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An Emendation of *Rhodocactus*, a Genus Segregated from *Pereskia* (*Cactaceae*)

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The genus *Pereskia* Mill. (*Cactaceae*), distributed in Latin America, is an archaic cactus characterized by the developed leaf blades. A molecular analysis of the genus (Edwards et al. 2005) found that *Pereskia* s.l. was grouped into three clades; 'Andean', 'southern South American (SSA)' and 'Northern'. Accordingly, a new genus, *Leuenbergeria*, was established for the 'Northern' clade based on some morphological differences (Lodé 2013). The 'Andean' and the 'SSA' clades have usually not been treated as independent genera, even though they are sister groups. Moreover, the 'Andean' and the 'SSA' clades differ in presence/absence of foliage leaves on brachyblast. We here propose to apply *Pereskia* s. str. for the 'Andean' clade and *Rhodocactus* (A. Berger) F. M. Knuth for the 'SSA' clade. We here describe and provide new combinations for five species under *Rhodocactus*.

Key words: *Cactaceae*, cactus, *Leuenbergeria*, *Pereskia*, *Pereskioideae*, *Rhodocactus*.

Cactaceae are characterized by a succulent habit and spines with areoles, a kind of brachyblast. They comprise 1,816 species in 124 genera (Hunt 2006). The family was classified into three tribes: *Pereskieae*, *Opuntieae* and *Cereeae* (Britton and Rose 1919), or three subfamilies: *Pereskioideae*, *Opuntioideae* and *Cereoideae* (Backeberg 1958, Ito 1988). Fearn (1996) proposed that the genus *Maihuenia* placed in the *Maihuenioideae*. The *Cactaceae* are therefore classified as including four subfamilies: *Pereskioideae*, *Maihuenioideae*, *Opuntioideae* and *Cactoideae* (= *Cereoideae*) (Anderson 2001, Hunt 2013).

The *Pereskioideae*, characterized by foliage leaves and distributed from forested areas to dry groves in Latin America, are thought to be the most primitive members of *Cactaceae* based on the unique foliage character and have traditionally been treated as a single genus, *Pereskia* (e.g. Hunt 2006). As such, *Pereskia* comprises 17 species.

A molecular analysis of *Cactaceae*, especially focusing on *Pereskia*, revealed that *Pereskia* s.l. is polyphyletic (Edwards et al. 2005) and divisible into three clades: 'Andean', 'southern South American (SSA)' and 'Northern'. Although dendrograms showed different topologies depending on the study (Butterworth and Wallace 2005, Crozier 2005, Arakaki et al. 2011), the 'Andean', 'SSA' and 'Northern' clades consistently formed distinct

groups in all of those studies, except one species, *P. lychnidiflora*, that was assigned to different positions in some cases. Accordingly, a new genus, *Leuenbergeria*, was established for the 'Northern' clade based on some morphological differences (Lodé 2013). For the remaining clades, the 'Andean' and the 'SSA' clades were always shown to be polyphyletic or paraphyletic. Arakaki et al. (2011) reported the genetic affiliation between the 'Andean' and 'SSA' clades to be comparable to the genetic affiliation among *Cactoideae*, *Maihuenioideae* and *Opuntioideae*, indicating that the 'Andean' and 'SSA' clades diverged earlier than other genera in *Cactaceae*.

The 'Northern' clade has such ancestral characteristics, as stems without stomata and bark formed precociously, that are not shared by other clades (Edwards and Donoghue 2006). The 'SSA' clade is distinctly arborescent, produces pink flowers and has foliage leaves on brachyblasts (brachyblast leaves), whereas the 'Andean' clade are climbers or undershrubs, produces smaller flowers and does not have brachyblast leaves but has spines on brachyblast (Leuenberger 1986).

