VARIATIONS ON A THEME: REPEATED EVOLUTION OF SUCCULENT LIFE FORMS IN THE PORTULACINEAE (CARYOPHYLLALES)

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Abstract: The succulent life form is a tried and true strategy for plants living in arid environments. It has evolved in many distantly related lineages comprising 12,500 species from 70 flowering plant families and has spawned remarkable radiations. Three major groups are generally recognized: (1) stem succulents (that is, leafless cactus-like growth forms), (2) leaf succulents, and (3) caudiciform and pachycaul succulents. All three lifeform groups are represented in the relatively small suborder Portulacineae. Here we suggest that this diversity provides a unique opportunity to evaluate early cactus evolution within a richer contextual framework. We briefly review what we know about the phylogenetic relationships within the suborder Portulacineae (that is, Basellaceae, Cactaceae, Didiereaceae, and Portulacaceae) and the morphology and ecology of all major Portulacineae lineages. We then outline what we believe to be key areas for future research on these understudied plants and discuss several hypothetical "pre-adaptations" and conditions in ancestral Portulacineae that may have promoted the repeated evolution of unusual succulent life forms.

Key words: Caryophyllales, Portulacineae, Montiaceae, succulence, life form, functional trait, cactus, evolution

Introduction

Trained botanists and amateurs alike have regarded the cacti with awe for centuries (Rowley 1997). The copious production of spines, lack of leaves, bizarre architecture due to the formation of stem succulence, and the impressive ability to persist in warm arid deserts under some of the harshest environmental conditions on Earth are all traits that have entitled this lineage to be recognized as a prominent textbook example for adaptive evolution in biology (for instance, Futuyma 1997; Niklas 1997). *Pereskia*, a group of relatively non-succulent, leafy shrubs and small trees (Fig 1), has long been considered the "evolutionary link" between "ordinary" perennial plants and leafless cacti (Rauh 1979; Gibson and Nobel 1986; Mauseth and Landrum 1997; but see Griffith 2004). The cactus-form of representatives of the subfamilies Cactoideae and Opuntioideae is the result of the following modifications: (1) leaves highly reduced, (2) short shoots (areoles) bear spines derived from leaf primordia, (3) branching reduced or absent, (4) long-lived stem epidermis with delayed bark formation, and (5) cortex and pith are expanded to form a water-storage tissue. Recent work on the phylogenetics of *Pereskia* (Edwards and others 2005; Butterworth and Wallace 2005), as well as studies of *Pereskia* anatomy (Ogburn 2007), physiology, and ecology (Martin and Wallace 2000; Edwards 2006; Edwards and Donoghue 2006) has revealed that this genus, indeed, has much to tell about early events in the evolution of the cactus life form (summarized in Edwards and Donoghue 2006).

Here we argue that there is even more to gain by looking beyond *Pereskia*. It is now clear that the cactus family is only one of several

lineages of succulent life forms emerging from what was once recognized as the family Portulacaceae (Hershkovitz and Zimmer 1997; Applequist and Wallace 2001; Nyffeler 2007). In addition to the cacti, there has been the evolution of (1) perennial rosette-forming herbs with persistent succulent leaves (such as *Lewisia* in western North America; Fig 2), (2) perennial herbs with fleshy roots and highly succulent or greatly reduced leaves (*Anacampseros* and *Avonia*; Figs 3, 4), (3) annual herbs with prostrate, fleshy stems and succulent leaves (including *Portulaca oleracea*, *P. afra*, and their relatives; Figs 5, 6), (4) small, pachycaulescent shrubs or trees with succulent leaves (*Ceraria* from southern Africa; Fig 7) and long shoot–short shoot differentiation (*Didierea* in Madagascar; Fig 8), (5) subwoody shrubs with tuberous roots and herbaceous leaves (*Talinum paniculatum* and relatives; Figs 9–11), and (6) slightly succulent scramblers or vines with a thickened stem base (such as *Basella* and related genera mainly from the tropics of the New World; Fig 12).

This new phylogenetic picture allows us to place the evolution of Cactaceae within a richer context and ask the following questions: (1) What do the cacti have in common with their other succulent relatives, and how do they differ? (2) What did the ancestral Portulacineae look like, and where did it arise? (3) Can we infer the ecological conditions that may have triggered such dramatic morphological innovation in these lineages, and were they similar in each case? (4) Can we infer anatomical or functional pre-conditions that enable the evolution of succulence?

Here we review what we currently know about the evolutionary relationships, ecology, and vegetative morphology of the Portulacineae and outline what we believe to be key areas for future research on these understudied plants.

Phylogenetics of the suborder Portulacineae

Today, the methods of molecular systematics allow us to reconstruct phylogenetic relationships among groups of organisms in detail and with good measures of statistical support. Molecular phylogenetic investigations of the past decade (for instance, Hershkovitz and Zimmer 1997, 2000; Applequist and Wallace 2001; Cuénoud and others 2001) have clearly shown that the traditional families Basellaceae, Cactaceae, Didiereaceae, and Portulacaceae (that is, suborder Portulacineae) are closely related to each other. Overall, this evolutionary lineage comprises about 2200 species, of which about 90% are classified as succulents (Eggli 2002; Anderson 2005; Hunt 2006). Relationships among the members of suborder Portulacineae have recently been further clarified (Nyffeler 2007). The family Portulacaceae s.l. is found to be paraphyletic; some of its species are more closely related to either Cactaceae or Didiereaceae rather than to some other species of the same family (Fig 13).

