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"That's *Opuntia*, that was!", again: a new combination for an old and enigmatic *Opuntia* s.l. (Cactaceae)

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Abstract

The genus *Opuntia* is one of the most emblematic of the cactus family (Cactaceae) and a species-rich clade within subfamily Opuntioideae. After molecular phylogenetic studies showed that the traditional broad circumscription of *Opuntia* could not be retained as the genus was polyphyletic, various segregated genera were recognize based on both morphological data and phylogenetic studies. Here, we reassessed an old and enigmatic taxon, *O. schickendantzii*, through molecular and morphological investigations. Our results support that *O. schickendantzii* was best circumscribed within the *Salmonopuntia* lineage based on molecular and morphological features. As a consequence, a new combination is proposed, and an epitype from the herbarium BAF is designated. An updated description of the taxon with illustrations is also given.

Keywords: cacti, *Opuntia schickendantzii*, Opuntieae, prickly pear, *Salmonopuntia*, taxonomy

Introduction

Reconciling traditional taxonomy with modern molecular systematics is one of the major foci for evolutionary biologists (Podani 2009). Many different issues have been reported as challenges, i.e. parallel and convergent evolution of morphological characters (Wu *et al.* 2015), hybridization and reticulate evolution (Morales-Briones *et al.* 2018), cryptic speciation (Surveswaran *et al.* 2018), as well as incongruence between different molecular markers (Zhang *et al.* 2015). Although novel classification systems have been proposed to classify organisms through a strict phylogenetic framework (Queiroz & Gauthier 1994), the traditional hierarchical Linnaean system is still largely useful to recognize biological groups in a practical way (Schuh 2003), but nomenclature must reflect monophyletic groups, at least above the species level (De Queiroz 2007).

Cacti are a fascinating clade of seed plants exhibiting an enormous diversity of growth forms, morphology, and intriguing niche occupancy across the Americas (Britton & Rose 1919, Anderson 2001, Hunt *et al.* 2006, Hernández-Hernández *et al.* 2011). The taxonomy and systematics of Cactaceae have long been based on morphological characters (Schumann 1899, Britton & Rose 1919, Backeberg 1958). However, with the advance of molecular data to reconstruct phylogenies, systematic biologists have been able to produce more reliable hypothesis about the relationships of this peculiar group, which is replete with homoplasious morphological characters (Nyffeler 2002, Nyffeler & Eggli 2010, Hernandez-Hernandez *et al.* 2011, Bárcenas *et al.* 2011).

Three major well-supported clades are currently circumscribed as subfamilies in Cactaceae: Opuntioideae K.Schum., Maihuenioideae P.Fearn, and Cactoideae Eaton (Guerrero *et al.* 2018), whereas the traditional "Pereskioideae" subfamily has been revealed as a basal grade including the two major perennial-leafy lineages of cacti (Edwards *et al.* 2005). Opuntioideae are the most widespread subfamily and the second major lineage of cacti in the number of species, comprising three tribes: Cylindropuntieae Doweld, Tephrocacteae Doweld, and Opuntieae DC. (Köhler *et al.* 2020a).

Tribe Opuntieae currently consists of the following seven genera: *Brasiliopuntia* (K.Schumann 1899: 651) A.Berger (1926: 17), *Consolea* Lemaire (1862: 174), *Miqueliopuntia* Frič ex F.Ritter (1980a: 869), *Opuntia* Miller (1754: without pagination), *Salmonopuntia* P.V.Heath (1999: 41), *Tacinga* Britton & Rose (1919: 39), and *Tunilla* D.R.Hunt & Iliff (2000: 10) (Majure & Puente, 2014, Köhler *et al.* 2020a). However, most of the species have been historically lumped in a broadly circumscribed *Opuntia* s.l., including members of other tribes, such as Cylindropuntieae and Tephrocacteae (Schumann 1899, Britton & Rose 1919, Backeberg 1958). After molecular studies showed that *Opuntia* (s.l.) was polyphyletic (Wallace & Dickie, 2002, Griffith & Porter 2009), many segregated genera have been recognized based on morphological characters and well-supported clades (Stuppy 2002, Taylor *et al.* 2002, Majure *et al.* 2013, Majure & Puente 2014).

