Agave oteroi (Asparagaceae/Agavoideae)

a new species from North-central Oaxaca, Mexico

Abstract: A new species, *Agave oteroi*, is described from the Rio Hondo and side drainages near the Calapa bridge along Mexico Federal Highway 135D on the border of Puebla and Oaxaca, Mexico. Its vegetative and flower morphology place this species in the group *Marginatae*. *Agave oteroi* is compared to *A. kerchovei*, *A. quiotepecensis,* and *A. titanota* of the *Marginatae*. The addition of *Agave oteroi* brings the total number of taxa in the *Marginatae* to 30; the group ranges from Texas throughout much of mainland Mexico into Guatemala.

Keywords: *Agave*, Agavaceae, *Marginatae*, Oaxaca, Puebla, endemic

Introduction

The genus *Agave* is wholly New World consisting of roughly 276 named taxa (Smith & Figueiredo 2014). Baker (1877) was the first to divide the genus into subgenera based on inflorescence characteristics. He split the genus into three subgenera, *Euagave*, *Littaea*, and *Manfreda*, and Berger (1915) agreed with this assessment. However, Gentry (1982) did not consider the subgenus *Manfreda* as part of *Agave* and divided the genus into two subgenera: *Littaea* and *Agave* with each subgenus further divided into groups. The *Marginatae* group falls under the subgenus *Littaea* and, at the time Gentry produced his monograph, was comprised of 21 species. However, recently there have been seven new species described and reconsideration of the status of two others to bring the current total to 28 species and 1 subspecies. The seven new species are: *Agave arcedianoensis* and *A. chazaroi* (Vázquez-García 2007) from Jalisco; *A. doctorensis* (Hernández & Magallán 2014) from Queretaro; *A. garciae-mendozae* (Galván & Hernández 2002) from Hidalgo, Querétaro, and San Luis Potosí; *A. megalodonta* (García-Mendoza, et. al. 2019) from Oaxaca, Puebla, and Guerrero; *A. montium-sancticaroli* (García-Mendoza, et. al. 2007) from Tamaulipas; and *A. quiotepecensis* (García-Mendoza, et. al. 2019) from Oaxaca. *Agave convallis* Trelease has been resurrected (García-Mendoza 2011) and *A. obscura* Schiede has been changed to *A. horrida* Lemaire ex Jacobi subsp. *perotensis* Ullrich (Ullrich 1990).The distribution of *Marginatae* ranges from Texas in the southwestern United States south throughout much of mainland Mexico and Guatemala.

In 1984, seeds of an unidentified *Agave* were collected in the Sierra Mixteca by Felipe Otero and distributed under his collection number FO-076. The plants exhibited some variability in cultivation but were recognizable as different from any other known *Marginatae*. About twenty years later, seed labeled as *Agave titanota* from Rancho Tambor became available to cultivation, and the resulting plants have shown a wide diversity in leaf form and color. Although referred to as coming from Rancho Tambor (the type locality of *Agave titanota*), that the seeds actually came directly from that locality has not been confirmed; additionally, the collector referred to the plants known as *Agave* FO-076 without published analysis to be the same as *Agave titanota*, which has since raised questions about the parameters of *Agave titanota*. To research the relationship of *Agave* FO-076 and *A. titanota*, the authors made several trips (2004, 2016, 2017 & 2018) to Rancho Tambor (the type locality for *Agave titanota*), the Rio Hondo (where *Agave* FO-076 is found), La Huerta in the Rio Xiquila drainage (this could be considered the epicenter of *A. titanota* distribution), and the arid countryside between Rancho Tambor and La Huerta. Based on the data accumulated during this fieldwork, it is evident that *Agave* FO-076 is closely related to *A. titanota*, yet distinct morphologically, separated geographically, and inhabiting different substrates, necessitating the description of a new species.

[1]Southwest Center College of Social and Behavioral Sciences, University of Arizona, Tucson, AZ 85719. email: gregdstarr@gmail.com. [2] 210 N. Leoma Ct., Chandler, AZ 85225.

