

THE SPECIES OF *MENTZELIA* (LOASACEAE) IN MEXICO, PART 2: *MENTZELIA* SECTION *BARTONIA* LAS ESPECIES DE *MENTZELIA* (LOASACEAE) EN MÉXICO, PARTE 2: *MENTZELIA* SECCIÓN *BARTONIA*

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Abstract

Background: *Mentzelia* (Loasaceae) is primarily distributed in western North America. The genus is classified into six monophyletic sections, among which species of section *Bartonia* are particularly poorly understood.

Questions: What species of *Mentzelia* section *Bartonia* occur in Mexico? What are the species distribution ranges and what are their defining attributes?

Study species: *Mentzelia* section *Bartonia*.

Methods: Field, herbarium, distribution, and scanning electron microscopy studies were conducted to assess species diversity. Seed coat microsculpture patterns were evaluated to confirm species identities and understand their distributions throughout Mexico.

Results: Six species from section *Bartonia* were recognized, with taxa distributed into either the Chihuahuan or Sonoran deserts. *Mentzelia longiloba* var. *pinacatensis* is the only Mexican endemic.

Conclusions: Although this work comprehensively addressed the species of section *Bartonia* in Mexico, two groups will continue to present identification challenges: the *M. longiloba* and *M. mexicana*-*M. saxicola* complexes. Overlapping and variable characters will continue to complicate species identification in the *M. longiloba* complex, while the late-season loss of primary leaves will obscure species identification between *M. mexicana* and *M. saxicola*.

Keywords: Chihuahuan Desert, desert flora, plant taxonomy, Sonoran Desert

Resumen

Antecedentes: *Mentzelia* (Loasaceae) se distribuye principalmente en el oeste de Norteamérica. El género se clasifica en seis secciones monofiléticas, entre las cuales las especies de la sección *Bartonia* son particularmente poco entendidas.

Preguntas: ¿Cuáles son las especies de *Mentzelia* sección *Bartonia* en México?, ¿Cuáles son sus rangos de distribución y cuáles son los atributos que las distinguen?

Especies de estudio: *Mentzelia* sección *Bartonia*.

Métodos: Se realizaron estudios de campo, herbario, distribución y microscopía electrónica de barrido para evaluar la diversidad de especies. Se analizaron los patrones de microescultura de la testa de la semilla para confirmar la identidad de las especies y comprender su distribución en México.

Resultados: Se reconocieron seis especies de la sección *Bartonia*, con taxones distribuidos en los desiertos Chihuahuense o Sonorense. *Mentzelia longiloba* var. *pinacatensis* es el único taxón endémico de México.

Conclusiones: Aunque este trabajo abordó exhaustivamente las especies de la sección *Bartonia* en México, dos grupos continuarán presentando desafíos de identificación: los complejos de *M. longiloba* y *M. mexicana*-*M. saxicola*. Los caracteres superpuestos y variables continuarán complicando la identificación en el complejo *M. longiloba*, mientras que la pérdida en temporada tardía de las hojas primarias dificultará la identificación entre *M. mexicana* y *M. saxicola*.

Palabras clave: Desierto Chihuahuense, Desierto Sonorense, flora del desierto, taxonomía vegetal.

Mentzelia L. is a New World genus centered in western North America. The genus is classified into six monophyletic sections (Hufford *et al.* 2003), of which section *Bartonia* (Torrey & A. Gray) Benth. & Hooker f. is the most species-rich, with approximately 51 species. Taxonomy of section *Bartonia* has been notably problematic (Thompson & Powell 1981, Holmgren & Holmgren 2002, Schenk & Hufford 2011a). Recent floristic work has clarified the species concepts within the United States as part of the Flora of North America (Hufford *et al.* 2016), the Californian flora in the Jepson Manual (Brokaw *et al.* 2012), and the North American intermountain region (Holmgren *et al.* 2005), but the species in Mexico have not been critically examined and substantial taxonomic confusion remains.

The most comprehensive study on Mexican *Mentzelia* was conducted by Thompson & Powell (1981), which focused exclusively on species of the Chihuahuan Desert. In section *Bartonia*, the authors recognized three species: *M. multiflora* (Nutt.) A.Gray, *M. saxicola* H.J.Thomps. & Zavort., and *M. mexicana* H.J.Thomps. & Zavort. Recent fieldwork, collections, and taxonomic reevaluations, however, have revealed species in Mexico that were not previously recognized to occur there, and that *M. multiflora* is a misapplied name in Mexico. Schenk & Hufford (2011b), for example, recognized *M. multiflora* as occurring only along the eastern edge of the Rocky Mountain Front Range in the United States, which begs the question: If collections previously treated as *M. multiflora* are misapplied, what species are they?

Seed coat microsculpture patterns provide reliable characters that can be essential for the identification of species in section *Bartonia* (Schenk *et al.* 2016). Thompson & Powell (1981) differentiated among species based on the curvature of the testal anticlinal wall, which Schenk *et al.* (2016) characterized as straight, wavy, or sinuate, as well as the number of small spherical bumps on the periclinal wall of the testa called papillae. Although Schenk *et al.* (2016) determined that variation in seed coat microsculpturing patterns are correlated with seed size, microsculpture patterns have provided reliable characters to differentiate among species (Schenk & Hufford 2011a) and might be useful for determining what species of *Mentzelia* occur in Mexico.

Recent floristic work demonstrates why detailed taxonomic studies in *Mentzelia* are needed. Villaseñor (2016), for example, recognized *M. hintoniorum* B.L. Turner & A.L. Hempel, *M. multiflora*, *M. oreophila* J.Darl., *M. pumila* Nutt., and *M. sinuata* (Rydb.) R.J.Hill in Mexico, all species that are either synonyms of species that do oc-

cur in Mexico or are not recognized as occurring in Mexico by Schenk & Hufford (2020). In addition to the four previously mentioned species, Villaseñor (2016) recognized *M. mexicana* H.J.Thomps. & Zavort., *M. reverchonii* (Urb. & Gilg) H.J.Thomps. & Zavort., and *M. saxicola* H.J.Thomps. & Zavort. Although there is good support for the latter three species as occurring in Mexico, how species are distributed across their respective range is poorly characterized and they are often confused in herbarium collections. Issues surrounding uncertain determinations and misapplied names are not unique to Villaseñor (2016). It is because of the historic taxonomic issues in section *Bartonia* that similar species recognition are echoed in other treatments (*e.g.*, Sosa *et al.* 2018) and especially on labels of collections in herbaria. In order to clarify the taxonomic uncertainties, a treatment of the Mexican species and their ranges is needed in section *Bartonia*.

In a companion article to this one, Schenk *et al.* (2021), surveyed the species of *Mentzelia* in Mexico. The authors recognized 25 species, of which six are placed in section *Bartonia*. In this paper, a formal taxonomic treatment of section *Bartonia* is presented that includes distribution maps of all taxa and an evaluation of seed coat microsculpture patterns. Through the present work, we hope to clarify persistent taxonomic issues of what species of section *Bartonia* occur in Mexico, what their respective ranges are, and how they are differentiated.

Materials and methods

We evaluated 313 herbarium specimens collected from Mexico for morphological variation and distribution data. Twelve collections were made from natural populations in Mexico and studied alongside herbarium specimens previously deposited at 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), Schenk & Hufford (2011a), and Schenk & Hufford (2020).

Species distribution data were collated from field and herbarium collections. 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). Maps were generated in ArcMap v.10.7 (ESRI, Redland, California, USA).

We evaluated the seed coat microsculpture patterns of species, with a particular focus on the Chihuahuan Desert

species that have historically been difficult to understand. Seeds were mounted onto a carbon tab and sputter coated with gold for 1 minute at 30-40 milliamps, then imaged with a JEOL JSM6610LV scanning electron microscope (JEOL Ltd., Tokyo, Japan) with 15 kV at 25X, 150X, and 200X.

