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Cornelia Klak
University of Cape Town

Terry Hedderson
University of Cape Town

MOLECULAR PHYLOGENETICS

A phylogeny and new classification for Mesembryanthemoideae (Aizoaceae)

Cornelia Klak, Peter V. Bruyns & Terry A.J. Hedderson

Bolus Herbarium, University of Cape Town, 7701 Rondebosch, South Africa. Cornelia.Klak@uct.ac.za (author for correspondence)

We present a phylogeny for Mesembryanthemoideae (Aizoaceae) based on sampling of nearly all species and subspecies of the subfamily and analysis of cp*trnL-F*, *rbcL-atpB, rps16*, nrITS1 and morphology. The larger genera *Phyllobolus* and *Mesembryanthemum* are not monophyletic. Although some clades can be circumscribed with morphological (often homoplasious) synapomorphies, several clades are impossible to characterise morphologically. We recognise a single genus, *Mesembryanthemum*, in Mesembryanthemoideae. The genera *Aptenia*, *Aridaria*, *Aspazoma*, *Brownanthus*, *Caulipsolon*, *Dactylopsis*, *Phyllobolus*, *Prenia*, *Psilocaulon*, *Sceletium*, and *Synaptophyllum* are reduced to synonymy. *Mesembryanthemum*, which now consists of 101 species without recognised sections, can be distinguished by several uniquely derived morphological characters. *Mesembryanthemum longipapillosum*, which had recently been reduced to synonymy, is reinstated.

KEYWORDS: Aizoaceae, classification, ITS1, Mesembryanthemoideae, phylogeny, *rbcL-atpB*, *rps16*, *trnL-F*

INTRODUCTION

Four subfamilies are currently recognised in Aizoaceae: Sesuvioideae, Aizooideae, Ruschioideae, and Mesembryanthemoideae. These were each shown to be monophyletic by means of chloroplast (Klak & al., 2003b) and nuclear markers (Thiede, 2004). The two subfamilies Mesembryanthemoideae and Ruschioideae, where succulence is most highly developed, are largely restricted to southern Africa. Of these, Ruschioideae, with approximately 1,600 species, is the most speciose subfamily, while Mesembryanthemoideae, with 100 species, is considerably smaller (Hartmann, 2001). Schwantes (1947) was the first to recognise the Mesembryanthemoideae, though he used "Aptenioideae" for it. Since this was not validly published it was later replaced by the name Mesembryanthemoideae (Ihlenfeldt & al., 1962). The defining features of the subfamily are koilomorphic nectaries, axile placentation and the presence in the fruits of purely septal expanding keels that reach from the central columella to the tips of the valves (e.g., Ihlenfeldt & al., 1962; Hartmann, 1991). Many members of this subfamily have flattened mesomorphic leaves and, in many of them, both leaves and stems are covered with conspicuous bladder cells. It is noteworthy that, while these vegetative characteristics are absent from almost all members of Ruschioideae, they are nevertheless present in the few members of the ruschioid tribes Apatesieae and Dorotheantheae, which are sisters to the remainder of Ruschioideae (Klak & al., 2003b).

Most of the genera in Mesembryanthemoideae have been revised (e.g., Gerbaulet, 1996a, b, c, 1997; Klak & Linder, 1998; Klak & al. 2006) and several were recircumscribed on the basis of morphological characters (e.g., Ihlenfeldt & Bittrich, 1985; Bittrich, 1986; Gerbaulet, 1995). Currently 12 genera are recognised (Table 1).

The Mesembryanthemoideae are remarkable among the succulent Aizoaceae for their diversity of life- and growth-forms. There are both annuals and perennials, leaf- as well as stem-succulents, geophytes, highly compact dwarf-shrubs as well as tall, woody shrubs that may exceed 1 m in height. Furthermore, the leaves are often deciduous (e.g., *Phyllobolus deciduus*) or the branches are partly deciduous (e.g., *P. oculatus*).

Phyllobolus is the largest genus within the subfamily (Table 1). While it includes mostly shrubby perennials, there are also several geophytes. Many of the non-geophytic species have stems with a cork layer and/or deciduous leaves. Since it was described by Brown (1925) this genus has often been modified. Bolus (1964) was the

Table 1. Genera and number of species in Mesembryanthemoideae after Hartmann (2001) and Klak & al. (2006).

Genus	Species	Subspecies
Aptenia N.E. Br.	4	–
Aridaria N.E. Br.	4	2
Aspazoma N.E. Br.	1	–
Brownanthus Schwantes	14	–
Caulipsolon Klak	1	–
Dactylopsis N.E. Br.	1	1
Mesembryanthemum L.	16	–
Phyllobolus N.E. Br.	31	1
Prenia N.E. Br.	6	3
Psilocaulon N.E. Br.	13	–
Sceletium N.E. Br.	8	–
Synaptophyllum N.E. Br.	1	–

first to broaden the generic concept, when she merged *Sphalmanthus* N.E. Br. and *Phyllobolus*. Bittrich (1986) promoted an even broader circumscription of *Phyllobolus* which included *Amoebophyllum* N.E. Br., *Aridaria*, *Prenia*, and *Sceletium*. Although he made no formal taxonomic changes he proposed subdivision of the enlarged *Phyllobolus* into five subgenera (*P.* subg. *Aridaria*, *Phyllobolus*, *Prenia*, *Sceletium*, *Sphalmanthus*). Since Gerbaulet (1995) was unable to find a synapomorphy for Bittrich's broad concept of *Phyllobolus*, she recognised the genera *Aridaria*, *Phyllobolus*, *Prenia*, and *Sceletium* and provided putative synapomorphies for each. In addition, she modified the generic concepts of *Prenia* and *Aridaria* (Gerbaulet, 1995). *Phyllobolus* included only *P.* subg. *Phyllobolus* and *Sphalmanthus*, the *Aridaria splendens*-group and the monotypic genera *Amoebophyllum* and *Dactylopsis* N.E. Br. (Gerbaulet, 1995). More recent investigations showed that *Dactylopsis*, together with *Aspazoma*, is sister to *Brownanthus* (Klak & al., 2003b) so that it is not closely allied to *Phyllobolus*. Consequently it was reinstated as a monotypic genus (Klak & al., 2006). This remarkable endemic of the Knersvlakte is compact and almost stemless and is the only member of the Mesembryanthemoideae with highly succulent, fleshy leaves. During the resting period the leaves dry out completely to provide a protective cover under which new leaves develop.

Bittrich (1986) incorporated all the annual species into *Mesembryanthemum* (apart from the single member of *Synaptophyllum*) and recognised several of the earlier genera as subgenera (*M.* subg. *Cryophytum* and subg. *Opophytum*). The morphological heterogeneity in *Mesembryanthemum* is reflected in this subgeneric division. *Mesembryanthemum* subg. *Cryophytum* is characterised by large, flat leaves with conspicuous bladder cells, whereas in *M.* subg. *Opophytum* the leaves are cylindrical with flattened bladder cells. The latter subgenus also includes *M. eurystigmatum*, an endemic of the Tanqua Karoo, that was previously the monotypic genus *Eurystigma* L. Bolus. Members of *M.* subg. *Mesembryanthemum* all have much smaller leaves than those of the other two subgenera. Bittrich (1986) regarded *M.* subg. *Mesembryanthemum* as the most heterogeneous subgenus. Within it, on the basis of differences in leaf shape and in pollen and seed morphology, the *M. aitonis* group (flat-leaved species) and the *M. nodiflorum* group (cylindrical-leaved species) could be recognised. Several hypothetically plesiomorphic characters (annual life-form, flattened broad leaves with conspicuous bladder cells, leafy inflorescences, narrow petaloid staminodes), led him to also suggest that *M.* subg. *Cryophytum* is sister to the remainder of the Mesembryanthemoideae. In the most recent treatment of *Mesembryanthemum* 16 species are recognised (Gerbaulet, 2001), but no synapomorphies were found for *Mesembryanthemum*.

The four genera *Aptenia*, *Aspazoma*, *Brownanthus*, and *Psilocaulon* all exhibit stem succulence and as a consequence were considered to be closely related (Gerbaulet, 1995). Here the stems remain green and succulent and generally only the oldest parts become woody. Leaves are produced during the growing season and dry up during the summer period. The molecular study by Klak & al. (2003b) showed that *Aspazoma*, *Brownanthus* and *Psilocaulon* are closely related, but that *Aptenia* is sister to *Sceletium*. The monotypic genus *Caulipsolon*, that was removed from *Psilocaulon* by Klak & Linder (1998), and the name later validated by Klak & Gerbaulet (2001), was found to be sister to *Psilocaulon* (Klak & al., 2003b).

The phylogenetic position of *Synaptophyllum*, a monotypic genus endemic to the Lüderitz area of Namibia and the only genus of Mesembryanthemoideae not included in the molecular study by Klak & al. (2003b), has so far been obscure. On account of the flat leaves and the much reduced epidermal bladder cells, Bittrich (1986) thought that it might be closely related to *Prenia*. On the other hand, the presence of neotenic seeds (Ihlenfeldt, 1971), leafy inflorescences and aspects of the floral morphology suggested an equally likely close relationship to *Mesembryanthemum* (Bittrich, 1986).

Only 16 species of Mesembryanthemoideae were included in Klak & al. (2003b). They indicated that several genera were not monophyletic and that generic limits needed re-investigation. Here we reconstruct phylogenetic relationships within the group from a nearly complete sampling of the species and subspecies, using both molecular and morphological data (Table 1). We address two questions: (1) Are the currently recognised genera monophyletic, and (2) how are the genera and the species related?

MATERIALS AND METHODS

Taxon sampling. — A total of 108 accessions of Mesembryanthemoideae were included (Appendix 1). Taxa not included are *Aptenia lancifolia* L. Bolus, *Dactylopsis digitata* subsp. *littlewoodii* (L. Bolus) Klak, *Mesembryanthemum gariusanum* Dinter, *Phyllobolus amabilis* Gerbaulet & Struck, *P. melanospermus* (Dinter & Schwantes) Gerbaulet, *Prenia pallens* subsp. *lancea* (Thunb.) Gerbaulet, and *Psilocaulon dimorphum* (Welw. ex Oliver) N.E. Br. Several of these are rare and more expensive, time-consuming field work would have been required to collect them. For several variable species more than one accession was included. Eighteen outgroup taxa were chosen: these were selected from the remaining subfamilies of Aizoaceae and one species each from the closely related families Molluginaceae, Phytolaccaceae and Nyctaginaceae (Klak & al., 2003b).

We sampled three chloroplast regions; the *rps16* intron (125 accessions), the *trnL-F* intergenic spacer (including the *trnL* intron) and the *atpB-rbcL* intergenic spacer, (123 accessions each). In addition, we sampled one nuclear gene region, the internal transcribed spacer (ITS1), for 82 taxa: 11 members for the outgroup and 71 taxa of Mesembryanthemoideae (Appendix 1). That we only managed to generate 52 new sequences, may be due to non-identical copies of the ITS1 region. However, the use of cloning techniques, which would have overcome this problem, was beyond the scope of this study. In total, 339 new sequences were generated from material collected in the field. The rest were obtained from GenBank.

Plant material, DNA extraction, PCR, sequencing and alignment. — Taxa, voucher information and accession numbers of the DNA sequences are listed in Appendix 1. Total DNA was isolated from fresh leaf material using the 2XCTAB method outlined in Doyle & Doyle (1987). Samples were ground in 700 µl of extraction buffer and a pinch of polyvinylpyrrolidone (PVP-40). In some cases, where initial polymerase chain reaction (PCR) amplification did not yield a product, the DNA was further purified by using the QIAquick™ PCR purification kit, following the manufacturer's instructions. The four DNA regions were amplified from total DNA by the PCR. The following primer pairs were used to amplify DNA regions: c and f (Taberlet & al., 1991) for the *trnL-F* region (consisting of the adjacent *trnL* intron and *trnL-F* intergenic spacer), *rps*F and *rps*R2 (Oxelman & al., 1997) for the *rps16* intergenic spacer, 2 and 5 (Manen & al., 1994) for the intergenic spacer between the *atpB* and *rbcL* genes, and 18KRC (Klak & al., 2006) and ITS2 (Baldwin, 1992) for ITS1. PCRs were performed using 0.75 units of BIOTAQ™ DNA polymerase (Bioline) in 30 µl volumes also containing 1× NH_4 buffer and 5 mM $MgCl_2$, 0.1 mM of each dNTP, 0.3 µM of each primer, and 3 µl of unquantified DNA template. Thermocycling was carried out on a Hybaid Sprint set to the following thermal conditions: initial denaturation at 97°C for 2 mins., followed by 30 cycles of 97°C for 1 min., 52°C for 1 min., 72°C for 2 mins., with a final polymerisation step of 72°C for 7 mins. The PCR products were cleaned using the QIAquick® PCR purification kit (Qiagen). Both strands of the PCR products were cycle sequenced, as per manufacturer's instructions, using the ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit Version 3.0 (Applied Biosystems). The primers used for amplification were also used for the sequencing reactions. The samples were run on an Applied Biosystems 377 automated DNA sequencer.

Data files were assembled and edited using GeneDoc version 2.6.002 (Nicholas & Nicholas, 1997) and Chromas version 1.43 (McCarthy, 1996–1997). Sequences were aligned by eye. Ambiguous positions were coded using appropriate IUPAC ambiguity symbols so as to maximise the retention of information. Gaps were coded as present or absent using the simple indel coding method (Simmons & Ochoterena, 2000).

Morphological characters. — Forty-one morphological characters were analysed (Appendices 2, 3 in the electronic supplement). The morphological characters were scored from field collected plants and based on information available in the literature (e.g., Bittrich, 1987; Gerbaulet, 1996a, b, c). Missing, inapplicable or variable characters were coded as "?".

Phylogenetic analyses. — Cladistic analyses were performed using the maximum parsimony (MP) algorithm of the software package PAUP* version 4.0b4 (Swofford, 2000). Characters were given equal weight and states were unordered. Each data matrix was analysed using 1,000 replicates of random taxon-addition to find local minima among the trees, TBR branch swapping with MULPARS on and all character transformations treated as equally likely (Fitch, 1971). A limit of two trees saved on each replicate was set to minimise time spent swapping on local minima. All trees found in the initial 1,000 replicates were then used as starting trees for a second round of TBR swapping. At most 30,000 of the most parsimonious trees (MPTs) were saved and their strict consensus is referred to below as the MP tree. Nodal support was evaluated by use of the Jackknife (10,000 replicates with 36.79% of characters deleted at each replicate, emulate "Jac" resampling, "Fast" stepwise-addition) as implemented in PAUP*. Only groups with jackknife support percentages (JK) > 50 were retained and clades with JK ≥ 63 are regarded as supported by the data, as they are supported by at least one uncontradicted character (Farris & al., 1996).

Five separate analyses were performed. (1) Combined chloroplast data (125 accessions). These were analysed only in a combined matrix since the chloroplast genome is uniparentally inherited and so any incongruence should not be due to different histories. (2) Morphological and chloroplast data (125 accessions). (3) Nuclear data (82 taxa; *Carpanthea pomeridiana* was included in this analysis as a representative for the Apatesiae). (4) Combined nuclear and chloroplast data (82 taxa). No specific tests of congruence were performed before combining the data, since such tests can fail and cannot be considered proof of incongruence (Yoder & al., 2001). (5) Total evidence: all molecular and morphological data (82 taxa). In all analyses the gap coding was included.

