Expanded circumscription of Didiereaceae and its division into three subfamilies

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ABSTRACT
Three genera of Portulacaceae (*Calyptrotheca, Ceraria* and *Portulacaria*) that are more closely allied to Didiereaceae than to other Portulacaceae are transferred to Didiereaceae. The family is divided into three subfamilies, Calyptrothecoideae, Didiereoideae and Portulacarioideae.

MOTS CLÉS
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RÉSUMÉ
Extension de la circonscription des Didiereaceae et leur subdivision en trois sous-familles.
Trois genres de Portulacaceae (*Calyptrotheca, Ceraria* et *Portulacaria*) qui sont plus proches de Didiereaceae que d'autres Portulacaceae sont transférés dans les Didiereaceae. La famille est ainsi constituée de trois sous-familles, Calyptrothecoideae, Didiereoideae et Portulacarioideae.

INTRODUCTION

The four families Portulacaceae, Basellaceae, Cactaceae and Didiereaceae form an alliance, first recognized by THORNE (1968), whose monophyly has been confirmed by cladistic studies (RETTIG et al. 1992; DOWNIE et al. 1997). Within this alliance, ITS and *ndhF* sequence data suggest that the latter three families evolved from within a paraphyletic Portulacaceae (HERSHKOVITZ & ZIMMER 1997; APPLEQUIST & WALLACE 2001). A classification reflecting monophyletic groups has not yet been achievable, as relationships among major lineages within the alliance are for the most part poorly if at all supported. The position of the endemic Malagasy family Didiereaceae is an exception: molecular data show that their closest relative is *Calyptrotheca*

Table 1. — Some morphological features distinguishing the Malagasy genera of **Didiereaceae** from ***Calyptrotheca*** and from ***Ceraria*** and ***Portulacaria***. Chromosome counts from NYANANYO (1987) and SCHILL et al. (1974).

	Didiereaceae (Didiereoideae)	***Calyptrotheca***	***Portulacaria* and *Ceraria***
Habit	Trees or shrubs with highly reduced brachyblasts, bearing both foliar leaves and spines	Shrubs without spines, sometimes climbing or arborescent	Shrubs or small trees without spines, leaves sometimes borne on short shoots or in fascicles
Sexual condition	Dioecious or rarely gynodioecious	Flowers hermaphroditic	Dioecious in *Ceraria*; flowers hermaphroditic in *Portulacaria*
Perianth	Sepals 2; petals 4	Sepals 2; petals 5	Sepals 2; petals 5, fused in *Portulacaria*
Androecium	Stamens 8-10	Stamens numerous	Stamens 5, free in *Ceraria*; 4-7(-10), adnate to perianth in *Portulacaria*
Fruit condition	Fruit 1-seeded, indehiscent	Fruit 1-seeded (but initially with up to 6 ovules), dehiscing by 6 valves	Fruit 1-seeded, indehiscent
Chromosome numbers	2n = 48, 192, 240	(Not determined)	2n = 44, 48, 72

(APPLEQUIST & WALLACE 2000, 2001), an East African genus of 2 species. The sister group of this clade is Portulacarieae (APPLEQUIST & WALLACE 2001), comprising *Portulacaria* and *Ceraria*. While this relationship is only weakly supported by cpDNA sequence data (and weakly contradicted by ITS data; HERSHKOVITZ & ZIMMER 1997), morphological resemblances among Didiereaceae and Portulacarieae (both woody, succulent and often dioecious) provide further evidence for their relatedness. LANDRUM (2002) observed several shared anatomical features: druses and mucilage cells in parenchymatous tissues of the stem and leaves, and the presence of tannins and collenchyma in the leaf mesophyll. RAUH & SCHÖLCH (1965) also noted similarities between Didiereaceae and *Ceraria* that included characters of the inflorescence and flowers, as well as the occurrence of short shoots (brachyblasts) that in *Ceraria namaquensis* Pearson & Stephens created some resemblance to a species of *Alluaudia* (Didiereaceae). In fact, *Calyptrotheca* resembles Didiereaceae far less than do Portulacarieae (Table 1), so that its position would remain uncertain if not for the many molecular synapomorphies. *Ceraria, Portulacaria* and *Calyptrotheca* are also united by geography; unlike most Portulacaceae, they are native to arid regions of southern or eastern Africa from whence dispersal to Madagascar may have occurred.

