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Peperomia accentus (Piperaceae), a new geophytic species endemic to the Sierra Madre Occidental, Mexico

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Abstract

Peperomia accentus is described and illustrated as a new species of Piperaceae from the state of Zacatecas, Mexico, in the Sierra Madre Occidental mountain range. This new taxon belongs to the subgenus *Tildenia,* which includes species characterized by their geophytic habit. It can be distinguished from its congeners mainly by the combination of roots at the apex of the globose tuber, peltate leaves, numerous simple inflorescences and flowers with long and geniculated styles of a reddish color. A preliminary threat assessment is provided for the new species based on IUCN Red List guidelines. We provide a comprehensive analysis of the distribution patterns of the Mesoamerican species of *Peperomia* subgenus *Tildenia*. Finally, we include a key for species distributed north of the Trans-Mexican Volcanic Belt.

Key words: endemic, geophyte, Neotropics, *Tildenia*

Introduction

Peperomia Ruiz & Pavon (1794: 8) is a highly diverse genus within the Piperaceae family comprising approximately 1400–1700 species (Callejas-Posada 2020). *Peperomia* species display remarkable morphological diversity and are primarily distributed across the tropical and subtropical regions of the world. Several subgenera are recognized within *Peperomia*, among which the subgenus *Tildenia* (Miquel) Miquel (1843: 45) is easily distinguished by its acaulescent, geophytic habit, typically featuring peltate leaves. In this group peduncles arise directly from a tuber and the flowers exhibit styles clearly distinct and separate from the ovary (Samain *et al.* 2011; Frenzke *et al.* 2015). The subgenus comprises approximately 60 species primarily distributed throughout the Neotropics, with two principal areas of diversity located from Peru to Bolivia with 31 species, and Mesoamerica with 24 species (Trelease 1922, Mathieu *et al.* 2011, Symmank *et al*. 2011, Villaseñor 2016, Mathieu 2017, Samain & Tebbs 2020, Pino *et al*. 2023, eFloraMex 2025).

Until recent decades, taxonomic knowledge for this group could have been considered incipient, as only in the last 15 years, about 50% (28 spp.) of the species that include this subgenus were described (Mathieu *et al.* 2011; Mathieu 2017; Pino *et al.* 2023). These not only greatly contributed to the taxonomic knowledge of the group, but also allowed for the exploration of evolutionary questions pertaining the origin and evolution of this lineage (Symmank *et al*. 2011). Several reasons can be attributed to why so much diversity was unknown only until these recent developments, one being that most species described in the last decades were considered as morphological variation of the more common and widespread species (Mathieu *et al.* 2011; Mathieu 2017; Pino *et al.* 2023). Second, these plants are often inconspicuous, as most species are small herbs that only appear above ground during certain times of the year. Additionally, information that is usually lost during herbarium processing is necessary to arrive at trustworthy identifications, such as features of flowering and fruiting material, as well as from tubers. It is also advisable to

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consider attributes that are only observable in live specimens, such as coloration, which is taxonomically informative but tends to deteriorate in *exsiccatae* (Symmank *et al.* 2011).

In this study, we aim to enhance understanding of *Peperomia* subgenus *Tildenia* in Mesoamerica in three ways. First, during fieldwork conducted by the first author to document the floristic diversity in the Sierra de los Cardos, located in Zacatecas, Mexico (Hurtado-Reveles *et al.* 2022), specimens of *Peperomia* were collected. Upon closer examination, we found that these specimens exhibited a unique combination of characteristics that distinguishes them from other known species of the subgenus *Tildenia* in Mexico. Consequently, we propose and describe these specimens from Zacatecas, including some previously classified in herbaria as *P. bracteata* A.W.Hill (1907: 55), as a new species based on their morphological features. This discovery increases the number of the subgenus *Tildenia* species in Zacatecas to three and those in Mexico to 22. Second, we provide information regarding richness and distribution patterns of *Tildenia* species from Mesoamerica, which can inform and elicit further questions regarding the evolution of this group of plants. Finally, we provide an identification key for *Peperomia* subgenus *Tildenia* species found north of the Trans-Mexican Volcanic Belt.

Materials and methods

Taxonomic treatment

During botanical explorations in July 2025 in the pine-oak forests of the Sierra de los Cardos in Jerez, Zacatecas, Mexico, a single population of *Peperomia* with a combination of morphological characteristics different from previously reported species was found growing in rock crevices and shallow soils. The Sierra de los Cardos is a small mountain range that is part of the larger Sierra Madre Occidental, which extends from northwestern to western Mexico. These plants were vegetatively similar to the sympatric *P. bracteata*, but they had thicker inflorescences, tinted reddish instead of green and featured long conspicuous styles. Eight individuals were collected, six of which were assigned as herbarium specimens and two were kept alive for later observation. The botanical material was processed and deposited in the herbarium MEXU (acronym according to Thiers 2025), and the living specimens were kept at the Instituto de Biología, Universidad Nacional Autónoma de México (IB-UNAM) at room temperature. These specimens were observed and photographed, noting details of the inflorescence, flowers, and fruits, following Samain *et al.* (2011).

Dichotomous keys, monographs, regional floras, images, and specimens collected in Mesoamerica of *Peperomia* subgenus *Tildenia* deposited in the MEXU herbarium, as well as digitized specimens available at GBIF, were consulted (Mathieu *et al.* 2011, Mathieu 2017, Callejas-Posada 2020, Samain & Tebbs 2020, eFloraMex 2025, GBIF 2025). We compared specimens of the species morphologically closest to the new species (*P. ovatopeltata* Candolle (1866: 4), *P. schizandra* Trelease (1922: 73)) as well as those distributed in the state of Zacatecas (*P. bracteata*, *P. monticola* Miquel (1843: 71)). We found that the new species had already been collected in Zacatecas but had been identified as *P. campylotropa* A.W. Hill. (1907: 2), which is an illegitimate superfluous name for *P. bracteata*.

