

AGAVE × MADRENSIS (ASPARAGACEAE), A PUTATIVE HYBRID FROM THE
SIERRA MADRE ORIENTAL, MEXICO

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ABSTRACT

A putative hybrid in *Agave* is described and illustrated from southern Nuevo Leon state in Mexico. **Agave × madreensis** is believed to be a natural, crossbreeding hybrid between *Agave gentryi* and *Agave lechuguilla*. A morphometric analysis between the parental species and the hybrid was created to assess the parentage of the individuals in question. A multivariate analysis (MANOVA) and a discriminant analysis are used to support the hypothesis of the existence of a natural occurrence of this hybrid. Plant illustrations are included.

KEY WORDS: *Agave × madreensis*, Asparagaceae, Nuevo León, México, hybridization, morphometric analysis

RESUMEN

Se describe un supuesto híbrido en *Agave* con material proveniente del sur del estado de Nuevo León, México. **Agave × madreensis** se cree es un cruzamiento natural entre *Agave gentryi* y *Agave lechuguilla*. Se realizó un análisis morfométrico de las especies involucradas para evaluar la posible relación en el parentesco del híbrido. Un análisis multivariado (MANOVA) y uno discriminante se usan para apoyar la hipótesis de la existencia de un híbrido natural intermedio entre las especies parentales. Se incluyen ilustraciones de la planta.

Agave is a genus endemic to America. It has approximately 200 species and 247 taxa, of which 75 per cent are found in Mexico, most of them growing in arid and semiarid regions (García 2002). Natural hybridization is not rare in *Agave* (Gentry 1967), as shown below. Hybrids are known in elements of the same subgenus, as in *A. nickelsiae* Gosselin and *A. lechuguilla* Torr., both of subgenus *Littaea* (González et al. 2011), but are more frequent between species of different subgenera, as in *A. marmorata* Roezl (subg. *Agave*) and *A. kerchovei* Lem. (subg. *Littaea*) of central Mexico (Valverde et al. 1996), *A. asperrima* Jacobi (subg. *Agave*) and *A. nickelsiae* Gosselin (subg. *Littaea*) (Gentry 1982; González et al. 2011) and *A. asperrima* Jacobi (subg. *Agave*) and *A. victoria-reginae* T. Moore (subg. *Littaea*) both from northern Mexico (Verduzco et al. 2009). Most of them were described at the specific level. Several putative hybrids are also known from the southwestern United States and include *A. × arizonica* Gentry & J.H. Weber, *A. × ajoensis* W.C. Hodgs. and probably *A. schottii* Engelm. var. *treleasei* (Toumey) Kearney & Peebles (Reveal & Hodgson 2001).

Sixteen taxa are reported to occur in Nuevo Leon (Villarreal & Estrada 2008). A recent collection from the Sierra Madre Oriental of Mexico included a specimen of *Agave* that is morphologically unlike any known species. Plants with large leaves and a racemose inflorescence led us to the idea of hybridization between *Agave gentryi* and *A. lechuguilla*, the only two species growing in the area. As both species are frequent in the mountains of north and central Mexico and the probability of a potential hybrid between them is present, the hybrid deserves to be named and recognized as a taxonomic element. A statistical analysis of morphometric traits was

TABLE 1. Means and standard deviations of the characters used in the morphometric study.

	<i>A. lechuguilla</i>	<i>A. gentryi</i>	putative hybrid
Plant diameter (d)	68.600±5.621	248.100±18.935	131.667±10.408
Leaf length (ll)	40.900±4.483	84.800±9.601	65.000±15.000
Leaf width (lw)	2.960±0.212	16.500±1.958	10.333±1.528
Number of leaves (nl)	39.200±5.116	48.500±6.346	49.000±7.937
Spines distance (sd)	1.840±0.196	3.380±0.319	2.467±0.503
Number of spines (ns)	15.400±2.171	30.300±3.622	14.667±2.517
Terminal spine length (tsl)	1.560±0.232	7.270±0.460	3.333±0.577
Valveredian distance (vd)*	2.390±0.614	12.000±3.197	9.667±1.528
Inflorescence length (il)	1.170±1.526	2.250±3.631	5.333±4.726
Inflorescence width (iw)	4.700±6.075	42.300±68.131	23.333±20.817

*valveredian distance = distance between the upper spine and the terminal spine

TABLE 2. Means and standard deviations of the ratios used in the morphometric analysis.

