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Echinoagave nievesiorum (Agavaceae, Asparagales): A new species from the Sierra Madre Occidental, Jalisco, Mexico

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Abstract

Echinoagave nievesiorum (Agavaceae, Asparagales), a new species endemic to the Sierra Wixárika (Huichola), part of the Sierra Madre Occidental, Jalisco, Mexico, is described. This species shares morphological characteristics with *Echinoagave rzedowskiana* but it differs from the latter by having narrower and striate leaves; leaf sheaths shorter, triangular and wider at the base; narrower ovary width; shorter tube length; tepal lobes at anthesis converging and tightening the filaments; larger filament length to flower length ratio; fruiting spikes thicker and denser with the peduncle covered by the capsules and the bracts usually deciduous; capsules broadly ellipsoid with dorsally blackish valves. A distribution map with biogeographic provinces is provided to place the species in an ecological and evolutionary context.

Key words: Allopatric speciation, endemic species, *Group Striatae*, subgen. *Littaea*

Resumen

Se describe *Echinoagave nievesiorum* (Agavaceae, Asparagales), una especie nueva endémica de la Sierra Wixárika (Huichola), Jalisco, México. Esta especie comparte características morfológicas con *Echinoagave rzedowskiana* pero se diferencia de esta última en tener hojas evidentemente estriadas, más estrechas en la parte más ancha y en la mitad de las hojas; vainas de las hojas más cortas, triangulares y más anchas en la base; ancho de ovario más estrecho; longitud del tubo más corta; lóbulos del tépalo en la antesis convergiendo y apretando los filamentos; mayor relación entre la longitud del filamento y la longitud de la flor; espigas en fructificación más gruesas y densas con el pedúnculo cubierto por las cápsulas y las brácteas generalmente caducas; cápsulas ampliamente elipsoides con las valvas dorsalmente negruzcas. Se proporciona un mapa de distribución con provincias biogeográficas para ubicar la especie en un contexto ecológico y evolutivo.

Palabras-clave: Endémica, especiación alopátrica, Grupo *Striatae*, Sierra Huichola, subgen. *Littaea*

Introduction

The circumscription of the family Agavaceae Dumortier (1829: 57) and that of the genus *Agave* Linnaeus (1753: 323), have changed historically with the emergence of new lines of evidence (Bentham & Hooker 1883, Engler & Prantl 1888, McKelvey & Sax 1933, Hutchinson 1934, Takhtajan 1980, Cronquist 1981, Dahlgren & Clifford 1982, Dahlgren *et al.* 1985, Chase *et al.* 1993, Duval *et al.* 1993, Eguiarte *et al.* 2000, APG II 2003, APG III 2009, APG IV 2016). However, recent treatments on the classification of Angiosperms adopt the concept of Agavaceae as an independent family (Judd *et al.* 2016, Thiede & Egli 2020, Thiede 2020) since a broad sense of Asparagaceae is not useful for gaining a better understanding of relationships between different clades due to its low support (Kim *et al.* 2010, Givnish *et al.* 2018). Likewise, *Agave* sensu lato being polyphyletic (Jiménez-Barrón *et al.* 2020) prompted Thiede *et al.* (2019) to merge *Manfreda* Salisbury (1866: 78), *Polianthes* Linnaeus (1753: 316) and *Prochnyanthes* Watson (1887: 457) into the same *Agave* concept, maintaining monophyly. However, instead of having a huge genus *Agave* an alternative is to recognize new genera, for highly supported lineages with substantial evolutionary and/or morphological change (Thiede & Egli 2020). Following this alternative three new genera of Agavaceae (Asparagales) were recently erected based on genetics, morphology, and estimated divergence times: *Echinoagave* A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 4), *Paleoagave* A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 5) and *Paraagave* A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 5).

