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AGAVE ROSALESII (SECT. *INERMES*, ASPARAGACEAE), SEGREGATED FROM *AGAVE ELLEMEETIANA* K. KOCH (SECT. *CHORITEPALAE*): A NEW SPECIES FROM THE MIXTECA ALTA OF WESTERN OAXACA, MEXICO

AGAVE ROSALESII (SECCIÓN *INERMES*, ASPARAGACEAE), SEGREGADA DE *AGAVE ELLEMEETIANA* K. KOCH (SECCIÓN *CHORITEPALAE*): UNA NUEVA ESPECIE DE LA MIXTECA ALTA DEL OCCIDENTE DE OAXACA, MÉXICO

 J. ANTONIO VÁZQUEZ-GARCÍA^{1*},  JOACHIM THIEDE²,  JULIA ETER³ AND  MARTIN KRISTEN³

¹ Herbario IBUG, Instituto de Botánica, Departamento de Botánica y Zoología, Universidad de Guadalajara, Zapopan, Jalisco, México.

² Independent researcher Hamburg, Germany.

³ Independent researcher, Atotonilco el Alto, Jalisco, México

*Author for correspondence: talaumaofelia@gmail.com

Abstract

Background: *Agave ellemeetiana* (*A.* sect. *Choritepalae*) features soft and “spineless” leaves and occurs in two disjunct and ecologically differentiated populations classified as subspecies. An incidental look at the flowers of *A. ellemeetiana* ssp. *subdentata* unveiled that these did not match those of *A. ellemeetiana* s. str. nor those of sect. *Choritepalae*.

Questions: Do these disjunct populations differ in flower and fruit morphology? Do they belong to the same section within *Agave*?

Hypotheses: The floral morphology of populations of *Agave ellemeetiana* ssp. *subdentata* from western Oaxaca places this species in *A.* sect. *Inermes*, and the set of qualitative and quantitative differences is sufficient to recognize it as a distinct species.

Studied species: *Agave ellemeetiana*, *Agave pedunculifera*.

Study site and dates: Putla District, western Oaxaca, December 2011 and April 2014.

Methods: We conducted an alpha-taxonomic study of the *Agave ellemeetiana* species complex, involving two fieldwork expeditions, review of literature, online images, and herbarium specimens.

Results: Differences in flower, fruit and vegetative morphology and habitat support the segregation of the populations (from the Putla District, Oaxaca) from the *Agave ellemeetiana* complex as a new species, *A. rosalesii* spec. nov. The presence of an evident corolla tube places the proposed taxon close to *A. pedunculifera* and within *A.* sect. *Inermes*.

Conclusions: The populations from the Putla District are sufficiently distinct in their morphology and ecology to merit recognition as a new species, *Agave rosalesii*, placed in *A.* sect. *Inermes*.

Keywords: *Agave ellemeetiana* ssp. *subdentata*, *Agave* sect. *Choritepalae*, *Agave* sect. *Inermes*, corolla tube, endemic, montane pine-oak forest.

Resumen

Antecedentes: *Agave ellemeetiana* (*A.* sect. *Choritepalae*) presenta hojas suaves e “inermes” y ocurre en dos poblaciones disyuntas, ecológicamente diferenciadas y clasificadas como subespecies. Una mirada incidental a las flores de *A. ellemeetiana* ssp. *subdentata* reveló que éstas no coincidían con las de *A. ellemeetiana* s. str. ni con las de sección *Choritepalae*.

Preguntas: ¿Se diferencian estas poblaciones disyuntas en su morfología floral y frutal? ¿Corresponden a la misma sección de *Agave*?

Hipótesis: La morfología floral de las poblaciones de *Agave ellemeetiana* ssp. *subdentata* del occidente de Oaxaca, las ubica en *Agave* sección *Inermes*, y el conjunto de diferencias cualitativas y cuantitativas son suficientes para reconocerlas como especies distintas.

Especies de estudio: *Agave ellemeetiana*, *Agave pedunculifera*.

Sitio y años de estudio: Distrito de Putla, Oaxaca occidental, diciembre del 2011 y abril del 2014.

Métodos: Realizamos un estudio alfa-taxonómico del complejo de especies de *Agave ellemeetiana*, que incluyó dos expediciones de trabajo de campo, revisión de literatura, imágenes en línea y especímenes de herbario.

Resultados: Las diferencias en la morfología floral, frutal, y vegetativa y en el hábitat apoyan la segregación de las poblaciones de Putla, Oaxaca, consideradas parte del complejo *Agave ellemeetiana*, como una nueva especie, *A. rosalesii*. La presencia de un tubo de corola evidente ubica al taxón propuesto cerca de *A. pedunculifera*, en *A.* sección *Inermes*.

Conclusiones: Las poblaciones de Putla son lo suficientemente distintas en su morfología y ecología para merecer el reconocimiento como una nueva especie, *Agave rosalesii*, incluida en *A.* sección *Inermes*.

Palabras clave: *Agave ellemeetiana* ssp. *subdentata*, *Agave* sección *Choritepalae*, *Agave* sección *Inermes*, bosque montano de pino-encino, endémica, tubo de la corola.



The genus *Agave* s. l. currently includes ca. 265 species (Thiede 2020). Approximately, 226 of these species correspond to *Agave* s. str., of which 153 (68 %) are native to Mexico, the center of origin of the group, 40 (18 %) are native to the Caribbean, 21 (9 %) to the United States, 13 (6 %) to Central America, six (3 %) to northern South America, and nine (4 %) are only known from cultivation (García-Mendoza 2002, Vázquez-García *et al.* 2007a, García-Mendoza *et al.* 2019, Thiede 2020). On a broader scale, Western Mexico or Nueva Galicia (Rzedowski & McVaugh 1966) is considered to have the highest concentration of *Agave* species in the world (Vázquez-García *et al.* 2007b, c, 2016, Cuevas-Guzmán *et al.* 2010). On a smaller scale, the Valle de Tehuacán and its surroundings are the center of highest species diversity (Reichenbacher 1985, García-Mendoza & Galván-Villanueva 1995, Thiede 2020, Eguiarte *et al.* 2021).

