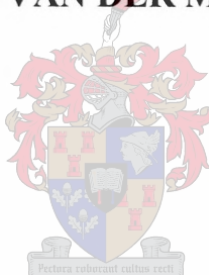


A BIOSYSTEMATIC STUDY OF THE SEVEN MINOR GENERA OF THE HYACINTHACEAE

by

ALISON M. VAN DER MERWE



Dissertation presented for the Degree of Doctor of Philosophy at the University of
Stellenbosch

Promoter: Dr. E.M. Marais
Co-promoter: Prof. D.U. Bellstedt

March 2002

ABSTRACT

Declaration

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and has not previously in its entirety or in part been submitted at any university for a degree

Signature

Date

ABSTRACT

A biosystematic revision of the seven minor genera of the Hyacinthaceae, including twenty-two species, was undertaken. Müller-Doblies & Müller-Doblies (1997) considered these seven genera (*Amphisiphon* Barker, *Androsiphon* Schltr., *Daubenya* Lindl., *Massonia* Thunb. ex Houtt., *Neobakeria* Schltr., *Polyxena* Kunth and *Whiteheadia* Harv.) together with the genus *Eucomis* L'Hérit. to form the subtribe *Massoniinae* of the tribe *Massonieae*. Previous revisions of the group were based only on morphological characters (Jessop 1976; Müller-Doblies & Müller-Doblies 1997).

The subtribe *Massoniinae* is characterised by the large variety of floral forms exhibited by the different species in the group. In the past this has led to the establishment of many monotypic genera for species thought to have unique floral structures. Morphological, leaf anatomical, palynological, geographical and molecular data were studied in order to delimit the taxa and determine the phylogenetic relationships within the group. This showed that most of the unique floral structures are probably only adaptations to pollination strategies and all except one of the monotypic genera are now placed in the genus *Daubenya*. In the genus *Massonia* there is a great deal of variation in leaf morphology and this resulted in the establishment of many invalid species, now mostly reduced to synonymy.

A new species was described, several name changes made and several species were reduced to synonymy.

UITTREKSEL

‘n Biosistematiese hersiening van die sewe kleiner genera van die Hyacinthaceae, insluitende twee-en-twintig spesies, is onderneem. Müller-Doblies & Müller-Doblies (1997) sluit hierdie sewe genera (*Amphisphon* Barker, *Androsiphon* Schltr., *Daubenyia* Lindl., *Massonia* Thunb. ex Houtt., *Neobakeria* Schltr., *Polyxena* Kunth and *Whiteheadia* Harv.) saam met die genus *Eucomis* L’Hérit. in die subtribus *Massoniinae* van die tribus *Massonieae* in. Vorige hersienings van die groep was meestal net op morfologiese kenmerke gebaseer (Jessop 1976; Müller-Doblies & Müller-Doblies 1997).

Die subtribus *Massoniinae* word gekenmerk deur die groot variasie in blomstrukture wat by die verskillende spesies in die groep voorkom. In die verlede het dit gelei tot die beskrywing van verskeie monotipiese genera gegrand op wat geblyk het, unieke blomstrukture te wees. Morfologiese, blaar anatomiese, palinologiese, geografiese en molekulêre data is bestudeer om die verskillende taksons af te baken en terselfdertyd die filogenetiese verwantskappe binne die groep te bepaal. Dit het aangetoon dat die unieke blomkenmerke eerder aanpassings aan bestuiwings-strategieë is en dat al hierdie monotipiese genera, behalwe een tot die genus *Daubenyia* behoort. In die genus *Massonia* is daar baie variasie in blaarmorfologie en dit het veroorsaak dat ‘n groot aantal spesies beskryf is, waarvan baie nou as sinonieme beskou word.

Een nuwe spesies is beskryf, verskeie naamsveranderinge is gemaak, en ‘n aantal van die spesies is tot sinonieme verander.

1. INTRODUCTION

2. MATERIAL AND METHODS

3. RESULTS

3.1 Macroecology

3.2 Leaf Anatomy

3.3 Palynology

3.4 Distribution and ecology

Nothing in the world can take the place of persistence.

Talent will not; nothing is more common than
unsuccessful men with talent.

Genius will not; unrewarded genius is almost a proverb.

Education will not; the world is full of educated failures.

Persistence and determination alone are omnipotent.

- Calvin Coolidge

7. TAXONOMIC TREATMENT OF THE GENUS *MARONIA* THREL. EX DOUTI

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7.2 *Maronia ciliolata* L.

7.3 *Maronia lutea* L.

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7.5 *Maronia parviflora* L.

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CHAPTER 1

INTRODUCTION

The restructuring of the Liliaceae was proposed by several authors. Dahlgren and Clifford (1982) in their comparative study of the monocotyledons, regard it "of crucial importance that the families comprise reasonably homogeneous groups in an evolutionary sense and that they are arranged according to relationships as far as can be ascertained from comparative studies".

The genera previously placed within the Liliaceae *sensu lato* are now allocated to separate families falling within one of the two closely related orders the Liliales or Asparagales. The combined characters used to separate the new families from Liliaceae *sensu lato* are mainly the habit (e.g. climbers, herbs, trees and shrubs), underground parts (e.g. bulbs, corms, stem tubers, tuberous roots), inflorescence (e.g. umbel or raceme) and fruits (capsule or berry; Perry 1985).

The order Asparagales, as relates to southern African taxa, consists of six new families formed by genera from the Liliaceae *sensu lato* as well as genera from the families Amaryllidaceae, Hypoxidaceae and Tecophilaeaceae (Perry 1985). The order Asparagales as presently circumscribed was first recognized by Huber (1969) and is believed to be a monophyletic group, a concept based mainly on fruit and seed characters. One of the prominent characters used is the complete collapse of the inner integument of the seed coat in the ripe seeds, forming a thin, brown or colourless membrane. The outer wall of the epidermis of the testa in nearly all capsule-fruited members as well as in some berry-fruited genera, is provided with a more or less thick layer of phytomelan. In the Asparagales the flowers generally have septal nectaries, the tepals are non-patterned and the style is usually simple. In contrast, members of the order Liliales have nuclear endosperm formation, perigonal nectaries (or a lack of septal nectaries) and a variegated pattern on the tepals (Dahlgren, Clifford & Yeo 1985).

Within the Asparagales nuclear endosperm formation and baccate fruits may be synapomorphic for one group of families which include the Philesiaceae, Lizuriagaceae, Convallariaceae, Asparagaceae, Ruscaceae, Herreriaceae, Dracaenaceae and Nolinaceae. The Philesiaceae show some similarities to the Alstroemeriaceae of the Liliales, but whether they serve as a "link" between Asparagales and Liliales is not yet clear (Dahlgren, Clifford & Yeo 1985). A second possible monophyletic group of families within the order Asparagales comprises the Asphodelaceae, Hemerocallidaceae, Doryanthaceae, Phormiaceae, Ixioliriaceae, Tecophilaeaceae and Cyanastraceae, all of which are characterized by simultaneous microsporogenesis (Dahlgren, Clifford & Yeo 1985). Another apparently closely allied group is the Hyacinthaceae, Alliaceae and Amaryllidaceae, most of which have bulbs and all of which have a leafless, frequently fleshy scape that carries a determinate inflorescence, varying in appearance from spicate in the Alliaceae to umbel-like in the Alliaceae and Amaryllidaceae (Dahlgren, Clifford & Yeo 1985).

The family Hyacinthaceae is characterized by geophytes with the underground part a bulb, inflorescence a simple raceme, perianth segments free or united at the base and the fruit a

capsule, and includes amongst others the following South African genera: *Amphisiphon* Barker, *Androsiphon* Schltr., *Daubenya* Lindl., *Massonia* Thunb. ex Houtt., *Neobakeria* Schltr., *Polyxena* Kunth and *Whiteheadia* Harv. (Perry 1985).

The genus *Hyacinthus* was described by Linnaeus in 1753, but the South African species, *H. corymbosus* was only described in 1771 in his Mantissa. This species was transferred to *Massonia* in 1807 and then to *Scilla* in 1812 by Ker-Gawler as it was thought to differ from other *Hyacinthus* species in "having a scape not shorter than the leaves, a raceme not erect and corymbose and by its large rootsheath and nearly obsolete bracts". Kunth (1843) transferred *H. corymbosus* to *Periboea* Kunth, however, most authors have continued to treat *H. corymbosus* as correctly assigned to *Hyacinthus* (Jessop 1976).

Houttuyn (1780) described *Massonia* based on a manuscript name proposed by Thunberg.

Lindley (1835) described *Daubenya aurea* and regarded *Daubenya* as a new genus because, although it agrees remarkably in habit with *Massonia* it differs in its tubular, not campanulate, very irregular perianth and in the absence of the nectaries typical in *Massonia*. Two more *Daubenya* species were described, *D. fulva* by Lindley (1839) and *D. coccinea* by Baker (1871); based on a manuscript name of Harvey, but Marloth (Phillips 1922c) suggested that the genus be treated as monotypic.

Polyxena ensifolia (Jacq.) Kunth was described by Kunth (1843) for a species previously placed in *Polyanthes* by Jacquin. Species were transferred from *Mauhlia* Thunb., *Agapanthus* (Thunb.) Willd., *Massonia* and *Hyacinthus* to *Polyxena* by Schönland (1910). Baker (1897) recognised ten species within the genus, whereafter another four have been included.

Harvey (1868) erected a new genus *Whiteheadia*, for a species formerly included in *Eucomis* L'Hérit., *Basilea* Poir. or *Melanthium* Andr. *Whiteheadia* has always been regarded as a monotypic genus, but Müller-Doblies & Müller-Doblies (1997) described *Whiteheadia etesionamibensis* from Namibia as a second species in the genus.

Baker (1897) recognized five genera in the *Massonia* group namely *Daubenya*, *Hyacinthus*, *Massonia*, *Polyxena* and *Whiteheadia*. He placed *Massonia* and *Daubenya* in the tribe *Allieae* based on their umbels, which are subtended by 1–2 or more membranous bracts. The two genera are distinguished from one another by the regular perianth limb of *Massonia* and an irregular perianth limb of *Daubenya*. Within *Polyxena* Baker (1897) recognized two subgenera, namely subgenus *Astemma* consisting of six species and subgenus *Eupolyxena* with four species.

Schlechter (1924) described *Androsiphon* and *Neobakeria* as two new genera. He considered *Androsiphon* to show affinities with *Massonia* but clearly distinct from it because of the presence of a gynostegium (staminal tube). Only a single species of *Androsiphon* was recognized. Schlechter (1924) considered the subgenus *Astemma* (genus *Polyxena*) of Baker (1897) to be sufficiently distinct to justify the generic status of *Neobakeria*.

Barker (1936) described *Amphisiphon* as a monotypic genus, and regarded it to be linked with *Androsiphon* because of its long staminal tube. It differs however, in lacking a disc at the distal end of this staminal tube, as is present in *Androsiphon*.

Krause (1930), Hutchinson (1959) and Phillips (1951) provided the most important reviews of the genera of the Liliaceae since Baker (1897). Krause (1930) recognized six genera in the *Massonia* group, all those already described at that time except for *Neobakeria*, which he considered synonymous with *Polyxena*. He included all the genera within the tribe *Scilloideae* Krause. Hutchinson (1959) also regarded *Neobakeria* as a synonym for *Polyxena* and *Amphisiphon* synonymous with *Androsiphon*, whereas *Massonia* and *Daubenya* were placed in the tribe *Massonieae*. Phillips (1951) linked *Massonia* with *Polyxena*, *Neobakeria*, *Whiteheadia*, *Neopatersonia* Schön. and *Androsiphon* on the basis of their connate stamens. He also regarded *Amphisiphon* as a synonym for *Androsiphon*.

Jessop (1975) proposed that the genera *Massonia*, *Neobakeria*, *Polyxena*, *Hyacinthus* L., *Daubenya*, *Androsiphon*, *Amphisiphon*, *Ledebouria* Roth, *Drimiopsis* Lindl. & Paxt., *Lachenalia* Jacq. f. ex Murray, *Veltheimia* Gled and *Eucomis* L'Hérit. should be grouped together as a tribe. Within this tribe Jessop (1976) considered *Massonia*, *Polyxena*, *Hyacinthus* (Cape species only), *Daubenya*, *Androsiphon*, *Amphisiphon* and *Whiteheadia* to comprise a natural group to which he refers as the "*Massonia* group". Jessop (1976) united *Massonia* and *Neobakeria* under the older name *Massonia*, because of the close correlation between the characters of the bulb and the filaments. He regarded *Neobakeria* to be closer to *Massonia* than to *Polyxena* mainly because all the filaments are inserted on the same level on the perianth of *Massonia* and *Neobakeria* but in two distinct levels in *Polyxena* and *Hyacinthus*. Jessop (1976) proposed that the Cape species of *Hyacinthus* (*H. corymbosa*) be placed in *Polyxena* because of the similarities in floral characters and the extreme isolation of the Cape *Hyacinthus* species from the rest of the genus in the northern hemisphere. Other genera recognized by Jessop (1976) are *Daubenya*, *Androsiphon*, *Amphisiphon* and *Whiteheadia*. He separated *Amphisiphon* from *Androsiphon* on the characters pointed out by Barker (1936).

Müller-Doblies and Müller-Doblies (1997) published a partial revision of the tribe *Massonieae* dividing the *Massonieae* into three subtribes *Ledebouriinae*, *Lachenaliinae* and *Massoniinae*. Within the subtribe *Massoniinae* they recognized the following genera: *Eucomis*, *Whiteheadia*, *Namophila* U. & D.M-D., *Periboea* Kunth., *Polyxena*, *Androsiphon*, *Amphisiphon*, *Neobakeria* and *Daubenya*.

Pfossor and Speta (1999), who completed the most recent work on the family Hyacinthaceae, investigated the monophyly of the family and the generic relationships by sequencing the trnL intron and the trnL-trnF intergenic spacer region of chloroplast DNA for 105 taxa in the Hyacinthaceae and 18 species of related families. They proposed four subfamilies: Oziroideae Speta (including South American Hyacinthaceae); Urgineoideae Speta; Ornithogaloideae Speta and the largest and most advanced subfamily Hyacinthoideae Link. The latter consists of tribe *Massonieae* Baker (including species from Africa south of the Sahara and from India) and the

Mediterranean/Asian tribe *Hyacintheae* Dumort. Pfosser & Speta (1999) pointed out that southern African taxa occur at basal positions in all subfamilies, thus indicating a southern African origin of the Hyacinthaceae.

Not much information has been published on the chromosome numbers, anatomy, palynology or chemotaxonomy of the group. Dahlgren, Clifford and Yeo (1985) looked at the vegetative morphology of most of the monocotyledons, but concentrated mainly on family characteristics and not those of the genera. At family level they examined the vegetative anatomy, floral morphology as well as the fruit and seed characters. They did not attempt to survey the chromosome numbers in the monocotyledons, as they found the numbers in most families to be too variable to be of much use in the phylogenetic evaluation. The Jodrell laboratory at Kew is examining the cytology of the *Massonieae*, but as yet the chromosome numbers of only *Amphisiphon stylosa* ($2n = 32$) and *Androsiphon capense* ($2n = 34$) have been published (Brandham 1990). The karyotypes of both of these species have proved to be bimodal, a feature which is said to be shared by other *Massonieae* (Brandham 1990). It was hoped that a detailed study of the chromosome numbers of the *Massonieae* would shed light on their inter-relationships, however Pfosser & Speta (1999) found that chromosome numbers may be constant within some genera but highly variable in others, resulting in aneuploid series that are difficult to interpret. Chromosome studies have proved very difficult as the root tips break off very easily when plants are lifted from the soil. In this study an attempt was made to cultivate the plants in hydroponics to examine the chromosomes, but this also proved unsuccessful. Jessop (1975) studied the seed surface characters of many of the *Massonieae* and other species and was able to make suggestions as to their inter-relationships from the data he obtained. No publications were found pertaining to the palynology or the chemical compounds of the group.

For no plant family is it more true than for the Hyacinthaceae that the interpretation of single morphological characters resulted in highly erratic classifications when delineating tribal and subfamilial relationships. No character, from bulb morphology to pistils or seeds, or even karyological data has proven to be reliable (Pfosser & Speta 1999). In order to compile a proper classification all available information had to be assembled and combined. The aim of this study was to combine all existing information on the South African *Massonieae* with new information on the morphology and anatomy of the taxa, as well as with new data gathered through the assessment of molecular data from DNA studies, and to produce a realistic and reliable phylogenetic tree. In the DNA analysis sequence data from the intron and spacer of the trnL-F chloroplast region was studied to determine the phylogenetic relationships within the subtribe *Massoniinae* of the tribe *Massonieae* (Hyacinthaceae), using species from *Eucomis*, *Crinum* L., *Ledebouria*, *Galtonia* Decaisne and *Veltheimia* as outgroups.

The commercial importance of this group lies in its horticultural potential as most of the species are very beautiful and those that are not are at least interesting enough to be attractive. Most beautiful of all must be *Daubenya aurea* with its striking red or yellow flowers, already recognized by Lindley (1835) as "truly among the flora gems in the South African flora".

Amphisiphon stylosa and *Androsiphon capense* have a delicate beauty all of their own and there is no doubt that the *Neobakerias* and *Massonias* are all very attractive, if not striking. The *Polyxena* species with their delicate mauve, pink or white flowers are pleasantly fragranced and just as attractive. The plants all grow easily from seed, taking one season from germination to the formation of the first bulb. Bulbils have also been observed at the base of the bulbs of many of the species, illustrating the ease at which these plants can multiply. The plants are easy to cultivate and will grow in containers or the open garden, they flower in autumn and winter and thus provide a good alternative to spring flowering annuals. The medicinal value of these plants is not yet known and there may well be valuable compounds in the bulbs, leaves or inflorescences. The group is not thought to be toxic as the plants are readily eaten by sheep and other grazing animals, including porcupines.

CHAPTER 2

MATERIAL AND METHODS

This revision is based on macro-morphological, leaf anatomical, palynological and DNA data. The material and methods used for the DNA study will be dealt with in Chapter four. An extensive literature study was undertaken and all available literature on the Hyacinthaceae and more specifically the Massonieae was studied. Table 2.1 lists all the specimens studied, names used are those accepted at the start of the study.

Herbarium specimens were studied at, or obtained on loan from, the following herbaria [abbreviations are from Holmgren and Keuken (1974)]:

BOL Bolus Herbarium, University of Cape Town, Cape Town

NBG Compton Herbarium, National Botanical Institute, Cape Town

K Royal Botanic Gardens, Kew

SAM South African Museum Herbarium, National Botanical Institute, Cape Town

STE Herbarium, National Botanical Institute, Stellenbosch (now incorporated in NBG)

STEU Herbarium, Department of Botany, University of Stellenbosch, Stellenbosch

Macromorphology

Living specimens were collected in the field and then grown in pots in the Botanical garden at Stellenbosch. These were then studied together with herbarium specimens for macro-morphological data. Where possible, at least five herbarium specimens from each taxon were studied in detail and measurements taken. The descriptive terminology used in this study was based on Radford *et al.* (1974).

Leaf anatomy

Leaf anatomical studies were done on fresh leaf material from potted plants that had been growing for more than one season, ensuring that all material studied was from plants growing under the same conditions for at least one season. Leaf material was fixed in F.A.A. (formaldehyde-acetic acid-acetone), dehydrated and infiltrated with Paraplast following the tertiary Buthanol method (Johansen 1940). Transverse sections were cut through the mid-section of the lamina with a rotary microtome, mounted on microscope slides using Haupt's reagent as glue and 4% formalin and then stained using the Alcian Green-Safranin method (Joel 1983). Cross sections were examined under the Leitz Laborlux light microscope and line drawings were made.

Pollen morphology

Pollen grains of all the species were collected from the potted plants and in some cases also from plants growing in the wild. All pollen specimens were prepared using the acetolysis method (Erdtman 1966), mounted in glycerine jelly and studied with the light microscope.

Geographical distribution and ecology

The geographical distribution of each specimen was cited according to the grid reference method proposed by Leistner and Morris (1976). A distribution map was compiled for each taxon using this data.

Taxonomy

The taxonomic treatment has been arranged according to the guidelines for contributors to the South African Journal of Botany. This includes the format for literature references and the specimens cited.

DNA analysis

The molecular phylogenetic relationships in the subtribe Massoniinae was prepared as a self-standing publication and is included as chapter four of the thesis. Parts of the introduction and discussion of the paper overlap with that of the thesis. I generated all the sequences myself and the work was done, as was the rest of the thesis, under the leadership of Prof. D.U. Bellstedt and Dr. E.M. Marais. The computer analysis of the DNA sequences was done by Prof. E. H. Harley. The aligned sequence files of the trnL intron and the trnL-trnF spacer are attached as Appendix 2 and 3 respectively, at the end of chapter four.

Table 2.1. List of specimens used in this study (names of species as accepted at the start of the study; * indicates studies undertaken).

Species	Collector	Locality	DNA	Leaf Anatomy	Pollen
<i>Amphisiphon stylosa</i> Barker	<i>Van der Merwe 119</i>	Nieuwoudtville	*	*	*
<i>Androsiphon capense</i> Schltr.	<i>Van der Merwe 152</i>	Nieuwoudtville	*	*	*
<i>Daubenya alba</i> A.M.v.d. Merwe	<i>Van der Merwe 195</i>	Middelpos	*	*	*
<i>Daubenya aurea</i> Lindl. (red)	<i>Van der Merwe 182</i>	Sutherland	*	*	*
<i>Daubenya aurea</i> Lindl. (yellow)	<i>Van der Merwe 183</i>	Sutherland	*		

Species	Collector	Locality	DNA	Leaf Anatomy	Pollen
<i>Eucomis regia</i> (L.) L'Hérit.	<i>Summerfield s.n.</i>	Drayton	*		
<i>Lachenalia pusilla</i> Jacq.	<i>Van der Merwe 193</i>	Piketberg	*		
<i>Massonia depressa</i> Houtt.	<i>Van der Merwe 106</i>	Robertson	*	*	*
<i>Massonia echinata</i> L.f.	<i>Van der Merwe 120</i>	Nieuwoudtville	*	*	*
<i>Massonia echinata</i> L.f.	<i>Van der Merwe 145</i>	Vanrhynspass	*	*	
<i>Massonia grandiflora</i> Lindl.	<i>Van der Merwe 140</i>	Nieuwoudtville	*	*	
<i>Massonia hirsuta</i> Link & Otto	<i>McMaster s.n.</i>	Graaf Reinet	*	*	
<i>Massonia hirsuta</i> Link & Otto	<i>Anderson s.n.</i>	Barkly West	*	*	
<i>Massonia jasminiflora</i> Burch. ex Baker	<i>Van der Merwe 179</i>	Stutterheim	*	*	
<i>Massonia pustulata</i> Jacq.	<i>Van der Merwe 101</i>	Bredasdorp	*	*	
<i>Massonia sessiliflora</i> (Dinter) U. & D. M-D.	<i>Snijman 1807</i>	Alexander Bay	*		
<i>Neobakeria angustifolia</i> (L.f.) Schltr.	<i>Van der Merwe 181</i>	Saldanha	*	*	*
<i>Neobakeria angustifolia</i> (L.f.) Schltr.	<i>Van der Merwe 134</i>	Sutherland			
<i>Neobakeria comata</i> (Burch. ex Baker) Schltr.	<i>Manning 2327</i>	De Aar	*		
<i>Neobakeria heterandra</i> Isaac	<i>Van der Merwe 177</i>	Kamiesberg	*	*	
<i>Neobakeria namaquensis</i> Schltr.	<i>Van der Merwe 199</i>	Springbok	*		
<i>Polyxena corymbosa</i> (L.) Kunth	<i>Van der Merwe 143</i>	Gordon's Bay	*	*	*
<i>Polyxena corymbosa</i> (L.) Kunth	<i>Van der Merwe 197</i>	Lionshead	*	*	
<i>Polyxena ensifolia</i> (Thunb.) Schönl.	<i>Van der Merwe 185</i>	Nieuwoudtville	*	*	*
<i>Polyxena longituba</i> A.M. v.d. Merwe	<i>Van der Merwe 194</i>	Komsberg	*	*	*
<i>Polyxena maughanii</i> Barker	<i>Van der Merwe 139</i>	Nieuwoudtville	*	*	

Species	Collector	Locality	DNA	Leaf Anatomy	Pollen
<i>Polyxena paucifolia</i> (Barker) A.M. v.d. Merwe & J.C. Manning	Van der Merwe 192	Vredenburg	*	*	
<i>Polyxena pygmaea</i> (Jacq.) Kunth	Van der Merwe 178	Rooiberg	*	*	
<i>Polyxena pygmaea</i> (Jacq.) Kunth	Van der Merwe 102	Bredasdorp	*	*	
<i>Whiteheadia bifolia</i> (Jacq.) Baker	Van der Merwe 99	Garies	*	*	*

CHAPTER 3

RESULTS

3.1 MACRO-MORPHOLOGY

Morphological features or the external appearance of a plant, has always been the type of data used most frequently in plant classification (Stuessy 1990). The reason for this has always been that morphological characters are easily noticeable and therefore much value is placed on the variability in morphology. The taxa included in this study have been placed in their present groupings based mainly on floral morphology. The taxonomic history of these taxa reflects the significance that has traditionally been attached to floral differences among the Hyacinthaceae. As a result of this several monotypic genera were established between 1835 and 1936 for newly discovered species which had more or less distinctive flowers. With further study it has become evident that the morphological characters on which these various genera were based, represent nothing more than extreme adaptations to a variety of pollination and seed dispersal strategies (Goldblatt & Manning 2000), and although there are differences in floral morphology, many of the taxa accord perfectly in their vegetative morphology. According to Stuessy (1990), vegetative characters are repeating units of structure without fixed numbers of parts, in contrast to floral features which are more definite in number. This he ascribed to the narrow, but obviously important, role of floral features in reproduction. He regarded the features of the vegetative organs to be more plastic and/or variable and therefore more difficult to use for taxonomic purposes. Nevertheless, in the Hyacinthaceae, leaves do reveal variation which can be a useful taxonomic tool. To eliminate any confusion when mentioning the various species all genus names have been written out in full.

Bulb

There is very little variation in the bulb morphology within the species of the minor genera of the Hyacinthaceae. The bulbs are mostly globose, subglobose or ovoid ranging from 15mm to 45mm in diameter. The smallest bulbs are found in the genus *Polyxena* where the bulbs are generally globose to ovoid and seldom exceed 15mm in diameter. A feature identified as common to the members of this genus and not found in any other of the genera in this study, is the inner membranous sheath of the bulb which encloses the base of the leaves and scape. In the genus *Daubenyia* the bulbs are turbinate, to globose or ovoid and between 20–35mm in diameter. The shape and size of the bulbs of *Amphisiphon stylosa*, *Androsiphon capensis*, *Neobakeria angustifolia*, *Neobakeria comata*, *Neobakeria heterandra* and *Neobakeria namaquensis* also fall into this group. Another bulb feature which combines all of the above species except for

Neobakeria heterandra is the outermost bulb tunics which split on drying and extend as a neck in narrow, flat papery segments. *Whiteheadia bifolia* also has bulbs which are approximately 25mm in diameter, but there is no papery neck evident in this species. Species of the genus *Massonia* have the largest bulbs of the study group, they are ovoid and vary from 30–45mm in diameter.

Leaves

Amphisiphon stylosa, *Androsiphon capensis*, *Daubenya alba* and *Daubenya aurea*, all have two prostrate or spreading, glabrous leaves, which are rather glossy above with impressed longitudinal striations along the main veins (Figure 3.1.1). The leaves are lanceolate to ovate in shape and measure 40–150mm x 25–50mm. Within the genus *Polyxena* there are two leaf types, the paired lanceolate or ovate leaves of *Polyxena pygmaea*, *Polyxena maughanii* and *Polyxena ensifolia* (Figure 3.1.2) and the narrow, linear leaves found in *Polyxena corymbosa*, *Polyxena paucifolia* and *Polyxena longituba*, of which there can be from two to six. The leaves of *Polyxena longituba* are also highly canaliculate (Figure 3.1.3) which makes this species very easy to identify. Within the genus *Massonia* there is a large variation in leaf morphology, but the leaves are always paired, usually prostrate or spreading and the bases enfold the peduncle for up to 50mm. The leaves of *Massonia* vary in shape and are oblong or orbicular to elliptic and sometimes even lanceolate. The leaf surfaces are also highly variable and may be glabrous, echinate, pustulate or even hairy. In *Massonia jasminiflora* individuals can have either glabrous or coriaceous leaves (Figure 3.1.4). The leaf markings in the genus *Massonia* are also highly variable and this is especially evident in *Massonia depressa* where the leaves can be green or green with red or maroon flecks (Figure 3.1.5) to an almost solid maroon colour. This is probably why early botanists described so many new species, now mostly included in the synonymy of *Massonia depressa*, as they over emphasized the taxonomic value of the differences in leaf colour. *Massonia pustulata*, as the name implies, is most easily recognised by its pustulate leaves (Figure 3.1.6). Minute pustules are sometimes seen in specimens of *Massonia echinata* where the echinate leaf surface appears more pustulate than echinate (Figure 3.1.7), but then the pustules are much smaller than those of *Massonia pustulata* and never as evenly distributed as in *Massonia pustulata*. The leaves of *Massonia echinata* and *Massonia pustulata* often have conspicuous longitudinal grooves similar to those found in the *Daubenya* group. *Massonia hirsuta*, as the name suggests, has hairy leaves and the hairs vary from short and bristly to long and silky. Although the leaves of *Neobakeria heterandra* are much smaller than the leaves of the *Massonia* species, they have the same shape and are very similar in appearance to those of *Massonia hirsuta*. The leaf surface in *Neobakeria heterandra* is also highly variable and can be glabrous, papillate or even pustulate, but where it is pustulate there are always simple hairs extending from the pustules (Figure 3.1.8). The leaves of *Whiteheadia bifolia* are very characteristic of the species and differ from the leaves of all the other genera included in this study.

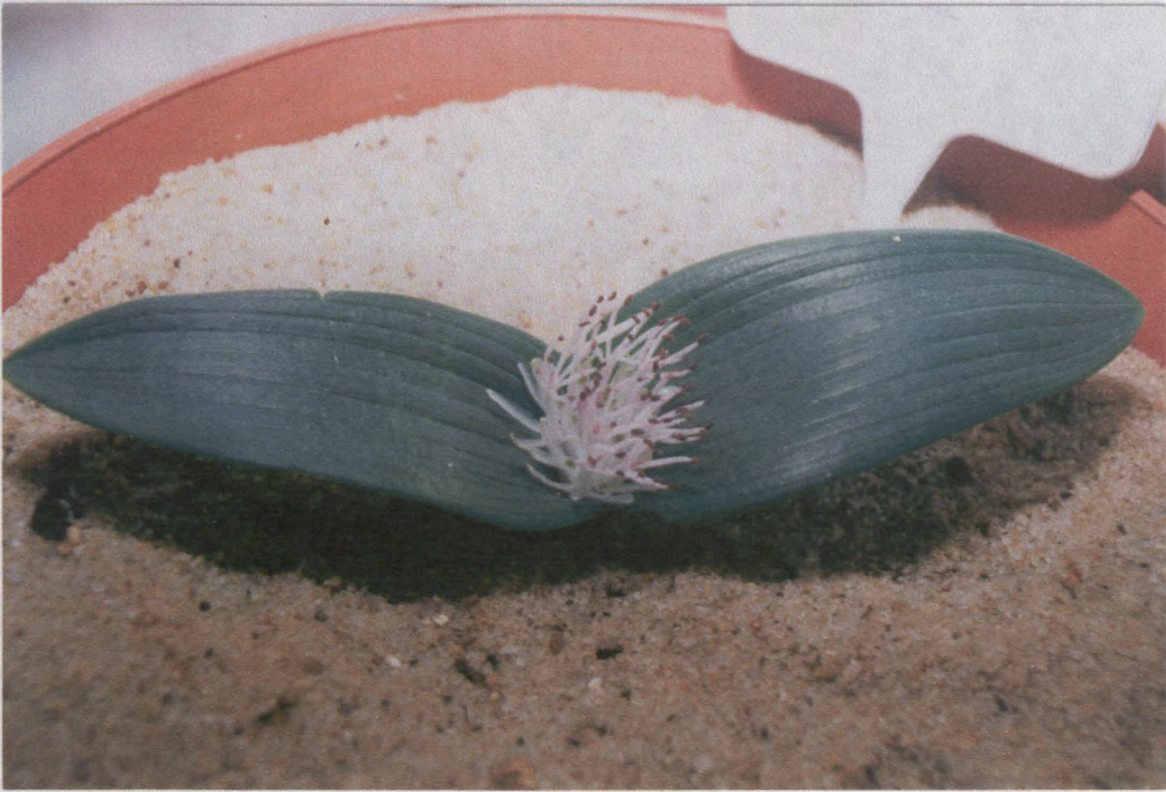


Figure 3.1.1 *D. alba* (Van der Merwe 195, STEU) with impressed longitudinal striations on leaves.



Figure 3.1.2 Paired, ovate leaves of *Polyxena ensifolia* (Van der Merwe 185, STEU)



Figure 3.1.3 Canaliculate leaves of *Polyxena longituba* (Van der Merwe 193, STEU)



Figure 3.1.4 Coriaceous leaves of *Massonia jasminiflora* (Van der Merwe 179, STEU).

Here the paired leaves are large and pale green, glabrous and fleshy to almost succulent but very fragile (even water dripping on the leaves can cause an injury). They also have conspicuous depressed longitudinal veins similar to those present in the *Daubenya* group (Figure 3.1.9).

Inflorescence

In *Daubenya aurea*, *Daubenya alba*, *Androsiphon capense* and the *Neobakeria angustifolia* specimen from Saldanha, the inflorescence is corymbose and capitate. In *Daubenya aurea* (Figure 6.2.2) the bracts are large and green, acropetally decreasing in size and the inflorescence protrudes approximately 50mm above the leaves. The inflorescence of this species also carries two different flower forms, here the lower flowers are zygomorphic and the upper ones actinomorphic. In *Daubenya alba* (Figure 3.1.1) the bracts are small and the inflorescence protrudes approximately 20mm above the leaves. In *Androsiphon capense* (Figure 3.1.10) the lower bracts are larger and the inflorescence protrudes approximately 40mm above the leaves. In the *Neobakeria angustifolia* specimen from Saldanha the bracts increase in size acropetally and the upper bracts form an inconspicuous green coma (Figure 3.1.11). In the *Amphisiphon stylosa* and the *Neobakeria angustifolia* specimen from Sutherland the inflorescence is subspicate and capitate or conical and protrudes for up to 50mm above the leaves in *Amphisiphon stylosa* and for up to 60mm in the *Neobakeria* specimen. In the *Neobakeria angustifolia* specimen from Sutherland the uppermost bracts are larger than the lower ones, with no flowers or flower buds in their axils, forming a conspicuous green to orange coma (Figure 3.1.12). In *Amphisiphon stylosa* the bracts acropetally increase in size reaching up to 10mm in length and there is a small coma present in this species (Figure 3.1.13). In *Neobakeria comata* the inflorescence is subspicate and capitate and protrudes approximately 20mm above the leaves (Figure 6.4.2). The bracts increase in size acropetally to form a small green, sometimes pinkish, coma. A very conspicuous green or pink coma of bracts is also present at the top of the inflorescence in *Neobakeria namaquensis*, where the inflorescence is subspicate and conical and protrudes for approximately 90mm above the leaves (Figure 6.6.2).

Within the genus *Polyxena*, *Polyxena brevifolia* and *Polyxena paucifolia* have racemose inflorescences while the inflorescences of *Polyxena ensifolia*, *Polyxena maughanii*, *Polyxena longituba* and *Polyxena pygmaea* are sub-corymbose, and *Polyxena corymbosa* is the only species with a corymbose inflorescence. While mounting herbarium sheets I noticed that the *Polyxena corymbosa* specimens from Gordon's Bay did not have a corymbose inflorescence at all, but rather a distinctly racemose one. Consulting the original description, I realized that the inflorescence should be a corymb, as indicated by the name and as evident in the *Polyxena corymbosa* specimen from Lion's Head, and not a raceme. Furthermore *Periboea gawleri* Kunth was described in 1843 and then transferred to *Hyacinthus* by Baker in 1897. According to Barker (1941) the supposed difference between *Polyxena corymbosa* and *Hyacinthus gawleri* was the corymbose inflorescence



Figure 3.1.5 Maroon flecked leaves of *Massonia depressa* (Van der Merwe 97, STEU).



Figure 3.1.6 Pustulate leaves of *Massonia pustulata* (Van der Merwe 101, STEU).



Figure 3.1.7 Echinat leaves of *Massonia echinata* (Van der Merwe 122, STEU).



Figure 3.1.8 *Neobakeria heterandra*, pustulate leaves with simple hairs extending from the pustules (Van der Merwe 177, STEU)

of *Polyxena corymbosa* as opposed to the racemose one of *Hyacinthus gawleri*. In the original description of *Periboea gawleri* no locality was given for the specimen, but an iconotype exists for *Scilla brevifolia* Ker-Gawl. (Curtis's Botanical Magazine 36: t. 1468 (1812)). Since *Periboea gawleri* Kunth and *Scilla brevifolia* Ker-Gawl. are conspecific the correct name should be *Scilla brevifolia*. As it would seem that this species belongs in the genus *Polyxena*, I suggest that it be transferred to *Polyxena* and should be referred to as *Polyxena brevifolia* (Ker-Gawl.) A.M. vd Merwe. In all the *Polyxena* species the bracts subtending the pedicels are small and inconspicuous or obsolete.

In the genus *Massonia* the inflorescence is capitate, surrounded by large bracts (varying from green to red in colour) and carried between the leaves, nestled on the leaf surfaces (Figure 3.1.6). *Neobakeria heterandra* (Figure 3.1.8) shares this type of inflorescence with the *Massonia* species.

The inflorescence of *Whiteheadia bifolia* is a spike which can reach 150mm in length and can extend to 300mm when in fruit. At the basal end of the inflorescence each flower is nestled in a large, persistent green bract. At the distal end of the inflorescence the bracts are without any flowers or flower buds, forming a terminal tuft or coma of green bracts at the top of the inflorescence (Figure 3.1.9). This coma, conspicuous or less conspicuous, is also present in *Amphisiphon stylosa*, *Neobakeria comata*, *Neobakeria angustifolia* and *Neobakeria namaquensis*.

Flower

There is a large variation in the flower morphology of the species included in this study. However, Goldblatt & Manning (2000) concluded that these differences in floral structure represent nothing more than extreme adaptations to a variety of pollination and seed dispersal strategies. The most striking of all the flowers are those of *Daubenya aurea* (Figure 6.2.2). The flowers of this species vary between a brilliant red or canary yellow, and the outer and inner flowers of the inflorescence differ considerably from one another. The outermost flowers are strongly zygomorphic and bilabiate, with the three lower tepals much enlarged to form a prominent lip (Figure 6.2.1). In these flowers, the perianth tube is 15–25mm long on the ventral side and 20–40mm long on the dorsal side. The smaller upper tepals measure only 2–4 x 1.5–2mm, whereas the larger lower tepals measure 20–40 x 5–13mm. Sometimes the median lower tepal is slightly larger than the other two. The innermost flowers are actinomorphic or weakly zygomorphic, with the tepals much smaller and equal in length and the perianth tube 13–20mm in length (Figure 6.2.1). The stamens in both flower types are basally fused into a short tube of ca. 2mm, although the lower three filaments are free in the outermost flowers. The zygomorphy evident in *Daubenya aurea* is also present, although to a lesser degree, in *Neobakeria namaquensis* where it can be observed in the bilabiate lower, older flowers and in *Neobakeria comata*, where the lowermost flowers are very slightly bilabiate. In



Figure 3.1.9 *Whiteheadia bifolia*, leaves with conspicuous depressed longitudinal veins (Van der Merwe 99, STEU).



Figure 3.1.10 Flowering plant of *Androsiphon capense* (Van der Merwe 152, STEU).



Figure 3.1.11 Flowering plant of *Neobakeria angustifolia* from Saldanha (Van der Merwe 181, STEU).



Figure 3.1.12 Flowering plant of *Neobakeria angustifolia* from Sutherland (Van der Merwe 134, STEU).

Daubinya alba there is a slight zygomorphy evident in the fusion of the stamens (Figure 6.1.2). In *Neobakeria namaquensis* the perianth tube in the lower flowers is 13–15mm long, cylindrical or dorsally slightly flattened with the ventral side of the perianth tube slightly longer than the dorsal side, and with a pronounced sinus separating the upper three tepals from the lower ones. In the upper flowers the perianth tube is 9–10mm long. The linear-oblongate perianth segments spread from the base and curve upwards. The stamens in *Neobakeria namaquensis* are erect to slightly spreading and sub-equal or the inner ones may be slightly longer, the three filaments on the ventral side of the perianth are basally fused for 5mm whereas the dorsal filaments are completely free (Figure 6.6.1)

In *Neobakeria comata* the lowermost flowers are very slightly bilabiate caused by a slight asymmetry in the perianth tube, as a result of the ventral side of the perianth tube that is slightly longer than the dorsal side, with a short sinus separating the three upper tepals from the lower ones. The perianth tube is also cylindrical or dorsally slightly flattened and can reach up to 45mm in length in the lower flowers and 15mm in length in the upper flowers. The upper flowers are actinomorphic. The perianth segments spread from the base, are slightly recurved and linear-oblong to narrowly oblanceolate. In *Neobakeria comata* the stamens are free and erect, becoming slightly spreading. The filaments are subequal or the inner ones may be slightly longer and they are inserted onto or 1mm above the base of the tepals (Figure 6.4.1).

In *Daubinya alba* the flowers are slightly zygomorphic and the perianth tube is 10–25mm long, with patent, linear to narrowly lanceolate perianth segments. Only the stamens reveal a degree of zygomorphy, because of the unequal fusion of the filaments which form a tube of about 20mm long. The free parts of the filaments are up to 15mm long, suberect or with tips slightly incurved. (Figure 6.1.1).

The flowers of *Neobakeria angustifolia* from the Sutherland locality (Figure 6.5.2) are noticeably different from those of the Saldanha locality (Figure 6.8.2). Those from Saldanha are white and papery in texture, while the flowers from the Sutherland specimens are yellow and firm textured. In the Sutherland specimens the perianth tube is cylindrical and slightly flattened, 10–20mm long and 2–3mm in diameter. The perianth segments are lanceolate and suberect with the inner three connate for about 1mm beyond the outer three. In these specimens the stamens are basally fused for up to 2.5mm into a wide-mouthed staminal collar. The filaments are yellow or orange and suberect to slightly incurved (Figure 6.5.1). In the Saldanha specimens the perianth tube is also cylindrical, slightly flattened at the mouth and up to 20mm long, however, it is only 1.5–2mm in diameter. The perianth segments are lanceolate, spreading at the base and then suberect. In these specimens the

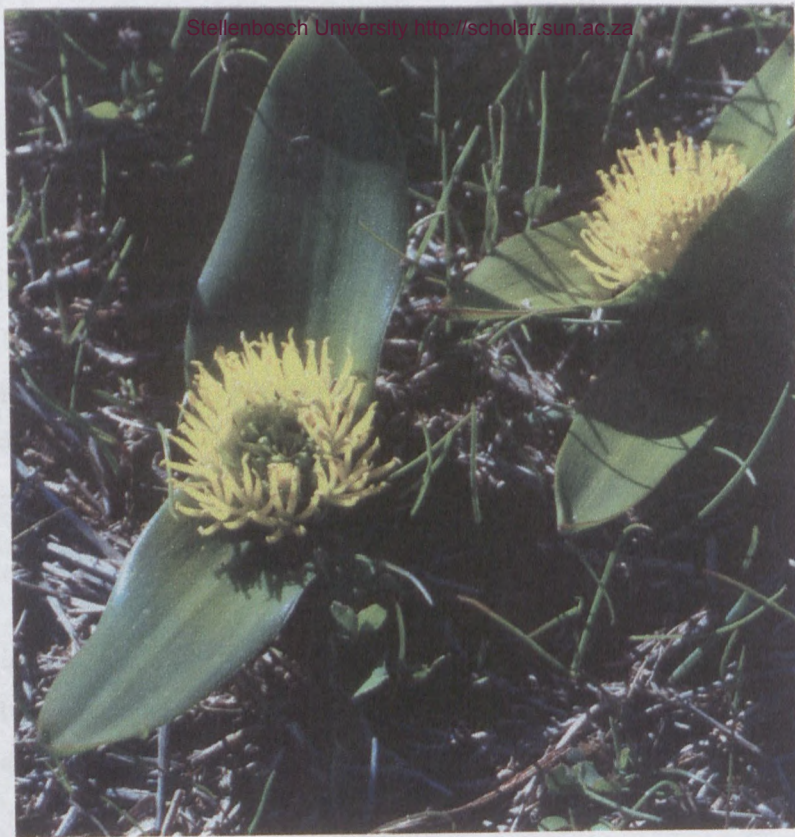


Figure 3.1.13 Flowering plant of *Amphisiphon stylosa* (Van der Merwe 119, STEU).



Figure 3.1.14 Flowering plant of *Polyxena pygmaea* (Van der Merwe 178, STEU).

stamens are connate for up to 1.5mm in a wide, purple staminal collar (Figure 6.8.1). The filaments are red and suberect.

Amphisiphon stylosa is the only species in which the tepals are almost completely fused with only minute free tepal lobes. The fused tepals form a tube of up to 20mm long around the staminal column. The stamens are connate for about 15mm to form a tube arising from about half way up the perianth tube. The free portion of the filaments are bright yellow, erect-spreading and arcuate (Figure 6.7.1).

In *Androsiphon capense* the flowers are very similar to those of *Amphisiphon stylosa*, but the tepals are erect or spreading, linear to oblanceolate and 11–15mm in length. The stamens are basally connate for 10–12mm to form a tube protruding from the mouth of the perianth tube. The top of the staminal tube is covered by a convex disc through which the style emerges and the free portion of the filaments are suberect with slightly incurved tips (Figure 6.3.1).

In the genus *Polyxena* the flowers are actinomorphic and pedicillate. The perianth is fused, forming a long or a short tube and the perianth segments are more or less oblong, erect, spreading or recurved. The stamens are attached to the perianth tube at two different levels and the filaments are free. *Polyxena brevifolia* (Figure 8.1.2) and *Polyxena corymbosa* (Figure 8.2.2) both have pink to lilac flowers with a very short perianth tube. The lanceolate-oblong tepals are four times the length of the perianth tube and are erect but spreading with age. In *Polyxena paucifolia* (Figure 8.5.2) the flowers are dark lilac to purple and the perianth tube is equal in length to the tepals. The perianth tube is 6–7mm long and the tepals are subequal and oblong. The stamens are very short (1mm) and are included within the perianth tube.

Polyxena pygmaea and *Polyxena longituba* are both characterised by a long perianth tube. In *Polyxena pygmaea* the flowers are white or lilac and the perianth tube is 20mm long, three times longer than the tepals. The tepals are oblong-lanceolate, spreading from the base and are strongly recurved. The stamens exert beyond the recurved segments, with the three longer stamens almost equal in length to the tepals (Figure 3.1.14). In *Polyxena longituba* (Figure 8.4.2) the flowers are also white to pale lilac and the perianth tube is 15–25mm long, at least twice the length of the tepals. The tepals are narrowly oblong-lanceolate, slightly involute, recurved and becoming more so with age. The stamens are fused with the tepals for the length of the perianth tube. The free portion of the filaments of the inner whorl equals one third of the length of the tepals and that of the outer whorl equals up to half the length of the tepals.

The flowers of *Polyxena ensifolia* (Figure 8.3.2) are white to pale lilac and the perianth tube (12–20mm long) is approximately twice the length of the tepals. The tepals are oblong and erect to spreading. The stamens are inserted at the base of the perianth segments and alternate filaments are



Figure 3.1.15 Flowering plant of *Massonia depressa* (Van der Merwe 106, STEU).



Figure 3.1.16 Flowering plant of *Massonia depressa* (Van der Merwe 97, STEU).

longer. The three longer stamens exert beyond the mouth of the perianth tube, equaling two thirds of the length of the tepals and the three shorter ones are sometimes included in the perianth tube. The flowers of *Polyxena maughanii* (Figure 8.3.4) are the same as those of *Polyxena ensifolia*, differing only in the length of the stamens, which are all included in the perianth tube with the three longest stamens just reaching to the mouth of the perianth tube.

In the genus *Massonia* the tepals of the flowers display a highly characteristic orientation not found in other genera of the family. Here the tepals are initially reflexed from the base, then curving outwards, forming a sigmoid fold in the longitudinal axis of the tepal. This characteristic is also found in flowers of *Neobakeria heterandra*, but is sometimes lacking in *Massonia depressa* and *Massonia jasminiflora*. In *Massonia depressa* the flowers are robust and fleshy with a large variation in colour of both the tepals and the stamens (Figure 3.1.15 & 3.1.16). The tepals can be erect or recurved with the sigmoid fold present. The perianth tube of *Massonia depressa* is cup-shaped, 5–10mm long and much wider (6–10mm) than any of the other *Massonia* species. The tepals are oblong, slightly broader at the base and equal in length to the tube. The stamens are all of equal length (10–18mm) and inserted at the mouth of the tube.

The flowers of *Massonia echinata* and *Massonia pustulata* are very similar, differing only in the length of the stamens and style, which in *Massonia echinata* are much shorter than those of *Massonia pustulata*. In *Massonia echinata* the perianth tube is 2–16mm long and 2–3mm wide and the tepals are oblong to narrowly lanceolate, reflexed with a sigmoid curve (Figure 7.2.1). The stamens are 5–8mm long and all of equal length and the style is 5–10mm long. In *Massonia pustulata* the perianth tube is 6–14mm long and 3–5mm in diameter and the tepals are oblong and more or less reflexed with a sigmoid curve (Figure 7.5.1). The stamens are 17–24mm long and all of equal length with the style measuring 10–30mm.

The flowers of *Massonia hirsuta* are almost identical to those of *Massonia echinata* with a perianth of 4–16mm long and 2–3mm wide and reflexed, narrowly lanceolate tepals with a sigmoid curve. The stamens are all of equal length but differ from the other species in the stoutness of the filaments (Figure 7.3.1)

In *Massonia jasminiflora* the flowers are characterised by a long (12–20mm) and narrow (less than 3mm in diameter) perianth tube which is at least twice the length of the tepals. The tepals are linear-lanceolate, spreading from the mouth of the perianth tube and can be ascending or reflexed. The stamens are very short (about 5mm long), all of equal length and inserted at the mouth of the perianth tube (Figure 7.4.1).

The flowers of *Neobakeria heterandra* are very similar to the flowers of *Massonia hirsuta*, *Massonia echinata* and *Massonia pustulata*, except that the stamens in *Neobakeria heterandra*, as



Figure 3.1.17 Fruiting plant of *Amphisiphon stylosa* showing the persistent styles on top of the capsules

the name implies, are of two different lengths. The perianth tube is 6–17mm long and up to 2mm wide and the tepals are 4–7mm long, linear-oblong and erect to spreading. The stamens (2.5–8mm long) are distinctly of two different lengths and inserted at the mouth of the perianth tube (Figure 7.6.1).

In *Whiteheadia bifolia* the flowers are fleshy with a wide, cup-shaped perianth tube, superficially resembling those of *Massonia depressa*. The perianth tube is 4–8mm long and 15–20mm wide with deltoid to ovate tepals, semi-erect, 5–7mm long. The stamens are fused at the base of the perianth tube for 2.5mm forming a white open cup at the mouth of the perianth tube. The upper part of the filaments are free, firm and 8mm long, curving inwards (Figure 9.1.2)

Capsules

In *Daubenya alba*, *Daubenya aurea* and *Neobakeria angustifolia* the capsules are loculicidal and trilobed, green and fleshy when young, becoming papery with age. In *Androsiphon capense* the capsules are papery, narrowly ovoid and tri-winged. In *Neobakeria comata*, the capsules are papery, obovoid, 3-angled rather than 3-winged, and do not appear to dehisce, but rather fragment when mature. The capsules in *Neobakeria namaquensis* are papery, obovoid and somewhat inflated, dehiscing loculicidally from the apex. *Amphisiphon stylosa* can easily be identified by its capsule which is green, obtusely angled and laterally compressed with a persistent style which remains at the top of the capsule like a conspicuous beak (Figure 3.1.17). Unlike the capsules of the rest of the taxa, the capsule of *Amphisiphon stylosa* dehisces septicidally from the base. In *Polyxena* there is no variation in the morphology of the capsules and all the members of this genus have small, green tri-lobed capsules which dehisce loculicidally. In *Massonia* there is also little variation in capsule morphology amongst the species. The capsule characteristics of this genus include an obovoid, 3-winged shape, fleshy to start but becoming papery with age and loculicidal dehiscence. The capsule of *Neobakeria heterandra* shares these features with *Massonia*. The capsule of *Whiteheadia bifolia* is obtriangular with three broad, obtuse, papery wings, basally surrounded by a persistent perianth. The capsule of *Whiteheadia bifolia* also has a persistent style attached at the apex, similar to that of *Amphisiphon stylosa* although much shorter.

