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The Desert Ignored: Early Cactus Evolution and Interpretation

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ABSTRACT—Cacti are important members of the Chihuahuan Desert flora. Botanists have proposed that stem succulence and reduced or absent leaves represent derived character states for Cactaceae. This hypothesis may be influenced by bias towards temperate, mesic contexts. Molecular phylogenetic papers often present data that does not support the traditional view. Cultural contexts that may affect bias towards traditional cactus evolution hypotheses are explored, and other contexts are demonstrated. I propose estimating early cactus evolution through objective, inclusive use of molecular data, which has less potential bias. As there is conflict among phylogenies for the Cactaceae, an objective view will consider all available works, and not select one phylogeny over others based on congruence with previous hypotheses. A consensus of available molecular data supports the following: the nearest outgroups of Cactaceae are diminutive, succulent Portulacaceae; the relationships among subfamilies are not resolved; most deep lineages of cacti include diminutive succulent plants, with the exception of *Pereskia*. A parsimonious view of character evolution is that early cacti were diminutive succulents, and *Pereskia* represents reversal to broad, non-succulent leaves. Even if *Pereskia* does represent the earliest diverging cacti, *Pereskia* wood, leaves, and size may represent character state reversals rather than transitional forms between succulent Portulacaceae and other cacti.

INTRODUCTION—Cacti are one of the most conspicuous yet most threatened features of the Chihuahuan Desert flora (Fig. 1). Cactaceae are mostly stem succulent plants generally restricted to the New World (Benson 1982; Gibson and Nobel 1986; Anderson 2001). Cacti are believed to have accompanied Columbus on his first return to Lisbon in 1493 (Anderson 2001). Cacti have fascinated naturalists of the Old World since their introduction there in the late 15th century and for much longer in the New World (Anderson 2001). Many economic uses of cacti have long been documented (Emmart 1940 among many others). Cacti have often been thought of as unusual plants, as stem succulence, spinosity, and leaflessness are not found in all dicots. This determination of unusuality may be culturally or contextually influenced, and such possible bias may have influenced interpretation of character state polarity in the Cactaceae.

Many interpretations of character evolution in Cactaceae represent stem succulence and leaflessness as derived features; this interpretation fits best if cacti are considered derived from a hypothetical outgroup that includes broad leaves and woody shoots,



FIG. 1—Cacti are a conspicuous feature of the Chihuahuan Desert flora. *Opuntia aureispina*, Rooney's place, Brewster County, Texas.

features associated with many dicots. The concept of a normal dicot varies between contexts, however. When succulent Portulacaceae (Fig. 2a) are considered the nearest outgroup of Cactaceae (see Hershkovitz and Zimmer 1997; also Applequist and Wallace 2001), this interpretation of character state polarity becomes less parsimonious. Newer data types may be able to inform early character evolution in cacti, but the interpretation has sometimes been subjective (see below).

EXTANT DIVERSITY OF CACTACEAE—Many subfamilial divisions of Cactaceae have been authored. Within the last century, these have mostly divided Cactaceae into three subfamilies based mainly on aspects of the areole (a feature of cacti derived from the short shoot) and the leaf. Subfamily Cactoideae (Fig. 2b) is marked by leafless areoles. Subfamily Opuntioideae (Fig. 2c) has areoles with deciduous spines (termed glochids), and mostly ephemeral leaves. Additionally, bony seed arils mark the opuntiid subfamily (Schumann 1895; Stuppy 2002). The third traditionally recognized subfamily, Pereskioideae (Fig. 2d), possesses broad, non-succulent leaves, and semi- to non-succulent shoots. In addition to these three subfamilies, some recent workers have erected two new groups. Maihuenioideae (Wallace 1995; Fearn 1996; Anderson 2001), containing two species of the genus *Maihuenia* (Fig. 2e), has terete-succulent, persistent leaves, and semi- to fully-succulent stems. The difficulty of placing *Maihuenia* is marked by its various inclusion in the three traditional subfamilies in different treatments (Schumann 1895; Britton and Rose 1919–1923; Benson 1982). Recent DNA research (Nyffeler 2002; Crozier 2004) has prompted the erection of Blossfeldioideae (Crozier 2004), containing the monotypic genus *Blossfeldia* (Fig. 2f). *Blossfeldia liliputiana* is marked by the restriction of stomata to areolar crypts, is entirely leafless at maturity, and is unique among the cacti by being poikilochlorophyllous (Barthlott and Porembski 1996).

