

1 **A Running title:** Reassessment of *Opuntia canterae* (Cactaceae), an endemic cactus of Uruguay

2

3

4

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

7

8

9

10 MATIAS KÖHLER^{1,2,*}, LUCAS C. MAJURE²

11

12

13 1 – Programa de Pós-Graduação em Botânica, Departamento de Botânica, Universidade Federal
14 do Rio Grande do Sul, Porto Alegre, RS, Brazil

15 2 - University of Florida Herbarium (FLAS), Florida Museum of Natural History, Gainesville,
16 Florida, United States

17

18

19 * Corresponding author: matias.k@ufrgs.br

20

21

22

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

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

36 **Key results** – *Opuntia canterae* is reassessed as a distinct species separated from its
37 previous synonym (*O. elata*) by the elliptic to long-oblancheolate stem segments, acute to conical
38 flower bud apex and long-obconic fruits. An epitype is here designate for purposes of the precise
39 designation of the name to the taxon. The species is considered endemic to Uruguay and is assessed
40 as Vulnerable (VU) using IUCN criteria, but more fieldwork will be necessary to provide a more
41 precise conservation status.

42

43 **Keywords:** biodiversity, Caryophyllales, cacti, endemic, Pampa, Pampean, threatened species

44

45

46 Introduction

47 *Opuntia* Mill. is the most widespread genus of Cactaceae, naturally occurring from
48 southern South America (Argentina) to northern North America (Canada) (Britton and Rose 1919;
49 Anderson 2001; Majure et al. 2012). The group has a putative origin during the Late Miocene (~7-
50 5 Mya) in southwestern South America with subsequent dispersal events of lineages to northern
51 South America, the Caribbean region, Central America and to the North American deserts
52 (Arakaki et al. 2011; Majure et al., 2012). The group exhibits a variety of morphological characters
53 such as a shrubby or tree growth form, dry/fleshy fruit, epidermis and seeds either pubescent or
54 glabrous, dioecy/monoecy, ornithophilic/melittophilic pollination, as well as other discrete and
55 phenotypically plastic characters (Schumann 1899, Britton and Rose 1919, Backeberg 1958,
56 Anderson 2001, Hunt et al. 2006, Majure and Puente 2014, Majure et al. 2017).

57 Eight major clades have been recovered within *Opuntia* s.str. (Majure et al, 2012; Köhler
58 et al., *in prep.*), and the South American species are mainly nested in two of these clades:
59 *Macbridei* and *Elatae* (sensu Majure et al. 2012, Köhler et al. *in prep.*). The *Macbridei* clade
60 includes species occurring in the northern part of South America, from central Peru to central
61 Colombia (Britton and Rose 1919, Anderson 2001, Madsen 1989, Vega 2013, Majure and Puente
62 2014), while the *Elatae* clade includes the southern South American lineages occupying mainly
63 the Pampa and the Chaco regions, as well as the Galapagos Island species (Britton and Rose 1919,
64 Leuenberger 2002, Majure et al. 2012, Font 2014, Las Peñas et al. 2017, Köhler et al. 2018, Köhler
65 et al. *in prep.*).

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

79 *Opuntia canterae* was described by Arechavaleta (1905) as a distinct species based on his
80 knowledge of the Uruguayan flora and neighbouring areas. The description included a
81 comprehensive diagnosis with a complementary description accompanied by personal
82 observations about the ecology and distribution of the species (Arechavaleta 1905). This taxon
83 was further treated as a doubtful species by Britton & Rose (1919), which merely transcribed the
84 original description of Arechavaleta without mentioning the detailed knowledge about the ecology,
85 etc., of the species. Bertram (1929, 1931) reported his success in growing *Opuntia* species in
86 Germany, illustrating a flowering prickly pear identified as *O. canterae* by Hern W. Weingart.
87 Herter (1957) included the species in his study of the Uruguayan flora and illustrated the species
88 with narrow and spineless stem segments, with visibly pointed apex flower buds. Backeberg

89 (1958) reproduced Arechavaleta's description providing a photograph of ambiguous assignment,
90 without providing any additional information. Anderson (2001) listed the species in his treatment
91 based on the previous, sparse descriptions. Leuenberger (2002), in the first attempted taxonomic
92 revision of a series from the sSA species of *Opuntia* (series *Armatae* K. Schum. = *Elatae* Britton
93 & Rose), was unable to critically assess the identity of the taxon, and suggested that it may belong
94 in *O. elata* Salm-Dyck or *O. cardiosperma* K.Schum.

