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Cactaceae at Caryophyllales.org – a dynamic online species-level taxonomic backbone for the family

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Abstract: This data paper presents a largely phylogeny-based online taxonomic backbone for the *Cactaceae* compiled from literature and online sources using the tools of the EDIT Platform for Cybertaxonomy. The data will form a contribution of the *Caryophyllales* Network for the World Flora Online and serve as the base for further integration of research results from the systematic research community. The final aim is to treat all effectively published scientific names in the family. The checklist includes 150 accepted genera, 1851 accepted species, 91 hybrids, 746 infraspecific taxa (458 heterotypic, 288 with autonyms), 17,932 synonyms of accepted taxa, 16 definitely excluded names, 389 names of uncertain application, 672 unresolved names and 454 names belonging to (probably artificial) named hybrids, totalling 22,275 names. The process of compiling this database is described and further editorial rules for the compilation of the taxonomic backbone for the *Caryophyllales* Network are proposed. A checklist depicting the current state of the taxonomic backbone is provided as supplemental material. All results are also available online on the website of the *Caryophyllales* Network and will be constantly updated and expanded in the future.

Key words: *Cactaceae*, *Caryophyllales*, checklist, cybertaxonomy, database, EDIT Platform, taxonomy, TEN, Taxonomic Expert Network, WFO, World Flora Online

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Data published through: http://caryophyllales.org/cactaceae/Checklist

Introduction

Cactaceae are a New World plant family that comprises many endangered species (Goettsch & al. 2015; IUCN 2021). Almost the entire family is cited in CITES Appendix II as protected and a number of species are cited in Appendix I as threatened with extinction (CITES 2021). Abundant new knowledge has been generated in the last 15 years as a result of molecular phylogenetic studies. Here, we present a largely phylogeny-based taxonomic

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backbone for the *Cactaceae* detailing the species and infraspecific levels. It represents a synthesis of available published evidence for the current understanding of species and generic circumscriptions and combines insights from phylogenetic studies, corresponding synoptic treatments, recent revisions and monographs and regional treatments in floras and checklists. We have made an effort to include all validly published (Turland & al. 2018) scientific names in *Cactaceae*, as well as the numerous invalid names found in the literature, in order to resolve all existing names in *Cactaceae* and avoid future erroneous use.

The Global *Caryophyllales* Initiative provided the framework for this work. This initiative aims at creating an online global synthesis of species diversity in the order *Caryophyllales* by a network of taxonomic specialists (Borsch & al. 2015). A family and genus-level checklist of the *Caryophyllales* was first published in 2015 (Hernández-Ledesma & al. 2015) and has since then been continuously updated on the *Caryophyllales* website (*Caryophyllales* Network 2015+; http://caryophyllales.org/). The next step was to implement species-level taxonomic backbones for the different families and genera of the order, building on the same technical solution used for the generic checklist, namely the EDIT Platform for Cybertaxonomy (Ciardelli & al. 2009; Berendsohn 2010; EDIT 2019). A concerted effort was made to use the Platform's ability to explicitly reference all underlying sources of the data from literature citations to type specimen information, thus crediting the originators of the information. This includes the possibility to state the sources for an explicit taxonomic concept with accepted names and synonyms, for the (later) assignment of synonyms to taxa, for the assignment of a nomenclatural status, for type information, and for factual data and notes of all kinds. This is part of the *Caryophyllales* Network's underlying intention to fully support FAIR principles (Wilkinson & al. 2016; Wilkinson & al. 2019) in data management. Our approach is also in line with the principles for creating global species lists outlined by Garnett & al. (2020).

In this way, the *Caryophyllales* initiative also contributes directly to the World Flora Online (WFO) (CBD 2014; Wyse Jackson & Miller 2015; Borsch & al. 2020), which is becoming the consistent and authoritative information source on the world's angiosperms, gymnosperms, ferns and allies and bryophytes. The *Caryophyllales* Network constitutes one of the Taxonomic Expert Networks (TENs) responsible for a specific "slice" of the taxonomic backbone of the World Flora Online, and the treatment of *Cactaceae* presented here will be incorporated into the WFO taxonomic backbone in a process that can be repeated whenever substantial updates of the *Caryophyllales* Network database occur (see http://about.worldfloraonline.org/wfodocuments.shtml, document "WFO Guidelines for Taxonomic Backbone Contributors, Version 2.06").

Enormous progress toward understanding phylogenetic relationships in the *Cactaceae* has been made in the last 10–15 years. Several family-wide phylogenetic studies have been published (Nyffeler 2002; Nyffeler & Eggli 2010; Bárcenas & al. 2011; Hernández-Hernández & al. 2011; Guerrero & al. 2019a), representatives of most *Cactaceae* genera have by now been included in detailed molecular phylogenetic analyses, including some of the most speciose clades of *Cactaceae* such as *Echinopsis* Zucc. (Schlumpberger & Renner 2012), *Mammillaria* Haw. (Breslin & al. 2021) and *Opuntia* Mill. (Majure & al. 2012). These studies were often based on a comprehensive sampling of a given genus, although they did not always result in well-resolved trees and largely relied on plastid sequence data. Nevertheless, many of the so-far published phylogenetic frameworks provide very useful information for phylogeny-based synopses or monographic treatments, an approach that is becoming the standard in the community. Examples include *Aylostera* Speg. (Ritz & al. 2016), *Copiapoa* Britton & Rose (Larridon & al. 2015; Larridon & al. 2018a), *Disocactus* Lindl. (Cruz & al. 2016), *Cephalocereus* Pfeiff. (Tapia & al. 2017), *Echinocactus* Link & Otto (Vargas-Luna & al. 2018), *Epithelantha* F. A. C. Weber ex Britton & Rose (Aquino & al. 2019), *Eriosyce* Phil. (Guerrero & al. 2019b), *Harrisia* Britton (Franck 2012; Franck & al. 2013; Franck 2016), the *Hylocereeae* (Korotkova & al. 2017), *Pfeiffera* Salm-Dyck (Korotkova & al. 2010), *Turbinicarpus* (Backeb.) Buxb. & Backeb. (Vázquez-Sánchez & al. 2019) and several more.

So, while there now is a solid phylogenetic framework for many *Cactaceae* genera, for many others there are phylogenetic studies that delimit their circumscription with varying support, or sometimes also contradicting conclusions, but do not provide a phylogenetically informed taxonomic treatment at the species level. And for still other genera, the phylogenetic results have so far remained inconclusive for various reasons, mostly attributable to insufficient taxon sampling or low node support. Examples include some genera in *Cacteae* (Vázquez-Sánchez & al. 2013) or the *Echinopsis* alliance (Schlumpberger & Renner 2012). Final conclusions regarding the monophyly and generic limits of *Coryphantha* (Engelm.) Lem., *Escobaria* Britton & Rose and *Mammillaria* must also await a more extensive sampling (Breslin & al. 2021).

Our species-level checklist therefore represents a snapshot of the current knowledge. Using a joint database to dynamically capture new knowledge generated by the taxonomic community and to fix nomenclatural problems in a persistent manner is instrumental for the development of an integrated view on the taxonomy of a complex group such as the *Cactaceae*.

Material and methods

General approach and editorial standards

The backbone classification follows phylogeny-based taxonomic treatments as far as they are available; otherwise, appropriate classical or conventional taxonomic works are used as the basis. The classification with respect to the acceptance of taxa follows treatments that were published, in press or at least submitted during the compilation of the present checklist. The taxonomic concept or circumscription of the accepted taxa is indicated by the secundum ("sec.") reference (Berendsohn 1995). Orthographical corrections may have been applied independently. In addition, several necessary combinations and validations of names are made here (see Nomenclatural novelties below). For those names that we have excluded from the core checklist (unresolved names, names of uncertain application, artificial hybrids), the sec. reference normally indicates the source for the respective placement of the name. For synonyms, the "syn. sec." reference indicates the assignment of the synonym to the concept of either the accepted name or one of its homotypic synonyms; this may or may not be the same reference as that of the secundum of the taxon. The statement of the nomenclatural status can also be independent of the sec. or syn. sec. reference of a name and is referenced separately; the sources are given on the website http://caryophyllales.org/cactaceae/Checklist, as well as in the online Supplemental content of the present publication.

