



<https://doi.org/10.11646/phytotaxa.327.1.1>

A phylogenetic framework for the Hylocereeae (Cactaceae) and implications for the circumscription of the genera

NADJA KOROTKOVA¹, THOMAS BORSCH¹ & SALVADOR ARIAS²

¹Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin, Königin-Luise-Str. 6-8, 14195 Berlin, Germany, n.korotkova@bgbm.org, t.borsch@bgbm.org

²Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), Circuito exterior s.n., Ciudad Universitaria, Ap. postal 70-614, México D.F. 04510, Mexico, sarias@ib.unam.mx

Abstract

The tribe Hylocereeae are represented by mainly Central American-Mexican epiphytic, hemi-epiphytic and climbing cacti. They are popular due to their spectacular nocturnal flowers and have some importance as crops grown for their edible fruits. We present the first comprehensive phylogenetic study of the Hylocereeae sampling 60 out of the 63 currently accepted species and 17 out of 19 infraspecific taxa. Based on four plastid regions (*trnK/matK*, the *rpl16* intron, *rps3-rpl16*, and *trnL-F*) we find a highly supported core Hylocereeae clade that also includes *Acanthocereus* and *Peniocereus p.p.*, while *Strophocactus* is depicted as polyphyletic and is resolved outside of the Hylocereeae tribe. The clades found within Hylocereeae agree, in general terms, with the currently accepted genera but none of the genera are entirely monophyletic in their current circumscription. A new concept for the Hylocereeae is presented to include the genera *Acanthocereus* (incl. *Peniocereus p.p.*), *Aporocactus*, *Disocactus*, *Epiphyllum*, *Selenicereus* (incl. *Hylocereus* and *Weberocereus p.p.*), *Pseudorhipsalis*, *Kimmachia* gen. nov., and *Weberocereus*. New nomenclatural combinations are provided to make these genera monophyletic. The genus *Deamia* is reinstated for *Strophocactus testudo* and *S. chontalensis*, while *Strophocactus* is newly circumscribed to include *S. wittii*, *Pseudoacanthocereus brasiliensis*, and *P. sicariguensis*. Both genera are excluded from Hylocereeae. A taxonomic synopsis of Hylocereeae is provided.

Key words: Caryophyllales, *Deamia*, epiphytes, generic concept, *Hylocereus*, *Kimmachia* gen. nov., *Pseudorhipsalis*, *Selenicereus*, *Strophocactus*, taxonomy, *Weberocereus*

Introduction

The family Cactaceae Juss. constitutes a well-defined lineage within the angiosperm order Caryophyllales Berchtold & J. Presl (see e.g., Brockington *et al.* 2015, Cuénoud *et al.* 2002, Schäferhoff *et al.* 2009). The general understanding of evolutionary relationships in Cactaceae has improved in recent years as a result of molecular phylogenetic studies (Hernández-Hernández *et al.* 2011, Korotkova *et al.* 2011, Korotkova *et al.* 2010, Nyffeler 2002, Nyffeler & Egli 2010, Schlumpberger & Renner 2012, Vázquez-Sánchez *et al.* 2013). Nevertheless, parts of the Cactaceae phylogenetic tree remain to be resolved, in particular concerning the relationships of major clades and relationships at the species level. Many genera have been recognized as para- or polyphyletic but limitations in taxon sampling, lack of statistical confidence of relevant nodes, or missing morphological analyses have so far prevented a consistent implementation of a phylogeny-based classification system. For the tribal and subtribal level, a revised classification for the whole family was proposed by Nyffeler and Egli (2010), which entails a more natural circumscription of taxa compared to previous classifications, albeit being not yet fully substantiated by phylogenetic data.

Cactaceae show complex patterns of convergent evolution in life forms, pollination syndromes and other traits (e.g. Gibson & Nobel 1986, Hernández-Hernández *et al.* 2011, Schlumpberger & Renner 2012). The obvious morphological characters and their states associated with these traits have frequently been used for diagnosing genera but they are often homoplastic and genera based on those characters are therefore often shown as not monophyletic.



FIGURE 1. Stem and flower morphology of the Hylocereeae. A) *Acanthocereus chiapensis* (Arias 1021); B) *A. tetragonus* (Arias 2166); C) *Disocactus quezaltecus* (Veliz 42515); D) *D. phyllanthoides* (Arias 1432); E) *Aporocactus flagelliformis* (Arias 1236); F) *Epiphyllum cartagense* (Hammel 19793); G) *E. chrysocardium* (cultivated, Botanical Garden UNAM); H) *E. hookeri* subsp. *hookeri* (Arias 1560); I) *E. thomsonianum* (Hammel 22020); J) *Pseudorhipsalis himantoclada* (Hammel 20806); K) *P. ramulosa* (Ferrufino 718); L) *Hylocereus monacanthus* (Hammel 26600); M) *H. undatus* (cultivated, Botanical Garden UNAM); N) *Selenicereus anthonyanus* (Hammel, cultivated); O) *S. dorschianus* (Arias 2221); P) *S. pteranthus* (Garcia 874); Q) *Weberocereus glaber* (Bravo s.n.) [photos by S. Arias (A–H, K, M, O–Q), and B. Hammel (I, J, L, N)].

The most recent taxonomic backbone of Caryophyllales that summarizes the current understanding of genus concepts in this order still had to accept several poly- or paraphyletic genera in Cactaceae (Hernández-Ledesma *et al.* 2015). Striking examples are *Echinopsis* Zuccarini (Anceschi & Magli 2013, Schlumberger & Renner 2012) or *Ferocactus* Britton & Rose (Vázquez-Sánchez *et al.* 2013).

A network of institutions and researchers has developed an integrated approach of research and biodiversity informatics with the goal to provide an up-to-date synthesis on the Caryophyllales, including an online taxonomic information source (Borsch *et al.* 2015). This approach takes into account that we are currently in a transition phase from predominantly alpha-taxonomic species treatments to the evolutionary analysis of species limits with a subsequent independent classification step. Knowledge generation and classification thereby advance in a stepwise process, and are fuelled by new methods such as next generation sequencing and computational advances, as well as structured data and reproducible work flows (Borsch *et al.* 2015, Kilian *et al.* 2015).

In the present study, we focus on the Hylocereeae Buxbaum as one of the major groups of Cactaceae that have not yet been analysed with phylogenetic methods using an overall representative sampling of species. They are a predominantly Mesoamerican and Caribbean (most diverse in southern Mexico, Guatemala, and Costa Rica) group of epiphytic or climbing cacti. Many species are popular ornamentals, especially *Disocactus* Lindley and *Epiphyllum* Haworth, while *Hylocereus* (A. Berger) Britton & Rose and *Selenicereus* (A. Berger) Britton & Rose are widely cultivated for their edible fruits (known as pitahaya or dragon fruit). Selected species are shown in Figure 1.

The composition of the Hylocereeae has been changing constantly. Past treatments have either separated sub-lineages (Barthlott & Hunt 1993, Britton & Rose 1923) or merged all epiphytic cacti under the name Hylocereeae (Backeberg 1959, Buxbaum 1958, 1962), Table 1). There are also no clear synapomorphies of the Hylocereeae, regardless of their circumscription. They have mostly been delimited as a Mexican/Mesoamerican group of hemi- or holo-epiphytes with large flowers and adventitious roots. The epiphytic growth form was used as main uniting characteristic while their distribution was the main rationale for separating the Hylocereeae from the likewise epiphytic, but small-flowered and predominantly South American tribe Rhipsalideae (Barthlott & Hunt 1993).

The current Hylocereeae classification and recognized genera date back to the treatment by Barthlott & Hunt (1993) and include: *Hylocereus*, *Selenicereus*, *Weberocereus* Britton & Rose, *Disocactus*, *Pseudorhipsalis* Britton & Rose and *Epiphyllum*. Two nomenclatural changes were recently proposed: three species of *Selenicereus* were transferred to *Strophocactus* Britton & Rose by Bauer (2003a) and *Aporocactus* Lemaire was reinstated by Cruz *et al.* (2016).

The phylogenetic position of the Hylocereeae as part of Cactoideae, close to Echinocereae, could be well established in previous studies, as well as their separation from the other epiphytic lineages, the tribes Rhipsalideae DC. and Lymanbensonieae N. Korotkova & Barthlott (see Hernández-Hernández *et al.* 2011, Korotkova *et al.* 2010). However, the monophyly of Hylocereeae still remains to be tested. So far, clades containing Hylocereeae species were either weakly supported (Arias *et al.* 2005, 67% BS, 57% JK, Hernández-Hernández *et al.* 2011, 75% MLBS) or not supported at all (Bárcenas *et al.* 2011). *Acanthocereus* (Englemann ex A. Berger) Britton & Rose and *Peniocereus* Britton & Rose subgen. *Pseudoacanthocereus* Sánchez-Mejorada were resolved in a clade together with the “core Hylocereeae” (Arias *et al.* 2005, 94% BS/91% JK, Nyffeler 2002, 84% BS). This was a notable finding since these genera are terrestrial rather than epiphytic and they used to be assigned to the Echinocereae (Britton & Rose) Buxbaum (Barthlott & Hunt 1993). On the other hand, Nyffeler and Egli (2010) suggested that *Strophocactus* may not be part of the Hylocereeae, but that was based on hitherto unpublished sequence data.

The Hylocereeae offer a good example for unstable generic limits and excessive splitting. In fact, 23 generic names have been published, many of them monotypic segregates (Table 1). Nevertheless, most of the genera in Hylocereeae are not well defined. So far, only three of them have been evaluated in a phylogenetic context. A study using plastid (*rpl32-trnL*, *trnQ-rps16*, *psbB-trnT*) and nuclear sequences (ITS, *phyC*, *Vatp1*) showed *Hylocereus* to be nested within a paraphyletic *Selenicereus* (Plume *et al.* 2013). Cruz *et al.* (2016) carried out a comprehensive sampling of *Disocactus*, redefined the genus, and provided a species-level synopsis that can serve as taxonomic backbone for it.

One of the specific objectives of the present study is to provide a comprehensive phylogenetic framework for the entire Hylocereeae based on plastid data and a dense taxon sampling covering more than 90% of the currently accepted species. For this purpose, we have selected four plastid regions: *trnK/matK*, the *rps3-rpl16* intergenic spacer and the *rpl16* intron as well as the *trnL-F* region. The rationale for this selection was twofold: first, we wanted to represent the Cactoideae as well as possible to be able to test the monophyly of the Hylocereeae and the positions of species that might go outside. These three plastid regions have been sequenced for Cactaceae in a family-level phylogenetic study (Hernández-Hernández *et al.* 2011) thus many sequences are available in GenBank that can be used as outgroups since the monophyly of the Hylocereeae needs to be evaluated. Second, the high phylogenetic utility of these regions,

especially the *rpl16* intron, for reconstructing species-level trees in Cactaceae has been demonstrated (Korotkova *et al.* 2011, Korotkova *et al.* 2010). Another objective is to evaluate the currently used generic concepts in light of the obtained phylogenetic hypothesis. Based on this phylogenetic study we provide an updated taxonomic synopsis of the Hylocereeae with all species that should be currently included.

TABLE 1. Historical background of Hylocereeae in monographic Cactaceae treatments.

Schumann (1899)	Britton & Rose (1920, 1923)	Buxbaum (1958)	Backeberg (1959)	Barthlott & Hunt (1993)
Tribe Echinocactaeae	Tribe Cereaeae³	Tribe Hylocereeae	Tribe Hylocereeae	Tribe Hylocereeae
<i>Phyllocactus</i> Link	Subtribe Epiphyllanae	Subtribe 3. Epiphyllinae	Subtribe Phyllocactinae	<i>Disocactus</i>
<i>Epiphyllum sensu</i> Haworth p.p.	<i>Chiapasia</i>	<i>Epiphyllum</i>	<i>Bonifazia</i>	<i>Aporocactus</i>
<i>Disocactus</i>	<i>Disocactus</i>	<i>Marniera</i>	<i>Chiapasia</i> .	<i>Wittia</i>
<i>Disisocactus</i>	<i>Eccremocactus</i>		<i>Cryptocereus</i>	<i>Heliocereus</i>
<i>Phyllocereus</i>	<i>Epiphyllanthus</i>	Subtribe Disocactinae	<i>Disocactus</i>	<i>Chiapasia</i>
	<i>Epiphyllum</i>	<i>Bonifazia</i>	<i>Eccremocactus</i>	<i>Nopalxochia</i>
	<i>Nopalxochia</i>	<i>Chiapasia</i>	<i>Epiphyllum</i> .	<i>Bonifazia</i>
	<i>Schlumbergera</i>	<i>Disocactus</i>	<i>Lobeira</i>	<i>Lobeira</i>
	<i>Wittia</i>	<i>Lobeira</i>	<i>Marniera</i>	<i>Pseudonopalxochia</i>
		<i>Nopalxochia</i>	<i>Nopalxochia</i>	<i>Wittiocactus</i>
		<i>Pseudorhipsalis</i>	<i>Pseudonopalxochia</i>	<i>Epiphyllum</i>
		<i>Wittia</i>	<i>Wittia</i>	<i>Hylocereus</i> (incl. <i>Wilmattea</i>)
<i>Epiphyllum sensu</i> Pfeiffer	<i>Zygocactus</i>	-	-	<i>Selenicereus</i> (incl. <i>Marniera</i>)
<i>Epiphyllum</i> p.p.				<i>Strophocactus</i>
<i>Zygocactus</i>				<i>Deamia</i>
<i>Cereus</i> Miller	Subtribe Hylocereanae	Subtribe Hylocereinae	Subtribe Hylocereinae	<i>Mediocactus</i>
	<i>Aporocactus</i>	<i>Aporocactus</i>	<i>Aporocactus</i>	<i>Cryptocereus</i>
Reihe Triangulares	<i>Deamia</i>	<i>Cryptocereus</i>	<i>Deamia</i>	<i>Pseudorhipsalis</i>
	<i>Hylocereus</i>	<i>Deamia</i>	<i>Hylocereus</i>	<i>Weberocereus</i> (incl. <i>Werckleocereus</i>)
	<i>Mediocactus</i>	<i>Eccremocactus</i>	<i>Mediocactus</i>	<i>Eccremocactus</i>
	<i>Selenicereus</i>	<i>Hylocereus</i>	<i>Selenicereus</i>	
	<i>Strophocactus</i>	<i>Mediocactus</i>	<i>Strophocactus</i>	
	<i>Weberocereus</i>	<i>Selenicereus</i>	<i>Weberocereus</i>	
	<i>Werckleocereus</i>	<i>Strophocactus</i>	<i>Werckleocereus</i>	
	<i>Wilmattea</i>	<i>Weberocereus</i>	<i>Wilmattea</i>	
		<i>Werckleocereus</i>		
		<i>Wilmattea</i>		
Tribe Rhipsalideae	Tribe Rhipsalideae	Subtribe Rhipsalinae	Subtribe Rhipsalidinae	Tribe Rhipsalideae
<i>Hariota</i>	<i>Acanthorhipsalis</i>	<i>Acanthorhipsalis</i>	<i>Acanthorhipsalis</i>	<i>Hattiora</i>
<i>Pfeiffera</i>	<i>Erythrorhipsalis</i>	<i>Erythrorhipsalis</i>	<i>Epiphyllanthus</i>	<i>Rhipsalidopsis</i>
<i>Rhipsalis</i>	<i>Hattiora</i>	<i>Hattiora</i>	<i>Epiphyllopsis</i>	<i>Epiphyllopsis</i>
<i>Lepismium</i>	<i>Lepismium</i>	<i>Pseudozygocactus</i>	<i>Erythrorhipsalis</i>	<i>Pseudozygocactus</i>
	<i>Pfeiffera</i>	<i>Lepismium</i>	<i>Hattiora</i>	<i>Lepismium</i>
	<i>Pseudorhipsalis</i>	<i>Pfeiffera</i>	<i>Lepismium</i>	<i>Pfeiffera</i>
	<i>Rhipsalidopsis</i>	<i>Rhipsalidopsis</i>	<i>Pseudorhipsalis</i>	<i>Acanthorhipsalis</i>
	<i>Rhipsalis</i>	<i>Epiphyllopsis</i>	<i>Pseudozygocactus</i>	<i>Lymanbensonia</i>
		<i>Rhipsalis</i>	<i>Rhipsalidopsis</i>	<i>Rhipsalis</i>
		<i>Schlumbergera</i>	<i>Rhipsalis</i>	<i>Erythrorhipsalis</i>
		<i>Zygocactus</i>	<i>Schlumbergera</i>	<i>Schlumbergera</i>
		<i>Epiphyllanthus</i>	<i>Zygocactus</i>	<i>Zygocactus</i>
				<i>Epiphyllanthus</i>

Material and methods

Plant material and taxon sampling

The plant material used was obtained from the living collections of the Botanical Garden Berlin and the Botanical Gardens of the University of Bonn, Germany. The taxonomic synopsis of the Hylocereeae, including verification of types and an extensive synonymy provided by Bauer (2003a) was taken as name source and to guide the taxon sampling. We have sampled 60 species including 17 infraspecific taxa. Taxa missing in the sampling are *Disocactus aurantiacus* (Kimmach) Barthlott, *D. salvadorensis* Cerén, J. Menjívar & S. Arias, *Epiphyllum grandilobum* Britton & Rose, *E. hookeri* subsp. *pittieri* (F.A.C. Weber) Ralf Bauer, *E. laui* Kimmach, *Hylocereus escuintlensis* Kimmach, *H. guatemalensis* (Eichlam ex Weingart) Britton & Rose, *H. purpusii* (Weingart) Britton & Rose, *H. trigonus* Safford, *Weberocereus bradei* (Britton & Rose) G.D. Rowley, and *W. alliodorus* Gómez-Hinostrosa & H.M. Hernández. If possible, we included several accessions from the same species from different localities. To verify the monophyly of the Hylocereeae, the clade that includes the Hylocereeae, the Pachycereeae Buxbaum and Echinocereeae (Hernández-

Hernández *et al.* 2011) was represented with its major sublineages as part of the ingroup. *Calymmanthium substerile* F. Ritter, *Copiapoa coquimbana* (Karwinsky ex Rümpler) Britton & Rose, *Frailea pumila* Britton & Rose and *Blossfeldia liliputana* Werdermann were used as outgroup taxa. All sampled taxa with their origins and voucher information are listed in Appendix 1.

Isolation of genomic DNA

For isolation of total genomic DNA, most of the water-storing tissue was removed from the stems and the remaining cortex tissue was dried over silica-gel in a drying chamber for two days at 50°C. This treatment significantly lessened the amount of mucilage during extraction. The dried plant material was homogenized using a mixer mill (Retsch MM200, Haan, Germany) and extracted using a CTAB protocol as described in Korotkova *et al.* (2011). Concentration and purity of the DNA (A260/A280 and A260/A230 ratios) were measured using a spectrophotometer (NanoDrop, peqLab, Erlangen, Germany). The original genomic DNA was stored at -30°C and working dilutions with a standard concentration of 10ng/μl were made for use in PCR.

Amplification and sequencing

The *trnK/matK* region was amplified in overlapping halves using the primer pair *trnK-F* (Wicke & Quandt 2009) and ROSmatK655R (Worberg *et al.* 2009) for the 3' fragment and ACmatK500F (Müller & Borsch 2005) *trnK-2R* (Johnson & Soltis 1995) or *psbA5'R* (Shaw *et al.* 2005) for the 5' fragment. The use of the reverse primer *psbA5'R* that anneals to the *psbA* gene allows to obtain the full sequence at the 5' end of the *trnK* intron, and additionally covers the *trnK-psbA* intergenic spacer. Amplification conditions were: an initial denaturation step 1 min 30 sec at 96°C followed by 30 sec at 95°C, 1 min at 50°C, 1 min 30 sec at 72°C, for 34 cycles and a final extension step of 20 min at 72°C. The *rps3-rpl16* intergenic spacer and the *rpl16* intron were co-amplified using the primers CARps3F, which anneals to the *rps3* exon, and CARpl16R (Korotkova *et al.* 2010), which anneals to the *rpl16* 3' exon. Amplifying from the *rps3* exon allows obtaining reads covering the *rpl16* intron in full. Amplification conditions were: an initial denaturation step 2 min at 95°C, followed by 35 cycles of 30 sec at 95°C, 1 min at 55°C, 1 min 30 sec at 72°C and a final extension step of 15 min at 72°C. The *trnL-F* region was amplified using the universal primers C and F (Taberlet *et al.* 1991). Amplification conditions were the same as for *rpl16*, except that the annealing temperature was set to 52°C. The amplification primers were also used for sequencing. The *trnL-F* region could mostly be completely covered by just the read of primer F and an additional read of primer C was only necessary when pherograms were not readable after large polyA/Ts in the 3' end of the *trnL* intron. Amplification reactions for all regions contained 4 μl DNA template with a concentration of 10 ng/μl, 5 μl Taq buffer S (PeqLab, Erlangen, Germany), 2 μl of each primer (20 pm/μl), 10 μl dNTPs (each 1.25 mM), and 1.5 units of Hot Taq DNA Polymerase (PeqLab). Ultrapure H₂O was added to obtain a total volume of 50 μl. While the other PCR fragments were purified directly using the Geneaid Gel/PCR DNA Fragments Extraction Kit before sequencing, the *trnL-F* products were electrophoresed for 2 hours on a 2% agarose gel and then excised. This was necessary because of frequent non-specific bands. Sequencing was performed by Macrogen Europe (Amsterdam, The Netherlands). Pherograms were examined for sequencing errors by eye and the reads corrected if necessary, sequences were assembled using the program PhyDE v. 0995 (Müller *et al.* 2005+).

Sequence alignment, coding of length mutational events

Sequences were initially aligned using MUSCLE (Edgar 2004) and manually adjusted using PhyDE v. 0995 (Müller *et al.* 2005+) following a motif alignment approach and the rules laid out by Kelchner (2000) and Löhne & Borsch (2005). Seventeen sequence parts of uncertain homology (online supplement Table S1) had to be excluded; otherwise sequences could be aligned unambiguously. Indels were coded according to the Simple Indel Coding method (Simmons & Ochoterena 2000) using the Indel Coder option in SeqState v. 1.40 (Müller 2005b). Inversions were placed separately during alignment and reverse-complemented prior to subjecting the matrices for phylogenetic analysis. They were not coded as previous datasets have shown inversions within Cactaceae plastid regions to be homoplastic (Korotkova *et al.* 2011). The alignments are available in TreeBase (<http://www.treebase.org>, study ID S21224) or from the authors.

Phylogenetic analyses and topological tests

The search for the most parsimonious tree was carried out in PAUP* v. 4.0b10 (Swofford 1998) using the parsimony ratchet (Nixon 1999). A command file for PAUP* containing the ratchet commands was generated using PRAP (Müller 2004). Ratchet settings were 200 iterations with 25% of the positions randomly upweighted (weight = 2) during each replicate and 10 random addition cycles. Tree lengths and homoplasy indices (CI, RI, and RC) were calculated in PAUP. Support for the nodes found by the parsimony ratchet was calculated by jackknifing (JK, (Farris *et al.* 1996)) using the

settings based on the optimal parameters (Müller 2005a), with 10.000 replicates, tree-bisection-reconnection (TBR) branch swapping, 36.788% of characters being deleted in each replicate, and one tree held during each replicate.

The best-fitting nucleotide substitution models were evaluated with jModeltest 2.1.7 (Darriba *et al.* 2012) with 11 substitution schemes and an ML optimized base tree. Each intron and intergenic spacer as well as the *matK* CDS were analysed separately. Model fit was evaluated using the Akaike Information Criterion as implemented in jModeltest. The models selected were: *trnK* intron and *matK*: TVM+I+G, *rps3-rpl16* spacer: TIM2, *rpl16* intron: TIM1+I+G, *trnL* intron: TVM+I+G, *trnL-F* spacer: TVM+G. The model was set for each of the partitions individually, including the base frequencies, substitution rates, proportions of invariable positions and the shape parameters were set as priors for each partition as well. Bayesian MCMC Inference was performed using MrBayes 3.2.2 (Ronquist & Huelsenbeck 2003). Analyses were performed in combination with coded indels, then applying the restriction site (binary) model for the indel partition. Four simultaneous runs of Metropolis-coupled Markov Chain Monte Carlo (MCMCMC) analyses, each with four parallel chains, were performed for 20 million generations, saving one tree every 1000th generation, starting with a random tree. The burn-in was determined using Tracer v1.6 (Rambaut *et al.* 2014) and set after the first two million generations, the remaining trees were summarized in a majority rule consensus tree. Maximum Likelihood (ML) analyses were performed with RAxML (Stamatakis 2014) using RAxML GUI v. 1.3. (Silvestro & Michalak 2012), using the GTR+G +I model of sequence evolution and the “ML + thorough bootstrap” option with 10.000 bootstrap replicates (Stamatakis *et al.* 2008). Tree annotation and layout of the BI and ML trees were done using TreeGraph2 (Stöver & Müller 2010).

Alternative topologies regarding the placement of *Pseudorhizalis ramulosa* (Salm-Dyck) Barthlott were evaluated using topological tests. As the exact position species was unresolved, we wanted to exclude the possibility that the dataset may still contain signal for this taxon to be sister to any of the subclades. The Bayesian topology with *P. ramulosa* unresolved was taken as reference and three alternative topologies to be tested were manually constructed using TreeGraph2: 1) *P. ramulosa* sister to the rest of the *Pseudorhizalis* clade, 2) *P. ramulosa* sister to the *Epiphyllum* clade, 3) *P. ramulosa* unresolved within the *Disocactus* clade. Alternative topologies were evaluated under the parsimony and likelihood criteria in PAUP*. A Templeton test (Templeton 1983) was performed under parsimony in PAUP* with the combined nucleotide matrix. A Kishino-Hasegawa (KH) test (Kishino & Hasegawa 1989) was performed with the combined matrix under the likelihood criterion in PAUP* and TIM1+I+G model settings as obtained using jModeltest 2.1.7 as described above for the combined dataset.

Results

Sequence characteristics

The final alignment contained 5367 characters. After exclusion of parts of uncertain homology (see Appendix 2) and trimming the uneven beginning and end, the resulting sequence matrix comprised 4915 nucleotide characters of which 3931 characters were constant, 511 variable but not informative and 437 characters were parsimony-informative. Of the 229 coded indels, three were constant, 141 were uninformative and 85 coded indels were parsimony-informative. The *rps3-rpl16* spacer and the *rpl16* intron provided the highest percentage of variable characters (13 %, Table 2) as a single locus.

Five inversions were detected in the dataset, one in the *matK* CDS and four in the *rpl16* intron (Table 2, 3).

TABLE 2. Sequence characteristics of the individual partitions in the dataset.

