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Mapping the Cacti of Mexico



Part II *Mammillaria*

Héctor M. Hernández & Carlos Gómez-Hinostrosa

Succulent Plant Research

Volume Nine

Mapping the Cacti of Mexico

*Their geographical distribution
based on referenced records*

Héctor M. Hernández & Carlos Gómez-Hinostrosa

*Departamento de Botánica, Instituto de Biología,
Universidad Nacional Autónoma de México*

*Part II
Mammillaria*



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Mapping the Cacti of Mexico Part II: *Mammillaria*

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Mapping the Cacti of Mexico: *Mammillaria*

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Summary. We present 54 range maps displaying the global distribution of all the 155 species of *Mammillaria*, the largest genus in the cactus family, and one of the largest and most emblematic in the Mexican flora. We used 4397 geographically referenced *Mammillaria* records, the best available set of verifiable data taken from herbarium specimens. In order to ensure the verifiability of data used in the mapping process, a list of all herbarium records is included in an Appendix; a list of the herbarium records utilized in the first volume of this series is also included here. The species of *Mammillaria* may be found from the southern portions of California, Arizona, New Mexico and western Texas, with few, marginal records in Nevada and Utah, and the genus is absent northwards and in all of the south-eastern states. Southwards, *Mammillaria* occurs in almost every major Mexican region and in numerous locations of Central America, although no records exist for Belize, Costa Rica and Panama. In addition, three species occur sporadically in the West Indies and in a few localities in the northern Andean regions of Venezuela and Colombia. Most species inhabit areas with arid or semi-arid climates covered by desert scrub, although they may also be found in tropical deciduous or thorn forest, and even in more mesic areas occupied by pine, oak, pine-oak or juniper forest or woodland, and even in grassland and chaparral. These plants occur from sea level to a maximum of 3250 m, although the greatest proportion of populations occurs at moderate elevations (1000–2000 m). A total of 98.7% of all *Mammillaria* species occur in Mexico, 88.2% being restricted to the geographical limits of this country. Six major areas of high species richness exist in Mexico: one is located in the Sonoran Desert (Baja California Sur), four in the Chihuahuan Desert (Jaumave, Guadalcázar, San Luis Potosí and Meridional subregion), and another one in the Tehuacán-Cuicatlán Valley. A significant factor conferring a high conservation value to some of these high-diversity areas is the presence of 12 unique, microendemic species within them. Two thirds of the species (102 or 65.8%) in the genus are partially or totally protected inside Natural Protected Areas in Mexico. However, unfortunately 28, out of the 53 unprotected species, are threatened according to IUCN criteria. Conservation actions are imperative in order to protect these species from extinction.

Resumen. Presentamos aquí 54 mapas que muestran la distribución global de las 155 especies de *Mammillaria*, el género más grande de la familia Cactaceae y uno de los más grandes y emblemáticos de la flora Mexicana. Usamos 4397 registros geográficamente referenciados, mismos que representan el mejor conjunto verificable de datos derivado de especímenes de herbario. Para asegurar la veri-

ficabilidad de los datos usados en la elaboración de los mapas, incluimos en un Apéndice una lista de los registros de herbario de cada especie; la lista de los registros utilizados en el primer volumen de esta serie también se incluye aquí. Las especies de *Mammillaria* pueden ser encontradas desde las porciones sureñas de California, Arizona, Nuevo México y el oeste de Texas, con unos registros marginales en Nevada y Utah, estando ausentes hacia el norte y en todos los estados del sureste de los Estados Unidos. Hacia el sur, *Mammillaria* se encuentra en casi todas las regiones de México, así como en numerosas localidades de Centro América, aunque no existen registros de Belice, Costa Rica y Panamá. Además, existen tres especies que se distribuyen esporádicamente en las Antillas y en unas pocas localidades del norte de los Andes de Venezuela y Colombia. Las mayoría de las especies habitan áreas con climas áridos y semi-áridos cubiertos con matorrales xerófilos, aunque también se les puede encontrar en zonas de bosque tropical caducifolio o bosque espinoso, y más aún en regiones templadas y más húmedas pobladas por bosque de pino, encino, pino-encino, así como en pastizal o chaparral. Las especies de *Mammillaria* crecen desde el nivel del mar hasta un máximo de 3250 m, aunque la mayor parte de las poblaciones se concentran entre 1000 y 2000 m de altitud. Del total de las especies que se reconocen en el género, 98.7% existen en México y 88.2% son endémicas a este país. De hecho, se reconocen en México seis áreas principales de alta riqueza de especies: una se localiza en el Desierto Sonorense (Baja California Sur), cuatro en el Desierto Chihuahuense (Jaumave, Guadalcázar, San Luis Potosí y Subregión meridional) y la última en el Valle de Tehuacán-Cuicatlán. Un factor importante que otorga un alto valor de conservación a algunas de estas áreas críticas es la presencia de 12 especies micro-endémicas restringidas. Dos tercios de las especies del género (102 o 65.8% de las especies) están parcial o totalmente resguardadas dentro de Áreas Naturales Protegidas de México. No obstante, de las 53 especies que están totalmente fuera de estas áreas, 28 están bajo algún nivel de riesgo de extinción (CR, EN o VU) de acuerdo con los criterios de la IUCN. Es claro que se requieren acciones para garantizar la conservación de estas especies.

INTRODUCTION

In August 2011 the first of a series of contributions intended to present detailed distribution maps of all the Mexican species of Cactaceae was published (Hernández & Gómez-Hinostrosa 2011). The book contains high quality maps of 33 small cactus genera and 114 species, corresponding to 20% of the estimated 560 species occurring in Mexico.

The spirit of the project rests on the idea that the study and interpretation of the geographical patterns of the Cactaceae would bring us to a better understanding of this emblematic plant family in several fields of knowledge, such as evolutionary biology, biogeography, ecology, conservation biology, natural resource management, etc.

At this second stage of the project we have decided to concentrate on *Mammillaria*, a highly emblematic, primarily Mexican genus, holding the distinction of being the largest of all the Cactaceae in terms of number of species, as well as one of the largest genera of Mexican Angiosperms. We present global range maps of all the species, including two West Indian and South American species not occurring in México.

The genus may be recognized by several morphological characteristics, including the small, globular, depressed or short-cylindrical, tuberculate stems; the dimorphic areoles lacking an adaxial groove running from the apical spine-bearing areole to the axillary flowering areole; the flowers produced in lateral (not apical) areoles; and the pitted seed cell-walls. However, recent phylogenetic investigations based on DNA sequences show that *Mammillaria*, as currently conceived taxonomically, is not monophyletic (Butterworth et al. 2002; Butterworth & Wallace 2004; Bárcenas et al. 2011; Hernández-Hernández et al. 2011). In this work we have opted to consider this genus as traditionally understood (Hunt 2006), in the hope that future systematic work will establish its taxonomic limits with a greater degree of scientific certainty.

METHODS

The characteristics of the database of herbarium specimens used in the mapping process and the methods employed in the production of the maps themselves were described in Hernández & Gómez-Hinostrosa (2011). Following the basic criteria established at the beginning of the project, all maps were built exclusively with the best available set of verifiable data taken from herbarium specimens. Here we used a subset of the database containing 4397 geographically referenced *Mammillaria* records. The complete cactus database currently contains over 43000 records taken from 68 herbaria.

The average number of records by *Mammillaria* species was 28 ($n=155$ species); however, the range varies significantly. For instance, numerous microendemic species were mapped with only a few existing records (<5), whereas many records were available for the widely distributed species [e.g., *M. compressa* (141), *M. magnimamma* (172), *M. crinita* (190), *M. dioica* (214), *M. formosa* (271) and *M. heyderi* (372)]. Appendix 1 shows the list of the 155 species mapped, their geographical distribution at state level, their altitudinal range and the total number of records used in mapping.

The 54 maps presented here display the global distribution of all of the *Mammillaria* species recognized by Hunt (2006) as taxonomically valid, including most of those listed as provisionally accepted. According to this author, numerous species comprise two or more subspecies, very often recognized on the basis of weak morphological characters. In many of these cases, when the differences between subspecies were not clear to us, or when we were unable to discriminate them in the herbarium specimens, we decided to map the species without consideration of infra-specific categories.

