Phytotaxa 550 (2): 079–098
https://www.mapress.com/pt/
Copyright © 2022 Magnolia Press

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.550.2.1

Towards a unified taxonomic catalogue for the Chilean cacti: assembling molecular systematics and classical taxonomy

HELMUT E. WALTER[1,5] & PABLO C. GUERRERO[2,3,4,6,*]
[1]*The EXSIS Project: Cactaceae Ex-Situ & In-Situ Conservation, 31860, Emmerthal, Germany.*
[2]*Departamento de Botánica, Facultad de Ciencias Naturales & Oceanográficas, Universidad de Concepción, Casilla 160C, Concepción, Chile.*
[3]*Institute of Ecology and Biodiversity (IEB), Victoria 631, Barrio Universitario, Concepción, Chile.*
[4] *Millennium Institute Biodiversity of Antarctic and Sub-Antarctic Ecosystems (BASE), CP 7800003, Santiago, Chile.*
[5] *hw582133@gmail.com; https://orcid.org/0000-0001-8614-0159*
[6] *pabloguerrero@udec.cl; https://orcid.org/0000-0003-1034-1899*
**Author for correspondence*

Abstract

The competition between floristic catalogues and the nomenclatural issues of the treated taxa, is a problem for the botanical knowledge of countries. Consequently, it seems to be necessary to merge former taxonomical proposals into a unified list based on phylogenetic hypotheses, the rules of nomenclature and dichotomous keys to the Chilean subfamilies, tribes and genera. With this approach we here propose an updated catalogue of the Chilean cacti. It would be necessary to merge the various taxonomic proposals into a unified list based on both phylogenetic hypotheses and the rules of nomenclature. With this approach, we here propose to updated the catalogue of Chilean cactus. A neotype was designated for *Echinocactus jussieui*. In addition, we present a dichotomous taxonomic key to the Chilean subfamilies, tribes, and genera.

Keywords: Cactaceae, Caryophyllales, Flora of Chile, succulents, taxonomy, typification

Resumen

La competencia entre los catálogos florísticos y la inestabilidad de nomenclatura de los taxones tratados, es un problema para el conocimiento botánico de los países. Es necesario fusionar las distintas propuestas taxonómicas en una lista unificada basada tanto en las hipótesis filogenéticas como en las reglas de nomenclatura. Con este enfoque, aquí proponemos actualizar el catálogo de cactus chilenos. Se designa un neotipo para *Echinocactus jussieui*. Además, presentamos una clave taxonómica dicotómica de las subfamilias, tribus y géneros chilenos.

Palabras clave: Cactaceae, Caryophyllales, Flora de Chile, suculentas, taxonomía, tipificación

Introduction

National lists of species are key pieces of information of biodiversity as they become part of the heritage of nations and are used by stakeholders in public policies such as conservation and land-use planning. However, the task of obtaining lists of stable species taxonomy over time can be arduous, since it is influenced by several factors (e.g., morphological convergence, hybridization, different stages of speciation, among others). The uncertainty of taxonomic classifications decreases when the information from molecular and morphological data decants into a list of nomenclatural valid names and represents natural units (see e.g. "dual" concept *sensu* Bregnan 2002). Some biological groups show a high uncertainty due to the exacerbated generation of new taxa, as is the case of cacti that run into > 13 thousand published specific names (WFO 2021), while it is estimated that the number of species amounts to approximately 1.800 (Nyffeller & Eggli 2010).

Accepted by Duilio Iamonico: 8 May 2022; published: 14 Jun. 2022

The taxonomic treatment of the family Cactaceae Juss. in the modern *Flora of Chile Initiative* (Marticorena & Rodríguez 2011) aims at stabilizing the classification of the Chilean cacti based on the compilation of molecular phylogenies and morphological data taken from literature and field work, broader inclusion of historically published names (i.e. the inclusion of taxa banned to synonymy by previous authors or not accepted new taxa). We here compare two taxonomic works [the widely used work Hunt *et al.* (2006, 2013, 2016) and Rodríguez *et al.* (2018)] with the Flora of Chile. These catalogues only list "accepted species" but do not include keys at species-level and detailed arguments about the taxonomic decisions. Both classifications are mainly based on morphological similarities, but not on a phylogenetic- and molecular-based perspective. A concept on this basis must be regarded as highly subjective and instable (Bregman 2002). Moreover, similarities among taxa may be due to convergent evolution caused by similar micro-climates and hybridization (Guerrero *et al.* 2019a, Merklinger *et al.* 2020). Additionally, a conservative trend towards broad circumscriptions of genera (e.g. *Opuntia* Mill. s.l., *Echinopsis* Zucc. s.l.), and especially, of broadly circumscribed species (so-called "species complexes") resulted in an inflationary use of the rank of subspecies and varieties or in a wave of synonymization of formerly published species (Hoffmann 1989, Kattermann 1994, Anderson 2001, Hoffmann & Walter 2004, Hunt *et al.* 2006, 2013, Rodríguez *et al.* 2018). Yet, with the development of molecular tools, the use of efficient analytical methods (Nyffeler & Eggli 2010), a much broader sampling (see Schlumpberger & Renner 2012, Larridon *et al.* 2015, Guerrero *et al.* 2019b, Merklinger *et al.* 2021), the inclusion of recently published new taxa not accepted by Kattermann (1994), Hunt *et al.* (2006, 2013), Hunt (2016), and Rodríguez *et al.* (2018), the majority of these conservative concepts were not corroborated by molecular data (Nyffeler & Eggli 2010, Schlumpberger & Renner 2012, Ritz *et al.* 2012, Larridon *et al.* 2015, 2018a,b, Guerrero *et al.* 2019b). As a consequence, many previously published taxa banned to synonymy had to be reinstalled and taxa formerly treated as subspecies or varieties had to be upgraded in rank, if molecular-based phylogenetic analyses indicated that taxa previously placed in a species-complex did not cluster with the "super-species" (Larridon *et al.* 2015, 2018a,b, Guerrero *et al.* 2019b, Guerrero & Walter 2019, Tables 2–7). Fourteen species-complexes in the genera *Copiapoa* Britton & Rose*, Cumulopuntia* F. Ritter, *Eriosyce* (Phil.), *Eulychnia* (Phil.), and *Maihueniopsis* Speg. (but see Hunt 2016) were split (see in the text below, Tables 3–7 and list of species). The taxonomic treatment here presented will be used to update the Catálogo de las plantas vasculares de Chile (Rodríguez *et al.* 2018).

Material and methods

The here proposed classification of Chilean Cactaceae follows phylogeny-based taxonomic treatments by i.e. Wallace & Dickie (2002); Nyffeler (2002); Edwards, Nyffeler & Donogue (2005); Nyffeler & Eggli (2010); Ritz *et al.* 2012; Schlumpberger & Renner (2012), Larridon (2015, 2019), Guerrero *et al.* (2019b) as well as classical morphology-based taxonomic works, i.e. Britton & Rose (1922); C. Backeberg (1958-62); F. Ritter (1980); Hoffmann (1989); Kattermann (1994); Hoffmann & Walter (2004); Hunt (2006, 2013, 2016). Further, we reviewed papers published in specialized journals such as *CactusWorld*, *Bradleya*, *Englera*, *Willdenowia*, *Haseltonia*, and *The Cactus Journal* among others.
All accepted taxa indicated by Hunt *et al.* (2006, 2013, 2016) and Rodríguez *et al.* (2018) were merged in a new proposal by using phylogeny-based studies to fit the primary principle of monophyly in an updated taxonomic classification (Stuessy 2009). The taxonomic studies concept is provided in the text to support our classification proposal.

Results and discussion

The relevance of classifying the Cactaceae family into different subfamilies helps to better understand the subdivision into clades that differ morphologically (see key below). On the other hand, the delimitation of some subfamilies has shown to been difficult (for example the paraphyly of the Pereskioideae K.Schum. and the ambiguous relationships of the Maihuenioideae P.Fearn with other subfamilies). Also, the tribes within the Opuntioideae K.Schum. and Cactoideae Eaton have undergone several changes, as molecular-based phylogenies provided new information about evolutionary relationships of its members. Most of the proposed changes at these taxonomic levels have an impact on the classification of Chilean cacti because the cactus flora in the Atacama Desert, the Altiplano, the Mediterranean area, and the Chilean Patagonian steppe harbours three of the four subfamilies and seven of the ten tribes.

1. Stems with functional leaves, at least on immature shoots; a 739 bp non-coding intron region in the chloroplast-encoded gene *rpo*C1 present 2
- Stems without functional leaves; a 739 bp non-coding intron region in the chloroplast-encoded gene *rpo*C1 is lost (subfam. Cactoideae) 3
- Stems without functional leaves; a 739 bp non-coding intron region in the chloroplast-encoded gene *rpo*C1 is lost (*Subfamily CACTOIDEAE*) 10
2. Leaves persistent, terete; glochids on areoles absent; seeds without funicular envelope; stems astomatous, barky ... (subfam. Maihuenioideae) .... **12. Maihuenia**
- Leaves ephemeral, flat; areoles with spines and glochids; seeds encased in a funicular envelope; stems stomatous, bark formation delayed (subfam. Opuntioideae) 4
4. Branch segments flat to subterete; shrubs to 20 cm high **22.Tunilla**
- Segments cylindric; shrubs to 1.5 m high .... **14. Miqueliopuntia**
3. Branches flattened to subterete or cylindric .... Tribe OPUNTIEAE
- Branch segments never flattened, terete in cross-section 5
5. Shrubs to 60 cm high, then mound-forming; segments to 10 cm, with determinate growth; spines without sheath .... TEPHROCACTEAE (pro parte)
- Shrubs to 1.5 m; branch segments to 30 cm, with indeterminate growth; spines with a papery sheath (CYLINDROPUNTIEAE) .... **6. Cylindropuntia**
6. Flowers dark red; petaloids few, <10; fruits 1cm, dark red, glabrous, pulp red .... **21. Tephrocactus** (*nigrispinus*)
- Flowers not dark red; petaloids >10; fruits 2–5 cm, greenish yellow, not glabrous, pulp never red 7
7. Seeds laterally compressed; perisperm large 8
- Seeds ± globose; perisperm small 9
8. Flowers immersed into apex; funicular girdle of seed formed into a papery wing .... **17. Pterocactus**
- Flowers not immersed; seeds not winged .... **13. Maihueniopsis**
9. Segments ±globose, etuberculate, easily detaching; spines on segments and fruits < 5cm; areoles evenly distributed; fruits subglobose; seeds lack lateral ridges .... **20. Sphaeropuntia**
- Segments ±conical, tuberculate; not detaching; spines much longer; areoles crowded towards apex; fruits cylindric; lateral ridges present .... 5**. Cumulopuntia**
10. Hypanthium shorter than pericarpel; stems always cylindric (PHYLLOCACTEAE subtribe CORRYOCACTINAE) 11
- Hypanthium longer than pericarpel; stems cylindric or not 13
11. Plants low, branches 10–50 cm; central spines <4 cm; flowers with few small bracts; fruits 2-5 cm .... 1**. Austrocactus**
- Plants tall, 0.8–5 m; central spines longer, to 15 cm; flowers densely covered with large bracts; fruits 5–10 cm 12
12. Flowers to 7 cm, whitish, narrow funnelform .... **8. Eulychnia**
- Flowers 8–11 cm, yellow, campanulate .... **4. Corryocactus**
13. Stems ±globose to elongating, small to medium-sized; flowers 1.5-6 cm; fruits never with pulp 14
- Stems cylindric, (subcylindric in *Lobivia ferox*), mostly tall; flowers large,7-18 cm; fruits with pulp or pulpless (CEREEAE) ... 17
14. Fruit dehiscing apically, funiculi juicy at fruit maturity (seed ant-dispersed) (INCERTAE SEDIS) .... **3. Copiapoa**
- Fruit dehiscion not as above; funiculi dry at fruit maturity (seed not ant-dispersed) (Tribe NOTOCACTEAE) 15
15. Flowers 2–7 cm, bract scales numerous, axils woolly and bristly; fruit always dehiscing basally (except for *Eriosyce rodentiophila*) .... **7. Eriosyce**
- Flowers small, to 2 cm, bract scales few, axils naked; fruit dehiscence lateral or basal 16
16. Stems 1–3 cm, areoles subtended by tiny persistent leaf; fruits elongating to 3 cm, dehiscing basally .... **18. Rimacactus**
- Stems to 15 cm diam., leaf absent; fruits <1 cm, dehiscing laterally .... **15. Neowerdermannia**
17. Flower scales large, fleshy, imbricate; axils naked; stems with densely branched crown (subtribe REBUTIINAE).. **2. Browningia**
- Flower scales small, not fleshy, not imbricate; axils with ± wool (subtribe TRICHOCEREINAE) 18
18. Flowers brightly carmine red, zygomorphic; fruits without pulp, dehiscing basally .... **6. Oreocereus**
- Flowers never carmine red, actinomorphic; fruits, with pulp never dehiscing basally 19
19. Stamens inserted in a single series; fruits indehiscent .... 9**. Haageocereus**
- Stamens inserted in two series; fruits dehiscent 20
20. Plants >0.5 m, branches columnar or thickly cylindric 21
- Plants <50(-70) cm, globose, elongating with age .... **11. Lobivia**[*ferox*]
21. Plants ±branching, shrubby or treelike; flowers narrowly funnelform, whitish .... **10. Leucostele**
- Plants usually unbranched, thickly cylindric; flowers campanulate, yellow .... **19. Soehrensia**

The comparison of the taxonomic classifications shows that there are important differences in the number of Chilean genera and species (Table 1). Hunt's classification (2006, 2013, 2016) includes the lowest number of species (95), whereas Rodríguez *et al.* (2018) reports the lowest number of genera (17). The percentage of endemic species also varies: 73% by Hunt *et al.* (2006, 2013, 2016), 74% by Rodríguez *et al.* (2018), 81% in the present study. These results highlight the importance of updating the taxonomic classifications in the Flora of Chile, because underestimating the endemism and number of species may have major negative effects on conservation (see e.g., Mace 2004, Duarte *et al.* 2014). The number of species accepted here means that the Cactaceae represent 6% of the Chilean native angiosperms and 5% of endemic species of Chile (Rodríguez *et al.* 2018).

