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## **Disintegrating Portulacaceae: A new familial classification of the suborder Portulacineae (Caryophyllales) based on molecular and morphological data**

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# Disintegrating Portulacaceae: a new familial classification of the suborder Portulacineae (Caryophyllales) based on molecular and morphological data

## Abstract

Traditional classifications of the suborder Portulacineae recognize six families: Basellaceae, Cactaceae, Didiereaceae, Halophytaceae, Hectorellaceae, and Portulacaceae. However, phylogenetic analyses based on molecular sequence data indicate that the traditional family Portulacaceae is paraphyletic and consists of three distinct lineages that also include Cactaceae, Didiereaceae, and Hectorellaceae. We use sequence data from the chloroplast genes *matK* and *ndhF* representing 64 species of Portulacineae and outgroups to reconstruct their phylogenetic relationships with Bayesian and maximum parsimony inference methods. Evidence from these molecular phylogenetic analyses as well as from comparative morphological investigations allow us to propose a revised familial classification of the suborder Portulacineae. We recognize eight monophyletic families: Anacampserotaceae (*Anacampseros*, *Grahamia*, *Talinopsis*), Basellaceae, Cactaceae, Didiereaceae (incl. *Calyptrotheca*, *Ceraria*, *Portulacaria*), Halophytaceae, Montiaceae (incl. *Hectorellaceae*, *Calandrinia*, *Cistanthe*, *Claytonia*, *Lewisia*, *Montia*, *Phemeranthus*), Portulacaceae (*Portulaca* only), and Talinaceae (*Amphipetalum*, *Talinella*, *Talinum*). We provide a synopsis for this revised family classification with an identification key mainly based on habit and fruit characters, and family diagnoses with information on distribution, taxonomic diversity, and a brief discussion on phylogenetics and classification.

# Disintegrating Portulacaceae: A new familial classification of the suborder Portulacineae (Caryophyllales) based on molecular and morphological data

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**Abstract** Traditional classifications of the suborder Portulacineae recognize six families: Basellaceae, Cactaceae, Didiereaceae, Halophytaceae, Hectorellaceae, and Portulacaceae. However, phylogenetic analyses based on molecular sequence data indicate that the traditional family Portulacaceae is paraphyletic and consists of three distinct lineages that also include Cactaceae, Didiereaceae, and Hectorellaceae. We use sequence data from the chloroplast genes *matK* and *ndhF* representing 64 species of Portulacineae and outgroups to reconstruct their phylogenetic relationships with Bayesian and maximum parsimony inference methods. Evidence from these molecular phylogenetic analyses as well as from comparative morphological investigations allow us to propose a revised familial classification of the suborder Portulacineae. We recognize eight monophyletic families: Anacampserotaceae (*Anacampseros*, *Grahamia*, *Talinopsis*), Basellaceae, Cactaceae, Didiereaceae (incl. *Calyptrotheca*, *Ceraria*, *Portulacaria*), Halophytaceae, Montiaceae (incl. Hectorellaceae, *Calandrinia*, *Cistanthe*, *Claytonia*, *Lewisia*, *Montia*, *PheMERanthus*), Portulacaceae (*Portulaca* only), and Talinaceae (*Amphipetalum*, *Talinella*, *Talinum*). We provide a synopsis for this revised family classification with an identification key mainly based on habit and fruit characters, and family diagnoses with information on distribution, taxonomic diversity, and a brief discussion on phylogenetics and classification.

**Keywords** Anacampserotaceae; description; familial classification; molecular phylogenetics; Montiaceae; Portulacaceae; Talinaceae

## ■ INTRODUCTION

Molecular sequence techniques and rigorous analytical methods have had a profound impact on the higher classification of flowering plants (e.g., Soltis & al., 2005; Judd & al., 2007). Recently, a well-supported clade consisting of the families Basellaceae, Cactaceae, Didiereaceae, Halophytaceae, Hectorellaceae, and Portulacaceae was identified on the basis of several molecular systematic studies (Hershkovitz & Zimmer, 1997; Applequist & Wallace, 2001; Cuénoud & al., 2002; Hilu & al., 2003; Müller & Borsch, 2005; Applequist & al., 2006; Nyffeler, 2007). This monophyletic group largely corresponds to the suborder Portulacineae as originally proposed by Engler (1898) and recently recognized by Thorne (1976, 2000 [as Cactineae]) and Takhtajan (1997). Furthermore, these molecular studies indicate that the traditional family Portulacaceae consists of three distinct lineages of which one includes Cactaceae (e.g., Hershkovitz & Zimmer, 1997; Nyffeler, 2007), one includes Didiereaceae (Applequist & Wallace, 2001, 2003), and one includes Hectorellaceae (Applequist & al., 2006; Wagstaff & Hennion, 2007). Basellaceae and the monotypic Halophytaceae represent two additional major lineages of suborder Portulacineae (Cuénoud & al., 2002; Müller & Borsch, 2005). The circumscription of Portulacineae previously received support from studies in palynology (Nowicke, 1996) and wood anatomy (Carlquist, 1997).

The family Portulacaceae was first established by Adanson (1763) and was later taken up by de Jussieu (1789), to whom

the name must be ascribed under *ICBN* Art. 13.1(1) (McNeill & al., 2006). Adanson included a total of 34 genera belonging to more than 20 currently recognized families, including Portulacaceae, Aizoaceae, and Cactaceae, and the unrelated Begoniaceae, Cuscutaceae, Saxifragaceae, Theophrastaceae, and Turneraceae. De Jussieu (1789) provided a considerably narrower circumscription of the family Portulacaceae (as ‘Portulaceae’) and placed it between Cactaceae (as ‘Cacti’) and Aizoaceae (as ‘Ficoideae’). Floral characters such as petal number and arrangement, ovary position, and fruit morphology were used by him to differentiate Portulacaceae from their allies. He included the genera *Portulaca* L., *Talinum* Adans., *Montia* L., and *Claytonia* L. along with some genera currently placed in Aizoaceae, Caryophyllaceae, Gisekiaceae, and Molluginaceae and the unrelated families Plantaginaceae sensu lato (s.l.), Tamaricaceae, and Turneraceae.

For more than two hundred years the circumscription of Portulacaceae was debated, modified, and adjusted up to the most recent treatment by Carolin (1993). Portulacaceae, as traditionally (i.e., in the sense of Carolin, 1993) understood, comprise 30 genera and about 450 species, mainly characterized by the presence of two sepals, often five fastly withering petals, and capsular fruits consisting of usually three fused carpels. This suite of characters is primarily responsible for the traditional circumscription of Portulacaceae remaining unchallenged for so long (e.g., Cronquist, 1981; Carolin, 1993; Takhtajan, 1997, 2009). The claim that Portulacaceae are “a very natural and easily recognized family” (Brummitt, 2002:

36) reflects the selective characterization of this taxon mainly by sustaining an established tradition. Basellaceae (Sperling & Bittrich, 1993) and the traditional Didiereaceae (Kubitzki, 1993) also have flowers with two sepals very similar to those of Portulacaceae, but have been maintained as distinct families mainly based on their twining or cactus-like xerophytic habit. Furthermore, a critical comparative evaluation of all relevant taxa of Portulacineae for different morphological and anatomical characters was hampered by the very distinctive nature of the family Cactaceae. For decades, this family was retained in a separate monofamilial order allied with Parietales (e.g., Engler, 1925) or Cucurbitales (e.g., Hutchinson, 1973), respectively, despite solid contrasting arguments (e.g., de Candolle, 1828; Schumann, 1899; Chorinsky, 1931). Only recently, the family Cactaceae was considered for comparative investigations of the closely related families now included in Portulacineae (e.g., Hershkovitz, 1993).

Starting very early, two different concepts of the family Portulacaceae were proposed: (1) a narrower concept favored by de Candolle (1828) and Bartling (1830) that includes genera of current Portulacaceae and Basellaceae, and (2) a much broader concept proposed by Fenzl (1836, 1839), and supported by Endlicher (1840) and Baillon (1886a), that in addition includes also some genera of current Aizoaceae, Caryophyllaceae, and Molluginaceae. Later, the treatments by Pax (1889) and Pax & Hoffmann (1934), that adhered to the narrower concept as outlined by Bentham (1862a,b), brought along a consensus to recognize Portulacaceae with its narrower circumscription. Franz (1908), based on comparative morphological and anatomical investigations of various characters (i.e., inflorescences, flowers, fruits, and pollen as well as stem vasculature and stomata), argued to retain the genera of Basellaceae in Portulacaceae. In contrast, Pax (1889) and Pax & Hoffmann (1934) excluded them and placed them in their own family. Furthermore, while Pax (1889) placed *Hectorella* Hook. f. in Portulacaceae, Pax & Hoffmann (1934) included it in Caryophyllaceae along with the closely related genus *Lyallia* Hook. f. During the past few decades, separate families (e.g., Halophytaceae, Hectorellaceae) were recognized for taxa with ambiguous or unresolved relationships (e.g., Dahlgren, 1980; Kubitzki & al., 1993; Takhtajan, 1997; Thorne, 2000). Only Cronquist (1981) and Cronquist & Thorne (1994) opted to retain *Hectorella* and *Lyallia* in Portulacaceae and *Halophytum* Sp. in Chenopodiaceae. On the other hand, recent molecular phylogenetic studies provided ample evidence that the genera *Dendroportulaca* Egli and *Pleuropetalum* Hook. f., which were originally included in Portulacaceae (Hooker, 1846; Egli, 2002), are representatives of Amaranthaceae (Applequist & Pratt, 2005; Müller & Borsch, 2005). Furthermore, similar studies confirm that *Talinella* Baill. unambiguously belongs in Portulacaceae (e.g., Hershkovitz & Zimmer, 1997; Applequist & Wallace, 2001; Nyffeler, 2007), despite its unique fruit type (mucilaginous berry rather than dry capsule). On the other hand, *Calyptrorhiza* Gilg, first described as a member of Caparaceae, was subsequently included in Portulacaceae and is currently included in an expanded concept of Didiereaceae (Applequist & Wallace, 2001, 2003).