In addition we performed two analyses using Bayesian inference (BI): one on the combined chloroplast and morphological data and the other on the total evidence. In both analyses the gap coding was included. Both analyses were conducted with MrBayes 3.0b4 (Ronquist & Huelsenbeck, 2003). Each of the analyses was done using three independent runs, each with four Markov chains (random starting trees), one of which was cold and the remainder heated. Each chain was run for 10^6 generations (ngen = 10^6), with trees sampled and printed every 100 generations (samplefreq = 100, printfreq = 100) and with a variable prior distribution. Following the recommendation by Huelsenbeck & Rannala (2004) the most complex substitution model was selected for the molecular and morphology datasets (set partition = datasets; prset ratepr = variable; lset applyto = [1,2,4] nst = 6; rates = invgamma; unlink shape = [all]; pinvar = [all]; statefreq = [all]; revmat = [all]). Plots of the –log likelihoods against generation time, as well as comparison of posterior probabilities (PP) across independent runs, were used to determine whether and when stationarity was achieved and thus to determine the 'burn-in' period. Based on this the first 500 of the sampled trees were discarded as "burnin" prior to the calculation of the Bayesian PP.

RESULTS

Statistics, including numbers of variable positions, numbers of coded indels and measures of character fit, are given for each analysis in Table 2.

Combined chloroplast analysis. — For the *trnL-F* region, data were not available for one accession of *Phyllobolus splendens* subsp. *splendens* (*Bruyns 9554*) and for *Aridaria noctiflora* subsp. *noctiflora*. For the *atpB-rbcL* intergenic spacer, data were not available for *M. nodiflorum* and for one accession of *P. oculatus* (*Klak 898*). The *trnL-F* region and the *rps16* intron contributed an almost equal number of coded indels, i.e., 32 and 29 respectively, whereas the *atpB-rbcL* intergenic spacer contributed only 9 indels to the combined data matrix. A phylogram of one of the 30,000 MPTs (not shown) reveals many very short branches within Mesembryanthemoideae, indicating that very few molecular changes have occurred between many of the genera. Relationships deep in the MP tree (Fig. 1) are well resolved and well supported, whereas there is much less resolution and support towards the tips of the branches. The *Mesembryanthemum aitonis* group, which is part of *Mesembryanthemum* subg. *Mesembryanthemum*, is sister to the remainder of the Mesembryanthemoideae (JK = 98). The remainder falls into three main clades (A, B, C). Clade A (JK = 86) incorporates *Aptenia*, *Mesembryanthemum* subg. *Cryophytum* and the *Phyllobolus* alliance (*Aridaria*, *Phyllobolus*, *Prenia*, *Sceletium*). Within clade A, all species currently in *Mesembryanthemum* subg. *Cryophytum* are sister to two well-supported subclades. The first consists of a polytomy including *Aptenia*, *Phyllobolus splendens*, and *Sceletium* (JK = 98). This is sister to a large polytomy, made up of *Aridaria*, the remainder of *Phyllobolus*, and *Prenia* (JK = 96). Very few relationships are resolved and well supported. Clade B consists of a polytomy with two larger and several smaller clades. The stem-succulent genera *Aspazoma*, *Brownanthus*, and *Dactylopsis* are resolved in one clade (JK = 97). A second well supported clade (JK = 90) consists of *Synaptophyllum* which is sister to *Psilocaulon*, with *Caulipsolon* nested in *Psilocaulon*. In addition, Clade B incorporates five species of *Mesembryanthemum*: four from *Mesembryanthemum* subg. *Mesembryanthemum* and *M. eurystigmatum* from *M.* subg. *Opophytum*. The remainder of the species of *M.* subg. *Opophytum* lie in clade C (JK = 100).

Combined chloroplast and morphology analysis. — The MP tree (not shown) is very similar to the tree based only on the chloroplast data (Fig. 1), but is more resolved. Several genera or subgenera, which were left in a polytomy in the chloroplast analysis, are resolved into clades in the MP tree. These are *Aptenia* (JK = 87), *Sceletium* (JK = 90), the four accessions of *P. splendens* (JK = 69), *Aridaria* (JK = 95), *Prenia* (JK = 78),

Table 2. Summary of characters included in parsimony analyses, together with tree statistics.

Data partition	Chars. incl.	Chars. var.	PICs	MPTs	Length	CI	RI	Indels
Combined chloroplast matrix: 125 taxa								
trnL-trnF		168	213					32
atpB-rbcL		114	110					9
rps16		152	195					29
Chloroplasts	2,748	437	588	30,000	1,293	0.619	0.860	70
Chloroplasts + morphology	2,789	438	628	30,000	1,543	0.546	0.837	70
Reduced data matrix: 82 taxa								
ITS1	634	64	127	30,000	1,490	0.593	0.790	10
trnL-trnF		177	167					25
atpB-rbcL		117	93					7
rps16		156	160					21
ITS1 + chloroplasts		654	610	30,000	1,490	0.593	0.790	63
Total evidence		649	524	30,000	1,671	0.554	0.780	63

Note: Column headings are as follows: Chars. incl., number of included characters; chars. var., number of variable characters; PICs, number of potentially parsimony informative characters; MPTs, number of most parsimonious trees; CI, consistency index; RI, retention index.

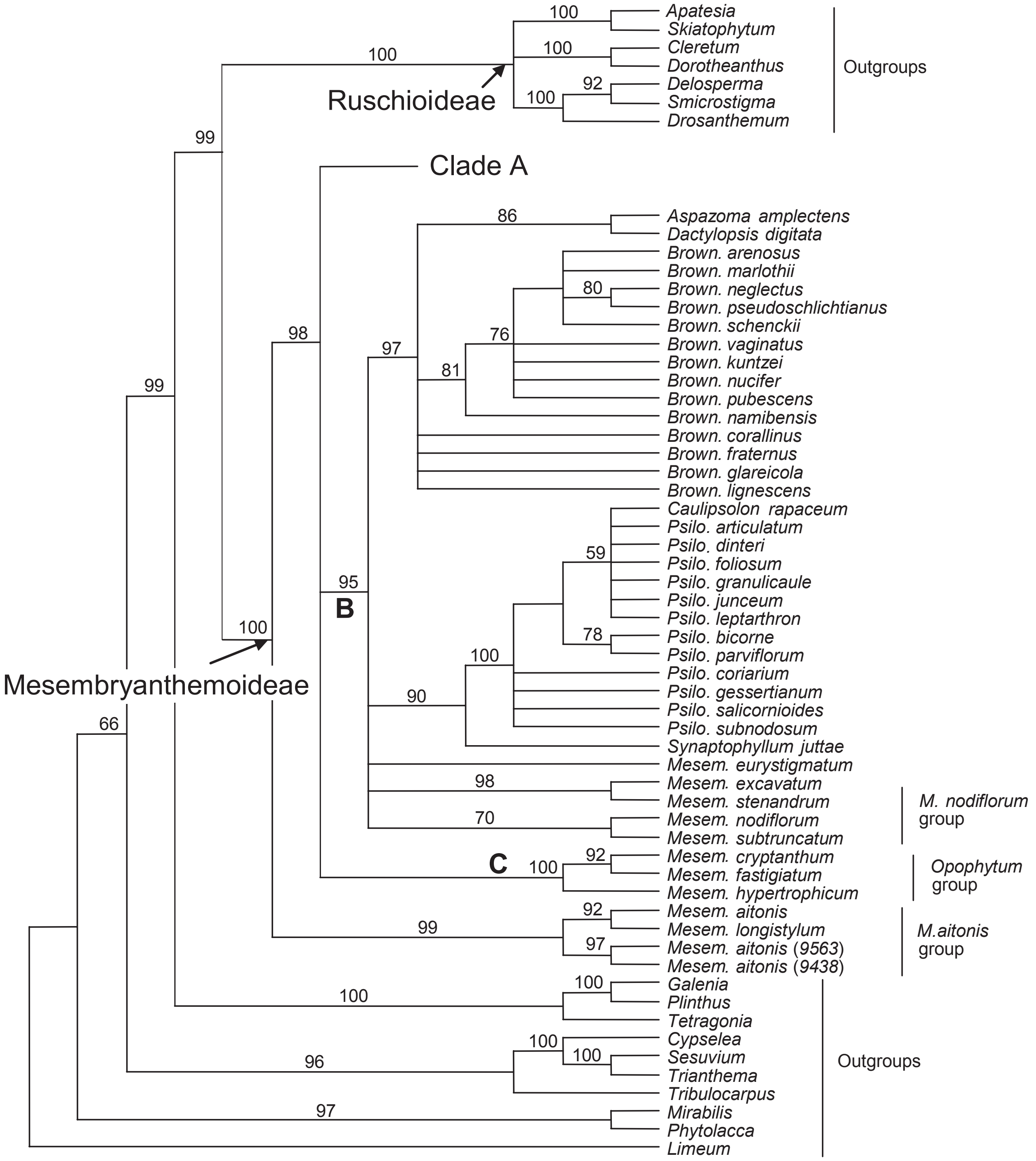

Fig. 1 (continued overleaf). Strict consensus tree of maximum parsimony (MP) analysis based on chloroplast data only; jackknife percentages above or equal to 50% are indicated above the branches.

Brownanthus (JK = 57), and *Mesembryanthemum* subg. *Cryophytum* (JK = 71). *Mesembryanthemum eurystigmatum* is sister to *Brownanthus* + *Aspazoma* + *Dactylopsis*, but this lacks any statistical support.

The BI tree (Fig. 2) for the combined chloroplast & morphology matrix for 125 accessions compares well with the MP tree. Similar to the MP tree, all of the deeper nodes have high PP values (PP = 1.00). There are also high PP values towards the tips of the branches. For example, *M. inachabense* is placed with a high posterior probability (PP) of 0.99 as sister to the remainder of *M.* subg. *Cryophytum*, as opposed to JK = 71 in the MP tree. Similarly,

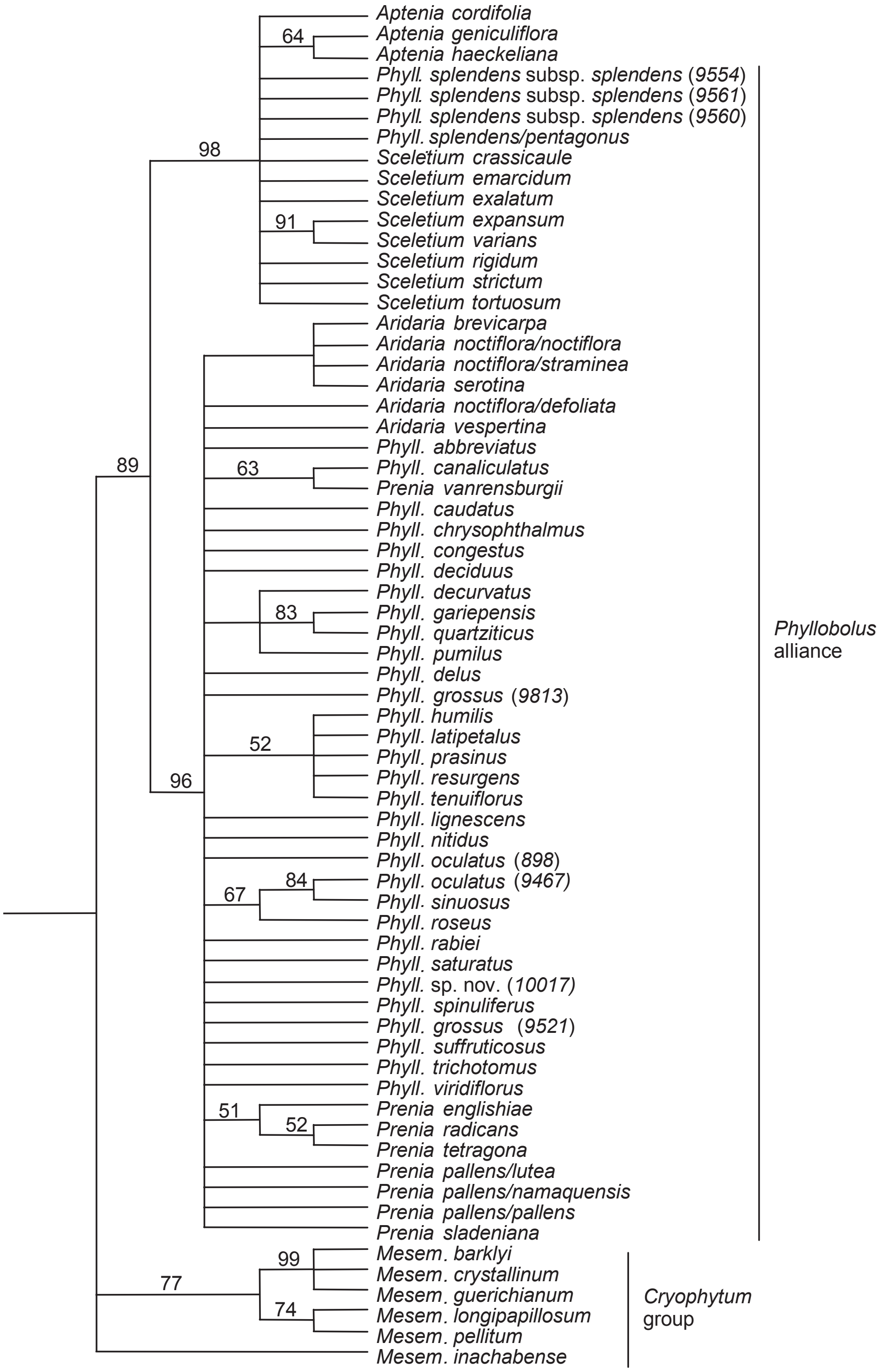

Fig. 1 continued. Clade A of the strict consensus tree of maximum parsimony (MP) analysis based on chloroplast data only; jackknife percentages above or equal to 50% are indicated above the branches.

the clade consisting of *M. subtruncatum* + *M. nodiflorum* has a high PP (PP = 0.99), whereas it gained little support (JK = 62) in the MP tree.