Description

Agave oteroi Starr & Davis **sp. nov.**

Type: México: Oaxaca: District of Coixtlahuaca, municipality of Tepelmeme, side drainage of the Rio Hondo, Sierra Mixteca, 18.15995 N, 97.25711 W, 1015 m. 15 January 2018. Starr 2018-011. (Holotype: ARIZ #436146; Isotypes MEXU). Additional specimens examined: **México:** Oaxaca: District of Coixtlahuaca, municipality of Tepelmeme, side drainage of the Rio Hondo, Sierra Mixteca, 18.15803 N, 97.25800 W, 1090 m, 15 January 2018, Starr 2018-010 (Paratype: ARIZ #436145; paratype to MO).

1. Classic form of *Agave oteroi* as seen at the type locality in a side drainage of the Rio Hondo near the Calapa bridge.

2. A small grouping of *Agave oteroi* near the type locality above the Rio Hondo.

Diagnosis: *Agave oteroi* appears to be closest to *A. titanota* from which it may be distinguished by its green, mostly obovate leaves, broader woody margin, and extremely pronounced woody margin below the terminal spine on the back of the leaves.

Plants multiannual, solitary or surculose, few-leaved. **Rosettes** open, 30–70 cm tall by 45–100 cm in diameter (Figs. 1 & 2). **Leaves** 20–50 per rosette, 25–45 cm long by 9–14 cm wide at the widest point above the middle, broadly obovate to oblanceolate, rigid, smooth to lightly asperous, thick and spongy, medium green to dark green, occasionally dull green, usually with a light yellow or greenish yellow central stripe, plane to deeply concave above and convex below; **leaf margin** straight, lightly undulate, to irregularly wavy, rarely deeply crenate, frequently cupped and in-rolled towards the tip, large and woody on abaxial surface (Fig. 3); **marginal teeth** 2–30 mm long, the larger teeth more numerous and thin to heavy, the smaller teeth towards the leaf base; teeth either very closely spaced or more remote, with or without smaller interstitial teeth, straight to variously flexed, reddish-brown to brown on new leaves, aging to gray on old leaves, frequently with deep bud prints on both surfaces; **terminal spine** 20–30 mm long with broad, shallow groove in lower one-half, groove narrowing and deepening, becoming rounded and awl-like, reddish-brown to brown on new leaves, aging to gray on old leaves. **Inflorescence** 2.4–3.5 m long (Fig. 4); **sterile peduncle** 1–2.5 m, comprising about one-half to two-thirds the overall length; lower **bracts** 105–120 mm long by 14–15 mm wide at the base tapering to 1–2 mm wide near the tip, becoming smaller 27–30 mm long by 3–5 mm wide at the base quickly tapering to 1 mm wide near the tip; **fertile spike** 0.9–1.75 m long, comprising about one-third to one-half the total length of the stalk, densely packed with yellow to yellowish green flowers, sometimes flushed with red or purplish-red. **Flowers** 2 per node, 36–46 mm long; **pedicels** 3–6 mm long; **flower buds** green; **tepals** green on the outside, occasionally lighter green, yellowish green, or yellow on the edges, yellow or light yellowish green on the inside when fully open, cup-shaped to narrowly campanulate at anthesis; **ovary** 15–18 mm long, neck 2–5 mm long; **tube** 2–3 mm long by 4–5 mm wide; **tepals** 17–20 mm long by 5–8

3. The back of a leaf of *Agave oteroi* showing the typically large, woody margin below the terminal spine.

4. The inflorescence of *Agave oteroi,* compare to Fig. 8 showing the inflorescence of *A. kerchovei* and Fig. 9 the inflorescence of *A. quiotepecensis*.

mm wide; **filaments** 40–55 mm long, yellow or green; **anthers** yellow or greenish yellow.

Phenology

Agave oteroi blooms from December to February with fruit setting from February to June.

Etymology

The species name commemorates Felipe Otero who first collected seed of this striking agave.