Results

Six species of *Mentzelia* section *Bartonia* occur in Mexico: *M. longiloba* J.Darl., *M. mexicana*, *M. procera* (Wooton & Standl.) J.J.Schenk & L.Hufford, *M. puberula* J.Darl., *M. reverchonii*, and *M. saxicola*. Three of the four varieties of *M. longiloba* occur in Mexico, *M. longiloba*

var. *chihuahuensis* J.J.Schenk & Hufford, *M. longiloba* var. *longiloba*, and *M. longiloba* var. *pinacatensis* J.J.Schenk & Hufford.

Even though the morphological characteristics of the seed coat can be analyzed by means of a common stereoscopic microscope, in order to better observe its micromorphology, sixty-two seeds were visualized with scanning electron microscopy to examine their gross morphology and microsculpturing patterns (Figures 1, 2). Although seed coat traits are easiest to view at high magnification with a SEM, microsculpture traits can be observed with a 10x hand lens or stereoscopic microscope. Seed coat microsculpture patterns in section *Bartonia* revealed pat-

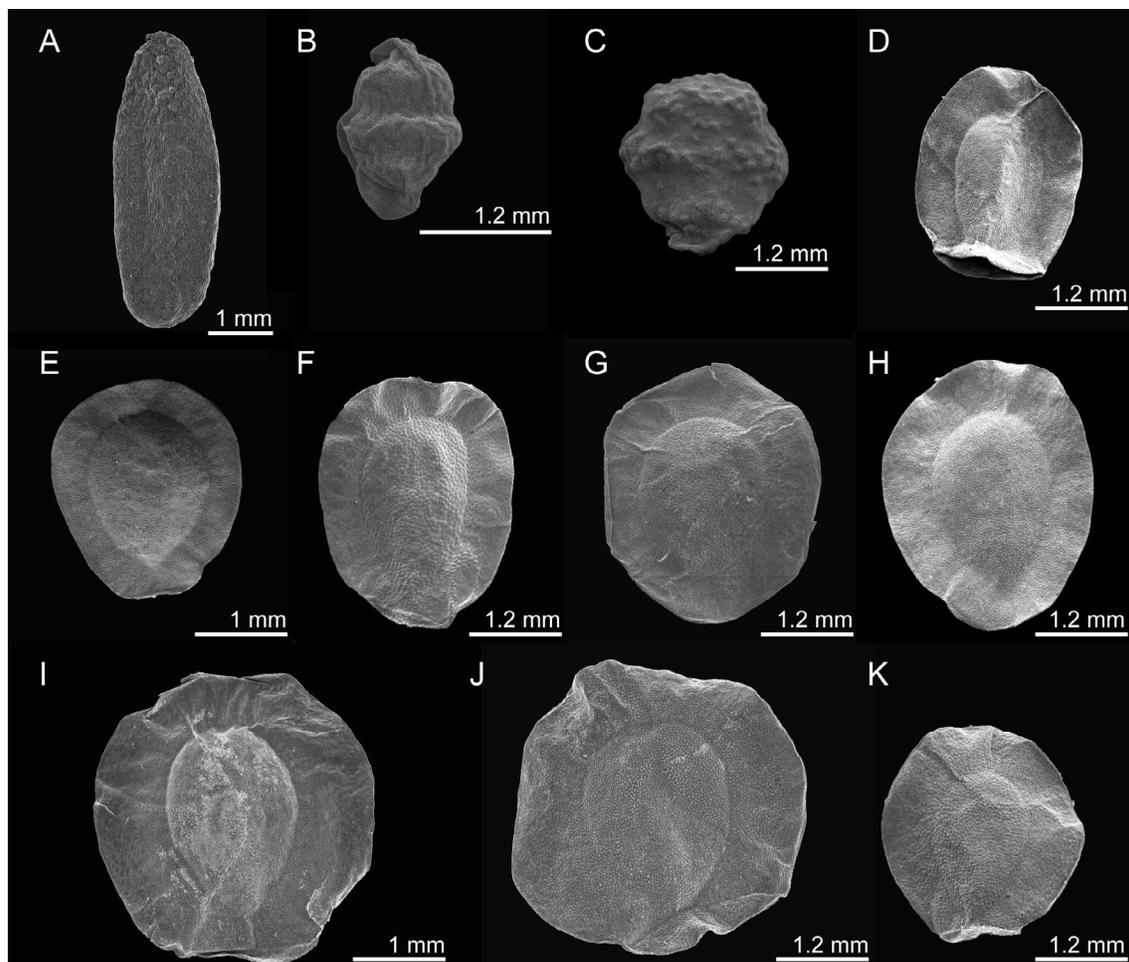


Figure 1. Seeds of *Mentzelia* species that occur in Mexico. A. *M. asperula* from *Mentzelia* section *Mentzelia* (Reina 2017-566, ARIZ). B. *M. hirsutissima* from *Mentzelia* section *Bicuspidaria* (Hufford 2680, WS). C. *M. involucrata* from *Mentzelia* section *Bicuspidaria* (Hufford 4065, WS). D-K: seeds from *Mentzelia* section *Bartonia*. D. *M. puberula* (Schenk 1224, WS), E. *M. longiloba* var. *chihuahuensis* (Granados Mendoza & Schenk 812, MEXU), F. *M. longiloba* var. *longiloba* (Schenk 1225, WS), G. *M. longiloba* var. *pinacatensis* (Sherbrooke s.n. April 9, 1983, ARIZ), H. *M. reverchonii* (Hufford 4310, WS), I. *M. mexicana* (Granados Mendoza & Schenk 802, MEXU), J. *M. saxicola* (Granados Mendoza & Schenk 813, MEXU), and K. *M. procera* (Schenk 1032, WS).

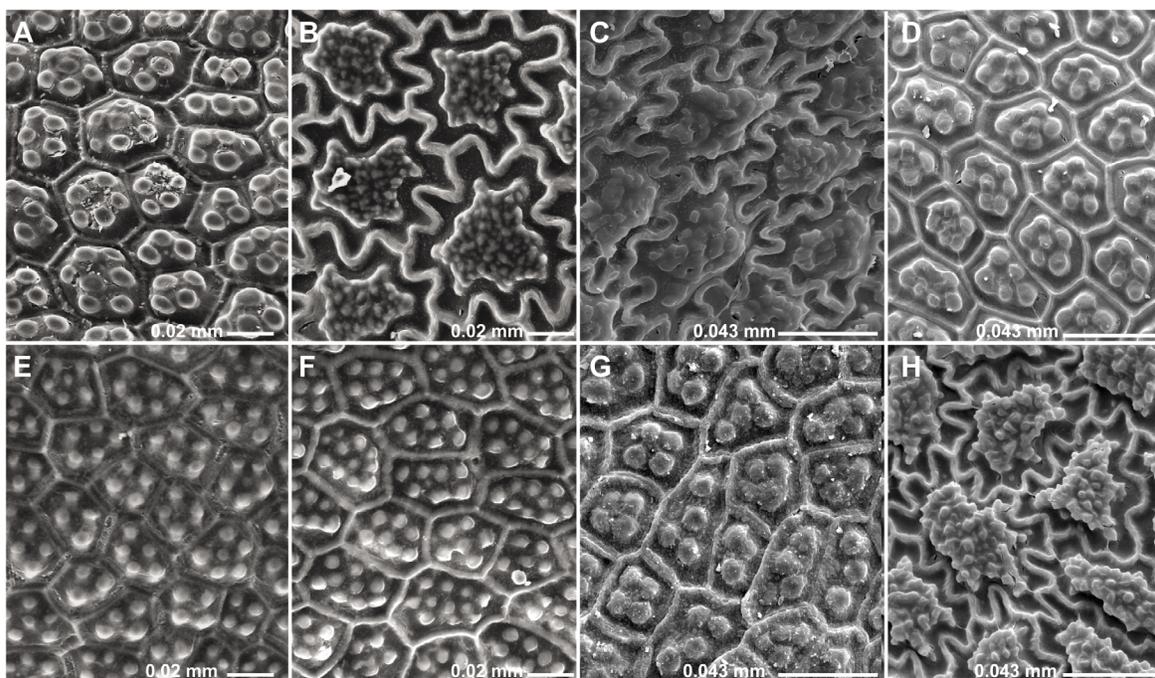


Figure 2. Seed coat surfaces of *Mentzelia* section *Bartonia* in Mexico. A. *M. longiloba* var. *chihuahuensis* (Spellenberg 12305, ARIZ), B. *M. longiloba* var. *longiloba* (White s.n., ARIZ), C. *M. longiloba* var. *pinacatensis* (9 Apr 1983, Sherbrooke s.n., ARIZ), D. *M. reverchonii* (Hufford 4310, WS), E. *M. mexicana* (Granados Mendoza & Schenk 802, MEXU), F. *M. saxicola* (Granados Mendoza & Schenk 813, MEXU), G. *M. puberula* (Schenk 1224, WS), and H. *M. procera* (Schenk 1032, WS).

