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A new endemic species of *Mammillaria* (*Cactaceae*) from San Luis Potosí, Mexico

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Abstract: We describe a new endemic densely spined *Mammillaria* from San Luis Potosí, Mexico. The new species, named *M. morentiniana*, is distinctive by the presence of a globose to shortly cylindric stem with several glabrous, reddish central spines, radial spines that protrude from the plant like white needle-bristles, and small flowers with pale yellow, lanceolate tepals. We compare it with similar and sympatric species of *M.* ser. *Stylothelae*. We include data about habitat and the preliminary status of conservation of the new taxon.

Keywords: *Cactaceae*, *Cacteae*, *Mammillaria*, *Mammillaria* ser. *Stylothelae*, Mexico, morphology, multivariate statistics, new species, species delimitation

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Introduction

Mammillaria Haw. is considered the most diverse lineage of *Cactaceae*, despite the segregation of *Cochemiea* (K. Brandegee) Walton as an independent genus (Breslin & al. 2021). *Mammillaria* includes 143 species (Korotkova & al. 2021), divided into five subgenera, three sections and 16 series (Hunt & al. 2006). The number of species in the genus is under discussion, and taxonomic work is necessary on many species complexes. Specialists estimate that the genus ranges between 164 and 200 species (e.g. Hunt 2016; Breslin & al. 2021). *Mammillaria* is well distributed in the Mexican territory, 98% of the species inhabit Mexico, but some species are present in the S United States, Central America, Colombia and Venezuela (Hernández & Gómez-Hinostrosa 2015). In Mexico, San Luis Potosí state has the highest richness in cactus species (Godinez-Alvarez & Ortega-Baes 2007), where *Mammillaria* is represented by c. 26 species, of which 14 species are endemic (Hernández & Gómez-Hinostrosa 2015; De-Nova & al. 2018). During field surveys in S San Luis Potosí, we found a population of densely spined plants of *Mammillaria*, which belong to *M.* ser. *Stylothelae* (Pfeiff.) K. Schum (Hunt 2006 & al. 2006). *Mammillaria* ser. *Stylothelae* (Hunt 2006) (= *M.* ser. *Stylothelae* group *Crinita*, Hunt 1981) represents a monophyletic group supported by chloroplast DNA sequences (Butterworth & Wallace 2004). Particularly, species of *M.* ser. *Stylothelae* share the deletion of the *rpl16* intron in the plastid genome (Butterworth & al. 2007). Members of this series present straight central spines with a hooked tip, bristles in the tubercle axils, spaced testa pits and a flowering time between March and August (Hunt & al. 2006). The collected plants exhibit contrasting morphological characters compared with other species of *M.* ser. *Stylothelae* distributed in the region, even those densely spined species of the series. We describe them as a new species.

Material and methods

Taxa sampling — Field work was carried out in the vicinity of the municipality of Santa María del Río, San Luis Potosí. We made six visits to the locality from August

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Table 1. Taxon and population sampling, voucher information and acronyms used in the morphological analyses.

Taxon (Korotkova & al. 2021)	**Locality** (Mexico: state, municipality)	**Specimen voucher**	**Population acronym**	**Species acronym**
Mammillaria sp.	San Luis Potosí, Santa María del Río	*P. González-Zamora 11* (IBUG)	sp	sp
M. bocasana Polselg.	San Luis Potosí, Mexquitic de Carmona	*P. González-Zamora 13* (IBUG)	bocasana_SLP	bocasana
M. bocasana	San Luis Potosí, San Luis Potosí	*P. González-Zamora 26* (IBUG)	bocasana_SLP2	bocasana
M. crinita DC.	Hidalgo, Zimapán	*P. González-Zamora 25* (IBUG)	c_crinita_HGO	c_crinita
M. crinita	Querétaro, Tolimán	*P. González-Zamora 22* (IBUG)	c_crinita_QRO	c_crinita
M. crinita	Hidalgo, Ixmiquilpan	*P. González-Zamora 24* (IBUG)	c_crinita_HGO2	c_crinita
M. crinita	Querétaro, Colón	*P. González-Zamora 23* (IBUG)	c_crinita_QRO2	c_crinita
M. crinita	Guanajuato, San Luis de la Paz	*P. González-Zamora 20* (IBUG)	c_crinita_GTO	c_crinita
M. crinita subsp. *leucantha* (Boed.) D. R. Hunt	San Luis Potosí, Charcas	*P. González-Zamora 12* (IBUG)	c_leucantha	c_leucantha
M. crinita subsp. *wildii* (A. Dietr.) D. R. Hunt	Hidalgo, Metztitlán	*P. González-Zamora 21* (IBUG)	c_wildii	c_wildii
M. schwarzii Shurly	Guanajuato, San Felipe	*P. González-Zamora 27* (IBUG)	schwarzii	schwarzii
M. nana Backeb.	San Luis Potosí, Lourdes	*P. González-Zamora 10* (IBUG)	nana	nana

2019 to June 2021. Also, we documented 11 populations of *Mammillaria* ser. *Stylothelae* through field work in the Mexican states of Guanajuato, Hidalgo, Querétaro and San Luis Potosí (Table 1) from 2019 to 2021. Sampling is representative of the morphological variation of the taxa for this comparative study; it included taxa sympatric with and morphologically similar to the putative new species. We discarded other species of the series due to clear differences in morphology, such as the presence of pink flowers (e.g. *M. fittkaui* Glass & R. A. Foster), sparse radial spination (e.g. *M. mathildae* Krähenb. & Krainz) or the presence of only one central spine (e.g. *M. scheinvariana* R. Ortega V. & Glass). For the record, we considered the presence or remains of reproductive structures. Specimen vouchers were preserved and later deposited in the herbarium IBUG (herbarium code according to Thiers 2022+).