Microscopic photography of reproductive structures was conducted with the aim of obtaining high resolution images for description and illustration using both light and scanning electron microscope (SEM) in the Biodiversity Photography and Microscopy Laboratory (LANABIO by its acronym in Spanish) at IB-UNAM. For SEM photographs, a Hitachi SU1510® microscope (Hitachi City, Japan) was used, for which the samples were mounted on metal sample holders and covered with gold. For light microscope photographs, fresh flowering material was taken from live specimens and shot with a Zeiss Axio Zoom V16 microscope (ZEISS, Germany), motorized for multifocal and mosaic photography. Photographs were taken with the Axiocam 305 color (5 megapixels) camera equipped with the microscope.

Based on herbarium labels, field-collected data, and observations on iNaturalist (www.inaturalist.org), which were verified here, a distribution map for the new species was elaborated. Derived from the known localities, the preliminary conservation status for *P. accentus* was assessed by calculating its Extent of Occurrence (EOO) and Area of Occupancy (AOO) using GeoCAT (Bachman *et al.* 2011) and applying the IUCN Red List Categories and Criteria (IUCN 2024). Finally, based on our findings regarding the distribution of *Peperomia* subgenus *Tildenia* species, available literature for those species and authors' field and herbarium observations we generated an identification key for those species distributed north of the Trans-Mexican Volcanic Belt (Mathieu *et al.* 2011, Mathieu 2017, Callejas-Posada 2020, Samain & Tebbs 2020, eFloraMex 2025, GBIF 2025).

Distribution patterns in Mesoamerica

A list of *Peperomia* subg. *Tildenia* species, native to Mesoamerica, was compiled based on Mathieu *et al*. (2011) and Mathieu (2017). For these species, we downloaded all available records from the GBIF (Global Biodiversity Information Facility) database, including records for synonyms (GBIF.org, 2025). The database was completed with records of species with known areas of distribution not represented in the database, manually inserting records obtained from literature and from herbarium specimens. Finally, records for the new species were inserted into the database.

The database was filtered to remove unreliable records for analysis. This involved removing records outside the study area and generalized locations (such as country or state centroids). Next, each record was curated by displaying them and their associated information with QGIS v. 3.40 (QGIS Development Team 2025). A record was deemed accurate when it was identified by an expert in the taxonomic group or when it matched existing information published in specialized literature (Mathieu *et al.* 2011, Mathieu 2017, Samain & Tebbs 2020; eFloraMex 2025).

A map of the world terrestrial ecoregions (Olson *et al*. 2001) was used to identify those with high species richness. Additionally, a map was created to pinpoint regions that harbor numerous rare species with narrow distribution, including those known from a single locality. The last map included an overlay showing extensions included in the World Database on Protected Areas to observe which regions harboring rare species are under protection (UNEP-WCMC and IUCN 2025). All maps were elaborated with QGIS v. 3.40 (QGIS Development Team 2025) and minor map editing and final composition of figures were done in Inkscape v. 1.4.2 (Inkscape Project 2024).

Results

Taxonomic treatment

Peperomia accentus Reveles & Amancio, *sp*. *nov*. (Figs. 1–4).

Type:—MEXICO: Zacatecas: Municipality Jerez, Sierra de los Cardos, 4 km West of Jomulquillo, pine and oak forests, on pockets of soil on large rocks, frequent, 22°40’56.9”N 103°05’43.1”W, 2614 m, 11 July 2025, *L. Hurtado-Reveles 3091* (holotype MEXU!, isotypes CHAPA!, GENT!).

Diagnosis:—*Peperomia accentus* can be differentiated from the rest of the geophytic species of *Peperomia* subgenus *Tildenia* by the following combination of characters: globose tubers without trunk-like outgrowths, green to wine-colored inflorescences (green to black *in sicco*), and flowers with geniculate styles 1.5–2.5 mm long, which remain longer than the ovaries after anthesis, persistent in fruit.

Description:—Geophytic, lithophytic herbs, 5–25 cm tall, entirely glabrous, with a tuber 5–10 mm in diameter, globose, rooting from the apex. Leaves simple, 2–8 per plant, originating directly from the apex of the tuber; lamina irregularly orbicular, 1–6 cm in diameter, margin entire, centrally peltate, apex acute to obtuse, palmately 7–10-veined, membranous; adaxial surface light green to dark green *in vivo*, abaxial surface light green to white in vivo; veins light green, faintly visible; petiole slender, 3–10 cm long, directly originating from the tuber and inserted around the center of the lamina. Inflorescences simple spadices, very rarely bifurcating, 1–12 per plant, green to wine *in vivo*, green to black *in sicco*; peduncle 3–9 cm long, 1–1.5 mm thick, slender, directly originating from the tuber; rachis 3–23 cm long, 1–1.5 mm thick, longer than the peduncle, slender, erect or ascending, rarely splitting near the apex; flowers clustered toward the apex, the cluster becoming increasingly diffuse as the inflorescence matures; floral bracts orbicular, peltate, with an acute apex, margin slightly undulate. Stamens 2, light pink to wine-colored, filament 1–2 mm long, anthers ca. 0.3 × 0.4 mm; pistil 1, ovary ovate, 0.5–1 mm long, style conical to cylindric, geniculate, 1.5–2.5 mm long, stigma apical, ca. 0.2 × 0.3 mm, papillate *in vivo*, penicillate *in sicco*. Fruits globose, ca. 1.5 mm in diameter, sessile, centrally attached at the base, pericarp granulose, style conical to filiform, 1.5–2.5 mm long, bent upwards to curving downwards.

Distribution and habitat:—*Peperomia accentus* is only known from Mexico, distributed in the southeasternmost portion of the Sierra Madre Occidental, where it intersects with the Central Mexican Plateau, in the Sierra de los Cardos (Sierra de las Candelas), municipality of Jerez, Sierra de Valparaíso, municipality of Valparaíso, and the Sierra de Órganos, municipality of Sombrerete, all in the state of Zacatecas (Fig. 4). The last locality is situated close to the limits between Zacatecas and Durango and therefore, the species is expected to also be distributed in the latter state.