	<i>trnK</i> intron	<i>matK</i>	<i>rps3-rpl16</i>	<i>rpl16</i> intron	<i>trnL</i> intron	<i>trnL-F</i> spacer
Dataset including hotspots						
Position in the alignment	1–754, 2295–2601	755–2294	2602–2762	2772–4088	4089–4848	4899–5341
Aligned length	1061	1540	161	1317	760	443
Mean length (SD)	881 (178)	1471 (293)	113 (65)	888 (280)	500 (131)	337 (79)
% GC	32,893	32,623	27,993	29,868	28,085	31,735
Number of inversions	0	1	0	4	0	0
Dataset excluding hotspots						
Position in the alignment	1–687, 2224–2442	688–2223	2443–2595	2605–3815	3816–4443	4494–4915
Aligned length	906	1536	153	1219	627	453
Mean length (SD)	794 (157)	1530 (1,46)	107 (62)	933 (153,4)	479,6 (56)	343,3 (5,6)
% variable characters	14,2	13,6	23,5	28,5	25,7	21,1
% informative characters	7	5,4	16,3	13,7	12,9	11,4
Number of coded indels	21	5	8	83	58	42

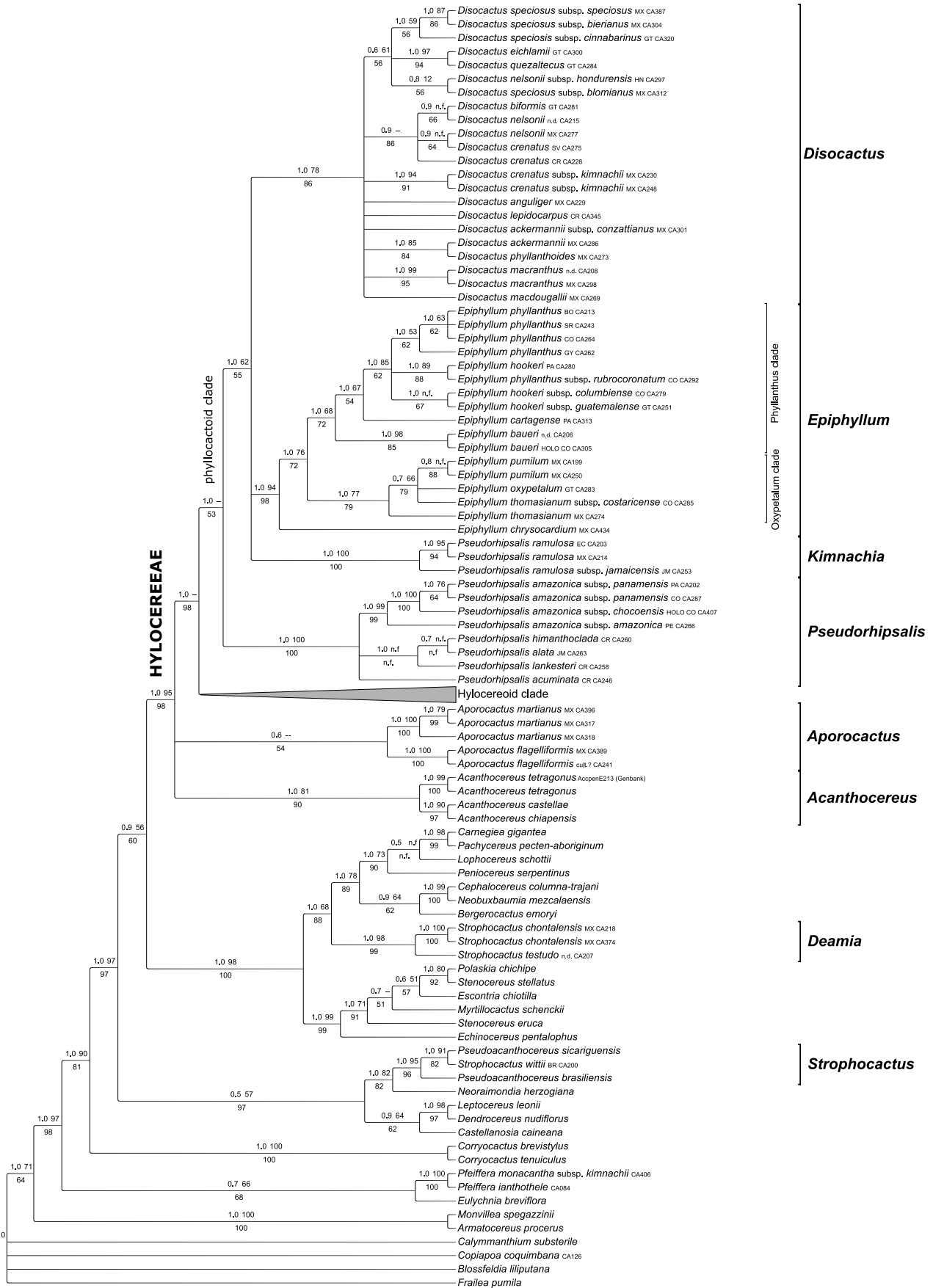


FIGURE 2A. Majority-rule consensus tree from Bayesian inference. Values above branches are Posterior Probabilities (left) and Bootstrap support values from Maximum Likelihood (10.000 replicates) calculated with RAxML GUI using the “ML + thorough bootstrap” option, values below branches are Jackknife support values (10.000) calculated in PAUP. (-- denotes ML BS support below 50, n.f.: node not found). Taxon names in the cladogram reflect hitherto accepted names (Bauer 2003a, Hunt 2006), with the exception of new names in *Disocactus* published by Cruz *et al.* (2016). The new/updated generic concepts presented here are annotated with brackets.

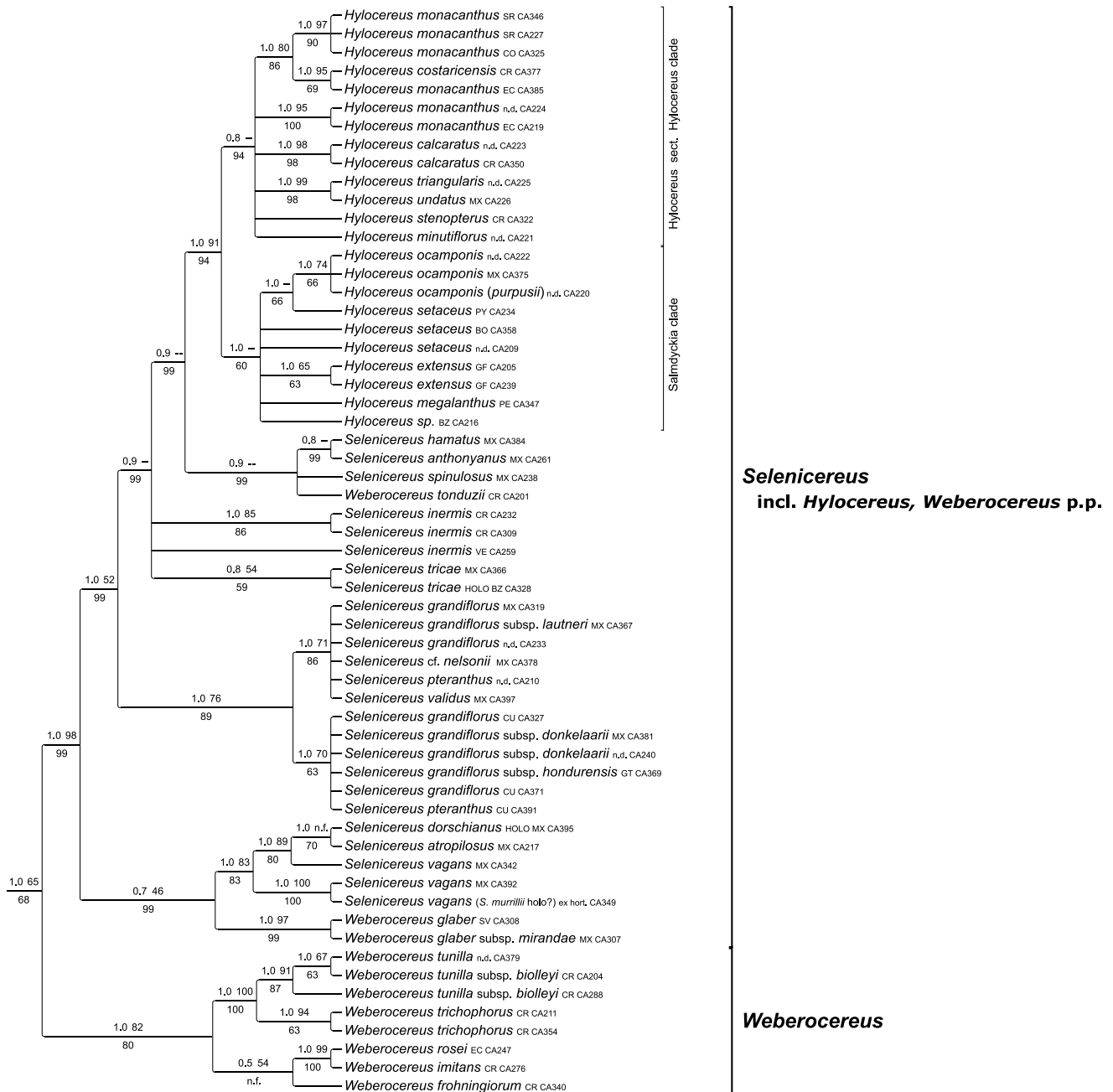


FIGURE 2B. The hylocereoid clade.

TABLE 3. Inversions found in the dataset.

Position in alignment	region	length	Motif—original state/inverted state	Occurrence
1531–1534	<i>matK</i>	4 nt	MAAA / TTTK	throughout the dataset
3097–3102	<i>rpl16</i> intron	6 nt	TAGAAA / TTTCTA	<i>Aporocactus flagelliformis</i> isolate CA389
3441–3444	<i>rpl16</i> intron	6 nt	TTCA / TGAA	<i>Aporocactus flagelliformis</i> isolate CA389
3561–3570	<i>rp16</i> intron	10 nt	GCAITGCTAA / TTAGCAATGC	<i>Hylocereus</i> , <i>Selenicereus</i> and <i>Weberocereus glaber</i>
3581–3604	<i>rpl16</i> intron	24 nt	GCAITGCTAAAATAAAAATAAGAGC / GCTCTTATTTTATTTTAGCAATGC	<i>Weberocereus</i> (not <i>W. glaber</i>), <i>Aporocactus</i> , outgroup except <i>Blossfeldia</i> , <i>Calymmanthium</i> , <i>Copiapoa</i>

Phylogenetic inference

The trees obtained from Maximum Parsimony (MP, not shown), Bayesian Inference (BI) and Maximum Likelihood (ML) are congruent regarding the major clades found. Figure 2 shows the Bayesian majority-rule consensus tree. The phylogram from the ML analysis is shown in the online supplement. The support from BI and ML differs notably—

many nodes that receive high (>0.95 PP) or maximum support from BI are only moderately supported by MLBS and some terminal nodes are not found.

The Hylocereeae clade and its major subclades

A Hylocereeae clade is highly supported in all analyses (1 PP, 95% MLBS, 98% JK), but the Hylocereeae as currently circumscribed are polyphyletic (Fig. 2). They would become monophyletic if *Acanthocereus* (Engelmann ex A. Berger) Britton & Rose were to be included and *Strophocactus* was excluded.

The well supported clade of the Hylocereeae as depicted here includes four main lineages: first, the *Acanthocereus* (incl. *Peniocereus* subg. *Pseudoacanthocereus*) clade, *Acanthocereus* with three species included is found as a highly supported lineage (1 PP, 81 % MLBS, 90 % JK), second, the two species of *Aporocactus* (represented by several samples) are depicted in an only weakly supported lineage, and two larger subclades that we refer to as the hylocereoid clade and the phyllocactoid clade.

The hylocereoid clade (1 PP, 65% MLBS, 68% JK) contains the genera *Hylocereus*, *Selenicereus*, and *Weberocereus*. *Hylocereus* and *Selenicereus* together form a highly supported clade (1 PP, 98% MLBS, 99% JK). *Selenicereus* is polyphyletic and for the most part forms a grade with a highly supported (1 PP, 91% MLBS, 94% JK) monophyletic genus *Hylocereus* nested in it. Five species of *Weberocereus* (including the type species, *W. tunilla* Britton & Rose) are recovered as a monophyletic group (1 PP, 82 % MLBS, 80 % JK) and are sister to the *Selenicereus*/*Hylocereus* clade. However the remaining two species [*W. tonduzii* (F.A.C. Weber) G.D. Rowley and *W. glaber* (Eichlam) G.D. Rowley, including subsp. *glaber* and subsp. *mirandae* (Bravo) U. Guzmán] appear within the *Selenicereus* grade. The phyllocactoid clade is maximally supported by Bayesian Inference but not recovered by Maximum Likelihood and only supported with 53% JK. It contains four subclades corresponding largely to the genera *Epiphyllum*, *Disocactus* and *Pseudorhipsalis*, yet *Pseudorhipsalis* is found polyphyletic with *P. ramulosa* (Salm-Dyck) Barthlott resolved separately from *Pseudorhipsalis* in a tritomy with *Epiphyllum* and *Disocactus*.

Strophocactus falls entirely outside the Hylocereeae clade and is itself polyphyletic. Its three species are resolved at two different positions with high to maximal support. The first clade (1 PP, 82% MLBS, 82% JK) contains *S. witti* (K. Schumann) Britton & Rose, *Pseudoacanthocereus sicariguensis* (Croizat & Tamayo) N.P. Taylor, *P. brasiliensis* (Britton & Rose) F. Ritter and *Neoraimondia herzogiana* (Backeberg) Buxbaum & Krainz. The second clade (1 PP, 98% MLBS, 99% JK) is resolved within the Echinocereae and contains *Strophocactus testudo* (Karwinsky ex Zuccarini) Ralf Bauer and *S. chontalensis* (Alexander) Ralf Bauer.

Discussion

The Hylocereeae clade

The main characteristic of the Hylocereeae is their predominantly hemi- or holoepiphytic habit; no clear morphological synapomorphies can be reported for this group. The members of Hylocereeae are highly variable in morphology and the inclusion of *Acanthocereus* makes them even more heterogeneous. As depicted here, the Hylocereeae contain terrestrial, scandent, hemiepiphytic and holoepiphytic species. Many of the species form aerial roots. The stems can be ribbed and spiny and succulent to various degrees, or flattened and leaf-like. Flowers and floral syndromes are very diverse: there are very large, nocturnal flowers as well as bright red flowers, presumably bird-pollinated, and small, white flowers. The two major Hylocereeae subclades are also distinguishable morphologically as pointed out by Cruz *et al.* (2016). The hylocereoid clade (1.0 PP, 65% MLBS, 68% JK) contains predominantly scandent or epiphytic species with spiny and ribbed stems, and nocturnal flowers. In contrast, the phyllocactoid clade (1.0 PP, 62% MLBS, 55% JK) contains mainly the epiphytic species with flattened, spineless leaf-like stems.

Internal relationships within Hylocereeae and clades corresponding to genera

The *Acanthocereus* (including *Peniocereus* subgen. *Pseudoacanthocereus*) clade

We find a clade of *Acanthocereus tetragonus* (Linnaeus) Hummelinck as sister to *A. castellae* (Sánchez-Mejorada) Lodé and *A. chiapensis* Bravo supported by 1 PP, 81% MLBS, 90% JK.

Acanthocereus had been included in Hylocereeae by previous authors (e.g., Gibson & Nobel 1986), but was later placed in Echinocereae (Barthlott & Hunt 1993), Pachycereae (Anderson 2001), and most recently in Phyllocactae-Corryocactinae (Nyffeler & Eggl 2010). The sister relationship of *Peniocereus* subg. *Pseudoacanthocereus* and

Acanthocereus has also been shown before (Arias *et al.* 2005, Nyffeler 2002). Nevertheless, only recently the species included in *Peniocereus* subgen. *Pseudoacanthocereus* were transferred to *Acanthocereus* (Lödé 2013) but without any proper analysis of further data.

Our results confirm the results by Arias *et al.* (2005) that *Acanthocereus* is only monophyletic if it includes *Peniocereus* subgen. *Pseudoacanthocereus*. *Peniocereus* was studied in detail by Arias *et al.* (2005) who found *Peniocereus* subgen. *Pseudoacanthocereus* intermixed with species of *Acanthocereus*, albeit hardly any support for the clade (55% JK, based on *trnL-F*). *Acanthocereus* previously included one to six species (Anderson 2001), and it was characterized by long infundibuliform flowers, and pericarpels with few spines. *Peniocereus* subgen. *Pseudoacanthocereus* includes nine species (Bravo-Hollis 1978) and the recently described *Peniocereus canoensis* P.R. House, Gómez-Hinostrosa & H.M. Hernández from Honduras (House *et al.* 2013) all of which possessing dimorphic stems. The current circumscription of *Acanthocereus* (see the taxonomic synopsis provided herein) includes all of these species. Young stems have 3–10 ribs, and adult stems have 3 or fewer ribs, or are cylindrical. Flowers are long or medium-sized, infundibuliform or tubular-infundibuliform, and areoles have flexible spines on pericarpels. Two species, namely *P. canoensis* and *A. hesperius* D.R. Hunt were not included in our molecular phylogenetic analyses. However, the mentioned morphological characters are synapomorphic. As these phylogenetically unsampled species also possess the same morphological characters, we assume that they are part of the *Acanthocereus* clade. The species grow in the tropical deciduous forests between Mexico and Costa Rica, in coastal regions up to 1000 m a.s.l.

The *Aporocactus* clade

Aporocactus is weakly supported as monophyletic (0.6 PP, --MLBS, 54% JK). Its position within the Hylocereeae remains unresolved. Nevertheless, our results are congruent with those of Cruz *et al.* (2016) who likewise found *Aporocactus* distant from *Disocactus*. *Aporocactus* was originally established as a genus by Lemaire (1860) but it was not generally accepted afterwards and was included in *Cereus* [a more detailed classification history of *Aporocactus* was given by Hunt (1989)]. Only Britton & Rose (1920) reinstated the genus *Aporocactus*. Later authors followed the latter proposal (see *e.g.* Backeberg 1959, Bravo-Hollis 1978) until Barthlott (1991) included *Aporocactus* in *Disocactus* because all the species form hybrids with other *Disocactus* taxa (W. Barthlott, pers. comm. to N. K.).

Cruz *et al.* (2016) argued for reinstating *Aporocactus* as a separate genus and we follow this view (see Taxonomic synopsis). *Aporocactus* is endemic to Mexico, where it preferably inhabits tropical montane cloud forests. Apart from a further clarification of relationships of *Aporocactus* within the Hylocereeae, work is needed to more reliably delimit species within the genus, since only two species are accepted (Bauer 2003a) while the morphological variation among populations is significant and still needs to be evaluated to support species recognition.

The *Hylocereus* / *Selenicereus* clade

Hylocereus is confirmed as monophyletic while *Selenicereus* forms a grade in which *Hylocereus* is nested (Fig. 2B).

Within *Hylocereus*, there are two highly supported clades that largely correspond to the two current sections, but neither of them is monophyletic. The clade of *Hylocereus* sect. *Hylocereus* (Fig. 2B) contains the type species *H. triangularis* Britton & Rose and corresponds to *Hylocereus* in its traditional circumscription, *e.g. sensu* Britton & Rose (1920). This clade includes the earlier-proposed monotypic genus *Wilmattea* Britton & Rose [*W. minutiflora* (Britton & Rose) Britton & Rose], that was originally separated from *Hylocereus* due to its smaller flowers and the lack of a floral tube.

The second clade (*Salmdyckia* clade, Fig. 2B) contains most of *Hylocereus* sect. *Salmdyckia* D.R. Hunt. It was transferred from *Selenicereus* to *Hylocereus* only recently by Bauer (2003a). This section was based on the genus *Mediocactus* Britton & Rose that was characterized by having characters of both *Hylocereus* and *Selenicereus* [see Hunt (1989) for a detailed classification history and notes on typification]. Buxbaum (1962) regarded *Mediocactus* to be close to *Hylocereus*, while Hunt (1989) suggested including it in *Selenicereus* and this was followed in subsequent treatments (*e.g.*, Anderson 2001, Barthlott & Hunt 1993). The transfer of *Selenicereus* sect. *Salmdyckia* D.R. Hunt to *Hylocereus* was based on unpublished DNA sequence data of Robert Wallace presented at an IOS congress in 1996 and was adopted by Bauer (2003a), Taylor & Zappi (2004), and Hunt (2006). Most species comprising the *Salmdyckia* clade are native to South America, except *H. ocamponis*, which occurs in Mexico.

The *Selenicereus* grade is formed by three lineages and several accessions of *S. inermis* (Otto) Britton & Rose that do not form a clade and remain unresolved (Fig. 2B). They are also not found closely related to the *Salmdyckia* clade, contrary to the classification according to Bauer (2003a). The monotypic genus *Cryptocereus* Alexander [*C. anthonyanus* Alexander \equiv *Selenicereus anthonyanus* (Alexander) D.R. Hunt] is resolved within *Selenicereus*. Backeberg (1959) additionally included *Werckleocereus imitans* Kimmach & Hutchison in *Cryptocereus* and suggested

a close relationship to phyllocactoid genera, *i.e.* the *Epiphyllum* alliance. These species differ from typical members of *Selenicereus* having flat-stemmed epiphytes with stems resembling fernleaves (Fig. 3). Our data confirm the proposal by Hunt (1989) who pointed out a possible affinity with *Werckleocereus* Britton & Rose, as well as its inclusion in *Selenicereus* because it shares the spiny pericarpel.

The genera *Hylocereus* and *Selenicereus* are morphologically similar as both contain scrambling or climbing cacti with large, usually white nocturnal flowers. Britton & Rose (1920) originally defined *Hylocereus* to possess pericarpels covered by scales while the pericarpels in *Selenicereus* have hairs or spines. The transfer of *Selenicereus* sect. *Salmodyckia* to *Hylocereus* (Bauer 2003a) included species with spines on the pericarpel in *Hylocereus* so that the original concept of Britton & Rose did not apply anymore. Bauer (2003a) had justified this transfer only by unpublished sequence data of Wallace, referred to in Taylor and Zappi (2004) and did not mention any morphological characters to substantiate his new concept of *Hylocereus*.

Our results confirm the finding of earlier molecular phylogenetic studies, using either plastid or nuclear DNA sequences. All of them have shown that there is no separation between *Hylocereus* and *Selenicereus*, although only few species were sampled (Arias *et al.* 2005, Bárcenas *et al.* 2011, Cruz *et al.* 2016, Hernández-Hernández *et al.* 2011, Plume *et al.* 2013). The most extensive dataset generated so far (plastid *rpl32-trnL*, *trnQ-rps16* and *psbD-trnT* and nuclear ITS) also found *Hylocereus* nested in a paraphyletic *Selenicereus* (Plume *et al.* 2013). The same conclusion was reached using a morphological and anatomical comparison of *Hylocereus* and *Selenicereus* (Gómez-Hinostroza *et al.* 2014). Therefore, we merge both genera under the name *Selenicereus* and provide the necessary new combinations (see Taxonomic synopsis). A next level of study is required in *Selenicereus* concerning the delimitation of several species which remain insufficiently known, *e.g.* *Selenicereus ocamponis*/*S. purpusii*, *S. triangularis*/*S. trigonus*, *S. vagans*/*S. murrillii*, and *S. costaricensis*/*S. monacanthus*. These taxa require insights from extensive field studies and a combination of molecular, morphological and ecological data.

The *Weberocereus* clade

Weberocereus is depicted as polyphyletic. A clade containing five species, including *W. tunilla* (F.A.C. Weber) Britton & Rose—the type species—is supported with 1 PP, 82% MLBS, 80% JK, but *W. glaber* and *W. tonduzii* are resolved at different positions within *Selenicereus*. The *Weberocereus* clade has two subclades: *W. tunilla* and *W. trichophorus* are resolved as sisters with maximum support. These two species are morphologically similar, with thin (less than 15 mm in diameter), pendent stems, campanulate flowers, and purple fruit pulp. The second subclade contains *Weberocereus frohningiorum* Ralf Bauer, *W. imitans* and *W. rosei* (Kimmach) Buxbaum, but is supported by only 0.5 PP, 54% MLBS and is not found by the MP analysis, although *W. rosei* and *W. imitans* are highly supported as sister species. These three species constitute the *Eccremocactus* group *sensu* Bauer (2003a) and are morphologically characterized by flattened or 3-ribbed stems, and white fruit pulp. Among the hylocereoid clade, *W. imitans* and *W. rosei* share the flat stems with *Selenicereus anthonyanus*, and together the three species were included in *Cryptocereus* (Backeberg 1959). However, our results show that *Weberocereus* species are not related to *S. anthonyanus*. The flat stem character state is convergent between clades within Hylocereeae and also occurs in *Disocactus*, *Epiphyllum* and *Pseudorhipsalis*. *Weberocereus* is morphologically heterogeneous in the current circumscription and is not well separated from *Hylocereus* or *Selenicereus*. The main difference is that the flowers of *Weberocereus* are smaller (less than 7 cm in length) compared to those of *Hylocereus*/*Selenicereus*. *Weberocereus glaber* and *W. tonduzii* (type species of *Werckleocereus*) represent the *Werckleocereus* group (*sensu* Bauer 2003a) and are resolved within the *Hylocereus*/*Selenicereus* assemblage, with which they share 3-ribbed stems and white nocturnal flowers with dark spiny pericarpels. So, morphologically, they do fit well within the *Hylocereus*/*Selenicereus* assemblage.

The *Epiphyllum* clade

A clade corresponding to *Epiphyllum* and including the type *E. phyllanthus* (Linnaeus) Haworth is supported with 1 PP, 94% MLBS, 98% JK, while three former species [*E. crenatum* (Lindley) G. Don, *E. anguliger* (Lemaire) H.P. Kelsey & Dayton and *E. lepidocarpum* Britton & Rose] are part of *Disocactus*. Our results are thus consistent with those obtained by Cruz *et al.* (2016) to exclude these three species. *Epiphyllum chrysocardium* Alexander is resolved as sister to the rest of *Epiphyllum*. It is a remarkable species with large white flowers and broad stems resembling fern leaves, known only from few collections from Chiapas and Tabasco, Mexico (Figs. 1G, 3A). It was originally described as a member of *Epiphyllum*, subsequently Backeberg (1959) placed it in his genus *Marniera* Backeberg, emphasizing that *Marniera* has hairy or bristly pericarpels while *Epiphyllum* has naked pericarpels. *Marniera* as a genus was later no longer accepted because its type *M. macroptera* (Lemaire) Backeberg cannot be satisfactorily identified (Kimmach 1991), although the generic name as such was never formally rejected. Until recently *E. chrysocardium* was treated

under *Selenicereus* because it has spiny fruits, which is untypical for *Epiphyllum* (Bauer 2003a, Kimmach 1991). Our data and those obtained by (Cruz *et al.* 2016) confirm this species to be part of *Epiphyllum*.

The rest of *Epiphyllum* consists of two well supported clades. The *Oxypetalum* clade (1 PP, 77% MLBS, 79% JK) is characterized by stamens in two series. The *Phyllanthus* clade (1 PP, 68% MLBS, 72% JK) includes *E. baueri* R. Dorsch and *E. cartagense* (F.A.C. Weber) Britton & Rose and a subclade (1 PP, 85% MLBS, 62% JK) of species that have been regarded as taxonomically difficult within *Epiphyllum*. Numerous subspecies were described within this complex, but in the other extreme, they have been all treated under the name *E. phyllanthus* (Dodson & Gentry 1977, Kimmach 1964). Currently two species are recognized within this complex (Bauer 2003a): *E. hookeri* Haworth with three subspecies [subsp. *columbiense* (F.A.C. Weber) Ralf Bauer, subsp. *guatemalense* (Britton & Rose) Ralf Bauer and subsp. *pittieri*], and *E. phyllanthus* with one subspecies [subsp. *rubrocoronatum* (Kimmach) Ralf Bauer]. Our data show all *E. phyllanthus* accessions forming a clade (1 PP, 63% MLBS, 62% JK) while *E. phyllanthus* subsp. *rubrocoronatum* is not part of that clade but resolved as sister to *E. hookeri* (1 PP, 89% MLBS, 88% JK). The two subspecies of *E. hookeri* that were sampled are found as sisters to each other, but do not cluster with the third *E. hookeri* accession. Therefore, a more comprehensive evolutionary analysis including morphological and molecular characters and all known taxa related to the *E. phyllanthus*/*E. hookeri* complex is required to understand species limits (our study did not include *E. grandilobum*, *E. hookeri* subsp. *pittieri* or *E. laui*).

Epiphyllum, as it is currently circumscribed, is a morphologically distinct genus and easily recognisable by flattened stems with often crenate or lobed stem margins and large, white nocturnal flowers with a well-developed floral tube. Its confusing classification history has been reviewed several times (Backeberg 1959, Britton & Rose 1923, Buxbaum 1969).

