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NEW GENERA AND NEW COMBINATIONS IN AGAVACEAE (ASPARAGALES)

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ABSTRACT

Three new genera of Agavaceae (Asparagales) are proposed based on genetics, morphology, and estimated divergence times: **ECHINOAGAVE** Vázquez, Rosales, & García-Mor., **gen. nov**., forms a highly supported clade that differs from *Agave* sensu stricto by having polycarpic rosettes of hedgehog shape, striate-sulcate leaves and a different divergence time (Early Pliocene) from the latter. **PALEOAGAVE** Vázquez, Rosales. & García-Mor., **gen. nov.**, differs from *Agave* sensu stricto in having unarmed, curling leaves — it is the lineage with the earliest estimated divergence time, dating from the Late Miocene. **PARAAGAVE** Vázquez, Rosales, & García-Mor., **gen. nov**., differs from *Paleoagave* in having few-leaved rosettes, non-curling leaves, and longer and wider corolla lobes — it represents a well-supported lineage with estimated divergence time from *Echinoagave* in the Early Pliocene. Our proposal contributes toward providing a more accurate taxonomy and diagnosability of the species groups most recently recognized in *Agave*.

The taxonomic placement of the genus *Agave* L. and the circumscription of the family Agavaceae Dumort have changed historically with the emergence of new lines of evidence. The Agavaceae, first proposed in 1829 and termed Agavineae, included the genus *Agave* within the tribe *Agaveae*. The long-established taxonomic systems of Bentham and Hooker (1883) and Engler and Prantl (1988) transferred *Agave* and other liliaceous genera into the family Amaryllidaceae J. St.-Hil., mainly based on their inferior ovaries. Regardless of the ovary position, Hutchinson´s system (1934) and the long-used Cronquist system (1981) included *Agave* and other more or less fibrous-leaved, woody genera in the Agavaceae. However, only *Yucca* and *Agave* shared a unique karyotype (n=30, 25 small + 5 large chromosomes) (McKelvey & Sax 1933). Some interpreted *Hosta*, with its *Agave*-like karyotype, as a member of the Agavaceae (Takhtajan 1980), while others viewed it as convergent evolution (Dahlgren & Clifford 1982). The system of Dahlgren et al. (1985), adding chemical characters, reduced the Agavaceae to the tribes Yucceae and Agaveae, which was later supported by

rbcL data (Chase et al. 1993; Duval et al. 1993). At the start of this century, Agavaceae was still recognized (Eguiarte et al. 2000; APG System II 2003), but Agavaceae later became part of a larger family Asparagaceae Juss. (Angiosperm Phylogeny Group III 2009; Angiosperm Phylogeny Group IV 2016). Likewise, the concept of *Agave* was broadened to include several genera traditionally recognized as morphologically distinct, such as *Manfreda*, *Polianthes*, and *Prochnyanthes* (Thiede et al. 2020).

In recent treatments on the classification of Angiosperms, the Agavaceae has regained its taxonomic rank as an independent family (Judd et al. 2016; Thiede & Eggli 2020; Thiede 2020) under the statement that the broad sense of Asparagaceae is not useful to gain a better understanding of relationships between different clades due to its low support (Kim et al. 2010; Givnish et al. 2018). Evidence from recent phylogenetic studies shows that the genus *Agave* sensu lato is polyphyletic (Jiménez-Barrón et al. 2020). Results from recent phylogenetic studies prompted Thiede (2020) to expand the de *Agave* concept by merging *Manfreda*, *Polianthes*, and *Prochnyanthes* into the same concept, maintaining monophyly. An alternative to having a huge genus *Agave* is the recognition of several highly supported lineages; we adopted this alternative, which implies taxonomical and nomenclatural changes to recognize, as new genera, clades or isolated lineages with high support or substantial evolutionary and/or morphological change (Thiede & Eggli 2020).

