

# A new infrageneric classification for *Mesembryanthemum* (Aizoaceae: Mesembryanthemoideae)

CORNELIA KLAK<sup>1†</sup> & PETER V. BRUYNS<sup>1</sup>

**Keywords:** Aizoaceae, classification, *Mesembryanthemum*, section, subgenus

## ABSTRACT

We present a new infrageneric classification for *Mesembryanthemum* L. (Aizoaceae: Mesembryanthemoideae), based on a phylogeny of the genus published in 2007. We re-affirm that a broad generic circumscription for *Mesembryanthemum* (including all 103 species of the Mesembryanthemoideae) is the only group in the subfamily that can be recognized unambiguously by synapomorphies. We divide *Mesembryanthemum* into five subgenera, of which two are new: *M.* subg. *Mesembryanthemum*, *M.* subg. *Cryophytum* (N.E. Br.) Bittrich, *M.* subg. *Opophytum* (N.E. Br.) Bittrich, *M.* subg. **Phyllobolus** (N.E. Br.) Klak and *M.* subg. **Volkeranthus** (Gerbaulet) Klak. Furthermore, we recognize five sections in subg. *Mesembryanthemum*, six sections in subg. *Phyllobolus* and two sections in *M.* subg. *Cryophytum*. Descriptions and keys to all infrageneric taxa are provided.

## INTRODUCTION

The Mesembryanthemoideae is one of four subfamilies currently recognized in Aizoaceae (Klak *et al.* 2003) and includes 103 species (Klak *et al.* 2007). The Mesembryanthemoideae include both annuals and perennials, leaf- as well as stem-succulents, geophytes, highly compact, dwarf shrubs as well as woody shrubs that may exceed 1 m in height. Many members of this subfamily have flattened, mesomorphic leaves and, in many of them, both the leaves and the stems are covered with conspicuous bladder cells. 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. Bittrich & Hartmann 1988; Hartmann 1991).

Most of the genera in the Mesembryanthemoideae have been revised (e.g. Gerbaulet 1996a, 1996b, 1996c, 1997; Klak & Linder 1998; Klak *et al.* 2006) and several were re-circumscribed on the basis of morphological characters (e.g. Ihlenfeldt & Bittrich 1985; Bittrich 1986; Gerbaulet 1995). Over the last 40 years, generic concepts have been modified frequently within the subfamily (Table 1). Bittrich (1986) was the first to consider the relationships between the genera and species in detail and this led him to put forward broad generic concepts for *Phyllobolus* and *Mesembryanthemum*, in which he incorporated several of the previously recognized genera (Table 1). Although he made no formal taxonomic changes, he proposed subdivision of the enlarged genus *Phyllobolus* into five subgenera (*P.* subg. *Aridaria*, *Phyllobolus*, *Prenia*, *Sceletium*, and *Sphalmanthus*). Since Gerbaulet (1995) was unable to find a synapomorphy for Bittrich's broad concept of *Phyllobolus*, she recognized the genera *Aridaria*, *Phyllobolus*, *Prenia* and *Sceletium* and provided putative synapomorphies for each. In addition, she modified the generic

concepts of *Aridaria* and *Prenia* and included the monotypic genera *Amoebophyllum* and *Dactyloopsis* N.E.Br. in *Phyllobolus* (Gerbaulet 1995). More recent investigations showed that *Dactyloopsis*, together with *Aspazoma*, is sister to *Brownanthus* (Klak *et al.* 2003), so that it is not closely allied to *Phyllobolus*. Consequently it was reinstated as a monotypic genus (Klak *et al.* 2006).

In *Mesembryanthemum*, Bittrich (1986) included all the annual species of the Mesembryanthemoideae (apart from *Synaptophyllum*) and recognized several of the earlier genera as subgenera (*M.* subg. *Cryophytum* and subg. *Opophytum*), but he was not able to find synapomorphies for *Mesembryanthemum*.

A preliminary molecular study by Klak *et al.* (2003), which included 16 species of the Mesembryanthemoideae, showed that *Mesembryanthemum* was polyphyletic and that the generic limits needed re-investigation. This was followed by a densely sampled molecular assessment of the Mesembryanthemoideae, which confirmed the polyphyly of *Mesembryanthemum* (Klak *et al.* 2007). It showed, in addition, that *Phyllobolus* was not monophyletic and that one of its species, *P. splendens* (= *Mesembryanthemum splendens*), was much more closely related to the *Aptenia*- and *Sceletium*-groups than to the remainder of *Phyllobolus* (Klak *et al.* 2007).

Klak *et al.* (2007) found that there were exceptionally high levels of homoplasy among the Mesembryanthemoideae. In particular, the *M. aitonis*-clade (*M. aitonis* and *M. longistylum* DC.) and the *P. splendens*-clade (*P. splendens* only) were new entities that can only be circumscribed using homoplasious characters (as discussed in detail by Klak *et al.* 2007). Placing these clades in separate genera would have made them extremely difficult to identify and any newly discovered species may be placed in such a generic framework only using molecular techniques. Consequently, a new classification of the Mesembryanthemoideae was proposed by Klak *et al.* (2007) with only the single genus *Mesembryanthemum*. Although not all relationships between the species were resolved, many of the clades in the Mesembryanthemoideae were well supported and these clades were

<sup>1</sup> Bolus Herbarium, Department of Biological Sciences, University of Cape Town, 7701 Rondebosch, South Africa. E-mail: †cornelia.klak@uct.ac.za (corresponding author).

TABLE 1.—Classification of Mesembryanthemoideae over the last four decades showing the fluctuation in the number of genera recognized (in bold)

