hall-Martin* 429 (14) PRE. *Handel Hamer* in BOL 16964 (11) BOL. *Harvey* 116 (9a) K; 148 (7) K; s.n. (5) BM, K, W. *Harwood* s.n. (14) PRE. *Hayes Palmer* s.n. (11) NBG. *Haynes* 304 (5) STE; 528 (5) STE. *Hendrickx* 3465 (14) PRE. *Hermann* 871 (4a) NBG. *Hill* 2 (14) K. *Hilliard & Burtt* 10404 (14) NU. *Huysteen* s.n. (6) STE.

Immelmann 246 (4a) BOL.

James in BOL 23178 (11) BOL. *Jameson* s.n. (6) K. *Jenkins* 8228 (14) PRE. Jeppe in PRE 3383 (5) PRE; in PRE 33384 (4b) PRE; in PRE 33385 (11) PRE. *Johnson* s.n (14) K. *Joubert* s.n. (5) K.

Karsten s.n. (14) NBG. *Keet* 1154 (11) GRA. *Kennedy* s.n. (5) PRE. *Kensley* 280 (11) GRA. *Kensit* 9339 (8) BOL. *Kerfoot* 1632 (16) K. *Kettle* 18 (13) PRE. *Kettlewell* in BOL 25392 (6) BOL. *Keulder* s.n. (9a) STE. *Kirk* s.n. (14) K. *Kolbe* 2412 (9a) GRA. *Krauss* s.n. (5) M.

Lavis s.n. (4a) BOL. *Leach* 4121 (14) K, SRGH; 14941 (14) BOL, SRGH; 21121 (14) S. *Lees* 99 (14) K. *Leighton* 402 (4a) BOL; 3067 (11) BOL, PRE. *Leipoldt* 601 (4a) BOL; 3233 (4a) BOL; 3234 (4a) BOL; 3810 (4a) BOL; 4243 (11) BOL; in BOL 11379 (5) PRE; s.n. (4a) BOL. *Lewis* 828 (8) SAM; 1837 (4a) SAM; 2402 (6) SAM; 2404 (7) SAM; 2680 (4a) SAM; 4737 (4a) SAM; 5202 (4a) NBG. *Liebenberg* 7805 (11) K, PRE. *Linder* 759 (6) BR, BOL; 1244 (4a) BOL; 1245 (4a) BOL; 1453 (4a) BOL; 1458 (4a) BOL; 1460 (4a) BOL; 1471 (4a) BOL; 1549 (4a) BOL, BR, K; 1656 (10) BOL; 1714 (11) BOL; 1729 (11) BOL; 1731 (11) BOL; 1743 (10) BOL; 1763 (5) BOL; 1806 (7) BOL. *Long* 165 (9a) K; 494 (9a) K; 507 (11) K, PRE; 520 (11) K, PRE. *Luyt* in BOL 10571 (3) BOL, PRE; 11379 (5) BOL.

MacOwan 700 (9a) BM, GRA, K, SAM; 1045 (11) BM, GRA, K, SAM; 1045b (5) SAM, W; 2587 (4a) SAM; 2690 (9a) SAM; s.n. (5) NBG. *MacOwan & Bolus* 166 (7) BM, BOL, K, P, W, ZT; 167 (5) BM, BOL, K, P, SAM, UPS, W, ZT; 494 (9a) BOL, P, PRE, W, Z, ZT. *MacNicol* s.n. (11) NBG. *Magennis* s.n. (4a) BOL, PRE. *Mahon* s.n. (14) K. *Marloth* 332 (6) BOL, PRE; 425 (5) PRE; 483 (10) PRE; 1601 (9a) BOL; 2310 (4a) PRE; 6678 (10) BOL, PRE; 7273 (7) PRE; 7941 (4a) PRE; 8337 (10) PRE; 8435 (4a) PRE; 8847 (9a) PRE; 10061 (11) PRE; 11008 (9a) PRE; s.n. (5) BOL; s.n. (6) SAM. *Marsh* 1408 (4b) PRE, SRGH. *Matthews* 28 (14) SRGH. *Mauve* 5005 (14) PRE. *McClounie* 10 (14) K; 92/3 (14) BM. *McLoughlin* 362 (14) BOL; 92/3 (14) K, P, PRE, S, UPS; s.n. (11) BOL. *Mgaza* 488 (14) K. *Michael* et al. 971 (13) SRGH. *Middlemost* 1721 (4a) NBG; 1954 (11) NBG. *Minicki* s.n. (1) BOL. *Moorshead sub Moss* 17594 (11) BM. *Morris* 52 (14) K; in BOL 13478 (4a) BOL. *Moss* 15432 (14) K, PRE; 17594 (11) BM, 18237 (11) BM. *Muir* 621 (11) PRE; 908 (9a) BOL, PRE, SAM; in PRE 16266 (9a) PRE; s.n. (4a) PRE. *Munch* 274 (14) SRGH; 327 (15) K, SRGH. *Myburg* s.n. (9a) NBG.