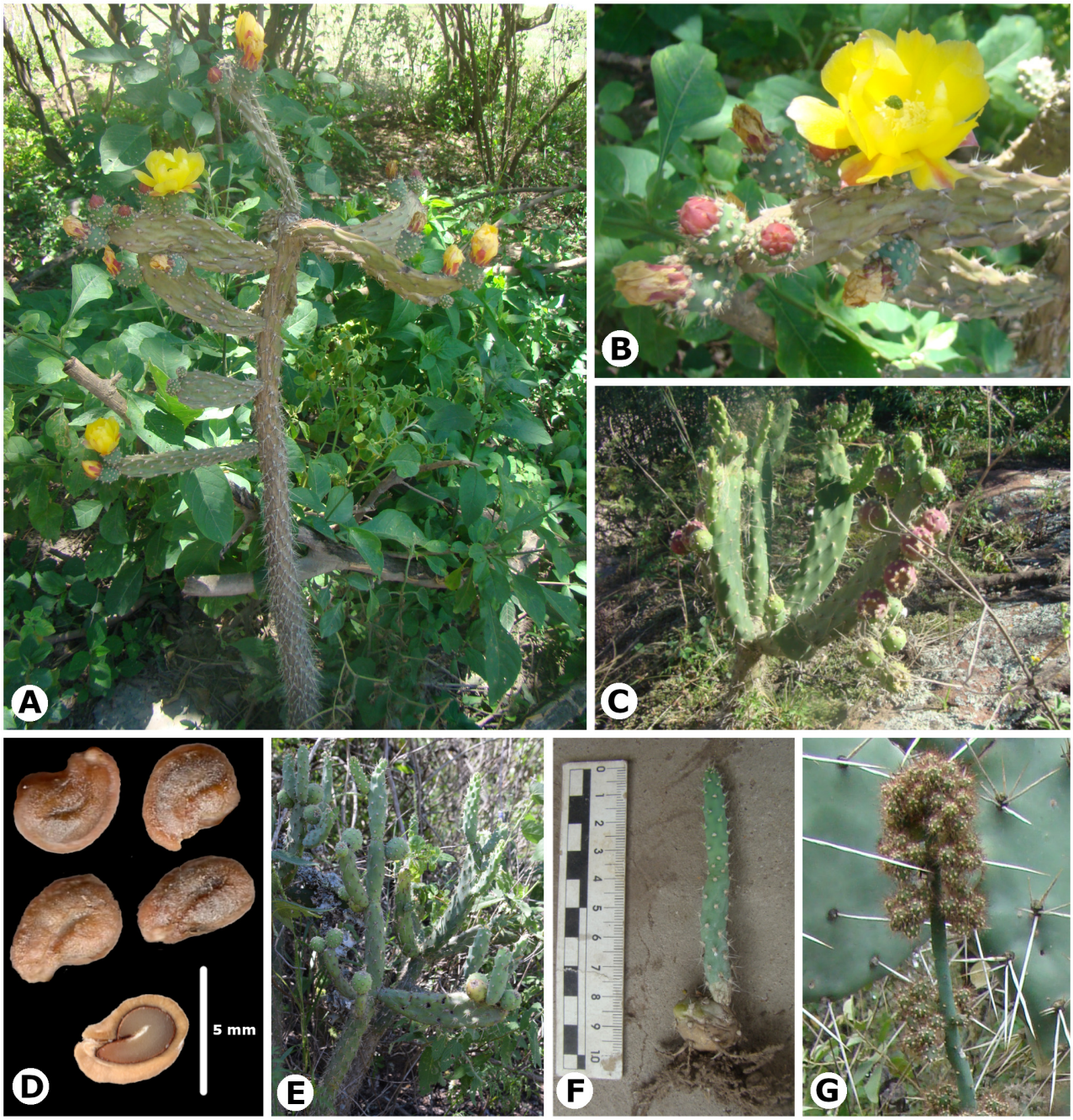

FIGURE 1. Morphological features of *Salmonopuntia*: *S. schickendantzii* (A−F) and *S. salmiana* (G). **A.** Plant in habitat showing the primary monopodial terete stem (Quebrada de Escoipe, Salta, Argentina). **B.** Detail of the secondary flattened stem, acute flower bud apex, bright yellow tepals, and the emerald stigma (Ibid.). **C.** Detail of the fruits and spherical immature propagules (*Font 660*). **D.** Seeds, and cross-section of a seed showing the hoop-shaped embryo (*Font 660*). **E.** Detail of the spherical propagules (Chicoana, Salta, Argentina). **F.** Juvenile plant growing from the spherical propagule (*Font 660*). **G.** Detail of the spherical propagules of *S. salmiana* (Catamarca, Argentina, *Font 494*). All photographs by F. Font, except E by Lucas Kaminski.

