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The species of *Mentzelia* (Loasaceae) in Mexico, part 1: Sectional diversity

Las especies de *Mentzelia* (Loasaceae) en México, parte 1: Diversidad seccional

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Abstract

Background: *Mentzelia* (Loasaceae) is a genus of approximately 95 species that are largely distributed in western North America; however, much ambiguity remains regarding species in Mexico.

Questions: What species of *Mentzelia* occur in Mexico and how can they be distinguished?

Study species: *Mentzelia*

Methods: Fieldwork, herbarium studies and scanning electron microscopy were carried out to determine the diversity of *Mentzelia* species in Mexico.

Results: Twenty-five species of *Mentzelia* occur in Mexico, of which four taxa are endemic to the country. Five of the six sections of *Mentzelia* occur in Mexico. *Mentzelia* section *Mentzelia* was the most species rich in Mexico (8 spp.), followed by section *Trachyphytum* (7 spp.), section *Bartonia* (6 spp.), section *Bicuspidaria* (3 spp.), and section *Dendromentzelia* (1 sp.). The sections have different distribution patterns, with some restricted to few areas and one widespread across most of Mexico.

Conclusions: This study is the first treatment of *Mentzelia* that encompasses all species and regions of Mexico, which includes approximately 26 % of the worldwide *Mentzelia* species. In-depth studies of the species in the region are needed to abate gaps in our knowledge on the extent of species distributions and to clarify species boundaries among some problematic species complexes.

Keywords: Desert flora, Madrean floristic region, misapplied nomenclature, plant systematics

Resumen

Antecedentes: *Mentzelia* (Loasaceae) es un género de aproximadamente 95 especies que están ampliamente distribuidas en Norteamérica occidental; sin embargo, sigue habiendo mucha ambigüedad respecto a las especies en México.

Preguntas: ¿Qué especies de *Mentzelia* se distribuyen en México y cómo pueden distinguirse?

Especies de estudio: *Mentzelia*.

Métodos: Se realizó trabajo de campo, herbario y microscopía electrónica de barrido para determinar la diversidad de especies de *Mentzelia* en México.

Resultados: Veinticinco especies de *Mentzelia* se distribuyen en México, de las cuales cuatro taxones son endémicos. Cinco de las seis secciones de *Mentzelia* se encuentran en México. *Mentzelia* sección *Mentzelia* fue la más rica en especies en México (8 spp.), seguida por la sección *Trachyphytum* (7 spp.), sección *Bartonia* (6 spp.), sección *Bicuspidaria* (3 spp.) y sección *Dendromentzelia* (1 sp.). Las secciones tienen diferentes patrones de distribución, con algunas de ellas restringidas a unas pocas áreas y una ampliamente distribuida en la mayor parte de México.

Conclusiones: Este estudio es el primer tratamiento de *Mentzelia* que engloba a todas las especies y regiones de México, lo que incluye aproximadamente el 26 % de las especies de *Mentzelia* a nivel mundial. Se necesitan estudios exhaustivos de las especies en la región para reducir las brechas en nuestro conocimiento sobre la extensión de la distribución de especies y para clarificar los límites de las especies en algunos complejos de especie problemáticos.

Palabras clave: Flora del desierto, Región florística Madreana, nomenclatura mal empleada, sistemática vegetal.

Mentzelia L. (Loasaceae) is a monophyletic genus of approximately 95 species that are mainly distributed in western North America (Hufford *et al.* 2016). Recent floristic, systematic, and revisionary work has clarified many of the taxonomic problems that have long-plagued the genus (Holmgren & Holmgren 2002, Holmgren *et al.* 2005, Schenk & Hufford 2009, Schenk *et al.* 2010, Schenk & Hufford 2010, 2011, Brokaw *et al.* 2012, Schenk *et al.* 2013, Hufford *et al.* 2016, Schenk & Hufford 2020), especially for species that occur in the United States and Canada as part of Flora of North America (Hufford *et al.* 2016), the North American intermountain region (Holmgren *et al.* 2005), New Mexico (Schenk *et al.* 2020), and California (Brokaw *et al.* 2012). The Mexican species, however, have received much less attention, and significant impediments remain to understand their diversity.

Species of *Mentzelia* are classified into six monophyletic sections (Hufford *et al.* 2003, Figure 1). Five of the sections occur in Mexico, which includes sections *Bartonia* (Torrey & A. Gray) Bentham & Hooker f., *Bicuspidaria* S.Watson, *Dendromentzelia* Urb. & Gilg, *Mentzelia* L., and *Trachyphytum* (Torrey & A. Gray) Bentham & Hooker f. The monotypic section *Micromentzelia*, represented by *M. torreyi* A.Gray, occurs in California, Nevada, and Idaho in the southwestern United States, and does not occur in Mexico. Previous works noted taxonomic problems in the genus (Thompson & Powell 1981, Calderón de Rzedowski 1992), and in its geographic range that has not been directly studied, such as in Mexico, those taxonomic problems persist. Recent floristic works focused on various regions in Mexico (*e.g.*, Calderón de Rzedowski 1992, Villaseñor 2016) have reiterated many historically misapplied names, perpetuating taxonomic problems, which call to attention the urgent need of taxonomic assessments of the species in Mexico. Herbarium collections of *Mentzelia* from Mexico are often identified to misapplied names and require reevaluated in light of current taxonomy.