For the nomenclature, the 'Andean' clade contains type species of *Pereskia*, *P. aculeata* Mill. Since the type species of *Rhodocactus*, *R. grandifolius* (Haw.) F. M. Knuth is assignable to the 'SSA' clade, all the species in that clade should belong to *Rhodocactus*. *Rhodocactus*, however, cannot be applied to the 'SSA' clade in the original sense.

Rhodocactus was described by Berger (1926) as a subgenus of *Pereskia* and later elevated to generic level by Knuth (1935). *Rhodocactus* was defined on the basis of having parietal placentation and a more developed receptacle surrounding the ovary. Knuth (1935) listed 11 species in the genus, but all of the species of *Rhodocactus*, except for *R. grandifolius* are in the 'Andean' or 'Northern' clades, not in the 'SSA' clade (Edwards et al. 2005). The 'Andean' clade should be included in *Pereskia*. We here redefine *Rhodocactus* as comprising five species: *R. grandifolius*, *R. bahiensis* (Gürke) I. Asai & K. Miyata, *R. nemorosus* (Rojas) I. Asai & K. Miyata, *R. sacharosa* (Griseb.) Backeb., and *R. stenanthus* (F. Ritter) I. Asai & K. Miyata.

Key to the genera of *Pereskioideae* (*Cactaceae*)

1. Stem without stomata; bark precocious .... *Leuenbergeria*
1. Stem with stomata (except in *R. nemorosus*); bark formation delayed (except in *P. aculeata*);
   2. Brachyblast leaves present ... *Rhodocactus*
   2. Brachyblast leaves absent (spines only present) ..... *Pereskia*

Taxonomic treatment

Rhodocactus (A. Berger) F. M. Knuth, Kaktus-ABC: 96 (1935). Emended here.

Pereskia subg. *Rhodocactus* A. Berger, Kakteen [Backeb. & Knuth]: 43 (1929).

Type: *Rhodocactus grandifolius* (Haw.) F. M. Knuth (= *Pereskia grandifolia* Haw.)

Trees, 3–7 m tall. Bark formation delayed. Brachyblast leaves present. Flowers 3–5 cm in diam. 'SSA' clade in molecular phylogenetics (Edwards et al. 2005).

Distribution: Brazil, Bolivia, Paraguay, N Argentina, NW Uruguay.

Key to the species of *Rhodocactus*

1. Stem without stomata ..... 3. *R. nemorosus*
1. Stem with stomata
   2. Flower petals erect or ascending .... 5. *R. stenanthus*
   2. Flower petals spreading
      3. Leaves mostly narrowly elliptic-obovate to elliptic-lanceolate; lateral veins 10–13 ..... 1. *R. grandifolius*
      3. Leaves mostly obovate or elliptic-obovate; lateral veins 4–7
         4. Tomentum of areoles pale gray; stomata present only around areoles ..... 4. *R. sacharosa*
         4. Tomentum of areoles brown at least

in youth; stomata scattered on whole stem ..... 2. *R. bahiensis*

1. ***Rhodocactus grandifolius*** (Haw.) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 97 (1935). Neotype (Leuenberger 1986): Cult. hort. Kew. "raised from seed collected by Bowie & Cunningham in 1816 in the neighbourhood of Rio de Janeiro." Drawing by T. Duncanson, June 11, 1824 (K).

Pereskia grandifolia Haw., Revis. Pl. Succ. 85 (1821).

Cactus grandifolius (Haw.) Link, Enum. Hort. Berol. Alt. **2**: 25 (1822).

subsp. ***grandifolius***.

Pereskia ochnocarpa Miquel, Bull. Sci. Phys. Nat. Neerl. **1**: 48 (1838). Type: Brazil. Illustration of *Cactus rosea* Vellozo (nom. nud.), Fl. flum. **5**: 27. (1827).

Pereskia rosea Hort. ex A. Dietrich, Allg. Gartenzeitung **19**: 152 (1851). Type: Cult. hort. Berol. "recieved from F. A. Haage, Erfurt, a specimen of unknown origin." Not preserved.