In this project, considerable emphasis has been laid on the quality and verifiability of data being used in mapping. For this reason, a list at all geographically ref-

erenced herbarium records used in the construction of the maps is included in Appendix 2. Records, most of which are deposited in the National Herbarium of Mexico (MEXU), are ordered alphabetically by species (or subspecies), country and state. It is important to mention that the first instalment of this project (Hernández & Gómez-Hinostrosa 2011) did not contain a list of exsiccatae, and we have judged convenient to include it here as Appendix 3.

RESULTS AND DISCUSSION

Geographical distribution

As mentioned in the previous section, a total of 4397 records were used to map all of the 155 species of *Mammillaria* recognized here. All of these records are plotted in the map of Figure 1 exhibiting the general distribution of the genus. In general terms, the northern limit of distribution of *Mammillaria* corresponds to populations of several species located in south-western United States, in the southern segments of CALIFORNIA, ARIZONA (mostly south of the Mogollón Rim), NEW MEXICO and western TEXAS. The northernmost records correspond to populations of *M. tetrancistra* from NEVADA (Esmeralda county, Conrad 6745) and UTAH (Parry s.n.). The genus is absent northwards, as well as in all of the south-eastern states.

South of the United States-Mexico border, the genus occurs in almost every major Mexican region, including the peninsular and continental portions of the Sonoran Desert Region; all of the states of the Mexican Pacific slope, from SONORA to the Central Depression of CHIAPAS; the Sierra Madre Occidental and Oriental; the Chihuahuan Desert Region; the Trans-Mexican Volcanic Belt; the Tehuacán-Cuicatlán Valley; and the driest portions of the Balsas Basin and the state of OAXACA.

However, the map of Figure 1 also reveals extensive areas within Mexico where *Mammillaria* is absent, probably due to ecological or historical reasons. The most evident are great extensions of the Sierra Madre del Sur of GUERRERO and OAXACA and the corresponding coastal plain, from western GUERRERO to the Huatulco area in OAXACA, and the coastal plains of CHIAPAS and Guatemala. Furthermore, with the exception of several populations from the eastern extreme of the Trans-Mexican Volcanic Belt (Sierra de Chiconquiaco) in central VERACRUZ, there is a clear absence of *Mammillaria* records in the wet, eastern slopes of the Sierra Madre Oriental and the northern mountains of OAXACA and CHIAPAS, as well as all across the Atlantic plain from southern TAMAULIPAS to north-western YUCATÁN. In particular, there is not a single record of the genus from CAMPECHE, TABASCO and QUINTANA ROO. The dry, narrow coastal belt of northern YUCATÁN is the only area within the Yucatán peninsula where species of *Mammillaria* have been recorded.

In Central America, *Mammillaria* is distributed across an east-west strip in the median portion of Guatemala, and in locations of south-eastern Honduras and

western Nicaragua. The southernmost record of the genus in Central America corresponds to a marginal population of *M. voburnensis* located west of Lake Nicaragua, MANAGUA (*Stevens 11131*). However, *Mammillaria* is absent in vast areas within this region, especially in those with high precipitation regimes of northern Guatemala, and large parts of Honduras and Nicaragua. Furthermore, no records exist for Belize, Costa Rica and Panama. There is one report of *M. columbiana* from El Salvador (José Linares, pers. comm.), but this has not been documented.

Finally, *M. nivosa* and *M. mammillaris*, which occur sporadically in the West Indies, set the eastern distributional limit of the genus. Likewise, *M. mammillaris* and *M. columbiana* subsp. *columbiana* mark the southern boundary of the genus in the northern segment of the Andes in Venezuela and Colombia. The southernmost documented population corresponds to a specimen of *M. columbiana* subsp. *columbiana* collected in HUILA (municipality of Colombia), Colombia (*Llanos 1100*).

Habitat

Most species of *Mammillaria* inhabit areas with arid or semi-arid climates covered by desert scrub or comparable vegetation types. Less frequently, these plants may be found in forest regions with highly seasonal, tropical climates (i.e., areas covered by tropical deciduous forest or thorn forest), or even in more mesic areas occupied by pine, oak, pine-oak or juniper forest or woodland, and even in grassland and chaparral. In contrast, *Mammillaria* species appear to be unable to survive in high precipitation areas where there is a dense, evergreen vegetation cover greatly reducing the availability of light, and when there is a lack of land features, such as rock outcrops, providing safe sites for the plants to establish and reproduce. In connection to this, it is likely that the lack of *Mammillaria* species in areas described in the previous section is a direct consequence of the absence of suitable habitats.

However, some gaps observed in Figure 1 also reflect limitations of the data that are being used in the construction of the maps. In fact, the figure shows extensive areas theoretically suitable for *Mammillaria*, but where there is an apparent absence of species of this genus. The most conspicuous examples include eastern and western COAHUILA, eastern CHIHUAHUA, and extensive portions of the Sierra Madre Occidental, in CHIHUAHUA and DURANGO. The absence of records of *Mammillaria* in these largely inaccessible areas undoubtedly is the result of poor collecting effort.

Elevation pattern

Examination of the elevation records ($n = 3469$) indicates that the *Mammillaria* populations may be found from sea level to a maximum elevation of 3250 m. As shown in Figure 2, about one quarter of all recorded populations (26.2%) occurs below 1000 m, 52.4% is found at moderate altitudes (1000–2000 m) and a further 18.2%

between 2000 and 2500 m. Only a small fraction of the populations exists at elevations above 2500 m.

Pattern of species richness

Figure 3 shows the pattern of distribution of *Mammillaria* species. In a general perspective, six major areas of high species richness are identified. In order to analyse each one of these areas, the distribution of species richness in a 15' latitude × 15' longitude grid was calculated (Figures 4 and 5A–C). Species richness by grid square varied from zero to 13, and 39 grid squares, those having more than seven species, define six discrete areas of high species richness (Figure 5A–C). The approximate area of each grid square is 709 km². The main characteristics of each of these high-diversity areas is summarised in the following paragraphs (Figure 5A–C and Table 1):

I. *Baja California Sur*. This area comprises two disjunct grid squares located at the southern tip of the Baja California peninsula. The area is part of the Central Gulf Coast subdivision of the Sonoran Desert Region and contains nine *Mammillaria* species.

II. *Jaumave*. Located at the Eastern subregion of the Chihuahuan Desert in south-western TAMAULIPAS, this area is formed by two grid squares and contains 16 species. The Eastern subregion of the Chihuahuan Desert is notorious by the proliferation of endemic genera and species of Cactaceae (Hernández et al. 2004b; Hernández & Gómez-Hinostrosa 2005).

III. *Guadalcázar*. This area contains 15 *Mammillaria* species in four grid squares situated in north-central SAN LUIS POTOSÍ, at the south-eastern edge of the Main subregion of the Chihuahuan Desert. This area corresponds almost entirely to the Huizache hotspot, an exceptional area containing the world's highest concentration of Cactaceae globally (Hernández et al. 2001).

IV. *San Luis Potosí*. Found in south-western SAN LUIS POTOSÍ, this area is composed by four grid squares and contains a total of 14 *Mammillaria* species. Contrasting with the other five species-rich areas described here, which are influenced by desert or semi-desert climates, this area is transitional between the Main and Meridional subregions of the Chihuahuan Desert, and is affected by a more mesic climate.

