



Updated checklist and conservation status of Cactaceae in the state of Durango, Mexico

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Abstract

An updated and annotated checklist of Cactaceae in the Mexican state of Durango is provided, supported by a thorough examination of specialized literature and herbarium specimens, as well as field work. Additionally, geographical distribution, endemism and conservation status of the species were analyzed based on a compiled data matrix with 2326 georeferenced records. Cactaceae comprises 137 species and 29 genera in Durango, which represent a high proportion of the Mexican cactus flora: 46–58% at the generic level and 20–23% at the specific level. The estimated richness according to Chao-2 and Jackknife-1 is 143 and 151 species respectively, which means that the inventory we present here for the Cactaceae of Durango is complete in 91 to 96%. Since no herbarium specimens nor registers in reliable data bases were found to support their presence in the area, 46 taxa were excluded; even so, this inventory increases by 30% the cacti richness previously reported for Durango and provides new information on the distribution range of many species. The richest genera are *Mammillaria*, *Opuntia*, *Coryphantha* and *Echinocereus*. The highest concentration of species occurs in the arid and semiarid zone of eastern Durango, although there are also some spots with significant richness in the tropical region on the western slopes of the Sierra Madre Occidental. 75% of the species are endemic to Mexico, 41% are regional endemics and 5% are restricted to Durango. New records and relevant novelties are also discussed.

Key words: cacti, Chihuahuan Desert, distribution, richness, Sierra Madre Occidental

Resumen

Se presenta una lista actualizada y comentada de las cactáceas de Durango respaldada en una revisión exhaustiva de literatura especializada, especímenes de herbario y trabajo de campo. Además, se analiza la distribución geográfica, endemismo y estatus de conservación de las especies con base en una matriz de datos con 2326 registros georreferidos. Cactaceae incluye 137 especies de 29 géneros en Durango, lo que representa una alta proporción de la flora cactológica mexicana: 46–58% de los géneros y 20–23% de las especies. La riqueza estimada según Chao-2 y Jackknife-1 es 143 y 151 especies, respectivamente, lo que significa que el inventario de Cactaceae de Durango que presentamos aquí está completo en 91 a 96%. Se excluyó un gran número de taxones (46), ya que no se encontraron especímenes de herbario, ni registros en bases de datos confiables que apoyen su presencia en el área de estudio; aun así, este inventario incrementa en 30% la riqueza de cactus registrada antes para Durango y provee información novedosa sobre los rangos de distribución de muchas especies. Los géneros más ricos son *Mammillaria*, *Opuntia*, *Coryphantha* y *Echinocereus*. La mayor concentración de especies ocurre en la región árida y semiárida del oriente de Durango, aunque también hay algunos puntos con riqueza considerable en la región tropical en la vertiente occidental de la Sierra Madre Occidental. 75% de las especies registradas son endémicas a México, 41% lo son a la región y 8% se restringen a Durango. También se discuten registros nuevos y novedades relevantes.

Palabras clave: cactus, Desierto Chihuahuense, distribución, riqueza, Sierra Madre Occidental

Introduction

Cactaceae are the most emblematic plants of the Mexican flora. Due to its richness, this family occupies one of the first places after Asteraceae, Fabaceae, Poaceae and Orchidaceae (Villaseñor 2003, 2004, 2016), and includes one genus, *Mammillaria* Haworth (1812: 177), that is among the five most diverse genera in the country (Villaseñor 2004, 2016, Hernández & Gómez-Hinostrosa 2015). Mexico embraces the highest richness and endemism of cacti worldwide (Bravo-Hollis & Sánchez-Mejorada 1991a, 1991b, Hernández & Godínez 1994, Guzmán *et al.* 2003, Hernández & Gómez-Hinostrosa 2011), being one of the main centers of diversity of the family, and, considering richness-area ratio, species density is larger than expected (Ortega-Baes & Godínez-Álvarez 2006).

Cacti are one of the most important groups of plants listed as endangered or threatened under national and international agreements (Hernández & Godínez 1994, Arias *et al.* 2005a, Hernández-Oria *et al.* 2007, SEMARNAT 2010, CITES 2016, IUCN 2016). Nevertheless, such lists are neither exhaustive nor accurate, due in part to the scarcity of information contained in collections and data matrices. Regional inventories are useful to improve conservation strategies of these plants (Ortega-Baes *et al.* 2010), since they provide reliable information on their distribution and abundance.

The taxonomic study of cacti presents great difficulties. The main problems are the poor typification and diagnosis of many taxa and the huge number of scientific names published, many of which are not valid. Among the causes of this are: a) the laboriousness of collecting and preparing specimens has led to a lack of adequate herbarium material, b) the enormous interspecific morphological variation, c) the great similarity between some species, d) the processes of hybridization and vegetative reproduction, common in Cactaceae, and e) the fact that many species have been described by horticulturists based on cultivated plants. Opinions differ on the number of genera and species known throughout their distribution range; the two most recent synoptic treatments recognize a total of 1896 species and 127 genera (Anderson 2001, 2005) or 1438 species and 124 genera (Hunt *et al.* 2006). The same discrepancy occurs in Mexico, where Cactaceae richness estimations range from 50 genera and 593 species (Hunt 2016) to 69 genera and 669 species (Guzmán *et al.* 2003), or 62 genera and 677 species (Villaseñor 2016).

Among 196 plant families in the state of Durango, Cactaceae ranks fourth in species number, surpassed only by Asteraceae, Fabaceae and Poaceae (González-Elizondo *et al.* 2017). Many specific and infraspecific taxa of Cactaceae have been described based on specimens collected in Durango. Some of them have been synonymized according to nomenclatural updates and recent taxonomical reviews, but others, at least 20 of the taxa described from Durango, are currently accepted, e.g., *Coryphantha durangensis* (Runge ex Schumann 1899: 478) Britton & Rose (1923: 40), *C. echinoidea* (Quehl 1913: 42) Britton & Rose (1923: 30), *C. kracikii* Halda *et al.* (2002: 12), *C. longicornis* Bodeker (1931: 249), *C. recurvata* subsp. *canatlanensis* Dicht & Luthy (2003: 57), *Echinocereus adustus* subsp. *schwarzii* (Lau 1982: 28) Taylor (1997: 8), *E. pamanesiorum* subsp. *bonatzii* (Roemer 1995: 98) Roemer (1997: 45), *Mammillaria guelzowiana* Werdermann (1928: 356), *M. mercadensis* Patoni (1910: 54), *M. pennispinosa* Krainz (1948: 20), *M. theresae* Cutak (1967: 237) and *Opuntia durangensis* Britton & Rose (1908: 518).

Despite the relevance of the cacti richness in Durango, there are only two publications that try to integrate knowledge about this important family in the region: a checklist including 86 names of species with no taxon authorities nor voucher specimens (Gold 1967), and the floristic checklist of Durango (González-Elizondo *et al.* 1991) including 129 species of cacti, only 52 based on voucher specimens and the rest based on literature. Some species, such as *Ariocarpus kotschoubeyanus* (Lemaire 1842: unpagged) Schumann in Engler & Prantl (1897: 259) and *Lophophora williamsii* (Lem. ex Salm-Reifferscheidt-Dyck 1845: 385) Coulter (1894: 131), although referred to Durango in old references, are not recorded for the state in recent integrative works such as the *Mexican Cacti Catalog* (Guzmán *et al.* 2003) and *Mapping the Cacti of Mexico I and II* (Hernández & Gómez-Hinostrosa 2011, 2015), probably due to either the lack of voucher specimens deposited in herbaria or of reliable geographic data.

Floristic studies, biological collections and data matrices are the source of information that support management and conservation strategies as well as taxonomic, ecological and phytogeographical studies. This paper aims to integrate, update and expand knowledge about cacti of Durango, and thus fill a gap of information about the diversity and distribution of this important family in an area that, according to what has been mentioned above, might contain a high diversity. We present and analyze an updated and annotated checklist for this family in the state based on more than 10 years of field work, critical review of herbaria specimens and reliable data bases. The representativeness of cacti from Durango in scientific collections through time, richness distribution, geographical extent of the distribution of each species and completeness of the inventory are also analyzed.

Material & Methods

Study area

The state of Durango is located in central northwestern Mexico. With an area of 123181 km² it represents 6.3% of the total area of the country. Its extreme coordinates are: 26°53'–22°16'N, 102°29'–107°16'W (INEGI 2005) (Figure 1) and it presents a wide range of elevations, from 130 to 3340 m. The Sierra Madre Occidental mountain range occupies more than half of the territory of Durango; it has a NNW orientation with a width of up to 250 km, and is the axis of the complex physiography of the region.

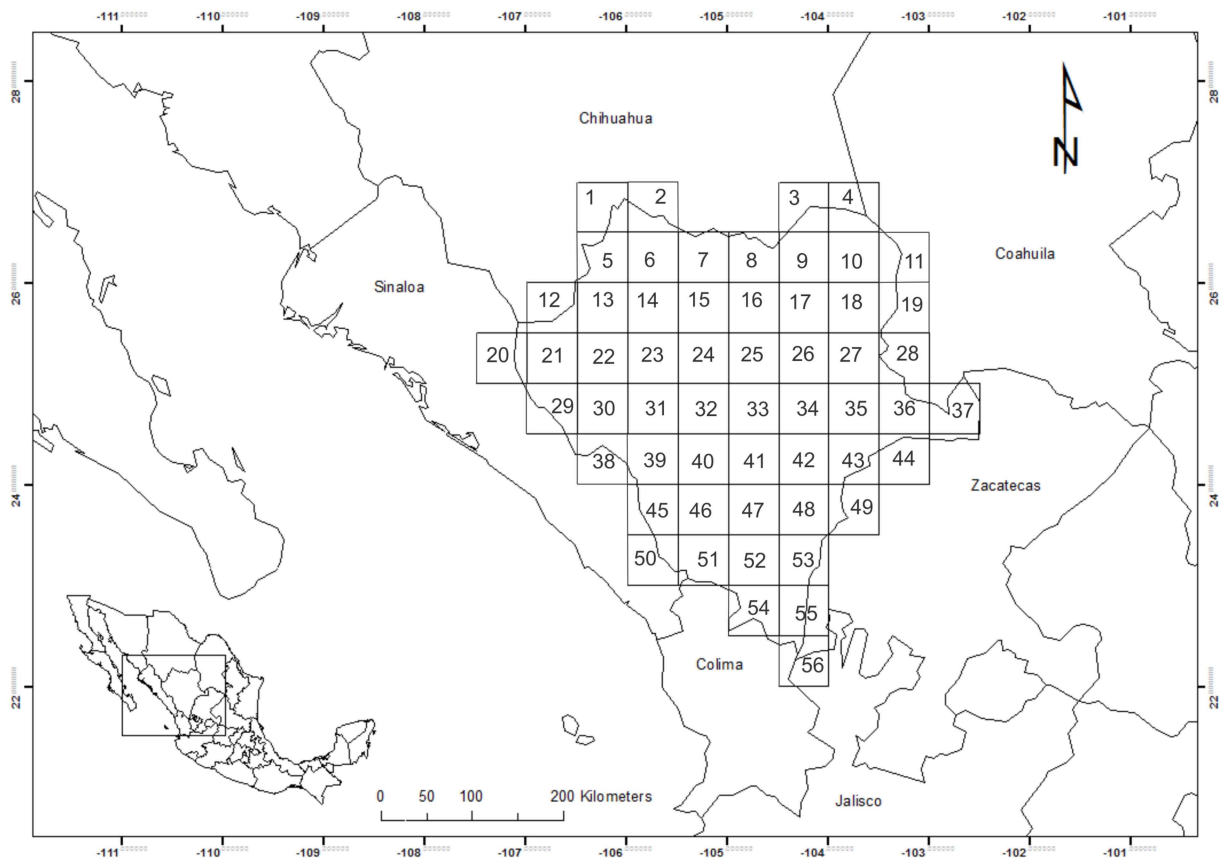


FIGURE 1. Location of Durango State in Mexico and its division in 56 cells of 0.5 × 0.5 degree.