Table 2. Vegetative quantitative characters measured for statistical comparison and acronyms used.

Character	**Acronym**
Length of stem	LSTEM
Diameter of stem	DSTEM
Number of central spines	NCENSP
Length of central spines	LCENSP
Number of radial spines	NRADSP
Length of radial spines	LRADSP
Length of areole	LARE
Width of areole	WARE

Comparative analyses — We took photographs of ten specimens *in situ* using several planes and accompanied by a millimetric scale. We selected eight vegetative characters (Table 2) and recorded them in each population on ten specimens and five to ten areoles per specimen. We measured and counted those characters using the image analyser ImageJ (Schneider & al. 2012). Then, we calculated central tendency and dispersion of the data, and constructed box-plots for each quantitative character in order to visually describe the distribution of the data (Mendenhall & al. 2010). We transformed character values using the logarithm function and performed a linear discriminant analysis (LDA) to evaluate the quantitative vegetative characters to discriminate taxa. We made all statistical analyses and plots in PAST (Hammer & al. 2001). We performed analyses by using populations and recognized taxa (Korotkova & al. 2021) as group variables. Complementary to this, we reviewed specialized literature (Britton & Rose 1923; Craig 1945; Bravo-Hollis 1991; Reppenhagen 1992; Pilbeam 1999; Anderson 2001; Hunt & al. 2006) and herbarium specimens to corroborate morphological variation of the compared taxa (see Appendix 1). Finally, we presented a comparison of the discriminant quantitative and qualitative characters for the included taxa.

Conservation — We estimated the area of occupancy (AOO) and extent of occurrence (EOO) by using the Geospatial Conservation Assessment Tool (GeoCAT; http://geocat.kew.org/; Bachman & al. 2001) in order to assess the provisional conservation status of the putative new species.

Results

The vegetative quantitative character NCENSP (Table 2) separates *Mammillaria* sp. (i.e. the putative new species) and *M. schwarzii* Shurly from the remaining populations. The characters LSTEM and DSTEM by themselves did not distinguish *Mammillaria* sp. from the comparative groups; however, the stem of *Mammillaria* sp. is twice as long as wide. Descriptive statistics by population and by taxon of the analysed vegetative characters, and boxplots of the variation of the vegetative characters by population and by taxon, are available in the Supplemental content online. The LDA plot by population (Fig. 1A) suggested *Mammillaria* sp. as a distinctive morphological group. Also, the LDA plot discriminated the population of *M. schwarzii*, one population of *M. bocasana* Polselg. (bocasana_SLP), and a group formed by the population of *M. crinita* subsp. *wildii* (A. Dietr.) D. R. Hunt and one