Herre (1971): 18 genera	Bittrich (1986): 9 genera	Gerbaulet (2001): 11 genera	Gerbaulet (2012): 16 genera
<i>Aptenia</i> N.E.Br.	<i>Aptenia</i> N.E.Br. (incl. <i>Platythyra</i> )	<i>Aptenia</i> N.E.Br. (incl. <i>Platythyra</i> )	<i>Aptenia</i> N.E.Br. (incl. <i>Platythyra</i> )
<i>Platythyra</i> N.E.Br.			
<i>Aspazoma</i> N.E.Br.	<i>Aspazoma</i> N.E.Br.	<i>Aspazoma</i> N.E.Br.	<i>Aspazoma</i> N.E.Br.
<i>Brownanthus</i> Schwantes	<i>Brownanthus</i> Schwantes  <i>Pseudobrownanthus</i> Ihlenf.&Bittrich	<i>Brownanthus</i> Schwantes (incl. <i>Pseudobrownanthus</i> )	<i>Brownanthus</i> Schwantes (incl. <i>Pseudobrownanthus</i> )
<i>Mesembryanthemum</i> L. (incl. <i>Callistigma</i> , <i>Cryophytum</i> )  <i>Eurystigma</i> L.Bolus  <i>Halenbergia</i> Dinter <i>Hydrodea</i> N.E.Br. <i>Opophytum</i> N.E.Br.	<i>Mesembryanthemum</i> L. (incl. <i>Cryophytum</i> , <i>Callistigma</i> , <i>Eurystigma</i> , <i>Halenbergia</i> , <i>Hydrodea</i> , <i>Opophytum</i> )	<i>Mesembryanthemum</i> L. (incl. <i>Callistigma</i> , <i>Cryophytum</i> , <i>Eurystigma</i> , <i>Halenbergia</i> , <i>Hydrodea</i> , <i>Opophytum</i> )	<i>Mesembryanthemum</i> L.  <i>Callistigma</i> Dinter & Schwantes <i>Cryophytum</i> N.E.Br. <i>Eurystigma</i> L.Bolus <i>Opophytum</i> N.E.Br. (incl. <i>Halenbergia</i> , <i>Hydrodea</i> )
<i>Dactyloopsis</i> N.E.Br.  <i>Aridaria</i> N.E.Br. <i>Phyllobolus</i> N.E.Br.  <i>Prenia</i> N.E.Br. <i>Sceletium</i> N.E.Br. <i>Amoebophyllum</i> N.E.Br. <i>Sphalmanthus</i> N.E.Br.	<i>Dactyloopsis</i> N.E.Br.  <i>Phyllobolus</i> (incl. <i>Amoebophyllum</i> , <i>Aridaria</i> , <i>Prenia</i> , <i>Sceletium</i> , <i>Sphalmanthus</i> )	<i>Phyllobolus</i> N.E.Br. (incl. <i>Amoebophyllum</i> , <i>Dactyloopsis</i> , <i>Sphalmanthus</i> ) <i>Aridaria</i> N.E.Br.  <i>Prenia</i> N.E.Br. <i>Sceletium</i> N.E.Br.	<i>Dactyloopsis</i> N.E.Br.  <i>Aridaria</i> N.E.Br. <i>Phyllobolus</i> N.E.Br. (incl. <i>Sphalmanthus</i> , <i>Amoebophyllum</i> ) <i>Prenia</i> N.E.Br. <i>Sceletium</i> N.E.Br.
<i>Psilocaulon</i> N.E.Br.	<i>Psilocaulon</i> N.E.Br.	<i>Psilocaulon</i> N.E.Br. <i>Caulipsolon</i> Klak	<i>Psilocaulon</i> N.E.Br. (incl. <i>Caulipsolon</i> )
<i>Synaptophyllum</i> N.E.Br.	<i>Synaptophyllum</i> N.E.Br.	<i>Synaptophyllum</i> N.E.Br.	<i>Synaptophyllum</i> N.E.Br.  <i>Volkeranthus</i> Gerbaulet

also recovered in an analysis including both molecular and morphological characters (Klak *et al.* 2007) so that they were recognized as informal groups.

Recently, these changes have been challenged and it has been claimed that the results of Klak *et al.* (2007) can easily be accommodated within the ‘traditional classification’ by reinstating a couple of older genera and describing one new genus, *Volkeranthus*, for the clade consisting of *M. aitonis* and *M. longistylum* (Gerbaulet 2012). This resulted in a new classification for the Mesembryanthemoideae involving 16 genera and reverting to a generic system similar to that of Herre (1971, Table 1).

Gerbaulet (2012: 189) based much of her discussion and conclusions on a ‘new’ and ‘simplified cladogram derived from Klak *et al.* (2007) and with new assessments of character states’. The data and methods used to generate this cladogram are not given, nor is it clear on what material the new assessments of characters are based. The new cladogram differs from that in Klak *et al.* (2007) in that the *Aptenia*-, *Aridaria*-, *Phyllobolus*-, *Prenia*- and *Sceletium*-groups form a polytomy, whereas in Klak *et al.* (2007), *M. splendens* (= *Phyllobolus splendens*) was much more closely related (with high statistical support) to the *Aptenia*- and *Sceletium*-groups

than to the *Phyllobolus*-group. Gerbaulet (2012: 191) erroneously interprets *Phyllobolus* as ‘unresolved’, since she was not able to find any synapomorphy to support the position of *M. splendens* (= *Phyllobolus splendens*) as sister to the *Aptenia*- and *Sceletium*-groups.

Apart from our objections to the use of this ‘cladogram’, we are unable to accept Gerbaulet’s conclusions for several other reasons:

- (1) The arguments for the creation of a new genus, *Volkeranthus*, for *M. aitonis* and *M. longistylum*, are flawed. Firstly, Gerbaulet (2012: 188) claimed that Bittrich (1986) had already identified these two species as the ‘*M. aitonis* group’. Bittrich (1986) had principally distinguished two groups in *M.* subg. *Mesembryanthemum* and provided morphological circumscriptions of these two groups, citing a ‘primitive leaf shape and brown papillate seeds’ as characteristic of the *M. aitonis*-group and ‘slender, cylindrical leaves with a central water-storing tissue and smooth seeds’ as characteristic of the *M. nodiflorum*-group. However, he never explicitly stated which other species belonged to the *M. aitonis*-group and which belonged to the *M. nodiflorum*-group. *M. longistylum* is intermediate between the two groups, since it possesses almost cylindrical, slightly chan-



nelled leaves with central water-storing tissue and papillate seeds (Gerbaulet 2001b). Thus, Gerbaulet's (2012) reference to Bittrich's '*M. aitonis*-group' as consisting of *M. aitonis* and *M. longistylum* is incorrect. Secondly, Gerbaulet (2012: 194) claimed that 'epidermal cells with a central papilla at the base of the stamens' characterizes the new genus *Volkeranthus* (*M. aitonis* and *M. longistylum*). She referred to Bittrich (1986) for evidence of this synapomorphy. However, Bittrich (1986: 26) did not state in which species this feature is present, apart from *M. aitonis*. Gerbaulet (2012) presented no new data and consequently her claim that 'epidermal cells with a central papilla at the base of the stamens are unique to *M. aitonis* and *M. longistylum*' is not justified. The failure to present such data is particularly problematic, since this was the only feature that characterized *M. aitonis* and *M. longistylum* as a distinct genus.

(2) A further example of a hypothesis for which no data were provided is the character 'bladder cells very large, especially on the receptacle' (Gerbaulet 2012: 194), which is given as a synapomorphy for *Cryophytum*. However, no evidence for it exists either in Bittrich (1986) or in any other paper by Gerbaulet.

