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UNIVERSITY OF CAPE TOWN

**PHYLOGENY AND CHARACTER EVOLUTION IN THE *LAMPRANTHUS* -  
GROUP (AIZOACEAE - RUSCHIOIDEAE)**

Thesis submitted for the degree of

DOCTOR OF PHILOSOPHY

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University of Cape Town

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**ABSTRACT**

The phylogenetic position of the *Lampranthus* – group (Ruschioideae, Aizoaceae), with particular emphasis on the large genus *Lampranthus*, was studied using morphological characters and DNA sequences from the *trnL* – *trnF* region of the chloroplast genome, the nuclear ribosomal internal transcribed spacer (ITS) region and the 5S non-transcribed spacer. Phylogenies of 59 species in 29 genera of succulent Aizoaceae, including two species from subfamily Mesembryanthemoideae, are presented. Due to an inadequate number of informative sites within the Ruschioideae (31 for *trnL* – *trnF*,  $ri = 0.840$ ; 57 for ITS,  $ri = 0.457$ ), the *trnL* – *trnF* and ITS regions are found to be unsuitable for phylogenetic investigations at specific and generic level. The 5S spacer proves useful at generic level, but fails to reveal well-supported phylogenies above generic level. On account of the relatively low number of informative sites across the Ruschioideae a recent diversification of the succulent Aizoaceae is hypothesized. Although each of the separate analyses, i.e. the morphological data and each of the three gene regions, yielded very poorly resolved and poorly supported phylogenies, the combined analysis of all available data resulted in a single highly resolved tree. It is shown that *Lampranthus* N.E.Br. in its present circumscription is not monophyletic. A “core” of species of *Lampranthus* is well supported with numerous species of *Lampranthus* more closely related to other genera. At a higher taxonomic level, the data also do not support a monophyletic *Lampranthus* - group. However, many of the intergeneric relationships remain poorly supported so that a redefinition of the *Lampranthus*-group is premature. The circumscription of the informal groups within the Ruschioideae, including the *Lampranthus* – group, has so far mainly been based on the shared presence of a particular type of fruit. Fruits of the *Lampranthus* – group are characterized by long diverging expanding keels, broad valve wings and the absence of a closing body. The present data implies that this fruit type is homoplasious.

Three new genera are recognized (*Ruschiella*, *Cornigeria*, *Pustulesia*). *Braunsia*, *Enarganthe*, *Zeuktophyllum*, *Oscularia* and *Lampranthus* are recircumscribed and a conspectus for *Lampranthus* is provided.

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**Note**

Data sets referred to in the text, including details of the exclusion sets, are stored as a Nexus file for use with PAUP\* (Swofford 2000) on a discette included with this thesis.

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## CHAPTER 1

### GENERAL INTRODUCTION

#### 1. 1. Introduction

Aizoaceae Martynov consists predominantly of succulent, annual to perennial herbs, subshrubs or shrubs. One hundred and twenty seven genera, comprising ca. 2500 species, are distributed in arid parts of the tropical and subtropical zones of both hemispheres, with the majority of species found in the winter rainfall region of Southern Africa (Hartmann 1991, 1993). Their diversity has been highlighted by various authors (e.g. Jürgens 1986, Hartmann 1991, Ihlenfeldt 1994). The succulent Aizoaceae include both leaf and stem succulents and range from woody shrubs which may grow to 3 m tall (e.g. *Stoeberia*) to highly reduced, compact and sunken forms (e.g. *Lithops*, *Fenestraria*).

Over the last 100 years there has been extensive research into the morphology and taxonomy of the succulent Aizoaceae, most notably by N. E. Brown (1921, 1929), L. Bolus (1950a-b, 1954, 1958, 1962, 1965), G. Schwantes (1947, 1952, 1957), H.-D. Ihlenfeldt (1960, 1971a-c; 1975, 1985, 1994) and H. E. K. Hartmann (1977, 1979, 1981, 1983, 1988, 1989, 1991, 1993, 1996, 1998a-c, 1999). In contrast to many other groups where numerous floral differences exist among species and groups, floral morphology is relatively uniform among the succulent Aizoaceae. Therefore, other character suites have had to provide the basis for classification in this group. The early botanists, such as De Candolle, Haworth and Salm Dyck, based their classification on vegetative structures. Later a classification was developed that was based largely on the morphology and the number of nectaries (e.g. Rappa 1912, Rappa & Camarrone 1953). This classification coexisted for many years with the currently accepted one, based primarily on placentation and fruit morphology (e.g. Brown 1921, Schwantes 1947, 1952, 1957). Although in both classifications the groupings of the two subfamilies Ruschioideae and Mesembryanthemoideae corresponded, they showed marked differences in generic delimitations. Ihlenfeldt (1960) later proposed that Schwantes' (1947) classification, although it needed improvement, appeared more natural as it gave fruit characters the greatest priority followed by floral and vegetative characters.

In the past, most attention has focused on the highly succulent groups, such as *Lithops*, *Conophytum*, *Cheiridopsis*, *Glottiphyllum* and *Faucaria*. For many of the shrubby groups such as *Ruschia*, *Drosanthemum*, *Delosperma*, *Antimima* and *Lampranthus*, which make up about a quarter of the succulent Aizoaceae (Table 1. 1), no workable taxonomies exist. A comprehensive summary of the taxonomic literature is given by Hartmann (1991).

#### 1. 2. Classification of the Aizoaceae

Bittrich and Hartmann (1988) reviewed the taxonomic history of the Aizoaceae and its various circumscriptions, which also incorporated the *Mollugo* - group (e.g. Pax 1889, Ihlenfeldt & Straka 1962).

Arguments based on non-molecular characters have been put forward, which suggest that, after separation of the *Mollugo* – group (as done by Hutchinson, 1926, by establishing the Molluginaceae), the Aizoaceae form a monophyletic group (Bittrich & Hartmann 1988). That the Molluginaceae are not closely related to the Aizoaceae *sensu stricto* was later confirmed by *rbcL*, 18S and *atpB* sequences (Rettig *et al.* 1992, Chase *et al.* 1993, Savolainen *et al.* 2000, Soltis *et al.* 1997, Soltis *et al.* 2000) as well as variation in the structure and inverted repeat restriction sites of chloroplast DNA (Downie & Palmer 1994). The presence of bladder cells in the epidermis, the hygrochastic capsule and the perianth stamen tube, may be synapomorphies for the Aizoaceae *sensu stricto* (Bittrich and Hartmann 1988).

In the most recent classification of the family (Hartmann 1993) five subfamilies are recognized: Aizooideae, Tetragonioideae, Sesuvioideae, Ruschioideae and Mesembryanthemoideae (Table 1. 1). Controversy still exists over the level at which these five groups should be recognized. Whereas some workers uphold the view that none of the subfamilies are sufficiently distinct to justify their recognition as formal taxonomic units (Bittrich 1986, Bittrich & Hartmann 1988), other authors disagree and favour a division of the group into several small families (e.g. Friedrich 1955, Ihlenfeldt & Straka 1962). Most frequently used and best established is the name Mesembryanthemaceae Fenzl. Under this family the subfamilies Mesembryanthemoideae and Ruschioideae are included, since both groups share the synapomorphy of petaloid staminodes. On the other hand the three remaining subfamilies share a basic chromosome number of  $n=8$  and a perianth that is petaloid inside and sepaloid outside and these are considered to be synapomorphies of these three groups. However, Bittrich (1986) suggests that there is a close relationship between the Mesembryanthemoideae and the Aizooideae, and that these differ in several respects from the Ruschioideae. In the absence of a formal cladistic analysis, relationships among the five subfamilies, remain uncertain.

Members of the Ruschioideae and Mesembryanthemoideae, comprising 116 genera and about 1900 species, were originally all included in the genus *Mesembryanthemum* L. Sonder (1862) recognised numerous sections in this huge genus, which he largely attributed to earlier classifications by Haworth, Salm Dyck and De Candolle. In many cases N. E. Brown (1921) and L. Bolus used the sections established by the previous workers as a basis to erect new genera. Although the characters of the fruits formed the primary focus in setting up the new genera, habit and other morphological characters continued to be of taxonomic importance.

Several molecular studies exist which explore the phylogenetic position of the Aizoaceae within the order Caryophyllales (Chase *et al.* 1993, Rettig *et al.* 1992, Downie & Palmer 1994, Downie *et al.* 1997, Soltis *et al.* 1997, Soltis *et al.* 2000, APG 1998, Savolainen *et al.* 2000). In all the studies the Aizoaceae are represented by a single species only, i.e. either *Trianthema* (Sesuvioideae), or *Tetragonia* (Tetragonioideae) or *Delosperma* (Ruschioideae). The studies are largely congruent and place the Aizoaceae as sister to a clade comprising Nyctaginaceae and some members of the polyphyletic Phytolaccaceae, with the Molluginaceae as sister to this entire clade. The only exception is that in the analyses of Soltis *et al.* (2000),

based on 18S rDNA, *rbcL*, and *atpB* sequences, the Molluginaceae are placed sister to the Cactaceae and Portulacaceae. So far, the molecular studies have not incorporated enough taxa from the different groups within the Aizoaceae to corroborate the hypothesis of monophyly of this family.

The currently accepted classification of Aizoaceae, based on non-molecular characters (Table 1. 1, Bittrich & Hartmann 1988, Hartmann 1993, 1998b), was followed in this study.

### 1. 2. 1. Classification of subfamily Ruschioideae

Schwantes (1947, 1957) was the first to set up a tribal classification for the Ruschioideae, which he subdivided into five tribes and 22 subtribes (Schwantes 1971). Several of Schwantes' subtribes have been investigated and subsequently amended (e.g. Leipoldtiinae, Hartmann 1983; Erepsiinae, Liede 1989; Ruschiinae, Dehn 1992).

Later Hartmann (1988, 1990) replaced Schwantes' classification and arranged the genera into 12 groups based primarily on fruit structure (Hartmann 1988, 1991). In addition, Ihlenfeldt & Hartmann (1982) discovered that the leaf epidermal surfaces differ considerably between taxa and this could be used to delimit groups (e.g. Ihlenfeldt & Bittrich 1985). Therefore, in addition to a much revised and refined system based on fruit-types (Hartmann 1988), Hartmann (1991, 1998b) also took leaf epidermal and anatomical features into consideration to set up groups within the Ruschioideae (Table 1. 1). Apart from these proposed relationships which may or may not delimit natural groups (Hartmann 1988), no comprehensive study of relationships among genera in the subfamily has been undertaken.

In a study of relationships among the genera of the Ruschiinae, Dehn (1992) suggested that the Lampranthinae, Ruschiinae and Leipoldtiinae form a monophyletic group within the Ruschioideae. Synapomorphies for the group are firm, complete covering membranes with additional closing devices at their distal ends and much sclerotinized fruits (Dehn 1992). In the Ruschiinae and Leipoldtiinae the locules are partially to completely concealed by the presence of a closing body at the exit, which is considered to be a derived characteristic. In contrast, in the Lampranthinae, the locules are blocked by sterile funicles and lack closing bodies (Dehn 1992). However, the hypothesis of a sister group relationship between Lampranthinae and Ruschiinae -Leipoldtiinae has not yet been tested explicitly

### 1. 2. 2. Classification of the *Lampranthus* - group

Schwantes (1957) included six genera in the Lampranthinae Schwantes. These were *Lampranthus* N.E.Br., *Oscularia* Schwantes, *Ebracteola* Schwantes, *Braunsia* Schwantes, *Cerochlamys* N.E.Br. and *Disphyma* N.E.Br. In a slightly amended version of his classification, *Dicrocaulon* N.E.Br. was also included (Schwantes 1971). The subtribe consists of shrubs or stemless shrubs, with 5-locular fruits having covering membranes and occasionally also having closing bodies.

In contrast, Hartmann's *Lampranthus* - group is much enlarged and consists of 14 genera (including ± 286 names of species), but excludes some of the genera originally placed in the Lampranthinae Schwantes

(Table 1. 1). Instead, numerous mono- or bitypic genera have been tentatively included in the *Lampranthus* - group (Hartmann 1988). The uncertainty associated with placement of many genera in the *Lampranthus* - group is reflected in Schwantes' classification, where *Carpobrotus* was placed in its own tribe, whereas *Amphibolia*, *Enarganthe*, *Namaquanthus*, *Scopelogenia*, *Wooleya* and *Zeuktophyllum* were not assigned to any tribe or subtribe. Although *Amphibolia* is no longer part of the *Lampranthus* - group, most of the species then placed in *Amphibolia* are now included in *Lampranthus* (Hartmann 1998a).

As with most of Hartmann's classification, the morphology of the fruits formed the basis for placement of a genus in the *Lampranthus* - group. The diagnostic characters of the *Lampranthus* - group are the same as for the *Lampranthinae sensu* Dehn, but also include mesomorphic to xeromorphic leaves with a thin crystal layer or none at all (Hartmann 1991). However, the group appears to be poorly defined and no phylogenetic study investigating the monophyly of the group has been conducted. In the following discussion, taxonomic and phylogenetic questions surrounding these genera are highlighted.

### 1. 2. 3. The genera of the *Lampranthus* - group

#### *Antegibbaeum* Schwantes ex C.Weber

*Antegibbaeum fissoides* (Haw.) Schwantes is the only species assigned to this genus. The species is a short, clump-forming perennial, with large purple flowers and 6-locular fruits. It occurs in South Africa, from Matjiesfontein to the western part of the Little Karoo. The area receives March and November rain of no more than 250 mm per annum. The plants grow on quartz patches or slopes, often with species of *Gibbaeum*.

Nel (1953) included *A. fissoides* in *Gibbaeum*. However, based on the presence of a holo-nectary and the bracts subtending the flowers in *Antegibbaeum*, this placement is no longer considered justified. It has been suggested that *Ruschia intrusa* (Kensit) L.Bolus, which somewhat resembles *A. fissoides* in habit and leaf morphology, may be a close relative (Hartmann, 1999).

#### *Braunsia* Schwantes

Six species are placed into *Braunsia* (*B. geminata*, *B. apiculata*, *B. stayneri* and *B. vanrensburgii*, as well as the insufficiently known *B. nelii* Schwantes). *B. maximilianii*, which L. Bolus (1965) placed in *Lampranthus*, has recently been reinstated (Klak, 2000a).

The most common and widespread species are *B. geminata* and *B. apiculata*, which are erect dwarf perennials, found from the Cedarberg to Laingsburg and the Little Karoo. *B. stayneri*, *B. vanrensburgii* and *B. maximilianii* are creeping species, which are found on flat rocky surfaces in shallow soil. The latter three species are more localized: *B. stayneri* has been collected only around Soutpan on the northern Ceres Karoo, whereas *B. vanrensburgii* is known from a small area on limestone near Bredasdorp. *B. maximilianii* is known from the area around Nieuwoudtville, in the Vanrhynsdorp district. *B. maximilianii* and *B. apiculata* have remarkable papillate epidermal surfaces, whereas the remaining species have smooth, shiny leaves.

The thick, trigonous, keeled leaves and the echinate seeds have long been considered to be the main

features of the genus. For example, the lack of echinate seeds in one of the species *B. maximilianii*, prompted L. Bolus (1965) to place it rather in *Lampranthus*. This view stood in contrast to the earlier opinion of N. E. Brown (1929). He considered the presence or absence of echinate seeds to be unimportant in terms of generic boundaries, since he had noticed that this character is found in completely unrelated taxa (e.g. some species of *Astridia*, Glen 1986; *Glottiphyllum*, Hartmann & Gölling 1993). The genus has not been revised and relationships to other genera in the group are obscure.

#### *Carpobrotus* N.E.Br.

*Carpobrotus* is a small group of trailing plants with a very uniform appearance. They all possess thick triquetrous leaves, large flowers and fleshy fruits. The latter character is unique within the family. Whereas *Sarcozona*, a bi-typic genus endemic to Australia, has in the past been treated by some as a separate genus (e.g. Prescott & Venning 1984), it was placed in the synonymy of *Carpobrotus* by Hartmann (1993). The Australasian taxa were revised by Blake (1969), while the South African species recently have been treated taxonomically by Wisura and Glen (1993). However the latter treatment did not take into account either the American or the Australian species of *Carpobrotus*.

Seven species are endemic to South Africa. A further seven species (including *Sarcozona*) are restricted to Australia, Tasmania and New Zealand. *C. chilensis* occurs only in Chile and Baja California. The majority of species inhabits low flats at or near the coast. Two exceptions are *C. edulis* subsp. *parviflorus* and *C. mellei*, which are restricted to the mountains of the south-western Cape (Wisura & Glen 1993). *Carpobrotus edulis* subsp. *edulis* is the most widespread species, occurring from Namaqualand to the Eastern Cape and growing both along the coast and inland (Wisura & Glen 1993). *Carpobrotus edulis* is naturalized in many parts of the world, notably in the British Isles (Preston 1988, Preston & Sell 1988) and in areas with a Mediterranean-type of climate (Wisura & Glen 1993).

The presence of fleshy fruits, and therefore loss of many of the capsule features found in other groups, has made it difficult to place *Carpobrotus*. From studies of floral development, Haas (1976) suggested a close relationship to the Leipoldtiinae, whereas Hartmann (1991) placed it tentatively in the *Lampranthus* – group.

#### *Circandra* N.E.Br.

*Mesembryanthemum serratum* was described by Linnaeus (1793). It was later placed by N. E. Brown (1930) in *Circandra* and by L. Bolus (1950a) in *Erepsia*. The species is a sparsely branched shrub to 60 cm tall, with sharply triquetrous leaves that are toothed along the margins. The flowers are yellow and may reach a diameter of 50 mm. Liede (1989) showed that *E. serrata* lacks the typical flower structure, i.e. the presence of a hypanthium, which defines *Erepsia*. As a consequence *Circandra* was reinstated with its single species *C. serrata*. On account of its floral and fruit morphology, a close relationship to some of the yellow flowered species of *Lampranthus* has been proposed (Liede 1989).

*C. serrata* has not been recollected since 1913. The low-lying areas between Tulbagh and Villiersdorp

in the south western Cape, where the few extant herbarium collections were made, have been extensively cultivated and it is now thought that the species is likely to be extinct (Hilton-Taylor 1996).

#### *Enarganthe* N.E.Br.

*Mesembryanthemum octonaria* was described by L. Bolus in the Flowering Plants of South Africa in 1927 and in 1930 it was placed by N.E. Brown into its own genus, *Enarganthe*. The plants form erect woody shrubs with somewhat club-shaped leaves. They produce large purple flowers and multi-locular capsules with tiny closing bodies.

*E. octonaria* (L.Bolus) N.E.Br. is found in a small area in the extremely arid coastal part of Namaqualand, and has been recorded between Augrabies Mountain and the Ploegberg in the Richtersveld. In this area it is common and grows on quartzite and schist slopes.

#### *Erepsia* N.E.Br.

*Erepsia* is a small group of shrubby perennials, of which most species are confined to the south-western Cape. The majority of its species is closely associated with *fynbos* vegetation and are found in both lowland and montane habitats. Liede's revision (1989) recognises 27 species in four sections. Two monotypic genera, *Semnanthe* and *Kensitia*, were also transferred by Liede to *Erepsia*, mainly due to the presence of a hypanthium and awn-like keels in the fruits. Recently, two further species, *E. aristata* and *E. dumensis*, were moved from *Ruschia* and *Lampranthus*, respectively, and included in *Erepsia* (Hartmann 1998a, Klak 2000a). *Erepsia aristata* is remarkable since it represents a disjunction of the genus to Uitenhage, in the Eastern Cape, while the remaining taxa are found from Clanwilliam to George, in the Western Cape.

Some species of *Erepsia*, in particular those of the section *Intectatae*, do not develop a complete hypanthium and these may be closely related to taxa placed in *Lampranthus*. A close relationship to both *Lampranthus* and *Esterhuysenia* has been suggested, based on similar leaf epidermal surfaces and fruit morphology (Liede 1989).

#### *Esterhuysenia* L.Bolus

The genus was established for the single species *E. alpina* L.Bolus, which lacks the broad valve wings typically found in *Lampranthus* and the closing bodies of *Ruschia*. The species was later moved to *Lampranthus* (Rowley 1978). The genus was recently reinstated (Hartmann 1998a) and three species previously placed in *Ruschia* transferred to it, (*E. stokoei*, *E. inlaudens* and *E. drepanophylla*) bringing the total number of species currently in *Esterhuysenia* to four.

The plants form low, often compact cushions that are found in rocky places, often at more than 2000 m.

It is known only from the south-western Cape, where it ranges from Worcester, Ceres and Robertson to

Caledon.

*Hammeria* P.M.Burgoyne

Hartmann (1998a) transferred *Ruschia salteri* to *Lampranthus*, whereas Burgoyne *et al.* (1998) erected the genus, *Hammeria* P.M.Burgoyne, for this species. At the same time a second species, *H. gracilis* P.M.Burgoyne was described (Burgoyne *et al.* 1998). Later, three synonyms of *R. salteri* L.Bolus were found (Klak 2000a). The morphological characters are inconsistent with a placement near *Lampranthus*, and a relationship to the *Titanopsis* - group has been suggested, based on leaf characteristics (Klak 2000a). The plants form low, sprawling shrublets to 30 cm diameter and are found growing occasionally in the flats of the Ceres Karoo and parts of the Great Karoo.

*Lampranthus* N.E.Br.

*Lampranthus* was established by N. E. Brown in 1930 and contains by far the most species in the *Lampranthus* Group. Smith *et al.* (1999) list 227 names, including 13 varieties. However, there are likely to be numerous synonyms and a more realistic estimate of the number of species lies between 60-80. The distribution of the genus extends from Namibia in the north to the south-western Cape. Towards the east *Lampranthus* grows as far as Pondoland in Natal. One species, *L. debilis*, which is found in the south-western Cape, is also found in Australia, where it was probably introduced. Species inhabit lowland areas and are also found at medium to high altitudes in the mountains of the Western Cape.

There is considerable diversity of habit. Some species are slender and prostrate while others are erect subshrubs and a few are robust erect shrubs reaching 70 cm in height. The morphology of the leaves is diverse showing very slender, minutely scabrid leaves to smooth, fairly robust leaves. Leaf shape varies from lunate, falcate to linear or recurved. The colour of the flowers is most commonly pink, purple or white or a combination of these, while yellow, orange and red are rarer. Similarly the size of the flowers varies greatly among the species, ranging between 1-7 cm in diameter.

The differences in habit, leaf and flower morphology were used to group the plants into 13 sections, several of which were manuscript names. The sections are *Aurea* Haw., *Reptantia* Salm Dyck, *Falcati* DC, *Multiradiatus* L.Bolus ined., *Lunati* Willd., *Eximii* L.Bolus ined., *Suffrutices* L.Bolus ined., *Haworthiani* DC, *Tenuifolii* Salm Dyck, *Adunci* (Salm Dyck) Schwantes, *Scabridi* (Haw.) Schwantes, *Amoeni* (Salm) Schwantes and *Blandi* (Haw.) Schwantes. Several species remained unplaced in a section. However, most of the sections are very poorly defined, so that for numerous species a placement in a different section appears equally possible. The sections are defined largely on the morphology of the leaves, followed by the flower size and colour, with one section incorporating only plants with a creeping or mat-forming habit. A broad overview and summary of the characteristics of the sections is given below.

Section *Aurea* contains only yellow- or orange- flowered species. The flowers are solitary, 4-5 cm in diameter and always lack filamentous staminodes. Yet several yellow-flowered species such as *L.*

*promontorii* (*Falcati*), *L. bicolor* (*Tenuifolii*) or *L. explanatus* (*Reptantia*) were not included in this section.

Sections *Eximii*, *Haworthiani*, *Amoeni*, *Blandi* and *Multiradiati* are very similar and include most of the erect, large flowered (4-7 cm in diameter) species of *Lampranthus*. The species included here have 1-3(5)-flowered inflorescences, with pink, purple or white flowers.

In Section *Suffrutices*, the flowers are smaller and usually arranged in a many-flowered inflorescence, which is rare in *Lampranthus*.

Species placed in section *Reptantia* share the characteristic of creeping stems, which root at the nodes. However, numerous species with creeping stems are found outside this section such as *L. spectabilis* (*Amoeni*), *L. tenuifolius* (*Tenuifolii*) and *L. filicaulis* (*Adunci*). No additional characters are present which circumscribe this section, so that it appears unnatural. Recently two species of section *Reptantia*, i.e. *L. maximilianii* and *L. dunensis*, were excluded from *Lampranthus* and moved to *Braunsia* and *Erepsia* respectively (Klak 2000a).

Species placed in section *Tenuifolii* have stems which are often horizontal, but may also be erect and do not root. The leaves are linear and usually punctate.

The largest number of names is found in section *Scabridi*, which consists of species with slender stems and slender, punctate-scabrous leaves. The flowers are always pink, purple or white or a combination of it, ranging between 1-3 cm in diameter. About half of the species included have flowers with their filamentous staminodes collected into a cone, whereas filamentous staminodes are altogether lacking in the remaining species of this section.

Both Sections *Falcati* and *Lunati* have glaucous leaves and the leaves are falcate or lunate respectively. All species in Section *Lunati* have recently been moved to *Oscularia*, including *L. falciformis* from Section *Falcati* (Hartmann 1998a). This genus is characterized by thick, glaucous, trigonous leaves, many-flowered inflorescences, the presence of meronectaries and only slightly sclerified fruits (Hartmann 1998a).

Species placed in Section *Adunci* have slender incurved leaves which are hooked at the apex and this unusual leaf-shape is unique to the species in this section. The flowers are solitary, with their filamentous staminodes and stamens collected into a cone.

More recently, Hartmann (1998a) moved several species from other genera, mainly *Ruschia* and *Amphibolia*, into *Lampranthus*. All the species moved to *Lampranthus* possess fruits with broad, mostly rectangular, valve wings in combination with the absence of an endocarpal closing body. Several species transferred from *Amphibolia* had previously been placed in *Lampranthus* or in *Stoeberia*. This relatively frequent movement among genera suggests that their placement has been traditionally difficult. In addition, two very similar species were excluded from *Drosanthemum* and re-established as species of *Lampranthus*, i.e. *L. otzenianus* (Dinter) Friedrich and *L. uniflorus* (L.Bolus) L.Bolus (Hartmann & Bruckmann 2000). None of the species recently moved to *Lampranthus* have been placed into any of the existing sections.

Investigations into *Lampranthus* were made by L. Bolus (unpubl., mostly as an arrangement of

herbarium specimens at BOL) and later by H. F. Glen (1978). However, in neither case was a workable taxonomy produced. More recent studies in the Ruschioideae (Dehn 1992) indicate that *Lampranthus*, in its present circumscription, does not form a monophyletic group. Dehn (1992) suggested three major groups within *Lampranthus*, which he characterized by the morphology of their fruits. However, he remained uncertain at which taxonomic level these groups may be recognized and to which genera they are most closely related. In a study of the Erepsiinae, Liede (1989) suggested that part of *Lampranthus*, a group of yellow-flowered species, were more closely related to *Circandra*, whereas another group in *Lampranthus*, consisting of small pink-flowered species, were more closely related to *Esterhuysenia*. Both Liede (1989) and Dehn (1992) gave no reference to the existing classification or names of the species of *Lampranthus* they investigated. Nevertheless, Liede's groups most likely refer to Section *Aurei* and Section *Scabridi* respectively.

#### *Namaquanthus* L.Bolus

*Namaquanthus vanheerdei* is an erect, woody shrub to about 30 cm tall. L. Bolus created the genus for this single species and noted that it shares the large purple flowers with *Enarganthe*, but differs from it in that the leaves have an almost circular cross-section, the fruits have more locules and lack closing bodies and the seeds are echinate (Bolus 1954).

*N. vanheerdei* is only known from two localities on north-facing quartzite slopes near Port Nolloth, in the coastal part of Namaqualand. Here it forms large populations of 100-200 plants and is the dominant element in these spots.

#### *Scopelogenia* L.Bolus

*Mesembryanthemum verruculatum* was already known to Linnaeus and had been introduced to England in the early 1730's (Dillenius 1732). It was moved to *Lampranthus* by Bolus (1950b), who subsequently (1962) placed it in its own genus and described a second species *Scopelogenia gracilis*. The reasons for the creation of a new genus were the apparent absence of valve wings and the fact that the capsules do not close once wetted. This characteristic is not found in *Lampranthus*. On the other hand it could not be included in *Ruschia*, since it lacks any closing bodies. Recently, *S. gracilis* has been shown to be a synonym of *S. verruculata* and a second species, *S. bruynsii*, was described (Klak 2000a). Both species form large cushions, with very soft leaves with an almost circular cross-section. The flowers are mostly yellow or more rarely pink or white and are arranged in a many-flowered inflorescence. The fruits of the second species open and close repeatedly, so that this characteristic no longer defines *Scopelogenia* (Klak 2000a). The relationships to other genera have never been investigated.

*S. verruculata* is found from the Cape Peninsula to George, whereas *S. bruynsii* is found from Namaqualand to the Ceres Karoo and Clanwilliam. Both species inhabit rocky sandstone cliffs or outcrops of sandstone.

*Smicrostigma* N.E.Br.

*Smicrostigma viride* is a low, shrubby, erect perennial, which becomes woody with age. Its leaves are fused at the base and continuous with the stem, and consequently it resembles species placed in *Ruschia* Sect. *Ruschia*. The fruits are multi-locular. This species was previously placed in the *Erepsia*ae. It was shown to differ in numerous characters from *Erepsia* and, in particular, the flowers do not exhibit the hypanthium typical for *Erepsia*. Liede (1989) suggested a possible close relationship to *Zeuktophyllum calycinum*, based on the morphology of the fruits.

*Smicrostigma* is found in the Little Karoo, from Robertson to Oudtshoorn, Western Cape.

*Vlokia* S.A.Hammer

The single species of this genus was only discovered in 1990. It is a dwarf succulent, which is sparsely branched and forms a prostrate trail of old stems to 10 cm long. The leaves are boat-shaped, with sessile, solitary flowers and 5-7-locular capsules.

The species is known from a single locality from north of Montagu, Western Cape. There *V. ater* grows in shallow gritty pans at an altitude of 1340 m. The plants are rare where they occur.

*Antegibbaeum* and *Esterhuysenia* have been cited as possible close relatives of *Vlokia* (Hammer 1994).

*Wooleya* L.Bolus

*Wooleya farinosa* was first described as *Namaquanthus farinosus* (L.Bolus 1958). However, in the absence of fruits L.Bolus was uncertain about her decision and placed a question mark next to the name in the protologue. Later she was able to examine some fruits and decided to establish a new genus for this species on account of differences in fruit, flower and seed morphology. Among the characters that differ from *Namaquanthus*, most noticeable are the expanding keels of the fruits, which are parallel for almost their entire length. These diverge from about the middle in *Namaquanthus*. In addition, the filamentous staminodes and stamens are collected in a central cone in *Wooleya*. In *Namaquanthus* filamentous staminodes are absent, and although the stamens are initially gathered into a cone they spread later during anthesis.

The species is restricted to a small area between Hondeklip Bay and Kleinsee, Namaqualand, where it grows close to the sea at an altitude of less than 10 m.

*Zeuktophyllum* N.E.Br.

Members of this genus are small compact shrubs to 12 cm tall with 3-angled leaves and multi-locular fruits. The type of the genus, *Z. suppositum*, was described by L. Bolus in 1925, based on a collection by J. Muir made at Phisantfontein in the Little Karoo. This remained the only collection and the only species of the genus until very recently, when a second species, *Z. calycinum*, was moved from *Octopoma* to *Zeuktophyllum* (Hartmann 1998a). Both species are very similar in their vegetative appearance. *Z. calycinum* can be

recognized by its finely apically toothed leaves, which are altogether smooth in *Z. suppositum*.

*Z. suppositum* was recently rediscovered near Phisantefontein, but is rare and remains known from this area only. The second species is more widespread and occurs over a large area in the Little Karoo. Both species grow on flattish patches of quartz gravel.

Liede (1989) suggested a close relationship between *Z. calycinum* and *Smicrostigma viride*. Based on the presence of woody fruits, which lack closing bodies, *Zeuktophyllum* was tentatively placed in the *Lampranthus* - group (Hartmann 1988).

### 1. 3. Aims of the thesis

It is evident that much of the taxonomy and systematics of the *Lampranthus* – group is as yet poorly understood. The circumscription of the *Lampranthus* – group is particularly problematic since *Lampranthus*, which forms the bulk of the group, has never been revised. In addition, much of the taxonomy and classification is based on fruit characters. However, over-reliance on fruit characters as phylogenetic indicators may be misleading. A good example of this problem is provided by the *Delosperma* – type of fruit that is shared among very divergent taxa. This particular fruit type is characterized by very simple and reduced structures and is found in, for example, *Delosperma*, *Conophytum* and *Lithops*. These three genera share essentially identical fruits, but are placed in three different groups, i.e. the *Delosperma* -, *Dracophilus* - and *Titanopsis* - groups respectively (Table 1. 1). Whether the three groups form a monophylum or represent different evolutionary lines remains uncertain (Hartmann 1988).

Any system based primarily on one structure (in this case the fruit) remains dubious, and the conventional tests by congruence cannot be applied. It is possible that a solution to this problem for the Ruschioideae may be found by using molecular data as an independent test of the phylogenetic relationships implied by the fruit structures. In several cases molecular systematic studies have led to new and better-supported phylogenies in the angiosperms (e.g. Chase *et al.* 1993, Soltis *et al.* 2000). Similarly they may also provide an independent means of resolving the phylogenetic relationships of the *Lampranthus* - group. The advantages of molecular data (reviewed by Hillis 1987) include the availability of a multitude of gene regions which may be used to address questions at different taxonomic levels and which may yield a potentially large number of characters. Although molecular analyses, in general, retrieve better supported phylogenies than morphological analyses due to a larger set of informative characters, morphological characters may enhance the results of purely molecular analyses (Doyle 1992, Endress *et al.* 2000). Examples of combined studies with large data sets are Doyle *et al.* 1994, Baum *et al.* 1998, Sennblad *et al.* 1998, Kron *et al.* 1999, and Schwarzbach & Ricklefs 2000.

Since no molecular phylogenetic studies have been conducted to investigate relationships within the Aizoaceae, it is first necessary to determine which region of the DNA might prove useful for resolving relationships at different taxonomic levels. In this study data from three independent gene regions,

representing both the nuclear and chloroplast genome, were analysed to investigate phylogenetic relationships in the *Lampranthus* – group (Ruschioideae, Aizoaceae). A fourth data set consisting of discrete morphological characters was also analysed and combined with the molecular data sets.

The regions sequenced were:

1. The non-coding chloroplast DNA region between the transfer RNA genes *trnL* and *trnF*
2. The internal transcribed spacer (ITS) region of the 18S-26S nuclear ribosomal RNA cistron
3. The 5S non-transcribed spacer region (5S-NTS) of nuclear ribosomal DNA

These regions have been found useful in species and generic level analyses in a number of studies (see 2.

- 1). Due to time and financial constraints extensive screening of further suitable gene regions was not possible. On account of these considerations, this study focused on these three gene regions.

The construction of a phylogenetic hypothesis for *Lampranthus* and the *Lampranthus* – group will provide a fundamental systematic framework for a revised and detailed account of *Lampranthus* and for the genera placed in the *Lampranthus* – group.

This study aims to :

- (1) investigate relationships among genera of the *Lampranthus* - group
- (2) test the monophyly of the *Lampranthus* - group proposed by Hartmann (1991)
- (3) test the value of fruit characters as indicators of phylogenetic relationship, both at generic and higher level
- (4) better the understanding of character evolution in the *Lampranthus* – group
- (5) produce a more concise circumscription of *Lampranthus*
- (6) elucidate relationships among species of *Lampranthus*
- (7) produce a conspectus of species currently placed in *Lampranthus*

**Table 1. 1** Classification of Aizoaceae (Hartmann 1993, 1998b). Several genera have been erected since, which were not placed in any group. *Hammeria* P.M. Burgoyne has been tentatively placed in the *Lampranthus* – group.

Subfamily	Group	Genera	Species	
Aizooidae		<i>Acrosanthes</i> Ecklon & Zeyher	4	
		<i>Aizoanthemum</i> Dinter ex Friedrich	4	
		<i>Aizoon</i> L.	11	
		<i>Galenia</i> L.	± 15	
		<i>Gunniopsis</i> Pax in Engler & Prantel	14	
		<i>Plinthus</i> Fenzl	± 4	
Sesuvioideae Lindley (1853)		<i>Cypselea</i> Turpin	1	
		<i>Sesuvium</i> L.	± 12	
		<i>Trianthema</i> L.	± 17	
		<i>Zaleya</i> Burm.f.	± 6	
Tetragonioideae Lindley (1853)		<i>Tetragonia</i> L.	± 85	
		<i>Tribulocarpus</i> S. Moore	1	
Mesembryanthemoideae Ihlenfeldt, Schwantes & Straka (1962)		<i>Aptenia</i> N.E.Br.	4	
		<i>Aridaria</i> N.E.Br.	4	
		<i>Aspazoma</i> N.E.Br.	1	
		<i>Brownanthus</i> Schwantes	11	
		<i>Caulipsolon</i> Klak	1	
		<i>Mesembryanthemum</i> L.	16	
		<i>Prenia</i> N.E.Br.	4	
		<i>Phyllobolus</i> N.E.Br.	32	
		<i>Psilocaulon</i> N.E. Br.	14	
		<i>Sceletium</i> N.E.Br.	8	
Ruschioideae Schwantes in Ihlenf., Schwantes & Straka emend. Bittrich & Hartmann (1988)	<i>Apatesia</i>	<i>Apatesia</i> N.E.Br.	3	
		<i>Carpanthea</i> N.E.Br.	1	
		<i>Caryotophora</i> Leistner	1	
		<i>Conicosia</i> N.E.Br.	2	
		<i>Hymenogyne</i> Haw.	2	
		<i>Saphesia</i> N.E.Br.	1	
		<i>Skiatophytum</i> L.Bolus	1	
		<i>Cleretum</i>	<i>Aethephyllum</i> N.E.Br.	1

Subfamily	Group	Genera	Species	
Ruschioideae	<i>Cleretum</i>	<i>Cleretum</i> N.E.Br.	2	
		<i>Dorothenathus</i> Schwantes	7	
	<i>Mitrophyllum</i>	<i>Dicrocaulon</i> N.E.Br.	7	
		<i>Diplosoma</i> Schwantes	2	
		<i>Disphyma</i> N.E.Br.	± 3	
		<i>Glottiphyllum</i> N.E.Br.	16	
		<i>Jacobsenia</i> L.Bolus & Schwantes	3	
		<i>Meyerophytum</i> Schwantes	2	
		<i>Mitrophyllum</i> Schwantes	6	
		<i>Monilaria</i> (Schwantes) Schwantes	5	
		<i>Oophytum</i> N.E.Br.	2	
		<i>Delosperma</i>	<i>Corpuscularia</i> Schwantes	8
	<i>Delosperma</i> N.E.Br.		± 120	
	<i>Drosanthemum</i> Schwantes		± 100	
	<i>Gibbaeum</i> N.E.Br.		16	
	<i>Malephora</i> N.E.Br.		14	
	<i>Mestoklema</i> N.E.Br.		7	
	<i>Oscularia</i> Schwantes		23	
	<i>Trichodiadema</i> Schwantes		34	
	<i>Stomatium</i>		<i>Chasmatophyllum</i> (Schwantes) Dinter & Schwantes	± 6
			<i>Faucaria</i> Schwantes	6
		<i>Frithia</i> N.E.Br.	2	
		<i>Mossia</i> N.E.Br.	1	
		<i>Neohenricia</i> L.Bolus	2	
		<i>Orthopterum</i> L.Bolus	2	
		<i>Rabiea</i> N.E.Br.	± 4	
		<i>Rhinephyllum</i> N.E.Br.	14	
		<i>Stomatium</i> Schwantes	40	
		<i>Titanopsis</i>	<i>Aloinopsis</i> Schwantes	13
	<i>Deilanthus</i> N.E.Br.		3	
	<i>Didymaotus</i> N.E.Br.		1	
	<i>Dinteranthus</i> Schwantes		6	
	<i>Ihlenfeldtia</i> H.E.K. Hartmann		2	

Subfamily	Group	Genera	Species
		<i>Lapidaria</i> (Dinter & Schwantes) Schwantes ex N.E.Br.	1
		<i>Lithops</i> N.E.Br.	35
		<i>Nananthus</i> N.E.Br.	± 7
		<i>Schwantesia</i> Dinter	8
		<i>Tanquana</i> H.E.K.Hartmann & Liede	3
		<i>Titanopsis</i> Schwantes	± 6
		<i>Vanheerdea</i> L.Bolus ex H.E.K.Hartmann	2
	<i>Dracophilus</i>	<i>Conophytum</i> N.E.Br.	86
		<i>Dracophilus</i> (Schwantes) Dinter & Schwantes	3-4
		<i>Jensenobotrya</i> Herre	1
		<i>Juttadintera</i> Schwantes	± 5
		<i>Namibia</i> Dinter & Schwantes ex Schwantes	1
		<i>Nelia</i> Schwantes	± 2
		<i>Psammophora</i> Dinter & Schwantes	4
		<i>Ruschianthus</i> L.Bolus	1
	<i>Bergeranthus</i>	<i>Bergeranthus</i> Schwantes	6
		<i>Bijlia</i> N.E.Br.	2
		<i>Carruanthus</i> (Schwantes) Schwantes	2
		<i>Cerochlamys</i> N.E.Br.	3
		<i>Hereroa</i> (Schwantes) Dinter & Schwantes	± 29
		<i>Machairophyllum</i> Schwantes	10
		<i>Rhombophyllum</i> (Schwantes) Schwantes	5
	<i>Lampranthus</i>	<i>Antegibbaeum</i> Schwantes ex C.Weber	1
		<i>Braunsia</i> Schwantes	6
		<i>Carpobrotus</i> N.E.Br.	15
		<i>Circandra</i> N.E.Br.	1
		<i>Enarganthe</i> N.E.Br.	1
		<i>Erepsia</i> N.E.Br.	29
		<i>Esterhuysenia</i> L.Bolus	4
		<i>Hammeria</i> P.M. Burgoyne	2
		<i>Lampranthus</i> N.E.Br.	± 220
		<i>Namaquanthus</i> L.Bolus	1
		<i>Scopelogenia</i> L.Bolus	2

Subfamily	Group	Genera	Species	
Ruschioideae	<i>Lampranthus</i>	<i>Smicrostigma</i> N.E.Br.	1	
		<i>Vlokia</i> S.A. Hammer	1	
		<i>Wooleya</i> L.Bolus	1	
		<i>Zeuktophyllum</i> N.E.Br.	2	
	<i>Eberlanzia</i>	<i>Amphibolia</i> H.E.K.Hartmann	5	
		<i>Eberlanzia</i> Schwantes	8	
		<i>Stoeberia</i> Dinter & Schwantes	5	
		<i>Ruschianthemum</i> Friedrich	1	
	<i>Ruschia</i>	<i>Acrodon</i> N.E.Br.	5	
		<i>Arenifera</i> Herre	4	
		<i>Astridia</i> Dinter	7	
		<i>Ebracteola</i> Dinter & Schwantes	5	
		<i>Khadia</i> N.E.Br.	6	
		<i>Marlothistella</i> Schwantes	1	
		<i>Polymita</i> N.E.Br.	2	
		<i>Ruschia</i> Schwantes	± 220	
		<i>Stayneria</i> L.Bolus	1	
		<i>Leipoldtia</i>	<i>Antimima</i> N.E.Br. emend. Dehn	102
			<i>Argyroderma</i> N.E.Br.	11
			<i>Cephalophyllum</i> N.E.Br.	31
			<i>Cheiridopsis</i> N.E.Br.	23
			<i>Cylindrophyllum</i> Schwantes	± 5
			<i>Fenestraria</i> N.E.Br.	1
	<i>Hallianthus</i> H.E.K. Hartmann		1	
	<i>Jordaaniella</i> H.E.K.Hartmann		1	
	<i>Leipoldtia</i> L.Bolus		8	
	<i>Octopoma</i> N.E.Br.		8	
	<i>Odontophorus</i> N.E.Br.		3	
	<i>Ottosonderia</i> L.Bolus		2	
	<i>Pleiospilos</i> N.E.Br.		4	
	<i>Schlechteranthus</i> Schwantes	2		
	<i>Vanzijlia</i> L.Bolus	1		

## CHAPTER 2

### MOLECULAR PHYLOGENETICS

#### 2. 1. Introduction

The rates of nucleotide substitution vary greatly among gene regions (Wolfe *et al.* 1987, Johnson & Soltis 1994). Therefore the choice of which gene region to study depends on the level of taxonomic investigation. The two primary sources for molecular phylogenetic studies in plants are the chloroplast genome and the ribosomal RNA repeat region of the nuclear genome (Olmstead & Palmer 1994). The circular chloroplast DNA (cpDNA) is highly conserved in both its structure and rate of nucleotide substitution (Böhle *et al.* 1994). In the chloroplast genome the rates of substitution are generally more conservative compared to nuclear genes (Wolfe *et al.* 1987). Contrary to some nuclear genes the chloroplast genes evolve as single copy genes (Olmstead & Palmer 1994), which provide orthologous characters suitable for phylogenetic investigation. Chloroplast genes have shown their greatest utility at higher taxonomic levels (e.g. Chase *et al.* 1993, Savolainen *et al.* 2000, Soltis *et al.* 1997, Soltis *et al.* 2000), whereas they often have less phylogenetic value at lower taxonomic levels.

The chloroplast region that will be investigated in this study is the region between the transfer RNA genes *trnL* (UAA, 85 bp) and *trnF* (GAA, 73 bp) (Taberlet *et al.* 1991). The region contains an intron (390–615 bp long) within the *trnL* gene and a spacer (160–440 bp long) between the *trnL* and *trnF* region. The *trnL* – *trnF* region has been used successfully in numerous studies to reconstruct hypotheses of relationship at the family and genus level (e.g. Gielly *et al.* 1996, Kim *et al.* 1996, Mes *et al.* 1997), while in most cases species-level relationships were not resolved (e.g. Böhle *et al.* 1994, Mes *et al.* 1997).

The nuclear rRNA gene regions may often contain multiple copies of tandemly repeated arrays (e.g. Baldwin *et al.* 1995, Sastri *et al.* 1992, Cronn *et al.* 1996). The individual repeats may evolve in unison and retain a high degree of uniformity due to homogenising forces referred to as concerted evolution (Zimmer *et al.* 1980). However, if this process of concerted evolution is not complete, the different repeats are not uniform and may represent different evolutionary histories (Sanderson & Doyle 1992). If non-homogeneous copies are present in a taxon, amplifications will often produce more than one band and direct sequencing will not produce a single unambiguous sequence. Under these circumstances cloning techniques need to be incorporated into the study.

Two nuclear regions, both of which are present in many thousands of copies arranged in tandem repeats in the plant nuclear genome (Baldwin *et al.* 1995, Sastri *et al.* 1992, Cronn *et al.* 1996), were investigated in this study. The first is the internal transcribed spacer (ITS) region of the 18S-26S nuclear-encoded ribosomal RNA cistron. The ITS region is situated between the 18S and 26S subunits of the nuclear rDNA and comprises the 5.8S subunit flanked by two spacers, ITS 1 and ITS 2. This region, < 700 bp long in angiosperms, has shown its greatest utility in phylogeny reconstruction at intrafamilial levels (e.g.

Gonzalez *et al.* 1990, Lee and Taylor 1992, Baldwin *et al.* 1995, Eldenäs *et al.* 1998), and is at present the DNA region most widely used to address questions at lower taxonomic levels.

The second nuclear gene region investigated here is the non-transcribed spacer of the nuclear-encoded 5S rRNA gene (5S NTS). The 5S region consists of a basic unit that is present in tandem repeats in the nuclear genome. The unit comprises a 120 bp gene that codes for the 5S ribosomal subunit and a nontranscribed spacer. The spacer is said to vary in length between 100 – 700 bp in plants (Sastri *et al.* 1992), although much larger spacers may occur as well (Gottlob-Mchugh *et al.* 1990). Owing to its relatively high variation rate, the 5S gene provides valuable information at low taxonomic levels for most groups studied (e.g. Kellogg *et al.* 1996, Udovicic *et al.* 1995). In contrast to the ITS region, where homogenisation across the tandem repeats is mostly complete, many studies of the 5S NTS have encountered high intra-genomic polymorphisms (e.g. Reddy & Appels 1989, Appels *et al.* 1992, Baker *et al.* 2000a). Despite the disadvantage of potential intra-genomic polymorphism, the 5S spacer is considered to provide valuable information for phylogeny reconstruction.

In this study amplifications of the two nuclear gene regions yielded, in the majority of cases, single bands that could also be sequenced successfully (but see also discussion below). This indicated that the copies were homogeneous, and no cloning was required to allow phylogenetically informative comparisons to be made between homologous nucleotide sequences.

### 2. 1. 1. Congruence and total evidence

The strongest evidence of an accurate phylogenetic hypothesis is congruence amongst data sets (e.g. Doyle 1992, Page & Holmes 1998). The availability of different data sets addressing the same systematic questions has sparked off a continued debate regarding combination of data sets (Swofford 1991, Chippendale and Wiens 1994, de Queiroz *et al.* 1995, Huelsenbeck *et al.* 1996, Sullivan 1996). De Queiroz *et al.* (1995) reviewed the arguments against and in favour of combined analysis of data sets. Kluge & Wolf (1993) questioned whether different classes of evidence existed at all. If there were no different classes of evidence, data sets from different sources would not need to be analyzed separately. However, studies have shown that morphological data and data generated from different gene regions each need to be recognized as different classes of evidence since they differ in properties such as rates of evolution, gene duplication and substitution patterns (e.g. Bull *et al.* 1993, Miyamoto & Fitch 1995).

One of the major arguments against combining data sets is the view that any phylogeny assumes a model of evolution (Bull *et al.* 1993). Differences between phylogenetic hypotheses must, as a consequence, be attributed to different evolutionary rules (Bull *et al.* 1993). The advantages of separate analyses are to detect such incongruencies (e.g. as a result of different evolutionary rates, gene duplication, hybridization or lineage sorting) which can promote further investigations and result in re-evaluation of character homologies (Bremer 1996). If incongruencies are found the data sets should not be combined unless the implemented method can account for the incongruencies (Bull *et al.* 1993).

If significant differences are caused by a single terminal taxon, the taxon can be removed from the analysis and the data sets combined (de Queiroz *et al.* 1995). If significant differences involve multiple taxa, then any combination of data obscures the history of the genes (Kellogg *et al.* 1996).

Although incongruence amongst data sets may suggest that data sets should not be combined, there are numerous arguments in favour of combined analyses. Total evidence or consensus methods exist that try to incorporate all the available information (Barret *et al.* 1991, Kitching *et al.* 1998). Two general approaches have been proposed to estimate the phylogeny of a group: (i) the consensus approach, which analyses each data set separately and then combines the resulting trees using a consensus method (de Queiroz *et al.* 1995, Kitching *et al.* 1998, Page & Holmes 1998); or (ii) the total evidence approach where all available characters are analyzed simultaneously in a single data set (Brower *et al.* 1996, Kitching *et al.* 1998, Page & Holmes 1998). One of the major advantages of the simultaneous approach is that it can maximise the explanatory power of the data and may provide resolution of relationships unresolved by partitioned data sets (e.g. Kluge & Wolf 1993, Nixon & Carpenter 1996, Chase & Cox 1998). In addition, a recent study which examined the effect of combining different data sets showed that, although the major clades were recovered in each of the separate analyses, they were only well supported in the combined analyses whilst also reducing the number of most parsimonious trees (MPTs) (Chase & Cox 1998).

The advantages of the total evidence (method ii) as compared to the consensus approach (method i) is its greater explanatory power (Barrett *et al.* 1991, Kluge & Wolf 1993). Further criticisms against consensus methods were raised, since they were shown to be less parsimonious than the combined trees (Miyamoto 1985). For the reasons outlined above there is merit in evaluating the results from each analysis separately (Albert 1994, Bremer 1996) before combining the data. If the data sets cannot be shown to be significantly different they can be combined (de Queiroz *et al.* 1995, Kitching *et al.* 1998). In this study the data were therefore first analyzed separately to identify possible incongruencies and then combined using the total evidence approach.

### 2. 1. 2. Estimating support and successive weighting

Tests of support. There are several methods of testing data informativeness and cladogram stability, and there is much discussion as to their applicability (Carpenter 1988, Goloboff 1991, Källersjö *et al.* 1992, Hillis & Bull 1993, Trueman 1993, Bremer 1994). The three main tests of support are: Bremer support analysis (Bremer 1988) to obtain integer values of node support, and bootstrap (Felsenstein 1985) and parsimony jackknifing (Farris *et al.* 1996) to determine presence and frequency of clades.

Bremer support analysis examines how many steps of character transformation are needed to lose a branch in a consensus of near-most parsimonious trees. Bootstrap analysis is performed by random resampling, with replacement, of the characters in the original data matrix followed by analysis of the permuted matrix. This procedure is repeated and a consensus tree of the minimal trees from each replicate,

showing the frequencies of occurring clades, is generated. Bootstrapping is sensitive to character number and the degree of homoplasy. The more unambiguous characters supporting a node, the less chance that the random resampling causes the node to collapse and the higher the frequency with which it appears in the performed replicates.

Parsimony jackknifing, as executed by the program "Jac" (Farris *et al.* 1996), combines jackknifing with parsimony analysis. Like the bootstrap it reanalyses the original data matrix, but at each "Jac" replicate a reduced matrix generated by randomly omitting a (specified) number of characters, in this case  $e^{-1}$  is analysed. For analyses of large data sets the major advantages of parsimony jackknifing is its far greater speed and its greater ability to detect poorly-supported groups compared to existing programs (Farris *et al.* 1996). Parsimony jackknifing was therefore used in this study to test clade support.

Farris *et al.* (1996) have shown that with a removal probability of 36.79% (~ 37%, Backlund & Bremer 1997) jackknife values of more than 63% correspond to a node supported by at least one uncontradicted character. Consequently, the percentage of deleted characters for all jackknife parsimony analyses in this study was fixed at 36.79%. Only groups with frequency greater than 50% were retained and clades with jackknife values greater than or equal to 63% are regarded as supported by the data (Farris *et al.* 1996, Backlund & Bremer 1997, Bakker *et al.* 1998).

Clade support was determined by performing 10,000 replications of parsimony jackknifing using PAUP\* version 4.0b4a (PPE) with options selected so as to emulate the conditions discussed by Farris *et al.* (1996) (collapse branches if minimum length is zero, jackknife with 36.79% deletion, emulate "Jac" resampling, "Fast" stepwise-addition). Only groups or nodes with frequency > 50% were retained in the jackknife consensus tree.

Successive weighting: The data set was further analysed using a successive weighting approach (Farris 1969, Goloboff 1993, Kitching *et al.* 1998). Successive approximated weighting is an *a posteriori* procedure for weighting characters according to their cladistic consistency as measured by their consistency index or rescaled consistency index on a given set of trees. As the weights can affect both the number and topology of the resulting cladograms, it is necessary to ensure that the weights stabilize (Kitching *et al.* 1998). By repeating the reweighting procedure until the weights assigned to each character in two successive iterations are identical ensures that the weights stabilize (Kitching *et al.* 1998).

Lidén (1999) has criticized the performance of bootstrapping (or jackknifing) on internally weighted characters (according to Farris' (1969) successive approximation approach). However, Lidén (1999) does not offer an alternative method to measure support for nodes on internally weighted characters. Apart from Lidén's objections there has so far been no unanimous rejection of this method in the literature and the implications of jackknifing on internally weighted characters on branch support have nowhere else been discussed. Since it is logical to examine also branch support of weighted characters, this method is used here as the best estimate of clade support.

## 2. 2. Materials and Methods

### 2. 2. 1. Ingroup and outgroup sampling

Fifty-nine exemplars were chosen to reflect as much of the morphological variation in the *Lampranthus* – group as possible. Since this morphological variation is largely encapsulated in the existing taxonomy, the current classification is used as shorthand for describing this variation. Consequently, for mono- and bitypic genera one species was selected as representative. *Circandra* was not included in the study, since no populations of the species could be located. In *Erepsia* and *Lampranthus*, the partly informal sections were used as a baseline for selection. Four species of *Lampranthus*, not placed to section (including an as yet undescribed species), were included to test whether they do belong in this genus.

Exemplars representing at least two genera of the proposed close relatives were selected. In the absence of an existing phylogenetic study, additional taxa were selected from Hartmann's groups to encompass a broad range of ruschioid morphology. These were used to provide an effective test for the monophyly of the *Lampranthus* – group. Two species were chosen to represent the Mesembryanthemoideae. Since there is sufficient morphological evidence that the Mesembryanthemoideae are not nested within the Ruschioideae (e.g. Hartmann 1991), one of the two species, *Brownanthus pubescens*, was used to root the tree.

### 2. 2. 2. DNA extraction and amplification of template DNA.

Total DNAs were isolated from fresh leaf material of the 59 sampled species by the method of Saghai-Marooof *et al.* (1984) as modified by Doyle & Doyle (1987). In some cases, where initial PCR amplification did not yield a product, DNAs were further purified by using the QIAquick™ PCR Purification Kit, following the manufacturer's instructions.

The three DNA regions were amplified from total DNA by polymerase chain reaction (PCR). The *trnL-trnF* and ITS regions were amplified using primers c and f (Taberlet *et al.* 1991) and universal primers ITS5 and ITS4 respectively (White *et al.* 1990). The 5S spacer was amplified using primers P3 and P4 described by Cox *et al.* (1992). The sequences of the primers are given in Table 2. 1. 25µl reactions were prepared, which contained 19 µl of sterile water, 2.5 µl of 10X PCR buffer, 1 µl of 10mM dNTPs in equimolar ratio, 0.75 µl of each 10 µM primer, 0.5 µl of 25 mM MgCl<sub>2</sub>, 0.125 µl of Taq DNA polymerase (5 U/µl) and 0.5 µl of genomic DNA. In general, a 10x dilution of the extraction product was used as template DNA. For the ITS amplifications, which in numerous cases yielded more than one product, 0.25µl of DMSO per reaction was added. The thermal reactions were carried out as follows: first 2 min at 97° C to ensure denaturation of double-stranded template DNA, 1 cycle; denaturing step of 95°C for 1 min, annealing step of X °C for 45 sec (X = 52 for *trnL-trnF* region, 49 for ITS, 55 for the 5S spacer) and extension step of 72° C for 2 min; the three cycle steps were repeated 30 times and were finally followed by one extension step for 8 min at 72°C to complete unfinished DNA strands. The reactions were cleaned using the QIAquick PCR purification kit from Qiagen and the purified products were eluted in 30 µl of TE.

### 2. 2. 3. Sequencing and alignments

Both strands of the PCR products were cycle sequenced, using the ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit from PE Biosystems. The primers used for amplification were also used for the sequencing reactions. In addition, for some samples the internal *trnL-F* region primers d and e were used (Taberlet *et al.* 1991, Table 2. 1). The cycle sequencing reactions were carried out following manufacturers instructions. The samples were run on an Applied Biosystems 377 automated DNA sequencer.

Data files were assembled and edited using DAPSA version 4.04 (Harley 1997). Sequences were aligned by eye. Ambiguous positions were coded using appropriate IUPAC ambiguity symbols so as to maximize retention of information. Alignment of some portions of the 5S and *trnL-F* datasets was ambiguous. These regions were excluded from all analyses described below. For all sequences a blast search in Genbank was performed to make sure that the correct gene region had been amplified.

Gaps, which result from the alignment of sequences of unequal length during primary homology assessment, are considered to contain valuable phylogenetic information (e.g. Giribet & Wheeler 1999). Different methods of treating gaps have been discussed and these may influence the outcome of a phylogenetic analysis (e.g. Eernisse & Kluge 1993, Vogler & DeSalle 1994, Simons & Mayden 1997). Simmons & Ochoterena (2000) recently reviewed and evaluated the different methods of gap coding (e.g. Barriol 1994, Wheeler 1996, Giribet & Wheeler 1999). In their method all gaps (including gaps that are one position long) are coded as separate present/absence characters and not as fifth character state since they do not represent alternative forms of bases. Some workers have also treated single gap positions independently of adjacent gap positions. Whereas some have treated contiguous gap positions as the result of independent indels (Eernisse & Kluge 1993) others consider them the result of a single indel and thus treat them as single characters (Lloyd & Calder 1991, van Dijk *et al.* 1999). Contiguous gap positions are generally thought to result from a single insertion or deletion (Pascarella & Argos 1992, Gu & Li 1995). Furthermore Simmons & Ochoterena (2000) argue further that the parsimony criterion favours the interpretation of coding contiguous gap positions as a single character. They proposed two methods to code gaps, simple indel coding and complex indel coding. Their method of simple indel coding, although it does not incorporate all available information, is far easier to implement compared to the complex indel coding. In addition, gaps found in this study could easily be aligned by eye and the simple indel coding procedure was sufficient to retrieve the phylogenetic information. In this study all gaps were treated as single sites regardless of their length and were coded as binary characters to be added to the data matrices and included in the analyses.

**Table 2. 1** Primer sequences used in this study for amplification and sequencing of the *trnL-F*, ITS and 5S NTS gene regions.

Primer	Sequence 5'-3'
C	CGAAATCGGTAGACGCTACG
D	GGGGATAGAGGGACTTGAAC
E	GGTTC AAGTCCCTCTATCCC
F	TTTGA ACTGGTGACACGAG
ITS 4	TCCTCCGCTTATTGATATGC
ITS 5	GGAAGTAAAAGTCGTAACAAGG
P3	GAGAGTAGTACATCGATGGG
P4	GGAGTTCTGACGGGATCCGG

#### 2. 2. 4. Cladistic Analyses

The data matrix was analysed using PAUP\* version 4.0b4a (PPE) (Swofford 2000) under the maximum parsimony optimality criterion with all parsimony-uninformative characters excluded and all included characters left unordered. Initially, each DNA region was analysed separately. The first step in each of these analyses involves an initial sweep of the tree space in an attempt to increase the chances of identifying all islands of MPT's (Maddison 1991, Olmstead & Palmer 1994). For this, five thousand consecutive heuristic searches were conducted using random stepwise taxon addition with tree-bisection-reconnection (TBR) branch swapping, MULPARS and steepest decent in effect. Zero length branches were collapsed. During each replicate of random taxon addition only 2 trees were saved. All of these trees were then used as starting trees for the next search with tree-bisection-reconnection (TBR) branch swapping, MULPARS and steepest decent in effect. Again branches with maximum length of zero were collapsed. Due to the limited memory of the computer, the maximum number of trees saved for each search was set to 30,000. To assess clade support, the data set was analysed using the "jackknife" option as implemented in PAUP\*, following the procedure outlined above.

The ITS region could not be amplified for *Phyllobolus rabiei*, *Ruschia intrusa*, *Braunsia maximiliani*, *Lampranthus dregeanus* and *Lampranthus peacockiae*, and amplification of the 5S NTS region was unsuccessful for *Phyllobolus rabiei*. The *trnL-trnF* region was successfully sequenced for all sampled species. *Brownanthus pubescens* and *Dorotheanthus bellidiformis* were excluded from the 5S data set, as sequences obtained could not be aligned with the remaining exemplars. In total, 59 taxa were included in the *trnL-trnF* data set, 56 species in the 5S NTS data set and 54 species in the ITS data set (Appendix 1). With the exception of *Phyllobolus rabiei*, each taxon was represented by at least two data sets. In combined analysis 1 and 2 (see below), missing regions were coded as '?'

In addition to the separate analyses, the following combined analyses were performed. These used the same PAUP settings as the individual analyses except where indicated.

Simultaneous Analysis 1. A data set comprising the *trnL-trnF*, ITS and 5S sequences was constructed. Analysis unweighted. Fifty-eight taxa for which data from at least two regions were available were included.

Simultaneous Analysis 2. The total data set was analyzed using the successive approximation weighting scheme (Farris 1969; 1989; Goloboff 1993). Using the optimal trees from analysis 1, characters were reweighted by their rescaled retention indices (using base weight 10). The trees recovered were used for a second round of reweighting and analysis. The process was repeated until the topology stabilized. The weight set of the final round of successive approximations weighting was used in a jackknife analysis in PAUP\*.

Simultaneous Analyses 3 and 4. Due to the problem of missing data, unweighted and weighted simultaneous analyses 2 were re-run including only those taxa for which sequences of all three DNA regions were available (Appendix 1).

### 2.3. Results

Numerous indels are present in the *trnL-F* gene region. The longest deletion, recorded for *Hammeria meleagris* and *Lampranthus henricii*, was 361 bp long. Consequently the sequence in both species only measured 554 bp, whereas the longest, found in *Phyllobolus*, was 987 bp. The ITS region, in contrast, had mostly single bp indels, with the exception of *Brownanthus* and *Astridia*, which have deletions between 11-17 bp. The shortest sequence, found in *Brownanthus*, measured 594 bp, whereas the longest amounted to 614 bp (found in several species).

In the 5S spacer, indels of varying length were recorded: *Namaquanthus* and *Titanopsis* had the longest (almost identical) indel, measuring 153 and 144 bp respectively. Sequence length varied between 165 - 348 bp, with the shortest sequence observed in *Lampranthus filicaulis* and the longest in *Namaquanthus*. *Brownanthus pubescens* was too divergent to be alignable to the rest of the taxa. *Phyllobolus rabiei* and *Dorotheanthus bellidiformis* could not be sequenced; the presence of multiple peaks at most positions in both sequences suggests that multiple copies of the spacer are present. In addition, a long homo-polymer region, consisting of a string of T's up to 24 bp, was located about 60 bp downstream from the 5' end. The sequence was unreadable after this region. With few exceptions the same applied when reading from the 3' end. This region of ambiguity was excluded from the analysis.

Statistics, including numbers of variable positions and measures of consistency are given for each analysis in Tables 2. 2 and 2. 3.

*TrnL-trnF* Analysis. The strict consensus (Fig. 2. 1) of the 30,000 trees recovered ( $ci = 0.862$ ,  $ri = 0.840$ ,  $rc = 0.724$ ) is largely unresolved. The Ruschoideae are resolved as a very strongly supported monophyletic group (JK = 100) within which *Dorotheanthus* is sister to a strongly supported clade (JK = 100) comprising the remaining genera. Among the remaining Ruschioid genera, a moderately well

supported (JK = 73) lineage comprising *Drosanthemum*, *Hammeria* and *Lampranthus henricii* is sister to a weakly supported (JK = 58) group comprising the rest of the sampled species. The remaining species form a large polytomy, within which the only grouping resolved is a well-supported clade (JK = 86) comprising *Lampranthus amphibolius* and *Lampranthus sp. nov.* Lack of resolution within the Ruschioideae appears to be due to lack of variation rather than character conflict; only 30 informative characters are available when the data set is restricted to the Ruschioideae. In addition, any homoplasy (although low for the *trnL-F* data set,  $ri = 0.840$ ) will lead to no statistical support at the nodes.

**ITS Analysis.** The strict consensus (Fig. 2. 2) of the 30,000 recovered ITS trees ( $ci = 0.491$ ,  $ri = 0.457$ ,  $rc = 0.225$ ) is also largely unresolved: *Dorotheanthus* forms the sister taxon to all remaining taxa, which form a polytomy. Within this large polytomy, only five clades are resolved of which only the group comprising the four species of *Erepsia* is well supported (JK = 87).

**5S Analysis.** The 5S tree, restricted to members of the Ruschioideae because of inability to align potential outgroups, shows more resolution than the ITS or *trnL-F* trees. The strict consensus of 30,000 recovered trees (Fig. 2. 3,  $ci = 0.519$ ,  $ri = 0.743$ ,  $rc = 0.386$ ) is rooted to *Drosanthemum* based on the well-supported results from the *trnL-F* region. The Ruschioideae form a large polytomy within which several clades are well supported. One major clade (clade C, *Lampranthus* clade) consists of a “core” of species of *Lampranthus* (13 out of the 21 sampled species) and also includes *Oscularia falciformis* (JK = 75). *Lampranthus debilis* is sister to *Oscularia guthrieae*, which in turn is sister to the “core” of *Lampranthus*, but without statistical support for inclusion into the “core” group of *Lampranthus*. In addition, several species of *Lampranthus* are placed outside this clade, and form closer relationships with other taxa. *Lampranthus argenteus* and *L. henricii* are sister to *Antimima* (clade A, JK = 75), whereas *Lampranthus mucronatus* is sister to *Esterhuysenia* (JK = 63). The relationships of *Lampranthus filicaulis*, *L. amphibolius* and *L. sp. nov.* to the other taxa are unresolved. Among the members of the *Lampranthus* – group, *Zeuktophyllum* and *Smicrostigma* are well-supported sister species (JK = 87).