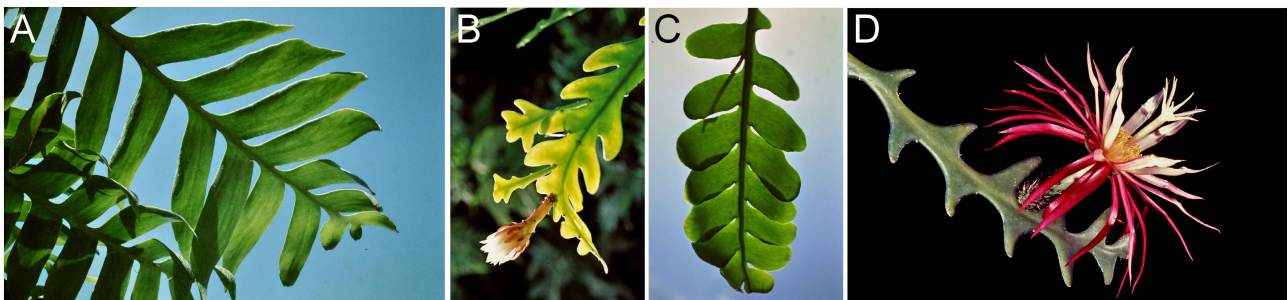


FIGURE 3. Convergent fern-like flattened stems in A) *Epiphyllum chrysocardium*, B) *Weberocereus imitans*, C) *Epiphyllum anguliger*, D) *Selenicereus (Cryptocereus) anthonyanus* (photos by W. Barthlott, Lotus-Salvinia.de).

The *Disocactus* clade

The clade that includes the nomenclatural type *D. biformis* (Lindley) Lindley is supported with 1 PP, 78% MLBS, 86 % JK. This confirms the results of Cruz *et al.* (2016), who recovered a *Disocactus* clade with the same composition with higher support from 96% BS and 96% JK, and 1 PP from Bayesian Inference (ML not calculated therein). Resolution and node support within *Disocactus* are generally low.

Disocactus was originally described by Lindley (1845) for *D. biformis* and was characterized by dimorphic stems and small flowers. The widely-used concept of *Disocactus* was established by Barthlott (1991), who amplified the genus by including the genera *Aporocactus*, *Nopalxochia* Britton & Rose, and *Heliocereus* (A. Berger) Britton & Rose, all with diurnal, large, bright red or pink flowers, to *Disocactus*. In this sense, *Disocactus* is polyphyletic, since *Aporocactus* is resolved outside and three *Epiphyllum* species (see above) are resolved within *Disocactus* with high confidence. This is also consistent with the results obtained by Cruz *et al.* (2016), who also already published the necessary new combinations for these *Epiphyllum* species under *Disocactus*. *Disocactus crenatus* (Lindley) M.Á. Cruz & S. Arias (2016: 157) has diurnal flowers, what had always appeared as unusual within the exclusively night-flowering *Epiphyllum*. Flowers of *D. crenatus* and *D. anguliger* (Lemaire) M.A. Cruz & S. Arias (2016: 157) have in fact stamens inserted in two series, a character that is common in *Disocactus* such as the flowers that open in the evening and last for several days. Furthermore, both species can hybridize with other species of *Disocactus*, but not of *Epiphyllum* (Bauer 2009).

The *Pseudorhipsalis* clade and the position of *P. ramulosa*

All species and subspecies were sampled in our study and *Pseudorhipsalis* is found as polyphyletic. A *Pseudorhipsalis* clade including the nomenclatural type *P. alata* (Swartz) Britton & Rose receives maximum support in all analyses, but *P. ramulosa* is not part of that clade, its exact position within the phyllocactoid clade remains unresolved. *Pseudorhipsalis*

amazonica (K. Schumann) Ralf Bauer is resolved as part of the *Pseudorhipsalis* clade with maximal support. This species is unusual as it is the only cactus to have blue tepals. Schumann regarded this as so unique that he placed it in an own monotypic genus *Wittia* K. Schumann (Schumann 1903). A new generic name *Wittiocactus* Rauschert (1982: 558) was published later to replace Schumann's illegitimate name *Wittia* because *Wittia* Pantocsek (1889: 110) is a genus of Bacillariophyta. *Wittiocactus* was then included in *Disocactus* (Hunt & Taylor 1990), yet still unresolved. Bauer (2002) moved it to *Pseudorhipsalis* because of many common characters, e.g. seedling morphology. The clade of *P. lankesteri* (Kimmach) Barthlott, *P. himantoclada* (Roland-Gosselin) Britton & Rose and *P. alata* (Swartz) Britton & Rose is supported by 1 PP but not found by the MP analysis. These three species are unique by forming pollen tetrads, a character found in no other Cactaceae species (Barthlott 1975, Leuenberger 1976).

Pseudorhipsalis was first described by Britton & Rose (1923: 213) with *P. alata* and *P. himantoclada*, two species that had been previously placed in *Rhipsalis*, and remained in this circumscription until the 1990ies. Subsequently two different generic concepts were suggested: Kimmach (1993) included *Pseudorhipsalis* in *Disocactus*, while Barthlott (1991) treated *Pseudorhipsalis* as distinct genus and expanded it to include six further Central American species showing small flowers. Barthlott's concept is largely confirmed by the plastid tree obtained here, while our data show no indication for merging *Pseudorhipsalis* into *Disocactus*.

Pseudorhipsalis ramulosa is resolved outside the *Pseudorhipsalis* clade and found in a polytomy with *Disocactus* and *Epiphyllum*. We tested alternative topologies for *P. ramulosa* being sister to either *Epiphyllum*, *Disocactus* or the rest of *Pseudorhipsalis*. The tree with *P. ramulosa* unresolved was significantly favoured over the alternative topologies tested (online supplement S3). The affinities of *P. ramulosa* were unclear for a long time. It was originally described as *Cereus ramulosus* Salm-Dyck (1834: 340), then treated as *Rhipsalis ramulosa* (Salm-Dyck) Pfeiffer, and still included in *Rhipsalis* by Britton & Rose (1920) after they had established the genus *Pseudorhipsalis*. They mentioned its similarity with *Pseudorhipsalis* but did not include it therein (Britton & Rose 1920). Kimmach (1961) included *P. ramulosa* in *Disocactus* whereas Barthlott (1991) combined it into *Pseudorhipsalis*. This taxon is generally similar to other *Pseudorhipsalis* species in vegetative and floral morphology, but there are also some differences. The floral tube is less pronounced in contrast to the other *Pseudorhipsalis* species. *P. ramulosa* sets fruits without pollination, while pollination is necessary in the other species of *Pseudorhipsalis* (Kimmach 1961). It is also widely distributed in tropical America, from Mexico and Central America to western South America and Antilles (Haiti, Jamaica) while the other *Pseudorhipsalis* species are much more restricted in their distribution, most are found only in Costa Rica and Panama (Barthlott *et al.* 2015). It has been suggested that the self-fertility, and also the berry-like sticky fruits adapted for bird-dispersal could explain the large distribution of *P. ramulosa* (Kimmach 1961). It could be a lineage within Hylocereeae that was especially successful in colonizing a comparatively large area by adapting to selfing and bird-dispersal. This is very similar to *R. baccifera* (Solander) Stearn, an epiphytic cactus with likewise small white flowers, self-pollination and sticky, bird-dispersed fruits that has the largest distribution of all cacti (Barthlott 1983, Barthlott *et al.* 2015). This independently evolved evolutionary strategy of *R. baccifera* and *P. ramulosa* would be another example for marked convergences in cacti.

To continue in recognizing *Pseudorhipsalis ramulosa* under *Pseudorhipsalis* and thus accepting a polyphyletic *Pseudorhipsalis* is not a good option in our opinion. We therefore propose to establish a new monotypic genus *Kimmachia* *gen. nov.* for *P. ramulosa* (see the Taxonomic synopsis).

The phylogenetic position of the *Strophocactus* species

Our results show that the epiphytic genus *Strophocactus* is not closely related to the core Hylocereeae but is in fact represented by two independent epiphytic lineages within Cactaceae. This is a very similar case to the earlier finding of *Lymanbensonia* Kimmach to constitute an epiphytic lineage independent from *Pfeiffera* Salm-Dyck and *Lepismium* Pfeiffer (Korotkova *et al.* 2010), in which it used to be included. Our finding of *Strophocactus* and *Deamia* as separate lineages shows that epiphytism in Cactaceae evolved up to six times independently.

Strophocactus sensu Bauer (2003a) is polyphyletic. Its nomenclatural type *S. wittii* is found nested within *Pseudoacanthocereus* F. Ritter, as sister to *P. sicariguensis*. *Strophocactus wittii* is an epiphyte from the inundation forests in the Amazonian Igapó region. It has flattened stems that adhere to the trunks of trees through numerous aerial roots and it is unique in Cactaceae in having water-dispersed seeds (Barthlott *et al.* 1997). Barthlott and Hunt (1993) included it in *Selenicereus* because of the large, white flowers with spines and bristles on the receptacle it shares with the other *Selenicereus* species. The two *Pseudoacanthocereus* species are scrambling or decumbent shrubs, with thin stems (up to 4.5 cm in diameter), variable number of ribs (2–7) and tuberous roots; the flowers are tubular-infundibuliform, with ribbed podaria, and areoles with bristles, and yellow to brown fruits, bearing podaria and deciduous areoles, and white pulpe (Taylor & Zappi 2004, Taylor *et al.* 1992). The genus *Pseudoacanthocereus* and *S. wittii* share the flower

shape, areoles with bristles, and fruit colour. Notably, *P. sicariguensis* occasionally forms flattened stem-segments which are highly similar to those of *S. wittii* (Fig. 4). This could be regarded as a morphological character supporting their close relationship. Furthermore, the distribution of these three species seems more gradual, because *S. wittii* is Amazonian (Brazil, Colombia, Peru), *P. sicariguensis* is native to the Maracaibo region (Colombia, Venezuela), and *P. brasiliensis* is native to the Eastern Caatinga-agreste (Brazil) (Barthlott *et al.* 2015). Therefore, we suggest a single genus for these three species and merge them under the oldest name *Strophocactus*. The necessary new combinations are provided in the Taxonomic synopsis.

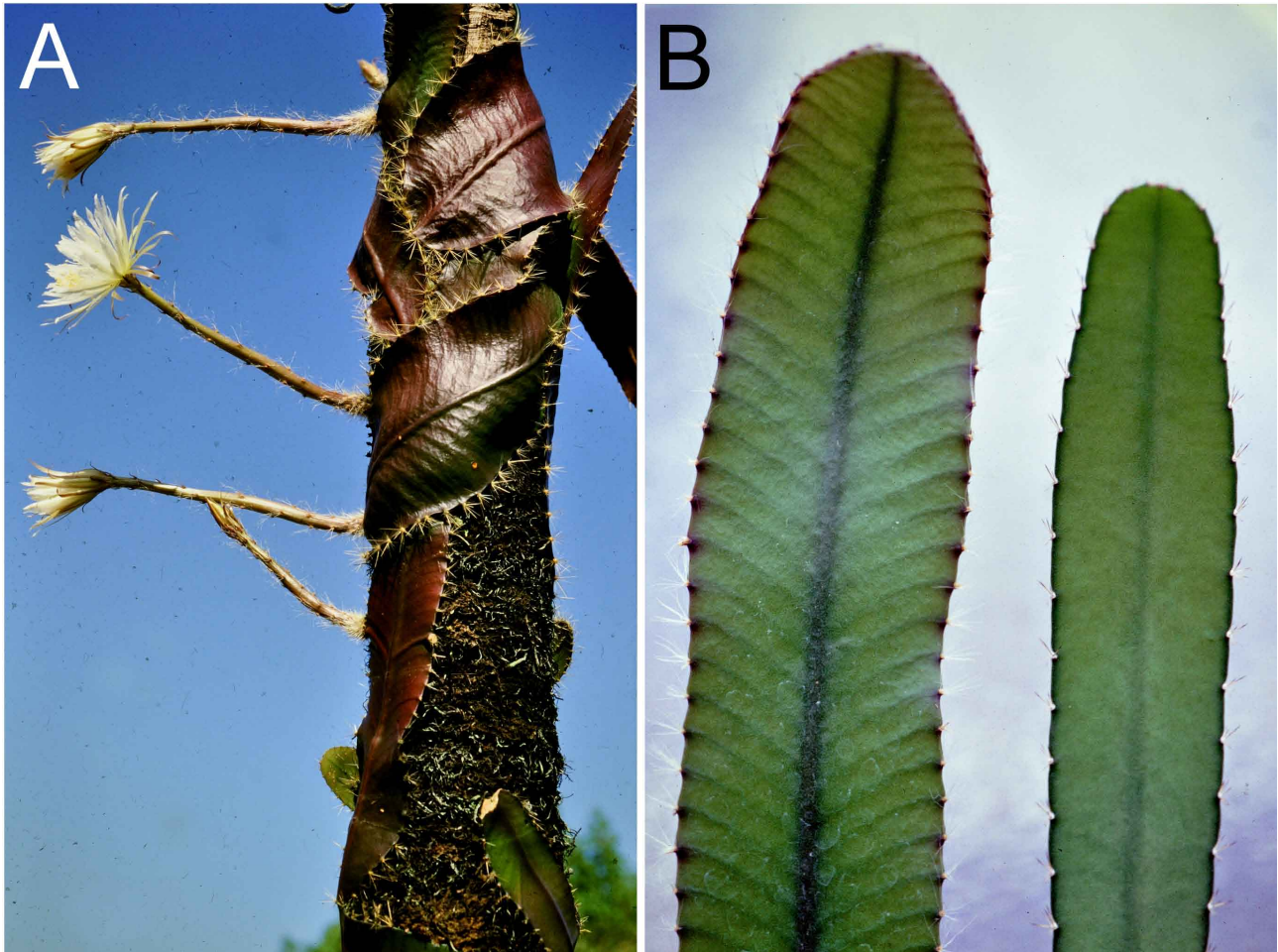


FIGURE 4. *Strophocactus*. A) *S. wittii*, flowering specimen (Schmidt s.n., cultivated at the Botanic Garden Bonn). B) *Strophocactus wittii* (left) and *Strophocactus (Pseudoacanthocereus) sicariguensis* (right), both forming flattened stems [photos by W. Barthlott, Lotus-Salvinia.de].

Strophocactus testudo and *S. chontalensis* (Fig. 5) form a highly-supported clade (1 PP, 98% MLBS, 99% JK), which is found as sister to the subtribe Pachycereinae. *Strophocactus testudo* [\equiv *Deamia testudo* (Karwinsky) Britton & Rose] is the nomenclatural type of *Deamia*, a monotypic genus originally established by Britton & Rose (1920: 212) and maintained as such until Buxbaum (1965) placed it in *Selenicereus* because of its flowers. Barthlott and Hunt (1993) maintained the species within *Selenicereus* because of the flower shape, spines and bristles on the stems and flowers, and spines persistent in fruit. *Strophocactus chontalensis* has originally been described as *Nyctocereus chontalensis* Alexander (1950: 131), for sharing the thin, cylindrical stems and ribs, although the roots are fibrous and the flowers shorter. Then it was moved to *Selenicereus* by Kimnach (1991) considering the presence of aerial roots and spines on the flowers. Most recently it was transferred to *Deamia* by Doweld (2002a) because it shares the micro-morphology of the seeds with *D. testudo*.

Strophocactus was originally established as a monotypic genus (Britton & Rose 1913: 262) and remained in this circumscription (Table 1), based on the flattened stems, the epiphytic habit, and very close areoles on the margin of the ribs, with flexible spines. In fact Berger (1905) and Britton & Rose (1920) pointed out a similarity to *Epiphyllum* by the 2-winged stems, and to *Selenicereus* by large flowers with hairs and bristles. Taking these characters into account, Hunt (1989) transferred *Strophocactus* to *Selenicereus*. The reinstatement of *Strophocactus* with three species

previously placed in *Selenicereus* was suggested by Bauer (2003a) and was based on unpublished sequence data of Robert Wallace reported by Hunt (2000), which is also clearly mentioned in Bauer's text. Hunt (2006) adapted this newly circumscribed *Strophocactus*, even though R. Wallace never published his data. Nyffeler and Egli (2010) additionally included *Cryptocereus anthonyanus* Alexander in *Strophocactus*, yet again based on unpublished data of R. Nyffeler and coworkers.



FIGURE 5. *Deamia*. A) *D. chontalensis* in habitat (M. Yañez 04); B) *D. chontalensis*, stem (M. Yañez 05); C) *D. testudo*, flower (M. Yañez 02) (photos by S. Arias).

Authors of all earlier treatments that accepted *Strophocactus* and *Deamia* as separate genera placed them together with the other Hylocereeae (or the equivalent group). Nevertheless, Bauer (2003a) excluded *Strophocactus* from Hylocereeae and suggested it might be closely related to *Acanthocereus* and *Peniocereus*. At the same time, there was also some evidence that these two genera might as well be part of the Hylocereeae (Arias *et al.* 2005, Nyffeler 2002), so the affinities of *Strophocactus* remained unclear. Nyffeler & Egli (2010) then placed *Strophocactus* within their Phyllocactaeae-Echinocereinae (= Pachycereeae). So, although there were these hints that *Strophocactus* is certainly not part of *Selenicereus* and possibly not part of the Hylocereeae, our study is the first to show this with high confidence. We consider it reasonable to reinstate *Deamia* to include *D. chontalensis* (Alexander) Doweld and *D. testudo*, as member of Echinocereae. Both species are clambering or pendent shrubs, with determinate growth, wax deposits on young stems, with hairs and spines on the flowers, red fruit and clear pulps. They are native to the Mesoamerican region, from central Mexico (Veracruz) to Costa Rica (Heredia) (Barthlott *et al.* 2015, Bravo-Hollis 1978).

Inversions in the plastid regions used here

Inversions are a common kind of microstructural mutations in plastid regions used for phylogeny inference. If an inversion is overlooked, the multiple sequence alignment will contain non-homologous, variable nucleotide characters (Ochoterena 2009), that will result in false phylogenetic signal. We therefore point out the very common presence of inversions in Cactaceae datasets, as several inversions have been found in the present study (Table 3).

The inversion in the *matK* CDS was reported earlier from Cactaceae (Korotkova *et al.* 2011) and is highly homoplastic. The inferred secondary structure (Fig. 6) shows this inversion to affect only the terminal loop of a hairpin and such hairpin-associated inversions have been shown to easily switch between closely related species and even at population level (Quandt *et al.* 2003, Quandt & Stech 2004). A translation of the *matK* CDS shows that only one amino acid is changed by the inversion (state "A" = lysine, state "T" = phenylalanine, asparagine or leucine) (Fig. 6). *MatK* is one of the fastest evolving genes in the plastid genome (Hilu & Liang 1997, Johnson & Soltis 1995), with a high proportion of substitutions even at the 1st and 2nd codon positions, so that it can be assumed that the amino acid substitution caused by this inversion does not affect the gene and therefore occurs repeatedly.

The inversions in the *rpl16* intron found here have not yet been reported from other Cactaceae datasets that use this region, although we would not exclude the possibility that they do occur therein. There are two inverted motifs directly adjacent to each other and that makes them particularly difficult to spot. Therefore, high attention needs to be paid when aligning plastid datasets for Cactaceae, as it is obvious that small inversions are extremely frequent in Cactaceae plastid genomes and pose a potential source of homoplasy when overlooked. This will be especially problematic when just automated alignment algorithms are used.

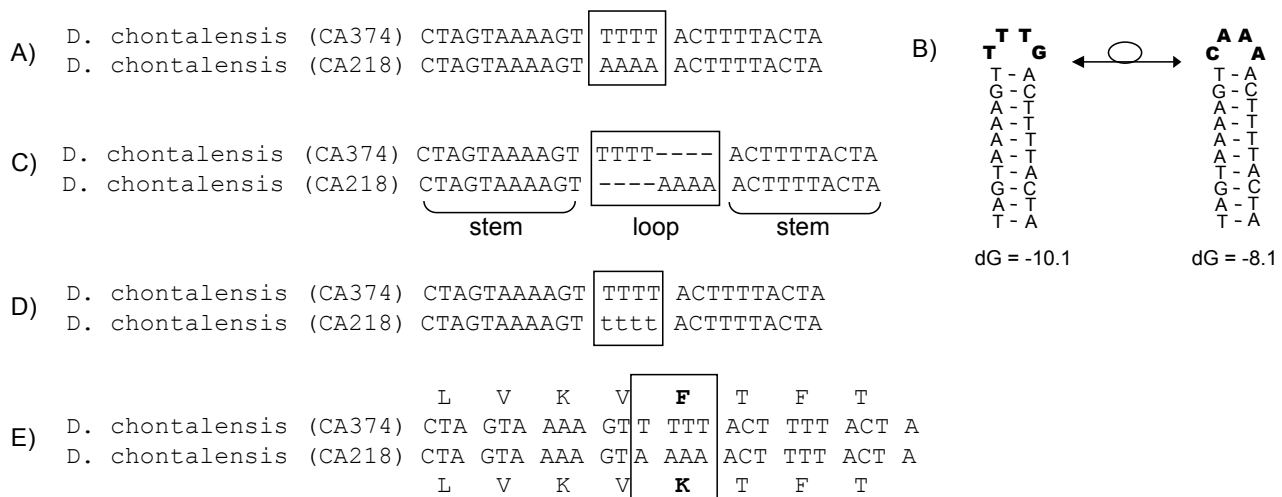


FIGURE 6. Inversion in the *matK* gene. A) Four independent substitutions will be assumed if the inversion is overlooked in the alignment. B) The inverted motif corresponds to the terminal loop of a hairpin and can easily switch from one state to another. If aligned in different columns, two independent substitution events will be assumed. C) The inverted motif reverse-complemented prior to phylogenetic analysis represents the most accurate homology assessment. D) The motif re-inverted prior to phylogenetic analysis. E) Only one amino acid is substituted by the inversion.

Conclusions and outlook

We have provided a first phylogenetic framework for the Hylocereeae and identified clades with high confidence that allow a reliable re-circumscription of the Hylocereeae genera. The dense taxon sampling in the presented phylogenetic trees can also be used to support a species-level synopsis. We are aware that relationships hypothesized on the base of plastid data still need to be corroborated using nuclear sequences, as taxa within Hylocereeae are known to hybridize. However, ITS, the most commonly used nuclear region for phylogeny inference, is not concerted in Cactaceae and therefore phylogenetically misleading (Harpke & Peterson 2006, Ritz *et al.* 2012). Other single-locus nuclear markers used, e.g. *phyC* and *ppc* (Hernández-Hernández *et al.* 2011, Ritz *et al.* 2012), do not significantly improve tree resolution and support over plastid markers and in general, there are so far hardly any nuclear datasets for Cactaceae. Therefore, a more in-depth approach to develop nuclear markers is needed and future work towards this aim will include phylogenomic approaches and next-generation-sequencing. Further sampling of sequence characters is still needed to improve our understanding of the relationships between the major clades of the Hylocereeae which so far could only be resolved in part. At the same time, a phylogenetically informed checklist at species-level will be a useful reference.

Taxonomy

Synopsis of the Hylocereeae

Our main criterion for suggesting taxonomic and nomenclatural adjustments here is the well-supported monophyly of the respective genera. We also believe that relationships found with molecular characters should be generally supported, or at least not be contradicted by the morphology of the plants (see discussion above). Narrow or wide circumscription of monophyletic entities as genera will therefore depend on the consistency of morphological variation and the possibility to recognise genera as easily as possible.

We suggest to re-define Hylocereeae to include eight genera in total: *Acanthocereus*, *Aporocactus*, *Disocactus*, *Epiphyllum*, *Kimnachia* gen. nov., *Pseudorhopsalis*, *Selenicereus*, and *Weberocereus*. *Deamia* and *Strophocactus* are excluded from the Hylocereeae and assigned to the Echinocereae. A few changes on generic level compared to the generic checklist of the Caryophyllales (Hernández-Ledesma *et al.* 2015) are proposed. First, we suggest amplifying *Selenicereus* to include *Hylocereus* and *Weberocereus glaber* and *W. tonduzii*, the type species of *Werckleocereus*. Therefore, *Werckleocereus* needs to become a new synonym of *Selenicereus*, not *Weberocereus*. Furthermore, we establish a new genus *Kimnachia* for *Pseudorhopsalis ramulosa*. We reinstate *Deamia* to include two species. The combination *Deamia chontalensis* (Alexander) Doweld is available while *D. testudo* is the type species of the genus. Finally, we newly circumscribe *Strophocactus* to include *Pseudoacanthocereus*.

To achieve the often-desired nomenclatural stability and practicability, we have attempted to retain the generic names that have been used for many decades as far as. Our data support reinstating earlier-proposed small segregate genera (*Deamia*, *Aporocactus*, *Strophocactus*). At the same time, we find also strong support for amplifying genera, especially *Selenicereus* that is twice its previous size in our new circumscription. Other clades at the generic level remain with their moderate species numbers between 10–20 (*Disocactus*, *Epiphyllum*). Of all the Hylocereeae genera as they were circumscribed by Barthlott and Hunt (1993), *Selenicereus* is least congruent with the results as found here.

We provide a complete synonymy and information on the types. This synopsis will be also available online through the online Caryophyllales checklist (caryophyllales.org) in the near future.



FIGURE 7. *Kimmachia ramulosa* f. *ramulosa* (left) and f. *angustissima* (right) (photo by W. Barthlott, Lotus-Salvinia.de). The specimen of f. *angustissima* pictured here originates from the collections of Marnier-Lapostolle at Lés Cedrés, and was very likely a clonotype from the plant Weber had described as *Rhipsalis angustissima*. A specimen is preserved at the Herbarium Berolinense (B-810013745, in spirit).

Hylocereeae Buxbaum (1958: 179).

1. *Acanthocereus* (Engelmann ex A. Berger) Britton & Rose (1909: 432) ≡ *Cereus* subsect. *Acanthocereus* Engelmann ex A. Berger (1905: 77).

Type:—*Acanthocereus baxaniensis* (Karwinsky 1837: 109) Borg (1937: 132).

= *Monvillea* Britton & Rose (1920: 21).

Type:—*Monvillea cavendishii* (Monville 1840: 219) Britton & Rose (1920: 21).

= *Peniocereus* subg. *Pseudoacanthocereus* Sánchez-Mejorada (1974: 38)

Type:—*Cereus maculatus* Weingart (1933: 14).

Accepted species:—13.

1.1 *Acanthocereus canoensis* (P.R. House, Gómez-Hinostrosa & H.M. Hernández) S. Arias & N. Korotkova, *comb. nov.* ≡ *Peniocereus canoensis* P.R. House, Gómez-Hinostrosa & H.M. Hernández (2013: 1077).

Type:—HONDURAS. Francisco Morazán: 1 km O de la comunidad de Río Hondo, 07 July 2009, House, Vega & Rivera 5110 (holotype TEFH!, isotype MEXU-1369109!).

1.2 *Acanthocereus castellae* (Sánchez-Mejorada) Lodé (2013: 2) ≡ *Peniocereus castellae* Sánchez-Mejorada (1974: 12).

Type:—MEXICO. Michoacan: 30 km N Playa Azul, 550 m, May 1971, Sánchez-Mejorada 71–0506 (holotype MEXU-159005!).

1.3 *Acanthocereus chiapensis* Bravo (1972: 117) ≡ *Peniocereus chiapensis* (Bravo) Gómez-Hinostrosa & H.M. Hernández (2005: 131).

Type:—MEXICO. Chiapas: entre Soyaló y Bochil, 23 March 1967, Bravo 5584 (holotype MEXU-118868!).

