

Reassessment and typification of *Opuntia canterae* (Opuntioideae, Cactaceae), an endemic prickly pear cactus of Uruguay

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Background and aims – *Opuntia* is the most widespread genus of Cactaceae, naturally occurring throughout arid and semi-arid areas of the Americas. Many of the species have taxonomic problems resulting from incomplete original descriptions, lack of type designations, a paucity of taxonomic revisions and, in general, difficult species delimitation resulting from hybridization, morphological plasticity, and poor specimen preparation. However, efforts are being undertaken to fill the gaps in our distributional, morphological and phylogenetic knowledge of the group. Here, we reassess the name *Opuntia canterae*, providing an updated description, typification, photographs, distribution map, conservation assessment and additional notes.

Material and methods – Extensive fieldwork was conducted, along with comprehensive herbarium and literature review. Morphological characters were assessed based on the commonly used characters used for prickly pears. Species delimitation is proposed based on our morphological studies, taxonomic and literature revision, as well as preliminary phylogenetic studies. The IUCN guidelines were followed to provide a conservation assessment of the species.

Key results – *Opuntia canterae* is reassessed as a distinct species separated from its previous synonym (*O. elata*) by the elliptic to long-oblancheolate stem segments, acute to conical flower bud apex and long-obconic fruits. An epitype is here designated to further clarify the morphological features of the species, which, heretofore, were only represented by a photo. The species is considered endemic to Uruguay and is provisionally assessed as Endangered (EN) using IUCN criteria, but more fieldwork will be necessary to provide a further precise conservation status.

Keywords – Biodiversity; Caryophyllales; cacti; endemic; Pampa; Pampean; threatened species.

INTRODUCTION

Opuntia Mill. is the most widespread genus of Cactaceae, naturally occurring from southern South America (Argentina) to northern North America (Canada) (Britton & Rose 1919; Anderson 2001; Majure et al. 2012). The group has a putative origin during the Late Miocene (11.6–5.3 Mya)

in southwestern South America with subsequent dispersal events of lineages to northern South America, the Caribbean region, Central America and to the North American deserts (Arakaki et al. 2011; Majure et al. 2012). The group exhibits a variety of morphological characters such as a shrubby or tree growth form, dry/fleshy fruit, epidermis and seeds either pubescent or glabrous, dioecy/monoecy, ornithophilic/

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melittophilic pollination, as well as other discrete and phenotypically plastic characters (Schumann 1899; Britton & Rose 1919; Backeberg 1958; Anderson 2001; Hunt et al. 2006; Majure & Puente 2014; Majure et al. 2017).

Eight major clades have been recovered within *Opuntia* s. str. (Majure et al. 2012; Köhler et al. unpubl. res.), and the South American species are mainly nested in two of these clades: *Macbridei* and *Elatae* (*sensu* Majure et al. 2012; Köhler et al. unpubl. res.). The *Macbridei* clade includes species occurring in the northern part of South America, from central Peru to central Colombia (Britton & Rose 1919; Anderson 2001; Madsen 1989; Vega 2013; Majure & Puente 2014), while the *Elatae* clade includes the southern South American lineages occupying mainly the Pampa and the Chaco regions, as well as the Galapagos Islands (Britton & Rose 1919; Leuenberger 2002; Majure et al. 2012; Font 2014; Las Peñas et al. 2017; Köhler et al. 2018; Köhler et al. unpubl. res.).

Some of the southern South American (sSA) species of *Opuntia* have a confused taxonomic history. Many of these taxa were described based on materials collected by Old World naturalists that were travelling to the New World and sending biological materials to European gardens (Pontes et al. 2017). That routine led to many names, which were poorly described, based on morphotypes grown under greenhouse conditions, with insufficient diagnoses or use of characters and usually without the designation of nomenclatural types (Haworth 1812; Pfeiffer 1837; Salm-Dyck 1850). Beyond that, many European naturalists that migrated to the New World and started to contribute to the knowledge of local floras also often failed to cite original materials or provide precise descriptions of the novel species proposed (Spegazzini 1899, 1901, 1902, 1905, 1925; Arechavaleta 1905). Recently, major efforts have been made to better assess the identity and the interpretation of many of these names with typifications and a handful of taxonomic revisions (Crook & Mottram 1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005; Leuenberger 1993, 2001a, 2001b, 2002; Font 2014; Las Peñas et al. 2017).

Opuntia canterae was described by Arechavaleta (1905) as a distinct species based on his knowledge of the Uruguayan flora and neighbouring areas. The description included a comprehensive diagnosis with a complementary description accompanied by personal observations about the ecology and distribution of the species (Arechavaleta 1905). This taxon was later treated as a doubtful species by Britton & Rose (1919), whom merely transcribed the original description of Arechavaleta without mentioning the detailed knowledge about the ecology, etc., of the species. Bertram (1929, 1931) reported his success in growing *Opuntia* species in Germany, illustrating a flowering prickly pear identified as *O. canterae* by Hern W. Weingart. Herter (1957) included the species in his study of the Uruguayan flora and illustrated the species with narrow and spineless stem segments, with acute flower buds. Backeberg (1958) reproduced Arechavaleta's description providing a photograph of ambiguous assignment, and without providing any additional information. Anderson (2001) listed the species in his treatment based on these prior, depauperate descriptions. Leuenberger (2002), in the first attempted taxonomic revision of a series from the sSA spe-

cies of *Opuntia* (series *Armatae* K.Schum. = *Elatae* Britton & Rose), was unable to critically access the identity of the taxon, and suggested that it may belong in *O. elata* Salm-Dyck or *O. cardiosperma* K.Schum.