General editorial standards regarding the citation of author names and nomenclatural references in many respects follow the rules formulated by Kilian & al. (2009+) for the *Cichorieae* Network, another initiative using the EDIT Platform. Titles of monographs are abbreviated in conformity with *Taxonomic literature*, ed. 2 (Stafleu & Cowan 1976–1988; Stafleu & Mennega 1992–2000; Dorr & Nicolson 2008, 2009), but all components start with capital letters. Titles of monographs not listed in *Taxonomic literature* follow the version used in IPNI, with the exception that work's editor is not included in the title. Titles not mentioned in any of these sources are abbreviated as in serials. Titles of serials are abbreviated in conformity with *Botanico-periodicum-huntianum* (Bridson & al. 2004, online edition); titles not listed there are abbreviated according to the standards therein defined. The publication year always refers to the actual year of publication of the page cited. If a work has been published in parts and its publication dates have been established, the publication year is one of the corresponding parts and can then differ from the year(s) on the (main) title page of that work. In the case of known differences between the year given and the real publication date, the former is cited in square brackets and set in quotation marks. Series that form part of the title are normally included in the standard abbreviation for nomenclatural citations.

The tools

The EDIT Platform for Cybertaxonomy (https://cybertaxonomy.eu/), (Ciardelli & al. 2009; Berendsohn 2010; EDIT 2019) is a suite of open-source software tools and services, which has been developed over the past 20 years with the aim of covering all aspects of an integrative taxonomic workflow (Borsch & al. 2015; Kilian & al. 2015; Henning & al. 2018). The underlying Common Data Model (CDM) has been constantly refined to mirror the intricacies of nomenclatural and taxonomic information, including all aspects of monographic and floristic work. The taxonomic editor software, online data portal and publication pipelines of the EDIT Platform are used in the *Caryophyllales* Network to capture, process, attribute, document, publish and maintain the data. Its role in the context of the *Caryophyllales* synthesis and the features that distinguish it from other tools for taxonomic compilations are more fully detailed in Borsch & al. (2015) and Berendsohn & al. (2018). It should be mentioned that the ongoing work on species-level checklists of core *Caryophyllales* families is carried out in a single underlying CDM database, providing synergies with respect to jointly used resources such as reference citations.

Data compilation and principal sources

Subfamilies and tribes — We have refrained from including an infrafamilial and tribal classification at this time. All genera can be assigned to subfamilies, with the majority belonging to the two major subfamilies *Opuntioideae* and *Cactoideae*. The genera *Leuenbergeria* Lodé, *Maihuenia* (Phil. ex F. A. C. Weber) K. Schum. and *Pereskia* Mill., which form the basal *Cactaceae* grade, would have to be placed in their respective monogeneric subfamilies; the names do exist. Tribes could be given for most taxa as well, yet some genera have not yet been sampled in phylogenetic analyses or poor node support so far did not allow placing them confidently at the tribal level. The names of subfamilies and tribes can certainly be included at a later stage to make the checklist more complete, but the current simple alphabetical list of genera is intended to make it easier for users to find taxa.

Accepted generic names — Accepted generic names and their synonyms were taken from the *Caryophyllales* genus-level checklist (Hernández-Ledesma & al. 2015), with additions from more recent phylogenetic studies that included changes to generic concepts. In the (rare) cases of conflicting treatments, the respective editor of the partial treatment simply decided on a source to follow and documented it in the notes accompanying the genus entry.

Infrageneric names (i.e. names at ranks below genus and above species) were not included, unless the currently accepted generic name was based on an earlier infrageneric name.

We have defined five categories to assess the robustness of the circumscriptions of genera, described in more detail below. Table 1 gives an overview of this assessment, as well as the literature used as circumscription

Table 1. Overview of accepted genera, their species numbers and an assessment of the monophyly and the phylogenetic knowledge of each genus (see text for more details). – A: genera that are monophyletic based on a complete or very comprehensive phylogenetic study, and a phylogeny-based taxonomic synopsis was published; B: genera that are monophyletic based on phylogenetic studies that support the clade based on a sufficiently dense or even complete sampling or support a monotypic genus as a distinct lineage; C: genera that are probably monophyletic, but too few of the species were sampled in phylogenetic studies to reliably establish monophyly; D: genera that are polyphyletic, paraphyletic or nested in another genus; E: genera for which no assessment of monophyly has yet been possible, because only a few species were sampled or no phylogenetic study has been conducted so far. See the Discussion for a more detailed explanation of these categories. The column "Names total" does not count the name of the genus itself.

Genus	Species	Infraspecies	Autonyms	Hybrid species	Synonyms	Names total	Secundum	Assessment
Acanthocalycium Backeb.	5	2	4	0	94	105	Schlumpberger in this publication	B
Acanthocereus (Engelm. ex A. Berger) Britton & Rose	15	0	0	0	70	86	Korotkova & al. (2017)	A
Acharagma (N. P. Taylor) Glass	2	1	1	0	12	16	Vázquez-Sánchez & al. (2013)	B
Airampoa Frič	16	0	0	0	86	102	Doweld (2002a)	E
Aporocactus Lem.	2	0	0	1	26	29	Cruz & al. (2016), Korotkova & al. (2017)	A
Ariocarpus Scheidw.	7	1	1	3	91	103	Vázquez-Sánchez & al. (2013)	B
Armatocereus Backeb.	7	2	2	0	31	42	Hunt (2006)	C
Arrojadoa Britton & Rose	6	1	1	1	34	45	Hunt (2016)	E
Arthrocereus A. Berger	4	2	1	0	21	28	Hunt (2016), Schlumpberger & Renner (2012)	B
Astrophytum Lem.	6	0	0	0	99	105	Vázquez-Lobo & al. (2015)	B
Austrocactus Britton & Rose	10	1	1	0	32	44	Hunt (2006)	E
Austrocylindropuntia Backeb.	7	1	1	0	127	136	Ritz & al. (2012)	B
Aylostera Speg.	9	0	0	0	525	534	Ritz & al. (2016)	A
Aztekium Boed.	3	0	0	0	2	5	Vázquez-Sánchez & al. (2013)	B
Bergerocactus Britton & Rose	1	0	0	0	2	3	Arias & al. (2005), Bárcenas & al. (2011), Hernández-Hernández & al. (2011)	B
Blossfeldia Werderm.	1	0	0	0	21	22	Bárcenas & al. (2011), Hernández-Hernández & al. (2011), Nyffeler (2002)	B
Borzicactus Riccob.	19	7	4	0	210	240	Hunt (2016)	E
Brachycereus Britton & Rose	1	0	0	0	1	2	Hunt (2006)	E
Brasilicereus Backeb.	3	0	0	0	11	14	Hunt (2016)	E
Brasiliopuntia (K. Schum.) A. Berger	2	0	0	0	22	24	Köhler in this publication	B
Browningia Britton & Rose	11	1	1	0	33	45	Hunt (2016)	E
Calymmanthium F. Ritter	1	0	0	0	4	5	Korotkova & al. (2010)	B
Carnegiea Britton & Rose	1	0	0	0	3	4	Parfitt & Gibson (2003)	D
Castellanosia Cárdenas	1	0	0	0	1	2	Bárcenas & al. (2011), Hernández-Hernández & al. (2011), Nyffeler (2002)	B
Cephalocereus Pfeiff.	16	0	0	0	123	139	Tapia & al. (2017)	A
Cereus Mill.	31	4	4	0	243	282	Franco & al. (2017), Hunt (2016)	D
Chamaecereus Britton & Rose	4	0	0	0	28	32	Hunt (2016)	B
Cipocereus F. Ritter	5	1	1	0	20	26	Franco & al. (2017), Taylor & Zappi (2004)	D