Echinoagave, formerly known as *Agave* Linnaeus (1753: 323), subgenus *Littaea* (Tagliabue 1816: 106) Baker (1888: 164), sect. *Juncineae* Salm-Dyck (1861: 182), or Group *Striatae* Baker (1877: 171), includes species such as *E. dasyliroides* (Jacobi & C.D. Bouché in Jacobi 1865: 344) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 6), putatively considered to hold a basal position in the genus, by bearing “primitive” (plesiomorphic) morphology (leaves serrulate and scarcely succulent, inflorescences relatively simple, ovary incompletely inferior, tepals all equal, lobes nearly of equal length) (Gentry 1982). Molecular data support Gentry’s hypothesis since *Echinoagave* is a sister group to the great majority of species of *Agave* s.l. (Bogler & Simpson 1996, Bogler *et al.* 2006, Gil-Vega *et al.* 2007, Hernández-Vera 2007, Hernández-Vera *et al.* 2007, Archibald *et al.* 2015 and Jiménez-Barrón *et al.* 2020).

In Mexico, there are twelve species of *Echinoagave*: *E. albopilosa* (I.Cabral, Villarreal & A.E.Estrada in Cabral-Cordero *et al.* 2007: 52) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 6), from Nuevo León; *E. cryptica* (G.D.Starr & T.J.Davis in Starr *et al.* 2021: 275) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 6), from NE Mexico; *E. cremnophila* (G.D.Starr, Etter & Kristen in Starr *et al.* 2018: 40) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 6), from Oaxaca; *E. dasyliroides*, from the states of Mexico and Morelos; *E. graciela* (Galván & Zamudio 2013: 2) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 6), from Queretaro and San Luis Potosí; *E. kavandivi* (García-Mendoza & Chávez-Rendón 2013: 1071) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 6), from Oaxaca; *E. lexii* (García-Mor., García-Jim. & Iamónico in García-Morales *et al.* 2019: 1) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 7), from Tamaulipas; *E. petrophila* (García-Mendoza & Martínez 1998: 627) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 7), from Guerrero and Oaxaca; *E. rzedowskiana* (P.Carrillo, Vega & R.Delgad. in Carrillo-Reyes *et al.* 2003: 240) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 7), from Central Jalisco; *E. striata* (Zuccarini 1833: 678) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 7), from Central-Northeast Mexico; *E. stricta* (Salm-Dyck 1859: 94) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 7), from Puebla; and *E. tenuifolia* (Zamudio & Sánchez 1995: 48) A.Vázquez, Rosales & García-Mor. in Vázquez-García *et al.* (2024: 7), from Querétaro (Gentry 1982, Vázquez-García *et al.* 2007a, 2007b, Thiede 2020).

In Jalisco, the first record of an *Echinoagave* species was made in 1990, from La Toma [=Los Alisos], Bolaños, southern end of the Sierra Madre Occidental, by Agustín Flores-Macias, however, this species was initially confused with *E. dasyliroides* (Vigueras 1993), subsequently, with *E. striata* subsp. *falcata* (Engelmann 1875: 304) Gentry (1982: 245) (Cházaro-Basáñez *et al.* 2004a, 2004b, 2004c), and later with *E. rzedowskiana* (Carrillo *et al.* 2003, Cházaro-Basáñez *et al.* 2004a, Vázquez-García *et al.* 2004a, 2004b, 2007a, 2007b, Hernández-Vera 2007, Thiede 2020).

Here we propose that the populations from the Sierra Wixarika, in Bolaños, formerly treated under *Echinoagave rzedowskiana* are significantly distinct from the latter and deserve to be described as a new species named *Echinoagave nievesiorum*.

Methods

Recently, during the spring of 2021, a living specimen of this species, previously collected in 2013, bloomed on the rooftop of the home of one of the authors, Ana Nuño, at Huentitán El Alto, Guadalajara, Jalisco, and it was possible to understand in detail its flower morphology and phenology. One of the authors, García-Morales, looked closely at the specimens of several populations of the *E. rzedowskiana* complex and found differences among them in the leaves, spine, and serrulate margins. In the autumn of 2022, a couple of visits to Sierra de Bolaños, allowed us to obtain fruiting material from the vertical cliffs. Voucher specimens collected from these field surveys were made following Bridson & Forman (1989) and were deposited at IBUG herbarium.

