A taxonomic revision of the genera of the subtribe Dracophilinae (Aizoaceae: Ruschioideae).

A thesis submitted in fulfillment of the
requirements for the degree of

MASTER OF SCIENCE
of
Rhodes University

by
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January 2006

ABSTRACT

Namibia, Juttadinteria and *Dracophilus,* the three genera belonging to the subtribe Dracophilinae Schwantes (Aizoaceae: Ruschioideae) were revised. Macro-morphology, leaf anatomy and micro-morphology of leaf epidermides, pollen, tapetal orbicules and seed were studied in order to test taxon limits, to determine relationships between taxa, and to improve knowledge of their characteristics as well as the taxonomy of the subtribe.

The investigation was based on herbarium specimens, field observations and cultivated, living plants. Phenetic cluster analyses were used to confirm species while intergeneric and interspecific relationships of the taxa so indicated were later tested by means of a phylogenetic analysis.

The existence of the three genera was provisionally upheld by this study although phylogenetic analysis showed *Namibia* nested as a strongly supported monophyletic group within a poorly supported *Juttadinteria*. Further work is needed to clarify whether *Namibia* should be sunk into *Juttadinteria.* The latest treatments of *Juttadinteria* and *Dracophilus* by Hartmann (2001) were supprted. However, in contrast to her latest treatment of *Namibia, N. pomonae* was sunk into *N. cinerea* and *N. ponderosa* was reinstated and typified. *Juttadinteria* was found to be a poorly resolved genus with many intergrading and overlapping characters, possible due to recent speciation. Possible subspecific groups within *J. deserticola* and *J. simpsonii* were indicated by the phenetic study but further work is needed before any formal infraspecific taxonomic rank can be assigned to them.

Detailed descriptions of the nine elucidated species and the three genera as well as new keys for their identification are provided in order to facilitate further work in this group. Distribution maps are provided for the genera and species, and the subtribe. Variation of character states within the subtribe, distribution area, ecology and biology are discussed.

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PREFACE

The research work described in this thesis was undertaken in the Department of Botany, Rhodes University, Grahamstown, under the supervision of Prof. N.P. Barker.

These studies represent original work by the author and have not been submitted in any form to another university. Where use was made of the work of others it has been duly acknowledged in the text.

CHAPTER 1 INTRODUCTION

Aizoaceae is the largest leaf succulent family worldwide (Klak 2004). Within this group the combined Mesembryanthemoideae and Ruschioideae (previously Mesembryanthemaceae Fenzl, a term which I will use here for ease of reference) were identified by Chesselet *et al.* (1995) as a taxonomic priority in southern Africa, where they represent 63% of the succulent flora and exhibit a high proportion of endemism at both species and genus levels (Chesselet *et al.* 2000).

Commonly known as 'mesembs' or 'vygies', this family exercises an addictive fascination for those who work on it, yet suffers from a paucity of herbarium material (especially in southern Africa) and, as indicated by Chesselet *et al.* (1995), a lack of expertise in identification and species-level taxonomic treatments. The recent renaissance in mesemb taxonomy, notably in South Africa (e.g. Klak & Linder 1998; Klak 2000, 2001; Chesselet & Van Wyk 2002; Chesselet *et al.* 2002, 2003; Dold 2002; Klak *et al.* 2003a), may be attributed to a certain extent to the stimulus provided by the work of Chesselet *et al.* (1995), in which they summarised the status of the taxonomy, particularly at genus and species level, and offered suggestions for research priorities in the group. Prior to this much of the more recent work in the Mesembryanthemaceae had been done overseas by workers such as Hartmann (e.g. 1978, 1986, 1987, 1988), Bittrich (1986) and Ihlenfeldt (e.g. 1960, 1994) in Germany, and Hammer (e.g. 1993, 1995) in the United States of America.

Several factors complicate taxonomic work in the Mesembryanthemaceae. These include their (often extremely) succulent nature and phenotypic plasticity. The latter problem affects in particular the plants' vegetative morphology, which varies greatly in response to environmental conditions such as moisture and insolation, especially in cultivation but also to a certain extent *in situ*. As a result of succulence herbarium material is often inadequate or poor, and for the purpose of taxonomic revision extensive field observations and the study of live specimens are virtually mandatory. In addition, the use of more constant (usually reproductive) characters is necessary for the production of a working taxonomy and useful keys to facilitate plant identification. These keys are a fundamental requirement for the practice of taxonomy and are also the most useful products for many end-users of taxonomic information.

Subtribe Dracophilinae Schwantes

Suprageneric classification in the Mesembryanthemaceae has thus far proved to be an intractable problem (Chesselet *et al.* 1995, 2000), however recently this challenge has been taken up by a number of South African taxonomists, resulting in a new tribal classification based on floral nectaries (Chesselet *et al.* 2001, 2002). In the scheme proposed by Schwantes which was revised and completed in collaboration with Straka and Ihlenfeldt (in Herre 1971), *Dracophilus, Juttadinteria* and *Namibia* were assigned to the subtribe Dracophilinae. The characteristics they used to delineate the subtribe are broad, superficial and not very useful, although obvious similarities do exist:

" Compact, prostrate shrubs with thick leaves. Capsules many-celled, with developed or small rudimentary cell lids or without these."

In her informal and provisional grouping of mesemb genera, Hartmann (1991,1993) assigned these three genera to the much larger Dracophilus group. The features listed for the group are quite broadly stated and vary greatly between genera:

" Plants perennial, leaves xeromorphic with distinct differences in cell sizes, i.e. heterocellular, surface rarely sticky; flowers mostly solitary, with a lophomorphic nectary ring, rarely five separate glands; without, rarely with filamentous staminodes; capsules mostly 5-locular, with or without covering membranes, without closing bodies, with broad valve wings."

Perhaps the most useful synthesis of the features shared by the three genera was provided by Walgate (1939):

"The group is distinguished by its solitary, terminal flowers, 4-5 sepals, pink or white petals, absence of staminodes, stamens collected into a cylinder or a cone, yellow anthers, white filaments, usually pubescent at the base, annular, crenulate disc, 5-25 yellow-green, narrow-subulate stigmas, valves of the capsule expanding widely, and parietal, brown seeds. The plants are low-growing with woody stems, whitish succulent leaves, and thick, woody roots."

The work of Chesselet *et al.* (2002) did not affect placement of the subtribe Dracophilinae in the tribe Ruschieae Schwantes, Ihlenf., Schwantes & Straka within the subfamily Ruschioideae Schwantes, where it may be regarded as one of the highly succulent groups.

Taxa included in this subtribe occur in the winter-rainfall area of the Namib Desert in the south-western reaches of Namibia and the extreme northern reaches of the Richtersveld in South Africa, between 26° and 28° 45' southern latitude and 15° to 17° eastern longitude. Most of the species are strict Namibian endemics, with several of very restricted habitat and distribution within that range. Their highly succulent nature may be regarded as a response to harsh and arid climatic conditions where median annual rainfall is less than 100 mm (Mendelsohn *et al.* 2002), solar insolation can be relatively high (although it is fog-mediated (Olivier 1995)), and prevailing persistent southerly and south-westerly winds often exceed speeds of 40 km/h (Mendelsohn *et al.* 2002), resulting in sand abrasion of any plant or object in their paths. This is discussed in more detail in Chapter 8.

Although Chesselet *et al.* (1995) suggested that revision of the genera of the subtribe Dracophilinae was only a medium priority, the fact that in Namibia they occur largely in very limited habitats within the Sperrgebiet raises their priority status. Previously this area ("Diamond Area No. 1") received *de facto* protection by virtue of highly restricted and controlled access due to an exclusive mining license agreement. The year 2001 saw the end of the NAMDEB (previously De Beers) monopoly on the area and economic prospecting licenses covering almost the entire area were snapped up by mining companies. A new land use plan addressing broad conservation concerns has been drawn up and the area is to become a National Park. However, mining and various other commercial activities will be allowed within the new park, so it remains essential that species of special concern, such as those of extremely limited distribution, be defined and their distribution/habitat mapped. Useful keys to facilitate identification of these species is also a priority. Most of the species of the Dracophilinae are almost entirely restricted to the Sperrgebiet. They form a small and discrete (probably natural) group within the mesembs that includes a number of species of highly restricted occurrence. The need for this study was identified during routine fieldwork in the Sperrgebiet during the period 1996 to 2000, when it was found that none of the current taxonomic concepts for the group were entirely consistent with field observations and that available species descriptions and keys were often confusing.

The following treatment of the three genera is based on field observations and collections undertaken between 1996 and 2005, and on herbarium specimens from B, BOL, HBG, K, M, NBG, PRE and WIND .

Taxonomic review

The earliest records of species to later be included in the Dracophilinae were those of *Mesembryanthemum cinereum* and *M. deserticolum*, collected at Angra Pequena (now Lüderitzbucht) by Dr. R. Marloth in 1910 during his extensive travels in Great Namaqualand. During the next twelve years three more species were described, including *M. dealbatum* from a specimen brought back by Prof. Pearson from the Percy Sladen Expedition to the Orange River in 1910, *M. elizae*, now considered a synonym of *J. deserticola*, and *M. ausense*.

The year 1923 saw Dinter publish an account of his travels in the then South West Africa, in which he listed a further six species – *M. pomonae, M. simpsonii, M. kovisimontanum, M. montis draconis, M. delaetianum* and *M. suavissimum*. No Latin diagnoses were offered, but rather full descriptions in German, with localities, collection numbers and brief discussions comparing them to other taxa. *M. pomonae* had the highest number of stigmata ever recorded for a mesemb (25), but has never reliably been recorded or collected since his original collection, for which no type material is available. It is here also that he noted a relationship between six species of *Mesembryanthemum* (*M. pomonae, M.*

cinereum, M. deserticolum, M. kovisimontanum, M. simpsonii and *M. suavissimum*) all of which were later placed in *Juttadinteria* or *Namibia*. Although he described *M. montis draconis* and *M. delaetianum* (later assigned to *Dracophilus*) at the same time, he did not include them in the group.

The genus *Juttadinteria* was established by Dr. G. Schwantes in 1926 and divided into three subgenera, namely *Eu-Juttadinteria, Dracophilus* and *Namibia*. At that time he assigned all eight of the above species plus *M. ausense* and *M. ponderosum* to *Juttadinteria* (Table 1.1), mentioned that he had not examined flowers of subgenus *Namibia*, and indicated that he would propose the name *Namibia* Dinter and Schwantes should it prove to be an independent genus. *Mesembryanthemum tugwelliae* was also included in this work but later transferred to *Hereroa* by Louisa Bolus (1928-1935).

In 1927 Schwantes established *Namibia* (1927a) and *Dracophilus* (1927b) as separate genera, effectively limiting the application of *Juttadinteria* to species included in the subgenus *Eu-Juttadinteria*.

Table 1.1: Taxa assigned to the subgenera of *Juttadinteria* by Schwantes (1926)

Subgenus	**Assigned species**
Dracophilus	*M. delaetianum* Dinter = *J. delaetiana* (Dinter) Schwantes *M. montis draconis* Dinter = *J. montis draconis* (Dinter) Schwantes *M. tugwelliae* L. Bolus = *J. tugwelliae* (L. Bolus) Schwantes
Eu-Juttadinteria	*M. suavissimum* Dinter = *J. suavissima* (Dinter) Schwantes *M. simpsonii* Dinter = *J. simpsonii* (Dinter) Schwantes *M. deserticolum* Marloth = *J. deserticola* (Marloth) Schwantes *M. kovisimontanum* (Dinter) = *J. kovisimontana* (Dinter) Schwantes *M. ausense* L. Bolus = *J. ausensis* (L. Bolus) Schwantes
Namibia	*M. cinereum* Marloth = *N. cinerea* (Marloth) Schwantes *M. pomonae* (Dinter) = *N. pomonae* (Dinter) Schwantes

Between 1927 and 1939, the year in which Walgate published the first complete revision of the three genera, a number of additional species were assigned to them. Louisa Bolus described *J. longipetala* and *J. tetrasepala* and transferred *J. insolita* and *J. albata* from *Mesembryanthemum* (Bolus 1928-1935). Schick and Tischer (1933) described *J. decumbens* and Walgate (1939) added *J. attenuata* and transferred *D. dealbatus* and *D. proximus*. Walgate also mentioned *J. elizae as* a dubious species and regarded *M. ponderosum* as invalidly published. Thus after Walgate *Juttadinteria, Dracophilus* and

Namibia were composed of eleven, four and two species respectively. According to her, all these species were distributed only in south-western Namibia and northern Namaqualand, with eleven of the seventeen being endemic to Namibia, three to South Africa, and three found in both countries, as indicated in Table 1. 2.

Table 1.2: Taxa included in *Juttadinteria, Dracophilus* and *Namibia* by Walgate (1939).

Species	Distribution	
	Namibia	**South Africa**
Dracophilus dealbatus (N.E. Br.) Walgate	●	●
D. delaetianus (Dinter) Dinter & Schwantes	●	
D. montis draconis (Dinter) Dinter & Schwantes	●	
D. proximus (L. Bolus) Walgate	●	●
Juttadinteria albata L. Bolus	●	●
J. attenuata Walgate	●	
J. ausensis (L. Bolus) Schwantes	●	
J. decumbens Schick. & Tisch.		●
J. deserticola (Marloth) Schwantes	●	
J. insolita L. Bolus		●
J. kovisimontana (Dinter) Schwantes	●	
J. longipetala L. Bolus	●	
J. simpsonii (Dinter) Schwantes	●	
J. suavissima (Dinter) Schwantes	●	
J. tetrasepala L. Bolus		●
Namibia cinerea (Marloth) Dinter & Schwantes	●	
N. pomonae (Dinter) Dinter & Schwantes	●	

Subsequent workers have questioned the number of species accepted by her, and/or suggested that several are of an extremely variable nature:

In 1970 Friedrich treated this group for *Prodromus einer Flora von Südwestafrika* (Merxmüller (Ed.)1967-1972). He chose to lump all the species into *Juttadinteria,* although his key clearly divides them into three distinct groups corresponding to the three separate genera. Fundamental differences in characters such as capsule structure, number of sepals and leaf surface morphology make this treatment questionable.

Hartmann (1993) suggested that the number of species of *Namibia* is in reality only one, in *Juttadinteria* about five, and in *Dracophilus* three to four. However, this treatment was not accepted by Smith *et al.* (1998). Hartmann (2001) has recently done more work in which she has raised the number of species in *Namibia* to two, left *Juttadinteria* at five and reduced *Dracophilus* to two. This treatment, which differs substantively from Smith *et al.*, has been accepted by Germishuizen and Meyer (2003). Table 1.3 summarises these differences, comparing them to Walgate (1939).

Table 1.3: Species accepted by recent treatments, compared to Walgate 1939.

Taxon	**Walgate 1939**	**Smith *et al.* 1998**	**Hartmann 2001**
Dracophilus dealbatus	●	●	●
Dracophilus delaetianus	●	●	●
Dracophilus montis draconis	●	●	
Dracophilus proximus	●	●	
Juttadinteria albata	●	●	●
Juttadinteria attenuata	●	●	●
Juttadinteria ausensis	●	●	●
Juttadinteria deserticola	●	●	●
Juttadinteria elizae		●	
Juttadinteria insolita	●	●	
Juttadinteria kovisimontana	●	●	
Juttadinteria longipetala	●		
Juttadinteria suavissima	●	●	
Juttadinteria simpsonii	●	●	●
Namibia cinerea	●	●	●
Namibia pomonae	●		●
Namibia ponderosa		●	

In order to compare the merits of the various treatments to field observations (i.e. 'intuitive species') and reduce confusion, especially for workers in the field, this study uses morphological, anatomical and phenological characters in an attempt to:

- confirm or establish genus and species limits and produce a useful taxonomy
- provide detailed descriptions
- provide distribution maps and useful field keys to the genera and species.

Chapter 6 looks at intergeneric relationships, while Chapter 7 offers a brief overview of the characters of the subtribe as a whole. A discussion on distribution, ecology and biology forms the final chapter.

CHAPTER 2: MATERIALS AND METHODS

In this thesis each genus in the subtribe Dracophilinae is first studied separately in order to establish species limits and to determine and describe the key features of each species. The following three chapters discuss the genera *Namibia, Juttadinteria* and *Dracophilus* respectively. As these three chapters use the same methodology, the methods employed are provided here as a separate chapter.

Fieldwork, collections and observations

The study is based on field observations and collections of 158 live plants made during field trips to the southern Namib (1996-2005). Material was also collected *in situ*, fixed in FAA, and preserved in 70% ethanol for later examination. In addition, four hundred and ninety three dried collections from B, BOL, HBG, K, M, NBG, PRE, and WIND were investigated. All gross measurements of leaves, flowers and capsules were done using a Vernier calliper. Leaf width and thickness were taken at the widest point, which was sometimes at the base and sometimes below the apex. Flowers were sectioned for measuring of individual parts but overall flower diameter was measured as it is seen in the fresh flower, without spreading the petals flat. Qualitative characters such as colour, sharpness of leaf apex and seed shape were subjectively asssessed. Some characters appear in different forms (e.g. leaf lenth minimum, maximum and mean) in the analysis, which affect the results of a phenetic analysis. The decision to include several data points for a single character in order to reflect variation adequately was influenced by the following:

- Leaves in this group are very long-lived, and appear to grow throughout their lives. It is not possible decide at which point a leaf is mature. Variation is thus considerable.
- The size of organs, in particular reproductive organs, appeared to be influenced by moisture availability.
- Many of the herbarium specimens were *ex hort* and their characters might thus also be expected to be somewhat distorted. This phenotypic plasticity has been discussed in Chapter 1.

Obtaining comprehensive, or even reasonably complete, data sets for each sample proved to be extremely difficult. The study area is very remote (a round trip of over 2000 km), and permits to enter the highly restricted diamond area as well as the Namib-Naukluft National Park have to be applied for well in advance, making *ad hoc* access impossible. Information on rain and conditions (such as flowering) prevailing in the area is virtually unavailable with the result that, more often than not, the plants were not in flower or were flowering very poorly during the study period, which unfortunately covered an extended drought period in the southern Namib. Due to poor flowering as a result of the drought, capsules were often very old and did not yield seed. Collecting large numbers of live plants was out of the question due to the taxa being protected and often rare and/or range restricted. In cultivation few or no capsules or seeds mature, suggesting that cross-pollination (xenogamy) is required in order to set viable seed. Herbarium material is often poor and, by virtue of being pressed, never yields a full data set.

Species delimitation: Phenetics and search for diagnostic characters

A phenetic species concept, relying on gaps in character variation, was followed in this thesis, although phylogenetic analysis was also undertaken to assess evolutionary relationships between the putative groups.

A phenetic character variation analysis was undertaken on each genus in order to test similarity and resolve species limits. These studies were undertaken using NT-SYS-pc^{TM} version 2.02k. Data sets for phenetic analysis were recorded in Excel^{TM} spreadsheets. Details regarding numbers and types of characters used, as well as the results of the analyses are given for each genus individually in Chapters 3 to 5. Missing data points were recorded as 999. As a result of problems associated with acquiring material in all stages of flowering and fruiting, most data sets were data deficient to a greater or lesser degree. However, samples with missing data were nevertheless retained unless severely data deficient. It must also be noted that the software utilized (NTSYS-pc; Rohlf 1988) only compares pairs of Operational Taxonomic Units on the basis of characters for which data are mutually available.

The process of finalising a suitable character set for each genus was not a haphazard affair. Initially a large number of characters were recorded uncritically. Analysis of these data sets revealed that some characters and / or states were poorly defined and coded. These were re-worked or excluded and the data reanalyzed until a final character set was obtained which included those characters that appeared to reflect observable differences.

The final data set for each genus was standardized, and triangular matrices of similarities were calculated using both the Manhattan and the Euclidian distance algorithms. Clustering algorithms, which estimate similarity between objects and are useful in summarising relationships (Crovello 1970), were used to generate phenograms. The unweighted pair-group method with arithmetic averages (UPGMA) was favoured here because it usually produces the best phenograms as measured by the Cophenetic Correlation Coefficient (CCC), a measure of how effectively the original similarity matrix has been summarized by the 2-dimensional phenogram. Although the Manhattan distance algorithm is affected less by different scales of measurement in the original matrix than Euclidean distance calculations (Duncan & Baum 1981), comparison of the phenograms and the Cophenetic Correlation Coefficients indicated that these methods produced very similar results. The phenograms shown in this thesis were produced using the Euclidian distance algorithm. These phenograms were inspected visually in order to make taxonomic decisions and confirm or refute intuitive species concepts based on field observations.

In order to further discriminate and describe the species obtained in the phenetic analyses, additional characters were sought by means of SEM studies of leaf epidermides, pollen and seed surfaces of selected, representative samples collected in the field. All studies were done on at least three, often more specimens per putative species, whenever possible from different populations. Vouchers are listed in the applicable chapters for each genus.

Once the phenetic analysis had identified putative taxa (species), additional characters were sought to further distinguish and delimit these. This additional information came from studies on leaf, seed and pollen using light and scanning electron microscopy.

Leaf anatomy

Leaf anatomy of six species was investigated for generic comparison. Vouchers are listed in Table 2.1. Material for sectioning was dehydrated in an alcohol series, embedded in wax and sectioned at 15 μm using a Leitz Wetzler rotary microtome. Sections were floated in a water bath at 45 °C, then onto slides. Slides were dried at 45 °C for 12 hours and then dewaxed with a xylol and alcohol series before immersion in safranin for 12 hours. They were then dehydrated in an alcohol series, stained in Fast Green for 15 seconds, immersed in Clove oil and cleared with a xylol series. The sections were then permanently mounted using Canada Balsam and dried for 7 days. Slides were examined and photographed using an Olympus BX50 light microscope and camera mount.

Table 2.1: Voucher specimens for anatomical study.

Species	Voucher
Namibia cinerea	*CM 1399*
Namibia ponderosa	*CM 1693*
Dracophilus dealbatus	*CM 1524C*
Juttadinteria albata	*CM 2236*
Juttadinteria deserticola	*CM 1682*
Juttadinteria kovisimontana	*CM 1661*

Scanning electron microscopy

All SEM studies were carried out using a JEOL-JSM 840 scanning electron microscope at the Electron Microscope Unit, Rhodes University. All material was air-dried, attached to SEM stubs using double-sided tape, sputter-coated with gold, using a Balzers coating unit, and examined at 12 kV.

Leaf material for SEM was sectioned and air-dried in the field to prevent possible alteration of epicuticular waxes by oven-drying and to exclude changes that might occur *in hort*. Sections examined were taken from the middle of lateral leaf surfaces as these areas are most exposed to harsh environmental elements such as wind-blown sand and so may be expected to exhibit most clearly any adaptive characters. The sections were examined with and without epicuticular waxes in order that both waxes and surface structures might be seen more clearly. Wax was removed by twenty minutes immersion in chloroform with gentle agitation every five minutes. No critical-point drying was done because this dissolves epicuticular waxes in mesembs (Hartmann 1979, 1991).

Pollen for SEM was removed directly from anthers. No acetolysis was done, as this process is primarily for the purpose of removing excess organic material from pollen samples (Faegri & Iversen 1989). This was regarded as superfluous because the pollen was removed directly from flowers, not collected in soil samples. Pollen grains were measured on SEM micrographs using a Vernier calliper. Counts of luminae in and spinulae on the tectum were performed on an area of 25 μm^2 on the mesocolpium at a point equidistant from both the poles and from the adjacent colpi. Cardboard frames were used to delineate the count areas on the scanning electron micrographs.

Seed for SEM was obtained by wetting ripe seed capsules to induce hydrochastic opening and seeds were removed directly.

Statistical analyses

Statistical analyses were done using STATISTICA Release 7. Where two groups were involved, and the data met the prerequisites (i.e. were normally distributed), samples were compared by means of a t-test and, similarly, those with more than two groups were compared by means of a one-way ANOVA utilizing the post-hoc Scheffé test. When data were not normally distributed simple "box-and-whisker" plots (indicating the minimum-mean-maximum) were used for illustrative purposes.

Provisional Red Data assessment

Species were assessed and assigned IUCN List Categories (IUCN 2001) using RAMAS (Akçakaya & Ferson 2001).

"What's the use of their having names" the Gnat said, "if they don't answer to them?"

"No use to them", said Alice, "but it's useful to the people that name them I suppose."

Alice through the Looking Glass
Lewis Carroll
December 1872

CHAPTER 3. *Namibia*

As discussed in Chapter 1, past workers have recognized different species of *Namibia.* Smith *et al.* (1998) recognised *N. cinerea* and *N. ponderosa,* while in the most recent treatment Hartmann (2001) recognised *N. cinerea* and *N. pomonae.* She mentioned that *N. cinerea* may be white or pink-flowering, and noted that the white-flowering *N. pomonae* is poorly known, with no type material available. In fact no material belonging to this taxon could be found at all. The "botanic garden at Lichtenstein" referred to by Dinter in his original description is presumably the garden of the Rusch family on Farm Lichtenstein near Windhoek, where he says that the few plants he found at the type locality near Pomona were planted and subsequently flowered. There is no sign of them there today. *Namibia cinerea* is the only one of the three described species of *Namibia* whose validity is undisputed.

Field observations strongly indicated that two species of *Namibia* exist, one pink-flowering species with a more northerly distribution on granitic-gneiss slopes and one white-flowering species distributed further south, mainly on dolomitic and quarzitic substrates. To clarify this issue, a phenetic study of 51 specimens was undertaken in order to resolve species number and limits. Character types and sources are listed in Table 3.1. The characters used and the full data set are presented as Appendix 1. The phenogram obtained (Figure 3.1) supports the existence two taxa, the characters of which best coincide with the type descriptions of *N. cinerea* and *N. ponderosa*, indicating that the relative data deficiency of the matrix had not skewed the data such that it provided no insight to the group. The Cophenetic Correlation Coefficient for the phenogram was 0.665.

Table 3.1: Summary of character types and sources used in the phenetic study of *Namibia.*

Organ/Source	Binary	Multistate	Quantitative
Leaf	4		
Flower		3	13
Fruit/Seed	1	1	7

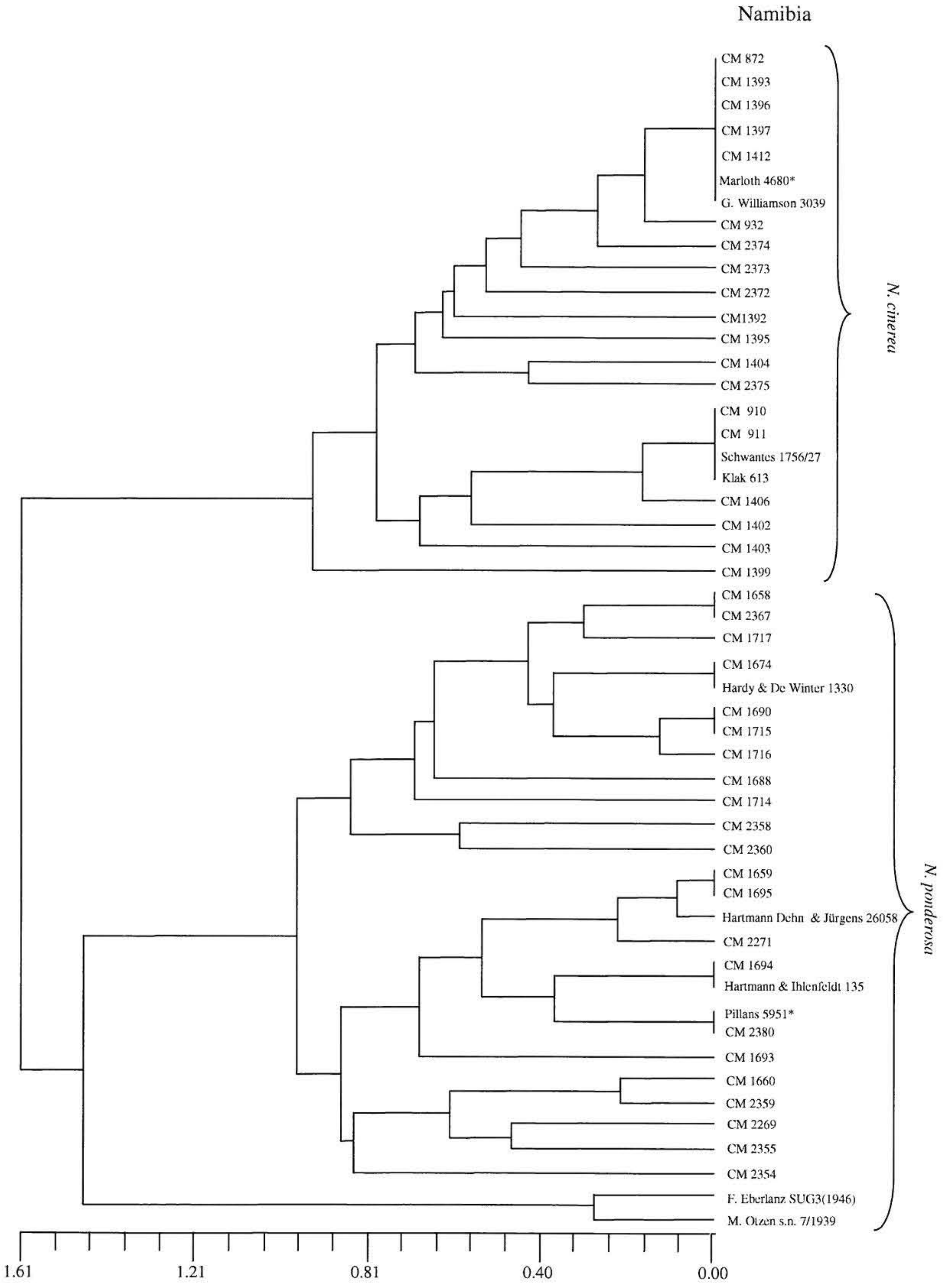


Figure 3.1: UPGMA phenogram for *Namibia* based on 29 characters. The data were standardized, and a triangular matrix of similarities calculated using the Manhattan distances algorithm. * = type specimen: Marloth 4680 = holotype *N. cinerea*; Pillans 5951 = holotype *Juttadinteria longipetala* (= *N. ponderosa*). CM = Coleen Mannheimer. CCC = 0.665.

Sixty-eight herbarium sheets and 37 live plants were inspected and additional micro-morphological investigations of leaf epidermides, pollen and seed of a small subset of samples were undertaken to assess differences between these two putative species. Voucher numbers for micromorphology are listed in Table 3.2.

Table 3.2: *Namibia* voucher specimens examined by SEM for micromorphological characters. * = specimen included in the phenetic study.

Species	**Voucher**	**Leaf surface**	**Pollen**	**Seed**
Namibia cinerea	*CM 1392**			●
	*CM 1399**			●
	*CM 1402**		●	●
	*CM 1404**	●		●
	*CM 2372**	●	●	
	*CM 2373**	●	●	
Namibia ponderosa	*CM 1693**	●	●	●
	*CM 1715**	●		
	*CM 1716**	●		●
	*CM 2269**			●
	*CM 2354**	●		
	*CM 2367**		●	
	CM 2369	●		
	*CM 2380**	●	●	

The *cinerea* group in the phenogram includes *Marloth 4680*, the holotype for *N. cinerea*. *Pillans 5951*, which falls into the *ponderosa* group, is the holotype for *Juttadinteria longipetala,* a synonym of *Namibia ponderosa. Namibia ponderosa* is therefore reinstated. *Namibia pomonae* is sunk into synonymy with *N. cinerea*. Character variation in and distinguishing features between the two species found here are discussed in the following pages.

3.1 Morphological characters

3.1.1 Habit

Namibia almost always exhibits a compact growth form with internodes entirely enclosed by the leaves, rarely developing one or two longer, more exposed, and spreading branches with age. The habit is essentially similar in both species.

3.1.2 Roots

Both species of *Namibia* have a short but distinct taproot and a spreading system of secondary roots. Root characters are not taxonomically useful.

3.1.3 Leaves

3.1.3.1 Macro-morphology and colour

Namibia leaves are all hypersucculent and fat-trigonous, but they differ between the two species in colour, and in character of the margins and apex. In *N. cinerea* leaves usually appear grey to grey-brown, and have rounded margins and blunt apices that always lack a mucro. In *N. ponderosa* the leaves usually appear pale green to light orange-brown, with distinct brownish margins that culminate in a recurved apex that often carries a blunt, but distinct and hard, mucro (Figures 3.2 A,B and 3.3). In addition to this, *N. ponderosa* occasionally carries a few rudimentary teeth on the leaf margin near the apex (Figure 3.3), another character never observed in *N. cinerea*. Leaf morphological characters are thus taxonomically useful in distinguishing the two species of *Namibia*.

Figure 3.2: *Namibia* leaves. A. *Namibia cinerea* (*C. Mannheimer CM 404*) showing grey leaf colour and blunt leaf apex; B. *N. ponderosa* (*C. Mannheimer CM 1716*) showing light green leaf colour and recurved, mucronate leaf apex.

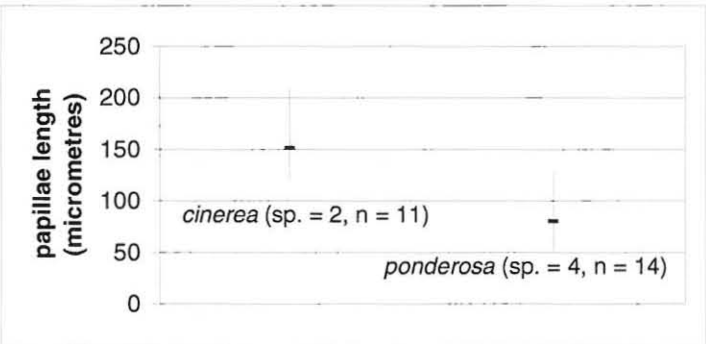
Figure 3.3: *Namibia ponderosa* (*C. Mannheimer CM 1695*) leaf pair, showing rudimentary marginal teeth and apical mucro.

3.1.3.2 Micro-morphology

Namibia leaves exhibit the xeromorphic-heterocellular condition, Type X6 as described by Ihlenfeldt and Hartmann (1982)) in which the cells vary in size. Leaf epidermal cells in both species of *Namibia* have isodiametric anticlinal walls, and periclinal walls with tapering papillae that result in a characteristic velvety appearance and texture. The length of these papillae varies between 52 and 110 μm. There is a statistically significant difference at the 95% confidence level between papillae length in the two species, with the papillae of *N. cinerea* being longer (Figure 3.4). The papillae of *N. cinerea* are large, slender, and closely spaced to one another (Figure 3.5 A), while those of *N. ponderosa* have a smaller but stouter appearance, and are more widely spaced (Figure 3.5 B). A t-test also confirmed a significant difference between counts of papillae per unit area (250 x 250 μm) at the 99% confidence level. Mean number of papillae in *N. cinerea* was 7 (sp. = 3, n = 14), compared with a mean of 10 in *N. ponderosa* (sp. = 6, n = 14), indicating that the overall size of the papillae is greater in *N. cinerea*. This difference is visible using a 10X handlens, and was mentioned by Dinter (1928) in his original publication of the species, together with flower colour. It is taxonomically useful in distinguishing the two species of *Namibia*.

Figure 3.4: A comparison of leaf papillae length range in *Namibia*

(horizontal bar = mean, sp.= specimens, n = papillae measured).



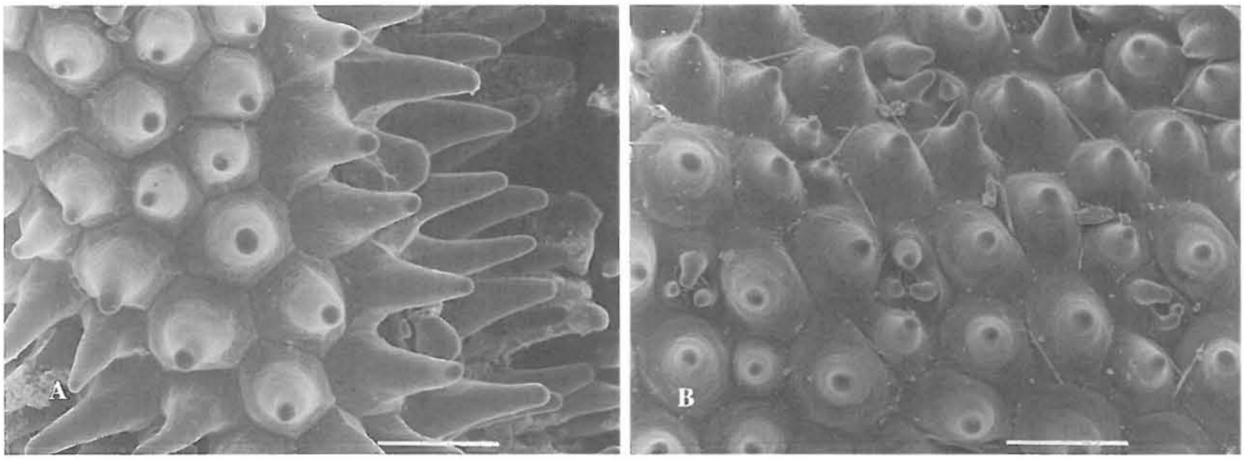


Figure 3.5: *Namibia* leaf epidermal papillae with wax removed, x 200. A. *Namibia cinerea* (*C. Mannheimer CM 1404*); B. *N. ponderosa* (*C. Mannheimer CM 1693*). Scale bars 100 μm.

3.1.3.3 Stomata

In *Namibia* the smallest epidermal cells are peristomatal cells with papillae that surround and often overarch the guard cells of the stomata (Figure 3.6) to form the 'hidden' stomatal type described by Ihlenfeldt and Hartmann (1982). The stomata are thus not sunken , but this configuration of cells results in the formation of what might loosely be described as an 'antestomatal chamber'. Lyshede (1979) suggests that such chambers retain moist air, thus decreasing residual stomatal transpiration by lengthening the water vapour diffusion pathway. Stomatal characters are not taxonomically useful in *Namibia.*

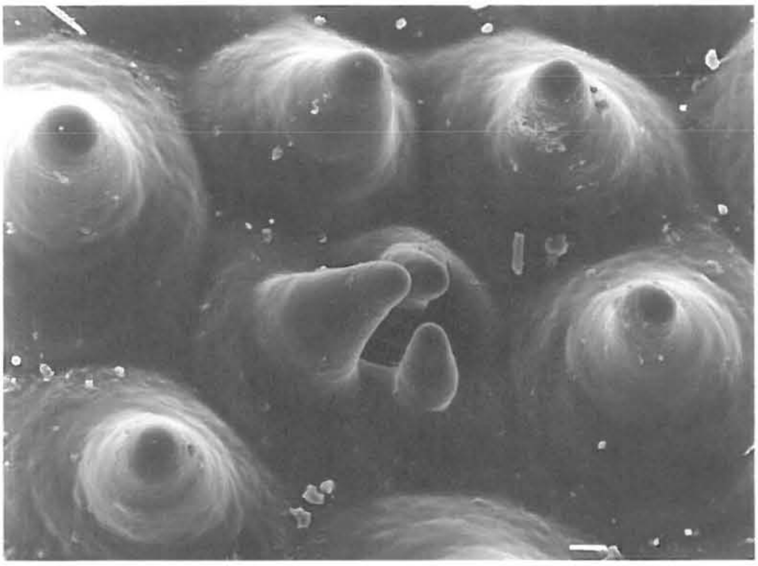


Figure 3.6: *Namibia ponderosa* (*C. Mannheimer CM 1693*), showing 'hidden' stomatal structure x 500 (after Ihlenfeldt and Hartmann 1982). Wax removed. Scale bar 10 μm.

3.1.3.4. Epicuticular waxes

The two species of *Namibia* differ in the expression of their epicuticular waxes. In both species the basal layer of wax occurs as thick, encrusting plates that fracture above the anticlinal walls (Figures 3.7 A and B). However, in *N. cinerea* there are scattered small blocks of wax on the upper surface of the plates (Figure 3.7 A and C), while in *N. ponderosa* the plates are usually covered by fine platelets that become fewer then disappear towards the apices of the papillae (Figure 3.7 B and D). The expression of epicuticular waxes is taxonomically useful at species level, but use is limited as they can only be viewed using an SEM.

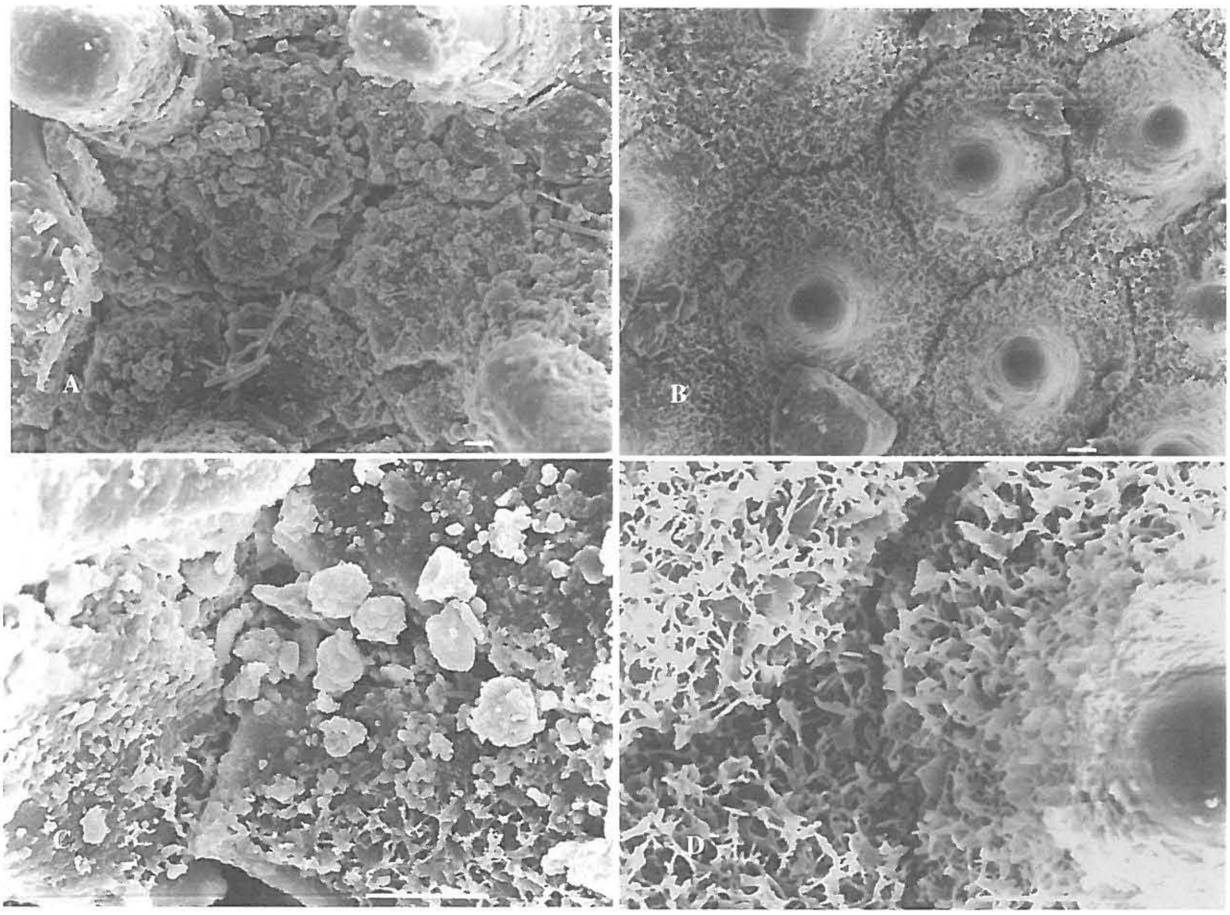


Figure 3.7: *Namibia* leaf epicuticular wax layer. A. *N. cinerea* x 500 (*C. Mannheimer CM 1404*); B. *N. ponderosa* x 500 (*C. Mannheimer CM 1716*); C. *N. cinerea* x 2000, showing scattered small blocks (*C. Mannheimer CM 2372*); D. *N. ponderosa*, showing fine platelets (*C. Mannheimer CM 1716*). Scale bars 10 μm.

3.1.4 Flowers

Namibia flowers appear sessile, as they are carried deep between pairs of very succulent leaves. They usually have a somewhat rectangular appearance (Figure 3.8 A - C) due to them being constrained by one pair of very succulent sepals and the uppermost leaf pair. The 'petals' are arranged in a single series.

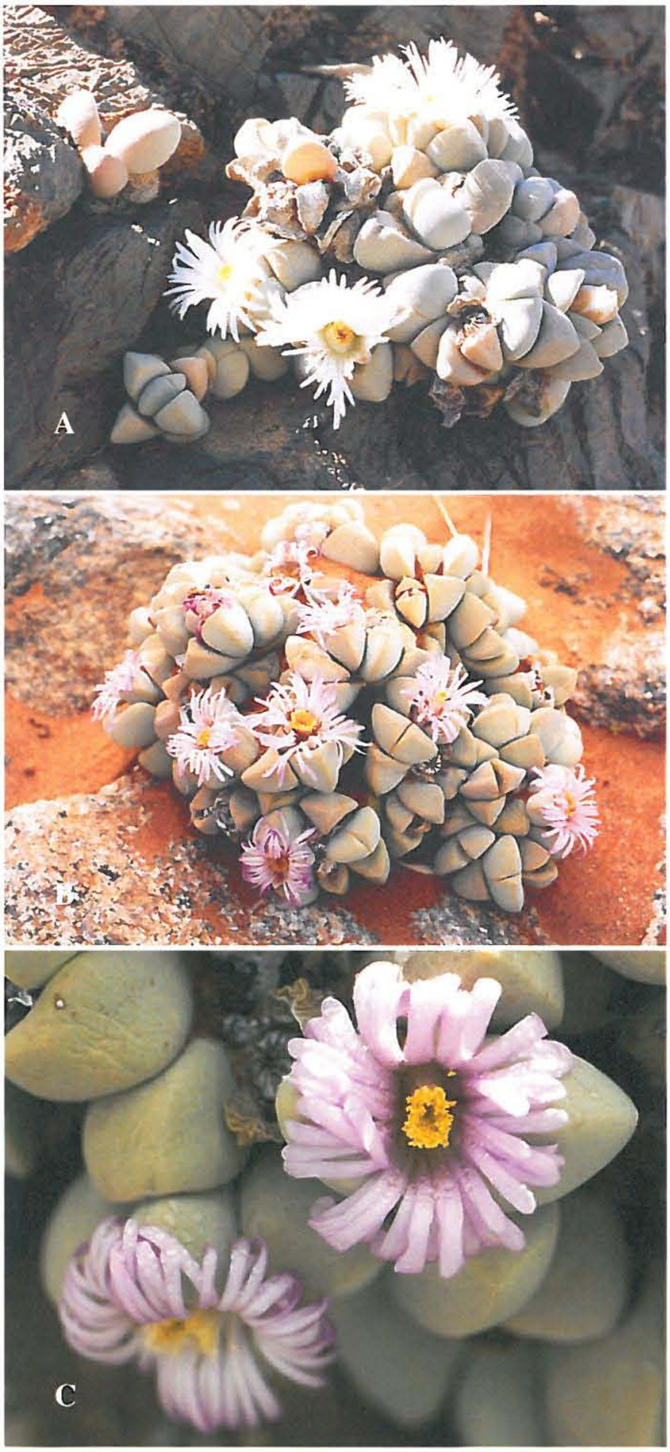


Figure 3.8: *Namibia* habit and flowers. A. *N. cinerea (C. Mannheimer CM 2374)*, showing white flowers. B. *N. ponderosa (C. Mannheimer CM 2367)*, showing pink flowers. C. *N. ponderosa (C. Mannheimer CM 2367)* showing sessile flower with typically square outline due to one pair of very fleshy sepals at right angles to the top pair of leaves.

3.1.4.1 Receptacle and Calyx

The receptacle in *Namibia* is bowl-shaped. Sepal number varies between four and seven. In *N. ponderosa* the most commonly observed number was four, while in *N. cinerea* it was five. One pair of sepals (the pair that is opposed to the uppermost leaf pair) is always very succulent and distinctly keeled (almost appearing like a very small pair of leaves), while the other sepals are thinly fleshy, not keeled, and have a membranous margin.

Neither the shape of the receptacle or sepal characters are taxonomically useful at species level. However, *N. cinerea* always has five or more sepals, while *N. ponderosa* may have four (frequently) or more. This character is of some taxonomic use at species level.

3.1.4.2 Flower colour and size

Flowers of *N. cinerea* are pure white (Figure 3.8 A), while those of *N. ponderosa* vary from white (although white is rare) to pale pink to deep rose-pink (Figure 3.8 B and C), fading to dirty white with age. Flower colour is taxonomically useful at species level in *Namibia*.

Flower size is extremely variable, the diameter ranging from 29 to 73 mm. In *N. cinerea* observed flower diameter varied between 29 and 50 mm, while in *N. ponderosa* the range was between 30 and 73 mm (Table 3.3).

Table 3.3: Flower dimensions in *Namibia*.

Species	Diameter range mm	Petal length range (mm)
Namibia cinerea	29 – 50	13 – 33
Namibia ponderosa	30 – 73	16 – 39

Thus, although there is much overlap (Figure 3.9), there is a clear tendency for *N. ponderosa* to have far larger flowers and correspondingly longer 'petals' (Figure 3.10), which is what inspired Louisa Bolus (1928) to ascribe the epithet *longipetala* to this taxon. The 'petals' of *Namibia* are by far the longest in the subtribe.

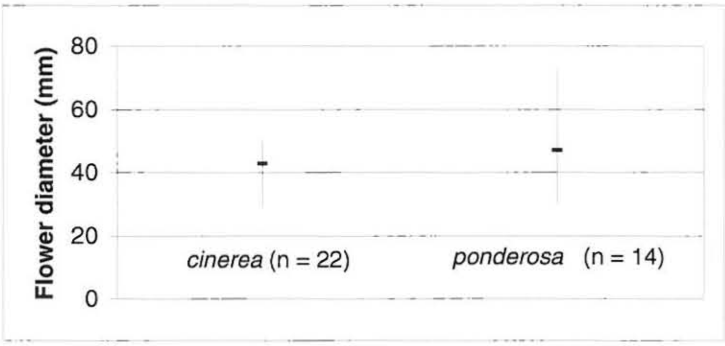


Figure 3.9: A comparison of flower diameters in *Namibia* (vertical bar = range, horizontal bar = mean).

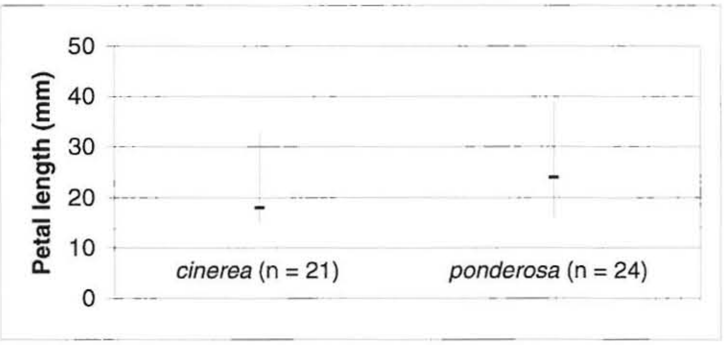


Figure 3.10: Petal lengths in *Namibia* (vertical bar = range, horizontal bar = mean)

3.1.4.3 Androecium

The stamens are numerous, and initially arranged in a cone which opens out to become more cylinder-like as anthesis progresses towards the female phase. Inner series of filaments are shorter than outer, with lengths overall varying between 2 and 14 mm. All filaments are pure white and pubescent at the base.

The anthers are elongate-elliptic and dorsifixed, varying between 0.6 and 1.7 mm in length. Their attachment is versatile. The thecae are parallel and exhibit longitudinal extrorse dehiscence. Stamen characters are not taxonomically useful at species level.

3.1.4.4 Stigmata

The stigmata are narrow-subulate, typical for the subtribe. In *Namibia* they are pale yellow-green and vary in number between 8 and 25. They are free, or virtually so, at the base, and the inner surface is covered by short stigmatic papillae. At first they are of a similar length to the stamens, but elongate during anthesis to protrude beyond them. Their characters are not taxonomically useful.

3.1.4.5 Ovary

Due to the wide, bowl-shape of the receptacle the ovary is shallow in relation to its width, and placentation appears basi-parietal rather than simply parietal as in other members of the subtribe. However, the depth is increased considerably by the fact that the tip of the columella is raised, with the septa rising from the outer wall of the capsule towards the centre. The upper surface is concave at first, becoming domed as the numerous ovules ripen. Ovary characters are similar in both species.

3.1.4.6 Floral nectary

The nectary is a narrow, shallowly crenulate ring (i.e. a lophomorphic holonectary). It is pale green to apple green, and produces a small amount of colourless to very pale straw-coloured nectar. No scent was discernable. The characters of the nectary are not taxonomically useful at species level.

3.1.5 Pollen

3.1.5.1 Colour

Pollen of *Namibia* is bright golden-yellow, fading to pale yellow with age.

3.1.5.2 Shape

Pollen grains of *Namibia* are symmetric, isopolar, prolate, tricolpate, and somewhat rounded-triangular in polar view. In equatorial view the poles sometimes appear more-or-less truncate (Fig. 3.12 A). The mesocolpi are convex, and the apertures are positioned at the angles between them, equidistant to one another and parallel to the polar axis. This morphology is not unusual in the Mesembryanthemaceae (e.g. Klak & Linder 1998, Hartmann 1991), although subspheroid pollen grains are regarded as typical (Dupont 1977, 1980).

3.1.5.3 Size

Namibia pollen grains are longiaxial, i.e. the polar axis (P) is longer than the equatorial axis (E). The P/E ratio varies from 1.1 to 1.5. In *N. cinerea* the mean value of this ratio is lower (1.2) than in *N. ponderosa* (1.3). This is due to the length of *N. ponderosa* pollen, which was shown by a t-test to be significantly greater than that of *N. cinerea* at the 99% confidence level (Figure 3.11). There was no significant difference in pollen width between the two species. Table 3.4 shows pollen dimensions for these two species.

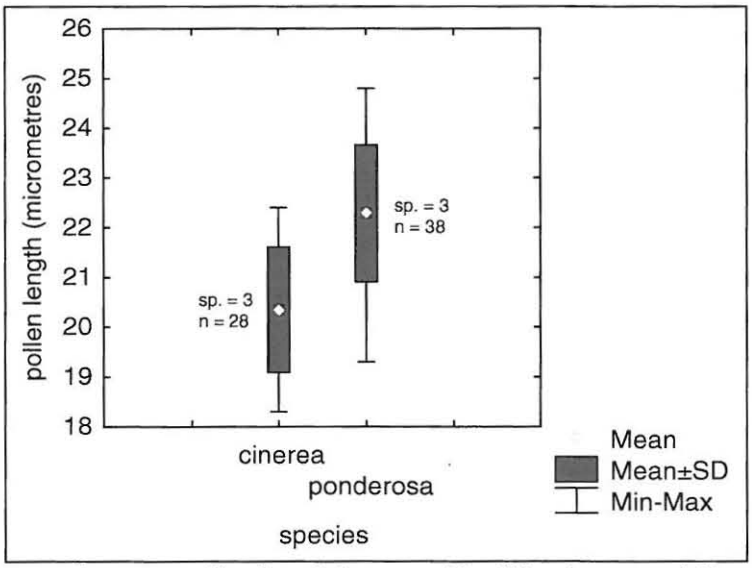


Figure 3.11: Difference in mean pollen length between *Namibia cinerea* and *N. ponderosa* (t = -5.8478; df = 64; p = 0.0000; F = 1.2017; sp = specimens examined; n = pollen grains examined).

Table 3.4: Pollen measurements and tectum structures in *Namibia*.

	Namibia cinerea	*Namibia ponderosa*
Length μm min - mean – max (std. dev.)	18.3 – 20.4 – 22.4 – 1.25	19.3 – 22.3 – 24.8 – 1.38
Width μm min - mean - max (std. dev.)	14.8 – 16.7 – 18.4 – 1.1	14.2 – 16.7 – 18.3 – 1.0
No. perforations (min – mean – max)	12 – 27 – 53	8 – 14 – 26
No. spinulae (min – mean – max)	33 – 38 – 42	38 – 56 – 68

3.1.5.4 Exine structure

The exine varies from tectate-perforate to semitectate-reticulate, and is always ornamented with spinulae. Micro-perforations of the tectum and free baculae on the nexine are often present. Reticulate and reticulate-spinulate conditions are regarded as advanced in angiosperms generally (Walker 1974), as well as in the Mesembryanthema in particular (Hartmann 1991).

3.1.5.5 Perforations and sculpturing

Perforations vary from micro-perforations to large, irregular luminae that result in the reticulate condition (Figure 3.12 A, B and C). The number of perforations varies from 9 to 53 μm in an area of 25 μm^2, counted on the mesocolpium at a point equidistant from both the poles, and the adjacent colpi. *Namibia cinerea* exhibits both the tectate-perforate and the semitectate-reticulate condition, sometimes within a single flower, while in *N. ponderosa* only the semitectate-reticulate condition was observed. Although there was no statistically significant difference, the mean number of perforations (luminae) was far lower in *N. ponderosa* (14) than in *N. cinerea* (27) (Figure 3.13). In *N. ponderosa* the muri appear wider and the luminae larger. The higher mean in *N. cinerea* may be ascribed to the inclusion of tectate-perforate as well as semitectate-reticulate pollen grains in the counts as well as to the occurrence of larger luminae in *N. ponderosa*. A larger sample size and a more accurate measure of exine extent being applied might offer greater clarity and serve to test the result of this small sample. The tendency of *N. ponderosa* to be less tectate than *N. cinerea* suggests that the former is more advanced in pollen characters.