Newbould & Jefford 1849 (14) K. *Newdigate* in BOL 6327 (2) BOL; s.n. (11) BOL.

O'Brien s.n. (9a) BM; s.n. (11) K, Z. *O'Connor* 216 (14) NU; 368 (14) NU. *Oldevig-Roberts* s.n. (11) S. *Oliver* 3181 (9a) PRE, STE; 3006 (6) PRE; in STE 29974 (10) PRE.

Pappe 38 (4a) SAM; 39 (9a) BOL, SAM; 377 (9a) BOL, GRA, SAM; in BOL 4393 (4a) BOL; s.n. (4a) K; s.n. (11) K, SAM. *Parker* s.n. (6) BOL. *Paterson* 106 (5) GRA; 488 (11) GRA, Z; 1277 (11) BOL, GRA; s.n. (6) BOL. *Pattison* in BOL 14455 (10) BOL. *Pawek* 1409 (13) SRGH; 3800 (14) K; 10275 (14) SRGH. *Penther* 50 (11) BM, M, W; 154 (5) M, W; 251 (4a) W; in PRE 10575 (11) PRE. *Peters* s.n. (4a) SAM. *Pillans* 3530 (6) PRE; 4056 (5) PRE; 4125 (1) BOL; 8275 (8) BOL; 9723 (10) BOL. *Plowes* 2807 (15) K, SRGH; 2808 (14) K, SRGH. *Pott* 1278 (9a) PRE. *Powrie* 168 (10) BOL. *Prentice* s.n. (4a) PRE.

Rattray in BOL 15770 (8) BOL. *Rauh & Schlieben* 9761 (14) M, PRE. Rehmen 529 (11) BM, Z; 571 (5) Z. *Reynolds* 4200 (14) PRE.

Richards 6804 (14) K; 18500 (14) K; 22561 (14) K; 22574 (14) K, P. *Robinson* 6259 (13) K, M, SRGH. *Robson* 297 (14) K; 358 (14) BM, K, SRGH. *Rogers* 10550 (5) Z; 16554 (11) Z; 19079 (14) PRE; 19767 (14) GRA, K, P, S; 21404 (14) BOL, K, Z; 26487 (11) Z; 26865 (11) Z; 27643 (11) Z; 30155 (14) BR, K, P, Z. *Rosenbruck* in BOL 27817 (1) BOL. *Rycroft* 2559 (4a) NBG. *Ryder* in NBG 40/28 (11) BOL, K; s.n. (3) K.

