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What did the first cactus look like? An attempt to reconcile the morphological and molecular evidence

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THE EXTANT DIVERSITY OF CACTUS FORM

Cacti have fascinated students of natural history for many millennia. Evidence exists for use of cacti as food, medicine, and ornamental plants by peoples of the New World for at least 9,000 years (Anderson, 2001), and cacti have captivated the attention of Old World plant scholars, agriculturists, and hobbyists since their introduction in the late 15th century. The striking visual aspect of the succulent, spiny, often leafless plants has received much attention, and botanists have been pondering their evolutionary relationships for over a century.

Three subfamilial groups have been traditionally recognized within Cactaceae. The easiest group to circumscribe morphologically is Opuntioideae, with minute, barbed, deciduous spines (termed glochids), and small, often ephemeral leaves. Additionally, Opuntioideae have a bony seed aril (Vaupel, 1925; Anderson, 2001). This subfamily includes the familiar prickly pears of the genus *Opuntia* Mill. (Fig. 1A), plus many other morphotypes. Another large group of cacti are subfamily Cactoideae, which include leafless, spiny stem succulents such as the genus *Trichocereus* Riccob. (Fig. 1B). Cactoideae are very diverse in habit and morphology, and the vast majority of described cactus species fall into this group. The remaining subfamily Pereskioideae includes leafy, spiny, often non-succulent trees and shrubs of the genus *Pereskia* Mill. (Fig. 1C).

In addition to these three long- and widely-recognized subfamilies, recent molecular evidence supports the recognition of a fourth subfamily of cacti, the monogeneric Maihuenioideae (Wallace, 1995a, b; Nyffeler, 2002). *Maihuenia* Phil. contains two little-studied species of smaller, succulent, cushion-forming cacti that are restricted to western and southern South America (Leuenberger, 1992a, b; 1997; Mauseth, 1999), and were variously included in Opuntioideae and Pereskioideae [and at times in a broadly circumscribed Cactoideae: Vaupel, 1925 (as Malacospermae); Hunt & Taylor, 1986].

EARLY HYPOTHESES ON CACTUS EVOLUTION

To estimate evolutionary relationships many authors determine which morphological features are primitive or ancestral versus advanced or derived. One assumption often made (Bessey, 1915; Cronquist, 1981) is that a common morphological state (one shared by many members of a group) should be considered a primitive condition. Among cacti, many traits are common, such as spininess and polytepaly, and we might safely assume that these represent ancestral conditions for the extant cacti. But, as cacti are highly specialized plants, it is difficult to determine which character states are ancestral or derived relative to other angiosperms.

The question of the Cactaceae's relationship to other plants has long been addressed morphologically. In an extremely influential early work, N. L. Britton and J. N. Rose (1919) hypothesized that the leafy genus *Pereskia* (Fig. 1C) was the closest relative to other angiosperms, and the leafy opuntoid genus *Peresklopsis* Britton & Rose (Fig. 1D) was the closest relative of *Pereskia* among the other cacti; in other words, *Pereskia* represented a primitive morphology, Opuntioideae a somewhat more advanced morphology, and Cactoideae (Cereae sensu Britton & Rose) a very derived morphology (Fig. 2). This early phylogenetic hypothesis (*Pereskia*-as-primitive) has had a great impact upon further work. Most subsequent treatments advance this hypothesis without taking a strong stand on the other subfamilial relationships (e.g., Cronquist, 1981; also Gibson & Nobel, 1986; Barthlott & Hunt, 1993), while some recent phylogenetic papers even state this hypothesis as well-supported (Hershkovitz & Zimmer, 1997; Martin & Wallace, 2000), even when the data cited or presented therein may not support this conclusion (see below). Morphological and anatomical studies of *Pereskia* also support that these plants possess characters found in other dicot families (Leuenberger, 1986; Mauseth & Landrum, 1997; Landrum, 2002) including ordinary dicot wood and broad leaves. Most notably however, some *Pereskia* species possess superior ovaries (*Rhodocactus* (A. Berg.) Knuth), a character state that is