Ever since the publication of the monumental *Agave* monograph nearly four decades ago (Gentry 1982), the number of *Agave* s. str. species has increased considerably (53 spp.), six of the 30 sections in the subgenera *Agave* and *Littaea* (Thiede *et al.* 2019) include 70 % of the newly described species: 10 in *A.* sect. *Heteracanthae* Salm-Dyck (Galván-Villanueva & Hernández-Sandoval 2002, García-Mendoza *et al.* 2007, Vázquez-García *et al.* 2007a, González-Elizondo *et al.* 2011), Hernández-Sandoval & Magallán-Hernández 2015, García-Mendoza *et al.* 2019, Hernández-Vera *et al.* 2019, Starr & Davis 2019, Starr 2020), followed by eight in *A.* sect. *Juncineae* Salm-Dyck (Zamudio-Ruiz & Sánchez-Martínez 1995, García-Mendoza & Martínez-Salas 1998, Carrillo-Reyes *et al.* 2003, Cabral-Cordero *et al.* 2007, Galván-Villanueva & Zamudio-Ruiz 2013, García-Mendoza & Chávez-Rendón 2013, Starr *et al.* 2018, García-Morales *et al.* 2019), seven in *A.* sect. *Ditepalae* Hochstätter (Hodgson & Sluson 1995, Hodgson 2001, Vázquez-García *et al.* 2012, Hodgson & Salywon 2013, Hodgson *et al.* 2018, García-Mendoza *et al.* 2019), five in *A.* sect. *Marmoratae* (A.Berger) Thiede & Gideon F.Sm. (Cházaro-Basáñez *et al.* 2005, Vázquez-García *et al.* 2013), five in *A.* sect. *Micracanthae* Salm-Dyck (Cházaro-Basáñez 1995, Cházaro-Basáñez *et al.* 2010, Cházaro-Basáñez & Vázquez-García 2013, Arzaba-Villalba *et al.* 2018, Beutelspacher & Hernández-Najarro 2021), and four in *A.* sect. *Inermes* Salm-Dyck, including the one here proposed as new (Cházaro-Basáñez *et al.* 2006, Vázquez-García *et al.* 2007a, b, Cuevas-Guzmán *et al.* 2012). Most of the newly described species (73 %) are from western Mexico (13 spp.), Oaxaca-Puebla-Guerrero (12), eastern Mexico (8), and northern Mexico (6).

The populations from western Oaxaca here described as a new species, *A. rosalesii*, were first placed in *A. ellemeetiana* K.Koch (1865), a species with stemless rosettes of few soft and flat, entire leaves without a terminal spine and yellow flowers with a very short corolla tube. *Agave ellemeetiana* was published from plants cultivated in Europe (Thiede 2014); its habitats were unknown for more than 150 years until its confirmed occurrence in central Veracruz and northern Oaxaca (Cházaro-Basáñez *et al.* 2012, Thiede 2014).

Further populations ascribed to *A. ellemeetiana*, but differing in its finely dentate leaf margins, were reported from the Putla / Tlaxiaco area in western Oaxaca (Köhres 2008). Thiede (2014) applied the forgotten name *A. ellemeetiana* var. *subdentata* Trelease (1914) to these plants; this name and the plants were unknown to Gentry (1982). Thiede (2014) had only photographs and small cultivated plants raised from field-collected seeds at hand, from which he preserved several leaves as neotype. He wanted to leave Trelease's name as it was published, pending field studies assessing the characteristics, variability and differences of the plants from the Putla / Tlaxiaco area to decide whether to recognize them as subspecies of *A. ellemeetiana* or a species in its own right. However, on behalf of one of the reviewers, Thiede (2014) had to publish the new combination *A. ellemeetiana* K.Koch ssp. *subdentata* (Trel.) Thiede, thus raising Trelease's name to subspecific rank.

A molecular genetic study using AFLP markers (Gil-Vega *et al.* 2007) displays a clear separation between *A. ellemeetiana* (ssp. *ellemeetiana*) and the Putla populations corresponding to *A. ellemeetiana* ssp. *subdentata* (Thiede 2014), grouping the latter with *A. pedunculifera* (from Guerrero), *A. vilmoriniana* and *A. bracteosa*. Similarly, *A. attenuata* (ssp. *attenuata*) groups with *A. garciae-mendozae* Galván & L.Hern., clearly separate from *A. pedunculifera* (from Tlacotepec, Guerrero). In the light of this genetic evidence, *A. pedunculifera* can be maintained as a species distinct from *A. attenuata* and not as a subspecies of the latter, as proposed by Ullrich (2006).

Recent field studies unveiled that the flowers of the populations from the Putla District, Oaxaca, exhibit a distinct corolla tube and thus do not correspond to *A.* sect. *Choritepalae* (type species: *A. ellemeetiana*) with a very short corolla tube, but instead to *A.* sect. *Inermes* (lectotype species: *A. attenuata*) with a distinct corolla tube. Thus, there

is no reason to keep the Putla populations as a subspecies of *A. ellemeeetiana*, instead, we here propose a distinct new species placed in the *Inermes* section. A closer look at the flowers shows additional differences in flower shape, color and length, as well as in the color of the filaments and styles. Furthermore, we highlight the habitat and ecological differences among similar taxa in both the *Choritepalae* and *Inermes* sections.