The spatial heterogeneity in Durango is related to the broad diversity of soils and climates in the region. In the center and west dominate outcrops of volcanic origin; to the east, sedimentary rock outcrops of marine origin; whereas the vast valleys and the Chihuahuan Desert are covered by residual and alluvial deposits. According to the FAO-UNESCO classification (FAO 1988), in nearly half of the state dominate Leptosols, followed by Calcisols, Regosols, Cambisols and Haplic Phaeozems. A wide range of climates are found in the state: dry (B) in the north and east, temperate (C) and semicold (C(E)) in the mountains, and warm (A) on the lowland zones west of the Sierra Madre Occidental (González-Elizondo *et al.* 2007).

Four ecoregions and 14 types of vegetation are represented in Durango (González-Elizondo *et al.* 2007). The ecoregions and vegetation types include: a) Arid and Semiarid Zone in the north and east of the state (xerophytic vegetation, halophyllous and gypsophyllous vegetation), b) Valleys and high plains in the central portion and inserted between the mountains (grasslands, dry-temperate scrub), c) Sierra Madre Occidental in the west, ranging from north to south (chaparral, pine-oak woodland, conifer forest, mixed forest, oak forest and mesophytic forest), and d) Quebradas or deep ravines on the western slopes of the Sierra Madre Occidental (tropical deciduous forest, tropical subdeciduous forest and thorn forest). Additionally, the state is located in the transition zone between the Nearctic and Neotropical regions which promotes a high diversity of ecosystems and the unique composition of its flora. Neotropical elements are dominant in the Quebradas region and common in the Arid zone, whereas in the Sierra and the Valles regions nearctic elements are abundant, although the mixture of origins is the most common pattern. Almost all vegetation types proposed by Rzedowski (1978) for Mexico are represented in the entity.

Data matrix

We made a data matrix in Access (version 2010) with taxonomic, curatorial and environmental information about Durango cacti from three main sources: 1) a critical review of floristic, and taxonomic literature (Bravo 1978, Bravo & Sánchez-Mejorada 1991a, 1991b, González-Elizondo *et al.* 1991, Guzmán *et al.* 2003, Hernández & Gómez-Hinostrosa 2011, 2015, Hernández *et al.* 2004, Hunt *et al.* 2006, Villaseñor 2016), 2) examination of Cactaceae specimens deposited in selected herbaria (ANSM, ASU, CIIDIR, DES, ENCB, GBH, and MEXU), plus records of herbarium specimens, not viewed, from US and NY) obtained from reliable sources, 3) new records were obtained on several field trips, carried out mainly between 2006 and 2015, that were conducted considering two criteria: to include the different ecoregions present in the entity, and to locate populations of species previously recorded for the region and not represented in the CIIDIR Herbarium. Many of the new records were made based on photographs of individuals *in situ*; however, some herbarium collections were also made in order to have the largest possible number of species represented in the collections. For each specimen examined, the identity of the species was verified, the nomenclature was updated, and the taxonomic and geographic information were recorded. The identifications were achieved using specialized resources (Britton & Rose 1919, 1920, 1922, 1923, Craig 1945, Bravo 1978, Taylor 1985, Bravo & Sánchez-Mejorada 1991a, 1991b, Pilbeam 1996, 1999, 2011, Pilbeam & Bowdery 2005, Dicht & Lüthy 2005). Voucher specimens were deposited at CIIDIR.

The data matrix was filtered to include only georeferenced records or those with enough geographical information allowing to assign coordinates; however, some important historical collections that lack this information or those of species with very few collections (such as the type specimen of *Echinocereus ortegae* Rose in González-Ortega (1929: unpagued) and one specimen of *Mammillaria moelleriana* Bödeker (1924: 213) were georeferenced approximately in order to be included in the numerical analysis. Also, valuable historical collections with very imprecise geographic information, such as Edward Palmer's collections deposited at US, were used only to build a species accumulation curve through time. The data matrix did not include subspecies, nor cultivated or escaped species.

Checklist

We prepared an updated and annotated checklist of the cacti from Durango following the proposal of generic nomenclature by Hernández-Ledesma *et al.* (2015), and that of Guzmán *et al.* (2003) for species delimitation, except in cases where more recent taxonomic information is available, for example: a) in the series *Triglochidiati* of *Echinocereus* Engelman in Wislizenus (1848: 91) we followed in part the criterion of Sánchez *et al.* (2013), b) according to Hunt *et al.* (2006) and Montanucci (2008), we recognized *Astrophytum coahuilense* (Moeller 1927: 54) Kayser (1932: 59) as a different species from *A. myriostigma* Lemaire (1839: 4), c) we accepted the reinstatement of *Nyctocereus* Berger (1905: 75) as a monotypic genus (Arias *et al.* 2005b), d) *Mammillaria sonorensis* Craig (1940: 155) was considered different from *M. standleyi* (Britton & Rose 1923: 97) Orcutt (1926: 8) in accordance with Pilbeam (1999) and Hunt *et al.* (2006), and e) *Opuntia rufida* Engelman (1856: 298) as different from *O. microdasys* (Lehmann 1827: 16) Pfeiffer (1837: 154) according to Hunt *et al.* (2006). Data source (voucher, photographic record or literature), geographical amplitude, endemic category and conservation status assigned in national and international instruments for each species were provided.

Based on a critical review of literature (Guzmán *et al.* 2003; Hernández *et al.* 2004; Hernández & Gómez-Hinostrosa 2011, 2015; Hunt *et al.* 2006; Lebgue-Keleng *et al.* 2011; Lebgue-Keleng & Quintana-Martínez 2013; Paredes-Aguilar *et al.* 2000; Villarreal-Quintanilla 2001; Villaseñor 2016) and field observations, the degree of endemism of each species was determined considering three levels: 1) Durango, taxa whose known distribution is restricted to the limits of the state of Durango; 2) Regional, taxa whose known distribution is restricted to the state of Durango plus one to three neighboring states; 3) Mexico, taxa whose known distribution is restricted to the territory of the Mexican Republic, generally in more than four states, including Durango.

The conservation status was considered according to the Mexican NOM-059-SEMARNAT-2010 (SEMARNAT 2010), the Red List of Threatened Species (IUCN 2016), and The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2016).

Analysis

In order to analyze the progress in the knowledge of Durango's cacti since the early twentieth century to the present, we built a species accumulation curve through time based on herbarium specimens, using as a measure of effort the number of species added by lustrum.

DIVA-GIS version 7.5 (Hijmans *et al.* 2012) was used to analyze richness distribution and species geographical amplitude within Durango, based on species presence/absence in a grid. Cell size was fixed as 30' × 30', resulting in 56 units (Figure 1). Geographical amplitude of each species within the state was estimated considering the number of cells in which these were recorded. Due to the latitudinal effect, there is difference in the area occupied by each cell; likewise, those located in the state limits have only a fraction of the territory within it. The size of the cell also may result in low spatial resolution, but is adequate for a preliminary analysis of the richness distribution and the degree of completeness of the inventory, estimating the α diversity (richness per cell) as well as the γ diversity (total richness of the state).

Sampling quality was assessed using EstimateS version 9.1.0 (Colwell, 2013) to construct species accumulation curves and to estimate potential richness using non-parametric estimators: Chao2 (Chao 1984) and Jackknife-1 (Burnham & Overton 1979).

The degree of completeness of the inventory (C) or percentage of known richness compared to the estimated was obtained by the coefficient C (Soberón *et al.*, 2007) by dividing the observed richness among the estimated one by each of the estimators.

Results

Representation of Durango cacti in scientific collections

A total of 1131 herbarium specimens collected in Durango were examined: ASU (83), ANSM (18), CIIDIR (864), DES (21), ENCB (11), GBH (1) and MEXU (133). Additionally, we used data of 121 specimens of Cactaceae collected in Durango which we did not examine nor include in the data matrix for numerical analysis, except for two species (*Epithelantha micromeris* and *Mammillaria moelleriana*) of which we obtained images. The United States National Herbarium (US) houses 119 specimens of cacti from Durango and The New York Botanical Garden herbarium (NY) houses only two. All of them were obtained from reliable data matrices and were included herein for their historical value, mainly to build a species accumulation curve through time. Records based on herbarium specimens examined, plus photographic records collected during the field work, and four out of the 121 herbarium specimens not examined allowed us to obtain a data matrix with a total of 2326 georeferenced records corresponding to 137 species and 29 genera. Of these, 131 species have vouchers deposited in recognized herbaria, mainly in Mexico and the USA, and were collected between 1896 and 2015. Records based on herbarium specimens examined visually, plus photographic records collected during the field work, and four out of the 121 not visually examined herbarium specimens allowed to obtain a data matrix with a total of 2326 georeferenced records corresponding to 137 species and 29 genera. Of these, 131 species have vouchers deposited in recognized herbaria, mainly in Mexico and the USA, and were collected between 1896 and 2015.

Richness and geographic extent of each species in Durango

The subfamily Cactoideae is represented in the state by 97 species (71%) and 25 genera (86%), whereas Opuntioideae is represented by 40 species (29%) grouped into four genera (14%). The genera with the highest species numbers are: *Mammillaria* (32), *Opuntia* (Miller (1754: unpagged) (29), *Coryphantha* (Engelmann 1856: 264) Lemaire 1868: 32 (15) and *Echinocereus* (14). The remaining 25 genera are represented in the state flora by one to five species each.

The distribution of the cactus richness in Durango is heterogeneous. Of the 56 cells in which the state was divided (Figure 1), only 4 (7%) lack cacti records in the data matrix (2, 11, 19 and 38), corresponding to cells located in the state limits and with only a fraction of the territory within it. The remaining 51 cells have records from one to 37 species each, with an average of 16 species per cell (Figure 2). The cells with the highest richness (27–37 species) in descending order are: 35, 37, 4, 18, 34, 25, 26 and 27; all of them located in the Arid and Semiarid Zone. The lowest richness (1 to 5 species) is found in the Sierra Madre Occidental and Quebradas regions (cells: 1, 5, 13, 22, 29, 30, 40 and 54). The size of the distribution range varies (Figure 3), from those recorded from a single cell (23 species) (Table 1), to those recorded in 16 or more cells (11 species) (Table 2).