A literature review was carried out. We reviewed and determined the specimens of *Agave* and *Echinoagave* deposited in the herbaria IBUG [herbarium acronym following Thiers (2023)]. Additionally, we revised the types and digitalized images from the corresponding herbaria and the iNaturalist website (<https://www.inaturalist.org/>). A map of the geographic distribution was made with the ArcMap software, v. 10.3 (ESRI 2016). To estimate the IUCN Red List category of *Echinoagave nievesiorum* we followed the guidelines and criteria B1 of the International Union for Conservation of Nature (IUCN 2022), and the Geospatial Conservation Assessment Tool (GeoCAT) from the Royal Botanic Gardens, Kew (Bachman *et al.* 2011) to calculate the Extent of Occurrence (EOO) and the Area of Occupancy (AOO), with the standard 2 × 2 km grid area.

Description of the new species

Echinoagave nievesiorum A. Vázquez, A.T. Nuño, Cházaro, Padilla-Lepe & García-Mor. *sp. nov.* (Figs. 1–4).

Type:—MEXICO. Jalisco: Municipio de Bolaños, Cercanías de Las Azucenas, Sierra Huichola, Cerro La Gallina, 21°52'18.20"N, 103°50'23.93"W, elev. 2286 m, con *Brahea sarukhanii* y *Dasyllirion acrotrichum* (floreó en cultivo en Huentitán El Alto, Guadalajara, 8 años después de haber sido recolectado), April 2021 (fl., bd.), J. Antonio Vázquez-García 10286 w/Ana Teresa Nuño-Rubio & Jesús Padilla-Lepe (holotype: IBUG!).

Diagnosis:—*Echinoagave nievesiorum* shares with *E. rzedowskiana* a similar rosette size and caespitose habit, rigid leaves, length of flowers, ovaries, tepal lobes, and size of capsules; however, it differs from the latter by having mature leaves bluish-white to whitish (vs. pale-green to green), narrower at the widest part (12.0–12.5 mm vs. 13.0–14.0 mm), and narrower at the middle of the leaves (6.0–6.5 mm vs. 7.0–10.0 mm); leaf sheaths shorter (9.0–11.0 mm vs. 28.0–34.0 mm), triangular and wider at the base (vs. rectangular and wider above the base); inflorescences usually straight and erect, sometimes vertically-curved or geniculate, rarely dropping (vs. usually horizontally-curved, often dropping and sinuous) narrower ovary width (4.5–5.1 mm vs. 5.7–7.5 mm); shorter tube length (5.5–6.4 mm vs. 7.0–10.0 mm); tepal lobes at anthesis converging and tightening the filaments (vs. diverging and not tightening the filaments); larger filament length to flower length ratio (2.0–2.3 vs. 1.8–1.9); fruiting spike narrowly pyramidal thicker (3.5–4.5 cm vs. 2.4–2.5 cm) and denser with the peduncle covered by the capsules and the bracts usually deciduous (vs. cylindroid, slim and lax, with the peduncle conspicuous and the bracts usually persistent); mature capsules broadly ellipsoid with dorsally blackish and opaque valves (vs. broadly ovoid, slightly depressed, with dorsally light brown and shiny valves) (Table 1).