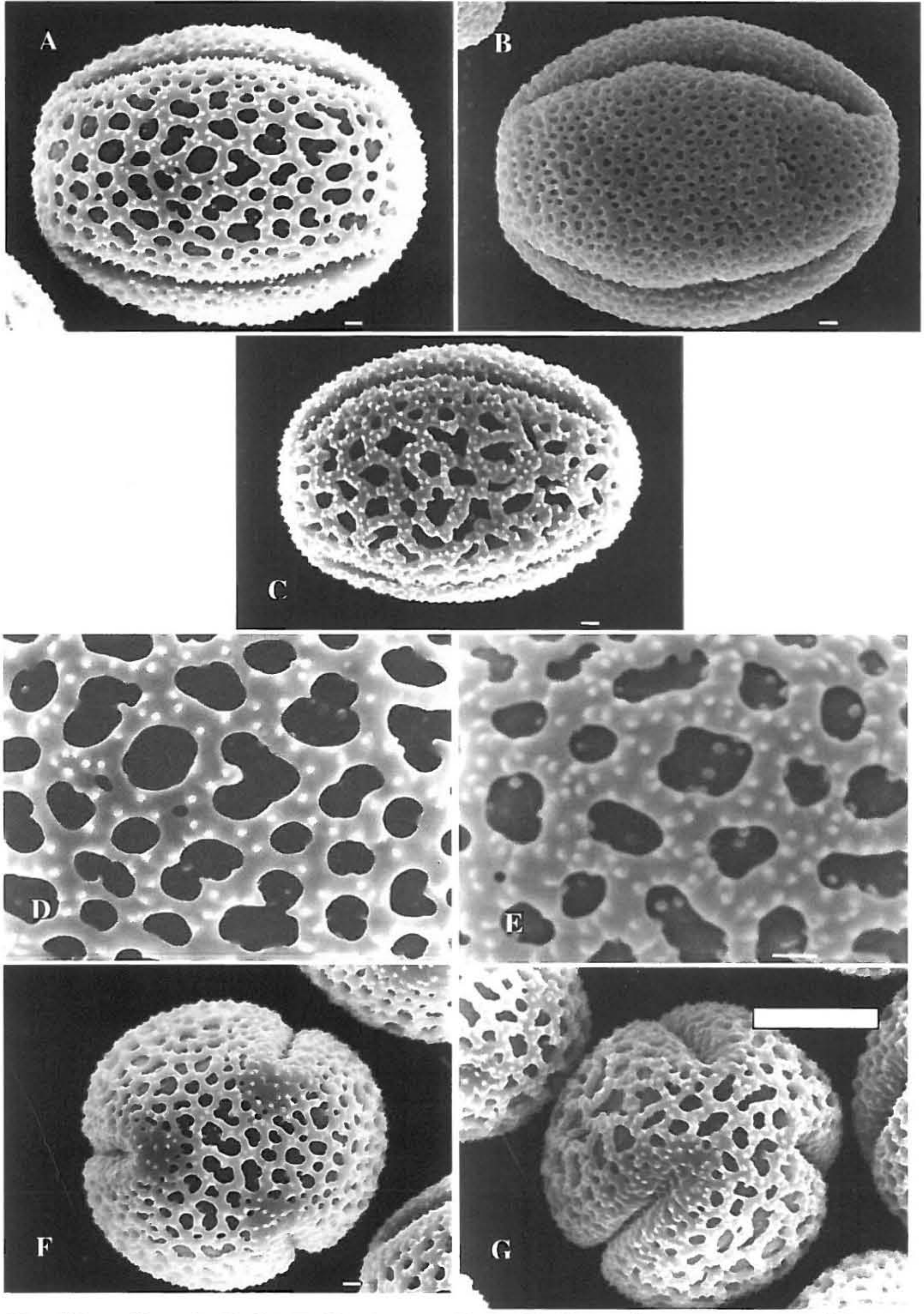


Figure 3.12: *Namibia* pollen. A, B, D, F. *N. cinerea*, C, E, G. *N. ponderosa*. A. equatorial view (*C. Mannheimer CM 2373*), showing truncate poles and semitectate-reticulate exine; B. equatorial view (*C. Mannheimer CM 1402*), showing tectate-perforate exine; C. equatorial view (*C. Mannheimer CM 2380*), showing semitectate-reticulate exine; D. exine at equator (*C. Mannheimer CM 2373*), showing muri; E. exine at equator (*C. Mannheimer CM 1693*), showing muri; F. polar view (*C. Mannheimer CM 2373*); G. colpus (*C. Mannheimer CM 2380*). D and E x 10 000, all others x 4000. Scale bars 1 μm.

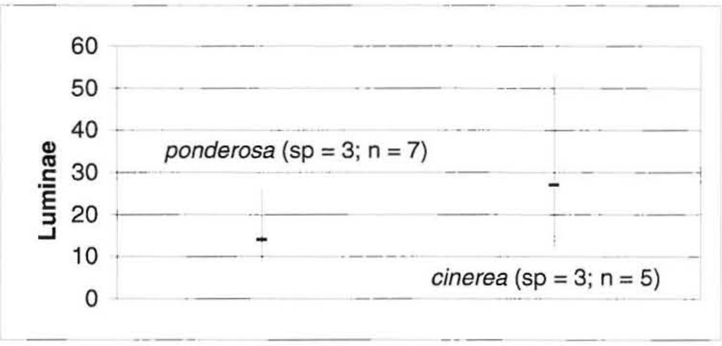


Figure 3.13: Range in number of luminae per 25 μm^2 pollen surface in *Namibia* (horizontal bar = mean, sp = specimens examined; n = pollen grains examined).

In contrast to the perforations, the number of spinulae in *N. cinerea* (mean 38) was significantly lower at the 95% confidence level than in *N. ponderosa* (mean 56), (Figure 3.14, Figure 3.12 D and E). This might be a taxonomically useful character but it should be tested using a larger data set.

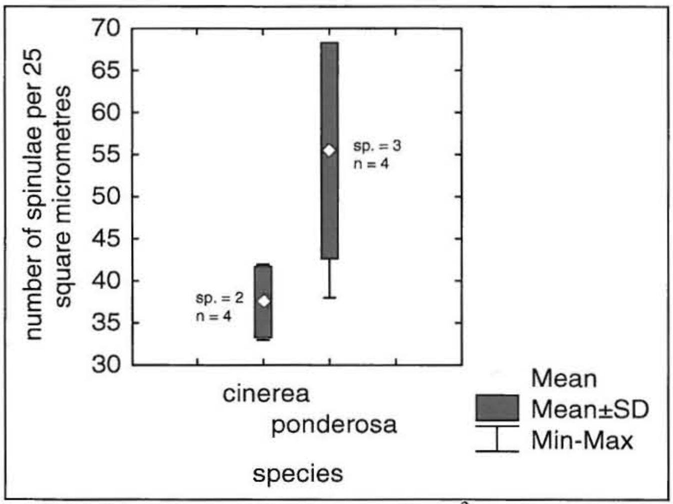


Figure 3.14: Number of spinulae per 25 μm^2 on *Namibia* pollen

($t = -2.6685$; $df = 6$; $p = 0.0371$; $F = 9.3019$; sp = specimens examined; n = pollen grains examined).

The polar regions exhibit the same characters as the mesocolpi , but at the margins of the colpi there are far fewer perforations, and often only micro-perforations are found. In some areas, particularly close to the poles, the exine may lack pores (Figure 3.12 F).

3.1.5.6 Apertures

As may be seen in figure 3.12 G, the colpi are closed.

3.1.6 Fruit

With the exception of size there is little difference in fruit characters between the two species of *Namibia*. Capsule size varies between 7 and 14 mm in diameter, and is significantly wider at the 95% confidence level in *N. cinerea* (Figure 3.15). However, there is considerable overlap so this character is not taxonomically useful.

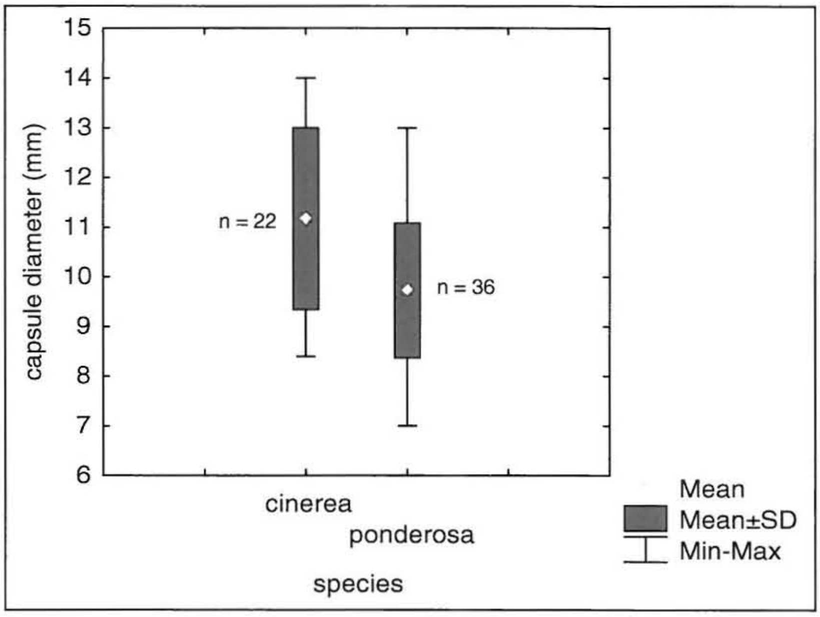


Figure 3.15: A comparison of mean capsule width in *Namibia* ($t = 3.4503$; $df = 56$; $p = 0.001$; $F = 1.8242$)

The base of the capsule is the same shape as the receptacle, i.e. bowl-shaped, and the lid is domed (Figures 3.16 B,C and 3.17 A). It is carried deep between the leaves of the uppermost leaf pair (Figure 3.17 B). Seen from above it is often somewhat ovate, possibly due to being constricted between the very fleshy leaves on two sides (Figure 3.17 C). Figure 3.16 A shows a generalized diagram of an open *Namibia* capsule.

Locule number varies between 8 and 25, but is most often between 11 and 13. The septa rise from their insertion on the wall of the receptacle towards the tip of the columella (Figure 3.17 D). The expanding keels are robust, radial, and parallel from the base, diverging only distally. They are about as high as they are broad. Their colour varies from beige to light to dark brown and appears to darken with age. The valve wings are slender-rectangular to rounded-rectangular to oblong, 0.6 to 2.2 mm wide, and lack awns. T-tests showed no statistical difference between the species regarding locule number or valve wing width.

Covering membranes are lacking or extremely vestigial, and are more often seen in fresh capsules (i.e. capsules from the latest season). Figure 3.17 E shows these vestigial membranes in a fresh capsule of *N. ponderosa,* in which the valves were eaten away by insect predators. In fruit types with parallel, radial keels this tissue is thought to be of septal, not valvar origin (Hartmann 1988). Closing bodies are completely absent. When wetted the valves open completely, to a reflexed position, (Figure 3.17 D), arching over the rim of the receptacle. Dehn and Hartmann (in Hartmann 1991) term this fruit type, typified by the radial keels, virtual or total absence of covering membranes and a lack of closing bodies, the *Delosperma* type. The lack of covering membranes is a feature shared with the Mesembryanthemoideae, suggesting that this is a primitive feature. This however, is questioned by Hartmann (1991) who points out that it is correlated with parallel, radial expanding keels, and that in this condition there is a reduction in the area of tissue available to develop into the central part of the covering membrane. She suggests that further work is necessary before this issue may be resolved. The ecological implications of the combination of capsule features seen in *Namibia* are discussed in Chapter 8.

Placentation is basi-parietal rather than parietal.

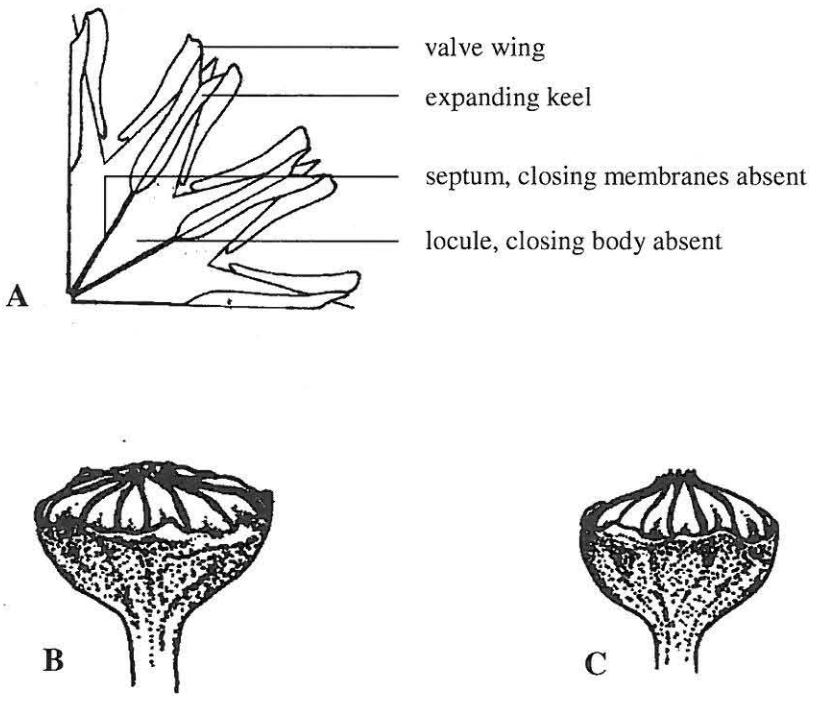


Figure 3.16: *Namibia* capsules. A. generalized diagram of internal structure. B. *N. cinerea* (*C. Mannheimer CM 2375*). C. *N. ponderosa* (*C. Mannheimer CM 2357*).

Figure 3.17: *Namibia* capsules. A, B, C, E. *N. ponderosa*. D. *N. cinerea*. A. Lateral view (*C. Mannheimer CM 2357*). B. capsule carried deep between uppermost leaf pair (*C. Mannheimer CM 2359*). C. ovate outline of capsule from above (*C. Mannheimer CM 2357*). D. the septa rise from the outer edge towards the columella and the valves reflex when wet (*C. Mannheimer CM 2375*) E. showing insect predation and revealing vestigial covering membranes (*C. Mannheimer CM 2359*).

3.1.7 Seed

Namibia seeds are ovate to pear-shaped, with the ventral region slightly flattened and the dorsal region somewhat convex. Their length varies between 0.7 and 1.2 mm. Although seeds of *N. cinerea* tend to be longer than those of *N. ponderosa* (Figure 3.18) there is considerable overlap. Thus seed size is not of taxonomic significance in this genus.

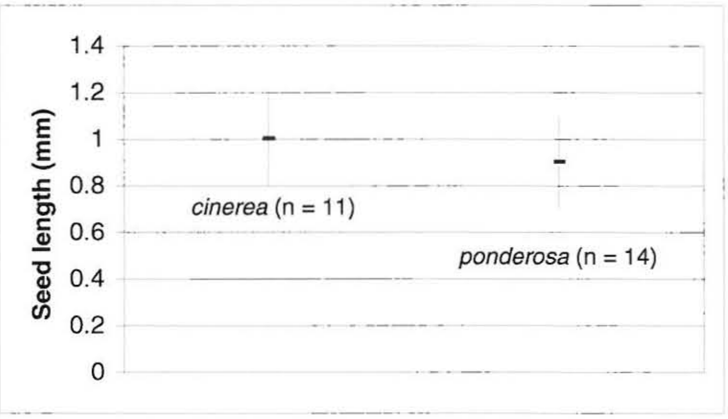


Figure 3.18: Seed length range in *Namibia* (horizontal bar = mean, n = specimens examined)

The seeds vary in colour from apricot or tan through to dark brown. The micropylar region is produced forwards, slightly more so in *Namibia ponderosa* than in *N. cinerea* (Figure 3.19 A and B). The testa fold is deeper and longer in *Namibia ponderosa* (about 25% the length of the seed, Figure 3.18 b) than in *N. cinerea* (about 12% the length of the seed, Figure 3.19 A). It is oriented at an angle of approximately 45° to the long axis of the seed and may be deeper either above or below the hilum.

The shape of the testa cells is elongated in areas where these cells are ordered in rows, such as in the micropylar, lower perisperm, hilar and ventral regions. Elongated cells have their longitudinal axes parallel to the long axis of the seed (Figure 3.19 A and B). In areas such as the perisperm region where the cells are less ordered their shape is more variable. Anticlinal walls are sunken to a greater or lesser degree, and vary from almost straight to very undulate, the undulations being S-shaped. Periclinal cell walls are gently convex, with less elongated cells more convex than longer ones (Figure 3.19 C and D). These more domed cells are found in rows on the dorsal and rear regions of the seeds. Along the testa fold the cells are small, elongated and narrow.

Namibia cinerea appears to carry waxy platelets on the surface of the testa cells whereas *N. ponderosa* appears rugose and carries tiny white verrucae (Figure 3.18 C and D). These epicuticular microstructures were not investigated in detail. In both species the cell surface is slightly lumpy.

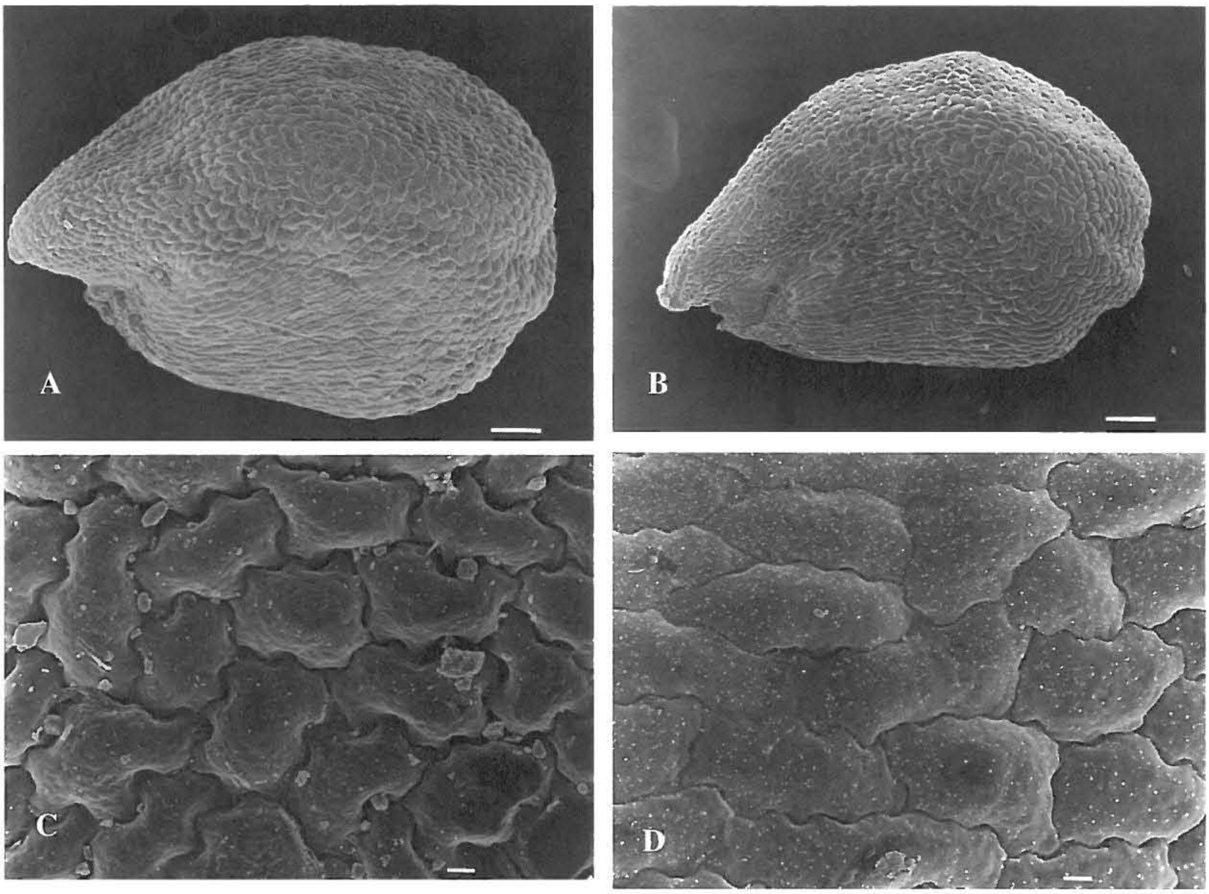


Figure 3.19: Seed testa in *Namibia*. A,C. *N. cinerea*. B,D. *N. ponderosa*. A. seed lateral view (*C. Mannheimer CM 1399*). B. seed lateral view (*C. Mannheimer CM 1693*). C. testa cells (*C. Mannheimer CM 1392*). D. testa cells (*C. Mannheimer CM 2269*). A, B. x 75, scale bars 100 μm. C, D. x 500, scale bars 10 μm.

3.2 Taxonomic treatment

Namibia (Schwantes) Dinter & Schwantes in Schwantes, Zeit. F. Sukk. 3: 106 (1927-1928); Schwantes, Zeit. F. Sukk. 2: 182-184 (1926); v. Pöllnitz, F. Rep. Sp. Nov. 32: 56 (1933); Jacobsen, Succ. Pl. 221 (1935); Jacobsen, F. Rep. Sp. Nov. 106: 153 (1938); Walgate in Bolus, Notes on Mes. 3: 186 (1939); Jacobsen, Herre & Volk, Mesembr.: 77, 119 (1950); Jacobsen, Handb. Sukk. Pfl.: 1563 (1955); Schwantes, Fl. Stones.: 137 (1957); Jacobsen, Handbook Succ. Pl.: 953 (1960); Jacobsen, Sukk. Lex.: 471 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 62-64 (1970); Herre, Gen. Mesem.: 224 (1971); Court, Succ. Fl. sthn. Afr.: 46 (1981); Smith *et al*, Mesembs: 120 (1998); Court, Succ. Fl. sthn. Afr.: 20-21 (2000); Leistner (Ed.), Seed Pl. sthn. Afr.: 397 (2000); Van Jaarsveld *et al*, Vygies: 160 (2000); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: 180-181 (2001). Type: *Namibia cinerea* (Marloth) Dinter & Schwantes.

Juttadinteria subg. *Namibia* Schwantes, Zeit.f. Sukk. 2: 184 (1926).

Etymology: Namib, coastal desert along western Namibia.

Plants perennial, compact, forming almost hemispherical bodies; branches short, woody-fibrous, three to several, each carrying one to three leaf pairs. *Leaves* opposite, light green to orange, or grey to grey-brown, up to 45 x 29 mm, up to 35 mm thick, usually less than twice as long as wide, frequently deeper than wide, rounded-trigonous, laterally bulging; margins entire or rarely sparingly notched or dentate; keel rounded or more distinct and flushed orange; apex obtuse; base pustulate; epidermis velutinous, papillate. *Flowers* solitary, terminal, ebracteate, sessile to subsessile, often with a squarish or rectangular appearance, open permanently, up to 70 mm in diameter; receptacle papillate; sepals 4–7, fleshy, papillate, margins membranous; outer sepals larger, keeled, 6.8–14.0 x 4.0–15.0 mm; inner sepals 5.2–11.0 x 1.7–11.0 mm. *Staminodes* petaloid, 51–92, uniseriate, white to pink, 15–39 x 1.1–3.3 mm, linear to linear-ligulate, reflexed. *Androecium* conical becoming cylindrical with age; stamens numerous; filaments white, unequal, 2–14 mm long, bases papillate; outer filaments longest; anthers dorsifixed, pale yellow, 0.6–1.7 mm long, extrorse, dehiscence longitudinal, thecae narrowly elliptic. *Pollen* prolate, bright yellow, 18–25 μm x 14–18 μm, tricolpate, exine tectate-perforate or semitectate-reticulate, spinulate. *Nectary* continuous, crenulate, green; nectar almost colourless. *Gynoecium* stigmas 8–25, narrow-subulate, pale yellow-green, inner surface with stigmatic papillae; ovary synovarious, base shallowly cupular, above convex; placentation basi-parietal. *Capsule* hygrochastic, 8–25 locular, 7–14 mm in diameter; base broadly and shallowly cupular, top convex; septa rising to centre; expanding keels radial, parallel, diverging distally, light brown to orange-brown or dark brown; valve wings elongate-rectangular, awns absent; covering membranes absent or vestigial; closing bodies absent. *Seed* ovate to pear-shaped, 0.8–1.2 mm long, light brown to light brown to rust-brown.

Key to species

- Flowers white; leaves grey to grey-brown, leaf epidermal papillae densely packed, usually with a long and slender appearance; sepals five or more... *N. cinerea*
- Flowers pink; leaves pale green to light orange-brown, leaf epidermal papillae well-spaced, with a relatively short and stout appearance; sepals four or more.. *N. ponderosa*

1. Namibia cinerea (Marloth) Dinter & Schwantes in Schwantes, Zeit. F. Sukk. 3: 106 (1927); Schwantes, Zeit. F. Sukk. 2: 182-184 (1926); v. Pöllnitz, F. Rep. Sp. Nov. 32: 56 (1933); Jacobsen, Succ. Pl. 221 (1935); Jacobsen, F. Rep. Sp. Nov. 106: 153 (1938); Walgate in Bolus, Notes on Mes. 3: 186-187 (1939); Schwantes, Fl. Stones.: 137 (1957); Jacobsen, Handbook Succ. Pl.: 953 (1960); Jacobsen, Sukk. Lex.: 471 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 62 (1970); Herre, Gen. Mesem.: 224 (1971); Court, Succ. Fl. sthn. Afr.: 46 (1981); Smith *et al*, Mesembs: 120 (1998); Court, Succ. Fl. sthn. Afr.: 20-21 (2000); Leistner (Ed.), Seed Pl. sthn. Afr.: 397 (2000); Van Jaarsveld *et al*, Vygies: 160 (2000); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: 180-181 (2001). Type: A few miles east of Prince of Wales Bay in Great Namaqualand, *Marloth 4680* (PRE!,holo; BOL!, NBG! iso).

Mesembrianthemum cinereum Marloth, Trans. Roy. Soc. S.A. 1: 487 (1910). *Juttadinteria cinerea* (Marloth) Schwantes, Zeit.f. Sukk. 2: 184 (1926).

Mesembrianthemum pomonae Dinter, Fedd. Rep. Sp. Nov. Reg. Veg. XIX:125 (1923). *Juttadinteria pomonae* (Dinter) Schwantes, Zeit. Sukk. Kunde 2:184 (1926) nomen invalid. *Namibia pomonae* (Dinter) Dinter & Schwantes ex Walgate, in H.M.L. Bolus Notes on Mes. & All. Gen. 3 (1939). Type: Between Pomona and Alicetal pump station, *Dinter 3787* (lost).

Etymology: *cinerei* (Latin), ash-grey, alluding to the greyish colour of the leaves.

Leaves grey to grey-brown, up to 45 x 29 mm, up to 35 mm thick; margins and keel entire, rounded; apex obtuse; epidermal papillae closely packed, long, with slender appearance; epicuticular wax in thick, encrusting plates with scattered small blocks. *Flowers* up to 50 mm in diameter; *s*epals 5–7; outer sepals 6.8–12.6 x 7.2–11.2 mm; inner sepals 6.7–9.9 x 3.1–8.7 mm. *Staminodes* 62–92, up to 33 mm long, up to 3.3 mm wide, shining white, fading to dirty white with age. *Androecium* filaments 2–14 mm long. *Pollen* exine tectate-perforate to semitectate-reticulate, 18–22 μm long, 15–18 μm in diameter. *Capsule* (9–)12–13(–25) locular 8–14 mm in diameter. *Seeds* 0.8–1.2 mm long.

Distinguishing characters: *Namibia cinerea* is distinguished by its grey-brown leaves with long, slender epidermal papillae and its pure white flowers. The leaf margins and keel are usually rounded and indistinct. Generally it has larger leaves than *N. ponderosa*, but this is a very variable character that depends to a great extent on the age of the leaf and of the plant as a whole. Large, old plants of both species often have smaller leaves than smaller and younger or senescent plants.

Distribution: Endemic to the southern Namib. Restricted to a small area south and south-east of Lüderitzbucht (Figure 3.20).
Habitat: Typically grows in crevices on dolomite, limestone and quarzitic outcrops, slopes and ridges.
Altitude: 44 – 263 m.
Flowering: August to September.
Provisional Namibian Red Data status: VU B1ab(v)+2ab(v).
Illustrations: Jacobsen, Sukk. Lex.: 471 (1970); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: XX (2001).

Discussion: *Namibia pomonae*, which has always been a controversial species, is sunk here. Its unique character was the high number of stigmata (25, with those of *N. cinerea* previously recorded as up to 14). Plants otherwise indistinguishable from *N. cinerea* were found to have up to 17 locules (e.g. *CM1402*, *CM1407*, WIND) in the *N. pomonae* type locality, where it was recorded by Dinter (1923) as occurring sympatrically with *N. cinerea*. Diligent searching over several years has failed to turn up any plants not referable to *N. cinerea*, either in the *N. pomonae* type locality or elsewhere.

The *N. cinerea* isotype in BOL is a piece of the holotype from PRE, removed by Louisa Bolus. The PRE sheet is thus annotated by her.

2. Namibia ponderosa (Dinter) Dinter & Schwantes ex H. Jacobsen, Succ. Pl. 222 (1935); Jacobsen, F. Rep. Sp. Nov. 106: 153 (1938); Walgate in Bolus, Notes on Mes. 3: 186-187 (1939); Schwantes, Fl. Stones.: 137 (1957); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 63-64 (1970); Herre, Gen. Mesem.: 225 (1971); Court, Succ. Fl. sthn. Afr.: 46 (1981); Court, Succ. Fl. sthn. Afr.: 20-21 (2000); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: 181 (2001). Type: *Dinter 3747* (B†). Neotype (here designated): Kovis Mountains, *C.A. Mannheimer 2632* (WIND!, BOL!, K!, MISS!, PRE! iso).

Mesembrianthemum ponderosum Dinter, Feddes Rep. Sp. Nov. Beih. 53:103 (1928)

A *Namibia cinerea (Marloth) Dinter & Schwantes* foliis viridibus pallidis, interdum complains croceis, cum papillis conicis humilis, apicibus recurvis interdum mucronatis; sepalis 4 – 7; petalis pallidis usque ad atroroseus, raro albis differt.

Etymology: *ponderosus* (Latin), weighty or heavy, possibly referring to the large size of some of the plants.

Leaves light green to orange, up to 42 x 22 mm, up to 31 mm thick; margins and keel rounded, often flushed orange, rarely sparingy notched or dentate; apex obtuse, usually with a small, recurved mucro; epidermal papillae short, well-spaced; epicuticular wax in thick, encrusting plates covered by fine platelets. *Flowers* up to 70 mm in diameter; sepals 4–7; outer sepals 7.0–14.0 x 4.0–15.0 mm; inner sepals 5.2–11.0 x 1.7–11.0 mm.. *Staminodes* 51–73, up to 39 mm long, up to 2.6 mm wide, very pale pink to deep rose pink, rarely white, fading to dirty white with age. *Filaments* 2–14 mm long. *Pollen* exine semitectate-reticulate, 19–25 μm x 14–18 μm in diameter. *Capsule* (8–)11–13(–15) locular, 7–13 mm in diameter. *Seeds* 0.8–1.1 mm long.

Distinguishing characters: *Namibia ponderosa* is distinguished by its light green to orange leaves with short, stubby, well-spaced epidermal papillae and its pink flowers. The leaf margins and keel are usually quite distinct, flushed orange-brown and terminate in a recurved apex that often carries a hard, blunt to sharp mucro. The flower often only has four sepals.

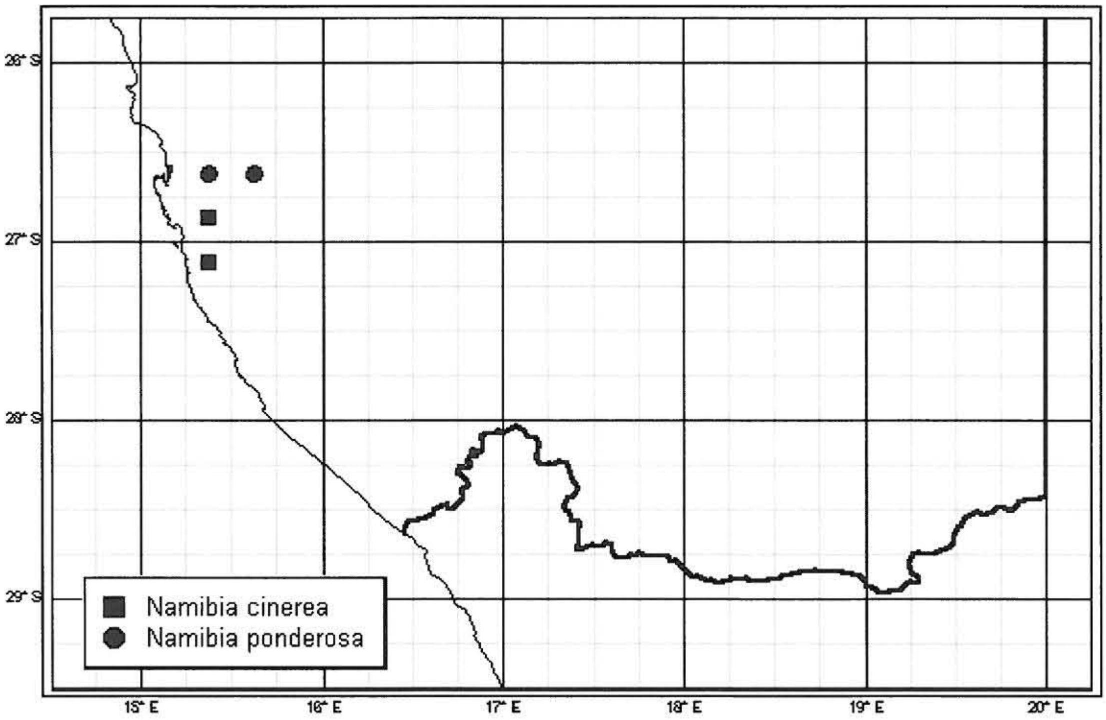
Distribution: Endemic to the southern Namib. Restricted to a small area north-east of Lüderitzbucht (Figure 3.20).
Habitat: Typically occurs on the slopes of granitic-gneiss and granite rock outcrops and slopes.
Altitude: 390 – 550 m.
Flowering: August to September.
Provisional Namibian Red Data status: VU D1+2.

Illustrations: B.O. Carter, *Pillans 5951* (BOL 1835); M. Walgate, *M. Otzen 1939* (BOL 2441); Walgate in Bolus, Notes on Mes. 3: 186-187 (1939); Herre, Gen. Mesem.: 225 (1971).

Discussion: *C.A. Mannheimer 2632* was chosen as the neotype because no material seen by Dinter could be found and very few of the older available specimens are fertile. Of those that are fertile there is no duplicate material.

The flower of *N. ponderosa* is open permanently, not only in the afternoon as noted in Hartmann (2001).

Figure 3.20: Distribution of *Namibia cinerea* and *N. ponderosa.*



CHAPTER 4. *Juttadinteria*

In the latest treatment of *Juttadinteria* Hartmann (2001) recognized five species compared to the nine recognized by Walgate (1939) and Smith *et al* (1998). The latter two treatments differ in that Smith *et al* recognized *J. elizae,* which was regarded as a dubious species by Walgate, while Walgate (with reservations, and noting its resemblance to *Namibia*) recognized *J. longipetala,* which was not accepted by Smith *et al.* Hartmann placed *J. elizae* in synonymy with *J. deserticola.*

Although the type specimen of *J. elizae* (*Dinter 1010*) is lost, and can thus not be consulted, this placement, which is accepted here, is supported both by the type description, which generally fits that of the genus, and (particularly) by the locality of the type specimen, the gneiss ridges at Lüderitzbucht, where *J. deserticola* is commonly found. The occurrence of five sepals is anomalous for the genus but the collection may have been atypical or an error of record may have occurred as no other similar mesemb species have been recorded for that area. As clarified in Chapter 3, *J. longipetala* is synonymous with *Namibia ponderosa.*

In order to assess limits of the remaining taxa a phenetic study of 50 specimens was undertaken. Character types and sources used are shown in Table 4.1. The full data set is presented as Appendix 2. Not all characters are taxonomically useful, but all are described for purposes of completeness. Despite the relative data deficiency of the matrix, the results were found to be reasonably intuitive, reflecting field observations.

Table 4.1: Summary of character types and sources used in the phenetic study of *Juttadinteria.*

Organ/Source	Binary	Multistate	Quantitative
Growth form		2	
Leaf	6	7	10
Flower	9	6	4
Fruit/Seed	3	9	8

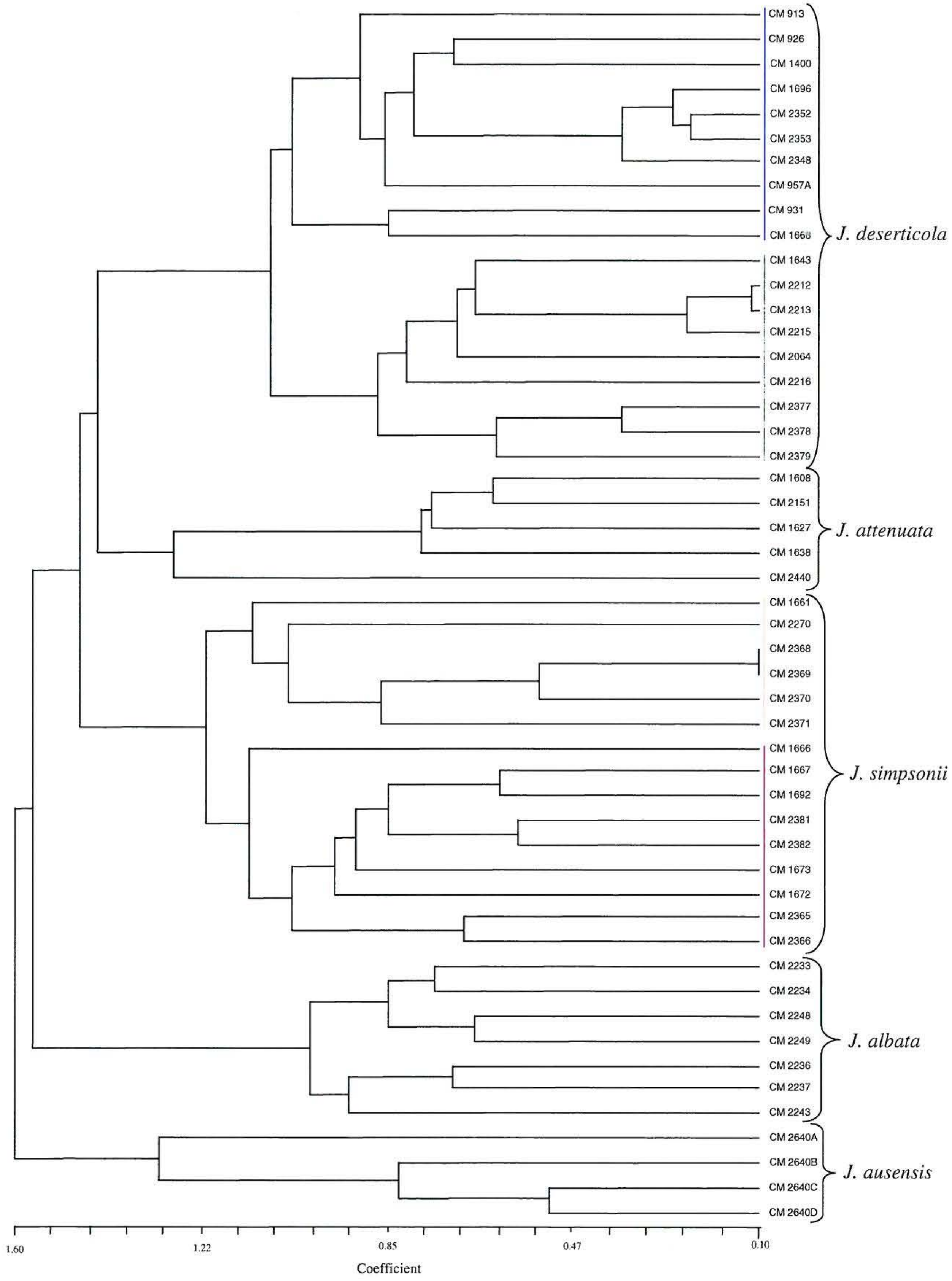


Figure 4.1: UPGMA phenogram for *Juttadinteria* based on 64 characters. The data were standardized, and a triangular matrix of similarities calculated using the Manhattan distances algorithm. CM = Coleen Mannheimer. Coloured bars indicate subgroups within *J. deserticola* and *J. simpsonii*. CCC = 0.777.

This phenogram (Figure 4.1) supports the presence of five taxa, coinciding with the species accepted by Hartmann (2001). It had a Cophenetic Correlation Coefficient of 0.777.

Within both the *J. deserticola* and the *J. simpsonii* clusters two subgroups can be distinguished, and these should be further assessed to decide whether they deserve formal infraspecific taxonomic status, possibly as varieties or forms. However, in both cases the taxa occur sympatrically and recent fieldwork has resulted in collection of specimens that appear to have intermediate characters. These data have not yet been included in the analysis. This argues against the erection of subspecific categories until further work has been undertaken. Further discussion regarding these subgroups is offered in Section 4.2.

In order to better differentiate between and describe the species, additional macro-morphological investigations were undertaken. Altogether 65 living plants, most of them in the field, and 246 herbarium specimens were examined, a total of 311 specimens. Micro-morphological investigations of leaf epidermides, pollen and seed by means of SEM of a small subset of samples were undertaken to assess additional differences between the species. Voucher numbers are listed in Table 4.2.

Table 4.2: ***Juttadinteria*** voucher specimens examined by SEM for micromorphological characters. * = specimen included in the phenetic study.

Species	**Voucher**	**Leaf surface**	**Pollen**	**Seed**
J. albata	*CM 2165*	●	●	
	*CM 2236**	●	●	
	*CM 2249**	●	●	●
	CM 2322			●
	CM 2366	●	●	
J. attenuata	*CM 1525*	●	●	●
	CM 1571B	●	●	●
	*CM 1608**	●	●	
	*CM 1627**			●
	*CM 1638**	●		
	CM 2188	●		

	CM 2425	●	●	
	*CM 2440**	●	●	
	CM 2446	●	●	
J. ausensis	*Hartmann, Dehn, Last & Rust 20909*	●	●	
	Hartmann, Dehn & Jürgens 26032	●		
	*CM 2640A**	●	●	●
	*CM 2640B**	●	●	
	*CM 2640C**	●	●	●
J. deserticola	*CM 931**	●	●	●
	CM 1682	●		●
	*CM 2216**	●	●	●
	*CM 2348**	●	●	
	*CM 2353**	●	●	
	*CM 2377**	●	●	
	*CM 2378**	●	●	
	CM 2548	●		●
	CM 2720	●	●	●
J. simpsonii	*CM 1661**	●	●	●
	*CM 1666**			●
	*CM 1672**	●	●	●
	*CM 1673**			●
	*CM 1692**			●
	*CM 2270**	●	●	●
	CM 2356	●	●	
	*CM 2368**		●	
	*CM 2369**	●	●	
	*CM 2381**	●	●	

4.1 Morphological characters

Few morphological characters are totally distinct or unique to a single species in *Juttadinteria* . As indicated in the discussion below, most overlap or intergrade, and thus few were found to be of taxonomic use unless combined with other characters. This relative absence of distinguishing characters is discussed further in Chapter 6.

4.1.1 Habit

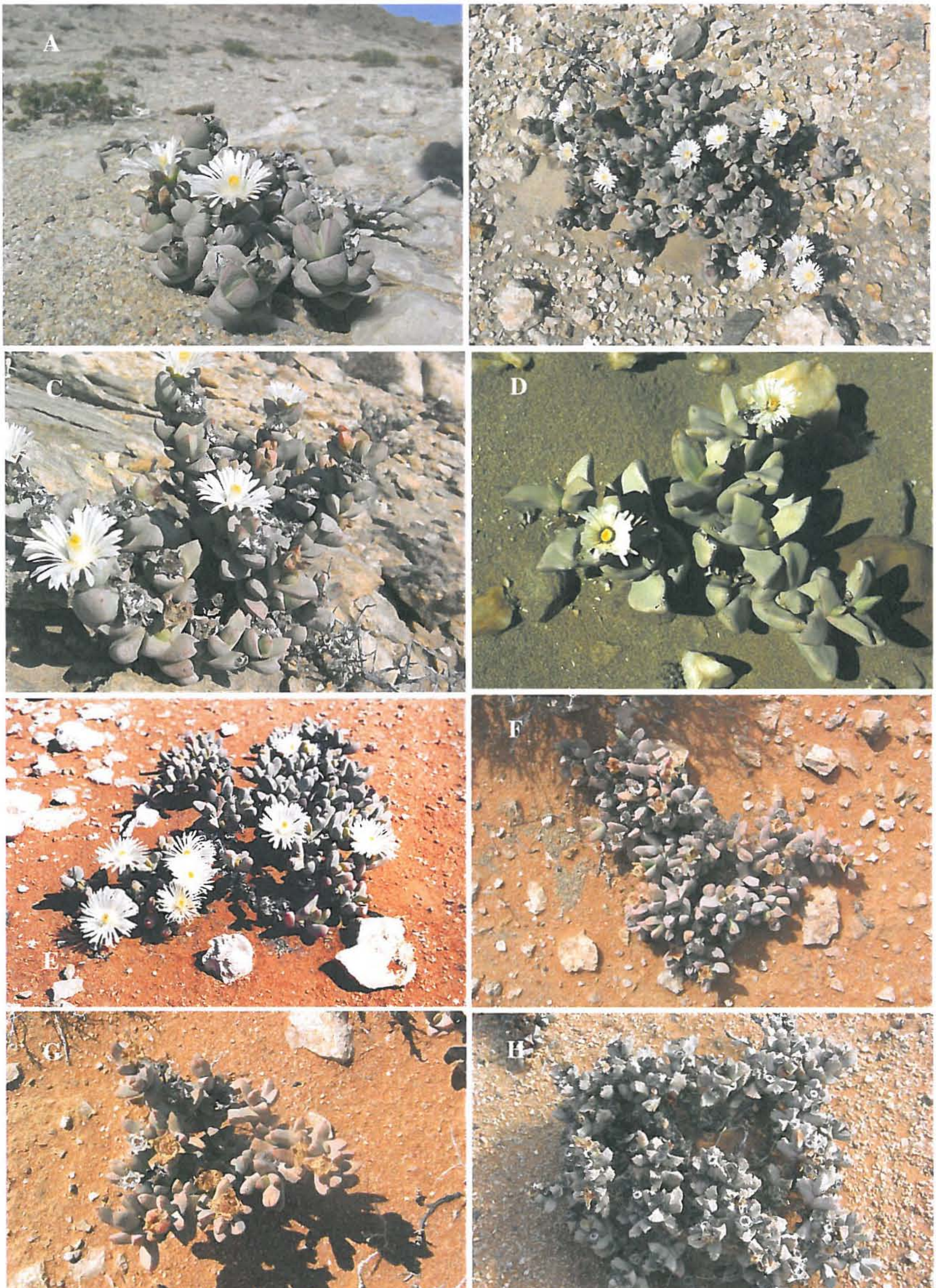
Juttadinteria is diverse in habit. It occurs in the form of compact tufts (Figure 4.2 A, *J. deserticola*), or may be distinctly branched. Branched forms may be prostrate and spreading (Figure 4.2 E *J. attenuata*), or procumbent to erect dwarf shrubs (Figure 4.2 B,C,D,F,G and H). The internodes may be enclosed or visible. Four species of *Juttadinteria* occur in more than one form (Table 4.3), and thus this character is of very limited taxonomic use.

Table 4.3: Lifeforms in *Juttadinteria* species

	compact tufts	**procumbent**	**shrubby**
J. albata		●	●
J. attenuata		●	
J. ausensis		●	●
J. deserticola	●	●	●
J. simpsonii		●	●

4.1.2 Roots

All species of *Juttadinteria* have one or two roots that spread from the base of the plant. They do not have a distinct taproot.



(Caption overleaf…)

Figure 4.2: *Juttadinteria* habit. A, B, C. *J. deserticola* A. tuft, mainly found coastal flats (*C. Mannheimer CM 2353*); B. procumbent form (*C.Mannheimer CM 2720*); C. shrubby form (*C. Mannheimer CM 2720*); D. *J. albata*, procumbent form (*C. Mannheimer CM 2249*); E. *J. attenuata* with prostrate, spreading branches (*C. Mannheimer CM 2764*); F. *J. ausensis* procumbent form (*C. Mannheimer CM 2640B*); G. *J. ausensis* shrubby form (*C. Mannheimer CM 2640C*); H. *J simpsonii* dwarf shrub (*C. Mannheimer CM 1666*).

4.1.3 Leaves

4.1.3.1 Macro-morphology and colour

Juttadinteria leaves are all hypersucculent, trigonous and often have a somewhat skewed appearance due to an oblique keel (Figure 4.3 D). They differ between the species in size, shape, and character of the margins and apex as well as in colour. In *J. albata, J. attenuata* and *J. deserticola* the leaves usually taper from base to apex (Figure 4.3 A, C, E) although in the first two species they sometimes broaden out briefly before narrowing to the tip. The margins are entire or may carry some very small cartilaginous teeth near the tip. The tip may be finely mucronate. In *J. ausensis* and *J. simpsonii* the leaves are wider and deeper just behind the tip, in *J. simpsonii* sometimes extremely so, and the margins, apex and (usually) keel are usually quite heavily toothed. Some teeth may also occur on the sides of the leaves. The teeth may be quite sharp (Figure 4.3 D) or just blunt knobs (Figure 4.3 F). *Juttadinteria deserticola, J. simpsonii* and *J. albata* have grey-green to blue-green leaves. In *J. albata* the colour is often very pale and this character is the source of the specific epithet. *Juttadinteria ausensis* has grey-green to brown-green leaves, the latter particularly when it is moisture-stressed. *Juttadinteria attenuata* has green leaves with distinct dark green spots due to pronounced tannin cells below the epidermis (Figure 7.5). Overall leaf shape, colour and leaf teeth characters are taxonomically useful at species level.

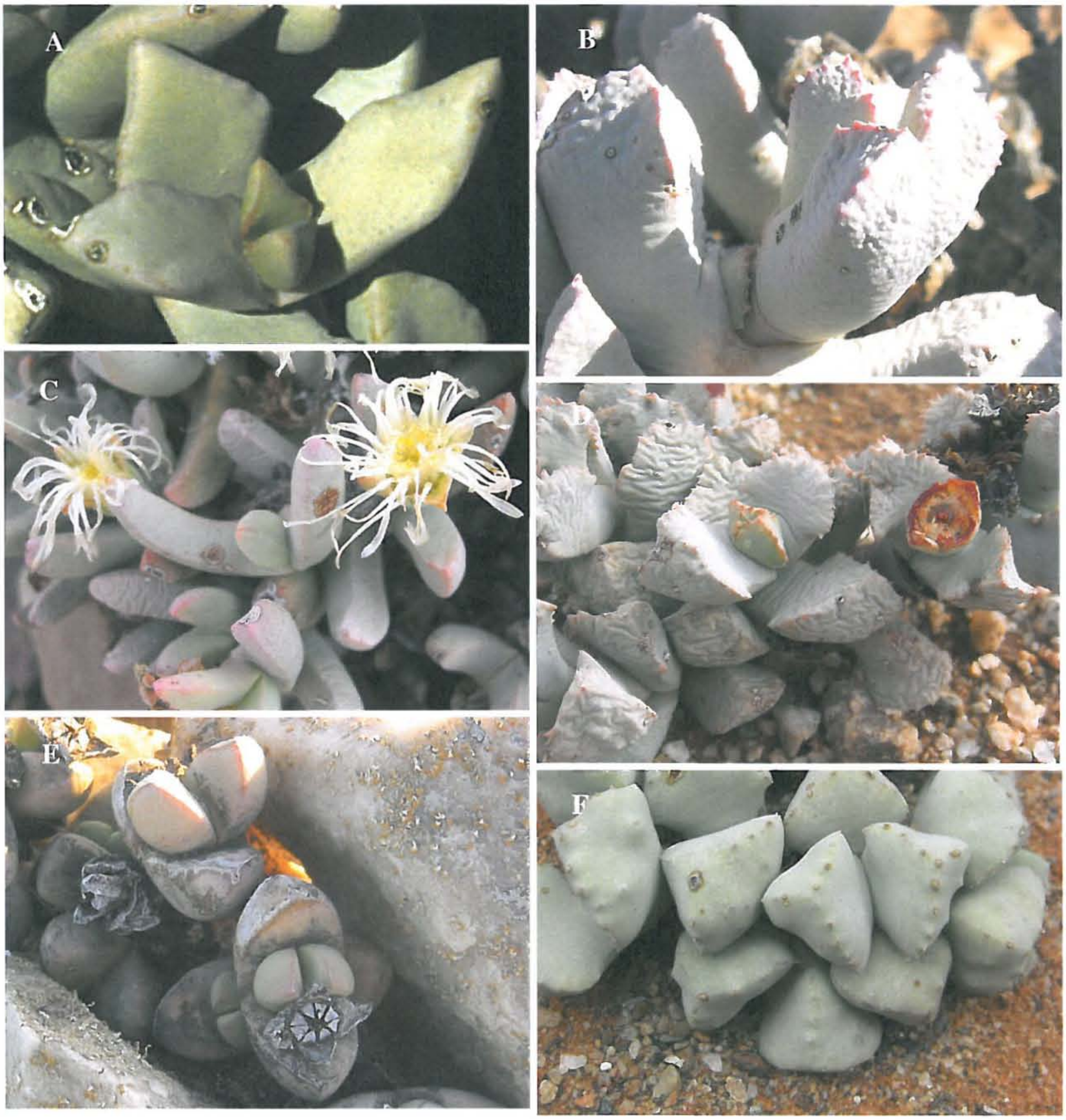


Figure 4.3: *Juttadinteria* leaves. A, D, E, F. x 1.5; B x 2; C x 1 (approximately). A. *J. albata* tapering to a sharp point (*C. Mannheimer CM 2249*). B. *J. ausensis* showing slight widening below tip, with toothed margin. and keel (*C. Mannheimer CM 2640A*). C. *J. attenuata* with slender, elongate leaves (*C. Mannheimer CM 2764*). D. *J. simpsonii* showing pronounced widening below tip and sharp teeth (*C. Mannheimer CM 1666*). E. *J. deserticola* with margin almost entire and short, broad leaves that taper to the tip (*C. Mannheimer CM 2649*). F. *J. simpsonii* with velvety, chunky leaf and small cartilaginous teeth (habit found in the Kovis Mountains *C. Mannheimer CM 2370*).

Considerable overlap is found in leaf length in *Juttadinteria* as indicated in Figure 4.4. The shortest leaves are found in *J. deserticola* while the longest by far are found in *J. albata*. This is of some taxonomic use at species level, if considered together with other characters. To a certain extent leaf proportions provide information too, because in *J. albata* and *J. attenuata* the leaves are always at least 2.5 times as long as wide, whereas in *J. ausensis* and *J. simpsonii* they are usually less than twice as long as wide. In *J. deserticola* this character is more variable.

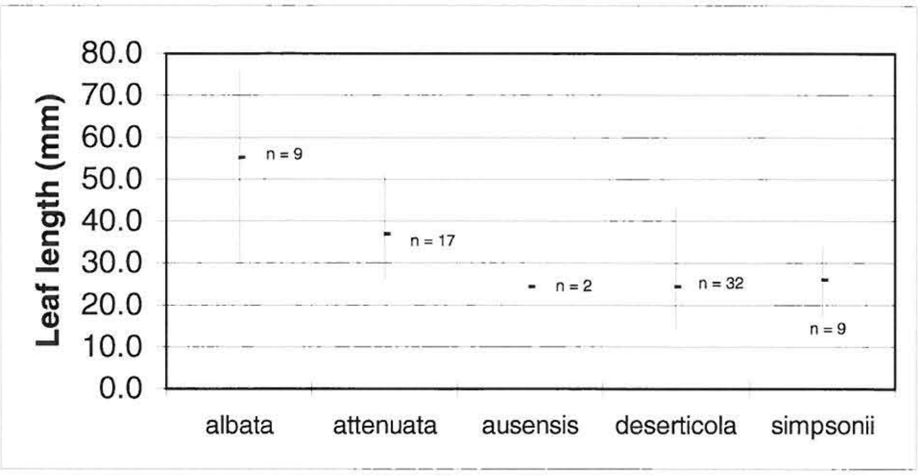


Figure 4.4: A comparison of leaf length ranges in *Juttadinteria* (horizontal bar = mean, n = specimens examined)

4.1.3.2 Micro-morphology

Juttadinteria leaves exhibit the xeromorphic-heterocellular condition as described by Ihlenfeldt and Hartmann (1982) in that the cells vary in size. Leaf epidermal cells in *Juttadinteria* have isodiametric anticlinal walls. In *J. albata*, *J. attenuata* and *J. deserticola* the periclinal walls are completely or almost flat (Figure 4.5 A, B, and C) while in the other two species they rise gradually towards the centre to form conical or elongate papillae of variable height. Occasionally *J. deserticola* has slightly rounded, nippled or domed periclinal walls (Figure 4.5 D). In *J. ausensis* only low conical papillae are found (Figure 4.5 E), whereas in *J. simpsonii* both conical and elongate papillae (Figure 4.5 F) occur. However in any given individual of *J. simpsonii* only one type occurs. Leaves of individuals with elongate papillae are velvety to the touch, all others are smooth. Leaf texture and epidermal cell characters are of limited taxonomic use at species level.