– *Acanthocereus griseus* Backeberg (1965: 103–106), *nom. inval.* (Art. 37.1).

1.4 *Acanthocereus cuixmalensis* (Sánchez-Mejorada) Lodé (2013: 2) ≡ *Peniocereus cuixmalensis* Sánchez-Mejorada (1973: 91).

Type:—MEXICO. Jalisco: La Huerta, playa Blanca de Careyitos, 30 m, November 1969, Sánchez-Mejorada 69–1102 (holotype MEXU-159003!).

1.5 *Acanthocereus fosterianus* (Cutak) Lodé (2013: 2) ≡ *Peniocereus fosterianus* Cutak (1946: 19).

Type:—MEXICO. Guerrero: Tierra Colorada, 1500 ft, 1935, Foster *s.n.* (holotype MO-054010!).

= *Peniocereus fosterianus* var. *nizandensis* Sánchez-Mejorada (1974: 49)

Lectotype (designated here):—[illustration] fig. 27 “Flor de *Peniocereus fosterianus* var. *nizandensis*” in Sánchez-Mejorada (1974).

= *Peniocereus fosterianus* var. *multitepalum* Sánchez-Mejorada (1974: 50).

Lectotype (designated here):—[illustration] fig. 28 “Flor de *Peniocereus fosterianus* var. *multitepalum*” in Sánchez-Mejorada (1974).

Notes:—*Peniocereus fosterianus* var. *nizandensis* was based on a specimen collected by Thomas MacDougall (*A-56*, Mexico, Oaxaca, Nizanda), and dispatched to Hernando Sánchez-Mejorada (*72-4066*) who described it and deposited the specimen in MEXU. At present there is no herbarium specimen in MEXU (missing), nor in NY and US where MacDougall also deposited cacti samples. We therefore designate a lectotype (Art. 9.2), based on the unique drawing that accompanies the protologue and associated with this taxon.

As in the previous case, *Peniocereus fosterianus* var. *multitepalum* was associated with a specimen collected by T. MacDougall (*A-56*, Mexico, Oaxaca, San Pedro) and refers to H. Sánchez-Mejorada (*72-4067*). The protologue clearly states that it was deposited in MEXU, however the specimen was not found in that herbarium (missing), nor in NY and US. Consequently, we designate as lectotype the only illustration that accompanies the publication (Art. 9.2).

1.6 *Acanthocereus hesperius* D.R. Hunt (2016: 9) ≡ *Peniocereus occidentalis* Bravo (1963: 80)

Type:—MEXICO. Oaxaca: San Pedro Pochutla, cerca de 20 km de Pochutla camino a río Copalito, 27 March 1963, Bravo *s.n.* [reg. 91] (holotype MEXU-072916!).

1.7 *Acanthocereus hirschtianus* (K. Schumann) Lodé (2013: 2) ≡ *Cereus hirschtianus* K. Schumann (1897: 130) ≡ *Nyctocereus hirschtianus* (K. Schumann) Britton & Rose (1909: 424) ≡ *Peniocereus hirschtianus* (K. Schumann) D.R. Hunt (1991: 90).

Type:—NICARAGUA. Ringgold & Rodgers Expedition, 1853-1856, *Wright s.n.* (holotype GOET-000502!, isotypes MO-313100!, US-177028!).

= *Nyctocereus guatemalensis* Britton & Rose (1913: 240) ≡ *Cereus guatemalensis* (Britton & Rose) Vaupel (1913: 86) ≡ *Peniocereus guatemalensis* (Britton & Rose) D.R. Hunt (2006: 14).

Type:—Guatemala. El Progreso: El Rancho, 4 April 1905, *Maxon 8510* [3767] (holotype US-535977).

= *Cereus neumannii* K. Schumann ex Loesener (1900: 99) ≡ *Nyctocereus neumannii* (K. Schumann) Britton & Rose (1909: 424)

Neotype (designated here):—NICARAGUA. Matagalpa: Hwy. 1 at bridge over Río Grande de Matagalpa, at ca. Km 83.5, ca. 3.6 km N of Las Calabazas, 31 August 1978, *Stevens & Krukoff 10224* (MO-2803392!).

Notes:—The protologue of *Cereus hirschtianus* is based on a sample collected by C. Wright during the expedition of Ringgold and Rodgers (1853–1856) to Nicaragua. According to the original publication, the original material used for the description is to be found in the Göttingen herbarium (Schumann 1897: 131). Therefore the herbarium specimen in GOET is the holotype (Art. 9.1). Two additional specimens (MO, US) include the same printed label and information, and represent isotypes. The sample in MO includes an additional hand-written distribution data: Island of Omotepe [Department of Rivas].

Schumann in Loesener (1900: 99–100) described *Cereus neumannii*, from a specimen collected by Rothschild (558 Nicaragua, Matagalpa, Chiquitillo). We have not found original material for this name. Therefore a neotype is designated (Art. 9.7), considering the closest to the locality and representing stem and flower as described in the protologue.

1.8 *Acanthocereus macdougallii* (Cutak) Lodé (2013: 2) ≡ *Peniocereus macdougallii* Cutak (1947: 87)

Type:—MEXICO. Oaxaca: on Cerro Arenal west of Tehuantepec, 550–800 m, 26 February 1947, *Cutak s.n.* (holotype MO-054009!).

– *Peniocereus macdougallii* var. *centrispinus* Backeberg (1962: 3843) *nom. inval.* (Art. 37.1).

1.9 *Acanthocereus maculatus* Weingart ex Bravo (1933: 398) ≡ *Cereus maculatus* Weingart ex Bravo (1933: 14) ≡ *Acanthocereus maculatus* (Weingart ex Bravo) F.M. Knuth (1935: 303) ≡ *Peniocereus maculatus* (Weingart ex Bravo) Cutak (1951: 76)

Lectotype (designated by Hunt & Taylor 2006: 10):—[illustration] unnumbered figure in Weingart (1933: 14).

1.10 *Acanthocereus oaxacensis* (Britton & Rose) Lodé (2012: 2) ≡ *Nyctocereus oaxacensis* Britton & Rose (1920: 120) ≡ *Peniocereus oaxacensis* (Britton & Rose) D.R. Hunt (1991: 90).

Type:—MEXICO. Oaxaca: about Lagunas, 850 ft, 05 June 1895, *Nelson 2643* [non 2543] (holotype US-115770!, isotype NY-385966!).

1.11 *Acanthocereus rosei* (J.G. Ortega) Lodé (2013: 3) ≡ *Peniocereus rosei* J.G. Ortega (1926: 189).

Lectotype (designated by Egli in Anderson 2005: 524):—[illustration] unnumbered figure in González Ortega (1926: 191).

1.12 *Acanthocereus tepalcatepecanus* (Sánchez-Mejorada) Lodé (2013: 3) ≡ *Peniocereus tepalcatepecanus* Sánchez-Mejorada (1974: 14)

Type:—MEXICO. Michoacan: La Huacana, 2 km N. El Infernillo, 360 m, September 1970, *Sánchez-Mejorada 70–0701* (holotype MEXU-159004!).

1.13 *Acanthocereus tetragonus* (Linnaeus) Hummelinck (1938: 165) ≡ *Cactus tetragonus* Linnaeus (1753: 466) ≡ *Cereus tetragonus* (Linnaeus) Miller (1768: unpagged)

Neotype (designated by Hummelinck 1938):—CURAÇAO. *Hummelinck 196, 170* (U).

= *Acanthocereus pentagonus* (Linnaeus) Britton & Rose (1920: 122) ≡ *Cactus pentagonus* Linnaeus (1753: 466) ≡ *Cereus pentagonus* (Linnaeus) Haworth (1812: 180)

Type:—Not designated.

= *Acanthocereus baxaniensis* (Karwinsky ex Pfeiffer) Borg (1937: 132) ≡ *Cereus baxaniensis* Karwinsky ex Pfeiffer (1837: 10)

Type:—Not designated.

= *Acanthocereus horridus* Britton & Rose (1920: 122)

Type:—GUATEMALA. Without locality, 1909, *Eichlam s.n.* (holotype NY-00118675!, isotypes US-00115577, US-00115578, U-0000928!).

= *Acanthocereus subinermis* Britton & Rose (1920: 125)

Type:—MEXICO. Oaxaca: between Mitla and Oaxaca City, 6 September 1908, *Rose 11304* (holotype US-115512!).

= *Acanthocereus occidentalis* Britton & Rose (1920: 125)

Type:—MEXICO. Sinaloa, vicinity of San Blas, near the river in thickets, 4 March 1910, *Rose et al. 13431* (holotype US-115513!).

Notes:—Hummelinck (1938) designated as lectotype of *Cereus tetragonus* two samples collected by him in Curaçao [*Hummelinck* 196 (flower), 170 (fruit) U], but Hunt (1991: 82, 1998: 16) and Egli (in Anderson 2005: 70) corrected its designation as neotype. However, this cannot be accepted according to the Art. 9.17. The designation of one of the specimens as neotype is currently in discussion (Hunt 2006).

Possible typification of *Cactus pentagonus* is not resolved (Hunt 1991: 83, Hunt 2006: 25). Eventual typification of *Cereus baxaniensis* is under discussion, since its identity and provenance is uncertain (Hunt 1998: 15, 2006: 25).

2. *Aporocactus* Lemaire (1860: 67)

Type:—*Aporocactus flagelliformis* (Linnaeus) Lemaire.

Accepted species:—2

2.1 *Aporocactus flagelliformis* (Linnaeus) Lemaire (1860: 68) ≡ *Cactus flagelliformis* Linnaeus (1753: 467) ≡ *Cereus flagelliformis* (Linnaeus) Miller (1768: unpagged) ≡ *Disocactus flagelliformis* (Linnaeus) Barthlott (1991: 87).

Lectotype (designated by Bauer 2003a: 12):—[illustration] in Plukenet (1692: t. 158, f. 6).

Epitype (designated by Bauer 2003a: 12):—MEXICO. Hidalgo: Along Mex 85, north of Parque Natural de los M[ar]moles, north of Cuesta Colorada, *Lautner* L00/241 (ZSS-22701!).

= *Aporocactus flagriformis* (Zuccarini ex Pfeiffer) Lemaire (1868: 58) ≡ *Cereus flagriformis* Zuccarini ex Pfeiffer (1837: 111).

Type:—Not designated.

= *Aporocactus leptophis* (A.P. de Candolle) Britton & Rose (1909: 435) ≡ *Cereus leptophis* A.P. de Candolle (1828: 117)

Type:—Not designated.

Notes:—Both *Cereus flagriformis* and *C. leptophis* are not typified. The description of *C. flagriformis* was based on material introduced by Karwinsky collected near San José de l'Oro, Oaxaca, Mexico. Bravo (1978) assumed that *A. flagriformis* might be merely a form of *A. flagelliformis*. Hunt (1989) mentions a plate of Pfeiffer & Otto (1839, t. 12) that could serve as iconotype, but the plant pictured has no significant differences to *A. flagelliformis*.

No type specimen or other verifiable material of *C. leptophis* appears to exist. De Candolle (1828) mentions a collection of Thomas Coulter No. 32 in the protologue, but does not cite any herbarium vouchers. He reports to have received a collection of living plants from Mexico from Coulter; the number 32 and other numbers mentioned in the same work refer to that collection. It is not clear whether herbarium specimens exist, they could not be located so far—if such a specimen could be located, it would be the type.

Both names require further investigations from the nomenclatural point of view.

2.2 *Aporocactus martianus* (Zuccarini) Britton & Rose (1920: 220) ≡ *Cereus martianus* Zuccarini (1832: 66) ≡ *Disocactus martianus* (Zuccarini) Barthlott (1991: 88) ≡ *Eriocereus martianus* (Zuccarini) Riccobono (1909: 240)

Neotype (designated by Bauer 2003a: 13):—MEXICO. Oaxaca: San Juan del Estado, 1500 m, *Lau* 1331 (ZSS-22702!).

= *Aporocactus conzattii* Britton & Rose (1920: 220) ≡ *Cereus conzattii* (Britton & Rose) A. Berger (1929: 110).

Type:—MEXICO. Oaxaca: Cerro San Felipe, 1912, *Conzattii* s.n.[#18] (holotype US-00115579!, isotypes K-000062686!, NY-118684!).

3. *Disocactus* Lindley (1845: 31)

Type:—*D. biformis* (Lindley) Lindley

= *Cereus* subsect. *Heliocereus* A. Berger (1905: 78) ≡ *Heliocereus* (A. Berger) Britton & Rose (1909: 433)

= *Chiapasias* Britton & Rose (1923: 203)

Type:—*Chiapasias nelsonii* (Britton & Rose) Britton & Rose

= *Nopalxochia* Britton & Rose (1923: 204)

Type:—*Nopalxochia phyllanthoides* (A.P. de Candolle) Britton & Rose

= *Bonifazia* Standley & Steyermark (1944: 66)

Type:—*Bonifazia quezalteca* Standley & Steyermark

= *Pseudonopalxochia* Backeberg (1958: 69)

Type:—*Pseudonopalxochia conzattiana* (T. MacDougal) Backeberg

= *Lobeira* Alexander (1944: 177)

Type:—*Lobeira macdougallii* Alexander

= *Trochilocactus* Lindinger (1942: 383)

Type:—*Trochilocactus eichlamii* (Weingart) Lindinger

Notes:—Our results support those obtained by Cruz *et al.* (2016) to recognize *Disocactus* as a monophyletic genus, including three erstwhile *Epiphyllum* species. Also the inclusion of *D. macdougallii* (Alexander) Barthlott and *D. ackermannii* subsp. *conzattianus* (T. MacDougal) U. Guzmán in this genus is confirmed. These taxa have not been included in the aforementioned study. A species-level synopsis of *Disocactus* has already been provided by Cruz *et al.* (2016) and is therefore not presented here.

Accepted species:—15 (7 infraspecific taxa).

4. *Epiphyllum* Haworth (1812: 197)

Type:—*Epiphyllum phyllanthus* (Linnaeus) Haworth ≡ *Cactus phyllanthus* Linnaeus

≡ *Phyllocactus* Link (1829: 10), *nom. illeg. et superfl.* (Art. 52.2).

= *Marniera* Backeberg (1950: 22)

Type:—*Marniera macroptera* (Lemaire) Backeberg

= *Chiapasophyllum* Doweld (2002: 32)

Type:—*Chiapasophyllum chrysocardium* (Alexander) Doweld

Accepted species:—10 (5 infraspecific taxa).

4.1. *Epiphyllum baueri* Dorsch (2003: 6)

Type:—COLOMBIA. Chocó: Nuquí, between Río Piedra Piedra and Río Terco, below Cerro Corrizalito, 150 m, 7 March 1999, *Bauer 32* (holotype ZSS-22456!).

4.2. *Epiphyllum cartagense* (F.A.C. Weber) Britton & Rose (1913: 256) ≡ *Phyllocactus cartagensis* F.A.C. Weber (1902: 462)

Neotype (designated by Bauer 2003a: 19):—COSTA RICA. Alajuela: Río Barranca, near San Juan de San Ramon, 1500–1600 m, 1913, *Tonduz 17850* (G).

= *Phyllocactus cartagensis* var. *refracta* F.A.C. Weber (1902: 462)

Type:—Not designated.

4.3. *Epiphyllum chrysocardium* Alexander (1956: 4) ≡ *Marniera chrysocardium* (Alexander) Backeberg (1959: 737) ≡ *Selenicereus chrysocardium* (Alexander) Kimmach (1991: 91) ≡ *Chiapasophyllum chrysocardium* (Alexander) Doweld (2002: 32)

Type:—MEXICO. Chiapas: Selva Negra, between Tapalapa and Blanca Rosa near Santa Lucía and Río Napak, 9 February 1951, *MacDougal A 198* (holotype NY-455205).

4.4. *Epiphyllum grandilobum* (F.A.C. Weber) Britton & Rose (1913: 257) ≡ *Phyllocactus grandilobus* F.A.C. Weber (1902: 464)

Lectotype (designated by Bauer 2003a: 27):—COSTA RICA. San José: La Hondura, 800 m, 1900, *Wercklé s.n.* (P-05003211!).

= *Epiphyllum gigas* Woodson & Cutak (1958: 87).

Type:—PANAMA. Cerro Trinidad, 800–100 m, 20 October 1946, *Allen 3772* [holotype MO-148233! (sheet 1), MO-148232! (sheet 2)].

4.5. *Epiphyllum hookeri* Haworth (1829: 108)

≡ *Cereus hookeri* (Haworth) Pfeiffer (1837: 125) ≡ *Phyllocactus hookeri* (Haworth) Salm-Dyck (1842: 38) ≡ *Epiphyllum phyllanthus* var. *hookeri* (Haworth) Kimmach (1964: 113) ≡ *Epiphyllum phyllanthus* subsp. *hookeri* (Haworth) U. Guzmán (2003: 17)

Type:—[illustration] “*Cactus phyllanthus*” in Sims (1826: t. 2692), holotype, image available at <http://www.biodiversitylibrary.org/item/14337#page/235/mode/1up>.

4.5a. *Epiphyllum hookeri* subsp. *hookeri*

= *Cereus marginatus* Salm-Dyck (1834: 340).

Type:—Not designated.

= *Phyllocactus stenopetalus* C.F. Förster (1846: 441) ≡ *Epiphyllum stenopetalum* (C.F. Förster) Britton & Rose (1913: 259).

Type:—Not designated.

= *Phyllocactus strictus* Lemaire (1854: 107) ≡ *Epiphyllum strictum* (Lemaire) Britton & Rose (1913: 259).

Type:—Not designated.

4.5b. *Epiphyllum hookeri* subsp. *columbiense* (F.A.C. Weber) Ralf Bauer (2003: 26) ≡ *Phyllocactus phyllanthus* var. *columbiensis* F.A.C. Weber (1898: 957) ≡ *Epiphyllum phyllanthus* var. *columbiense* (F.A.C. Weber) Backeberg (1959: 746) ≡ *Epiphyllum columbiense* (F.A.C. Weber) Dodson & A.H. Gentry (1977: 31).

Neotype (designated by Bauer 2003a: 26):—COLOMBIA. Chocó: Nuquí, Coquí, mangrove swamp El Estero, 1 m, 9 March 1999, *Bauer 36* (ZSS-19792).

4.5c. *Epiphyllum hookeri* subsp. *guatemalense* (Britton & Rose) Ralf Bauer (2003: 25) ≡ *Epiphyllum guatemalense* Britton & Rose (1913: 78) ≡ *Phyllocactus guatemalensis* (Britton & Rose) Vaupel (1913: 116) ≡ *Epiphyllum phyllanthus* var. *guatemalense* (Britton & Rose) Kimmach (1964: 110) ≡ *Epiphyllum phyllanthus* subsp. *guatemalense* (Britton & Rose) U. Guzmán (2003: 17).

Type:—GUATEMALA. Locality unknown, 1910, *Eichlam s.n.* (holotype US-691401, isotype US-385785!, US-385786!).

4.5d. *Epiphyllum hookeri* subsp. *pittieri* (F.A.C. Weber) Ralf Bauer (2003: 26) ≡ *Phyllocactus pittieri* F.A.C. Weber (1898: 957) ≡ *Epiphyllum pittieri* (F.A.C. Weber) Britton & Rose (1913: 258) ≡ *Epiphyllum phyllanthus* var. *pittieri* (F.A.C. Weber) Kimmach (1964: 115)

Neotype (designated by Bauer 2003a: 26):—COSTA RICA. Limón: Atlantic coast near Cahuita, *Horich s.n.* (ZSS-19793).

4.6. *Epiphyllum laui* Kimmach (1990: 194)

Type:—MEXICO. Chiapas: north of Tumbala, 2200 m, December 1979, *Lau 1319* (holotype HNT-0000085!).

4.7. *Epiphyllum oxypetalum* (A.P. de Candolle) Haworth (1829: 109) ≡ *Cereus oxypetalus* A.P. de Candolle (1828: 470) ≡ *Phyllocactus oxypetalus* (A.P. de Candolle) Link ex Walpers (1843: 341).

Lectotype (designated by Bauer 2003a: 23):—[illustration] “*Cereus oxipetalus*” in Candolle (1828: t. 14). image available at <http://www.biodiversitylibrary.org/item/84594#page/161/mode/1up>

= *Cereus latifrons* Pfeiffer (1837: 735) ≡ *Epiphyllum latifrons* Pfeiffer (1837: 125) ≡ *Phyllocactus latifrons* (Pfeiffer) Walpers (1843: 341).

Type:—Not designated.

= *Epiphyllum acuminatum* K. Schumann (in Martius 1890: 222) ≡ *Phyllocactus acuminatus* (K. Schumann) K. Schumann (1897: 213)

Lectotype (designated here):—[illustration] t. 45 “*Epiphyllum acuminatum*” in Martius (1890: 222). image available at <http://www.biodiversitylibrary.org/page/138734#page/224/mode/1up>.

= *Phyllocactus grandis* Lemaire (1847: 255) ≡ *Epiphyllum grande* (Lemaire) Britton & Rose (1913: 257).

Type:—Not designated

= *Phyllocactus purpusii* Weingart (1907: 34) ≡ *Epiphyllum oxypetalum* var. *purpusii* (Weingart) Backeberg (1959: 747).

Lectotype (designated here):—[illustration] “*Phyllocactus Purpusii* Weing. n. sp. Nach einer von C. A. Purpus aufgenommenen Photographie” in Weingart (1907: 35 [unpaged]). image available at <http://www.biodiversitylibrary.org/item/49873#page/51/mode/1up>

Notes:—Both for *Epiphyllum acuminatum* and for *Phyllocactus purpusii* there are no holotype indications in the protologues (Martius 1890: 222, and Weingart 1907: 34, respectively). The illustrations provided are here designated as lectotypes.

4.8. *Epiphyllum phyllanthus* (Linnaeus) Haworth (1812: 197) ≡ *Cactus phyllanthus* Linnaeus (1753: 469)

Lectotype (designated by Leuenberger 1997: 17):—[illustration] “*Cereus scolopendrii folio brachiato*” in Dillenius (1732: t. 64. fig. 74. 1732).

4.8a. *Epiphyllum phyllanthus* subsp. *phyllanthus* ≡ *Cereus phyllanthus* (Linnaeus) A.P. de Candolle (1828: 469) ≡ *Rhipsalis phyllanthus* (Linnaeus) K. Schumann (1890: 298) ≡ *Phyllocactus phyllanthus* (Linnaeus) Link (1831: 11) ≡ *Opuntia phyllanthus* (Linnaeus) Miller (1768: unpagged).

= *Rhipsalis macrocarpa* Miquel (1838: 49) ≡ *Hariota macrocarpa* (Miquel) Kuntze (1891: 263).

Type:—Not designated

= *Epiphyllum gaillardae* Britton & Rose (1913: 240) ≡ *Phyllocactus gaillardae* (Britton & Rose) Vaupel (1913: 88).

Type:—PANAMA. Canal zone, 6 August 1909, *Gaillard s.n.* (holotype US-691240!).

= *Phyllocactus phyllanthus* var. *boliviensis* F.A.C. Weber (1898: 957) ≡ *Epiphyllum phyllanthus* var. *boliviense* (F.A.C. Weber) Backeberg (1959: 746).

Type:—Not designated

= *Phyllocactus phyllanthus* var. *paraguayensis* F.A.C. Weber (1898: 957) ≡ *Epiphyllum phyllanthus* var. *paraguayense* (F.A.C. Weber) Backeberg (1959: 756).

Type:—Not designated

= *Epiphyllum phyllanthus* var. *schnetteri* Peukert (1991: 255).

Type:—COLOMBIA. Departamento de Cundinamarca: entre Viot y Mesitas del Colegio, December 1970, 900 m, *Schnetter s.n.* (holotype COL-256856!, isotype COL-291368!).

4.8b. *Epiphyllum phyllanthus* subsp. *rubrocoronatum* (Kimmach) Ralf Bauer (2003: 25) ≡ *Epiphyllum phyllanthus* var. *rubrocoronatum* Kimmach (1964: 110) ≡ *Epiphyllum rubrocoronatum* (Kimmach) Dodson & A.H. Gentry (1977: 31).

Type:—ECUADOR. Chimborazo: along Rio Chimbo at the station of La Isla on the railroad to Quito, 100 m, 1958, *Horich s.n.* (holotype HNT-0000086!, isotypes K-000101442!, US-00173517!, UC-1229076!, UC-1229080!).

= *Epiphyllum trimetrale* Croizat (1946: 353).

Type:—COLOMBIA. Departamento del Valle: Costa del Pacifico; Rio Yurumangu: Veneral, 11 February 1944, *Cuatrecasas 15863* (holotype GH-00063119!, isotypes: GH-00063120!, COL-000003016, COL-000003017!, COL-000003018!, GH-00063120).

4.9. *Epiphyllum pumilum* Britton & Rose (1913: 258) ≡ *Phyllocactus pumilus* (Britton & Rose) Vaupel (1913: 117)

Type:—GUATEMALA. Locality unknown, 1910, *Eichlam s.n.* (holotype US-691392!).

= *Epiphyllum caudatum* Britton & Rose (1913: 256) ≡ *Phyllocactus caudatus* (Britton & Rose) Vaupel (1913: 116).

Type:—MEXICO. Oaxaca: Near Comaltepec, 30 July 1894, *Nelson 919* (holotype US- 00115643!).

4.10. *Epiphyllum thomsonianum* (K. Schumann) Britton & Rose (1913: 259) ≡ *Phyllocactus thomsonianus* K. Schumann (1895: 6)

Lectotype (designated by Bauer 2003c: 247):—[illustration] “*Phyllocactus Thomsonianus* K. Sch.”, Fig. by B. Esh in Schumann (1895: unpagued). Image available at <http://www.biodiversitylibrary.org/item/49871#page/13/mode/1up>

Epitype (designated by Bauer 2003c: 247):—[Illustration] “Fig. A *Epiphyllum thomsonianum* (Schum.) Britt. & Rose var. *thomsonianum*, *Birdsey 314*, [cult.] UCBG 53.512”, in Kimmach (1965: 165).

4.10a. *Epiphyllum thomsonianum* subsp. *thomsonianum* ≡ *Epiphyllum macropterum* var. *thomsonianum* (K. Schumann) Borg (1937: 359)

= *Phyllocactus ruestii* Weingart (1914: 123) ≡ *Epiphyllum ruestii* (Weingart) F.M. Knuth (1936: 163).

Type:—Not designated.

4.10b. *Epiphyllum thomsonianum* subsp. *costaricense* (F.A.C. Weber) Ralf Bauer (2003: 22) ≡ *Phyllocactus costaricensis* F.A.C. Weber (1902: 463) ≡ *Epiphyllum costaricense* (F.A.C. Weber) Britton & Rose (1913: 256) ≡ *Epiphyllum thomsonianum* var. *costaricense* (F.A.C. Weber) Kimmach (1965: 168).

Lectotype (designated by Bauer 2003a: 22):—[illustration] “Fig. C. The lectotype of *Phyllocactus costaricensis*, collected by Biolley in 1898” in Kimmach (1965: 167).

Epitype (designated by Bauer 2003a: 22):—[illustration] “Fig. B *Epiphyllum thomsonianum* var. *costaricensis* (Web.) Kimm., *Horich s.n.*, [cult.] UCBG 57001 (Costa Rica)” in Kimmach (1965: 166).

= *Phyllocactus macrocarpus* F.A.C. Weber (1902: 464) ≡ *Epiphyllum macrocarpum* (F.A.C. Weber) Backeberg (1959: 754).

Type:—COSTA RICA. Pedras Negras, 1901, *Pittier 12* (holotype P-02273071!).