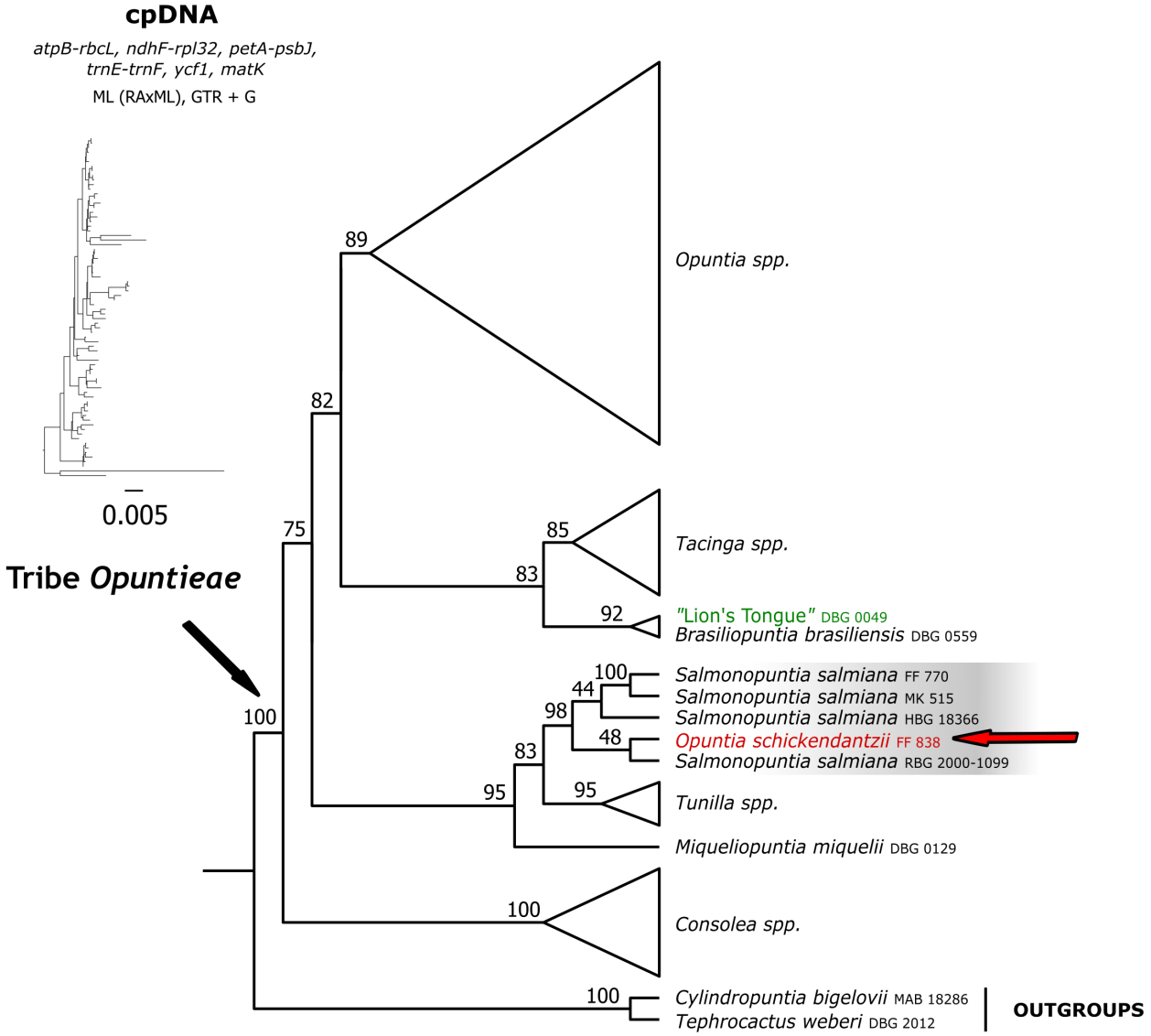

FIGURE 2. Phylogenetic placement of *Opuntia schickendantzii* (red arrow and tip label) in the tribe Opuntieae within the *Salmonopuntia* lineage (gray highlighted). Analysis based on combined plastid sequences and a maximum likelihood inference from RAxML. Bootstrap support values are shown above the branches and the phylogram is represented in small size with substitution rate scaled upper-left.

Opuntia schickendantzii F.A.C.Weber (in Bois 1898: 898) is an old and enigmatic species described based on material from Catamarca and Tucumán (Argentina), in the subgenus *Cylindropuntia* Engelmann (1856: 302) (Bois 1898). The description comprises diagnostic characters that conform to wild plants that currently occur along the northwestern mountainous region of Argentina (Catamarca, Jujuy, Salta, and Tucumán Provinces) and Bolivia (Cochabamba, Chuquisaca, and Tarija Departments), such as the green-glaucescent cylindrical primary stem, spiny areoles, bright-yellow flowers with emerald-green stigma and the prolific production of immature globose sterile fruits that generate vegetative propagules (Bois 1898, Fig. 1). After the original description, the species followed a long taxonomic rearrangement due to its particular morphological characters, being tentatively treated in *Cylindropuntia* (Engelmann 1856: 302) F.M.Knuth (1930: 102) (Backeberg & Kunth 1936), *Austrocylindropuntia* Backeberg (1938: without pagination) (Backeberg 1951), or *Salmiopuntia* Frič ex Kreuzinger (1935: 41) (Kreuzinger 1935), but frequently as *incertae sedis* (Hunt & Taylor 2002).

Recently, molecular studies suggested that *Opuntia schickendantzii* was part of the *Brasiliopuntia* clade (Majure *et al.* 2012), and a new combination was proposed, *B. schickendantzii* (F.A.C.Weber) R.Puente & Majure (Majure & Puente 2014). However, no obvious morphological feature linking wild accessions of *O. schickendantzii* and *Brasiliopuntia* supported this circumscription, other than the monopodial principle stems. Further, additional analyses revealed that