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

102 During a broad taxonomic, systematic and floristic revision of the southern South
103 American species of *Opuntia*, a distinct morphotype have been observed in the Pampean region of
104 Uruguay, and further analyses were carried out to assess the identity for those materials, which
105 conform to *Opuntia canterae*. Here, we propose a reassessment of *O. canterae*, providing a
106 typification, an updated description, photographs, conservation assessment and additional notes
107 about the species.

108

109 **Material and Methods**

110 Extensive field trips were carried out in southern South America encompassing the main
111 natural ecoregions to obtain data about natural populations of *Opuntia*. The region is represented
112 by subtropical grasslands permeated by rocky outcrops that compose the Pampa or Río de La Plata
113 grassland (Andrade et al., 2018) and the Chaco region (Pennington et al., 2000). Major herbaria
114 from the region have been revisited to check distribution records and specimen identification of all
115 *Opuntia*: BA, BAF, BCWL, CORD, CTES, HAS, ICN, LIL, LP, MCN, MVFA, MVJB, MVM,
116 SI (herbarium abbreviations following Thiers (2020+, continuously updated), except BCWL,
117 non-indexed herbarium of the Biological Control of Weeds Laboratory (FuEDEI), Hurlingham,
118 Buenos Aires, Argentina). The digital database of Brazilian collections was also consulted through
119 the SpeciesLink platform (2019) to check herbaria from disparate geographical regions.

120 A literature review was carried out comprising the main magnum opus that contains
121 description of southern South American *Opuntia* species (Arechavaleta 1905; Spegazzini 1901,
122 1905, 1925; Schumann 1890, 1899a,b; Britton and Rose 1919; Backeberg 1958, 1966; Ritter 1979,
123 1980), as well as recent revisions, floras and taxonomic treatments (Kiesling 1999, 2005; Kiesling
124 and Ferrari 2005; Kiesling et al. 2008; Machado et al. 2008; Leuenberger 2002; Font 2014; Las
125 Peñas et al. 2017). The morphological characters used for identification of the southern South
126 American species of *Opuntia* followed those proposed by Font (2014) and Las Peñas et al. (2017),
127 which have been reported as useful for species delimitation in other sSA *Opuntia* species (Köhler
128 et al. *under review*). For the conservation status assessment of the species, the GeoCAT tool
129 (Bachman et al. 2011) was used to evaluate the area of occupancy (AOO) and the extent of
130 occurrence (EOO), using a cell width of 5 km based on our observations. The criteria followed
131 those proposed by the IUCN Red List (IUCN, 2019).

132

133 Results and Discussion

134

135 *Opuntia canterae* has been treated as a doubtful taxon (Britton & Rose 1919; Leuenberger
136 2002; Kiesling et al. 2008), valid species (Anderson 2001), or more recently as synonym of *O.*
137 *elata* (Font 2014; Las Peñas et al. 2017). During our recent field expeditions, a distinct morphotype
138 has been observed in the Pampean region of Uruguay, and none of the previous taxonomic
139 treatments included its morphological features under the circumscription of the species proposed,
140 nor within the identification key provided. The combined features in *O. canterae* of the elliptic to
141 long-oblong stem segments, acute flower bud apices and long-obconic ripe fruits (Fig. 1),
142 separate the species from *Opuntia elata*, which includes specimens with obovate-oblong stem
143 segments, rounded/globose flower bud apices and pyriform fruits. Our preliminary phylogenetic
144 studies of the sSA species of *Opuntia* (Köhler et al., *in prep.*) reinforces *O. canterae* as a distinct
145 evolutionary lineage of the *Elatae* clade (sensu Majure et al. 2012), which led us to propose a
146 reassessment of the species.

147

148 Taxonomic treatment

149 *Opuntia canterae* Arechav., *Anales del Museo Nacional de Montevideo, Tomo II* (Arechavaleta
150 1905: 278–280, as *O. canterai*) Figs. 1–4.

151 **Type:** Not designated; **Neotype:** designated by Las Peñas et al. 2017, Lám. LX in Osten (1941);
152 **Epitype (designated here):** URUGUAY. Canelones: Neptunia, 34°47'2.73"S, 55°53'11.75"W, 6
153 December 2017, *M. Köhler et al. 316* (ICN 201773, barcode 00043878, isopitype: MVM).