Botanists have been pondering the evolutionary relationships of these groups for almost a century. One of the most influential early treatments was that of Britton and Rose (1919), which stated, “cacti are certainly very different [from other plants],

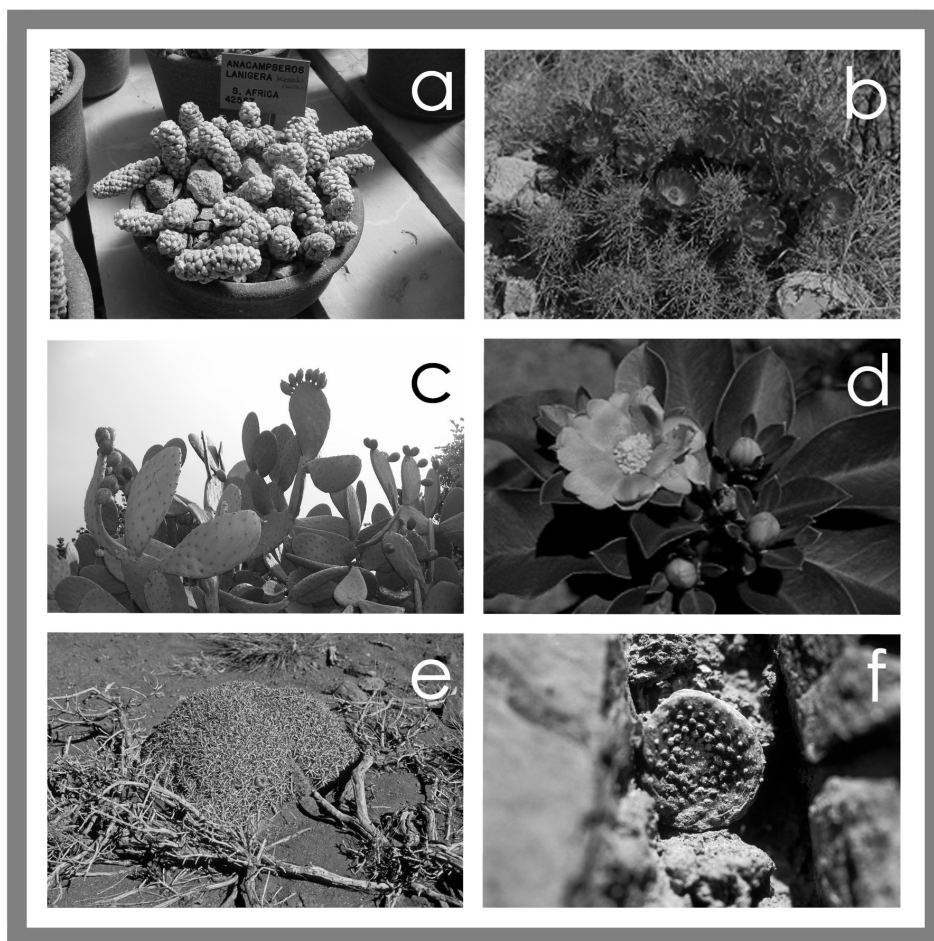


FIG. 2—Deep lineages and close relatives of Cactaceae. a) *Anacampseros lanigera* (Portulacaceae). Diminutive succulents like this are some of the closest relatives to the Cactaceae. b) *Echinocereus coccineus*; the Chihuahuan Desert has a high diversity of Cactoideae, marked by the absence of leaves (Photo: A. M. Powell). c) *Opuntia ficus-indica*; Opuntioideae are marked by glochids, and species in the Chihuahuan Desert region possess ephemeral leaves. d) *Pereskia grandifolia*; cacti of the Pereskioideae have broad, persistent, nonsucculent leaves (Photo: A. M. Powell). e) *Maihuenia poeppigii*; recent workers recognize Maihuenioideae (with terete-succulent, persistent leaves) as a deep lineage of Cactaceae (Photo: J. D. Mauseth). f) *Blossfeldia liliputiana*; this diminutive (rarely exceeding 3 cm wide) dessication-tolerant succulent is a deep lineage in the Cactaceae (Photo: J. D. Mauseth).