the material used in Majure *et al.* (2012) was from cultivated provenance ("Lion's Tongue" from Boyce Thompson Southwestern Arboretum, BTA, Arizona, USA), without original collection data (https://livingcollections.org/dbg/Accession/596081). During a broad floristic, taxonomic, and systematic study of the southern South American species of *Opuntia* s.l., phylogenetic analyses based on molecular data from wild material revealed that *O. schickendantzii* was closely related to *Salmonopuntia*, not to *Opuntia* s.str. or *Brasiliopuntia*. Here, we further carried out molecular analyses and morphological studies to reassess the relationship of *O. schikendantzii* with the closest relative taxa of tribe Opuntieae, and we herein propose a new combination in *Salmonopuntia*.

Materials and Methods

DNA sampling, sequence alignment and phylogenetic analyses

We first gathered molecular sequences available on GenBank. The previous sequenced materials from Majure *et al.* (2012) and Köhler *et al.* (2020a) were downloaded using functions of R package *ape* (Paradis *et al.* 2004, R Core Team, 2017), and imported into Geneious 11.1.5 (Biomatters, Auckland, New Zealand). These sequences correspond to the chloroplast intergenic spacers *atpB-rbcL, ndhF-rpl32, petA-psbJ, trnE-trnF*, and to the *ycf1* and *matK* genes, covering a comprehensive taxon sampling of all members of tribe Opuntieae (*Consolea*, *Miqueliopuntia*, *Tunilla*, *Salmonopuntia*, *Brasiliopuntia*, *Tacinga,* and *Opuntia*), and two outgroups of tribes Cylindropuntieae and Tephrocacteae. We newly sequenced a wild-collected sample of *O. schickendantzii,* and two new accessions of *S. salmiana* via genome-skimming following methods described in Köhler *et al.* (2020a,b). Then, a reference mapping pipeline was pursued using the Geneious mapper to assemble the same molecular markers downloaded from GenBank for the newly sequenced materials (for additional methodological details, see Köhler *et al.* 2020b). Information for all sampled materials and sequences analyzed are available in Table S1.