(3) By placing *M. splendens* once more in *Phyllobolus*, Gerbaulet (2012) created a paraphyletic *Phyllobolus*. This contradicts the principles of Backlund & Bremer (1998), who argued that only monophyletic groups should be recognized as genera.

We therefore maintain that a broad generic circumscription for *Mesembryanthemum* (including all 103 species of the Mesembryanthemoideae) is the only arrangement that accurately reflects the most recently acquired information on the subfamily and is the only group that can be recognized unambiguously by synapomorphies. The aim of this paper is therefore to formalize the arrangement of species into groups by Klak *et al.* (2007) as an infrageneric classification for *Mesembryanthemum*. The major lineages within *Mesembryanthemum* are recognized as subgenera, while the clades within these lineages are recognized as sections. The subgenera and sections have been created here for ease of reference but, due to the high levels of homoplasy in the Mesembryanthemoideae, not all are easy to recognize. This applies particularly to *M.* subg. *Volkeranthus* and *M.* sect. *Splendens*. Therefore, the keys to the subgenera and sections provided below are not easy to use and often have exceptions. Nevertheless they provide a first step in the identification of groups of species in the Mesembryanthemoideae. Where possible, the sections consist of groups that were previously recognized as genera. All of the subgenera and sections are monophyletic, except for *M.* sect. *Canaliculata*, which forms a polytomy together with sections *Vesperifolia* (monophyletic) and *Flaviflora* (monophyletic). Resolution obtained so far is inadequate to argue for or against the monophyly of sect. *Canaliculata*, but we recognize this group of taxa at the rank of section for ease of identification. The subgenera and sections have been mapped onto a simplified version of the cladogram of Klak *et al.* (2007: Figure 3), which shows the support for and relationships between them.

Haworth (1795) appears to have been the first to split up the large Linnaean genus *Mesembryanthemum* (which then already included 162 species) into groups, but without assigning them a formal rank. He intended to provide 'a numerical index of the species and varieties, arranged after [my] own method' (Haworth 1795: 473). Several years later, Haworth (1803) arranged the species into 13 sections and provided short diagnoses ('*characteres sectionum*') for each of them. Most of the 13 sections were further subdivided but without an indication of the rank of these segregates. Salm-Dyck (1820:13) refined Haworth's system and further subdivided *Mesembryanthemum* ('*subdivisionis generis*'), providing names and diagnoses for his divisions. Although Haworth (1821:71) referred to Salm-Dyck's subdivisions as 'the Prince's divisions and sections', Salm-Dyck (1820) assigned no formal rank to them. Due to the growing number of species in *Mesembryanthemum*, Haworth (1821) considered it necessary to modify the divisions and he recognized eight sections, which were further broken into 69 numbered but unranked subdivisions. Haworth (1821:79) noted at the end of his sections that several of his groups could be regarded as 'true and natural genera'. Since his 69 subdivisions were unranked, their names need not to be taken into consideration for nomenclatural purposes.

The species currently placed in the Mesembryanthemoideae were included in five of the 13 sections of Haworth (1803), namely *Subacaulia*, *Planifolia*, *Canaliculata*, *Vesperifolia* and *Flaviflora*. Whereas sections *Subacaulia* and *Flaviflora* each included only a single species from the Mesembryanthemoideae, most species of the Mesembryanthemoideae were placed in sections *Planifolia* and *Canaliculata*. All five sections had many subdivisions, except for section *Vesperifolia*, which included only *M. defoliatum* Haw., *M. noctiflorum* L. and *M. stramineum* Haw. Haworth (1821) placed all species of the Mesembryanthemoideae in section *Papulosa* ('*foliis fere semper plus minus papulosis*'), except for the more-or-less stemless, clump-forming, highly succulent *M. digitatum*, which he included in section *Acaulia*. However, section *Papulosa* also included many taxa which belong to the Ruschioideae, such as various species of *Delosperma* and *Cleretum*.

Candolle (1828) based his classification on the earlier works of Haworth and Salm-Dyck, and used many of Haworth's 'sections' at the rank of 'subdivision' and Haworth's groupings within a section at the rank of 'sections'. He recognized eight 'subdivisions' and 54 'sections', including some new sections. Candolle (1828) made many changes to the membership and circumscription of the groupings of Haworth and Salm-Dyck, but regarded two species, i.e. *M. ciliatum* Ait. (= *M. vaginatum* Lam.) and *M. corallinum* Thunb. as insufficiently known and did not place them in any section (1828: 451). These two species were later included by Sonder (1862) in sect. *Juncea*.

Most sections listed below were thus previously validly published, but not typified. As their membership has changed repeatedly since they were set up, they are typified below and are more accurately circumscribed.

## TAXONOMIC TREATMENT

**Mesembryanthemum** L., Species plantarum 1: 480 (1753), nom. cons. Type: *Mesembryanthemum nodiflorum* L., typ. cons.

Key to subgenera of *Mesembryanthemum*

1. Seeds whitish to light brown, rarely dark brown and sculptured . . . 2
  1. Seeds dark brown, much sculptured (whitish and smooth in *M. inachabense* but then stigmas red) . . . . . 3
  - 2.(1) Annuals; leaves highly succulent, cylindrical and 7–15 mm diam. . . . . 3. *M.* subg. *Opophytum*
  2. Annuals or perennials, if annuals then leaves flat or if ± cylindrical then 2–5 mm diam. . . . . 2. *M.* subg. *Mesembryanthemum*
  - 3.(1') Plants perennial; testa cells convex or with central raised papillae . . . . . 4. *M.* subg. *Phyllobolus*
  - 3'. Plants annual or short-lived perennials; testa cells with central raised papillae . . . . . 4
  - 4.(3') Petaloid staminodes free, filamentous staminodes absent . . . . . 5. *M.* subg. *Volkeranthus*
  - 4'. Petaloid staminodes fused into tube, filamentous staminodes present (rarely absent) . . . . . 1. *M.* subg. *Cryophytum*

1. **M.** subg. **Cryophytum** (N.E.Br.) Bittrich in Mitteilungen aus dem Institut für allgemeine Botanik Hamburg 21: 72 (1986). *Cryophytum* N.E.Br.: 412 (1925). Lectotype (Bittrich 1986: 72): *M. crystallinum* L.

*Callistigma* Dinter & Schwantes in Schwantes: 644 (1928). Type: *Callistigma inachabense* (Engler) Dinter & Schwantes (= *Mesembryanthemum inachabense* Engler).