Cleistocactus Lem.	20	7	6	0	174	207	Hunt (2016)	E
Cochemiea (K. Brandegee) Walton	38	6	5	0	314	363	Breslin & al. (2021)	A
Coleocephalocereus Backeb.	6	2	2	0	39	49	Taylor & Zappi (2004)	E
Consolea Lem.	9	3	3	0	35	50	Majure in this publication	B
Copiapoa Britton & Rose	34	10	6	1	161	212	Larridon & al. (2015)	B
Corryocactus Britton & Rose	13	0	0	0	60	73	Hunt (2006)	E
Coryphantha (Engelm.) Lem.	43	12	10	0	325	390	Breslin & al. (2021), Hunt (2006)	D
Cremnocereus M. Lowry & al.	1	0	0	0	0	1	Lowry & Winberg (2017)	E
Cumarinia (F. M. Knuth) Buxb.	1	0	0	0	4	5	Breslin & al. (2021)	B
Cumulopuntia F. Ritter	11	4	2	0	169	186	Hunt (2016), Ritz & al. (2012)	B
Cylindropuntia (Engelm.) F. M. Knuth	40	17	8	9	290	364	Hunt (2016), Majure & al. (2019)	B
Deamia Britton & Rose	3	0	0	0	12	15	Korotkova & al. (2017)	A
Denmoza Britton & Rose	1	0	0	0	21	22	Hunt (2006)	B
Discocactus Pfeiff.	12	2	1	0	108	123	Hunt (2016)	E
Disocactus Lindl.	16	7	4	0	166	193	Cruz & al. (2016), Korotkova & al. (2017)	A
Echinocactus Link & Otto	2	1	1	1	74	78	Vargas-Luna & al. (2018)	B
Echinocereus Engelm.	83	46	28	4	592	753	Sánchez & al. (2014)	B
Echinopsis Zucc.	15	7	2	0	373	397	Schlumpberger & Renner (2012), Schlumpberger in this publication	B
Epiphyllum Haw.	10	6	3	0	81	100	Korotkova & al. (2017)	A
Epithelantha F. A. C. Weber ex Britton & Rose	10	0	0	0	41	51	Aquino & al. (2019)	A
Eriosyce Phil.	55	12	9	0	862	938	Guerrero & al. (2020)	B
Escobaria Britton & Rose	17	5	5	0	253	280	Breslin & al. (2021)	D
Escontria Rose	1	0	0	0	3	4	Arias & al. (2012), Hernández & Gómez-Hinostrosa (2011)	B
Espostoa Britton & Rose	11	4	2	0	52	69	Hunt (2006)	E
Espostoopsis Buxb.	1	0	0	0	7	8	Taylor & Zappi (2004)	B
Estevesia P. J. Braun	1	0	0	0	0	1	Franck in this publication	E
Eulychnia Phil.	9	2	2	0	21	33	Larridon & al. (2018b)	B
Facheiroa Britton & Rose	3	1	1	0	22	27	Taylor & Zappi (2004)	E
Ferocactus Britton & Rose	29	14	9	0	363	415	Hunt (2016), Vázquez-Sánchez & al. (2013)	D
Frailea Britton & Rose	17	6	5	0	151	179	Hunt (2006)	E
Geohintonia Glass & W. A. Fitz. Maur.	1	0	0	0	2	3	Vázquez-Sánchez & al. (2013)	B
Grusonia F. Rchb. ex Britton & Rose	21	1	1	0	69	91	Majure in this publication	B
Gymnocalycium Pfeiff. ex Mittler	61	14	7	3	604	689	Charles (2009), Demaio & al. (2011), Hunt (2016)	B
Haageocereus Backeb.	13	7	3	1	230	254	Hunt (2006)	E

continued on next page

Genus	Species	Infraspecies	Autonyms	Hybrid species	Synonyms	Names total	Secundum	Assessment
Harrisia Britton	19	0	0	0	103	122	Franck (2016)	A
Hatiora Britton & Rose	2	1	1	0	45	49	Korotkova & al. (2011)	B
Homalocephala Britton & Rose	3	1	1	0	18	23	Vargas-Luna & al. (2018)	B
Isolatocereus Backeb.	1	0	0	0	5	6	Arias & Aquino (2019)	B
Jasminocereus Britton & Rose	1	0	0	0	13	14	Hunt (2006)	E
Kadenicarpus Doweld	2	3	1	0	53	59	Vázquez-Sánchez & al. (2019)	A
Kimnachia S. Arias & N. Korotkova	1	2	2	0	23	28	Korotkova & al. (2017)	A
Kroenleinia Lodé	1	0	0	0	5	6	Vargas-Luna & al. (2018)	B
Lasiocereus F. Ritter	2	0	0	0	0	2	Hunt (2006)	E
Lemaireocereus Britton & Rose	2	0	0	0	12	14	Arias & al. (2012)	E
Leocereus Britton & Rose	1	0	0	0	11	12	Taylor & Zappi (2004)	B
Lepismium Pfeiff.	5	2	2	0	85	94	Barthlott & Taylor (1995), Korotkova & al. (2011)	B
Leptocereus (A. Berger) Britton & Rose	20	0	0	0	31	51	Barrios & al. (2019)	A
Leuchtenbergia Hook.	1	0	0	0	0	1	Hunt (2006)	D
Leucostele Backeb.	13	4	2	0	114	133	Schlumpberger in this publication	B
Leuenbergeria Lodé	8	0	0	0	43	51	Lodé (2013)	B
Lobivia Britton & Rose	33	9	6	0	573	621	Schlumpberger in this publication	B
Lophocereus (A. Berger) Britton & Rose	3	0	0	0	57	60	Arias & al. (2012)	B
Lophophora J. M. Coult.	3	0	0	0	51	54	Vázquez-Sánchez & al. (2013)	B
Lymanbensonia Kimnach	5	0	0	0	21	26	Korotkova & al. (2010)	A
Maihuenia (Phil. ex F. A. C. Weber) K. Schum.	2	0	0	0	21	23	Hunt (2006), Leuenberger (1997)	B
Maihueniopsis Speg.	20	0	0	0	115	135	Hunt (2016), Ritz & al. (2012)	B
Mammillaria Haw.	143	61	37	1	2090	2332	Breslin & al. (2021), Hunt (2016)	B
Marshallocereus Backeb.	1	0	0	0	21	22	Arias in this publication	B
Matucana Britton & Rose	17	8	3	0	123	151	Hunt (2016)	E
Melocactus Link & Otto	43	14	9	3	407	476	Hunt (2006)	E
Micranthocereus Backeb.	10	1	1	0	36	48	Hunt (2006)	E
Micropuntia Daston	1	0	0	0	20	21	Majure & al. (2019)	B
Mila Britton & Rose	1	1	1	0	36	39	Hunt (2006)	B
Miqueliopuntia Frič ex F. Ritter	1	0	0	0	8	9	Majure & al. (2012)	B
Morangaya G. D. Rowley	1	0	0	0	2	3	Sánchez & al. (2014)	B
Myrtillocactus Console	4	0	0	0	26	30	Hunt (2006)	B
Neoraimondia Britton & Rose	2	0	0	0	19	21	Hernández-Hernández & al. (2011), Hunt (2006)	B
Neowerdermannia Frič	2	0	0	0	13	15	Hunt (2006)	D
Nyctocereus (A. Berger) Britton & Rose	1	0	0	0	19	20	Arias & Aquino (2019)	B

Obregonia Frič	1	0	0	0	2	3	Vázquez-Sánchez & al. (2013)	B
Opuntia Mill.	154	30	11	18	826	1039	Hunt (2016)	B
Oreocereus (A. Berger) Riccob.	11	2	1	0	100	114	Hunt (2006)	E
Oroya Britton & Rose	2	0	0	0	27	29	Hunt (2006)	E
Pachycereus (A. Berger) Britton & Rose	7	0	0	0	48	55	Arias & Terrazas (2009)	B
Parodia Speg.	65	0	0	0	1200	1265	Anceschi & Magli (2018)	E
Pediocactus Britton & Rose	9	1	1	0	79	89	Hunt (2016)	E
Pelecyphora Ehrenb.	2	0	0	0	7	9	Vázquez-Sánchez & al. (2013)	D
Peniocereus (A. Berger) Britton & Rose	8	1	1	0	32	41	Arias & al. (2005)	B
Pereskia Mill.	9	2	2	0	62	75	Korotkova in this publication, Leuenberger (1986)	B
Pereskiopsis Britton & Rose	6	0	0	0	28	34	Hunt (2006), Majure & al. (2019)	B
Pfeiffera Salm-Dyck	6	1	1	0	51	58	Korotkova & al. (2010)	A
Pilosocereus Byles & G. D. Rowley	51	10	8	1	337	407	Calvente & al. (2017), Franck in this publication	B
Polaskia Backeb.	2	0	0	0	13	15	Arias & al. (2012)	E
Praecereus Buxb.	2	4	1	0	64	71	Franco & al. (2017), Taylor & Zappi (2004)	D
Pseudorhipsalis Britton & Rose	5	2	1	0	30	38	Korotkova & al. (2017)	A
Pterocactus K. Schum.	10	0	0	0	16	26	Griffith & Porter (2009), Ritz & al. (2012)	B
Punotia D. R. Hunt	1	0	0	0	20	21	Hunt (2011), Ritz & al. (2012)	B
Pygmaeocereus H. Johnson & Backeb.	2	1	1	0	13	17	Hunt (2006), Schlumpberger & Renner (2012)	B
Quiabentia Britton & Rose	2	0	0	0	12	14	Griffith & Porter (2009), Hunt 2006)	E
Rapicactus Buxb. & Oehme	5	2	2	0	52	61	Vázquez-Sánchez & al. (2019)	A
Rauhocereus Backeb.	1	1	1	0	2	5	Hunt (2006)	B
Rebutia K. Schum.	7	1	1	0	241	250	Kiesling & al. (2014), Ritz & al. (2007)	B
Reicheocactus Backeb.	2	0	0	0	35	37	Hunt (2006), Schlumpberger & Renner (2012)	B
Rhipsalidopsis Britton & Rose	2	0	0	1	31	34	Barthlott & Taylor (1995), Korotkova & al. (2011)	B
Rhipsalis Gaertn.	45	18	10	0	265	338	Barthlott & Taylor (1995), Korotkova & al. (2011), Korotkova in this publication	B
Rimacactus Mottram	1	0	0	0	2	3	Guerrero & al. (2020)	B
Salmonopuntia P. V. Heath	2	0	0	0	32	34	Griffith & Porter (2009), Majure & al. (2012)	B
Samaipaticereus Cárdenas	1	0	0	0	0	1	Hunt (2006)	B
Schlumbergera Lem.	7	1	1	4	84	97	Barthlott & Taylor (1995), Korotkova & al. (2011)	B
Sclerocactus Britton & Rose	23	4	4	0	192	223	Hunt (2016), Vázquez-Sánchez & al. (2013)	B
Selenicereus (A. Berger) Britton & Rose	31	5	3	0	210	249	Korotkova & al. (2017)	A
Setiechinopsis Backeb.	1	0	0	0	8	9	Hunt (2016)	B
Soehrensia Backeb.	28	6	3	0	309	346	Schlumpberger & Renner (2012), Schlumpberger in this publication	B