3.2 ANATOMY

Leaf anatomy is often ignored as a taxonomic tool and yet anatomical characters can be taxonomically useful in pointing out differences between taxa, or lending support to existing groupings. Within the minor genera of the Hyacinthaceae no existing information on leaf anatomical studies could be found, therefore it was deemed important to include an investigation of the leaf anatomy in this study. Leaf anatomical characters revealed differences on generic level,

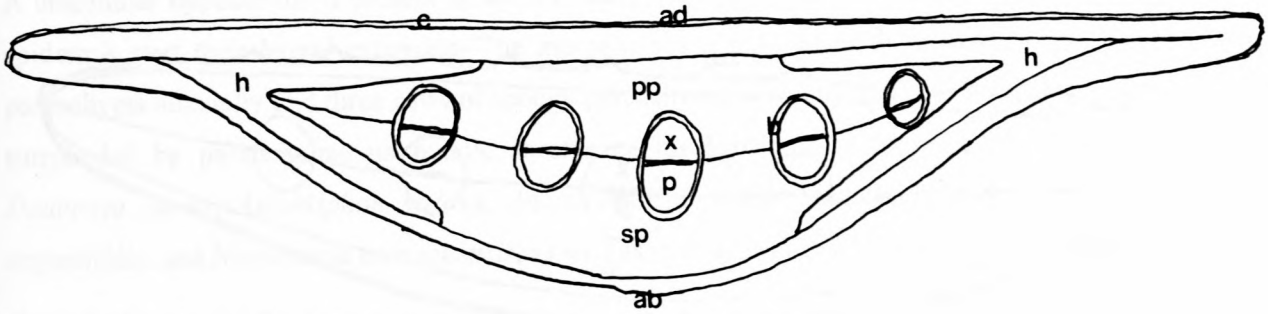


Figure 3.2.1 Diagrammatic representation of anatomical leaf type 1; ab = abaxial surface; ad = adaxial surface; b = bundle sheath; c = cuticle; h = hypodermis; p = phloem; pp = palisade-like parenchyma; sp = spongy parenchyma; x = xylem.

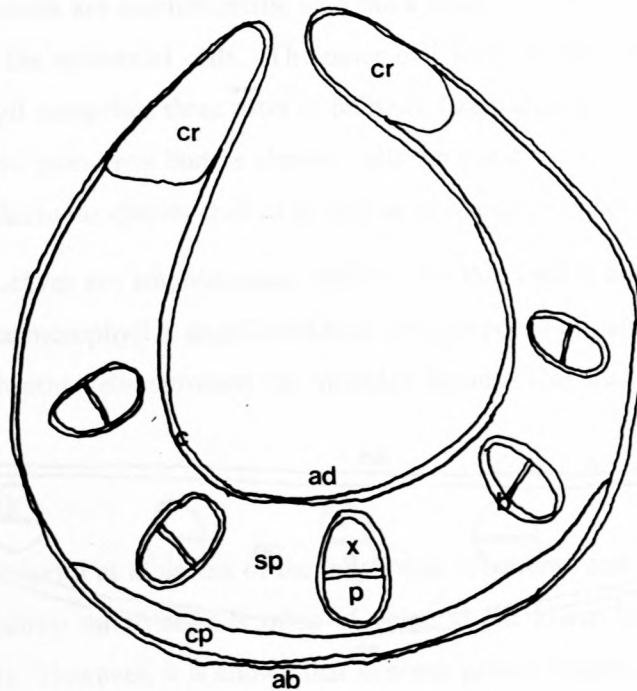


Figure 3.2.2 Diagrammatic representation of anatomical leaf type 2; ab = abaxial surface; ad = adaxial surface; b = bundle sheath; c = cuticle; cp = collenchymatic parenchyma; cr = collenchymatic ridge; p = phloem; sp = spongy parenchyma; x = xylem.

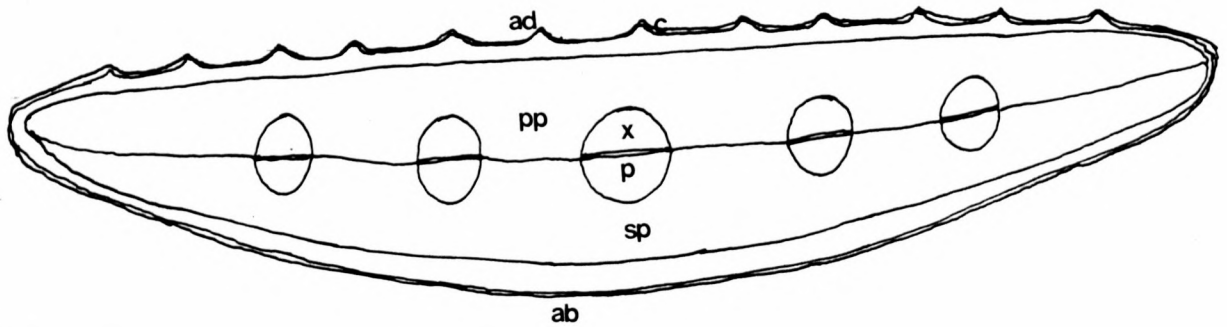


Figure 3.2.3 Diagrammatic representation of anatomical leaf type 3; ab = abaxial surface; ad = adaxial surface; c = cuticle; p = phloem; pp = palisade-like parenchyma; sp = spongy parenchyma; x = xylem.

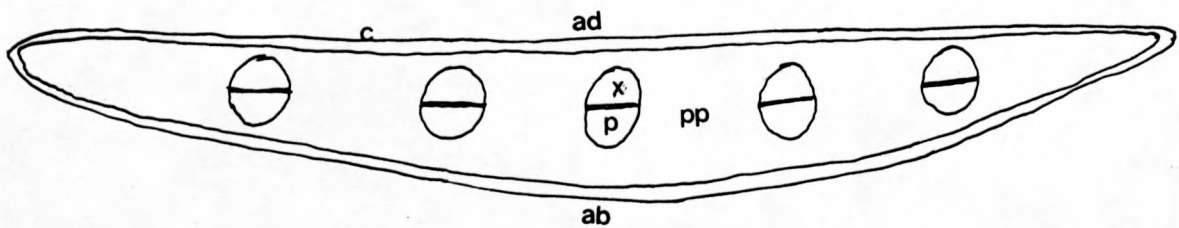


Figure 3.2.4 Diagrammatic representation of anatomical leaf type 4; ab = abaxial surface; ad = adaxial surface; c = cuticle; p = phloem; pp = palisade-like parenchyma; x = xylem.

which proved useful in grouping the taxa. Within the species of the minor genera of the Hyacinthaceae there appear to be four basic anatomical leaf types.

Type 1 (Figure 3.2.1): Leaves are amphistomatic with a thick, waxy cuticle. The adaxial and abaxial epidermis extend laterally at the leaf margins without any mesophyll in between. In this region of the extended epidermis the cell wall are slightly thickened, strengthening the leaf margins. A unicellular hypodermis is present at the leaf margins in the area where the adaxial and abaxial epidermis start their lateral extension. The mesophyll is composed of three rows of palisade-like parenchyma adaxially and three rows of spongy parenchyma abaxially and the vascular bundles are surrounded by parenchymatous bundle sheaths. This leaf type is found in *Daubenya alba*, *Daubenya aurea*, *Amphisphon stylosa*, *Androsiphon capense*, *Neobakeria comata*, *Neobakeria angustifolia*, and *Neobakeria namaquensis*, as well as in *Polyxena ensifolia* and *Polyxena pygmaea*.

Type 2 (Figure 3.2.2): Leaves are amphistomatic with a thick waxy cuticle. The mesophyll is composed of three rows of spongy parenchyma adaxially and three rows of collenchymatic parenchyma abaxially in the central part of the leaf. Collenchymatic ridges are also present along the leaf margins. Parenchymatous bundle sheaths surround the vascular bundles. This leaf type is found in *Polyxena brevifolia*, *Polyxena corymbosa*, *Polyxena longituba* and *Polyxena paucifolia*.

Type 3 (Figure 3.2.3): Leaves are amphistomatic with thick waxy cuticles, sometimes with pustules or hairs extending from the epidermal cells. The outer cell walls of the epidermal cells are also thickened. The mesophyll comprises three rows of palisade-like parenchyma adaxially and spongy parenchyma abaxially. No prominent bundle sheaths cells surround the vascular tissues. This leaf type is found in all the *Massonia* species studied as well as in *Neobakeria heterandra*.

Type 4 (Figure 3.2.4): Leaves are amphistomatic with a very thin cuticle and no thickening of the epidermal cell walls. The mesophyll is undifferentiated and composed of palisade-like parenchyma. No prominent bundle sheaths cells surround the vascular tissues. This leaf type is only found in *Whiteheadia bifolia*.

3.3 PALYNOLOGY

Data from pollen can be useful at all levels of the taxonomic hierarchy, and data obtained with the use of the scanning electron microscope is often of value at the lower levels of the taxonomic hierarchy (Stuessy 1990). However, it is known that in some genera remarkable variations of great and obvious taxonomic value occur, whereas in others there are no significant differences to be found between different species (Marais 1994). Unfortunately the minor genera of the Hyacinthaceae fall into the latter group. The pollen grains of this group are all monosulcate as is typical for the majority of the monocotyledons and primitive dicotyledons. Monosulcate pollen grains are boat-shaped and have one long germinal furrow and one germinal aperture (Walker

1976). The tectum in all the species of this group is without ornamentation and there was no significant variation in the size of the pollen grains. Walker and Doyle (1975) concluded that, with some exceptions, pollen morphology is consistent with the levels of advancement and the relationships shown in the Takhtajan & Cronquist systems of classification.

3.4 DISTRIBUTION AND ECOLOGY

The genus *Daubenia* is restricted to the winter rainfall region of Southern Africa and both *Daubenia alba* and *Daubenia aurea* occur along the edge of the Bokkeveld and Roggeveld escarpments from Nieuwoudtville and Calvinia in the north towards Sutherland in the South. *Amphisiphon stylosa* and *Androsiphon capense* are local endemics that are also restricted to the winter rainfall region and both species occur in the immediate vicinity of Nieuwoudtville. *Neobakeria angustifolia* occurs mainly in the winter rainfall region along the Roggeveld escarpment, but is not restricted to it and extends into the summer rainfall region near Fraserburg. This species also occurs on calcareous sands near Saldanha. *Neobakeria comata* has a very widespread distribution and is also the only species that occurs mainly in the summer rainfall region. *Neobakeria namaquensis* is another local endemic and occurs at the edge of the summer rainfall region in Bushmanland to the east of Springbok. Although *Neobakeria angustifolia*, *Neobakeria comata* and *Neobakeria namaquensis* all occur in the summer rainfall region they all respond to rain from autumn thundershowers and are therefore also winter growing. *Neobakeria heterandra* is restricted to the mountain ranges of the Western and Northern Cape Provinces in the winter rainfall region. The genus *Massonia* is widespread in the Western, Northern and Eastern Cape Provinces. *Massonia jasminiflora* is the only species restricted to the summer rainfall region and occurs in the Eastern Cape, the Free State and Lesotho, as well as near Kimberley in the Northern Cape. *Massonia depressa* is widespread in the winter rainfall regions of the Western Cape and Namaqualand, also occurring in the Karoo. *Massonia echinata* is widespread in the Western, Northern and Eastern Cape Provinces, occurring in both winter and summer rainfall areas. *Massonia hirsuta* is known from few isolated populations in Namaqualand, but has a wide inland and southern coastal distribution, occurring mainly in areas with summer rainfall. *Massonia pustulata* is mainly restricted to the winter rainfall region of the Western Cape Province and occurs from Calvinia in the North to Bredasdorp in the South and as far as Port Elizabeth in the East where it enters the summer rainfall region. The genus *Polyxena* is restricted to the winter rainfall area, with only *Polyxena ensifolia* extending towards the summer rainfall region, near Port Elizabeth. Many of the *Polyxena* species have very limited distribution ranges. *Polyxena brevifolia* is restricted to the Western Cape Province and occurs in scattered populations from Harmony flats between Gordon's Bay and Strand, to Stellenbosch, Paarl, Tulbagh and Ceres extending as far north as the Clanwilliam area. *Polyxena corymbosa* is restricted to the Cape Peninsula and occurs in

isolated patches around Greenpoint, Bantry Bay and Camps Bay. *Polyxena maughanii* has a very limited distribution in the Western Karoo and Bokkeveld mountains. *Polyxena longituba* is another very localised species occurring in the Komsberg area in the Northern Cape. *Polyxena paucifolia* is restricted to the coastal granite and limestone outcrops of the Paternoster and Langebaan areas in the Western Cape Province. *Polyxena pygmaea* is known from two different areas, occurring in the Riversdale area in the south and also to the north in Namaqualand. *Whiteheadia bifolia* occurs in the winter rainfall region of the western part of the Western Cape Province and Namaqualand and has also been recorded where it enters the summer rainfall region, to the extreme south of Namibia.

CHAPTER 4

DNA STUDY

VAN DER MERWE ET AL. – TRNL-TRNF PHYLOGENY OF MASSONIINAE
(HYACINTHACEAE)

PHYLOGENETIC RELATIONSHIPS IN THE SUBTRIBE MASSONIINAE OF THE TRIBE
MASSONIEAE (HYACINTHACEAE) BASED ON NON-CODING TRNL-TRNF
CHLOROPLAST SEQUENCES

Alison M. van der Merwe^{1,4}, Dirk U. Bellstedt², Elizabeth M. Marais¹ and Eric H. Harley³

¹Department of Botany, University of Stellenbosch, Stellenbosch, Private Bag X1, Matieland 7602, South Africa; and

² Department of Biochemistry, University of Stellenbosch, Stellenbosch, Private Bag X1, Matieland 7602, South Africa; and

³ Department of Chemical Pathology, University of Cape Town Medical School, Mowbray 7700, South Africa

⁴ Author for correspondence (e-mail: alisonvdm@xsinet.co.za)

Abstract

Sequence data from the intron and spacer of the trnL-F chloroplast region was studied to determine the phylogenetic relationships within the subtribe Massoniinae of the tribe Massonieae (Hyacinthaceae). Within Massoniinae, one species of *Amphisiphon* Barker, one of *Androsiphon* Schltr., two of *Daubenia* Lindl., seven of *Massonia* Thunb. ex Houtt., seven of *Polyxena* Kunth, four of *Neobakeria* Schltr. and one of *Whiteheadia* Harv. were included with two species from *Eucomis* L'Hérit in the ingroup. Species from *Veltheimia* Gled., *Ledebouria* Roth, *Galtonia* Decaisne and *Crinum* L. were included as outgroups.

Phylogenetic analysis using parsimony revealed three distinct lineages. Firstly, the *Massonia* clade including *Neobakeria heterandra* Isaac, secondly, the *Lachenalia*-*Polyxena* clade and thirdly, the *Daubenia* clade which includes *Amphisiphon*, *Androsiphon*, *Neobakeria angustifolia* (L. f.) Schltr., *Neobakeria comata* (Burch. ex Bak.) Schltr. and *Neobakeria namaquensis* Schltr. *Whiteheadia* is closely related to *Massonia* but is distinct enough to retain its generic status. The phylogenetic tree obtained here gives greater definition to the high order tree of Pfosser and Speta (1999). The results of the molecular phylogeny indicate that too much emphasis has been placed on the differences in floral morphology and that the morphological characters of some of the taxa should be re-evaluated.

Key words: Massoniinae; Massonieae; molecular phylogeny; Hyacinthaceae; trnL-trnF

The restructuring of the Liliaceae was proposed by several authors. Dahlgren and Clifford (1982), in their comparative study of the Monocotyledons, regarded it "of crucial importance that the families comprise reasonably homogeneous groups in an evolutionary sense and that they are arranged according to relationships as far as can be ascertained from comparative studies".

According to Perry (1985), the genera previously placed within the Liliaceae *sensu lato*, are now allocated to separate families falling within one of the two closely related orders, the Liliales or Asparagales. The combination of characters used to separate the new families from Liliaceae *sensu lato* were obtained mainly from the habit (eg. climbers, herbs, trees and shrubs), underground parts (eg. bulbs, corms, stem tubers, tuberous roots), inflorescence (eg. umbel or raceme) and fruits (capsule or berry; Perry 1985).

The southern African taxa of the order Asparagales consists of six new families formed by genera from the Liliaceae *sensu lato* as well as genera from the families Amaryllidaceae, Hypoxidaceae and Tecophilaeaceae (Perry 1985). The order Asparagales, as presently circumscribed, was first recognized by Huber (1969) and is believed to be a monophyletic group, a concept based mainly on fruit and seed characters. One of the main characters used in this demarcation is the complete collapse of the inner integument of the seed coat in ripe seeds, forming a thin, brown or colourless membrane. The outer wall of the epidermis of the testa in almost all capsule-fruited members as well as in some berry-fruited genera is provided with a rather thick layer of phytomelan. In the Asparagales the flowers generally have septal nectaries, the tepals are non-patterned and the style usually simple. In contrast, members of the order Liliales have nuclear endosperm formation, perigonal nectaries (or a lack of septal nectaries) and a variegated pattern on the tepals (Dahlgren, Clifford & Yeo 1985).

Within the order Asparagales the family Hyacinthaceae is characterized by geophytes with the underground part a bulb, inflorescence a simple raceme, perianth segments free or united at the base and the fruit a capsule, and includes, amongst others, the following South African genera: *Amphisiphon* Barker, *Androsiphon* Schltr., *Daubenya* Lindl., *Massonia* Thunb. ex Houtt., *Neobakeria* Schltr., *Polyxena* Kunth and *Whiteheadia* Harv. (Perry 1985).

Krause (1930), Hutchinson (1959) and Phillips (1951) provided the most important reviews of the genera of the Liliaceae since Baker (1897). Krause (1930) recognized six genera in the *Massonia* group, thus including all the genera which were described at that time except for *Neobakeria* which he considered synonymous with *Polyxena*. He included all the genera within the tribe *Scilloideae* Krause. Hutchinson (1959) also regarded *Neobakeria* as a synonym for *Polyxena* and *Amphisiphon* synonymous with *Androsiphon*, whereas *Massonia* and *Daubenya* were placed in the tribe *Massonieae*. Phillips (1951) linked *Massonia* with *Polyxena*,

Neobakeria, *Whiteheadia*, *Neopatersonia* Schön. and *Androsiphon* because of the shared possession of connate stamens. He also regarded *Amphisiphon* as a synonym for *Androsiphon*.

Jessop (1976) proposed that the genera *Massonia*, *Neobakeria*, *Polyxena*, *Hyacinthus* L., *Daubenia*, *Androsiphon*, *Amphisiphon*, *Ledebouria* Roth., *Drimiopsis* Lindl. & Paxt., *Lachenalia* Jacq. f. ex Murray, *Veltheimia* Gled. and *Eucomis* L' Hér. should be grouped as a tribe. Within this tribe Jessop (1976) believed that *Massonia*, *Polyxena*, *Hyacinthus* (Cape species only), *Daubenia*, *Androsiphon*, *Amphisiphon* and *Whiteheadia* comprised a natural group to which he referred to as the "*Massonia* group". Jessop (1976) united *Massonia* and *Neobakeria* under the older name *Massonia* because of the close correlation between the characters of the bulb and the filaments. He regarded *Neobakeria* to be closer to *Massonia* than to *Polyxena*, mainly because all the filaments are inserted on the same level on the perianth of *Massonia* and *Neobakeria*, but in two distinct levels in *Polyxena* and *Hyacinthus*. Jessop (1976) proposed that the Cape species of *Hyacinthus* (*H. corymbosus* L.) be placed in *Polyxena* based on the similarities in floral characters and the extreme isolation of the Cape *Hyacinthus* species from the rest of the genus in the northern hemisphere. Other genera recognized by Jessop (1976) are *Daubenia*, *Androsiphon*, *Amphisiphon* and *Whiteheadia*. He separated *Amphisiphon* from *Androsiphon* based on the same characters used by Barker (1936).

The most recent taxonomic treatment of the family was done by Müller-Doblies and Müller-Doblies (1997) who published a partial revision of the tribe Massonieae. They divided the Massonieae into the three subtribes Ledebouriinae, Lachenaliinae and Massoniinae. Within the subtribe Massoniinae they recognized the following genera: *Eucomis*, *Whiteheadia*, *Namophila* U. & D.M-D., *Periboea* Kunth., *Polyxena*, *Androsiphon*, *Amphisiphon*, *Neobakeria* and *Daubenia*.

Molecular data has been found to be particularly informative in resolving complex phylogenetic relationships. Thus Pfosser and Speta (1999), who did the most recent work on the family Hyacinthaceae, investigated the monophyly of the family and the generic relationships by sequencing the trnL intron and the trnL-trnF intergenic spacer region of chloroplast DNA for 105 taxa in the Hyacinthaceae and 18 species of related families. They proposed the following four subfamilies: Oziroëideae Speta (including South American Hyacinthaceae); Urgineoideae Speta; Ornithogaloideae Speta and the largest and most advanced subfamily Hyacinthoideae Link. The latter consists of the tribe Massonieae Baker (including species from Africa south of the Sahara and from India) and the Mediterranean/Asian tribe Hyacintheae Dumort. Pfosser and Speta (1999) pointed out that southern African taxa occur at basal positions in all subfamilies, thus indicating a southern African origin of the Hyacinthaceae.

For no plant family is it more true than for the Hyacinthaceae that the interpretation of single morphological characters resulted in highly erratic classifications when delineating tribal and

subfamilial relationships. No character, from bulb morphology to pistils or seeds, or even karyological data, has proven to be reliable (Pfosser and Speta 1999). In order to compile a proper classification all available information had to be assembled and combined. The aim of the present study was to provide new information gathered through the assessment of molecular data from DNA studies in order to produce a more realistic and reliable phylogenetic tree. This information could later be combined with morphological data to produce a more informative phylogenetic tree.

MATERIALS AND METHODS

The intron and spacer of the trnL-F chloroplast region of twenty-nine species of Hyacinthaceae were sequenced (Appendix 1). Duplicates of five of these species were collected from different localities. In *D. aurea* both the red- and the yellow-flowered forms were sampled. *Lachenalia pusilla* was originally included in the study because its position within *Lachenalia* was questioned. Its habit shows similarities with that of many *Polyxena* species and it is quite different from other *Lachenalia* species. Based on morphology alone, it appeared that *L. pusilla* should rather be included in *Polyxena*. The trnL-F sequences of a number of the taxa studied by Pfosser and Speta and others were obtained from Genbank and included in this study (also shown in Appendix 1). These included some species of *Lachenalia*, *Whiteheadia etesionamibensis* and some species of the more remotely related genera *Veltheimia*, *Eucomis*, *Ledebouria*, *Drimiopsis* and *Galtonia* with *Crinum* serving as the proximal outgroup.

Fresh material was used for all species, except for *N. comata* and *M. sessiliflora*, where silica-dried leaf material was used. Total genomic DNA was extracted using the hexacetyltrimethylammonium bromide (CTAB) method of Doyle and Doyle (1987). The trnL intron and the trnL-F spacer region of the chloroplast genome were amplified using the “c” and “d” primers and the “e” and “f” primers respectively (Taberlet *et al.*, 1991) by PCR using standard techniques at a 2.5 mM MgCl₂ concentration. Automated sequencing with an automated ABI sequencer was employed to sequence all taxa, using all four of the above primers.

Sequences were aligned using the DNA and Protein Sequence Alignment (DAPSA) programme developed by Harley (1998). Redundant sequence data at the ends of some sequences was trimmed, after which the sequence data were combined. Sequences from both regions were submitted to GenBank as indicated in Appendix 1.

Character by taxon matrices were generated by DAPSA and these were analyzed using PAUP version 4.1. Parsimony was used for tree construction, since maximum likelihood is difficult to codify for a mix of indels and single base changes, and indels contributed a major component of

the character data. The entire data set was analyzed either with indels assigned a weight of 1 and coded as a fifth character, or without indels. This was done to investigate the impact of indels on the data set. Indels were identified and analyzed by the method of Giribet and Wheeler (1999). The most parsimonious trees were sought by step-wise addition followed by a TBR search, holding only 5 trees for each of 500 random taxon entry replicates, as implemented in PAUP (Swofford, 1993). The resulting set of most parsimonious trees were then entered into a TBR search with MULPARS on, in order to find all possible most parsimonious trees. This protocol is designed to avoid islands of parsimony (Maddison, 1991). Where multiple most parsimonious trees were obtained, the strict consensus tree was calculated. Nodal support was investigated using the bootstrap (BS, Felsenstein, 1985) using 1000 replicates of random taxon selections, and MAXTREES set at 200.

RESULTS

Alignment and *trnL*, *trnL-trnF* characteristics – Sequences of the *trnL* intron and *trnL-trnF* spacer were aligned using DAPSA. DAPSA was also used to generate a cartoon of aligned sequences which is useful for the visualization of the data set (Figures 1 and 2), illustrating distinct indel patterns. Thus three distinct indel patterns emerged in the *Massonia* clade, the *Lachenalia*/*Polyxena* clade and the *Daubenya* clade.

Five species were sampled from two different localities each (*Massonia echinata* from Nieuwoudtville and Vanrhyns Pass, *M. hirsuta* from Graaff Reinet and Barkly West, *Polyxena corymbosa* from Gordon's Bay and Lion's Head, *P. pygmaea* from Bredasdorp and Kamiesberg and *Neobakeria angustifolia* from Sutherland and Saldanha). Samples of both the red form and the yellow form of *Daubenya aurea* were also included to see whether there would be any differences in sequence data. Although no noteworthy morphological variation was recognized in specimens of *M. echinata*, *M. hirsuta* or *P. pygmaea* from the different localities, the material was sequenced to assess sequence variation within these species. Quite considerable morphological variation occurs between specimens of *N. angustifolia* from the two different localities and between the two specimens of *P. corymbosa* from the two localities. Both specimens of each species were sequenced in an attempt to find support for the differences in the morphological data. No variation was found within *M. echinata*, *M. hirsuta*, *D. aurea* or *P. pygmaea* and thus only one sequence for each species was included in the final data set. In *N. angustifolia* variation was found between the sequence of the specimen from Sutherland and the one from Saldanha. The specimen from Sutherland shared an identical sequence with *Amphisiphon stylosa* from Nieuwoudtville, whereas the specimen from Saldanha differed in the *trnL* intron in having a deletion from bp 519-525, a deletion at 527, an autapomorphic substitution at bp 633 of A to T, and in the *trnL-trnF* spacer in having a deletion at 176-179 and an insertion at 435-437. In *P. corymbosa* there were also differences in the sequences of the two samples (Lion's Head vs. Gordon's Bay). The sequence obtained from *P. corymbosa* from

Lion's Head was identical to that obtained by Pfosser and Speta (1999), but the sequence of *P. corymbosa* from Gordon's Bay differed at bp 466 (autapomorphic substitution of a G to T) in the trnL intron and an addition of a T at bp 73, at bp 300 (an autapomorphic substitution of an A to G), at bp 308 (T instead of a C), and a four base insertion from 348-352 in the trnL-trnF spacer.

The sequence of *Whiteheadia etesionamibensis* U. & D. M-D. differs from that of *W. bifolia* only in that there is a large deletion from bp 95-206 in the trnL-trnF spacer in *W. etesionamibensis*.

The final length of the aligned data set of the trnL intron was 641 bp and of the trnL-trnF spacer was 461 bp resulting in a final matrix alignment with a total length of 1102 bp of which 129 were phylogenetically informative characters (60 indels and 69 transition/transversion characters). The information contained in the data set is summarized in Table1.

Repeat motifs within trnL sequences— In this data set, poly A repeats were found from bp 121-129 in the trnL intron. An TA microsatellite was also found from bp 338-375 in the trnL intron as can be seen in the sequence cartoon (Figure 1). Routinely, poly A sequences and microsatellite repeats are omitted from sequence data to be used for molecular systematic analyses. Due to the limited number of taxa used by Pfosser and Speta (1999) in their analysis, these regions were also omitted in their sequence analysis. However, in this study it was found that these poly A rich regions and the TA microsatellite were of constant length within genera and that they were phylogenetically informative. For this reason, they were not removed from the data set. In *D. alba* the TA microsatellite was repeated more times than in the rest of the genus.

Phylogenetic trees reconstructed by parsimony—Phylogenetic trees were constructed using parsimony on the full data set with 1000 bootstrap replicates. The strict consensus tree which was obtained in this way is shown in Figure 3. In addition, phylogenetic trees bootstrapped in a similar way were produced using the data set either without indels or with indels and these are shown in Figures 4 and 5 respectively.

The main phylogenetic analysis (figure 3) revealed a number of clades with very strong bootstrap support. Strong support at the basal node revealed a monophyletic Massoniae, with the successive emergence of the *Merwillia* clade with 99% bootstrap support and the *Ledebouria/Drimiopsis* clade with 100% bootstrap support (as established by Pfosser and Speta (1999)). The subtribe Massoniinae subsequently emerged as a trichotomy with poor support. This trichotomy consisted of the strongly supported *Eucomis* and *Daubenya* clades both with 100% bootstrap support and a further clade consisting of the rest of the subtribe, with a low bootstrap support of 55%. In this clade *Veltheimia* appears basally, followed by a clade consisting of a strongly supported *Lachenalia/Polixena* clade (100% bootstrap support) and a

less strongly supported *Whiteheadia*/*Massonia* clade (61% bootstrap support). Both of these clades were poorly resolved with the two *Whiteheadia* taxa appearing separately at the base of the strongly supported (97% bootstrap support) *Massonia* clade. Thus within the Massoniinae four distinct clades, with very high levels of bootstrap support emerge. These are the *Eucomis* clade, the *Massonia* clade, *Lachenalia*/*Polyxena* clade and the *Daubenya* clade. Additional resolution was found within the *Daubenya* clade. *Androsiphon capense* and *Daubenya alba* grouped together strongly as sister to the rest of *Daubenya* which unites into a strongly supported clade with 86% bootstrap support. Within this clade *Massonia zeyheri* and *Amphisiphon stylosa* form a sister relationship in a more proximal, strongly supported clade.

If the trees generated with the full data set (Figure 3) are compared with the trees generated with the data set without indels and with indels alone (Figures 4 and 5 respectively), the impact of the indel data is clearly evident. The eight nodes with the strongest support in the tree based on the full data set are also found in both indel and single base data sets, demonstrating strong congruence between single base change and indel data. The only obvious discordance between indel and base change data is found within the *Ledebouria*/*Drimiopsis* clade. In the data set without indels the resolution within many clades is lost and the tree shows many more polytomies, although some clades still appear with strong bootstrap support.

DISCUSSION

Sequence variation within species— Three of the five species which were each sampled from two different localities (*M. echinata*, *M. hirsuta* and *P. pygmaea*) have identical sequences. In *D. aurea*, the sequences of the red and yellow forms are also identical. The sequences of the two *P. corymbosa* specimens from Gordon's Bay and Lion's head differ quite considerably as mentioned in the results. These differences in sequences lend support to the morphological differences between the two specimens. While mounting herbarium specimens, it was noticed that the *P. corymbosa* specimens from Gordon's Bay have a racemose inflorescence. From the original description it was clear that the inflorescence should indeed be a corymb, as indicated by the name and as is evident in the *P. corymbosa* specimen from Lion's Head. From the literature it is evident that the correct name for this *P. corymbosa* specimen should have been *Scilla brevifolia* Ker-Gawl. As this species should be transferred to the genus *Polyxena* the name assigned to it is *Polyxena brevifolia* (Ker-Gawl.) A.M. vd Merwe. The sequences of the two *N. angustifolia* specimens differed considerably confirming the morphological differences between the specimens of the two different localities and supporting the splitting of the species. The sequence of *W. etesionamibensis* U. & D. M-D differs from the sequence of *W. bifolia* only with respect to a large deletion in the sequence of *W. etesionamibensis*. According to the description of Müller-Doblies & Müller-Doblies (1997), the two species of *Whiteheadia* differ only with respect to the length of the perianth tube and tepals.

Utility of the *trnL-trnF* region — The utility of the *trnL-trnF* region in resolving the phylogenetic relationships within the Massoniineae gives reasonably good resolution between genera. Within genera, however, the resolution is poor except for within the *Daubenyia* clade. If the trees generated with the full data set are compared with the trees generated with indel characters alone and with the data set excluding indels, it is evident that the substitution characters in the data set are highly informative in establishing the relationships between the clades, whilst the indel characters are important in the establishment of the monophyly of the clades. It also appears that the exclusion of the indel characters in the combined data set in actual fact improves tree resolution.

Monophyly of the major clades of the Massoniinae — The greatest value of the analysis is the fact that three strongly supported monophyletic clades appear in the Massoniinae i.e. the *Lachenalia/Polyxena* clade, *Massonia* clade and the *Daubenyia* clade. In view of the fact that many taxa were incorrectly placed in the past, this analysis clearly highlights these discrepancies and is thus of particular value in resolving the numerous nomenclatural errors in this subfamily. However, in order to analyse the relationships within genera, other analyses in which more informative (faster evolving) genes are sequenced, will have to be used.

Phylogeny within Massoniineae — The study of Pfosser and Speta (1999), which was primarily aimed at resolving the familial and subfamilial relationships within the Hyacinthaceae, included a limited number of species within the tribe Massoniae and the subtribe Massoniinae. In the present study, all known South African species within this subtribe were analysed (as far as is known only *W. etesiamibensis* occurs in the neighbouring Namibia). The species within the *Massonia* clade are *M. pustulata*, *M. grandiflora*, *M. echinata*, *M. depressa*, *M. jasminiflora*, *M. hirsuta*, *M. sessiliflora* and *N. heterandra*. The relationships between *M. pustulata*, *M. echinata*, *M. depressa* and *M. jasminiflora* are unresolved, but they are all obviously closely related. Although the morphology of *M. echinata* and *M. pustulata* lends support to the lumping of *M. echinata* and *M. pustulata*, the sequence variation between the two species may justify their separate species status. *M. depressa*, although also closely related to *M. echinata* and *M. pustulata* shows sufficient morphological variation with regard to both leaf and floral structure to retain its species status. *M. grandiflora* is morphologically identical to *M. depressa*, except for an increase in plant size, which is probably due to the effects of habitat. Inclusion within *M. depressa* should be considered. The separate species status of *M. hirsuta*, which is morphologically distinct, especially with regard to the leaf structure, is also supported. The sequence of *M. sessiliflora* is identical to that of *M. hirsuta* which confirms the morphological similarities between the two species and lends support to the reduction of *M. sessiliflora* to synonymy under *M. hirsuta*. The evidence presented here strongly supports the transfer of *N. heterandra* to the genus *Massonia*. This finding is in agreement with that of Müller-Doblies & Müller-Doblies (1997), who argued that the correct name of *N. heterandra* should be *Massonia*

pygmaea Kunth. Although their research was based on morphology with no contribution of molecular data, it appears that they were correct in their assignment of the name *M. pygmaea*. The synapomorphic morphological characters supporting this clade and found in all the species within the clade are the tepals with a sigmoid curve (although this character sometimes undergoes a reversal in *M. depressa*) and the inflorescence that is surrounded by large bracts. The large bracts are also found in *Whiteheadia*.

The *Polyxena/Lachenalia* clade includes the species *P. ensifolia*, *P. longituba*, *P. maughanii*, *P. pygmaea*, *P. paucifolia*, *P. corymbosa*, *P. brevifolia* (Ker-Gawl) A.M. vd Merwe and *Lachenalia pusilla*. The latter was included in the analysis because of the differences in morphology between it and other *Lachenalia* species and the similarities to species in the genus *Polyxena*. *Polyxena brevifolia* is the correct name of the *P. corymbosa* specimen from Gordon's Bay. Jessop (1976) considered *Scilla brevifolia* Ker-Gawl to be a synonym of *P. corymbosa* but according to the original description this species has a racemose inflorescence whereas the inflorescence of *P. corymbosa* is corymbose. Sequence data supports the morphological differences between the two species and supports the species status of *P. brevifolia*. The tree confirms the position of this species within the *Lachenalia* clade. At the same time the tree shows the close relationship between the genera *Lachenalia* and *Polyxena*, as was also found by Pfosser and Speta (1999). *Polyxena* and *Lachenalia* group together into a single highly unresolved clade, but due to the vast number of *Lachenalia* species a larger sampling of *Lachenalia* species is required before a final conclusion can be drawn. The apparent close relationship of all the *Polyxena* species indicates that lumping of some of the species may be considered. However, this can only be done after more *Lachenalia* species have been added to the analysis. According to the molecular tree, *P. maughanii* and *P. ensifolia* appear to be very closely related. Morphologically they differ only in the length of their stamens. In *P. maughanii* the stamens are included in the perianth tube and in *P. ensifolia* they are exerted beyond the tube. Both species share the same overall distribution pattern with *P. maughanii* being restricted to limestone outcrops, while *P. ensifolia* has a less specific substrate preference. The data presented here would support lumping these two taxa into a single species with separate varieties providing for the minor difference in stamen length and the preference of *P. maughanii* for limestone substrates. The molecular data presented here also supports the species status of *P. longituba*, which, although also very closely related to *P. ensifolia*, has sufficient morphological variation both in flower and leaf shape to retain its species rank. *P. pygmaea* shows significant variation, both molecularly and morphologically to retain its species status. *P. corymbosa* and *P. paucifolia* are very closely related, but differ in flower morphology as well as in the number of leaves per species, with *P. paucifolia* only having two leaves per plant, whereas *P. corymbosa* has six. The flowers of *P. corymbosa* are pink with the perianth tube about one third of the length of the perianth segments. In *P. paucifolia* the flowers are dark lilac to purple and the perianth tube equals the perianth segments in length. *P. brevifolia* shows sufficient molecular

variation to support its species status. This is also supported by the morphology of the species with the most noticeable difference being the inflorescence type, which is racemose in *P. brevifolia* and corymbose in *P. corymbosa*. The synapomorphic morphological characters supporting the *Polyxena* clade are biseriate stamens and a membranous basal sheath that encloses the base of the leaves and scape. It is not clear whether these characters are present in all species of *Lachenalia* or whether they are only characteristic of *Polyxena*.

The monotypic genera *Amphisiphon*, and *Androsiphon*, as well as *N. comata*, *N. namaquensis*, *N. angustifolia*, *M. marginata*, *M. zeyheri*, *D. aurea* and *D. alba* clearly resolve into a single clade. Thus molecular data strongly supports that these taxa should be lumped into a single genus. As *Daubenia* is the oldest genus within the group all the other species will be transferred to *Daubenia*. In this study, two collections of *N. angustifolia* were made, one from Sutherland and the other from Saldanha. The sequences of these two specimens differed significantly, which was confirmed by morphological differences. This supports the splitting of the species and it has since been determined that the respective names of the species should be *Massonia marginata* Willd. ex Kunth (Manning & Van der Merwe in press*) and *Massonia zeyheri* Kunth (Müller-Doblies & Müller-Doblies 1997). *Amphisiphon stylosa* shows a sister relationship with *M. zeyheri* and *M. marginata*, but there are sufficient morphological differences to retain their separate species status. *N. comata*, *N. namaquensis* and *D. aurea* appear together on a branch with 86% bootstrap support on the strict consensus tree, this then branches further with *M. zeyheri*, *Amphisiphon stylosa* and *M. marginata* grouped together on a branch with 91% bootstrap support. The sequences of *M. marginata* and *Amphisiphon stylosa* are identical apart from a few minor differences, but the two species differ considerably in floral morphology. Although *Androsiphon capense* and *D. alba* appear together as sister taxa on a branch with 98% bootstrap support, they differ morphologically in that the flowers of *D. alba* are white to pale-lilac whereas those of *Androsiphon capense* are bright yellow to orange. Another significant difference is that there is a disc present on the top of the staminal tube in *Androsiphon capense* that is lacking in *D. alba*. The synapomorphic morphological characters that support the *Daubenia* clade are longitudinal leaf striations and bulb tunics which extend as a long papery bulb neck. These morphological characters are found in all the taxa in the *Daubenia* clade.

Whiteheadia bifolia is the only species that retains its monotypic status. It appears on a branch of its own at the base of the *Massonia* clade. Here the molecular data supports the unique morphology of the species. According to Müller-Doblies and Müller-Doblies (1997) there is another species of *Whiteheadia*, *W. etesionamibensis* U.& D.M-D., which is confined to Namibia. The sequence of *W. etesionamibensis* appears to differ from that of *W. bifolia* only with regard to a large, autapomorphic deletion in the trnL-trnF spacer of *W. etesionamibensis*. The limited molecular variation found here indicates that further examinations of the validity of this species should be undertaken.

Of all the previous authors, Phillips' classification (1951) agrees best with the molecular analyses presented here regarding the taxonomic position of the species of the '*Massonia* group'. Phillips (1951) united *Amphisiphon* with *Androsiphon*, which is confirmed by this analysis. He also recognized *Neobakeria* as a different taxon from *Massonia*, whereas many taxonomists have followed Jessop (1976) and Müller-Doblies & Müller-Doblies (1997) and continued to include it in *Massonia*. Although the present study does not justify a generic status for *Neobakeria*, the molecular data shows differences that may justify its separation from *Massonia*. The molecular analysis does however, show that only *N. heterandra* belongs to *Massonia*. Krause (1930) and Hutchinson (1959) both treated *Neobakeria* as a synonym of *Polyxena*, but this study shows conclusively that there are no *Neobakeria* species belonging to *Polyxena*. Although this study rejects Jessop's (1976), assumption of *Neobakeria* being united with *Massonia*, it supports his inclusion of the Cape species of *Hyacinthus* (*H. corymbosus*) in the genus *Polyxena*. The taxonomic position of the genus *Neobakeria* has always been problematic (it was recognized by some authors and completely ignored by others), but the additional information from the analysis presented here, indicates that a better re-positioning of *Neobakeria* species within the group is possible. At the same time the genus *Daubenyia* is newly demarcated. Of the four *Neobakeria* species (*N. angustifolia*, *N. comata*, *N. heterandra* and *N. namaquensis*) all except *N. heterandra* will be transferred to the genus *Daubenyia*. *N. heterandra* moves into *Massonia* and the older name of *M. pygmaea* is re-instated (Müller-Doblies & Müller-Doblies, 1997). As a result of the differences in morphology as well as molecular differences of the *N. angustifolia* specimens from the two different localities, the species is split into two. Specimens from Sutherland correspond to *N. angustifolia* (L.f.) Schltr., but recent studies of the type specimens have revealed that *N. angustifolia* is a later homonym and the correct name should have been *M. marginata* Willd. ex Kunth (Manning & Van der Merwe in press*). As the species has since been transferred to *Daubenyia*, the correct name assigned to it is *Daubenyia marginata* (Willd. ex Kunth) J.C. Manning & A.M. van der Merwe. The specimen from Saldanha corresponds to the type specimen of *M. zeyheri* (Müller-Doblies & Müller-Doblies, 1997) and the correct name is *D. zeyheri* (Kunth) J.C. Manning & A.M. van der Merwe.

Perspectives — This analysis has clarified many of the nomenclatural and taxonomic anomalies that have dogged the subfamily Massoniinae in the past and is a clear illustration of the power of molecular systematics in resolving complex relationships. The contribution of indels is a particularly interesting feature of this (non-coding) data set. An extensive sampling within the Genus *Lachenalia*, which contains approximately 120 species, will, however be required before a clarification of the validity of the genus *Polyxena* and therefore a full phylogeny of the subfamily can be established.

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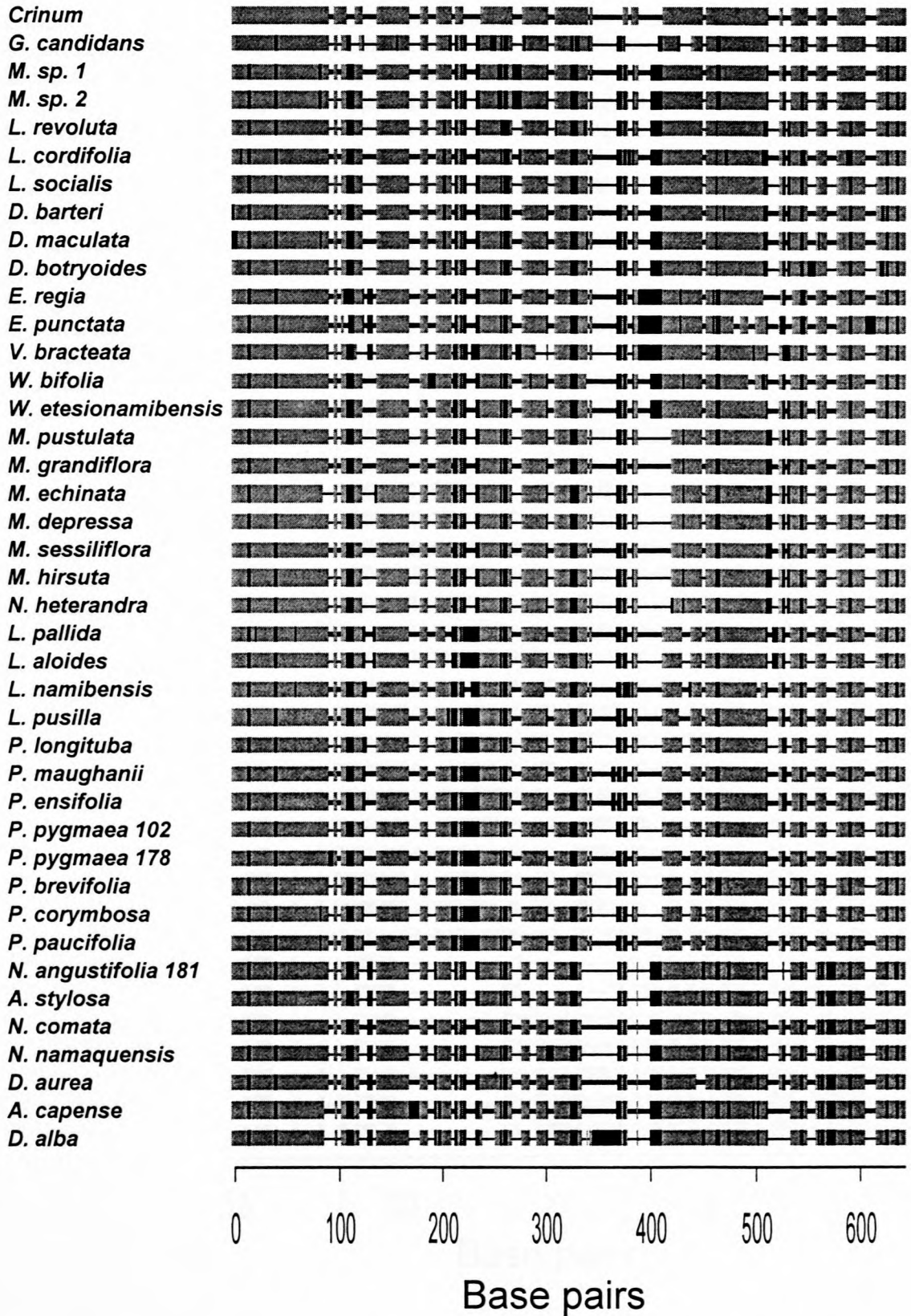


Figure 1. Sequence cartoon of the aligned sequences of the trnL intron of taxa included in this study. Homologous sequences are indicated as grey bars, mutations (substitutions and insertions) are indicated as full width black bars and gaps are indicated as lines

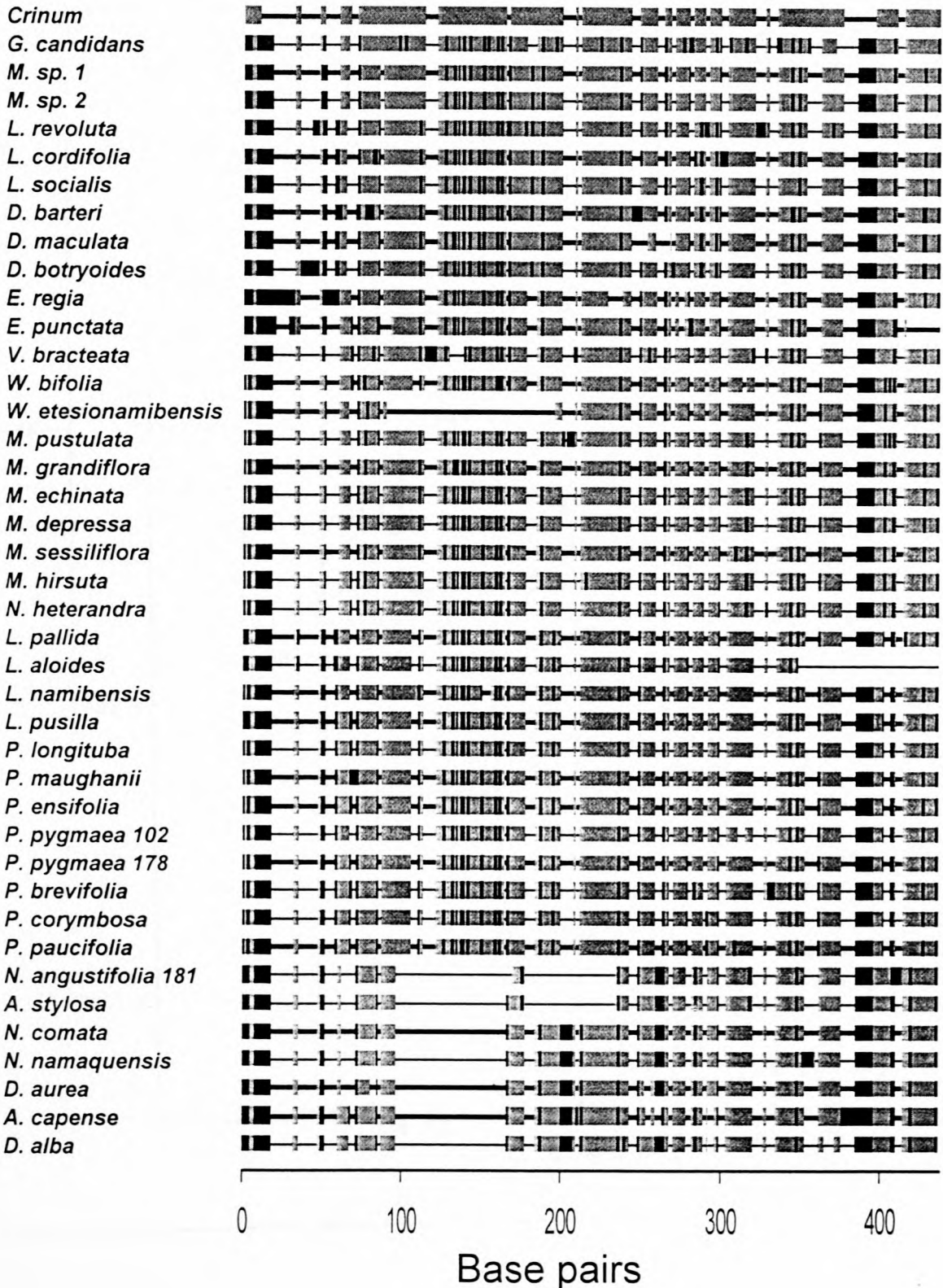


Figure 2. Sequence cartoon of the aligned sequences of the trnL-trnF spacer of the taxa included in this study. Homologous sequences are indicated as grey bars, mutations (substitutions and insertions) are indicated as black bars and gaps are indicated as lines.

P A U P * 1000 bootstraps

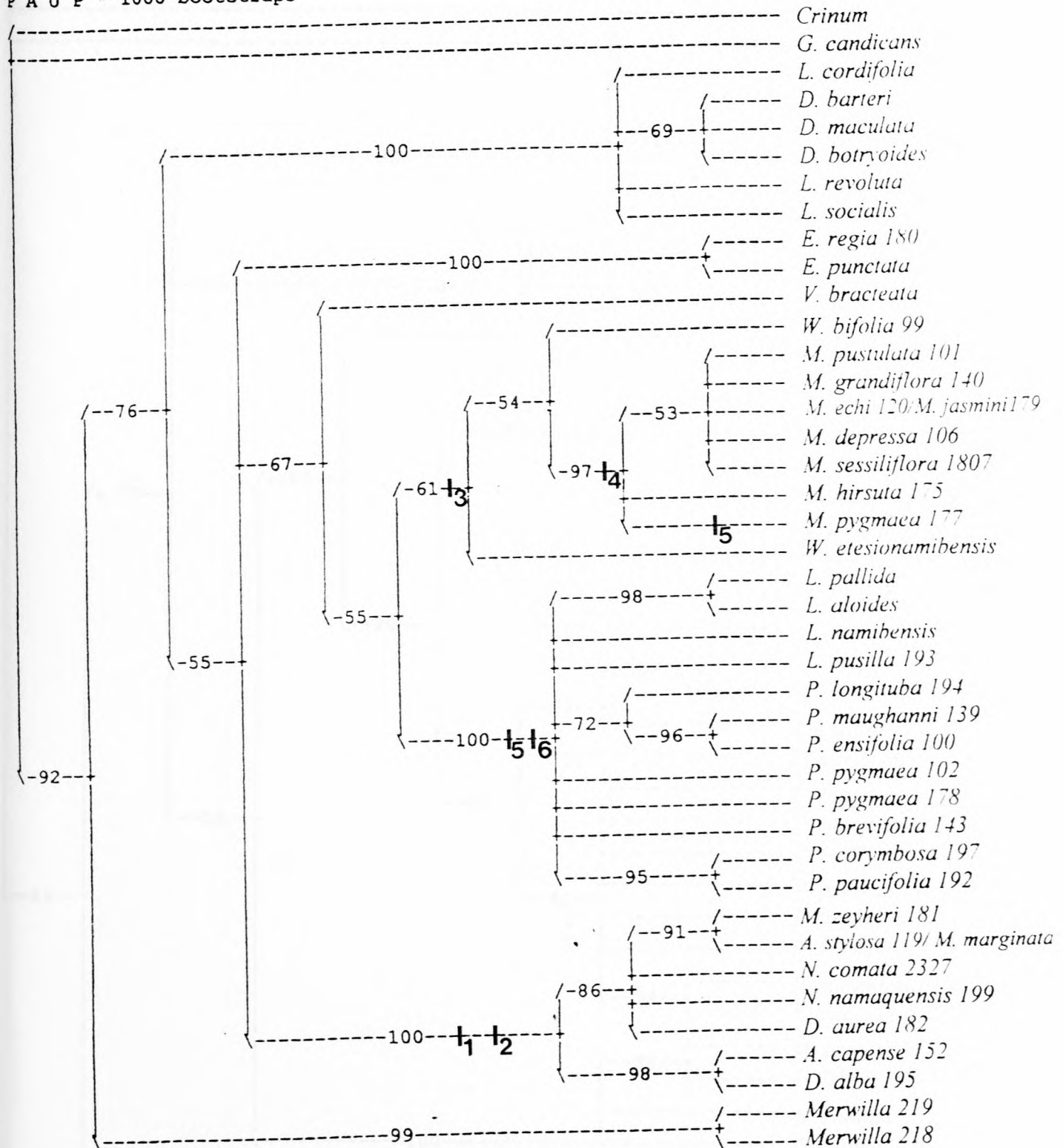


Figure 3. Strict consensus tree using full data set. Numbers on branches are bootstrap values. Bootstrap of less than 50% not indicated. Synapomorphic morphological characters supporting the main clades were plotted directly onto the tree: character 1. = longitudinal leaf striations; 2 = outer bulb tunics extend as bulb neck; 3 = inflorescence surrounded by large bracts; 4 = tepals with sigmoid fold; 5 = stamens biseriate; 6 = leaves & scape surrounded by membranous basal sheath.