Sequences of each marker from each taxon were concatenated as one sequence, and a multiple sequence alignment was performed across all samples using the MAFFT v. 7 (Katoh & Standley 2013) plugin in Geneious with default settings, and then manually adjusted. Phylogenetic inference was performed using the Maximum Likelihood (ML) approach implemented in RAxML 8.2.4 (Stamatakis 2014) on the CIPRES Science Gateway Web Portal (Miller *et al.* 2010). The alignment was partitioned by marker and the GTR+G model was employed as model of molecular evolution for each partition since the GTR model has been demonstrated to be accurate when topological reconstructions are the desired output skipping model selection (Abadi *et al.* 2019). Statistical support values were estimated by implementing 1000 rapid bootstrapping iterations (-f a function).

Data collection for morphological features and taxon circumscription

Extensive fieldwork was carried out in southern South America during 2006 to 2019 encompassing the main natural ecoregions to obtain data about natural populations of *Opuntia* s.l. in the area. The following herbaria were checked: BA, BAF, CORD, CTES, ICN, LIL, LP, SI, as well as digitalized materials from GBIF.org that corresponded to GH, K, NY, MO (herbarium codes according to Thiers 2021 [continuously updated]) and human observations from GBIF.org. The relevant literature was also analyzed (Arechavaleta 1905, Spegazzini 1901, 1905, 1925, Schumann 1890, 1899a, 1899b, Britton & Rose 1919, Backeberg 1958, 1966, Ritter 1979, 1980a, 1980b, Kiesling 1999, 2005, Kiesling & Ferrari 2005, Kiesling *et al.* 2008, Leuenberger 2002, Font 2014, Las Peñas *et al.* 2017). Since the important feature of the curvature of the embryo and the amount of perisperm to generic circumscription within Opuntioideae (Stuppy 2002), we also investigated the embryo of *Opuntia schickendantzii*. We were unable to survey seeds of *S. salmiana,* since the fruits found hitherto were sterile.

Results

Phylogenetic analyses

The resulting alignment consisted of 5,802 sites in length for 74 taxa, with 4,993 (86%) constant sites and 303 parsimony informative sites. Tribe Opuntieae was resolved as monophyletic (bootstrap, bs, = 100) with four major, well-

supported clades: (1) *Consolea* (bs = 100), (2) *Miqueliopuntia* + *Tunilla* + *Salmonopuntia* (bs = 95), (3) *Brasiliopuntia* + *Tacinga* (bs = 83) and (4) *Opuntia* (bs = 89) (Fig. 2). *Salmonopuntia* was well-supported as sister to *Tunilla* (bs = 98) (*Salmonopuntia* + *Tunilla* clade had bs = 83). The wild accession of *Opuntia schickendantzii* (FF 838) was embedded within the *Salmonopuntia* clade (Fig. 2, red arrow and tip label), while *S. salmiana*, represented by four accessions, was recovered as a polyphyletic species. The cultivated material of *O. shickendantzii* from Boyce Thompson Arboretum (BTA), used in Majure *et al.* (2012) and Majure & Puente (2014) was resolved within the *Brasiliopuntia* clade (bs = 92, Fig. 2, green tip label), as sister to *Brasiliopuntia brasiliensis*.

Morhological data

Thirteen preserved herbarium specimens were found for *Opuntia schickendantzii* (see 'specimens examined' below). Seven additional observation records of *O. schickendantzii* were found (human observations at GBIF.org), three from Argentina and four from Bolivia (see Supplementary Table S2 for complete details). Our observations revealed that the primary terete stem with mostly monopodial growth (Fig. 1A), and the prolific production of immature, unripe and/or sterile globose fruits that generate propagules, were useful morphological features to circumscribe the *Salmonopuntia* lineage (Fig. 1E–G). The analysis of the embryo of *O. schickendantzii* showed it to be hook-shaped (Fig. 1D).