TABLE 1. Taxonomic diversity of the Chilean cacti according to three classifications.

	Hunt (2013, 2016)	**Rodríguez *et al.* (2018)**	**Present study**
Genera	20	17	22
Species	95	102	134
Infraspecific taxa	124	129	143
% endemism at species level	73%	74%	81%

Chilean Maihuenioideae ("Maihuenias")

The monogeneric subfamily Maihuenioideae is widely accepted, although its position within the Cactaceae is still not clear. Nyffeler & Eggli's (2010) reported the subfamily in a polytomy with the Opuntioideae and Cactoideae. On the other hand, Maihuenioideae appears to be basal and sister of the rest of the Cactaceae in Griffith & Porter (2009). Nyffeler (2002) indicated Maihuenioideae as sister to the Opuntioideae, but in Edwards *et al.* (2005), Moore *et al.* (2017), Walker *et al.* (2018) and Arakaki *et al.* (2011) Maihuenioideae and Opuntioideae appear as sister of the Cactoideae. Finally, in Hernández-Hernández *et al.* (2011) *Maihuenia* (Phil. ex F.A. C. Weber) K.Schum. is placed between the Caribbean *Pereskia nychlidiflora* DC. and the Andean *Pereskias* Mill. such as *P. diaz-romeroana* Cárdenas, *P. aculeata* Mill., and *P. weberiana* K.Schum. Barcenas *et al.* (2011) placed Maihuenioideae between Opuntioideae and Cactoideae. Since the position of the Maihuenioideae is not resolved, we follow the middle-way concept of Nyffeler & Eggli (2010). Both members of the Maihuenioideae are native to Chile and Argentina.

Chilean Opuntioideae: a mainly andean clade

The subfamily Opuntioideae is well supported by molecular data (Wallace & Dickie 2002, Edwards *et al.* 2005, Barcenas *et al.* 2011, Hernández-Hernández *et al.* 2011, Majure *et al.* 2012, Moore *et al.* 2017, Walker *et al.* 2018) and includes the following three tribes, but issues in tribal delimitation arised, as several phylogenetic analyses remain unresolved for lack of sufficient taxon sampling.

Tribe Cylindropuntieae Doweld:—The only species in this tribe occurring in Chile [*Cylindropuntia tunicata* (Lehmann) Knuth] has been introduced from Northern Mexico and Arizona.

Tribe Opuntieae:—The membership of the two Chilean genera (*Miqueliopuntia* Frič ex F.Ritter and *Tunilla* D.Hunt & Iliff) in the Opuntieae is corroborated by various studies (e.g. Wallace & Dickie 2002, Griffith & Porter 2009, Majure *et al.* 2012).

Tribe Tephrocacteae Doweld:—According to phylogenetic analyses (Ritz *et al.* 2012, Walker *et al.* 2018, Majure *et al.* 2019), the monophyletic clade "Tephrocacteae" represents a widely distributed group which includes the genera *Pterocactus* K.Schum*.*, *Maihueniopsis* Speg*.*, *Tephrocactus* Lem., *Austrocylindropuntia* Backeb., and *Cumulopuntia* F.Ritter. The study by Ritz *et al.* (2012) retrieved two main clades, one of which comprises *Pterocactus* and *Maihueniopsis* and the other one harbours *Tephrocactus* and the sister pair *Cumulopuntia* and *Austrocylindropuntia*. Former taxonomic concepts (e.g. Hunt *et al.* 2006: p. 12) suggested a close relationship between *Maihueniopsis* and *Cumulopuntia* mainly for their shared gross morphology. Wallace & Dickie's (2002) results suggest a close relationship between *Maihueniopsis* and *Thephrocactus* and, furthermore, *Pterocactus* was treated as a tribe, an opinion shared by Nyffeler & Eggli (2010). Yet, in Griffith & Porter (2009), *Pterocactus* was not isolated but was placed together with *Maihueniopsis* in a basal grade to the rest of the terete-stemmed Opuntioideae. Ritz *et al.* (2012) showed that *Pterocactus* is not isolated, appearing as sister to *Maihueniopsis*. This finding supports Stuppy's (2001) assumption that the genus might be closely related to *Maihueniopsis*. Although some morphological characters of *Pterocactus* are unique in the tribe and the Opuntioideae (the base of the glochids is rounded; the flowers are immersed into the apex of the segment; at an early oncological stage the fruit is not clearly separated from the surrounding tissue of the segment; the funicular girdle of the seed forms a broad papery and undulating wing), it shares some important morphological characters with *Maihueniopsis*. According to all these findings our classification follows the results of Ritz *et al.* (2012). According to the results of Ritz *et al.* one large species-complex was split: *Cumulopuntia boliviana* (Salm-Dyck) F.Ritter (Table 2).

TABLE 2 (1/4). Updated checklist of Chilean genera and species in comparison with works by Hunt *et al.* (2006, 2013, 2016) and Rodríguez *et al.* (2018). Names in bold highlight differences among the works. Symbols: - = new taxa backed by molecular data but not accepted by Hunt *et al.* (2006, 2013, 2016) and Rodríguez *et al.* (2018); numbers in brackets ( ) = supported by following relevant studies: 1 = Larridon *et al.* (2015), 2 = Ritz *et al.* (2012); 3 = Guerrero *et al.* (2019b); 4a= Larridon *et al.* (2018a); 4b = Larridon *et al.* (2018b), 5a = Schlumpberger & Renner (2012); 5b = Schlumpberger (2012); 6 = Nyffeler & Eggli (2010); 7 = Wallace & Dickie (2001); 8 = Griffith & Porter (2009); 9 = Nyffeler 2002; 10 = Edwards *et al.* 2005; 11 = Ritz *et al.* 2007; 12 = Lendel 2006; 13 = Hernández-Hernández *et al.* 2011; 14= Walter (2011); 15 = Eggli & Walter (2012); 16 = Wilson (2016); 17 = Vergara (2011, cited in Guerrero *et al.* 2019b); 18 = Walter (2019); 19 = Guerrero, unpublished data; 20 = Merklinger *et al.* (2021); * = taxa "alternatively" accepted by Hunt (2016). Taxa in *italics* not still included in the sampling of relevant molecular studies.

Hunt *et al.* (2013; 2016)	Rodríguez *et al.* (2018)	Present study
Austrocactus	*Austrocactus*	*Austrocactus*
A. bertinii	***A. patagonicus***	*A. coxii* (18)
A. hibernus	***A. philippii***	*A. hibernus*
A. spiniflorus	*A. spiniflorus*	*A. spiniflorus*
Browningia	Browningia	Browningia (11); (13)
B. candelaris	B. candelaris	B. candelaris
Copiapoa	Copiapoa	Copiapoa (1)
C. angustiflora	-	C. angustiflora
-	-	C. aphanes
-	-	C. armata
C. calderana subsp. atacamensis	**C. calderana subsp. atacamesis**	C. atacamensis
C. humilis	-	C. australis
	C. boliviana	
C. calderana	C. calderana	C. calderana
C. cinerascens	C. cinerascens	C. cinerascens
C. cinerea subsp. cinerea	**C. cinerea var. cinerea**	C. cinerea subsp. cinerea
C. cinerea subsp. columna-alba	**C. cinerea var. columna-alba**	C. cinerea subsp. columna-alba
C. krainziana	**C. krainziana**	C. cinerea subsp. krainziana
C. ahremephiana	**C. ahremephiana**	C. conglomerata (14)
C. coquimbana	C. coquimbana	C. coquimbana
C. dealbata	C. dealbata	C. dealbata
C. decorticans	C. decorticans	C. decorticans
C. taltalensis subsp. desertorum	**C. rupestris**	C. desertorum
C. megarhiza subsp. echinata	**C. echinata**	
C. echinoides	C. echinoides	C. echinoides
	C. **eremophila**	
C. esmeraldana	**C. humilis var. esmeraldana**	C. esmeraldana
C. fiedleriana	**C. coquimbana var. fiedleriana**	C. fiedleriana
C. cinerea subsp. haseltoniana	**C. cinerea var. gigantea**	C. gigantea (4b)
C. grandiflora	C. grandiflora	C. grandiflora
C. humilis subsp. humilis	**C. humilis var. humilis**	C. humilis subsp. humilis
C. humilis subsp. tenuissima	**C. humilis var. tenuissima**	C. humilis subsp. tenuissima
C. humilis subsp. tocopillana	**C. humilis var. tocopillana**	C. humilis subsp. tocopillana
C. humilis subsp. varispinata	**C. humilis var. varispinata**	C. humilis subsp. varispinata
C. hypogaea subsp. hypogaea	**C. hypogaea var. hypogaea**	C. hypogaea
C. krainziana	**C. krainziana**	
C. hypogaea subsp. laui	C. laui	C. laui
-	-	C. leonensis
C. humilis subsp. humilis	**C. humilis var. longispina**	C. longispina
C. longistaminea	C. longistaminea	C. longistaminea
C. marginata	C. marginata	C. marginata
C. megarhiza subsp. megarhiza	C. megarhiza	C. megarhiza
C. montana	**C. hypogaea var. hypogaea**	C. mollicula
C. montana	**C. hypogaea var. montana**	C. montana
	C. rarissima	
C. taltalensis subsp. taltalensis	C. rupestris	C. rupestris
C. serpentisulcata	C. serpentisulcata	C. serpentisulcata
C. solaris	C. solaris	C. solaris
C. taltalensis subsp. taltalensis	**C. humilis var. taltalensis**	C. taltalensis