	<i>A. lechuguilla</i>	<i>A. gentryi</i>	putative hybrid
Plant diameter/number leaves	4.530±0.695	8.288±1.087	9.078±0.885
Leaf length/width	13.853±1.602	5.211±0.889	6.241±0.599
Spines number/distance	8.395±1.016	9.097±1.787	5.972±0.293
Terminal spine length/ valveredian distance*	0.701±0.233	0.669±0.277	0.293±0.346
Inflorescence length/width	1.358±1.785	0.184±0.297	1.431±1.344

*valveredian distance = distance between the upper spine and the terminal spine

used to test the hypothesis that a hybrid should be expected to be morphologically intermediate between the putative parents.

MATERIALS AND METHODS

Ten plants belonging to each parental species were randomly selected in two populations in the area, and three plants of the putative hybrid. Three leaves were evaluated and the average computed for each individual. The morphometric measures are: rosette diameter (d), number of leaves (nl), leaf length (ll), leaf width (lw), number of spines by side (ns), distance between spines (ds), terminal spine length (tsl), and distance between the last and the terminal spine—valveredian distance (vd). The length (il) and width (iw) of three inflorescences of parental and putative hybrid were included.

The data were statistically evaluated by a discriminant analysis using a multivariate analysis (MANOVA) with the Wilk's test (Everitt & Hothorn 2010), included in the PAST software, version 2.01 (Hammer & Harper 2006).

RESULTS

Means and standard deviations of the characters used in the morphometric study are shown in the Table 1. Five character means (leaf length, leaf width, number of leaves, valveredian distance and inflorescence length) are closer to *Agave gentryi*, while four (plant diameter, spines distance, number of spines and the terminal spine length) are for *A. lechuguilla*; and one (inflorescence width) is intermediate between both species. Seven means of the putative hybrids lay between the means of the parental species, and three (number of leaves, number of spines and inflorescence length) are slightly exceeded from a parental mean.

The ratios and standard deviation used in the discriminant analysis are shown in the Table 2. The plot derived from the analysis (Fig. 1) includes three groups clearly separated in the discriminant space. It can be concluded that the ratios of *A. lechuguilla* and *A. gentryi* are different and the putative hybrid is intermediate, according the Wilk's test ($p < 0.001$) with a Wilk's Lambda = 0.01692. However, direct breeding studies are