The genera *Ceraria* and *Portulacaria* are most closely related to traditional Didiereaceae, while the genera *Anacampseros*, *Avonia*, *Grahamia* s. l. (including *Talinaria*, *Talinopsis*, and *Xenia*—in composite referred to as tribe Anacampseroteae; Rowley 1994, 1995), as well as *Portulaca* and *Talinum* (the latter in a revised circumscription excluding the members of the former section *Phemeranthus* but including the Madagascan endemic genus *Talinella*), form a well supported clade together with the family Cactaceae. This clade was referred to as the "ACPT clade" (that is, Anacampseroteae, Cactaceae, *Portulaca*, *Talinum*) by Nyffeler (2007). These findings receive good statistical support from molecular sequences of the chloroplast genome. Furthermore, morphological and anatomical characteristics provide additional evidence in favor of these inferred relationships (Ogburn 2007; Nyffeler and Eggli submitted).

Overall, we may recognize four major lineages in Portulacineae (Fig 13): (1) The resurrected family Montiaceae, here represented by the three genera *Claytonia*, *Lewisia*, and *Phemeranthus*, includes about 200 species mainly with herbaceous, rosettiform habits and clasping, non-constricted leaf bases. This family is most prominent in the western parts of North and South America. (2) The family Basellaceae forms a distinct and morphologically well characterized clade of about 20 species that are distributed in the tropics of the New World, Africa, and Madagascar. (3) The family Didiereaceae is here used in the expanded circumscription (Applequist and Wallace 2003) that includes *Ceraria*, *Portulacaria*, and possibly also *Calyptrotheca*. These taxa generally form large woody trees or shrubs, some with a distinct cactus-like habit, and occur in eastern and southern Africa and Madagascar. (4) The ACPT clade consists of the family Cactaceae as well as three distinct subclades from the traditional family Portulacaceae. The genus *Talinum* (including the genus *Talinella*, Nyffeler 2007) takes a cladistically basal position and forms the sister group to a subclade consisting of Anacampseroteae (*Anacampseros*, *Avonia*, and

Grahamia), Cactaceae, and *Portulaca*. This latter group is well characterized by the presence of axillary hairs or scales. The present hypothesis (Fig 13; Nyffeler 2007) favors a sister-group relationship between Anacampseroteae and Cactaceae, though this result only receives moderate statistical support. These findings have a profound bearing on the family classification of the ACPT clade. If Cactaceae should further on be recognized in its familiar form, we either need to propose additional families for the three subclades of former Portulacaceae, or we accept a recircumscribed paraphyletic Portulacaceae* that only includes Anacampseroteae, *Portulaca*, and *Talinum*.

Description of typical taxa of the major Portulacineae lineages

Montiaceae

Phemeranthus Raf.

Description Perennial; presumably long-lived herbs with taproots or underground tubers; stems usually none to short with contracted internodes, herbaceous; leaves rosulate, herbaceous, terete, slightly succulent, annually more or less deciduous (Fig 14).

Distribution North, Central, and South America, open areas, dry woodland to rocky slopes.

Systematics and evolution Previously conceived as a subgenus of *Talinum*, but recent molecular work (Hershkovitz and Zimmer 1997, 2000; Applequist and Wallace 2001; Nyffeler 2007) has shown that this group of about 30 species is not at all related to *Talinum* but belongs to the group of genera now recognized to belong to Montiaceae, where it likely occupies a cladistically basal sister-group position relative to the rest of the family (Nyffeler 2007). The rather herbaceous, or only slightly woody, rosulate habit is typical for Montiaceae.

Physiology Predominantly C3, facultative CAM (inducible CAM-cycling) is reported by Guralnick and Jackson (2001).

Lewisia Pursh

Description Perennial long-lived herbs with fleshy taproot; stem none to short, contracted, enlarged and forming a caudex; leaves rosulate, herbaceous, slightly to strongly succulent, annually deciduous or long-lived, flat to terete (Fig 2).

Figure 1. *Pereskia sacharosa* (Bolivia). **Figure 2.** *Lewisia rediviva* (US). **Figure 3.** *Anacampseros* sp. **Figure 4.** *Avonia papyracea.*

Distribution North America (W half of the continent only, SW Canada to NW Mexico), on rocks or gravel in usually open places.

Systematics A genus of about 16 species (Hershkovitz and Hogan 2002; Hershkovitz and Hogan 2003). *Lewisia tweedyi*, formerly classified as *Cistanthe,* has now been segregated as monotypic genus *Lewisiopsis*.

Physiology Predominantly C3, facultative CAM (inducible CAM-cycling) is reported by Guralnick and Jackson (2001).

Claytonia L.