continued on next page

Genus	Species	Infraspecies	Autonyms	Hybrid species	Synonyms	Names total	Secundum	Assessment
Stenocactus (K. Schum.) A. W. Hill	21	2	2	0	242	267	Hunt (2006)	D
Stenocereus (A. Berger) Riccob.	24	1	1	0	198	224	Hunt (2016)	B
Stephanocereus A. Berger	2	0	0	0	15	17	Taylor & Zappi (2004)	E
Stetsonia Britton & Rose	1	0	0	0	4	5	Hunt (2006)	B
Strombocactus Britton & Rose	2	1	1	0	22	26	Vázquez-Sánchez & al. (2013)	B
Strophocactus Britton & Rose	3	1	1	0	11	16	Korotkova & al. (2017)	A
Tacinga Britton & Rose	10	1	1	2	31	45	Griffith & Porter (2009), Majure & al. (2012)	B
Tephrocactus Lem.	12	4	3	0	132	151	Las Peñas & al. (2019)	B
Thelocactus (K. Schum.) Britton & Rose	13	8	3	1	207	232	Hunt (2016)	D
Trichocereus (A. Berger) Riccob.	6	2	2	0	72	82	Schlumpberger & Renner (2012), Schlumpberger in this publication	B
Turbinicarpus (Backeb.) Buxb. & Backeb.	23	13	3	36	160	235	Aquino in this publication, Vázquez-Sánchez & al. (2019)	B
Uebelmannia Buining	3	3	1	0	11	18	Taylor & Zappi (2004)	E
Vatricania Backeb.	1	0	0	0	5	6	Schlumpberger & Renner (2012)	B
Weberbauerocereus Backeb.	9	0	0	0	43	52	Arakaki (2003)	E
Weberocereus Britton & Rose	6	1	1	0	19	26	Korotkova & al. (2017)	A
Weingartia Werderm.	20	1	1	0	435	457	Kiesling & al. (2014), Ritz & al. (2007)	B
Xiquexique Lavor, Calvente & Versieux	3	1	1	0	23	28	Lavor & al. (2020)	A
Yavia R. Kiesling & Piltz	1	0	0	0	1	2	Guerrero & al. (2020)	B
Yungasocereus F. Ritter	1	0	0	0	2	3	Hunt (2006)	B
Totals	**1851**	**458**	**288**	**91**	**17,932**	**20,613**		

references for the genera ("sec." references). Discussion notes in the actual checklist provide more detailed information about the current state of knowledge in terms of monophyly or phylogenetic relationships.

Accepted species names and synonyms — A list of all *Cactaceae* names with nomenclatural references used in the World Flora Online backbone based on The Plant List 1.1 (TPL 2013) was received from the WFO Data Centre in February 2018. These 17,531 names had each received a unique WFO-identifier (a unique number) and were to be resolved completely, to be able to reimport the new backbone without disrupting the data linked to the names in the WFO database. The names were converted into a standard format so as to enable cut-and-paste data entry into the EDIT Platform's Taxonomic Editor software, which then automatically parses names and nomenclatural references into the corresponding fully atomized fields in the relational database. Additional names from literature were entered similarly.

Data entry started with those genera for which a phylogeny-based treatment, including a synopsis of species and their synonyms, was available and which therefore could be directly adopted for this backbone.

For the more common cases, where phylogenetic studies establish the circumscription of the genus but do not provide a new taxonomic treatment at the species level, a suitable recent taxonomic work or monograph was used. For genera that lack a sufficient level of phylogenetic robustness or have not been sampled in a phylogenetic study so far, available treatments as detailed below were used to compile the list of species, complemented with more recently described new taxa. Works considered suitable for this purpose were monographs of genera or subgenera or sections, checklists of tribes or genera, lexicographic family-wide treatments, floristic treatments and regional checklists. Among the most important sources in the latter three categories were *The new cactus lexicon* (Hunt 2006), the 3rd edition of the *CITES Cactaceae checklist* (Hunt 2016), the *Catálogo de cactáceas Mexicanas* (Guzmán & al. 2003), the *Cacti of eastern Brazil* (Taylor & Zappi 2004), the *Flora do Brasil* (Flora do Brasil 2020), the *Catálogo de las plantas vasculares de Bolivia* (Kiesling & al. 2014), the *Cactaceae* treatment in the *Flora of North America* (Parfitt & Gibson 2003), the *Opuntioideae* checklist for North and Central America (Hernández & al. 2014) and *Mapping the cacti of Mexico* (Hernández & Gómez-Hinostrosa 2011, 2015). Further references are cited in Table 1 and a complete list of all sec. references used for the checklist can be found in the Supplemental content online (see https://doi.org/10.3372/wi.51.51208) and at http://caryophyllales.org/cactaceae/bibliography.

For many genera, there was more than one suitable reference that could be used, and the final choice of a secundum reference was left to the contributors for the individual genera. When deciding as to which sec. reference would be used for accepted species, priority was given to phylogenetic and taxonomic research published in peer-reviewed journals, monographs, floras, country/regional checklists and family-wide lexicographic treatments. Newer works were often preferred over older works. Taxonomic synopses in non-peer-reviewed journals and amateur journals were used if the editor responsible for the respective genera considered them of sufficient quality, no alternative was available and if the information therein was necessary from a nomenclatural standpoint. Online databases were normally not used as sec. references for accepted taxa but were commonly used for synonyms. Finally, there are several cases where the present checklist implements new generic concepts for the first time, in which cases the respective partial treatment itself is the sec. reference.

Remaining synonyms, unresolved names, and names of uncertain application — Close to 8000 names were included into the backbone after completing the working process as described above, still leaving almost 10,000 names from the WFO backbone. Of those, only 124 represented duplicates or artefacts and three were synonyms applicable to taxa in other families — these cases are reported to WFO for their elimination from the WFO backbone and are not treated any further. The remainder included names that had never been used in a recent treatment, e.g. names in segregate genera not accepted by later authors, names not validly published, names not listed in synonymies and names of hybrids. The vast majority of these names were combinations based on basionyms already covered in the list and were therefore easily resolved through IPNI (2020), Tropicos (2020) and Plants of the World Online (POWO 2019), as well as the original World Flora Online backbone dataset based on The Plant List 1.1 (TPL 2013). Many names published in the 19^{th} century and not listed in either Tropicos or POWO had been included in the monograph of Britton & Rose (1919–1923) and could thus be resolved. The resulting database of 18,686 names was matched with the World Checklist of Vascular Plants (WCVP) received from Royal Botanic Gardens, Kew in December 2019 (WCVP 2019), which resulted in some 4000+ further names, in their majority infraspecific names, that had not been covered in The Plant List or recent monographs, as well as numerous names of artificial hybrids. After identifying misspellings and orthographical variants, these names were also incorporated into the backbone.

For names that could not be classified as belonging to one of the taxa, so-called "pseudotaxa" were created and included in the taxonomic hierarchy immediately underneath the family. This allowed including the names in the database, finding them in searches and indicating their special status.

