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A new endemic species and species richness distribution of the genus Pinguicula (Lentibulariaceae) in the Trans-Mexican Volcanic Belt, Mexico

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Abstract
Background: The genus *Pinguicula* harbors 110 species, of which 53 are distributed in Mexico. The formation of the Mexican mountains has favored the *Pinguicula* diversification. *Pinguicula* specimens collected in the State of México, along the Trans-Mexican Volcanic Belt (TMVB) do not correspond with any known species.
Questions: Do the collected specimens belong to a new species? What is its conservation status? How many *Pinguicula* species are there along the TMVB and how do they differentiate? How is the *Pinguicula* species richness distributed?
Studied species: *Pinguicula*.
Study site and dates: TMVB, 2005-2023.
Methods: Based on herbarium specimens and recently collected material, a morphological analysis and description were made. Conservation status was assessed following IUCN Red List Categories and Criteria. Herbarium specimens and digital records of *Pinguicula* from the TMVB were examined to generate a list and key. We analyzed the richness distribution of *Pinguicula* by states, vegetation types, elevation ranges, and grid cells.
Results: *Pinguicula tlahuica* is proposed as a new species. It is distinguished by the linear-spatulate summer leaves. The new species falls into the Endangered (EN) category. Along the TMVB, 16 species of *Pinguicula* are distributed. The State of México, Hidalgo and Michoacán, and the pine-oak forest were the richest. *Pinguicula* appeared between 759-3,427 m asl. The grid cell analyses revealed different areas with high richness.
Conclusions: Along the TMVB, the *Pinguicula* species richness centered on the Eastern and Western sectors. *Pinguicula crassifolia*, *P. michoacana*, *P. tlahuica*, and *P. zamudioana* are endemic to the TMVB.
Keywords: butterworts, carnivorous plants, diversification, Mexican Transition Zone, *Pinguicula* section *Orcheosanthus*.

Resumen
Antecedentes: *Pinguicula* agrupa 110 especies, 53 crecen en México. La formación de las montañas mexicanas ha favorecido su diversificación. Ejemplares provenientes del Estado de México, en la Faja Volcánica Trans-Mexicana (FVTM) no corresponden con alguna especie conocida.
Preguntas: ¿Los ejemplares recolectados representan una especie nueva? ¿Cuál es su estado de conservación? ¿Cuántas especies de *Pinguicula* crecen en la FVTM y cómo se diferencian? ¿Cómo se distribuye la riqueza de especies en la FVTM?
Especies estudiadas: *Pinguicula*.
Lugar y fechas del estudio: FVTM, 2005-2023.
Métodos: Con base en especímenes de herbario y muestras recolectadas recientemente se realizaron un análisis morfológico y una descripción. El estado de conservación se evaluó siguiendo las Categorías y Criterios de la Lista Roja de la UICN. Ejemplares de herbario y registros digitales de *Pinguicula* en la FVTM fueron examinados para generar una lista de especies y una clave. La riqueza fue analizada por estados, tipos de vegetación, rangos de elevación y celdas.
Resultados: *Pinguicula tlahuica* es propuesta como especie nueva, distinguible por las hojas de verano linear-espatuladas. Es considera dentro de la categoría En Peligro (EN). En la FVTM crecen 16 especies de *Pinguicula*. El Estado de México, Hidalgo y Michoacán, y el bosque de pino-encino son los más ricos. *Pinguicula* crece entre 759-3,427 m snm. Los análisis de celdas recuperaron distintas áreas con riqueza alta.
Conclusiones: En la FVTM, la riqueza de especies de *Pinguicula* está en los sectores Oriental y Occidental. *Pinguicula crassifolia*, *P. michoacana*, *P. tlahuica* y *P. zamudioana* son endémicas de la FVTM.
Palabras clave: diversificación, *Pinguicula* sección *Orcheosanthus*, pinguiculas, plantas carnívoras, Zona de Transición Mexicana.

Lentibulariaceae is a family of carnivorous plants that includes the genera *Genlisea* A.St.-Hil. with 30 species, *Pinguicula* L. with 110 species, and *Utricularia* L. with 271 species. *Pinguicula* is distinguished by the presence of true roots, leaves grouped in a basal rosette, and bractless peduncles with a terminal flower (Casper 1966). Based on morphological characters, Casper (1966) divided *Pinguicula* into *P*. subg. *Isoloba* Barnhart, *P.* subg. *Pinguicula* L., and *P*. subg. *Temnoceras* Barnhart. *Pinguicula* subg. *Isoloba* includes species with actinomorphic corollas, subequal lobes, white to white-purplish corolla, and trichomes arranged in three rows inside the corolla tube. In contrast, *P*. subg. *Pinguicula* harbors species with bilabiate, blue or violet corollas, and with the tube trichomes dispersed. Finally, *P*. subg. *Temnoceras* includes species with whitish bilabiate corollas, crenate or cleft apex lobes, the lobes of the upper lip shorter than the lower, and the tube trichomes arranged in three rows.

Pinguicula grows in Eurasia, the Americas, and the Caribbean islands (Shimai *et al*. 2021). All three subgenera are represented in Mexico, where 53 species have been recorded, 45 of which are endemics (López-Pérez *et al.* 2024). In addition, in Mexico, the species of *Pinguicula* grows almost exclusively in the mountain chains. Due to the large number of species and high endemism, Mexico represents a center of diversity for the group.

The Trans-Mexican Volcanic Belt morphotectonic province (TMVB) crosses central Mexico from east to west between the 18° 30’ N and 21° 30’ N parallels. It includes, at least partially, the states of Colima, Guanajuato, Hidalgo, Jalisco, Mexico, Mexico City, Michoacán, Morelos, Nayarit, Puebla, Querétaro, Tlaxcala, and Veracruz (Ferrusquía-Villafranca 2007). The TMVB includes mountain ranges, volcanic structures, and intermountain plateaus at different elevations ranging from Cerro San Juan in Nayarit to the Sierra de Chiconquiaco in Veracruz (Gámez *et al*. 2012). The province is divided into the Eastern, Central and Western sectors (Ferrusquía-Villafranca *et al*. 2007, Ferrari *et al*. 2012) and merges three major mountain ranges. The Eastern sector meets the Sierra Madre Oriental and the Sierra Madre del Sur. Whereas the Western sector connects with the Sierra Madre Occidental and the Sierra Madre del Sur. Whereby, the TMVB represents the nucleus of the Mexican Transition Zone (MTZ; Halffter & Morrone 2017).