There are several clades which are only retrieved in the BI tree although they do not have a high PP (PP < 0.95). Within clade A, *P. splendens* is sister to *Aptenia* + *Sceletium* (PP = 0.89). There is strong support for the monophyly of *Aridaria* (PP = 1.0) and *Prenia* (PP = 0.99). A clade consisting of *P. decurvatus*, *P. gariepensis* + *P. quartziticus* (PP = 0.90) is weakly supported (PP = 0.91)

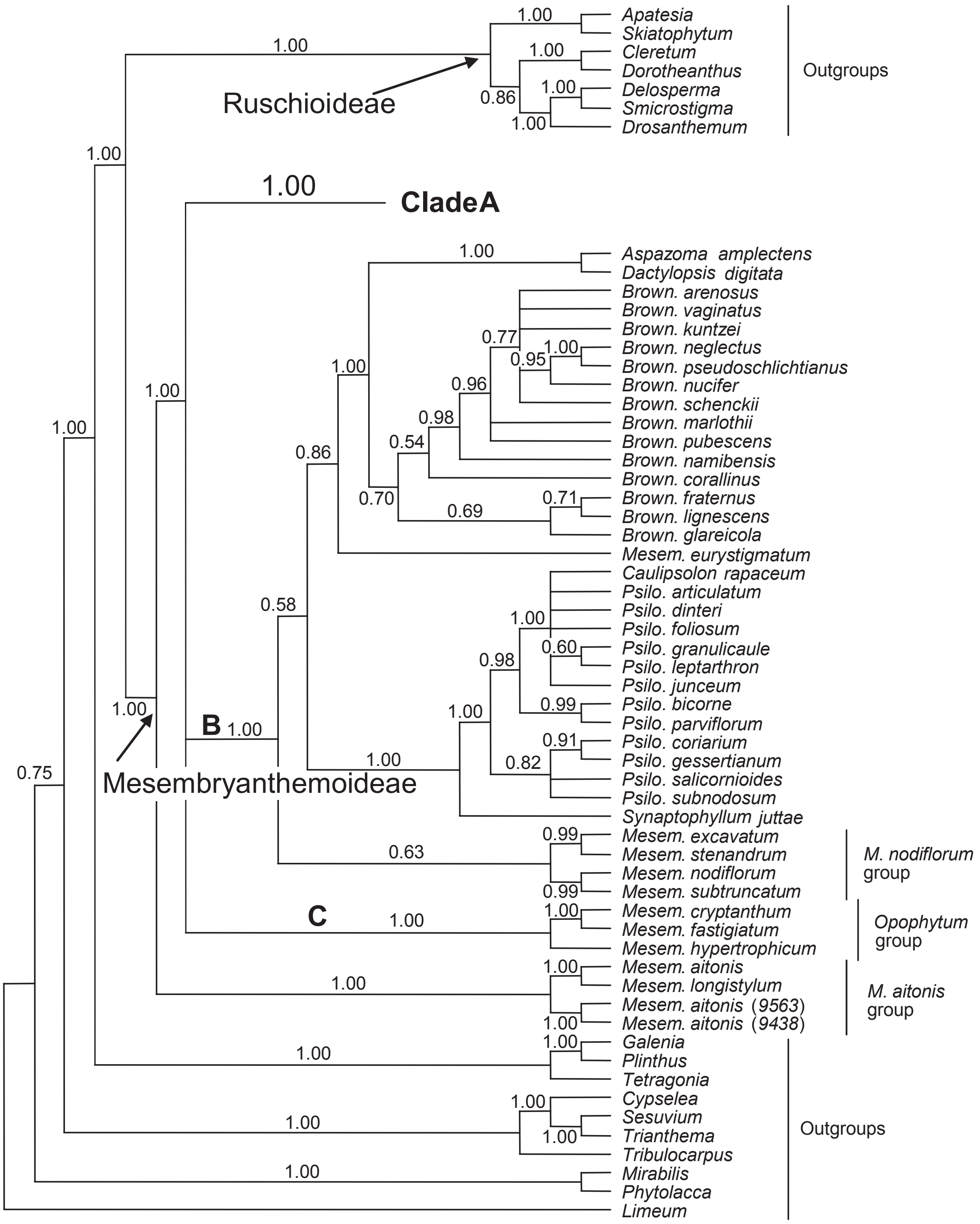

Fig. 2 (continued overleaf). Bayesian inference (BI) tree based on chloroplast data and morphology; posterior probability (PP) values are indicated at the branches.

as sister to the remainder of *Phyllobolus* (excl. *P. splendens*) which falls into a polytomy including also *Prenia* and *Aridaria*. The relationship of these two clades to the remainder of *Phyllobolus* is uncertain. Nevertheless there are several groups of species of *Phyllobolus*, which are retrieved with high PP values within this polytomy (e.g., *P. delus* + *P. rabiei* + *P. spinuliferus* + *P. viridiflorus* [PP = 0.99] and *P. humilis* + *P. latipetalus* + *P. prasinus* + *P. resurgens* + *P. tenuiflorus* [PP = 1.0]). In clade B, *M. excavatum* + *M. stenandrum* and *M. nodiflo-*

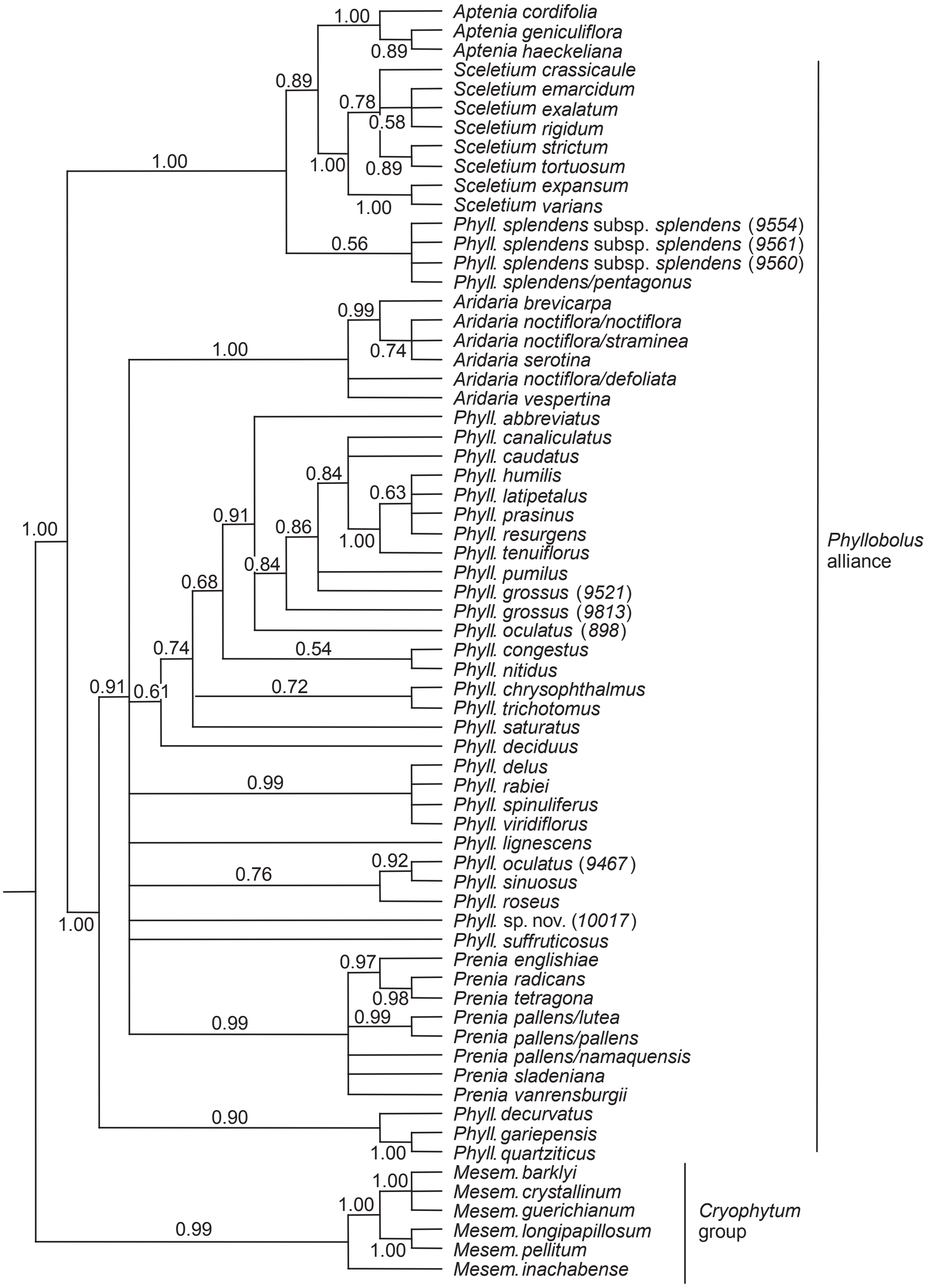

Fig. 2 continued Clade A of the Bayesian inference (BI) tree based on chloroplast data and morphology; posterior probability (PP) values are indicated at the branches.

rum + *M. subtruncatum* are retrieved as sisters with a low PP (PP = 0.63) which is sister to the remainder of clade B. However, the relationship of the *M. nodiflorum* group to the remainder of clade B remains uncertain (PP = 0.58). Similarly, the position of *M. eurystigmatum* as sister to *Aspazoma* + *Brownanthus* + *Dactylopsis* gained only moderate PP values (PP = 86, MP tree: JK < 50). However, there is more confidence concerning the position of the monotypic *Caulipsolon*. Whereas in the MP tree *Caulipsolon* lies in a polytomy with the species of *Psilo-*

caulon, in the BI tree it is nested in *Psilocaulon* (PP = 1.0). Among its closest relatives are other species of *Psilocaulon* (except *P. granulicaule*) from the dry winter-rainfall area of southern Africa (Namaqualand and the southern Namib). The position of clade C, consisting of part of *M.* subg. *Opophytum*, remains uncertain. This is consistent with the results obtained in the MP tree.

Nuclear analysis. — The resolution and support in the MP tree (not shown) is very low and not even the Mesembryanthemoideae form a monophylum. The species in clade A of the chloroplast analysis are also grouped together by the nuclear data, but they fall within a large polytomy (JK < 50) in which there are also three members of Ruschioideae and *Psilocaulon bicorne*. Clade B is not retrieved. Within this large polytomy very few clades are resolved and well supported. Nevertheless, amongst them there are clades which were not retrieved by the chloroplast data (Fig. 1). These are *Aridaria* (JK = 69), *Sceletium* (JK = 85), and *Brownanthus marlothii* + *B. pubescens* (JK = 95). The two clades *Mesembryanthemum crystallinum* + *M. guerichianum* (JK = 59) and *M. stenandrum* + *M. excavatum* (JK = 73), which were also present in analyses of the chloroplast data, are less supported by the nuclear data.

Combined chloroplast and nuclear analysis. — The MP tree (not shown) is similar to the chloroplast tree (Fig. 1), but is more resolved. New clades are *Aridaria* (JK = 78) and *Sceletium* (JK = 96). Furthermore, *M. cryptanthum* (the only representative of clade C of the chloroplast analysis), which occupied an uncertain position in all previous analyses, is now sister to clade A. However, this relationship is without statistical support.

Total evidence analysis. — The MP tree (not shown) has an identical topology and very similar levels of nodal support to the combined chloroplast & nuclear analysis. Noteworthy is the increase in nodal support for *Aridaria* (JK = 100, up from JK = 78 without morphology). The BI tree (Fig. 3) is largely congruent with the MP tree. One of the few important differences between the chloroplast & morphology analysis (Fig. 2) and that including the nuclear data (Fig. 3) is in the position of *M. cryptanthum* (the only representative of clade C). In both the MP tree and the BI tree (Fig. 3) this species is sister to clade A. Although this relationship has negligible support in the MP tree (JK < 50), the BI analysis shows fairly high PP values (PP = 0.94).

DISCUSSION

Polyphyly of *Mesembryanthemum*. — One of the most striking results of our study is the polyphyly of *Mesembryanthemum*, though its morphological diversity may have led one to expect this. Here the 16 species fall into five evolutionary lineages (Fig. 2) and none of the three subgenera is monophyletic. *Mesembryanthemum inachabense*, which Gerbaulet (2001) placed in *M.* subg. *Mesembryanthemum*, is sister to *M.* subg. *Cryophytum*, where Bittrich (1986) had placed it. Gerbaulet (2001) reduced *M. longipapillosum* to synonymy with *M. inachabense*, but these two are shown to be distinct species. Members of *M.* subg. *Cryophytum* typically have flowers with many narrow staminodes and many stamens. In *M. inachabense*, on the other hand, the petals are broader and are not especially numerous, the seeds are neotenic (i.e., light brown to white with raised to almost smooth testa cells) and the leaves are not particularly large (25–50 mm long) with only moderately sized epidermal bladder cells. Thus, in many features *M. inachabense* is more similar to members of *M.* subg. *Mesembryanthemum*. Characters linking it to *M.* subg. *Cryophytum* are the deep nectaries, the fusion of the androecial parts into a connate tube and the valve wings which are erect or inflexed over the valves in the fruits. In contrast, in *M.* subg. *Mesembryanthemum* all species have tubular nectaries, the androecial parts are free towards the bases and the valve wings are reflexed and fused in pairs.

Mesembryanthemum subg. *Mesembryanthemum* is also polyphyletic and falls into two clades (Fig. 2). The first (containing *M. aitonis*), incorporates two species. In our phylogeny one of the three accessions of *M. aitonis* is resolved as sister to *M. longistylum* (PP = 1.00, Fig. 2). Gerbaulet (2001) regarded *M. aitonis* as a highly variable and widespread species, under which she included several taxa. A more detailed study of *M. aitonis* is necessary to establish why the three accessions are not monophyletic. One possible explanation is that *M. aitonis* includes more than one species, which might require for some taxa currently included under *M. aitonis* to be reinstated. Although the *M. aitonis*-clade and its sister-relationship to the remainder of the Mesembryanthemoideae gained high support (PP = 1.00, Fig. 2), this clade cannot easily be characterised morphologically. The two groups distinguished by Bittrich (1986) and Gerbaulet (2001) are shown here not to be monophyletic, since *M. longistylum* is part of the *M. aitonis*-clade. According to Bittrich (1986), the *M. nodiflorum* group is characterised by leaves with enlarged, central, water-storing cells, punctate-foveolate to reticulate pollen and neotenic seeds. On the other hand, the *M. aitonis* group lacks enlarged, central, water storing cells, but has punctate-microspinulose pollen and brown seeds with raised testa cells. However, information on these characters and their variability is not available for all members of both clades, so it is not certain whether these characters delimit them. Although there are several morphological characters which can be used to circumscribe the *M. nodiflorum* group, this clade is only well supported in the total evidence analysis (PP = 1.00, Fig. 3).

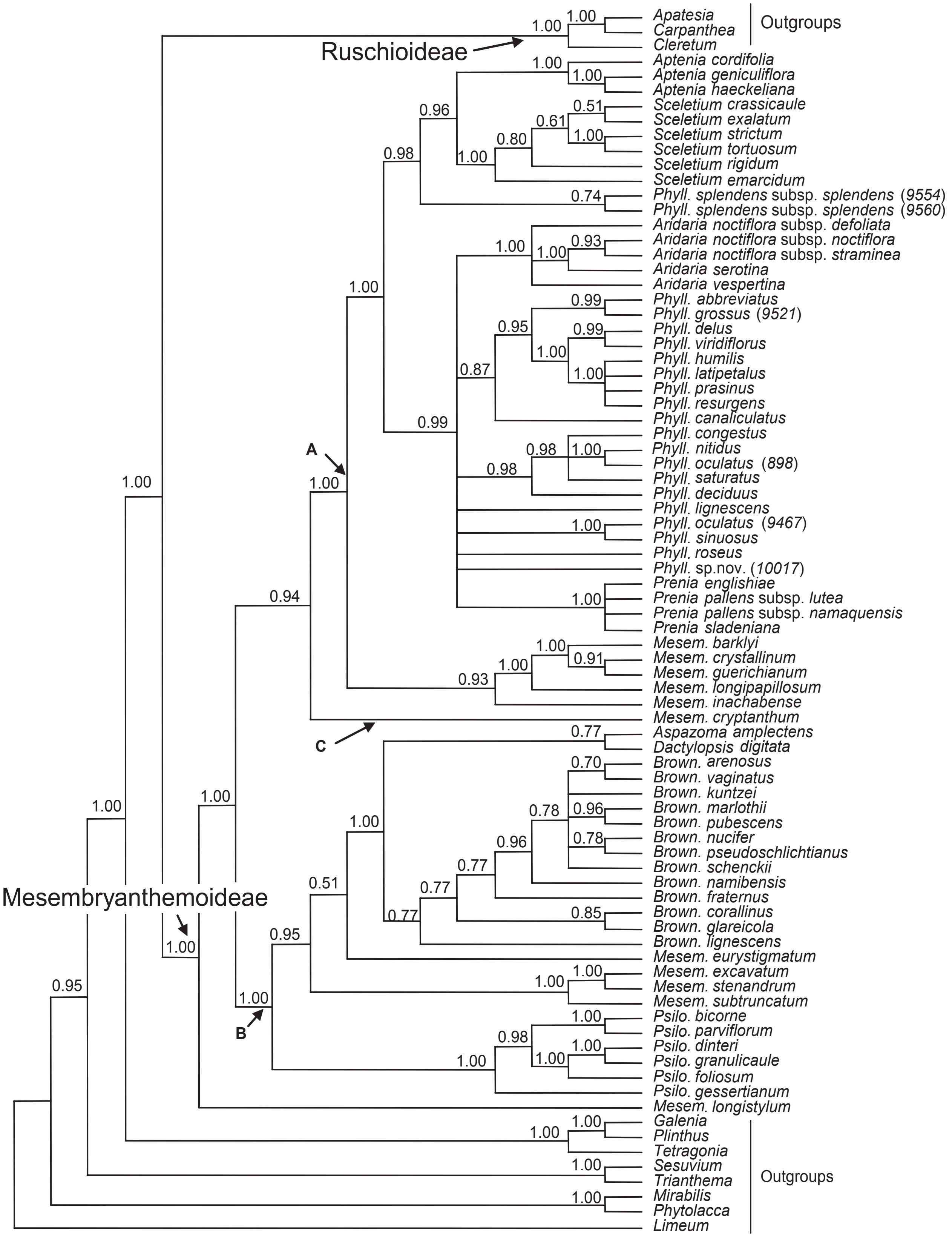

Fig. 3. BI tree based on combined chloroplast, nuclear and morphology data; PP values are indicated at the branches.