Description:—Perennial, caespitose rosette 35.0–55.0 cm in diameter, 20.0–40.0 cm tall, hemispherical, compact, bluish-white to whitish. Leaves 29.5–32.0 × 1.2–1.25 × 0.2–0.4 cm, sheath length 9.0–11.0 mm, linear-triangular, straight or falcate, rigid, acuminate at the apex, grooved on both surfaces, bluish-white to whitish when mature, green when young; margin non-hyaline, crenate-dentate, 19 teeth per cm; spines 2.5–2.8 × 1.6–2.2 mm; terminal spine blackish at apex, base brown. Inflorescence 130.0–155.0 × 4.3–4.7 cm, usually straight and erect, sometimes curved or geniculate, rarely sinuous or dropping; fertile portion 17.5–38.0 cm, spike narrowly pyramidal dense, oblongoid to obtrullate, truncate at the base and acute at the apex; peduncle bracts 6.5–9.0 × 0.4–0.5 cm, linear, broadest at the sheath base, narrowing towards the apex, needle-like, greyish-white, brown base; flower bracts 2.0–2.3 × 1.0–1.5 cm, longer than flowers, triangular, caudate at apex, greyish-white. Flowers 65–70 pairs per spike, 21.7–23.5 × 14.0–16.0 mm, funnel-shaped, red to pink; pedicels 2 mm long on fruit. Ovary 7.0–7.8 × 4.5–5.1 mm, cylindrical to fusiform, glabrous. Corolla tube 5.5–6.4 × 10.0–12.0 mm; tepals 4.5–5.5 mm long, adaxially concave, the outer ones wider than the inner ones. Filaments 4.3–4.6 cm long, brown at anthesis then turning purple. Anthers 9.0–12.0 mm long, centric, arched, oblong, and rounded at both ends, brownish to yellow or pinkish-purple. Style 4.5–6.0 cm long, filiform, sinuate to straight. Fruiting spike 18–21 × 3.5–4.5 cm, narrowly pyramidal, covering ¼ of the length of the peduncle, capsules densely appressed hiding the peduncle, bracts usually deciduous. Capsules 0.8–1.1 × 0.8–1.0 cm, broadly

ellipsoid, apically dehiscent, valves dorsally blackish and opaque; perianth deciduous. Seeds 3.24–3.53 × 1.68–2.15 mm, laminate, lunate (“D” shape), one of the angles right, the other a cleft, the cleft 0.10–0.25 mm deep, black (Fig. 7).



FIGURE 1. *Echinoagave nievesiorum*. A. Fructing rosette on top of Sierra Wixárika, Cerro El Gallo, Bolaños, Jalisco. B. Stages of flower and inflorescence development, from a specimen cultivated at Huentitán El Alto, Jalisco, México. C. Miguel Cházaro on Cerro El Gallo, Bolaños, Sierra Wixárika. D. At moist vertical cliffs with *Dasylirion acrotrichum* and *Brahea sarukhanii* at El Nalgazo, Bolaños, Photographs: A by M. Chazaro, B by A.T. Nuño-R. (April 2021); C & D by J.A. Vázquez-García (April 2004 and October 2022, respectively).



FIGURE 2. Differences in leaves, spines, margins (upper row), flowers (mid row), and fruits (bottom row) among *Echinoagave* sp. from Concordia, Sinaloa (A); *E. rzedowskiana* from San Cristóbal de La Barranca, Jalisco (B); and *E. nievesiorum* from Bolaños, Jalisco (C). Photographs: Leaves, spines, margins, flowers (A), and fruits (A–B) by L.J. García-Morales; flowers (B) by S. Rosales; flowers (C) by A.T. Nuño-R.; and fruits (C) by J.A. Vázquez-G.



FIGURE 3. Inflorescences of three species of *Echinoagave*: A. *E. sp.* from Concordia, Sinaloa, Vega-Aviña & Gutiérrez-García 1000 (MEXU). B. *E. rzedowskiana* from San Cristóbal de la Barranca, Jalisco. C. *E. nievesiorum* from La Toma, Bolaños, Jalisco, Flores-M. & Flores-M. 2734 (WIS), D. *E. nievesiorum* from E of Astillero, Bolaños, Calónico-Soto & Flores-Franco 3199 (MEXU). Photographs: A, C & D from the MEXU and WIS herbaria virtual collections; and B by J. G. Morales-Padilla (left), by S. Rosales-M. (central top and right) and by M. Cházaro (central bottom).