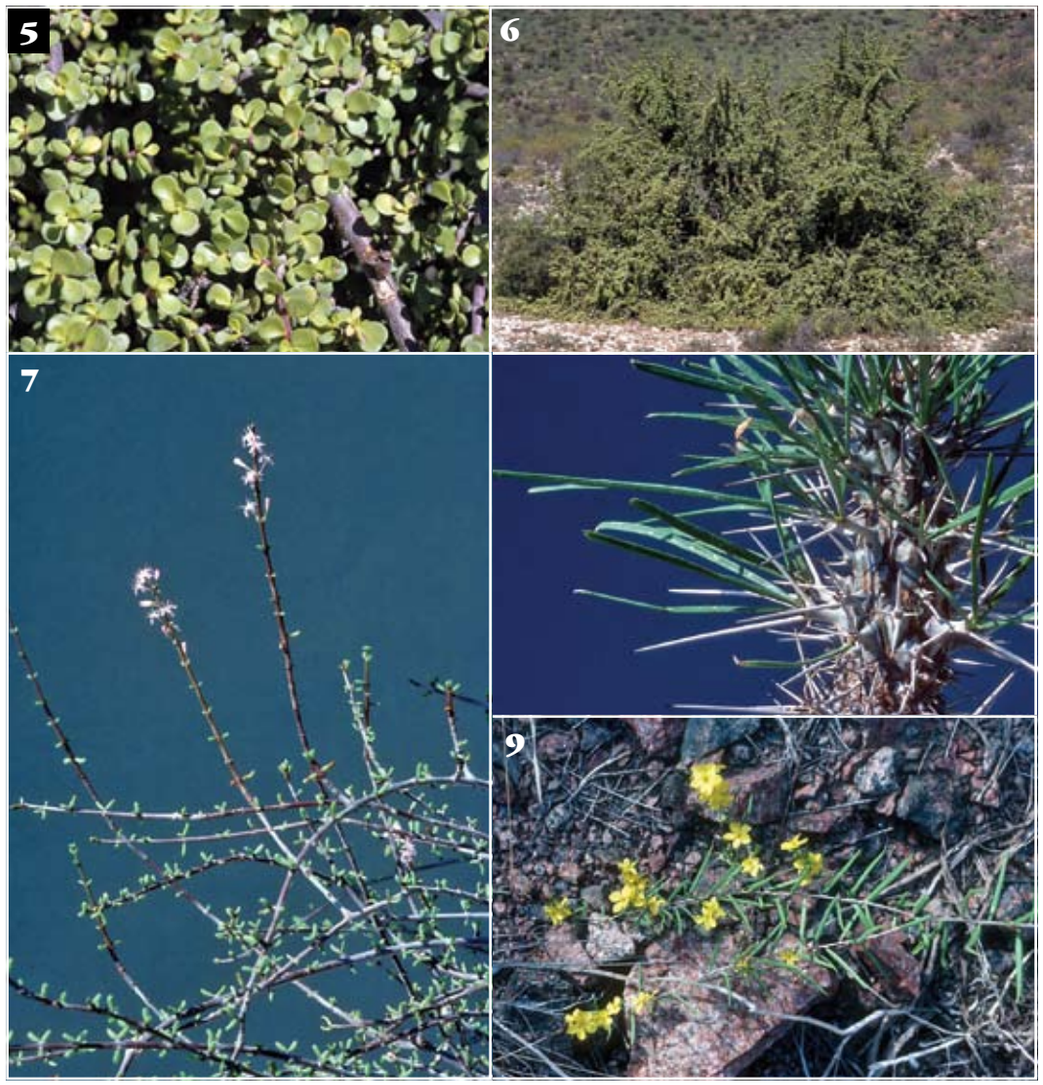
Description Annual to perennial herbs usually with fibrous roots; stem short, as underground tuber, caudex or rhizome; leaves rosulate, herbaceous, thin-textured to slightly succulent, annually deciduous, flat to narrowly linear.

Distribution North and Central America, northeast Asia (Mongolia, Siberia), usually moist places (seepages, river banks, snow-covered depressions) but some extending to dry grassland and rocks.

Systematics A genus of 26 species. Closely related to *Montia* (ca. 12 species, northern hemisphere circumboreal).

Physiology Predominantly C3, facultative CAM (inducible CAM-cycling or minimal true CAM) is reported by Guralnick and Jackson (2001).

Figure 5. *Portulacaria afra.* **Figure 6.** *Portulacaria afra.* **Figure 7.** *Ceraria fruticulosa.* **Figure 8.** *Didierea madagascariensis.* **Figure 9.** *Talinum polygaloides.*



Notes on other genera of Montiaceae

The three genera included in our survey do not depict the whole range of life forms present in the family. Several taxa of *Cistanthe* show pronounced stem succulence, *Hectorella* and *Lyallia* (previously recognized as a separate family; Applequist and others 2006) are tight cushion plants occurring in alpine and sub-antarctic habitats (such as South Island of New Zealand and Kerguelean Island), and *Montiopsis* species are small herbs to diminutive shrublets without any succulence. The genera included in this resurrected family Montiaceae are representatives of the so-called PAW clade (from *Phemeranthus*, Australian *Calandrinia*, western American Portulacaceae; Hershkovitz 1993; Hershkovitz and Zimmer 2000). The systematics of the groups dismantled from the former genus *Calandrinia* (where *Cistanthe* and *Montiopsis* have been traditionally placed) is still largely unresolved (Hershkovitz 2006).

Basellaceae

***Basella* L.**

Description Perennial vines with tuberous underground roots and often basally swollen stems; stems slender, herbaceous, scrambling to twining; leaves alternate, flat, slightly fleshy, evergreen (Fig 12).

Distribution Madagascar, east Africa, one species pantropical, usually in semi-deciduous to evergreen forests.

Systematics A genus of five species.

Physiology C3 (Mabry 1977).

Notes on other genera of Basellaceae

This small family has only four genera and about 20 species. Almost all produce either tuberous roots or thickened tuberous stem bases and have weakly decumbent to twining, herbaceous stems and flat, slightly succulent leaves. The combination of spicate inflorescences and uniformly small and pale-colored flowers also set the Basellaceae apart from the rest of the Portulacineae. Some species of *Anredera* have functionally unisexual flowers (Sperling and Bittrich 1993).

Didiereaceae

***Ceraria* Phearson & Stephens**

Description Perennial woody shrublets to shrubs; stems thin and lignescent, or contracted, much thickened and stubby, with contracted invisible short-shoots in the primary leaf axils; leaves alternate or opposite, flat to terete, succulent, annually deciduous, or short-lived evergreen (Fig 7).

Distribution South Africa (Namibia, RSA).

