

THE STUDY OF CACTUS EVOLUTION: THE PRE-DNA ERA

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Abstract: We provide a short history of the development of phylogenetic concepts for the cactus family in the pre-molecular (here meaning pre-DNA) era, beginning from the creation of the first artificial classification systems, over to natural systems, and on to the progress made in the Post-Darwinian era. Although several authors have presented their ideas on the evolution of Cactaceae, it was the botanists Alwin Berger and Franz Buxbaum who made the most essential contributions towards a cactus phylogeny during the 20th century. In the second half of that century, new techniques and detailed studies (phytochemistry, anatomy, SEM) helped formulate new concepts or revised established concepts about the evolution of cacti.

Key words: Cactaceae, phylogeny, evolution, history of botany

Introduction

Plants are a major component of the human environment; moreover, they are an essential resource for human life. Ancient humans needed to distinguish those plants of significance (edible, medicinal, source of wood, poisonous, etc). The people of former or primeval cultures categorized plants according to characters shared in common and passed on their attributes and (vernacular) names to others. This has to be regarded as the basis for systematics. Early plant classifications were basically utilitarian. Whether names were assigned to single species or plant groups depended on their significance to human life. Folk taxa of edible or poisonous plants are often equivalent to those taxa accepted by today's modern taxonomy, whereas useless plants were classified into large groups or remain unnamed.

When humans migrated from Asia to North America about 12,000 years ago they were confronted with plants they had never known before. Upon reaching arid areas, they encountered plants even more strange, including members of the family Cactaceae. These plants were incorporated into the life and culture of the different tribes in manifold ways. Although archaeological records in arid areas are sparse, what appears to be the oldest evidence of plant domestication was found in present-day Mexico, where opuntias have

been used by humans for perhaps 12,000 years (Casas and Barbera 2002). Not much is known about early cactus classifications; much of the traditional knowledge was either undocumented or lost to the Spanish invasion. However, the preservation of information in some isolated tribes and some publications from the 16th century prove the importance of cacti for the native people (Anderson 2001; Backeberg 1961; Bravo-Hollis 1978).

Although early folk classification systems, vernacular namings of cacti, and pre-Linnean classifications may be progenitors of cactus taxonomy, they all lack an essential component of modern systematics: recognition of the natural relationships and evolutionary histories of organisms. Since the beginning of systematics as a scientific discipline there has been a long journey towards the modern cactus phylogeny (Barthlott 1988; Gibson and others 1986; Wallace 2002). Here we give an overview of this journey, from the progenitors of cactus taxonomy to the study of their evolutionary history, up to the point where the first molecular studies began to influence cactus systematics.

We here use the term “pre-molecular era” for the period prior to the establishment of DNA studies in cactus systematics in the mid-1990s. Macromolecules (such as proteins) and micromolecules (for instance, alkaloids and

flavonoids) were by then already widely used in plant systematics, but these studies have been commonly summarized under “chemosystematics” or “biochemical systematics” (Wallace 1986; Crawford 2000), whereas “molecular systematics” is today generally associated with the use of RNA and DNA to infer relationships among organisms (Judd and others 1999), and in this sense it is appropriate to name the period considered in this paper as “pre-molecular era.”

Classification is the process of establishing and defining systematic groups and arranging entities in some sort of order. Today, classification is linked to phylogeny, as only monophyletic groups are generally accepted as taxa in current classification systems (Jones and Luchsinger 1986; Judd and others 1999; but for rejection of the monophyletic dogma see Brummitt 2002; Rowley 1997a). Here we will consider some early classifications of the pre-

Darwinian period, because several taxonomic groups circumscribed on the basis of morphological characters by early authors have been confirmed by molecular cladistic studies in the 1990s—or, in other words, today those ancient groupings have been proven to represent natural monophyletic groups.

The Linnean period—artificial systems

Although Carl von Linné (1707–1778) was not the first to provide a classification system independent of whether the plants had significance for human use, he is regarded as father of taxonomic botany (and zoology). With his works, the period of classifications based on the habit of plants was replaced by a period of artificial systems based on numerical classifications (Lawrence 1951).

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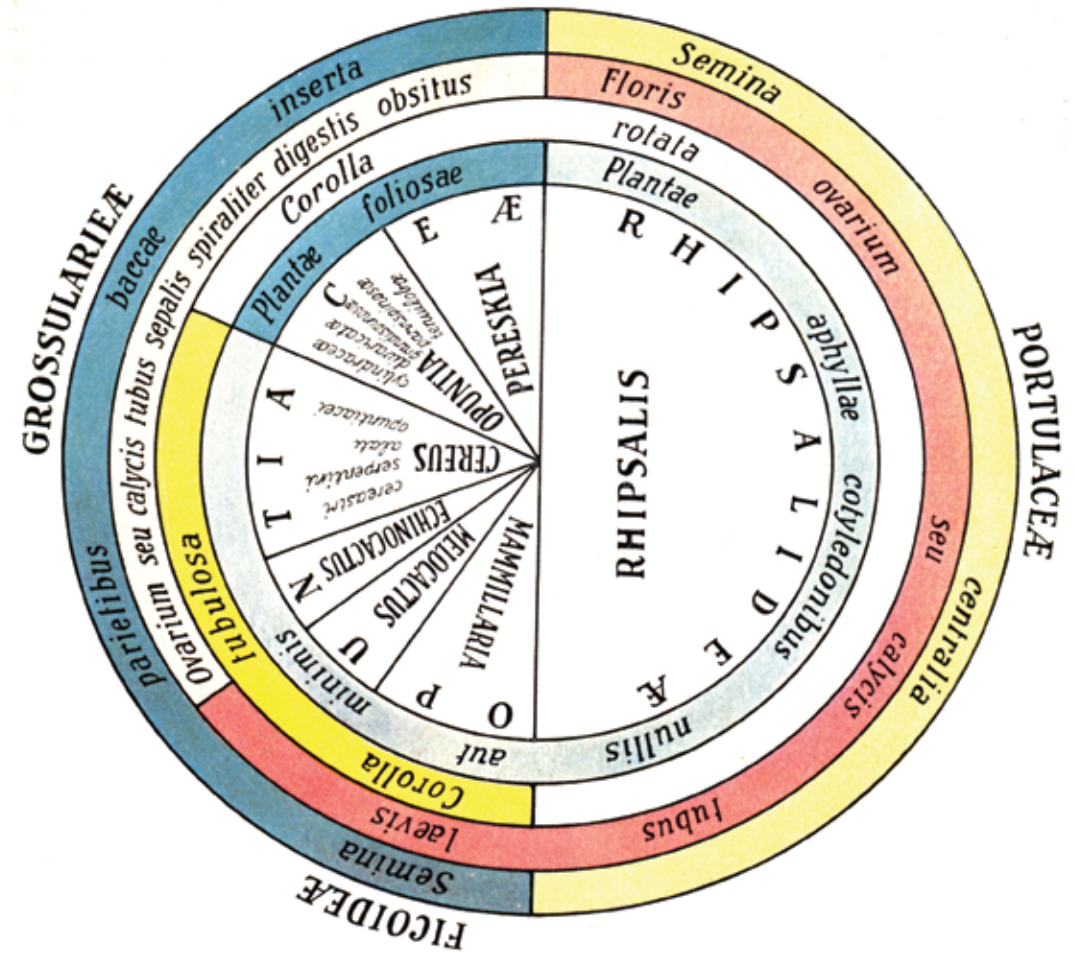


Figure 1. Circular diagram showing the classification and relationships of Cactaceae, published by De Candolle in 1828.

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prise different aspects, and the number of publications about his works is enormous.

In the first edition of *Species Plantarum*, published in 1753, he was the first to consistently use a binomial nomenclature, the naming system we still use today. Previous to *Species Plantarum*, each species was named with a more or less short, descriptive, and non standardized phrase. For instance, "*Cactus subrotundus tectus tuberculis ovatis barbtis*" was a naming phrase used in Linnaeus's "Hortus Cliffortianus" (1737) for a plant that Linnaeus (1753) later named *Cactus mammillaris* [= *Mammillaria mammillaris* (L.) KARSTEN]. But nomenclature is only the allocation of names to the taxa produced by classification (Jeffrey 1989), although classification below genus rank is partly reflected by the Linnean naming system.

The classification system created by Linnaeus, his "Sexual (or Natural) System," provided 24 classes for all plants based on the number, union, and length of stamens; classes were subdivided by the number of styles in a flower. The fact that the system was mainly based on quantitative characters, and that male characters (number of stamens) *a priori* have been weighted more than female ones (number of styles) led researchers to classify naturally related taxa in separated classes (Lawrence 1951). So, although the Linnean arrangement is now recognized to be rather artificial, and is therefore no longer used, the basic idea of aggregating plants according to natural affinities is basically the same we use for the construction of phylogenetic classifications, albeit now made with the help of computer programs and molecular analysis. Between these two extremes, we can find a great number of intermediate approaches. It has to be said that at the time of Linnaeus the idea of creation was still dominant and indisputable. Linnaeus knew about the weak points of his classification system and later attempted to develop a system that considered more-natural relationships.