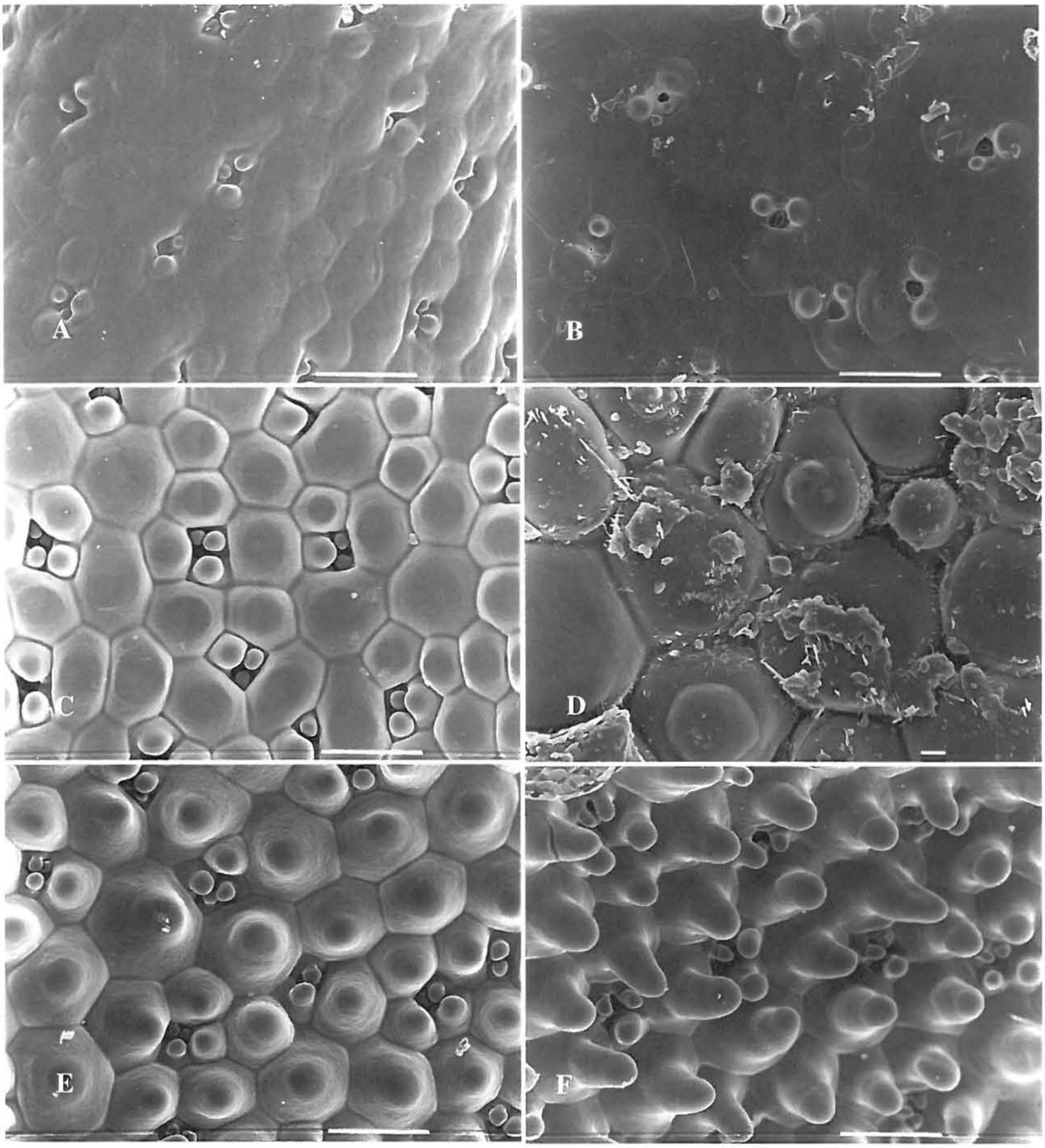


Figure 4.5: *Juttadinteria* leaf epidermal cells. A, B, C, E, F x 200. D x 500. A. *J. albata* with flat periclinal walls (*C. Mannheimer CM 2236*); B. *J. attenuata* with flat periclinal walls (*C. Mannheimer CM*); C. *J. deserticola* with flat periclinal walls (*C. Mannheimer CM*); D. *J. deserticola* with slightly rounded and nippled periclinal walls (*C. Mannheimer CM*); E. *J. ausensis* showing domed periclinal walls (*C. Mannheimer CM*); F. *J. simpsonii* showing elongate papillae. Wax removed. Scale bars 100 μm.

4.1.3.3 Stomata

In *Juttadinteria* the smallest epidermal cells are peristomatal cells with papillae that surround and often overarch the guard cells of the stomata (Figure 4.6) to form the 'hidden' stomatal type as described by Ihlenfeldt and Hartmann (1982). A discussion on this configuration is offered in section 3.1.3.3. Stomatal characters are essentially similar in all *Juttadinteria* species

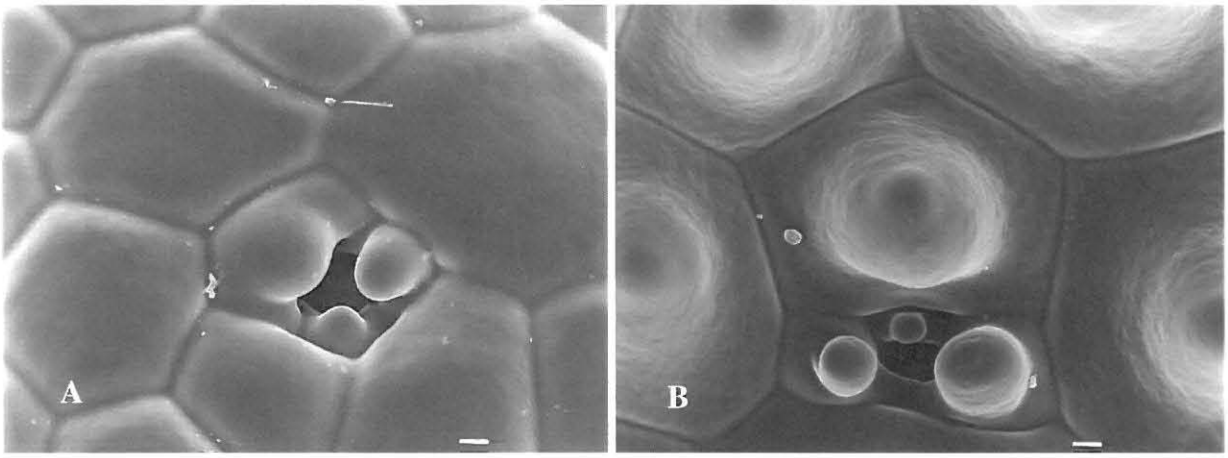


Figure 4.6: Peristomatal structure in *Juttadinteria* x 500. A. *J. deserticola* (*C. Mannheimer CM 1682*); B. *J. simpsonii* (*C. Mannheimer CM 1661*). Wax removed. Scale bar 10 μm.

4.1.3.4. Epicuticular waxes

The species of *Juttadinteria* differ in the expression of their epicuticular waxes. In all species the basal layer of wax occurs as thick, encrusting plates that fracture above the anticlinal walls (e.g. Figures 4.7 A and B). However, in *J. albata, J. attenuata* and *J. deserticola* there are almost always small, thin platelets of wax sparsely scattered on the upper surface of the plates, while in *J. ausensis* these are absent (e.g. Figure 4.7 B). These platelets sometimes appear to be denser on the top of the cells that surround the stomata (Figure 4.7 C). Additional wax crystals in *J. simpsonii* are often similar to those in the first three species, but in the individuals with the elongate papillae there is a far heavier layer of platelets. This layer is particularly dense on the sides of the papillae (Figure 4.7 D). All *Juttadinteria* species also have small blocks of wax sparsely scattered on the surface of the basal layer (Figure 4.7 A and B). The expression of epicuticular waxes is of limited taxonomic use at species level.

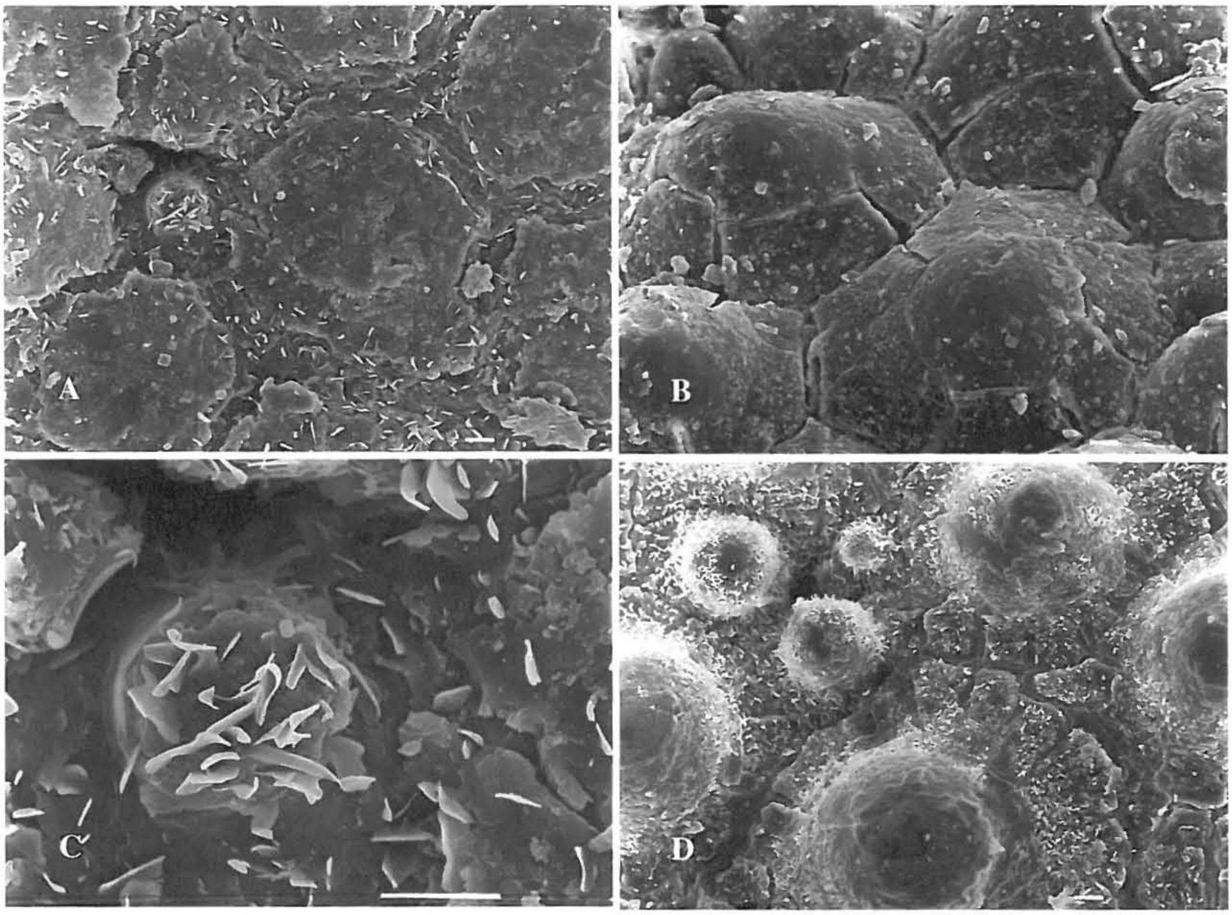


Figure 4.7: Epicuticular waxes in *Juttadinteria* . A, B, D x 500, C x 2000. A, C. *J. albata.* B. *J. ausensis.* D. *J. simpsonii.* A. thick basal layer of wax with scattered small wax platelets and wax blocks (*C. Mannheimer CM 2165*); B. thick basal wax layer without wax platelets (*C. Mannheimer CM 2640C*); C. wax platelets concentrated on top papillae of peristomatal cells (*C. Mannheimer CM 2165*); D. dense layer of wax platelets, most pronounced on sides of papillae (*C. Mannheimer CM 1661*). Scale bars 10 μm.

4.1.4 Flowers

Juttadinteria flowers (e.g. Figure 4.8 A and B) are solitary, terminal, almost sessile and ebracteolate. They are circular or somewhat squarish in outline, and with their numerous, shining 'petals' they provide a very attractive show when the plants are in full flower.

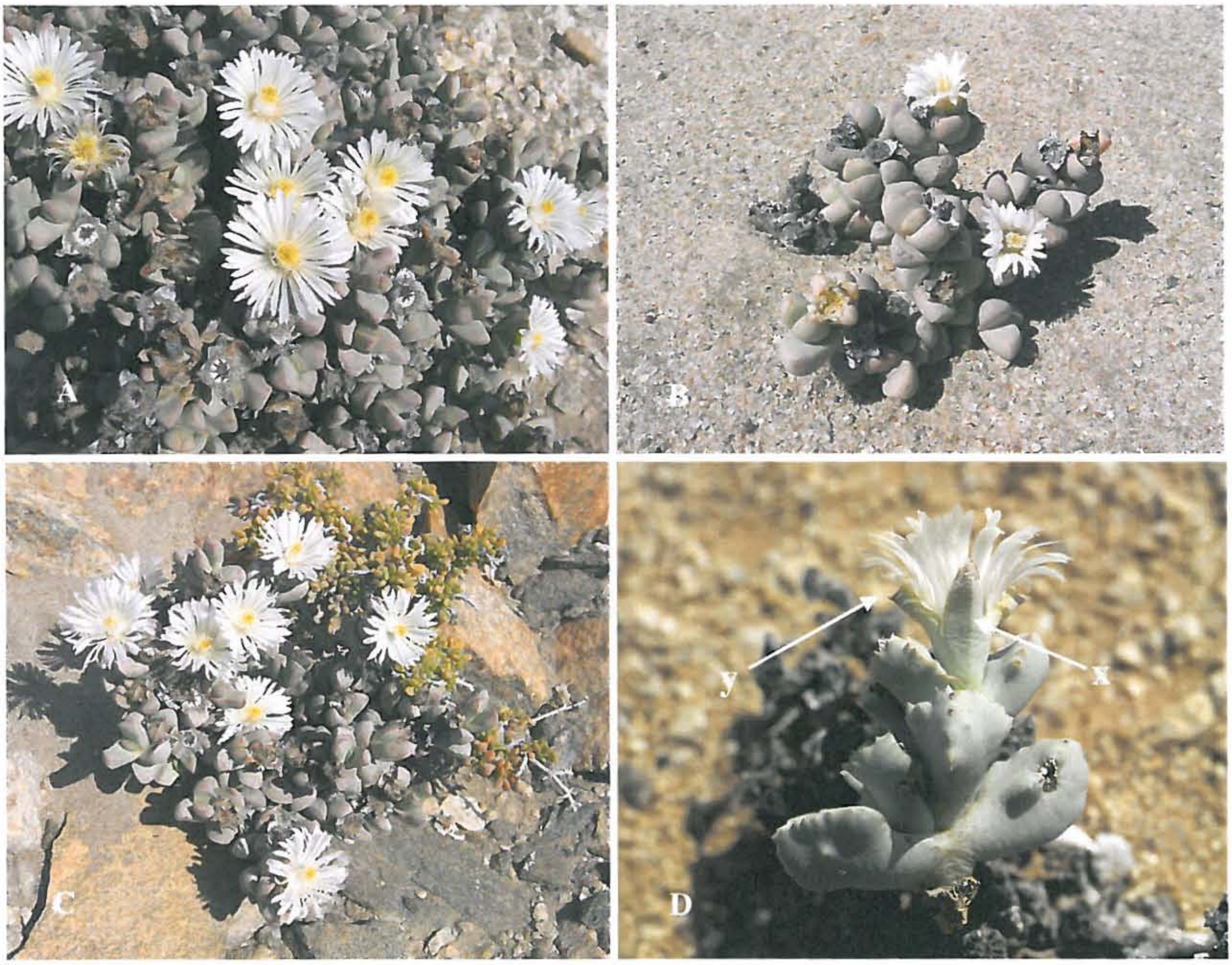


Figure 4.8: *Juttadinteria* habit and flowers. A, B, C. *J. deserticola*. A. Round flowers (*C. Mannheimer CM 2720*); B. Squarish flowers (*C. Mannheimer CM 2353*); C. Plant in full flower (*C. Mannheimer CM 2720*); D. *J. simpsonii* showing larger keeled sepal (x) and smaller sepal with membranous margin and subterminal tooth (y) (*C. Mannheimer CM 1672*).

4.1.4.1 Receptacle and Calyx

The receptacle in *Juttadinteria* is always funnel-shaped.

There are always four fleshy sepals arranged in two unequal pairs. The outer, larger pair is very fleshy, and keeled (Figure 4.8 D), and may be ornamented with terminal or subterminal teeth as well as teeth on the margins and/or keel. The inner pair is smaller, has membranous margins and usually has a terminal or subterminal tooth (Figure 4.8 D) and very rarely marginal teeth as well. None of these characters differ consistently between *Juttadinteria* two species. However, as indicated in Figure 4.9, the longest sepals are found in *J. albata* and *J. attenuata*, the species that also have the longest leaves. This figure shows length of the larger sepal pair, but the trend is the same for both pairs. Thus neither sepal characters nor sepal size are taxonomically useful at species level.

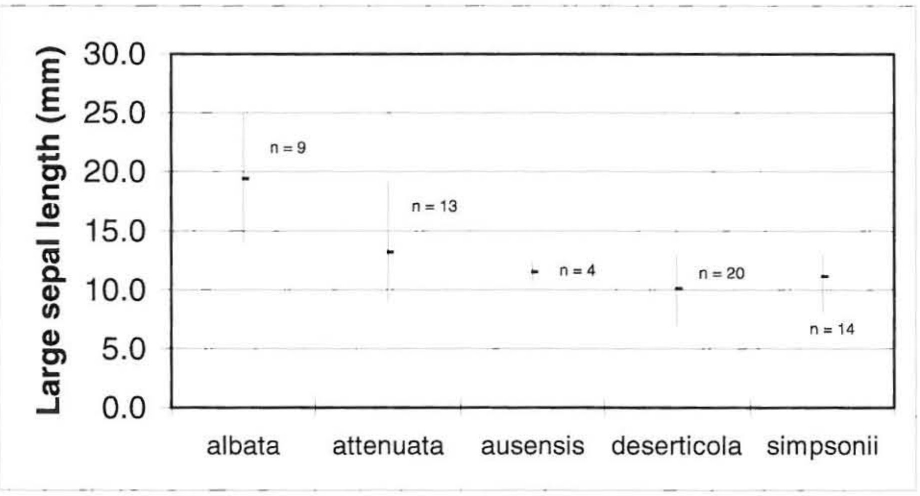


Figure 4.9: Length range of large sepals in *Juttadinteria* (horizontal bar = mean, n = specimens examined)

4.1.4.2 Flower colour and size

Flower colour in *Juttadinteria* is almost invariably white. In *J. deserticola,* extremely rarely, the flowers have a very faint pink flush.

Flowers range from 15 to 55 mm in diameter. As indicated in Figure 4.10 the highest mean is found in *J. albata*, a species that is generally more robust than the others in all aspects except fruit and seed characters. However flowers of *J. attenuata* do occasionally exceed those of *J. albata* in diameter. As might be expected, petal length showed a similar trend. However, as anthesis progresses flower diameter increases, making it difficult to standardize measurements and due to the overlap flower size is not regarded as taxonomically useful at species level.

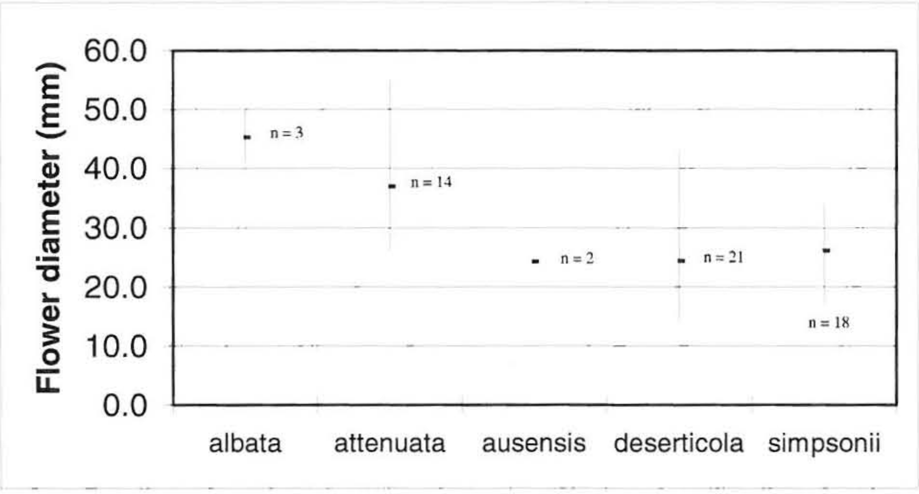


Figure 4.10: Flower diameter range in *Juttadinteria* (horizontal bar = mean, n = specimens examined)

'Petal' number varies between 38 and 72. Mean 'petal' number was found to show extensive overlap between all species, with the lowest in *J. deserticola* (48), and the highest in *J. ausensis* (65). It is thus not a taxonomically useful character at species level.

4.1.4.3 Androecium

The stamens are numerous. Initially they are arranged into a cone (Figure 4.11) which opens out to become cylindrical as anthesis progresses towards the female phase. Filaments become longer during this progression. Inner series of filaments are shorter than outer, with lengths overall varying between 2 and 11 mm. Those of *J. albata* reach a length of 11 mm and those of *J. attenuata* 10 mm, with those of the other three reaching a maximum of 9 mm. All filaments are pure white and pubescent at the base. The anthers are elongate-elliptic and dorsifixed. Their attachment is versatile. They vary between 0.3 and 1.2 mm in length, with considerable overlap between species. The thecae are parallel and exhibit longitudinal extrorse dehiscence. Androecial characters are not taxonomically useful at species level.

4.1.4.4 Stigmata

The stigmata are narrow-subulate, typical for the subtribe. In *Juttadinteria* they are pale yellow to yellow-green and vary in number between 6 and 11. In *J. albata* and *J. attenuata* there are almost always 8 while in *J. deserticola* 6 or 7 are sometimes found. In *J. simpsonii* 8 is most common but 9 or 10 stigmata are not unusual, while in *J. ausensis* up to 11 occur. With the exception of *J. ausensis,* in which the stigmata are usually free (n = 4), they are fused for a short distance at the base, sometimes with a somewhat lumpy appearance there, and the inner surface is covered by short stigmatic papillae. At first they are of a similar length to the stamens, but elongate during anthesis to protrude beyond them (Figure 4.11). Stigmatal number is of limited taxonomic use at species level, but should be considered in conjunction with other characters.

Figure 4.11: Androecium and stigmata in *Juttadinteria attenuata,* stamens collected into a cone and stigmata protruding beyond anthers.

4.1.4.5 Ovary

The ovary is shallowly to quite deeply obconical, with a flat top. Placentation is parietal, as is common in the subfamily Ruschioideae. The ovules are numerous. Ovary characters are not taxonomically useful at species level.

4.1.4.6 Floral nectary

The nectary is a crenulate ring (i.e. lophomorphic holonectary). It is apple green to dark green and produces pale straw-coloured to pale yellow nectar. No scent is discernable. Nectary characters are not taxonomically useful at species level.

4.1.5 Pollen

4.1.5.1 Colour

Pollen of *Juttadinteria* is bright golden-yellow, fading to pale yellow with age.

4.1.5.2 Shape

Pollen grains of *Juttadinteria* are symmetric, isopolar, prolate, tricolpate and somewhat rounded-triangular in polar view (Figure 4.12 C). In equatorial view the poles sometimes appear more-or-less truncate (Figure 4.12 A and B). The mesocolpi are convex and the apertures are positioned at the angles between them, equidistant to one another and parallel to the polar axis. *Juttadinteria* pollens grains are longiaxial, i.e. the polar axis (P) is longer than the equatorial axis (E). The P/E ratio varies from 0.8 to 1.5, with a mean of 1.2 in all species except *J. ausensis,* which has a mean of 1.3.

4.1.5.3 Size

Juttadinteria ausensis has a significantly longer mean pollen length than both *J. attenuata* and *J. simpsonii* (Figure 4.13). Its pollen grains are also significantly narrower than those of *J. attenuata* and *J. deserticola* (Figure 4.14). However, there is no significant difference in pollen dimensions between the other *Juttadinteria* species (Table 4.4).

Table 4.4: Pollen dimensions and tectum structures in *Juttadinteria.*

	Length μm min– mean –max – std. dev.	Width μm min– mean –max – std. dev.	No. perforations min– mean –max – std. dev.	No. prominences min– mean –max – std. dev.
J. albata	18.8 – 21.6 – 23.7 – 1.19	15.0 – 17.6 – 19.4 – 1.14	40 – 58 – 82 – 15	69 – 92 – 173 – 28
J. attenuata	16.2 – 20.9 – 25.4 – 1.67	15.6 – 17.8 – 20.4 – 1.51	38 – 47 – 65 – 9	54 – 73 – 99 – 18
J. ausensis	19.6 – 22.3 – 24.6 – 1.46	15.0 – 16.7 – 18.5 – 0.91	41 –56 – 68 –11	56 – 87 – 110 – 25
J. deserticola	19.2 – 21.7 – 25.8 – 1.47	15.6 – 17.9 – 22.3 – 1.20	38 – 51 – 63 – 10	56 – 82 – 102 – 14
J. simpsonii	17.5 – 21.1 – 23.8 – 1.53	13.4 – 17.4 – 20.0 – 1.14	20 – 41 – 61 – 15	31 – 86 – 133 – 33

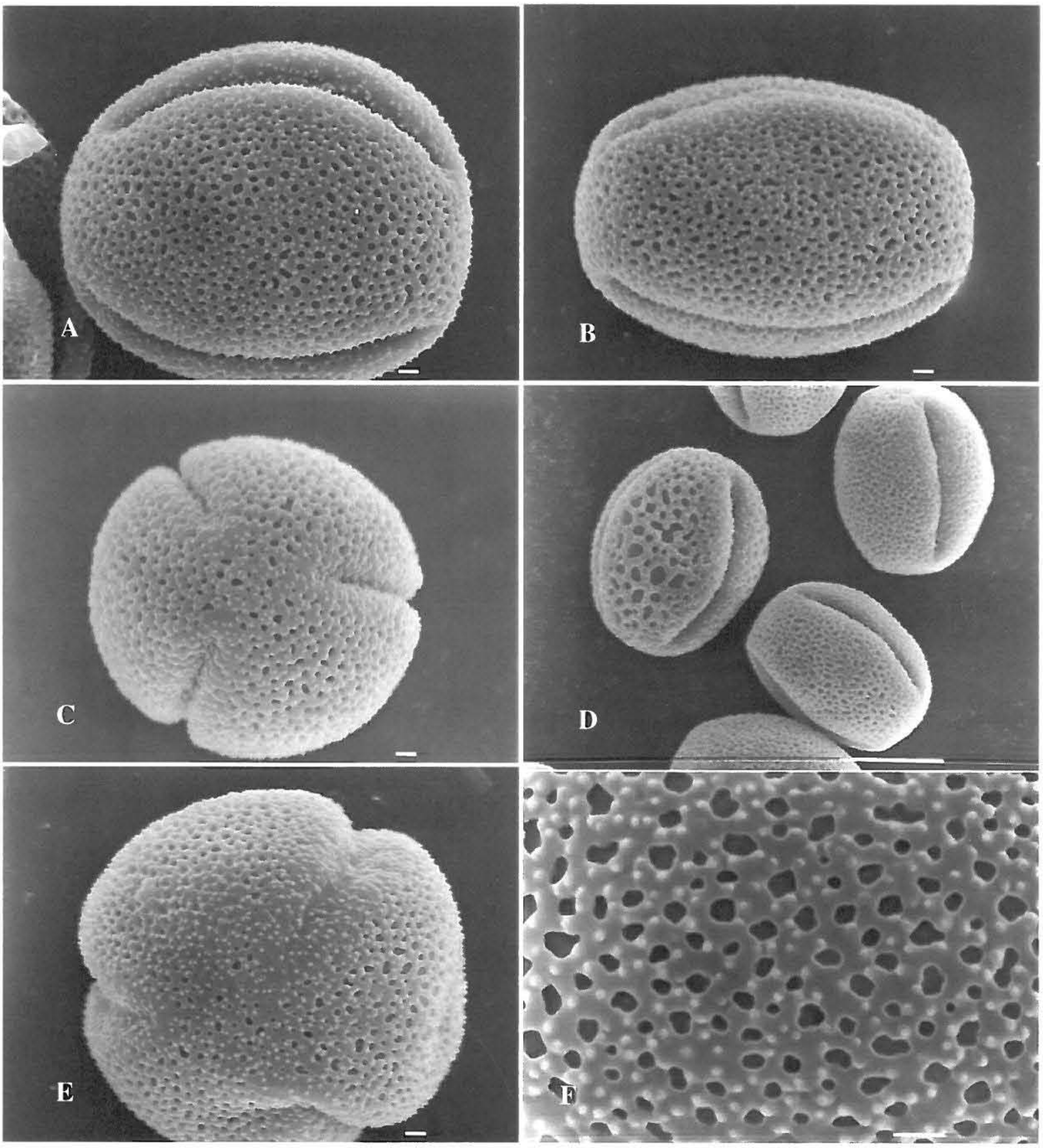


Figure 4.12: ***Juttadinteria*** pollen. A, B, C, E. x 4000, D x 2000, F x 10 000. A, E, F. *J. deserticola*. B, C, D. *J. simpsonii*. A. Equatorial view (*C. Mannheimer CM 2348*); B. Equatorial view showing truncate poles (*C. Mannheimer CM 1673*); C. Polar view showing colpi with narrow gape (*C. Mannheimer CM 2381*); D. Two different tectum types in a single flower (*C. Mannheimer CM 2369* from the Kovis Mountains); E. Polar view showing wide colpus gape and almost entire exine near colpi and poles (*C. Mannheimer CM 2348*); F. Equatorial view of tectate-perforate exine showing spinulae and luminae of varying sizes (*C. Mannheimer CM 2378*). Scale bars 1 μm except D. D scale bar 10 μm.

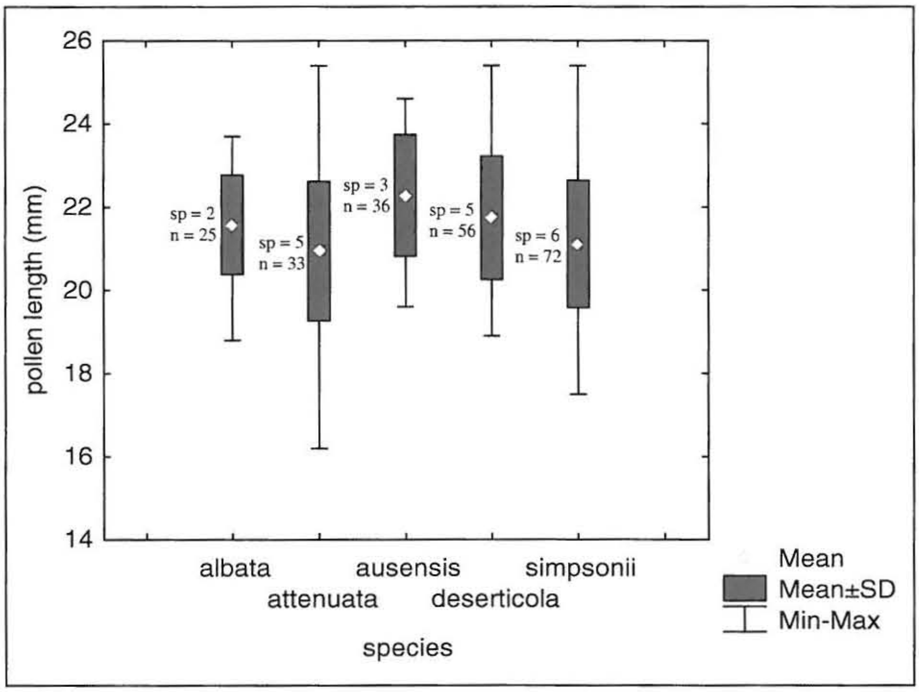


Figure 4.13: A comparison of pollen length in *Juttadinteria*

(F(4, 216) = 5.1733; p = 0.0005; sp = specimens; n = pollen grains measured).

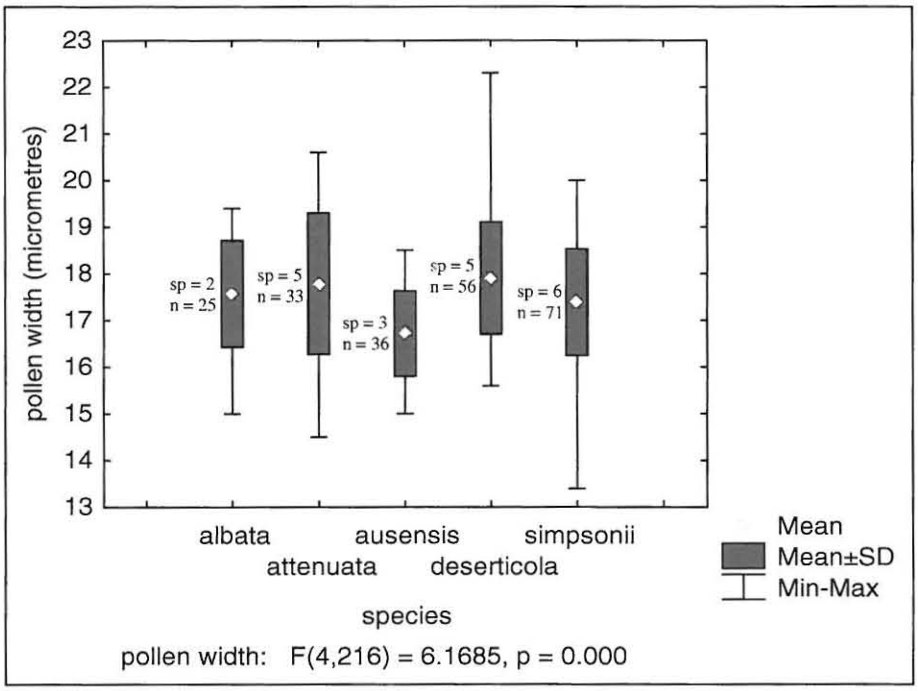


Figure 4.14: A comparison of pollen width in *Juttadinteria.*

(F(4, 216); p = 0.0001; sp = specimens; n = pollen grains measured).

4.1.5.4 Exine structure

The exine in all *Juttadinteria* species except *J. simpsonii* is consistently tectate-perforate. In *J. simpsonii* it varies from tectate-perforate to semitectate-reticulate, sometimes even in a single flower (Figure 4.14 D). However the latter condition is found only in plants from the Kovis Mountains that also have a velvety epidermis. In all species the tectum is always ornamented with pointed spinulae. Micro-perforations of the tectum and free baculae on the nexine are often present.

4.1.5.5 Perforations and sculpturing

Perforations vary from micro-perforations to irregular luminae that result in the reticulate condition. The number of perforations varies from 20 to 82 in an area of 25 μm^2, counted on the mesocolpium at a point equidistant from both the poles and the adjacent colpi. The mean number of perforations was lowest in *J. simpsonii* (41, n=16) and highest in *J. albata* (58, n=12) (Table 4.4).

The mean number of spinulae was lowest in *J. attenuata* (73) and highest in *J. albata* (92).

Although mean numbers of perforations and spinulae differ to quite an extent in this genus, these characters do overlap greatly and are not regarded as taxonomically useful at species level. If a more accurate measure of exine extent was applied to a larger sample size it would be possible to reassess these characters.

The polar regions exhibit the same characters as the mesocolpi , but at the margins of the colpi there are far fewer perforations and often only micro-perforations are found. In some areas, particularly close to the poles, the exine may lack pores (Figure 4.12 E).

4.1.5.6 Apertures

As may be seen in figure 4.12 E, the colpi are closed. There is variation in the gape of the colpi (e.g. Figure 4.12 C and E), however this appears to occur in all species of *Juttadinteria.*

4.1.6 Fruit

Juttadinteria fruit differ in size as well as in a number of other characters. Capsule diameter varies between 4.7 and 13.0 mm. By means of a one-way ANOVA the mean was found to be significantly different between species at the 99 % confidence level (Figure 4.15), despite the fact that considerable overlap in ranges exists. *Juttadinteria deserticola* has the smallest capsules and *J. albata* and *J. ausensis* have the largest. The capsule in all species is obconical with the upper surface flat to slightly raised towards the centre (Figure 4.16 A and B). The edges are sometimes rounded (Figure 4.16 B), and the valve tips often recurved when mature.

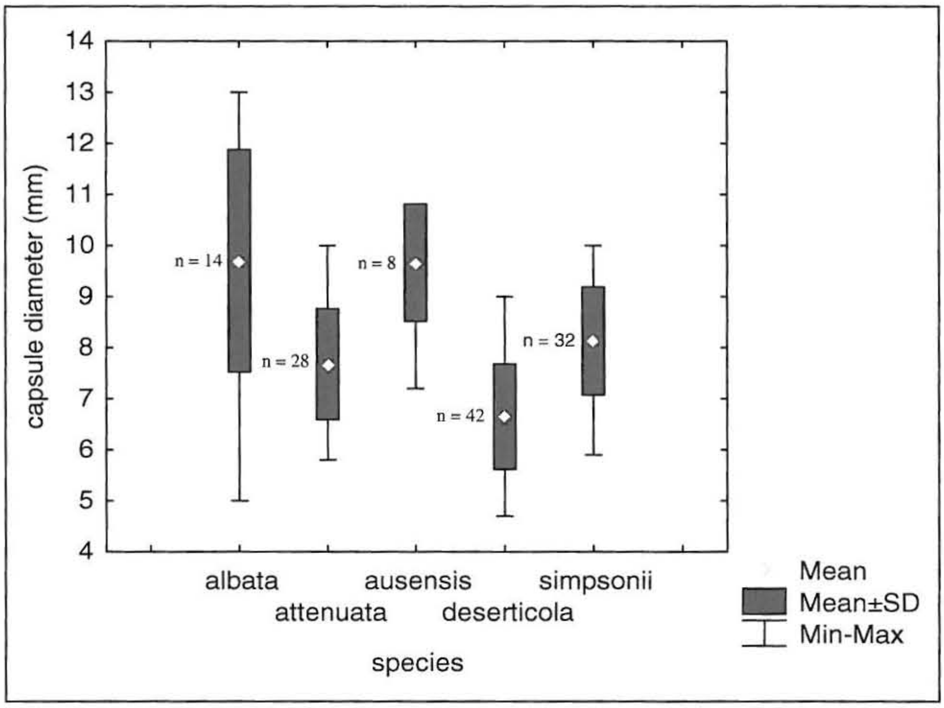


Figure 4. 15: A comparison of mean capsule diameter between *Juttadinteria* species.

(F(4, 119) = 22.7294; p = 0.0000)

Locule number varied between 6 and 12, with the most frequent number overall being 8. Mean locule number was not significantly different between *Juttadinteria* species. In *J. deserticola* maximum locule number is 10, while all other *Juttadinteria* species may have up to 12. Capsule size and locule number may be regarded as of some taxonomic use at species level, providing they are considered together with other characters.

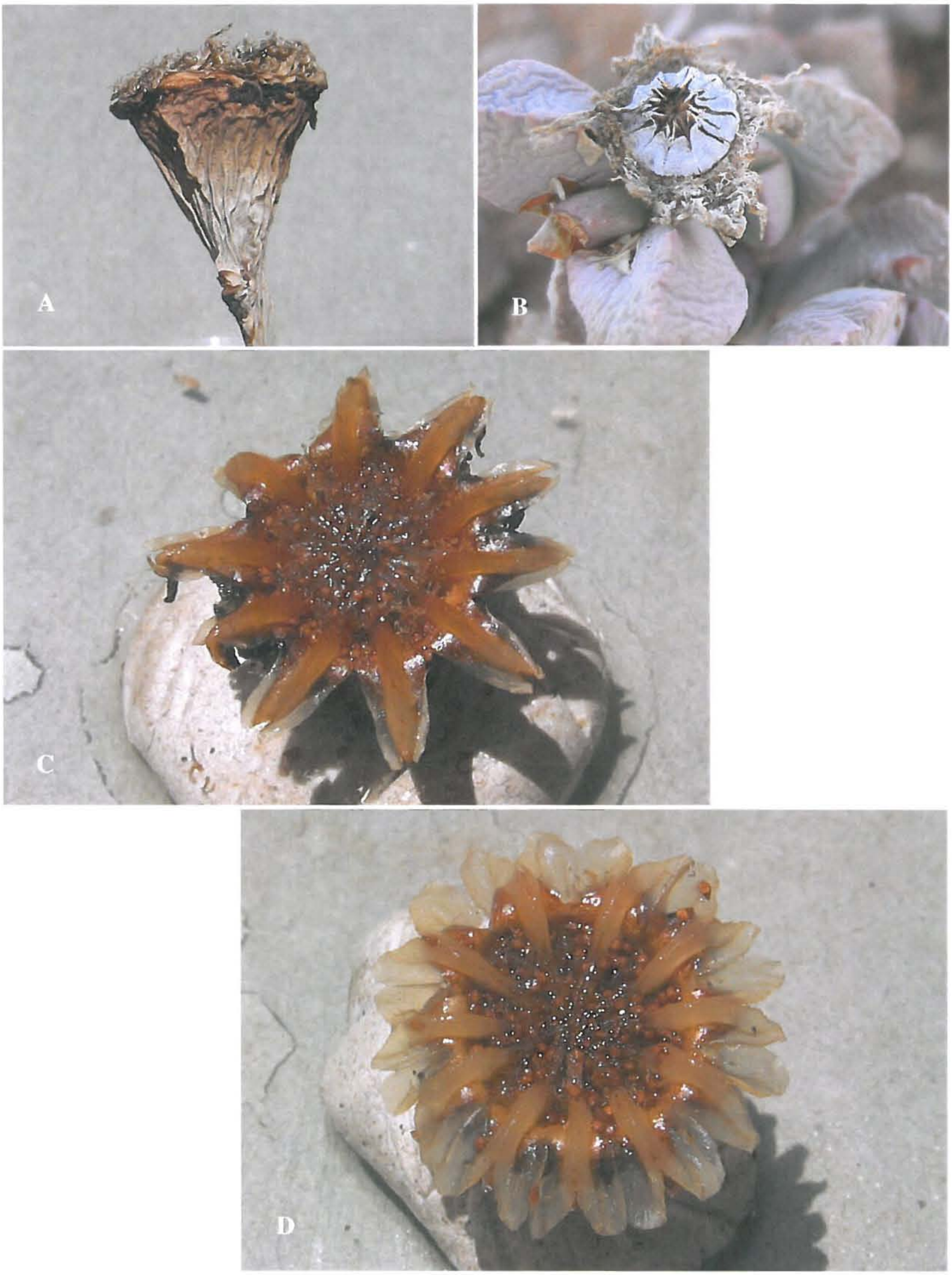


Figure 4.16: *Juttadinteria* capsules. A. *J. albata* showing obconical general shape (Hartmann 8426); B. *J. ausensis* showing rounded edges and recurved valve tips (*C. Mannheimer CM 2640A*); C. *J. simpsonii* open capsule with parallel keels and narrow-rectangular valve wings (*C. Mannheimer CM 2382*); D. *J. simpsonii* with vestigial covering membranes and broad-rectangular valve wings (*C. Mannheimer CM 2356* Kovis Mountains).

The septa extend evenly from their insertion on the wall of the receptacle to the tip of the columella. The expanding keels are radial and parallel from the base (Figure 4.16 C), diverging distally and (occasionally) at the fulcrum where the valve bends slightly when open. Rarely, in *J. deserticola,* they diverge very slightly from the base all the way along. They are higher than broad and slightly lacerate. Their colour varies from pale yellow-orange to light to dark brown and appears to darken with age. The valve wings are narrowly to broadly rectangular (Figure 4.16 C and D) or crescent-shaped, 0.2 to 1.6 mm wide and occasionally have short awns. There is no significant difference between species regarding valve wing width. They equal or exceed the valve and/or the keels in length, with the exception of *J. ausensis*, in which they are shorter than the valve. Covering membranes are present but often poorly developed (Figure 4.16 D). They are translucent, and seldom meet, collapsing inwards after seed dispersal. In *J. albata, J. ausensis* and *J. deserticola* they never meet (e.g. Figure 4.17 A), whereas in *J. attenuata* and *J. simpsonii* (e.g. Figure 4.17 B) they do occasionally meet in the middle of the locule. Closing bodies are completely absent and the valves open completely to a flat or even reflexed position when wetted (Figure 4.16 D). The fruit type appears to fall between the *Titanopsis* type and the *Delosperma* type as described by Hartmann 1988. because the covering membranes are vestigial in many individuals but vary within species such that all were also found to exhibit crescent-shaped covering membranes. *Juttadinteria attenuata* occasionally even has membranes that broaden distally. The ecological implications of the combination of capsule features seen in *Juttadinteria* are discussed in chapter 8. As a result of high intraspecific variation capsule structure is not taxonomically useful at species level in *Juttadinteria.*

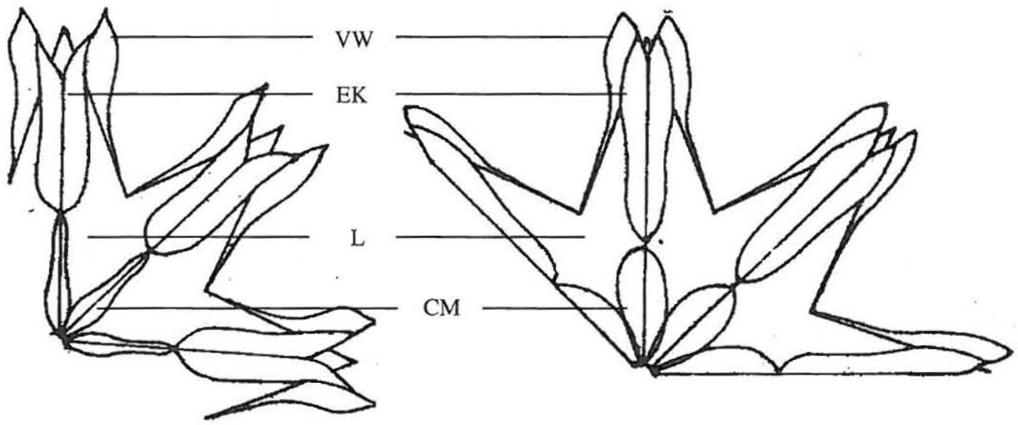


Figure 4.17: Examples of Juttadinteria capsules. A. *J. deserticola* (*C.Mannheimer CM 2348*). B. *J. simpsonii* (*C. Mannheimer CM 2382*). VW = valve wing; EK = expanding keel; L = locule; CM = covering membrane.

4.1.7 Seed

Juttadinteria seeds are similar in all species. They are fat comma-shaped (Figure 4.18 A)and vary in colour from light brown to apricot or gold-brown to rust-brown. The micropylar region is produced well forwards. Seed length varies between 0.5 and 1.0 mm. There is no difference in seed length between species.

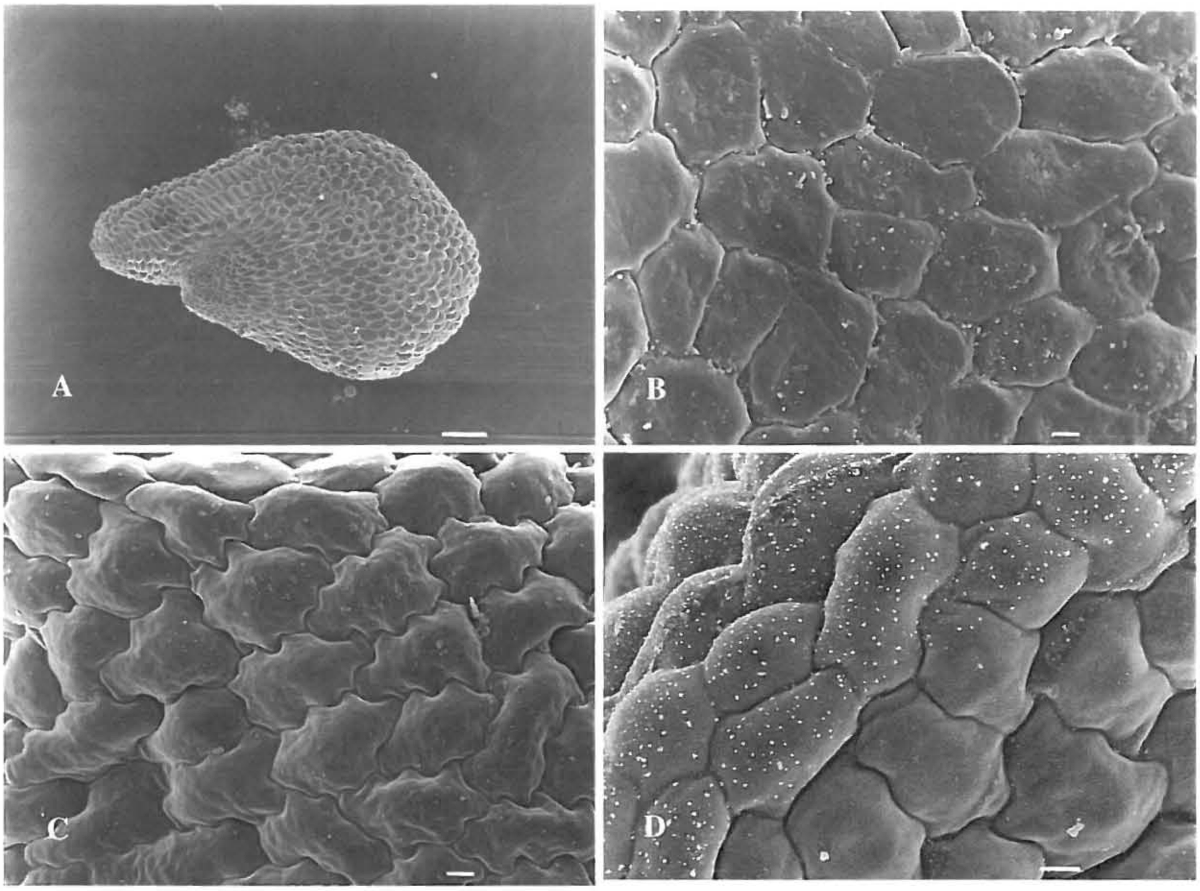


Figure 4.18: *Juttadinteria* seed. A x 75, B, C. x 500, D x 700. A. *J. deserticola* x 75 (*C. Mannheimer CM 2720*), scale bar 100 µm; B. *J. albata* with flattish periclinal walls (*C. Mannheimer CM 2165*); C. *J. simpsonii* with undulate anticlinal walls, surface somewhat lumpy (*C. Mannheimer CM 1666*); D. *J. simpsonii* with velvety texture and white granulation (*C. Mannheimer CM 2270*). Scale bars 10 µm.

The shape of the testa cells is variable. Where they are ordered in rows, i.e. in the micropylar and hilar regions, they are narrower than elsewhere. In areas such as the perisperm region, where the cells are less ordered their shape is more variable. Anticlinal walls are sunken to a greater or lesser degree, and vary from almost straight (Figure 4.18 B) to very undulate, with S-shaped undulations (Figure 4.18 C).

Periclinal cell walls are flattish (e.g. Figure 4.18 B) to distinctly convex (e.g. Figure 4.18 C and D), with less elongated cells more convex than longer ones. The testa fold is oriented at an angle of approximately 45% to the long axis of the seed. In all species testa cell surfaces appear textured (e.g. Figure 4.18 D), but this texturing is variable within species and the small sample size did not allow for any definite conclusions to be drawn as to constant specific differences. Seed characters are not regarded as taxonomically useful at species level in *Juttadinteria*.

4.2 Taxonomic treatment

Juttadinteria Schwantes, Zeit. F. Sukk. 2: 182-183 (1926); Jacobsen, Sukk. Pl. : 141 (1933); v. Pöllnitz, F. Rep. Sp. Nov. 32: 46-47 (1933); Jacobsen, Succ. Pl. 190 (1935); Jacobsen, F. Rep. Sp. Nov. 106: 94-95 (1938); Walgate in Bolus, Notes on Mes. 3: 173 (1939); Jacobsen, Succ. Pl.:190 (1935); Jacobsen, Herre & Volk, Mesembr.: 66, 77, 99 (1950);Jacobsen, Handb. Sukk. Pfl.: 1418 (1955); Jacobsen, Handbook Succ. Pl.: 953 (1960); Jacobsen, Sukk. Lex.: 435 (1970); Friedrich in Merxmüller, Prodromus FSWA (Juttadinteria) 27: 58-64 (1970); Herre, Gen. Mesem.: 184 (1971); Court, Succ. Fl. sthn. Afr.: 46 (1981); Smith *et al.*, Mesembs: 148 (1998); Court, Succ. Fl. sthn. Afr.: 20 (2000); Leistner (Ed.), Seed Pl. sthn. Afr.: 393 (2000); Van Jaarsveld *et al.*, Vygies: 130 (2000); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: 70-71 (2001). Type: *Juttadinteria kovisimontana* (Dinter) Schwantes

Etymology: Named after Jutta Dinter, the wife of Professor K. Dinter, a German botanist who worked extensively in Namibia.

Plants succulent, perennial, clump-forming, caespitose or prostrate, procumbent or erect dwarf shrubs; branches 3-5, woody-fibrous, internodes enclosed by leaf bases or exposed, up to 30 mm long. *Leaves* opposite, connate; broadly trigonous, elongate-trigonous or rhomboid-spatulate; light grey-green to blue-green or green with darker green spots; up to 73 x 26 mm, up to 23 mm thick, up to more than four times as long as wide; margins, keels and lateral surfaces sometimes flushed pink or orange; margins and keel entire or minutely denticulate to fiercely or rather bluntly dentate; keel often oblique, prominent at the apex; apex blunt, tapering, rounded or acute, often with a small, hard mucro; base pustulate; epidermis glabrous with flat, rounded or domed cells or velutinous and papillate; epicuticular wax in thick encrusting plates, sparsely ornamented with small wax blocks, sometimes with additional, scattered wax platelets or rodlets; stomata hidden by overarching papillae. *Flowers* solitary, ebracteolate, sessile to subsessile, sometimes appearing squarish, opening from early afternoon until dusk, up to 55 mm in diameter; receptacle epidermal cells rounded to domed or papillate. *Sepals* 4, unequal, fleshy, epidermal cells rounded to domed or papillate; outer sepals keeled, larger than inner sepals, sometimes with terminal, subterminal, marginal or keel teeth variously combined, 6.8–25.0 x 4.8–13.0 mm; inner sepals with membranous margin, 4.0–17.0 x 3.0–9.0 mm. *Staminodes* petaloid, 30–71, in two to three series, exceeding the sepals, shining white, rarely with slight pink flush, 7–30 mm long, linear to linear-ligulate, reflexed. *Androecium* conical to columnar with age; stamens numerous; filaments white, unequal, 0.8–11 mm long, bases finely papillate; outer filaments longest; anthers dorsifixed, pale yellow, 0.5–1.2 mm long, extrorse, dehiscence longitudinal. *Pollen* prolate, bright yellow, 16–26 μm long, tricolpate, exine tectate-perforate to semitectate-reticulate, spinulate. *Nectary* continuous, crenulate green to olive-brown; nectar clear, pale green, pale yellow to straw-coloured, rarely golden yellow. *Gynoecium* stigmas 6–11, yellow, narrow-subulate, free or briefly basally fused, inner surface with stigmatic papillae; ovary synovarious, shallowly to deeply obconical, almost flat above; placentation parietal. *Capsule* hygrochastic, 6–13 locular, 5–13 mm in diameter; base obconical, top flat or almost so; expanding keels radial and parallel, diverging slightly distally or at the fulcrum, various shades of brown; awns absent; valve wings crescent-shaped, narrow to broad-rectangular or broad-triangular; covering membranes vestigial, crescent-shaped or widening distally; closing bodies absent. *Seeds* comma-shaped to ovate, 0.5 – 1 mm long, light brown, light apricot or rust-brown.

Key to species

1a	Leaves very pale grey-green, tapering sharply, often almost in a straight line, from a broad base to a sharp tip, minimum width at base 12 mm, usually far wider................	*J. albata*
b	Leaves blue-green to green, sometimes with darker green dots, tapering in a gentle curve or gradually to the tip, which may be rounded or quite sharp, width at base usually up to 15 mm, usually narrower, rarely up to 18 mm..	2
2a	Leaf margins and keel untoothed or with few minute teeth..	3
b	Leaf margins distinctly toothed, teeth numerous, large..	4
3a	Leaves broadly boat-shaped, up to twice as long as wide.............................	*J. deserticola*
b	Leaves elongate-trigonous, more than twice a long as wide..........................	*J. attenuata*
4a	Leaf forming a distinct but narrow triangular section below the apex (Figure 4.3 B)	*J. ausensis*
b	Leaf widest below the tip, forming a broad and deep spathulate section (Figure 4.3 D and F)...	*J. simpsonii*

1. Juttadinteria albata (L. Bolus) L. Bolus, S.A. Gard. 1928c: 249; Jacobsen, Succ. Pl.:190-191 (1935); Jacobsen, F. Rep. Sp. Nov. 106: 94 (1938); Walgate in Bolus, Notes on Mes. 3: 173 (1939); Jacobsen, Sukk. Lex.: 435 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 58-64 (1970); Court, Succ. Fl. sthn. Afr.: 46 (1981); Smith *et al.*, Mesembs: 148 (1998); Van Jaarsveld *et al.*, Vygies: 130 (2000); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: 71 (2001). Type: Hill west of Arris Drift, Little Namaqualand, *Pillans 5039* (BOL!, holo).

Mesembryanthemum albatum L. Bolus, Ann. Bol. Herb. 4: 97-98 (1928d).

Etymology: albatum (Latin), white, probably referring to the pale leaves.

Plants succulent, perennial, procumbent or erect dwarf shrubs up to 30 cm high; internodes enclosed by leaf bases or very short. *Leaves* elongate-trigonous, flat above, light grey-green, sometimes dotted darker green; up to 76 x 23 mm, and up to 23 mm thick, two to four times as long as wide; keel oblique, prominent at the apex; margins and keels entire or sparsely and minutely denticulate, sometimes flushed pink or orange; apex tapering to a point, sometimes with a small, hard mucro; epidermis very smooth; epicuticular wax with additional, scattered wax platelets. *Flowers* radially symmetric to slightly squarish, up to 50 mm in diameter; receptacle and sepal epidermal cells rounded; outer sepals with minute terminal, subterminal, marginal or keel teeth variously combined, 14.0–25.0 x 7.0–11.0 mm; inner sepals 7.6–17.0 x 5.2–8.5 mm. *Staminodes* petaloid, 50–70, shining white, linear-ligulate, 13–30 x 1.5–4.2 mm. *Androecium* filaments 2–11 mm long; anthers 0.5–0.8 mm long. *Pollen* 19–24 x 15–19 μm; exine tectate-perforate. *Nectary* a green crenulate ring, nectar clear to pale yellow or straw-coloured, rarely golden yellow. *Gynoecium* stigmas 7–9, briefly basally fused; ovary shallowly obconical. *Capsule* 7.3–12.0 mm in diameter, 8–12 locular; base shallowly obconical; keels radial and parallel, diverging slightly distally, light brown to tan; valve wings narrowly to broadly rectangular or crescent-shaped; covering membranes vestigial to (seldom) crescent-shaped, not meeting. *Seeds* comma-shaped, 0.6–1.0 mm long, light brown to light apricot.