P A U P * 1000 bootstraps with indels left out.

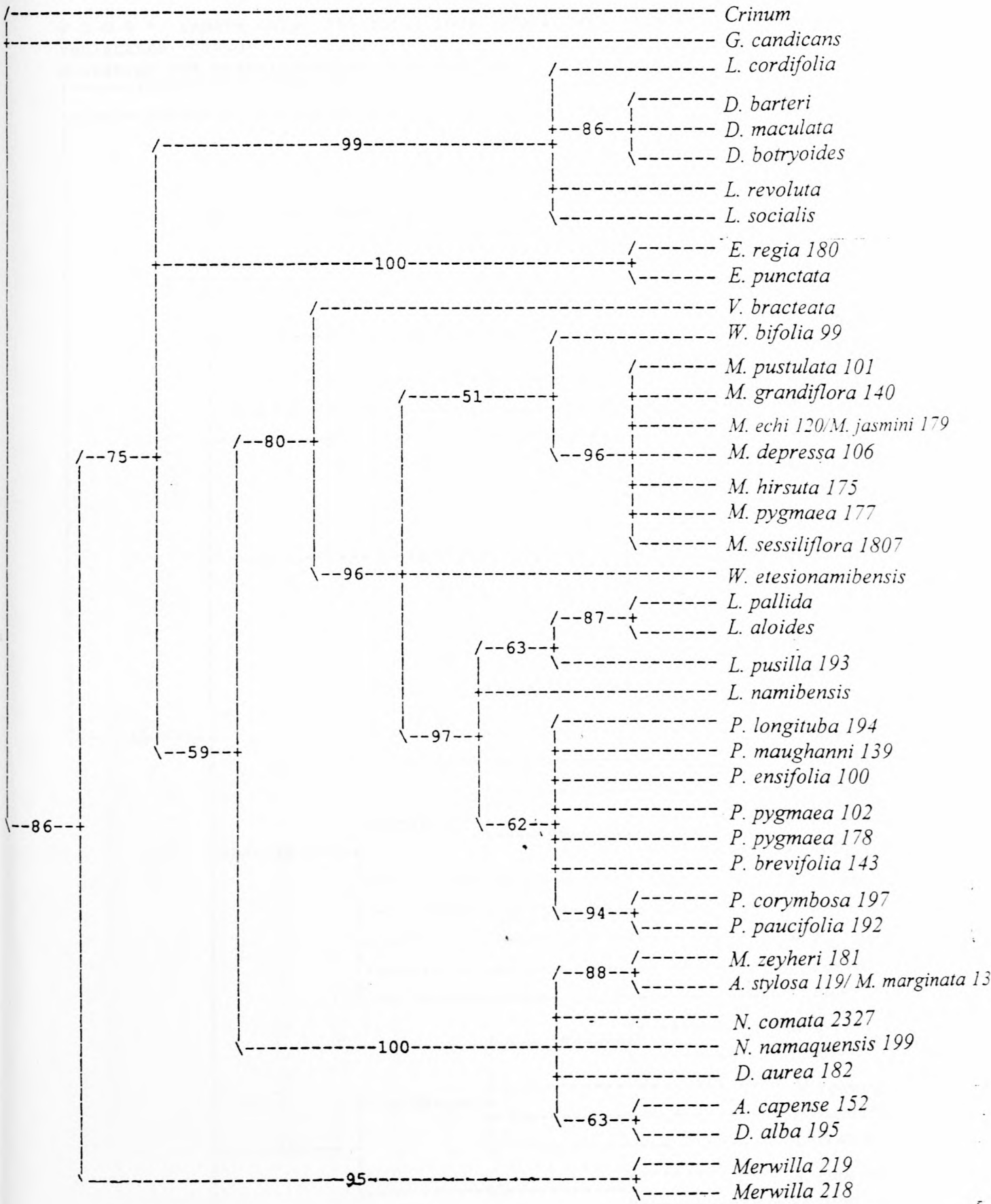


Figure 4. Phylogenetic tree constructed from data set with indels left out.

P A U P * indels only (59 total indel characters) Number of bootstrap replicates = 1000

Bootstrap 50% majority-rule consensus tree

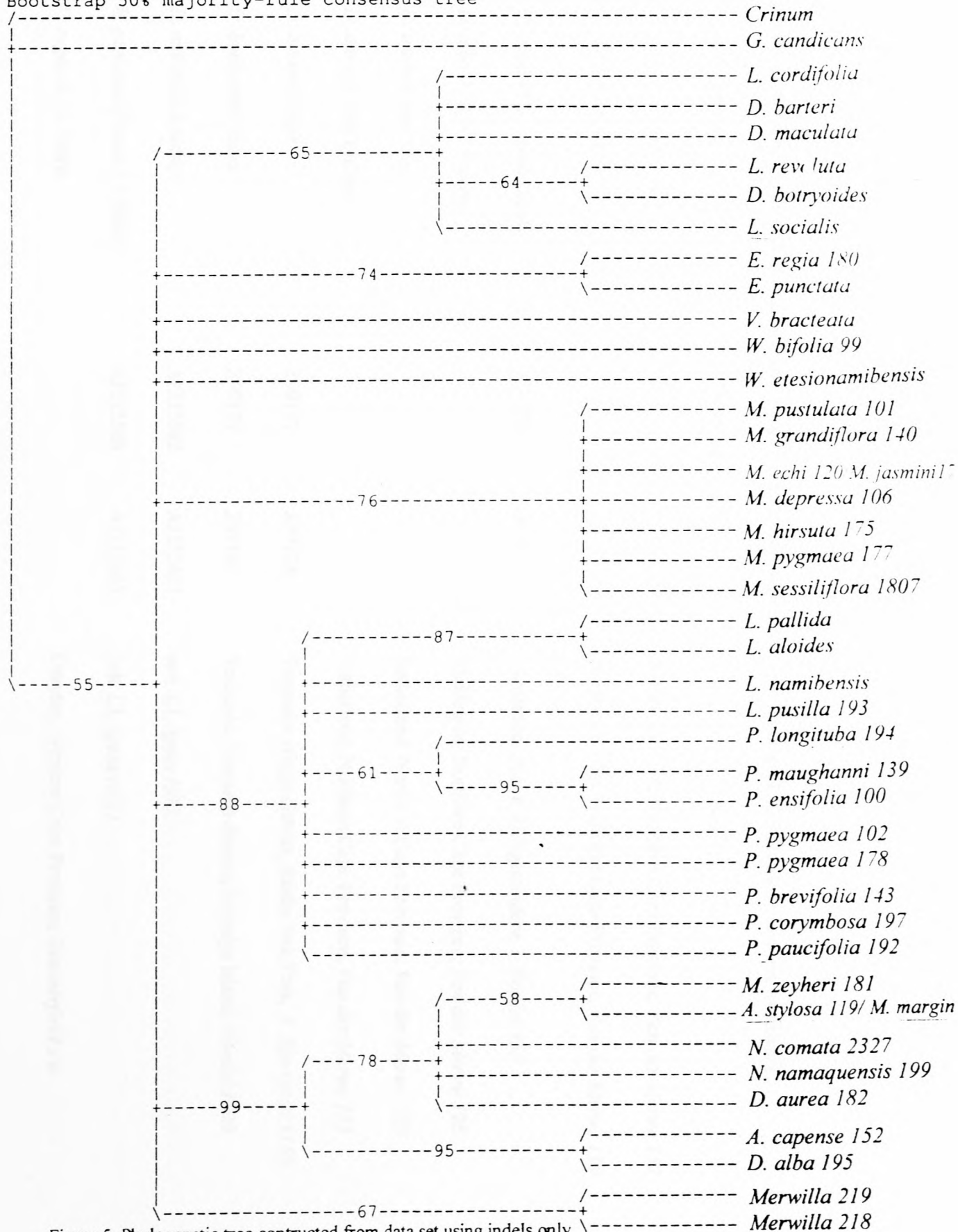


Figure 5. Phylogenetic tree constructed from data set using indels only

Appendix 1. Species analyzed, arranged alphabetically by genera, including collector's data and GenBank accession numbers.

Genus	Species	GenBank Accession no.	Source
<i>Androsiphon</i>	<i>A. capense</i> Schltr.		Nieuwoudtville, Northern Cape Province, <i>Van der Merwe 152</i>
<i>Amphisiphon</i>	<i>A. stylosa</i> Barker		Nieuwoudtville, Northern Cape Province, <i>Van der Merwe 119</i>
<i>Crinum</i>	<i>C. jagus</i> (Thomson) Dandy	X74729 X74580	Cameroon: 3km E of Ngaoundere, <i>I. Nordal 952</i>
<i>Daubinya</i>	<i>D. alba</i> A.M. vd Merwe		Middelpos, Northern Cape Province, <i>Van der Merwe 195</i>
	<i>D. aurea</i> Lindl. (red)		Sutherland, Northern Cape Province, <i>Van der Merwe 182</i>
	<i>D. aurea</i> Lindl. (yellow)		Sutherland, Northern Cape Province, <i>Van der Merwe 183</i>
<i>Drimiopsis</i>	<i>D. barteri</i> Baker	Z99137 Z99138	Tanzania: Iringa district, Ruaha Nat. Park, <i>A. Bjornstad 1158</i>
	<i>D. botryoides</i> Baker	Z99139 Z99140	Tanzania: Uzaramo district, Mbudya island, <i>Nordal 1600</i>
	<i>D. maculata</i> Lindley	AJ232502 AJ232625	cult. LI, <i>Speta H002</i>
<i>Eucomis</i>	<i>E. punctata</i> (Thunb.) L'Hérit.	AJ232500 AJ232623	cult. LI, <i>Speta H221</i>
	<i>E. regia</i> (L.) L'Hérit.		Drayton, Western Cape Province, <i>Summerfield s.n.</i>

<i>Galtunia</i>	<i>G. candicans</i> (Baker) Decne.	AJ232472	AJ232595	Cult. LI, <i>Speta H233</i>
<i>Lachenalia</i>	<i>L. aloides</i> (L.f.) Engl.	AJ232508	AJ232631	cult. B.G. Vienna, <i>Pfossen H159</i>
	<i>L. namibensis</i> Barker	AJ232505	AJ232628	Namibia, <i>Miller-Doblies H059</i>
	<i>L. pallida</i> Aiton	AJ232507	AJ232630	cult. B.G. Vienna, <i>Pfossen H021</i>
	<i>L. pusilla</i> Jacq.			Piketberg, Western Cape Province, <i>Van der Merwe 193</i>
<i>Ledebouria</i>	<i>L. cordifolia</i> (Baker) Stedje & Thulin	Z99143	Z99144	Malawi: Nyika plateau, Kongolo hills, <i>Nordal & Stedje 2409</i>
	<i>L. revoluta</i> (L.f.) Jessop	Z99146	Z99147	Zimbabwe: 8km SW of Selous, <i>Nordal 2082</i>
	<i>L. socialis</i> (Baker) Jessop	AJ232501	AJ232624	cult. B.G. Vienna, <i>Pfossen H014</i>
<i>Mervilla</i>	<i>M. sp. 1</i>	AJ232499	AJ232622	cult. B.G. Vienna, <i>Puff H219</i>
	<i>M. sp. 2</i>	AJ232498	AJ232621	cult. B.G. Vienna, <i>Puff H218</i>
<i>Massonia</i>	<i>M. depressa</i> Houtt.			Robertson, Western Cape Province, <i>Van der Merwe 106</i>
	<i>M. echinata</i> L.f.			Nieuwoudtville, Northern Cape Province, <i>Van der Merwe 120</i>
	<i>M. echinata</i> L.f.			Vanrhynspass, Northern Cape Province, <i>Van der Merwe 145</i>
	<i>M. grandiflora</i> Lindl.			Nieuwoudtville, Northern Cape Province, <i>Van der Merwe 140</i>

M. hirsuta Link & Otto

Graaf Reinet, Eastern Cape Province, *McMaster s.n.*

M. hirsuta Link & Otto

Barkly West, Eastern Cape Province, *Anderson s.n.*

M. jasminiflora Burch. ex Baker

Stutterheim, Eastern Cape Province, *Van der Merwe 179*

M. pustulata Jacq.

Bredasdorp, Western Cape Province, *Van der Merwe 101*

M. sessiliflora (Dinter) U. & D. M-D.

Alexander Bay, Northern Cape Province, *Snijman 1807*

Neobakera

N. angustifolia (L.f.) Schltr.

Saldanha, Western Cape Province, *Van der Merwe 181*

N. angustifolia (L.f.) Schltr.

Sutherland, Northern Cape Province, *Van der Merwe 134*

N. comata (Burch. ex Baker) Schltr.

De Aar, Eastern Cape Province, *Manning 2327*

N. heterandra Isaac

Kamiesberg, Northern Cape Province, *Van der Merwe 177*

N. namaquensis Schltr.

Springbok, Namaqualand, *Van der Merwe 199*

Polyxena

P. corymbosa (L.) Kunth

Gordon's Bay, Western Cape Province, *Van der Merwe 143*

P. corymbosa (L.) Kunth

Lionshead, Western Cape Province, *Van der Merwe 197*

P. ensifolia (Thunb) Schönl.

Nieuwoudtville, Northern Cape Province, *Van der Merwe 185 (100)*

P. longituba A.M. vd Merwe

Komsberg, Northern Cape Province, *Van der Merwe 194*

<i>P. maughanii</i> Barker			Nieuwoudville, Northern Cape Province, <i>Van der Merwe 139</i>	
<i>P. paucifolia</i> (Barker) A.M. vd Merwe & J.C. Manning			Vredenburg, Western Cape Province, <i>Van der Merwe 192</i>	
<i>P. pygmaea</i> (Jacq.) Kunth			Rooiberg, Namaqualand, <i>Van der Merwe 178</i>	
<i>P. pygmaea</i> (Jacq.) Kunth			Bredasdorp, Western Cape Province, <i>Van der Merwe 102</i>	
<i>Veltheimia</i>	<i>V. bracteata</i> Harv. ex Baker	AJ232503	AJ232626	cult. LI, <i>Speta H060</i>
<i>Whiteheadia</i>	<i>W. bifolia</i> (Jacq.) Baker			Garies, Northern Cape Province, <i>Van der Merwe 99</i>
<i>W. etesionamibensis</i> U. & D. M-D.		AJ232504	AJ232627	Namibia: Namskluft, Lavranos & Pehlemann H444

Appendix 2. The full aligned file data matrix of the trnL intron

						60
Crinum	GGAAACCTGC	TAAGTGGTAA	CTTCCAAATT	CAGAGAAACC	CCGGAACTAA	AAATGGGCAA
GalcanPf	•T.....
Merw219C..	•T.....
Merw218C..	•T.....
LedrevC..	•T.....
LedcorPfA.C..	•T.....
LedsocC..	•T.....
Dribar	N.....C..	•T.....
Drimac	NNNN.....C..	•T.....
DribotC..	•T.....
Er180C..	•T.....
EpPfC..	•T.....
VbPfC..	•T.....
Wb99C..	•T.....
WbPfC..	•T.....
Mpl01C..	•T.....
Mgl40C..	•T.....
Mel20C..	•T.....
Mdl06C..	•T.....
MsJMC..	•T.....
Mhl75C..	•T.....
Mpy177C..	•T.....
LpPfC..	•C.....	•T.....
LaPfC..	•T.....
LnPfC..	•T.....
Lp193C..	•T.....
Pl194C..	•T.....
Pml39C..	•T.....
Pe100C..	•T.....
Pp102C..	•T.....
Pp178C..	•T.....
Pb143C..	•T.....
Pc197C..	•T.....
Ppa192C..	•T.....
Dz181C..	•T.....
Ds119C..	•T.....
DcJMC..	•T.....
Dnl99C..	•T.....
Dal82C..	•T.....
Dca152C..	•T.....
Dal195C..	•T.....

Crinum	TCCTGAGCCA	AATCTTTATT	TTTAGAAAAA	CAA---GGGT	TTTAAAAACT	-----AGAAT
GalcanPf	AGAC-----
Merw219C.....	AGACT.....
Merw218C.....	AGACT.....
Ledrev	AGACT.....
LedcorPf	AGACT.....
Ledsoc	AGACT.....
Dribar	AGACT.....
DrimacT.....	AGACT.....
Dribot	AGACT.....
Er180G..	ATACT.....
EpPf	-TACT.....
VbPf	AGACT.....
Wb99	AGACT.....
WbPf	AGACT.....
Mpl01	AGACT.....
Mg140	AGACT.....
Mel20	AGACT.....
Md106	AGACT.....
MsJM	AGACT.....
Mh175	AGACT.....
Mpy177	AGACT.....
LpPf	N.....	AGACT.....
LaPf	AGACT.....
LnPf	C.....	AGACT.....
Lp193	AGACT.....
Pl194	AGACT.....
Pml39	AGACT.....
Pel00	AGACT.....
Pp102	AGACT.....
Pp178CAA...	AGACT.....
Pb143	AGACT.....
Pc197T.....	AGACT.....
Ppa192T.....	AGACT.....
Dz181	AGACT.....
Ds119	AGACT.....
DcJM	AGACT.....
Dn199	AGACT.....
Dal82	AGACT.....
Dca152	AGACT.....
Dal195	AGACT.....

Crinum	AAAAA-----	-----GGGA	TAGGTGCAGA	GACTCAATGG	AAGCTGTTCT	-----A
GalcanPfAA---	-----C..	-----
Merw219-----	-----	-----
Merw218-----	-----	-----
Ledrev-----	-----	-----
LedcorPf-----	-----	-----
Ledsoc-----	-----	-----
Dribar-----	-----	-----
Drimac-----	-----	-----
Dribot-----	-----	-----
Er180A---T	AAAAA-....	-----
EpPfA---T	AAAAA-....	-----
VbPf	-----T	AAAAA-....	-----
Wb99-----	-----	-----
WbPf-----	-----	-----
Mp101-----	-----	-----
Mg140-----	-----	-----
Mel20-----	-----A..	-----
Md106-----	-----	-----
MsJM-----	-----	-----
Mh175-----	-----	-----
Mpy177-----	-----	-----
LpPfAAA--	-----G...	-----
LaPfAAA--	-----G...	-----
LnPfAAAA-	-----	-----
Lp193AAA--	-----	-----
Pl194AAAA-	-----	-----
Pml39AAA--	-----	-----
Pe100AAA--	-----	-----
Pp102AA--	-----	-----
Pp178AA--	-----	-----
Pb143AA--	-----	-----
Pc197AA--	-----	-----
Ppa192AA--	-----	-----
Dz181	-----T	AAAAA-....	-----
Ds119	-----T	AAAAA-....	-----
DcJM	-----T	AAAAA-....	-----
Dn199	-----T	AAAAA-....	-----
Da182	-----T	AAAAA-....	-----
Dca152	-----T	AAAAA-....	AACGATTCT
Dal195	-----T	AAAAA-....	-----

Crinum	ACGAATGGA-	----GTTGAC	TACGTTGCGT	T--GGTAACT	GG-----	-----CTA
GalcanPf	-----AA....A	..AAT-----	---CCTT...
Merw219	-----A....A	..AAT-----	---CCTT...
Merw218	-----A....A	..AAT-----	---CCTT...
Ledrev	-----	...A.....A....A	..AAT-----	---CCTT...
LedcorPf	-----	...A.....A....A	..AAT-----	---CCTT...
Ledsoc	-----	...A.....A....A	..AAT-----	---CCTT...
Dribar	-----	...A.....A....A	..AAT-----	---CCTT...
Drimac	-----	...A.....A....A	..AAT-----	---CCTT...
Dribot	-----	...A.....A....A	..AAT-----	---CCTT...
Er180	-----A....A	..AAT-----	---CCTT...
EpPf	-----A....A	..AAT-----	---CCTT...
VbPfA...	-----	--AA....A	..AACAG--G	AATCCTT...
Wb99A	TGGA.....	--AA....A	..AAT-----	---CCTT...
WbPf	-----	--AA....A	..AAT-----	---CCTT...
Mp101	-----	--AA....A	..AAT-----	---CCTT...
Mg140	-----	--AA....A	..AAT-----	---CCTT...
Me120	-----	--AA....A	..AAT-----	---CCTT...
Md106	-----	--AA....A	..AAT-----	---CCTT...
MsJM	-----	--AA....A	..AAT-----	---CCTT...
Mh175	-----	--AA....A	..AAT-----	---CCTT...
Mpy177	-----	--AA....A	..AAT-----	---CCTT...
LpPf	-----	ATAA....A	..AATAGAAT	AATCCTT...
LaPf	-----	ATAA....A	A..AATAGAAT	AATCCTT...
LnPf	-----	ATAA....A	..AA-----T	AATCCTT...
Lp193	-----T..	ATAA....A	..AATAGAAT	AATCCTT...
Pl194	-----	ATAA....A	..AATAGAAT	AATCCTT...
Pml39	-----	ATAA....A	..AATAGAAT	AATCCTT...
Pe100	-----	ATAA....A	..AATAGAAT	AATCCTT...
Pp102	-----	ATAA....A	..AATAGAAT	AATCCTT...
Pp178	-----	ATAA....A	..AATAGAAT	AATCCTT...
Pb143	-----	ATAA....A	..AATAGAAT	AATCCTT...
Pc197	-----	ATAA....A	..AATATAAT	AATCCTT...
Ppa192	-----	ATAA....A	..AATATAAT	AATCCTT...
Dz181	----A.....	---A....A	..AAT-----	---CCTT...
Ds119	----A.....	---A....A	..AAT-----	---CCTT...
DcJM	----A.....	---A....A	..AAT-----	---CCTT...
Dn199	----A.....	---A....A	..AAT-----	---CCTT...
Da182	----A.....	---A....A	..AAT-----	---CCTT...
Dca152	----A....T	---A....A	..AAT-----	---CCTT...
Dal195	----A....T	---A....A	..AAT-----	---CCTT...

Crinum	TCGAAATTAA	AGAAAGGATG	GCATATAT--	-----ATCT	AATACGTACG	TATACATACT
GalcanPfC.	·A.....G·	A·C.....	-----G
Merw219A·G·	A·C.....AT	CTATAT....
Merw218A·G·	A·C.....AT	CTATAT....
LedrevGG·	A·CCG.....	-----
LedcorPfG·	A·CC.....	----AT....
LedsocG·	A·CC.....	-----
DribarG·	A·CC.....	-----
DrimacG·	A·CY.....	-----
DribotG·	A·CC.....	-----
Erl80G·	A·C.....	-----
EpPfG·	A·C.....	-----
VbPfG·	A·C.....	-TATAT....	-----
Wb99G·	A·C.....	-----A.....
WbPfG·	A·C.....	-----
Mp101G·	A·C.....	-----
Mg140G·	A·C.....	-----
Me120G·	A·C.....	-----
Md106G·	A·C.....	-----
MsJMG·	A·C.....	-----
Mh175G·	A·C.....	-----
Mpy177G·	A·C.....	-----
LpPfG·	A·C.....	-----
LaPfG·	A·C.....	-----
LnPfG·	A·G.....	-----	-----
Lp193G·	A·C.....	-----
Pl194G·	A·C.....	-----
Pm139G·	A·C.....	-----
Pe100G·	A·C.....	-----
Pp102G·	A·C.....	-----
Pp178G·	A·C.....	-----
Pb143G·	A·C.....	-----
Pc197G·	A·C.....	-----
Ppa192G·	A·C.....	-----
Dz181G·	A·C.....	-----
Ds119G·	A·C.....	-----
DcJMG·	A·C.....	-----
Dn199G·	A·C.....	-----
Dal82G·	A·C.....	-----
Dcal52	-----G·	A·C.....	-----
Dal195	-----G·	A·C.....	-----

Crinum	GGC----	ATA	TCAAACGATT	AATCGCGAAC	CGAATCCATA	-TAT-----	-----
GalcanPf	·A·-----	·	·	·A·CT	·	A·-----	-----
Merw219	·A·-----	·	·	·AT·C·	·	·-----	-----
Merw218	·A·-----	·	·	·AT·C·	·	·-----	-----
Ledrev	·A·-----	·G	·	·AT·C·	·	·T·	-----
LedcorPf	·A·-----	·	·	·AT·C·	·	·-----	-----
Ledsoc	·-----	·	·	·AT·C·	·	·-----	-----
Dribar	·A·-----	·	·	·AT·C·	·	·-----	-----
Drimac	·A·-----	·	·	·AT·C·	·	·C	-----
Dribot	·A·-----	·	·	·AT·C·	·	·-----	-----
Er180	·A·-----	·	·	·AT·C·	·	·-----	-----
EpPf	·A·-----	·	·	·AT·C·	·	·-----	-----
VbPf	·A·-----	·	·	·AT·C·	·	·-----	-----
Wb99	·A·-----	·	·	·AT·C·	·	·-----	-----
WbPf	·A·-----	·	·	·AT·C·	·	·-----	-----
Mp101	·A·-----	·	·	·AT·C·	·	·-----	-----
Mg140	·A·-----	·	·	·AT·C·	·	·-----	-----
Me120	·A·-----	·	·	·AT·C·	·	T·	-----
Md106	·A·-----	·	·	·AT·C·	·	·-----	-----
MsJM	·A·-----	·	·	·AT·C·	·	·-----	-----
Mh175	·A·-----	·	·	·AT·C·	·	·-----	-----
Mpy177	·A·-----	·	·	·AT·C·	·	·-----	-----
LpPf	·A·-----	·	·	·AT·C·	·	·-----	-----
LaPf	·A·-----	·	·	·AT·C·	·	·G	-----
LnPf	-----	·	·	·AT·C·	·	·-----	-----
Lp193	·A·-----	·	·	·AT·C·	·	·-----	-----
Pl194	·A·-----	·	·	·AT·C·	·	·-----	-----
Pm139	·A·-----	·	·	·AT·C·	·	·-----	-----
Pe100	·A·-----	·	·	·AT·C·	·	·-----	-----
Pp102	·A·-----	·	·	·AT·C·	·	·-----	-----
Pp178	·A·-----	·	·	·AT·C·	·	·-----	-----
Pb143	·A·-----	·	·	·AT·C·	·	·-----	-----
Pc197	·A·-----	·	·	·AT·C·	·	·-----	-----
Ppa192	·A·-----	·	·	·AT·C·	·	·-----	-----
Dz181	·A·-----	·	·	·AT·C·	·	·-----	-----
Ds119	·A·-----	·	·	·AT·C·	·	·-----	-----
DcJM	·A·-----	·	·	·AT·C·	·	·-----	-----
Dn199	·A·TGAC·	·	·	·AT·C·	·	·-----	-----
Da182	·A·-----	·	·	·AT·C·	·	·-----	-----
Dca152	·A·-----	·	·	·AT·C·	·	·-----	-----
Dal195	·A·-----	·	·	·AT·C·	·	·ATATAT	ATATATATAT

Crinum	-----	--ATGCAT--	ATATATAT--	-----	-----G	CAATATATGC
GalcanPf	-----TAT	AT..AT----	-----	-----	-----GC.
Merw219	-----TAT	AT..A.....	--G.....	-----	GCAATATGC.
Merw218	-----TAT	AT..A.....	--G.....	-----	GCAATATGC.
Ledrev	-----TAT	AT..AG....	--G.....	-----	GCAATATGC.
LedcorPf	-----TAT	AT..A...AC	..G.....	-----	GCAATATGC.
Ledsoc	-----TAT	AT..A.....	--G.....	-----	GTAATATGC.
Dribar	-----TAT	AT.....	--G.....	-----	GCAATATGT.
Drimac	-----TAT	AT..A.....	--G.....	-----	GCAATATGT.
Dribot	-----TAT	AT..A.....	--G.....	-----	GCAATATGT.
Er180	-----TAT	AT..A.....	--G.....GC	AATATTATAT	GCAATATGC.
EpPf	-----TAT	AT..A.....	--G.....GC	AATATTATAT	GCAATATGC.
VbPf	-----TAT	AT..A.....	--G.....GC	AATATTATAT	GTAATATGC.
Wb99	-----TAT	AT..A.....	--G.....	-----	GCAATATGC.
WbPf	-----TAT	AT..A.....	--G.....	-----	GCAATATGC.
Mp101	-----TAT	AT..A.....	--G.....	-----	-----	-----
Mg140	-----TAT	AT..A.....	--G.....	-----	-----	-----
Me120	-----TAT	AT..A.....	--G.....	-----	-----	-----
Md106	-----TAT	AT..A.....	--G.....	-----	-----	-----
MsJM	-----TAT	AT..A.....	--G.....	-----	-----	-----
Mh175	-----TAT	AT..A.....	--G.....	-----	-----	-----
Mpy177	-----TAT	AT..A.....	--G.....	-----	-----	-----T
LpPf	-----TAT	AT..A..C--	--G.....	-----	-----	-----
LaPf	-----TAT	AT..A..C--	--G.....	-----	-----	-----
LnPf	-----TAT	AT..A..CGT	..G.....	-----	-----	-----
Lp193	-----TAT	AT..A..C--	--G.....	-----	-----	-----
Pl194	-----TAT	AT..A..C--	--G.....	-----	-----	-----
Pm139	---TATA-AT	AT..A..C--	--G.....	-----	-----	-----
Pe100	---TATA-AT	AT..A..C--	--G.....	-----	-----	-----
Pp102	-----TAT	AT..A..C--	--G.....	-----	-----	-----
Pp178	-----TAT	AT..A..C--	--G.....	-----	-----	-----
Pb143	-----TAT	AT..A..C--	--G.....	-----	-----	-----
Pc197	-----TAT	AT..A..C--	--G.....	-----	-----	-----
Ppa192	-----TAT	AT..A..C--	--G.....	-----	-----	-----
Dz181	-----T	AT..A.....	-----	-----	GCAATATGC.
Ds119	-----T	AT..A.....	-----	-----	GCAATATGC.
DcJM	-----T	AT..A.....	-----	-----	GCAATATGC.
Dn199	-----T	AT..A.....	-----	-----	GCAATATGC.
Da182	-----T	AT..A.....	-----	-----	GCAATATGC.
Dca152	-----TAT	AT..A.....	-----	-----	GCAATATGC.
Dal195	ATATATATAT	AT..A.....	-----	-----	GCAATGTGC.

Crinum	AAAATTCAGA	GTTATTGTGG	ATCTATTC--	CAATCGAAGT	TAAAGGAAGA	ATCGAATATT
GalcanPfG.---	-----	-----	-----	.G.C.
Merw219	-----	-----	.G.C.
Merw218	-----	-----	.G.C.
Ledrev	-----	-----	.G.
LedcorPf	-----	-----	.G.	G.
Ledsoc	-----	-----	.G.
Dribar	-----	-----	.G.T.
Drimac	-----	-----	.G.
Dribot	-----	-----	.G.
Erl80G.	-----A.	.G.C.
EpPfG.	-----A.	.G.C.	-----
VbPf	-----	-----	.G.C.
Wb99	A.	-----	-----	.G.C.
WbPf	-----	-----	.G.C.
Mp101	A.	-----	-----	.G.T.
Mg140	A.	-----	-----	.G.T.
Me120	A.	-----	-----	.G.T.
Md106	A.	-----	-----	.G.T.
MsJM	A.	-----	-----	.G.T.
Mh175	A.	-----	-----	.G.T.
Mpy177	A.	-----	-----	.G.T.
LpPf	-----	-----	-----	.G.C.
LaPf	-----	-----	-----	.G.C.
LnPf	-----A.	-----	-----	.G.C.
Lp193	-----	-----	-----	.G.C.
Pl194	-----	-----	-----	.G.C.
Pm139	-----	-----	-----	.G.C.
Pe100	-----	-----	-----	.G.C.
Pp102	-----	-----	-----	.G.C.
Pp178	-----	-----	-----	.G.C.
Pb143	-----	-----	-----	.G.C.T.
Pc197	-----	-----	-----	.G.C.
Ppa192	-----	-----	-----	.G.C.
Dz181TCG.C.T.
Ds119TCG.C.T.
DcJMTCG.C.T.
Dn199TCG.C.T.
Dal82	-----G.C.T.
Dca152TCG.C.T.
Dal195TCG.C.T.

Crinum	CAGTGATCAA	ATCATTTCATT	CCAGAGTTTG	-----A	TAGAC-----	TTTTTTGAAA
GalcanPfA	-----CC--
Merw219A	-----CC--
Merw218A	-----CC--
LedrevC·A	-----CC--T
LedcorPfTC·A	-----CC--T
LedsocC·A	-----CC--T
DribarC·A	-----CC--T
DrimacC·A	-----CC--T
DribotC·A	-----CC--T
Erl80	-----CC--
EpPf	-----	-----A	-----	·A·CC--	-----
VbPfT·A	-----CCTTT
Wb99	-----A·A	-----CC--
WbPfA	-----CC--T
Mp101A	GTTTA----CC--T
Mg140A	GTTTA----CC--T
Me120A	GTTTA----CC--T
Md106A	GTTTA----CC--T
MsJMA	GTTTA----CC--T
Mh175A	GTTTA----CC--T
Mpy177A	GTTTA----CC--T
LpPfA	----ATAG·CCC--
LaPfA	----ATAG·CCC--
LnPfA	-----CCC--
Lp193A	-----CCC--
Pl194A	-----CCCC--
Pml39A	-----CCCC--
Pe100A	-----CCCC--
Pp102A	-----CCC--
Pp178A	-----CCC--
Pb143A	-----CCC--
Pc197A	-----CCC--
Ppa192A	-----CCC--
Dz181	T·.....A	-----	----C--
Ds119	T·.....A	-----CC--
DcJM	T·.....A	-----CC--
Dn199	T·.....A	-----CC--
Da182	T·.....A	-----CC--
Dca152T·	T·.....A	-----	-----
Dal195	T·.....A	-----	-----

Crinum	AAATGATTA-	----ATCGGA	CGAGAAT---	----AAAGAG	AGAGTCCCAT	TCTACATGTC
GalcanPf	..C.....	-----	-----
Merw219	..C.....	-----	-----
Merw218	..C.....	-----	-----
Ledrev	..C.....	-----	-----G.
LedcorPf	..CG.....	-----	-----AAAG.
Ledsoc	..C.....	-----	-----G.
Dribar	..C.....	-----	-----G.
Drimac	..C.....	-----A.	-----G.
Dribot	..C.....G	ATTA.....	-----G.
Erl80	..CG.....	-----	-----G.
EpPf	..CG.....	-----	-----G.
VbPf	..C.....	-----	-----G.
Wb99	..C.....	-----	-----G.
WbPf	..C.....	-----T.	-----G.
Mp101	..C.....	-----	-----G.
Mg140	..C.....	-----	-----G.
Me120	..C.....	-----	-----G.
Md106	..C.....	-----	-----G.
MsJM	..C.....	-----	-----G.
Mh175	..C.....	-----	-----G.
Mpy177	..C.....	-----	-----G.
LpPf	..C.....	-----	-----G.
LaPf	..C.....	-----	-----G.
LnPf	..C.....	-----	-----G.
Lp193	..C.....	-----	-----G.
P1194	..C.....	-----	-----G.
Pml39	..C.....	-----	-----G.
Pe100	..C.....	-----	-----G.
Pp102	..C.....	-----	-----G.
Pp178	..C.....	-----	-----G.
Pb143	..C.....	-----	-----G.
Pc197	..C.....	-----	-----G.
Ppa192	..C.....	-----	-----G.
Dz181	..T.....	-----A.	A.....CGA	GAAT.....G.
Ds119	..T.....	-----A.	A.....CGA	GAAT.....G.
DcJM	..T.....	-----A.	A.....CGA	GAAT.....G.
Dn199	..T.....	-----A.	A.....CGA	GAAT.....G.
Da182	..T.....	-----A.	A.....CGA	GAAT.....G.
Dca152	..T.....	-----A.	A.....CGA	GAAT.....G.
Dal195	..T.....	-----A.	A.....CGA	GAAT.....G.

Crinum	AATA-----	--CCGACAAC	AATTAAATTT	ATACTAAGAG	G
GalcanPf	-----	...G.....	...G.....	.
Merw219	-----	...G.....	...G.....	.
Merw218	-----	...G.....	...G.....	.
Ledrev	-----	...G.....	...G.....	.
LedcorPf	-----	...G.....	...G.....	.
Ledsoc	-----	...G.....	...G.....	.
Dribar	-----	...G.....	...G.....	.
Drimac	-----	...G.....	...G.....	.
Dribot	-----	...G.....	...G.....	.
Er180	-----	...G.....	...G.....	.
EpPfTGTC	AA TA.....	...G.....	...G.....	.
VbPf	-----	...G.....	...G.....	.
Wb99	-----	...G.....	...G.....	.
WbPf	-----	...G.....	...G.....	.
Mp101	-----	...G.....	...G.....	.
Mg140	-----	...G.....	...G.....	.
Me120	-----	...G.....	...G.....	.
Md106	-----	...G.....	...G.....	.
MsJM	-----	...G.....	...G.....	.
Mh175	-----	...G.....	...G.....	.
Mpy177	-----	...G.....	...G.....	.
LpPf	-----	...G.....	...G.....	.
LaPf	-----	...G.....	...G.....	.
LnPf	-----	...G.....	...G.....	.
Lp193	-----	...G.....	...G.....	.
Pl194	-----	...G.....	...G.....	.
Pm139	-----	...G.....	...G.....	.
Pe100	-----	...G.....	...G.....	.
Pp102	-----	...G.....	...G.....	.
Pp178	-----	...G.....	...G.....	.
Pb143	-----	...G.....	...G.....	.
Pc197	-----	...G.....	...G.....	.
Ppa192	-----	...G.....	...G.....	.
Dz181	-----	...G.....	...TG.....	.
Ds119	-----	...G.....	...G.....	.
DcJM	-----	...G.....	...G.....	.
Dn199	-----	...G.....	...G.....	.
Da182	-----	...G.....	...G.....	.
Dca152	-----	...G.....	...G.....	.
Dal195	-----	...G.....	...G.....	.

Appendix 3. The full aligned file data matrix of the trnL-trnF spacer.

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Crinum	AACTATTTAT	C-----	-----	--TATTT--	-----AT	CTT-----
GalcanPf	GC·C····TA	·TTCTTAAC-	-----	-----	-----	·C-----
Merw218	GC·C····TA	·TTCTTAAC-	-----	-----	-----	TC·C-----
Merw219	GC·C····TA	·TTCTTAAC-	-----	-----	-----	TC·C-----
Ledrev	GC·C····TA	·TTCTTTAC-	-----	-----	---ATCC·	·C·C-----
LedcorPf	NC·C····TA	·TTCTTTAC-	-----	-----	-----	·C·C-----
Ledsoc	GC·C····TA	·TTCTTTAC-	-----	-----	-----	·C·C-----
Dribar	GC·C····TA	·TTCTTTAC-	-----	-----	-----	·C·C-----
Drimac	GC·C····TA	·TTCTTTAC-	-----	-----	-----	·C·C-----
Dribot	GC·C····TA	·TTCTTTAC-	-----	-----	-----	·C·C-----
Er180	GC·CG···TA	·TTCTTAACT	ATTTAACAAT	AC·-----	-----	·C·CTTATCC
EpPf	GC·CG···TA	·TTCTTAACT	A-----T	AC·-----	-----	·C·C-----
VbPf	GC·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Wb99	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
WbPf	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Mp101	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Mg140	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Me120	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Md106	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
MsJM	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Mh175	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Mpy177	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
LpPf	G·T····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
LaPf	G·T····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
LnPf	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Lp193	G·TC····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Pl194	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Pm139	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Pe100	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Pp102	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Pp178	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Pb143	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Pc197	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Ppa192	G·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Dz181	GC·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Ds119	GC·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
DcJM	GC·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Dn199	GC·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Da182	GC·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Dca152	GC·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----
Dal195	GC·C····GA	·TTCTTAAC-	-----	-----	-----	·C·C-----

Crinum	--CTTTTTTT	T---CATAAG	CGGTTCAAAG	AAAATTCAAT	ATCTTTCTCA	TTCATTCTAC
GalcanPf	-----	----G....T...T...
Merw218	-----	----G....
Merw219	-----	----G....
Ledrev	CC-----	----G....T	-----A...
LedcorPf	CC-----	----G....NN..T	-----A...
Ledsoc	CC-----	----G....T	-----A...
Dribar	CC.G-----	----AG....	NNNNN...T	-----A...
Drimac	CC-----	----G....T	-----A...
Dribot	CC-----	----G....T	-----A...
Er180	CC-----	----G....T	-----A...
EpPf	-----	.T--G....TT	-----A...
VbPf	-----	.TT-G....T..T	-----A...
Wb99	-----	.TT-G...AT	-----A...
WbPf	-----	----G....	.N.....T	-----	-----	-----
Mp101	-----	----G....	T.....T	-----A...
Mg140	-----	----G....	T.....T	-----A...
Me120	-----	----G....	T.....T	-----A...
Md106	-----	----G....	T.....T	-----A...
MsJM	-----	----G....	T.....T	-----A...
Mh175	-----	.T--G....	T.....T	-----A...
Mpy177	-----	.T--G....	T.....T	-----A...
LpPf	CC-----	----G....T	-----	-----A...
LaPf	CC-----	----G....T	-----	-----A...
LnPf	-C-----	----G....T	-----A...
Lp193	-C-----	.TT-G....T	-----	-----A...
Pl194	-T-----	.TT-G....T	-----	-----A...
Pml39	-T-----	.TTT-G....T	-----	-----A...
Pe100	-T-----	.TT-G....T	-----	-----A...
Pp102	-T-----	----G....T	-----	-----A...
Pp178	-T-----	.T--G....T	-----	-----A...
Pb143	-T-----	.TT-G....T	-----	-----A...
Pc197	-T-----	.T--G....T	-----	-----A...
Ppa192	-T-----	.T--G....T	-----	-----A...
Dz181	-----	----G....T	-----	-----	-----
Ds119	-----	----G....T	-----	-----	-----
DcJM	-----	----G....T	-----	-----	-----
Dn199	-----	----G....T	-----	-----	-----
Da182	-----	----G....T	-----	-----	-----
Dca152	-----	.T--G....T	-----	-----	-----
Dal195	-----	----G....T	-----	-----	-----

Crinum	-----TCT	TTCACAAATG	GACCCGAACA	TAAATCTTTT	GATCTTATAC	CAATT-TGGT
GalcanPf	-----	...G.....	..T...G...	G.....G	..C.....C	·T...-A...
Merw218	-----	...G.....A	..T...G...	G.....GC	·T...-A...
Merw219	-----	...G.....A	..T...G...	G.....GC	·T...-A...
Ledrev	-----	...G.....A	..T...G...	G.....C..GC	·T...TA...
LedcorPf	-----	...G.....A	..T...G...	G.....C..GC	·T...-A...
Ledsoc	-----	...G.....A	..T...G...	G.....C..GC	·T...-A...
Dribar	-----	...G.....A	..T...G...	G.....C..GC	·T...-A...
Drimac	-----	...G...GA	..T...G...	G.....C..GC	·T...-A...
Dribot	-----	...G.....A	..T...G...	G.....C..GC	·T...-A...
Er180	-----	...G.....A	..T...G...GC	·T...-A...
EpPf	-----	...G.....A	..T...G...GC	·T...-A...
VbPf	TCTATAC...	...G.....	-----G-	G.....GC	·T...-A...
Wb99	-----	...G.....A	..T...GG-	G.....GCT	·T...-A...
WbPf	-----	-----	-----	-----	-----	-----
Mp101	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Mg140	-----	...G.....A	A..T...GG-	G.....GC	·T...-A...
Me120	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Md106	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
MsJM	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Mh175	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Mpy177	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
LpPf	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
LaPf	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
LnPf	-----	...G.....A	..T...GG-	G.....G	-----C	·T...-A...
Lp193	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Pl194	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Pm139	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Pe100	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Pp102	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Pp178	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Pb143	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Pc197	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Ppa192	-----	...G.....A	..T...GG-	G.....GC	·T...-A...
Dz181	-----	-----	-----	-----	-----	-----
Ds119	-----	-----	-----	-----	-----	-----A...
DcJM	-----	-----	-----	-----	-----	-----A...
Dn199	-----	-----	-----	-----	-----	-----A...
Da182	-----	-----	-----	-----	-----	-----A...
Dca152	-----	-----	-----	-----	-----	-----A...
Dal195	-----	-----	-----	-----	-----	-----A...

Crinum	TTGAATAGAT	ATGATACCCG	TACAAATGAA	CA-----T	AT-ATGGTCA	AGGAATTCCC
GalcanPf-T.A..T..
Merw218C.....T.
Merw219C.....T.
LedrevC.	.C.....T.
LedcorPfC.....T.
LedsocC.....T.
DribarC.....T.
DrimacT.
DribotC.....T.
Er180T.
EpPfT.
VbPfT.	-----G	G.....
Wb99T.
WbPf	-----	-----
Mp101T.TA-AACA.
Mg140T.
Me120T.
Md106T.
MsJMT.
Mh175T.K.
Mpy177T.
LpPfT.C.
LaPfT.C.
LnPfT.C.
Lp193T.C.
Pl194T.C.
Pml39T.C.
Pe100T.C.
Pp102T.C.
Pp178T.C.
Pb143T.C.
Pc197T.C.
Ppa192T.C.
Dz181T.-	-----	-----	-----	-----	-----
Ds119T.-	-----	-----	-----	-----	-----
DcJMT.TATAACA.A.
Dn199T.TATAACA.A.
Dal82T.TATAACA.A.
Dca152T.TATAACA.	..T..A.
Dal195T.TATAACA.A.

Crinum	ATTATTGAAT	CATTCACA--	--GTCCATAT	CATTA---TT	CTTA-CATTC	ACAAAG-AAA
GalcanPf	T.....	---C.....C	·A···AA···
Merw218	T.....	---C.....CA-···
Merw219	T.....	---C.....CA-···
Ledrev	T.....	---C.....C-···
LedcorPf	T.....	---C.....CA·G·
Ledsoc	T.....	---C.....CA-···
Dribar	T.....CA	CA·C.....CA-···
Drimac	T.....	-----	-----	-----A-···
Dribot	T.....	---C.....C	···A···A-···
Erl80	-----	-----	---C.....C	-----A-···
EpPf	T.....	---C.....C	-----AA···
VbPf	T.....	---C···CCA-···
Wb99	T.....	---C.....CA-···
WbPf	T.....	---C.....CA-···
Mp101	T.....	---C.....CA-···
Mg140	T.....	---C.....CA-···
Me120	T.....	---C.....CA-···
Md106	T.....	---C.....CA-···
MsJM	T.....	---C.....CA-···
Mh175	T.....	---C.....CA-···
Mpy177	T.....	---C.....CA-···
LpPf	T.....	---C.....CA-···
LaPf	T.....	---C.....CA-···
LnPf	T.....	---C.....CA-···
Lp193	T.....	---C.....CA-···
Pl194	T.....	---C.....CA-···
Pm139	T.....	---C.....CA-···
Pe100	T.....	---C.....CA-···
Pp102	T.....	---C.....CA-···
Pp178	T.....	---C.....CA-···
Pb143	T.....	---C.....CA-···G
Pc197	T.....	---C.....CA-···
Ppa192	T.....	---C.....CA-···
Dz181	-----	T.....	---C.....	····TTA·C-···
Ds119	-----	T.....	---C.....	····TTA·C-···
DcJM	T.....	---C.....	····TTA·C-···
Dn199	T.....	---C.....	····TTA·C-···
Da182	T.....	---C.....	····TTA·C-···
Dca152	T.....	---C.....	-----C-···
Dal195	T···A···	---C.....	····TTA·C-···

Crinum	GTCTTC-TTT	TTGAAA----	ATCTAAGAAA	TTCGGGGAC-	----TAGG--	--TCAAAATT
GalcanPfA..G----	..T.....	..A.....	-----A--	--C.C.....
Merw218G----	-----	-----
Merw219G----	-----	-----
Ledrev	..T..TT..	..A..G----T	ACAC.....	-----
LedcorPf	..T.....	..A..GATCT	-----	-----
Ledsoc	..T.....	..A..G----	-----	-----
Dribar	..T.....	..A..G----	-----	-----
Drimac	..T.....	..A..G----	-----	-----
Dribot	..T.....	..A..G----	-----	-----
Erl80G----	-----	-----
EpPfG----	-----	-----
VbPfG----G-	-----G-	-----
Wb99G----	-----	-----
WbPfG----	-----	-----
Mp101G----A.....	-----	-----
Mg140G----A.....	-----	-----
Me120G----A.....	-----	-----
Md106G----A.....	-----	-----
MsJMG----T..	..A.....	-----	-----
Mh175G----A.....	-----	-----
Mpy177G----A.....	-----A-	-----
LpPfG----	-----	-----
LaPfG----	-----	-----
LnPfG----	-----	-----
Lp193G----	-----	-----
Pl194G----	-----	-----
Pm139G----	-----	-----
Pe100G----	-----	-----
Pp102G----	-----	-----
Pp178G----	-----	-----
Pb143G----	-----TA	GG.....
Pc197-C..G----	-----	-----
Ppa192-C..G----T..	-----	-----
Dz181	T.....G----A..	-----	-----
Ds119	T.....G----A..	-----	-----
DcJM	T.....G----	-----	-----
Dn199	T.....G----	-----	-----
Da182	T.....G----	-----	-----
Dca152	T.....G----	-----	-----
Dal195	T.....G----	-----	-----

Crinum	TTGAATACTT	TTTTTTTAGTT	TAGTCTATTT	AATTTAC---	-----	-----AT
GalcanPf	..T....G..	...C.-----	-----	-----ATA	CATATTAC..
Merw218	..T....G..	-----	-----ATA	CATATTAC..
Merw219	..T....G..	-----	-----ATA	CATATTAC..
Ledrev	..T....G..A	-----	-----ATA	CATATTACG.
LedcorPf	..T....G..	-----	-----ATA	CATATTACG.
LedsocG..	-----	-----ATA	CATATTACG.
Dribar	..TT...G..	-----	-----ATA	CATATTACG.
Drimac	..T....G..	-----	-----ATA	CATATTACG.
Dribot	..T....G..	-----	-----ATA	CATATTACG.
Er180	..T....G..	-----	-----ATA	CATATTAC..
EpPf	..T....G..	-----	-----ATA	CATATTAC..
VbPf	..T....G..	-----	-----ATA	CATATTAC..
Wb99	..T....G..	-G.....	-----	-----ATA	CATATTAC..
WbPf	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Mp101	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Mg140	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Me120	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Md106	..T....G..	-G.....	-----	-----ATA	CATATTAC..
MsJM	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Mh175	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Mpy177	..T....G..	-G.....	-----	-----ATA	CATATTAC..
LpPf	..T....G..	-G.....	-----	-----ATA	CATATTAC..
LaPf	..T....G--	-----	-----	-----	-----	-----
LnPf	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Lp193	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Pl194	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Pm139	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Pe100	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Pp102	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Pp178	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Pb143	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Pc197	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Ppa192	..T....G..	-G.....	-----	-----ATA	CATATTAC..
Dz181G..	-----	-----ATA	CATATTAC..
Ds119G..	-----	-----ATA	CATATTAC..
DcJMG..	-----	-----ATA	CATATTAC..
Dn199G..	·A·AG·TT·	-----	-----ATA	CATATTAC..
Da182G..	-----	-----ATA	CATATTAC..
Dca152G..ATA	TTACAATTTA	CATATTAC..	CATATTAC..
Dal195G..	-----	-----ATA	CATATTAC..