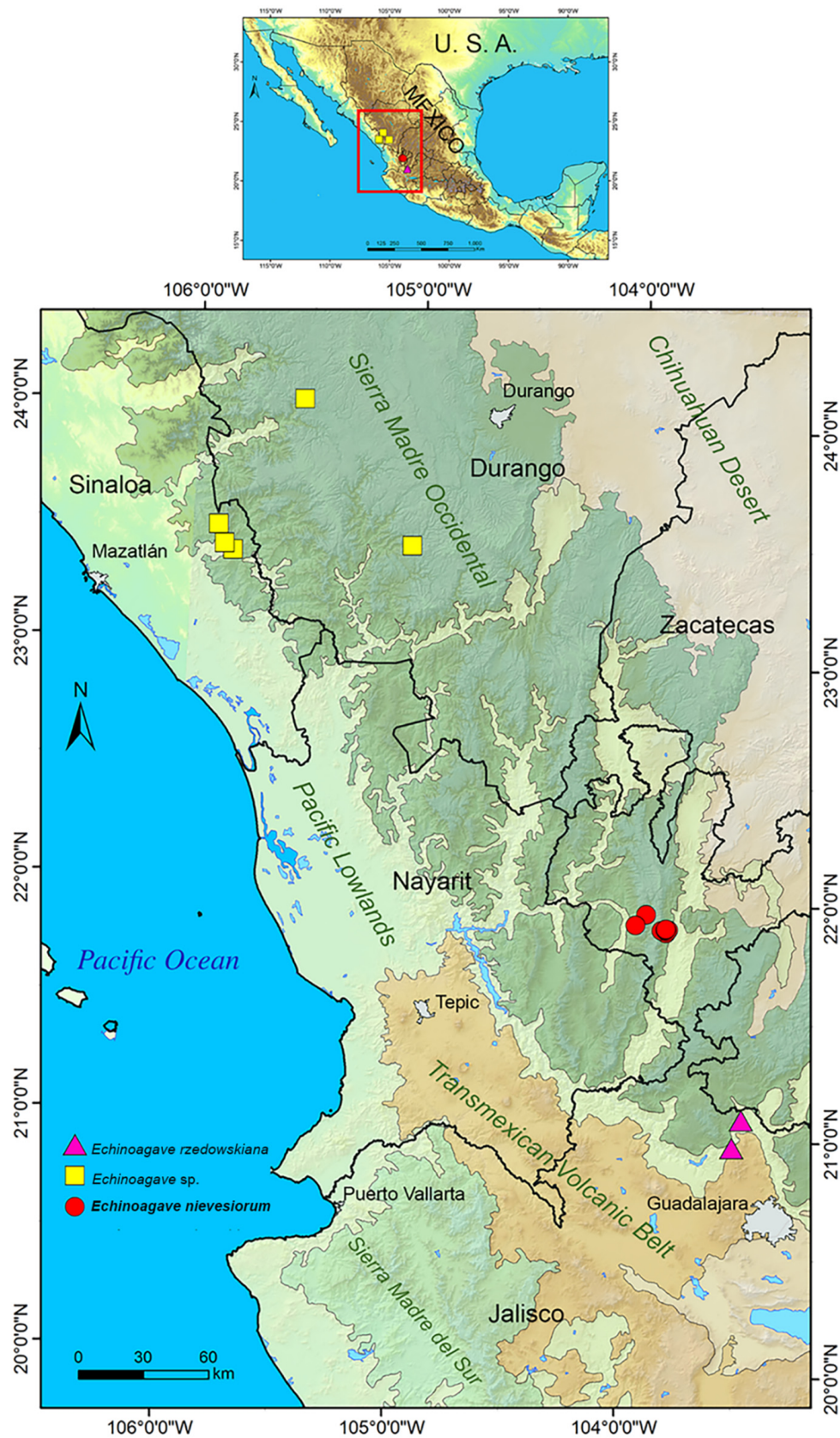


FIGURE 4. Map of *Echinoagave nievesiorum* and morphologically similar species. Different colors represent the biogeographic provinces *sensu* Morrone *et al.* (2017).

TABLE 1. Differences among *Echinoagave nievesiorum* and morphologically close species (Gentry 1982, García-Mendoza & Martínez 1998, Carrillo-Reyes *et al.* 2003).