This is especially surprising, as *M. stenandrum* and *M. nodiflorum* are not easy to tell apart and differ mainly in the diameter of their flowers.

The relationship of the *M. nodiflorum* group to the remaining species in clade B remains uncertain. Morphologically, the *M. nodiflorum* group shares several characters with *Synaptophyllum*. These include the leafy inflorescences, floral morphology and the neotenic seeds. Neotenic seeds are shared by most members of clade B (*Aspazoma*, *Brownanthus*, *Dactylopsis*, *Psilocaulon*), but are also characteristic of the polyphyletic *M.* subg. *Opophytum*. Again, the members of this subgenus (including *M. eurystigmatum*) look superficially very similar, as they all have very succulent, more or less smooth, cylindrical leaves and (except for *M. cryptanthum*) have flowers with many petals, filamentous staminodes and stamens. These floral features are otherwise only found in the *Cryophytum* clade (except for *M. inachabense*). Despite this similarity, *M. eurystigmatum* belongs to clade B and is sister to the *Aspazoma* + *Brownanthus* + *Dactylopsis* clade (with low support: MP, JK < 50; BI, PP = 0.86). One of the few differences between *M. eurystigmatum* and other species of the *Opophytum* clade are that in the fruits the valve wings are inflexed over the valves and free in *M. eurystigmatum*, but reflexed and fused in pairs in the others. In addition, in *M. eurystigmatum* the stigmas are basally shortly connate with the ovary, which is an autapomorphy within the subfamily. It is noteworthy that *M. eurystigmatum* is geographically isolated from the other members of *M.* subg. *Opophytum*. *Mesembryanthemum fastigiatum* is geographically the closest member and occurs in the Knersvlakte, approximately 100 km away from the Ceres Karoo, where *M. eurystigmatum* is endemic.

Thus, the *Opophytum* clade can only be delimited using homoplasious morphological characters. The *Cryophytum* clade (except *M. inachabense*) and the *Opophytum* clade (except *M. cryptanthum*) share a very similar floral morphology, supporting the position of *Opophytum* as sister to clade A (the *Cryophytum* clade + the *Phyllobolus* alliance, PP = 0.94, Fig. 3). Nevertheless, the *Opophytum* group (and *M. inachabense*) differ from members of clade A by its smallish, smooth, pale (neotenic) seeds, features that characterise clade B. In clade A and in the *M. aitonis* group, the seeds are dark, with a much sculptured testa. Therefore, we must also interpret neotenic seeds as a homoplasious synapomorphy.

The *Phyllobolus* alliance (*Aptenia, Aridaria, Phyllobolus, Prenia, Sceletium*). — A further unexpected outcome is that *Phyllobolus splendens* is more closely allied to *Aptenia* and *Sceletium* than to the remainder of *Phyllobolus*. *Phyllobolus splendens* previously belonged to *Aridaria*, but Gerbaulet (1995) found numerous derived characters shared with *Phyllobolus* and suggested *P. decurvatus*, *P. saturatus* and *P. suffruticosus* as its closest relatives. With these, *P. splendens* shares woody stems with only few cortical bundels, flowers with filamentous staminodes where stamens and stigmas are not concealed, cylindrical leaves with weakly developed, central, water-storing tissue and small, somewhat flattened bladder cells (Gerbaulet, 1995, 1997). In an attempt to circumscribe the genera of the *Phyllobolus* alliance more precisely, the character "branches partly deciduous" was used as a synapomorphy for *Phyllobolus* (Gerbaulet, 1995). However, this feature is only present in some species (e.g., *P. lignescens* and *P. oculatus*) and is not found in *P. splendens*. Numerous species of *Phyllobolus* lose their leaves during the dry season and Gerbaulet (1995) also claimed that this was a synapomorphy for *Phyllobolus*. However, this phenomenon is widespread throughout Mesembryanthemoideae (e.g., *Aptenia*, *Aridaria*, *Psilocaulon*, *Brownanthus*) so that it is also a homoplasious synapomorphy for *Phyllobolus*. The presence of a pair of crests along the seed was cited as a further possible synapomorphy for *Phyllobolus*. Again, this feature is present in some species, while others lack it (e.g., *P. oculatus*). Consequently, no non-homoplasious synapomorphy appears to exist for *Phyllobolus*. Gerbaulet (1995) also proposed synapomorphies for *Aptenia, Aridaria, Prenia*, and *Sceletium*, each of which form highly supported clades in the combined chloroplast & morphological analysis (Fig. 2). Although *Aridaria* and *Prenia* each prove to be monophyletic, our study places them in a polytomy with species of *Phyllobolus*. Both *Aridaria* and *Prenia* possess leaves with much flattened bladder cells and a comparatively thick, epidermal wax layer. Gerbaulet (1995) used these two characters to suggest that the two genera were sisters, since the leaves in *Phyllobolus* (incl. *P. splendens*) generally have more prominent bladder cells. In a few cases, the leaves have smaller, xeromorphic bladder cells (*P. trichotomus*), but then they usually lack the grey, waxy layer typical of *Aridaria* and *Prenia*. One exception is *P. decurvatus,* which has grey leaves with very small bladder cells, so that plants may closely resemble *Prenia tetragona*.

In Mesembryanthemoideae, the stems are mostly slightly woody towards the base only. Nevertheless, there are some species with quite brittle, woody stems. In clade A this mainly involves members of *Phyllobolus* (e.g., *P. lignescens*, *P. splendens*, *P. trichotomus*) and all species of *Aridaria* have especially brittle and woody stems. While Gerbaulet (1995) recognised that woody stems had evolved in parallel in *Phyllobolus* and in *Aridaria*, she used the same character to propose a close relationship between *P. splendens*, the *P. decurvatus* group and the *P. trichotomus* group (Gerbaulet, 1995, 1997). Our results show that this grouping is not monophyletic. Moreover, "woodiness" and "corkiness" are expressed to varying degrees in the different species. For example, *P. prasinus* and *P. spinuliferus* have thick cork layers and others thin ones (*P. nitidus*). Similarly, the entire stem may be woody (e.g., *Aridaria*) or only the stem bases (e.g., *M. longistylum*).

The phenomenon of convergent evolution is equally evident in *P. splendens*, which is sister to *Aptenia* and *Sceletium*. There are no characters known to distinguish *P. splendens* from the clade containing the other species of *Phyllobolus*. Similarly, there are no defining morphological characters for the clade including *Aptenia*, *P. splendens*, and *Sceletium*. *Aptenia* and *Sceletium* are characterised by broad flat leaves (except in *A. geniculiflora*) and a climbing habit (also widespread in *Phyllobolus*). *Phyllobolus splendens*, on the other hand, has subcylindrical leaves and grows in the open. Gerbaulet (1995) identified "seeds with convex-papillose testa cells" as a synapomorphy for the genera *Sceletium* and *Phyllobolus* (incl. *P. splendens*). In *Aptenia*, *Aridaria* and *Prenia* the testa cells have a central papilla. The phylogeny reveals that both seed characteristics are homoplasious within the *Phyllobolus* alliance. A further feature of the seed, found in all members of the *Phyllobolus* alliance, is the manner in which the testa cells are arranged in distinct rows, more rarely in indistinct rows (e.g., *Aridaria*). In the remainder of Mesembryanthemoideae the testa cells are usually not arranged in rows, though in *Mesembryanthemum* subg. *Cryophytum* they may be in indistinct rows. In addition, members of the *Phyllobolus* alliance tend to have medium to large seeds (medium: 1.1–1.5 mm long in *Aptenia*, *Aridaria*, *Prenia*; large: 1.4–2.0 mm long in *Phyllobolus*, *Sceletium*), whereas the other Mesembryanthemoideae usually have smaller seeds (0.5–1.2[–1.5] mm long). Rarely, large seeds are also found outside the *Phyllobolus* alliance, as in *Aspazoma* (to 2.2 mm long). Although the seed sizes overlap, most of the taxa in clade B and clade C have either almost smooth seeds or the testa cells are not arranged in distinct rows, whereas in the *Cryophytum* and the *M. aitonis* clade seeds range only between 0.5–1.0 mm in length (Gerbaulet, 2001). Thus, a combination of seed characteristics could be used to recognise the *Phyllobolus* alliance (i.e., seeds brown to black, medium to large, testa cells convex-papillose or central-papillose). This expanded generic concept, including *Aptenia*, *Aridaria*, *Phyllobolus*, *Prenia*, and *Sceletium*, would reflect to a large extent Bittrich's concept of *Phyllobolus* (1986).

The stem succulent genera (*Aptenia*, *Aspazoma*, *Brownanthus*, *Psilocaulon*). — On account of the shared feature of the persistent green succulent cortex, the genera *Aptenia*, *Aspazoma*, *Brownanthus*, and *Psilocaulon* (including "*Caulipsolon*") were thought to be closely related (Gerbaulet, 1995). In these genera, usually most of the stem is succulent. However, in *Brownanthus lignescens* and *Psilocaulon foliosum* this succulence is restricted to the youngest internodes and so, strictly speaking, these two are not stem succulents. In addition, details of the epidermis of the stem differ among these four genera. Ihlenfeldt & Bittrich (1985) showed that the species of *Psilocaulon* s.l. fell into two groups defined by differences in epidermal morphology. In one group the surface of the stem has much flattened bladder cells, while the bladder cells are tall and more xeromorphic in the other. Thus, *Psilocaulon* was re-circumscribed to contain the first group and the second was placed in *Brownanthus* (Ihlenfeldt & Bittrich, 1985). In addition, *Aptenia*, *Aspazoma*, and *Dactylopsis* also possess a similar, xeromorphically modified epidermis. The monotypic *Dactylopsis* is unusual, since its stems are much shortened and more or less completely hidden by the clasping leaves. In addition, in *Dactylopsis* the stems possess a thick cork layer. For this reason Bittrich (1986) and Gerbaulet (1995) postulated that it was closer to *Phyllobolus*, since corky stems are widely present in *Phyllobolus* but not known elsewhere in Mesembryanthemoideae. The phylogeny suggests that corky stems have evolved independently in the two major clades A and B. Although *Aptenia*, *Aspazoma* and *Brownanthus* lack corky stems characteristic of *Dactylopsis*, these genera share a peculiar epidermal feature, viz., epidermal morphology of leaves different to that of stems. In *Psilocaulon*, however, these cells are similar. In *Aspazoma*, *Brownanthus*, and *Dactylopsis* the bladder cells are much thickened (though less so in *Dactylopsis*). In *Aptenia* on the other hand, they are thin-walled (Klak & al., 2006).

The monotypic *Caulipsolon* is part of *Psilocaulon* (Fig. 2), where it was previously placed. This species differs from all others in *Psilocaulon* by its floral morphology (which is suggestive of *M. nodiflorum*) and the geophytic habit (which suggests a close relationship to *Phyllobolus*) and consequently it was placed in a genus of its own (Klak & Linder, 1998). It shares several homoplasious features with *Psilocaulon,* namely articulated stems, flattened bladder cells on both stems and leaves, deep locules in the capsules and neotenic seeds,.

The phylogeny suggests that, whereas stem succulence is homoplasious, similar epidermal features may indeed be indicative of a close phylogenetic relationship. Nevertheless, the case of *Caulipsolon* shows that even epidermal characters may be homoplasious, since flattened epidermal bladder cells are also characteristic for *Prenia*.

TAXONOMIC CONCLUSIONS

A new classification for Mesembryanthemoideae. — Morphologically, Mesembryanthemoideae are well characterised by several synapomorphies, as discussed in the introduction. The monophyly of the subfamily is also well supported by molecular characters (e.g., JK = 100, Fig. 1). Whereas in the Ruschieae (Ruschioideae) there was very poor resolution and support even among the larger taxonomic groupings (Klak & al., 2003b), many of the internal clades in the Mesembryanthemoideae are well supported (e.g., the *M. aitonis* clade, the *Aridaria*-*Phyllobolus*-*Prenia* clade, the *Aptenia*-*P. splendens*-*Sceletium* clade). The phylogram (not shown) of the chloroplast analysis reveals that numerous molecular changes separate Mesembryanthemoideae from the other subfamilies of Aizoaceae. On the other hand, the short branches at the bases of many clades show that the number of molecular changes within Mesembryanthemoideae is much lower.

To uphold the currently recognised genera and keep all taxa monophyletic, it would be necessary to erect numerous further genera. However, the morphological delimitation of most of these clades is difficult. Several genera, such as *Brownanthus* (Klak & al., 2006), *Psilocaulon* (Klak & Linder, 1998) and *Sceletium* (Gerbaulet, 1996a) have uniquely derived characters. Also monotypic genera such as *Dactylopsis* and *Synaptophyllum* have autapomorphies, which may justify their monotypic status (Klak & al., 2006). However, groupings such as the *M. aitonis* clade, the *M. nodiflorum* clade, the *Phyllobolus splendens* clade and the *Phyllobolus* s.str. clade lack any uncontradicted morphological synapomorphies and can only be circumscribed with homoplasious characters. Even, the *Psilocaulon* clade, which has a synapomorphy includes *Caulipsolon*, which lacks this synapomorphy (Klak & Linder, 1998). In several other cases, the synapomorphies listed by Gerbaulet (1995, 2001) for *Phyllobolus* and for the subgenera/groups of *Mesembryanthemum* prove to be homoplasious. Even for the deeper, well supported nodes in the tree (e.g., clade A, clade B), no morphological synapomorphies could be found.