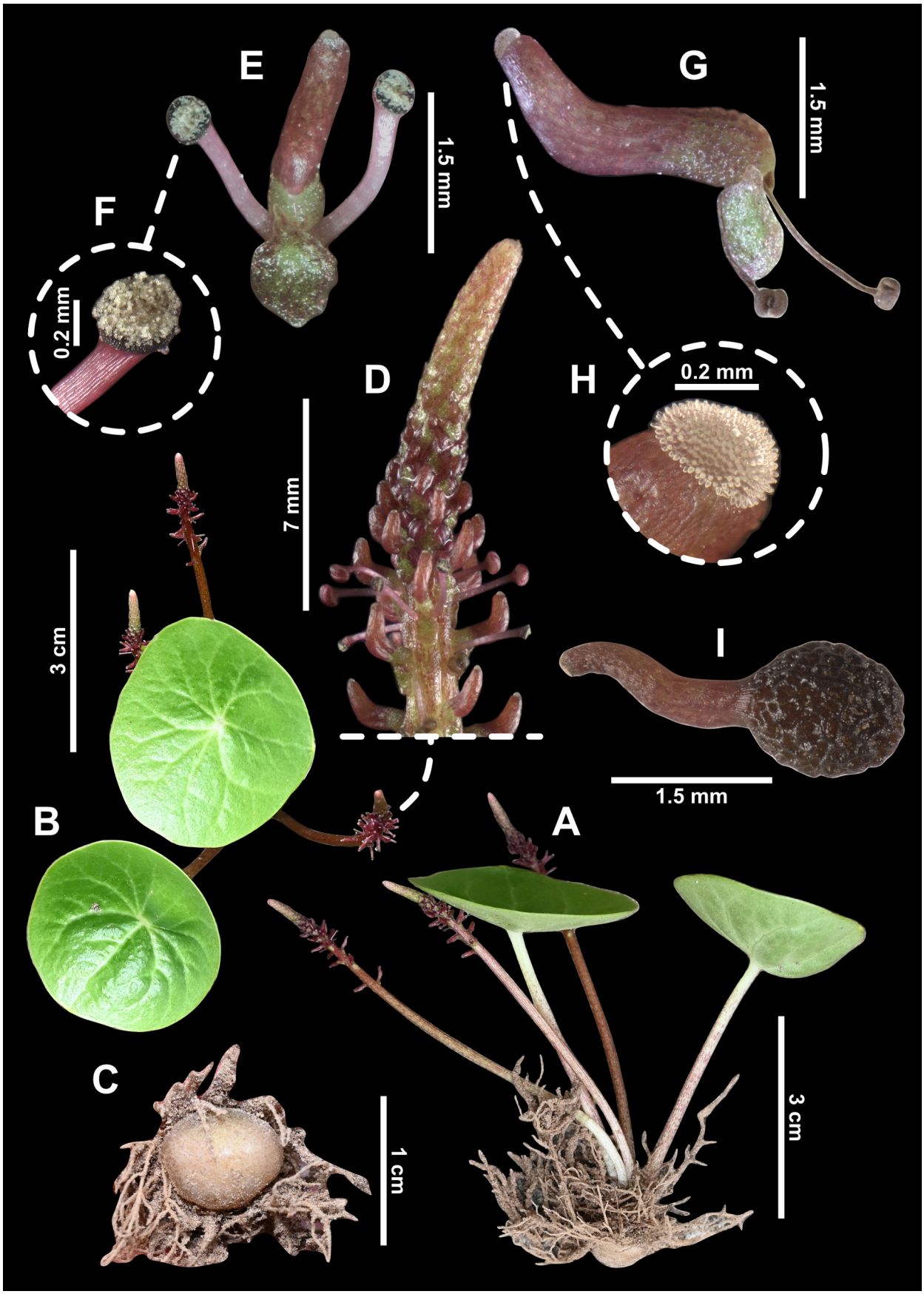

FIGURE 1. *Peperomia accentus* morphology. A. General view of a flowering specimen from a lateral perspective. B. General view from an upper perspective. C. Tuber from the bottom. D. Apex of a developing inflorescence with flowers in different anthesis stages. E. Flower with mature stamens from a front and bottom perspective. F. Close-up of a mature anther. G. Sideways perspective of a flower in anthesis. H. Closeup of a receptive stigma. I. Lateral perspective of a developing fruit.

However, herbarium or digital records have yet to be reported, if that is the case. The plant communities in which it has been found consist of subtemperate pine-oak mixed forests, typically established in young, shallow soils. It has also been found on rock outcrop vegetation growing in protected crevices or on pockets of soil accumulated underneath larger lithophytic vascular plants such as *Agave schidigera* Lemaire (1861: 289) (Fig. 2). In terms of elevation, it ranges between 2300 and 2700 m.