Distribution and Habitat

Agave oteroi (Figs. 3–6) is found in the Sierra Mixteca in both Puebla and Oaxaca, along the Rio Hondo and its principal side drainages, from near the Calapa bridge, west and south to near the Santa Lucia bridge along Mexico Federal Highway 135D. The agaves are found growing in shallow to deep soil on open, exposed slopes, and rocky outcrops along the embankment of the river and its side drainages. The elevation range is from 975–1160 m. The region is tropical deciduous forest, and associated plants include: *Acacia* sp., *Agave macroacantha*, *Agave kerchovei*, *Agave titanota*, *Bursera* sp., *Ceiba parvifolia*, *Cephalocereus columna-trajani*, *Cnidoscolus tubulosus*, *Hechtia* sp., *Jatropha* sp., *Mammillaria albilanata*, *Myrtillocactus geometrizans, Neobuxbaumia tetetzo*, *Opuntia pubescens*, *Parkinsonia praecox*, and *Pilosocereus chrysacanthus*.

Taxonomy

Of the *Marginatae*, Gentry (1982) wrote, "the flowers are so uniform as to be of little or only secondary use in the delineation of species." He went on to say that the evolution of flowers has been very conservative while leaf and inflorescence structure have greatly diversified. This uniformity of flowers leaves the agave taxonomist with vegetative characters including leaf shape, thickness, color, and armature, plant size, rosette density, and inflorescence structure to use in determining species. Because some leaf characters are not always apparent on herbarium specimens, it is always best to visit the type locality of a species to set a baseline for comparisons.

García-Mendoza (2011) listed seven species of *Agave* in the group *Marginatae* occurring in the Valle

5. *Agave oteroi* showing the broadly obovate leaf shape that is commonly seen on plants at the type locality.

6. Several *Agave oteroi* showing the consistent green leaf color.

de Tehuacán-Cuicatlán: *A. angustiarum* Trelease, *A. convallis* Trelease, *A. ghiesbreghtii* Lemaire ex Jacobi, *A. kerchovei* Lemaire, *A. peacockii* Croucher, *A. titanota* Gentry, and *A. triangularis* Jacobi. García-Mendoza & S. Franco (2019) recently described *Agave quiotepecensis,* which occurs near Santiago Quiotepec in the Valle de Tehuacán-Cuicatlán. *Agave angustiarum*, *A. ghiesbreghtii*, and *A. triangularis* are distinct by virtue of their narrower, more deltoid to triangular leaves and freely offsetting habit so are not compared to *Agave oteroi* here. *Agave convallis* is distinct based on the dense rosettes of lanceolate to ovate-lanceolate leaves and smaller teeth. *Agave peacockii* is presumed to be of hybrid origin with *A. kerchovei* as one parent and *A. marmorata* as the other and as such, it is distinctive and not easily confused with any other species. *Agave oteroi* grows syntopically[2] with *A. kerchovei* and *A. titanota s.s.* near Calapa bridge, with a variety of hybrids with all three species resulting in a hybrid swarm; therefore, *A. oteroi* is compared to both.

[2] Syntopy is a specific form of sympatry in which two or more species occur in the same habitat at the same time, often used in cases with closely-related species that may hybridize.

Because *A. quiotepecensis* resembles *A. oteroi,* it is also compared. The distribution of these four agave taxa is shown in Map 1.

Agave oteroi is easily separated from *A. kerchovei* based on leaf shape (Figs. 1 & 7) and inflorescence (Figs. 4 & 8). The leaves of *A. oteroi* are ovate, ovate-lanceolate, broadly obovate, or broadly oblanceolate with the widest point at or above mid-blade, while those of *A. kerchovei* are medium green to dark green, sometimes with a bronze tinge, long linear-triangular to triangular-lanceolate with the widest point towards the base. The inflorescence on *Agave oteroi* is shorter with the fertile section consisting of yellow to lightly greenish yellow flowers, while the inflorescence on *A. kerchovei* is taller with the fertile section consisting of greenish or yellowish flowers, frequently tinged with red, or the flowers nearly all reddish-purple (Fig. 8). *Agave oteroi* differs from *A. quiotepecensis* by a combination of plant size, leaf size and shape, and inflorescence. *Agave oteroi* is a smaller, more compact plant than *A. quiotepecensis* (30–70 cm tall by 50–100 cm across versus 55–115 cm tall by 115–160 cm across). The inflorescence on *A. oteroi* (Fig. 4) is shorter with the sterile peduncle comprising one-half to two-thirds