Before 1925, the large and inhomogeneous genus *Mesembryanthemum* included all species of Mesembryanthemoideae and Ruschioideae. Brown (1925) began the dismemberment of *Mesembryanthemum* into smaller units and since then the trend has been to recognise ever smaller genera, many including only one or two species (e.g., *Aspazoma*, *Caulipsolon*, *Dactylopsis*, *Synaptophyllum*). In Mesembryanthemoideae this trend was partly reversed by Bittrich (1986), who proposed broader concepts for *Phyllobolus* and *Mesembryanthemum*. Gerbaulet (1995), however, again favoured smaller genera and proposed synapomorphies for her recircumscribed genera. These fluctuating taxonomic concepts were partly due to the fact that many studies dealt with only parts of Mesembryanthemoideae (Gerbaulet, 1995; Klak & al., 2006). Our study includes almost all species of Mesembryanthemoideae for the first time. Furthermore, it reveals that convergent evolution is even more prevalent than was previously thought and we have shown that it is impossible to circumscribe all the monophyletic clades that we found using non-homoplasious morphological characters. This means that any newly discovered species may only be assigned to the appropriate monophyletic clade by means of molecular evidence. This would contradict Backlund & Bremer (1998), who maintained that a classification should maximise the principles of stability, phylogenetic information, support for monophyly and ease of identification.

In the absence of reliable and easy-to-use characters indicating generic boundaries and, since the characters defining the subfamily are the only reliable, easy-to-use synapomorphies, we propose that Mesembryanthemoideae should consist of the single genus *Mesembryanthemum*. This approach may seem drastic to users of the current classification, since now *Mesembryanthemum* encompasses considerable morphological diversity. However, *Mesembryanthemum* in its new circumscription will not be an unusual genus, since there are numerous genera of equal or larger size and greater morphological diversity which are also found in the Greater Cape flora (e.g., *Euphorbia* L., *Othonna* L., *Oxalis* L., *Pelargonium* L'Hér. ex Aiton, *Senecio* L.). More than half of the species and subspecies of Mesembryanthemoideae already have names in *Mesembryanthemum*. Here only new combinations, new names and new synonymy are given and the reader is referred to Hartmann (2001) for the others. We omit the new generic circumscription for *Mesembryanthemum*, since it is identical to that of Mesembryanthemoideae in Hartmann (2001). We provide an informal grouping for the species of Mesembryanthemoideae and a diagnosis for each group.

Mesembryanthemoideae Ihlenf. & al. in Taxon 11: 53. 1962 – Type: *Mesembryanthemum* L.

Mesembryanthemum L., Sp. Pl.: 480. 1753, nom. cons. – Type: *Mesembryanthemum nodiflorum* L., typ. cons.

Aptenia N.E. Br. in Gard. Chron. ser. 3, 78: 412. 1925, **syn. nov.** – Type (designated by N.E. Brown in J. Bot. 66: 139. 1928): *Aptenia cordifolia* (L. f.) Schwantes.

Aridaria N.E. Br. in Gard. Chron. ser. 3, 78: 433. 1925, **syn. nov.** – Type (designated by N.E. Brown in J. Bot. 66: 140. 1928): *Aridaria noctiflora* (L.) Schwantes.

Aspazoma N.E. Br. in Gard. Chron. ser. 3, 78: 413. 1925, **syn. nov.** – Type (designated by N.E. Brown in E.P. Phillips, Gen. S. African Fl. Pl.: 244. 1926): *Aspazoma amplectens* (L. Bolus) N.E. Br.

Brownanthus Schwantes in Z. Sukkulentenk. 3: 14, 20. 1927 (≡ *Trichocyclus* N.E. Br. non Dulac), **syn. nov.** – Type: *Brownanthus ciliatus* (W. Aiton) Schwantes = *Brownanthus vaginatus* (Lam.) Chesselet & M. Pignal)

Caulipsolon Klak in Hartmann, Ill. Handb. Succ. Pl. A–E: 103. 2001 (in Bot. Jahrb. Syst. 120: 364. 1998, non rite publ. [Art. 37.6]), **syn. nov.** – Type: *Caulipsolon rapaceum* (Jacq.) Klak.

Dactylopsis N.E. Br. in Gard. Chron. ser. 3, 78: 413. 1925, **syn. nov.** – Type (designated by N.E. Brown in E.P. Phillips, Gen. S. African Fl. Pl.: 244. 1926): *Dactylopsis digitata* (Aiton) N.E. Br.

Phyllobolus N.E. Br. in Gard. Chron. ser. 3, 78: 413. 1925, **syn. nov.** – Type (designated by Gerbaulet in Taxon 43: 75, 76. 1994): *Phyllobolus resurgens* (Kensit) Schwantes.

Prenia N.E. Br. in Gard. Chron. ser. 3, 78: 412, 413. 1925, **syn. nov.** – Type (designated by N.E. Brown in Gard. Chron., ser. 3, 84: 268. 1928): *Prenia pallens* (Aiton) N.E. Br.

Psilocaulon N.E. Br. in Gard. Chron. ser. 3, 78: 433. 1925, **syn. nov.** – Type (designated by N.E. Brown in E.P. Phillips, Gen. S. African Fl. Pl.: 244. 1926): *Psilocaulon articulatum* (Thunb.) N.E. Br.

Pseudobrownanthus Ihlenf. & Bittrich in Bot. Jahrb. Syst. 105: 319. 1985, **syn. nov.** – Type: *Pseudobrownanthus nucifer* Ihlenf. & Bittrich.

Sceletium N.E. Br. in Gard. Chron. ser. 3, 78: 412. 1925, **syn. nov.** – Type (designated by N.E. Brown in E.P. Phillips, Gen. S. African Fl. Pl.: 245. 1926): *Sceletium tortuosum* (L.) N.E. Br.

Synaptophyllum N.E. Br. in Gard. Chron. ser. 3, 78: 412. 1925, **syn. nov.** – Type (designated by E.P. Phillips, Gen. S. African Fl. Pl., ed. 2: 322. 1951): *Synaptophyllum juttae* (Dinter & A. Berger) N.E. Br.

One species, which was placed in synonymy in the latest treatment of *Mesembryanthemum* (Gerbaulet, 2001) is reinstated here based on our molecular results and a study of herbarium material.

Mesembryanthemum longipapillosum Dinter is not a synonym of *M. inachabense*. Our results show that it is more closely related to *M. barklyi*, *M. crystallinum*, *M. guerichianum*, and *M. pellitum* (Fig. 2). This species had with some doubt been placed into synonymy with *M. inachabense* (Gerbaulet 2001: 151). Dinter (1928: 19) had compared this plant with *M. guerichianum*, from which it apparently differed by its calyx being covered by long papillae and the entire plant having a red tinge. While the leaves in *M. longipapillosum* are similar in size to those in *M. inachabense*, they are much smaller than in the other species of the *Cryophytum* clade. In *M. longipapillosum* the leaves are erect and are conspicuously crystalline from raised idioblasts, whereas they spread horizontally close to the ground in *M. inachabense* with much flattened and inconspicuous idioblasts. The flowers of *M. longipapillosum* are white, cream or pale pink with a yellow centre and yellow anthers (see also Dinter 1928: 19) and the reproductive parts are not concealed. In contrast in *M. inachabense* the flowers are bright yellow with red stigmas and the reproductive parts (including the red stigmas) are at least partly concealed.

Representative specimens: Garius, *Dinter 4944* (BOL!); Grootfontein-Süd, *Dinter 8058* (BOL!); near Inachab, *Strey SUG 12563* (BOL!); between Aus and Rosh Pinah, *Mannheimer CM2654* (BOL!, WIND), *Loots SL26* (BOL!, WIND); ca. 30 km north of Oranjemund, *Williamson 2721* (BOL!).

Mesembryanthemum aitonis group

M. aitonis Jacq., *M. longistylum* DC.

Prostrate, ascending or erect annuals or biennials, leaves flat and broad or narrow, with conspicuous or flattened bladder cells, flowers with androecial parts free or shortly fused towards bases; fruits 5-locular, valve wings inflexed over the valves or reflexed and fused in pairs; seeds small (0.5–1.2[–1.5] mm long), brown with rough testa.

Clade A

Flowers with androecial parts fused into a petal-stamen tube, seeds brown to black, usually medium to large (1.1–2.0 mm long), testa usually rough.

Aptenia group

Mesembryanthemum lancifolium (L. Bolus) Klak, **comb. nov.**: *Aptenia lancifolia* L. Bolus in J. S. African Bot. 25: 371. 1959.

Further taxa: *M. cordifolium* L. f., *M. geniculiflorum* L., *M. haeckelianum* A. Berger.

Prostrate to scandent or climbing perennials, stems with persistent green succulent cortex, leaves broad and flat or rarely almost cylindrical; fruits 4-locular, with or without valve wings, valve wings inflexed over the valves; seeds rough, testa cells central papillose.

Aridaria group

Mesembryanthemum brevicarpum (L. Bolus) Klak, **comb. nov.**: *Aridaria brevicarpa* L. Bolus, Notes Mesembryanthemum 2: 33. 1929.

Mesembryanthemum noctiflorum L. subsp. ***defoliatum*** (Haw.) Klak, **comb. et stat. nov.**: *Mesembryanthemum defoliatum* Haw., Misc. Nat.: 64. 1803.

Mesembryanthemum noctiflorum L. subsp. ***stramineum*** (Haw.) Klak, **comb. et stat. nov.**: *Mesembryanthemum stramineum* Haw., Observ. Mesembryanthemum: 252. 1795.

Mesembryanthemum occidentale Klak, **nom. nov.**, pro *Aridaria vespertina* L. Bolus in Ann. Bolus Herb. 4: 127 (1928), non *Mesembryanthemum vespertinum* A. Berger (1908) = *Bergeranthus vespertinus* (A. Berger) Schwantes.

Mesembryanthemum serotinum (L. Bolus) Klak, **comb. nov.**: *Aridaria serotina* L. Bolus in J. Bot. 66: 196. 1928.

Further taxon: *Mesembryanthemum noctiflorum* L. subsp. *noctiflorum*.

Low growing or to 1 m tall, erect, shrubby perennials, stems woody, with thickened root stock; leaves almost cylindrical, epidermal bladder cells much flattened, deciduous; flowers large (to 4.0 cm diam.); fruits 4-locular, valve wings inflexed over the valves; seeds rough, testa cells central papillose.

Cryophytum group

Mesembryanthemum barklyi N.E. Br., *M. crystallinum* L., *M. gariusanum* Dinter, *M. guerichianum* Pax, *M. inachabense* Engler, *M. longipapillosum* Dinter, *M. pellitum* Friedrich.

Prostrate to ascending annuals or biennial herbs, leaves flat and often very broad, margins often undulating, epidermis with conspicuous bladder idioblasts; flowers cream to pale yellow (yellow in *M. inachabense*) with many fine petals, filamentous staminodes and stamens (few in *M. inachabense*); fruits 5-locular, valve wings inflexed over the valves; seeds rough or rarely smooth, testa cells central papillose.

Opophytum group

Mesembryanthemum cryptanthum Hook. f., *M. fastigiatum* Thunb., *M. hypertrophicum* Dinter.

Annuals, leaves very succulent and cylindrical with much flattened epidermal bladder cells; flowers to 6 cm diam., rarely much reduced and only 1 cm diam.; fruits 5-locular, valve wings reflexed and fused in pairs or inflexed over the valves; seeds smooth.

Phyllobolus group

Mesembryanthemum amabile (Gerbaulet & Struck) Klak, **comb. nov.**: *Phyllobolus amabilis* Gerbaulet & Struck in Haseltonia 4: 24. 1996.

Mesembryanthemum baylissii (L. Bolus) Klak, **comb. nov.**: *Sphalmanthus baylissii* L. Bolus in J. S. African Bot. 29: 45. 1963 = *Phyllobolus saturatus* (L. Bolus) Gerbaulet in Bot. Jahrb. Syst. 119: 186. 1997.

Mesembryanthemum caducum Klak, **nom. nov.**, pro *Aridaria congesta* L. Bolus, Notes Mesembryanthemum 2: 178. 1930, non *Mesembryanthemum congestum* Salm-Dyck (1854) = *Ruschia congesta* (Salm-Dyck) L. Bolus.

Mesembryanthemum chrysophthalmum (Gerbaulet & Struck) Klak, **comb. nov.**: *Phyllobolus chrysophthalmus* Gerbaulet & Struck in Haseltonia 4: 25. 1996.

Mesembryanthemum deciduum (L. Bolus) Klak, **comb. nov.**: *Aridaria decidua* L. Bolus in S. African Gard. 17: 256. 1927.

Mesembryanthemum decurvatum (L. Bolus) Klak, **comb. nov.**: *Aridaria decurvata* L. Bolus in S. African Gard. 17: 433. 1927.

Mesembryanthemum gariepense (Gerbaulet & Struck) Klak, **comb. nov.**: *Phyllobolus gariepensis* Gerbaulet & Struck in Haseltonia 4: 26. 1996.

Mesembryanthemum holense Klak, **nom. nov.**, pro *Sphalmanthus humilis* L. Bolus in J. S. African Bot. 28: 291, 292. 1962, non *Mesembryanthemum humile* Haw. (1795).

Mesembryanthemum latipetalum (L. Bolus) Klak, **comb. nov.**: *Aridaria latipetala* L. Bolus, Notes Mesembryanthemum 2: 111. 1929.

Mesembryanthemum lignescens (L. Bolus) Klak, **comb. nov.**: *Sphalmanthus lignescens* L. Bolus in J. S. African Bot. 29: 137. 1963.

Mesembryanthemum ligneum (L. Bolus) Klak, **comb. nov.**: *Aridaria lignea* L. Bolus, Notes Mesembryanthemum 2: 50. 1929 = *Phyllobolus melanospermus* (Dinter & Schwantes) Gerbaulet in Bot. Jahrb. Syst. 119: 179. 1997.

Mesembryanthemum lilliputanum Klak, **nom. nov.**, pro *Aridaria abbreviata* L. Bolus, Notes Mesembryanthemum 2: 177. 1930, non *Mesembryanthemum abbreviatum* Haw. (1926) = *Carpobrotus virescens* (Haw.) Schwantes

Mesembryanthemum prasinum (L. Bolus) Klak, **comb. nov.**: *Aridaria prasina* L. Bolus, Notes Mesembryanthemum 2: 6. 1928.

Mesembryanthemum pumilum (L. Bolus) Klak, **comb. nov.**: *Aridaria pumila* L. Bolus, Notes Mesembryanthemum 2: 214, 215. 1930.

Mesembryanthemum quartziticola Klak, **nom. nov.**, pro *Aridaria quartzitica* L. Bolus, Notes Mesembryanthemum 2: 69. 1929, non *Mesembryanthemum quartziticum* Dinter (1923) = *Antimima quartzitica* (Dinter) H.E.K. Hartmann.

Mesembryanthemum rabiei (L. Bolus) Klak, **comb. nov.**: *Aridaria rabiei* L. Bolus in S. African Gard. 17: 433. 1927.

Mesembryanthemum suffruticosum (L. Bolus) Klak, **comb. nov.**: *Cryophytum suffruticosum* L. Bolus, Notes Mesembryanthemum 2: 230. 1931.

Mesembryanthemum vanheerdei (L. Bolus) Klak, **comb. nov.**: *Sphalmanthus vanheerdei* L. Bolus in J. S. African Bot. 30: 41. 1964 = *Phyllobolus roseus* (L. Bolus) Gerbaulet in Bot. Jahrb. Syst. 119: 186. 1997.