The species of *Mentzelia* in Mexico have not been comprehensively assessed. Although floristic projects have contributed to our understanding of the species in Mexico, because of their narrow geographic scope, they often only include one or two representative species (*e.g.*, Rzedowski & Rzedowski 2005, Villarreal-Quintanilla *et al.* 2017), rendering comparisons of the genus across floristic treatments cumbersome. To produce the first comprehensive evaluation of all species of *Mentzelia* that occur in Mexico, species are reevaluated while accounting for recent phylogenetic, taxonomic, and floristic works that have clarified many of the previous problems. Through field and herbarium collection surveys, we reevaluate the species to better understand what species occur in Mexico and the extent of their distributions. To assist in the identification of species, a key is included that distinguishes all species of *Mentzelia* in Mexico.

Materials and methods

We studied herbarium specimens collected from Mexico to confirm identifications and to assess their distributions. Specimens were collected from natural populations in the field, or consulted from the following herbaria (herbarium abbreviations follows Thiers 2020): ARIZ, F, GH, ID, LA, MEXU, MO, N, NMC, NY, OKL, P, RSA, TEX, UCR, US, and WS. Taxonomic treatments followed Hufford *et al.* (2016), Grissom (2014), Brokaw & Schenk (2020), and Schenk & Hufford (2020). Species distribution data were collated from field and herbarium collections and supplemented with collections on The Global Biodiversity Information Facility (GBIF 2012). Latitude and longitude were taken directly from herbarium specimen labels when present, or were georeferenced with GEOLocate (Rios & Bart 2010) or GoogleEarth (Google LLC., Mountain View, CA). In total, we plotted 3,343 data locality points in ArcMap v. 10.7 (ESRI, Redlands, California, USA).

Results

Five of the six *Mentzelia* sections were confirmed to occur in Mexico (Table 1). *Mentzelia* section *Bartonia* was determined to consist of six species in Mexico, which included three of the four varieties of *M. longiloba* J.Darl. Three of the six species in section *Bicuspidaria* were determined to occur in Mexico. The monotypic section *Dendromentzelia* was represented by *M. arborescens* Urb. & Gilg (Figure 2A) in southern Mexico. Section *Mentzelia* was represented by eight species, the most species among all sections in Mexico. Seven species from section *Trachyphytum* were confirmed to occur in Mexico. A total of 25 *Mentzelia* species occur in Mexico (Table 1).

Species of *Mentzelia* were distributed across all of Mexico (Figure 3). Sections *Bartonia*, *Bicuspidaria*, and *Trachyphytum* were distributed primarily in northern Mexico (Figure 3A). Section *Dendromentzelia* was distributed in southern Mexico (Figure 3B). Section *Mentzelia* occurred throughout the country, except for the northern limits of the Mexican Chihuahuan Desert (Figure 3B).

Four taxa were determined to be Mexican endemics: *M. longiloba* J.Darl. var. *pinacatensis* J.J.Schenk &

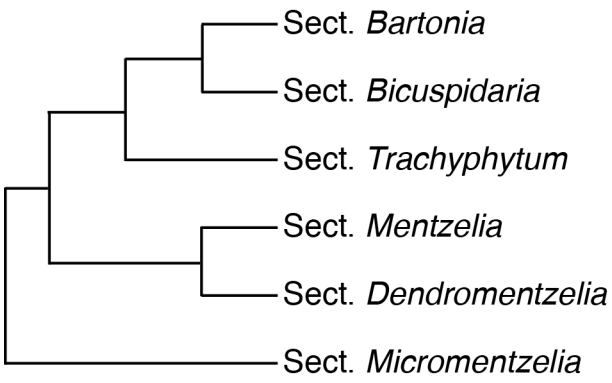

Figure 1. Phylogenetic relationships among the six monophyletic sections of *Mentzelia*, based on Hufford *et al.* (2003). All sections have representatives in Mexico except for section *Micromentzelia*, which only occurs in western United States.

L.Hufford (section *Bartonia*); *M. nesiotes* (I.M.Johnst.) Brokaw & J.J.Schenk (section *Bicuspidaria*); *M. adhaerens* Benth (section *Mentzelia*; Figure 2F-G); and *M. arborescens* (section *Dendromentzelia*). All other species had ranges that either extended northward into the United States, southward into Guatemala, or were widespread across the New World (*e.g.*, *M. aspera*).

Ten names are misapplied in Mexico, which include *M. albescens* (Gill. ex Arn.) Griseb., *M. desertorum* (Davidson) H.J.Thomps. & J.E.Roberts, *M. dispersa* S.Watson, *M. isolata* Gentry, *M. multiflora* (Nutt.) A.Gray, *M. nitens* Greene, *M. oligosperma* Nutt. ex Sims, *M. oreophila* J.Darl., *M. pumila* Torr. & A.Gray, and *M. sinuata* (Rydb.) R.J.Hill. Eleven taxa were inferred to be synonyms of other species that were confirmed to occur in Mexico, which included *M. conzattii* Greenm. (= *M. arborescens*), *M. gracilis* Urb. & Gilg (= *M. lindheimeri* Urb. & Gilg), *M. gypsophila* B.L.Turner (= *M. asperula* Wooton & Stanley), *M. hintoniorum* B.L.Turner & A.L.Hempel (= *M. reverchonii* [Urb. & Gilg] H.J.Thomps. & Zavort.), *M. incisa* Urb. & Gilg (= *M. lindheimeri*), *M. karwinskii* Urb. & Gilg (= *M. hispida* Willdenow), *M. orizabae* Urb. & Gilg (= *M. hispida*), *M. sessilifolia* Urb. & Gilg (= *M. asperula*), *M. stenophylla* Urb. & Gilg (= *M. hirsutissima* S.Watson), *M. strigosa* Kunth (= *M. hispida*), and *M. texana* Urb. & Gilg (= *M. lindheimeri*).