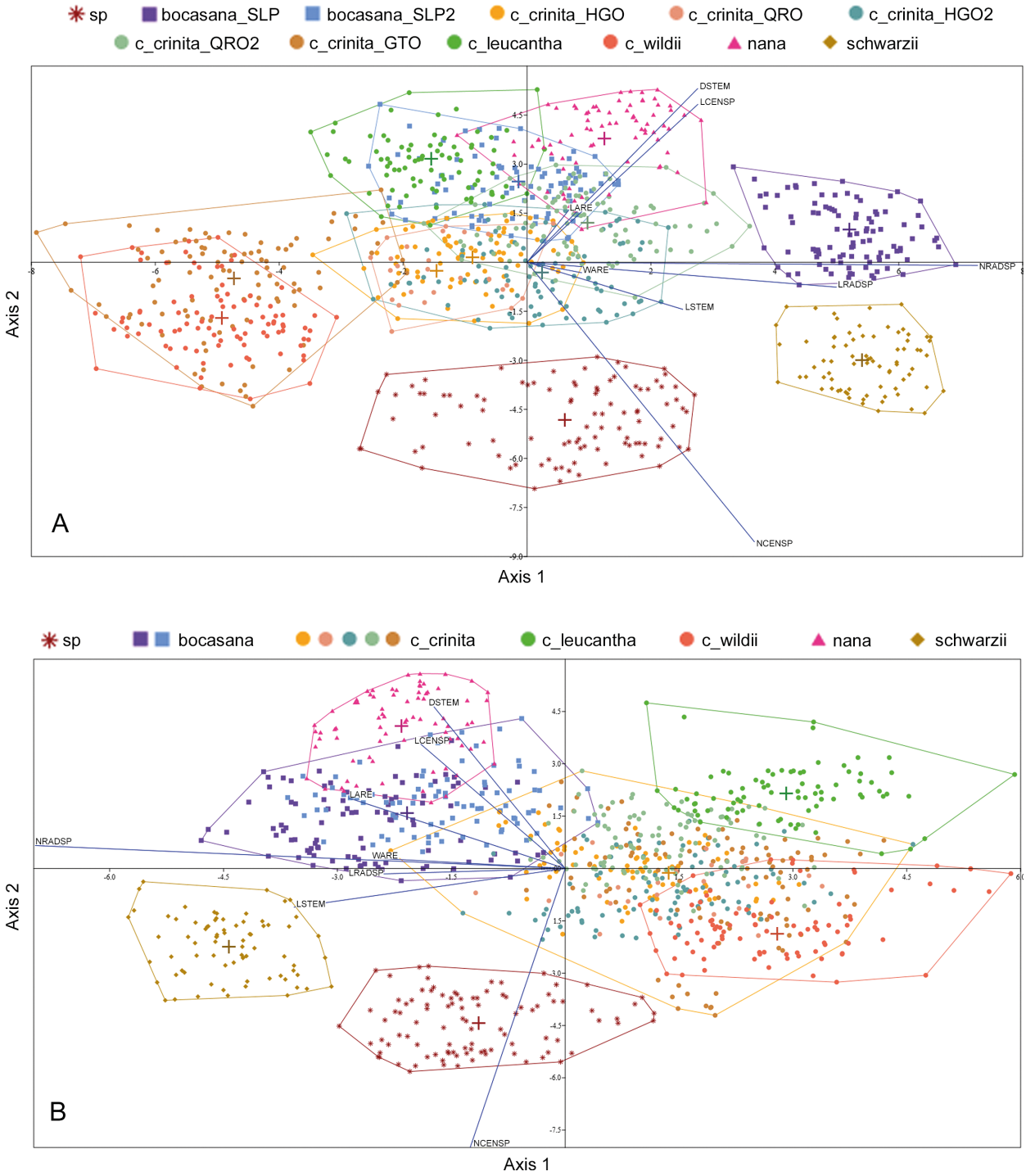

Fig. 1. Linear discriminant analyses (LDA) of the eight vegetative characters. – A: LDA by population, axis 1 (*x*) vs axis 2 (*y*); B: LDA by taxon, axis 1 (*x*) vs axis 2 (*y*). – For population and species acronyms see Table 1; for character acronyms see Table 2.

Table 3. Morphological comparison of the populations of *Mammillaria* ser. *Stylothelae* included in the analysis.

Population acronym (see Table 1)	**Growth form**	**Areole mean length / mean width**	**Root type**	**Central spines number**	**Radial spines number**	**Spines indumentum**	**Radial spines type**	**Inner tepals colour**	**Seed aril**
sp	shortly cylindric	0.76 / 0.76 mm	fibrous	(3 or)4–6(–8) mean = 5.02	(17–)19–28(–32) mean = 24.49	glabrous	straight	pale yellow	absent
bocasana_SLP	shortly cylindric	1.03 / 0.98 mm	fibrous	(1 or)2–4(or 5) mean = 3.57	30–36(–40) mean = 36.02	glabrous	tortuous	yellow with reddish middle stripe	present
bocasana_SLP2	globose	1.33 / 1.09 mm	fibrous	1–3(or 4) mean = 2.63	17–21(–25) mean = 21.79	glabrous	straight	yellow with reddish middle stripe	absent
c_crinita_HGO	globose	0.94 / 0.87 mm	fibrous	(1 or)2–4 mean = 3.44	16–25(–27) mean = 20.69	pubescent	straight	yellow with brown middle stripe	absent
c_crinita_HGO2	globose	0.75 / 0.70 mm	fibrous	3 or 4 mean = 3.71	(14–)16–25(–27) mean = 21.16	pubescent	tortuous	white with pink middle stripe	absent
c_crinita_GTO	globose	1.01 / 0.88 mm	fibrous	1–4 mean = 2	10–20 mean = 14.14	glabrous	straight	yellow with darker yellow middle stripe	absent
c_crinita_QRO	globose	0.86 / 0.78 mm	fibrous	3 or 4 mean = 3.88	16–24 mean = 19.68	pubescent	straight	yellow with brown middle stripe	absent
c_crinita_QRO2	globose	0.71 / 0.65 mm	fibrous	2–4 mean = 3.21	19–26(–30) mean = 23.18	pubescent	tortuous	yellow with brown middle stripe	absent
c_leucantha	globose	0.98 / 0.93 mm	tuberous	(1–)3 or 4(or 5) mean = 3.79	14–21 mean = 12.84	pubescent	straight	yellow with green middle stripe	present
c_wildii	globose	1.07 / 1.08 mm	fibrous	3 or 4(or 5) mean = 3.28	10–15 mean = 12.84	glabrous	straight	white with brown middle stripe	absent
nana	depressed globose	1.26 / 0.93 mm	tuberous	1 or 2 mean = 1.09	(23–)26–29(–32) mean = 28.18	pubescent	straight	yellow with reddish middle stripe	absent
schwarzii	globose	1.36 / 1.39 mm	fibrous	5–9 mean = 7.08	(32–)35–40(–44) mean = 38.67	glabrous	straight	pale yellow with reddish middle stripe	absent

population of *M. crinita* DC. (c_crinita_GTO). The first two axes explained 71.64% of the morphological variation (45.17% and 26.47%, respectively) on the compared populations of *Mammillaria*. NRADSP (axis 1) and NCENSP (axis 2) were the characters with more load (Fig. 1A). The confusion matrix of the LDA by population indicated that all replicates of *Mammillaria* sp. were correctly assigned to their population (Supplemental content online). In the same way, the plot of the LDA by taxon discriminated unambiguously to *Mammillaria* sp. and *M. schwarzii* (Fig. 1B). The first two axes explained 80.75% of the morphological variation (41.27% and 39.48%, respectively) in the compared taxa (Fig. 1B). As in the previous analysis, the characters NRADSP and NCENSP had the highest loadings (Fig. 1B). The confusion matrix of the LDA by taxon showed that all replicates of *Mammillaria* sp. were correctly classified (Supplemental content online).

In addition to the analysed vegetative characters, *Mammillaria* sp. presents a shortly cylindric growth form, fibrous roots, glabrous spines, white, straight radial spines, reddish central spines, and outer tepals without the conspicuous, reddish middle stripe. Table 3 shows the unique combination of characters that defined each taxon included in this study.