Later, Font (2014), in an attentive revision of the series *Armatae*, proposed a novel set of morphological characters for a comprehensive circumscription of the species within the group. Besides the commonly used morphological characters of the stem segments (cladodes), spination and habit of the species, Font (2014) introduced the morphology of the flower bud apices, stigma colour and the inner pericarpel tissue colour as useful characters to diagnose taxonomic entities that have been problematic historically. Even so, Font (2014) broadly circumscribed *O. elata* to include *O. canterae*, and later Las Peñas et al. (2017) retained it in the synonymy of *O. elata* s. lat.

During a broad taxonomic, systematic and floristic revision of the southern South American species of *Opuntia*, a distinct morphotype was observed in the Pampean region of Uruguay, and further analyses suggested that it conformed to *Opuntia canterae*. Here, we propose a reassessment of *O. canterae*, providing a typification, an updated description, photographs, conservation assessment and additional notes about the species.

MATERIAL AND METHODS

Extensive field trips were carried out in southern South America encompassing the principle ecoregions to obtain data about natural populations of *Opuntia* in the area. The region is represented by subtropical grasslands permeated by rocky outcrops that compose the Pampa or Río de La Plata grassland (Andrade et al. 2018) and the Chaco region (Pennington et al. 2000). Major herbaria from the region have been revised to check distribution records and specimen identification of all *Opuntia*: BA, BAF, CORD, CTES, HAS, ICN, LIL, LP, MCN, MVFA, MVJB, MVM, SI (herbarium abbreviations following Thiers continuously updated). The digital database of Brazilian collections was also consulted through the SpeciesLink platform (2019) to check herbaria from disparate geographical regions.

A literature review was carried out comprising the main magna opera that contain descriptions of southern South American *Opuntia* species (Arechavaleta 1905; Spegazzini 1901, 1905, 1925; Schumann 1890, 1899a, 1899b; Britton & Rose 1919; Backeberg 1958, 1966; Ritter 1979, 1980), as well as recent revisions, floras and taxonomic treatments (Kiesling 1999, 2005; Kiesling & Ferrari 2005; Kiesling et al. 2008; Machado et al. 2008; Leuenberger 2002; Font 2014; Las Peñas et al. 2017). The morphological characters used for identification of the southern South American species of *Opuntia* followed those proposed by Font (2014) and Las Peñas et al. (2017), which have been reported as useful for species delimitation in other sSA *Opuntia* species (Köhler et al. 2020). For the conservation status assessment of the species, the GeoCAT tool (Bachman et al. 2011) was used to evaluate the area of occupancy (AOO) and the extent of occurrence (EOO), using a cell width of 5 km based on our observations. The criteria followed those proposed by the IUCN Red List (IUCN 2019). A distribution map was