Four kinds of pseudotaxa were defined: (1) "names of uncertain application", including nomina nuda; (2) names of artificial hybrids (natural hybrids are listed in the core checklist); (3) "unresolved names", including all further names that could not be assigned to one of the preceding categories; and (4) *incertae sedis*, gathering species or subspecies that should probably be accepted, but their placement in a genus is not clear. Under the heading "excluded", are names that could be positively excluded for a certain reason, which is given with the name.

Revision and community input — The initial compilation of the checklist was mainly done by the first author of this publication. After its completion, *Cactaceae* taxonomists, systematists and phylogeneticists were invited to revise the treatments for genera that they were free to select, and most of those invited responded positively. The same approach had also been successfully used before for the *Caryophyllales* genus-level checklist (Hernández-Ledesma & al. 2015).

The revisions encompassed reviewing and adjusting the status of the accepted species names and synonyms, adding potentially missing names, adjusting sec. references used in the respective partial treatment, writing taxonomic notes and, if needed, providing new combinations, validations and typifications. This contribution was the basis to be listed as a co-author of the checklist and of this publication. To facilitate the revision process, a database output was provided as a simple Word file and all revisions and comments were made therein; the changes in the database were subsequently made by the first author. The extent to which the partial treatments had to be revised differed between the different genera and was expectedly higher for genera, for which no up-to-date treatment was available, and therefore the revisions took between several weeks to about two months to complete.

Results

The database — The database created as the result of the aforementioned work is the first comprehensive treatment of the entire family that attempts to consistently document and attribute taxonomic concepts at the species and infraspecific levels. Such a treatment at the species level conforms with the needed basis for the incorporation of new research results and with the needs of users of taxonomic data, such as the global conservation community. As mentioned before, the resulting checklist of taxa and names in the *Cactaceae*, published in the Supplemental content online and on the data portal, is currently restricted to generic, specific and infraspecific ranks. Additional taxonomic data, such as morphological descriptions, identification keys, distribution data, as well as additional nomenclatural information, such as types and type image links for species and infraspecific names, and sources of the nomenclatural status, is so far only available for some taxa and is accessible in the online portal only.

The checklist is divided into the "core checklist" of accepted genera, species and infraspecies, and into a collection of names that were not included in the core for various reasons stated in their "pseudotaxon" heading. No attempt was made to completely compile all effectively published hybrid or horticultural names. Natural hybrids were included in the core checklist, and names of artificial hybrids were listed separately, but only if they appeared in the WFO or Kew WCVP datasets. Admittedly this is still somewhat inconsistent, with artificial hybrids sometimes also listed in the core checklist.

The database currently includes 22,275 scientific names (of any rank and standing). In the core checklist, 2835 names (including the family name) are accepted as correct taxon names, i.e. representing natural taxa excluding artificial hybrids: 150 genera, 1851 species, 91 hybrid species, 458 heterotypic infraspecific taxa (including 2 hybrids) and 288 infraspecific taxa carrying autonyms. 16 names were definitely excluded. 17,932 names are assigned to the taxa of all ranks as synonyms or as designations of no nomenclatural standing (including names not validly published) that are clearly referable to the specific taxon (including later isonyms, nomina nuda or later citations that have been mistaken for original publications). Of these, 596 are marked as being not validly published or otherwise of no nomenclatural standing and 121 are considered illegitimate names (the data portal provides further details available for status designations). Outside the core checklist, there are 454 names that are presently considered to belong to named (probably artificial) hybrids (including 197 of generic rank and 69 synonyms). 389 names are of uncertain application (including 151 mostly nomenclatural synonyms). 672 (including 151 synonyms) are currently listed as unresolved names, i.e. names that could not be clarified with the sources used and need further investigation.

Table 1 provides an overview of all accepted genera with the numbers of species and infraspecific taxa accepted therein, along with the total number of synonyms currently included in the core checklist.

Comparison of different online sources — The Plant List included a total of 17,007 names for the *Cactaceae*, of which 2715 were considered accepted, 8444 synonyms, 1 unplaced and 5847 as unassessed. The WFO dataset, largely based on TPL, listed 17,454 names for the family: 444 at generic rank (158 accepted, 146 synonyms, 140 unchecked); 13,163 at specific rank (2232 accepted, 5418 synonyms, 5510 unchecked and 3 misapplied); and 3520 at infraspecific rank (482 accepted, 3021 synonyms, 343 unchecked).

The Kew-WCVP dataset (as of December 2020) contained 17,046 names: 636 at generic rank (148 accepted, 88 artificial hybrids, 327 synonyms, 73 unplaced); 11,777 at specific rank (1717 accepted, 18 artificial hybrids, 9519 synonyms, 523 unplaced); and 4633 at infraspecific rank (425 accepted, 4206 synonyms, 2 unplaced).

The Plant List will not be further updated *per se*, but the WFO backbone serves as a successor and will be updated using the dataset here provided. Our dataset will also be made available to the authors of the Kew-WCVP dataset in a suitable form for their consideration.

Discussion

The checklist published here is a consensus view of classification at the genus level, with appropriate notes where circumscriptions are ambiguous or contested, as well as the state of current knowledge about the published names in the *Cactaceae*. The online portal is and will be a dynamic standard reference source for the family providing an up-to-date taxonomic backbone and additional data.

The results confirm that compiling a taxonomically consistent list of names in *Cactaceae* is feasible by combining available databases supplemented by published lexica and papers so that previous work done in this respect can be united in a sustainable and updatable information resource. The checklist presented here differs from previous ones (Britton & Rose 1919–1923; Backeberg 1958–1962; Anderson 2001, 2005; Hunt 2006) in several respects. It is the most comprehensive in terms of names covered and information on taxa as currently interpreted. It is online, open access, updatable and sustainable, because there is a declared institutional commitment of the Botanic Garden and Botanical Museum Berlin to the continued hosting and support of its technical base. Likewise, it represents a first attempt to clearly credit the originators of the information, not only the compilers (albeit this still has limits, see below). Therefore, the backbone itself is not *the* "authoritative" source – rather, when using the taxonomic concepts represented by the accepted taxon names, the original taxonomic works indicated as secundum references should be cited.

Assessment of the state of phylogenetic knowledge for genera

Table 1 provides an assessment of the reliability of the generic circumscriptions. Hunt (2006) in *The new cactus lexicon*, attempted a scheme to indicate the reliability of the taxonomy, qualifying the information source as: (A) monograph; (B) regional or partial specimen-based revision; (C) semi-popular handbook/study-group publication and/or older regional treatment; and (D) provisional assessment, often protologue-based. Because most phylogenetic studies based on DNA sequences in *Cactaceae* were published only after 2006, this can now be used as a further indicator. Here we use the extent of the phylogenetic knowledge included in the work as the main indicator of taxonomic stability, using five categories:

- A The genus is monophyletic based on a complete or very comprehensive phylogenetic study, and a phylogeny-based taxonomic synopsis was published, usually together with the phylogenetic study or in a follow-up taxonomic paper by the same authors.
- B The genus is monophyletic based on phylogenetic studies that support the clade based on a sufficiently dense or even complete sampling, or support a monotypic genus as a distinct lineage, but do not provide a new taxonomic treatment at the species level. In many cases, older classical taxonomic synopses or a monographic treatment exist for these genera providing a reliable assessment of the species included.
- C The genus is probably monophyletic, but only some of the species were sampled in phylogenetic studies, too few to reliably establish its monophyly.
- D The genus is polyphyletic, paraphyletic or nested in another genus.
- E No assessment of monophyly has yet been possible, because only a few species were sampled or no phylogenetic study has been conducted so far.

Fig. 1 compares the numbers of genera per category, with encouraging results. Most of the genera have already been included in phylogenetic studies and fall in either category A (21 genera) or category B (84 genera). Therefore, over two-thirds of all *Cactaceae* genera have already been confirmed as monophyletic based on phylogenetic studies.

The recent trend has clearly been reinstating earlier-described genera or segregating small genera based on phylogenetic studies, which consistently recover small clades corresponding to genera and support the many previously published monotypic genera as isolated lineages. Thirty-six genera are monotypic and a further 40 have between two and five species.

Species numbers in *Cactaceae*

The main achievement of this checklist is an updated phylogeny-based, species-level taxonomic backbone. As for the reliability of the overall species number, this varies between different genera and is linked to the taxonomic stability of the genera, as explained above.

The most reliable basis for such a species-level backbone is a phylogeny-based synopsis or monograph (category A). These include 21 genera with 225 species and 37 heterotypic infraspecific taxa, which is slightly above 14% of all *Cactaceae* for which we have this reliable assessment of species diversity. Most genera fall into category B, and while no synopsis was published based on the phylogenetic study, there are often older classical treatments or one of the recent family-wide synopses that provide a rather reliable basis for the species to be included and accepted in these genera. This concerns 84 genera containing 1104 species plus 291 heterotypic infraspecific taxa. So, in terms of species numbers, almost 60% of the family has a solid basis for the accepted species, or 72% if all taxa, including heterotypic infraspecific taxa, are considered.