Pereskia tampicana F. A. C. Weber, Bull. Mus. Hist. Nat. (Paris) **4**: 167 (1898). Type: Mexico. Tamaulipas: Nr. Tampico, at El Paso de Doña Cecilia on the Río Pánuco, ca. 1895, Heese s.n. Not preserved.

Rhodocactus tampicanus (F. A. C. Weber) Backeb., Cactaceae **1**: 115 (1958).

Distribution: E Brazil.

subsp. ***violaceus*** (Leuenb.) I. Asai & K. Miyata, **comb. nov.**

Basionym: *Pereskia grandifolia* Haw. var. *violacea* Leuenb. in Mem. New York Bot. Gard. **41**: 116 (1986). Type: BRAZIL. Minas Gerais: Mun. de Santana do Riacho, area do futuro Parque Estadual da Serra do Cipó, 650 m, 23 Sep 1981, da Silva 89 (HRB–holotype).

Pereskia grandifolia Haw. subsp. *violacea* (Leuenb.) N. P. Taylor & Zappi, *Cactaceae* Consensus Init. **3**: 7 (1997).

Distribution: Espírito Santo and Minas Gerais, E Brazil.

2. ***Rhodocactus bahiensis*** (Gürke) I. Asai & K. Miyata, **comb. nov.**

Basionym: *Pereskia bahiensis* Gürke in Monatsschr. Kakteenk. **18**: 86 (1908). Lectotype (Leuenberger 1986): BRAZIL. Bahia: Calderão, Oct 1906, E. H. G. Ule 7050 (HBG).

Distribution: Bahia, Brazil.

3. ***Rhodocactus nemorosus*** (Rojas Acosta) I. Asai & K. Miyata, **comb. nov.**

Basionym: *Pereskia nemorosa* Rojas Acosta, Cat. Hist. Nat. Corrientes: 64 (1897). Neotype (Leuenberger 1986): ARGENTINA. Corrientes: Poso de los Libres, 10 Mar 1917, J. A. Shafer 127 (NY).

Pereskia amapola F. A. C. Weber, Dict. Hort. [Bois]: 939 (1898). Type: PARAGUAY. Asunción, Mar 1877, Balansa 2671 (P–holotype).

Pereskia argentina F. A. C. Weber, Dict. Hort. [Bois]: 939 (1898). Type: Not cited. Description based on young, sterile plant grown from seed from Argentina.

Pereskia amapola var. *argentina* (F. A. C. Weber) F. A. C. Weber, Monatsschr. Kakteenk. [Weingart] **14**: 87 (1904). Type: Not preserved. Description based on living plant grown from seed collected by Grosse in Paraguay, ca. 1899.

Distribution: S Brazil, Paraguay, NE Argentina, NW Uruguay.

4. ***Rhodocactus sacharosa*** (Griseb.) Backeb., Kakteenlexikon 397 (1966). Type: ARGENTINA. Salta: Orán, frequens in sepibus, 1873, Lorentz & Hieronymus 410 (GOET–holotype).

Pereskia sacharosa Griseb. in Abh. Königl. Ges. Wiss. Göttingen **24**: 141 (1879).

Pereskia moorei Britton & Rose, Cactaceae (Britton & Rose) **1**: 15 (1919). Type: BRAZIL. Matto Grosso: Corumbá, Tannay, 1891–92, Moore 955 (BM–holotype).

Pereskia saipinensis Cárdenas, Cactus (Paris) **19**: 17 (1964). Type: BOLIVIA. Santa Cruz: Prov. Caballero, nr. Saipina, 1500 m, Nov 1962,

Cárdenas 6122 (Herb. Cardenasianum, specimen not located).

Rhodocactus saipinensis (Cárdenas) Backeb., Kakteenlexikon: 397 (1966).

Pereskia sparsiflora Ritter, Kakteen Südamerika **2**: 482 (1980). Type: BOLIVIA. Tarija: Villa Montes, 1958, Ritter 640 p.p. (U–holotype).