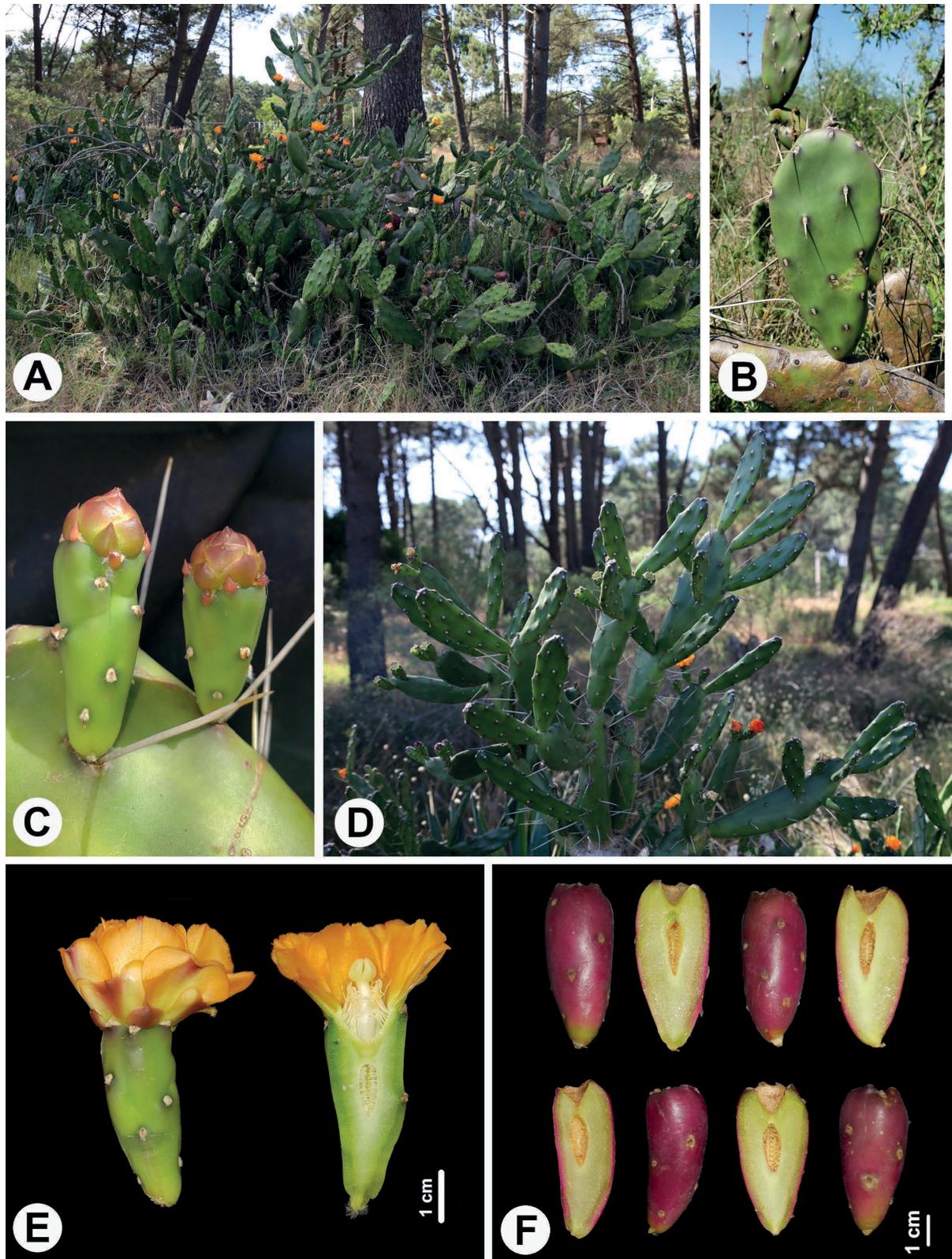


Figure 1 – Morphological features of *Opuntia canterae*. **A.** Plant in habitat (*M. Köhler 316*). **B.** Detailed stem segment resembling morphotype designated as neotype (*M. Köhler 550*). **C.** Detail of the acute flower bud apex (*M. Köhler 550*). **D.** Elliptic to long-oblancoelate stem segments, showing growing cladodes with protuberant areoles encircled with dark-violet coloration from betalain pigmentation (*M. Köhler 316*). **E.** Flower in longitudinal section showing orange tepals, obconic pericarpel, sterile stamens and obovate to elliptical ovary (*M. Köhler 550*). **F.** Longitudinal section of the long-obconic dark-purple ripe fruits showing the sterile ovaries and light green inner pericarpel tissue (*M. Köhler 316*). All photographs by M. Köhler.

generated using the free and Open Source Geographic Information System QGIS v. 3.10.2 (QGIS Development Team 2020) with the public domain map dataset available at Natural Earth (<https://www.naturalearthdata.com/>).

RESULTS AND DISCUSSION

Opuntia canterae has been treated as a doubtful taxon (Britton & Rose 1919; Leuenberger 2002; Kiesling et al. 2008), valid species (Anderson 2001), or more recently as a synonym of *O. elata* (Font 2014; Las Peñas et al. 2017). During our recent field expeditions, a distinct morphotype was observed in the Pampean region of Uruguay, and none of the previous taxonomic treatments included the morphological features that are found in our circumscription of the species. The combined features in *O. canterae* of the elliptic to long-oblong stem segments, acute flower bud apices and long-obconic ripe fruits (fig. 1), separate the species from *Opuntia elata*, which includes specimens with obovate-oblong stem segments, rounded/globose flower bud apices and pyriform fruits. Our preliminary phylogenetic studies of the sSA species of *Opuntia* (Köhler et al. unpubl. res.) reinforces *O. canterae* as a distinct evolutionary lineage of the *Elatae* clade (*sensu* Majure et al. 2012), which led us to propose a reassessment of the species.

Knowledge about the biology of the species is still lacking. As pointed out by Arechavaleta (1905) and confirmed by our field work, *O. canterae* frequently has sterile stamens and

fruits (fig. 1E–F). All populations we were able to study had sterile stamens and fruits, but Arechavaleta (1905), although mentioning these features, also reported developed seeds. Thus, it will be necessary to further investigate putative dioecy in this species, as reported for other *Opuntia* species (Reyes-Agüero et al. 2006; Díaz & Cocucci 2008; Majure & Puente 2014). However, a hybrid origin for *O. canterae* must also be considered. Natural hybridization is widely reported and well known in *Opuntia* (Grant & Grant 1979; Griffith 2001; Rebman & Pinkava 2001; Majure et al. 2012; Majure & Puente 2014). During our fieldwork, we observed *O. canterae* occurring both isolated, as well as in sympatry with other *Opuntia* species, such as *O. rioplatense* Font, *O. elata* Link & Otto, *O. aurantiaca* Lindl. and *O. anacantha* Speg., but no obvious putative parents can be inferred. So, additional studies must be carried out to assess the chromosome number and reproductive biology of *O. canterae*. If evidence is generated suggesting that *O. canterae* may be of hybrid origin and always is a sterile, with only vegetative reproduction, wherein cladodes disarticulate and are later deposited on the ground rooting and forming clones of the parent plant, it would be an efficient way for the species to maintain its dispersion over time. However, regardless of the origin of *O. canterae*, considering the currently known distribution of the species over several sites, phylogenetic position (Köhler et al. unpubl. res.) and the ease of recognition based on several morphological characters, satisfying the morphological phe-