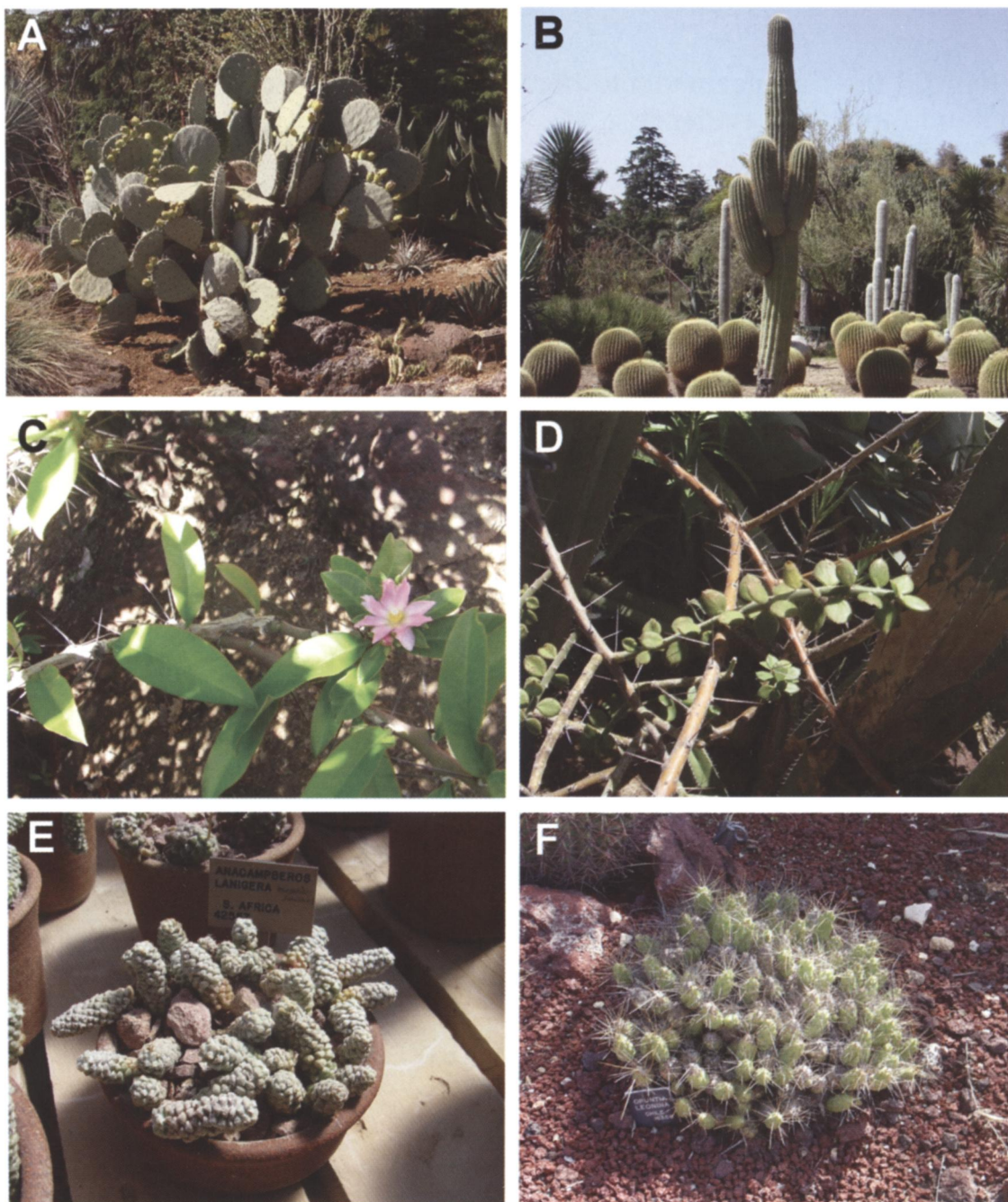


Fig. 1. Examples of the diversity of extant cactus form that may illuminate early cactus evolution. All plants pictured here are growing at the Huntington Botanical Gardens, San Marino, California, U.S.A. A, an example from subfamily Opuntioideae: *Opuntia robusta* Wendl. The jointed stems are typical for this subfamily, although the stem segments may be of various shapes. Glochids and bony seed arils also hold this group together morphologically. B, a representative of Cactoideae: *Trichocereus pasacana* Britton & Rose. Members of this subfamily lack leaves and glochids. Other architectural diversity of this subfamily can be seen in the background and foreground. C, *Pereskia grandifolia*, in Pereskioideae. The non-succulent woody shoots and abundant foliage of these plants may have led Britton and Rose (1919) to declare them the most primitive cacti. D, *Pereskiaopsia aquosa* (F. A. C. Weber) Britton & Rose. The glochids and seed structure led Britton & Rose (1919) to place this taxon in Opuntioideae, and this has been confirmed by molecular analyses (Griffith, 2002; Wallace & Dickie, 2002). E, *Anacampseros lanigera* Burch. (Portulacaceae). Diminutive, succulent plants like this are the closest extant relatives of Cactaceae (Hershkovitz & Zimmer, 1997; Applequist & Wallace, 2001). F, *Maihueniopsis glomerata* (Haw.) R. Kiesling (Opuntioideae). Such a taxon is probably plesiomorphic within Opuntioideae, and may possibly represent many character states of the earliest cacti.

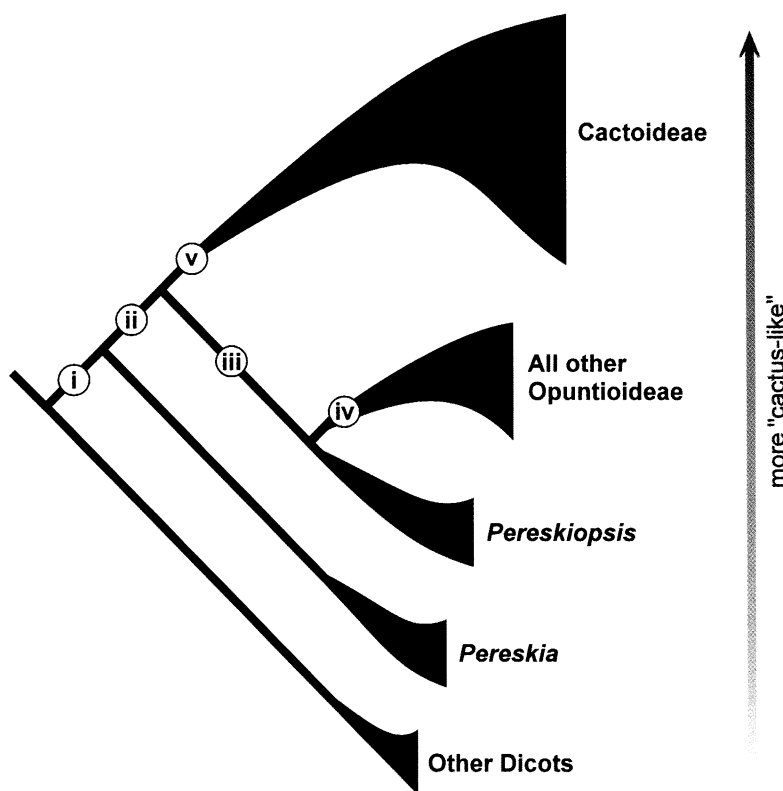