It is clear that the closest affinities of *Portulacaria* and *Ceraria* are with *Calyptrotheca* and Didiereaceae rather than with Basellaceae or with any of the more speciose major clades of Portulacaceae. As shown by the wealth of contradictory literature (e.g. MCNEILL 1974; CAROLIN 1987; NYANANYO 1990; HERSHKOVITZ 1993; HERSHKOVITZ & ZIMMER 1997; APPLEQUIST & WALLACE 2001), intergeneric relationships within Portulacaceae as presently circumscribed are complex and controversial; prior efforts at formal classification were hampered by the failure to recognize paraphyletic relationships involving three other families. To resolve one of the obvious discrepancies between past classification and current phylogenetic understanding, we therefore propose that *Portulacaria*, *Ceraria* and *Calyptrotheca* be transferred to Didiereaceae. This action not only recognizes the demonstrably close relationship among these genera, leaving Didiereaceae (in our expanded sense) a small monophyletic group with many shared features, but also renders the remaining Portulacaceae a somewhat less heterogeneous group by removing two clades that are only distantly related to the family's core lineages and in many ways dissimilar to them.

As the four endemic Malagasy genera are very distinctive, we divide Didiereaceae sensu lato into three subfamilies, fully cited below: Didiereoideae encompasses the Malagasy genera, while the African genera transferred from Portulacaceae fall into Calyptrothecoideae (an existing name, initially placed within Capparidaceae) and Portulacarioideae. *Calyptrotheca*, as sister to Didiereoideae, cannot be grouped with *Portulacaria* and *Ceraria*, but it is too unlike the Didiereoideae to be placed therein; thus, three subfamilies are required despite the small number of genera to be included.

DIDIEREOIDEAE Appleq. & R.S. Wallace, **subfam. nov.**

Based on Didiereaceae Drake, Bull. Mus. Hist. Nat. (Paris) 9: 36 (1903).

TYPUS. — *Didierea* Baill., Bull. Mens. Soc. Linn. Paris 1: 258 (1880).

This subfamily comprises the four genera and 11 species traditionally included in Didiereaceae sensu stricto (see RAUH 1963; RAUH & SCHÖLCH 1965), all of which are endemic to southwestern Madagascar. In addition to *Didierea*, which comprises 2 species (RAUH 1963; see also RAUH 1961), the subfamily includes the following genera:

— *Alluaudia* (Drake) Drake, Bull. Mus. Hist. Nat. (Paris) 9: 37 (1903), a genus of 6 species (see CHOUX 1934; RAUH 1961; RABESA 1982).
— *Alluaudiopsis* Humbert & Choux, Compt.-Rend. Hebd. Séances Acad. Sci. 149: 1651 (1934), which includes 2 species (RAUH 1961, 1963).
— *Decaryia* Choux, Mém. Acad. Malgache 18: 62 (1934), a monotypic genus (RAUH 1963).

CALYPTROTHECOIDEAE Pax & Gilg

In Engl. & Prantl, Nat. Pflanzenfam., Nachtrag zu II-IV: 178 (1897. — Type: *Calyptrotheca* Gilg, Bot. Jahrb. Syst. 24: 307 (1897).

Calyptrothecoideae include a single genus, *Calyptrotheca*, which has just two species, both endemic to tropical East Africa (BRENAN 1949; NYANANYO 1986; PHILLIPS 2002).

PORTULACARIOIDEAE Appleq. & R.S. Wallace, **subfam. nov.**

Frutices vel arbusculae, ramosi, glabri, caulibus crassis. Folia opposita vel fasciculata, succulenta, glabra. Flores cymosi, dioeci vel hermaphroditi. Sepala 2, brevia, membranacea, persistentia. Petala 5. Stamina 4-10. Ovarium superum, trigonum, ovulo uno. Fructus indehiscens. Pollen tricolpatum.

TYPUS. — *Portulacaria* Jacquin, Collect. 1: 160 (1787).

Portulacarioideae comprise two genera:

— *Portulacaria*, with two species mostly in South African and disjunct in Kenya (PAX & HOFFMAN 1934; VAN JAARSVELD 1984; PHILLIPS 2002).
— *Ceraria* H. Pearson & Stephens (Ann. S. Afr. Mus. 9: 32, 1912), which has 4-5 species in South Africa (PAX & HOFFMANN 1934; PODLECH 1967; ROWLEY 1996; GLEN 2002).

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