154

155 **Shrub**, erect, 1.5–2(>2) m tall. **Stem segments (cladodes)** 13–30 x 4–6 cm, 2–2.5(–3) cm thick,
156 elliptic to long-oblong, dark green, apex rounded to obtuse, base attenuate, occasionally
157 forming subterete proximal stems. **Areoles** 6–9 at midsection of cladode, 0.4–0.6 cm in diameter,
158 circular to elliptic, frequently protuberant on growing cladodes, circled with dark-violet stains.
159 **Leaves** conic, dark-violet, 3–4 mm, usually only on the apex of new cladodes or pericarpel, quickly
160 ephemeral. **Glochids** present but not developed, poorly exerted outside of the areoles, ferruginous.
161 **Spines** 0–1(–2) per areole, acicular, white to light grey, reflexed (when < 3 cm) to straight (when
162 > 4–10 cm). **Pericarpel** 3.5–4 x 1.5(–2) cm, obconic. **Flower bud apex** acute to conical, external
163 tepals reddish, obcordate with mucronulate apex; inner tepals orange, largely obovate with
164 mucronulate apex; flower at anthesis 3–5 cm in diameter. **Stamens** numerous with pale yellow
165 filaments and anthers when present; frequently sterile. **Stigma** 6–7 lobed, connivent, cream-
166 colored. **Style** cylindrical to obclaviform, 1.7–2 x 0.3–0.5 cm. **Ovary** 1–1.3 x 0.4–0.7 cm, obovoid,
167 in the upper third of the pericarpel. **Fruit** 5.5–7 x 2.5–3 cm, long-obconic, red to dark-purple when
168 ripe, inner pericarpel light greenish. **Seeds** flattened (not seen in recent specimens).

169 **Specimens examined** — URUGUAY. Montevideo, Pocitos, December 1921, *C. Osten 16016*
170 (MVM). San José: Rincón del Pino, 34°30'8.61"S, 56°50'7.37"W, 4 December 2017, *M. Köhler et*
171 *al. 299* (ICN), *M. Köhler et al. 302* (ICN); Libertad, 34°39'48.17"S, 56°35'3.69"W, 4 December
172 2017, *M. Köhler et al. 303* (ICN). Canelones: Neptunia, 34°47'2.73"S, 55°53'11.75"W, 6

173 December 2017, *M. Köhler et al. 316* (ICN). Río Negro: Nuevo Berlin, 32°53'10.9"S,
174 58°02'42.4"W, 23 January 2020, *M. Köhler et al. 550* (ICN).

175 **Distribution** — Only recorded in Uruguay near Río de la Plata and Río Uruguay (Esteros and
176 Algarrobales del Río Uruguay) in the departments of Canelones, Río Negro, San José and
177 Montevideo (Fig. 2).

178 **Habitat** — The species is originally described as occurring along the Uruguayan coastal plain of
179 the “Río de La Plata” river, on sandy or rocky (granite) soils, where it has been sparsely observed.
180 New records have been observed in the extreme northwest part of the “Río de La Plata”, on the
181 margins of the “Río Uruguay”, in the “Esteros y Algarrobales del Río Uruguay”, suggesting a
182 broader distribution that must be further investigated.

183 **Conservation assessment** — The currently known records of the species are reduced to only four
184 localities. Although many of the natural areas of Uruguay has been converted to agroindustry
185 plantations of *Eucalyptus* spp., *Glycine max* (soybean) or to smallholder livestock ranching and
186 annual agriculture, we expect that there are more localities where the species occurs but have not
187 been reported yet. Based on the known distribution, the extent occurrence (EOO) of the species is
188 estimated to be ~6,400 km², which places it under the Vulnerable (VU) category, whereas its area
189 of occupancy (AOO) is estimated to be 100 km², which put it under the category of Endangered
190 (EN) using the subcriterion B2a of IUCN (2019). Admitting that there are still lacking appropriate
191 data to make an adequate assessment of its risk of extinction, a Data Deficient category (DD)
192 would be most appropriate for this taxon. However, considering that the species has long been
193 ignored as a doubtful taxa or synonym of *O. elata*/*O. cardiosperma*, with few known records, and
194 lives in an highly threatened environment, we are giving a precautionary IUCN Red List Category
195 of Vulnerable: VU B1a,b(ii,iii)+2a,b(iii), suggesting that more fieldwork is necessary to critically
196 evaluate the conservation status of this species.

197 **Phylogenetic relationships** — This species was not sampled in previous phylogenetic analyses
198 (Majure et al. 2012, Majure and Puente 2014, Realini et al. 2014, Majure et al. 2020). However,
199 newly generated data has revealed the species as a distinct lineage in the *Elatae* clade (Köhler et
200 al., *in prep.*, sensu Majure et al. 2012), being closely related with some species treated in series
201 *Armatae* K.Schum. such as *O. elata* and *O. megapotamica* (sensu Font 2014).