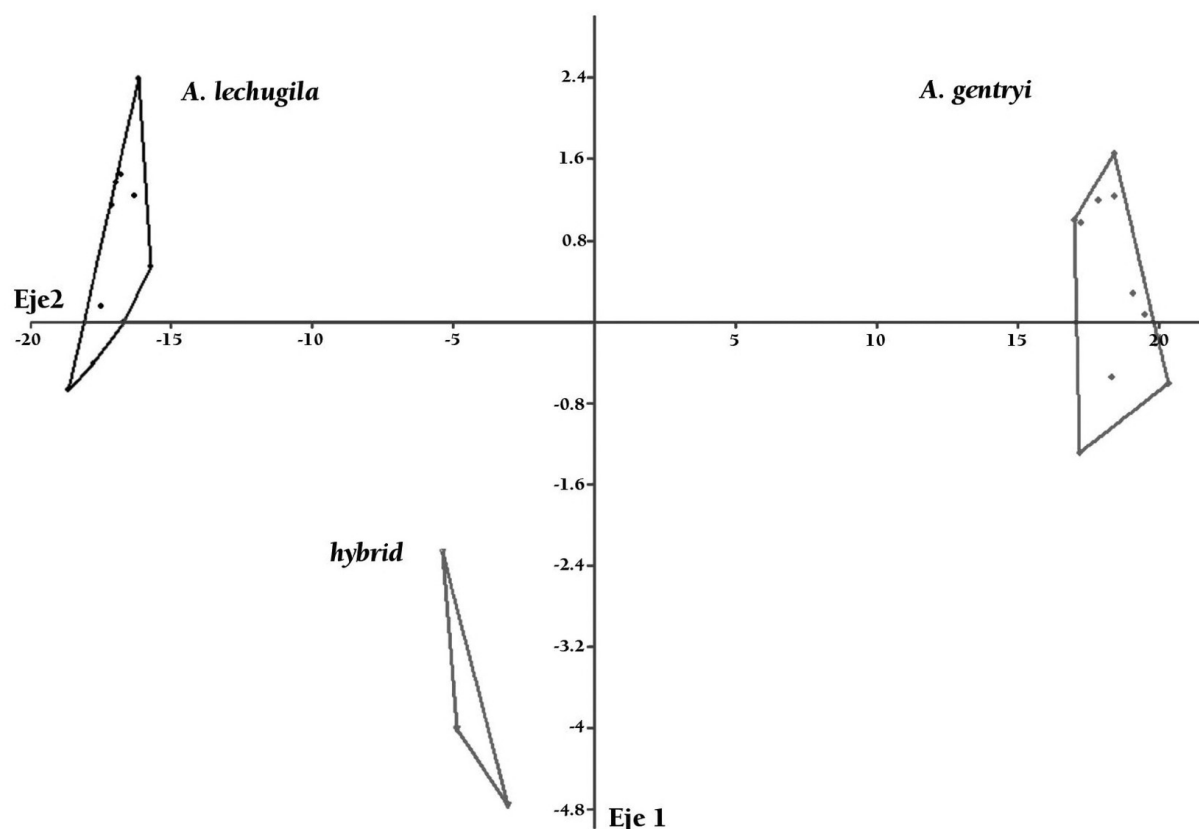


FIG. 1. Plot that shows the results of the use of the Discriminant analysis applied to the five morphometric ratios listed in the Table 2.

needed for more conclusive evidence. As the two parental species belong to different subgenera we are considering that the plant is a putative intersubgeneric hybrid and is described as a new taxonomic entity.

Agave × madrensis Villarreal, A. Ramírez, & A.E. Estrada, hybrid nov. (Figs. 2–3). TYPE: MÉXICO. NUEVO LEÓN: Municipio de Galeana, cerro El Potosí, camino a las antenas. Bosque esparcido de *Pinus hartwegii* y encinar enano, 2654 m, 21 Aug 2012, A. Ramírez 106 (HOLOTIPO: MEXU; ISOTYPES: ANSM, CFNL, ENCB, TEX; to be distributed).

Similar to *Agave montium-sancticaroli* García-Mend., but with lanceolate leaves 50–80 cm long, inflorescence 7–9 m long with 80–150 floriferous branches and distribution in the Sierra Madre Oriental.

Perennial single plants, acaulescent, moderately suckering; rosettes hemispheric, openly spreading, 120–140 cm wide, 80–100 cm high. Leaves 40–55 per plant, lanceolate, concave toward apex, 50–80 cm long, 9–12 cm wide, ascending, glaucous to green-yellowish when mature, the base slightly enlarged, the apex acuminate, the margins straight, the terminal spine 3–4 cm long and 6–7 mm wide at the base, brown, the marginal teeth 12–17 pairs, straight to slightly retrorse, 2–3 cm apart, 4–7 mm high, brown. Flowering stalk 7–9 m tall, the inflorescence a racemose panicle, congested, largely oblong (fusiform), 4–5 m long and 30–40 cm wide, the peduncles 8–12 cm diameter, bracteates; bracts long triangular, 20–28 long, 5–6 cm wide at the base, chartaceous, the margins entire, the apex with a short and weak spine; branches of the inflorescence 15–20 cm long, spaced 10–15(–20) cm apart, green-purple; bracts like those of the peduncle, largely triangular, 12–18 cm long. Flowers 18–26 per umbel, 5–6 cm long, narrowly campanulate, succulent, green-yellowish, flushed with purple; pedicels 4–12 mm long; tepal lobes largely triangular, 18–20 mm long, 3–5 mm wide, succulent, the outer ones slightly larger than the inner, the margins involute, the apex cucullate; floral tubes 5–6 mm long, 7–10 mm diameter distally, slightly sulcate; filaments 45–55 mm long, inserted above mid-tube (3–4 mm), yellowish distally flushed with purple; anthers dorsifixed, 20–25 mm long, 2 mm wide, yellow; ovary cylindric, 20–26 mm long, 6–8 mm wide, green, the neck 2–4 mm long, the style 5–6 cm long, the stigma



FIG. 2. *Agave* × *madrensis*. A. Flowering plant. B. Rosette of leaves. C. Inflorescence close-up. D. Close-up of flowers and pollinators. Photos by A. Ramirez G.

claviform, trilobate. Capsules oblong to slightly ovate, 4–6 cm long and 20–25 mm wide, rostrate, dark brown; seeds lunulate, flattened, 5–6 mm long, 4–5 mm wide, black.