continued on the next page

TABLE 2 (2/4) (Continued**)**

Hunt *et al.* (2013; 2016)	**Rodríguez *et al.* (2018)**	**Present study**
Corryocactus	*Corryocactus*	*Corryocactus* (12); (13)
C. brevistylus	*C. brevistylus*	*C. brevistylus*
Cumulopuntia	Cumulopuntia	Cumulopuntia (2)
C. boliviana subsp. dactylifera	C. dactylifera	C. dactylifera
C. boliviana subsp. echinacea	C. echinacea	C. echinacea
C. boliviana subsp. ignescens	C. ignescens	C. ignescens
C. leucophaea		
C. sphaerica	**C. sphaerica**	
Cylindropuntia	*Cylindropuntia*	*Cylindropuntia*
C. tunicata	*C. tunicata*	*C. tunicata*
	Echinopsis	
Eriosyce	Eriosyce	Eriosyce (3)
E. napina subsp. aerocarpa	**E. napina**	E. aerocarpa
E. curvispina subsp. armata	**E. curvispina var. tuberisulcata**	E. armata
E. aspillagae	E. aspillagae	E. aspillagae subsp. aspillagae
E. aspillagae	**E. aspillagae**	E. aspillagae subsp. maechlerorum
E. eriosyzoides subsp. atroviridis	**E. eriosyzoides**	E. atroviridis
E. aurata	E. aurata	E. aurata
	E. aurata var. spinibarbis	
E. calderana	**E. taltalensis subsp. pygmaea**	E. calderana
E. iquiquensis	E. caligophila	E. caligophila
E. subgibbosa subsp. subgibbosa	**E. subgibbosa subsp. subgibbosa**	E. castanea
E. chilensis	E. chilensis	E. chilensis
	E. chilensis var. albidiflora	
E. **subgibbosa subsp. clavata**	**E. subgibbosa subsp. clavata**	E. clavata
E. senilis subsp. coimasensis	**E. senilis**	E. coimasensis
E. confinis	**E. confinis**	
E. crispa subsp. crispa	**E. crispa**	E. crispa subsp. crispa
E. crispa subsp. totoralensis	**E. eriosyzoides**	E. crispa subsp. totoralensis
E. curvispina subsp. curvispina	**E. curvispina var. curvispina**	E. curvispina
E. napina subsp. lembckei	**E. napina**	E. duripulpa
E. senilis subsp. senilis	**E. senilis**	E. elquiensis
E. engleri	E. engleri	E. engleri
E. eriosyzoides	E. eriosyzoides	E. eriosyzoides
E. esmeraldana	E. esmeraldana	E. esmeraldana
E. napina subsp. tenebrica	**E. tenebrica**	E. fankhauseri
E. napina subsp. glabrescens	**E. napina**	E. fulva
E. garaventae	E. garaventae	E. garaventae
E. napina subsp. glabrescens	**E. odieri subsp. glabrescens**	E. glabrescens
E. heinrichiana	E. heinrichiana	E. heinrichiana
	E. ihotzkyana	
E. iquiquensis	E. iquiquensis	E. iquiquensis
E. islayensis	E. islayensis	E. islayensis
E. heinrichiana	**E. heinrichiana**	E. jussieui
E. odieri subsp. krausii	E. krausii	E. krausii
E. confinis	**E. eriosyzoides**	E. kunzei (17)
	E. lapampaensis	
E. laui	**E. laui**	
E. curvispina subsp. armata	**E. curvispina subsp. curvispina**	E. limariensis
E. subgibbosa subsp. subgibbosa	**E. subgibbosa subsp. subgibbosa**	E. litoralis
E. odieri subsp. krausii	**E. odieri subsp. malleolata**	E. malleolata
E. curvispina subsp. marksiana	**E. curvispina subsp. marksiana**	E. marksiana
	E. megacarpa	
E. napina subsp. napina	**E. napina**	E. napina subsp. napina
E. napina subsp. lembckei	**E. napina**	E. napina subsp. lembkei
E. subgibbosa subsp. subgibbosa	**E. subgibbosa subsp. clavata**	E. nigrihorrida
E. odieri	E. odieri	E. odieri
E. occulta	E. occulta	E. occulta
E. paucicostata subsp. paucicostata	E. paucicostata subsp. paucicostata	E. paucicostata subsp. paucicostata
E. paucicostata subsp. echinus	*E. paucicostata subsp. echinus*	*E. paucicostata subsp. echinus*
E. paucicostata subsp. floccosa	*E. paucicostata subsp. floccosa*	*E. paucicostata subsp. floccosa*
E. recondita	E. recondita	E. recondita
-	-	E. riparia

continued on the next page

TABLE 2 (3/4) (Continuned**)**

Hunt *et al.* (2013; 2016)	Rodríguez *et al.* (2018)	Present study
Eriosyce	Eriosyce	Eriosyce (3)
E. rodentiophila	E. rodentiophila	E. rodentiophila
E. senilis	E. senilis	E. senilis
E. simulans	E. simulans	E. simulans
E. sociabilis	E. sociabilis	E. sociabilis
-	**E. napina**	E. spectabilis
E. subgibbosa subsp. subgibbosa	E. subgibbosa subsp. subgibbosa	E. subgibbosa
E. taltalensis subsp. taltalensis	E. taltalensis subsp. taltalensis	E. taltalensis subsp. taltalensis
E. taltalensis subsp. pygmaea	E. taltalensis subsp. pygmaea	E. taltalensis subsp. pygmaea
	E. taltalensis subsp. pilispina	
E. napina subsp. tenebrica	E. tenebrica	E. tenebrica
E. subgibbosa subsp. vallenarensis	**E. subgibbosa**	E. vallenarensis
E. villosa	E. villosa	E. villosa
E. subgibbosa subsp. wagenknechtii	**E. subgibbosa subsp. clavata**	E. wagenknechtii
Eulychnia	Eulychnia	Eulychnia (4a); (20)
E. acida	E. acida	E. acida
	E. aricensis	
E. breviflora	**E. breviflora**	E. barquitensis
E. breviflora	E. breviflora	E. breviflora
E. castanea	E. castanea	E. castanea
E.chorosensis	-	E. chorosensis
E. iquiquensis	E. iquiquensis	E. iquiquensis
E. iquiquensis	E. saint-pieana	E. saint-pieana
E. taltalensis	**E. breviflora var. taltalensis**	E. taltalensis
-	-	E. vallenarensis
Haageocereus	*Haageocereus*	*Haageocereus*
H. chilensis	***H. fascicularis***	*H. chilensis*
H. decumbens	*H. decumbens*	*H. decumbens*
Leucostele*	**Echinopsis**	Leucostele (5a)
L. atacamensis*	E. atacamensis	L. atacamensis (5a)
L. chiloensis subsp. litoralis	***E. chiloensis subsp. litoralis***	*L. bolligeriana*
L. chiloensis*	E. chiloensis	L. chiloensis (5a)
L. chiloensis subsp. litoralis	***E. chiloensis subsp. litoralis***	*L. litoralis*
L. coquimbana	***E. coquimbana***	*L. nigripilis* (15), (16)
L. deserticola	***E. deserticola***	
	E. glauca	
L. chiloensis subsp. skottsbergii	***E. skottsbergii***	*L. skottsbergii*
Lobivia*	**Echinopsis**	Lobivia (5a,b)
L. ferox*	**E. ferox**	L. ferox
Maihuenia	Maihuenia	Maihuenia (9); (10)
M. patagonica	M. patagonica	M. patagonica
M. poeppigii	M. poeppigii	M. poeppigii
Maihueniopsis	Maihueniopsis	*Maihueniopsis* (2); (19)
M. glomerata	**M. glomerata**	
M. archiconoidea	M. archiconoidea	M. archiconoidea
M. atacamensis	*M. atacamensis*	*M. atacamensis*
M. camachoi	*M. camachoi*	*M. camachoi*
M. colorea	*M. colorea*	*M. colorea*
M. conoidea	**M. glomerata**	M. conoidea
M. crassispina	*M. crassispina*	*M. crassispina*
M. darwinii	*M. darwinii*	*M. darwinii*
M. domeykoensis	M. domeykoensis	M. domeykoensis
M. grandiflora	*M. grandiflora*	*M. grandiflora*
M. reicheana		
		M. leoncito
	M. nigrispina	
M. ovata	*M. ovata*	*M. ovata*
	M. rahmeri	
M. wagenknechtii	*M. wagenknechtii*	*M. wagenknechtii*

continued on the next page

TABLE 2 (4/4) (Continuned)

Hunt *et al.* (2013; 2016)	Rodríguez *et al.* (2018)	Present study
Miqueliopuntia	Miqueliopuntia	Miqueliopuntia (7)
M. miquelii	M. miquelii	M. miquelii
Neowerdermannia	Neowerdermannia	Neowerdermannia (6)
N. chilensis	N. chilensis	N. chilensis
Oreocereus	*Oreocereus*	*Oreocereus*
O. hempelianus	*O. hempelianus*	*O. hempelianus*
O. leucotrichus	*O. leucotrichus*	*O. leucotrichus*
Pterocactus	*Pterocactus*	*Pterocactus*
P. australis	*P. australis*	*P. australis*
P. hickenii	*P. hickenii*	*P. hickenii*
-	-	Rimacactus (6), (3)
Eriosyce laui	**Eriosyce laui**	R. laui
Soehrensia*	**Echinopsis**	Soehrensia (5a)
S. formosa*	**E. formosa**	S. formosa
-	-	Sphaeropuntia (2) (7) (8)
Cumulopuntia sphaerica	**Cumulopuntia sphaerica**	S. sphaerica
Cumulopuntia leucophaea		
Tephrocactus	**Maihueniopsis**	Tephrocactus (2) (7) (8)
T. nigrispinus	**M. nigrispina**	T. nigrispinus
Tunilla	Tunilla	Tunilla (2)
T. soehrensii	T. soehrensii	T. soehrensii

Notes on some genera belonging to the Tribe Tephrocacteae follow:

Maihueniopsis **Speg.:**—Hunt's *et al.* (2016) and Hunt's (2013) circumscription of the genus *Maihueniopsis* includes only four species occurring in Chile, i.e. the two endemics *M. archiconoidea* F.Ritter and *M. conoidea* F.Ritter, and two species occurring also in Argentina (*M. darwinii* Hnsl. and *M. ovata* Pfeiff.). These authors merged the rest of the Chilean species described by Ritter (1980) and Espinosa (1933) into the widespread Argentinean species *M. glomerata* (Haw.) R.Kiesling without any evidence (i.e. detailed descriptions, morphological keys, and/or molecular phylogenies). They did not realize, however, that the Chilean *Maihueniopsis* are clearly divided into two main groups (the "*glomerata*- group" and the "*domeykoensis*-group") when all members of the *domeykoensis* group [*M. camachoi* (Espinosa) F.Ritter, *M. colorea* F.Ritter, *M. crassispina* F.Ritter, *M. domeykoensis* F.Ritter, *M. grandiflora* F.Ritter, and *M. wagenknechtii* F.Ritter] are included in the sampling. All members of the *domeykoensis* group are endemic to the western slopes of the Chilean Andes. Populations of *M. glomerata* s.str. had not yet been documented in Chile. The molecular-based phylogeny presented by Ritz *et al.* (2012) shows that *M. domeykoensis* [a species that was lumped into *M. glomerata* by Hunt (2011)] is sister to the rest of the nine taxa (all of them being members of the *glomerata* group). Ritz *et al.* (2012) found it "interesting" that *M. domeykoensis* was not placed within the "*glomerata*" group. Their sampling was unbalanced, as they included nine species assigned to the "*glomerata*" group (see above) but only one assigned to the "*domeykoensis*" group (i.e. *M. domeykoensis*).

Maihueniopsis domeykoensis is likely a separate lineage. So, we conclude that a) as *M. domeykoensis* did not cluster with *M. glomerata* (or other members of the *glomerata*-clade), it cannot be considered a synonym of *M. glomerata*, and thus b) the rest of the members of the *domeykoensis* group, who share the same morphological characters with *M. domeykoensis*, cannot be considered synonyms of *M. glomerata*. This conclusion is corroborated by a broadly sampled (i.e. all the members of the *domeykoensis* group) molecular phylogeny (Guerrero, in preparation) that showed that *Maihueniopsis* is split into two groups congruent with the above presented morphylogy-based groups (a morphology-based key is reported below). According to the results of the phylogenetic analyses one large species-complex was split: *Maihueniopsis glomerata*. However, Hunt (2016) withdrew his opinion and reinstalled all of the formerly not accepted species of the domeykoensis-clade.