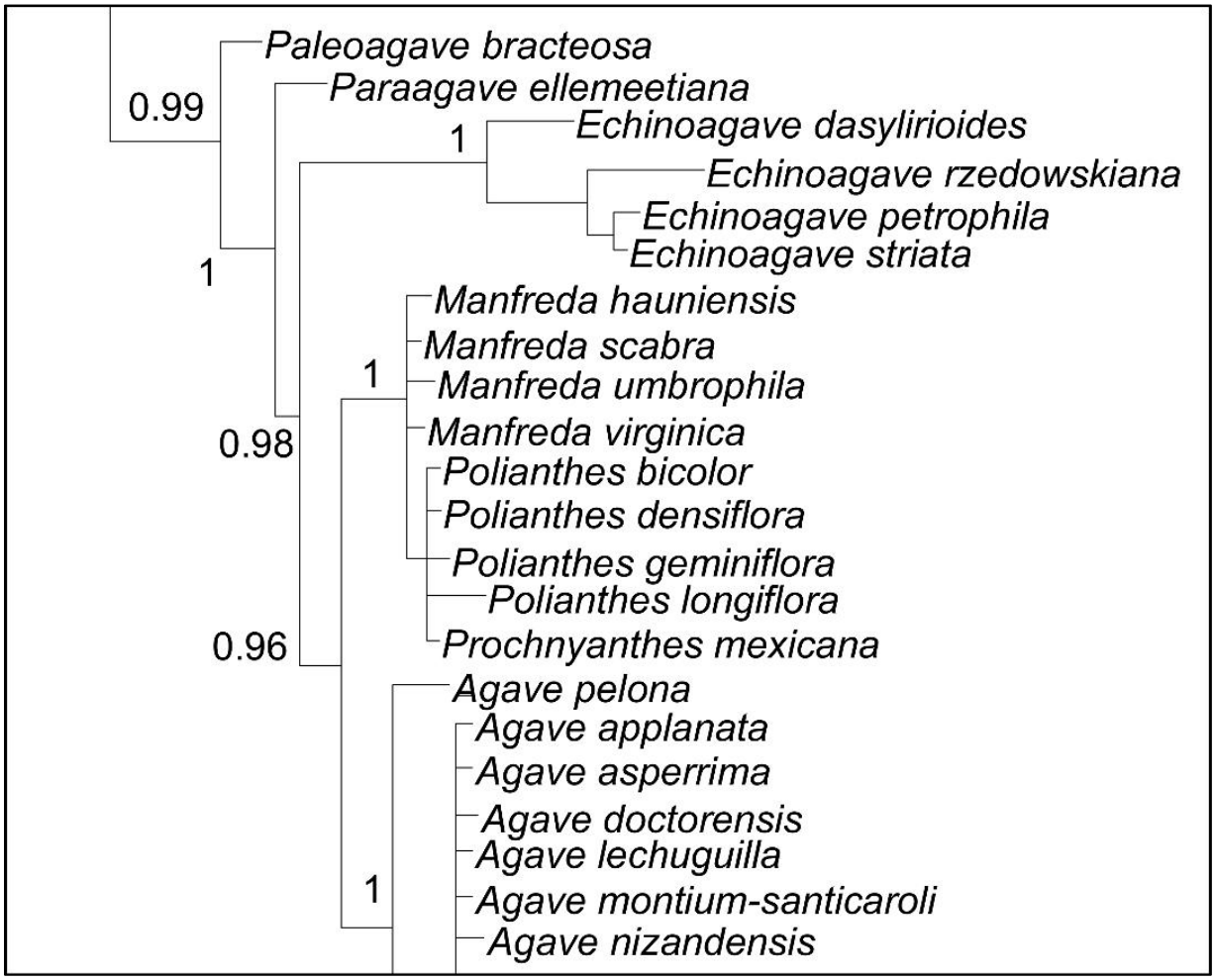

Figure 1. Phylogeny of *Agave* sensu lato, from ITS sequences and using a Bayesian inference analysis, from Jiménez-Barrón et al.. (2020). The numbers next to the nodes indicate the posterior probability values above 0.70.

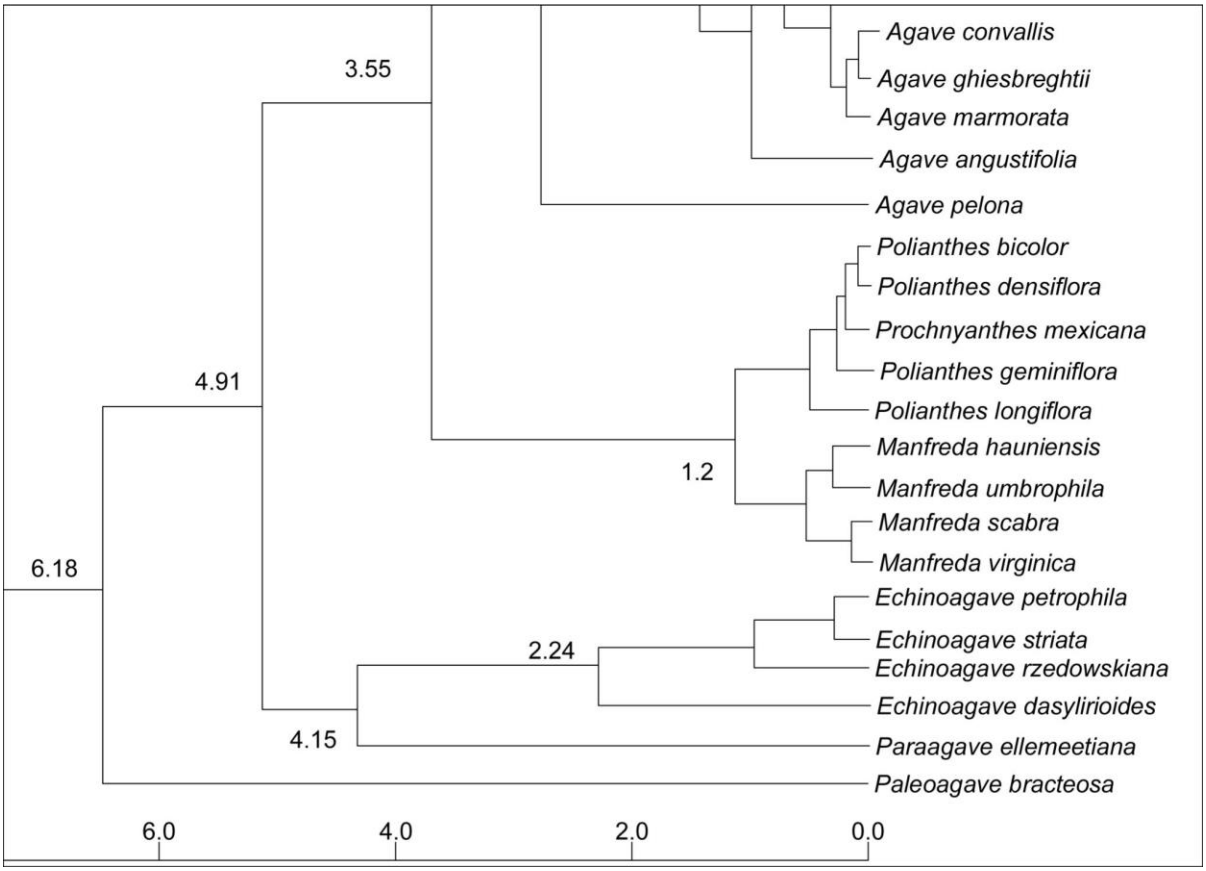

Figure 2. Divergence times of *Agave* sensu lato, derived from the maximum clade credibility tree using BEAST, adapted from Jiménez-Barrón et al.. (2020). Numbers indicate mean divergence times and mean ages.