Distribution and ecology.—The plant grows in southern Nuevo Leon state on steep slopes in limestone soils, at 2500 to 2700 m. The area is dominated by a dwarf oak community, mainly of *Quercus greggii*, and other shrubs such as *Arctostaphylos pungens*, *Arbutus xalapensis*, *Ceanothus buxifolius*, *Pinus culminicola*, *Cercocarpus* sp., and *Agave gentryi*, with sparse forest components of *Pinus hartwegii* and *Pseudotsuga menziesii*. Additional immature specimens believed to be conspecific were observed, considering a probable wider distribution, possibly tracking the occurrence of *Agave gentryi* in the Sierra Madre Oriental. Four plants were found in the area, all of them close to a roadside, as might be expected of an association with disturbance. The incidence of hybrids in disturbed environment was discussed by Grant (1971).

Phenology.—Flowering during the summer, fruiting at the end of summer and beginning of autumn.

Etymology.—The specific epithet refers to the Sierra Madre Oriental where the plant is distributed.

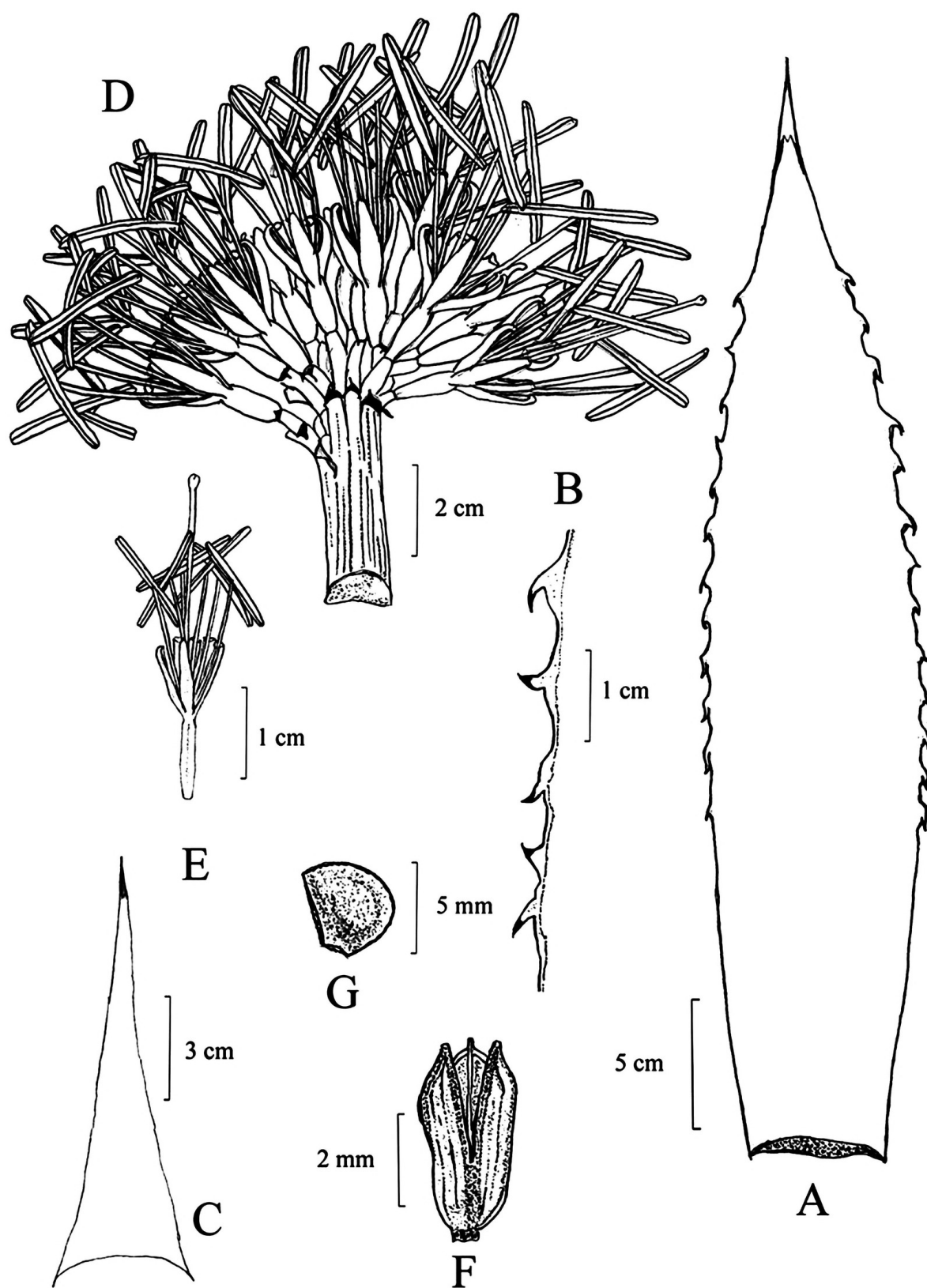


FIG. 3. *Agave × madrensis*. A. Leaf. B. Leaf margin. C. Bract. D. Cluster of flowers. E. Flower. F. Fruit. G. Seed.

TABLE 3. Comparison of select character states of *Agave* × *madrensis*, *A. gentryi*, *A. lechuguilla*, and *A. montium-sancticaroli*.

Character	<i>A. × madrensis</i>	<i>A. gentryi</i>	<i>A. lechuguilla</i>	<i>A. montium-sancticaroli</i>
Leaf length	50–80 cm	60–100 cm	25–50 cm	100–120 cm
Leaf shape	lanceolate	triangular	linear-lanceolate	linear-lanceolate
Leaves/plant	40–55	30–45	30–45	50–80(100)
Flower stalk	7–9 m	3–5 m	2.5–3.5 m	5.5–7 m
Infl. length	$\frac{3}{5}$	$\frac{1}{3}$ – $\frac{1}{2}$	$\frac{1}{3}$ – $\frac{1}{4}$	$\frac{1}{2}$ – $\frac{3}{5}$
Infl. shape	fusiform	elliptic	cylindrical	fusiform
Infl. branches	80–150	16–20	80–120	60–80(140)
Branch length	15–20 cm	50–80 cm	4–6 mm	8–13 cm
Flower length	50–60 mm	70–90 mm	30–45 mm	40–50(–60) mm
Distribution	SMO	SMO	CDR	LLCG y SSC