but *Pereskia* is the closest relative to the other plant families.” Additionally, the authors postulated a close relationship between *Pereskia* and *Peresklopsis* (Opuntioideae). The phylogeny inferred by these statements of relationship is depicted in Fig. 3. The outgroup used for predicting this relationship is simply “other plant families.” Without

reference to a specific outgroup, estimation of relationships may be performed through a cognitive rather than strictly comparative estimation of character evolution, or a comparative estimation that uses an imaginary outgroup. I propose here that this conceptual, unidentified outgroup is derived from the composite experience of the observer, and the observer's context.

POSTMODERNISM AND CACTI —The observation that ideas are shaped by contexts (and are therefore subjective) is one of the most influential developments in late 20th century thought. Often termed 'postmodernism,' (James 1979; Blais 1997; among many others)

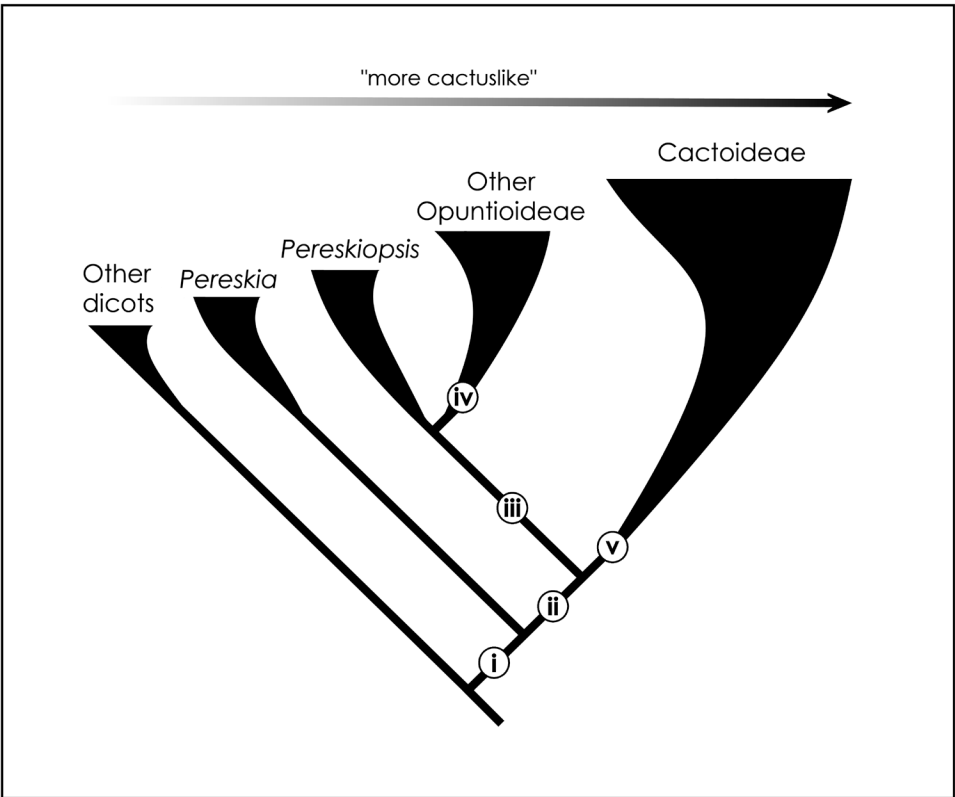


FIG. 3—Phylogram depicting traditional morphological phylogeny of Cactaceae, based on Britton and Rose (1919–1923), with a primitive *Pereskia* and highly derived Cactoideae (Cereae sensu Britton and Rose). *Pereskia* have long been thought of as transitional forms between broadleaved angiosperms and leafless cacti. 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). Adapted from Griffith (2004a, b).