5. *Selenicereus* (A. Berger) Britton & Rose (1909: 429)

Type:—*S. grandiflorus* (Linnaeus) Britton & Rose

≡ *Cereus* subsect. *Selenicereus* A. Berger (1905: 76)

= *Hylocereus* (A. Berger) Britton & Rose (1909: 428) ≡ *Cereus* subg. *Hylocereus* A. Berger (1905: 72)

Type:—*H. triangularis* (Linnaeus) Britton & Rose

= *Werckleocereus* Britton & Rose (1909: 432)

Type:—*Werckleocereus tonduzii* (F.A.C. Weber) Britton & Rose

= *Wilmattea* Britton & Rose (1920: 195).

Type:—*Wilmattea minutiflora* (Vaupel) Britton & Rose

= *Mediocactus* Britton & Rose (1920: 210), excl. the type, see Hunt (1989) for a detailed explanation. Type:—*Mediocactus coccineus* (Salm-Dyck ex A.P. de Candolle) Britton & Rose ≡ *Selenicereus* sect. *Salmdyckia* D.R. Hunt (1989: 91). Type:—*Selenicereus setaceus* (Salm-Dyck ex A.P. de Candolle) Werdermann
= *Cryptocereus* Alexander (1950: 164).
Type:—*Cryptocereus anthonyanus* Alexander

Notes:—Our study provides strong evidence that *Hylocereus* and *Selenicereus* share a common origin and therefore suggest they should be merged under one generic name. The support for the clade of *Hylocereus* and *Selenicereus* is 1 PP, 98% ML BS, 99 % JK and this clade includes additionally two *Weberocereus* species. *Hylocereus* and *Selenicereus* were both originally established by Berger (1905), *Hylocereus* as a subgenus and *Selenicereus* as a subsection of *Eucereus* Engelmann. Both were raised to generic rank by Britton & Rose (1909) and the names *Hylocereus* and *Selenicereus* therefore had equal priority according to the Art. 11.5 of ICN, “When, for any taxon of the rank of family or below, a choice is possible between legitimate names of equal priority in the corresponding rank ... the first such choice to be effectively published ... establishes the priority of the chosen name...”. Recently, Hunt (2017) merged *Hylocereus* and *Selenicereus* and published the necessary new combinations in *Selenicereus*. He thus established priority of *Selenicereus* by explicitly citing *Hylocereus* to synonymy.

There would have been several reasons for maintaining *Hylocereus* instead of *Selenicereus*. First, *Selenicereus* has always been a genus without a clear concept, and several times became an assemblage of various segregate genera. Berger (1929) for example treated *Selenicereus* including *Deamia*, *Weberocereus*, *Werckleocereus* and *Wilmatea*, while Hunt (1989) included *Mediocactus*, *Cryptocereus*, *Deamia* and *Strophocactus* in *Selenicereus*. *Hylocereus*, in contrast has been much more consistent in terms of its circumscription. In addition, from an economic or utility perspective, *Hylocereus* has an international market for edible fruits (pitahaya in Latin America, dragon fruit in China), while *Selenicereus* does not. Although *Selenicereus grandiflorus* is better known in Europe as an ornamental than some species of *Hylocereus*, this has a regional connotation. Therefore maintaining the name *Hylocereus* would have also been relevant for CITES and for trade. Nevertheless, as the new combinations in *Selenicereus* by Hunt (2017) must be regarded as effectively published and the name now has priority over *Hylocereus*, we have to accept *Selenicereus*. The recognized species are listed and some further necessary new combinations are provided below.

Accepted species:—31, 3 infraspecific taxa.

5.1. *Selenicereus anthonyanus* (Alexander) D.R. Hunt (1989: 93) ≡ *Cryptocereus anthonyanus* Alexander (1950: 165).

Lectotype (designated by Bauer 2003a: 50):—[illustration] “Fig. 64” of Alexander (1950: 166).

5.2. *Selenicereus alliodorus* (Gómez-Hinostrosa & H.M. Hernández) S. Arias & N. Korotkova, *comb. nov.* ≡ *Weberocereus alliodorus* Gómez-Hinostrosa & H.M. Hernández (2014: 250).

Type:—MEXICO. Oaxaca: Distrito Pochutla, Municipio San Miguel del Puerto, ca. 1.5 km al N de Finca Monte Carlo, camino a Las Lobas. Finca Monte Carlo se encuentra a 11 km al NO de Sta. María Xadani, 16°00′11″N, 96°06′26″W, 1238 m, 18 January 2013, Gómez-Hinostrosa, Hernández & Pascual 2601 (holotype MEXU-01380036!, isotypes ASU, CR, HNT, IEB, MO, NY).

5.3. *Selenicereus atropilosus* Kimmach (1978: 270)

Type:—MEXICO. Jalisco: on road from Mascota to Puerto Vallarta, 3 miles past turnoff to San Sebastian, ca. 870 m, 8 February 1970, Boutin & Kimmach 3190 (holotype HNT-1267!).

5.4. *Selenicereus calcaratus* (F.A.C. Weber) D.R. Hunt (2017: 30) ≡ *Cereus calcaratus* F.A.C. Weber (1902: 458) ≡ *Hylocereus calcaratus* (F.A.C. Weber) Britton & Rose (1909: 428)

Neotype (designated by Bauer 2003a: 32):—[illustration] “*Hylocereus calcaratus* (Web.) Britt. & Rose, Lankaster s.n. [cult.] UCBG 52.1085 (Costa Rica)” in *Cact. Succ. J.* (Los Angeles) 39(3): 103. 1967.

Notes:—The neotype was designated by Bauer (2003a: 32) because the original Pittier collection can not be located at the Paris herbarium.

5.5. *Selenicereus costaricensis* (F.A.C. Weber) S. Arias & N. Korotkova, *comb. nov.*

≡ *Cereus trigonus* var. *costaricensis* F.A.C. Weber (1902: 457) ≡ *Hylocereus costaricensis* (F.A.C. Weber) Britton & Rose (1909: 428).
Type:—Not designated.

Notes:—The protologue mentions a photograph by Tonduz (Herborisations au Costa-Rica, Bull. de l'herbier Boissier 3. 1895) that could serve as a lectotype but so far has not been possible to locate; currently under discussion (Bauer 2003a).

5.6. *Selenicereus dorschianus* Ralf Bauer (2009: 64)

Type:—MEXICO. Jalisco: c. 42 km south of Puerto Vallarta, about half-way (22 km) from El Túito eastwards to an abandoned mine (Cuale-San Sebastián), ca. 1100–1500 m, June 1989, *Böhme s.n.* (holotype ZSS-22551!).

5.7. *Selenicereus escuintlensis* (Kimmach) D.R. Hunt (2017: 31)

≡ *Hylocereus escuintlensis* Kimmach (1984: 177)

Type:—GUATEMALA. Escuintla, just south of Escuintla, near cemetery, 1 July 1953, *Birdsey 313*, cult. UCBG 53.511 at Huntington Bot. Gard. 15092 (holotype HNT-0000024!, isotypes F-0052882F!, K-000101238!, MEXU-01283225!, MO-054008!, NY-00803905!, UC-1229087!, US-00115679!).

5.8. *Selenicereus extensus* (Salm-Dyck ex A.P. de Candolle) Leuenberger (2001: 56)

≡ *Cereus extensus* Salm-Dyck ex A.P. de Candolle (1828: 469) ≡ *Hylocereus extensus* (Salm-Dyck ex A.P. de Candolle) Ralf Bauer (2003: 28) ≡ *Mediocactus extensus* (Salm-Dyck ex A.P. de Candolle) Doweld (2002: 42).

Neotype (designated by Leuenberger 2001: 56):—FRENCH GUIANA. Gobaya Soula, Bassin du Maroni, Atachi Bacca mountains (Camp 1), Hany river, 100 m, 1 February 1989, *Granville et al. 10991* (B!).

5.9. *Selenicereus glaber* (Eichlam) S. Arias & N. Korotkova, *comb. nov.* ≡ *Cereus glaber* Eichlam (1910: 150) ≡ *Werckleocereus glaber* (Eichlam) Britton & Rose (1917: 13) ≡ *Weberocereus glaber* (Eichlam) G.D. Rowley (1982: 46)

Lectotype (designated by Bauer 2003a: 50):—GUATEMALA. locality unknown, '1910', *Eichlam s.n.* (US-68419).

Epitype (designated by Bauer 2003a: 50):—GUATEMALA. Road to Antigua, July 1909, *Deam s.n.* (US-68420!).

5.9a. *Selenicereus glaber* subsp. *glaber*

5.9b. *Selenicereus glaber* subsp. *mirandae* (Bravo) S. Arias & N. Korotkova, *comb. nov.* ≡ *Selenicereus mirandae* Bravo (1967: 52) ≡ *Werckleocereus glaber* var. *mirandae* (Bravo) Kimmach (1978: 270) ≡ *Werckleocereus glaber* subsp. *mirandae* (Bravo) Doweld (2002: 43).

Type:—MEXICO. Chiapas: El Sumidero, 22 March 1967, *Bravo s.n.* (holotype MEXU- 01231772!).

5.10 *Selenicereus grandiflorus* (Linnaeus) Britton & Rose (1909: 430) ≡ *Cactus grandiflorus* Linnaeus (1753: 467) ≡ *Cereus grandiflorus* (Linnaeus) Miller (1768: unpagged)

Lectotype (designated by Lourteig 1991: 406):—Herb. Cliff. 182, Cactus 10 (BM-000628597!).

Epitype (designated by Bauer 2003a: 44):—MEXICO. Veracruz: Palma Sola, 10–50 m, 7 May 1978, *Lau 1285* (ZSS-5477!).

5.10a. *Selenicereus grandiflorus* subsp. *grandiflorus*

= *Cereus coniflorus* Weingart (1904: 118) ≡ *Selenicereus coniflorus* (Weingart) Britton & Rose (1909: 430).

Neotype (designated here):—[illustration] “Flower on branch of *Selenicereus coniflorus*“ in Britton & Brown (1920: pl 35).

= *Cereus jalapaensis* Vaupel (1913: 85).

Type:—Not designated

= *Cereus paradisiacus* Vaupel (1913: 87).

Type:—Not designated

= *Cereus roseanus* Vaupel (1913: 85).

Type:—Not designated

= *Cereus urbanianus* Gürke & Weingart (1904: 158) ≡ *Selenicereus urbanianus* Britton & Rose (1913: 242).

Type:—Not designated

= *Selenicereus maxonii* Rose (1909: 430).

Type:—CUBA. [Santiago de Cuba]: Province of Oriente, near Berraco, 8 miles east of Daiquiri, 13 April 1907, *Maxon 4024* (holotype US-00313059!, isotypes GH-00063201!, NY-00386183, P-04947361!).

= *Selenicereus pringlei* Rose (1909: 431).

Type:—MEXICO. Veracruz: near Jalapa, 3500 ft, 3 April 1899, *Pringle 7841* (US-00037467!).

– *Selenicereus hallensis* Weingart ex Borg (166. 1937), *nom. inval.* (Art. 36.1).

5.10b. *Selenicereus grandiflorus* subsp. *donkelaarii* (Salm-Dyck) Ralf Bauer (2003: 46) ≡ *Cereus donkelaarii* Salm-Dyck (1845: 355) ≡ *Selenicereus donkelaarii* (Salm-Dyck) Britton & Rose (1920: 200).

Neotype (designated by Bauer 2003a: 46):—MEXICO. Yucatan: Chichén Itzá, al the lip of a cenote, *Johnson s.n.* (US-2830673!).

5.10c. *Selenicereus grandiflorus* subsp. *hondurensis* (K. Schumann ex Weingart) Ralf Bauer (2003: 45) ≡ *Cereus hondurensis* K. Schumann ex Weingart (1904: 147) ≡ *Selenicereus hondurensis* (K. Schumann ex Weingart) Britton & Rose (1909: 430)

Neotype (designated by Doweld 2002a: 43):—HONDURAS. Atlántida: 5 miles east of Tela, 13 August 1934, *Yuncker 5019* (MO-108719).

Epitype (designated by Bauer 2003a: 46):—GUATEMALA. Izabal: Lago de Izabal near Castillo de San Felipe, *Bauer 8* (ZSS-21377!).

Notes:—An epitype was designated because Doweld's (l.c.: 43) neotype is a damaged specimen (c.f. Bauer 2003a).

5.10d. *Selenicereus grandiflorus* subsp. *lautneri* Ralf Bauer (2003: 45)

Type:—MEXICO. Oaxaca: San Pedro Huamelula, c. 50 m, 20 February 1990, *Lautner L90/55* (holotype ZSS-22536).

5.11. *Selenicereus guatemalensis* (Eichlam ex Weingart) D.R. Hunt ≡ *Cereus trigonus* var. *guatemalensis* Eichlam ex Weingart (1911: 68) ≡ *Cereus guatemalensis* (Eichlam ex Weing.) A. Berger (1929: 121) ≡ *Hylocereus guatemalensis* (Eichlam ex Weingart) Britton & Rose (1920: 184)

Neotype (designated by Doweld 2002b: 13):—GUATEMALA. Guatemala: Fiscal, ca. 1230 m, 6 June 1909, *Deam 6195* (MO-3057468 (sheet 3 of 3), MO-3057469 (sheet 1 of 3), MO-3057470 (sheet 2 of 3), isoneotype S-09-28483!).

5.12. *Selenicereus hamatus* (Scheidweiler) Britton & Rose (1909: 430) ≡ *Cereus hamatus* Scheidweiler (1837: 371)

Neotype (designated by Bauer 2003a: 50):—MEXICO. Veracruz: south of Palma Sola, 3 km from the coast, *Stolzenburg s.n.* (ZSS-21397).

= *Cereus rostratus* Lemaire (1838: 29).

Type:—Not designated

5.13. *Selenicereus inermis* (Otto ex Pfeiffer) Britton & Rose (1920: 207) ≡ *Cereus inermis* Otto ex Pfeiffer (1837: 116) ≡ *Mediocactus inermis* (Otto ex Pfeiffer) Doweld (2002: 42)

Neotype (designated by Doweld 2002a: 42):—VENEZUELA. Carabobo: carr. Puerto-Cabello-San Esteban, Sitio called "Montero", 21 May 1985 *Trujillo & Pulido 19360* (MO-3905799!).

= *Cereus karstenii* Salm-Dyck (1849: 218).

Type:—Not designated

= *Cereus wercklei* F.A.C. Weber (1902: 460) ≡ *Selenicereus wercklei* (F.A.C. Weber) Britton & Rose (1920: 208) ≡ *Mediocactus wercklei* (F.A.C. Weber) Doweld (2002a: 42).

Neotype (designated by Doweld 2002a: 42):—COSTA RICA. Guanacaste, 31 August 1990, *Solomon 19104* (MO).

= *Selenicereus rubineus* Kimmach (1993: 17).

Type:—MEXICO. Oaxaca: Tehuantepec, Santo Domingo Petapa, "Platanillo", ca 2,000 ft, 1 July 1957, *MacDougall A.245* (holotype HNT-0000016!, isotypes MEXU-01283233!, 01283234!, US-2830720!).

= *Epiphyllum steyermarkii* Croizat (1974: 19).

Type:—VENEZUELA. Miranda: Selva de Guatopo, Parque Nacional Guatopo, 27 April 1973, *Steyermark 108741* (holotype VEN-95337!).

5.14. *Selenicereus megalanthus* (K. Schumann ex Vaupel) Moran (1953: 325) ≡ *Cereus megalanthus* K. Schumann ex Vaupel (1913: 284) ≡ *Mediocactus megalanthus* (K. Schumann ex Vaupel) Britton & Rose (1920: 212) ≡ *Hylocereus megalanthus* (K. Schumann ex Vaupel) Ralf Bauer (2003: 28)

Lectotype (designated by Bauer 2003a: 28):—[illustration] "*Cereus megalanthus* auf einer grossen *Ficus* bei Tarapoto (Peru)" in Karsten & Schenck (1904: t. 5).

Epitype (designated by Bauer 2003a: 28):—PERU. Huánuco: Tingo Marfa, valley of Río Huallaga, *Johnson s.n.* (US-2906780!).

5.15. *Selenicereus minutiflorus* (Britton & Rose) D.R. Hunt (2017: 33) ≡ *Hylocereus minutiflorus* Britton & Rose (1913: 240) ≡ *Cereus minutiflorus* (Britton & Rose) Vaupel (1913: 87) ≡ *Wilmattea minutiflora* Britton & Rose (1920: 195).

Type:—GUATEMALA. Izabal: Lago de Izabal, 1907, *Peters s.n.* (holotype US-00115680!).

5.16 *Selenicereus monacanthus* (Lemaire) D.R. Hunt (2017: 33) ≡ *Cereus monacanthus* Lemaire (1841: 60) ≡ *Hylocereus monacanthus* (Lemaire) Britton & Rose (1920: 190)

Neotype (designated by Bauer 2003a: 33):—COLOMBIA. Magdalena: Parque Tayrona, Playa Arrecifes, 2 m, 20 March 1999, *Bauer 46* (ZSS-22705!).

= *Cereus lemairei* Hooker (1854: t. 4814) ≡ *Hylocereus lemairei* (Hooker) Britton & Rose (1909: 428).

Lectotype (designated by Leuenberger 1997: 22):—[illustration] in Hooker (1854: t. 4814).

= *Cereus polyrhizus* F.A.C. Weber in K. Schumann (1897: 151) ≡ *Hylocereus polyrhizus* (F.A.C. Weber) Britton & Rose (1920: 185).

Neotype (designated by Bauer 2003a: 41):—VENEZUELA. Cojedes: Hato Piñero, *Delascio 14484* (VEN-249248!).

= *Cereus scandens* Salm-Dyck (1850: 219) ≡ *Hylocereus scandens* (Salm-Dyck) Backeberg (1959: 817).

Neotype (designated by Bauer 2003a: 40):—SURINAME. Brokopondo district: 12 km south of village Afobaka, forest along Sara Creek, February 1965, *Donselaar 2119* (U-212602).

= *Cereus trinitatis* Lemaire & Herment (1859: 642) ≡ *Hylocereus trinitatis* (Lemaire & Herment) Berger (1929: 341).

Neotype (designated by Bauer 2003a: 41):—TRINIDAD. Government farm St. Joseph, 21 April 1975, *Philcox & Andrews 7710* (K-000101193!).

= *Hylocereus venezuelensis* Britton & Rose (1920: 226) ≡ *Wilmattea venezuelensis* (Britton & Rose) Croizat (1972: 39).

Lectotype (designated by Bauer 2003a: 41):—VENEZUELA. [Carabobo]: Near Valencia, 1917, *Rose 21835* (US-1038847!).

= *Hylocereus estebanensis* Backeberg (1957: 11).

Neotype (designated by Bauer 2003a: 41):—[illustration] “Abb. 730. *Hylocereus estebanensis* Backbg.” in Backeberg (1959: 814).

= *Hylocereus peruvianus* Backeberg (1937: [2])

Neotype (designated by Bauer 2003a: 41):—PERU. Tumbes: Prov. Zarumilla, about 0,5 km from Campo Verde along the road, Bosque Nacional de Tumbes, 17 December 1967, *Simpson & Schunke 400* (US-2750703!).

– “*Cereus extensus* Salm-Dyck ex A.P. de Candolle” *sensu* Hooker (1844: 4066).

Notes on *Cereus polyrhizus*:—Bauer (2003a: 41) noted that the the neotype designated by Doweld (2002b: 13): PANAMA. Panama, 2 m, 4 December 1984, *Bravo & Scheinvar 4008* (MO) had to be rejected as it is in strong conflict with the protologue and apparently there are even two different species on that sheet.

Notes on *Cereus scandens*:—Bauer l.c. noted that he designated this neotype because Doweld’s neotype [Doweld 2002b: 13: VENEZUELA. Bolivar: 260 m, May 1986, *Fernandez 3035* (MO)] could not be found at MO and therefore had to be rejected as neotype.

5.17. *Selenicereus murrillii* Britton & Rose (1920: 206) ≡ *Mediocactus murrillii* (Britton & Rose) Doweld (2002: 42).

Lectotype (designated by Doweld 2002a: 42):—MEXICO. Colima: near Colima, 1910, *Murril s.n.* (NY-386172!).

5.18. *Selenicereus nelsonii* (Weingart) Britton & Rose (1923: 283) ≡ *Cereus nelsonii* Weingart (1923: 33).

Lectotype (designated by Bauer 2003a: 49):—MEXICO. Locality unknown, from material sent by Dr J. L. Slater to C. Z. Nelson, of which cuttings were sent to Britton & Rose (US-2947536A!).

5.19. *Selenicereus ocamponis* (Salm-Dyck) D.R. Hunt (2017: 34) ≡ *Cereus ocamponis* Salm-Dyck (1850: 220) ≡ *Hylocereus ocamponis* (Salm-Dyck) Britton & Rose (1909: 429)

Neotype (designated by Bauer 2003a: 32):—[illustration] watercolour of *Hylocereus ocamponis* by Mary Emily Eaton, US.

5.20 *Selenicereus pteranthus* (Link ex A. Dietrich) Britton & Rose (1909: 431) ≡ *Cereus pteranthus* Link ex A. Dietrich (1834: 209–210).

Lectotype (designated by Bauer 2003b: 43):—[illustration] “*Cereus nycticaulis*” in Dietrich (1834: t. 4).

Image available at <http://www.biodiversitylibrary.org/item/106684#page/356/mode/2up>

5.20a. *Selenicereus pteranthus* f. *pteranthus*

= *Cereus boeckmannii* Otto ex Salm-Dyck (1850: 217) ≡ *Selenicereus boeckmannii* (Otto ex Salm-Dyck) Britton & Rose (1909: 429).

Neotype (designated here):—[illustration] “Flower of *Selenicereus boeckmannii*” in Britton & Rose (1920: pl. 36, fig. 2).
 = *Selenicereus brevispinus* Britton & Rose (1920: 278).
 Type:—CUBA. Camagüey: Cayo Romano, 1909, *Shafer 2811* (holotype US-1821063!, isotypes K-000101294!, NY-00386176!).
 = *Cereus irradians* Lemaire (1864: 74) ≡ *Selenicereus grandiflorus* var. *irradians* (Lemaire) Borg (1951: 206).
 Type:—Not designated.
 = *Cereus kunthianus* Hort. Berol. ex Salm-Dyck (1850: 217) ≡ *Selenicereus kunthianus* (Hort. Berol. ex Salm-Dyck) Britton & Rose (1909: 430).
 Type:—Not designated.
 = *Cereus vaupelii* Weingart (1912: 106).
 Type:—Not designated.

Notes:—Britton & Rose (1909) mentioned a plant sent under this name to J. N. Rose from the Berlin Botanical Garden in 1909, pictured in their fig. 277. A corresponding specimen could not be located. Also, Britton & Rose note that this plant does not exactly match the protologue, according to which this species would have 7-angled to 10-angled stems, whereas the plant from Berlin had 5-angled stems.

5.20b. *Selenicereus pteranthus* f. *macdonaldae* (Hooker) Ralf Bauer (2003: 44) ≡ *Cereus macdonaldiae* Hooker (1853: 4707) ≡ *Selenicereus macdonaldae* (Hooker) Britton & Rose (1909: 430)

Lectotype (designated by Bauer 2003a: 44):—[illustration] in Hooker (1853: t. 4707). Image available at <http://www.biodiversitylibrary.org/item/14357#page/64/mode/1up>
 = *Cereus grusonianus* Weingart (1905: 54).
 Type:—Not designated.
 = *Cereus rothii* Weingart (1922: 146).
 Type:—Not designated.

5.21. *Selenicereus purpusii* (Weingart) S. Arias & N. Korotkova, *comb. nov.* ≡ *Cereus purpusii* Weingart (1909: 150) ≡ *Hylocereus purpusii* (Weingart) Britton & Rose (1920: 184).

Neotype (designated by Doweld 2002b: 14):—MEXICO. Nayarit: Tepic, 600 m, 27 August 1948, *Dressler 336* (MO-1718059!).

5.22 *Selenicereus setaceus* (Salm-Dyck ex A.P. de Candolle) Werderman (1933: 87) ≡ *Cereus setaceus* Salm-Dyck ex A.P. de Candolle (1828: 469) ≡ *Mediocactus setaceus* (Salm-Dyck ex A.P. de Candolle) Borg (1951: 213) ≡ *Hylocereus setaceus* (Salm-Dyck ex A.P. de Candolle) Ralf Bauer (2003: 29).

Neotype (designated by Bauer 2003a: 29):—[illustration] “*Cereus setaceus*” in Pfeiffer & Otto (1839: t. 16).
 Image available at <http://www.biodiversitylibrary.org/item/107302#page/50/mode/1up>
 = *Cereus hassleri* K. Schumann (1900: 45) ≡ *Mediocactus hassleri* (K. Schumann) Backeberg (1959: 798).
 Type:—PARAGUAY. Cordillera [de Altos] Inter 200-280 lat. merid. et 590-630 long occ., December 1895, *Hassler 1716* (holotype K-000250212!, syntypes G-00095956!, NY-00120658! P-04947370!, P-04947368!).
 = *Cereus lindbergianus* F.A.C. Weber ex K. Schumann (1897: 151).
 Type:—Not designated.
 = *Cereus lindmanii* F.A.C. Weber ex K. Schumann (1897: 163) ≡ *Mediocactus lindmanii* (F.A.C. Weber ex K. Schumann) Backeberg (1959: 798).
 Type:—Not designated.
 = *Mediocactus coccineus* (Salm-Dyck) Britton & Rose (1920: 211) ≡ *Cereus coccineus* Salm-Dyck ex DC. (1828: 469).
 Type:—Not designated.
 = *Selenicereus rizzinii* Scheinvar (1974: 251).
 Type:—BRAZIL. Rio de Janeiro: Araruama, 29 January 1974, *Rizzini s.n.* (holotype RB, isotype MEXU-00166614!).

5.23. *Selenicereus spinulosus* (A.P. de Candolle) Britton & Rose (1909: 431) ≡ *Cereus spinulosus* A.P. de Candolle (1828: 117) ≡ *Mediocactus spinulosus* (A.P. de Candolle) Doweld (2002: 42).

Neotype (designated by Doweld 2002a: 42):—MEXICO. Tamaulipas: 14 miles east of El Salto, 4 March 1969, *Harmon 1347* (UMO-92557).
 = *Selenicereus pseudospinulosus* Weingart (1931: 255).
 Type:—Not designated.

5.24. *Selenicereus stenopterus* (F.A.C. Weber) D.R. Hunt (2017: 35) ≡ *Cereus stenopterus* F.A.C. Weber (1902: 458) ≡ *Hylocereus stenopterus* (F.A.C. Weber) Britton & Rose (1909: 429).
Lectotype (designated by Bauer 2003a: 32):—COSTA RICA. Sur les troncs des forêts de Las Hueltas, Tucuniqué, May 1899, *Tonduz 13053* (US-795790!, isoelectotype G-00236582! syntype P-02273103!).

5.25. *Selenicereus tonduzii* (F.A.C. Weber) S. Arias & N. Korotkova, *comb. nov.* ≡ *Cereus tonduzii* F.A.C. Weber (1902: 459) ≡ *Werckleocereus tonduzii* (F.A.C. Weber) Britton & Rose (1909: 432) ≡ *Weberocereus tonduzii* (F.A.C. Weber) G.D. Rowley (1982: 46).
Neotype (designated by Bauer 2003a: 50):—COSTA RICA. Limón: near base of Rio Chirripó, in Indian territory, 11 February 1957, *Horich s.n.* (K-1470).