202 **Notes** — Las Peñas et al. (2017) designated a neotype based on a photographic plate provided by
203 Osten (1941, LAM. LX). The same photography was found in the MVM herbarium on a duplicate
204 herbarium sheet, with one them being accompanied by personal notes of C. Osten (Fig. 3) which
205 were almost entirely transcribed in Osten (1941). Our field studies allowed us to observe the same
206 features provided by the photograph, as well as the original descriptions of Arechavaleta (1905),
207 in those populations sampled (Fig 1A–B, D). However, considering that the neotype is a
208 photograph of a putative juvenile plant, lacking important characters to be critically identified, we
209 designate here an epitype containing features applied for the precise designation of the name of
210 the species (Fig. 4). The species is still lacking knowledge about its biology. As pointed in
211 Arechavaleta (1905) and confirmed in our field work, *O. canterae* frequently has sterile stamens
212 and fruits, thus, it will be necessary to further investigate putative dioecy in this species, as reported
213 for other *Opuntia* species (Díaz & Cocucci 2008; Majure & Puente 2014). Additionally,
214 chromosome counts must be explored in *O. canterae*, since there are no information about it ploidy
215 level yet.

216

217 **Acknowledgements**

218 We thanks to Dr. Jefferson Prado (Instituto de Botânica, Herbarium SP) for providing helpful
219 comments about nomenclature and typification; Anderson S. Mello, Philip Weber, Lucas
220 Kaminski, Luis Volkmann and Curtis Callaghan for providing help during fieldwork; Ivan Grela
221 (UPM) for permission of studies in the protected area of the “Esteros y Algarrobales del Río
222 Uruguay (Río Negro)” in Uruguay; Andrés González and Meica Valdivia for helping digitalizing
223 MVM material and permission for use it; and the staff from ICN herbarium for support in
224 digitalizing the epitype. MK is grateful to the American Society of Plant Taxonomists (ASPT),
225 Cactus and Succulent Society of America (CSSA), International Association for Plant Taxonomy
226 (IAPT) and IDEA WILD for supporting part of the research here reported; MK also thanks the
227 Brazilian National Council for Scientific and Technological Development (Conselho Nacional de
228 Desenvolvimento Científico e Tecnológico - CNPq) for his PhD scholarship, and the
229 PDSE/CAPES for support his period as Visiting Researcher at the Florida Museum of Natural
230 History (FLMNH, University of Florida, UF, USA). This study was also financed in part by the
231 Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) - Finance Code
232 001 and start-up funds to LCM from UF and the Florida Museum of Natural History.

233

234 **Figure captions**

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

243 **Figure 2.** Distribution map of *Opuntia canterae*. The white dots indicate the known records of
244 distribution, while the green area indicate a potential distribution of the taxon that must be further
245 investigated.

246 **Figure 3.** Herbarium specimen from Cornelius Osten Herbarium (MVM 23484, *C. Osten 16016*),
247 which includes the photograph designated as the neotype by Las Peñas et al. (2017), accompanied
248 by personal notes from C. Osten.

249 **Figure 4.** Epitype of *Opuntia canterae* (ICN 201773, barcode 00043878, *M. Köhler et al. 316*),
250 which includes important characters to critically apply the name to the taxon, such as the elliptic
251 to long-oblong stem segments, acute flower bud apices and long-obconic fruits.

252

253 **References**

254

255 Anderson E.F. (2001) The cactus family. Portland, Timber Press.

256 Andrade B.O., Marchesi E., Burkart S., Setubal R.B., Lezama F., Perelman S., Schneider A.A.,
257 Trevisan R., Overbeck G.E., Boldrini I.I. (2018) Vascular plant species richness and
258 distribution in the Río de la Plata grasslands. *Botanical Journal of the Linnean Society* 188:
259 250–256. <https://doi.org/10.1093/botlinnean/boy063>

260 Arakaki M., Christin P.-A., Nyffeler R., Lendel A., Eggli U., Ogburn R.M., Spriggs E., Moore
261 M.J., Edwards E.J. (2011) Contemporaneous and recent radiations of the world's major
262 succulent plant lineages. *Proceedings of the National Academy of Sciences* 108: 8379–8384.
263 <https://doi.org/10.1073/pnas.1100628108>

264 Arechavaleta J. (1905) Anales del Museo Nacional de Montevideo. Volumen 5, Tomo II.
265 Montevideo.

266 Bachman S., Moat J., Hill A., Torre J. de la, Scott B. (2011) Supporting Red List threat
267 assessments with GeoCAT: geospatial conservation assessment tool. *ZooKeys* 150: 117–
268 126. <https://doi.org/10.3897/zookeys.150.2109>

269 Backeberg C. (1958) Die Cactaceae, Band I. Jena, Gustav Fischer Verlag.

270 Backeberg C. (1966) Das Kakteenlexikon. Stuttgart, Gustav Fischer Verlag.

271 Bertram P. (1929) *Opuntia canterai* Arech. *Monatsschrift der Deutschen Kakteen-Gesellschaft*
272 1(12): 239–241.

273 Bertram P. (1931) *Opuntia canterai* Arech. *Monatsschrift der Deutschen Kakteen-Gesellschaft*
274 3(11):259–260

275 Britton N.L., Rose J.N. (1919) The Cactaceae. Washington, Carnegie Institute.

276 Crook R., Mottram R. (1995) *Opuntia* Index Part 1 : Introduction and A-B. *Bradleya* 1995: 88–
277 118. <https://doi.org/10.25223/brad.n13.1995.a10>