Prostrate to ascending or erect annuals or short-lived perennials, stems often angled or winged, epidermis of stems with conspicuously raised bladder cells, roots fibrous. *Leaves* flat and often very broad, decussate and shortly connate at the base or becoming alternate in the inflorescences, margins often undulating, epidermis with conspicuous bladder idioblasts, without enlarged central water storing cells. *Flowers* in cymes, 10–60 mm diam., cream to pale or rarely dark yellow, petaloid staminodes fused into tube, petaloid and filamentous staminodes and stamens very numerous and filiform, rarely filamentous staminodes absent and petaloid staminodes and stamens few (*M. inachabense*); stigmas free or rarely basally connate and red (*M. inachabense*), nectaries shell-shaped, often deep. *Fruits* 5-locular, valve wings erect or inflexed over valves. *Seeds* brown, rarely whitish, rough with testa cells central papillose, rarely smooth.

Key to sections of *M.* subg. *Cryophytum*

1. Margins of leaves not undulate; flowers 10–20 mm diam.; filamentous staminodes absent, petaloid staminodes and stamens few . . . . . 1.1. *M.* sect. *Callistigma*
- 1'. Margins of leaves undulate; flowers 15–60 mm diam.; petaloid staminodes, filamentous staminodes and stamens numerous . . . . . 1.2. *M.* sect. *Papulosa*

1.1. **M.** sect. **Callistigma** (Dinter & Schwantes) Klak, comb. et stat. nov. *Callistigma* Dinter & Schwantes in Gartenwelt 32: 644 (1928). Type: *Mesembryanthemum inachabense* Engler (= *Callistigma inachabense* (Engler) Dinter & Schwantes).

Decumbent annuals, stems terete or 2-edged. *Leaves* flat, oblong, margins not undulate, epidermis with conspicuous bladder idioblasts. *Flowers* 10–20 mm diam., petaloid staminodes pale to dark yellow, filamentous staminodes absent, petaloid staminodes and stamens few; stigmas basally connate and red, nectaries deep. *Fruits* 5-locular, valve wings erect or inflexed over the valves. *Seeds* whitish, testa smooth.

Species (1): *Mesembryanthemum inachabense* Engler

1.2. **M.** sect. **Papulosa** Haw., Revisiones plantarum succulentarum : 79 (1821). Type (designated here): *Mesembryanthemum crystallinum* L.

Prostrate to ascending or erect annuals or short-lived perennials, stems often angled or winged. *Leaves* flat and often very broad, margins usually undulate, decussate and shortly connate at the base or becoming alternate in inflorescences, epidermis with conspicuous bladder idioblasts. *Flowers* 15–60 mm diam., cream to pale yellow, with numerous filiform petaloid staminodes, filamentous staminodes and stamens; stigmas free, greenish-yellow, nectaries shell-shaped. *Fruits* 5-locular, valve wings inflexed over valves. *Seeds* dark or light brown, rough, testa cells with central papillae.

*Typification*: Haworth (1803) included all species of Mesembryanthemoideae and Ruschioideae with flat leaves and a prostrate to decumbent habit in section *Planifolia*, including *M. crystallinum* (*Cryophytum*-group), *M. cordifolium* (*Aptenia*-group), *M. expansum* (*Sceletium*-group) and *M. pallens* (*Prenia*-group) (see also typification for sections *Planifolia* and *Flaviflora*). In a subsequent publication, however, all species of Mesembryanthemoideae (except *M. digitatum*) were accommodated in section *Papulosa* (Haworth 1821). Section *Papulosa* included annuals, biennials and perennials, with more-or-less papillate leaves ('*Suffrutices; annua, biennia, perenniave: foliis fere semper plus minus papulosis*' (Haworth 1821). Although most members of the Mesembryanthemoideae have distinctly papillate leaves, the size of the papillae are most striking in the *Cryophytum*-group. We therefore selected section *Papulosa* to accommodate all those members of subgenus *Cryophytum* that have particularly large and striking bladder cells. Since *M. crystallinum* was the only species from this group to be known and included in section *Papulosa* by Haworth, we chose this species as the type of section *Papulosa*.

Species (6): *M. barklyi* N.E.Br., *M. crystallinum* L., *M. gariusanum* Dinter, *M. guericchianum* Pax, *M. longipapillosum* Dinter, *M. pellitum* Friedrich

2. **M.** subg. **Mesembryanthemum**

Annuals or perennials, prostrate, decumbent or erect shrubs, rarely geophytes, stems cylindrical, often with ephemeral leaves and surface remaining green and photosynthetic, roots fibrous or rarely thickened, epidermis of stems with conspicuously raised bladder cells, or bladder cells reduced and flattened. *Leaves* deciduous or marcescent, epidermal bladder cells distinct or flattened, without or with central enlarged water storing cells. *Flowers* in cymes or solitary, 5–20(–30) mm diam., sepals remaining erect during anthesis or spreading, pet-

aloid staminodes, filamentous staminodes and stamens not particularly numerous, with or without filamentous staminodes, petaloid staminodes white, cream, pink or pale yellow, rarely much reduced, nectaries shell-shaped or tubular, rarely absent. *Fruits* (3)4 or 5-locular, rarely nut-like, valve wings inflexed over valves or reflexed and fused in pairs, locules deep or shallow. *Seeds* smooth or testal cells with central raised papillae, light coloured (rarely brown), rarely with crest.

Key to the sections of *M.* subg. *Mesembryanthemum*

1. Annuals ..... 2  
 1.' Perennials ..... 4  
 2. (1) Flowers 5–30 mm diam.; filamentous staminodes absent; petaloid staminodes and stamens not particularly numerous ..... 2.4. *M.* sect. *Mesembryanthemum*  
 2.' Flowers  $\pm$  60 mm diam.; petaloid staminodes, filamentous staminodes and stamens very numerous ..... 2.2. *M.* sect. *Eurystigma*  
 3. (1') Leaves free, with tubular stem-clasping sheath ..... 2.5. *M.* sect. *Subacaulia*  
 3.' Leaves free or shortly connate, without tubular stem-clasping sheath ..... 4  
 4. (3') Epidermis of stems with cylindrical, closely packed, xeromorphic bladder cells resembling cobblestones ..... 2.1. *M.* sect. *Brownanthus*  
 4.' Epidermis of stems with much flattened epidermal bladder cells, smooth, sometimes with widely-spaced, rounded or hair-like bladder cells ..... 2.3. *M.* sect. *Juncea*

2.1. **M.** sect. **Brownanthus** (*Schwantes*) Klak, comb. et stat. nov. *Brownanthus* Schwantes in Zeitschrift für Sukkulentenkunde 3: 20 (1927). Type: *Mesembryanthemum vaginatum* Lam. (= *Brownanthus vaginatus* (Lam.) Chesselet & M. Pignal.