5.26. *Selenicereus triangularis* (Linnaeus) D.R. Hunt (2017: 35) ≡ *Cactus triangularis* Linnaeus (1753: 468) ≡ *Cereus triangularis* (Linnaeus) Haworth (1812: 180) ≡ *Hylocereus triangularis* (Linnaeus) Britton & Rose (1909: 429).
Lectotype (designated by Doweld 2002b: 12):—[illustration] in Plukenet (1691: t. 29. fig. 3).
Epitype (designated by Doweld 2002b: 12):—JAMAICA. Manchester: Marshalls Pen, ca. 2.25 miles due NW of Mandeville, ca. 700 m, 31 August 1979, *Proctor 38288* (MO-3433296).
= *Cereus compressus* Miller (1768: without pagination) ≡ *Hylocereus compressus* (Miller) Y. Itô (1981: 122), *comb. illeg.* (Art. 33.3).
Lectotype (designated by Doweld 2002b: 12):—[illustration] in Plukenet (1691: t. 29. fig. 3).
= *Hylocereus cubensis* Britton & Rose (1920: 188).
Type:—CUBA. La Habana, Jata Hills, near Guanabaca, 14 July 1913, *León 3719* (holotype NY-00385836!, isotypes NY-00385835!, NY-00385834!, NY-00385833!).

Notes on *Selenicereus triangularis*:—The publication year of Plukenet’s *Phytographia* containing the lectotype was incorrectly given by Doweld l.c. as 1696. The original image is available at http://bibdigital.rjb.csic.es/ing/Carga.php?Pagina=A_PLU_Op_Bot_1/PLU_Op_Bot_1_049.pdf

Notes on *Cereus compressus*:—Miller (1768) described *Cereus compressus* as different from *Cereus triangularis*. Yet in the protologue of *C. compressus*, he cited Plukenet’s illustration from the “*Phytographia*” (Plukenet 1691). Miller apparently confused the figure of Plukenet, that was originally associated with the name *Cactus triangularis* by Linnaeus and associated it with his name *Cereus compressus*. Doweld (2002b) designated Plukenet’s illustration as the lectotypes of both, *Cactus triangularis* Linnaeus and *Cereus compressus* Miller. Therefore *Cereus compressus* Miller has to be a homotypic synonym of *Cactus triangularis* Linnaeus.

The name *Cereus triangularis* (Linnaeus) Miller is therefore not a combination of *Cactus triangularis* Linnaeus because it is based on a different type. However it is unclear what exactly Miller based this name on. Therefore Miller’s name was probably not used or mentioned by later authors and should best be formally rejected.

5.27. *Selenicereus tricae* D.R. Hunt (1989: 91) ≡ *Mediocactus tricae* (D.R. Hunt) Doweld (2002: 42) ≡ *Hylocereus tricae* (D.R. Hunt) Ralf Bauer (2003: 29) ≡ *Selenicereus inermis* subsp. *tricae* (D.R. Hunt) Ralf Bauer (2010: 12).
Type:—BELIZE. Cayo: secondary forest west of Augustine, 500 m, 13 July 1969, *Hunt 7076* (holotype K-29047.259).

5.28. *Selenicereus trigonus* (Haworth) S. Arias & N. Korotkova *comb. nov.* ≡ *Hylocereus trigonus* (Haworth) Safford (1909: 553, 556) ≡ *Cereus trigonus* Haworth (1812: 181).
Lectotype (designated by Howard 1989: 404):—[illustration] “Tab. CC cactus caule triangulari articulato” of Plumier (1758: pl. 200. fig. 2).
Lectotype (designated by Bauer 2003a: 41):—US VIRGIN ISLANDS: St. Thomas: Magens Bay, 29 August 2000, *Acevedo-Rodríguez 11250* (US-3408457!).
= *Cereus napoleonis* Graham (1836: 3458) ≡ *Hylocereus napoleonis* Britton & Rose (1909: 429).
Neotype (designated here):—[illustration] in Hooker (1836: t. 3458). Image available at <http://www.biodiversitylibrary.org/item/14342#page/3/mode/1up>
= *Cereus plumieri* Roland-Gosselin (1908: 668) ≡ *Hylocereus plumieri* (Roland-Gosselin) Lourteig (1991: 406)
Lectotype (designated here):—[illustration] “Tab. CXCIX cactus repens” of Plumier (1758: pl. 199).
= *Hylocereus antiguensis* Britton & Rose (1920: 193)
Lectotype (designated by Howard 1989: 404):—ANTIGUA AND BARBUDA. Antigua, 4-16 April 1913, *Rose, Fitch & Russell 3297* (US-00115678!, isoelectotypes GH-00063130!, NY-00385830!).

5.29. *Selenicereus undatus* (Haworth) D.R. Hunt (2017: 35) ≡ *Cereus undatus* Haworth (1830: 110) ≡ *Hylocereus undatus* (Haworth) Britton & Rose (1918: 256)

Neotype (designated by Taylor 1995: 119):—[illustration] “*Cactus triangularis*” in Sims (1817: t. 1884).

= *Cereus tricostatus* Roland-Gosselin (1908: 664) ≡ *Hylocereus tricostatus* (Roland-Gosselin) Britton & Rose (1909: 429).

Type:—Not designated.

5.30. *Selenicereus vagans* (K. Brandegee) Britton & Rose (1913: 242) ≡ *Cereus vagans* K. Brandegee (1904: 191) ≡ *Mediocactus vagans* (K. Brandegee) Doweld (2002: 42).

Neotype (designated by Bauer 2003a: 47):—MEXICO. Sinaloa: El Faro, the light-house at Mazatlán, 12 November 1964, *Kimmach 532* (HNT-2061!).

= *Cereus longicaudatus* F.A.C. Weber (1904: 384).

Type:—Not designated.

5.31. *Selenicereus validus* S. Arias & U. Guzmán (1995: 27–28).

Type:—MEXICO. Michoacán: Mun. Villa Victoria, 7 km south of Villa Victoria, 600 m, 19 October 1987, *Sánchez-Mejorada et al. 4254* (holotype MEXU-1304620!).

Kimmachia S. Arias & N. Korotkova *gen. nov.*

Type:—*Kimmachia ramulosa* (Salm-Dyck) S. Arias & N. Korotkova, *comb. nov.*

Diagnosis:—Plants shrubby with pendent stems, differentiated into primary and secondary stems (dimorphic), primary stems terete, secondary stems flattened and broadened in the apical part, margins of flattened stem segments crenate or obtusely serrate, stems often suffused purple, especially when exposed to sunlight; areoles inconspicuous, lacking spines. Flowers actinomorphic, 1–2 per areole, 7–12 mm long and for up to 15 mm in diameter, pericarpel with small scales, floral tube inconspicuous, ca. 2–4 mm long, green to reddish brown, perianth whitish/yellowish. Fruit globose to ovoid, 4–8 mm in diameter, whitish, pulp whitish.

Accepted species:—1 (2 infraspecific taxa).

Etymology:—We name this new genus after our dear colleague Myron Kimmach. He is an outstanding expert on the epiphytic cacti, and in particular on the Hylocereeae and his publications were a significant contribution to our knowledge on this group of plants. It is therefore our great pleasure to honour his works by dedicating this genus to him.

6.1 *Kimmachia ramulosa* (Salm-Dyck) S. Arias & N. Korotkova, *comb. nov.*

Basionym ≡ *Cereus ramulosus* (Salm-Dyck) (1834: 340).

Lectotype (designated by Kimmach 1993: 126):—US, photo of destroyed type at herbarium Berolinense (B), collector and locality unknown, collected before 1834.

6.1a *Kimmachia ramulosa* subsp. *ramulosa* ≡ *Rhipsalis ramulosa* (Salm-Dyck) Pfeiffer (1837: 130) ≡ *Hariota ramulosa* (Salm-Dyck) Lemaire (1839: 75) ≡ *Disocactus ramulosus* (Salm-Dyck) Kimmach (1961: 14) ≡ *Pseudorhipsalis ramulosa* (Salm-Dyck) Barthlott (1991: 90).

= *Rhipsalis coriacea* Polakowski (1877: 562) ≡ *Hariota coriacea* (Polakowski) Kuntze (1891: 262).

Lectotype (designated here):—COSTA RICA. Cartago: In arboribus prope Cartago, 20 June 1875, *Polakowsky 156* (BM-000776843!).

= *Rhipsalis purpusii* Weingart (1918: 78)

Lectotype (designated here):—MEXICO. Chiapas: [illustration] “*Rhipsalis purpusii* Weing. spec. nov.” in Weingart (1918: 79).

Image available at <http://www.biodiversitylibrary.org/item/110868#page/341/mode/1up>

= *Rhipsalis leiophloea* Vaupel (1923: 20).

Lectotype (designated by Kimmach 1993: 127):—COSTA RICA. San José, 1857, *Hoffman 498* (MO-148525!).

Notes on *Rhipsalis coriacea*:—Polakowski noted that the type was deposited in Berlin, and was destroyed. A second original copy deposited in BM is here designated as lectotype.

Notes on *Rhipsalis purpusii*:—The original sample was collected in 1913 by C. A. Purpus, in Cerro de Boqueron southwest of Chiapas, Mexico. However, Weingart does not refer to a type specimen deposited. An image of *Rhipsalis purpusii* included in the protologue is here designated as lectotype.

6.1b *Kimnachia ramulosa* f. *angustissima* (F.A.C. Weber) S. Arias & N. Korotkova, *comb. nov.* ≡ *Rhipsalis angustissima* F.A.C. Weber (1902: 465) ≡ *Disocactus ramulosus* var. *angustissimus* (F.A.C. Weber) Kimnach (1987: 67) ≡ *Pseudorhipsalis ramulosa* f. *angustissima* (F.A.C. Weber) Barthlott (1991: 90) ≡ *Disocactus ramulosus* f. *angustissimus* (F.A.C. Weber) Kimnach (1993: 127).

Type:—COSTA RICA. [Cartago]: Caché, au S.E. de Cartago, dans la vallée du Reventazon, 1000 m, 1902, *Biolley s.n.* (holotype P-04556957!).

6.1c *Kimnachia ramulosa* subsp. *jamaicensis* (Britton & Harris) S. Arias & N. Korotkova, *comb. nov.* ≡ *Rhipsalis jamaicensis* Britton & Harris (1909: 159) ≡ *Disocactus ramulosus* var. *jamaicensis* (Britton & Harris) Kimnach (1993: 129) ≡ *Pseudorhipsalis ramulosa* subsp. *jamaicensis* (Britton & Harris) Doweld (2002: 42).

Type:—JAMAICA. Trelawny: Troy, ca. 730 m, 1906, *Britton 551* (holotype NY-886148!).

Distribution:—Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Peru, Venezuela; subspecies *jamaicensis*: Haiti, Jamaica.

7. *Pseudorhipsalis* Britton & Rose (1923: 213)

Type:—*P. alata* (Swartz) Britton & Rose

= *Wittia* K. Schumann (1903: 117), *nom. illeg.* (Art. 53.1)

= *Wittiocactus* Rauschert (1982: 558)

Type:—*Wittiocactus amazonicus* (K. Schumann) Rauschert

= *Disisorhipsalis* Doweld (2002: 40)

Type:—*Disisorhipsalis macrantha* (Alexander) Doweld, *nom. inval.* (Art. 73)

Accepted species:—5 (2 infraspecific taxa).

7.1. *Pseudorhipsalis acuminata* Cufodontis (1933: 196) ≡ *Rhipsalis acuminata* (Cufodontis) Standley (1938: 1560) ≡ *Disocactus acuminatus* (Cufodontis) Kimnach (1961: 14).

Type:—COSTA RICA. Limón: Cairo Branch, near La Castilla-Los Negritos, 30 m, 6 May 1930, *Cufodontis 494* (holotype W, isotype F-0052905F!).

= *Pseudorhipsalis horichii* (Kinnach) Barthlott (1991: 90).

Type:—COSTA RICA. [Alajuela]: Sarapiquí región, laguna del Cerro Congo: 650 m, 1 July 1962, *Horich s.n.* (holotype HNT-0000078!).

7.2. *Pseudorhipsalis alata* (Swartz) Britton & Rose (1923: 213)

≡ *Cactus alatus* Swartz (1788: 77) ≡ *Epiphyllum alatum* (Swartz) Haworth (1819: 84) ≡ *Cereus alatus* (Swartz) A.P. de Candolle (1828: 410) ≡ *Rhipsalis alata* (Swartz) K. Schumann (1890: 288) ≡ *Hariota alata* (Swartz) Kuntze (1891: 262) ≡ *Disocactus alatus* (Swartz) Kimnach (1961: 14).

Lectotype (designated by Kimnach 1993: 122):—JAMAICA. Locality unknown, *Swartz s.n.* (S-R-798!, syntype BM-001008538!).

= *Rhipsalis swartziana* Pfeiffer (1837: 131) ≡ *Hariota swartziana* (Pfeiffer) Lemaire (1839: 75).

Type:—Not designated.

= *Rhipsalis harrisii* Gürke (1908: 180) ≡ *Pseudorhipsalis harrisii* (Gürke) Y. Itô (1952: 160).

Type:—Not designated.

7.3. *Pseudorhipsalis amazonica* (K. Schumann) Ralf Bauer (2003: 101) ≡ *Wittia amazonica* K. Schumann (1903: 117), *nom. illeg.* ≡ *Disocactus amazonicus* (K. Schumann) D.R. Hunt (1982: 2) ≡ *Wittiocactus amazonicus* (K. Schumann) Rauschert (1982: 559).

Lectotype (designated by Kimnach 1993: 117):—PERU. Loreto: Leticia, July 1902, *Ule 6189* (G-00236720!).

7.3a. *Pseudorhipsalis amazonica* subsp. *amazonica*

7.3b. *Pseudorhipsalis amazonica* subsp. *chocoensis* Ralf Bauer (2002: 108–109)

Type:—COLOMBIA. Chocó: near Nuquí, 6 March 1999, *Bauer 29* (holotype ZSS-22545!).

7.3c. *Pseudorhipsalis amazonica* subsp. *panamensis* (Britton & Rose) Ralf Bauer (2003: 106) ≡ *Wittia panamensis* Britton & Rose (1913: 241) ≡ *Wittiocactus panamensis* (Britton & Rose) Rauschert (1982: 559).
Type:—PANAMA. Panamá: above Chepo, 15 October 1911, *Pittier 4571* (holotype US-691299!, isotype NY00386208!).

7.4. *Pseudorhipsalis himantoclada* (Roland-Gosselin) Britton & Rose (1923:213) ≡ *Rhipsalis himantoclada* Roland-Gosselin (1908: 694) ≡ *Wittia himantoclada* (Roland-Gosselin) Woodson (1958: 88) ≡ *Disocactus himantocladus* (Roland-Gosselin) Kimnach (1961: 14).
Neotype (designated by Kimnach 1993: 117):—COSTA RICA. Puntarenas: Pozo Azul de Pirris, ca. 170 m, 1915, *Lankester s.n.* (US-2386472!, isoneotype P-04556965!).
= *Wittia costaricensis* Britton & Rose (1913: 261).
Type:—COSTA RICA. At the west coast, 1907, *Wercklé s.n.* (holotype US-691402!).

7.5. *Pseudorhipsalis lankesteri* (Kinnach) Barthlott (1991: 90)
Type:—COSTA RICA. Puntarenas: Valle de El General, ca. 670 m, ca. 1940, *Lankester s.n.* (holotype HNT-1214!).

8. *Weberocereus* Britton & Rose (1909: 431).
Type:—*W. tunilla* (F.A.C. Weber) Britton & Rose.
= *Eccremocactus* Britton & Rose in Contr. U.S. Natl. Herb. 16: 261. 1913.
Type:—*Eccremocactus bradei* Britton & Rose.

Accepted species:—6 (1 infraspecific taxon).

8.1. *Weberocereus bradei* (Britton & Rose) G.D. Rowley (1974: 10).
≡ *Eccremocactus bradei* Britton & Rose (1913: 262) ≡ *Phyllocactus bradei* (Britton & Rose) Vaupel (1913: 118) ≡ *Epiphyllum bradei* (Britton & Rose) Standl. (1937: 753).
Lectotype (designated by Bauer 2003a: 52):—COSTA RICA. Puntarenas: near Santo Domingo, Turrubares, 200 m, 1905, *Brade s.n.* (NY-120685!).

8.2. *Weberocereus frohningiorum* Ralf Bauer (2001: 228).
Type:—COSTA RICA. locality and collector unknown, cult. Hort. *H. & U. Frohning s.n.* (holotype ZSS-19806, isotype K-000100018!).

8.3. *Weberocereus imitans* (Kinnach & Hutchison) Buxbaum (1978: 125) ≡ *Werckleocereus imitans* Kinnach & Hutchison (1956: 154) ≡ *Cryptocereus imitans* (Kinnach & Hutchison) Backeberg (1959: 734) ≡ *Eccremocactus imitans* (Kinnach & Hutchison) Kimnach (1962: 82).
Type:—Costa Rica. Puntarenas: Valle de El General, near Cañas, ca. 1940, *Lankester s.n.* (holotype UC-052593!).

8.4. *Weberocereus rosei* (Kinnach) Buxbaum (1978: 125) ≡ *Eccremocactus rosei* Kinnach (1962: 80) ≡ *Cryptocereus rosei* (Kinnach) Backeberg (1963: 5).
Type:—ECUADOR. Chimborazo: canyon of Río Chanchan between Naranjapata and Olimpio, 700–1000 m, September 1958, *Horich s.n.* (holotype UC-229129!).

8.5. *Weberocereus trichophorus* H. Johnson & Kimnach (1963: 205).
Type:—COSTA RICA. Limón: Peralta, ca. 330 m, *Lankester s.n.* (holotype UC-229160!).

8.6. *Weberocereus tunilla* (F.A.C. Weber) Britton & Rose (1909: 432).
≡ *Cereus tunilla* F.A.C. Weber (1902: 460).
Neotype (designated by Bauer 2003a: 51):—COSTA RICA. Cartago: canyon of Río Birris, 1100 m, 7 January 1958, *Horich s.n.* (ZSS-000274!).

8.6a. *Weberocereus tunilla* subsp. *tunilla*
= *Cereus gonzalezii* F.A.C. Weber (1902: 460).
Type:—Not designated.

8.6b. *Weberocereus tunilla* subsp. *biolleyi* (F.A.C. Weber) Ralf Bauer (2003: 243) ≡ *Rhipsalis biolleyi* F.A.C. Weber (1902: 476) ≡ *Cereus biolleyi* F.A.C. Weber in K. Schumann (1903: 60).

Neotype (designated by Bauer 2003a: 51):—COSTA RICA. Limón: northern Llanura de Santa Clara, along Río Sucio, 100–150 m, *Horich s.n.* (ZSS-21351).

= *Weberocereus panamensis* Britton & Rose (1920: 215).

Type:—PANAMA. Province of Colon: Rio Fato Valley, above Nombre de Dios, July 1911, *Pittier 3903* (holotype US-00117135!, isotypes NY-00386199!, NY-00386200!, NY-00386198!, K-000101169!, K-000101168!).

A synopsis of *Strophocactus*

Our results show a highly supported clade containing *Strophocactus wittii* and *Pseudoacanthocereus*. The latter genus is currently accepted including two species *P. sicariguensis* and *P. brasiliensis* (Hunt 2006). We argue for combining both *Pseudoacanthocereus* species into *Strophocactus* because all three species share morphological characters as discussed above. Therefore we suggest a single genus for these three species and merge them under the oldest name *Strophocactus*. The necessary new combinations are provided below. *Strophocactus* is assigned to the tribe Echinocereae.

Strophocactus Britton & Rose (1913: 262).

Type:—*Strophocactus wittii* (K. Schumann) Britton & Rose.

Accepted species:—3

Strophocactus brasiliensis (Britton & Rose) S. Arias & N. Korotkova, *comb. nov.* ≡ *Acanthocereus brasiliensis* Britton & Rose (1920: 125) ≡ *Pseudoacanthocereus brasiliensis* (Britton & Rose) F. Ritter (1979: 47).

Type:—BRAZIL. Bahia: vicinity of Machado Portella, 1915, *Rose 19903* (holotype US-762245!).

Strophocactus sicariguensis (Croizat & Tamayo) S. Arias & N. Korotkova, *comb. nov.* ≡ *Acanthocereus sicariguensis* Croizat & Tamayo (1947: 75) ≡ *Pseudoacanthocereus sicariguensis* (Croizat & Tamayo) N.P. Taylor (1992: 30).

Type:—VENEZUELA. Lara: Torres, Sicarigua, *Tamayo 3296* (holotype VEN-46728!).

Strophocactus wittii (K. Schumann) Britton & Rose (1913: 262) ≡ *Cereus wittii* K. Schumann (1900: 154) ≡ *Selenicereus wittii* (K. Schumann) Rowley (1986: 36).

Type:—BRAZIL. Amazonas: near Manaus, 1900, *Witt s.n.* (holotype B-810006832!; isotypes: US-535998!, K-000250213!).

Notes:—The specimen at US is annotated as lectotype by Hutchison 1960, assuming the type at B had been destroyed, which is however not the case.

Synopsis of *Deamia*

Deamia Britton & Rose (1920: 212).

Type:—*Deamia testudo* (Karwinsky ex Zuccarini) Britton & Rose (1920: 213).

Accepted species:—2

Deamia chontalensis (Alexander) Doweld (2002: 41) ≡ *Nyctocereus chontalensis* Alexander (1950: 132) ≡ *Strophocactus chontalensis* (Alexander) Ralf Bauer (2003: 54).

Lectotype (designated by Bauer 2003a: 55):—[illustration] “Flower of *Nyctocereus chontalensis* sp. nov., x 0.6” in Alexander (1950: 129).

Deamia testudo (Karwinsky ex Zuccarini) Britton & Rose (1920: 213).

≡ *Cereus testudo* Karwinsky ex Zuccarini (1837: 682) ≡ *Selenicereus testudo* (Karwinsky ex Zuccarini) Buxbaum ex Krainz (1965: C.IIa) ≡ *Strophocactus testudo* (Karwinsky ex Zuccarini) Ralf Bauer (2003: 55).

Neotype (designated by Bauer 2003a: 55):—MEXICO. Veracruz: near Minatitlán, 1958, *King s.n.* (HNT-2055).

= *Deamia diabólica* Clover (1938: 570).

Type:—BELIZE. Corozal, 1931–1932, *Gentle 490* (holotype MICH-1003450A!).

Acknowledgements

This study would not have been possible without the living collections in the Botanic Garden Berlin and the Botanic Gardens of the University of Bonn. We are therefore most grateful to the garden staff members who have been caring for these collections during the last years or even decades with great enthusiasm. We first need to thank N. Köster, curator of the tropical plant collection of the Berlin Botanic Garden, for his care of the cacti collection and his support for this study. We also greatly acknowledge the efforts of B. E. Leuenberger (deceased 2010) who originally built up the Hylocereeae living collection in Berlin as a curator. We have especially to thank the horticultural staff of the Berlin Botanic Garden: S. Gasper, M. Krinelcke, C. Neuenfeldt, A. Moldenhauer, and B. Radtke who care for the living collection of cacti in Berlin. From Bonn, we thank W. Lobin (curator) and the horticulturalists O. Kriesten and B. Emde. We also thank R. Bauer (Offenburg) who contributed valuable material from his collection. B. Hammel (CR) provided photographs and information on Costa Rican species. Several people have provided very helpful tips on earlier versions of the manuscript and the taxonomic synopsis: we thank E. von Raab-Straube and N. Turland (both BGBM) for advice on nomenclatural questions, to W. Barthlott (Bonn) for many fruitful discussions, and to K. Jones and J. Marquardt (BGBM) for proof-reading of the manuscript. We are grateful to the laboratory team at the BGBM, especially K. Govers, J. Pfitzner, T. Pfalzgraff, D. Weigel, and H. Fleischer-Notter for their support in generating the data. S. A. thanks for support from DGAPA PAPIIT (IN208315), N. K. and T. B. appreciate financial support from the Verein der Freunde des Botanischen Gartens und Botanischen Museums Berlin-Dahlem e.V.

References

- Alexander, E.J. (1950) A new *Nyctocereus* from southern Mexico. *Cactus and Succulent Journal (Los Angeles)* 22: 131–133.
- Anceschi, G. & Magli, A. (2013) The new monophyletic macrogenus *Echinopsis*. No risk of paraphyly, and the most convincing hypothesis in phylogenetic terms. *Cactaceae Systematics Initiatives* 31: 24–27.
- Anderson, E.F. (2001) *The Cactus Family*. Timber Press, Portland, 776 pp.
- Anderson, E.F. (2005) Das große Kakteen-Lexikon. Eugen Ulmer KG, Stuttgart, 744 pp.
- Arias, S., Terrazas, T., Arreola-Nava, H.J., Vazquez-Sanchez, M. & Cameron, K.M. (2005) Phylogenetic relationships in *Peniocereus* (Cactaceae) inferred from plastid DNA sequence data. *Journal of Plant Research* 118: 317–328.
<https://doi.org/10.1007/s10265-005-0225-3>
- Backeberg, C. (1959) *Die Cactaceae. Band II. Cereoideae (Hylocereeae-Cereae [Austrocereinae])*. VEB Gustav Fischer Verlag, Jena, 1360 pp.
- Bárcenas, R.T., Yesson, C. & Hawkins, J.A. (2011) Molecular systematics of the Cactaceae. *Cladistics* 27: 1–20.
<https://doi.org/10.1111/j.1096-0031.2011.00350.x>
- Barthlott, W. (1975) Zur systematischen Stellung von *Disocactus himantocladus* (Roland-Gosselin) Kimmach. *Kakteen und andere Sukkulente* 26: 246–249, 278–280.
- Barthlott, W. (1983) Biogeography and evolution in neo- and palaeotropical Rhipsalinae (Cactaceae). In: Kubitzki, K. (Ed.) *Proceedings of the International Symposium Dispersal and Distribution*. Sonderbände des Naturwissenschaftlichen Vereins in Hamburg 7, pp. 241–248.
- Barthlott, W. (1991) *Disocactus*, *Lepismium* and *Pseudorhipsalis*. In: Hunt, D. & Taylor, N.P. (Eds.) *Notes on miscellaneous genera of Cactaceae. Bradleya* 9: 81–92.
- Barthlott, W. & Hunt, D.R. (1993) Cactaceae. In: Kubitzki, K. (Ed.) *The families and genera of vascular plants, Vol. II*. Springer, Berlin Heidelberg New York Tokyo, pp. 161–197.
https://doi.org/10.1007/978-3-662-02899-5_17
- Barthlott, W., Porembski, S., Kluge, M., Hopke, J. & Schmidt, L. (1997) *Selenicereus wittii* (Cactaceae): An epiphyte adapted to Amazonian Igapo inundation forests. *Plant Systematics and Evolution* 206: 175–185.
<https://doi.org/10.1007/BF00987947>
- Barthlott, W., Burstedde, K., Geffert, J.L., Ibisch, P.L., Korotkova, N., Rafiqpoor, D., Stein, A. & Mutke, J. (2015) Biogeography and biodiversity of cacti. *Schumannia* 7. Universitätsverlag Isensee, Oldenburg, 205 pp.
- Bauer, R. (2002) The genus *Pseudorhipsalis* Britton & Rose. *Haseltonia*: 94–120.
- Bauer, R. (2003a) A synopsis of the tribe Hylocereeae F. Buxb. *Cactaceae Systematics Initiatives* 17: 3–63.
- Bauer, R. (2003b) The typification of *Cereus pteranthus* Link ex A. Dietr. (*Selenicereus pteranthus* (Link ex A. Dietr.) Britt. & Rose. *Haseltonia* 9: 78–79.