Twenty-two cactus species were designated by Linnaeus (1753), all classified within a single genus: *Cactus*. Based on habit, the genus was divided into *Echino-Melocacti subrotundi* (columnar and globular cacti), *Cerei erecti stantes per se* (erect columnar cacti), *Cerei repentis radiculis lateralibus* (climbing epiphytes), and *Opuntiae compressae articulis proliferis* (opuntias, *Pereskia* and *Epiphyllum*). Although genus names like *Cereus*, *Pereskia*, and *Opuntia* had already been used by prior authors, they were not employed by Linnaeus (Barthlott 1988).

All four genus names, *Cactus*, *Cereus*, *Pereskia*, and *Opuntia*, were re-established in subsequent editions of Miller's "Dictionary of Gardening" (published in 1754 and 1768; see Barthlott 1988). Two additional genera, *Mammillaria* and *Epiphyllum*, were instated by Haworth (1812) in his *Synopsis Plantarum Succulentarum* and, together with *Rhipsalis*, Haworth used seven genus names for the cacti known in his time.

The first "natural" systems

Since the beginning of the second half of the 18th century, travellers and explorers brought to Europe many hitherto unknown plants from across the globe, and it became increasingly evident that Linnaeus' system failed to sufficiently reflect natural relationships. The meaning of the word "natural" changed during the different phases of human culture (Staffeu 1967). Based on form relationships, the so-called natural systems of the 18th century showed the knowledge of plant diversity at that time, and were supposed to reflect God's plan of creation (Jones and Luchsinger 1986). The theory of evolution was still primordial, and "natural" systems were not, as yet, phylogenetic.

Augustin Pyramus de Candolle (1778–1841) tried to compile a monumental work encompassing all the plant species known at the time, *Prodromus systematis naturalis regni vegetabilis*. For the cacti he retained the seven genera already in use by Haworth and listed 174 species. Regarding cactus classification, an old diagram of cactus relationships made by de Candolle (1828, reproduced by Backeberg 1958: 13; Fig 1) is of particular interest. Although this diagram (and others we will mention in this note) did not contain evolutionary considerations, it did try to reflect relationships within the family and with other families.

De Candolle's subdivision of the Cactaceae into "Rhipsalideae" (with *Rhipsalis*) and Opuntiaceae (all other genera), is from today's perspective a classification with a polyphyletic group of epiphytes and a paraphyletic group of non-epiphytes (Barthlott 1988), this classification was nevertheless long accepted, even by Berger (1929) and Backeberg (1966).

Cactus systematics after Darwin

Although there had been previous essays on the subject of evolution (for instance, by Erasmus Darwin), it was Charles Darwin (1809–1882) who was first successful in widely unearthing early ideas about organic evolution.

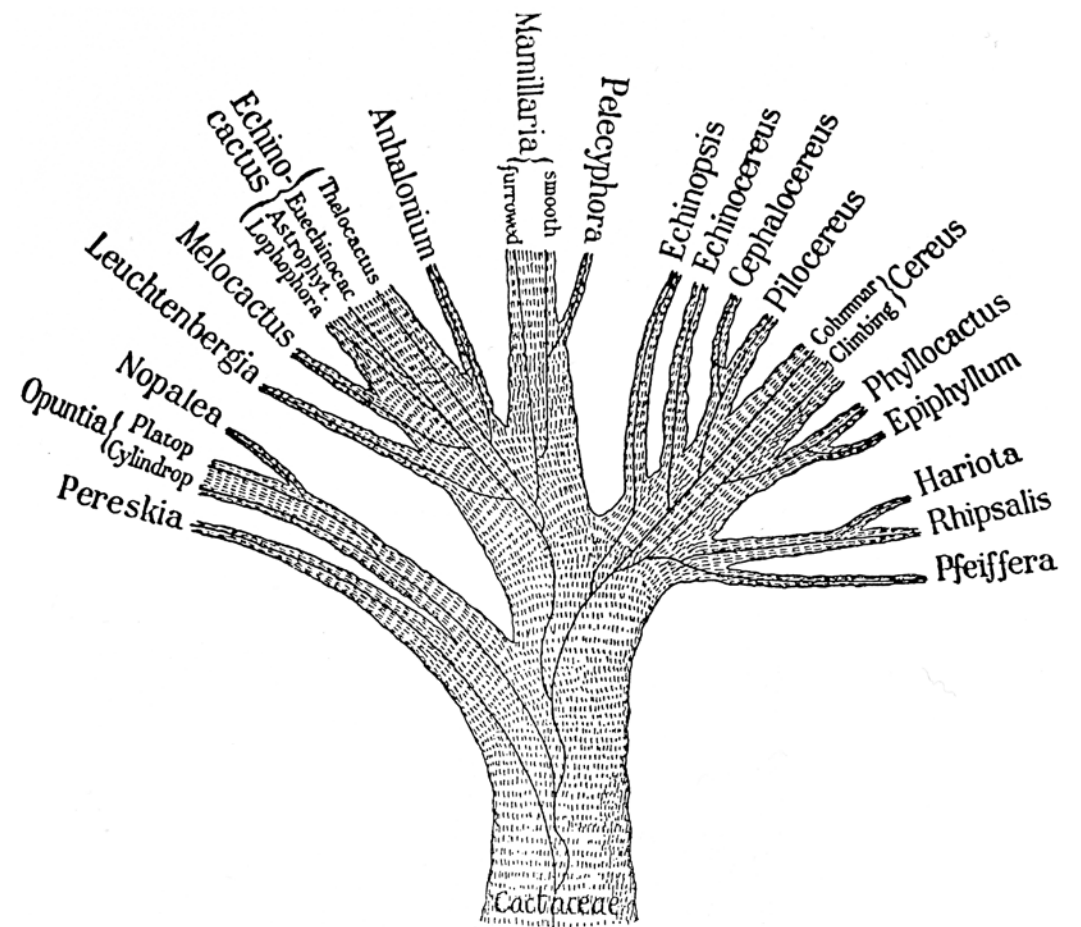


Figure 2. Early phylogenetic tree for the Cactaceae, drawn by Ganong (1898).

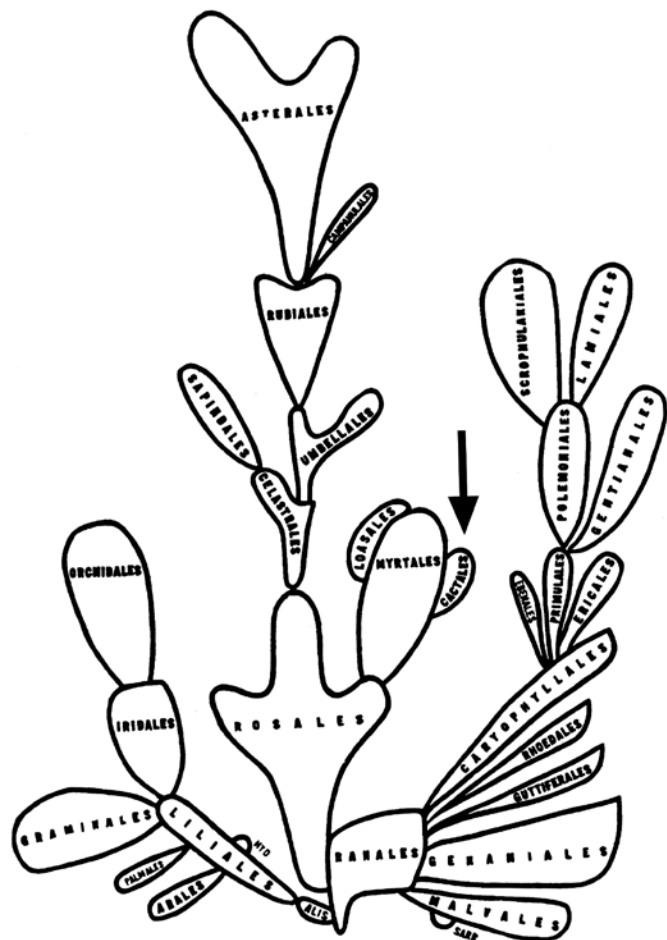
With the publication of his *The Origin of Species* in 1859, biology was no longer the same. The idea of descent with modification conspicuously influenced biological classification from then on, even though for many years Darwin's ideas faced wide resistance for theological reasons (and as an anachronism, the recent rise in popularity of creationism, and its evil twin "intelligent design," has picked up these irrational thoughts again).