A nomenclatural note on the no validly published name "*Maihueniopsis leoncito* (Werderm.) F.Ritter" is necessary. According to Art. 41.5 ICN (Turland *et al.* 2018), Ritter's "*Maihueniopsis leoncito*" is invalid because it does not include the place of publication of the basyonym. The correct name *Maihueniopsis leoncito* (Werdermann ex F.Ritter) P.C. Guerrero & Helmut Walter was recently published by Guerrero & Helmut Walter (2019);

1. Branch segments ≤5 cm; spines ± flattened; mature fruits unspined, ±ovoid or cylindric; seeds pale yellow, with short trichomes ("*glomerata*-group") 2
- Branch segments 5–10 cm, spines terete in cross-section; fruits spiny, obconical urn-shaped; seeds brown, with long trichomes ("*domeykoensis*-group") 7
2. Spines strongly flattened and broad at base, often deflexed 3
- Spines less flattened, not broad at base, thinner, not deflexed 4
3. Compact, large cushions 20–60 cm high; segments to 4 cm, broadly conical, apex acute; spines to 4 cm, pointed downwards to porrect .... **10. *M. leoncito***
- Small, loose cushions up to 20 cm diam. and 10 cm high; segments <2.5 cm, conoid to globose, apex obtuse; spines ≤2 cm, deflexed or appressed to segment .... **1. *M. archiconoidea***
4. Branch segments <5 cm; spines 3-4 cm 5
- Branch segments 1.5–3 cm; spines <3cm 6
5. Shrubs forming compact cushions up to 50 cm wide and 35 cm high; areoles numerous, 4-5 mm, upper 2/3 spiniferous; stigma-lobes green .... 7**. *M. darwinii***
- Cushions loose, to 10 cm high; areoles few, 1–2 mm, only upper third to upper half spiniferous; stigma-lobes red .... **11. *M. ovata***
6. Small, loose cushions; spines directed sideward to ±downwards, new ones blackish-violet; fruits cylindric, areoles wooly .... **5. *M. conoidea***
- Large compact cushions; spines porrect to erect, new ones yellowish; fruits ovoid, areoles not woolly .... **2. *M. atacamensis***
7. Areole number <40, only upper 2/3 of areoles spiniferous; spineslong, 5–12 cm 8
- Areole number 40-60, even basalmost ones spiniferous, spines 2–3 cm .... 12. ***M. wagenknechtii***
8. Spines red-brown, base whitish; seeds small 9
- Spines white or light honey-brown; seeds large 10
9. Stigma lobes red; spines to 12 cm .... **3**. ***M. camachoi***
- Stigma lobes green; spines to 6 cm .... **4**. ***M. colorea***
10. Shrubs up to 2 m diam.; spines white, those on flowers and fruits contorted .... **9**. ***M. grandiflora***
- Shrubs to 50 cm diam.; spines honey-brown, stiff 11
11. Segments light yellowish-green; most spines directed upwards; stigma green .... **8**. ***M. domeykoensis***
- Segments bluish grey-green; most spines directed; sideward or downwards; stigma ruby-red .... **6**. ***M. crassispina***

***Sphaeropuntia* Guggi:**—Nyffeler & Eggli (2010) remarked that the exclusively West-Andean species *Cumulopuntia sphaerica* (C.F.Först.) F. Anderson "is unambiguously shown as a separate lineage", as it appears in a trichotomy with *Austrocylindropuntia* Backeb. and *Cumulopuntia* F. Ritter (Wallace & Dickie, 2002). Also, in Griffith and Porter (2009) the two accessions of *C. sphaerica* were not placed within the *C. boliviana* clade, but in a strongly supported trichotomy with *Austrocylindropuntia*. Finally, Ritz *et al.* (2012) showed that the well-supported *C. sphaerica* clade is sister to the *C. boliviana* clade.

The morphology of *Sphaeropuntia* support above mentioned findings. In fact this genus differs from *Cumulopuntia* in many character states: shrubs low, 10–15 cm high, forming loose groups < 50 cm diameter (20–50 cm high, forming compact mounds 0.5–2.0 m diameter); stem segments easily despatching (not so), spherical to short ovoid (long conical to nearly cylindric), epidermis with white wax (not so), not or only slightly tuberculate (strongly tuberculate); areoles evenly dispersed all over the segment (only upper third, crowding near apex), large, 5–10 mm (small, ≤ 5mm), prominent (not so), closely set (more apart); spines 3–5 cm (3–15 cm), present on all areoles (only superior ones spiniferous); floral areoles dispersed all over pericarpel and hypantium (only rim of hypanthium); pericarpel short and broader than long (isodiametric or long); fruits globose to obconical, often broader than high (cylindric), 2.0–2.5(–3.5) cm, areoles large, spiny all over (small, spines only at rim); flank of seeds not ridged (ridges present; see also Stuppy 2002). Moreover, both occur in different habitats: *Sphaeropuntia* is distributed between the latitudes of 33° S and 18°S and from sea-level to the Pre-Cordillera (100–3700 m), while members of the genus *Cumulopuntia* are mainly distributed in the Altiplano regions (3700–4300 m). According to these findings we accept *Sphaeropuntia* Gucchi.

***Tephrocactus* Lem.:**—Kiesling (1984) and Rodríguez *et al.* (2018) placed *Tephrocactus nigrispinus* (K.Schum.) Backeb. within the genus *Maihueniopsis*. This assumption was not supported by molecular studies (Wallace & Dickie 2002, Griffith & Porter 2009, Ritz *et al.* 2012).

Chilean Cactoideae
The monophyly of various taxa is supported by the molecular study by Wallace & Cota (1996).

Tribe Phyllocacteae Salm-Dyck:—Nyffeler & Eggli (2010) stated that the monophyly of the tribe is well supported by Nyffeler (2002) and Crozier (2005). Moreover, for nomenclatural reasons, the name Phyllocacteae (incl. Echinocereeae Buxb.) must be used because it has priority over all the other relevant tribal names, i.e. Hylocereeae Buxb., Leptocereeae Buxb., Pachycereeae Buxb. and Peniocereeae Doweld. Despite of this, Hunt *et al.* (2013) placed the three Chilean genera (*Austrocactus* Britton & Rose*, Eulychnia* Phil., and *Corryocactus* Britton & Rose) within Echinocereeae Buxb., Nyffeler & Eggli (2010) proposed the following three subtribes, one of which (Subtribe Corryocactinae Buxb.) includes the three Chilean genera. The relationships between *Austrocactus*, *Eulychnia*, and *Corryocactus* was corroborated by various molecular-based studies (e.g. Nyffeler 2002, Hernández-Hernández *et al.* 2011, Bárcenas *et al.* 2011).

***Austrocactus*:**—The *Austrocactus* species from around the town of Chile Chico was shown to be *A. coxii* (K.Schum.) Backeb. (see Walter 2019) and not *A. patagonicus* Hosseus according to Rodríguez *et al.* (2018) and Hunt *et al.* (2013, 2016). *A. coxii* can easily be distinguished from *A. patagonicus* (= *A. bertinii* Britton & Rose) by large multi-headed cushions (*vs*. simple, rarely few-headed in *A. patagonicus*), branches 10–15 cm long (*vs*. 50–60 cm) and 5 cm thick (*vs*. to 15 cm), all spines straight (*vs*. hooked), centrals 2.0–2.5 cm (*vs*. 2–4 cm), flowers yellow to orange (*vs*. pinkish to white).

***Eulychnia*:**—The genus includes two main clades according to Larridon *et al.* (2018) and Merklinger *et al.* (2021). The two groups are morphologically and phylogenetically supported and clearly associated with geographical changes in the Atacama Desert (a proposed key is reported below). According to the results of the phylogenetic analyses three former species-complexes were resolved: *Eulychnia acida* Phil., *E. breviflora* Phil., and *E. iquiquensis* (K.Schum.) Britton & Rose.

1. Ribs steep and narrow; flowers and fruits densely covered with wool; perianth segments lanceolate (“*breviflora*-group”) 2
- Ribs broad and flattened; flowers and fruits with less and shorter wool; perianth segments spathulate (“*acida*-group”) 6
2. Spines numerous, central ones very long; seed large .... **3.** ***E. breviflora***
- Spines less numerous and shorter; seed smaller 3
3. Pulp orange; areoles with long wool; plants low to medium-sized 4
- Pulp whitish; areoles with shorter wool; plants higher 5
4. Plants shrubby; branches sub-prostrate, thin .... **2.** ***E. barquitensis***
- Plants arborescent; branches ascending, thicker .... **7.** ***E. saint-pieana***
5. Areoles far apart, wool dark brown .... **8.** ***E. taltalensis***
- Areoles closely set, wool greyish .... **6.** ***E. iquiquensis***
6. Flower and fruit areoles spiny .... **4.** ***E. castanea***
- Flower and fruit areoles spineless 7
7. Plants shrubby; branches (sub)prostrate with superior portions pointing upwards; ribs 8–12 8
- Plants arborescent; branches ascending to erect; ribs up to 16 .... **1.** ***E. acida***
8. Shrubs low; branches thin, grey-green; flowers with short wool; new areoles with abundant white felt .... **5.** ***E. chorosensis***
- Shrubs higher; branches thicker, yellowish-green; flowers with in conspicuous hairs; areoles with short grey felt .... **9.** ***E. vallenarensis***

Tribe Notocacteae Buxb.:—The Notocacteae had long been a heterogeneous group of South American genera (*Parodia* Speg., *Eriosyce* Phil., *Blossfeldia* Werderm., *Frailea* Britton & Rose, *Copiapoa*, *Eulychnia*, *Neowerdermannia* Frič, and *Austrocactus*). Nyffeler's (2002) DNA-based study, however, showed that Notocacteae *sensu* Hunt *et al.* (2006) is highly polyphyletic and, therefore, he reduced the tribe to the strongly supported monophyletic group (“core Notocacteae”) comprising *Eriosyce s.l.*, *Parodia* Speg. *s.l.*, and *Neowerdermannia*. Nyffeler & Eggli (2010) showed that the two monotypic genera *Rimacactus* Mottram and *Yavia* Kiesling & Pilz, as well as *Eriosyce*, *Parodia*, and *Neowerdermannia*, form a strongly supported monophyletic clade (“Notocacteae”). Finally, the results of Guerrero *et al.* (2019) corroborated the monophyly of the tribe, yet Hunt *et al.* (2013) upheld the inclusion of *Blossfeldia* Werderm. and *Frailea* Britton & Rose within tribe Notocacteae.

***Copiapoa* Britton & Rose:**—This endemic genus has formerly been regarded as a member of the tribe Notacacteae Buxb., e.g. by Barthlott & Hunt (1993), Anderson (2001), Hoffmann & Walter (2004), and Hunt *et al.* (2006). Molecular studies by Nyffeler (2002), Korotkova *et al.* (2010), Nyffeler & Eggli (2010), Arakaki *et al.* (2011), and Hernández-Hernández *et al.* (2011) suggested that *Copiapoa* is not a member of this tribe as it appears isolated on its own clade. Nyffeler & Eggli (2010) treated *Copiapoa* as a genus of uncertain relationship (*incertae sedis*), whereas Korotkova *et al.* (2010) suggested a close relation between *Copiapoa* and *Calymmanthium* F.Ritter, although morphology, ecology, and distribution of the two genera are very different. In Nyffeler (2002) and Hernández-Hernández *et al.* (2011), both genera appear together in a polytomy. Finally, Hunt *et al.* (2013) accepted Doweld`s (2002) recognition of a "tribe Copiapoae". In consideration of the complex situation and the lack of data, we here consider Nyffeler & Eggli's (2010) concept (*incertae sedis*).

Several infrageneric classifications of *Copiapoa* based on morphological characters had been proposed by Ritter (1980) [two subgenera (subgenus *Pilocopiapoa* F.Ritter and subgenus *Copiapoa* F.Ritter) and five unnamed sections]. Doweld (2002) proposed three sections (sect. *Pilocopiapoa* (F.Ritter) Doweld (one serie), sect. *Echinopoa* Doweld (two series: *Echinoidei* Doweld and *Cinerei* Doweld), and sect. *Copiapoa* (two series: *Humilis* Doweld and *Copiapoa*); mainly based on general morphological data (Hunt 2001) and stem mucilage and/or root types. Taylor (2001) proposed two subgenera (subgen. *Pilocopiapoa* (F.Ritter) F.Ritter) and subgen. *Copiapoa* (five unformal "groups": "*marginata*", "*cinerea*", "*hypogaea*", "*cinerascens*", and "*humilis*"). None of these concepts were corroborated by the molecular phylogeny presented by Larridon *et al.* (2015) whose data retrieved the four well supported sections: sect. *Pilocopiapoa* (with 1 species), sect. *Mammilopoa* Helmut Walter & Larridon (1 species), sect. *Copiopoa* [with two subsections: subsect. *Cinerei* (Doweld) Helmut Walter & Larridon (2 species), subsect. *Copiapoa* (22 species)], sect. *Echinopoa* (Doweld) Helmut Walter & Larridon (5 species) and two basal unnamed monotypic clades ("*Copiapoa australis*" and "*Copiapoa laui*") (see the proposed key below). According to the results of the phylogenetic analyses five species-complexes were split: *C. humilis* (Phil.) Hutchison*, C. cinerea* (Phil.) Britton & Rose, *C. taltalensis* (Werderm.) Looser, *C. montana* F.Ritter, and *C. coquimbana* (Rümpler) Britton & Rose.