Fig. 2. Phylogram depicting traditional (and widely accepted) morphological phylogeny of Cactaceae, adapted from Britton & Rose (1919), with a primitive *Pereskia* and highly derived Cactoideae (Cereae sensu Britton & Rose). Character evolution depicted here: i, a woody, broad-leaved common ancestor of Cactaceae, reduction of short shoots into areoles and bud scales into spines; ii, development of succulent stems; iii, development of glochids and bony seed arils (Opuntioideae); iv, reduction of leaves to terete-succulent and mostly ephemeral; v, complete loss of leaves (Cactoideae).

often relictual (Cronquist, 1981; Takhtajan, 1991). Shared morphological characters, however, may occasionally reflect convergent adaptation via natural selection instead of, or in addition to, reflecting close evolutionary relationship.

The *Pereskia*-as-primitive hypothesis is supported by other evolutionary considerations. One often-proposed mechanism for evolution in Cactaceae that is a natural corollary of the *Pereskia*-as-primitive idea is pedomorphic reduction or neotony (Boke, 1944; Buxbaum, 1956; Anderson, 1986). If the first cacti were leafy trees or shrubs, many extant cacti would be considered reduced forms. Recent theoretical work, however, proposes that increased size (of plants with a conserved shape) may be adaptive in cacti (Mauseth, 2000, 2004), and might then represent a derived character state in some Cactoideae and Opuntioideae. This would not apply to *Pereskia*, however, as this genus probably has the highest surface area/volume ratio of any cacti.