Distinguishing characters: *Juttadinteria albata* may be confued with *J. attenuata* It is distinguished by its large, pale, very smooth and almost untoothed leaves that taper to a narrow apex and its procumbent to erect habit.

Distribution: Endemic to the southernmost reaches of the southern Namib, where it is most common on the gravel terraces of the Orange (Gariep) River. (Figure 4.21).
Habitat: Typically occurs in sandy soil on rocky slopes and south-facing gravel river terraces where fog is periodically trapped.
Altitude: 20 – 72 m
Flowering: September.
Provisional Namibian Red Data status: CR A3c+4c;D2.
Illustrations: Jacobsen, Succ. Pl.:Fig. 170 (1935); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: Pl. 10 (2001).

2. Juttadinteria attenuata Walgate in Bolus, Notes on Mes. 3: 178 (1939); Jacobsen, Sukk. Lex.: 435 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 58-64 (1970); Smith *et al.*, Mesembs: 148 (1998); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: 71 (2001). Type: Locality unknown, *Holloway 3* (BOL!, holo).

Etymology: attenuatus (Latin), drawn out, referring to the slender, elongate leaves.

Plants succulent, perennial, prostrate to slightly procumbent; internodes enclosed by leaf bases or exposed, up to 30 mm long. *Leaves* elongate-trigonous, usually slender, slightly rounded above, green, with conspicuous, often raised, punctae due to large subepidermal tannin cells, up to 43 x 15 mm, up to 12 mm thick, far longer (up to more than four times)than wide; keel oblique, prominent at the apex; margins and keel entire, rarely sparsely and minutely denticulate, sometimes flushed pink; apex tapering to a slender or rounded point, sometimes with a small, hard mucro; epidermis very smooth, with flat cells; epicuticular wax with additional, scattered wax platelets. *Flowers* radially symmetric, up to 55 mm in diameter; receptacle and sepal epidermal cells rounded to domed; outer sepals with minute terminal, subterminal or keel teeth variously combined, 9.0–19.1 x 5.2–13.0 mm; inner sepals 5.0–15.2 x 3.0–7.8 mm. *Staminodes* petaloid, 38–70, shining white, linear-ligulate, 10–24 x 1.338–70, 2.7 mm. *Androecium* filaments 3–10 mm long; anthers 0.5–1.1 mm long. *Pollen* 16–25 x 16–20 μm; exine tectate-perforate. *Nectary* green; nectar clear to pale green, pale yellow or straw-coloured. *Gynoecium* stigmas 8; base briefly fused; ovary shallowly obconical. *Capsule* 5.8–10.0 mm in diameter, 8–12 locular; base obconical; keels radial and parallel, diverging slightly distally and sometimes at the fulcrum, yellow brown to orange brown; valve wings narrowly to broadly rectangular or crescent-shaped; covering membranes vestigial to crescent-shaped or widening distally, meeting or not meeting. *Seeds* comma-shaped, 0.7 mm long, light brown.

Distinguishing characters: *Juttadinteria attenuata* is distinguished from *J. albata* and *J. deserticola* by its long, relatively slender, dotted, almost untoothed leaves and its prostrate habit.

Distribution: Endemic to the central plains and koppies of the southern Namib (Figure 4.21).
Habitat: Typically occurs in sandy soil, often with calcrete inclusions, on rocky slopes, gentle slopes or plains.
Altitude: 263 – 768 m.
Flowering: August to September.
Provisional Namibian Red Data status: LC.

Illustrations: Walgate in Bolus, Notes on Mes. 3: 179 (1939); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: Pl. 10 (2001).

3. Juttadinteria ausensis (L. Bolus) Schwantes, Zeit. Sukk. Kunde 2: 183 (1926); Jacobsen, F. Rep. Sp. Nov. 106: 94 (1938);Walgate in Bolus, Notes on Mes. 3: 173 (1939); Jacobsen, Sukk. Lex.: 435 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 58-64 (1970); Smith *et al.*, Mesembs: 148 (1998); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: 71 (2001). Type: South West Africa, Aus, *Lewis 543/18* (BOL!, lecto).

Mesembryanthemum ausense L. Bolus, Ann. Bol. Herb. 3: 123 (1922).

Juttadinteria suavissima sensu Dinter: 138-139 (1923) *pro parte*.

Etymology: Aus, after the small town in southern Namibia that lies closest to the distribution area of the species.

Plants succulent, perennial, decumbent or erect dwarf shrubs up to 20 cm high; internodes enclosed by leaf bases or exposed and up to 20 mm long. *Leaves* elongate-trigonous, flat above, blue-green to grey-green becoming dirty pink when stressed, up to 25 x 12 mm, up to 10 mm thick, up to twice as long as wide; keel oblique, prominent at the apex; margins parallel; margins and keel distinctly dentate, with fleshy teeth; apex narrowly triangular, tapering to a point, sometimes with a small, hard mucro; epidermis smooth with domed cells; epicuticular wax covering lacking additional, scattered wax platelets. *Flowers* slightly squarish, up to 55 mm in diameter; receptacle epidermal cells conelike; sepal epidermal cells domed; outer sepals with or without subterminal and marginal teeth, keel teeth absent, 10.7–12.3 x 6.7–8.8 mm; inner sepals 5.7–9.1 x 4.8–6.7 mm. *Staminodes* petaloid, 56–72, shining white, linear-ligulate, 11–18 x 1.0–2.8 mm. *Androecium* filaments 2–9 mm long; anthers 0.7–1.0 mm long. *Pollen* 20–25 x 15–19 μm; exine tectate-perforate. *Nectary* green; nectar pale yellow or straw-coloured. *Gynoecium* stigmas 8–11, free at the base; ovary obconical. *Capsule* 7.2–10.7 mm in diameter, 8–12 locular; base obconical; keels radial and parallel, diverging slightly distally, yellow brown to orange brown; valve wings narrowly to broadly rectangular; covering membranes crescent-shaped, not meeting. *Seeds* comma-shaped, 0.8 mm long, light brown.

Distinguishing characters: *Juttadinteria ausensis* distinguished from *J. simpsonii* by its leaves that form a distinct but not very pronounced triangle below the apex, this thickening is far more pronounced in *J. simpsonii*.

Distribution: Endemic to the central-northern and central reaches of the southern Namib south-west of Aus (Figure 4.21).

Habitat: Typically occurs on gravelly-sandy plains with heavy calcrete inclusions and some quartz, occasionally on mountain slopes.

Altitude: 640 – 980 m.

Flowering: September.

Provisional Namibian Red Data status: EN B1ab(v).

Illustrations: Smith *et al.*, Mesembs: 149 (1998); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: Pl. 10 (2001).

4. Juttadinteria deserticola (Marloth) Schwantes, Zeit. Sukk. Kunde 2: 183 (1926); Jacobsen, Succ. Pl.: 191 (1935); Jacobsen, F. Rep. Sp. Nov. 106: 94 (1938); Walgate in Bolus, Notes on Mes. 3: 173 (1939); Jacobsen, Sukk. Lex.: 435 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 58-64 (1970); Smith *et al.*, Mesembs: 148 (1998); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: 71 (2001). Type: Near Angra Pequena,in Great Namaqualand, *Marloth 4688* (BOL!, holo).

Mesembyanthemum deserticolum Marloth. Trans. Roy. Soc. S. Afr. 2: 34 (1910-1912).

Juttadinteria suavissima sensu Dinter: 138-139 (1923) *pro parte.*

Juttadinteria buchubergense Dinter in F. Rep. Sp. Nov. 21: 169 (1931) *nomen nudum.*

Juttadinteria decumbens Schick & Tisch. Kakt. 48 (1933). Type: photograph pg. 48 *Tischer 1933* (lecto).

Mesembrianthemum elizae Dinter & Berger. Bot. Jahrb. Supp. 50: 587-588 (1914). *Juttadinteria elizae* (Dinter & Berger) L. Bolus. S. A. Gard. 18: 249 (1928). Type: Lüderitzbucht, Great Namaqualand, *Dinter 1010* (B, †).

Mesembryanthemum insolitum L. Bolus. Ann. Bol. Herb. 4: 75 (1928). *Juttadinteria insolita* (L. Bolus) L. Bolus. S.A. Gard. 18: 249 (1928). Type: Karroid hills between Dun Vley and Groot Doorn above S. bank of Orange River, *Pillans 5692* (BOL!, holo).

Juttadinteria tetrasepala L. Bolus. Notes on Mes. 2: 343-344 (1932). Type: Richtersveld, Swartwater, *Herre S.U.G. 9046* (BOL!, holo).

Etymology: referring to the desert habitat.

Plants succulent, perennial, tufted or branched and procumbent or erect dwarf shrubs up to25 cm high; internodes enclosed by leaf bases or very short. *Leaves* broad-trigonous to elongate-trigonous, flat to slightly rounded above, up to 29 x 18 mm, up to 12 mm thick, up to three times as long as wide, usually less than twice as long as wide, grey-green to blue-green,; keel sometimes oblique, often indistinct; margins and keels sometimes flushed pink, entire or sparsely and minutely denticulate; apex tapering to a rounded point, sometimes with a small, hard mucro; epidermis smooth with flat to rounded cells; epicuticular wax with additional, scattered wax platelets. *Flowers* radially symmetric to slightly squarish, up to 37 mm in diameter, often smaller; receptacle and sepal epidermal cells rounded to domed; outer sepals usually with terminal, marginal and keel teeth variously combined, 6.8–13.0 x

4.8–9.3 mm; inner sepals 4.0–10.4 x 3.7–7.0 mm. *Staminodes* petaloid 30–56, shining white, linear to linear-ligulate, 7–19 x 1.0–3.0 mm. *Androecium* filaments 2–9 mm long; anthers 0.3–1.2 mm long. *Pollen* 19–26 x 16–22 μm; exine tectate-perforate. *Nectary* green to very dark green; nectar clear to pale green, pale yellow or straw-coloured. *Gynoecium* stigmas 7–10, bases briefly fused; ovary obconical. *Capsule* 4.7–9.0 mm in diameter, 7–9 locular; base obconical,;keels radial and parallel, diverging slightly distally, or diverging slightly from the base, various shades of brown; valve wings narrowly to broadly rectangular or broadly triangular; covering membranes vestigial to crescent-shaped, not meeting. *Seeds* comma-shaped, 0.6–1.0 mm long, various shades of brown from light brown to apricot or rust-brown.

Distinguishing characters: *Juttadinteria deserticola* is distinguished from *J. albata* and *J. attenuata* by its short, blue-green leaves that are almost always less than twice as long as wide and often appear fat boat-shaped. They almost always have a few very fine teeth on the margins and a hard apical mucro.

Distribution: Endemic to the western reaches of the southern Namib (Figure 4.21).
Habitat: Occurs on flat patches of gravelly sand near the coast, flat gravel plains or (less often) on rocky dolomite or granitic-gneiss slopes in sandy and stony soil. Individuals growing in flats near the ocean often have particularly small, square flowers.
Altitude: 13 – 249 m.
Flowering: August to September.
Provisional Namibian Red Data status: LC.

Illustrations: B.O. Carter, *Pillans 5692* (BOL 132828), *Nat. Bot. Gardens 1731/27* (BOL 132823), *S.U.G. 9046* (BOL); M. Walgate *Holloway, H.M. 98A* (BOL 132824); M.M. Page *Staber 442/24* (BOL 132834); *Erni 881/28* (BOL 132827); Jacobsen, Sukk. Lex. Fig. 171/3 (1970); Smith *et al.*, Mesembs: 149 (1998); Van Jaarsveld *et al.*, Vygies: 130 (2000); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: Pl. 10 (2001).

Discussion: In her latest treatment of *Juttadinteria* Hartmann (2001) indicated that *J. deserticola* varies across its distribution range, with the leaf shape in northern populations shorter and broader than those in more southern populations. She also mentioned that west of the Klinghardt Mountains a semi-erect to erect form with slender leaves resembling those of the southern populations occurs. This form of *J. deserticola* is typical of the one subgroup indicated by the *Juttadinteria* phenogram (Figure 4.1, green line). In view of recent field observations and collection of what appear to be intermediate forms, further work is needed in order to establish whether these subgroups should be assigned a formal taxonomic status.

The branched and erect forms of *J. deserticola* conform in appearance with that of the lectotype of *J. suavissima* (*Range 1885*, B), which was sunk into *J. ausensis* by Hartmann (2001). It is probable that *J. suavissima sensu* Dinter (1923) included elements of both *J. deserticola* and *J. ausensis* because the two localities mentioned in the type description are occupied separately by those two species, those on the large plain between Kuckaus and Pockenbank being *J. ausensis* and those east of Pomona being the erect to branched form of *J. deserticola.* On one hand the type description (*Dinter 1923*), which describes the leaves as triangular and with one to six lateral teeth, coincides best with *J. ausensis,* but the type specimen is lost. On the other hand the fact that the specimens from one of the type localities resemble the lectotype designated by Hartmann (2001), and group with *J. deserticola* rather than *J. ausensis* supports the view that *J. suavissima* was composed of two separate species and should therefore be sunk *pro parte* into both. Athough Hartmann sunk *J. suavissima in toto* into *J. ausensis* (both shrubby species), noting their similarly parallel leaf margins, the *pro parte* inclusion of *J. suavissima* with *J. deserticola* is supported not only by a flat to slightly rounded leaf epidermal cell structure and the denticulate rather than heavily dentate margins in both, but also by habitat type and distribution patterns. Clumped and tufted forms of *J. deserticola* are found near the coast and branched/erect forms further east on coarse sandy to gravelly plains as far west as the Klinghardt Mountains. *Juttadinteria ausensis* occurs further east, from Drachenberg towards the eastern and northeastern reaches of the Sperrgebiet on sandy plains with heavy calcrete inclusions. It has heavily dentate leaves with domed epidermal cells.

5. Juttadinteria simpsonii (Dinter) Schwantes, Zeit. F. Sukk. 2: 183 (1926); Jacobsen, Succ. Pl.: 191 (1935); Jacobsen, F. Rep. Sp. Nov. 106: 94 (1938);Walgate in Bolus, Notes on Mes. 3: 173 (1939); Jacobsen, Sukk. Lex.: 435 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 58-64 (1970); Smith *et al.*, Mesembs: 148 (1998); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: 72 (2001). Type: Great Namaland, Halenberg Station, *Dinter 3742* (lost), *Dinter 54* (HBG!, lecto B!, BOL!, isolecto).

Mesembrianthemum simpsonii Dinter, F. Rep. Sp. Nov. 19: 134 (1923).

Mesembrianthemum kovisimontanum Dinter, F. Rep. Sp. Nov. 19: 135 (1923). *Juttadinteria kovisimontana* (Dinter) Schwantes, Zeit. Sukk. Kunde 2: 183 (1926). Type: Great Namaland, at the base of a gneiss mountain in the Kovis Mountains, approx. 25 km east of Lüderitzbucht, *K. Dinter 3881* (B, †).

Etymology: named after Mr. & Mrs. Simpson of Halenberg station in whose garden the first plants were found.

Plants succulent, perennial, procumbent or erect dwarf shrubs up to 15 cm high; internodes enclosed by leaf bases or very short. *Leaves* short and thick, trigonous with pronounced rhomboidal thickening behind the apex, flat above, grey-green to blue-green, up to 34 x 26 mm, up to 20 mm thick, up to twice as long as wide; keel oblique, pronounced at apex; margins and keels sometimes flushed pink, heavily dentate, often sides also dentate; apex tapering to a point, usually with a hard mucro; epidermis smooth with conical cells or velutinous due to papillate cells; epicuticular wax with additional, scattered wax platelets; wax platelets dense on sides of papillae. *Flowers* usually radially symmetric when fully open, up to 47 mm in diameter; receptacle and sepal epidermal cells domed, conelike or papillate; outer sepals with minute terminal, marginal or keel teeth variously combined, 8.1–13.0 x 5.6–10.0 mm; inner sepals 4.5–12.0 x 4.7–12.0 mm. *Staminodes* petaloid 47–71, shining white, linear-ligulate, 11–25 x 1.2–3.5 mm. *Androecium* filaments 2–9 mm long; anthers 0.5–1.1 mm long. *Pollen* 17–24 μm x 13–20 μm; exine tectate-perforate or tectate-reticulate. *Nectary* green; nectar clear to pale green, pale yellow or straw-coloured. *Gynoecium* stigmas 7–10, free or briefly basally fused; ovary obconical. *Capsule* 5.9–10.0 mm in diameter, 7–12 locular; base obconical; keels radial and parallel, diverging slightly distally, rarely diverging only at the fulcrum, light brown or tan to yellow brown or orange brown; valve wings narrowly to broadly rectangular or crescent-shaped; covering membranes vestigial to crescent-shaped, most often not meeting. *Seeds* comma-shaped, 0.5–0.9 mm long, various shades of brown from light brown to apricot or rust-brown.

Distinguishing characters: *Juttadinteria simpsonii* may be confused with *J. ausensis*. It is distinguished by the pronounced rhomboidal thickening below the apex.

Distribution: Endemic to the southern Namib in localized populations on footslopes in the Kovis Mountains and at Halenberg (Figure 4.21).
Habitat: Typically occurs on granitic-gneiss ridges and foothills and coarse gravelly-sandy slopes.
Altitude: 390 – 606 m.
Flowering: July to October.
Provisional Namibian Red Data status: VU B1ab(v)+2ab(v).

Illustrations: M. Walgate *Schwantes 1928 1759/27* (BOL 132833), *Otzen 1938* (BOL 132830); M.M. Page *Morant, F. 17329* (BOL 132832); *Pillans 5863* (BOL 132835); Jacobsen, Succ. Pl.:Fig. 171 (1935); Smith *et al.*, Mesembs: 149 (1998); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. F-Z: Pl. 10 (2001).

Discussion: Plants similar to *J. simpsonii* but with distinct leaf epidermal papillae and far chunkier leaves were found in the Kovis Mountains, occurring sympatrically with that species and with *N. ponderosa*. These agreed with the type description of *J. kovisimontana*, a taxon that had been sunk into *J. simpsonii* by Hartmann with a note that the 'peculiar roughness' of the leaf surface was due to incompletely developed teeth. These specimens formed a subgroup within the *J. simpsonii* cluster in the *Juttadinteria* phenogram (Figure 4.1, orange line). In most characters observed during this study, including flower and fruit characters, they resemble *J. simpsonii* but they exhibit some characters intermediate between *J. simpsonii* and *N. ponderosa*. In both forms of *J. simpsonii* the leaf margins diverge distally to produce a rhomboid tip but the overall appearance in the papillate form is far more bulky, and the margins, keel and teeth are less pronounced (compare Figures 4.19 A, B and C). The papillate form has leaf epidermal papillae that appear intermediate between the domed to conelike cells of *J. simpsonii* and the distinct epidermal papillae of *N. ponderosa* (compare Figures 4.20 A, B and C), and it produces both tectate-perforate and semitectate-reticulate pollen, sometimes within a single flower (Figure 4.12D). The pollen of *J. simpsonii* is tectate perforate whereas that of *N. ponderosa* is semitectate reticulate.

This suggests a possible hybrid origin for *J. kovisimontana* and supports the opinion of Hartmann (2001), who sunk it into *J. simpsonii,* although the roughness of the leaves, as noted by Dinter (1926) in his original discussion of this taxon, is due to the epidermal papillae and not incompletely developed teeth as suggested by her. According to Ihlenfeldt (1994) genetic barriers between related species in the same or closely related genera in the Mesembryanthemaceae may be absent or weak, and the rarity of hybrids between these taxa in nature is usually due to geographic separation, differing phenology or floral structure, or differing ploidy levels. As *N. ponderosa* and *J. simpsonii* occur sympatrically, they flower at the same time of year, the opening times of their flowers overlap and they have a similar flower structure a possible hybrid origin for the papillate form of *J. simpsonii* cannot be ruled out. Further work on populational variation and cytology is needed to determine ploidy levels and to establish whether hybridization has taken place before a decision can be made on whether any formal taxonomic status should be assigned to the different forms of *J. simpsonii.* At present it is not clear whether speciation has occurred or whether these specimens represent a hybrid swarm.

Figure 4.19: Leaf shapes of the Dracophilinae occurring in the Kovis Mountains. A. *Juttadinteria simpsonii (C. Mannheimer CM 1666)*; B. *J. kovisimontana (C. Mannheimer CM 2371)*; C. *Namibia ponderosa (C. Mannheimer CM 2811)*.

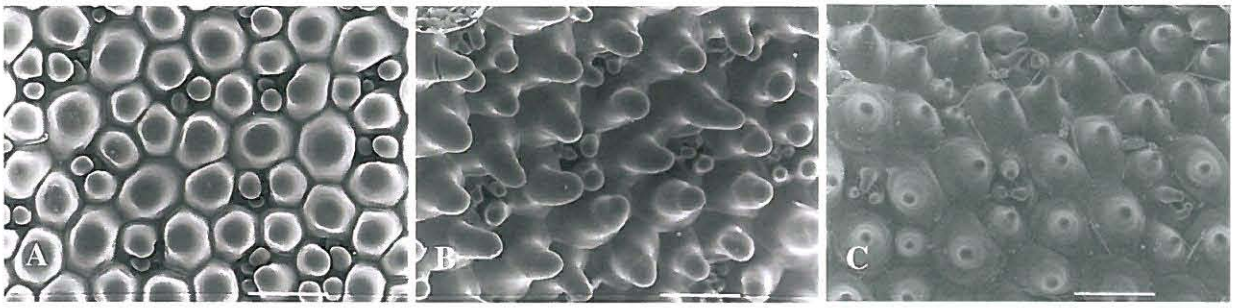


Figure 4.20: Leaf papillae of the Dracophilinae occurring in the Kovis Mountains x 200. A. *Juttadinteria simpsonii* (*C. Mannheimer CM 2381*); B. *J. kovisimontana* (*C. Mannheimer CM 2369*); C. *Namibia ponderosa* (*C. Mannheimer CM 1693*). Scale bars 100 μm.

Excluded names

Juttadinteria tugwelliae (L. Bolus) Schwantes, Zeit. Sukk. ii: 184 (1926), based on *Mesembryanthemum tugwelliae* L. Bolus = *Bijlia tugwelliae* (L. Bolus) S.A. Hammer.

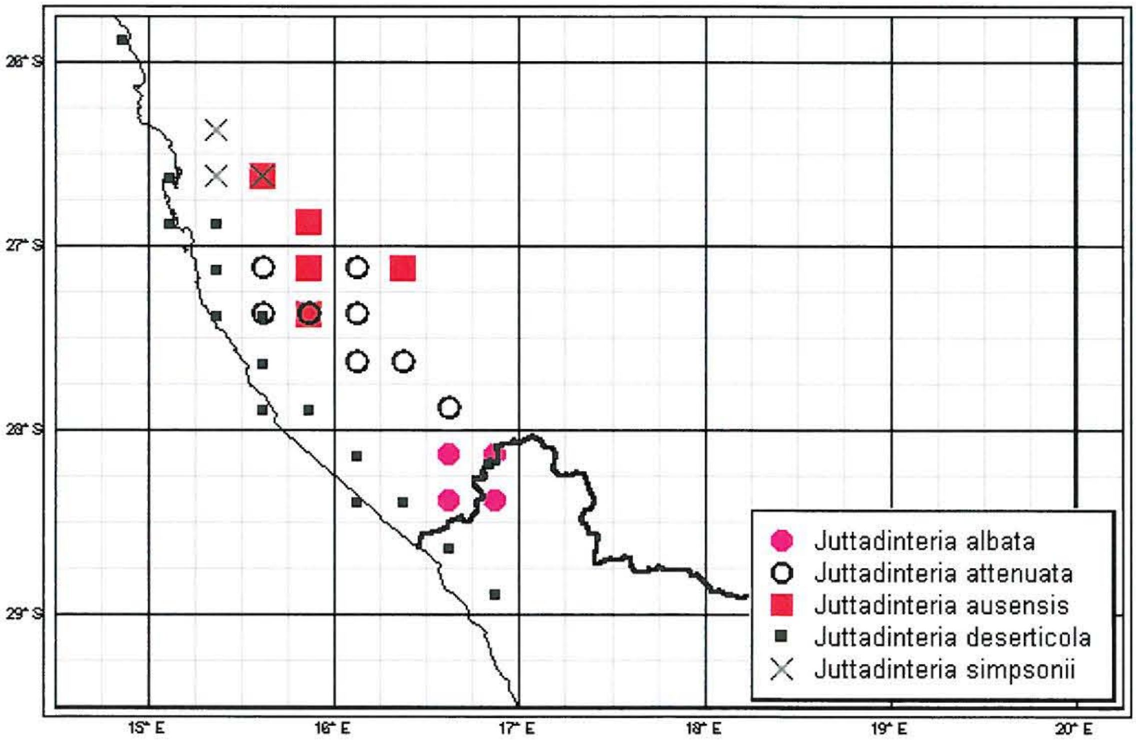


Figure 4.21: Distribution of *Juttadinteria.*

CHAPTER 5. *Dracophilus*

Although both Walgate (1939) and Smith *et al* (1998) recognized four species of *Dracophilus* (*D. delaetianus, D. dealbatus, D. montis-draconis* and *D. proximus*), field observations lent support the latest treatment of *Dracophilus* (Hartmann 2001), in which only *D. delaetianus* and *D. dealbatus* were recognized with the other two species being subsumed into *D. dealbatus*. In order to confirm this a phenetic study of 33 specimens was undertaken. Character types and sources used are shown in Table 5.1. The full data set is presented as Appendix 3. Not all characters are taxonomically useful, but all are described for purposes of completeness. Despite the relative data deficiency of the matrix, the results were found to support field observations and the work of Hartmann (2001).

Table 5.1: Summary of character types and sources used in the phenetic study of *Dracophilus*

Organ/Source	**Binary**	**Multistate**	**Quantitative**
Leaf	5	6	10
Flower	9	9	29
Fruit/Seed	4	6	8

The phenogram obtained (Figure 5.1) clearly supports the presence of two taxa (Cophenetic Correlation Coefficient 0.721), the characters of which best coincide with the type descriptions of *D. delaetianus* and *D. dealbatus*. The This, as well as further micro-morphological investigations corroborate the existence of two species, as proposed by Hartmann (2001).

In order to better assess differences between taxa and assist in their description, additional morphological investigations were undertaken. Altogether 56 living plants, most of them in the field, and 188 herbarium specimens were examined, a total of 244 specimens. Micro-morphological investigations of leaf epidermides, pollen and seed by means of SEM of a small subset of samples were undertaken to assess further differences between these two species. Voucher numbers are listed in Table 5.2.

The *dealbatus* group in the phenogram includes *Dinter 3784*, the holotype for *D. montis-draconis* and *N.S. Pillans 5720* the holotype for *D. proximus*, confirming their synonymy with *D.dealbatus*. In order to provide a comprehensive overview of the genus, character variation in and distinguishing features between the two valid species are discussed in the following pages.

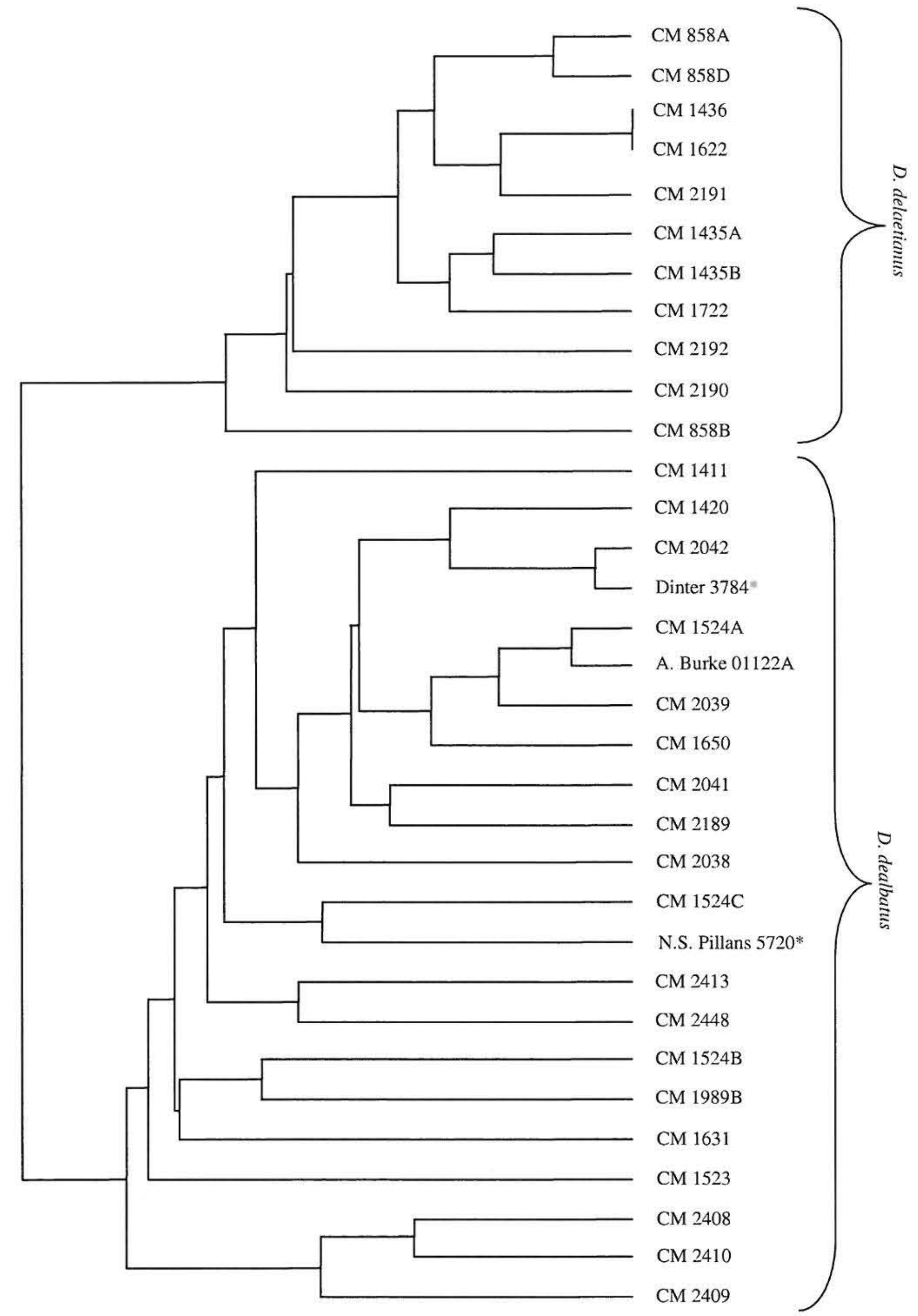


Figure 5.1: UPGMA phenogram for *Dracophilus* based on 86 characters. The data were standardized, and a triangular matrix of similarities calculated using the Manhattan distances algorithm. * = type specimen: N.S. Pillans 5720 = holotype *Dracophilus proximus* (= *D. dealbatus*); Dinter 3784 = holotype *Mesembrianthemum montis-draconis* (= *D. dealbatus*). CM = Coleen Mannheimer. CCC = 0.721.

Table 5.2: ***Dracophilus*** voucher specimens examined by SEM for micromorphological characters. * = specimen included in the phenetic study.

Species	Voucher	Leaf surface	Pollen	Seed
Dracophilus dealbatus	*CM 963 A*	●		
	*CM 1524A**	●		●
	*CM 1524B**			●
	*CM1524C**	●	●	●
	*CM 1631**	●	●	●
	*CM 1650**			●
	CM 1973			●
	*CM 2038**	●	●	●
	*CM 2041**	●	●	
	CM 2137	●	●	●
	CM 2164	●		
	*CM 2189**	●	●	●
	CM 2209			●
	*CM 2408**	●	●	
Dracophilus delaetianus	*CM 858A**	●	●	●
	*CM 858B**			●
	*CM 1622**			●
	CM 2135			●
	CM 2144			●
	*CM 2190**		●	
	*CM 2192**	●	●	●
	CM 2193	●		
	CM 2385	●		
	CM 2386		●	

5.1 Morphological characters

5.1.1 Habit

Dracophilus almost exclusively exhibits a compact growth form with internodes entirely enclosed by the leaves, rarely developing one or two longer, more exposed, and spreading branches in very old plants (Figures 5 .2 A and B). The habit is similar in both species. The overall size of *D.dealbatus* is generally larger than that of *D. delaetianus* however younger plants of the former are often within the general size range of the latter, resulting in extensive overlap.

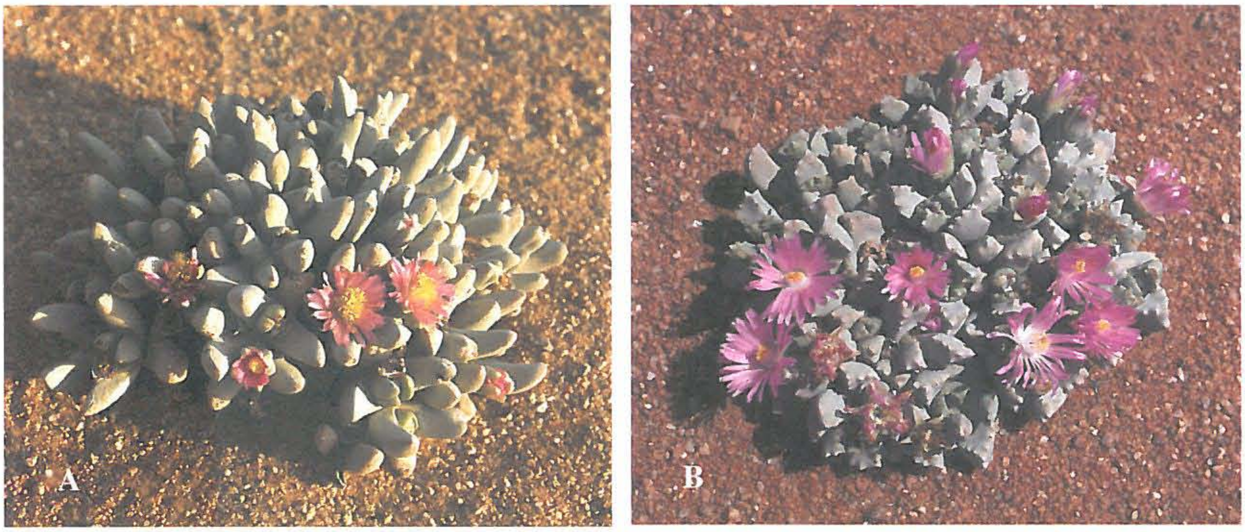


Figure 5.2: *Dracophilus* habit. A. *D. dealbatus* (*C. Mannheimer CM 1524A*); B. *D. delaetianus* (*C.Mannheimer CM 2135*).

5.1.2 Roots

Both species of *Dracophilus* have a short but distinct taproot and a spreading system of secondary roots.

5.1.3 Leaves

5.1.3.1 Macro-morphology and colour

Dracophilus leaves are all hypersucculent, blue-green, and elongate-trigonous and usually have a somewhat skewed appearance due to an oblique keel (Figure 5.3 A and B). They differ between the two species in size, shape, and character of the margins and apex. In *D. dealbatus* the leaves have entire margins and usually taper from base to apex although sometimes they broaden out briefly to form blunt 'shoulders' before narrowing to the tip (Figure 5.3 B). In *D. delaetianus* the leaves are usually distinctly wider and sometimes also deeper just behind the tip, and the margins, apex and (usually) keel are distinctly toothed. The teeth may be quite sharp (Figure 5.3 C) or just small, blunt knobs (Figure 5.3 D). Overall leaf shape and presence or absence of leaf teeth are taxonomically useful characters at species level.

Figure 5.3: *Dracophilus* leaves. A, B. *D. dealbatus*. C, D. *D. delaetianus*. A. showing unequal sides with one convex and the other concave due to the oblique keel (*C. Mannheimer CM 2041*); B. oblique keel (arrow) and "shoulders" as found on some individuals (*C. Mannheimer CM 2162*); C. sharp teeth (*C.Mannheimer CM 2136*); D. blunt teeth (*C. Mannheimer CM 2143*).

Because *Dracophilus* leaves are long-lived and appear to continue growing for several years, at least *in hort*, the difference in variance of leaf sizes between these two species is too great for them to be compared by means of a t-test. Younger plants tend to have much smaller leaves than older plants (age being judged by size of the tuft). Nevertheless, the leaves of *D. dealbatus* reach a far greater maximum length (mean 38 mm, maximum 59 mm) than those of *D. delaetianus* (mean 25 mm, maximum 35 mm). Leaves of *D. dealbatus* are consistently more than twice as long as wide, while those of *D. delaetianus* are less than twice as long as wide. This is of some taxonomic use at species level, if considered together with other characters.

5.1.3.2 Micro-morphology

Dracophilus leaves exhibit the xeromorphic-heterocellular condition, Type X6 as described by Ihlenfeldt and Hartmann (1982). Leaf epidermal cells in *Dracophilus* have isodiametric anticlinal walls. The periclinal walls are domed (Figure 5.4 A), sometimes with a nipple-like apex (Figure 5.4 B), or rise gradually towards the centre to form conical papillae of variable height (Figure 5.4 C). Generally speaking this character is variable and does not differ between the two species. However in some populations of *D. dealbatus*, particularly those east of the Klinghardt Mountains, the papillae are pronounced enough to give a distinctly rough texture to the leaf (Figure 5.4 C). In other populations the leaf may be very smooth or almost smooth, and those of *D. delaetianus* are always smooth to the touch. Leaf texture and epidermal cell characters are therefore not very useful at species level.

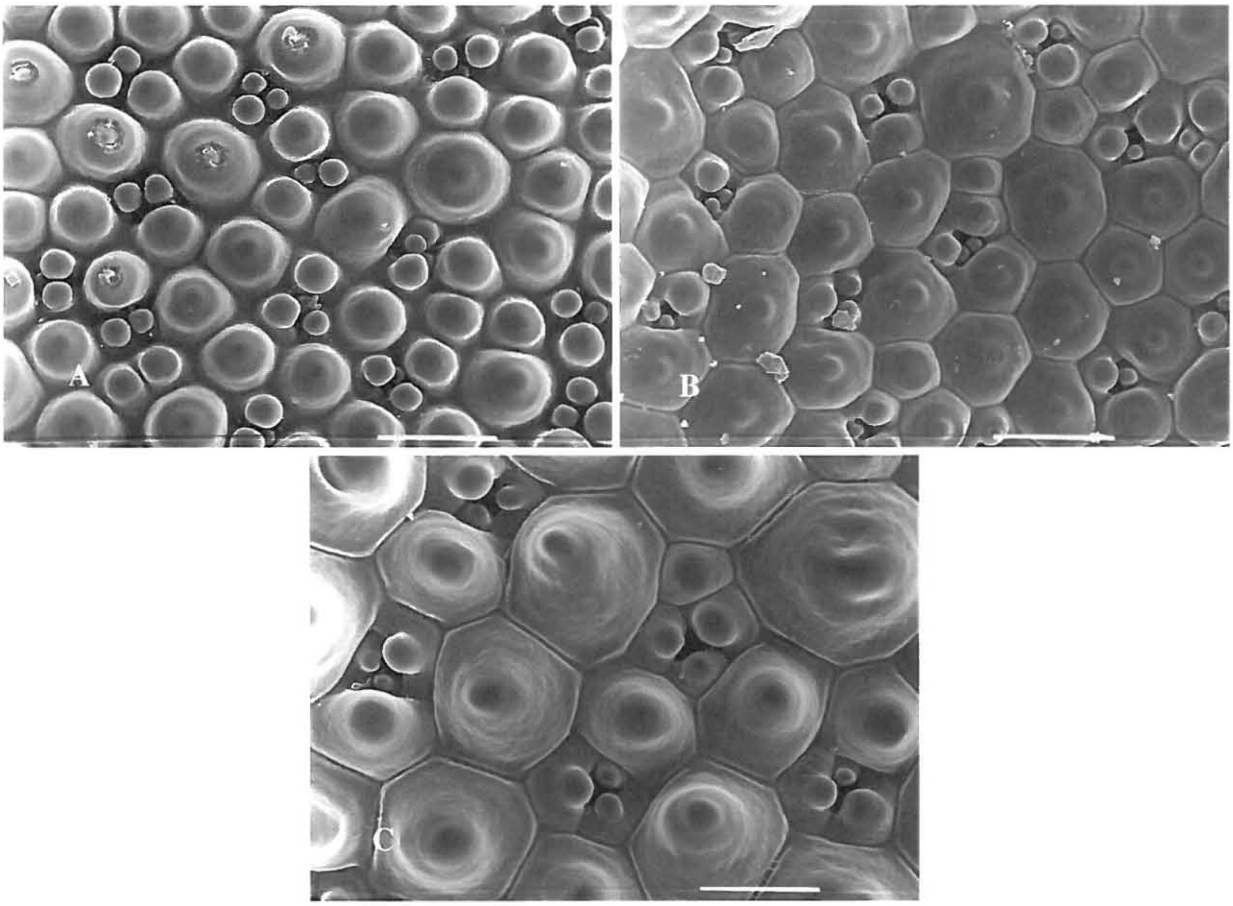


Figure 5.4: *Dracophilus* leaf epidermal cells x 200. A. *D. delaetianus*. B, C. *D. dealbatus*. A. Domed periclinal walls (*C. Mannheimer CM 2162*); B. Nipple-like apex of some rounded periclinal walls (*C. Mannheimer CM 2038*); C. Conical papillae (*C. Mannheimer CM 2164*). Scale bars 100 μm.

5.1.3.3 Stomata

In *Dracophilus* the smallest epidermal cells are peristomatal cells with papillae that surround and often overarch the guard cells of the stomata (Figure 5.5). A discussion on this configuration is offered in section 3.1.3.3. Stomatal characters are not taxonomically useful in *Dracophilus*.

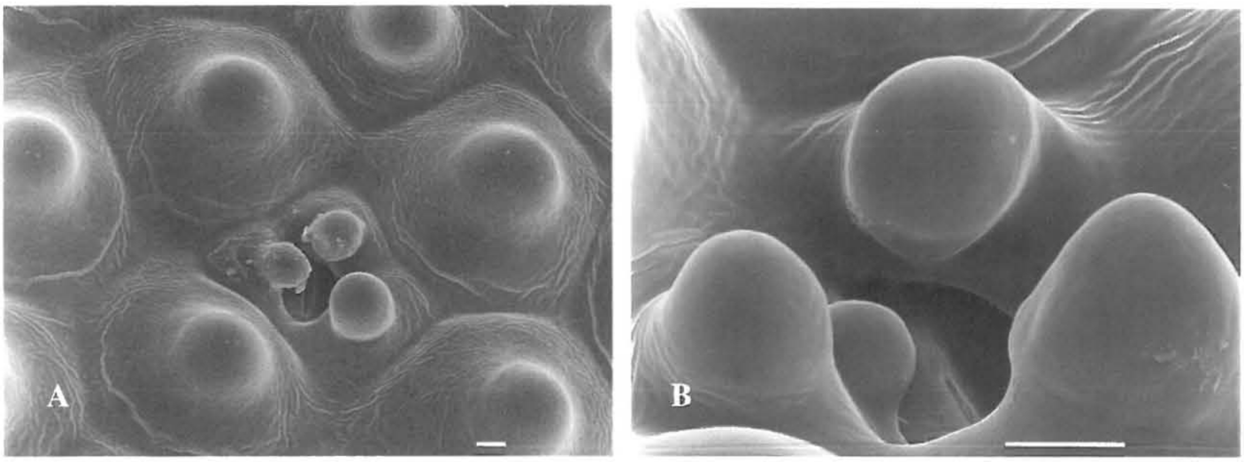


Figure 5.5: Perisomatal structure in *Dracophilus*. A. *D. dealbatus* x 500 (*C. Mannheimer CM 2137*); B. *D. delaetianus* x 2000 (*C. Mannheimer CM 858A*). Scale bars 10 μm.

5.1.3.4. Epicuticular waxes

The two species of *Dracophilus* differ only slightly in the expression of their epicuticular waxes. In both species the basal layer of wax occurs as thick, encrusting plates that fracture above the anticlinal walls (Figures 5.6 A and B). However, in *D. dealbatus* there are almost always small, thin flakes of wax on the upper surface of the plates, most prominently on the top of the papillae (Figure 5.6 C), while in *D. delaetianus* these are often, but not always, absent. These flakes sometimes also appear to orientate themselves in a single general direction, although the degree to which they do it is variable. Both species also exhibit small blocks of wax scattered on the surface of the basal layer (Figure 5.6 D).

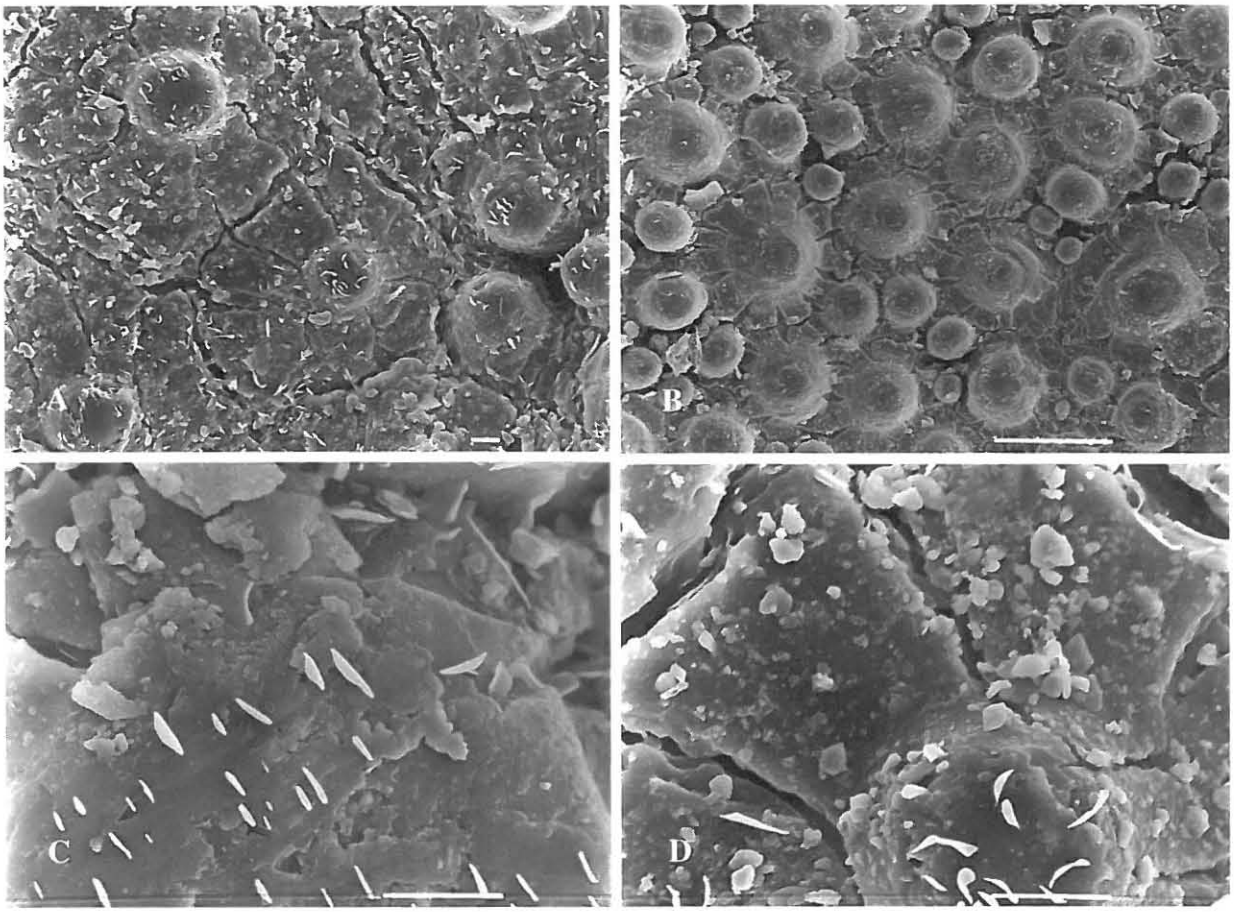


Figure 5.6: Epicuticular waxes in *Dracophilus*. A, B. x 500. C,D. x 2000. A, C, D. *D. dealbatus*. B. *D. delaetianus*. A. thick basal plates of wax (*C. Mannheimer CM 2408*). B. thick basal plates of wax (*C. Mannheimer CM 2192*). C. thin flakes orientated in one direction on top of papilla (*C. Mannheimer CM 2041*). D. small wax blocks on top of basal layer (*C. Mannheimer CM 2408*). Scale bars 10 μm.

5.1.4 Flowers

Dracophilus flowers (Figure 5.7 A and B) are solitary, terminal, carried on distinct, fleshy pedicels and subtended by a pair of small, fleshy bracts. They are circular in outline, but may (very rarely) have five indistinct groups of petaloid staminodes rather than an even spread.

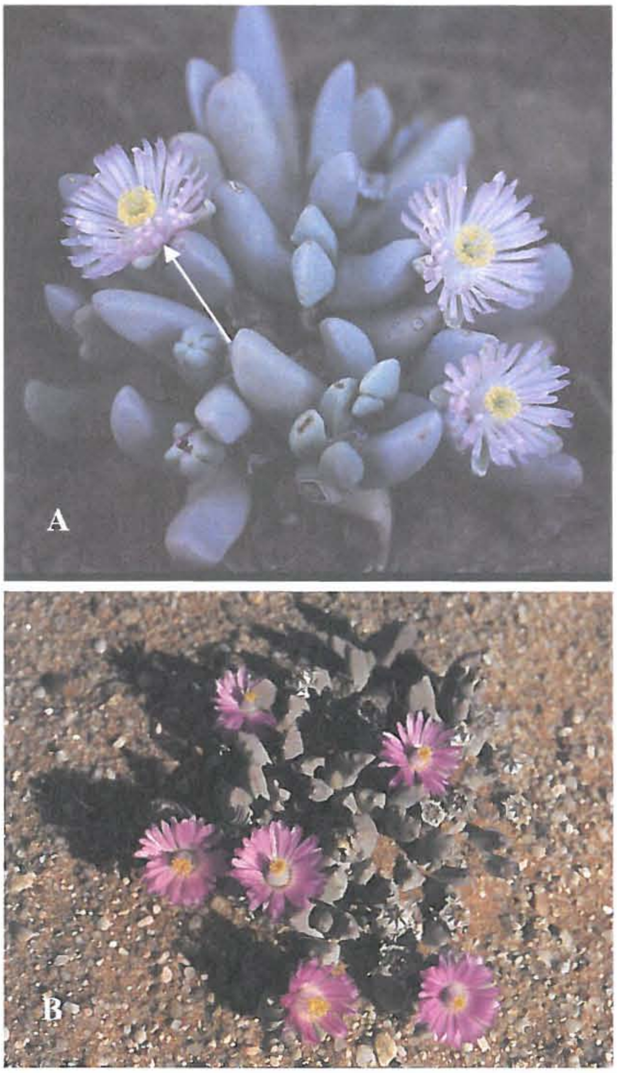


Figure 5.7: *Dracophilus* habit and flowers. A. *D. dealbatus* (*C. Mannheimer CM 1989A*) showing recurved petals; B. *D. delaetianus* (*C. Mannheimer CM 804*).

5.1.4.1 Receptacle and Calyx

The receptacle in *Dracophilus* is always shallowly funnel-shaped.

There are always five unequal, thinly fleshy sepals. The inner, smaller pair are far narrower than the other three, and have broad, membranous margins and a slight terminal thickening below the apex. Of the other three, two are usually similar and have only a vestigial membranous margin, whereas the other one is usually of a similar size but has a far more pronounced membranous margin, thus showing characters intermediate between the other two pairs. These larger sepals also usually have pronounced thickening below the apex and the thickened area may sometimes appear somewhat toothlike. None of these characters differ consistently between the two species. However, the sepals are significantly bigger at the 95% confidence level in *D. dealbatus*. Thus only sepal size is taxonomically useful at species level.

5.1.4.2 Flower colour and size

Flower colour in *Dracophilus* varies from white (rarely) to deep rose-pink and cerise. In *D. dealbatus* all shades are found (Figure 5.8 A.) but in *D. delaetianus* the flowers are virtually always pinky-cerise (Figure 5.8 B) and only rarely does one see a white-flowered individual (only one was found during this study). Flower colour is not taxonomically useful at species level.

Figure 5.8: Flower colour in *Dracophilus*. A. *D. dealbatus*, indicating colour range (*C. Mannheimer CM 2008 to 2011*); B. Bright pinky-cerise shades are almost invariable in *D. delaetianus* (*C. Mannheimer CM 2136*).

Flowers range from 22 to 40 mm in diameter. In *D. dealbatus* flower diameter varied between 27 and 40 mm, whereas in *D. delaetianus* the range was between 22 and 34 mm. A t-test indicated a significant difference between their means at the 99% confidence level. As might be expected, petal length showed a similar trend. However, as anthesis progresses flower diameter increases, making it difficult to standardize measurements and due to the overlap flower size is not regarded as taxonomically useful at species level.

Average 'petal' number was found to be significantly lower in *D. delaetianus* (mean 45, range 41 – 51) than in *D. dealbatus* (mean 61, range 50 – 72) at the 99% confidence level (Figure 5.9). Thus there is very little overlap and, in conjunction with other characters, petal number is a taxonomically useful character at species level.

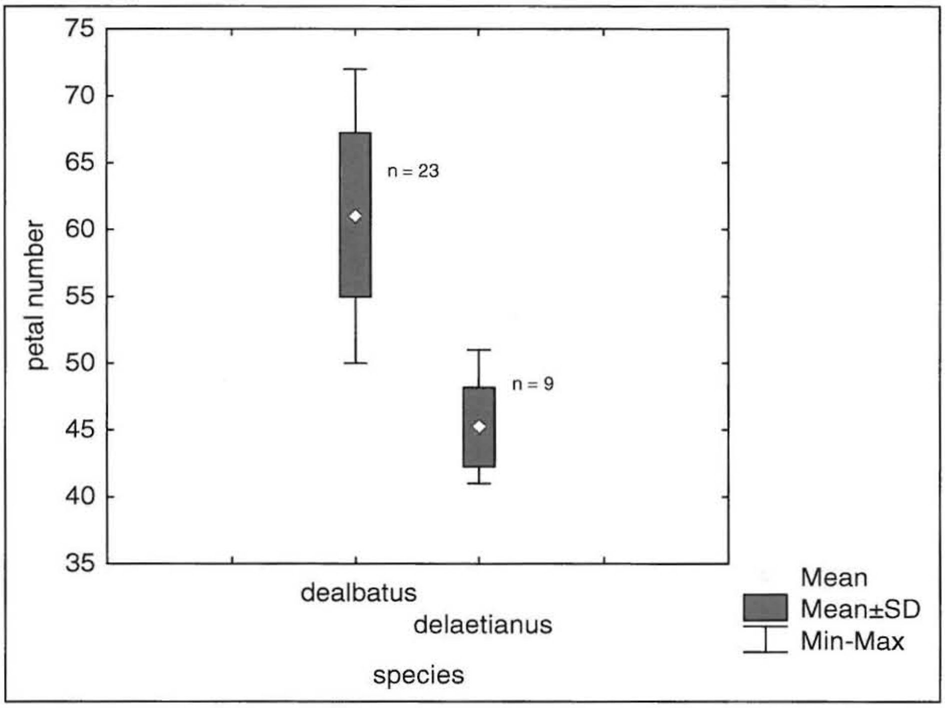


Figure 5.9: Comparison of mean 'petal' number between *D. dealbatus* and *D. delaetianus*.

(t = 7.3858; df = 30; p = 0.0000; F = 4.3174)

5.1.4.3 Androecium

The stamens are numerous. Initially they are arranged into a cone which opens out to become more cylindrical as anthesis progresses towards the female phase. Filaments become longer during this progression. Inner series of filaments are shorter than outer, with lengths overall varying between 2 and 11 mm. Those of *D. dealbatus* vary between 3 and 11 mm and those of *D. delaetianus* between 2 and 9 mm. All filaments are pure white and pubescent at the base. The anthers are elongate-elliptic and dorsifixed. Their attachment is versatile. They vary between 0.6 and 1.4 mm in length. The thecae are parallel and exhibit longitudinal extrorse dehiscence. Androecial characters are not taxonomically useful at species level.

5.1.4.4 Stigmata

The stigmata are narrow-subulate, typical for the subtribe. In *Dracophilus* they are pale yellow-green and vary in number between 7 and 16. In *D. dealbatus* they vary between 9 and 16 (mean 11) although there are usually 10 to 12, whereas in *D delaetianus* the range is 7 to 11 (mean 9), with 8 to 10 being most commonly found. The means were found to be significantly different at the 95% confidence level. They are fused for a short distance at the base, sometimes with a somewhat lumpy appearance there, and the inner surface is covered by short stigmatic papillae. At first they are of a similar length to the stamens, but elongate during anthesis to protrude beyond them. Stigmatal number is of limited taxonomic use at species level, but should be considered in conjunction with other characters.

5.1.4.5 Ovary

The ovary is broadly and shallowly obconical, with a flat top. Placentation is parietal, as is common in the subfamily Ruschioideae. The ovules are numerous. Ovary characters are not taxonomically useful at species level.

5.1.4.6 Floral nectary

The nectary, which is similar in the two species of *Dracophilus,* is a robust crenulate ring (i.e. lophomorphic holonectary). It is orange to dark brown and produces bright yellow nectar. No scent is discernable.

5.1.5 Pollen

5.1.5.1 Colour

Pollen of *Dracophilus* is bright golden-yellow, fading to pale yellow with age.