Discussion

The original description of *Opuntia schickendantzii* largely agrees with a wild extant prickly pear cactus that currently occurs along the northwestern mountainous region of Argentina (Catamarca, Jujuy, Salta, and Tucumán provinces) and southern Bolivia (Cochabamba, Chuquisaca, and Tarija departments). Our results (molecular and morphological) conform to those previously revealed by Realini *et al.* (2015), which shows *O. schickendantzii* more closely related to *Salmonopuntia salmiana*. Based on these analyses, *O. schickendantzii* is best circumscribed within the genus *Salmonopuntia*, and the new combination is proposed below. Concenring the embryo of *O. schickendantzii*, which is hook-shaped (Fig. 1D), it reinforces the position of this taxon outside of *Opuntia* s.str., which exhibits a coiled/spirally enrolled embryo (see Stuppy 2002, Majure *et al.* 2013).

The genus *Salmonopuntia* P.V.Heath is occasionally referred to as *Salmiopuntia* Frič or *Salmiopuntia* Frič ex Guiggi as a mistake. *Salmiopuntia* Frič is an invalid name (Art. 39.1; Mottram, 2014, Turland *et al.* 2018), and *Salmiopuntia* Frič ex Guiggi is an illegitimate name (Art. 52.1; Mottram, 2014, Turland *et al.* 2018); while *Salmonopuntia* was validly published as a replacement name (*nom. nov.*) based on the *Salmianae* Britton & Rose (1919: 44, *pro ser. Opuntia* (L.) Mill.), which includes the type *O. salmiana* J.Parm. ex Pfeiffer (1837: 172).

The material previously identified as *Opuntia schickendantzii* ("Lion's Tongue" from BTA) in Majure *et al.* (2012) and Majure & Puente (2014) was again supported within the *Brasiliopuntia* clade. However, our comparison of that material with wild materials of *O. schickendantzii* revealed that the cultivated material on which the previous analyses were based do not belong to the wild type material of *O. schickendantzii.* The material cultivated at Boyce Thompson Arboretum is a different morphotype that does not correspond to the wild type of *O. schickendantzii*, as it lacks the true primary monopodial, terete stem, as well as the prolific production of immature, unripe and/or sterile globose fruits that generate propagules, and is usually spineless. This same morphotype is worldwide reported as an invasive cactus escaped from cultivation and wrongly identified as *O. schickendantzii*. In Australia, numerous records are available at the Atlas of Living Australia (ALA, www.ala.org.au) and GBIF.org reporting this morphotype as *O. schickendantzii*, and more recently it has also been reported in Spain (Ortíz & Gonyalons, 2014, Aymerich, 2015, Senar & Cardero, 2019, Verloove & Guiggi, 2019). However, analyses of those materials cited for Europe and the Australian alloctone flora, as well as from the Boyce Thompson Arboretum, revealed that they do not correspond to *O. schickendantzii*. In all these cases, the commercial cultivar or ornamental clone named "Lion's Tongue" is represented, which is widely distributed in private and public collections of cacti and succulents around the world and still of unknown origin. We consider it could be of hybrid origin based on its morphological characters. So, further studies should be carried out to assess its origins and to appropriately circumscribe that taxon (Köhler & Font, submitted).

Taxonomic treatment

Salmonopuntia schickendantzii (F.A.C.Weber) Font & M.Köhler, *comb. nov.* Bas. *Opuntia schickendantzii* F.A.C.Weber (1898: 898) ≡ *Mortolopuntia schickendantzii* (F.A.C.Weber) Guiggi (2015: 1) ≡ *Brasiliopuntia schickendantzii* (F.A.C.Weber) R.Puente & Majure (2014: 25) ≡ *Austrocylindropuntia schickendantzii* (F.A.C.Weber) Backeb. (1951: 14) ≡ *Cylindropuntia schickendantzii* (F.A.C.Weber) Backeb. (1936: 122) ≡ *Salmiopuntia schickendantzii* (F. A. C. Weber) Kreuz. (1935: 41), *nom. inval.*

Neotype (designated by Guiggi 2015):—Ex cult hort. Mortolensi, 11 June 1905, *Berger s.n*. (HMGBH, fl., image!)