Discussion

Linear discriminant analyses (Fig. 1) and the unique combination of characters (Table 3) suggested *Mammillaria* sp. as a distinctive group based on the number of central and radial spines (Fig. 2), growth form, and colour of inner tepals. In this study, we included a wide variation of the closest species, *M. crinita*, which comprises populations with a high morphological variation (Fig. 2). However, it is important to note that high variation occurs between populations and not inside populations (Supplemental content online). The lump concept of *M. crinita* (Fitz-Maurice & Fitz-Maurice 2009) has changed, and some "forms" are now recognized as independent taxa, such as *M. crinita* subsp. *leucantha* (Boed.) D. R. Hunt, *M. crinita* subsp. *wildii*, *M. nana* Backeb. and *M. scheinvariana*. The two subspecies of *M. crinita* were recovered by the analyses as independent morphological groups (Fig. 1, Table 3), and some qualitative characters separate them from the typical *M. crinita*. The status of those taxa should be corroborated in posterior analyses. Despite the morphological variation documented for *M. crinita*, Fitz-Maurice & Fitz-Maurice (2009) never mentioned a "form" with four to eight central spines. *Mammillaria* sp. was also recovered as a separate group from *M. bocasana*, even though we included two distinctive populations of this taxon. Interestingly, one population of *M. bocasana* (*P. González-Zamora 59*, IBUG) corresponded to the neotype location of *M. bocasana* subsp. *eschauzieri* (J. M. Coult.) W. A. Fitz Maur. & B. Fitz Maur. (Fitz-Maurice & Fitz-Maurice 1995), which was discriminated in the LDA by population. Once again, a directed analysis of this *M. bocasana* complex is necessary. Finally, morphological variation and the lack of efficient scientific communication in the past century promoted the publication of several names for *M. bocasana* and *M. crinita*. The comparison of the distinctive characters and distribution of *Mammillaria* sp. with the protologue of those heterotypic synonyms (Korotkova & al. 2021) showed that any of those names correspond to *Mammillaria* sp. (Appendix 2 and 3). *Mammillaria haehneliana* Boed. and *M. knebeliana* Boed. share the number of central and radial spines with *Mammillaria* sp. (Appendix 3). However, both species were described as having red central spines with a yellow base and reddish brown seeds, typical characters of *M. bocasana*. By contrast, *Mammillaria* sp. has completely red central spines and black seeds. In addition, the seeds of *Mammillaria* sp. do not have an aril, whereas the seeds *M. haehneliana* were described with one. In this context, we describe and illustrate a new species of *Mammillaria*.

Taxonomic treatment

Mammillaria morentiniana Gonz.-Zam., D. Aquino, J. Mohl & Dan. Sánchez, **sp. nov.** – Fig. 3.
Holotype: Mexico, San Luis Potosí, Santa María del Río, 2056 m, 28 Aug 2019, *P. González-Zamora 11* (IBUG 215375; isotype: SLPM).

Diagnosis — *Mammillaria morentiniana* is distinguishable from *M. bocasana*, *M. crinita* and *M. nana* by the presence of more than 4 central spines (mean = 5), and differs from *M. schwarzii*, which presents, on average, 7 thinner central spines (Supplemental content online; Fig. 2). *Mammillaria morentiniana* bears fewer than 32 straight radial spines (mean = 24.49), whereas *M. schwarzii* bears more than 32 straight radial spines (mean = 38.98). *Mammillaria morentiniana* has completely red central spines and black, non-arillate seeds, whereas *M. bocasana* has red central spines with a yellow base and reddish brown, arillate seeds. *Mammillaria morentiniana* has glabrous spines and straight radial spines, whereas *M. crinita* has pubescent spines and tortuous or straight radial spines. *Mammillaria morentiniana* differs from the sympatric *M. nana* because the latter has tuberous roots and 0 or 1 pubescent central spines.

Description — *Roots* slender branched. *Stem* simple to branched, 2.2–4(–6) cm tall, 1.5–2.6 cm in diam., growth form globose to shortly cylindric, latex watery; *tubercles* 2–3.5 mm long, 1.5–2.5 mm in diam., axils with tortuous bristles; *areoles* circular, 0.6–1 mm wide; *central spines* (3 or)4–6(–8), reddish, acicular, (3.7–)5–8(–9.4) mm long, glabrous, 1 or 2 of them uncinate; *radial spines* (17–)19–28(–32), white, acicular, (0.4–)0.5–

Fig. 2. Comparison of the stem (left), areole, central and radial spines (right) in the populations of *Mammillaria* ser. *Stylothelae* included in the analysis. – A: *Mammillaria* sp.; B: *M. bocasana* (bocasana_SLP); C: *M. bocasana* (bocasana_SLP2); D: *M. crinita* (c_crinita_QRO); E: *M. crinita* (c_crinita_QRO2); F: *M. crinita* (c_crinita_GTO); G: *M. crinita* subsp. *leucantha* (c_leucantha); H: *M. crinita* subsp. *wildii* (c_wildii); I: *M. nana* (nana); J: *M. schwarzii* (schwarzii). – Scale bars: A–E, G, I, J = graduations of 1 mm; F, H = 10 mm.

Fig. 3. Morphology of *Mammillaria morentiniana* during dry and rainy seasons. – A: plant flowering in habitat; B: stem and roots; C: stems during dry season covered by radial spines resembling white needle-bristles; D: stems during rainy season showing hydrated and expanded tubercles; E: close-up of tubercle and areole bearing six central spines; F: plant bearing red and claviform fruits; G: flower in longitudinal section, outside and inside views; H: seeds. – Scale bars: A = primary graduations of 1 cm, secondary graduations of 1 mm; B = 10 mm; E = graduations of 0.5 mm; G = 10 mm; H = 1 mm.

0.7(–9.2) mm long, glabrous. *Flowers* infundibuliform, 7–9 mm long; *outer tepals* pale yellow with reddish middle stripe, lanceolate, margin entire; *inner tepals* pale yellow, lanceolate, margin entire; *filaments* pale yellow; *anthers* yellow; *style* pale yellow; *stigma* pale yellow, 4-lobed. *Fruit* pink, claviform, 10–20 mm long; *seeds* black, c. 1.1 mm in diam.; *aril* absent; *testa* pitted.

Phenology — Flowering from April to June; fruiting from June to August.