5.1.5.2 Shape

Pollen grains of *Dracophilus* are symmetric, isopolar, prolate, tricolpate and somewhat rounded-triangular in polar view. In equatorial the poles sometimes appear more-or-less truncate (Figure 5.10 A and B). The mesocolpi are convex and the apertures are positioned at the angles between them, equidistant to one another and parallel to the polar axis. *Dracophilus* pollens grains are longiaxial, i.e. the polar axis (P) is longer than the equatorial axis (E). The P/E ratio varies from 1.2 to 1.5, with a mean in both species of 1.4.

5.1.5.3 Size

There is no significant difference in pollen dimensions between the two species (Table 5.3). Pollen size and shape are therefore not taxonomically useful at species level.

Table 5.3: Pollen dimensions and tectum structures in *Dracophilus*

	D. dealbatus	***D. delaetianus***
Length μm (min - mean - max)	18.0 – 21.7 – 25.4	17.8 – 22.4 – 25.6
Width μm (min - mean - max)	12.7 – 15.8 – 18.5	13.8 – 16.7 – 18.5
No. perforations (min – mean – max)	18 – 31– 66	32 – 41 – 48
No. prominences (min – mean – max)	27 – 32 – 51	38 – 58 - 83

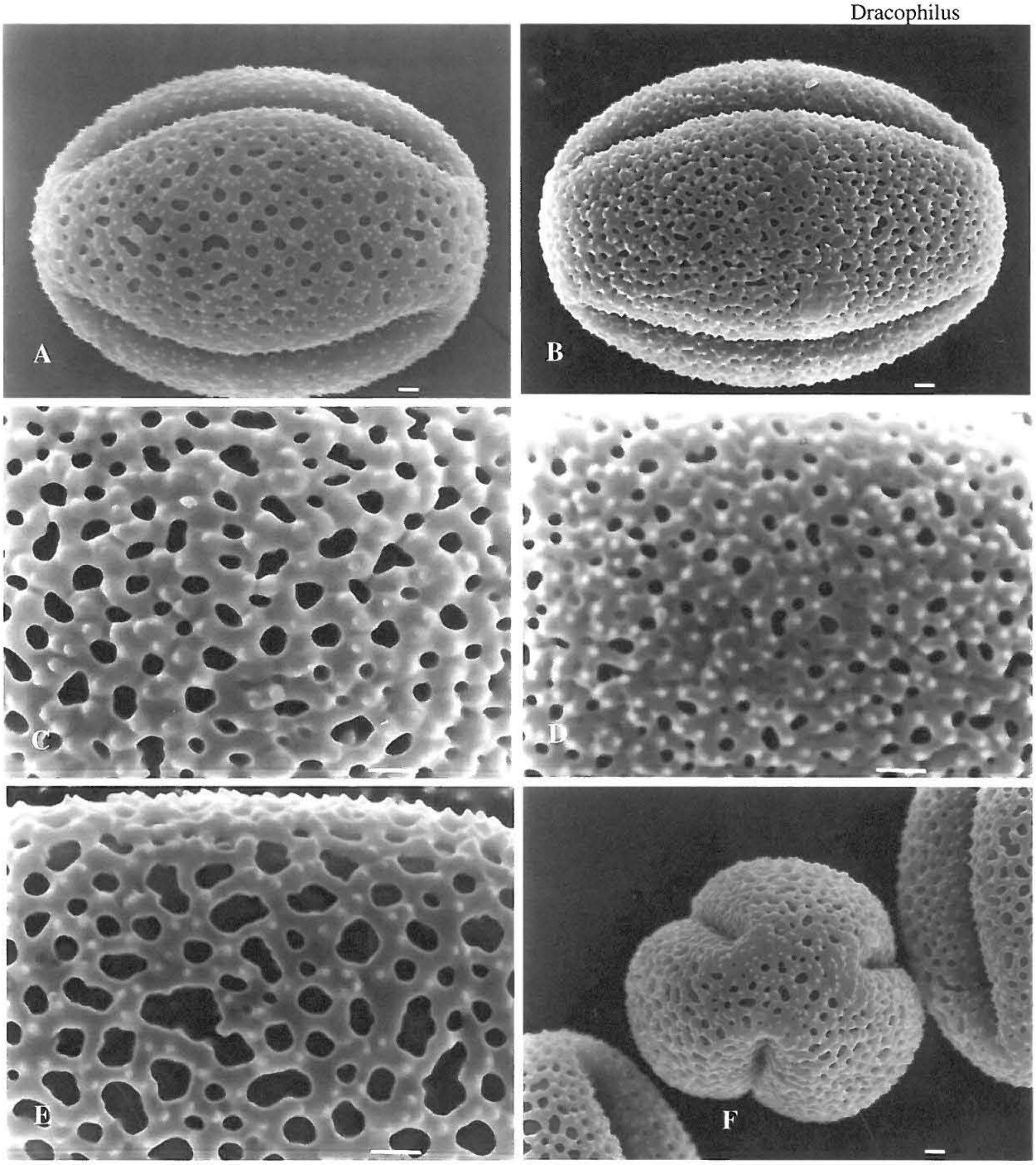


Figure 5.10: *Dracophilus* pollen. A, B, F. x 4000. C, D, E. x 10 000. A, C, E, F. *D. dealbatus*. B, D. *D. delaetianus*. A. equatorial view (*C. Mannheimer CM 2408*); B. equatorial view (*C. Mannheimer CM 2385*); C. equatorial view (*C. Mannheimer CM 2041*) showing semitectate-reticulate exine; D. equatorial view (*C. Mannheimer CM 858A*) showing tectate-perforate exine; E. equatorial view (*C. Mannheimer 2189*) showing slightly more semitectate-reticulate exine; F. polar view (*C. Mannheimer 2189*). Scale bars 1 μm.

5.1.5.4 Exine structure

The exine varies from tectate-perforate to semitectate-reticulate and is always ornamented with pointed spinulae. *Dracophilus dealbatus* exhibits both the tectate-perforate and the semitectate-reticulate conditions whereas in *D. delaetianus* only the tectate-perforate condition was observed.

Micro-perforations of the tectum and free baculae on the nexine are often present.

5.1.5.5 Perforations and sculpturing

Perforations vary from micro-perforations to irregular luminae that result in the reticulate condition (Figure 5.10 C, D and E). The number of perforations varies from 18 to 66 in an area of 25 μm^2, counted on the mesocolpium at a point equidistant from both the poles and the adjacent colpi. The mean number of perforations was lower in *D. dealbatus* (31, n=16) than in *D. delaetianus* (41, n=6). This might be due to the tendency of *D. dealbatus* towards the reticulate condition, in which the luminae are far larger and therefore occupy more space on the exine.

The mean number of spinulae in *D. dealbatus* (mean 32) was also lower than in *D. delaetianus* (mean 58). This might also be ascribed to the lower exine surface area available due to the reticulate tendency of the former species.

Although mean numbers of perforations and spinulae differ to quite an extent in this genus, these characters do overlap greatly and are not regarded as taxonomically useful at species level. If a more accurate measure of exine extent were applied to a larger sample size it may be possible to reassess these characters.

The polar regions exhibit the same characters as the mesocolpi, but at the margins of the colpi there are far fewer perforations and often only micro-perforations are found. In some areas, particularly close to the poles, the exine may lack pores (Figure 5.10 F).

5.1.5.6 Apertures

As may be seen in figure 5.11 A, the colpi are closed. There is variation in the gape of the colpi (e.g. Figure 5.11 B and C), however this appears to be common to both species

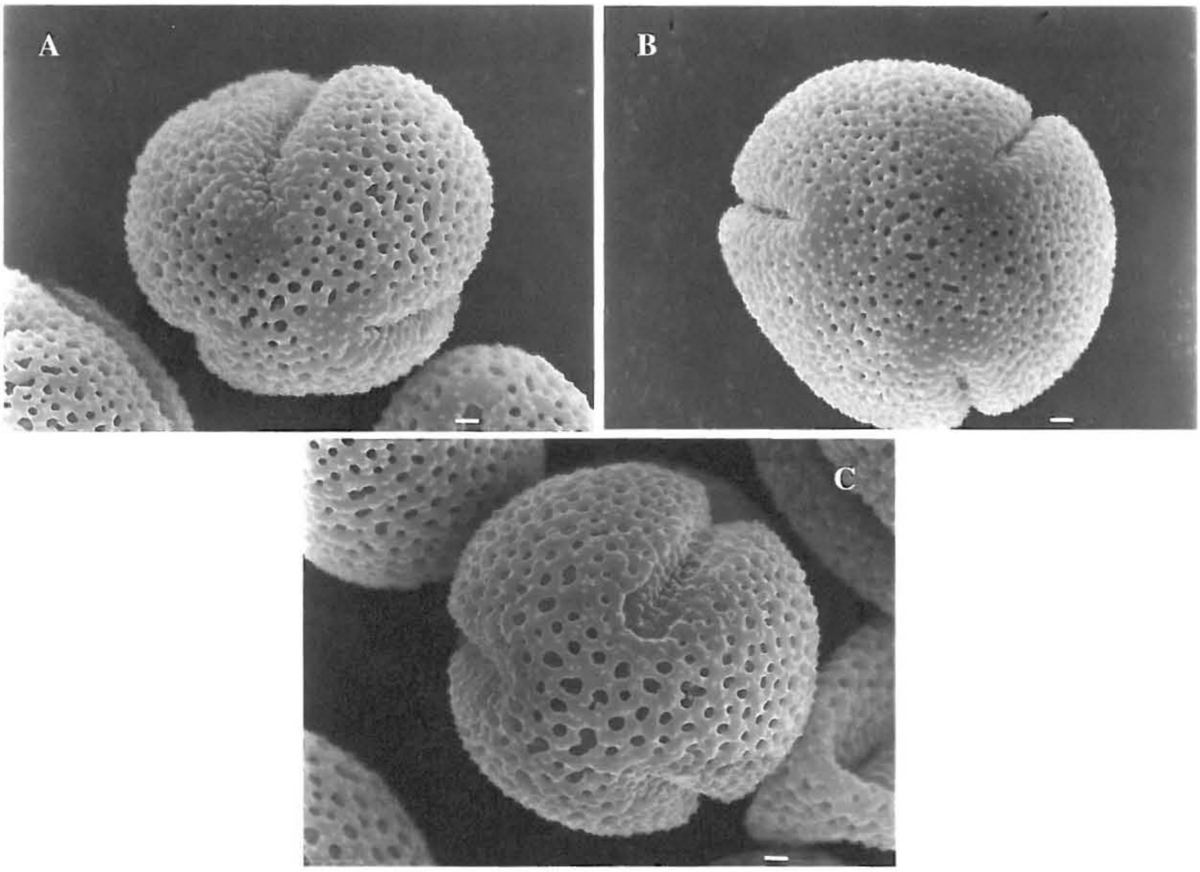


Figure 5.11: *Dracophilus* pollen x 4000. A, C. *D. dealbatus.* B. *D. delaetianus.* A. closed colpus (*C. Mannheimer CM 2041*); B. narrow colpus gape (*C. Mannheimer CM 858A*); C. wide colpus gape (*C. Mannheimer CM 2408*). Scale bars 1 μm.

5.1.6 Fruit

With the exception of size and locule number there is little difference in fruit characters between the two species of *Dracophilus*. Capsule diameter varies between 5 and 11 mm. By means of a t-test the mean was found to be significantly larger in *D. dealbatus* at the 99 % confidence level (Figure 5.12). In *D. delaetianus* capsule diameter varied between 5 and 9 mm (mean 7 mm, n = 35) whereas in *D. dealbatus* the range was between 7 and 11 mm (mean 9 mm, n = 71).

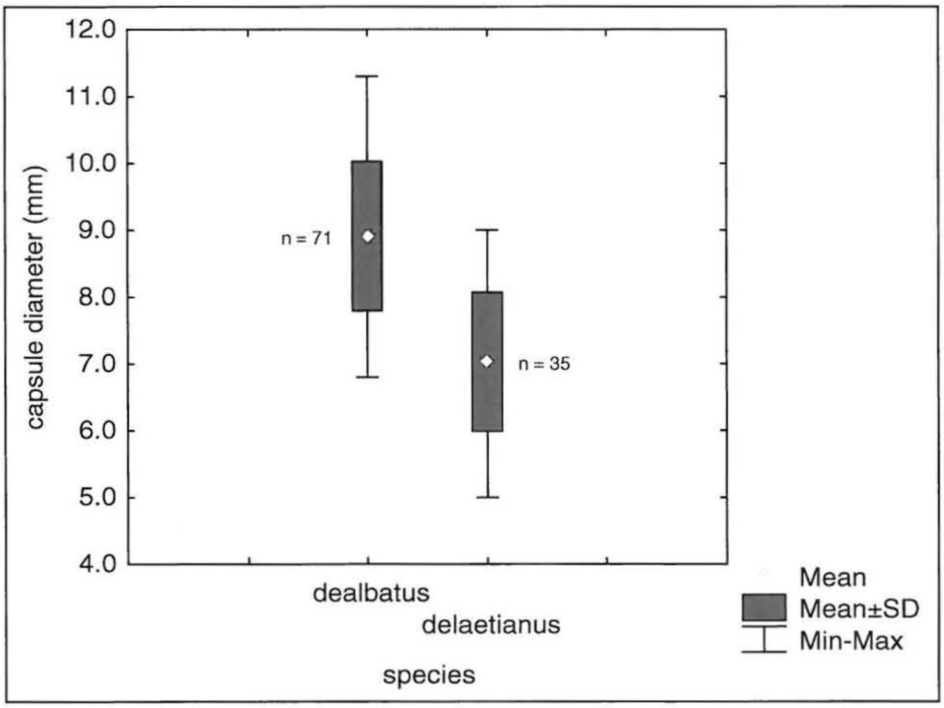


Figure 5. 12: A comparison of mean capsule diameter between *Dracophilus dealbatus* and *D. delaetianus*. (t = 8.3428; df = 104; p = 0.0000; F = 1.1554)

Mean locule number was found to be significantly different at the 99% confidence level between the two species of *Dracophilus* (Figure 5.13). It varied between 7 and 17, with the most frequent number being 10. In *D. dealbatus* locule number is mostly 10 to 13 (85 per cent of capsules; range 8 to 17) and is seldom fewer than 10 (9 per cent of those measured) whereas in *D. delaetianus* locules usually number between 8 and 10 (68 per cent of capsules; range 7 to 11), with 8 and 9 being common (50 % of those measured). Capsule size and locule number may be regarded as of some taxonomic use at species level, providing they are considered together with other characters.

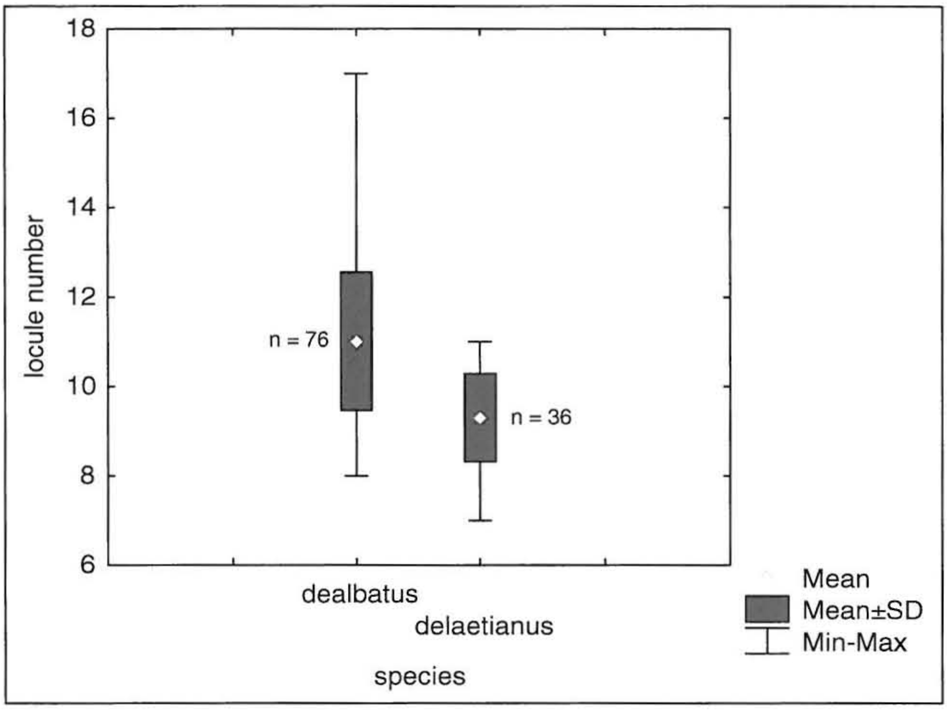


Figure 5.13: A comparison of mean locule number between *Dracophilus dealbatus* and *D. delaetianus*. (t = 6.0705; df = 110; p = 0.0000; F = 2.4831)

The capsule is shallowly and broadly obconical with the upper surface flat to slightly concave, and with recurved valve tips when mature (Figure 5.14 A). It is carried on a distinct pedicel.

The septa extend evenly from their insertion on the wall of the receptacle to the tip of the columella. The expanding keels are radial and parallel from the base (Figure 5.14 B and C), diverging distally and (occasionally) at the fulcrum where the valve bends slightly when open. They are higher than broad and slightly lacerate. Their colour varies from pale yellow-orange to light to dark brown and appears to darken with age. The valve wings are somewhat rectangular to (more often) crescent-shaped, 0.5 to 1.3 mm wide (average 0.9 in both species), and sometimes have short awns. A t-test showed no statistical difference between the species regarding valve wing width. Covering membranes are present and well developed. They are somewhat textured and translucent, and cover approximately two thirds of the locule area, meeting in the middle (Figure 5.15). Occasionally they show a slight tendency towards a distal ledge. They collapse inwards after seed dispersal. Closing bodies are completely absent and the valves open completely to a flat position at 90° to the axis, when wetted (Figure 5.14 B). Hartmann (1988) terms this fruit type (typified by the radial keels, compound covering membranes and very small or absent closing bodies) as the *Titanopsis* type. The ecological implications of the combination of capsule features seen in *Dracophilus* are discussed in Chapter 8.

Capsule structure is not taxonomically useful at species level in *Dracophilus*.

Figure 5.14: *Dracophilus* capsules. A, B. *D. dealbatus* (*C. Mannheimer 1524B*); C. *D. delaetianus* (*C. Mannheimer 858D*). A. capsule closed, lateral view, showing shallow base and recurved valve tips. B, C. capsule open showing valves, expanding keels, valve wings with small awns and well developed covering membranes.

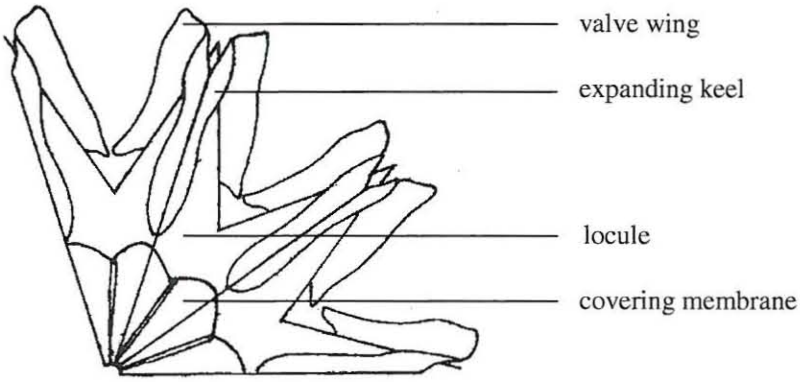


Figure 5.15: Diagram of *Dracophilus delaetianus* capsule internal structure (*C. Mannheimer CM 2385*).

5.1.7 Seed

Dracophilus seeds are similar in both species (Figure 5.16 A and B). They are fat comma-shaped and vary in colour from light brown to apricot or gold-brown to rust-brown. The micropylar region is produced forwards. Seed length varies between 0.4 and 1.1 mm. Although the average length of *D. dealbatus* seeds is 0.7 mm, while that of *D. delaetianus* is 0.6 mm, there is considerable overlap.

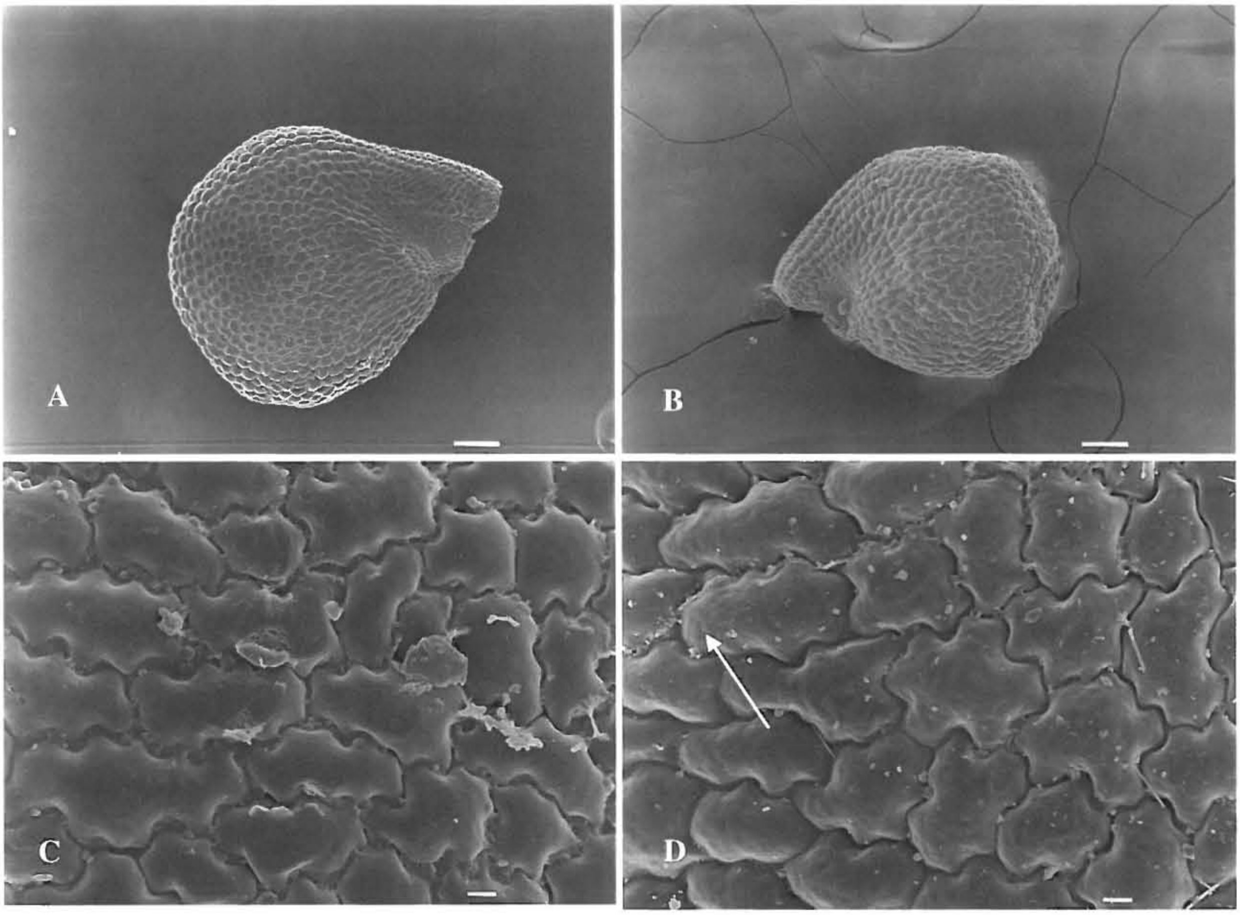


Figure 5.16: *Dracophilus* seed. A, B. x 75. C, D. x 500. A, C, D. *D. dealbatus*. B. *D. delaetianus*. A. lateral view (*C. Mannheimer CM 1524C*); B. lateral view showing general shape (*C. Mannheimer CM 1622*); C. testa showing undulate anticlinal walls (*C. Mannheimer CM 1524A*); D. testa with slightly lumpy texture (*C. Mannheimer CM 1631*). A, B. scale bars 100 μm; C, D. scale bars 10 μm.

The shape of the testa cells is variable. Where they are ordered in rows, i.e. in the micropylar and hilar regions, they are smaller than elsewhere. In areas such as the perisperm region, where the cells are less ordered their shape is more variable. Anticlinal walls are sunken to a greater or lesser degree, and vary from almost straight to very undulate, with S-shaped undulations (Figure 5.16 C). Periclinal cell walls are distinctly convex, with less elongated cells more convex than longer ones. The testa fold is oriented at an angle of approximately 45° to the long axis of the seed. In both species testa cell surfaces sometimes appear slightly lumpy (Figure 5.16 D) but are more often smooth. Seed characters are not regarded as taxonomically useful at species level in *Dracophilus*.

Taxonomic treatment

Dracophilus (Schwantes) Dinter & Schwantes in Schwantes, Möll. Deutsch. Gärtnerztg 15: 187 (1927); Schwantes, Zeit. F. Sukk. 2: 182-184 (1926); v. Pöllnitz, F. Rep. Sp. Nov. 32: 39-40 (1933); Jacobsen, F. Rep. Sp. Nov. 106: 70-71 (1938); Walgate in Bolus, Notes on Mes. 3: 182 (1939); Jacobsen, Herre & Volk, Mesembr.: 77, 95 (1950); Jacobsen, Handb. Sukk. Pfl.: 1335 (1955); Schwantes, Fl. Stones.: 339 (1957); Jacobsen, Handbook Succ. Pl.: 953 (1960); Jacobsen, Sukk. Lex.: 413 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 58-62 (1970); Herre, Gen. Mesem.: 140 (1971); Court, Succ. Fl. sthn. Afr.: 46 (1981); Smith *et al*, Mesembs: 140 (1998); Court, Succ. Fl. sthn. Afr.: 20 (2000); Leistner (Ed.), Seed Pl. sthn. Afr.: 387 (2000); Van Jaarsveld *et al*, Vygies: 94 (2000); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. A-E: 225-226 (2001). Type: *Dracophilus delaetianus* (Marloth) Dinter & Schwantes.

Juttadinteria Schwantes subg. *Dracophilus* Schwantes, Zeit.f. Sukk. 2: 184 (1926). Type *Juttadinteria delaetiana* (Dinter) Schwantes (lecto).

Etymology: Gk dracon = dragon; philos = friend, after the dragon rock at Pomona.

Plants succulent, clump-forming, somewhat branched with age; branches short, woody-fibrous. . *Leaves* opposite, grey-green to blue-green, often flushed pinkish; trigonous to rounded-trigonous, up to 45 x 29 mm, up to 35 mm thick, up to three times as long as wide, seldom deeper than wide; margins and keel rounded or distinct and flushed pink; margins entire or dentate; apex obtuse or acute; base pustulate; epidermis smooth, cells domed, conelike or slightly nippled; epicuticular wax in thick encrusting plates. *Flowers* solitary, terminal, bracteolate, pedicellate, radially symmetric, opening late afternoon, closing at dusk, 22–40 mm in diameter; receptacle epidermis similar to that of leaf; sepals 5, slightly unequal, slightly fleshy; outer sepals larger than inner, with narrow membranous margin, usually with subapical knoblike or toothlike appendage, 6.0–16.9 x 2.5–9.1 mm; inner sepals with broad membranous margin, 5.1–16.6 x 2.0–6.0 mm. *Staminodes* petaloid, 41–72, in two to three series, rarely more-or-less gathered into five groups, 7–17 x 0.9–3.0 mm, white to deep pink or cerise, linear to linear-ligulate, reflexed to a greater or lesser degree, sometimes distally recurved. *Androecium* arranged into a central cone or column; stamens numerous, outer ones much longer than inner; filaments white, 2–11 mm long, outer much longer than inner; bases finely papillate; anthers dorsifixed, pale yellow, 0.6–1.7 mm long, extrorse, dehiscence longitudinal; thecae narrowly elliptic. *Pollen* prolate, bright yellow, 18–25 x 14–19 μmr, tricolpate, exine tectate-perforate to semitectate-reticulate, ornamented with spinulae. *Nectary* continuous, crenulate, orange to dark brown; nectar bright golden yellow. *Gynoecium* stigmas 7–16, pale yellow-green to pale yellow, narrow-subulate, inner surface with stigmatic papillae; ovary synovarious, shallowly obconical below, flat above, rising slightly to base of stigmata; placentation parietal. *Capsule* 5–11 mm in diameter; 7–17 locular; base shallowly obconical, top flat; valve tips somewhat elevated and recurved; expanding keels radial and parallel, diverging distally, yellow- to orange-brown, or light brown to tan; awns present, small; valve wings almost rectangular to (more often) crescent-shaped; covering membranes present, well developed, textured, translucent, covering approximately two thirds of the locule area, meeting in the middle, declining into locule after seed dispersal, additional closing devices absent or very slight closing ledge present; closing bodies absent. *Seed* fat comma-shaped, 0.4 – 1.1 mm long, light brown to apricot or gold- to rust-brown.

Key to species

— Leaves at least twice as long as wide, untoothed or with very few small and indistinct teeth or knobs; 'petals' 50 or more...*D. dealbatus*

—Leaves less than twice as long as wide, margins (and sometimes keels and sides) dentate; 'petals' fewer than 52...*D. delaetianus*

1. Dracophilus dealbatus (N.E. Br.) Walgate, in Bolus, Notes on Mes. 3: 184-185 (1939); Schwantes, Fl. Stones.: 339 (1957); Jacobsen, Handbook Succ. Pl.: 953 (1960); Jacobsen, Sukk. Lex.: 413 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 62 (1970); Court, Succ. Fl. sthn. Afr.: 46 (1981); Smith *et al*, Mesembs: 140 (1998); Court, Succ. Fl. sthn. Afr.: 20 (2000); Van Jaarsveld *et al*, Vygies: 94 (2000); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. A-E: 226 (2001). Type: Little Namaqualand, *Pearson 6062* (K!, holo).

Mesembryanthemum dealbatum N.E. Br., Kew Bull. 357 (1911); *Juttadinteria dealbata* (N.E. Br.) L. Bolus, S. Afr. Gard. 18: 249 (1928).

Dracophilus foetens Dinter, F. Rep. Sp. Nov. Reg. Veg. 27:169 (1931) nom. nud. Type: unknown, possibly *Dinter 6698* (B).

Mesembrianthemum montis draconis Dinter, F. Rep. Sp. Nov. Reg. Veg. 19: 136 (1923); *Juttadinteria montis draconis* (Dinter) Schwantes, Zeit. Sukk. K. 2: 184 (1926); *Dracophilus montis draconis* (Dinter) Dinter & Schwantes in Schwantes, Möll. Deu. Gaert.Zeit.: 187 (1927). Type: Drachenberg 13 km east of Pomona, *Dinter 3784* (B!, holo).

Juttadinteria proxima L. Bolus, Fl. Pl. S.A.: t. 273 (1927); *Dracophilus proximus* (L. Bolus) Walgate, N. Mes. 3:185 (1939). Type: Little Namaqualand between Sendelingsdrift and Arris Drift, *Pillans 5720* (BOL!, holo).

Mesembrianthemum rheolens L. Bolus, Ann. Bol. Herb. 4: 76 (1928); *Dracophilus rheolens* (L. Bolus) Schwantes, Zeit. Sukk. K.: 106 (1927). Type: Little Namaqualand, karroid hills above south bank of the Orange River, between Dun Vley and Groot Doorn, *Pillans 5644* (BOL!, holo).

Etymology: dealbatus (Latin) – covered with a white powder, "whitewashed", referring to the leaves, which often appear very pale.

Leaves up to 59 mm x 19 mm, up to 20 mm thick, up to three times as long as wide, seldom deeper than wide; margins entire or indistinctly dentate; apex blunt to pointed. *Flowers* 27–40 mm in diameter, opening late afternoon, closing at about 22h00; outer sepals usually lacking appendage, or with slight thickening or knob, rarely with subterminal toothlike appendage. *Staminodes* 50–72, white to deep pink or cerise, sometimes distally recurved, 8–17 mm long. *Androecium* filaments 3 – 11 mm long; anthers 0.6-1.4 mm long. *Pollen* 18–25 μm x 13–19 μm. *Gynoecium* stigmas 9–16. *Capsule* 7–11 mm in diameter; (8–)10–13(–17) locular. *Seed* 0.4–0.9 mm long.

Distribution: Southern Namib on central and eastern plains (Figure 5.17).
Habitat: Red sandy plains with calcrete and quarz inclusions and gravel plains, occasionally mountain slopes.
Altitude: 90 – 811 m
Flowering: August to September.
Provisional Namibian Red Data status: LC.

Illustrations: B.O. Carter, *Pillans 5720* (BOL 131808); B.O. Carter, *Pillans 5644,* (BOL 1198); Jacobsen, Sukk. Lex.: 413 (1970); Smith et al, Mesembs: 141 (1998); Van Jaarsveld *et al*, Vygies: 94 (2000).

Discussion: This species was originally described from a plant that flowered at Kew. The present type sheet comprises only a leaf.

2. Dracophilus delaetianus (Dinter) Dinter & Schwantes, Möll. Deutsch. Gärtnerztg 15: 187 (1927); Schwantes, Zeit. F. Sukk. 2: 182-184 (1926); Labarre (ed.), Mesembr.: 209 (1931); v. Pöllnitz, F. Rep. Sp. Nov. 32: 39-40 (1933); Jacobsen, F. Rep. Sp. Nov. 106: 70 (1938);Schwantes, Fl. Stones.: 339 (1957); Jacobsen, Handbook Succ. Pl.: 953 (1960); Jacobsen, Sukk. Lex.: 413 (1970); Friedrich in Merxmüller, Prodromus FSWA (*Juttadinteria*) 27: 62 (1970); Court, Succ. Fl. sthn. Afr.: 46 (1981); Smith *et al*, Mesembs: 140 (1998); Court, Succ. Fl. sthn. Afr.: 20 (2000); Hartmann (Ed.), Ill. Handb. Succ. Pl. Aiz. A-E: 226 (2001). Type: Kukausberge near the Kessel water point, *Dinter 3652* (lost). Lectotype: Locality unknown, *Dinter, s.n. 18.8.1922* (HBG!, lecto).

Mesembrianthemum dealaetianum Dinter, F. Rep. Sp. Nov. Reg. Veg. 19: 137 (1923); *Juttadinteria delaetiana* (Dinter) Schwantes, Zeit. Sukk. K. 2: 184 (1926).

Etymology: De Laet – a belgian succulent collector, particularly of cacti, whose plants drew many people to the cactus hobby.

Leaves up to 35 x 15 mm, up to 15 mm deep, usually about twice as long as wide, rarely three times, seldom deeper than wide; margins usually very distinctly dentate; apex usually distinctly pointed, sometimes with rounded point. *Flowers* 22–34 mm in diameter, opening late afternoon, closing at about 21h00; outer sepals usually lacking appendage, usually with slight thickening or knob, rarely with terminal or subterminal toothlike appendage. *Staminodes* 41–51, white to cerise, reflexed to a greater or lesser degree, 7–15 mm long. *Androecium* filaments 2–9 mm long; anthers 0.6–1.1 mm long. *Pollen* 18–26 x 14 – 19 μm. *Gynoecium* stigmas 7–11. *Capsule* 5–9 mm in diameter; (7–)8–10(–11) locular. *Seed* 0.4–1.1 mm long.

Distribution: Southern Namib in several localised populations (Figure 5.17).
Habitat: Red sandy plains with calcrete and quarz inclusions, usually near mountain bases, occasionally granite or sandstone slopes or sandy washes.
Altitude: 536 – 1065 m.
Flowering: August to September.
Provisional Namibian Red Data status: LC.

Illustrations: M. Page, *Dinter s.n.* Oct. 1922, (BOL 1202); B.O. Carter, *Dinter sp .n.* (BOL 131806); M. Walgate, *Holloway 101 & 102,* BOL 1201; Labarre (ed.), Mesembr.: 209 (1931); Jacobsen, Succ. Pl.: 169 (1935); Jacobsen, Handbook Succ. Pl.: 953 (1960); Smith *et al*, Mesembs: 140 (1998); Van Jaarsveld *et al*, Vygies: 94 (2000).

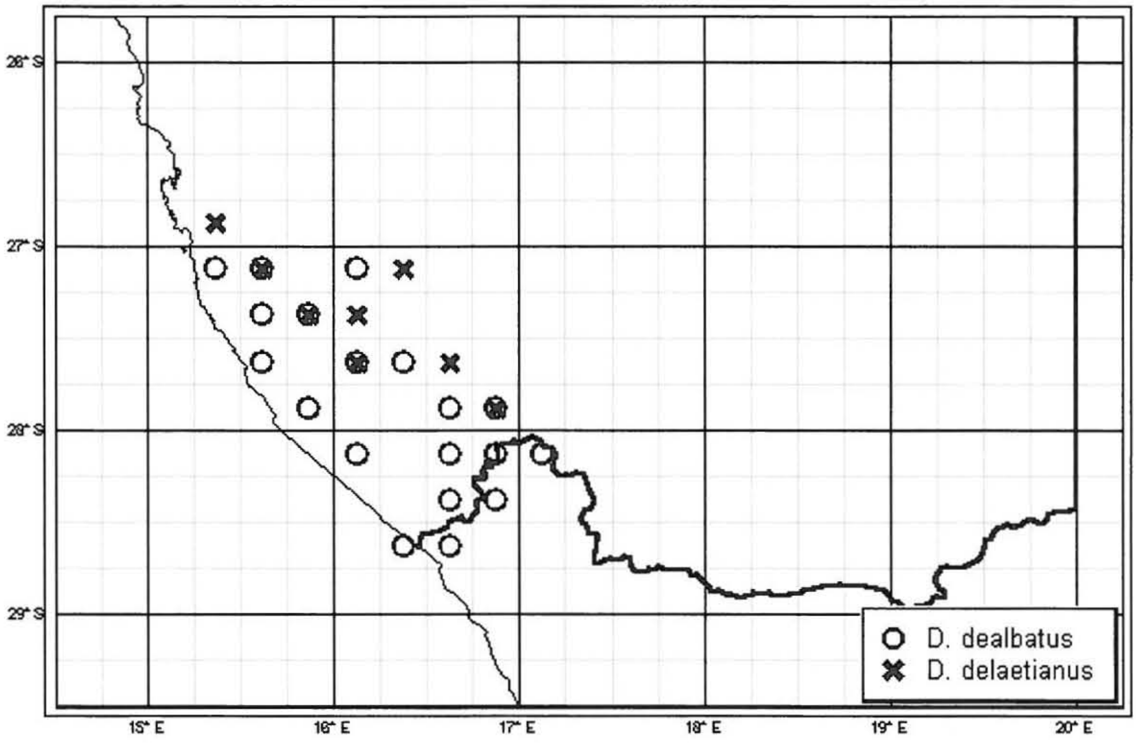


Figure 5.17: Distribution of *Dracophilus dealbatus* and *D. delaetianus*.

CHAPTER 6 PHYLOGENY

Phylogenetic analysis

A phylogenetic analysis of morphological and phenological data of the taxa indicated by the phenetic analysis was undertaken with the aim of clarifying and confirming relationships within the subtribe. The analysis was based on 24 characters, 23 morphological and 1 phenological (Table 6.1)

For the phylogenetic analysis characters that exhibited discrete states for the majority of the groups were selected, although there were a few instances where a character was polymorphic for a particular species. The final character set was selected to best represent clear disjunctions in character states from a range of plant structures. These vary from the macroscopic to the microscopic. Each of these is discussed briefly below.

1. All species in the Dracophilinae are branched. The branches may be so short that the plants appear tuft-forming (state 0; Figures 3.8B, 5.2B) or they may be well-developed (state 1; Figure 4.2D).

2. Distinct taproots (state 1) or only a spreading root system without a taproot (state 0) are found.

3. Leaves in the Dracophilinae have a skewed appearance due to a displaced keel (state 0; Figure 5.3 B). This character becomes indistinct in the oldest leaves of some species, such that the leaves have a bilaterally symmetric appearance (state 1; Figure 3.2A).

4. Leaf margins may be entire (state 0; Figure 5.3A), bear a few minute, sharp, cartilaginous teeth (state 1; Figure 4.3A), or be heavily dentate with fleshy teeth (state 2; Figure 7.1B).

5. Leaf margins may taper from the base to the apex (state 0; Figure 3.2A), be parallel for most of their length (state 1; Figure 4.3C), or diverge in the distal half such that the leaf is broadest just behind the apex (state 2; Figure 4.3D).

6. Leaf keels may be indistinct such that the ventral outline is a curve (state 0; Figure 3.2A), distinctly angled but rounded (state 1; Figure 4.3A) or very pronounced and sharply defined, forming an acute angle (state 2; Figure 7.1B).

7. Leaf epidermal cells may be very flat to slightly rounded (Figure 4.5C), domed to conelike (Figure 4.5E), or papillate with long, tapering papillae (Figure 3.5A).

8. Leaf colour may be grey to grey-brown (state 0; Figure 3.2A), very light green (state 1; Figure 4.3A), blue-green (state 2; Figure 5.2B) or green (state 3; Figure 4.3C).

9. Leaf size ratios were recorded as less than twice as long as wide (state 0) or more than twice as long as wide (state 1).

10. Flowers were ebracteolate (state 0)or bracteolate (state 1).

11. Flowers were recorded as sessile or almost so if the pedicel was not visible without pulling the upper pair of leaves apart (state 0; Figure 3.8C). If the pedicel was clearly visible they were recorded as pedicellate (state 1).

12. Sepals number four or more (state 0) or five or more (state 1). Some species have strictly four (i.e. *Juttadinteria* spp.) or strictly five (i.e. *Dracophilus* spp.), while the two species of *Namibia* have either predominantly four or predominantly five sepals. This has been discussed in more detail in section 7.5.1.

13. Sepals, in particular the larger outer petals may be slightly fleshy, such that they are easily flexible without damaging them (state 0) or very thick and fleshy, such that they are inflexible (state 1; Figure 4.8D).

14. Flowers in some species are invariably white (state 0), while in others white flowers predominate to a great extent in all populations with pink flowers rarely found (state 1), or otherwise pink flowers predominate in all populations and white flowers are rarely found (state 2).

15. Petals are either in a single row (state 0) or are 2 to 3-seriate (state 1).

16. Inner and outer filament length may be slightly unequal which results in the inner side of the androecium having a ring of anthers near the top (state 0) or extremely unequal, with the inner ones very short compared to the outer such that the inner side of the androecium appears to be entirely lined by anthers (state 1).

17. Usually all the anthers are similar and elongate (state 0), they rarely exhibit two forms in a single species, both elongate and short and fat anthers being present (state 1).

18. Three flower opening times occur - afternoon (state 0), evening (state 1) or all day(state 2).

19. Pollen may be tectate-perforate, in which the area covered by the tectum is greater than that not covered and the luminae are perforations (state 0) or tectate-reticulate, in which the tectate area is less than the open area and the luminae are large, irregular and reticulate (state 1).

20. Nectary crenulations vary between very low and inconspicuous such that the nectary looks like a simple ring unless magnified (state 0), medium, in which the height of the crenulations was estimated to be less than that of the basal ring (state 1) and very pronounced, in which the height of the crenulations was estimated to be as high or higher than that of the basal ring (state 2).

21. Nectaries were either of such a pale green that they were almost colourless (state 0), truly green to very dark green (state 1) or orange to brown (state 2).

22. The capsule base may be cupular (bowl shaped, state 0; Figure 3.17A), shallowly funnel-shaped with the diameter greater than the depth (state 1; Figure 5.14A) or deep funnel shaped with the diameter less than or equal to the depth (state 2; Figure 4.16A).

23. Covering membranes meet in the centre of the locule (state 0; Figure 5.14C) or are reduced to the point where they do not meet (state 1; Figure 3.17E).

24. Covering membranes may be absent or extremely vestigial (state 0; Figure 3.17 D), crescent-shaped (state 1; Figure 5.14B) or widen distally (so as to appear somewhat deltoid, state 2; Figure 5.14C).

Parsimony analysis was done using PAUP Version 4.0b10 (Swofford 2000). An heuristic search was done (HSEARCH), using the TBR branch swapping algorithm with ACTRAN ON. All multistate characters were considered as unordered, and multiple states for a character were considered as polymorphisms. Bootstrap values were obtained from 1000 bootstrap iterations. *Hartmanthus pergamentaceus* (L. Bolus) S.A. Hammer was chosen as the outgroup because it occurs within the distribution area of the subtribe Dracophilinae and the genus *Hartmanthus* was included by Hartmann (1991, 1993) into her informal Dracophilus group together with the three genera of the subtribe. However, it is possible that a more suitable outgroup will become apparent once more inclusive phylogenetic studies become available.

Cladistic analysis of 12 taxa resulted in three equally parsimonious trees of 46 steps with a CI of 0.772 and an RI of 0.772. These trees differ in the internal arrangement of the *Juttadinteria* clade. Figure 6.1 shows one of the possible three solutions.

Because only a single outgroup was used it was impossible to assess the validity of the subtribe as a monophyletic lineage. The study group divides into two clades, one containing the two members of *Dracophilus* (100% bootstrap support) and the other containing the members of both *Juttadinteria* and *Namibia*, rendering *Juttadinteria* paraphyletic. However bootstrap support for the clade is poor, and several synapomorphies set the two species of *Namibia* (which receives 96% bootstrap support within this clade) apart from species of *Juttadinteria*. They differ in root system, their flowers are permanently open, their capsule is bowl-shaped rather than obconical, they exhibit basi-parietal rather than parietal placentation, their seeds differ in shape and they have papillate leaf epidermal cells. The latter character is shared within the subtribe only with some examples of *J. simpsonii* that were previously named *J. kovisimontana*. These may be hybrid between *N. ponderosa* and *J. simpsonii* (see Section 4.2). In addition to these differences *Namibia* has a pronounced tendency towards multiplication of structures such as sepals, stigmata and locules, with the 25 stigmata recorded for *N. cinerea* very high within the Aizoaceae. In view of the poor bootstrap support for the *Juttadinteria* clade and the distinct characters of the nested *Namibia* clade further evidence from molecular, cytological and embryological studies should be assessed before sinking *Namibia* into *Juttadinteria.* At present nomenclatural stability will best be maintained by upholding *Namibia* as a distinct genus.

The *Dracophilus* clade enjoys strong bootstrap support (100%) and its monophyly is well supported by several synapomorphies, including nocturnally opening bracteolate flowers with slightly fleshy sepals. All other members of the subtribe have ebracteolate flowers with very fleshy sepals that either open in the afternoon and close at dusk or stay open permanently.

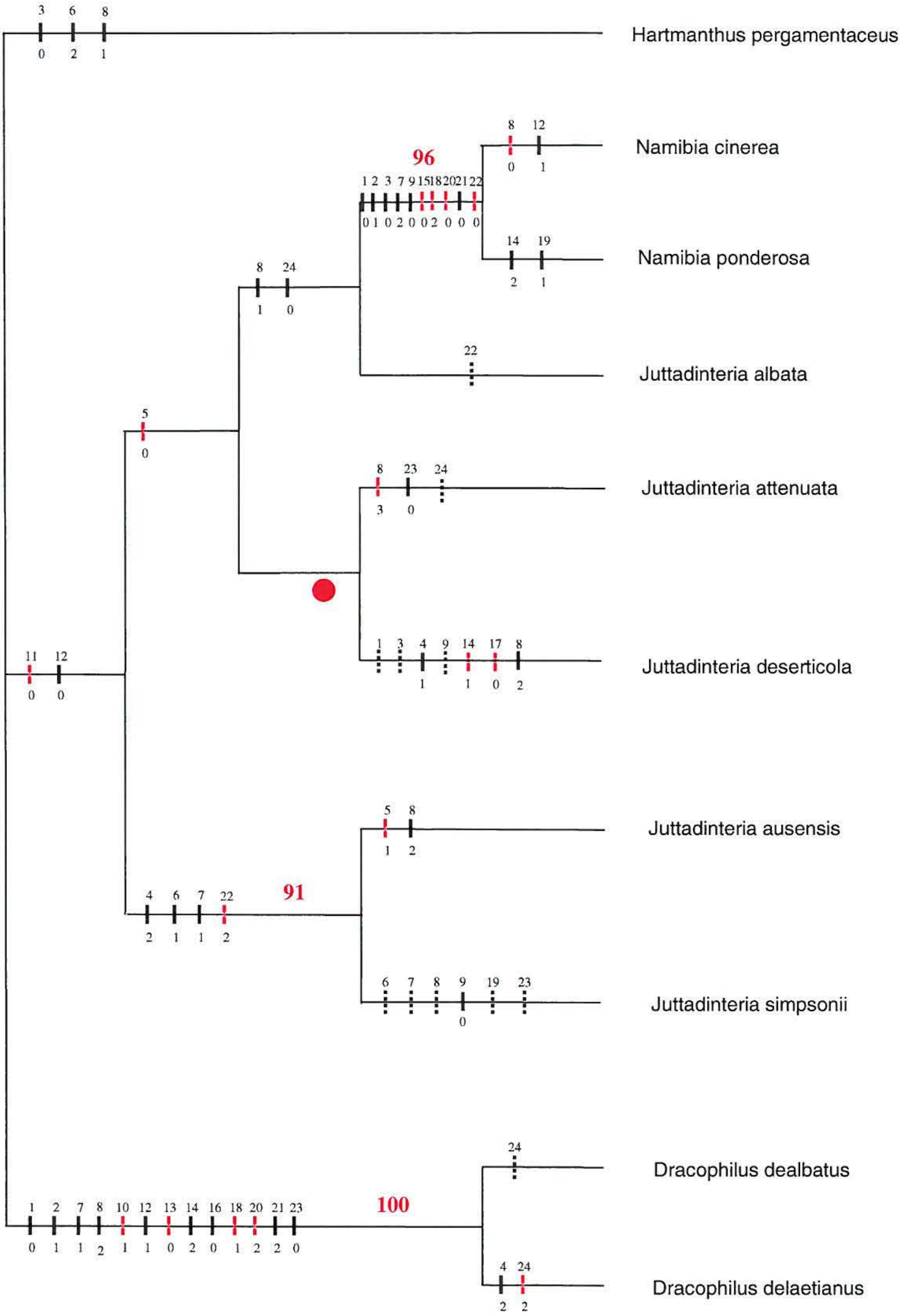


Figure 6.1: One of the three most parsimonious trees obtained from the phenological and morphological data (length = 46 steps; CI = 0.772; RI = 0.772). Solid dots indicate nodes that collapse in the strict consensus tree. Numbers above the nodes are bootstrap values from 1000 iterations. Red bars represent non-homoplasic character transformations. Broken bars represent variable characters.

The *Juttadinteria* clade is not well supported and contains one node that collapses in the strict consensus tree. *Juttadinteria* appears to be a complex of closely related species that are difficult to delimit due to a profusion of intergrading, overlapping and reticulate characters. This phenomenon is recognized as a trait of the Mesembryanthemaceae (Ihlenfeldt 1994) and may indicate relatively recent or even incomplete speciation in *Juttadinteria.* Ihlenfeldt (1994) maintains that this trait is a confounding factor in cladistic analysis and elucidation of phylogeny that impedes delimitation of natural taxonomic units. Certainly there appears to be a distinct tendency towards intermediate forms in *Juttadinteria,* particularly where distribution areas meet or overlap. Many characters are polymorphic in some species of *Juttadinteria,* e.g. leaf dentition, leaf shape, shape of covering membranes and many characters that were not utilized in this analysis, including flower shape, valve wing width and shape and seed colour, amongst others

Juttadinteria attenuata shows similar leaf epidermal characters and denticulation to *J. deserticola* (characters 7 and 4 respectively) but differs in its longer leaves (character 9), extremely pronounced subepidermal tannin cells (Figure 7.5) and in the character of the covering membranes in the capsule (character 23). *Juttadinteria albata* has the flattest leaf epidermal cells in the subtribe (Figure 7.3 A). Its robust leaves taper to a distinct point (character 5) and are an unusual whitish green colour reminiscent of the colour of putty (character 8). Hartmann (2001) mentions very small seed as a distinguishing character for this taxon, but during this study considerable overlap of this character between all *Juttadinteria* species was observed.

The *J. ausensis-J. simpsonii* clade forms what appears to be a well supported (91% bootstrap) natural group that has distinctly keeled leaves with heavily dentate margins and domed to papillate epidermal cells. The group is allopatric with respect to *J. deserticola.* There is some overlap between *J. deserticola* and *J. attenuata* and between *J. attenuata* and *J. ausensis*

Juttadinteria ausensis is allopatric with respect to *J. simpsonii* (Although the distribution map shows them overlapping in the 2715BD quarter-degree square (Figure 4.21) they are in fact geographically separated within that square.). Its leaves are usually more than twice as long as wide (character 9) with tips that are slightly triangular and thickened whereas those of *J. simpsonii* are less than twice as long as wide with pronounced rhomboidal thickening below the tip. While *J. simpsonii* occurs on sandy footslopes and lower slopes of granitic-gneiss koppies and mountains *J. ausensis,* as previously mentioned, prefers sandy plains with heavy calcrete inclusions.

Based on the evidence used in this study the validity of the five species of *Juttadinteria* as proposed by Hartmann (2001) is upheld. However *J. suavissima* is placed in synonymy with *J. deserticola* as well as with *J. ausensis.* This was discussed in the taxonomic treatment of *Juttadinteria* in Chapter 4.

Table 6.1: Characters and data set used in the phylogenetic analysis of the Dracophilinae.

	H. pergamentaceous	N. cinerea	N. ponderosa	D. dealbatus	D. delaetianus	J. albata	J. attenuata	J. ausensis	J. deserticola	J. simpsonii
1Habit tufted (0) branched (1)	1	0	0	0	0	1	1	1	{01}	1
2Roots adventitious (0) taproot (1)	0	1	1	1	1	0	0	0	0	0
3Oldest leaves symmetric (0) distinctly asymmetric with displaced keel (1)	0	0	0	1	1	1	1	1	{01}	1
4Leaf margins and keels entire (0) with few minute teeth (1) heavily dentate (2)	0	0	{01}	0	2	{01}	{01}	2	1	2
5Leaf margins tapering to apex (0) parallel (1) diverging to apex (2)	2	0	0	{02}	2	0	{01}	1	0	2
6Leaf keel indistinct (0) distinct but rounded (1) very pronounced (2)	2	0	0	0	0	0	0	1	0	{12}
7Leaf epidermal cells flat or slightly rounded (0) domed to conelike (1) papillate (2)	0	2	2	1	1	0	0	1	0	{12}
8Leaf colour greyish (0) very light green (1) blue-green (2) green (3)	1	0	1	2	2	1	3	2	2	{12}
9Leaf < twice as long as wide (0) > twice as long as wide (1)	1	0	0	1	1	1	1	1	{01}	0
10Flower ebracteolate (0) bracteolate (1)	0	0	0	1	1	0	0	0	0	0
11Flower sessile or almost so (0) pedicellate (1)	1	0	0	1	1	0	0	0	0	0
12Sepals four or more (0) five or more (1)	1	1	0	1	1	0	0	0	0	0
13Sepals slightly fleshy (0) very fleshy (1)	1	1	1	0	0	1	1	1	1	1
14Flower white (0) white rarely pink (1) pink rarely white (2)	0	0	2	2	2	0	0	0	1	0
15Petals 1-seriate (0) 2 to 3-seriate	1	0	0	1	1	1	1	1	1	1
16Filament length slightly unequal (0) very unqual (1)	1	1	1	0	0	1	1	1	1	1
17Anthers sometimes short and fat (0) always elongate (1)	1	1	1	1	1	1	1	1	0	1
18Flower open afternoon (0) evening (1) all day (2)	0	2	2	1	1	0	0	0	0	0
19Pollen tectate-perforate (0) tectate-reticulate (1)	?	{01}	1	{01}	0	0	0	0	0	{01}
20Nectary crenulations low (0) medium (1) high (2)	1	0	0	2	2	1	1	1	1	1
21Nectary pale green (0) green (1) orange or brown (2)	1	0	0	2	2	1	1	{12}	1	1
22Capsule base bowl-shaped (0) shallow funnel-shaped (1) deep funnelshaped (2)	1	0	0	1	1	{12}	1	2	1	2
23Covering membranes meeting (0) not meeting (1)	1	1	1	0	0	1	0	1	1	{01}
24Covering membranes absent or extremely vestigial (0) crescent-shaped (1) widening distally (2)	1	0	0	{12}	2	0	{12}	1	{01}	1

CHAPTER 7: SUBTRIBE DRACOPHILINAE Schwantes

With species limits now ascertained, and most species relationships elucidated, intergeneric variation in characters is examined and discussed.

The unifying characters of the subtribe Dracophilinae, composed at present of three genera (*Namibia, Juttadinteria* and *Dracophilus*) may at present be summarized as follows:

Plants low-growing. Leaves hypersucculent with large subepidermal tannin cells and thick epicuticular wax layers. Stomata overarched by papillate peristomatal cells. Flowers solitary, terminal, white or pink; 'petals' 1 to 3 seriate; filaments numerous, white, pubescent at the base, gathered into a cone or cylinder. Stigmata narrow-subulate, covered in stigmatic papillae on the inner surface. Nectary a crenulate ring. Capsules with valves expanding widely, covering membranes absent, vestigial or poorly developed and lacking additional closing mechanisms, closing bodies absent.

Variation in characters between genera is briefly discussed below.

7.1 Roots

All three genera have reddish woody-fibrous roots that lack a storage function. In *Dracophilus* and *Namibia* there is usually a more-or-less distinct taproot with several secondary roots, whereas *Juttadinteria* has a more spreading system with two or more roots from the base. Roots without a specialised storage function were regarded as possibly primitive in the Mesembryanthemceae by Bittrich and Struck (1989). Root anatomy was not investigated. Root morphology is thus taxonomically useful at genus level.

7.2 Habit and life forms

According to the system in Jürgens (1990) the members of the subtribe Dracophilinae are all chamaephytes. Within this category all the species are usually microchamaephytes (height 5-15 cm) or mesochamaephytes (height 15-25 cm) when adult. Exceptionally *J. albata* and *J. deserticola* reach heights over 25 cm.