	<i>E. nievesiorum</i>	<i>E. petrophila</i>	<i>E. rzedowskiana</i>	<i>E. dasyliroides</i>
Rosette diameter (cm)	35.0–55.0	50.0–80.0	25.0–45.0 (–65.0)	(60.0–)100.0–200.0
Rosette habit	Cespitose	Cespitose	Cespitose	Solitary
Leaves				
Length (cm)	29.5–32.0	40.0–70.0	(11.0)20.0–35.0(–50.0)	(40.0–)60.0–100.0
Width at the widest part (mm)	12.0–12.5	?	13.0–14.0	?
Width at the middle (mm)	6.0–6.5	4.0–9.0	7.0–10.0	20.0–38.0
Shape	Straight to falcate	Straight	Straight to falcate	Straight
Margins	Sparsely serrulate	Denticulate	Densely serrulate	Inconspicuously and sparsely serrulate
Sheath length (mm)	9.0–11.0	?	28.0–34.0	26.8–30.0
Sheath Shape	Triangular, widest at the base	?	Rectangular, narrower at the base	Trapezoid, widest at the base
Flower length (mm)	21.7–23.5	20–25	22.0–24	25.0–39.0
Ovary length (mm)	7.0–7.8	7.0–10.0	7.0–9.0	9.0–13.0
Width (mm)	4.5–5.1		5.7–7.5	
Tube length (mm)	5.5–6.4	3.0–4.0	7.0–10.0	8.0–15.0
Tepal lobes length (mm)	4.5–5.5	9.0–11.0	4.0–8.0	9.0–13.0
Tepal shape	Converging and tightening the filaments	Diverging and not tightening the filaments	Diverging and not tightening the filaments	Diverging and not tightening the filaments
Filaments insertion	Half of the tube	Apex of tube	Half of the tube	Half of the tube
Filament length to flower length ratio (mm)	2.00–2.30	1.36–1.43	1.80–1.90	1.08–1.10
Inflorescence (fruiting spike)				
Thickness (cm)	3.5–4.5	3.7–3.9	2.4–2.5	4.0–6.0
Density	Dense, peduncle covered	Lax, peduncle visible	Lax with, peduncle visible	Dense, peduncle covered
Bracts	Usually deciduous	Persistent	Persistent	Persistent
Capsule size (mm)	8.0–11.0 × 8.0–10.0	9.0–10.0 × 8.0–9.0	7.0–13.0 × 6.0–9.0	10.0–20.0 × 6.0–9.0
Shape	Broadly ellipsoid	Globose	Broadly ovoid	Ellipsoid to oblongoid
Color of valves	Dorsally blackish	Dorsally brown-blackish	Dorsally brownish green	Dorsally blackish
Habitat	Pine-oak forests	Tropical dry forest	Pine-oak forests	Pine-oak forest
Elevation (m a.s.l.)	2000–2600	850–1300	1501–1700	1900–2500
Distribution	N of Jalisco	E Guerrero, S Puebla, W & N Oaxaca	Central Jalisco	San Luis Potosí and Morelos

TABLE 2. The elevational disjunct distribution *E. nievesiorum* and morphologically close species

	801–	901–	1001–	1101–	1201–	1301–	1401–	1501–	1601–	1701–	1801–	1901–	2001–	2101–	2201–	2301–	2401–	2501–
	900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300	2400	2500	2600
<i>E. petrophila</i> , E Guerrero, S Puebla, W & N Oaxaca	x	x	x	x	x													
<i>E. rzedowskiana</i> , Central Jalisco							x	x										
<i>E. nievesiorum</i> , N of Jalisco													x	x	x	x		x
<i>E. dasytiritoides</i> , San Luis Potosí and Morelos												x	x	x	x	x	x	x