Pereskia certainly does resemble other non-cactaceous plants morphologically and anatomically, but

whether it represents the early morphology of Cactaceae is not clear. It is difficult to draw phylogenetic inferences and determine plesiomorphies without reference to a specific outgroup. The work of Britton and Rose remains an invaluable contribution to our knowledge of cacti, but it is possible that the morphological evolutionary hypotheses presented therein may be influenced by possible bias toward the temperate, mesic, broad-leaved regions that they (and many 19th and 20th century botanists) inhabited and knew so thoroughly; even if a broadleaf shrub can (perhaps) be thought of as a typical dicot, the closest relatives to cacti still might not fit this concept.

Morphologies of organisms are subject to and influenced by environmental pressures; natural selection operates on the forms of plants, resulting in the diverse adaptations we now see. Perhaps the non-cactus-like shoots and leaves of *Pereskia* represent an example of convergent evolution via natural selection. Recent phylogenetic research may provide insight into this question.

WHAT IS THE MOLECULAR EVIDENCE?

An extremely useful feature of molecular phylogenetics is its ability to inform us about character evolution. Molecular phylogenetic research of Cactaceae has been slower to develop than in other groups, but a growing body of evidence is now available to begin to test hypotheses about cactus evolution. Recently published work presents independent molecular phylogenies that are not entirely consistent with the *Pereskia*-as-primitive hypothesis. Although some do advance this hypothesis, often uninformative data, or data that are in conflict with that conclusion, are presented. This work is briefly reviewed and summarized below:

Wallace, 1995a. — This important early paper on the molecular phylogenetics of Cactaceae presented a phylogeny of the genus *Pereskia* in which five lineages were shown forming a basal polytomy for the group. In other words, the relationships among these five lineages were unclear. A landmark paper in cactus evolution (Hershkovitz & Zimmer, 1997; discussed below) cited Wallace (1995a) as providing molecular evidence that Pereskioideae are basalmost within Cactaceae, but this conclusion was not stated or supported. Wallace presented either three (*Maihuenia*, *Pereskia* + Cactoideae, and Opuntioideae), or four (each subfamily) distinct early-diverging lineages, not fully resolved by the data. Interestingly, in one analysis *Pereskia* and one representative cactoid (*Leptocereus quadricostatus* Britton & Rose) formed an unresolved clade distinct from *Maihuenia* and Opuntioideae; this relationship actually suggested that *Maihuenia* and/or Opuntioideae may be relatively older than *Pereskia*.

Wallace 1995b. — This important work began a recent movement to recognize a fourth subfamily of Cactaceae, Maihuenioideae (Wallace, 1995b; Anderson, 2001), as it represents a deep lineage within the family. This monogeneric subfamily contains two species of diminutive, mat- or cushion-forming cacti with terete-succulent leaves; i.e., one of the earliest-diverging cactus groups would be comprised of diminutive succulents. *Maihuenia* was found to be as different from the other subfamilies as they are from each other.

Hershkovitz & Zimmer, 1997. — This paper sampled three genera of cacti believed to be relictual (*Maihuenia*, *Pereskia*, and *Peresklopsis*), but the resolution among these genera (in different subfamilies) was unclear. The very important conclusion (and focus of this paper) however, was that Cactaceae are nested within Portulacaceae. Some nearest relatives of Cactaceae predicted by this work are *Anacampseros* L. (Fig. 1E), *Talinum* Adans., and *Talinella* Baill., which are diminutive and often succulent (and not broadleaf, semisuccu-

lent shrubs and trees similar to *Pereskia*). Also mentioned (briefly) was the possibility that cacti in non-arid environments might be descended from cacti that were arid-adapted, although this was not discussed in context of the *Pereskia*-as-primitive hypothesis.

Martin & Wallace, 2000. — This important paper investigated the photosynthetic modes of cactus leaves in a phylogenetic context. The authors advanced the phylogenetic hypothesis that *Pereskia* represents an ancestral character suite and basal lineage among Cactaceae, and that persistent leafiness is a primitive character state within Opuntioideae and Cactaceae. However, the pattern of relationships displayed (derived from restriction site and *rpl16* cpDNA sequence data) actually supports three equivocally deep clades (Opuntioideae, Maihuenioideae, and *Pereskia* + Cactoideae), again suggesting that opuntioids or *Maihuenia* may be relatively older than *Pereskia*. Phylogenetic relationships were not the main focus of this paper, however.