Contrary to the ITS analysis, only three of the four species of *Erepsia* are placed in a highly supported clade (clade B); *Erepsia inlaudens* is placed instead as sister to *Oscularia guthrieae* and the “core” group of *Lampranthus* species. Forcing the monophyly of *Erepsia* (with *E. inlaudens* as sister to the three other species of *Erepsia*), increases tree length from 231 to 243 steps. A subsequent comparative analysis of the constrained and unconstrained tree with the Kishino-Hasegawa and the Templeton Wilcoxon tests showed that the differences between the two trees were significant ( $P^* = 0.0010$  and  $P^* = 0.0018$  respectively). This result suggests that the monophyly of *Erepsia* is significantly contradicted by the 5S data. However, if for the ITS data set, *E. inlaudens* was forced sister to *O. guthrieae* (placement in the 5S topology), the length of the constrained tree is only three steps longer than the unconstrained tree (175 versus 178 steps). In addition, the Kishino-Hasegawa and Templeton Wilcoxon tests for these two trees suggested that there was no significant difference ( $P^* = 0.4711$  and  $P^* = 0.7905$  respectively). This suggests that there is no real conflict between the 5S and ITS data sets.

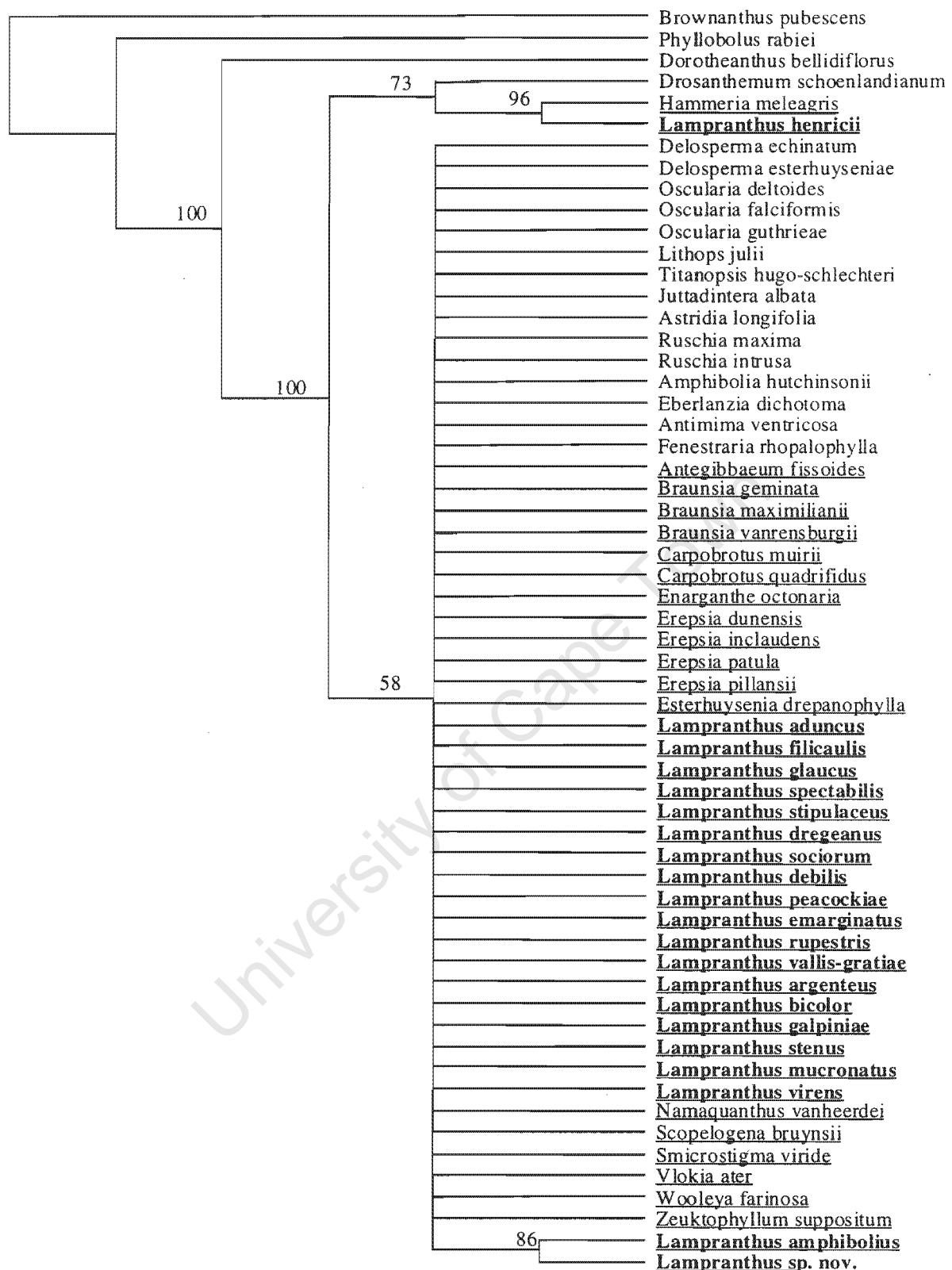
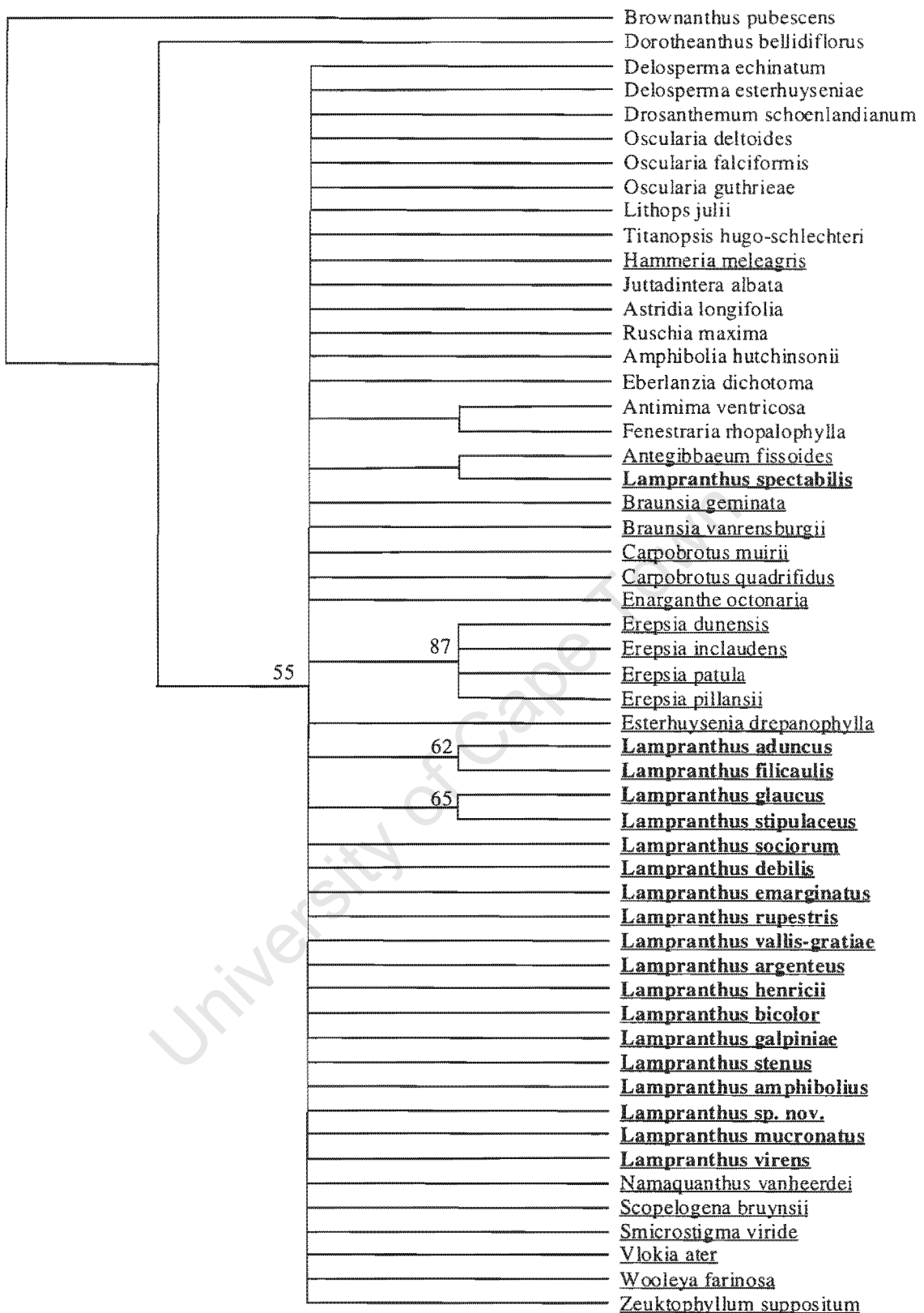
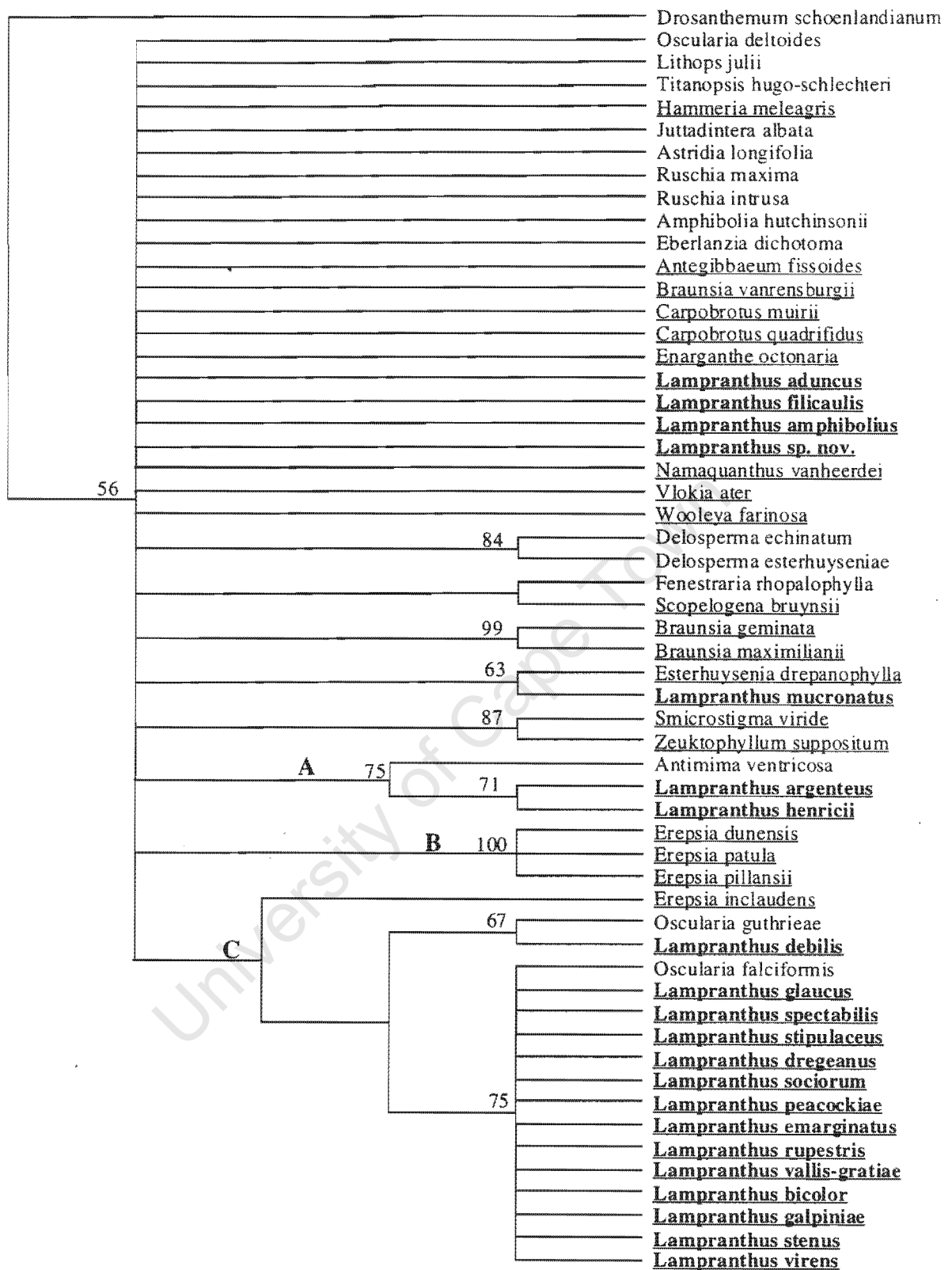


Fig. 2. 1 Strict consensus of 30,000 most parsimonious trees ( $l=189$ ,  $ci=0.862$ ,  $ri=0.840$ ,  $rc=0.724$ ) recovered during heuristic search 1 of the *trnL-trnF* data set for 59 taxa. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.



**Fig. 2. 2** Strict consensus tree of 30,000 most parsimonious trees ( $l=175$ ,  $ri=0.491$ ,  $ri=0.457$ ,  $rc=0.225$ ) recovered during heuristic search 2 of the ITS data set for 54 taxa. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.



**Fig. 2. 3** Strict consensus of 30,000 most parsimonious trees (l=231, ci=0.519, ri=0.743, rc=0.386) recovered during heuristic search 3 of the 5S data set for 56 taxa. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.

Simultaneous Analysis 1. The strict consensus of 30,000 equally parsimonious trees ( $ci = 0.474$ ,  $ri = 0.589$ ,  $rc = 0.280$ ) from combined analysis 1, including 58 taxa (excluding *Phyllobolus*), resolves similar clades to the 5S analysis, but shows greater resolution (Fig. 2. 4). *Enarganthe* is sister to a clade consisting of the two species of *Delosperma* and *Namaquanthus* as sister of a large polytomy. The remainder fall into an unsupported lineage within which six clades are resolved that participate in a polytomy with 13 individual species.

In clade D *Scopelogenia* and *Fenestraria* are sister to species of *Erepsia* and *Braunsia*, which each form well supported clades (JK = 99 and 96). However, *E. inlaudens* and *B. vanrensburgii* are each placed in a separate clade (clade C and E respectively).

Clade E consists of five mono- or bitypic genera at present placed in the *Lampranthus* - group, as well as *Ruschia intrusa* and *Braunsia vanrensburgii*. Within this clade relationships are largely unresolved, and only *Smicrostigma* and *Zeuktophyllum* are well-supported sister taxa (JK = 82).

In contrast to the 5S analysis, *Antimima* and the two species of *Lampranthus* are no longer statistically supported by the combined data. On the other hand *Astridia* and *Wooleya* form a clade not retrieved by the 5S analysis, but the clade is statistically unsupported.

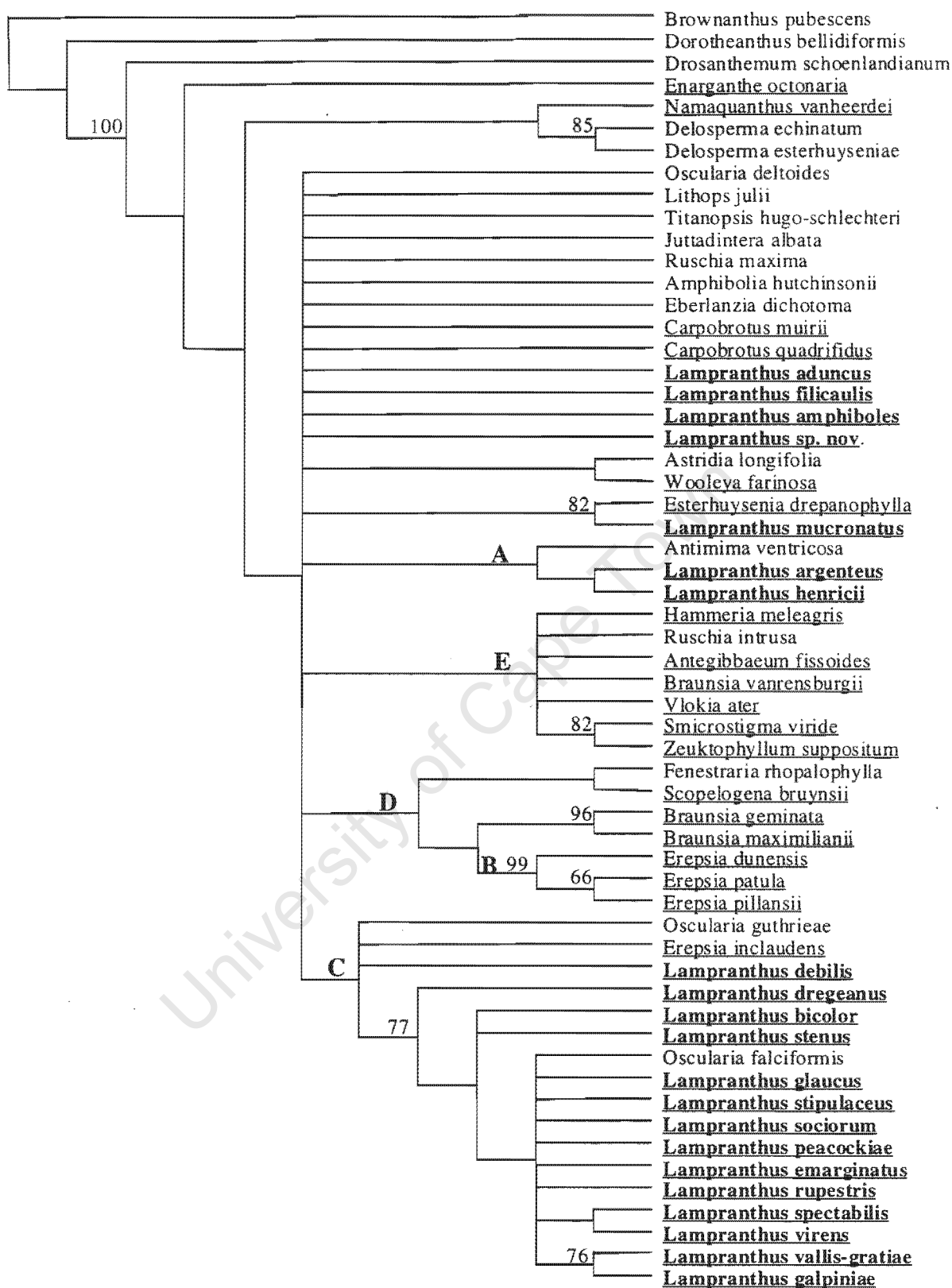
Simultaneous Analysis 2. Successively-approximated weighting of the above topology of the strict consensus tree (Fig. 2. 4) progressively increased the number of trees and the topology did not stabilize. The search was therefore stopped and no results recorded.

Simultaneous Analysis 3. In this analysis only taxa represented in all three data sets (52 taxa) were included. Removal of taxa with missing data yields a strict consensus tree (not shown) recovered from 30,000 trees ( $ci = 464$ ,  $ri = 0.594$ ,  $rc = 0.276$ ) which is almost identical to that of simultaneous analysis 1 (full data set). The only difference found was a lack of resolution in the *Lampranthus* clade (clade 6), where all the unsupported nodes were collapsed. In addition, jackknife support for several of the nodes retrieved in simultaneous analysis 1 are higher. Notably the “core” of *Lampranthus* is now highly supported (JK = 96 compared to JK = 77 in simultaneous analysis 1).

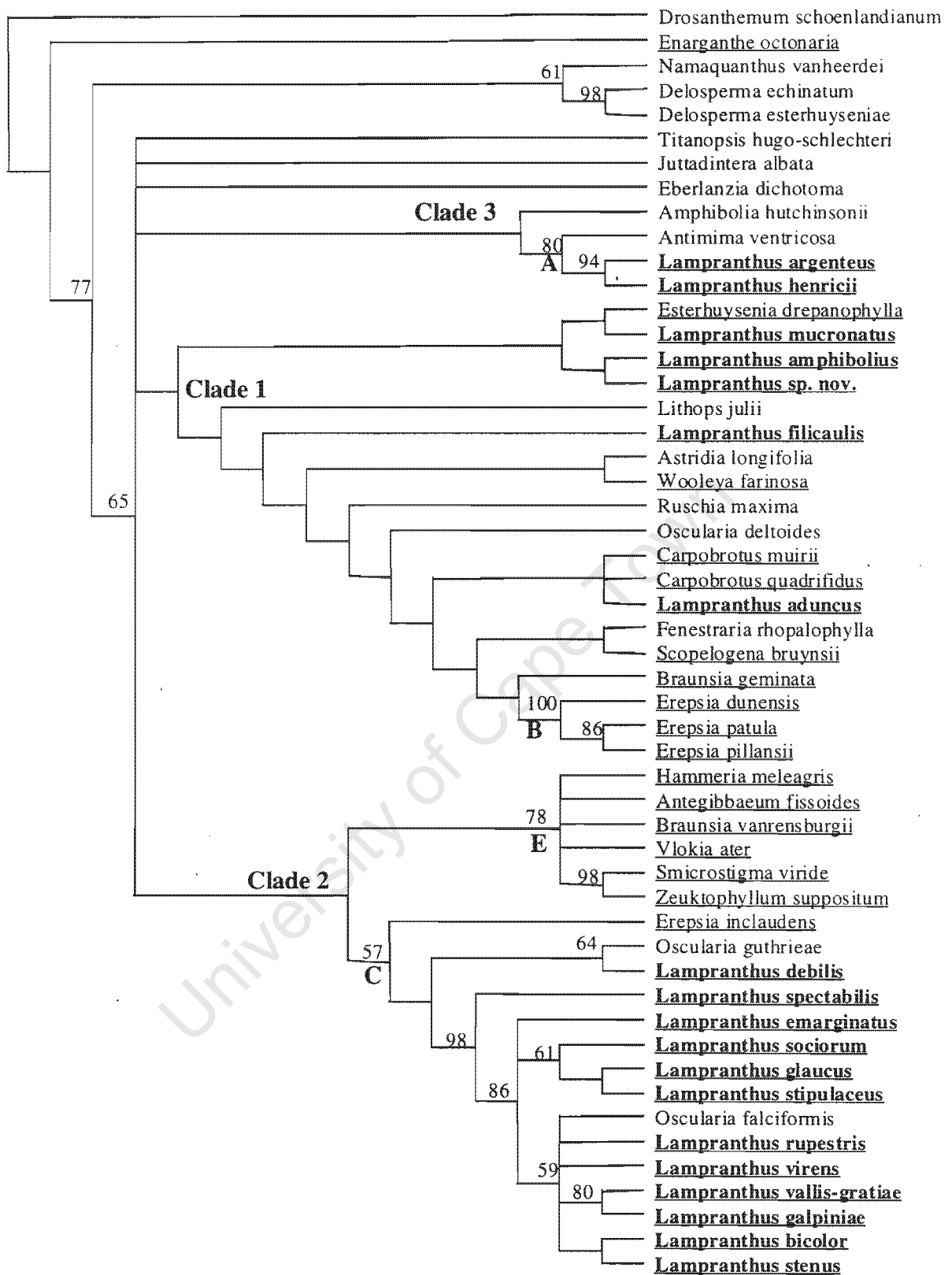
Simultaneous Analysis 4. Three rounds of successive weighting were necessary to stabilise the topology. The strict consensus of 56 equally parsimonious trees ( $ci = 0.595$ ,  $ri = 0.837$ ,  $rc = 0.498$ ) (Fig. 2. 5) after successively approximated weighting shows considerably more resolution than the previous analyses.

Clade D (shown in Fig. 2. 4) is now nested within an assemblage of taxa that are scattered among the *Ruschia* -, *Delosperma* - and *Lampranthus* – groups, including *Lampranthus aduncus* and *Lampranthus filicaulis*. Sister to this clade are *Esterhuysenia* and *L. mucronatus*, which in turn are sister to *Lampranthus sp. nov.* and *L. amphibolius*, a relationship that is statistically unsupported.

As in the 5S analysis, *Lampranthus henricii* and *L. argenteus* are placed in a well-supported clade as sister to *Antimima*.



**Fig. 2. 4** Strict consensus of 30,000 most parsimonious trees ( $l=548$ ,  $ci=0.474$ ,  $ri=0.589$ ,  $rc=0.280$ ) recovered during heuristic search 1 of the combined data set (not weighted) for 58 taxa. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.



**Fig. 2. 5** Strict consensus of 56 most parsimonious trees ( $ci=0.595$ ,  $ri=0.837$ ,  $rc=0.498$ ) recovered during heuristic search 4 of the combined data set (weighted) for 52 taxa. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.

The *Lampranthus* clade (clade C) is poorly supported (JK = 57). Within this clade *Erepsia inlaudens* is sister to a clade which comprises two lineages: the first comprises the highly supported “core” of *Lampranthus*, including *Oscularia falciformis* (JK = 98), and the second consists of *O. guthrieae* and *L. debilis* (JK = 64). Sister to the *Lampranthus* clade (but statistically unsupported) are several of the monotypic genera of the *Lampranthus* – group (clade E), with the latter clade fairly well supported (JK = 78).

Overall, there is a very apparent lack of jackknife support, in particular for the middle to lower branches of the topology.

**Table 2.2** Statistics for maximum parsimony analysis of *trnL-F*, ITS and 5S NTS sequences.

Analysis	Taxa	Total characters	Indels	Informative characters	Tree length	Tree number	CI	RI	RC
<i>trnL-F</i>	59	946	16	84	189	30,000	0.862	0.840	0.724
ITS	54	625	12	66	175	30,000	0.491	0.457	0.225
5S	56	191	5	73	231	30,000	0.519	0.743	0.386
Combined 1	58	1762	33	191	548	30,000	0.474	0.589	0.280
Combined 3	52	1762	33	147	446	30,000	0.460	0.584	0.269
Combined 4 (weighted)	52	1762	33	147	-	56	0.595	0.837	0.498

**Table 2.3** Number of informative and variable characters (in brackets) for different sets of taxa for the *trnL-F*, ITS and 5S NTS data sets.

Informative characters (variable uninformative characters)	<i>trnL-F</i>	ITS	5S NTS
All taxa included (Appendix 1)	84 (71)	66 (142)	-
Ruschioideae (Appendix 1)	31 (83)	57 (121)	-
<i>Brownanthus</i> , <i>Phyllobolus</i> , <i>Dorotheanthus</i> excluded	30 (53)	49 (117)	73 (29)
<i>Lampranthus</i> - group	23 (35)	30 (60)	57 (29)

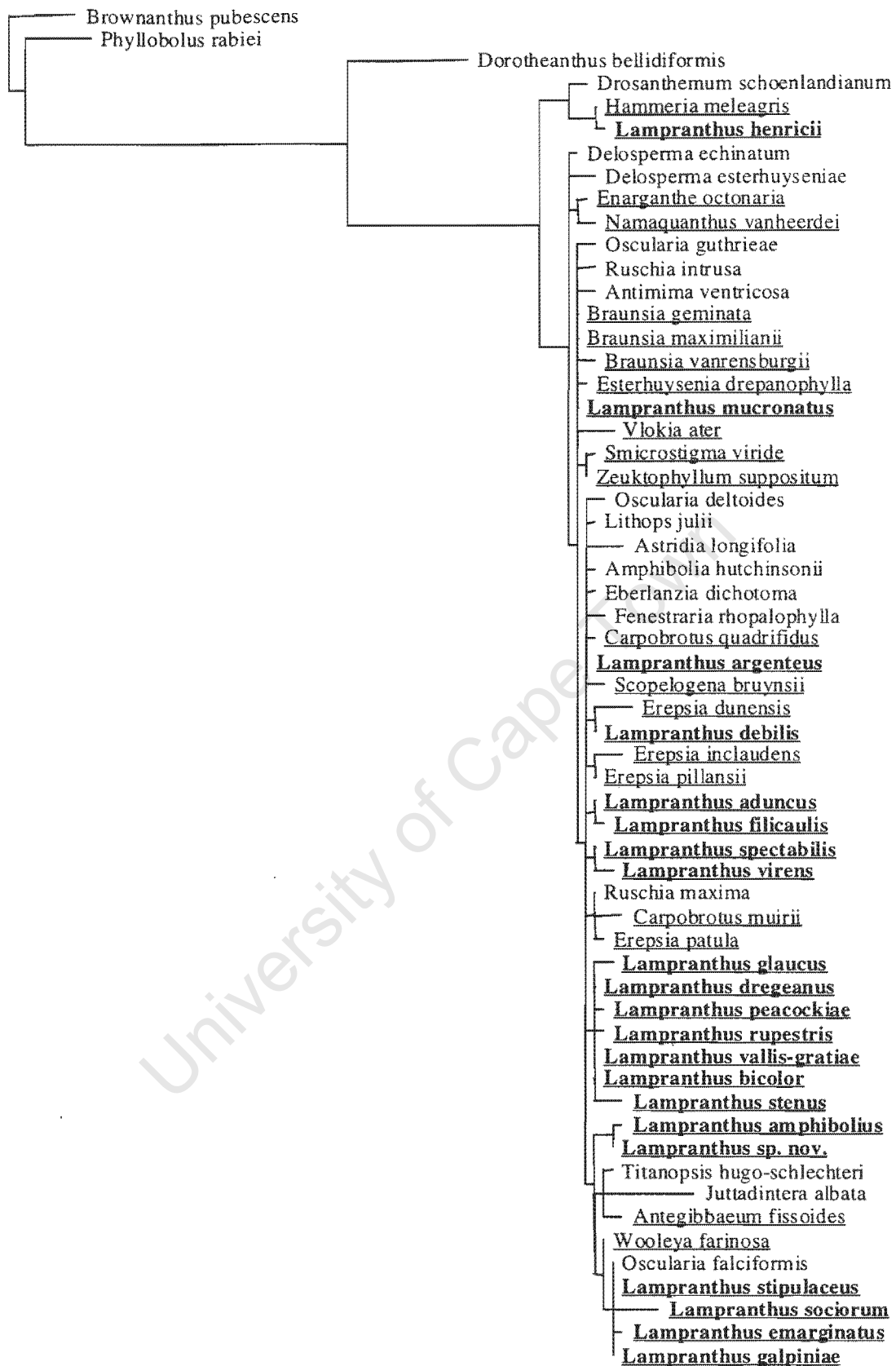
## 2. 4. Discussion

### 2. 4. 1. Utility of the DNA regions for phylogeny reconstruction

There is a surprising lack of resolution in two of the gene regions, namely ITS and *trnL-F*. Lack of resolution may either be a result of character conflict or of a paucity of characters. In this study the retention index (ri) is high for the *trnL-F* data set, so that the lack of resolution may be attributed to inadequate numbers of informative characters (Table 2. 3). In addition, exclusion of the distantly related outgroups, i.e. the Mesembryanthemoideae and *Dorotheanthus*, shows that comparatively few informative characters (30 for *trnL-F* including 56 taxa, 49 for ITS including 52 taxa) are found among the remaining genera of the Ruschioideae with even fewer observed in the *Lampranthus* – group (23 for *trnL-F*, 30 for ITS, Table 2. 3). In the *trnL-F* data set pairwise distances between the *Lampranthus* – group and the Mesembryanthemoideae ranged between 6.3-7.0%. Pairwise distances between the *Lampranthus* – group and the distantly related outgroups (*Drosanthemum* and *Delosperma*) ranged only between 0.2-1.1% and within the *Lampranthus* – group between 0.0-0.8%. These values furthermore suggest that most character changes occur in the deep branches (see also Fig. 2. 6), with considerably fewer changes occurring in the Ruschioideae (after exclusion of *Dorotheanthus*). If the ITS data set was restricted to the Ruschioideae (excluding *Dorotheanthus*) pairwise distances between the *Lampranthus* – group and the most distantly related outgroups (*Drosanthemum* and *Delosperma*) measured between 1.4-2.6% and ranged within the *Lampranthus* – group between 0.4-2.2%. These measurements indicate that within the Ruschioideae (excluding *Dorotheanthus*) the character changes in the ITS data set are higher compared to the *trnL-F* data set and are also somewhat more evenly distributed (Fig. 2. 7).

In contrast in a comparative study at subfamily level (Calamoideae, Palmeae), some 415 informative sites were recorded for the 60 included taxa for the ITS region (Baker *et al.* 2000a). Similarly, in a study of the ITS region of five tribes of Brassicaceae which included 37 taxa, 196 informative sites were present (Mitchell & Heenan 2000). Thus both studies yielded 4.5-6.5 times as many informative characters as taxa investigated. However, in this study there were always considerably fewer informative characters than included terminals, if the data set was restricted to the Ruschioideae. A very similar lack of informative characters has also been reported for the *trnL-F* region in palms (Baker *et al.* 1999), where for 65 sampled species (representing the major tribes and subtribes within the family) only 57 informative characters were obtained. Low numbers of informative characters may at least partly account for the low levels of resolution observed in this study.

In the ITS data set, however, the retention index is comparatively low suggesting that the characters most involved in synapomorphy are quite homoplasious. Therefore character conflict in this data set might be substantial. The number of informative characters after exclusion of the distantly related outgroups is only slightly higher than in the *trnL-F* data set (30 for *trnL-F*, 49 for ITS). However, the number of variable characters is considerably higher, suggesting that adding more taxa may help to obtain a better-resolved



– 1 change

**Fig. 2. 6** Phylogram of one of 30,000 most parsimonious trees ( $l=189$ ,  $ci=0.862$ ,  $ri=0.840$ ,  $rc=0.724$ ) recovered during heuristic search 1 of the *trnL-trnF* data set for 59 taxa. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.

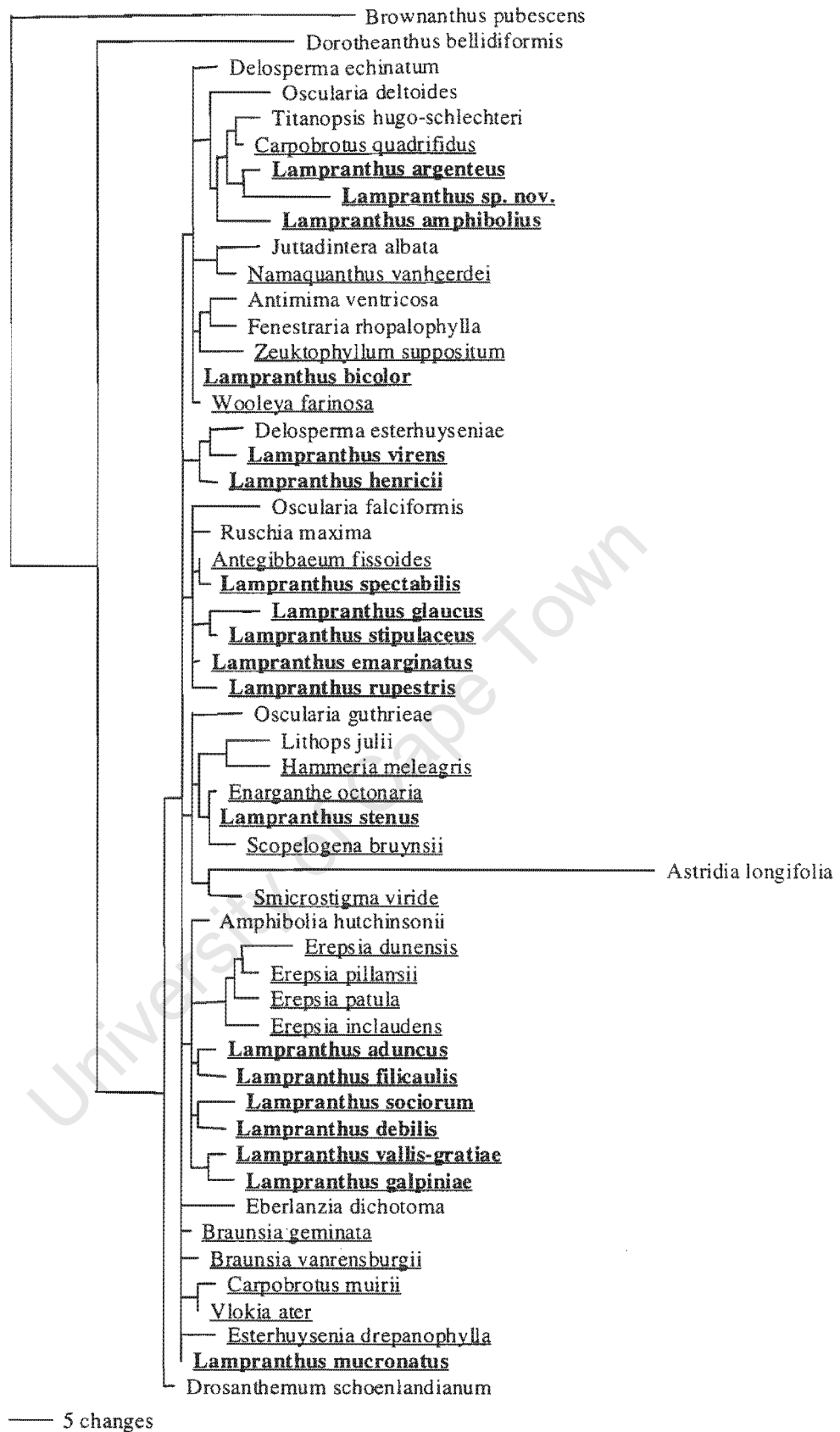


Fig. 2. 7 Phylogram of one of 30,000 most parsimonous trees ( $l=175$ ,  $ci=0.491$ ,  $ri=0.457$ ,  $rc=0.225$ ) recovered during heuristic search 2 of the ITS data set for 54 taxa. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.

topology for the Ruschioideae (83 for *trnL-F*, 121 for ITS).

For both the *trnL-F* and ITS data sets the number of variable characters across the two subfamilies suggests that these two regions are likely to be extremely useful for resolving major lineages within the two subfamilies. While both gene regions appear to be useful for resolving the major lineages within the Aizoaceae, they appear of little utility within the *Lampranthus* - group. If only the *Lampranthus* - group is considered, the *trnL-F* and the ITS data sets (Table 2. 3) show both a low number of informative as well as variable characters (which may become informative if more taxa were added). This result is surprising, since the *trnL-F* region has been used successfully in numerous studies to reconstruct hypotheses of relationship at generic level (e.g. Gielly *et al.* 1996; Kim *et al.* 1996; Mes *et al.* 1997), although in most cases species level relationships were not resolved (e.g. Böhle *et al.* 1994; Mes *et al.* 1997). On the other hand, the ITS region frequently resolves relationships among species (e.g. Eldenäs *et al.* 1998; Meerow *et al.* 2000, Baldwin & Wessa 2000).

In the 5S spacer data set, the retention index and the rescaled consistency index were higher than in the ITS data set, suggesting that there was less homoplasy (Table 2. 2). The region was found to be informative at the generic level, where nodes were in four cases highly supported with jackknife values above 80 (Fig. 2. 3). The number of informative characters for the *Lampranthus* - group is almost double compared to the ITS gene region, suggesting that it is more informative than the ITS region at lower taxonomic levels. Above generic level some nodes were resolved, but statistically unsupported. At the specific level, hardly any resolution could be obtained (Fig. 2. 3), which contrasts with many previous studies which have shown the 5S spacer to be particularly useful at the specific level (e.g. Udovicic *et al.* 1995; Kellogg *et al.* 1996; Baker *et al.* 2000b). This may have been also due to a greater number of informative characters as reported for a study of *Calamus*, where the number of informative characters far exceeded the number of sampled taxa (by 6.4 times, Baker *et al.* 2000b) compared to 1.3 times in the present study, Table 2. 1).

#### 2. 4. 2. Congruence between trees

The strict consensus trees generated from the three different data sets are largely congruent. In part this is because the trees based on the ITS and *trnL-F* data sets are poorly resolved, rendering them of very limited use in corroborating the better resolved relationships found in the 5S analysis. Nevertheless there are some areas of disagreement. In the *trnL-F* strict consensus tree, *Drosanthemum* forms a clade with *Hammeria* and *Lampranthus henricii*. In the 5S strict consensus tree, *L. henricii* is placed sister to *L. argenteus*, with the latter two placed next to *Antimima*. However, in the reduced and weighted analysis (simultaneous analysis 4), *L. henricii* and *L. argenteus* are well-supported sister taxa (JK = 94), suggesting that both data sets provide characters indicating this relationship. The ITS data yield only one well supported clade (JK = 87), which comprises the four species of *Erepsia*. Yet, in the 5S and the combined analysis (reduced and weighted), *E. inclaudentis* is placed outside the *Erepsia* clade and is sister to *O.*

*guthrieeae* and the “core” of *Lampranthus*, although with no statistical support. The Kishino-Hasegawa and the Templeton-Wilcoxon tests showed that the differences between the two trees were significant, suggesting that the monophyly of *Erepsia* is significantly contradicted by the 5S data. An explanation that mixed up DNA samples may be the cause for this different placement could be rejected on the grounds that re-sequencing (using the same DNA extraction as for the ITS analysis) of the 5S spacer produced the same sequence for *E. inclaudentis* as in the first instance. Although the ITS analysis indicated a high jackknife value (JK = 87) for the clade which contained all four species of *Erepsia*, it was shown above that the ITS data do not significantly contradict the placement of *E. inclaudentis* as sister to *O. guthrieeae*. Thus, the two data sets are considered congruent.

The ITS data place *L. spectabilis* sister to *Antegibbaeum*, whereas in the 5S analysis and in the combined analyses these are clearly unrelated. Since the relationship found in the ITS analysis is unsupported by the jackknife, the node may be due to random convergence. Similarly, in the ITS tree *Zeuktophyllum* appears as sister to *Antimima* and *Fenestraria*, whereas the three taxa are placed in different clades in the 5S (Fig. 2. 3) and combined analyses (Fig. 2. 4, 2. 5). Again, the nodes in the ITS tree are unsupported by jackknife values. Since the arrangement shown in the 5S tree is also retrieved in the combined analyses, the nodes retrieved in the ITS tree may be spurious.

Noteworthy is also the relatively long branch leading to *Astridia* in the ITS tree, whereas the same taxon had a relatively shorter branch in both the trnL-F and 5S (not shown) analyses. For a particular taxon such length variation among different gene regions have been observed in other plant groups (Hedderson, pers. comm.). Since all of the sequences had been blasted at genbank, it was verified that the correct region and taxonomic group had been amplified.

Incongruence between molecular data sets necessarily raises the question of whether the genes actually reflect species relationships. Many mechanisms (e.g. introgression, lineage sorting or gene conversion) are known by which genes might have different histories and which may be fundamentally incongruent with the true species phylogeny (Doyle 1992, Kellogg *et al.* 1996). In addition, for multi-copy genes, more than one versions may be present due to incomplete concerted evolution. For nuclear genes, especially for the 5S NTS spacer, intragenome polymorphisms have been recorded (Kellogg *et al.* 1996, Baker *et al.* 2000b). However, in these cases, the majority of multiple clones obtained from individual species were resolved as monophyletic groups, suggesting that gene trees mostly coalesce within species.

In order to test the validity of inferring a species phylogeny from a gene tree or trees, the molecular data set should be combined with all the available data (e.g. morphological data) to obtain a globally parsimonious result (Doyle 1992). In the present study, since two of the data sets were poorly resolved, it is not possible to meaningfully evaluate conflicts. Therefore, apart from non-molecular data, a further gene region, preferably of chloroplast or mitochondrial origin, should be investigated to test the hypothesized relationships among the taxa included in this study.

### 2. 4. 3. Monophyly and relationships of the genera placed in the *Lampranthus* – group

The molecular data provide no support for the monophyly of *Lampranthus* in its present circumscription. The 5S and the combined analyses retrieve a well-supported “core” of *Lampranthus*, whereas numerous species of *Lampranthus* are placed well outside this “core”.

The “core” of *Lampranthus* includes some species whose close relationship to *Lampranthus* has been questioned in the past. This applies to *L. virens*, which was recently transferred from *Drosanthemum* to *Lampranthus* (Hartmann & Bruckmann 2000). In addition, Liede (1989) suggested that a group of yellow-flowered species of *Lampranthus* were more closely related to *Circandra*, whereas a group of pink flowered species was more closely related to *Esterhuysenia* and *Erepsia*. Although Liede omits all names of species she investigated, the yellow-flowered group would certainly include *L. glaucus*, whereas *L. vallisgratae* matches her diagnosis of a species of the pink-flowered group. If the molecules used here do reflect the phylogeny of the species (and not just the genes), this study shows that they are all part of the “core” of *Lampranthus*.

Furthermore, two species of *Oscularia*, *O. falciformis* and *O. guthrieae*, recently transferred from *Lampranthus* to *Oscularia* (Hartmann 1998a), also fall within or are sister to the “core” of *Lampranthus*. Both species lack (at least some) the main morphological features of *Oscularia*, viz. aggregate inflorescences, flowers with their filamentous staminodes conically collected and five distinct nectar glands (meronectaries). Instead *O. falciformis* has 1-3 - flowered inflorescences, lacks filamentous staminodes and has a ring of nectaries (holonectary) - all characters that are shared with most species of *Lampranthus*. *O. guthrieae* shares these characters as well, but its nectaries are arranged in five groups (although not very distinctly) rather than in a ring. The data indicate a weakly-supported relationship (JK = 64) between *Oscularia guthrieae* and *L. debilis* but provide only relatively weak support (JK = 57) for inclusion into the “core” of *Lampranthus*.

Several species at present included in *Lampranthus* are shown not to be part of the *Lampranthus* clade and form closer relationships with other taxa:

*Lampranthus aduncus* is placed in the combined analysis in a clade with *Carpobrotus* (Fig. 2. 5), whereas it is placed as sister to *L. filicaulis* in the ITS analysis. Both species are currently included in Section *Adunci* and share the same floral morphology and the unusual slender, smooth and scimitar-shaped leaves. Although the combined analysis does not resolve the two species as sister taxa, the evidence from morphology and the ITS analysis suggests that they are closely related. However, their relationship to the genera of Ruschioideae remains uncertain.

Two further species, *L. sp. nov.* and *L. amphibolius*, the latter of which has been traditionally difficult to place, show no close association with either *Lampranthus* or *Amphibolia*. Possibly the most unusual features they share are the sculptured epidermis and the xeromorphic leaves, which distinguishes them clearly from the “core” of *Lampranthus*. Their relationship to other genera within the Ruschioideae remains unresolved in all the analyses, except in combined analyses 4 (Fig. 2. 5), where the two species are

placed as sister to *Esterhuysenia* and *L. mucronatus*. Morphologically the two clades do not share any obvious similarities. Instead, a much closer similarity may be found with *Eberlanzia*, which also displays sculptured leaves and a similar capsule morphology (Hartmann 1998a). However, no close relationship between the taxa is indicated by the molecular data.

*L. mucronatus* is shown to be most closely related to *Esterhuysenia* (Fig. 2. 5). Morphologically *L. mucronatus* is very similar to species placed in *Esterhuysenia*, in particular to *Esterhuysenia inlaudens* (L.Bolus) H.E.K.Hartmann. All species of *Esterhuysenia* have solitary flowers, top-shaped fruits with no closing bodies and narrow valve wings (Hartmann 1998a). Typically the old stems and leaves have a blackish colour and the leaves dry up on the stem and do not fall off. In addition, Liede (1989) pointed out that the leaves of *Esterhuysenia alpina* L.Bolus do not possess any reduced bladder cell idioblasts (Ihlenfeldt & Jürgens 1982) as found in both *Erepsia* and *Lampranthus*. The more xeromorphic type of epidermis, which can be observed in all species of *Esterhuysenia*, appears to be an important feature which delimits the genus from *Lampranthus* and *Erepsia*, with which it otherwise shares a very similar fruit morphology.

In addition, two members of Section *Suffrutices*, *Lampranthus argenteus* and *L. henricii*, appear not to be closely related to the “core” of *Lampranthus*. The *trnL-F* analysis places *L. henricii* with very high support (JK = 96) as sister to *Hammeria*. However, the combined analysis shows a highly supported clade consisting of *L. henricii* and *L. argenteus* (JK = 94) which is most closely related to *Antimima* (Fig. 2. 5). The association with *Antimima* has been unsuspected until now, since no morphological characters are as yet evident which would support such a placement.

*Erepsia* forms a highly supported clade from which *E. inlaudens* is excluded. This result is surprising since morphologically all species of *Erepsia* are characterised by the presence of a hypanthium. A hypanthium is a rare feature in the Ruschioideae (but also present in *Argyroderma*, *Rabiea*, several species of *Carpobrotus*) and suggests that this species is part of *Erepsia*. However, one important difference between *E. inlaudens* and the other three species of *Erepsia* sampled in this study, constitutes the presence of a meronectary in *E. inlaudens* as opposed to a holonectary in the other three species. However, *E. inlaudens* shares this character state with *Oscularia guthrieae*, a species placed near it in the 5S (Fig. 2. 3) and combined analyses (Figs. 2. 4 & 2. 5). The nectary structure is generally conservative within a genus and the generic circumscription of *Erepsia* has so far been unusual for incorporating both types of nectary structures. However, the interpretation of which nectary type is present is not always unambiguous. Recent research of the nectary structure of *Machairophyllum* suggests that what may superficially appear as a meronectary is indeed a holonectary with few raised areas (H. Kurzweil, pers. comm.). Thus, although the majority of species of *Erepsia* have a holonectary, there are several others which also differ by the possession of (what appears to be) a meronectary. These are *E. pentagona* (L.Bolus) L.Bolus, *E. lacera* (Haw.) Liede, *E. forficata* (L.) Schwantes and *E. heteropetala* (Haw.)

Schwantes. In addition, a further species currently placed in *Lampranthus*, *L. schlechteri* (Zahlbr.) L. Bolus, also exhibits both a hypanthium and meronectaries, characters that are absent from any species considered to be part of the “core” of *Lampranthus*. Therefore, if the presence of a meronectary is indicative of a close phylogenetic relationship, this study predicts that these species may be more closely related to *E. inclaudens* than to the remainder of the species placed in *Erepsia* or *Lampranthus*. Clearly, more sampling within *Erepsia* is needed to test this hypothesis.

*Braunsia geminata* and *B. maximilianii* form a highly supported clade (Fig. 2. 4), which is corroborated by several floral and fruit characters typical for *Braunsia* (Klak 2000a). However, *B. vanrensburgii* appears to be unrelated to the other species of *Braunsia*. The fruit morphology of this species differs in having widely diverging expanding keels, whereas they are parallel in all other species of *Braunsia*. The fruit morphology therefore corroborates the molecular results which suggest that *B. vanrensburgii* is not part of *Braunsia*. In the combined analysis 4 (Fig. 2. 5) the species is placed in a well-supported clade (JK = 78) with several mono- and bitypic genera at present placed in the *Lampranthus* - group. There are as yet no known morphological characters that characterize the clade in which *B. vanrensburgii* is placed.

*Smicrostigma* forms a strong alliance with *Zeuktophyllum* (e.g. Fig. 2. 5) corroborating an earlier hypothesis of a close relationship between these two genera (Liede 1989). The latter genus comprises two species of very close morphological resemblance, which differ slightly in their fruit and flower morphology. *Smicrostigma* shares with both species the fused, trigonous xeromorphic leaves, sessile solitary flowers and many-locular fruits with similar internal structures. Based on the molecular evidence, which is corroborated by the morphology, *Smicrostigma* should be considered part of *Zeuktophyllum*. Both genera are placed with members of the *Lampranthus* - group and *Ruschia intrusa* into one clade (Fig. 2. 4), with the latter species suspected of misplacement in *Ruschia*. The present study supports Hartmann's (1998a) suggestion of a close relationship between this species and *Antegibbaeum*, since both taxa share a very similar habit and floral morphology (but differ in most of their fruit characters). The analysis excluding *Ruschia intrusa* (due to missing data) results in a higher support for the clade (Fig. 2. 5).

The relationship of several other mono- or bitypic genera of the *Lampranthus* - group remains uncertain. For example, *Namaquanthus* and *Enarganthe* show a closer relationship with *Drosanthemum* and *Delosperma* than with any of the genera at present placed in the *Lampranthus* - group. *Enarganthe* and *Namaquanthus* are found in the dry winter rainfall area of Namaqualand, with the latter genus only known from two localities. Morphologically the two taxa share numerous features, which they do not share with either *Drosanthemum* or *Delosperma*. These are leaves with flattened bladder cell idioblasts, multi-locular fruits with narrow valve wings and sharply pointed expanding keels which are parallel for most of their length. Thus, a close relationship between the two taxa is possible but needs to be investigated further.

*Wooleya* is placed with very low statistical support as sister to *Astridia* (Fig. 2. 5). Similarly,

*Scopelogenia* is placed next to *Fenestraria* without any support. *Scopelogenia* and *Fenestraria* bear no morphological resemblance to each other. Although there are similarities in the habit, floral and leaf morphology between *Astridia* and *Wooleya*, both taxa differ greatly in their fruit morphology. The indicated relationships are therefore viewed with great caution.

It is evident then that several genera such as *Erepsia* (see discussion for *E. inlaudens*), *Braunsia* after exclusion of *B. vanrensburgii*) and the “core” of *Lampranthus* are well supported in this analysis and supported by numerous morphological characters. However, relatively little confidence can be placed in the relationships among the genera of the *Lampranthus* - group, which do not form a clade.

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## CHAPTER 3

### MORPHOLOGY AND CLADISTIC ANALYSIS OF THE *LAMPRANTHUS* - GROUP

#### 3. 1. Introduction

Despite the wide application and use of molecular methods in systematic biology, morphological, ontogenetic and anatomical characters are still critical for providing independent sources of evidence for testing phylogenetic hypotheses derived from molecular data (e.g. Doyle 1992). Therefore a careful and comprehensive morphological analysis remains essential for substantiating a hypothesis of phylogenetic relatedness (Stevens 1991, Endress *et al.* 2000).

The molecular study of *Lampranthus* and the *Lampranthus* – group was undertaken because of a perceived deficiency of morphological characters other than from fruits, and the consequent strong bias towards fruit structures in all previously proposed hypotheses of phylogenetic relationships. Although in the past evolution of particular characters has been considered and presumed apomorphic or synapomorphic characters defining particular groups were provided, numerical cladistic analyses have generally been lacking (e.g. Dehn 1992, Gerbault 1995). The question as to which characters are synapomorphic or which are plesiomorphic has so far been based on outgroup comparison with the other subfamilies of the Aizoaceae (Bittrich & Hartmann 1988, Bittrich & Struck 1989). However, these polarity assessments have not been tested in a formal cladistic context. Therefore, although the problem of the possible repeated evolution of “derived” characters such as the closing body has been raised (Hartmann 1988), a phylogenetic tree has not been constructed to demonstrate homoplasy of these structures.

Since numerous characters have never been studied in detail (e.g. ontogenetic investigations), the assessment of whether characters are homologous is a difficult task. However, this study would be flawed if an assessment of morphological characters were not undertaken in concert with the molecular data (Doyle 1992, Luckow & Bruneau 1997). Furthermore, homology and evolution of morphological characters in *Lampranthus* and the *Lampranthus* – group can be evaluated by optimization of characters on phylogenetic trees (Luckow & Bruneau 1997). This can be done either by plotting the morphological characters on the tree obtained from the combined molecular data or on the tree derived from the total evidence analysis (combining the morphological data with the molecular data).

In this chapter a hypothesis of phylogenetic relationships is constructed based on a study of morphological characters. A matrix of characters is presented for the *Lampranthus* - group and the characters and their codings are discussed in detail.

#### 3. 2. Phylogenetic analysis

##### 3. 2. 1. Homology assessment and matrix construction

Homology occupies a central position in comparative studies in various fields (e.g. Jardine 1969,

Guedes & Dupuy 1976, Blackmore & Barnes 1987, Patterson 1988, Coddington 1994, McKittrik 1994) and forms the basis of most generalisations about biological phenomena (de Pinna 1991). In its basic form, homology is understood as 'equivalence of parts' and serves as a sorting procedure to investigate the validity of comparative information (de Pinna 1991). The proposition of homology involves two stages, which have been termed by de Pinna (1991) as 'primary and secondary homology assessment'. A primary homology statement reflects the expectation that there is a correspondence of parts that can be detected on the basis of similarities. The secondary homology assessment is the outcome of a congruence test (e.g. a cladistic analysis) and it essentially tests the hypotheses generated during the primary homology assessment.

A primary homology assessment forms the basis of any data matrix construction and it involves two stages (Brower & Schawaroch 1996). Firstly, a study of variation in morphology is used to find those characters that may prove useful. Secondly, the states for individual characters are partitioned so that they may be coded. The states are assigned to a terminal taxon and are presented as one column in the data matrix. "The data matrix can thus be viewed as a statement of the primary homology assessment" (Hawkins *et al.* 1997). Primary homology assessment therefore forms the main determinant of the outcome of any cladistic analysis, as different codings can yield different cladograms (Bryant 1989, Maddison 1993). In aligned DNA sequences the character states can usually be clearly defined. However, morphological variation may involve complex characters that give scope for alternative approaches to representing this variation as characters and their states (Wilkinson 1995). Thus, the construction of the data matrix, i.e. the primary homology assessment, has been perceived as subjective (e.g. de Pinna 1991, Stevens 1991). This view appears to have been confirmed in a survey of primary homology assessments, which showed that different botanists code characters in different ways (Hawkins 2000).

Although fundamental to phylogenetic inference, there has been far less discussion of methods and problems of character documentation compared with discussion of constructed matrices. Baum (1988), Stevens (1991), Thiele (1993) and Gift & Stevens (1997) provided extensive discussion of how to code quantitative characters. Quantitative characters often show a considerable amount of variation, and are essentially continuous. According to Stevens (1991) such continuous characters are not suitable as cladistic characters, in which the different states have to be discrete. Thus quantitative data are only considered cladistic and may be useful only when the data show widely discontinuous patterns of variation (Stevens 1991, Kitching *et al.* 1998). In this study quantitative characters were coded as discrete states if taxa could in the majority of cases be unambiguously assigned one of the states. Taxa which took up an intermediate position were coded with a "?".

Whereas Stevens (1991) discussed qualitative versus quantitative data and delineation of different character states within a character, others have focused on delineation problems in the relation between characters and character states (Pimentel & Riggins 1987, Pleijel 1995, Wilkinson 1995, Hawkins *et al.* 1997, Strong & Lippscomb 1999, Lee & Bryant 1999). One of the main issues discussed is whether characters should be coded as multistate variables or as present/absent. Pimentel & Riggins (1987) rejected

the coding of characters as absent/present on the basis that it may result in the selection of less parsimonious trees (Meier 1994). Pleijel (1995) on the other hand argued that presence/absence coding (coding each observable feature as a separate character) avoids problems with non-applicable states. However, Seitz *et al.* (2000) showed that the problem of inapplicable data persists independent of whether characters were coded as absent/present or with two or more states. They concluded in accordance with Strong & Lipscomb (1999) that, although flawed, inapplicable characters are currently best coded with a '?'. A solution to this problem is only to be found in the development of new algorithms that distinguish between inapplicable and missing data (Maddison 1993, Hawkins *et al.* 1997, Lee & Bryant 1999).

In this study Pleijel's method C is followed for most character codings, which is in accordance with the coding method proposed by Hawkins *et al.* (1997), where the absence/presence of feature X is considered as a separate character from for example the shape and colour of feature X. Inapplicable characters were coded with a '?'. In the case of binary character-states, character polarity is determined by the resultant topology after analyzing outgroup and ingroup taxa simultaneously (Farris 1972, Nixon & Carpenter 1993). In the case of the question of whether to order and how to order multi-state characters, no consensus has been reached in the literature (e.g. Hauser & Presch 1991, Wilkinson 1992). Whereas ordered characters are generally perceived as being more informative, Hauser & Presch (1991) found that this was not necessarily the case. They found that ordered characters can produce more, equal numbers or fewer parsimonious trees and can increase as well as decrease or have no effect on tree resolution. It has been further argued that, if the best criterion for assessing character evolution is congruence with other characters, the practice of ordering multistate characters is unnecessary (Hauser & Presch 1991). Ordering characters would thus only add more assumptions into the analysis and these may consequently weaken the confidence with which one can interpret the results. Therefore in this study, only unordered or non-additive character transformations were considered. Several methods were proposed to code polymorphisms, e.g. as missing data (Pimentel & Riggins 1987), each as a separate character state in a multistate transformation series (e.g. Wiens 1995) or as implemented by PAUP (Swofford 2000). The various methods were evaluated by Kornet & Turner (1999) who concluded that polymorphism is best coded as the plesiomorphic state, unless the plesiomorphic state is unknown, in which case coding as ambiguous was recommended. However, in many cases it is difficult to assess prior to analysis to assess whether a character state is plesiomorphic. Their second recommendation therefore closely follows the method implemented by PAUP where polymorphic characters are coded as ambiguous and this was followed in this study.

### 3.3. Materials and Methods

#### 3.3.1. Ingroup and outgroup sampling.

The same species were used in the morphological study as in the molecular analysis presented in chapter 2. In total 2654 herbarium specimens in BOL and 615 field collected plants were examined for the morphological study. In addition, *Circandra* was included to test whether it formed part of *Lampranthus*.

Since no living material could be located (see pages 5-6), the characters of this taxon had to be scored from dried material, from information given in the literature (Liede 1989) and from notes on the herbarium sheets. The details of the palynological investigation followed the methods outlined by Klak & Linder (1998).

### 3.3.2. Character list

#### General habit and stem

1. Habit: decumbent to erect and never rooting at nodes (0), trailing to mat-forming and mostly rooting at nodes (1)

Most species form small erect shrubs, 15-35 cm tall, with only relatively few species forming more substantial, woody shrubs varying from 30-60 cm in height (e.g. *Scopelogena*). Numerous species form elongated, slender, decumbent or prostrate branches which root at the nodes and trail along the ground and these may also form dense mats. *Lampranthus stenus* has a very variable habit ranging from trailing plants to erect shrubs.

2. Plants shrubby with stems visible between the nodes (0), dwarf, clump-forming with stems very reduced (1) stemless (2)

#### Leaves (macroscopic)

3. Leaves glaucous green (0), bright yellow-green (1)
4. Leaves triquetrous (0), trigonous (1), half-cylindrical to cylindrical (2), flat to spatulate (3)
5. Leaves < 6 mm thick (0), leaves conspicuously thickened and > 8 mm thick (1)

Thickness refers here to the depth of the leaves. Although the character coding may appear arbitrary, taxa can be assigned with little difficulty to either state. Leaf thickness can vary depending on the availability of water. However such variation is almost exclusively observed in species with thickened leaves and not in species with very slender leaves.

6. Leaves not connate or very shortly connate (0), fused for a quarter of their length (1), fused for a third to more than one half of their length (2), completely fused (3)

In leaves “fused for a quarter of their length” the fused parts of the leaves are much shorter than the free parts, whereas in leaves “fused for a third to more than one half”, the free parts are considerably shorter compared to state (1). It may be argued that this character should be ordered since the states appear to represent a morphocline (Mickevich & Weller 1990, Wilkinson 1992). However, Ihlenfeldt (1971a, b)

suggested that abbreviations in the ontogeny (e.g. neoteny or the loss of some of the intermediate stages) may result in very different leaf shapes arising in closely related taxa. On account of these observations it may be possible that character state (0) may change to state (3) in one step without going through the intermediate stages. Therefore, *a priori* hypotheses of the direction of change cannot be made since the sequence of transformations may vary.

7. Leaves incurved, i.e. sickle shaped (0), leaves recurved (1), leaves more or less straight (2)

All three states are frequently found throughout the succulent Aizoaceae. Within species no variation has been observed. The state "leaves recurved" does not refer to apically recurved leaves, which could equally be termed mucronate or hooked. Instead the leaf is recurved for some of its length.

8. Leaves mucronate (0), without a mucro (1)

Leaves (microscopic)

The anatomy and the surfaces of the leaves and succulent stems of the succulent Aizoaceae were studied by various authors (e.g. Reule 1937, Öztig 1940, Dupont 1968, Barthlott & Ehler 1977, Hartmann 1979, Ihlenfeldt & Hartmann 1982, Ihlenfeldt & Jürgens 1982, Jürgens 1985). Whereas the surface and anatomy of the leaves and/or stems has been investigated in most generic revisions in the succulent Aizoaceae (e.g. Liede 1989, Klak & Linder 1998, Groen & van der Maesen 1999), developmental studies of epidermal surfaces, in particular those with a very similar appearance, are very rare (e.g. Niesler 1996). The different ontogeny of the very similar cuticular folds found in *Synaptophyllum* and *Faucaria* (Niesler 1996) suggests that further studies should be undertaken in order to establish homologous features.

9. Outsized water storing bladder cells present, cell diameter large (0), absent or cell diameter small (1)

Outsized water storing bladder cells with large cell diameter are typical for members of the Mesembryanthemoideae, but are also found in the Ruschioideae, such as in *Delosperma* and *Dorotheanthus*. Due to their large size, they can easily be observed with the naked eye (Plate 1 A). Numerous modifications in size, shape, density and anatomy have been described for these outsized bladder cells (e.g. Ihlenfeldt & Hartmann 1982, Ihlenfeldt & Jürgens 1982, Klak & Linder 1998). However, since these modifications are mainly present in a few of the outgroups and since they often represent autapomorphies, they were not coded separately. Large cell diameters ranged from 350-600  $\mu\text{m}$  (Plate 1 A) and small diameters range from 8-160  $\mu\text{m}$  (Plate 1 B-I). The measurement was taken at the broadest diameter.

10. Bladder idioblasts much reduced (0), flattened, but clearly elevated (1) surface smooth, with epidermal cells not elevated (2)

This character state refers only to those taxa where outsized bladder idioblasts are absent.

Numerous taxa in the Ruschioideae have a finely papillate, often referred to as “velvety” (Plate 1 B, E) or “scabrid” (Plate 1 F) epidermal surface, which can mostly be observed with a 10X magnification lens. These surfaces were coded as “much reduced”. The second and third character states can no longer be observed with a 10X magnification lens. Whereas in state (1) the borders of the cells are still clearly visible (Plate 1 C), they are much obscured in state (2), where the cells are completely flattened (Plate 1 D, H).

11. Epidermal cells raised in groups into hills (0), not raised in groups (1)

In several genera of *Ruschioideae* the epidermal cells are conspicuously raised out of the surface in irregular groups (Plate 1 E).

12. All cells raised (0), only single cells raised (1)

If the cells are raised above the surface, every cell may be raised (Plate 1 A-C), or only single cells may be raised above the level of the others (Plate 1 F).

13. Epidermal cells pointed (0), raised into a mound (1)

The two states are easily distinguished and are illustrated in Plate 1 B for state (0) and e.g. Plate 1 E, F for state (1).

14. Leaves without dark dots (0), with dark dots (1)

The dark dots on the leaves are tannin idioblasts, which lie in the assimilating tissue just below the surface of the leaves (e.g. Liede 1989). Such tannin idioblasts are common, but are usually positioned in the water-storing tissue of the leaves, so that the leaves are of a uniformly green or grey colour. The subepidermal positioning of the tannin idioblasts characterizes several genera such as *Pleiospilos* and *Erepsia*. Nevertheless in *Erepsia* there are also exceptions with light green leaves without dark subepidermal tannin idioblasts, such as *E. inclaudentis*. In *Lampranthus* the tannin idioblasts are visible only in a few species, such as in *L. glaucus*.