Gentry (1982) noted that *Agave bracteosa* S. Wats. ex Engelm. and *Agave ellemeetiana* K. Koch, among few other species, shared two distinctive characters, unarmed leaves and discoid floral receptacles with distinct corolla segments, which separate these species into a different group, the *Choritepalae*, recently formalized as *Agave* sect. *Choritepalae* Hochstätter (2015): "this distinctive flower structure together with the unarmed leaves without terminal spine, could justify removal from *Agave* to a separate genus" (Gentry 1982). Its peculiarity led Ullrich (1990b) to assign it within a reconsidered monotypic group *Serrulatae* Baker (Thiede 2020). Recent phylogenetic analyses (Jiménez-Barrón et al. 2020) using plastid and nuclear DNA sequences support the early separation of *Agave bracteosa* from *Agave* sensu lato with a mean estimated age of ca. 6.18 Ma, and also the separation of *Agave ellemeetiana* with a mean estimated age of 4.25 Ma from species of sect. *Juncineae* Salm-Dyck, and the latter from *Agave* sensu stricto with the same mean estimated age. The early divergence of sect. *Juncineae* Salm Dyck (1861), formerly treated as the *Striatae* group (Gentry 1982), was previously supported by several studies using molecular markers (Bogler & Simpson 1995; Bogler et al. 2006; Gil-Vega et al. 2007; Hernández-Vera et al. 2007).

Previous authors (Dahlgren et al. 1985; Hernández-Vera 2007) proposed the inclusion of *Manfreda*, *Polianthes*, and *Prochnyanthes* within *Agave* for a monophyletic classification of *Agave* (Thiede 2012, 2015; Thiede & Eggli 1999, 2020; Govaerts & Thiede 2013). However, this classification results in a large genus which is unusually diverse in morphology. Alternatively, we use three types of evidence: genetic, morphological, and estimated divergence times (Good-Ávila et al. 2006; Eguiarte et al. 2000; Jiménez-Barrón et al. 2020) to propose a more accurate circumscription

of *Agave*, segregating three new genera: *Echinoagave*, *Paleoagave*, and *Paraagave*. We base our proposal on recent phylogenetic analyses of Jiménez-Barrón et al. (2020) (Fig. 1), using both Bayesian inference (BI) and maximum likelihood (ML) on a concatenated matrix of plastid and nuclear DNA sequences, which supports the early separation of *Agave bracteosa* from *Agave* sensu lato in the Late Miocene, with a mean estimated age of ca. 6.18 Ma. Moreover, this phylogeny also supports the separation between *Agave ellemeetiana* and *Striatae* group (sect. *Juncineae* Salm-Dyck) with a mean estimated age of 4.15 Ma, and the separation of both from *Agave* sensu stricto, estimated to have occurred in the Early Pliocene at ca. 4.91 Ma. (Fig. 2).

Our aim to segregate these new genera from *Agave* is to provide a more accurate classification within Agavaceae based on more natural or monophyletic groups as supported by recent studies. It also implies that the clade consisting of *Manfreda*, *Polianthes*, and *Prochnyanthes* is separate from the monophyletic *Agave* sensu stricto (Jiménez-Barrón et al. 2020). Our proposal leaves open the possibility of better-resolving relationships among *Manfreda*, *Polianthes*, and *Prochnyanthes* (with a larger sampling of taxa and characters).

We consider that this new proposal contributes to the taxonomic and nomenclatural stability and diagnosability within the Agavaceae.

KEY TO *AGAVE* AND SEGREGATED GENERA

1. Rosettes with epigeous axillary offsets or branches, leaf margins minutely serrulate.

   2. Leaves non-striate and curled apically without a terminal spine, flowers with alternate unequal free tepals segments ..... **PALEOAGAVE**
   2. Leaves striate non-curled apically with a terminal spine, flowers with alternate equal fused tepals segments, forming a tube ..... **ECHINOAGAVE**

1. Rosettes with hypogeous offsets, leaf margins non-minutely serrulate:

   3. Leaves without a terminal spine with the tip calloused ..... **PARAAGAVE**
   3. Leaves with a terminal spine or with the tip fraying ..... **AGAVE** sensu stricto

ECHINOAGAVE Vázquez, Rosales, & García-Mor., **gen. nov. TYPE SPECIES: Echinoagave rzedowskiana (**Carrillo, Vega, & Delgad.) Vázquez, Rosales, & García-Mor. [= sect. *Juncineae* Salm-Dyck (1861) = group *Striatae* Baker (1877) = subsect. *Striatae* (Baker) A. Terracciano (1885) = sect. *Schoenagave* A. Berger (1915); incl. Abtheilung *Loriformes* Jacobi (1864) = sect. *Chonanthagave* A. Berger (1915), syn. nov.]. Figure 3

Echinoagave shares with *Agave* sensu stricto its rosette habit with a terminal spine, but it differs from the latter by having a polycarpic habit and usually a compact "hedgehog-like" shape, with leaves cylindrical to subcylindrical to flattened, hard, firm, striate-sulcate and serrulate margins. All species of *Echinoagave* included in a phylogeny (Jiménez-Barrón et al.. 2020) form a highly supported basal clade of early divergence, with a stem age of ca. 4.15 Ma and a crown age of ca. 2.24 Ma. (Figs. 1 and 2).

Rosettes perennial, single or caespitose, axillary branching. Leaves numerous, striate-sulcate, narrow, linear, hard, thick. Margin scabrous, serrulate, with thin hyaline yellow borders, grayish green, to yellow-green, reddish or purplish, the tip pungent, but fragile. Inflorescence spike-like, 1.5-3 m, long pedunculate, bracteate, flowering in upper half or 1/4/ of shaft. Flowers mostly geminate, campanulate to cylindric, variously colored, and persisting dry on the capsule. Tubes well developed, frequently longer than tepals. Filaments elongate, inserted in the middle of the tube, frequently at two levels. Capsules threeangulate, the valves with indented dorsal ribs. Seeds black, usually semi-spheroid, small, thick.

Etymology. The word *Echinoagave* means “hedgehog agave” and is composed of the Greek prefix ekhinos (*ἐχῖνος*, “hedgehog”) meaning "prickly; spiny" and the Greek suffix “agauós” **(***ἀγαυός,* "illustrious, noble"). The name refers to the rosette spiny shape appearance of the *Agave* species belonging to this genus, resembling a hedgehog shape.