1.	Bract scales numerous distributed all over pericarpel and hypanthium, axils very woolly; ribs to 3.5 cm high (Sect. PILOCOPIAPOA)	**31. *C. solaris***
-	Bract scales few, mainly near hypanthium rim, axils only rarely with fine tiny hairs; ribs ≤2 cm high	2
2.	Ribs in mature plants dissolved into ±conical tubercles; stems soft to the touch	3
-	Ribs not dissolved into conical tubercles (except for *C. longispina*), stems soft or not so	4
3.	Tubercles obtuse; epidermis ±pruinose; ribs 8-10 (unnamed Section)	**5. *C. australis***
-	Tubercles pronounced; epidermis not pruinose; ribs more numerous	5
4.	Stems dwarf (1–2 cm diam.); tubercles and spines minute (Unnamed Section	**21. *C. laui***
-	Stems to 8 cm diam.; tubercles large, spines much longer (Sect. HUMILIS)	**19. *C. humilis***
5.	Plants usually mound-forming; ribs to 2 cm high; fruits large, 1.5–2.0 cm (Sect. ECHINOPOA)	6
-	Plants mound-forming or not; ribs lower; fruits <1.5 cm (Sect. COPIAPOA)	10
6.	Tubercles inconspicuous; roots fascicular	7
-	Tubercles well pronounced; taproots of different lengths	8
7.	Mounds up to 2 × 1.5 m; stems often pruinose; ribs to 30; areoles far apart	**11. *C. dealbata***
-	Mounds much smaller, ribs to 15; stems never pruinose; areoles closely set	**14. *C. echinoides***
8.	Stems 5–8 cm diam.; tubercles with large chins	**16. *C. fiedleriana***
-	Stems 8–18 cm diam., usually chinless	9
9.	Stems 8–12 cm diam.; new spines black, to 4 cm	**10. *C. coquimbana***
-	Stems to 18 cm diam.; new spines brownish, later golden yellow, to 6 cm	**3. *C. armata***
10.	Rib number up to 40; roots always fascicular; stem tissue very hard (Subsect. CINAREI	11
-	Rib number <26, roots various; stem tissue not very hard (Subsect. COPIAPOA)	12
11.	Plants forming loose groups or solitary; apical wool grey	**8. *C. cinerea***
-	Plants forming large dense mounds; apical wool (orange)-brown	**17. *C. gigantea***
12.	Ribs dissolved into conical tubercles	**23. *C. longispina***
-	Ribs not so	13
13.	Stem tissue somewhat hard (except for C. hypogaea)	14
-	Stem tissue ±soft-fleshy	29
14.	Bract-scales on hypanthium and fruits large, broad and fleshy; hilum very large	**26. *C. megarhiza***
-	Bract scales and hilum not as above	15
15.	Rib number usually 15–25	24
-	rib number usually low (8–15)	16
16.	Roots fascicular	17
-	Roots usually tuberous or long to short taproots	18
17.	Stem diam. 4–7 cm	**9. *C. conglomerata***
-	Stem diam. larger, to 15 cm	**23. *C. longistaminea***
18.	Interior perianth segments yellow, without red mid-stripes; style whitish-yellow	19
-	Interior perianth segments yellowish with red mid-stripes of different widths; style pink to red	22
19.	Plants mound-forming; stems elongating; spines short (1.5–2.5 cm), straight	20
-	Plants solitary to few-headed; stems only slightly elongating; spines long (to 5 cm), partly curved	**32. *C. taltalensis***
20.	Rib tubercles much pronounced, furrows undulate	**30. *C. serpentisulcata***
-	Ribs only somewhat tuberculate, furrows not undulate	21
21.	Plants forming loose mounds; stems ca. 8 cm diam.; longer ones prostrate; fruit 1cm	**12. *C. decorticans***
-	Plants forming compact mounds; stems apically flattened, to 15 cm diam.; stems not prostrate; fruit 1.5 cm	**7. *C. cinerascens***
22.	Plants mound-forming; stems green, not pruinose, to12 × 50 cm; flowers 3.0–4.5 cm, funnel-form; spines to 5 cm, thick	

…… 23

\- Plants solitary to few-headed; stems grey-green, ±pruinose, to 8 × 20 cm; flowers small, (2.5 cm), campanulate; spines short, to 2.5 cm, thin …… **2. *C. aphanes***

23\. Mounds usually loose, spines to 10, (red)-brown, partly curved …… **29. *C. rupestris***

\- Mounds compact, spines to 20, completely hiding stem, black, straight …… **13. *C. desertorum***

24\. Plants large, forming loose or dense mounds; rib tubercles inconspicuous, areoles closely set in older plants …… 25

\- Plants small to medium-sized, not much elongating, few-headed, rib tubercles pronounced; areoles not crowded …… 27

25\. Plants forming large, dense mounds; stems to 15 cm diam., pruinose …… **4. *C. atacamensis***

\- Mounds smaller, loose; stems to 10 cm diam., only sometimes pruinose …… 26

26\. Stems light grey-green, sometimes pruinose, spines to 3 cm …… **6. *C. calderana***

\- Stems green, never pruinose, spines to 5 cm …… **25. *C. marginata***

27\. Plants subglobose, temporarily geophytic; epidermis grey-brown …… **20. *C. hypogaea***

\- Plants globose to somewhat elongate; epidermis grey-green …… 28

28\. Stems to 10 cm diam., not pruinose; areoles large …… **28. *C. montana***

\- Stems 4–7 cm diam.; ± pruinose; areoles smaller …… **22. *C. leonensis***

29\. Plants mound-forming; stems to 10 cm diam.; tubercles not chinned …… **18. *C. grandiflora***

\- Plants solitary to few-headed; stems 3–7 cm diam.; tubercles ±chinned …… 30

30\. Ribs broad and flattened …… **27. *C. mollicula***

\- Ribs narrower and deeper …… 31

31\. Flowers large, broadly campanulate; stems to 7 cm diam. green, not pruinose …… **15. *C. esmeraldana***

\- Flowers small, narrowly funnel-form; stems to 4 cm, grey-brown, somewhat pruinose …… **1. *C. angustiflora***

Several new taxa in the genus *Copiapoa* were recently proposed in different journals. As none of them had been included in the sampling of a molecular-based study, we decided not to accept them as long as they are not corroborated by molecular phylogenies: *Copiapoa coquimbana* subsp. *rubrispina* Piombetti in Xerophilia 4(3): 76. 2015; *Copiapoa longispinea* subsp. *imperialis* Piombetti in Xerophilia 4(3): 78. 2015; *Copiapoa corralensis* Schaub & Keim in Cactus Explorer 16: 48. 2016; *Copiapoa fusca* Schaub, Cactus Explorer 16: 42. 2016; *Copiapoa humilis* subsp. *matancillensis* Schaub & Keim in Cactus & Co 20(1): 15. 2016.

Concerning *Copiapoa gigantea* Backeb., Hunt *et al.* (2006) use the epithet "*haseltoniana*" (instead of "*gigantea*") in the combination *C. cinerea* subsp. *haseltoniana* (Backeb.) N.P.Taylor (see species list). The results by Larridon *et al.* (2015, 2018b) suggest that this taxon is not closely related to *C. cinerea* and should thus be considered as a valid species. Also, *C. gigantea* has priority over *C. haseltoniana* at species level (ICN, Art. 11.2) as below reported.

Copiapoa gigantea Backeb., Jahrb. Deutsche Kakt. Ges. 1: 104. 1936.

Type:—Not designated.

= *Copiapoa eremophila* F. Ritter, Kakt. Südam. 3: 1104–1105. 1980.

Type:—CHILE, östl. Paposo, *s.d.* [1956], *Ritter 208b* [holotype SGO124843, (corpus), areoles, spines].

Notes:—Backeberg (1936: 104) gave a vague type locality ("Chile: Provinz Antofagasta, auf nachts oft nebelfeuchten Berggipfeln" = "Chile: Province Antofagasta, on mountain peaks that are often damp at night") in the protologue of his *Copiapoa gigantea*. Later, the same author (Backeberg 1977: 107) specified the locality as "above Paposo". Ritter (1980: 1100) accepted Backeberg's species for plants occurring east of Paposo area ("Gegen die Wüste des Hinterlandes wächst sie aber nur gegen Süden, während sie im gleichen Klima und in gleicher Höhenlage etwas nördlicher, nämlich östlich von PAPOSO ..." = "Towards the desert of the hinterland, however, it [*Copiapoa gigantea* var. *gigantea*] only grows towards the south, while in the same climate and at the same altitude it grows a little further north, namely east of PAPOSO ...") and proposed *C. haseltoniana* Backeb. at variety rank of *C. gigantea* (Ritter 1980: 1101) for plant occurrring in "... nördlich Paposo an der Küste ..." (= "... north of Paposo on the coast ...").

Concerning *Copiapoa eremophila*, Ritter (1980: 1105) reported "Typusort. östlich von PAPOSO am Rand der Vollwüste als einzige noch wachsende Kakteenart; nur von hier bekannt. Von mir entdeckt 1956. Nr. FR 476 (=208a)", the "Typusort" can be considered as "holotype". We traced this specimen at SGO. Its morphology corresponds to the current concept of *C. gigantea* (see e.g., Larridon *et al.* 2015).

The "current" concept of *Copiapoa gigantea* (based on molecular evidence) is Larridon 2015. There are no other works occupying with the status of *C. gigantea*. Former concepts treated *C. gigantea* as a synonym of *C. cinerea* subsp. *haseltonia* (Hunt *et al.*, Hoffmann & Walter (2004), Anderson (2001) as a synonym of *Copiapoa haseltonia* and Slaba, (in Kaktussy (special) 33: 3. 1997) as *C. cinerea* subsp. *gigantea* for sharing the following characters: Apical wool orange-brown; large dense multi-headed mounds; stem diameter 10–25 cm, farina-covered; spines honey-coloured, later turning greyish-blackish, more numerous at higher elevations; young areoles orange brown. Accordingly, and since the type locality of *C. eremophila* is nearly the same of that of *C. gigantea* (Paposo), we here propose to synonymize the two names.

Eriosyce **Phil.** (see a proposed key below)**:**—The results of the molecular phylogeny by Guerrero *et al.* (2019b) show that *Eriosyce s.l.* (see also Kattermann 1994) species from Chile, Perú, and Argentina form a strongly supported monophyletic clade, but only with the exclusion of *Rimacactus laui* (Lüty) Mottram, a species that had been included within *Eriosyce* section *Neoporteria* subsection *Chileosyce* by Kattermann (1994, *as Eriosyce laui* Lüthy) and within the "*Islaya*-group" by Hunt *et al.* (2006, 2013, as *Eriosyce laui*).

TABLE 3. Comparison among different species concepts of *Eriosyce kunzei* (C.F.Först.) Katt. 1 Zoll (Saxony) = 2.36 cm; 1 Lin. = 1/12 saxonian Zoll = 1.96 mm.

	Pyrrhocactus kunzei	*Echinocactus kunzei*	*Eriosyce kunzei*
Material	Ritter refers *Echinocactus kunzei* to the plants from the vicinity of Copiapó Atacama, *FR 220*, Paipote	Förster: Type not extant nor illustrated. "Chile" as distribution	Kattermann refers *Echinocactus kunzei* to the plants from the vicinity of the Elqui Valley, Coquimbo. Type (neo): **Elqui, Guanta**, *FK 459* and equated *Echinocactus kunzei* (Först.) Katt. with *Horridocactus eriosyzoides* F. Ritter; Type **Guanta**
Climatology	1.The plants are **sometimes** covered by light snow. A recent snow episode occurred in the area around the Copiapó Valley (Vergara 2011). 2. Ritter gave six locations: not only "Sierra Hornillos"; the town Paipote located in high mountains east of Copiapó is one of the six (Eggli *et al.* (1995) and Hunt (2003)	The plants are **sometimes** covered by light snow	1."The plants are covered by snow for ***long periods***". This statement is not correct 2. "It never snows in the Sierra Hornillos"
Stems	Subglobose (0.7 – 12 cm in diameter) to slightly elongating with age	Globose, somewhat appressed; 4 Zoll high (= 9.4 cm); 5-5 ½ Zoll (11.8-12.98 cm) in diameter	"10 (– 20) x 13 – 14 cm, somewhat elongating with age)" This description is not correct. The plants from Guanta grow much longer: Hoffmann (1989) under *Neoporteria eriosyzoides*: "30 – 40 cm", and Lam. 56. Ritter under *Pyrrhocactus eriosyzoides* (F.Ritter) F.Ritter: "globose, later elongating" Another illustration shows a plant three times higher than wide Fig. 300.3 in Hunt (2006).
Areoles	Very long and narrow 7 – 13 x 3 – 5 mm: see specimen of *Pyrrhocactus kunzei* F.Ritter 220, loc. 2, SGO 121486	Very long and narrow; 1 Lin. wide (=2 mm) and 4-6 Lin. long (=8-12 mm)	"Areoles 10 – 15 x 2.5 mm" This description is not correct (areoles 6 times longer than wide!). The areoles of the plants from the upper Elqui Valley are oval: F.Ritter (1980: 937, *Pyrrhocactus eriosyzoides* from upper Elqui Valley: "Areoles 7 – 10 mm long and 3 – 5 mm wide" (= oval). Hunt *et al.* (2006: Fig. 300.2, *Eriosyce eriosyzoides*) shows a well visable areole measuring 5 mm long and 3 mm wide (= oval); Hoffmann (1998: Lam. 56: *Neoporteria eriosyzoides*) shows clearly oval-shaped areoles*;* Kattermann (1994: Plate 9.3) shows oval-shaped and not extremely long and narrow areoles.
Spines	New ones grey-brown, with darker tips, later turning grey	Brown, ash-grey with age	"First yellowish, later ash grey". This description is not correct. Hoffmann (1998: Lam. 56: *Neoporteria eriosyzoides*) shows an old plant with yellowish spines; Hunt (2006: Fig. 3) shows an old plant with yellow spines