FIG. 4a—Semiotic communication of culturally-dependant “normal” context through landscaping. Above: Humble administrator’s garden, Suzhou, China, 2004 (Photo M. Zhou). Western and Chinese observers of Chinese gardens interpret the aesthetic differently, due to differing reference points. Chinese gardening can communicate untranslatable elements of Buddhist and Daoist philosophy in its presentation; although this aesthetic requires much maintenance, Western observers may sense busy, unpruned plants, lack of space (Zhou 2007), and a sense of external observation of the landscape.

this philosophy has seen broad and varied application in the fields of art, architecture, literature, cultural studies, and history, but rarely in the sciences. Science is not entirely free of contextual bias; although evolution by natural selection provides an apt analogy to postmodernism, evolutionary scientists sometimes do not acknowledge the cultural contexts that may shape their hypotheses. One example involves the differences between 20th century Soviet and Western evolutionary science, with their respective emphases on interspecific and intraspecific competition; the prevailing philosophical climate projected strong influence on hypotheses tested and theories developed (Todes 1989).

What contextual elements might influence the study of botany? Plants are often a feature of the academic environment. Many of the interpreters of cactus evolution live within a temperate, mesic environment. Those that live in arid regions often function within a temperate, mesic landscape. Landscaping is an important part of many

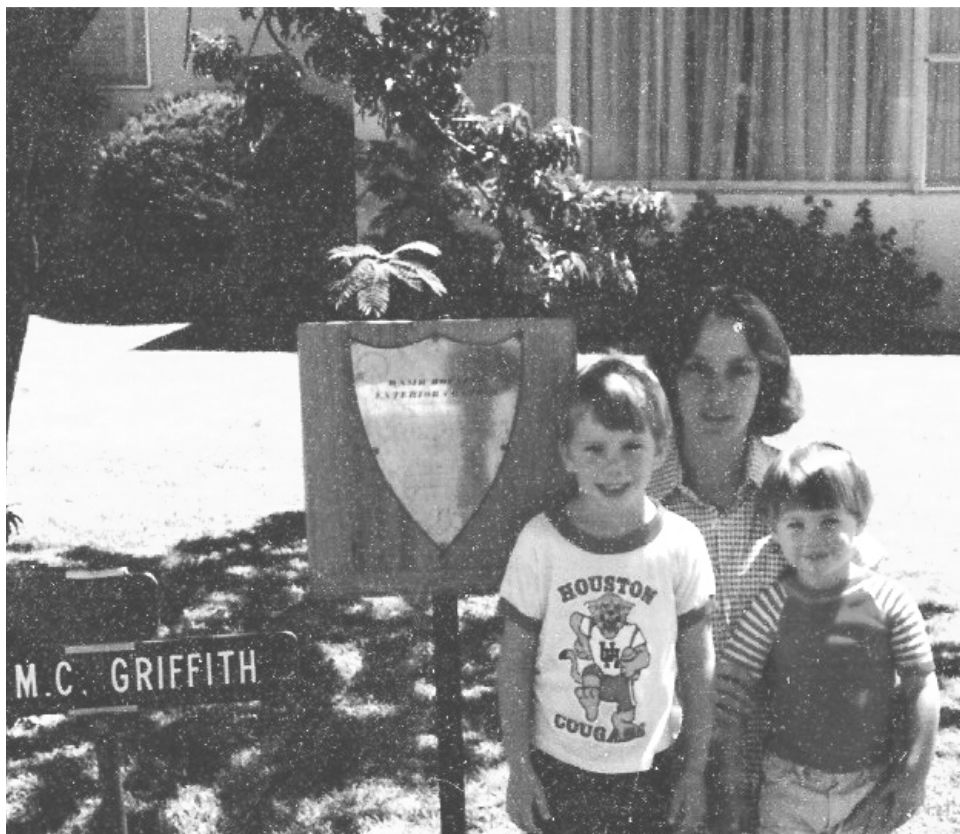


FIG. 4b—Traditional American landscaping in the arid Chihuahuan Desert, White Sands, New Mexico, 1979. This landscape aesthetic communicates stability and dependability among westerners (Nassauer, 1995; Kaufman, 2000), whereas other observers may sense overpruned vegetation and unfilled space (Zhou 2007). This family is posing with an award won for exemplifying ideal landscaping within their community (Photo: M. C. Griffith).