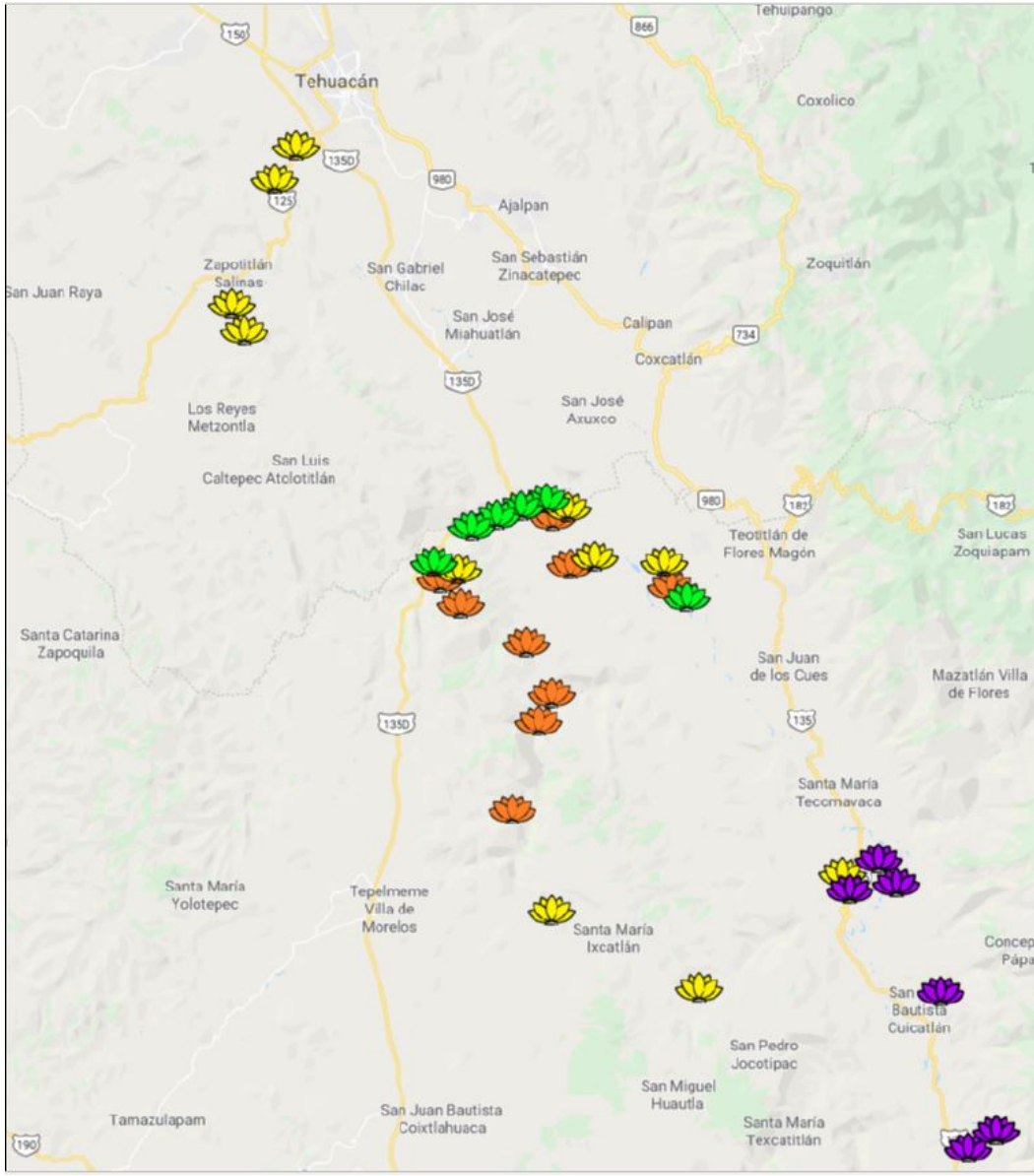
7. *Agave kerchovei* showing the long linear-triangular leaf shape and lack of marginal teeth in the upper portion of the leaf; compare to Fig. 1 showing the compact, obovate leaf shape commonly seen on *Agave oteroi*.