Crinum	AGATACAAGT	ATTC---TAC	TAGGATGATG	CGCGGGAAAT	C
GalcanPf	·C·-----	G
Merw218	·C·-----	·A·.....	G
Merw219	·C·-----	·A·.....	G
Ledrev	·C·-----	·A·.....	G
LedcorPf	·C·-----	·A·.....	G
Ledsoc	·C·-----	·A·.....	G
Dribar	·C·-----	TA·.....	G
Drimac	·C·-----	TA·.....	G
Dribot	·C·-----	TA·.....	G
Er180	·C·A-----	·A·.....	G
EpPf	·C·A-----	-----	-----	-
VbPf	·C·-----	·A·.....	G
Wb99T·T·	·A·-----	·A·.....	G
WbPfT·	·C·-----	·A·.....	G
Mp101T·A·	·C·-----	·A·.....	G
Mg140T·	·C·-----	·A·.....	G
Me120T·	·C·-----	·A·.....	G
Md106T·	·C·-----	·A·.....	G
MsJMT·	·C·-----	·A·.....	G
Mh175T·	·C·-----	·A·.....	G
Mpy177T·	·C·-----	·A·.....	G
LpPfT---	CA·-----T	·A·.....	G
LaPf	-----	-----	-----	-----	-
LnPfT---	CA·-----	·A·.....	G
Lp193T---	CA·-----	·A·.....	G
Pl194T---	CA·-----	·A·.....	G
Pml39T---	CA·-----	·A·.....	G
Pe100T---	CA·-----	·A·.....	G
Pp102T---	CA·-----	·A·.....	G
Pp178T---	CA·-----	·A·.....	G
Pb143T---	CA·-----	·A·.....	G
Pc197T---	CA·-----	·A·.....	G
Ppa192T---	CA·-----	·A·.....	G
Dz181	·C·TTTT·	···T·	G
Ds119	·C·T-----	···T·	G
DcJM	·C·T-----	···T·	G
Dn199	·C·T-----	···T·	G
Da182	·C·T-----	···T·	G
Dca152	·C·T-----	···T·	G
Dal195	·C·T-----	···T·	G

CHAPTER 5

DISCUSSION AND CONCLUSION

The family Hyacinthaceae is characterized by geophytes of which the underground part is a bulb, the inflorescence a simple raceme, the perianth segments free or united at the base and the fruit a capsule. It includes, amongst others, the following South African genera: *Amphisiphon*, *Androsiphon*, *Daubenya*, *Massonia*, *Neobakeria*, *Polyxena* and *Whiteheadia*.

The taxonomic history of the minor genera of the Hyacinthaceae largely reflects the significance that has been placed on morphological differences among the Hyacinthaceae in the past. Particular value has been placed on floral differences, resulting in the description of several monotypic genera for newly discovered species that were more or less distinctive in their flowers. The first of these monotypic genera to be established was *Daubenya*, which was described by Lindley in 1835 to accommodate *Daubenya aurea* with its highly zygomorphic flowers. This degree of zygomorphy is rarely encountered in the family Hyacinthaceae. In his treatment of the sympetalous genera of the Hyacinthaceae, Baker (1871) allied *Daubenya* with the genus *Massonia* in his tribe Massonieae on the basis of the reduced peduncle. However, Bentham (Bentham & Hooker 1883) later included both genera in his tribe Allieae based on their congested inflorescences, in which the flowers are subtended by large bracts. They reminded him of the umbel-like inflorescences found in the Alliaceae. This is an extremely superficial resemblance, but resulted in Baker (1897) placing several other related species with less well-developed bracts in the subgenus *Astemma* of the genus *Polyxena*. The creation of subgenus *Astemma* of the genus *Polyxena* was done after Endlicher (1836) had already established a subgenus *Astemma*, but in the genus *Massonia*. Baker's subgenus *Astemma* was completely unrelated to the subgenus *Astemma* of Endlicher, however *Polyxena* subgenus *Eupolyxena* Baker (1897) is a synonym of *Massonia* subgenus *Astemma* Endlicher (1836). In 1924 Schlechter segregated *Polyxena* subgenus *Astemma* as a distinct genus (on the basis of their uniseriate stamens), which he named *Neobakeria*. In describing *Neobakeria namaquensis* Schlechter dissected only the upper actinomorphic flowers, overlooking the more diagnostic zygomorphy of the lower flowers. This character was also overlooked by Jessop (1976) who confused this species with *Massonia marginata*. It was only in 1997 that this character was emphasized when Müller-Doblies and Müller-Doblies used it to restrict the circumscription of *Neobakeria* as a monotypic genus to include *Neobakeria namaquensis* as the only species. Although they recognized the zygomorphy of the flowers of this species, they failed to recognize that the same floral zygomorphy is pronounced in *Daubenya aurea* and also occurs, although to a lesser extent in *Neobakeria comata*. At the same time as he named *Neobakeria*, Schlechter (1924) also established the genus *Androsiphon* for a species with an unique morphology of the androecium

which had been discovered a few years earlier by his brother. In 1936 the trend towards the establishment of monotypic genera for species with unusual flowers was continued by Barker with the description of *Amphisiphon stylosa*. Phillips (1951) considered *Amphisiphon* and *Androsiphon* to be the same genus, but this suggestion was ignored by subsequent workers like Dyer (1976) and Jessop (1976), and later also by Müller-Doblies and Müller-Doblies (1997). With further study it has become evident that the characters on which these various genera were based, represent nothing more than extreme adaptations to a variety of pollination and seed dispersal strategies (Goldblatt & Manning 2000).

Great significance was also attached to differences in leaf morphology, resulting in several new species of *Massonia*, which are now placed mostly in synonymy under *Massonia depressa* or *Massonia echinata*. Within the Hyacinthaceae, the taxonomic position of the genus *Neobakeria* has always been problematic as it has been recognized by some authors and completely ignored by others. Krause (1930) and Hutchinson (1959) both treated *Neobakeria* as a synonym of *Polyxena*, but Jessop (1976) united the genus with *Massonia*.

With the advancement in science and technology more tools become available for unraveling taxonomic relationships. One of the latest tools, the DNA analysis, was used in this study and provided a useful phylogenetic analysis of the minor genera of the Hyacinthaceae. The main phylogenetic analysis revealed three distinct lineages i.e. *Massonia*, *Polyxena* and *Daubenya* with *Whiteheadia bifolia* remaining on a branch of its own outside of the *Massonia* clade.

The species within the *Massonia* clade are *Massonia depressa*, *Massonia echinata*, *Massonia grandiflora*, *Massonia jasminiflora*, *Massonia hirsuta*, *Massonia sessiliflora* and *Neobakeria heterandra*. Within this clade there is very little resolution which could point to the very close relationship between the species. It is possible that the analysis of a different gene could provide more resolution within this genus. However, there are very few differences between the sequences of the different species in this clade which clearly indicates that the species are very closely related. Therefore lumping of the species in the *Massonia* clade should be considered. The DNA data indicates that *Neobakeria heterandra* should be transferred to the genus *Massonia*. Morphological evidence also supports this as both the flowers, with the characteristic sigmoid curve in the perianth and the paired, ovate to suborbicular leaves of *Neobakeria heterandra* are very similar to that of the other *Massonia* species. The leaf anatomy of *Neobakeria heterandra* is also the same as that of the other *Massonia* species. Müller-Doblies and Müller-Doblies (1997) stated that the correct name for *Neobakeria heterandra* should be *Massonia pygmaea* Schlechtendal ex Kunth. Apparently when Jessop (1976) examined the isotype of *Massonia pygmaea* he did not notice the differences in the length of the filaments and included it in the synonymy of *Massonia echinata*. Although Müller-Doblies and Müller-Doblies (1997) based their research purely on the study of herbarium

specimens, with no contribution of DNA data, they were correct in the assignment of the name *Massonia pygmaea*. *Massonia grandiflora* differs from *Massonia depressa* only in the size of the flowers and leaves, which are slightly larger in *M. grandiflora*. *Massonia grandiflora* has, however, often been considered deservant of its species rank by previous authors. DNA data shows the genetic sequence of *M. grandiflora* to be identical to that of *M. depressa*, thus indicating that it should be reduced to the synonymy of *M. depressa*. In the past too much value has been placed on the increased size of the plants of *M. grandiflora*, but this is probably due to the habitat in which the plants grow. Jessop (1976) considered *Massonia hirsuta* to be a synonym of *Massonia echinata*, but Müller-Doblies and Müller-Doblies (1997) resuscitated it to species level, with which I agree. *M. hirsuta* shows sufficient morphological variation, especially with regard to the leaf morphology and the hairy bracts (which are not found in any other species) to deserve its species status. The DNA data also supports the retention of species status. *Massonia sessiliflora* is a species transferred from *Haemanthus* by Müller-Doblies and Müller-Doblies (1997) from a specimen originally described as *Haemanthus sessiliflorus* Dinter. The DNA analysis shows that the genetic sequence of this species is almost identical to that of *M. hirsuta*. Unfortunately I have not had the opportunity to study a live specimen, but from their description and the floral diagram, I could not see any remarkable differences separating this species from *M. hirsuta*. As the species within the genus *Massonia* are all so closely related to one another with so little resolution within the clade, I am reluctant to recognize yet another species and believe that *M. sessiliflora* should rather be placed in synonymy under *M. hirsuta*. Morphological characters supporting the *Massonia* clade and found in all the species include ovoid bulbs; paired prostrate, spreading leaves; inflorescence which is borne between the leaves, nestled on the leaf surface and the three-winged, loculicidal capsule. All the taxa in this clade also share the same leaf anatomy, with leaves being amphistomatic with thick waxy cuticles. The outer walls of the epidermal cells are thickened and the mesophyll comprises three rows of palisade-like parenchyma adaxially, with spongy parenchyma abaxially. No prominent bundle sheaths are present around the vascular bundles.

The *Polyxena* clade includes the species: *Polyxena brevifolia*, *Polyxena corymbosa*, *Polyxena longituba*, *Polyxena maughanii*, *Polyxena paucifolia*, *Polyxena pygmaea* and *Lachenalia pusilla*. The latter was included in the DNA study because of the differences in morphology exhibited between it and other *Lachenalia* species, as well as the similarities it showed to species in the genus *Polyxena*. The DNA results showed a close relationship between the genus *Lachenalia* and *Polyxena*, as found also found by Pfosser and Speta (1999). *Polyxena* and *Lachenalia* together form a single monophyletic group. Due to the vast number of *Lachenalia* species, a further analysis including sequences for a larger number of *Lachenalia* species is required before a final conclusion can be drawn about the relationship between these two genera. There are also a high percentage of

similarities in the DNA sequences of all the *Polyxena* species, which indicates that lumping of some of the species should be considered. However, this can only be done accurately once more *Lachenalia* species have been added to the analysis. *Polyxena brevifolia* (Ker-Gawl.) A.M. van der Merwe is the correct name of the '*Polyxena corymbosa*' specimens from Gordon's Bay. Jessop (1976) considered *Scilla brevifolia* Ker-Gawl. to be a synonym of *Polyxena corymbosa*, but according to the original description *Polyxena corymbosa* has a corymbose inflorescence whereas *Polyxena brevifolia* has a racemose one. Sequence data supports the morphological differences between the two species and justifies the species status of *Polyxena brevifolia*. According to the phylogenetic tree (Figure 3) there appears to be a very close relationship between *Polyxena maughanii* and *Polyxena ensifolia*. Morphologically the two species differ only in the length of their stamens, which in *Polyxena maughanii* are included in the perianth tube with the three longest ones just reaching to the mouth of the tube, while in *Polyxena ensifolia* the three longest stamens are exerted beyond the tube. Both species share the same general distribution area, but *Polyxena maughanii* is restricted to limestone outcrops within this area. It appears that these two taxa should be lumped into a single species with separate varieties *Polyxena ensifolia* var. *ensifolia* and *Polyxena ensifolia* var. *maughanii*, providing for the minor difference in stamen length and the preference of *Polyxena maughanii* for limestone substrates. *Polyxena longituba*, although also very closely related to *Polyxena ensifolia*, reveals sufficient morphological variation both in flower shape and size and leaf shape to retain its specific rank. *Polyxena pygmaea* shows sufficient variation, both in the DNA data set and morphological characters to retain its species status. *Polyxena paucifolia* and *Polyxena corymbosa* are very closely related, but they differ in flower morphology as well as in the number of leaves per species, with *Polyxena paucifolia* only having two leaves per plant, whereas *Polyxena corymbosa* has four to six. The pink flowers of *Polyxena corymbosa* are characterised by a short perianth tube, which is only about one third of the length of the perianth segments, while in *Polyxena paucifolia* the flowers are dark lilac to purple with a perianth tube that is equal in length to the perianth segments. Leaf anatomical studies show two different anatomical leaf types within the genus *Polyxena*, which correspond with the two different leaf forms present in the genus. *Polyxena ensifolia* and *Polyxena pygmaea* with their paired ovate-lanceolate leaves share leaf type one (Figure 3.2.1) with *Daubinya alba*, *Daubinya aurea*, *Amphisiphon stylosa*, *Androsiphon capense*, *Neobakeria comata*, *Neobakeria angustifolia* and *Neobakeria namaquensis*. *Polyxena brevifolia*, *Polyxena corymbosa*, *Polyxena longituba* and *Polyxena paucifolia* with their linear, sometimes canaliculate leaves, all share leaf type two (Figure 3.2.2). Morphological characters supporting the clade and found in all the species include the small, globose to ovoid bulbs with the inner membranous sheath that encloses the base of the leaves and scape; small, inconspicuous or obsolete bracts subtending the pedicels and the actinomorphic flowers with biseriate stamens.

The *Daubenia* clade includes all the monotypic genera (except for *Whiteheadia bifolia*), as well as *Neobakeria comata*, *Neobakeria namaquensis* and *Neobakeria angustifolia*. Two collections of *Neobakeria angustifolia* were made, one from Sutherland and one from Saldanha. These two specimens differ remarkably with regard to both inflorescence type and flower morphology. In the specimen from Saldanha the inflorescence is corymbose and capitate with the bracts acropetally increasing in size and the upper bracts having no buds in their axils, forming an inconspicuous green coma. The inflorescence of the Sutherland specimen is subspicate and capitate or conical with the bracts also acropetally increasing in size and with the uppermost bracts forming a conspicuous green to orange coma. The flowers of the *Neobakeria angustifolia* specimen from Sutherland are yellow and firm textured, with yellow or orange stamens, while those of the specimen from Saldanha are white with a papery texture and purple stamens. In the Saldanha specimens the perianth tube is also much narrower than that of the Sutherland specimen. DNA analysis also reveals two different genetic sequences for the trnL-trnF regions of the two different specimens, confirming the morphological differences and justifying splitting the species into two. It has since been determined that the respective names of the species should be *Massonia marginata* Willd. ex Kunth (Manning & Van der Merwe in press*) for the Sutherland specimen and *Massonia zeyheri* Kunth (Muller-Doblies & Muller-Doblies 1997) for the Saldanha specimen. It is especially in this clade where it is most evident that too much emphasis has been placed on floral differences in the past. The monotypic genera included in the *Daubenia* clade were all established for new species that were thought to be very distinct in their floral morphology and unrelated to any of the existing genera. However, all of these taxa share the same leaf morphology and leaf anatomy and now DNA studies confirm their close relationship.

DNA data shows that *Amphisiphon* shares a close relationship with *Massonia zeyheri* and *Massonia marginata*, but there are sufficient morphological differences to retain separate species status. DNA data also shows that *Daubenia aurea* is closely related to *Amphisiphon stylosa*, *Massonia marginata* and *Massonia zeyheri*. Although *Androsiphon capense* and *Daubenia alba* appear together on a branch with a very high bootstrap support, they differ morphologically in that the flowers of *Daubenia alba* are white to pale lilac, whereas those of *Androsiphon capense* are bright yellow to orange. Another significant difference is the disc present on the top of the staminal tube in *Androsiphon capense*, that is lacking in *Daubenia alba*. DNA data clearly shows that the species in the *Daubenia* clade (*Daubenia alba*, *Daubenia aurea*, *Amphisiphon stylosa*, *Androsiphon capense*, *Massonia marginata*, *Massonia zeyheri*, *Neobakeria comata* and *Neobakeria namaquensis*) should be placed together in a single genus. As *Daubenia* is the oldest genus within the group, the other species will all be transferred to *Daubenia* and will be known as *Daubenia alba*, *Daubenia aurea*, *Daubenia stylosa*, *Daubenia capensis*, *Daubenia marginata*, *Daubenia*

zeyheri, *Daubenya comata* and *Daubenya namaquensis*. The morphological characters shared by all the species and thus support the clade include the bulbs of which the outermost tunics extend as a neck in narrow, flat, papery segments and the glossy, green, prostrate to spreading leaves with prominent longitudinal striations on the upper surface, the bases of which clasp the peduncle for some distance below the ground.

The differences in the floral morphology of the species of *Daubenya* can most likely be attributed to the extreme adaptations that these species show to a variety of pollination strategies (Goldblatt & Manning 2000). The area in which these plants occur is also one of the floristically richest areas known. Plants have had to adapt and evolve in order to be successful. It seems plausible that species that are very closely related have evolved different floral forms in order to attract pollinators with minimum competition. A very clever adaptation is that of producing two different floral forms on a single inflorescence. In *Daubenya aurea* the outer flowers are extremely zygomorphic with large showy tepals, while the inner flowers are smaller and actinomorphic with reduced tepals. Proctor *et al.* (1996) believe that the particular advantage of the composite head where many small flowers open over a period of a week or two, is that it allows a very wide range of different pollinations to take place. The two different floral forms in *D. aurea* are probably designed to attract different pollinators, or at least to be able to make use of different pollinators to ensure successful pollination. According to Proctor *et al.* (1996), the flowers that have achieved the closest adaptation in form to their pollinators are those that have become, like their pollinators, bilaterally symmetrical. From personal observations the pollinators of *Daubenya aurea* appear to be monkey beetles, but bees have also been observed on the flowers. In other species within this group two types of flowers are also found on the same inflorescence, although the zygomorphy is never as prominent as in *Daubenya aurea*. Where the two flower forms differ in the length of the perianth tubes, it is most probably an opportunistic adaptation to be able to make use of different pollinators. In *Daubenya comata*, where the lower flowers are slightly zygomorphic and the upper flowers actinomorphic, the species is known to be visited by bees during the day and small moths at night. This pattern is repeated in *Daubenya namaquensis* where the lower flowers are also zygomorphic and the upper ones actinomorphic, and visitors to the flowers are also bees during the day and moths at night. The flowers of *Daubenya marginata* are unscented and appear to be bird pollinated, as Malachite sunbirds come to feed on the nectar that accumulates in the wide-mouthed staminal collar (Manning & Van der Merwe in press**). The flowers of *Daubenya capensis* have a firm texture and a yeasty smell reminiscent of flowers of *Massonia depressa*, which is rodent pollinated (Johnson *et al.* 2001). The flowers of *Daubenya stylosa* are also visited by diurnal and nocturnal pollinators, bees and butterflies during the day and moths during the night. It is evident that there

are a huge variety of pollination strategies that have developed in this group, ensuring the success of the various species but adding to the confusion in the classification of the taxa.

Whiteheadia bifolia is the only species that retains its monotypic status, and the DNA analysis supports the unique morphology of the species as it appears on a branch of its own on the outside of the *Massonia* clade. Müller-Doblies and Müller-Doblies (1997) described a new *Whiteheadia* species from Namibia (*Whiteheadia etesionamibensis*), thus altering the monotypic status of the genus. According to their description this species differs from *Whiteheadia bifolia* with respect to the perianth tube which is shorter (2–3mm) than that of *Whiteheadia bifolia* (4–8mm) and also the perianth segments which are much longer (9.5–14mm) than those of *Whiteheadia bifolia* (5–7mm). Unfortunately, although they state that an isotype of this species is housed at the Compton herbarium (NBG), the herbarium has not as yet received the specimen and I am unable to verify the validity of this species. Genetic analysis reveals that the sequence *W. etesionamibensis* differs from that of *W. bifolia* with regard to an autapomorphic deletion in the trnL-trnF spacer region in *W. etesionamibensis*.

CONCLUSION

Of all the work by previous authors the classification of Phillips (1951) agrees best with the DNA analyses regarding the taxonomic position of the species of the 'Massonia group'. Phillips (1951) united *Amphisiphon* and *Androsiphon*, a decision confirmed by the phylogenetic tree. He was also one of the only authors to recognize *Neobakeria* as a different taxon to *Massonia*, whereas many taxonomists have followed Jessop (1976) and later Müller-Doblies and Müller-Doblies (1997) and continued to include it in *Massonia*. Although the present study does not justify a generic status for *Neobakeria*, the DNA of three of the species differs sufficiently from *Massonia* to justify their separation. The DNA analysis shows that only *Neobakeria heterandra* belongs to *Massonia* and this species will now correctly be referred to as *Massonia pygmaea*. Krause (1930) and Hutchinson (1959) both treated *Neobakeria* as a synonym of *Polyxena*, but this study proves that there are no *Neobakeria* species belonging to *Polyxena*. Although this study rejects Jessop's (1976) assumption that *Neobakeria* should be united with *Massonia*, it supports his inclusion of the Cape species of *Hyacinthus* (*Hyacinthus corymbosus*) in the genus *Polyxena*. The DNA data has proven beyond a doubt that this species belongs in *Polyxena*. As previously mentioned, the taxonomic position of the genus *Neobakeria* has always been problematic, but with the additional information provided by the DNA analysis, a better re-positioning of the *Neobakeria* species within the group is possible. Of the four *Neobakeria* species (*N. angustifolia*, *N. comata*, *N. heterandra* and *N. namaquensis*) all, except *N. heterandra*, are transferred to the genus *Daubenya*. *Neobakeria heterandra* moves into *Massonia* and the older name of *Massonia pygmaea* is re-instated (Müller-Doblies & Müller-Doblies 1997). As a result of the differences in morphology as well as in the DNA of the *N.*

angustifolia specimens from the two different localities, the species is split into two. Specimens from Sutherland correspond to *N. angustifolia* (L.f.) Schltr., but recent studies of the type specimens have revealed that *N. angustifolia* is a later homonym and the correct name should have been *Massonia marginata* Willd. ex Kunth (Manning & Van der Merwe in press*). The true identity of *M. marginata* has been misunderstood ever since Baker confused the species with *Massonia angustifolia* as early as 1871. This mistake was perpetuated by subsequent authors until Manning and Van der Merwe (2001, in press*) showed that *M. angustifolia* is actually conspecific with *M. echinata* L. The species known by Baker and later authors as *M. angustifolia* was in fact first described as *M. marginata* by Kunth (1843). The collector and place of collection of the type specimen are not known and the species was later redescribed by Baker (1888) as *Polyxena haemanthoides* Baker, based on a plant collected by Bolus on the Nuweveld mountains near Fraserburg in 1886. Baker had not seen type material of *M. marginata* and therefore described it as a new species. As the species has now been transferred to *Daubenya*, the correct name assigned to it is *Daubenya marginata* (Willd. ex Kunth) J.C. Manning & A.M. van der Merwe. The specimen from Saldanha corresponds to the type specimen of *Massonia zeyheri* (Muller-Doblies & Muller-Doblies 1997) and the correct name is *Daubenya zeyheri* (Kunth) J.C. Manning & A.M. van der Merwe. Table 5.1. lists the species finally recognized in the present study, together with their synonyms.

In the past most taxonomic classifications have been based solely on morphological differences or similarities, and although some of these classifications are still viewed as valid, many others have been proven incorrect as new data has become available. Morphological characters are the easiest to use when classifying taxa, as they are the most obvious to the eye. However, it is sometimes difficult to exercise objectivity when viewing them, as very often there are superficial resemblances between plants that support the pre-conceived ideas we have as to the relationships between them. It is vital that we make use of as much information as possible about the taxa we are attempting to classify in order to attain objectivity. With the help of DNA analysis this has become possible, as it gives a more objective view of the phylogeny of taxa. In many cases the DNA results support the morphologically based classifications previously used, but in others they dispute it forcing us to re-evaluate the value that was placed on the morphological characters used in earlier classifications. The most reliable and realistic phylogeny can only be produced through the combination of all known data on the taxa, including morphological, anatomical, palynological and molecular information. In this thesis phylogenetic characters were used to bring clarity to the morphological characters and the morphological characters were used to test the phylogenetic tree. It is hoped that the information provided in this thesis is one more step towards the unraveling of the relationships between taxa in the family Hyacinthaceae.

Table 5.1. List of species currently recognized together with their synonyms

Species	Synonyms
Genus <i>Daubenya</i>	
<i>D. alba</i> A.M. vd Merwe	-
<i>D. aurea</i> Lindl.	<i>Daubenya fulva</i> Lindl. <i>Daubenya coccinea</i> Harv. ex Baker <i>Daubenya aurea</i> var. <i>coccinea</i> (Harv.) Marloth
<i>D. capensis</i> (Schltr.) A.M. vd Merwe & J.C. Manning	<i>Androsiphon capense</i> Schltr.
<i>D. comata</i> (Burch. ex Bak.) J.C. Manning & A.M. vd Merwe	<i>Massonia comata</i> Burch. ex Baker <i>Polyxena comata</i> (Burch. ex Baker) Baker <i>Neobakeria comata</i> (Burch. ex Baker) Schltr.
<i>D. marginata</i> (Willd. ex Kunth) J.C. Manning & A.M. vd Merwe	<i>Massonia marginata</i> Willd. ex Kunth <i>Polyxena marginata</i> (Willd. ex Kunth) Baker <i>Massonia rugulosa</i> Lichtenst. ex Kunth <i>Polyxena rugulosa</i> (Lichtenst. ex Kunth) Baker <i>Polyxena haemanthoides</i> Baker <i>Neobakeria haemanthoides</i> (Baker) Schltr. <i>Massonia angustifolia</i> auct. non <i>M. angustifolia</i> (= <i>M. echinata</i> L.)
<i>D. namaquensis</i> (Schltr.) A.M. vd Merwe	<i>Neobakeria namaquensis</i> Schltr.
<i>D. stylosa</i> (Barker) A.M. vd Merwe & J.C. Manning	<i>Amphisiphon stylosum</i> ['stylosa'] Barker
<i>D. zeyheri</i> (Kunth) J.C. Manning & A.M. vd Merwe	<i>Massonia zeyheri</i> Kunth <i>Polyxena zeyheri</i> (Kunth) Dur. & Schinz <i>Massonia pedunculata</i> Baker <i>Massonia burchellii</i> Baker <i>Neobakeria burchellii</i> (Baker) Schltr. <i>Massonia angustifolia</i> auct. non <i>M. angustifolia</i> (= <i>M. echinata</i> L.)
Genus <i>Massonia</i>	
<i>M. depressa</i> Houtt.	<i>Massonia latifolia</i> L.f. <i>Massonia sanguinea</i> Jacq. <i>Massonia obovata</i> Jacq. <i>Massonia grandiflora</i> Lindl. <i>Massonia brachypus</i> Baker

- Massonia triflora* Compton
- Massonia echinata* L.f.
- Massonia scabra* Thunb.
- Massonia muricata* Ker-Gawl.
- M. longifolia* Jacq. var *candida* Burch. ex Ker-Gawl
- Massonia huttonii* Baker
- Massonia setulosa* Baker
- Massonia tenella* Soland. ex Baker
- Massonia versicolor* Baker
- Massonia calvata* Baker
- Massonia latebrosa* Masson ex Baker
- Massonia amygdalina* Baker
- Massonia parvifolia* Baker
- Massonia dregei* Baker
- Massonia cocinna* Baker
- Massonia candida* Burch. ex Baker
- Massonia modesta* Fourc.
- Neobakeria visserae* Barnes
- Massonia angustifolia* L.f.
- Polyxena angustifolia* (L.f.) Baker
- Neobakeria angustifolia* (L.f.) Schltr.
- M. hirsuta* Link & Otto
- Massonia orientalis* Baker
- Massonia bolusia* Barker
- Massonia inexpectata* Poelln.
- Massonia sessiliflora* (Dinter) U. & D. M-D.
- M. jasminiflora* Burch. ex Baker
- Massonia bowkeri* Baker
- Massonia greenii* Baker
- M. pustulata* Jacq.
- Massonia schlechtendalii* Baker
- Massonia longipes* Baker
- M. pygmaea* Schlechtendal ex Kunth
- Polyxena bakeri* Dur. & Schinz
- Neobakeria heterandra* Isaac
- Massonia heterandra* (Isaac) Jessop
- Genus *Polyxena***
- P. brevifolia* (Ker-Gawl.) A.M. vd Merwe
- Scilla brevifolia* Ker-Gawl.
- Dipcadi brevifolium* (Thunb.) Fourc.
- Scilla brachyphylla* Roem. et Schultes
- Periboea gawleri* Kunth

- P. corymbosa* (L.) Jessop
- P. ensifolia* (Thunb) Schönl. var. *ensifolia*
- P. ensifolia* var. *maughanii* (Barker) A.M. vd Merwe
- P. longituba* A.M. vd Merwe
- P. paucifolia* (Barker) A.M. vd Merwe & J.C. Manning
- P. pygmaea* (Jacq.) Kunth
- Genus *Whiteheadia***
- W. bifolia* (Jacq.) Baker
- Hyacinthus gawleri* (Kunth) Baker
- Hyacinthus corymbosus* L.
- Massonia corymbosa* (L.) Ker-Gawl.
- Scilla corymbosa* (L.) Ker-Gawl.
- Periboea corymbosa* (L.) Kunth
- Polyxena ensifolia* (Thunb) Schönl.
- Mauhlia ensifolia* Thunb.
- Agapanthus ensifolius* (Thunb.) Willd.
- Massonia ensifolia* (Thunb.) Ker-Gawl.
- Massonia odorata* Hook.f.
- Polyxena odorata* (Hook.f.) Baker
- Massonia uniflora* Sol. ex Baker
- Polyxena uniflora* (Sol. ex Baker) Dur. & Schinz
- Polyxena calcioli* U. & d. M-D.
- Polyxena maughanii* Barker
-
- Hyacinthus paucifolius* Barker
- Periboea paucifolia* (Barker) U. & D. M-D.
- Periboea oliveri* U. & D. M-D.
- Polyanthes pygmaea* Jacq.
- Hyacinthus bifolius* Boutelou ex Cav.
- Massonia violacea* Andr.
- Eucomis bifolia* Jacq.
- Basilea bifolia* (Jacq.) Poir.
- Melanthium massoniaefolium* Andr.
- Whiteheadia latifolia* Harv.

CHAPTER 6

TAXONOMIC TREATMENT OF THE GENUS *DAUBENYA* LINDL.

6. *Daubenia* Lindley in Botanical Register 21: t. 1813 (1835); Baker: 394 (1871); Baker: 417 (1897); Marloth: t. 71 (1922); Engler: 350 (1930); Phillips: 193 (1951); Hall: 13 (1970); Dyer: 940 (1976); Jessop: 431 (1976); Lavranos & Craib: 22 (1997); Müller-Doblies & Müller-Doblies: 91 (1997); Goldblatt & Manning: 96 (2000); Williams: 614 (2000). Type – *D. aurea* Lindl.

Massonia Thunb. ex Houtt.: 1780 p.p. excl. type specimen.

Polyxena Kunth. subgenus *Astemma* Baker (excl. *P. angustifolia*): 419 (1897). Lectotype: *P. comata*

[*Polyxena* Kunth subgenus *Astemma* Baker (1897), non *Massonia* Thunb. ex Houtt. subgenus *Astemma* Endlicher (1836)]

Androsiphon Schltr.: 148 (1924); Barker: 21 (1936); Jessop: 432 (1976); Brandham: 124, t. 155 (1990); Müller-Doblies & Müller-Doblies: 86 (1997); Williams: 612 (2000). Type: *A. capense* Schltr.

Neobakeria Schltr.: 150 (1924); Müller-Doblies & Müller-Doblies: 86 (1997). Type: *N. namaquensis* Schltr.

Amphisiphon Barker: 19 (1936); Jessop: 432 (1976); Brandham: 58, t. 123 (1989); Müller-Doblies & Müller-Doblies: 86 (1997); Williams: 611 (2000). Type: *A. stylosa* Barker.

Bulb: turbinate to globose or ovoid, usually deeply buried; *outermost tunics* leathery, dark brown to almost black, extending as a neck in narrow, flat, papery segments. *Leaves*: two, prostrate to spreading, lanceolate to ovate, with prominent longitudinal striations on upper surface, glabrous, glossy green, the bases clasping the peduncle for some distance below the ground. *Inflorescence*: corymbose or racemose to subspicate, the peduncle slightly or well-exserted, sometimes elongating as fruits mature; *bracts* small or large, often forming a coma; *pedicels* suberect, reduced or well-developed in lower flowers, decreasing in length in upper flowers, sometimes elongating in fruit. *Flowers*: white to lilac-tinged, greenish yellow to orange or red, scented or unscented, actinomorphic or zygomorphic with the lower flowers slightly or strongly bilabiate, gamopetalous; *perianth tube* cylindrical or slightly dorso-ventrally compressed, shorter in upper flowers, in lower flowers the adaxial or abaxial side of tube is sometimes longer than the opposite side; *tepals* suberect to spreading or recurved, rarely erect and connate, linear to oblanceolate, usually subsimilar, but sometimes lower three much enlarged. *Stamens*: 6, erect to slightly spreading, filaments equal or the inner ones slightly

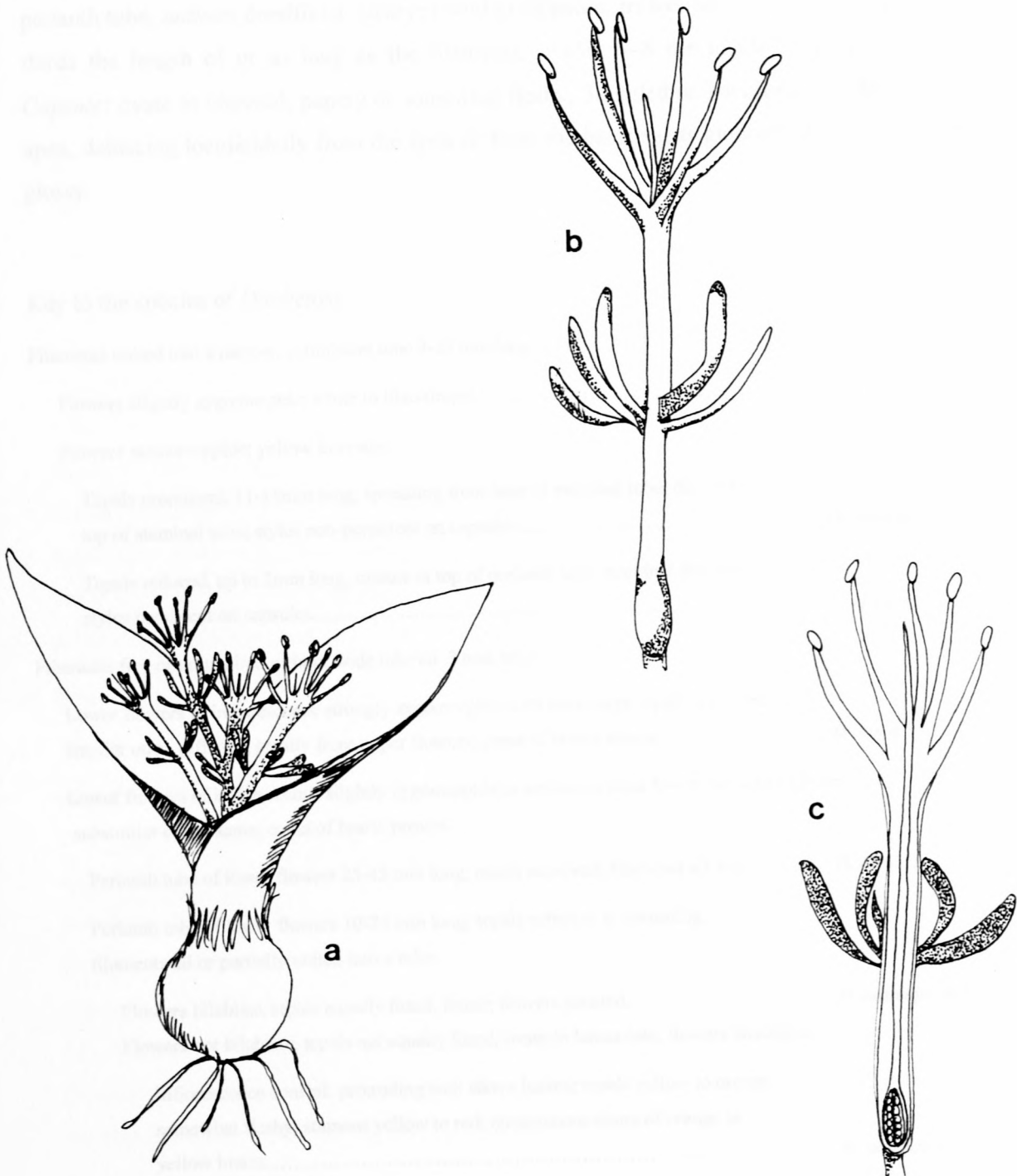


Figure 6.1.1 *Daubenya alba* (a) flowering plant x 1; (b) flower x 4; (c) longitudinal section of flower x 4.

longer, free or basally fused into a short or long tube, inserted at the base of the tepals or sometimes tepals fused above filament insertion and then the filaments arising from inside the perianth tube; *anthers* dorsifixed. *Ovary*: ovoid to ellipsoid, tri-locular. *Style*: usually up to two-thirds the length of or as long as the filaments; *ovules* 6–8 per locule; *stigma* penicillate. *Capsule*: ovate to obovoid, papery or somewhat fleshy, 3-angled or 3-winged and obtuse at the apex, dehiscent loculicidally from the apex or from the base; *seeds* globose, black, smooth and glossy.

Key to the species of *Daubenya*

Filaments united into a narrow, cylindrical tube 9–20 mm long

Flowers slightly zygomorphic; white to lilac-tinged..... *D. alba*

Flowers actinomorphic; yellow to orange

Tepals prominent, 11–15 mm long, spreading from base of staminal tube; disc present on top of staminal tube; styles non-persistent on capsules..... *D. capensis*

Tepals reduced, up to 2 mm long, minute at top of perianth tube; staminal disc absent; styles persistent on capsules..... *D. stylosa*

Filaments free or united into a short, wide tube *ca.* 3 mm long

Lower flowers of inflorescence strongly zygomorphic with three large tepals and three smaller ones, differing greatly from upper flowers; coma of bracts absent *D. aurea*

Lower flowers of inflorescence slightly zygomorphic or actinomorphic; lower and upper flowers subsimilar or the same; coma of bracts present

Perianth tube of lower flowers 25–45 mm long; tepals recurved; filaments all free..... *D. comata*

Perianth tube of lower flowers 10–25 mm long; tepals suberect or spreading; filaments all or partially united into a tube

Flowers bilabiate, tepals equally fused, linear; flowers scented..... *D. namaquensis*

Flowers not bilabiate, tepals not equally fused, ovate to lanceolate; flowers unscented

Inflorescence conical, protruding well above leaves; tepals yellow to orange, somewhat fleshy; stamens yellow to red; conspicuous coma of orange or yellow bracts..... *D. marginata*

Inflorescence capitate, hardly protruding above leaves; tepals white, papery; stamens red with purple base; inconspicuous coma of small green bracts..... *D. zeyheri*

6.1 *Daubenya alba* A.M. v.d. Merwe, sp. nov., foliis glabris, distincte striatis, inflorescentia corymbosa, floribus parum zygomorphis albis vel lilacineis tinctis, tubo staminali longo, tepalis apice viridibus. *Daubenya* capensi similis, sed structura coloreque florum, absentia disco staminalis differt.

TYPE- Northern Cape Province, 3120 (Williston): Farm Bo-tuin, 25km SW of Middelpos, roadsides between ploughed lands in heavy doleritic clay soil (-CC), *A.M. van der Merwe* 195 (NBG, holo.).

Bulb: subglobose, 20–35mm in diameter; outer layers leathery, dark brown, extending in a short papery neck to 5mm. *Leaves*: 2, suberect or somewhat spreading, ovate-lanceolate, acuminate, dark green, glabrous, with prominent longitudinal striations on adaxial surface, 45–100mm x 20–55 mm, leaf bases purple-red, enfolding peduncle for ca. 5mm. *Inflorescence*: corymbose, capitate, protruding ca. 20mm above the leaves, peduncle elongating as fruit matures; *bracts* small, ovate-lanceolate; *pedicels* well-developed, 10–20mm long, elongating slightly in fruit. *Flowers*: slightly zygomorphic, white to lilac-tinged, tepals tipped with green, filaments and style lilac-tinged; *perianth tube* 10–25mm long, 1.5–2mm in diameter; *perianth segments* patent, linear to narrowly oblanceolate, 10–18mm x 1.5–2mm. *Stamens*: 6, zygomorphic, filaments fused unequally, forming a tube ca. 20mm long, free parts suberect or with tips slightly incurved, up to 15mm long; *anthers* purple, ca. 2mm long. *Ovary*: ovoid, tri-locular, ca. 4mm long; *style* up to 55mm long, protruding from the middle of the staminal tube, reaching 2mm beyond the anthers; *stigma* penicillate. *Capsule*: loculicidal, trilobed, ca. 15mm long; *seeds* ellipsoid, black, glossy. (Figure 6.1.1)

Diagnostic features and affinities

Daubenya alba (Figure 6.1.2) is characterised by its delicate white to lilac-tinged flowers and a long staminal tube. It is similar to *D. capensis* (Schltr.) v.d. Merwe & Manning with regard to the floral structure and the presence of a staminal tube, but differs in flower colour and size as well as the lack of a staminal disc. The flowers are also much smaller than those of *D. capensis* and show slight zygomorphy, of the stamens. This zygomorphy is shared by other members of the genus *Daubenya*. Examples include *D. aurea* Lindl. where the outer flowers are strongly zygomorphic (with three much enlarged tepals and three small ones), *D. namaquensis* (Schltr.) J.C. Manning & Goldblatt where zygomorphy can be observed in the lower, older flowers, and *D. comata* (Burch. ex Baker) Manning & vd Merwe, where the lowermost flowers are very slightly bilabiate. Molecular studies reveal a close affiliation between *D. alba* and *D. capensis*.

Geographical distribution and ecology

Daubenya alba occurs in scattered colonies along the edge of the Roggeveld escarpment, between Calvinia and Middelpos (Figure 6.1.3). The species grows in heavy doleritic clay, as do most of the other *Daubenya* species. Plants appear to be restricted to the lower-lying drainage areas. The flowers are strongly scented during the day and night. Flowering time is from May to June.

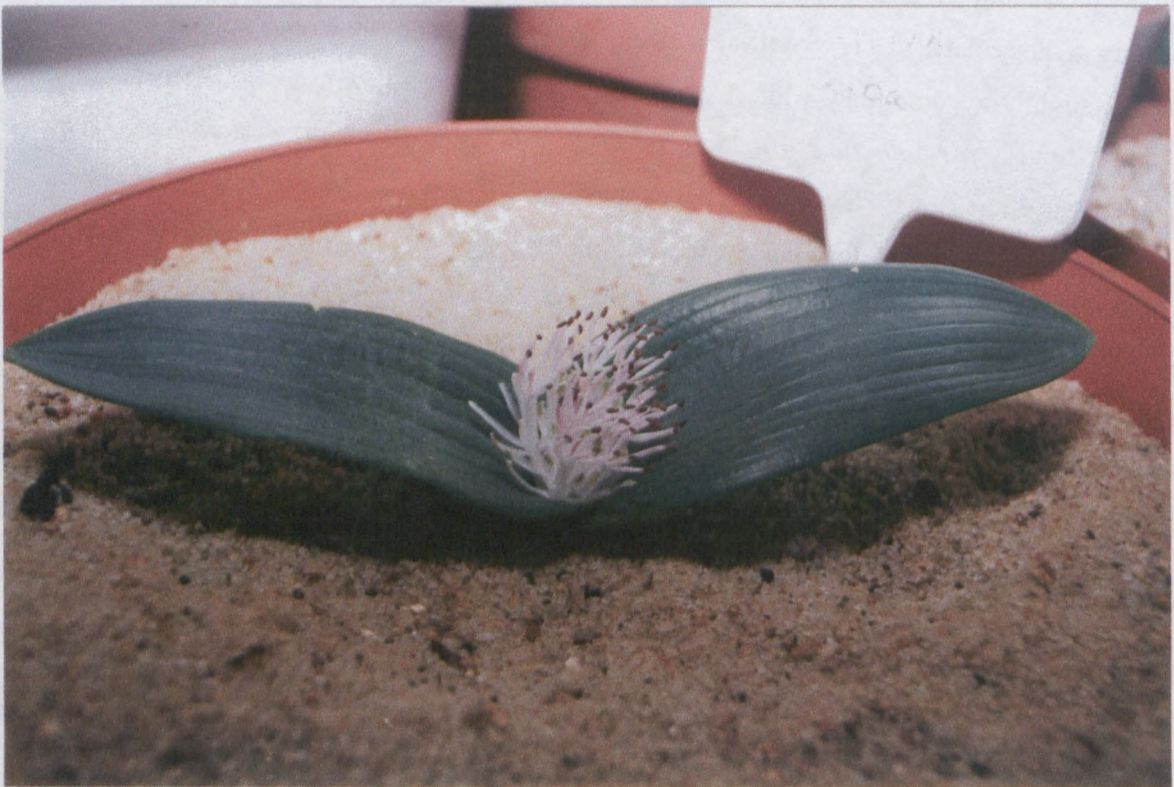


Figure 6.1.2 *Daubenya alba* (Van der Merwe 195, STEU).

Material studied

-3120 (Williston): Roggeveld, Farm Vaalhoek, 25km SW of Middelpos, dolerite outcrop 1km E of homestead behind old shed (-CC), Manning 2345 (NBG); Farm Bo-Tuin, 25km SW of Middelpos, at roadside between ploughed lands in heavy doleritic clay soil (-CC), Van der Merwe 195 (NBG).

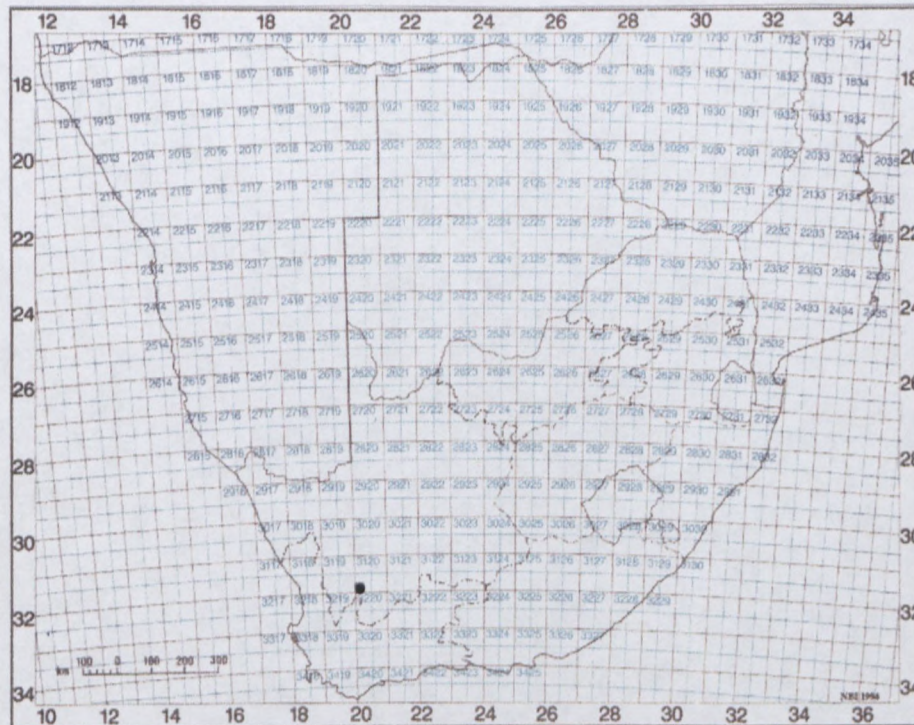


Figure 6.1.3. Geographical distribution of *Daubenya alba*

6.2 *Daubenya aurea* Lindley in Botanical Register 21: t. 1813 (1835); Kunth: 301 (1843); Baker: 389 (1871); Baker: 420 (1897); Phillips: pl. 71 (1922c); Hall: 13 (1970); Jessop: 431 (1976); Müller-Doblies & Müller-Doblies: 91 (1997); Goldblatt & Manning: 713 (2000). Type: South Africa, Cape, without locality or collector, cultivated by Messrs Young of Epsom. Iconotype: Lindley, Botanical Register 21: t. 1813 (1835).

Daubenya fulva Lindl.: pl. 53 (1839); Kunth: 300 (1843); Baker: 389 (1871); Baker: 420 (1897). Type: Received from Cape of Good Hope, with other bulbs, but mistakenly believed to have been collected somewhere on the East Coast of Africa or in Madagascar, cultivated by Robert Barchard, Wandsworth (CGE, holo.).

Daubenya coccinea Harv. ex Baker: 395 (1871); Baker: 420 (1897). *Daubenya aurea* var. *coccinea* (Harv.) Marloth in Phillips: 71 (1922c). Type: Cap. B. Spei, Harvey s.n. (TCD, holo.).

Bulb: subglobose to turbinate, 20–35mm diameter, usually shallowly buried; *outer tunics* leathery, blackish brown, extending in a short, papery neck *ca.* 10mm long. **Leaves:** 2, dark green, suberect to spreading, ovate to lanceolate, 50–150mm x 20–75mm, the bases clasping

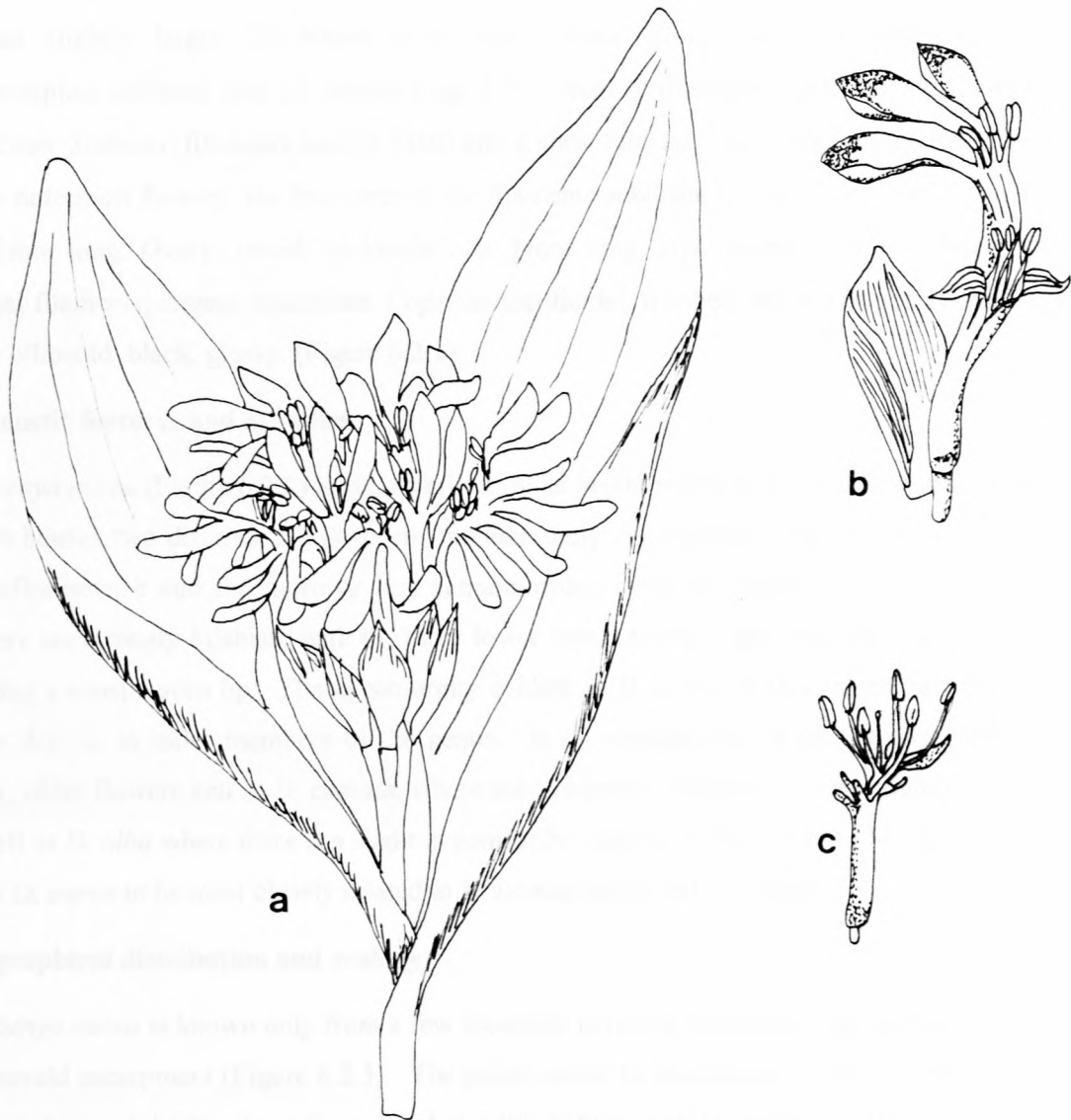


Figure 6.2.1 *Daubenya aurea* (a) flowering plant x 1;(b) zygomorphic, lower flower x 1;(c) actinomorphic, upper flower x 1.

the peduncle for 5–50mm. *Inflorescence*: corymbose, capitate, exserted to 50mm above the leaves, *peduncle* elongating slightly as fruit matures; *bracts* large, decreasing in size acropetally, greenish, the lowermost ovate to oblanceolate, 25–35mm x 10–15mm long; *pedicels* suberect, the lowermost 5–10mm long, the uppermost *ca.* 3mm long. *Flowers*: brilliant red or canary yellow or more rarely orange; *outermost flowers* strongly zygomorphic and bilabiate with three lower tepals much enlarged and forming a prominent lip, *perianth tube* obliquely cylindrical, 15–25mm long on ventral side and 20–40mm long on dorsal side, 3–4mm in diameter; *upper tepals* oblong-ovate, 2–4mm x 1.5–2mm; *lower tepals* oblanceolate to obovate, subequal or the median slightly larger, 20–40mm x 5–13mm; *inner flowers* actinomorphic or weakly zygomorphic, *perianth tube* 13–20mm long, 2.5–3.5mm in diameter, *tepals* oblong, 2–4mm x 1.5–2mm. *Stamens*: filaments basally fused into a short tube *ca.* 2mm long, but the lower 3 free in the outermost flowers, the free parts of the filaments suberect, 4–8mm long; *anthers* yellow, 2.5–3mm long. *Ovary*: ovoid, tri-locular, *ca.* 8mm long; *style* equal to or just longer than adaxial filaments; *stigma* penicillate. *Capsule*: loculicidal, trilobed, becoming papery with age; *seeds* ellipsoid, black, glossy. (Figure 6.2.1)

Diagnostic features and affinities

Daubenya aurea (Figure 6.2.2) is characterised by its bright red or yellow capitate inflorescence which houses two different floral forms, the extremely zygomorphic outer or older flowers in the inflorescence and the more or less actinomorphic inner or younger flowers. The outer flowers are strongly bilabiate with the three lower tepals much larger than the upper three and forming a conspicuous lip. The zygomorphy evident in *D. aurea* is also present, although to a lesser degree, in other members of the genus. In *D. namaquensis* it can be observed in the lower, older flowers and in *D. comata*, where the lowermost flowers are very slightly bilabiate, as well as *D. alba* where there is a slight zygomorphy evident in the stamens. Molecular studies show *D. aurea* to be most closely related to *D. namaquensis* and *D. comata*.