278 Crook R., Mottram R. (1996) *Opuntia* Index Part 2: Nomenclatural note and C-E. *Bradleya*
279 1996: 99–144. <https://doi.org/10.25223/brad.n14.1996.a15>

280 Crook R., Mottram R. (1997) *Opuntia* Index Part 3: Nomenclatural note and F. *Bradleya* 1997:
281 98–112. <https://doi.org/10.25223/brad.n15.1997.a12>

282 Crook R., Mottram R. (1998) *Opuntia* Index Part 4: G-H. *Bradleya* 1998: 119–136.
283 <https://doi.org/10.25223/brad.n16.1998.a11>

284 Crook R., Mottram R. (1999) *Opuntia* Index Part 5: Nomenclatural note and I-L. *Bradleya* 1999:
285 109–131. <https://doi.org/10.25223/brad.n17.1999.a8>

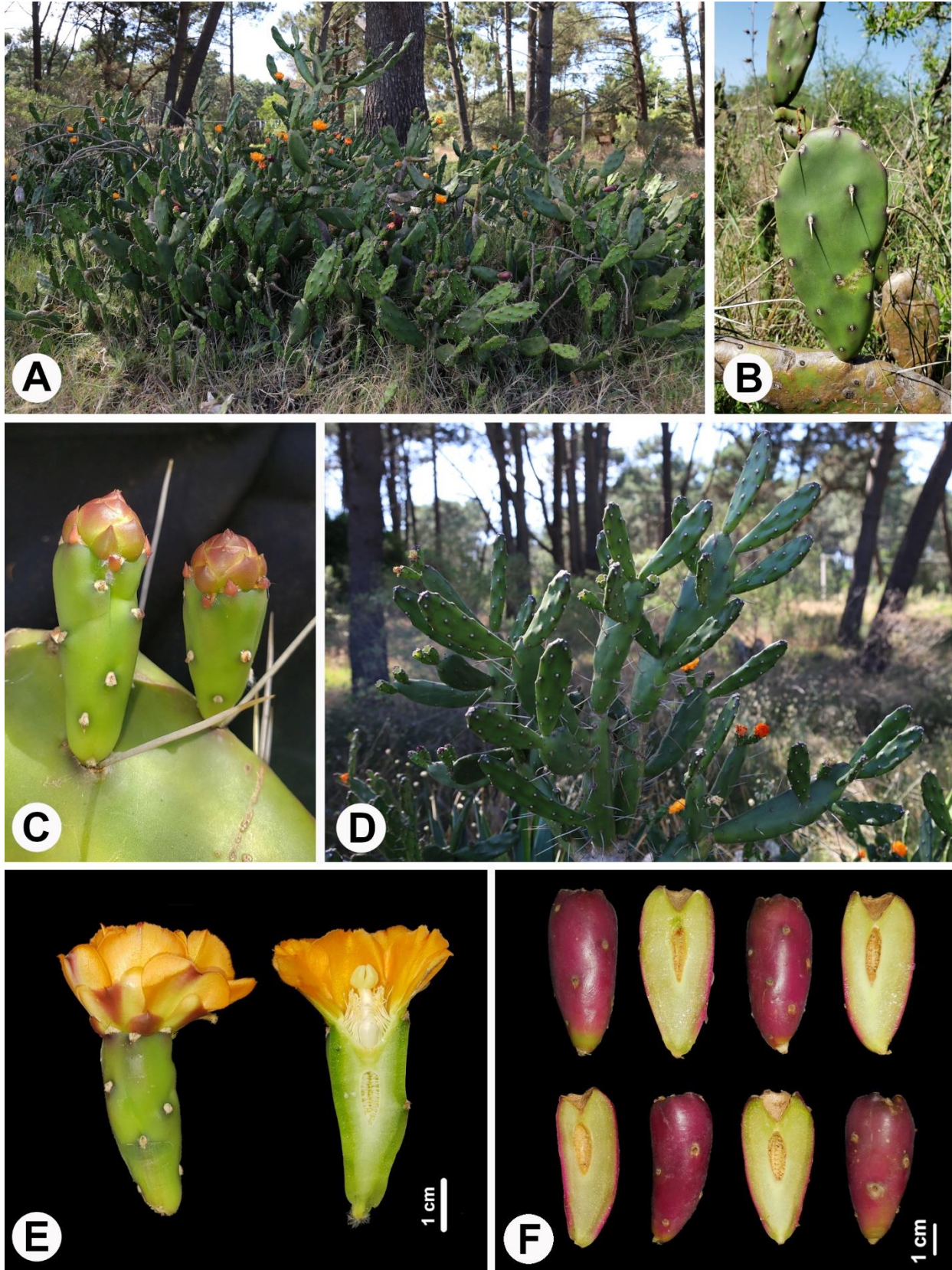
286 Crook R., Mottram R. (2000) *Opuntia* Index Part 6: M-O. *Bradleya* 2000: 113–140.
287 <https://doi.org/10.25223/brad.n18.2000.a9>