terns consistent with previous studies. Straight to slightly wavy anticlinal cell walls were identified in the testa of *M. longiloba* var. *chihuahuensis*, *M. mexicana*, *M. saxicola*, *M. reverchonii*, and *M. puberula*. The testal anticlinal cell walls were sinuate in *M. longiloba* var. *longiloba*, *M. longiloba* var. *pinacatensis*, and *M. procera*. Variation in the periclinal wall included size and shape differences of papillae, as well as differences in the number of papillae per cell. Substantial variation was observed among the varieties of *M. longiloba*. In Mexico, *M. longiloba* var. *longiloba* contained 34-77 papillae per cell, *M. longiloba* var. *chihuahuensis* contained 3-7 papillae per cell, and *M. longiloba* var. *pinacatensis* contained 26-51 papillae per cell. The distantly related *M. puberula* contained 3-5 papillae per cell. The Chihuahuan Desert taxa consisted of *M. mexicana* with 3-14 papillae per cell, *M. saxicola* contained 3-11 papillae per cell, *M. reverchonii* contained 4-8 papillae per cell, and *M. procera* contained 32-47 papillae per cell.

Taxa occurred in either the Sonoran or Chihuahuan deserts (Figures 3, 4). The Sonoran Desert taxa included *M. longiloba* var. *longiloba*, *M. longiloba* var. *pinacatensis*, and *M. puberula* (Figure 3). The Mexican endemic *M. longiloba* var. *pinacatensis* had the narrowest distribution

in Mexico, likely due to specializing on the volcanic soils of the Pinacate Region. The distribution of *M. longiloba* var. *longiloba* approaches *M. longiloba* var. *pinacatensis*, but it has not been collected directly from the volcanic field. The range of *M. longiloba* var. *longiloba* is one of the most widespread when compared to other taxa of section *Bartonia* in Mexico (Figure 3), with a range that includes most of the Sonoran Desert and extends northward into the United States. The distribution of *M. puberula* is mostly associated with the Colorado River throughout its range in Mexico and the United States, with some notable extensions away from the river (Figure 3).

Section *Bartonia* is more diverse in the Chihuahuan Desert, where it is represented by *M. longiloba* var. *chihuahuensis*, *M. mexicana*, *M. procera*, *M. reverchonii*, and *M. saxicola*. All five taxa are distantly related to one another based on previous phylogenetic analyses. The distributions of *M. procera* and *M. longiloba* var. *chihuahuensis* are relegated to the northern portions of the Chihuahuan Desert (Figure 4). *Mentzelia reverchonii* is more widespread throughout the Chihuahuan Desert and northward in the United States, but its populations are sporadically distributed. *Mentzelia mexicana* and *M. saxi-*

cola have overlapping ranges throughout northern Mexico in the Chihuahuan Desert.

Discussion

When examining herbarium collections and floristic works, numerous names of section *Bartonia* are misapplied in Mexico. Among the more commonly misapplied names, *M. albescens* (Gillies ex Arn.) Griseb., *M. multiflora*, *M. oreophila*, *M. pumila*, and *M. sinuata* are currently not known to occur in Mexico. Future collecting efforts have the potential to discover *M. albescens* and *M. oreophila* in Mexico, given that both species ranges approach the northern Mexican border from the United States. The ranges of the remaining species, all of which are endemic to the Rocky Mountains and its Front Range, are far enough north to have a low probability of also occurring in Mexico.

Below, a taxonomic treatment for the species of section *Bartonia* modified from Schenk & Hufford (2020) is presented. Selected Mexican specimens that were evaluated as part of this project are indicated in supplementary data. A key to identify species in section *Bartonia*, as well as other *Mentzelia* species in Mexico, is provided in Schenk *et al.* (2021).

Taxonomic treatment of Mentzelia section Bartonia in Mexico.

Mentzelia longiloba J.Darl. var. *chihuahuensis* J.J.Schenk & L.Hufford. *Madroño* 57: 256. 2011. Type: United States, Texas, Brewster Co., Rte 118, S of 898, on W side of rd with E exposure, 30.098 °N, 103.596366 °W, 1385 m elevation, 7 Aug 2004, J. Schenk 901 (holotype: WS!; isotypes: ARIZ!, NY!, TEX!, UNM!, US!).

Biennial herbs, 3.2-5.5 dm tall. Stems primary aerial axis arising at or above the soil surface, erect, straight; axillary branches on distal half of primary axis or along the entire primary axis. Leaves 35-110 × 7.4-27.1 mm, intersinus distance at widest point 2.4-15.3 mm; leaves on proximal third of primary axis oblanceolate to elliptic, dentate with 12-20 teeth 8.4-12.5 mm apart, teeth opposite, perpendicular to leaf axis, regular, 2.3-9 × 4-5 mm with rounded to acute apices; leaves on distal third of primary axis lanceolate, serrate to pinnatilobate with 8-14 teeth or lobes 6.1-9.4(14.1) mm apart, lobes opposite, slightly angled towards leaf apex, regular, 2.9-7.5 × 3.7-4.8 mm with rounded to acute apices. Petals golden yellow, narrowly spatulate, 11.3-16.3 × 3.1-5.1 mm. Androecium golden yellow; anthers remaining straight after dehiscence; outer whorls of stamens staminodial and fertile, five outermost

stamens in median antesealous positions petaloid, narrowly spatulate, 11.2-15.4 × 2.4-4 mm, without anthers, second whorl of stamens all fertile. Capsule cup-shaped to cylindrical, 9.1-15(20.5) × 6.1-9.1 mm, base round to tapering; hypanthium 0.9-2 mm. Seeds 2.9-3.2 mm long; seed coat anticlinal cell walls straight (occasionally slightly wavy), central papillae generally 3-7 per cell.

Distribution. Throughout the entire Chihuahuan Desert, occurring at 548-2,378 m in Mexico (Figure 4).

Habitat. Sandy and/or rocky soils, along roadsides, flats, hills, dunes, or in arroyos, but also occasionally associated with clay or volcanic soils.

Common names. Chihuahuan blazingstar, pega ropa.

Mentzelia longiloba var. *chihuahuensis* has been recognized as *M. multiflora*, a name misapplied to populations across North America and now more narrowly recognized as being localized to the eastern edge of the Rocky Mountain Front Range (Schenk & Hufford 2011a). Phylogenetic analyses recovered *M. longiloba* var. *chihuahuensis* in a polytomy with other *M. longiloba* varieties, plus *M. nuda* (Pursh) Torr. & A.Gray, *M. sinuata*, *M. speciosa* Osterh., *M. strictissima* (Wooton & Standl.) J.Darl., and *M. reverchonii* (Schenk & Hufford 2011b), the latter of which also occurs in the Chihuahuan Desert. We follow Schenk & Hufford (2011a) in continuing to recognize the taxon as a variety of *M. longiloba*.

Mentzelia longiloba var. *chihuahuensis* is unique among the varieties of *M. longiloba* in seed testal cells. Unlike the other varieties that contain sinuate anticlinal cell walls with over 26 papillae per cell, *M. longiloba* var. *chihuahuensis* has straight walls with 3-7 papillae per cell (Figure 2). Schenk & Hufford (2020) reported 4-6 papillae per cell, but our estimates widen the range slightly more.