Systematics and evolution A genus of seven species. *Ceraria* has traditionally been placed in Portulacaceae and was only recently recognized as a close relative of the formerly Madagascar-endemic Didiereaceae (Applequist and Wallace 2003). It forms a clade with *Portulacaria* (two species, leaves flat, Namibia and South Africa), which is the sister-group to traditional Didiereaceae.

Physiology Leaves predominantly C3, CAM-cycling (Rundel and others 1999) or inducible full-CAM (Guralnick and Jackson 2001); stems with slightly higher CAM activity (von Willert and others 1992; Gibson 1996, Edwards and others in Winter and Smith 1996: 128).

***Didierea* Baill.**

Description Long-lived perennial shrubs or tree-like; stems woody, moderately succulent (medulla, cortex), eventually becoming woody, with contracted short-shoots in the primary leaf axils; leaves linear, deciduous, slightly succulent; short shoots first producing four spines, later producing a couple of leaves each season (Fig 8).

Distribution South and southwest Madagascar, dry forest.

Systematics A genus of two species.

Physiology No data available for *Didierea*, but facultative CAM appears to be ubiquitous in Didiereaceae s. str. (Kluge and Ting 1978; Kluge and others 2001).

Notes on other genera of Didiereaceae

In the traditional sense, the family embraced four genera with 11 species, all from Madagascar, and with the exception of the monotypic *Decarya* (Fig 15) all show moderate stem succulence. Applequist and Wallace (2003) found in a molecular analysis that the South African genera *Ceraria* and *Portulacaria* (both weakly to pronouncedly stem-succulent shrubs) as well as the east African genus *Calyptrotheca* (weakly leaf-succulent shrubs with or without tuberous roots) belong here.

ACPT Clade—Portulacaceae*

***Talinum* Adans.**

Description (*Talinum* s. str. excl. *Talinella*) Perennial herbs to small shrubs, usually with tuberous roots; stems elongate and lignescent to elongate and herbaceous, sometimes basally thickened and forming a caudex, sometimes upper parts deciduous; leaves alternate, slightly fleshy, deciduous to semi-deciduous (Figs 9, 10).

Distribution Africa, Arabia, North and South America, some species pantropical but perhaps introduced, seasonally mesic sites, semi-deciduous to deciduous forests and scrub.

Systematics and evolution A genus of 27 (15 excluding *Talinella*) species. In traditional classifications *Talinum* also embraced *Phemeranthus*, now removed to Montiaceae on molecular grounds. On the other hand, the Malagasy endemic, former genus *Talinella* has been found to be nested within *Talinum* s. str. (Nyffeler 2007). *Talinella* species (excluded from the above description) are small to large and sometimes lianoid shrubs. The stems are hardly thickened, but at least one taxon produces a fleshy taproot and basal stem swelling, and the leaves of most taxa are slightly thickened. Furthermore, *Talinum* s. str. and *Talinella* both often have a dense cover of papillae on young stems (Figs 10, 11).

Physiology Predominantly C3; inducible CAM-cycling and weak full CAM (Guralnick and Jackson 2001). For *Talinella* we do not have any data.

***Portulaca* L.**

Description Annual to perennial (but predominantly short-lived) diminutive to conspicuous herbs or diminutive shrublets, with fibrous to tuberous roots; stems herbaceous, slightly succulent (rarely thin and lignescent, or strongly succulent with flaking bark), internodes long to short; leaves alternate or opposite, flat to terete, slightly to strongly succulent, not deciduous (but sometimes whole stems deciduous), axils appearing naked but always with hardly noticeable to conspicuous tufts of hairs (rarely bristles or scales), rarely with a contracted short-shoot producing leaves (Figs 5, 6).

Distribution Worldwide in tropical to temperate regions but with centers of diversity in South America, Africa, and Oceania, usually open arid to semi-arid sandy to rocky places, in scrub and deciduous forests, but also opportunistic and as weeds.

Systematics A genus of 60–100 species of unequivocal circumscription.

Physiology CAM appears to be widespread (Kluge and Ting 1978). *Portulaca grandiflora* shows inducible CAM in the stem and CAM-cycling in combination with C4 photosynthesis in the leaves (Guralnick and others 2002). Kranz anatomy is widespread (Nyananyo 1988) and perhaps even characteristic. According to Franz (1908), *Portulaca* is the only genus of Portulacineae showing Kranz anatomy, indicating C4 metabolism.

***Grahamia* Gill. s. str. (only *G. bracteata*)**

Description Perennial, presumably long-lived small shrubs with fleshy taproot; stems with long internodes, lignescent and not succulent; leaves alternate, terete, succulent, annually ± deciduous or shortly persistent (Fig 16).

Distribution South America (Argentina), dry scrub (*monte*).

Systematics and distribution Recent molecular systematic studies (Hershkovitz and Zimmer 1997; Nyffeler 2007) indicate that *Grahamia* s. lat. (Rowley 1994, 1995) does not represent a monophyletic group but rather a cladistically basal grade. The monotypic *Grahamia* s. str. and the morphologically similar monotypic genus *Talinopsis* from southern United States (New Mexico, W Texas) and neighboring Mexico form a basal grade within the tribe Anacampseroteae (Nyffeler 2007).

Physiology No data available.

***Anacampseros* Mill. s. lat. (incl. *Avonia* (Fenzl) G. D. Rowley)**

Description Dwarf, perennial, presumably long-lived herbs with tuberous roots or taproots; stems usually contracted and short with short internodes, sometimes forming a swollen basal caudex with slender short-lived short aerial shoots; leaves usually alternate and arranged in rosettes, flat but much thickened and strongly succulent, axils with hairs and/or bristles or a rigid to papery scale.