V. *Meridional subregion*. This is the largest and richest of all *Mammillaria*-rich areas as it contains an aggregation of 17 grid squares found throughout the Meridional subregion of the Chihuahuan Desert, holding a total of 30 species. This area, also known as the Querétaro-Hidalgo Arid Zone, corresponds to several disjunct, relatively small, semi-arid land fragments of GUANAJUATO, QUERÉTARO and HIDALGO, holding a biota phylogenetically linked to that of the other subregions of the Chihuahuan Desert (Hernández et al. 2004b; Hernández & Gómez-Hinostrosa

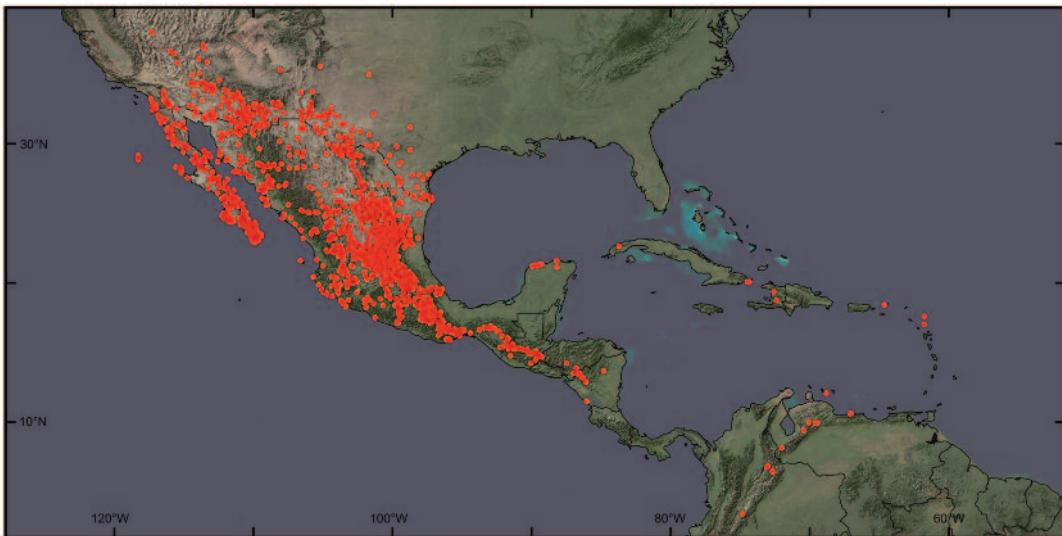


Figure 1. General geographical distribution of *Mammillaria* based on 4397 geographically referenced records. Each circle represents the occurrence of one to several species in a given locality.

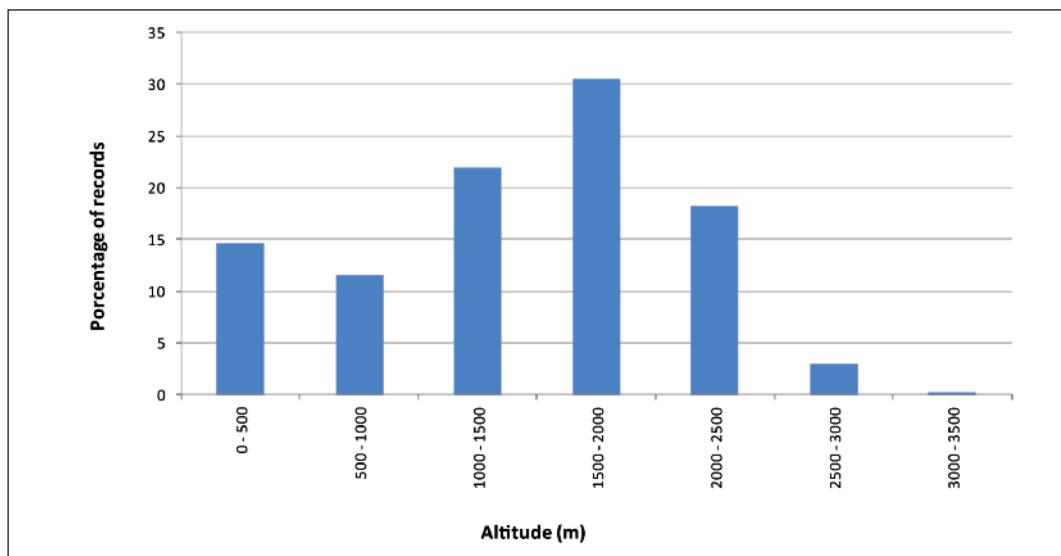


Figure 2. Frequency distribution of the elevation records.

2005). Our results clearly indicate that this exceptional area is the richest centre of species diversity of *Mammillaria* globally.

VI. *Tehuacán-Cuicatlán*. This area comprises a conglomerate of 10 grid squares situated in south-eastern PUEBLA and north-western OAXACA, holding 19 *Mammillaria* species. It corresponds entirely to the Tehuacán-Cuicatlán Valley, the southernmost semi-arid, disjunct area in North America, recognized by its highly endemic flora (Méndez-Larios et al. 2004).

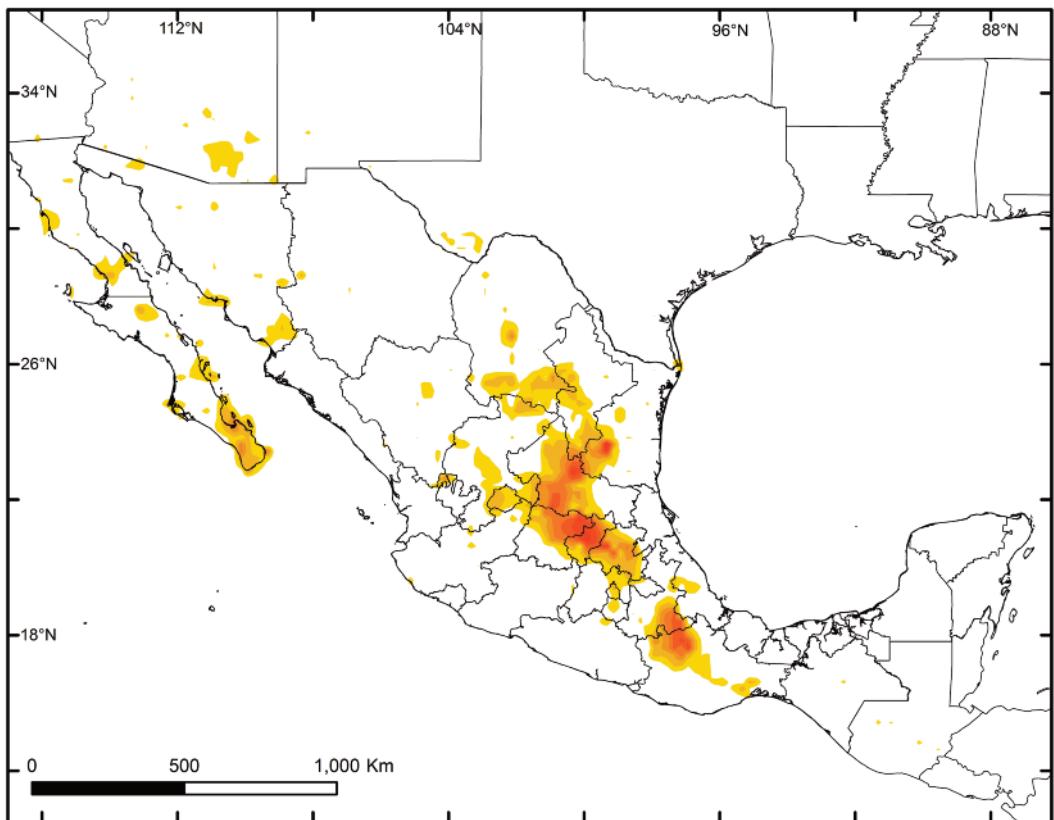


Figure 3. General pattern of *Mammillaria* species richness. The deep-red areas indicate the areas of highest species diversity.

An important factor conferring a high conservation value to some of these high-diversity areas is the presence of unique, microendemic species within them. As it is indicated in Tables 1 and 2, a total of 12 species are restricted to three of these areas, the most important of which is the Meridional subregion (Figure 5B) holding seven exclusive species. The presence of unique species within these areas makes them irreplaceable and essential objects for conservation actions.

Endemism

With 98.7% of its species occurring in Mexico and 88.2% being restricted to the geographical limits of this country, *Mammillaria* is eminently a Mexican genus. Table 3 compares some of the most species-rich genera of flowering plants occurring in Mexico, revealing that *Mammillaria* ranks above all these genera in terms of incidence in this country and level of endemism. Consequently, *Mammillaria* may be distinguished as the most representative member of the Mexican flora.