The first infrafamilial classification of traditional Portulacaceae was proposed by Franz (1908). He recognized two subfamilies, one of which was divided into two tribes and four subtribes using morphological features (i.e., pollen morphology, form of the ovary base, number of carpels, number of ovules, micropyle orientation, and number of sepaloid organs). Pax & Hoffmann (1934) only slightly modified this classification by recognizing the tribe Baselleae of subfamily Montioideae as a separate family, and by treating the genera *Ceraria* Pearson & Stephens, *Portulacaria* Jacq., and *Philippiamra* Kuntze as “intermediate between Portulacaceae and Basellaceae” (Pax & Hoffmann, 1934: 244). More recently, infrafamilial classifications by McNeill (1974), Carolin (1987, 1993), and Nyananyo (1990) recognized either seven, five or four, and eight tribes, respectively (for details see table 1 in Applequist & Wallace, 2001). The number of recognized genera ranges from 17 (Nyananyo, 1990) or 18 (McNeill, 1974) up to 28 or 29 (Carolin, 1987, 1993). These observations clearly indicate the widely differing views on the relationships among the taxa of Portulacaceae and their circumscriptions.

Evidence is growing that the traditional, vaguely characterized family Portulacaceae represents an assembly of different evolutionary lineages (e.g., Bittrich, 1993a; Hershkovitz & Zimmer, 1997; Applequist & Wallace, 2001; Cuénoud & al., 2002; Nyffeler, 2007), and this is the main rationale for the present study. Available data from molecular phylogenetic investigations and from comparative investigations of morphological characters allow us to propose a revised classification of the suborder Portulacineae. We suggest a recircumscription of the family Portulacaceae and the recognition of three additional families that are either new or have not been recently used. The objectives of the present study are (1) to present a molecular phylogenetic analysis of Portulacineae based on the cpDNA markers *matK* and *ndhF* from a representative sample of individuals, (2) to transform the inferred relationships into a hierarchical classification of monophyletic families, and (3) to provide a concise taxonomic treatment of all families recognized in Portulacineae. We chose to use a ‘supermatrix’ approach (de Queiroz & Gatesy, 2006) by relying primarily on the *ndhF* data to provide information on the core relationships and by further resolving relationships towards the tips with a more densely sampled *matK* dataset.

## ■ MATERIALS AND METHODS

**Taxon sampling and markers.** — In our analysis of suborder Portulacineae we included 59 representatives of the traditional families Basellaceae, Cactaceae, Didiereaceae, Halophytaceae, Hectorellaceae, and Portulacaceae. These ingroup taxa were carefully selected from published sequences in order to fully represent the taxonomic diversity of the study group. Furthermore, we included five samples from the families Aizoaceae, Molluginaceae, Nyctaginaceae, and Phytolaccaceae as outgroups. Overall, 53 sequences of *matK* and 37 sequences of *ndhF* from previously published studies (Olmstead & al., 2000; Applequist & Wallace, 2001;

Cuénoud & al., 2002; Nyffeler, 2002, 2007; Edwards & al., 2005; Müller & Borsch, 2005; Applequist & al., 2006) were obtained from GenBank (<http://www.ncbi.nlm.nih.gov/>) and seven *matK* sequences were newly generated. Four species of *Talinum* (incl. *Phemeranthus* Raf.) were newly added in order to address the recent observation that this genus, as traditionally circumscribed, might be polyphyletic (Hershkovitz & Zimmer, 1997; Applequist & Wallace, 2001; Ferguson, 2001). Two species of *Portulaca* were also added to the present study to increase the taxon sampling of this species-rich lineage. Finally, the sampling of Cactaceae subfamily Opuntioideae was expanded by sequencing *Maihueniopsis subterranea* (R.E. Fr.) E.F. Anderson.

#### DNA extraction, PCR amplification and sequencing.

— Total DNA was extracted from silica gel–dried stem or leaf material using the DNeasy Plant Mini Kit (Qiagen Corp.). External primers trnK-3914F and trnK-2R were used for amplification of *trnK/matK* (Johnson & Soltis, 1994). The 20- $\mu$ l PCR reactions contained 10 mM Tris-HCl, 50 mM KCl, 2.5 mM MgCl<sub>2</sub>, 0.2 mM of each dNTP, 0.4 mM of each primer, and 0.8 units of AmpliTaq polymerase (Perkin-Elmer Applied Biosystems). The PCR temperature profile for the reactions was 95°C for 5 min, then 35 cycles of 94°C for 30 s, 48°C for 60 s, 72°C for 90 s, followed by a final extension of 72°C for 5 min. Double-stranded PCR products were cleaned using QIAquick columns (Qiagen Corp.) and directly sequenced for the *matK* gene using the internal primers trnK-23F, trnK-41R, trnK-44F, trnK-52F, and trnK-71R (Nyffeler, 2002). The products were cleaned with Microspin G-50 (Amersham Pharmacia Biotech) using multiscreen plates to remove excess Big Dye Terminator before loading on the automated sequencer ABI PRISM 3100 Genetic Analyzer (Perkin-Elmer Applied Biosystems). All seven newly created *matK* sequences were checked and assembled using the software Sequencher v.4.2 (Gene Codes Corporation, 2000) and are available from GenBank (Accession numbers EU834746–EU834752; see Appendix 1).

**Phylogenetic analyses.** — For 29 out of the 64 representatives only one of the two cpDNA markers were available (see Appendix 1). Combining sequences of several different molecular markers into a combined matrix, in particular if they are derived from the same genome, is widely used today (e.g., de Queiroz & Gatesy, 2006). Furthermore, the issue of missing data is no longer regarded as a major problem when dealing with incompletely coded taxa (Kearny, 2002) if “there are sufficient characters in one broadly sampled dataset to allow the position of these taxa to be resolved” (Wiens, 2003: 536). Alignment of the two partitions was done by eye and these were combined into a single matrix. Only very few informative indels were located, and therefore not further considered. We conducted maximum parsimony (MP) and Bayesian inference (BI) analyses using PAUP\* v.4.0b10 (Swofford, 2002) and MrBayes v.3.1.1 (Huelsenbeck & Ronquist, 2001). The parsimony analysis was based on 100,000 heuristic search replicates using random taxon addition and TBR branch swapping with MULTREES on. Bootstrap support values were calculated using 10,000 replicates, each with simple taxon addition and MAXTREES set to 1000. We also conducted individual

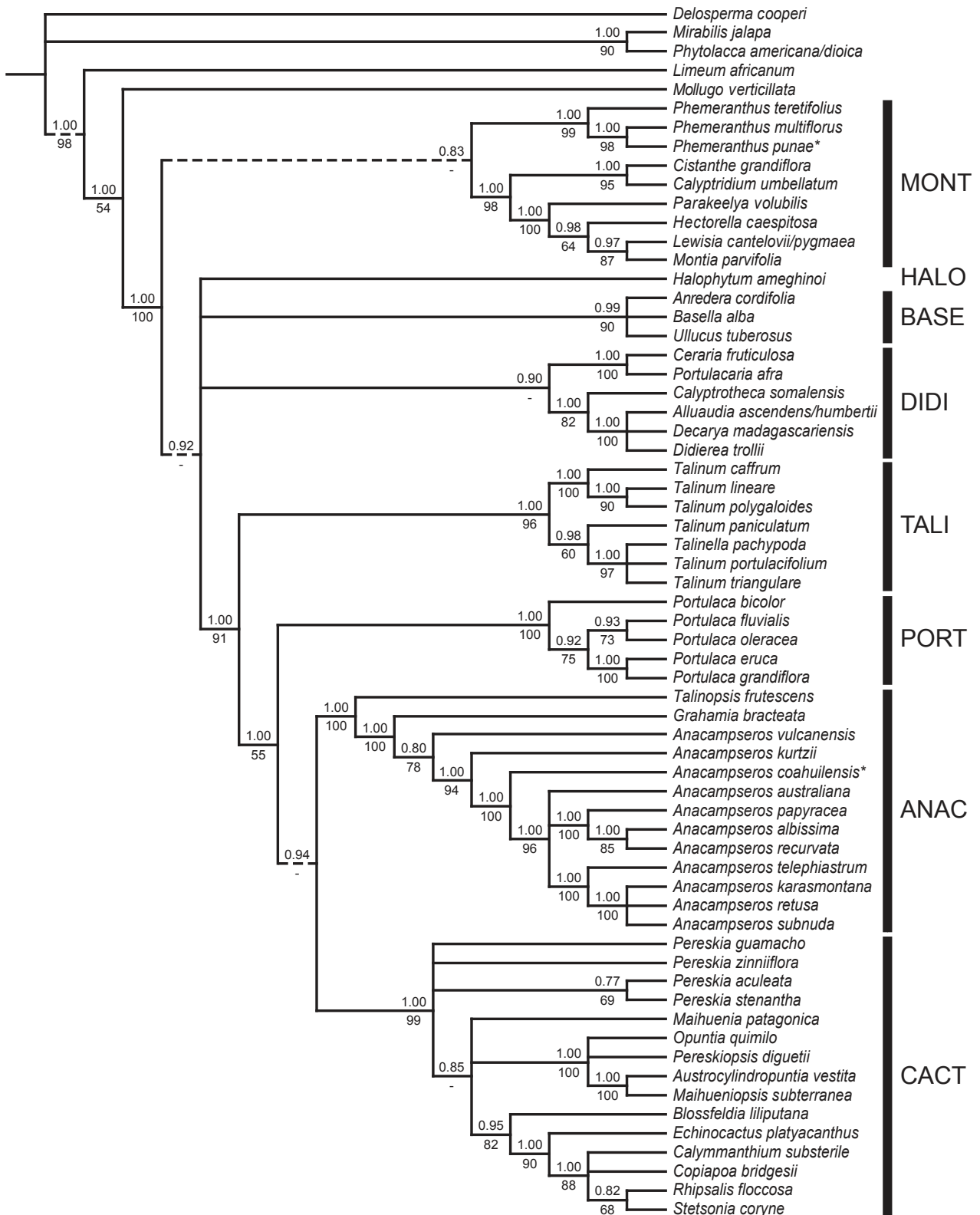
analyses of the *matK* and *ndhF* datasets comprising 60 and 37 samples, respectively. Then, we compared the topologies of the two majority-rule consensus trees from the bootstrap analyses for possible incongruence and sampling effects.