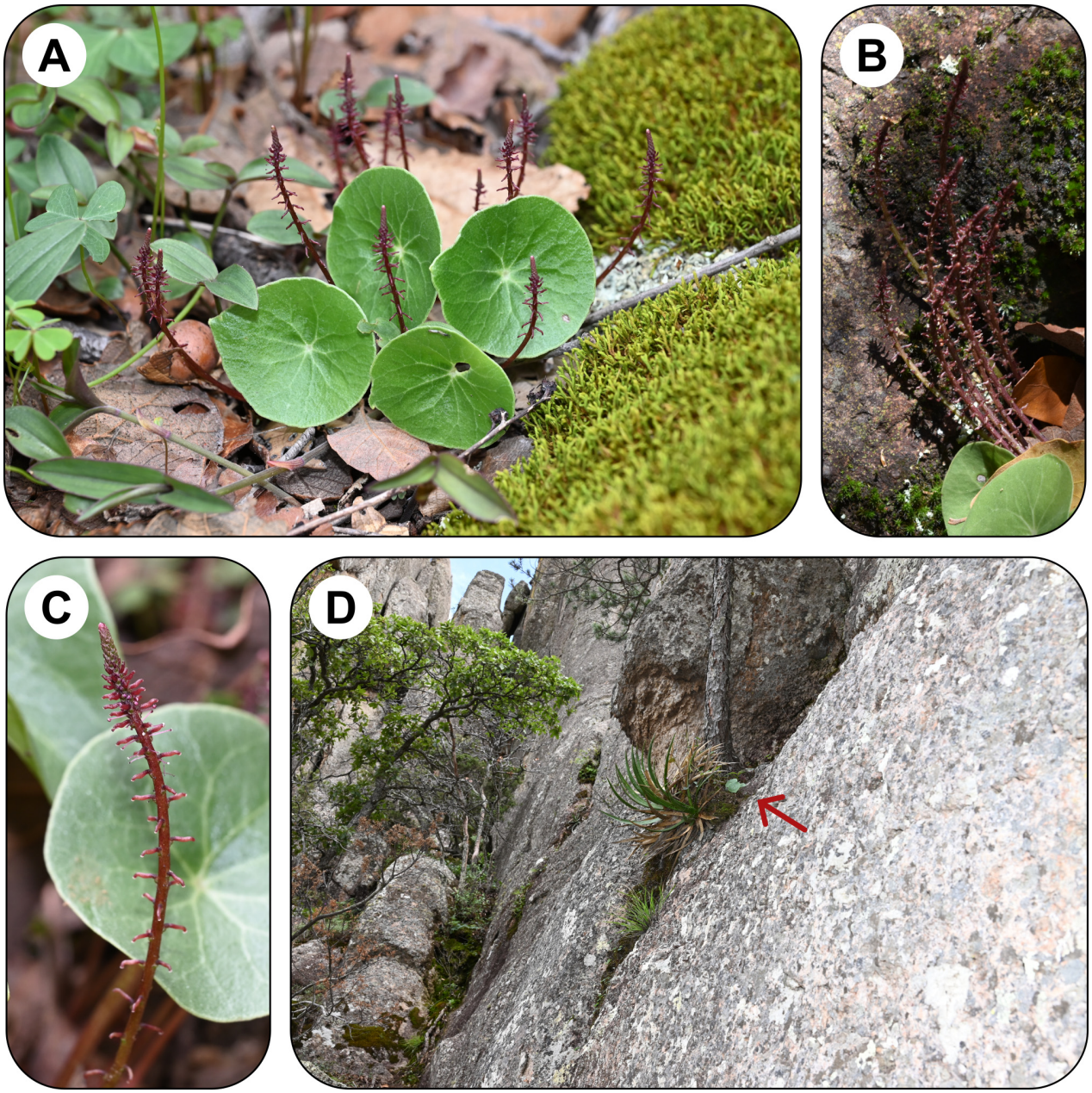

FIGURE 2. Photographs of *Peperomia accentus* in habitat. A. General view of a flowering specimen. B. Mature inflorescences. C. Closeup of a single inflorescence. D. Specimen growing in a sheltered soil pocket on a rock outcrop.

Preliminary conservation status:—According to Criterion B established by the IUCN Red List (2024), with an EOO of 2,676.44 km^2, AOO is 24 km^2, and four known locations, *P. accentus* can be considered Endangered (EN) (B1,2ab(i)(iii)). The distribution of this species is narrow and limited across the pine-oak forests of Zacatecas, in the highlands, which represents the southernmost region of the Sierra Madre Occidental. These forests are being impacted by land-use change, deforestation, illegal trade in species, and overgrazing (Dinerstein *et al*. 1995, Hernández-Ramírez 2020).

Phenology:—The species has been found flowering from July to October, which is also the known period when it can be observed above ground.

Etymology:—The specific epithet alludes to the common shape of the pistil in developing flowers: a wavy line which resembles a tilde (~). Tildes are graphemes commonly used as diacritic (accent) in several scripts.

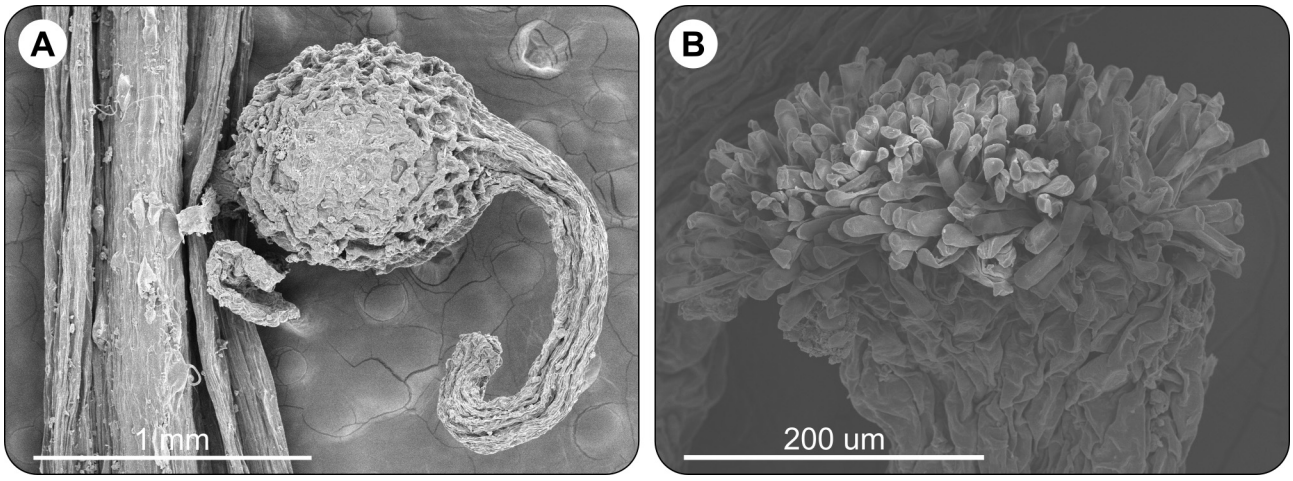

FIGURE 3. Scanning Electron Microscope photographs of floral structures *in sicco*. A. Developed fruit. B. Receptive stigma.