Distribution. *Echinoagave* species have a wide distribution range in the dry and subtropical regions of the Chihuahuan Desert, the Hidalgo-Querétaro arid region, the Tehuacán-Cuicatlán arid region, the Sierra Madre Oriental, the Sierra Madre Occidental, and the Sierra Madre del Sur.

PALEOAGAVE Vázquez, Rosales, & García-Mor., **gen. nov.** **TYPE SPECIES**: **Paleoagave bracteosa** (S. Wats. ex Engelm.) Vázquez, Rosales, & García-Mor. [= *Agave* sect. *Choritepalae* Hochstätter (2015) (including group *Choritepalae* Gentry (1982) (nom. inval. Art 37.1.), syn. nov.]. Figure 4.

Paleoagave differs morphologically from *Agave* sensu stricto by having unarmed (finely serrulate), soft, curling leaves and a floral discoid receptacle instead of a corolla tube, with tepals unequally distinct. Genetically, its separation as an isolated lineage is highly supported by Bayesian Inference and Maximum Likelihood methods. Furthermore, it is the earliest and only Late Miocene diverging lineage from *Agave* sensu lato, with a stem age of ca. 6.18 Ma. (Figs. 1 and 2).

Rosettes of medium size, few-leaved, open, caespitose, axillary budding. Leaves lanceolate, widest near the base, arching and curling at the tip, succulent, with weak fibers, asperous, plane above, convex below in the basal ⅓. Margins minutely serrulate. Terminal spine absent, the tip drying early, yellowish. Inflorescence 1.2-1.7 m, ascending to erect, densely flowered in the upper third of the shaft. Peduncular bracts erect, triangular-acuminate. Flowers white to pale yellow, geminate. Bractlets navicular at the base, long caudate at the apex. Ovary fusiform, neckless. Tube replaced by a discoid receptacle. Tepals alternate, unequal, spreading, hyaline, distinct, the outer overlapping inner, lanceolate, acute, the inner broadly ovate, obtuse, both floccose at tips. Filaments long exserted, white, persisting, elongating in post-anthesis, inserted on the receptacle. Anthers sagittate, yellow, pistil eventually exceed the stamens. Capsules obtuse, thin-walled, stipitate. Seeds half round shaped.

Etymology. The word *Paleoagave* means “ancient agave” and is composed of the Greek prefix “paleo” (παλαιός, palaios, ancient) and the Greek suffix agauós **(***ἀγαυός,* "illustrious, noble"). The name refers to the earliest diverging genus within *Agave* sensu lato.

Distribution. *Paleoagave bracteosa* is a narrow endemic to the northern end of the Sierra Madre Oriental in Nuevo León and Coahuila, on dry limestone cliffs from 500 to 1200 m elevation frequently in the transition areas with the Chihuahuan Desert.

PARAAGAVE Vázquez, Rosales, & García-Mor. **gen. nov.** **TYPE SPECIES**: **Paraagave ellemeetiana** (K. Koch) Vázquez, Rosales, & García-Mor. [= *Agave* sect. *Choritepalae* Hochstätter (2015) (including group *Choritepalae* Gentry (1982) (nom. inval. Art 37.1.), syn. nov.]. Figure 5.

Paraagave shares with *Paleoagave* the absence of a corolla tube; however, it differs from *Paleoagave* by having few leaved larger rosettes with margins entire or rarely sparsely denticulate and large non-curling leaves, and flowers with equal tepals in length and shape. The flowers are typical of *Agave* sect. *Choritepalae* Hochstätter 2015, including group *Choritepalae* Gentry 1982 (nom. inval., ICN Art. 37.1), and an early divergence from *Agave* sensu lato (Jiménez Barrón et al.. 2020). Furthermore, it represents a well-supported lineage with an estimated diverging age from *Echinoagave* of ca. 4.25 Ma. From *Agave* sensu stricto it differs by having a floral discoid receptacle instead of a corolla tube. (Figs. 1 and 2).

Rosettes nearly acaulescent, monocarpic, open, unarmed, few-leaved. Leaves light bright green, thickly soft-succulent, smooth, ovate to oblong, acuminate, somewhat recurved, reclining at maturity, adaxially concave to flat, abaxially flat beyond the thick base, widest in the middle, the short acuminate tip slightly calloused. Margins thin, sometimes reddish or finely serrulate toward the apex. Inflorescence erect, densely flowered from near the base. Peduncular bracts ovate, caudate-acuminate. Flowers pale greenish-yellow, campanulate, mostly on fours, on a pair of dichotomous pedicels. Ovary flask-shaped, with a long neck. Tube replaced by a discoid receptacle. Tepals lanceolate, concave, hooded at the tip, the inner ones wider. Filaments erect, inserted on the discoid receptacle. Anthers yellow. Capsules trigonous, woody, light brown, rounded at the base, beaked. Seeds black, shiny.

Etymology. The word *Paraagave* means "close to agave" and is composed of the Greek prefix "pará" (παρά, "beside; next to, near, from; against, contrary to") and the Greek suffix agauós (ἀγαυός, "illustrious, noble"). The name refers to the occurrence of this genus within the topology of phylogenetic trees, being close to *Agave* sensu stricto.

Distribution. Endemic to the boundaries of the Sierra Madre Oriental and Sierra Madre del Sur in southeastern Veracruz and northern Oaxaca.

New combinations

We propose the following new nomenclatural combinations for include the recognized taxa within the new genera here described:

1. **ECHINOAGAVE ALBOPILOSA** (Cabral, Villarreal, & Estrada) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave albopilosa* Cabral, Villarreal, & Estrada, Acta Bot. Mex. 80: 52. 2007. **TYPE**: **MEXICO**. **Nuevo León**. *Cabral 1612* (holotype: MEXU; isotypes: ANSM, CFNL, CIIDIR, ENCB, UNL).