The Bayesian inference analysis was performed on the combined dataset, allowing model parameters to be independently estimated for the two partitions. We used MrModeltest v.2.2 (Nylander, 2004) to identify the best available model of molecular evolution where the Akaike information criterion favored the GTR+G+I model for both partitions. We conducted three independent Markov chain Monte Carlo runs, each consisting of four linked chains with standard settings that were run for five million generations (sampling every 100 generations). The burn-in was set to 500,000 generations, after comparing plots of log-likelihood values against generation time across independent runs. Furthermore, topologies derived from the three majority rule consensus trees and clade posterior probabilities were compared to check for good mixing during the BI analysis. The 135,003 post-burn-in trees of the three independent runs were then combined into a single majority rule consensus phylogram using the SUMT command, which also estimated the branch lengths. The aligned data matrix and the majority rule consensus tree of the Bayesian inference analysis are available at TreeBase (<http://www.treebase.org/>; study accession number = S2283, matrix accession number = S2283).

## RESULTS

**Dataset.** — The aligned matrix of the combined *matK* and *ndhF* dataset comprises 3706 characters, of which 2306 are constant, 632 are variable but parsimony uninformative, and 768 are parsimony informative. Overall, the average percentage of missing characters for the combined dataset is 33.4% (nucleotides in gaps of the aligned matrix not considered). In the *matK* data partition (1563 characters aligned) 16.4% of nucleotides are missing, while in the *ndhF* partition (2143 characters aligned) 45.9% of nucleotides are missing.

**Parsimony analysis.** — The MP analysis of the combined dataset yielded 98,559 most parsimonious trees (length = 2852; consistency index, CI = 0.656; retention index, RI = 0.704; RI excluding uninformative characters = 0.539). The strict consensus tree, of which the topology largely corresponds to the majority rule consensus tree of the BI analysis (Fig. 1), resolves 45 clades, but does not provide unambiguous information for a sister-group relationship between ANAC (*Anacampseros* L., *Grahamia* Hook., *Talinopsis* A. Gray) and CACT (Cactaceae), nor for the monophyly of MONT (*Phemeranthus* as part of a clade including *Cistanthe* Spach, *Lewisia* Pursh, and *Montia*). Bootstrap support values are listed below the branches onto the majority-rule consensus tree derived from the BI analysis (Fig. 1). The bootstrap majority-rule consensus trees of the individual analyses identified almost all highly supported clades that are also present in the combined analysis, and did not yield any incongruence in the topologies and underlying datasets.



**Fig. 1.** Majority rule consensus of 135,003 trees derived from a Bayesian inference (BI) analysis of the suborder Portulacineae. Dashed branches collapse in the strict consensus cladogram of the maximum parsimony (MP) analysis. Numbers above branches denote posterior probabilities of the BI analysis, numbers below branches indicate bootstrap values of the MP analysis. Eight distinct major clades are marked with character codes; we propose that they are recognized as the families Anacampteroaceae (ANAC), Basellaceae (BASE), Cactaceae (CACT), Didiereaceae (DIDI), Halophytaceae (HALO), Montiaceae (MONT), Portulacaceae (PORT), and Talinaceae (TALI). An asterisk marks new species combinations (see Appendix 2).

**Bayesian analysis.** — The three independent BI runs yielded similar topologies with minimal variation in clade posterior probabilities of the post-burn-in majority-rule consensus trees. The three individual tree pools were combined into one majority-rule consensus tree (Fig. 1). Posterior probability values for the different clades are given above the branches (Fig. 1). This consensus tree does not support a sister-group relationship of Basellaceae with Halophytaceae. In contrast, such a close relationship was indicated by the strict consensus of the MP analysis, though with less than 50% bootstrap support.

## ■ DISCUSSION

**Comparison with previous molecular phylogenetic studies.** — The present study is based on a combined analysis of the two molecular markers *matK* and *ndhF* from the chloroplast genome, which have been used most often so far to infer relationships within and among families of Portulacineae (Applequist & Wallace, 2001; Cunéoud & al., 2002; Applequist & al., 2006; Nyffeler, 2007). For the first time, this study provides a concise but well-balanced sampling of all eight major lineages of this suborder to infer their interrelationships and to recircumscribe all the families included. The resulting topology (Fig. 1) is congruent, for clades that receive reasonable statistical support, with previous studies relying on the same molecular markers (e.g., Applequist & Wallace, 2001; Applequist & al., 2006; Nyffeler, 2007). A major challenge remains to identify possible sister-group relationships among the eight major lineages identified here. So far we encounter the strongest support for a clade consisting of ANAC, CACT, PORT, and TALI (Fig. 1; ACPT clade of Nyffeler, 2007).

**Character interpretation.** — Floral envelope characters, in combination with aspects of the habit, have been used in the past for the circumscription of the family Portulacaceae (e.g., Carolin, 1993). In particular, the presence of two, often unequal sepaloid floral parts is commonly listed as a key character for Portulacaceae (e.g., Geesink & al., 1981; Cullen, 1997), even though it is not consistent nor unique. Many species of *Lewisia* have five to nine sepaloid elements, while the members of the traditionally segregated families Basellaceae and Didiereaceae also have two sepaloids. Furthermore, this character is inconsistently identified and termed either as ‘sepals’ (e.g., Geesink, 1969; Cronquist, 1981; Carolin, 1993), ‘sepaloid bracts’ (Legrand, 1949), ‘pseudosepals’ (Legrand, 1953), or ‘bracteoles’ (Zomlefer, 1995; Judd & al., 2007). Pax & Hoffmann (1934) were the first to recognize that these ‘sepals’ correspond to involucral bracts, and that the ‘petals’ are elements of a perigone. Already Payer (1857; cited in Friedrich, 1956) pointed out that Portulacaceae do not have ‘true’ petals. This interpretation is now widely recognized (see also Eckardt, 1976). Erbar & Leins (2006), in a study of Didiereaceae, suggest that this condition applies to all higher Caryophyllales.

Traditional Portulacaceae and related families show a wealth of different fruit types. Capsular fruits are prominent, either opening at the base or near the top by valves (e.g., *Anacamperos*, *Calandrinia* Kunth, *Calyptrotheca*, *Talinum*,

etc.) or by a circumscissile lid (i.e., *Amphipetalum* Bacigalupo, *Lewisia*, *Lewisiopsis* Govaerts, *Portulaca*). More rare are various forms of indehiscent nutlets (e.g., *Halophytum*, *Hectorella*, *Lyallia*, *Philippiamra*), which are in some cases enclosed by different parts of the floral envelope (e.g., *Ceraria*, *Portulacaria*, Basellaceae), and berries (*Talinella*). Furthermore, in *Halophytum* the one-seeded nutlets are deeply sunken into the inflorescence axis and form a slightly woody infructescence (Bittrich, 1993b). Most taxa have two to three carpels, though, one carpel is typical for *Ceraria* and *Portulacaria*, five to eight and up to a dozen for Cactaceae, *Lewisia*, and *Portulaca*.

Berry-like (baccate) fruits are considered diagnostic for *Talinella*, and are unique in the suborder Portulacineae. Applequist (2005: 50) reports, however, that thin-walled dry capsules apically dehiscent by shallow valves have been found in a single specimen, and argues that capsular fruits might be more common in the genus than reported so far. Moreover, young ovaries have in the past been described as having two or more distinct locules (Baillon, 1886b), which would be unique within the suborder. Anatomical studies are needed to corroborate or falsify this undocumented observation.