*Pseudobrownanthus* Ihlenf. & Bittrich: 319 (1985). Type: *Pseudobrownanthus nucifer* Ihlenf. & Bittrich. (= *Mesembryanthemum nucifer* (Ihlenf. & Bittrich) Klak).

Decumbent to erect perennial shrubs, at least youngest stems succulent and green, articulate, epidermis of stems with closely packed, xeromorphic bladder cells. *Leaves* decussate, deciduous or marcescent, epidermal bladder cells mesomorphic, with central enlarged water storing cells. *Flowers* solitary or in cymes, 5–10(–20) mm diam., sepals remaining erect during anthesis, petaloid staminodes cream to white, free, filamentous staminodes absent, nectaries narrow. *Fruits* 3–5-locular, valve wings inflexed over valves, lower part of fruit shallow, occasionally with seed bags, rarely nut-like. *Seeds* brown to cream, testa rough or  $\pm$  smooth, rarely with crest.

*Typification:* *Mesembryanthemum vaginatum* is the type of *Brownanthus* and thus the type for section *Brownanthus*.

Species (14): *M. arenosum* Schinz, *M. corallinum* Thunb., *M. glareicola* (Klak) Klak, *M. kuntzei* Schinz, *M. marlothii* Pax, *M. namibense* Marloth, *M. napierense* Klak, *M. neglectum* (Pierce & Gerbaulet) Klak, *M. nucifer* (Ihlenf. & Bittrich) Klak, *M. pseudoschlichtianum*

(Pierce & Gerbaulet) Klak, *M. schenckii* Schinz, *M. springbokense* Klak, *M. tomentosum* Klak, *M. vaginatum* Lam.

2.2. **M.** sect. **Eurystigma** (*L. Bolus*) Klak, comb. et stat. nov. *Eurystigma* L. Bolus in Notes on Mesembrianthemum and allied genera 2: 179 (1930). Type: *Mesembryanthemum eurystigmatum* Gerbaulet (= *Eurystigma clavatum* L. Bolus).

Decumbent annuals to 20 cm tall, internodes terete, to 4 mm diam. *Leaves* cylindrical, to 70  $\times$  10 mm, bladder cells flattened, with central enlarged water storing cells. *Flowers* in cymes, deeply funnel-shaped, to 60 mm diam., petaloid staminodes straw-coloured to yellow, very narrow, connate into tube, petaloid staminodes, filamentous staminodes and stamens very numerous; stigmas basally shortly connate with ovary, thick and broad, subulate, or rather filiform, yellow, nectaries tubular. *Fruits* 5-locular, valve wings inflexed over valves. *Seeds* whitish to light brown, testa smooth.

Species (1): *M. eurystigmatum* Gerbaulet

2.3. **M.** sect. **Juncea** Haw. ex DC., Prodomus systematis naturalis regni vegetabilis 3: 446 (1828). [Unranked] *Juncea* Haw.: 175 (1821). Lectotype (designated here): *Mesembryanthemum juceum* Haw.

*Psilocaulon* N.E.Br.: 433 (1925). Type: *Psilocaulon articulatum* (Thunb.) N.E.Br. (= *Mesembryanthemum articulatum* Thunb.).

*Caulipsolon* Klak: 364 (1998). Type: *Caulipsolon rapaceum* (Jacq.) Klak (= *Mesembryanthemum rapaceum* Jacq.).

*Synaptophyllum* N.E.Br.: 412 (1925). Type: *Synaptophyllum juttæ* (Dinter & A. Berger) N.E.Br. (= *Mesembryanthemum juttæ* Dinter & A. Berger).

[Unranked] *Articulata* Salm-Dyck: 24 (1820).

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, without central enlarged water storing cells. *Flowers* in cymes, rarely solitary, 5–25 mm diam., petaloid staminodes free or very shortly connate at base, filamentous staminodes and stamens conically collected, rarely petaloid staminodes or filamentous staminodes absent, nectaries narrowly shell-shaped or absent. *Fruits* 4 or 5-locular, valve wings inflexed over valves, rarely reflexed and fused in pairs, usually with deep locules. *Seeds* usually light brown to ochre, rarely whitish, testa slightly sculptured, with central raised papillae, rarely smooth.

*Typification:* Salm-Dyck (1820) created subdivision 'Articulata' (without formal rank) to include three species from the *Psilocaulon*-group, which Haworth (1821) placed in his subdivision 'Juncea' (without formal rank) within section *Papulosa*: *M. junceum*, *M. parviflorum* (= *M. micranthon* Haw., = *M. tenue* Haw.) and *M. rapaceum*. Constricted green stems and deciduous leaves were mentioned by both authors in the diagnoses

of their respective subdivision, although these characteristics are also found in sections *Brownanthus* and *Geniculiflora*. Candolle (1828) treated Haworth's subdivision 'Juncea' as a section, thereby validating it for the first time at this rank. In addition, he only included taxa currently placed in the *Psilocaulon*-group, making it the correct name for this group at the rank of section. Since *M. juncea* is the eponymous species of this group we selected it as the type of sect. *Juncea*.

Species (15): *M. articulatum* Thunb., *M. bicornis* 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. juncea* Haw., *M. juttiae* Dinter & A.Berger, *M. leptarthron* A.Berger, *M. neofoliosum* Klak, *M. parviflorum* Jacq., *M. rapaceum* Jacq., *M. salicornioides* Pax, *M. subnodosum* A.Berger

#### 2.4. *M.* sect. *Mesembryanthemum*

Annual, prostrate or erect shrublets, internodes terete. *Leaves* ± cylindrical or somewhat channelled to narrowly obovate or oblong or almost truncate, epidermal bladder cells distinct or inconspicuous, with enlarged central water storing cells. *Flowers* in cymes, petaloid staminodes free or connate into short tube, 5–30 mm diam., petaloid staminodes yellow, white to pale pink or pink, filamentous staminodes absent, nectaries tubular. *Fruits* 5-locular, valve wings reflexed and fused in pairs. *Seeds* whitish to light brown, testa smooth.

Species (4): *M. excavatum* L.Bolus, *M. nodiflorum* L., *M. stenandrum* (L.Bolus) L.Bolus, *M. subtruncatum* L.Bolus

2.5. *M.* sect. *Subacaulia* Haw. in *Miscellanea naturalia*: 17 (1803): Lectotype (designated here): *Mesembryanthemum digitatum* Aiton

*Aspazoma* N.E.Br.: 413 (1925). Type: *Aspazoma amplexens* (L.Bolus) N.E.Br.

*Dactyloopsis* N.E.Br.: 413 (1925). Type: *Dactyloopsis digitata* (Aiton) N.E.Br.