Geographical distribution and ecology

Daubenya aurea is known only from a few localities between Sutherland and Middelpos on the Roggeveld escarpment (Figure 6.2.3). The plants occur in abundance in colonies, in low-lying areas in heavy doleritic clay. *D. aurea* shares this habitat with *D. marginata* (Willd. ex Kunth) J.C. Manning & A.M. van der Merwe, although the two species do not flower at the same time. The flowering time of *D. marginata* stretches from May to June and that of *D. aurea* from August to September. *D. aurea* occurs in two colour forms, the more abundant brilliant red form and the less common canary yellow form. Occasionally a dull orange form has also been observed. The two colour forms seem to differ slightly in flowering time, with the yellow form coming into flower a few weeks before the red one and the fruits also taking longer to reach maturity, remaining green long after the fruits of the red form have dehisced.



Figure 6.2.2 *Daubenya aurea* (Van der Merwe 183, STEU).

Material studied

–3220 (Sutherland): Modderfontein (-AB), *Meiring 2775/15* (BOL); Fransplaas (-AB), *Hall s.n.* (NBG); Fransplaas, SE of Bleskop (-AB), *Oliver 8932* (NBG); near Voëlfontein farm (-AB), *Hall 3240* (NBG); junction of Quaggasfontein and Visrivier roads NW of Sutherland (-AB), *Oliver 4412* (NBG); Farm Steenkamp's Hoek (-AB), *Cloete & Haselau 96* (NBG); Meintjiesplaas, clay area just S of derelict farm Danielskuil (-AB), *Oliver 8972* (NBG); Sutherland (-AB), collected by student in Sept 1951 and grown in Stellenbosch University gardens, *van Niekerk 3851* (BOL); Near Fishriver (-AB), *Marloth 10415* (BOL); 40 miles NW of Sutherland (-AB), *Hall 3269* (NBG); Sutherland (-AB), *Meterlekamp 355/37* (NBG); At South entrance to Fransplaas (-AB), *Perry 3511* (NBG).

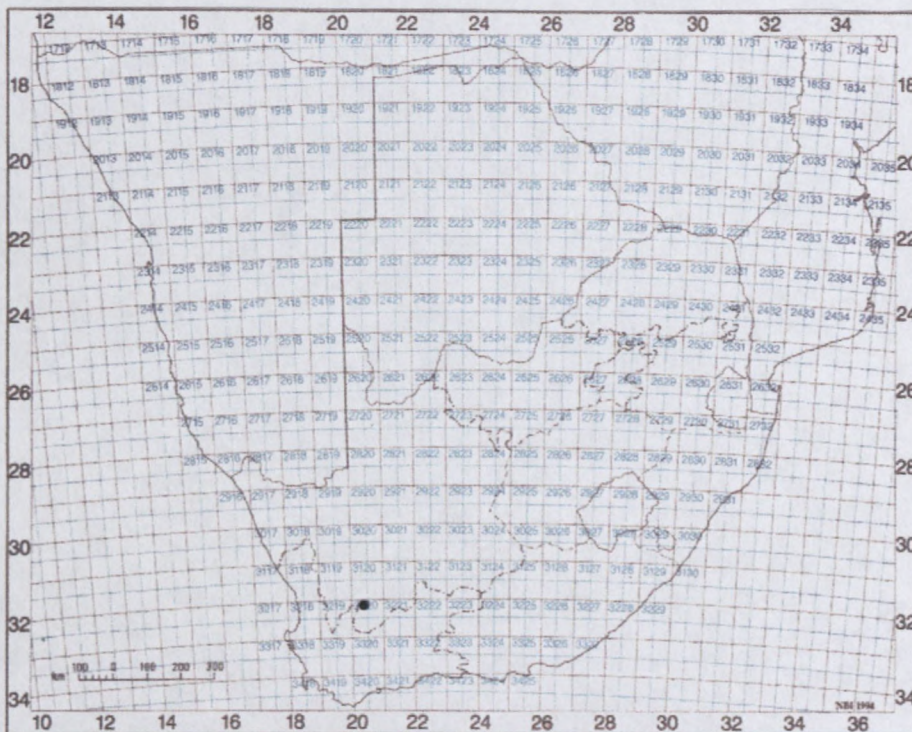


Figure 6.2.3. Geographical distribution of *Daubenya aurea*

6.3 *Daubenya capensis* (Schltr.) A.M. van der Merwe & J.C. Manning in Goldblatt & Manning, *Cape Plants*: 713 (2000). Type: South Africa, Northern Cape, Calvinia District, Onder-Bokkeveld, Oorlogskloof, July 1897, *R. Schlechter 10969* (B holo., BOL!, G, GRA, PRE, Z).

Androsiphon capense Schltr.: 148 (1924); Barker: 21 (1936); Jessop: 432 (1976); Brandham: 124, t. 155 (1990); Müller-Doblies & Müller-Doblies: 86 (1997); Williams: 612 (2000). Type: South Africa, Northern Cape, Calvinia District, Onder-Bokkeveld, Oorlogskloof, July 1897, *R. Schlechter 10969* (B holo., BOL!, G, GRA, PRE, Z).

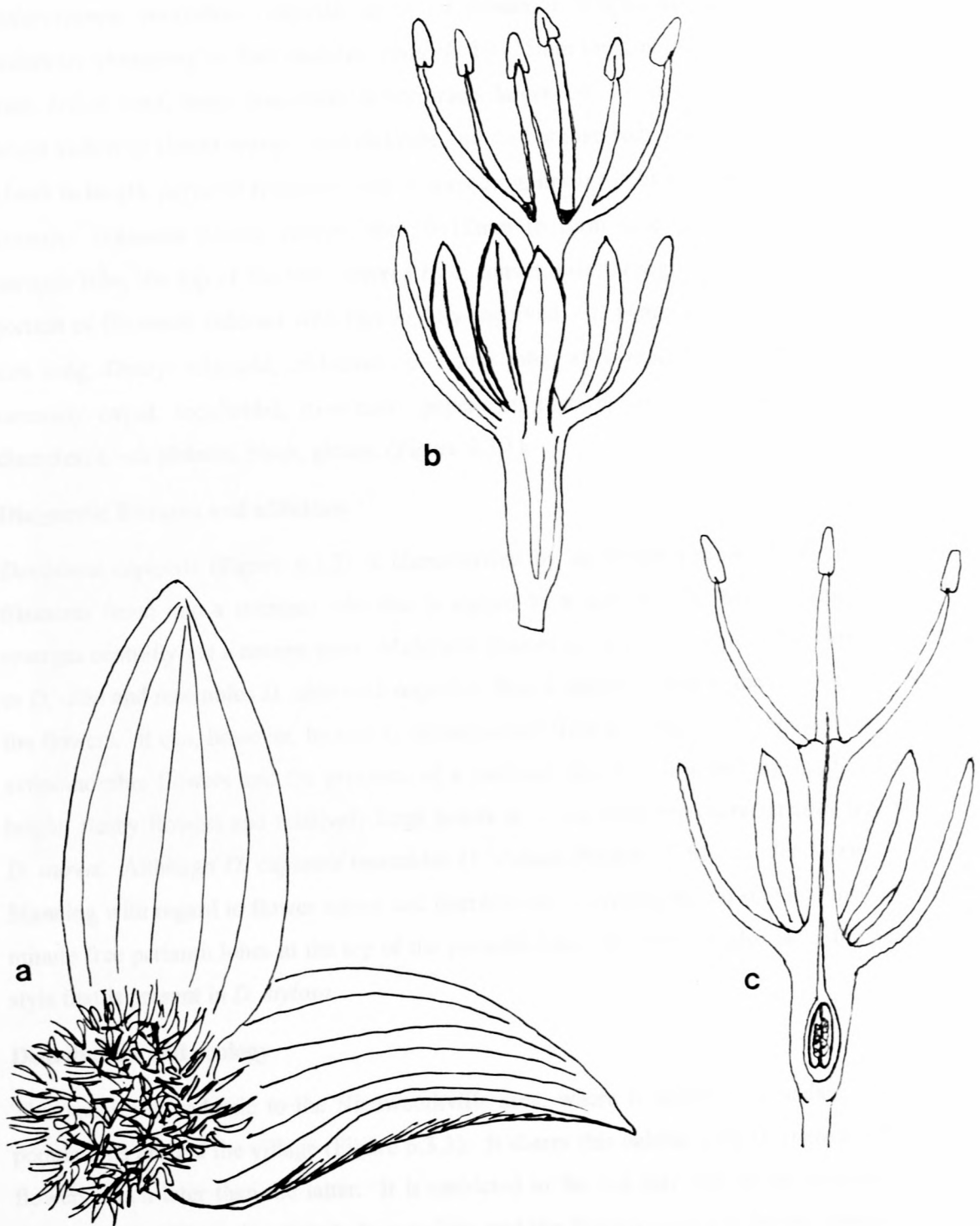


Figure 6.3.1 *Daubinya capensis* (a) flowering plant x 1; (b) flower x 4; (c) longitudinal section of flower x 4.

Bulb: subglobose, 20–30 mm in diameter, outer tunics dark brown, leathery, extending as a short papery neck for *ca.* 5mm. *Leaves*: 2, dark green, suberect, ovate-lanceolate to elliptic, apiculate, 50–150mm x 25–90mm, leaf bases clasping the peduncle for 25–80mm. *Inflorescence*: corymbose, capitate, up to *ca.* 40mm in length, nestled between the leaves; *peduncles* elongating as fruit matures; *pedicels* 10–25mm long, elongating up to *ca.* 30mm in fruit; *bracts* erect, linear-lanceolate, lower bracts larger, *ca.* 30mm in length. *Flowers*: fleshy, bright yellow to almost orange, staminal tube and disc orange-red; *perianth tube* cylindrical, 6–11mm in length, *perianth segments* erect or spreading, linear to oblanceolate, 11–15mm x 3mm. *Stamens*: filaments basally connate for 10–12mm to form tube protruding from mouth of perianth tube, the top of the tube covered by a convex disc through which style emerges, free portion of filaments suberect with tips slightly incurved, *ca.* 14mm long; *anthers* yellow, 2–3 mm long. *Ovary*: ellipsoid, tri-locular, 6–9 mm long; *style* erect 20–25mm long. *Capsule*: narrowly ovoid, loculicidal, tri-winged, papery in texture, *ca.* 30mm long and 12mm in diameter; *seeds* globose, black, glossy. (Figure 6.3.1)

Diagnostic features and affinities

Daubenya capensis (Figure 6.3.2) is characterised by its bright yellow, fleshy flowers and filaments fused into a staminal tube that is topped by a convex disc through which the style emerges centrally via a narrow pore. Molecular studies show that *D. capensis* is closely related to *D. alba* and resembles *D. alba* with regard to flower shape as well as the distinct pedicels of the flowers. It can, however, be readily distinguished from *D. alba* by its yellow, more robust, actinomorphic flowers and the presence of a staminal disc which is lacking in *D. alba*. The bright, fleshy flowers and relatively large bracts of *D. capensis* are characteristics shared with *D. aurea*. Although *D. capensis* resembles *D. stylosa* (Barker) A.M. van der Merwe & J. C. Manning with regard to flower colour and distribution, *D. stylosa* has no staminal disc and only minute free perianth lobes at the top of the perianth tube. *D. capensis* also lacks the persistent style that is present in *D. stylosa*.

Distribution and ecology

This species is endemic to the Nieuwoudtville area, where it occurs in abundance in several populations around the village (Figure 6.3.3). It shares this habitat with *D. stylosa*, although it flowers much later than the latter. It is restricted to the red clay soil of the seasonally moist doleritic flats. Flowering time is June to July and the flowers emit a rather unpleasant, yeasty smell.

Material studied

–3119 (Calvinia): Nieuwoudtville klipkoppies, sticky clay soil (-AC), Barker 9366 (NBG);
 Nieuwoudtville, Glen Lyon, sticky clay soil (-AC), Barker 9389 (NBG);
 Nieuwoudtville District, Karoo clay soil (-AC), Compton NBG 1531/26 (NBG);



Figure 6.3.2 *Daubenya capensis* (Van der Merwe 152, STEU).

Leipoldt 796 (NBG); dolerite outcrops east of Nieuwoudtville waterfall, hard clay soil with a few shrubs (-AC), *Vlok 633* (NBG); Oorlogskloof, red porous clay (-AD), *Van Wyk 2578* (BOL).

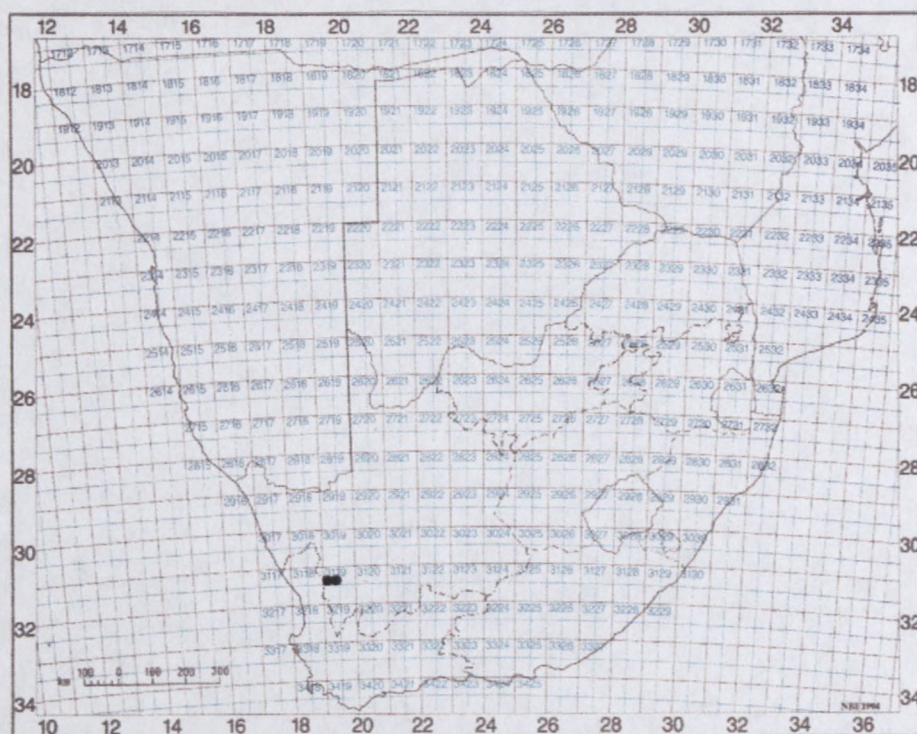


Figure 6.3.3. Geographical distribution of *Daubenya capensis*

6.4 *Daubenya comata* (Burch. ex Baker) J.C. Manning & A.M. van der Merwe, *comb. nov.*

Massonia comata Burch. ex Baker: 392 (1871); Jessop: 421 (1976); Müller-Doblies & Müller-Doblies: 68 (1997). *Polyxena comata* (Burch. ex Baker) Baker: 419 (1897). *Neobakeria comata* (Burch. ex Baker) Schltr.: 150 (1924). Type: Northern Cape, Noupoot district, Carolus Poort, 19 March 1813, *Burchell 2751* (K, holo!).

Bulb: subglobose, 20–35mm in diameter, deeply buried; *outer tunics* leathery, dark brown, extending in a papery neck for up to ca. 30mm. **Leaves:** 2, dark green, sometimes flushed with maroon, spreading to prostrate, ovate-lanceolate, 50–150mm x 30–90mm, the bases clasping the peduncle for up to 80mm. **Inflorescence:** capitate, exerted up to 20mm beyond the leaves; *bracts* acropetally increasing in size, lowermost bracts linear becoming broader and ovate-lanceolate, uppermost ones without flowers or flower buds in axils, forming a coma, green or tinged with pink; *pedicels* minute, lowermost flowers subsessile, uppermost pedicels slightly longer, not elongating in fruit. **Flowers:** white or pink-tinged, weakly dimorphic, lower flowers slightly bilabiate, upper flowers actinomorphic; *perianth tube* cylindrical or dorsally slightly flattened, up to 45mm long in lower flowers and 15mm long in upper flowers, 2–3mm in diameter; in the lower flowers the ventral side of the perianth tube is slightly longer than the dorsal side with a short sinus separating the upper three tepals from the lower three; *perianth*

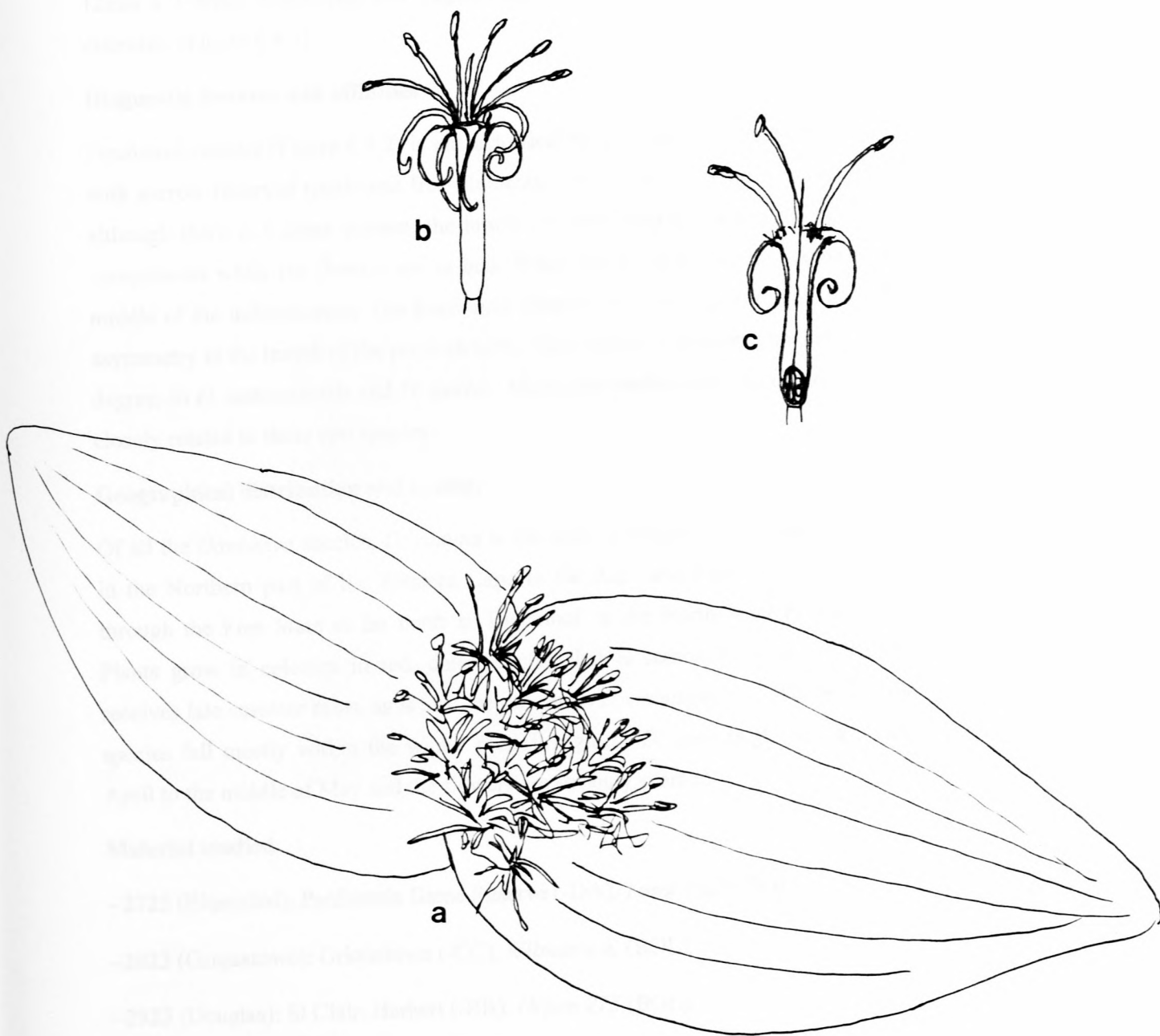


Figure 6.4.1 *Daubenya comata* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

segments spreading from the base, slightly recurved, linear-oblong to narrowly oblanceolate, 7mm x 1.5–2mm. *Stamens*: free, erect, eventually slightly spreading, filaments subequal or inner ones slightly longer, inserted onto or 1mm above the base of the tepals, 15–35 mm long; *anthers* pink, 2.5–3mm long. *Ovary*: ovoid, *ca.* 3mm long; *style* subequal or slightly longer than filaments, 20–40mm long; *stigma* penicillate. *Capsule*: obovoid, papery, 3 angled, 10–12mm x 7–8mm, indehiscent and fragmenting; *seeds* globose, smooth and glossy, *ca.* 2mm in diameter. (Figure 6.4.1)

Diagnostic features and affinities

Daubenya comata (Figure 6.4.2) is characterised by its capitate inflorescence of white flowers with narrow recurved tepals and free filaments. The name *D. comata* is rather misleading as, although there is a coma present, the bracts are small and green and the coma is only really conspicuous while the flowers are in bud. When the flowers open the coma is hidden in the middle of the inflorescence. The lowermost flowers are very slightly bilabiate through a slight asymmetry in the length of the perianth tube. This feature is present, although to a much greater degree, in *D. namaquensis* and *D. aurea*. Molecular studies also show that *D. comata* is most closely related to these two species.

Geographical distribution and ecology

Of all the *Daubenya* species, *D. comata* is the most widespread, occurring from Beaufort West in the Northern part of the Western Cape to De Aar and Colesberg in the Northern Cape, through the Free State as far north as Bloemhof in the North-West Province (Figure 6.4.3). Plants grow in colonies in red, doleritic clay that is seasonally waterlogged. This species receives late summer rains, as is also the case with *D. namaquensis*. The rest of the *Daubenya* species fall mostly within the winter rainfall region. *D. comata* flowers from the middle of April to the middle of May and the flowers are strongly scented.

Material studied

- 2725 (Bloemhof): Panfontein Game Reserve (-DA), Louw 1828 (BOL).
- 2823 (Griquatown): Griquatown (-CC), Wilman s.n. (BOL).
- 2923 (Douglas): St Clair, Herbert (-BB), Orpen 275 (BOL).
- 2925 (Jagersfontein): Fauresmith (-CB), In drift sand round solid rock, Verdoorn s.n. (BOL).
- 3024 (De Aar): 20 km SE of De Aar (-CC), Manning 2329 (NBG); 40 km SE of De Aar, Farm Dieprivier (-CD), Manning 2327 (NBG).
- 3123 (Victoria West): Richmond, 3 km SE of town on Graaff Reinet road (-BD), Manning 2321 (NBG).



Figure 6.4.2 *Daubinya comata* (Manning 2327, NBG).

-3124 (Hanover): Naauwpoort, (-AB), *Denoon* 38 (BOL); Waschbanks river, near Ruigtefontein, Carolus Poort. Colesberg division, damp localities near running water (-BB), *Burchell* 2751 (K).

-3222 (Beaufort West): Beaufort West (-BC), *Macarthy s.n.* sub SAM 23080 (SAM).

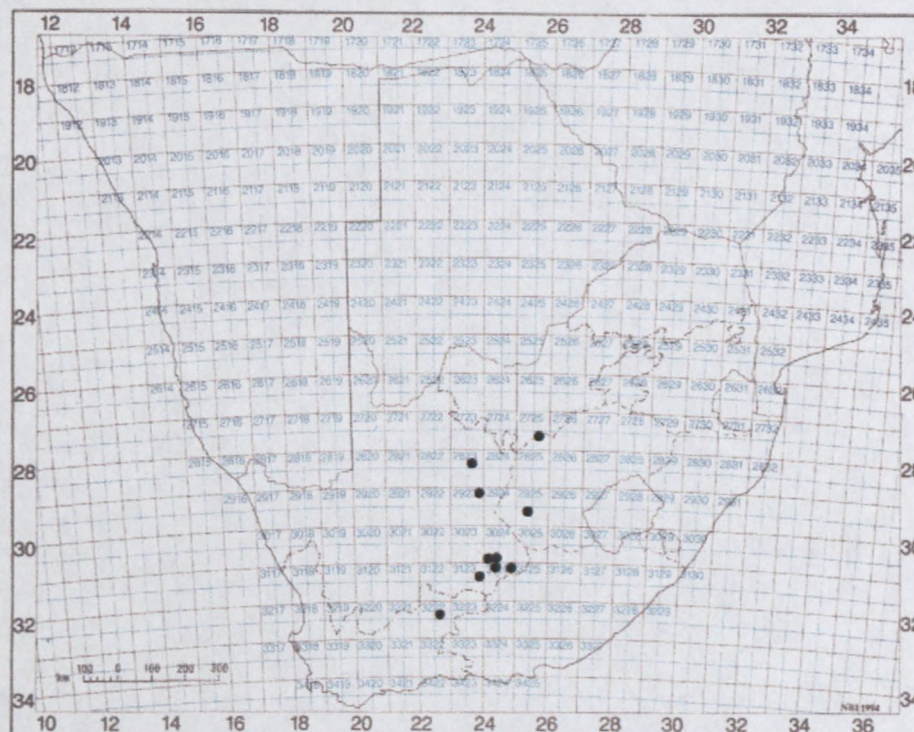


Figure 6.4.3. Geographical distribution of *Daubenya comata*

6.5 *Daubenya marginata* (Willd. ex Kunth) J.C. Manning & A.M. van der Merwe *comb. nov.*

Massonia marginata Willd. ex Kunth: 299 (1843). *Polyxena marginata* (Willd. ex Kunth) Baker: 420 (1897). *Neobakeria marginata* (Willd. ex Kunth) Schltr.: 150 (1924). Type: South Africa, Cap. B. Spei. (*B-WILLD* 6373, holo., NBG, photograph!).

Massonia rugulosa Lichtenst. ex Kunth: 299 (1843). *Polyxena rugulosa* (Lichtenst. ex Kunth) Baker: 420 (1897). *Neobakeria rugulosa* (Lichtenst. ex Kunth) Schltr.: 150 (1924). Type: Cap. B. Spei., *Lichtenstein* 224 (B, holo., ?destroyed).

Polyxena haemanthoides Baker: pl. 1727 (1888); Phillips: pl. 56 (1922b). *Neobakeria haemanthoides* (Baker) Schltr.: 150 (1924). Type: South Africa, Nuweveld Mountains near Fraserburg, April 1886, *Bolus* 5493 (BOL, lecto.!, designated here, G, SAM!).

Massonia angustifolia auct. non *M. angustifolia* L.f.

Bulb: subglobose, 20–30mm in diameter, shallowly buried, *outer tunics* leathery, dark brown, extending as a narrow papery neck for up to 40mm. **Leaves:** 2, spreading, ovate to elliptic, apiculate, dark green, sometimes flushed with maroon, 50–100mm x 25–50mm, the base

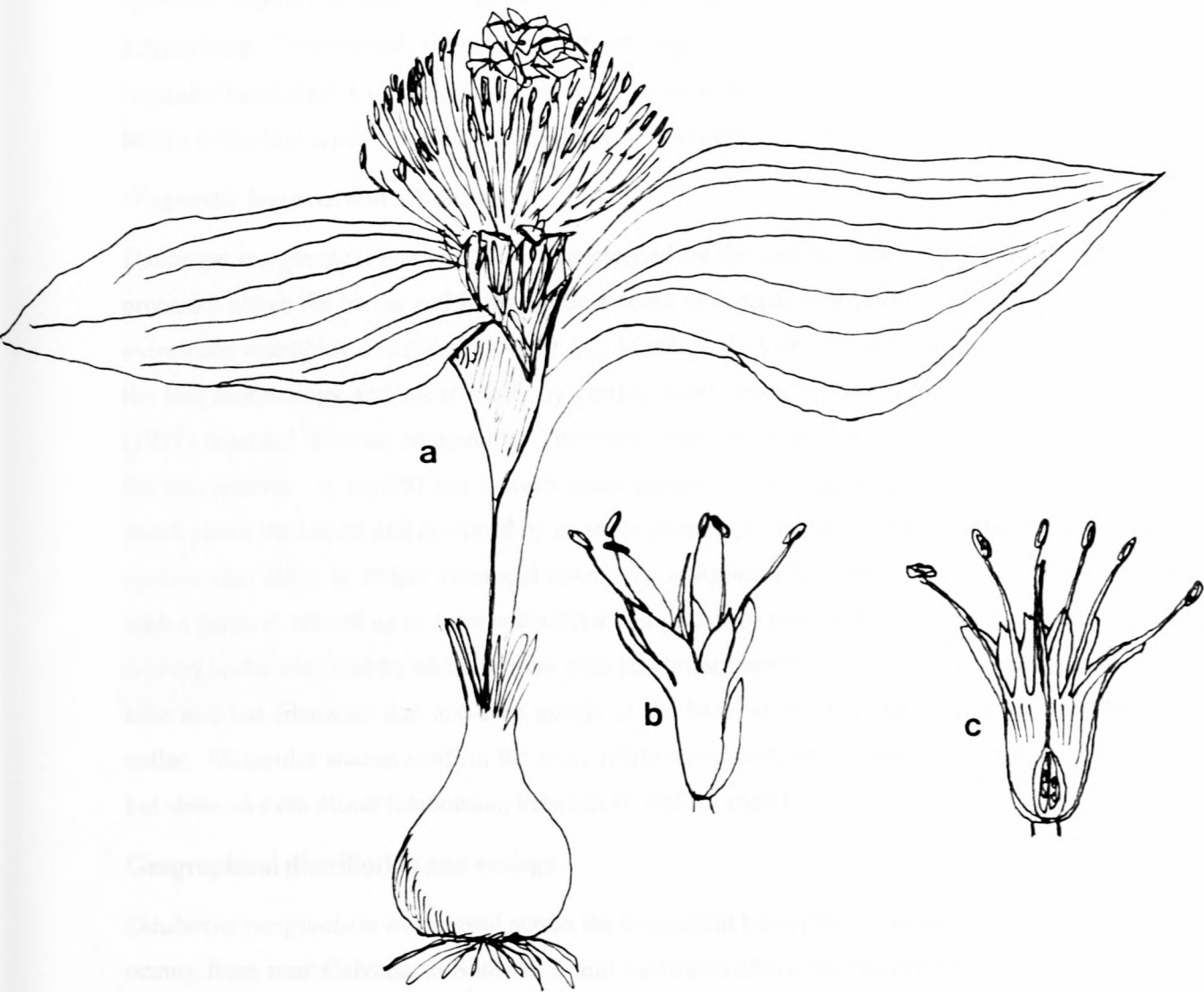


Figure 6.5.1 *Daubenya marginata* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

clasping the peduncle for 20–30mm. *Inflorescence*: subspicate, capitate or conical, protruding for 20–60mm above the leaves, *peduncle* elongating slightly as fruits mature; *pedicels* 1–2.5mm long; *bracts* erect, acropetally increasing in size, lowermost bracts triangular, up to 5mm long, uppermost ones oblanceolate, up to 10mm long, without flowers or flower buds in axils, imbricate and forming a green to orange coma. *Flowers* greenish yellow, *perianth tube* cylindrical, slightly flattened, 10–20mm long and 2–3mm in diameter, *perianth segments* suberect, the inner 3 connate for ca. 1mm beyond the outer 3, lanceolate, conduplicate, 6–8mm x 2.5mm. *Stamens*: basally fused for up to 2.5mm into a wide-mouthed staminal collar, filaments suberect or slightly incurved, yellow or orange, 10–20mm long; *anthers* yellow, 2–2.5mm long. *Ovary* ovoid, tri-locular, ca. 6mm long; *style* 11–20mm long; *stigma* penicillate. *Capsule*: loculicidal, tri-lobed, ca. 15mm long, green and fleshy when young, drying to papery before dehiscing; *seeds* ellipsoid, black, glossy. (Figure 6.5.1).

Diagnostic features and affinities

Daubenya marginata (Figure 6.5.2) is characterised by the conical yellow inflorescence, which protrudes above the leaves and is topped by a coma of conspicuous yellow or orange bracts. *D. marginata* resembles *D. zeyheri* (Kunth) J.C. Manning & A.M. van der Merwe with regard to the leaf morphology and superficially by certain floral characteristics, so much so that Jessop (1977) regarded them as conspecific. There are, however, many obvious differences between the two species. *D. zeyheri* has a much more capitate inflorescence, which does not protrude much above the leaves and is topped by an inconspicuous coma of small green bracts. The two species also differ in flower form and colour. *D. marginata* has firm-textured yellow flowers with a perianth tube of up to 3mm in diameter and yellow to orange or red filaments, whereas *D. zeyheri* is characterised by white flowers with an almost papery texture, a more slender perianth tube and red filaments that are deep purple at the base where they are fused into a shallow collar. Molecular studies confirm the close relationship between *D. marginata* and *D. zeyheri*, but show an even closer relationship between *D. stylosa* and *D. marginata*.

Geographical distribution and ecology

Daubenya marginata is widespread across the Roggeveld Escarpment and the western Karoo. It occurs from near Calvinia to Sutherland and eastwards along the Nuweveld scarp and inland near Fraserburg and Loxton. There are also a few isolated populations on the Knersvlakte, north of Vanrhynsdorp (Figure 6.5.3). In the Sutherland area plants occur together with *D. aurea* in red doleritic clays in seasonally moist depressions. In other areas they are more often found in silt or gritty clay. Flowering time is May to July, but sometimes extends into August.

Material studied

–3018 (Kamiesberg): Kamiesberg (-AC), *Van Berkel* 334 (NBG).



Figure 6.5.2 *Daubenya marginata* (Van der Merwe 134, STEU).

- 3118 (Vanrhynsdorp): Knersvlakte, Kalkgat farm, Soutrivier floodplain (-BB), *Boucher 5153* (NBG); Knersvlakte, flats NE of Kwaggaskop, sandy open flats with grass and low shrublets (-BC), *Oliver 9464* (NBG).
- 3119 (Calvinia): Zuringrug Vlake, 6 miles N of Downes Station (-BD), *Salter 4452* (BOL); Uitkomst, W of Tafelberg SE of Calvinia, dry, stony, karroid flats (-DB), *Thompson 2439* (NBG).
- 3120 (Williston): Williston (-BD), *Stayner s.n.* (NBG); Williston (-CA), *Hall 4253* (NBG).
- 3121 (Fraserburg): 22.3 km SW of Fraserburg on Sutherland road, deep red sands along Grootfontein River, (-CD), *Manning 2263* (NBG); Fraserburg, (-DC), *Rossouw s.n.* (NBG).
- 3122 (Loxton): De Cypher SE of Carnarvon, shale and sandy flats, (-AB), *Thompson 3093* (NBG).
- 3220 (Sutherland): Middelpoos, Farm Fransplaas, dolerite flats among *D. aurea*, (-AB), *Manning s.n.* (NBG); Rietkuil, NW of Sutherland along Visrivier, open clay flats between scattered shrublets, growing with *D. aurea*, (-AB), *Oliver 4423* (NBG); Great Fish River, (-BC), *Compton 7470* (NBG); Roggeveld mountains, (-BC), *Compton 702/28* (NBG); Voëlfontein farm (-BC), *Hall 225* (NBG); *Hall 3242* (NBG).
- 3221 (Merweville): 12 miles SW of Fraserburg, farm Grootfontein, red loamy slopes with rocky outcrops, (-AB), *Coetzer 67* (NBG).

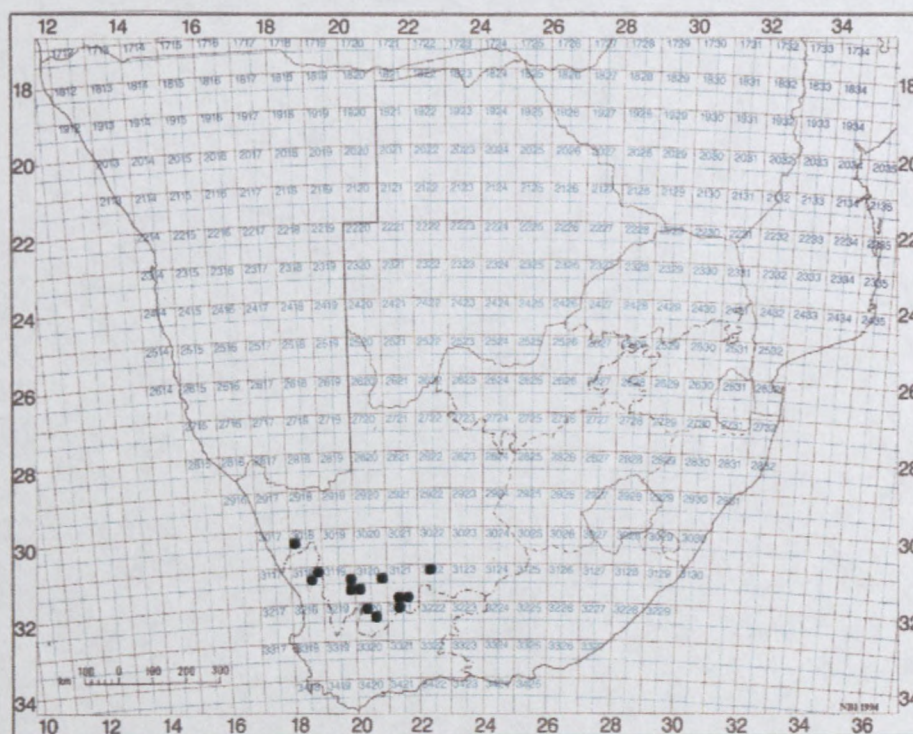


Figure 6.5.3 Geographical distribution of *Daubenya marginata*



Figure 6.6.1 *Daubenya namaquensis* (a) flowering plant x 1; (b) zygomorphic, lower flower x 1.5; (c) actinomorphic, upper flower x 1.5.

6.6 *Daubenya namaquensis* (Schltr.) J.C. Manning & Goldblatt, in Goldblatt & Manning, Cape Plants: 713 (2000).

Daubenya namaquana ['namaquensis'] (Schltr.) J.C. Manning & Goldblatt: 713 (2000).

Neobakeria namaquensis Schltr.: 150 (1924); Müller-Doblies & Müller-Doblies: 86 (1997). Type: South Africa, Northern Cape, Springbok District, Zabies (=Sabies), *M. Schlechter* 90 (B, holo., BOL!, GRA, PRE, SAM!, Z.).

Massonia angustifolia sensu Jessop: 419 (1976), p.p.

Bulb: turbate, 20–35mm in diameter, very deeply buried; outer tunics leathery, dark brown, extending into a papery neck for up to 30mm. *Leaves*: 2, dark green, spreading to prostrate, lanceolate, 100–150mm x 25–75mm, the bases clasping the peduncle for up to 100mm. *Inflorescence*: subspicate, conical, exserted for up to 90mm above the leaves; *bracts* acropetally increasing in size, the lowermost awl-shaped, white, up to 2mm long, the uppermost green or pink-tinged, spatulate, up to 8mm long, forming a coma; *pedicels* suberect, acropetally decreasing in length, lowermost ones up to 5mm long, uppermost ones only 0.5mm long and flowers subsessile, pedicels elongate slightly as fruits mature. *Flowers*: greenish yellow, dimorphic, the lower flowers slightly bilabiate, the upper flowers actinomorphic; *perianth tube* cylindrical or dorsally slightly flattened, 2mm in diameter, 13–15mm long in the lower flowers, 9–10mm long in the upper flowers; in the lower flowers the ventral side of the perianth tube is slightly longer than the dorsal side with a pronounced sinus separating the upper three tepals from the lower three; *perianth segments* spreading from the base, curving upwards, linear-oblongate, weakly cucullate at apex, 9–10mm x 1–1.5mm. *Stamens*: erect to slightly spreading, filaments subequal or inner ones slightly longer, 3 filaments on ventral side of perianth basally fused for 5mm, dorsal filaments completely free, inserted on the base of the tepals, 13–15mm long; *anthers* yellow, 2.5 mm long. *Ovary*: ovoid, ca. 3mm long; *style* equal to filaments or $\frac{2}{3}$ of their length, 15–25mm long; *stigma* penicillate. *Capsule*: obovoid, papery and somewhat inflated, triangular at base but tri-winged and obtuse at the apex, 20–23mm x 15mm, dehiscing loculicidally from the apex; *seeds* globose, black and glossy, ca. 2mm in diameter. (Figure 6.6.1)

Diagnostic features and affinities

Daubenya namaquensis (Figure 6.6.2) is characterised by a conical inflorescence of strongly scented, yellow flowers which are exserted well above the leaves. *D. namaquensis* superficially resembles *D. marginata* which also has a conical inflorescence topped by a coma of bracts. The two species were considered conspecific by Jessop (1976), but they are easily distinguished. The flowers of *D. marginata* are not scented and have pale- or greenish-yellow tepals and golden orange filaments that are fused at the base into a short collar. The flowers of *D. namaquensis* are dimorphic, with the lower flowers being noticeably bilabiate. The ventral side



Figure 6.6.2 *Daubenya namaquensis* (Van der Merwe 199, STEU).

of the perianth tube is extended almost 2mm beyond the dorsal side, forming a sinus which separates the upper and lower tepals. The upper flowers of *D. namaquensis* are actinomorphic. *D. namaquensis* shares this dimorphy with *D. aurea*, and zygomorphic flowers are also found in *D. comata* and *D. alba*. Molecular studies show a close relationship between *D. namaquensis*, *D. comata* and *D. aurea*.

Geographical distribution and ecology

Daubenya namaquensis is known only from a few collections from the semi-arid flats east of O'okiep and Springbok (Figure 6.6.3). This area lies on the extreme western edge of Bushmanland and is on the boundary between winter- and summer-rainfall regions. *D. namaquensis* occurs in small colonies in lower-lying drainage areas in deep red sands. The bulbs are extremely deeply buried enabling the plants to make full use of any soil moisture. Flowering time is from the middle of May to the middle of June and flowers are strongly scented.

Material studied

-2917 (Springbok): Zabies, Namaqualand (-BD), *Schlechter 90* (SAM, BOL); O'okiep (-DB), *Good s.n.* (BOL).

-2918 (Gamoep): 50 km NE of Springbok along Pofadder road, Farm Varsputs, just before gate to homestead, seasonally moist red sands (-AD), *Manning 2250* (NBG); 60 miles W of Pofadder (-BC), *Schlieben 9017* (BOL); 20 miles NE of Springbok (-CB), *Barker 6703* (NBG).

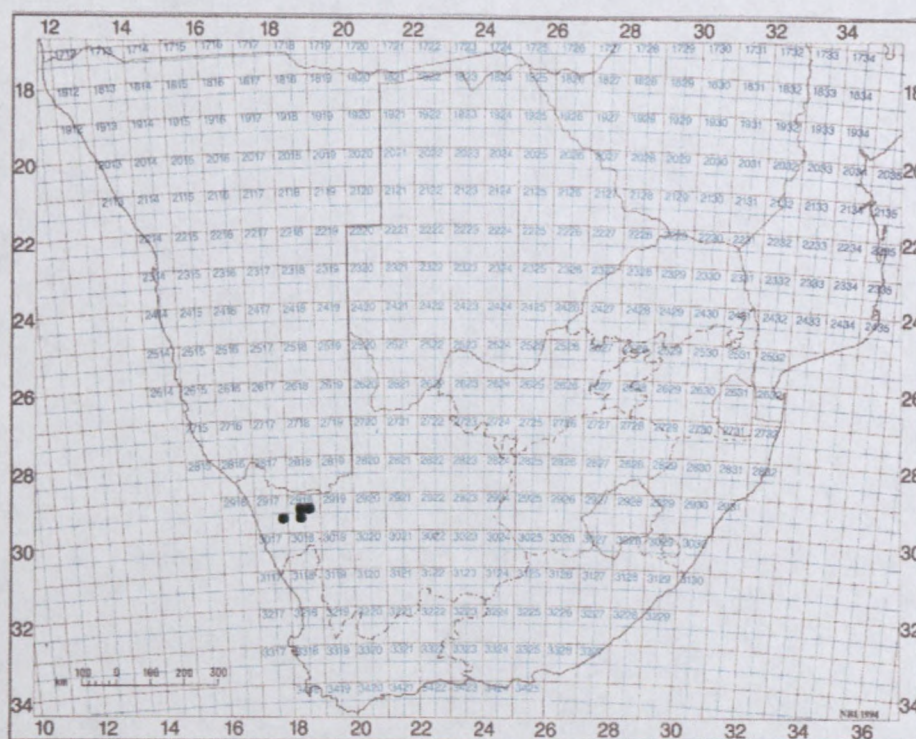


Figure 6.6.3. Geographical distribution of *Daubenya namaquensis*

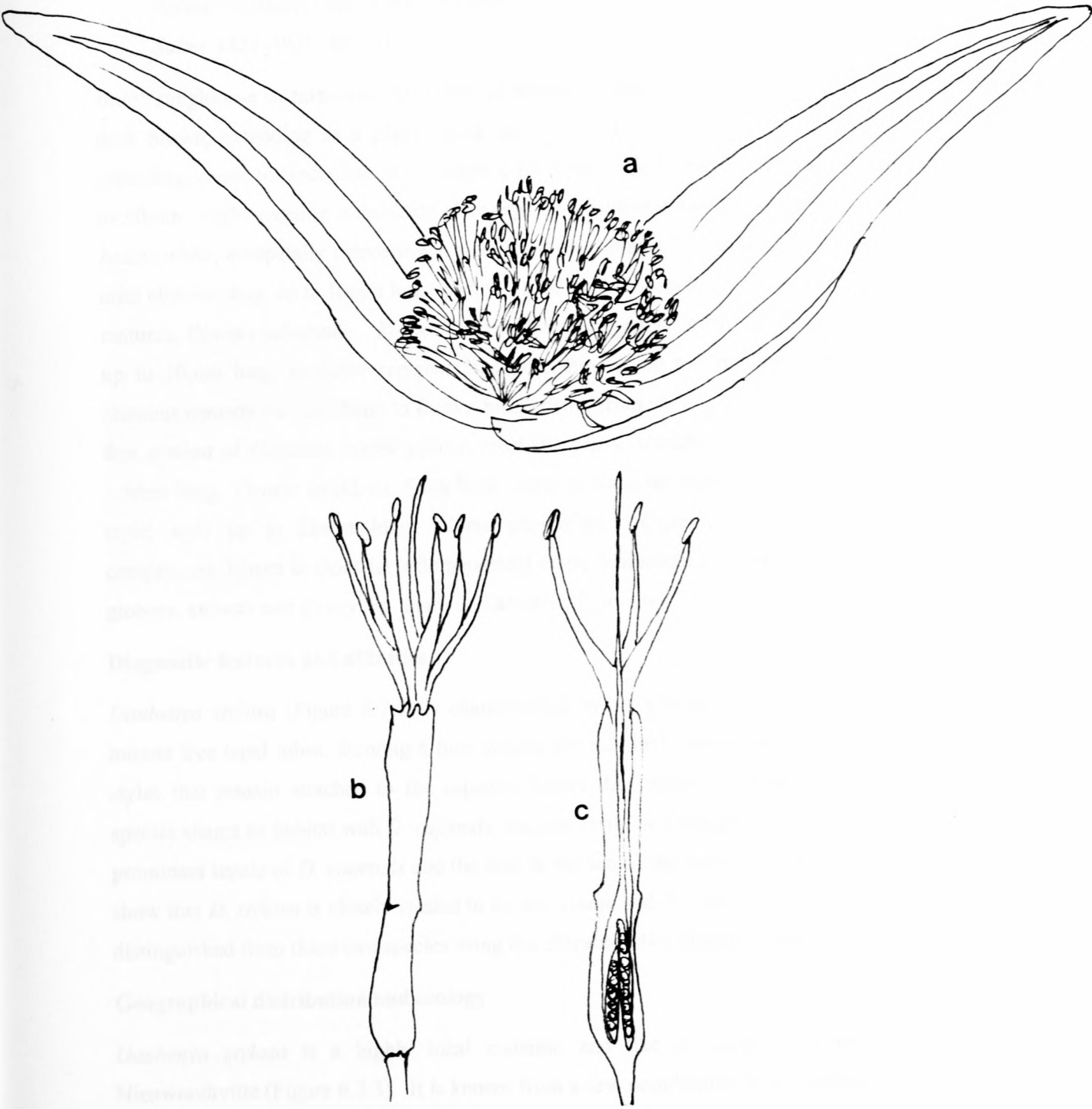


Figure 6.7.1 *Daubenya stylosa* (a) flowering plant x 1; (b) flower x 4; (c) longitudinal section of flower x 4.

6.7 *Daubenya stylosa* (Barker) A.M. van der Merwe & J. C. Manning, in Goldblatt & Manning, Cape Plants: 713 (2000).

Amphisphon stylosum ['*stylosa*'] Barker: 19 (1936); Jessop: 432 (1976); Brandham: 58 (1989); Müller-Doblies & Müller-Doblies: 86 (1997); Williams: 612 (2000). Type: South Africa, Northern Cape, Calvinia District, 3 miles north of Nieuwoudtville, 21 June 1934, *Salter 4552* (BOL, holo!).

Bulb: subglobose to turbinate, 20–35mm in diameter, shallowly buried; *outer tunics* leathery, dark brown, extending as a papery neck for *ca.* 5mm. *Leaves*: 2, dark green, suberect to spreading, ovate to lanceolate, 30–100mm x 15–50mm, the bases clasping the peduncle for up to 50mm. *Inflorescence*: subspicate or capitate, protruding above the leaves for up to 50mm; *bracts* white, acropetally increasing in size, lowermost bracts lanceolate up to 5mm long, upper ones oblanceolate, up to 10mm long; *pedicels* suberect, 1–3mm long, elongating slightly as fruit matures, flowers subsessile. *Flowers*: actinomorphic, yellow-green; *perianth tube* cylindrical, up to 20mm long, *perianth segments* reduced, minute, up to 2mm long and 1.5mm wide. *Stamens* connate for *ca.* 15mm to form a tube arising from about half way up the perianth tube, free portion of filaments bright yellow, erect-spreading, arcuate, 10mm long; *anthers* yellow, 1.5mm long. *Ovary*: ovoid, *ca.* 6mm long, 2mm in diameter, apex attenuated into long yellow style; *style* up to 28mm long; *stigma* penicillate. *Capsule*: obtusely angled, laterally compressed, 12mm in diameter with persistent style, dehiscing septicidally from the base; *seeds* globose, smooth and glossy, *ca.* 2mm in diameter. (Figure 6.7.1)

Diagnostic features and affinities

Daubenya stylosa (Figure 6.7.2) is characterised by its almost completely fused tepals with minute free tepal lobes, forming a tube around the staminal column and also by the persistent styles that remain attached to the capsules where they appear as conspicuous beaks. This species shares its habitat with *D. capensis*, but can easily be distinguished from it because of the prominent tepals of *D. capensis* and the disc at the top of the staminal tube. Molecular studies show that *D. stylosa* is closely related to *D. marginata* and *D. zeyheri*. *D. stylosa* can easily be distinguished from these two species using the characteristics already mentioned.

Geographical distribution and ecology

Daubenya stylosa is a highly local endemic and like *D. capensis* occurs only around Nieuwoudtville (Figure 6.7.3). It is known from a few populations in the immediate vicinity of the town, the Wildflower Reserve and the Farm Glenlyon. Plants are abundant in these populations and grow in the red doleritic clays so typical of this genus. Flowering time is May to June and the flowers are sweetly scented. Nectar is visible at the mouth of the staminal column.



Figure 6.7.2 *Daubenyia stylosa* (Van der Merwe 119, STEU).