Distribution: S Brazil, Bolivia, Paraguay, NW Argentina.

5. ***Rhodocactus stenanthus*** (F. Ritter) I. Asai & K. Miyata, **comb. nov.**

Basionym: *Pereskia stenantha* F. Ritter, Kakteen Südamerika **1**: 21 (1979). Type: BRAZIL. Bahia: Caetité, FR 1251 (U–holotype).

Distribution: Bahia, Brazil.

Species excluded from *Rhodocactus*, in the sense of present study

Rhodocactus antonianus Backeb., Descr. Cact. Nov. **3**: 13 (1963). Type: Cult. in coll. Backeberg. "Regio orientalis cordillerarum." Not preserved, but illustrated in Backeberg, Kakteenlexicon: 695, fig. 370; 696, fig. 371 (1966).

Correct name: *Pereskia weberiana* K. Schum., Gesamtbeschr. Kakt.: 762 (1898). Type: BOLIVIA. Cochabamba: Tunari mountains, May 1892, Kuntze s.n. (NY–lectotype, Leuenberger 1986).

Rhodocactus autumnalis (Eichlam) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 96 (1935). Type: GUATEMALA. Progreso: San Augustin, Eichlam s.n. (B–holotype, destroyed). A drawing by Weingart of a fruit sent by Eichlam is at NY (copy of B).

Correct name: *Leuenbergeria lychnidiflora* (D. C.) Lodé, Cact.-Avent. Int. **97**: 27 (2013). Type: Drawing of "*Cactus fimbriatus*" in Mociño, Fl. Mex. ined. no. 1689, preserved at the Hunt Inst. Bot. Doc., Pittsburgh.

Rhodocactus bleo (F. M. Knuth) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 97 (1935). Type: COLOMBIA. Bolívar: nr. Badillas on the Magdalena river, May 1805, Humboldt & Bonpland 1546 (P–lectotype, Leuenberger 1986).

Correct name: *Leuenbergeria bleo* (F. M. Knuth) Lodé, Cact.-Avent. Int. **97**: 26 (2013).

Rhodocactus colombianus (Britton & Rose) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 97 (1935). Type: COLOMBIA. Magdalena: Santa Marta, Bonda, 50 m, 5 Apr 1898/99, H. H. Smith 1886 (NY–lectotype, Leuenberger 1986).

Correct name: *Leuenbergeria guamacho* (F. A. C. Weber) Lodé, Cact.-Avent. Int. **97**: 26 (2013). Type: VENEZUELA. Bolívar: Ciudad Bolivar and vic. on the Orinoco, 70 m, Feb–Mar 1921, L. Bailey & E. Bailey 1351 (US–neotype, Leuenberger 1986).

Rhodocactus conzattii (Britton & Rose) Backeb., Cactaceae **1**: 118 (1958). Type: MEXICO. Oaxaca: Salina Cruz, 23 Jan (Feb?) 1913, Conzatti s.n. (US, NY–syntype); Tehuantepec, Apr 1913, Conzatti s.n. (US–syntype).

Correct name: *Leuenbergeria lychnidiflora* (D. C.) Lodé, Cact.-Avent. Int. **97**: 27 (2013).

Rhodocactus corrugatus (Cutak) Backeb., Cactaceae **1**: 118 (1958). Type: Cultivated at Missouri Bot. Gard., origin unknown, 10 Sep 1951, Cutak s.n. (MO).

Correct name: *Leuenbergeria bleo* (Weber) Lodé, Cact.-Avent. Int. **97**: 26 (2013).

Rhodocactus cubensis (Britton & Rose) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 96 (1935). Type: CUBA. Oriente, 1856–57, Wright 205 (US–lectotype, Leuenberger 1986).

Correct name: *Leuenbergeria zinniiflora* (D. C.) Lodé, Cact.-Avent. Int. **97**: 27 (2013). Type: Drawing of "*Cactus zinniaeflorus*" in Mociño, Fl. Mex. ined. no. 1012, preserved at the Hunt

Inst. Bot. Doc., Pittsburgh.