As shown in the maps presented in this book, a great number of the endemic species of *Mammillaria* have a wide distribution range covering extensive areas

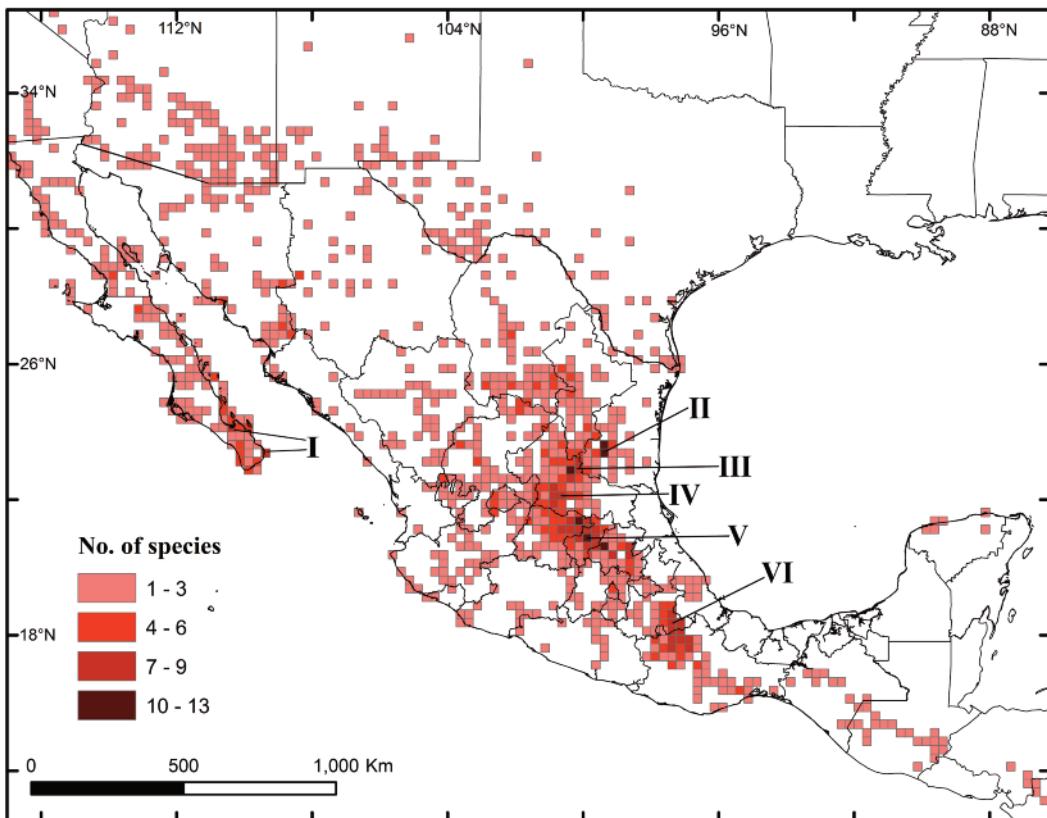


Figure 4. Pattern of *Mammillaria* species richness at a scale of 15' latitude × 15' longitude. The Roman numbers indicate the diversity centres mentioned in Table 1.

within Mexico. However, a significant proportion of the species (57 or 37%) are endemics restricted to a particular state, BAJA CALIFORNIA SUR (10 spp.), TAMAULIPAS (8 spp.) and OAXACA (7 spp.) being the richest in state endemics (Table 4). Furthermore, there is an additional group of *Mammillaria* species deserving special consideration from the phytogeographical and conservation perspectives. These are species occurring in extremely small geographical areas that are always known from only a few records. Examination of Appendix 1 shows that, in fact, virtually half of the species in the genus (77 or 49.6%) are known only from 10 records or less, confirming the frequent occurrence of microendemism in this genus.

Conservation status

Mammillaria is a highly threatened genus and a discussion on its conservation status cannot be avoided. There are three major factors threatening the existence of these plants: the destruction of its natural habitat, the high incidence of microendemisms and the fact that these plants are still being extracted from the natural populations to satisfy the demand from private collectors and illegal traders. The conservation

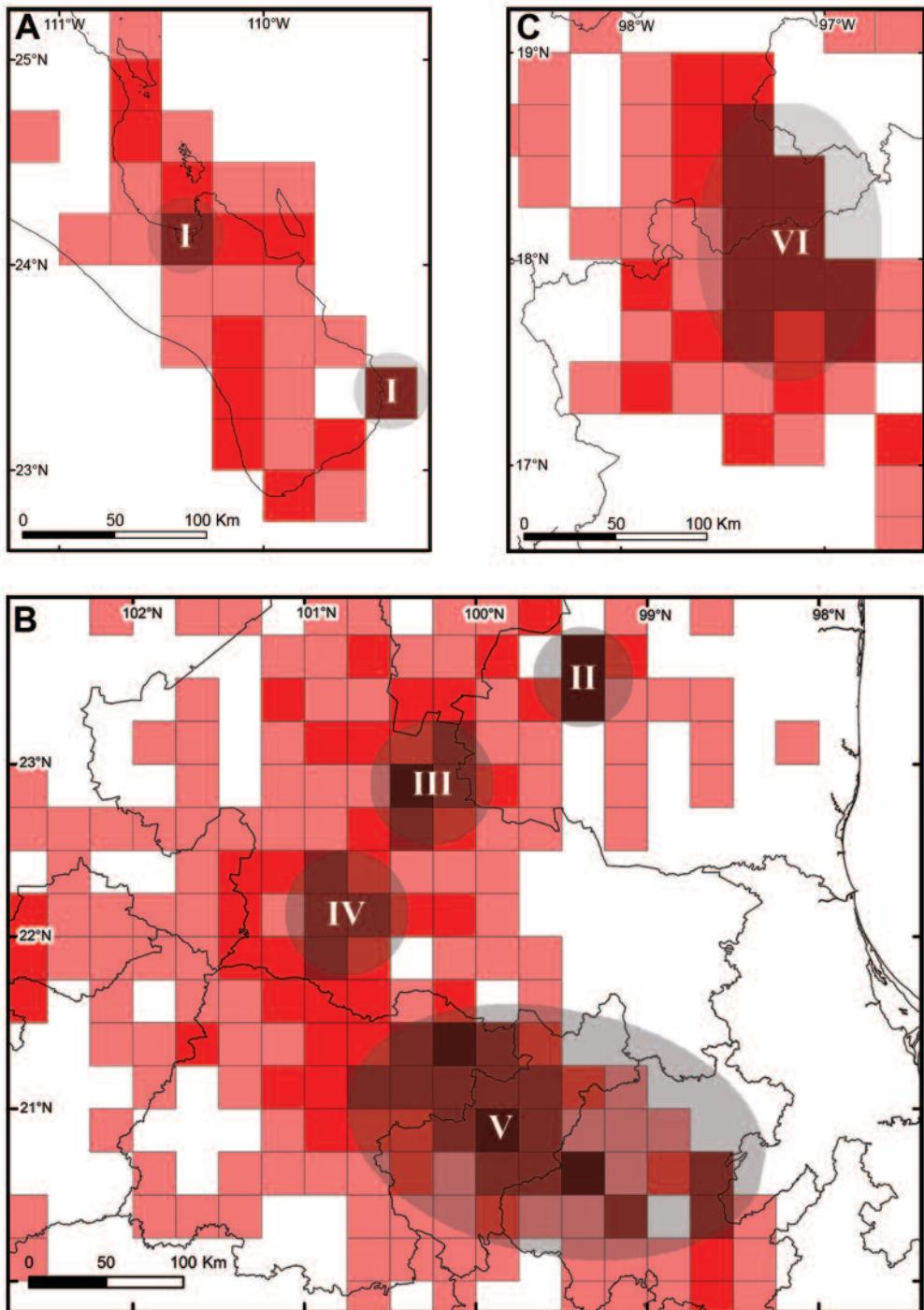


Figure 5. Detail of the diversity centres shown in Fig. 4. **A.** (I) = Baja California Sur. **B.** (II) = Jaumave, (III) = Guadalcázar, (IV) = San Luis Potosí, (V) = Meridional subregion. **C.** (VI) = Tehuacán-Cuicatlán (see Table 1).