Agave section *Inermes* currently includes 11 species, of which two are known from cultivation only: *A. gilbertii* A. Berger and *A. spicata* Cav. The rest is confined to the Pacific slopes of Mexico from Sonora to Oaxaca ([Figure 1](#)): *Agave attenuata* Salm-Dyck, *A. chazaroi* A. Vázquez & O.M. Valencia, *A. chrysoglossa* I.M. Johnst., *A. manantlani-cola* Cuevas & Santana-Mich., *A. nizandensis* Cutak, *A. ocahui* Gentry, *A. pedunculifera* Trel., *A. vazquezgarciae* Cházaro & J.A. Lomelí, and *A. vilmoriniana* A. Berger (Gentry 1982, McVaugh 1989, Cházaro-Basáñez et al. 2006, Vázquez-García et al. 2007a,b, Cuevas-Guzmán et al. 2012, Thiede 2020). Molecular studies revealed that *A. sect. Inermes* is not monophyletic (Gil-Vega et al. 2007, Hernández-Vera et al. 2007, Jiménez-Barron et al. 2020), but its long corolla tube remains an important taxonomic character.

We aimed to describe and illustrate *Agave rosalesii* from western Oaxaca, Mexico, as a species new to science, placed in *A. sect. Inermes* as its twelfth species.

Materials and methods

As a result of fieldwork in the montane pine-oak forest of the Putla District in the Oaxaca state, Mexico, we documented the morphology of *Agave ellemeeetiana* var. *subdentata* Trel. The collections of flowers were made in December 2011 and of the rosette morphology and variability in April 2014. After an analysis of the morphological structures of these plants, we compared with similar *Agave* species treated in taxonomic reference works, particularly spineless or soft-spined ones (Gentry 1982, Vázquez-García et al. 2007a, b, Thiede 2001, 2020), as well as with digital images of specimens deposited in the herbaria ARIZ, CORU, MEXU, MO, US, XAL and ZSS.

We readily realized that the populations from the Putla District, Oaxaca, previously treated as *Agave ellemeeetiana* K. Koch ssp. *subdentata* (Trel. in L. H. Bailey) Thiede, needed to be segregated from the *A. ellemeeetiana* complex as a separate species given their differing flower structure.

We confirmed vegetative characters of the *Agave* populations from the Oaxaca Putla District with the vegetative type specimen at the SSZ herbarium and color plates available in the literature. We compared the new species with both *A. ellemeeetiana* (sect. *Choritepalae*) and *A. pedunculifera* (sect. *Inermes*) ([Table 1](#)) and documented the habitat differences of both these species ([Table 2](#)).

Table 1. Morphological differences between *Agave rosalesii*, *A. ellemeeetiana* and *A. pedunculifera*.

	<i>A. pedunculifera</i>	<i>A. ellemeeetiana</i> s. s.	<i>A. rosalesii</i>
Habit (stem)	Acaulescent	Acaulescent	Sometimes caulescent
Rosette (branching)	Not offsetting	Surculose	Not offsetting
Height (cm)	70.0-90.0	35.0-50.0	50.0-70.0
Diam. (cm)	140.0-180.0	70.0-100.0	93.0-145.0
Leaf wax bloom	Present	Absent	Present
Leaf shape	Mostly ovate-acuminate or lanceolate	Ovate to oblong	Broadly oblanceolate to rarely elliptic
Leaf size	80.0-90.0 × 11.0-15.0 cm	50.0-70.0 × 12.0-20.0	43.0-70.0 × 14.0-30.0
Leaf margin	Narrowly lined with brown or white, with closely set denticles 0.5-2 mm long	Entire, sometimes finely serrulate towards the apex	Very minutely denticulate

	<i>A. pedunculifera</i>	<i>A. ellemeetiana</i> s. s.	<i>A. rosalesii</i>
Leaf length to width ratio	5.1-5.3	4.4-4.6	2.6-3.2
Terminal spine (mm)	Acicular, weak, 10 mm	Absent, but leaf tip shortly acuminate and slightly calloused	Shortly conic, 2-3 mm or inconspicuous, reddish
Inflorescence (m)	2.0-3.0, erect to recurving	3.0-4.5, erect	3.2-3.5, erect
Flower pedicel length (mm)	20.0-30.0	15.0-20.0	4.0-5.0
Flower length (cm)	3.7-5.2	2.8-4.0	3.3-3.5
Corolla tube	Evident, 2.0-4.0 mm (as in <i>A. sect. Inermes</i>)	Inconspicuous, 1.0-2.0 mm (as in <i>A. sect. Choritepalae</i>)	Evident, 4.0-5.5 mm (as in <i>A. sect. Inermes</i>)
Flower color	Pale yellow	Pale greenish-yellow to white	Yellow to pale yellow
Tepal lobes (size in mm)	12.0-18.0 × 5.0-6.0, erect	13.0-15.0 × 5.0, incurved	19.0-22.0 × 6.5-7.0, reflexed-rolled
Number of flowers per node	4	Usually 4	2
Filament length (cm)	4.0-5.5	5.0-6.0	6.0-6.5
Anther length (mm)	14.0-22.0	10.0-12.0	16.0-17.0
Style length (mm)	20.0-27.0, shorter than the filaments	50.0-60.0, as long as the filaments	40.0-53.0, shorter than the filaments
Fruit size (cm)	1.5-2.0 × 0.7-1.0	1.3-1.5 × 1.0	2.0-2.3 × 1.1-1.6

Table 2. Habitat differences between *Agave rosalesii*, *A. ellemeetiana*, and *A. pedunculifera*

	<i>A. pedunculifera</i>	<i>Agave ellemeetiana</i> s. s.	<i>A. rosalesii</i>
Latitudinal range (°N)	24.316667-19.747691	18.031346-18.913517	17.009966-17.157348
Distribution	Sinaloa, Nayarit, Jalisco	Veracruz, Oaxaca (N)	Oaxaca (W)
Altitude (m)	1,500-2,000	400-1,600	2,400-2,600
Vegetation type	Premontane pine-oak forest	Tropical subdeciduous forest to cloud forest	Montane pine-oak forest
Biogeographic province	Sierra Madre Occidental, Eje Neovolcánico Transversal	Sierra Madre del Sur (ESE)	Sierra Madre del Sur (SSE)
Physiography	Sierra de Tacuichamona Sierra de Tapalpa, Sierra de Tlacotepec	Sierra de Zongolica, Sierra Mazateca	Mixteca Alta
Hydrography (watersheds)	Río San Lorenzo, río Tapalpa, Bajo Balsas, Huetamo, La Salada	Papaloapan	Río Verde basin

We used GeoCat (Bachman et al. 2011) online application to calculate the Extent of Occurrence (EOO) and Area of Occupancy (AOO) for their conservation assessment.