Distribution and habitat — *Mammillaria morentiniana* is endemic to S San Luis Potosí, Mexico. The species inhabits NW-facing cliffs in a small group of igneous mountains at 1900–2100 m. The vegetation at this elevation is oak forest (Rzedowski 1978), which is surrounded by xerophytic scrub in the lower zones of the mountains and valleys. Dominant elements of the vegetation are *Quercus chihuahuensis* Trel., *Q. deserticola* Trel., *Dasylirion parryanum* Trel., *Beaucarnea hookeri* (Lem.) Baker and succulents such as *Echinocereus acifer* (Salm-

Dyck) Lem., *Mammillaria muehlenpfordtii* C. F. Först and *Pachyphytum hookeri* A. Berger.

Conservation — *Mammillaria morentiniana* is known in only one locality and represents a micro-endemism. Probably, the range-restricted *M. morentiniana* and *M. schwarzii* represent relict species with dense spination adapted to previous cold periods and now to winter frosts. We estimate that the population is composed of 250 adult and 150 juvenile plants, occupying an area of c. 0.087 km^2. Following the IUCN Red List categories and criteria (IUCN Standards and Petitions Committee 2022), we propose *M. morentiniana* as Critically Endangered, CR B1ab(iii)+2ab(iii); C1, based on an EOO of 0.317 km^2 (criterion B1) and an AOO of 0.140 km^2 (criterion B2). In addition, it is known from only one locality (criteria B1a and B2a), presents a poor quality of habitat (criteria B1b(iii) and B2b(iii)) and the population size is estimated to number fewer than 250 mature individuals (criterion C1).

Etymology — The specific epithet is dedicated to the Morentín family from Colima, Mexico. Don Marco and Doña Laura spent their lives preserving the flora in W Mexico. They inspired the first author to observe and admire the local and xerophytic flora.

Taxonomic comments — We suggest *Mammillaria morentiniana* as a part of *M.* ser. *Stylothelae*. Members of this series are characterized by having small seeds with spaced testa pits, bristles at the axils, straight central spines and at least one central spine with an uncinate tip (Hunt & al. 2006). Also, *M. morentiniana* flowers from April to June like most members of *M.* ser. *Stylothelae* (Butterworth & al. 2007). *Mammillaria* ser. *Stylothelae* is distributed in the foothills of the Chihuahuan Desert, Sierra Madre Oriental and Trans-Mexican Volcanic Belt, mainly on igneous soils (Hernández & Gómez-Hinostrosa 2015). Following Butterworth & al. (2007), deletion of the *rpl16* intron is shared by members of *M.* ser. *Stylothelae* (Hunt & al. 2006). Additional analyses are required to confirm the inclusion of *M. morentiniana* in this series. Despite their superficial similarity, *M. morentiniana* is distinctive from other close species of *M. ser. Stylothelae*, by the number of central and radial spines, spine pubescence and seed morphology (see Discussion and Diagnosis). The number of spines, areole dimensions and spine length have been valid for delimiting species in lineages such as *Mammillaria* (Zamudio & Guzmán 2017; Ortiz-Brunel & al. 2022), *Epithelantha* F. A. C. Weber ex Britton & Rose (Aquino & al. 2019) and *Echinocereus* Engelm. (Sánchez & al. 2020). Also, qualitative characteristics such as the presence of tuberous roots, pubescent spines, tortuous spines or a seed aril could provide characters useful for diagnosis. We propose that comprehensive fieldwork and statistical morphological analyses could support a better delimitation of *M.* ser. *Stylothelae*. We consider that including *M. morentiniana* as a part of *M. crinita* will complicate the taxonomy of the latter species. We end by rephrasing David Hunt (2008), who wrote "please, no more *crinita*" to criticize the superspecies concept of *M. crinita* (Fitz-Maurice & Fitz-Maurice 2006).

Identification key for *Mammillaria morentiniana* and closest species

1. Central spines pubescent **2**
– Central spines glabrous **4**
2. Areoles oval; central spines (0 or)1(or 2) . . ***M. nana***
– Areoles circular; central spines 2–4 . . . . . **3**
3. Stem (20–)27–34(–39) mm in diam.; roots fibrous . . . . . ***M. crinita*** subsp. ***crinita***
– Stem (36–)39–46(–52) mm in diam.; roots tuberous . . . . . ***M. crinita*** subsp. ***leucantha***
4. Central spines > 6 (on average) . . . . . ***M. schwarzii***
– Central spines ≤ 6 (on average) **5**
5. Radial spines > 30 . . . . . **6**
– Radial spines < 30 . . . . . **7**
6. Stem > 30 mm in diam.; radial spines tortuous; seeds with perceptible aril . . . . . ***M. bocasana***
– Stem < 30 mm in diam.; radial spines straight; seed aril absent . . . . . ***M. crinita*** subsp. ***wildii***
7. Central spines 1–3(or 4), to 23 mm long . . . . . ***M. bocasana***
– Central spines (3 or)4–6(–8), (3.7–)5–8(–9.4) mm long . . . . . ***M. morentiniana***

Author contributions

All four authors participated in the design of the investigation. PGZ conducted the field work, data collection and the conservation status assessment. JM provided most of the historical references, collaborated in data collection and analysis of the protologues. DA conducted the herbarium revision. DA and DS performed the comparative analyses. All four authors discussed and wrote the first draft of the manuscript. DS led the revision and editing of the final version of the manuscript.