Table 1. Centres of *Mammillaria* diversity. Grid squares were named after known cities or towns, and are ordered north to south and west to east. Centroids are expressed as north latitude / west longitude.

Diversity centre	Grid square	No. of species	Total species/ unique species	Centroid
I. Baja California Sur	La Paz	7	9 / 0	24°07' / 110°22'
	Cabo Pulmo	8		23°22' / 109°22'
II. Jaumave	San Antonio	13	16 / 2	23°37' / 99°22'
	Jaumave	11		23°22' / 99°22'
III. Guadalcázar	Puerto de la Clavellina	7	15 / 0	23°07' / 100°07'
	Huizache	11		22°52' / 100°22'
	Presa de Guadalupe	8		22°52' / 100°07'
	Guadalcázar	7		22°37' / 100°22'
IV. San Luis Potosí	Ventura	7	14 / 0	22°22' / 100°52'
	San Luis Potosí	7		22°07' / 100°52'
	Valle de los Fantasmas	7		22°07' / 100°37'
	Villa de Reyes	9		21°52' / 100°52'
V. Meridional subregion	Cañada Moreno	7	30 / 7	21°22' / 100°22'
	Xichú	10		21°22' / 100°07'
	El Guamúchil	8		21°22' / 99°52'
	Los Rodríguez	7		21°07' / 100°37'
	Doctor Mora	8		21°07' / 100°22'
	Tierra Blanca	7		21°07' / 100°07'
	Peña Miller	9		21°07' / 99°52'
	Pinal de Amoles	8		21°07' / 99°37'
	Colón	8		20°52' / 100°07'
	Tolimán	11		20°52' / 99°52'
	San Joaquín	8		20°52' / 99°37'
	Ezequiel Montes	7		20°37' / 99°52'
	Tecozautla	8		20°37' / 99°37'
	Zimapán	10		20°37' / 99°22'
	Mezquititlán	7		20°37' / 98°37'
VI. Tehuacán - Cuicatlán	Ixmiquilpan	8	19 / 3	20°22' / 99°07'
	Atotonilco el Grande	8		20°22' / 98°37'
	Chapulco	7		18°37' / 97°22'
	Tehuacán	7		18°22' / 97°22'
	Coxcatlán	7		18°22' / 97°07'
	Caltepec	7		18°07' / 97°22'
	Teotitlán del Camino	8		18°07' / 97°07'
	Tepelmeme	7		17°52' / 97°22'
	Tecomavaca	8		17°52' / 97°07'
	Cuicatlán	8		17°52' / 96°52'
	Teposcolula	7		17°37' / 97°22'
	Tepeuxila	9		17°37' / 96°52'

Table 2. The six major diversity centres of the genus *Mammillaria* and species restricted to them. It has to be noted that there are no species restricted to the Baja California Sur, Guadalcázar and San Luis Potosí centres.

I. Baja California Sur	V. Meridional subregion
II. Jaumave <i>M. carmenae</i> <i>M. laui</i>	<i>M. albiflora</i> <i>M. herrerae</i> <i>M. marcosii</i> <i>M. microhelia</i> <i>M. parkinsonii</i> <i>M. perbella</i> <i>M. scheinvariana</i>
III. Guadalcázar	
IV. San Luis Potosí	
	VI. Tehuacán-Cuicatlán <i>M. huitzilopochtli</i> <i>M. supertexta</i> <i>M. variaculeata</i>

Table 3. Diversity and endemism of large genera of Angiosperms in the Mexican flora.

Genus	Species worldwide	Species in Mexico (%)	Endemic species (%)	Source
<i>Mammillaria</i>	155	153 (98.7)	135 (88.2)	This book
<i>Salvia</i>	900	303 (33.7)	232 (75.6)	Martínez-Gordillo et al. (2013)
<i>Euphorbia</i>	2000	138 (6.9)	81 (58.7)	Martínez-Gordillo et al. (2002); Steinmann & Porter (2002)
<i>Dalea</i>	161	113 (70.2)	74 (65.5)	Sousa & Delgado (1993)
<i>Quercus</i>	400 ⁺	161 (40.2)	109 (67.7)	Valencia (2004)
<i>Mimosa</i>	500	110 (22)	60 (54.5)	Martínez-Bernal & Grether (2006)
<i>Desmodium</i>	300	100 (33.3)	50 (50)	Sousa & Delgado (1993)
<i>Agave</i>	200	159 (79.5)	119 (74.8)	García-Mendoza (2011)
<i>Croton</i>	1200	126 (10.5)	66 (52.4)	Martínez-Gordillo et al. (2002); Govaerts et al. (2000)
<i>Acalypha</i>	450	126 (28)	74 (58.7)	Martínez-Gordillo et al. (2002); Sagún et al. (2010)
<i>Tillandsia</i>	560	232 (41.4)	172 (74.1)	Espejo (2012)

Table 4. *Mammillaria* species endemic to one state.

Baja California	Guerrero	San Luis Potosí
<i>M. blossfeldiana</i>	<i>M. guerreronis</i>	<i>M. aureilanata</i>
<i>M. neopalmeri</i>		<i>M. erythrosperma</i>
		<i>M. orcutii</i>
Baja California Sur	Hidalgo	Sonora
<i>M. albicans</i>	<i>M. glochidiata</i>	<i>M. boolii</i>
<i>M. armillata</i>	<i>M. humboldtii</i>	<i>M. johnstonii</i>
<i>M. capensis</i>	<i>M. wiesingeri</i>	<i>M. multidigitata</i>
<i>M. cerralboa</i>		<i>M. tayloriorum</i>
<i>M. evermanniana</i>	Morelos	
<i>M. halei</i>	<i>M. knippeliana</i>	
<i>M. petrophila</i>		Tamaulipas
<i>M. phitauiana</i>	Nuevo León	<i>M. anniana</i>
<i>M. posegneri</i>	<i>M. linaresensis</i>	<i>M. baumii</i>
<i>M. schumannii</i>	<i>M. sanchez-mejoradae</i>	<i>M. carmenae</i>
	<i>M. weingartiana</i>	<i>M. cielensis</i>
Coahuila	Oaxaca	<i>M. klissingiana</i>
<i>M. gasseriana</i>	<i>M. deherdtiana</i>	<i>M. laui</i>
<i>M. luethyi</i>	<i>M. hernandezii</i>	<i>M. melaleuca</i>
	<i>M. huitzilopochtli</i>	<i>M. zublerae</i>
Durango	<i>M. kraehenbuehlii</i>	Veracruz
<i>M. guelzowiana</i>	<i>M. oteroii</i>	<i>M. sartorii</i>
<i>M. theresae</i>	<i>M. rekoi</i>	
	<i>M. tonalensis</i>	
Estado de México	Puebla	
<i>M. backebergiana</i>	<i>M. napina</i>	
	<i>M. variaculeata</i>	
Guanajuato	Querétaro	
<i>M. albiflora</i>	<i>M. herrerae</i>	
<i>M. marcosii</i>	<i>M. mathildae</i>	
<i>M. schwarzii</i>	<i>M. microhelia</i>	
<i>M. zeilmanniana</i>		

status of all species of *Mammillaria* has been recently evaluated as part of the Global Cactus Assessment, a project aimed at estimating the extinction risk of the entire cactus family. The results of this evaluation, which may be consulted at www.redlist.org, indicate that 31% of the species (48 spp.) in the genus are threatened with extinction: 9% critically endangered, 11.6% endangered and 10.3% vulnerable. Table 5 is a list of threatened *Mammillaria* species.

The creation and proper maintenance of Natural Protected Areas (NPA) is currently considered the most effective mechanism to protect species and their natural habitats. In connection to this, examination of the distribution area of all *Mammillaria* species in relation to all Mexican NPA indicates that at least part of the range of two thirds of them (102 species or 65.8%) occur inside NPA. In contrast, 53 species are totally unprotected and, unfortunately, more than half of them (28

Table 5. Conservation status of threatened *Mammillaria* species according to the IUCN criteria (www.redlist.org) and presence in Natural Protected Areas. CR = critically endangered, EN = endangered and VU = vulnerable; + = species present in Natural Protected Areas.