Discussion

Twenty-five species of *Mentzelia* occur in Mexico (approximately 26 %), which are placed in five of the six sections, and indicates that *Mentzelia*, and even Loasaceae, are more diverse in Mexico than previous estimates inferred when accounting for synonymy. Villanueva-Almanza (2011), for example, estimated that nine species of *Mentzelia* occurred in Mexico, just slightly over a third of what is recognized here. *Mentzelia hispida* was notable as not being included among the endemic taxa, as it is often regarded as a Mexican endemic (*e.g.*, Darlington 1934, Hufford *et al.* 2016). Our study documented Guatemalan collections on the other side of the Mexican border (*Molina 21388*, F: 1661991, US: 3543407; *Soto 1471*, MEXU: 1435246), suggesting the species is endemic to Mexico and Guatemala. Our list of Mexican endemics is different than that of Sosa *et al.* (2018), who recognized *M. adhaerens*, *M. arborescens*, *M. desertorum*, *M. isolata*, and *M. sinuata*. Our study overlaps in recognizing *M. adhaerens* and *M. arborescens*, but *M. desertorum* and *M. isolata* also occur in the United States. *Mentzelia sinuata* does not occur in Mexico, rather, its range is centered in the mid-northern Rocky Mountains in the U.S. (Schenk & Hufford 2020). Our list of endemics is also different from Villaseñor (2016), who recognized the same endemics as Sosa *et al.* (2018), but also recognized *M. conzattii*, *M. gypsophila*, and *M. hintoniorum*, all of which are treated as synonyms of other species that occur in Mexico (see below).

The sections of *Mentzelia* are geographically clustered in different parts of the country (Figure 3). Section *Bartonia* is distributed in the two northern deserts, but only partially overlaps with section *Bicuspidaria* (Figure 3A), which is localized in the Baja California Peninsula and the western edge of the Sonoran Desert adjacent to the Gulf of California (Figure 3A). Section *Trachyphytum* occurs exclusively in the Sonoran Desert and Baja California Peninsula. Section *Mentzelia* is widespread across the entire country (Figure 3B), extending northward into the United States, eastward into the Caribbean, and southward into Central and South America. Section *Dendromentzelia* is endemic to southern Mexico (Figure 3B).

The most recent taxonomic work that focused on the *Mentzelia* of the Chihuahuan Desert recognized three species in section *Bartonia* (Thompson & Powell 1981). Although we have expanded the geographical scope to include all of Mexico, we recognize the Mexican flora as including six species from section *Bartonia*, with *M. longiloba* represented by three of its four varieties. Unlike Thompson & Powell (1981), we recognize *M. multiflora* as a misapplied name in Mexico. Populations of *M. multiflora* reported by Thompson & Powell (1981) were most likely what we now recognized as *M. longiloba* var.

Table 1. The species of *Mentzelia* in Mexico grouped according to their section.

Bartonia	***Bicuspidaria***	***Dendromentzelia***	***Mentzelia***	***Trachyphytum***
M. longiloba	*M. hirsutissima*	*M. arborescens*	*M. adhaerens*	*M. affinis*
M. mexicana	*M. involucrata*		*M. aspera*	*M. albicaulis*
M. procera	*M. nesiotes*		*M. asperula*	*M. desertorum*
M. puberula			*M. hispida*	*M. micrantha*
M. reverchonii			*M. isolata*	*M. montana*
M. saxicola			*M. lindheimeri*	*M. obscura*
			M. pachyrhiza	*M. veatchiana*
			M. pattersonii	

chihuahuaensis or *M. procera*. The only other species that occurs in the geographic area outlined by the authors is *M. reverchonii* (Figure 2H-I), a species that H. Thompson, who described the species, would have been unlikely to confuse.

Mentzelia section *Bartonia* is the most species rich section of the genus worldwide, with approximately 51 species. The section is distributed in the northern half of Mexico in the Sonoran and Chihuahuan deserts (Figure 3A). The geographic associations among Mexican species are inconsistent with phylogenetic relationships (Schenk & Hufford 2011), suggesting that there have been multiple movements of species across floristic regions. *Mentzelia reverchonii*, for example, was sister to a clade of *M. nuda* and *M. strictissima* (Schenk & Hufford 2011) that occurs in the short-grass prairies of the Great Plains in the United States. Schenk (2013a) determined a center of origin for section *Bartonia* to be in the Colorado Plateau, and that movement across the North American southwestern deserts to be restricted. The Mexican species of section *Bartonia* represent this scenario well, where all of the species are more closely related to northern species from different floristic regions than they are to each other (Schenk 2013a). It can be hypothesized, although beyond the limits of this study that such distribution patterns occurred because of southward migrations driven by climate change associated with Pleistocene glacial cycles.