15. Crystal layer absent or incomplete (0), present, either thin or thick (1)

A thick layer of oxalate crystals is one of the characteristics of a xeromorphic type of epidermis, whereas a mesomorphic type of epidermis usually lacks such a crystal layer (e.g. Hartmann 1991). Naturally there are intermediates, from taxa with no trace of crystals in the subepidermal layers through an incomplete or very thin layer to a moderately thick or very thick layer of oxalate crystals. *Erepsia* is an example where species may have a continuous crystal layer, or it may be broken up (Liede 1989). In addition, the crystal layer may be unevenly distributed in the leaves, as in the case of *Erepsia*, where it is particularly thick at the keels (Liede 1989). Since there is a grade in the thickness of the crystal layer, a

continuous layer independent of its thickness was coded as a single character state (1). Variation in the thickness of the crystal layer in response to environmental variables, such as availability of water and intensity of sunlight may be possible. The character states were therefore broadly defined, in order to account also for possible variation within a taxon.

16. Stomata not sunken (0), slightly sunken (1), completely sunken (2)

Variation between the three character states has not been observed. Stomata that are not sunken are shown in Plate 1 C, D; slightly sunken stomata are found in, for example, *Namaquanthus vanheerdei* (Plate 1 F) and completely sunken stoma are shown in Plate 1 H, I.

17. Stomata not concealed by epidermal bladder idioblasts (0), concealed by epidermal bladder idioblasts (1)

The surface may be densely covered with bladder idioblasts, forming a second surface above the epidermal layer and these may completely conceal the stomata (Plate 1 E). In cases where the surface is only thinly covered with bladder idioblasts, the stomata may still be visible (Plate 1 B) and such cases were then coded as state (0).

18. Guard cells flattened (0), raised and overarching stoma (1)

In the majority of taxa the guard cells are flattened (e.g. Plate 1 C, G). In numerous, possibly unrelated taxa, the guard cells are conspicuously raised and overarch the stoma (Plate 1 I).

### Flowers

19. Receptacle not bicarinate (0), bicarinate (1)

20. Inflorescence with 1(-2) flowers (0), 1-5 flowers (1), 6-many flowers (2)

The inflorescences of the Aizoaceae principally follow a dichasial pattern in their construction as described by Troll & Weberling (1981). Several variations of this dichasial type have also been described (Troll 1969, Troll & Weberling 1981, Bittrich 1986, Hartmann & Rust 1994).

Single-flowered inflorescences are widespread, particularly in plants with much reduced growth form such as in *Argyroderma*, *Lithops* and *Conophytum* (Hartmann 1978, Hammer 1993), but are also found among shrubby species. In the *Lampranthus* - group and in *Lampranthus* single-flowered inflorescences are frequent, particularly among the species with creeping or trailing habits. Occasionally, a second flower is produced if plenty of water has been available. Species may also show a range of 1-5 flowers per inflorescence within a specimen. Inflorescences with 6-many flowers are rare in the *Lampranthus* - group.

21. Flowers small (< 3 cm diam.) (0), large (> 3.5 cm diam.) (1)

Although this subdivision may appear arbitrary, small and large flowered species can in most cases easily be distinguished. The size of the flower can vary, particularly if the plants are growing under unfavorable conditions. These circumstances were not taken into account, since they do not represent the norm. The flower diameters have been taken from the plant descriptions and from own observations.

22. Flowers more or less sessile or on short pedicels (< 2 cm long) (0), flowers on long pedicels (> 3-8 cm long) (1)

The length of the pedicels is variable. However, exceedingly long pedicels, which are those that are longer than 3 cm, are always clearly distinguishable from those which generally do not exceed 2 cm in length.

23. Flowers yellow, orange or red (0) never yellow, orange or red (1)

Both petaloid and filamentous staminodes are usually brightly coloured. In the succulent Aizoaceae the most frequently observed colours are pink, purple and white. Yellow flowers are common among members of the *Stomatium* – and *Bergeranthus* – groups. Otherwise yellow flowers are rare in the Ruschioideae. Even less common are orange- and red-coloured flowers. They are found in a few species of *Drosanthemum*, *Dorotheanthus*, *Conophytum* and occasionally in *Lampranthus*. The colour of flowers may vary considerably within a species (Hartmann 1981, 1988b, Ihlenfeldt & Struck 1987) and it has been observed that species with pink or purple flowers may have white-flowered forms and similarly those with yellow, orange or red flowers may also have white-flowered forms (e.g. *Lampranthus reptans* has both yellow and white-flowered forms and *L. watermeyeri* has both purple and white flowers). In addition, plants producing yellow flowers may sometimes produce orange or even red flowers so that further subdivision of this character is not possible. The fact that in *L. bicolor* the inside of the flower is yellow to orange and the outside is suffused with red also suggests that further subdivision would be artificial. The entire complex of flower pigments in the succulent Aizoaceae is as yet poorly understood and needs further investigation (reviewed by Hartmann 1991, p. 109).

24. Flowers with filamentous staminodes (0), without filamentous staminodes (1)

Ihlenfeldt (1960) distinguished between three types of androecia: 1, those where filamentous staminodes are not clearly distinguishable, i.e. where there is a grade from stamens into petals (Type 1); 2, those where filamentous and petaloid staminodes and stamens are clearly distinguishable (Type 2); 3, androecia where there are no filamentous staminodes (Type 3). In the majority of species in the Ruschioideae, the filamentous staminodes are clearly distinguishable. Occasionally transitions between fertile stamens and filamentous staminodes and between filamentous and petaloid staminodes occur.

25. Filamentous staminodes gathered into a cone (0), spreading (1), gathered together but with tips apically recurved (2)

If filamentous staminodes are present, they may either collect with the stamens around the stigmas to form a cone or they may spread to form open carpet flowers (Vogel 1954, Hartmann 1991). Cone-flowers are particularly common among the members of the *Ruschia* - and *Leipoldtia* - groups. In *Lampranthus* about half of the species has cone flowers, whereas the other half has open carpet flowers.

26. Staminodes and stamens free to bases (0), fused into a staminal tube (1)

Species of *Lampranthus* never form a staminal tube (not to be confused with a hypanthium) as in *Erepsia* and in some species of *Carpobrotus*.

27. Stamens papillate at base (0), without papillae (1)

In *Lampranthus* the stamens are mostly papillate, except for the majority of yellow-flowered species which have stamens without basal papillae.

28. Stamens erect (0), only inner ones pendulous (1), all pendulous (1)

The majority of species in the Aizoaceae has erect anthers. However, genera which possess a hypanthium, such as *Erepsia* or *Argyroderma* always have pendulous anthers. In some cases such as in *Erepsia* Sect. *Intectatae* only the inner stamens are pendulous while the outer ones are erect (Liede 1989). Nevertheless pendulous stamens are not restricted to species with a hypanthium (e.g. *Nelia*).

29. Top of ovary raised (0), flat or slightly concave (1)

Most species show no intraspecific variation between the two character states except for some species of *Carpobrotus* (Wisura & Glen 1993).

30. Hypanthium absent (0), present (1)

The presence of an extended receptacle wall, i.e. a hypanthium, is rare in the succulent Aizoaceae and occurs in several seemingly unrelated groups. The development of the hypanthium has been studied for *Erepsia* and *Argyroderma* (Haas 1976). Within a genus the length of the hypanthium can differ between species. For example, in *Erepsia* section *Intectatae* the hypanthium is very reduced and only reaches a maximum of 0.7 mm in length, with a maximum length for some species of *Erepsia* Sect. *Crassifoliae* of 2.0 mm long. In *Carpobrotus* only some of the species display a hypanthium. Variation in the length of the hypanthium found in *Carpobrotus* was never investigated.

31. Placentation axile (0), parietal to basal (1)

32. Stigmas short (i.e. shorter or the same length as shortest stamens) (0), long (i.e. longer than shortest stamens) (1)

In *Lampranthus* the length of the stigmas is closely connected to the floral morphology. Flowers with their filamentous staminodes and stamens conically collected have relatively long, slender stigmas, where the stamens are shorter or as long as the stigmas. In a carpet flower the stigmas are short and broad, and here the stigmas are never longer than the shortest stamens.

33. Columella broad, development in a radial direction (0), columella narrow, development early terminated (1)

The information used here was extracted from Haas (1976).

34. Nectaries in a ring (0), in five parts (1)

There is a ring of nectaries (holonectary) present in almost all species of the *Lampranthus*-group. Exceptions are the species placed by Liede (1989) in *Erepsia* Sect. *Erepsia* and Sect. *Crassifoliae*, which have their nectaries segmented into five parts (meronectaries). Meronectaries are absent in the closely related *Leipoldtia*- and *Ruschia*-groups, and are associated with the *Delosperma*- and *Drosanthemum*-groups. The meronectaries present in *Oscularia*, to where numerous species previously placed in *Lampranthus* have been moved, are considered indicative of a close relationship to the *Delosperma*- and *Drosanthemum*-groups (Hartmann 1991).

35. Nectaries shell-shaped (koilomorphic) (0), forming a ring or several groups of small teeth (lophomorphic) (1), forming a flat ring (2)

Shell-shaped nectaries are restricted to the Mesembryanthemoideae, whereas a flat, broad nectariferous ring is found in the *Cleretum* - and *Apatesia* - groups. A nectariferous ring consisting of groups of small teeth or a ring of small teeth is found in all remaining species in the Ruschioideae.

#### Pollen

There have been relatively few studies of the pollen morphology published in the succulent Aizoaceae (Dupont 1973, 1977, Dupont & Hartmann 1982, Bittrich 1986). One consequence of these studies is that a tricolpate, spinulose and punctate to micropunctate pollen is thought to be most common (Hartmann 1991) and this agrees with the position in most other centrosperms (Skvarla & Norwicke 1976, Norwicke & Skvarla 1977, 1979). Although the pollen characters were reportedly uniform within the Aizoaceae (Norwicke & Skvarla 1977), Bittrich found a surprising amount of variation in the Mesembryanthemoideae. A comprehensive survey of the pollen morphology across the Ruschioideae has not been undertaken as yet. In the present study this aspect was investigated to a limited degree: in several cases scarcity of flowering material meant that only one specimen per species was investigated.

## 36. Punctate (0), foveolate to reticulate (1)

Since the size of the perforations of the tectum varied fairly extensively across taxa, the categories were chosen very broadly to account for this variation. More detailed studies may show that this character may be partitioned further. Plate 2 A, D show punctate pollen. Examples of reticulate to foveolate pollen is shown in Plate 2 B, C.

## 37. Pollen microspinulate (0), spinulate (1)

Intermediates between the two states were not observed and taxa could generally unambiguously be assigned to one of the two states. Examples of the two states are shown in Plate 2 A-C (state 0) and Plate 2 D (state 1).

## 38. Pollen densely spinulate (0), sparsely set with spines (1)

The two states are shown in Plate 2 A-C (state 0) and Plate 2 D (state 1).

### Fruits

The fruits of the succulent Aizoaceae, in particular the fruits of the Ruschioideae, are very rich in characters. As a consequence, numerous studies have dealt extensively with the shapes and to some extent the anatomy of the fruit structures found over a broad range of species in the two subfamilies, Ruschioideae and Mesembryanthemoideae (e.g. Schwantes 1952, Straka 1955, Haas 1976, Hartmann 1988). A detailed account of each of the important structures found in the fruits such as the closing bodies, the covering membranes, the expanding keels and the valves was given by Hartmann (1988). The structures which are most frequently referred to are illustrated on Plate 3.

## 39. Fruits fleshy and in-dehiscent (0), a dehiscent hygrochastic capsule (1)

Within the Aizoaceae, *Carpobrotus* (including *Sarcozona*) is unusual in having fleshy fruits and this is considered to be an apomorphy for the genus.

## 40. Fruits woody (0), scarcely or not at all woody (1)

## 41. Fruit &gt; 7-locular (0), 4-6 (-7)-locular (1)

In the Mesembryanthemoideae, only (3-)4-5-locular capsules are found, whereas in the Ruschioideae capsules with up to 24 locules have evolved (e.g. *Argyroderma*). Generally low numbers of locules are constant within a species. Occasionally, species may have both 4- and 5-locular capsules (e.g. *Psilocaulon coriarium*, *Psilocaulon junceum*), but on one plant one number will usually predominate (Klak & Linder

1998). However, in capsules with more than seven locules, the locule number is rarely constant, even on the same plant. Exceptions are species placed in *Octopoma*, which always have 8-locular fruits. In addition to the greater variability in locule number, the ranges are larger than for low locule numbers. So, for example, it is common to find a range of 8-16 locules in fruits of *Namaquanthus vanheerdei*, or 14-20-locular fruits in *Argyroderma ringens* L.Bolus within the same specimen.

42. Fruit with low rims (0), with high rims (1)

43. Lower part of capsule bell-shaped (0), funnel-shaped (1), bowl-shaped (2), flattened (3)

The lower part of the capsule exhibits a variety of shapes. The shape is constant within a species and often also within a genus. This feature has been found to be useful at various taxonomic levels. At generic level it was used, for example, to separate species of *Brownanthus* from *Psilocaulon* (Ihlenfeldt & Bittrich 1985), or species of *Antimima* from *Ruschia* (Hartmann 1998). Even at a higher taxonomic level, Hartmann (1991) proposed deep capsules as a characteristic of the entire *Lampranthus* - group, although they are also found for example in *Ruschia*.

44. Base of fruit shallow (0), deep (1)

The base of the fruit was coded as shallow, when the diameter exceeded the depth.

45. Valve wings present (0), absent (1)

Although the mature fruits of *Ruschia maxima* lack valve wings, valve wings are formed during the early ontogeny of the flowers, but are not further developed during the later stages of development (Ihlenfeldt 1960). Therefore, valve wings were coded as "present" for this species.

46. Valve wings broad (0), narrow to very narrow, i.e. seam-like (1)

In both the Mesembryanthemoideae and the Ruschioideae a reduction from broad to narrow valve wings has occurred. Variation within a species is not known to occur. Very reduced valve wings are inconspicuous and consist of narrow rims, no broader than 0.5 mm but they remain clearly visible. Valve wings frequently disintegrate over time. As a consequence, old capsules have occasionally been found to lack valve wings (e.g. *Scopelogenia verruculata*, *Esterhuysenia alpina*), although very narrow seams are present in fresh material.

47. Fruits with expanding keels reaching from central columella to tip of valve (0), expanding keels not reaching the centre (1)

The presence of hygrochastic opening tissue is considered to be an apomorphy for the Aizoaceae (Bittrich & Hartmann 1988). The keels act as a lever mechanism to open and expose the contents of the

locules.

In the Mesembryanthemoideae, the keels are of septal origin and extend from the center to the outer edge of the locule (Plate 3 A, B). There are a few exceptions, where a small central portion of the lower part of the septum may form a translucent membrane (Hartmann 1988).

In the Ruschioideae, the tissue which swells up on being moistened is composed of an expanding keel and an expanding sheet (e.g. Ihlenfeldt 1960, Plate 3 C). However, in some cases, such as in *Dorotheanthus*, keels are absent and only an expanding sheet is present. In contrast to the purely septal expanding keels in the Mesembryanthemoideae, the keels in the Ruschioideae are mainly of valvar origin with only a small septal portion near the outer rim of the locule, never reaching the centre of the fruit (Plate 3 C).

48. Keels diverging from base and not touching (0), parallel at base and diverging from about middle towards the top (1), parallel and touching (2), parallel and not touching (3)

The valvar expanding keels can differ in their orientation and may be parallel (Plate 3 A) or divergent (Plate 3 C) (Schwantes 1952). In numerous cases, the keels are parallel in their basal region and diverge from about their middle. In the Ruschioideae, fruits with parallel keels have been referred to as the *Delosperma*-type, since they are typical for species of *Delosperma*, but this type is also found in numerous highly succulent genera, such as *Conophytum* and *Lithops*. In some cases the keels diverge right at the tips, such as in *Braunsia*.

49. Keels awn-like (0), blunt (1)

50. Keels short, valves only opening through  $90^\circ$  (0), keels long, valves opening through  $180^\circ$  (1)

In addition to the position of the expanding keels, their length may differ as well. In numerous species the keels may be much shortened and they may lack a radial extension towards the tip of the valves. This type of fruit is referred to as the *Ruschia*-type, since it is found in all species of *Ruschia* and in other members of the *Ruschia*-group such as *Astridia* and *Acrodon*. Since the keels are quite short, the capsule will only open so that the valves stand at  $90^\circ$  to the top of the capsule. More commonly found are keels which are extended radially and are much longer. In such a capsule, upon wetting, the valves open to  $180^\circ$  and frequently bend over even further.

51. Closing body absent (0), present (1)

The closing body is situated at the distal end of the locule and is considered to promote dispersal in both space (Lockyer 1932) and time (Volk 1960, Ihlenfeldt 1971c). Two types of closing bodies may be distinguished, namely endocarpal and placental (Hartmann & Liede 1986). Placental closing bodies are rare and species investigated for this study all have closing bodies that are of endocarpal origin. The presence of

closing bodies is restricted to capsules with complete or nearly complete covering membranes, although not all fruits with complete covering membranes have closing bodies. Variability in the presence or absence of a closing body within a species is rare and has so far been documented only for *Mitrophyllum* (Poppendieck 1976).

52. Closing body cylindrical and not apically enlarged (0), stalked and apically enlarged (1)

The shape of the closing body is characteristic for a species and usually for an entire genus (e.g. *Ruschia*). At a higher taxonomic level, the majority of species placed in the *Leipoldtia* - group has stalked closing bodies which are thickened at the top (Dehn 1992). This character state is considered an apomorphy for the *Leipoldtia* – group (Hartmann 1988, Dehn 1992).

53. Covering membranes completely covering the locule (0), only partly covering the locule (1), reduced to a narrow rim (2)

54. Covering membranes concave (0), convex (1)

55. Covering membranes with additional closing device (0), closing device inconspicuous (1) without any closing device (2)

56. Closing device cylindrical (0), ridge-like (1)

57. Placenta not apically free from endocarp (0), apically free from endocarp (1)

### Seeds

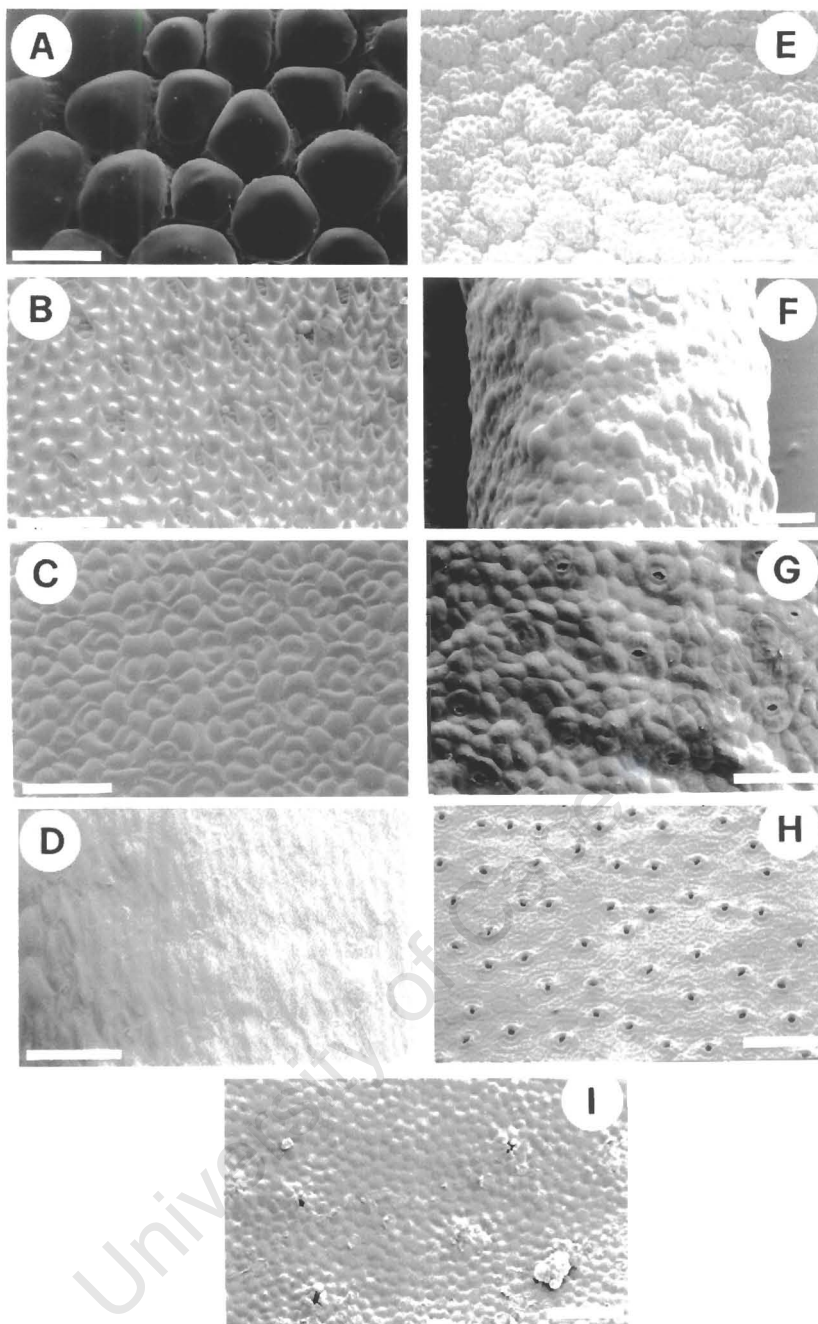
The anatomy and ontogeny of the seed coat has been studied for various species of the succulent Aizoaceae (Huber 1924, Schmid 1925, Woodcock 1930, Prakasch 1967, Ehler & Barthlott 1978). Studies of the seed coat across the Mesembryanthemoideae (Bittrich 1987) and (at least part of) the Ruschioideae (Haas 1976, Dehn 1992) were also conducted. As the sculpturing of the seed coat can be rather variable within species (e.g. *Erepsia anceps* (Haw.) Schwantes, Liede 1989) and within a genus (e.g. *Ruschia*, Dehn 1992) it has rarely been used in the delimitation of genera or species (e.g. Klak 2000a).

58. Outer wall of testa cell not raised out of the surface (0), raised but flattened (1), conspicuously raised (2)

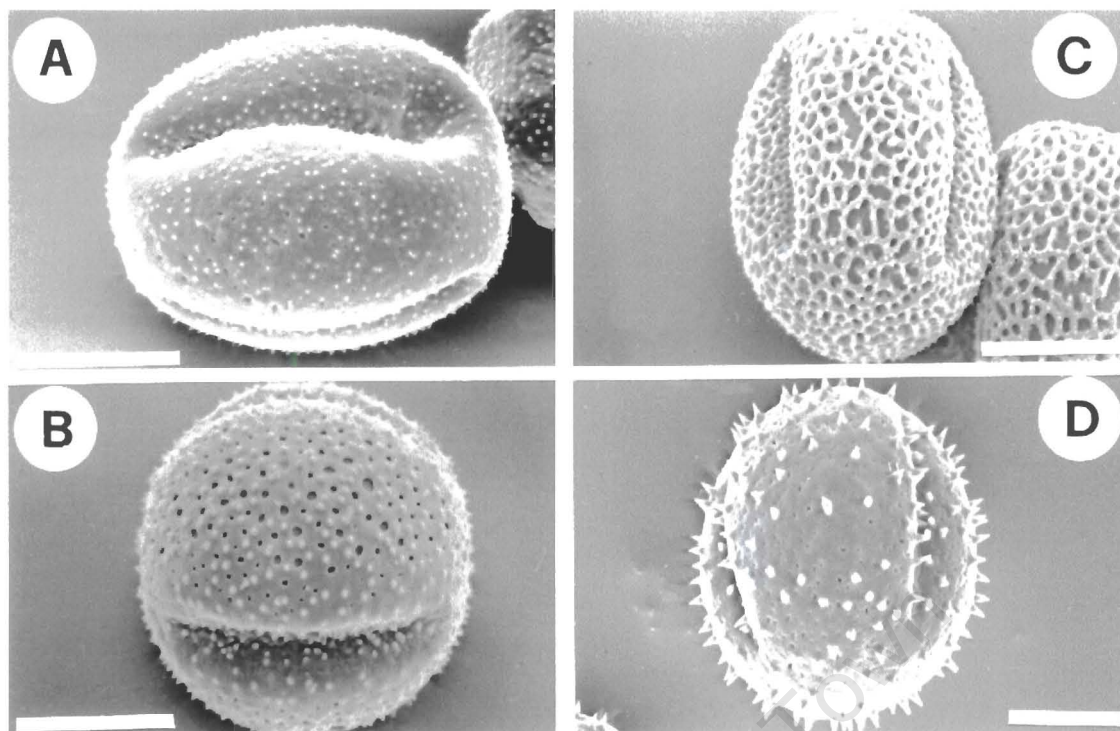
A (nearly) smooth seed surface is shown in Plate 4 A (0). Slightly raised testa cells are found in several species, e.g. *Lampranthus amoenus*, Plate 4 B. Plate 4 C-H illustrates conspicuously raised testa cells.

59. Outer wall of testa cell with central raised papilla (0), entire outer wall of testa cell convex (1), entire outer wall of testa cell raised into a short spike (2), entire outer wall of testa cell raised into a long spike (3)

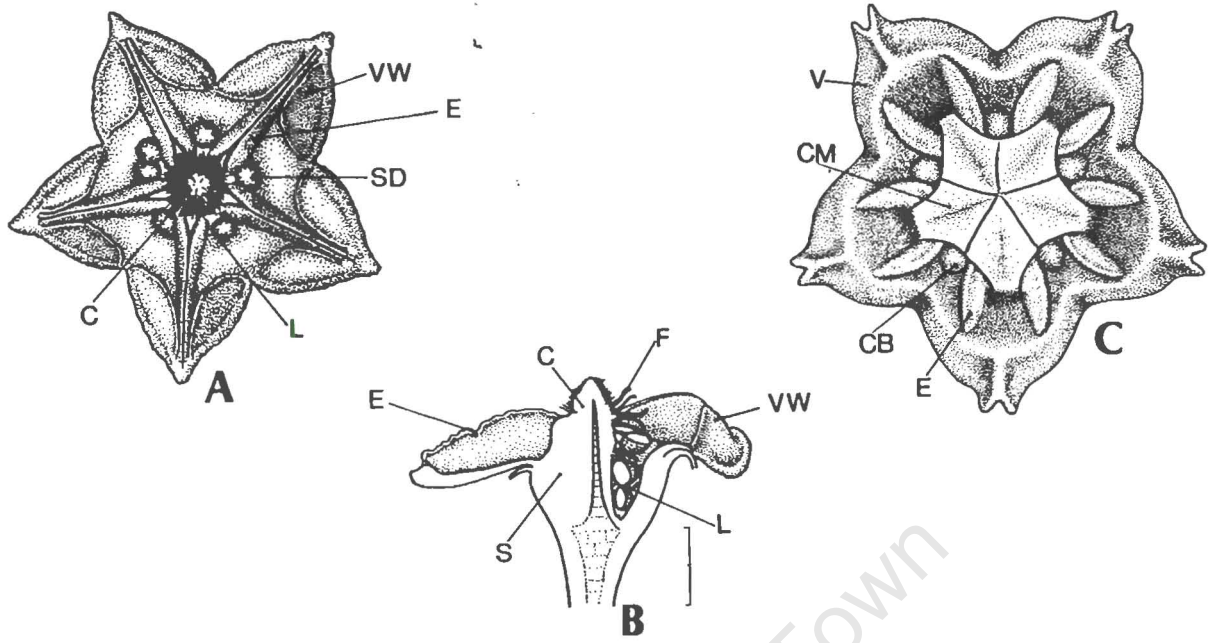
The shape of the raised testa cell can vary considerably: it may either be extended into a centrally raised papillae, Plate 4 C or the entire testa cell is convex, Plate 4 D. Rarely the testa cell is raised into a spike (Plate 4 E-H) and in such cases the seeds are commonly referred to as echinate. Echininate seeds are uncommon in the Ruschioideae and are found also in some species of *Astridia* (Glen 1986) and some species of *Glottiphyllum* (Hartmann & Gölling 1993). Whereas no further differences within echinate seeds have so far been recognized, this study shows that at least two different types can be distinguished: much shorter spikes are found in *Ruschia intrusa* (Plate 4 E) and *Braunsia vanrensburgii* (Plate 4 F) compared to *Namaquanthus* (Plate 4 G) and *Braunsia geminata* (Plate 4 H) where the spikes are much longer.



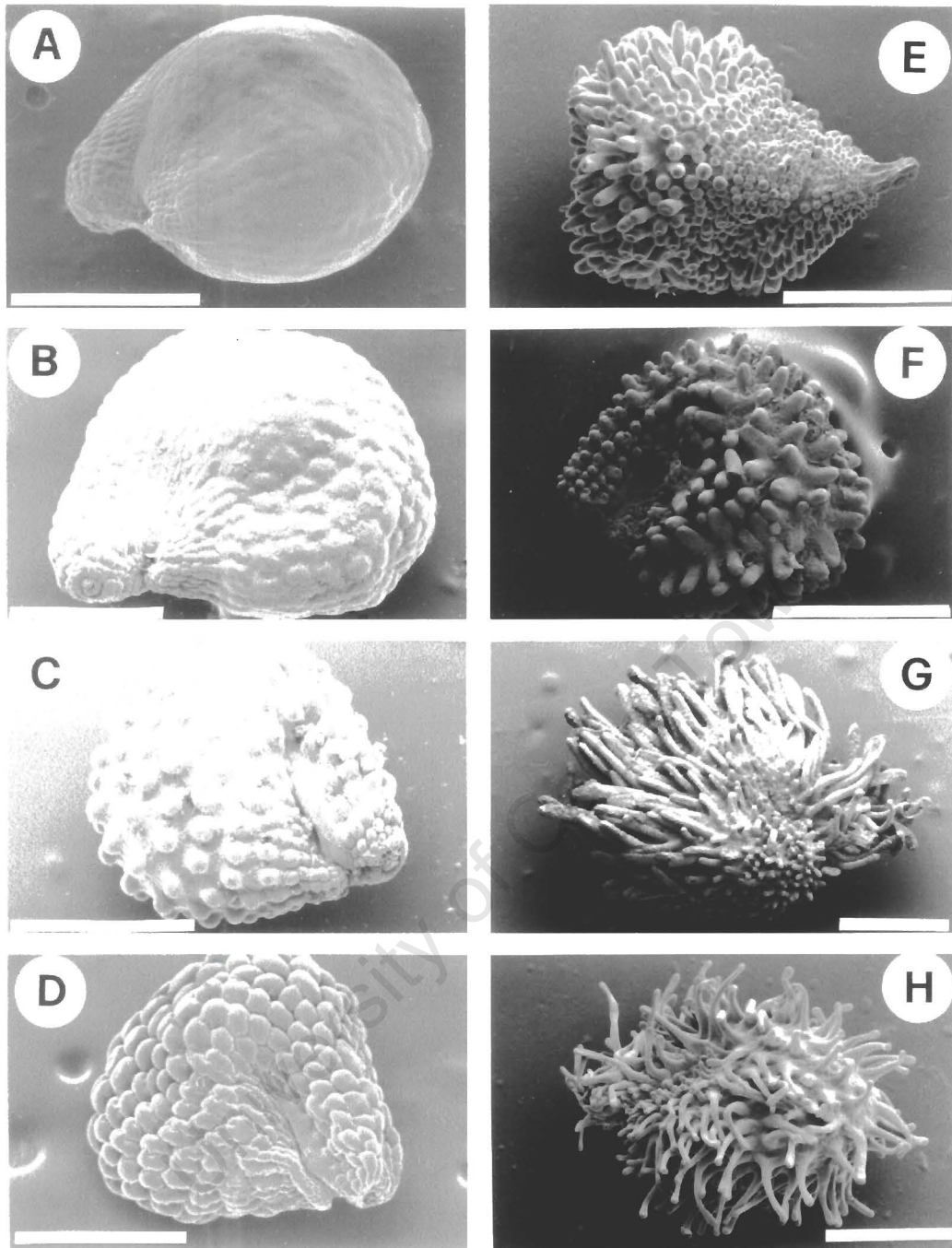
**Plate 1** SEM views of leaf surfaces.--- A, *Delosperma echinatum* (Klak 344), leaf covered with outsized water-storing cells (scale bar = 0.5 mm); B, *Antimima ventricosa* (Klak 457), epidermal cells much reduced compared to *Delosperma echinatum* but outer walls of each cell raised into acute papilla giving the surface a “velvety” texture (scale bar = 0.25 mm); C, *Oscularia deltooides* (Klak 215), outer walls of epidermal cells much flattened (scale bar = 0.25 mm); D, *Oscularia falciformis* (Klak 216), epidermal cells completely flattened and cell borders obscure (scale bar = 0.25 mm); E, *Lampranthus* sp. nov. (Klak 417a), epidermal cells raised in groups into hills with outer wall of each individual cell also raised (scale bar = 0.25 mm); F, *Lampranthus emarginatus* (Klak 708), occasional cells with raised outer wall conspicuously raised (scale bar = 0.25 mm); G, *Namaquanthus vanheerdei* (Klak 251), stomata slightly sunken (scale bar = 0.25 mm); H, *Carpobrotus quadrifidus* (Klak 705) stomata sunken (scale bar = 200  $\mu$ m); I, *Braunsia geminata* (Klak 205), guard cells overarch stomata (scale bar = 100  $\mu$ m).



**Plate 2** SEM views of pollen grains.--- A, *Astridia longifolia* (Bruyns 7302), punctate, microspinulate tectum (scale bar = 10  $\mu\text{m}$ ); B, *Lampranthus virens* (Klak 529), microspinulate, foveolate tectum (scale bar = 10  $\mu\text{m}$ ); C, *Lampranthus peacockiae* (Klak 391), microspinulate, reticulate tectum (scale bar = 10  $\mu\text{m}$ ); D, *Lampranthus spectabilis* (Klak 337), sparsely spinulate, punctate tectum (scale bar = 10  $\mu\text{m}$ ).



**Plate 3** A, top view of open capsule of *Psilocaulon* (Mesembryanthemoideae), there are no covering membranes and the keels extend to the centre of the fruit; B, longitudinal section through the same capsule; (scale bar = 2 mm); C, top view of open capsule of *Ruschia* (Ruschioideae), covering membranes form a "roof" over the locules, expanding keels do not reach to the centre of the fruit. --- CB = closing body; CM = covering membranes; C = columella; E = expanding keel; F = funicle; L = locule; S = septum; SD = seed; V = valve; VW = valve wing. Drawings by P.V. Bruyns.



**Plate 4** SEM views of seeds.--- A, *Amphibolia hutchinsonii* (Bruyns 7184), smooth surface; B, *Lampranthus godmaniae* (Klak 265), surface with flattened outer walls; C, *Lampranthus sociorum* (Klak 403), outer walls of testa cells each raised into a central papilla; D, *Erepsia dunensis* (Klak 453), entire outer wall of testa cell convex; E, *Ruschia intrusa* (Bruyns 7150) outer wall of each testa cell raised into a short spike; F, *Braunsia vanrensburgii* (Klak 218) outer wall of each testa cell raised into a short spike; G, *Namaquanthus vanheerdei* (Klak 251) outer wall of each testa cell raised into a long spike; H, *Braunsia geminata* (Klak 205) outer wall of each testa cell raised into a long spike; scale bars = 0.5 mm.

**Table 3.1** Morphological dataset used in the cladistic analysis. '?' indicates missing or inapplicable data; 'a' indicates polymorphism).

Taxa	Characters 1-30						
<i>Brownanthus pubescens</i>	00020	0210?	10100	?1?00	0011?	01000	
<i>Phyllobolus rabiei</i>	00020	0210?	10100	?1?00	11101	11000	
<i>Dorotheanthus bellidiformis</i>	01030	0210?	11100	00000	1101?	00000	
<i>Delosperma echinatum</i>	00120	0210?	10100	00000	00001	01000	
<i>Delosperma esterhuyseniae</i>	01030	0210?	10100	?1?00	0011?	00000	
<i>Drosanthemum schoenlandianum</i>	00120	0210?	10100	?1?00	0001?	00000	
<i>Oscularia deltoides</i>	00010	02111	10100	00002	00100	00000	
<i>Oscularia falciformis</i>	00010	00112	1??00	00001	1011?	00000	
<i>Oscularia guthrieae</i>	00020	00011	10101	20000	0011?	00010	
<i>Lithops julii</i>	02021	32111	10101	20000	0011?	00000	
<i>Titanopsis hugo-schlechteri</i>	01030	02111	10101	10000	0001?	00010	
<i>Hammeria meleagris</i>	00020	12111	10111	10000	00100	00000	
<i>Juttadintera albata</i>	00011	02111	10101	20100	1011?	00000	
<i>Astridia longifolia</i>	00021	02111	10101	20100	10000	00000	
<i>Ruschia maxima</i>	00011	00111	10101	20002	00100	00000	
<i>Ruschia intrusa</i>	00011	10112	1??01	00000	1111?	00000	
<i>Amphibolia hutchinsonii</i>	00010	02111	10101	00001	00100	00000	
<i>Eberlanzia dichotoma</i>	00020	02110	00001	20102	00100	00000	
<i>Antimima ventricosa</i>	00011	12110	10001	00000	10100	00000	
<i>Fenestraria rhopalophylla</i>	02021	32111	10101	00000	1101?	00000	
<i>Antegibbaeum fissoides</i>	01021	12112	1??01	00000	1011?	00000	
<i>Braunsia geminata</i>	00011	22111	10101	20100	10102	00010	
<i>Braunsia maximilianii</i>	10011	12110	10001	?1?00	00102	00010	
<i>Braunsia vanrensburgii</i>	10001	12112	1??01	20000	10102	00000	
<i>Carpobrotus muirii</i>	10001	02112	1??01	20000	1011?	00011	
<i>Carpobrotus quadrifidus</i>	10001	00112	1??01	20010	1011?	000?0	
<i>Enarganthe octonaria</i>	00021	02111	10101	00000	1011?	00000	
<i>Erepsia dunensis</i>	10000	02112	1??1?	10010	10101	11111	
<i>Erepsia inclaudens</i>	00110	00111	10100	00000	10101	10211	
<i>Erepsia patula</i>	00000	01110	11110	00001	00100	11211	
<i>Erepsia pillansii</i>	00001	00112	1??11	20010	10101	11211	
<i>Esterhuysenia drepanophylla</i>	00120	00011	10100	00000	00100	00010	
<i>Lampranthus aduncus</i>	00020	01112	1??00	00000	00100	00000	
<i>Lampranthus filicaulis</i>	10020	01112	1??00	00000	01100	00000	
<i>Lampranthus glaucus</i>	00010	02111	10110	00000	1001?	01010	
<i>Lampranthus spectabilis</i>	10010	02111	10100	00000	1111?	00000	
<i>Lampranthus stipulaceus</i>	00020	02111	10100	00001	1011?	00000	
<i>Lampranthus dregeanus</i>	00010	00111	10100	00001	0011?	00010	
<i>Lampranthus sociorum</i>	10020	02111	10100	00000	00100	00000	
<i>Lampranthus debilis</i>	10010	02111	10100	00000	00100	00000	
<i>Lampranthus peacockiae</i>	10020	02110	11100	00000	01100	00000	
<i>Lampranthus emarginatus</i>	00020	02110	11100	00001	0011?	00000	
<i>Lampranthus rupestris</i>	10020	02112	1??00	00000	0011?	00000	
<i>Lampranthus vallis-gratiae</i>	00020	00111	10100	00001	00100	00000	
<i>Lampranthus argenteus</i>	00020	02112	1??01	00001	00100	00000	
<i>Lampranthus henricii</i>	00020	02112	1??01	00000	00100	00000	
<i>Lampranthus bicolor</i>	00020	02110	11100	00001	1001?	01000	
<i>Lampranthus galpiniae</i>	00020	02111	10100	00000	1011?	00000	
<i>Lampranthus stenus</i>	a0020	02111	10100	00001	0011?	00000	
<i>Lampranthus amphibolius</i>	10020	12110	00101	?1?00	10100	00000	
<i>Lampranthus sp. nov.</i>	00020	12110	00101	?1?01	10100	00000	
<i>Lampranthus mucronatus</i>	00121	10012	1??01	00000	1011?	00010	
<i>Lampranthus virens</i>	00020	00111	10100	00000	00100	00000	
<i>Namaquanthus vanheerdei</i>	00021	02111	10101	10000	1011?	00000	
<i>Scopelogenia bruynsii</i>	00020	02111	10100	00002	00000	00000	
<i>Smicrostigma viride</i>	00010	21112	1??01	20000	00102	00010	
<i>Vlokia ater</i>	10011	02112	1??11	20000	00100	00010	
<i>Wooleya farinosa</i>	00021	02111	10101	20000	10100	00000	
<i>Zeuktophyllum suppositum</i>	00011	22113	1??01	20000	00102	00000	
<i>Circandra serrata</i>	00001	02112	1011?	??000	1101?	0?010	

Table 3. 1 cont.

Taxa	Characters 31-59						
<i>Brownanthus pubescens</i>	01?10	00011	10200	00211	0????	?00?	
<i>Phyllobolus rabiei</i>	01?10	00011	11111	?0211	0????	?021	
<i>Dorotheanthus bellidiformis</i>	10?02	00010	10300	1????	0?012	?00?	
<i>Delosperma echinatum</i>	10111	00011	10200	01211	0?212	?01?	
<i>Delosperma esterhuyseniae</i>	10111	10011	11200	01211	0?212	?01?	
<i>Drosanthemum schoenlandianum</i>	11111	10010	11010	01311	0?012	?00?	
<i>Oscularia deltoides</i>	11111	10010	10110	01011	0?011	1021	
<i>Oscularia falciformis</i>	10101	10010	10110	01011	0?011	1021	
<i>Oscularia guthrieae</i>	10111	10010	10110	11001	0?011	1021	
<i>Lithops julii</i>	11101	00010	11100	01211	0?212	?021	
<i>Titanopsis hugo-schlechteri</i>	10101	???10	10210	01211	0?012	?00?	
<i>Hammeria meleagris</i>	11?01	???10	112?0	01001	0?012	?00?	
<i>Juttadintera albata</i>	11101	10010	01110	01211	0?212	?020	
<i>Astridia longifolia</i>	11101	00010	11111	?1010	10010	1020	
<i>Ruschia maxima</i>	11101	10010	10110	?1111	10010	000?	
<i>Ruschia intrusa</i>	10?01	???10	10301	?1001	10012	?022	
<i>Amphibolia hutchinsonii</i>	11101	10010	10110	01111	10010	100?	
<i>Eberlanzia dichotoma</i>	11101	10010	10010	11111	10010	000?	
<i>Antimima ventricosa</i>	11?01	???10	11210	11010	11000	100?	
<i>Fenestraria rhopalophylla</i>	10001	11010	01300	01111	11000	1020	
<i>Antegibbaeum fissoides</i>	11101	10010	10210	01301	0?012	?022	
<i>Braunsia geminata</i>	11101	01110	10210	01211	0?112	?023	
<i>Braunsia maximilianii</i>	11101	???10	10210	01211	0?012	?020	
<i>Braunsia vanrensburgii</i>	11101	10010	10111	?1000	0?011	1022	
<i>Carpobrotus murii</i>	10001	???0?	0?21?	?????	?????	?0?	
<i>Carpobrotus quadrifidus</i>	10001	0110?	0?21?	?????	?????	?0?	
<i>Enarganthe octonaria</i>	10101	???10	00110	11101	10011	100?	
<i>Erepsia dunensis</i>	10101	???10	10110	01001	0?011	1021	
<i>Erepsia inclaudentis</i>	10111	01110	10111	?1001	0?011	1021	
<i>Erepsia patula</i>	10101	???10	10210	11001	0?011	1021	
<i>Erepsia pillansii</i>	10101	???10	00210	11101	0?011	1020	
<i>Esterhuysenia drepanophylla</i>	11101	10010	102?0	11111	0?011	1021	
<i>Lampranthus aduncus</i>	11101	10010	10110	01011	0?012	?121	
<i>Lampranthus filicaulis</i>	11101	10010	10110	01011	0?011	111?	
<i>Lampranthus glaucus</i>	10101	10110	10110	01011	0?010	111?	
<i>Lampranthus spectabilis</i>	10101	01110	10210	01011	0?011	1121	
<i>Lampranthus stipulaceus</i>	10101	11110	10110	01011	0?010	111?	
<i>Lampranthus dregeanus</i>	10101	10010	10210	01011	0?011	11??	
<i>Lampranthus sociorum</i>	11101	10010	10110	01011	0?010	1120	
<i>Lampranthus debilis</i>	11101	10010	10110	01011	0?011	1121	
<i>Lampranthus peacockiae</i>	11101	10010	10110	01011	0?010	1021	
<i>Lampranthus emarginatus</i>	10101	10010	10110	01011	0?011	1121	
<i>Lampranthus rupestris</i>	10101	???10	10110	01011	0?011	1121	
<i>Lampranthus vallis-gratiae</i>	11101	10010	10110	01011	0?011	1121	
<i>Lampranthus argenteus</i>	11101	10010	10010	01011	0?010	010?	
<i>Lampranthus henricii</i>	11101	10010	10010	01011	0?010	010?	
<i>Lampranthus bicolor</i>	10101	10010	10110	01011	0?011	1121	
<i>Lampranthus galpiniae</i>	10101	10010	10110	01011	0?011	1121	
<i>Lampranthus stenus</i>	10101	11110	10110	01011	0?011	111?	
<i>Lampranthus amphibolius</i>	11101	???10	10010	01111	0?010	011?	
<i>Lampranthus sp. nov.</i>	11101	???10	10010	01111	0?010	011?	
<i>Lampranthus mucronatus</i>	11101	10010	10110	01011	0?010	1021	
<i>Lampranthus virens</i>	11101	10010	10010	01311	0?012	?00?	
<i>Namaquanthus vanheerdei</i>	10101	???10	00210	01101	0?012	?023	
<i>Scopelogenia bruynsii</i>	11101	10011	10110	11011	0?010	1020	
<i>Smicrostigma viride</i>	10101	00010	00110	11101	0?012	?021	
<i>Vlokia ater</i>	11101	???10	10210	11101	0?011	?021	
<i>Wooleya farinosa</i>	10101	10010	00210	01211	0?012	?00?	
<i>Zeuktophyllum suppositum</i>	11101	10010	00211	-1101	0?112	?01?	
<i>Circandra serrata</i>	101??	10010	10110	01011	0?011	1?21	

### 3. 3. 3. Cladistic analysis

The data matrix (Table 3. 1) was analysed using PAUP\* version 4.0b4a (Swofford 2000) under the maximum parsimony optimality criterion. All characters were unordered and assigned equal weights (Fitch Parsimony, Fitch 1971). No autapomorphies were included in the analysis.

Search 1: The search procedure was the same as described in 2. 2. 4 in chapter 2. The trees were rooted using *Brownanthus pubescens* as the outgroup.

Search 2: The data set was analyzed using the successive approximation weighting scheme (Farris 1969, 1989; Goloboff 1993). Using the optimal trees from search 1, characters were reweighted by their retention indices, using base weight 10 and subjected to 500 consecutive heuristic searches under conditions employed in analysis 1. The process was repeated until the topology stabilized. The weight set of the final round of successive approximations weighting was used in a jackknife analysis in PAUP\*. The parameters were set as in search 1.

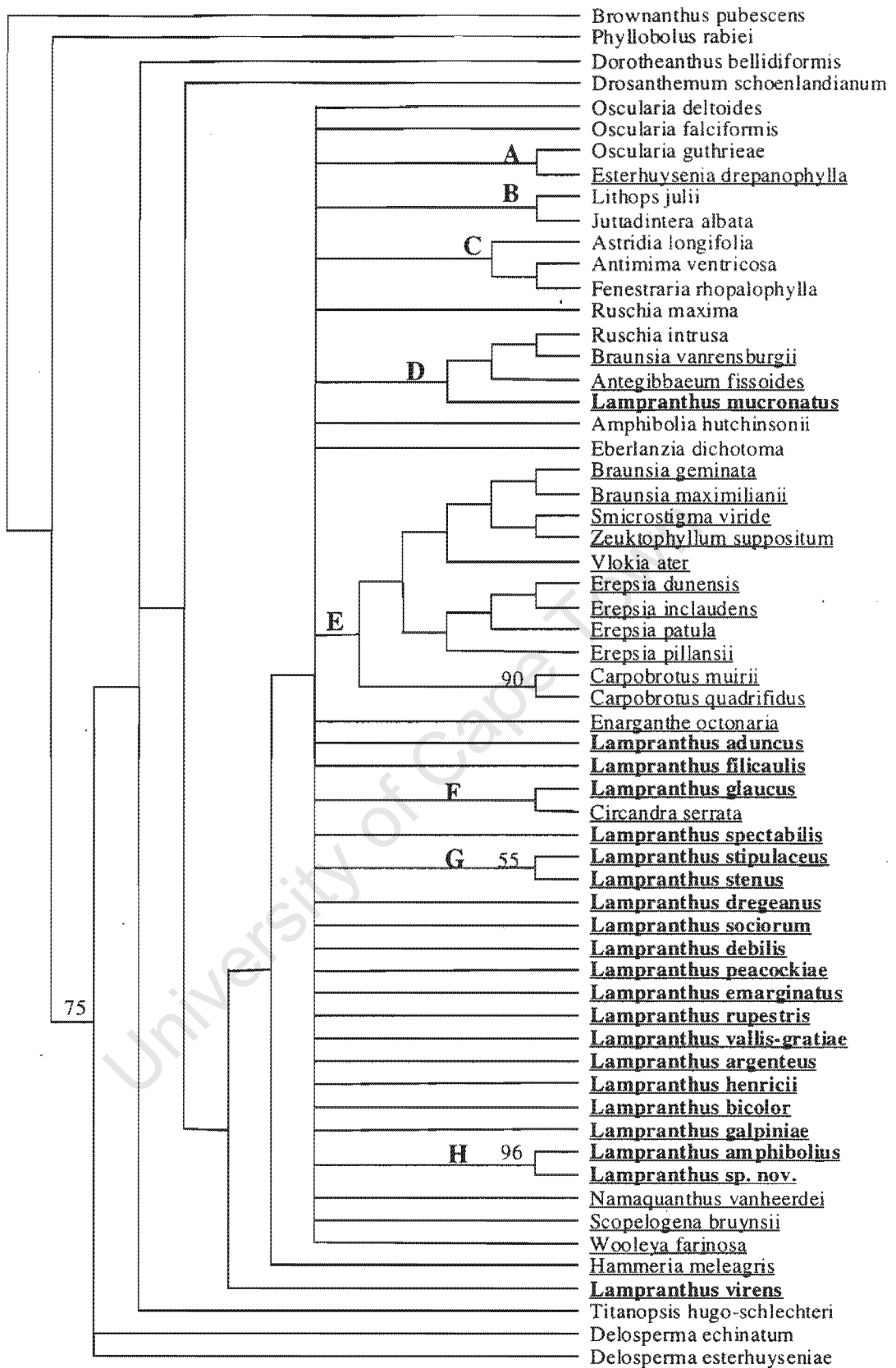
Search 3 & 4: For two of the taxa, *Carpobrotus muirii* and *C. quadrifidus*, numerous inapplicable data were recorded, which may cause loss of resolution (e.g. Maddison 1993). Therefore the data set was reanalyzed after exclusion of the two species of *Carpobrotus*. The search procedure outlined for search 1 and 2 was repeated for searches 3 & 4 respectively.

### 3. 4. Results

Search 1 Morphological data set. The strict consensus of 30,000 most parsimonious trees recovered during heuristic search 1 of 60 taxa and 59 morphological characters is presented in Fig. 3. 1 (length = 349, ci = 0.232, ri = 0.537, rc = 0.125). The strict consensus tree is poorly resolved, with the majority of species placed in a large polytomy. The Mesembryanthemoideae are sister to a fairly well supported clade (JK = 75) comprising the Ruschioideae. Within the Ruschioideae, *Delosperma* is sister to *Dorotheanthus* and *Titanopsis* which in turn are sister to *Drosanthemum*. Sister to *Drosanthemum* are two species placed in the *Lampranthus* – group, *Lampranthus virens* and *Hammeria meleagris*, which are sister to the remainder of the Ruschioideae and this falls into a large polytomy.

Within this large polytomy only eight major clades are resolved (A-H) and each of these clades mostly consist of only 2-4 species. The largest clade (E) consists of 11 species made up of *Carpobrotus*, *Erepsia*, two of the species of *Braunsia* and three mono- or bitypic genera from the *Lampranthus* - group. *Braunsia vanrensburgii* was retrieved in clade with *Ruschia intrusa* and *Antegibbaeum*.

Only four nodes are supported with JK > 50. A clade consisting of *Carpobrotus* and another comprising *Lampranthus amphibolius* and *L. sp. nov.* are highly supported (JK = 90 and JK = 96, respectively). In addition, *L. stenus* and *L. stipulaceus* form a poorly supported clade (JK = 55). Although the four species of *Erepsia* are placed in one clade, the jackknife support is below 50 %. Similarly, two of the species of *Braunsia*, *B. maximilianii* and *B. geminata*, are retrieved in a clade, but this is statistically very poorly supported.



**Fig. 3. 1** Strict consensus of 30,000 most parsimonious trees ( $l=349$ ,  $ci=0.232$ ,  $ri=0.537$ ,  $rc=0.125$ ) recovered during heuristic search 1 of the morphology data set for 60 taxa and 59 characters. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.

Search 2 Morphological data set weighted. Successive weighting did not achieve a reduction in the number of trees and the topology did not stabilise. The search was therefore terminated and no results were recorded.

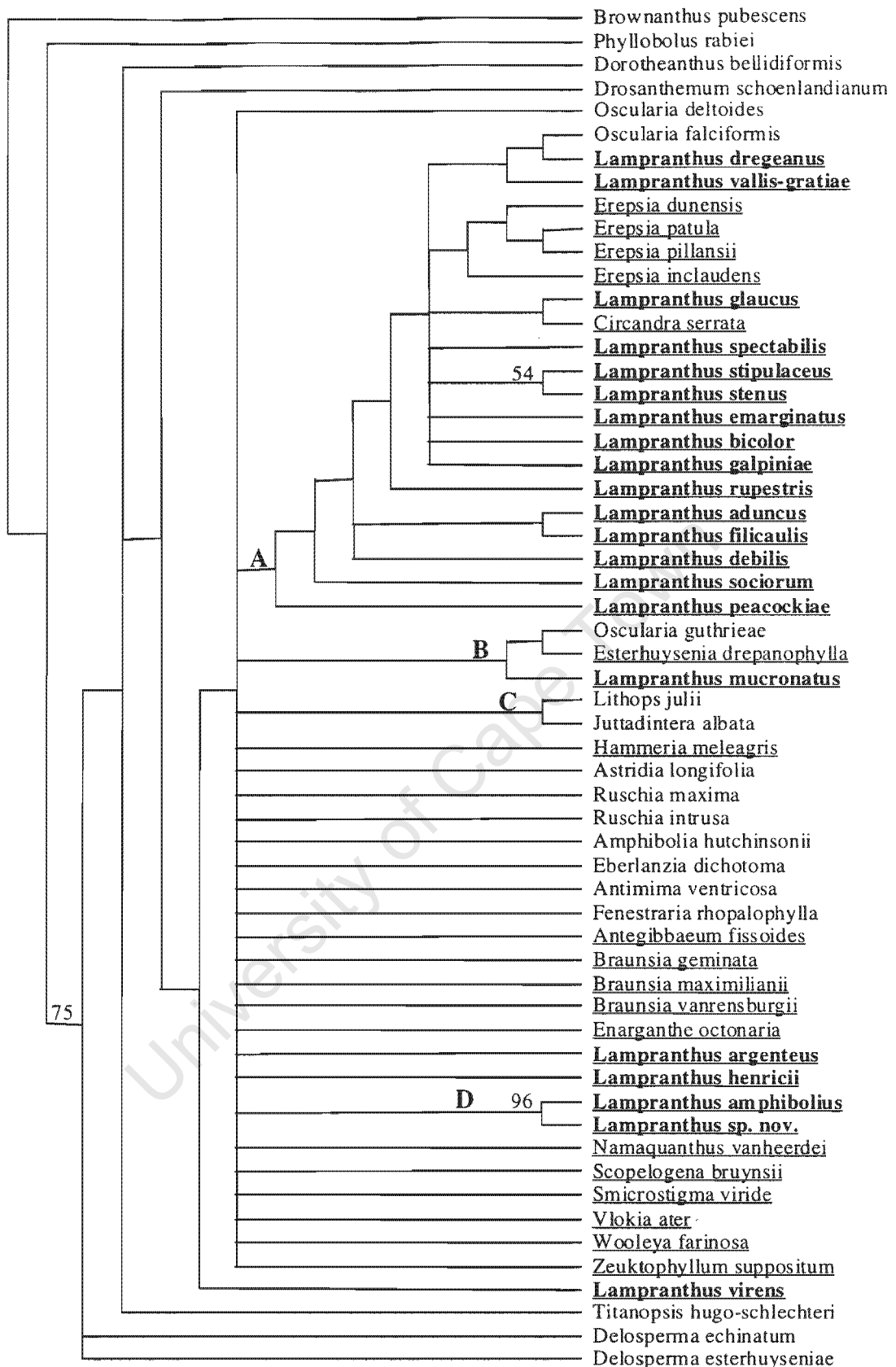
Search 3 Morphological data set with *Carpobrotus* excluded. The strict consensus of 3437 most parsimonious trees recovered during heuristic search 3 of 58 taxa and 57 informative morphological characters is presented in Fig. 3. 2 (length = 337, ci = 0.234, ri = 0.528, rc = 0.124). The topology retrieved is similar to the tree obtained when *Carpobrotus* was included (search 1). Differences are, however, found in the large polytomy, where instead of eight clades, only four clades were retrieved (A-D). In addition, within this polytomy two of the smaller clades (F, G) retrieved in search 1 (Fig. 3. 1) are part of a larger clade (A) which is made up of 15 (out of 21) species of *Lampranthus*, *Erepsia*, *Oscularia falciformis* and *Circandra*.

Exclusion of *Carpobrotus* does not yield better supported nodes, so that the same nodes as in search 1 are supported with JK > 50.

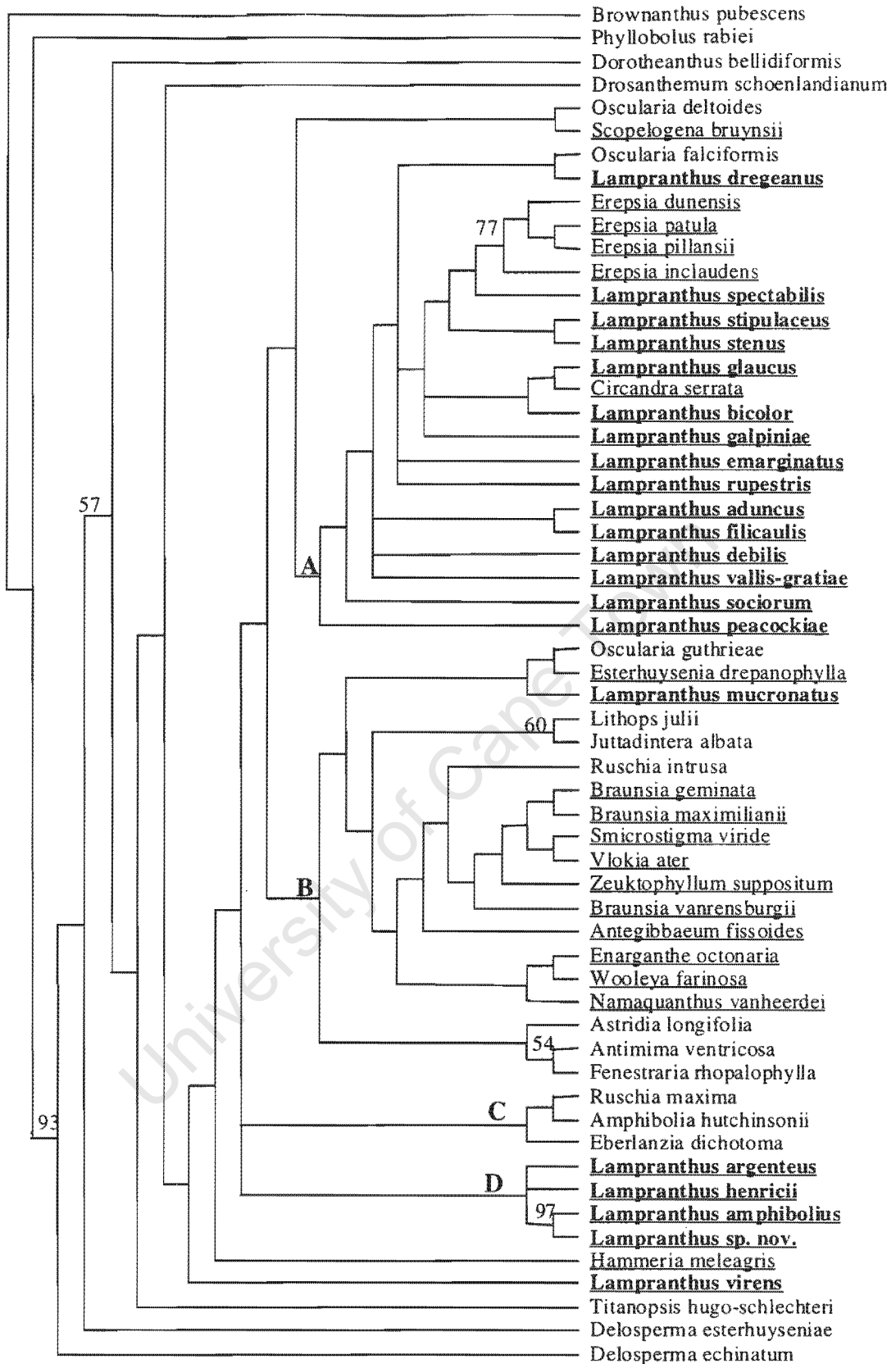
Search 4 Morphological data set weighted with *Carpobrotus* excluded. The strict consensus of 511 most parsimonious trees recovered during heuristic search 4 is presented in Fig. 3. 3 (ci = 0.268, ri = 0.622, rc = 0.167). Six rounds of successive weighting were required to stabilize the topology. The large polytomy retrieved in searches 1 and 3 is now well resolved. After successive weighting *Erepsia* is still nested within a “core” of *Lampranthus* with numerous species of *Lampranthus* placed outside this core. *L. aduncus* and *L. filicaulis* are part of the “core” in the morphological analysis, whereas they were placed outside this “core” in the combined molecular analysis. Sister to this core of *Lampranthus* is a clade comprising *Oscularia deltoides* and *Scopelogenia*.

Three of the monotypic genera placed in the *Lampranthus* – group, *Enarganthe*, *Wooleya* and *Namaquanthus* are resolved in a clade (JK < 50), which is sister to a clade similar to one retrieved by the molecular data (Fig. 2. 5). The clade comprises several mono- and bitypic genera from the *Lampranthus* – group (*Antegibbaeum*, *Vlokia*, *Smicrostigma*, *Zeuktophyllum*, *Braunsia vanrensburgii*) and *Ruschia intrusa*, but also includes *Braunsia maximiliani* and *Braunsia geminata* which were not part of this clade in the combined molecular analysis.

Although the tree is well resolved, there are only six nodes with JK > 50. In the weighted analysis the Ruschioideae are now highly supported (JK = 93) compared to much lower support (JK = 75) in the analysis with equal weights (search 1 & 3). The clade of four species of *Erepsia*, unsupported in search 3 (equal weights), is moderately well supported (JK = 77) after successive weighting.



**Fig. 3. 2** Strict consensus of 3437 most parsimonious trees ( $l=337$ ,  $ci=0.234$ ,  $ri=0.528$ ,  $rc=0.124$ ) recovered during heuristic search 3 (not weighted) of the morphology data set for 58 taxa (*Carpobrotus* excluded) and 57 characters. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.



**Fig. 3.3** Strict consensus of 511 most parsimonious trees ( $ci=0.268$ ,  $ri=0.622$ ,  $rc=0.167$ ) recovered during heuristic search 4 (weighted) of the morphology data set for 58 taxa (*Carpobrotus* excluded) and 57 characters. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.

### 3. 5. Congruence with molecular topologies and discussion

**The “core” of *Lampranthus*.** With few exceptions, the species retrieved in clade A are the same as those incorporated into the “core” of *Lampranthus* in the molecular analysis (Fig. 2. 5). In both the morphological and molecular trees (e.g. Figs. 2. 5 & 3. 2) *O. falciformis* is placed as sister to species of *Lampranthus*. Whereas *L. aduncus* and *L. filicaulis* are also part of clade A in the morphological analysis, they were not retrieved as part of the “core” by the molecular data. The morphological analysis differs further by the placement of *Erepsia* into the “core” of *Lampranthus*. The lack of a synapomorphic character, by means of which species of *Lampranthus* may be distinguished from *Erepsia*, may account for the nested position of *Erepsia* within the “core” of *Lampranthus*. As in the ITS analysis, the four species of *Erepsia* are grouped here in one clade (JK = 77). The position of *E. inclaudentis* as sister to *Oscularia guthrieae* and *Lampranthus debilis* in the 5S data has been discussed in detail in Chapter 2, but this position is not repeated in the morphological tree. *Oscularia guthrieae* appears in the morphological tree as sister to *Esterhuysenia*, but with a jackknife value below 50. Since morphological characters exist in *E. inclaudentis* which differ from most of the remaining species of *Erepsia* (such as the nectary structure, leaf morphology) the phylogenetic position of *E. inclaudentis* remains uncertain.

Further differences involve the position of *L. virens*, which is much removed from the “core” of *Lampranthus* and is placed as sister to *Drosanthemum* by the morphological analysis, whereas it was included with high support into this “core” in the molecular analyses (Fig. 2. 5). On account of morphological features, *Lampranthus virens* takes up an intermediate position, which may place it either in *Drosanthemum* (on account of the fruits) or in *Lampranthus* (on account of the leaf epidermal features and the nectarial structure). Depending on which characters were considered to indicate phylogenetic relatedness (Friedrich 1968), the taxonomic position of *L. virens* has in the past shifted between *Drosanthemum* and *Lampranthus*. As a consequence of the results obtained from the combined molecular and morphological analysis of the *Lampranthus* – group, the phylogenetic relationships of this species to *Drosanthemum* and *Lampranthus* are further discussed in chapter 4.

*Circandra* (not available for the molecular analysis) is resolved sister to *L. glaucus*. Liede (1989) had suggested a close relationship between the yellow-flowered species of *Lampranthus* (which includes *L. glaucus*) and *Circandra*. One of the striking features that they share is the large yellow flowers. Although in the combined molecular study *L. glaucus* is shown to be part of the “core” of *Lampranthus*, in the absence of molecular evidence it cannot be concluded that *Circandra* should be part of this “core” as well. In addition, the position of *Erepsia*, *L. aduncus* and *L. filicaulis* inside the “core” of *Lampranthus* in the morphological tree, which differs from the molecular tree (Fig. 2. 5), furthermore suggests that *Circandra* may not be part of the “core” of *Lampranthus*. Therefore, in the absence of any strong statistical or any unambiguous morphological support for the inclusion of *Circandra* into the “core” of *Lampranthus*, the phylogenetic relationships between *Circandra* and the “core” of *Lampranthus* remain uncertain.

As in the combined molecular analysis (Fig. 2. 5), several species of *Lampranthus* show closer

relationships to taxa placed outside the “core” of *Lampranthus*.

Both the combined molecular and the morphological analyses retrieved the clade comprising *Lampranthus amphibolius* and *L. sp. nov.* Although neither the ITS nor the 5S data retrieved this clade, there is high statistical support for this clade in the morphological analysis (JK = 97, Fig. 3. 3) and in the *trnL-F* analysis (JK = 86). The two species of *Lampranthus* are placed in a clade with *L. argenteus* and *L. henricii*, but the relationship remains poorly supported (JK < 50). In contrast in the combined molecular analysis, *L. henricii* and *L. argenteus* are reasonably well supported (JK = 80) as sister to *Antimima*.

In addition, the morphological and molecular analysis both placed *Lampranthus mucronatus* closer to *Esterhuysenia* than to the “core” of *Lampranthus*. In contrast to position in the molecular analysis, *Esterhuysenia* is still more closely related to *Oscularia guthrieae* than it is to *L. mucronatus*.