Dwarf, clump-forming or bushily branched, erect shrublets, epidermis of stem with closely packed bladder cells. *Leaves* cylindrical or slightly flattened, alternating, with tubular sheaths clasping one another, drying up completely during resting period, bladder cells much flattened or somewhat flattened, with central enlarged water storing cells. *Flowers* solitary, sepals and petaloid staminodes basally fused into short tube, petaloid staminodes white to cream, filamentous staminodes absent or present, if absent then reproductive parts concealed, nectaries shell-shaped. *Fruits* 4 or 5-locular, valve wings inflexed over valves or reflexed and fused in pairs. *Seeds* light brown to whitish, testa smooth.

*Typification*: Among several species of Ruschioideae, only a single species of Mesembryanthemoideae was included in section *Subacaulia* (Haworth 1803), which Haworth characterized as lacking stems or with very short stems and perennial roots ('*caulibus nullis vel brevissimis, radice perenni*'). Among the species of Mesembryanthemoideae currently known a seemingly stem-less habit is still unique to *M. digitatum*. The

closely related *M. amplexens* is a shrubby plant but shares the unique leaf morphology with *M. digitatum*.

Species (2): *M. amplexens* L.Bolus, *M. digitatum* Aiton subsp. *digitatum*, *M. digitatum* subsp. *littlewoodii* (L.Bolus) Klak

3. *M.* subg. *Opophytum* (N.E.Br.) Bittrich in *Mitteilungen aus dem Institut für allgemeine Botanik Hamburg* 21: 73 (1986). *Opophytum* N.E.Br.: 412 (1925). Lectotype (Bittrich 1986: 73): *Mesembryanthemum fastigiatum* Thunb.

*Halenbergia* Dinter ex H. Jacobsen: 158, 200 (1937). Type: *Halenbergia hypertrophica* (Dinter) Dinter ex H. Jacobsen (= *M. hypertrophicum* Dinter).

*Hydrodea* N.E.Br.: 412 (1925). Type: *Hydrodea cryptantha* (Hook.f.) N.E.Br. (= *M. cryptanthum* Hook.f.).

Prostrate annuals, internodes terete, roots fibrous, epidermis of stems with much flattened bladder cells. *Leaves* highly succulent, cylindrical or globular, decussate and shortly connate at base or sometimes alternate in inflorescence, becoming dry while plants are still in flower, with much flattened epidermal bladder cells, with enlarged central water storing cells. *Flowers* 20–60(–80) mm diam., rarely much reduced and only 10 mm diam., petaloid staminodes filiform, sepals and petaloid staminodes connate into short tube, petaloid staminodes, filamentous staminodes and stamens numerous, nectaries tubular. *Fruits* 5-locular, valve wings reflexed and fused in pairs. *Seeds* ochre, smooth.

Species (3): *M. cryptanthum* Hook.f., *M. fastigiatum* Thunb., *M. hypertrophicum* Dinter

4. *M.* subg. *Phyllobolus* (N.E.Br.) Klak, comb. et stat. nov. *Phyllobolus* N.E.Br. in *Gardener's Chronicle* 78: 413 (1925). Type: *Mesembryanthemum resurgens* Kensit (= *Phyllobolus resurgens* (Kensit) Schwantes).

Prostrate or erect shrubs or geophytes, stems herbaceous or corky or woody, roots fibrous or thickened, epidermis of stems with mesomorphic bladder cells, mostly distinct. *Leaves* subcylindrical to somewhat flattened or flat, decussate and shortly connate at base or becoming alternate in inflorescence, or alternate throughout, deciduous or marcescent or old dry leaves 'skeletonized', ± retaining shape through lignified veins, epidermal bladder cells distinct or flattened. *Flowers* in cymes or solitary, white, yellow, pink, greenish or greenish-blue, 10–40 mm diam, sepals spreading during anthesis, petaloid staminodes, filamentous staminodes and stamens not particularly numerous, with or without filamentous staminodes, reproductive parts sometimes concealed, nectaries shell-shaped. *Fruits* 4 or 5-locular, valve wings inflexed over valves or reflexed and fused in pairs, rarely absent, locules deep or shallow. *Seeds* dark brown, with testa cells convex or testa with central raised papillae, with or without a crest.

#### Key to the sections of *M.* subg. *Phyllobolus*

1. Old dry leaves 'skeletonized' (retaining their shape ± fully through lignified veins) . . . . . 4.4. sect. *Planifolia*

- 1.' Old dry leaves sometimes becoming spiny, but not 'skeletonized' ..... 2
- 2.(1') Epidermis of stems with tall, cylindrical, closely packed, xeromorphic bladder cells ..... 4.5. sect. *Geniculiflora*
- 2.' Epidermis of stems with much flattened bladder cells ..... 3
- 3.(2') Epidermis of leaves with thick wax layer, bladder cells flattened ..... 4
- 3.' Epidermis of leaves with inconspicuous wax layer, bladder cells rarely flattened. .... 5
4. Stems herbaceous or only weakly lignified; lower part of fruits conspicuously longer than upper part ..... 4.2. sect. *Flaviflora*
- 4.' Stems woody, leaves strictly decussate; lower part of fruit  $\pm$  as long as upper part ..... 4.3. sect. *Vesperifolia*
- 5.(3') Large woody shrubs, to 1 m tall, rarely cushion-like, leaves persistent, never marcescent or spiny, decussate becoming alternate in the inflorescences . . . 4.1. sect. *Splendentia*
- 5.' Decumbent or erect shrubs or prostrate to decumbent geophytes, if decumbent or erect shrubs, leaves usually deciduous, marcescent or spiny, rarely persistent, if persistent, new leaves tufted in old and dry leaves ..... 4.6. sect. *Canaliculata*

4.1. **M. sect. *Splendentia*** DC., Prodr. systematis naturalis regni vegetabilis 3: 445 (1828). Lectotype (designated here): *Mesembryanthemum splendens* L.

Erect perennial shrubs to 1 m tall, stems woody, roots not thickened. *Leaves* variable in shape, from subcylindrical to narrowly ovate, persistent, epidermal bladder cells small, central water storing cells indistinct. *Flowers* in cymes, 30–40 mm diam., petaloid staminodes cream, pale pink, pale salmon or pale yellow, filamentous staminodes present, reproductive parts not concealed. *Fruits* 5-locular, valve wings inflexed over valves. *Seeds* black or dark brown, with rough testa, crest distinct, indistinct or absent.

*Typification:* Most taxa included in sect. *Splendentia* by Candolle (1828) are now considered to be conspecific with *M. splendens*, but the section also included *M. longistylum* (now placed in subg. *Volkeranthus*) and two species of *Delosperma* (Ruschioideae).