Epitype (**designated here**):—ARGENTINA. Salta, Depto. Guachipas, Cuesta el Lajar, 25˚40'33.4"S 65˚29'43.8"W, 16 March 2010, *Font 660* (BAF13598!) [FF 838 in cult.].

= *Opuntia cochabambensis* Card. (1953: 20)

= *Platyopuntia conjungens* F.Ritter (1980b: 494) ≡ *Opuntia conjungens* (F.Ritter) P.J.Braun & Esteves (1995: 133)

Description:—*Shrub*, small to large, 0.5–1.0(–1.5) m tall, erect. *Stems* dimorphic, the primary terete, up to 5 cm in diam., lignified, indefinite growth narrowing towards the apex; secondary stems flattened, asymmetric ascending, oblanceolate to spathulate, 10–20 × 2–5 cm. *Epidermis* ashen green, glaucous. *Areoles* densely present on the primary stem, 1–2 cm distance between each other in diagonal; eventually subtuberculated on the secondary stems, gray to yellowish glochids. *Spines* setiform to acicular, radial, white-gray; conspicuous on the primary stem, 0–3(–5), 0.5–3.0 cm long; inconspicuous on the secondary stems, 0–3, 0.5–3.0 cm long. *Leaves* green, conic to subulates, 3–6 mm long, deciduous, not appressed, ascending. *Pericarpel* globose, rarely obovoid to obpyriform, 1.0–1.5(–2.0) cm in diameter. *Flower bud apex* acute, shades of red (claret to scarlet); inner tepals obovate to oblanceolate, bright yellow; flower at anthesis 2–3(–4) cm in diameter. *Stamens* numerous, pale yellow filaments and anthers. *Stigma* 5–6 lobed, connivent, emerald to dark green; style white. *Fruit* globose, 1.5–2.5 cm in diameter, indehiscent, dark purple to reddish when ripe, inner pericarpel green; glochids profusely developed, areoles 2 mm in diam. without propagules; generally fertile, up to 60–70 seeds per fruit; presence of immature, green, or sterile fruits functioning as clonal propagules just on the ground. *Seeds* elliptic to obovate, slightly curved, brownish, glabrous, 3–5 × 3 mm.

Distribution and habitat:—Argentina (Catamarca, Jujuy, Salta, Tucumán) and Bolivia (Cochabamba, Chuquisaca, Tarija). It grows between 1000–2000 m a.s.l.; orophilic, generally growing on cliffs and hillsides, rarely seen on flat terrain.

Specimens examined:—ARGENTINA. Catamarca: Depto. Ambato, Singuil, 1200 m, 2 December1951, *Vervoorst 3505* (LIL). **Jujuy**: Depto. Valle Grande, Pueblo (Lomadas), 15 November 1958, *Villa & Legname 766* (LIL). Ibid. 17 November 1958, *Villa & Legname 767* (LIL); Depto. Santa Bárbara, El Fuerte, 22 November 1970, *Cabrera & Fabris 21095* (LP). **Salta:** Depto. Chicoana, Quebrada de Escoipe, February 1972, *Kiesling 136* (LP). Depto. Guachipas, 10 km antes de Casa de Arcos, 23 November 2017, *Font 740* (BAF). Cuesta El Lajar, 16 March 2010, *Font 660* (BAF). Depto. La Candelaria, Unquillo, 1200 m, November 1931; *Schreiter 6730* (LIL). **Tucumán**: Depto. Tafí, La Hoyada, 1750 m; 11 December 1924, *Venturi 3559* (LIL, GH, NY). La Hoyada 1500 m, 17 December 1923, *Venturi s.n.* (LIL 66441); Quebrada de La Hoyada, October 1930, *Schreiter 2367* (LIL). La Hoyada, 1460 m, November 1932, *Schreiter 8765* (LIL). **BOLIVIA. Cochabamba**: December 1949, *Cárdenas 2549* (LIL 531554).