Distribution South and east Africa, Australia; dry to very dry sandy to rocky places.

Systematics and evolution A genus of about 25 species. Species with axillary scales are sometimes separated at generic level as *Avonia* (Rowley 1994, 1995). Three species of dwarf perennial herbs with rosulate succulent leaves from North and South America recognized either as monotypic genera (*Talinaria* and *Xenia*; Gerbaulet 1992) or included in *Grahamia* s. lat. (Rowley 1994, 1995) are best included in an expanded genus *Anacampseros* s. lat. based on insights from molecular phylogenetic investigations and morphological reasoning (Nyffeler 2007).

Physiology: C3 and inducible full CAM in *Anacamperos* sect. *Anacampseros* (Guralnick and Jackson 2001); reports for *Anacampseros* sect. *Avonia* differ between exclusively C3 (Schütte

and others 1967) and inducible CAM (Rundel and others 1999).

ACPT Clade—Cactaceae

Pereskia Mill.

Description Perennial, long-lived shrubs to small trees, roots fibrous or tuberous; stems with long internodes, slightly thickened and herbaceously succulent when young, soon becoming strongly woody and epidermis replaced by bark; leaves alternate, seasonally deciduous, flat, not or slightly fleshy; leaf axils with a contracted short shoot forming an indefinite number of spines and sometimes also seasonally deciduous leaves for many years.

Distribution Southern Mexico to northern Argentina and Peru, Caribbean; deciduous to semi-deciduous dry forest and open cactus scrub.

Systematics and evolution The genus (17 species; Leuenberger 1986) in its present circumscription is paraphyletic and falls into a northern clade (Pereskia I; Fig 13) and a southern clade (South America, Andean region) (Pereskia II) on molecular grounds (Edwards and others 2005; Butterworth and Edwards, this volume, pp 46–53). The southern *Pereskia* clade is united by the presence of stem stomata and a persistent green epidermis, which are traits they also share with other cacti (the "core cacti," consisting of Opuntioideae, Cactoideae, and *Maihuenia*—though it appears these traits were subsequently lost in *Maihuenia*)

Physiology CAM-cycling is present in leaves of all studied species of *Pereskia* even under well-watered conditions. Drought-induced full CAM has been recorded in leaves of *Pereskia guamacho* (Edwards and Diaz 2006). Significant CAM-cycling has also been found in the stems of some species (Martin and Wallace 2000).

Maihuenia Phil.

Description Perennial, long-lived, small cushion-forming shrublets with a fleshy taproot; stems short with short internodes, succulent (medulla, cortex) becoming slightly woody with age, epidermis rapidly covered by a translucent periderm; leaves linear, terete, succulent, seasonally mostly deciduous, axils with an areole producing spines only.

Distribution South America (Argentina, Chile); open gravelly to sandy places, cool climates.

Systematics and evolution A genus of two species (Leuenberger 1997) that was previously included in subfamily Pereskioideae due to the lack of any obvious synapomorphic characteristics. The succulent but hardly photosynthetic stems with stomata confined to the areolar pits are a remarkable development in a relictual lineage from alpine habitats (Mauseth 1999).

Physiology C3 with limited CAM-cycling in both stems and leaves (Nobel and Hartsock 1986; Mauseth 1999; Martin and Wallace 2000).

Opuntia

Description Perennial long-lived small shrubs to large trees with fibrous or rarely fleshy roots; stems succulent, flattened, segmented, green cladodes; leaves only as rapidly caducous, terete, green rudiments, axils with an areole producing an indefinite number of spines and numerous glochids (minutely barbed, bristle-like spines), often active for many years.

Distribution Southwest Canada to central Argentina with a center of diversity in

Figure 10. *Talinum triangulare.* **Figure 11.** *Talinella boiviniana.* **Figure 12.** *Basella excavata.*