Applequist & Wallace, 2001. — Further insight into the closest outgroups of Cactaceae is found in this paper, which demonstrates a close phylogenetic relationship between Cactaceae and diminutive, stem-succulent geophytic or caudiciform members of Portulacaceae, such as *Anacampseros* (Fig. 1E), *Grahamia* Gill., *Portulaca* L., *Talinum*, and *Talinopsis* A. Gray. As in Hershkovitz & Zimmer (1997), the relationships among subfamilies of cacti were not well resolved (although in one analysis Opuntioideae appear sister to Pereskioideae and Maihuenioideae). Again, the morphological relationships of these diminutive succulents to *Pereskia* were not addressed.

Nyffeler, 2002. — Recent, thorough work demonstrated that the deepest lineage within subfamily Cactoideae is the diminutive, succulent genus *Blossfeldia* Werderm. This finding generates controversy (Gorelick, 2002) because although it challenges morphological phylogenies based on the Britton and Rose concept, it parallels what the earlier papers (above) have predicted, and what current work (below) supports—that diminutive, stem-succulent (often geophytic) plants represent deep lineages in Cactaceae. Also supported here (but less robustly) is the traditional hypothesis that *Pereskia* species are early-diverging lineages in Cactaceae, yet they appear paraphyletic with respect to other cacti.

Wallace & Dickie, 2002. — A recent paper proposed that the (often leafy) genus *Austrocylindropuntia* Backeb. is deepest (“basal” sensu Wallace) within subfamily Opuntioideae, although their data actually do not support this conclusion (five equivocally deep lineages are shown, not one). However, the authors note contradiction with the Britton & Rose (1919) hypothesis that

Pereskioopsis is the most primitive opuntoid.

Griffith, 2002, 2003. — This work focusing on relationships among subfamily Opuntioideae provided preliminary evidence that Opuntioideae may be sister to all other cacti, i.e., that opuntoids might represent the deepest lineage. This research supports a deep lineage (and possibly an ancestral character suite) for Opuntioideae that is represented by extant members of the genus *Maihueiopsis* Speg., a diminutive, stem-succulent, often geophytic taxon (Fig. 1F). Additionally, this work demonstrates that persistent leafiness (as in the genera *Austrocylindropuntia*, *Pereskioopsis*, and *Quiabentia* Britton & Rose) represents a derived morphological character state in Opuntioideae.

PROBLEMS WITH THE MOLECULAR MODEL

A consensus of evolutionary inferences gleaned from molecular data suggests that an alternative to the *Pereskia*-as-primitive hypothesis might be considered. Some of the reasons for reopening this discussion are summarized below.

1. — The relationships among the subfamilies of Cactaceae are not clear. There is conflict among the deep lineages recovered by recent phylogenetic studies (Griffith, 2002; Nyffeler, 2002), although neither analysis is incorrect; both present statistically rigorous inferences of the history of the genes sampled. Other work does not fully resolve these lineages, yet often places *Pereskia* in a relatively derived position (Wallace, 1995a; Martin & Wallace, 2000; Applequist & Wallace, 2001). One paper that does restate the traditional view does not present or cite molecular phylogenetic support for it (Hershkovitz & Zimmer, 1997). *Pereskia* may represent a derived lineage, or perhaps there occurred a rapid radiation of cacti at their origin, and the currently available molecular phylogenetic data may not be enough to fully resolve this pattern of relationship (R. Nyffeler, pers. comm.).

2. — The species of *Pereskia* proposed as relictual (*P. aculeata* Mill. and *P. grandifolia* Haw.) are equivocally deep within a lineage that includes *P. diazromeroana* Cárdenas, *P. humboldtii* Britton & Rose, and *P. weberiana* K. Schum. (Wallace, 1995a), species possessing tuberous roots, a feature found in the deep lineages of Opuntioideae (Griffith, 2002), *Maihueiopsis* (Anderson, 2001), and among the outgroups of Cactaceae (Applequist & Wallace, 2001).

3. — There are interesting similarities among the deep lineages recovered for Cactoideae (Nyffeler, 2002), Opuntioideae (Griffith, 2002), and the genus *Maihueiopsis*.