Seed characters have not been explored for many representatives of Portulacineae. However, various observations on testa architecture, embryo shape, and amounts of perisperm indicate a potential as informative characters for larger taxa. Furthermore, various types of fleshy or spongy appendages (e.g., aril, strophiola) are reported and should be investigated in more detail. The embryo is only slightly curved in *Anacamperoteae*, but reported to be strongly curved or annular in most other families of Portulacineae. Perisperm is generally copious, but scanty in Basellaceae (Sperling & Bittrich, 1993).

Conspicuous axillary outgrowths are characteristic for Cactaceae, Didiereoideae (= Didiereaceae sensu stricto [s.str.]; Applequist & Wallace, 2003), *Anacamperos*, and *Portulaca*. In the case of Cactaceae, the axillary outgrowth is termed an areole, and it conforms to a contracted short shoot (brachyblast) of which the leaves have been transformed into spines, and which usually also produces abundant trichomes. The architecture of the axillary outgrowths of Didiereoideae is similar. Their brachyblasts differ from cactus areoles in having a small and definite number of spines, and no associated trichomes (Rauh, 1956). The axillary outgrowths of *Anacamperos* and *Portulaca* have been regarded as modified stipules (de Candolle, 1827: 186; Pax, 1889; Schönland, 1903). Chorinsky (1931) has shown, however, that such a derivation is unlikely, and since stipules are absent from all Portulacineae (Geesink, 1969), this interpretation can be dismissed. Chorinsky (1931) found that the axillary outgrowths of *Anacamperos* and the hairs and bristles of cacti are basically similar in nature, while Gerbault (1992: 489) stresses that the outgrowths of *Anacamperos* and *Portulaca* are homologous, but without reaching a conclusion about their possible anatomical derivation. Geesink (1969), based on the data presented by Chorinsky (1931), concluded that the axillary hairs and bristles of *Portulaca* are clearly derived from the axillary meristem of the foliage leaves. Recently, Ogburn (2007) identified proleptic leaves in the axils of *Talinum* s.str.



and noted that they are products of the axillary buds. It is therefore tempting to suggest that the axillary outgrowths of *Anacampseros*, *Portulaca*, and probably also *Talinum*, are the only remnants of a highly condensed axillary short shoot, and are thus homologous to the areoles of cacti, and hence, represent a potential synapomorphy for a large subclade of Portulacineae that also receives high statistical support from molecular phylogenetic analyses. Similar areolar structures are also present in Didiereaceae, indicating a possible close relationship with the ACPT clade (Nyffeler, 2007).

**Revised family classification.** — The present phylogenetic analysis of suborder Portulacineae identifies eight major lineages that are with the exception of the two clades DIDI and MONT (Fig. 1), well supported. However, only the clades BASE, CACT, and HALO correspond to traditionally circumscribed families, viz., Basellaceae, Cactaceae, and Halophytaceae, respectively. Members of Portulacaceae in a traditional sense are found to be part of the clades ANAC, DIDI (incl. Didiereaceae), MONT (incl. Hectorellaceae), PORT, and TALI. These findings, in particular in combination with morphological considerations (see below), lead us to propose the following families in the suborder Portulacineae: Anacampserotaceae, fam. nov. (ANAC; Fig. 1), Basellaceae (BASE), Cactaceae (CACT), Didiereaceae (DIDI), Halophytaceae (HALO), Montiaceae (MONT), Portulacaceae (PORT), and Talinaceae (TALI).

**Nomenclatural note on the name Portulacineae.** —

The suborder name Portulacineae was published by Engler (1898) in the second edition of his *Syllabus der Pflanzenfamilien*. It is predated by the suborder name Cactineae, published by Bessey (1895) in the eighth volume of *Johnson's Universal Cyclopaedia*. Since priority does not apply at ranks above family based on ICBN Art. 11.10 (McNeill & al., 2006), we disregard Recommendation 16B of the ICBN (McNeill & al., 2006), and continue to use the more familiar name Portulacineae (i.e., Nowicke, 1996; Carlquist, 1997; Nyffeler, 2007; Nyffeler & al., 2008; Ogburn & Edwards, 2009), which also more aptly circumscribes the taxon that includes all major lineages previously referred to traditional Portulacaceae.

■ **SYNOPSIS OF FAMILIES OF PORTULACINEAE**

Here, we provide a synopsis of the eight monophyletic families to be recognized in the suborder Portulacineae. The artificial key to the families is largely based on fruit and habit characteristics. Further comparative studies that include all relevant taxa will certainly make additional distinctive characteristics available.

**Key to the families of Portulacineae**

1. Fruits dry capsules, utricles, or nutlets . . . . . 2
1. Fruits fleshy berries (rarely dry and irregularly dehiscent at maturity). . . . . 11
2. Fruits aggregated into a dry infructescence; flowers unisexual, wind-pollinated . . . . . **Halophytaceae**

2. Fruits discrete, not aggregated into an infructescence; flowers animal-pollinated . . . . . 3
3. Fruits indehiscent (i.e., utricles or nutlets). . . . . 4
3. Fruits dehiscent (i.e., capsules) . . . . . 6
4. Shrubs to trees, usually stem-succulent, often with spines . . . . . **Didiereaceae** p.p.
4. Plants herbaceous to suffruticose, spineless . . . . . 5
5. Stems well-developed, usually herbaceous and semi-succulent, trailing to scandent and vine-like; inflorescences dichasia, spikes, racemes, or panicles; fruits enveloped in dry to fleshy perianth remains. . . . . **Basellaceae**
5. Stems contracted or well-developed, hardly succulent but stiff; inflorescences cymose, usually condensed; fruits enveloped in dry perianth remains . . . . **Montiaceae** p.p.
6. Fruit dehiscence circumscissile, top portion shed intact as a lid (operculum) . . . . . **Portulacaceae** s.str.
6. Fruit dehiscence variable but valvate, without true operculum . . . . . 7
7. Exocarp and endocarp not separating . . . . . 8
7. Exocarp and endocarp separating . . . . . 10
8. Fruit dehiscence valvate starting at the top. . . . . **Montiaceae** p.p.
8. Fruit dehiscence circumscissile at the base and splitting upwards into valves in the upper part . . . . . 9
9. Sparsely branched shrubs . . **Didiereaceae** (*Calypthrothea*)
9. Herbs with a basal sessile rosette of succulent leaves . . . . . **Montiaceae** (*Lewisia*)
10. Fruit dehiscence basal; seeds usually black and glossy, with a strophiole; embryo curved . . . . **Talinaceae** (*Talinum*)
10. Fruit dehiscence apical; seeds usually pale, without strophiole; embryo rather straight. . . . . **Anacampserotaceae**
11. Sarmentose lianoid shrubs; spines absent; flowers small, with 2–5 petaloids . . . . . **Talinaceae** (*Talinella*)
11. Usually spiny stem-succulents with mostly very reduced leaves; flowers usually showy, with 5 to many petaloids in a graded series . . . . . **Cactaceae**

**Anacampserotaceae** Eggl & Nyffeler, **fam. nov.** – Type: *Anacampseros* L., Opera Var.: 232. 1758.

Herbae vel suffrutices succulentae perennes axillis foliorum pilis axillaribus vel squamis albis foliis obtegentibus instructis; flores tricarPELLATI; fructi capsulae elaboratae partes exocarpi et endocarpi separandae, partes exocarpi caducis; seminis pelliculis siccis pallidis instructae.

Small shrubs to thick-stemmed perennial herbs, mucilaginous (except *Grahamia*), sometimes with a basal fleshy caudex or tuberous main root; leaves spiral, succulent to very succulent, terete to globose, rarely flattened, glabrous or tomentose; axils with hairs, bristles, or a pergamentaceous scale (*Anacampseros* sect. *Avonia* (Fenzl) Gerbault); inflorescence lateral or terminal few-flowered thyrsoids, sometimes with contracted internodes, sometimes with scorpioid partial inflorescences; flowers small to medium-sized, bisexual, usually showy; sepaloids 2, fleshy, persistent and becoming dry in fruit; petaloids 5; stamens 5–25; ovary superior, of 3 united carpels; calyptra formed by the perianth remains and stamens persistent at fruiting stage (*Grahamia*, *Talinopsis*) or deciduous

as an entity (*Anacampseros*); fruits loculicidally dehiscent capsules with the caducous exocarp separating from the endocarp (except *Grahamia*, Gerbault, 1992: 506; Hershkovitz, 1993), and the endocarp valves forming a small basket; seeds usually somewhat angular and voluminous, usually pale-colored to white, without strophiola or elaiosome, testa two-layered, the outer testa layer usually partially or almost completely separating from the inner layer of the seed; embryo parallel to the perisperm and rather straight (Franz, 1908; Kowal, 1961).

*Distribution.* – Southern and eastern Africa, Australia, Argentina, Bolivia, Mexico, United States.

*Genera and number of species.* – *Anacampseros* L. (ca. 34 species; incl. *Avonia* (Fenzl) G.D. Rowley, incl. *Talinaria* Brandegee, incl. *Xenia* Gerbault); *Grahamia* Hook. (1 species); *Talinopsis* A. Gray (1 species).

*Important taxonomic literature.* – Gerbault (1992 – monograph *Anacampseros*), Rowley (1994, 1995 – illustrated synopses).

*Discussion.* – Anacampserotaceae are easily recognized by the combination of elaborate fruits and pale-colored seeds with the outer testa layer becoming separate from the inner layer. The more derived representatives are found in Australia and arid southern and eastern Africa, while the species of the basal grade occur in North and South America. The migration between the continents was accompanied by the evolution of specialized diminutive leaf-succulent life forms (Nyffeler, 2007).