Ferrari *et al*. (2012) described the TMVB formation in four episodes. The first episode showed a volcanic arc during the Early and Mid Miocene (~20-10 Ma), followed by a pulse of mafic volcanism during the Late Miocene (~11-7 Ma). Then, between the Late Miocene and Early Pliocene (7.5-3 Ma), a silicic and bimodal episode was recorded. Lastly, an arc from the Late Pliocene to the Holocene (2.5 Ma-present) is observed (Gómez-Tuena *et al*. 2005, Ferrari *et al*. 2012). The TMVB displays the most recent orogenic processes with volcanism still active (Gámez *et al*. 2012) and its uplift has favored the biogeographic transition, speciation, and persistence of several taxa, such as the tribe Tigridieae B. M. Kittel (Munguía-Lino *et al*. 2015), *Solanum* L. sect. *Petota* Dumort (Murillo-Pérez *et al*. 2022), the genera *Cosmos* Cav. and *Lycianthes* (Dunal) Hassl. (Vargas-Amado *et al*. 2013, Anguiano-Constante *et al*. 2018), and populations of *Nolina parviflora* Hemsl. (Ruiz-Sanchez & Specht 2013).

During a systematic study of *Pinguicula* in Mexico, we collected material in the Eastern sector of the TMVB, which did not correspond with any previously known species. Here, we propose it as a new and endemic species. In addition, we analyzed the species richness distribution of *Pinguicula* along this province. The extreme sectors of the TMVB are the confluence of the three major mountain ranges. We expect that the species richness will be unevenly distributed.

Materials and methods

Taxonomic treatment. We examined the specimens of *Pinguicula* from the IBUG, IEB, and MEXU herbaria (herbarium acronyms per Thiers 2023). For the new species, the morphological description was accomplished based on fresh material and herbarium specimens. The terminology followed Casper (1966), Moreno (1984), and Zamudio (2001). We used the infrageneric classification proposed by Casper (1966). The color of the structures was designated in accordance with the RHS Colour Chart (Royal Horticultural Society 2015).

Conservation status. The conservation status of the new species was evaluated based on the IUCN Red List Categories and Criteria (IUCN 2022). The Area of Occupancy (AOO) was estimated with GeoCAT (Bachman *et al*. 2011).

Study area, database and species richness of Pinguicula. The TMVB is made up of volcanic successions, continental sedimentary deposits, and volcanic-sedimentary deposits situated in the intermountain depressions, whereby the study area was delimited under the morphotectonic province criterion of Ferrusquía-Villafranca (2007). A morphotectonic province has physiographic and geologic-tectonic features unique enough to distinguish it from such other neighboring provinces (Ferrusquía-Villafranca 1993). The records from CHAP, CHAPA, ENCB, FCME, HUAP, IBUG, IEB, INEGI, INIF, MEXU, QMEX, SLPM, and XAL herbaria (Thiers 2023), the digital herbaria CAS, K, MO, and US (Thiers 2023), as well as the information available in the Global Biodiversity Information Facility (GBIF 2023), the Southwest Environmental Information Network (Gilbert *et al*. 2019), and the Sistema Nacional de Información sobre Biodiversidad de México (CONABIO 2020) were compiled and curated into a database. To assure the taxonomic identity of the digital records, only specimens with images were examined. Specimens without geographical data were georeferenced using Google Earth Pro v. 9.191.0.0 (Google 2023), the Mapa Digital de México v. 6.1 (INEGI 2023a) and following the recommendations of Garcia-Milagros & Funk (2010). The specimens with ambiguous information were excluded. The species distribution maps were elaborated using the presence records of *Pinguicula* along the TMVB.

S*pecies richness distribution of Pinguicula along the TMVB*. The species richness distribution was quantified by 1) states, 2) vegetation types, 3) elevation ranges, and 4) grid cells. The shapes of states (INEGI 2018) and vegetation types (Rzedowski 1978) were clipped with the TMVB polygon of Ferrusquía-Villafranca (2007). The distribution richness analyses by states and vegetation types were carried out through a direct count of species documented in each polygon. Species richness by elevation ranges was quantified based on 500 m intervals. The Continuo de Elevaciones Mexicano 3.0 (INEGI 2023b) with a resolution of 15 m was used to assign the elevation value to each record. The grid cell richness analyses were performed using a cell size of 0.21 × 0.21° based on Suárez-Mota & Villaseñor (2011) method and 0.24 × 0.24° according to Oyala (2020) criterion.

Results

Pinguicula tlahuica López-Pérez & Zamudio, sp. nov. (Figures 1 and 2, Table 1).

Type. Mexico, Estado de México, municipio Ocuilan de Arteaga, parque Tlatucapa, Peña Redonda, 18° 57’ 56.6” N, 99° 24’ 58.5” W, 2,189 m snm, 12 April 2023, *J. López-Pérez & G. Munguía-Lino 641* (Holotype: IBUG; Isotype: MEXU).

Diagnosis. *Pinguicula tlahuica* is morphologically similar to *P. moranensis* Kunth in the form and size of the flowers, but it is distinguished from it by: the oblong to oblong-spathulate winter leaves; linear-spatulate summer leaves, 7.0-14.5 × 0.5-1.7 cm; blooming with winter rosette.