All three of the general growth forms distinguished by Hartmann (1991) for perennial mesembs are represented. These are compact forms, procumbent forms and shrub forms. *Dracophilus* and *Namibia* exhibit the compact form, with internodes entirely enclosed by the leaves, rarely developing longer, more exposed and spreading branches with age. *Juttadinteria* is more diverse in habit. It exhibits all three forms (Table 4.3), although the shrubby forms do not entirely conform to her description of that category. These lack the long internodes specified by her for the shrub group. Their internodes may be enclosed or visible but as they have semi-erect to erect branches they do not exhibit the strictly horizontal branch orientation specified by her for the procumbent form. They are placed in the shrub category because they are often, and perhaps best, described as dwarf shrubs. Four species of *Juttadinteria* occur in more than one form.

All the species in the subtribe have two to five branches. Internodes are usually concealed in *Namibia* and *Dracophilus*. In *Juttadinteria* the internodes may be enclosed or visible, with internodes most visible in *J. attenuata* and *J. ausensis.*

7.3 Stems

Stems in the subtribe are fibrous-woody and red-brown in colour. No anatomical investigation was undertaken. Stem morphology is not taxonomically useful.

7.4 Leaves

7.4.1 Macro-morphology

The leaves in all three genera are opposite, decussate, trigonous and fused at the base. They often have a characteristic skewed appearance which results from the presence of an oblique keel. One side of the leaf is convex, the other concave or flat, and the apex displaced to one side (e.g. Figure 5.3 B). Leaf shape varies from fat-trigonous to elongate-trigonous, and may taper from base to tip or widen out below the tip to form a rather chunky rhomboid to rhomboid-spatulate area (Figure 4.3 D). In the latter case the leaf may also become much deeper in the wide area, resulting in a somewhat gibbous outline.

Margins and keels may be distinct or rounded, and leaf margins may be entire or ornamented with blunt knobs (Figure 7.1 A) or sharp teeth. The teeth may be very small and fine, or larger and fiercer (Figure 7.1 B). To a certain extent this character appears to be environmentally controlled, because in cultivation fiercely toothed species become less so, and the converse is true of finely toothed species, which bear more teeth than usual. Teeth or knobs may also occur on the lateral surfaces of leaves (Figure 7.1 A). Usually most knobs or teeth are carried on the widened section (Figure 7.1 B), or near the apex of those species in which the leaves do not widen out. Heavily toothed species of both *Dracophilus* and *Juttadinteria* are found in the northern and eastern reaches of the distribution area of the subtribe. Leaf tips often bear a tiny, horny mucro, that may be blunt or quite sharp. In *N. ponderosa* the leaf tip is distinctly recurved (Figure 3.2 B).

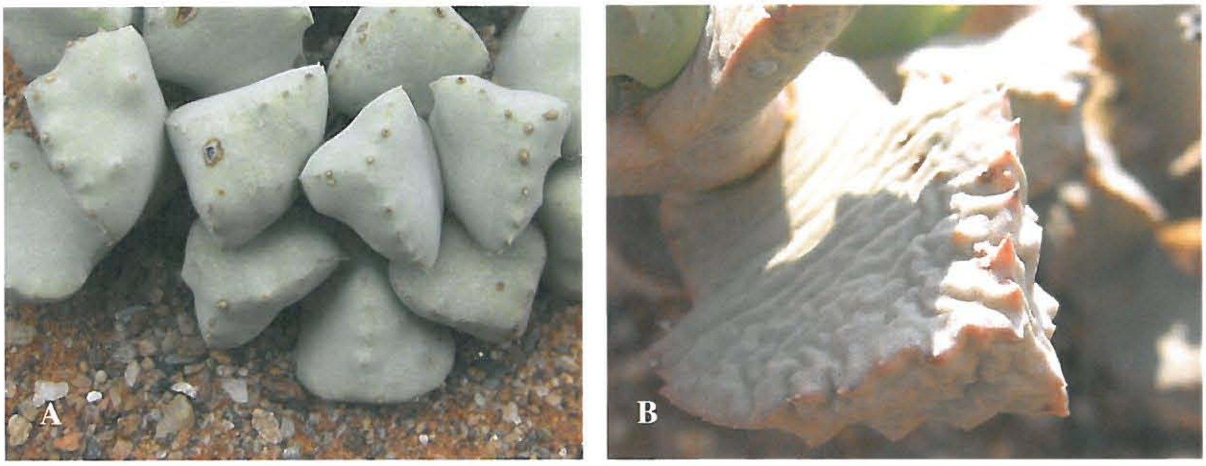


Figure 7.1: A. *Juttadinteria simpsonii* showing blunt knobs on leaf margins, keel and sides (C. Mannheimer CM 2370). B. *J. simpsonii* showing large teeth on margins, keel and sides (C. Mannheimer CM 1666).

All leaves have a basal-dorsal area called the pustule, where the epidermal layer is much thinner and more translucent, and the water storage tissue lies far closer to the surface than elsewhere. This pustule is generally inconspicuous and under dry conditions it is virtually concealed by the leaf above but during favourable moisture periods it swells, becoming far more prominent. According to Hartmann (1991) these pustules are quite common in the mesembs. Generally they have been interpreted as solar windows that allow greater penetration of sunlight into the leaf. In the Dracophilinae swelling of the pustule results in the leaf being orientated at a wider angle to the axis, permitting not only light penetration through the pustule surface but, possibly, also exposing more of the dorsal surface to insolation during favourable moisture periods.

Leaf macro-morphology is of taxonomic use at genus level.

7.4.2 Colour

In *Dracophilus* and *Juttadinteria* leaf colour varies from very light grey-green (e.g. *J. albata*) to blue-green (e.g. *D. delaetianus*) and the leaf may be flushed pink or reddish, especially on margins and keels. The leaves often have a rather glaucous appearance due to the presence of epicuticular waxes that are discussed in more detail in section 7.4.3. In *Namibia* leaf colour is light green to light orange or grey to grey-brown. The margins in *N. ponderosa* are often flushed orange and during dry periods exposed parts of the leaf surface may also have a light orange appearance. This character is of limited taxonomic use, mainly due to its subjective nature. Under conditions of severe moisture deficit leaves in all species flush a dull, dirty-pink colour. Leaf colour is not of taxonomic use at genus level.

7.4.3 Anatomy

According to Ihlenfeldt and Hartmann (1982) the Dracophilinae exhibit the 'xeromorphic' type of epidermis (Type X6). The following characters, considered typical of xerophytes, are present (Figure 7.2).

- A thick epicuticular wax layer, thought to reduce water translocation across the wall (Lyshede 1979).
- A thick cuticle.
- A cutinized wall layer in addition to the cuticle proper.
- Encrustation of the cell wall by calcium oxalate crystals resulting in crystal layers that may vary in thickness as well as in size and shape of crystals.
- Reduced cell lumenae due to the thick secondary cell wall layers.
- Stomata that, although they are not sunken, are of the 'hidden' type.

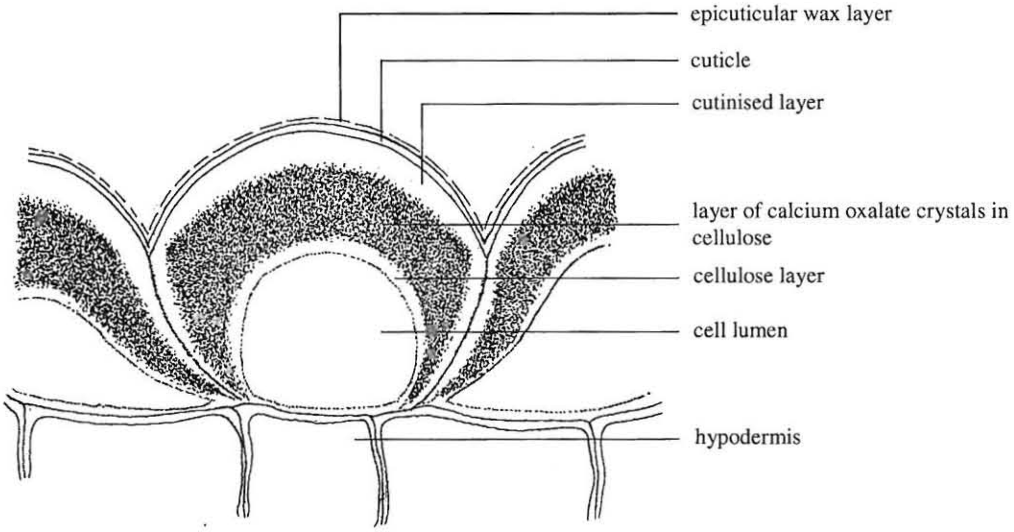


Figure 7.2: Generalised leaf epidermal anatomy in the subtribe Dracophilinae (adapted from Ihlenfeldt & Hartmann 1982).

Within the subtribe (distinguished by the degree of convexity of the periclinal cell wall) three main epidermis types occur. These are:

- cells flat to very slightly rounded
- cells distinctly rounded to domed or conelike
- cells papillate, with tapering papillae

The characters listed above for the xeromorphic type of epidermis appear to differ in their expression between these epidermal categories. As sectioning was limited to very few representatives of each group the discussion below should be viewed as preliminary. Measurements were rounded off to the nearest micrometre.

The cuticular layer, comprising the cuticle and cutinised layer as described by Hartmann and Ihlenfeldt (1982) is 2–6 μm thick in all three epidermis types. In the flat and rounded types it forms a thick, more-or-less uniform layer that fills the space between the anticlinal cell walls (Figures 7.3 A and 7.3 B). In the papillate type this layer is thickest at the tips of the papillae, tapering down towards the base of the cells (Figure 7.3 C).

Calcium oxalate crystals occur as crystal 'sand', i.e. granules up to 1 μm in diameter (as discussed by Hartmann 1981). In all the examined specimens the layer of calcium oxalate crystals in the flat and rounded epidermis types is far deeper (13–23 μm) than in the papillate type (5–7 μm). It appears to occur as a layer of variable thickness that partitions the cell lumen to some extent. Thus in transverse section, as shown here, what appear to be 'ribs' that extend further into the lumen than the rest of the crystal layer are seen as extentions of that layer or darker zones within the layer (Figure 7.4 A). To what extent these structures compartmentalise the cell might be clarified by examination of transverse sections of these cells. This was not undertaken during the present study. These structures might have a support function in the cell.

The stomata lie at the same level as the epidermal cells and are hidden by papillate peristomatal cells (Figure 7.4 B).

The mesophyll consists mainly of large undifferentiated cells with a water storage function. It is further characterised by the following elements (Figure 7.4 C):

- A narrow layer of relatively small hypodermal cells below the epidermis (Figure 7.4 C (a)).

- Large tannin idioblasts in the subhypodermal layers (Figure 7.4 C (b)). These are by far the largest cells in the mesophyll. Their surface visibility is an important taxonomic character at species level in *Juttadinteria*. They are thought to play a role in discouraging herbivory.

- Idioblasts containing crystal raphides of calcium oxalate (Figure 7.4 C (c)). These are also larger than the undifferentiated mesophyll cells.

- Transport vessels characterised by helical wide-band tracheids (Figures 7.4 C (d) and 7.4 D). These are common in the Ruschioideae and are also known from the Cactaceae and Portulacaceae.

In these the diameter of the secondary cell wall is increased, reducing the size of the cell lumen. They lack the cell perforations are found in vessel elements. When stained with safranin and fast green they show typical lignin staining as found in common tracheids and vessel elements. Wide-band tracheids are thought to prevent cell collapse under water stress (Landrum 2001). They might also provide some degree of additional structural support for these very heavy leaves.

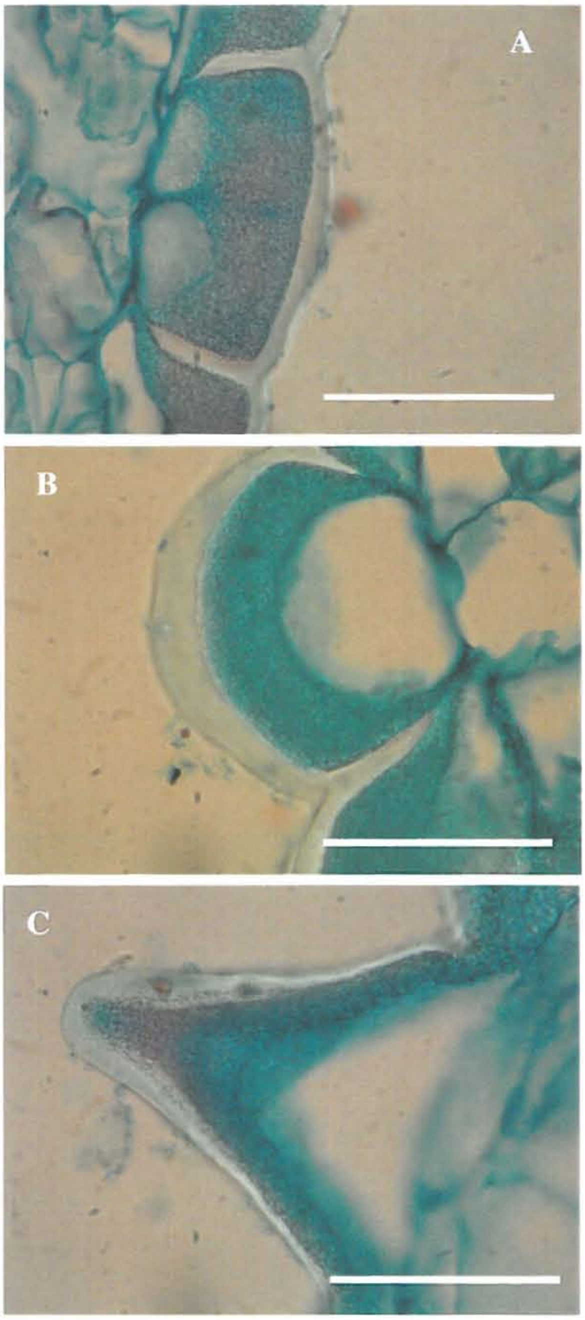


Figure 7.3: Cross section of epidermal cells showing cuticular layer, layer of calcium oxalate crystals and cell lumen x 1000. A. Flat epidermal cell in *Juttadinteria albata* (*C. Mannheimer CM 2236*); B. Rounded epidermal cell in *J. deserticola* (*C. Mannheimer CM 2216*); C. Papillate epidermal cell in *Namibia ponderosa* (*C. Mannheimer CM 1693*). Scale bars 50 μm.

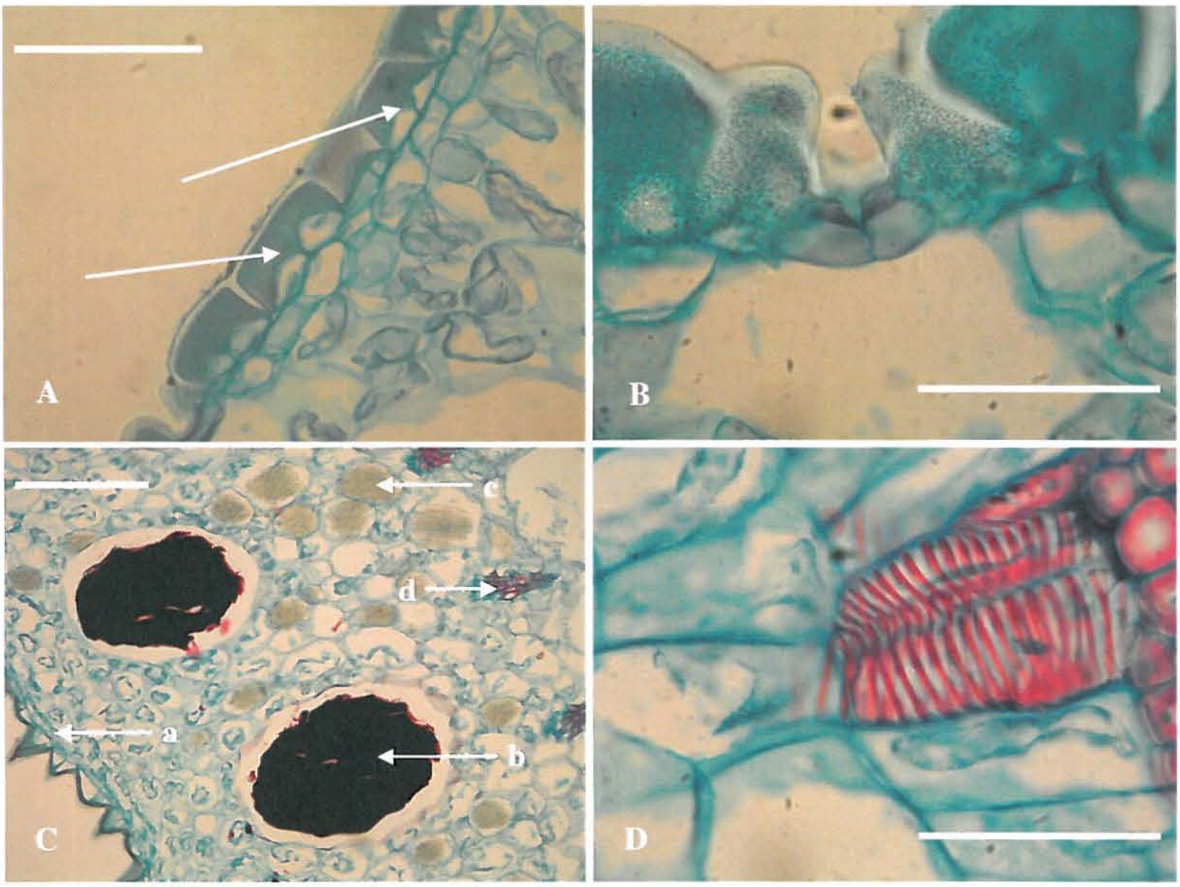


Figure 7.4: Leaf cross sections. A, B. *Juttadinteria albata* (*C. Mannheimer CM 2236*) A. Riblike thickening of calcium oxalate layers x 400, scale bar 100 μm; B. Stoma showing guard cells at the same level as other epidermal cells and overarching papillae x 1000, scale bar 50 μm; C. *Namibia ponderosa* (*C. Mannheimer CM 1693*) epidermis and mesophyll showing narrow layer of hypodermal cells (a), tannin idioblast (b), idioblasts containing calcium oxalate raphides (c) and transport vessels (d) x 100, scale bar 300 μm; D. Wide band tracheids in *Dracophilus dealbatus* (*C. Mannheimer CM 1524C*) x 1000, scale bar 50 μm.

7.4.4 Micro-morphology

All members of the subtribe Dracophilinae exhibit a heterocellular/xeromorphic epidermis with cells that differ in size. The epidermal cells, excluding guard cells, have isodiametric anticlinal walls (e.g. Figures 4.5 C and 5.4 C). In all members of the subtribe the stomata are surrounded by, and may also be overarched by, papillate subsidiary cells (e.g. Figures 3.6 and 4.6).

Types and size classes of leaf surface structures found in the Mesembryanthemaceae were listed by Ihlenfeldt and Hartmann (1982). Of these two are found in the Dracophilinae:

- Class II, protruberances of the epidermal cell of 20-50 μm in diameter and 120-150 μm in length

This type of sculpture occurs in the periclinal cell walls in several species of *Juttadinteria* in the form of short, tapered papillae or domelike papillae that in addition are occasionally nippled (Figures 4.5 E and D). They are also found in *Namibia*, in which both species have papillae that taper from the base to the tip (Figure 3.5). In species with domed epidermal cells the anticlinal walls are sometimes obscured because the walls of adjacent cells lie so close together (e.g. Figure 5.4 A).

- Class III, epicuticular wax structures of 1-10 μm in size.

All members of the subtribe have a thick epicuticular wax layer that tends to fracture above the anticlinal walls (e.g. Figure 4.7 A). They further exhibit additional small wax structures termed crystalloids by Engel and Barthlott (1988). These are of two types - blocks (Figure 5.6 D) and platelets (Figure 3.7 D). Their density differs between taxa. Density of the wax cover is greatly influenced by environmental factors (Hartmann 1979), reducing the usefulness of material grown *ex situ* and making assessment of several populations per taxon mandatory before any comparisons between taxa may be drawn. Wax crystalloids may be eroded during aging, and may completely disappear (Barthlott 1981).

Wax platelets in this group show an inclination, sometimes quite pronounced, towards orientation in a common direction on the surface of the leaf (Figure 5.6 C). This was reported as absent in centrospermous leaf and stem succulents by Engel and Barthlott (1988).

Epicuticular wax in seed plants consist of alkanes, long-chain alcohols, ketones and esters of long-chain fatty acids as well as cyclic compounds such as phytosterols and flavonoids (Barthlott 1981). Chemical composition of waxes in members of the subtribe was not investigated.

The tannin cells described earlier may be so large that they form clearly visible swellings of the epidermis, a character that is pronounced in *J. attenuata* (Figure 7.5).

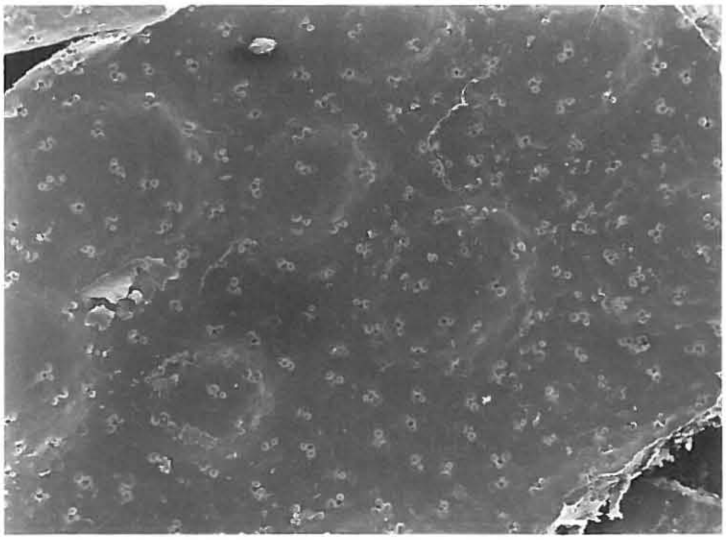


Figure 7.5: Large subepidermal tannin cells result in pronounced elevations on the surface of the leaves of *Juttadinteria attenuata* (*C. Mannheimer CM 1608*) x 40, scale bar 100 μm.

Although surface structures show considerable variation, they are, to a certain extent, influenced by environmental conditions. Thus, although they are helpful taxonomically, they should be used with caution and only together with other, more constant, characters.

7.5 Flowers

All three genera have solitary, terminal, protandrous (i.e. they have an early male phase followed by a female phase during anthesis), possibly melittophilous flowers (in *Juttadinteria* and Namibia, which open their flowers during the day) of the central cone type (Figure 7.6). The flowers are pedicellate, although those of *Juttadinteria* and *Namibia* (particularly) may appear sessile because they are carried deep between very succulent leaf pairs. *Dracophilus* flowers all have distinct pedicels, and, in further contrast to those in the other two genera, are subtended by two small, fleshy, leaflike, persistent bracts that are fused at the base. These are carried just above the last pair of leaves, and orientated in the same direction as they are. They sometimes carry subterminal teeth or knobs. Both pedicel and bracts enlarge through the several days of anthesis and both are also plastic in cultivation, making their consistent measurement difficult.

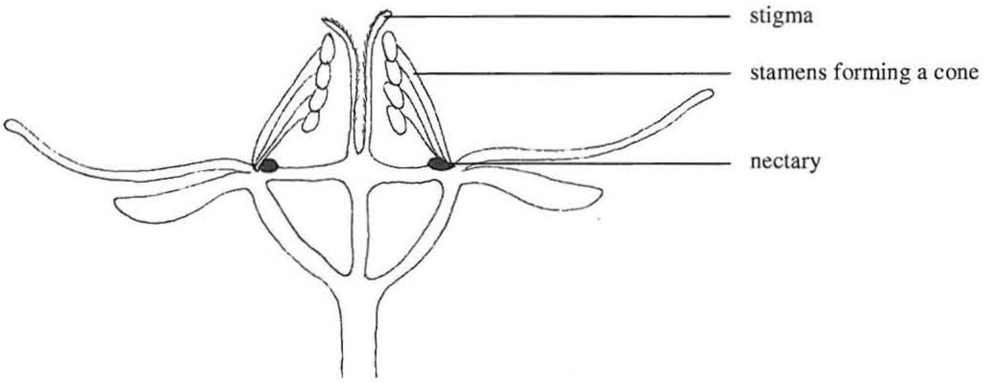


Figure 7.6: Generalised diagram showing cross-section of flowers in the Dracophilinae.

Flower diameter varies between 11 and 73mm, the smallest flowers found in *J. deserticola* and the largest in *N. ponderosa*. Basal growth of the androecial elements (stamens and 'petals') results in an increase in flower diameter through the (approximately) five to seven days of anthesis, as noted for *Cheiridopsis* by Hartmann and Dehn (1987). Ideally flower diameters should therefore all be measured at a specific stage of anthesis in order to try and standardise the measurement as far as possible. This was not possible due to time constraints in the field, and, obviously, also not on herbarium sheets. Measurements thus represented open flowers at all stages of anthesis.

Flower colour varies from white, through various shades of pink, to deep rose pink and cerise. *Juttadinteria* flowers are pure white, while those of *Dracophilus* vary from white (rarely) through pink to cerise within single populations (Figure 5.8 A), although the white condition is quite rare, especially in *D. delaetianus*. The shade of pink of *Dracophilus* flowers tends to fade through anthesis, gradually becoming paler and less intense. Both pink and white flowers are found in *Namibia*, but in this case the flower colour is more consistent in each of the two species. *Namibia cinerea* flowers are pure white whereas those of *N. ponderosa* are almost always a shade of pink, from very pale to deep rose pink (Figure 3.8 C). Pure white flowers were found to be rare in *N. ponderosa*, but the flowers invariably fade to a dirty white with age.

Flower shape in *Namibia* and *Juttadinteria* may be round, but is often somewhat rectangular to squarish (Figure3.8 and 4.8 B) due to them having reasonably robust outer sepals that prevent the petals from reflexing fully, particularly on the sides constrained by the larger, outer sepals. The morphology of the sepals is discussed in detail later. *Dracophilus* flowers are invariably round, rarely with the 'petals' indistinctly divided into five groups.

Opening time varies greatly within the subtribe. It is delayed or inhibited by very cold, overcast, or wet weather. Under suitable conditions *Juttadinteria* flowers open in the early afternoon (± 13h00-14h00) and close during the late afternoon (± 16h30- 17h00), *Dracophilus* flowers open in the mid to late afternoon (usually ± 17h00) and close during the night (±20h00-23h00), and *Namibia* flowers stay open permanently. In these, and other, species of mesembs flower opening occurs quite rapidly; Peter *et al* (2004) reported that in *Bergerathus* flower opening appeared to be related to temperature and relative humidity on any given day, but they indicate that the mechanism controlling flower opening overall has not yet been satisfactorily established.

7.5.1 Calyx

As is the case for all of the Mesembryanthemaceae (Hartmann 1991), the basal part of the calyx is fused with the gynoecium, forming an obconical structure in *Dracophilus* and *Juttadinteria* and a bowl-like one in *Namibia*. Sepal number in the subtribe varies between four and five, or up to seven, depending upon interpretation. According to almost all available literature (e.g. Walgate 1939, Herre 1971, Smith *et al* 1998, Leistner 2000) *Juttadinteria* has four sepals and the other two genera five. This, however, is not strictly the case. Certainly *Juttadinteria* and *Dracophilus* have four and five sepals respectively. Hartmann (2001) noted that in *Namibia* sepal number may be 4 to 6. *Namibia ponderosa* very often clearly has four sepals. This accounts for its description as a *Juttadinteria* by Louisa Bolus (1928). *Namibia cinerea* mostly has five sepals, but it was found that both species may appear to have up to six or (occasionally) seven, because their smaller sepals have a tendency to divide longitudinally (partially or fully to the base), with narrow segments or 'sepals' being formed. If each of these is counted as a sepal, then the number of sepals increases. If not, then even *N. cinerea* must perforce be counted as sometimes having only four sepals, because very often one of its five sepals is very small in comparison to the others. For the purposes of this study each section was counted as one sepal, and thus *Namibia* is regarded as having four to seven sepals.

In all members of the subtribe the outer and inner sepals within each flower are of unequal dimensions and more-or-less dissimilar appearance. Those in *Dracophilus* are less dissimilar and less fleshy than those in the other two genera. Sepals may be very fleshy or only slightly so, may or may not be keeled, may bear subapical, marginal or keel teeth in *Juttadinteria*, or subapical hoods or knobs in all three genera, or have membranous margins with conspicuous tannin cells. Outer sepals are always keeled in *Juttadinteria* (Figure 4.8 D) and *Namibia* but never in *Dracophilus*.

Sepal characters are taxonomically useful at genus level.

7.5.2 Petaloid staminodes ('petals')

In the Mesembryanthemaceae the petaloid parts, which form the visual attraction of the flower, are of androecial origin (e.g. Ihlenfeldt 1960), thus they are petaloid staminodes. For ease of reference they are here called 'petals'. In the subtribe they are flat, linear-acute to linear-ligulate, gradually widening from base to just below the tip, and one to three seriate. In *Dracophilus* and *Juttadinteria* they are two to three seriate, and may scarcely exceed or be distinctly longer than the sepals, whereas in *Namibia* they are one seriate and greatly exceed the sepals in length. The number of 'petals' per flower varies from 38 to 92, with the lowest numbers recorded in *Juttadinteria* and the highest in *Namibia*. Figure 7.7 shows the variation within and between genera. The apices are acute to rounded or emarginate, and the petals reflexed. In *Dracophilus* the tips are often also recurved (Figure 5.7 A). This is particularly noticeable in *D. dealbatus*. 'Petal' texture is reasonably robust, although the relatively great length of *Namibia* petals still makes them quite lax and fragile. 'Petal' length varies between 7 and 39 mm. Table 7.1 shows the ranges within genera. The longest 'petals' by far are found in *Namibia*. 'Petal' characters are not taxonomically useful at genus level.

Genus	Petal number range	Petal length range
Namibia	51 – 92	13 – 39
Juttadinteria	38 – 72	7 – 30
Dracophilus	41 – 72	7 – 17

Table 7.1: Range in 'petal' number and 'petal' length between genera in the Dracophilinae

7.5.3 Androecium

All species under consideration have numerous stamens collected into a cone that conceals the stigmata at the onset of anthesis (Figure 7.7). Petals are distinct from the stamens, and staminodes are absent (Androecium Type 3 after Ihlenfeldt 1960). The stamens ripen centripetally, becoming more erect and eventually forming a cylinder during the female phase of anthesis. In all three genera the inner series are shorter than the outer ones, but this is far more pronounced in *Juttadinteria* and *Namibia* than in *Dracophilus*. Filaments are white, with translucent papillae near the base. Most ruschioid genera have papillate filaments (Hartmann 1991), although position and density of papillae is variable. Papillate filaments are regarded as an advanced state by Bittrich and Struck (1989).

Figure 7.7: *Juttadinteria deserticola,* central cone flower with stamens concealing the stigmata in early anthesis (*C. Mannheimer CM 2216*).

The anthers are are yellow, elliptic to linear, and vary in length from 0.5 to 1.7 mm. Their attachment is dorsifixed and versatile. They exhibit longitudinal-extrorse dehiscence. All members of the Dracophilinae have similar verrucose tapetal orbicules on their inner anther walls (Figure 7.8). According to Retief *et al* (2001) the function of these structures is still obscure although they might provide a 'non-wettable surface from which pollen may easily detach'.

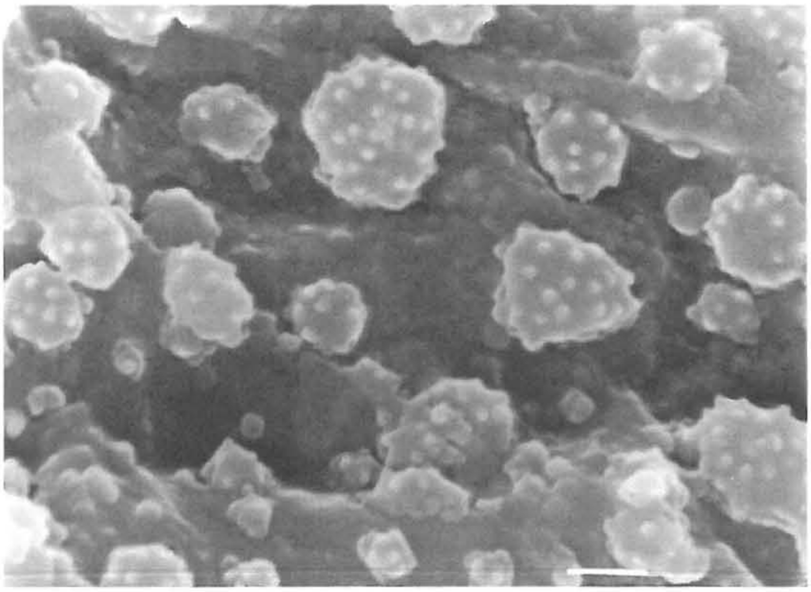


Figure 7.8: *Juttadinteria simpsonii.* Inner surface of anther showing verrucose tapetal orbicules x 10000 (*C. Mannheimer CM 2356*). Scale bar 1 μm.

Pollen is profuse, bright golden-yellow or yolk-yellow when young, fading to pale yellow with age. Pollen length in the Dracophilinae is between 17 and 26 μm, and width between 13 and 22 μm. The P/E ratio varies from 0.8 to 1.5. Pollen dimensions are most variable in *Juttadinteria*, possibly because it is the largest genus. The grains are longiaxial, tricolpate and tectate-perforate to semitectate-reticulate (in rare individual instances intectate). Generally the tectum has fewer luminae at the pole and around the colpi. In these areas it may be almost tectate. The tectum has raised ornamentation in the shape of spinulae. Baculae are sometimes visible on the exine. This may be more common than was observed, but is not always readily visible due to more tectate states in some genera.

According to Hartmann (1981) most pollen grains in her Mesembryanthema group (= Mesembryanthemoideae and Ruschioideae) are tricolpate, spinulose and punctate to micropunctate. Given that the ornamentation on the pollen of the Dracophilinae could be termed either spinulose or verrucose, their pollen agrees well with this general pattern. The reticulate condition found in a few of the species is regarded as a rare type (Hartmann 1981). Reticulate and reticulate-spinulate conditions are regarded as advanced in angiosperms generally (Walker 1974and in the Mesembryanthema in particular (Hartmann 1991), implying that within the Dracophilinae *Namibia* might be the most derived group. However whether any given state for a character is considered primitive or derived is contentious because it may have arisen homoplasiously (Judd *et al.* 1999). Dupont (1977) maintains that infrageneric variation is great, but this is not the case in the Dracophilinae. Pollen characters are not useful at genus level.

7.5.4 Stigmata

Stigmata vary in number between 6 and 25. They are linear-subulate, with dense stigmatic papillae on the inner surface, and are often shortly fused at the base. When young they are erect, loosely coherent, and usually reach a height below or equivalent to the outer stamen series during the early (male) phase of anthesis. As anthesis progresses into the female phase they elongate, extending beyond the stamens and recurving to expose the stigmatic papillae on their inner surfaces (Figure 4.11).

7.5.5 Ovary

As in all Ruschioids, the ovary in the Dracophilinae is inferior. The upper surface of the ovary is flat or slightly concave and raised in the centre at the base of the stigmata in *Dracophilus* and *Juttadinteria*. In *Namibia* it is concave at first, becoming domed as it ripens. There are distinct lines radiating from the centre where the valve margins will develop in the mature fruit. Locules are deeper in relation to width in *Juttadinteria* than in *Dracophilus* and *Namibia*. Placentation is parietal in *Dracophilus* and *Juttadinteria*, but basi-parietal in *Namibia*. Ovary characters are of limited taxonomic use at genus level.

7.5.6 Floral nectary

Nectaries in the subtribe Dracophilinae are lophomorphic holonectaries. They are pale green and low-crenulate in *Namibia,* medium green to very dark green and moderately crenulate in *Juttadinteria* and bright orange to brown with pronounced crenulation in *Dracophilus*. Nectar production is never profuse, but is far more plentiful in *Dracophilus* than in *Juttadinteria* and *Namibia.*

7.6 Fruit

Fruits in the family Mesembryanthemaceae are multilocular hydrochastic capsules. They exhibit a highly specialised structure that is related to their seed dispersal mechanisms, i.e. moisture or rain-mediated release or expulsion.

Capsule shape in lateral view is obconical in *Dracophilus* and *Juttadinteria*, with that of the latter genus generally far deeper than the former. In *Namibia* the fruit is bowl-shaped and has a domed lid.

Expanding keels in the subtribe are quite robust and parallel, diverging distally and sometimes also at the fulcrum provided by the edge of the receptacle when the capsule opens. Covering membranes are absent or extremely vestigial in a number of taxa, notably both species of *Namibia*, or when present may be crescent shaped to narrowly deltoidal. Their texture is thin and no additional closing hooks or ledges are present. Closing bodies are completely absent in all members of the subtribe.

7.7 Seed

Two general seed shapes are found in the Dracophilinae. In *Namibia* the seeds are ovate to pear-shaped, while in the other two genera they are comma-shaped. Surface cells have isodiametric and (often) undulate anticlinal walls. The periclinal walls are raised, giving the surface a finely tuberculate appearance. Seed size varies from 0.4 to 1.2 mm. In colour the seed varies from light brown to light apricot, gold-brown or dark brown. It appears to darken with age.

7.8 Taxonomically useful characters at genus level

The characters most useful for distinguishing the three genera of the Dracophilinae, particularly in the field, are leaf morphology , leaf epidermal characters, presence or absence of flower bracts, nectary colour, flower opening time and capsule characters. A key to the genera is provided below.

Key to genera

1a Leaf epidermis velvety..2
b Leaf epidermis smooth or rough...3
2a Most leaves with margins entire.. *Namibia*
b Most leaf margins with distinct knobs or teeth.. *J. simpsonii*
3a Sepals five; flowers bracteolate, usually pink (rarely white) and opening mid to late afternoon, closing during the night; nectary orange to brown.. *Dracophilus*
b Sepals four; flowers ebracteolate, always white, opening early afternoon, closing before dusk; nectary green.. *Juttadinteria*

CHAPTER 8: DISTRIBUTION, HABITAT, ECOLOGY AND CONSERVATION STATUS.

8.1 DISTRIBUTION

The subtribe Dracophilinae is restricted to the low rainfall zone (< 200 mm p.a.) of the core region of the Mesembryanthema described by Hartmann 1981, within the 14-genera isocline. Its members occur in the southern Namib desert roughly between 26° and 28°45' south and 15° to 17° east (Figure 8.1). This area falls into the Gariep Centre, one of the five centres of diversity designated by Hartmann (1991) for the Mesembryanthemaceae. Most of the species are strict Namibian endemics, with the distribution area of just three species (*J. deserticola, J. albata* and *D. dealbatus*) extending to just south of the Orange River. The most northerly records are of *J. deserticola* from the vicinity of Spencer Bay.

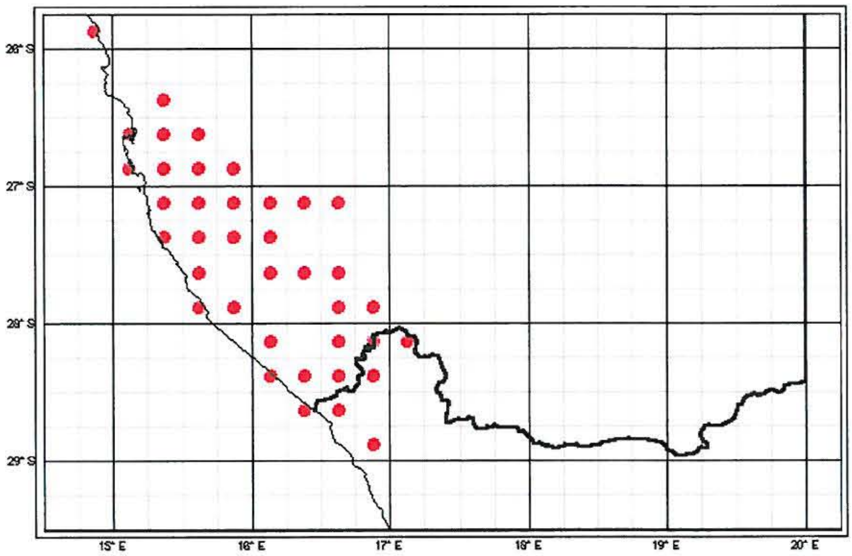


Figure 8.1: Distribution of the subtribe Dracophilinae.

The area of occurrence forms the northern extent of the Succulent Karoo Biome (Rutherford 1997), an area recognised as a biodiversity hotspot of global significance (Myers *et al.* 2000). Van Wyk and Smith (2001) provide a comprehensive overview of the phytogeographical significance of the area. In the Namibian context the area is home to 25 per cent of the vascular plant flora (Burke & Mannheimer 2004) and is further considered to be a centre of endemism (Maggs *et al* 1998).

Juttadinteria is the most widely distributed of the three genera within the distribution area (Figure 4.21) with *J. deserticola* having the widest distribution within its genus and the subtribe. The other *Juttadinteria* species have far smaller ranges, probably due to far more restricted areas of suitable habitat. *Dracophilus dealbatus* is more widely distributed than all the other species with the exception of *J. deserticola*. As a result of this *Dracophilus* is quite a widespread genus in the southern Namib despite the fact that *D. delaetianus* occurs in only very few isolated populations. *Namibia* has the most restricted spread, known area of occurrence being only four quarter-degree squares south and east of Lüderitz and even within that area a only a few discrete populations have been recorded. Reasons for such limited distribution areas have been discussed in chapter 6.

8.2 HABITAT

As previously mentioned, *Namibia* prefers rocky slopes of koppies and mountains or rocky ridges. *Namibia cinerea* usually occurs on limestone, dolomitic or quarzitic slopes (Figure 8.2), while *N. ponderosa* is found on granitic-gneiss or granitic substrates (Figure 8.3). They are often associated with species of *Juttadinteria*. In the case of *N. cinerea* the association is with *J. deserticola* while in *N. ponderosa* it is with *J. simpsonii*. Other species associated with *N. cinerea* include *Antimima dolomitica* (Dinter) H.E.K. Hartmann, *Euphorbia hamata* (Haw.) Sweet, *E.decussata* E. Mey. ex Boiss., *Pelargonium cortusifolium* L'Hér. and *P. crassicaule* L'Hér.. *Namibia ponderosa* is found with *Commiphora capensis* (Sond.) Engl., *Rhus populifolia* E. Mey. ex Sond., *Aloe dichotoma* Masson, *P. cortusifolium* and *Hermannia pfeilii* K. Schum.. It occurs in the open, but quite often establishes below and is 'nursed' by larger plants in the association, a phenomenon not seen in *N. cinerea* but common in the southern Namib.

Figure 8.2: Dolomite slope at Grillental. Typical habitat for *Namibia cinerea*.

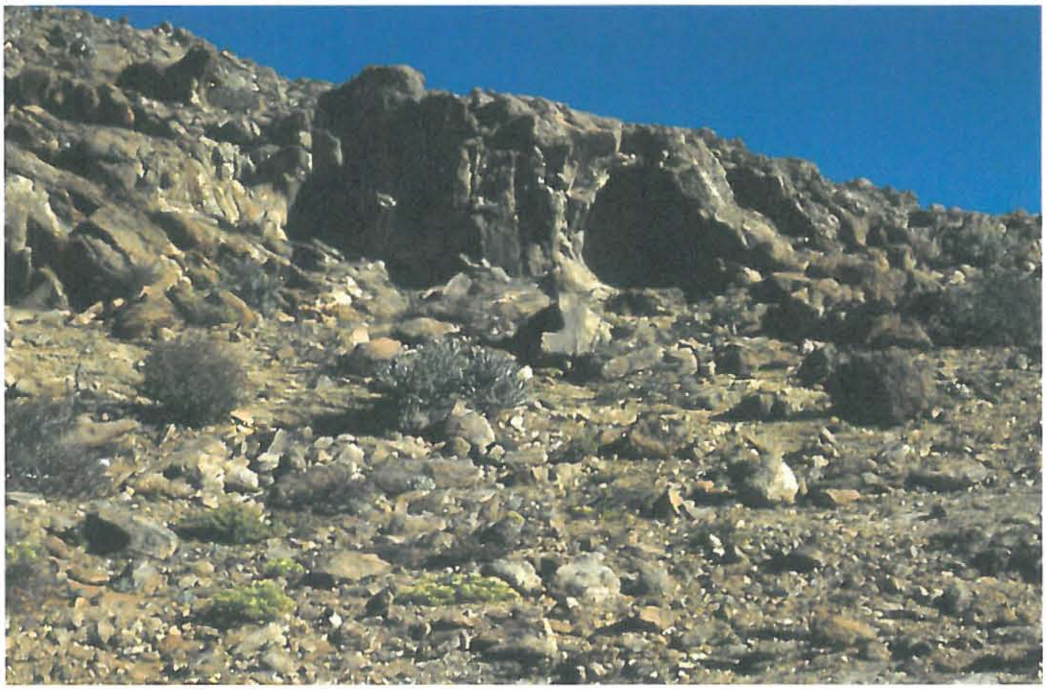


Figure 8.3: Granitic-gneiss slope in the Kovis Mountains. Typical habitat for *Namibia ponderosa.*

Both species of *Dracophilus* prefer red sandy plains or gentle slopes with calcrete and/or quarz inclusions (Figure 8.4) or gravel plains, and are rarely found anywhere else. *Dracophilus dealbatus* is found associated with *Psammphora modesta* (Dinter & A. Berger) Dinter & Schwantes, *P. nissenii* (Dinter) Dinter & Schwantes, *J. deserticola, J. attenuata and J. albata*, *Ruschia* spp., *Aridiaria sp.*, *Pteronia pomonae* Merxm. and (sometimes) *Cheiridopsis robusta* Haw.) N.E. Br.. In contrast, *D. delaetianus* associates with *Brownanthus ciliatus* (Aiton) Schwantes subsp. *schenckii* (Schinz) Ihlenf. & Bittrich, *Euphorbia namibensis* Marloth, *Zygophyllum longicapsulare* Schinz and *Salsola* sp.in the east of its distribution area while in the more western populations it is found in stands where few other perennials occur. Both species of *Dracophilus* may be found in localised stands, but *D. dealbatus* also occurs in large, loosely scattered populations.

Figure 8.4: Sandy plain, the preferred habitat for both species of *Dracophilus*. *Juttadinteria attenuata* also occurs on these plains.

Juttadinteria albata is found in the south of the distribution area of the subtribe. It prefers rocky slopes, including the diamondiferous gravel terraces of the Orange (Gariep) River. Associated species include *D. dealbatus*, *Phyllobolus oculatus* (N.E. Br.) Gerbaulet, *B. marlothii*, *P. modesta* and *E. chersina*. *Juttadinteria attenuata* is found on rocky slopes associated with *P. cortusifolium* or on sandy plains with calcrete inclusions, where it occurs in associations with *D. dealbatus*, *Drosanthemum curtophyllum* L. Bolus, *Eberlanzia sedoides* (Dinter & A. Berger) Schwantes and others. *Juttadinteria ausensis* prefers sandy-calcrete plains with a high calcrete gravel content,as well as quarz inclusions, where it is found in association with *Ruschia odontocalyx* (Schltr. & Diels) Schwantes, *P. modesta*, *P. pomonae*, *Salsola* sp. and *Zygophyllum* spp. As previously mentioned, *J. simpsonii* is often found in association with *N. ponderosa* on footslopes of koppies and mountains but also occurs on gentle coarse sandy slopes in localised populations interspersed with *E. gummifera*. *Juttadinteria deserticola* occurs on gravelly-sandy plains and flats (Figure 8.5) as well as rocky slopes. It is associated with a variety of species that includes *E. sedoides*, *P. modesta*, *N. cinerea*, *D. dealbatus*, *A. dolomitica*, *P. cortusifolium*, *P. crassicaule*, *Othonna furcata* (Lindl.) Druce, *E. hamata* and many others. The species composition depends upon the location of the site and its proximity to the ocean. The leaves of *J. deserticola* often appear black, or fungus-infected due to a lichen that grows on them.

Figure 8.5: *Juttadinteria deserticola* on a gravelly flat near the ocean (Lüderitz peninsula)

8.3 CLIMATE

Average rainfall in the distribution area of the subtribe is even lower than that of the low rainfall zone mentioned earlier. Here annual precipitation from rain very seldom exceeds 100 mm p.a., and is extremely variable. Within the area annual means range from approximately 20 mm in coastal areas to 60 mm in the eastern reaches. Much of this falls as winter rain, although the area may be regarded as a transitional zone between winter and summer rainfall regimes, with a winter → summer trend from the south east to the north west. The moisture deficit resulting from such meagre rainfall is ameliorated by precipitation from condensing, advective fog, an important and reliable source of moisture for biota in the area (Louw & Seely 1982), particularly in summer when the highest number of fog days occur (Olivier 1995). Fog forms as air is cooled over the cold Benguela current of the Atlantic ocean on the western border and is carried inland by wind.

Frequent moderately strong winds are characteristic of narrow coastal deserts (Louw & Seely 1982) and this is the case in the Namib where persistent winds, particularly in the coastal zones, are an important climatic factor. Pomona, situated in the north-western section of the southern Namib, has the highest wind velocities in southern Africa with recorded wind speeds of up to 80 km/h (Pallet (Ed.) 1995). The most prevalent winds are cool, moist, southerly to south-westerly winds that blow off the cold ocean surface as a result of intense insolation inland. However in winter strong easterly winds generated by high pressures over the southern African interior occasionally bring warm, dusty and dessicating conditions to the southern Namib. The prevailing cool winds moderate temperatures, providing a convective cooling effect, and also carry fog that acts as an important source of additional moisture, but they also have a considerable sand-blasting action that offers an additional challenge to plants in this area.

Although extremes of temperature do occur in the area, with maxima sometimes exceeding 35°C and minima sometimes below 0°C, temperatures in general are mild with an overall mean of around 18 to 22°C due to the moderating influence of the cold waters of the Atlantic Ocean to the west (Pallet (Ed.) 1995). Nevertheless, due to low water vapour content of the air and a lack of cloud cover desert organisms are often exposed to intense loads of both direct and indirect solar radiation (Louw & Seely 1982).

8.4 LEAF ADAPTATIONS

The most important challenges faced by plants in the southern Namib are moisture deficit, high solar radiation and sand abrasion. Loss of water in plants is due to transpiration, including moisture lost through the stomata during photosynthesis as well as that lost through the cuticle. This loss is influenced by temperature, radiation, vapour pressure gradients and wind speed which interact to determine transpiration rates and adaptive responses of the plant to the climatic conditions under which it lives (Louw & Seely 1982). As the epidermis is the functional border between the plant and its environment, through which all interactions take place, one may look to this organ for adaptive structures for survival under adverse conditions, in particular because the Dracophilinae do not have roots that are elaborately adapted for water storage or acquisition.

It is clear that the xeromorphic adaptations of both the leaf as a whole and the leaf epidermis in the subtribe Dracophilinae play an important role in their ability to survive and reproduce. The thick epicuticular wax layers, some with additional sculpturing, may have various functions:

- Reduction of water loss across the leaf cuticle. Water loss due to cuticular transpiration is largely controlled by the thickness of the epicuticular wax layer and the cutin in the cuticle (Louw & Seely 1982). The increased thickness of the cuticle due to the additional cuticular layer below may thus also restrict cuticular transpiration.
- Reduction of contamination due to increased water repellency. Adhesion of dust particles and pathogens is reduced in cell surfaces with secondary or tertiary sculptures, and contaminants may be washed off by water (Barthlott 1981).
- Temperature control (and thus reduced heat stress) due to increased reflection of incoming radiation as recorded by Schultze *et al.* (1980) for *Welwitschia mirabilis*. Reflection may be as high as 30 – 50% (Eller 1979).

- Temperature control due to sculpturing increasing turbulence at the leaf surface, thus promoting heat exchange between the leaf surface and the surrounding air (Barthlott 1981).
- Protection of the leaf surface from sand abrasion.

According to Louw and Seely (1982) the nature of the outer covering of plants can influence the reflectance, absorbance and transmittance of solar radiation and thus solar load. In the xeromorphic type of epidermis in the Mesembryanthemaceae the rate of reflection is high and the rate of transmission relatively low, possibly due to the thick layer of calcium oxalate sand in the outer cell wall below the cuticular layer (Ihlenfeldt 1983). As noted previously, reflectance may also be increased by the epicuticular wax layer, which is thick in the Dracophilinae. Reduction of surface area exposed to radiation is also reduced in the subtribe by the hypersucculent nature of the leaves that results in a small surface area to volume ratio. As mentioned earlier, orientation of the leaves is affected by water availability with increased availability causing swelling of the basal pustule and resulting in the leaves being held at a greater angle to the axis and thus more surface being exposed to direct solar radiation than when conditions are poor. Obviously, as in all leaf succulents, the water-storage capacity of these very succulent leaves is in itself a major adaptation to survival in an arid environment.

As mentioned previously, in all the species of the Dracophilinae the smallest epidermal cells are peristomatal cells with papillae that surround and often overarch the guard cells of the stomata (Figure 4.5) to form the 'hidden' stomatal type as described by Ihlenfeldt and Hartmann (1982). The stomata are thus not sunken , but this configuration of cells results in the formation of what might loosely be described as an 'antestomatal chamber'. Lyshede (1979) suggests that such chambers retain moist air, thus decreasing residual stomatal transpiration by lengthening the water vapour diffusion pathway. It may be possible that water stress results in partial collapse of these papillae, which would further enclose such a chamber.

Temperature control due to sculpturing increasing turbulence at the leaf surface as suggested by Barthlott 1981 for secondary and tertiary sculptures may also be a function of the papillae seen in many members of this subtribe.

Wide-band tracheids are found in leaves of all members of the Dracophilinae. They have greatly thickened secondary walls that extend into the cell lumen (Figure 7.4 D) and it has been suggested that they prevent cell collapse under water stress (Landrum 2001). The fact that they show typical lignin staining when stained with safranin and fast green suggests that they might possibly provide some strengthening or support to these very heavy succulent leaves. Klak *et al* (2003b) are of the opinion that they represent an important innovation that facilitated the major radiation of the core Ruschioideae, allowing them to occupy arid habitats in the Succulent Karoo where today they dominate in terms of numbers of species as well as coverage density. Plowes (2003) suggests that speciation in xerophytic plants is encouraged because they occupy marginal habitats that are easily affected by small climatic oscillations, leaving relict pockets of survivors.

It is probable that, in common with other members of the Mesembryanthemaceae, the members of the Dracophilinae are able to take up water directly from the atmosphere when conditions are favourable and there is a positive vapour gradient from outside to inside the leaf. This requirement is usually met in the southern Namib when fog is present at night or in the early morning. While its presence has not yet been demonstrated in the Dracophilinae, CAM is thought to be a widespread phenomenon in the Mesembryanthemaceae (Von Willert *et al.* 1977).

8.5 FLOWER ADAPTATIONS AND POLLINATORS

Flowering in the species of these genera is synchronised within populations, a phenomenon that increases pollinator attraction and also promotes gene exchange within populations (Ihlenfeldt 1994). The main flowering period is from July to October (winter to spring), peaking in September when temperatures begin to rise and thus more pollinator activity can be expected. Rain is probably important to induce flowering because in poor rainy seasons few flowers are produced.

All three genera in the Dracophilinae have protandrous central cone flowers with numerous stamens that form a dense brush and produce prolific pollen that must provide a substantial reward for pollinators. None of the species produce profuse nectar, and nectar production was not measured. However *Dracophilus*, which opens late afternoon into the night appears to produce the most nectar of the three genera while *Namibia*, which has flowers that remain permanently open appears to produce the least. *Juttadinteria* flowers are open only from just after midday until late afternoon, closing as soon as the light begins to fade. Although *J. deserticola* and *D. dealbatus* have been reported to have sweetly scented flowers (Dinter 1923, Bolus 1927 respectively) this was not found to be so during this study.

The fact that flowers in these three genera open and close at different times of the day or night and produce varying but very limited amounts of nectar but prolific pollen suggests that not only should their suites of pollinators should be different, but one might expect that pollen would provide the main reward for non-destructive visitors. *Namibia* might further be expected to have the widest range of visitors, given that it is open day and night.

Despite repeated efforts to collect pollinators no serious contenders were ever found. This may in part be ascribed to the restricted time available in the study area and the almost invariably cold and windy weather. The flowers were always occupied by numerous thrips and were occasionally visited by nonpilose monkey beetles (Coleoptera: Scarabaeidae) or buprestid beetles (Buprestidae) but these are usually destructive visitors or thieves rather than pollinators (S. Gess, pers. comm.). No masarine (pollen wasps) or other wasps, or bees, (i.e. Hymenoptera) other than small black ants were seen visiting the flowers. Nocturnal observations were difficult because light in itself attracts insects but random observations of *D. dealbatus* revealed only occasional small crickets that were probably living in the plants rather than pollinating them and a few small moths.

Although abundant pollen as an adaptation for wind pollination has been mooted for the Mesembryanthemaceae by Bittrich (1987), the consensus of opinion is that this requires further investigation (Ihlenfeldt 1994, Chesselet *et al* 2001), and recently Peter *et al* (2004) refuted it in *Bergeranthus multiceps*. Specific opening and closing time, inhibition of flower opening by cold or wet weather, supply of pollen and nectar and synchronized flowering and bright, shiny petals all point to insect pollination, and this has been accepted by most workers (e.g. Smith *et al* 1998, Groen & van der Maesen 1999, Chesselet *et al* 2002, Peter *et al* 2004)as being the case as a rule for mesembs.