Mentzelia longiloba J.Darl. var. *longiloba*. *Ann. Missouri Bot. Gard.* 21: 176. 1934; *Mentzelia multiflora* (Nutt.) A.Gray subsp. *longiloba* (J.Darl.) Felger, *Desert Plants* 2: 108. 1980. *Mentzelia multiflora* (Nutt.) A.Gray var. *longiloba* (J.Darl.) Kartesz, *Synth. N. Amer. Fl.* version 1, 1999. Type: United States, California, hayfields, 15 Sep 1931, M.E. Jones s.n. (holotype: MO!; isotype: UC!).

Biennial herbs, 2.6-6.3 dm tall. Stems primary aerial axis arising at or above the soil surface, erect, straight; axillary branches on distal half of primary axis or along the entire primary axis. Leaves 38-112 × 10-24.6 mm, intersinus distance at widest point 3.6-13.7 mm; leaves on proximal third of primary axis oblanceolate or elliptic, pinnatilobate with 12-30 lobes 4.2-15.8 mm apart, lobes opposite, perpendicular to leaf axis, irregular or regular,

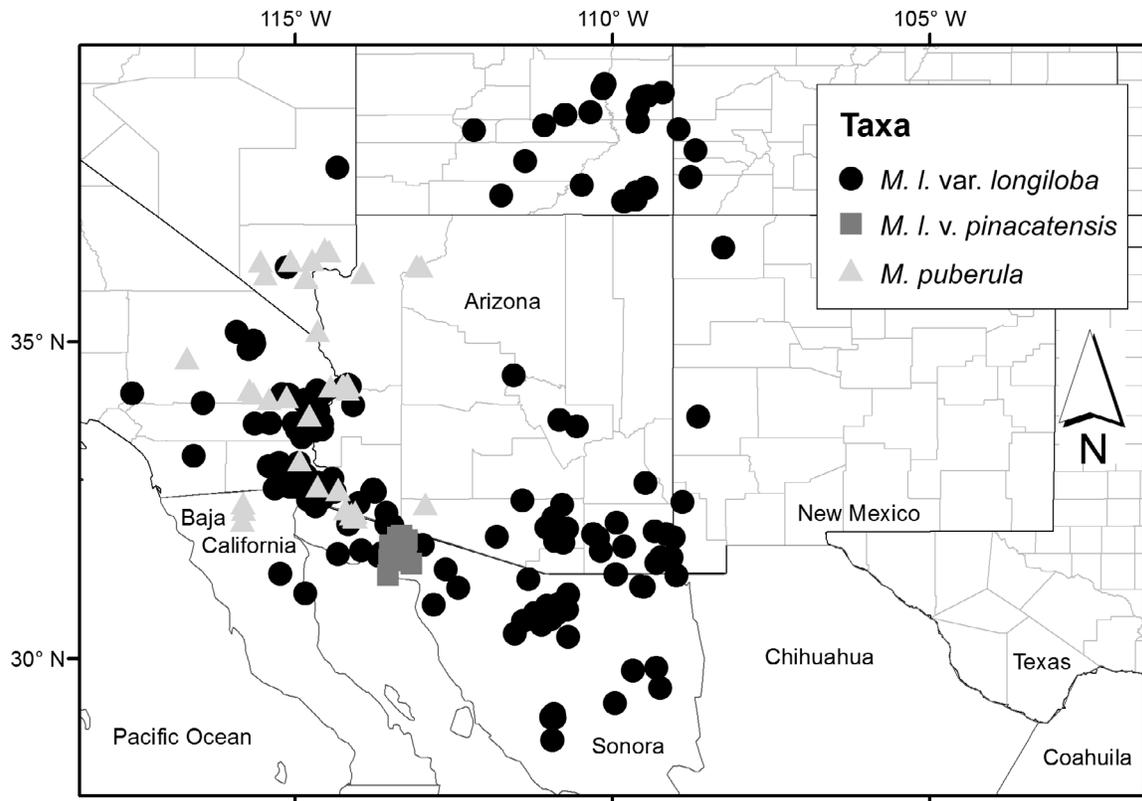


Figure 3. Distribution of *Mentzelia* section *Bartonia* in the Sonoran Desert. *Mentzelia longiloba* is abbreviated as *M. l.*

1.4-6.6 × 1.9-6.1 mm with rounded to acute apices; leaves on distal third of primary axis lanceolate, pinnatilobate with 10-28 lobes 5-15.8(20.8) mm apart, lobes opposite, perpendicular to leaf axis, irregular or regular, 2.3-8.6 × 1.8-5.8 mm with rounded to acute apices. Petals golden yellow, narrowly spatulate, 12.2-20.4 × 3.7-7.2 mm. Androecium golden yellow; anthers remaining straight after dehiscence; outer whorls of stamens staminodial and fertile, five outermost stamens in median antesealous positions petaloid, narrowly spatulate, (6.7)10.6-15.5 × 1.9-5.2 mm, without (occasionally with) anthers, second whorl of stamens all fertile. Capsule cup-shaped to cylindrical, 9.6-16.4 × 6-9.2 mm, base rounded; hypanthium 0.7-1.7 mm. Seeds 3.3-4 mm long; seed coat anticlinal cell walls sinuate, central papillae generally 67-106 per cell.

Distribution. Occurs throughout the Sonoran Desert in Mexico and the Colorado Plateau in the United States. In Mexico, populations occur in Baja California and Sonora at 15-1,470 m in elevation (Figure 3).

Habitat. Sandy compacted soils or loose sand dunes.

Common names. Dune blazingstar, hierba del piquete, hierba pegajosa.

Mentzelia longiloba var. *longiloba* has been recognized as *M. multiflora* ssp. *longiloba* (Felger 2000). Schenk & Hufford (2011b) inferred *M. longiloba* to be distantly related to *M. multiflora*, supporting its recognition at the specific level and they further recognized four varieties that exhibit notable geographic, phylogenetic, and morphologic variation.

Seed coat microsculpture patterns were consistent with Schenk & Hufford (2020) in having sinuate anticlinal cell walls. Along the periclinal wall, however, we identified additional variation. Schenk & Hufford (2020) reported 34-106 papillae per cell, while we identified 34-77 papillae per cell (Figure 2). The discrepancy in papillae number suggests variation across populations and the range of *M. longiloba* var. *longiloba*.

Mentzelia longiloba J.Darl. var. *pinacatensis* J.J.Schenk & L.Hufford. Madroño 57: 257. 2011. Type: Mexico, Sonora, Pinacate Region, 1.1 km N of Pinacate Peak, 31.7847222 °N; 113.4902778 °W, 950 m elevation, 13 Oct 1986, R.S. Felger & G.E. Joseph 86-432 (holotype: ARIZ!; isotypes: ARIZ!, RSA!).

Biennial herbs, 1.5-5 dm tall. Stems primary aerial axis arising at or above the soil surface, erect, straight; axillary branches along the entire primary axis. Leaves 24-78 × 5.5-13.8 mm, intersinus distance at widest point 1.9-7.3 mm; leaves on proximal third of primary axis elliptic, dentate to pinnatilobate with 12-50 teeth or lobes, 2.9-18.2 mm apart, teeth or lobes opposite, perpendicular to leaf axis, irregular or regular, 2.8-6.9 × 1.5-3.1 mm with acute apices; leaves on distal third of primary axis elliptic to lanceolate, dentate to pinnatilobate with (6)8-28 teeth or lobes 2.1-5.5 mm apart, teeth or lobes opposite, perpendicular to leaf axis, irregular or regular, 1.7-8.9 × 1.3-3.1 mm with acute apices. Petals golden yellow, narrowly spatulate, 11.9-14.1 × 4.7-6.7 mm. Androecium golden yellow; anthers remaining straight after dehiscence; outer whorls of stamens staminodial and fertile, five outermost stamens in median antesealous positions petaloid, narrowly spatulate, 9.7-13.6 × 3.3-5.9 mm, without anthers, second whorl of stamens all fertile. Capsule cup-shaped, 7.6-13.2 × 5.8-8.5 mm, base rounded; hypanthium 0.5-1.1 mm. Seeds 2.9-3.4 mm long; seed coat anticlinal cell walls sinuate, central papillae generally 26-51 per cell.