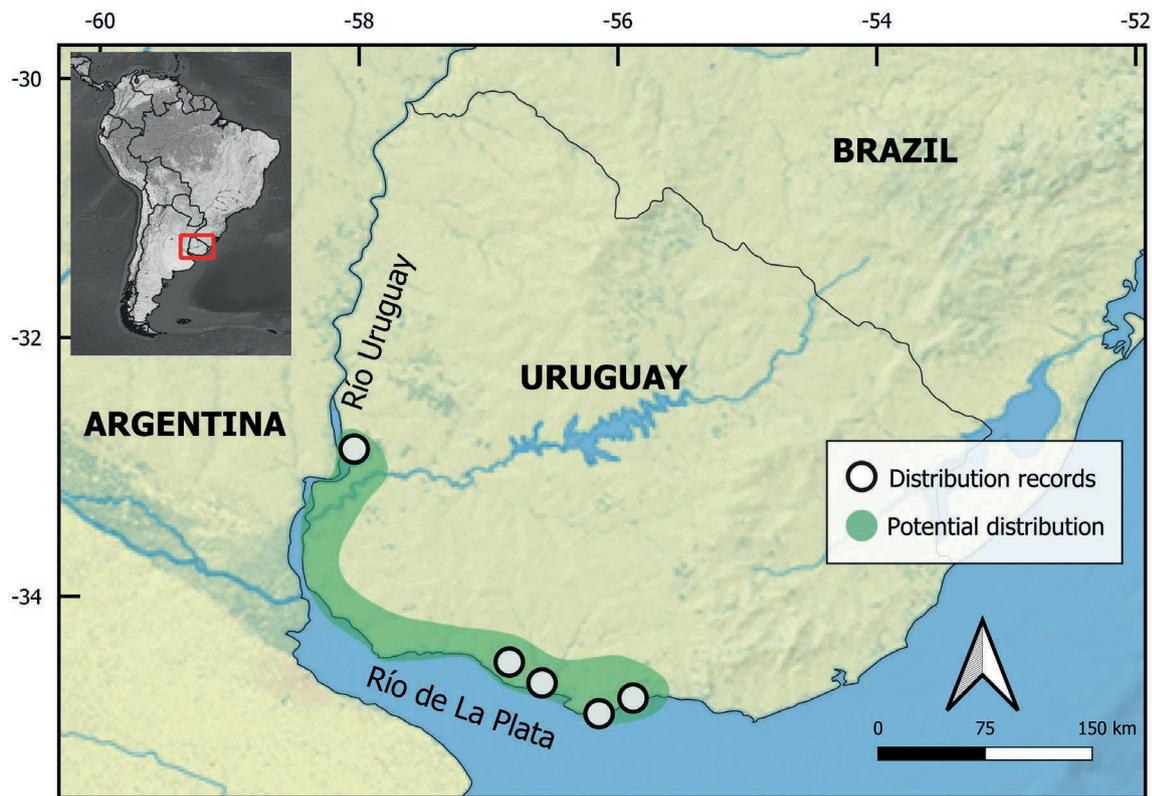


Figure 2 – Distribution map of *Opuntia canterae*. The white dots indicate the known records of distribution, while the green area indicates a potential distribution of the taxon that must be further investigated. Map created using QGIS v.3.10.2 (QGIS Development Team 2020) with dataset available at Natural Earth (<https://www.naturalearthdata.com/>).

netic (Judd 2007) and diagnostic (Wheeler & Platnick 2000) species concepts, its specific status is warranted and justified.

Taxonomic treatment

Opuntia canterae Arechav. (Arechavaleta 1905: 278–280, as *O. canterai*).

Figs 1–4

Type – Not designated.

Neotype – Designated by Las Peñas et al. 2017, Lám. LX in Osten (1941). See photograph on fig. 3.

Epitype (designated here) – Uruguay: Canelones, Neptunia, 34°47'2.73"S, 55°53'11.75"W, 6 Dec. 2017, *M. Köhler et al. 316* (holoepitype: ICN, ICN 201773, barcode 00043878; isoeptype: MVM).

Description – **Shrub**, erect, 1.5–2(> 2) m tall. **Stem segments (cladodes)** 13–30 × 4–6 cm, 2–2.5(–3) cm thick, elliptic to long-oblongate, dark green, apex rounded to obtuse, base attenuate, occasionally forming subterete proximal stems. **Areoles** 6–9 per cladode face, 0.4–0.6 cm in diameter, circular to elliptic, frequently protuberant on growing cladodes, encircled with dark-violet betalain pigments. **Leaves** conic, dark-violet, 3–4 mm long, usually only on the apex of new cladodes or pericarpel, quickly ephemeral. **Glochids** present, but not well-developed (hardly exerted above the areoles), ferruginous. **Spines** 0–1(–2) per areole, acicular, white to light grey, reflexed (when < 3 cm) to straight (when > 4–10 cm). **Pericarpel** 3.5–4 × 1.5(–2) cm, obconic. **Flower bud apex** acute to conical, external tepals reddish, obcordate with mucronulate apex; inner tepals orange, largely obovate with mucronulate apex; flower at anthesis 3–5 cm in diameter. **Stamens** numerous with pale yellow filaments and anthers when present; frequently sterile. **Stigma** 6–7 lobed, connivent, cream-colored. **Style** cylindrical to obclaviform, 1.7–2 × 0.3–0.5 cm. **Ovary** 1–1.3 × 0.4–0.7 cm, obovoid, in the upper third of the pericarpel. **Fruit** 5.5–7 × 2.5–3 cm, long-obconic, red to dark-purple when ripe, inner pericarpel light greenish. **Seeds** flattened (not seen in recent specimens).

Specimens examined – **Uruguay: Montevideo:** Pocitos, Dec. 1921, *C. Osten 16016* (MVM). **San José:** Rincón del Pino, 34°30'8.61"S, 56°50'7.37"W, 4 Dec. 2017, *M. Köhler et al. 299* (ICN), *M. Köhler et al. 302* (ICN); Libertad, 34°39'48.17"S, 56°35'3.69"W, 4 Dec. 2017, *M. Köhler et al. 303* (ICN). **Canelones:** Neptunia, 34°47'2.73"S, 55°53'11.75"W, 6 Dec. 2017, *M. Köhler et al. 316* (ICN). **Río Negro:** Nuevo Berlin, 32°53'10.9"S, 58°02'42.4"W, 23 Jan. 2020, *M. Köhler et al. 550* (ICN).

Distribution – Only recorded in Uruguay near Río de la Plata and Río Uruguay (Esteros and Algarrobales del Río Uruguay) in the departments of Canelones, Río Negro, San José and Montevideo (fig. 2).