- Bauer, R. (2003c) Typisierung von *Phyllocactus thomasi* K. Schumann. *Kakteen und andere Sukkulente* 54: 245–247.
- Bauer, R. (2009) *Epiphyllum anguliger* (Lemaire) Don ex Loudon, eine botanische interessante Art aus dem westlichen Mexico. *EPIG* 63: 5–15.
- Berger, A. (1905) A systematic revision of the genus *Cereus* Mill. *Missouri Botanical Garden Annual Report* 1905: 57–86.
<https://doi.org/10.2307/2400072>
- Berger, A. (1929) *Kakteen*. Eugen Ulmer, Stuttgart, 346 pp.
- Borsch, T., Hernandez-Ledesma, P., Berendsohn, W.G., Flores-Olvera, H., Ochoterena, H., Zuloaga, F.O., von Mering, S. & Kilian, N. (2015) An integrative and dynamic approach for monographing species-rich plant groups—Building the global synthesis of the angiosperm order Caryophyllales. *Perspectives in Plant Ecology, Evolution and Systematics* 17: 284–300.
<https://doi.org/10.1016/j.ppees.2015.05.003>
- Bravo-Hollis, H. (1978) *Las Cactaceas de Mexico, Vol. 1*. Universidad Nacional Autonoma de Mexico, Mexico City, 743 pp.
- Britton, N.L. & Rose, J.N. (1909) The genus *Cereus* and its allies in North America. *Contributions from the United States National Herbarium* 12: 413–437, 474.
- Britton, N.L. & Rose, J.N. (1913) The genus *Epiphyllum* and its allies. *Contributions from the United States National Herbarium* 16: 255–262.
- Britton, N.L. & Rose, J.N. (1920) *The Cactaceae. Descriptions and illustrations of plants of the cactus family, Vol. 2*. Carnegie Institute, Washington, 248 pp.
- Britton, N.L. & Rose, J.N. (1923) *The Cactaceae. Descriptions and illustrations of plants of the cactus family, Vol. 4*. Carnegie Institute, Washington, 248 pp.
- Brockington, S.F., Yang, Y., Gandia-Herrero, F., Covshoff, S., Hibberd, J.M., Sage, R.F., Wong, G.K.S., Moore, M.J. & Smith, S.A. (2015) Lineage-specific gene radiations underlie the evolution of novel betalain pigmentation in Caryophyllales. *New Phytologist* 207: 1170–1180.
<https://doi.org/10.1111/nph.13441>
- Buxbaum, F. (1958) The phylogenetic division of the subfamily Cereoideae, Cactaceae. *Madroño* 14: 177–206.
- Buxbaum, F. (1962) Das phylogenetische System den Cactaceae. In: Krainz, H. (Ed.) *Die Kakteen*. Franck'sche Verlagshandlung, Stuttgart, pp. 1–21.
- Buxbaum, F. (1965) Gattung *Selenicereus*. In: Krainz, H. (Ed.) *Die Kakteen*. Franck'sche Verlagshandlung, Stuttgart, p. C II a.
- Buxbaum, F. (1969) Gattung *Epiphyllum*. In: Krainz, H. (Ed.) *Die Kakteen*. Franck'sche Verlagshandlung, Stuttgart, p. C II b.
- Candolle, A.P. de (1828) Revue de la famille des Cactées. *Mémoires du Muséum d'histoire naturelle* 31: 1–119.
- Cruz, M.Á., Arias, S. & Terrazas, T. (2016) Molecular phylogeny and taxonomy of the genus *Disocactus* (Cactaceae), based on the DNA sequences of six chloroplast markers. *Willdenowia* 46: 145–164.
<https://doi.org/10.3372/wi.46.46112>
- Cuénoud, P., Savolainen, V., Chatrou, L.W., Powell, M., Grayer, R.J. & Chase, M.W. (2002) Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbcL*, *atpB*, and *matK* DNA sequences. *American Journal of Botany* 89: 132–144.
<https://doi.org/10.3732/ajb.89.1.132>
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772–772.
<https://doi.org/10.1038/nmeth.2109>
- Dietrich, A. (1834) Beschreibung des *Cereus nycticaulis* Link. *Verhandlungen des Vereins zur Beförderung des Gartenbaues in den Königlich Preussischen Staaten* 10: 372–375.
- Dillenius, J.J. (1732) *Hortus Elthamensis (Vol. 1)*. Sumptibus auctoris, Londini, 204 pp.
- Dodson, C.H. & Gentry, A.H. (1977) *Epiphyllum phyllanthus* and its allies in Ecuador. *Selbyana* 2: 30–31.
- Doweld, A.B. (2002a) Re-classification of Rhipsalideae, a polyphyletic tribe of the Cactaceae. *Sukkulenty* 1–2: 25–45.
- Doweld, A.B. (2002b) A typification of the species of *Hylocereus*. *Turczaninowia* 1: 11–16.
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res* 32: 1792–1797.
<https://doi.org/10.1093/nar/gkh340>
- Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D. & Kluge, A.G. (1996) Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 12: 99–124.
<https://doi.org/10.1111/j.1096-0031.1996.tb00196.x>
- Gibson, A. & Nobel, P.S. (1986) *The cactus primer*. Harvard University Press, Cambridge, 286 pp.
<https://doi.org/10.4159/harvard.9780674281714>
- Gómez-Hinostrosa, C., Hernández, H.M., Terrazas, T. & Correa-Cano, M.E. (2014) Studies on Mexican Cactaceae. V. Taxonomic notes on *Selenicereus tricae*. *Brittonia* 66: 51–59.
<https://doi.org/10.1007/s12228-013-9308-y>

- González Ortega, J. (1926) *Peniocereus rosei* sp. n. *Revista Mexicana de Biología* 6: 189–191.
- Harpke, D. & Peterson, A. (2006) Non-concerted ITS evolution in *Mammillaria* (Cactaceae). *Molecular Phylogenetics and Evolution* 41: 579–593.
<https://doi.org/10.1016/j.ympev.2006.05.036>
- Hernández-Hernández, T., Hernández, H.M., De-Nova, J.A., Puente, R., Eguiarte, L.E. & Magallón, S. (2011) Phylogenetic relationships and evolution of growth form in Cactaceae (Caryophyllales, Eudicotyledoneae). *American Journal of Botany* 98: 44–61.
<https://doi.org/10.3732/ajb.1000129>
- Hernández-Ledesma, P., Berendsohn, W.G., Borsch, T., von Mering, S., Akhani, H., Arias, S., Castañeda-Noa, I., Eggli, U., Eriksson, R., Flores-Olvera, H., Fuentes-Bazán, S., Kadereit, G., Klak, C., Korotkova, N., Nyffeler, R., Ocampo, G., Ochoterena, H., Oxelman, B., Rabeler, R.K., Sanchez, A., Schlumpberger, B.O. & Uotila, P. (2015) A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales. *Willdenowia* 45: 281–383.
<https://doi.org/10.3372/wi.45.45301>
- Hilu, K.W. & Liang, H.P. (1997) The *matK* gene: Sequence variation and application in plant systematics. *American Journal of Botany* 84: 830–839.
<https://doi.org/10.2307/2445819>
- Hooker, W.J. (1836) *Cereus Napoleonis*. Napoleon's *Cereus*. *Curtis's Botanical Magazine* 63: t. 3458.
- Hooker, W.J. (1854) *Cereus Lemaireii*. Lemaire's *Cereus*. *Curtis's Botanical Magazine* 80: t. 4814.
- Hooker, W.J. (1853) *Cereus MacDonaldiae*—Mrs. MacDonald's Great Night-Flowering *Cereus*. *Curtis's Botanical Magazine* 79: t. 4707.
- House, P.R., Gómez-Hinostrosa, C. & Hernández, H.M. (2013) Una especie nueva de *Peniocereus* (Cactaceae) de Honduras. *Revista Mexicana de Biodiversidad* 84: 1077–1081.
<https://doi.org/10.7550/rmb.32720>
- Howard, R.A. (1989) *Flora of the Lesser Antilles, Vol. 5 (2)*. Harvard University Jamaica Plain, Massachusetts, 658 pp.
- Hummelink, P.W. (1938) Over *Cereus repandus*, *Cephalocereus lanuginosus*, *Lemaireocereus griseus* en *Acanthocereus tetragonus*. III. *Succulenta* 20: 165–171.
- Hunt, D.R. (1984) The Cactaceae of Plumier's Botanicum Americanum. *Bradleya* 2: 39–64.
- Hunt, D.R. (1989) Notes on *Selenicereus* (A.Berger) Britton & Rose and *Aporocactus* Lemaire (Cactaceae-Hylocereinae). *Bradleya* 7: 89–96.
- Hunt, D.R. (1991) Notes on miscellaneous genera of Cactaceae. *Bradleya* 9: 82–83.
- Hunt, D.R. (1998) Further notes on *Acanthocereus* (Engelmann ex Berger) B. & R. *Cactaceae Consensus Initiatives* 5: 15–17
- Hunt, D.R. (2000) *Selenicereus*. *Cactaceae Systematics Initiatives* 9: 18.
- Hunt, D.R. (2006) *The New Cactus Lexicon*. dh books, Milborne Port, 371 pp.
- Hunt, D.R. (2017) *Selenicereus*. *Cactaceae Systematics Initiatives* 36: 29–36.
- Hunt, D.R. & Taylor, N.P. (1990) The genera of the Cactaceae: progress towards consensus. *Bradleya* 8: 85–107.
- Hunt, D.R. & Taylor, N.P. (2006) Notulae Systematicae Lexicon Cactacearum Spectantes VII. *Cactaceae Systematics Initiatives* 21: 4–10.
- Johnson, L.A. & Soltis, D.E. (1995) Phylogenetic inference in Saxifragaceae s.str. and *Gilia* (Polemoniaceae) using *matK* sequences. *Annals of the Missouri Botanical Garden* 82: 149–175.
<https://doi.org/10.2307/2399875>
- Karsten, G. & Schenck, H. (1905) *Vegetationsbilder (Vol. 2. Reihe, Heft 1)*. Gustav Fischer Verlag, Jena, 218 pp.
- Kelchner, S.A. (2000) The evolution of non-coding chloroplast DNA and its application in plant systematics. *Annals of the Missouri Botanical Garden* 87: 482–498.
<https://doi.org/10.2307/2666142>
- Kilian, N., Henning, T., Plitzner, P., Müller, A., Güntsch, A., Stöver, B.C., Müller, K.F., Berendsohn, W.G. & Borsch, T. (2015) Sample data processing in an additive and reproducible taxonomic workflow by using character data persistently linked to preserved individual specimens. *Database* 2015: bav094.
<https://doi.org/10.1093/database/bav094>
- Kimmach, M. (1961) *Disocactus ramulosus*. *Cactus and Succulent Journal (Los Angeles)* 33: 11–16.
- Kimmach, M. (1964) *Epiphyllum phyllanthus*. *Cactus and Succulent Journal (Los Angeles)* 36: 105–115.
- Kimmach, M. (1965) *Epiphyllum thomsonianum*. *Cactus and Succulent Journal (Los Angeles)* 37: 162–168.
- Kimmach, M. (1967) *Hylocereus calcaratus*. *Cactus and Succulent Journal (Los Angeles)* 39: 102–105.
- Kimmach, M. (1991) *Selenicereus*. In: Hunt, D. & Taylor, N.P. (Eds.) *Notes on miscellaneous genera of Cactaceae*. *Bradleya* 9: 81–92.
- Kimmach, M. (1993) The genus *Disocactus*. *Haseltonia* 1: 95–139.
- Kishino, H. & Hasegawa, M. (1989) Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA

- sequence data, and the branching order in Hominoidea. *Journal of Molecular Evolution* 29: 170–179.
<https://doi.org/10.1007/BF02100115>
- Korotkova, N., Zabel, L., Quandt, D. & Barthlott, W. (2010) A phylogenetic analysis of *Pfeiffera* and the reinstatement of *Lymanbensonia* as an independently evolved lineage of epiphytic Cactaceae within a new tribe Lymanbensoniaceae. *Willdenowia* 40: 151–172.
<https://doi.org/10.3372/wi.40.40201>
- Korotkova, N., Borsch, T., Quandt, D., Taylor, N.P., Müller, K. & Barthlott, W. (2011) What does it take to resolve relationships and to identify species with molecular markers? An example from the epiphytic Rhipsalideae (Cactaceae). *American Journal of Botany* 98: 1549–1572.
<https://doi.org/10.3732/ajb.1000502>
- Lemaire, C. (1860) Des Cactées. A propos d'un genre nouveau de cette famille. *L'illustration horticole* 7: 66–68.
- Leuenberger, B.E. (1976) *Die Pollenmorphologie der Cactaceae und ihre Bedeutung für die Systematik*. J. Cramer, Ganter Verlag, Vaduz, 321 pp.
- Leuenberger, B.E. (1997) Cactaceae. In: Görts-van Rijn, A.R.A. (Ed.) *Flora of the Guianas Ser. A*. Koeltz Königstein, pp. 1–60.
- Leuenberger, B.E. (2001) *Selenicereus extensus* (Cactaceae), new combination and taxonomic history. *Botanische Jahrbucher für Systematik, Pflanzengeschichte und Pflanzengeographie* 123: 47–62.
- Lindley, J. (1845) *Disocactus biformis*. *Edwards' s Botanical Register* 31: t. 9.
- Lödé, J. (2013) New combinations. *Cactus Adventures International. Supplement* 98: 2–3.
- Löhne, C. & Borsch, T. (2005) Molecular evolution and phylogenetic utility of the *petD* group II intron: A case study in basal angiosperms. *Molecular Biology and Evolution* 22: 317–332.
<https://doi.org/10.1093/molbev/msi019>
- Lourteig, A. (1991) Nomenclatura plantarum americanum XVI. Cactaceae. *Bradea* 5: 400–411.
- Miller, P. (1768) *The gardeners dictionary* (8 ed.). Printed for the author and sold by John and Francis Rivington, London, without pagination.
- Müller, K. (2004) PRAP—computation of Bremer support for large data sets. *Molecular Phylogenetics and Evolution* 31: 780–782.
<https://doi.org/10.1016/j.ympev.2003.12.006>
- Müller, K. (2005a) The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. *BMC Evolutionary Biology* 5: 58.
<https://doi.org/10.1186/1471-2148-5-58>
- Müller, K. (2005b) SeqState—primer design and sequence statistics for phylogenetic DNA data sets. *Applied Bioinformatics* 4: 65–69.
- Müller, K. & Borsch, T. (2005) Phylogenetics of Amaranthaceae based on *matK/trnK* sequence data—Evidence from Parsimony, likelihood, and Bayesian analyses. *Annals of the Missouri Botanical Garden* 92: 66–102.
- Müller, J., Müller, K., Neinhuis, C. & Quandt, D. (2005) [Continuously update] *PhyDE: Phylogenetic Data Editor*. Available from: www.phyde.de (accessed 28 September 2011)
- Nixon, K.C. (1999) The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414.
<https://doi.org/10.1111/j.1096-0031.1999.tb00277.x>
- Nyffeler, R. (2002) Phylogenetic relationships in the cactus family (Cactaceae) based on evidence from *trnK/matK* and *trnL-trnF* sequences. *American Journal of Botany* 89: 312–326.
<https://doi.org/10.3732/ajb.89.2.312>
- Nyffeler, R. & Eggli, U. (2010) A farewell to dated ideas and concepts—molecular phylogenetics and a revised suprageneric classification of the family Cactaceae. *Schumannia* 6: 109–151.
- Ochoterena, H. (2009) Homology in coding and non-coding DNA sequences: a parsimony perspective. *Plant Systematics and Evolution* 282: 151–168.
<https://doi.org/10.1007/s00606-008-0095-y>
- Pantocsek, J. (1889) *Beiträge zur Kenntnis der Fossilen Bacillarien Ungarns. Teil II*. Brackwasser Bacillarien. Anhang: Analyse de marine Depots von Bory, Bremia, Nagy-Kurtos in Ungarn; Ananio und Kusnetz in Russland. Buchdruckerei von Julius Platzko, Nagy-Tapolcsány, 123 pp.
- Pfeiffer, L. & Otto, F. (1839) *Abbildung und Beschreibung Blühender Cacteen*. Theodor Fischer, Cassel, without pagination.
- Plukenet, L. (1691) *Phytographia, sive stirpium illustriorum & minus cognitarum icones, Vol. 1*. Sumptibus Autoris, Londini, without pagination.
- Plukenet, L. (1692) *Phytographia, sive stirpium illustriorum & minus cognitarum icones, Vol. 3*. Sumptibus Autoris, Londini, without pagination.
- Plume, O., Straub, S. C. K., Tel-Zur, N., Cisneros, A., Schneider, B. & Doyle, J. J. (2013) Testing a hypothesis of intergeneric allopolyploidy in vine cacti (Cactaceae: Hylocereeae). *Systematic Botany* 38: 737–751.
<https://doi.org/10.1600/036364413X670421>

- Plumier, C. & Burman, J. (1758) *Plantarum americanarum, Fasc. 8*. Amstelaedami: Lugd. Batav.: Sumtibus Auctoris, without pagination.
- Quandt, D. & Stech, M. (2004) Molecular evolution and phylogenetic utility of the chloroplast *trnT-trnF* region in bryophytes. *Plant Biology* 6: 545–554.
<https://doi.org/10.1055/s-2004-821144>
- Quandt, D., Müller, K. & Huttunen, S. (2003) Characterisation of the chloroplast DNA *psbT-H* region and the influence of dyad symmetrical elements on phylogenetic reconstructions. *Plant Biology* 5: 400–410.
<https://doi.org/10.1055/s-2003-42715>
- Rambaut, A., Suchard, M.A. & Drummond, A.J. (2014) *Tracer v1.6*. Available from: <http://beast.bio.ed.ac.uk/> (accessed 18 February 2015)
- Rauschert, S. (1982) Nomina nova generica et combinationes novae Spermatophytorum et Pteridophytorum. *Taxon* 31: 554–563.
<https://doi.org/10.2307/1220694>
- Ritz, C.M., Reiker, J., Charles, G., Hoxey, P., Hunt, D.R., Lowry, M., Stuppy, W. & Taylor, N. (2012) Molecular phylogeny and character evolution in terete-stemmed Andean opuntias (Cactaceae-Opuntioideae). *Molecular Phylogenetics and Evolution* 65: 668–681.
<https://doi.org/10.1016/j.ympev.2012.07.027>
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
<https://doi.org/10.1093/bioinformatics/btg180>
- Sánchez-Mejorada, H. (1974) Dos nuevas variedades de *Peniocereus fosterianus*. *Cactáceas y Suculentas Mexicanas* 19:48–55.
- Schäferhoff, B., Müller, K.F. & Borsch, T. (2009) Caryophyllales phylogenetics: disentangling Phytolaccaceae and Molluginaceae and description of Microteaceae as a new isolated family. *Willdenowia* 39: 209–228.
<https://doi.org/10.3372/wi.39.39201>
- Schlumpberger, B.O. & Renner, S.S. (2012) Molecular phylogenetics of *Echinopsis* (Cactaceae): Polyphyly at all levels and convergent evolution of pollination modes and growth forms. *American Journal of Botany* 99: 1335–1349.
<https://doi.org/10.3732/ajb.1100288>
- Schumann, K.M. (1895) *Phyllocactus Thomasianus* K. Sch. *Monatsschrift für Kakteenkunde* 5: 6.
- Schumann, K.M. (1897–1899) *Gesamtbeschreibung der Kakteen (Monographia Cactacearum)*. Neumann, Neudamm, 832 pp.
- Schumann, K.M. (1900) Cactaceae. In: Loesener, T. (Ed.) Beiträge zur Kenntnis der Flora von Central-Amerika (einschließlich Mexico) II. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 29: 99–100.
- Schumann, K.M. (1903) *Wittia Amazonica* K. Sch. n. gen. et spec. *Monatsschrift für Kakteenkunde* 13: 117–119.
- Shaw, J., Lickey, E.B., Beck, J.T., Farmer, S.B., Liu, W., Miller, J., Siripun, K.C., Winder, C.T., Schilling, E.E. & Small, R.L. (2005) The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany* 92: 142–166.
<https://doi.org/10.3732/ajb.92.1.142>
- Silvestro, D. & Michalak, I. (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution* 12: 335–337.
<https://doi.org/10.1007/s13127-011-0056-0>
- Simmons, M.P. & Ochoterena, H. (2000) Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369–381.
<https://doi.org/10.1093/sysbio/49.2.369>
- Sims, J. (1817) *Cactus triangularis*. Triangular creeping *Cereus*, or Strawberry Pear. *Curtis's Botanical Magazine* 44: t. 1884.
- Sims, J. (1826) *Cactus phyllanthus*. Spleenwort-leaved cactus. *Curtis's Botanical Magazine* 53: t. 2692.
- Stamatakis, A. (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.
<https://doi.org/10.1093/bioinformatics/btu033>
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57: 758–771.
<https://doi.org/10.1080/10635150802429642>
- Stöver, B. & Müller, K. (2010) TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics* 11: 7.
<https://doi.org/10.1186/1471-2105-11-7>
- Swofford, D.L. (1998) *PAUP*. Phylogenetic Analysis Using Parsimony (*and other Methods)*. Sinauer Associates, Sunderland.
- Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. (1991) Universal primers for amplification of three non-coding regions of the chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.
<https://doi.org/10.1007/BF00037152>
- Taylor, N.P. & Zappi, D.C. (2004) *Cacti of Eastern Brasil*. Kew Publishing, London, 499 pp.

- Taylor, N.P., Zappi, D.C. & Egli, U. (1992) *Pseudoacanthocereus*. *Bradleya* 10: 28.
- Templeton, A.R. (1983) Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37: 221–244.
<https://doi.org/10.1111/j.1558-5646.1983.tb05533.x>
- Vázquez-Sánchez, M., Terrazas, T., Arias, S. & Ochoterena, H. (2013) Molecular phylogeny, origin and taxonomic implications of the tribe Cacteeae (Cactaceae). *Systematics and Biodiversity* 11: 103–116.
<https://doi.org/10.1080/14772000.2013.775191>
- Weingart, W. (1907) *Phyllocactus Purpusii* Weing. n. sp. *Monatsschrift für Kakteenkunde* 17: 34–38.
- Weingart, W. (1918) *Rhipsalis Purpusii* spec. nov. *Monatsschrift für Kakteenkunde* 27–28: 78–82.
- Weingart, W. (1933) *Cereus maculatus* Spec. nov. *Kakteenkunde* 1: 14–15.
- Wicke, S. & Quandt, D. (2009) Universal primers for the amplification of the plastid *trnK/matK* region in land plants. *Anales Del Jardín Botánico De Madrid* 66: 285–288.
<https://doi.org/10.3989/ajbm.2231>
- Worberg, A., Alford, M.H., Quandt, D. & Borsch, T. (2009) Huerteales sister to Brassicales plus Malvales, and newly circumscribed to include *Dipentodon*, *Gerrardina*, *Huertia*, *Perrottetia*, and *Tapiscia*. *Taxon* 58: 468–478.

Appendix 1. Material and sequences used in this study

Abbreviations: BG B: Botanical Garden Berlin, B: Herbarium Berolinense, B GH: garden herbarium of the Herbarium Berolinense, ZSS: Züricher Sukkulentens-Sammlung, K: Herbarium of the Royal Botanic Gardens Kew.

Acanthocereus castellae.—*trnK/matK* DQ100014.1 (Arias *et al.* 2005), *rpl16* DQ099945.1 (Arias *et al.* 2005).

Acanthocereus chiapensis.—*trnK/matK* HM041754.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* DQ099985.1 (Arias *et al.* 2005), *trnL-F* HM041335.1 (Hernandez-Hernandez *et al.* 2011).

Acanthocereus tetragonus.—*trnK/matK* HM041645.1, *rpl16* HM041378.1, *trnL-F* HM041223.1 (all from Hernandez-Hernandez *et al.* 2011); isolate AccpenE213 *trnK/matK* AY015295.1 (Nyffeler 2002), *trnL-F* AY015386.1 (intron), AY015345.1 (spacer) (Nyffeler 2002).

Armatocereus procerus.—*trnK/matK* HM041650.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041384.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041229.1 (Hernandez-Hernandez *et al.* 2011).

Aporocactus flagelliformis.—isolate CA389: MEXICO. Hidalgo, *Schrempf s.n.* (B), living BG B 156431230 *trnK/matK* LT745632, *rpl16* LT745515, *trnL-F* LT745401; isolate CA241: as “Netherlands Antilles” St. Vincent (probably cultivated, occurrence outside the natural distribution range) *Innes s.n.* (B GH 33610), living BG B 001018330, *trnK/matK* LT745631, *rpl16* --, *trnL-F* LT745400.

Aporocactus martianus.—isolate CA396: MEXICO. Oaxaca, *Lau 1275* (B), living BG B 155371230, *trnK/matK* LT745635, *rpl16* LT745518, *trnL-F* LT745404; isolate CA318: MEXICO. Oaxaca, *Lautner L05/18* (B), living BG B 156401230, *trnK/matK* LT745634, *rpl16* LT745517, *trnL-F* LT745403.

Bergerocactus emoryi.—*trnK/matK* HM041654.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041388.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* DQ099925.1 (Arias *et al.* 2005)

Blossfeldia liliputana.—*trnK/matK* AY015284.1 (Nyffeler 2002) *rpl16* HM041389.1 (Hernandez-Hernandez *et al.* 2011) *trnL-F* AY064303.1 (Nyffeler 2002).

Calymmanthium substerile.—*trnK/matK* AY015291.1 (Nyffeler 2002), *rpl16* FN673676.1 (Korotkova *et al.* 2010), *trnL-F* DQ099926 (Arias *et al.* 2005).

Carnegiea gigantea.—*trnK/matK* HM041657.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041391.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041236.1 (Hernandez-Hernandez *et al.* 2011).

Castellanosia caineana.—*trnK/matK* AY015298.1 (Nyffeler 2002), *rpl16* --, *trnL-F* AY015389.1 (Nyffeler 2002).

Cephalocereus columna-trajani.—*trnK/matK* HM041658.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041392.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041237.1 (Hernandez-Hernandez *et al.* 2011).

Copiapoa coquimbana.—isolate CA126, *trnK/matK* FN995677 (Korotkova *et al.* 2010), *rpl16* FN673557.1 (Korotkova *et al.* 2010), *trnL-F* --.

Corryocactus aureus.—*trnK/matK* HM041669.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041404.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041249.1 (Hernandez-Hernandez *et al.* 2011).

Corryocactus brevistylus.—*trnK/matK* AY015302.1 (Nyffeler 2002), *rpl16* --, *trnL-F* AY015393.1 (Nyffeler 2002).

Corryocactus tenuiculus.—*trnK/matK* AY015303.1 (Nyffeler 2002), *rpl16* --, *trnL-F* AY015394.1 (Nyffeler 2002).

Deamia chontalensis.—isolate CA218: MEXICO. Oaxaca, *Lautner LW 85 33* (B), living BG B 266059430 *trnK/matK* LT745733, *rpl16* LT745616, *trnL-F* LT745500; isolate CA374: MEXICO. Oaxaca, *Lautner s.n.* (B) *trnK/matK* LT745734, *rpl16* LT745617, *trnL-F* LT745501.

Deamia testudo.—isolate CA207: without locality data (B), living BG B 014857483 *trnK/matK* LT745735, *rpl16* LT745618, *trnL-F* LT745502.

Dendrocereus nudiflorus.—*trnK/matK* --, *rpl16* DQ099998.1 (Arias *et al.* 2005), *trnL-F* DQ099929.1 (Arias *et al.* 2005).

Disocactus ackermannii.—isolate CA286: MEXICO. Oaxaca, *Lautner L98/57* (B) *trnK/matK* LT745636, *rpl16* LT745519, *trnL-F* LT745405.

Disocactus ackermannii subsp. *conzattianus*.—isolate CA301: MEXICO. Oaxaca, *Lautner L98/49* (B), living BG B 155881230 *trnK/matK* LT745637, *rpl16* LT745520, *trnL-F* LT745406.

Disocactus anguliger.—isolate CA229: MEXICO. Oaxaca, *Lau L1265* (B), living BG B 069111230, *trnK/matK* LT745638, *rpl16* LT745521, *trnL-F* LT745421.