288 Crook R., Mottram R. (2001) *Opuntia* Index Part 7: Nomenclatural note and P–Q. *Bradleya*
289 2001: 91–116. <https://doi.org/10.25223/brad.n19.2001.a11>

- 290 Crook R., Mottram R. (2002) *Opuntia* IndexPart 8: R. *Bradleya* 2002: 51–66.
291 <https://doi.org/10.25223/brad.n20.2002.a9>
- 292 Crook R., Mottram R. (2003) *Opuntia* Index Part 9: S. *Bradleya* 2003: 63–86.
293 <https://doi.org/10.25223/brad.n21.2003.a13>
- 294 Crook R., Mottram R. (2004) *Opuntia* Index Part 10: T-V. *Bradleya* 22: 53–76.
295 <https://doi.org/10.25223/brad.n22.2004.a7>
- 296 Crook R., Mottram R. (2005) *Opuntia* Index Part 11: W-Z, cultivars. *Bradleya* 2005: 57–78.
297 <https://doi.org/10.25223/brad.n23.2005.a8>
- 298 Díaz L., Cocucci A.A. (2008) Functional gynodioecy in *Opuntia quimilo* (Cactaceae), a tree
299 cactus pollinated by bees and hummingbirds. *Plant Biology* 5(5): 531–539.
300 <https://doi.org/10.1055/s-2003-44783>
- 301 Font F. (2014) A revision of *Opuntia* series *Armatae* K. Schum. (*Opuntia* ser. *Elatae* Britton &
302 Rose) (Cactaceae - Opuntioideae). *Succulent Plant Research* 8: 51–94.
- 303 Haworth A. H. (1812) *Synopsis plantarum succulentarum*. London, Richardi Taylor et Soch.
304 <https://doi.org/10.5962/bhl.title.9462>
- 305 Herter G.G. (1957) *Estudios botánicos en la región Uruguaya*. 14(2): without pagination.
306 Montevideo.
- 307 Hunt D., Taylor N., Charles G. (2006) *The New Cactus Lexicon*. Milborne Port, DH Books.
- 308 IUCN (2019) *Guidelines for using the IUCN Red List Categories and Criteria*. Version 13.
309 Prepared by the Standards and Petitions Sub-Committee. Available at
310 <https://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf> [accessed 15 Dec. 2019].
- 311 Kiesling R. (1999) Cactaceae. In: Zuloaga F.O., Morrone, O. (eds.) *Catálogo de las plantas*
312 *vasculares de la República Argentina II: Dicotyledoneae*. Monographs in Systematic
313 Botany 74: 423–489. St. Louis, Missouri Botanical Garden Press.
- 314 Kiesling R. (2005) Cactaceae. In: Trancoso N.S., Bacigalupo, N.M. (eds.) *Flora ilustrada de*
315 *Entre Ríos (Argentina). Dicotyledoneas Arquiclamídeas. B. Geraniales a Umbelifloriales*.
316 Buenos Aires, INTA.
- 317 Kiesling R., Ferrari O. (2005) *100 cactus Argentinos*. Buenos Aires, Albatros.
- 318 Kiesling R., Larocca J., Faúndez L., Metzging D., Albesiano S. (2008) Cactaceae: *Opuntia*. In:
319 Zuloaga F., Morrone O., Belgrano M. (eds.) *Catálogo de las plantas vasculares del cono*
320 *sur*. Vol. 2. Dicotyledoneae: Acanthaceae–Fabaceae. Monographs in Systematic Botany
321 107. St. Louis, Missouri Botanical Garden Press.
- 322 Köhler M., Font F., Souza-Chies T.T. (2018) First record of *Opuntia rioplatense* (Cactaceae) for
323 the Brazilian Flora. *Phytotaxa* 379(4): 293–296.
324 <http://dx.doi.org/10.11646/phytotaxa.379.4.3>
- 325 Las Peñas M.L., Oakley L., Moreno N.C., Bernardello G. (2017) Taxonomic and cytogenetic
326 studies in *Opuntia* ser. *Armatae* (Cactaceae). *Botany* 95: 101–120.
327 <https://doi.org/10.1139/cjb-2016-0048>