**The *Lampranthus*-group.** The morphological analysis retrieved *Oscularia deltoides* and *Scopelogenia* as sister to the “core” of *Lampranthus* and *Erepsia*. *Oscularia deltoides*, which is the type of the genus, was placed into the *Delosperma* – group by Hartmann (1991). However, it appears to be more closely related to taxa placed in the *Lampranthus* – group than to *Delosperma* and *Drosanthemum*, both of which are members of the *Delosperma* - group. As in the combined molecular analyses, *Antegibbaeum*, *Vlokia*, *Ruschia intrusa*, *Braunsia vanrensburgii*, *Smicrostigma* and *Zeuktophyllum* are retrieved in a clade in the morphological analysis. However, the two remaining species of *Braunsia*, which form the sister group to *Smicrostigma* and *Vlokia* in the morphological tree, are not closely related to these taxa in the molecular tree (Fig. 2. 5). In a similar manner to the 5S and combined molecular analyses (Fig. 2. 3-2. 5), *Braunsia geminata* and *B. maximilianii* are retrieved as closely related species by the morphology, with *B. vanrensburgii* more closely related to *Zeuktophyllum* and *Ruschia intrusa* than to the other two species of *Braunsia*.

Sister to this latter clade are the three monotypic genera from Namaqualand, i.e. *Wooleya*, *Enarganthe* and *Namaquanthus*. The latter clade did not appear in any of the molecular analyses. A further clade not retrieved by any of the molecular analyses is the one made up of the two species of *Carpobrotus* (Fig. 3. 1), and this clade is at the same time also very well supported (JK = 90).

Two main explanations may be offered to account for incongruence between the morphological and the molecular analyses.

#### (1) Incorrect homology assessment

Very few studies have investigated similar looking structures to determine whether they are in fact the “same”. Thus, for example, a different ontogenetic development was observed for the very similar looking cuticular folds of *Synaptophyllum* (Mesembryanthemoideae) and *Faucaria* (Ruschioideae) (Niesler 1996). Similarly, a comparative investigation of the fruits of *Pleiospilos* subgen. *Punctillaria* and *P.* subgen. *Pleiospilos* showed that the closing bodies in the two subgenera differed in their anatomy and that a

distinction between endocarpal and placental closing bodies should be made (Hartmann & Liede 1986). The different anatomy found in the two types of closing body furthermore suggests that the two structures may have different ontogenies. Ihlenfeldt (1960) showed that *Ruschia maxima* develops valve wings during the early stages of floral development, but that these do not further develop in the mature fruits. These examples highlight the dangers of assuming that similar structures are in fact homologous. Similar considerations apply to the pollen. Dupont (1977) pointed out that what are apparently similar grains sometimes ought to be classified in different groups. However, only studies of pollen-grain sections could resolve this problem and so far these have never been undertaken in the succulent Aizoaceae. Equally the question arises as to whether the development of the surface structure of the seed is always identical for a given type of sculpturing. In order to ascertain this it would be necessary to follow the development of the seeds. There are few ontogenetic or anatomical investigations of morphological structures such as the nectaries, closing bodies, expanding keels and valve wings, despite their importance in the classification of the succulent Aizoaceae. Therefore the chances of incorrect homology assessment are reasonably high since unless shown to be different, the initial assumption of homology assessment has to be based on similarity.

(2) A disproportionately large number of homoplasious characters in the data set

The levels of homoplasy observed in the equally weighted ( $ci = 0.234$ ) and successively weighted data set ( $ci = 0.268$ ) were high. When there is a high noise:signal ratio the phylogenetic signal could be considerably reduced and inferred relationships may be the result of parallelisms or a convergence in morphological characters (Patterson *et al.* 1993). The molecular bases of morphological character transformations among species are still too poorly understood to allow generalizations on the sources of morphological homoplasy (Doyle 1996). On the other hand parallelisms and convergences in morphological characters can often be detected by careful anatomical and developmental studies (e.g. Jürgens 1985) or by mapping morphological characters onto a tree generated with molecular data.

Despite the problem of incorrect homology assessment and high levels of homoplasy, the successively weighted morphological analysis uncovered several clades similar to those retrieved by the combined molecular analysis. Both the molecular and morphological analysis showed that several of the genera placed in the *Lampranthus* – group are not monophyletic and are in many cases more closely related to taxa placed outside the *Lampranthus* – group. The results of the morphological analysis suggest that phylogenetic relationships can be retrieved using morphological characters. However, it has also become evident that far more detailed ontogenetic and anatomical morphological studies are needed in order to discover homologous structures.

## CHAPTER 4

### TOTAL EVIDENCE AND CHARACTER EVOLUTION

#### 4. 1. Introduction

The use of molecular data in phylogenetic studies has become commonplace, so that most systematic journals today contain phylogenetic studies based on molecular characters alone or in combination with morphological studies. The use of molecular data has set off a debate about the reliability of molecular versus morphological data sets (reviewed by Hillis 1987). It is generally desirable to discuss the outcome of a molecular study with reference of supporting morphological data (Doyle 1992, Bremer 1996, see chapter 2. 1. 1). Furthermore, the existence of diagnostic morphological characters is desirable when making nomenclatural changes based on a molecular phylogeny (Doyle 1992).

Separate hypotheses of phylogenetic relationships among the members of the *Lampranthus* - group have been obtained from analyses of four independent data sets: the first based on morphology, the second on chloroplast DNA sequences and two sets based on nuclear DNA sequences. Individual data sets yielded either very poorly resolved or poorly supported phylogenies (chapters 2 & 3). Combining the three molecular data sets considerably improved both resolution and support. Although disagreements between the morphological and combined molecular phylogenetic trees exist, these are confined to nodes with very low jackknife support ( $JK < 50$ ). It is therefore argued that there is no real conflict between the data sets and that the data can be combined.

A total evidence approach, including morphological data, is therefore undertaken here. This should provide the best phylogenetic hypothesis for the *Lampranthus* – group given the currently available data, and will provide a framework in which the evolution of characters can be evaluated. In particular, the evolution of characters previously thought to be important in the taxonomy of the group is evaluated, especially fruit characters. This chapter also discusses the implications of the total evidence analysis for taxonomy and classification.

#### 4. 2. Materials and Methods

##### 4. 2. 1. Cladistic analysis

The coding of morphological characters is discussed in chapter 3 and the collection of DNA sequence data is detailed in chapter 2. The DNA sequences incorporated in the combined data were extracted from the data used in chapter 2. The same 59 taxa extracted from the molecular data were extracted from the morphological data matrix, with identical coding as in chapter 3. *Circandra* was excluded from the analyses, since no molecular sequence data are available.

The cladistic analyses were conducted using PAUP\* version 4.0b4a (PPE) (Swofford 2000). All

analyses were conducted under the maximum parsimony optimality criterion. Characters that were parsimony uninformative were excluded prior to analyses. All characters were unordered.

Combined search 1. The combined data were analysed as for the combined molecular data sets (chapter 2).

Combined search 2. The combined data was analysed using a successive weighting strategy and jackknifing protocol as described in Chapter 2.

Combined search 3 & 4. The data was re-analysed following the same protocol as in the combined searches 1 & 2, but included only those taxa for which data for all three gene regions were available. The same 52 taxa used in Chapter 2 were incorporated in the search.

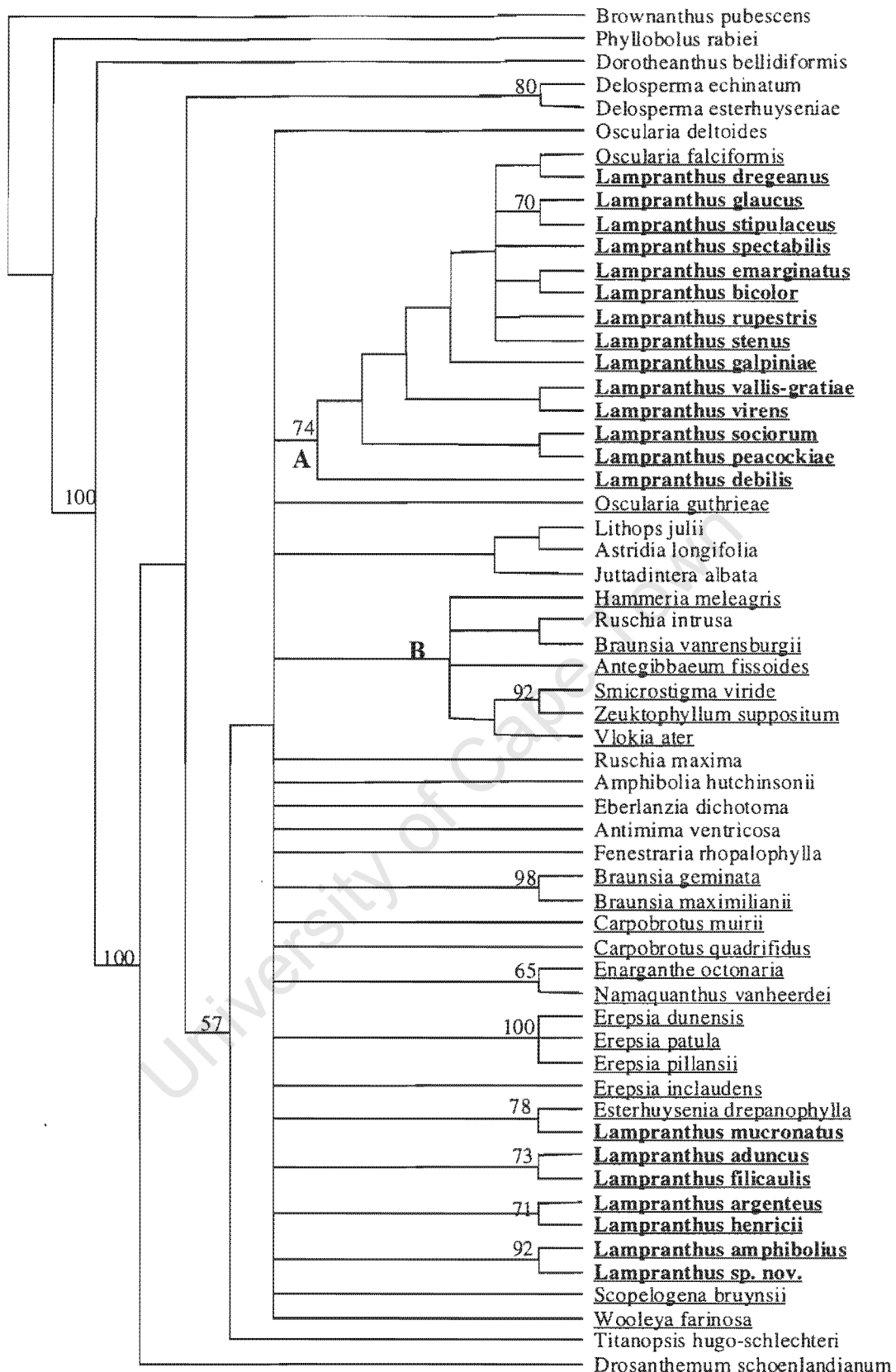
Character optimization. Morphological characters were optimised onto trees from the total analysis using MacClade version 3.06 (Maddison & Maddison 1996). Equivocal character states were optimized to show all most parsimonious states at each node.

### 4.3. Results

Statistics for each parsimony analysis are given in Table 4. 1.

Combined search 1. The strict consensus tree of 3894 equally parsimonious trees including all 59 taxa is presented in Fig. 4. 1 (length = 996, ci = 0.376, ri = 0.532, rc = 0.200). The Ruschioideae form a highly supported clade (JK = 100). Within the Ruschioideae *Dorotheanthus* is sister to a highly supported clade (JK = 100) comprising *Drosanthemum* and *Delosperma* and this clade is in turn sister to the remainder of the Ruschioideae which form a large polytomy (JK = 57). *Titanopsis* is sister to this large polytomy within which two larger clades (A & B) and several small clades each consisting of 2-3 taxa are resolved, leaving 12 species unresolved. The "core" of clade A, which incorporates 13 species of *Lampranthus* (out of 21 sampled) and *Oscularia falciformis*, is reasonably well supported (JK = 74). Although *L. debilis* is sister to the "core" of *Lampranthus* there is no statistical support for its inclusion into this "core" group. In contrast to the combined molecular analysis two pairs of species are newly resolved (although neither is well-supported) by the total analysis. These are *Enarganthe* and *Namaquanthus* (JK = 65) and *L. aduncus* and *L. filicaulis* (JK = 73). It is, however, noteworthy that both clades were retrieved by the morphology (Fig. 3. 7). Several of the species pairs retrieved by the combined molecular analysis are also found in the total evidence analysis and are highly supported (e.g. *Braunsia geminata* and *B. maximilianii*, JK = 98; *Smicrostigma* and *Zeuktophyllum*, JK = 92; *Esterhuysenia* and *Lampranthus mucronatus*, JK = 78; *L. amphibolius* and *L. sp. nov.*, JK = 92).

As in the combined molecular analysis, the total analysis retrieves a clade of mono- and bitypic genera (clade B) but it remains very poorly supported (JK < 50). Also as in the combined molecular analyses, three species of *Erepsia* comprise a highly supported clade that excludes *E. inlaudens*. The latter species remains unresolved within the large polytomy.



**Fig. 4. 1** Strict consensus of 3894 most parsimonious trees ( $l=996$ ,  $ci=0.376$ ,  $ri=0.532$ ,  $rc=0.200$ ) recovered during heuristic search 1 of the total evidence analysis (not weighted) for 59 taxa. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.

Combined search 2. Eight MPTs were obtained after successive weighting. The strict consensus tree is presented in Fig. 4. 2 ( $ci = 0.508$ ,  $ri = 0.529$ ,  $rc = 0.268$ ). The topology stabilized after four rounds of successive weighting. The tree is far better resolved after successive weighting compared to the analysis with equal weights. In addition to clades A and B retrieved in the unweighted analysis, several other larger clades are now resolved (clades C-G). *Drosanthemum* and *Delosperma* are sister to a much better supported clade ( $JK = 75$ , compared to  $JK = 57$  in the previous search) comprising the majority of the Ruschioideae. Within this clade, *Enarganthe* and *Namaquanthus*, instead of *Titanopsis*, are sister to the remaining species of Ruschioideae. In contrast to the combined molecular analysis (Fig. 2. 5) which placed *E. inlaudens* well outside the well-supported clade comprising the three remaining species of *Erepsia*, it is placed here as sister to this clade, but with no apparent support for its inclusion ( $JK < 50$ ).

In agreement with the morphological and combined molecular analyses several species of *Lampranthus* do not form part of the “core” of *Lampranthus*: clade G incorporates the well-supported clade comprising *Lampranthus amphibolius* and *L. sp. nov.* ( $JK = 99$ ), which are sister to *Eberlanzia*. This sister relationship to *Eberlanzia* was not shown by the combined molecular analysis (Fig. 2. 5), which had placed *Esterhuysenia* and *L. mucronatus* as closest relatives to *Lampranthus amphibolius* and *L. sp. nov.* Furthermore, the clade comprising *Lampranthus henricii* and *L. argenteus* is placed closer to *Antimima*, rather than to the “core” of *Lampranthus*.

In contrast to the morphological analysis where *Lampranthus aduncus* and *L. filicaulis* are part of the “core” of *Lampranthus* they are placed now as sister to a clade comprising *Oscularia deltoides*, *Ruschia maxima* and *Scopelogenia*. Again, there is poor support for these relationships.

It is noteworthy that *Ruschia maxima* was placed as sister to *Eberlanzia* in the morphological analysis, but it is placed here as sister to *Scopelogenia*. This clade in turn is sister to *Oscularia deltoides*. A close relationship between *O. deltoides* and *R. maxima* was also shown in the combined molecular analysis, but in that case *Scopelogenia* was resolved in a clade with *Fenestraria*.

*Carpobrotus*, a clade previously only retrieved and well-supported in the morphological tree, is highly supported in the weighted total evidence analysis ( $JK = 95$ ). Relationships of *Carpobrotus* to the other taxa placed in Clade E may be spurious, since they are unsupported ( $JK < 50$ ).

Whereas the combined molecular analysis placed the “core” of *Lampranthus*, including *O. guthrieae* and *E. inlaudens* as sister to clade B (incorporating *Hammeria*, *Vlokia*, *Smicrostigma*, *Zeuktophyllum*, *Antegibbaeum* and *B. vanrensburgii*), the total analysis places it as sister to clade C (comprising *Esterhuysenia*, species of *Lampranthus*, *Scopelogenia* and *Oscularia*).

Although relationships among the major clades (A-G) are resolved, they are unsupported ( $JK < 50$ ).

Combined search 3. The strict consensus tree of the 4480 most parsimonious trees found after analysis of the reduced data set (including 52 taxa represented in all data sets) is presented in Fig. 4. 3 (length = 805,  $ci = 0.350$ ,  $ri = 0.507$ ,  $rc = 0.177$ ). Based on the results of combined searches 1 & 2, *Drosanthemum* was used to root the tree. The topology is almost identical with the unweighted combined

search 1 (including 59 taxa), but differs in that *Carpobrotus* is resolved as monophyletic (JK = 90).

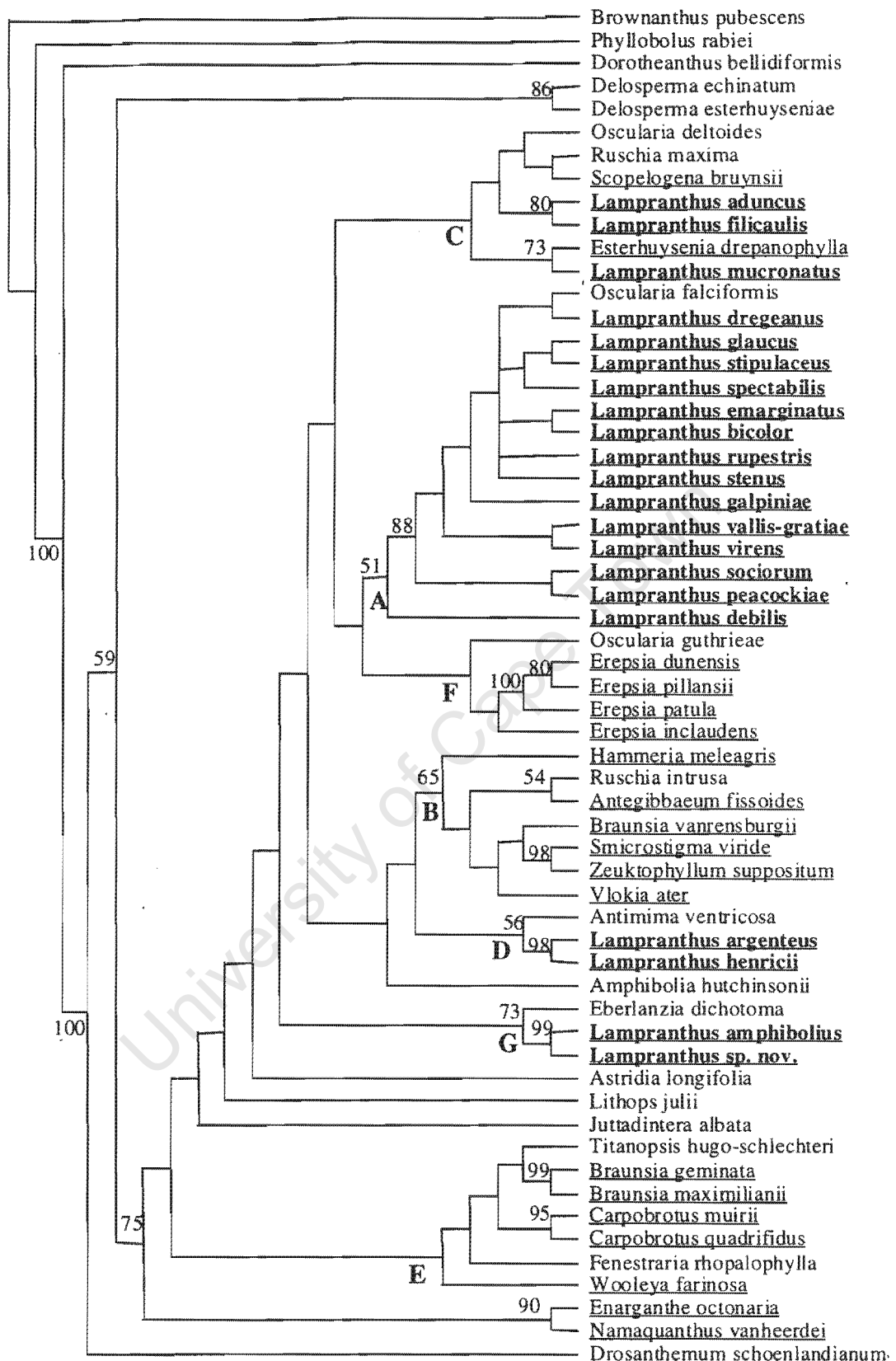
Furthermore, after the exclusion of *Ruschia intrusa* from the data set, *B. vanrensburgii* is part of a polytomy in which *Vlokia* and the clade comprising *Smicrostigma* and *Zeuktophyllum* are also present.

In the reduced data set several nodes are better supported. The statistical support for the “core” of *Lampranthus* is considerably increased (JK = 85) compared to what was achieved in the combined search 1. Also the Ruschioideae, excluding *Delosperma* and *Drosanthemum*, are better supported with JK = 69, compared to 57 in the unreduced and unweighed analysis (Fig. 4. 1).

Combined search 4. The single most parsimonious tree found in search 4 is presented in Fig. 4. 4 (ci = 0.390, ri = 0.696, rc = 0.272). Three rounds of successive weighting were necessary to stabilize the topology. The tree is highly resolved compared to the unweighted tree, but without statistical support (i.e. JK < 50) for the newly resolved nodes. The major clades (A-G) retrieved in this tree are largely congruent with the weighted topology from combined search 2 (including 59 taxa). Different relationships between the two topologies were retrieved for the taxa placed in clade C and for clades A-D & G. *Drosanthemum* and *Delosperma* are now sister to a well-supported clade (JK = 83) comprising the remainder of the Ruschioideae. Within this clade many nodes are still statistically very poorly unsupported (JK < 50). The highest support values (JK > 75) are for the “core” of *Lampranthus* and for various pairs of taxa. In addition, some of the nodes statistically unsupported in search 2 and 3 here obtained low jackknife values between 53 and 71. *Lampranthus debilis* is now placed (with low support of JK = 55) as sister to the “core” of *Lampranthus*. In contrast to the combined molecular analysis, *Antimima* is placed here with very low support (JK = 58, compared to JK = 80) as sister to *Lampranthus argenteus* and *L. henricii*. There is slightly more support for clade B (JK = 80) in the total analysis, compared to JK = 78 when only the molecular data were analysed. Under successive weighting, clade B is well-resolved, placing *B. vanrensburgii* as sister to *Vlokia*.

**Table 4. 1** Statistics for maximum parsimony analysis of the total evidence data set.

Analysis	Number of taxa	Number of characters	Informative characters	Tree length	Tree number	CI	RI	RC
Combined 1	59	1821	282	996	3894	0.376	0.532	0.200
Combined 2 (weighted)	59	1821	282		8	0.508	0.529	0.268
Combined 3	52	1821	204	805	4480	0.350	0.507	0.177
Combined 4 (weighted)	52	1821	204		1	0.390	0.696	0.272



**Fig. 4. 2** Strict consensus of 8 most parsimonious trees ( $ci=0.508$ ,  $ri=0.529$ ,  $rc=0.268$ ) recovered during heuristic search 2 of the total evidence analysis (weighted) for 59 taxa. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.

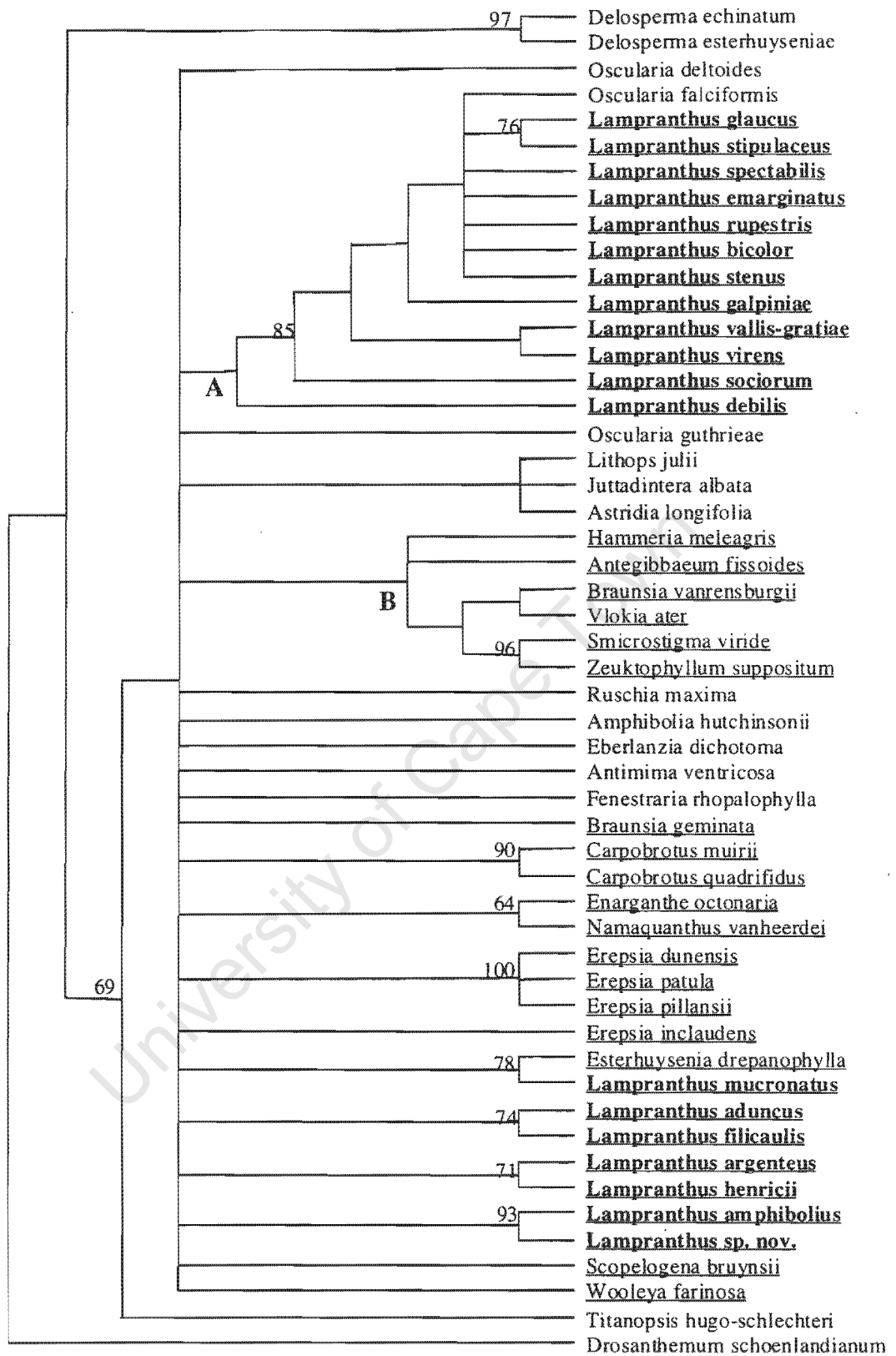
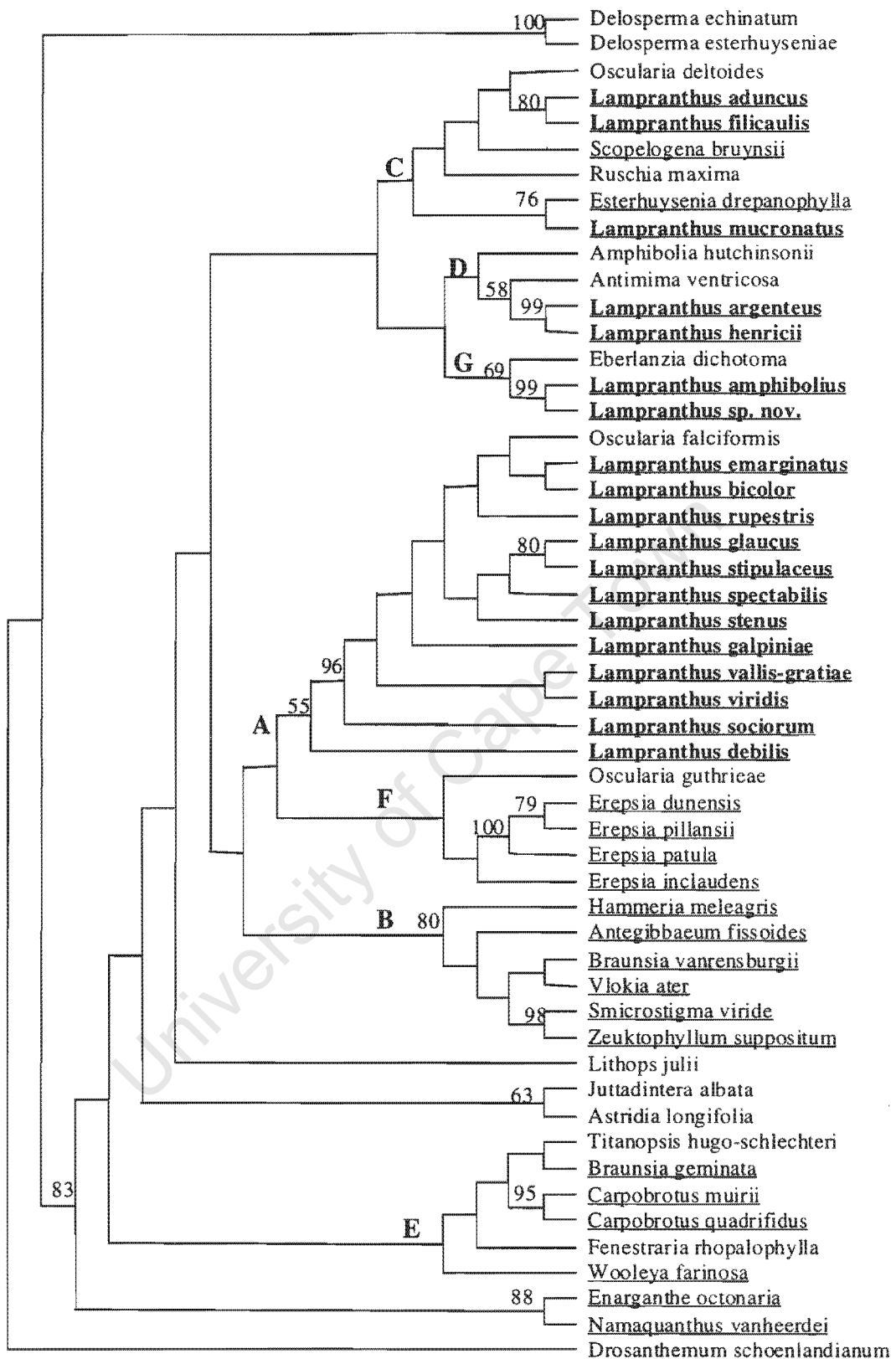


Fig. 4. 3 Strict consensus of 4480 most parsimonious trees ( $l=805$ ,  $ci=0.350$ ,  $ri=0.507$ ,  $rc=0.177$ ) recovered during heuristic search 3 of the total evidence analysis (not weighted) for 52 taxa. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.



**Fig. 4. 4** Single most parsimonious tree ( $ci=0.390$ ,  $ri=0.696$ ,  $rc=0.272$ ) recovered during heuristic search 4 of the total evidence analysis (weighted) for 52 taxa. Numbers indicate jackknife values. Members of the *Lampranthus* - group are underlined; species of *Lampranthus* in bold and underlined.

## 4. 4. Discussion

### 4. 4. 1. Phylogenetic relationships

The topologies of the two unweighted total analyses are neither well-resolved nor well-supported. After successive weighting the topologies are fully resolved, but the new arrangements are only marginally better supported. In the tree (Fig. 4. 4) resulting from weighted analysis of the reduced data matrix 18 nodes (out of 50) are supported, compared to 12 (out of 23) nodes in the analysis with equal weights (Fig. 4. 3). In addition, in the combined (reduced) molecular tree (Fig. 2. 5) only 38 nodes are resolved, compared to 50 nodes when molecular and morphological data were combined (Fig. 4. 4). Although the morphological data alone did not retrieve a hypothesis of phylogenetic relationships for the genera placed in the *Lampranthus* - group, adding the morphological data to the molecular data set increased the explanatory power. The successively weighted analysis of the reduced data set, including 52 taxa, produced a single tree (Fig. 4. 4) where several nodes yielded a higher jackknife support than in the weighted analyses including all 59 taxa (Fig. 4. 2). Therefore, the tree given in Fig. 4. 4 is regarded as the best phylogenetic hypothesis for *Lampranthus* and the genera placed in the *Lampranthus* - group.

The lack of statistical support for many of the nodes in the morphological and combined molecular topologies has been very apparent. This is also the case in the total analysis, where only some of the deep branches and several of the branches near the tree tips are highly supported (JK > 80), but with no support for any of the middle branches. Overall, the phylogenetic relationships discussed for the combined molecular topology are largely corroborated by the total analyses. In the following I indicate the main differences between the analysis of the combined molecular data (Fig. 2. 5) and the total analysis (Fig. 4. 4). The well-supported phylogenetic groups that appear in the total analyses are also discussed.

#### (ii) Delimiting *Lampranthus*

As in the combined molecular analysis a "core" of species of *Lampranthus* was retrieved and is highly supported (JK = 96) in the total analysis (Fig. 4. 4). The "core" of *Lampranthus* differs from the closely related groups of taxa (clades C & F, which incorporate *Scopelogenia*, *Erepsia*, *Oscularia* and *Esterhuysenia*) by the presence of mesomorphic leaves (i.e. crystal layer absent or incomplete), 1-5-flowered inflorescences, the presence of a holonectary (Fig. 4. 8) and no hypanthium (Fig. 4. 9), fruits with funnel-shaped bases and (usually) raised tops and broad valve wings. Whereas the combined molecular analysis placed *L. debilis* as sister to *Oscularia guthrieae* (but JK = 64), the total analyses placed it as sister to the "core" of *Lampranthus* (Figs. 4. 1 – 4. 4). Although support (JK = 55) for this clade is very low, it suggests that the morphological characters place this species closer to *Lampranthus* than to *Oscularia guthrieae*. *Lampranthus debilis* differs from *O. guthrieae* by the presence of a holonectary (meronectary in *O. guthrieae*, Fig. 4. 8) as well as in having less xeromorphic leaves (e.g. distinct crystal layer in *O. guthrieae*, Fig. 4. 7). In addition, the upper parts of the fruits are flattened and the keels have awn-like extensions in *O. guthrieae* and *Erepsia*, whereas the tops are raised and the keels are blunt in *L. debilis*. *Lampranthus debilis*

shares all of these characters with *Lampranthus*. Although the same combination of characters is not found in the closely related genera, they are all homoplasious characters.

Within the well-resolved “core” of *Lampranthus* (Fig. 4. 4) there is only one supported node. In addition, nodes which were supported in the combined molecular analysis are no longer supported in this total analysis. For example, *L. vallis – gratiae* and *L. galpiniae*, are resolved in a fairly well-supported clade (JK = 80) in the combined molecular analysis, whereas the former species is shown to be more closely related to *L. virens* in the total analysis (JK < 50). Furthermore, Sect. *Scabridi* and Sect. *Tenuifolii*, which were each represented by three species in the total analysis (Fig. 4. 4), do not resolve as clades in either the total or the combined molecular analyses. However, since the sampling is very incomplete, the validity of the sections and the relationships between them cannot be deduced from the present study. Relationships within *Lampranthus* remain ambiguous.

Whereas *Erepsia inlaudens* and a clade consisting of *O. guthrieae* and *L. debilis* were placed by the combined molecular analysis as the closest relatives to the “core” of *Lampranthus*, in the total evidence analysis, *E. inlaudens* is sister to the remaining species of *Erepsia*. However, the absence of strong statistical support suggests that the relationship of *E. inlaudens* to the three other species of *Erepsia* may be based on homoplasious characters. As discussed earlier, a future investigation needs to focus on those species of *Erepsia* that, like *E. inlaudens*, have meronectaries. In addition, these species need to be studied in conjunction with those very poorly known species of *Lampranthus* with a hypanthium (*L. simulans*, *L. schlechteri*) and meronectaries (*L. schlechteri*). These two species are discussed further in chapter 6.

Species placed in two other sections of *Lampranthus*, Sect. *Adunci* and Sect. *Suffrutices*, are shown to be more closely related to some of the outgroups than to the “core” of *Lampranthus*. Sect. *Suffrutices* was resolved even in the combined molecular analysis and was statistically supported there as well. Another section of *Lampranthus*, Sect. *Adunci*, is also distinguished by the total analysis (Fig. 4. 4) and is also more closely related to the outgroups than to the “core” of *Lampranthus*. This clade, comprising *L. aduncus* and *L. filicaulis*, was previously resolved in the ITS, the morphological and total evidence analyses, but was fairly well-supported (JK = 80) only by the total evidence analysis (Fig. 4. 4). Members of this clade share several morphological characters with *Esterhuysenia* and *L. mucronatus*: these are green-reddish, recurved, apiculate, almost cylindrical leaves and solitary flowers. However, in the reduced total evidence analysis (Fig. 4. 4) *L. filicaulis* and *L. aduncus* are placed as sister to *Oscularia deltoides*, which is characterized by grey, trigonous leaves and an elaborate, many-flowered inflorescence. Thus in terms of their morphological characters the two species of *Lampranthus* are rather dissimilar from *Oscularia*. In the absence of strong statistical or morphological support the relationships of *L. filicaulis* and *L. aduncus* to the other taxa remains ambiguous.

*Lampranthus amphibolius* and *L. sp. nov.*, two species that were never placed in a section within *Lampranthus*, lie in a highly supported clade, but with no close relationships to any other species of

*Lampranthus*. *Lampranthus amphiboli* and *L. sp. nov.* were placed without statistical support as sister to *Esterhuysenia* and *L. mucronatus* in the combined molecular analysis. In the total evidence analysis they are modestly well supported as sister to *Eberlanzia* (JK = 69). *Eberlanzia* shares with the two species of *Lampranthus* a similar leaf epidermal sculpturing, i.e. the epidermal cells are raised in groups into hills. Although leaf epidermal sculpturing can vary within a genus (e.g. smooth surface in *Braunsia geminata* compared to velvety in *B. maximilianii*), the case of *Lampranthus gydouwensis* and *L. sp. nov.* shows that a very different epidermal surface may be indicative of different phylogenetic histories. In the past differences in the leaf epidermal surfaces have been used usually only in conjunction with divergent fruit characters in the delimitation of genera (e.g. for *Psilocaulon* and *Brownanthus*, Ihlenfeldt & Bittrich 1985; *Amphibolia* and *Eberlanzia*, Hartmann 1996, but also see discussion for *Glottiphyllum* below). In genera, such as *Ruschia* or *Antimima*, where the fruit morphology is very similar amongst species, the very different epidermal surfaces found among the species has largely been ignored. The results of this study show that leaf epidermal differences can reveal phylogenetic relationships between unrelated taxa that otherwise share very similar fruit morphology.

The two species of *Lampranthus* differ from *Eberlanzia* by the presence of closing bodies, which have so far been considered to constitute an important difference in generic delimitation. The fairly low support and the absence of a closing body in the fruits in the two species of *Lampranthus* suggest that they are not part of *Eberlanzia*.

The clade incorporating *Lampranthus argenteus* and *L. henricii* is placed as sister to *Antimima ventricosa* in both the combined molecular and the total evidence analyses (Fig. 4. 2 & 4. 4). However, the relationship with *Antimima* lost support in the total evidence analysis, with JK = 58 (Fig. 4. 4), as compared to the combined molecular analysis where it had JK = 80 (Fig. 2. 5). The two species of *Lampranthus* share no close morphological similarities with *Antimima*, that could support their sister relationship. Also problematic in this respect is that *Antimima* (comprising about 100 species) has not been revised to species level, so that generic delimitation rests entirely on the fruit morphology (Dehn 1988, Hartmann 1998). However, the high support for this clade gained in the combined molecular analysis suggests that *Antimima* is not as closely related to members of the *Leipoldtia*-group (e.g. *Fenestraria*) as previously thought. This relationship therefore needs further investigation. In terms of their habit, leaf, floral and also inflorescence morphology, the two species of *Lampranthus* are most similar to *Ruschia* Sect. *Spinosa*, from which they differ mainly in their fruit morphology. In the present study only two species (possibly not representative) of the very large genus *Ruschia* (which contains ca. 200 species) were included. A future study would therefore need to include further species of *Ruschia* to test possible relationships.

#### (ii) Delimiting the *Lampranthus* - group

The total evidence analyses (Figs. 4. 1 – 4. 4) retrieved three well supported nodes among the deep branches. These are interpreted to represent three distinct lineages within the sampled taxa:

The Mesembryanthemoideae and Ruschioideae are morphologically very distinct, in terms of their placentation, fruit and nectary structure and their floral ontogeny (Ihlenfeldt 1960). On account of the many differences between the two subfamilies, the morphology resolved the Ruschioideae as a well-supported clade (JK = 93) and this is further strengthened (JK = 100) in the total evidence analyses (Fig. 4. 1, 4. 2). Within the Ruschioideae, *Dorotheanthus* is the only representative of a lineage sister to the remainder of the Ruschioideae. The morphology did not retrieve *Dorotheanthus* as a separate lineage, but this is achieved in the total analysis (Fig. 4. 1, 4. 2). This corroborates the fact that the *Cleretum* – group, to which *Dorotheanthus* belongs, is morphologically distinct from the remainder of the Ruschioideae. Members of this group are annuals, with flat leaves covered with prominent bladder cells. In addition, the *Cleretum*-group has much reduced expanding keels, which are well developed in (almost) all other species of Ruschioideae (exceptions are the *Apatesia* - group and *Ruschianthemum*). In addition, it was recently shown that (almost all) taxa placed outside the *Cleretum* - and *Apatesia* – groups possess wide band tracheids, whereas they are absent in all other species of Aizoaceae (Landrum 2001). This further corroborates the position of *Cleretum* – group (and probably also the *Apatesia* – group which was not sampled in this study) as sister to the remainder of the Ruschioideae.

The second well-supported lineage (Fig. 4. 1- 4. 4) includes *Delosperma* and *Drosanthemum*, which are both members of the *Delosperma* – group. This clade does not include *Oscularia* (in particular the type of the genus, *O. deltoides*, does not belong to it) previously placed here by Hartmann (1991, Table 1. 1). As pointed out earlier, most species of *Oscularia* were included in *Lampranthus* Section *Lunati* and *Oscularia* formed part of the *Lampranthinae* in Schwantes' (1971) classification. The main differences between the *Lampranthus* - and the *Delosperma* - group are the more or less prominent bladder cells on the leaves and flowers with five separate nectaries in the latter group (Hartmann 1991). In the *Lampranthus* - group the nectaries are arranged in a ring (except in a few species of *Erepsia*) and the epidermal bladder cells are much flattened. Morphologically *Oscularia* occupies an intermediate position between the *Delosperma*- and the *Lampranthus*.- group: although most species have their nectaries in five separate groups, their leaf epidermal bladder idioblasts are much flattened. This study suggests that the presence of “much reduced bladder cell idioblasts” found in all species sister to *Delosperma* and *Drosanthemum* represents a synapomorphy for this clade into which *Oscularia* is placed (Fig. 4. 5 and see discussion below).

The remainder of the Ruschioideae forms the third lineage (JK = 75, Fig. 4. 2; JK = 83, Fig. 4. 4), which incorporates all other sampled groups. Within this third lineage none of the groups delimited by Hartmann (1991, Table 1. 1) are retrieved. *Enarganthe* and *Namaquanthus*, both members of the *Lampranthus* – group, form a well-supported clade (JK > 87) in the total evidence analyses (Figs. 4. 2, 4. 4) sister to the remainder of the third lineage. It is noteworthy that only the morphology retrieved the two taxa in a clade (but unsupported), whereas in the combined molecular analysis *Enarganthe* was sister to a reasonably well-supported clade (JK = 77), which consisted of *Namaquanthus* as sister to *Delosperma* (Fig. 2. 4). These results show that a clade not retrieved or unsupported by individual analyses, may gain fairly

high support in a total analysis (cf. Doyle 1992). The single species of *Wooleya*, which at one time was placed in *Namaquanthus* (L. Bolus 1958) and was sister to *Enarganthe* and *Namaquanthus* in the morphological analysis (Fig. 3. 7), is in the total evidence analysis placed in a clade with *Carpobrotus*, *Fenestraria*, *Titanopsis* and *Braunsia geminata*. However, the intergeneric relationships between these genera differ in the total evidence analysis from those suggested by the combined molecular analysis (Fig. 2. 5). Since the intergeneric relationships are supported in both the combined molecular and the total evidence analyses with JK < 60, they are considered unreliable.

In the total evidence analyses the same terminal branches are highly supported as is the case in the combined molecular analysis (e.g. *Erepsia* excluding *E. inlaudens*, *Braunsia* excluding *B. vanrensburgii*, *Delosperma*). However, in addition, the total evidence analyses (Figs. 4. 2 – 4. 4) retrieved *Carpobrotus* as a highly supported clade (JK > 89). *Carpobrotus* had been retrieved as a well-supported clade only by the morphology (Fig. 3. 5), whereas it remained unsupported and unresolved in a clade with *Lampranthus aduncus* in the combined molecular analysis (Fig. 2. 5). Hartmann (1991) allied *Carpobrotus* to the *Lampranthus* – group, whereas developmental studies by Haas (1976) suggested that *Carpobrotus* is most closely related to the *Leipoldtia* – group (which excluded *Antimima* at that stage). In Fig. 4. 4 *Fenestraria* (*Leipoldtia* – group) is placed sister to a clade comprising *Carpobrotus*, *Titanopsis* and *Braunsia geminata*. However, no other members of the *Leipoldtia*- group, apart from *Antimima* (see discussion below) were sampled in this study. *Carpobrotus* shares with the *Leipoldtia* – group a broad columella and multi-locular fruits (Haas 1976). There are no obvious morphological characters that may support the clade into which *Carpobrotus*, *Titanopsis* and *Braunsia geminata* are placed. In the absence of strong statistical support in the total evidence analysis, the relationship of *Carpobrotus* to members of the Ruschioideae remains unclear.

The clade comprising numerous mono- and bitypic genera (*Hammeria*, *Antegibbaeum*, *Vlokia*, *Smicrostigma* and *Zeuktophyllum*) and *Braunsia vanrensburgii* is best-supported and resolved in the total evidence analysis (Fig. 4. 4). So far there are no known morphological synapomorphies which could be used to characterize this clade. The fruit morphology is fairly diverse within this clade: it includes taxa with 5-, 6-, and 5-7-locular fruits, as well as 7-10-locular fruits found in *Zeuktophyllum* and *Smicrostigma*. *Ruschia intrusa* appears to belong to this clade as well, since both the combined molecular and some of the total analyses (Fig. 4. 1, 4. 2) retrieved this species in a clade with the above taxa. The presence of 6- or 7-locular fruits or a range of 5-7-locular fruits within a species is a rare feature in the Ruschioideae, but is also found in some species of *Ruschia* (e.g. *Ruschia knysnana*, *R. leucosperma* L.Bolus, *R. middlemostii* L.Bolus, *R. namusmontana* Friedrich). In addition, *Hammeria*, *Vlokia*, *Braunsia vanrensburgii* and *Ruschia intrusa* share widely diverging expanding keels, whereas they are parallel in *Antegibbaeum*. In addition, the seeds of *B. vanrensburgii*, *Antegibbaeum* and *Ruschia intrusa* are shortly echinate, whereas the testa cells are much flattened in the other taxa placed in this clade. It is noteworthy that seeds of *Braunsia vanrensburgii* and *Braunsia geminata* were both referred to previously as being “echinate”. This study shows that the

seeds are shortly-echinate in *B. vanrensburgii* (Fig. 3. 4 E, F) whereas they are long-echinate in *B. geminata* (Fig. 3. 4 G, H). This seed character, in addition to the differing fruit morphology (keels diverging in *B. vanrensburgii* compared to parallel keels in all remaining species of *Braunsia*, Klak 2000a), supports the conclusion based on molecular and total evidence analyses that *B. vanrensburgii* is not closely related to the rest of *Braunsia*.

Common to all the taxa in this clade are keels with awn-like extensions and flexible covering membranes with no additional closing devices at their lower surfaces. However, awn-like keels (e.g. *Erepsia*, *Namaquanthus*) and flexible covering membranes (e.g. *Namaquanthus*, *Drosanthemum*) are homoplasious characters. Even the combination of these two fruit characters is found in some species of the *Bergeranthus* – group, such as in *Cerochlamys*. *Cerochlamys* on the other hand differs in possessing meronectaries, as opposed to a holonectary in all other taxa placed in this clade (clade B). Further sampling in the Ruschioideae may show that further taxa may belong here. As in the case of *Lampranthus*, only a combination of homoplasious characters can so far be listed to delimit this clade.

The different relationships found among clades A-D in the unreduced total analysis (including 59 taxa, Fig. 4. 2) compared to the reduced total analysis (including 52 taxa, Fig. 4. 4) and the absence of well-supported nodes indicates that the relationships among the larger clades (A-D & G) remain ambiguous. Nevertheless, the *Lampranthus* – group in its present circumscription cannot be upheld, since part of it shows closer relationships to taxa placed outside the *Lampranthus* – group and taxa from outside the group are nested within it. It therefore does not constitute a natural group. However a recircumscription of the *Lampranthus* – group is problematic. This is partly since the nodes of the middle branches of the topology are not well supported but also since this study indicates that taxa from outside the group also need to be brought into consideration. This very much broadens the necessary scope of further investigations. In view of the contrasting positions of and the low support for the larger clades in the different analyses, adding more taxa or data may very well rearrange the larger clades.

#### 4. 4. 2. Character optimization and evolution

Character evolution in the *Lampranthus* – group was studied by optimization of certain characters which were chosen either because they were frequently used in the classification of the succulent Aizoaceae or because they were used in the circumscription of the *Lampranthus*- group (Hartmann 1991).

##### A. Evolution of leaf morphology and of a xeromorphic type of epidermis

An epidermis with thin-walled, water-storing bladder cells is considered to be a derived character for the entire Aizoaceae (Bittrich 1986, Bittrich & Hartmann 1988). According to Ihlenfeldt & Hartmann (1982) and Jürgens (1985) the epidermis has been modified in two different ways. In the first, the bladder idioblasts are more and more reduced and finally lost (Ihlenfeldt & Hartmann 1982, Ihlenfeldt & Jürgens

1982) while in the second the outer cells of the idioblasts are progressively thickened (Ihlenfeldt 1985, Jürgens 1986). Only the first evolutionary modification has been considered in this study.

Outsized bladder idioblasts are present in all of the most basal groups, including *Dorotheanthus* and the Mesembryanthemoideae and the bladder idioblasts are much reduced in all of the taxa that are sister to *Drosanthemum* and *Delosperma* (Fig. 4. 5). This study corroborates earlier hypotheses that the large bladder cells are the plesiomorphic state within the succulent Aizoaceae (Bittrich & Struck 1989). Since the entire clade sister to *Drosanthemum* and *Delosperma* is characterized by much reduced bladder cell idioblasts, this character may be a synapomorphy for this clade. However, this would only be the case if also taxa with reduced bladder cell idioblasts that were not sampled in this study were restricted to this clade. In addition, numerous taxa with outsized bladder idioblasts were not sampled in this study (e.g. members of the *Apatesia*-, *Mitrophyllum*- and the *Delosperma* – groups). Therefore adding a *Delosperma* – group member with outsized bladder cells could very well make the reconstruction ambiguous and call into question the results of this study that large bladder cells are the plesiomorphic state. Therefore further sampling is necessary to substantiate these hypotheses.

The epidermal surface may show different modifications of the epidermal cell. Within a genus the surface structures can differ considerably. A good example of this is provided by the highly supported clade comprising two species of *Braunsia* (Fig. 4. 2) where *B. maximilianii* has a papillate surface, while it is completely smooth in *B. geminata*. On the other hand, the unusually sculptured leaves found in *Eberlanzia*, *Lampranthus sp. nov.* and *L. amphibolius* represent a synapomorphy for this clade and distinguishes it from the “core” of *Lampranthus*, with which it shares a very similar fruit morphology (Fig. 4. 6). However, a similar sculpturing of the epidermis is also found in species of *Octopoma*. Species of this polyphyletic genus (Hartmann 1998a) were not included in this study, but should be studied in more detail to test whether they may also form part of this clade.

A subepidermal crystal layer has been listed as an important indicator of a xeromorphic type of epidermis (e.g. Ihlenfeldt & Jürgens 1982). Figure 4. 7 traces the evolution of this character. *Dorotheanthus*, *Drosanthemum* and *Delosperma* all of which lack a subepidermal crystal layer, form a basal grade to a large clade spanning the node leading to *Enarganthe* and the rest of the “ingroup”, most of which have a distinct and often thick crystal layer. The gain of the crystal layer happened in the common ancestor of this large clade. Subsequently there have been at least three independent losses. Since the optimization at the base of the clade which incorporates *O. guthrieae* and *Erepsia* is equivocal, there is as yet no hard evidence for an independent gain of a distinct crystal layer.

### B. Evolution of floral characters

Within the succulent Aizoaceae, the nectaries are always located shortly below the insertion of the stamens. In the succulent Aizoaceae shell-shaped (koilomorphic) or crested (lophomorphic) nectaries have been distinguished (e. g. Rappa 1912). In the other three non-succulent subfamilies of the Aizoaceae the

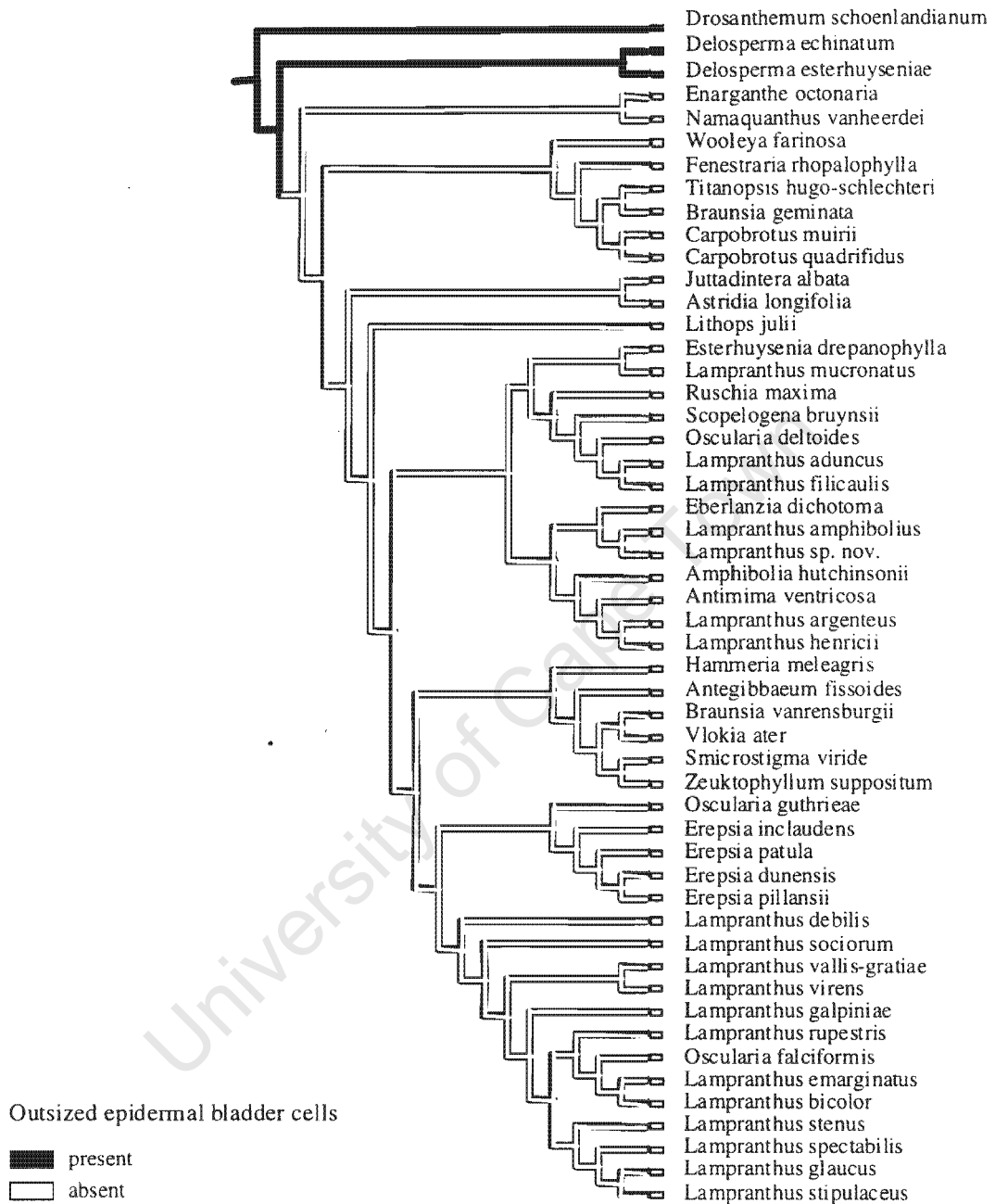


Fig. 4.5 Optimisation of outsized epidermal bladder cell character

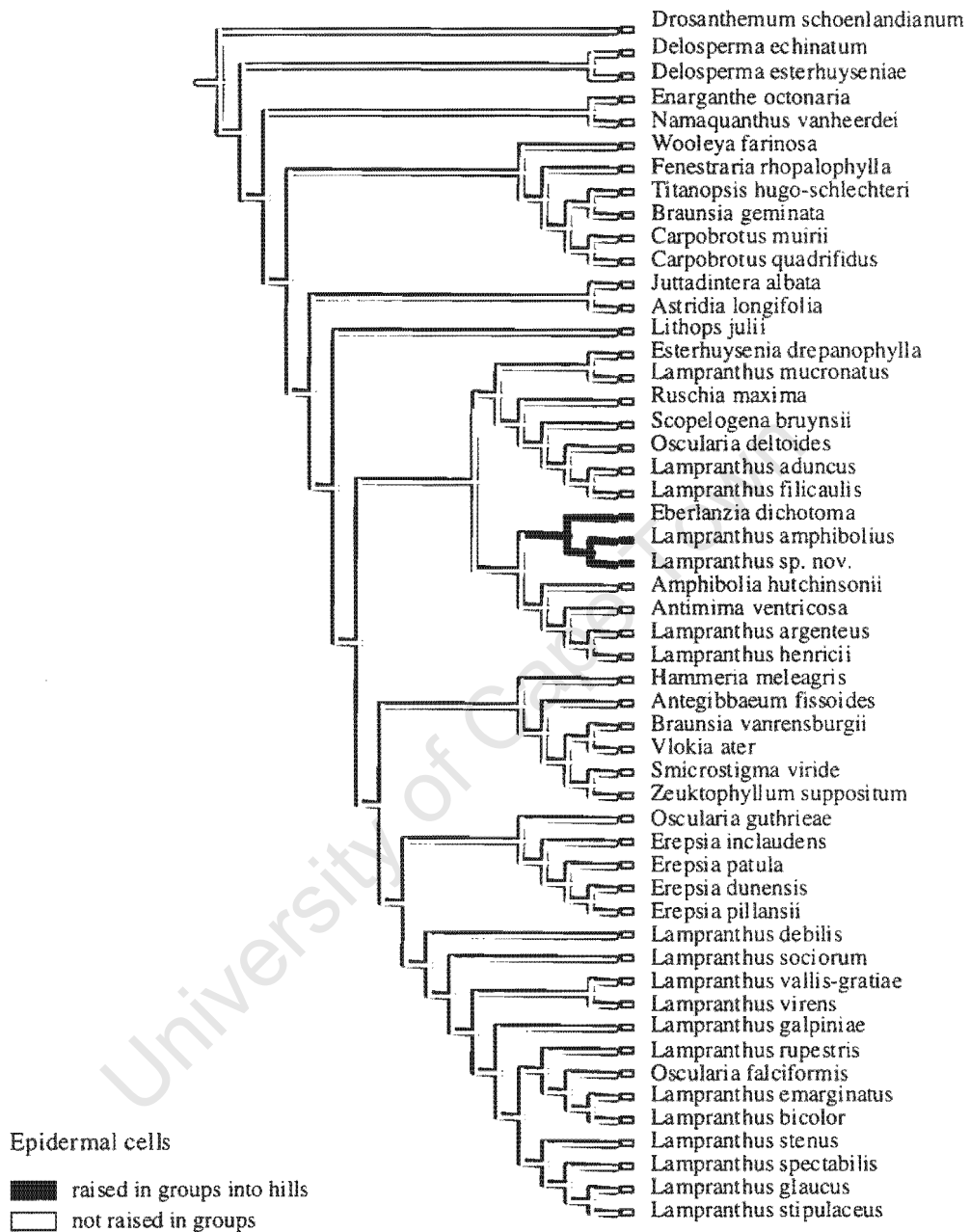


Fig. 4. 6 Optimisation of epidermal cell character

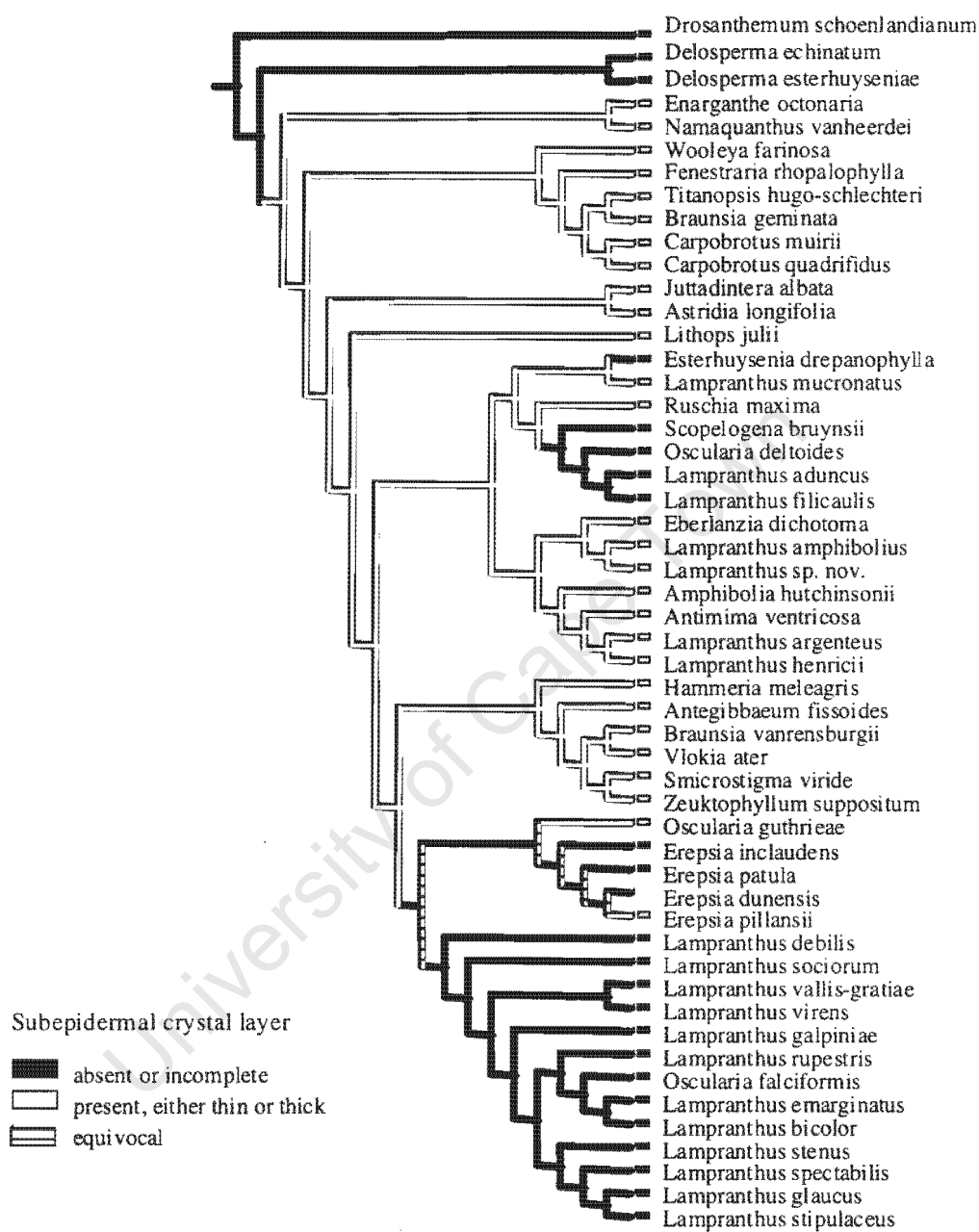


Fig. 4. 7 Optimisation of subepidermal crystal layer character

nectary forms a flat, smooth, continuous ring, i.e. it is a holonectary (Zandonella 1977). Holonectaries are found in all other taxa placed in the Centrospermae (Zandonella 1977), but those of the Ruschioideae differ from other members of the group in that they are crested. Rappa (1912) interpreted the holonectaries found in the other three subfamilies of the Aizoaceae as plesiomorphic, and regarded shell-shaped and crested nectaries as derived. The presence of flat, smooth nectaries (usually meronectaries) found in the *Cleretum* - and *Apatesia* - groups, as opposed to the crested nectaries in all other Ruschioideae, led to the hypothesis that the *Cleretum* - group constituted an early phylogenetic separation from the rest of the Ruschioideae (Bittrich & Struck 1989). The distribution of the three nectary types, i.e. coilomorphic (Mesembryanthemoideae), flat ring (*Dorotheanthus*) and lophomorphic (the remainder of the sampled Ruschioideae) corresponds to the three highly supported lineages within the succulent Aizoaceae recognized in this study (Fig. 4. 2). Although *Dorotheanthus* was the only representative of the *Cleretum* - group, the topology presented here lends support to Bittrich & Struck's and Landrum's (2001) hypothesis of an early phylogenetic separation of the *Cleretum* - group from the rest of the Ruschioideae.

Within the Ruschioideae, lophomorphic nectaries may either form a ring (holonectary) or be separated (meronectaries). On account of the predominant occurrence of meronectaries in the *Cleretum* - group and in the Mesembryanthemoideae, meronectaries have in the past been considered to be the plesiomorphic state within the Ruschioideae compared to a holonectary (Bittrich & Struck 1989). When the evolution of these character states is traced (Fig. 4.8), it is shown that the two genera which are sister to *Dorotheanthus*, i.e. *Drosanthemum* and *Delosperma*, have five distinct nectary glands. Although sampling is not complete within the Ruschioideae, the topology supports the hypothesis of Bittrich and Struck (1989), suggesting that the holonectary is the derived state within the Ruschioideae. However, meronectaries are also found in several other taxa (*Oscularia deltoides*, *Erepsia inclaudentis*, *Oscularia guthrieae*), which are neither closely related to *Drosanthemum* or *Delosperma* nor necessarily to each other. The presence of distinct meronectaries in *Oscularia deltoides* is therefore not indicative of a close phylogenetic relationship to the *Delosperma* - group where it has so far been placed and where members typically possess meronectaries. Among the taxa sampled in this study, distinct meronectaries have evolved independently at least twice. Since the character optimization at the base of the clade comprising *O. guthrieae* and *Erepsia* is equivocal, there is as yet no hard evidence for an independent gain of a holonectary.