Although Ihlenfeldt (1994) maintains that a wide range of pollinators are admitted by the Mesembryanthemaceae, detailed data on these pollinators are sparse (Hartmann 1991), although recorded vectors include bees, wasps, butterflies and moths (Chesselet *et al* 2002). Gess & Gess (2004a) recorded 54 species of the Masarinae (pollen wasps) visiting mesembs in southern Africa, of which 30 were found to exhibit a specialization for a plant taxon. More recent work has added to this number (Gess & Gess, pers. comm.). They also recorded 76 species of non-masarine wasps and 98 species of non- *Apis* bees on Aizoaceae, but found that they exhibited less plant taxon specialization than pollen wasps (Gess & Gess 2004b). Peter *et al* (2004) found that a single bee species, *Allodapula variegata* was the most important pollinator for *Bergerathus multiceps* although eight other species of Hymenoptera and two species of Diptera (flies) also had significant pollen loads. Other visitors included chrysomelid, monkey and blister beetles and a number of flies. These studies suggest that the Hymenoptera are prime candidates for pollination of the Dracophilinae, with the pollen wasps as the most obvious. The arid and semi-arid areas of southern Africa host the highest diversity of pollen wasps in the world (Gess & Gess 2004c). Many of these wasps require water for nest-building, restricting their distribution in an arid zone like the Namib Desert, but a number of species have adapted to use nectar instead and one genus, *Quartinia*, has retained the ability to spin silk for nest construction as adults. In fact, *Quartinia* is highly desert adapted in a number of other ways too, including their small size, which allows them to survive and reproduce with minimal resources and to nest in small pockets of stable sand such as that trapped in snail shells (empty shells of the desert snail genus *Trigonephrus* are common in sandy areas of the southern Namib), and they are able to fly and forage at high and low temperatures, even in gale force winds. Nevertheless, to date no pollen wasps (or other obvious pollinators) have been found on the Dracophilinae, even with some assistance from the Gesses themselves, and thus pollen vectors in the subtribe remain uncertain.

8.6 FRUIT ADAPTATIONS AND SEED DISPERSAL

Seed dispersal in the Mesembryanthemaceae is mediated by water (hydrochory), often rain (ombrohydrochory). Highly specialized mechanisms in the fruit capsules restrict seed release, spreading it over time and restricting it to favourable moisture periods. The fruit capsules have hygroscopic structures such as expanding sheets and keels that take up water, swell, and open the capsule when conditions are favourable for germination and establishment of seedlings, as well as further specialized structures, such as closing membranes, closing bodies (actually placental tubercles) and closing ledges, that reduce risk by spreading seed release over time and restrict seed dispersal to only the most favourable conditions. These capsule characters vary greatly between taxa, and Hartmann (1991) has outlined four different mechanisms for hydrochoric seed dispersal, of which two appear to be present in the Dracophilinae.

The combination of capsule features seen in *Namibia*, i.e. no or vestigial covering membranes, lack of a closing body, bowl-shaped base and complete reflexing of the valves when wet results in seeds being easily dispersed by a wash-out mechanism. They are exposed once the capsule opens fully, and dispersed by water overflowing the edges. Although the valve wings are not particularly broad, as is usually seen in species with a wash-out dispersal mechanism (Hartmann 1988), the multilocularity and total valve reflexion of this species still results in an arrangement that promotes seed dispersal by this mechanism. Due to the fact that these plants occur mainly on slopes, it may be assumed that dispersal over several metres might be possible, depending on the amount of moisture available. The area in which the plants occur has an average rainfall of <100 mm p.a., but lies within a zone where fog provides a consistent and significant source of moisture (Olivier 1995, Mendelsohn et al 2002). It is known that ambient moisture is sufficient to open the capsules of mesembs (Hartmann, 1991), and during a heavy fog the moisture collecting on the plants, which often stand well above the substrate and are frequently presented at an angle to the horizontal, might well be sufficient to wash out seeds, thus reducing the need for ombrohydrochory (dispersal by rainwater) in an area with extremely low rainfall. This is, however, speculative. The conservative advantage offered by hydrochory (that of spreading the dispersal of seed over time and thus reducing the risk of releasing all the seeds at once, another being release of the seeds only when sufficient moisture is available) is probably maintained in *Namibia* by the fact that, as a result of multilocularity, the locules are deep in comparison to their width, and thus some seeds may be retained in the narrow base of the locules over a longer period. In contrast to species in the other two genera of the subtribe, placentation is basi-parietal rather than parietal, which, due to the seeds being deep in the locules, may also assist in retaining seed over longer periods.

The combination of capsule features seen in *Dracophilus*, particularly the well-developed closing membranes, results in most, of the seeds being dispersed by the spring-board mechanism, in which seeds are ejected by pressure of raindrops hitting the covering membranes once the seed cup has been filled with water. It has been suggested by Hartmann (1988) that the sagging of the covering membranes into the locules once most of the seeds have gone might result in the last few being dispersed by the wash-out mechanism as described for *Namibia.*

Most *Juttadinteria* species have vestigial or poorly developed covering membranes and thus may generally be expected to exhibit a similar seed dispsersal mechanism to *Namibia.* In *J. attenuata* and (particularly) *J. ausensis* these membranes are sometimes slightly better developed, and here there may be a slight tendency towards the spring-board mechanism as found in *Dracophilus.*

Seed retention is an important adaptation in arid area with erratic and unpredictable rainfall. It not only promotes germination when conditions are favourable and spreads the risk of failure over time, but also protects the seeds from deterioration and predation. Some mesemb seed has been known to remain viable for several decades (Hartmann 1991). Capsule structure in the Dracophilinae is simple and includes few pronounced mechanisms to promote seed retention such as firm or well-developed closing membranes or closing bodies. This may be ascribed to the low rainfall experienced in their area of occurrence as well as the type of rain received. Rain in the area generally falls in the form of gentle showers or drizzle and fog (as previously mentioned) is an important moisture source that may play a part in seed dispersal of some species. If the capsules of these species needed hard or heavy rain to ensure their release then seed would very seldom escape the capsule. The relative lack of impediments promotes release of at least some seed when moisture is available.

Neither fruits nor seeds in the Dracophilinae are adapted for long-range dispersal (telechory), and seedlings usually establish near the mother plant. This is thought to ensure that the seeds remain within the (often restricted) area ecologically suitable for their survival (Ihlenfleldt 1994). It does, however, greatly restrict gene flow between populations. Ellner and Shmida (1981) suggest that in many desert plants mechanisms to ensure that seeds continue to occupy a favourable site in otherwise unsuitable territory represent atelechory rather than antitelechory, which involves adaptations that actually hinder dispersal.

8.7 PREDATION

Vegetative structures in the Dracophilinae do not appear to be subject to any meaningful predation by either vertebrate or invertebrate predators. Very rarely *Dracophilus* plants are uprooted, either deliberately or inadvertently, probably by gemsbok, but these are usually not consumed. Very little evidence of insect damage to the leaves was seen during the study period. This is probably due the large subepidermal tannin idioblasts that make the leaves bitter and unpalatable, because previous observations suggest that mesembs that lack tannin idioblasts in their leaves are eaten readily (Hartmann 1991) and that plant parts of otherwise tanniniferous plants plants that lack tannin cells (e.g. ovules and young seeds) are predated. This is a common occurrence in the Dracophilinae, particularly in *Juttadinteria* and *Namibia*, in which the stamens, 'petals', receptacle lid and ovules are often found to be chewed away (Figure 3.17 E). The only predators observed doing this were armoured crickets (Orthoptera: Hetrodinae). These insects appear to do considerable damage during poor rain years when few annuals are available, and may seriously compromise seed production in those years.

8.8 CONSERVATION STATUS

All the species in the subtribe Dracophilinae (i.e. *Juttadinteria* sensu Friedrich in Merxmüller 1967 – 1972) are protected in Namibia by means of the Nature Conservation Ordinance No. 4 of 1975, under which their collection for any purpose is controlled by a permit system. Threats in general include mining and prospecting, illegal collection and climate change, especially in the drier northern sections of their distribution area, which receives less winter rainfall than the rest of the area and very little summer rainfall.

Because population numbers and sizes are not known for certain the software "RAMAS" (Akçakaya & Ferson 2001), which allows for uncertainty in data, was used to assign provisional Namibian Red Data categories (IUCN 2001) to the various species. Several species had previously been assigned categories (Loots 2001) but these will change due to changes in taxonomy.

Three species are near- endemic and so responsibility for their well-being is shared between South Africa and Namibia. Of these two are the most common and widespread species in the subtribe, i.e. *D. dealbatus* and *J. deserticola*. These both fall into the Least Concern (LC) category. The third, *J. albata*, has been assessed as Vulnerable (VU). This is because its very restricted area of occurrence and habitat have already been impacted by mining activities and projections are that due to these impacts the population size will reduce by up to 30% or more in the next ten years or three generations. During the period of this study, assistance was offered to a company mining in this area, which undertook a detailed survey to establish the extent of threat to this species in order to try and mitigate damage and loss as far as possible (Burke 2004).

The other six species are strict Namibian endemics. *Dracophilus delaetianus* and *J. attenuata* are relatively widespread. They each occur in a number of populations, of which none appear to be declining or at risk due to mining, prospecting or illegal collecting at present and were both provisionally assigned Least Concern. However, the former is a very appealing species and will be particularly at risk from collectors when and if the proposed National Park is open to visitors.

Juttadinteria ausensis has a restricted extent of occurrence and is known only from a few locations, although one population is quite extensive. In addition to this numerous dead mature individuals were found during fieldwork. These factors resulted in it receiving a provisional Endangered (EN) listing. The apparent high mortality rate could be due to an extended drought that the area has been experiencing or to climate change. Either way this species should be field assessed as soon as possible to provide a baseline for future monitoring.

Juttadinteria simpsonii, N. cinerea and *N. ponderosa* were given provisional listings of Vulnerable (VU). In each case the area of occurrence is small, as is the area of occupancy, and they occur in only a few locations. In the case of *J. simpsonii* this is compounded by an apparent loss of mature individuals as well as illegal collecting in the Halenberg population, which is near the main road between Aus and Lüderitz. *Namibia cinerea* also appears to be suffering a considerable mortality in mature individuals, while the remaining number of *N. ponderosa* individuals is estimated to be not more than 2500 individuals. Their occurrence in the northern reaches of the winter rainfall area would make climate change towards a drier regime an additional threat. Detailed field assessments of these species should also be undertaken as soon as possible.

CONCLUSION

After five years of field, herbarium and laboratory work the taxonomy of the genera in the subtribe Dracophilinae can now considered to be "stable" apart from assessment of the possible subgroups in *J. deserticola* and *J. simpsonii.* Detailed descriptions and new keys should reduce confusion and contribute to a better understanding of this largely endemic and restricted group, allowing more accurate appraisal of their conservation status in order to ensure that suitable precautionary measures are in place when the proposed National Park is opened as well as during any commercial activities that may impact on their habitat or distribution area in future.

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ACKNOWLEDGEMENTS

SABONET for financial support.

Professor N.P. Barker, my promotor, for his patience, assistance and encouragement.

Curators of all the herbaria from which material was borrowed.

Staff and fellow postgraduate students at Rhodes University. In particular Jai Narsai, Dave Forsdyke, Syd Ramdhani, Seranne Howis, Robert McKenzie and Louise Donaldson.

Staff of the Microscopy and Graphics Departments at Rhodes University. In particular Shirley Pinchuck and Bronwen McLean.

My colleagues at the NBRI. In particular Gillian Maggs-Kölling for support and encouragement, Silke Rügheimer and Sonja Loots for field assistance and help with Red Data assessments, Esmerialda Klaassen and Sonja Schubert for database queries, Salomé Kruger and Kerta Kolberg for literature and John Irish for endless help with computer glitches.

My colleagues at other institutions whose help, suggestions and guidance were invaluable. In particular Elizabeth Retief, Priscilla Burgoyne, Dr. Otto Leistner and Gerrit Germishuizen of SANBI, Cornelia Klak of BOLUS and Dr. R. Brummitt of the Royal Botanic Gardens, Kew.

Dr. Peter Bruyns for the Latin diagnosis for *Namibia ponderosa* and Hugh Glen for checking translations of all other Latin diagnoses as well as taxonomic advice and assistance.

Trygve Cooper, chief warden of the Sperrgebiet National Park for field assistance as well as his energy, enthusiasm and willingness to search for obscure localities.

Antje Burke for field assistance and encouragement.

Fred and Sarah Gess of the Albany Museum for advice on pollinators, field assistance, photographs and hospitality in Grahamstown.

NAMDEB for assisting me to obtain access to the restricted areas, for permitting me to work in their mining license areas and for providing escorts several times.

The Ministry of Environment and Tourism of Namibia and Northern Cape Nature Conservation for permits.

My family, especially my husband John, who provided love and support as well as field assistance throughout.

Appendix 1: Data set for Namibia phenogram. CM = Coleen Mannheimer; cin = cinerea; pon = ponderosa.

	Specimen number	CM 872	CM 910	CM 911	CM 932	CM 1392	CM 1393	CM 1395	CM 1396
	Species abbreviations	cin	cin	cin	cin	cin	cin	cin	cin
	CHARACTER								
1.	Leaf apex: 0=blunt; 1=rounded/pointed	0	0	0	0	0	0	0	0
2.	Leaf colour: 0= grey brown/green; 1=light green or orange	0	0	0	0	0	0	0	0
3.	Leaf margins and/or tip: 0=flushed orange; 1=same as leaf	1	1	1	1	1	1	1	1
4.	Leaf papillae: 0=long/slender; 1=short/fat	0	0	0	0	0	0	0	0
5.	Receptacle cell papillae:0=domed;1=domed and nippled;2=tapered	999	999	999	999	2	2	999	999
6.	Sepal #: 0=4;1=5;2=4 or 5, occasionally 6 ; 3=6 or 7	999	999	999	999	2	1	2	999
7.	Flower: 0=white;1=pale pink; 2=pink to deep rose pink	999	999	999	999	0	0	0	999
8.	Flower: diameter (mm average)	999	999	999	999	40	999	37	999
9.	Flower max diameter	999	999	999	999	50	999	50	999
10.	Flower min diameter	999	999	999	999	30	999	29	999
11.	Petal # (average)	999	999	999	999	999	999	999	999
12.	Petal length (mm average)	999.0	999.0	999.0	999.0	18.4	999.0	17.0	999.0
13.	Petal max length	999.0	999.0	999.0	999.0	21.4	999.0	19.4	999.0
14.	Petal min length	999.0	999.0	999.0	999.0	14.9	999.0	15.2	999.0
15.	Petal width at widest point (mm average)	999.0	999.0	999.0	999.0	2.1	999.0	1.9	999.0
16.	Petal max width at widest point	999.0	999.0	999.0	999.0	2.2	999.0	2.1	999.0
17.	Petal min width at widest point	999.0	999.0	999.0	999.0	2.0	999.0	1.8	999.0
18.	Filaments: min length mm	999.0	999.0	999.0	999.0	7.5	2.0	5.3	999.0
19.	Filaments: max length mm	999.0	999.0	999.0	999.0	10.4	10.0	10.4	999.0
20.	Stigma # (average)	999	999	999	999	14	12	10	999
21.	Capsule average # locules	12	16	16	12	11	999	12	999
22.	Capsule min # locules	10	14	999	12	9	999	8	999
23.	Capsule max # locules	12	17	999	12	12	999	13	999
24.	Capsule average diameter (mm)	999.0	12.0	999.0	11.0	9.2	999.0	12.0	999.0
25.	Capsule max diameter (mm)	999.0	13.4	999.0	13.0	10.6	999.0	14.0	999.0
26.	Capsule min diameter	999.0	10.4	999.0	10.0	8.4	999.0	10.0	999.0
27.	Covering membranes: 0=absent; 1=vestigial	999	999	999	999	1	999	1	999
28.	Valve wings: 0=narrow-rectangular; 1=broad-rectangular; 2=crescent-shaped	999	999	999	999	0	999	0	999
29.	Valve wing width (average mm)	999.0	999.0	999.0	999.0	0.9	999.0	1.2	999.0

CM 1397	CM 1399	CM 1402	CM 1403	CM 1404	CM 1406	CM 1412	CM 1658	CM 1659	CM 1660	CM 1674	CM 1688	CM 1690	CM 1693	CM 1694	CM 1695	CM 1714	CM 1715
cin	**cin**	**cin**	**cin**	**cin**	**cin**	**cin**	**pon**	**pon**	**pon**	**pon**	**pon**	**pon**	**pon**	**pon**	**pon**	**pon**	**pon**
0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	999	1	1
0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	999	1	1
1	1	1	1	1	1	1	0	0	999	0	999	0	999	999	999	999	999
0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
2	999	999	999	2	999	999	0	2	2	999	999	999	2	2	999	0	0
999	1	1	1	999	999	999	0	0	0	0	1	0	0	1	0	0	0
999	0	0	0	999	999	0	1	0	999	1	999	2	2	2	999	0	2
999	43	999	40	999	999	999	999	999	999	999	999	999	35	999	37	30	999
999	45	999	45	999	999	999	999	999	999	999	999	999	40	999	40	999	999
999	40	999	35	999	999	999	999	999	999	999	999	999	30	999	33	999	999
999	999	999	999	999	999	999	999	999	999	999	999	999	58	57	999	51	999
999.0	16.1	999.0	19.1	999.0	999.0	999.0	18.0	999.0	999.0	999.0	999.0	18.0	21.4	29.0	26.0	19.0	999.0
999.0	18.2	999.0	19.6	999.0	999.0	999.0	21.2	999.0	999.0	999.0	999.0	999.0	27.0	39.0	999.0	999.0	999.0
999.0	14.6	999.0	18.4	999.0	999.0	999.0	15.7	999.0	999.0	999.0	999.0	999.0	15.7	24.5	999.0	999.0	999.0
999.0	1.9	999.0	1.5	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	1.3	1.3	999.0	2.0	999.0
999.0	2.1	999.0	1.6	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	1.6	1.3	999.0	999.0	999.0
999.0	1.5	999.0	1.3	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	1.1	1.2	999.0	999.0	999.0
999.0	7.0	3.0	3.7	999.0	999.0	999.0	6.2	999.0	999.0	999.0	999.0	999.0	4.5	6.0	999.0	999.0	999.0
999.0	7.1	14.0	8.5	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	8.0	10.0	999.0	999.0	999.0
999	11	16	999	999	999	999	12	12	12	999	999	999	11	999	999	999	999
999	13	16	14	13	15	999	12	11	13	10	11	10	11	999	999	9	999
999	9	15	14	12	15	999	11	999	11	9	999	8	11	999	999	8	999
999	13	17	14	14	16	999	13	999	15	12	999	12	12	999	999	10	999
999.0	12.0	11.2	14.0	15.0	13.0	999.0	8.3	11.0	13.0	8.0	9.0	10.0	9.0	999.0	999.0	10.0	999.0
999.0	12.0	12.0	13.0	999.0	14.0	999.0	11.0	999.0	13.0	8.3	10.0	10.0	9.0	999.0	999.0	11.0	999.0
999.0	9.0	10.4	999.0	999.0	11.0	999.0	7.0	999.0	11.0	7.9	8.0	9.0	11.0	999.0	999.0	9.0	999.0
999	1	1	999	0	999	999	999	999	999	1	0	0	0	999	999	0	999
999	2	0	999	0	999	999	999	999	999	1	1	1	1	999	999	0	999
999.0	0.8	0.9	999.0	0.7	999.0	999.0	999.0	999.0	999.0	1.9	2.2	1.8	1.1	999.0	999.0	1.5	999.0

CM 1716	CM 1717	CM 2269	CM 2271	Marloth 4680 (holo)	Schwantes 1756/27	Pillans 5951	Williamson 3039	Klak 613	Hardy & De Winter 1330	F. Eberlanz SUG3(1946)	M. Otzen s.n. 7/1939
pon	pon	pon	pon	cin	cin	pon	cin	cin	pon	pon	pon
1	1	1	0	0	999	999	0	0	1	1	1
1	1	1	1	0	999	999	0	999	999	0	999
999	999	0	0	1	999	999	999	999	999	999	999
1	1	1	1	0	999	999	999	999	999	999	999
0	0	1	999	999	999	999	999	999	999	999	999
0	0	0	0	1	1	999	999	999	999	999	2
999	999	999	999	0	999	999	999	999	999	999	999
999	999	999	999	20	999	999	999	999	999	999	999
999	999	999	999	999	999	999	999	999	999	999	999
999	999	999	999	999	999	999	999	999	999	999	999
999	999	999	999	999	999	999	999	999	999	999	999
999.0	999.0	999.0	999.0	11.0	18.0	999.0	999.0	999.0	999.0	20.0	18.0
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	22.0	19.0
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	18.0	17.0
999.0	999.0	999.0	999.0	999.0	0.8	999.0	2.0	999.0	999.0	1.6	1.5
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0
999.0	999.0	999.0	999.0	999.0	6.0	999.0	999.0	999.0	999.0	4.0	4.0
999.0	999.0	999.0	999.0	999.0	9.0	999.0	999.0	999.0	999.0	8.0	8.0
999	999	999	999	999	16	999	999	999	13	12	999
10	12	12	12	999	999	999	999	999	999	999	999
999	11	999	11	999	999	999	999	999	999	999	999
999	12	999	12	999	999	999	999	999	999	999	999
11.0	9.0	11.2	9.9	8.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0
999.0	10.0	11.4	10.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0
999.0	9.0	10.9	9.8	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0
0	0	0	0	999	999	999	999	999	999	999	999
1	0	1	1	999	999	999	999	999	999	999	999
1.6	0.8	1.0	0.6	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0

Hartmann, Dehn & Jűrgens 26058	Hartmann & Ihlenfeldt 135	CM 2354	CM 2355	CM 2358	CM 2359	CM 2360	CM 2367	CM 2372	CM 2373	CM 2374	CM 2375	CM 2380
pon	pon	pon	pon	pon	pon	pon	pon	cin	cin	cin	cin	pon
0	0	1	1	1	1	1	999	0	0	0	0	0
999	999	1	1	1	1	1	999	0	0	0	0	1
999	999	0	0	0	0	0	999	1	1	1	1	0
1	1	1	1	1	1	1	1	0	0	0	0	1
999	2	2	2	2	2	2	999	2	2	2	2	2
999	999	0	0	0	0	0	999	1	1	1	1	0
999	999	2	2	2	1	2	999	0	0	0	0	2
999	999	70	51	999	63	41	999	45.8	41.3	42.2	48	59
999	999	999	55	999	999	999	999	48.7	999	47.8	48.7	65
999	999	999	45	999	999	999	999	43.3	999	36.5	47.2	53
999	999	66	72	999	73	999	999	76	86	62	999	66
999.0	999.0	31.8	30.0	22.2	26.6	21.9	999.0	28.2	23.3	25.2	25.2	28.5
999.0	999.0	32.8	32.1	23.9	28.2	22.9	999.0	32.5	24.1	25.8	26.9	28.5
999.0	999.0	30.8	23.2	19.9	24.9	20.4	999.0	23.2	22.5	24.5	23.4	28.5
999.0	999.0	2.1	1.7	2.1	1.7	2.4	999.0	2.1	2.7	2.1	2.2	1.7
999.0	999.0	2.5	1.8	2.5	1.8	2.6	999.0	2.5	3.3	2.3	2.3	2.2
999.0	999.0	1.6	1.6	1.8	1.6	2.1	999.0	1.1	2.0	2.0	2.0	1.2
999.0	999.0	6.9	5.5	6.3	999.0	3.7	999.0	6.7	4.5	3.3	8.5	5.2
999.0	999.0	9.2	9.7	10.5	999.0	7.7	999.0	10.4	9.6	9.8	11.3	9.8
999	999	12	13	12	999	12	999	12	12	11	13	13
11	12	12	13	12	13	12	999	10	12	11	13	13
10	12	12	12	12	999	12	999	10	11	999	999	11
12	13	12	13	12	999	12	999	11	12	999	999	15
10.4	10.5	10.2	10.7	8.4	12.0	8.6	999.0	9.7	10.0	10.7	13.4	9.6
10.5	11.5	10.7	11.4	8.7	999.0	9.7	999.0	11.4	10.4	999.0	999.0	11.2
10.2	9.5	9.7	9.8	8.0	999.0	7.5	999.0	8.6	9.6	999.0	999.0	8.4
999	999	1	0	0	0	0	999	0	0	0	0	0
999	999	1	1	1	1	1	999	0	0	0	0	1
999.0	999.0	1.1	1.0	1.1	1.5	1.2	999.0	1.5	1.4	1.3	1.1	1.5

Appendix 2: Data set for Juttadinteria phenogram. CM = Coleen Mannheimer; alb = albata; att = attenuata; aus = ausensis; des = deserticola; kov = kovisimontana; sim = simpsonii; sua = suavissima.

	Specimen number	CM 913	CM 926	CM 931	CM 957A	CM 1400	CM 1608	CM 1627
	Species abbreviations	des	des	des	des	des	att	att
	CHARACTER							
1.	Habit: 0=tuft;1=erect shrub;2=procumbent shrub	2	2	2	2	2	2	2
2.	Internodes: 0=hidden;1=exposed;2=occasionally exposed	1	0	1	0	0	2	1
3.	Leaf: 0=asymmetric;1=symmetric/hardly asymmeric	1	1	1	1	1	999	0
4.	Leaf: 0=broadest at base, narrowing to tip; 1=widening out below tip; 2=widening out below tips, forming flattish knobs/blunt teeth	0	0	0	0	0	0	0
5.	Leaf: 0=deepest at base; 1=slightly deeper around middle; 2=distinctly deepest below tip	0	1	1	0	0	2	1
6.	Leaf: 0=margins/keels distinct/sharp;1=margins/keels distinct/rounded	0	0	0	0	0	1	1
7.	Leaf: 0=untoothed; 1=minute/slight/small teeth; 2=distinct/fierce teeth	0	1	1	1	1	1	0
8.	Leaf: 0=teeth only on margins & keel;1=teeth on other surfaces too	0	0	0	0	0	0	999
9.	Leaf apex: 0=blunt; 1=rounded/pointed; 2=distinctly pointed	2	2	2	2	1	1	1
10.	Leaf: 0=subepidermal tannin idioblasts visible;1=invisible or almost so	1	1	1	1	1	0	0
11.	Leaf length (mm, average)	18	14	19	16	21	34	30
12.	Leaf length max	22	17	22	17	22	43	34
13.	Leaf length min	15	13	14	15	19	29	23
14.	Leaf breadth (mm, average)	10	999	12	11	14	11	11
15.	Leaf breadth max	11	999	14	11	18	12	13
16.	Leaf breadth min	9	999	10	10	11	11	9
17.	Leaf depth (mm, average)	7	7	8	8	8	12	10
18.	Leaf depth max	8	7	9	9	9	12	11
19.	Leaf depth min	6	7	7	7	7	11	9
20.	Proportion leaf length to breadth	2	999	2	2	2	3	3
21.	Leaf epidermal cells 0=flat to slightly rounded;1=domed;2=cone-shaped; 3=papillate	0	0	0	0	0	0	0
22.	Leaf texture: 0=smooth;1=rough;2=velvety	0	0	0	0	0	0	0
23.	Leaf colour: 0=blue/grey-green; 1=green; 2= grey brown/green	0	0	0	0	0	1	1
24.	Leaf margins and/or tip: 0=flushed pink/purple/orange; 1=same as leaf	1	0	0	1	0	0	1
25.	Leaf surface flushed 0=pink/purple/orange; 1=not flushed	1	999	1	1	1	1	1
26.	Receptacle cells:0=rounded;1=domed;2=domed and nippled/papillate;3=conelike/papillate	1	0	1	1	0	1	1
27.	Receptacle: 0=tannin idioblasts visible; 1=hardly visible (deep); 2=invisible	2	999	2	0	2	0	0
28.	Top of receptacle: 0=flat; 1=raised at base of stigmas	1	999	1	1	1	0	0
29.	Sepals l/s: 0=with terminal tooth; 1=subterminal tooth;2=without	0	0	0	0	0	0	1
30.	Sepals l/s: 0=with marginal teeth;1=without marginal teeth	0	1	1	0	0	0	0
31.	Sepals l/s: 0=with keel teeth; 1=without keel teeth	1	1	1	1	1	0	0
32.	Sepals s/s: 0=with subterminal tooth;1=without;2=knob or thickened tip only	0	0	0	0	0	0	0
33.	Sepals s/s: 0=with marginal teeth;1=without	1	1	1	1	1	1	1
34.	Sepals cells: 0=rounded;1=domed;2=domed and nippled/papillate;3=domed to conelike or papillate	1	999	1	1	0	0	1
35.	Flower: 0=squarish;1=round or oval	0	999	0	0	999	0	0
36.	Petal # (average)	42	999	42	47	30	55	54
37.	Petals: 0=only slightly longer than sepals; 1=distinctly longer than sepals	999	999	0	0	999	1	1
38.	Filaments: min length mm	5.0	999.0	3.0	3.0	999.0	5.1	5.0

CM 1638	CM 1643	CM 1661	CM 1666	CM 1667	CM 1668	CM 1672	CM 1673	CM 1692	CM 1696	CM 2064	CM 2151	CM 2212	CM 2213	CM 2215	CM 2216	CM 2233	CM 2234
att	**sua**	**kov**	**sim**	**sim**	**des**	**sim**	**sim**	**sim**	**des**	**sua**	**att**	**sua**	**sua**	**sua**	**sua**	**alb**	**alb**
2	1	2	2	2	2	2	2	2	999	1	2	2	2	2	1	2	2
1	2	0	0	2	0	2	0	2	999	2	1	1	1	1	1	1	2
0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
0	0	1	1	1	0	1	1	1	0	0	1	0	0	0	0	999	0
1	0	2	2	2	0	2	2	2	0	0	1	0	0	0	0	999	0
1	0	1	0	0	0	0	0	0	999	0	1	0	0	0	0	1	1
1	1	2	2	2	1	2	2	2	1	1	1	1	1	1	1	1	0
0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	999
0	2	0	2	2	1	2	2	2	999	2	0	2	2	2	2	2	2
0	1	1	1	1	1	1	1	1	999	1	0	1	1	1	1	999	999
34	30	27	25	26	17	26	25	27	16	28	31	24	22	28	28	50	41
35	32	34	28	28	21	29	27	27	18	30	35	999	24	29	35	51	46
32	28	20	22	23	14	23	22	27	14	25	28	999	20	27	26	48	38
11	13	18	17	16	14	16	16	18	13	14	12	10	10	10	10	12	15
13	14	25	20	17	15	19	16	19	14	15	13	999	11	11	12	13	20
9	11	11	13	15	12	14	16	17	12	13	10	999	8	8	8	11	12
10	10	15	13	11	10	10	13	14	9	9	11	7	8	9	8	11	11
12	11	20	15	12	11	12	14	16	9	11	12	999	8	10	8	12	12
7	10	10	10	10	9	8	11	12	8	8	10	999	7	7	8	10	11
3	2	2	1	2	1	2	2	2	1	2	3	2	2	3	3	4	3
0	0	2	1	1	0	0	1	1	999	0	0	999	999	0	0	0	0
0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
1	0	1	0	0	1	0	0	1	999	0	0	0	0	0	1	0	0
1	1	1	1	1	1	1	1	1	999	1	1	1	1	1	1	1	1
0	1	1	1	1	0	2	1	1	999	1	999	999	999	999	1	999	999
0	2	0	0	999	999	999	0	999	999	2	999	999	999	999	1	999	999
0	1	1	0	1	1	0	0	1	999	1	999	999	999	0	0	999	999
0	0	0	0	0	0	0	0	0	999	0	999	999	0	0	0	999	999
0	0	0	0	0	1	0	0	0	999	0	999	999	0	0	0	0	0
0	1	1	0	0	1	0	0	0	999	1	999	999	999	999	1	0	0
0	0	0	0	0	0	0	0	0	999	0	999	0	0	0	0	0	0
1	1	1	0	1	1	1	1	1	999	1	999	999	999	1	1	1	1
0	1	3	1	999	999	1	1	1	999	0	999	999	999	0	0	999	999
999	999	1	1	999	999	0	1	999	0	1	999	999	999	999	1	999	999
38	55	62	48	999	999	57	49	52	45	55	999	999	999	999	53	999	999
1	999	1	999	999	999	1	1	1	999	1	999	999	999	999	1	999	999
3.6	3.1	1.6	2.2	999.0	999.0	3.3	3.0	3.7	4.0	4.1	999.0	999.0	999.0	1.8	3.0	999.0	999.0

CM 2236	**CM 2237**	**CM 2243**	**CM 2248**	**CM 2249**	**CM 2270**	**CM 2348**	**CM 2352**	**CM 2353**	**CM 2365**	**CM 2366**	**CM 2368**	**CM 2369**	**CM 2370**	**CM 2371**	**CM 2377**	**CM 2378**	**CM 2379**
alb	**alb**	**alb**	**alb**	**alb**	**kov**	**des**	**des**	**des**	**sim**	**sim**	**kov**	**kov**	**kov**	**kov**	**sua**	**sua**	**sua**
1	2	2	1	1	2	0	0	0	2	2	2	2	2	2	1	1	1
1	1	1	1	1	2	0	0	0	2	2	2	2	2	2	2	2	2
0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
1	1	1	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0
1	1	1	0	0	2	0	0	0	2	2	2	2	2	2	0	0	0
0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0
1	1	1	0	0	2	1	1	1	2	2	2	2	2	2	1	1	1
0	0	0	999	999	1	0	0	0	1	1	1	1	1	1	0	0	0
2	2	2	2	2	0	2	2	2	2	2	0	0	0	0	2	2	2
0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
52	47	51	52	60	25	14.8	17.4	15.4	22.1	25.4	999	999	28.2	22.4	24.8	24.5	999
61	50	55	55	73	26	16.5	19.7	16	23.1	27	999	999	25.7	24.5	26	25.8	999
40	45	47	49	53	24	13.9	15	15	21.1	23.6	999	999	19.8	20	22.7	22.3	999
18	19	16	19	14	15	11.2	11.2	11.5	19.1	21.5	999	999	17.6	17.2	12.7	10.6	999
20	21	17	999	15	15	12.4	11.7	12.1	20.3	25.7	999	999	20.7	18.9	13.7	11	999
16	18	14	999	12	14	9.8	10.5	11.2	17.9	18.5	999	999	13.9	14	11.9	10.3	999
16	17	15	17	14	14	7.9	8.6	9	13.7	11.9	999	999	11.7	14	10.1	8.7	999
17	23	16	999	16	14	9.1	9.1	9.6	16	12.5	999	999	13.7	14.6	11.6	9	999
14	12	12	999	12	14	6.3	8.3	8.6	11.3	11.6	999	999	11.3	13.5	8.9	8.3	999
3	2	3	3	4	2	1	2	1	1	1	999	999	2	1	2	2	999
0	0	0	0	0	2	0	0	0	1	1	3	3	2	2	0	0	0
0	0	0	0	0	2	0	0	0	0	0	2	2	2	2	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	999	999	3	0	999	0	1	1	3	3	3	3	0	0	0
0	0	0	999	999	999	0	999	0	0	0	1	1	1	1	1	1	1
0	1	0	999	1	0	0	999	0	0	0	0	0	0	0	0	0	0
0	0	0	999	0	0	0	999	1	1	1	0	0	0	999	0	0	0
0	0	1	999	999	0	0	999	0	0	0	0	0	0	0	0	0	1
0	0	1	999	999	0	1	999	1	1	0	0	0	0	0	1	1	1
0	0	0	0	0	0	1	999	1	0	0	0	0	0	2	1	0	0
1	1	1	1	1	1	1	999	1	1	1	1	1	1	1	1	1	1
0	0	0	999	999	3	0	999	0	1	1	3	3	3	2	0	0	0
0	0	0	999	999	999	0	999	0	1	1	1	1	1	0	1	1	1
70	999	55	999	999	999	999	999	999	999	71	999	999	55	53	46	47	56
1	0	1	999	999	999	0	999	0	1	1	1	1	1	1	1	1	1
3.0	2.0	4.0	999.0	3.6	999.0	2.3	999.0	3.1	3.6	4.8	3.2	3.0	4.1	2.5	4.8	4.3	5.1

CM 2381	CM 2382	CM 2440	CM 2640A	CM 2640B	CM 2640C	CM 2640D
sim	sim	att	aus	aus	aus	aus
2	2	2	2	2	2	2
2	2	1	1	1	1	1
0	0	0	0	0	0	0
1	1	2	0	0	0	0
2	2	2	0	0	0	0
0	0	1	0	0	0	0
2	2	1	2	2	2	2
1	1	0	0	0	0	0
2	2	2	2	2	2	2
1	1	0	1	1	1	1
20.8	25.6	31.8	999	21.9	22.7	999
25.4	27.5	37.9	999	24	24.6	999
18.4	21	28	999	19.2	20.7	999
16.6	12.9	11.5	999	11.8	11.3	999
18.1	14.1	14.4	999	12.2	12.0	999
13.8	11.1	9.2	999	11.4	10.6	999
11.7	10.9	10.1	999	8.7	8.5	999
13.6	11.8	11.4	999	9.4	9.4	999
10.1	9.4	8.9	999	8.3	7.7	999
1	2	3	1	2	2	1
0	0	0	1	1	1	1
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
1	1	1	0	0	0	0
3	1	0	3	3	3	3
1	1	999	0	0	0	0
0	0	999	0	0	0	0
0	0	2	2	1	1	2
0	0	0	1	0	0	0
0	0	1	1	1	1	1
0	0	1	0	2	2	2
1	1	0	1	1	1	1
1	1	0	1	1	1	1
1	1	1	1	1	1	1
55	47	66	70	72	56	63
1	1	1	0	1	1	1
3.5	4.2	3.5	2.6	2.3	3.0	5.0

39.	Filaments: max length mm	7.0	999.0	7.0	5.0	999.0	6.0	9.0
40.	Nectary colour:0=green;1=brown/olive-brown	0	999	0	0	999	0	0
41.	Nectar colour: 0=clear or pale green;1=golden yellow;2=straw-coloured or pale yellow	0	999	0	0	999	999	0
42.	Stigma # (average)	8	999	8	10	999	8	8
43.	Stigmas: 0=free at base;1=fused at base	1	999	1	1	999	1	1
44.	Stigmas: 0=slender; 1=robust/sturdy	0	999	1	1	999	1	999
45.	Capsule average # locules	8	8	8	8	8	999	8
46.	Capsule min # locules	8	8	8	8	999	999	8
47.	Capsule max #locules	8	8	8	8	999	999	8
48.	Capsule average diameter (mm)	6.0	6.0	7.0	5.5	8.0	999.0	6.8
49.	Capsule max diameter (mm)	7.0	6.4	7.0	6.4	999.0	999.0	7.4
50.	Capsule min diameter	5.0	5.3	7.0	4.7	999.0	999.0	6.3
51.	Valve tips: 0=curved back when dry; 1=not	999	999	999	999	999	999	0
52.	Covering membranes: 0=absent; 1=vestigial/almost so; 2=crescent-shaped; 3=broadening towards outside	1	2	1	2	2	999	3
53.	Covering membranes: 0=not meeting; 1=meeting	0	0	0	0	0	999	1
54.	Keels: 0=shorter than valves; 1=as long as valves; 2=longer than valves	1	999	1	999	1	999	1
55.	Keels: 0=touching for most of length, diverging distally; 1 =meeting along most of length, may be slightly divergent at fulcrum only	0	0	0	0	0	999	0
56.	Keels: 0=yellow/orange-brown; 1=light brown/tan; 2=dark brown	1	1	1	0	999	999	0
57.	Valve wings: 0=narrow-rectangular; 1=broad-rectangular; 2=crescent to rectangular; 3=broad-triangular	0	0	1	1	1	999	0
58.	Valve wings: 0=extending beyond valves; 1=same reach as valves; 2=shorter than valves	999	999	1	999	0	999	0
59.	Valve wings: 0=extending beyond keels; 1=same reach as keels	1	999	1	0	0	999	0
60.	Valve wing width (average mm)	0.2	0.3	0.7	0.5	0.8	999	0.6
61.	Seed: 0=pear-shaped; 1=comma-shaped; 2=ovate	1	1	0	1	1	999	1
62.	Seed: 0=light brown; 1=light apricot; 2=rust/golden brown	2	2	2	2	2	999	0
63.	Seed surface: 0=fine, flattish cells; 1=medium/rounded cells; 2=smooth or slightly striate; 3=finely tuberculate	1	1	0	1	1	999	3
64.	Seed length mm	0.7	0.7	0.9	1.0	0.8	999.0	0.7

3.9	7.0	8.0	6.3	999.0	999.0	7.0	8.6	6.7	5.0	7.9	999.0	999.0	999.0	7.0	9.0	999.0	999.0
999	999	0	0	999	999	0	0	999	999	0	999	999	999	999	0	999	999
999	999	2	2	999	999	999	2	999	999	2	999	999	999	999	0	999	999
8	10	10	10	8	7	8	9	8	8	8	999	999	999	999	8	999	999
999	1	1	1	999	1	1	0	1	999	1	999	999	999	999	1	999	999
999	1	0	0	999	1	1	1	1	999	1	999	999	999	999	0	999	999
8	8	9	8	8	8	8	8	8	999	8	8	999	999	999	8	8	8
8	8	8	8	8	7	7	8	8	999	8	999	999	999	999	8	999	999
8	8	12	10	9	8	9	12	8	999	8	999	999	999	999	8	999	999
8.1	8.7	8.0	8.0	9.0	8.0	10.0	8.0	8.0	999.0	7.6	7.0	999.0	999.0	999.0	7.2	11.0	10.0
8.2	999.0	8.0	9.0	9.0	8.0	10.0	9.0	9.0	999.0	8.1	999.0	999.0	999.0	999.0	7.3	12.0	11.0
8.0	999.0	7.0	7.0	8.0	8.0	9.0	7.0	8.0	999.0	7.2	999.0	999.0	999.0	999.0	7.1	10.0	8.0
999	999	0	0	999	0	0	0	0	999	0	0	999	999	999	0	0	0
2	1	2	2	999	999	2	2	2	999	1	999	999	999	999	1	999	1
1	0	0	1	999	999	1	1	0	999	0	999	999	999	999	0	999	0
999	2	2	1	999	999	1	1	1	999	999	999	999	999	999	1	999	2
0	0	0	0	999	999	0	0	0	999	0	999	999	999	999	1	999	0
999	999	0	0	999	999	0	0	1	999	0	999	999	999	999	0	999	1
0	1	1	1	999	999	1	0	1	999	3	999	999	999	999	3	999	1
999	999	0	0	999	999	0	1	0	999	999	999	999	999	999	0	999	0
0	0	1	0	999	999	0	1	0	999	0	999	999	999	999	0	999	0
0.7	1.4	0.6	1.1	999	999	0.9	0.5	1.3	999	0.7	999	999	999	999	0.7	999	1.6
1	999	1	1	999	999	1	1	1	999	1	999	999	999	999	1	999	1
0	999	0	0	999	999	0	1	1	999	1	999	999	999	999	0	999	0
1	999	0	3	999	999	3	3	3	999	3	999	999	999	999	3	999	1
0.7	999.0	0.7	0.6	999.0	999.0	0.5	0.7	0.8	999.0	0.7	999.0	999.0	999.0	999.0	0.6	999.0	0.6

9.5	9.0	11.0	999.0	8.8	999.0	4.7	999.0	4.8	7.4	7.6	7.8	7.0	8.4	6.9	7.0	6.4	6.9
0	0	0	0	999	1	0	999	0	0	0	0	0	0	0	0	0	0
2	1	0	999	999	999	999	999	999	2	2	2	2	0	0	2	2	0
8	8	8	999	999	7	8	999	8	8	8	9	999	8	8	8	8	8
1	1	1	999	999	1	999	999	0	1	999	1	1	1	0	0	0	0
1	1	0	999	999	1	999	999	1	1	999	0	0	0	1	1	1	1
8	8	999	999	8	8	8	8	8	8	8	9	999	8	8	8	8	8
8	999	999	999	999	8	8	8	8	8	8	8	999	8	8	8	8	8
10	999	999	999	999	8	8	8	9	8	9	10	999	8	8	8	8	8
999.0	999.0	999.0	999.0	11.0	9.0	6.1	6.1	6.3	7.7	8.0	7.9	999.0	7.7	8.6	7.5	6.8	6.1
999.0	999.0	999.0	999.0	12.0	9.2	7.0	6.3	7.2	8.0	9.3	8.6	999.0	8.5	8.8	8.4	7.0	6.3
999.0	999.0	999.0	999.0	10.0	8.8	5.2	5.7	5.4	7.4	6.2	7.0	999.0	7.2	8.3	6.6	6.6	5.8
0	999	0	0	0	0	1	1	1	0	0	0	999	0	0	1	1	1
1	999	999	999	999	2	1	1	1	2	2	2	999	2	2	2	2	2
0	999	999	999	999	1	0	0	0	0	0	0	999	0	0	0	0	0
999	999	999	999	999	1	1	1	1	1	1	1	999	1	1	1	1	1
999	999	999	999	999	0	0	0	0	1	1	0	0	0	0	0	0	0
999	999	999	999	999	0	2	2	2	0	0	0	0	0	0	0	0	0
999	999	999	999	999	1	0	1	0	2	1	1	999	1	1	1	1	0
999	999	999	999	999	1	1	1	1	1	1	1	999	0	0	1	1	1
999	999	999	999	999	1	0	0	0	1	1	0	999	0	0	1	1	1
999	999	999	999	999	0.6	0.5	0.7	0.6	0.7	1.1	0.8	999	1.4	1.1	1.1	0.7	0.5
1	999	999	999	999	1	1	1	1	1	1	1	1	1	1	1	1	999
0	999	999	999	999	1	2	2	2	1	2	0	999	0	0	1	1	999
0	999	999	999	999	2	1	1	1	0	3	1	999	1	1	1	1	999
0.9	999.0	999.0	999.0	999.0	0.6	0.8	0.9	0.9	0.7	0.9	0.8	999.0	0.7	0.8	0.8	0.7	999.0

6.9	7.4	7.5	5.8	5.2	8.5	7.9
0	0	0	0	0	1	1
0	0	2	999	999	2	2
9	9	8	11	10	8	10
0	0	999	0	0	0	0
1	1	999	0	0	0	0
9	9	8	11	9	8	8
8	8	8	9	8	8	8
9	9	9	12	11	8	8
7.0	7.4	6.9	9.9	9.6	9.7	10.0
7.5	8.7	7.6	10.0	10.7	10.7	10.4
6.4	5.9	5.9	9.6	7.2	9.1	9.6
1	1	0	0	0	0	0
2	2	2	2	2	2	2
0	1	1	0	0	0	0
1	1	1	0	0	0	0
0	0	0	0	0	0	0
1	1	0	0	0	0	0
0	0	0	0	1	1	1
0	0	0	2	2	2	2
0	0	0	0	0	0	0
0.5	0.5	0.8	0.4	1.2	0.7	0.9
1	1	1	1	1	1	1
0	2	0	0	0	0	0
0	1	1	3	3	3	3
0.7	0.7	0.7	0.8	0.8	0.8	0.8

Appendix 3: Data set for Dracophilus phenogram. CM = Coleen Mannheimer; dea = dealbatus; del = delaetianus.

	Specimen number	CM 858A	CM 858B	CM 858D	CM 1411	CM 1420	CM 1435A	CM 1435B	CM 1436
	Species abbreviations	del	del	del	dea	dea	del	del	del
	CHARACTER								
1.	Leaf: 0=broadest at base, narrowing to tip; 1=widening out below tip; 2=widening out below tips, forming flattish knobs/blunt teeth	1	1	1	2	0	1	1	1
2.	Leaf: 0=deepest at base; 1=slightly deeper around middle; 2=distinctly deepest below tip	2	2	2	0	0	1	0	1
3.	Leaf: 0=margins/keels distinct/sharp;1=margins/keels distinct/rounded	0	0	0	1	1	0	0	0
4.	Leaf: 0=untoothed; 1=minute/slight/small teeth; 2=distinct/fierce teeth; 3=knobs	2	2	2	0	0	2	1	2
5.	Leaf: 0=teeth only on margins & keel;1=teeth on other surfaces too	1	0	1	999	999	1	0	1
6.	Leaf apex: 0=blunt; 1=rounded/pointed; 2=distinctly pointed	2	2	2	1	1	2	2	2
7.	Leaf length (mm, average)	23.0	26.0	27.0	37.0	26.0	23.0	25.0	21.0
8.	Leaf length max	26.0	28.0	28.0	47.0	26.0	33.0	27.0	26.0
9.	Leaf length min	21.0	24.0	25.0	29.0	25.0	13.0	23.0	17.0
10.	Leaf breadth (mm, average)	11.0	11.0	10.0	15.0	13.0	10.0	11.0	11.0
11.	Leaf breadth max	12.0	12.0	11.0	16.0	14.0	11.0	12.0	12.0
12.	Leaf breadth min	9.0	9.0	9.0	14.0	12.0	9.0	9.0	10.0
13.	Leaf depth (mm, average)	10.0	11.0	10.0	14.0	11.0	11.0	10.0	10.0
14.	Leaf depth max	12.0	12.0	12.0	14.0	12.0	12.0	12.0	11.0
15.	Leaf depth min	7.0	8.0	8.0	13.0	10.0	10.0	8.0	9.0
16.	Proportion leaf length to breadth	2	2	3	2	2	2	2	2
17.	Leaf epidermal cells 0=flat to slightly rounded;1=domed;2=cone-shaped; 3=papillate; 4=domed and nippled	1	1	1	2	2	0	0	999
18.	Leaf texture: 0=smooth;1=rough;2=velvety; 3=very rough	0	0	0	1	1	0	0	0
19.	Leaf margins and/or tip: 0=flushed pink/purple/orange; 1=same as leaf	0	0	0	1	0	0	0	1
20.	Leaf surface flushed 0=pink/purple/orange; 1=not flushed	1	1	1	1	1	1	1	1
21.	Bract epidermal cells: 0=rounded;1=domed;2=cone-shaped	1	1	1	2	2	0	1	1
22.	Bract length (ave mm) (but they enlarge through anthesis)	5	4	4	7	7	6	7	3
23.	Bracts: 0=with subterminal knob or tooth; 1=lacking such	0	1	1	1	1	0	0	1
24.	Receptacle cells:0=rounded;1=domed;2=domed and nippled (papillae);3=conelike (papillae)	1	1	1	1	1	0	1	2
25.	Receptacle: 0=tannin idioblasts visible; 1=hardly visible (deep); 2=invisible	1	1	1	999	999	999	2	999
26.	Large sepals: 0=with terminal tooth; 1=with subterminal tooth; 2=without either; 3=with knob only	3	3	3	2	3	3	3	2
27.	Large sepals length (mm average)	7.0	8.0	7.0	11.4	10.1	6.9	9.0	7.5
28.	Large sepal length max	9.0	9.0	7.0	14.0	11.1	7.0	9.0	8.0
29.	Large sepal length min	6.0	7.0	7.0	10.1	10.3	6.7	8.0	6.9
30.	Large sepals breadth (mm average)	4.0	5.0	5.0	6.6	6.5	3.3	6.0	4.0
31.	Large sepal breadth max	5.0	5.0	5.0	6.9	6.8	4.0	6.0	4.0
32.	Large sepal breadth min	4.0	4.0	4.0	6.1	6.4	2.5	5.0	3.9
33.	Small sepals: 0=with subterminal tooth; 1=without; 2=knob or thickened tip only	1	1	1	2	2	2	1	1
34.	Small sepals: 0=with marginal teeth;1=without	1	1	1	1	1	1	1	1

CM 1523	CM 1524A	CM 1524B	CM 1524C	CM 1622	CM 1631	CM 1650	CM 1722	CM 1989B	CM 2038	CM 2039	CM 2041	CM 2042	CM 2189	CM 2190	CM 2191	CM 2192
dea	**dea**	**dea**	**dea**	**del**	**dea**	**dea**	**del**	**dea**	**dea**	**dea**	**dea**	**dea**	**dea**	**del**	**del**	**del**
0	0	2	0	1	0	2	1	0	0	0	2	2	2	1	1	1
0	0	0	0	2	1	0	0	1	0	0	0	0	0	2	2	2
0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0
0	0	3	0	2	0	3	2	0	0	0	1	1	3	2	2	2
999	999	999	999	999	999	999	0	999	999	999	0	0	0	1	1	1
2	1	0	1	2	1	1	1	1	1	1	2	1	2	2	2	2
29.0	32.6	32.5	34.0	23.0	28.0	33.0	25.0	39.7	34.0	37.0	27.0	28.0	28.9	29.0	27.0	26.9
30.0	36.0	34.0	40.0	24.0	29.0	39.0	28.0	999.0	37.0	41.0	30.0	30.0	34.0	31.0	27.0	35.0
28.0	30.0	30.0	29.0	22.0	28.0	28.0	20.0	999.0	31.0	29.0	24.0	25.0	23.2	26.0	26.0	21.1
15.0	12.3	13.8	12.0	11.0	15.0	13.0	9.0	11.0	9.0	14.0	11.0	12.0	10.7	12.0	11.0	11.9
16.0	13.0	17.0	14.0	14.0	15.0	15.0	10.0	999.0	8.0	17.0	12.0	11.0	12.0	13.0	11.0	15.0
13.0	12.0	11.0	11.0	9.0	13.0	11.0	7.0	999.0	10.0	11.0	10.0	13.0	8.7	11.0	10.0	10.5
13.0	11.0	12.3	12.0	10.0	13.0	13.0	9.0	10.9	11.0	14.0	10.0	11.0	11.6	14.0	12.0	10.6
15.0	13.0	15.0	14.0	11.0	13.0	14.0	11.0	999.0	12.0	15.0	11.0	11.0	14.0	15.0	13.0	13.0
12.0	10.0	10.0	9.0	9.0	12.0	11.0	7.0	999.0	10.0	12.0	8.0	10.0	8.7	13.0	11.0	7.2
2	3	2	3	2	2	3	3	4	4	3	2	2	3	2	2	2
1	1	2	0	0	2	2	0	1	2	2	1	2	1	999	1	3
0	0	1	0	0	1	3	0	0	1	3	0	1	3	0	0	2
1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1
1	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1
2	1	2	1	0	2	1	1	2	2	2	2	2	2	1	1	2
8	6	7	7	5	7	7	4	8	9	8	7	9	6	999	6	7
1	1	1	1	999	1	1	1	1	1	1	1	1	1	0	1	0
0	1	1	1	999	3	1	0	2	1	1	0	0	1	1	2	1
1	2	999	1	999	0	1	999	1	1	1	1	1	2	2	2	2
3	3	999	3	999	2	2	3	3	3	3	2	3	999	1	3	0
6.2	10.2	999.0	10.2	8.0	11.7	10.1	6.9	16.0	9.4	12.8	9.6	10.0	11.4	7.0	7.0	7.3
999.0	10.7	999.0	14.0	9.0	13.0	11.0	7.7	16.9	9.7	13.3	10.9	10.5	12.1	7.1	7.2	8.5
999.0	9.3	999.0	15.0	7.0	9.5	7.3	6.2	15.3	9.1	12.3	9.2	9.5	11.0	6.7	6.9	6.0
4.3	6.6	999.0	12.0	4.0	6.8	7.5	4.0	8.4	5.4	6.5	7.2	5.6	6.8	4.9	3.7	4.7
999.0	6.7	999.0	7.0	4.0	7.3	8.0	5.6	9.1	5.5	6.9	7.4	5.6	7.1	5.2	3.8	4.8
999.0	6.4	999.0	8.0	3.0	5.7	7.0	2.9	7.9	5.2	6.0	7.1	5.5	6.4	4.7	3.6	4.5
2	2	1	2	999	1	2	1	2	2	2	1	2	2	2	2	0
1	1	1	1	999	1	1	1	1	1	1	1	1	1	1	1	1

AB 01122A	**Pillans 5720**	**K. Dinter 3784**	**CM 2408**	**CM 2409**	**CM 2410**	**CM 2413**	**CM 2448**
dea	dea (holo D. proximus)	dea (holo D. montis-draconis)	dea	dea	dea	dea	dea
		B-2					
0	0	999	0	0	0	0	2
0	999	999	0	0	0	0	0
1	1	999	1	1	1	1	1
0	0	999	0	0	0	0	3
999	999	999	999	999	999	999	999
1	1	999	1	1	1	1	1
32.0	31.0	28.0	34.6	26.1	32.1	36.9	30.1
38.0	45.0	34.0	36.0	31.2	35.9	39.4	33.7
27.0	24.0	20.0	33.2	18.7	29.0	34.7	26.1
13.0	13.0	999.0	10.7	9.8	11.0	12.2	14.1
14.0	14.0	999.0	11.3	10.5	12.3	12.5	15.4
12.0	999.0	999.0	10.0	8.7	9.6	11.9	13.1
12.0	999.0	12.0	9.9	9.0	9.9	11.2	12.1
13.0	999.0	13.0	10.9	9.9	11.3	12.0	13.0
9.0	999.0	11.0	8.9	7.6	8.5	10.7	11.6
2	2	999	3	3	3	3	2
1	0	2	0	2	4	2	2
1	0	1	1	1	1	1	3
0	999	999	0	0	0	0	0
0	999	999	0	0	0	1	0
2	999	999	999	1	1	2	2
8	999	999	999	999	999	999	999
1	999	999	0	0	0	0	0
1	999	999	2	0	2	2	3
999	999	999	1	1	1	1	1
3	1	999	3	3	3	3	3
11.0	999.0	999.0	999.0	11.0	999.0	12.6	11.1
12.0	999.0	999.0	999.0	999.0	999.0	13.1	11.7
10.0	999.0	999.0	999.0	999.0	999.0	12.4	10.5
7.0	999.0	999.0	999.0	6.3	999.0	7.9	6.9
8.0	999.0	999.0	999.0	999.0	999.0	8.3	7.4
6.0	999.0	999.0	999.0	999.0	999.0	7.6	6.3
2	2	999	0	0	0	1	1
1	1	999	1	1	1	0	0