Distribution. Endemic to the volcanic Pinacate Re-

gion of northwestern Sonora at 130-950 m in elevation (Figure 3).

Habitat. Only on volcanic cinder cone soils.

Common name. Pinacate blazingstar.

Among the varieties of *M. longiloba*, *M. longiloba* var. *pinacatensis* has the most limited range. Populations are localized in the Sierra Pinacate, a volcanic field in the northern Sonoran Desert, which is also home to other endemic plants and animals (Felger 2000).

Phylogenetic analyses recovered *M. longiloba* var. *pinacatensis* as sister to *M. longiloba* var. *yavapaiensis* (Schenk & Hufford 2011b), a taxon that is currently considered endemic to Arizona (Schenk & Hufford 2020). In Mexico, *M. longiloba* var. *pinacatensis* is most likely confused with *M. longiloba* var. *longiloba*, but the two taxa can be differentiated by the larger leaves and fruits of *M. longiloba* var. *longiloba* (Figure 5).

Mentzelia mexicana H.J.Thomps. & Zavort. Wrightia 4: 21. 1968. Type: Mexico, Coahuila, La Rosa, 7 Sep 1940, F. Shreve & E. Tinkham 9908 (holotype: GH!; isotypes: ARIZ!, MICH).

Biennial herbs, 1-4 dm tall. Stems primary aerial axis

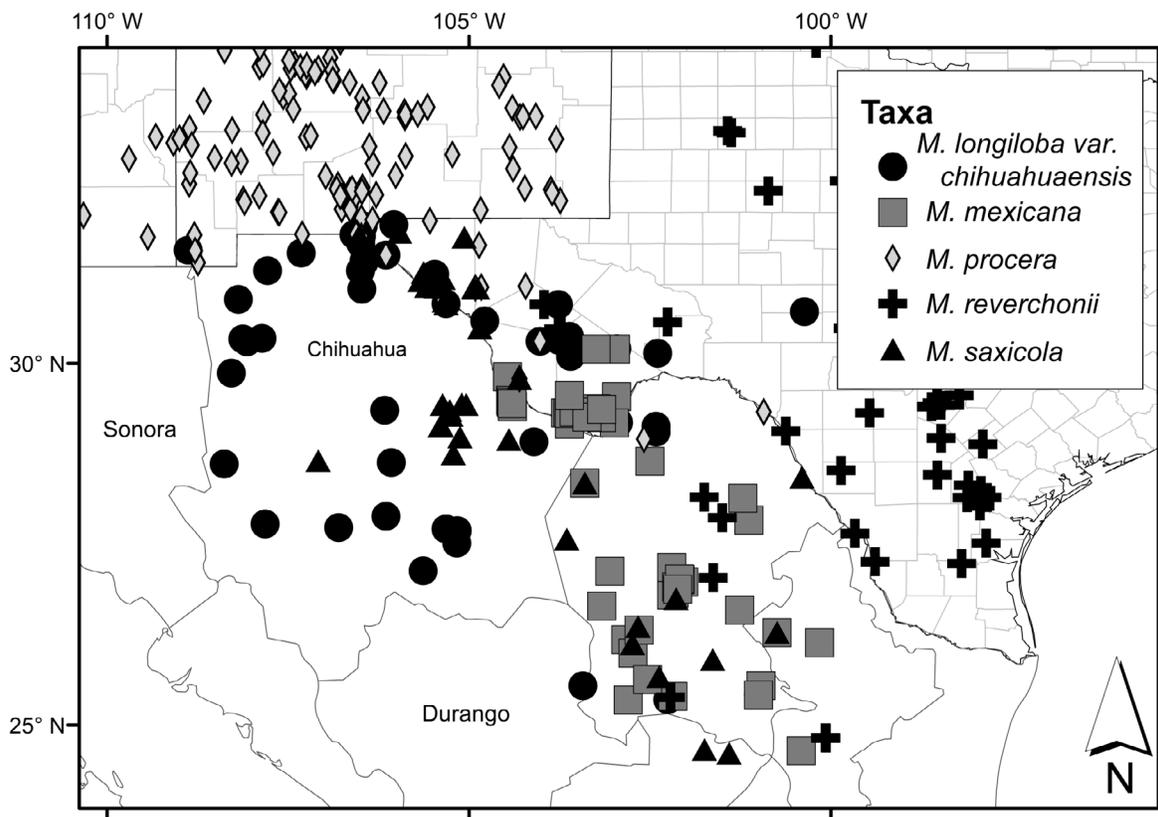


Figure 4. Distribution of *Mentzelia* section *Bartonia* in the Chihuahuan Desert.

arising at or above the soil surface, erect, straight; axillary branches on distal half of primary axis or along the entire primary axis. Leaves 24–82 × 11.7–29.1 mm, intersinus distance at widest point 3.4–18.8 mm; leaves on proximal third of primary axis oblanceolate or elliptic, dentate, serrate, or pinnatilobate with 6–16 teeth or lobes 5.7–13.3 mm apart, teeth or lobes opposite or nearly opposite, slightly angled towards leaf apex or perpendicular to leaf axis, regular, 1.4–5.1 × 2.4–6.4 mm with rounded to acute apices; leaves on distal third of primary axis elliptic to lanceolate with usually non-clasping bases, margins dentate, serrate, or pinnatilobate with 6–12 teeth or lobes 5.8–13.1 mm apart, teeth or lobes opposite or nearly opposite, slightly angled towards leaf apex or perpendicular to leaf axis, regular, 2.5–6.7 × 1.8–4.9 mm with rounded to acute apices. Petals golden yellow, narrowly spatulate, 10.2–15.3(17) × 2.5–6.2 mm. Androecium golden yellow; anthers remaining straight after dehiscence; outer whorls of stamens staminodial and fertile, five outermost stamens in median antesealous positions petaloid, narrowly spatulate, 9.9–14.4(16.7) × 2–4.8 mm, without anthers, second whorl of stamens all fertile. Capsule cup-shaped, 6.5–12.8 × 5.6–8.4 mm, base rounded; hypanthium 0.4–1.2 mm. Seeds 2.2–2.9 mm long; seed coat anticlinal cell walls straight, central papillae generally 3–14 per cell. See [Figure 6](#).

Distribution. Eastern Chihuahua, Coahuila, and Nuevo León at 740–1,525 m in Mexico ([Figure 4](#)).

Habitat. Clay soils largely composed of gypsum, often growing on steep hillside slopes, roadcuts, or arroyos.

Common name. Mexican blazingstar.

Mentzelia mexicana is a Chihuahuan Desert endemic that occurs along the northeastern Mexican states and extends northward into southwestern Texas in the United States. The distribution of *M. mexicana* overlaps substantially with *M. saxicola* ([Figure 4](#)). [Thompson & Powell \(1981\)](#) emphasized elevational differences among *M. mexicana* (their report: 600–1,300 m), *M. saxicola* (their report: 800–1,900 m), and *M. longiloba* var. *chihuahuensis* (treated by the authors as *M. multiflora*, their report: above 1,400 m). Although the authors' general sentiment of *M. mexicana* and *M. saxicola* occurring at lower elevations is supported here, additional collections since their work have revealed much greater overlap in elevations. In Mexico, *M. mexicana* occurs at 740–1,525 m, *M. saxicola* occurs at 850–1,843, and *M. longiloba* var. *chihuahuensis* occurs at 548–2,378 m. Relative to *M. mexicana* and *M. saxicola*, the elevation of *M. reverchonii* does not overlap, occurring at 1,860–2,050 m in Mexico (but it occurs at 50–2,134 in the United States). Given the paucity

of *M. procera* collections, we do not have a good sense of the elevational variation that populations occur at, but we know that it occurs at 970–2,470 m throughout its range in the United States and our two collections indicate an elevational range of 1,250–2,406 m in Mexico, suggesting populations are situated at higher elevations than *M. mexicana* and *M. saxicola*.