But after 1900, opposition also arose from the early geneticists the likes of W Johannsen, H de Vries, and W Bateson, who were influenced by the rediscovery of Mendel's principles of heredity and which saw the driving force of evolution in discontinuous variation, or macromutations. At the dawn of population genetics, based on the Hardy-Weinberg law and elaborated by S Wright, RA Fisher, JBS Haldane, and TG Dobzhansky, genetics and Darwinism were finally united into a synthetic theory of evolution in the 1930s (Jahn 1998; Mayr 1982).

The Darwinian theory of natural evolution was adapted by succeeding biologists, some of whom began to integrate evolution into new and extant classification systems. They tried to order plant groups according to their supposed natural sequences, from the most simple to the most complex, and to develop evolutionary classification systems beginning in the late 19th and early 20th centuries.

When Moritz K Schumann (1851–1904) published his monograph *Gesamtbeschreibung der Kakteen* (Schumann 1897–1898), a milestone in cactus systematics, phylogenetic aspects were scarcely considered, although there are hints in the text that ideas about cactus evolution were already in mind. He postulated *Pereskia* as beginning the sequence of cactus forms. He saw the leaf-like sprouts of some epiphytic cacti as derivations from the *Cereus* form. And when he discussed the origin of the African *Rhipsalis*, he wrote about the cactus family as a relatively young group with a still-in-progress splitting of single lineages.

Figure 3. Bessey's 1915 phylogenetic tree for the angiosperms resembles a prickly pear. The order Cactales is placed close to the order Myrtales (here indicated by the arrow).



Subdivision of the cacti into three subfamilies, Cereoideae, Opuntioideae, and Peireskioideae (Schumann 1890)¹, is esteemed as an important innovation in Schumann's classification system (Barthlott 1988), although this subdivision had been previously proposed by Engelman in 1876 (Crozier 2004, 2005). In fact, this division remained in use up to the mid-1990s, when molecular studies by Robert Wallace (1995a) led to the creation of a fourth subfamily, the Maihuenioideae².

Motivated by his intensive studies during the preparation of *Gesamtbeschreibung der Kakteen*, and the amount of available material, Schumann took a closer look at the natural relationships of cacti in his subsequent publica-

tions (Schumann 1899, 1903). He upheld the three subfamilies, but changed their order, identifying Pereskioideae as the group with the most-primitive characters, followed by Opuntioideae and Cereoideae. He called this classification a "natural system."

Canadian botanist, historian, and cartographer William Francis Ganong (1864–1941) employed Schumann's classification in a diagram that represents the first published illustration of cactus phylogeny (Fig 2, from Ganong 1898; reproduced by Rowley 1997b). The expression of phylogeny is evident from his explanation: "The outline of the main trunks and branches is intended to express the appearance of the whole group as it appears to us at the present day, while the axial lines are intended to represent the probable historical relations of the different genera, their place and relative time of origin from one another" (Ganong 1898: 469). Ganong combined his own studies on the morphology of cactus embryos and seedlings with data provided by other researchers to outline the evolution of the cactus

family. The first line branching off his main trunk bears *Pereskia* and the opuntias (not necessarily in accord with modern phylogenies), while the epiphytic cacti (*Hariota*, *Rhipsalis*, and *Pfeiffera*, today classified as Rhipsalidoideae) are shown as an early split from the rest (the core cacti). Ganong shows the epiphytic cacti to be derived from cereus-like forms, as had been proposed by Schumann (1897–1898), but Ganong's phylogeny of the globular and columnar cactus genera is scarcely in accord with our recent knowledge of cactus evolution, since Schumann had neglected the high diversity and divergence within the still-large genera *Echinocactus* and *Cereus*. Recognizing this diversity remained for subsequent authors.

¹For nomenclatural reasons, today Cereoideae must be named Cactoideae, and Peireskioideae ought to be Pereskioideae.

²For the sake of completeness we must also mention the establishment of Blossfeldioideae by Crozier (2004, 2005), who also resurrected Rhipsalidoideae.

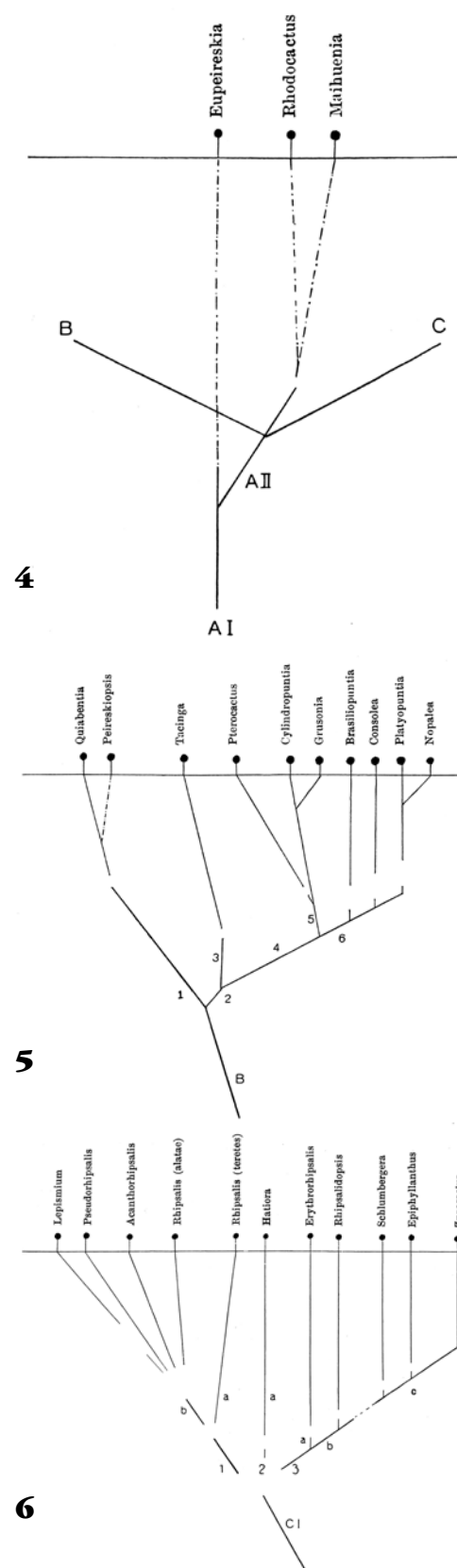


Figure 4. Phylogenetic scheme by Alwin Berger (1926) for the subdivision of the subfamily Pereskioideae, and the lineages of the other subfamilies (AI = Pereskioideae, with primitive ovary; AII = perfect ovary; B = ancestors of Opuntioideae; C = ancestors of Cereoideae). **Figure 5.** Phylogenetic scheme of Berger (1926) for the subdivision of the subfamily Opuntioideae. Note that the numbers in the diagram represent new (apomorphic) characters for the particular lineages (B = ancestors of Opuntioideae; 1 = broad leaves; 2 = leaves reduced; 3 = stems little succulent, virgate; 4 = stronger tendency towards succulence; 5 = cylindrical stems; 6 = stems converting to cladodes). **Figure 6.** Phylogenetic scheme by Berger (1926) for the subdivision of the tribe Rhipsalidoideae into 10 genera (C I = ancestors of Rhipsalidoideae; 1 = Eurhipsalidoideae; 2 = *Hariota*; 3 = Erythrohipsalidoideae; a = stems cylindrical; b = tendency towards cladodes; c = flowers zygomorphic).

Twenty years after Schumann, Britton and Rose (1919–1923) published their monograph in four volumes. Their main innovation was the splitting of many large genera into smaller ones, 124 in total. They presented no ideas about a phylogeny of the family, and their suprageneric classifications had nearly no influence on modern classifications (Barthlott 1988). However, their splitting was certainly the result of an attempt to establish natural entities, and in many cases Britton and Rose seemed to be successful (Gibson and Nobel 1986).

Alwin Berger and the phylogeny of Cactaceae

One of the first botanists to seriously study phylogenetic relationships of cacti in the early 20th century was Alwin Berger (1871–1931). He was a curator at the botanical garden La Mortola (Italy), where he had the opportunity to study many living columnar cacti (Barthlott 1988). In 1905 he divided the genus *Cereus* into several subgenera (Berger 1905)—decisions upheld, for the most part, by subsequent authors (Riccobono 1909; Britton and Rose 1909).

From a phylogenetic perspective, his *Die Entwicklungslinien der Kakteen* (Berger 1926) is the starting point of modern cactus phylogenies. There we find the tree branching in an attempt to show the diversification of cacti during evolutionary history (Figs 4–6). These trees are amazingly modern, because they were constructed using derived features inherited from the immediate ancestor of the group, with mostly dichotomous branching, hence applying principles of cladistics long before the cladistic school founded by Willi Hennig in the 1950s became accepted by the taxo-

nomic community (cf Jones and Luchsinger 1986). Berger did not rely on intuition alone, however; his studies considered a large number of characters, including vegetative, floral, and embryological.