Blossfeldia, *Maihueiopsis*, and *Maihueiopsis* in many cases share the following characters: morphological reduction, terete or globular stem shape, and absence of broad, persistent, nonsucculent leaves. Additionally, *Maihueiopsis* and *Maihueiopsis* include geophytic species. Also, all three genera are restricted to western and southern South America, where Cactaceae are presumed to have arisen (Griffith, 2002; Nyffeler, 2002; Wallace & Dickie, 2002).

4. — The nearest outgroups predicted for Cactaceae by recent phylogenetic studies are diminutive portulacaceous succulents, including the genera *Anacampseros*, *Talinum*, *Talinella*, and *Portulaca* (Hershkovitz & Zimmer, 1997; Applequist & Wallace, 2001). None of these could rightly be considered a woody, broad-leaved tree or shrub similar to *Pereskia*; in fact, *Pereskia* wood may be considered uniquely ordinary in all of Caryophyllales (J. Mauseth, pers. comm.).

The consensus. — The relationships among the subfamilies are not clearly understood, and Opuntioideae may represent the deepest lineage of Cactaceae. The deep lineages of all subfamilies include geophytic storage tissues, and all deep lineages except Pereskioideae are architecturally simpler plants. The nearest relatives to cacti are not woody, broadleaf shrubs and trees like *Pereskia*, but succulent Portulacaceae, often with reduced leaves and geophytic tissues. All deep lineages of Cactaceae are found in west-central and southern South America (Anderson, 2001). A conceptual model of cactus evolution based on a consensus of the new data is presented in Fig. 3. Looking only at the available molecular evidence, it seems possible that the first cactus may have been a diminutive, portulacaceous succulent (and possible geophyte) that evolved spines, and diversified into the extant cactus flora we now observe. *Pereskia* may represent an early (but not necessarily the earliest) lineage of cacti, which evolved broad leaves and woody stems as it adapted to a non-arid environment, gaining an overall appearance more convergent with ordinary dicots.

We have evidence that essentially leafless lineages of cacti have the potential to derive persistent, often broad leaves (Wallace & Dickie, 2002; Griffith, 2002): *Pereskioopsis*, *Quiabentia*, and *Austrocylindropuntia* (all derived members of Opuntioideae) possess persistent leaves of various degrees of succulence. If we note that a more recently evolved genus, *Pereskioopsis*, has leaves that are less broad, less vascularized, and more succulent than *Pereskia*, we can conceive of what the ancestors of *Pereskia* might have looked like as they began to adapt to more humid regimes. This model contradicts the phylogenetic hypotheses of Britton & Rose, as we imagine ancient, smaller cacti (like *Blossfeldia*, *Maihueiopsis*, and *Maihueiopsis*), gaining a more erect, open habit, with