Description. Perennial herbs. Leaves dimorphic, arranged into basal rosettes; winter rosette compact, subhypogeous, 1.2-1.9 cm in diameter, leaves 55-70, succulent, petiole 0.5-2.5 mm long, oblong, spathulate to oblong-spathulate, 2.5-8.0 × 1.0-3.0 mm, acute to obtuse, pubescent; summer rosette lax, leaves 4-8, sessile, ascending, linear-spatulate, 7.0-14.5 × 0.5-1.7 cm, acute to obtuse, margin revolute, pubescent on the upper surface with sessile and stipitate glandular trichomes. Peduncles 1-6 per plant, 4.0-12.0 cm long, pilosulose with stipitate glandular trichomes. Flowers 3.0-5.0 cm long, including the spur; calyx bilabiate, outer surface pilosulose with stalked glandular trichomes; upper lip trilobate, triangular lobes, 2.0 × 1.0 mm; lower lip bilobate, lobes triangular to lanceolate, 2.0 × 0.5 mm; corolla bilabiate, blue-violet (violet-blue group 95A), with a white macula at the base of lower lip that extends to the throat; upper lip bilobate, lobes oblong to obovate, 8.0-12.0 × 3.5-7.0 mm, truncate to obtuse; lower lip trilobate,

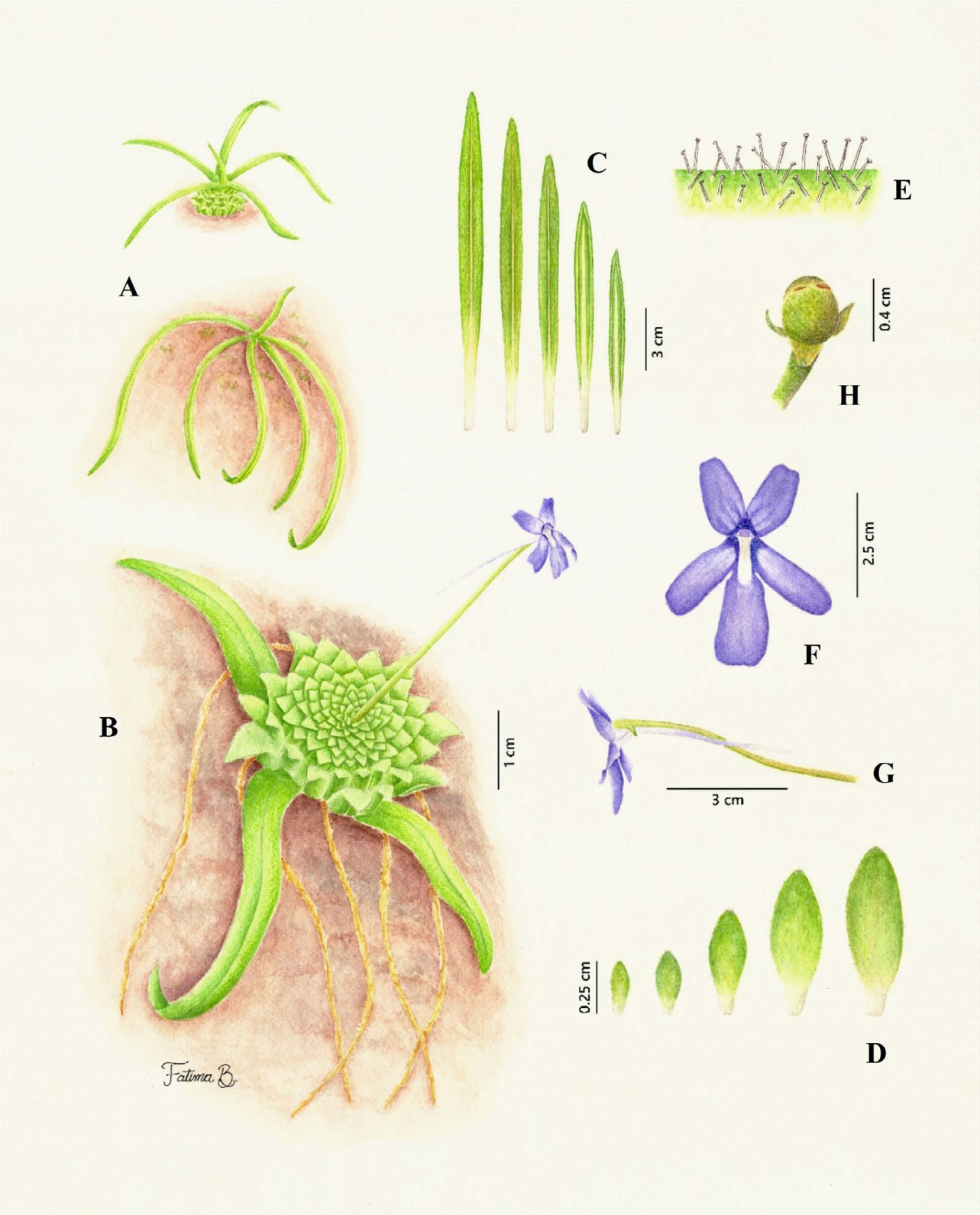

Figure 1. *Pinguicula tlahuica*. A) Summer rosette. B) Flowering winter rosette. C) Summer leaves. D) Winter leaves. E) Stipitate glands on the leaf. F) Flower frontal view. G) Flower lateral view. H) Fruit. Illustrated by Fatima Bracamontes based on type material (*J. López-Pérez & G. Munguía-Lino 641*).