cultures (Hunt 1991), often communicating aspects of form and meaning inscrutable to the foreign observer (Tuan 1974; Hunt 1996; Feleppa 1988; Zhou 2007; Fig. 4a & b). Academic botanists always come from, and often work in, two similar and related institutions: the college and the botanic garden. Britton and Rose (1919–1923) were both scientists employed by the New York Botanical Garden (NYBG) in the Bronx, New York. Guests of NYBG enjoy a world-class horticultural institution, a true cultural landmark. Reflecting a natural confluence of the climate, soil, tastes, and history of New York City, NYBG's landscape aesthetic draws largely from the English estate garden, with its emphasis on broad lawns and tall, stately trees (Darian-Smith 1999). The lawn-and-tree aesthetic is repeated in most landscaped areas in North America (Nassauer 1995; Kaufmann 2000). The North American desire for this landscape expression is

strongly attested to: in areas where local climate does not readily support the lawn-and-tree style, large bodies of water have been depleted for landscaping hundreds of miles away (e.g. Los Angeles and Owens Lake; Ewan 2000). This landscape aesthetic reaches its zenith on college campuses (Fig. 5).

What effect has this context had upon the study of cactus evolution? Although this is hard to measure directly, there remains a trend towards recognizing *Pereskia* as a primitive morphology among cacti and near outgroups, in spite of published works that suggest otherwise. Even as more narrowly circumscribed outgroups have been identified by subsequent authors (Mabry et al. 1963 [Caryophyllales]; Hershkovitz and Zimmer 1997 [Portulacaceae]), the influence of Britton and Rose's (1919–1923) hypotheses and the context of the academiscap have led recent authors to echo relationships that are not the most parsimonious inferences, given their own data.

THE (HORTI)CULTURAL CONTEXT—Noting the lack of parsimony between recently published data and the traditional (*Pereskia*-as-primitive) views expressed in recent papers, I decided to investigate possible sources of bias. One of the most proximate sources may be immersion within a landscaped environment of a certain type. To explore the proximate horticultural environment, a recent study (Griffith 2004b) explored the concept of 'normal' leaves within two contexts: the academiscap (Fig. 5), and one of an infinite number of alternative contexts, the Whipple Mountains of

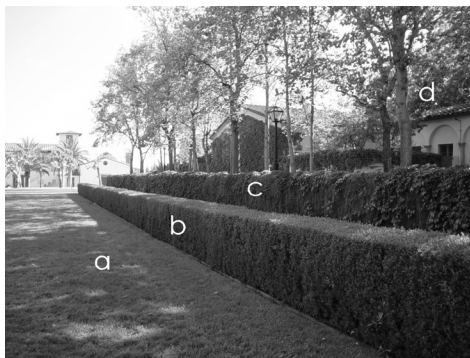


FIG. 5—The academiscap: Scripps College, Claremont, California. College campuses in North America are landscaped with four elements: (a) broad lawns; (b) evergreen hedges; (c) ivy-covered walls, and (d) hardwood trees. In spite of widely diverse climates, soils, and precipitation, this landscape aesthetic differs little throughout North American campuses. Adapted from Griffith (2004b). See also Fig. 7.



FIG. 6—One of an infinite number of possible alternative landscapes: Whipple Mountains, San Bernardino, California. Leaf morphology here necessarily differs from the academiscap. See Fig. 7, right.

Southern California (Fig. 6). Randomly chosen dicot leaves from both contexts were morphologically averaged to produce single composite images (Fig. 7). These images represent cognitive archetypes (of ‘normal’ leaves) for each regime.