[Thompson & Powell \(1981\)](#) described chromosome polymorphism in *M. mexicana*. Populations in the northern edge of the species range from Big Bend National Park in Texas, United States, were reported as $n = 9$. Populations from Coahuila, however, were reported as $n = 10$. The authors identified no morphological distinctions between the $n = 9$ and $n = 10$ populations, a result corroborated here. [Schenk & Hufford \(2011b\)](#) identified evidence for recent hybridization between *M. mexicana* and an unknown member from their clade-1e. If the true chromosome number of *M. mexicana* is $n = 10$, individuals from clade-1e that could be the parental cross include *M. longiloba* var. *chihuahuensis* and *M. reverchonii* because of their geographic proximity and their chromosome number of $n = 9$. If the true chromosome number of *M. mexicana* is $n = 9$, however, the parental cross would likely be with *M. saxicola*, which overlaps in its range and has a chromosome number of $n = 10$.

In this study, we sought to determine how populations of *M. mexicana* and *M. saxicola* were distributed ([Figure 4](#)). We determined the two species to have overlapping ranges throughout their distribution. For example, *Grados Mendoza & Schenk 802* and *803* (MEXU) were identified as *M. mexicana* and *M. saxicola*, respectively, both of which were collected at the same locality in Nuevo León. In the aforementioned population, *M. saxicola* was less common and occurred along the flat area at the base of a roadcut, while *M. mexicana* occurred along the base of the roadcut slope, thus, there remained some spatial separation syntopically. Whether introgression occurs is yet to be determined, but remains a possibility given their proximity, and introgression might be an explanation for why the two distantly related species are so difficult to differentiate morphologically.

Mentzelia procera (Wootton & Standl.) J.J.Schenk & L.Hufford. *Madroño* 57: 247. 2011; *Nuttallia procera* Wootton & Standl., *Contr. U.S. Natl. Herb.* 16: 150. 1913; *Mentzelia pumila* Torr. & A.Gray var. *procera* (Wootton & Standl.) J.Darl., *Ann. Missouri Bot. Gard.* 21: 169. 1934. Type: United States, New Mexico, White Sands, 18 Aug 1907, *E.O. Wootton & P.C. Standley s.n.* (holotype: US!; isotype: NMC!).

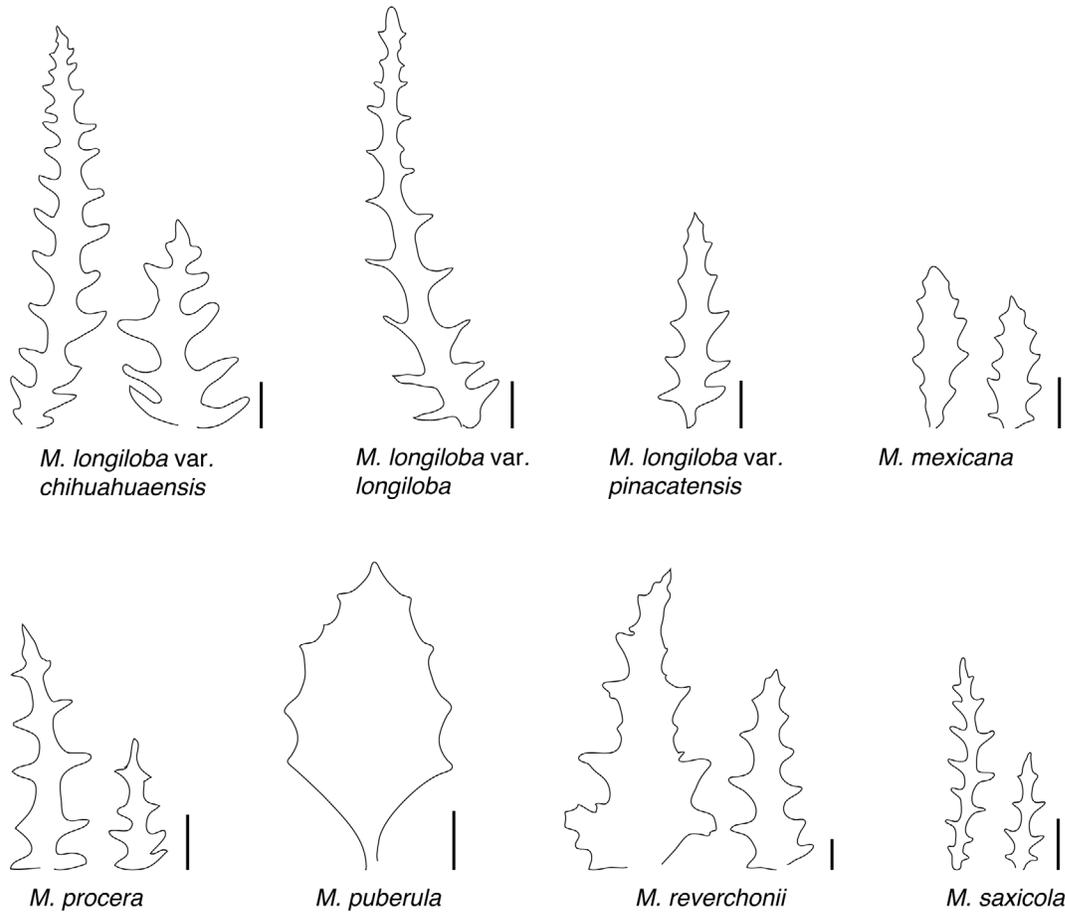


Figure 5. Representative leaf outlines of Mexican taxa of *Mentzelia* section *Bartonia*. *Mentzelia longiloba* var. *chihuahuensis* is based on the isotype and *Granados Mendoza & Schenk 812* (MEXU), *M. longiloba* var. *longiloba* is based on *Gentry & Engard 23284* (MEXU), *M. longiloba* var. *pinacatensis* is based on *Felger 86-432* (ARIZ, RSA), *M. mexicana* is based on *Henrickson 24086* (MEXU), *M. procera* is based on *Wootton s.n.* (P), *M. puberula* is based on *Schenk 1224* (WS), *M. reverchonii* is based on *Granados Mendoza & Schenk 806* (MEXU), and *M. saxicola* is based on *Granados Mendoza & Schenk 813* (MEXU).

Biennial herbs, 2.7-9.4 dm tall. Stems primary aerial axis arising at or above the soil surface, erect, straight; axillary branches on distal half of primary axis or occasionally along the entire primary axis. Leaves 38.3-108 × 5.3-14.9 mm, intersinus distance at widest point 1.7-3.9 mm; leaves on proximal third of primary axis oblanceolate to elliptic, pinnatilobate with 14-22(26) lobes 5.6-12.1 mm apart, lobes opposite, perpendicular to leaf axis, regular, 1.8-4.5 × 1.3-3.8 mm with rounded to acute apices; leaves on distal third of primary axis elliptic to lanceolate with non-clasping bases, pinnatilobate with 6-18 lobes 3.4-12.8 mm apart, lobes opposite to alternate, perpendicular to leaf axis, regular, 1-4.5 × 1.2-3.8 mm with rounded to acute apices. Petals light to occasionally golden yellow, narrowly spatulate, 9.5-16.8 × 3.4-5.6 mm. Androecium light

yellow; anthers remaining straight after dehiscence; outer whorls of stamens staminodial and fertile, five outermost stamens in median antesealous positions petaloid, narrowly spatulate, 8.2-14.6 × 2.3-3.4 mm, without anthers, second whorl of stamens all fertile. Capsule cup-shaped to cylindrical, 9.8-18.8 × 5.2-7.3 mm, base tapering; hypanthium 0.6-1.3 mm. Seeds 2.5-3.1 mm long; seed coat anticlinal cell walls sinuate, central papillae generally 28-68 per cell.

Distribution. The range of *M. procera* is more extensive in the United States, but spans the Mexican border into the northern parts of Chihuahua and Coahuila, at 1,250-2,400 m in elevation ([Figure 4](#)).

Habitat. Sandy soils, roadsides, arroyos, and hillsides.

Common name. Upright blazingstar, pega-pega.