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Appendix 1. Additional specimens examined

Mammillaria bocasana Poselg. — México: San Luis Potosí: 1.2 km de Valle Umbroso, hacia el N, 26 Apr 2010, *S. Arias & al. 2042* (MEXU); SW of Derramaderos, 12 May 1984, *W. A. Fitz Maurice & B. Fitz Maurice 1520* (MEXU); N of Ahualulco toward Moctezuma, 17 Jul 1989, *W. A. Fitz Maurice & B. Fitz Maurice 1928* (MEXU); El Aguaje, SLP Periférico, 22 Aug 1989, *W. A. Fitz Maurice & B. Fitz Maurice 1933* (MEXU); Fracción el Aguaje, 25 Nov 2021; *P. González-Zamora 26* (IBUG); near cemetery at Agua Prieta, 6 Sep 1989, *W. A. Fitz Maurice & B. Fitz Maurice 1942* (MEXU); NE of Valle Umbroso, 8 Nov 1989. *W. A. Fitz Maurice & B. Fitz Maurice 1946* (MEXU); SW of Mexquitic, 12 Nov 1989, *W. A. Fitz Maurice & B. Fitz Maurice 1954* (MEXU); Puente Tecolote, 27 Nov 1989, *W. A. Fitz Maurice & B. Fitz Maurice 1965* (MEXU); near Tulillo, 6 Oct 1989, *W. A. Fitz Maurice & B. Fitz Maurice 1970* (MEXU); SE of San Pedro, 9 Oct 1989, *W. A. Fitz Maurice & B. Fitz Maurice 1973* (MEXU); Los Ojitos, al N de la Ciudad de San Luis Potosí, Apr 1990, *W. A. Fitz Maurice & B. Fitz Maurice 1996* (MEXU); E of Mantiquillas, 7 Apr 1990, *W. A. Fitz Maurice & B. Fitz Maurice 1996A* (MEXU); S of La Aduana, 23 Nov 1993, *W. A. Fitz Maurice & B. Fitz Maurice 2274* (MEXU); SE of Bocas, 25 Nov 1993, *W. A. Fitz Maurice & B. Fitz Maurice 2276* (MEXU); Mexquitic de Carmona, 5 Jul 2020, *P. González-Zamora 13* (IBUG). — Zacatecas: N of KM 62 #49 to Zacatecas, 27 Sep 1989, *W. A. Fitz Maurice & B. Fitz Maurice 1966* (DES); near Presa San Carlos, 27 Sep 1989, *W. A. Fitz Maurice & B. Fitz Maurice 1967* (MEXU); NW of Pinos, 23 Jul 1989, *W. A. Fitz Maurice & B. Fitz Maurice 2257* (MEXU); NW of Pinos at microondas, 23 Jul 1989, *W. A. Fitz Maurice & B. Fitz Maurice 2258* (MEXU).

Mammillaria crinita DC. subsp. ***crinita*** — México: Hidalgo: SW of Ixmiquilpan, 8 Dec 1993, *W. A. Fitz Maurice & B. Fitz Maurice 2298A* (MEXU); E of Aguas Blancas, 12 Dec 1994, *W. A. Fitz Maurice & B. Fitz Maurice 2346* (MEXU); Ixmiquilpan, al S de Panales, 17 Nov 2021, *P. González-Zamora 24** (IBUG); S shore of Presa Zimapán, 28 Mar 1995, *W. A. Fitz Maurice & B. Fitz Maurice 2372* (MEXU); E shore of Presa Zimapán, 17 Jul 1995, *W. A. Fitz Maurice & B. Fitz Maurice 2379* (MEXU); near Nueva Aljibe, 25 Oct 1997, *W. A. Fitz Maurice & B. Fitz Maurice 2401* (MEXU); Zimapán, Botha, 21 Nov 2021, *P. González-Zamora 25** (IBUG); SW of Actopan, 26 Ago 2000, *W. A. Fitz Maurice & B. Fitz Maurice 2423* (MEXU). — Guanajuato: aproximadamente 5 a 6 km sobre la terracería Aldama-Atarjea, 19 Jun 2014, *S. Arias & D. Aquino 2225* (MEXU); 1 km al N de El Tepehuaje, c. 72 km de Cañada de Moreno sobre la terracería a Mineral El Refugio; la desv. [desviación] a Mineral el Refugio está a 28 km de Cañada de Moreno sobre la terracería a Xichú, 11 Mar 1995, *R. T. Bárcenas & C. Gómez Hinostrosa 481* (MEXU); c. 2 km al N de Puerto de Palmas sobre camino a Álamos de Martínez, 17 Mar 1995, *R. T. Bárcenas & al. 817* (MEXU); E of San Luis de la Paz, 17 Mar 1987, *W. A. Fitz Maurice & B. Fitz Maurice 1641* (MEXU); San Luis de la Paz, carretera MEX 57, 10 Apr 2021, *P. González-Zamora 20** (IBUG); Río El Aguacate, al SO de El Realito, 29

Feb 2012, *U. Guzmán 3541* (IEB); +/- 9 km de Xichú, por la brecha a Atarjea, 30 May 1996, *E. Pérez-Calix & S. Zamudio 3340-A* (IEB). — Querétaro: N of Colón, 18 Oct 1991, *W. A. Fitz Maurice & B. Fitz Maurice 2182* (MEXU); km 48 S of Tolimán, 1 Mar 1992, *W. A. Fitz Maurice & B. Fitz Maurice 2187* (MEXU); near Molinitos, 21 Dec 1994, *W. A. Fitz Maurice & B. Fitz Maurice 2384* (MEXU); Alrededores de presa Colón, 29 May 2021, *P. González-Zamora 23** (IBUG); Panales, 19 Nov 1986, *U. Guzmán 685* (ANSM); km 49.3 de la carretera Bernal-Tolimán, 25 Apr 2013, *O. Rubio 523* (QMEX); 2.6 km al OSO de San Martín, 20 May 2014, *O. Rubio 876* (IEB); San Pablo Toliman-Higuerillas, 8 Feb 2002, *E. Sánchez 122* (MEXU); laderas de rocas ígneas cercanas a Tolimán, Querétaro, 27 Nov 1973, *H. Sánchez-Mejorada 2193* (MEXU); Tolimán, La Vereda, 27 Apr 2021, *P. González-Zamora 22** (IBUG).