When estimating relationships morphologically without the use of a specific outgroup, the estimator may rely upon a semiotically obtained concept of a normal plant. As the academic’s ‘normal’ leaf (Fig. 7, left) is broad, green, simple, and entire, other forms are determined as derived. This character state polarity is parsimonious when compared with a traditional concept of cactus phylogeny (Fig. 3). If the context differs, the semiotically obtained outgroup may force a different determination of character state polarity; if the observer comes from an arid context, *Pereskia* leaves may appear derived. In light of the conflicting interpretations possible, I propose an objective view. The most objective view will consider all available molecular data, and will not choose one phylogeny over another based on degree of congruence with existing hypotheses (Ioannidis 2005).

MOLECULAR PHYLOGENETICS OF CACTI: A CONSENSUS—A growing body of molecular evidence (Wallace 1995; Hershkovitz and Zimmer 1997; Martin and Wallace 2000; Applequist and Wallace 2001; Griffith 2002, 2005; Nyffeler 2002, 2007; Wallace and Dickie 2002; Crozier 2004, 2005; Edwards et al. 2005; Butterworth and Wallace 2005) exists for testing the morphologically derived relationships proposed by previous workers. Many papers repeat the traditional (*Pereskia*-as-primitive) view of cactus phylogeny, even as the data does not support that conclusion (Griffith 2004a). In using phylogenetic trees to test evolutionary hypotheses, the tree should be derived from characters independent of the hypotheses being studied (Felsenstein 1985; MacLeod 2001; Pisani et al. 2002). In order to investigate morphological evolution, therefore, phylogenies of cacti based on the primitive morphology of *Pereskia* should be discarded *a priori*. To take the broadest and most objective, non-circular view possible, and incorporate these data into a model of what is currently known about cactus phylogeny, I derived a consensus phylogeny based on all currently available molecular phylogenies, (Wallace 1995; Hershkovitz and Zimmer 1997; Martin and Wallace 2000; Applequist and Wallace 2001; Griffith 2002; Nyffeler 2002, 2007; Crozier 2004, 2005; Edwards et al. 2005; Butterworth and Wallace 2005). This consensus was modeled by comparing and compiling information about sister-group relationships among subfamilies; no unique sister group relationship between subfamilies was consistent among all phylogenies. This consensus is presented in Fig. 8.