Distribution, habitat and phenology:—*Echinoagave nievesiorum* is endemic to Sierra Huichola (Sierra Wixarika), in the Bolaños municipality, Jalisco, Mexico (Fig. 8). It inhabits rocky outcrops on top of the mountains or vertical cliffs, usually found between 2000–2600 m in elevation, on pine-oak forests with some woody species such as *Alnus jorullensis* Kunth (1817: 20), *Arbutus glandulosa* Martens & Galeotti (1842: 533), *Arctostaphylos pungens* Kunth (1818: 278), *Brahea sarukhanii* Quero Rico (2000: 110), *Comarostaphylys glaucescens* (Kunth 1818: 278) Zucc. ex Klotzsch (1851: 76), *Pinus lumholtzii* Robinson & Fernald (1895: 122), and *Quercus gentry* Muler (1942: 474), it may also coexist with a great diversity of herbaceous or shrubby species including *Dasylyrion acrotrichum* Zuccarini (1843: 228), *Agalinis peduncularis* (Bentham 1835: 209) Pennell (1918: 135), *Ageratina* sp., *Bletia roezlii* Reichenbach f. (1877: 7), *Castilleja* sp., *Cuphea* sp., *Dalea* sp., *Echeveria dactylifera* Walther (1972: 179), *Echinocactus* sp., *Epidendrum* sp., *Euclidia* sp., *Gaultheria* sp., *Gaura* sp., *Graptopetalum amethystinum* (Rose 1905: 11) Walther (1931: 12), *Lamourouxia viscosa* Kunth (1817: 338), *Lobelia laxiflora* Kunth (1818: 311), *Lupinus madrensis* Seemann (1856: 278), *Milla biflora* Cavanilles (1793: 76), *Oncidium graminifolium* (Lindley 1840: 384) Lindley (1841: sub t. 48), *Pellaea ternifolia* (Cavanilles 1802: 266) Link (1841: 59), *Penstemon* sp., *Phaseolus* sp., *Pinaropappus diguetii* McVaugh (1972: 373), *Pippenalia delphiniifolia* (Rydberg 1924: 419) McVaugh (1972: 470), *Plantago* sp., *Salvia* sp., *Sedum jaliscanum* Watson (1890: 148), *Seymeria* sp., and *Tillandsia* sp. Flowering from March to April and fruiting from September to October.

Etymology:—The specific epithet honors the family members of Prof. Gregorio Nieves Hernández, who have contributed notably for over a decade to the knowledge of vascular flora and ethnobotany of the Sierra Wixarika.

Conservation status:—The known geographic distribution of *Echinoagave nievesiorum* covers an extent of occurrence (EOO) of 54.96 km². According to the IUCN Red List Criteria (IUCN 2022), *E. nievesiorum* could be categorized as Critically Endangered CR B1+B2ab(ii,iii) due to its EOO <100 km² (B1 criterion), and an area of occupancy (AOO) of 16 km² (B2) with severely fragmented locations [condition (a)] and an estimated continuing decline of its area of occupancy [condition (b)(ii)], and quality of habitat (b)(iii). Further exploration is required in neighboring municipalities and states to determine if this species may have a wider distribution.

Additional specimens examined:—MEXICO. **Jalisco:** Municipio de Bolaños, La Toma, Cerro La Gallina, km 20[22] hacia Puente de Camotlán, 16 June 1990 (young fr.), *A. Flores M., G. Martínez P. & N.P. Ramos G. 1890* (IBUG, IEB, MEXU); La Toma, 30[22] km NW of Bolaños, 1 July 1991 (young fr.), *A. Flores M. & J.M. Flores M. 2734* (IEB, MEXU, WIS). Cerros cercanos a La Toma, km 17 del camino a Tuxpan de Bolaños, 21°53'N, 103°50'W, elev. 2100–2170 m, 12 March 2001 (fr.), *P. Carrillo-Reyes & M. Barba 1515* (IBUG, IEB); Los Alisos (arriba de depósito de agua, “La Toma”), Cerro La Gallina, km 22 al NW de Bolaños, rumbo a Crucero Banderitas (Tuxpan de Bolaños-Bajío del Tule), 15 November 2003 (sterile), *J. A. Vázquez-García, 7614 w/G. López D. & M. Mantilla B.* (IBUG), same locality, elev. 2100 m, 8 April 2004 (sterile), *J. A. Vázquez-García 7790 w/M. Cházaro & R. Perez M.* (IBUG); Cerro El Gallo, km 29 al NW de Bolaños, elev. 2600 m, rumbo a crucero banderitas, 9 April 2004 (fl. buds and old infructescence); *J.A. Vázquez-García, M. Cházaro & R. Perez M. 7813* (IBUG); Frente a El Nalgazo, 23 km al NW de Bolaños, rumbo a Crucero Banderitas, elev. 2180 m, 21 October 2022 (sterile), *Vázquez-García, González-Villegas & Romero González 10205* (IBUG); Same locality, 29 Octubre 2022 (fr.), *J.A. Vázquez-García, J. Padilla-Lepe, A. Prinz, J.L. Lomeli-Hernández, A. Chavarín & S. Cristóbal-Gabriel 10216a* (IBUG); El Nalgazo, elev. 2200 m, 29 October 2022 (fr.), *S. Cristóbal-Gabriel, A. Prinz & J.L. Lomeli-Hernández 10216b* (IBUG).