Berger (1926) only briefly addressed the issue of cactus relationships with other families, but he was repeating Schumann's findings (1899). The focus of his *Entwicklungslinien der Kakteen* lays the framework for the study of the infrafamilial evolutionary history of cacti. For genera, he largely used the nomenclature developed by Britton and Rose (1919–1923), as he considered the new, small genera to be more appropriate for displaying the evolution of the family. Berger indicated a paraphyly of *Pereskia* with *Eupereskia* as the sister group of *Rhodocactus*, *Maihuenia*, and all other cacti (Fig 4; cf discussion by Leuenberger 2008). The paraphyly of *Pereskia* has since found support in modern studies, but the basal relationships he delineated within Cactaceae have been largely rejected (Edwards and others 2005; other papers herein). His phylogeny of the subfamily, wherein he accepted ten genera, is not supported by recent studies. Berger saw *Quiabentia* and *Peresklopsis* as sister groups of all other Opuntioideae (Fig 5), again not supported by the latest studies (Wallace and Dickie 2002; Wallace and Gibson 2002). For the Cactoideae (“Cereoideae”), Berger outlined four independent branches (the subtribes Rhipsalideae, Epiphyllae, Hyllocereae and Cereae; Fig 6), but he could not resolve their phylogeny in detail.

In *Kakteen*, Berger (1929) presented a new classification that rejected most of the small genera proposed earlier by Britton and Rose and himself: in all, he accepted only 41 genera, classifying other former genera as subgenera. This scheme threw into confusion the validity of many species-rank combinations attributed to Berger (for instance, Metzging and others 1995; Nyffeler and Egli 1996; Doweld and Greuter 2001); but these were only nomenclatural concerns and did not affect knowledge of the evolutionary history of the family. Berger upheld the division of cacti into three subfamilies, but divided the Cereoideae into two tribes: Rhipsalideae and Cereae, as had been suggested by De Candolle in 1828. The monophyly of Rhipsalideae has been supported by recent molecular data (Nyffeler 2002). Berger was the first to discern the basal features of a natural division of cacti, but partly failed to make this clear, as he cleaved to the old, large genera (Barthlott 1988). Although Berger (1926) did not

alter the common nomenclature (only partially doing so in 1929), his studies strongly influenced subsequent classifications.

A curiosity: the diagram of Frič and Schelle

The study of cacti has never been confined to skilled botanists; it has long been the bailiwick of amateur botanists, naturalists, and horticulturists, whose activities were mainly to collect plants or find novelties. But some tried to discover the ways of evolution—the phylogeny of cactus species. Amateurs often obtain their knowledge by growing plants or observing them in nature during collecting trips. One example of such a study, which seems to be based more on imagination than on systematic research, is a diagram attributed to Frič and Schelle. It was first presented in a paper about the cactus explorer Alberto V Frič (Weingart 1931), and then reproduced in a widespread version of Kreuzinger's commercial catalogue (1935).

It is an extraordinarily lovely and complicated picture (Fig 7) depicting a unique cactus phylogeny: attached to the base (or trunk) there is another family name mentioned, Asclepiadaceae, suggesting this as a closely related family. The branch of the ‘Lignoseminae’ (with the opuntoid genera and *Pereskia*) merges with (or diverges from/toward?) the family Rosaceae—indicating a relationship not supported by any modern phylogeny, and here perhaps Frič was influenced by the old Linnean classification. Other branches are divergent but then remerge (!), but it is not clear whether the authors intended to indicate reticulate evolution or were merely illustrating biogeographic histories (the migration of some groups from North to South America or vice versa). The top of each ramification is quaintly set with the shape of the different plants (globular, columnar, etc), globular forms represented in a size-appropriate fashion: *Echinocactus* is big, globular, and spiny; *Rebutia* little larger than a point.

Perhaps because of space limitations, epiphytic cacti with short flowers (*Rhipsalis* and others) are placed at another level (to the right, between *Cephalocereus* and *Melocactus*). The last genus at the right is *Malacocarpus*, but at the left end of the central tree (the authors' subfamily ‘Lepidocalycieae’, which today we call Cactoideae) is an arrow pointed to “Malac.,” as if the authors had a circular view of this part of the tree (perhaps influenced by De Candolle's circular classification schemes of 1828). The tops of some of the branches

Figure 7. Diagram illustrating relationships of the family Cactaceae (“genealogic table”), from Kreuzinger's commercial catalogue (1935, where it is attributed to “Frič & Schelle, 1931”). The branches include the letters SA and NA, for South and North America, corresponding to the main distribution of genera included in those branches. Nearly illegible at the top of the figure are the latitudes, longitudes, and altitudes of the distribution areas given for the particular genera.