Although a hypanthium is a rare feature within the succulent Aizoaceae, it is known that this structure also evolved independently in apparently unrelated genera such as *Argyroderma*, which differs from species of *Erepsia* and *Carpobrotus* by a very different habit, leaf and fruit morphology. It is also noteworthy that in *Carpobrotus*, there are several species that form a hypanthium (e.g. *C. murii*, *C. dimidiatus* (Haw.) L.Bolus), whereas it is absent in others (e.g. *C. quadrifidus*, *C. mellei* (L.Bolus) L.Bolus) (Fig. 4. 9). Unfortunately, in their revision of the South African species of *Carpobrotus*, Wisura & Glen (1993) paid little attention to this character and its possible variability within species. Assuming that the presence of a hypanthium within a species is not variable, this study suggests that the hypanthium has

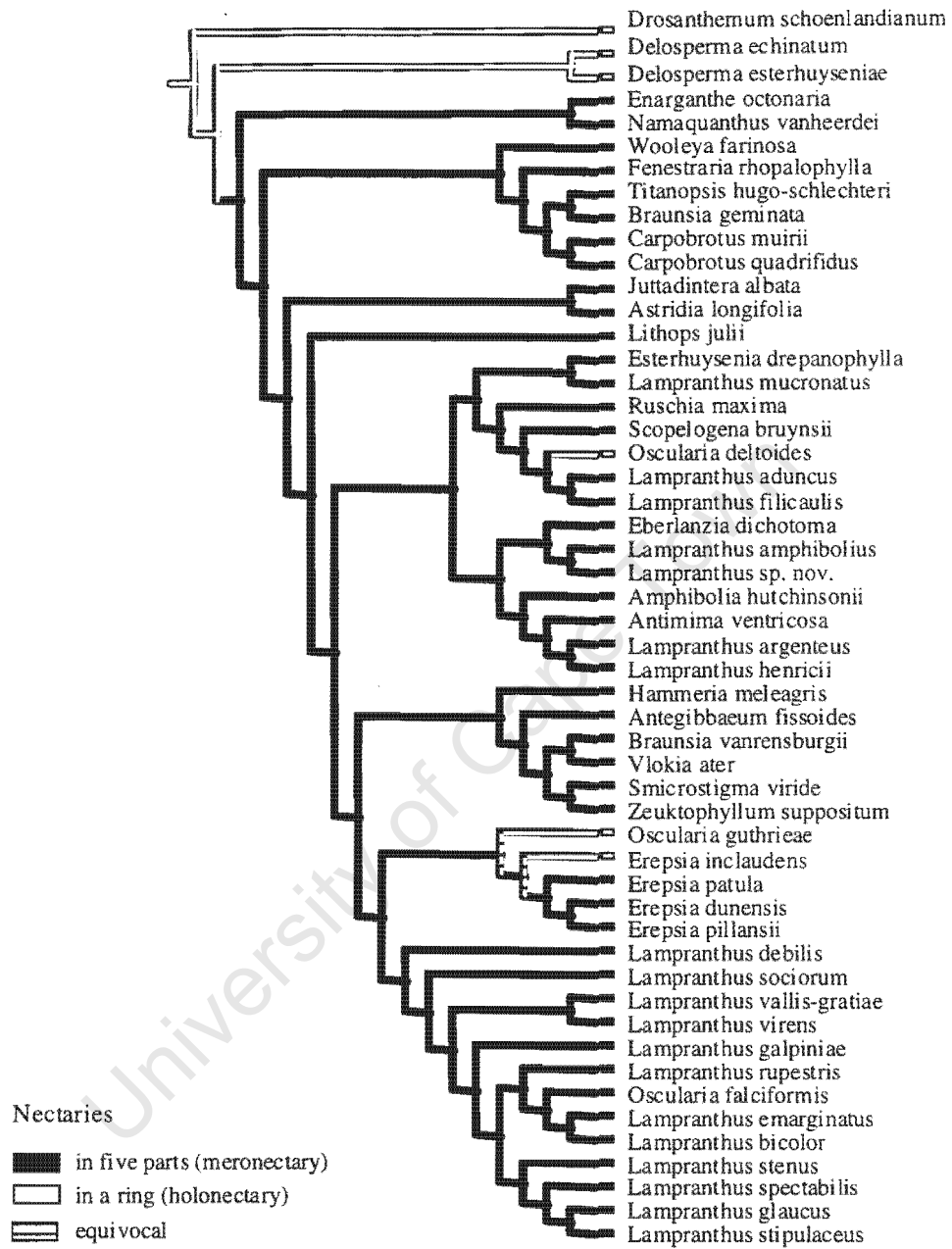


Fig. 4. 8 Optimisation of nectarial character

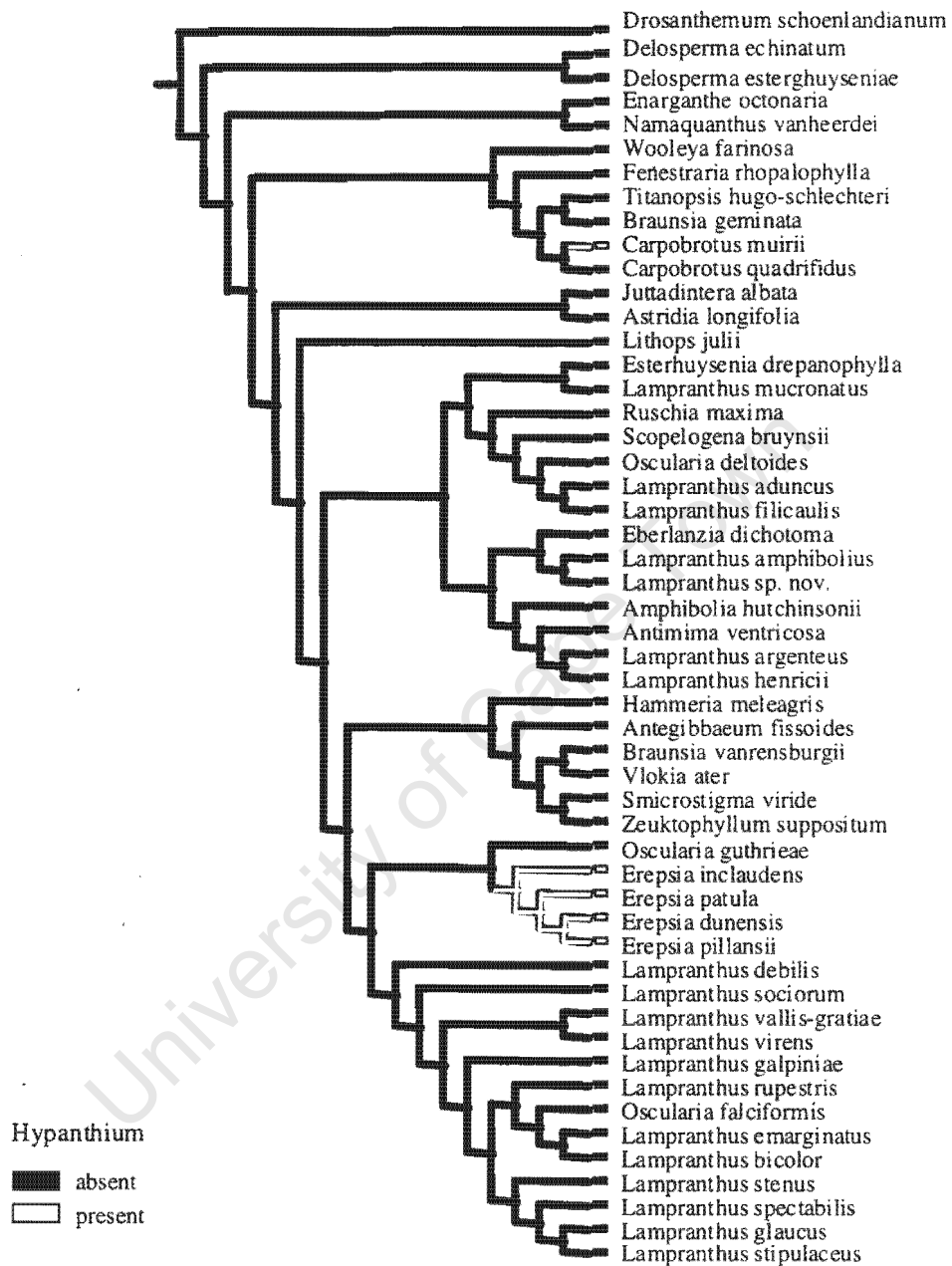


Fig. 4. 9 Optimisation of hypanthium character

evolved independently at least twice within the sampled Ruschioideae.

### C. Evolution of fruit characters

Hartmann (1988) postulated that the combination of fruit structures in the Ruschioideae could be used to classify the fruits into groups or fruit types to which she assigned genera, though in numerous cases only tentatively. Here, particular attention is paid to the "*Lampranthus* fruit type", which is characterized by a combination of characters. The different characters of the fruits and their states are therefore discussed separately.

(i) The absence of a closing body is listed as one of the main features of the *Lampranthus* fruit-type (Hartmann 1988, 1991; Dehn 1992), and the distribution of this character state is shown in Fig. 4. 10. The absence of a closing body in the Mesembryanthemoideae and in the most basal groups within the Ruschioideae suggests that it is the plesiomorphic state, which confirmed earlier hypotheses (e.g. Bittrich & Struck 1989). On the other hand, taxa with a closing body, such as *Astridia* and *Ruschia* (both members of the *Ruschia* - group) appear to have closer relationships to taxa without a closing body than to others possessing a closing body. The closing body appears to have evolved independently at least five times. Since the optimization of the character is equivocal at the base of the clade comprising *Eberlanzia*, *Amphibolia*, *Antimima* and four species of *Lampranthus*, there is no evidence for an independent loss of the closing body.

The apically enlarged closing body present in *Antimima* and *Fenestraria*, which has been proposed as a synapomorphy for the members of the *Leipoldtia* - group, has evolved independently twice. It needs, however, to be re-emphasized that the anatomy of closing bodies has never been comprehensively investigated across the Ruschioideae. Similarly, developmental studies of the closing bodies are entirely absent, so that it is possible that not all these structures are homologous. The closing bodies found in *Glottiphyllum* are noteworthy. These are listed as a striking case of parallel evolution, since they resemble those found in the *Leipoldtia* - group but actually differ from them both in shape and anatomy (Hartmann 1988). The presence of outsized epidermal bladder cells on the leaves of species of *Glottiphyllum* (as opposed to much flattened bladder cells in the *Leipoldtia* - group), had already earlier led to the conclusion that overall similarity in fruit structures was not necessarily indicative of a close phylogenetic relationship (Hartmann 1983). Unfortunately, *Glottiphyllum* was not included in the present study, so that these hypotheses still need to be substantiated.

(ii) Instead of a closing body, sterile funicles or seed-stalks can block the exit of the locule - opening in order to regulate the dispersal of the seeds from the capsule (e.g. Dehn 1992). Hartmann (1991) suggested that the presence of sterile funicles at the locule - opening is characteristic for the *Lampranthus* - group. Generally it is difficult to determine whether a funicle is sterile or no longer has a seed attached to it. Bunches of funicles placed at the exit of the locules were found in all members of the *Lampranthus* - group, but were also present among the genera placed outside the *Lampranthus* - group (e.g. *Juttadintera*,

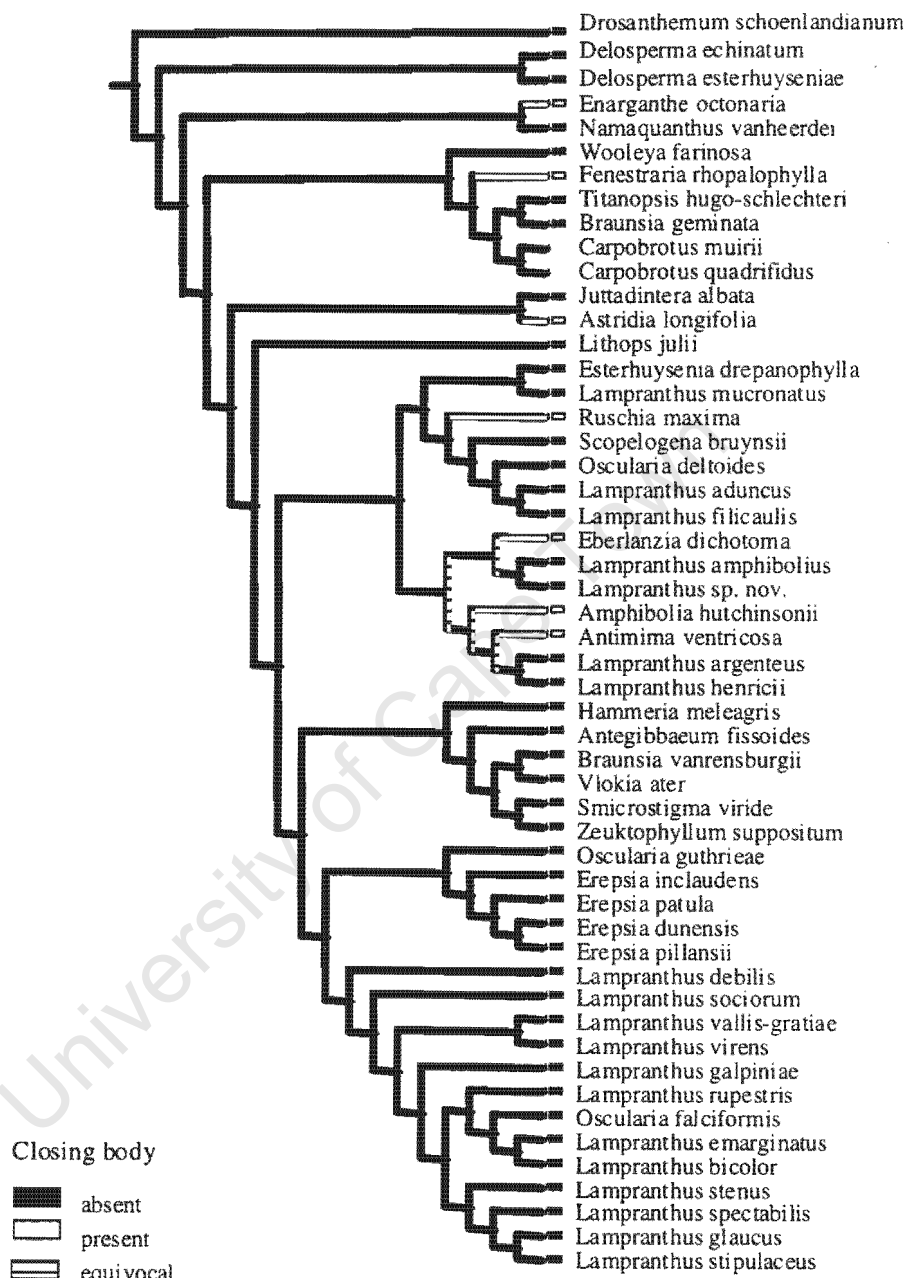


Fig. 4. 10 Optimisation of closing body character

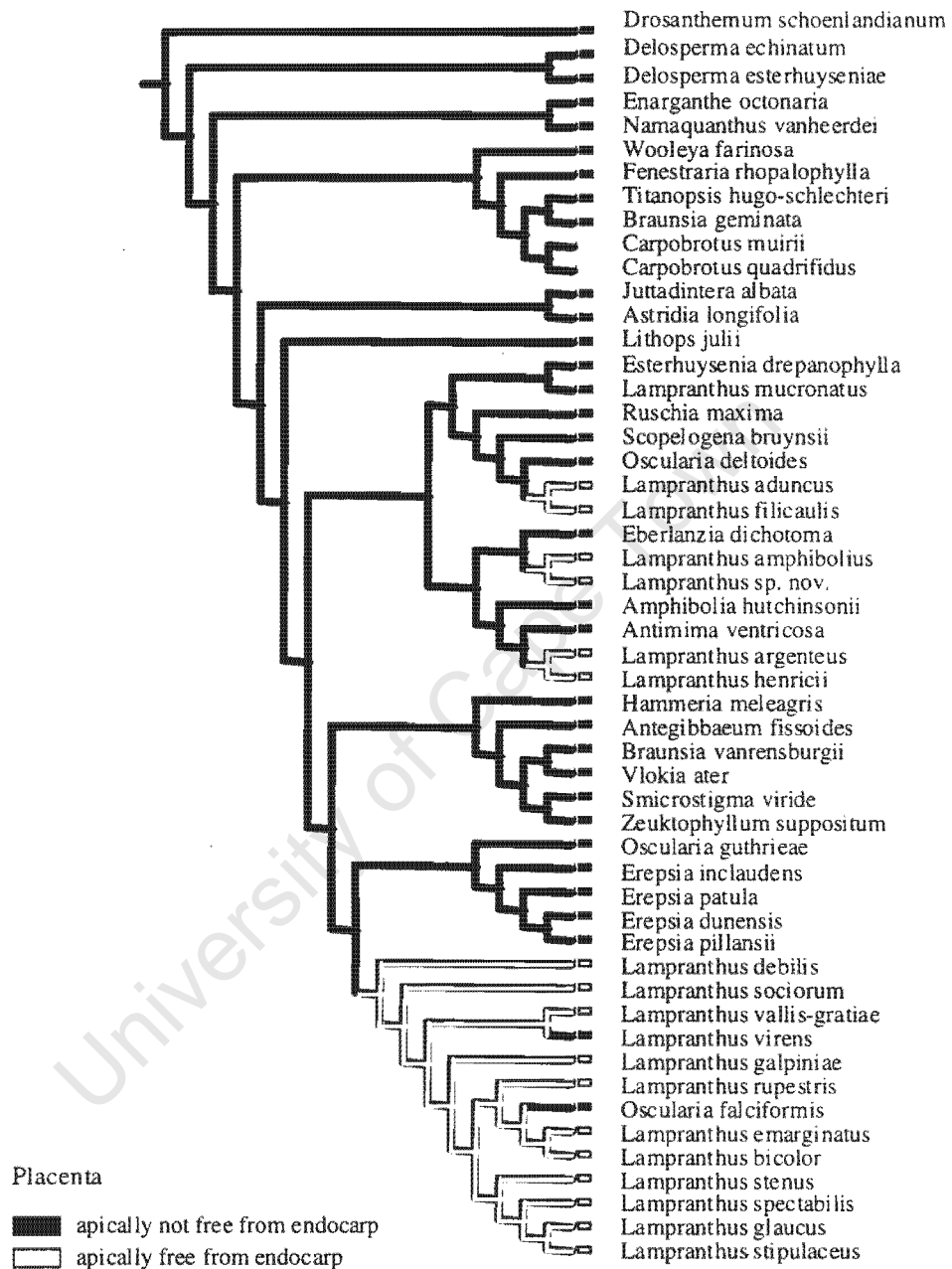


Fig. 4. 11 Optimisation of placental character

*Oscularia*, *Trichodiadema*). This character therefore has to be considered to be homoplasious (not traced). In addition, it was noticed that in some taxa the placenta may be apically separated from the endocarp (Hartmann & Dehn 1989, Dehn 1992). If the evolution of this character state is traced (Fig. 4. 11), it becomes evident that within the “core” of *Lampranthus* the majority of species has their placenta apically separated from the endocarp. However, in *O. falciformis* and *L. virens*, the placenta is not apically separated. Furthermore, this character state is also present in all other species of *Lampranthus* sampled (except *L. mucronatus*), which are placed outside the “core” of *Lampranthus*. In total, a placenta which is apically free from the endocarp has evolved independently four times, whereas there are two independent gains of a placenta which is apically attached to the endocarp.

(iii) The covering membranes, common in the Ruschioideae, are entirely absent in the Mesembryanthemoideae and the other subfamilies of the Aizoaceae. Although they are reduced to a narrow rim in several ruschioid genera (e.g. *Delosperma*, *Juttadintera*, *Lithops*), they are considered to be a synapomorphy for the subfamily Ruschioideae (Bittrich & Hartmann 1988, Bittrich & Struck 1989). Convex covering membranes are listed as characteristic for the *Lampranthus* – group (Hartmann 1991). If this character state is traced on the topology (Fig. 4. 12), it resolves as the plesiomorphic and most widespread character state within the Ruschioideae, as compared to the concave covering membranes. Concave covering membranes are rare in the Ruschioideae and are believed to be a synapomorphy for the members placed in the *Leipoldtia* - group. However, in both the combined molecular and total evidence analyses *Antimima* is apparently more closely related to *Lampranthus argenteus* and *L. henricii* than it is to *Fenestraria*. On account of the 5-locular fruits and a very similar floral morphology, most species of *Antimima* used to be part of *Ruschia*. However, the discovery of stalked, apically enlarged closing bodies and concave covering membranes in the fruits of *Antimima*, suggested a closer relationship to the *Leipoldtia* – group (Dehn 1992). Concave covering membranes are, however, also found in *Glottiphyllum*, a genus that is thought to be unrelated to the *Leipoldtia* – group, as mentioned above. The present analysis suggests that concave covering membranes have evolved independently at least twice.

(iv) Hartmann (1991) further lists additional closing devices below the distal ends of the covering membranes as a characteristic for the members of the *Lampranthus* – group. The evolution of an additional closing device is traced in Fig. 4. 13, which shows that numerous taxa placed in the *Lampranthus* – group do not possess any additional closing devices (e.g. *Wooleya*, *Antegibbaeum*, *Braunsia*, *Namaquanthus*). Since *Drosanthemum* and *Delosperma* do not develop additional closing devices, the presence of a closing device is shown to be the derived state. Additional closing devices are shown to be widespread among the ruschioid taxa (e.g. *Ruschia*, *Antimima*, *Eberlanzia*, *Amphibolia*) and have evolved independently five times. In several species such as *Lampranthus* and *Erepsia* the closing device is often fairly inconspicuous, which has evolved independently five times. This study also suggests that additional closing devices have been lost independently twice. This shows that inconspicuous or conspicuous closing devices are highly homoplasious character states.

(v) Divergent expanding keels have been listed as a further characteristic for the *Lampranthus*- type of fruit and these were supposed to be found in *Braunsia*, *Wooleya*, *Namaquanthus*, *Enarganthe* and *Zeuktophyllum* (Hartmann 1988). If this character (Fig. 4. 14) is traced, it shows that several species placed in the *Lampranthus* – group have keels which are parallel for most of their length (e.g. *Braunsia geminata*, *Wooleya*, *Zeuktophyllum*). One might argue that in multi-locular fruits (*Wooleya*, *Zeuktophyllum*) no space for diverging keels exists and they therefore need to be parallel. However, the many-locular fruits found in members of the *Leipoldtia* – group exhibit both divergent keels and many locules and provide a counter-example, disproving this argument. Expanding keels that diverge from the base are shown to be the derived state compared to keels which are parallel for at least some of their length. Optimization of the character states in the clade sister to *Lithops* is equivocal: if the ancestral state at this nodes were “keels diverging from middle” then the state “keels diverging from base” would have evolved six times independently. If the state “keels diverging from base” were the ancestral condition at base of this node then the state “keels parallel and diverge from middle” would have evolved at least six times. This shows that keel morphology is very homoplasious.

The discussion of the different characters used to define the *Lampranthus* – type of fruit shows that a combination of all the characters listed for this “type” are found in only a few taxa, i.e. *Lampranthus*, *Erepsia*, *Esterhuysenia* and *Scopelogenia*. All other genera so far listed with a *Lampranthus* – fruit type, usually fail to satisfy several of the other characteristics listed by Hartmann for the group. This shows that fruit “types” do not make characters. However, the individual characters themselves may provide considerable phylogenetic information. Groups which were highly supported in this study, such as the “core” of *Lampranthus* or *Braunsia*, also share numerous fruit characters. It follows that members of a genus with very different fruit morphology are unlikely to be close relatives and this was demonstrated here for *Braunsia vanrensburgii* (chapter 2). So one may conclude that fruit morphology may provide phylogenetically informative characters.

On the other hand, this study of the *Lampranthus* – group and of *Lampranthus* also shows that species with a very similar fruit morphology need not be part of the same genus or need not even be closely related. A good example is provided by *Delosperma*, *Lithops* and *Conophytum*, which all share the same fruit-type. Here habit, flower morphology and epidermal features differ quite substantially among the three genera and a close relationship is unlikely (Hartmann 1988, 1991). In the past the morphological features of the species in *Lampranthus* and the *Lampranthus* - group have mainly been interpreted in the light of the fruit morphology. However, the present study shows that fruit characters may also be homoplasious, so that a careful analysis of all available characters (i.e. leaf, floral morphology etc.) is needed to retrieve the relationships.

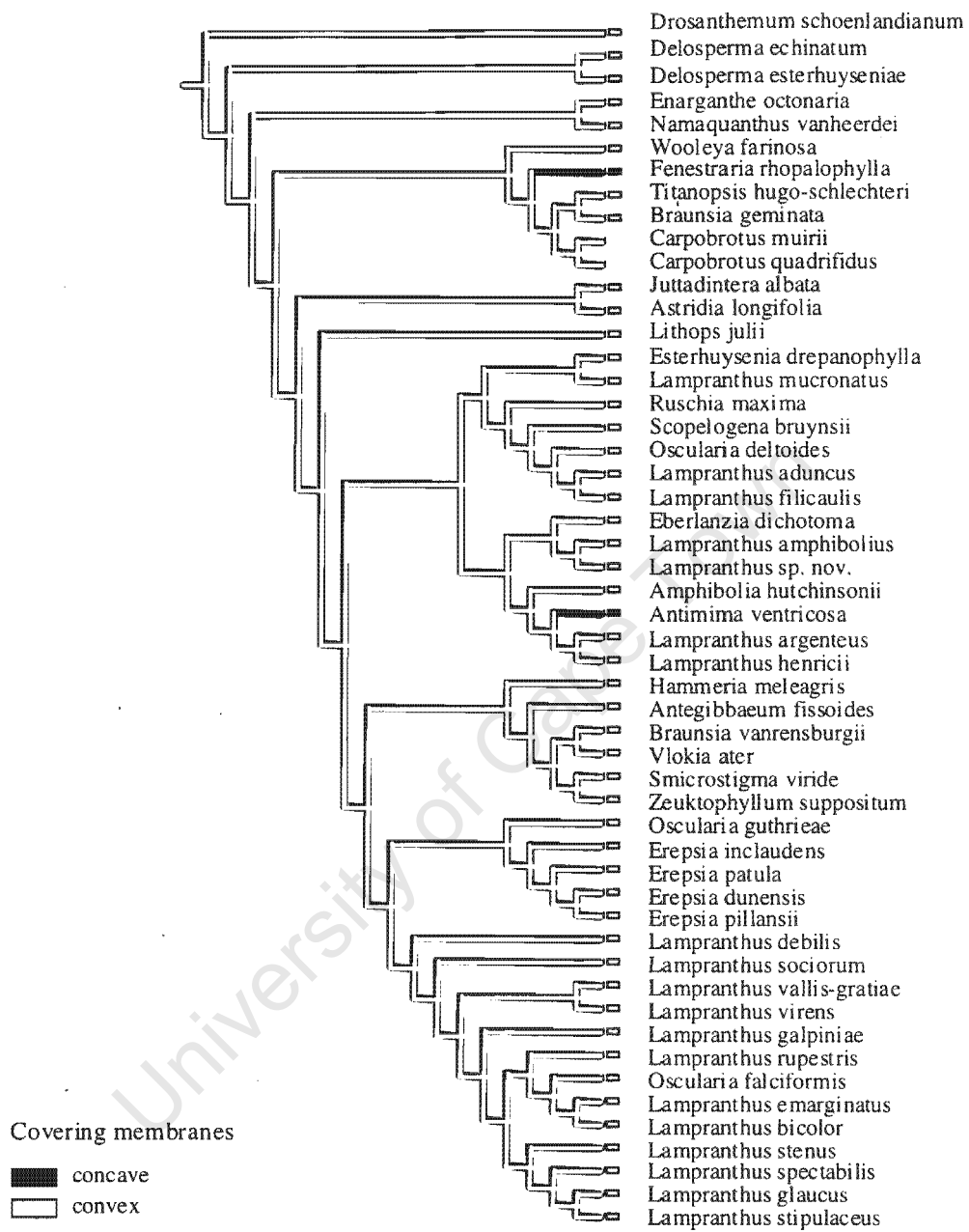


Fig. 4. 12 Optimisation of covering membrane character

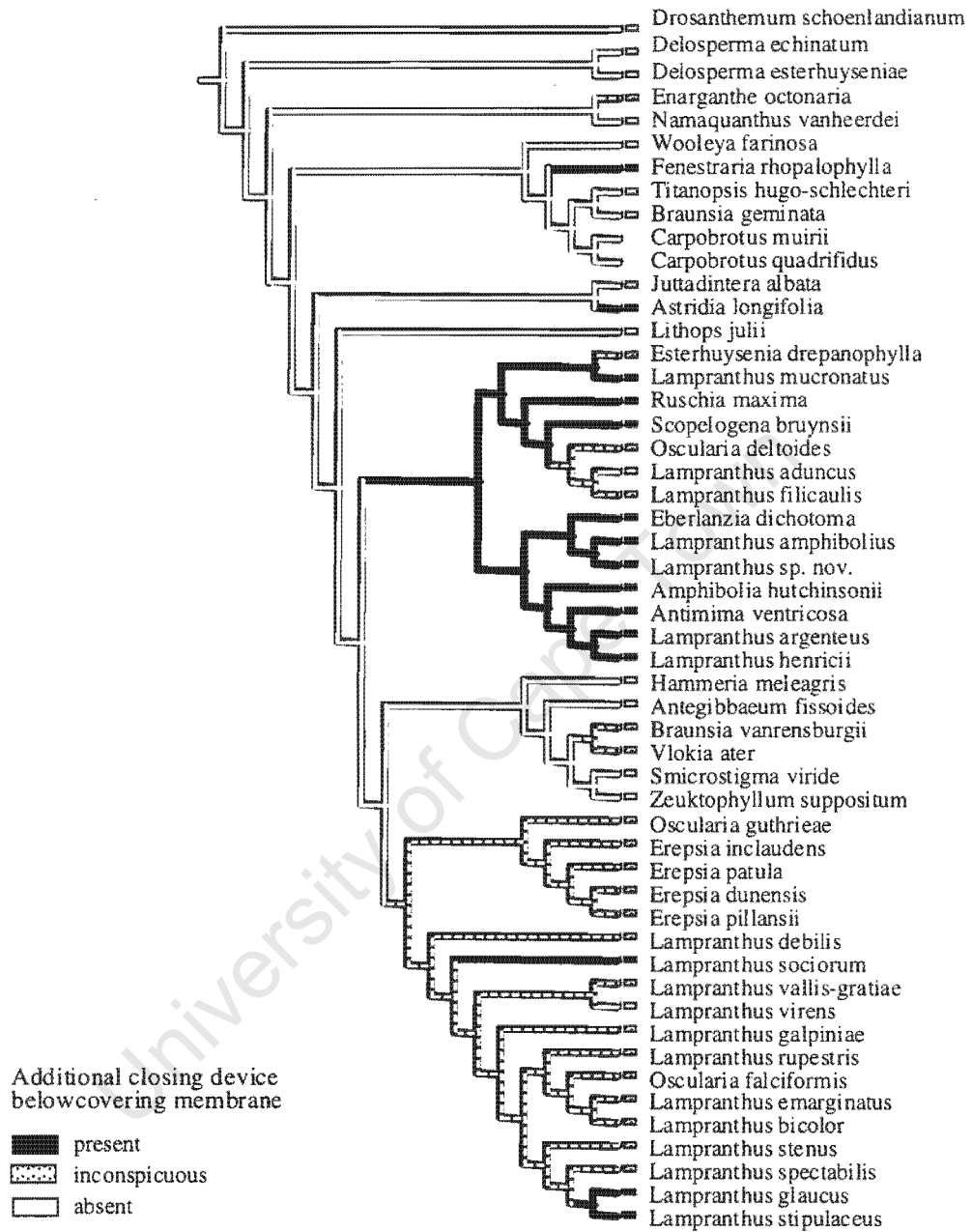


Fig. 4. 13 Optimisation of additional closing device character

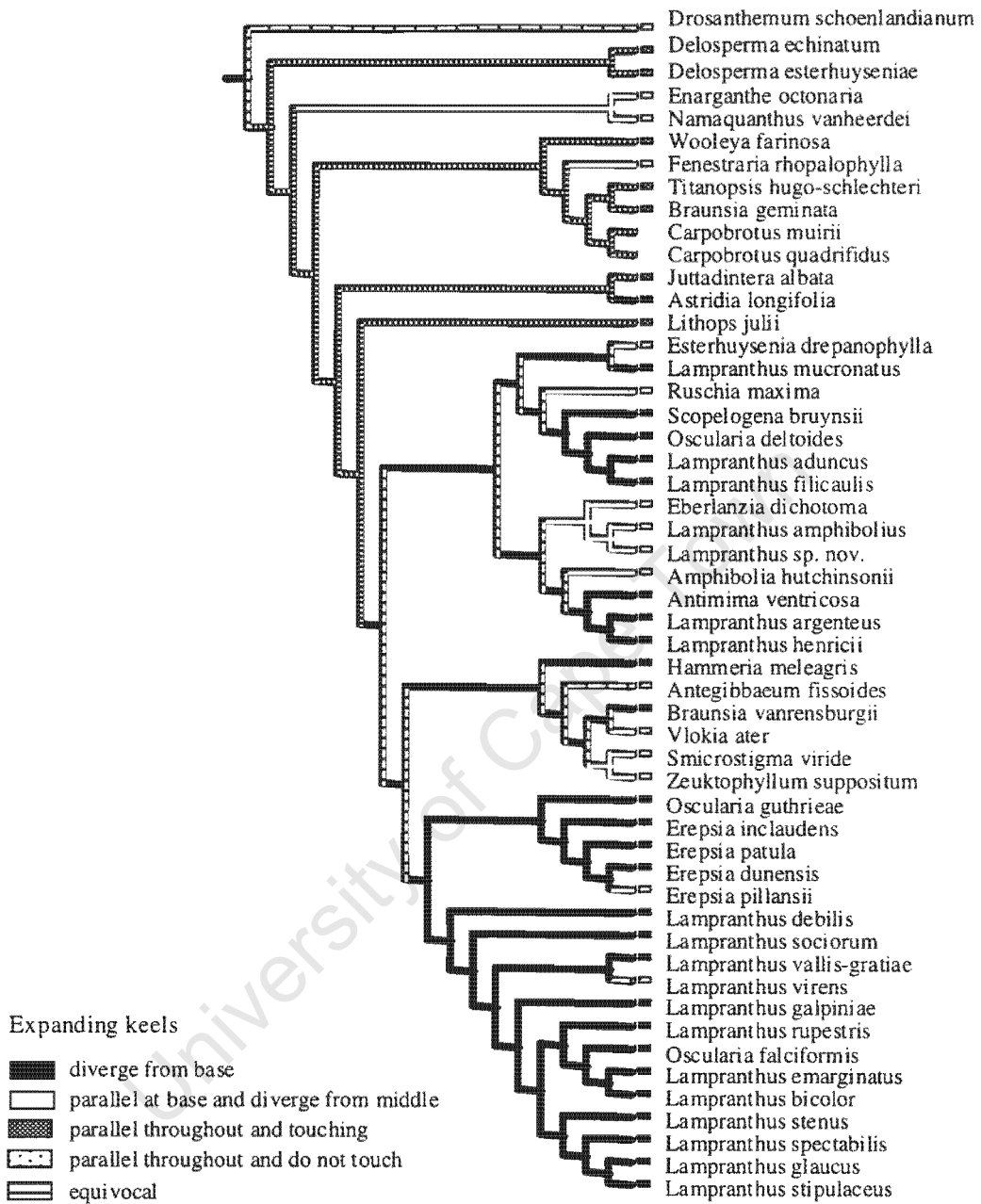


Fig. 4. 14 Optimisation of expanding keel character

## CHAPTER 5

### GENERAL DISCUSSION

#### 5. 1. Summary and appraisal of results

The *trnL-F* and the ITS region provided relatively few informative characters at generic level. The 5S spacer proved to be most informative at generic and to some extent at specific level. Whereas each of the separate molecular and morphological analyses produced very poorly supported and often also poorly resolved trees, the combination of all available data had the greatest explanatory power. The total analysis produced the fewest alternative phylogenetic hypotheses for the *Lampranthus* - group and showed the highest degree of resolution. The cladistic analysis of both morphological and molecular data improved not only the resolution within the tree but in most cases also the support for the topology.

Despite the inclusion of four data sets in a simultaneous analysis, many ambiguities in the relationships between the members of the *Lampranthus* - group persist. A lack of phylogenetically informative characters, incorrect homology assessments, parallelisms and convergence in the morphological characters may have contributed to the loss of statistical support for the clades. Yet, some of the basal nodes defining the main lineages within the ruschioid taxa that were sampled were well-supported. In addition, high jackknife support was achieved for the terminal branches delimiting genera.

On the basis of the current analysis a number of firm conclusions may be drawn:

- (i) Several genera, such as *Lampranthus*, *Oscularia* and *Braunsia*, are polyphyletic. The largest of these genera, *Lampranthus*, was shown to consist of a well-supported “core” of species which is considered to represent *Lampranthus s. str.* Various other species of *Lampranthus* are placed with good support outside this “core” and, show closer relationships to other ruschioid genera than to the core *Lampranthus* clade.
- (ii) Relationships of several mono- and bitypic genera which were previously difficult to place have been elucidated in this study: High statistical support and the presence of at least one shared derived character (e.g. multi-locular fruits) suggest that *Enarganthe* and *Namaquanthus* form a well defined monophyletic group and ought to be placed in a single genus. Similarly, *Smicrostigma* and *Zeuktophyllum* should be recognized as a single genus.

In addition, *Antegibbaeum*, *Vlochia*, *Hammeria*, *Smicrostigma*, *Zeuktophyllum*, *Braunsia vanrensburgii* and *Ruschia intrusa* were retrieved as a well supported clade. The presence of shortly-echinate seeds appears to be unique to this clade, but is not shared by all the taxa and is only present in *Antegibbaeum*, *B. vanrensburgii* and *Ruschia intrusa*. Keels with awn-like extensions may represent a synapomorphy for this clade.

- (iii) The *Lampranthus* - group, largely circumscribed by a particular fruit “type”, i.e. the *Lampranthus* - type of fruit, is found not to be monophyletic. This fruit “type” is only present in some genera of the *Lampranthus* - group. This shows that here the type of fruit fails to circumscribe a natural group and the possibility arises

that the present classification of the Ruschioideae may also fail to represent natural groupings, since it is similarly largely based on fruit typology. However, the individual characters of the fruits may still be phylogenetically informative. The presence of homoplasy in the fruits suggests that a broader suite of characters needs to be considered in order to retrieve the phylogeny.

(iv) Many of the species investigated in this study were shown to be less closely related to one another than was previously thought to be the case. The polyphyly of many of the genera and groups previously thought to be well defined by various morphological characters, suggests that these characters need to be re-evaluated. This applies not only to *Lampranthus* and the genera incorporated by Hartmann (1988, 1991) in the *Lampranthus* – group, but also to some of the outgroups. A good example of this is provided by the two representatives of the *Leipoldtia* – group that were sampled: although this group shares the morphological features of stalked, apically enlarged closing bodies and concave covering membranes they did not group together in this analysis and these characters proved to be homoplasious. Concerns were also raised about the monophyly of *Erepsia*, a genus assumed to be well defined by floral characters. On account of the present study the position of *Erepsia inclaudentis* needs to be further investigated in conjunction with more sampling within *Erepsia* and *Lampranthus*.

(v) The phylogenetic hypothesis presented in this study has important implications for an increased understanding of the evolution of the morphological characters. Although homoplasy was suspected in numerous characters, including the fruit characters, this is the first study to reveal homoplasy in a phylogenetic framework. An increased understanding of the evolution of the morphological characters ultimately aids in understanding the evolution of the Aizoaceae.

(vi) The clades retrieved in this study conflict in many ways with the present classification of the succulent Aizoaceae. The fact that none of Hartmann's groups were retrieved in a clade suggests that a much broader study is needed to reveal the relationships among the Ruschioideae. The phylogenetic tree found in the total evidence analysis (Fig. 4. 4) provides an important framework for further phylogenetic studies in the Ruschioideae.

(vii) On the basis of the morphologically and statistically well supported clades a new classification is proposed in chapter 6. This classification includes new generic circumscriptions and a conspectus of the large genus *Lampranthus*.

## 5. 2. Estimating the possible age of the succulent Aizoaceae and the age of their diversification

The succulent Aizoaceae, in particular the Ruschioideae, are remarkable for their richness in species and the high levels of endemism in the succulent Karoo (e.g. Jürgens 1986, Hartmann 1991). The diversification of the succulent Aizoaceae has been suggested to be both recent and rapid: Ihlenfeldt (1994) thought that the group is unlikely to be older than five million years and that in view of the high number of species the tempo of diversification must have been rapid. On the other hand Cowling & Pierce (1999) suggested that the diversification of the succulent Aizoaceae may have taken place within the last 12,000

years.

Various methods exist for estimating the age of the succulent Aizoaceae:

#### A. Fossil evidence

Cowling and Pierce (1999) based their hypothesis largely on the fossil and geological evidence. The points listed below provide an overview of what fossil and geological evidence exists to substantiate or refute the proposed hypothesis. However they show that the evidence obtained from the geological and fossil data remains ambiguous as to the onset and speed of diversification of the succulent Aizoaceae and it is not possible to produce estimates based on this evidence alone.

##### (1) Arid to semi-arid conditions in the Namib date back to 80 mya.

Geological evidence from sediments found in the Namib suggest that arid to semi-arid conditions, interspersed with wetter periods, dominated the climate of the Namib since the Cretaceous about 80 mya (Ward *et al.* 1983, Ward & Corbett 1990). This fact has not been universally recognised and some authors have considered the Namib to be a “young” desert (Tankard & Rodgers 1978). Ward *et al.* (1983) show that many of these arguments are based on misinterpretations of fossil data and they cite numerous examples where extrapolations of the existence of extensive wooded grasslands in the Miocene were based on the presence of mammal fossils in the sediments. Since faunal distributions are often related to the major rivers that traverse the Namib, their fossil assemblages may be associated with their river sediments which are essentially islands within an arid environment and say nothing about conditions prevailing more widely (Ward *et al.* 1983).

This suggests that succulents may have been present in these areas and in turn implies that the Aizoaceae may be very ancient. On the other hand even if the family may be very old, it still does not predict the age of the modern species and genera of Aizoaceae.

##### (2) Moister conditions suggesting subtropical to tropical forest 10-15 mya in several spots in the south-western Cape.

Although the greatest diversity of the succulent Aizoaceae is in the arid winter-rainfall area of Namaqualand (Jürgens 1986, 1990, 1997), there are many species that are found on the west coast of the Cape today (Klak 2000b). In this area, early to mid-Miocene deposits (i.e. from 10-15 mya) indicate a luxurious broad-leafed flora (Coetzee & Muller 1984) and a fauna adapted to forest and woodland with summer rainfall (Hendey 1982). Faunal remains from Langebaan in the south-western Cape, suggest that, by the late Miocene (i.e. 5-10 mya), the forest and woodland were being replaced by more open savanna under markedly drier conditions (Hendey 1982). Since these earlier floras are entirely different from what is now found in the region, these observations are generally taken as evidence that

- (i) there was considerable climatic change around the end of the Miocene and the beginning of the Pliocene (i.e. about 5 mya)

(ii) the present Cape Flora is of comparatively recent origin and diversified dramatically after the beginning of the Pliocene, i.e. about 5 mya (e.g. Linder *et al.* 1992, Goldblatt & Manning 2000).

However, the evidence for this is superficial. In particular, these conclusions are based on extrapolations from two fairly small sites to whole regions. For these extrapolations there is no corroborating evidence so that the same objections raised by Ward *et al.* (1983) apply here as well.

(3) The establishment of the Benguela Current, ca. 10 mya.

The Benguela Current has a cooling and aridifying effect along the adjacent coastal region and the hinterland (Logan 1960) and there is no doubt that the present arid conditions in the Namib are maintained by its influence (Koch 1962, Van Zinderen Bakker 1975, Siesser 1977, Tankard & Rodgers 1978). It is believed to have originated in the early late Miocene, that is about 10 mya (Siesser 1980). The Benguela Current is considered to have exercised a major influence on the vegetation in the south-western Cape and its establishment is considered to be reflected in changes in the species composition in the fossil record from Langebaan that were noted above (Hendey 1982, Coetzee & Muller 1984). However, complications arise in that the influence of the Benguela Current does not appear to have been continuous and fluctuations in the intensity of the upwelling have been recorded, corresponding to variation in the Antarctic continental ice volumes (Meyers 1992). Therefore the climate must have fluctuated during these cycles as well, suggesting that arid periods were interspersed with moister periods. These fluctuations make it all the more difficult to pinpoint the time of establishment of the Cape Flora, including its succulent Aizoaceae.

(4) Establishment of the winter-rainfall region ca. 5 mya

Although the succulent Aizoaceae are found in both summer- and winter-rainfall regions of southern Africa, they have their greatest diversity in the arid winter-rainfall area of Namaqualand (Jürgens 1986, 1990, 1997). The winter-rainfall area is floristically very diverse and consists of part of the Cape Floristic Region and part of the Succulent Karoo Region (Jürgens 1991). There are 624 species of succulent Aizoaceae in the Cape Floristic Region and several genera included in the present study, such as *Lampranthus*, *Erepsia*, *Oscularia* and *Esterhuysenia*, are almost entirely restricted to the south-western Cape, where they experience relatively high winter-rainfall (Klak 2000b).

The vegetation of the Cape Region prior to the establishment of the winter-rainfall climate is thought to have been very different from that now found here, implying that the winter-rainfall regime with summer droughts was the primary selective force in shaping the vegetation of the Cape Region as we know it today (Axelrod & Raven 1978: 112, Goldblatt & Manning 2000). However, there is no conclusive evidence of a change in the seasonality of the rainfall. Generally the strong development of the present Macchia vegetation in the Pliocene and the presence of plants typically associated with summer-rainfall in the south-western Cape 5-10 mya, were seen as an indicator of increasing summer aridity in the south-western Cape (Coetzee 1980). Similarly, plants that are usually associated with tropical wet climates, such

as Gunneraceae, Cyatheaceae which were present in the Arnot flora of 60-70 mya (Scholz 1985) are now entirely absent from Namaqualand (though *Gunnera* still occurs along permanently wet streambanks in the Cedarberg further to the south).

It appears equally possible that a general increase in aridity, due to the cold Benguela current, may have led to the changes in the vegetation that have been observed. Since the timing of onset of the Benguela current dates back about 10 mya, the diversification of the succulent Aizoaceae may date back to 10 mya.

#### (5) Considerable increases in Aizoaceous pollen at Eksteenfontein over the last 10,000 years

Palynological data from spring deposits at Eksteenfontein in the Richtersveld show a marked change from sediments dominated by Chenopodiaceae, Amaranthaceae and different Asteraceous pollen in the Late Pleistocene (before 10,700 ya), to assemblages totally dominated by pollen of the Aizoaceae in the Holocene (10,700 – 8450 ya) (Scott *et al.* 1995).

One interpretation of this data is that the diversification of the succulent Aizoaceae is very recent. However, due to the scarcity of corroborating data from comparable sites and from earlier assemblages, it is also possible to argue that the succulent Aizoaceae were diverse elsewhere prior to the Holocene, but spread later over larger areas of the country. The palynological evidence is generally scarce due to poor preservation (e.g. summarized in Scott *et al.* 1997) and evidence of centrosperous pollen in the early pollen assemblages is only ambiguous. Thus for example, pollen samples from Namaqualand, dating from the Paleocene (60-70 mya), possibly include species of Cactaceae (Scholz 1985). Similarly, among the pollen flora identified from the Pliocene (c. 5 mya) from the south-western Cape the dominant type (c. 92%) is Aizoaceous, although also here the identity of the pollen was ambiguous (Tankard & Rodgers 1978).

#### (6) Increase of Aizoaceous pollen in the south-western Cape after 14,000 ya

Investigations of a continuous series of pollen samples from hyrax middens in the south-western Cape showed that, between 20,000 – 14,000 ya dry asteraceous  *fynbos* was more prevalent, but after 14,000 ya the investigated samples showed more elements of subtropical thicket along with succulent karoo elements such as Aizoaceae and *Aloe* (Scott 1994). In addition, a study of charcoal remains from Elands Bay, in the south-western Cape, reveals a greater dominance of mesic elements prior to 12,000 ya (Cowling *et al.* 1999). Thus, both studies suggest that arid elements were less prevalent at these latitudes prior to Holocene warming. However, in these two cases the evidence is based in each instance on a single study site, from which again extrapolations have been made to the entire area. In addition, although it could be true that xeric elements may have become more common in relatively recent times, the evidence does not necessarily point to the onset of diversification in the succulent Aizoaceae but just that they became more plentiful. Since the pollen can usually only be identified to family level, its presence says nothing about the levels of diversity that existed at any given time.

## B. Morphology

Some authors have suggested that the morphological characteristics of plants may be indicative of the mode of radiation: quantitative changes, such as shape and size, are thought to be associated with recent radiations as compared to qualitative changes (e.g. development and biosynthetic pathways) which happen over longer periods of time (Chase *et al.* 2000). The Ruschioideae is well known for its diversity of life forms: there are a few annuals and the majority of species are perennials. While most species are leaf succulents, there are also a few stem succulents and species with partly or completely deciduous stems or leaves. The group includes large woody shrubs up to 3 m tall, small shrubs (the most common habit), mat forming plants and even highly reduced forms, which may only consist of a single pair of leaves. Similarly, leaf shape, leaf epidermal features (e. g. Ihlenfeldt & Hartmann 1982) and fruit structures are very diverse.

In the Mitrophyllinae (Ruschioideae, Aizoaceae) differences among species (e.g. *Mitrophyllum*) were interpreted as quantitative (e.g. Ihlenfeldt 1971a, b) and the radiation of this group may therefore be recent. However, quantitative versus qualitative differences are not always easily distinguished no attempts have been made to generalize this hypothesis to other groups within the Ruschioideae. In the absence of studies that investigate quantitative versus qualitative morphological variation across a wide taxonomic range in the Ruschioideae the mode and time of radiation cannot be deduced.

## C. Molecular methods

Attempts have been made to estimate the age and rate of diversification of organisms based on molecular evidence (e.g. Baldwin & Sanderson 1998, Richardson *et al.* 2001). It could be argued that the relatively low levels of divergence observed in the ITS and *trnL-F* region in the Ruschioideae, as indicated by the very short branches at the base of many genera within the Ruschioideae (Fig. 2. 6, 2. 7), is indicative of a recent radiation, since molecular changes had little time to accumulate. However, this may not necessarily be the case: for example, the genus *Protea*, that also shows extensive morphological variation and little molecular divergence, is thought to be a relatively ancient lineage, originating ca. 36 mya (Reeves pers. comm.). Similarly, a molecular phylogenetic study of the morphologically diverse palm family (Palmae) found the *trnL-F* region to be highly conserved (Baker *et al.* 1999) whereas the fossil record indicates that the palms are a very ancient group with the earliest unequivocal records dating from the Upper Cretaceous, ca. 65 mya (Uhl & Dransfield 1987). A possible interpretation of these studies is that the age of divergence may not necessarily be closely linked to molecular divergence. On the other hand, although the palms may be an ancient lineage, the modern species may be more recent.

The maximum likelihood approach has been used to estimate divergence times in some plant groups (e.g. Baldwin & Sanderson 1998). Maximum likelihood analyses are driven by one of a myriad of process models, each of which requires justification (Kitching *et al.* 1998). In order to calculate likelihoods, probabilities of nucleotide substitution must be calculated along a branch. The length of a branch on a tree represents the expected number of substitutions per site along this branch (Swofford *et al.* 1996). The

length of a branch can then be calibrated using paleoclimatic and fossil data to place an earliest date for the onset of diversification and it then represents the length of the period of evolution. A calibration for the Aizoaceae is difficult due to the very poor fossil finds in Namaqualand (dating 60-70 mya) and the uncertainty of the identity of the pollen (Scholz 1985, see discussion of fossil evidence above). Much younger pollen samples have been identified (although ambiguously) as belonging to species of Aizoaceae from the Pliocene (c. 5 mya) from the south-western Cape (Tankard & Rodgers 1978). Also, since the pollen only identifies the family and not the genera, it is not possible to make an internal calibration.

The separation of land masses due to continental drift offers another possibility to date the age of a lineage. The majority of the genera is found in southern Africa and only a few, such as *Disphyma* (Australia, New Zealand), *Carpobrotus* (e.g. coastal areas of North and South America, Australia), *Mesembryanthemum* (Mediterranean) and *Delosperma* (Madagascar, Réunion, southern Arabia), occur naturally outside Africa. The methods of their dispersal to these areas have not been studied sufficiently (e.g. Hartmann 1991). In the case of *Carpobrotus* the disjunct distribution has been attributed to long-distance dispersal (Carlquist 1983), which is generally rare in the succulent Aizoaceae (e.g. Hartmann 1991). Until there is more information about the mode of dispersal of the other genera with a disjunct distribution, this biogeographic information cannot be used with confidence for internal calibration.

It was beyond the scope of this study to use the maximum likelihood approach to estimate the age and rate of diversification in the succulent Aizoaceae. However, the method merits exploration in the future.

#### D. Modelling by computer

A further hypothesis relating to the onset and mode of diversification of key groups (e.g. succulent Aizoaceae) of the Succulent Karoo Biome has been put forward suggesting that dispersal to novel sites during biome expansion facilitated bursts of speciation (Midgley *et al.* in press). Bioclimatic modelling of the succulent Karoo and *fynbos* biomes has suggested that the *fynbos* biome was of much greater extent and covered much of Namaqualand ca. 18,000 ya. At the same time the succulent Karoo was of far lesser extent, extending further north into the southern and central coastal regions of Namibia (Midgley *et al.* in press). This model also identified areas of relictual retreats for succulents in the northern Cape (Richtersveld mountains), the Knersvlakte and the Tanqua Karoo, which were then completely surrounded by *fynbos*. This model further suggested that the warming between 15,000 – 12,000 ya and again at 6,000 ya led to an expansion of the succulent Karoo (Midgley *et al.* in press) along a North-South axis into the south-western Cape.

The model, however, still does not allow predictions to be made about the time of diversification of the taxa such as *Lampranthus*, *Oscularia*, *Esterhuysenia* and *Erepsia* that are found in the south-western Cape. On account of their only slightly xeromorphic features they may have existed in their present habitat for a very long time prior to the warming and aridification of the Cape Region. Although the “core” of

*Lampranthus* and *Erepsia* are among the most derived clades in the tree (Fig. 4. 5) adding more taxa, in particular the highly specialized ones of which only very few were sampled, may well re-arrange the topology. The model by Midgley *et al.* may be tested further by generating a phylogeny that incorporates a much broader range of taxa of succulent Aizoaceae.

### 5. 3. An agenda for future phylogenetic research in the Ruschioideae

Numerous questions concerning the genera of the *Lampranthus* – group were answered in this study, but most of the phylogenetic relationships among the ruschioid genera remain obscure. Several points are listed below which need to be taken into consideration for future phylogenetic research in the succulent Aizoaceae:

#### (A) The need for more comprehensive sampling

Thorough sampling will generally produce better estimates of phylogeny (Olmstead *et al.* 1992, 1993, Chase *et al.* 1993, Chase & Cox 1998). This study highlighted the need for an overview of the generic relationships among the Ruschioideae and the Mesembryanthemoideae. In such a broad phylogenetic study all genera should be sampled and special attention should be given to the very speciose genera (*Ruschia*, *Antimima*, *Drosanthemum*, *Delosperma*), which may represent polyphyletic assemblages.

Once an overview has been produced which identifies the higher groupings within the Ruschioideae, studies at lower taxonomic level can be approached more easily. For these, far denser sampling is needed in order to unravel the evolution of and the relationships among the taxa, as has become evident for the taxa placed in the *Lampranthus* – group. In this study parts of *Lampranthus* (*L. gydouwensis*, *L. sp. nov.*, *L. henricii* and *L. argenteus*) were shown to be more closely related to *Antimima* and species placed in the *Eberlanzia* – group. Both the *Eberlanzia* – group and *Antimima* have in the past been closely allied to *Ruschia* (Dehn 1988, Hartmann & Stüber 1993), with the latter genus only represented by two species in this study. Therefore further studies in the *Lampranthus* – group need to take all of these genera into consideration.

#### (B) Morphological studies

The present study highlights the need for more detailed morphological studies, in particular anatomical and palynological research. The recent discovery of wide-band tracheids in leaves of genera of Aizoaceae (Landrum 2001), suggests that detailed surveys of anatomical characters can yield very valuable phylogenetic information. Although many of the revisions of the succulent Aizoaceae include a study of the pollen morphology of the genus under study, there has been no survey across the entire Ruschioideae (Hartmann 1991). The discovery of a very similar pollen tectum in genera that are not closely related suggests that sections of the pollen should be prepared to facilitate primary homology assessment.

Particular attention should also be given to those structures that have frequently been used in the classification of the Aizoaceae. These are the structures found in the fruits (closing bodies, valve wings,

covering membranes) and the leaf epidermal characters. As very little developmental work on these morphological structures has been undertaken (e.g. floral development: Ihlenfeldt 1960, Haas 1976; leaf surface development: Niesler 1996), future ontogenetic research needs to investigate whether similar features are homologous.

### (C) Molecular studies

Although three gene regions were investigated in this study, the ITS and *trnL-F* region showed low numbers of phylogenetically informative sites compared with most studies in other groups using these gene regions (see chapter 2). However, the ITS region displayed a fairly high number of variable sites across the taxa sampled in the Ruschioideae. This suggests that further sampling among the genera in the Ruschioideae may increase the number of phylogenetically informative sites and thus help to resolve the deep to middle branches in the tree.

Since particularly the deep to middle branches lacked statistical support, a further gene region should be sampled. Several possibilities exist and future investigations may revolve around them.

(i) Particularly suitable may be the *rps16* intron, which is found in the large single-copy region of the chloroplast genome that codes for the ribosomal protein small subunit 16. The *rps16* displays two to three times lower sequence divergence than the ITS region and this would make it useful for taxonomic studies below family level and above species level (Lidén *et al.* 1997, Oxelman *et al.* 1997). For example, it has been found useful to resolve relationships of the genera within the tribe *Sileneae* in the Caryophyllaceae (Oxelman *et al.* 1997). Although, this gene was found to display relatively low levels of variation in the Calamoideae (Palmae), the major lineages could nevertheless be resolved (Baker *et al.* 2000b). In addition, in this case, when the data were combined with ITS gene sequences, a well-resolved and well-supported phylogeny was obtained (Baker *et al.* 2000b).

(ii) Comparative sequencing of the maturase-encoding chloroplast gene *matK* was shown to have high potential for reconstructing phylogenetic relationships not only at family, but also at generic level (Johnson & Soltis 1995). Although pairwise comparisons of two species of *Gilia* indicated on average a 1.9 - fold greater level of nucleotide differences per site in the ITS region compared to *matK*, the latter gene region has the potential to yield far more characters because of its greater length.

(iii) The regions flanking the *matK* gene, referred to as *trnK*, may also prove useful. Whereas the 5' flanking region showed slightly less variability than the *matK* gene itself, it was considerably higher for the 3' flanking region (Johnson & Soltis 1995). Recent studies in the Polygonaceae and the Fabaceae using these gene regions (or parts thereof) obtained well-resolved and well-supported clades (Ohsako & Ohnishi 2000, Lavin *et al.* 2001). Ohsako & Ohnishi used, in addition to the *trnK* region (including *matK*), a further region referred to as the *trnC* (GCA)-*rpoB* spacer. A combined analysis of these two gene regions was shown to be able to resolve the intra- and interspecific phylogeny within *Fagopyrum* (Ohsako & Ohnishi 2000).

#### (D) Molecular developmental research

A further promising area of research is molecular developmental biology which aims to understand how plant organs evolve (reviewed by Zimmer 1994, Endress *et al.* 2000). This area of research is rather recent and one of the first published studies dealt with the genetic control of floral development (Coen & Meyerowitz 1991). Since then, numerous other studies were dedicated to understanding genetic control of floral development and its implication for phylogenetic studies (e.g. Albert *et al.* 1998, Kramer & Irish 1999, Theissen & Saedler 1999). Most challenging in this regard is how to interpret the results of developmental genetics in order to better understanding of the driving forces of plant diversification and evolution (e.g. Gleissberg & Kadereit 1999, Graham *et al.* 2000, Iltis 2000).

Ihlenfeldt (1971 a, b, 1994) suggested that developmental genetics may in fact represent the key to the understanding of diversification in the succulent Aizoaceae. On account of studies in the Mitrophyllinae, where growth forms vary from medium-sized shrubs (e.g. *Mitrophyllum*, *Meyerophytum*) to highly reduced and sunken forms (e.g. *Oophytum*, *Diplosoma*), differences among species were attributed to differences in the timing of genes controlling the development of plant organs (e.g. Ihlenfeldt 1971a, b). The advances in molecular developmental research may allow one to test Ihlenfeldt's hypothesis.

This phylogenetic study of the *Lampranthus* – group constitutes a major contribution towards unravelling the relationships within this group. The results of this study reach far beyond proposing new generic limits and relationships for several genera. Their major contribution is an increased understanding of the evolution of morphological characters, in particular the fruit characters, where the level of homoplasy is far higher than had been anticipated. It has been revealed as well that the current classification of the succulent Aizoaceae probably does not reflect natural groups and this work sets the stage for a reinvestigation of the entire group.

## CHAPTER 6

### TAXONOMY

#### 6. 1. A revised classification of *Lampranthus* and the genera placed in the *Lampranthus* – group

The *Lampranthus* – group as circumscribed by Hartmann (1991) is clearly not monophyletic, since members of other groups turn out to be nested within it. Although a single tree was obtained in the total analysis (which included 52 taxa), most intergeneric relationships are very poorly supported. Adding more taxa or data may well change the topology and would then require further taxonomic changes. Therefore, based on the present study, it is not possible to establish which genera form the *Lampranthus* – group. Before the different elements of the *Lampranthus* – group can be assigned to their correct position, a much broader survey is needed and this was well outside the scope of the present study.

The cladistic analysis has shown that several genera (or parts thereof) that are currently or were previously placed in the *Lampranthus* – group are not monophyletic in their present circumscriptions and this is especially true of *Oscularia*, *Lampranthus* and *Braunsia*. In cases where both statistical support (JK > 74) and morphological characters suggests that a taxon belongs to a different genus, this transfer is made below. Therefore *Oscularia falciformis* is reinstated as *Lampranthus falciformis* and *Lampranthus mucronatus* is moved to *Esterhuysenia*. Based on the same reasoning, *Namaquanthus* is included in *Enarganthe*, and *Smicrostigma* is transferred to *Zeuktophyllum*.

However, in the cases of *Oscularia guthrieae*, *Braunsia vanrensburgii* and several species of *Lampranthus*, which were shown to be more closely related to some of the other taxa, there is neither high statistical support nor morphological support for their inclusion in any of the existing genera. The species of *Lampranthus* placed well outside the “core” of the genus occupy three well-supported clades. These are: (1) *L. amphibolius* and *L. sp. nov.*; (2) *L. henricii* and *L. argenteus*; (3) *L. aduncus* and *L. filicaulis*. This leads to the question of which monophyletic groups should be raised to generic level. Although there are no definite rules, several criteria have been put forward (Judd *et al.* 1999). The first criterion is the strength of support for the clade; the second is the presence of one or more obvious morphological characters to characterize the clade; a third criterion is the size of the group involved and a fourth is the need to create entities that are nomenclaturally stable.

For all three clades these criteria are considered to be fulfilled. The strength of support is very high for the first two clades and even for the third clade is still considered sufficiently high to distinguish it from other clades. All three clades have morphological characters by which they can be distinguished, and based on these morphological characteristics additional species can be transferred from *Lampranthus* to these clades. Furthermore, adding more taxa is unlikely to cause the nomenclatural collapse of these new entities. If these clades are not treated as separate genera, *Lampranthus* would be left paraphyletic. Since only monophyletic, but not paraphyletic groups are named in cladistic classification, the three clades and the

“core” of *Lampranthus* (i.e. that clade which contains the type of the genus) will be recognized at generic level.

However, in contrast to the above cases, *Oscularia guthrieae* and *Braunsia vanrensburgii*, are not part of any well-supported clade, which can be diagnosed by an obvious morphological character. In addition, further sampling within the Ruschioideae may well show that these taxa are part of other well-defined clades, which can be morphologically characterized. Although taxa with uncertain phylogenetic position are unsatisfactory, it is equally unsatisfactory to create new genera, in this case monotypic, for these two taxa. They are therefore listed at the end of their respective genera.

The species which constitute the “core” of *Lampranthus* are grouped into four informal sections, i.e. *Amoeni*, *Aurei*, *Scabridi* and *Tenuifolii* and a key is provided for these. The sections are unlikely to be monophyletic and are upheld only as an aid to users for identification. In order to test the monophyly of the sections complete sampling would be required, which may be attempted in a future study.

A revised taxonomic account for the species of *Lampranthus* is given below. A morphological survey of all the described species in *Lampranthus* has furthermore shown that numerous names are conspecific or that several species should be moved to other genera with which they share derived morphological character-states. Here the nomenclature and synonymy are listed and a short diagnosis, flowering time and distribution is given for each species. In total 68 species (including one subspecies) of *Lampranthus* are recognized. However, this account represents a conspectus only and includes several poorly known species, some of which are only known from the type. It is therefore not yet possible to present a key to the species. A revision of the genus may still lead to further taxonomic changes though they are unlikely major, and will consist mainly of a further reduction of the number of species that are recognized.

The exclusion or transfer of species necessitates re-circumscriptions of several genera and these are given below.

## 6. 2. New generic circumscriptions

**Braunsia** Schwantes, Gartenwelt 32: 644 (1928). Type: *Braunsia geminata* (Haw.) L.Bolus.

Dwarf erect or prostrate perennials. **Leaves** opposite, about equal, pair of leaves 1/4 to 1/2 of its length connate, crescent, trigonous, keeled, velvet-like or smooth, with white cartilaginous margin. **Flowers** solitary or in cymes, shortly pedicellate, about 4 cm diameter, pink or white, filamentous staminodes present, conically collected around the stamens and apically recurved, filaments bearded. Ovary more or less flattened, nectaries inconspicuous, in a ring. **Fruits** 5-locular, woody, lower part of capsule deeply bowl-shaped, covering membranes reduced without additional closing devices, expanding keels parallel, upper parts of keels broadened, with valve wings, closing body absent. **Seeds** short, echinate or papillate.

Species included:

*Braunsia apiculata* (Kensit) L.Bolus

*Braunsia geminata* (Haw.) L.Bolus

*Braunsia maximiliani* (Schltr. & A. Berger) Schwantes

*Braunsia stayneri* (L.Bolus) L.Bolus.

Insufficiently known species: *Braunsia nelii* Schwantes.

Species excluded: *Braunsia vanrensburgii* L.Bolus.

**Enarganthe** N.E.Br., Gard. Chron. 87: 71, 151 (1930), in key. Type: *Enarganthe octonaria* (L.Bolus) N.E.Br.

*Namaquanthus* L.Bolus, Notes Mesembryanthemum 3: 257 (1954). Type: *Namaquanthus vanheerdei* L.Bolus.

Erect shrubs, to 30 cm tall. **Leaves** free or shortly united at the base, trigonous or terete, obtuse, smooth, 3.5-6 cm long, 1-1.5 cm diam. **Flowers** solitary or ternate, shortly stalked, 5-6 cm diam. violet-red or purple, sepals 4, unequal, filamentous staminodes absent, filaments bearded. Ovary flat or convex, nectaries in a ring. **Fruits** 8-12 (-16)-locular, with covering membranes, with or without very small closing body, expanding keels parallel at base, later on diverging, ending in awns, with narrow valve wings. **Seeds** echinate or smooth.

**Enarganthe vanheerdei** (L.Bolus) Klak **comb. nov.** *Namaquanthus vanheerdei* L.Bolus, Notes Mesembryanthemum 3: 257 (1954). Type: Namaqualand, Steenbok, off the road between Spektakel and Port Nolloth, 6 Jul. 1953, *P. van Heerde sub BOL 25193* (BOL, holo.).

Species included:

*Enarganthe octonaria* (L.Bolus) N.E.Br.

*Enarganthe vanheerdei* (L.Bolus) Klak.