Discussion

Echinoagave nievesiorum is sufficiently morphologically distinct from *E. rzedowskiana* to warrant its recognition as a distinct species. Additionally, they inhabit different biogeographic provinces and are ecologically disjunct along the elevational gradient (Table 2). Populations from Durango may correspond to *E. nievesiorum*, but further morphological study of populations from Durango is needed. *Echinoagave nievesiorum* differs from *E. petrophila* in having shorter leaves 29.5–32.0 vs. 40.0–70.0 cm, leaf margins sparsely serrulate vs. denticulate margins; longer tube length (5.5–6.4 vs. 3.0–4.0 mm); shorter tepal lobes (4.5–5.5 vs. 9.0–11.0 mm) and these converging and tightening the filaments vs. diverging and not tightening the filaments, filament insertion at the middle of the tube vs. at the apex; inflorescence dense and covering the peduncle vs. lax with the peduncle visible; bracts usually deciduous vs. persistent; and capsules broadly ellipsoid vs. globose. *Echinoagave nievesiorum* differs from *E. dasylyrioides* in having shorter rosettes (35.0–55.0 vs. 60.0–200.0 cm), caespitose vs. solitary; shorter leaves 29.5–32.0 vs. 40.0–100.0 cm); leaves narrower at the middle (6.0–6.5 vs. 20.0–38.0 mm); leaf sheath shorter (9.0–11.0 vs. 26.8–30.0 mm) and triangular vs. trapezoid;

flowers shorter (21.7–23.5 vs. 25.0–39.0 mm); ovary shorter (7.0–7.8 vs. 9.0–13.0 mm), tubes shorter (5.5–6.4 vs. 8.0–15.0 mm); tepal lobes shorter (4.5–5.5 vs. 9.0–13.0 mm), these converging and tightening the filaments vs. diverging and not tightening the filaments; and bracts usually deciduous vs. persistent.

Echinoagave nievesiorum adds up to a total of 13 species in genus *Echinoagave*, and together with *E. rzedowskiana*, are the only two species of the genus for Jalisco, the two endemic to the state.

The relatively close morphological and geographical proximity between *E. rzedowskiana* and *E. nievesiorum* suggest that the two belong to the basal and monophyletic *Striatae* clade (Hernández-Vera 2007, Hernández-Vera *et al.* 2007, Gil-Vega *et al.* 2007), recently erected as *Echinoagave* (Vázquez-García *et al.* 2024). *Echinoagave rzedowskiana*, is an endemic to the Trans-Mexican Volcanic Belt province in Jalisco, meanwhile *E. nievesiorum* is endemic to the Sierra Madre Occidental province; both species may have derived from a common ancestor distributed along the Sierra Madre Occidental from which migration into the relatively recent Trans-Mexican Volcanic Belt led to exposure to new environmental selective pressures allowing speciation.

It should be noted that floristically these two *Echinoagave* species hardly share cohabiting species in common, among the 37 species listed in the habitat of *E. nievesiorum* only one species, *Comarostaphylis glaucescens* (Carrillo-Reyes *et al.* 2003), occurred in the habitat of both species, representing 2.7% similarity among these distant plant communities. This is partly due to the geographical distance, ecological differences, and the different biogeographic provinces where they inhabit (Morrone *et al.* 2017). Particularly, *E. nievesiorum* is found in a colder climate on cliffs and on top of high mountains in the southern Sierra Madre Occidental biogeographic province, while *E. rzedowskiana* is in a subtropical warmer climate, on cliffs of highly eroded mid-elevation plateaus, within the Trans-Mexican Volcanic Belt province in Jalisco.

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