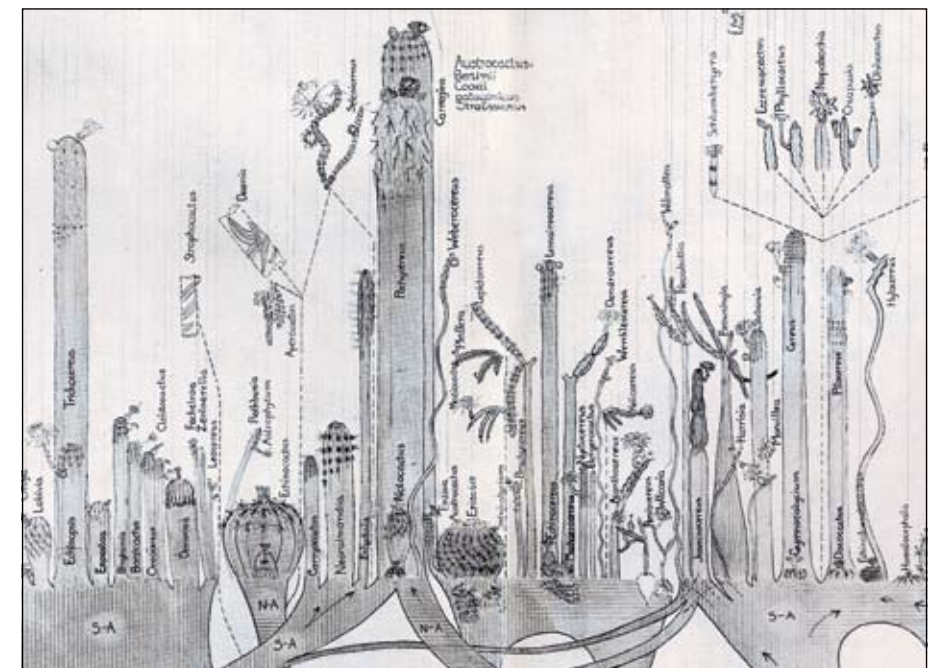
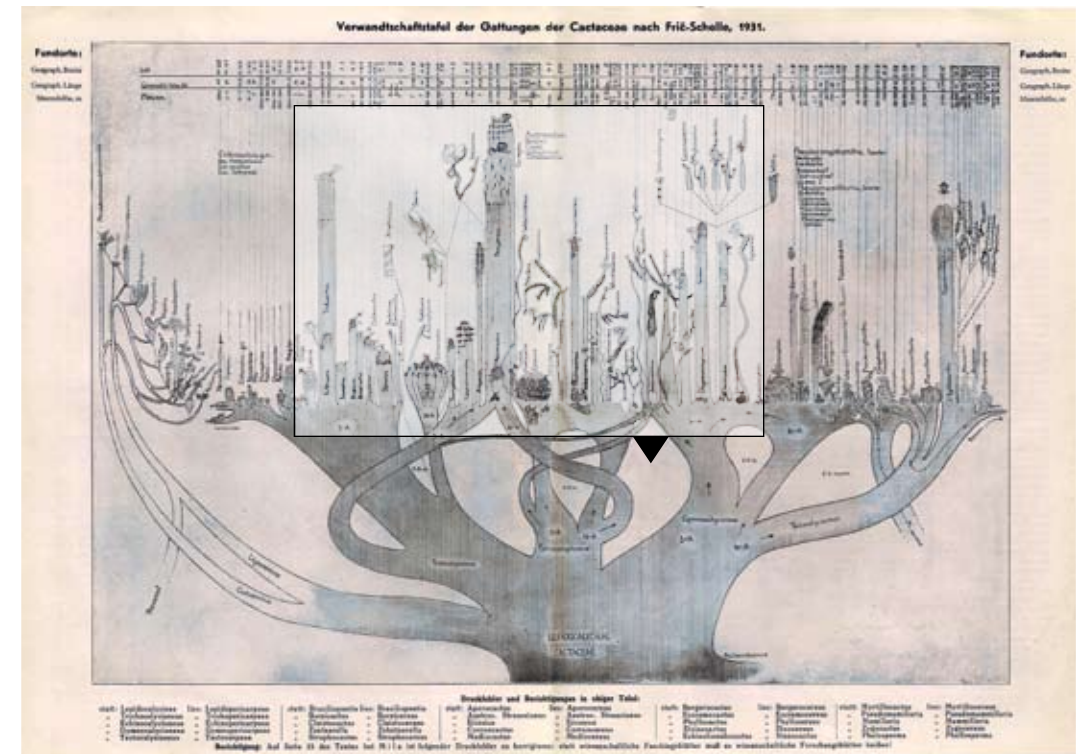
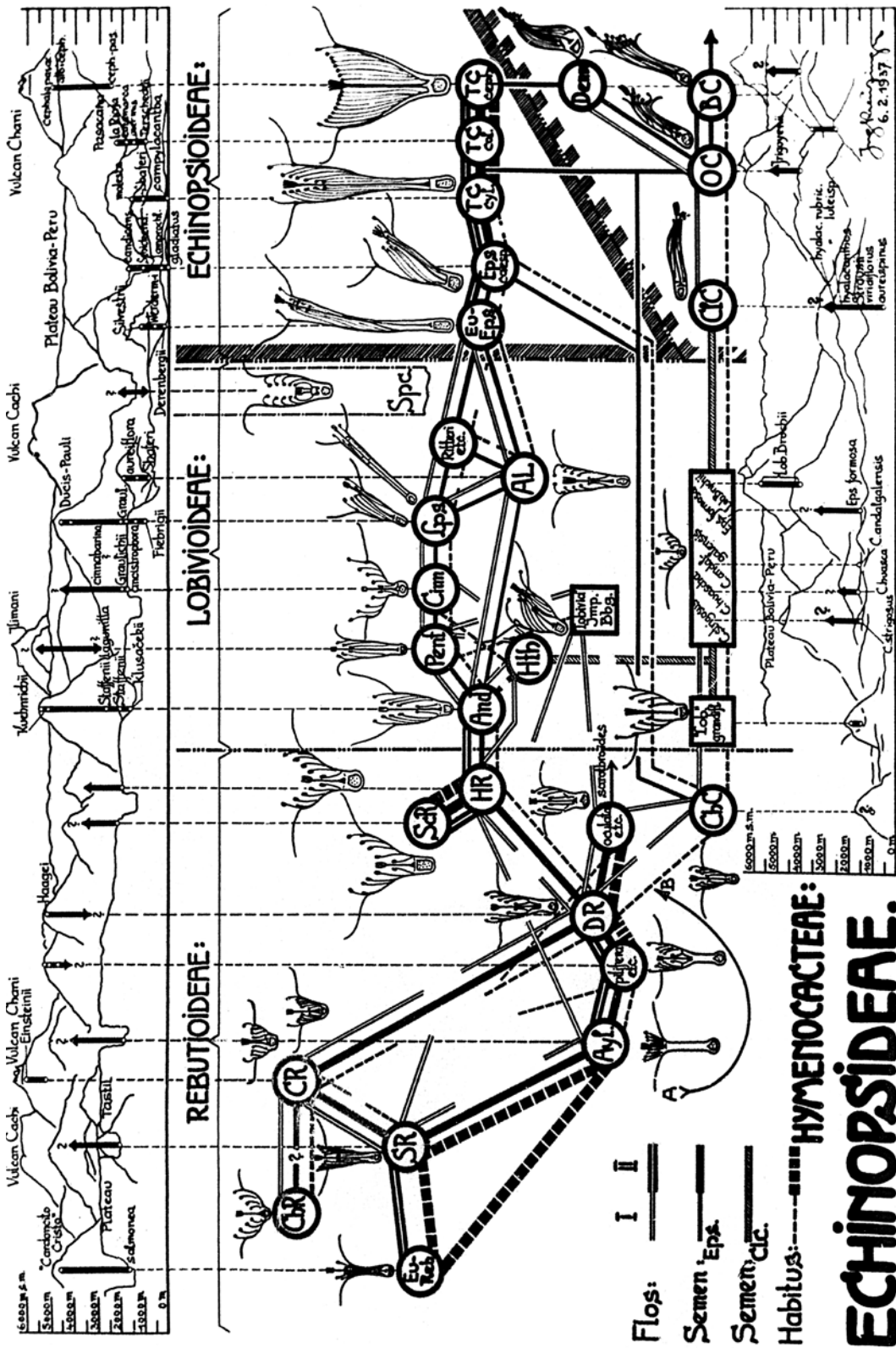


Figure 8. Kreuzinger's diagram of the "Echinopsidae" (unpublished?).



overlap. For instance, at the front of the big *Trichocereus* column there is a smaller one for *Echinopsis*, as if showing its close relationship. The same happens with *Cereus*, having *Gymnocalycium* at its base (perhaps considered to be related because of its partially overlapping South American distribution and nude receptacle). One pale branch at the left includes the genera of the Opuntioideae (with the uncommon name 'Lignoseminae'), and another branch, 'Cactoseminae', includes *Pereskia*, *Maihuenia*, and "Pseudotephrocactus."

Rowley (1997b) commented that this illustration is like "the Book of Genesis visualized by Walt Disney, maybe." Indeed, we cannot take this diagram as a serious reflection of evolutionary history today, but it shows its authors' interest in geographic distribution, evolution, and migration of cacti. Although lacking in modern methods and concepts, they had perhaps the same concern as did skilled botanists for disclosing how cacti have evolved.

Another drawing from the 1930s, about the "Echinopsidae" signed "Kreuzinger 6.2.1937" is reproduced in Figure 8. We do not know whether it was formally published; it may only have been distributed with photos of plants sold by Kreuzinger's nursery. It has several lines connecting the different abbreviations of plant names, flower diagrams, and a couple of schemas (at base and top) representing the mountains where the plants are growing: a perspective from northern Argentina to Peru. It attempts to reflect morphological relationships among several species groups and their distributions, rather than the evolutionary history of this group.

Backeberg's evolutionary history of cacti

Influenced by personal contacts with AV Frič, German merchant, plant collector, cactus trader, and author Curt Backeberg (1894–1966) began his engagement with the cactus family in the late 1920s. His output of articles and books about horticultural and taxonomical aspects of cacti is enormous, as is the scope of his new names and combinations (Eggl 1987). In 1936 he presented his ideas of evolutionary relationships in the family, with an emphasis on the Cereoideae (Backeberg 1936; Fig 9). He considered Peireskia to be the most primary group, from which the Opuntieae branched off. Two groups of epiphytic cacti, the rhipsaloid Cereoideae and the cereoid Hylocereae, he supposed, evolved from the Cereoideae. The main crux of his