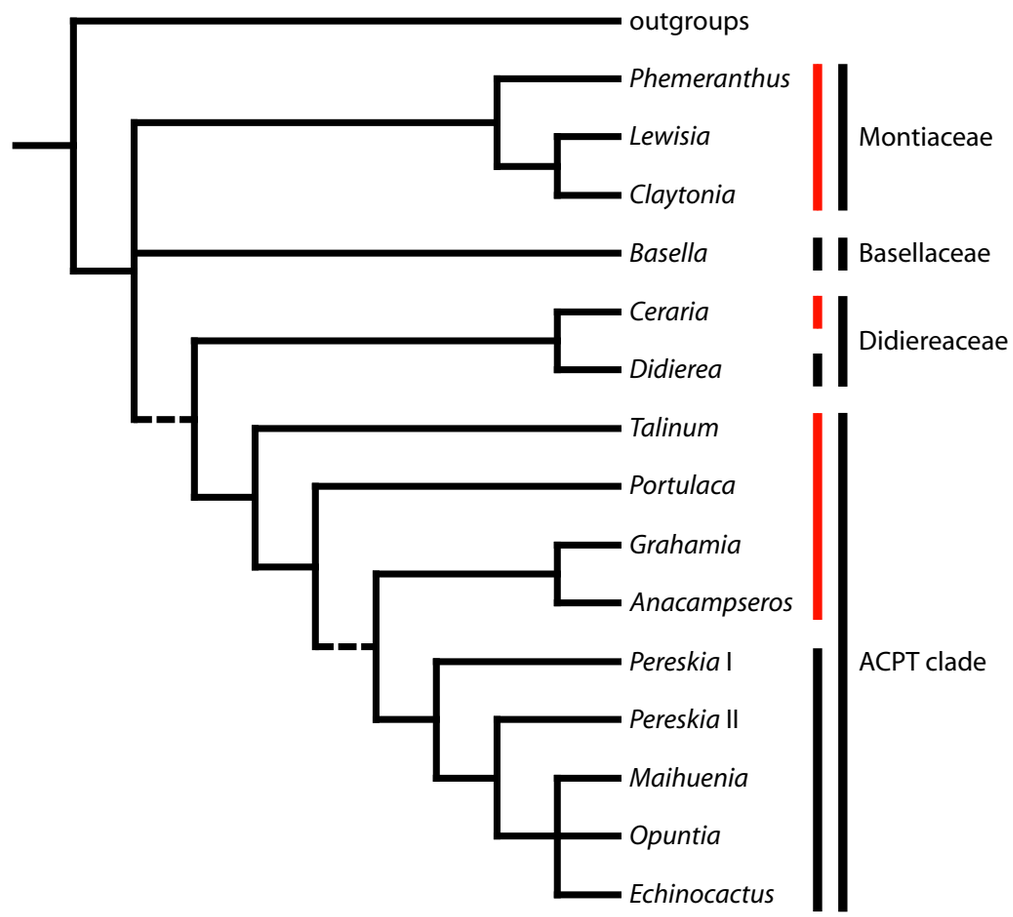


Figure 13. Summary topology of 15 representatives of the suborder Portulacineae classified into three monophyletic families (that is, Montiaceae, Basellaceae, Didiereaceae) and the ACPT clade. This latter subclade consists of a grade of three genera from traditional Portulacaceae and a monophyletic Cactaceae (based on Nyffeler 2007). Red bars mark representatives of traditional Portulacaceae (for instance, Carolin 1993). Dashed branches indicate limited statistical support for the corresponding clade.

Mexico and the southern USA; usually open places or among deciduous to semi-deciduous scrub or forest.

Systematics and evolution While some authors treat the genus in a broad sense (that is, including the vast majority of the species of subfamily Opuntioideae), Wallace and Dickie (2002) have found that this results in a paraphyletic classification. In the narrow sense, *Opuntia* (~180 species, still the largest genus of the family) is restricted to the "prickly pears," with their typically flattened and jointed stem segments (aka cladodes or pads). In these "platyopuntias" only rudimentary and early caducous leaves are formed, but the genera *Pereskiopsis* and *Quiabentia* of the same subfamily produce fleshy, seasonally deciduous leaves as main photosynthetic organs. The seeds, which are covered with bony hard aril, are diagnostic for the subfamily (except *Pterocactus* with flattened winged seeds). The second diagnostic character for the subfamily is the presence of glochids.

Physiology Obligate full CAM appears to be ubiquitous in Opuntioideae (Gibson and Nobel 1986; Nobel 1988; for lists of taxa see Gibson 1996: 118 and Sayed 2001).

Echinocactus Link & Otto

Description Perennial long-lived one- to several-headed stem-succulents; stem grossly enlarged, barrel-shaped, with vertically oriented ribs; leaves as microscopic rudiments only; axils with a well-developed areole producing a small but indefinite number of spines and then becoming dormant; flowers solitary from the upper end of the areole, architecture of flower

and fruits as in *Pereskia* but ovary inferior; seeds brown to black, without strophiole.

Distribution North America (southern USA, Mexico), in open, semi-arid to highly arid rocky or gravelly places.

Systematics A genus of six species, here standing as representative of subfamily Cactoideae, which embraces about 80% of total cactus diversity.

Physiology As for *Opuntia*.

The cacti: just another weird Portulacineae

Even without detailed analyses, several clear themes emerge when looking at the distribution of traits across these lineages. (1) It appears that virtually all Portulacineae exhibit some degree of succulence, whether in leaf, stem or root tissue. (2) Crassulacean acid metabolism is prevalent as CAM-cycling, and it seems likely that all Portulacineae species have some ability to at least recycle respired CO_2 during times of drought. (3) With the notable exception of some Montiaceae (that is, *Claytonia*, some *Lewisia*, *Montia*), most Portulacineae inhabit warm, drought-prone environments. Due to their ubiquitous distribution, it is highly probable that these traits are plesiomorphic for the group and thus also characterize ancestral Cactaceae (for similar arguments see Griffith 2004). This allows us to begin to develop a picture of the ecological and morphological conditions that preceded, and potentially promoted, the transition to the cactus life form in Portulacineae.

Using anatomical, physiological, and environmental data from extant *Pereskia* populations, Edwards and Donoghue (2006) hypothesized that several key functional traits were present in cacti prior to the evolution of the cactus life form, including (1) intolerance of large water deficits in tissues, (2) high photosynthetic water-use efficiency, (3) conservative stomatal behavior with inducible CAM photosynthesis, (4) distribution in warm, seasonally dry habitats, (5) a shallow root system that can quickly absorb water from infrequent and unpredictable rainfall events, and (6) some ability to buffer water deficits through the release of water stored in various tissues (that is, succulence). This model of the ancestral cactus is highly consistent with inferences (using the above summaries of ecological and morphological characteristics) of Portulacineae ecological function, suggesting that these traits not only preceded the evolution of the cactus lifeform, but may also have been the condition from which the highly specialized *Anacampseros* lineage of the succulent Karoo and the pachycaulescent Didiereaceae of Madagascar and Africa evolved. This parallel evolution of distinct succulent life-forms among three closely related lineages and from potentially very similar ancestral conditions presents an unequaled opportunity for comparative studies of the different ways to "be" a succulent plant. How do these groups compare in terms of water storage capacity, drought tolerance, stomatal behavior, or growth rates? Do these different succulent strategies occupy a similar breadth of ecological space? At the outset, the cacti stand apart from the others in several important ways: they are the only Portulacineae lineage to transfer all photosynthetic function to stem cortical tissue (with the potential exception of *Decarya*, but functional studies are needed), and they are also the only lineage to evolve obligate CAM photosynthesis. They are also undeniably more "successful," whether this is measured by sheer ecological abundance or species diversity. This may lead one to infer that these traits confer some large advantages over the other growth forms, but there are many historical contingencies to consider. Are the cacti much older than Didiereaceae or Montiaceae? Does biogeography and timing matter (for instance, were the cacti just in the "right place at the right time")? Dating the Portulacineae phylogeny, combined with more rigorous analyses of historical biogeography in this group, should provide us with key information in this regard.