8. The tall, narrow inflorescence of *Agave kerchovei* showing the reddish tinged flowers and smaller, sparser bracts; compare to Fig. 4 showing the relatively thicker fertile section and the noticeably longer, denser bracts.

9. The inflorescence of *Agave quiotepecensis* showing the fertile section starting just above the leaf tips and the very short sterile peduncle.

the total length, compared to the inflorescence on *A. quiotepecensis,* which has a very short sterile peduncle and long fertile section comprising up to 90 percent of the total length (Fig. 9); this difference in inflorescence is very distinctive in flowering plants despite not being identified as such in the original description (García-Mendoza & S. Franco 2019).

Although *Agave oteroi* (Figs. 3–6) has a leaf shape that can look like that of *A. titanota* (Figs. 10 & 11), the leaf color of each is distinctive. *Agave oteroi* leaves are dull pale green to dark green, rarely bright green, and most commonly with a noticeable lighter yellowish green mid-stripe. Leaves of *Agave titanota* are glaucous white to blue-white, very rarely blue-green and most commonly lacking a noticeable mid-stripe. *Agave oteroi* occurs in alluvial, shallow, and moderately deep soils, and occasionally on rocky outcrops of sandstone, or rarely limestone, along the Rio Hondo and its side drainages with the center of distribution near Puente Calapa at the Puebla-Oaxaca border. *Agave titanota* grows exclusively on limestone cliffs and outcrops from Rancho Tambor (the type locality) south to La Huerta in the Rio Xiquila (sometimes spelled Jiquila) drainage and reaching its southernmost point near Puerto Mixteco, with outlier populations near the Calapa bridge



Map 1. Distribution of *Agave oteroi* and similar species. *A. oteroi*, *A. titanota*, *A. kerchovei* and *A. quiotepecensis.*

to the north, the Santa Lucia bridge to the west, and Cerro Tepetzezonga to the east (Map 1).

Discussion

The center of distribution for *Agave oteroi* (Map 1) is along Mexico Federal Highway 135D, and the Rio Hondo and its principal side drainages from east of the Calapa bridge west and south to near the Santa Lucia bridge. Plants grow on the open, exposed slopes, and rocky ledges and outcrops above the river bottom between 975–1160 m elevation. It is roughly 16 km by trail from the south side of the Calapa bridge to Rancho Tambor. The trail initially drops roughly 20–25 m in elevation from the road before climbing about 40 m, at which point it levels off before starting a gradual climb to Rancho Tambor. Within the first 500 meters from the highway, *Agave oteroi* disappears and is not seen again even upon reaching Tambor, where thousands of *A. titanota* are seen on the limestone that makes up the primary substrate in the canyon. In addition to the thousands of *Agave titanota*, there are a handful of *A. kerchovei* and the rare hybrid between the two. *Agave titanota*

10. A young *Agave titanota* showing a leaf shape similar to *Agave oteroi* yet the classic blue-white color lacking a central stripe.

11. An older *Agave titanota* on the trail to La Huerta with more elongated leaves having grown out of the juvenile stage of shorter, more obovate shape.