Species (1): *M. splendens* L. subsp. *splendens*, *M. splendens* subsp. *pentagonum* (L.Bolus) Klak

4.2. **M. sect. *Flaviflora*** Haw. in *Miscellanea naturalis*: 19 (1803). Lectotype (designated here): *Mesembryanthemum tetragonum* Thunb.

*Prenia* N.E.Br.: 412 (1925). Type: *Prenia pallens* (Aiton) N.E.Br. (= *M. pallens* Aiton).

Prostrate to rarely ascending (*M. tetragonum*) perennials, stems weakly lignified, roots fibrous. *Leaves*  $\pm$  flat and obscurely triquetrous, obtusely trigonous or almost cylindrical, persistent, epidermal bladder cells much flattened, without enlarged central water storing cells. *Flowers* in cymes, 20–40 mm diam., petaloid staminodes white yellow or pink, sepals and petaloid staminodes connate into short tube, filamentous staminodes present, nectaries shell-shaped. *Fruits* 4 or 5 locular, locules deep, valve wings inflexed over valves. *Seeds* black, rough, testa cells central papillose, with or without indistinct crest.

*Typification:* Haworth (1803) included several species of Ruschioideae and only one species of Mesembryanthemoideae in section *Flaviflora*, i.e. *M. tetragonum* Thunb. We take this species as the type of this section. It was included by Haworth on the 'authority of Thunberg', who thought it was related to *M. molle* Aiton (= *Malephora mollis* (Aiton) N.E.Br.). Section *Flaviflora* was characterized by slightly woody, often erect stems, triquetrous leaves and yellow, orange, or deep red petaloid staminodes ('*caulibus suffrutulentibus saepe erectis, foliis triquetris saepe brevissimis, petalis flavis, aurantiis, vel coccineis*') (Haworth 1803: 19).

Species (6): *M. englishiae* L.Bolus, *M. pallens* subsp. *lanceum* (Thunb.) Klak, *M. pallens* subsp. *luteum* (L.Bolus) Klak, *M. pallens* subsp. *namaquense* (Gerbaulet) Klak, *M. pallens* Aiton subsp. *pallens*, *M. radicans* (L.Bolus) Klak, *M. sladenianum* L.Bolus, *M. tetragonum* Thunb., *M. vanrensburgii* (L.Bolus) Klak

4.3. **M. sect. *Vesperifolia*** Haw. in *Miscellanea naturalis*: 18 (1803). Type: *Mesembryanthemum noctiflorum* L.

*Aridaria* N.E.Br.: 433 (1925). Type: *Aridaria noctiflora* (L.) Schwantes (= *M. noctiflorum* L.).

Low to tall erect shrubs to 1 m high, roots thickened. *Leaves* subcylindrical, decussate, deciduous, bladder cells small and much flattened, with enlarged central water storing cells. *Flowers* in cymes, large (to 40 mm diam.), diurnal or nocturnal, petaloid staminodes white or pink inside, suffused with various shades of yellow, copper, pink, or red on reverse, sepals and petaloid staminodes connate into short tube, filamentous staminodes absent, nectaries shell-shaped. *Fruits* 4-locular, valve wings inflexed over valves, breaking off easily with stalks becoming spiny. *Seeds* brown or dark brown, rough, testa cells central papillose, with or without crest.

*Typification:* Haworth (1803) included three species in sect. *Vesperifolia* (i.e. *M. noctiflorum*, *M. stramineum* and *M. defoliatum*). The last two are now subspecies of *M. noctiflorum*, which therefore becomes the type of the section.

Species (4): *M. brevicarpum* (L.Bolus) Klak, *M. noctiflorum* subsp. *defoliatum* (Haw.) Klak, *M. noctiflorum* L. subsp. *noctiflorum*, *M. noctiflorum* subsp. *stramineum* (Haw.) Klak, *M. occidentale* Klak, *M. serotinum* (L.Bolus) Klak

4.4. **M. sect. *Planifolia*** Haw. in *Miscellanea naturalis*: 18 (1803). Lectotype (designated here): *Mesembryanthemum tortuosum* L.

*Sceletium* N.E.Br.: 412 (1925). Type: *Sceletium tortuosum* (L.) N.E.Br. (= *M. tortuosum* L.).

Prostrate to erect small perennials, often scrambling in other bushes, roots fibrous. *Leaves* flat, ovate, dry leaves persistent and 'skeletonized' through lignified veins, without enlarged central water storing cells. *Flowers* in few-flowered cymes, more rarely solitary, stalked or sessile, 20–40 mm diam., petaloid staminodes white, various shades of yellow, pale pink, or pale salmon, sepals and petaloid staminodes basally connate

into short tube, filamentous staminodes present, sometimes concealing reproductive parts. *Fruits* 4–6-locular, with or without valve wings, valve wings inflexed over valves, breaking off easily to be dispersed by wind. Seeds rough, testa cells convex and arranged in concentric rows, with distinct or indistinct crest.

*Typification:* Haworth (1803) placed all species of Mesembryanthemoideae and Ruschioideae with flat leaves and a prostrate to decumbent habit in sect. *Planifolia* ('*foliis planis saepe subcarinatis, caulibus saepe decumbenti—prostrates effusis*'). From Mesembryanthemoideae, he included *M. crystallinum*, *M. cordifolium*, *M. expansum*, *M. emarcidum*, *M. tortuosum*, *M. varians* and *M. pallens*. Although all of these species fit the description of the section well, they are unrelated and cannot be placed in the same section. Since most species listed fall into the *Sceletium*-group we elected to associate sect. *Planifolia* with this group, by selecting *M. tortuosum* as the type of the section.

Species (8): *M. archeri* Klak, *M. crassicaule* Haw., *M. emarcidum* Thunb., *M. exalatum* (Gerbaulet) Klak, *M. expansum* L., *M. ladismithiense* Klak, *M. tortuosum* L., *M. varians* Haw.

4.5. **M. sect. *Geniculiflora*** DC. in Prodrromus systematis naturalis regni vegetabilis 3: 445 (1828). Type: *Mesembryanthemum geniculiflorum* L.

*Aptenia* N.E.Br.: 412 (1925), Type: *Aptenia cordifolia* (L.f.) Schwantes (= *M. cordifolium* L.f.).

*Platythyra* N.E.Br.: 412 (1925), Type: *Platythyra haeckeliana* (A.Berger) N.E.Br. (= *M. haeckelianum* A.Berger).

*M. sect. *Cordifolia** DC.: 449 (1828). Type: *Mesembryanthemum cordifolium* L.f.