Mammillaria crinita subsp. ***leucantha*** (Boed.) D. R. Hunt — México: San Luis Potosí: c. 35 km al N de Río Verde sobre carretera a Cerritos, 4 Nov 1997, *R. T. Bárcenas 1501* (MEXU); near Flor de Calabaza, 11 Sep 1986, *W. A. Fitz-Maurice & B. Fitz-Maurice 1602* (MEXU); Leoncito, N of Hacienda Solís, 14 Sep 1986, *W. A. Fitz-Maurice 1603* (DES); W of Peotillos, 12 oct 1986, *W. A. Fitz-Maurice & B. Fitz-Maurice 1603A* (MEXU); N of Zaragoza, 29 Oct 1986, *W. A. Fitz-Maurice & B. Fitz-Maurice 1605* (MEXU); Cerro El Picacho, 6 Sep 1989, *W. A. Fitz-Maurice & B. Fitz-Maurice 1941* (MEXU); 3 km al N de la carretera San Luís Potosí - Entronque Huizache en dirección a El Peyote, 1 May 2005, *B. Goettsch 687* (MEXU), Charcas, Rancho los Álamos, 6 Dec 2019, *P. González-Zamora 12** (IBUG).

Mammillaria crinita subsp. ***wildii*** (A. Dietr.) D. R. Hunt — México: Hidalgo: El 18, km 81 de la carretera federal 105, Venados a Metzquititlán, 19 Mar 2005, *S. Arias & al. 1493* (MEXU); N of Metzquititlán, 3 Mar 1992, *W. A. Fitz-Maurice & B. Fitz-Maurice 2190* (MEXU); above Metztitlán, 13 Dec 1994, *W. A. Fitz-Maurice & B. Fitz-Maurice 2349* (MEXU); near Puente Venados, 14 Dec 1994, *W. A. Fitz-Maurice & B. Fitz-Maurice 2350* (MEXU); 12 Apr 2021, *P. González-Zamora 21** (IBUG).

Mammillaria morentiniana Gonz.-Zam.& al. — México: San Luis Potosí: Santa María del Río, 2 Sep 2022, *D. Aquino & P. González-Zamora 529* (MEXU).

Mammillaria nana Backeb. — México: Guanajuato: brecha a Vergel de Guadalupe, 9 Dec 2015, *S. Arias & D. Aquino 2255* (MEXU); carretera a San Pedro Almoloyan, 16 Dec 2016, *S. Arias & D. Aquino 2278* (MEXU); 1.5 km N del cruce del libramiento Dolores Hidalgo y camino a la estación de ferrocarril de San Miguel de Allende, 16 Aug 1992, *R. T. Bárcenas 8* (MEXU); c. 21 km al NE de Ocampo sobre el camino a San Pedro Almoloyan. La desviación a San Pedro Almoloyan está a 8 km al O de Ocampo sobre el camino a San Felipe, 15 Oct 1995, *R. T. Bárcenas & C. Gómez-Hinostrosa 804* (MEXU); N of San Luís de la Paz, 27 Jan 1990, *W. A. Fitz Maurice & B. Fitz Maurice 1988* (MEXU); microondas W of km 113, carretera 57, 27 Jan 1990, *W. A. Fitz Maurice & B. Fitz Maurice 1989* (MEXU); W of El Vergel de Guadalupe, 27 Mar 1995, *W. A. Fitz Maurice & B. Fitz Maurice 2371* (MEXU); near of San Miguel de Allende, 19 Mar 1997, *W. A. Fitz Maurice & B. Fitz Maurice 2400* (MEXU); c. 21 km al NE de Ocampo, sobre el camino a San Pedro Almoloya, la desviación a San Pedro está a 8 km al O de Ocampo sobre el camino a San Felipe, 13 Oct 1995, *C. Gómez-Hinostrosa & R. T. Bárcenas 464* (MEXU). — San Luis Potosí: SE of Zaragoza, 29 Oct 1986, *W. A. Fitz Maurice & B. Fitz Maurice 1606* (MEXU); SW of Zaragoza, 29 Oct 1986, *W. A. Fitz Maurice & B. Fitz Maurice 1607* (MEXU); Cañón Yáñez, 7 Nov 1986, *W. A. Fitz Maurice & B. Fitz Maurice 1609* (MEXU); k[km] 175 SE of SLP, 7 Nov 1986, *W. A. Fitz Maurice & B. Fitz Maurice 1610* (MEXU); O del balneario de Lourdes, 20 Jul 2019, *P. González-Zamora 10** (IBUG).

Mammillaria schwarzii Shurly — México: Guanajuato: southeast of El Cubo, 3 Oct 1987, *W. A. Fitz Maurice & B. Fitz Maurice 1687B* (MEXU); 29 Nov 2021, *P. González-Zamora 27** (IBUG).

Appendix 2. Comparison of distinctive characters of *Mammillaria* sp. versus protologues of the accepted name *M. bocasana* (in bold) and heterotypic synonyms (based on Korotkova & al. 2021). An asterisk (*) indicates complementary information from Bravo-Hollis & Sánchez-Mejorada (1991); a dash (–) indicates that the character state is not mentioned in either.