Habitat – The species is originally described as occurring along the Uruguayan coastal plain of the Río de La Plata, on sandy or rocky (granite) soils, where it has been sparsely observed. New records have been observed in the extreme northwest part of the Río de La Plata, on the margins of the Río Uruguay, in the Esteros y Algarrobales del Río Uruguay,

suggesting a broader distribution that must be further investigated.

Conservation assessment – Currently, 6 herbarium specimens of *Opuntia canterae* are known, collected between 1921 and 2020. These represent 5 unique occurrences, but the species has not been found again at the oldest locality (*C. Osten 16016* - Pocitos, Montevideo), where the capital city of Uruguay has developed. So, based on the presently known distribution, the extent of occurrence (EOO) of the species is estimated to be ~6,400 km², which places it under the Vulnerable (VU) category under criterion B1, whereas its area of occupancy (AOO) is estimated to be 100 km², which places it under the Endangered (EN) category under criterion B2 (IUCN 2019). The 6 herbarium specimens represent 2 locations, which places the species in the Endangered category under subcriterion 'a' of criterion B2. Many of the natural areas of Uruguay have been converted to agroindustry plantations of *Eucalyptus* spp., *Glycine max* (L.) Merr. (soybean), threatening one of the locations, whereas residential and commercial development threatens the other location. We therefore infer a reduction in the extent and quality of the habitat of *O. canterae*. Because of the low AOO (< 500 km²), the low number of locations (2) and the inferred reduction in the extent and quality of the habitat, we give a provisional IUCN assessment of Endangered EN B2ab(ii,iii). We suggest that more fieldwork is necessary to increase our knowledge of *O. canterae*, its distribution and the threats it faces after which the conservation status of this species should be re-evaluated.

Phylogenetic relationships – This species was not sampled in previous phylogenetic analyses (Majure et al. 2012; Majure & Puente 2014; Realini et al. 2015; Majure et al. 2020). However, newly generated data has revealed the species as a distinct lineage in the *Elatae* clade (Köhler et al. unpubl. res.; *sensu* Majure et al. 2012), being closely related to some species treated in series *Armatae* K.Schum., such as *O. elata* and *O. megapotamica* (*sensu* Font 2014).

Notes – Las Peñas et al. (2017) designated a neotype based on a photographic plate provided by Osten (1941: Lám. LX). The same photograph was found in the MVM herbarium on a duplicate herbarium sheet, which was also accompanied by personal notes of C. Osten (fig. 3) that were almost entirely transcribed in Osten (1941). Our field studies allowed us to observe the same features provided by the photograph, as well as the original descriptions of Arechavaleta (1905), in those populations sampled (fig. 1A–B, D). However, considering that the neotype is a photograph of a putatively juvenile plant, which lacks important characters to be critically identified, we here designate an epitype showing the morphological features necessary for the precise identification and designation of the name of the species (fig. 4).

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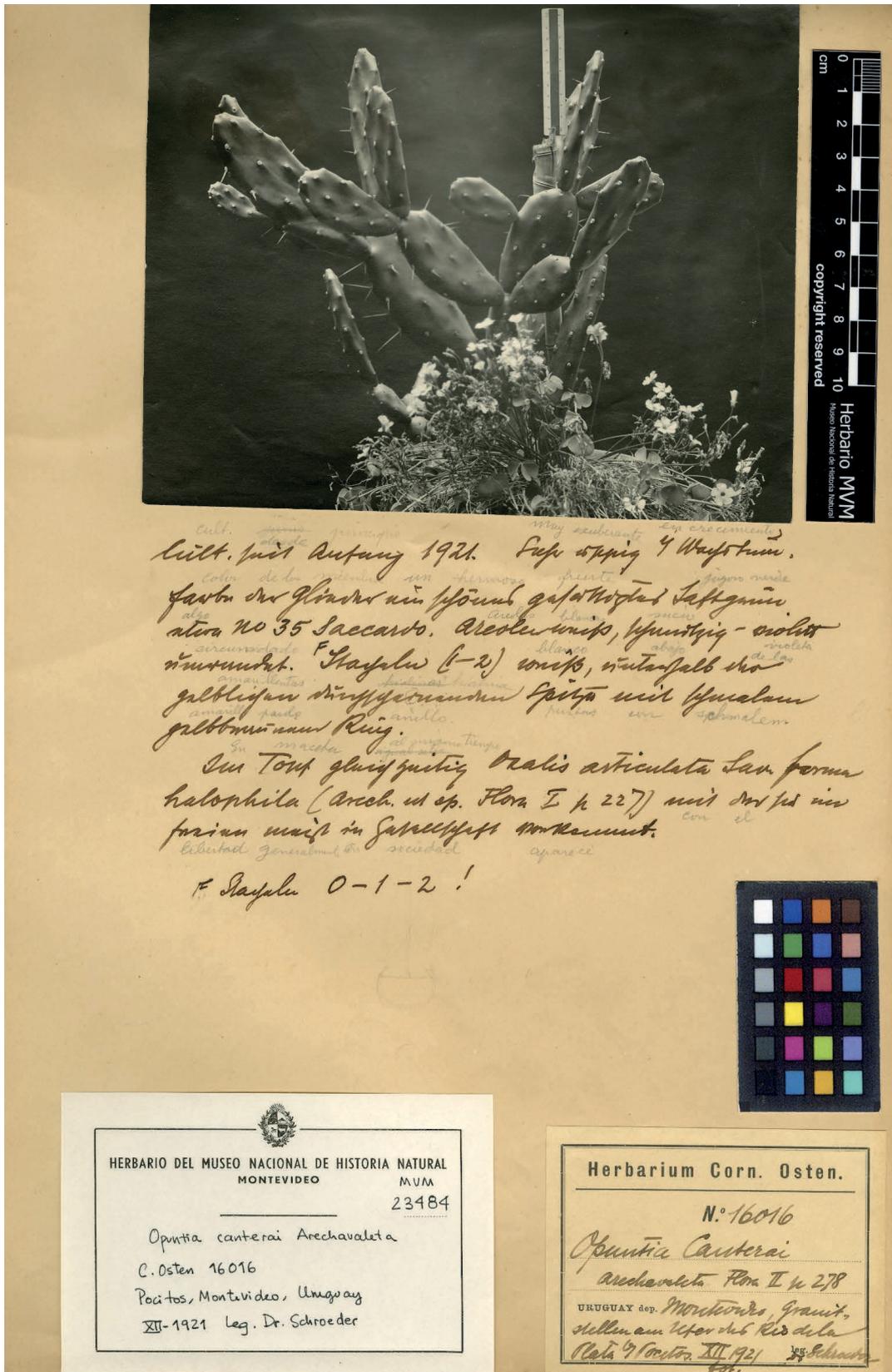