12. A mass of *Agave titanota* on the limestone cliffs near La Huerta which is the center of distribution.

as originally described by Gentry (1982) was known only from Rancho Tambor, which is not a ranch at all but a watering spot for goats as they are herded through the arid countryside. Gentry speculated that exploration of the area would likely result in the discovery of more *A. titanota* populations, and that was exactly the case. While the *Agave titanota* distribution ranges primarily from Rancho Tambor in the north to at least La Huerta along the Rio Xiquila (Jiquila) in the south, the center of distribution is within the Xiquila river drainage where thousands of plants can be seen growing on the steep, nearly vertical limestone walls (Fig. 12). There are outlier populations to the north along the Rio Hondo at the Calapa bridge, to the west on Cerro Verde and near the Santa Lucia bridge, to the south at Puerto Mixteco, and to the east at Cerro Tepetzezonga and are found between 1100–1830 m elevation. Wherever this species is found, the plants are always on the limestone and not in soil, while other species of *Marginatae* occur in the shallow or deep soils of slopes and ledges.

13. Putative hybrid between *Agave oteroi* and *Agave kerchovei* showing an elongated leaf more characteristic of *Agave kerchovei* and the marginal teeth present nearly to the tip that is more indicative of *Agave oteroi*.

14. Putative hybrid between *Agave titanota* and *Agave oteroi*.

The population of agaves near the Calapa bridge consists of at least three species of *Marginatae*: *A. kerchovei, A. oteroi,* and *A. titanota.* While *Agave oteroi* is the most numerous species found there, many are presumed hybrids between *A. oteroi* and *A. kerchovei* (Fig. 13), *A. oteroi* and *A. titanota* (Fig. 14), and *A. kerchovei* and *A. titanota* (Figs. 15 & 16), resulting in a hybrid swarm with many intermediate forms. Although there are similarities between *A. oteroi* and *A. titanota*, their distributions only overlap at the perimeter of the range of *A. titanota* (Map 1) where the latter's impact seems to be quite low; the genetic exchange is overwhelmed by the sheer numbers of *A. oteroi*. On the other hand, there are relatively few *A. kerchovei* within the main distribution area of *A. oteroi*, yet the genetic exchange appears to be more pronounced as witnessed by the larger amount of phenotypic variation of characters between *A. oteri* and *A. kerchovei* exhibited in the populations with overlap. Conversely, the genetic exchange between *A. kerchovei* and *A. titanota* is somewhat limited due to their relatively low numbers found at the *A. oteroi* population, but there are clear examples of hybridization occurring (Figs 15, 16, & 17). Variation manifests itself more profusely in plants grown in cultivation where there is not the same pressure on survival as there is in the harsh, arid environment in the Tehuacán-Cuicatlán region of northern Oaxaca and southern Puebla, and where the differences in substrates that may impact distribution and phenotypic variation are eliminated. The wide range of cultivated morphological forms and associated loose nomenclature has led to the speculation that *Agave titanota* and *Agave* FO-076 (=*A. oteroi*) are but one variable species and has led to universal confusion regarding true species limits. However, a thorough examination of the populations involved in the wild reveals three distinct species (*A. kerchovei, A. oteroi, A. titanota*) that maintain their individual identities when not growing syntopically.

The areas of overlap and hybridization may result when historically distinct substrates or other habitat variables come together locally because of changes in climate or other historical factors. Areas of secondary contact that result in hybridization demonstrate that the evolutionary mechanisms that resulted in distinct lineages did not include incompatibility of pollination and do not necessarily indicate close relationship. That distinct species of *Agave* can hybridize in areas of overlap but maintain their distinctive characteristics outside of these hybrid zones is not novel (e.g., *Agave* ×*arizonica*, *Agave* ×*glomeruliflora*, *Agave* ×*peacockii*). Based on flower morphology and other similarities, *A. oteroi* and *A. titanota* are clearly closely related and might even be considered sister species; however, consideration of distribution, substrate, and phenotypic appearance in wild populations demonstrates these two taxa are on separate evolutionary

15. Putative hybrid between *Agave titanota* and *Agave kerchovei* showing the open rosette and longer leaves indicative of *Agave kerchovei* and the characteristic leaf color of *Agave titanota*.

pathways and have reached a level of divergence best represented by separate species.