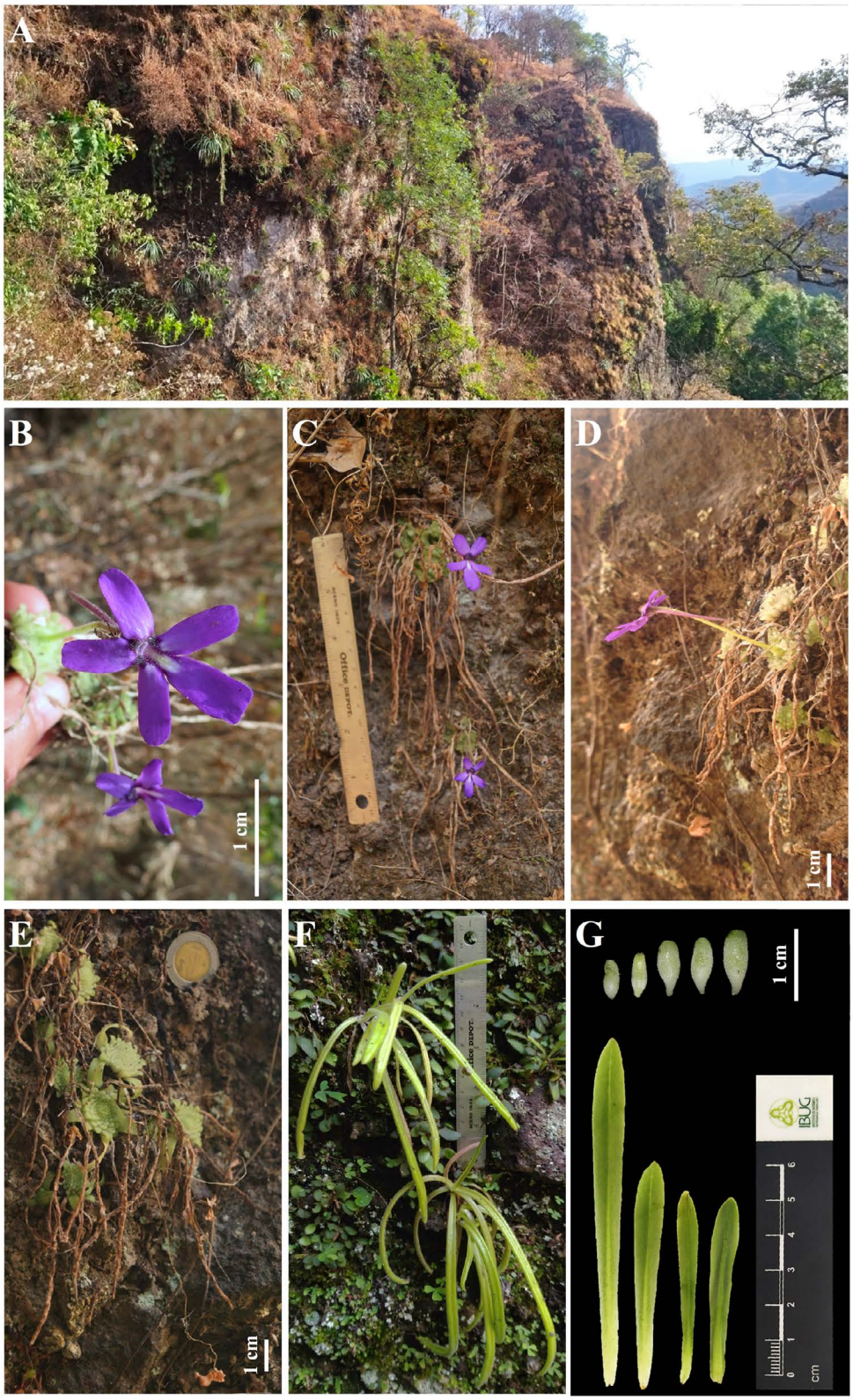

Figure 2. *Pinguicula tlahuica*. A) Habitat. B) Flower frontal view. C-D) Winter rosette with flowers. E) Sterile winter rosette. F) Summer rosette. G) Transition among winter and summer leaves. A-G by Jorge López-Pérez.

lobes oblong to obovate, truncate to obtuse, lateral lobes 7.0-8.0 × 3.0-6.0 mm, the medium larger than the lateral ones, 8.0-10.0 × 4.0-6.5 mm; corolla tube infundibuliform, 2.5-4.0 × 2.0-2.5 mm, pilosulose with stalked glandular trichomes; spur cylindrical-subulate, 2.0-3.0 cm long, brown to green-greyish (brown group N200A, greyed-green group 197B); ovary subglobose, 1.5 mm in diameter, glandular pilosulose; stigma bilobate, blue-violet (violet-blue group 95A). Capsule globose, 4-5 mm in diameter. Seeds not seen.

Distribution and ecology. *Pinguicula tlahuica* is endemic to the TMVB. It grows in the municipalities of Ocuilan de Arteaga, State of México, and Cuernavaca, Morelos (Figure 3). The area is part of a mega-stratovolcanoes alignment in the Eastern sector of the TMVB (Ferrusquía-Villafranca 2007). *Pinguicula tlahuica* inhabits in ravines, on northeastern facing igneous rock walls, within the oak forest at elevations of 1,860-2,190 m asl (Figure 2A). The plants grow in compact groups, associated with mosses, and in sympatry with *Bomarea edulis* (Tussac) Herb., *Calochortus pringlei* B.L.Rob., *Dahlia merckii* Lehm., *Svenkoeltzia congestiflora* (L.O.Williams) Burns-Bal, *Hechtia* sp., *Nolina* sp., and *Pitcairnia* sp.

Table 1. Morphological comparison among *Pinguicula gypsicola*, *P. moranensis*, and *P. tlahuica*.

Character	*P. gypsicola*	*P. moranensis*	*P. tlahuica*
Winter rosette			
Life form	Subhypogeous	Epigeous, hypogeous, and subhypogeous	Subhypogeous
Rosette diameter (cm)	1.5-2	1-3	1.2-1.9
Leaf number	41-42	30-80	55-70
Leaf size (cm)	0.5-1.5 × 0.1-0.2	1-3 × 0.2-0.6	0.25-0.8 × 0.1-0.3
Leaf shape	Spatulate to elliptic-lanceolate	Lanceolate to oblong-lanceolate	Spatulate to oblong-spatulate
Summer rosette			
Leaf orientation	Ascendent	Adpressed	Ascendent
Leaf number	6-17	4-12	4-8
Leaf size (cm)	2.2-11 × 0.3-0.6	3.5-9.5 × 2.5-7.5	7-14.5 × 0.5-1.7
Leaf shape	Linear lanceolate, ciliate at the base	Elliptic, obovate to suborbicular, not ciliate	Linear-spatulate, not ciliate
Flower length (cm)	3-4	2.5-6	3-5
Corolla upper lobes size (mm)	7-10 × 2-5	7-18 × 4-11	8-12 × 3.5-7
Corolla lower lobes size (mm)	6-11 × 3-7	6.5-11.5 × 4.5-9	7-8 × 3-6
Corolla lower median lobe size (mm)	7-13 × 3-7	8-18.5 × 5-10	8-10 × 4-6.5
Spur length (mm)	14-22	15-37	20-30
Flowering time	June to October, with summer rosette	All year, with winter and summer rosettes	April to May with winter rosette
Habitat	Gypsum soils in xeric scrublands	Limestone rock walls, soils in xeric scrublands, igneous rock walls in pine-oak forest, cloud forest, tropical deciduous forest	Igneous rock walls in oak forest

Conservation status. *Pinguicula tlahuica* is known only from two localities. It grows along a few ravines on igneous rock walls. GeoCAT calculated an AOO of 12 km^2. According to the IUCN Red List Categories and Criteria, we preliminary recommend the category of Endangered (EN), criterion B2ab(iii).