Figure 14. *Phemeranthus spinescens.* **Figure 15.** *Decarya madagascariensis.* **Figure 16.** *Grahamia bracteata*

The road to succulence: a one-way street?

It is also tempting to view evolution in the Portulacineae as a repeated, inevitable transition from mild succulence to extreme succulence. The evolution of the core cacti from woody, mildly succulent *Pereskia*-like ancestors, for example, appears to be mirrored in the evolution of succulent *Anacampseros* from the woody, thin-stemmed, mildly succulent *Grahamia*. Is this a reversible trend? Currently, we don't have much evidence of evolution occurring in the opposite direction, though some species of Cactaceae (for instance, *Disocactus*, *Epiphyllum*, *Lepismium*, *Rhipsalis*) appear to have lost much of their succulence during evolution. We are only at the outset of investigating aspects of the adaptive strategy to evolve succulent shoots under different environmental conditions (for instance, Mauseth 2000).

Better phylogenetic resolution of some of the less well known and more variable groups (*Talinum*, *Portulaca*) will be critical for addressing this question (and critical also for more accurate reconstructions of ancestral character states in Portulacineae).

In conclusion, we feel there is much to learn about early cactus evolution from gaining a deeper understanding of the evolutionary history of the cacti's close relatives—a veritable potpourri of enigmatic and woefully understudied succulents with different life form characteristics.

Literature Cited

Anderson EF. 2005. *Das grosse Kakteenlexikon*. Ulmer Verlag. Stuttgart. (Augmented and corrected German translation of the original English edition of 2001: *The cactus family*. Timber Press. Portland.)

Applequist WL, Wallace RS. 2001. Phylogeny of the portulacaceous cohort based on *ndhF* sequence data. *Systematic Botany* 26: 406–419.

Applequist WL, Wallace RS. 2003. Expanded circumscription of Didiereaceae and its division into three subfamilies. *Adansonia* ser. 3 25: 13–16.

Applequist WL, Wagner WL, Zimmer EA, Nepokroeff M. 2006. Molecular evidence resolving the systematic position of *Hectorella* (Portulacaceae). *Systematic Botany* 31: 310–319.

Butterworth CA, Wallace RS. 2005. Molecular phylogenetics of the leafy cactus genus *Pereskia* (Cactaceae). *Systematic Botany* 30: 800–808.

Cuénoud P, Savolainen V, Chatrou, LW, Powell M, Grayer RJ, Chase MW. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbcL*, *atpB*, and *matK* DNA sequences. *American Journal of Botany* 89: 132–144.

Edwards EJ. 2006. Correlated evolution of stem and leaf hydraulic traits in *Pereskia* (Cactaceae). *New Phytologist* 172: 479–489.

Edwards EJ, Diaz M. 2006. Ecological physiology of *Pereskia guamacho*, a cactus with leaves. *Plant Cell and Environment* 29: 247–256.

Edwards EJ, Donoghue MJ. 2006. *Pereskia* and the origin of the cactus life-form. *American Naturalist* 167: 777–793.

Edwards EJ, Nyffeler R, Donoghue MJ. 2005. Basal cactus phylogeny: implications of *Pereskia* (Cactaceae) paraphyly for the transition to the cactus life-form. *American Journal of Botany* 92: 1177–1188.

Eggli U, editor. 2002. *Illustrated handbook of succulent plants*: *dicotyledons*. Springer Verlag. Berlin.

Franz E. 1908. Beiträge zur Kenntnis der Portulacaceen und Basellaceen. *Botanisches Jahrbuch für Systematik*, *Pflanzengeschiche und Pflanzengeographie 42* (*Beiblatt 97*): 1–46.

Gerbaulet M. 1992. Die Gattung *Anacampseros* L. (Portulacaceae). I. Untersuchungen zur Systematik. *Botanische Jahrbücher für Systematik*, *Pflanzengeschiche und Pflanzengeographie* 113: 477–564.

Gibson AC. 1996. *Structure-function relations of warm desert plants. Adaptations of desert organisms*. Springer-Verlag. Berlin.

Gibson AC, Nobel PS. 1986. *The cactus primer*. Harvard University Press. Cambridge, Massachusetts.

Griffith MP. 2004. What did the first cactus look like? An attempt to reconcile the morphological and molecular evidence. *Taxon* 53: 493–499.

Guralnick LC, Jackson MD. 2001. The occurrence and phylogenetics of Crassulacean Acid Metabolism in the Portulacaceae. *International Journal of Plant Sciences* 162: 257–262.

Guralnick LC, Edwards G, Ku MSB, Hockema B, Franceschi VR. 2002. Photosynthetic and anatomical characteristics in the C4-crassulacean acid metabolism-cycling plant, *Portulaca grandiflora*. *Functional Plant Biology* 29: 763–773.