Mexican species of section *Bartonia* that occur in the Chihuahuan Desert are often associated with gypsum outcrops. The evolution of species that are limited to gypsum-rich soils has occurred at least five times in section *Bartonia* (Schenk 2013b). It is notable that the species that occur on gypsum in the Chihuahuan Desert do not appear to be obligated to these soil types. Three species associated with gypsum soils, *M. mexicana*, *M. reverchonii*, and *M. saxicola* all occur on soils that show no evidence of being gypsum derived in the northern parts of their respective ranges.

Three names have been misapplied in Mexico for section *Bartonia*. *Mentzelia albescens*, which is amphitropically disjunct between Texas in the United States and Argentina and Chile in South America (Schenk & Saunders 2017), approaches the Mexican border, but no collections have been made, as far as we know, in Mexico. *Mentzelia oreophila* occurs in the Sonoran Desert in the United States, but collections are not known from Mexico. The misapplication is likely the result of Prigge's (1993) treatment of *M. puberula*, a species that does occur in Mexico, as a synonym of *M. oreophila*. Brokaw *et al.* (2012) later recognized *M. puberula* as a distinct species, a treatment followed here. *Mentzelia procera* had historically been treated as a variety of the Rocky Mountain endemic *M. pumila* (Schenk & Hufford 2010), and previous works and herbarium collections have recognized *M. procera* as *M. pumila*, which is misapplied in Mexico.

Mentzelia section *Bicuspidaria* consists of six annual species worldwide, three of which occur in Mexico: *M. hirsutissima*, *M. involucrata* S.Watson (Figure 2B), and *M. nesiotes*. The three species are each other's closest relatives, with *M. hirsutissima* being more closely related to *M. involucrata* than the morphologically similar *M. nesiotes* (Brokaw *et al.* 2020). Despite the cryptic differences between *M. hirsutissima* and *M. nesiotes*, the two species are geographically isolated and occur in ecologically distinct climates (Brokaw & Schenk 2020). All three species occur in the California Peninsula and/

or the western edge of Sonora. Although the ranges of *M. involucrata* and *M. hirsutissima* overlap in southern California and Baja California, *M. nesiotes* is allopatric in the Vizcaíno fog desert west of the Peninsular Ranges (Brokaw & Schenk 2020). We were unable to locate and verify the collection of *M. hirsutissima* reported from near Coxcatlán, which was considered introduced into the area (Villanueva-Almanza 2011). We agree with Brokaw *et al.* (2020), Brokaw & Schenk 2020 in treating *M. stenophylla* as a synonym of *M. hirsutissima* on the basis of overlapping characters that prohibit clear species boundaries as well as phylogenetic results that recovered representatives mixed within a clade.

The monotypic section *Dendromentzelia* is located in southern Mexico (Figure 3B), and it is notably different compared to sections *Bartonia*, *Bicuspidaria*, and *Trachyphytum* in being a small tree with opposite leaves, versus herbaceous to subshrubby with alternate leaves. *Mentzelia arborescens* has long been associated with section *Mentzelia* (Darlington 1934), but more recent phylogenetic studies have identified support for its placement as sister to section *Mentzelia* (Hufford *et al.* 2003, Grissom 2014, Figure 1). We continue to observe the importance of the tree habit in recognizing *M. arborescens* within *Dendromentzelia*. Mexican collections have historically been treated as *M. conzattii*, but we agree with Darlington (1934) and Weigend (2007a) in recognizing the taxon as a synonym of *M. arborescens*.

Mentzelia section *Mentzelia* is the most diverse section in Mexico with eight species. Grissom (2014) identified a Sonoran Desert origin for the Mexican species of section *Mentzelia*. From the Sonoran Desert, lineages dispersed into the Mexican Highlands, West Indian region, Central America, and South America. The Sonoran Desert origin of section *Mentzelia* contrasts with section *Bartonia*, which has an estimated origin further north in the Colorado Plateau of the United States (Schenk 2013a).

Mentzelia hispida, *M. aspera* L., and *M. lindheimeri* from section *Mentzelia* are especially widespread throughout Mexico and represent considerable taxonomic challenges (Grissom 2014). The concept of *M. hispida* is one of the most confused among section *Mentzelia* because of its wide range that encompasses much phenotypic variation (Villanueva-Almanza 2011). Darlington (1934) recognized *M. strigosa*, which she identified as a Mexican endemic, but did not cite a single specimen in her monograph. We treat *M. strigosa* as a synonym of *M. hispida*, as well as *M. karwinskii* Urb. & Gilg and *M. orizabae* Urb. & Gilg, both of which have been synonymized in other works (Darlington 1934, Calderón de Rzedowski 1992, Villanueva-Almanza 2011).

Mentzelia aspera is considered a tropical weed (Thompson & Powell 1981) and has the widest distribution of all species in *Mentzelia* (Reyes 1999, Weigend 2007b, Hufford *et al.* 2016), occurring from Arizona in the United States southward to Argentina, and extending eastward into Brazil. *Mentzelia aspera* is commonly confused with other annual species from section *Mentzelia*, a trait that appears to have evolved multiple times from perennial ancestors throughout the genus. In Mexico, *M. aspera* is common in all places except the Chihuahuan Desert, where it rarely occurs along its periphery. Differentiating *M. aspera* from *M. isolata* can be difficult, but *M. aspera* tends to have longer pedicled fruits and more stamens (see key below).