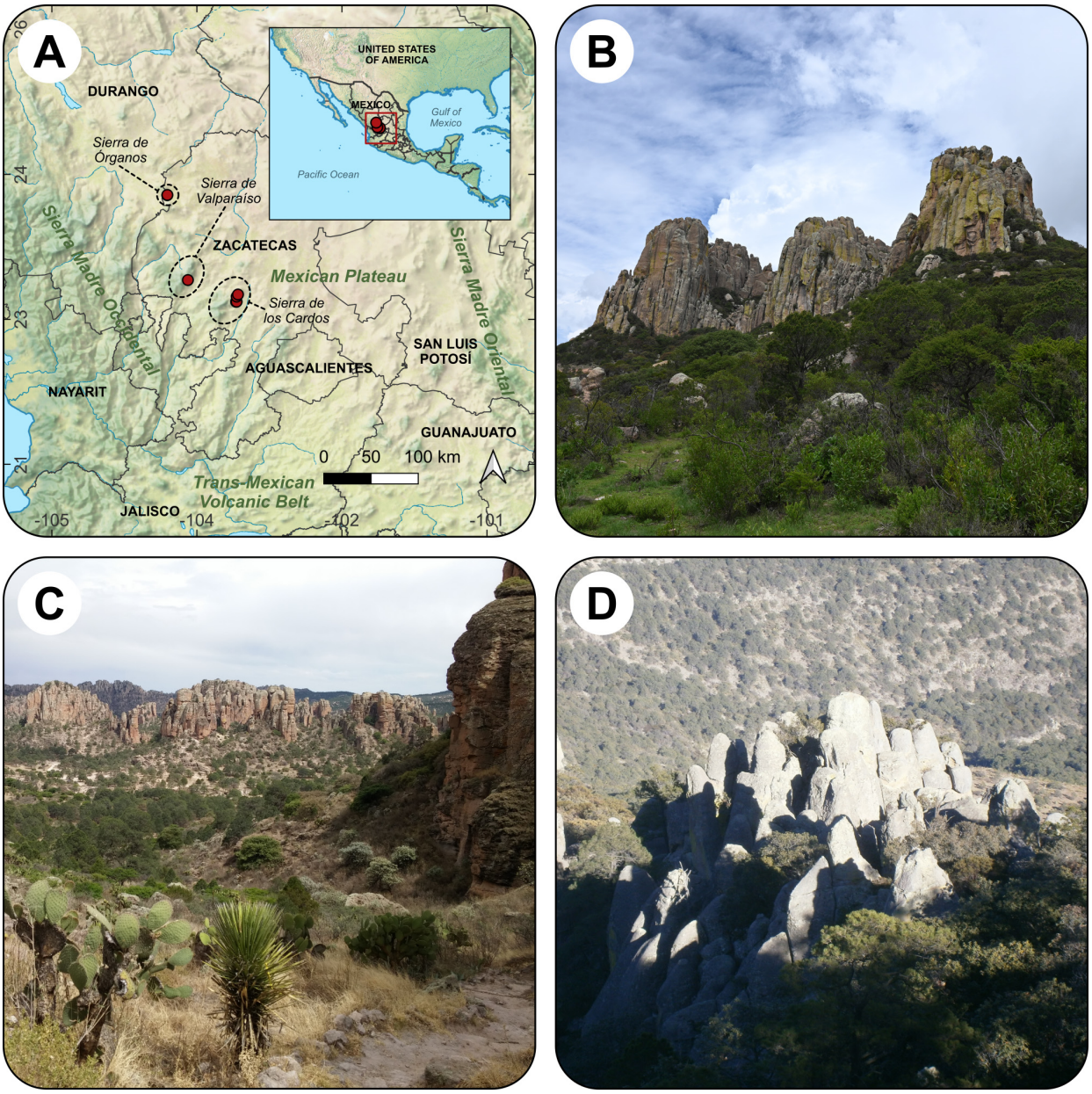

FIGURE 4. Distribution and habitat of *Peperomia accentus*. A. Distribution of *P. accentus*, maroon circles represent known localities. B. Sierra de los Cardos (Jerez, Zacatecas). C. Sierra de Órganos (Sombrerete, Zacatecas). D. Sierra de Valparaíso (Valparaíso, Zacatecas; (photo by Robhiga in Wikimedia Commons).

Notes:—A detailed comparison between *P. accentus* and the two most morphologically similar species, *P. ovatopeltata* and *P. schizandra*, is available in Table 1.

TABLE 1. Morphological comparison between *Peperomia accentus* and morphologically related species.

	P. accentus	*P. ovatopeltata*	*P. schizandra*
Leaf diameter	up to 6 cm	up to 4 cm	up to 5.5 cm
Adaxial leaf color	Completely green or green with light green veins	Dark green to purple	Completely green or green with light green veins
Abaxial leaf color	Light green to white	Light green with purple veins	Green to white
Number of inflorescences per plant	1 to 12	1 to 3	1 to 6
Rachis length	up to 23 cm	up to 10 cm	up to 15 cm
Rachis width	1 to 1.5 mm	less than 1 mm	less than 1 mm
Style shape	Conical to cylindrical, geniculate	Conical, slender and straight	Conical and short
Style length	1.5 to 2.5 mm	0.8 to 1 mm	less than 0.5 mm
Filament length	1 to 2 mm	less than 1.5 mm	less than 0.5 mm
Distribution	Mexico (Zacatecas)	Guatemala, Honduras, Mexico (Chiapas, Guanajuato, Guerrero, Michoacán, Oaxaca)	Mexico (Colima, Guerrero, Jalisco, Michoacán, Oaxaca, Puebla)