Results

Agave rosalesii A. Vázquez, Thiede, Etter & Kristen, spec. nov. ([Figures 2-4](#)). Type. Mexico, Oaxaca, distrito de Putla, municipio Santa Cruz Itundujia, paraje Los Monos, Col. El Chamizal, Buena Vista, bosque de encino-pino, creciendo sobre promontorios de roca con crasuláceas y *Salvia*, 16° 54' 24.4" N, 97° 37' 22.4" W, 2,549 m asl, 27 November 2013, Vicencio Aparicio-Barrios 278 w/ Kenia Velasco-Gutiérrez & Javier Juárez-Sierra (holotype: MEXU).

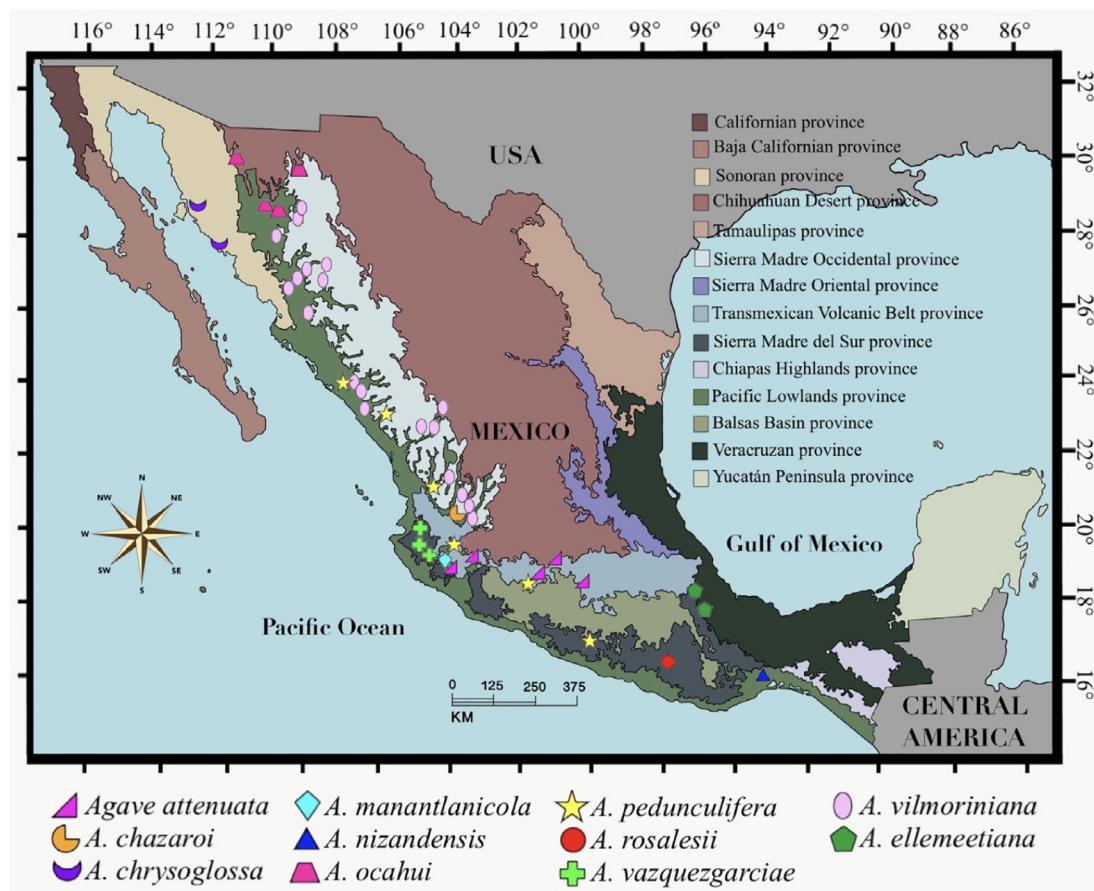


Figure 1. Distribution of the species of *Agave* sect. *Inermes* and of *A. ellemeetiana* (sect. *Choritepalae*) in the biogeographic provinces of Mexico (Morrone 2017).

= *Agave ellemeetiana* var. *subdentata* Trel. in L. H. Bailey, Stand. Cycl. Hort. 1: 236 (1914)

≡ *Agave ellemeetiana* ssp. *subdentata* (Trel. in L. H. Bailey) Thiede, Bradleya 32: 157 (2014), syn. nov. - Type (neotype, designated by Thiede 2014: 157): ex cult., J. Thiede s.n., 8th October 2014; from living plants raised from seed collected in Mexico, Oaxaca, between Putla and Tlaxiaco, ca. 2400 m; J. Spath & K. Griffin s.n. (ZSS digital image seen!).

Diagnosis. *Agave rosalesii* shares with *A. ellemeetiana* the soft leaves, inflorescence size and shape, but differs from the latter in having rosettes non-offsetting (vs. surculose); leaf wax bloom present (vs. absent); leaves broadly oblanceolate to rarely elliptic (vs. ovate to oblong); leaf margin very minutely denticulate (vs. entire and sometimes finely

serrulate towards the apex); leaf length to width ratio 2.6-3.2 (vs. 4.4-4.6); terminal spine 2.0-3.0 mm or inconspicuous (vs. absent); pedicels 4.0-5.0 mm long (vs. 15-20 mm); the number of flowers per node 2 (vs. usually 4); corolla tube 4.0-5.5 mm long (vs. 1-2 mm); tepal lobes reflexed-rolled, 19.0-22.0 × 6.5-7.0 mm (vs. incurved, 13.0-15.0 × 5.0 mm); anthers 16.0-17.0 mm long (vs. 10.0-12.0 mm); style 40.0-53.0 mm long (vs. 50.0-60.0 mm); and fruit size 2.0-2.3 × 1.1-1.6 cm (vs. 1.3-1.5 × 1.0 cm) ([Table 1](#)).