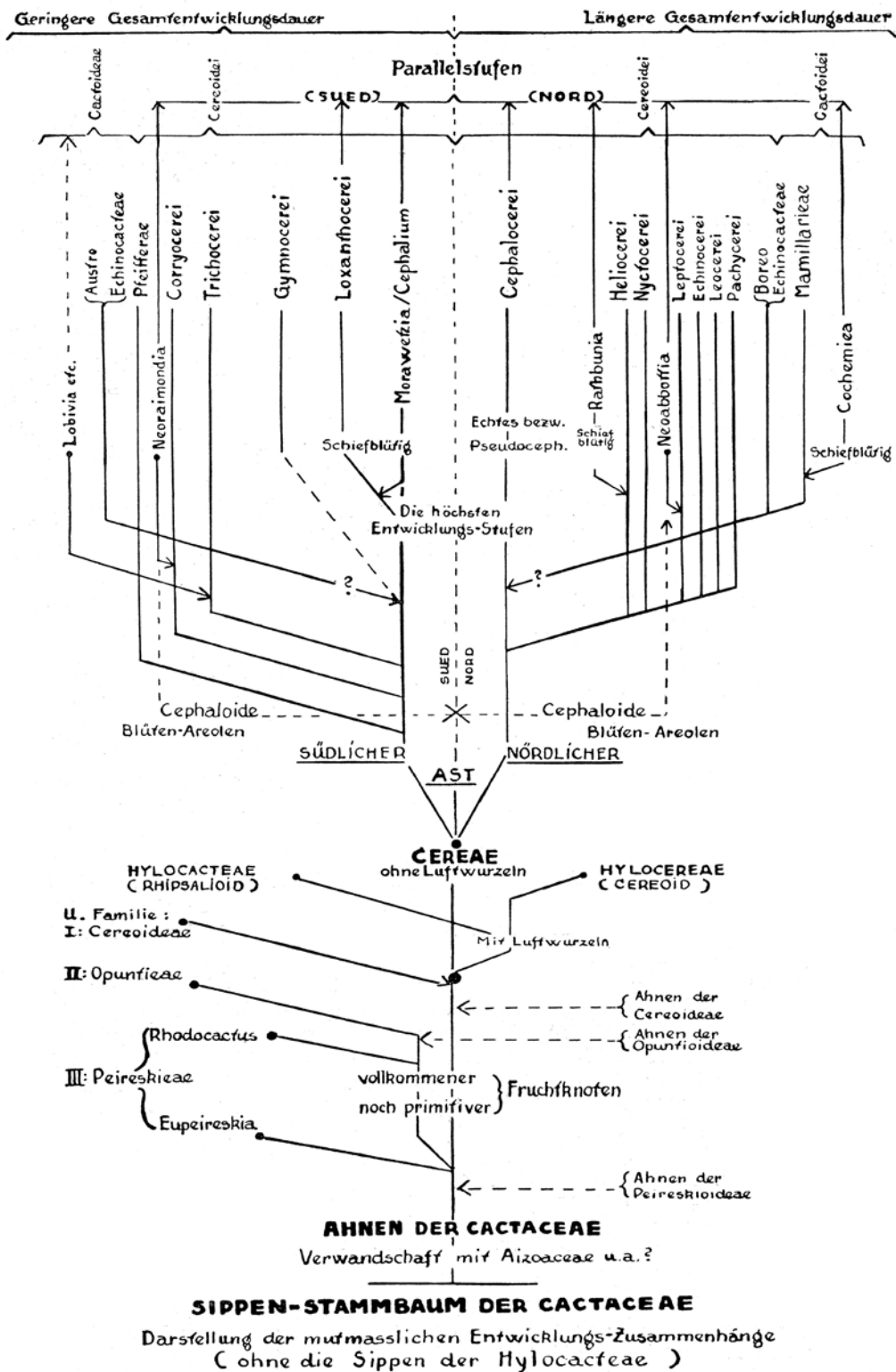
theory involves the dichotomous branching of all remaining globular and columnar cacti along southern and northern lineages, thus forming a "bipolar distribution." He assumed that the evolutionary origin of cacti was in Central America, with subsequent migration north and south (Backeberg 1942). Distribution was an important character in his classification (see Backeberg 1958), where, for instance, he splits the tribe Cereae into subtribes Austrocereae and Boreocereae. As it is based on a wrong assumption (cacti do not appear to have originated in Central America), Backeberg's system is now regarded as artificial in many aspects.

Backeberg tried to correlate his cactus phylogeny with the history of Earth. He assumed that the oldest forms of cacti must have evolved during the Cretaceous (65–144 million years BP) in tropical Central America. In this period, fast evolution led to the first progenitors of the Opuntioideae and Cereoideae (= Cactoidae). At that time, *Rhipsalis* could still jump over the disappearing connection between Africa and America. Our present knowledge, based solely on hypothesized rates of molecular change, is that cacti are not quite so old; they probably first appeared in the mid-Tertiary (ca. 30 million years BP) (Edwards and others 2005; Hershkovitz and Zimmer 1997; Nyffeler 2002). Consequently Backeberg's cactus evolution is misdated. He probably failed here in large part because of his desire to explain the occurrence of *Rhipsalis baccifera* in Africa without invoking a trans-oceanic dispersal event. To this day the distribution of *Rhipsalis* remains incompletely understood, although it is evident that *Rhipsalis* is not a Gondwana relict (see Barthlott 1983 and Buxbaum 1980 for two different views concerning its dispersal from the Americas to Africa).

Phylogenetic studies of Franz Buxbaum

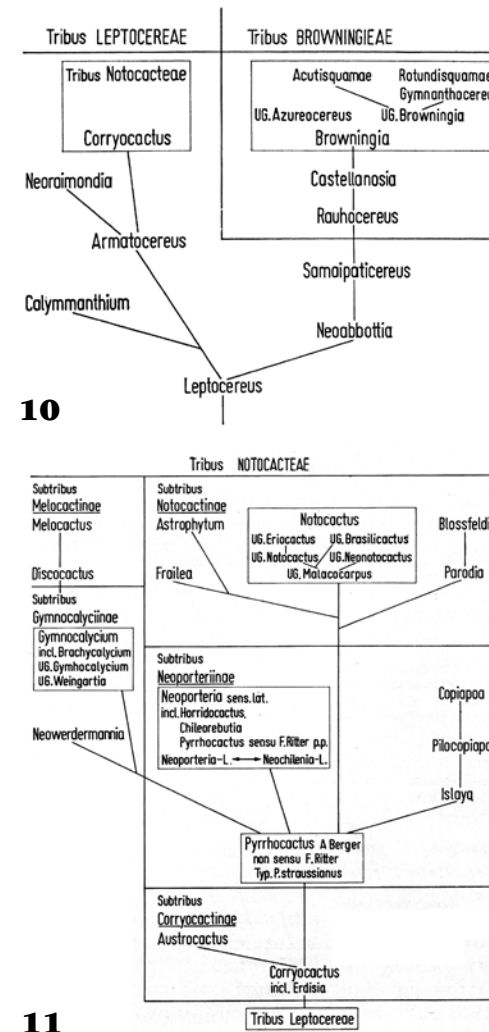
After Berger, it was the Austrian botanist Franz Buxbaum (1900–1979), an experienced plant morphologist, who continued the study of cactus phylogeny. Buxbaum published 343 papers between 1918 and 1980, about half of which concern cacti (Leuenberger 1980). His *Morphology of cacti* is the classic and still current work on cactus morphology (Buxbaum 1951–1955; German edition: Buxbaum 1957–1960). Although many of his papers deal with morphology, one of the earlier (Buxbaum 1949) and several of his later papers focus on phylogeny, the last in 1969. In collaboration with J Endler he published his ideas about cactus phylogeny

Figure 9. Phylogenetic tree for the cacti drawn by Backeberg (1936).



Entwurf des Schemas : C. Backeberg.

Dez. 1936



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Figure 10. Phylogeny of the tribes Leptocereeae and Browningieae, from Buxbaum (1967). Figure 11. Phylogeny of the tribe Notocacteeae, from Buxbaum (1967).

and the resulting classification in a popular little book (Endler and Buxbaum 1958, 1966, 1974). From 1969 to 1980, most of his publications were introductions for many genera compiled in *Die Kakteen* (Krainz 1956–1975), which was published serially in 63 fascicles and largely follows his phylogenetic system.

Buxbaum retained the three subfamilies as proposed by Schumann and further divided the subfamilies into nine tribes, as was similarly outlined by Britton and Rose. These tribes were further divided into subtribes and lines. With some improvements, his system has been accepted in recent studies (Hunt and Taylor 1986, 1990; Barthlott and Hunt 1993; Anderson 2001).

As examples of his several phylogenetic studies, we discuss his paper on “The origin of the tribe Browningieae” (Buxbaum 1966, enlarged in 1967; Fig 10). For understanding the diagrams, Buxbaum’s related statement (1967: 9) should be taken into account. For instance, the diagram depicted in Fig 10 does not mean that the recent genus *Leptocereus* is the ancestor of *Calymmanthium* or *Neobottia*. It should be read that the morphological type of *Calymmanthium* or *Neobottia* derive from the morphological type of *Leptocereus*. As can be seen in the illustration, Buxbaum postulated the Caribbean genus *Leptocereus* as the ancestral genus of the subfamily Cactoideae, or a big part of it. Buxbaum regarded *Corryocactus* as the most primitive group within the Notocacteeae (Fig 11). Recent molecular analyses verify *Corryocactus* as a basal genus of Cactoideae, related to members of the tribes Leptocereeae and Pachycereeae (Wallace 2002), which is commensurate with our phylogenies based on morphological data. Both *Leptocereus* and *Corryocactus* retain ancestral characters and both can be considered “current representatives” from the origin of different lineages. The significance of Buxbaum’s studies has been discussed in detail for Pachycereeae and other columnar cacti by Gibson and Nobel (1986), Gibson and others (1986), Wallace (2002), and Wallace and Gibson (2002).

Buxbaum also assigned the results from his phylogenetic research to biogeography and outlined probable migration routes of cacti in a chapter entitled “Die Entwicklungsweg der Kakteen” (Buxbaum 1969), where he presents the results of his studies concerning cactus relationships. Thereafter, Buxbaum believed that cacti are most closely related to the Phytolaccaceae, which is not supported by recent studies (although both families belong to the order Caryophyllales). He further speculated an evolutionary lineage from the Phytolaccaceae to the basal angiosperms *Illicium* and *Magnolia*.