Additional specimens examined:—MEXICO. Zacatecas: Municipality Jerez: Sierra de las Candelas, Central portion, approximately 5 km southeast of La Barca, stream, pine-oak mixed forest, 22°45’26”N, 103°4’32”W, 2531 m, 8 October 2013, *J. J. Balleza C. et al. 20214* (MEXU!); Southern region, northwest oriented slope, approximately 1.25 km in a straight line northeast from Parral de las Huertas, *Pinus* forest, 22°44’9”N, 103°5’20”W, 2372 m, 20 July 2012, *J. J. Balleza C. et al. 19541* (MEXU!); Río Florido Ejido, stream located approximately 3 km southeast from La Barca, pine-oak mixed forest, 22°47’14”N, 103°5’27”W, 2375 m, 13 September 2013, *J.J. Balleza C. et al. 20080* (MEXU!).

Distribution patterns of Tildenia species in Mesoamerica

Most of *Tildenia* species-rich ecoregions are found in central Mexico along or adjacent to the Trans-Mexican Volcanic Belt formation. In particular, the ecoregion known as the Trans-Mexican Volcanic Belt pine-oak forests is the richest, with 11 native species, followed by the Balsas dry forests and the Sierra Madre del Sur pine-oak forests with nine species each and the Central American pine-oak forests with eight species (Fig. 5). Most areas harboring rare or restricted distribution species fall within the four aforementioned ecoregions (Fig. 6). Notably, the Amacuzac Basin (with three endemic species) and the Cutzamala Basin (with two) in the Trans-Mexican Volcanic Belt, along with the Sierra de los Cuchumatanes in Guatemala and the Cordillera de Talamanca in Costa Rica (each with two endemic species), are particularly prominent (Fig. 6). In terms of conservation, Fig. 6 shows that areas with rare species are scarcely represented in Protected areas according to the World Database on Protected Areas (UNEP-WCMC and IUCN 2025).

Discussion

Peperomia accentus displays the most common vegetative morphological characteristics for *Peperomia* subg. *Tildenia*, an underground non-branching tuber and orbicular peltate leaves. Among those species, this species stands out for its showy inflorescences with very long, geniculated styles. The inflorescences and vegetative characters of *P. accentus* resemble those of *P. ovatopeltata* which is distributed in the Trans-Mexican Volcanic Belt, but the latter species has smaller (up to 1 mm) and straight styles, which are around the same length as the ovary vs. longer than the ovary (1.5–2.5 mm) and geniculate styles in *P. accentus*. Additionally, *P. accentus* has darker and red-tinted floral structures

vs. light-colored floral structures with seldom dark-tinted styles in *P. ovatopeltata*. Vegetatively, the most conspicuous differences are that *P. ovatopeltata* displays a purple-tinted adaxial leaf surface while *P. accentus* is light green to white.