We propose, on the basis of our molecular phylogenetic analyses and previous morphological investigations (Nyffeler, 2007), that the genus *Anacampseros* is recircumscribed to include all dwarf herbaceous species with rosulate leaf arrangement, including *Talinaria coahuilensis* (S. Watson) P. Wilson and *Xenia vulcanensis* (Añón) Gerbault. We retain the monotypic genera *Grahamia* and *Talinopsis* for the two species from North and South America that form woody subshrubs with distinct internodes (Nyffeler, 2007). The new combination required for the former *Talinaria* species is provided in Appendix 2.

**Basellaceae** Raf., Fl. Tellur. 3: 44. 1837 (nom. cons.) – Type: *Basella* L.

Vines or trailing herbs, usually glabrous, slightly to distinctly fleshy, mucilaginous, sometimes with tuberous roots; leaves alternate to subopposite at the stem base; inflorescences axillary or terminal spikes, racemes, panicles, or dichasia; flowers bisexual (functionally unisexual in *Anredera vesicaria* (Lam.) C.F. Gaert.), rather small and inconspicuous, sometimes cleistogamous; sepaloids two, free or partly united, sometimes hardly different from the petaloids; petaloids (4–)5(–13), connate only at the base to more than half their length, sometimes becoming black in fruit; stamens (4–)5(–9), basally connate and adnate to the petaloids; ovary superior, consisting of three united carpels, with a single basal ovule; fruits thin-walled nutlets surrounded by the dry or fleshy perianth remains.

*Distribution.* – Tropics and subtropics of the New World, few species in Africa and Madagascar, one species pantropical due to cultivation.

*Genera and number of species.* – *Anredera* Juss. (ca. 12 species; incl. *Boussingaultia* Kunth); *Basella* L. (5 species); *Tourneria* Moq. (1 species); *Ullucus* Caldas (1 species).

*Important taxonomic literature.* – Eriksson (2007 – synopsis), Sperling (1987 – family monograph), Sperling & Bittrich (1993 – synopsis).

*Discussion.* – Basellaceae are well-characterized by the combination of a subsucculent to herbaceous, trailing to scandent, vine-like growth form, often spicate inflorescences with small, pale-colored flowers, and nutlets or drupes with one seed enclosed by the perianth remains.

**Cactaceae** Juss., Gen. Pl.: 310. 1789 (nom. cons.) – Type: *Cactus* L. (nom. rejic. ≡ *Mammillaria* Haw., nom. cons.).

Perennial trees to shrubs, or dwarfs, usually stem succulent and mucilaginous; roots fibrous, rarely tuberous; foliage leaves usually absent (but present as minute microscopical vestiges; Mauseth, 2007) or present, if present either flat and weakly to distinctly fleshy (*Pereskia*), or terete, then either persistent for a vegetation period (*Maihuenia*) or early caducous and only present on young growth (Opuntioideae); axils developed into a spiniferous (rarely spineless) areole, usually with some wool or felt; flowers solitary (rarely several together or in succession) from the areoles, small to very large, usually showy, usually bisexual, usually actinomorphic, short- to long-lived, consisting of a pericarpel with some to many spiniferous or spineless areoles, a perianth tube of varying length and with few to many spiniferous or spineless areoles, and a usually graded series of perianth elements varying from scales to sepaloids to petaloids; stamens usually numerous, inserted in one or two distinct series, or over the length of the perianth tube; ovary inferior (superior or semi-inferior in *Pereskia*), included in the pericarpel, composed of up to ten and more carpels, unilocular with numerous ovules; fruit normally a fleshy to juicy berry, rarely spontaneously dehiscent capsules (e.g., *Copiapoa*) or slowly weathering over time (e.g., *Tephrocactus*); seeds variable, often with diagnostic color and testa cells, sometimes with a conspicuous spongy hilum-micropyle region (Cactoideae) or completely enveloped into a hard bony aril (Opuntioideae); embryo strongly curved around the perisperm to almost straight.

*Distribution.* – North and South America (southern Canada to South-Central Argentina and South Chile) and 1 species (*Rhipsalis baccifera* (J.S. Muell.) Stearn) also in Africa, Madagascar, Sri Lanka and various islands of the Indian Ocean.

*Number of genera and species.* – 126 genera and ca. 1900 species (Anderson, 2001, 2005); 124 genera and 1438 species (Hunt, 2006). Refer to these two sources for recent, slightly contrasting lexicographic treatments of the family.

*Important taxonomic literature.* – Anderson (2001 – lexicon; 2005 – updated lexicon), Barthlott & Hunt (1993 – synopsis; 2000 – seed atlas), Butterworth & al. (2002 – phylogeny), Buxbaum (1950 – morphology), Endler & Buxbaum (1973 – classification), Hunt (1967 – classification; 2006 – lexicon), Leuenberger (1976 – palynology), Mauseth (2006 – morphology, anatomy), Stuppy (2002 – synopsis Opuntioideae).

*Discussion.* – All members of Cactaceae are immediately recognized on account of the usually spine-bearing areoles, the

wide-spread stem-succulence in conjunction with the lack of foliage leaves, and the flower morphology involving a pericarp formed by stem tissue with areoles, and a graded series of perianth elements. Cacti are a very prominent group of stem succulents, and it is often thought that this applies to the whole family. However, succulence is only vaguely present in the cladistically most basal and paraphyletic genus *Pereskia* Mill. (Edwards & al., 2005), and has been lost again to a large degree in highly specialized epiphytes such as *Rhipsalis* Gaertn., *Disocactus* Lindl. p.p. or *Epiphyllum* Haw. p.p.

A concise overview of the suprageneric classification of Cactaceae is found in Anderson (2001, 2005). The traditional division of the family into the three subfamilies Pereskioideae, Opuntioideae and Cactoideae dates back to Schumann (1897–1898). Maihuenioideae were recently erected for the single genus *Maihuenia* Phil. (Fearn, 1996).

**Didiereaceae** Radlk. in Engler & Prantl, Nat. Pflanzenfam. 3(5): 462. 1896 – Type: *Didierea* Baill.

Slightly stem-succulent trees or shrubs, sometimes with spines (Didiereoideae), medulla and cortex with mucilage ducts and older stems with conspicuous tannin deposits (Didiereoideae and Portulacarioideae, unknown for *Calyptrotheca*); leaves deciduous, leathery to succulent, flat to terete; axillary buds of primary leaves developing into short spur-shoots (*Calyptrotheca*), or as contracted short-shoots producing only leaves or spines and leaves; inflorescences panicles to cymes, often fasciculate, often many-flowered, or flowers in small groups; flowers regular, unisexual (but rudiments of the opposite sex present) on dioecious or gynodioecious (some *Ceraria*; Swanepoel, 2007) plants, or bisexual (*Calyptrotheca*, *Portulacaria*), minute to small (or large and showy in *Calyptrotheca* and *Alluaudiopsis marnieriana* Rauh); sepals 2, persistent and dry at fruiting time (except *Calyptrotheca*); petals 4 or 5; stamens (4–)5–12 (up to 60 in *Calyptrotheca*); ovary superior, formed by (2–)3(–4) united carpels, ovule 1 or up to 6 (*Calyptrotheca*), basal; fruits 1-seeded indehiscent nutlets enclosed by dry bracts (Didiereoideae), indehiscent dry or slightly fleshy nutlets with membranous wings (Portulacarioideae), or basally circumscissile, 6-valved, 1- (rarely 2-) seeded capsules (*Calyptrotheca*); seeds with a small funicular strophiole or an aril; embryo strongly curved around the perisperm.

*Distribution.* – Southern and eastern Africa, Madagascar.

*Genera and number of species.* – *Alluaudia* (Drake) Drake (6 species), *Alluaudiopsis* Humbert & Choux (2 species), *Calyptrotheca* Gilg (2 species), *Ceraria* Pearson & Stephens (4–5 species), *Decarya* Choux (1 species), *Didierea* Baill. (2 species), *Portulacaria* Jacq. (2 species).

*Important taxonomic literature.* – Applequist & Wallace (2000 – molecular phylogeny; 2003 – expansion of family, infrafamilial classification), Kubitzki (1993 – synopsis), Nowicke (1996 – palynology), Rauh (1956 – morphology, anatomy; 1961 – growth form; 1963 – monograph), Rauh & Reznik (1961 – chemistry), Rauh & Schölch (1965 – lower morphology, embryology), Rowley (1992 – illustrated synopsis).

*Discussion.* – The systematic position of the Didiereaceae was enigmatic for a long time, and it was variously associated

with Euphorbiaceae or placed in Sapindales (e.g., Hutchinson, 1969). Its placement in core Caryophyllales was first suggested by Radlkofer (1896), and later confirmed by Rauh & Reznik (1961) based on the presence of betalains. Rauh (1961) and Rauh & Reznik (1961) stress the morphological and anatomical similarities (i.e., long and short shoot organization, short shoots as areoles, presence of oxalate druses and conspicuous mucilage idioblasts in the primary cortex) with Cactaceae. Hence, some authors (e.g., Rowley, 1992) refer to them as “cacti of the Old World”. Palynologically, the family is readily recognizable due to the 5–7-zonocolpate pollen with a finely spinate aperture, which is unique for the whole order (Nowicke, 1996).