38.	Small sepals length min	7.0	7.0	7.0	8.3	9.4	5.1	8.0	6.3
39.	Small sepals breadth (mm average)	3.0	3.0	4.0	4.2	3.6	2.6	2.9	2.9
40.	Small sepals breadth max	3.0	3.0	4.0	4.4	4.4	3.2	3.4	3.0
41.	Small sepals breadth min	2.0	3.0	3.0	3.9	3.2	2.0	2.5	2.8
42.	Flower: 0=white;1=pale pink; 2=pink to magenta	2	2	2	2	2	2	2	2
43.	Pink flowers: 0=petals just pink;1=petals fading to almost white at base	1	0	0	0	0	0	0	0
44.	Flower: diameter (mm average)	24	25	27	999	29	26	31	25
45.	Flower max diameter	26	26	34	999	999	999	34	999
46.	Flower min diameter	22	20	23	999	999	999	29	999
47.	Flower opening: 0=afternoon; 1=late afternoon;2=night	1	1	1	999	999	999	1	1
48.	Petal # (average)	41	51	43	999	999	999	44	999
49.	Petal length (mm average)	11.0	11.0	12.0	10.5	10.3	10.0	10.1	12.0
50.	Petal max length	12.0	12.0	14.0	11.1	10.5	11.0	13.0	14.0
51.	Petal min length	9.0	10.0	11.0	9.9	10.0	8.0	8.3	10.0
52.	Petal width at widest point (mm average)	1.7	2.4	1.9	1.4	1.7	1.3	1.3	1.3
53.	Petal max width at widest point	2.0	3.0	2.2	1.6	1.7	1.3	1.5	999.0
54.	Petal min width at widest point	1.5	2.0	1.8	1.2	1.6	1.2	1.2	999.0
55.	Petals 0=evenly distributed; 1=in 5 groups; 2=both	0	1	0	0	999	0	0	0
56.	Petals: 0=straight or slightly downcurved; 1=petal tips distinctly recurved	0	0	0	999	999	999	0	0
57.	Petals: 0=only slightly longer than sepals; 1=distinctly longer than sepals	0	0	0	0	0	999	1	999
58.	Filaments: min length mm	5.0	7.0	6.0	5.9	6.2	4.0	4.7	3.0
59.	Filaments: max length mm	7.0	9.0	7.0	8.9	7.8	7.0	8.0	7.0
60.	Anther ave length mm	999.0	999.0	999.0	999.0	999.0	999.0	0.7	999.0
61.	Anther min length mm	999.0	999.0	999.0	999.0	999.0	999.0	0.6	999.0
62.	Anther max length mm	999.0	999.0	999.0	999.0	999.0	999.0	0.8	999.0
63.	Nectary colour: 0=brown/olive-brown; 1=orange/orange-brown	0	0	0	1	1	0	0	999
64.	Nectar colour: 0=golden yellow; 1=straw-coloured or pale yellow	1	1	1	0	999	999	1	999
65.	Stigma # (average)	8	10	10	13	11	10	9	9
66.	Stigma colour:0=pale yellow;1=pale green-yellow	0	0	0	999	999	1	1	1
67.	Stigmas: 0=slender; 1=robust/sturdy	1	1	1	0	0	0	0	999
68.	Capsule average # locules	8	10	10	13	11	10	10	9
69.	Capsule min # locules	7	8	9	13	12	9	9	8
70.	Capsule max #locules	8	10	11	13	10	10	10	10
71.	Capsule average diameter (mm)	7.3	7.4	7.3	9.9	9.1	6.7	6.5	6.0
72.	Capsule max diameter (mm)	8.0	8.0	7.8	10.0	9.4	6.9	9.0	999.0
73.	Capsule min diameter	6.9	7.0	6.4	9.7	9.0	6.6	5.0	6.0
74.	Covering membranes: 0=crescent-shaped; 1=broadening distally	1	1	1	1	0	1	0	999
75.	Covering membranes: 0=not meeting; 1=meeting; 2=overlapping	1	1	1	0	0	1	0	999

3	1	999	1	999	1	1	0	1	1	1	0	1	999	999	999	0
6.0	9.7	999.0	12.0	8.0	11.4	10.5	6.4	15.0	7.8	11.0	8.9	10.3	9.3	5.9	5.9	4.4
999.0	9.9	999.0	14.0	9.0	13.0	11.0	6.6	16.6	7.8	11.6	9.7	10.8	9.6	6.2	6.3	7.5
999.0	9.5	999.0	10.0	7.0	9.4	10.0	6.2	13.8	7.7	10.4	8.2	9.9	9.0	5.3	5.6	4.7
4.1	5.2	999.0	5.0	3.0	4.5	4.4	3.0	5.9	4.5	4.6	5.0	4.0	3.2	2.9	3.3	3.4
999.0	5.7	999.0	6.0	3.0	5.0	5.0	3.0	6.0	4.7	5.3	5.5	4.4	3.7	3.0	3.8	3.8
999.0	4.7	999.0	4.0	2.0	3.8	4.0	2.9	5.9	4.3	3.8	4.4	3.6	3.0	2.7	2.9	2.7
2	2	2	2	2	0	999	2	1	2	2	2	2	2	2	2	2
1	0	0	0	999	0	999	0	0	1	0	1	1	0	0	0	0
30	999	999	999	999	38	999	23	32	27	32	33	31	999	22	22	27
999	30	999	999	999	40	999	999	36	27	35	36	33	999	22	24	32
999	999	999	999	999	35	999	999	29	25	28	31	30	999	21	20	23
2	999	999	999	999	2	999	1	2	2	2	2	2	999	1	1	1
999	69	999	68	999	55	60	44	66	55	60	72	67	59	44	46	48
11.7	13.0	999.0	15.2	7.5	19.0	9.8	10.1	14.8	9.2	11.8	10.9	14.0	10.0	8.4	10.4	12.0
999.0	16.0	999.0	17.0	999.0	20.1	999.0	11.2	15.9	10.4	14.0	13.1	14.1	11.4	9.1	11.1	14.5
999.0	11.4	999.0	13.4	999.0	17.7	999.0	9.0	14.0	8.1	10.5	9.8	13.8	8.6	7.4	10.0	10.2
1.2	1.6	999.0	1.6	999.0	1.5	1.8	1.3	1.3	1.8	1.8	1.8	1.6	1.9	1.4	1.3	1.8
999.0	1.7	999.0	1.7	999.0	1.6	2.0	1.3	1.6	2.1	1.8	1.9	1.6	2.0	1.5	1.4	2.0
999.0	1.6	1.5	1.5	999.0	1.5	1.5	1.2	1.2	1.6	1.7	1.6	1.5	1.8	1.2	1.1	1.4
0	0	0	0	999	0	0	0	0	0	0	0	0	0	0	0	0
1	1	999	1	999	1	1	0	1	0	1	1	999	999	0	0	0
0	0	999	1	1	1	0	1	0	0	0	0	0	0	1	1	1
6.9	7.4	999.0	7.0	999.0	8.0	6.1	7.5	9.0	4.7	6.2	7.3	7.3	6.4	1.9	6.4	3.2
9.2	7.8	999.0	10.0	999.0	10.0	8.3	7.5	10.5	9.8	10.8	8.4	9.3	6.4	6.3	7.5	8.0
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	0.9	1.3	0.8	0.8	999.0	999.0	999.0	0.8
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	0.8	1.2	0.7	0.7	999.0	999.0	999.0	0.6
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0	0.9	1.4	0.9	0.8	999.0	999.0	999.0	1.0
0	999	999	1	1	0	1	0	1	1	0	1	1	1	0	0	0
0	999	999	0	0	0	0	0	0	1	0	0	0	0	1	1	0
10	12	9	10	11	10	12	7	10	10	10	11	11	12	9	10	8
0	1	1	1	999	1	999	999	1	1	1	1	1	1	999	1	0
0	0	999	0	1		0	0	0	1	0	0	1	0	1	0	0
10	11	11	11	10	12	13	10	10	11	10	11	11	13	10	10	10
999	11	9	10	9	11	12	9	10	10	10	11	10	13	9	999	8
999	11	12	14	10	12	13	10	11	12	10	11	12	12	10	999	11
7.0	9.3	8.6	9.0	8.0	8.4	8.0	7.0	9.8	8.8	9.0	8.8	9.1	10.0	7.8	7.0	8.3
999.0	9.8	9.0	10.0	8.0	9.0	9.0	7.0	9.8	9.7	9.9	9.0	9.5	11.0	999.0	8.0	9.0
999.0	9.0	8.2	8.0	6.0	7.7	7.0	6.0	9.7	7.8	8.0	8.6	8.7	9.0	999.0	7.0	7.5
999	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
999	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1

1	0	999	2	1	1	2	3
11.0	999.0	999.0	999.0	9.0	999.0	11.7	10.3
12.0	999.0	999.0	999.0	999.0	999.0	11.9	10.6
9.0	999.0	999.0	999.0	999.0	999.0	11.6	9.8
5.0	999.0	999.0	999.0	4.3	999.0	5.0	5.7
5.0	999.0	999.0	999.0	999.0	999.0	5.5	6.0
3.0	999.0	999.0	999.0	999.0	999.0	4.8	5.3
2	2	999	0	1	2	2	2
0	0	999	0	0	0	0	0
34	999	999	30	31	32	27	999
38	30	999	31	34	32	999	999
30	999	999	29	27	31	999	999
999	1	999	2	2	2	2	999
59	999	999	66	69	61	50	999
14.0	13.0	999.0	11.6	10.8	11.6	13.3	999.0
15.0	13.0	999.0	12.3	11.5	12.0	14.2	999.0
13.0	12.0	999.0	11.2	10.0	11.2	12.3	999.0
1.8	1.9	999.0	1.6	1.9	1.9	1.7	1.9
2.0	2.0	999.0	1.7	2.3	2.3	1.8	1.9
1.5	1.8	999.0	1.5	1.6	1.4	1.7	1.8
0	0	999	0	0	0	0	0
1	999	999	1	1	1	1	999
1	0	999	0	0	0	0	999
7.0	8.0	999.0	5.8	4.8	7.8	8.0	6.3
9.0	11.0		6.9	7.0	8.3	10.0	7.6
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0
999.0	999.0	999.0	999.0	999.0	999.0	999.0	999.0
1	0	999	0	1	1	0	0
0	999	999	0	0	0	0	0
9	12	999	10	999	999	11	12
1	999	999	1	1	1	999	999
1	0	999	0	0	1	999	999
10	12	999	10	18	10	11	12
9	999	999	10	999	9	10	999
10	999	999	10	999	10	12	999
10.0	999.0	999.0	8.6	9.0	8.5	8.1	9.2
10.0	999.0	999.0	999.0	999.0	8.8	8.7	999.0
8.0	999.0	999.0	999.0	999.0	8.2	7.7	999.0
1	999	999	1	1	1	1	1
1	999	999	2	2	2	2	0

76.	Keels: 0=shorter than valves; 1=as long as valves	1	1	1	999	0	1	1	999
77.	Keels: 0=touching for most of length, diverging distally; 1=touching at base, then slightly separated along length, diverging distally; 2=meeting along most of length, may be slightly divergent at fulcrum only; 3=touching at base, diverging halfway along	2	2	2	999	0	2	2	999
78.	Valve wings: 0=narrow-rectangular; 1=broad-rectangular; 2=crescent-shaped; 3=crescent to rectangular	1	2	2	1	1	2	2	999
79.	Valve wings: 0=extending beyond valves; 1=same reach as valves; 2=shorter than valves	1	1	1	999	999	1	1	999
80.	Valve wings: 0=extending beyond keels; 1=same reach as keels	1	1	1	0	0	1	1	999
81.	Valve wing width (average mm)	0.9	1.2	1.0	1.0	1.3	0.6	0.6	999.0
82.	Placenta: 0=forming a slight knob at tip; 1=not	1	0	0	999	1	0	0	999
83.	Seed: 0=light brown; 1=light apricot; 2=rust/golden brown	0	0	2	1	1	2	2	999
84.	Seed surface: 0=fine, flattish cells; 1=medium/rounded cells; 2=finely tuberculate	0	0	0	1	0	2	2	999
85.	Seed length mm	0.6	0.5	0.6	0.7	0.7	0.5	0.6	999.0
86.	Diameter of tuft cm (Dracophilus, Namibia)	999	999	999	999	999	999	11	12

999	1	0	0	999	1	1	1	0	1	1	1	1	1	999	999	1
999	2	0	0	0	0	2	2	0	0	2	2	2	2	0	0	2
999	1	3	1	1	1	2	3	2	2	1	2	2	1	2	2	1
999	1	2	0	999	1	1	1	999	0	1	0	1	1	999	999	1
999	1	1	0	1	1	1	1	1	0	1	0	1	1	0	1	1
999.0	1.0	0.8	0.7	0.6	1.9	1.0	0.5	1.2	1.0	1.0	0.5	1.0	0.8	1.6	0.7	0.6
999	1	0	1	1	1	0	1	1	1	999	0	1	1	1	1	0
999	1	1	0	1	1	0	0	1	1	1	999	0	1	1	1	2
999	2	2	2	0	2	1	2	2	1	2	999	1	2	0	0	1
999.0	0.6	0.6	0.6	0.6	0.5	0.6	0.7	0.7	0.6	0.6	999.0	0.6	0.4	0.7	0.6	0.4
12	20	17	23	999	999	999	999	999	17	999	14	14	999	999	999	999

1	999	999	1	1	1	1	1
0	0	999	3	2	1	0	0
2	999	999	1	2	2	0	2
1	1	999	1	1	0	1	1
1	1	999	0	1	0	1	1
0.6	999.0	999.0	1.0	0.7	0.9	0.6	0.9
1	999	999	999	999	999	999	999
0	999	999	0	1	0	0	2
2	0	999	1	0	0	0	0
0.6	999.0	999.0	0.8	0.6	0.9	0.6	0.8
999	999	999	999	999	999	999	999

Appendix 4: Specimens examined.

Dracophilus dealbatus

NAMIBIA.—2715 (Lüderitz): Gabis, south-east from mast (–AB), *Hartmann & Dehn 15296* (HBG, WIND); Gabis (mast), 1.5 km from main road (–AB), *Hartmann & Ihlenfeldt 376* (HBG, WIND); Along main road Lüderitz-Oranjemund (–AB), *Mannheimer, C.A. CM 1650* (BOL, WIND); 3.5 km towards Drachenberg, eastern mountains (–AB), *Hartmann 8542* (HBG, WIND); Turn-off to Drachenberg, 15 km south of Grillental (–AB), *Hartmann 8537* (HBG, WIND); Drachenberg 13 km east of Pomona (–AB), *K. Dinter 3784* (B); 10.7 km south of Schwarzenberg (–AB), *Hartmann, Dehn & Jürgens 26123* (HBG, WIND); Just after turn-off towards Pomona (–AB), *Mannheimer, C.A. CM 1394* (WIND); On way into Pomona (–AB), *Mannheimer, C.A. CM 1411* (PRE, WIND); Diamond Area No. 1, Sperrgebiet (–AB), *Mannheimer, C.A. CM 1413* (NBG, WIND); Tsabiams mountain (–BA), *Mannheimer, C.A. CM 2209, CM 2210* (WIND); Footslopes east of Tsabiams mountain (–BA), *Mannheimer, C.A. CM 2189* (WIND); Road between Lüderitz and Oranjemund (–BC), *Mannheimer, C.A. CM 2217* (WIND); Along main road (–BC), *Mannheimer, C.A. CM 1642* (PRE, WIND); Lüderitz-Oranjemund road near central Klinghardts turnoff (–BC), *Mannheimer, C.A. CM 2066* (WIND); North road into Klinghardts (–BC), *Mannheimer, C.A. CM 1653, CM 2448* (WIND); Sandy plain west of Klinghardt mountains, near northern entry road (–BC), *Mannheimer, C.A. CM 1419, CM 1420* (WIND); Western Klinghardt mountains (–BC), *Hartmann & Dehn 15299* (HBG, WIND); At the south-junction to Klinghardt (–BC), *Hartmann & Ihlenfeldt 537* (HBG, WIND); Rocky koppie, north-eastern Klinghardts (–BC), *Mannheimer, C.A. CM 2163A, CM 2164* (WIND); Area of relevés west of Klinghardts (–BC), *Mannheimer, C.A. CM 963A* (WIND); Northern Pietab 2 (–BC), *Hartmann & Dehn 15151* (HBG, WIND); 2 km south-east of Buntfeldschuh (–BC), *Hartmann 8569* (HBG, WIND); 23 km away from camp towards the west, down in sand (–BC), *Hartmann & Ihlenfeldt 522* (HBG, WIND); Western side of main Oranjemund-Lüderitz road, in from Klinghardts turnoff (–BC), *Mannheimer, C.A. CM 963A* (WIND); Klinghardts southern turnoff (–BC), *Mannheimer, C.A. CM 1005* (PRE, WIND); Hill west of Klinghardt (–BC), *Hartmann 8556* (HBG, WIND); West of Klinghardt mountains (–BC), *Hartmann 8566* (HBG, WIND); Klinghardt mountains (–BD), *Mannheimer, C.A. CM 1432A* (WIND); Western Pietab 2, three lighter mountains (–BD), *Hartmann & Dehn 15166* (HBG, WIND); Foot of the Quellkuppe (–BD), *Hartmann & Dehn 15227* (HBG, WIND); Below the Sleepkoppie (–BD), *Hartmann & Ihlenfeldt 504* (HBG, WIND); Gabusib (–BD), *Hartmann & Dehn 15189* (HBG, WIND); Plain north of Dieters camp (–BD), *Mannheimer, C.A. CM 2137, CM 2138, CM 2139, CM 2140* (WIND); Along road from Dieters camp (–BD), *Mannheimer, C.A. CM 2441* (WIND); Red sandy plain with patches of calcrete (–BD), *Mannheimer, C.A. CM 1625A, CM 1625B, CM 1625C, CM 1626* (WIND), *CM 1631* (BOL, WIND); Middle of Dracophilus population near first campsite (–BD), *Mannheimer, C.A. CM 1628* (WIND); Buntfeldschuh, below Kakaomountains (–DA), *Hartmann & Dehn 15309* (HBG, WIND); 4.4 km south of the turn-off to Buntfeldschuh (–DA), *Hartmann 8581* (HBG, WIND); Chameis to Eisenkuppe (–DD), *Hartmann & Dehn 15144* (HBG, WIND); Between Chamnaib and Bogenfels (–DD), *Mannheimer, C.A. CM 2048* (PRE, WIND).

—2716 (Ai-Ais): South of Hoher Rücken (–AA), *Hartmann & Ihlenfeldt 653* (HBG, WIND); Mountain 805, 650-780 m (–CA), *Hartmann, Dehn, Last & Rust 20855* (HBG, WIND); Chamnaub, south-western foothills (–CA), *Mannheimer, C.A. CM 2038, CM 2041* (WIND); NW of Aurus; north of Roter Kamm, on gently sloping coarse red-sandy slopes at base of mountain (–CA), *Mannheimer, C.A. CM 1524A* (BOL, WIND), *CM 1524B* (WIND), *CM 1524C* (PRE, WIND); Koppie west of Aurus (–CA), *Mannheimer, C.A. CM 1510* (WIND); Between turn-off from river and campsite NW of Aurus (–CA), *Mannheimer, C.A. CM 1519* (WIND); South of Uguchab river, to west of Aurus range (–CA), *Mannheimer, C.A. CM 1518B* (BOL, WIND); Chamnaub, southwestern foothills (–CA), *Mannheimer, C.A. CM 2039* (WIND), *CM 2042* (live plant, died); Campsite northwest of Aurus (–CA), *Mannheimer, C.A. 1523* (live plant, died); Towards bowl of Aurus mountains (–CB), *Mannheimer, C.A. CM 1572* (WIND); Plain in bowl of Aurus mountains (–CB), *Mannheimer, C.A. CM 1573* (PRE, WIND); About 6-7 km north of Aurus-holding (–CB), *Hartmann & Ihlenfeldt 1090* (HBG, WIND); Rooiberg (–CB), *Hartmann & Ihlenfeldt 1047* (HBG, WIND); Southern Obib (–DC), *Hartmann & Dehn 15072* (HBG, WIND); Obib huts, north-west of Wasser (–DC), *Mannheimer, C.A. CM 2408, CM 2409, CM 2410, CM 2411* (WIND); North-west of Obib, towards Red Dunes (–DC), *Mannheimer, C.A. CM 1114* (WIND); Plain at NE corner of Skorpion (–DC), *Burke, A. 01122A* (WIND); About 5 km south of Schlafkuppe (–DC), *Burke, A. 01123* (WIND); South of Schlafkuppe (–DC), *Burke, A. 01124* (WIND); Scorpion Mine site, Sperrgebiet, plain below limestone koppie (–DC), *Mannheimer, C.A., Loots, S. & Bartsch, S. CM 794(a)* (WIND); Rosh Pinah to the west, about 8 km (–DC), *Hartmann & Dehn 15057* (HBG, WIND); Obib, 8.3 km north of Rosh Pinah golf course (–DC), *Hartmann 8462* (HBG, WIND); Namuskluft plain (–DD), *Mannheimer, C.A. CM 1973* (WIND); Entrance to Namuskluft (from junction in the steam valley to the left) (–DD), *Hartmann & Ihlenfeldt 973* (HBG, WIND); Entrance to Namuskluft (–DD), *H. Chr. Friedrich 518* (M), *Mannheimer, C.A. 1978* (WIND); Side valley of Namuskluft, 12 km from Rosh Pinah (–DD), *Hartmann & Ihlenfeldt 941* (HBG, WIND); 2 km from Rosh Pinah (–DD), *Hartmann 8483* (HBG, WIND); About 5 km SE of Rosh Pinah (–DD), *Burke, A. 01127* (WIND); Witputz (–DD), *Giess, W. 12873* (M, PRE).

—2816 (Alexander Bay): Karingarab, 8 km from road, flat below first terrace (–AA), *Hartmann & Ihlenfeldt 583* (HBG, WIND); Karingarab, 13 km from road (–AA), *Hartmann & Ihlenfeldt 592* (HBG, WIND); Karingarab, 20 km from road (–AA), *Hartmann & Ihlenfeldt 602* (HBG, WIND); Patrol road along the Obib dune (–BA), *Hartmann & Dehn 15087* (HBG, WIND); On footslope between red dunes and Obib ridge (–BA), *Mannheimer, C.A. CM 2413* (PRE, WIND); Alluvial plain at the eastern foot of the Schakal mountains (–BA), *Hartmann 8646* (HBG, WIND); Western Schakal mountains, 29.4 km north of the turn-off to Daberas (–BA), *Hartmann 8655* (HBG, WIND); West of

Daberas dune (–BA), *Hartmann 8644* (HBG, WIND); Obib mountains (–BA), *Hartmann 8439, 8444* (HBG, WIND); Obib mountains, south (–BA), *Hartmann 8437* (HBG, WIND); Obib mountains about 4 km north of Obib fountain (–BA), *Hartmann 8451* (HBG, WIND); Obib mountains 4.7 km north of Obib fountain, second valley (–BA), *Hartmann 8447* (HBG, WIND); To Obib in the Gumtsavib valley (–BB), *Hartmann & Dehn 15025* (HBG, WIND); 8 km north of Dreigratdrift (–BB), *Hartmann 8429* (HBG, WIND); Valley, north-east behind Lorelei (–BB), *Hartmann 8423* (HBG, WIND); Plain before Lorelei (–BB), *Hartmann 8410* (HBG, WIND); 3 km from Neck (entrance) 6.8 km north of waterfall, neck over sand, before entrance in broad stream valley (–BB), *Hartmann & Ihlenfeldt 1006* (HBG, WIND); Lorelei, on hills near road (–BB), *Hartmann & Ihlenfeldt 1024* (HBG, WIND); Gomtsavib mountain, western side (–BB), *Hartmann & Ihlenfeldt 1001* (HBG, WIND); Gomtsavib, western slope (–BB), *Hartmann & Dehn 15039* (HBG, WIND); Gomtsavib towards the north (–BB), *Hartmann & Dehn 15047* (HBG, WIND); Sendelingsdrift, wash along main road next to gravel plains (–BB), *Mannheimer, C.A. CM 2255* (WIND); Just off main road at turnoff to Skilpad (–BC), *Mannheimer, C.A. CM1085* (WIND); Turn-off at the western side of the Schakal mountains from bridge (= 8 km from Oranjemund gate) (–BC), *Hartmann 8629* (HBG, WIND); Western Schakalsmountains, 12.8 km north of junction to Daberas (–BC), *Hartmann 8659* (HBG, WIND); West edge of Schakal mountains, 2 km north of junction, at dumping place (–BC), *Hartmann & Ihlenfeldt 810* (HBG, WIND); West of Daberas dune (–BD), *Hartmann 8641* (HBG, WIND); Hohenfels, 20km east of Oranjemund (–CB), *G. Williamson 4512* (WIND).

—2817 (Alexander Bay): Nuab pediment (–AA), *B. Strohbach 91* (WIND); Lorelei diamond mine (–AA), *Mannheimer, C.A. CM 1989A, CM 1989B* (WIND).

NORTHERN CAPE.—2816 (Alexander Bay): Just beyond Sendelingsdrift Gate, before Potjiespram turnoff. Richtersveld National Park (–BB), *Mannheimer, C.A. CM 1885,CM 1886, CM 1887* (NBG, WIND); Road out of Richtersveld National Park to Alexander Bay (–BD), *Mannheimer, C.A. CM 1893, CM 1894, CM1895* (NBG, WIND); Road to Alexander Bay (–BD), *Mannheimer, C.A. CM 1896, CM 1897, CM 1898* (WIND); Beauvallon (–DA), *G. Williamson 2950* (BOL); Arris (–DA), *H.W.R. Marloth 6921* (PRE).

UNCERTAIN. — Between Arris Drift and Sendelingsdrift, *Pillans 5720* (BOL); Little Namaqualand, *Pearson 6062* (K); Namaqualand, *G. Williamson 3185* (BOL); Little Namaqualand, Richtersveld, Arris, *Marloth, H.W.R. 6921* (PRE). No locality given, *H.M. Holloway 51, 53, 54, 104* (BOL); *K. Dinter July 1929*; *S.U.G. 75, 8757* (BOL).

D. delaetianus

NAMIBIA.—2615 (Lüderitz): Rotkop gate, 17.7 km towards south (–CD), *Hartmann 8525* (WIND); *Hartmann, Dehn & Jürgens 26116* (HBG, WIND).

—2715 (Lüderitz): Between Jagdkuppe and Tsabiams (–BA), *Hartmann, Dehn, Last & Rust 20912* (HBG, WIND); Plain and footslope west of Tsabiams mountain (–BA), *Mannheimer, C.A. CM 2190, CM 2191, CM 2192, CM 2193* (WIND); Klinghardt mountains - Schlafkuppe (–BC), *Hartmann & Ihlenfeldt 388* (HBG, WIND); North of Namiams (–BD), *Hartmann & Dehn 15198* (HBG, WIND); Between Namiams and Gabusib, two black sandstone hills 800-820 (–BD), *Hartmann & Dehn 15224* (HBG, WIND); Between Namiams and Gabusib (–BD), *Hartmann & Dehn 15218* (HBG, WIND); Namiams plain and saddle (–BD), *Mannheimer, C.A. CM 2135* (BOL, WIND), *CM 2136* (WIND); Plain north of population assessed for Red Data (–BD), *Mannheimer, C.A. CM 1435A* (BOL, WIND), *CM 1435B* (WIND); Klinghardt mountains (–BD), *Mannheimer, C.A, CM 1436* (WIND); Ridge near Namiams (–BD), *Mannheimer C.A. CM 1622* (WIND); Namiams, on footslope (–BD), *Mannheimer, C.A. CM 2147* (WIND); Eastern Sperrgebiet, north of Namiams (–BD), *Mannheimer, C.A. CM 2143* (WIND); Plain east of Klinghardts Mounatins (–BD), *Mannheimer, C.A. CM 2442* (WIND).

—2716 (Ai-Ais): Road verge between Rosh Pinah and Aus (–AB), *Mannheimer, C.A., Bartsch, S. & Loots, S. CM 804* (WIND); Aus - Rosh Pinah road (–AB), *Mannheimer, C.A., Mannheimer, J. & Burke, A. CM 1722* (BOL, WIND): Road between Aus and Rosh Pinah (–AB), *Mannheimer, C.A. CM 2385* (WIND); Aus - Rosh Pinah road, red sandy plain (–AB), *Mannheimer, C.A. CM 858A* (BOL, PRE, WIND), *CM 858B, CM 858D* (WIND); Aus to Witpütz one and a half miles past Pockenbank (–AB), *H.M. Holloway 102* (BOL); About 1 km behind junction towards the east (–AB), *Hartmann & Ihlenfeldt 1110* (HBG, WIND); Near Pockenbank (–AB), *M. Otzen December 1938* (BOL); Near Uguchab (–AC), *Hartmann, Dehn & Jürgens 26007* (HBG, WIND); Stream valley north of the Aurus mountains (–AC), *Hartmann, Dehn, Last & Rust 20869* (HBG, WIND); Pockenbank (–BA), *Dinter 6220* (B, HBG); Campsite in riverbed, just north of Aurus range (–CA), *Mannheimer, C.A. CM 1486* (WIND); Near Witpütz (–DA), *Otzen s.n.* (BOL); Swartkloof mountain, about 9 km from farmhouse towards Witpütz (–DA), *Hartmann 8400* (HBG, WIND); Witpütz to Rooiberg 2 miles west of Witpütz (–DA), *H.M. Holloway 202* (BOL); Farm Zebrafontein , LU87 (–DD), *Giess, J.W.H., Volk, O.H. & Bleissner, B. 5352* (WIND); East of Farm Namuskluft 88 (–DD), *Giess, J.W.H., Volk, O.H. & Bleissner, B. 5352a* (WIND).

—2816 (Alexander Bay): Obib Mountains, 20 miles northwest of Sendelingsdrift (–BA), *L. Bolus (for Dinter) 1941* (PRE).

UNCERTAIN. — Great Namaqualand, *F.Frith 1925* (K); Lüderitzbucht, *Dinter s.n.* (PRE); S.W.A., *Merxmüller 6089* (PRE); Government Gardens Windhoek, *H.M. Holloway 98* (BOL); No locality given, *Dinter October 1922* (K), *N.S. Pillans 1922* (K), *K. Dinter s.n. 18.8.1932* (HBG); *Rev. L.A. Rogers 15.11.1924* (BOL); *S.U.G. 9.6.1932* (BOL).

J. albata

NAMIBIA. —2816 (Alexander Bay): Schakalsberge, (–BA), *Merxmüller 2631* (PRE); Southern Schakalsberge, (–BA), *H. Merxmüller & W. Giess 2631* (M); Dreigrat Mountain, (–BB), *Hartmann & Ihlenfeldt 1014* (HBG, WIND), *Wood, P. PW1, PW2, PW3, PW4, PW5, PW6, PW7, PW8, PW9* (WIND); 4.4 km north of Dreigratdrif towards Rosh Pinah, (–BB), *Hartmann 8426* (HBG, WIND); Dreigratberg southern slope, (–BB), *Noli, D. DN12* (WIND); Dreigratberg foot, southern side, (–BB), *Noli, D. DN9* (WIND); Dreigratberg western slopes, (–BB), *Noli, D. DN11* (WIND); Dreigratberg foot, eastern side, (–BB), *Noli, D. DN10* (WIND); Direction Rosh-Pinah-Lorelei, (–BB), *Hartmann 8405* (HBG, WIND); Daberas Site, (–BB), *Mannheimer, C.A. CM 802* (WIND); Daberas Orange River Mine near administration block, (–BB), *Mannheimer, C.A., Burke, A. & Woods, P. CM 2321* (WIND); Daberas east, (–BB), *Noli, D. DN14* (WIND); Obib upper, (–BB), *Noli, D. DN13* (WIND); Sendelingsdrift ridge, (–BB), *Noli, D. DN 1, DN2, DN3, DN4, DN5, DN6, DN7* (WIND); Sendelingsdrift ridge north, (–BB), *Noli, D. DN8* (WIND); Sendelingsdrif terraces, (–BB), *Mannheimer, C.A., Burke, A. & Woods, P. CM 2322* (WIND); Sendelingsdrif Mine Area in gullys above river, gravel terrace, (–BB), *Mannheimer, C.A. CM 2233, CM 2235, CM 2236, CM 2237, CM 2243, CM 2248, CM 2249* (WIND), *Mannheimer, C.A. CM 2234* (PRE, WIND); Sendelingsdrif, (–BB), *Ihlenfeldt 1360* (HBG, M, PRE), *H.-Chr. Friedrich* 507b (M), *Merxmüller & Giess 2551, 3524* (M), *H. Hall 27.10.1955* (BOL), *H. Hall* 1340 (NBG), *J. Luckhoff July* 1934 (BOL), *P.A.B. van Breda* 904 (BOL), *Mannheimer, C.A. CM 2266* (WIND);Slope of mountain to east of Sendelings security gate, (–BB), *Noli, D. DN31* (WIND); 5km up valley to east of Sendelings Pump Station, (–BB), *Noli, D. DN30* (WIND); North of Orange River, (–BB), *Hartmann & Dehn 15055* (HBG, WIND); Kahanstal, (–BB), *Dinter 4736* (K), *8195* (B, HBG, M); Southern end of "albata" valley, base of koppie, (–BB), *Noli, D. DN32* (WIND); Auchas lower, top of mountain range overlooking deposit, on stony koppie, (–BC), *Noli, D. DN28, DN29* (WIND); North of Daberas. Prominent dolomite koppie, western slope, (–BC), *Noli, D. DN21* (WIND); Daberas Meso, very far up river in gulley, northern slope, (–BD), *Noli, D. DN27* (WIND); Daberas, Kalkrücken Mountain, (–BB), *Noli, D. DN15, DN16, DN17* (WIND); Daberas, Kalkrücken Mountain, northern end, western slope, (–BD), *Noli, D. DN18* (WIND); Daberas koppie to south-east of Kalkrücken, (–BD), *Noli, D. DN19* (WIND); Daberas, (–BD), *Noli, D. DN22, DN23, DN24, DN25, DN26* (WIND); Daberas west, dolomite koppie, (–BD), *Noli, D. DN20* (WIND); Nach Obib, (–BD), *Hartmann & Dehn 15018* (HBG, WIND).

NORTHERN CAPE. —2816 (Alexander Bay): Richtersveld, few miles south of Sendelingsdrif, (–BB), *J.P. Roux 924* (BOL); Hill west of Arris Drift, Little Namaqualand, (–BB), *Pillans 5039* (BOL).

UNCERTAIN. —Richtersveld, *J. Archer A741.*

J. attenuata

NAMIBIA. —2715 (Lüderitz): South-western slopes of Tsabiams mountain, (–BA), *Mannheimer, C.A. CM 2194* (WIND); Rocky koppie north of dune poort on road into north Klinghardts and Tsabiams, (–BC), *Mannheimer, C.A. 2446* (WIND), *Mannheimer, C.A. CM 1638* (PRE, WIND); Plain east of Klinghardts, (–BC), *Mannheimer, C.A. CM 2151* (live plant, died); Klinghardt Mountains - Schlafkuppe/N-junction towards north-west, (–BC), *Hartmann & Ihlenfeldt 387* (HBG, WIND); North-eastern Klinghardts, (–BD), *Mannheimer, C.A. CM 2152* (WIND); Klinghardts main basin, (–BD), *Mannheimer, C.A. CM 1003, CM 2764* (WIND); Rocky slope, north-eastern Klinghardts, (–BD), *Mannheimer, C.A. CM 2174* (WIND); Plain north of Dieters camp (Gabusib), (–BD), *Mannheimer, C.A. CM 2142* (WIND); Along road north from Dieters camp (Gabusib), near the camp, (–BD), *Mannheimer, C.A. CM 2440* (WIND); Red sandy plain, (–BD), *Mannheimer, C.A. CM 1627* (WIND).

—2716 (Ai-Ais): Witpűtz, Tsaus Sandberg, (–AA), *W. Wendt 18/7* (HBG, WIND); Phyllobolus plain near Heioab, (–AC), *Mannheimer, C.A. CM 1608* (WIND); North-west of Aurus, north of Roter Kamm, (–CA), *Mannheimer, C.A. CM 1525* (WIND); Mountain top, (–CA), *Mannheimer, C.A. CM 1522* (WIND); Mountain 805, (–CA), *Hartmann, Dehn, Last & Rust 20856* (HBG, WIND); Aurus basin, (–CB), *Mannheimer, C.A. CM 1571, CM 2425* (WIND); Plain near Aurus mountain camp, (–CB), *Mannheimer, C.A., Loots, S. & Bartsch, S. CM 782* (WIND); Obib Mountains, (–DC), *Hartmann & Dehn 15070* (HBG, WIND); Between Obib and Schlafkuppe, (–DC), *Hartmann & Dehn 15075* (HBG, WIND).

—2816 (Alexander Bay): Schakals Mountains, hill north of Rooilepel, (–BA), *Hartmann 8650* (HBG, WIND); Schakals Mountains, 8.9 km north of turn-off to Daberas, (–BC), *Hartmann 8668* (hbg, WIND); Junction at the western side of the Schakal Mountains at bridge 8 km from Oranjemund gate, (–BC), *Hartmann 8628* (HBG, WIND); West margin of Schakal Mountains, 2 km north of junction, at dumping site, (–BC), *Hartmann & Ihlenfeldt 807* (HBG, WIND); West margin of Schakal Mountains, about 3 km south-west of Rooilepel, (–BC), *Hartmann & Ihlenfeldt 822* (HBG, WIND);

Schakalsberge, (–BC), *H. Merxmüller & W. Giess 2677* (M); Southern Schakalsberge, *H. Merxmüller & W. Giess 2643* (M); Skilpad, (–BC), *Mannheimer, C.A. CM 1083* (WIND).

UNCERTAIN. — *H. Holloway 28* (BOL); Government Gardens Windhoek, *H.M.Holloway 3* (BOL); *S.U.G. 9256* (BOL).

Juttadinteria ausensis

NAMIBIA. —2615 (Lüderitz): 6 km from junction to Letterkuppe, (–DA), *Hartmann, Dehn & Jűrgens 26032* (HBG, WIND); 1.2 km east of Tsauchaib neck, (–DA), *Hartmann & Ihlenfeldt 236* (HBG, WIND); Just east of the Tsauchaib koppies, (–DA), *Mannheimer, C.A. CM 2640A, CM2640B, CM2640C, CM 2640D, CM 2773 , CM2800, CM 2801, CM 2802* (WIND), *CM 2803* (Bol, PRE, WIND); Tsauchaib, on the plain, (–DA), *Hartmann & Ihlenfeldt 175* (HBG, WIND); 18 km from Kaukausib camp, left of the road, (–DC), *Hartmann & Ihlenfeldt 360* (HBG, WIND); 36 km from Kaukausib fountain, (–DD), *Hartmann & Ihlenfeldt 276* (HBG, WIND); 3 km north-east of junction, Mountain 914, (–DD), *Hartmann, Dehn, Last & Rust 20894* (HBG, WIND); South of Agab, 10 km south of junction from mountain, (–DD), *Hartmann, Dehn, Last & Rust 20883* (HBG, WIND).

—2715 (Lüderitz): Numitsoab, south-western slope, (–BB), *Hartmann, Dehn, Last & Rust 20909* (HBG, WIND); South of the Jagdkuppe, limestone koppie, (–BB), *Hartmann, Dehn, Last & Rust 20911* (HBG, WIND); Hőchster, east of Schlafkuppe, (–BD), *Hartmann & Ihlenfeldt 468* (HBG, WIND); Southern side of Schlafkuppe, (–BD), *Hartmann & Ihlenfeldt 425* (HBG, WIND); Western Pietab 2, three pale mountains (–BD), *Hartmann & Dehn 15173* (HBG, WIND); Between Namiams and Gabusib, two black sandstone hills, (–BD), *Hartmann & Dehn 15221* (HBG, WIND).

—2716 (Ai-Ais): Tsaus border, about 1 km before the junction in mountains towards east (–AB), *Hartmann & Ihlenfeldt 1105* (HBG, WIND).

UNCERTAIN. —Aus, *E. Phillips s.n**. (K); *Lewis 543/18:G.L.Phillips 381/19** (BOL); *De Winter 6553* (PRE).

*Many of the old collectors recorded Aus as a locality localities for almost anywhere in the vicinity of that town, probably due to it being the closest town. These have been listed locality uncertain because the species has not been seen or recorded by any other workers in the Aus quarter-degree square.

J. deserticola

NAMIBIA. —2514 (Spencer Bay): Spencer Bay, about 1 km from the sea, (–DD), *Mannheimer, C.A., Mannheimer, J. & Burke, A. CM 1682* (WIND); Top of steep rocky hill in the middle of the dune sea west of Spencer Bay (–DD), *Mannheimer, C.A., Mannheimer, J. & Burke, A. CM 1687* (WIND).

—2615 (Lüderitz): Near Angra Pequena (–CA), *Marloth 4688* (BOL); Lüderitz Bay (–CA), *Frith, F. M3* (K), *Dinter Feb. 1929* (B), *Engler, A. 6830* (BOL), *Merxmüller, H. & Giess, W. 2437* (M); Lüderitzbucht, between the harbour bay and Diaz Point (–CA), *Friedrich, H.-Chr. 529/1, 529/2* (M); Lüderitz Peninsula, (–CA), *Mannheimer, C.A., Maggs-Kölling, G.L. & Loots, S. CM 2635* (WIND), *Archer 306, 606* (BOL), *Mrs. J. Heydt S.U.G. 12588* (BOL); Lüderitz Peninsula on road to black ridge, (–CA), *Mannheimer, C.A., Mannheimer, J. & Burke, A. CM 1696* (GRA, WIND); Lüderitz area, road to Diaz Point, (–CA), *Mannheimer, C.A. CM 2352, CM 2353* (WIND); 2.3 km south of Diaz Point to Halifax, just after junction, (–CA), *Hartmann 8511* (WIND); Lüderitz , at Fjord, (–CA), *Mannheimer, C.A. CM 2348* (WIND); Lüderitz, 2 km south of town, where railway and road to peninsula part, (–CA), *Hartmann 8500* (WIND); Agate-beach, north of Lüderitz on summit near beach, (–CA), *Hartmann & Ihlenfeldt 247* (WIND); Nautilus hill (–CA), *Mannheimer, C.A. CM 2720, CM 2721, CM 2722 (CHECK WHERE!!!!)*; Sandy ravine east of Nautilus, Lüderitz (–CA), *Giess, W. & van Vuuren, D. 725* (K, M, WIND); Lüderitzbucht hills (–CA), *Pillans 5863?* (BOL); Next to main road between Lüderitz and Aus (–CA), *Mannheimer, C.A. CM 1657* (WIND); 11.6 km south of Kolmanskop (–CA), *Hartmann 8516* (HBG, WIND); South of Klein Bootbaai (–CA), *Hartmann, Dehn & Jürgens 26099* (HBG, WIND); Elizabeth Bay (–CC), *Hartmann 8520* (HBG, WIND); Between Elizabeth Bay and Kolmanskop, towards coast, along old mine road, (–CC), *Mannheimer, C.A. CM 2001* (WIND); 11.6 km from junction to Elizabeth Bay (–CC), *Hartmann 8524* (HBG, WIND); Proposed wind farm site, east of Grosse Bucht, (–CC), *Mannheimer, C.A., Mannheimer, J. & Burke, A. CM 1708* (WIND); Valley east of mine plant at Elizabeth Bay (–CD), *Williamson, G. 4550* (WIND); Grillental above the houses (–CD), *Hartmann & Dehn 15289* (HBG, WIND); Zutowkopf (–CD), *Range 1885* (B!).

—2715 (Lüderitz): Dreizackberg (–AB), *Mannheimer, C.A. CM 2732, CM 2733* (WIND); Turn-off to Drachenberg, 15 km south of Grillenthal (–AB), *Hartmann 8538* (HBG, WIND); Drachenberg (–AB), *Mannheimer, C.A. CM 2740, CM 2741* (WIND); Pomona, (–AB), *G. Williamson 5103* (WIND); Pomona, southern part, excavation fields (–AB), *Hartmann & Dehn 15247* (HBG, WIND); Pomona pumphouse at blue ridge (–AB), *Mannheimer, C.A. CM 1398, 1400, 1401* (WIND); Road to Pomona (–AB), *Mannheimer, C.A. CM1410* (WIND); About 10 km from Pomona town by winding road (–AB), *Mannheimer, C.A. CM 913* (BOL, WIND); Just north of Pomona (–AB), *Mannheimer, C.A. CM 926* (PRE, WIND), *Mannheimer, C.A. CM 931* (live plant, died); 5 km north of Pomona (–AB), *Hartmann & Dehn 15252* (HBG, WIND); Van Rheenen Bay, (–AB), *Mannheimer, C.A., Maggs-Kölling, G.L. & Loots, S. CM 2649* (WIND); Pomona to Grillental (–AB), *Hartmann & Dehn 15261* (HBG, WIND); Gabis Mast, 1.5 km from the main road (–AB), *Hartmann & Ihlenfeldt 371* (HBG, WIND); Northern turn-off to Albatross Rock (Prinzenbay) (–AB), *Hartmann & Dehn 15255* (HBG, WIND); House near Schwarzeberg (–AD), *Hartmann 8553* (HBG, WIND); Road between Pomona and Bogenfels (–AD), *Mannheimer, C.A. CM 951* (WIND); About 13 km south of Pomona on road to Bogenfels, (–AD), *Mannheimer, C.A. CM 957* (BOL, WIND); Near Bogenfels (–AD), *Hartmann & Dehn 15233* (HBG, WIND); Bogenfels towards Pomona (–AD), *Hartmann & Dehn 15239* (HBG, WIND); Pomona town (–AD), *Mannheimr, C.A. CM 1668* (live plant, died); Along main road between Lüderitz and Oranjemund (–BC), *Mannheimer, C.A. CM 1643* (WIND), *Mannheimer, C.A. CM 2212, CM 2213, CM 2215, 2216* (WIND); Near central Klinghardts turnoff (–BC), *Mannheimer, C.A. CM 2065* (WIND), *Mannheimer, C.A. CM 2064* (live plant, lost); Western side of main Oranjemund-Lüderitz road, in from Klinghardts turnoff, (–BC), *Mannheimer, C.A. CM 972* (WIND); Just off of main road between Lüderitz and Oranjemund along the road to Bogenfels (–BC), *Mannheimer, C.A. CM 2377, 2378, 2379* (WIND); Base of the Klinghardts Mountains (–BC), *Williamson, G. 3257* (BOL); At the south junction to the Klinghardts (–BC), *Hartmann & Ihlenfeldt 535* (HBG, WIND); 23 km from camp towards west, below in sand (–BC), *Hartmann & Ihlenfeldt 521* (HBG, WIND); Hill in the west of Klinghardt (–BC), *Hartmann 8555, 8557* (HBG, WIND); Klinghardts Mountains (–DA), *Williamson, G. 3451/8451 28.4.1985* (BOL); Buntfeldschuh (–DA), *Dr. Schäfer 622* (BOL); Buntfeldschuh – at the edge of the clifftop (–DA), *Hartmann 8575* (HBG, WIND); 4.4 km south of the turn-off towards Buntfeldschuh (–DA), *Hartmann 8580* (HBG, WIND); South of Buntfeldschuh (–DA), *Merxmüller, H. & Giess, W. 2462* (M, PRE); 15.9 km north of Chameis gate (–DA), *Hartmann 8583* (HBG, WIND); 98 km north of Oranjemund entry to mine WNW of Klinghardt Mountains on road to Pomona (–DC), *Williamson, G. 4949* (WIND); 4.6 km north of Chameis Gate (–DC), *Hartmann 8589* (HBG, WIND); 10 km south of Chameis gate (110 km north of Oranjemund) WNW of Klinghardt Mountains on road to Pomona (–DC), *Williamson, G. 5079* (WIND); Hills east of Bakers Bay (–DC), *Williamson, G. 5122* (WIND); Chameis Bay (–DC), *Hartmann 8593* (HBG, WIND);Chameis Bay, 6 km towards the east (–DC), *Hartmann 8598* (HBG, WIND); 6 km south of Chameis gate, in plain behind first chain (–DD), *Hartmann & Ihlenfeldt 567* (HBG, WIND); Chameis gate – south, 14.6 km (–DD), *Hartmann 8601* (HBG, WIND); Chameis to Eisenkuppe (–DD), *Hartmann & Dehn 15148* (HBG, WIND); Sandy plain at the Buchubergen (–DD), *Dinter 6517* (B, HBG, K, M, NBG, SAM); Buchuberg (–DD), *Range, P. 603, 2639a* (HBG); South of Buchuberg (–DD), *Range, P. May 1909* (B); Boegoeberg, plain in east (–DD), *Hartmann & Dehn 15138* (HBG, WIND);

—2716 (Ai-Ais): High ridge, 19 km north of Karingarab/39 km north of junction (–CC), *Hartmann & Ihlenfeldt 634* (HBG, WIND);

—2815 (Oranjemund): Coastal mining area, Affenrücken, behind old buildings, (–BB), *Bartsch, S., Klaassen, E.S. & Loots, S. SB 1375* (WIND); Boegoeberg, west, about 13.7 km from the mountain peak (–BB), *Hartmann 8620* (HBG, WIND);

—2816 (Alexander Bay): Karingarab, 13 km from road, (–AA), *Hartmann & Ihlenfeldt 591* (WIND); Karingarab, 8 km from road/9 km from the junction (–AA), *Hartmann & Ihlenfeldt 658* (HBG, WIND); Karingarab, 20 km from road (–AA), *Hartmann & Ihlenfeldt 603* (HBG, WIND); 18 km south of Wolwekop (–AC), *Hartmann 8624* (HBG, WIND); 14 km north of Oranjemund gate (–AD), *Hartmann 8626* (HBG, WIND);

NORTHERN CAPE. —2816 (Alexander Bay): Karroid hills between Dun Vley and Groot Doorn above S. bank of Orange River (–DA), *Pillans 5692* (BOL); Kortdoorn, near Alexander Bay (–DA), *Roux, J.P. 48* (BOL); Grootderm (–DA), *Hall, H. 18.2.1953* (BOL), *Hall, H. 591* (NBG); Swartwater, Little Namaqualand (–DD), *H. Herre S.U.G. 9046* (BOL);

—Locality uncertain: no locality given, *Marloth, R. s.n. 1928* (K), *Range, P. 1739*; Namaqualand, *Dr. A. Tischer 1928* , *Marloth 8* (K); *Williamson, G. 3443* (BOL); *Holloway, H.M. 98A* (BOL); *Nat. Bot. Gardens 1731/27* (BOL); Great Namaqualand *Brown, N.E. April 1929* (K).

J. simpsonii

NAMIBIA. —2615 (Lüderitz): Southern Koichab, in front at the mountain range (–AD), *Hartmann & Ihlenfeldt 10* (HBG, WIND); South Koichab, second mountain range, to the right, (–AD), *Hartmann & Ihlenfeldt 104* (HBG, WIND); Kovisberge foothills, (–CB), *Mannheimer, C.A. CM 1661* (WIND); Kovisberge, (–CB), *Hartmann 8495* (HBG, WIND), *W. Giess 2408* (M), *Mannheimer, C.A. CM 1689, CM 1692, CM2270* (WIND), *Hardy & De Winter 1331* (BOL); Northern Kovis Mountains, (–CB), *Hartmann, Dehn & Jűrgens 26056* (HBG, WIND); Kovisberge, northern koppies, (–CB), *Hartmann & Ihlenfeldt 139* (HBG, WIND), *Mannheimer, C.A. CM 2368, CM 2369, CM 2370, CM 2371* (WIND); Kovis camp area, (–CB), *Mannheimer, C.A. CM 2365, CM 2366* (WIND); South-eastern face of the Kovisberg, (–CB), *Merxműller & Giess 28484* (M); Kovisberge, valley east of mountain and north-eastern slopes, (–CB), *Mannheimer, C.A. CM 2633* (WIND); Kovisberge south, (–CB), *Mannheimer, C.A. CM 2356* (WIND); Koichab Pan, southern side of the west-east mountain range, (–CB), *Hartmann & Ihlenfeldt 54* (HBG, WIND); Southern Koichab, mountain chain to right, (–CB), *Hartmann & Ihlenfeldt 104* (HBG, WIND); On face further south, (–CB), *Hartmann & Ihlenfeldt 127* (HBG, WIND); 40 miles east of Lüderitzbucht (–DA), *Otzen, M 7.7. 1939* (BOL); Halenberg, (–DA), *Dinter s.n.* (B, K), *Dinter 6014* (B, HBG, M), *Herre s.n. 1966* (M), *Merxműller & Giess 3456* (M), *Mannheimer, C.A. CM 1672* (BOL, WIND), *Mannheimer, C.A., CM 1673* (PRE, WIND), *NBG 1759/27* (BOL), *Pillans,N.S. 5861* (BOL); Halenberg, north of road, (–DA), *Hartmann 8489* (HBG, WIND); Near Halenberg about 25 km E. of Lüderitzbucht (–DA), *J. Luckhoff 7/34* (BOL); Just west of Halenberg, koppie north of road (Hőhlenberg), (–DA), *Mannheimer, C.A. CM 1666, CM 1667* (WIND); Halenberg quarry, (–DA), *Mannheimer, C.A. CM 2381* (WIND), *Mannheimer, C.A. CM 2382* (PRE, WIND).

UNCERTAIN. — *K. Dinter 54* (B, BOL, HBG)
Morant, F. (BOL 17329), *Dinter s.n.* (B 2001-11), *Holloway, H.M. 99* (BOL), *Otzen, M. s.n. in hort Dec. 1938* (BOL), *NBG 520/55* (BOL).

N. cinerea

NAMIBIA.—2615 (Lüderitz): Grillental, (–CD), *Hartmann & Dehn 15288* (HBG, WIND), *Mannheimer, C.A., Loots, Dauth & Roberts CM 872* (WIND), *Mannheimer, C.A. CM 1392* (PRE, WIND), *Mannheimer, C.A. CM 1393* (live plant, died), *Mannheimer, C.A. & Mannheimer CM 2372* (PRE, WIND); 18.5 km from CDM gate at Rotkop direction Oranjemund, (–CD), *Hartmann 8533* (HBG,WIND); windy valley near Pomona, (–CD), *Mannheimer, C.A. CM 1395* (PRE, WIND), *Mannheimer, C.A. CM 1396* (live plant, died), *Mannheimer, C.A. CM 1397, CM 2374* (WIND); 30 km south of Rotkop, near Lüderitz, (–CD), *G. Williamson 3039* (BOL).

—2715 (Lüderitz): Pomona to Grillenthal, (–AB), *Dinter s.n. 1939* (BOL), *Hartmann & Dehn 15262* (HBG, WIND); Dreizackberg, (–AB), *Mannheimer, C.A. CM 2729* (PRE, WIND); 4 km east of Pomona, (–AB), *G. Williamson 5108* (WIND); near Pomona, (–AB), *C. Klak 613* (BOL); 10 km from Pomona, (–AB), *Mannheimer, C.A. CM 910* (BOL, PRE, WIND), *Mannheimer, C.A. CM 911* (PRE, WIND); north of Pomona (–AB), *Mannheimer, C.A. CM 932* (WIND); Pomona Pumphouse west at blue ridge, (–AB), *Mannheimer, C.A. CM 1399* (PRE, WIND), *Mannheimer, C.A. CM 1402, CM 1404, CM 1405, CM 1406, CM 1407* (WIND), *Mannheimer, C.A. CM 1403* (PRE), *Mannheimer, C.A. CM 2375* (WIND), *Mannheimer, C.A. CM 2644* (K, WIND); Schwarzeberg, (–AB), *Mannheimer, C.A. CM 1412, CM 2373* (WIND).

UNCERTAIN.—Angra Pequena, (2615CB??), *Marloth 4680** (BOL, NBG, PRE); S.W. Expedition, *Schwantes 1756/27* (BOL).

*Many of the old collectors recorded "Angra Pequena", "Lüderitz" or "Lüderitzbucht" as localities for almost anywhere in the Sperrgebiet (Diamond Areas 1 & 2). This has been listed locality uncertain because the species has not been seen or recorded by any other workers in the Lüderitz quarter-degree square.

N. ponderosa

NAMIBIA.—2615 (Lüderitz): Lüderitzbucht (–CB), *F. Eberlanz S.U.G.3(1946)* * (BOL); North of Sturmhaube (–CB), *Hartmann & Ihlenfeldt 11, 117* (HBG, WIND); Kovisbergen (–CB), *Hardy & De Winter 1330* (BOL), *Hartmann 8494* (HBG, WIND), *Mannheimer, C.A., Mannheimer, J. & Burke, A. CM 2271* (BOL, WIND), *Mannheimer, C.A., Mannheimer, J. & Burke, A. CM 1690,CM 2269* (PRE, WIND), *Mannheimer, C.A., Mannheimer, J. & Burke, A. CM 1688, CM 1693, CM 1694* (WIND); Northern Kovisbergen (–CB), *Hartmann, Dehn & Jürgens 26058* (HBG, WIND); Kovisbergen, northern slopes (–CB), *Mannheimer, C.A. & Mannheimer, J. CM 2367* (PRE, WIND); Kovisbergen, northern koppies (–CB), *Hartmann & Ihlenfeldt 135* (HBG, WIND); Kovisbergen, north-eastern slopes (–CB), *Mannheimer, C.A. CM 2632* (BOL, K, MISS, PRE, WIND); Southern Kovisbergen (–CB), *Giess 2049* (M), *Mannheimer, C.A., Mannheimer, J. & Burke, A. CM 1714, CM 1715, CM 1716, CM 1717* (WIND), *Mannheimer, C.A. & Mannheimer, J. CM 2355* (BOL, WIND), *Mannheimer, C.A. & Mannheimer, J. CM 2354, CM 2357, CM 2358, CM 2359, CM 2360* (WIND); Kovisbergen foothills (–CB), *Mannheimer, C.A. CM 1660* (BOL), *Mannheimer, C.A. CM 1658, CM 1695* (PRE, WIND), *Mannheimer, C.A. CM 1659* (WIND); Koppie NW of Höhlenberg (–DA), *Mannheimer, C.A. CM 1674* (BOL, PRE, WIND), *Mannheimer, C.A. CM 2811* (WIND); Halenberg quarry (–DA), *Mannheimer, C.A. CM 2380* (PRE, WIND); Halenberg, on mountain near quarry (–DA), *Mannheimer, C.A. CM 2630* (K, WIND); Halenberg (–DA), *Pillans 5951* (BOL), *M. Otzen s.n., July 1939* (BOL, K), *Merxmüller & Giess 3458* (M), *Hartmann 8492* (HBG, WIND).

* Many of the old collectors recorded "Angra Pequena", "Lüderitz" or "Lüderitzbucht" as localities for almost anywhere in the Sperrgebiet (Diamond Areas 1 & 2). It is unlikely that *N. ponderosa* was actually found at Lüderitzbucht.