Further taxa: *Mesembryanthemum canaliculatum* Haw., *M. caudatum* L. Bolus, *M. delum* L. Bolus, *M. grossum* Aiton, *M. nitidum* Haw., *M. oculatum* N.E. Br., *M. resurgens* Kensit, *M. sinuosum* L. Bolus, *M. spinuliferum* Haw., *M. tenuiflorum* Jacq., *M. trichotomum* Thunb., *M. viridiflorum* Aiton.

Perennials, prostrate to erect shrubs to minute geophytes, stems corky or woody, long or much shortened, roots often thickened; leaves almost cylindrical or flattened, deciduous, marcescent or persistent, epidermal bladder cells mostly distinct; flowers (1–)2–4 cm diam., reproductive parts in several species conceiled; fruits 4–5-locular, valve wings inflexed over the valves; seeds with a rough testa, testa cells convex and arranged in concentric rows.

Phyllobolus splendens group

Mesembryanthemum splendens L. subsp. ***pentagonum*** (L. Bolus) Klak, **comb. et stat. nov.**: *Aridaria pentagona* L. Bolus, Notes Mesembryanthemum 2: 35, 36. 1929.

Further taxa: *Mesembryanthemum splendens* L. subsp. *splendens*.

Erect perennial shrubs to 1 m tall, stems woody, roots not thickened; leaves almost cylindrical, narrowly ovate, persistent, epidermal bladder cells small; flowers 3–4 cm diam.; fruits 5-locular, valve wings inflexed over the valves; seeds with a rough testa, testa cells convex and arranged in concentric rows.

Prenia group

Mesembryanthemum pallens (Aiton) subsp. ***lanceum*** (Thunb.) Klak, **comb. et stat. nov.**: *Mesembryanthemum lanceum* Thunb., Prod. Fl. Cap. 1: 83. 1794.

Mesembryanthemum pallens (Aiton) subsp. ***luteum*** (L. Bolus) Klak, **comb. nov.**: *Prenia pallens* var. *lutea* L. Bolus, Notes Mesembryanthemum 3: 259. 1954 (≡ *P. pallens* subsp. *lutea* (L. Bolus) Gerbaulet in Bot. Jahrb. Syst. 118: 32. 1996).

Mesembryanthemum pallens (Aiton) subsp. ***namaquense*** (Gerbaulet) Klak, **comb. nov.**: *Prenia pallens* subsp. *namaquensis* Gerbaulet in Bot. Jahrb. Syst. 118: 34. 1996.

Mesembryanthemum radicans (L. Bolus) Klak, **comb. nov.**: *Aridaria radicans* L. Bolus in Ann. Bolus Herb. 4: 102. 1927.

Mesembryanthemum vanrensburgii (L. Bolus) Klak, **comb. nov.**: *Prenia vanrensburgii* L. Bolus, Notes Mesembryanthemum 3: 258. 1954.

Further taxa: *Mesembryanthemum englishiae* L. Bolus, *M. pallens* Aiton subsp. *pallens*, *M. sladenianum* L. Bolus, *M. tetragonum* Thunb.

Prostrate to rarely ascending (*M. tetragonum*) perennials, stems weakly lignified, roots fibrous; leaves flat, flatly triquetrous, obtusely trigonous or almost cylindrical, persistent, epidermal bladder cells much flattened; flowers 2–4 cm diam.; fruits 4–5-locular, locules deep, valve wings inflexed over the valves; seeds rough, testa cells central papillose.

Sceletium group

Mesembryanthemum archeri (L. Bolus) Klak, **comb. nov.**: *Sceletium archeri* L. Bolus, Notes Mesembryanthemum 2: 16. 1928 = *Sceletium rigidum* L. Bolus in S. African Gard. 18: 279. 1928.

Mesembryanthemum exalatum (Gerbaulet) Klak, **comb. nov.**: *Sceletium exalatum* Gerbaulet in Bot. Jahrb. Syst. 118: 17. 1996.

Mesembryanthemum ladismithiense Klak, **nom. nov.**, pro *Sceletium strictum* L. Bolus in S. African Gard. 17: 399. 1927, non *Mesembryanthemum strictum* Haw. (1803).

Further taxa: *Mesembryanthemum crassicaule* Haw., *M. emarcidum* Thunb., *M. expansum* L., *M. tortuosum* L., *M. varians* Haw.

Prostrate to erect small perennials, often scrambling in other bushes, roots fibrous; leaves flat, ovate, dry leaves persistent and 'skeletonised' through lignified veins; flowers 2–4 cm diam.; fruits 4–6-locular, with or without valve wings, valve wings inflexed over the valves; breaking off easily and dispersed by wind; seeds rough, testa cells convex and arranged in concentric rows.

Clade B

Flowers with androecial parts free or shortly fused towards bases, rarely fused into a petal-stamen tube (*Aspazoma* group), seeds usually small (0.5–1.2[–1.5]) mm long), testa mostly almost smooth.

Aspazoma group

Mesembryanthemum digitatum Aiton subsp. ***littlewoodii*** (L. Bolus) Klak, **comb. et stat. nov.**: *Dactylopsis littlewoodii* L. Bolus in J. S. African Bot. 29: 11. 1963.

Further taxa: *Mesembryanthemum amplectens* L. Bolus, *M. digitatum* Aiton subsp. *digitatum*.

Dwarf, erect, clump-forming perennials; leaves alternating, with tubular sheaths clasping one another, drying up completely during the resting period; fruits 4–5-locular, valve wings inflexed over the valves or reflexed and fused in pairs; seeds cream.

Brownanthus group

Mesembryanthemum glareicola (Klak) Klak, **comb. nov.**: *Brownanthus glareicola* Klak in Bothalia 30: 37. 2000.

Mesembryanthemum napierense Klak, **nom. nov.**, pro *Brownanthus fraternus* Klak in Bothalia 30: 37. 2000, non *Mesembryanthemum fraternum* N.E. Br. (1913) = *Conophytum fraternum* (N.E. Br.) N.E. Br.

Mesembryanthemum neglectum (Pierce & Gerbaulet) Klak, **comb. nov.**: *Brownanthus neglectus* Pierce & Gerbaulet in Aloe 34: 43. 1997.

Mesembryanthemum nucifer (Ihlenf. & Bittrich) Klak,

comb. nov.: *Pseudobrownanthus nucifer* Ihlenf. & Bittrich in Bot. Jahrb. Syst. 105: 320. 1985.

Mesembryanthemum pseudoschlichtianum (Pierce & Gerbaulet) Klak, **comb. nov.**: *Brownanthus pseudoschlichtianus* Pierce & Gerbaulet in Aloe 34: 43. 1997.

Mesembryanthemum springbokense Klak, **nom. nov.**, pro *Brownanthus lignescens* Klak in Bradleya 21: 114. 2003, non *Mesembryanthemum lignescens* (L. Bolus) Klak.

Mesembryanthemum tomentosum Klak, **nom. nov.**, pro *Trichocyclus pubescens* N.E. Br. ex C.A. Maass in Z. Sukkulentenk. 3: 234, 322. 1928, non *Mesembryanthemum pubescens* Haw. (1795) = *Gibbaeum pubescens* (Haw.) N.E. Br.

Further taxa: *Mesembryanthemum arenosum* Schinz, *M. corallinum* Thunb., *M. kuntzei* Schinz, *M. marlothii* Pax, *M. namibense* Marloth, *M. schenckii* Schinz, *M. vaginatum* Lam.

Decumbent to erect perennial shrubs, at least youngest stems succulent and green, articulate, epidermis of stems with closely packed, xeromophic bladder cells; leaves deciduous or marcescent, epidermal bladder cells mesomorphic; flowers small (0.5–1.0[–2.0]) cm diam.), petals cream to white, sepals remaining erect during anthesis; fruits 4–5-locular, valve wings inflexed over the valves, lower part of fruit shallow.

Mesembryanthemum nodiflorum group

M. excavatum L. Bolus, *M. nodiflorum* L., *M. stenandrum* (L. Bolus) L. Bolus, *M. subtruncatum* L. Bolus.

Annuals, prostrate or erect small herbs; leaves more or less cylindrical or somewhat channelled, linear to very narrowly obovate or oblong or almost truncate, epidermal bladder cells distinct or flattened; flowers without filamentous staminodes, 0.5–3.0 cm diam.; fruits 5-locular, valve wings reflexed and fused in pairs.

Psilocaulon group

Mesembryanthemum neofoliosum Klak, **nom. nov.**, pro *Psilocaulon foliosum* L. Bolus, Notes Mesembryanthemum 2: 100, 142. 1929, non *Mesembryanthemum foliosum* Haw. (1803) = *Ruschia foliosa* (Haw.) Schwantes.

Further taxa: *Mesembryanthemum articulatum* Thunb., *M. bicorne* Sonder, *M. coriarium* Burch. ex N.E. Br., *M. dimorphum* Welw. ex Oliver, *M. dinteri* Engler, *M. gessertianum* Dinter & A. Berger, *M. granulicaule* Haw., *M. junceum* Haw., *M. juttae* Dinter & A. Berger, *M. leptarthron* A. Berger, *M. parviflorum* Jacq., *M. rapaceum* Jacq., *M. salicornioides* Pax, *M. subnodosum* A. Berger.

Small to large prostrate to erect shrubby perennials or rarely annuals or geophytes (*M. rapaceum*), at least youngest stems succulent and green, usually articulate, epidermis of stems and leaves similar, with much flattened bladder cells; leaves cylindrical to slightly trigonous, rarely flat and broad, deciduous; flowers 0.5–2.5 cm diam., filamentous staminodes and stamens conically collected, rarely petals or filamentous staminodes absent; fruits 4–5-locular, valve wings inflexed over the valves, rarely reflexed and fused in pairs, usually with deep locules; seeds small (0.5–1.2 mm long).

Ungrouped

Mesembryanthemum eurystigmatum Gerbaulet.

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Appendix 1. List of taxa with voucher information, and GenBank/EMBL accession numbers for each DNA region.

Species, voucher (herbarium acronym, country where voucher is stored), *trnL-F* GenBank accession, *rps16* GenBank accession, *atpB-rbcL* GenBank accession, ITS1 GenBank accession.

Outgroups:

Limeum africanum Burm., *Trinder-Smith 279* (BOL, RSA), AJ558034[b], AJ532730[b], AJ532610, AJ532594[c]; ***Mirabilis jalapa*** L., *Klak 986* (BOL, RSA), AJ558035[b], AJ532731[b], AJ532611, AJ532596[c]; ***Phytolacca dioica*** (L.) Moq., *Klak 988* (BOL, RSA), AJ558037[b], AJ532733[b], AJ532612, AJ532595[c]; ***Cypselea humifusa*** Turpin, *Ahart 9922* (BOL, RSA), AM161379, AM161196, –, –; ***Sesuvium sesuvioides*** (Fenzl) Verdcourt, *Bruyns 8876* (BOL, RSA), AJ558038[b], AJ532734[b], AJ532613, AJ532597[c]; ***Trianthema crystallina*** Vahl., *Bruyns 8876a* (BOL, RSA), AJ558039[b], AJ532735[b], AJ532614, AJ532598[c]; ***Tribulocarpus dimorphantha*** (Pax) S. Moore, *Mannheimer 1900* (BOL, RSA), AJ558049[b], AJ532743[b], –, –; ***Galenia africana*** L., *Klak 713* (BOL, RSA), AJ558043[b], AJ532739[b], AJ532615, AJ532600[c]; ***Plinthus karooicus*** I. Verdoorn, *T. Anderson & van Heerden 1070* (BOL, RSA), AJ558047[b], AJ532743[b], AJ531616, AJ532599[c]; ***Tetragonia fruticosa*** L., *Goldblatt & Manning 11662* (MO, U.S.A.), AJ558048[b], AJ532744[b], AJ531617, AJ532601[c]; ***Apatesia helianthoides*** (Aiton) N.E. Br., *Klak 800* (BOL, RSA), AJ558064[b], AJ532762[b], AJ532623, AJ532604[c]; ***Carpanthea pomeridiana*** (L.) N.E. Br., *Klak 801* (BOL, RSA), –, –, –, AJ532605[c]; ***Skiatophytum tripolium*** (L.) L. Bolus, *Klak 1030* (BOL, RSA), AM161451, AM161268, –, –; ***Cleretum papulosum*** (L. f.) L. Bolus, *Bruyns 8825a* (BOL, RSA), AJ558070[b], AJ532768[b], –, AJ532606[c]; ***Dorotheanthus bellidiformis*** (Burm.) N.E. Br. subsp. ***bellidiformis***, *Klak 627* (BOL, RSA), AJ439000[b], AJ532769[b], AJ532621, –; ***Delosperma echinatum*** (Lam.) Schwantes, *Klak 344* (BOL, RSA), AJ439001[b], AJ532775[b], AJ532629, –; ***Drosanthemum zygophylloides*** (L. Bolus) L. Bolus, *Klak 830* (BOL, RSA), AJ558081[b], AJ532783[b], AJ532637, –; ***Smicrostigma viride*** (Haw.) N.E. Br., *Klak 180* (BOL, RSA), AJ439051[b], AJ532812[b], AJ532666, –;

Mesembryanthemoideae:

Aptenia cordifolia (L.) Schwantes, *Klak 1019* (BOL, RSA), AM161373, AM161176, AM161270, AM162352; ***Aptenia geniculiflora*** (L.) Bittrich ex Gerbaulet, *Bruyns 8947* (BOL, RSA), AJ558050[b], AJ532746[b], AJ532619, AJ532602[c]; ***Aptenia haeckeliana*** (A. Berger) Bittrich ex Gerbaulet, *Bruyns 8933* (BOL, RSA), AM161374, AM161177, AM161271, AM162353; ***Aridaria brevicarpa*** L. Bolus, *Bruyns 9469* (BOL, RSA), AM161374, AM161178, AM161272, –; ***Aridaria noctiflora*** subsp. ***defoliata*** (Haw.) Gerbaulet, *Klak 1173* (BOL, RSA), AM161376, AM161179, AM161273, AM162354; ***Aridaria noctiflora*** (L.) Schwantes subsp. ***noctiflora***, *Bruyns 9576* (BOL, RSA), –, AM161180, AM161274, AM162355; ***Aridaria noctiflora*** subsp. ***straminea*** (Haw.) Gerbaulet, *Bruyns 9804* (BOL, RSA), AM161377, AM161181, AM161275, AM162356; ***Aridaria serotina*** L. Bolus, *Klak 790* (BOL, RSA), AJ558051[b], AJ532747[b], AM161276, AM162357; ***Aridaria vespertina*** L. Bolus, *Bruyns 9873* (MO, U.S.A.), AM161378, AM161182, AM161277, AM162358; ***Aspazoma amplectens*** (L. Bolus) N.E. Br., *Bruyns 6751* (BOL, RSA), AJ558052[b], AJ532748[b], AM161278, AY996760[d]; ***Brownanthus arenosus*** (Schinz) Ihlenf. & Bittrich, *Pierce 68* (BOL, RSA), AY993963[d], AM161183, AM16127, AY996761[d]; ***Brownanthus corallinus*** (Thunb.) Ihlenf. & Bittrich, *Klak 459* (BOL, RSA), AY993966[d], AM161185, AM161281, AY996764[d]; ***Brownanthus fraternus*** Klak, *Klak 171* (BOL, RSA), AY993967[d], AM161186, AM161282, AY996765[d]; ***Brownanthus glareicola*** Klak, *Klak 458* (BOL, RSA), AY993968[d], AM161187, AM161283, AY996766[d]; ***Brownanthus kuntzei*** (Schinz) Ihlenf. & Bittrich, *Bruyns 8072* (BOL, RSA), AY993969[d], AM161188, AM161284, AY996767[d]; ***Brownanthus lignescens*** Klak, *Bruyns 8254* (E, GB), AY993970[d], AM161189, AM161285, AY996768[d]; ***Brownanthus marlothii*** (Pax) Schwantes, *Klak 607* (BOL, RSA), AY993971[d], AM161190, AM161286, AY996769[d]; ***Brownanthus namibensis*** (Marloth) Bullock, *Klak 604* (BOL, RSA), AY993972[d], AM161191, AM161287, AY996770[d]; ***Brownanthus neglectus*** Pierce & Gerbaulet, *Klak 233* (BOL, RSA), AY993973[d], AM161192, AM161288, –; ***Brownanthus nucifer*** (Ihlenf. & Bittrich) Pierce & Gerbaulet, *Klak 248* (BOL, RSA), AY993974[d], AM161193, AM161289, AY996771[d]; ***Brownanthus pseudoschlichtianus*** Pierce & Gerbaulet, *Pierce 67* (BOL, RSA), AY993975[d], AM161194, AM161290, AY996772[d]; ***Brownanthus pubescens*** (N.E. Br. ex Maas) Bullock, *Klak 242* (BOL, RSA), AJ438998[a], AJ532749[b], AJ532618, AY996773[d]; ***Brownanthus schenckii*** (Schinz) Schwantes, *Klak 230* (BOL, RSA), AY993965[d], AM161195, AM161291, AY996763[d]; ***Brownanthus vaginatus*** (Lam.) Chesselet & M. Pignal, *Klak 651* (BOL, RSA), AY993964[d], AM161184, AM161280, AY996762[d]; ***Caulipsolon rapaceum*** (Jacq.) Klak, *Klak 750* (BOL, RSA), AJ558053[b], AJ532750[b], AM161292, –; ***Dactylopsis digitata*** (Aiton) N.E. Br. subsp. ***digitata***, *Klak 788* (BOL, RSA), AJ558058[b], AJ532755[b], AM161293, AY996776[d]; ***Mesembryanthemum aitonis*** Jacq., *Bruyns 9563* (BOL, RSA), AM161381, AM161197, AM161295, –; ***Mesembryanthemum aitonis*** Jacq., *Bruyns 9438* (BOL, RSA), AM161382, AM161198, AM161296, –; ***Mesembryanthemum aitonis*** Jacq., *Klak 1172* (BOL, RSA), AM161380, AM161207, AM161294, –; ***Mesembryanthemum barklyi*** N.E. Br., *Klak 767* (BOL, RSA), AJ558054[b], AJ532751[b], AJ532620, AJ532603[c]; ***Mesembryanthemum cryptanthum*** Hook. f., *Mannheimer 2274* (BOL, RSA), AM161383, AM161199, AM161297, AM162359; ***Mesembryanthemum crystallinum*** L., *Klak 1020* (BOL, RSA), AM161384, AM161200, AM161298, AM162360; ***Mesembryanthemum eurystigmatum*** Gerbaulet, *Klak 796* (BOL, RSA), AM161385, AM161201, AM161299, AM162361; ***Mesembryanthemum excavatum*** L. Bolus, *Klak 1032* (BOL, RSA), AM161386, AM161202, AM161300, AM162362; ***Mesembryanthemum fastigiatum*** Thunb., *Klak 791* (BOL, RSA), AJ558055[b], AJ532752[b], AM161301, –; ***Mesembryanthemum guerichianum*** Dinter, *Bruyns 9557* (MO, U.S.A.), AM161387, AM161203, AM161302, AM162363; ***Mesembryanthemum hypertrophicum*** Dinter, *Bruyns 9465* (MO, U.S.A.), AM161388, AM161204, AM161303, –; ***Mesembryanthemum inachabense*** Engler, *Bruyns 10087* (BOL, RSA), AM161389, AM161205, AM161304, AM162364; ***Mesembryanthemum longipapillosum*** Dinter, *Mannheimer 2654* (BOL, RSA), AM161390, AM161206, AM161305, AM162365; ***Mesembryanthemum longistylum*** DC, *Klak 767* (BOL, RSA), AJ558056[b], AJ532753[b], AM161306, AY996774[d]; ***Mesembryanthemum nodiflorum*** L., *Klak 982* (BOL, RSA), AM161391, AM161208, –, –; ***Mesembryanthemum pellitum*** Friedrich, *Bruyns 9464* (BOL, RSA), AM161392, AM161209, AM161307, –; ***Mesembryanthemum stenandrum*** (L. Bolus) L. Bolus, *Bruyns 9550* (MO, U.S.A.), AM161393, AM161210, AM161308, AM162366; ***Mesembryanthemum subtruncatum*** L. Bolus, *Bruyns 9575* (E, GB), AM161394, AM161211, AM161309, AM162367; ***Phyllobolus abbreviatus*** (L. Bolus) Gerbaulet, *Bruyns 9930* (BOL, RSA), AM161395, AM161212, AM161310, AM162368; ***Phyllobolus canaliculatus*** (Haw.) Gerbaulet, *Nowell 112* (BOL, RSA), AJ558057[b], AJ532754[b], AM161311, AY996775[d]; ***Phyllobolus caudatus*** (L. Bolus) Gerbaulet, *Klak 973* (BOL, RSA), AM161396, AM161213, AM161312, –; ***Phyllobolus chrysophthalmus*** Gerbaulet, *Bruyns 9510* (K, GB), AM161397,

Appendix 1. Continued.

Species, voucher (herbarium acronym, country where voucher is stored), *trnL-F* GenBank accession, *rps16* GenBank accession, *atpB-rbcL* GenBank accession, ITS1 GenBank accession.

AM161214, AM161313, –; ***Phyllobolus congestus*** (L. Bolus) Gerbaulet, *Bruyns 9908* (BOL, RSA), AM161398, AM161215, AM161314, AM162369; ***Phyllobolus deciduus*** (L. Bolus) Gerbaulet, *Bruyns 9860* (BOL, RSA), AM161399, AM161216, AM161315, AM162370; ***Phyllobolus decurvatus*** (L. Bolus) Gerbaulet, *Bruyns 9489* (BOL, RSA), AM161400, AM161217, AM161316, –; ***Phyllobolus delus*** (L. Bolus) Gerbaulet, *Bruyns 9501* (BOL, RSA), AM161401, AM161218, AM161317, AM162371; ***Phyllobolus gariepensis*** Gerbaulet & Struck, *Bruyns 9882* (BOL, RSA), AM161402, AM161219, AM161318, –; ***Phyllobolus grossus*** (Aiton) Gerbaulet, *Bruyns 9521* (BOL, RSA), AM161421, AM161239, AM161339, AM162386; ***Phyllobolus grossus*** (Aiton) Gerbaulet, *Bruyns 9813* (BOL, RSA), AM161403, AM161220, AM161319, –; ***Phyllobolus humilis*** (L. Bolus) Klak, *Bruyns 9913* (BOL, RSA), AM161404, AM161221, AM161320, AM162372; ***Phyllobolus latipetalus*** (L. Bolus) Gerbaulet, *Desmet s.n.* (BOL, RSA), AM161405, AM161222, AM161321, AM162373; ***Phyllobolus lignescens*** (L. Bolus) Gerbaulet, *Bruyns 9453* (BOL, RSA), AM161406, AM161223, AM161322, AM162374; ***Phyllobolus nitidus*** (Haw.) Gerbaulet, *Bruyns 9509* (BOL, RSA), AM161407, AM161224, AM161323, AM162374; ***Phyllobolus oculatus*** (N.E. Br.) Gerbaulet, *Bruyns 9467* (BOL, RSA), AM161408, AM161225, AM161324; AM162376; ***Phyllobolus oculatus*** (N.E. Br.) Gerbaulet, *Klak 898* (BOL, RSA), AM161409, AM161226, –, AM162377; ***Phyllobolus prasinus*** (L. Bolus) Gerbaulet, *Bruyns 9899* (BOL, RSA), AM161410, AM161227, AM161325, AM162378; ***Phyllobolus pumilus*** (L. Bolus) Gerbaulet, *Bruyns 9999* (BOL, RSA), AM161411, AM161228, AM161326, –; ***Phyllobolus quartziticus*** (L. Bolus) Gerbaulet, *Bruyns 9868* (BOL, RSA), AM161412, AM161229, AM161327, –; ***Phyllobolus rabiei*** (L. Bolus) Gerbaulet, *Klak 589b* (BOL, RSA), AJ438999[a], AJ532756[b], AM161328, –; ***Phyllobolus resurgens*** (Kensit) Schwantes, *Bruyns 9503* (K, GB), AM161413, AM161230, AM161329, AM162379; ***Phyllobolus roseus*** (L. Bolus) Gerbaulet, *Klak 870* (BOL, RSA), AJ558059[b], AJ532757[b], AM161330, AM162380; ***Phyllobolus saturatus*** (L. Bolus) Gerbaulet, *Bruyns 9499* (BOL, RSA), AM161414, AM161231, AM161331, AM162381; ***Phyllobolus sinuosus*** (L. Bolus) Gerbaulet, *Bruyns 9892* (BOL, RSA), AM161415, AM161232, AM161332, AM162382; ***Phyllobolus*** **sp. nov.**, *Bruyns 10017* (BOL, RSA), AM161416, AM161233, AM161333, AM162383; ***Phyllobolus spinuliferus*** (Haw.) Gerbaulet, *Bruyns 9508* (BOL, RSA), AM161417, AM161234, AM161334, –; ***Phyllobolus splendens*** (L.) Gerbaulet subsp. ***splendens***, *Bruyns 9554* (MO, U.S.A.), –, AM161235, AM161335, AM162384; ***Phyllobolus splendens*** (L.) Gerbaulet subsp. ***splendens***, *Bruyns 9561* (BOL, RSA), AM161418, AM161236, AM161336, –; ***Phyllobolus splendens*** (L.) Gerbaulet subsp. ***splendens***, *Bruyns 9560* (BOL, RSA), AM161419, AM161237, AM161337, AM162385; ***Phyllobolus splendens*** subsp. ***pentagonus*** (L. Bolus) Gerbaulet, *Bruyns 9801* (BOL, RSA), AM161420, AM161238, AM161338, –; ***Phyllobolus suffruticosus*** (L. Bolus) Gerbaulet, *Bruyns 9543* (BOL, RSA; K, GB), AM161422, AM161240, AM161340, –; ***Phyllobolus tenuiflorus*** (Jacq.) Gerbaulet, *Bruyns 9909* (BOL, RSA), AM161423, AM161241, AM161341, –; ***Phyllobolus trichotomus*** (Thunb.) Gerbaulet, *Helme 2802* (BOL, RSA), AM161424, AM161242, AM161342, –; ***Phyllobolus viridiflorus*** (Aiton) Gerbaulet, *Bruyns 9920* (K, GB), AM161425, AM161243, AM161343, AM162387; ***Prenia englishiae*** (L. Bolus) Gerbaulet, *Bruyns 9558* (MO, U.S.A.; K, GB), AM161426, AM161244, AM161344, AM162388; ***Prenia pallens*** subsp. ***lutea*** Gerbaulet, *Klak 1022* (BOL, RSA), AM161427, AM161245, AM161345, AM162389; ***Prenia pallens*** subsp. ***namaquensis*** Gerbaulet, *Klak 759* (BOL, RSA), AM161428, AM161246, AM161346, AM162390; ***Prenia pallens*** (Aiton) N.E. Br. subsp. ***pallens***, *Klak 983* (BOL, RSA), AM161429, AM161247, AM161347, –; ***Prenia radicans*** (L. Bolus) Gerbaulet, *Bruyns 9798* (BOL, RSA), AM161430, AM161248, AM161348, –; ***Prenia sladeniana*** (L. Bolus) L. Bolus, *Bruyns 8848a* (BOL, RSA), AJ558060[b], AJ532758[b], AM161349, AM162391; ***Prenia tetragona*** (Thunb.) Gerbaulet, *Bruyns 8866a* (BOL, RSA), AJ558061[b], AJ532759[b], AM161350, –; ***Prenia vanrensburgii*** L. Bolus, *Bruyns 9439* (MO, U.S.A.), AM161431, AM161249, AM161351, –; ***Psilocaulon articulatum*** (Thunb.) N.E. Br., *Bruyns 9512* (BOL, RSA), AM161432, AM161250, AM161352, –; ***Psilocaulon bicorne*** (Sonder) Schwantes, *Bruyns 9556* (NBG, RSA), AM161433, AM161251, AM161353, AM162392; ***Psilocaulon coriarium*** (Burch. ex N.E. Br.) N.E. Br., *Klak 990* (BOL, RSA), AM161434, AM161252, AM161354, –; ***Psilocaulon dinteri*** (Engler) Schwantes, *Bruyns 9511* (MO, U.S.A.), AM161435, AM161253, AM161355, AM162393; ***Psilocaulon foliosum*** L. Bolus, *Bruyns 9452* (MO, U.S.A.), AM161436, AM161254, AM161356, AM162394; ***Psilocaulon gessertianum*** (Dinter & A. Berger) Dinter & Schwantes, *Bruyns 10100* (BOL, RSA), AM161438, AM161255, AM161357, AM162395; ***Psilocaulon granulicaule*** (Haw.) Schwantes, *Bruyns 9559* (E, GB), AM161439, AM161256, AM161358, AM162396; ***Psilocaulon junceum*** (Haw.) Schwantes, *Bruyns 9524* (MO, U.S.A.), AM161440, AM161257, AM161359, –; ***Psilocaulon leptarthron*** (A. Berger) N.E. Br., *Klak 989* (E, GB), AM161441, AM161258, AM161360, –; ***Psilocaulon parviflorum*** (Jacq.) Schwantes, *Klak 699* (BOL, RSA), AJ558062[b], AJ532760[b], AM161361, AY996777[d]; ***Psilocaulon salicornioides*** (Pax) Schwantes, *Mannheimer 2670* (BOL, RSA), AM161442, AM161259, AM161362, –; ***Psilocaulon subnodosum*** (A. Berger) N.E. Br., *Bruyns 9466* (BOL, RSA), AM161443, AM161260, AM161363, –; ***Sceletium crassicaule*** (Haw.) L. Bolus, *Dold 7000* (BOL, RSA), AM161444, AM161261, AM161364, AM162397; ***Sceletium emarcidum*** (Thunb.) L. Bolus ex Jacobsen, *Bruyns 9835* (BOL, RSA), AM161445, AM161262, AM161365, AM162398; ***Sceletium exalatum*** Gerbaulet, *Bruyns 9859* (K, GB), AM161446, AM161263, AM161366, AM162399; ***Sceletium expansum*** (L.) L. Bolus, *Bruyns 9926* (K, GB), AM161447, AM161264, AM161367, –; ***Sceletium rigidum*** L. Bolus, *Bruyns 9834* (BOL, RSA), AM161448, AM161265, AM161368, AM162400; ***Sceletium strictum*** L. Bolus, *Bruyns 9562* (BOL, RSA), AM161449, AM161266, AM161369, AM162401; ***Sceletium tortuosum*** (L.) N.E. Br., *Klak 816* (BOL, RSA), AJ558063[b], AJ532761[b], AM161370, AM162402; ***Sceletium varians*** (Haw.) Gerbaulet, *Bruyns 9577* (E, GB), AM161450, AM161267, AM161371, –; ***Synaptophyllum juttae*** (Dinter & A. Berger) N.E. Br., *Mannheimer 2273* (BOL, RSA), AM161437, AM161269, AM161372, –.