It is now interesting to compare this checklist with earlier family-wide treatments and estimates of species numbers. Table 2 shows a comparison to the two recent reference works covering the whole family, and notably our results match the treatment of Anderson (2001, 2005) very closely, although the taxa are certainly only partly congruent. Hunt (2006) on the other hand took a much more conservative approach in accepting genera and species.

Many new taxa have been described since 2006: 217 new species, 4 new hybrid species, 101 new subspecies, 35 varieties and 9 forms, yet not all of them are currently accepted here.

Many *Cactaceae* species are known to have a large number of synonyms, mostly resulting from their variability, popularity in collections and a long history of cultivation, and from changing generic concepts and moving species from one genus to another. Table 3 lists the three species with the most synonyms, with *Aylostera pygmaea* (R. E. Fr.) Mosti & Papini being the most extreme example with 256 synonyms in total, but *Melocactus macracanthos* (Salm-Dyck) Link & Otto having the most heterotypic synonyms: 124 homotypic groups in total, compared to only 81 homotypic groups in *A. pygmaea*.

We are aware that estimating species limits using current phylogenetic methods is generally harder than inferring generic limits and that the results of such approaches generally harder to interpret due to individuals of the same species or infraspecific taxon not being resolved as monophyletic. Also, many phylogenetic studies do not include enough individuals to be able to infer species limits in detail. And certainly there are species or species complexes that are not sufficiently understood and require more detailed study. An approach to flag species with the current state of research on species delimitation has been taken by Borsch & al. (2018) for the genus *Iresine* P. Browne (*Amaranthaceae*).

But disregarding the shortcomings, this checklist is not only phylogeny-based, but also expert-revised, making it a reliable source for the species diversity of the *Cactaceae*.

Secundum references

Currently, some ambiguity exists with respect to the secundum references as cited in the checklist. In the EDIT Platform, there are two possibilities to cite references for the context of a taxon: (1) the circumscription reference, coined as the secundum (sec.) reference by Berendsohn (1997), should cite a publication where the circumscription of the taxon or its differentiation from other (related) taxa of the same rank is treated; (2) the placement reference, which is the source for the assignment of an already defined taxon to a place in a given classification (in the core checklist: the placement in a taxonomic group of higher rank). In analogy to (2), the "syn. sec." reference depicts the placement of a name in the synonymy of a taxon, and the "err. sec." reference (not yet used in the *Cactaceae* dataset) is the source of the inclusion of a taxon that has been misnamed in its sec. reference elsewhere (which is then cited as "sensu"). However, in the present state of our data, the sec. reference in some cases represents the source of a name (particularly when the taxonomic position of that name is not yet clear), or the reference for the placement (especially if the placement resulted in a changed name), or even the reference for the source of a name or taxon under one of the categories excluded from the core checklist. Furthermore, the data entry does not at present support multiple sec. references, so the responsible editor must choose one over others that may be equally relevant. These issues are being discussed in the EDIT Platform's user and developer communities and will be solved as soon as possible.

Table 2. Comparison of the numbers of accepted taxa in the two most widely used works and our results.

	Genera	Species + heterotypic infraspecies
Anderson (2005)	145	1882 + 474
Hunt (2006)	124	1438 + 378
This paper	150	1851 + 458

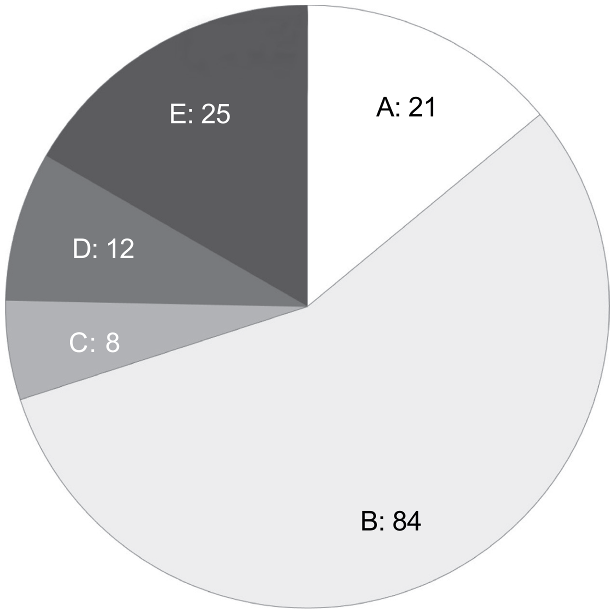

Fig. 1. Comparison of the numbers of genera per category of monophyly and taxonomic robustness. – A: genera that are monophyletic based on a complete or very comprehensive phylogenetic study, and a phylogeny-based taxonomic synopsis was published; B: genera that are monophyletic based on phylogenetic studies that support the clade based on a sufficiently dense or even complete sampling or support a monotypic genus as a distinct lineage; C: genera that are probably monophyletic, but too few of the species were sampled in phylogenetic studies to reliably establish monophyly; D: genera that are polyphyletic, paraphyletic or nested in another genus; E: genera for which no assessment of monophyly has yet been possible, because only a few species were sampled or no phylogenetic study has been conducted so far. See the Discussion for a more detailed explanation of these categories.

Table 3. Species with the most synonyms.

Aylostera pygmaea (R. E. Fr.) Mosti & Papini	256 synonyms	81 homotypic groups
Melocactus macracanthos (Salm-Dyck) Link & Otto	131 synonyms	124 homotypic groups
Aylostera deminuta (F. A. C. Weber) Backeb.	123 synonyms	61 homotypic groups

Future work, interaction with the World Flora Online and some technical aspects

As a joint community effort within the *Caryophyllales* Network, the taxonomic backbone for *Cactaceae* will be continuously updated according to newly published results of phylogenetic and taxonomic research and with respect to further names that may be found in obscure and hard-to-get historical publications once they become digitized and freely available. The addition of further nomenclatural information, such as links to protologues and to images of type specimens, will be an ongoing task. Also, further work on the currently unresolved names is needed.

The backbone serves as a very useful tool for future monographic and floristic treatments, because taxonomic and nomenclatural decisions accumulate and do not have to be entered anew, and the output from the EDIT Platform can be taken as a baseline. It is also planned to provide the output from this database to other providers of taxonomic or nomenclatural data, especially those that have directly or indirectly contributed to the data (Kew WCVP, Tropicos). Providing data to the Catalogue of Life (https://www.catalogueoflife.org/) is planned as well and will be done through WFO.

Outputs in various formats are possible from the EDIT Platform database. One of them, the so-called CDM-light format (Luther & al. 2019), consists of a series of interrelated, comma-separated value (CSV) tables that, e.g., provided the base for the statistics drawn from the data and for the transformation of the data into the formatted checklist published here in the Supplemental content online. The document-type output also greatly facilitates input from collaborators who do not interact directly with the database. Another platform output format follows the standard Darwin Core Archive format defined by the WFO consortium, so that a pipeline from the *Caryophyllales* Taxonomic Expert Network to the WFO database is established. The checklist data will be provided to the WFO gatekeeper as a replacement of the current, TPL-based taxonomic backbone for the WFO portal. As part of the *Caryophyllales* Network's responsibilities as a Taxonomic Expert Network for WFO, all previously used WFO name IDs were revised, and 4695 new IDs were assigned to names that were not previously present. This will also allow future straightforward input and machine-readable interaction with WFO. Specific outputs can be requested from the *Caryophyllales* secretariat at caryophyllales@bgbm.org.

The EDIT Platform also allows entering further information that can be associated with a taxon, such as morphological descriptions, specimens and specimen descriptions, molecular data, photographs, common names, etymology, chromosome counts, anatomical information, state of conservation, etc.

The first species-level taxonomic backbone treatment that was completed in the context of the *Caryophyllales* initiative was that for *Nepenthaceae* (176 spp.) (Berendsohn & al. 2018; *Caryophyllales* Network 2015+; http://caryophyllales.org/nepenthaceae/home). In comparison to the present *Cactaceae* treatment, the *Nepenthaceae* treatment exemplifies the additional inclusion of descriptive and other monographic information. A possible further goal for *Cactaceae* would be to add distribution data, first at TDWG level (https://www.tdwg.org/), which are currently exemplarily available in the portal for the *Rhipsalideae* only. The ultimate aim is to provide referenced information for distributions, either by means of area records, as exemplified by the Euro+Med PlantBase (Korotkova & Raab-Straube 2017+) or by means of voucher specimens. Distribution data for *Cactaceae* are available at the country level in basically all family-level synopses and on a finer scale in floras, regional treatments and synopses. Species-level distribution maps based on such literature sources have also already been published for the whole family (Barthlott & al. 2015). Hence, literature data already contain area records for the whole family, which can be added to the backbone in the future. This can be complemented by links to global aggregators of species occurrence data, such as GBIF (https://www.gbif.org/). However, distribution information for taxa with a defined concept considering expert-revised voucher and/or publication information will continue to provide the most reliable source for, e.g., decision-making in conservation.