Hershkovitz MA. 2006. Ribosomal chloroplast DNA evidence for diversification of western American Portulacaceae in the Andean region. *Gayana Botanica* 63: 13–74.

Hershkovitz MA, Hogan SB. 2002. *Lewisia*. *Illustrated Handbook of succulent plants*: *dicotyledons*. Eggli U, editor. Springer Verlag. Berlin. pp 388–394.

Hershkovitz MA, Hogan SB. 2003. *Lewisia*. *Flora of North America*. FNA Editorial Committee. Oxford University Press. New York. 4: 476–485.

Hershkovitz MA, Zimmer EA. 1997. On the evolutionary origins of the cacti. *Taxon* 46: 217–242.

Hershkovitz MA, Zimmer EA. 2000. Ribosomal DNA evidence and disjunctions of western American Portulacaceae. *Molecular Phylogenetics and Evolution* 15: 419–439.

Hunt DR, editor. 2006. *The new cactus lexicon*. DH Books. Millborne Port.

Kluge M, Ting IP. 1978. Crassulacean Acid Metabolism. Analysis of an Ecological Adaptation. *In* Billings WD, Golley F, Lage OL, Olson JS, editors. *Ecological Studies*. *Analysis and Synthesis*. Vol. 30. Springer-Verlag. Berlin.

Kluge M, Razanoelisoa B, Brulfert J. 2001. Implications of genotypic diversity and phenotypic plasticity in the ecophysiological success of CAM plants, examined by studies in the vegetation of Madagascar. *Plant Biology* 3: 214–222.

Leuenberger BE. 1986. *Pereskia* (Cactaceae). *Memoirs of the New York Botanical Garden* 41: 1–141.

Leuenberger BE. 1997. *Maihuenia*—monograph of a Patagonian genus of Cactaceae. *Botanische Jahrbücher für Systematik*, *Pflanzengeschiche und Pflanzengeographie* 119: 1–92.

Mabry TJ. 1977. The order Centrospermae. *Annals of the Missouri Botanical Garden* 64: 210–220.

Martin CE, Wallace RS. 2000. Photosynthetic pathway variation in leafy members of two subfamilies of the Cactaceae. *International Journal of Plant Sciences* 161: 639–650.

Mauseth JD. 1999. Anatomical adaptations to xeric conditions in *Maihuenia* (Cactaceae), a relictual, leaf-bearing cactus. *Journal of Plant Research* 112: 307–315.

Mauseth JD. 2000. Theoretical aspects of surface-to-volume ratios and water-storage capacities of succulent shoots. *American Journal of Botany* 87: 1107–1115.

Mauseth JD, Landrum JV. 1997. Relictual vegetative anatomical characters in Cactaceae: the genus *Pereskia*. *Journal of Plant Research* 110: 55–64.

Nobel PS. 1988. *Environmental biology of agaves and cacti*. Cambridge University Press. Cambridge, Massachusetts.

Nobel PS, Hartsock T. 1986. Leaf and stem CO_2 uptake in the three subfamilies of the Cactaceae. *Plant Physiology* 80: 913–917.

Nyananyo BL. 1988. Leaf anatomical studies in the Portulacaceae (Centrospermae), with regards to photosynthetic pathways. *Folia Geobotanica Phytotaxonomica* 23: 99–101.

Nyffeler R. 2007. The closest relatives of cacti: insights from phylogenetic analyses of chloroplast and mitochondrial sequences with special emphasis on relationships in the tribe Anacampseroteae. *American Journal of Botany* 94: 89–101.

Ogburn RM. 2007. *Anatomical variation in Cactaceae sensu lato*. Master Thesis, University of Missouri. St Louis.

Rauh W. 1979. *Kakteen an ihren Standorten*. Verlag Paul Parey. Hamburg, Germany.

Rowley GD. 1994. *Anacampseros* and allied genera. A reassessment. *Bradleya* 12: 105–112.

Rowley GD. 1995. *Anacampseros*, *Avonia*, *Grahamia*. *A grower's handbook*. British Cactus and Succulent Society.

Rowley GD. 1997. *A History of Succulent Plants*. Strawberry Press. Mill Valley, California.

Rundel PW, Esler KJ, Cowling RM. 1999. Ecological and phylogenetic patterns of carbon isotope discrimination in the winter-rainfall flora of the Richtersveld, South Africa. *Plant Ecology* 142: 133–148.

Sayed OH. 2001. Crassulacen Acid Metabolism 1975–2000, a check list. *Photosynthetica* 39: 339–352.

Schütte KH, Steyn R, van der westhuizen M. 1967. Crassulacean Acid Metabolism in South African succulents: A preliminary investigation into its occurrence in various families. *Journal of South African Botany* 33: 107–110.

Sperling CR, Bittrich V. 1993. Basellaceae. *The families and genera of vascular plants*. Kubitzki K, editor. Springer Verlag. Berlin. 2: 143–146.

von Willert DJ, Eller BM, Werger MJA, Brinckmann E, Ihlenfeldt HD. 1992. *Life strategies of succulents in desert with special reference to the Namib desert*. Cambridge University Press. Cambridge, Great Britain.

Wallace RS, Dickie SL. 2002. Systematic implications of chloroplast DNA sequence variation in the Opuntioideae. *Studies in the Opuntioideae* (*Cactaceae*). Hunt DR, Taylor NP, editors. David Hunt. Sherborne. 6: 9–24.

Winter K, Smith JAC, editors. 1996. *Crassulacean Acid Metabolism*. *Biochemistry*, *ecophysiology and evolution*. Springer Verlag. Berlin.