We conservatively treat *M. gracilis*, *M. incisa*, and *M. texana* as synonyms under *M. lindheimeri*. Hufford *et al.* (2016) recognized the latter two taxa as synonyms of *M. lindheimeri*, but Grissom (2014) advocated for their continued recognition, in addition to *M. gracilis*. Representatives of *M. gracilis*, *M. incisa*, and *M. lindheimeri* formed a clade in phylogenetic analyses of Grissom (2014), which also included *M. floridana* Nutt. ex Torr. & A.Gray. The aforementioned clade has a unique biogeographic pattern, forming a band around the northern portion of the Gulf of Mexico (Grissom 2014). Additional systematic work is needed to assess the species status of the taxa, as well as their relationships.

We treat *M. sessilifolia* and *M. gypsophila* under *M. asperula*. Grissom (2014) recovered all three taxa in a clade, but the relationships within the clade were weakly supported. *Mentzelia sessilifolia* had been treated as a synonym of *M. hispida* by Darlington (1934), but representatives analyzed by Grissom (2014) were recovered as being too distantly related to be consistent with Darlington's treatment. Additional work is needed in this clade to determine whether *M. sessilfolia* and *M. gypsophila* should be recognized as distinct species in regard to *M. asperula*.

Many of the reported occurrences of *M. oligosperma* in the northeastern portion of Mexico (*e.g.*, Turner 2004) were likely *M. pattersonii* B.L.Turner. *Mentzelia oligosperma* approaches the Mexico border in southwestern Texas, but current herbarium collections provide no evidence that it ever crosses the border (although future collecting efforts might reveal that it does indeed occur in Mexico). The two taxa are sister (Grissom 2014) and can be differentiated by the greater number of stamens in *M. oligosperma* (15-45 versus approximately 10). Turner