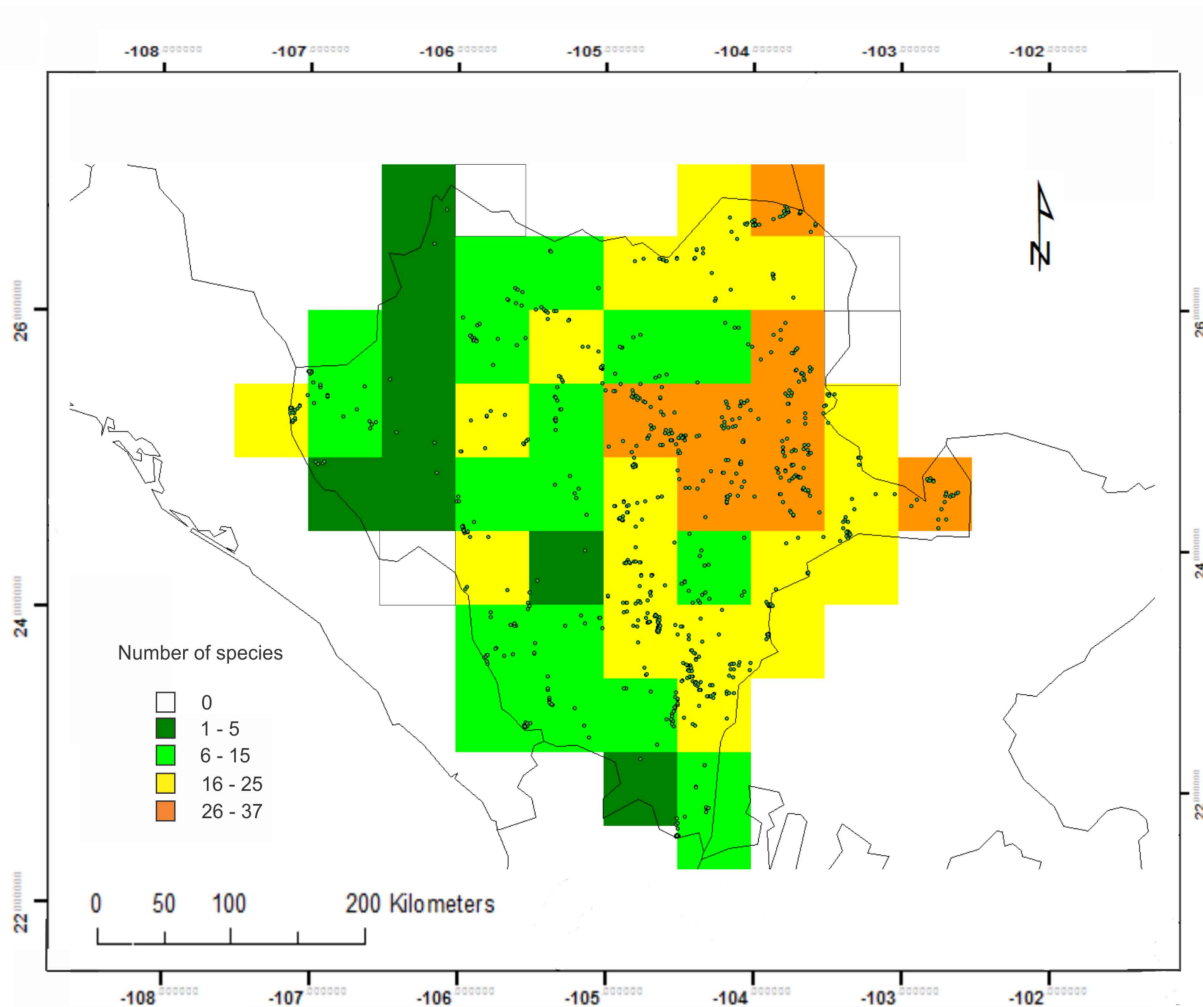


FIGURE 2. Species richness distribution within the 56 $0.5^\circ \times 0.5^\circ$ cells.

TABLE 1. Species present in a single cell.

Species	Cell
<i>Ariocarpus kotschoubeyanus</i>	37
<i>Echinocereus coccineus</i>	18
<i>Echinocereus palmeri</i>	7
<i>Epithelantha micromeris</i>	4
<i>Escobaria dasyacantha</i>	18
<i>Escobaria henricksonii</i>	4
<i>Ferocactus alamosanus</i>	12
<i>Ferocactus schwarzii</i>	20
<i>Mammilloidia candida</i>	36
<i>Mammillaria chionocephala</i>	18
<i>Mammillaria coahuilensis</i>	37
<i>Mammillaria densispina</i>	55
<i>Mammillaria guelzowiana</i>	25
<i>Mammillaria lindsayi</i>	31
<i>Mammillaria magallanii</i>	18
<i>Mammillaria moelleriana</i>	43

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TABLE 1. (Continued)

Species	Cell
<i>Mammillaria saboae</i>	41
<i>Mammillaria sinistrohamata</i>	44
<i>Mammillaria standleyi</i>	20
<i>Mammillaria theresae</i>	33
<i>Opuntia auberi</i>	21
<i>Opuntia neochrysacantha</i>	37
<i>Stenocactus dichroacanthus</i>	41

TABLE 2. Species present in 11 or more cells.

Species	Number of Cells
<i>Cylindropuntia kleiniae</i>	11
<i>Echinocereus stramineus</i>	11
<i>Glandulicactus uncinatus</i>	12
<i>Mammillaria lasiacantha</i>	12
<i>Opuntia leucotricha</i>	12
<i>Echinocereus enneacanthus</i>	13
<i>Mammillaria senilis</i>	13
<i>Thelocactus heterochromus</i>	13
<i>Opuntia macrocentra</i>	14
<i>Cylindropuntia leptocaulis</i>	15
<i>Echinocereus acifer</i>	15
<i>Echinomastus unguispinus</i>	15
<i>Mammillaria pottsii</i>	15
<i>Thelocactus bicolor</i>	15
<i>Ferocactus hamatacanthus</i>	16
<i>Opuntia durangensis</i>	17
<i>Opuntia engelmannii</i>	18
<i>Opuntia rufida</i>	19
<i>Echinocactus horizonthalonius</i>	20
<i>Opuntia robusta</i>	21
<i>Echinocereus polyacanthus</i>	22
<i>Opuntia phaeacantha</i>	25
<i>Echinocereus pectinatus</i>	26
<i>Cylindropuntia imbricata</i>	28
<i>Mammillaria heyderi</i>	29

Endemism and conservation status

A total of 103 species (75%) are endemic to Mexico; of these, 56 are regional endemics (41%) including 7 restricted to Durango (Table 3).

TABLE 3. Taxa endemic to Durango.

<i>Coryphantha kracikii</i> Halda, Chalupa & Kupcák
<i>Coryphantha longicornis</i> Boed.
<i>Coryphantha pseudonickelsiae</i> Backeb.
<i>Echinocereus schereri</i> G. Frank
<i>Mammillaria guelzowiana</i> Werderm.
<i>Mammillaria pennispinosa</i> Krainz
<i>Mammillaria theresae</i> Cutak

Of the 137 species recorded to date for Durango, 23% (31 species) are included in the NOM-059-SEMARNAT-2010 (SEMARNAT 2010), 83% (114 species) are listed on the IUCN Red List of Threatened Species (IUCN 2016), of which 8% (11 species) are considered to have some degree of risk (Table 4), another nine are recorded as having insufficient data (DD) and the rest are listed under the least concern category (LC). Appendices I and II of CITES include almost all species of the family Cactaceae. Among the Durango cacti, the species of *Ariocarpus* Scheidweiler (1838: 491) are included in the Appendix I; the rest, with the exception of the species of *Pereskopsis* Britton & Rose (1907: 331), are included in Appendix II (CITES, 2016).

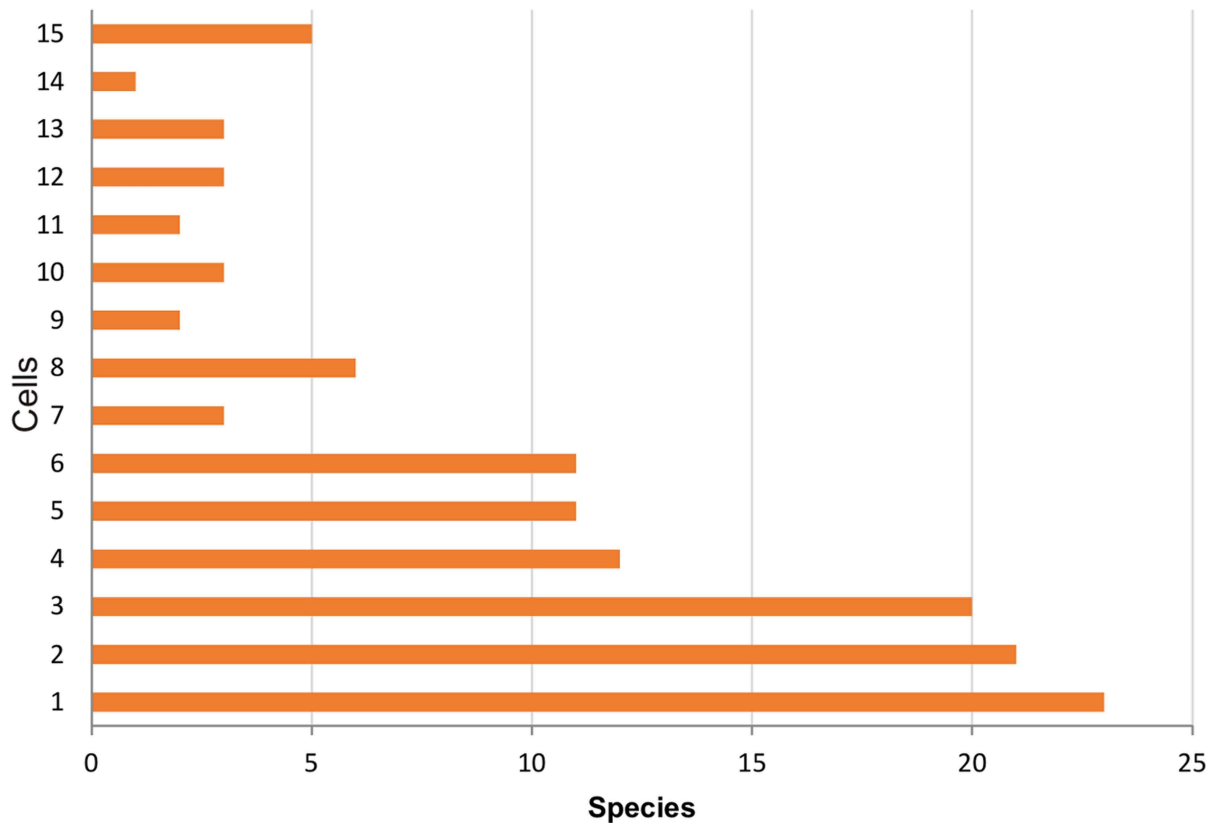


FIGURE 3. Range size of 126 species according its presence in 1 to 15 cells

TABLE 4. Cactaceae of Durango with some degree of risk according to IUCN Red List.

Species	IUCN
<i>Ariocarpus kotschoubeyanus</i> (Lem.) K. Schum.	NT
<i>Astrophytum coahuilense</i> (H.Moeller) K.Kayser	VU
<i>Ferocactus alamosanus</i> (Britton & Rose) Britton & Rose	NT
<i>Ferocactus histrix</i> (DC.) G.E. Linds.	NT
<i>Grusonia bulbispina</i> (Engelm.) H. Rob.	EN
<i>Lophophora williamsii</i> (Lem. ex Salm-Dyck) J.M. Coult.	VU
<i>Mammillaria coahuilensis</i> (Boed.) Moran	EN
<i>Mammillaria gasseriana</i> Boed.	EN
<i>Mammillaria jaliscana</i> (Britton & Rose) Boed.	VU
<i>Mammillaria pennispinosa</i> Krainz	CE
<i>Mammillaria theresae</i> Cutak	CE

Quality of sampling (Completeness)

The estimated richness for the whole state (gamma diversity), based on Chao-2 and Jackknife-1, is 143 and 151 species, respectively; the corresponding completeness index indicates that the Durango cacti inventory is complete in 91 to 96%, which means that between 6 and 14 species are still lacking in the records (Figure 4).

The sample quality analysis per cell indicates that, of the 56 cells, 19 (34%) have medium to low completeness values (less than 0.7). The rest exceeds that value, indicating an acceptable to good level of exploration; however, only 9 cells (16%) have completeness values larger than 0.9.