Rhodocactus guamacho (F. A. C. Weber) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 97 (1935).

Correct name: *Leuenbergeria guamacho* (F. A. C. Weber) Lodé, Cact.-Avent. Int. **97**: 26 (2013).

Rhodocactus higueranus (Cárdenas) Backeb., Kakteenlex: 396 (1966). Type: BOLIVIA. Vallegrande: Near Higuera, 1600 m, Apr 1954, Candia s.n. in Herb. Cardenasianum no. 6123 (holotype not located, isotype indicated for US, but not located).

Correct name: *Pereskiopsis diguetii* (F. A. C.Weber) Britton & Rose, Smithsonian Misc. Collect. **50**: 332 (1907). Type: MEXICO. Etat de Jalisco: environs de Guadalajara, Diguet s.n. Mus. Natl. Hist. Nat. P00077252 (P–lectotype, Hutchison 1960).

Rhodocactus horridus (F. M. Knuth) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 97 (1935). Type: PERU. Jaén de Bracamoros, in collibus siccis, ad flumen Marañón, Aug 1802, Humboldt & Bonpland 3594 (P–lectotype, Leuenberger 1986).

Correct name: *Pereskia horrida* D. C., Prodr. [A. P. de Candolle] **3**: 475 (1828).

Rhodocactus lychnidiflorus (D. C.) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 97 (1935). Type: Drawing of "*Cactus fimbriatus*" in Mociño, Fl. Mex. ined. no. 1689, preserved at the Hunt Inst. Bot. Doc., Pittsburgh.

Correct name: *Leuenbergeria lychnidiflora* (D. C.) Lodé, Cact.-Avent. Int. **97**: 27 (2013).

Rhodocactus nicoyanus (F. A. C. Weber) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 97 (1935). Neotype (Leuenberger 1986): Nicoya, May 1900, Tonduz 14001 (US).

Correct name: *Leuenbergeria lychnidiflora* (D. C.) Lodé, Cact.-Avent. Int. **97**: 27 (2013).

Rhodocactus portulacifolius (L.) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 96 (1935). Lectotype (Leuenberger 1986): Haïti. le Fond Parisien, Cul de Sac, Plumier 1758, Pl. amer. tab. 197, fig. 1 (drawing).

Correct name: *Leuenbergeria portulacifolia* (L.) Lodé, Cact.-Avent. Int. **97**: 27 (2013).

Rhodocactus zinniiflorus (D. C.) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth]: 96 (1935).

Correct name: *Leuenbergeria zinniiflora* (D. C.) Lodé, Cact.-Avent. Int. **97**: 27 (2013).

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Lodé J. 2013. *Leuenbergeria*, a new genus in *Cactaceae*. Cact.-Avent. Int. **97**: 25–27.

浅井一作[a]，宮田一範[b, c]：**サボテン科ロドカクトゥス属の訂正 ― ペレスキア属からの分離**

ラテンアメリカに分布するサボテン科 *Pereskia* 属は，葉身を発達させる原始的なサボテンとされる．近年，広義の *Pereskia* 属は ‘Andean’，‘southern South American (SSA)’，‘Northern’ の 3 系統よりなることが報告され (Edwards et al. 2005)，2013 年には ‘Northern’ 系統に対して，早期の樹皮化という形質をもとに *Leuenbergeria* 属が設立された (Lodé 2013)．一方，‘Andean’ 系統と ‘SSA’ 系統は姉妹群とされるにもかかわらず，通常は別属として扱われていない．また，両群は短枝上の普通葉の有無ではっきりと区別される．そこで，‘Andean’ 系統に対して狭義の *Pereskia* 属を，‘SSA’ 系統に対して *Rhodocactus* 属を適用し，必要な記載の訂正と新組み合わせをおこなった．

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