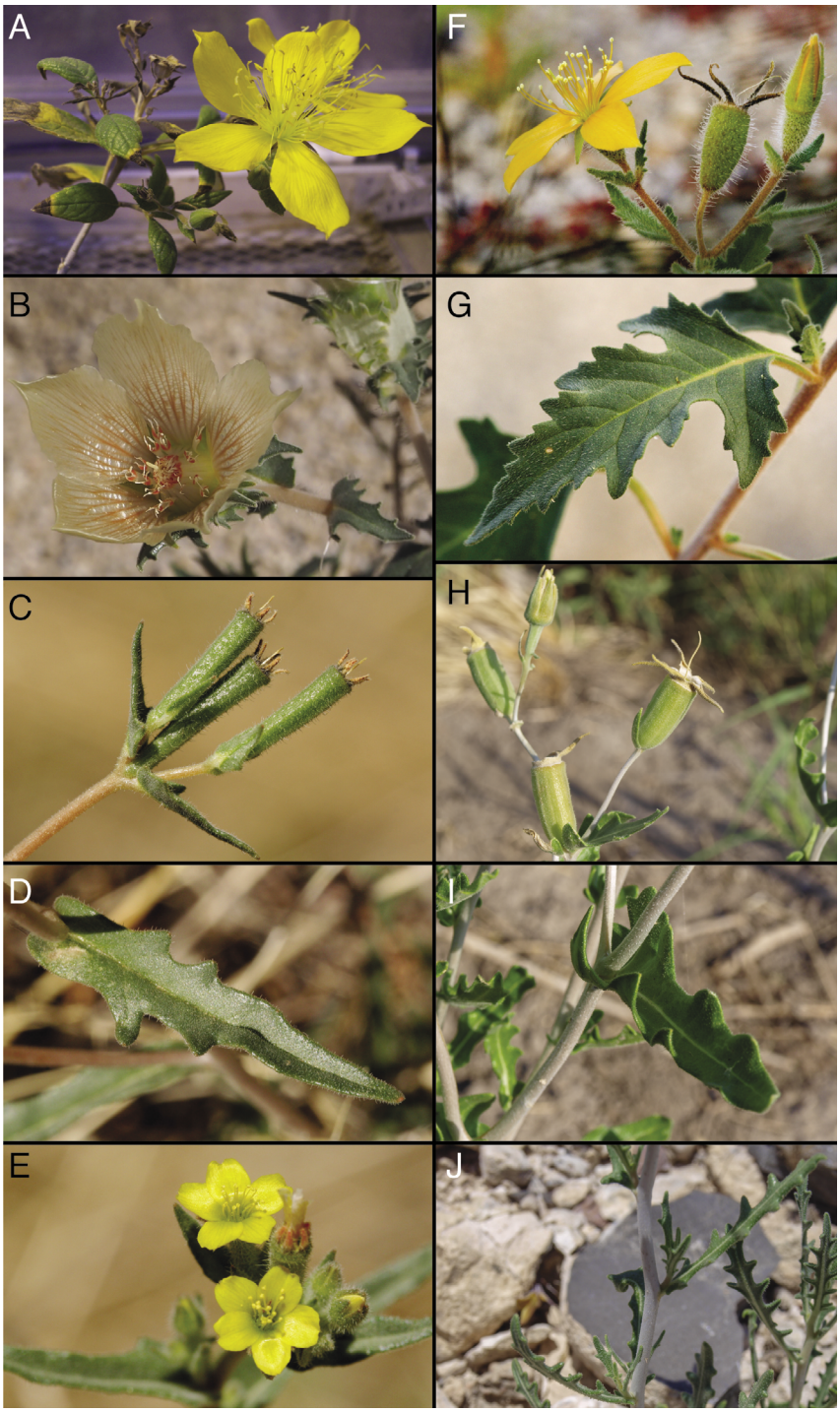

Figure 2. Representative *Mentzelia* species from the five sections that occur in Mexico. A. *M. arborescens* from section *Dendromentzelia*, cultivated in the Washington State University greenhouse; B. *M. involucrata* flower with bifid stamens from section *Bicuspidaria*, photograph from Riverside Co., California, USA, by Joe Decruyenaere; C. *M. montana* fruits from section *Trachyphytum*, demonstrating the gradual tapering from the apex to the base, from Doña Ana County, New Mexico, USA, photograph by Patrick J. Alexander; D. *M. montana* leaf from Doña Ana County, New Mexico, USA, photograph by Patrick J. Alexander; E. *M. montana* flowers from Doña Ana County, New Mexico, USA, photograph by Patrick J. Alexander; F. *M. adhaerens* flower and fruit from Baja California, photograph by Patrick J. Alexander; G. *M. adhaerens* leaf from Baja California, photograph by Patrick J. Alexander; H. *M. reverchonii* fruits and pre-anthesis flower from Coahuila, Mexico; I. Leaf of *M. reverchonii* from Coahuila, Mexico; and J. *M. saxicola* leaf from Zacatecas, Mexico.

(2004) cited the larger petals (15-20 × 8-10 mm) of *M. pattersonii* as a distinguishing character, but we note that although *M. pattersonii* petals can be slightly larger than *M. oligosperma*, those measurements overlap greatly with those reported by Hufford (2016) as (6-)8-18.5 × (3-)4-10.5 mm. *Mentzelia oligosperma* and *M. pattersonii* form a clade that is closely related to the Chihuahuan endemic *M. pachyrhiza* I.M.Johnston (Grissom 2014).

Mentzelia section *Trachyphytum* is the second most species-rich section in *Mentzelia* world-wide with approximately 22 species. Individuals are all annual herbs, about half of which are polyploids, including tetraploids, hexaploids, and octoploids (Brokaw & Hufford 2010). *Mentzelia veatchiana* Kellogg, for example, is hypothesized to be an allohexaploid (6x) between the tetraploid *M. montana* (Davidson) Davidson & Moxley (or possibly *M. ravenii* H.J.Thomps. & J.E.Roberts) and the diploid *M. pectinata* Kellogg (Brokaw & Hufford 2010). Such complex evolutionary histories render distinguishing species on the basis of morphological characters challenging (*e.g.*, see *M. veatchiana* and *M. montana* in key below). In Mexico, section *Trachyphytum* is represented by seven species: *M. affinis* Greene, *M. albicaulis* (Dougl.) Dougl. ex Torr. & A.Gray, *M. desertorum*, *M. micrantha* (Hooker & Arnott) Torr. & A.Gray, *M. montana* (Figure 2C–E), *M. obscura* H.J.Thomps. & J.E.Roberts, and *M. veatchiana*. All seven species occur in either Baja California Peninsula and/or the Sonoran Desert (Figure 3A). Given that the center of diversity in section *Trachyphytum* is in California, it is not surprising to observe representatives of the section in the peninsula and western Sonora Desert of Mexico.

Distinguishing among *M. albicaulis*, *M. desertorum*, and *M. obscura* is challenging because of the great degree of morphological variation in the species and because *M. obscura* is morphologically intermediate between *M. albicaulis* and *M. desertorum* (Brokaw 2016). The species occur sympatrically, creating further challenges to their identifications, but do not appear to be currently hybridizing (Brokaw 2016). The most reliable characters to distinguish among the three taxa are seed characteristics. When observing the seeds at 10X magnification, the periclinal walls of the cells can be seen as being either flat to slightly convex or domed. The wall shapes are best observed when looking at cells that occur along the ridge of the polygonal seed.

Specimens collected from Sonora have been identified as *M. nitens* and *M. dispersa*. We determined those names to be misapplied. Collections attributed to *M. nitens* belonged to section *Mentzelia*, which can be distinguished on the basis of the broad lobing patterns on the proximal leaves. The collections labeled *M. dispersa* were also better placed in section *Mentzelia* for the same reason as above, but others were reidentified as *M. montana*. *Mentzelia montana* can be differentiated from *M. dispersa* on the basis of seeds situated in two rows within capsules (vs. one row in *M. dispersa*), the usually white bases of bracts subtending flowers (vs. green bases), and capsule lengths 6-17(-20) mm (vs. 7-30 mm; Brokaw 2016). We continue to recognize both *M. nitens* and *M. dispersa* as species that occur only in the United States.

Key to Mentzelia species in Mexico.