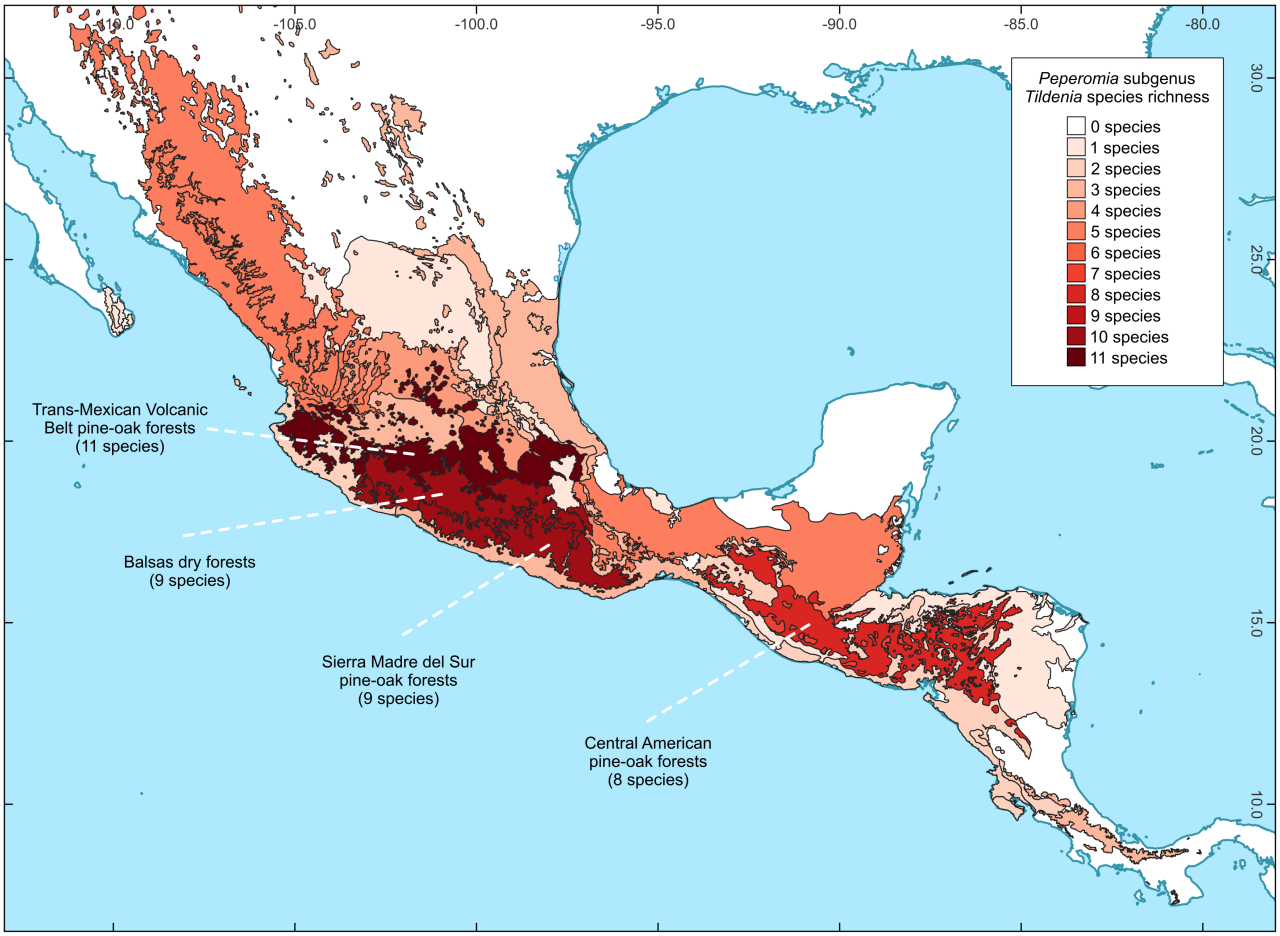

FIGURE 5. Species richness distribution for Mesoamerican species of *Peperomia* subgenus *Tildenia* according to ecoregions.

The fact that this new species was previously collected and circumscribed as the widespread *P. bracteata*, despite not fitting that description, is a common occurrence in this group of *Peperomia* (Mathieu *et al*. 2011). This issue is amplified by the overall inconspicuous nature of the subgenus *Tildenia* and its seasonal phenology, which limits its representation in herbarium collections (Mathieu *et al*. 2011). Furthermore, the state of Zacatecas, where *P. accentus* is distributed, is considered one of the least surveyed regions in terms of botanical exploration (Hurtado-Reveles *et al.* 2022).

Though dry specimens of *P. accentus* are easily discernible from other *Peperomia* in herbarium collections by their large styles, diagnostic characters like inflorescence color and floral structure can only be observed on live specimens. This highlights the need for the use of fresh material in the taxonomy of this group (Mathieu *et al*. 2011). Our findings emphasize the need for more further exploration and botanical research in under-surveyed regions of Mexico, along with careful review of herbarium specimens. This publication raises the total number of *Peperomia* subgenus *Tildenia* species in Mexico to 22.

Distribution patterns of Tildenia species in Mesoamerica

The three most diverse ecoregions for this group (Trans-Mexican Volcanic Belt pine-oak forests, Balsas dry forests, and Sierra Madre del Sur pine-oak forests) are all part of what is known in biogeography as the Mexican Transition Zone, a topographical complex region in which Nearctic and Neotropical biotas overlap, as well as physical and environmental features have contributed to a disproportionately high diversity of species (Barthlott *et al*. 2005; Morrone 2020). A defining feature in the Mexican Transition Zone is the development of the Trans-Mexican Volcanic Belt in the Pliocene and Pleistocene, which has been cited as a key event in the diversification of *Peperomia* subg. *Tildenia* (Samain *et al*. 2011, Symmank *et al*. 2011).

FIGURE 6. Areas in Mesoamerica harboring *Peperomia* subgenus *Tildenia* species that are known from a single or a few localities.

As shown in Fig. 6, regions that harbor unique diversity for this group are also underrepresented in protected areas and are near densely populated urban areas. This, along with the fact that the demographic status and conservation of populations for this group of *Peperomia* are not well understood, raises concerns about the need for more thorough evaluations.

Peperomia accentus is the third known native species of this group for Zacatecas, and its first endemic species. Interestingly, it is the only species exclusively north of the Trans-Mexican Volcanic Belt. The locations where it has been recorded, although part of the Sierra Madre Occidental mountain chain, are situated at the transition to the Mexican Plateau, and are isolated from the montane continuum by flat plains and valleys. Although on a regional scale, *P. accentus* seems to grow sympatrically with *P. bracteata* during surveys conducted for this work, both species were consistently found on different slopes or ravines. They appear remarkably similar vegetatively, but both species are easy to distinguish in reproductive structures: *P. accentus* has red-tinted inflorescences and flowers with long and geniculated styles as well as long filaments, while *P. bracteata* has light-green-tinted inflorescences and flowers with very short styles and filaments. This local distribution of species aligns with what has been hypothesized as a promoter of the high diversity of species of *Peperomia* subg. *Tildenia*, in which topographically complex areas have served as microrefugia, which in turn favored allopatric speciation (Rahbek & Graves 2001, Symmank *et al.* 2011). Furthermore, for the two species mentioned above, *P. accentus* is a species of restricted distribution, while *P. bracteata* is one of the most widely distributed ones. This opens up further questions regarding the local evolutionary mechanisms that underly speciation and this group.

Identification key for *Peperomia* subgenus *Tildenia* found north of the Trans-Mexican Volcanic Belt Key

1. Style longer than the ovary or fruit, geniculate ..... *Peperomia accentus* Reveles & Amancio
- Style shorter or as long as the ovary or fruit, conical or flat ..... 2.
2. Fruit centrally attached at base by a short, broad pseudopedicel ..... *Peperomia albonervosa* G. Mathieu
- Fruit sessile, not centrally attached at the base by a pseudopedicel ..... 3.

3. Fruit cylindrical ..... *Peperomia monticola* Miq.
- Fruit globose ..... 4.
4. Style flattened ..... *Peperomia painteri* Trel.
- Style conical ..... *Peperomia bracteata* A. W. Hill

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References

Bachman, S., Moat, J., Hill, A.W., De La Torre, J. & Scott, B. (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *ZooKeys* 150: 117–126. https://doi.org/10.3897/zookeys.150.2109

Barthlott, W., Mutke, J., Rafiqpoor, D., Kier, G. & Kreft, H. (2005) Global centers of vascular plant diversity. *Nova Acta Leopoldina NF* 92: 61–83.