**Zeuktophyllum** N.E.Br., Gard. Chron. 81: 12 (1927, in key). Type: *Zeuktophyllum suppositum* (L.Bolus) N.E.Br.

*Smicrostigma* N.E.Br., Gard. Chron. 87: 186 (1930, in key). Type: *Smicrostigma viride* (Haw.) N.E.Br.

Low shrubby perennials, branches succulent, becoming woody with age. **Leaves** opposite, united at the base and continuous with the stem, 3-angled, margins smooth or with minute teeth towards the apex, glabrous, free parts 0.5-3.0 cm long. **Flowers** solitary, terminal, sessile, 2.5-3.0 cm diam., straw yellow, white or pale pink, filamentous staminodes numerous, conically collected and apically recurved. Ovary top flattish, nectaries in a ring. **Fruits** 7-10-locular, without or with very narrow wings, contiguous at the basal part, with diverging

acute or awned tips without marginal wings, covering membranes present, without additional closing device, closing body absent. **Seeds** minutely tuberculate or smooth, blackish or brown.

**Zeuktophyllum viride** (Haw.) Klak **comb. nov.** *Smicrostigma viride* (Haw.) N.E.Br., Gard. Chron. 87: 186 (1930, in key). *Ruschia viridis* (Haw.) G. D. Rowley, Cact. Succ. J. (US) 33: 9 (1978).

*Mesembryanthemum viride* Haw., Obs. Gen. Mesemb.: 314 (1795). Type: missing.

*Ruschia integra* (L.Bolus) Schwantes, Zeitschr. Sukkulantenk. 2: 187 (1926). *Mesembryanthemum integrum* L.Bolus, Ann. Bolus Herb. 3: 134 (1922). Type: Robertson div., Ashton, Nov. 1921, *F. A. Rogers sub BOL 17175* (BOL, holo.).

*Erepsia viridis* L.Bolus, Flowering Pl. S. Africa 7: t 270 (1927). Type: Flowering Pl. S. Africa 7: t 270.

Species included:

*Zeuktophyllum calycinum* (L.Bolus) H.E.K.Hartmann

*Zeuktophyllum suppositum* (L.Bolus) N.E.Br.

*Zeuktophyllum viride* (Haw.) Klak.

**Esterhuysenia** L.Bolus, J. S. African Bot. 33: 308 (1967). Type: *Esterhuysenia alpina* L.Bolus.

Low, often compact shrubs or cushions, to 30 cm tall. **Leaves** free or fused into a sheath to 8 mm long, trigonous to terete, with a prominent mucro or at least shortly acuminate, yellowish or reddish green, old leaves often persistent and drying up on the stem, smooth, with distinct crystal layer in outer epidermis wall, epidermal bladder cells completely flattened, stoma not sunken or sunken. **Flowers** solitary or rarely 2-3, bracteoles midway on the pedicel or below, embracing the calyx, white or purple, 1.7-4.0 cm diam., filamentous staminodes absent or present; nectaries in a ring. **Fruits** upper part flattened, lower part usually bowl-shaped or funnel-shaped, with keels parallel at base and later diverging, covering membranes with closing ledge, closing body absent, valve wings very narrow (often disintegrating with age) to moderately narrow 5(-6)-locular. **Seeds** brown, testa cells convex.

**Esterhuysenia mucronata** (L.Bolus) Klak **comb. nov.** *Lampranthus mucronatus* L.Bolus, J. S. African Bot. 32: 201 (1966). Type: Cape, Ceres Karoo, 15 miles west of Skitterykloof, Sep. 1965, *Stayner sub KG 998/61* (BOL, holo.).

Compact shrublet, to 15 cm tall. Leaves fused into a sheath to 8 mm long, apiculate, 2-3.5 cm long, 5 mm diam. Flowers solitary, sessile or pedicels 5 mm long, white, to 4 cm diam., without filamentous staminodes. Sep. On sandstone; Katbakkies, Cedarberg.

Species included:

*Esterhuysenia alpina* L.Bolus

*Esterhuysenia drepanophylla* (Schltr. & A.Berger) H.E.K.Hartmann

*Esterhuysenia inclaudens* (L.Bolus) H.E.K.Hartmann

*Esterhuysenia mucronata* (L.Bolus) Kläk

The genus consisted until recently of a single species, *E. alpina* L.Bolus. In a recent treatment the genus was amended to contain four species (Hartmann 1998a). The species are, however, still little known and confusion has arisen about the identity of *E. alpina*. In several publications the far more common *E. drepanophylla* (Schltr. & A.Berger) H.E.K. Hartmann, has been misidentified as *E. alpina* (Hartmann 1998a: 82, fig. 49; Smith et al. 1998: 281). The two species differ in their leaves (larger in *E. drepanophylla*) and in their floral morphology. In particular, *E. alpina* does not possess any filamentous staminodes, whereas *E. drepanophylla* has its filamentous staminodes collected into a cone around the stamens.

**Oscularia** Schwantes, Möller's Deutsche Gärtn.-Zeitung 42: 187 (1927). Type: *Oscularia deltoides* (Haw.) Schwantes.

Small subshrubs with erect or spreading branches. **Leaves** trigonous, thicker than broad, keeled, dentate in some species, glaucous from a thick covering of wax, crystal layer absent, with slightly convex epidermal bladder cells, to 2 cm long, 1.3 cm broad. **Flowers** in aggregate inflorescences, shortly pedicelled, white or pink, to 15 mm diam., filamentous staminodes and stamens conically collected, flowers remain open after anthesis; nectaries consisting of 5 distinct glands or in a ring with raised areas. **Fruits** base funnel-shaped, top raised, covering membranes complete with an inconspicuous closing ledge, closing body absent, keels diverging, broadened, valve wings broad and rectangular, locules 5. **Seeds** brown or black, testa cells with central papillae raised.

Three names at present listed under *Lampranthus* are transferred to *Oscularia*:

1. *Lampranthus comptonii* (L.Bolus) N.E.Br. var. *angustifolius* (L.Bolus) L.Bolus ex H. Jacobsen, Feddes Repert. Beih. 106: 98 (1938).

Hartmann (1998a) transferred all forms and varieties of *Lampranthus comptonii* to *Oscularia*, except for the variety *angustifolius*. A water colour painting of the type of this variety by M. Page in the Bolus Herbarium shows the typical floral features found in species of *Oscularia* (i.e. flowers which are arranged in aggregate inflorescences, with their filamentous staminodes and stamens conically collected). The type specimen of the variety and the illustration of it agree well with the type of *Lampranthus comptonii* and consequently the variety *angustifolia* is considered to be conspecific with *Oscularia comptonii*.

2. *Lampranthus ebracteatus* L.Bolus, J. S. African Bot. 28: 294 (1962).

This species has so far been included in *Lampranthus* Section *Lunati*. Although Hartmann (1998a)

moved all other names from this section to *Oscularia*, this name was left in *Lampranthus*. However, the species belongs in *Oscularia* as it possesses the features described above as typical for *Oscularia*.

Furthermore, the overall similarity in leaf, flower and fruit characters suggests that it is conspecific with *Oscularia comptonii*. A complete list of synonyms for *Oscularia comptonii* is given below.

### 3. *Lampranthus profundus* (L.Bolus) H.E.K.Hartmann

On account of the presence of valve wings and the absence of a closing body, *Ruschia profunda* L.Bolus had been transferred by Hartmann (1998a) to *Lampranthus*. The species is only known from the type collection. However, a water-colour painting by M. Page of the type specimen is lodged at BOL. The illustration shows that there is a striking similarity between this species and species of *Oscularia*, both in terms of leaf and floral morphology: the leaves are trigonous, lunate and apically serrated. In addition, the flowers are arranged in cymes, with their filamentous staminodes conically collected. These characteristics clearly exclude it from *Lampranthus*. Interestingly, the nectaries are described by L.Bolus and painted by M. Page as an inconspicuous holonectary with a few raised areas. Although for most species of *Oscularia* a meronectary is typical, a few species (e.g. *O. cedarbergensis*, *O. alba*) have a holonectary with a few raised areas, suggesting an intermediate position between a mero- and a holonectary. Also unusual are the fairly narrow valve wings found in *L. profundus*, whereas species of *Oscularia* have large valve wings. However, since the morphology of valve wings can vary considerably within a genus (e.g. *Erepsia*, Liede 1989), *L. profundus* is still considered to form part of *Oscularia*. The new combination with synonymy is given below.

***Oscularia comptonii*** (L.Bolus) H.E.K. Hartmann, *Bradleya* 16: 76 (1998). *Lampranthus comptonii* (L.Bolus) N.E.Br., *Gard. Chron. ser. 3*, 87: 212 (1930). *Mesembryanthemum comptonii* L.Bolus, *Ann. Bolus Herb.* 3: 162 (1923). Type: Klawer, Jul. 1923, *Compton sub NBG 295/22* (BOL, holo.).

*Lampranthus comptonii* f. *roseus* (L.Bolus) G.D. Rowley, *Natl. Cact. Succ. J.* 13: 77 (1958). *Lampranthus comptonii* var. *roseus* (L.Bolus) L.Bolus ex H. Jacobsen, *Feddes Repert. Beih.* 106: 96 (1938). *Mesembryanthemum comptonii* var. *roseum* L.Bolus, *Notes Mesembryanthemum* 2: 409 (1933). Lectotype (designated here): Clanwilliam, *Herre 8566* (BOL).

*Lampranthus comptonii* var. *angustifolius* (L.Bolus) L.Bolus ex H. Jacobsen, *Feddes Repert. Beih.* 106: 98 (1938). *Mesembryanthemum comptonii* var. *angustifolium* L.Bolus, *Notes Mesembryanthemum* 2: 409 (1933). Type: Cape, near Springbok, *Herre sub SUG 8997* (BOL, holo.).

*Lampranthus ebracteatus* L.Bolus, *J. S. African Bot.* 28: 294 (1962). Type: Cape, Vanrhynsdorp distr., Papendorp, Nov. 1961, *H. Hall sub NBG 613/57* (BOL, holo.).

***Oscularia profunda*** (L.Bolus) Klak **comb. nov.** *Lampranthus profundus* (L.Bolus) H.E.K. Hartmann, *Bradleya* 16: 70 (1998). *Ruschia profunda* L.Bolus, *Notes Mesembryanthemum* 3: 16 (1936).

Type: Piquetberg distr., Piquetberg mountain, Kapitein's Kloof, Sep. 1935, *Pillans 7711* (BOL, holo.).

Species included:

*Oscularia alba* (L.Bolus) H.E.K.Hartmann  
*Oscularia caulescens* (Miller) Schwantes  
*Oscularia cedarbergensis* (L.Bolus) H.E.K.Hartmann  
*Oscularia compressa* (L.Bolus) H.E.K.Hartmann  
*Oscularia comptonii* (L.Bolus) H.E.K.Hartmann  
*Oscularia copiosa* (L.Bolus) H.E.K.Hartmann  
*Oscularia deltoides* (L.) Schwantes  
*Oscularia excedens* (L.Bolus) H.E.K.Hartmann  
*Oscularia lunata* (Willd.) H.E.K.Hartmann  
*Oscularia major* (Weston) Schwantes  
*Oscularia ornata* (L.Bolus) H.E.K.Hartmann  
*Oscularia paardebergensis* (L.Bolus) H.E.K.Hartmann  
*Oscularia pedunculata* (N.E.Br.) Schwantes  
*Oscularia piquetbergensis* (L.Bolus) H.E.K.Hartmann  
*Oscularia prasina* (L.Bolus) H.E.K.Hartmann  
*Oscularia primiverna* (L.Bolus) H.E.K.Hartmann  
*Oscularia profunda* (L.Bolus) Klak  
*Oscularia steenbergensis* (L.Bolus) H.E.K.Hartmann  
*Oscularia superans* (L.Bolus) H.E.K.Hartmann  
*Oscularia thermarum* (L.Bolus) H.E.K.Hartmann  
*Oscularia vernicolor* (L.Bolus) H.E.K.Hartmann  
*Oscularia vredenburgensis* (L.Bolus) H.E.K.Hartmann.

Species excluded:

*Oscularia falciformis* = ***Lampranthus falciformis***

The transfer of *L. falciformis* to *Oscularia* by Hartmann (1998a) appears to be based on misidentified material. The drawing by Duncanson at Kew, which Hartmann selected as the lectotype, matches neither her description nor the photograph she cites (Hartmann 1998a: 83, Fig. 60) for *Oscularia falciformis*. However, the specimen on the photograph (Hartmann's Fig. 60) possesses flowers typical of *Oscularia*, where the stamens and staminodes are conically collected. This is not true of Duncanson's lectotype, which matches in all characteristics the species traditionally known as *Lampranthus falciformis*: this has 1-3 flowered inflorescences and flowers without any filamentous staminodes.

*Oscularia guthrieae* (L.Bolus) H.E.K. Hartmann, *Bradleya* 16: 77 (1998). *Lampranthus guthrieae* (L.Bolus) N.E.Br., *Gard. Chron.*, ser. 3, 87: 212 (1930). *Mesembryanthemum guthrieae* L.Bolus, *Ann. Bolus Herb.* 4: 101 (1927). Type: Cape, Ceres Flower Show, 4 Oct. 1926, *L. Guthrie sub BOL 18531* (BOL, holo.).

In the following account each species recognized is provided with a synonymy, a brief diagnostic description (or how it differs from closely related species) after which flowering time, ecology and distribution are listed. A question mark indicates that the relevant information is unknown.

**Cornigeria Klak gen. nov.**, a *Esterhuysenia carinis in fructibus latioribus et parte inferiore capsulae tubata differt*; a *Lamprantho foliis fere cylindricis subulatis aduncis distinguenda est*. Type: *Cornigeria adunca* (Haw.) Klak.

Slender shrubs with decumbent or spreading branches, to 30 cm tall, or prostrate and creeping, with short erect flowering branchlets, 3-10 cm long. Roots fibrous. Stems brown, smooth or slightly scabrid, rooting at nodes. **Leaves** free or shortly fused towards bases, crowded at the tips of the branches, curved inwards and recurved at the tip, semi-cylindrical to almost cylindrical in cross-section, to 25 mm long, 1-4 mm diam., epidermal bladder cells much flattened, dark green, often reddish. **Flowers** solitary, pedicels 10-50 mm long, top of ovary raised or nearly flattened, filamentous staminodes and stamens conically collected, 2-3 cm diam., reddish or pink, coppery red reverse; stigmas either thick or slender; nectaries in a conspicuous ring. **Fruits** 5-locular, deep, trumpet-shaped, keels diverging, valve wings narrow or broad, without closing body. **Seeds** brown, with flattened or raised testa cells.

*Ecology*: Flowering time from April to August. Usually on shale, in seasonally wet depressions.

*Distribution*: Clanwilliam, Tulbagh to Cape Town.

Species included: 3

Note: The genus is largely identical with the species formerly placed in *Lampranthus* Sect. *Adunci*.

**Cornigeria adunca** (Haw.) Klak, **comb. nov.** *Lampranthus aduncus* (Haw.) N.E.Br., *Gard. Chron.*, ser. 3, 87: 211 (1930). *Mesembryanthemum aduncum* Willd., *Enum. Pl.* 534 (1809), *nom. illegit.* *Mesembryanthemum aduncum* Haw., *Misc. Nat.*: 87 (1803). Lectotype (designated here): Watercolour original by T. Duncanson (920) (K!).

*Lampranthus curvifolius* (Haw.) N.E.Br., *Gard. Chron.*, ser. 3, 87: 212 (1930). *Mesembryanthemum curvifolium* Haw., *Misc. Nat.*: 88 (1803). Lectotype (designated here): Cape Town, Hout Bay, June 1915, *J. W. Mathews 1650/15* (BOL). A watercolour painting by M. Page (plate 1874) of this specimen is lodged at BOL.

*Mesembryanthemum ceratophyllum* Willd., Enum. Pl. Hort. Berol. Suppl.: 36 (1813). Type: missing.

*Lampranthus curvifolius* var. *minus* (Salm-Dyck) G.D.Rowley, Natl. Cact. Succ. J. 13: 77 (1958).

*Mesembryanthemum curvifolium* var. *minus* Salm-Dyck, Monogr.: § 47 (1836). Lectotype (here designated): Monogr.: § 47, 2 (1836).

*Lampranthus flexifolius* (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum*

*flexifolium* Haw., Suppl. Pl. Succ.: 96 (1819). Lectotype (designated here): Watercolour original by T. Duncanson (K!).

*Mesembryanthemum flexifolium* var. *perviride* Haw., Rev. Pl. Succ.: 153 (1821). Type: missing.

*Lampranthus wordsworthiae* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum*

*wordsworthiae* L.Bolus, Ann. Bolus Herb. 3: 126 (1922). Type: Cape, mountains near Sir Lowry's Pass, Aug. 1919, *R. Wordsworth sub NBG 1899/17* (BOL, holo.).

Low shrub with erect or spreading branches, stems often rough. Leaves fused towards bases, crowded at the tips of branches, with short shoots in axils, tapering, spreading and recurved at the tip, 15-28 mm long, 3-5 mm thick, smooth. Flowers solitary, terminal, to 18-27 mm diam., red, stigmas long and slender, top of ovary raised. Fruits with broad valve wings. Apr.-Jul. At c. 500 m; Clanwilliam to Cape Town.

**Cornigeria spiniformis** (Haw.) Klak, **comb. nov.** *Lampranthus spiniformis* (Haw.) N.E.Br., Gard. Chron.,

ser. 3, 87: 212 (1930). *Mesembryanthemum spiniforme* Haw., Obs. gen. Mesemb.: 240 (1795). Lectotype (designated here): Monogr.: § 47, 1 (1836).

*Lampranthus inconspicuus* (Haw.) Schwantes ex H.Jacobsen, Feddes Repert. Spec. Nov. Regni. Veg. 43:

229 (1938). *Mesembryanthemum inconspicuum* Haw., Till. Phil. Mag. 68: 128 (1826). Lectotype (designated here): Watercolour original by T. Duncanson (993) (K!).

*Lampranthus nelii* L.Bolus, J. S. African Bot. 31: 308 (1965). Type: Cape, Fisantekraal, July 1965, *Nel sub BOL 27732* (BOL, holo.).

Very similar to *L. aduncus*, but leaves more slender. Flowers with thick and short stigmas, top of ovary flattened. Fruits with narrow valve wings. May-Jun. In disturbed spots, Clanwilliam to Cape Town.

**Cornigeria filicaulis** Klak, **comb. nov.** *Lampranthus filicaulis* (Haw.) N.E.Br., Gard. Chron., ser. 3, 87:

212 (1930). *Mesembryanthemum filicaule* Haw., Misc. Nat.: 87 (1803). Lectotype (designated here): Watercolour original by T. Duncanson (949) (288) (K!).

Mat-forming succulent, to 10 cm. Leaves crowded at the tip of the branches, curved inwards and recurved at the tip, to 25 mm long, 3 mm diam., smooth. Flowers solitary, on long pedicels to 10 cm long, to 20 mm diam., rose to magenta, filamentous staminodes gathered into a cone around the stamens. Fruits c. 6 mm diam. Jun.-Jul. In damp or wet depressions overlaying Ouklip; Tulbagh to Peninsula and Cape Flats.

**Pustulesia** Klak **gen. nov.**, a *Ruschia*, *Eberlanzia*, *Octopomaque tuberculo absentis*; a *Lamprantho foliis papillatis connatisque strato crystallino subepidermali differt*. Type: *Pustulesia unca* (L.Bolus) Klak.

Erect stiffly branched woody shrubs, to 60 cm tall or rarely prostrate and trailing, with fibrous roots.

**Stems** brown, smooth. **Leaves** fused basally into a short sheath, free parts trigonous to half-cylindrical, minutely papillate, apiculate and apically recurved, with a distinct subepidermal crystal layer. **Flowers** solitary or in cymes, short pedicelled with bracts, filamentous staminodes few or numerous, usually two-coloured and conically collected with stamens, petals pink or white; nectaries in a ring. **Fruits** 5-locular, lower part of fruit bell-shaped, rarely funnel-shaped, with large rectangular valve wings, covering membranes with additional appendages, keels usually parallel at base, later diverging, without closing body. **Seeds** brown, papillate.

Most of the species listed below had been placed by L. Bolus in *Amphibolia*. Several species currently included in *Ruschia* are also considered to form part of this group and are listed below. Numerous species are poorly known, so that the list given here forms the basis for future investigations.

A. *Leaves thick (to 6 mm diam.)*

**Pustulesia amphibolia** (G.D. Rowley) Klak, **comb. nov.** *Lampranthus amphibolius* (G.D. Rowley)

H.E.K. Hartmann, *Bradleya* 16: 67 (1998). *Ruschia amphibolia* G.D. Rowley, *Natl. Cact. Succ. J.* 33: 7 (1978). *Amphibolia hallii* (L. Bolus) L. Bolus, *J. S. African Bot.* 31: 169 (1965), *comb. invalid.* *Amphibolia hallii* (L. Bolus) L. Bolus ex Toelken & Jessop, *Bothalia* 12: 64 (1976). *Stoeberia hallii* L. Bolus, *J. S. African Bot.* 26: 161 (1960). Type: Ceres distr., Karooport, 8 Jul. 1959, *H. Hall 1741* (BOL, holo.).

Plant creeping, stems to 30 cm long. Leaves connate for 3-4 mm, free parts 20-35 mm long, 4-6 mm diam., almost terete, tapered, papillate. Flowers solitary, pedicels 15-25 mm long, to 35 mm diam., pink, hardly any filamentous staminodes. Fruits as for genus. Jul. Among rhenoster vegetation; Karooport.

**Pustulesia franciscii** (L. Bolus) Klak, **comb. nov.** *Lampranthus franciscii* L. Bolus, *J. S. African Bot.* 27: 113 (1961). Type: Cape, Karooport, Nov. 1960, *Stayner sub KG 240/60* (BOL, holo.).

Erect robust shrub to 60 cm tall and 90 cm diam. Leaves fused at their bases into a sheath for 4-5 mm, 25-40 mm long, 3-6 mm thick and wide, shortly tapered, papillate, pale green, velvety. Flowers in a 3-4-partite inflorescence, pedicels 3-10 mm long, 30-45 mm diam., pink, without filamentous staminodes. Fruits as for genus. Oct.-Nov. ?, Ceres.

**Pustulesia incumbens** (L. Bolus) Klak, **comb. nov.** *Ruschia incumbens* L. Bolus, *Notes*

*Mesembryanthemum* 2: 212 (1930). Type: Clanwilliam distr., betw. Klawer and Clanwilliam, Apr.

1929, *Leipoldt sub BOL 19246* (BOL, holo.).

*Lampranthus gydouwensis* L.Bolus, J. S. African Bot. 29: 13 (1963). *Amphibolia gydouwensis* (L.Bolus) L.Bolus, J. S. African Bot. 33: 306 (1967), *comb. invalid.* *Amphibolia gydouwensis* (L.Bolus) L.Bolus ex Toelken & Jessop, Bothalia 12: 64 (1976). Type: Cape, Gydo Pass, Oct. 1939, *Leipoldt 4801* (BOL, holo.).

Shrub to 38 cm tall, with stems to 1 cm diam. Leaves fused, sheath to 3.5 mm long, apiculate, to 35 mm long, 3-4 mm diam, papillate. Flowers in a many-flowered inflorescence. 18 mm diam., purple, filamentous staminodes and stamens conically collected. Fruits as for genus. Oct. ?; Clanwilliam area. Note: Hartmann (1999) retained *Ruschia incumbens* in *Ruschia*, since there were no fruits on the type. In this study *Ruschia incumbens* was found to agree in fruit, floral and leaf morphology with *Lampranthus gydouwensis*, so that they are regarded as conspecific.

***Pustulesia mentiens* Klak, sp. nov.**, a *P. franciscii foliis brevioribus et connatis brevius discedit*, a *P. incumbenti foliis latioribus et fructibus grandioribus differt*. Type: Western Cape Province, Ceres Karoo, Vaalkloof near Karoopoort, 1 May 1998, *Klak 417a* (BOL, holo.).

Plants erect, 25-35 cm tall. Stems dark brown, smooth; internodes 2.5-4.0 cm long. Leaves shortly fused, semi-cylindrical, mucronate, with recurved tips, 13-25 mm long, 4-6 mm broad and thick., velvety. Flowers in a few-flowered inflorescence, pedicels to 12 mm long with bracts positioned midway, otherwise unknown. Fruits as for genus. ? On sandstone, Ceres Karoo, Cedarberg.

Etymology: The epithet "*mentiens*" refers to the similarity of this species to *P. franciscii*.

#### B. Leaves slender

***Pustulesia dissimilis* (G.D. Rowley) Klak, comb. nov.** *Lampranthus dissimilis* (G.D.Rowley)

H.E.K.Hartmann, *Bradleya* 16: 67 (1998). *Ruschia dissimilis* G.D.Rowley, *Natl. Cact. Succ. J.* 33: 62 (1978). *Amphibolia stayneri* L.Bolus ex Toelken & Jessop, *Bothalia* 12: 64 (1976). *Amphibolia stayneri* L.Bolus, J. S. African Bot. 32: 126 (1966), *nom. illegit.* Type: Ceres div., between Matroosberg and Theronsberg Pass, 4000 ft., Sep. 1965, *Stayner sub KG 258/65* (BOL, holo.).

Plant to 7 cm tall, branches slender, root tuberous to 6 cm long. Leaves fused into a short sheath to 1.5 mm long, acute, papillate, green, 17 mm long, 1.5-2 mm diam. Flowers solitary, pedicels 5-10 mm long, to 2 cm diam., filamentous staminodes and stamens conically collected. Fruits with moderately broad valve wings. Sep. In sandstone; Ceres.

Note: Based on the tuberous rootstock and the lack of a additional closing device below the covering membranes, this species was thought to be a possible close relative to *Mestoklema* (Hartmann & Dehn 1989). However, species of *Mestoklema* have outsized bladder idioblasts, whereas the epidermis found in *Pustulesia dissimilis* has the unusually sculptured leaves typical for this genus.

**Pustulesia persistens** (L.Bolus) Klak, **comb. nov.** *Lampranthus persistens* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum persistens* L.Bolus, Notes Mesembryanthemum 2: 235 (1931). Type: Calvinia distr., Grasberg, near Nieuwoudtville, Oct. 1930, Mathews sub BOL 19383 (BOL, holo.).

*Lampranthus arenicola* L.Bolus, J. S. African Bot. 30: 38 (1964). Type: Cape, south of the Witteberg, Nov. 1963, Esterhuysen 30524 (BOL, holo.; K).

Erect shrub, to 25 cm tall, with stiffly erect slender branches. Leaves fused towards bases, erect, tips conspicuously recurved, to 25 mm long, papillate. Flowers in a many-flowered dichasium, pedicels 25-40 mm long, to 14 mm diam., purplish, filamentous staminodes and stamens collected into a cone, smooth. Fruits as for genus. Oct.-Nov. Sandy valley; Grasberg, near Nieuwoudtville, Witteberg.

**Pustulesia unca** (L.Bolus) Klak, **comb. nov.** *Lampranthus uncus* (L.Bolus) Schwantes, Natl. Cact. Succ. J. 4: 58 (1949). *Ruschia unca* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 220 (1950). *Mesembryanthemum uncum* L.Bolus, Notes Mesembryanthemum 1: 136 (1928). Type: Cape, Nieuwoudtville, Dec.-Feb., Compton sub NBG 2275/25 (BOL, holo.).

*Lampranthus uncus* var. *gydouwensis* (L.Bolus) Schwantes, Natl. Cact. Succ. J. 4: 58 (1949).

*Mesembryanthemum uncum* var. *gydouwense* L.Bolus, Notes Mesembryanthemum 3: 55 (1937). Type: Cape, Gydouw Pass, Sep. 1936, G.J. Lewis sub BOL 21821 (BOL, holo.).

*Lampranthus dubitans* L.Bolus, Notes Mesembryanthemum 3: 168 (1939). *Ruschia dubitans* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 220 (1950). *Mesembryanthemum dubitans* L.Bolus, Notes Mesembryanthemum 2: 119 (1929). Type: Ceres distr., at foot of Matroosberg, fl. Jun.-Jul. 1929, Cook sub NBG 1459/24 (BOL, holo.).

*Lampranthus francesiae* H.E.K Hartmann, Bradleya 16: 68 (1998). *Ruschia leightoniae* L.Bolus, Notes Mesembryanthemum 2: 499 (1935). Type: Clanwilliam distr., Kromme Rivier, Cedarbergen, Sep. 1934, Leighton sub BOL 21422 (BOL, holo.).

*Lampranthus marginatus* (L.Bolus) H.E.K. Hartmann, Bradleya 16: 68 (1998). *Ruschia marginata* L.Bolus, Notes Mesembryanthemum 2: 500 (1935). Type: Clanwilliam distr., near Pakhuis, Sep. 1933, L. Bolus sub NBG 1505/33 (BOL, holo.).

Erect shrub, branches spreading, elongated, 25 cm long. Leaves fused into a short sheath for 2-3 mm, apiculate, 10-25 mm long, 3 mm wide and thick, set with small papillae. Flowers solitary or 1-2, pedicels 5 mm long, 18 mm diam., pale pink, filamentous staminodes and stamens conically collected. Sep. ?; Nieuwoudtville to Clanwilliam.

**Ruschiella** Klak **gen. nov.**, a *Ruschia carinis longis et valvis capsulae expansae alatis*; a *Pustulesia foliis laevibus libris breviter connatusve*; a *Lamprantho strato crystallino subepidermali carinisque*

*angustioribus distinguenda est.* Type: *Ruschiella lunulata* (A.Berger) Klak.

Erect loosely branched and spreading shrubs, to 1 m tall, with fibrous roots. **Leaves** free or very shortly fused to bases, usually obtusely trigonous, rarely trigonous to subfalcate with serrulate keel, epidermal bladder cells much flattened, subepidermal crystal layer present. **Flowers** solitary or in a few to many-flowered inflorescence, pedicels 5-15 mm long, 8-17 mm diam., filamentous staminodes two-coloured and conically collected around stamens; nectaries in ring. **Fruits** with bell-shaped lower parts, upper part raised, rims low, 4-5 mm diam., covering membranes convex with rodlet-shaped appendages, without closing body, occasionally with small placental knob, valve wings broad or rarely narrow, rectangular, expanding keels long and rather narrow, diverging from base. **Seeds** ochre, smooth.

**Ruschiella argentea** (L.Bolus) Klak, **comb. nov.** *Lampranthus argenteus* (L.Bolus) L.Bolus, J. S. African Bot. 33: 306 (1967). *Mesembryanthemum argenteum* L.Bolus, Ann. Bolus Herb. 4: 8 (1925).

Type: Clanwilliam distr., Graafwater, *Compton sub NBG 962/22* (BOL, holo.).

*Lampranthus montaguensis* (L.Bolus) L.Bolus, J. S. African Bot. 33: 306 (1967). *Mesembryanthemum montaguense* L.Bolus, Ann. Bolus Herb. 4: 9 (1925). Type: near Montagu, 800 ft., fl. Aug., *Page sub BOL 17692* (BOL, holo.).

*Lampranthus nardouwensis* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum nardouwense* L.Bolus, Notes Mesembryanthemum 2: 407 (1933). Type: Clanwilliam distr., Nardouw Pass, about 5 miles from the road between Clanwilliam and Klawer, 5 Aug. 1933, *Salter 3531* (BOL, holo.).

Small shrublets to 23 cm tall, with spreading branches. Leaves free towards bases, 2 cm long, 3-4.5 mm broad, glaucous. Flowers ternate, pedicels 5-7 mm long, ca. 12 mm diam., pale pink or white, filamentous staminodes white with pink tips. Fruit base bell-shaped, covering membranes with small closing rodlets, valve wings broad and rectangular. May-Aug. On sandstone, Clanwilliam to Paarl, Montagu.

**Ruschiella henricii** (L.Bolus) Klak, **comb. nov.** *Lampranthus henricii* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum henricii* L.Bolus, Ann. Bolus Herb. 3: 168 (1924).

Lectotype (designated here): Cape, Koudeberg near Wupperthal, 5 Oct. 1897, *Bolus 9006* (BOL).

*Lampranthus mariae* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum mariae* L.Bolus, Notes Mesembryanthemum 2: 329 (1932). Type: Ceres distr., Oct. 1931, *M. Lavis sub NBG 1764/31* (BOL, holo.).

Stiff, erect shrublet, to 20 cm, internodes black with age. Leaves inclined, falcate, blunt to acute, glaucous, 7 mm long, 1.5 mm thick. Flowers solitary, 14 mm diam., purplish. Fruit base bell-shaped, covering membranes with small closing rodlets, valve wings broad and rectangular. Sep.-Oct. Sandy slopes; Cedarberg and Ceres Karoo.

**Ruschiella lapidicola** (L.Bolus) Klak, **comb. nov.** *Ruschia lapidicola* L.Bolus, Notes Mesembryanthemum 3: 283 (1954). Type: Clanwilliam distr., Pakhuis Peak, "stony soil and rock basins", alt. 3500 foot. Sep. 1953, *Esterhuysen 21720* (BOL, holo.).

Freely branched shrub to 30 cm tall. Leaves free towards bases, falcate, acute, bluntly keeled, 9-15 mm long, 3-6 mm diam., smooth. Flowers 1-3, pedicels 6-15 mm long, 15 mm diam., magenta, filamentous staminodes and stamens conically collected. Fruits with narrow valve wings, very small placental closing body. Sep. Among rocks, in sandstone, Nieuwoudtville to Clanwilliam.

**Ruschiella lunulata** (A.Berger) Klak, **comb. nov.** *Lampranthus lunulatus* (A.Berger) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum lunulatum* A.Berger, Bot. Jahrb. Syst. 57: 638 (1922). Type: Cape, Olifants River west of Clanwilliam, 3 Sep. 1900, *Diels 344* (B, holo.).

*Lampranthus edwardsiae* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum edwardsiae* L.Bolus, Ann. Bolus Herb. 3: 163 (1923). Type: Clanwilliam distr., Oliphant's River Valley 1914, *Edwards sub NBG 2600/14* (BOL, holo.).

*Mesembryanthemum capornii* f. *fera* L.Bolus, Notes Mesembryanthemum 2: 405 (1933). Type:

Clanwilliam distr., near the road between Pakhuis Pass and Oumuur, Sep. 1933, *L. Bolus sub BOL 20764* (BOL, holo.).

*Mesembryanthemum capornii* var. *longifolium* L.Bolus, Notes Mesembryanthemum 2: 405 (1933). Type: Vanrhynsdorp distr., near Klawer, among rocks, Aug. 1932, *L. Bolus sub NBG 1947/32* (BOL, holo.).

*Lampranthus convexus* L.Bolus, Notes Mesembryanthemum 3: 168 (1939). *Mesembryanthemum convexum* L.Bolus, Notes Mesembryanthemum 2: 18 (1928). Type: Tulbagh distr., between town and waterfall, *Hutchinson 406*. Fl. Sep. 1928. (BOL, holo.).

*Lampranthus arenarius* H.E.K. Hartmann, *Bradleya* 16: 67 (1998). *Ruschia arenosa* L.Bolus, Notes Mesembryanthemum 2: 411 (1933). Type: Calvinia distr., in sand, Oorlog's Kloof, near Nieuwoudtville, Sep. 1930, *L. Bolus sub BOL 19304* (BOL, holo.).

*Lampranthus hiemalis* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum hiemale* L.Bolus, Notes Mesembryanthemum 2: 189 (1930). Type: Clanwilliam distr., near the road between Clanwilliam and Vanrhynsdorp, Apr. 1929, *Leipoldt sub BOL 19117* (BOL, holo.).

*Lampranthus pakpassensis* H.E.K. Hartmann, *Bradleya* 16: 70 (1998). *Ruschia pakhuisensis* L.Bolus, Notes Mesembryanthemum 2: 414 (1933). Type: Clanwilliam distr., Pakhuis Pass, on summit, Sep. 1933, *L. Bolus sub BOL 20749* (BOL, holo.).

*Lampranthus pleniflorus* L.Bolus, J. S. African Bot. 28: 293 (1962). Type: Cape, De Doorns, Jun.--July 1962, *P.A.B. van Breda sub NBG 1710/62* (BOL, holo.).

Branched erect shrub, 20-30 cm tall. Leaves shortly fused towards bases, 3-angled, blunt, glaucous. Flowers small, numerous, 3 together, filamentous staminodes gathered around stamens, white to pale pink. Fruit without a closing body, 3.5-5 mm diam., valve wings broad, rims low. Jul.-Sep. In sand among stones;

Vanrhynsdorp to Paardeberg.

### 6. 3. A conspectus of *Lampranthus* N. E. Br.

**Lampranthus** N.E.Br., Gard. Chron., ser. 3, 87: 71 (1930). Type: *Lampranthus multiradiatus* (Jacq.) N.E.Br.

*Aristanthus* Schwantes, Zeitschr. Sukkulentenk. 3: 28 (1927), *nom. nud.*

*Mesembryanthus* Necker ex Rothmaler, Notizbl. Bot. Gart. Berlin-Dahlem 15: 413 (1941). Type:

*Mesembryanthus tenuifolius* (L.) Rothmaler.

Erect to creeping shrubs, stems woody, occasionally with thickened root stock. **Leaves** free to shortly fused, without a crystal layer or crystal layer incomplete, green or glaucous, epidermal bladder cells flattened, smooth or slightly scabrid, trigonous or semi-cylindrical. **Flowers** solitary to ternate, to 60 mm diam.; petaloid staminodes yellow, pink, purple, red or white, filamentous staminodes absent or present; nectaries in a ring. **Fruits** grey or brown, persistent, base funnel-shaped or rarely globular, top raised or almost flat, covering membranes complete, with a distal rim and (often inconspicuous) closing ridges below, closing bodies absent, expanding keels diverging from base or occasionally parallel but do not touch, valves with broad, mostly rectangular valve wings, locules 5. **Seeds** ochre to dark brown, pear- to D-shaped, papillate to almost smooth.

*Ecology:* Most species grow in the wetter winter rainfall areas of the south-western Cape.

*Distribution:* Southern Namibia, Namaqualand to Cape Town; from Cape Town, Little Karoo to Eastern Cape and Natal. Few species in Australia where they have probably been introduced.

#### Key to the sections:

1. Leaves trigonous (2.5-7 mm diam.), flowers yellow, orange, red or white, top of fruit flattened.....**Sect. Aurei**
- Leaves half-cylindrical or trigonous, flowers purple, pink, or white, more rarely yellow or red, top of fruit raised.....2
2. Leaves smooth, 3-6 mm diam, flowers > 4 cm diam (only smaller in *L. virens*)..... **Sect. Amoeni**
- Leaves scabrid (rarely smooth), slender (1-2 mm diam.), flowers small or large .....3
3. Flowers 0.7-3.5 cm diam., purple, pink or white, leaves 4-15(-30) mm long.....**Sect. Scabridi**
- Flowers 4-6 cm diam.(rarely 14-35 mm diam.), pink, purple, red, yellow or white, petals mostly very numerous and often threadlike, leaves (10-)15-40 mm long.....**Sect. Tenuifolii**

#### **Sect. Amoeni**

Plants small to medium sized woody shrubs. Leaves smooth, shortly fused or free towards their

bases, semi-cylindrical, rarely triquetrous, glaucous. Inflorescence 1-3(-5)-flowered, pedicels 5-50 mm long. Flowers white, purple or pink, 3-7 cm diam., filamentous staminodes present or absent. Fruits large, 5-16 mm diam. Seeds large, wedge-shaped, testa cells convex, rarely with central papillae raised or flattened. Note: Section *Amoeni* includes those species previously placed in sections *Haworthii*, *Amoeni*, *Blandi* and *Falcati*.

*A. Flowers with filamentous staminodes*

**Lampranthus dependens** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum dependens* L.Bolus, Ann. Bolus Herb. 3: 134 (1922). Type: Robertson distr., hanging over damp cliffs in Cogman's Kloof and in the cave, near Montagu Baths, fl. Oct. 1921, Page sub BOL 17156 (BOL, holo.).

Decumbent shrub, young branches 3-angled. Leaves shortly fused towards bases, spreading to recurved, green, acute, set with fine green papillae, covered with white dots, 35-55 mm long, 3-4 mm thick. Flowers ternate or 1-2 by abortion, pedicels 3-4.5 cm long, pale mauve, to 6 cm diam, filamentous staminodes and stamens collected. Oct. Cool slopes, ledges on cliffs; Worcester, Montagu, Uniondale, Humansdorp.

Note: Similar to *L. haworthii*, but grows on sandstone.

**Lampranthus godmaniae** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum godmaniae* L.Bolus, Notes Mesembryanthemum 2: 141 (1929). Lectotype (designated here): Namaqualand, near Springbok, *L. Bolus sub BOL 18992* (BOL).

*Lampranthus godmaniae* var. *grandiflorus* (L.Bolus) L.Bolus ex H.Jacobsen, Handb. Sukk. Pfl. 3: 1435 (1955). *Mesembryanthemum godmaniae* var. *grandiflora* L.Bolus, Notes Mesembryanthemum 2: 326 (1932). Type: between Patats River and Karoopoort, Sep. 1931, *Compton 3719* (BOL, holo.).

Erect shrublet to 400 mm. Leaves free towards bases, slightly spreading, cylindrical to trigonous, to 40 mm long, grey. Flowers ternate, pedicels 2-7 cm long, white or purple, 35-40 mm diam., filamentous staminodes present. Sep.-Oct. Sandy flats; Namaqualand.

**Lampranthus haworthii** (Donn ex Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Erepsia*

*haworthii* (Donn ex Haw.) Schwantes, Gartenflora 78: 68 (1928). *Mesembryanthemum haworthii* Donn ex Haw., Misc. Nat.: 65 (1803). Lectotype (designated here): Watercolour original by T. Duncanson (959) (132) (K!).

*Lampranthus cyathiformis* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Erepsia cyathiformis* (L.Bolus) Schwantes, Gartenflora 78: 68 (1928). *Mesembryanthemum cyathiforme*, L.Bolus, Ann. Bolus Herb. 3: 165 (1923). Type: without locality, Sep. 1922, *Arbuthnot sub BOL 17255* (BOL, holo.).

*Lampranthus affinis* L.Bolus, J. S. African Bot. 28: 12 (1962). Type: Cape, Meiringspoort, Oct.-Nov. 1961, *Stayner sub KG 794/60* (BOL, holo.).

*Lampranthus egregius* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939). *Mesembryanthemum egregium* L.Bolus, Notes Mesembryanthemum 3: 12 (1936). Type: Montagu distr., 2 miles from Montagu along the old road to Ladismith, Sep. 1935, *Esterhuysen sub BOL 21640* (BOL, holo.).

Erect, freely branched shrublet, 40-60 cm tall. Leaves shortly fused, ascending to spreading, densely pruinose with grey, 25-40 mm long, 3-4 mm wide. Flowers 1-3, pedicels c. 4 cm, light purple, to 7 cm diam., filamentous staminodes incurved over the stamens. Sep.-Oct. ?; Clanwilliam, Montagu.

**Lampranthus littlewoodii** L.Bolus, J. S. African Bot. 27: 114 (1961). Type: Cape, 2 miles north of Khamieskroon, Nov. 1960, *Littlewood sub KG 581/59* (BOL, holo.).

Plants straggling, 23 cm tall. Leaves free towards bases, somewhat falcate, acute, laterally compressed, 1.25 cm long, 1.5-2 mm diam. Flowers 2-3, pedicels short, pink, 2.3-3 cm diam., very few filamentous staminodes. Oct. ?; Khamieskroon.

Note: The species is only known from the type collection. Description taken from the protologue.

**Lampranthus productus** (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum productum* Haw., Till. Phil. Mag. 64: 425 (1824). Lectotype (designated here): Monogr.: § 40, 4 (1837).

*Lampranthus productus* var. *lepidus* (Haw.) Schwantes ex H.Jacobsen, Feddes Repert. Beih. 106: 100 (1938). *Mesembryanthemum productum* var. *lepidum* (Haw.) Salm-Dyck., Monogr.: § 40, 4. *Mesembryanthemum lepidum* Haw., Till. Phil. Mag. 68: 130 (1826). Type: Cape of Good Hope, 1824, *Bowie* (missing). Lectotype (designated here): Watercolour original by T. Duncanson (24) (245?) (K!).

*Lampranthus stephanii* (Schwantes) Schwantes, Feddes Repert. Spec. Nov. Regni. Veg. 43: 230 (1938). *Mesembryanthemum stephanii* Schwantes, Möller's Deutsche Gärtn.-Zeitung 42: 159 (1927). Type: Hort. Kiel, *Stephan* (KIEL, holo., K).

*Lampranthus mutans* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum mutans* L.Bolus, Notes Mesembryanthemum 2: 18 (1928). Type: Humansdorp div., Zuurbron, Sep.-Oct. 1928, *H.G. Fourcade 3336* (BOL, holo.).

*Lampranthus algoensis* L.Bolus, J. S. African Bot. 26: 159 (1960). Type: Cape, Algoa Park, Oct. 1959, *Feinauer sub NBG 691/59* (BOL, holo.).

Plants erect, to 35 cm tall. Leaves shortly fused, triangulate, 1-1.5 cm long, 1-2 mm wide and thick, apiculate, tip recurved. Flowers ternate, to 36 mm diam., pink with yellow centre or white, filamentous staminodes present. Sept.-Oct. ?; Humansdorp to Port Elizabeth.

**Lampranthus virens** (Haw.) Klak **comb. nov.** *Delosperma virens* (Haw.) L.Bolus, *§. Afr. Gard.* 18: 16 (1928).

*Mesembryanthemum virens* Haw., *Rev. Pl. Succ.*: 121 (1821). Type: missing.

*Lampranthus uniflorus* (L.Bolus) L. Bolus, *Notes Mesembryanthemum* 3: 170 (1939). *Drosanthemum uniflorum* (L.Bolus) Friedrich ex Jacobsen, *Sukkulentenlexikon*: 418 (1970), *nom. illegit.*

*Mesembryanthemum uniflorum* L.Bolus, *Ann. Bolus Herb.* 3: 135 (1922). Type: Beaufort West distr., Klipbank, May 1921, *Rogers sub BOL 17066* (BOL, holo.).

Branched shrub, somewhat rambling, 20-45 cm tall. Leaves shortly fused towards bases, slightly falcate, almost cylindrical, smooth, light green, 20-28 mm long, 3-4 mm diam. Flowers solitary, pedicels 7-35 mm long, 20-35 mm diam., pink to purplish, filamentous staminodes and stamens conically collected. Sep. Often in disturbed spots, on shale, in flats; Namaqualand to Little Karoo, parts of Great Karoo.

Note: The fruits are unusual for having a false placenta and parallel keels.

**Lampranthus otzenianus** (Dinter) Friedrich, *Mitt. Bot. Staatssamml. München* 3: 565 (1960).

*Drosanthemum otzenianum* (Dinter) Friedrich, *Mitt. Bot. Staatssamml. München* 7: 217 (1968).

*Psilocaulon otzenianum* (Dinter) L.Bolus, *Notes Mesembryanthemum* 2: 31 (1928).

*Mesembryanthemum otzenianum* Dinter, *Feddes Rep. Spec. Nov. Regni. Veg.* 19: 152 (1923). Type: Namibia, Buntfeldschuhplateau and at the eastern foot of the Zwartkop, Sep. 1922, *Dinter 3789* (B, holo.).

*Lampranthus uniflorus* var. *spathulatus* L.Bolus ex Jacobsen, *Handb. Succ. Pl.* 3: 1212 (1960).

*Mesembryanthemum spathulatum* L.Bolus, *Notes Mesembryanthemum* 1: 136 (1928), *nom. illegit.*

Type: Namaqualand, between Sendlingsdrift and Doornpoort, Oct. 1926, *Pillans 5719* (BOL, holo.).

Very similar to *L. virens*, but leaves more succulent and fruits without false placenta. *L. otzenianus* has a more northerly distribution and occurs from southern Namibia to Namaqualand, where it meets *L. virens*. As the two species can be found growing together in certain areas (e.g. at Louriesfontein), this suggests that they are distinct species. However, since there are still areas of uncertainty with respect to their distribution it appears worthwhile to examine these two species in more detail.

**Lampranthus zeyheri** (Salm-Dyck) N.E.Br., *Gard. Chron.*, ser. 3, 87: 212 (1930). *Mesembryanthemum zeyheri* Salm Dyck, *Monogr.*: § 40, 5 (1849). Lectotype (designated here): *Monogr.*: § 40, 5 (1849).

*Lampranthus stayneri* (L.Bolus) N.E.Br., *Gard. Chron.*, ser. 3, 87: 212 (1930). *Mesembryanthemum stayneri* L.Bolus, *Ann. Bolus Herb.* 4: 6 (1925). Type: Cape, Bedford, Mar. 1924, *F. J. Stayner sub NBG 81/21* (BOL, holo.; K, PRE).

*Lampranthus productus* var. *purpureus* (L.Bolus) H.Jacobsen, *Feddes Repert. Beih.* 106: 100 (1938).

*Mesembryanthemum productum* Haw. var. *purpureum* L.Bolus, Notes Mesembryanthemum 2: 43 (1929). Lectotype (designated here): Peddie road, 25 miles from Grahamstown, Apr. 1928, R. A. Dyer 1323 (BOL).

*Lampranthus praecipitatus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum praecipitatum* L.Bolus, Notes Mesembryanthemum 2: 330 (1932). Type: Albany distr., Dassie Krantz, near Grahamstown, Dec. 1931, Britten 25 (BOL, holo.).

*Lampranthus swartkopensis* Strohschneider, Oesterr. Bot. Z. 84: 292 (1935). Type: Port Elizabeth, Swartkop, 1909, J. Brunthaler (W, holo., missing). Lectotype (designated here): Photo of type in Oesterr. Bot. Z. 84: 293 (1935).

Robust, many-branched shrub, to 20 cm tall, branches spreading. Leaves erect, shortly fused; semicylindrical to trigonous, shortly acuminate, glaucous, 15-25 mm long, 3 mm diam. Flowers ternate, pedicels short, purple, 30-35 mm diam., filamentous staminodes present. Dec.-Mar. ?; Bedford to Grahamstown.

#### B. Flowers without filamentous staminodes

**Lampranthus borealis** L.Bolus, J. S. African Bot. 26: 160 (1960). Type: Namibia, Witpütz, May 1959, Herre sub *SUG 14513* (BOL, holo.).

Erect glabrous shrub, with stems 9-18 cm long and internodes to 2.5 cm long. Leaves free towards bases, bluntly trigonous, 2.4 cm long, 3-5 mm thick. Flowers solitary, pedicels to 2.5 cm long, 4-5 cm diam., pale rose, without filamentous staminodes. Sep. ?; Witpütz.

**Lampranthus coralliflorus** (Salm-Dyck) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Erepsia coralliflora* (Salm-Dyck) Schwantes, Gartenflora 78: 68 (1928). *Mesembryanthemum coralliflorum* Salm Dyck, Monogr.: § 40, 2 (1836). Lectotype (designated here): Monogr.: § 40, 2 (1836).

Erect, freely branched shrublet, to 40-60 cm. Leaves shortly fused, ascending to spreading, densely pruinose with grey, 25-40 mm long, 3-4 mm wide. Flowers 1-3, pedicels 18-35 mm long, light purple, to 7 cm diam., inner petals form filamentous staminodes which are incurved over the stamens. Oct. ?; Uniondale.

**Lampranthus densipetalus** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939).

*Mesembryanthemum densipetalum* L.Bolus, Notes Mesembryanthemum 2: 218 (1930). Type: Namaqualand, between Garies and Kamieskroon, Aug. 1929, L. Bolus sub *BOL 19249* (BOL, holo.).

*Lampranthus plautus* N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum latum* L.Bolus, Notes Mesembryanthemum 2: 141 (1929) *nom. illegit.* Type: Cape, between Khamieskroon and Springbok, Aug. 1929, Pillans 6267 (BOL, holo.).

Erect, loosely branched shrub, 26 cm tall. Leaves shortly fused towards bases, spreading to erect,

upper side flattened, glaucous, 2 cm long, 3 mm thick. Flowers solitary, pedicels 14 mm long, to 35 mm diam., white, without filamentous staminodes. Jun.-Aug. On shale; Garies to Khamieskroon.

**Lampranthus dregeanus** (Sond.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Erepsia dregeana* (Sond.) Schwantes, Gartenflora 78: 68 (1928). *Mesembryanthemum dregeanum* Sond., Fl. Cap. 2: 414 (1862). Syntypes: Cape, Tulbagh and Vogelvalley, *Ecklon & Zeyher TCD 107* (TCD); Cape, Tulbagh and Vogelvalley, *Drège s.n.* herb. Sonder (TCD).

Erect shrublet, to 600 mm, stems red, finely pruinose, branches compressed 2-angled. Leaves free towards bases, compressed trigonous, finely denticulate, to 16 mm long and 6 mm diam. Flowers almost sessile, 1-3, white, without filamentous staminodes. Sep.-Oct. On lower rocky sandstone slopes, near water; Tulbagh to Montagu.

**Lampranthus falciformis** (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Oscularia falciformis* (Haw.) H.E.K.Hartmann, Bradleya 16: 77 (1998). *Mesembryanthemum falciforme* Haw., Syn. Pl. Succ.: 299 (1812). Lectotype: drawing 947/11 (K!).

*Lampranthus laxifolius* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum laxifolium* L.Bolus, Ann. Bolus Herb. 4: 86 (1927). Type: Riversdale div., Feb. 1925, *Muir sub NBG 2173/23* (BOL, holo.).

*Lampranthus falciformis* var. *maritimus* L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum maritimum* L.Bolus, Notes Mesembryanthemum 3: 55 (1937), *nom. illegit.*

Type: Stellenbosch distr., Rooiels, near Gordon's Bay, Jan. 1936, *Pillans 8352* (BOL, holo.).

Decumbent to erect shrubs, to 300 mm with reddish stems. Leaves free towards bases, acinaciform to falcate, with big dots, glaucous. Flowers in terminal fastigiate cymes, pedicels short, petals pink, 4-5 cm diam., without filamentous staminodes. Nov.-Feb. Sandstone slopes or pans; Cape Peninsula, Langeberg near Riversdale, Mossel Bay.

**Lampranthus gracilipes** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum gracilipes* L.Bolus, Notes Mesembryanthemum 2: 73 (1929). Type: Piquetberg distr., Oct. 1924, *Anon. sub BOL 17883* (BOL, holo.).

*Lampranthus globosus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum globosum* L.Bolus, Notes Mesembryanthemum 2: 234 (1931). Type: Vanrhynsdorp distr., Van Rhyn's Pass, Oct. 1930, *Mathews sub BOL 19384* (BOL, holo.).

*Lampranthus dulcis* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939). *Mesembryanthemum dulce* L.Bolus, Notes Mesembryanthemum 2: 328 (1932). Type: Clanwilliam distr., Oliphant's River valley, near Warm Baths, Oct. 1931, *Leipoldt sub BOL 19332* (BOL, holo.).

*Lampranthus esterhuyseniae* L.Bolus, Notes Mesembryanthemum 3: 331 (1958). Type: Cape, Khamieskroon, Oct. 1954, *Esterhuysen 23638* (BOL, holo.).

*Lampranthus vanheerdei* L.Bolus, J. S. African Bot. 30: 39 (1964). Type: Cape, about 12 miles west of Springbok, Nov. 1963, *P. van Heerde sub BOL 27493* (BOL, holo.).

*Lampranthus gracilipes* f. *luxurians* L.Bolus, J. S. African Bot. 32: 232 (1966). Type: Cape, Pakhuis Pass, Oct. 1965, *H. Hall 3039* (BOL, holo.).

Erect laxly branched shrub, 20-40 cm tall, branches 4-angled. Leaves free towards bases, spreading, subfalcate, 7 (-35) mm long, to 4 mm diam. Flowers 2-3, pedicels 15-20 mm long, 32 mm diam., pale pink, without filamentous staminodes. Oct.-Nov. In sandstone; Khamieskroon to Villiersdorp.

**Lampranthus hallii** L.Bolus, Notes Mesembryanthemum 3: 272 (1954). Type: Cape, Cloete's Pass near Herbertsdale, Aug. 1952, *H. Hall sub NBG 521/52* (BOL, holo.).

Erect shrub, to 36 cm, later decumbent. Leaves shortly fused, ascending to erect, acutely to bluntly keeled, laterally compressed, green, 2-8 cm long, 2-4 mm diam. Flowers solitary or rarely ternate, pedicels 25-45 mm long, 30-35 mm diam., pink, without filamentous staminodes. Sep. ?; Cloetes Pass, Langebergen, Riversdale.

**Lampranthus hoerleinianus** (Dinter) Friedrich, Mitt. Bot. Staatssammlung München 3: 566 (1960).

*Mesembryanthemum hoerleinianum* Dinter, Feddes Rep. Spec. Nov. Regni. Veg. 19: 153 (1923).

Type: Namibia, Bundtfeldschuh Plateau, 10 Sep. 1922, *Dinter 3788* (B, holo.; PRE, HBG).

*Lampranthus brachyandrus* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 211 (1930). *Mesembryanthemum brachyandrum* L.Bolus, Notes Mesembryanthemum 2: 3 (1928). Type: Cape, between Ooghrabies Poort and Port Nolloth, Oct. 1926, *Pillans 5803* (BOL, holo.; K).

Plants to 70 cm tall, stems light grey-brown. Leaves very shortly fused, light blue green. Flowers in a few-flowered inflorescence, without filamentous staminodes. Sep.-Oct. ?; Southern Namibia to northern Namaqualand.

Note: Similar to *L. stipulaceus*, but stems grey.

**Lampranthus holensis** L.Bolus, J. S. African Bot. 28: 294 (1962). Type: Cape, Vanrhynsdorp, Hol River, Aug. 1962, *H. Hall 2568* (= *NBG 745/62*) (BOL, holo.).

Plants shrubby, stems 20 cm long. Leaves shortly fused towards bases, acute, cylindrical, very slender, 4.5-5.5 cm long, 4-5 mm diam. Flowers solitary, pedicels 2-4 cm long, to 5.5 cm diam., petals white, no filamentous staminodes present. Aug. ?; Vanrhynsdorp div., Hol River to Rooiberg.

**Lampranthus hollandii** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum hollandii* L.Bolus, Notes Mesembryanthemum 2: 274 (1931). Type:

Alexandria distr., Apr.-Jun. 1931, *Galpin sub BOL 19640* (BOL, holo.).

Erect shrub to 20 cm tall. Leaves shortly fused, spreading to erect, dull green, 20-27 mm long, 2-3

mm diam. Flowers solitary, pedicels 15-25 mm long, pink to purple, 4.5 cm diam., no filamentous staminodes present. Apr.-Jun. Occasional on grassy slopes; Alexandria.

Note: This species has its flowering time in autumn, which is rare in *Lampranthus*.

**Lampranthus lavisii** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum lavisii* L.Bolus, Notes Mesembryanthemum 2: 156 (1929). Type: Humansdorp distr., Assegaibosch, Nov. 1927, *Lavis* sub *BOL 18762* (BOL, holo.).

*Lampranthus lavisii* var. *concinus* L.Bolus, J. S. African Bot. 26: 158 (1960). Type: Cape, Kabega Park near Port Elizabeth, Oct.--Nov. 1959, *MacKenzie* sub *NBG 595/58* (BOL, holo.).

Erect shrub, 25-35 cm tall. Leaves shortly fused towards bases, erect, back surface keeled, 25-35 mm long, 2.0-2.5 mm thick. Flowers 1-3, pedicels 15-30 mm long, pink, 4 cm diam., filamentous staminodes absent. Oct.-Nov. ?; Port Elizabeth.

**Lampranthus multiradiatus** (Jacq.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum multiradiatum* Jacq., Fragm. Bot.: 44. n. 152 t. 53 f. 1 (1809). Lectotype (designated here): Fragm. Bot.: t. 53 f. 1 (1809).

*Lampranthus blandus* (Haw.) Schwantes, Feddes Repert. Spec. Nov. Regni. Veg. 43: 229 (1938).

*Mesembryanthemum blandum* Haw., Suppl. Pl. Succ.: 95 (1819). Lectotype (designated here): Lodd. Bot. Cab. 6: t. 599 (1821).

*Lampranthus incurvus* (Haw.) Schwantes ex H.Jacobsen, Feddes Repert. Spec. Nov. Regni. Veg. 43: 230 (1938). *Mesembryanthemum incurvum* Haw., Misc. Nat.: 70 (1803). Type: missing.

*Lampranthus roseus* (Willd.) Schwantes ex H.Jacobsen, Feddes Repert. Spec. Nov. Regni. Veg. 43: 230 (1938). *Mesembryanthemum incurvum* var. *roseum* (Willd.) DC., Prodr. 3: 433 (1828).

*Mesembryanthemum roseum* Willd., Enum. Pl. Hort. Berol.: 535 (1809). Type: Hort. Berlin, Willdenow (B-W, holo.).

*Lampranthus curviflorus* (Haw.) H.E.K Hartmann, Bradleya 16: 67 (1998). *Lampranthus curviflorus* (Haw.) N.E.Br. ex H. Jacobsen, Handb. Sukk. Pfl. 3: 1429 (1955), *nom. invalid.*

*Mesembryanthemum blandum* var. *curviflorum* (Haw.) A.Berger, Mesemb. Portulac.: 163 (1908).

*Mesembryanthemum curviflorum* Haw., Rev. Pl. Succ.: 147 (1821). Type: Ross (K, holo.).

Spreading shrublet, to 60 cm. Leaves shortly fused, compressed trigonous, smooth, 1.5-2.5 cm long, 2-4 mm diam. Flowers 1-3, stalked, 4.5-5 cm diam., pale pink or white, without filamentous staminodes. Aug.-Nov. On sandstone slopes, Peninsula.

Very similar to *L. falciformis*, but leaves longer and flowers larger. Flowering time earlier, from Aug.-Nov., whereas *L. falciformis* flowers from Nov.-Feb.

**Lampranthus spectabilis** (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum*

*spectabile* Haw., Obs. Gen. Mesemb.: 385 (1795). Lectotype (designated here): Bot. Mag. 11: t. 396 (1797).

*Lampranthus turbinatus* (Jacq.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum turbinatum* Jacq., Hort. Schoenbr.: t. 476 (1804). Lectotype (designated here): Hort. Schoenbr.: t. 476.

*Lampranthus formosus* (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum formosum* Haw., Rev. Pl. Succ.: 145 (1821). Lectotype (designated here): Watercolour original by T. Duncanson (951) (K!).

*Lampranthus macrocarpus* (A.Berger) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum macrocarpum* A.Berger, Bot. Jahrb. Syst. 57: 634 (1922). Lectotype (designated here): Redhouse, Sep. 1908, *Paterson 207* (GRA).

*Lampranthus macrosepalus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum macrosepalum* L.Bolus, Notes Mesembryanthemum 2: 219 (1930). Type: Humansdorp distr., Assegaibosch, Nov. 1927, *Lavis sub BOL 18761* (BOL, holo.).

*Lampranthus fugitans* L.Bolus, Notes Mesembryanthemum 3: 330 (1958). Type: Natal, 3 miles inland from Port Edward, *H. Hall sub NBG 496/56* (BOL, holo.).

Robust, prostrate to ascending shrublet. Leaves shortly fused, tufted ascending, trigonous, 5-8 cm long, 6 mm diam. Flowers solitary or rarely 1-3, long-stalked, 5-7 cm diam., purple or rarely white, without filamentous staminodes. Sep.-Oct. ?; Eastern Cape to Port Edward.

***Lampranthus stipulaceus*** (L.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Erepsia stipulacea* (L.) Schwantes, Gartenflora 78: 68 (1928). *Mesembryanthemum stipulaceum* L., Sp. Pl.: 484 (1753). Lectotype (designated here): "*M. stipulaceum*", S.205 7 (LINN).

*Lampranthus conspicuus* (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum conspicuum* Haw., Syn. Pl. Succ.: 240 (1812). Lectotype (designated here): Watercolour original by T. Duncanson at Kew (K).

*Lampranthus amoenus* (Salm-Dyck ex DC.) N.E.Br., Gard. Chron., ser. 3, 87: 211 (1930).

*Mesembryanthemum amoenum* Salm-Dyck ex DC., Prod. 3: 436 (1828). Lectotype (designated here): Monogr.: §27, 2 (1837).

*Lampranthus suavissimus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum suavissimum* L.Bolus, Notes Mesembryanthemum 2: 220 (1930). Type: Namaqualand, near Hondeklip Bay, Oct. 1924, *Pillans sub BOL 17929* (BOL, holo.; K).

*Lampranthus suavissimus* f. *fera* (L.Bolus) L.Bolus ex H.Jacobsen, Handb. Sukk. Pfl. 3: 1449 (1955).

*Mesembryanthemum suavissimum* f. *fera* L.Bolus, Notes Mesembryanthemum 2: 221 (1930). Type: Cape, near Wallekraal, Aug. 1929, *L.Bolus sub BOL 19250* (BOL, holo., missing).

*Lampranthus suavissimus* var. *oculatus* (L.Bolus) L.Bolus ex H.Jacobsen, Handb. Sukk. Pfl. 3: 1449

(1955). *Mesembryanthemum suavissimum* var. *oculatum* L.Bolus, Notes Mesembryanthemum 2: 221 (1930). Type: Cape, near Hondeklip Bay, Oct. 1924, *Pillans 6060* (BOL, holo.).

*Lampranthus subtruncatus* var. *wupperthalensis* L.Bolus, J. S. African Bot. 27: 114 (1961). Type: Cape, Wupperthal, Sep. 1959, *R. C. Littlewood sub KG 380/59* (BOL, holo.).

Erect, robust densely branched shrublet, to 45 cm, stems brown. Leaves ascending, shortly fused towards bases, falcately incurved, acute or tapering, glaucous, to 35 mm long. Flowers ternate, short stalked, purple, to 4 cm diam., without filamentous staminodes. Oct. In deep sand on flats and among rocks; Namaqualand to Cape Town.

**Lampranthus vernalis** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum vernale* L.Bolus, Ann. Bolus Herb. 4: 93 (1927). Type: *Arbuthnot sub BOL 17305* (BOL, holo.).

*Lampranthus arenosus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939). *Mesembryanthemum arenosum* L.Bolus, Notes Mesembryanthemum 2: 367 (1932). Type: Malmesbury distr., Saldanha Bay, near Langebaan, in hills, Oct.-Nov. 1932, *L.Bolus sub BOL 20202* (BOL, holo.).

*Lampranthus salicola* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939). *Mesembryanthemum salicola* L.Bolus, Notes Mesembryanthemum 3: 12 (1936). Type: Piquetberg distr., in saline flats between Veldrift and St. Helenafontein, Oct. 1935, *L.Bolus sub BOL 21641* (BOL, holo.).

Erect shrub, 20-30 cm tall. Leaves shortly fused, erect to ascending, semicylindrical, shortly acuminate, glaucous to yellow-green, 15-20 mm long, 3 mm wide and thick. Flowers 1-3, stalked, to 4 cm diam., pink, no filamentous staminodes present. Sep.-Oct. In coastal habitats, on salt plain; Langebaan, St. Helena Fontein, Vredenburg.

**Lampranthus watermeyeri** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum watermeyeri* L.Bolus, Ann. Bolus Herb. 3: 72 (1921). Type: Calvinia distr., Nieuwoudtville, *Watermeyer sub NBG 2256/15* (BOL, holo.).

*Lampranthus saturatus* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum saturatum* L.Bolus, Ann. Bolus Herb. 3: 169 (1924). Type: Vanrhynsdorp div., Jul. 1923, *H.S. van Zijl s.n.* (BOL, holo.).

*Lampranthus dyckii* (A.Berger) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum dyckii* A.Berger, Bot. Jahrb. Syst. 57: 635 (1922). Holotype: Monogr.: §27, 1 (1837).

*Lampranthus vanputtenii* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum vanputtenii* L.Bolus, Notes Mesembryanthemum 2: 98 (1929), as *M. pittenii*, see J. S. African Bot. 33: 308 (1967). Lectotype (designated here): Lambert's Bay, 18 Jul. 1928, *van Pitten sub NBG 1045/25* (BOL, holo.).

*Lampranthus disgregus* (N.E.Br.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum*

*disgregum* N.E.Br., Bull. Misc. Inform. Kew 2: 59 (1929). Type: Fl. Pl. S. Africa: t. 253 (1927).