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[a]Klak & al., 2003a; [b]Klak & al., 2003b; [c]Klak & al., 2004; [d]Klak & al., 2006.

Appendix 2. Morphological characters used for the cladistic analyses of Mesembryanthemoideae and outgroups.

Life-form: 1. Perennial (0), annual or short-lived (1); **Roots:** 2. Roots fibrous (0), thickened (1), tuberous (2); **Growth form:** 3. Prostrate (0), decumbent to erect (1); 4. Non-scrambling habit (0), scrambling habit (1); **Stems and Branches:** 5. Stems without persistent green cortex (0), with persistent green cortex (1); 6. Branches are retained (0), branches deciduous or partly deciduous (1); 7. Stems weakly lignified (0), stems woody (1); 8. Stems without a cork layer (0), stems with a cork layer (1); 9. Epidermis with closely packed, tall bladder cell idioblasts (0), without (1); 10. Without or weakly developed additional vascular bundels in the cortex (0), distinct (1); 11. Dry primary cortex soon fading away (0), persistent and white (1); **Leaves:** 12. Pairs of leaves clasping the stem (0), not clasping (1); 13. Bladder cell idioblasts absent (0), present (1); 14. Bladder cell idioblasts prominent (0), reduced (1); 15. Leaves persistent (0), leaves deciduous or remain dried up on the stem (1); 16. Leaves becoming spincescent (0), not spinescent (1); 17. Old leaves drying up and sheathing the new leaves and/or stem (0), old leaves not sheathing (1); 18. Leaf veins not lignified (0), leaf veins lignified (1); 19. Leaves broad and flat (0), leaves much thickened, triangular to (half-)cylindrical in cross section (1); 20. Central water storing tissue absent or only weakly developed (0) distinct (1); **Flowers:** 21. Petaloid staminodes absent (0), present (1); 22. Filamentous staminodes present (0), absent (1); 23. Filamentous staminodes thread-like and narrow (0), broad and translucent (1); 24. Filamentous staminodes and/or stamens very numerous (0), not numerous (1); 25. Sepals open into a horizontal position 180° (0), sepals remain erect during anthesis (1); 26. Androecial parts free or very shortly fused towards bases (0), fused into a petal stamen tube (1); 27. Stamens and stigmas visible (0), conceiled (1); 28. Flowers in a few-many flowered inflorescence, i.e., > 3 flowers per inflorescence (0), solitary or 1–3 (1); 29. Nectaries shell-shaped (0), tubular (1); 30. Koilomorphic nectaries absent (0), present (1); 31. Nectaries crested (0), not crested (1); 32. Nectaries a flat ring (0), not a flat ring (1); **Fruits:** 33. Fruit a hygrochastic capsule (0), not a hygrochastic capsule (1); 34. Capsule hygrochastic (0) capsule xerochastic (1); 35. Fruits with deep locules (0), with shallow locules (1); 36. Fruits (3–)4 locular (0), 5(–7) locular (1), more than 7 locules (2); 37. Valve wings inflexed (0), valve wings reflexed, sometimes reflexed and fused in pairs (1); 38. Fruits not anemochorous (0), fruits anemochorous (1); **Seeds:** 39. Testa cells raised (0), much flattened (1); 40. Testa cells central papillose (0), convex papillose (1); 41. Testa cells arranged in concentric rows (0), not arranged in concentric rows (1).

Appendix 3. Matrix of the morphological chararacter states in Mesembryanthemoideae and outgroups used in the cladistic analyses.

OUTGROUPS	1–10	11–20	21–30	31–40	41
Limeum africanum	001000001?	010?0110??	0??10????0	1?1????0??	?
Mirabilis jalapa	011001001?	010?0110??	0??10??0?0	1?1????0??	?
Phytolacca dioica	000100101?	010?0110??	0??10????0	1?1????0??	?
Cypselea humifusa	10000?001?	0111011000	01?10?01?0	1?1???????	?
Sesuvium sesuvioides	101?00001?	01100110??	0??10??1?0	1?1????0??	?
Trianthema crystallina	00??00??1?	011?0110??	0??10????0	1?1????0??	?
Tribulocarpus dimorphantha	001000101?	0111011000	01?10?00?0	??1???????	?
Galenia africana	001000101?	011?0110??	0??10??0?0	1?1????0??	?
Plinthus karooicus	001000101?	011?0110??	0??10??0?0	1?00???0??	?
Tetragonia fruticosa	000000??1?	011?0110??	0??10??0?0	1?1????0??	?
Apatesia helianthoides	10100?001?	?111?11100	1000000?0	1000121 0??	?
Skiatophytum tripolium	1110010010	0111?11000	11?00000?0	1001?1?00?	?
Cleretum papulosum	10100?001?	?110?11000	1??10001?0	1000111 0??	?
Dorotheanthus bellidiformis subsp. *bellidiformis*	10100?001?	?110?11000	11?10001?0	100011101?	?
Delosperma echinatum	001000101?	011001101?	1001000 1?0	0100111 0??	?
Drosanthemum zygophylloides	001000101?	011001101?	1001000 0?0	0100111 0??	?
Smicrostigma viride	001000101?	0111011011	1001001 1?0	010002100?	?
INGROUP					
Aptenia cordifolia	0011100001	0111011000	11?1010101	110010?000	0
Aptenia geniculiflora	0011100001	0111111010	1001010001	1100100000	0
Aptenia haeckeliana	0011100001	0111011000	11?1010101	1100100000	0
Aridaria brevicarpa	0110001010	0111111011	11?1010001	1100100000	0
Aridaria noctiflora subsp. *defoliata*	0110001010	0111111011	11?1010001	1100100000	0
Aridaria noctiflora subsp. *noctiflora*	0110001010	0111111011	11?1010001	1100100000	0
Aridaria noctiflora subsp. *straminea*	0110001010	0111111011	11?1010001	1100100000	0
Aridaria serotina	0110001010	0111111011	11?1010001	1100100000	0
Aridaria vespertina	0110001010	0111111011	11?1010001	1100100000	0
Aspazoma amplectens	0010100001	0010101011	1001010101	11001?001?	?
Brownanthus arenosus	0010100001	0110111011	11?1100001	11001?0000	1
Brownanthus corallinus	0010100001	0110111011	11?1100101	1100110000	1
Brownanthus fraternus	0010100001	0111111011	11?1100101	1100110000	1
Brownanthus glareicola	0010100001	0111111011	11?1100101	1100110000	1
Brownanthus kuntzei	0010100001	0110111011	11?1100001	1100110000	1
Brownanthus lignescens	0010101001	0111111011	11?1100101	1100110000	1

Appendix 3. Continued.

INGROUP	**1–10**	**11–20**	**21–30**	**31–40**	**41**
Brownanthus marlothii	0010100001	0110111011	11?1100101	1100110000	1
Brownanthus namibensis	0010100001	0110111011	11?1100101	1100110000	1
Brownanthus neglectus	0010100001	0110111011	11?1100001	1100100000	1
Brownanthus nucifer	0010100001	0110111011	11?1100001	111?100000	1
Brownanthus pseudoschlichtianus	0010100001	0110111011	11?1100001	1100100000	1
Brownanthus pubescens	0010100001	0110111011	11?1100101	1100110000	1
Brownanthus schenckii	0010100001	0110111011	11?1100001	1100110000	1
Brownanthus vaginatus	0010100001	0110111011	11?1100001	1100110000	1
Caulipsolon rapaceum	0200010011	01111??010	11?1000001	1100011000	1
Dactylopsis digitata subsp. *digitata*	0110110101	0011101011	11?1011101	110011101?	?
Mesembryanthemum aitonis (Bruyns 9438)	10000?0011	0110???000	11?1010011	1100111000	1
Mesembryanthemum aitonis (Bruyns 9563)	10000?0011	0110???000	11?1010011	1100111000	1
Mesembryanthemum aitonis (Klak 1172)	10000?0011	0110???000	11?1010011	1100111000	1
Mesembryanthemum barklyi	10100?0011	0110???000	1000010001	1100110000	1
Mesembryanthemum cryptanthum	10000?0011	0111???011	1011001111	110001??11	1
Mesembryanthemum crystallinum	10000?0011	0110???000	1000010001	1100110000	1
Mesembryanthemum eurystigmatum	10100?0011	0111???011	1000010011	110011001?	?
Mesembryanthemum excavatum	10000?0011	0110???011	1110001111	1100110??	?
Mesembryanthemum fastigiatum	10000?0011	0111???011	1000010011	1100110?0	1
Mesembryanthemum guerichianum	10000?0011	0110???000	1000010001	1100110000	1
Mesembryanthemum hypertrophicum	10000?0011	10111???01	1000010011	110011101?	?
Mesembryanthemum inachabense	10000?0011	0110?11000	1001010011	1100100??	?
Mesembryanthemum longipapillosum	10000?0011	0110???000	11?1010011	110011001?	?
Mesembryanthemum longistylum	10100?0011	0111???011	11?1010011	1100111000	1
Mesembryanthemum nodiflorum	10000?0011	0110???011	11?1000011	110011101?	?
Mesembryanthemum pellitum	10100?0011	0110???000	1000010001	1100110000	1
Mesembryanthemum stenandrum	10?00?0011	0110???011	11?1010011	110011101?	?
Mesembryanthemum subtruncatum	10000?0011	0111???011	11?1010011	110011?0??	?
Phyllobolus abbreviatus	0200010011	0110011010	1001010001	1100110001	0
Phyllobolus canaliculatus	0200010011	0110011010	1001010101	1100110001	0
Phyllobolus caudatus	0201010011	0110011010	1001010101	1100110001	0
Phyllobolus chrysophthalmus	0210001011	0110111010	11?1011001	1100110001	0
Phyllobolus congestus	0010000111	0110111010	1001010001	1100110001	0
Phyllobolus deciduus	0010001011	0110111010	1001010101	1100110001	0
Phyllobolus decurvatus	0010001011	0111011010	1001010001	11001?0001	0
Phyllobolus delus	0010001011	0111011010	11?1011001	1100110001	0
Phyllobolus gariepensis	0010000011	0110011010	1001010001	1100110001	0
Phyllobolus grossus (Bruyns 9521)	0201011011	0110011010	1001010101	1100110001	0
Phyllobolus grossus (Bruyns 9813)	0201010011	0110011010	1001010101	1100110001	0
Phyllobolus humilis	0210010111	0110011010	11?1011?01	1100110001	0
Phyllobolus latipetalus	0010001111	0110110010	1011001101	1100001011	1
Phyllobolus lignescens	0010001010	0110110010	1001010001	1100110001	0
Phyllobolus nitidus	0011000111	0110011010	1001010001	11001?0001	0
Phyllobolus oculatus (Bruyns 9467)	0200010011	0110011010	1001010001	1100110001	0
Phyllobolus oculatus (Klak 898)	0200010011	0110011010	1001010001	1100110001	0
Phyllobolus prasinus	0210010111	0110011010	11?1011001	1100110001	0
Phyllobolus pumilus	021001001?	011011101?	10010001?1	1100010001	0
Phyllobolus quartziticus	0010000111	0111011010	1001010001	11001?0001	0
Phyllobolus rabiei	0010000111	0111011010	1001011101	1100110001	0
Phyllobolus resurgens	0210010111	0110011010	11?1011101	1100110001	0
Phyllobolus roseus	0010001011	0110110010	1001010101	1100110001	0
Phyllobolus saturatus	0011001011	0111110010	1001010001	1100110001	0
Phyllobolus sinuosus	0011000011	0110011010	1001010001	1100110001	0
Phyllobolus sp. nov. *(Bruyns 10017)*	0?100?????	?110???01?	1????????1	1100??0???	?
Phyllobolus spinuliferus	0010000111	0111011010	1001010001	1100100001	0
Phyllobolus splendens subsp. *pentagonus*	0010001011	0111011010	1001010101	1100110001	0
Phyllobolus splendens subsp. *splendens (Bruyns 9554)*	0010001011	0111011010	1001010101	1100110001	0
Phyllobolus splendens subsp. *splendens (Bruyns 9560)*	0010001011	0111011010	1001010101	1100110001	0
Phyllobolus splendens subsp. *splendens (Bruyns 9561)*	0010001011	0111011010	1001010101	1100110001	0
Phyllobolus suffruticosus	0010001011	0111111010	1001010001	1100110001	0
Phyllobolus tenuiflorus	0200010111	0110011010	11?1011101	1100110001	0

Appendix 3. Continued.

INGROUP	1–10	11–20	21–30	31–40	41
Phyllobolus trichotomus	0010001011	0111011010	11?1011001	1100100001	0
Phyllobolus viridiflorus	0210010111	0110011010	11?1011001	1100110001	0
Prenia englishiae	0000000011	1111011010	1001010001	1100000000	0
Prenia pallens subsp. *lutea*	0000000011	1111011010	1001010001	11000?0000	0
Prenia pallens subsp. *namaquensis*	0000000011	1111011010	1001010001	11000?0000	0
Prenia pallens subsp. *pallens*	0000000011	1111011010	1001010001	11000?0000	0
Prenia radicans	0000000011	1111011010	1001010001	1100000000	0
Prenia sladeniana	0000000011	1111011000	1001010001	1100000000	0
Prenia tetragona	0010000011	1111011010	1001010001	1100000000	0
Prenia vanrensburgii	0000000011	1111011000	1001010001	1100010000	0
Psilocaulon articulatum	?0?0100011	0111111010	1011010001	1100010000	1
Psilocaulon bicorne	0000110011	0111111010	1011010101	1100010000	1
Psilocaulon coriarium	0010100011	0111111010	1011010001	1100010000	1
Psilocaulon dinteri	00?0100011	0111111010	1011010001	1100010000	1
Psilocaulon foliosum	0010100011	0111111010	1011010001	1100010000	1
Psilocaulon gessertianum	1010100011	0111111010	1011010001	1100010000	1
Psilocaulon granulicaule	1000100011	0111111010	1011010101	1100010000	1
Psilocaulon junceum	0010100011	0111111010	1011010001	11000?0000	1
Psilocaulon leptarthron	0010100011	0111111010	1011010101	1100010000	1
Psilocaulon parviflorum	0000100011	0111111010	1011010101	1100000000	1
Psilocaulon salicornioides	?010100011	0111111010	1011010001	1100010000	1
Psilocaulon subnodosum	0010100011	0111111010	1011010001	1100010000	1
Sceletium crassicaule	0011000011	0110001100	1001010001	1100110101	0
Sceletium emarcidum	0011000011	0110000100	1001010101	11001?0101	0
Sceletium exalatum	0011000011	0110000100	1001010?01	110010?101	0
Sceletium expansum	0011000011	0110000100	1001011001	1100110101	0
Sceletium rigidum	0011000011	0110000100	1001010101	110010?101	0
Sceletium strictum	0011000011	0110000100	1001010001	11001?0101	0
Sceletium tortuosum	0011000011	0110000100	1001010001	11001?0101	0
Sceletium varians	0011000011	0111000100	1001011001	1100110101	0
Synaptophyllum juttae	10000?0011	0111???000	11?1000001	110010001?	?

"?" = polymorphic, non-applicable or missing.