2. **ECHINOAGAVE CRYPTICA** (Starr & Davis) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave cryptica* Starr & Davis, Cact. Succ. J. 93: 275. 2021. **TYPE**: **MEXICO**. **Nuevo León**. *Starr 2021-006* (holotype: ARIZ; isotype: MEXU).

3. **ECHINOAGAVE CREMNOPHILA** (Starr, Etter, & Kristen) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave cremnophila* Starr, Etter, & Kristen, Cact. Succ. J. 90: 40, 2018. **TYPE: MEXICO. Oaxaca**. *Starr 2017-013* (holotype: ARIZ; isotypes: MEXU, MO).

4. **ECHINOAGAVE DASYLIRIOIDES** (Jacobi & Bouché) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave dasylirioides* Jacobi & Bouché, Hamburg. Gart.- & Blumenzeit. 21: 344. 1865. **NEOTYPE** (designated by Thiede 2014): **GERMANY.** Ex-cult. BG Berlin, "v. Jacoby / h. Berol Jan 1863", *anonymous* s.n. (neotype: B 101068481).

5. **ECHINOAGAVE GRACIELAE** (Galván & Zamudio) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave gracielae* Galván & Zamudio, Acta Bot. Mex. 105: 2. 2013. **TYPE: MEXICO. Querétaro**. *E. González 569* (holotype: IEB; isotypes: ENCB, MEXU, XAL).

6. **ECHINOAGAVE KAVANDIVI** (García-Mend. & Chávez) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave kavandivi* García-Mend. & Chávez-Rendón, Rev. Mex. Biodiv. 84: 1071. 2013. **TYPE: MEXICO. Oaxaca**. *A. García-Mendoza et al. 10184* (holotype: MEXU; isotypes: ENCB, MO, OAX).

7. **ECHINOAGAVE LEXII (**García-Mor., García-Jim., & Iamonico) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave lexii* García-Mor., García-Jiménez, & Iamonico, Novon 27: 201. 2019. **TYPE: MEXICO. Tamaulipas**. *L. García 5580* (holotype: ITCV; isotypes: ANSM, CIIDIR, GBH, HFLA).

8. **ECHINOAGAVE PETROPHILA (**García-Mend. & Martínez) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave petrophila* García-Mendoza & Martínez, Sida 18: 627. 1998. **TYPE: MEXICO. Guerrero**. *Martínez & al. 2639* (holotype: MEXU; isotypes: BRIT, ENCB, K, MO).

9. **ECHINOAGAVE RZEDOWSKIANA** (Carrillo, Vega, & Delgad.) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave rzedowskiana* Carrillo, Vega, & Delgad., Brittonia 55: 240. 2003. **TYPE: MEXICO. Jalisco**. *Carrillo-Reyes & Cabrera 1503* (holotype: IBUG; isotypes: GUADA, MEXU, NY).

10. **ECHINOAGAVE STRIATA (**Zucc.) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave striata* Zuccarini, Flora 15: 2(Beiblatt 2): 98. 1832. **NEOTYPE** (designated by Gentry 1982): **U.K.** Ex-cult. RBG Kew, from Real del Monte [Hidalgo], 15 Dec 1880, *Anonymous s.n.* (neotype: K294235).

11. **ECHINOAGAVE STRICTA (**Salm-Dyck) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave stricta* Salm-Dyck, Bonplandia 7: 94. 1859. **NEOTYPE** (designated by Gentry 1982): **MEXICO. Puebla**. 4-10 miles southwest of Tehuacán, along road to Zapotitlán, Aug 1953[1963], *H.S. Gentry & al. 20226* (neotype: US00163595; isoneotypes: MEXU [00376351 + 00129982]).

12. **ECHINOAGAVE TENUIFOLIA (**Zamudio & Sánchez) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave tenuifolia* Zamudio & Sánchez, Acta Bot. Mex. 37: 48. 1995. **TYPE: MEXICO. Querétaro**. *Carranza 1905* (holotype: IEB; isotypes: MEXU, TEX).

13. **PALEOAGAVE BRACTEOSA** (S. Wats. ex Engelm.) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave bracteosa* S. Wats. ex Engelm., Gard. Chron., ser. nov. 18: 776. 1882. **LECTOTYPE** (designated by Ulrich 1990**)**: Gard. Chron. 2:18, 776, fig 138, 139. 1882.

14. **PARAAGAVE ELLEMEETIANA** (K. Koch) Vázquez, Rosales, & García-Mor., **comb. nov.** *Agave ellemeetiana* K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 8: 103 [1 Apr]. 1865. **NEOTYPE** (designated by Gentry 1982): **U.K.** Ex-cult. Hort Kew, 10 Mar 1877, *Anonymous s.n.* (K 524804; isoneotypes: K 524801, 524802, 524803).