Buxbaum (1969) believed that the origin of cacti must have been in South America, as suggested later by Gibson and Nobel (1986), Mauseth (1990), and Edwards and others (2005). Buxbaum suggested that the geographic origin of the Cactaceae in northern South America, home of *Pereskia* and the genus *Phytolacca*. He explained the occurrence of the putative most-primitive members of *Pereskia* (*P. weberiana*, *P. humboldtii*, and *P. varagaisana*) in Bolivia and northern Peru by a subsequent migration of this less-

derived lineage away from the center of origin, whereas the most derived forms (*P. aculeata*) evolved geographically farther away. He assumed that the origin of the Opuntioideae was also in South America (Buxbaum 1969). For the Cactoideae, Buxbaum (1967, 1969) still assumed the Caribbean Sea as the center of origin, which recent findings contradict (see Edwards and others 2005). However, Buxbaum suggested that the Andes were the primary migration route and main center of Cactoideae diversity.

Insights from anatomy since the 1960s

In the 1960s Irwing W Bailey (1884–1967), professor of botany at the Harvard University, published a series of papers dealing with anatomical features and classification of *Pereskia*, as well as similar papers on the subfamily Opuntioideae, including *Quiabentia*, *Pereskiaopsis*, and others (for a list of his papers see Gibson 1975; Gibson and Nobel 1986). He elucidated characters of the most “primitive” cacti in order to infer their relationships with other families. Bailey was also interested in the issue of how succulence evolved. For *Pereskia* he proposed a subdivision of the genus into three groups, all of them largely supported by current studies (Edwards and others 2005), except the position of *Pereskia lychnidiflora*.

For several years now, James D Mauseth, professor of botany at the University of Texas, has devoted his research to detailed anatomical studies of cacti, with a secondary aim to understand phylogenetic relations of the Cactaceae. His long series of papers on cactus wood, emphasizing its nearly-unique characteristics, wide-band tracheids (discovered before, but systematically investigated mainly by him), and other anatomical characters (Mauseth and others 1995; Mauseth 2004). A hypodermis is generally present in members of the Opuntioideae, but lacking in the Pereskioideae (Mauseth and Landrum 1997); cortical bundles are restricted to the Cactoideae, but lacking in the Pereskioideae and Opuntioideae (Mauseth 1995); medullary bundles are relictually absent in the family (Mauseth 1993). The latter are present in some tribes of Cactoideae, but lacking, for instance, in most members of the derived tribe Cacteeae. These are only a few examples where anatomical studies have helped us understand the differentiation and phylogeny of cacti.

Mauseth not only studied cactus anatomy, but had wider concerns, as can be seen in his popular, but well documented, note on

the origin of the family (Mauseth 1990). He postulated the area of origin in central South America, at the eastern base of the Andes, an opinion now widely accepted. (An origin of cacti in northwestern South America had been suggested by Leuenberger 1986). He assumed the period between 70 and 40 million years ago as the starting point for the cactus family.

Karyological data have shown that the basic chromosome number in the Cactaceae is $n = 11$; most species are diploid ($2n = 22$). No polyploid species have been found in the Pereskioideae, but they are present in the Opuntioideae and Cactoideae, where about 15% are polyploid (mainly tetraploid) (Barthlott and Hunt 1993; Pinkava and others 1985, 1992; Ross 1981). Chromosome numbers may help us understand relationships and evolution within and among major seed plant groups (Ehrendorfer 1976) as well as within or among species (for instance Barthlott 1983), but unfortunately they provide no good data to test most cactus phylogenetic hypotheses.

Placement of Cactaceae within Caryophyllales

The goal of providing classification systems that reflect natural relationships and evolutionary lineages has not been restricted to the family itself. Regarding suprafamilial relationships of cacti, different attempts and concepts have been put forth by many authors.

Linnaeus (1753) placed the cacti known to him within class XII Icosandria, subclass Monogynia, together with other species today assigned to the families Myrtaceae, Hydrangeaceae, and Rosaceae.

Michael Adanson (1764) in volume 2 of his *Familles des Plantes* classified cacti as members of a family “Portulacae” resp. “Pourpiers.” Although this placement looks intuitive (and the circumscription of Adanson’s Portulacae is different from the modern concept of Portulacaceae), only by the mid-20th century did embryological and chemical studies demonstrate the close relationship between the Cactaceae and Portulacaceae, now confirmed by molecular studies (Downie and Palmer 1993; Hershkovitz and Zimmer 1997). De Candolle (1828) also indicated a close relationship between the Portulacaceae and Cactaceae in his diagram (Fig 1).

Eichler (1878) established the name Centrospermae (today Caryophyllales), including the Cactaceae, although the relationships among the families involved had been proposed earlier (Braun 1864). During the first



Figure 12. A bubble diagram showing the presumed phylogenetic relationships within the Cactaceae, from Barthlott (1979). The size of the bubbles corresponds to the number of species, the arrangement of the genera to the presumed relationships.

half of the 20th century, the family Cactaceae was placed in its own order, the Opuntiales, or Cactales, because of its bizarre, near-unique growth forms, which seem to have no close relationship with other families.

The statement that cacti are closely related to portulacae and mesembs, as vaguely indicated by Adanson (1764), was adopted by Schumann (1899). He saw parallels among cactus areoles, the axillary hair tufts of some Portulacaceae, as well as the diadems of *Trichodiadema* (Aizoaceae); additional arguments in support of these linkages included similar characters in ovules and seeds as well as the occurrence of succulence in these groups. Furthermore, Schumann affirmed the classification of Cactaceae as a family within the Centrospermae.

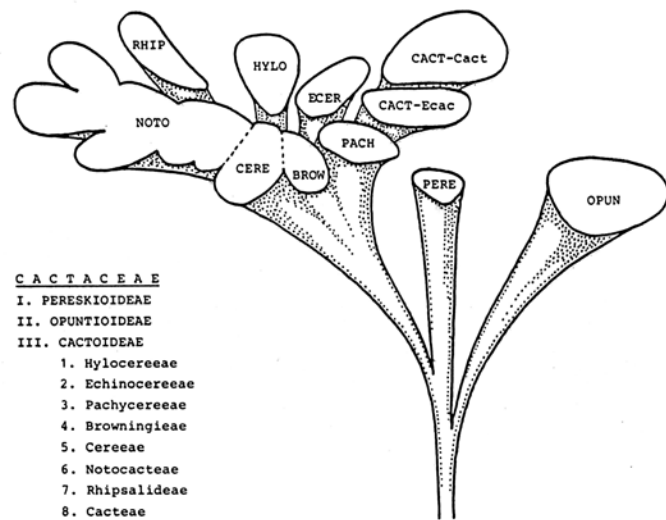
The taxonomic system devised by Charles E Bessey was substantially influenced by Darwin’s evolutionary theory (Jones and Luchinger 1986). His diagram for the angiosperm phylogeny (Bessey 1915; Fig 3), presented as a cactus-like phylogenetic tree (also known as “Bessey’s cactus”), shows the order Cactales placed close to the Myrtales, separated from the Caryophyllales that belong to another of the three major evolutionary lineages.

Huber (1936) denied the proposed relationship between cacti and Centrospermae. Buxbaum (1948) summarized his findings from

morphological studies of flowers and seeds to confirm the placement of cacti within the Centrospermae. Cronquist (1957), in a general synthesis of the evidence for the relationship between cacti and Caryophyllales. Whereas in the 12th edition of Engler’s *Syllabus* (Eckardt 1964) the cacti were still classified in their own order, Cactales, they were later subordinated by Cronquist (1968) to the rank of a family within Caryophyllales (1968).

In the 1970s it became more evident that the Cactaceae had to be classified within the Caryophyllales (Eckardt 1976). Biochemical studies demonstrated that cacti contain betalains, water soluble pigments restricted to the Caryophyllales (except absent in the Caryophyllaceae and Molluginaceae) (Mabry 1974). Further evidence came from ultrastructural studies, where the existence of special plastids in sieve tube members provided a unique feature of the Caryophyllales (Behnke 1976). Other shared characters of cacti and other families of the Caryophyllales are the perisperm as storage tissue of the seed, 3-celled pollen grains, curved ovules and embryos, and anomalous secondary thickening. However, the immediate ancestors of the Cactaceae still remained unknown (Boke 1980). The exact placement and phylogeny of cacti within the Caryophyllales could not be resolved before molecular

Figure 13. Three-dimensional diagram from Barthlott (1988) reflects the presumed evolution of the main lineages of Cactaceae.



techniques became available, although several attempts have been made (Bittrich 1993; Downie and Palmer 1994; Gibson and Nobel 1986; Wallace and Gibson 2002).

The last decades of the pre-DNA era

In his comprehensive study of cactus pollen, Leuenberger (1976) evaluated the phylogenetic significance of pollen morphology of the Cactaceae. The close relationship between the Cactaceae and the Caryophyllales could be confirmed by pollen characters. The comparison of pollen data and cactus phylogeny as proposed by Buxbaum revealed congruencies in some lineages, but differences in others.