<i>M. albicoma</i>EN	+	<i>M. luethyi</i>	VU	+
<i>M. albiflora</i>CR		<i>M. marcosii</i>	CR	+
<i>M. anniana</i>CR	+	<i>M. mathildae</i>	EN	
<i>M. armillata</i>VU	+	<i>M. melaleuca</i>	EN	
<i>M. aureilanata</i>EN	+	<i>M. microhelia</i>	EN	
<i>M. bocensis</i>VU		<i>M. multidigitata</i>	VU	+
<i>M. bombycinia</i>	VU	<i>M. oteroii</i>	VU	
<i>M. capensis</i>	EN	+	<i>M. parkinsonii</i>	EN
<i>M. carmenae</i>	CR	+	<i>M. pectinifera</i>	EN
<i>M. carretii</i>	VU		<i>M. peninsularis</i>	EN
<i>M. coahuilensis</i>	EN		<i>M. pennispinosa</i>	CR
<i>M. crucigera</i>	EN	+	<i>M. perbella</i>	VU
<i>M. deherdtiana</i>	VU	+	<i>M. petrophila</i>	VU
<i>M. duwei</i>	CR		<i>M. pringlei</i>	VU
<i>M. eriacantha</i>	VU		<i>M. sanchez-mejoradae</i>	CR
<i>M. gasseriana</i>	EN		<i>M. schiedeana</i>	VU
<i>M. glochidiata</i>	CR		<i>M. schumannii</i>	EN
<i>M. halei</i>	VU		<i>M. schwarzi</i>	CR
<i>M. hernandezii</i>	EN		<i>M. supertexta</i>	EN
<i>M. herrerae</i>	CR		<i>M. surculosa</i>	EN
<i>M. humboldtii</i>	CR		<i>M. tayloriorum</i>	VU
<i>M. johnstonii</i>	EN		<i>M. theresae</i>	CR
<i>M. laui</i>	CR	+	<i>M. zeilmanniana</i>	CR
<i>M. longimamma</i>	VU	+	<i>M. zublerae</i>	EN

species) are threatened: 10 critically endangered, 9 endangered and 9 vulnerable (Table 5). Obviously, urgent conservation actions must be implemented to protect the threatened species occurring outside NPA.

TEXTS AND MAPS

SUBGENUS OEHMEA

Mammillaria beneckeii (Figure 6), the only member of this subgenus, is a widespread species distributed along the Pacific slope of Mexico, from SINALOA to southeastern OAXACA. It has been found growing in tropical dry forest areas, on limestone and igneous-derived soils, at altitudes ranging from near sea level to 850 m. Its distribution area appears to be extremely fragmented with records being concentrated in particular areas of coastal NAYARIT, JALISCO, MICHOCÁN and GUERRERO, as well as in numerous locations of the Balsas river basin in MICHOCÁN, GUERRERO and ESTADO DE MÉXICO, and on Cerro Guiengola, OAXACA. No herbarium records exist for SINALOA, but Glass & Foster (1971) reported it growing near Río Elota, approximately 60 miles north of Mazatlán.

SUBGENUS DOLICHOTHELE

This subgenus comprises six distinct species, five of which are endemic to the Chihuahuan Desert Region (Figure 7). *Mammillaria longimamma*, the southernmost species, is restricted to the Meridional subregion of the Chihuahuan Desert (Hernández & Gómez-Hinostrosa 2005). Its distribution range extends along a relatively narrow strip in the southern slopes of the Sierra Gorda, from the municipality of Victoria, GUANAJUATO ($100^{\circ} 12' 49''$ W longitude) to Barranca de Santiago ($98^{\circ} 31'$ W longitude), municipality of Huayacocotla, VERACRUZ, including numerous records in QUERÉTARO and HIDALGO. It is usually found growing in desert scrub areas, on limestone, and less frequently rhyolitic, substrates, from 1000–2100 m altitude.

Mammillaria surculosa (Figure 7) has only been reported from a small area located at the south-eastern portion of the main body of the Chihuahuan Desert. The available records of this species come from three contiguous municipalities of SAN LUIS POTOSÍ (Ciudad del Maíz and Guadalcázar) and TAMAULIPAS (Tula), between 940 and 1290 m altitude. It grows in areas covered by typical Chihuahuan Desert vegetation, on limestone and, rarely, igneous substrates.

North-east from the distribution area of *M. surculosa*, right at some of the branches of the Sierra Madre Oriental, two species belonging to subgenus *Dolichothele* are found. *Mammillaria melaleuca* (Figure 7) is restricted to a small



Mammillaria beneckei in habitat; Santa María Mixtequilla, Oaxaca (Gómez-Hinostrosa 2220).

Photo: C. Gómez-Hinostrosa.

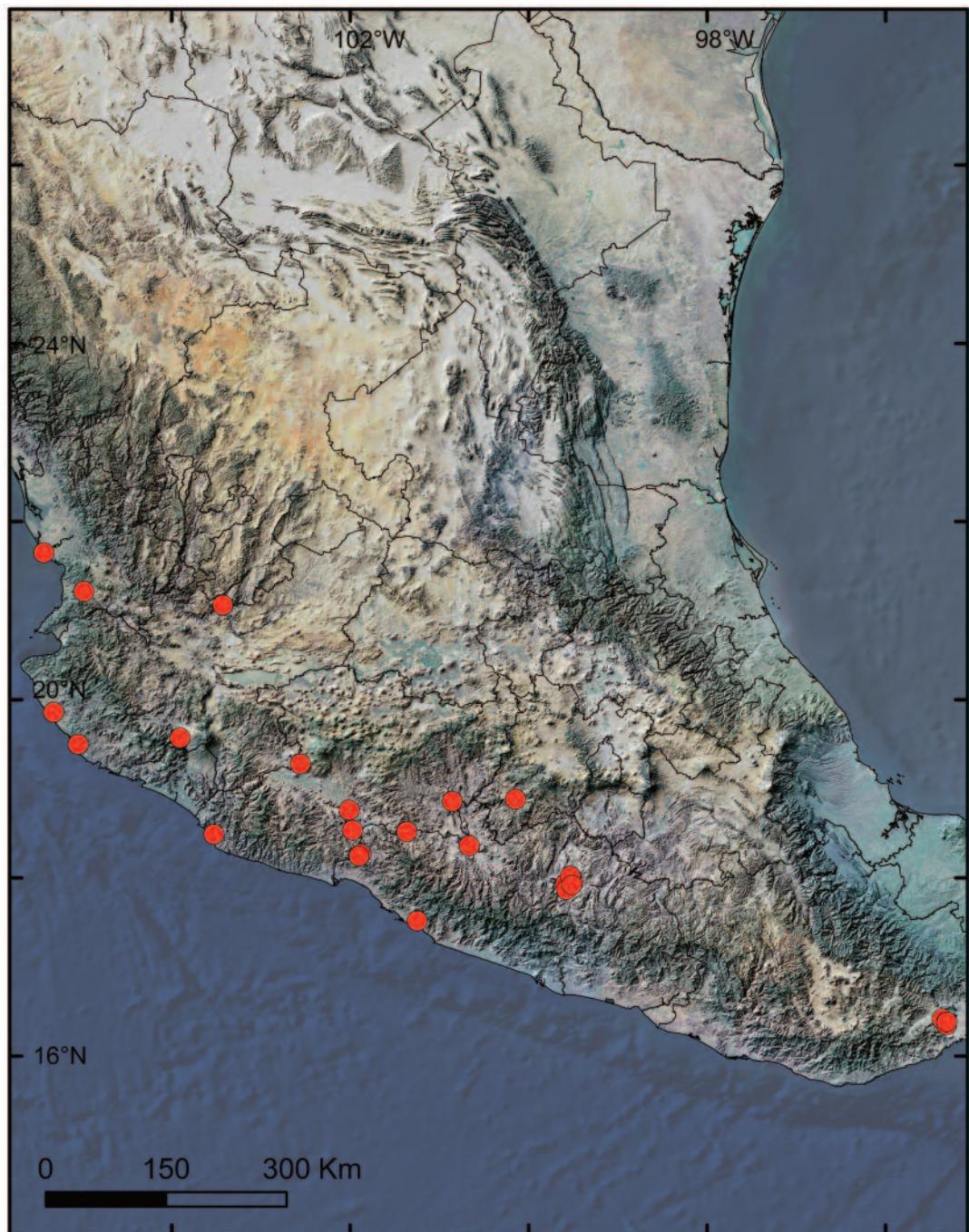


Figure 6. Geographical distribution of subgenus *Oehmea*. *Mammillaria beneckei* (red circles).