As traditionally circumscribed, the family consisted only of the four Madagascan genera now included in subfamily Didiereoideae. Molecular studies by Applequist & Wallace (2001, 2003) and Nyffeler (2007) have shown that the two genera *Ceraria* and *Portulacaria*, traditionally placed in Portulacaceae s.l., are closely related to Didiereaceae s.str. and should be placed here. In addition, the genus *Calyptrotheca*, also formerly included in Portulacaceae, is part of this major lineage of Portulacineae too. These additions, and in particular *Calyptrotheca*, make Didiereaceae a rather heterogeneous assemblage as to gross vegetative morphology and floral characters. The presence of tannin deposits (no reports available for *Calyptrotheca*), otherwise only known for Talinaceae, is potentially diagnostic for this family.

**Halophytaceae** A. Soriano in Bol. Soc. Argent. Bot. 23: 161. 1984 – Type: *Halophytum* Speng.

Annual, glabrous, leaf-succulent monoecious herbs; leaves sessile, alternate, subterete with flattened upper face, without axillary elements, but occasionally fascicled on short shoots; flowers unisexual, small, usually with 2 (male flowers) or 2–4 (female flowers) bracts or bracteoles, female flowers 4–5 together in the axils of upper leaves, male flowers numerous, densely aggregated in a condensed spike-like inflorescence from the axils of the upper leaves; sepals none; petals none in female flowers, 4 in male flowers, membranous, whitish; stamens 4; ovary superior, 3-carpellate, unilocular, with 1 ovule; fruit a thin-walled, indehiscent, 1-seeded nutlet partly embedded into the axial tissue of the inflorescence, which as a whole becomes hard and forms a fusiform syncarp consisting of several nutlets; embryo annular.

*Distribution.* – Argentina.

*Genera and number of species.* – *Halophytum* Speng. (1 species only: *H. ameghinoi* Speng.).

*Important taxonomic literature.* – Bittrich (1993b – synopsis).

*Discussion.* – The phylogenetic relationships of this monotypic family remained unresolved for long, and it was either associated with Aizoaceae (esp. *Tetragonia* L.) or Chenopodiaceae. Ehrendorfer (1976: 102) placed it in Portulacaceae as a “more isolated derivative”, and Bittrich (1993b) associated the taxon with the ‘portulacoid’ group of families. In the present study *Halophytum* is found to be part of a polytomy that also includes Basellaceae, Didiereaceae and the ACPT clade. Cuboidal pollen and flowers, as well as fruits, embedded into

the floral axis are also found in Basellaceae (esp. *Basella excavata* Scott-Eliot). Further investigations are needed to clarify whether, indeed, *Halophytum* might share closer relationships with Basellaceae. Anemophily is unique in the whole suborder.

**Montiaceae** Raf. in Ann. Gén. Sci. Phys. 5: 349. 1820 – Type: *Montia* L. (incl. Hectorellaceae Philipson & Skipw. in Trans. Roy. Soc. New Zealand, Bot. 1: 31. 1961).

Perennial to annual herbs, frequently stemless, rarely subshrubs, very rarely semiaquatic (*Montia* spp.), sometimes with thickened roots and/or stems; leaves spiral, often in rosettes, commonly succulent, sometimes with clasping base, usually glabrous, leaf axils naked; inflorescences terminal or lateral, usually cymose, often scorpioid, or flower solitary and axillary, flowers sessile to pedicellate, bisexual (bisexual or unisexual in *Hectorella*), actinomorphic; sepals 2 or more (up to 9 in *Lewisia*), often persistent and dry at fruiting stage; petals 4 or 5 or up to 19 (*Lewisia*), usually free, sometimes basally connate; stamens as many as petals, or numerous (to 100); ovary superior, unilocular, consisting of 2–8 united carpels; fruits 2 to 3-valved capsules with usually persistent valves (deciduous in *Phemeranthus*), or basally circumscissile (*Lewisia*, *Lewisiopsis*), or 1-seeded utricles (indehiscent or tardily dehiscent in *Lenzia*, irregularly dehiscent or indehiscent in *Philippiamra*), or 1 to 2-seeded indehiscent capsules disintegrating with time (*Hectorella* and *Lyallia*), sometimes with a deciduous calyptra formed by the dry perianth remains and stamens; seeds often minutely papillate, with or without a strophiole or elaiosome, rarely with a thin-textured fleshy or chartaceous aril ('pellicle', *Phemeranthus*); embryo curved around the perisperm.

**Distribution.** – North and South America (predominantly western parts), northern Asia to northern Europe (circumboreal), Australia, New Zealand.

**Genera and number of species.** – *Calandrinia* Kunth (14 species; incl. *Monocosmia* Fenzl); *Calyptridium* Torr. & A. Gray (14 species; incl. *Spraguea* Torr.); *Cistanthe* Spach (20 species); *Claytonia* L. (27 species; incl. *Limnia* Haw.); *Hectorella* Hook. f. (1 species); *Lenzia* Phil. (1 species); *Lewisia* L. Pursh (16 species; incl. *Erocallis* Rydb., *Oreobroma* Howell); *Lewisiopsis* Govaerts (1 species); *Lyallia* Hook. f. (1 species); *Montia* L. (12 species; incl. *Claytoniella* Jurtzev, *Crunocallis* Rydb., *Limnalsine* Rydb., *Maxia* O. Nilsson, *Mona* O. Nilsson, *Montiastrum* Rydb., *Naiocrene* Rydb., *Neopaxia* O. Nilsson); *Montiopsis* Kuntze (40 species; incl. *Calandriniopsis* E. Franz); *Parakeelya* Hershk. (40 species); *Phemeranthus* Raf. (ca. 30 species); *Philippiamra* Kuntze (8 species; incl. *Diazia* Phil., *Silvaea* Phil.); *Schreiteria* Carolin (1 species).

**Important taxonomic literature.** – Applequist & al. (2006 – relationships of Hectorellaceae), Carolin (1993 – synopsis Portulacaceae), Davidson (2000 – monograph *Lewisia*), Heenan (1999 – monograph *Montia* p.p. [*Neopaxia*]), Hershkovitz (1991 – phylogeny Portulacaceae), Hershkovitz (1993 – phylogeny Portulacaceae), Hershkovitz (2006 – phylogeny Portulacaceae), Hershkovitz & Hogan (2003 – flora monograph *Lewisia*), Kiger (2003 – flora monograph *Phemeranthus*),

Mathew (1989 – monograph *Lewisia*), Miller & Chambers (2006 – monograph *Claytonia*), Philipson (1993 – Hectorellaceae synopsis), Wagstaff & Hennion (2007 – relationships of Hectorellaceae).

**Discussion.** – The genera included here (except for *Hectorella* and *Lyallia*, formerly Hectorellaceae), were previously placed in Portulacaceae (Carolin, 1993). The genera now placed in the family Montiaceae were previously dispersed among different tribes of Portulacaceae s.l. (see McNeill, 1974). However, the present circumscription was suggested by Hershkovitz (1993, 2006) and Hershkovitz & Zimmer (2000), as their informal “Western American Portulacaceae” subgroup, on the basis of vegetative morphology as well as molecular phylogeny analysis. The reestablishment of the genus *Phemeranthus* exemplifies very well the previous lack of solid knowledge to resolve issues in Portulacaceae classification: molecular phylogenetic investigations provide clear evidence that the traditional concept of *Talinum* is polyphyletic and consists of two distinct lineages; one (i.e., *Phemeranthus*) takes up a cladistically basal position in Montiaceae and the other (i.e., *Talinum* s.str.) forms the sister-group to a clade consisting of the families Anacampserotaceae, Cactaceae, and Portulacaceae s.str. (Hershkovitz & Zimmer, 1997; Applequist & Wallace, 2001). Differences in the morphology between the two clades (i.e., *Phemeranthus* and *Talinum* s.str.) were discussed by Ferguson (2001) and the necessary new combinations for the *Phemeranthus* species of North America have been published in the recent past (Hershkovitz & Zimmer, 1997; Kiger, 2001; Ocampo, 2002, 2003). However, so far no combination for *Phemeranthus* is available for the disjunct species *Talinum punae* (R.E. Fr.) Carolin from higher altitudes in northern Argentina. Our phylogenetic analysis (Fig. 1) supports its close relationships with North American *Phemeranthus* species, and the necessary new combination is provided in Appendix 2. Morphologically, *P. punae* groups with other *Phemeranthus* species on account of the terete leaves and the scapose, richly branched inflorescence.

The family Montiaceae is by far the most diverse group within Portulacineae. A predominance of herbaceous plants with weakly expressed succulence is notable, and some genera (e.g., *Montiopsis*, *Lenzia*, *Hectorella*, *Lyallia*) can hardly be termed succulent at all. The placement of the monotypic *Schreiteria* in Montiaceae is preliminary. This enigmatic genus has not been found again in the past 80 years or so, and was not available for our analysis.