Prostrate to scandent or climbing perennials, stems with persistent green succulent cortex, internodes 4-angled or terete, with closely packed, xeromorphic bladder cells, roots fibrous, rarely fleshy. *Leaves* flat or rarely almost cylindrical, cordate, ovate, lanceolate or linear, petiolate or sessile, bladder cells mesomorphic and loosely arranged, without enlarged central water storing cells. *Flowers* solitary or in few-flowered cymes, shortly stalked, 15–35 mm diam., petaloid staminodes white, pale yellow or pink, basally connate into short tube, with or without filamentous staminodes, nectaries shell-shaped. *Fruits* 4-locular, with or without valve wings, valve wings inflexed over valves. *Seeds* rough, testa cells central papillose, without a crest.

*Typification:* Candolle (1828) included only a single species in sect. *Geniculiflora*, thus its type. Sect. *Cordifoliae* DC. (1828), described only a few pages after section *Geniculiflora*, is included here in sect. *Geniculiflora*. Four sepals and papillate leaves are among the diagnostic characters for sect. *Geniculiflora* (Candolle 1828) and his mention of 5 sepals for sect. *Cordifoliae* is evidently incorrect (Gerbaulet, 2001a).

Species (4): *M. cordifolium* L.f., *M. geniculiflorum* L., *M. haeckelianum* A.Berger, *M. lancifolium* (L.Bolus) Klak.

4.6. **M. sect. *Canaliculata*** Haw. in Miscellanea naturalia: 18 (1803). Lectotype (designated here): *Mesembryanthemum canaliculatum* Haw.

*Amoebophyllum* N.E.Br.: 433 (1925). Type: *Amoebophyllum angustum* N.E.Br. (= *M. vanheerdei* (L.Bolus) Klak).

*Phyllobolus* N.E.Br.: 413 (1925). Type: *Phyllobolus resurgens* (Kensit) Schwantes (= *M. resurgens* Kensit).

*Sphalmanthus* N.E.Br.: 433 (1925). Type: *Sphalmanthus canaliculatus* (Haw.) N.E.Br. (= *M. canaliculatum* Haw.).

[Unranked] *Canaliculata. Spinulifera* Haw.: 56 (1803).

[Unranked] *Spinulifera* Haw.: 176 (1821).

Perennials, prostrate to erect shrubs to minute geophytes, stems corky or woody, long or much shortened, roots often thickened. *Leaves* subcylindrical or flattened, deciduous, marcescent or persistent, epidermal bladder cells mostly distinct, central water storing cells indistinct. *Flowers* in cymes or solitary, petaloid staminodes in various shades of green, yellow, orange, red, or pink or almost white, (10–)20–40 mm diam., sepals and petaloid staminodes basally fused into short tube, filamentous staminodes present and reproductive parts not concealed or filamentous staminodes absent and reproductive parts concealed, nectaries shell-shaped. *Fruits* 4- or 5-locular, valve wings inflexed over valves. *Seeds* rough, testa cells convex and arranged in concentric rows, with or without crest, sometimes with additional crests on sides.

*Typification:* Whereas sect. *Planifolia* included taxa with flat, often broad leaves, sect. *Canaliculata* (Haw. 1803: 18) accommodated taxa with more slender leaves ('*foliis linearibus, junioribus canaliculatis subtus convexis*'). Taxa with slender leaves are found in unrelated clades within Mesembryanthemoideae. Section *Canaliculata* had been subdivided further into the unranked subdivisions '*Canaliculata. Spinulifera*' (Haw. 1803:56) and '*Canaliculata. Varia*' (Haw. 1803:58). Of these two groups, '*Canaliculata. Spinulifera*' incorporated several species previously placed in *Phyllobolus*, whereas '*Canaliculata. Varia*' included taxa that fall into various unrelated clades. We therefore elected that sect. *Canaliculata* should correspond to the group of taxa previously placed in *Phyllobolus*. Surprisingly many species from this group were already known to Haworth, including *M. canaliculatum*, *M. grossum*, *M. nitidum*, *M. spinuliferum* and *M. viridiflorum*. Since slightly channelled leaves are common to all of these species, we chose *M. canaliculatum* as the type of the section.

Species (32): *M. amabile* (Gerbaulet & Struck) Klak, *M. baylissii* Klak, *M. bulletrapense* Klak, *M. canaliculatum* Haw., *M. caudatum* L.Bolus, *M. chrysophthalmum* (Gerbaulet & Struck) Klak, *M. deciduum* (L.Bolus) Klak, *M. decurvatum* (L.Bolus) Klak, *M. delum* L.Bolus, *M. flavidum* Klak, *M. gariense* (Gerbaulet & Struck) Klak, *M. grossum* Aiton, *M. holense* Klak, *M. knolfonteinense* Klak, *M. latipetalum* (L.Bolus) Klak, *M. lignes-*

*cens* (L.Bolus) Klak, *M. ligneum* (L.Bolus) Klak, *M. liliputatum* Klak, *M. nitidum* Haw., *M. oculatum* N.E.Br., *M. oubergense* (L.Bolus) Klak, *M. prasinum* (L.Bolus) Klak, *M. quartziticola* Klak, *M. rabiei* (L.Bolus) Klak, *M. resurgens* Kensit, *M. sinuosum* L.Bolus, *M. spinuliferum* Haw., *M. suffruticosum* (L.Bolus) Klak, *M. tenuiflorum* Jacq., *M. trichotomum* Thunb., *M. vanheerdei* (L.Bolus) Klak, *M. viridiflorum* Aiton.

5. **M. subg. Volkeranthus** (*Gerbaulet*) Klak, comb. et stat. nov. *Volkeranthus* Gerbaulet in *Bradleya* 30: 196 (2013). Type: *Volkeranthus aitonis* (Jacq.) Gerbaulet (= *Mesembryanthemum aitonis* Jacq.).

Prostrate to ascending, annual to biennial, herbaceous plants, epidermis of stems with mesomorphic, rounded bladder cells, roots fibrous. *Leaves* flat and broad or almost cylindrical to flattened, slightly channelled, linear to narrowly oblong, decussate and shortly connate at base or becoming alternate in inflorescences, epidermis with mesomorphic, rounded bladder cells, with or without enlarged central water storing cells. *Flowers* in cymes, to 25 mm diam., white, sometimes suffused pink or yellowish, sepals shortly connate, petaloid staminodes narrowly lanceolate, filamentous staminodes absent, petaloid staminodes and stamens free, nectaries as deep as locules and tubular. *Fruits* 5-locular, valve wings reflexed and fused in pairs or free and incurved over valves. *Seeds* brown with rough testa, without crest.

Species (2): *M. aitonis* Jacq., *M. longistylum* DC.

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