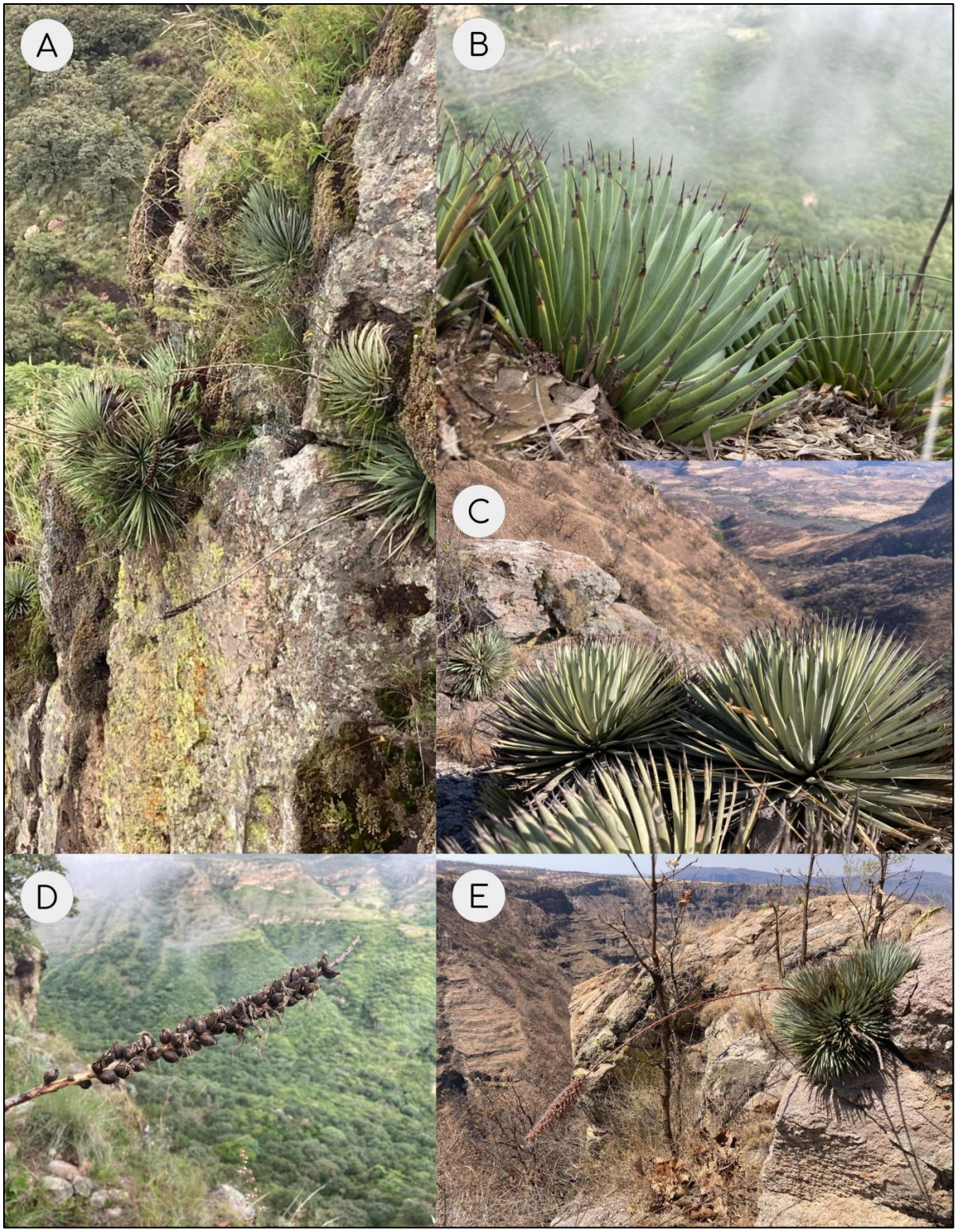

Figure 3. Representative specimens of *Echinoagave rzedowskiana*, the type species of *Echinoagave*. A. Habitat. B. Rosette during the rain season. C. Rosette during the dry season. D. Infrutescence. E. Plant with inflorescence. Photographs: Santiago Rosales.

Figure 4. Representative plants of *Paleoagave bracteosa*. A. Inflorescences. B. Inflorescence close up. C-E. Rosette variability. Photographs: A-B by Miguel A. González Botello, C-E by Daniel Hernández Campos.

Figure 5. Illustration of *Paraagave ellemeetiana* (K. Koch) Vázquez, Rosales, & García-Mor. (from Hooker´s Curtis´s Botanical Magazine, 1888, Tab. 7027).

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LITERATURE CITED

Angiosperm Phylogeny Group II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.

Angiosperm Phylogeny Group III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161: 105–121.

Angiosperm Phylogeny Group IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181: 1–20.

Archibald, J.K., S.R. Kephart, K.E. Theiss, A.L. Petrosky, and T.M. Culley. 2015. Multilocus phylogenetic inference in subfamily Chlorogaloideae and related genera of Agavaceae–Informing questions in taxonomy at multiple ranks. Molec. Phylogenet. Evol. 84: 266–283.

Baker, J.G. 1887. *Agave* (*Eu-Agave*) *morrisii* Baker n. sp. Gard. Chron., ser. 3, 1: 543, fig. 105 (p. 549).

Bentham, J. and J.D. Hooker. 1883. Genera Plantarum. Vol. 3, part 2. Lovell Reeve & Co - Williams & Norgate, London.

Berger, A. 1915. Die Agaven. Beiträge zu einer Monographie. Verlag Gustav Fischer, Jena.

Bogler, D.J. and B.B. Simpson. 1995. A chloroplast DNA study of the Agavaceae. Syst. Bot. 20: 191–205.

Bogler, D.J., J.C. Pires, and J. Francisco-Ortega. 2006. Phylogeny of Agavaceae based on ndhF, rbcL, and its sequences. Aliso 22: 313–328.

Cabral-Cordero, I., J.A.Villarreal-Quintanilla, and A.E. Estrada Castillón. 2007. *Agave albopilosa* (Agavaceae, subgenus *Littaea*, group *Striatae*), a new species from the Sierra Madre Oriental in northeastern Mexico. Acta Bot. Mex. 80: 51–57.

Carrillo-Reyes, P., R.V. Aviña, and R. Ramírez-Delgadillo. 2003. *Agave rzedowskiana*, a new species in subgenus *Littaea* (Agavaceae) from western Mexico. Brittonia 55: 240–244.

Chase, M.W., D.E. Soltis, R.G. Olmstead, D. Morgan, D.H. Les, B.D. Mishler, M.R. Duvall, R. Price, H.G. Hills, Y. Qui, K. Akron, J.H. Rettig, E. Conti, J.D. Palmer, J.R. Manhart, K.J. Sytsma, H.J. Michaels, W.J. Kress, K.G. Karol, W.D. Clark, M. Hedren, B.S. Gaut, R.K. Jansen, K. Kim, C.F. Wimpee, J.F. Smith, G.R. Furnier, S.H. Strauss, Q. Xiang, G.M. Plunkett, P.S. Soltis, S.M. Swernsen, S.E. Williams, P.A. Gadek, C.J. Quinn, L.E. Eguiarte, E. Golenberg, G.H. Learn Jr., S. Graham, S.C.H. Barrett, S. Dayanandan, and V.A. Albert. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene rbcL. Ann. Missouri Bot. Gard. 80: 528–580.