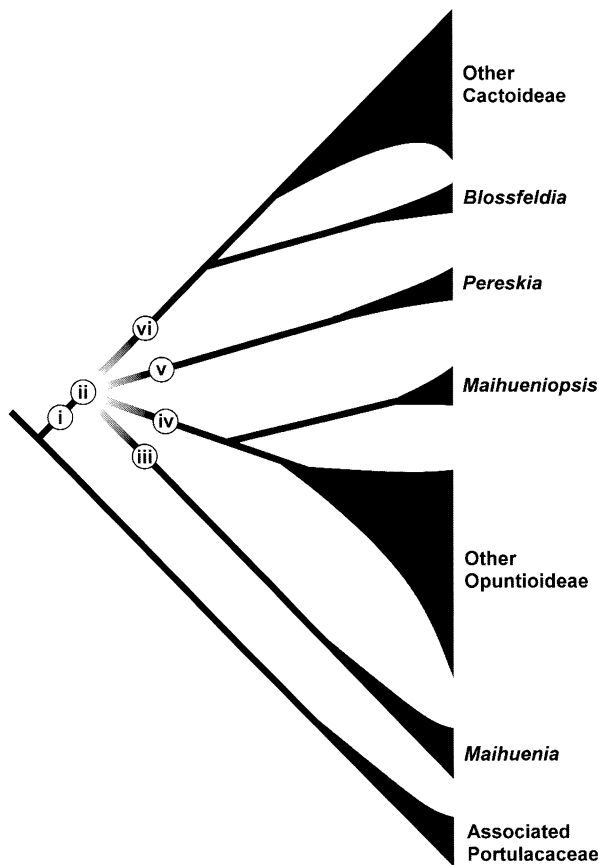


Fig. 3. Conceptual model of the phylogeny of Cactaceae, based on consensus of recent molecular work (see text). Numerated points are as follows: i, a diminutive, succulent, portulacaceous common ancestor of Cactaceae; reduction of short shoots into areoles and bud scales into spines; ii, the relationships among the subfamilies are not resolved; iii, a deep lineage of Cactaceae maintains a smaller, cushion-like, succulent habit (Maihuenioideae); iv, evolution of glochids and bony arils (Opuntioideae); v, one lineage of cacti evolves broad leaves and loses much succulence (Pereskioideae); vi, complete loss of leaves (Cactoideae). This model is open for testing with further research.

persistent leaves (as some *Austrocylindropuntia*), developing broad leaves (such as *Pereskioopsis* and *Quiabentia*), and losing succulence (e.g., *Pereskia*) as they adapt a higher surface area to volume ratio over time.

PROBLEMS WITH THE MOLECULAR MODEL

This model for cactus evolution is difficult to reconcile with the relictual morphological and anatomical features found in *Pereskia*. Several conflicting character

states are reviewed below.

1. — *Pereskia* species with superior ovaries. Some species of *Pereskia* [*Rhodocactus* (A. Berg) Knuth] possess superior ovaries, a trait considered plesiomorphic (Takhtajan, 1991). Superior ovaries are also a character of some Portulacaceae, which is considered the nearest outgroup to Cactaceae. The possession of superior ovaries by these *Pereskia* species supports the idea that *Pereskia* are relictual members of Cactaceae. However, at least one genus of Portulacaceae (*Portulaca* L.) has partially inferior ovaries (Cronquist, 1981), and this genus is supported as a close relative of cacti. The molecular and morphological evidence, then, are both unclear with reference to the polarity of this trait in this group.

2. — *Pereskia* leaves. The leaves of *Pereskia* have a strong midrib and pinnate venation (Leuenberger, 1986), whereas the leaves of *Pereskioopsis* and *Quiabentia* do not (pers. observ.). It may be difficult to conceive of broad, semi- to non-succulent *Pereskia* leaves evolving from a small, succulent-leaved ancestral cactus to superficially resemble those of other dicots. However, the leaves of the related Portulacaceae (e.g., *Anacampseros*, *Talinum*) are fleshy to succulent and lack strong venation (Guralnick & Jackson, 2001). Even if *Pereskia* is relictual amongst cacti, the evolution of its leaf form is still puzzling.

3. — Apparent relictual corollas in *Pereskia*. *Pereskia diaz-roemeriana* has a corolla that consists of five petals, in contrast to the polytepalate corollas of most cacti. This pentapetaly could be considered a primitive trait among cacti. It is possible to conceive of the five-petaled corolla being a derived trait in *P. diaz-roemeriana*. A similar corolla may be found in *Rhipsalis* Gaertn., however, a genus well-supported as derived in the Cactoideae (Nyffeler, 2002). Furthermore, oligomerization of the perianth may also be considered a derived trait among angiosperms (Takhtajan, 1991).

4. — Wood characters of *Pereskia*. *Pereskia* possesses ordinary dicot wood compared to other members of Cactaceae (Anderson, 2001; J. D. Mauseth, pers. comm.); non-pereskioid cacti have massive parenchymatous rays (Terrazas Salgado & Mauseth, 2002). A *Pereskia* lineage, independently deriving ordinary dicot wood characters from a succulent, geophytic ancestor, would involve numerous, synchronous character state changes, and no heterobathmous character states have yet been documented. It is widely held that secondarily derived woody lineages would show anatomical differences from primary woody lineages (e.g., in Asteraceae, Cucurbitaceae; Takhtajan, 1991). However, *Pereskia* is exceptional in its ordinary wood anatomy among Caryophyllales, as most members of this order are marked by anomalous stem structure of some kind (Cronquist, 1981), and we have good support that the

cacti are nested within a derived lineage of the Portulacaceae (Hershkovitz & Zimmer, 1997; Applequist & Wallace, 2001).

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