Mammillaria longimamma in habitat; Metztitlán, Hidalgo (Gómez-Hinostrosa 1791).

Photo: C. Gómez-Hinostrosa.

area south-west of the Jaumave Valley, in south-western TAMAULIPAS, at altitudes ranging from 1220 to 1400 m. This area is covered by submontane scrub (sensu Rzedowski 1956) and has a calcareous substrate. On the other hand, right on the opposite side of the Jaumave Valley, there is *M. baumii*. This species, recorded from several locations within a small area of TAMAULIPAS, has been usually found growing under nurse *Prosopis* sp. individuals, in places covered by xerophytic and thorn scrub on limestone, at 550–910 m altitude. The distribution area of these two Tamaulipan endemics corresponds to the Eastern subregion of the Chihuahuan Desert (Hernández & Gómez-Hinostrosa 2005).

One additional microendemic in this group is *M. carretii* (Figure 7), a poorly known and presumably rare species only found in a small area near the borderline between NUEVO LEÓN and COAHUILA. It has been reported to occur in barren slopes covered by *Agave-Hechtia* xerophytic scrub.

Mammillaria sphaerica (Figure 7) is the only species belonging to subgenus *Dolichothele* found outside the proper limits of the Chihuahuan Desert. It is a relatively wide ranging species found primarily in the Tamaulipan biotic province east of the Sierra Madre Oriental, with the majority of the known populations found disjunctly in south-eastern TEXAS, eastern NUEVO LEÓN and TAMAULIPAS. During the 1990's, two additional populations were discovered in north-central SAN LUIS

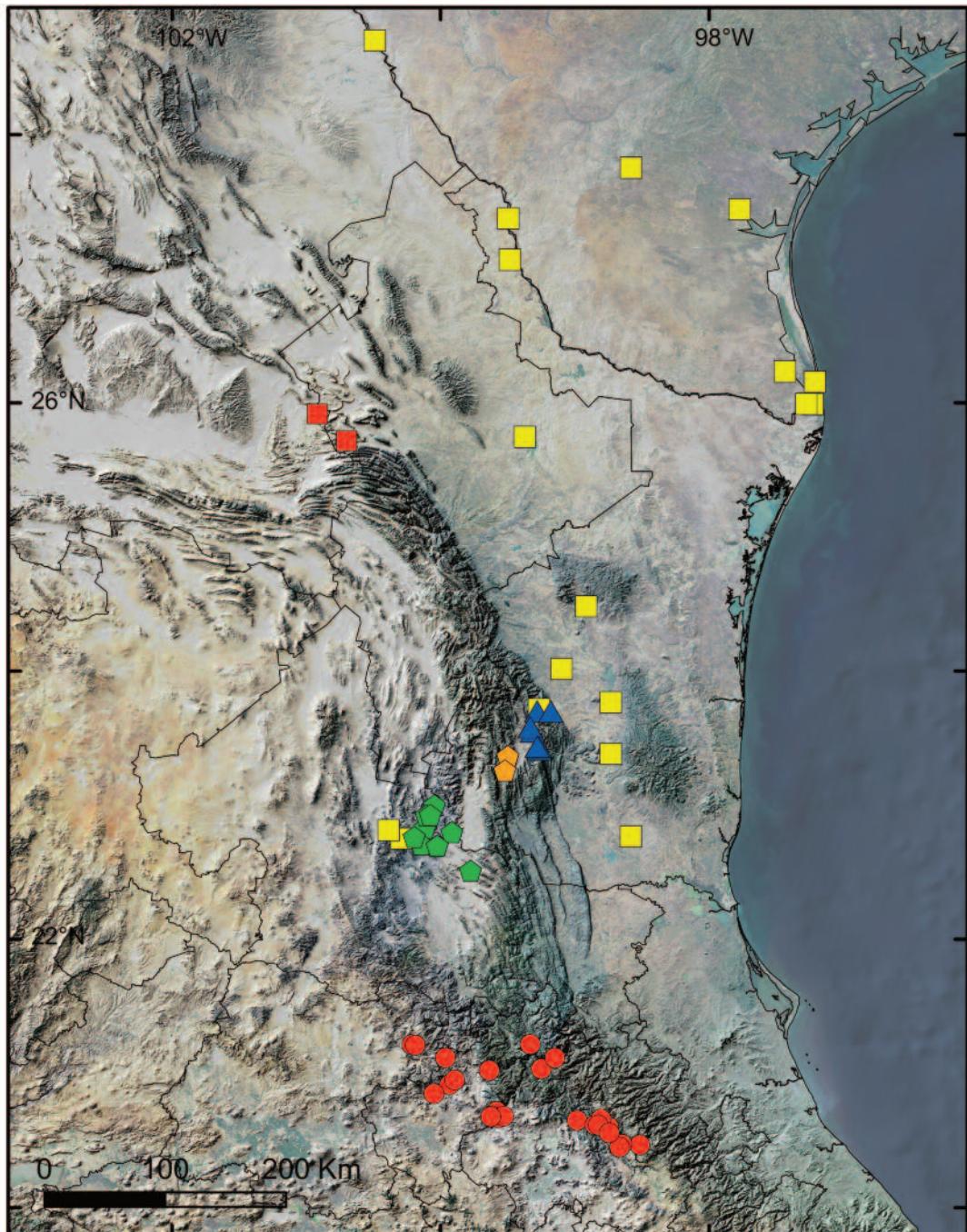


Figure 7. Geographical distribution of subgenus *Dolichothele*. *Mammillaria baumii* (blue triangles), *M. carretii* (red squares), *M. longimamma* (red circles), *M. melaleuca* (orange diamonds), *M. sphaerica* (yellow squares) and *M. surculosa* (green diamonds).

POTOSÍ. This species inhabits a variety of environments across its wide altitudinal range (90–2080 m), including *Juniperus-Quercus* and *Quercus* woodlands, chaparral, and Tamaulipan thorn scrub, in areas of limestone and, occasionally, volcanic substrates.

SUBGENUS PHELLOSPERMA

This subgenus comprises five species, four of which are distributed in parts of north-western Mexico and south-western United States (Figures 8 and 9). *Mammillaria tetrancistra*, in particular, marks the northern limit of distribution of the genus, reaching some localities of NEVADA and UTAH, in the Mohave Desert. In contrast, *M. zephyranthoides* occurs in scattered locations of central and southern Mexico, on both sides of the Trans-Mexican Volcanic Belt.

Mammillaria zephyranthoides (Figure 8) occurs sporadically in several disjunct areas. The northernmost one is in SAN LUIS POTOSÍ, in the municipality of Armadillo de los Infante. Then, a few populations are distributed in GUANAJUATO within the municipalities of San Miguel de Allende, Dolores Hidalgo, San Luis de la Paz and Victoria. South-east of this area, there are some additional populations near San Juan del Río, QUERÉTARO, Huichapan and Tula, HIDALGO, and Nopala, ESTADO DE MÉXICO. Then, it appears again in a distant area of north-western OAXACA, in the



Mammillaria zephyranthoides* subsp. *zephyranthoides in habitat; San Miguel de Allende, Guanajuato.
Photo: R. Bárcenas.

Appendix 2

List of herbarium specimens used in mapping. Specimens are at MEXU unless otherwise indicated; other herbarium acronyms are in parenthesis.

Mammillaria albicans subsp. *albicans*

MEXICO. BAJA CALIFORNIA SUR: *DeBach* 28 (UCR), 304 (UCR), *Johnston* 3912 (ARIZ, K, US), 3923 (K, US), 3943 (ARIZ, K, US), *León de la Luz* 7284, 7586BIS, 7686, 7894 (all at HCIB), *Lindsay* 3301, 3302, 3305, 3313, 3322, *Rebman* 5702 (BCMEX, SD), *Rose* 16842 (types of *Neomammillaria albicans*: SD, US).