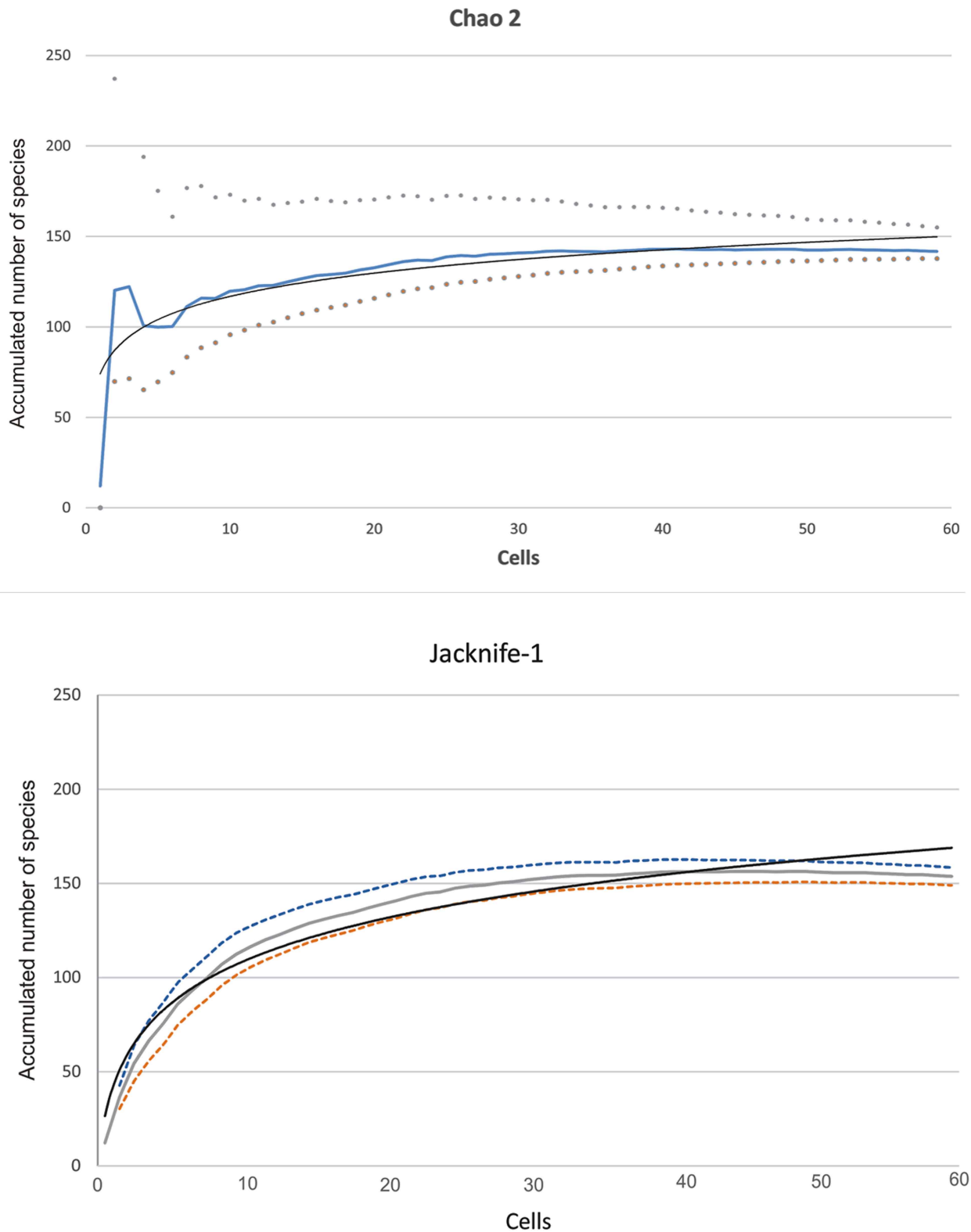


FIGURE 4. Richness accumulation curves according to non-parametric estimators CHAO 2 and Jackknife 1. In each case the mean value and standard deviation of the estimated number of species is shown. For comparison purposes, each panel shows the estimated asymptotic richness value.

Discussion

Representation of Durango cacti in herbaria

The review of 1131 herbarium specimens and information compiled from online sources of other collections show that, prior to the year 2000, Cactaceae specimens collected in Durango and deposited in recognized collections were very scarce. In addition, the labels of many of the specimens collected prior to that year recorded very poor information. The earliest specimens of Cactaceae from Durango are found in the United States National Herbarium (US), most of them without accurate information on localities, such as some of these might actually come from neighboring states (Coahuila and Zacatecas) instead. For example, there is an unidentified *Neobuxbaumia* Backeberg (1938: 20) collected by Hugh H. Iltis (673a) labeled as from Durango, which was discarded in our inventory, since the northern distribution limit of this genus is the state of Jalisco.

Most specimens deposited in US were collected between 1896 and 1946, and only five were collected from 1960 to 1997. Of the Mexican National Herbarium (MEXU) 97 out of 133 cacti specimens from Durango were collected before the year 2000, and only 64 contained enough geographic information to georeference the collection sites.

Another herbarium with a significant amount of Durango cacti is ASU (The University of Arizona herbarium), with 83 specimens collected between 1971 and 1997. All these specimens are valuable since they include types and were considered here to construct the accumulation curve of species collected in Durango through time (Figure 5). However, many of them are of little or no value for distribution studies since they lack precise geographical information.

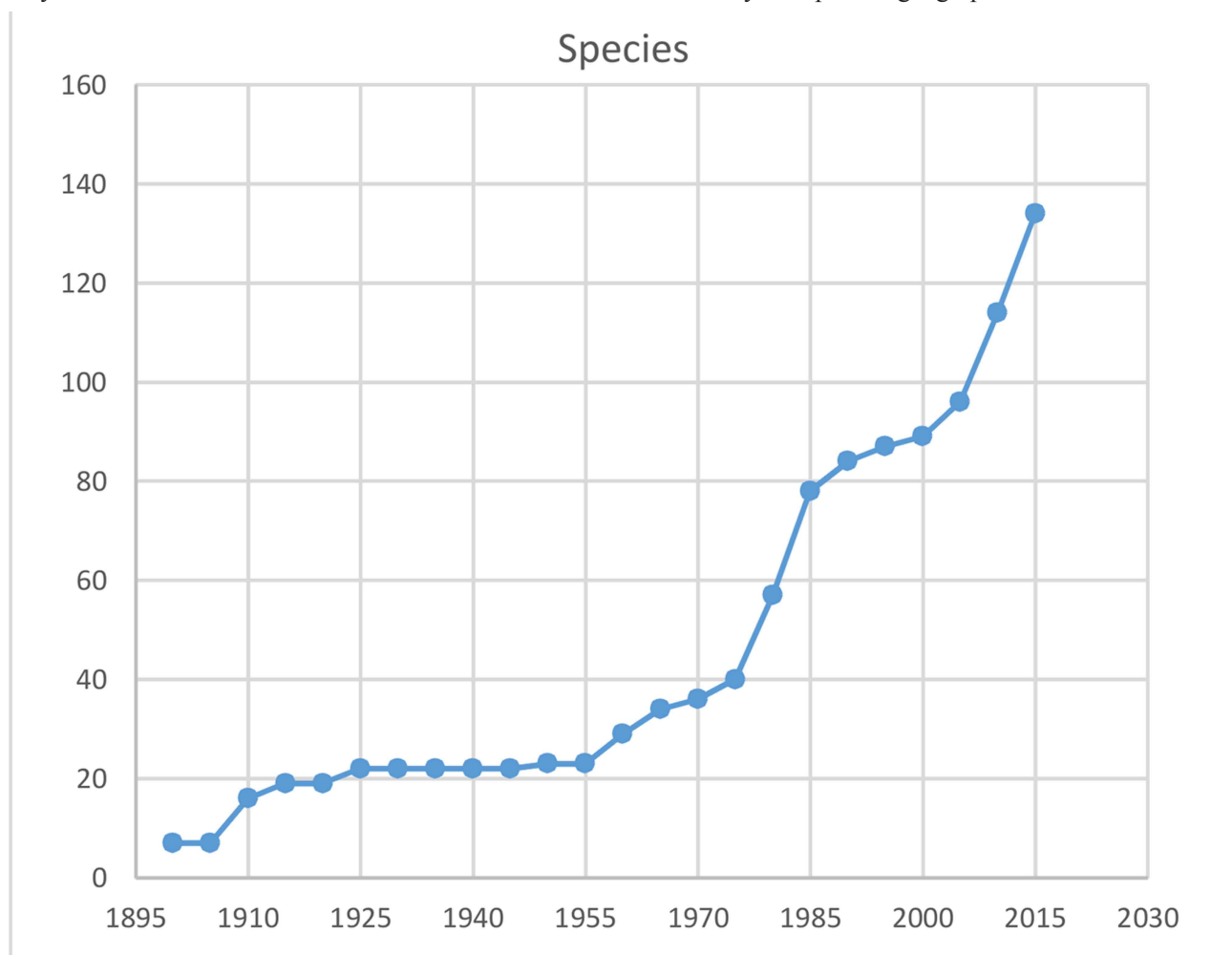


FIGURE 5. Accumulation curve of cactus species collected in Durango and deposited in recognized herbaria.

Hence, the herbarium CIIDIR, with 864 specimens of 126 species, houses the largest collection of cacti from Durango. Of these, only 94 specimens (11%) and 52 species (42%) were collected before the year 2000; hence, most are recent collections with enough geographical data for biogeographic studies. Five additional species are recorded at CIIDIR only by photographic specimens (with geographic and environmental data): *Escobaria henricksonii* Glass & Foster (1977: 195), *Mammillaria candida* Scheidweiler (1838: 496), *M. sinistrohamata* Bodeker (1932: 162), *Opuntia*

cantabrigiensis Lynch (1903: 98), and *O. neochrysacantha* Bravo (1974: 20). Another six species included in the checklist are not represented in CIIDIR but are so in other herbaria: *Echinocereus schererii* Frank (1990: 159) and *Mammillaria jaliscana* (Britton & Rose 1923: 160) Bödeker (1933: 35) at MEXU; *Epithelantha micromeris* (Engelmann 1856: 260) Weber ex Britton & Rose (1922: 93) and *M. moelleriana* at US; *Grusonia grahamii* (Engelmann 1856: 304) Robinson (1973: 176) at ASU, and *Opuntia erinacea* Engelmann & Bigelow (Engelmann 1856: 301) at ANSM. We checked specimens of four out of these six species and review images of those of *E. micromeris* and *M. moelleriana*.

The species accumulation curve (Figure 5) shows that the collections of cacti in Durango were poor from 1896 to 1955, with only 23 species accumulated. Since then, two well-defined stages of a strong collection effort can be appreciated: from 1975 to 1985 (38 species in a decade, 78 accumulated), and from 2005 to 2015 (34 species, 131 accumulated). To date, only two species (*Epithelantha micromeris* and *Mammillaria moelleriana*) included in the present checklist are based on ancient specimens (before 1955) and have not been verified with recent field collections or observations, thus it is unclear if these are still present in Durango. *Epithelantha micromeris* is a species of wide distribution in the Chihuahuan Desert (northern Mexico and southwestern United States of America), it has been reported for Durango by several authors but with no voucher citation (Guzmán *et al.* 2003, Hunt *et al.* 2006, Hernández *et al.* 2010, Sánchez Salas *et al.* 2014, Villaseñor 2016). To date, the only herbarium specimens of this species allegedly from Durango are one of *A.F. Möller* (US 2983341) and another of *E. Chaffey* (US 2979599). This species is also mentioned from the Mapimí Biosphere Reserve (Cornet 1985), located very close to the boundaries between the states of Coahuila and Durango. Its presence is not ruled out in the municipalities of Tlahualilo and/or San Juan de Guadalupe. On the other hand, *Mammillaria moelleriana* was described from the Sierra de Santa María, Durango (Glass & Foster 1970), without a recorded collector and preserved type specimen (Pilbeam 1999, Hunt *et al.* 2006). However, in the US herbarium there are three specimens of this species collected in Durango by *Möller* in 1924 (US 3045720) and 1925 (US 3045721 and US 3045719).