Acknowledgements

The lead author would like to thank Carol for her never-ending support of these endeavors, and the second author would like to similarly thank Jacob. Also, thank you to Jeff Chemnick for his help in the field and for his language skills when securing guides, garnering permission to travel on community land, and solving general miscommunications. Thank you to Silvia Hortensia Salas Morales for securing the official federal collecting permit SEMARNAT-03-058-A. Many thanks to the following for funding this ongoing research project: Tucson Cactus and Succulent Society, Cactus and Succulent Society of America, Central Arizona Cactus and Succulent Society, Tim Gregory Agave Research Project. I extend my gratitude to the Tepelmeme Villa de Morelos and Santiago Quiotepec communities for their assistance and permission for collecting voucher specimens. A belated thank you to Jeff Chemnick for suggesting the species name for the previously published *Agave cremnophila*.

16. Putative hybrid between *Agave titanota* and *Agave kerchovei* showing the tall, narrow inflorescence with reddish tinged flowers indicative of *Agave kerchovei* and the characteristic leaf color of *Agave titanota*.

Literature cited

Key to Species

1. Inflorescence ratio of fertile section to overall length of stalk 0.87–0.93 ..... *A. quiotepecensis*
1. Inflorescence ratio of fertile section to overall length of stalk 0.33–0.72 2
2. Leaves long linear-lanceolate to triangular-lanceolate; teeth lacking in the upper 1/3–1/2 of the leaf; leaf length 60–125 cm long ..... *A. kerchovei*
2'. Leaves linear-ovate to deltoid-ovate, ovate, ovate-lanceolate, broadly obovate, or broadly oblanceolate; leaf length to width ratio 2.5–3.9 3
3. Leaves liner-ovate, deltoid-ovate, broadly lanceolate or spatulate; leaf color glaucous white to blue-white, rarely blue-green, very rarely with a faint lighter blue-green central stripe ..... *A. titanota*
3'. Leaves ovate, ovate-lanceolate, broadly obovate to broadly oblanceolate; leaf color dull green, pale green to dark green, rarely bright green, frequently with a lighter green central stripe ..... *A. oteroi*

Table 1. Vegetative and floristic comparison of *Agave oteroi* and its four near relatives in the Valle de Tehuacán-Cuicatlán.

	Agave oteroi	*A. kerchovei*	*A. quiotepecensis*	*A. titanota*
Height	30–70 cm	60–100 cm	55–115 cm	50–95 cm
Width	50–100 cm	100–150 cm	115–160 cm	75–140 cm
# of leaves	18–30	30–50	15–25	20–30
Leaf color	Dull pale green to dark green, rarely bright green, frequently with a lighter green central stripe.	Dark green, rarely with a faint, light green mid-stripe.	Bright, shiny green to dark green, occasionally dull, glaucous blue-green, frequently flushed with red or purplish red on one or both sides during the dry season, usually with a light yellow or greenish yellow mid-stripe.	Glaucous white to blue-white, very rarely blue-green, and rarely with a faint light blue-green mid-stripe.
Leaf shape	Ovate, ovate-lanceolate, broadly obovate, or broadly oblanceolate	Long linear-triangular to triangular-lanceolate.	Ovate-lanceolate.	Linear-ovate to deltoid-ovate.
Leaf length	20–45 cm	60–125 cm	45–75 cm	35–55 cm
Leaf width	8–14 cm	5–12 cm	12–17 cm	12–14 cm
Leaf margin	Undulate to crenate, broadly corneous, very widely corneous at apex below terminal spine.	Straight, narrowly corneous.	Undulate, narrowly to broadly corneous on back.	Straight, undulate to crenate, narrowly to broadly corneous
Teeth	Small to large and wide, 2–18 mm long x 1–8 mm wide, variously curved and flexed.	Small to medium, few and remotely spaced, straight to slightly curved, lacking in upper portion.	Small to large, 1–13 mm long, straight to variously curved.	Small to medium, numerous and closely spaced to fewer and more widely spaced, straight to curved.
Terminal spine	2–3 cm long, deeply grooved to rolled, very widely corneous below, particularly on the abaxial surface.	3–6 cm long, deep groove that is broad or narrow.	2–4 cm long, broadly and shallowly grooved becoming rounded at tip.	2–4 cm long, with short, deeply in-rolled groove.
Inflorescence	2.5–3.5 m	2.5–5 m	3–4 m	2–4 m
Sterile peduncle	1–2.5 m	1.3–1.6 m	0.3–0.5 m	1–2 m
Fertile spike	1–1.75 m	1.2–3.4 m	2.6–3.7 m	1–2 m
Fertile/overall ratio	0.33–0.50	0.48–0.68	0.87–0.93	0.50
Floral bracts	11–13 cm	Not available	8.5–11.5 cm	Not available
Flower color	Yellow to greenish yellow, rarely tinged with red at tepal tips.	Greenish or yellowish, frequently tinged with red, or nearly all reddish-purple.	Green, lighter green on tepal edges and inside.	Yellow, rarely flushed with lavender or red on tepal tips.
Pedicel length	4–6 mm	1–3 mm	4–13 mm	2–15 mm
Flower length	39–43 mm	38–54 mm	36–53 mm	36–52 mm
Ovary length	15–18 mm	18–21 mm	13–23 mm	11–25 mm
Neck length	3–5 mm	3–6 mm	3–7 mm	3–6 mm
Tube length	2–3 mm	2–6 mm	1–3 mm	2–4 mm
Tube width	4–5 mm	7–10 mm	3–7 mm	6–10 mm
Tepal length	17–20 mm	15–21 mm	15–24 mm	17–25 mm
Tepal width	5–8 mm	6–9 mm	5–9 mm	4–10 mm
Filament length	40–53 mm	40–50 mm	37–65 mm	36–70 mm