Material studied

-3119 (Calvinia): Nieuwoudtville district, Glenlyon (-AC), *Barker 9390* (NBG); Glenlyon farm (-AC), *Barker 10545* (NBG); Nieuwoudtville Reserve, flatish areas among dolerite koppies (-AC), *Perry & Snijman 2132* (NBG); along trekpath through Glenlyon, local in damp depressions in red doleritic clay (-AC), *Snijman 1705* (NBG); Nieuwoudtville Wildflower Reserve, in red clay dolerite koppies (-AC), *Snijman 1228* (NBG); 3 miles N of Nieuwoudtville (-AD), *Salter 1558/34* (BOL); Oorlogskloof, red clay but more sandy that *Androsiphon* habitat, (-AD), *Van Wyk 2579* (BOL).

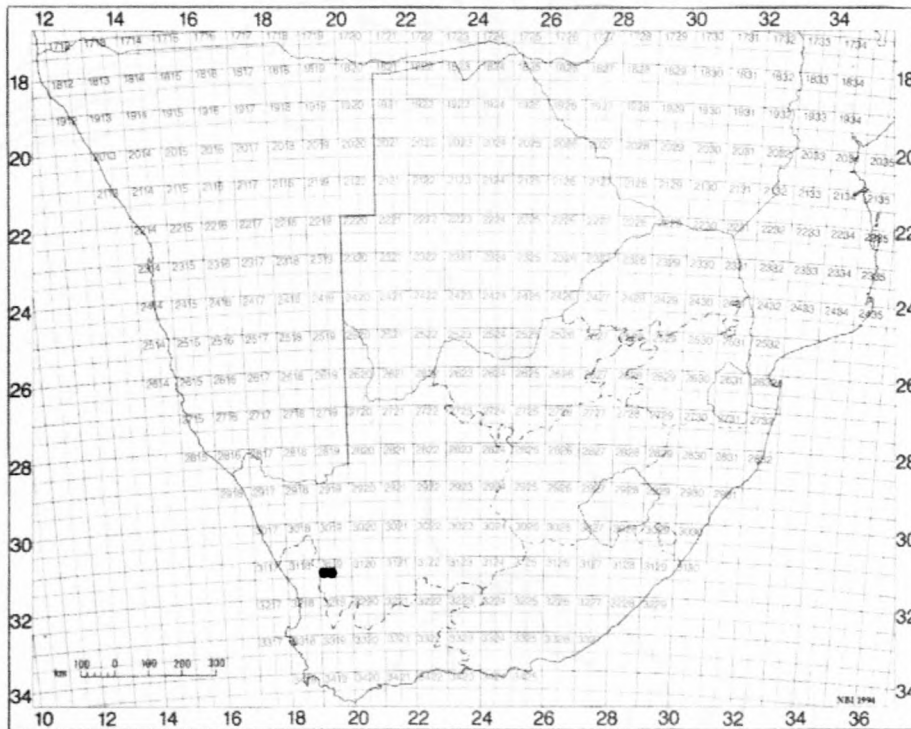


Figure 6.7.3. Geographical distribution of *Daubenya stylosa*

6.8 *Daubenya zeyheri* (Kunth) J.C. Manning & A.M. van der Merwe *comb. nov.*

Massonia zeyheri Kunth: 298 (1843); Müller-Doblies & Müller-Doblies: 77 (1997).

Polyxena zeyheri (Kunth) Dur. & Schinz: 367 (1895). Type: *M. zeyheri*, Zeyher 298, no locality (K, holo.!).

Massonia pedunculata Baker: 8 (1892). Type: Vicinity of Hopefield. Malmesbury division, *Bachmann 2043* (K, holo.!).

Massonia burchellii Baker: 393 (1871). *Polyxena burchellii* (Baker) Baker: 420 (1897).

Neobakeria burchellii (Baker) Schltr.: 150 (1924). Type: South Africa, Cap. B. Spei., *Burchell s.n.* (K, holo.!, BOL, drawing!).

Massonia angustifolia auct. non *M. angustifolia* L.f.

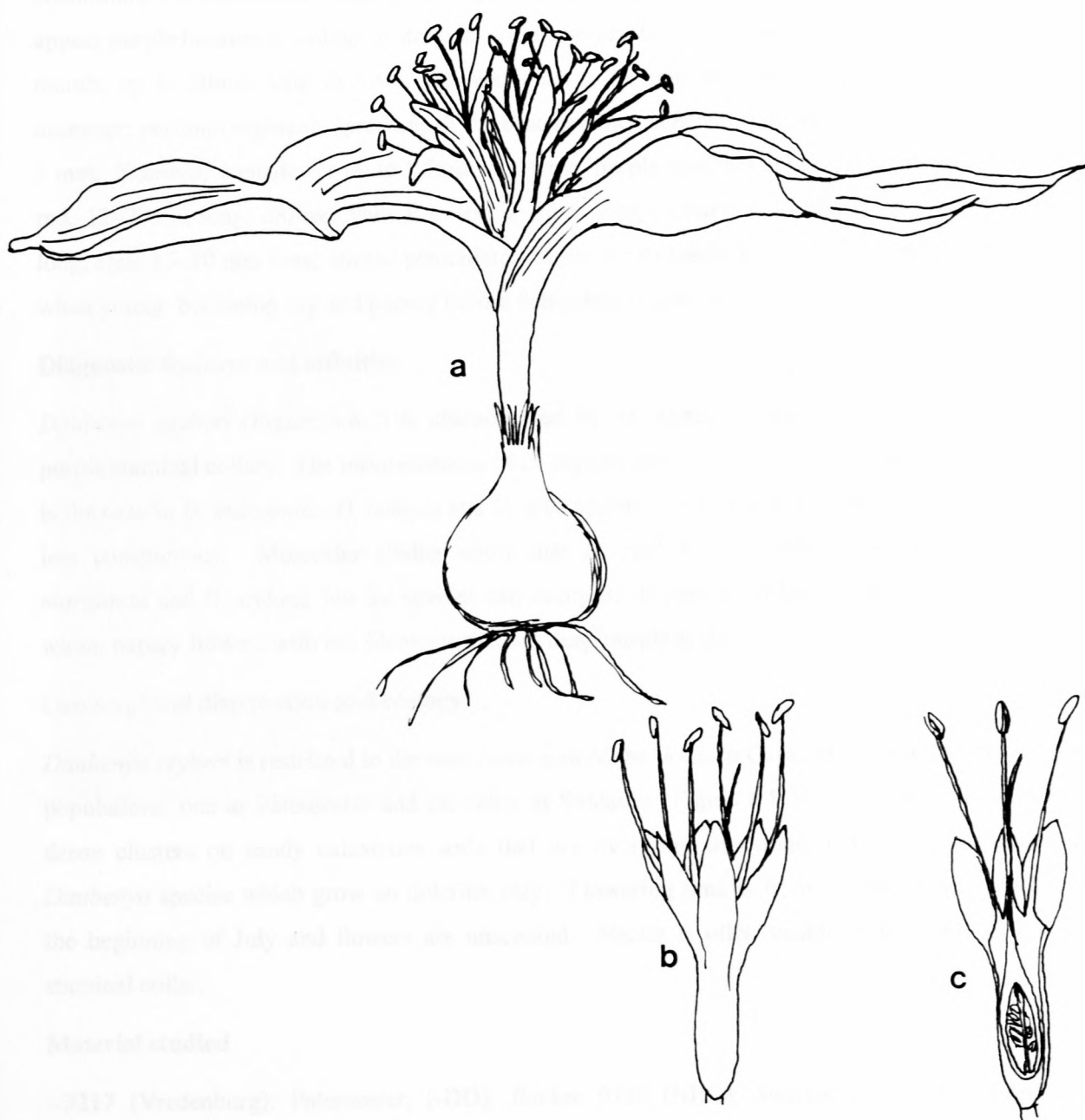


Figure 6.8.1 *Daubenya zeyheri* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

Bulb: subglobose, 20–30mm in diameter, outer tunics leathery, dark brown, extending as a papery neck for up to 10mm. *Leaves*: spreading, elliptic to lanceolate, apiculate, dark green, 60–150mm x 20–80mm, the bases clasping the peduncle for up to 100mm. *Inflorescence*: corymbose, capitate, 20–40mm in length, hardly protruding above the leaves; *bracts* erect, acropetally increasing in size, the lowermost triangular, up to 3mm long, the uppermost lanceolate, up to 8mm long, forming an inconspicuous coma; *pedicels* 2–10 mm long. *Flowers*: actinomorphic, translucent white, pink-tinged on the tube, papery in texture, centre of flowers appear purple because of colour of staminal collar; *perianth tube* cylindrical, slightly flattened at mouth, up to 20mm long in lower flowers, only to 13 mm in upper flowers, 1.5–2mm in diameter; *perianth segments* spreading at the base and then suberect, lanceolate, 6–10mm x 2.5–3 mm. *Stamens*: connate for up to 1.5mm in a wide, purple staminal collar, filaments suberect, red, 12–20mm long; *anthers* yellow to red, 2–3mm long. *Ovary* tri-locular, ovoid, ca. 4mm long; *style* 15–30 mm long; *stigma* penicillate. *Capsule* : tri-lobed, loculicidal, green and fleshy when young, becoming dry and papery before dehiscing. (Figure 6.8.1)

Diagnostic features and affinities

Daubenya zeyheri (Figure 6.8.2) is characterised by its white, papery-textured flowers with purple staminal collars. The inflorescences of *D. zeyheri* are also topped by a coma of bracts, as is the case in *D. marginata*, *D. comata* and *D. namaquensis*, although in *D. zeyheri* this coma is less conspicuous. Molecular studies show that *D. zeyheri* is closely related to both *D. marginata* and *D. stylosa*, but the species can easily be distinguished from both because of its white, papery flowers with red filaments that are deep purple at the base.

Geographical distribution and ecology

Daubenya zeyheri is restricted to the west coast area of the Western Cape. It is known from two populations, one at Paternoster and the other at Saldanha (Figure 6.8.3). The plants grow in dense clusters on sandy calcareous soils that are overlying limestone, unlike all the other *Daubenya* species which grow on doleritic clay. Flowering time is from the end of May until the beginning of July and flowers are unscented. Nectar is often visible in the ring of the staminal collar.

Material studied

–3217 (Vredenburg): Paternoster, (-DD), *Barker* 9736 (NBG), *Steytler s.n.* (NBG); Cape Columbine Lighthouse (-DD), *Barker* 10179 (NBG); Paternoster, hillside behind hotel (-DD), *Barker* 10237 (NBG); Hopefield (-DD), *Barker* 10244 (NBG); Paternoster, sandy flats on limestone (-DD), *Manning* 2175 (NBG).



Figure 6.8.2 *Daubenya zeyheri* (Van der Merwe 181, STEU).

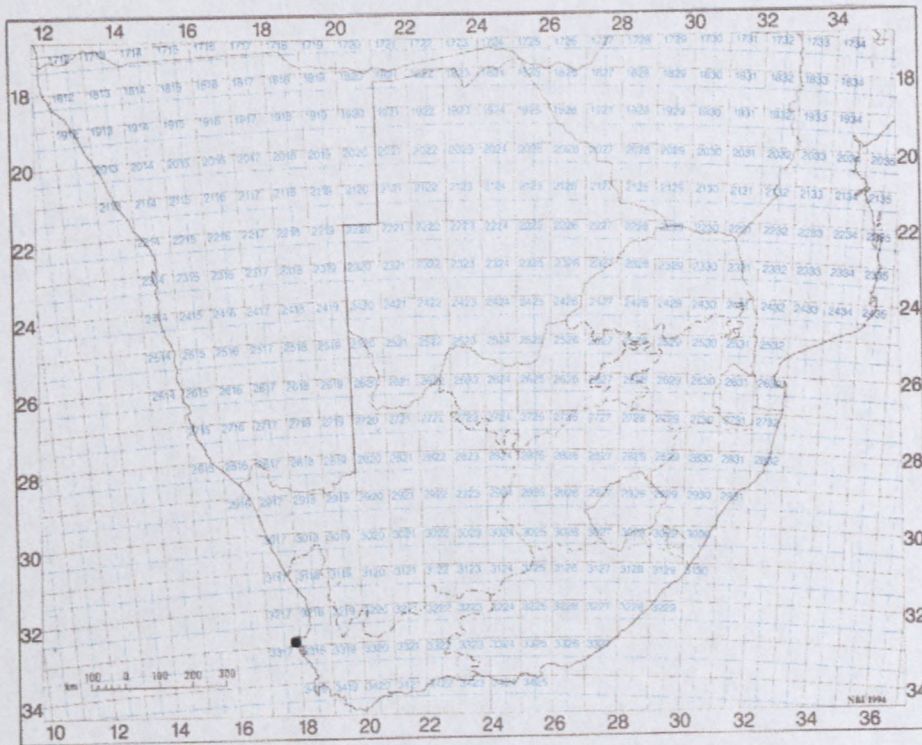


Figure 6.8.3. Geographical distribution of *Daubenya zeyheri*

CHAPTER 7

TAXONOMIC TREATMENT OF THE GENUS *MASSONIA* THUNB. EX HOUTT.

Massonia Thunb. ex Houtt. *Natuurlijke Historie*, 2 (12): 424 (1780); Linn.f.: 193 (1782); Kunth: 294 (1843); Baker: 408 (1897); Engler: 350 (1930); Merrill: 331 (1938); Obermeyer: t. 1451 (1965b); Merxmüller & Roessler: 83 (1973); Jessop: 406 (1976); Hilliard: 35 (1990); Müller-Doblies and Müller-Doblies: 66 (1997); Williams: 614 (2000); Goldblatt & Manning: 104 (2000). Type: *M. depressa* Houtt.

Massonia Thunb. ex Linn.f. subgenus *Massonia* Endl.: 145 (1836). Lectotype: *M. depressa* Houtt.

Neobakeria Schltr.: 150 (1924) p.p.; Müller-Doblies & Müller-Doblies: 68 (1997). Type: *N. heterandra* Isaac.

Bulb: ovoid, up to 45mm in length, scales tubular, fleshy; *outermost tunics* membranous, dark brown. *Leaves*: 2, prostrate, spreading, often tightly adpressed to the ground, varying greatly in shape from oblong or orbicular to elliptic, sometimes lanceolate, glabrous or ciliate, scabrous or pustulate, sometimes with fine hairs or bristles. *Inflorescence*: borne between leaves, nestled on leaf surface. *Peduncles*: solitary, carrying a condensed subcapitulate raceme; *bracts* large, surrounding inflorescence, green to red in colour, upper bracts much smaller. *Flowers*: white, cream, pale pink or green, actinomorphic, pedicellate; *perianth tube*, completely surrounding ovary, equal in length to ovary or longer; *perianth segments* more or less oblong, sometimes linear, usually with a sigmoid fold in the longitudinal axis towards the base, often minutely papillate at the apex. *Stamens*: 6, uniseriate or biseriate, attached at the mouth of the perianth tube; *filaments* free or shortly connate at the base; *anthers* dorsifixed, oblong to linear, straight or slightly arcuate. *Ovary*: sessile, oblong to ovoid; *ovules* 15–25. *Style*: sublinear, usually slightly longer than the stamens; *stigma* simple, subcapitate. *Capsule*: 3-winged, loculicidal, *seeds* many, black, globose.

Key to the species of *Massonia*

Flowers robust and fleshy, perianth tube cup-shaped, 6–10mm in diameter..... *M. depressa*

Flowers delicate and membranous, perianth tube narrow, up to 5mm in diameter

Outermost bracts hairy, coma of green bracts present in centre of inflorescence..... *M. hirsuta*

Outermost bracts glabrous, coma of green bracts absent from centre of inflorescence

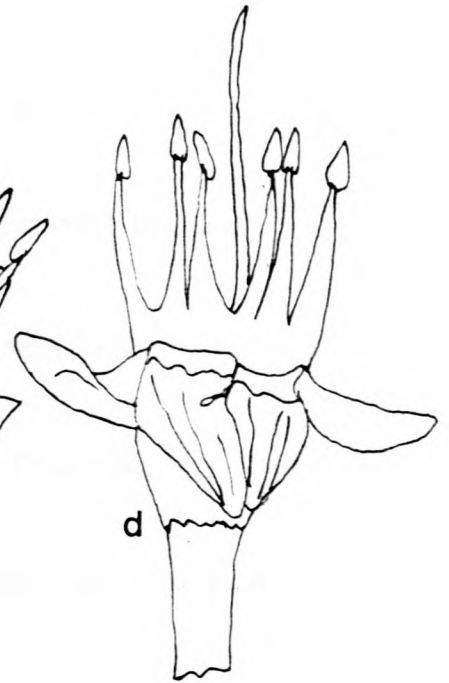
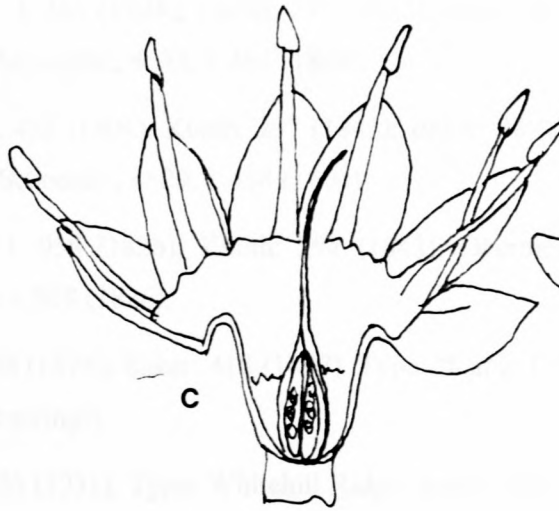
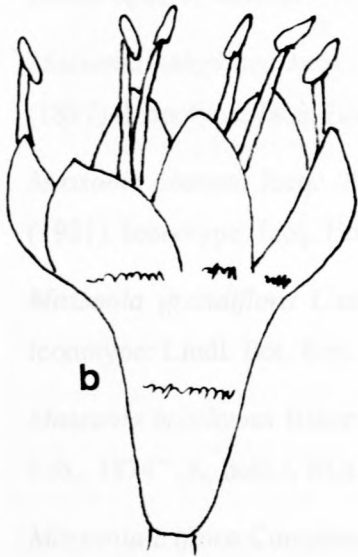
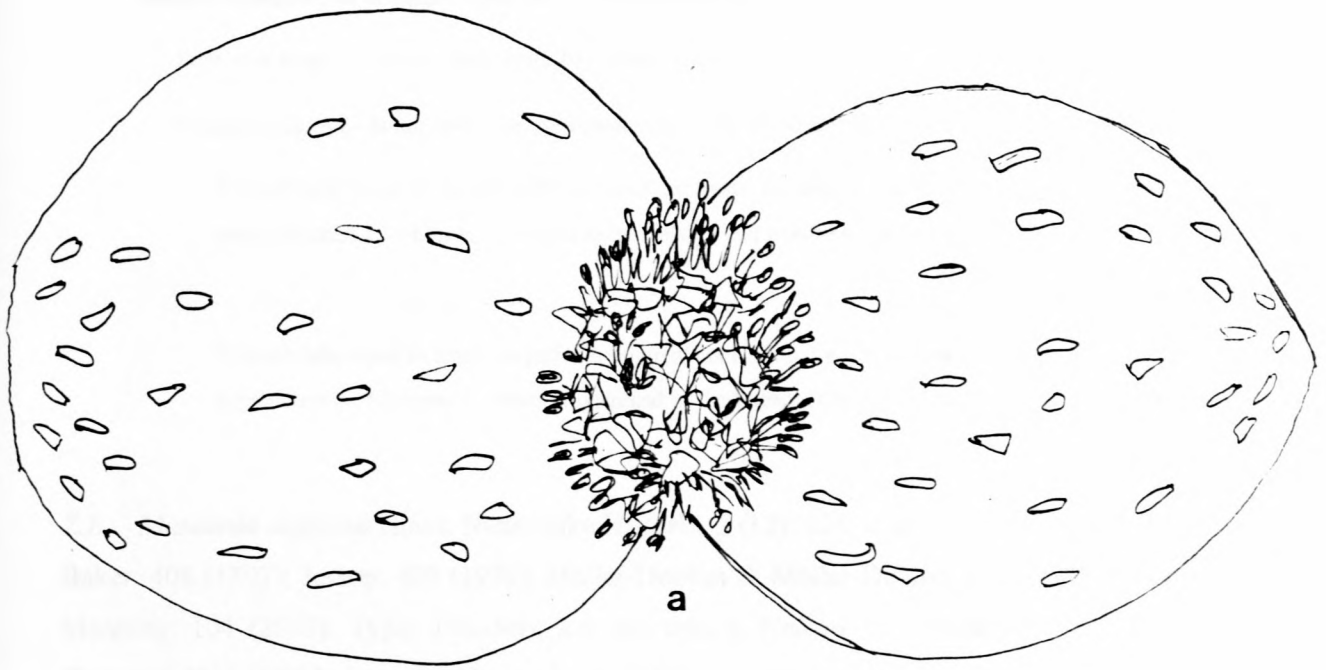


Figure 7.1.1 *Massonia depressa* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5; (d) flower with reflexed petals x 1.5.

Stamens biseriate, of 2 lengths; leaves glabrous or pustulate but then with long hairs..... *M. pygmaea*

Stamens uniseriate, all of equal length, leaves glabrous, echinate or pustulate, but seldom hairy

Filaments long, 17–24mm; style long, 10–30mm; leaves pustulate..... *M. pustulata*

Filaments short, 2–8mm; style short 5–10mm; leaves glabrous, echinate or minutely pustulate

Perianth tube twice the length of the perianth segments, perianth segments sometimes lacking sigmoid curve; filaments 2–4.5mm; restricted to the Eastern and Northern Cape Provinces & Lesotho

..... *M. jasminiflora*

Perianth tube equal in length to perianth segments or slightly longer; perianth segments with sigmoid curve; filaments 5–8mm; widespread in the Western Cape Province..... *M. echinata*

7.1. *Massonia depressa* Houtt. *Natuurlijke Historie*, 2 (12): 424, t. 85 (1780); Kunth: 294 (1843); Baker: 408 (1897); Jessop: 409 (1976); Müller-Doblies & Müller-Doblies: 67 (1997); Goldblatt & Manning: 104 (2000). Type: *Thunberg s.n.* not traced; Neotype - Whitehill Ridge, South side, *Compton 3515* (BOL), designated here. (Type of *Massonia triflora* Compton.)

Massonia latifolia L.f.: 193 (1782); Aiton: 3 (1789); Thunb.: 188 (1794); Jacq.: t. 455 (1804); Kunth: 297 (1843); Baker: 389 (1871); Baker: 418 (1897); Phillips: t. 46 (1922c). Type: “Cap. Bonae Spei, *F. Masson*”; not located.

Massonia sanguinea Jacq.: 31, t. 461 (1804); Kunth: 297 (1843); Baker: 389 (1871); Baker: 418 (1897). Iconotype: Jacq. Hort. Schoenbr., 4: 31, t. 461 (1804).

Massonia obovata Jacq.: 29, t. 458 (1804); Kunth: 297 (1843); Baker: 389 (1871); Compton: 276 (1931). Iconotype: Jacq. Hort. Schoenbr., 4: 29, t. 458 (1804).

Massonia grandiflora Lindl.: t. 958 (1826); Kunth: 294 (1843); Obermeyer: t. 1451 (1965b). Iconotype: Lindl. Bot. Reg. 12: t. 958 (1826).

Massonia brachypus Baker: 368 (1874); Baker: 418 (1897). Type: “Caput Bonae Spei, Hort. Kew., Feb., 1874” (K, holo.!, BOL, drawing!).

Massonia triflora Compton: 276 (1931). Type: Whitehill Ridge, south side, *Compton 3515* (BOL, holo.!).

Bulb: ovoid, up to 45mm long; *outer tunics* brown and membranous. *Leaves*: 2, varying greatly in shape and size, orbicular to oblong, acute or apiculate, prostrate, often adpressed to the ground, somewhat fleshy, glabrous, 50–250mm x 40–100mm, varying greatly in colour from light to dark



Figure 7.1.2 *Massonia depressa* (Van der Merwe 108, STEU).

green, sometimes with red or maroon markings. *Inflorescence*: abbreviated raceme, capitate, 20–30 flowers; *peduncle* very short, enclosed by leaves; *outer bracts* large, conspicuous, lanceolate to ovate, glabrous, fleshy, up to 60mm long and 40mm broad, green often reddish towards the base; *pedicels* 5–20mm long, ca. 4mm in diameter. *Flowers*: varying greatly in colour from white to cream or green or reddish brown, often with red or dark green or brown in the middle of the flower; *perianth tube* 5–10mm long and widening to 6–10mm at mouth of the tube; *perianth segments* oblong, slightly broader at the base, equal to the length of the tube, reflexed with a sigmoid curve in the tepals towards the base, or erect without the sigmoid curve, 5–10mm long. *Stamens*: 6, uniseriate, of equal length, inserted at the mouth of the tube, 10–18mm long, connate into a tube at the base for up to 2mm, cream, yellow, green or red; *anthers* 2–4mm long. *Ovary*: obovoid; *style* equal to or longer than the stamens, up to 20mm long, subterete; *stigma* simple. *Capsule*: obovoid, 3-winged, fleshy, green, loculicidal, 10–15mm long; *seeds* globose, black (Figure 7.1.1).

Diagnostic features and affinities

Massonia depressa (Figure 7.1.2) is characterised by its larger more fleshy flowers, with a wide cup-shaped perianth tube that is at least 6mm wide, and widening up to 10mm towards the mouth of the tube. The six stamens of equal length are basally connate for up to 2mm, forming a cup in which the nectar accumulates. The pedicels of *M. depressa* are also longer than in the other *Massonia* species, often measuring up to 20mm. DNA studies show that *M. depressa* is closely related to *M. echinata*, but *M. depressa* can easily be distinguished from *M. echinata* by its more robust, fleshy flowers with the cup-shaped perianth tube of 6–10mm in width, whereas the perianth tube of *M. echinata* is only 2–3mm in diameter.

Geographical distribution and ecology

Massonia depressa is widespread in the winter rainfall regions of the Western Cape and Namaqualand and also occurs in the Karoo (Figure 7.1.3). This species occurs in a wide range of habitats on both sandy flats and rocky slopes, either growing in the shade of other plants or in the open sun. Flowering occurs in July and August. The flowers usually have a yeasty scent and produce large amounts of nectar which accumulates in the cup formed by the short staminal tube. According to Johnson *et al.* (2001), *M. depressa* is pollinated by rodents which visit the plants at night to consume the nectar.

Material studied:

- 2817 (Vioolsdrif): 2 km W of Eksteenfontein (-DA), *Williamson 3902* (NBG).
- 2917 (Springbok): Kookfontein, Namaqualand minor (-BC), *Bolus 6596* (BOL); Namaqualand, Nigramoep (-DA), *Wikner s.n.* (SAM); 2 miles E of Springbok (-DB), *Lewis 2975* (SAM); 2 miles N of Concordia, Namaqualand (-DB), *Rourke 811* (NBG).
- 3017 (Hondeklipbaai): 3 miles E of Soebatsfontein, Namaqualand (-AB), *Hall 2901* (NBG); Grootvlei, a few miles W of Kamieskroon (-BB), *Rourke 797* (NBG).
- 3018 (Kamiesberg): Ezelsfontein, 14 miles W of Springbok (-AC), *Hall 3058* (NBG); Kamiesberg, 500m E of Leliefontein village (-AC), *Van Berkel 335* (NBG); Aalwynsfontein (-BC), *Herre s.n.* (BOL); 22 miles N of Garies (-CA), *Booyesen 14* (NBG).
- 3019 (Loeriesfontein): Hill above Graafwater (-CC), *Pamphlett 99* (NBG); 4 miles N of Loeriesfontein (-CD), *Hall 408/53* (NBG).
- 3024 (De Aar): Taaiboschpoort, Petrusville (-DA), *van der Walt s.n.* (BOL).
- 3026 (Aliwal North): Winnaarsbaken, rocky hill slopes, Burgersdorp division (-CC), *Thorne 51960* (SAM); Vlakplaats (-DB), *Bolus 13831* (BOL).
- 3118 (Vanhynsdorp): Vredendal road from Vanrhynsdorp (-CB), *Barker 5698* (NBG); Widouw river, 6 miles S of Vanrhynsdorp (-DA), *Barker 6347* (NBG); 16km E of Vredendal (-DA), *Hall 4010* (NBG); Vanrhynsdorp (-DA), *Smith 110/46* (NBG); 6 miles S of Widouw river (-DB), *Lewis 2976* (SAM); Between Vanrhynsdorp & Klawer (-DC), *Compton 20713* (NBG); Gifberg, Vanrhynsdorp (-DC), *Compton 20840* (NBG).
- 3119 (Calvinia): Nieuwoudtville, Calvinia div. (-AC), *Leipoldt 189/46* (NBG); Foot of Hantam mts, between Hantams peak & Akkerdam (-BC), *Lewis 2973* (SAM); 5 miles SW of Calvinia (-BD), *Stokoe s.n.* (SAM); Top of Botterkloof Pass, Calvinia district (-CD), *Lewis 2979* (SAM).
- 3120 (Williston): Near Matjiesfontein (-CB), *Compton 3972* (NBG).
- 3123 (Victoria West): Murraysburg (-DD), *Tyson s.n.* (SAM).
- 3217 (Vredenburg): Hopefield, Stompneus (-DB), *Hall s.n.* (NBG); *Rourke 781* (NBG).

- 3218 (Clanwilliam): 5 miles W of Clanwilliam on Lamberts Bay road (-AB), *Lewis* 2978 (SAM); Clanwilliam (-BB), *Leipoldt* 270 (SAM); 8 miles N of Clanwilliam (-BB), *Lewis* 2977 (SAM).
- 3219 (Wuppertal): Pakhuisberg (-AA), *Schlechter* 10808 (BOL); North Cedarberg, in shelter of overhanging rock (-AC), *Esterhuysen* 12199 (NBG); Near waterfalls between Citrusdal & Elandskloof (-CA), *Stokoe* 7421 (BOL).
- 3220 (Sutherland): Voëlfontein farm (-BC), *Hall* 207 (NBG); Sutherland (-BC), *Stayner* s.n. (NBG).
- 3319 (Worcester): Karoopoort, Ceres (-AD), *Barker* 3055 (NBG); Hex River Valley (-BD), *Davidson* s.n. (SAM); Langerug pavements (-CB), *Bolus* 13213 (BOL); In Convalle, Hex River (-CD), *Walters* 2086 (NBG); Over Hex (-DA), *Barker* 5380 (NBG); 10 miles from Worcester on the Robertson road (-DD), *Barker* 8259 (NBG).
- 3320 (Montagu): Whitehill (-BA), *Archer* 58 (BOL); Whitehill ridge, southside (-BA), *Compton* 3515 (BOL, NBG); Near the baths, Montagu (-CC), *Page* s.n. (BOL); Near Barrydale off road from Warmwaterberg (-DC), *Van Niekerk* 571 (BOL).
- 3321 (Ladismith): Hills N of Huisriver Pass, near Bergplaas (-CB), *Wurts* 1632 (NBG).
- 3322 (Oudtshoorn): De Rust (-BC), *Marais* 543/60 (NBG); Meiringspoort (-BC), *Stoekoe* s.n. (SAM).
- 3418 (Simonstown): Steenberg Cove (-AB), *Barker* 9720 (NBG).
- 3419 (Caledon): River Zonder Einde (-AB), *Pappe* s.n. (SAM); Caledon (-AB), *Zeyher* s.n. (SAM).
- 3421 (Riversdale): Riversdale (-AB), *Ferguson* s.n. (BOL).

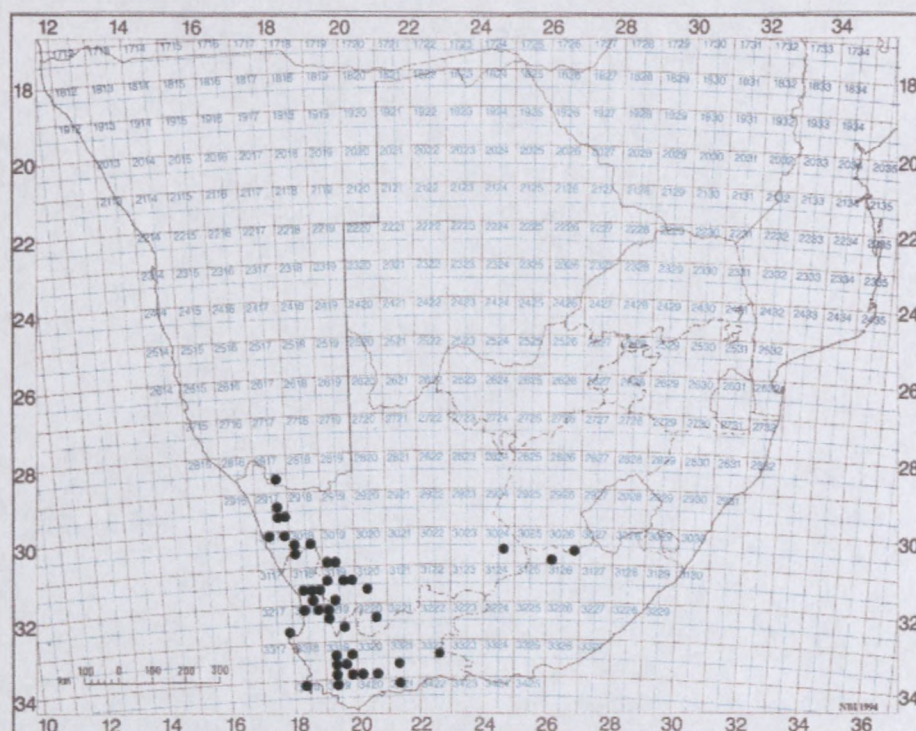


Figure 7.1.3 Geographical distribution of *Massonia depressa*

7.2. *Massonia echinata* L.f. Supplementum Plantarum ed 8: 193 (1782); Thunb.: 188 (1794); Kunth: 294 (1843); Baker: 389 (1871); Baker: 414 (1897). TYPE: "Cap. bonae. spei, Thunberg" (UPS-7988, holo., microfiche!).

Massonia scabra Thunb.: 188 (1800). Type: Cape, without further locality, Thunberg s.n. (UPS-7992, holo., microfiche).

Massonia muricata Ker-Gawl.: t. 559 (1802b). Iconotype: Ker-Gawl. 16: t. 559 (1802b).

Massonia longifolia Jacq. var. *candida* Burch. ex Ker-Gawl.: 694 (1823). Type: "Raised at Mr. Colvill's nursery from a plant that had been raised two years before from seed from Mr. Burchell"; "Little Brak River, Mossel Bay Div," Burchell 5746 (K, holo.!).

Massonia huttonii Baker: 389 (1871). Type: "Cap. b. spei", Masson s.n. (BM, lecto., BOL, drawing!); Drège 3509 (K!, BOL, drawing!).

Massonia setulosa Baker: 389 (1871). Type: "Cap. b. spei", Ecklon & Zeyher s.n. (TCD, holo.).

Massonia tenella Soland. ex Baker: 389 (1871); Baker: 420 (1897). Type: Witte Bergen. Aliwal North division, Drège 3509 (K, holo.!).

Massonia versicolor Baker: 184 (1876). Type: C.B.S. in argillaceis apricis fluminis Klyn Visch rivier, alt. 2500 pedes", MacOwan 2178 (K, holo.!).

Massonia calvata Baker: 321 (1878). Type: Cape colony, eastern district, Bolus 749 (K, holo.!).

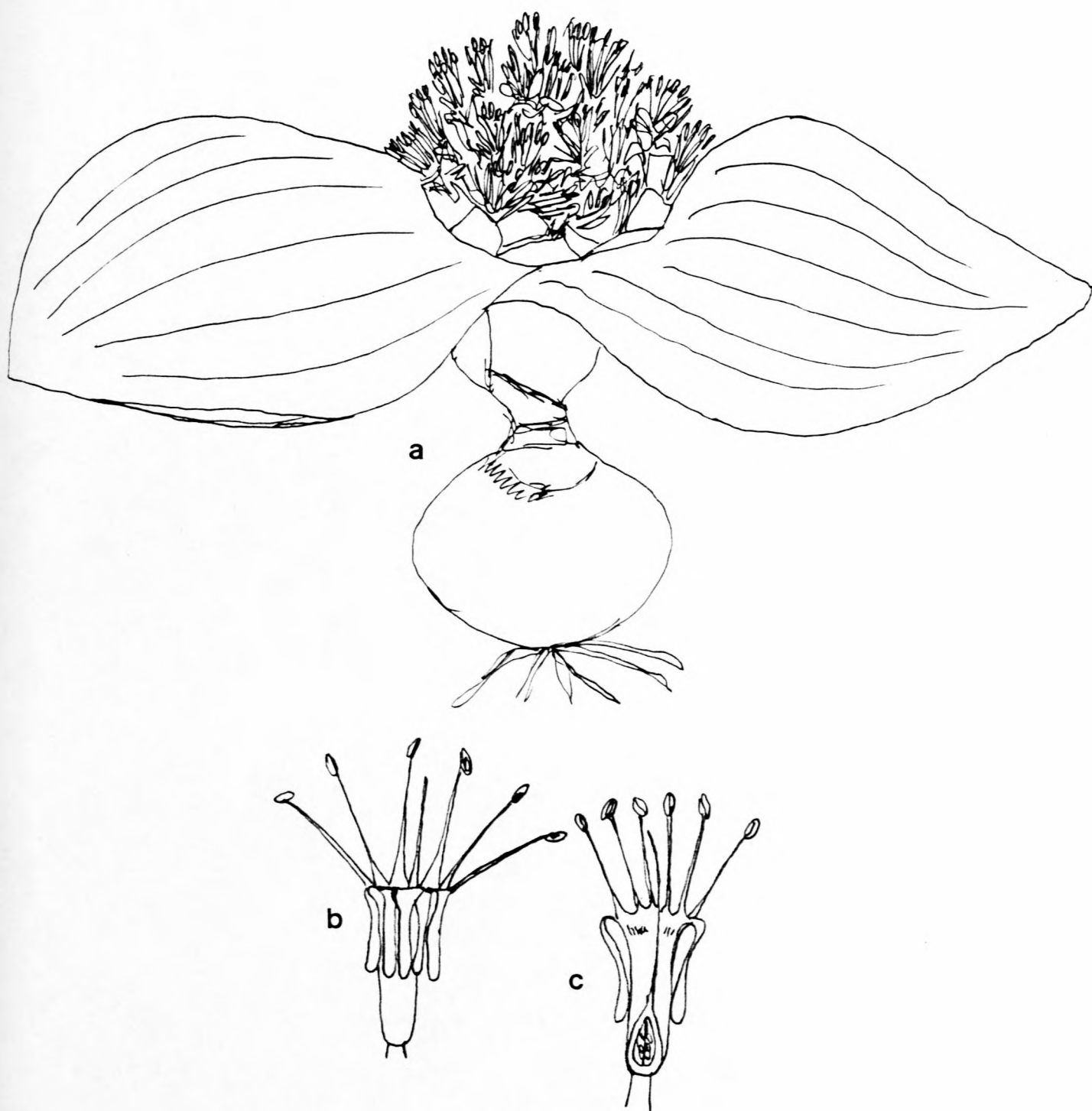


Figure 7.2.1 *Massonia echinata* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

Massonia latebrosa Masson ex Baker: 336 (1886). Type: "Bokveld, Aug 1792", *Masson s.n.* (BM, drawing, holo., BOL, copy!).

Massonia amygdalina Baker: 715 (1889). Type: plant cultivated by Sir C.W. Strickland (K, holo.!, BOL, drawing!).

Massonia parvifolia Baker: 8 (1892). Type: "Cap. B. spei", *Ecklon & Zeyher Asphod.* 25 (B, holo.).

Massonia dregei Baker: 412 (1897). Type: "Clanwilliam Div., Lange Vallei", *Drège* 2688 (K, holo.!, BOL, drawing!; G: HAL; L).

Massonia cocinna Baker: 414 (1897). Type: "Stockenstrom Div.; stony ground above the waterfall, Elands River", *Scully* 54 (K, holo., BOL, drawing!; SAM!)

Massonia candida Burch. ex Baker: 415 (1897). Type: Little Brak River, *Burchell* 6197/5 (K, holo.!).

Massonia modesta Fourc.: 79 (1934). Type: "Div. Humansdorp: Karreedouw", *Jeppe s.n.* sub *Fourcade* 4592 (BOL-FOURCADE, holo.!).

Neobakeria visserae Barnes: 72 (1933). Type: Lamberts Bay, *Visser s.n.* sub *BOL* 19616 (BOL, holo.!).

Massonia angustifolia L.f.: 193 (1782); *Polyxena angustifolia* (L.f.) Baker: 419 (1897); *Neobakeria angustifolia* (L.f.) Schltr.: 150 (1924). Type: "Cap. spei", *Thunberg s.n.* (UPS, microfiche).

Illegitimate name: *Massonia scabra* Andr.: t. 220 (1802); non Thunb. (1800). Iconotype: Plant introduced to Britain, in the year 1796, by Messrs. Lee and Kennedy, Andr. Bot. Rep. 4: t. 220 (1802).

Bulb: ovoid, 10–40mm long; *outermost tunics* brown and membranous. *Leaves*: 2, ovate to oblong, acute or obtuse, usually adpressed to the ground, coriaceous, echinate, sometimes minutely pustulate, often with conspicuous longitudinal grooves, sometimes with ciliate margins, 50–200mm x 30–150mm, green, often with red or purple flecks or patches, leaf bases enfolding peduncle for 25–50mm long. *Inflorescence*: capitate, with 5–25 flowers; *lower bracts* conspicuous, ovate to obovate, 10–30mm x 5–10mm, green, sometimes marked with red or purple; *pedicels* 4–12mm long. *Flowers*: white, sometimes tinged with pale pink; *perianth tube* 4–16mm long, 2–3mm in diameter, often pink in colour in older flowers; *perianth segments* oblong to narrowly lanceolate, reflexed with a sigmoid curve in the longitudinal axis towards the base, 4–9mm x 0.75–1.5mm. *Stamens*: 6, uniseriate, of equal length, sublinear or narrowly conical, slightly broader at the base, free or shortly connate, 5–8mm long; *anthers* purple, ca. 1.25mm long. *Ovary*: obovoid, tri-locular;



Figure 7.2.2 *Massonia echinata* (Van der Merwe 145, STEU).

style 5–10mm long; stigma simple. Capsule: tri-winged, narrowly obovoid, 15–40mm long; seeds globose, black. (Figure 7.2.1)

Diagnostic features and affinities

Massonia echinata (Figure 7.2.2) is characterised by white or pink tinged flowers with narrow perianth tubes (2–3mm) and short filaments (5–8mm long). The filaments are all of equal length and subequal in length to the style (5–10mm long). Leaves are coriaceous or sometimes minutely pustulate. *M. echinata* is similar in appearance to *M. pustulata*, but the filaments of *M. pustulata* are much longer (17–24mm) and the leaves are dark green or purple with uniform pustules without trichomes. DNA studies show that *M. echinata* is closely related to *M. depressa*, but the two species can easily be distinguished from each other as the flowers of *M. depressa* are more robust and fleshy and the perianth tube is cup-shaped and much wider (6–10mm) than that of *M. echinata* (2–3mm).

Geographical distribution and habitat ecology

Massonia echinata is widespread in the Western, Northern and Eastern Cape Provinces from Calvinia in the north to Riversdale in the south and as far east as Middelburg in the Eastern Cape (Figure 7.2.3). *M. echinata* occurs in open, sandy areas, clay soils or rock crevices, mostly in the full sun. Flowering time is from May to July and flowers are sweetly scented.

Material studied

- 3119 (Calvinia): Summit of Vanrhyns Pass, in shallow rock pans (-AC), *Hall* 3583 (NBG); *Barker* 9440 (NBG); Grasberg, Nieuwoudtville (-AC), *Martin* 1557/37 (NBG); Montagu via Ouberg, Rooihoogte Pass, Touws river road (-BC), *Thomas s.n.* (NBG).
- 3125 (Steynsburg): Bangor farm, Middelburg div. (-AC), *Bolus* 19615 (BOL).
- 3218 (Clanwilliam): 5 miles from Lamberts Bay, on a klip koppie (-AB), *Broom* 19616 (BOL); Lamberts Bay, Clanwilliam (AB), *Hall s.n.* (NBG).
- 3219 (Wuppertal): Voëlfontein farm, 40 miles NW of Sutherland (-CB), *Hall* 225 (NBG).
- 3319 (Worcester): Ertjieskloof, Ceres (-AD), *Barker* 3062 (NBG); Hill near Brandvlei (-CB), *Barker* 10701 (NBG).
- 3323 (Willowmore): Rocky hill N of Joubertinia (-DD), *Fourcade* 2684 (BOL).

- 3421 (Riversdale): Oude Huis, near Albertinia (-BA), *Muir* 918 (SAM); Bothas farm (-BA), without collector, *NBG* 210/67 (NBG); Farm Tierfontein, near to Platvlei, N of Albertinia (-BA), *Snijman* 790 (NBG).
- 3424 (Humansdorp): Humansdorp, Karreedouw (-AA), *Fourcade* 4592 (BOL); Elandsriver, among stones (-AA), *Scully* 54 (SAM).

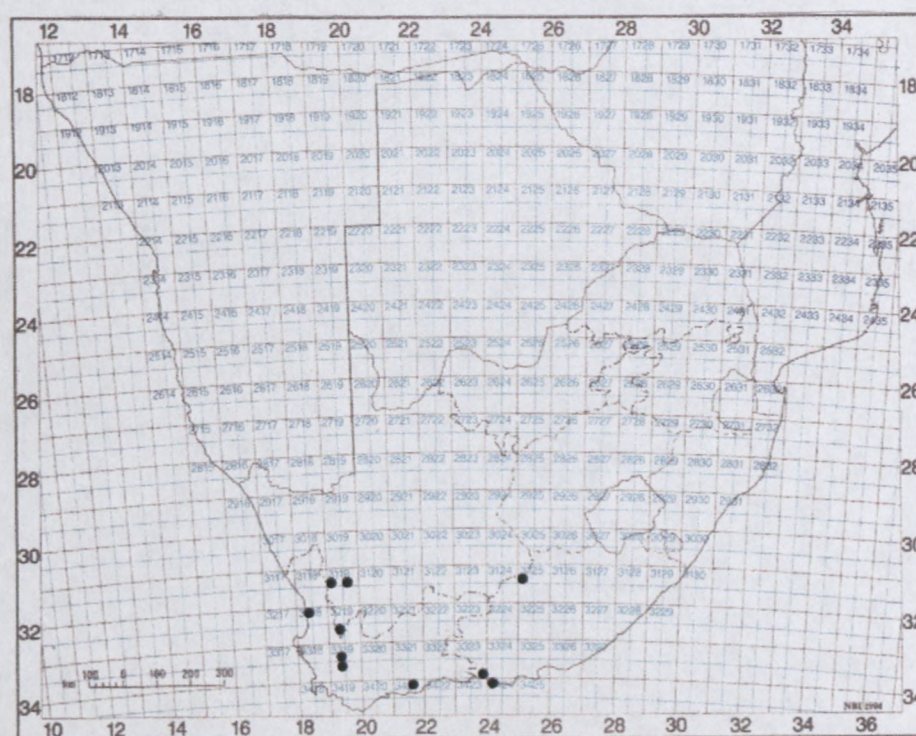


Figure 7.2.3 Geographical distribution of *Massonia echinata*

7.3. *Massonia hirsuta* Link & Otto in *Icones Plantarum Rariorum* 1: t. 1 (1828); Müller-Doblies & Müller-Doblies: 72 (1997). Iconotype: *Icones Pl. Rar.* t.1 (1828).

Massonia orientalis Baker: 321 (1878); Müller-Doblies & Müller-Doblies: 72 (1997). Type: Cape – 3325 (Port Elizabeth): Sand dunes at Port Elizabeth (-DC), *Bolus* 2239 (BOL, holo.!).

Massonia bolusiae Barker: t. 429 (1931b); Müller-Doblies & Müller-Doblies: 72 (1997). Type: Cape – 3125 (Steynsburg): Farm Bangor near Middelburg (-AC), *Bolus s.n. sub BOL* 19615 (BOL, holo.).

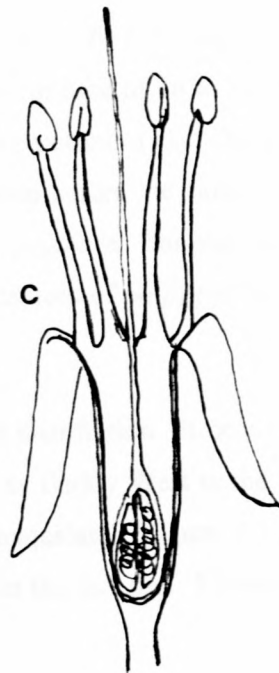
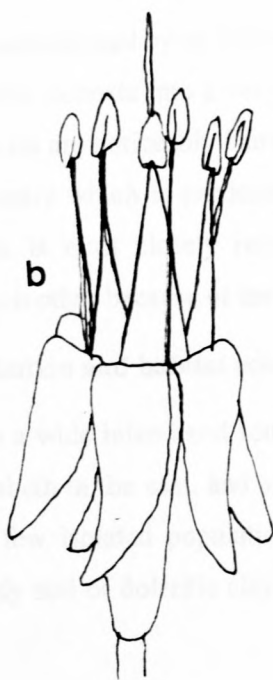
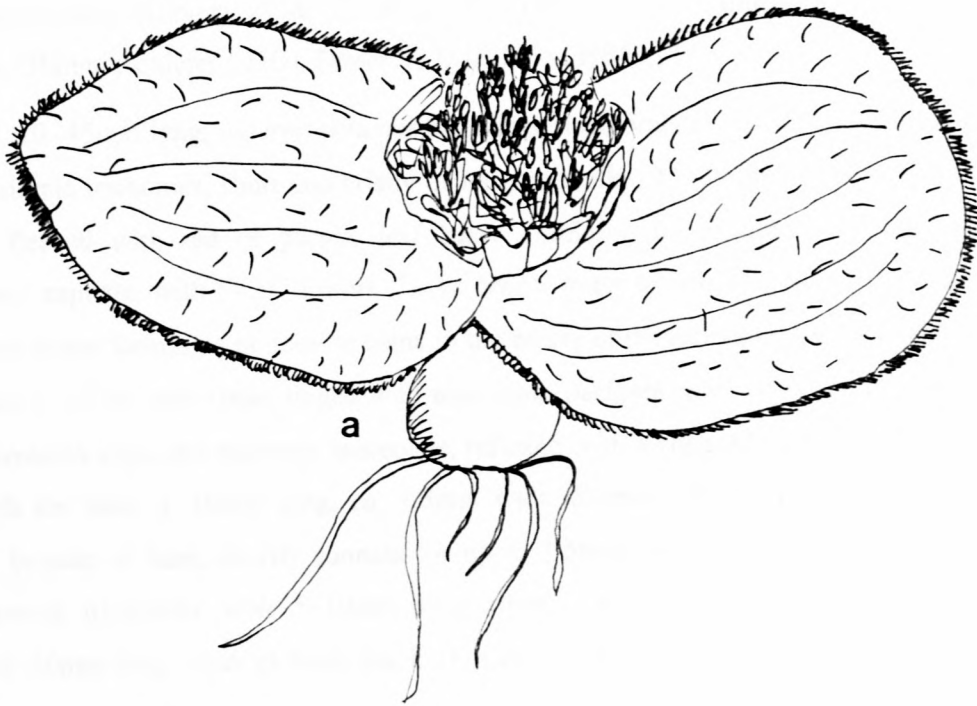


Figure 7.3.1 *Massonia hirsuta* (a) flowering plant x 1; (b) flower x 2; (c) longitudinal section of flower x 2.

Massonia inexpectata Von Poelln.: 384 (1945); Müller-Doblies & Müller-Doblies: 72 (1997). Type: Cape- 3325 (Port Elizabeth): Zwartkopsrivier, villa Paul Maré to Uitenhage (-CD), Ecklon & Zeyher 2.11. (WRS� holo., BTU photo).

Massonia sessiliflora (Dinter) U. & D. M-D.: 70 (1997). Type: Namibia -2715 (Bogenfels): Buchuberge, Glimmerschiefer (-DD), Dinter 6471 (B holo., HBG, M).

Bulb: ovoid, 10–45mm long; *outermost tunics* brown and membranous. *Leaves* 2, ovate to oblong, covered in simple trichomes, short and bristly or long and silky, 45–190mm x 25–150mm, green, sometimes flecked with red or purple, leaf bases enfolding the peduncle for up to 50mm. *Inflorescence*: capitate, with 5–25 flowers; *lower bracts* ovate to obovate, hairy, 10–40mm x 5–10mm, green bracts forming a noticeable coma in the centre of the inflorescence; *pedicels* 5–15mm long. *Flowers*: white, sometimes tinged with pale pink; *perianth tube* 4–16mm long, 2–3mm in diameter; *perianth segments* narrowly lanceolate, reflexed with a sigmoid curve in the longitudinal axis towards the base, 4–10mm long, ca. 1.5mm wide. *Stamens*: 6, uniseriate, of equal length, acuminate, broader at base, shortly connate for up to 1.5mm; *anthers* purple, ca. 1.25mm long. *Ovary*: obovoid, tri-locular; *style* 5–10mm long; *stigma* simple. *Capsule*: tri-winged, narrowly obovoid, 15–40mm long; *seeds* globose, black. (Figure 7.3.1)

Diagnostic features and affinities

Massonia hirsuta is characterised by an inflorescence of white flowers with stamens of equal length that have stout filaments connate into a very short filament tube of up to 1.5mm long. The bracts and leaves of this species are noticeably hairy. The inflorescence is also characterised by a coma of green bracts in the centre which is particularly noticeable before the flowers open. DNA studies show that *M. hirsuta* is most closely related to *M. pygmaea*, but the two species are easily distinguished from each other because of the biseriate stamens of *M. pygmaea*.