In the last 15 years, the representativeness of Durango cacti at the CIIDIR herbarium has increased substantially. However, there are still species reported for the region without reference specimens in this herbarium, and many others are poorly represented. Nevertheless, the amount of information available to date could be adequate for biogeographic and systematic studies.

Updated checklist, new records and other novelties

The updated and annotated checklist (Appendix 1) is the first of its kind for the state in over 25 years. This includes 49 species not mentioned for the entity in the Mexican Cactus Inventory (Guzmán *et al.* 2003), including eight genera (*Astrophytum* Lemaire (1839: 3), *Hylocereus* (Berger 1905: 72) Britton & Rose (1909: 428), *Leuchtenbergia* Hooker (1848: pl. 4393), *Lophophora* Coulter (1894: 131), *Nyctocereus* (Berger 1905: 75) Britton & Rose (1909: 423), *Pachycereus* (Berger 1905: 63) Britton & Rose (1909: 420), *Pilosocereus* Byles & Rowley (1957: 66) and *Stenocereus* (Berger 1905: 25) Riccobono 1909: 253). Nevertheless, many of these taxa had already been mentioned for Durango (González-Elizondo *et al.* 1991) based on ancient references (e.g., Standley 1920–1926, Bravo 1937, Gentry 1957 and Gold 1967) that did not include vouchers. Some other of these 49 taxa were mentioned previously for Durango only on the basis of literature in the Chihuahuan Desert cacti checklist (Hernández *et al.* 2004), in The New Cactus Lexicon (Hunt *et al.* 2006), or in monographs (Dicht & Lüthy 2005, Pilbeam 1999, Pilbeam and Bowdery 2005).

Among the species that were recently recorded in Durango, not mentioned in the country study (Guzmán *et al.* 2003), *Lophophora williamsii* and *Leuchtenbergia principis* Hooker (1848: pl. 4393) are remarkable. Both of them were cited for Durango several decades ago (Bravo 1937) without specimens of reference or specific locations, as a consequence of which in subsequent publications the same author did not mention them anymore for this entity (Bravo and Sánchez-Mejorada 1991a). Both species were reported for Durango by Hernández *et al.* (2004) based on data matrices, but without citing reference specimens. Here we confirm the presence of *Lophophora* in the municipalities of San Juan de Guadalupe and Tlahualilo, and of *Leuchtenbergia* in San Juan de Guadalupe, Cuencamé and Nazas.

In the flora of Durango, as in that of Mexico (Guzmán *et al.* 2003), the four genera of Cactaceae with the highest species richness are: *Mammillaria* (± 160 in México/32 in Durango), *Opuntia* ($\pm 83/29$), *Echinocereus* ($\pm 56/14$) and *Coryphantha* (45/15). This has also been noted for other regions of the country (González-Botello 2004, Lebgue-Keleng *et al.* 2013, Martínez-Avalos & Jurado 2005). *Opuntia* and *Coryphantha* stand out in the flora of Durango since they represent about one-third of the total species known from the country.

The known distribution range of several species is expanded, among others: *Mammillaria coahuilensis* (Bödeker 1926: 210) Moran (1953: 324) and *Thelocactus hexaedrophorus* (Lemaire 1839: 27) Britton & Rose (1922b: 251) grow in several localities of San Juan de Guadalupe, in the eastern region of the state, and a peripheral population of

Mammillaria candida Scheidweiler (1838: 496) was recorded in the municipality of General Simón Bolívar, about 100 km west of the previously known populations. *Nyctocereus serpentinus* (Lagasca & Rodríguez 1801: 261) Britton & Rose (1909: 423), previously recorded for several states in central and western Mexico, was located in Pueblo Nuevo and Topia, Durango, apparently naturalized. *Acanthocereus occidentalis* Britton & Rose (1920: 125) has been mentioned for Durango at least since almost four decades (Martínez 1979) and is cited for the state in the *Catalog of Mexican Cacti* (Guzmán *et al.* 2003). However, Gómez-Hinostrosa *et al.* (2013) do not include Durango in the distribution range of *A. tetragonus* (Linnaeus 1753: 466) Hummelinck (1938: 165) [= *A. occidentalis*, according to several authors] due to the lack of *vouchers*. We found this species in several sites in tropical vegetation in Durango. We confirmed the presence in Durango of *Hylocereus purpusii* (Weingart 1909: 150) Britton & Rose (1920: 184), which was cited for Durango without reference specimens by Cáliz de Dios (2004), and we registered for the first time *H. ocamponis* (Salm-Reifferscheid-Dyck 1850: 220) Britton & Rose (1909: 429). García Rubio *et al.* (2015), in a study on the distribution range of *Hylocereus* in Mexico, record *H. purpusii* on the Pacific coast but discard its presence in Durango due to the lack of reference specimens in the herbaria consulted. Both taxa were collected in tropical deciduous forest in the municipalities of Pueblo Nuevo, San Dimas and Tamazula, thereby expanding the known distribution of both species.

Two species of *Ferocactus* Britton & Rose (1922: 123) growing on rocky walls in deciduous tropical forest are also novelties for the flora of Durango: *Ferocactus alamosanus* (Britton & Rose 1913: 239) Britton & Rose (1922: 137) at 1300 m elevation, and *F. schwarzii* Lindsay (1955: 70) at 250 m elevation. The first, although mentioned for Durango by Gold (1967), had no voucher; it is known of less than 10 localities (Van Devender 2013) in Álamos Sonora region and nearby areas of the states of Chihuahua and Sinaloa. *Ferocactus schwarzii* is a little-known species that had been considered to date as endemic to the state of Sinaloa and had not been collected recently (Hernández *et al.* 2013).

We also confirm the occurrence in Durango of several *Mammillaria* species previously mentioned for this region with no vouchers: *M. densispina* (Coulter 1894: 96) Orcutt (1926: 7), *M. chionocephala* Purpus (1906: 41), *M. grusonii* Runge (1889: 105), *M. petterssonii* Hildmann (1886: 185) and *M. scrippsiana* (Britton & Rose 1923: 84) Orcutt (1926: 8).

Mammillaria saboae Glass (1966: 55–56) was found in the municipality of Canatlán, in the center of Durango (Rischer & Krüger 2003), ca. 500 km south of its previously known range in Chihuahua and Sonora. Despite its discovery in Durango, more than a decade ago, the lack of herbarium specimens and data matrix records did not allow its inclusion in reviews such as those of Hunt *et al.* (2006), Hernández and Gómez Hinostrosa (2015) and Villaseñor (2016). Its inclusion in this work is based on field data and a voucher.

Mammillaria standleyi was mentioned for Durango by Guzmán *et al.* (2003). The lack of specimens cited in that work, plus the omission of Durango among the Mexican entities where this species is represented in data matrix leads to suppose that that reference was based exclusively on the type of *M. xanthina* (Britton & Rose 1923: 164) Bödeker (1933: 47), which is considered as a synonym of the former, and it was purportedly collected near the Monte Mercado, close to Durango city. Considering that for more than 90 years it has not been observed again in this locality, besides that it seems quite improbable for any taxa of the group of *M. standleyi* to be found in that region since the group is distributed on the western slopes of the Sierra Madre Occidental, we consider that either the circumscription of *M. xanthina* as part of the *M. standleyi* complex must be reconsidered, or the type specimen comes from a different locality. This paper confirms the presence in Durango of *M. standleyi*, previously known from Chihuahua and Sonora, but in the ravines region on the western slopes of the Sierra Madre.

Mammillaria chaletii (Plein & Rogozinski 2013: 99), whose type comes from the Quebradas region in Durango, was not considered in the checklist presented here. After collating the description, illustrations and photographs, we decided that this fits well into morphological variation of *M. sonorensis*. The latter was circumscribed as part of *M. standleyi* by Guzmán *et al.* (2003), although our field observations and collections support the recognition of both as distinct taxa, coinciding with the differentiation made by Pilbeam (1999) and Hunt *et al.* (2006). This criterion was also followed by Hernández and Gómez-Hinostrosa (2015), who mentioned both species only for the states of Chihuahua and Sonora. Here we confirm the presence of both *M. sonorensis* and *M. standleyi* in Durango.

Following our field explorations in recent years the number of *Opuntia* species known for Durango doubled. Guzmán *et al.* (2003) list 14 species, of which we excluded two. Hence, 17 of the 29 species included in our updated checklist are not mentioned for Durango by these authors. Three of them (*O. macrorhiza* Engelman in Gray (1850: 206), *O. megacantha* Salm-Reifferscheid-Dyck (1834: 363) and *O. polyacantha* Haworth (1819: 82) were mentioned for Durango by Hernández *et al.* (2004) without citing reference specimens. Here we verify the presence in Durango of these three species, plus 12 out of 14 species cited by Guzmán *et al.* (2003), as well as 14 additional taxa that constitute new records for the state (See Appendix).

Furthermore, the presence in the state of four large columnar species is confirmed: *Pilosocereus alensis* (Weber in Roland-Gosselin 1905: 508) Byles & Rowley (1957: 66), *P. purpusii* (Britton & Rose 1920: 56) Byles & Rowley (1957: 67), *Stenocereus montanus* (Britton & Rose 1920: 97) Buxbaum (1961: 101), and *S. queretaroensis* (Weber 1891: 27) Buxbaum (1961: 101). The first was mentioned for Durango by Hunt *et al.* (2006) and the third by Gold (1967), in both cases without reference specimen.

Taxa provisionally excluded

Since no herbarium specimens were found that support their presence in Durango and, in most cases, their presence is doubtful, 46 taxa that have been mentioned for the state in taxonomic and floristic literature (González-Elizondo *et al.* 1991, Guzmán *et al.* 2003, Hernández *et al.* 2004, Pilbeam 2011, Sánchez-Salas *et al.* 2014, Villaseñor 2016) are provisionally excluded from the flora of Durango (Table 5).

Nevertheless, the presence of some of them in Durango would not be unexpected. For instance, in the southern portion, in the boundaries with Zacatecas, *Ferocactus latispinus* (Haworth 1824: 41) Britton & Rose (1922: 143) might be found. *Opuntia chaffeyi* Britton & Rose (1913: 241) and *Echinocereus poselgeri* Lemaire (1868: 57) are species difficult to locate in the field, and according to their ecological requirements and distribution they could eventually be discovered in the municipality of San Juan de Guadalupe. *Mammillaria barbata* Engelmann in Wislizenus (1848: 105) is known from the southwestern United States of America and from the Sierra Madre Occidental in Chihuahua and can be present in temperate areas in Durango. The presence of *Selenicereus vagans* (Brandege 1905: 191) Britton & Rose (1913: 242) is also probable given its wide distribution from southern Sonora to Chiapas in tropical deciduous and sub-deciduous forest (Terrazas *et al.* 2013), plant communities scarcely explored in Durango in part because of the inaccessibility of the areas where they grow. Some other species mentioned previously for Durango in ancient references may have a similar ecological affinity as the former one: *Mammillaria bocensis* Craig (1945: f 38), *Stenocereus kerberi* (Schumann 1899: 89) Gibson & Horak (1978: 1007)) and *S. quevedonis* (González-Ortega 1928: 7) Buxbaum (1961: 101)). The taxonomic revision of some genera for which unidentified species have been cited from Durango could reveal the presence of some other species like *Escobaria zilziana* (Bödeker 1930: 233) Backeberg (1961: 2957) and *Grusonia moelleri* (Berger 1929: 57) Anderson (1999: 325). However, all of these are provisionally excluded from the flora of Durango until having reliable references.