Wilhelm Barthlott, professor of Botany in Bonn, published several papers dealing with the taxonomy of the Cactaceae as well as micro-morphological studies of plant surfaces (for instance, Barthlott 1981; Barthlott and Ehler 1977; Barthlott and Voit 1979; Schill and others 1973). His studies of cactus seeds (for a survey see Barthlott and Hunt 2000) strongly influenced cactus taxonomy. Although he was not the first to study the seeds of cacti, the SEM technique he applied brought many new data and insights for the classification and phylogeny of the family (and other families, as well).

A book devoted mainly to amateurs written by Barthlott (1979) contains a “bubble diagram” (Fig 12) in which the author represents the affinities, or evolutionary lineages, of cacti in a two-dimensional diagram based

on Buxbaum’s classification system (Endler and Buxbaum 1974), but including new insights, mostly drawn from SEM studies. Letter colors represent North or South American distribution and reflect the concern of the author for internal relationships and geographic distributions. The epiphytic cacti are placed in two different evolutionary groups (Rhipsalideae and Hylocereae). The Trichocereae and Notocactae are united in one group. This system was later revised, together with a three-dimensional version of the diagram including the time parameter (Barthlott 1988; Fig 13). In the three-dimensional diagram, the Opuntioideae

are shown as a basal split from the main lineage, which is not supported by recent molecular phylogenies (for instance, Nyffeler 2002; Edwards and Butterworth 2008). The study of stomatal types (Eggl 1984) confirmed the separation of the subfamilies Pereskioideae and Opuntioideae from the rest of the family, the Cactoideae.

Gibson and Nobel (1986) published a textbook with chapters about nearly all aspects of the cactus family, including morphology, anatomy, physiology, chemistry, and geography. Two chapters are devoted to “Phylogeny and Speciation” and “Evolutionary relationships”, which includes a comprehensive synthesis of cactus phylogeny and evolution, summarizing the published literature and their own studies. Their main conclusions about the phylogeny of Cactaceae can be summarized as follows:

- The Cactaceae are members of the order Caryophyllales.
- The closest relative of the Cactaceae is the family Portulacaceae.
- The Cactaceae has its geographic origin in northern South America.
- The Opuntioideae did not start their evolution in the west Indies.
- Within the Cactoideae, the tribe Leptocereae possesses the most primitive characters.
- The poorly defined tribe Hylocereae includes terrestrial and epiphytic cacti; the latter evolved from terrestrial forms.

Gibson and Nobel place special focus on the phylogeny of the Pachycereae (Fig 14), and

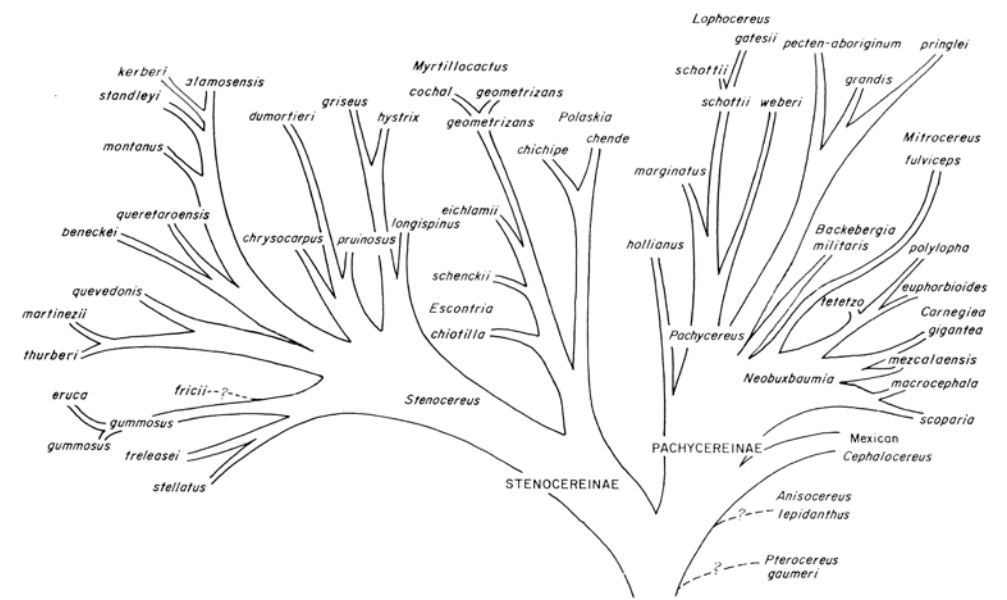


Figure 14. Phylogeny of the tribe Pachycereae after Gibson and Horak (1978; reprinted from Gibson and others, 1986).

their studies (for instance, Gibson and Horak 1978) have provided new insights with comparison to Buxbaum’s older studies (for instance, Buxbaum 1967). Gibson and Nobel divided the Pachycereae into two lineages (subtribes Stenocereinae and Pachycereinae), largely confirmed by recent molecular studies (Wallace and Gibson 2002).

Bregman (1992) provided a more recent phylogenetic study of another well-defined group of genera, the Borzicactinae, dealing with morphological data (mainly of seeds) as well as climatic and geographic data. He presents a cladogram for all seven accepted genera, with *Cleistocactus* as the most basal genus. Although no fossil or palynological records were available, it is speculated that their geographic origin lies on the eastern slopes of the rising Andes, where the subtribe started to evolve during the Neogene (beginning 24 million years BP).

In 1990, Mottram published a useful list of suprageneric and supraspecific names of Cactaceae, including a cladogram for the family (Fig 15), without further explanation. It is not exactly clear from the text whether this diagram represents a phylogeny of cacti, or rather reflects the keys to the subfamilies and subordinated taxa, although these keys are mentioned as “close to ‘natural’ as possible.” He accepts two subfamilies, Opuntioideae and Cactoideae, the latter with two tribes, Pereskieae and Cacteae. The Cacteae are di-

vided into two subtribes, one with a mainly North American distribution area (Echinocactinae), the other occurring mainly in South America (Cactinae). We have seen a similar overestimation of “bipolar distribution” in Backeberg’s concept.

The contribution of Barthlott and Hunt (1993) was the last qualified survey of cactus systematics at the end of the pre-molecular era. Aside from their own studies, it was much influenced by Buxbaum’s classification system as well as by the revised list of genera (consensus list, Hunt and Taylor 1990) worked out by a group of specialists within International Organisation for Succulent Plant Study

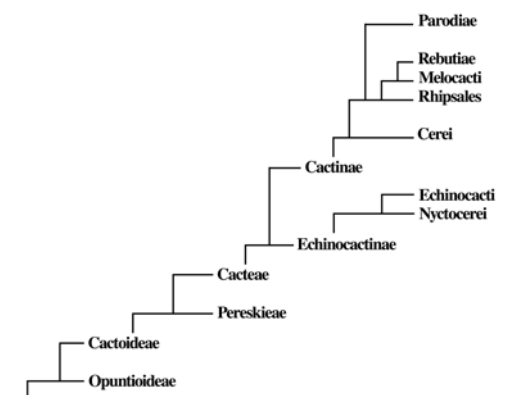


Figure 15. A phylogeny of the Cactaceae, redrawn after the original from Mottram (1990).

(IOS). The “Dahlgrenogram” revised from an earlier version (Barthlott 1988) shows the current knowledge of presumed evolutionary relationships among cactus genera, although it does not deal with the phylogeny of the family in detail.

The pre-molecular era ends

Molecular techniques, and especially those using DNA, became available in the early 1980s (Crawford 2000). When studying the phylogeny of the Caryophyllales, Downie and Palmer (1993) included only one cactus sample in their analysis. It was Robert Wallace who acted as pioneer in the molecular systematic study of the cactus family as a further development of his micro- and macromolecular studies (Wallace 1995b). He and other scholars from his working group and other universities in several countries strongly spurred the molecular study of cactus phylogeny. Progress achieved in laboratory techniques, theoretical advances in systematics, and new software and computer power now make it possible to conduct such studies even at smaller institutions and to process the enormous amount of data. Much new knowledge concerning the phylogeny of cacti has been gained over the last decade.

We wanted to pay homage to those who seriously started the study of cactus phylogeny, such as Berger and Buxbaum, to concerned amateurs, such as Frič and Backeberg, and to others who have explored the complex anatomy of mucilaginous cactus tissues or the diversity of surfaces, such as Mauseth and Barthlott. Molecular techniques cannot simply neglect morphological, anatomical, or biogeographic studies (cf Gorelick 2002). Quite to the contrary, new phylogenies derived using molecular techniques will bring new questions about how particular traits evolved, about the role of character complexes, where and when single lineages evolved, and what the environmental conditions were in those times. Existing morphological or anatomical data have to be reassessed in the context of new hypotheses (for instance, Landrum 2002; Griffith 2008; Nyffeler and others 2008). The use of all available data, methods, and techniques will give us a more accurate view of the complicated landscape of cactus diversity, phylogeny, and evolution in the (near?) future.

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