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

Dahlgren, R.M. and H.T. Clifford. 1982. The Monocotyledons: A Comparative Study. Academic Press. London.

Dahlgren, R.M.T., H.T. Clifford, and P.F. Yeo. 1985. The Families of the Monocotyledons: Structure, Evolution, and Taxonomy. Springer Verlag, Berlin/Heidelberg.

Duvall, M.R., M.T. Clegg, M.W. Chase, W.D. Clark,W.J. Kress, H.G. Hills, L.E. Eguiarte, J.F.Smith, B.S. Gaut, E.A. Zimmer and G.H. Learn, Jr. 1993. Phylogenetic hypotheses for the monocotyledons constructed from rbcL sequence data. Ann. Missouri Bot. Gard. 80: 607–619.

Dumortier, B.C.J. 1829. Agavineae. Anal. Fam. Pl: 57-58.

Eguiarte, L.E., M.R. Duvall, G.H. Learn Jr., and M.T. Clegg. 1994. The systematic status of the Agavaceae and Nolinaceae and related Asparagales in the monocotyledons: An analysis based on the rbcL gene sequence. Bol. Soc. Bot. Méx. 54: 36–56.

Eguiarte, L.E. 1995. Hutchinson (Agavales) vs. Huber and Dahlgren (Asparagales). Análisis moleculares sobre filogenia y evolución de la familia Agavaceae *sensu* Hutchinson dentro de las monocotiledóneas. Bol. Soc. Bot. Méx. 56: 45–56.

Eguiarte, L.E., V. Souza, and A. Silva-Montellano. 2000. Evolución de la familia Agavaceae: filogenia, biología reproductiva y genética de poblaciones. Bot. Sci. 66: 131–150.

Engler, A. and K. Prantl. 1888. Die Natürlichen Pflanzenfamilien Teil 2, Abteil 5. Verlag von Wilhelm Engelmann, Leipzig.

Galván, R. and S. Zamudio. 2013. Una nueva especie de *Agave* subgénero *Littaea* (Agavaceae) del estado de Querétaro, México. Acta Bot. Mex. 105: 1–10.

García-Mendoza, A. J. and E. Martínez. 1998. Una nueva especie de *Agave*, subgénero *Littaea* (Agavaceae) de Guerrero y Oaxaca, México. Sida 18: 227–230.

García-Mendoza, A.J. and C. Chávez-Rendón. 2013. *Agave kavandivi* (Agavaceae: grupo *Striatae*), una especie nueva de Oaxaca, México. Rev. Mex. Biodiv. 84: 1070–1076.

García-Morales, L.J., J. García-Jiménez, and D. Iamonico. 2019. *Agave lexii* (Asparagaceae: Agavoideae), a new species from Mexico. Novon 27: 201–204.

Gentry, H.S. 1982. Agaves of Continental North America. Univ. of Arizona Press., Tucson.

Gil-Vega, K.C., C.E. Díaz-Quezada, A. Nava-Cedillo, A. García Mendoza, and J. Simpson. 2007. Análisis AFLP del género *Agave* refleja la clasificación taxonómica basada en caracteres morfológicos y otros métodos moleculares. Pp. 23–39, in P. Colunga-García Marín, A. Larqué Saavedra, L.E. Eguiarte, and D. Zizumbo-Villarreal (eds.). En lo ancestral hay futuro: Del tequila, los mezcales y otros Agaves. Centro de Investigación Científica de Yucatán A.C., Mérida.

Givnish, T.J., A. Zuluaga, D. Spalink, M. Soto Gomez, V.K. Lam, J.M. Saarela, and C. Ané. 2018. Monocot plastid phylogenomics, timeline, net rates of species diversification, the power of multi-gene analyses, and a functional model for the origin of monocots. Amer. J. Bot. 105: 1–23

Good-Avila, S.V., V. Souza, B.S. Gaut, and L.E. Eguiarte. 2006. Timing and rate of speciation in *Agave* (Agavaceae). Proc. Nat. Acad. of Sci. 103-24: 9124-9129.

Govaerts, R. and J. Thiede. 2013. Transfer of *Polianthes geminiflora* into *Agave* (Asparagaceae): new combinations (Nomenclature of Agave II). Willdenowia 43: 331–333.

Hernández-Vera, G. 2003. Inventario de especies silvestres del género *Agave* en el Estado de Jalisco y relaciones filogenéticas inferidas mediante marcadores AFLP. Universidad de Guadalajara - CUCEI - Centro de Investigación y Asistencia en Tecnología y Diseño del Estado de Jalisco, A.C, Guadalajara.

Hernández-Vera, G., E.P. Flores-Berrios, and M. Cházaro-Basáñez. 2007. Los Agaves de Jalisco, México: Análisis de relaciones genéticas mediante marcadores AFLP. In: Vázquez-García J.A., M. Cházaro-Basáñez, G. Hernández-Vera, E. Flores-Berrios, and Y.L. Vargas-Rodríguez (eds). Agaves del Occidente de México. Serie Fronteras de Biodiversidad 3. Universidad de Guadalajara - Consejo Regulador del Tequila A.C. - Centro de Investigación y Asistencia en Tecnología y Diseño del Estado de Jalisco A.C. - Comisión Nacional Forestal, Guadalajara, pp. 92–99.

Hochstätter, F. 2015. *Agave* Linné *(*Agavaceae). Digitally published by the author, Mannheim, Germany.