Figure 3 – Herbarium specimen from the Cornelius Osten Herbarium (MVM 23484, C. Osten 16016), which includes the photograph designated as the neotype by Las Peñas et al. (2017), accompanied by personal notes from C. Osten. © Museo Nacional de Historia Natural (Uruguay), all rights reserved; reproduced with permission. This image is not distributed under the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder.



Figure 4 – Epitype of *Opuntia canterae* (ICN 201773, barcode 00043878, *M. Köhler et al.* 316), which includes important characters to critically identify and apply the name to the taxon, such as the elliptic to long-oblong stem segments, acute flower bud apices and long-obovate fruits. © Herbário ICN/UFRGS, all rights reserved; reproduced with permission. This image is not distributed under the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder.

del Río Uruguay (Río Negro)” in Uruguay; Andrés González and Meica Valdivia for helping digitising MVM material and permission to use it; and the staff of the ICN herbarium for support in digitising the epitype. M. Köhler is grateful to the American Society of Plant Taxonomists (ASPT), Cactus and Succulent Society of America (CSSA), International Association for Plant Taxonomy (IAPT) and IDEA WILD for supporting part of the research here reported; M. Köhler also thanks the Brazilian National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq) for his PhD scholarship, and the PDSE/CAPES (Process number 88881.186882/2018-01) for supporting his period as Visiting Researcher at the Florida Museum of Natural History (FLMNH, University of Florida, UF, USA). This study was also financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) - Finance Code 001 and start-up funds to L.C. Majure from the University of Florida and the Florida Museum of Natural History (UF, FLMNH). Two anonymous reviewers provided valuable comments that improved the manuscript.