Four other Mexican species are cultivated in the region and were occasionally observed growing spontaneously in the field: *Hylocereus undatus* (Haworth 1830: 110) Britton & Rose in Britton (1918: 256), *Lophocereus marginatus* (De Candolle 1828: 116) Arias & Terrazas (2009: 82), *Opuntia ficus-indica* (Linnaeus 1753: 468) Miller (1768: appears in alphabetical order, unpagged) and *Stenocereus stellatus* (Pfeiffer 1836: 258) Riccobono (1909: 253). From the latter, there are no previous reports, we found a senile individual growing spontaneously in an area far from any village. None of these four species are included in our updated checklist.

In spite of these 46 exclusions, the total richness registered here means an increase of little more than 30% to the cactus species previously known from Durango according to Guzmán *et al.* (2003). The native cacti in the state represent 46% of the genera and 20.5% of the total species in the country registered by those authors. Or, if we take as baseline the checklist of Mexican native vascular plants of Villaseñor (2016), 156 species in 32 genera are recorded from Durango, which represent 53% of the genera and 23% of the species of the country, respectively. According to the proposal for generic nomenclature and species delimitation of Hunt (2016), in Durango exist ca. 122 of the 593 species (20.5%) and 29 of the 50 genera (58%) included in the updated checklist of Cactaceae from Mexico. Those discrepancies result from the differences in taxonomic circumscriptions, methodological approaches and amplitude of each publication. However, either way, it is clear that Durango embraces a surprisingly high proportion of the Mexican cactus flora, ranking 46–58% at the generic level and 20–23% at the specific level.

Endemism and conservation status

The percentage of cactus species endemic to Mexico in Durango is very similar to that of endemic cacti in the country (75 and 77%, respectively). Of the 103 Mexican endemic species present in Durango, 56 are regional endemic, which highlights the importance of the study of the cacti of this region for the knowledge of the Mexican flora, particularly *Coryphantha* and *Opuntia*. Additionally, 7 species are strictly endemic to Durango. *Mammillaria theresae*, *M. guelzowiana* and *M. pennispinosa* are microendemic species that are known from very localized areas. Other species have broader distribution ranges but are known from few sites, where in addition, they are usually very scarce, for example, *Echinocereus palmeri* Britton & Rose (1922: 34) which is known from a few sites in the states of Chihuahua, Durango, and Zacatecas, and *M. guillauminiana* Backeberg (1952: 81), which has been considered extinct in the wild (Arias *et al.*, 2005a) due to its extreme rarity.

TABLE 5. Species cited for Durango in literature that we provisionally exclude from the floristic list due to lack of evidence of its presence in the entity.

Ariocarpus retusus Scheidw.
Astrophytum capricorne (A. Dietr.) Britton & Rose
Coryphantha glanduligera (Otto & A. Dietr.) Lem.
Coryphantha robustispina subsp. *scheeri* (Lem.) N.P. Taylor
Coryphantha vaupeliana Boed.
Coryphantha werdermannii Boed.
Echinocactus platyacanthus Link & Otto
Echinocereus chisoensis W.T. Marshall subsp. *fobeanus* (Oehme) Taylor
Echinocereus dasyacanthus Engelm. subsp. *dasyacanthus*
Echinocereus longisetus (Engelm.) Lem.
Echinocereus mapimiensis E.F. Anderson, W. Hodgs. & P. Quirk
Echinocereus posegeri Lem.
Echinocereus reichenbachii (Terscheck ex Walp.) Haage
Echinocereus rigidissimus (Engelm.) F. Haage
Echinocereus stoloniferus W.T. Marshall
Escobaria chihuahuensis Britton & Rose
Escobaria zilziana (Boed.) Backeb.
Ferocactus latispinus (Haw.) Britton & Rose
Ferocactus wislizeni (Engelm.) Britton & Rose
Grusonia bradtiana (J.M. Coulter) Britton & Rose
Grusonia moelleri (A. Berger) E.F. Anderson
Mammillaria barbata Engelm.
Mammillaria berkiana A.B. Lau
Mammillaria bocensis R.T. Craig
Mammillaria magnimamma Haw.
Mammillaria spinosissima Lem. subsp. *spinosissima*
Mammillaria uncinata Zucc. ex Pfeiff.
Opuntia chaffeyi Britton & Rose
Opuntia jaliscana Bravo
Opuntia megarhiza Rose
Opuntia scheeri F.A.C. Weber
Opuntia stenopetala Engelm.
Pachycereus pringlei (S. Watson) Britton & Rose
Pereskia porteri (K. Brandegee ex F.A.C. Weber) Britton & Rose
Pilosocereus cometes (Scheidw.) Byles & G.D. Rowley
Pilosocereus leucocephalus (Poselg.) Byles & G.D. Rowley
Selenicereus vagans (K. Brandegee) Britton & Rose
Stenocactus heteracanthus (Muehlenpf.) A.W. Hill
Stenocactus obvallatus (DC.) A.W. Hill
Stenocactus vaupelianus (Werderm.) F.M. Knuth in Backeb. & F.M. Knuth
Stenocereus kerberi (K. Schum.) A.C. Gibson & K.E. Horak
Stenocereus quevedonis (J.G. Ortega) Buxb.
Stenocereus thurberi (Engelm.) Buxb.
Thelocactus conothelos (Regel & Klein) Backeb. & F.M. Knuth
Thelocactus rinconensis (Poselg.) Britton & Rose
Turbincarpus mandragora (Fric ex A. Berger) A.D. Zimmerman

A high proportion of cacti are included in national and international lists as deserving a degree of protection (Álvarez *et al.* 2004). The vulnerability of cacti is due to their biological and ecological characteristics: many are slow growing plants, with long life cycles, little recruitment and restricted distribution patterns since they inhabit sites with very particular environmental conditions (Hernández & Godínez 1994). In contrast, some species (particularly those of *Opuntia* and *Cylindropuntia* (Engelmann 1856:302) Knuth (1930: 102) invade areas degraded by overgrazing, forming very dense thickets because of their vegetative propagation. Among the Durango cacti, 35 species (25%) are included in NOM-059-SEMARNAT 2010 (SEMARNAT 2010) and / or in the IUCN Red Book (IUCN 2016). *Ariocarpus* spp. are also listed in Appendix I of CITES (CITES 2016).

Mammillaria theresae and *M. pennispinosa* are strictly endemic to Durango, both are classified as Critically Endangered (CE) according to the IUCN Red List (Fitz-Maurice & Fitz-Maurice 2013, Fitz-Maurice *et al.* 2013c), additionally, the first is considered in danger (P) and the other in the category of conservation priority (Pr) according to NOM-059-SEMARNAT 2010 (SEMARNAT 2010). Three other taxa (*M. guelzowiana*, *M. saboae* and *Echinocereus adustus*) are listed as threatened (A) in NOM-059-SEMARNAT-2010 (SEMARNAT 2010) and as Least Concern (LC) in the Red List. In contrast, other species included in NOM-059-SEMARNAT-2010 (SEMARNAT 2010) with the category of special protection (Pr) are considered of minor concern (LC) in the IUCN evaluations, e.g.: a) *Coryphantha durangensis*, a quasi-endemic species of Durango that is distributed in eastern Durango and the southwestern extreme of the state of Coahuila, b) *Sclerocactus unguispinus* (Engelmann in Wislizenus 1848: 111) Taylor in Hunt & Taylor (1987: 94) (as *Echinomastus* Britton & Rose (1922: 147) in NOM-059), an abundant and widely distributed species from Chihuahua to San Luis Potosí, c) *Peniocereus greggii* (Engelmann in Wislizenus 1848: 102) Britton & Rose (1909: 428), which occurs in a wide area in northern Mexico and southwestern United States of America, but in scarce and isolated populations.

On the other hand, there are some species not included in the NOM-059-SEMARNAT-2010 (SEMARNAT 2010) despite their low population densities and their restricted distribution, such as *Echinocereus schererii*, known only from the type locality and classified as Data Deficient in the Red List (Fitz-Maurice *et al.* 2013b); *Escobaria henricksonii*, micro -endemic of a small area in Chihuahua and Durango, has not yet been assessed for the IUCN Red List; and *Mammillaria gasseriana* Bödeker (1927: 75), known only from three localities in Coahuila and Durango and whose total occupancy area is estimated to be less than 10 km² is included in the IUCN Red List as Endangered (Fitz-Maurice *et al.* 2013a). Of these three species, *Echinocereus schererii*, and *Escobaria henricksonii*, along with a few other taxa of restricted distribution should be studied to define their conservation status.

Of the 31 species of Durango cacti listed in NOM-059-SEMARNAT-2010 (SEMARNAT 2010), 23 thrive in the Chihuahuan Desert, at the northeast of the state, six in temperate forests in the Sierra Madre Occidental and other mountains, and two more inhabit the Quebradas region.

Richness distribution and geographic extent of each species in the state

Cacti species are distributed throughout the state of Durango. However, as expected, the cells with the highest richness are mostly concentrated in the Arid and Semi-arid region with xerophytic vegetation, whereas those with lower richness are located in the higher parts of the Sierra Madre Occidental region, with temperate forests. An analysis of the ecoregional distribution of Cactaceae in Durango (in prep.) indicates that approximately 53% of the species occur in the Arid and Semiarid Zone (xerophytic vegetation, halophyllous and gypsophyllous vegetation), 25% in the Quebradas region (tropical deciduous forest, tropical subdeciduous forest, thorn forest), 18% in the Sierra Madre Occidental (woodland and various temperate forests), 19% in the Valleys and high plains region (grasslands and transitional vegetation between temperate forests and xerophytic vegetation), and 14% are distributed in more than one ecoregion.

Our results coincide with a pattern found in several biogeographic studies (McLaughlin 1995, Arita *et al.* 1997, Balleza *et al.* 2005, Miguel-Talonia *et al.* 2014) related to the existence of a large number of species with restricted distribution and a smaller number of species with wide range distribution (Figure 4). Of the 137 cactus species registered in Durango, 64 (47%) have a restricted distribution to one to three cells, while only 11 species (8%) are distributed in 16 or more cells (Table 2). The size of the distribution area has been related to rarity (Arita & Rodríguez 2001, Balleza *et al.* 2005) and to the vulnerability of species (Gómez-Hinostrosa and Hernández 2000). However, in the case of regional studies, such as the present, to estimate the rarity of a species, it is important to consider also the total extent of its distribution, as pointed out by Miguel-Talonia *et al.* (2014). Hence, of the 23 species of Durango restricted to a single cell (Table 1), eight are in fact wide-ranging species that reach their limit in the state of Durango, such as *Ariocarpus kotschoubeyanus*, with a wide distribution in the Chihuahuan Desert. Twelve are of regional distribution and only three are endemic to Durango. In contrast, two taxa endemic to Durango, *Coryphantha pseudonickelsiae*

Backeberg (1949: 8) and *C. recurvata* subsp. *canatlanensis* are recorded in 8 and 6 cells respectively, showing a wide distribution within the state.