Geographical distribution and habitat ecology

Massonia hirsuta has a wide inland and southern coast distribution. It occurs from Mossel Bay in the west to Port Elizabeth in the east, and as far north as Barkly West in the Kimberley area. It is also known from a few isolated populations in Namaqualand (Figure 7.3.2). *Massonia hirsuta* occurs mostly in sandy soil or doleritic clay, growing in the full sun. Flowering time is from May to July.

Material studied

- 2824 (Kimberley): South of Barkley West, Platfontein farm (-DA) *Anderson s.n.* (STEU).
- 2917 (Springbok): Little Namaqualand (-DA), *Zeyher 1717* (SAM).
- 3224 (Graaf Reinet): Along the road between Nieuw Bethesda & Graaf Reinet (-BC), *McMaster s.n.* (STEU).
- 3324 (Steytlerville): Assegaaibosch (-CD), *Rogers 30900* (BOL); Assegaaibosch, W of Hotel (-CD), *Fourcade 5369* (BOL).
- 3325 (Port Elizabeth): Kommadagga, Somerset East (-BB), *Bayliss s.n.* (NBG); Swartkops river (-DB), *Ecklon & Zeyher 130* (SAM); Port Elizabeth (-DC), *West 309* (BOL); *Drège 43* (BOL); Redhouse near P.E. (-DC), *Paterson 1115* (BOL).
- 3422 (Mossel Bay): Hills E of Great Brak river (-AA), *Fourcade 3949* (BOL); Mossel Bay (-AA), *Lewis 1094/37* (NBG).
- 3424 (Humansdorp): Duineveld, Jeffreys Bay (-BB), *Fourcade 3294* (BOL).

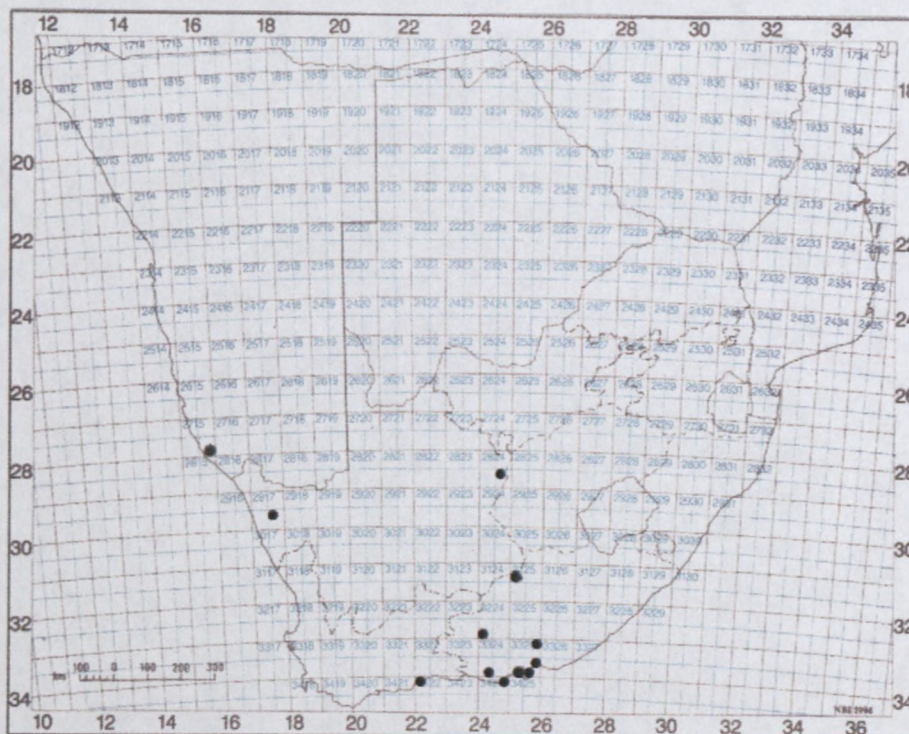


Figure 7.3.2 Geographical distribution of *Massonia hirsuta*

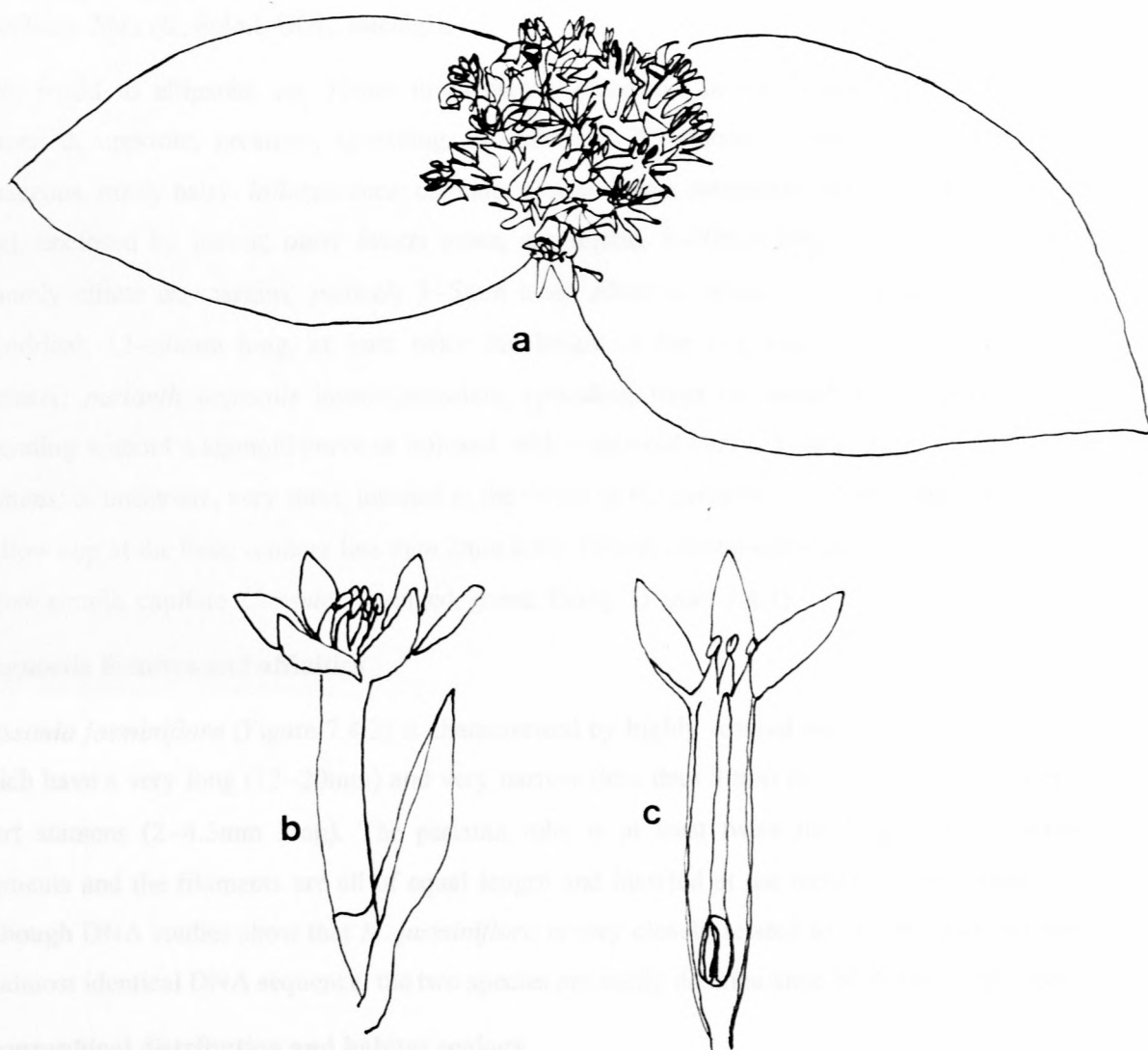


Figure 7.4.1 *Massonia jasminiflora* (a) flowering plant x 1; (b) flower x 2; (c) longitudinal section of flower x 2.

7.4. *Massonia jasminiflora* Burch. ex Baker in Journal of the Linnaean Society Botany 11:390 (1871); Baker: 420 (1897); Phillips: t. 367 (1930); Jessop: 423 (1976); Müller-Doblies & Müller-Doblies: 68 (1997). TYPE: Cape – 2723 (Kuruman): Pellat Plains, at Jabiru Fontein near Takun (-BB), *Burchell Bulb* no. 7 (K, holo!).

Massonia bowkeri Baker: 390 (1871). Type: “Orange Free State”, *Barber s.n.* (TCD, holo.).

Massonia greenii Baker: 413 (1897). Type: “Griqualand West, stony places near Kimberley”, *MacOwan* 2842 (K, holo., BOL, tracing!).

Bulb: ovoid to ellipsoid, *ca.* 15mm in diameter; *outermost tunics* brown, firm, membranous. *Leaves*: 2, opposite, prostrate, spreading, 30–60mm x 20–45mm, broadly oblong, glabrous or coriaceous, rarely hairy. *Inflorescence*: capitate, globose head, surrounded by bracts; *peduncle* very short, enclosed by leaves; *outer bracts* ovate, acuminate, 8–30mm long, 6–20mm wide, rarely minutely ciliate on margins; *pedicels* 3–5mm long. *Flowers*: white or pale pink; *perianth tube* cylindrical, 12–20mm long, at least twice the length of the free segments, less than 3mm in diameter; *perianth segments* linear-lanceolate, spreading from the mouth of the perianth tube, ascending without a sigmoid curve or reflexed with a sigmoid curve, 5–8mm long, *ca.* 2mm wide. *Stamens*: 6, uniseriate, very short, inserted at the throat of the perianth, 2–4.5mm long, united into a shallow cup at the base; *anthers* less than 2mm long. *Ovary*: oblong-obovoid; *style* 12–15mm long; *stigma* simple, capitate. *Capsule*: 3-winged, green, fleshy. (Figure 7.4.1)

Diagnostic features and affinities

Massonia jasminiflora (Figure 7.4.2) is characterised by highly scented white to pale pink flowers which have a very long (12–20mm) and very narrow (less than 3mm) perianth tube and extremely short stamens (2–4.5mm long). The perianth tube is at least twice the length of the perianth segments and the filaments are all of equal length and inserted at the mouth of the perianth tube. Although DNA studies show that *M. jasminiflora* is very closely related to *M. depressa* and shares an almost identical DNA sequence, the two species are easily distinguished by floral morphology.

Geographical distribution and habitat ecology

M. jasminiflora occurs in the summer rainfall area of the Eastern Cape, the Free State and Lesotho, extending to the west near Kimberley in the Northern Cape (Figure 7.4.3). *M. jasminiflora* occurs mostly in open grassveld, or sometimes in limestone gravel or calcrete. Flowering time is from May to June and flowers are highly scented.

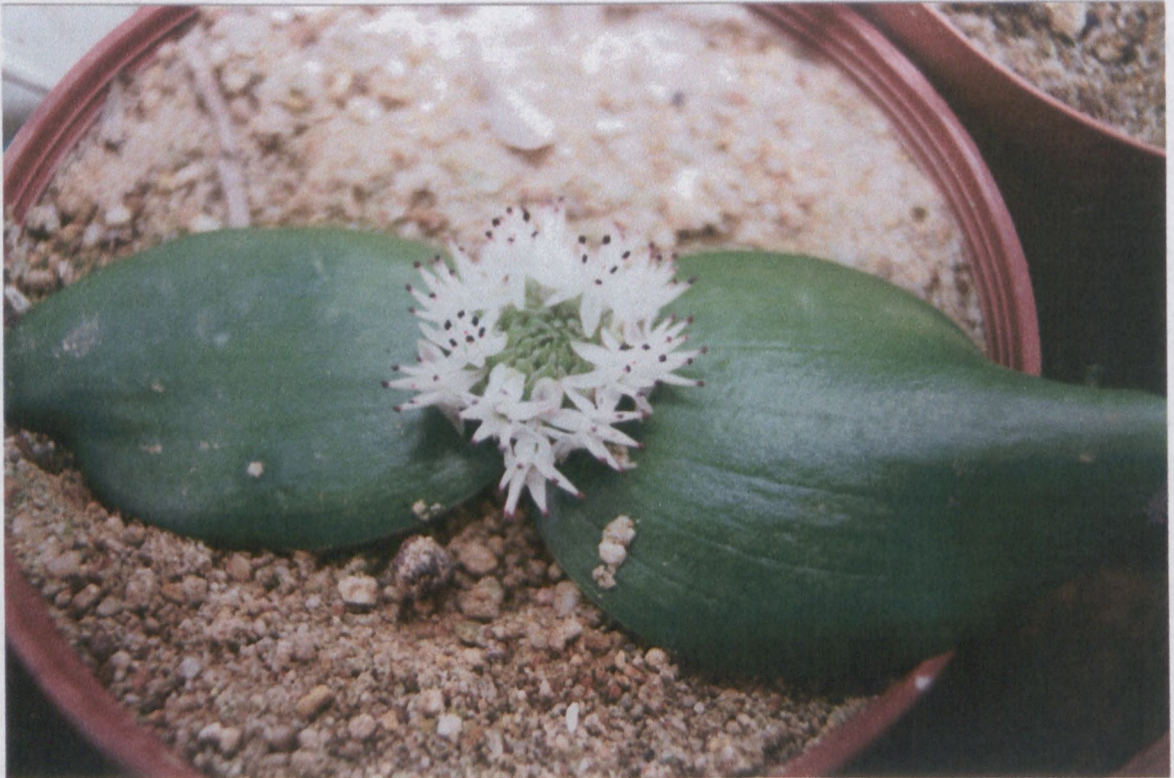


Figure 7.4.2 *Massonia jasminiflora* (Van der Merwe 179, STEU).

Material studied

- 2824 (Kimberley): Kimberley, in patches in veld (-DB), *Fogarty* 2157/14 (BOL).
- 2827 (Senekal): Willem Pretorius Game Reserve, Allemanskraal (-AC), *Feinauer* 324/64 (BOL);
Winburg (-CA), *Radloff* 17733 (BOL); Marquard (-CB), *Joubert* 1190/30 (BOL).
- 2828 (Bethlehem): Leribe (-CC), *Dieterlen* 724 (SAM).
- 2927 (Maseru): Maseru (-AD), *Griffith* 1730 (SAM).
- 3026 (Aliwal North): Dordrecht, Tafelberg (-BA), *Bayliss* 2237 (NBG); Elandshoek near Aliwal
North (-DA), *Bolus* 85 (BOL); Aliwal North (-DA), *Oliver s.n.* (NBG).
- 3027 (Lady Grey): Lady Grey (-CA), *Matthaer s.n.* (NBG).
- 3126 (Queenstown): Bowkers kop (-DD), *Galpin* 1817 (BOL).
- 3226 (Fort Beaufort): Amatola mountain range, E. Cape (-DB), *McMaster s.n.* (STEU).
- 3227 (Stutterheim): Hogsback, Stockenstroom (-CA), *King* 146/56 (NBG).

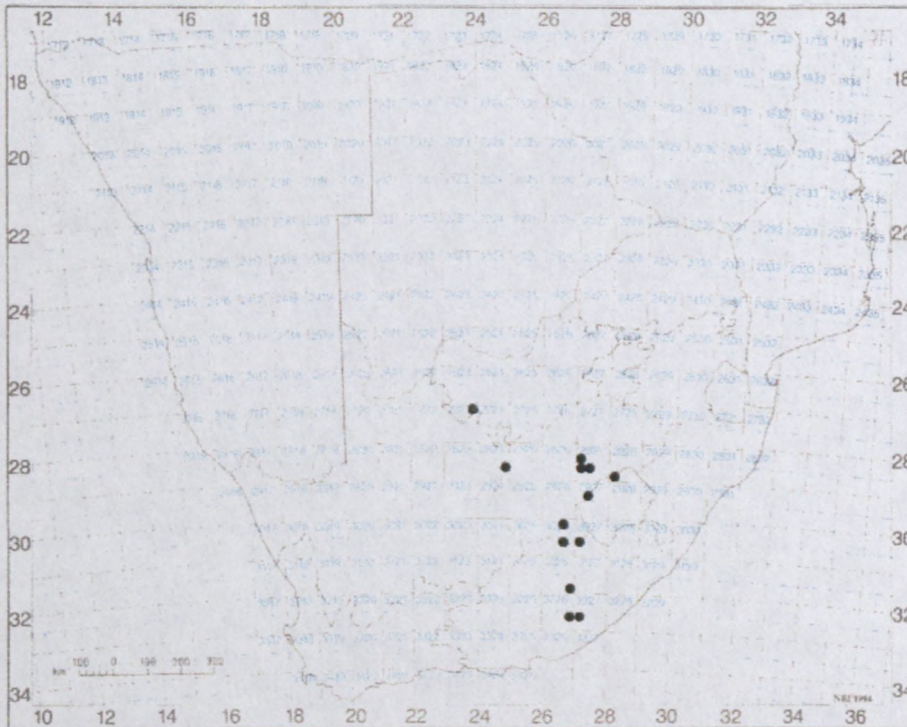


Figure 7.4.3 Geographical distribution of *Massonia jasminiflora*

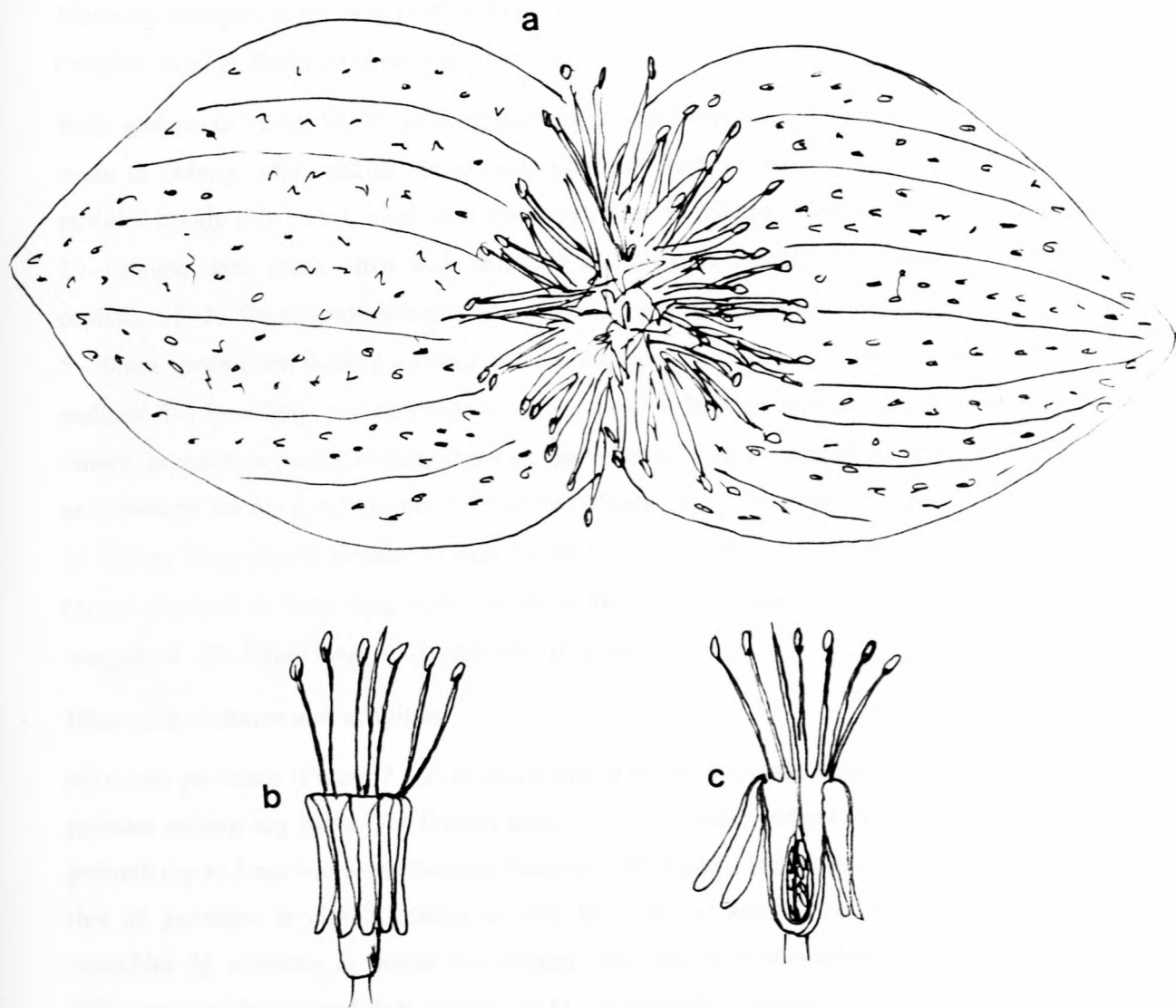


Figure 7.5.1 *Massonia pustulata* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

7.5. *Massonia pustulata* Jacq. *Collectanea* 4: 177 (1791); Jacq.: t. 454 (1804); Kunth: 294 (1843); Baker: 389 (1871); Baker: 5 (1874); Baker: 420 (1897); Leighton: t. 915 (1943); Jessop: 417 (1976); Müller-Doblies & Müller-Doblies: 68 (1997); Goldblatt & Manning: 104 (2000). Iconotype: Cape, without locality. Jacq. Hort. Schoenbr., 4: t. 454 (1804).

Massonia schlechtendalii Baker: 389 (1871); Baker: 5 (1874). Type: Cap. b. Spei, *Schlechtendal s.n.* (G-DC, holo.)

Massonia longipes Baker: 420 (1897). Type: Cape -3419CB (Caledon). From near Danger Point, Caledon division, *Bolus* 5973 (K, holo.).

Bulb: globose to ovoid, 10–35mm long; *outermost tunics* firm, brown and membranous. *Leaves*: 2, ovate to oblong, adpressed to the ground, subfleshy with conspicuously depressed veins, with pustules evenly distributed, often with minutely ciliate to minutely dentate margins, 30–150mm x 20–120mm, dark green often with dark red markings or completely maroon. *Inflorescence*: capitate, 15–25 flowers, lower bracts conspicuous, ovate to obovate, acute, glabrous, 15–40mm x 5–20mm, green often marked with red towards the margins and base. *Flowers*: white to pale pink, pedicels 5–15mm long, *perianth tube* 6–14mm long, 3–5mm in diameter widening slightly at the mouth, *perianth segments* oblong, more or less reflexed with a sigmoid curve in the longitudinal axis towards the base, 4.5–14mm x 1.5x3mm. *Stamens*: 6, uniseriate, of equal length, filaments 17–24mm long, shortly connate at base for up to 1mm; *anthers* yellow or reddish, 1–2mm long. *Ovary*: obovoid, 5–8mm long; *style* 10–30mm long; *stigma* minute, simple. *Capsule*: obovoid, 3-winged, ca. 30–35mm long, 12–20mm wide (Figure 7.5.1).

Diagnostic features and affinities

Massonia pustulata (Figure 7.5.2) is characterised by its pustulate leaves with evenly distributed pustules without any hairs. The flowers are white to pale pink, and are characterised by the narrow perianth (up to 5mm wide) and the long filaments (all of equal length) and style. DNA studies show that *M. pustulata* is closely related to both *M. depressa* and *M. echinata*. *M. pustulata* also resembles *M. echinata* in flower morphology, but can be distinguished from it because of the differences in filament and style lengths. In *M. pustulata* the filaments are 17–24mm long, whereas in *M. echinata* they are only 5–8mm in length. The style in *M. pustulata* is also much longer (10–30mm) than that of *M. echinata* (5–10mm).



Figure 7.5.2 *Massonia pustulata* (Van der Merwe 101, STEU).

Geographical distribution and habitat ecology

M. pustulata is quite widespread in the Western Cape Province occurring from Calvinia in the north to Bredasdorp in the south and as far as Port Elizabeth in the east (Figure 7.5.3). It usually grows in the open in coastal sand, in dry inland areas and sometimes on clay. Flowering time is from June to September and flowers are sweetly scented.

Material studied

- 3119 (Calvinia): Near Grasberg, Nieuwoudtville (-AC), *Barker 9370* (NBG); summit of Hantamsberg (-BC), *Viviers s.n.* (NBG).
- 3218 (Clanwilliam): Elands Bay on hill near school, Piketberg (-AD), *Barker 10435* (NBG); Pakhuispeak (-BB), *Thorne s.n.* (SAM).
- 3219 (Wuppertal): Cedarberg, Middelberg (-AC), *Kerfoot 5932* (NBG).
- 3319 (Worcester): Ceres, top of Theronsberg Pass (-AD), *Levyns 150* (BOL); Karooport (-BC), *Barker 3066* (NBG); Orchard (-BC), *Esterhuysen 10349* (BOL); Kaaimansgat, Worcester (-BD), *Hall 2791* (NBG).
- 3320 (Montagu): Mountainview, Karoo National Park (-BA), *Bruyns 3358* (BOL); Montagu baths (-BA), *Page 16781* (BOL).
- 3322 (Oudtshoorn): Flat rock, Wilderness (-DC), *Bayliss 2954* (NBG).
- 3419 (Caledon): Caledon district (-AB), *Lamb 1758* (SAM); Hermanus (-AC), *Werner 389/48* (NBG); De Kelders hotel, Gansbaai (-CB), *Lawder s.n.* (NBG); Hagelkraal, between Dangerpoint and Quoin point (-DA), *Lewis 2974* (SAM); Quoin point, Bredasdorp area (-DC), *Oliver s.n.* (NBG).
- 3420 (Bredasdorp): Ratelriver (-AA), *Compton 14768* (NBG); Farm Witkop near Swellendam (-AB), *Bayliss 639* (NBG); 2 miles from National road on Cape Infanta road (-BD), *Thomas s.n.* (NBG); San Sebastian point, Cape Infanta (-BD), *Thomas s.n.* (NBG); Witsand, Swellendam division (-BD), *Pocock s.n.* (BOL); De Hoop (-CA), *without collector* (NBG); Arniston, near the sea (-CA), *Van Rensburg s.n.* (NBG); Struisbaai (-CC), *Esterhuysen 3869* (BOL).
- 3421 (Riversdale): Bothas farm, Albertinia (-BA), *without collector* (NBG); near Sports ground, Albertinia commonage (-BA), *Muir 918* (NBG).
- 3423 (Knysna): Formosa, Plettenberg Bay (-AB), *Fourcade 3733* (BOL).

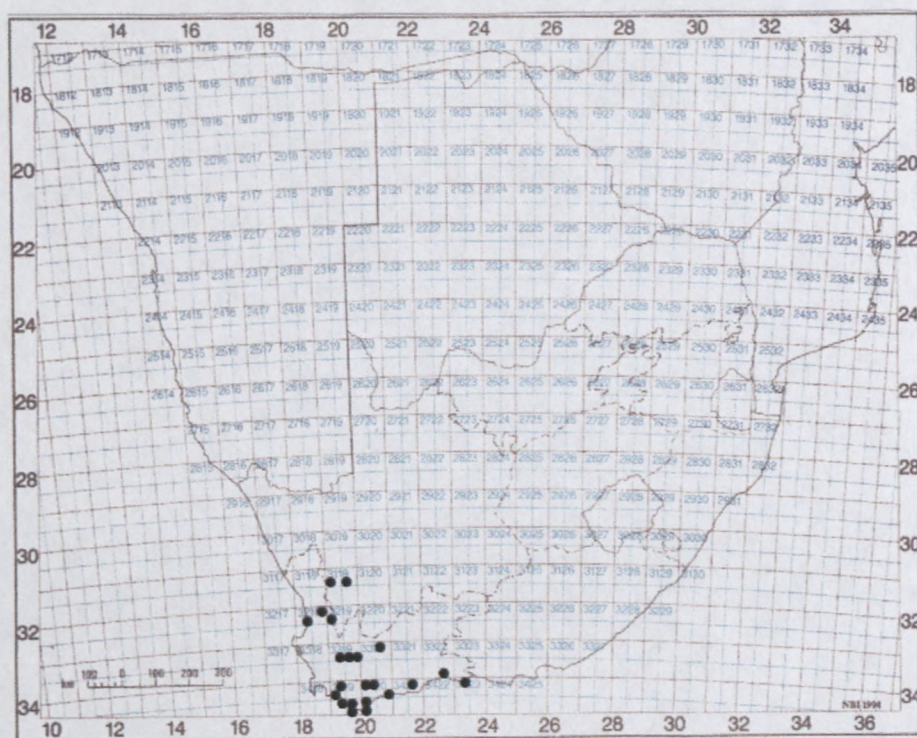


Figure 7.5.3 Geographical distribution of *Massonia pustulata*

7.6 *Massonia pygmaea* Schlechtendal ex Kunth in Enumeratio Plantarum 4: 298 (1843); Müller-Doblies & Müller-Doblies: 68 (1997); Goldblatt & Manning: 104 (2000). TYPE: Cap. B. Spei, “Koude Bokkeveld, Geitow”, *Mund & Maire s.n.* (B, holo., G, HAL)

Polyxena bakeri Dur. & Schinz: 366 (1895), nom. novum pro *Massonia pygmaea* Kunth [nominis pristini *Polyxena pygmaea* (Jacq.) Kunth causa]. Type: Cap. B. Spei, “Koude Bokkeveld, Geitow”, *Mund & Maire s.n.* (B holo., G, HAL).

Neobakeria heterandra Isaac: t. 729 (1939). *Massonia heterandra* (Isaac) Jessop: 426 (1976). Type: Cape –3319CD (Worcester): Louw’s Hoek, Villersdorp, *Stokoe s.n. sub BOL 22309* (BOL, holo., PRE, SAM!).

Bulb: ovoid, 15–25mm long; **outermost tunics** firm, brown and membranous. **Leaves:** 2, glabrous, papillate or pustulate, but then with simple hairs extending from pustules, hairs sometimes only in region of leaf tips, green with or without maroon markings, erect-spreading to spreading, ovate to obovate or suborbicular, apex acute, 20–45mm x 10–25mm. **Inflorescence:** capitate to shortly

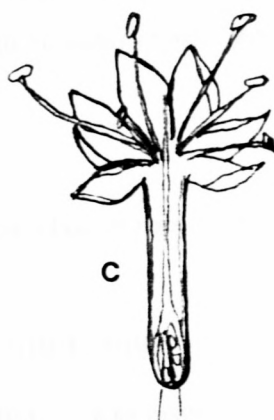
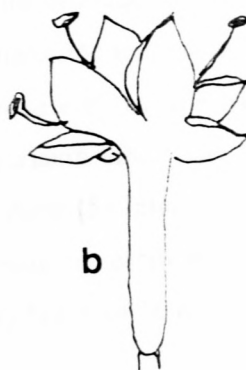
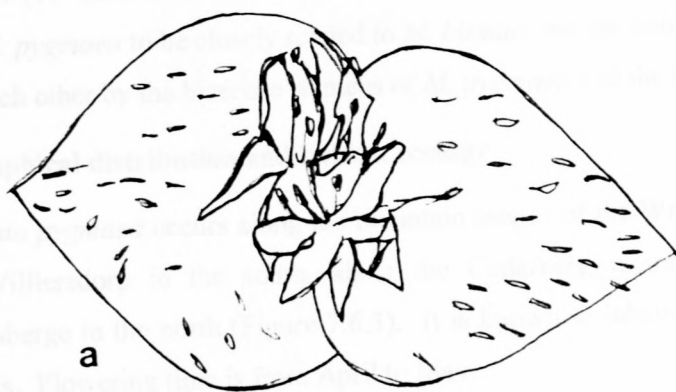


Figure 7.6.1 *Massonia pygmaea* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

corymbose, few-flowered; *lower bracts* oblanceolate to obovate, acute, 10–20mm long, 3–5mm wide; *pedicels* 5–12mm long. *Flowers*: pink or white, *perianth tube* 6–17mm long, up to 2mm wide; *perianth segments* erect to spreading, linear-oblong, 4–7mm long, up to 2mm wide. *Stamens*: 6, biseriate, 2.5–8mm long; *filaments* inserted at the mouth of the perianth tube, connate to 1mm at base; *anthers* purple-black, ca. 1mm long. *Ovary*: ellipsoid, green, 3–4mm long; *style* 10–12mm long; *stigma* simple. *Capsule*: obovoid, shortly acute at the apex, 5–7mm long; *seeds* small, black globose. (Figure 7.6.1)

Diagnostic features and affinities

Massonia pygmaea (Figure 7.6.2) is the only *Massonia* species with biseriate stamens, with the inner filaments 2–3mm longer than the outer ones. *M. pygmaea* shares the long, narrow perianth tube with *M. jasminiflora*, but can easily be distinguished from it because of the short equal length stamens of *M. jasminiflora* that are inserted in the throat of the perianth tube. The style in *M. pygmaea* (11–12mm) is also much longer than that of *M. jasminiflora* (5–7mm). DNA studies show *M. pygmaea* to be closely related to *M. hirsuta*, but the two species can easily be distinguished from each other by the biseriate stamens of *M. pygmaea* and the hairy bracts of *M. hirsuta*.

Geographical distribution and habitat ecology

Massonia pygmaea occurs along the mountain ranges of the Western and Northern Cape Provinces from Villiersdorp in the south, along the Cedarberg mountain range to Leliefontein in the Kamiesberge in the north (Figure 7.6.3). It is known to inhabit high altitudes in sand and in rock crevices. Flowering time is from April to May.

Material studied

- 3018** (Kamiesberg): Koringlandskloof, 1km on Leliefontein road from Garies road (-AC), *Van der Merwe* 177 (STEU).
- 3219** (Wuppertal): Cedarberg, Tafelberg (-AC), *Esterhuysen* 21370 (BOL, NBG)
- 3319** (Worcester): Hansiesberg (-AB), *Esterhuysen* 25722 (BOL); Kaaimans Peak (-BD), *Esterhuysen* 32132 (BOL); Wemmershoek Tafelberg (-CC), *Stokoe s.n.* (BOL); Louw's Hoek (-CD), *Stokoe s.n. sub BOL* 22309 (BOL); Villiersdorp (-CD), *Stokoe s.n. sub SAM* 52826 (SAM).



Figure 7.6.2 *Massonia pygmaea* (Van der Merwe 177, STEU).

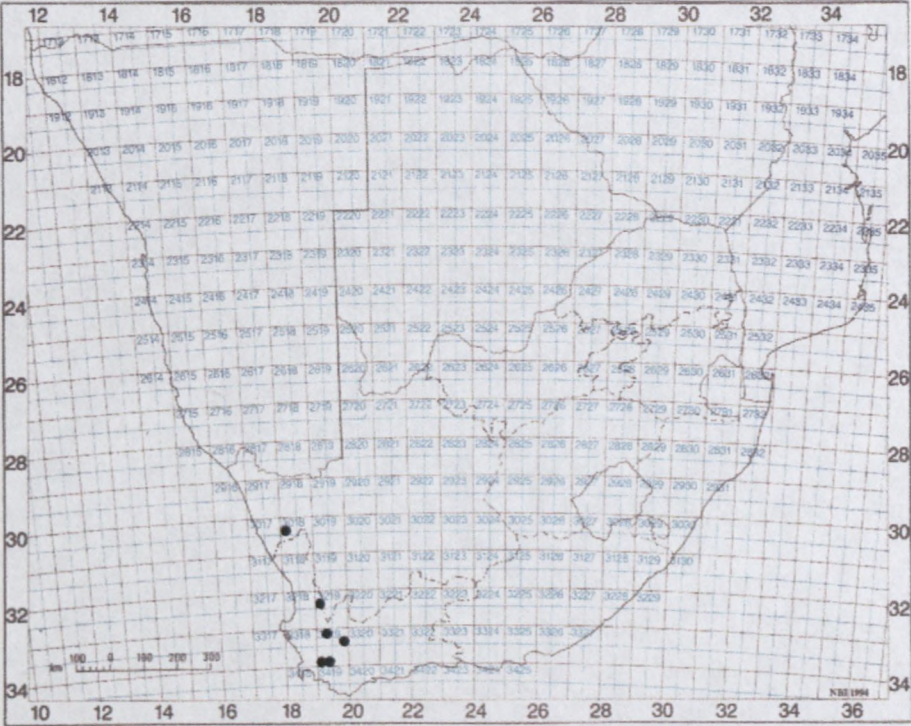


Figure 7.6.3 Geographical distribution of *Massonia pygmaea*

CHAPTER 8

TAXONOMIC TREATMENT OF THE GENUS *POLYXENA* KUNTH.

8. *Polyxena* Kunth in Enumeratio Plantarum 4: 294 (1843); Baker: 420 (1897) p.p., excluding subgenus *Astemma* Baker; Schönland: 443 (1910); Phillips: 190 (1951); Jessop: 426 (1976); Mathew: 5 (1988); Müller-Doblies & Müller-Doblies: 84 (1997); Goldblatt & Manning: 107 (2000); Williams: 615 (2000). Type—*Polyxena pygmaea* (Jacq.) Kunth.

Massonia Thunb. ex Houtt. subgenus *Astemma* Endlicher: 145 (1836) = *Polyxena* Kunth subgenus *Eupolyxena* Baker: 419 (1897). Lectotype: *Polyxena odorata* Baker (= *P. ensifolia* (Thunb.) Schönl.)

Periboea Kunth: 293 (1843).

Bulb small, globose to ovoid; *outer tunics* brown and membranous; inner membranous sheath enclosing base of leaves and scape. *Leaves* 2–6, usually erect, sometimes spreading, linear to broadly lanceolate or obtuse, sometimes canaliculate, glabrous, margins sometimes ciliate. *Inflorescence* racemose, subcorymbose or corymbose, *bracts* small and inconspicuous or obsolete, subtending the pedicels; *flowers* actinomorphic, pedicillate, purple, lilac, pink or white; *perianth* fused to form a long or short tube; *perianth segments* more or less oblong, erect, spreading or recurved, often minutely papillate at the apex. *Stamens* 6, biseriate, attached to the perianth tube at 2 different levels, *filaments* free, sublinear; *anthers* minute, dorsifixed. *Ovary* sessile, ellipsoid; style sublinear, usually slightly longer than stamens, stigma simple, subcapitate. *Capsule* loculicidal; *seeds* globose, black, ca. 2mm in diameter.

Key to the species of *Polyxena*

Leaves narrow, linear and canaliculate, 2–6 per plant

Inflorescence distinctly corymbose *P. corymbosa*

Inflorescence subcorymbose or racemose

Perianth tube very short, $\frac{1}{4}$ of the length of the perianth segments, inflorescence

distinctly racemose, flowers campanulate.....*P. brevifolia*

Perianth tube equal in length to perianth segments or longer, inflorescence

subcorymbose, flowers funnel-shaped

Perianth tube equal in length to perianth segments, stamens included

in perianth tube, leaves always 2..... *P. paucifolia*

Perianth tube at least double the length of the perianth segments,

stamens exerted above recurved perianth segments, leaves 2 or 3..... *P. longituba*

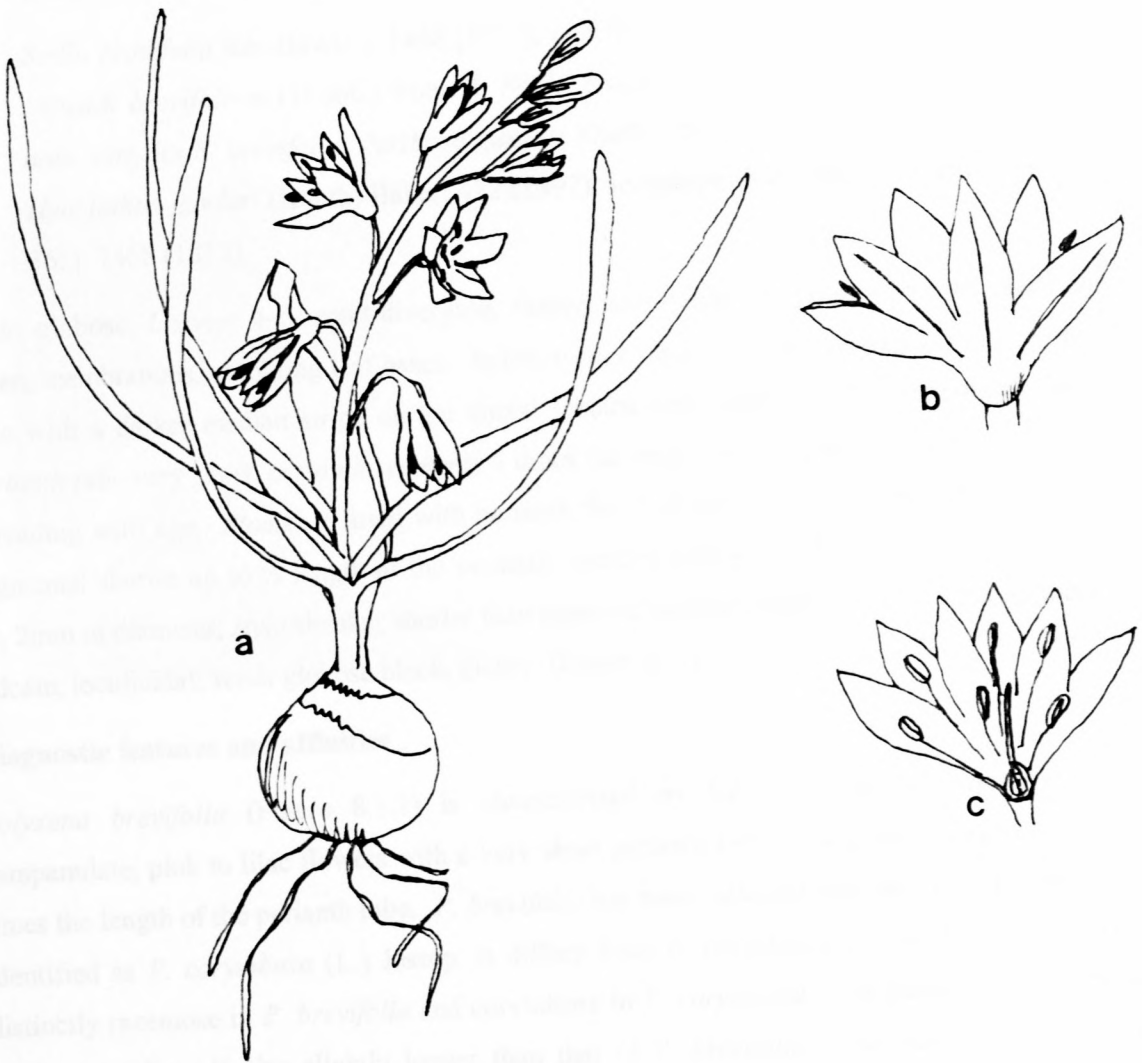


Figure 8.1.1 *Polyxena brevifolia* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

Leaves lanceolate or ovate, obtuse, 2 per plant

Perianth tube 3x the length of the perianth segments, perianth segments strongly recurved.....*P. pygmaea*

Perianth tube up to double the length of the perianth segments, perianth segments erect to spreading

Stamens included in throat of the perianth tube..... *P. ensifolia* var. *maughanii*

Stamens exerted beyond the throat of the tube..... *P. ensifolia* var. *ensifolia*

8.1 *Polyxena brevifolia* (Ker-Gawl.) A.M. van der Merwe *comb. nov.* Iconotype: Ker-Gawl., in Curtis's Botanical Magazine 36: t. 1468 (1812).

Scilla brevifolia Ker-Gawl.: t. 1468 (1812), non *Hyacinthus brevifolius* Thunb. 63 (1794) [= *Dipcadi brevifolium* (Thunb.) Fourc.]; *Scilla brachyphylla* Roem. et Schultes: 573 (1829) *nom. nov.* for *S. brevifolia*; *Periboea gawleri* Kunth: 293 (1843) *nom. nov.* for *S. brevifolia*; *Hyacinthus gawleri* (Kunth) Baker: 472 (1897). Iconotype: Ker-Gawl. in Curtis's Bot. Mag. 36: t. 1468 (1812).

Bulb: globose. *Leaves*: 4–5, erect-diverging, fleshy, semi-terete to linear, subacute; basal sheath green, membranous, enfolding leaf bases. *Inflorescence*: racemose, 6–8 flowered. *Flowers*: pink to lilac with a darker median stripe on the dorsal surface, campanulate; *bracts* minute or obsolete; *perianth tube* very short, *perianth segments* 4 times the length of the tube, lanceolate-oblong, erect, spreading with age. *Stamens*: fused with perianth for $\frac{1}{4}$ of their length, longest equal to perianth segments, shorter up to $\frac{2}{3}$ length of the perianth; *anthers* yellow, *ca.* 1mm long. *Ovary*: trigonal, *ca.* 2mm in diameter; *style* slender, shorter than stamens; *stigma* simple. *Capsule*: membranous, trisulcate, loculicidal; *seeds* globose black, glossy. (Figure 8.1.1)

Diagnostic features and affinities

Polyxena brevifolia (Figure 8.1.2) is characterised by the racemose inflorescence of 6–8 campanulate, pink to lilac flowers with a very short perianth tube. The perianth segments are four times the length of the perianth tube. *P. brevifolia* has been collected over the years and mistakenly identified as *P. corymbosa* (L.) Jessop. It differs from *P. corymbosa* in that the inflorescence is distinctly racemose in *P. brevifolia* and corymbose in *P. corymbosa*. The perianth tube in flowers of *P. corymbosa* is also slightly longer than that of *P. brevifolia*. This species was originally described by Ker Gawler as *Scilla brevifolia*, but was only ever known from the drawing in Curtis's Botanical magazine. Barker (1941) in her description of *P. paucifolia* (Barker) A.M. van der Merwe & J.C. Manning mentions that at that time *Hyacinthus* was only represented by two South African species, *H. corymbosus* L. and *H. gawleri* Baker. When compared, they appear to be closely related, differing only in the inflorescence which is corymbose in the former and racemose



Figure 8.1.2 *Polyxena brevifolia* (Van der Merwe 143, STEU).

in the latter. Molecular data shows a close relationship between *P. brevifolia*, *P. corymbosa* and *P. paucifolia*, but shows clear differences in the sequence data of the three and thus lends support to the morphological differences and backs the species status of *P. brevifolia*.

Geographical distribution and ecology

P. brevifolia is restricted to the Western Cape Province and occurs in scattered populations from Harmony flats between Gordon's Bay and Strand, to Stellenbosch, Paarl, Tulbagh and Ceres and as far north as the Clanwilliam area (Figure 8.1.3). The plants grow in low-lying drainage areas in sandy or clayey soil. Flowering time is April to June and flowers are pleasantly scented.

Material studied

- 3218 (Clanwilliam): Warm baths, Clanwilliam (-BB), *Edwards 14437* (NBG).
- 3318 (Cape Town): Malmesbury, Mamre hills (-CB), *Hall 243/48* (NBG); Near Raapenberg, E of Mowbray (-CD), *Bolus 8966* (BOL); Outskirts of Paarl on road to Wellington (-DB), *Leighton 1647* (BOL); Paarl, gravel flats (-DB), *Barker 4026* (NBG); Stellenbosch, (-DD), *Duthie 417* (BOL).
- 3319 (Worcester): Tulbagh (-AC), *Bolus 5363* (NBG); Between Ceres and Karooport (-AD), *Leipoldt s.n.* (BOL).
- 3418 (Simonstown): Sandy flats, Strand to Gordon's Bay, (-BB), *Parker 4320* (NBG).

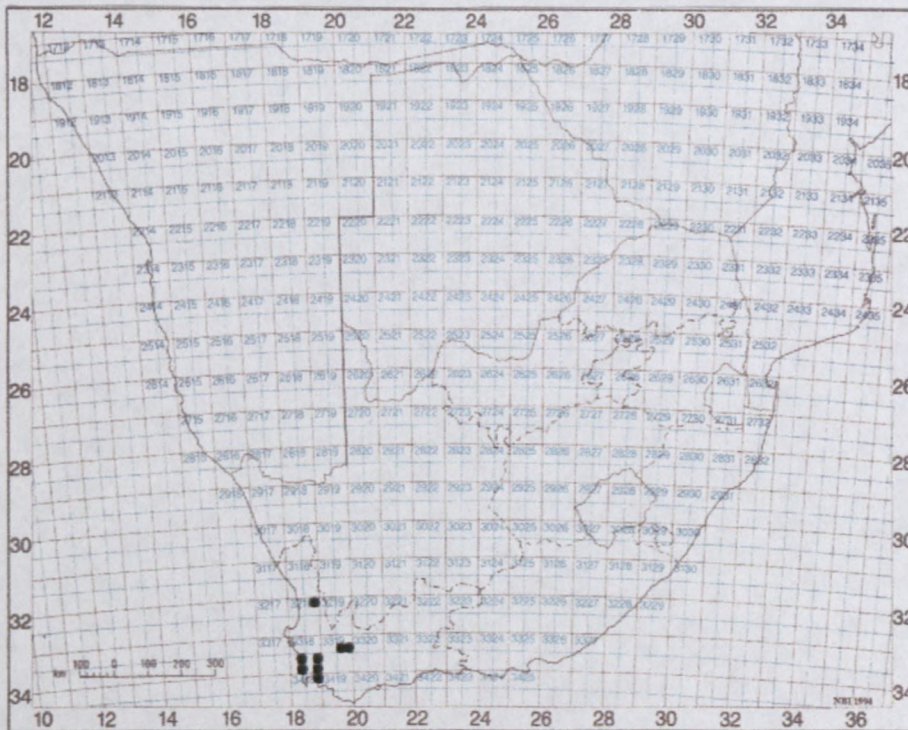


Figure 8.1.3. Geographical distribution of *Polyxena brevifolia*

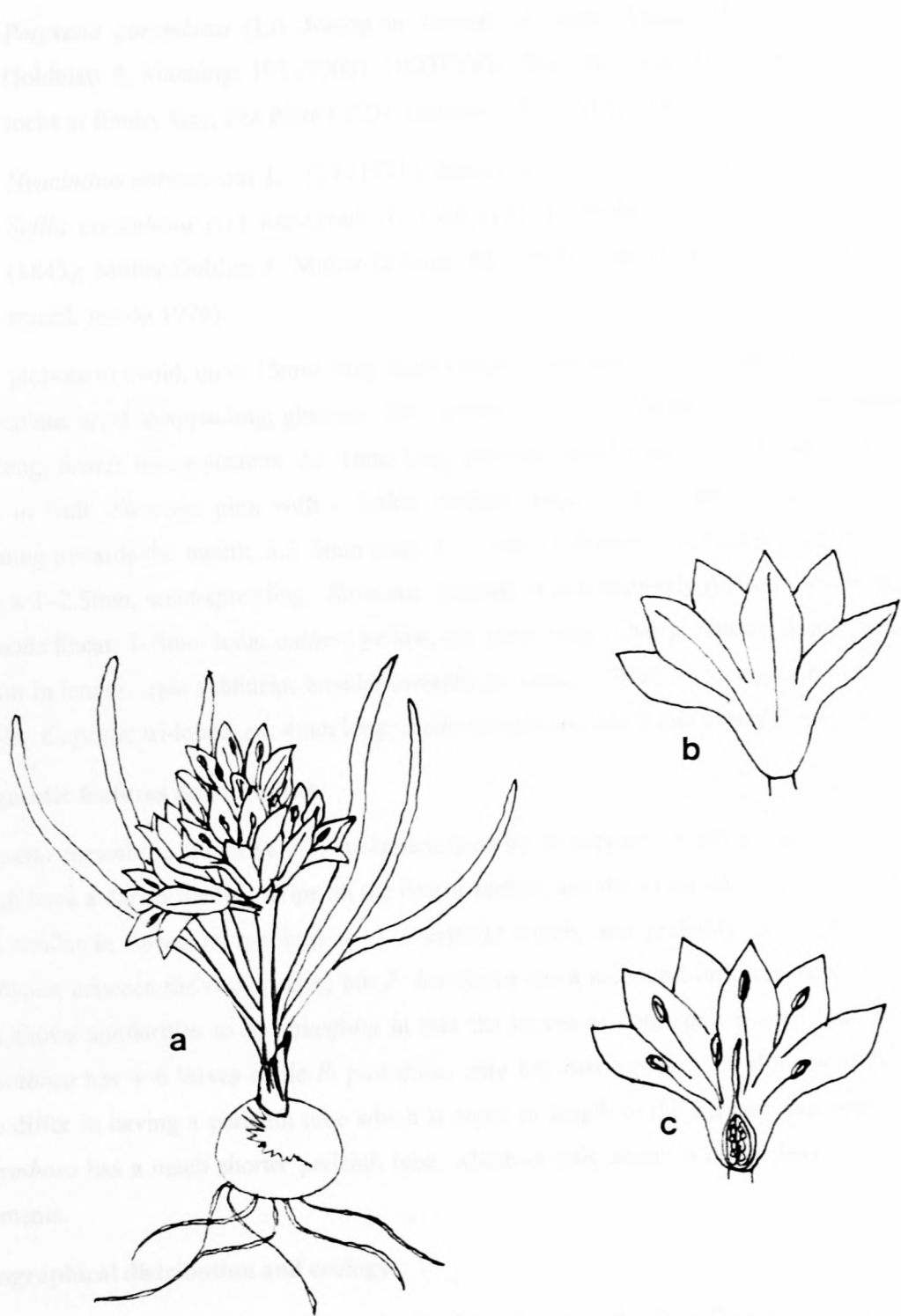


Figure 8.2.1 *Polyxena corymbosa* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

8.2 *Polyxena corymbosa* (L.) Jessop in Journal of South African Botany 42: 429 (1976); Goldblatt & Manning: 107 (2000). NEOTYPE- Western Cape, 3318 (Cape Town): On the rocks at Bantry Bay, Sea Point (-CD), *Guthrie 17218* (NBG). Designated here.