1. Distal appendages flanking the anthers present on most stamens (section *Bicuspidaria*).
   2. Bracts subtending flowers white-scarious at the base. *M. involucrata*
   2’ Bracts subtending flowers green at the base.
      3. Occurring in Baja California north of 28.5° N and in the northwestern Sonoran Desert; capsules 1.7-3.1 cm long. *M. hirsutissima*
      3’ Occurring in Baja California Sur and surrounding islands south of 28.5° N; capsules 1.1-2.1 cm long. *M. nesiotes*

1’ Distal appendages flanking the anthers absent or present in only the outer stamen whorl (in *M. micrantha*).
   4. Plants arborescent; leaves opposite (section *Dendromentzelia*). *M. arborescens*
   4’ Plants herbaceous to suffrutescent; leaves alternate.
      5. Seeds wingless, variously polygonal, prismatic, ovoid, or pyriform; filaments of outermost antesepalous stamens filiform (rarely laminar).
         6. Leaf blades with broad basal lobes; plants annual or perennial (section *Mentzelia*).
            7. Plants annual.
               8. Leaf blades on primary axis ≤ 5 cm long.
                  9. Petals 11-15 mm long; fruits 8-14 mm long; occurring in Sonora and Baja California Peninsula. *M. adhaerens*
                  9’ Petals 5-8 mm long; fruits 12-25 mm long; occurring throughout Mexico. *M. asperula*
               8’ Leaf blades on primary axis > 5 cm long.
                  10. Pedicles of fruits ≥ 1 mm long; stamens more than 15; occurring throughout Mexico. *M. aspera*
                  10’ Pedicles of fruits < 1 mm long; stamens less than 15; occurring in Sonora. *M. isolata*
            7’ Plants perennial.
               11. Capsules with rounded base. *M. lindheimeri*

11’ Capsules with cuneate base.

12. Petioles of proximal leaves along main shoot ≤ 3 mm long; upper leaves sessile. *M. pattersonii*

12’ Petioles of proximal leaves along main shoot generally ≥ 3 mm long; upper leaves with petiole 1 mm.

13. Petals 17-30 mm long; occurring throughout Mexico. *M. hispida*

13’ Petals 5-11.5 mm long; occurring in the Chihuahuan Desert. *M. pachyrhiza*

6’ Leaf blades without broad basal lobes; plants annual (section *Trachyphytum*).

14. Stamen filaments heteromorphic, with the five outermost stamen broad with two distal appendages flanking the anther, the inner stamen filaments filiform and without distal appendages flanking the anther. *M. micrantha*

14’ Stamen filaments monomorphic, all filiform and without distal appendages flanking the anther.

15. Seeds in one row in distal half of fruit; capsules narrowly cylindric. *M. affinis*

15’ Seeds in two rows in distal half of fruit; capsules clavate (occasionally cylindric in *M. montana*).

16. Bracts obovate, green with white base (rarely with green base), 3-7 lobes along the margin (rarely entire).

17. Petals orange to orange-yellow distally; styles (3-)3.5-6 mm long at anthesis; sepals 2-5 mm long; leaves to 17 cm long; capsules 8-28 mm long. *M. veatchiana*

17’ Petals yellow distally; styles 1.5-3.5(-6) mm long at anthesis; sepals 1-4 mm long; leaves to 13 cm long; capsules 6-17(-20) mm long. *M. montana*

16’ Bracts orbiculate to ovate to lanceolate, green, margins three-lobed, sinuate, or entire.

18. Periclinal surface of mature seed cells flat to convex; bracts subtending flowers entire. *M. desertorum*

18’ Periclinal surface of mature seed cells domed; bracts subtending flowers entire to three-lobed.

19. Domes of periclinal surface of mature seed cells ≥ 1/2 as tall as wide; leaf margins deeply to shallowly lobed; bracts subtending flowers entire to three-lobed. *M. albicaulis*

19’ Domes of periclinal surface of mature seed cells < 1/2 as tall as wide; leaf margins few lobed to entire; bracts subtending flowers entire. *M. obscura*

5’ Seeds with peripheral wings, dorsoventrally flattened, lenticular-ovoid; filaments of outermost antesepalous stamens laminar, sometimes petaloid (section *Bartonia*).

20. Plants with multiple branches arising from a subterranean branching caudex; median antesepalous stamens with anthers; fruits cup-shaped; anthers twisting after dehiscence. *M. puberula*

20’ Plants with a single primary branch or multiple branches arising from a single region at or above the soil surface; median antesepalous stamens generally without anthers; fruits cup-shaped or cylindrical; anthers remaining straight (or sometimes twisting in *M. saxicola*) after dehiscence.

21. Cauline leaves, at least some, with teeth or lobes that are angled toward the leaf apex.

22. Seed central domes with 4-6 papillae per cell as viewed at 10X magnification; plants 3.2-5.5 dm tall; leaves 35-110 mm long with 8-20 lobes or teeth. *M. longiloba* var. *chihuahuaensis*

22’ Seed central domes with 8-45 papillae per cell as viewed at 10X magnification; plants 1-4 dm tall; leaves 16.5-82 mm long with 4-16 lobes or teeth.

23. Primary leaves dentate (sometimes nearing pinnatilobate), 11.7-29.1 mm wide, most intersinus distances 3.4-12.8 mm. *M. mexicana*

23’ Primary leaves pinnatilobate, 5.8-11.2 mm wide, intersinus distances 1.6-3.4 mm. *M. saxicola*

21’ Cauline leaves with teeth or lobes always perpendicular to the leaf central axis.

24. Anticlinal walls of seed coats straight, 5-7 papillae per cell as viewed at 10X magnification; leaves 24.2-54 mm long; proximal leaves with 10-20 teeth or lobes; petals 2.5-4.2(5.5) mm wide; Chihuahuan Desert. *M. reverchonii*

24’ Anticlinal walls of seed coats sinuate, 26-106 papillae per cell as viewed at 10X magnification; leaves 24-112 mm long; proximal leaves with 12-50 teeth or lobes; petals 3.7-7.2 mm wide; Sonoran or Chihuahuan Desert.