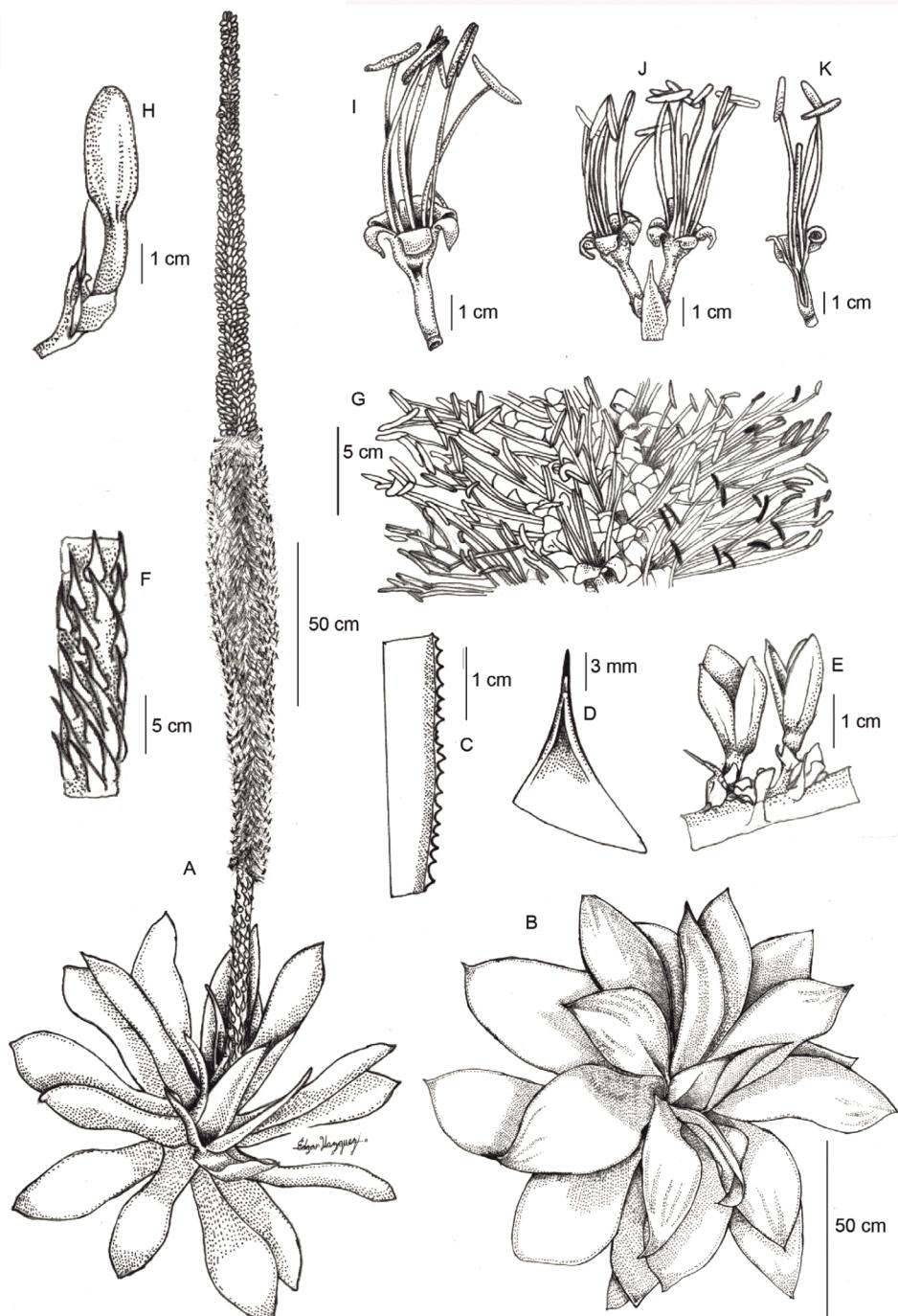


Figure 2. *Agave rosalesii*. A. Habit. B. Rosette. C. Leaf margin. D. Terminal spine. E. Capsules. F. Peduncle segment. G. Inflorescence segment. H. Flower bud. I. Fully developed flower. J. Geminata flowering node. K. Dissected flower. Mostly from photographs by Julia Etter & Martin Kristen, except E. from E. Solano w/ R. Rios 1976 (MEXU). Illustration by Edgar Vázquez-Verdejo.