- 328 Leuenberger B.E. (1993) Interpretation and typification of *Cactus opuntia* L., *Opuntia vulgaris*
329 Mill., and *O. humifusa* (Rafin.) Rafin. (Cactaceae). *Taxon* 42: 419–429.
330 <https://doi.org/10.2307/1223152>
- 331 Leuenberger B.E. (2001a) *Opuntia paraguayensis* (Cactaceae) reassessed. *Willdenowia* 31: 181–
332 187. <https://doi.org/10.3372/wi.31.31116>
- 333 Leuenberger B.E. (2001b) The type specimen of *Opuntia cardiosperma* (Cactaceae), new
334 synonyms and new records from Argentina and Paraguay. *Willdenowia* 31: 171–179.
335 <https://doi.org/10.3372/wi.31.31115>
- 336 Leuenberger B.E. (2002) The South American *Opuntia* ser. *Armatae* (= *O.* ser. *Elatae*)
337 (Cactaceae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und*
338 *Pflanzengeographie* 123 (4): 413–439.
- 339 Machado M. (2008) Notes on Brazilian taxa of series *Armatae* (*Elatae*). *Cactaceae Systematics*
340 *Initiatives* 24: 33–35.
- 341 Madsen J.E. (1989) *Opuntia*. In: Harling G., Andersson L. (eds) *Flora of Ecuador* 45. Cactaceae.
342 Berlings, Azlov.
- 343 Majure L.C., Judd W.S., Soltis P.S., Soltis D.E. (2017) Taxonomic revision of the *Opuntia*
344 *humifusa* complex (Opuntieae: Cactaceae) of the eastern United States. *Phytotaxa* 290: 1–
345 65. <https://doi.org/10.11646/phytotaxa.290.1.1>
- 346 Majure L.C., Puente R. (2014) Phylogenetic relationships and morphological evolution in
347 *Opuntia* s. str. and closely related members of tribe Opuntieae. *Succulent Plant Research* 8:
348 9-30.
- 349 Majure L.C., Puente R., Griffith M.P., Judd W.S., Soltis P.S., Soltis D.E. (2012) Phylogeny of
350 *Opuntia* s.s. (Cactaceae): clade delineation, geographic origins, and reticulate evolution.
351 *American Journal of Botany* 99: 847–864. <https://doi.org/10.3732/ajb.1100375>
- 352 Majure L.C., Köhler M., Font F. (2020) North American *Opuntias* (Cactaceae) in Argentina?
353 Remarks on the phylogenetic position of *Opuntia penicilligera* and a closer look at *O.*
354 *ventanensis*. *Phytotaxa* 428 (3): 279–289. <http://dx.doi.org/10.11646/phytotaxa.428.3.9>
- 355 Pennington R.T., Prado D.E., Pendry C.A. (2000) Neotropical seasonally dry forests and
356 Quaternary vegetation changes. *Journal of Biogeography* 27: 261–273.
357 <https://doi.org/10.1046/j.1365-2699.2000.00397.x>
- 358 Pfeiffer L.G.K. (1837) *Enumeratio diagnostica Cactearum hucusque cognitarum*. Berlin, L.
359 Oehmigke. <https://doi.org/10.5962/bhl.title.15207>
- 360 Pontes R.C., Marchiori J.N.C., Neto L.W. (2017) Notas históricas sobre a família Cactaceae no
361 Rio Grande do Sul (Brasil) e Uruguai. I – Período Clássico (1818-1950): viajantes
362 naturalistas e botânicos europeus. *Balduinia* 0: 01–11.
363 <https://doi.org/10.5902/2358198026215>
- 364 Realini M.F., González G.E., Font F., Picca P.I., Poggio L., Gottlieb A.M. (2014) Phylogenetic
365 relationships in *Opuntia* (Cactaceae, Opuntioideae) from southern South America. *Plant*
366 *Systematics and Evolution* 301: 1123–1134. <https://doi.org/10.1007/s00606-014-1154-1>