REFERENCES

- Anderson E.F. (2001) The cactus family. Portland, Timber Press.
- Andrade B.O., Marchesi E., Burkart S., Setubal R.B., Lezama F., Perelman S., Schneider A.A., Trevisan R., Overbeck G.E., Boldrini I.I. (2018) Vascular plant species richness and distribution in the Río de la Plata grasslands. *Botanical Journal of the Linnean Society* 188(3): 250–256. <https://doi.org/10.1093/botlinnean/boy063>
- Arakaki M., Christin P.-A., Nyffeler R., Lendel A., Eggli U., Ogburn R.M., Spriggs E., Moore M.J., Edwards E.J. (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(20): 8379–8384. <https://doi.org/10.1073/pnas.1100628108>
- Arechavaleta J. (1905) Cactáceas [Flora Uruguaya]. *Anales del Museo Nacional de Montevideo* 5(2): 161–291.
- Bachman S., Moat J., Hill A., Torre J. de la, Scott B. (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *ZooKeys* 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Backeberg C. (1958) Die Cactaceae, Band I. Jena, Gustav Fischer Verlag.
- Backeberg C. (1966) Das Kakteenlexikon. Stuttgart, Gustav Fischer Verlag.
- Bertram P. (1929) *Opuntia canterai* Arech. *Monatsschrift der Deutschen Kakteen-Gesellschaft* 1(12): 239–241.
- Bertram P. (1931) *Opuntia canterai* Arech. *Monatsschrift der Deutschen Kakteen-Gesellschaft* 3(11): 259–260.
- Britton N.L., Rose J.N. (1919) The Cactaceae: descriptions and illustrations of plants of the cactus family, vol. 1. Washington, Carnegie Institute.
- Crook R., Mottram R. (1995) *Opuntia* Index Part 1: Introduction and A-B. *Bradleya* 1995(13): 88–118. <https://doi.org/10.25223/brad.n13.1995.a10>
- Crook R., Mottram R. (1996) *Opuntia* Index Part 2: Nomenclatural note and C-E. *Bradleya* 1996(14): 99–144. <https://doi.org/10.25223/brad.n14.1996.a15>
- Crook R., Mottram R. (1997) *Opuntia* Index Part 3: Nomenclatural note and F. *Bradleya* 1997(15): 98–112. <https://doi.org/10.25223/brad.n15.1997.a12>
- Crook R., Mottram R. (1998) *Opuntia* Index Part 4: G-H. *Bradleya* 1998(16): 119–136. <https://doi.org/10.25223/brad.n16.1998.a11>
- Crook R., Mottram R. (1999) *Opuntia* Index Part 5: Nomenclatural note and I-L. *Bradleya* 1999(17): 109–131. <https://doi.org/10.25223/brad.n17.1999.a8>
- Crook R., Mottram R. (2000) *Opuntia* Index Part 6: M-O. *Bradleya* 2000(18): 113–140. <https://doi.org/10.25223/brad.n18.2000.a9>
- Crook R., Mottram R. (2001) *Opuntia* Index Part 7: Nomenclatural note and P-Q. *Bradleya* 2001(19): 91–116. <https://doi.org/10.25223/brad.n19.2001.a11>
- Crook R., Mottram R. (2002) *Opuntia* Index Part 8: R. *Bradleya* 2002(20): 51–66. <https://doi.org/10.25223/brad.n20.2002.a9>
- Crook R., Mottram R. (2003) *Opuntia* Index Part 9: S. *Bradleya* 2003(21): 63–86. <https://doi.org/10.25223/brad.n21.2003.a13>
- Crook R., Mottram R. (2004) *Opuntia* Index Part 10: T-V. *Bradleya* 2004(22): 53–76. <https://doi.org/10.25223/brad.n22.2004.a7>
- Crook R., Mottram R. (2005) *Opuntia* Index Part 11: W-Z, cultivars. *Bradleya* 2005(23): 57–78. <https://doi.org/10.25223/brad.n23.2005.a8>
- Díaz L., Cocucci A.A. (2008) Functional gynodioecy in *Opuntia quimilo* (Cactaceae), a tree cactus pollinated by bees and hummingbirds. *Plant Biology* 5(5): 531–539. <https://doi.org/10.1055/s-2003-44783>
- Font F. (2014) A revision of *Opuntia* series *Armatae* K. Schum. (*Opuntia* ser. *Elatae* Britton & Rose) (Cactaceae - Opuntioideae). *Succulent Plant Research* 8: 51–94.
- Grant V., Grant K.A. (1979) Hybridization and variation in the *Opuntia phaeacantha* group in Central Texas. *Botanical Gazette* 140(2): 208–215. <https://doi.org/10.1086/337077>
- Griffith M. (2001) Experimental hybridization of Northern Chihuahuan Desert Region *Opuntia* (Cactaceae). *Aliso: A Journal of Systematic and Evolutionary Botany* 20(1): 37–42. <https://doi.org/10.5642/aliso.20012001.06>
- Haworth A.H. (1812) Synopsis plantarum succulentarum. London, R. Taylor et Soch. <https://doi.org/10.5962/bhl.title.9462>
- Herter G.G. (1957) Estudios botánicos en la región Uruguaya, vol.14(2). Montevideo.
- Hunt D., Taylor N., Charles G. (2006) The New Cactus Lexicon. Milborne Port, DH Books.
- IUCN (2019) Guidelines for using the IUCN Red List Categories and Criteria. Version 13. Prepared by the Standards and Petitions Sub-Committee. Available at <https://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf> [accessed 15 Dec. 2019].
- Judd W.S. (2007) Revision of *Miconia* sect. *Chaenopleura* (Miconiaceae, Melastomataceae) in the Greater Antilles. *Systematic Botany Monographs* 81: 1–235. <https://www.jstor.org/stable/i25027960>
- Kiesling R. (1999) Cactaceae. In: Zuloaga F.O., Morrone O. (eds) Catálogo de las plantas vasculares de la República Argentina II: Dicotyledoneae. *Monographs in Systematic Botany* 74: 423–489. St. Louis, Missouri Botanical Garden Press.
- Kiesling R. (2005) Cactaceae. In: Trancoso N.S., Bacigalupo, N.M. (eds) Flora ilustrada de Entre Ríos (Argentina). Dicotiledoneas Arquiclamídeas. B. Geraniales a Umbelifloriales. Buenos Aires, INTA.
- Kiesling R., Ferrari O. (2005) 100 cactus Argentinos. Buenos Aires, Albatros.