Decumbent to erect robust shrub, to 30 cm. Leaves free towards bases, semicylindrical, 20-25 mm long, to 6 mm diam. Flowers mostly solitary, long stalked, to 7 cm diam., purple or white, without filamentous staminodes. Jul.-Oct. In sandy soils; Vanrhynsdorp, Nieuwoudtville to Lamberts Bay.

Note: L. Bolus (in Notes Mesembryanthemum 2: 192, 1930) explicitly stated that the *Mesembryanthemum stipulaceum* that she was dealing with was that of Linnaeus and she did not describe a new species with this name as N.E. Brown seems to have assumed.

### Section *Aurei*

Small erect or creeping shrubs. Leaves free towards bases, 3-angled, often set with raised dots. Flowers yellow, orange, red or white, to 6 cm diam, no filamentous staminodes, anthers apapillose, ovary top flattened. Fruits with lower part funnel-shaped, slightly raised to flattened, covering membranes with a fine protruding ridge.

Note: Section *Aurei* includes the old section *Aurei* and some species previously placed in Sect. *Tenuifolii* and Sect. *Reptantes*.

**Lampranthus acrosepalus** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum acrosepalum* L.Bolus, Notes Mesembryanthemum 3: 11 (1936). Type: Piquetberg distr., plateau on Kapitein's Kloof Mountain, Piquetberg Range, 3340 ft., Oct. 1935, Pillans 7752 (BOL, holo.).

**Lampranthus rubroluteus** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum rubroluteum* L.Bolus, Notes Mesembryanthemum 3: 11 (1936). Type: Piquetberg distr., north side of plateau on Kapitein's Kloof Mountain, Piquetberg Range, 3350 ft., Oct. 1935, Pillans 7749 (BOL, holo.).

Erect shrub 18-25 cm tall, branches virgate, 3 mm thick. Leaves ascending, sides compressed and tapering, sharply keeled, slender, 17-30 mm long. Flowers solitary, to 60 mm diam., orange or white. Oct. Among rocks at 1100 m; Kapitein's Kloof.

**Lampranthus aurantiacus** (Haw.) Schwantes ex H.Jacobsen, Feddes Repert. Spec. Nov. Regni. Veg. 43:

229 (1938). *Mesembryanthemum aurantiacum* Haw., Misc. Nat.: 84 (1803), as "*aurantium*".

Lectotype (designated here): Monogr.: § 25, 2 (1836).

**Lampranthus matutinus** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Lampranthus matutinus*

(L.Bolus) Schwantes ex H. Jacobsen, Natl. Cact. Succ. J. 4: 58 (1949). *Mesembryanthemum matutinum* L.Bolus, Notes Mesembryanthemum 1: 135 (1928). Type: Piquetberg distr.?, Aug.-Sep. 1927, Immelman sub BOL 18713 (BOL, holo.).

**Lampranthus marcidulus** N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum flaccidum*

L.Bolus, Ann. Bolus Herb. 3: 164 (1924), *nom. illegit.* Type: between Montagu and Montagu Baths, Sep. 1921, *Page sub BOL 17258* (BOL, holo., missing). Lectotype (designated here): Watercolour original by M. Page of the type plant (BOL).

*Lampranthus hurlingii* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum hurlingii* L.Bolus, Notes Mesembryanthemum 2: 427 (1934). Type: Robertson distr., between Bushman's River and McGregor, Sep. 1933, *Hurling & Neil sub BOL 21015* (BOL, holo.).

*Lampranthus stanfordiae* L.Bolus, Notes Mesembryanthemum 3: 158 (1939). Type: Malmesbury distr., Yzerfontein, Sep. 1938, *Stanford sub BOL 21851* (BOL, holo.).

*Lampranthus amabilis* L.Bolus, Notes Mesembryanthemum 3: 330 (1958). Type: Cape, Potberg, Sep. 1954, *Esterhuysen 23153* (BOL, holo.).

Slender erect shrublet 20-25 cm tall, also decumbent and trailing with floral branches 2.5-6 cm long. Leaves free towards bases, bluntly trigonous, acute, scabrid, to 17 mm long, to 2.5 mm broad. Flowers 1-3, stalked, 35-52 mm diam., deep orange, more rarely orange – yellow or white occasionally with a pink tinge, filamentous staminodes absent. Aug.-Sep. Sandy flats, among lowland *fynbos*; Yzerfontein to Cape Town, Robertson and Montagu, Bredasdorp.

***Lampranthus aureus*** (L.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum aureum* L., Syst. Nat., ed. 10: 1060 (1759). Lectotype (designated here): Bot. Mag. 8: t. 262 (1794).

Very similar to *L. aurantiacum*, but flowers and leaves larger, i.e. leaves 5 cm long, flowers to 6 cm diam. Only known from the area around Saldanha Bay.

***Lampranthus glaucus*** (L.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum glaucum* L., Sp. Pl.: 486 (1753). *Mesembryanthus glaucus* (L.) Rothm., Notizb. Bot. Gart. Berlin-Dahlem 15: 413 (1941).). Lectotype (designated here): "*M. glaucum*", S.206 3 (LINN).

*Lampranthus glaucus* var. *tortuosus* (Salm-Dyck) Schwantes ex H.Jacobsen, Hand. Sukk. Pfl. 3: 1434 (1955). *Mesembryanthemum glaucum* var. *tortuosum* Salm-Dyck, Monogr.: § 25 (1840). Lectotype (designated here): Monogr.: § 25, 1 (1840).

*Lampranthus citrinus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939). *Mesembryanthemum citrinum* L.Bolus, Notes Mesembryanthemum 2: 326 (1932). Type: Malmesbury distr., between Kalabas Kraal and Malmesbury, Mar. 1931, *Leipoldt sub BOL 19925* (BOL, holo.).

*Lampranthus palustris* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum palustre* L.Bolus, Notes Mesembryanthemum 2: 325 (1932). Type: Stellenbosch distr., between Bottelary and Stellenbosch, Sep. 1931, *L.Bolus sub BOL 19927* (BOL, holo.).

*Lampranthus longistamineus* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum longistamineum* L.Bolus, Notes Mesembryanthemum 1: 149 (1929). Type: Clanwilliam distr., near Pakhuis Pass, fl. July 1927, *C.L. Leipoldt sub BOL 18810* (BOL, holo.).

Erect, stiff shrublet, to 15 cm tall. Leaves free towards bases, set with dark slightly elevated dots. ascending to spreading, bluntly trigonous, dull glaucous, to 25 mm long, 7 mm thick. Flowers stalked. solitary, 4-5 cm diam., golden yellow. Jul.-Sep. In seasonally wet spots. Gifberg to Peninsula.

**Lampranthus reptans** (Aiton) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum reptans* Aiton, Hort. Kew., ed. 1, 2: 185 (1789). Lectotype (designated here): Watercolour original by T. Duncanson (110) (M/63) (K!).

*Mesembryanthemum crassifolium* Thunb., Prodr. Pl. Cap.: 90 (1800). Type: Cape, Swartland, Malmesbury Div., Thunberg A (UPS).

*Lampranthus serpens* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum serpens* L.Bolus, Notes Mesembryanthemum 2: 221 (1930). Type: Caledon distr., near Kleinmond, Jan. 1929, Edwards sub BOL 19247 (BOL, holo.).

*Lampranthus woodburniae* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum woodburniae* L.Bolus, Notes Mesembryanthemum 2: 1 (1928). Type: Cape, Orchard, M. Woodburn sub NBG 595/25 (BOL, holo.).

Mat-forming perennial, with erect flowering branchlets 4-8 cm tall. Leaves crowded in tufts from which the elongated branches arise, erect, 15-25 mm long, 5-6 mm wide. Flowers solitary, pedicels 2-4.5 cm long, 4-4.5 cm diam., white or yellow, without filamentous staminodes. Aug.-Oct. Sandy flats; Kalbaskraal to Cape Flats, Caledon.

**Lampranthus vanzijliae** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum vanzijliae* L.Bolus, Ann. Bolus Herb. 3: 126 (1922). Type: Cape, Worcester, Aug. 1921, D. van Zijl sub BOL 17141 (BOL, holo.).

*Lampranthus antonii* L.Bolus, J. S. African Bot. 32: 232 (1966). Type: Cape, north of Ceres at western foot of Agterwitzenberg Pass, Sep. 1965, A.V. Hall 1053 (BOL, holo.).

Mat-forming perennial, with creeping stems, 5-12 cm long. Leaves free towards bases, acute, apiculate, 2-5 cm long, 2-5 mm diam. Flowers solitary, pedicels 7-13 mm long. 5-6.6 cm diam., red, white to pale pink, filamentous staminodes absent. Aug. Common on moist rocks; Ceres, Agterwitzenberg and near Worcester.

Note: Similar to *L. reptans*, but leaves longer (to 55 mm) and flowers larger (to 60 mm diam.).

#### Section *Scabridi*

Small dainty shrubs to 40 cm tall. Leaves free to bases, slender, often with conspicuously raised epidermal bladder cells or more rarely flattened. Flowers in a 1-5 flowered inflorescence, pink or white, 0.7-30 mm diam., with or without filamentous staminodes, filamentous staminodes conically collected or spreading. Seeds with convex testa cells, rarely with central papillae raised.

Note: Species placed here incorporate most of the species previously placed in section *Sabridi*. In addition, several species from Sect. *Reptantes* were transferred here.

A: with filamentous staminodes

**Lampranthus caudatus** L.Bolus, Notes Mesembryanthemum 3: 226 (1950). Type: Cape, Bredasdorp distr., Strandkloof, Apr. 1946, *Leighton 1631* (BOL, holo.).

Erect, densely leafy slender shrub, to 30 cm tall. Leaves spreading to ascending, recurved at the tip, rough, glaucous, 9-14 mm long. Flowers 1-3, pedicels 10-20 mm long, to 20 mm diam., pink to pale pink. filamentous staminodes few, collected into a cone with stamens. Apr. ?; Bredasdorp distr., Strandkloof.

Note: Similar to *L. deflexus*, but flowers in April. A poorly known species.

**Lampranthus calcaratus** (Wolley-Dod) N.E.Br., Gard. Chron., ser. 3, 87: 211 (1930).

*Mesembryanthemum calcaratum* Wolley Dod, J. Bot. London 38: 170 (1900). Lectotype (designated here): Cape Town, Claremont Flats, 5 Sep. 1897, *Wolley Dod 2857* (BOL).

*Lampranthus tenuis* L.Bolus, J. S. African Bot. 35: 144 (1969). Type: Cape, Kenilworth Race Course, Sep. 1968, *Esterhuysen 32044* (BOL, holo.).

Erect, very slender shrublet to 26 cm tall. Leaves erect, acute, 6-11 mm long. Flowers solitary, pedicels 5-6 mm long, 16-20 mm diam., pink, filamentous staminodes and stamens conically collected. Fruit with conspicuously funnel-shaped base, without valve wings. Jun.-Sep. Marshy, sandy area; Malmesbury to Cape Peninsula.

**Lampranthus debilis** (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum debile* Haw., Till. Phil. Mag. 68: 330 (1826). Lectotype (designated here): Watercolour original by T. Duncanson (401) (K!).

*Lampranthus tegens* (F. Muell.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum tegens* F. Muell., Fragm., Phytogr. Austral. 5: 157 (1865-66). Syntypes: Port Phillip, *F. von Mueller MEL 74972, 74973* (MEL).

*Lampranthus caespitosus* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 211 (1930). *Mesembryanthemum caespitosum* L.Bolus, Ann. Bolus Herb. 3: 4 (1920). Type: Cape, near Paarl, 1914, *Rohland sub NBG 1712/14* (BOL, holo.; K).

*Lampranthus caespitosus* var. *luxurians* (L.Bolus) H.Jacobsen, Feddes Repert. Beih. 106: 96 (1938).

*Mesembryanthemum caespitosum* f. *luxurians* L.Bolus, Notes Mesembryanthemum 2: 487 (1935). Type: Cape, Worcester Veld Reserve, Dec. 1934, *Van Breda 197* (BOL, holo.).

*Lampranthus ernestii* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939). *Mesembryanthemum ernestii* L.Bolus, Notes Mesembryanthemum 2: 327 (1932). Type: Bredasdorp distr., near Bredasdorp, Dec. 1930, *E. E. Galpin sub NBG 2663/30* (BOL, holo.).

*Lampranthus arbuthnotiae* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum arbuthnotiae* L.Bolus, Ann. Bolus Herb. 4: 8 (1925). Type: *Arbuthnot sub BOL 17397* (BOL, holo.).

Mat-forming dainty perennial, rooting at nodes, floral branches erect, 10-15 mm long. Leaves ascending, 3-angled, acute, to 8 mm long, rough. Flowers solitary, to 16 mm diam., purplish with paler centre, pedicels 6-12 mm long, filamentous staminodes and stamens conically collected. Aug.-Oct. In light stony calcareous sandy flats or in seasonally inundated areas; Darling, Peninsula to Bredasdorp, Swellendam; Australia (probably introduced).

**Lampranthus deflexus** (Aiton) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum deflexum* Aiton, Hort. Kew. ed. 1, 2: 187 (1789). Lectotype (designated here): Cape Town, Milnerton, 8 Sep. 1927, *L.Bolus sub BOL 20161* (BOL).

*Lampranthus elegans* (Jacq.) Schwantes, Feddes Repert. Spec. Nov. Regni. Veg. 43: 229 (1938).

*Mesembryanthemum elegans* Jacq., Hort. Schoenbr. 4: 18, t. 436 (1804). Lectotype (designated here): Hort. Schoenbr. 4: t. 436 (1804).

*Mesembryanthemum versicolor* Haw., Misc. Nat.: 70 (1803). Lectotype (designated here): *BOL 20164* (BOL). Watercolour original by B. O. Carter, plate 1938, of this specimen (BOL 20164) is lodged at BOL.

*Mesembryanthemum retroflexum* Haw., Misc. Nat.: 71 (1803). Lectotype (designated here): Watercolour original by T. Duncanson (1000/) (299) (K!).

**Lampranthus flexilis** (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum flexile* Haw., Rev. Pl. Succ.: 140 (1821). Lectotype (designated here): Cape Town, Signal Hill, south slopes above Fort, *Lavis sub BOL 20162* (BOL).

**Lampranthus polyanthon** (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum polyanthon* Haw., Syn. Pl. Succ.: 270 (1812). Lectotype (designated here): Watercolour original by T. Duncanson, (215) (M/113) (K).

**Lampranthus laetus** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum laetum* L.Bolus, Notes Mesembryanthemum 2: 189 (1930). Type: Montagu distr., near Montagu Bath Ravine, on the rocky cliffs, Sep. 1921, *Page sub BOL 17157* (BOL, holo.).

**Lampranthus rustii** (A.Berger) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum rustii* A.Berger, Bot. Jahrb. Syst. 57: 636 (1922). Type: Cape, bei Riversdale, 1891 - 1893, *Rust 312* (B, holo.; BOL).

**Lampranthus prominulus** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum prominulum* L.Bolus, Notes Mesembryanthemum 2: 408 (1933). Type: George distr.?, Sep. 1933, *sub BOL 20825* (BOL, holo.).

**Lampranthus liberalis** L.Bolus, Notes Mesembryanthemum 3: 170 (1939). *Mesembryanthemum liberale* L.Bolus, Notes Mesembryanthemum 3: 128 (1938). Type: *sub BOL 21843* (BOL, holo.).

Erect shrub, to 35 cm, branches stiff. Leaves erect, with recurved tips, scabrid, 12-20 mm long, c. 2 mm wide and thick. Flowers stalked, 25 mm diam., purple, pink or white, filamentous staminodes conically collected and apically recurved. Sep.-Oct. ?; Cape Peninsula to Montagu and George.

**Lampranthus diffusus** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum diffusum* L.Bolus, Notes Mesembryanthemum 1: 137 (1928). Type: Near Ceres, Nov. 1927, W.R. Way sub BOL 18759 (BOL, holo.).

*Lampranthus microstigma* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum microstigma* L.Bolus, Notes Mesembryanthemum 2: 142 (1929). Type: Cape, ? Piquetberg div., Oct. 1929, Anon. sub BOL 19871 (BOL, holo.).

*Lampranthus occultans* L.Bolus, Notes Mesembryanthemum 3: 225 (1950). Type: Cape, Hex River Valley, Nov. 1949, Esterhuysen 10942 (BOL, holo.).

*Lampranthus rabiesbergensis* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum rabiesbergense* L.Bolus, Notes Mesembryanthemum 3: 13 (1936). Type: Worcester distr., Langebergen, between Robertson and Worcester, in crevices on the Rabiesberg, Sep. 1935, Lewis sub BOL 21642 (BOL, holo.).

Woody, spreading, loosely branched shrub, to 30-40 cm tall. Leaves narrow, rough, 15-25 mm long, 1(-1.5) mm diam. Flowers solitary or rarely 2-3, to 30 mm diam., white to purplish, pedicels 35 mm long, with filamentous staminodes. Oct.-Dec. Slopes; Ceres to Worcester.

**Lampranthus dilutus** N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum pallidum* L.Bolus, Notes Mesembryanthemum 2: 119 (1929), *nom. illegit.* Type: Cape, near Porterville, Aug. 1923, Mathews sub NBG 1196/26 (BOL, holo.).

*Lampranthus bolusiae* Schwantes ex H. Jacobsen, Feddes Repert. Spec. Nov. Regni. Veg. 43: 229 (1938).

*Lampranthus recurvus* (L.Bolus) Schwantes, Natl. Cact. Succ. J. 4: 58 (1949). *Mesembryanthemum recurvum* L.Bolus, Notes Mesembryanthemum 2: 367 (1932), *nom. illegit.* Type: Tulbagh distr., in damp places between the Tulbagh station road and the village of Tulbagh, Sep. 1932, L.Bolus sub BOL 20166 (BOL, holo.).

*Lampranthus argillosus* L.Bolus, Notes Mesembryanthemum 3: 227 (1950). *Mesembryanthemum*

*tulbaghense* L.Bolus, Notes Mesembryanthemum 2: 364 (1932), *nom. illegit.* Type: Tulbagh distr., near the road between Tulbagh and Tulbagh road, 17 Sep. 1932, L.Bolus sub BOL 18470 (BOL, holo.).

*Lampranthus creber* L.Bolus, Notes Mesembryanthemum 3: 332 (1958). Type: Cape, 20 miles from Albertinia towards Mossel Bay, 28 July 1955, R. du Plessis 15 (BOL, holo.).

*Lampranthus neostayneri* L.Bolus, J. S. African Bot. 27: 58 (1961). Type: Cape, between Porterville and Twenty-four Rivers, 30 Aug. 1945, L.Bolus BOL 26980 (BOL, holo.).

*Lampranthus proximus* L.Bolus, J. S. African Bot. 32: 127 (1966). Type: Cape, Fisantekraal near the Klappmuts turn-off to Agter-Paarl, Sep. 1965, *Nel* sub BOL 27738 (BOL, holo).

Erect, robust shrublet, 15-30 cm tall, stems spreading. Leaves spreading to recurved, rough, upper side convex, laterally compressed, 8-13 mm long. Flowers 1-3, pedicels 7-13 mm long. 18- (45) mm diam., purplish-pink. Jul.-Sep. In shale; Clanwilliam to Cape Flats to Albertinia.

Note: Very similar to *L. deflexus*, but flowers with their filamentous staminodes and stamens conically collected, filamentous staminodes two coloured (apically recurved and one coloured in *L. deflexus*).

**Lampranthus leptaleon** (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum leptaleon* Haw., Rev. Pl. Succ.: 140 (1821). Lectotype (designated here): Somerset Strand, on grass veld, Oct. 1922, *M. Page* sub BOL 17262 (BOL).

*Mesembryanthemum deflexum* Salm Dyck, Obs.: 27 (1820), *nom. illegit.*

*Lampranthus parvus* N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum tenue* L.Bolus, Notes Mesembryanthemum 2: 1 (1928), *nom. illegit.* Type: Near Caledon, Sep. 1927, *Pillans* sub BOL 18844 (BOL, holo.).

*Lampranthus altistylus* N.E.Br., Gard. Chron., ser. 3, 87: 211 (1930). *Mesembryanthemum longistylum* L.Bolus, Notes Mesembryanthemum 2: 2 (1928), *nom. illegit.* Type: Cape, between Cape Town and Kalabas Kraal, Sep. 1927, *L. Bolus* sub BOL 18823 (BOL, holo.).

*Lampranthus maturus* N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum praecox* L.Bolus, Notes Mesembryanthemum 2: 3 (1928), *nom. illegit.* Type: Paarl distr., near Klappmuts, Sep. 1928, *L. Bolus* sub NBG 1045/24 (BOL, holo.).

*Lampranthus microsepalus* L.Bolus, J. S. African Bot. 27: 261 (1961). Type: Cape, Kleinberg near Tulbagh, July 1928, *Duthie* sub SUG 1410 (BOL, holo).

Very delicate short decumbent shrublet, rarely rooting, to 100 mm. Leaves ascending to spreading, free to bases, somewhat falcate, minutely papillose, to 4 mm long. Flowers solitary, short-stalked, 19 mm diam, pink, petaloid and filamentous staminodes white towards bases, filamentous staminodes and stamens conically collected. Aug.-Oct. On shale and sandy loamy plains; Tulbagh to Cape Town, Hermanus.

**Lampranthus lewisiae** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum lewisiae* L.Bolus, Notes Mesembryanthemum 3: 54 (1937). Type: Ceres distr., Gydouw Pass, Sep. 1936, *Lewis* sub BOL 21820 (BOL, holo.).

Plants erect to 7.5 cm tall. Leaves slightly scabrid, pointed, very shortly fused, 1.2(-1.4) cm long, 2 mm diam. Flowers solitary, pedicels 1.5-1.8 cm long, pink, ca. 25 mm diam., filamentous staminodes present. Sep. In sandstone; Ceres, distr., top of Gydouw Pass.

Note: Similar to *L. diffusus*, but more densely leafy, leaves pointed, dotted, very shortly fused.

Superficially also resembles *Erepsia esterhuyseniae* and *E. aperta*, but fruits of both species of *Erepsia* without valve wings, whereas broad valve wings in *L. lewisiae*; flowering time for *L. lewisiae* in September, whereas both species of *Erepsia* flower in summer (Dec.-Feb.).

**Lampranthus obconicus** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum obconicum* L.Bolus, Notes Mesembryanthemum 2: 220 (1930). Type: Calvinia distr., on hills near Nieuwoudtville, Sep. 1930, *L. Bolus sub BOL 19230* (BOL, holo.).

*Lampranthus paucifolius* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum paucifolium* L.Bolus, Notes Mesembryanthemum 1: 138 (1928). Type: Calvinia distr., Nieuwoudtville, Sep. 1927, *Compton sub NBG 1509/26* (BOL, holo.).

Erect shrub, 20-30 cm high, stems shiny brown. Leaves ascending, trigonous, slightly rough, to 1 cm long. Flowers 1-3, 27 mm diam., pink, filamentous staminodes and stamens conically collected. Sep. In sand; near Nieuwoudtville.

Note: Very similar to *L. staminodiosus*, but flowering time in Sep. (Dec. in *L. staminodiosus*).

**Lampranthus pauciflorus** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum pauciflorum* L.Bolus, Ann. Bolus Herb. 4: 90 (1927). Type: Cape, Noetzie, Knysna, 24 Sep. 1925, *Phillips sub BOL 18552* (BOL, holo.; K).

*Lampranthus swartbergensis* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum swartbergense* L.Bolus, Notes Mesembryanthemum 1: 137 (1928). Type: Cape, Swartberg, Jul. 1926, *M. A. Pocock 96* (BOL, holo.).

*Lampranthus subaequalis* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum subaequale* L.Bolus, Notes Mesembryanthemum 3: 56 (1937). Type: Uniondale distr., *Fourcade sub NBG 1883/34* (BOL, holo.).

*Lampranthus sparsiflorus* L.Bolus, Notes Mesembryanthemum 3: 332 (1958). Type: Cape, Plettenberg Bay, Feb. 1955, *Esterhuysen 24218* (BOL, holo.).

Small shrublet, to 30 cm, with angled branches. Leaves erect or ascending, subfalcately incurved, 18 mm long, 3 mm thick. Flowers 1(-3), pedicels 2-4 cm long, 3-4 cm diam., purple often with yellow base, petals merge into filamentous staminodes. Oct.- Dec. In sandstone, to 1440 m, Plettenberg Bay to Uniondale.

**Lampranthus peacockiae** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939).

*Mesembryanthemum peacockiae* L.Bolus, Ann. Bolus Herb. 3: 71 (1921). Lectotype (designated here): Darling, Sep. 1917, *W. Peacock sub NBG 1659/17* (BOL).

Creeping to decumbent slender shrublet, flowering branchlets erect, 2-4 cm long. Leaves free towards bases, almost terete, papillate, glaucous, 6-9 mm long, 1.5 mm diam. Flowers solitary, pedicels 7-

10 cm long, 2.5-3 cm diam., rose or pale rose, filamentous staminodes and stamens conically collected.

Aug.-Sep. At 80 m, in shale among rhenosterveld; Darling to Lion's Head.

Note: Similar to *L. filicaulis*, but leaves much shorter and more slender, slightly papillate.

**Lampranthus scaber** (L.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum scabrum* L.

Sp. Pl.: 483 (1753). Lectotype: *Dillenius*, Hort. Eltham.: t. 197, fig. 251 (1732).

*Lampranthus paarlensis* L.Bolus, J. S. African Bot. 27: 261 (1961). Type: Cape Prov., Paarl div.,

Daljosaphat, Aug. 1937, *A. J. Middlemost sub NBG 1360/37* (BOL, holo.).

*Lampranthus virgatus* L.Bolus, J. S. African Bot. 27: 262 (1961). Type: Cape, 1 mile from Alpha towards

Algeria, Sep. 1938, *L. Bolus sub BOL 27100* (BOL, holo.).

Richly and irregularly basitonically branched shrublet, 20-30 cm high; rootstock tuberous, c. 10-15 cm long. Leaves linear, trigonous, scabrid, partly or occasionally completely deciduous, 10-20 mm long, 2-4 mm wide. Flowers mostly solitary, to 30 mm diam., pale lilac, shiny, filamentous staminodes and stamens conically collected. Aug.-Sep. Plateau of granite hills in rhenosterveld and in seasonally wet areas, at 100-400 m; Algeria to Cape Flats.

Note: Liede & Meve (1990) discussed the identity of this species in detail. Whereas the authors cited only two known localities for *L. scaber* from the Darling area, several new locations have been discovered since. Nevertheless the species remains rare, since most of its habitat has been severely reduced.

**Lampranthus sociorum** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum*

*sociorum* L.Bolus, Ann. Bolus Herb. 3: 132 (1922). Lectotype (designated here): Darling, Sep.

1917, *W. Peacock & L. Bolus sub NBG 1666/17* (BOL).

Low creeping slender shrub, with elongated branches, rooting at nodes. Leaves subfalcate, acute towards apex, set with fine dots, to 15 mm long, narrow. Flowers solitary, pedicels 6-20 mm long, to 35 mm diam., purplish, filamentous staminodes and stamens conically collected. Aug.-Nov. Sandy flats or lower slopes; Citrusdal to Darling.

**Lampranthus staminodiosus** (L.Bolus) Schwantes ex H.Jacobsen, Natl. Cact. Succ. J. 4: 58 (1949).

*Mesembryanthemum staminodiosum* L.Bolus, Notes Mesembryanthemum 3: 76 (1937). Type:

Cape, Elands Kloof, Cedarberg, 24 Nov. 1936, *G.J. Lewis sub BOL 21839* (BOL, holo.).

*Lampranthus macrostigma* L.Bolus, Notes Mesembryanthemum 3: 274 (1954). Type: Cape, Cedarberg,

Driehoek Valley, Dec. 1950, *Esterhuysen 18608* (BOL, holo.).

Erect shrub, to 13-22 cm tall. Leaves somewhat falcate, rough, glaucous, 7-14 mm long, 1.75 mm wide and thick. Flowers solitary, pedicels 1-1.8 cm long, 12 mm diam., white or dark purple to maroon, filamentous staminodes and stamens conically collected. Nov.-Dec. On sandstone; Cedarberg, Phisantefontein.

Note: Very similar to *L. obconicus*, but flowering time in summer (spring in *L. obconicus*).

**Lampranthus subluxus** L.Bolus Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum laxum* L.Bolus, Notes Mesembryanthemum 2: 406 (1933), *nom. illegit.* Type: amongst plants collected at Nieuwoudtville, Sep. 1930, *L.Bolus sub BOL 20165* (BOL, holo.).

*Lampranthus intervallaris* L.Bolus, J. S. African Bot. 26: 160 (1960). Type: Cape, 10 miles south of Clanwilliam, Aug. 1959, *H. Hall 1785* (BOL, holo.)

Laxly branched shrub, to 16 cm tall. Leaves tapered, obtuse to acute, green, 1.5-2.0 cm long, slender. Flowers 1-3, pedicels 25-30 mm long, 2.2-2.8 cm diam., pale pink, filamentous staminodes and stamens conically collected. Aug. ?; Nieuwoudtville to Clanwilliam.

**Lampranthus vallis-gratiae** (Schltr. & A. Berger) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930).

*Mesembryanthemum vallis-gratiae* Schltr. & A. Berger, Bot. Jahrb. Syst. 57: 634 (1922). Type: Cape, Genadendal, 1 Apr. 1897, *Schlechter 10303* (B, holo.; BOL, BM, K, PRE).

*Lampranthus verecundus* (L.Bolus) L.Bolus, Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum verecundum* L.Bolus, Notes Mesembryanthemum 1: 134 (1928). Type: Riversdale div., Phisantefontein, Apr. 1926, *Muir 3865* (BOL, holo.).

*Lampranthus falcatus* var. *galpinii* (L.Bolus) L.Bolus ex H.Jacobsen, Feddes Repert. Beih. 106: 87 (1938).

*Mesembryanthemum falcatum* var. *galpinii* L.Bolus, Notes Mesembryanthemum 2: 234 (1931).

Type: Cape, near Bredasdorp, Nov.-Dec. 1930, *Galpin sub NBG 2669/30* (BOL, holo.).

*Lampranthus middlemostii* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum middlemostii* L.Bolus, Notes Mesembryanthemum 2: 329 (1932). Type: Caledon distr., near Houw Hoek, *Middlemost sub NBG 2071/28* (BOL, holo.).

Erect, dainty shrublet, 15-20 cm tall. Leaves subfalcate, set with round papillae, 4-6 mm long, to 3 mm diam, grey. Flowers 1-3, pedicels 10-20 mm long, 16-24 mm diam., white or pink, with few filamentous staminodes and stamens conically collected. Nov.-Jan. On mountains, in sandstone; Houw Hoek, Genadendal, Riversdale.

Note: Similar to *L. falcatus*, but more densely leafy and inflorescence 1-3-flowered.

*B: without filamentous staminodes*

**Lampranthus acutifolius** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 211 (1930). *Mesembryanthemum acutifolium* L.Bolus, Notes Mesembryanthemum 2: 59 (1929). Type: Malmesbury distr., Riebeeck's Kasteel, Jan. 1928, *Pillans BOL 18871* (BOL, holo.).

*Lampranthus leptosepalus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum leptosepalum* L.Bolus, Notes Mesembryanthemum 2: 489 (1935). Type:

Clanwilliam distr., Uitkyk Pass, Cedarberg mountains, 3500 ft., Dec. 1934, *Compton sub BOL 21430*

(BOL, holo).

*Lampranthus walgateae* L.Bolus, Notes Mesembryanthemum 3: 159 (1939). Type: Distr. Swellendam, Tradouw Pass, Oct. 1938, *Walgate sub BOL 21853* (BOL, holo.).

Erect, slender shrublet, to 40 cm tall. Leaves erect, narrowed towards tip, dull green, set with round papillae, 15-35 mm long, 2 mm thick and wide. Flowers 1-3, pedicels to 20 mm long, 30 mm diam., magenta or pink, no filamentous staminodes present, inner petals very short. Nov.-Mar. At 1170 m, rocky kloof; Uitkyk Pass, near Algeria, Tradouw Pass, near Swellendam.

Note: Similar to *L. leipoldtii*, but leaves longer, flowers 1-3 and flowering time later from Nov.-Mar.

**Lampranthus candidus** L.Bolus, Notes Mesembryanthemum 3: 156 (1939). Type: Piquetberg distr., Jonker's Klip, 2 miles north of Verloren Vlei and eastern slope of Muishoekberg, south side of Verloren Vlei, Oct. 1938, *Pillans 8852*. (BOL, holo.; K).

Erect, loosely branched, very slender shrub, 25-30 cm tall. Leaves spreading, subfalcate, rough, 6 mm long, 1.5-2 mm wide and thick. Flowers 1-5-flowered inflorescence, pedicels 10-17 mm long, to 2 cm diam., white. Oct. On sandstone; Piquetberg.

Note: Similar to *L. falcatus*, but plants more robust, with stiff branches. Flowers shortly stalked and flowers in October.

**Lampranthus emarginatus** (L.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum emarginatum* L., Sp. Pl., edn 2: 692 (1762). Lectotype: *Dillenius*, Hort. Eltham.: t. 197, fig. 250 (1732).

*Lampranthus emarginatoides* (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum emarginatoides* Haw., Obs. gen. Mesemb. 343 (1795). Lectotype (designated here): Watercolour original by M. Page, plate 1934, based on *BOL 17302*, BOL.

*Lampranthus violaceus* (DC.) Schwantes ex H.Jacobsen, Feddes Repert. Spec. Nov. Regni. Veg. 43: 230 (1938). *Mesembryanthemum violaceum* DC, Pl. Grass.: t. 84 (1799). Lectotype (designated here): Pl. Grass.: t. 84 (1799).

*Lampranthus emarginatus* var. *puniceus* (Jacq.) Schwantes ex H.Jacobsen, Feddes Repert. Beih. 106: 97 (1938). *Mesembryanthemum puniceus* Jacq., Hort. Schoenbr.: t. 442 (1804). Lectotype (designated here): Hort. Schoenbr.: t. 442 (1804).

*Mesembryanthemum polyphyllum* Haw., Rev. Pl. Succ.: 141 (1821). Lectotype (designated here): Watercolour original by T. Duncanson (99/) (930) (M/114) (K!).

*Lampranthus imbricans* (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum imbricans* Haw., Suppl. Pl. Succ.: 94 (1819). Lectotype (designated here): Watercolour original by T. Duncanson (181?) (K!).

- Erepsia urbaniana* (Schltr.) Schwantes, Gartenflora 78: 68 (1928). *Mesembryanthemum urbanianum* Schltr., Bot. Jahrb. Syst. 24: 445 (1897). Type: Cape, Sir Lowry's Pass, 17 Jan. 1896, *Schlechter* 7280 (B, holo.!, BOL).
- Lampranthus subrotundus* L.Bolus, Notes Mesembryanthemum 3: 170 (1939). *Mesembryanthemum subglossum* L.Bolus, Notes Mesembryanthemum 3: 56 (1937). Type: *sub* *SUG* 1477a (BOL, holo.). Erect shrub, to 20 cm, with slender branches. Leaves erect, slender, dull green, set with round papillae, 10-15 mm long. Flowers stalked, 1-3, 34 mm diam., pale pink to pink. Oct.-Jan. ?; Cape Peninsula and Gordon's Bay.
- Note: Similar to *L. deflexus* (Aiton) N.E.Br., but filamentous staminodes absent and flowering in summer (spring for *L. deflexus*).
- Lampranthus falcatus** (L.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum falcatum* L., Sp. Pl.: 484 (1753). Lectotype (designated here): *Dillenius* (OXF).
- Lampranthus tulbaghensis* (A.Berger) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum tulbaghense* A.Berger, Bot. Jahrb. Syst. 57: 637 (1922). Type: Tulbagh waterfall, 15 Jan. 1896, *Schlechter* 7477 (B, holo; K, E, S, G, PRE!).
- Lampranthus framesii* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum framesii* L.Bolus, Notes Mesembryanthemum 1: 137 (1928). Type: Cape, between Hermanus and Bredasdorp, Feb., *P. Ross Frames sub* *NBG* 318/27 (BOL, holo.).
- Lampranthus capillaceus* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum capillaceum* L.Bolus, Notes Mesembryanthemum 1: 137 (1928). Type: Tulbagh distr., near Tulbagh, Jan. 1928, *Stokoe sub* *BOL* 18781 (BOL, holo.).
- Erect, dainty shrub, to 30 cm, with slightly hirsute branches. Leaves 3-angled, shortly acuminate, rough, 5-10 mm long, slender. Flowers numerous, pedicels 3-4 cm long with bracts midway, to 26 mm diam., purple, pink to white. Jan.-Feb. Rocky and moist places in mountains, on sandstone; Tulbagh, Worcester, Hermanus to Swellendam.
- Lampranthus glomeratus** (L.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum glomeratum* L., Syst. Nat., ed. 10: 1060 (1758). Lectotype (designated here): *Dillenius s.n.* (OXF).
- Mesembryanthemum falcatum* Lam., Encyc. 2: 482 (1788). Lectotype (designated here): Cape Peninsula, north-eastern slopes of Karbonkelberg, Dec. 1919, *Pillans* 4147 (BOL).
- Lampranthus furvus* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum furvum* L.Bolus, Notes Mesembryanthemum 1: 134 (1928). Type: Cape, near Gordon's Bay, Nov.--Dec. 1927, *Lavis sub* *BOL* 18760 (BOL, holo.).
- Lampranthus austriicola* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939).
- Mesembryanthemum austriicola* L.Bolus, Notes Mesembryanthemum 2: 453 (1934). Type: Cape

Peninsula, between Smitswinkel and Olifantsbosch, Jan. 1934, *Salter 4264* (BOL, holo.).

*Lampranthus aestivus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939). *Mesembryanthemum aestivum* L.Bolus, Notes Mesembryanthemum 2: 188 (1930). Type: Caledon distr., near Kleinmond, Jan. 1929, *Edwards sub BOL 19098* (BOL, holo.).

Erect shrublet, 20-30 cm tall with slender stiff or decumbent branches. Leaves acute, green, 12-18 mm long, slender, with prominent dots. Flowers numerous, pedicels 2 (-4) cm long with bracts midway, to 25 mm diam., violet or rose-purple. Dec.-Jan. On lower sandstone slopes; Cape Town to Hermanus.

***Lampranthus leipoldtii*** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum leipoldtii* L.Bolus, Notes Mesembryanthemum 2: 156 (1930). Type: Worcester distr., road between Worcester and Villiersdorp, Oct. 1928, *Leipoldt sub BOL 18997* (BOL, holo.).

*Lampranthus purpureus* L.Bolus, Notes Mesembryanthemum 3: 157 (1939). Type: Clanwilliam Div., Olifants River Valley, hills one mile south-east of Keerom, Nov. 1938, *Pillans 8670* (BOL, holo.).

Loosely branched shrub, to 400 mm. Leaves erect, rough, glaucous, 15-35 mm long, slender. Flowers solitary, rarely 2-3, pedicels 34-45 mm long, to 30 mm diam., purplish. Oct.-Nov. In sand; Keerom, Villiersdorp and Worcester.

Note: Similar to *L. emarginatus*, but flowers solitary. Differs from *L. acutifolius*, see above.

***Lampranthus pocockiae*** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum pocockiae* L.Bolus, Ann. Bolus Herb. 4: 80 (1927). Type: Prince Albert div., Swartberg, Jun. 1926, *M.A. Pocock S.158* (BOL, holo.).

*Lampranthus brevistamineus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939).

*Mesembryanthemum brevistamineum* L.Bolus, Notes Mesembryanthemum 2: 155 (1929). Type: Worcester distr., at foot of Matroosberg, *Stokoe sub NBG 855/25* (BOL, holo.; K).

Dainty tangled shrublet, to 14 cm. Leaves cuneate to sabre-shaped, short-tapered, to 11 mm long, 2 mm wide and thick. Flowers short-stalked, solitary, 20-30 mm diam., purplish, petaloid staminodes spatulate. Oct.-Dec. On sandstone, Matroosberg to Swartberg.

Note: Similar to *L. falcatus*, but flowers solitary.

***Lampranthus rupestris*** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum rupestre* L.Bolus, Notes Mesembryanthemum 1: 134 (1928). Type: Cape, Paardeberg, Sep., *Pillans sub BOL 18780* (BOL, holo.).

Slender shrublet, to 15 cm, branches spreading, prostrate to creeping. Leaves grey, rough, to 12 mm long, 2 mm diam. Flowers 1-3, pedicels c. 20 mm long, to 25 mm diam., white. Oct. Shallow depressions on granitic outcrop; Paardeberg.

Note: This species is only known from the Paardeberg.

### Section *Tenuifolii*

Plants erect or creeping and rooting at nodes. Leaves either shortly fused or free towards bases, long, slender, often papillate. Flowers solitary or ternate, mostly > 3 cm in diam., filamentous staminodes present or absent, occasionally collected around the stamens but never in a strict cone, all colours, petaloid staminodes often very numerous and threadlike. Seeds with flattened testa cells, occasionally with convex testa cells.

**Lampranthus bicolor** (L.) N.E.Br., Gard. Chron., ser. 3, 87: 211 (1930). *Mesembryanthus bicolor* (L.) Rothm., Notizbl. Bot. Gart. Berlin 15: 414 (1941). *Mesembryanthemum bicolor* L., Sp. Pl.: 485 (1753). Lectotype (designated here): "*M. bicolor*" as "*M. bicolorum*", S. 205 17 (LINN).

*Lampranthus inaequalis* (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Lampranthus bicolorus* var. *inaequalis* (Haw.) Schwantes ex H.Jacobsen, Feddes Repert. Beih. 106: 96 (1938).

*Mesembryanthemum bicolorum* var. *inaequale* (Haw.) A. Berger, Mesemb. Portulac.: 152 (1908).

*Mesembryanthemum inaequale* Haw., Syn. Pl. Succ.: 266 (1812). Lectotype (designated here):

Watercolour original by T. Duncanson (225) (K).

*Lampranthus antemeridianus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939).

*Mesembryanthemum antemeridianum* L.Bolus, Notes Mesembryanthemum 1: 135 (1928). Type: Cape, near Albertinia, Nov.-Feb., *Muir sub NBG 1505/21* (BOL, holo.).

*Mesembryanthemum antemeridianum* f. *flore-pleno*, Notes Mesembryanthemum 2: 404 (1933). Type: Riversdale distr., in sand dunes, on farm Welgevonden, Apr. 1933, *Ferguson sub BOL 20821* (BOL, holo.).

Stiff, erect shrublet, to 500 mm. Leaves almost trigonous, shortly fused towards bases, green, rough, 12-25 mm long. Flowers 1-3, stalked, yellow with scarlet or copper reverse, 2-3.5 cm diam.. Nov.-Feb. Deep sandy flats or lower slopes; Cape Flats and Peninsula to Albertinia.

Note: *Mesembryanthemum bicolorum* L. was transferred to *Lampranthus bicolorus* (L.) N.E.Br. ex Jacobsen (Jacobsen 1955: 1426). However, in Linnaeus (1762) all citations are identical to those in Linnaeus 1753: 485, except that he cites an additional figure in the second edition (Mill. Dict.: t. 177, fig. 1.). On account of the identical citations and the fact that fig. 1 in Miller's Dictionary depicts a typical specimen of *Lampranthus bicolor*, it can be deduced that Linnaeus did not intend to describe a new species.

**Lampranthus coccineus** (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum coccineum* Haw., Obs. gen. Mesemb.: 247 (1795). Lectotype (designated here): Watercolour original by T. Duncanson (196) (K).

*Lampranthus variabilis* (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum*

*variabile* Haw., Misc. Nat.: 85 (1803). Lectotype (designated here): Watercolour original by B. O. Carter, plate 2085 (BOL).

*Lampranthus brownii* (Hook. f.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum brownii* Hook. f., Bot. Mag. 114: t. 6985 (1888). Type: Hort. Kew, 7 July 1887 (K, holo.).

*Lampranthus sauerae* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum sauerae* L.Bolus, Notes Mesembryanthemum 2: 409 (1933). Type: Cape, near Ysterfontein, Sep. 1933, *M. Sauer sub* *SUG 9114* (BOL, holo.).

Erect or diffusely branched, 15-30 cm tall. Leaves free or very shortly fused towards bases (in young leaves), crowded on the short shoots, trigonous, to 25 mm long, dull grey green, covered with prominent grey-green dots. Flowers 1-3, pedicels 2-4 cm long, 35-40 mm diam., petals varying from reddish orange, which changes to various shades of pink as the flower withers. Sep.-Oct. ?; Saldanha Bay, Montagu, Stilbay.

Note: Very similar to *L. bicolor*, but flowers intensely reddish or various shades of pink and flowering time in spring (summer in *L. bicolor*).

***Lampranthus diutinus*** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum diutinum* L.Bolus, Ann. Bolus Herb. 3: 167 (1923). Type: Cape, Riversdale div., 1914, *Muir 2670* (= *NBG 1587/14*) (BOL, holo.).

*Lampranthus ceriseus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939). *Mesembryanthemum ceriseum* L.Bolus, Notes Mesembryanthemum 2: 327 (1932). Type: Riversdale distr., Melkhoutfontein, near Still Bay, Jan. 1931, *L. Bolus sub* *BOL 19926* (BOL, holo.).

*Lampranthus foliosus* L.Bolus, Notes Mesembryanthemum 3: 226 (1950). Type: Cape, Gansbaai, Baviaansfontein, Sep. 1940, *Stokoe sub* *BOL 22742* (BOL, holo.).

*Lampranthus salteri* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum salteri* L.Bolus, Notes Mesembryanthemum 2: 428 (1934). Type: Bredasdorp distr., Cape Agulhas, Nov.-Dec. 1933, *Salter 4099* (BOL, holo.).

Shrublet to 15 cm, branches spreading to prostrate to 20 cm long. Leaves fused towards bases, erect, acute or shortly acuminate, 15-30 mm long, 1.5-3 mm wide. Flowers short-stalked, solitary, c. 30 mm diam, petals reddish inside, purple reverse, without filamentous staminodes. Aug.-Dec. On limestone, Stilbay, Cape Agulhas.

***Lampranthus explanatus*** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum explanatum* L.Bolus, Ann. Bolus Herb. 3: 166 (1923). Type: Somerset Strand, Oct. 1919, *Page sub* *BOL 15201* (BOL, holo.).

Two subspecies are recognized:

*Lampranthus explanatus* subsp. *explanatus*

*Lampranthus sternens* L.Bolus, Notes Mesembryanthemum 3: 158 (1939). Type: Bredasdorp distr., Cape Agulhas, Jan. 1938, *Mathews sub BOL 21852*. (BOL, holo.).

Slender creeping shrublet with elongated branches, with erect flowering branchlets 3-8 cm tall. Leaves shortly fused, acute or obtuse, smooth 1.5-2.5 cm long, to 2 mm diam. Flowers solitary, pedicels 1-2.5 cm long, 3-5.5 cm diam., yellow, without filamentous staminodes. Aug.-Oct. Sandy flats: Cape Flats to Cape Agulhas.

**Lampranthus explanatus** subsp. **procumbens** subsp. nov. Type: Namaqualand, Koiingnaas, Skulpfontein, 24 Aug. 1999, *National Geographic – IPC tour 188* (BOL, holo.); *a subspecie explanato foliis brevioribus crassioribusque, ramulis florentibus brevioribus et physocellulis epidermalis planioribus differt.*

Plants prostrate, trailing, rooting at nodes, the flowering branchlets erect, to 5.5 cm tall. Stems brown, internodes 3 cm long. Leaves shortly fused towards bases, spreading to erect, trigonous, (11-)16-21 mm long, 2-3 mm broad and wide, glaucous, smooth. Flowers solitary, pedicels to 10 mm long, golden yellow, 4-5 cm diam., without filamentous staminodes, anthers papillate at base. Fruits 5-locular, base funnel-shaped, top raised, without closing body, valve wings broad, keels diverging. Aug. In sandy flats, among fynbos vegetation, Namaqualand.

Note: This taxon is so far only known from a single collection. The epithet “*procumbens*” refers to its creeping habit.

**Lampranthus fergusoniae** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939).

*Mesembryanthemum fergusoniae* L.Bolus, Notes Mesembryanthemum 2: 427 (1928). Type: near Riversdale, in calcareous dunes, Nov. 1933, *Ferguson sub BOL 21002* (BOL, holo.).

*Lampranthus fergusoniae* var. *crassistigma* L.Bolus, J. S. African Bot. 26: 159 (1960). Type: Cape, Shelly Beach near Bredasdorp, Dec. 1954, *H. Hall sub BOL 25655* (BOL, holo.).

*Lampranthus baylissii* L.Bolus, J. S. African Bot. 31: 240 (1965). Type: Cape, Knysna, Flat Rock, Nov. 1964, *Bayliss 1083 (= NBG 1103/62)* (BOL, holo.).

Prostrate to decumbent, slender shrub, to 15 cm tall, rooting at nodes. Leaves erect, shortly fused towards bases, compressed, back surface bluntly keeled, acute, rough, to 17 mm long, slender. Flowers solitary, pedicels 3-10 mm long, 3 cm diam., yellow or orange-red, without filamentous staminodes. Nov.-Dec. Limestone dunes; Riversdale, Sedgfield.

Note: Similar to *L. bicolor*, but prostrate to decumbent, growing on limestone.

**Lampranthus galpiniae** (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum galpiniae* L.Bolus, Notes Mesembryanthemum 2: 328 (1932). Type: Bredasdorp distr., Struisbay near Cape Agulhas, Jan. 1931, *M. Galpin sub NBG 2/31* (BOL, holo.).

Erect shrublet, to 10 cm tall with slender branches. Leaves erect, rarely falcate, semicylindrical, narrow, acute, to 22 mm long. Flowers solitary, to 60 mm diam., white with pink centre. Oct.-Nov. On limestone; Struisbay, Bredasdorp.

Note: Very similar to *L. diutinus*, but flowers white with purple centre. Possibly only a form of *L. diutinus*.

**Lampranthus immelmaniae** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum immelmaniae* L.Bolus, Notes Mesembryanthemum 1: 136 (1928). Type: Sep. 1926, *Immelman sub BOL 18715* (BOL, holo.).

*Lampranthus densifolius* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 168 (1939).

*Mesembryanthemum densifolium* L.Bolus, Notes Mesembryanthemum 1: 136 (1928). Type: Cape, near Vredenburg, without date, *J. W. Mathews sub NBG 1705/24* (BOL, holo.).

*Lampranthus eximius* L.Bolus, Notes Mesembryanthemum 3: 273 (1954). Type: Cape, Ysterfontein, Oct. 1951, *H. Hall sub NBG 1354/50* (BOL, holo.).

Shrub with prostrate stems, to 5 cm long, floral branches erect, 15-29 cm long. Leaves free towards bases, ascending to erect, acute, 15-22 mm long. Flowers 1-3, 4.5-5.5 cm diam., purplish, occasionally few filamentous staminodes collected into cone around stamens. Oct.-Nov. In sandy flats; Hopefield to Malmesbury; introduced in Australia.

Note: Similar to *L. tenuifolius*, but leaves free towards bases and flowers mostly ternate.

**Lampranthus multiseriatus** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 21(1930). *Mesembryanthemum multiseriatum* L.Bolus, Ann. Bolus Herb. 4: 128 (1928). Lectotype (designated here): Cape, Ou Tuin near Albertinia, Oct. 1921, *Muir 2416* (BOL).

*Lampranthus perreptans* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum humile* L.Bolus, Notes Mesembryanthemum 2: 73 (1929), *nom. illegit.* Type: Swellendam distr. ?, *van der Merwe NBG 1195/28* (BOL, holo.).

Prostrate to decumbent shrub, rooting at nodes, with erect flowering branchlets to 10 cm tall. Leaves free towards bases, subfalcate, shortly acuminate, dull green, to 20 mm long, 3 mm wide and thick. Flowers solitary, pedicels 2-4 cm long, 43 mm diam., pink, without filamentous staminodes, anthers not papillate. Oct. ?; Albertinia, Riversdale.

**Lampranthus pakhuisensis** L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum pakhuisense* L.Bolus, Notes Mesembryanthemum 2: 364 (1932). Type: Clanwilliam distr., Pakhuis Pass, Sep.-Oct. 1932, *Salter 2667* (BOL, holo.).

*Lampranthus martleyi* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum martleyi* L.Bolus, Notes Mesembryanthemum 2: 366 (1932). Type: Piquetberg distr., between

Piquetberg and Langebaan, *Martley sub BOL 20205* (BOL, holo.).

*Lampranthus plenus* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939). *Mesembryanthemum plenum* L.Bolus, Notes Mesembryanthemum 2: 407 (1933). Type: Clanwilliam distr., Olifants River Valley, between Modderfontein and Warm Bath, Oct. 1932, *L. Bolus sub BOL 20818* (BOL, holo.).

*Lampranthus leightoniae* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum leightoniae* L.Bolus, Notes Mesembryanthemum 2: 488 (1935). Type: Clanwilliam distr., Kromme River, Cedarberg mountains, Sep. 1934, *Leighton sub BOL 21424* (BOL, holo.).

*Lampranthus berghiae* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939). *Mesembryanthemum berghiae* L.Bolus, Notes Mesembryanthemum 3: 127 (1938). Type: Clanwilliam distr., in hills, between Pakhuis and Nardouw, Aug.-Sep. 1937, *Bergh sub BOL 21842* (BOL, holo.).

Erect shrub, to 50 cm, branches angled below, otherwise cylindrical, scin shiny brown. Leaves free towards bases, ascending, trigonous, glaucous, to 25 mm long, c. 3 mm wide and thick. Flowers 1-3, pedicels 7-10 mm long, to 40 mm diam., pink to pale pink, petaloid staminodes very numerous, filamentous staminodes and stamens collected. Aug.-Nov. On sandy stony slopes, often among Restionaceae; Clanwilliam to Kalbaskraal.

***Lampranthus peersii*** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum peersii* L.Bolus, Ann. Bolus Herb. 3: 131 (1922). Type: Cape, Graafwater, Sep., *Peers sub NBG 3002/15* (BOL, holo.).

Erect shrublet to 350 mm. Leaves free to bases, inclined or ascending, 3-angled, acute, glaucous, to 2 cm long. Flowers in a 3-5 flowered inflorescence, pedicels 4-4.5 cm long with bract midway, 35-44 mm diam., petaloid staminodes very numerous, golden-orange changing to red and finally rose-purple, filamentous staminodes filiform surrounding the stamens. Sep. ?, Clanwilliam distr, Graafwater.

Note: Very similar to *L. pakhuisensis*, but differs in the flower colour. A poorly known species.

***Lampranthus promontorii*** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum promontorii* L.Bolus, Ann. Bolus Herb. 4: 10 (1925). Type: Cape Peninsula, hills near Glencairn and slopes above the sea at Cape Point, *Arbuthnot sub BOL 17486* (BOL, holo.).

Erect shrublet to 200 mm, stems spreading. Leaves erect or spreading, fused towards bases, falcate, shortly acuminate, 10-23 mm long, 3 mm wide. Flowers 1-3, short-stalked, 14-23 mm diam., light yellow, without filamentous staminodes, stamens apapillate. Dec.-Jan. In sand often among rocks, Cape Peninsula.

***Lampranthus stenus*** (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum stenum* Haw., Till. Phil. Mag. 70: 420 (1831). Lectotype (designated here): Monogr.: § 46, 5 (1842).

*Lampranthus monticola* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 169 (1939).

*Mesembryanthemum monticola* L.Bolus, Notes Mesembryanthemum 2: 171 (1930). Type: Cape Peninsula, Table Mountain, Castle rock, at 540 m, *Cook sub NBG 1378/28* (BOL, holo.).

Many-branched slender erect shrub, to 30 cm tall, or straggling among bushes, or with elongated prostrate or creeping branches. Leaves shortly fused, subcylindrical, tapering, 12-30 mm long, 2 mm wide, often pale or whitish green. Flowers 1-3, pedicels 10 mm long, 2-3 cm diam., pale mauve, with threadlike petaloid staminodes, filamentous staminodes absent. Nov.-Feb. Sandy flats, Cape Peninsula, Cape Flats.

Note: Table Mountain, Castle rock which was given as the locality for *L. monticola* appears to be incorrect, see Notes Mesembryanthemum 3: 388 (1930).

***Lampranthus stenopetalus*** (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum stenopetalum* L.Bolus, Ann. Bolus Herb. 4: 10 (1927). Type: Cape, Graafwater, Oct. 1922, *Peers sub BOL 17830* (BOL, holo.).

*Lampranthus villiersii* (L.Bolus) L.Bolus, Notes Mesembryanthemum 3: 170 (1939). *Mesembryanthemum villiersii* L.Bolus, Notes Mesembryanthemum 2: 489 (1935). Type: Villiersdorp distr., Belgravia, *de Villiers sub NBG 2547/32* (BOL, holo.).

*Lampranthus subtruncatus* L.Bolus, Notes Mesembryanthemum 3: 159 (1939). Type: Piquetberg distr., eastern base of northern end of Piquetberg Mountain, Oct. 1938, *Pillans 8854* (BOL, holo.).

Erect shrublet, to 12 cm. Leaves free to bases, semicylindrical, scabrid, tapering, to 15 mm long, 1.5 mm wide and thick. Flowers short-stalked, 1-3, to 25 mm diam., pale pink or purple, filamentous staminodes and stamens collected into a cone. Nov. Sandy flats; Graafwater to Cape Peninsula.

Note: Similar to *L. stenus*, but more robust, leaves, free to bases, dark green and flowers purple.

***Lampranthus tenuifolius*** (L.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthus tenuifolius* (L.) Rothm., Notizbl. Bot. Gart. Berlin 15: 414 (1941). *Mesembryanthemum tenuifolium* L., Sp. Pl.: 484 (1753). Lectotype (designated here): *Linnaeus* in Hort. Cliff. (BM).

*Lampranthus magnificus* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum magnificum* L.Bolus, Ann. Bolus Herb. 4: 93 (1927). Type: Probably from the Paardeberg, exhibited at the Malmesbury flower show, Oct. 1926, *BOL 18532* (BOL, holo.).

Prostrate to decumbent shrublet, floral branches slender, ascending or erect. Leaves fused towards bases into a short sheath, erect, semicylindrical, acute, green, 25-45 mm long. Flowers long-stalked, solitary, 5 cm diam., crimson to reddish, petals numerous without filamentous staminodes. Oct. -Nov. Sandy flats, Malmesbury to Cape Peninsula to Struisbaai.

**Species already excluded from *Lampranthus***

*Lampranthus albus* L.Bolus = **Oscularia alba** (L.Bolus) H.E.K.Hartmann

*Lampranthus alpinus* (L.Bolus) G.D.Rowley = **Esterhuysenia alpina** L.Bolus

*Lampranthus capornii* (L.Bolus) L. Bolus = **Ruschia capornii** (L.Bolus) L.Bolus

Note: Although the type material of *Mesembryanthemum capornii* L.Bolus (Ann. Bolus Herb. 2: 30 1916) collected at Garies by *Caporn sub NBG 822/15* (BOL, holo.) did not bear any fruit, later collections of (presumably) the same species (*H. Hall NBG1060/50, NBG591/54*) fruited in Kirstenbosch. From an examination of the fruits of this garden material, L. Bolus placed the collection by Caporn in *Ruschia* (Notes Mesembryanthemum 3: 333, 1958). However, she placed *L. capornii* var. *longifolius* and *L. capornii* f. *fera* in synonymy with *Lampranthus lunulatus*. Recently, Hartmann (1999) included the latter two names in synonymy with *Ruschia capornii*. However, both types lack closing bodies in their fruits, so that the two latter names are still considered conspecific with *L. lunulatus*. Although the type of *R. capornii* could so far not be examined, the collections cited by L. Bolus (i.e. *H. Hall NBG1060/50* and *NBG591/54*) are distinct from *L. lunulatus*.

*Lampranthus cedarbergensis* (L.Bolus) L.Bolus = **Oscularia cedarbergensis** (L.Bolus) H.E.K.Hartmann

*Lampranthus compressus* L.Bolus = **Oscularia compressa** (L.Bolus) H.E.K.Hartmann

*Lampranthus comptonii* (L.Bolus) N.E.Br. = **Oscularia comptonii** (L.Bolus) H.E.K.Hartmann

*Lampranthus comptonii* var. *roseus* (L.Bolus) L.Bolus ex H.Jacobsen = **Oscularia comptonii** (L.Bolus)  
H.E.K.Hartmann

*Lampranthus comptonii* f. *roseus* (L.Bolus) G.D.Rowley = **Oscularia comptonii** (L.Bolus)  
H.E.K.Hartmann

*Lampranthus copiosus* (L.Bolus) L.Bolus = **Oscularia copiosa** (L.Bolus). H.E.K.Hartmann

*Lampranthus deltoides* (L.) Glen = **Oscularia deltoides** (L.) Schwantes

*Lampranthus drepanophyllus* (Schltr. & A.Berger) N.E.Br. = **Esterhuysenia drepanophylla** (Schltr. & A.  
Berger) H.E.K.Hartmann

*Lampranthus dunensis* (Sond.) L.Bolus = **Erepsia dunensis** (Sond.) Klak

*Lampranthus excedens* (L.Bolus) L.Bolus = **Oscularia excedens** (L.Bolus) H.E.K. Hartmann

*Lampranthus herrei* (L.Bolus) L.Bolus = **Ruschia sandbergensis** L.Bolus

*Lampranthus longisepalus* L.Bolus = **Hammeria meleagris** (L.Bolus) Klak

*Lampranthus lunatus* (Willd.) N.E.Br. = **Oscularia lunata** (Willd.) H.E.K.Hartmann

*Lampranthus maximilianii* (Schltr. & A.Berger) L.Bolus = **Braunsia maximilianii** (Schltr.& A.Berger)  
Schwantes

*Lampranthus meleagris* L.Bolus = **Hammeria meleagris** (L.Bolus) Klak

*Lampranthus ornatus* L.Bolus = **Oscularia ornata** (L.Bolus) H.E.K.Hartmann

*Lampranthus piquetbergensis* (L.Bolus) L.Bolus = **Oscularia piquetbergensis** (L.Bolus) H.E.K.Hartmann

*Lampranthus paardebergensis* (L.Bolus) L.Bolus = **Oscularia paardebergensis** (L.Bolus) H.E.K.Hartmann

- Lampranthus prasinus* L.Bolus = **Oscularia prasina** (L.Bolus) H.E.K.Hartmann  
*Lampranthus primivernus* (L.Bolus) L.Bolus = **Oscularia primiverna** (L.Bolus) H.E.K.Hartmann  
*Lampranthus punctulatus* L.Bolus = **Ruschia punctulata** (L.Bolus) L.Bolus ex H.E.K.Hartmann  
*Lampranthus ruber* L.Bolus = **Astridia rubra** (L.Bolus) L.Bolus  
*Lampranthus steenbergensis* (L.Bolus) L.Bolus = **Oscularia steenbergensis** (L.Bolus) H.E.K.Hartmann  
*Lampranthus stoloniferus* L.Bolus = **Hammeria meleagris** (L.Bolus) Klak  
*Lampranthus superans* (L.Bolus) L.Bolus = **Oscularia superans** (L.Bolus) H.E.K.Hartmann  
*Lampranthus tanquanus* H.E.K.Hartmann = **Hammeria meleagris** (L.Bolus) Klak  
*Lampranthus thermarum* (L.Bolus) L.Bolus = **Oscularia thermarum** (L.Bolus) H.E.K.Hartmann  
*Lampranthus utilis* (L.Bolus) Schwantes = **Stoeberia utilis** (L.Bolus) v.Jaarsveld  
*Lampranthus vernicolor* (L.Bolus) L.Bolus = **Oscularia vernicolor** (L.Bolus) H.E.K.Hartmann  
*Lampranthus verruculatus* (L.) L.Bolus = **Scopelogenia verruculata** (L.) L.Bolus  
*Lampranthus vredenburghensis* L.Bolus = **Oscularia vredenburghensis** (L.Bolus) H.E.K.Hartmann  
*Lampranthus zygophylloides* (L.Bolus) N.E.Br. = **Drosanthemum zygophylloides** (L.Bolus) L.Bolus (Note:  
this is not a species of *Lampranthus* as suggested by Hartmann & Bruckmann 2000: 108).

#### Proposed assignment of residual names in *Lampranthus*

The correct identity of *Lampranthus viatorum* (L.Bolus) N.E. Br.

Since no fruit material is present on the type of *Lampranthus viatorum* (L.Bolus) N.E.Br., the placement of this species is difficult. Leaf morphology, however, unambiguously excludes this species from *Lampranthus*. A note by M. Fenton on the herbarium sheet suggests it to be synonymous with *Antimima bina* (L.Bolus) H.E.K. Hartmann. The type of *L. viatorum* shows the typical leaf features characteristic for *Antimima bina* (Hartmann 1998c) and also matches the description of the flowers. The two species are therefore considered synonymous. Since *L. viatorum* is the older epithet a new combination is made.

**Antimima viatorum** (L.Bolus) Klak, **comb. nov.** *Lampranthus viatorum* (L.Bolus) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum viatorum* L.Bolus, Ann. Bolus Herb. 3: 136 (1922).  
Type: Cape, between Bitterfontein and Stinkfontein, Dec. 1910, Pearson PSME 5575 (BOL, holo.).  
*Antimima bina* (L.Bolus) H.E.K. Hartmann, Bothalia 28(1): 70 (1998). *Ruschia bina* L.Bolus, Notes Mesembrianthemum 2: 282 (1931). Type: Clanwilliam div., in stony places on the road near Doorn R. Bridge, 27 May 1931, Pillans sub BOL 19610 (BOL, holo.).

### Excluded and unplaced species of *Lampranthus*

#### 1. Relationships of *Lampranthus schlechteri* (Zahlbr.) L.Bolus and *Lampranthus simulans* L.Bolus to *Erepsia*.

A closer investigation of the species placed in *Lampranthus* shows that two species, *Lampranthus simulans* and *L. schlechteri* also possess a hypanthium, which excludes them from *Lampranthus*. The circumscription of *Erepsia* (Liede 1989) suggests that these floral characteristics in conjunction with the fruit morphology would place them in *Erepsia*.

However, as shown in the molecular and combined study, *Erepsia* may not be monophyletic. As discussed above, one of the major difference between *E. inlaudens* and the other three species of *Erepsia* sampled in this study, is the presence of a meronectary. Although the majority of species of *Erepsia* have a holonectary, there are several others (*E. pentagona* (L.Bolus) L.Bolus, *Erepsia lacera* (Haw.) Liede, *E. forficata* (L.) Schwantes and *E. heteropetala* (Haw.) Schwantes), which also differ by the possession of a meronectary.

As in *E. inlaudens*, *Lampranthus schlechteri* is also unusual in having meronectaries, which are occasionally found in *Erepsia*, but never in *Lampranthus*. The leaf morphology of this species diverges from that of a typical *Erepsia*. Instead of the triquetrous, hooked leaves, the species exhibits acute, almost filiform, obscurely terete leaves. Thus, the presence of the hypanthium and the meronectaries place it most closely to *E. inlaudens*.

Unfortunately, the nectary structure of *L. simulans* was not mentioned in the protologue nor does a drawing of the floral morphology exist. In addition, the species has not been recollected since the collection of the type by E. Esterhuysen, so that no fresh material has been investigated. The name of the species alludes to L. Bolus' view (stated in the protologue) that this species only simulates a species of *Erepsia*. However, she gives no details which would firmly exclude it from this genus. Liede (1989) was also aware of this species, but provided no discussion of whether or not it may be included in *Erepsia*. Until fresh material has been investigated the position of this species has to remain uncertain.

The synonymy with short descriptions are given below for the two species.

*Lampranthus schlechteri* (Zahlbr.) L.Bolus, Notes Mesembryanthemum 3: 227 (1950).

*Mesembryanthemum schlechteri* Zahlbr., Ann. K.K. Nat. Hofmus. 15: 35 (1900). Type: Berg River near Franschoek, 17 Nov. 1896, *Schlechter 9214* (B, holo; BM, BOL, E, GRA, K, PRE, S, iso.).