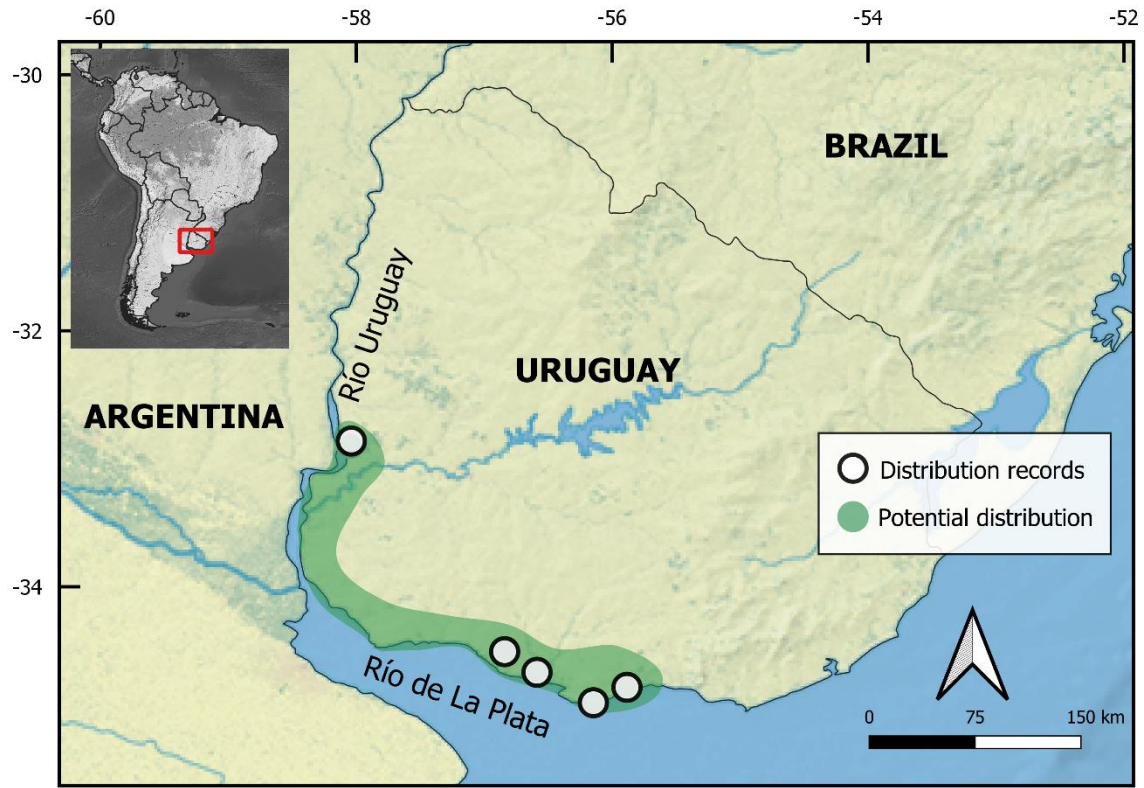
- 367 Ritter F. (1979) Kakteen in Südamerica 1. Brasilien/Uruguay/Paraguay. Spangenberg, F. Ritter.
- 368 Ritter F. (1980) Kakteen in Südamerica 2. Argentinien/Bolivien. Spangenberg, F. Ritter.
- 369 Salm-Dyck J. (1850) Cactae in Horto Dyckensi cultae anno 1849. Bonnae.
370 <https://doi.org/10.5962/bhl.title.120333>
- 371 Schumann K. (1890) Cactaceae. In: Martius C.F.P. *Flora Brasiliensis* Volume 4, Part 2.
372 <https://doi.org/10.5962/bhl.title.454>
- 373 Schumann K. (1899a) Die Cactaceen der Republik Paraguay. *Monatsschrift für Kakteenkunde* 9:
374 149–154.
- 375 Schumann K. (1899b) Gesamtbeschreibung der Kakteen (Monographia cactacearum).
376 Neudamm, Verlag J. Neumann. <https://doi.org/10.5962/bhl.title.10394>
- 377 SpeciesLink (2019) Digital database, CRIA. Available at <http://www.splink.org.br/> [accessed 12
378 Dec. 2019].
- 379 Spegazzini C. (1899) Nova addenda ad floram Patagonigam. *Anales de la Sociedad Científica*
380 *Argentina* 48: 44–59.
- 381 Spegazzini C. (1901) Contribución al estudio de la flora del Tandil. La Plata, Sesé, Larrañaga y
382 Renovales. <https://doi.org/10.5962/bhl.title.9302>
- 383 Spegazzini C. (1902) Nova addenda ad floram Patagonigam. *Anales de la Sociedad Científica*
384 *Argentina* 53: 275–292.
- 385 Spegazzini C. (1905) Cactacearum Platensium Tentamen. *Anales de la Sociedad Científica*
386 *Argentina* 3(5): 477–521.
- 387 Spegazzini C. (1925) Nuevas notas Cactológicas. *Anales de la Sociedad Científica Argentina* 99:
388 85–156.
- 389 Vega R.R. (2013) Distribución, variación morfológica y correlaciones ecológicas de *Opuntia*
390 Miller (Cactaceae) en Colombia. Montería, Zenú.
- 391



393

394

395



396

397

398

399