Disocactus biformis.—isolate CA281: GUATEMALA. Sololá, *Lautner L91/34* (ZSS 21337) *trnK/matK* LT745639, *rpl16* LT745522, *trnL-F* LT745407.

Disocactus crenatus.—isolate CA228: COSTA RICA. no further locality data, *Lau s.n.* (B), living BG B 069051260 as ‘chichicastenango’ *trnK/matK* LT745640, *rpl16* LT745523, *trnL-F* LT745423
isolate CA275: El Salvador, Santa Ana, *Vollmer 1111/85* (B) *trnK/matK* LT745641, *rpl16* LT745524, *trnL-F* LT745425.

Disocactus crenatus subsp. *kinnachii*.—isolate CA248: MEXICO. Chiapas: SW San Cristóbal, *Trost s.n.* (ZSS-22539, holotype) *trnK/matK* LT745643, *rpl16* LT745526, *trnL-F* LT745427; isolate CA230: MEXICO. Chiapas, *Hohmann s.n.* (B), living BG B 069081230 *trnK/matK* LT745642, *rpl16* LT745525, *trnL-F* LT745426.

Disocactus eichlamii.—isolate CA300: GUATEMALA. Escuintla, *Lautner L99/4a* (ZSS-21371) *trnK/matK* LT745644, *rpl16* LT745527, *trnL-F* LT745408.

Disocactus lepidocarpus.—isolate CA345: COSTA RICA. Heredia, *Kinnach 2440* (ZSS-22700, neotype Bauer 2003), living BG B 155451230 ex HBG 49676 *trnK/matK* LT745664, *rpl16* LT745528, *trnL-F* LT745431.

Disocactus macdougallii.—isolate CA269: MEXICO. Chiapas, *Kimnach, Bauml & Sanchez-Mejorada 622* (ZSS-21400, ZSS-29520): *trnK/matK* LT745645, *rpl16* LT745529, *trnL-F* LT745409.

Disocactus macranthus: isolate CA208.—without locality data (B GH 48382), living BG B 264-83-99-83: *trnK/matK* LT745646, *rpl16* LT745530, *trnL-F* LT745410; isolate CA298: MEXICO. Oaxaca, *MacDougall A 42* (HNT-1213, isotype, US-2301200, isotype), *trnK/matK* LT745647, *rpl16* LT745531, *trnL-F* LT745411.

Disocactus nelsonii subsp. *hondurensis*.—isolate CA297: HONDURAS. Comayagua, *Kimnach 394* (HNT, ZSS. B), living BG B 155751230 *trnK/matK* LT745650, *rpl16* LT745534, *trnL-F* LT745414.

Disocactus nelsonii subsp. *nelsonii*.—isolate CA215: without locality data, (B), living BG B 069371280 (ex BG Bonn 4639): *trnK/matK* LT745648, *rpl16* LT745532, *trnL-F* LT745412; isolate CA277: Mexico Chiapas, *Lautner L98/40*, (B), living BG B 155681230 *trnK/matK* LT745649, *rpl16* LT745533, *trnL-F* LT745413.

Disocactus phyllanthoides.—isolate CA273: MEXICO. Puebla, *Lautner L02/60 I* (ZSS-22584, ZSS-29527), living BG B 155861230 *trnK/matK* LT745651, *rpl16* LT745535, *trnL-F* LT745415.

Disocactus quezaltecus.—isolate CA284: GUATEMALA. Quezaltenango, *Lautner L99/21/3* (ZSS-21369), living BG B 155661230 *trnK/matK* LT745652, *rpl16* LT745536, *trnL-F* LT745416.

Disocactus speciosus subsp. *blomianus*.—isolate CA312: MEXICO. Chiapas, *MacDougall A 202* (HNT-1794, holotype, ZSS-21340, isotype, ZSS-27875, isotype; ex HBG 15865) *trnK/matK* LT745656, *rpl16* LT745540, *trnL-F* LT745420.

Disocactus speciosus subsp. *cinnabarinus*.—isolate CA320: GUATEMALA. San Marcos, *Krahn 915-I* (B), living BG B 156201230 *trnK/matK* LT745653, *rpl16* LT745537, *trnL-F* LT745417.

Disocactus speciosus subsp. *speciosus*.—isolate CA387: MEXICO. Estado de México, *Bauer 20* (ZSS 27871), living BG B 155341230 *trnK/matK* LT745654, *rpl16* LT745538, *trnL-F* LT745418.

Disocactus speciosus subsp. *bierianus*.—isolate CA304: MEXICO. Guerrero, *Köhres 9650-2* (ZSS 27903) *trnK/matK* LT745655, *rpl16* LT745539, *trnL-F* LT745419.

Echinocereus cinerascens.—*trnK/matK* HM041680.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041414.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041260.1 (Hernandez-Hernandez *et al.* 2011).

Echinocereus pentalophus.—*trnK/matK* AY015307.1 (Nyffeler 2002), *rpl16* KF783558.1 (Arias *et al.* 2005), *trnL-F* AY015396.1 (Nyffeler 2002).

Epiphyllum baueri.—isolate CA206: without locality data (B GH 50240), living BG B 087020970 *trnK/matK* LT745657, *rpl16* LT745542, *trnL-F* --; isolate CA305: Colombia Chocó, *Bauer 32* (K-000035667 isotype, K-000035668 isotype, K-000578667 isotype) *trnK/matK* LT745658, *rpl16* LT745543, *trnL-F* --.

Epiphyllum cartagense.—isolate CA314: PANAMA. Bocas del Toro, *Mangelsdorff RMP 4112* (B), living BG B 156341230 *trnK/matK* --, *rpl16* --, *trnL-F* LT745460.

Epiphyllum chrysocardium.—isolate CA434: without locality data, but the specimen very likely comes from the type collection (MEXICO. Chiapas, *MacDougall A198*): type clones had been distributed to several botanical gardens; voucher (B GH 9420), living BG B 014747483 *trnK/matK* LT745660, *rpl16* LT745545, *trnL-F* LT745424.

Epiphyllum hookeri.—isolate CA280: PANAMA. Chiriquí, *Mangelsdorff RMP 3141* (B), living BG B 156351230 *trnK/matK* LT745661, *rpl16* LT745546, *trnL-F* LT745428.

- Epiphyllum hookeri* subsp. *columbiense*.—isolate CA279: Colombia, Chocó, *Bauer 28* (ZSS-19790) *trnK/matK* LT745662, *rpl16* LT745547, *trnL-F* LT745429.
- Epiphyllum hookeri* subsp. *guatemalense*.—isolate CA251: GUATEMALA. San Marcos, *Vollmer 9951 98* (B) *trnK/matK* LT745663, *rpl16* LT745548, *trnL-F* LT745430.
- Epiphyllum oxypetalum*.—isolate CA283: GUATEMALA. Izabal, Lago de Izabal, *Lautner L97/5* (B), living BG B 155731230 *trnK/matK* LT745665, *rpl16* LT745549, *trnL-F* LT745432.
- Epiphyllum phyllanthus*.—isolate CA243: SURINAM. without locality data, *Brownsberg s.n.* (B), living BG B 177191060 *trnK/matK* LT745666, *rpl16* LT745550, *trnL-F* LT745433; isolate CA262: GUYANA. Georgetown, *Bauer 82* (B), living BG B 156061230 *trnK/matK* LT745667, *rpl16* LT745551, *trnL-F* LT745434; isolate CA213: BOLIVIA. Santa Cruz, *Ibisch 93.197* (BOLV, LPB, FR), living BG B 069011230 *trnK/matK* --, *rpl16* LT745541, *trnL-F* --; isolate CA264: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, *Bauer 40* (ZSS 19797) *trnK/matK* LT745668, *rpl16* LT745552, *trnL-F* LT745435.
- Epiphyllum phyllanthus* subsp. *rubrocoronatum*.—isolate CA292: COLOMBIA. Chocó, *Bauer 66* (B), living BG B 155851230 *trnK/matK* LT745669, *rpl16* LT745553, *trnL-F* LT745436.
- Epiphyllum pumilum*.—isolate CA199: MEXICO. Los Tuxlas, collector unknown (B GH 45760), living BG B 180190163 *trnK/matK* LT745670, *rpl16* LT745554, *trnL-F* LT745437; isolate CA250: MEXICO. Chiapas, *Haugg s.n.* (ZSS 21396) *trnK/matK* LT745671, *rpl16* LT745555, *trnL-F* LT745438.
- Epiphyllum thomsonianum*.—isolate CA274: MEXICO. Chiapas, *Ehlers 031112* (B), living BG B 156451230 *trnK/matK* LT745672, *rpl16* LT745556, *trnL-F* LT745439.
- Epiphyllum thomsonianum* subsp. *costaricense*.—isolate CA285: COLOMBIA. Magdalena, *Bauer 39* (B), living BG B 155551230 *trnK/matK* --, *rpl16* LT745557, *trnL-F* --.
- Escontria chiotilla*.—*trnK/matK* AY015308.1 (Nyffeler 2002), *rpl16* AY181608.1 (Arias *et al.* 2003), *trnL-F* AY015397.1 (Nyffeler 2002).
- Eulychnia breviflora*.—isolate CA137 *trnK/matK* FN669772 (Korotkova *et al.* 2010), *rpl16* FN673680.1 (Korotkova *et al.* 2010), *trnL-F* --.
- Frailea pumila*.—*trnK/matK* HM041698.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041433.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041279.1 (Hernandez-Hernandez *et al.* 2011).
- Kimnachia ramulosa*.—isolate CA203: ECUADOR. no further locality data, collector unknown (B), living BG B 153089243 *trnK/matK* LT745705, *rpl16* LT745588, *trnL-F* LT745473; isolate CA214: MEXICO. Chiapas, collector unknown (B), living BG B 055230640 *trnK/matK* LT745706, *rpl16* LT745589, *trnL-F* LT745474.
- Kimnachia ramulosa* subsp. *jamaicensis*.—isolate CA253: JAMAICA. Westmoreland Parish, *Fleming s.n.* (ZSS 19803), living BG B 155061230 *trnK/matK* LT745707, *rpl16* LT745590, *trnL-F* LT745475.
- Leptocereus leonii*.—*trnK/matK* AY015297.1 (Nyffeler 2002), *rpl16* --, *trnL-F* AY015388.1 (Nyffeler 2002).
- Lophocereus schottii*.—*trnK/matK* AY015309.1 (Nyffeler 2002), *rpl16* --, *trnL-F* AY015398.1 (Nyffeler 2002).
- Monvillea spegazzinii*.—*trnK/matK* HM041723.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041458.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041304.1 (Hernandez-Hernandez *et al.* 2011).
- Myrtillocactus schenckii*.—isolate T1668 *trnK/matK* FN997501.1 (Barcenas *et al.* 2011), *rpl16* AY181607.1 (Arias *et al.* 2005), *trnL-F* AY181633.2 (Arias *et al.* 2005).

Neobuxbaumia mezcalaensis.—*trnK/matK* HM041725.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041460.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041306.1 (Hernandez-Hernandez *et al.* 2011).

Neoraimondia herzogiana.—*trnK/matK* HM041728.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041463.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041309.1 (Hernandez-Hernandez *et al.* 2011).

Pachycereus pecten-aboriginum.—*trnK/matK* HM041750.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041487.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041331.1 (Hernandez-Hernandez *et al.* 2011).

Peniocereus serpentinus.—*trnK/matK* HM041756.1 (Hernandez-Hernandez *et al.* 2011).

Pfeiffera ianthothele.—isolate CA084 *trnK/matK* FR716764 (Korotkova *et al.* 2010), *rpl16* FR716775.1 (Korotkova *et al.* 2010), *trnL-F* LT745463.

Pfeiffera monacantha spp. *kimnachii*.—isolate CA406: BOLIVIA. Kessler 13425 (B) *trnK/matK* LT745696, *rpl16* --, *trnL-F* LT745464.

Polaskia chichipe.—*trnK/matK* HM041760.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041497.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* HM041341.1 (Hernandez-Hernandez *et al.* 2011).

Pseudorhipsis acuminata.—isolate CA246: COSTA RICA. Limón, Davidson & Donohue 8422 (ZSS-19801, ZSS-21362), living BG B 155461230 *trnK/matK* LT745697, *rpl16* LT745580, *trnL-F* LT745465.

Pseudorhipsis alata.—isolate CA263: JAMAICA. Cockpit Country, Kress s.n. (ZSS-22552), living BG B 155251230 *trnK/matK* LT745698, *rpl16* LT745581, *trnL-F* LT745466.

Pseudorhipsis amazonica subsp. *amazonica*.—isolate CA266: PERU. Ucayali: Chullachaqui, Pino 97-17 (ZSS 22555), living BG B 155771234 *trnK/matK* LT745699, *rpl16* LT745582, *trnL-F* LT745467.

Pseudorhipsis amazonica subsp. *chocoensis*.—isolate CA407: COLOMBIA. Chocó, Nuquí, Bauer 29 (ZSS-22545, holotype) *trnK/matK* LT745700, *rpl16* LT745583, *trnL-F* LT745468.

Pseudorhipsis amazonica subsp. *panamensis*.—isolate CA202: PANAMA. no locality data, collector unknown (B), living BG B 082018233 *trnK/matK* LT745701, *rpl16* LT745584, *trnL-F* LT745469; isolate CA287: Colombia, Magdalena, Sierra Nevada de Santa Marta, Bauer 43 (ZSS-21381), living BG B 155601230 *trnK/matK* LT745702, *rpl16* LT745585, *trnL-F* LT745470.

Pseudorhipsis himanthoclada.—isolate CA260: COSTA RICA. San José, Horich s.n. (HNT-1488, ZSS-21379), living BG B 155421230 *trnK/matK* LT745703, *rpl16* LT745586, *trnL-F* LT745471.

Pseudorhipsis lankesteri.—isolate CA258: COSTA RICA. San José, Cordillera Brunqueña, Horich s.n. (ZSS-21365), living BG B 155211230 *trnK/matK* LT745704, *rpl16* LT745587, *trnL-F* LT745472.

Selenicereus anthonyanus.—isolate CA261: MEXICO. Chiapas, Noller s.n. (B), living BG B 155811230 *trnK/matK* LT745708, *rpl16* LT745591, *trnL-F* LT745476.

Selenicereus atropilosus.—isolate CA217: MEXICO. Jalisco, San Sebastian, Boutin & Kimnach 3190 (B GH 15955 holotype), living BG B 001028330 *trnK/matK* LT745709, *rpl16* LT745592, *trnL-F* LT745477.

Selenicereus calcaratus.—isolate CA223: without locality data (B), living BG B 066048480 *trnK/matK* LT745673, *rpl16* LT745558, *trnL-F* LT745440; isolate CA350: COSTA RICA. Limón, Horich s.n. (B), living BG B 155471230 *trnK/matK* LT745674, *rpl16* LT745559, *trnL-F* LT745441.

Selenicereus cf. nelsonii.—isolate CA378: MEXICO. Chiapas, *Kimnach 3239* (B) *trnK/matK* LT745711, *rpl16* LT745594, *trnL-F* LT745479.

Selenicereus costaricensis.—isolate CA377: COSTA RICA. Puntarenas, *Becksteiner s.n.* (B), living BG B 155221230 *trnK/matK* LT745675, *rpl16* LT745560, *trnL-F* LT745442.

Selenicereus dorschianus.—isolate CA395: MEXICO. Jalisco, *Böhme s.n.* (MEXU-1248407, isotype), ZSS-22551, holotype), living BG B 155821230, ex BG Bonn 2302 *trnK/matK* LT745712, *rpl16* LT745595, *trnL-F* LT745480.

Selenicereus extensus.—isolate CA205: FRENCH GUIANA. Atachi Bacca mountains, *Granville et al.10991* (B, neotype), living BG B 039498920 *trnK/matK* LT745676, *rpl16* LT745561, *trnL-F* LT745443; isolate CA239: FRENCH GUIANA. Cayenne: Approuague-Kaw, *Scharf 101* (B), living BG B 193010630 *trnK/matK* LT745677, *rpl16* LT745562, *trnL-F* LT745444.

Selenicereus glaber.—isolate CA308: EL SALVADOR. Ahuachapan, *Vollmer 9911 97* (ZSS-21352) *trnK/matK* LT745738, *rpl16* LT745621, *trnL-F* LT745505.

Selenicereus glaber subsp. *mirandae*.—isolate CA307: MEXICO. Chiapas, El Mirador, *Dorsch s.n.* (B) *trnK/matK* LT745739, *rpl16* LT745622, *trnL-F* LT745506.

Selenicereus cf. grandiflorus.—isolate CA327: CUBA. Matanzas: Varadero peninsula, *Day s.n.* (B), living BG B 156331230 *trnK/matK* LT745714, *rpl16* LT745597, *trnL-F* LT745482.

Selenicereus grandiflorus.—isolate CA319: MEXICO. Chiapas, *Kimnach 3272* (B) *trnK/matK* LT745710, *rpl16* LT745593, *trnL-F* LT745478; isolate CA371: Cuba, Guantánamo, *MangelsdorffRMC 2177* (B), living BG B 156241230 *trnK/matK* LT745713, *rpl16* LT745596, *trnL-F* LT745481; isolate CA233: without locality data (B GH 18344), living BG B 055627480 as “*coniflorus*” *trnK/matK* LT745717, *rpl16* LT745600, *trnL-F* LT745485.

Selenicereus grandiflorus subsp. *donkelaarii*.—isolate CA381: MEXICO. Yucatán, *Campos 2579* (B), living BG B 155611230 *trnK/matK* LT745715, *rpl16* LT745598, *trnL-F* LT745483; isolate CA240: without locality data (B GH 18828), living BG B 043697480 *trnK/matK* LT745716, *rpl16* LT745599, *trnL-F* LT745484.

Selenicereus grandiflorus subsp. *lautneri*.—isolate CA367: MEXICO. Oaxaca, *Lautner L06/8* (B) *trnK/matK* LT745719, *rpl16* LT745602, *trnL-F* LT745487.

Selenicereus grandiflorus subsp. *hondurensis*.—isolate CA369: GUATEMALA. Izabal, Lago de Izabal, *Bauer 8* (ZSS 21377) *trnK/matK* LT745718, *rpl16* LT745601, *trnL-F* LT745486.

Selenicereus hamatus.—isolate CA384: MEXICO. Veracruz, *Lautner L06/4* (B) *trnK/matK* LT745720, *rpl16* LT745603, *trnL-F* LT745488.

Selenicereus inermis.—isolate CA259: VENEZUELA. Miranda, *Steyrmark 108741* (HNT-6254) *trnK/matK* LT745721, *rpl16* LT745604, *trnL-F* LT745489; isolate CA309: COSTA RICA. Guanacaste, *Lewis EPICR#104* (B) *trnK/matK* LT745722, *rpl16* LT745605, *trnL-F* LT745491; isolate CA232: COSTA RICA. Atlantic rainforest, *Horich s.n.* (B GH 35913), living BG B 112028920 *trnK/matK* LT745732, *rpl16* LT745615, *trnL-F* LT745499.

Selenicereus megalanthus.—isolate CA347: PERU. Amazonas, *Bauer 55 = Bauer & Kimnach 38* (B), living BG B 155781230 *trnK/matK* LT745678, *rpl16* LT745563, *trnL-F* LT745445.

Selenicereus minutiflorus.—isolate CA221: without locality data (B GH 15053), living BG B 175028180 *trnK/matK* LT745680, *rpl16* LT745565, *trnL-F* LT745447.

Selenicereus monacanthus.—isolate CA224: without locality data (B GH 31603), living BG B 052018230 *trnK/matK* LT745682, *rpl16* LT745567, *trnL-F* LT745449; isolate CA346: SURINAM. Raleigh Falls, *Ingham & Ingham s.n.* (B),

living BG B 156011230 ex HBG 33960 *trnK/matK trnK/matK* LT745685, *rpl16* LT745570, *trnL-F* LT745452; isolate CA385: ECUADOR. Chimborazo, *Krahn 1178* (B), living BG B 156301230 *trnK/matK* LT745686, *rpl16* LT745571, *trnL-F* LT745453; isolate CA325: COLOMBIA. Magdalena, *Bauer 46* (ZSS-22705 neotype Bauer 2003), living BG B 155581230 *trnK/matK* LT745684, *rpl16* LT745569, *trnL-F* LT745451; isolate CA219: ECUADOR. El Oro, *Madson* s.n. (B), living BG B 222029830 *trnK/matK* LT745681, *rpl16* LT745566, *trnL-F* LT745448; isolate CA227: SURINAM. Raleigh Falls, collector unknown (B GH 28417, 28417a), living BG B 187018830 *trnK/matK* LT745683, *rpl16* LT745568, *trnL-F* LT745450.

Selenicereus ocamponis.—isolate CA222: without locality data (B GH 41127), living BG B 258079380 *trnK/matK* LT745688, *rpl16* LT745573, *trnL-F* LT745455; isolate CA375: MEXICO. Nayarit, *Kimnach 535* (B) *trnK/matK* LT745689, *rpl16* LT745574, *trnL-F* LT745456; isolate CA220: without locality data (B GH 12787, 12787a), living BG B 012187480 *trnK/matK* LT745687, *rpl16* LT745572, *trnL-F* LT745454.

Selenicereus pteranthus.—isolate CA210: without locality data (B), living BG B 069261280 *trnK/matK* LT745727, *rpl16* LT745610, *trnL-F* LT745494; isolate CA391: CUBA. Holguín, *Schwerdtfeger* s.n. (B) *trnK/matK* LT745728, *rpl16* LT745611, *trnL-F* LT745495.

Selenicereus setaceus.—isolate CA358: BOLIVIA. Santa Cruz, *Krahn 1006* (B), living BG B 155951230 *trnK/matK* LT745692, *rpl16* LT745576, *trnL-F* LT745459; isolate CA209: without locality data (B) BG B 069321218 (ex BG Bonn 14394) *trnK/matK* LT745690, *rpl16* --, *trnL-F* LT745457; isolate CA234: PARAGUAY. Cerro Acahay Billiet, *Jadin* s.n. (B GH 44115), living BG B 232070230 *trnK/matK* LT745691, *rpl16* LT745575, *trnL-F* LT745458.

Selenicereus sp..—isolate CA216: BELIZE. without further locality data, *Vollmer* s.n. (B), living BG B 069131260 (ex BG Bonn 16416) *trnK/matK* LT745679, *rpl16* LT745564, *trnL-F* LT745446.

Selenicereus spinulosus.—isolate CA238: MEXICO. Oaxaca, *Lautner LW 81 /Q* (B GH 37937), living BG B 266029430 *trnK/matK* LT745729, *rpl16* LT745612, *trnL-F* LT745496.

Selenicereus stenopterus.—isolate CA322: COSTA RICA. Limón, *Horich* s.n. (B GH 49514), living BG B 069221230 (ex BG Bonn 6290) *trnK/matK* LT745693, *rpl16* LT745577, *trnL-F* --.

Selenicereus triangularis.—isolate CA225: without locality data (B GH 15049, 15049a, 15049b), living BG B 014967480 *trnK/matK* LT745694, *rpl16* LT745578, *trnL-F* LT745461.

Selenicereus tricae.—isolate CA328: BELIZE. Cayo, *Hunt 7076* (K-29047.259 holotype, in spirit), living RBG Kew 1969-3879 *trnK/matK* LT745724, *rpl16* LT745607, *trnL-F* LT745491; isolate CA366: MEXICO. Veracruz, *Hunt 7170* (ZSS 29372), living RBG Kew 1969-4129 *trnK/matK* LT745723, *rpl16* LT745606, *trnL-F* --.

Selenicereus undatus.—isolate CA226: MEXICO. Veracruz, *Leuenberger & Schiers 2500* (B GH 18378, 18378a), living BG B 003017810 *trnK/matK* LT745695, *rpl16* LT745579, *trnL-F* LT745462.

Selenicereus vagans.—isolate CA342: MEXICO. Michoacán, *Noller* s.n. (ZSS-28853), living BG B 155741230 *trnK/matK* LT745730, *rpl16* LT745613, *trnL-F* LT745497; isolate CA349: ex hort. without locality data collector unknown (ZSS-29368), probably the type clone of *Selenicereus murrilli* *trnK/matK* LT745726, *rpl16* LT745609, *trnL-F* LT745493; isolate CA392: MEXICO. Michoacán, *Hoxey 476.03* (ZSS-28854), living BG B 156121230 *trnK/matK* LT745725, *rpl16* LT745608, *trnL-F* LT745492.

Selenicereus validus.—isolate CA397: MEXICO. Michoacán, *Lautner L00/13* (B), living BG B 155871230 *trnK/matK* LT745731, *rpl16* LT745614, *trnL-F* LT745498.

Stenocereus eruca.—*trnK/matK* HM041777.1 (Hernandez-Hernandez *et al.* 2011), *rpl16* HM041514.1 (Hernandez-Hernandez *et al.* 2011) *trnL-F* HM041357.1 (Hernandez-Hernandez *et al.* 2011).

Stenocereus stellatus.—isolate T1652 *trnK/matK* FN997498.1 (Barcenas *et al.* 2011), *rpl16* HM041517.1 (Hernandez-Hernandez *et al.* 2011), *trnL-F* --.

Strophocactus wittii.—isolate CA200: BRAZIL, region of the Rio Negro, *Loki Schmidt s.n.* (B GH 46892), living BG B 240119930 *trnK/matK* LT745736, *rpl16* LT745619, *trnL-F* LT745503.

Strophocactus brasiliensis.—*rpl16* DQ100036.1 (Arias *et al.* 2005), *trnL-F* DQ099967.1 (Arias *et al.* 2005).

Strophocactus sicariguensis.—*rpl16* DQ100037.1 (Arias *et al.* 2005), *trnL-F* DQ099968.1 (Arias *et al.* 2005).

Weberocereus frohningiorum.—isolate CA340: COSTA RICA. no further locality data, ex. Palmengarten, cited as *Frohning 9067*. Frohning had obtained the plant 1994 from the Palmengarten Frankfurt (K-000100018 isotype, ZSS-19806 holotype) *trnK/matK* LT745737, *rpl16* LT745620, *trnL-F* LT745504.

Weberocereus imitans.—isolate CA276: COSTA RICA. San José, Valle de El General, *Kimmach, Horich & Linden 2463* (B) *trnK/matK* LT745740, *rpl16* LT745623, *trnL-F* LT745507.

Weberocereus rosei.—isolate CA247: ECUADOR. Chimborazo, *Madsen 87EC63877* (B) *trnK/matK* LT745741, *rpl16* LT745624, *trnL-F* LT745508.

Weberocereus tonduzii.—isolate CA201: COSTA RICA. Cordillera de Talamanca, *Horich s.n.* (B GH 35652), living BG B 112058920 *trnK/matK* LT745742, *rpl16* LT745625, *trnL-F* LT745509.

Weberocereus trichophorus.—isolate CA211: COSTA RICA. *Horich s.n.* (B), living BG B 069271230 (ex BG Bonn 6530) *trnK/matK* LT745743, *rpl16* LT745626, *trnL-F* LT745510; isolate CA354: COSTA RICA. Limón, *Wrage s.n.* (ZSS 19805, ZSS 21393) *trnK/matK* LT745744, *rpl16* LT745627, *trnL-F* LT745511.

Weberocereus tunilla.—isolate CA379: ex. Rainbow Gardens 1988, without locality data (B) *trnK/matK* LT745745, *rpl16* LT745628, *trnL-F* LT745512.

Weberocereus tunilla subsp. biolleyi.—isolate CA204: COSTA RICA. *Horich s.n.* (B GH 25043, 25043a), living BG B 271028220 *trnK/matK* LT745746, *rpl16* LT745629, *trnL-F* LT745513; isolate CA288: COSTA RICA. Alajuela, *Lau s.n.* (ZSS-22550) *trnK/matK* LT745747, *rpl16* LT745630, *trnL-F* LT745514.