*Mesembryanthemum sabulosum* Schltr., Bot. Jahrb. Syst. 27: 130 (1899). Type: Cape, Berg River near Franschoek, 17 Nov. 1896, *Schlechter 9214* (B, holo.; BM, BOL, E, GRA, K, PRE, S).

*Lampranthus perspicuus* (A.Berger) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum perspicuum* A.Berger, Bot. Jahrb. Syst. 57: 634 (1922). Type: as above, *Schlechter 9214*.

Shrublet with suberect to ascending branches, 13-20 cm tall. Leaves free to bases, included, acute, 1-2 cm long, 1 mm thick. Flowers 1-3, short-stalked, to 5 cm diam, salmon, nectaries in five parts, petaloid staminodes shorter towards the centre and largely concealing the reproductive parts, filamentous staminodes absent, walls of hypanthium erect, stamens apapillose and free towards bases, only inner ones hanging. Nov. Sandy plain; Stellenbosch and French Hoek.

*Lampranthus simulans* L.Bolus, Notes Mesembryanthemum 3: 273 (1954). Type: Cape, Brandfontein, Bredasdorp, Oct. 1951, *Esterhuysen 18960* (BOL, holo.).

Erect dainty, loosely branched shrub, 14-16 cm tall. Leaves shortly fused towards bases, ascending, narrowed towards the tip in profile, acute to somewhat obtuse, 10-17 mm long, sheath 2 mm long, 4-6 mm thick. Flowers solitary, rarely 2-3, pedicels 1-2 cm long, bracts slightly subtending the flower, petals silvery white with pink tips, 20-32 mm diam., nectaries unknown, walls of hypanthium sloped. Oct. In sand, on flats; Bredasdorp distr., Brandfontein.

## 2. The identity of *Lampranthus erratus* N.E.Br. and *Lampranthus glaucoides* (Haw.) N.E.Br.

Jacobsen (1970) listed *Lampranthus erratus* as an insufficiently known species, which was described and illustrated as *Mesembryanthemum virens* in 1840 by Salm Dyck. However, since this epithet had already been used by Haworth, N. E. Brown gave it a new name when he transferred it to *Lampranthus*. The new name, *Lampranthus erratus*, remained obscure and was not mentioned by Glen (1978). On account of certain very unusual characters displayed by this species (the 6-locular fruits without closing bodies, flowers with their filamentous staminodes collected) this name appears to be conspecific with *Ruschia knysnana* (L.Bolus) L.Bolus.

In addition, *Lampranthus glaucoides*, seems to be an even earlier name for this species. It had been placed by Berger (1908) and later by Jacobsen (1970) in synonymy with *L. aurantiacus*, whereas Glen (1978) believed it to be conspecific with *L. glaucus*. In the protologue Haworth pointed out the very striking similarity of this species with *Lampranthus glaucus*. According to Haworth, differences included the fact that the leaves were smooth and covered with pellucid dots in *L. glaucoides*. The most striking difference from *L. glaucus* is its reportedly purple flowers. Although no type material was cited, the detailed description given by Haworth matches quite accurately the plant depicted by Salm Dyck (1840) as *Mesembryanthemum virens*. Since the purple colour of the petaloid staminodes may fade into orange as the flower matures, *L. glaucoides* is unlikely to be conspecific with *L. aurantiacus*. In addition, like *L. glaucus* the latter species has a slightly rough epidermis, whereas the surface of the leaf was described as smooth in *L. erratus* and *L. glaucoides*.

Although there is as yet no species-level revision available for *Ruschia*, a list of the currently recognised species was compiled by Hartmann (1999). Although the species in the genus have almost exclusively 5(-6)-locular fruits with closing bodies, Hartmann retained a few species in *Ruschia* which lack

closing bodies. *Lampranthus erratus*, however, does not belong in *Lampranthus*, on account of its fruit and leaf epidermal characters. All species of *Lampranthus* have expanding keels, which are broadened, whereas they are narrow throughout in *L. erratus*. In addition, the epidermis is xeromorphic with sunken stomata and small cell diameters (45-48µm), which are never found in *Lampranthus*. Hartmann (1999) noted that the capsules most closely resemble fruits of *Erepsia* or *Esterhuysenia*. However, the floral morphology of *L. erratus* differs from *Erepsia* in that it does not have a hypanthium, but it does resemble closely the floral morphology of some species of *Esterhuysenia*, such as *E. drepanophylla*. Characteristic of *Ruschia knysnana* are the bright green leaves, which are present in all but one species of *Esterhuysenia* (*E. stokoei* (L. Bolus) H.E.K. Hartmann). Thus a close relationship between *Ruschia knysnana* and *Esterhuysenia* may be possible. However, at present it is not possible to assign this species unambiguously to *Esterhuysenia*, since not all species of *Esterhuysenia* were investigated in this study. On the other hand the fruit morphology, which diverges from most species placed in *Ruschia*, suggests that it does not belong in *Ruschia* and a better understanding of *Ruschia* and its generic limits is needed in order to place this species. Since “*glaucoides*” is the older epithet a new combination would be necessary. However, in the absence of clear evidence as to where this species should be placed, no new combinations are made. The nomenclature is listed below.

Hartmann (1999) also placed the variety *Ruschia knysnana* var. *angustifolia* L.Bolus into synonymy with *Ruschia knysnana*. Both type plants show a very similar fruit and floral morphology, but differ considerably in their leaf morphology. The leaves are much more narrow (c. 4 mm diam.) and in addition have a dark green colour. Until further investigation this variety should be upheld.

*Lampranthus glaucoides* (Haw.) N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum glaucoides* Haw., Obs. gen. Mesemb. 330 (1795). Lectotype (designated here): Port Elizabeth distr., Kabouga, at ca. 800 m, *Bruyns 8408* (BOL, lecto; K, MO).

*Lampranthus erratus* N.E.Br., Gard. Chron., ser. 3, 87: 212 (1930). *Mesembryanthemum virens* Salm Dyck, Monogr.: § 24, 1 (1840). Lectotype (designated here): Monogr.: § 24, 1 (1840).

*Ruschia knysnana* (L.Bolus) L.Bolus, Notes Mesembryanthemum 1: 146 (1928). *Mesembryanthemum knysnanum* L.Bolus, Ann. Bolus Herb. 4: 97 (1927). Type: Knysna, Feb. 1924, *Duthie 671* (BOL, holo.).

Shrubs mostly sparsely branched, 30-40 cm tall. Leaves triquetrous, apiculate, light and shiny green, translucent with dark dots, 33 mm long, 5 mm broad, 6 mm diam. Flowers 1-3, pedicels to 10 mm long, calyx 4-6-lobed, purple, 25 mm diam., filamentous staminodes conically collected around stamens. Fruit without closing body, keels diverging, ending in awns, 6-locular. Feb.-Mar. In sandstone, Knysna.

### 3. The phylogenetic position of *Lampranthus mutatus* (G.D.Rowley) H.E.K.Hartmann

*Ruschia mutata* has recently been transferred to *Lampranthus* (Hartmann 1998a), however, with

little justification provided for this transfer: The exclusion of this species from *Ruschia* appears to have been largely based on the presence of valve wings and a small placental closing body. As in the former case, this species is only known from the type collection. However, the presence of a placental closing body, the distinctly fused leaves (interpreted as a xeromorphic feature, cf. Dehn 1992) and the elaborate inflorescence excludes this species from *Lampranthus*. It also does not appear to belong to the newly described genus *Pustulesia*, where no placental closing bodies have been observed and the leaves are conspicuously velvety. Much difficulty with the placement of this species has to do with the very poorly understood taxonomy of *Ruschia*. As in the case of *Lampranthus*, the generic circumscription is largely based on a "typified" (*Ruschia*-type) fruit morphology (Hartmann 1999). However, no other characters have yet been investigated nor does a detailed survey of the fruit morphology exist.

*Lampranthus mutatus* (G.D.Rowley) H.E.K.Hartmann, *Bradleya* 16: 68 (1998). *Ruschia mutata*

G.D.Rowley, *Natl. Cact. Succ. J.* 33: 7 (1978). *Stoeberia littlewoodii* L.Bolus, *J. S. African Bot.* 26:

162 (1960). *Amphibolia littlewoodii* L.Bolus, *J. S. African Bot.* 31: 170 (1965), *nom. invalid.*

*Amphibolia littlewoodii* (L.Bolus) L.Bolus ex Toelken & Jessop, *Bothalia* 12: 64 (1976).

Lectotype: Ceres div., 15 miles east of Karooport on the road to Touws River, *Littlewood sub KG 522/59* (BOL, holo.).

Erect shrubs to 30 cm high with reddish internodes. Leaves trigonous, glabrous, connate for 2-3 mm with a distinct line, free parts 10-22 mm long, 3-4 mm diam. Flowers in ternate cymes, pedicels 15-25 mm long, pink, 43 mm diam., without filamentous staminodes. Fruits with small placental closing body and high rims. Sep. ?; Ceres division.

## REFERENCES

- APG 1998: An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* 85: 531-553.
- Albert, V. A. 1994: Cladistic relationships of the slipper orchids (Cypripedioidea: Orchidaceae) from congruent morphological and molecular data. *Lindleyana* 9: 115-132.
- Albert, V. A., M. H. G. Gustafsson & L. Di Laurenzio 1998: Ontogenetic systematics, molecular developmental genetics, and the angiosperm petal. In D. E. Soltis, P. S. Soltis & J. J. Doyle (eds.), *Molecular systematics of plants, II*. Pp. 349-374. Boston.
- Appels, R., B. R. Baum, B. C. Clarke 1992: The 5S DNA units of bread wheat (*Triticum aestivum*). *Plant Systematics and Evolution* 183: 183-194.
- Axelrod, D. I. & P. H. Raven 1978: Late Cretaceous and Tertiary vegetation history of Africa. In M. J. A. Werger, *Biogeography and ecology of southern Africa*. Pp. 77-130. Junk, The Hague.
- Backlund, A. & B. Bremer 1997: Phylogeny of the Asteridae s. str. based on *rbcL* sequences, with particular reference to the *Dipsacales*. *Plant Systematics and Evolution* 207: 225-254.
- Baker, W. J., C. B. Asmussen, S. C. Barrow, J. Dransfield & T. A. Hedderson 1999: A phylogenetic study of the palm family (Palmae) based on chloroplast DNA sequences from the *trnL* – *trnF* region. *Plant Systematics and Evolution* 219: 11-126.
- Baker W. J., T. A. Hedderson & J. Dransfield 2000a: Molecular Phylogenetics of *Calamus* (Palmeae) and related rattan genera based on 5S nrDNA spacer sequence data. *Molecular Phylogenetics and Evolution* 14: 218-231.
- Baker W. J., T. A. Hedderson & J. Dransfield 2000b: Molecular phylogenetics of subfamily Calamoideae (Palmae) based on nrDNA ITS and cpDNA *rps16* intron sequence data. *Molecular Phylogenetics and Evolution* 14: 195-217.
- Bakker F. T., D. Hellbrügge, A. Culham & M. Gibby 1998: Phylogenetic relationships within *Pelargonium* sect. *Peristera* (Geraniaceae) inferred from nrDNA and cpDNA sequence comparisons. *Plant Systematics and Evolution* 211: 273-287.

- Baldwin, B. G. & M. J. Sanderson 1998: Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proceedings of the National Academy of Sciences, USA* 95: 9402-9406.
- Baldwin, B. G., M. J. Sanderson, J. M. Porter, M. F. Wojciechowski, C. S. Campbell & M. J. Donoghue 1995: The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden* 82: 247-277.
- Baldwin, B. G. & B. L. Wessa 2000: Phylogenetic placement of *Pelucha* and new subtribes in Helenieae *sensu stricto* (Compositae). *Systematic Botany* 25: 522-538.
- Barrett, M., M. J. Donoghue & E. Sober 1991: Against consensus. *Systematic Zoology* 40: 486-493.
- Barriel, V. 1994: Molecular phylogenies and how to code insertions/deletions events. *Life Sciences* 317: 693-701.
- Barthlott, W. & N. Ehler 1977: Raster-Elektronenmikroskopie der Epidermis-Oberflächen von Spermatophyten. *Tropische und Subtropische Pflanzenwelt* 19: 363-467.
- Baum, B. R. 1988: A simple procedure for establishing discrete characters from measurement data, applicable to cladistics. *Taxon* 37: 63-70.
- Baum, D., R. Small & J. F. Wendel 1998: Biogeography and floral evolution of baobabs (*Adansonia*, Bombacaceae) as inferred from multiple data sets. *Systematic Biology* 47: 181-207.
- Berger, A. 1908. *Mesembryanthemen und Portulacaceen*. Ulmer. Stuttgart.
- Bittrich, V. 1986: Untersuchungen zu Merkmalsbestand, Gliederung und Abgrenzung der Unterfamilie Mesembryanthemoideae (Mesembryanthemaceae Fenzl.). *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 21: 5-116.
- Bittrich, V. & H. E. K. Hartmann 1988: The Aizoaceae – a new approach. *Botanical Journal of the Linnean Society* 97: 239-254.
- Bittrich, V. & M. Struck 1989: What is primitive in Mesembryanthemaceae? An analysis of evolutionary polarity of character states. *South African Journal of Botany* 55: 321-331.

- Blackmoore, S. & S. H. Barnes 1987: Embryophyte spore walls: origin, development and homologies. *Cladistics* 3: 185-195.
- Blake, S. T. 1969: A revision of *Carpobrotus* and *Sarcozona* in Australia, genera allied to *Mesembryanthemum* (Aizoaceae). *Contributions from the Queensland Herbarium* 7: 1-65.
- Bolus, H. L. M. 1950a: Notes on *Mesembryanthemum* and allied genera, part 3: 228.
- Bolus, H. L. M. 1950b: *Lampranthus verruculatus* (L.) L.Bolus. In R. S. Adamson & T. M. Salter, *Flora of the Cape Peninsula*. P. 385. Juta, Cape Town.
- Bolus, H. L. M. 1954: Notes on *Mesembryanthemum* and allied genera, part 3: 257.
- Bolus, H. L. M. 1958: Notes on *Mesembryanthemum* and allied genera, part 3: 334.
- Bolus, H. L. M. 1962: Notes on *Mesembryanthemum* and allied genera. *Journal of South African Botany* 28: 9-11.
- Bolus, H. L. M. 1965: Notes on *Mesembryanthemum* and allied genera. *Journal of South African Botany* 31: 172.
- Böhle U.-R., H. Hilger, R. Cerff & W. F. Martin 1994: Non-coding chloroplast DNA for plant molecular systematics at the infrageneric level. In B. Schierwater, B. Streit, G. P. Wagner & R. DeSalle (eds.), *Molecular ecology and evolution: approaches and applications*. Pp. 391-403. Birkhäuser, Basel.
- Bremer, B. 1996: Combined and separate analyses of morphological and molecular data in the plant family Rubiaceae. *Cladistics* 12: 21-40.
- Bremer, K. 1988: The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795-803.
- Bremer, K. 1994: Branch support and tree stability. *Cladistics* 10: 295-304.
- Brower, A. V. Z. & V. Schawaroch 1996: Three steps of homology assessment. *Cladistics* 12: 265-272.
- Brower, A. V. Z., R. DeSalle & A. Vogler 1996: Gene Trees, Species Trees, and Systematics: A Cladistic

Perspective. *Annual Review of Ecology and Systematics* 27: 423-450.

Brown, N. E. 1921: *Mesembryanthemum* and some genera separated from it. *Gardeners Chronicle* 151-152.

Brown, N. E. 1929: New species and critical notes on *Mesembryanthemum* and allied genera. *Bulletin of Miscellaneous Information Kew* 2: 56-62.

Bryant, H. N. 1989: An evaluation of cladistic and character analyses as hypothetico-deductive procedures, and the consequences of character weighting. *Systematic Zoology* 38: 214-227.

Bull, J. J., J. P. Huelsenbeck, C. W. Cunningham, D. L. Swofford & P. J. Wadell 1993: Partitioning and combining data in phylogenetic analysis. *Systematic Biology* 42: 384-397,

Burgoyne, P. M., G. F. Smith & P. Chesselet 1998: *Hammeria*, a new genus of Aizoaceae from South Africa. *Journal of the Cactus and Succulent Society of America* 70: 203-208.

Carlquist, S. 1983: Intercontinental dispersal. *Sonderband des naturwissenschaftlichen Vereins in Hamburg* 7: 37-47.

Carpenter, J. M. 1988: Choosing among multiple equally parsimonious cladograms. *Cladistics* 4: 291-296.

Chase, M. W., D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hillis, Y.-L. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedren, B. S. Gaut, R. K. Jansen, K.-J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. H. Strauss, Q.-Y. Quinn, L. E. Eguiarte, E. Golenberg, G. H. Learn, Jr, S. W. Graham, S. C. H. Barret, S. Dayanandran & V. A. Albert 1993: Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*. *Annals of the Missouri Botanical Garden* 80: 528-580.

Chase, M. W. & A. V. Cox 1998: Gene sequences, collaboration and analyses of large data sets. *Australian Systematic Botany* 11: 215-229.

Chase, M. W., M. F. Fay & V. Savolainen 2000: Higher-level classification in the angiosperms: new insights from the perspective of DNA sequence data. *Taxon* 49: 685-704.

Chippendale, P. T. & J. J. Wiens 1994: Weighting, partitioning, and combining characters in phylogenetic

analysis. *Systematic Biology* 43: 278-287.

Coen, E. S. & E. Meyerowitz 1991: The war of the whorls: genetic interactions controlling flower development. *Nature* 353: 31-37.

Coetzee, J. A. 1980: Tertiary environmental changes along the south-western African coast. *Palaeontologia Africana* 23: 197-203.

Coetzee, J. A. & J. Muller 1984: The phytogeographic significance of some extinct Gondwana pollen types from the Tertiary of the southwestern Cape (South Africa). *Annals of the Missouri Botanical Garden* 71: 1088-1099.

Coddington, J. A. 1994: The roles of homology and convergence in studies of adaptation. In P. Eggleton & R. I. Vane-Wright (eds.), *Phylogenetics and Ecology*. Pp. 53-78. London, Academic Press.

Cowling, R. M., C. R. Cartwright, J. E. Parkington & J. C. Allsopp 1999: Fossil wood charcoal assemblages from Elands Bay Cave, South Africa: implications for Late Quaternary vegetation and climates in the winter-rainfall fynbos biome. *Journal of Biogeography* 26: 367-378.

Cowling, R. M. & S. Pierce 1999: *Namaqualand*. Fernwood Press.

Cox, A. V., M. D. Bennett & T. A. Dyer 1992: Use of the polymerase chain reaction to detect spacer size heterogeneity in plant 5S-rRNA gene clusters and to locate such clusters in wheat (*Triticum aestivum* L.). *Theoretical and Applied Genetics* 83: 684-690.

Dehn, M. 1988: Untersuchungen zum Merkmalsbestand und zur Stellung der Gattung *Antimima* N.E.Br. emend. Dehn (Mesembryanthemaceae Fenzl). *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 22: 189-215.

Dehn, M. 1992: Untersuchungen zum Verwandtschaftskreis der Ruschiinae, Mesembryanthemaceae Fenzl. *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 24: 91-198.

de Pinna, M. C. C. 1991: Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7: 367-394.

De Queiroz, A., M. J. Donoghue & J. Kim 1995: Separate versus combined analysis of phylogenetic evidence. *Annual Review of Ecology and Systematics* 26: 657-681.

- Dillenius, J. J. 1732. *Hortus Elthamensis*: 268, t. 23, fig. 259. Londini, sumptibus auctoris.
- Downie, S. R. & J. D. Palmer 1994: A Chloroplast DNA Phylogeny of the Caryophyllales Based on Structural and Inverted Repeat Restriction Site Variation. *Systematic Botany* 19 (2) 236-252.
- Doyle, J. A., M. J. Donoghue & E. A. Zimmer 1994: Integration of morphological and ribosomal RNA data on the origin of angiosperms. *Annals of the Missouri Botanical Garden* 81: 405-418.
- Doyle, J. J. 1992: Gene trees and species trees: Molecular systematics as one-character taxonomy. *Systematic Botany* 17: 144-163.
- Doyle, J. J. 1996: Homoplasy connections and disconnections: genes and species, molecules and morphology. In M. J. Sanderson & L. Hufford (eds.), *Homoplasy. The recurrence of similarity in evolution*. Pp. 37-66. Academic Press.
- Doyle, J. J. & J. S. Doyle 1987: A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11-15.
- Dupont, S. 1968: Epidermes et plantules des Mésembryanthémacées. Systematique. Evolution. Bulletin de la Societe d'Histoire naturelle de Toulouse 104: 7-64.
- Dupont, S. 1973: Étude du pollen de Mésembryanthémacées très succulentes. C. R. Academie Scientifique Paris, série D 277: 2373-2376.
- Dupont, S. 1977: Notes on the pollen of the Mesembryanthemaceae. *Cactus and Succulent Journal of Great Britain* 39: 57-63.
- Dupont, S. & H. E. K. Hartmann 1982: Exine sculpture in pollen of the genus *Leipoldtia* L. Bol. A contribution towards a taxonomic revision of the genus. *Cactus and Succulent Journal of Great Britain* 44: 61-66.
- Eernisse D. J. & A. G. Kluge 1993: Taxonomic congruence versus total evidence, and Amniote phylogeny inferred from fossils, molecules, and morphology. *Molecular Biology and Evolution* 10: 1170-1195.
- Ehler, N. & W. Barthlott 1978: Die epicuticulare Skulptur der Testa-Zellwände einiger Mesembryanthemaceae. *Botanische Jahrbücher für Systematik* 99: 329-340.

- Eldenäs, P., A. A. Anderberg & M. Källersjö 1998: Molecular phylogenetics of the tribe *Inuleae* s. str. (Asteraceae), based on ITS sequences of nuclear ribosomal DNA. *Plant Systematics and Evolution* 210: 159-173.
- Endress, P. K., P. Baas & M. Gregory 2000: Systematic plant morphology and anatomy – 50 years of progress. *Taxon* 49: 401-434.
- Farris, J. S. 1969: A successive approximation approach to character weighting. *Systematic Zoology* 18: 374-385.
- Farris, J. S. 1972: Estimating phylogenetic trees from distance matrices. *American Naturalist* 106: 645-668.
- Farris, J. S. 1989: The retention index and the rescaled consistency index. *Cladistics* 5: 417-419.
- Farris, J. S., V. A. Albert, M. Källersjö, D. Lipscomb & A.G. Kluge 1996: Parsimony jack-knifing outperforms neighbor-joining. *Cladistics* 12: 99-124.
- Felsenstein, J. 1985: Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783-791.
- Fitch, W. M. 1971: Toward defining the course of evolution: minimal change for a specific tree topology. *Systematic Zoology* 20: 406-416.
- Friedrich, H. C. 1955: Beiträge zur Kenntnis einiger Familien der Centrospermae. *Mitteilungen der Botanischen Staatssammlung München* 2: 56-66.
- Friedrich, H. C. 1968: Mesembryanthemenstudien 3, Neue Sippen und Kombinationen. *Mitteilungen der Botanischen Staatssammlung München* 7: 211-218.
- Gerbault, M. 1995: *Phyllobolus* N.E.Br. emend. Bittrich (Aizoaceae): A reassessment of generic boundaries. *Botanische Jahrbücher für Systematik* 117: 385-399.
- Gielly, L., Y.-M. Yuan, P. Küpfer & P. Taberlet 1996: Phylogenetic use of noncoding regions in the genus *Gentiana* L.: Chloroplast *trnL* (UAA) intron versus nuclear ribosomal internal transcribed spacer sequences. *Molecular Phylogenetics and Evolution* 5: 460-466.

- Gift, N. & P. F. Stevens 1997: Vagaries in the delimitation of character states in quantitative variation – an experimental study. *Systematic Biology* 46: 112-125.
- Giribet, G. & W. C. Wheeler 1999: On gaps. *Molecular Phylogenetics and Evolution* 13: 132-143.
- Gleissberg, S. & J. W. Kadereit 1999: Evolution of leaf morphogenesis: evidence from developmental and phylogenetic data in Papaveraceae. *International Journal of Plant Science* 160: 787-794.
- Glen, H. F. 1978: A taxonomic monograph of *Lampranthus* and allied genera (Mesembryanthemaceae). Ph.D.-Thesis, University of Cape Town.
- Glen, H. F. 1986: Numerical taxonomic studies in the subtribe Ruschiinae (Mesembryanthemaceae) – *Astridia*, *Acrodon* and *Ebracteola*. *Bothalia* 16: 203-226.
- Goldblatt, P. & J. Manning 2000: Cape Plants. A conspectus of the Cape Flora of South Africa. *Strelitzia* 9. NBI, Missouri Botanical Garden.
- Goloboff, P. A. 1991: Homoplasy and the choice among cladograms. *Cladistics* 7: 215-232.
- Goloboff, P. A. 1993: Estimating character weights during tree search. *Cladistics* 9: 83-91.
- Gonzalez, I. L., J. E. Sylvester, T. F. Smith, D. Stambolian & R. D. Schmickel 1990: Ribosomal RNA gene sequences and hominid phylogeny. *Molecular Biology and Evolution* 7: 203-219.
- Gottlob-McHugh, S. C., M. Lévesque, K. MacKenzie, M. Olson, O. Yarosh & D. A. Johnson 1990: Organization of the 5S rRNA genes in the soybean *Glycine max* (L.) Merrill and conservation of the 5S rDNA repeat structure in higher plants. *Genome* 33: 486-494.
- Graham, L. E., M. E. Cook & J. S. Busse 2000: The origin of plants: body plan changes contributing to a major evolutionary radiation. *Proceedings of the National Academy of Sciences, USA* 97: 4535-4540.
- Groen, L. E. & L. J. G. van der Maesen 1999: Revision of the genus *Faucaria* (Ruschioideae: Aizoaceae) in South Africa. *Bothalia* 29: 35-59.
- Gu, X. & W.-H. Li 1995: The size distribution of insertions and deletions in human and rodent pseudogenes suggests the logarithmic gap penalty for sequence alignment. *Journal of Molecular Evolution* 40:

464-473.

- Guedes, M. & P. Dupuy 1976: Comparative morphology of lodicules in grasses. *Botanical Journal of the Linnaen Society* 73: 317-331.
- Haas, R. 1976: Morphologische, anatomische und entwicklungsgeschichtliche Untersuchungen an Blüten und Früchten hochsukkulenter Mesembryanthemaceen-Gattungen. Ein Beitrag zu ihrer Systematik. *Dissertationes Botanicae* 33.
- Hammer, S. 1993: *The genus Conophytum. A Conograph*. Succulent Plant Publications, Pretoria.
- Hammer, S. 1994: *Vlokia*, a new genus in Aizoaceae. *Journal of the Cactus and Succulent Society of America* 66: 255-258.
- Harley, E. H. 1997: DAPSA, A Program for DNA And Protein Sequence Analysis, version 4.04. Distributed by the author.
- Hartmann, H. E. K. 1977: Monographie der Gattung *Argyroderma* N.E.Br. (Mesembryanthemaceae Fenzl). *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 15: 121-235.
- Hartmann, H. E. K. 1979: Surface structures of leaves: their ecological and taxonomical significance in members of the subfamily Ruschioideae Schw. (Mesembryanthemaceae Fenzl). In D. F. Cutler & H. E. K. Hartmann, *Scanning electron microscope studies of the leaf epidermis of some succulents*. *Tropische und Subtropische Pflanzenwelt* 28: 31-55.
- Hartmann, H. E. K. 1981: Ecology, distribution and taxonomy in Mesembryanthemaceae as a basis for conservation decisions. In H. Synge (ed.), *The Biological Aspects of Rare Plant Conservation*. Pp. 297-303. John Wiley & Sons, Chichester.
- Hartmann, H. E. K. 1983: Untersuchungen zum Merkmalsbestand und zur Taxonomie der Subtribus Leipoldtiinae (Mesembryanthemaceae). *Bibliotheca Botanica* 136: 1-67.
- Hartmann, H. E. K. 1988: Fruit types in Mesembryanthema. *Beiträge zur Biologie der Pflanzen* 63: 313-349.
- Hartmann, H. E. K. 1989: Monographien der Subtribus Leipoldtiinae. VIII. Monographie der Gattung *Cephalophyllum* (Mesembryanthemaceae). *Mitteilungen aus dem Institut für Allgemeine Botanik*

Hamburg 22: 93-187.

Hartmann, H. E. K. 1991: Mesembryanthema. Contributions from the Bolus Herbarium 13: 75-157.

Hartmann, H. E. K. 1993: Aizoaceae. In: K. Kubitzki, J.G. Rohwer, V. Bittrich (eds.), *The Families and Genera of Vascular Plants, Vol.2*. Pp. 37-69. Berlin: Springer.

Hartmann, H. E. K. 1996: Miscellaneous taxonomic notes on Aizoaceae. *Bradleya* 14: 29-56.

Hartmann, H. E. K. 1998a: New combinations in Ruschioideae, based on studies in *Ruschia* (Aizoaceae). *Bradleya* 16: 44-91.

Hartmann, H. E. K. 1998b: Groupings in Ruschioideae (Aizoaceae). *Mesemb Study Group Bulletin* 13: 35-36.

Hartmann, H. E. K. 1998c: New combinations in *Antimima* (Ruschioideae, Aizoaceae) from southern Africa. *Bothalia* 28,1: 67-82.

Hartmann, H. E. K. 1999: An annotated list of the species placed in *Ruschia* (Aizoaceae). *Bradleya* 17: 38-74.

Hartmann, H. E. K. & C. Bruckmann 2000: The capsules of *Drosanthemum* Schwantes (Ruschioideae, Aizoaceae). *Bradleya* 18: 75-112.

Hartmann, H. E. K. & M. Dehn 1989: A re-examination of the genus *Amphibolia* (Mesembryanthemaceae). *Bothalia* 19: 179-182.

Hartmann, H. E. K. & H. Gölling 1993: A monograph of the genus *Glottiphyllum* (Mesembryanthema, Aizoaceae). *Bradleya* 11: 1-49.

Hartmann, H. E. K. & S. Liede 1986: Die Gattung *Pleiospilos s. lat.* (Mesembryanthemaceae). *Botanische Jahrbücher für Systematik* 106: 433-485 (1986).

Hartmann, H. E. K. & S. Rust 1994: Monographien der Leipoldtiinae. IX. Monographie der Gattung *Leipoldtia* L.Bolus *s. lat.* (Aizoaceae). *Verhandlungen des naturwissenschaftlichen Vereins Hamburg, Neue Folge* 34: 275-351.

- Hartmann, H. E. K. & D. Stüber 1993: On the spiny Mesembryanthea and the genus *Eberlanzia* (Aizoaceae). *Contributions from the Bolus Herbarium* 15: 1-75.
- Hauser, D. L. & W. Presch 1991: The effect of ordered characters on phylogenetic reconstruction. *Cladistics* 7: 243-265.
- Hawkins, J. A., C. E. Hughes & R. W. Scotland 1997: Primary homology assessment, characters and character states. *Cladistics* 13: 275-283.
- Hawkins, J. A. 2000: A survey of primary homology assessment: different botanists perceive and define characters in different ways. In R. Scotland & R.T. Pennington (eds.), *Homology and Systematics: Coding characters for phylogenetic analysis*. Taylor and Francis, London, pp 22-53.
- Hendey, Q. B. 1982: *Langebaanweg. A record of past life*. South African Museum, Cape Town.
- Hillis, D. M. 1987: Molecular versus morphological approaches to systematics. *Annual Review of Ecology and Systematics* 18: 23-42.
- Hillis, D. M. & J. J. Bull 1993: An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* 42: 182-192.
- Hilton-Taylor, C. 1996: Red Data List of Southern african plants. *Strelitzia* 4: 38.
- Huber, J. A. 1924: Zur Morphologie von Mesembrianthemum. *Botanisches Archiv* 5: 7-25.
- Hutchinson, J. 1926: *The Families of Flowering Plants I. Dicotyledons*. Pp. 128-129. London, MacMillan & Co.
- Ihlenfeldt, H.-D. 1960: Entwicklungsgeschichtliche, morphologische und systematische Untersuchungen an Mesembryanthenen. *Feddes Repertorium specierum novarum regni vegetabilis* 63: 1-104.
- Ihlenfeldt, H.-D. 1971a: Über ontogenetische Abbreviation und Zeitkorrelationsänderungen und ihre Bedeutung für Morphologie und Sytematik. *Berichte der Deutschen Botanischen Gesellschaft* 84: 91-107.
- Ihlenfeldt, H.-D. 1971b: Zur Morphologie und Taxonomie der Mitrophyllinae Schwantes

(Mesembryanthemaceae). *Berichte der Deutschen Botanischen Gesellschaft* 84: 655-60.

Ihlenfeldt, H.-D. 1971c: Some aspects of the biology of dissemination of the Mesembryanthemaceae. In Herre, H. (ed.), *The Genera of the Mesembryanthemaceae*. Tafelberg, Cape Town.

Ihlenfeldt, H.-D. 1975: Some trends in the evolution of Mesembryanthemaceae. *Boissiera* 24: 249-54.

Ihlenfeldt, H.-D. 1985: Lebensformen und Überlebensstrategien bei Sukkulente n. *Berichte der Deutschen Botanischen Gesellschaft* 98: 409-423.

Ihlenfeldt, H.-D. 1994: Diversification in an arid world: The Mesembryanthemaceae. *Annual Review of Ecology and Systematics* 25: 521-46.

Ihlenfeldt, H.-D. & V. Bittrich 1985: Morphologie, Gliederung und Abgrenzung der Gattung *Psilocaulon* N.E.Br. s. l. (Mesembryanthemaceae). *Botanische Jahrbücher für Systematik* 105: 289-322.

Ihlenfeldt, H.-D. & H.E.K. Hartmann 1982: Leaf surfaces in Mesembryanthemaceae. In: D. F. Cutler, F. L. Alvin & C. E. Price (eds.), *The plant cuticle*. Pp. 397-423. Academic Press, London.

Ihlenfeldt, H.-D. & N. Jürgens 1982: Epidermistypen mit reduzierten Blasen zell-Idioblasten bei Mesembryanthemaceae. *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 18: 103-115.

Ihlenfeldt, H.-D. & H. Straka 1962: Über die systematische Stellung und Gliederung der Mesembryanthemen. *Berichte der Deutschen Botanischen Gesellschaft* 74: 485-492.

Ihlenfeldt, H.-D. & M. Struck 1987: Morphologie und Taxonomie der Dorotheanthinae Schwantes (Mesembryanthemaceae). *Beiträge zur Biologie der Pflanzen* 61: 411-453.

Iltis, H. H. 2000: Homeotic sexual translocation and the origin of maize (*Zea mays*, Poaceae): a new look at an old problem. *Economic Botany* 54: 7-42.

Jacobsen, H. 1955: *Handbuch der Sukkulente n Pflanzen* 3. P. 1426. Jena, VEB Gustav Fischer.

Jacobsen, H. 1970: *Das Sukkulente nlexikon*. Fischer. Jena.

- Jardine, N. 1969: The observational and theoretical components of homology: a study based on the morphology of the dermal skull-roofs of rhipidistian fishes. *Botanical Journal of the Linnaen Society* 1: 327-361.
- Johnson, L. A. & D. E. Soltis 1994: *matK* DNA sequences and phylogenetic reconstruction in Saxifragaceae *s. str.* *Systematic Botany* 19: 143-156.
- Johnson, L. A. & D. E. Soltis 1995: Phylogenetic inference in Saxifragaceae sensu stricto and *Gilia* (Polemoniaceae) using *matK* sequences. *Annals of the Missouri Botanical Garden* 82: 149-175.
- Judd, S. W., C. S. Campbell, E. A. Kellogg, P. F. Stevens 1999: *Plant Systematics. A Phylogenetic Approach*. Pp. 9-33. Sinauer Associates, Inc. Sunderland, Massachusetts U.S.A.
- Jürgens, N. 1985: Konvergente Evolution von Blatt- und Epidermismerkmalen bei blattsukkulenten Familien. *Berichte der Deutschen Botanischen Gesellschaft* 98: 425-446.
- Jürgens, N. 1986: Untersuchungen zur Ökologie sukkulenter Pflanzen des südlichen Africa. *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 21: 139-365.
- Jürgens, N. 1990: Remarks on the biogeography of Mesembryanthemaceae and their possible use in other arid regions. *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 23B: 1047-1060.
- Jürgens, N. 1991: A new approach to the Namib Region. Part 1: Phytogeographic subdivision. *Vegetatio* 97: 21-38.
- Jürgens, N. 1997: Floristic biodiversity and history of African arid regions. *Biodiversity and Conservation* 6: 495-514.
- Källersjö, M., J. S. Farris, A. G. Kluge & C. Bult 1992: Skewness and permutation. *Cladistics* 8: 275-287.
- Kellogg, E. A., R. Appels & R. G. Mason-Gamer 1996: Why genes tell different stories: The diploid genera of Triticeae (Gramineae). *Systematic Botany* 21: 321-347.
- Kim, J. H., H.'T Hart & T. H. M. Mes 1996: The phylogenetic position of East Asian *Sedum* species (Crassulaceae) based on chloroplast DNA *trnL* (UAA) – *trnF* (GAA) intergenic spacer sequence variation. *Acta Botanica Neerlandica* 45: 309-321.

- Kitching, I. J., P. L. Forey, C. J. Humphries & D. M. Williams 1998: *Cladistics: The theory and practice of parsimony analysis*. Second edition. Oxford University Press, Oxford.
- Klak, C. 2000a: Taxonomic studies in the Aizoaceae from South Africa: three new species and some new combinations. *Bothalia* 30: 35-42.
- Klak, C. 2000b: Aizoaceae. In P. Goldblatt & J. Manning (eds.), *Cape Plants. A conspectus of the Cape Flora of South Africa*. Pp. 222-268. *Strelitzia* 9. NBI, Missouri Botanical Garden.
- Klak, C. & H. P. Linder 1998: Systematics of *Psilocaulon* N.E.Br. and *Caulipsolon* Klak gen. nov. (Mesembryanthemoideae, Aizoaceae). *Botanische Jahrbücher für Systematik* 120: 301-375.
- Kluge, A. G. & A. J. Wolf 1993: Cladistics: what's in a word? *Cladistics* 9: 183-199.
- Koch C. 1962: The Tenebrionidae of southern Africa XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum* 24: 61-106.
- Kornet, D. J. & H. Turner 1999: Coding Polymorphism for Phylogeny Reconstruction. *Systematic Biology* 48: 365-379.
- Kramer, E. M. & V. F. Irish 1999: Evolution of genetic mechanisms controlling petal development. *Nature* 399: 144-148.
- Kron, K. A., W. S. Judd & D. M. Crayn 1999: Phylogenetic analysis of *Andromedeae* (Ericaceae subfam. Vaccinioideae). *American Journal of Botany* 86: 1290-1300.
- Landrum, J. V. 2001: Wide-band tracheids in leaves of genera in Aizoaceae: the systematic occurrence of a novel cell type and its implications for the monophyly of the subfamily Ruschioideae. *Plant Systematics and Evolution* 227: 49-61.
- Lavin, M. R. T. Pennington, B. B. Klitgaard, J. E. Spret, H. C. de Lima & P. E. Gasson 2001: The dalbergioid legumes (Fabaceae): delimitation of a pantropical clade. *American Journal of Botany* 88: 503-533.
- Lee, D.-C. & H. N. Bryant 1999: A reconsideration of the coding of inapplicable characters: assumptions and problems. *Cladistics* 15: 373-378.

- Lee, S. B. & J. W. Taylor 1992: Phylogeny of five fungus-like protocistan (*Phytophthora*) species, inferred from the internal transcribed spacers of ribosomal DNA. *Molecular Biology and Evolution* 9: 636-653.
- Lidén, M., T. Fukuhara, J. Rylander & B. Oxelman 1997: Phylogeny and classification of Fumariaceae, with emphasis on *Dicentra* s.l., based on the plastid gene *rps16* intron. *Plant Systematics and Evolution* 206: 411-420.
- Lidén, M. 1999: Boots-traps. *Taxon* 48: 349-350.
- Liede, S. 1989: Untersuchungen zum Merkmalsbestand und zur Taxonomie der "Erepsiinae" (Mesembryanthemaceae). *Beiträge zur Biologie der Pflanzen* 64: 391-479.
- Liede, S. & U. Meve 1990: What is *Lampranthus scaber* (L.) N.E.Br.? *Bradleya* 8: 39-44.
- Linder, H. P., M. E. Meadows & R. M. Cowling 1992: History of the Cape Flora. In R. M. Cowling (ed.), *The ecology of fynbos: nutrients, fire and diversity*. Pp: 113-134. Cape Town.
- Linnaeus, C. 1753: *Species Plantarum*. P. 485. Salvius, Stockholm.
- Linnaeus, C. 1762: *Species Plantarum*, edn. 2. P. 695. Stockholm.
- Lloyd, D. G. & V. L. Calder 1991: Multi-residue gaps, a class of molecular characters with exceptional reliability for phylogenetic analyses. *Journal of Evolutionary Biology* 4: 9-21.
- Lockyer, S. 1932: Seed Dispersal from Hygroscopic *Mesembryanthemum* Fruits; *Bergeranthus scapigerus*, Schw., and *Dorotheanthus bellidiformis*, N.E.Br., with a Note on *Carpanthea pomeridiana* N.E.Br. *Annals of Botany* 46: 323-342.
- Logan, R. F. 1960. The central Namib Desert, South West Africa. *Publications of the National Academy of Sciences* 758: 1-141.
- Luckow, M. & A. Bruneau 1997: Circularity and independence in phylogenetic tests of ecological hypotheses. *Cladistics* 13: 145-151.
- Maddison, D. R. 1991: The discovery and importance of multiple islands of most-parsimonious trees.

Systematic Zoology 40: 315-328.

Maddison, W. P. 1993: Missing data versus missing characters in phylogenetic analysis. *Systematic Biology* 42: 576-581.

Maddison, W. P. & D. R. Maddison 1992: *MacClade*, 3.06. Sunderland, Massachusetts: Sinauer Associates.

McKittrik, M. C. 1994: On homology and the ontological relationships of parts. *Systematic Biology* 43: 1-10.

Meerow, A. W., C. L. Guy, Q.-B. Li & S.-L. Yang 2000: Phylogeny of the American Amaryllidaceae based on nrDNA ITS sequences. *Systematic Botany* 25: 708-726.

Meier, R. 1994: On the appropriateness of presence/absence recoding for non-additive multistate characters in computerized cladistic analyses. *Zoologischer Anzeiger* 232: 201-212.

Mes, T. H. M., G. J. Wiejers & H. T Hart 1997: Phylogenetic relationships in *Monanthes* (Crassulaceae) based on morphological, chloroplast and nuclear DNA variation. *Journal of Evolutionary Biology* 10: 193-216.

Meyers, P. A. 1992: Organic matter variations in sediments from DSDP sites 362 and 532: evidence of changes in the Benguela Current upwelling system. In C. P. Summerhayes, W. L. Prell and K. C. Emeis (eds), *Upwelling systems: evolution since the Early Miocene*. Pp. 323-329. Geological Society Special Publication no. 64, London.

Mickevich, M. F. & S. J. Weller 1990: Evolutionary character analysis: tracing character change on a cladogram. *Cladistics* 6: 137-170.

Midgley, G. F., L. Hannah, R. Roberts, J. Allsop & D. J. McDonald in press: Quaternary climatic oscillations as a driving force behind plant species richness in the greater Cape Mediterranean Region. *Journal of Mediterranean Ecology*.

Mitchell, A. D. & P. B. Heenan 2000: Systematic relationships of New Zealand endemic Brassicaceae inferred from nrDNA ITS sequence data. *Systematic Botany* 25: 98-105.

Miyamoto, M. M. 1985: Consensus cladograms and general classifications. *Cladistics* 1: 186-189.

Miyamoto, M. M. & W. M. Fitch 1995: Testing species phylogenies and phylogenetic methods with

congruence. *Systematic Biology* 44: 64-76.

Nel, G. C. 1953: *The Gibbaeum handbook*. Blandford Press. London.

Niesler, I. 1996: Unterschiedliche Ontogenie der Cuticularleisten bei den Gattungen *Synaptophyllum* N.E.Br. und *Faucaria* Schwantes (Mesembryanthemaceae Fenzl).  
Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg 26: 145-152.

Nixon, K. C. & J. M. Carpenter 1993: On outgroups. *Cladistics* 9: 413-426.

Nixon, K. C. & J. M. Carpenter 1996: On simultaneous analysis. *Cladistics* 12: 221-241.

Norwicke, J. W. & J. J. Skvarla 1977: Pollen morphology and the relationship of the Plumbaginaceae, Polygonaceae, and Primulaceae to the order Centrospermeae. *Smithsonian Contribution to Botany* 37: 1-64.

Norwicke, J. W. & J. J. Skvarla 1979: Pollen morphology: The potential influence in higher order systematics. *Annals of the Missouri Botanical Garden* 66: 633-700.

Ohsako, T. & O. Ohnishi 2000: Intra- and interspecific phylogeny of wild *Fagopyrum* (Polygonaceae) species based on nucleotide sequences of noncoding regions in chloroplast DNA. *American Journal of Botany* 87: 573-582.

Olmstead, R. G., H. J. Michaels, K. M. Scott & J. D. Palmer 1992: Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbcL*. *Annals of the Missouri Botanical Garden* 79: 249-265.

Olmstead, R. G., B. Bremer, K. M. Scott & J. D. Palmer 1993: A parsimony analysis of the Asteridae *sensu lato* based on *rbcL* sequences. *Annals of the Missouri Botanical Garden* 80: 700-722.

Olmstead, R. G. & J. D. Palmer 1994: Chloroplast DNA systematics: a review of methods and data analysis. *American Journal of Botany* 81: 1205-1224.

Oxelman, B., M. Lidén & D. Berglund 1997: Chloroplast *rps16* intron phylogeny of the tribe *Sileneae* (Caryophyllaceae). *Plant Systematics and Evolution* 206: 393-410.

- Öztig, Ö. F. 1940: Beiträge zur Kenntnis des Baues der Blattepidermis bei den Mesembrianthenen, im besonderen den extrem xeromorphen Arten. *Flora* 134: 105-144.
- Page, R. D. M. & E. C. Holmes 1998: *Molecular Evolution: A Phylogenetic Approach*. Blackwell Science Ltd., Oxford.
- Pascarella, S. & P. Argos 1992: Analysis of insertions / deletions in protein structures. *Journal of Molecular Biology* 224: 461-471.
- Patterson, C. 1988: Homology in classical and molecular biology. *Molecular Biology and Evolution* 5: 603-625.
- Patterson, C., D. M. Williams & C. J. Humphries 1993: Congruence between molecular and morphological phylogenies. *Annual Review of Ecology and Systematics* 24: 153-188.
- Pax, F. 1889: Aizoaceae. In A. Engler & K. Prantle (eds.), *Die natürlichen Pflanzenfamilien, part 3 (l.b.)*. Pp 33-51. Leipzig, W. Engelmann.
- Pimentel, R. A. & R. Riggins 1987: The nature of cladistic data. *Cladistics* 3: 201-209.
- Pleijel, F. 1995: On character coding for phylogeny reconstruction. *Cladistics* 11: 309-315.
- Poppendieck, H.-H. 1976: Untersuchungen zur Morphologie und Taxonomie der Gattung *Mitrophyllum Schwantes s. lat.* *Botanische Jahrbücher für Systematik* 97: 339-413.
- Prakasch, N. 1967: Gametogenesis and seed development in *Hereroa hesperantha* (Dtr.) Dtr. & Schwant. (Aizoaceae). *Australian Journal of Botany* 15: 425-435.
- Prescott, A. & J. Venning 1984: Aizoaceae. In *Flora of Australia* IV, pp. 19-62. Australia Government Publishing Service Canberra.
- Preston, C. D. 1988: Hottentot Fig, *Carpobrotus edulis* (L.) N.E.Br., in Guernsey. Report and transactions, société guernésiaise 22: 296-302.
- Preston, C. D. & P. D. Sell 1988: The Aizoaceae naturalized in the British Isles. *Watsonia* 17: 217-245.

- Rappa, F. 1912: Per una classificazione naturale dei Mesembrianthemii. Bollettino delle reale orto botanico e giardino coloniale de Palermo 11: 21-36.
- Rappa, F. & V. Camarrone 1953: La nuova sistematica di Mesembrianthemum. Lavori dell' istituto botanico e del giardino coloniale di Palermo 14.
- Reddy, P. & R. Appels 1989: A second locus for the 5S multigene family in *Secale* L.: sequence divergence in two lineages of the family. *Genome* 32: 4456-4467.
- Rettig, J. H., H. D. Wilson & J. R. Manhart 1992: Phylogeny of Caryophyllales – gene sequence data. *Taxon* 41: 201-209.
- Reule, H. 1937: Vergleichend-anatomische Untersuchungen in der Gattung *Mesembryanthemum* L. *Flora* 131: 400-424.
- Richardson, J. E., F. M. Weitz, M. F. Fay, Q. C. B. Cronk, H. P. Linder, G. Reeves & M. Chase 2001: Phylogenetic analysis of *Phyllica* L. (Rhamnaceae) with an emphasis on island species: evidence from plastid *trnL-F* and nuclear internal transcribed spacer (ribosomal) DNA sequences. *Taxon* 50: 405-427.
- Rowley, G. D. 1978: Reunion of some genera of Mesembryanthemaceae. *National Cactus and Succulent Journal* 33(1): 6-9.
- Saghai-Maroo, M. A., K. M. Soliman, R. A. Jorgensen, R. W. Allard 1984: Ribosomal DNA spacer-length polymorphisms in barley: Mendelian inheritance, chromosomal location and population dynamics. *Proceedings of the National Academy of Sciences, USA* 81: 8014-8018.
- Sanderson, M. J. & J. J. Doyle 1992: Reconstruction of organismal and gene phylogenies from data on multigene families: Concerted evolution, homoplasy, and confidence. *Systematic Biology* 41: 4-17.
- Sastri, D. C., K. Hilu, R. Appels, E. S. Lagudah, J. Playford & B. R. Baum 1992: An overview of evolution in plant 5S DNA. *Plant Systematics and Evolution* 183: 265-280.
- Savolainen, V., M. F. Fay, D. C. Albach, A. Backlund, M. van der Bank, K. M. Cameron, S. A. Johnson, M. D. Lledó, J.-C. Pintaud, M. Powell, M. C. Sheahan, D. E. Soltis, P. S. Soltis, P. Weston, W. M. Whitten, K. J. Wurdack & M. W. Chase 2000: Phylogeny of the eudicots: a nearly complete familial

analysis based on *rbcL* gene sequences. *Kew Bulletin* 55: 257-309.

Schmid, W. 1925: Morphologische, anatomische und entwicklungsgeschichtliche Untersuchungen an *Mesembryanthemum pseudotruncatellum* Berger. *Vierteljahrsschrift der Naturforschenden Gesellschaft Zürich* 70 (Beiblatt 8): 1-96.

Schmiedel, U. & N. Jürgens 1999: Community structure on unusual islands: quartz-fields in the Succulent Karoo, South Africa. *Plant Ecology* 142: 57-69.

Scholz, A. 1985: The palynology of the upper lacustrine sediments of the Arnot pipe, Banke, Namaqualand. *Annals of the South African Museum* 95: 1-109.

Schwantes, G. 1947: System der Mesembryanthemaceen. *Sukkulantenkunde* 1: 34-40.

Schwantes, G. 1952: Die Früchte der Mesembryanthemaceen. *Vierteljahrsschrift der Naturforschenden Gesellschaft Zürich* 97: 1-38.

Schwantes, G. 1957: *Flowering Stones and Mid-Day Flowers*. London.

Schwantes, G. 1971: The Classification of the Mesembryanthemaceae. In H. Herre, *The Genera of the Mesembryanthemaceae*. Tafelberg, Cape Town.

Schwarzbach, A. E. & R. E. Ricklefs 2000: Systematic affinities Rhizophoraceae and Anisophylleaceae, and intergeneric relationships within Rhizophoraceae, based on chloroplast DNA, nuclear ribosomal DNA, and morphology. *American Journal of Botany* 87: 547-564.

Scott, L. 1994: Palynology of late Pleistocene hyrax middens, southwestern Cape Province, South Africa: a preliminary report. *Historical Biology* 9: 71-81.

Scott, L., M. Steenkamp & P. B. Beaumont 1995: Palaeoenvironments in South Africa at the Pleistocene-Holocene transition. *Quaternary Science Reviews* 14: 937-47.

Scott, L., H. M. Anderson & J. M. Anderson 1997: Vegetation history. In R. M. Cowling, D. M. Richardson & S. M. Pierce (eds.), *Vegetation of southern Africa*. Pp. 62-84. Cambridge University Press.

Seitz, V., S. O. Garcia & A. Liston 2000: Alternative coding strategies and the inapplicable data coding

problem. *Taxon* 49: 47-54.

Sennblad, B., M. G. Endress & B. Bremer 1998: Morphology and molecular data in phylogenetic fraternity: the tribe *Wrightieae* revisited. *American Journal of Botany* 85: 1143-1158.

Siesser, W. G. 1977: Aridification of the Namib Desert: Evidence from oceanic cores. In E. M. Van Zinderen Bakker (ed.), *Antarctic Glacial History and Palaeoenvironments*. Pp. 105-112. Balkema, Rotterdam

Siesser, W. G. 1980: Late Miocene origin of the Benguela Upwelling System off Northern Namibia. *Science* 208: 283-285.

Simmons, M. P. & H. Ochoterena 2000: Gaps as Characters in Sequence-Based Phylogenetic Analyses. *Systematic Biology* 49: 369-381.

Simons, A. M. & R. M. Mayden 1997: Phylogenetic relationships of the creek chubs and the spine-fins: An enigmatic group of North America cyprinid fishes (Actinopterygii: Cyprinidae). *Cladistics* 13: 187-206.

Skvarla, J. J. & J. W. Norwicke 1976: Ultrastructure of pollen exine in centrosperous families. *Plant Systematics and Evolution* 126: 55-78.

Smith, G. F., P. Chesselet, E. J. van Jaarsveld, H. Hartmann, S. Hammer, B.-E. van Wyk, P. Burgoyne, C. Klak & H. Kurzweil 1998: *Mesembryaceae of the world*. Briza Publications.

Soltis, D. E., P. S. Soltis, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Sweere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, S. M. Chaw, L. J. Gillespie, W. J. Kress & K. M. Sytsma 1997: Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Annals of the Missouri Botanical Garden* 84: 1-49.

Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, K. C. Nixon & J. S. Farris 2000: Angiosperm phylogeny inferred from a combined data set of 18S rDNA, *rbcL*, and *atpB* sequences. *Botanical Journal of the Linnean Society* 133: 381-461.

Sonder O. W. 1862: Mesembryaceae Lindl. In W.H. Harvey & O.W. Sonder, *Flora Capensis* 2: 386-479.

Dublin, Cape Town.

- Stevens, P. F. 1991: Character states, morphological variation, and phylogenetic analysis: a review. *Systematic Botany* 16: 553-583.
- Straka, H. 1955: Anatomische und entwicklungsgeschichtliche Untersuchungen an Früchten paraspermer Mesembryanthemen. *Nova Acta Leopoldina, Neue Folge* 17, 118: 127-190.
- Strong, E. E. & D. Lipscomb 1999: Character coding and inapplicable data. *Cladistics* 15: 363-371.
- Sullivan, J. 1996: Combining data with different distributions of among-site rate variation. *Systematic Biology* 45: 375-380.
- Swofford, D. L. 1991: When are phylogeny estimates from molecular and morphological data incongruent ? In M. M. Miyamoto and J. Cracraft (eds.), *Phylogenetic analysis of DNA sequences*. Pp. 295-333. New York: Oxford University Press.
- Swofford, D. L. 2000: PAUP\*. Phylogenetic Analysis Using Parsimony (and Other Methods). Version 4.0b4. Sinauer Associates, Sunderland, Massachusetts.
- Swofford, D. L., G. J. Olsen, P. J. Waddell & D. M. Hillis 1996: Phylogenetic inference. In D. M. Hillis, C. B. Moritz & K. Mable (eds.), *Molecular Systematics*. Pp. 407-514. Sinauer Associates, Sunderland, Massachusetts.
- Taberlet, P., L. Gielly, G. Pautou & J. Bouvet 1991: Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105-1109.
- Tankard, A. J. & J. Rogers 1978: Late Cenozoic palaeoenvironments on the west coast of Southern Africa. *Journal of Biogeography*. 5: 319-337.
- Theissen, G. & H. Saedler 1999: The golden decade of molecular floral development (1990-1999): a cheerful obituary. *Developmental Genetics* 15: 1-13.
- Thiele, K. 1993: The holy grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics* 9: 275-304.

- Troll, W. 1969: *Die Infloreszenzen, Typologie und Stellung im Aufbau des Vegetationskörpers II/1*. Jena.
- Troll, W. & F. Weberling 1981: Infloreszenzstudien an Aizoaceen, Mesembryanthemaceen und Tetragoniaceen. *Tropische und Subtropische Pflanzenwelt* 35: 195-289.
- Trueman, J. W. H. 1993: Randomization confounded: a response to Carpenter. *Cladistics* 9: 101-109.
- Udovicic, R., G. I. McFadden, P. Y. Ladiges 1995: Phylogeny of *Eucalyptus* and *Angophora* based on 5S rDNA spacer sequence data. *Molecular Phylogenetics and Evolution* 4: 247-256.
- Uhl, N. W. & J. Dransfield 1987: *Genera Palmarum*. Allen Press, Lawrence, Kansas.
- van Dijk, M. A. M., E. Paradis, F. Catzefflis & W. W. De Jong 1999: The virtues of gaps: *Xenarthran* (Edentate) monophyly supported by a unique deletion in aA-crystallin. *Systematic Biology* 48: 94-106.
- van Zinderen Bakker E. M. Sr. 1975: The origin and palaeoenvironment of the Namib Desert biome. *Journal of Biogeography* 2: 65-73.
- Vogel, S. 1954: Blütenbiologische Typen als Elemente der Sippengliederung. In W. Troll & H. von Gutenberg (eds.), *Botanische Studien I*. Fischer, Jena.
- Vogler, A. P. & R. DeSalle 1994: Evolution and phylogenetic information content of the ITS-1 region in the tiger beetle *Cicindela dorsalis*. *Molecular Biology and Evolution* 11: 393-405.
- Volk, O. 1960: Flowers and Fruits of the Mesembryanthemums. In H. Jacobsen, *A Handbook of Succulent Plants* 3: 945-950.
- Ward, J. D., M. K. Seely & N. Lancaster 1983: On the antiquity of the Namib. *South African Journal of Science* 79: 175-183.
- Ward, J. D. & I. Corbett 1990: Towards an age of the Namib. *Transvaal Museum Monograph* 7: 17-26.
- Wheeler, W. 1996: Optimization alignment: The end of multiple sequence alignment in phylogenetics? *Cladistics* 12: 1-10.

- Wiens, J. J. 1995: Polymorphic characters in phylogenetic systematics. *Systematic Biology* 44: 482-500.
- Wilkinson, M. 1992: Ordered versus unordered characters. *Cladistics* 8: 375-385.
- Wilkinson, M. 1995: A comparison of two methods of character construction. *Cladistics* 11: 297-308.
- Wisura, W. & H. F. Glen 1993: The South African species of *Carpobrotus* (Mesembryanthema – Aizoaceae). *Contributions from the Bolus Herbarium* 15: 76-107.
- Wolfe, K. H., W. H. Li & P. M. Sharp 1987: Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast and nuclear DNAs. *Proceedings of the National Academy of Sciences, USA* 84: 9054-9058.
- Woodcock, E. F. 1930: Morphological studies on the seed of *Mesembryanthemum crystallinum* L. *Papers of the Michigan Academy of Sciences, arts and letters, New York* 13: 221-226.
- Zandonella, P. 1977: Apports de l'étude comparée des nectaires floraux à la conception phylogénétique de l'ordre des Centrospermales. *Berichte der Deutschen Botanischen Gesellschaft* 90: 105-125.
- Zimmer, E. A. 1994: Perspectives on future applications of experimental biology to evolution. In B. Schierwater, B. Streit, G. P. Wagner & R. DeSalle (eds.), *Molecular ecology and evolution: approaches and applications*. Pp. 607-616. Basel.
- Zimmer, E. A., S. L. Martin, S. M. Beverley, Y. W. Kan & A. C. Wilson 1980: Rapid duplication and loss of genes coding for the alpha chains of hemoglobin. *Proceedings of the National Academy of Sciences, USA* 77: 2158-2162.

**Appendix 1.** Exemplar species with voucher number used in the cladistic analysis of morphological and molecular data and their position in the classification of the Aizoaceae (Hartmann 1998a). "X" indicates the gene region that was sequenced.

Species	Section	Voucher (in BOL)	Trn L-F	ITS	5S
<b>Mesembryanthemoideae</b>					
<i>Brownanthus pubescens</i> (N.E.Br. ex Maas) Bullock		Klak 242	X	X	
<i>Phyllobolus rabiei</i> (L.Bolus) Gerbaulet		Klak 589b	X		
<b>Ruschioideae</b>					
<b>Cleretum – group</b>					
<i>Dorotheanthus bellidiformis</i> subsp. <i>bellidiformis</i> (Burm.) N.E.Br.		Klak 627	X	X	
<b>Delosperma – group</b>					
<i>Delosperma echinatum</i> (Lamarck) Schwantes		Klak 344	X	X	X
<i>Delosperma esterhuyseniae</i> L.Bolus		Bruyns 7141	X	X	X
<i>Drosanthemum schoenlandianum</i> (Schltr.) L.Bolus		Bruyns 7172	X	X	X
<i>Oscularia deltoides</i> (L.) Schwantes		Klak 215	X	X	X
<i>Oscularia falciformis</i> (Haw.) H.E.K.Hartmann		Klak 261	X	X	X
<i>Oscularia guthrieae</i> (L.Bolus) H.E.K.Hartmann		Bruyns 7361	X	X	X
<b>Titanopsis – group</b>					
<i>Lithops julii</i> subsp. <i>fulleri</i> (Dinter & Schwantes) N.E.Br.		Klak 701	X	X	X
<i>Titanopsis hugo-schlechteri</i> (Tischer) Dinter & Schwantes		Klak 702	X	X	X
<i>Hammeria meleagris</i> (L.Bolus) Klak		Klak 418	X	X	X
<b>Dracophilus – group</b>					
<i>Juttadintera albata</i> L.Bolus		Klak 244	X	X	X
<b>Ruschia – group</b>					
<i>Astridia longifolia</i> (L.Bolus) L.Bolus		Bruyns 7302	X	X	X
<i>Ruschia maxima</i> (Haw.) L.Bolus		Klak 704	X	X	X
<i>Ruschia intrusa</i> (Kensit) L.Bolus		Bruyns 7150	X		X
<b>Eberlanzia – group</b>					
<i>Amphibolia hutchinsonii</i> (L.Bolus) H.E.K. Hartmann		Bruyns 7184	X	X	X
<i>Eberlanzia dichotoma</i> (L.Bolus) H.E.K. Hartmann		Klak 497	X	X	X

Species	Section	Voucher (in BOL)	Trn L-F	ITS	5S
<b>Leipoldtia – group</b>					
<i>Antimima ventricosa</i> (L.Bolus) H.E.K.Hartmann		Klak 475	X	X	X
<i>Fenestraria rhopalophylla</i> subsp. <i>aurantiaca</i> (N.E.Br.) H.E.K.Hartmann		Klak 263	X	X	X
<b>Lampranthus – group</b>					
<i>Antegibbaeum fissoides</i> (Haw.) Schwantes		Klak 308	X	X	X
<i>Braunsia geminata</i> (Haw.) L.Bolus		Klak 205	X	X	X
<i>Braunsia maximilianii</i> (Schltr. & A.Berger) Schwantes		Helme 1678	X		X
<i>Braunsia vanrensburgii</i> (L.Bolus) L.Bolus		Klak 218	X	X	X
<i>Carpobrotus muirii</i> (L.Bolus) L.Bolus		Klak 706	X	X	X
<i>Carpobrotus quadrifidus</i> L.Bolus		Klak 705	X	X	X
<i>Enarganthe octonaria</i> (L.Bolus) N.E.Br.		Klak 491	X	X	X
<i>Erepsia dunensis</i> (Sond.) Klak	<i>Crassifolii</i>	Klak 453	X	X	X
<i>Erepsia inclaudentis</i> (Haw.) Schwantes	<i>Erepsia</i>	Bruyns 7181	X	X	X
<i>Erepsia patula</i> (Haw.) Schwantes	<i>Tectatae</i>	Klak 642	X	X	X
<i>Erepsia pillansii</i> (Kensit) Liede	<i>Crassifolii</i>	Klak 707	X	X	X
<i>Esterhuysenia drepanophylla</i> (Schltr. & A.Berger) H.E.K.Hartmann		Klak 213	X	X	X
<i>Lampranthus aduncus</i> (Haw.) N.E.Br.	<i>Adunci</i>	Klak 381	X	X	X
<i>Lampranthus amphibolius</i> (G.O.Rowley) H.E.K. Hartmann		Trinder- Smith 159	X	X	X
<i>Lampranthus argenteus</i> (L.Bolus) L.Bolus	<i>Suffrutices</i>	Klak 398	X	X	X
<i>Lampranthus bicolor</i> (L.) N.E.Br.	<i>Tenuifolii</i>	Klak 543	X	X	X
<i>Lampranthus debilis</i> (Haw.) N.E.Br.	<i>Reptantes</i>	Klak 316	X	X	X
<i>Lampranthus dregeanus</i> (Sond.) N.E.Br.	<i>Falcati</i>	Klak 619	X		X
<i>Lampranthus emarginatus</i> (L.) N.E.Br.	<i>Scabridi</i>	Klak 708	X	X	X
<i>Lampranthus filicaulis</i> (Haw.) N.E.Br.	<i>Adunci</i>	Bruyns 7176	X	X	X
<i>Lampranthus galpiniae</i> (L.Bolus) L.Bolus	<i>Tenuifolii</i>	Klak 279	X	X	X
<i>Lampranthus glaucus</i> (L.) N.E.Br.	<i>Aurei</i>	Klak 311	X	X	X
<i>Lampranthus</i> sp. nov.		Klak 417a	X	X	X
<i>Lampranthus henricii</i> (L.Bolus) N.E.Br.	<i>Suffrutices</i>	Klak 425	X	X	X

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<i>Lampranthus mucronatus</i> L.Bolus		Klak 709	X	X	X
<i>Lampranthus peacockiae</i> (L.Bolus) L.Bolus	<i>Scabridi</i>	Klak 391	X		X
<i>Lampranthus rupestris</i> (L.Bolus) N.E.Br.	<i>Scabridi</i>	Klak 320	X	X	X
<i>Lampranthus sociorum</i> (L.Bolus) N.E.Br.	<i>Reptantes</i>	Klak 390	X	X	X
<i>Lampranthus spectabilis</i> (Haw.) N.E.Br.	<i>Amoeni</i>	Klak 333	X	X	X
<i>Lampranthus stenus</i> (Haw.) N.E.Br.	<i>Tenuifolii</i>	Klak 313	X	X	X
<i>Lampranthus stipulaceus</i> (L.) N.E.Br.	<i>Haworthiani</i>	Klak 472	X	X	X
<i>Lampranthus vallis-gratiae</i> (Schltr. & A.Berger) N.E.Br.	<i>Scabridi</i>	Bruyns 7655	X	X	X
<i>Lampranthus virens</i> (Haw.) Klak comb. nov.		Klak 449	X	X	X
<i>Namaquanthus vanheerdei</i> L.Bolus		Klak 251	X	X	X
<i>Scopelogenia bruynsii</i> Klak		Klak 462	X	X	X
<i>Smicrostigma viride</i> (Haw.) N.E.Br.		Klak 180	X	X	X
<i>Vlokia ater</i> S.A. Hammer		Hammer & Vlok 1181	X	X	X
<i>Wooleya farinosa</i> (L.Bolus) L.Bolus		Klak 473	X	X	X
<i>Zeuktophyllum suppositum</i> (L.Bolus) N.E.Br.		Klak 375	X	X	X