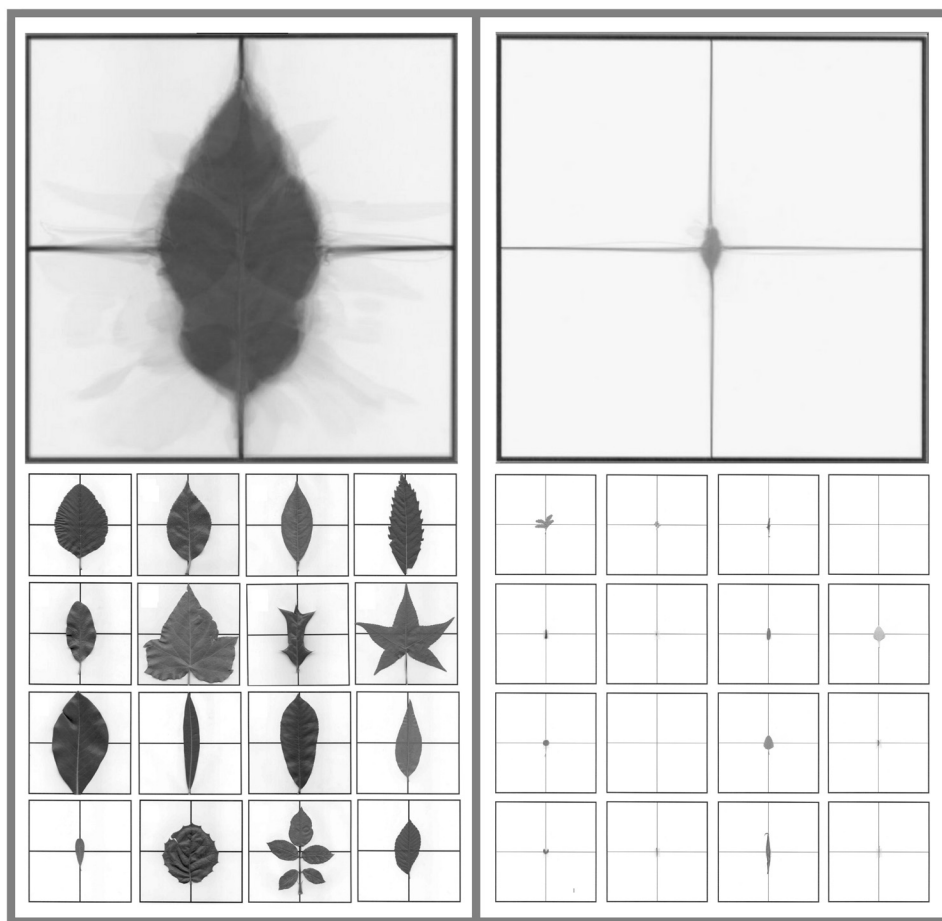


FIG. 7—Semiotic ‘normal’ leaves from two contexts. Freshly collected leaves were scanned and the resulting images averaged to produce leaf stereotypes representative of different contexts. Large boxes (above) depict morphological averages of 16 leaves (below) collected from one of two sites: left, the academiscap (see Fig. 5); right, alternative landscape context (see Fig. 6). Adapted from Griffith (2004*b*). All boxes are 12 cm.

When viewed as a consensus, the molecular data support a number of hypotheses. Firstly, a more specific outgroup has been identified: the nearest relatives of the Cactaceae are diminutive, succulent Portulacaceae. The relationships among the subfamilies are not fully resolved, as there is conflict among the phylogenies recovered. Perhaps further work may provide overwhelming evidence that one of these subfamilies is the absolute deepest lineage, but large amounts of data in different studies (Crozier 2005; Edwards et al. 2005; Butterworth and Wallace 2005) derive different topologies; each study supports two major lineages for *Pereskia*, but the species relate to the other subfamilies

in different ways. The phylogenies of genes are not necessarily the phylogenies of the organisms that carry them (Pamilo and Nei 1988). One way of explaining the conflict among phylogenies is that the cacti experienced a rapid diversification at their origin, and the basal polytomy depicted in Fig. 8 is an accurate estimation of the actual relationships. Forcing a dichotomous interpretation of relationships can obscure real patterns of divergence in some cases (Lamboy 1996).

Deep lineages in the cactus family share some interesting features. The positions of *Blossfeldia* and *Maihueniopsis* are important. *Blossfeldia*, a diminutive succulent, is alternately the deepest lineage in subfamily Cactoideae (Nyffeler 2002), or one of the subfamilies of Cactaceae (Crozier 2004). Either way, *Blossfeldia* is one of the deepest lineages in Cactaceae. *Maihueniopsis*, which is diminutive, succulent, and often geophytic, is the deepest lineage in the Opuntioideae (Griffith 2002, 2005). *Maihuenia*, which has semi- or fully-succulent stems, terete-succulent leaves, and sometimes tuberous roots, is one of the deepest lineages in Cactaceae (Wallace 1995; Crozier 2004; Edwards et al. 2005). *Pereskia* represents a deep lineage or set of lineages (Edwards et al. 2005), but