Phenology. The summer rosettes have been observed from May to September. In contrast, the winter rosettes appear from September to May. The plants bloom from April to May when the winter rosette is present.

Etymology. The specific epithet honors the Tlahuica ethnical people. The tlahuicas inhabit some villages in Ocuilan de Arteaga, State of México (Álvarez Fabela 2006).

Additional specimens examined. Mexico, Estado de México, municipio Ocuilan de Arteaga, Barranca y mirador Peña Redonda, 2,185 m snm, 18° 57' 57.3" N, 99° 24' 57.9" W, 29 September 2021, *A. Rodríguez et al. 8466* (IBUG, IEB, MEXU); Parque Tlatucapa, Peña Redonda, 2,185 m, 18° 57' 57.2" N, 99° 24' 59" W, 3 September 2022, *J. López-Pérez & G. Munguía-Lino 589* (IBUG, IEB, MEXU). Morelos, Cuernavaca, Barranca cerca del Tecolote, antigua vía de madera hacia Bella Vista del Monte, May 1955, *E. Lyonnet s/n* (MEXU, two sheets MEXU-699454 and MEXU-699473).

Species of Pinguicula in the TMVB. There are 16 species of *Pinguicula* recorded along the TMVB (Table 2, Figures 3, 4). *Pinguicula crassifolia*, *P. michoacana*, *P. tlahuica*, and *P. zamudioana* are exclusive to this morphotectonic province (Figures 3, 4). The *Pinguicula* species along the TMVB can be identified as follows:

1. Corolla isolobate to subisolobate, the superior and inferior lips lobes are almost equal…….. 2
2. Annual plants, with a single type of leaves (homophyllous); corolla lilac or white, palate diminute; tube with purple veins…… *P. lilacina*
2. Perennial plants, with two types of leaves during the annual cycle (heterophyllous); corolla white, occasionally with violet margin, palate absent; tube with green veins…….. 3
3. Corolla tube geniculate ..... *P. acuminata*
3. Corolla tube straight 4
4. Rupiculous plants; winter rosette epigeal, leaves entire, blade pubescent; summer leaves entire…….. *P. agnata*
4. Terrestrial plants; winter rosette hypogeal, leaves ciliate at the base, blade glabrous; summer leaves ciliate at the base……..... 5
5. Calyx accrescent, covering the capsule at maturity ……..... *P. casperi*
5. Calyx not accrescent, nor covering the capsule at maturity ..... *P. parvifolia*
1. Corolla bilabiate, with clear distinction between the superior and inferior lip lobes ….....…..... 6
6. Annual plants; flowers 3-7 mm long (including the spur); corolla lobes crenate or cleft……..... *P. crenatiloba*
6. Perennial plants; flowers larger than 10 mm (including the spur); corolla lobes entire, emarginate or erose…….. 7
7. Homophyllous plants, winter and summer rosettes undifferenciated during the annual cycle..... 8
8. Corolla white, lobes emarginate or erose, with evident purple veins ……..... .....*P. emarginata*
8. Corolla pink, lobes entire, with incospicuos veins or the same color as the lobes…..... *P. zamudioana*
7. Heterophyllous plants, winter and summer rosettes differentiated during the annual cycle…..... 9
9. Corolla red to purple-red; tube evident; spur equal or larger than the tube…..…..... *P. crassifolia*
9. Corolla blue, purple, pink or violet; tube diminute; spur larger than the tube……..……..... 10
10. Summer leaves linear-spatulate…..... *P. tlahuica*
10. Summer leaves cuneate, oblong, elliptic to suborbicular..... 11
11. Summer leaves ciliate at the base……..……..... 12
12. Winter rosette subhypogeal, leaves entire……..……..... *P. elizabetiae*
12. Winter rosette hypogeal, leaves ciliate at the base……..... 13
13. Winter rosette covered by a layer of dry membranous leaves, leaves 25-86, lanceolate…..... *P. oblongiloba*
13. Winter rosette without dry membranous leaves, leaves 20-40, ovate-lanceolate……. .....*P. michoacana*
11. Summer leaves entire..……..……..……..... 14
14. Winter rosette epigeal, laxa; flowers 2.4-2.8 cm long (including spur); corolla pink to whitish-purple, whit a yellow macula at the throat……..... *P. esseriana*
14. Winter rosette epigeal to hypogeal, compact; flowers 2.5-6 cm long (including spur); corolla purple, whit a white macula at the throat …..……..... 15
15. Winter rosette epigeal to subhypogeal, covered by dry membranous leaves..... *P. moranensis*
15. Winter rosette hypogeal, without dry membranous leaves..... *P. macrophylla*

Table 2. Species list and distribution of *Pinguicula* along TMVB. (*) Exclusive species of TMVB. States: CdMx) Mexico City; Gto) Guanajuato; Hgo) Hidalgo; Jal) Jalisco; Méx) State of México; Mich) Michoacán de Ocampo; Mor) Morelos; Nay) Nayarit; Pue) Puebla; Qro) Querétaro de Arteaga; Tlax) Tlaxcala; Ver) Veracruz de Ignacio de la Llave. Vegetation type: G) Grassland; Cf) Cloud forest; Tef) Tropical evergreen forest; Pof) Pine-oak forest; Tf) Thorn forest; Tdf) Tropical deciduous forest; Xs) Xeric scrubland.

Specie	State	Vegetation type
P. acuminata Benth.	CdMx, Hgo, Méx, Mich, Qro, Tlax	Pof, Xs, G
P. agnata Casper	Hgo	Xs
P. casperi H.D.Juárez & Zamudio	Jal	Pof
P. crassifolia Zamudio*	Hgo	Pof
P. crenatiloba DC.	Jal, Méx, Mich, Nay	Pof, Tdf
P. elizabethiae Zamudio	Hgo	Xs
P. emarginata Zamudio & Rzed.	Pue, Ver	Pof, Cf
P. esseriana B.Kirchn.	Hgo	Xs
P. lilacina Schltdl. & Cham.	Nay, Ver	Pof, Cf
P. macrophylla Kunth	Gto	Tdf
P. michoacana Zamudio & H.D.Juárez*	Mich	Tdf
P. moranensis Kunth	CdMx, Gto, Hgo, Méx, Mich, Mor, Pue, Qro, Tlax, Ver	Pof, Cf, Tdf, Tef, Xs, G
P. oblongiloba A.DC.	Gto, Jal, Méx, Mich	Pof, Tf, Tdf, G
P. parvifolia B.L.Rob.	Jal, Méx, Mich, Mor, Nay	Pof, Tf, Tdf
P. tlahuica López-Pérez & Zamudio*	Méx, Mor	Pof
P. zamudioana H.D.Juárez & Muñiz-Castro*	Jal	Tdf