Hooker. J.D. 1888. *Agave ellemeetiana*. Curtis's Bot. Mag.: tab. 7027.
Hutchinson, J. 1934. The Families of Flowering Plants. Vol. II. Monocotyledons. The Clarendon Press, Oxford.
Jacobi, G.A. von. 1864. Versuch zu einer systematischen Ordnung der Agaveen. Hamburg. Gart.- & Blumenzeit 20: 455–466, 498–515, 539–562.
Jacobi, G.A.von. 1865. Versuch zu einer systematischen Ordnung der Agaveen (Fortsetzung). Hamburg. Gart.- & Blumenzeit 21: 344–346.
Jiménez-Barrón, O., R. García-Sandoval, S. Magallón, A. García-Mendoza, J. Nieto-Sotelo, E. Aguirre-Planter, and L.E. Eguiarte. 2020. Phylogeny, diversification rate, and divergence time of *Agave* sensu lato (Asparagaceae), a group of recent origin in the process of diversification. Front. Pl. Sci. 11: 536135.
Judd, W.S., C.S. Campbell, E.A. Kellogg, P.F. Stevens, and M.J. Donoghue. 1999. Plant Systematics: A Phylogenetic Approach. Ecol. Mediterr. 25: 215.
Kim, J.H., D.K. Kim, F. Forest, M.F. Fay, and M.W. Chase. 2010. Molecular phylogenetics of Ruscaceae sensu lato and related families (Asparagales) based on plastid and nuclear DNA sequences. Ann. Bot. 106: 775–790.
Koch, K. 1865. Agaveen-Studien (II–IV). Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 8: 92–95, 100–104, 108–112.
McKain, M.R., J.R. McNeal, P.R. Kellar, L.E. Eguiarte, J.C. Pires, and J. Leebens-Mack. 2016. Timing of rapid diversification and convergent origins of active pollination within Agavoideae (Asparagaceae). Amer. J. Bot. 103: 1717–1729.
McKelvey, S.D. and K. Sax. 1933. Taxonomic and cytological relationships of *Yucca* and *Agave*. J. Arnold Arbor. 14-1: 76–81.
McVaugh, R. 1989. Bromeliaceae to Dioscoreaceae. Flora Novo-Galiciana 15: 1-398.
Nyffeler, R. and U. Eggli. 2010. An up-to-date familial and suprafamilial classification of succulent plants. Bradleya 28: 125–144.
Salm-Dyck, J. de. 1859. Bemerkungen über die Gattungen *Agave* und *Fourcroya* nebst Beschreibung einiger neuen Arten. Bonplandia 7: 85–96.
Salm-Dyck, J. de. 1861. Bemerkungen über die Familie der Agaveen. Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 2: 177–182.
Seberg, O., G. Petersen, J.I. Davis, J.C. Pires, D.W. Stevenson, M.W. Chase, M.F. Fay, D.S. Devey, T. Jorgensen, K.J. Sytsma, and Y. Pillon. 2012. Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. Amer. J. Bot. 99-5: 875–889.
Starr, G.D., J. Etter, and M. Kristen. 2018. *Agave cremnophila* (Agavaceae), a new species from Southeastern Oaxaca, Mexico. Cact. Succ. J. 90: 39–45.
Starr, G.D., T.J. Davis, and J.A. Villarreal-Quintanilla. 2021. A cryptic new species of *Agave* (Asparagaceae/Agavoideae) and an amplified description of *Agave tenuifolia*. Cact. Succ. J. 93: 273–285.
Terracciano, A. 1885. Primo Contributo ad una Monografia delle *Agave*. Barnaba Cons di Antonio, Napoli, 58 pp.
Takhtajan, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225-359
Thiede, J. 2012. Nomenclatural transfers from *Manfreda* Salisb., *Polianthes* L. and *Bravoa* Lex. to *Agave* L. (Agavaceae/ Asparagaceae). Haseltonia 17: 94–95.
Thiede, J. 2015. Transfers from *Polianthes* into *Agave* (Asparagaceae/Agavaceae): new combinations. Bradleya 33: 82–83.
Thiede, J. 2019. A review of *Agave ellemeetiana* K. Koch (Asparagaceae /Agavaceae). Bradleya 32: 146–163.
Thiede, J. 2020. *Agave* (Agavaceae). In: Eggli, U. and R. Nyffeler (eds.). Monocotyledons Second Ed. Springer Verlag, Berlin/Heidelberg, pp. 21–312.

Thiede, J., G. Smith, and U. Eggli. 2019. Infrageneric classification of *Agave* L. (Asparagaceae: Agavoideae / Agavaceae): a nomenclatural assessment and updated classification at the rank of section, with new combinations. Bradleya 37: 240–264.

Thiede, J. and U. Eggli, U. 1999. Einbeziehung von *Manfreda* Salisbury, *Polianthes* Linné und *Prochnyanthes* in *Agave* (Agavaceae). Kakt. and. Sukk. 50: 109–113.

Thiede, J. and U. Eggli. 2020. Agavaceae. In: U. Eggli & R. Nyffeler (eds.). Monocotyledons Second Ed. Springer Verlag, Berlin/Heidelberg, pp. 9–20.

Ullrich, B. 1990. *Agave bracteosa* S. Watson ex Engelmann. Kakt. and. Sukk. 41(5): centre-page pullout 1990/13, ills.

Verhoek-Williams, S. 1998. Agavaceae. Pp. 60–70, in K. Kubitzki (ed.). The Families and Genera of Vascular Plants. Monocotyledons: Lilianae (except Orchidaceae). Springer Berlin, Heidelberg.

Verhoek-Williams, S. and W.J. Hess. 2002. Agavaceae. Fl. N. Amer. N. Mex. 26: 413-465.

Watson, S. and G. Engelmann. 1882. *Agave bracteosa* S. Wats. ex Engelm. Gard. Chron. n. Ser. 18: 776–777.

Zamudio-Ruiz, S. and E.S. Martínez. 1995. Una nueva especie de *Agave* del subgénero *Littaea* (Agavaceae) de la Sierra Madre Oriental, México. Acta Bot. Mex. 32: 47–52.

Zuccarini, J. G. 1833. Über einige neue Pflanzen aus den Gattungen *Agave* und *Fourcroya*. Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 16: 659-679.