The concept of *M. procera* has changed through time, being first described as a variety of *M. pumila*, it was later recognized at the specific level by [Schenk & Hufford \(2011a\)](#), who emphasized that the two taxa are distantly related. The range of *M. procera* is almost entirely in the United States and only extends slightly into Mexico. Mexican populations have been difficult to locate in herbarium collections and more directed field sampling is needed to better understand the range of *M. procera* in Mexico.

In northern Mexico (and throughout the overlapping ranges in the United States), *M. procera* is likely to be confused with *M. longiloba* var. *chihuahuensis* and *M. reverchonii*. Seed characters best differentiate *M. procera* from *M. longiloba* var. *chihuahuensis*, where the anticlinal walls of the former are sinuate and the periclinal walls have 28-68 papillae per cell, compared to the straight anticlinal walls and 4-6 papillae per cell on the periclinal walls of the latter ([Figure 2](#)). The petals of *M. procera* tend to be a lighter yellow, which differentiates it from both aforementioned species. Capsules of *M. procera* exhibit a tremendous amount of variation in length, but tend to be smaller on average than those observed in *M. reverchonii*.

Mentzelia puberula J.Darl. Ann. Missouri Bot. Gard. 21: 177. 1934. Type: United States, California, San Bernardino Co., Kane Springs, Ord Mtns., 1 May 1906, *H.M. Hall & H.P. Chandler 6824* (holotype: UC!).

Short-lived perennial herbs, 1.4-5.4 dm tall. Stems primary/renewal aerial axes arising from a subterranean branching caudex, erect, straight; axillary branches along the entire primary axis. Leaves 18.8-62.7 × 11-36 mm, intersinus distance at widest point 8.9-28.8 mm; leaves on proximal third of primary axis broadly elliptic to obovate, dentate to serrate with 8-12 teeth 5-11.5 mm apart, teeth opposite, slightly angled towards leaf apex or perpendicular to leaf axis, regular, 1-4 × 1.7-6 mm with rounded to acute apices; leaves on distal third of primary axis oval, or obovate with non-clasping bases, dentate to serrate with 6-12 teeth 3.1-12.7 mm apart, teeth opposite, slightly angled towards leaf apex or perpendicular to leaf axis, regular, 1-3.5 × 2.6-7.3 mm with acute apices. Petals golden yellow, narrowly spatulate, 6.7-9.5(12.6) × 2.3-5.8 mm. Androecium golden yellow; anthers twisted after dehiscence; outer whorls of stamens all fertile, five outermost stamens in median antesealous positions petaloid, slightly clawed, narrowly spatulate, 5.4-9.2(11) × 1.3-2.7 mm, with anthers borne on stalks, second whorl of stamens all fertile. Capsule cup-shaped, 5-9.8 × 5-8 mm, base rounded; hypanthium 0.9-1.8 mm. Seeds 2.4-2.8 mm long; seed

coat anticlinal cell walls straight, central papillae generally 3-5 per cell.

Distribution. Baja California and northwestern edge of Sonora near the United States border, occurring at elevations of 90-460 m in Mexico ([Figure 3](#)).

Habitat. Near the bases of granite rock outcrops or occasionally in sandy arroyos.

Common name. Pubescent blazingstar.

Mentzelia puberula is the most distinct species of section *Bartonia* in Mexico. Phylogenetic analyses conducted by [Schenk & Hufford \(2011b\)](#) inferred that all species of section *Bartonia* belong to one of two sister clades that they referred to as clade-1 and clade-2. *Mentzelia puberula* was recovered in clade-2, which primarily consisted of short-lived perennials that have a woody caudex that branches underground. All other species of section *Bartonia* in Mexico were recovered in clade-1. *Mentzelia puberula*, consequently, is more distantly related to all other species of *Mentzelia* section *Bartonia* in Mexico and is the southernmost representative of clade-2. Only a few specimens of *M. puberula* from Mexico exist, and it is likely that additional field surveys in the Sonoran region will discover novel populations and expand its known range.

Mentzelia puberula was treated as a synonym of *M. oreophila* by [Prigge \(1993\)](#) and [Felger \(2000\)](#). The accounts of *M. oreophila* in Mexico (e.g., [Sosa et al. 2018](#)) likely reflect the treatment of *M. puberula* as a synonym of the former taxon. Although the two taxa are closely related ([Schenk & Hufford 2011b](#)), they are easily distinguished by the clasping leaf-bases of the upper leaves in *M. oreophila* versus the non-clasping bases in *M. puberula*. We follow [Brokaw et al. \(2012\)](#) in advocating for the recognition of the two taxa as distinct species. *Mentzelia oreophila* is a Mojave Desert endemic, distributed in California and Nevada, and it is not known to occur in Mexico.

Mentzelia reverchonii (Urb. & Gilg) H.J.Thomps. & Zavort. Wrightia 4: 24. 1968; *Mentzelia pumila* Torr. & A.Gray var. *reverchonii* Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 94. 1900; *Nuttallia reverchonii* (Urb. & Gilg) W.A.Weber, Phytologia 55: 9. 1984. Type: United States, Texas, Callahan Co., May 1882, *J. Reverchon 322* (lectotype: US!; isolectotypes: MO!, P!).

Mentzelia hintoniorum B.L.Turner & A.L.Hempel, Phytologia 79: 298. 1995. Type:

Mexico, Nuevo León, Mpio. Galeana, San Roberto to "Y," 24.6986111 °N, 100.1761111 °W, 2,015 m, 5 Sep

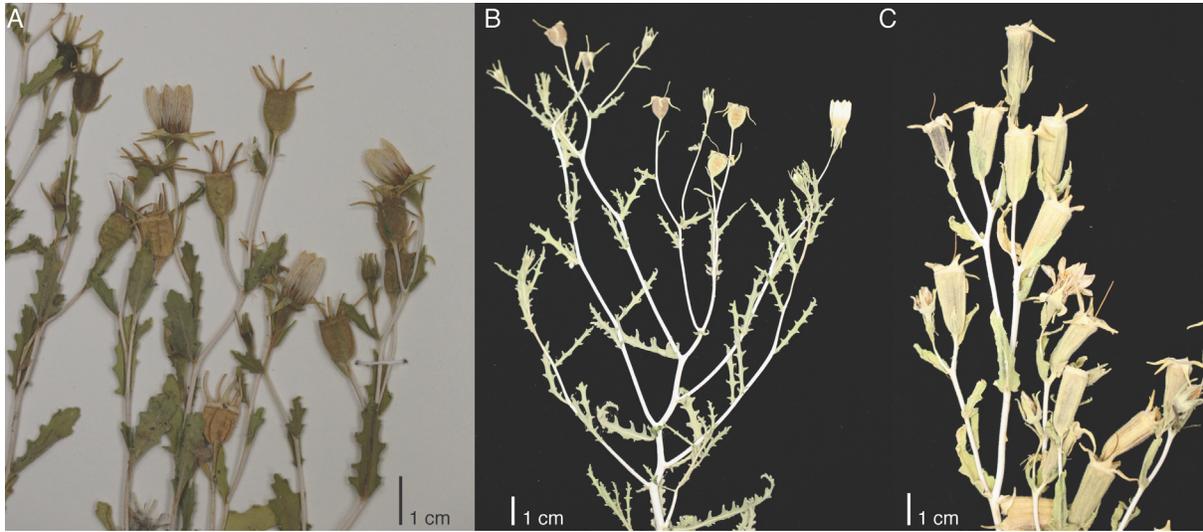


Figure 6. Inflorescences of *Mentzelia* section *Bartonia* from Mexico. A. *Mentzelia mexicana* from Coahuila (Henrickson 24086, MEXU), B. *M. saxicola* from Zacatecas (Granados Mendoza & Schenk 813, MEXU), and C. *M. reverchonii* from Coahuila (Granados Mendoza & Schenk 807, MEXU).

1995, G.B. Hinton *et al.* 25495 (holotype: TEX!; isotype: TEX!).