Species richness distribution of Pinguicula along the TMVB. The species richness distribution analyses indicated that Hidalgo, the State of México and Michoacán (six species each), and the pine-oak forest (10 species) were the richest states and vegetation type (Figure 5A, B, Table 2). While, Mexico City, Morelos, Puebla, Querétaro, and Tlaxcala registered two species each. *Pinguicula acuminata*, *P. casperi*, *P. crassifolia*, *P. crenatiloba*, *P. emarginata*, *P. lilacina*, *P. moranensis*, *P. oblongiloba*, *P. parvifolia*, and *P. tlahuica* were found in pine-oak forest. Only, *P. moranensis* was found in the tropical evergreen forest.

Along the TMVB, the species of *Pinguicula* appeared from 759 m asl to 3,427 m asl (Figure 5C), but these were found mainly between 1,500-1,999 m asl (Figure 5D). *Pinguicula moranensis* had the widest elevation distribution range (996-3,427 m asl, Figure 5C). Whereas, *P. michoacana* had the narrowest elevation distribution range (1,828-1,852 m asl, Figure 5C). Furthermore, *P. moranensis* reached the highest elevation (3,427 m asl, Figure 5C) and *P. lilacina* had the lowest elevation (759 m asl, Figure 5C).

The two cell grid sizes recovered different areas with high species values on the Eastern and Western sectors of the TMVB (Figure 6). The analysis with cells of 0.21 × 0.21° rescued one cell with the highest species richness value in the Eastern sector (Figure 6A). On the other hand, the 0.24 × 0.24° cell analysis highlighted two richest cells, one on the Eastern and the other in the Western sectors (Figure 6B).

Discussion

Taxonomic treatment. *Pinguicula tlahuica* was first collected in 1955 in the vicinity of Bella Vista del Monte, municipality of Cuernavaca, Morelos by *E. Lyonnet*. The second author searched for the plants in this locality from 2005 to 2016, but never found them. During a field expedition in 2021, it was rediscovered and collected in the vicinity of

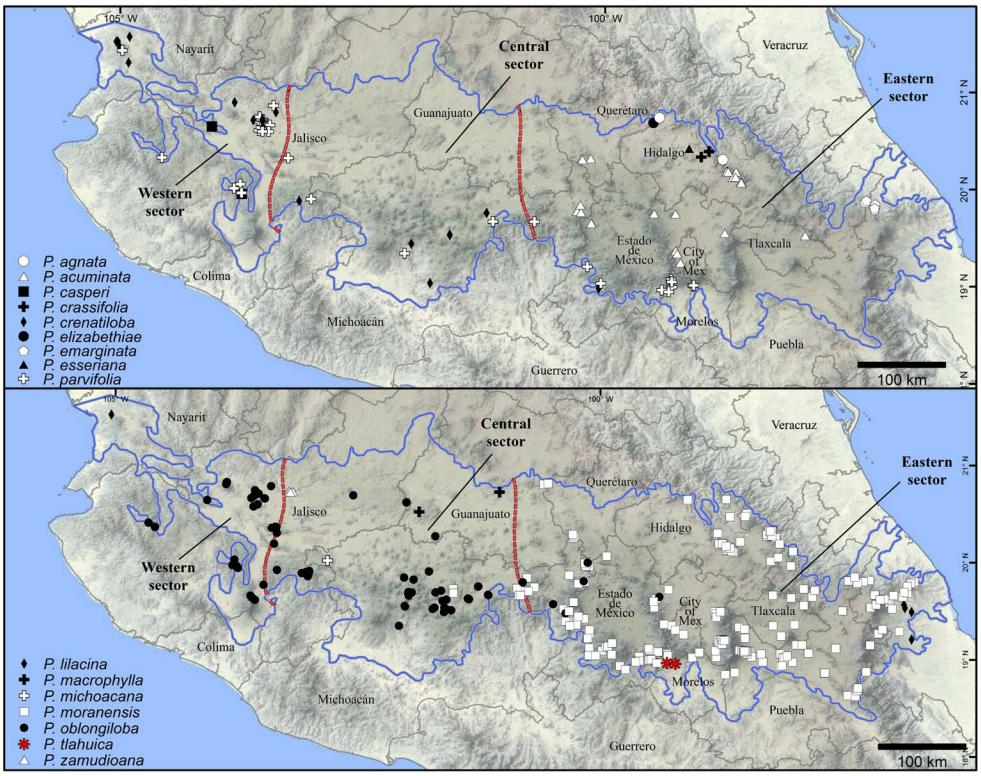

Figure 3. Species distribution map of *Pinguicula* along the TMVB. Blue line: TMVB limits. Red line: Sector limits. Grey line: State limits.

Ocuilan de Arteaga, State of México. The dimorphic leaves arranged in summer and winter rosettes, the blue-violet and bilabiate corollas, the short infundibuliform tube, and the long spur place the new taxon within *P*. subg. *Pinguicula* section *Orcheosanthus* A.DC. (Candolle 1844). Within this section, *P*. *tlahuica* is similar to *P*. *moranensis* and *P*. *gypsicola* Brandegee by the form and size of the flowers, but morphological characters and ecological preferences set it apart (Table 1). *Pinguicula tlahuica* differs from *P*. *moranensis* by the linear-spatulate and ascendant summer leaves (*vs*. elliptic to sub-orbicular and adpressed to the soil), and the flowering period with the presence of winter rosettes (*vs*. winter and summer rosettes). In addition, it differs from *P*. *gypsicola* by the linear-spatulate and entire at the base summer leaves (*vs*. linear-lanceolate and ciliate at the base), and niche preferences. *Pinguicula tlahuica* grows on igneous rock walls in the oak forest, whereas *P. gypsicola* is found on gypsum soils of the xeric scrubland. *Pinguicula tlahuica* adds up to 54 the taxonomic richness of *Pinguicula* in Mexico.