Taxon	Type locality	Growth form	Central spines	Radial spines	Spines indumentum	Areole shape	Inner tepals colour	Seed aril	Reference / Note
Mammillaria sp.	San Luis Potosí	shortly cylindric	(3 or)4–6(–8)	19–28	glabrous	circular	pale yellow	absent	–
M. bocasana Poselg.	San Luis Potosí	subglobose	1	25–30*	pubescent*	oval-circular*	pale yellow with pink stripe*	present*	Poselger (1853)
M. bocasana var. *kunzeana* Quehl	San Luis Potosí	globose to cylindric	2–4	25–30	pubescent	oval	pale yellow with pink stripe	–	Quehl (1916)
M. eschauzeri (J. M. Coult.) R. T. Craig	San Luis Potosí	depressed globose	1	15–20	pubescent	–	–	absent	Coulter (1894, as *Cactus eschauzieri* J. M. Coult.)
M. kunzeana Boed. & Quehl	–	globose to cylindric	3 or 4	20–25	pubescent	oval	pale yellow with pink stripe	present	Quehl (1912)
M. haehneliana Boed.	San Luis Potosí	globose	5–7	25	glabrous	–	pale yellow with pink stripe	present	Boedeker (1934)
M. hirsuta Boed.	–	globose	3 or 4	> 20	glabrous	circular	pale yellow with pink stripe	–	Boedeker (1919)
M. hirsuta var. *grandis* Repp.	Zacatecas	depressed globose to globose	2–4	26–33	glabrous	oval	pale yellow with pink stripe	absent	Reppenhagen (1987)
M. icamolensis Boed.	Nuevo León	shortly cylindric	4	16–20	glabrous	circular	pale pink with pink stripe	present	Boedeker (1933a) / We suggest this name to be a synonym of *M. carretii* Rebut ex K. Schum.
M. knebeliana Boed.	San Luis Potosí	shortly cylindric	5–7	20–25	glabrous	circular	pale yellow	–	Boedeker (1932)
M. longicoma (Britton & Rose) A. Berger	San Luis Potosí	globose	4	25	–	–	pale yellow with pink stripe	–	Britton and Rose (1923, as *Neomammillaria longicoma* Britton & Rose)

Appendix 3. Comparison of distinctive characters of *Mammillaria* sp. versus protologues of the accepted names of *M. crinita* (in bold) and heterotypic synonyms (based on Korotkova & al. 2021). An asterisk (*) indicates complementary information from Bravo-Hollis & Sánchez-Mejorada (1991); a dash (–) indicates that the character state is not mentioned in either.

Taxon	Type locality	Growth form	Central spines	Radial spines	Spines indumentum	Areole shape	Inner tepals colour	Seed aril	Reference / Note
Mammillaria sp.	San Luis Potosí	shortly cylindric	(3 or)4–6(–8)	19–28	glabrous	circular	pale yellow	absent	–
M. crinita DC.	–	depressed globose	4 or 5*	15–20	pubescent*	circular*	yellow with reddish stripe*	–	Candolle (1828)
M. erectohamata Boed.	San Luis Potosí	globose	2 or 3	25	–	–	pale yellow with pink stripe	present	Boedeker (1930b) / We suggest this name to be a synonym of *M. bocasana*.
M. mollihamata Shurly	–	broadly cylindric	4	28	pubescent	–	yellow with rose brown stripe	–	Shurly (1960)
M. pubispina Boed.	Hidalgo	globose	4	15	pubescent	circular*	white to pale yellow with pink stripe	–	Boedeker (1930a)
M. pygmaea (Britton & Rose) A. Berger	Querétaro	globose	4	15	pubescent	circular*	pale yellow	–	Britton and Rose (1923, as *Neomammillaria pygmaea* Britton & Rose)
M. schelhasei Pffeif.	Hidalgo*	subglobose	3	16–20	pubescent*	circular*	white with pink stripe	–	Pfeiffer (1838)
M. seideliana Quehl	Zacatecas	globose to shortly cylindric	3	> 20	pubescent	oval*	pale yellow with pink stripe	present*	Quehl (1911) / We suggest this name to be a synonym of *M. bocasana*.
M. crinita subsp. ***leucantha*** (Boed.) D. R. Hunt	San Luis Potosí	globose	3 or 4	18	pubescent	circular*	brownish olive	present	Boedeker (1933b, as *Mammillaria leucantha* Boed.)
M. aurihamata Boed.	Central Mexico	globose to ovoid	4	15–20	glabrous	circular	pale olive	–	Boedeker (1928)
M. brevicrinita Repp.	San Luis Potosí	depressed globose to globose	3 or 4	18–27	pubescent	–	White to yellow	absent	Reppenhagen (1987) / We suggest this name to be part of the *M. crinita* complex.
M. puberula Repp.	San Luis Potosí	depressed globose to globose	3 or 4	14–19	pubescent	circular	pale yellow with brown stripe	present	Reppenhagen (1987)
M. tezontle W. A. Fitz Maur. & B. Fitz Maur.	San Luis Potosí	depressed globose	1–4	14–20	pubescent	circular	yellow	present	Fitz-Maurice & Fitz-Maurice (1995)
M. crinita subsp. ***wildii*** (A. Dietr.) D. R. Hunt	Hidalgo*	globose to cylindric	4	9	glabrous	circular*	white to pale green with brown stripe	–	Dietrich (1836)
M. calleana Backeb.	Hidalgo	globose to cylindric	1	22	–	–	white	–	Backeberg (1951)

Supplemental content online

See https://doi.org/10.3372/wi.52.52305

Table S1. Descriptive statistics of the compared populations of *Mammillaria* ser. *Stylothelae*.

Fig. S1. Boxplots of the variation of the eight vegetative characters by population of *Mammillaria* ser. *Stylothelae* included in the analysis.

Table S2. Descriptive statistics of the compared taxa of *Mammillaria* ser. *Stylothelae*.

Fig. S2. Boxplots of the variation of the eight vegetative characters by taxon of *Mammillaria* ser. *Stylothelae* included in the analysis.

Table S3. Confusion matrix of the linear discriminant analysis by population.

Table S4. Confusion matrix of the linear discriminant analysis by taxon.

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