SMO = Sierra Madre Oriental, CDR = Chihuahuan Desert Region, LLCG = Llanura Costera del Golfo, SSC = Sierra de San Carlos.

The plants exhibit an inflorescence morphology which is intermediate between the broad panicles of subg. *Agave* with many-flowered partial inflorescences (branches), and the narrow-elongate, spike-like inflorescences of subg. *Littaea* with few-flowered partial inflorescences (branches), as shown in the Table 3. The plant seems to represent a natural hybrid between a member of subg. *Agave* (the sympatric *A. gentryi* B. Ullrich) and a member of subg. *Littaea* (*A. lechuguilla* Torr.).

The plant is morphologically similar to *A. montium-sancticaroli* García-Mend. from Tamaulipas (García et al. 2007). Both have a similar racemose paniculate inflorescence, but *A. × madrensis* differs by the shape and size of the leaves (see Table 3), lack of small interstitial teeth between the large teeth found in *A. montium-sancticaroli*, peduncular bracts 20–26 cm long (vs. 11–16 cm) (Table 1), and occurring in the Sierra Madre Oriental (vs. between Llanura Costera del Golfo and Sierra de San Carlos), at 2500–2700 m (vs. 150–800 m) in forest to oak scrubland habitat (vs. tamaulipan thornscrub habitat). *Agave montium-sancticaroli* is published at the rank of species, but exhibits intermediate inflorescence morphology and might also represents a natural hybrid between *A. angustifolia* Haw. and *A. lophantha* Schiede ex Kunth. In the protologue, *A. montium-sancticaroli* is compared to *A. × glomeruliflora* (Engelm.) A. Berger, the latter suggested to be a series of hybrids involving *A. lechuguilla* Torr. of subg. *Littaea* and *A. gracilipes* Trel., *A. havardiana* Trel. and *A. parryi* Engelm. var. *neomexicana* (Wooton & Standl.) McKechnie of subg. *Agave* (Gentry 1982). *Agave lechuguilla* is considered a “dono-species” by Gentry (1967), hybridizing with several other taxa.

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