Species richness distribution and endemism of Pinguicula along the TMVB. The MTZ represents the boundary between the Nearctic and Neotropical regions (Villaseñor *et al*. 2020). It includes the main mountainous chains of Mexico, Guatemala, Honduras, El Salvador, and Nicaragua (De Mendonça & Ebach 2020). The MTZ is a set of morphotectonic and physiographic provinces with different ages and origins (Ferrusquía-Villafranca 1993, Mastretta-Yanes *et al*. 2015). The orientation of the mountain ranges favors the dispersal of northern elements to the south and vice versa (Zunino & Halffter 1988). Shimai *et al.* (2021) explain the evolution within *Pinguicula* by ancient geographical expansions and gene flow, and subsequent vicariance with genetic drift. Whereas, Domínguez *et al*. (2024) highlight the effects of climatic changes over time in the mountain chains of the MTZ, favoring speciation and persistence, which is reflected in the high species richness and endemism of *Pinguicula* (López-Pérez *et al*. 2024).

Within the MTZ, the TMVB connects three major mountain ranges at both ends (Ferrusquía-Villafranca *et al*. 2007, Ferrari *et al*. 2012). Consequently, the TMVB represents a center of diversity, endemism, persistence, and

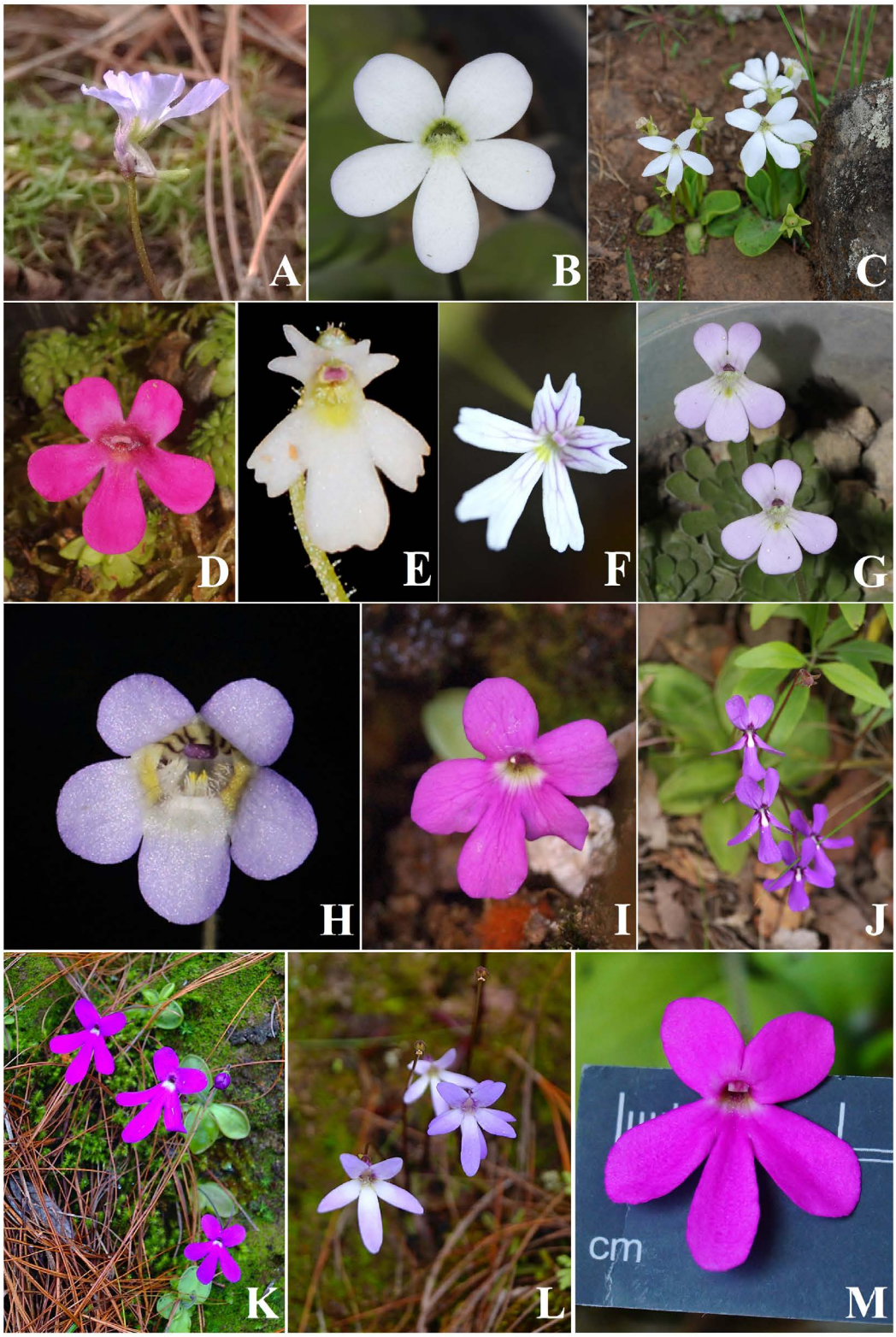

Figure 4. *Pinguicula* species in the TMVB. A) *P. acuminata*. B) *P. agnata*. C) *P. casperi*. D) *P. crassifolia*. E) *P. crenatiloba*. F) *P. emarginata*. G) *P. esseriana*. H) *P. lilacina*. I) *P. michoacana*. J) *P. moranensis*. K) *P. oblongiloba*. L) *P. parvifolia*. M) *P. zamudioana.* A-B, D-E, G-M by Jorge López-Pérez, C by Sergio Zamudio, and F by Alberto Lozano.