- Kiesling R., Larocca J., Faúndez L., Metzging D., Albesiano S. (2008) Cactaceae: *Opuntia*. In: Zuloaga F., Morrone O., Belgrano M. (eds) Catálogo de las plantas vasculares del cono sur. Vol. 2. Dicotyledoneae: Acanthaceae–Fabaceae. *Monographs in Systematic Botany* 107. St. Louis, Missouri Botanical Garden Press.
- Köhler M., Font F., Souza-Chies T.T. (2018) First record of *Opuntia rioplatense* (Cactaceae) for the Brazilian Flora. *Phytotaxa* 379(4): 293–296. <https://doi.org/10.11646/phytotaxa.379.4.3>
- Köhler M., Esser L.F., Font F., Souza-Chies T.T., Majure L.C. (2020) Beyond endemism, expanding conservation efforts: what new distribution records can reveal? *Perspectives in Plant Ecology, Evolution and Systematics*. <https://doi.org/10.1016/j.ppees.2020.125543>
- Las Peñas M.L., Oakley L., Moreno N.C., Bernardello G. (2017) Taxonomic and cytogenetic studies in *Opuntia* ser. *Armatae* (Cactaceae). *Botany* 95(2): 101–120. <https://doi.org/10.1139/cjb-2016-0048>
- Leuenberger B.E. (1993) Interpretation and typification of *Cactus opuntia* L., *Opuntia vulgaris* Mill., and *O. humifusa* (Rafin.) Rafin. (Cactaceae). *Taxon* 42(2): 419–429. <https://doi.org/10.2307/1223152>
- Leuenberger B.E. (2001a) *Opuntia paraguayensis* (Cactaceae) reassessed. *Willdenowia* 31(1): 181–187. <https://doi.org/10.3372/wi.31.31116>
- Leuenberger B.E. (2001b) The type specimen of *Opuntia cardio-sperma* (Cactaceae), new synonyms and new records from Argentina and Paraguay. *Willdenowia* 31(1): 171–179. <https://doi.org/10.3372/wi.31.31115>
- Leuenberger B.E. (2002) The South American *Opuntia* ser. *Armatae* (= *O.* ser. *Elatae*) (Cactaceae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 123(4): 413–439.
- Machado M. (2008) Notes on Brazilian taxa of series *Armatae* (*Elatae*). *Cactaceae Systematics Initiatives* 24: 33–35.
- Madsen J.E. (1989) *Opuntia*. In: Harling G., Andersson L. (eds) *Flora of Ecuador* vol. 45, Cactaceae. Berlings, Azlov.
- Majure L.C., Puente R. (2014) Phylogenetic relationships and morphological evolution in *Opuntia* s. str. and closely related members of tribe Opuntieae. *Succulent Plant Research* 8: 9–30.
- 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(5): 847–864. <https://doi.org/10.3732/ajb.1100375>
- Majure L.C., Judd W.S., Soltis P.S., Soltis D.E. (2017) Taxonomic revision of the *Opuntia humifusa* complex (Opuntieae: Cactaceae) of the eastern United States. *Phytotaxa* 290(1): 1–65. <https://doi.org/10.11646/phytotaxa.290.1.1>
- Majure L.C., Köhler M., Font F. (2020) North American Opuntias (Cactaceae) in Argentina? Remarks on the phylogenetic position of *Opuntia penicilligera* and a closer look at *O. ventanensis*. *Phytotaxa* 428(3): 279–289. <https://doi.org/10.11646/phytotaxa.428.3.9>
- Pennington R.T., Prado D.E., Pendry C.A. (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* 27(2): 261–273. <https://doi.org/10.1046/j.1365-2699.2000.00397.x>
- Pfeiffer L.G.K. (1837) Enumeratio diagnostica Cactearum hucusque cognitarum. Berlin, L. Oehmigke. <https://doi.org/10.5962/bhl.title.15207>
- Pontes R.C., Marchiori J.N.C., Neto L.W. (2017) Notas históricas sobre a família Cactaceae no Rio Grande do Sul (Brasil) e Uruguai. I – Período Clássico (1818-1950): viajantes naturalistas e botânicos europeus. *Balduinia* 56: 1–11. <https://doi.org/10.5902/2358198026215>
- QGIS Development Team (2020) QGIS Geographic Information System. Open Source Geospatial Foundation. Available at <https://qgis.org/en/site/index.html> [accessed 3 Apr. 2020].
- Realini M.F., González G.E., Font F., Picca P.I., Poggio L., Gottlieb A.M. (2015) Phylogenetic relationships in *Opuntia* (Cactaceae, Opuntioideae) from southern South America. *Plant Systematics and Evolution* 301: 1123–1134. <https://doi.org/10.1007/s00606-014-1154-1>
- Rebman J.P., Pinkava D.J. (2001) *Opuntia* cacti of North America: An overview. *The Florida Entomologist* 84: 474–483. <https://doi.org/10.2307/3496374>
- Reyes-Agüero J.A., Aguirre R. J.R., Valiente-Banuet A. (2006) Reproductive biology of *Opuntia*: A review. *Journal of Arid Environments* 64(4): 549–585. <https://doi.org/10.1016/j.jaridenv.2005.06.018>
- Ritter F. (1979) Kakteen in Südamerika 1. Brasilien/Uruguay/Paraguay. Spangenberg, F. Ritter.
- Ritter F. (1980) Kakteen in Südamerika 2. Argentinien/Bolivien. Spangenberg, F. Ritter.
- Salm-Dyck J. (1850) Cactaeae in Horto Dyckensi cultae anno 1849. Bonn, Henry & Cohen. <https://doi.org/10.5962/bhl.title.120333>
- Schumann K. (1890) Cactaceae. In: Martius C.F.P. (ed.) *Flora Brasiliensis* vol. 4, Part 2: 185–322, Tabs 39–63. Munich, C. Wolf & son.
- Schumann K. (1899a) Die Cactaceen der Republik Paraguay. *Monatsschrift für Kakteenkunde* 9: 149–154.
- Schumann K. (1899b) Gesamtbeschreibung der Kakteen (Monographia cactacearum). Neudamm [Dębno, Poland], Verlag J. Neumann. <https://doi.org/10.5962/bhl.title.10394>
- SpeciesLink (2019) SpeciesLink digital database, CRIA. Available at <http://www.splink.org.br/> [accessed 12 Dec. 2019].
- Spegazzini C. (1899) Nova addenda ad floram Patagonigam. *Anales de la Sociedad Científica Argentina* 48: 44–59.
- Spegazzini C. (1901) Contribución al estudio de la flora del Tandil. La Plata, Sesé, Larrañaga y Renovales. <https://doi.org/10.5962/bhl.title.9302>
- Spegazzini C. (1902) Nova addenda ad floram Patagonigam. *Anales de la Sociedad Científica Argentina* 53: 275–292.
- Spegazzini C. (1905) Cactacearum Platensium Tentamen. *Anales del Museo Nacional de Buenos Aires* 3(4): 477–521.
- Spegazzini C. (1925) Nuevas notas Cactológicas. *Anales de la Sociedad Científica Argentina* 99: 85–156.
- Vega R.R. (2013) Distribución, variación morfológica y correlaciones ecológicas de *Opuntia* Miller (Cactaceae) en Colombia. Montería, Zenú.
- Wheeler Q.D., Platnick N.I. (2000) The phylogenetic species concept. In: Wheeler Q.D., Meier R. (eds) *Species concepts and phylogenetic theory: a debate*: 55–69. New York, Colombia University Press.

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