Callejas-Posada, R. (2020) *In:* Davidse, G., Ulloa, C., Hernández, H. & Knapp, S. (Eds.) *Flora Mesoamericana, Vol. 2, parte 2, (Piperaceae)*. 1st ed. Missouri Botanical Garden, Universidad Nacional Autónoma de México (Instituto de Biología), The Natural History Museum (Londres), St. Louis (MO) U.S.A., 619 pp.

Candolle, A.C.P.de (1866) Piperaceae Novae. *Journal of Botany, British and Foreign* 4: 132–133.

Dinerstein, E.D., Olson, M., Graham, D.J., Webster, A.L., Primm, S.A., Bookbinder, M.P. & Ledec, G. (1995) Una evaluación del estado de conservación de las ecorregiones terrestres de América Latina y el Caribe. WWF, Washington. [ISBN 0-8213-3191-1]

eFloraMex (2025) *Peperomia* Ruiz & Pav. | eFloraMex—Flora de México en línea [bajo construcción]. *eFloraMex, La flora electrónica de México*. Available from: https://efloramex.ib.unam.mx/cdm_dataportal/taxon/a51e3ba5-3ade-4a6a-b4b2-736990727801 (accessed 1 August 2025)

Frenzke, L., Scheiris, E., Pino, G., Symmank, L., Goetghebeur, P., Neinhuis, C., Wanke, S. & Samain, M.-S. (2015) A revised infrageneric classification of the genus *Peperomia* (Piperaceae). *Taxon* 64: 424–444. https://doi.org/10.12705/643.4

GBIF.org (2025) GBIF Occurrence Download. Available from: https://www.gbif.org/occurrence/download/0075180-250717081556266 (accessed 23 August 2025)

Hernández-Ramírez, D. (2020) Resumen ejecutivo. *In*: *La biodiversidad en Zacatecas.* Estudio de Estado. CONABIO, México, pp. 352–354.

Hill, A.W. (1907) A revision of the geophilous species of *Peperomia*, with some additional notes on their morphology and seedling structure. *Annals of Botany* 2: 139–160. https://doi.org/10.1093/oxfordjournals.aob.a089128

Hurtado-Reveles, L., Burgos-Hernández, M., Vázquez-Sánchez, M., López-Acosta, J.C., Hurtado-Reveles, L., Burgos-Hernández, M., Vázquez-Sánchez, M. & López-Acosta, J.C. (2022) Contribución al conocimiento florístico de la Sierra de los Cardos, Susticacán, Zacatecas, México. *Botanical Sciences* 100: 247–262. https://doi.org/10.17129/botsci.2882

Inkscape Project (2024) Inkscape v. 1.4.

IUCN (2024) Guidelines for Using the IUCN Red List Categories and Criteria. Version 16. Prepared by the Standards and Petitions Subcommittee. Available from: https://www.iucnredlist.org/resources/redlistguidelines (accessed 10 September 2025)

Mathieu, G. (2017) *Peperomia tubericordata* (Piperaceae), a new geophytic species from Oaxaca, Mexico. *Phytotaxa* 313: 293–295.

https://doi.org/10.11646/phytotaxa.313.3.9

Mathieu, G., Symmank, L., Callejas, R., Wanke, S., Neinhuis, C., Goetghebeur, P. & Samain, M.-S. (2011) New geophytic *Peperomia* (Piperaceae) species from Mexico, Belize and Costa Rica. *Revista mexicana de biodiversidad* 82: 357–382. https://doi.org/10.22201/ib.20078706e.2011.2.1199

Miquel, F.A.W. (1843) *Systema piperacearum*. Kramers, 575 pp. https://doi.org/10.5962/bhl.title.151

Morrone, J.J. (2020) *The Mexican Transition Zone: A Natural Biogeographic Laboratory to Study Biotic Assembly*. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-47917-6

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51 (11): 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Pino, G., Samain, M.-S., Suclli, E., Alcalá, A. & Marquiegui, D. (2023) Two New Geophytic Species of *Peperomia* Subgenus *Tildenia* (Piperaceae) from Central Peru. *Haseltonia* 29. https://doi.org/10.2985/026.029.0105

QGIS Development Team (2025) QGIS Geographic Information System. v. 3.40.

Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences* 98: 4534–4539. https://doi.org/10.1073/pnas.071034898

Ruiz, H. & Pavón, J. (1794) *Florae Peruvianae, et Chilensis Prodromus*. en la imprenta de Sancha, Madrid.

Samain, M.-S., Mathieu, G., Pino, G., Symmank, L., Cieza, N., Neinhuis, C., Goetghebeur, P. & Wanke, S. (2011) The geophytic *Peperomia* subgenus *Tildenia* (Piperaceae) in the Andes with the description of new species in a phylogenetic framework. *Plant Ecology and Evolution* 144: 148–176. https://doi.org/10.5091/plecevo.2011.470

Samain, M.-S. & Tebbs, M.C. (2020) *Familia Piperaceae*. Instituto de Ecología A.C. Centro Regional del Bajío, Pátzcuaro, Michoacán, México, 62 pp.

Symmank, L., Samain, M.-S., Smith, J.F., Pino, G., Stoll, A., Goetghebeur, P., Neinhuis, C. & Wanke, S. (2011) The extraordinary journey of *Peperomia* subgenus *Tildenia* (Piperaceae): insights into diversification and colonization patterns from its cradle in Peru to the Trans-Mexican Volcanic Belt. *Journal of Biogeography* 38: 2337–2349. https://doi.org/10.1111/j.1365-2699.2011.02586.x

Trelease, W. (1922) The peltate peperomias of North America. *Botanical Gazette* 73 (2): 133–147. https://doi.org/10.1086/332965

UNEP-WCMC and IUCN (2025) Protected Planet: The World Database on Protected Areas. *WDPA*. Available from: www.protectedplanet.net (accessed 12 September 2025)

Villaseñor, J.L. (2016) Checklist of the native vascular plants of Mexico. *Revista mexicana de biodiversidad* 87 (3): 559–902. https://doi.org/10.1016/j.rmb.2016.06.017