Phylogenetic analyses retrieved seven major clades in the genus (Guerrero *et al.* 2019b). The first branching clade (Section *Eriosyce* Katt.) comprises two species from Chile, one from Argentina, and two from Perú. The next branching clade (Section *Campanulatae* P.C. Guerrero & Helmut Walter) comprised two taxa from southern-central Chile [*Eriosyce marksiana* (F.Ritter), *Eriosyce marksiana* var. *lissocarpa* (F.Ritter) Katt.]. Subsequently branching is a clade (Section *Pyrrhocactus* (A.Berger) P.C. Guerrero & Helmut Walter) harbouring four species endemic to Argentina. Then, a group of 12 taxa endemic to south and and northern-central Chile (Sect. Horridocactus (Backeb.) P.C. Guerrero & H.E. Walter). The next branching clade formed by three species endemic to north central Chile (Section *Diaguita* P.C.Guerrero & Helmut Walter). Subsequently branching is a clade comprising 15 taxa endemic to south and north-central Chile (Sect. Horridocactus (Backeb.) P.C. Guerrero & H.E. Walter), and finally, an unnamed clade composing 22 taxa from northern Chile. In Kattermann (1994), Wallace proposed an infrageneric classification with two sections [sect. *Eriosyce* (with subsect. *Eriosyce*, subsect. *Islaya* (Backeb.) Katt., and subsect. *Pyrrhocactus* (A.Berger) Katt. and sect. *Neoporteria* (with subsect. *Neoporteria* (Britton & Rose) Katt., subsect. *Horridocactus* (Backeb.) Katt., and subsect. *Chileosyce* Katt.), whereas Hunt *et al.* (2006, 2013) and Hoffmann & Walter (2004) proposed six "groups" (= subgenera) based on the former genera *Islaya* Backeb., *Pyrrhocactus* A.Berger, *Neoporteria* Britton & Rose, *Horridocactus* Backeb., *Thelocephala* Ito, and *Eriosyce* Phil. None of these concepts were corroborated by the results of the molecular phylogeny (Guerrero *et al.* 2019b). Moreover, at species level, the large "species complexes" *E. napina* (Phil.) Katt., *E. odieri* (Lem. ex Salm-Dyck) Katt., *E. heinrichiana* (Backeb.) Katt., *E. subgibbosa* (Haw.) Katt., (Backeb.) Katt and *E. curvispina* (Bertero ex Colla) Katt. were not supported by the results of Guerrero *et al.* (2019b) (see Table 2). In addition, the taxonomic delimitation of *E. curvispina* Bertero ex Colla including several infraspecies did not resist standing upright much longer, by not complying with the principle of monophyly as reported by Guerrero et al (2019b), and by new molecular data of several putative members of the *E. curvispina* complex (Villalobos-Barrantes *et al.* 2022).

Concerning *Eriosyce kunzei* (C.F. Först.) Katt., a nomenclatural note is necessary. In the protologue of *Echinocactus kunzei*, Förster gave "Chile" as the type locality but mentioned that the plants are sometimes covered by a light layer of snow in winter. F.Ritter (1980) referred Förster's *E. kunzei* to the plants from near Copiapó, that perfectly match Förster's description (see Table 3 F. Ritter, Kakteen in Südamerika, p.p. 955 and 956 and the specimen at SGO 121487, Ritter *220 loc. 2*) clearly shows the typically long and narrow areole of this taxon. Kattermann (1994), however, chose material from Guanta, Provincia de Elqui, *FK 459* (DBG) for his typification of *Eriosyce kunzei* and based his decision not to refer the plants from around Copiapó to Förster's *Echinocactus kunzei* (as proposed by F. Ritter, 1980) on the single argument that it never snows in this area. Yet, according to meteorological data (Vergara 2011) this assumption cannot be upheld. Hunt (2003) stated that "… the editorial preference would be to supersede Kattermann's neotypification and to substitute *FR 220* material from Paipote (SGO 121487)". Moreover, several relevant morphological characters (Kattermann 1994; stems, areoles and spines, see Table 3) of the plants from Guanta and its vicinity do not match Försters original description. We thus follow F. Ritter's proposal to refer Förster's *Echinocactus kunzei* to the plants from the vicinity of Copiapó. This makes *E. confinis* (F.Ritter) Katt. a heterotypic synonym of *E. kunzei* (C.F. Först.) Katt. (see list of species).

With regard to *Echinocactus jussieui* Monv. ex Salm Dyck a note is necessary. *E. jussieui* was published by Salm-Dyck (1849: 34, 170–171) in his *Hortus Dyckensis* with a short diagnosis ("*Caule aterrime virente*, *tuberculis gibberatis* in *costas 13 subconfluentibus, aculeisque brunneis ad praecedentem valde accedit; sed differt aculei centrali validissimo*"). No specimen referring to the original material could be traced and, therefore, a neotypification is required according to the Art. 9.8 of ICN (Turland *et al.* 2018). Ritter (1980) used the epiteth *jussieui* for plants occurring in the middle and upper Elqui Valley (*Pyrrhocactus jussieui* (Monv. ex Salm-Dyck) F.Ritter var. *jussieui* and var. *spinosior* F.Ritter), argueing that these plants match Salm-Dyck's original protologue (see below) based on "body blackish-green", "ribs 13", "ribs tuberculate", "spines brown", "strong central spine". Kattermann (1994: 156), however, considered *E. jussieui* as "a name of doubtful application, possibly referable to *Eriosyce heinrichiana* (Backeb.) Katt.". To avoid the epithet "jussieui", he chose the name *E. heinrichiana* subsp. *intermedia* var. *intermedia* (F.Ritter) Katt. for the plants in and around the Elqui Valley. Yet, Ritter's locality for his *P. setosiflora* var. *intermedia* was "60 km south of the Elqui Valley low coastal hills". The morphology of the plants occurring in this region differs in several character states from the plants in the middle- and upper Elqui Valley (plants from the Elqui Valley in brackets): stems subglobose to flat on the ground (globose to somewhat elongating), stem diameter 2–5 cm (6–9 cm), stem colour often reddish-brown (dark-green); spines thin (thick), mostly straight (mostly curved upward), 1.5–4.0 cm long (3–6 cm); flowers 4–6.5 (3–4.5); seeds small, 0.9 × 0.7 mm (1.2 × 0.9 mm). Moreover, Kattermann's "subspecies *intermedia*" is not at all related to *E. heinrichiana* subsp. *heinrichiana,* but a species in its own right (Guerrero *et al.* 2019b), thus the name *E. heinrichiana* subsp. *intermedia* can not be uphold and, consequently, a new name for the plants from the middle- and upper Elqui Valley must be found. Following Ritter's (1980) arguments, we here propose a new combination for these plants under the genus *Eriosyce* as well as a neotypification of *Echinocactus jussieui* based on a Ritter's collection:

Eriosyce jussieui (Monv. ex Salm-Dyck) P.C.Guerrero & Helmut Walter, *comb. nov.*

≡ *Echinocactus jussieui* Monv. ex Salm-Dyck, Cact. Hort. Dyck 1849: 170 (1850).

Type (neotype, designated here):—CHILE: Coquimbo, Elqui, 20 km West of Vicuña, *Ritter 252a* [SGO121545!, corpus, areoles, spines (includes a small rooted seedling)].

Another name which deserves attention is the combination *Eriosyce fulva* (F.Ritter) P.C.Guerrero & Helmut Walter. It is invalid, because its putative basyonym ("*Chileorebutia fulva* F.Ritter") is a nomen nudum (Arts. 36.1 and 37.1 of ICN). The valid basionym is *Thelocephala fulva* F.Ritter and we here propose its combination under *Eriosyce*:

Eriosyce fulva (F.Ritter) P.C. Guerrero & Helmut Walter *comb. nov.*

≡ *Thelocephala fulva* F.Ritter, Kakt. Südamer. 3: 1011. 1980.

Holotype:—CHILE: Atacama, Totoral, 1956, *Ritter 500* (U0249077! https://data.biodiversitydata.nl/naturalis/specimen/U%20%200249077).

1.	Stem diameters large; ribs many; areoles large; roots always fascicular	2
-	Stem diameters from very small to medium-sized; ribs less numerous; areoles smaller; roots various	5
2.	Seed testa cell appendages lacking or inconspicuous, interstices pitted or sunken; flowers funnel-form (Sect. ERIOSYCE)	3
-	Seed testa cell appendages present, interstices not pitted nor sunken; flowers campanulate (Sect. CAMPANULATAE)	**31. *E. marksiana***
3.	Flowers and fruits with erect spine-like bristles; fruits not elongating	4
-	Flowers and fruits not as above; fruits much elongating, balloon-like	**25. *E. islayensis***
4.	Stems very thick; fruits completely covered by wool; loculus pulpless; dehiscent by a basal pore	**5. *E. aurata***
-	Stems thinner; fruits not completely covered by wool; loculus with mucilagineous pulp; indehiscent	**39**. ***E. rodentiophila***
5.	Stems subglobose, globose to somewhat elongating; flowers always diurnal, always funnel-form, usually not fuchsia-colour, interior perianth segments directed outward; nectary small; seed notched below hilum or not	6
-	Stems elongating; flowers mostly tubular, fuchsia-colour, interior perianth segments inclining inward to erect; flowers usually remaining open during the night; nectar chamber usually very large; seeds never notched below hilum (sect. NEOPORTERIA)	37
6.	Nectary always tubular; ovary always elongate to isodiametric; roots various	7
-	Nectary widened at base; ovary compressed (with a few exceptions); roots never facicular (unnamed Section)	18
7.	Pericarpel, hypanthium and fruits with inconspicuous white wool and without bristles; tubercles arranged in parastichies (Sect. HORRIDOCACTUS)	8
-	Flowers and fruits always covered by long dense wool and numerous long porrect bristles; ribs not arranged in parastichies (Sect. DIAGUITA)	16
8.	Stems green, never pruinose, medium; fruits short, ovoid to barrel-shape, perianth remnant attachment area large; roots various	9
-	Stems grey-green to grey brown, often ±pruinose, small, fruits elongating, perianth remnant attachment area small; taproots always present	14
9.	Stems with a tendency towards basal branching	10
-	Stems not branching	11
10.	Fruit dry, dehiscing by partial circumscissile splitting; spines finely acicular; ribs low	**3. *E. aspillagae***
-	Fruit-wall fleshy when mature, dehiscing by a complete circumscissile slit; spines thicker; ribs steep	**2. *E. armata***
11.	Stems ±elongating, spines numerous, often obscuring stem	12
-	Stems subglobose to globose or somewhat elongating, spines less numerous	13
12.	Spines long, white to yellowish, tipped dark; floral bristles scant, only near hypanthium rim	**15. *E. engleri***
-	Spines shorter, yellow, not turning grey; bristles numerous, distributed all over hypanthium	**21. *E. garaventae***
13.	Ribs numerous; ovary much elongated; rootstock a long taproot; spines thickly acicular	**28. *E. limariensis***
-	Ribs fewer; ovary ±isodiametric; roots fascicular; spines thinner	**13. *E. curvispina***
14.	Ribs dissolved into tubercles arranged in parastichies; stems very small; spines very short	15
-	Ribs arranged in orthostichies; stems medium-sized; spines much longer	**44**. ***E. jussieui***
15.	Stems never elongating, tubercles large; spines black; flowers with brownish wool and black bristles	**32. *E. napina***
-	Stems elongating with age; tubercles small, spines horn-coloured to white; flowers with white wool and white bristles	**14. *E. duripulpa***
16.	Stems to 6 cm; ribs to 21 discernible, tubercles rhomboid	17
-	Stems 2-4 cm; ribs 12, tubercles rounded	**38. *E. riparia***
17.	Stems not branching; roots neckless; adult plants spineless; style yellow; seed large, hilum pyriform	**19. *E. fankhauseri***
-	Stems branching; roots with a narrow neck; spines present; style red; seed smaller, hilum oval	**47. *E. tenebrica***
18.	Stems medium-sized, ±globose sometimes elongated; spine length various, centrals always present	19
-	Stems very small, flattened to subglobose; spines ≤1.5 cm, centrals often absent	28