Inventory completeness

The results on the estimated richness indicate important advances in the general inventory of the cacti of Durango (91 to 96%). Among the 6 to 14 missing species could be some of those 46 that are temporarily excluded due to lack of evidence such as *Escobaria zilziana*, *Ferocactus latispinus*, *Opuntia chaffeyi*, *Selenicereus vagans* and *Stenocereus kerberi*.

In contrast, the alpha diversity (richness observed per cell) and estimated richness for the same geographic units according to estimators used, suggest that there are still some areas where further field exploration is required to document more accurately the species regional distribution.

It is interesting to note that the 11 cells with the highest values of completeness (0.90 to 0.97) are distributed throughout the range of observed richness, from 2 to 37 species (cells 22 and 35 respectively). However, coinciding partially with that reported by Miguel-Talonia *et al.* (2014), in general the cells with the lowest observed richness have high values (0.88 to 0.94) of completeness, which is related to their geographic location (cells 1, 5, 13, 22 and 30) in the Sierra Madre Occidental mountain range, with temperate to cold climates in which the presence of Cactaceae is scarce by nature.

On the other hand, the lowest values of completeness (≤ 0.5) correspond to four cells with low to medium richness (5 to 18 species); cell 39 stands out, with an observed richness of 17 species and an estimated of 58 according to the two indicators used, thus occupying the lowest value of completeness (0.29). It should be noted, however, that we consider this estimated richness disproportionately high, which may be due to the fact that the corresponding geographical area presents a complex mosaic of environmental conditions: it is found in the region of the Quebradas, with a wide altitudinal range (550 to 2550 m elevation) and it has both tropical and temperate vegetation. In addition, given the difficult access to this region, the records included in the data matrix are relatively few (31); furthermore, 13 of the 17 species are represented by a single record, that is, they appear as singletons in the analysis, raising as such the value of estimated richness in that particular cell. Etter and Kristen (2013), in an exploration with particular interest in succulent plants carried out in this area, mention several cacti species, only one different to the 17 registered here for the cell 39, raising to 18 the known richness of that area; less than a third of the estimated richness. The overestimation of richness in that cell is an example of the inaccuracies that result from the combination of a small sample and a heterogeneous environment.

Conclusions

The regional inventory presented here, despite the large number of excluded taxa, increases by 30% the cacti richness previously reported for Durango and provides new information on the distribution range of many species. The biological collection and the data matrix on which this information is based fill an important gap of knowledge and is a valuable tool for regional floristic studies, allowing to undertake taxonomic and ecological studies of particular groups as well as biogeographic studies at small scales.

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Appendix 1. Annotated checklist of Cactaceae in the state of Durango, Mexico.

Species	Voucher	NOM_059	IUCN Red List	Red	CITES	Geographical amplitude	Endemism
<i>Acanthocereus occidentalis</i> Britton & Rose	J.N. 94 (CIIDIR)		LC ¹		II	4	Mexico
<i>Ariocarpus fissuratus</i> (Engelm.) K. Schum.	M.G. 4169 (CIIDIR)		LC		I	4	
* <i>Ariocarpus kotschoubeyanus</i> (Lem.) K. Schum.	J.N. 261 (CIIDIR)	Pr	NT		I	1	Mexico
** <i>Astrophytum coahuilense</i> (H.Moeller) K.Kayser	J.N. 179 (CIIDIR)	A ²	VU		II	2	Regional
<i>Coryphantha compacta</i> (Engelm.) Britton & Rose	R.R. 168 (CIIDIR)		LC		II	8	Regional
<i>Coryphantha cornifera</i> (DC.) Lem.	M.G. 4253 (CIIDIR)		LC		II	3	Mexico
<i>Coryphantha delaetiana</i> (Quehl) A. Berger	M.G. 4083 (CIIDIR)		LC		II	9	Mexico
<i>Coryphantha delicata</i> L. Bremer	M.G. 4382 (CIIDIR)	Pr	LC		II	5	Mexico
<i>Coryphantha durangensis</i> (Runge ex K. Schum.) Britton & Rose	J.V. 51 (CIIDIR)	Pr	LC		II	10	Regional
<i>Coryphantha echinoidea</i> (Quehl) Britton & Rose	J.V. 79 (CIIDIR)	Pr	LC		II	3	Regional
* <i>Coryphantha</i> aff. <i>echinus</i> (Engelm.) Britton & Rose	M.G. 4725 (CIIDIR)		LC		II	3	Regional
<i>Coryphantha kracikii</i> Halda, Chalupa & Kupcák	J.V. 23 (CIIDIR)		DD		II	2	Durango
<i>Coryphantha longicornis</i> Boed.	M.G. 4088 (CIIDIR)		LC		II	3	Durango
<i>Coryphantha macromeris</i> (Engelm.) Lem.	M.G. 4077 (CIIDIR)		LC		II	6	
<i>Coryphantha ottonis</i> (Pfeiff.) Lem.	L.R. 831 (CIIDIR)		LC		II	5	Mexico
<i>Coryphantha poselgeriana</i> (A. Dietr.) Britton & Rose	M.G. 4115 (CIIDIR)	A	LC		II	8	Mexico
<i>Coryphantha pseudonickelsiae</i> Backeb.	M.G. 4082 (CIIDIR)		LC		II	8	Durango
<i>Coryphantha recurvata</i> (Engelm.) Britton & Rose	F.M. 362 (CIIDIR)		LC		II	6	Durango
* <i>Coryphantha</i> sp.	L.L. 664 (CIIDIR)				II	2	Regional
<i>Cylindropuntia imbricata</i> (Haw.) F.M. Knuth	J.N. 211 (CIIDIR)		LC		II	28	
<i>Cylindropuntia kleiniae</i> (DC.) F.M. Knuth	M.G. 4170 (CIIDIR)		LC		II	11	
<i>Cylindropuntia leptocaulis</i> (DC.) F.M. Knuth	L.L. 220 (CIIDIR)		LC		II	15	
<i>Cylindropuntia spinosior</i> (Engelm.) F.M. Knuth	L.L. 653 (CIIDIR)		LC		II	9	
<i>Cylindropuntia tunicata</i> (Lehm.) F.M. Knuth	D.R. 3625 (CIIDIR)		LC		II	2	
<i>Disocactus speciosus</i> (Cav.) Barthlott	J.N. 22 (CIIDIR)		NE		II	3	
<i>Echinocactus horizonthalonius</i> Lem.	L.L. 522 (CIIDIR)		LC		II	20	
* <i>Echinocactus texensis</i> Hopffer	A.G. 2921 (CIIDIR)		LC		II	2	
<i>Echinocereus acifer</i> (Otto ex Salm-Dyck) Jacobi	F.M. 229 (CIIDIR)		LC		II	15	Mexico
<i>Echinocereus adustus</i> Engelm. in Wisl.	J.N. 147 (CIIDIR)	A	LC		II	2	Durango
* <i>Echinocereus</i> aff. <i>coccineus</i> Engelm.	S.G. 7378 (CIIDIR)		LC		II	1	

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Appendix 1. (Continued)

Species	Voucher	NOM_059	IUCN List	Red	CITES	Geographical amplitude	Endemism
<i>Echinocereus enneacanthus</i> Engelm.	M.G. 4217 (CIIDIR)		LC		II	13	
<i>Echinocereus koehresianus</i> (G.Frank) Rischer	M.G. 2390 (CIIDIR)		NE		II	2	Regional
<i>Echinocereus ortegae</i> Rose ex J.G. Ortega	M.G. 2414 (CIIDIR)		DD		II	4	Regional
<i>Echinocereus palmeri</i> Britton & Rose	D.R. 3246 (CIIDIR)	P	LC		II	1	Regional
* <i>Echinocereus pamanesiorum</i> A.B. Lau	M.G. 1266 (CIIDIR)		LC		II	5	Regional
<i>Echinocereus pectinatus</i> (Scheidw.) Engelm.	M.G. 4090 (CIIDIR)		LC		II	26	
<i>Echinocereus polyacanthus</i> Engelm.	M.G. 2369 (CIIDIR)		LC		II	22	Regional
<i>Echinocereus scheeri</i> (Salm-Dyck) Scheer	F.M. 229 b (CIIDIR)		LC		II	2	Regional
<i>Echinocereus schereri</i> G. Frank	D.S.70 (MEXU)		DD		II	2	Durango
<i>Echinocereus stramineus</i> (Engelm.) Engelm ex. F. Seitz	M.G. 4387 (CIIDIR)		LC		II		
<i>Echinocereus subinermis</i> Salm-Dyck ex Scheer	J.M. 3 (CIIDIR)	Pr	DD		II	2	Regional
<i>Epithelantha micromeris</i> (Engelm.) F.A.C. Weber ex Britton & Rose	H.M sn (US); E.C. sn (US)	Pr	LC		II	1	
* <i>Escobaria dasyacantha</i> (Engelm.) Britton & Rose	R.R. 104 (CIIDIR)	Pr	LC		II	1	Regional
<i>Escobaria henricksonii</i> Glass & R.A.Foster	L.R. 744f (CIIDIR)		LC ³		II	1	Regional
<i>Escobaria tuberculosa</i> (Engelm.) Britton & Rose	M.G. 4613 (CIIDIR)		LC		II	6	
* <i>Ferocactus alamosanus</i> (Britton & Rose) Britton & Rose	D.R. 2337 (CIIDIR)		NT		II	1	Regional
<i>Ferocactus hamatacanthus</i> (Muehlenpf.) Britton & Rose	L.L. 563 (CIIDIR)		LC		II	16	
<i>Ferocactus histrix</i> (DC.) G.E. Linds.	M.G. 1262 (CIIDIR)	Pr	NT		II	3	Mexico
<i>Ferocactus pilosus</i> (Galeotti ex Salm-Dyck) Werderm.	M.G. 4385 (CIIDIR)	Pr	LC		II	4	Mexico
* <i>Ferocactus schwarzii</i> G.E. Linds.	I.R. 203 (CIIDIR)		DD		II	1	Regional
<i>Glandulicactus uncinatus</i> (Galeotti ex Pfeiff. & Otto) Backeb.	M.G. 4073 (CIIDIR)		NE		II	12	
<i>Grusonia bulbispina</i> (Engelm.) H. Rob.	I.R. 7a (CIIDIR)		EN		II	4	Mexico
* <i>Grusonia grahamii</i> (Engelm.) H. Rob.	D.P. 13864 (ASU)		LC		II	5	
* <i>Grusonia schottii</i> (Engelm.) H. Rob.	M.G. 4391 (CIIDIR)		LC		II	4	
<i>Grusonia vilis</i> (Rose) H. Rob.	M.G. 4747f (CIIDIR)		LC		II	5	Regional
** <i>Hylocereus ocamponis</i> (Salm-Dyck) Britton & Rose	M.G. 2345 (CIIDIR)		LC		II	3	Mexico
** <i>Hylocereus purpusii</i> (Weing.) Britton & Rose	I.R. 215 (CIIDIR)		NE		II	4	Mexico
** <i>Leuchtenbergia principis</i> Hook.	M.G. 4069 (CIIDIR)	A	LC		II	3	Mexico

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Appendix 1. (Continued)