Mammillaria albicans subsp. *fraileana*

MEXICO. BAJA CALIFORNIA SUR: *Alvarado* 32, *DeBach* 16AB, 19B, 20B (all at UCR), *Fitz Maurice* 1747, 1754, *Johnston* 3746, 3834, 4018 (all at US), *Larraín* 209, 250, *León de la Luz* 3057, 7366, 7965, 9993A, s.n. (all at HCIB), *Lindsay* 3012 (SD), *Pérez-Navarro* 1537 (HCIB), *Rebman* 2862 (ASU, BCMEX, DES, SD), *Rose* 16508 (types of *Neomammillaria fraileana*: SD, US), 16831 (US), s.n. (US), *Wiggins* 16109 (DS, US).

Mammillaria albicoma

MEXICO. NUEVO LEÓN: *Gómez-Hinostrosa* 920, *Hinton* 28237. SAN LUIS POTOSÍ: Bárrenas 1200, 1325, *Gómez-Hinostrosa* 509, H.M. Hernández 2956. TAMAULIPAS: *Goettsch* 315, 351, *Martínez-Ávalos* 1 (UAT).

Mammillaria albiflora

MEXICO. GUANAJUATO: Bárrenas 192, *Fitz Maurice* 5057, s.n., *Gómez-Hinostrosa* 380, *Scheinvar* 6151.

Mammillaria albilanata

MEXICO. CHIAPAS: *Bravo* s.n., *Dodson* s.n., *Gates* 113 (isotype of *M. tegelbergiana*), *Gómez-Hinostrosa* 2326, *Guzmán* 951. COLIMA: *Reppenhagen* 382 (types of *M. reppenhagenii*: K, ZSS). GUERRERO: *Aquino* 3, *Arias* 303, *Bravo* s.n., *Domínguez* 54, *Guízar* 5017, *Kruse* 2980, *Matuda* s.n., *Sánchez-Mejorada* 3912. JALISCO: *Arreola* 1180 (IBUG). OAXACA: *Aquino* 164, 171, *Arias* 1041, 2133, *Bravo* s.n., *Cedillo* 765, 1854, *Cruz-Espinosa* 1639, *García* 390A, *Gómez-Hinostrosa* 2175, 2603, *Guzmán* 829, H.M. Hernández 1641, *López Martínez* 1, *Martínez R.* 1200, *Martínez Salas* 33476, *Reyes* 3855, *Salas* 2875, *Salinas* 6584, 6803, *Sánchez-Mejorada* 4015, *Torres B.* 162, 183. GUATEMALA. BAJA VERAPAZ: *Véliz* 20032 (BIGU). HUEHUETENANGO: *Gómez-Hinostrosa* 2234, *Velásquez* 191 (BIGU), *Véliz* 12224, 12224bis, 12354, 12535, 15144, 16934, 17032, 17037, 17465, 18438, 19836, 19843, 19849, 19853, 21482 (all at BIGU). QUICHE: *Véliz* 19727, 19729 (both at BIGU).

Mammillaria anniana

MEXICO. TAMAULIPAS: *Fitz Maurice* 2193, *Lau* 1332 (isotype).

Mammillaria armillata

MEXICO. BAJA CALIFORNIA SUR: *Ahuatzin* 15, 16, Bárrenas 1860, *Brandegee* s.n. (probably a type: US), *Fitz Maurice* 1747, *Hunt* 8743 (K), *Larraín* 217, 247, *Lau* 55, *León de la Luz* 7016, 8108 (both at HCIB), *Lindsay* 3086, 3307, *Moran* 7352, *Pérez-Navarro* 1249 (HCIB), *Rebman* 2859 (ASU, BCMEX, SD), *Rivas* 1745, *Rose* 16374, 16445, 16455, 16938 (all at US), *Sanders* 3449 (ARIZ, ASU, UCR), *Wiggins* 5677 (US).

Mammillaria aureilanata

MEXICO. SAN LUIS POTOSÍ: Bárrenas 1500, Chicharo s.n., *Gómez-Hinostrosa* 413, H.M. Hernández 1537, 1740, 3296, 3304, R.E. Hernández 355 (SLPM).

Mammillaria backebergiana subsp. *backebergiana*

MEXICO. ESTADO DE MÉXICO: *Buchenau* 8599.

Mammillaria backerbergiana subsp. *ernestii*

MEXICO. ESTADO DE MÉXICO: *Fittkau* 171-1 (holotype of *M. ernestii*).

Mammillaria barbata

UNITED STATES. ARIZONA: *Benson* 11087 (ARIZ), 8873A, 14864, 16625, 16674 (all at POM), *Bertelsen* 89-396 (ARIZ), *Castetter* 1830 (UNM), *Clark* 1509 (ASU), *Felger* 01-372 (ARIZ), *Fishbein* 2086 (ARIZ), *Loomis* 142 (ARIZ), *Paradine* s.n. (WNMU), *Peebles* 14342, SF-1026, s.n. (all at ARIZ), *Toumey* s.n. (UC, US), *Wankum* s.n. (ARIZ), *West* 1134 (ARIZ), *Zimmerman* 1907, 1909, 1990, 2471, 2472, 2553, 2560 (all at WNMU). NEW MEXICO: *Metcalfe* 797 (US), 819 (UNM, US), 826 (US), *Zimmerman* 1879, 2496, 2643 (all at WNMU). **MEXICO.** CHIHUAHUA: *Arias* 1778, *Findley* s.n., H.M. Hernández 3581, *Laferrière* 1440, 2189 (both at ARIZ), 2328, *Rose* 11666 (US), *Wislichenus* s.n. (possibly a type: MO).

Mammillaria baumii

MEXICO. TAMAULIPAS: *Goettsch* 292, *Gómez-Hinostrosa* 1705, H.M. Hernández 2042, 2549, *Martínez-Ávalos* 328, 602, 623, 685, 712 (all at UAT), *Runyon* s.n. (US), *Sánchez-Mejorada* 2079.

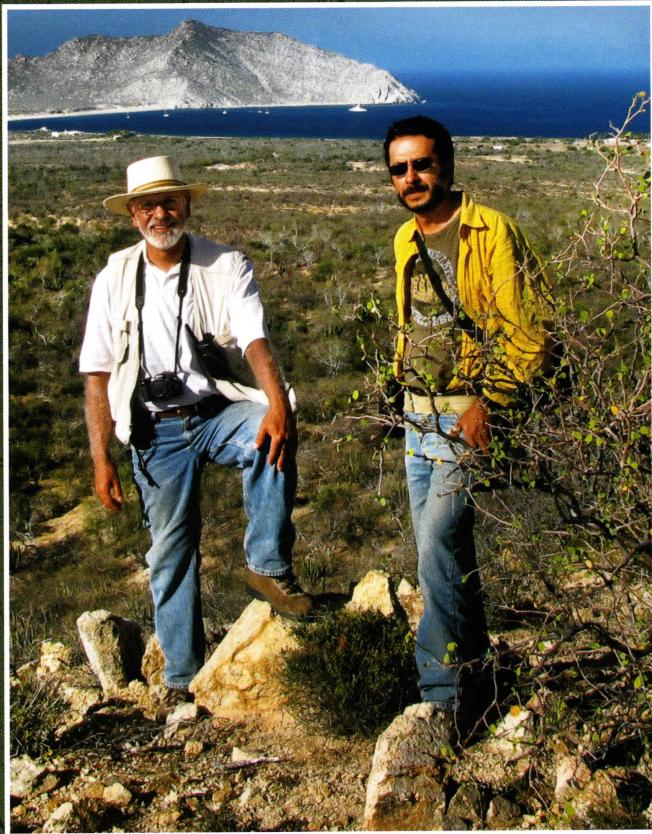
Mammillaria beneckeii

MEXICO. ESTADO DE MÉXICO: *Scheinvar* 6917.

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Accepted names (**in bold**) are followed by the most common synonyms.
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