Salter 8703 (8) NBG; 325/1 (5) BM; 325/2 (6) BM; 325/3 (7) BM; 325/4 (8) BM; in SAM 53195 (8) SAM. *Schelpe* 013 (14) NU; 826 (14) NU; 4267 (11) BOL; 4994 (11) BOL; 5006a (11) BOL; 6313 (9a) BOL. *Schlechter* 481 (5) P, Z; 2061 (5) BOL, Z; 4997 (4a) PRE, Z; 5165 (4a) BOL, GRA, P, W, Z; 5928 (11) Z; 9544 (8) BM, BR, GRA, K, PRE; s.n. (4a) BR, K. *Schlieben* 1366 (14) BM, G, M, P, S, Z. *Schmidt* 3 (5) M. *Schnisterhol* 213 (5) S. *Schonland* 1519 (9a) GRA, Z; 2410 (9a) PRE; 3662 (11) GRA; sub *Galpin* 4917 (5) PRE. *Seltzer* s.n. (9a) NBG. *Seltzer & Parke* s.n. (9a) BOL. *Shirley* 234 (14) NU. *Sidey* 490 (14) PRE; 1498 (14) PRE, S; 4057 (11) PRE. *Sim* 2457 (14) BOL, PRE. *Skead* 210 (14) NU. *South* 127 (9a) GRA; s.n. (11) GRA, PRE. *Stander* s.n. (11) STE. *Starke* 127/27 (11) BOL; NBG 60/27 (11) BOL. *Stewart* 8875 (14) GRA, PRE. *Stokoe* 2560 (1) BOL; 7324 (5) BOL, SAM; 7386 (5) BOL; 8679 (10) BOL; in SAM 54389 (11) SAM; in SAM 54714 (11) SAM; s.n. (5) SAM. *Stolz* 127 (14) BM, G, K, M, W, Z; 2192 (14) C, G, M, S, W, Z; 2193 (14) C, G, M, Z. *Strey* 9853 (14) PRE. *Sturgeon* in SRGH 30524 (14) K, SRGH. *Symons* 22 (14) SAM; in PRE 14847 (14) PRE.

Taylor 191 (14) NU; 634 (11) NBG; 1713 (14) NU; 1755 (14) NU; 1786 (14) NU, SRGH; 1791 (15) NU; 5455 (9a) STE; 6220 (5) STE. *Tennant* 5 (5) NBG. *Thode* A48 (5) PRE; A387 (14) K, PRE; A1022 (11) K, PRE; in STE 5247 (5) STE; in STE 5307 (11) STE; in STE 6104 (5) STE; in STE 6526 (11) STE; in STE 8128 (5) STE. *Thomas* s.n. (4a) NBG; s.n. (6) NBG. *Thorncroft* 2478 (14) K, PRE. *Thornton* s.n. (14) PRE. *Thulin & Mhoro* 1201 (14) K, UPS; 1207 (14) K. *Thunberg* 21429 (9) UPS; 21443 (11) UPS. *Trauseld* 412 (14) PRE. *Trimen* s.n. (12) BM; s.n. (9a) BM. *Tyrer* 726 (13) BM, SRGH; 966 (13) BM, SRGH; 978 (13) BM. *Tyson* 1537 (14) BOL.

Wahlberg s.n. (5) S. *Wall* s.n. (3) S; s.n. (4a) S; s.n. (5) S; s.n. (9a) S; s.n. (11) S. *Wallich* 113 (11) BM. *Watermeyer* 167 (13) K. *West* 256 (11) W. *Westwood* 694 (14) SRGH. *Whellan* 1493 (11) SRGH; 2137 (14) SRGH; 2145 (15) SRGH. *Whyte* 345 (14) K; s.n. (14) K; s.n. (14) K. *Wild* 1366 (14) K, SRGH; 3556 (14) PRE, SRGH; 4668 (14) SRGH; 4669 (14) K. *Willan* 176 (14) K; in BOL 24915 (14) BOL. *Williamson* 119 (14) K; 312 (13) K; 1023 (13) K, SRGH. *Wilms* 1406 (14) BM. *Wolley-Dodd* 358 (9a) BM; 359 (7) K; 391 (8) BM, K; 840 (5) BM; 885 (5) K; 1798 (9a) K; 2005 (6) BM, K. *Wood* 9290 (14) BOL, K; 10599 (14) K, PRE. *Worsdell* s.n. (4a) K; s.n. (9a) K; s.n. (14) K. *Wright* 2412 (14) NU. *Wurts* 558 (5) NBG; 2136 (11) NBG. *Wylie sub Wood* 10599 (14) GRA, PRE, SAM; in *Dümmer* 1502 (14) BM.

York 34 (9a) K.

Van Zinderen Bakker 56 (11) NBG. *Venter* 848 (14) PRE. *Venter & Vorster* 195 (14) PRE; 196 (14) PRE. *Vogelpoel* s.n. (14) BOL. *Voigt* in PRE 13199 (14) PRE.

Zeyher 504 (11) P; 628 (11) K; 1566 (9a) K, S, SAM; 1567 (7) K, P, SAM, W; 3917 (11) S; 3918 (10) BM, K, P, S, W; s.n. (5) SAM; s.n. (6) K. *Zinn* s.n. (5) SAM.

INDEX