Species	Voucher	NOM_059	IUCN List	Red	CITES	Geographical amplitude	Endemism
** <i>Lophophora williamsii</i> (Lem. ex Salm-Dyck) J.M. Coult.	A.G. 2715 (CIIDIR)	Pr	VU		II	2	
* <i>Mammillaria candida</i> Scheidw.	M.G. 4785f (CIIDIR)	A	LC ⁴		II	1	Mexico
<i>Mammillaria chionocephala</i> J.A. Purpus	R.R. 97 (CIIDIR)		NE		II	1	Mexico
* <i>Mammillaria coahuilensis</i> (Boed.) Moran	J.N. 262 (CIIDIR)	A	EN		II	1	Regional
<i>Mammillaria densispina</i> (J.M.Coult) Orcutt	M.G. 4435 (CIIDIR)		LC		II	1	Mexico
* <i>Mammillaria gasseriana</i> Boed.	M.G. 4755 (CIIDIR)		EN		II		Regional
* <i>Mammillaria grusonii</i> Runge	M.G. 4600 (CIIDIR)	Pr	LC		II	7	Regional
<i>Mammillaria guelzowiana</i> Werderm.	L.R. 328 (CIIDIR)	A	LC		II	1	Durango
<i>Mammillaria guillauminiana</i> Backeb.	M.G. 4417 (CIIDIR)		DD		II	2	Regional
<i>Mammillaria heyderi</i> Muehlenpf.	M.G. 4216 (CIIDIR)		LC		II	29	
* <i>Mammillaria jaliscana</i> (Britton & Rose) Boed.	M.G. 1228 (MEXU)		VU		II	2	Mexico
<i>Mammillaria lasiacantha</i> Engelm.	M.G. 4071 (CIIDIR)		LC		II	12	
<i>Mammillaria lindsayi</i> R.T. Craig	I.R. 204 (CIIDIR)	Pr	NE		II	1	Regional
<i>Mammillaria longiflora</i> (Britton & Rose) A. Berger	S.G. 5047 (CIIDIR)	A	LC		II	6	Regional
<i>Mammillaria magallanii</i> Schmoll ex R.T. Craig	M.G. 4179 (CIIDIR)		NE		II	1	Regional
<i>Mammillaria marksiana</i> Krainz	Y.C. 1 (CIIDIR)	Pr	LC		II	3	Regional
<i>Mammillaria mercadensis</i> Patoni	S.G. 2457 a (CIIDIR)	Pr	LC		II	6	Regional
<i>Mammillaria moelleriana</i> Boed.	H.M. 3 (US)	Pr	LC		II	1	Regional
<i>Mammillaria</i> cf. <i>ortegae</i> (Britton & Rose) Orcutt	I.R. 228, (CIIDIR)		NE		II	3	Regional
<i>Mammillaria pachycylindrica</i> Backeb.	M.G. 4117 (CIIDIR)		NE		II	3	Regional
<i>Mammillaria pennispinosa</i> Krainz	M.G. 4251 (CIIDIR)	Pr	CR		II	5	Durango
* <i>Mammillaria petterssonii</i> Hildm.	L.R. 293 (CIIDIR)		LC		II	8	Mexico
<i>Mammillaria pottsii</i> Scheer ex Salm-Dyck	M.G. 4229 (CIIDIR)		LC		II	15	
* <i>Mammillaria saboae</i> Glass	L.R. 367 (CIIDIR)	A	LC		II	1	Durango
<i>Mammillaria scrippsiana</i> (Britton & Rose) Orcutt	D.R. 3280 (CIIDIR)		LC		II	2	Regional
<i>Mammillaria senilis</i> G.Lodd. ex Salm-Dyck	S.G. 4603 (CIIDIR)	A	LC		II	13	Mexico
<i>Mammillaria sinistrohamata</i> Boed.	A.R. 65f (CIIDIR)		DD		II	1	Regional
* <i>Mammillaria sonorensis</i> R.T. Craig	M.G. 4456 (CIIDIR)		LC		II	4	Regional
<i>Mammillaria standleyi</i> (Britton & Rose) Orcutt	L.R. 899 (CIIDIR)		LC		II	1	Regional
<i>Mammillaria theresae</i> Cutak	L.L. 123 (CIIDIR)	P	CE		II	1	Durango

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Appendix 1. (Continued)

Species	Voucher	NOM_059	IUCN List	Red	CITES	Geographical amplitude	Endemism
<i>Mammillaria wagneriana</i> Boed.	J.N. 46 (CIIDIR)		DD		II	10	Regional
<i>Mammillaria zeyeriana</i> F. Haage ex K. Schum.	L.L. 779 (CIIDIR)		NE		II	3	Regional
<i>Myrtillocactus geometrizans</i> (Mart.) Console	M.G. 1275 (CIIDIR)		LC		II	3	Mexico
<i>Neolloydia conoidea</i> (DC.) Britton & Rose	M.G. 4624 (CIIDIR)		LC		II	2	Mexico
** <i>Nyctocereus serpentinus</i> (Lag. & Rodr.) Britton & Rose	I.R. 123 (CIIDIR)		LC		II	3	Mexico
* <i>Opuntia</i> aff. <i>auberi</i> Pfeiff.	D.R. 3225 (CIIDIR)		LC ⁵		II	1	Mexico
<i>Opuntia azurea</i> Rose	M.G. 4767 (CIIDIR)		NE		II	6	Regional
* <i>Opuntia cantabrigiensis</i> Lynch	A.R. 20f (CIIDIR)		NE		II	2	Mexico
<i>Opuntia durangensis</i> Britton & Rose	I.A. 103 (CIIDIR)		NE		II	17	Regional
<i>Opuntia engelmannii</i> Salm-Dyck	J.N. 74 (CIIDIR)		LC		II	18	
<i>Opuntia erinacea</i> Engelm. & Bigelow	J.E. 256 (ANSM)		NE		II	2	
* <i>Opuntia feroacantha</i> Britton & Rose	D.R. 3221 (CIIDIR)		NE		II	2	Regional
* <i>Opuntia fuliginosa</i> Griffiths	M.G. 3865 (CIIDIR)		LC		II	3	Mexico
* <i>Opuntia hyptiacantha</i> F.A.C. Weber	I.A. 135 (CIIDIR)		LC		II	5	Mexico
* <i>Opuntia</i> cf. <i>karwinskiana</i> Salm-Dyck	S.G. 6582 (CIIDIR)		NE		II	4	Mexico
* <i>Opuntia lasiacantha</i> Pfeiff.	I.A. 95 (CIIDIR)		LC		II	2	Mexico
<i>Opuntia leucotricha</i> DC.	I.A. 166 (CIIDIR)		LC		II	12	Mexico
<i>Opuntia macrocentra</i> Engelm.	M.G. 4210 (CIIDIR)		LC		II	14	Mexico
* <i>Opuntia macrorhiza</i> Engelm.	M.G. 4571 (CIIDIR)		LC		II	7	
* <i>Opuntia megacantha</i> Salm-Dyck	I.A. 157 (CIIDIR)		NE		II	6	Mexico
* <i>Opuntia microdasys</i> (Lehm.) Pfeiff.	M.G. 4673 (CIIDIR)		LC		II	2	Mexico
* <i>Opuntia neochrysacantha</i> Bravo	J.N. 306f (CIIDIR)		NE		II	1	Regional
<i>Opuntia phaeacantha</i> Engelm.	J.N. 140 (CIIDIR)		LC		II	25	
* <i>Opuntia polyacantha</i> Haw.	M.G. 4560 (CIIDIR)		LC		II	2	
<i>Opuntia puberula</i> Pfeiff.	M.G. 1312 (CIIDIR)		LC		II	6	
* <i>Opuntia pubescens</i> H.L. Wendl. ex Pfeiff.	M.G. 4465 (CIIDIR)		LC		II	8	
<i>Opuntia rastrera</i> F.A.C. Weber	A.G. 2942 (CIIDIR)		NE		II	10	Mexico
* <i>Opuntia</i> cf. <i>rileyi</i> J.G. Ortega	M.G. 4581 (CIIDIR)		NE		II	3	Regional
<i>Opuntia robusta</i> H.L. Wendl. ex Pfeiff.	J.N. 87 (CIIDIR)		LC		II	21	Mexico
<i>Opuntia rufida</i> Engelm.	M.G. 4211 (CIIDIR)		LC		II	19	

...continued on the next page

Appendix 1. (Continued)

Species	Voucher	NOM_059	IUCN List	Red	CITES	Geographical amplitude	Endemism
* <i>Opuntia</i> sp.	M.G. 4485 (CIIDIR)				II	5	Regional
<i>Opuntia streptacantha</i> Lem.	I.A. 72 (CIIDIR)		LC		II	5	Mexico
* <i>Opuntia tomentosa</i> Salm-Dyck	M.M. 151 (CIIDIR)		LC		II	4	
* <i>Opuntia</i> cf. <i>wilcoxii</i> Britton & Rose	I.R. 211f (CIIDIR)		LC		II	6	Mexico
** <i>Pachycereus pecten-aboriginum</i> (Engelm.) Britton & Rose	M.G. 4451 (CIIDIR)		LC		II	6	Mexico
<i>Peniocereus greggii</i> (Engelm.) Britton & Rose	L.L. 558 (CIIDIR)	Pr	LC		II	7	
<i>Pereskiaopsis aquosa</i> (F.A.C. Weber) Britton & Rose	M.G. 1311 (CIIDIR)		LC		Ex	5	Regional
<i>Pereskiaopsis blakeana</i> J.G. Ortega	M.G. 2536 (CIIDIR)		LC		Ex	4	Mexico
** <i>Pilosocereus alensis</i> (F.A.C. Weber) Byles & G.D. Rowley	M.G. 4464 (CIIDIR)		LC		II	6	Mexico
** <i>Pilosocereus purpusii</i> (Britton & Rose) Byles & G.D. Rowley	J.N. 97 (CIIDIR)		LC		II	3	Mexico
<i>Sclerocactus unguispinus</i> (Engelm.) N.P. Taylor	M.G. 4431 (CIIDIR)	A/Pr ⁶	LC		II	15	Mexico
<i>Stenocactus dichroacanthus</i> (Mart. Ex Pfeiff.) A. Berger ex Backeb. & F.M. Kunth	M.G. 1206 (CIIDIR)		NE		II	1	Mexico
<i>Stenocactus multicostatus</i> (Hildm. ex K. Schum.) A.W. Hill	L.L. 572 (CIIDIR)		DD		II	8	Mexico
** <i>Stenocereus montanus</i> (Britton & Rose) Buxb.	M.G. 4463 (CIIDIR)		LC		II	4	Regional
** <i>Stenocereus queretaroensis</i> (F.A.C. Weber) Buxb.	J.N. 237 (CIIDIR)		LC		II	3	Mexico
<i>Thelocactus bicolor</i> (Galeotti ex Pfeiff.) Britton & Rose	M.G. 4213 (CIIDIR)		LC		II	15	
<i>Thelocactus heterochromus</i> (F.A.C. Weber) van Oosten	M.G. 4089 (CIIDIR)	A	LC		II	13	Regional
* <i>Thelocactus hexaedrophorus</i> (Lem.) Britton & Rose	M.G. 3813a (CIIDIR)		LC		II	3	Mexico

Symbol preceding the name means: species (*) and genus (**) not mentioned in the country study (Guzmán *et al.* 2003) for Durango state; Geographical amplitude is expressed as number of cells in which the species was recorded.

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Categories of risk: **NOM-059**: Probably extinct in the wild (E), in danger of extinction (P), Threatened (A), subject to special protection (Pr). **IUCN**: Extinct (EX), Extinct in the wild (EW), Critically endangered (CR), Endangered (EN), Vulnerable (VU), Near threatened (NT), Least concern (LC), Data deficient (DD), Not evaluated (NE). **CITES**: Appendix I, II or exempted (ex).

¹As subspecies of *Acanthocereus tetragonus*; ²As subspecies of *Astrophytum myriostigma*; ³As subspecies of *Escobaria chihuahuensis*; ⁴As *Mammilloidya candida*; ⁵As *Nopalea auberi*; ⁶As *Echinomastus unguispinus* with two subspecies threatened (A) and one subject to special protection (Pr).