Such goals will also require further development of the collaborative workflows in taxonomy and their required technical bases. For example, linking and integrating flora treatments with global monographs is one of the principal challenges for the botanical community and a major research topic in biodiversity informatics.

As for the mechanisms of future updates, we intend to keep it as up-to-date as possible. There are no specific cycles of review planned, but the checklist will be updated whenever necessary and IPNI will be checked periodically for new names. The database output will also be published at irregular intervals as a citable PDF publication with a DOI through BGBM-Press (https://www.bgbm.org/en/publikationen-publications).

Experts on *Cactaceae* are invited to contribute as editors in the future. It is important to emphasize that this *Cactaceae* backbone is, and must remain, a community work.

Nomenclatural novelties

Acanthocalycium rhodotrichum subsp. ***chacoanum*** (Schütz) Schlumpb., **comb. nov.** ≡ *Echinopsis chacoana* Schütz in Kaktusář. Listy 17: 1. 1949.

Acanthocalycium thionanthum subsp. ***ferrarii*** (Rausch) Schlumpb., **comb. nov.** ≡ *Acanthocalycium ferrarii* Rausch in Succulenta (Netherlands) 55: 82. 1976.

Cochemiea hutchisoniana subsp. ***louisae*** (G. E. Linds.) Majure, **comb. nov.** ≡ *Mammillaria louisae* G. E. Linds. in Cact. Succ. J. (Los Angeles) 32: 169. 1960.

Consolea millspaughii subsp. ***corallicola*** (Small) Majure, **comb. nov.** ≡ *Consolea corallicola* Small in Addisonia 15: 25. 1930.

Cylindropuntia perrita (Griffiths) Majure, **comb. nov.** ≡ *Opuntia perrita* Griffiths in Rep. Missouri Bot. Gard. 22: 33. 1911.

Echinopsis aurea subsp. ***leucomalla*** (Wessner) Schlumpb., **comb. nov.** ≡ *Lobivia leucomalla* Wessner in Beitr. Sukkulentenk. Sukkulentenpflege 1938: 1. 1938.

Echinopsis tubiflora subsp. ***callochrysea*** (F. Ritter) Schlumpb., **comb. & stat. nov.** ≡ *Hymenorebutia aurea* var. *callochrysea* F. Ritter, Kakteen Südamerika 2: 468. 1980.
Note — This taxon was long seen as part of the *Echinopsis aurea* Britton & Rose complex, although it grows further north and isolated from the distribution area of *E. aurea*. It resembles *E. tubiflora* (Pfeiff.) Zucc. ex A. Dietr., with which it grows at least partly in sympatry, but differs from it in having yellow, diurnal and nectarless flowers. Molecular data suggest a close relationship to *E. tubiflora* (Schlumpberger & Renner 2012). [B. Schlumpberger]

Kadenicarpus heliae (García-Mor., Díaz-Salím & Gonz.-Bot.) D. Aquino, **comb. nov.** ≡ *Turbinicarpus heliae* García-Mor., Díaz-Salím & Gonz.-Bot. in Xerophilia 8(1): 3. 2015.
Note — With the recognition of *Kadenicarpus* Doweld by Vázquez-Sánchez & al. (2019), the inclusion of this taxon in this genus is proposed and the necessary new combination provided here. [D. Aquino]

Leucostele atacamensis subsp. ***pasacana*** (F. A. C. Weber ex Rümpler) Schlumpb., **comb. nov.** ≡ *Pilocereus pasacanus* F. A. C. Weber ex Rümpler, Handb. Cacteenk.: 678. 1885.

Leucostele chiloensis subsp. ***australis*** (F. Ritter) Schlumpb., **comb. nov.** ≡ *Trichocereus chiloensis* var. *australis* F. Ritter, Kakteen Südamerika 3: 1108. 1980.

Leucostele chiloensis subsp. ***eburneus*** (Phil. ex K. Schum.) Schlumpb., **comb. nov.** ≡ *Eulychnia eburnea* Phil. ex K. Schum., Gesamtbeschr. Kakt.: 59. 1897.

Leucostele chiloensis subsp. ***panhoplites*** (K. Schum.) Schlumpb., **comb. nov.** ≡ *Cereus chiloensis* var. *panhoplites* K. Schum., Gesamtbeschr. Kakt.: 63. 1897.

Leucostele faundezii (Albesiano) Schlumpb., **comb. nov.** ≡ *Trichocereus faundezii* Albesiano in Haseltonia 18: 128. 2012.

Leucostele pectinifera (Albesiano) Schlumpb., **comb. nov.** ≡ *Trichocereus pectiniferus* Albesiano in Haseltonia 18: 133. 2012.

Leucostele undulosa (Albesiano) Schlumpb., **comb. nov.** ≡ *Trichocereus undulosus* Albesiano in Haseltonia 18: 136. 2012.

Lobivia bridgesii subsp. ***vallegrandensis*** (Cárdenas) Schlumpb., **comb. nov.** ≡ *Echinopsis vallegrandensis* Cárdenas in Cactus (Paris) 64: 163. 1959.

Lobivia bridgesii subsp. ***yungasensis*** (F. Ritter) Schlumpb., **comb. nov.** ≡ *Echinopsis yungasensis* F. Ritter, Kakteen Südamerika 2: 631. 1980.

Pilosocereus armatus (Otto ex Pfeiff.) A. R. Franck, **comb. nov.** ≡ *Cereus armatus* Otto ex Pfeiff., Enum. Diagn. Cact.: 81. 1837.
Note — The earliest available basionym for the *Pilosocereus* Byles & G. D. Rowley cacti of Puerto Rico and the Virgin Islands appears to be *Cereus armatus*. The protologue of *C. armatus* described the stems as "vix glaucescens", which may pertain to cultivated young plants or stressed or older stems that are sometimes not as bluish glaucescent as are mature, vigorous stems. The use of *P. royenii* (L.) Byles & G. D. Rowley for these plants by Franck & al. (2019) cannot be followed because it overlooked the designation of neotype for *Cactus royenii* L. made by Mottram (2013). Both the neotype and the protologue of *C. royenii* (Linnaeus 1753) are ambiguous with regard to provenance and precise identity. [A. R. Franck]

Rapicactus zaragosae (Glass & R. A. Foster) D. Donati ex D. Aquino, **comb. nov.** ≡ *Gymnocactus subterraneus* var. *zaragosae* Glass & R. A. Foster in Cact. Succ. J. (Los Angeles) 50: 283. 1978 – *Rapicactus zaragosae* (Glass & R. A. Foster) D. Donati in Revis. Tasson. Gen. Turbinicarpus: 6. 2003, nom. inval.

Rhipsalis rhombea (Salm-Dyck) Pfeiffer, Enum. Diagn. Cact.: 130. 1837 ≡ *Cereus rhombeus* Salm-Dyck, Cact. Hort. Dyck.: 341. 1834. – **Neotype (designated here):** ex hort. BG Bonn Acc. No. 4477, pseudo Rauh No. 35834, ex collection Dr. Friedrich (B 10 0525912 !; isoneotypes: B 10 0676801 !, B 10 0676802 !).