Hyacinthus corymbosus L.: 223 (1771); *Massonia corymbosa* (L.) Ker-Gawl: t. 991 (1807); *Scilla corymbosa* (L.) Ker-Gawl.: t. 1468 (1812); *Periboea corymbosa* (L.) Kunth: 293 (1843); Müller-Doblies & Müller-Doblies: 84 (1997). Type: Cap. B. Spei, *Koenig s.n.* (not traced, Jessop 1976).

Bulb: globose to ovoid, up to 15mm long; outer tunics brown and membranous. *Leaves*: 2–6, linear caniliculate, erect to spreading, glabrous, 30–120mm x 1–3mm. *Inflorescence*: corymbose, 20–90 mm long; *bracts* inconspicuous, *ca.* 1mm long; *pedicels* usually up to 5mm long, lengthening to 8mm in fruit. *Flowers*: pink with a darker median stripe on the dorsal surface; *perianth tube* widening towards the mouth, 3.5–6mm long, 1.5–2mm in diameter; *perianth segments* oblong, 6–9mm x 1–2.5mm, erect-spreading. *Stamens*: inserted at two distinctly different levels in the tube; *filaments* linear, 1–5mm long; *anthers* yellow, *ca.* 1mm long. *Ovary*: oblong, deeply tri-lobed, *ca.* 3.5mm in length; *style* sublinear, broader towards the base, 1–7mm long; *stigma* minutely capitate, simple. *Capsule*: tri-lobed, *ca.* 4mm long; *seeds* subglobose, black and glossy (Figure 8.2.1).

Diagnostic features and affinities

Polyxena corymbosa (Figure 8.2.2) is characterised by its corymbose inflorescence of pink flowers which have a darker median stripe on the dorsal surface and the linear, slightly canaliculate leaves. It is similar in flower morphology to *P. brevifolia* which, was probably the main reason for the confusion between the two species, but *P. brevifolia* has a racemose inflorescence. *P. corymbosa* also shows similarities to *P. paucifolia* in that the leaves of both species are linear, however, *P. corymbosa* has 4–6 leaves while *P. paucifolia* only has two leaves. The flowers of *P. paucifolia* also differ in having a perianth tube which is equal in length to the perianth segments whereas *P. corymbosa* has a much shorter perianth tube, which is only about $\frac{1}{3}$ of the length of the perianth segments.

Geographical distribution and ecology

P. corymbosa is restricted to the Cape Peninsula and was originally collected on Lion's Head. The species occurs in isolated patches around Greenpoint, Bantry Bay and Camps Bay (Figure 8.2.3). Plants grow in sandy soil or sometimes in gravelly soils and rock crevices. Flowering time is from April to June and flowers are pleasantly scented.



Figure 8.2.2 *Polyxena corymbosa* (Van der Merwe 197, STEU).

Material studied

–3318 (Cape Town): Southern portion, Green Point common (-CD), *Bolus* 8967 (NBG); On the rocks at Bantry Bay, Sea Point (-CD), *Guthrie* 17218 (NBG); Sea Point, Camps Bay (-CD), *MacOwan* 943 (NBG). Green Point common (-CD), *Stokoe* 9037 (NBG).

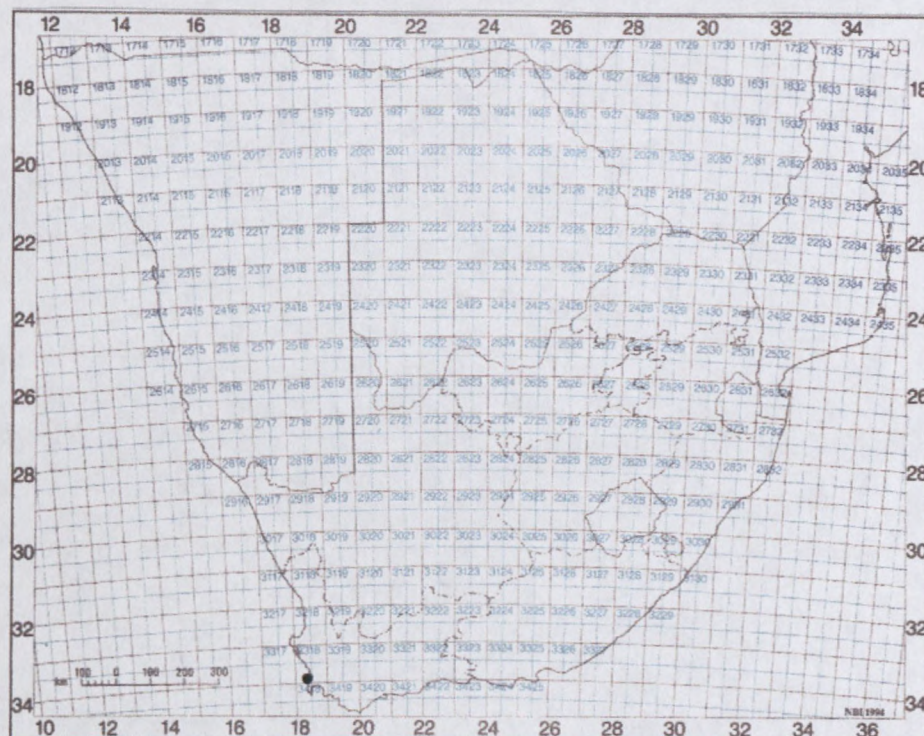


Figure 8.2.3. Geographical distribution of *Polyxena corymbosa*

8.3 *Polyxena ensifolia* (Thunb) Schönl. in Transactions of the Royal Society of South Africa 1: 443 (1910). Type: Cape, inter Sondags et Visch river *Thunberg* s.n. (UPS-Thunb 8002 holo., microfiche!)

Mauhlia ensifolia Thunb.: t. 1 (1794); *Agapanthus ensifolius* (Thunb.) Willd.: 48 (1799); *Massonia ensifolia* (Thunb.) Ker-Gawl.: t. 554 (1802a). Type: Cape, inter Sondags et Visch river *Thunberg* s.n. (UPS-Thunb 8002 holo., microfiche!)

Massonia odorata Hook.f.: t. 5891 (1871); *Polyxena odorata* (Hook.f.) Baker: 420 (1897). Type: Cape, Colesberg. *D. Arnot* s.n. (K, holo.!).

Massonia uniflora Sol. ex Baker: 393 (1871); *Polyxena uniflora* (Sol. ex Baker) Benth. & Hook ex Dur. & Schinz: 367 (1895); Baker: 421 (1897). Type: Cap. B. Spei. *Masson* s.n. (BM, holo.).

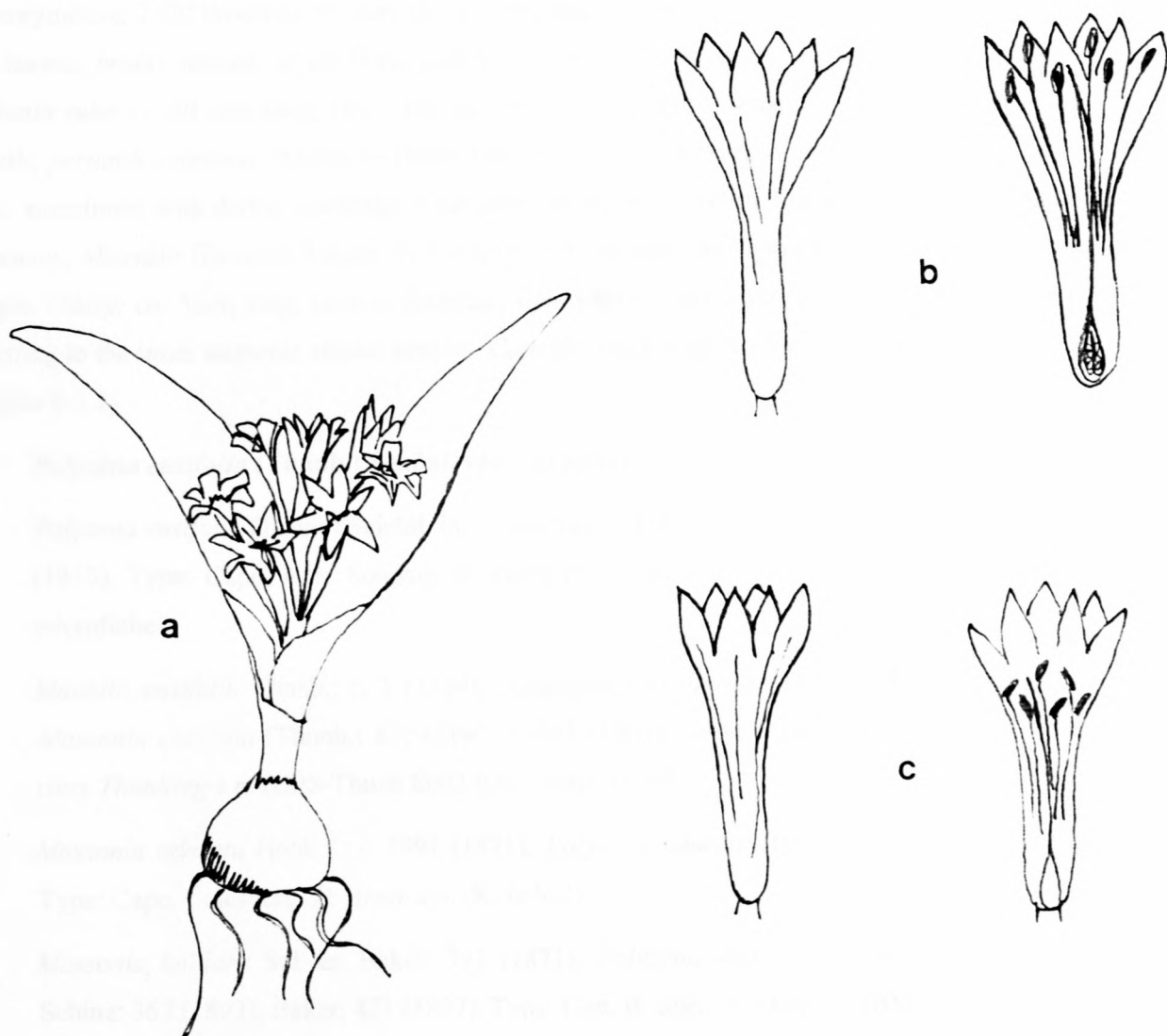


Figure 8.3.1 *Polyxena ensifolia* (a) flowering plant x 1; (b) flower of *P. ensifolia* var. *ensifolia* x 2; (c) flower of *P. ensifolia* var. *maughanii* x 2.

Polyxena calcicola U. & D. M-D.: 85 (1997). Type: Cape, De Hoop Nature Reserve, calcareous rocks. *Müller-Doblies* 84026a (PRE, holo; B, BOL, BTU, G, GRA, K, M, MO, NBG, P, S, UPS, Z).

Bulb: globose-ovoid, ca. 15mm in diameter. *Leaves*: 2, lanceolate to obtuse, glabrous with cartilagino-ciliate margins, ascending or prostrate, 50–130mm x 10–30mm. *Inflorescence*: subcorymbose, 7–20 flowered, flowers borne at the base of the leaves, peduncle short, enfolded by the leaves; *bracts* minute or obsolete; *pedicels* up to 5mm in length. *Flowers*: white, scented; *perianth tube* 12–20 mm long, twice the length of the perianth segments, slightly dilated at the mouth; *perianth segments* oblong, 6–10mm long, acute, erect to spreading, white and more rarely lilac, sometimes with darker markings at the tips. *Stamens*: 6, inserted at the base of the perianth segments, alternate filaments longer, $\frac{2}{3}$ the length of the perianth segments; *anthers* 1 mm long, purple. *Ovary*: ca. 5mm long, 1mm in diameter; *style* white, usually much shorter than the stamens, reaching to the inner stamens; *stigma* simple. *Capsule*: loculicidal, tri-lobed; *seeds* ellipsoid, black. (Figure 8.3.1)

Polyxena ensifolia* (Thunb.) Schönl. var. *ensifolia

Polyxena ensifolia (Thunb) Schönl. in Transactions of the Royal Society of South Africa: 443 (1910). Type: Cape, inter Sondags et Visch river *Thunberg s.n.* (UPS-Thunb 8002 holo., microfiche!).

Mauhlia ensifolia Thunb.: t. 1 (1794); *Agapanthus ensifolius* (Thunb.) Willd.: 48 (1799); *Massonia ensifolia* (Thunb.) Ker-Gawl.: t. 554 (1802). Type: Cape, inter Sondags et Visch river *Thunberg s.n.* (UPS-Thunb 8002 holo., microfiche!)

Massonia odorata Hook.f.: t. 5891 (1871); *Polyxena odorata* (Hook.f.) Baker: 420 (1897). Type: Cape, Colesberg. *D. Arnot s.n.* (K, holo!).

Massonia uniflora Sol. ex Baker: 393 (1871); *Polyxena uniflora* (Sol. ex Baker) Dur. & Schinz: 367 (1893); Baker: 421 (1897). Type: Cap. B. Spei. *Masson s.n.* (BM, holo.).

Polyxena calcicola U. & D. M-D.: 85 (1997). Type: Cape, De Hoop Nature Reserve, calcareous rocks *Müller-Doblies* 84026a (PRE, holo; B, BOL, BTU, G, GRA, K, M, MO, NBG, P, S, UPS, Z).

Diagnostic features and affinities

Polyxena ensifolia var. *ensifolia* (Figure 8.3.2) is characterised by its subcorymbose inflorescence of white to pale lilac flowers carried at the base of the leaves. The flowers are characterised by the perianth tube which is approximately twice the length of the perianth segments and the stamens which are exerted beyond the mouth of the perianth tube. *P. ensifolia* var. *ensifolia* is very similar



Figure 8.3.2 *Polyxena ensifolia* var. *ensifolia* (Van der Merwe 185, STEU).



Figure 8.3.4 *Polyxena ensifolia* var. *maughanii* (Van der Merwe 139, STEU).

to *P. ensifolia* var. *maughanii* and differs only in the length of the stamens, which in *P. ensifolia* var. *maughanii* are always included within the perianth tube and are not easily visible. In *P. ensifolia* var. *ensifolia* the three longer stamens are exerted beyond the mouth of the perianth tube, while the three shorter ones are sometimes included in the perianth tube. The perianth segments of *P. ensifolia* var. *ensifolia* are also more spreading than those of *P. ensifolia* var. *maughanii*. Molecular studies show that *P. ensifolia* var. *ensifolia* is closely related to *P. longituba* A.M. vd Merwe, but the two taxa can be easily distinguished from one another by leaf shape and flower structure. In *P. longituba* the longer perianth tube and highly recurved perianth segments of the flowers are very distinctive. The leaves of *P. longituba* are linear and canaliculate, whereas those of *P. ensifolia* var. *ensifolia* are lanceolate to obovate.

Geographical distribution and ecology

Polyxena ensifolia var. *ensifolia* is widely distributed and occurs mostly on clay or granite flats from Namaqualand through the Western Karoo, and as far east as Bathhurst (Figure 8.3.3). Flowering time is from April to June and flowers are strongly scented.

Material studied

- 3017 (Hondeklipbaai): Top of Studer's Pass, W of Garies (-AD), *Stayner s.n.* (NBG).
- 3018 (Kamiesberg): 20 miles NE of Garies (-CA), *Salter 916/37* (NBG).
- 3119 (Calvinia): Matjiesfontein (-BC), *Bolus 2048/14* (BOL); East of Nieuwoudtville (-CD), *Barker 9400* (NBG); 1 mile N of Botterkloof (-CD), *Heginbotham 105* (NBG); Farm Botterkloof, between Clanwilliam and Calvinia (-CD), *Snijman 1208* (NBG).
- 3220 (Sutherland): Voëlfontein farm (-AB), *Booyesen s.n.* (NBG); Voëlfontein farm (-AB), *Hall 223; 3243* (NBG); Top of Verlatenkloof (-BC), *Hall 3175* (NBG).
- 3222 (Beaufort West): Beaufort West (-BC), *Macarthy 23077* (NBG).
- 3225 (Somerset East): Basson's kloof (-DA), *Bayliss 2969* (NBG).
- 3319 (Worcester): Worcester division (-CB), *Dregé 2187* (NBG).
- 3320 (Montagu): Whitehill, Laingsburg (-BA), *Compton 14584* (NBG); Anysberg Nature Reserve (-BC), *Gie 18* (NBG);
- 3322 (Oudtshoorn): SE of Oudtshoorn (-BC), *Wurtz 2087* (NBG).
- 3323 (Willowmore): Uniondale (-CA), *Rycroft 425/62* (NBG).
- 3324 (Steytlerville): Near Hankey, Easton Cape (DD), *Bayliss 6386* (NBG).

- 3325** (Port Elizabeth): Uitenhage (-CD), *Ecklon & Zeyher* 23076 (BOL); Swartkops (-DC), *Bolus* 864/31 (BOL); Port Elizabeth (-DC), *Holland* 8228 (NBG).
- 3326** (Grahamstown): Grahamstown (BC), *Dennie* 23078 (BOL); Bushman's river, Alexandria (-DB), *J.R. & B.R.* 305 (BOL); Bushman's River mouth, Alexandria (-DB), *Leighton s.n.* (BOL); Bushman's river mouth, Bathhurst (-DB), *Leighton* 24933 (BOL); Bushman's River (-DB), *MacOwan* 751 (NBG).
- 3419** (Caledon): Riviersonderend (-BB), *Heginbotham* 128 (NBG); Elim (-DA), *Schlechter* 10471 (NBG).
- 3420** (Bredasdorp): Bredasdorp (-BB), *Brand* 874/29 (NBG); Potteberg (-BC), *Barker* 4547 (NBG); De Hoop (-CA), *Barker* 8742 (NBG).
- 3421** (Riversdale): Soetmelksfontein (-AB), *Muir* 291 (BOL); Albertinia (-BA), *Muir* 915 (BOL); Between Riversdale and Puntjie (-CB), *Esterhuysen* 16967 (BOL).

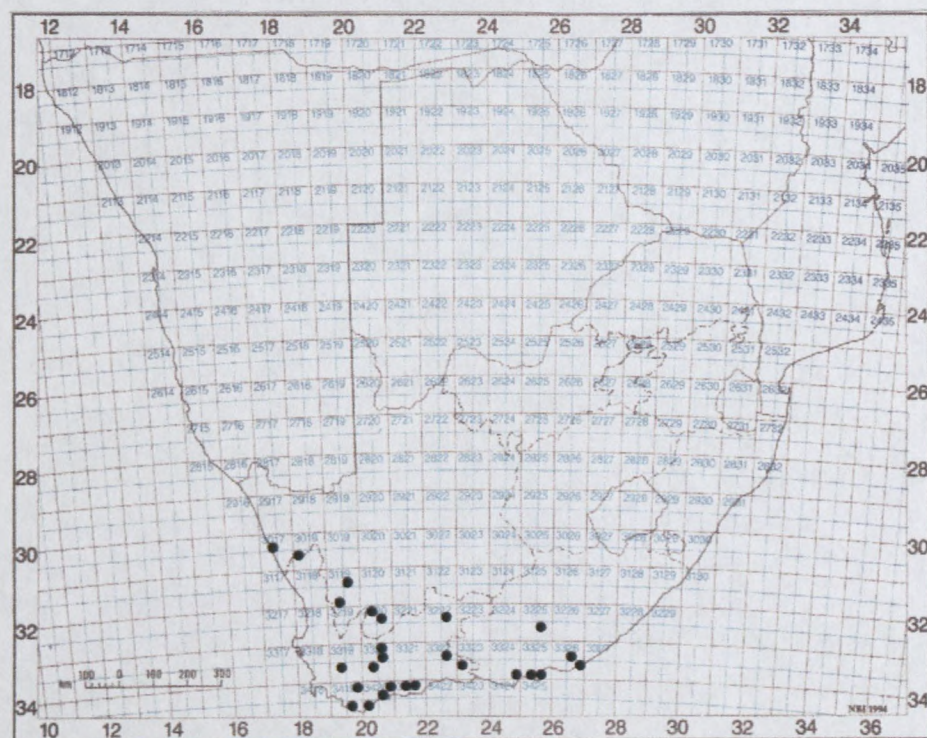


Figure 8.3.3. Geographical distribution of *Polyxena ensifolia* var. *ensifolia*

***Polyxena ensifolia* var. *maughanii* (Barker) A.M. van der Merwe comb. nov.**

Polyxena maughanii Barker in Flowering Plants of South Africa 11: t. 420 (1931a). Type: Nieuwoudtville, *Maughan Brown & Bolus s.n.* sub. *BOL 19613* (BOL, holo!).

Diagnostic features and affinities

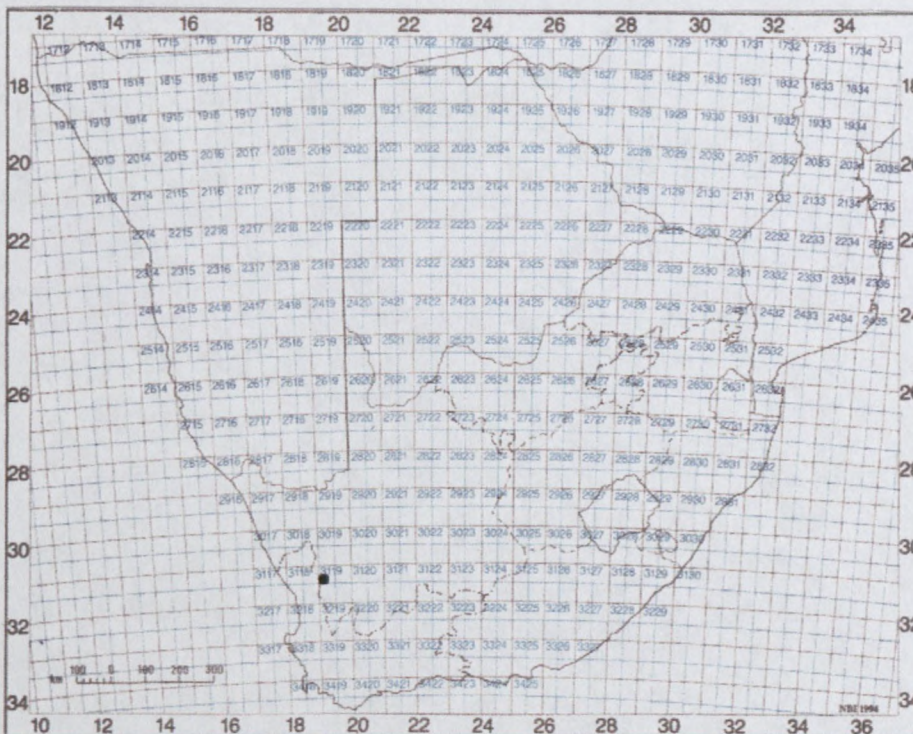
Polyxena ensifolia var. *maughanii* (Figure 8.3.4) is characterised by its subcorymbose inflorescence of white flowers which are carried at the base of the leaves. The perianth tube is twice the length of the perianth segments and the stamens are included in the perianth tube, with the three longest stamens just reaching to the mouth of the tube. *P. ensifolia* var. *maughanii* differs from *P. ensifolia* var. *ensifolia* only with regard to the length of the stamens, and in *P. ensifolia* var. *ensifolia* the three longest stamens are exerted beyond the mouth of the perianth tube, reaching up to $\frac{2}{3}$ of the length of the perianth segments. Molecular data shows that *P. ensifolia* var. *maughanii* is also closely related to *P. longituba* (as is *P. ensifolia* var. *ensifolia*), but is easily distinguished from *P. longituba* based on the characters previously mentioned.

Geographical distribution and ecology

P. ensifolia var. *maughanii* has a very limited distribution in the Western Karoo and Bokkeveld mountains. This variety shares its distribution area with *P. ensifolia* var. *ensifolia*, but is always restricted to dolerite outcrops. Flowering time is from May to June and flowers are pleasantly scented (Figure 8.3.5).

Material studied

-3119 (Calvinia): Nieuwoudtville (-AC), *Barker* 9670 (NBG); Nieuwoudtville Reserve (-AC), *Perry & Snijman* 2158 (NBG); Summit of Vanrhyns Pass (-AC), *Hall* 3579 (NBG).



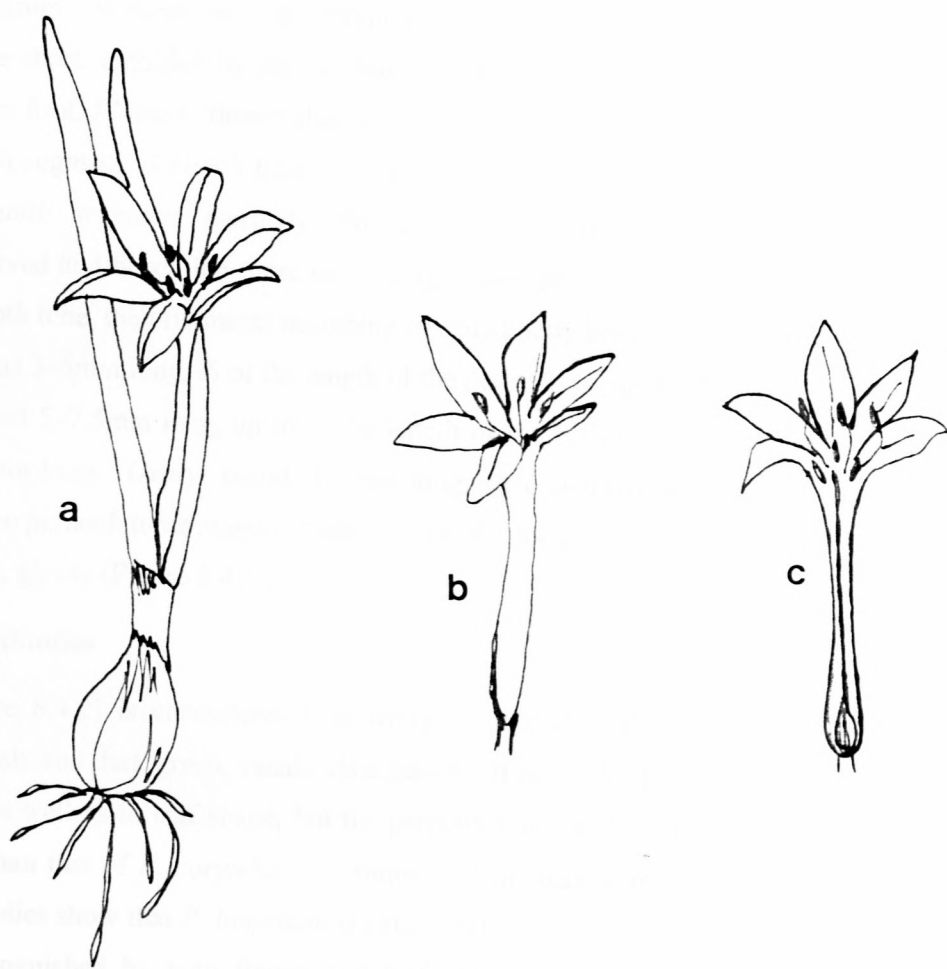


Figure 8.4.1 *Polyxena longituba* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

8.4 *Polyxena longituba* A.M. vd Merwe in South African Journal of Botany 67: 44 (2001).

Type: Northern Cape Province, 3220 (Sutherland): 5km N of Komsberg Pass summit (-DB), Manning 2165 (NBG, holo!).

Bulb: globose or ovoid, ca. 15mm in diameter. *Leaves*: 2 sometimes 3, erect or prostrate, narrowly lanceolate, acuminate, canaliculate, dark green, slightly fleshy, glabrous with cartilaginous, ciliate margins, 30–70mm x 2–6mm. *Inflorescence*: subcorymbose, 1–5 flowered, flowers borne at the base of the leaves; *scape* short, enfolded by leaves; *bracts* minute or obsolete; pedicels 2–4mm long, elongating slightly in fruit. *Flowers*: funnel-shaped, white to lilac, with a darker median stripe abaxially on each perianth segment; *perianth tube* 15–25mm long, at least twice the length of the perianth segments; *perianth segments* narrowly oblong-lanceolate, 10–15mm long, slightly involute, acuminate, recurved and becoming more so with age. *Stamens*: 6, fused with the tepals for the length of the perianth tube, then filaments becoming free, distinctly biseriate, free portions of filaments of the inner whorl 3–5mm long, $\frac{1}{3}$ of the length of the perianth segments, free portions of filaments of the outer whorl 5–7.5mm long, up to $\frac{1}{2}$ the length of the perianth segments; *anthers* dorsifixed, yellow, ca. 1mm long. *Ovary*: ovoid, 3–5mm long; *style* slender, up to 20mm long, reaching to the mouth of the perianth tube; *stigma* capitate. *Capsule*: loculicidal, tri-lobed, ca. 5mm long; *seeds* ellipsoid, black, glossy (Figure 8.4.1).

Diagnostic features and affinities

Polyxena longituba (Figure 8.4.2) is characterised by white to pale lilac flowers with a long perianth tube, recurved tepals and dark green, canaliculate leaves. It is similar to *P. corymbosa* in flower shape and colour, as well as in leaf shape, but the perianth tube of *P. longituba* is always much longer (15–25mm) than that of *P. corymbosa* (3–6mm) and the leaves are noticeably more canaliculate. Molecular studies show that *P. longituba* is closely related to *P. ensifolia*, but the two species can easily be distinguished by both flower and leaf characteristics. The leaves of *P. ensifolia* are ovate-elliptical with acute apices and the flowers are much smaller, with a shorter perianth tube (ca. 12mm) than those of *P. longituba* (15–25mm).

Geographical distribution and ecology

P. longituba occurs abundantly, but localised, in the Komsberg area in the Northern Cape (Figure 8.4.3), growing in damp lower-lying areas. Two separate populations are known, with one population having flowers that are off-white to pale pink and the other with more robust lilac flowers. Flowering time is from late April to May and the flowers emit a sweet, yeasty smell and they close at night. Flowers appear to be self-pollinated and the peduncles elongate during seed ripening.



Figure 8.4.2 *Polyxena longituba* (Van der Merwe 193, STEU).

Material studied

–3220 (Sutherland): Voëlfontein farm (-BC), *Hall* 226 (NBG); 3.5 km S of Sutherland (-BC), *Manning* 2163 (NBG); 5 km N of Komsberg Pass Summit (-DB), *Manning* 2165 (NBG).

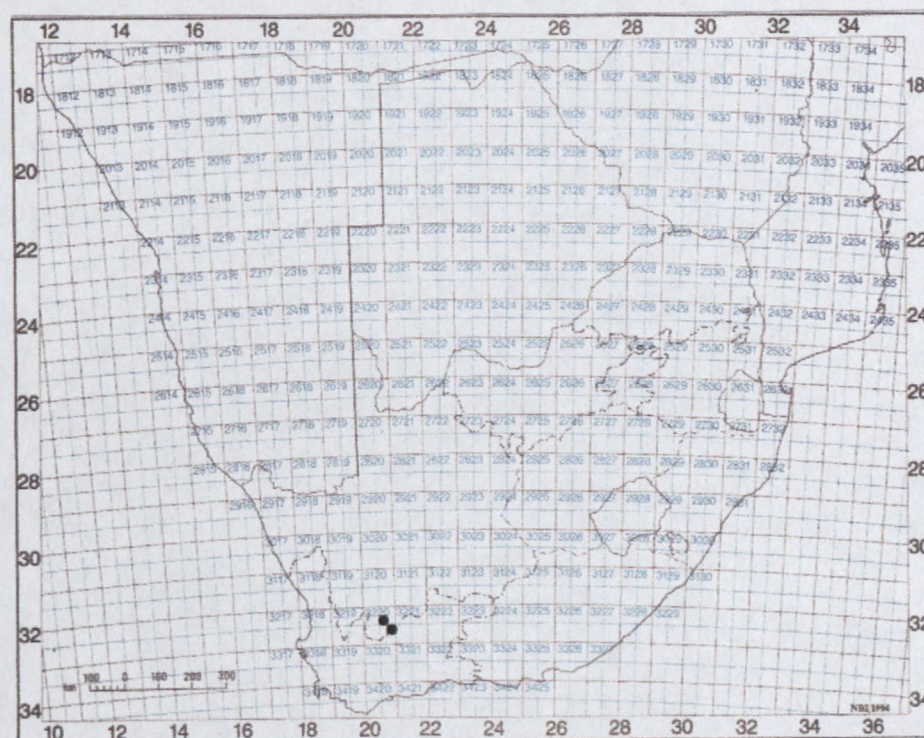


Figure 8.4.3. Geographical distribution of *Polyxena longituba*

8.5 *Polyxena paucifolia* (Barker) A.M. van der Merwe & J.C. Manning in Goldblatt & Manning, *Cape Plants*: 107 (2000). Type: Cape 3217 DD (Vredenburg), *Mathews* sub. NBG cult no. 689/30 (NBG, holo., K!, PRE).

Hyacinthus paucifolius Barker: 198 (1941); *Periboea paucifolia* (Barker) U. & D. M-D.: 84 (1997). Type: Cape 3217 DD (Vredenburg), *Mathews* sub. NBG cult no. 689/30 (NBG, holo., K!, PRE).

Periboea oliveri U. & D. M-D.: 84 (1997). Type: Cape, open ground near to the hotel at Paternoster, *Anderson s.n. sub BTU cultno.* 6390 (PRE, holo, B, BTU, K, M, MO, NBG, Z).

Bulb: globose, 10–15mm in diameter. **Leaves:** 2, spreading, linear, canaliculate, subacute, 50–100mm x 3mm; **peduncle** ca. 30mm long, enclosed by bulb sheath for most of its length. **Inflorescence:** racemose, usually few-flowered, lowermost pedicels up to 8mm long; **bracts** minute.

Figure 8.5.1 *Polyxena paucifolia* (a) flowering plant x 1; (b) flower x 1.5; (c) longitudinal section of flower x 1.5.

Flowers: dark lilac to purple, white at the base; *perianth tube* 6–7mm long, 2mm in diameter, perianth tube equal in length to perianth segments; *perianth segments* subequal, oblong, 6–8mm long. *Stamens*: 6, biseriate, included within the perianth tube; *filaments* very short, ca. 1 mm long, lowermost ones adnate to the midway up the tube. *Ovary*: oblong, 1.5mm in diameter; *style* short 1mm long. *Capsule*: trilobed, about 4mm long, loculicidal; *seeds* globose, black, glossy. (Figure 8.5.1)

Diagnostic features and affinities

Polyxena paucifolia (Figure 8.5.2) is characterised by its dark lilac to purple flowers without a median stripe on the perianth segments, and a perianth tube equal in length to the perianth segments. Another diagnostic character is the extremely short staminal filaments. Molecular studies show that *P. paucifolia* is closely related to *P. corymbosa*, but the two species can easily be distinguished because of the corymbose inflorescence of *P. corymbosa* and the racemose one of *P. paucifolia*. *P. paucifolia* also has only two leaves, whereas *P. corymbosa* usually has 4-6 leaves. The flowers of *P. corymbosa* are lighter in colour, with a darker median stripe on the dorsal surface of the perianth segments and the perianth tube is also slightly shorter in length than the perianth segments.

Geographical distribution and ecology

P. paucifolia is restricted to the coastal granite and limestone outcrops of the Paternoster and Langebaan areas in the Western Cape Province (Figure 8.5.3). The plants grow in quite densely populated colonies scattered in this area. Flowering time is from April to June.

Material studied

- 3217** (Vredenburg): Noordhulp farm, Hopefield (-DD), *Barker 10370* (NBG); Paternoster (-DD), *Barker 10238* (NBG); Witklip farm, S of Vredenburg, *Barker 10173* (NBG); Vredenburg (-DD), *Matthews s.n.* (NBG); Vredenburg (-DD), *Matthews 689/30* (NBG); Paternoster (-DD), *Stephens 549/31* (NBG).
- 3318** (Cape Town): 5km South of Langebaanweg (-AA), *Snijman 841* (NBG); Between Malmesbury & Hopefield near Oude Post (-BC), *Salter 4409* (BOL).



Figure 8.5.2 *Polyxena paucifolia* (Van der Merwe 192, STEU).

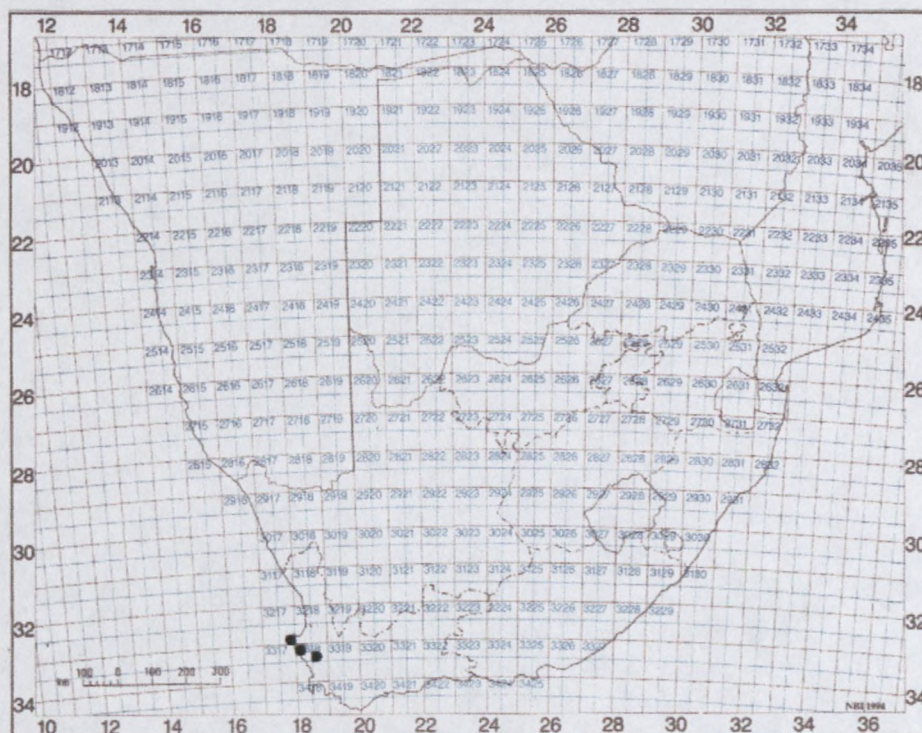


Figure 8.5.3. Geographical distribution of *Polyxena paucifolia*

8.6 *Polyxena pygmaea* (Jacq.) Kunth in Enumeratio Plantarum 4: 294 (1843); Müller-Doblies & Müller-Doblies: 85 (1997). Iconotype: Jacquin Icones 2 (16): t. 380 (1795).

Polyanthes pygmaea Jacq.: t. 380 (1795). Iconotype: Jacquin Icones 2 (16): t. 380 (1795).

Massonia violacea Andr.: t. 46 (1797). Iconotype: Andr. in Bot. Rep. 1: t46 (1797).

Hyacinthus bifolius Boutelou ex Cav.: 14 (1802). Iconotype: Cav. in Anal. Cienc. Nat. 5: 14 fig. 1 (1802).

Bulb: ovoid, ca. 12mm in diameter. **Leaves:** 2, lanceolate, erect, glabrous, narrowed gradually into the base, ca. 80mm x 25mm. **Inflorescence:** sub-corymbose; peduncle up to 15mm long; **bracts** small, lanceolate, membranous; **pedicels** 5–15mm long. **Flowers:** white to lilac, cylindrical, slightly dilated at the throat; **perianth tube** very narrow, ca. 20mm long, 3 times longer than the perianth segments; **perianth segments** oblong-lanceolate, falcate, spreading from the base, strongly recurved, ca. 6mm long. **Stamens:** 6, biseriate, strongly exserted beyond recurved segments, 3 longer stamens almost equal to perianth segments; **anthers** minute, oblong. **Ovary:** small, 4mm long, 1mm in diameter; **style** equal to the length of the tube, 20mm long; **stigma** minute, simple. **Capsule:** small, tri-lobed; **seeds** many, black, glossy (Figure 8.6.1).

Diagnostic features and affinities

Polyxena pygmaea (Figure 8.6.2) is characterised by white or lilac flowers with an extremely long and narrow perianth tube, strongly reflexed perianth segments and stamens which are exserted beyond the reflexed perianth. A long perianth tube can also be found in *P. longituba*, but the two

species can easily be distinguished on the base of leaf form, which is linear and canaliculate in *P. longituba* and lanceolate in *P. pygmaea*. The flowers of *P. longituba* are also more robust than the delicate flowers of *P. pygmaea*. Molecular studies show that *P. pygmaea* is most closely related to *P. corymbosa* and *P. paucifolia*, however, *P. pygmaea* can easily be distinguished from both of these species by leaf form and floral structure.

Geographical distribution and ecology

Polyxena pygmaea is known from two areas that are relatively isolated from each other, occurring in the Riversdale area and also in Namaqualand (Figure 8.6.3). The species grows on sandy flats, or sometimes in rocky localities on calcareous outcrops. Flowering time is from May to June and the flowers are highly scented.

Material studied

- 3018** (Kamiesberg): Rhebokskloof near Eselsfontein in the Kamiesberg (-AC), *Snijman 262* (NBG); Kamiesberg near Leliefontein (-AC), *Van Heerde s.n.* (BOL); Kamiesberg Namaqualand (-AC), *Van Heerde 59* (BOL); 20 miles NE of Garies (-CA), *Salter 6676* (BOL).
- 3421** (Riversdale): Riversdale (-AB), *Ferguson s.n.* (BOL); Middeldrift near Albertinia (-BA), *Muir 291* (BOL).

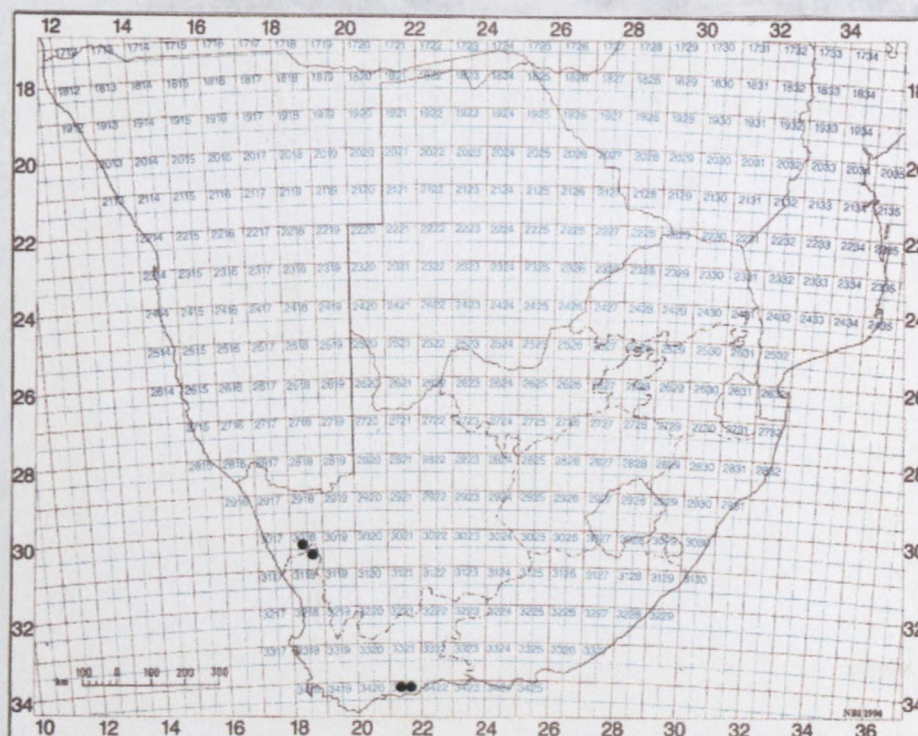


Figure 8.6.3. Geographical distribution of *Polyxena pygmaea*



Figure 8.6.2 *Polyxena pygmaea* (Van der Merwe 102, STEU).

CHAPTER 9

TAXONOMIC TREATMENT OF THE GENUS *WHITEHEADIA* HARVEY

9. ***Whiteheadia* Harv.** The genera of South African plants ed. 2; 396 (1868); Baker: 226 (1873); Baker: 418 (1897); Engler: 3 (1930); Phillips: 194 (1951); Obermeyer: t. 1450 (1965a); Sölch *et al.*: 74 (1970); Jessop: 433 (1976); Müller-Doblies & Müller-Doblies: 79 (1997); Goldblatt & Manning: 108 (2000); Williams: 617 (2000). Type: *Whiteheadia latifolia* Harv. = *W. bifolia* (Jacq.) Baker.

Bulb: subglobose, 20–30mm long, *ca.* 25mm in diameter. *Leaves*: 2, pale green, glabrous, fleshy to almost succulent but fragile, prostrate, 80–400mm x 60–250mm, elliptic, apex obtuse, with conspicuous depressed longitudinal veins. *Inflorescence*: spicate, 55–150mm in length with a terminal tuft of green bracts forming a coma, extending to 300mm when in fruit; bracts large, persistent, green, widely ovate, acuminate, 25–40mm x 12–20mm. *Flowers*: pale green with a thin, white margin, fleshy, nestling in an open spreading bract; *perianth tube* cup-shaped, 4–8mm long, 15–20mm wide; *perianth segments* deltoid to ovate, semi-erect, 5–7mm long. *Stamens*: 6, basally fused with the perianth tube; *filaments* erect, forming a white, open cup, 2.5mm high at the mouth of the perianth tube; upper part of filaments free, firm, curved inwards, 8mm long, greenish in colour; *anthers* 2.5–3.5mm long. *Ovary*: obtriangular, tapering to the base, dark green, 5mm long; *style* terete, 5mm long, slightly arched, tapered to the stigma; *stigma* simple, minute. *Capsule*: loculicidal, obtriangular, the side-walls extending into 3 broad, obtuse, papery, transparent wings, 15–25mm long, surrounded at the base by the persistent perianth with a persistent style; *seeds* many, shiny black, globose. (Figure 9.1.1)

A Monotypic genus

- 9.1 ***Whiteheadia bifolia* (Jacq.) Baker** in Journal of the Linnean Society, Botany 13: 226 (1873); Phillips: 194 (1951); Obermeyer: t. 1450 (1965a); Jessop: 433 (1976); Müller-Doblies & Müller-Doblies: 79 (1997); Goldblatt & Manning: 108 (2000). Iconotype: Cape of Good Hope, without precise locality or collector, Jacq., Icones 2 (16): 21, t. 449 (1795).

Eucomis bifolia Jacq.: 215 (1791); Jacq.: 21, t. 449 (1795); Jacq.: t. 840 (1805); *Basilea bifolia* (Jacq.) Poir.: 591 (1810). Iconotype: Cape of Good Hope, without precise locality or collector, Jacq., Icones 2 (16): 21, t. 449 (1795).



Figure 9.1.1 *Whiteheadia bifolia* (a) flowering plant x 1; (b) longitudinal section of the flower x 2.

Melanthium massoniaefolium Andr.: t. 368 (1804). Iconotype: “in the Hibbertian collection”, Andr. Bot. Rep. 6: t. 368 (1804).

Whiteheadia latifolia Harv.: 396 (1868); Baker: 418 (1897). Type: Modderfontein, Namaqualand, Rev. Henry Whitehead s.n. (TCD, holo).

Diagnostic features and affinities

Whiteheadia bifolia (Figure 9.1.2) is characterised by a spicate inflorescence with each flower nestled on a large open, spreading bract. The leaves are also characteristic in that they are large and fleshy to almost succulent, but extremely fragile and even drops of water dripping onto the leaves can injure them. DNA studies show that the genus *Massonia* is the closest genus to *Whiteheadia*. *W. bifolia* does not belong to the same clade as *Massonia*, but rather resolves on a branch of its own just outside of the *Massonia* clade. *W. bifolia* does show a superficial resemblance to *M. depressa* with regard to flower form, as both species have flowers with a wide, cup-shaped perianth tube. The two species can, however, be easily distinguished because of the differences in inflorescence, which is a spike in *W. bifolia* and capitate in *M. depressa*.

Geographical distribution and habitat ecology

Whiteheadia bifolia occurs in the western part of the Western Cape Province and Namaqualand and has also been recorded from the extreme south of Namibia (Figure 9.1.3). It grows amongst rocks and boulders, usually in pockets of humus-rich soil, in both dry and damp habitats. Flowering time is from June to July and flowers are unscented.

Taxonomic note: Müller-Doblies and Müller-Doblies (1997) described a new species of *Whiteheadia* from Namibia, thus altering the monotypic status of this genus. They have named the species *W. etesionamibensis* U. & D. M-D. According to their description, this species differs from *W. bifolia* with respect to the perianth tube which is much shorter (2–3mm) than that of *W. bifolia* (4–8mm) and the perianth segments which are much longer (in *W. etesionamibensis* 9.5–14mm and in *W. bifolia* 5–7mm). Unfortunately, although they state that an isotype of this newly described species is housed at the NBG herbarium, the herbarium has not as yet received such a specimen and I have been unable to verify the status of this species.

Material studied:

–2917 (Springbok): near Klipfontein (-BA), Bolus 6565 (BOL); Steinkopf (-BC), Marloth 6766 (STE); Mesklip (-DD), Lewis 1396 (SAM).

–3017 (Hondekliptaai): Kamieskroon (-BB), Thorne s.n. sub SAM 48856 (SAM); Brakdam (-BD), Leighton 1373 (BOL).



Figure 9.1.2 *Whiteheadia bifolia* (Van der Merwe 99, STEU).

- 3018 (Kamiesberg): Studer's Pass, Kamiesberg (-AC), *Thompson 425* (STE); Giftberg (-CB), *Compton 20842* (NBG).
- 3119 (Calvinia): Top of Botterkloof (-CD), *Esterhuysen 3871* (BOL).
- 3218 (Clanwilliam): Kransvleibergen (-BB), *Leipoldt 322* (SAM).
- 3219 (Wuppertal): Pakhuis Pass (-AA), *Esterhuysen 3157* (BOL).

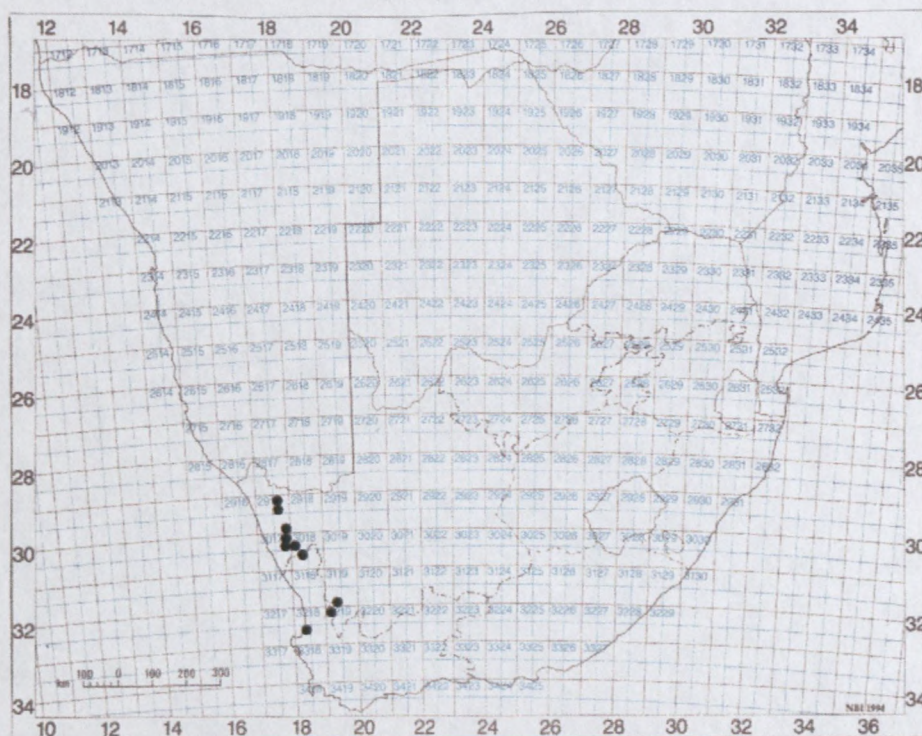


Figure 9.1.3. Geographical distribution of *Whiteheadia bifolia*

ACKNOWLEDGEMENTS

I would like to extend my most grateful thanks to the following:

- My promoter Dr. Bettie Marais for her enthusiasm, guidance and motivation, without which this thesis would never have reached completion.
- My co-promoter Prof. Dirk Bellstedt for his advice and guidance, especially with the molecular study.
- Mrs Coral de Villiers for her expert technical assistance with the molecular study.
- Prof. Eric Harley for doing the computer analysis of the molecular study
- The curators of the different herbaria listed in chapter 2, whose collections are on loan at the University of Stellenbosch or who allowed me to study their collections.
- Dr. John Manning for supplying me with leaf material of *M. sessiliflora* and *D. comata* and photos of *D. comata* and *D. namaquensis*.
- Rhoda and Cameron McMaster for collecting and sending to me specimens of *M. jasminiflora*.
- My mother for her love and support and for always being available for 'babysitting duties', without her help I would never have had the opportunity to work on this thesis.
- My father for his moral support and for all his help with collecting plants and looking after my living collection.
- My husband, Andie, for his continuous support and motivation and my children, Joshua, Jessica and Danielle for their patience with me finishing this thesis.
- My friends and family for their support and words of encouragement.

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