19.	Spines long, hair-like, flexible, often contorted; stem epidermis grey-brown, ±pruinose	**12. *E. crispa***
-	Spines shorter, not hair-like or flexible; epidermis usually green to grey-green, blackish-green or glaucous, not pruinose	20
20.	Spines numerous, occulting stems	21
-	Spines less numerous, not occulting stems	24
21.	Flowers purple, narrowly funnel-form; exterior perianth segments ±bent downwards	22
-	Flowers never purple; funnel-form; exterior perianth segments not as above	23
22.	Perianth segments concolourous; interior ones nearly erect; ribs numerous	**42. *E. sociabilis***
-	Perianth segments bicolourous; interior ones directed outward; ribs fewer	**46. *E. taltalensis***
23.	Stems elongating; areoles round-oval; spines yellow, not turning grey; fruit red and juicy when ripe	**17. *E. eriosyzoides***
-	Stems globose; areoles narrow; spines brownish, soon turning grey; fruit dry when ripe	**27. *E. kunzei***
24.	Fruits clavate; spines short; flowers very short	25
-	Fruits not clavate; spines longer; flowers longer	26
25.	Stems globose to somewhat elongating; flowers yellow; ribs to16	**24. *E. iquiquensis***
-	Stems small, subglobose; flowers reddish; ribs fewer	**7. *E. caligophila***
26.	Stems green or glaucous; ribs few; flowers whitish-yellowish	27
-	Stems blackish grey-green; ribs more numerous; flowers reddish	**4. *E. atroviridis***
27.	Stems (sub)globose, green, areoles not woolly; style whitish; fruits yellowish	**6. *E. calderana***
-	Stems ±elongating, glaucous, areoles woolly; style red; fruits red	**36. *E. paucicostata***
28.	Ribs dissolved into tubercles arranged in parastichies	29
-	Ribs arranged in orthostichies	35
29.	Hypanthium and pericarpel with long porrect bristles	30
-	Hypanthium and pericarpel not as above	33
30.	Stems branching, not elongating; spines often completely lacking, not interwoven, short	31
-	Stems often elongating with age, not branching; spines interwoven, to1 cm, always present	**1. *E. aerocarpa***
31.	Tubercles, areoles and spines tiny	**26. *E. krausii***
-	Tubercles and areoles larger, spines longer	32
32.	Stem apex with long white wool; fruit areoles on top of large nipple-shaped tubercles; seed testa surface shiny, smooth, cells lacking appendages	**30. *E. malleolata***
-	Stem apex not woolly; fruit etuberculate; seed testa opaque, rugose, cell appendages present; flowers whitish	**18. *E. esmeraldana***
33.	Stems to 6 cm diam.; spines radiating, straight; roots conical without a neck	**35. *E. odieri***
-	Stems <4 cm, spines appressed, recurved; roots a long taproot with a neck-like constricton	34
34.	Stems flat to the ground, not elongating; tubercles large, obtuse; spines few, often lacking; fruits with long white wool	**22. *E. glabrescens***
-	Stems elongating with age; tubercles smaller, pronounced; spines numerous; fruits with short wool	**20. *E. fulva***
35.	Fruits short barrel-shape; perianth remnant area and attach basal pore large; fruit-wall thick at maturity	**43. *E. spectabilis***
-	Fruits ellipsoid, elongating; perianth remnant area small, basal pore small; fruit-wall thin	36
36.	Stems hard, bluish grey-green; fruits with black bristles	**37. *E. recondita***
-	Stems soft, grey-brown; fruits with white bristles	**34. *E. occulta***
37.	Flowers tubular, always fuchsia, hypanthium long in relation to pericarpal length	40
-	Flowers (narrowly)funnel-form, fuchsia or not hypanthium short in relation to pericarpal length	38
38.	Stems much elongating; flowers fuchsia; roots fibrous	**9. *E. chilensis***
-	Stems only moderately or not elongating; flowers not fuchsia; taproots	39
39.	Stems somewhat elongating, apex woolly; flowers with plenty of white hairs and bristles	**41. *E. simulans***
-	Stems (sub)globose, apex not woolly; flowers not as above	**23. *E. heinrichiana***
40.	Roots tuberous or (short)taproots; perianth segments narrowly lanceolate with long tips	41
-	Roots fascicular; perianth segments broader, apex often rounded	49
41.	Flowers not exceeding spines; fruits medium-sized to small, ellipsoid or slender	42
-	Flowers exceeding spines; fruits ovoid to globose, larger	43
42.	Flowers medium-sized, carmine-fuchsia; fruits, medium-sized, ellipsoid	44
-	Flowers small, pale fuchsia; fruits small, slender	45
43.	Ribs up to16; spines numerous, acicular, often hair-like, contorted	**49. *E. villosa***
-	Ribs fewer; spines less numerous, thicker, never hair-like nor contorted	**48. *E. vallenarensis***
44.	Spines numerous, completely obscuring stems; these small; areoles small	**29. *E. litoralis***
-	Spines less numerous; stems thicker; areoles larger	**50. *E. wagenknechtii***
45.	Stems much elongating, clavate; ribs few; spines few, short	**10. *E. clavata***
-	Stems only moderately elongating; ribs more numerous; spines more numerous, longer	46
46.	Spines flexible, soft, completely hiding stems	47
-	Spines not as above	48
47.	Stems elongating; flowers very large, bristles inconspicuous	**40. *E. senilis***
-	Stems smaller; flowers smaller, bristles long and numerous	**16. *E. elquiensis***
48.	Flowers very large, bristles numerous; stems green	**11. *E. coimasensis***
-	Flowers smaller, bristles few; stems dark grey-green	**33. *E. nigrihorrida***
49.	Stems much elongating; stigma lobes not exserted beyond perianth segments	**45. *E. subgibbosa***
-	Stems only moderately elongating; stigma lobes exserted	**8. *E. castanea***

Tribe Cereeae Salm-Dyck:—Nyffeler & Eggli (2010) proposed a broader circumscription of the tribe Cereeae than traditional concepts (see e.g., Anderson 2001, 2005, Hunt *et al.* 2013). Lendel (2006) and Ritz *et al.* (2007) showed, in fact, that the traditionally circumscribed Cereeae and Trichocereeae are not monophyletic. Therefore, we follow Nyffeler & Eggli's (2010) concept of a tribe Cereeae with three subtribes, i.e. Cereinae Britton & Rose, Rebutiinae Donald (incl. Browningieae Buxb.) and Trichocereinae Britton & Rose.

Subtribe Rebutiinae Donald. (incl. Browningieae Buxb.):—Various molecular-based studies (e.g. Lendel *et al*. 2006, Ritz *et al.* 2007) showed that *Browningia* Britton & Rose is closely related to *Rebutia* K.Schum., while other authors using only morphology-based characters (e.g. Hunt *et al.* 2013, Anderson 2001, 2005) placed the two genera in different tribes: Hunt *et al.* (2013) placed *Browningia* in tribe Cereeae and *Rebutia* in tribe Trichocereeae, whereas Anderson (2001, 2005) placed *Rebutia* in Trichocereeae and *Browningia* in Browningieae (together with *Stetsonia* Britton & Rose, *Jasminocereus* Britton & Rose*, Armatocereus* Backeb. and *Neoraimondia* Britton & Rose). We here accept to include Browningieae in the tribe Rebutiinae.

Subtribe Trichocereinae Britton & Rose (1920):—Most of the genera in Subtribe Trichocereine are also found in the traditional concept "Trichocereae" and the same applies to all the five Chilean genera [*Haageocereus* Backeb., *Leucostele* Backeb., *Lobivia* Britton & Rose, *Oreocereus* (A.Berger) Riccob., and *Soehrensia* Backeb.] in the Subtribe Trichocereinae. Based on DNA sequences and a broad sampling, Schlumperger & Renner (2012) showed that the large genus *Echinopsis* Zucc. is polyphyletic. Consequently, many former segregate genera were reinstalled, and the names of the Chilean taxa needed to be changed from *Echinopsis* s.l. into *Leucostele* Backeb., *Lobivia* Britton & Rose, and *Soehrensia* Backeb. (Schlumpberger 2012). Hunt (2012, 2016, see Table 2), accepted Schlumperger's concept as "alternative", while Rodríguez *et al.* (2018) still upheld the *Echinopsis* s.l. concept.

Concerning the genus *Leucostele*, the old name *Cactus coquimbanus* Mol. has recently been rejected for being ambiguous (Eggli & Walter 2012) and Wilson (2016). Consequently, all combinations using this basionym must be abandoned. Among them is "*Leucostele coquimbana* (Mol.) Schlumpb.". A new combination of *Cereus nigripilis* Phil., which represents the shrubby columnar plants occurring along the coast from the Coquimbo- to the Atacama Region was recently proposed [*Leucostele nigripilis* (Phil.) P.C. Guerrero & Helmut Walter (see Guerrero & Walter 2019 and Table 2)]. Several new taxa in the genus *Leucostele* were also recently proposed in different journals. As none of them had been included in the sampling of a molecular-based study, we decided not to accept them as long as they are supported by molecular phylogenies: *L. faundezii* (Albesiano) Schlumpb., *L. pectinifera* (Albesiano) Schlumpb., and *L. undulosa* (Albesiano) Schlumpb. (Korotkova *et al.* 2021).

Acknowledgements

We thank B. Bates and U. Eggli (Sukkulenten-Sammlung, Zürich) by their comments on some species nomenclature. This study was funded by the Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT) 1211441 and ANID PIA/BASAL FB210006 grants.

References

Anderson, E.F. (2001) *The Cactus Family*. Portland, Timber Press, 776 pp.

Anderson, E.F. (2005) *Das große Kakteenlexicon*. Stuttgart, Ulmer, 744 pp.

Arakaki, M., Cristin, P.A., C., Nyffeler, R., Lendel, A. Eggli, U., Ogburn, R.M. Spriggs, E., Moore, M.J. & Edwards, E. (2011) Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proceedings of the National Academy of Sciences of the United States of America* 108: 8379–8384. https://doi.org/10.1073/pnas.1100628108

Backeberg, C. (1958–1962) *Die Cactaceae*, vol. 6. Jena, Gustav Fischer Verlag, 374 pp.

Backeberg, C. (1977) *Das Kakteenlexikon, Enumeratio diagnostica Cactacearum* (4.ed.). Stuttgart, Fischer Verlag, 822 pp.

Backeberg, C. (1936) *Jahrbücher der Deutschen Kakteengesellschaft in der Deutschen Gesellschaft für Gartenkultur* 1: 104. pp.144

Bárcenas, R.T., Yesson, C. & Hawkins, A. (2011) Molecular systematics of the Cactaceae. *Cladistics* 27: 1–20. https://doi.org/10.1111/j.1096-0031.2011.00350.x

Barthlott, W. & Hunt, D. (1993) Cactaceae Juss. *In*: Kubitzki, K (ed.) *The families and Genera of Vascular Plants*, vol. 2. Berlin, Springer Verlag, pp. 161–197.

https://doi.org/10.1007/978-3-662-02899-5_17

Bregnan, R. (2002) Some notes on the recent taxonomic confusion in cacti. *Cactaceae Systematics Initiatives* 13: 18–20.

Britton, N.L. & Rose, J.N. (1920) *The Cactaceae*, vol. 3. Washington, Carnegie Institution, 248 pp.

Crozier, B.S. (2005) *Systematics of Cactaceae Juss.: phylogeny cpDNA evolution and classification, with emphasis on the genus Mammilaria Haw.* Dissertation, The University of Texas at Austin, 154 pp.

Doweld, A.B. (2002) On the phylogeny and systematics of the genus *Copiapoa* Britton & Rose. *Sukkulenty 2001, series I–II* 4: 46–56.

Duarte, M., Guerrero, P.C., Carvallo, G. & Bustamante, R.O. (2014) Conservation network design for endemic cacti under taxonomic uncertainty. *Biological Conservation* 176: 236–242.
https://doi.org/ 10.1016/j.biocon.2014.05.028

Edwards, E.J., Nyffeler, R. & Donoghue, M.J. (2005) Basal cactus phylogeny: Implications of *Pereskia* (Cactaceae) paraphyly for the transition to the cactus life form. *American Journal of Botany* 92: 1177–1188.
https://doi.org/10.3732/ajb.92.7.1177

Eggli, U. & Walter, H.E. (2012) Proposal to reject the name *Cactus coquimbanus* (Cactaceae). *Taxon* 61: 686–687.
https://doi.org/10.1002/tax.613024

Eggli, U., Schick, E. & Leuenberger, B.E. (1995) Cactaceae of South America: The Ritter Collections. *Englera* 16: 1–646.
https://doi.org/10.2307/3776764

Espinosa, M.R. (1933) Una *Opuntia* nueva chilena. *Revista Chilena de Historia Natural* 37: 126–130.