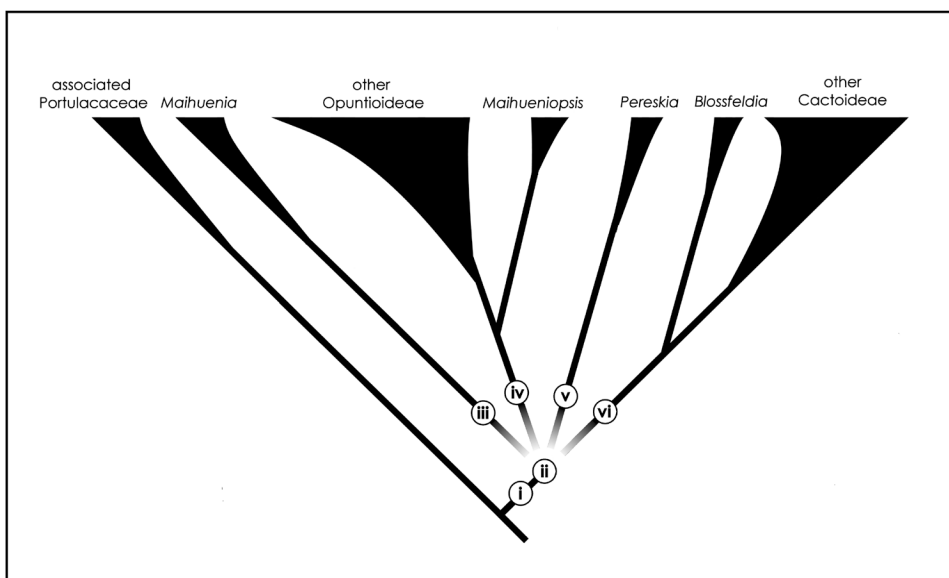


FIG. 8—New model of cactus evolution: consensus phylogeny of molecular phylogenies recovered since 1995. i) The nearest outgroups of Cactaceae are diminutive, succulent Portulacaceae; ii) the relationships among the subfamilies of cacti are not resolved; iii) one deep lineage of Cactaceae (*Maihuenia*) retains succulence and diminutive habit; iv) The Opuntioideae form a deep lineage in Cactaceae, and *Maihueniopsis* is the deepest lineage; v) *Pereskia* is a deep lineage in Cactaceae, but not necessarily the deepest; vi) Cactoideae are a deep lineage in Cactaceae, and *Blossfeldia* is the deepest lineage of cactoids - or alternately - Cactoideae + Blossfeldioideae form a deep lineage of cacti.

these plants are the exception among cacti and closely related Portulacaceae in having broad, non-succulent, persistent leaves.

Some features of *Pereskia* may be difficult to reconcile with the view of cactus evolution proposed here (Griffith 2004a); the origin of these features can be ambiguous, however. One of these features is the presence of superior ovaries in some species of *Pereskia*. These are exceptional in Cactaceae, as all other cacti have markedly inferior ovaries, often sunken into stem tissue replete with areoles (Gibson and Nobel, 1986). Inferior ovaries are generally considered to be a derived feature among angiosperms (Cronquist 1981; among others). One genus of Portulacaceae (*Portulaca*) has partially inferior ovaries, and this genus is supported as a close relative of Cactaceae (HersHKovitz and Zimmer 1997; Applequist and Wallace 2001). The morphology of *Pereskia* leaves is also puzzling when conceived of as a reversal from succulence. The leaves of *Pereskia* have a strong midrib and pinnate venation (Leuenberger 1986), whereas the leaves of *Quiabentia* and *Peresklopsis* (two persistent-leaved opuntoid genera) do not (pers. obs.). The leaves of closely related Portulacaceae are fleshy to succulent and lack strong venation (Guralnick and Jackson 2001); so even if *Pereskia* is basalmost within Cactaceae, the evolution of its leaf form is still mysterious. For further discussion see Griffith (2004a).

CONCLUSION—A parsimonious way to map diminutive succulence onto the consensus phylogeny is to view this character as a plesiomorphy for the entire Cactaceae, with character state reversals occurring in the lineages that lead to *Pereskia*. This implies that the earliest cacti were likely diminutive succulents, and *Pereskia* evolved broad leaves secondarily. If *Pereskia* does in fact represent the deepest lineage or lineages of Cactaceae, then the evolution of its broad leaf form, large size, and non-succulent wood still represent likely character state reversions, based on the nearest outgroups. Succulence and other cactus-associated characters may have evolved more than once in this case.

Estimating early plant evolution should be done as objectively as possible. Ranking one molecular phylogeny over another based on its degree of congruence with traditional thinking will not provide the most accurate estimate. Workers must be careful here: criticizing the data examined after viewing a result that differs from *a priori* assumptions can approach a form of theory-to-evidence reasoning. Instead, paring away cultural influence, and considering as much objective data as exists might allow us to perceive truths less relative.

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