**Portulacaceae** Juss., Gen. Pl.: 312. 1789 – Type: *Portulaca* L.

Perennial to annual, usually succulent and mucilaginous herbs with fibrous to tuberous roots, sometimes minute and ephemeral, rarely somewhat suffrutescent (*Portulaca suffrutescens* Engelm.); stems herbaceous to slightly succulent, rarely somewhat woody, or strongly succulent with flaking bark (*P. molokiniensis* R.W. Hobby); leaves alternate or rarely opposite, flat to terete, succulent, sessile, glabrous or rarely tomentose, axils appearing naked or commonly with few to numerous short to long hairs or scales (*P. somalica* N.E. Br., *P. wightiana* Wall.); inflorescence terminal, basically

cymose but much congested and head-like; flowers sessile to pedicellate; sepaloids 2; petaloids (4–)5(–8), very shortly connate, very delicate, usually showy in bright colors; stamens usually numerous, or as few as 4; ovary semi-inferior, composed of (4–)5–8 carpels, unilocular, ovules numerous; fruits circumscissile capsules (pyxidia) with few to numerous seeds, capsule lid (operculum) falling off intact together with the dry perianth remains, stamens and style as a cap-like structure (calyptra); seeds yellow, brown to black or grey, often with iridescent gloss, testa cells usually forming an intricate stellate pattern, sometimes with tubercles or short to long projecting spines; hilum with a small to large spongy aril; embryo curved.

*Distribution.* – Worldwide in the tropics and subtropics, very rare in temperate climates.

*Genera and number of species.* – *Portulaca* L. (116 species; incl. *Lamia* Endl., *Lemia* Vand., *Merida* Neck., *Sedopsis* Exell & Mendonça).

*Important taxonomic literature.* – Carolin (1993 – synopsis), Geesink (1969 – monograph Indo-Pacific and Australia), Gilbert & Phillips (2000 – monograph Africa and Arabia), Legrand (1962 – monograph New World), Phillips (2002 – monograph East Africa).

*Discussion.* – According to our results, Portulacaceae has to be restricted to the single genus *Portulaca*, which is in sharp contrast to the traditional circumscription of the family (e.g., Carolin, 1993; Egli & Ford-Werntz in Egli, 2002). The isolated position of *Portulaca* within the Portulacaceae s.l. was already recognized by Pax & Hoffmann (1934), who assigned it to the monogeneric subtribe Portulacinae, as well as by McNeill (1974), who recognized the monogeneric tribe Portulacaceae. The contracted, head-like inflorescences and the operculate capsules (pyxidia) are absolutely diagnostic. Such capsules are not known for other Portulacineae, but are found elsewhere in Caryophyllales (e.g., Aizoaceae subfam. Sesuvioideae, several genera of Amaranthaceae [Townsend, 1993]). Portulacaceae are also anatomically unique, as the leaves show Kranz anatomy associated with C4 photosynthesis (Nyananyo, 1988).

The genus *Portulaca* is usually divided into two subgenera: *P.* subg. *Portulaca* (leaves alternate or rarely opposite, axillary hairs present or seemingly absent, inflorescence capitate or flowers solitary; distribution world-wide) and *P.* subg. *Portulacella* (F. Muell.) Legrand (leaves opposite, axillary hairs absent, inflorescence somewhat lax cymes; Australia, Africa). Currently, molecular phylogenetic studies are in progress to evaluate this classification based on morphological data (Ocampo, pers. comm.).

**Talinaceae** Doweld, Tent. Syst. Pl. Vasc. (Tracheophyta): 42 [xlii]. 2001 – Type: *Talinum* Adanson.

Dwarf shrubs with often tuberous roots or rootstock; leaves alternate, flat and slightly succulent, mucilaginous, entire, glabrous or tomentose, axils appearing naked but usually with a rudimentary axillary short shoot; inflorescence terminal and basically paniculate, or flowers solitary from leaf axils; flowers small to medium-sized and showy, bisexual,

actinomorphic; sepaloids 2, deciduous or persistent at fruiting time; petaloids usually 5, sometimes 2–4 and not clearly separated from the sepaloids (*Talinella*, *Amphipetalum*); stamens 15–35; ovary superior, unilocular, composed of 3(–5) carpels; fruits many-seeded loculicidal capsules, or mucilaginous berries (*Talinella*), capsules covered by the dry remains of perianth, stamens and style which are shed in their entirety as a calyptra, capsules dehiscent from the tip and/or base and the valves deciduous, or the caducous exocarp separating from the persistent endocarp; seeds usually black and glossy, with a strophiola; embryo curved.

*Distribution.* – America, Africa, Madagascar, *Talinum paniculatum* and *T. triangulare* pantropical weeds.

*Genera and number of species.* – *Amphipetalum* Bacigalupo (1 species), *Talinella* (12 species; incl. *Sabouraea* Leandri), *Talinum* (ca. 15 species; excl. *Phemeranthus* Raf. which is now included in Montiaceae).

*Important taxonomic literature.* – Applequist (2005 – monograph *Talinella*), Egli (1997 – monograph *Talinella*), Tölken (1969 – monograph *Talinum* South Africa).

*Discussion.* – The small family Talinaceae is rather heterogeneous. The genus *Talinella* (endemic to Madagascar) is easily recognized on morphological grounds (sarmentose lianoid shrubs, inconspicuous and often numerous flowers in congested inflorescences, berry-like fruits unique for the whole suborder). Molecular phylogenetic studies repeatedly placed it in a clade together with *Talinum* s.str. (Hershkovitz & Zimmer, 1997; Applequist & Wallace, 2001; Nyffeler, 2007), which is certainly unexpected in view of the previous uncertainties regarding its relationships (Pax & Hoffmann, 1934; Nyananyo, 1986, Carolin, 1993). Interestingly enough, *Talinella* was closely associated with Didiereaceae s.l. by Hershkovitz (1993: 349). Pending further research towards a complete species phylogeny of *Talinum* s.l., we refrain from formally transferring *Talinella* species to *Talinum* here.

The axils of *Talinum* are usually described as naked, but Ogburn (2007) found scale-like and often paired prophylls. *Talinum* thus appears to possess axillary contracted shortshoots that are most likely homologous to the ‘areoles’ of the Cactaceae and Didiereaceae, and the axillary hairs and scales of Anacampteroideae and Portulacaceae s.str.

The monotypic genus *Amphipetalum* from Paraguay and Bolivia was not available for study. It is placed here based on general habit and inflorescence morphology.

**Excluded genera.** — *Dendroportulaca* and *Pleuropetalum* are excluded from Portulacaceae s.l. These genera clearly belong to the family Amaranthaceae, as confirmed by recent investigations (Applequist & Pratt, 2005; Müller & Borsch, 2005).

**Relationships of Portulacineae.** — The closest relationships of Portulacaceae s.l. has been debated in the past. Fenzl (1836) claimed that Aizoaceae (tribes Ficoideae and Mesembryanthemeae) and Caryophyllaceae (tribes Alsineae and Paronychieae) might represent the most closely related families. This view was shared by Pax (1889), who pointed out the half-inferior ovary of *Portulaca* and the elevated number

of sepals and petals of *Lewisia* as characters that are indicative of a close relationship to the family Aizoaceae. Other authors stressed the similarity between some members of Portulacaceae (i.e., *Anacampseros* and *Portulaca*) and Cactaceae on the basis of the presence of multiseriate hair-like structures (Chorinsky, 1931; see discussion above). Finally, Hutchinson (1969) suggested a close affinity to Primulaceae.

The most broadly sampled molecular phylogeny of Caryophyllales identifies various members of Molluginaceae (e.g., *Adenogramma* Rchb., *Glinus* L., and *Suessenguthiella* Friedrich) as the closest relatives of a generally well-supported Portulacineae (Cuénoud & al., 2002). However, sequence data available so far does not provide adequate information to settle this question.

### CONCLUDING REMARKS AND OUTLOOK

Resolving the family classification of traditional Portulacaceae in the light of new findings from phylogenetic analyses has been made public as a test case for the sensibility of traditional taxonomic practice to contrast the current obsession to create monophyletic taxa (Brummitt, 2002, 2006). Molecular phylogenetic analyses as well as insights derived from comparative morphological data of fruit characters clearly indicate that the traditional classification of Portulacineae into six families (i.e., Basellaceae, Cactaceae, Didiereaceae, Halophytaceae, Hectorellaceae, and Portulacaceae; Kubitzki & al., 1993) does not reflect the phylogenetic relationships among the members of this suborder, and makes inconsistent use of morphological characteristics to circumscribe these taxa. Hiding behind established tradition of Portulacaceae classification with the notion that “there are no characters by which anyone has ever thought to divide it [Portulacaceae] into two families” (Brummitt, 2002: 36) is not helpful to plant systematics in the long term. Discordance between molecular phylogenies and traditional classification practice should rather be seen as a challenge to further investigate morphological characteristics potentially useful for circumscribing and identifying taxa derived from inferred phylogenetic relationships.

We argue that we are in a much better position to work towards overcoming this obsolete traditional family classification and to replace it with one that better reflects phylogenetic hypotheses as well as provides well-supported overall taxon circumscriptions. In line with arguments by Albach (2008) we maintain that taxonomic stability will ultimately only be reached by making taxon delimitation congruent with well supported monophyletic groups of extant species. For the suborder Portulacineae we suggest that eight families (i.e., Anacampserotaceae, Basellaceae, Cactaceae, Didiereaceae, Halophytaceae, Montiaceae, Portulacaceae, Talinaceae) should be recognized as outlined in our synoptical treatment. This revised classification forms the framework for further phylogenetic analyses on the basis of molecular markers from the nuclear genome as well as detailed comparative structural investigations (Nyffeler & al., 2008; Ogburn & Edwards, 2009).

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**Appendix 1.** Accessions of Portulacineae and outgroups used for the molecular phylogenetic analysis. A dash indicates that the sequence was not available. Voucher specimen information is given for previously unpublished sequences. For taxon names with an asterisk new combinations are provided in Appendix 2 of this publication.