Baker, J. G. 1877. *The Gardener's Chronicle & Agricultural Gazette* 7(1): 527.

Berger, A. 1915 *Die Agaven: Beiträge zu einer Monographie*. 288 pp.

Galván, R. V., & L. G. Hernández S. 2002. *Agave garciae-mendozae*, a new species from central Mexico. *Cactus and Succulent Journal of America* 74(4):188–191.

García-Mendoza, A., C. Jacques-Hernández, y A. Salazar Bravo. 2007. Una Nueva Especie de *Agave*, subgénero *Littaea* (Agavaceae) de Tamaulipas, México. *J. Bot. Res. Inst. Texas* 1(1):79–84.

García-Mendoza, A. 2011. Agavaceae. *Flora del Valle de Tehuacán-Cuicatlán*. Fascículo 88, Instituto de Biología Universidad Nacional Autónoma de México. 98 pp.

García-Mendoza, A. J., I. S. Franco Martínez & D. Sandoval Gutiérrez. 2019. Cuatro especies nuevas de *Agave* (Asparagaceae, Agavoideae) del sur de México. *Acta Botanica Mexicana* 126:e1461. DOI: 10.21829/abm126.2019.1461

Gentry, H. S. 1982. *Agaves of Continental North America*. University of Arizona Press, Tucson, Arizona, USA. 670 pp.

Hernández-Sandoval, Luis and Fabiola Magallán-Hernández. 2014. *Agave doctorensis* (Agavaceae), a new species from Sierra El Doctor, Querétaro, México. *Brittonia* 67(1): 1-4.

Smith, Gideon and Estrela Figueiredo. 2014. State of our knowledge of online resources of the types of names of Agave L. (Agavaceae/Asparagaceae) with a list of names attributed to William Trelease with notes on types, online resources and etymology. *Phytotaxa* 170 (4): 221–249.

Trelease, William. 1920. Amaryllidaceae. In: Standley, P.C., Trees and Shrubs of Mexico. *Contributions to the U.S. National Herbarium*. 23:105–142.

Ullrich, Bernd. 1990. *Agave obscura* Schiede y *Agave horrida* Lemaire ex Jacobi ssp. ***perotensis*** Ullrich ssp. nov. *Cactáceas y Suculentas Mexicanas* 35(4): 80.

Vázquez-García, A. 2007. Agaves del Occidente de México, Universidad de Guadalajara, Guadalajara, México. 221 pp.