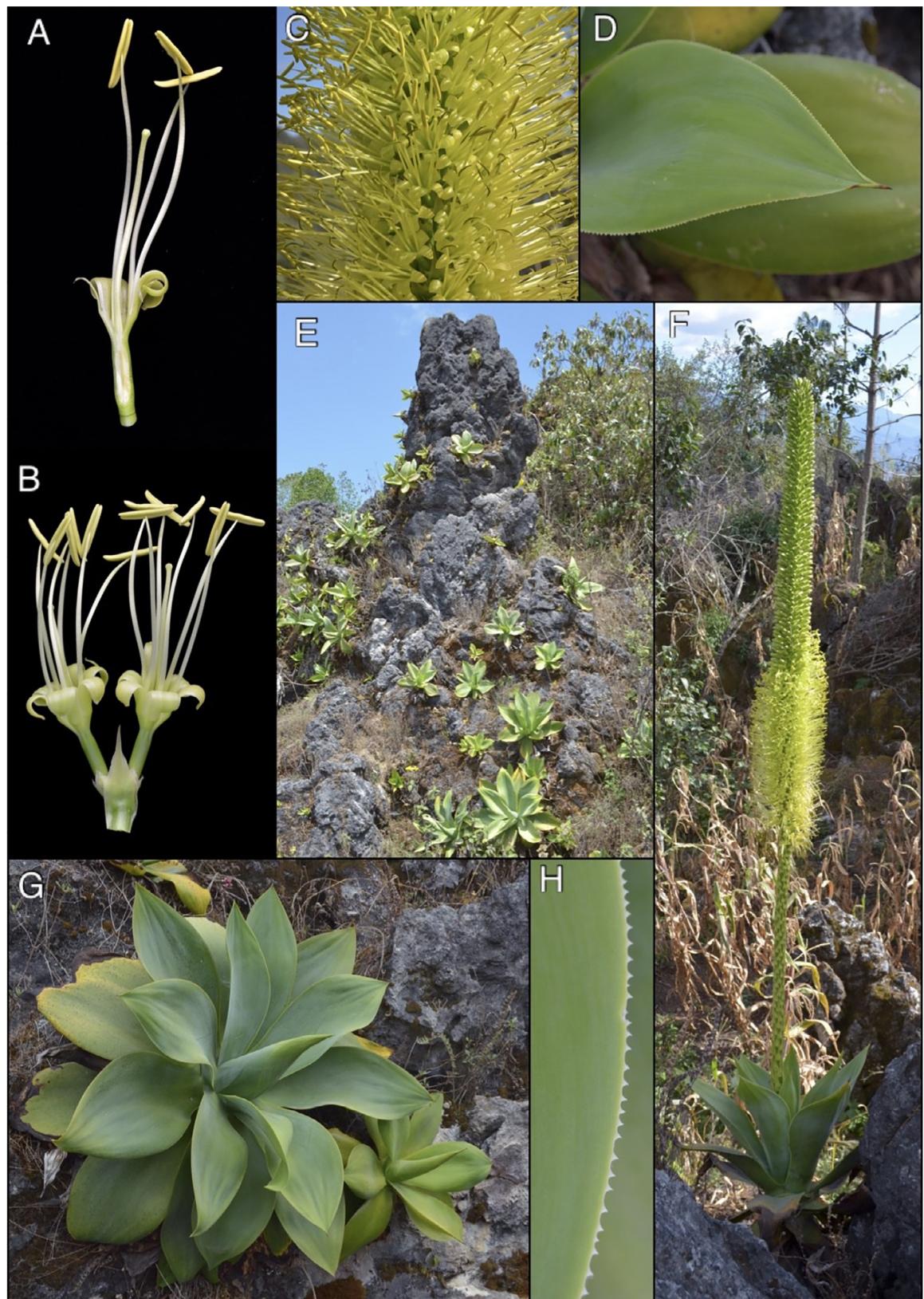


Figure 3. *Agave rosalesii*. A. Geminata flowering node with outer and inner floral bracts (bracteoles). B. Dissected flower showing corolla tube and ovary. C. Inflorescence close up. D. Leaf showing a terminal spine. E. Habitat. F. Habit in full bloom. G. Rosettes. H. Leaf margin. Photographs by Julia Etter & Martin Kristen.