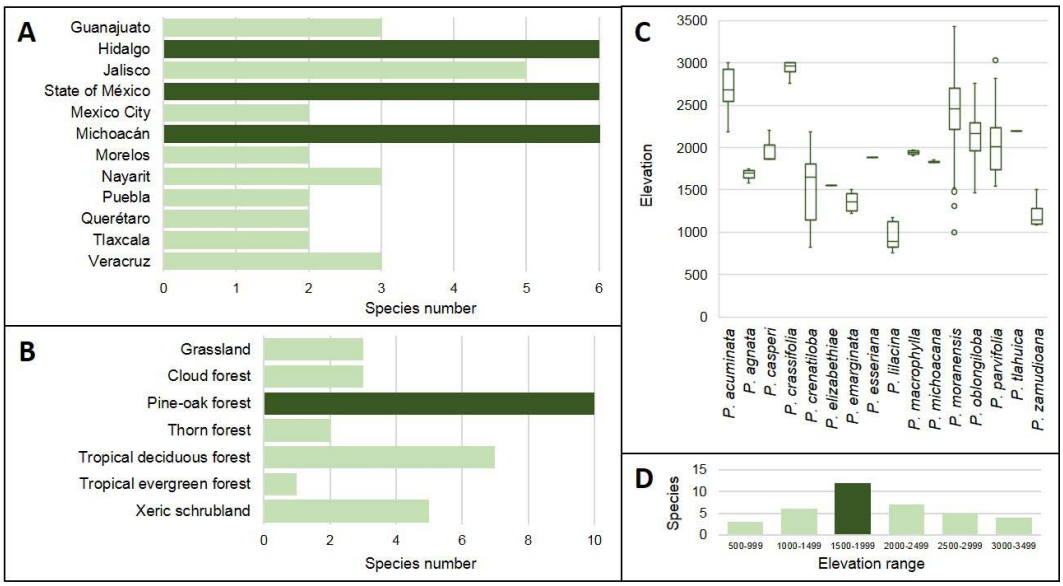

Figure 5. Species richness distribution of *Pinguicula* along the TMVB. A) Species richness by state. B) Species richness by vegetation type. C) Boxplot of distribution by elevation range. D) Species richness by elevation range. In dark green the richest class.

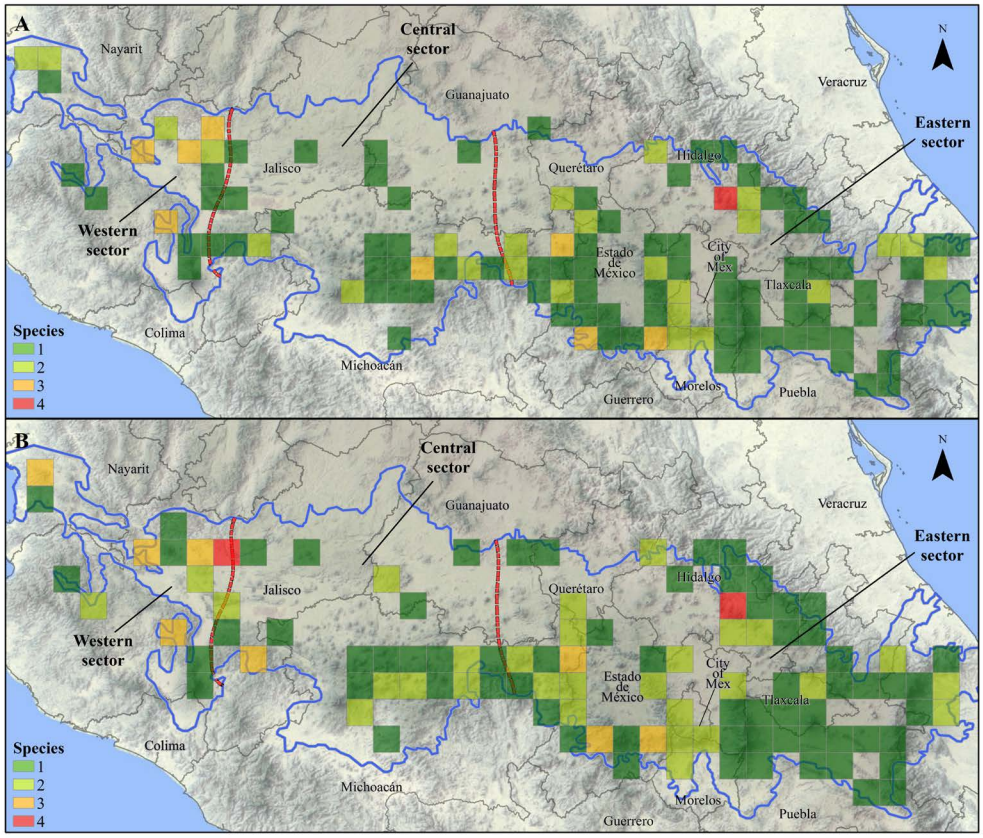

Figure 6. Species richness distribution of *Pinguicula* along the TMVB by grid cell. A) Cell size of 0.21° × 0.21°. B) Cell size of 0.24° × 0.24°. Blue line: TMVB limits. Red dot line: Sector limits. Gray line: State limits.

biogeographic transition of the Mexican biota (Halffter & Morrone 2017). Our results identified the species richness of *Pinguicula* centered at both extreme sectors of the TMVB. Contact zones among mountain ranges favored the species richness and has been observed in other groups of plants. Rodríguez *et al*. (2018), identified grid cells with high species richness and endemism values of angiosperms in the Eastern, Central and Western sectors. Meanwhile, Murillo-Pérez *et al*. (2022) showed high species richness of *Solanum* (Solanaceae) in the Eastern and Western sectors. Also, Vargas-Amado *et al*. (2013) rescued the richness of *Cosmos* (Asteraceae) in the Western sector. Sosa *et al*. (2018), Sosa & Loera (2017), and Sanginés-Franco *et al*. (2015) located the species richness of vascular plants, monocot geophytes, and ferns in the Eastern sector. Furthermore, Munguía-Lino *et al*. (2015) recognized this sector as the richest in Tigridieae (Iridaceae) species. In addition, this sector was highlighted as the species richest for *Lycianthes* (Solanaceae) and *Echeandia* Ortega (Asparagaceae) (Anguiano-Constante *et al*. 2018, 2021, Ortiz-Brunel *et al*. 2021). On the other hand, Ruiz-Sanchez & Specht (2013) correlated the TMVB uplifting with the population diversification of *Nolina parviflora* (Asparagaceae). In addition, Sosa *et al*. (2018) found a high phylogenetic diversity of Mexican vascular plants in this province. Finally, Romero-Soler *et al.* (2021) revealed evidence supporting the speciation of *Bakerantha* B.L.Sm. (Bromeliaceae) as a result of the TMVB uplift. All analyses support the importance of the geodiversity and the complex climatic history of this province which promoted the diversification of angiosperms, including *Pinguicula*.

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