25. Petals light yellow (rarely golden yellow); Chihuahuan Desert; cauline leaf intersinus distance all < 4 mm. *M. procera*

25. Petals golden yellow; Sonoran Desert;

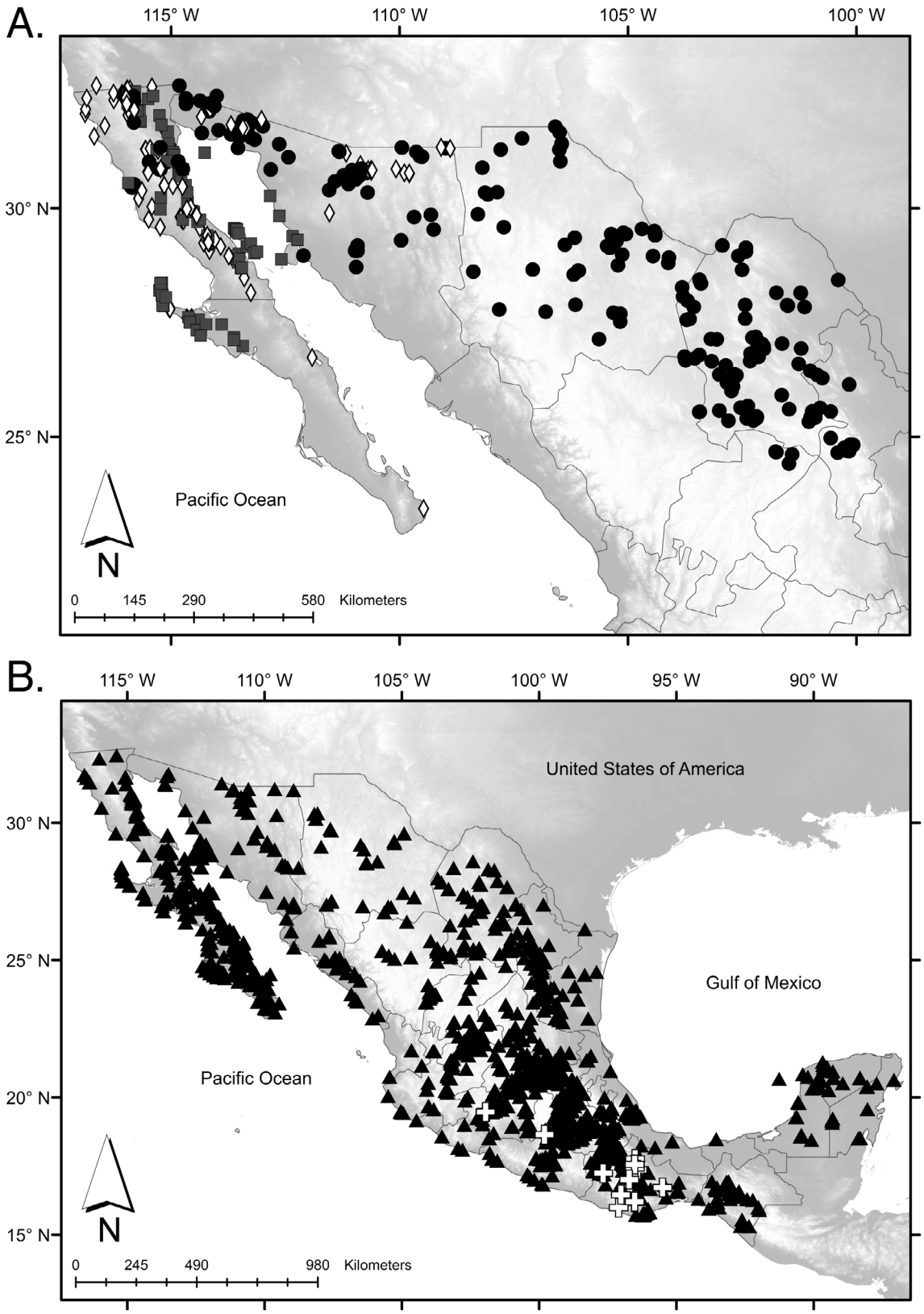

Figure 3. Distributions of *Mentzelia* sections in Mexico. A. Distribution of sections *Bartonia* (black circles), *Bicuspidaria* (gray squares), and *Trachyphytum* (white diamonds) in northern Mexico. B. Distribution of sections *Dendromentzelia* (white crosses) and *Mentzelia* (black triangles).

at least some cauline leaf intersinus distance ≥ 4 mm.

26. Leaves 38-112 × 10-24.6 mm, intersinus distances 3.6-13.7 mm; fruits cup-shaped to cylindrical, 9.6-16.4 mm long; seed central domes with 67-106 papillae per cell as viewed at 10X magnification. *M. longiloba* var. *longiloba*

26' Leaves 24-78 × 5.5-13.8 mm, intersinus distances 1.9-7.3 mm; fruits cup-shaped, 7.6-13.2 mm long; seed central dome with 26-51 papillae per cell as viewed at 10X magnification. *M. longiloba* var. *pinacatensis*

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