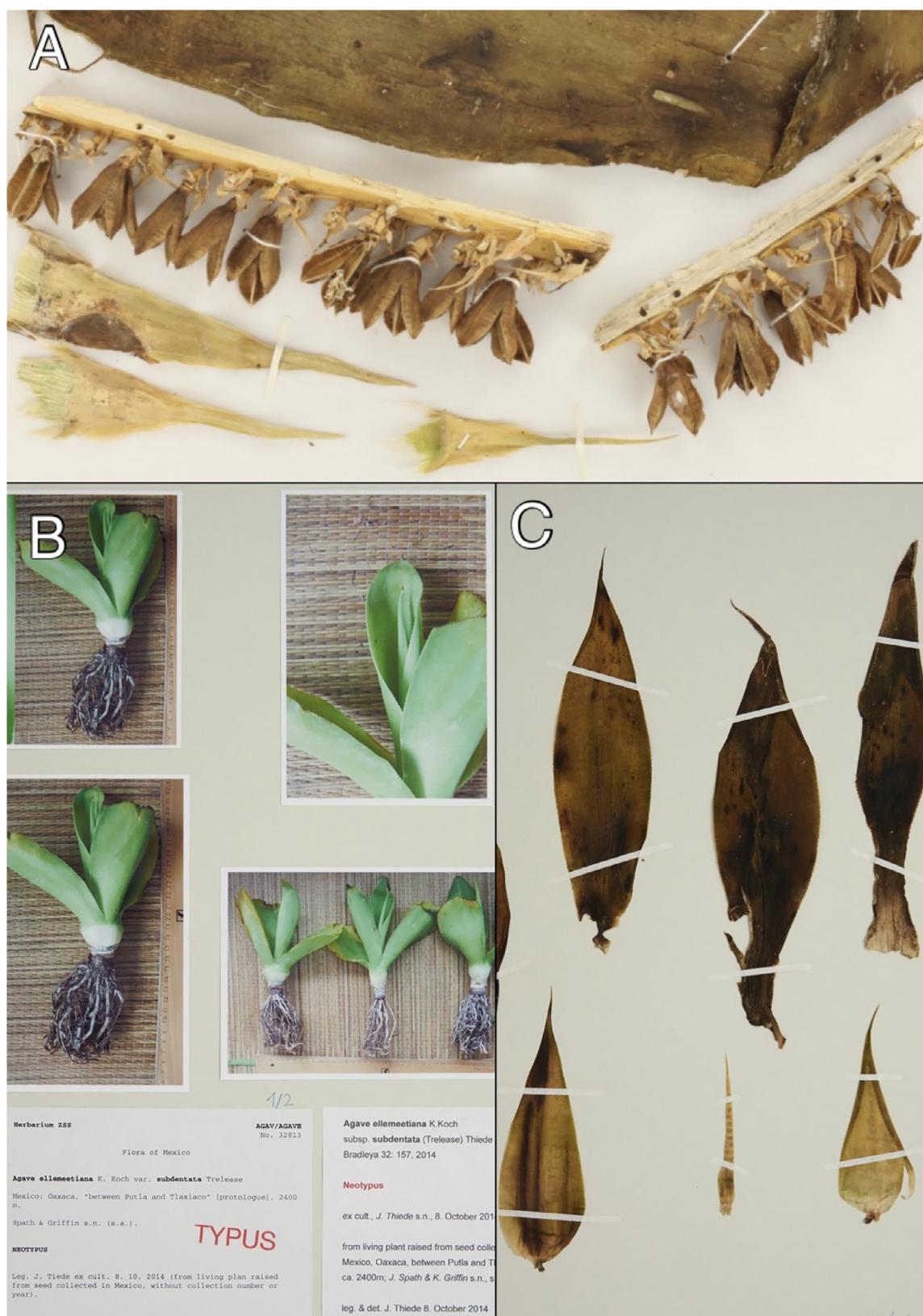


Figure 4. *Agave rosalesii*. A. Capsules, from E. Solano w/ R. Ríos 1976 (MEXU). B-C. Neotype of *Agave ellemeetiana* ssp. *subdentata*, J. Thiede s.n. (ZSS)

Agave rosalesii is also similar to *Agave pedunculifera* in having non-offsetting rosettes, a denticulate leaf margin, a distinct corolla tube, a similar tepal lobe size and anther length, but it differs from the latter in having leaves broadly oblanceolate to rarely elliptic vs. mostly ovate-acuminate or lanceolate; leaf size 43.0-60.0 × 14.0-30.0 cm (vs. 80.0-90.0 × 11.0-15.0 cm); leaf length to width ratio 2.6-3.2 (vs. 5.2); terminal spine 2.0-3.0 mm long (vs. 10.0 mm); inflorescence 3.2-3.5 m long (vs. 2.0-3.0 m); pedicels 4.0-5.0 mm long (vs. 20.0-30.0 mm); flower length 3.3-3.5 cm (vs. 3.7-5.2 cm); flower color yellow (vs. pale yellow); tepal lobes reflexed rolled, 19.0-22.0 × 6.5-7.0 mm (vs. erect, 12.0-18.0 × 5.0-6.0 mm); number of flowers per node 2 (vs. 4), filaments 60.0-65.0 mm long (vs. 40.0-55.0 mm); and style 40.0-53 mm long (vs. 20-27 mm) ([Table 1](#)).

Description. Plants perennial, sometimes caulescent and up to 100.0 cm long, stem usually absent or up to 50.0 cm long, rosettes 50.0-70.0 cm in height, 93.0-145.0 cm in diam., consisting of 14-28 leaves, not offsetting, leaves 43.0-70.0 × 14.0-30.0 cm, broadly oblanceolate or rarely elliptic, narrowed at the base, 10.0-15.0 cm wide, adaxially concave, glaucous-green to green-yellowish, with distinct leaf wax bloom, longitudinally wrinkled toward the apex, the apex arching outward, abaxially convex and pale bluish-green; leaf margin very minutely denticulate with soft herbaceous teeth, regularly spaced, whitish or reddish; terminal spine shortly conic, 2.0-3.0 mm or inconspicuous, reddish. Inflorescence spike-like, 320.0-350.0 × 24.0-26.0 cm, erect, densely flowered, the fertile part 250.0 cm long, peduncle 90.0-100.0 cm long, 4.5-5.0 cm in diam. at the base; upper peduncle bracts 6.0-7.0 × 1.0-1.2 cm at the base; outer floral bracts 1.4-1.5 cm long, inner flower bracts (bracteoles) 0.4-0.5 cm long; pedicels 4.0-5.0 mm long. Flowers geminate, 3.3-3.5 cm long, yellow; ovary 19.0-20.0 × 4.8-5.2 mm long; style shorter than the filaments, 40.0-53.0 mm long, yellow; stigma capitate, yellow; corolla tube evident, 4.0-5.5 mm long; tepal lobes 19.0-22.0 × 6.5-7.0 mm, reflexed-rolled, yellow to pale yellow; filaments 6.0-6.5 cm long, creamy white to pale yellow; anthers 16.0-17.0 mm long, yellow. Fruits 2.0-2.3 × 1.1-1.6 cm, obovoid, fruit pedicels 6.0-8.0 mm; seeds unknown.

Distribution and ecology. *Agave rosalesii* is endemic to the Putla District in western Oaxaca, in the municipalities of Santa Cruz Itundujía (paraje Los Monos), Santa María Yucuhiti (Yosonicaje) and Putla Villa de Guerrero (Las Mesas Santo Domingo), inhabiting rocky outcrops of montane pine-oak forest at 2,400-2,600 m in elevation within the Río Verde basin. It grows with *A. kavandivi*, *Echeveria* sp., *Furcraea* sp., *Pinguicula* sp., *Pinus* sp., and *Sprekelia* sp. ([Table 2](#), [Figure 1](#)).

Etymology. The species honors Carlos Santiago Rosales Martínez, a young enthusiastic agavologist, explorer, and horticulturist of succulents, who, in collaboration with the first author, unveiled that the Putla populations traditionally treated as belonging to *A. sect. Choritepalae*, actually belong to *A. sect. Inermes* due to the presence of a distinct corolla tube.

Conservation status. *Agave rosalesii* is locally abundant but confined to a few locations in a restricted area (EOO 45,941 Km² and AOO of 12,000 km²). This species, meeting the A3(c) criterion, is critically endangered (CR). We expect a population reduction for the following decades, given current trends in climate change that will deteriorate habitat quality at the top of the mountain, depleting the only space left for survival. Additionally, corn crop expansion is also a threat since it restricts the agaves to the rocky outcrops, where corn plants could not succeed. The species has the potential as an ornamental for temperate regions.