Förster, C.F. (1846) *Handbuch der Cacteenkunde*. Leipzig, Wöller Verlag, 559 pp.

Griffith, M.P. & Porter, J.M. (2009) Phylogeny of *Opuntioideae* (Cactaceae). *International Journal of Plant Science* 170: 107–116.
https://doi.org/10.1086/593048

Guerrero, P.C. & Walter, H.E. (2019) Nomenclatural novelties and a new species in Chilean Cactaceae. *Phytotaxa* 392: 89 – 92.
https://dx.doi.org/10.11646/phytotaxa.392.1.11

Guerrero, P.C., Majure, L.C., Cornejo-Romero, A. & Hernández-Hernández, T. (2019a) Phylogenetic relationships and evolutionary trends in the Cactus family. *Journal of Heredity* 110: 4–21.
https://doi.org/10.1093/jhered/esy064

Guerrero, P.C., Walter, H.E., Arroyo, M.K.T, Peña, C., Tamburrino, I., De Benedictis, M. & Larridon, I. (2019b) Molecular phylogeny of the large South American genus *Eriosyce* (Notocacteae, Cactaceae): Generic delimitation and proposed changes in infrageneric and species ranks. *Taxon* 68: 557–573.
https://doi.org/10.1002/tax.12066

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/10.1002/tax.12066

Hoffmann, A.E. (1989) *Cactáceas en la flora de Chile*. Fundacion Claudio Gay, Santiago de Chile, 272 pp.

Hoffmann, A.E. & Walter, H.E. (2004) *Cactáceas en la flora de Chile*, 2nd ed. Fundación Claudio Gay, Santiago de Chile, 307 pp.

Hunt, D. (2001) Coping with *Copiapoa* – continued. *Cactaceae Systematics Initiatives* 12: 15–17.

Hunt, D. (2003) Subg. *Horridocactus*. *Cactaceae Systematics Initiatives* 16: 9–10.

Hunt, D. (2011) Classification of the “cyndroid” opuntias of South America. *Cactaceae Systematics Initiatives* 25: 5–29.

Hunt, D. (2012) Tricky Trichos. *Cactaceae Systematics Initiatives* 28: 3–4.

Hunt, D. (2016) *CITES Cactaceae Checklist* Third Edition. Milborne Port, Remous Limited, 175 pp.

Hunt, D., Taylor, N. & Charles, G. (2006) *The New Cactus Lexicon*. DH Books, Milborn Port, 526 pp.

Hunt, D., Taylor, N. & Charles, G. (2013) *The New Cactus Lexicon, Atlas of Illustrations*. Dh Books, Milborn Port, 373 pp.

Kattermann, F. (1994) *Eriosyce* (Cactaceae) The genus revised and amplified. *Succulent Plant Research* 1: 5–176.

Kiesling, R. (1984) Estudios en Cactaceae de Argentina: *Maihueniopsis*, *Tephrocactus* y generosafines (Opuntioideae). *Darwiniana* 25: 171–215.

Korotkova, N., Zabel. I., T., Quandt, D. & Bartlott, W. (2010) A phylogenetic analysis of *Pfeiffera* and the reistatement of *Lymanbensonia* as an independently evolved lineage of epiphytic Cactaceae within a new tribe Lymanbensonieae. *Willdenowia* 40: 151–172.
https://doi.org/10.3372/wi.40.40201

Korotkova, N., Aquino, D., Arias, S., Eggli, U., Franck, A., Gómez-Hinostrosa, C., Guerrero, P.C., Hernández, H.M., Kohlbecker, A., Köhler, M., Luther, K., Majure, L.C., Müller, A., Metzing, D., Nyffeler, R., Sánchez, D., Schlumpberger, B. & Berendsohn, W.G. (2021) Cactaceae at Caryophyllales.org – a dynamic online species-level taxonomic backbone for the family. – *Willdenowia* 51: 251–270.
https://doi.org/10.3372/wi.51.51208

Labouret, M. (1853) *Monographie de la fámille des Cactées*. Dusaq, Paris, 682 pp.

Larridon, L., Walter, H.E., Guerrero, P.C., Duarte, M., Cisterna, M.A., Pena Hernández, C., Bauters, K., Asselmann, P., Goetghebeur, P.

& Samain, M-S. (2015) An integrative approach to understanding the evolution and diversity of *Copiapoa* (Cactaceae), a threatened endemic Chilean genus from the Atacama desert. *American Journal of Botany* 102: 1506–1520.
https://doi.org/10.3732/ajb.1500168

Larridon, L., Walter, H.E., Rosas, R., Vandomme, V. & Guerrero, P.C. (2018a) Evolutionary trends in the columnar catus genus *Eulychnia* (Cactaceae) based on molecular phylogenetics, morphology, distribution and habitat. *Systematics and Biodiversity* 16: 643–657.
https://doi.org/10.1080/14772000.2018.1473898

Larridon, I., Veltjen, E., Semmouri, I., Asselmann, P., Guerrero, P.C., Duarte, M., Walter, H.E., Cisternas, M.A. & M.-S. Samain (2018b) Investigating taxon boundareries and extinction risc in endemic Chilean cacti (*Copiapoa* subsection Cinerei, Cactaceae) using chloroplast DNA sequences, microsatellite data and 3D mapping. *Kew Bulletin* 73: 1–17.
https://doi.org/10.1007/s12225-018-9780-3

Lendel, A. (2006) Phylogenetic relationships in the tribe *Trichocereeae* (Cacteae) inferred from cpDNA sequence data analysis. *IOS Bulletin* 14: 11–12

Lüthy, J.M. (1994) *Eriosyce laui* J. Lüthy sp. nov. *In*: Kattermann, F. (Eds.) *Eriosyce (Cactaceae) the genus revised and amplified. Succulent Plant Research*, vol. 1. Privately published by David Hunt & Nigel Taylor, Richmont, pp. 5–176.

Mace, G.M. (2004) The role of taxonomy in species conservation. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 359: 711–719.
https://doi.org/10.1098/rstb.2003.1454

Majure, L.C., Puente, R., Griffith, M.P., Judd, W.S., Soltis, P.S. & Soltis, D.E. (2012) Phylogeny of *Opuntia* s.s. (Cactaceae): clade delineation, geographic origins, and reticulate evolution. *American Journal of Botany* 99: 847–864.
https://doi.org/10.3732/ajb.1100375

Majure, L.C., Baker, M.A., Cloud-Hughes, M., Salywon, A. & Neubig, K.M. (2019) Phylogenomics in Cactaceae: A case study using the chollas *sensu lato* (Cylindropuntieae, Opuntioideae) reveals a common pattern out of the Chihuahuan and Sonoran deserts. *American Journal of Botany* 106: 1327–1345.
https://doi.org/10.1002/ajb2.1364

Marticorena, C. & Rodríguez, R. (2011) *Flora de Chile*: *Misodendraceae a Zygophyllaceae.* Ediciones Universidad de Concepción, Concepción, 148 pp.

Merklinger, F.F., Böhnert, T., Arakaki, M., Weigend, M. & Quandt, D. (2021) Luebert F. Quaternary diversification of a columnar cactus in the driest place on earth. *American Journal of Botany* 108: 184–199.
https://doi.org/10.1002/ajb2.1608

Moore, A.J., De Vos, J.M., Hancock, L.P., Goolsby, E. & Edwards, E.J. (2017) Targeted enrichment of large gene families for phylogenetic inference: phylogeny and molecular evolution of photosynthesis genes in the *Portullugo* clade (Caryophyllales). *Systematic Biology* 67: 367–383.
https://doi.org/10.1093/sysbio/syx078

Mottram, R. (2001) *Rimacactus*, a new genus of Cactaceae. *Bradleya* 19: 75–82.
https://doi.org/10.25223/brad.n19.2001.a9

Nyffeler, R. (2002) Phylogenetic relationships in the Cactus family. *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: 109–149.

Philippi, R. (1860) *Florula Atacamensis*. Halle, Verlag Eduard Anton, 62 pp.

Ritter, F. (1980) *Kakteen in Südamerika*, vol. 3. Friedrich Ritter Selbstverlag, Spangenberg, 381 pp.

Ritz, C., Martins, L., Mecklenburg, R., Goremykin, V. & Hellwig, F.H. (2007) The molecular phylogeny of *Rebutia* (Cactaceae) and its allies demonstrates the influence of paleography on the evolution of South American mountain cacti. *American Journal of Botany* 94: 1321–1332.
https://doi.org/10.3732/ajb.94.8.1321

Ritz, C.M., Reiker, J., Charles, G., Hoxey, P., Hunt, D., 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

Rodríguez, R., Marticorena, C., Alarcón, D., Baeza, C., Cavieres, V., Finot, L., Fuentes, N., Kiessling, A., Mihoc, M., Pauchard, A., Ruiz, E., Sanchez, P. & Marticorena, A. (2018) Catálogo de las plantas vasculares de Chile. *Gayana Botánica* 75: 1–430.
http://dx.doi.org/10.4067/S0717-66432018000100001

Salm-Dyck, J. (1849) *Cactaceae Hortus Dyckensis* 34: 170–171.

Schlumpberger, B.O. (2012) New combinations in the *Echinopsis* alliance. *Cactaceae Systematic Initiatives* 28: 30–32.

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

Stuppy, W. (2002) Seed characters and the classification of the Opuntioideae. Studies in the Opuntieae (Cactaceae). *Succulent Plant Research* 6: 25–58.

Stuessy, T.F. (2009) *Plant taxonomy: the systematic evaluation of comparative data*, 2nd ed. Columbia University Press, 565 pp.

Taylor, N.P. (2001) Roots and mucilage in *Copiapoa. Cactaceae Systematics Initiative* 12: 18.

Vergara, E. (2011) *World's driest desert hits snow rain. NBC News*. Available from http://www.nbcnews.com (accessed 27 January 2022).

Villalobos-Barrantes, H.M., Meriño, B.M., Walter, H.E. & Guerrero, P.C. (2022) Independent evolutionary lineages in a globular cactus species complex reveals hidden diversity in a Central Chile biodiversity hotspot. *Genes* 13: 240. https://doi.org/10.3390/genes13020240

Wallace, R.S. (1994) Phylogenetic analysis of *Eriosyce*. *In*: Hunt, D & Taylor, N. (Eds.) *Eriosyc*e *(Cactaceae): The genus revised and amplified. Succulent Plant Research*, vol. 1. Privately published by David Hunt & Nigel Taylor, Richmond, pp. 5–176.

Wallace, R.S. & Cota, J.H. (1996) An intron loss in the chloroplast gene *rpo*C1 supports a monophyletic origin for the subfamily Cactoideae of the Cactaceae. *Current genetics* 29: 275–281. https://doi.org/10.1007/BF02221558

Wallace, R.S. & Dickie, S.L. (2002) Systematic implications of chloroplast DNA sequence variation in subfam. Opuntioideae (Cactaceae) Studies in the Opuntieae (Cactaceae). *Succulent Plant Research* 6: 9–24.

Walker, J.F, Yang, Y., Feng, T., Timoneda, A., Mikenas, J., Hutchison, V., Edwards, C., Wang, N., Ahluwalia, S., Olivieri, J., Walker-Hale, N., Majure, L.C., Puente, R., Kadereit, G., Lauterbach, M., Eggli, U., Flores-Olvera, H., Ochoterena, H., Brockington, S.F., Moore, M.J. & Smith, S.A. (2018) From cacti to carnivores: improved phylotranscriptomic sampling and hierarchical homology inference provide further insight into the evolution of Caryophyllales. *American Journal of Botany* 105: 446–462. https://doi.org/10.1002/ajb2.1069

Walter, H.E. (2011) Typification of *Copiapoa conglomerata* (Phil.) Lembcke: "A re–evaluation of the evidence for the correct identity of *Copiapoa conglomerata* and its neotypification *Cactus World* 29: 103–104.

Walter, H.E. (2019) The cacti of the Chilean Patagonia. *Cactus World* 37: 49–56.

Wilson, K.L. (2016) Report of the General Committee. *Taxon* 65: 878. https://doi.org/10.12705/654.15

WFO (2021) *World Flora Online*. Available at: http://www.worldfloraonline.org (accessed 27 January 2022).