*Taxon*, voucher, GenBank accession number: *matK* (original publication), *ndhF* (original publication).

**PORTULACINEAE:** *Alluaudia ascendens* (Drake) Drake, –, AY042541 (Cuénoud & al., 2002); *Alluaudia humbertii* Choux, AF194832 (Applequist & Wallace, 2001), –; *Anacampseros albissima* Marloth, –, DQ855856 (Nyffeler, 2007; as *Avonia albissima*); *Anacampseros australiana* J.M. Black, –, DQ855855 (Nyffeler, 2007; as *Grahamia australiana*); *\*Anacampseros coahuilensis* (S. Watson) Eggl & Nyffeler, –, DQ855854 (Nyffeler, 2007; as *Grahamia coahuilensis*); *Anacampseros kurtzii* Bacigalupo, –, DQ855853 (Nyffeler, 2007; as *Grahamia kurtzii*); *Anacampseros karasmontana* Dinter, DQ855872 (Nyffeler, 2007), DQ855859 (Nyffeler, 2007); *Anacampseros papyracea* Fenzl, –, DQ855857 (Nyffeler, 2007; as *Avonia papyracea*); *Anacampseros recurvata* Schönland, –, DQ855858 (Nyffeler, 2007; as *Avonia recurvata*); *Anacampseros retusa* Poelln., DQ855873 (Nyffeler, 2007), DQ855860 (Nyffeler, 2007); *Anacampseros subnuda* Poelln., DQ855874 (Nyffeler, 2007), DQ855861 (Nyffeler, 2007); *Anacampseros telephium* DC., DQ855875 (Nyffeler, 2007), DQ855862 (Nyffeler, 2007); *Anacampseros vulcanensis* Añón, –, DQ855852 (Nyffeler, 2007; as *Grahamia vulcanensis*); *Anredera cordifolia* (Ten.) Steenis, –, AY042547 (Cuénoud & al., 2002); *Austrocyliodropuntia vestita* (Salm-Dyck) Backeb., DQ855878 (Nyffeler, 2007), AY015278 (Nyffeler, 2002); *Basella alba* L., AF194834 (Applequist & Wallace, 2001), AY042553 (Cuénoud & al., 2002); *Blossfeldia liliputana* Werdermann, –, AY015284 (Nyffeler, 2002); *Calymanthium substerile* F. Ritter, –, AY015291 (Nyffeler, 2002); *Calyptidium umbellatum* (Torr.) Greene, AF194840 (Applequist & Wallace, 2001), –; *Calyptrotheca somalensis* Gilg, AF194839 (Applequist & Wallace, 2001), AY042563 (Cuénoud & al., 2002); *Ceraria fruticulosa* H. Pearson & Stephens, AF194841 (Applequist & Wallace, 2001), AY875371 (Edwards & al., 2005); *Cistanthe grandiflora* (Lindl.) Hershk., AF194842 (Applequist & Wallace, 2001), AY042568 (Cuénoud & al., 2002); *Copiopoa bridgesii* (Pfeiff.) Backeb., DQ855879 (Nyffeler, 2007), AY015293 (Nyffeler, 2002); *Decarya madagascariensis* Choux, AF194844 (Applequist & Wallace, 2001), AY042574 (Cuénoud & al., 2002); *Didierea trollii* Capuron & Rauh, AF194845 (Applequist & Wallace, 2001), AY042576 (Cuénoud & al., 2002); *Echinocactus platyacanthus* Link & Otto, –, AY015287 (Nyffeler, 2002); *Grahamia bracteata* Gill., AF194846 (Applequist & Wallace, 2001), AY015273 (Nyffeler, 2002); *Halophytum ameghinoi* Speg., –, AY514852 (Müller & Borsch, 2005); *Hectorella caespitosa* Hook. f., DQ093963 (Applequist & al., 2006); DQ267197 (Applequist & al., 2006); *Lewisia cantelovii* J.T. Howell, –, AY042607 (Cuénoud & al., 2002); *Lewisia pygmaea* (A. Gray) B.L. Rob., AF194847 (Applequist & Wallace, 2001), –; *Maihueunia patagonica* (Phil.) Britton & Rose, DQ855877 (Nyffeler, 2007), AY015281 (Nyffeler, 2002); *Maihueuniopsis subterranea* (R.E. Fr.) E.F. Anderson, –, EU834746 (this study; Bolivia: Potosí, *Rausch s.n.*; ZSS 28414); *Montia parvifolia* (DC.) Greene, AF194851 (Applequist & Wallace, 2001), AY042616 (Cuénoud & al., 2002); *Opuntia quimilo* K. Schum., –, AY015279 (Nyffeler, 2002); *Parakeelya volubilis* (Benth.) Hershk., AF194838 (Applequist & Wallace, 2001; as *Calandrinia volubilis*), –; *Pereskia aculeata* Mill., DQ855876 (Nyffeler, 2007), DQ855863 (Nyffeler, 2007); *Pereskia guamacho* F.A.C. Weber, –, AY015275 (Nyffeler, 2002); *Pereskia stenantha* F. Ritter, –, AY015276 (Nyffeler, 2002); *Pereskia zinniiflora* DC., –, AY015277 (Nyffeler, 2002); *Pereskiaops diguetii* (F.A.C. Weber) Britton & Rose, –, AY015280 (Nyffeler, 2002); *Phemeranthus multiflorus* (Rose & Standley) Ocampo, –, EU834747 (this study; Mexico: Queretaro, *Ocampo & Morales 1484*; ZSS 27389); *\*Phemeranthus punae* (R.E. Fr.) Eggl & Nyffeler, –, EU834748 (this study; Argentina: Salta, *Leuenerberger & Eggl 4867a*; ZSS 23769); *Phemeranthus teretifolius* Raf., –, EU834749 (this study; ex cult. Huntington Botanical Garden; HNT); *Portulaca* cf. *bicolor* F. Muell., DQ855870 (Nyffeler, 2007), DQ855848 (Nyffeler, 2007); *Portulaca eruca* Hauman, –, DQ855849 (Nyffeler, 2007); *Portulaca fluvialis* D. Legrand, –, EU834750 (this study; Uruguay: Río Negro, *Nyffeler & Eggl 1652*; ZSS 26796); *Portulaca grandiflora* L., AF194853 (Applequist & Wallace, 2001), EU834751 (this study; Uruguay: Paysandú, *Nyffeler & Eggl 1673*; ZSS 26698); *Portulaca oleracea* L., AY194867 (Applequist & Wallace, 2001), DQ855850 (Nyffeler, 2007); *Portulacaria afra* Jacq., AF194857 (Applequist & Wallace, 2001), AY042637 (Cuénoud & al., 2002); *Rhypsalis floccosa* Pfeiff., –, AY015342 (Nyffeler, 2002); *Stetsonia coryne* (Salm-Dyck) Britton & Rose, –, AY015320 (Nyffeler, 2002); *Talinella pachypoda* Eggl, DQ855868 (Nyffeler, 2007), DQ855846 (Nyffeler, 2007); *Talinopsis frutescens* A. Gray, DQ855871 (Nyffeler, 2007), DQ855851 (Nyffeler, 2007); *Talinum caffrum* (Thunb.) Eckl. & Zeyh., AY194859 (Applequist & Wallace, 2001), AY042662 (Cuénoud & al., 2002); *Talinum lineare* Kunth, –, EU834752 (this study; Mexico: Michoacán, *Ocampo & Morales 1460*; ZSS 27415); *Talinum paniculatum* (Jacq.) Gaertn., DQ855866 (Nyffeler, 2007), AY015274 (Nyffeler, 2002); *Talinum polygaloides* Arn., DQ855867 (Nyffeler, 2007), DQ855845 (Nyffeler, 2007); *Talinum portulacifolium* (Forssk.) Schweinf., DQ855869 (Nyffeler, 2007), DQ855847 (Nyffeler, 2007); *Talinum triangulare* (Jacq.) Willd., DQ855865 (Nyffeler, 2007), DQ855844 (Nyffeler, 2007); *Ullucus tuberosus* Caldas, AF194865 (Applequist & Wallace, 2001), –.

**OUTGROUP SPECIES:** *Delosperma cooperi* L. Bolus, DQ855864 (Nyffeler, 2007), DQ855843 (Nyffeler, 2007); *Limeum africanum* L., –, AY042608 (Cuénoud & al., 2002); *Mirabilis jalapa* L., AF194826 (Applequist & Wallace, 2001), AY042614 (Cuénoud & al., 2002); *Mollugo verticillata* L., AF194827 (Applequist & Wallace, 2001), DQ267195 (Applequist & al., 2006); *Phytolacca americana* L., AF130229 (Olmstead & al., 2000), –; *Phytolacca dioica* L., –, AY042631 (Cuénoud & al., 2002).

#### Appendix 2. New combinations.

*Anacampseros coahuilensis* (S. Watson) Eggl & Nyffeler, **comb. nov.** Basionym: *Talinum coahuilense* S. Watson in Proc. Amer. Acad. Arts 26: 132. 1891.  
*Phemeranthus punae* (R.E. Fr.) Eggl & Nyffeler, **comb. nov.** Basionym: *Calandrinia punae* R.E. Fr. in Nova Acta Regiae Soc. Sci. Upsal., ser. 4, 1: 149. 1905.