Note — The original neotypification of *Rhipsalis rhombea* made by Bauer & Korotkova (2020) was ambiguous, because an incorrect B specimen barcode (B 10 0525909) was cited along with the designation of the neotype, while the correct barcodes were cited only in the appendix, also referring to them as neotypes. Under a strict application of the *Code*, the neotype cannot be considered as effectively designated and we therefore correct this error here. [R. Bauer & N. Korotkova]

Rhipsalis trigonoides (Doweld) N. Korotkova, **comb. nov.** ≡ *Hylorhipsalis trigonoides* Doweld in Sukkulenty 4(1–2): 38. 2002 [“2001”].
Note — The neotypification of *Rhipsalis trigona* Pfeiff. by Barthlott & Taylor (1995: 54) was rejected by (Doweld 2002b: 38) because of the “serious conflict with the protologue of the species”, Pfeiffer’s plant supposedly being a *Lepismium* Pfeiff., as mentioned by Pfeiffer himself and by Barthlott & Taylor. Doweld therefore proposed *Hylorhipsalis trigonoides* as the name of a new species based on the specimen that Barthlott & Taylor had designated as the neotype of *R. trigona*. Because *Hylorhipsalis* Doweld, a genus he segregated from *Rhipsalis* Gaertn. is not accepted, and this species has no other validly published names in *Rhipsalis*, a new combination is provided here. [N. Korotkova]

Selenicereus costaricensis (F. A. C. Weber) S. Arias & N. Korotkova, **comb. nov.** ≡ *Cereus trigonus* var. *costaricensis* F. A. C. Weber in Bull. Mus. Hist. Nat. (Paris) 8: 457. 1902 – *Selenicereus costaricensis* (F. A. C. Weber) S. Arias & N. Korotkova in Phytotaxa 327: 25. 2017, nom. inval. – **Lectotype (designated here):** [illustration] “*Cactus triangularis* L. Pitahaya à San José” in Tonduz [Herborisations au Costa-Rica III] in Bull. Herb. Boissier 4: planche 2. 1896 [https://www.biodiversitylibrary.org/page/33638575].
Note — The illustration designated here as the lectotype was cited in the protologue of *Cereus trigonus* var. *costaricensis*. [S. Arias & N. Korotkova]

Soehrensia formosa subsp. ***kieslingii*** (Rausch) Schlumpb., **comb. nov.** ≡ *Lobivia kieslingii* Rausch in Kakteen And. Sukk. 28: 249. 1977.

Soehrensia formosa subsp. ***korethroides*** (Werderm.) Schlumpb., **comb. nov.** ≡ *Echinopsis korethroides* Werderm. in Backeberg, Neue Kakteen: 84. 1931.

Soehrensia formosa subsp. ***randallii*** (Cárdenas) Schlumpb., **comb. nov.** ≡ *Trichocereus randallii* Cárdenas in Cact. Succ. J. (Los Angeles) 35: 158. 1963.

Soehrensia formosa subsp. ***rosarioana*** (Rausch) Schlumpb., **comb. nov.** ≡ *Lobivia rosarioana* Rausch, Kakteen And. Sukk. 30: 284. 1979.

Soehrensia huascha subsp. ***robusta*** (Rausch) Schlumpb., **comb. nov.** ≡ *Lobivia huascha* var. *robusta* Rausch, Lobivia 85: 141, 72. 1987.

Soehrensia ×mendocina (Méndez) Schlumpb., **comb. nov.** ≡ *Trichocereus ×mendocinus* Méndez in Hickenia 3: 73. 2000.
Note — *Soehrensia candicans* (Gillies ex Salm-Dyck) Schlumpb. × *S. strigosa* (Salm-Dyck) Schlumpb.

Soehrensia sandiensis (Hoxey) Schlumpb., **comb. nov.** ≡ *Echinopsis sandiensis* Hoxey in Bradleya 34: 195. 2016.

Soehrensia serpentina (M. Lowry & M. Mend.) Schlumpb., **comb. nov.** ≡ *Echinopsis serpentina* M. Lowry & M. Mend. in CactusWorld 29(2): 95. 2011.

Soehrensia shaferi (Britton & Rose) Schlumpb., **comb. nov.** ≡ *Trichocereus shaferi* Britton & Rose, Cactaceae 2: 144. 1920.

Soehrensia tarijensis subsp. ***bertramiana*** (Backeb.) Schlumpb., **comb. nov.** ≡ *Trichocereus bertramianus* Backeb. in Blätt. Kakteenf. 1935(6): 2, genus 51, sp. 2. 1935.

Strophocactus sicariguensis (Croizat & Tamayo) S. Arias & N. Korotkova, **comb. nov.** ≡ *Acanthocereus sicariguensis* Croizat & Tamayo in Bol. Soc. Venez. Ci. Nat. 11: 75. 1947 – *Strophocactus sicariguensis* (Croizat & Tamayo) S. Arias & N. Korotkova in Phytotaxa 327: 33. 2017, nom. inval.
Note — This new combination was not validly published in 2017 because only an indirect reference to the basionym was given through the citation of the place of publication of the combination *Pseudoacanthocereus sicariguensis* (Croizat & Tamayo) N. P. Taylor. [S. Arias & N. Korotkova]

Turbinicarpus valdezianus (H. Moeller) Glass & R. A. Foster in Cact. Succ. J. (Los Angeles) 49: 174. 1977 ≡ *Pelecyphora valdeziana* H. Moeller in Deutsche Gärt.-Zeitung 45: 179, 207. 1930.
= *Pelecyphora plumosa* Boed. & Ritter in Monatsschr. Deutsch. Kakteen-Ges. 2: 116. 1930. – **Lectotype (designated here):** [illustration] “*Pelecyphora plumosa* Boed. sp. n. $^5/_4$ nat. Grösse.” in Bödeker in Monatsschr. Deutsch. Kakteen-Ges. 2: 117. 1930. [D. Aquino]

Turbinicarpus ysabelae (Schlange) John & Říha in Repert. Pl. Succ. 19: 22. 1983 ≡ *Thelocactus ysabelae* Schlange in Cact. Succ. J. (Los Angeles) 5: 551. 1934. – Type: Mexico, San Luís Potosí, Rancho El Vergel, on the railroad between Cd San Luís Potosí and Tampico, *A. F. Moeller s.n.* (not preserved). – **Lectotype (designated here):** [illustration] “*Thelocactus ysabelae* sp. nov.” in Schlange in Cact. Succ. J. (Los Angeles) 5: 551. 1934. [D. Aquino]

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Contribution of authors

All authors have contributed to the writing of the manuscript.

Data compilation editors — Nadja Korotkova (main editor and compiler), Walter G. Berendsohn (name matching with contributed datasets, nomenclatural issues, data quality control, generation of formatted documents from output from the EDIT Platform, editorial guidelines)

Taxonomic information

David Aquino: *Epithelantha*, *Kadenicarpus*, *Rapicactus*, *Turbinicarpus*

Salvador Arias: *Acanthocereus*, *Aporocactus*, *Astrophytum*, *Bergerocactus*, *Cephalocereus*, *Disocactus*, *Marshallocereus*, *Nyctocereus*, *Pachycereus*, *Peniocereus*, *Pereskiopsis*, *Selenicereus*, *Stenocereus*, *Strophocactus*

Urs Eggli: *Aylostera*, *Blossfeldia*, *Rebutia*, *Weingartia*, partial quality control of unresolved names

Alan R. Franck: *Cereus*, *Estevesia*, *Harrisia*, *Pilosocereus*, *Stenocereus*, *Xiquexique*

Pablo C. Guerrero: *Copiapoa*, *Eriosyce*, *Eulychnia*, *Rimacactus*

Héctor M. Hernández & Carlos Gómez-Hinostrosa: *Acanthocereus*, *Acharagma*, *Ariocarpus*, *Astrophytum*, *Aztekium*, *Bergerocactus*, *Cumarinia*, *Cylindropuntia*, *Echinocactus*, *Escontria*, *Grusonia*, *Lophophora*, *Mammillaria* p.p., *Melocactus* p.p., *Myrtillocactus*, *Neolloydia*, *Opuntia* p.p., *Peniocereus* p.p., *Sclerocactus*, *Thelocactus*, *Turbinicarpus* p.p.

Matias Köhler: *Airampoa*, *Brasiliopuntia*, *Opuntia* p.p., *Salmonopuntia*, *Tacinga*

Nadja Korotkova: *Deamia*, *Disocactus*, *Epiphyllum*, *Hatiora*, *Kimnachia*, *Lepismium*, *Leuenbergeria*, *Lymanbensonia*, *Pereskia*, *Pfeiffera*, *Pseudorhipsalis*, *Rhipsalidopsis*, *Rhipsalis*, *Schlumbergera*, *Selenicereus*, *Strophocactus*, *Weberocereus*

Lucas C. Majure: *Cochemiea*, *Consolea*, *Coryphantha*, *Cumarinia*, *Cylindropuntia*, *Grusonia*, *Kroenleinia*, *Leptocereus*, *Melocactus*, *Micropuntia*, *Opuntia* p.p.

Detlev Metzing: *Frailea*, *Gymnocalycium*, various other genera

Reto Nyffeler: *Parodia*

Daniel Sánchez: *Echinocereus*

Boris Schlumpberger: *Acanthocalycium*, *Echinopsis*, *Leucostele*, *Lobivia*, *Reicheocactus*, *Setiechinopsis*, *Soehrensia*, *Trichocereus*

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