Additional specimen examined (paratype). Mexico, Oaxaca, distrito de Putla, municipio de Putla Villa de Guerrero, Las Mesas Santo Domingo, 17° 09' 21.86" N, 97° 50' 37.37" W, 2,442 m asl, 13 April 2006 (fr), E. Solano w/ R. Ríos 1976 (MEXU).

Discussion

Agave populations from the Pacific slopes in the Putla District of western Oaxaca, formerly treated as *Agave el-lemetiana* ssp. *subdentata* (Thiede 2014) differ sufficiently in their flower and fruit morphology from disjunct

populations of *Agave ellemeetiana* s. s., occurring in the Atlantic slopes of central Veracruz and northern Oaxaca (Cházaro-Basáñez *et al.* 2012, Thiede 2014). This evidence supports the recognition of *A. ellemeetiana* ssp. *subdentata* as a different species, here proposed as *A. rosalesii* spec. nov., and also places it in the *A. sect. Inermes* and not in *A. sect. Choritepalae* due to the presence of an evident corolla tube. Thus, within *Agave*, this is the first record of an infraspecific taxon elevated as a species on a different section from the initial one, suggesting a revision of other poorly morphologically characterized taxa.

A phylogeny using 355 AFLP markers for 71 species of *Agave* s. str. also supports the separation of *A. rosalesii*, treated as *A. aff. pedunculifera*, from *A. ellemeetiana* s. str. (Gil-Vega *et al.* 2007). The Putla populations (*A. rosalesii*) cluster together with two species of *A. sect. Inermes*: *A. pedunculifera* and *A. vilmoriniana*. On the other hand, *A. ellemeetiana* was not clustered with any species. A cladogram based on nuclear DNA (ITS) shows *A. bracteosa* and *A. ellemeetiana* s. str., the two of *A. sect. Choritepalae*, as the most basal species in the genus (Jiménez-Barrón *et al.* 2020). This study shows that the Amolae and Choritepalae groups (now formally as *A. sect. Inermes* and *A. sect. Choritepalae*, respectively) are not monophyletic, suggesting the corolla tube is not a reliable predictor of phylogenetic relationships.

Ecological differences also separate these two taxa: *Agave rosalesii* is a montane species thriving from 2,400 to 2,600 m, while *A. ellemeetiana* s. s. grows in lowlands or mid-elevations, from 400 to 1,600 m (Cházaro-Basáñez *et al.* 2012) (Table 2). Among the species of *A. sect. Inermes*, only two grow at elevations above 2,400 m: *A. rosalesii* in the Mixteca Alta of western Oaxaca and *A. manantlanicola* in the Sierra de Manantlán of Western Mexico; the former with soft broad leaves, spineless or soft-spined and subdente margin, and the latter with stiff leaves, long firm-spine and corneous toothless margin (Cuevas-Guzmán *et al.* 2012, Thiede 2014). Also, the latitudinal range of *A. rosalesii*, growing at about 17° N, is further south than that of *A. ellemeetiana* s. s., growing from 18-19° N. Actually, *A. rosalesii* is the second southernmost species of *A. sect. Inermes*, and also the second recorded for Oaxaca (Figure 1). The two species inhabit different habitats: *A. rosalesii* grows in a montane pine-oak forest in the Pacific slopes within the Río Verde watershed with a mean annual rainfall of 1,800 mm, while *A. ellemeetiana* s. s. inhabits tropical deciduous to cloud forest in the Atlantic slopes of the Papaloapan watershed with a mean annual rainfall of 2,800 mm (Table 2) (Thiede 2014).

A conservation strategy needs to be designed, we strongly recommend setting aside a natural protected area to ensure the survival of the critically endangered species, *Agave rosalesii*, and all together protect the rich and the endemic flora of the montane pine-oak forest of the Mixteca Region, an area of numerous recent discoveries, such as the corncob flower, *Magnolia mixteca* (Vázquez-García *et al.* 2021), the cycad *Dioon planifolium* Salas-Mor., Chemnick & T.J. Greg. (Salas-Morales *et al.* 2016), *Salvia robertoana* Mart.Gord. & Fragoso (Martínez-Gordillo *et al.* 2016) and *Salvia tilantongensis* J.G. González & R. Aguilar-Santelises (González-Gallegos & Aguilar-Santelises 2014).

Key to species of *A. sect. Inermes* similar to *A. rosalesii*

1. Plants surculose; mature rosettes on stems longer than 50.0 cm.
2. Stems 20.0-25.0 cm diam.; leaf margin corneous, continuous and entire; terminal spine 30.0-45.0 mm long; tepals reddish outside *A. manantlanicola*
2. Stems less than 15.0 cm diam.; leaf margin smooth or serrulate; terminal spine absent; tepals yellowish green
- *A. attenuata*
1. Plants non-surculose; mature rosettes acaulescent or on stems less than 30.0 cm long.
3. Terminal spine 20.0 mm long or less.
4. Leaf margin closely denticulate; corolla tube 2.0-6.0 mm long
5. Leaves 80.0-90.0 × 11.0-15.0 cm, terminal spine 10.0 mm long, pedicels 20.0-30.0 mm long, tepal lobes 12.0-18.0 × 5.0-6.0 mm long and pale yellow, filaments 40.0-55.0 mm long, styles 20.0-27.0 mm long *A. pedunculifera*

5. Leaves 43.0-60.0 × 14.0-30.0 mm, terminal spine 2.0-3.0 mm long, pedicels 4.0-5.0 mm long, tepal lobes 19.0-22.0 × 6.5-7.0 mm long and yellow, filaments 60.0-65.0 mm long, styles 40.0-53.0 mm long *A. rosalesii*
4. Leaf margin entire; corolla tube 11.0-12.0 mm long *A. gilbertii*
3. Terminal spine 30.0-65.0 mm long.
6. Leaf margin entire; flowers 20.0-30.0 mm long; tepals ivory-white *A. chazaroii*
6. Leaf margin closely dentate; flowers 52.0-94.0 mm long, tepals greenish-yellow *A. vazquezgarciae*

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