Biennial to short lived perennial herbs, 1.6-8.5 dm tall. Stems primary/renewal aerial axis arising at or above the soil surface, erect, straight; axillary branches on distal half of primary axis. Leaves 24.2-54 × 6.6-29 mm, intersinus distance at widest point 5.4-13.5(22.4) mm; leaves on proximal third of primary axis oblanceolate to elliptic, dentate to pinnatilobate with 10-20 teeth or lobes 4.6-9.3 mm apart, teeth or lobes opposite, perpendicular to leaf axis, regular, 1.1-5 × 2.4-5.3 mm with rounded to acute apices; leaves on distal third of primary axis lanceolate with non-clasping bases, margins dentate with 8-14 teeth 2.8-8.4(11) mm apart, teeth opposite, perpendicular to leaf axis, regular, 0.6-3.8 × 1.6-5.8 mm with rounded to acute apices. Petals golden yellow, narrowly spatulate, (9.6)11.1-14.1(22) × 2.5-4.2(5.5) mm. Androecium golden yellow; anthers remaining straight after dehiscence; outer whorls of stamens staminodial and fertile, five outermost stamens in median antesealous positions petaloid, narrowly spatulate, 9.4-13.4(20) × 2.2-3.7(5) mm, without anthers, second whorl of stamens all fertile. Capsule cup-shaped to cylindrical, 9.4-25 × 6-10 mm, base tapering; hypanthium 1-1.8 mm. Seeds 3-3.1 mm long; seed coat anticlinal cell walls straight, central papillae generally 5-8 per cell. See [Figure 6](#).

Distribution. Coahuila and Nuevo León at 1,860-2,050 m in Mexico, but 50-2,134 m in the United States ([Figure 4](#)). Populations have not been collected in the northwest-

ern Tamaulipas panhandle, despite being collected on the other side of the border in Texas, and we recommend targeted collections in this area to identify potential populations.

Habitat. Occurring in a myriad of soil types, include loam, gypsum, clay, sandy, and rocky soils, along roadsides, in grasslands, alluvial river banks, and hills.

Common name. Reverchon's blazingstar.

We recognize *M. hintoniorum* as a synonym of *M. reverchonii* following [Schenk & Hufford \(2020\)](#). *Mentzelia hintoniorum* was not compared to *M. reverchonii* in the original description ([Turner & Hempel 1995](#)), despite documented collections of *M. reverchonii* from Nuevo León that existed in MEXU at the time it was described. When evaluating the morphological variation among the two taxa, the only distinguishing character between them is the enlarged woody base of *M. hintoniorum*, which is a wound response similar to other species of section *Bartonia*, such as *M. nuda*, *M. rusbyi* Wooton, and *M. strictissima* ([Schenk & Hufford 2020](#)).

Mentzelia reverchonii is morphologically similar to *M. longiloba* var. *chihuahuensis* in the Mexican Chihuahuan Desert. The easiest way to differentiate between the two species is the larger leaf lobes that are pointed to the distal end of the upper leaves in *M. longiloba* var. *chihuahuensis* compared to the perpendicular lobes in *M. reverchonii* (note that lower leaves are both perpendicularly situated). Other features that help to differentiate the two species, despite overlapping characters, include

M. reverchonii being a larger plant, 1.6-8.5 dm tall (vs. to 3.2-5.5 dm tall in *M. longiloba* var. *chihuahuaensis*), lower primary leaves up to 54 mm long (vs. up to 110 mm long), and fruits that are up to 25 mm long (vs. up to 15[20.5] mm long).

Mentzelia saxicola H.J.Thomps. & Zavort. *Wrightia* 4: 22. 1968. Type: United States, Texas, Hudspeth Co., 3 mi W of Van Horn on US 10, 100 yards W of the Hudspeth-Culberson Co. line, 17 Aug 1964, *P.R. Atsatt 500* (holotype: US!; isotypes: LA! [×2]).

Biennial herbs, 1.8-3 dm tall. Stems primary aerial axis or axes arising at or above the soil surface, erect, straight; axillary branches on distal half of primary axis or along the entire primary axis. Leaves 21-44.4 × 5.8-11.2 mm, intersinus distance at widest point 1.6-3.4 mm; leaves on proximal third of primary axis oblanceolate to elliptic, pinnatilobate with 6-14 lobes 4.1-11.6 mm apart, lobes opposite or alternate, slightly angled towards leaf apex, regular, 2.4-3.9 × 1.8-3 mm with rounded or acute apices; leaves on distal third of primary axis oblanceolate, elliptic, or lanceolate with non-clasping bases, pinnatilibate with 4-12 lobes 5.3-10.5 mm apart, lobes opposite or alternate, slightly angled towards leaf apex, regular, 1.8-3.9 × 1.3-3.1 mm with acute apices. Petals light to golden yellow, narrowly spatulate, 11.7-16.6 × 3-4.8 mm. Androecium light to golden yellow; anthers twisted or remaining straight after dehiscence; outer whorls of stamens staminodial and fertile, five outermost stamens in median antepetalous positions petaloid, narrowly spatulate, 10.4-14.6 × 2-3.8 mm, generally without anthers, second whorl of stamens all fertile. Capsule cup-shaped, 7-11.9 × 5.7-8.2 mm, base rounded; hypanthium 0.8-1.4 mm. Seeds 2.7-3.3 mm long; seed coat anticlinal cell walls straight, central papillae generally 3-13 per cell. See [Figure 6](#).

Distribution. Endemic to the Chihuahuan Desert and occurring in eastern Chihuahua, Coahuila, and Zacatecas, at 850-1,843 m elevation in Mexico and 510-2,100 m in the United States ([Figure 4](#)).

Habitat. Sandy or gypsum-clay soils, occurring in arroyos, cliffs, roadcuts, and steep hillsides.

Common name. El Paso blazingstar.

Despite the two taxa being distantly related ([Schenk & Hufford 2011b](#)), differentiating between *M. saxicola* and *M. mexicana* can be difficult in some collections ([Thompson & Powell 1981](#)) because flower, stamen, and capsule sizes overlap greatly ([Figure 6](#)). Characters of the primary leaves differentiate between them best if the leaves are on the plant when it is collected. The primary leaves of *M.*

saxicola are generally smaller (and particularly narrower) than those of *M. mexicana*, 21-44.4 × 5.8-11.2 mm (vs. 24-82 × 11.7-29.1 mm), and the lobes tend to be smaller on proximal leaves, 2.4-3.9 × 1.8-3 mm (vs. 1.4-5.1 × 2.4-6.4 mm; [Figure 5](#)). Leaves along the main shoot of *M. mexicana* are dentate to pinnatilobate, but almost always are pinnatilobate in *M. saxicola*. The intersinus distance of primary leaves along the main stem are narrower in *M. saxicola* (1.6-3.4 mm) than they are in *M. mexicana* (3.4-18.8 mm). Secondary leaves (those positioned along secondary branches that tend to persist longer than primary leaves throughout the growing season) overlap too greatly to be of utility in differentiating the species and are often the only leaves remaining on the plant if collected late in the season.

[Schenk & Hufford \(2020\)](#) estimated 38-48 papillae per cell for *M. saxicola* periclinal surfaces of the seed coat, a range that is markedly different than 3-11 papillae per cell reported here ([Figure 2](#)). Their estimates were based on seeds collected from the type locality, which as [Thompson & Zavortink \(1968\)](#) noted, is a hybrid population. Although [Thompson & Zavortink \(1968\)](#) suggested that *M. saxicola* was hybridizing with *M. multiflora*, [Schenk & Hufford \(2020\)](#) determined that *M. multiflora* was a misapplied name in Texas and that *M. saxicola* was hybridizing with *M. procera* at the type locality. *Mentzelia procera* has 26-68 (32-47 in our estimates from Mexico populations) papillae per cell ([Figure 2](#)), and it is likely that the [Schenk & Hufford \(2020\)](#) number reflects an introgression of papillae number from *M. procera*, and that the true number is much closer to those estimated by [Thompson & Zavortink \(1968\)](#); reported as 3-5) and here. It is likely that Thompson & Zavortink happened upon seeds that did not possess introgressed traits, as [Schenk & Hufford \(2020\)](#) did in their work.

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Supplementary material

Supplemental data for this article can be accessed here: <https://doi.org/10.17129/botsci.2828>

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