Notes:—Guiggi (2015) designated a neotype based on a sheet with a flower section preserved at the HMGBH from cultivated material at La Mortola. Considering that the neotype is not complete, we here designate an epitype showing complete morphological features necessary for the precise identification and designation of the name of the species.

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TABLE S1. Sampled taxa used in the molecular phylogenetic analysis. GenBank accessions are provided only for those generated in this study, the other ones can be checked in their Reference. Voucher information contains collector and herbarium acronym.

Species	**Reference (or Voucher)**	**GenBank**
Brasiliopuntia brasiliensis	Majure *et al.* 2012	see Majure *et al.* 2012
Consolea corallicola	Majure *et al.* 2012	see Majure *et al.* 2012
Consolea microcarpa	Majure *et al.* 2012	see Majure *et al.* 2012
Consolea nashii	Majure *et al.* 2012	see Majure *et al.* 2012
Consolea rubescens	Majure *et al.* 2012	see Majure *et al.* 2012
Consolea spinosissima	Majure *et al.* 2012	see Majure *et al.* 2012
Cylindropuntia bigelovii	Köhler *et al.* 2020a	see Köhler *et al.* 2020a
Miqueliopuntia miquelii	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia abjecta	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia arechavalatae	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia arenaria	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia auberi	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia aureispina	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia austrina	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia basilares	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia caracassana	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia chisosensis	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia chlorotica	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia cochenillifera	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia dejecta	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia drummondii	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia elata	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia ellisiana	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia excelsa	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia gaumeri	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia guatemalensis	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia inaperta	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia jamaicensis	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia karwinskiana	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia macbridei	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia macrocentra	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia macrorhiza	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia mesacantha	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia microdasys	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia pachyrhyza	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia polyacantha	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia pycnantha	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia quimilo	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia quitensis	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia retrorsa	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia rufida	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia sanguinea	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia santarita	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia scheerii	Majure *et al.* 2012	see Majure *et al.* 2012

Opuntia schickendantzii	This study - *F.Font 660* (BAF)	**MZ292557-62**
Opuntia schickendantzii (Lion's Tongue)	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia setispina	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia stenopetala	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia strigil	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia tapona	Majure *et al.* 2012	see Majure *et al.* 2012
Opuntia triacantha	Majure *et al.* 2012	see Majure *et al.* 2012
Salmonopuntia salmiana	This study - *F.Font 770* (BAF)	**MZ292545-50**
Salmonopuntia salmiana	This study – *M.Köhler 515* (ICN)	**MZ292551-56**
Salmonopuntia salmiana (HBG 18366)	Majure *et al.* 2012	see Majure *et al.* 2012
Salmonopuntia salmiana (Kew s.n.)	Majure *et al.* 2012	see Majure *et al.* 2012
Tacinga funalis	Majure *et al.* 2012	see Majure *et al.* 2012
Tacinga inamoena	Majure *et al.* 2012	see Majure *et al.* 2012
Tacinga lilae	Majure *et al.* 2012	see Majure *et al.* 2012
Tacinga palmadora	Majure *et al.* 2012	see Majure *et al.* 2012
Tacinga saxatilis	Majure *et al.* 2012	see Majure *et al.* 2012
Tephrocactus weberi	Köhler *et al.* 2020a	see Köhler *et al.* 2020a
Tunilla corrugata	Majure *et al.* 2012	see Majure *et al.* 2012
Tunilla longispina	Majure *et al.* 2012	see Majure *et al.* 2012
Tunilla soehrensii	Majure *et al.* 2012	see Majure *et al.* 2012

TABLE S2. Human observations of *O. schickendantzii* recorded at GBIF.org. Accessed at 22 Dec. 2020

Country	Reference
Argentina	https://www.gbif.org/occurrence/1986636765
Argentina	https://www.gbif.org/occurrence/2576507110
Argentina	https://www.inaturalist.org/observations/67093534
Bolivia	https://www.gbif.org/occurrence/1920783021
Bolivia	https://www.gbif.org/occurrence/2576483190
Bolivia	https://www.gbif.org/occurrence/2576501174
Bolivia	https://www.gbif.org/occurrence/2576360932