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Rediscovering the *Selaginella* flora of Puebla, Mexico: New records reveal underestimated richness

Redescubriendo la flora de *Selaginella* de Puebla, México: Nuevos registros revelan una riqueza subestimada

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Abstract:

Background and Aims: Puebla ranks as the seventh most diverse Mexican state in terms of plant species. Despite this, only 24 *Selaginella* species had been recorded for the state as of 2022, fewer than in neighboring Oaxaca (53 spp.) and Veracruz (33 spp.). This work aims to update current knowledge of *Selaginella* diversity in Puebla by documenting newly recorded species, comparing the state's taxonomic diversity with that of neighboring states, and providing an identification key for the species known from the state.

Methods: We conducted extensive fieldwork, reviewed herbarium specimens, and analyzed database records from 2014 to the present. We also calculated the *Selaginella* Taxonomic Biodiversity Index (TBI, taxa/lnA) for Puebla and its neighboring states.

Key results: We documented seven new species records, increasing the known diversity of *Selaginella* in Puebla to 31 species. This represents 38.75% of all *Selaginella* taxa reported in Mexico, of which eight are endemic to the country. To aid identification, a dichotomous key was developed. The TBI for Puebla (3.0 taxa/lnA) equaled that of Veracruz and represented approximately 65% of the value recorded for Oaxaca (4.6 taxa/lnA). The most frequently recorded species were *S. lepidophylla*, *S. pallescens*, and *S. stellata*. The highest species richness was found in montane cloud forests (16 spp.) and xeric scrublands (8 spp.), with most species distributed across the northeastern (16 spp.) and northwestern (15 spp.) mountain ranges.

Conclusions: The genus *Selaginella* is well represented in Puebla. Ongoing field collections and systematic review of herbarium specimens, particularly in underexplored southern areas of the state, are essential for refining the regional checklist and understanding species distribution patterns.

Key words: distribution, lycophytes, morphological diversity, state checklist, taxonomy, vegetation types.

Resumen:

Antecedentes y Objetivos: Puebla ocupa el séptimo lugar entre los estados de México con mayor diversidad de especies de plantas. A pesar de ello, hasta 2022 solo se habían registrado 24 especies de *Selaginella* en el estado, menos que en los estados vecinos de Oaxaca (53 spp.) y Veracruz (33 spp.). Este trabajo tiene como objetivo actualizar el conocimiento sobre la diversidad de *Selaginella* en Puebla mediante la documentación de especies registradas por primera vez, la comparación de la diversidad taxonómica del estado con la de los estados vecinos y la elaboración de una clave de identificación de las especies conocidas en el estado.

Métodos: Llevamos a cabo un extenso trabajo de campo, la revisión de ejemplares de herbario y el análisis de registros en bases de datos desde 2014 hasta la actualidad. Asimismo, calculamos el Índice de Biodiversidad Taxonómica de *Selaginella* (IBT, taxa/lnA) para Puebla y sus estados vecinos.

Resultados clave: Documentamos siete nuevos registros de especies, lo que eleva la diversidad conocida de *Selaginella* en Puebla a 31 especies. Esto representa el 38.75% de todos los taxones del género reportados en México, de los cuales ocho son endémicos. Para facilitar la identificación, se elaboró una clave taxonómica. El IBT para Puebla (3.0 taxa/lnA) es igual al de Veracruz y representó aproximadamente 65% del valor registrado para Oaxaca (4.6 taxa/lnA). Las especies más frecuentemente registradas fueron *S. lepidophylla*, *S. pallescens* y *S. stellata*. La mayor riqueza específica se encontró en los bosques mesófilos de montaña (16 spp.) y en los matorrales xerófilos (8 spp.), con la mayoría de las especies distribuidas en las sierras nororiental (16 spp.) y noroccidental (15 spp.).

Conclusiones: El género *Selaginella* está bien representado en Puebla. Las colectas de campo continuas y la revisión sistemática de ejemplares de herbario, especialmente en las zonas del sur poco exploradas, son fundamentales para afinar la lista florística regional y comprender los patrones de distribución de las especies.

Palabras clave: distribución, diversidad morfológica, licofitas, listado estatal, taxonomía, tipos de vegetación.

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Introduction

Selaginella P.Beauv. is the largest lineage of lycophytes and the only genus in the family Selaginellaceae (PPG I, 2016). It is cosmopolitan, with its highest diversity in the tropics and subtropics (Weststrand and Korall, 2016a). Mexico is one of the Earth's most megadiverse countries, with more than 23,314 vascular plant species, and is home to a remarkable variety of flora, including many endemic species (Villaseñor, 2016). Among seedless vascular plants in Mexico, *Selaginella* is the fourth-most-diverse in this category (Mickel and Smith, 2004).

Puebla, located in central-eastern Mexico, is characterized by a vast diversity of vegetation types shaped by its geographical location, geological history, and climatic variation, with 5415 vascular plant species recorded (Rodríguez-Acosta et al., 2014). In this context, Puebla harbors approximately 381 fern and lycophyte species (Tzompa-Coatl et al., 2022). The earliest documentation of *Selaginella* species from Puebla appears in the study of Alston (1955), who cited four taxa for the state (i.e., *S. apoda* (L.) C.Morren, *S. lepidophylla* (Hook. & Grev.) Spring, *S. porphyrospora* A.Braun, and *S. stellata* Spring). However, the first comprehensive account of *Selaginella* species from Puebla was documented by Mickel et al. (2004), who recorded 16 species, 2 of which (*S. extensa* Underw. and *S. landii* Greenm. & N.Pfeiff.) were cited as unverified collections. Subsequently, Rodríguez-Acosta et al. (2014) reported 20 species for the state, a number also recognized by Villaseñor (2016). However, there are variations in the species recognized between these authors.

Most collections of this genus have been made in the Sierra Norte region of Puebla, primarily in studies of fern and lycophyte floristics. Notable collections include a single species, *S. pallescens* (C.Presl) Spring, in the municipality of Teziutlán (Cerón-Carpio and Marín-Torres, 2004) and three species (i.e., *S. delicatissima* Linden ex A.Braun,

S. hoffmannii Hieron., and *S. schiedeana* A.Braun) in the municipality of Tlatlauquitepec (Cerón-Carpio et al., 2006). Additionally, three species (i.e., *S. pallescens*, *S. stellata*, and *S. stenophylla* A.Braun) were identified within the ten municipalities of Puebla forming the hydrographic basin of the Necaxa River (Cerón-Carpio et al., 2012). More recently, Tzompa-Coatl et al. (2022) reported 16 *Selaginella* species in the Sierra Norte of Puebla.

Another area with a high density of *Selaginella* collections is the southeastern region of Puebla. This genus has been recorded in the Tehuacán-Cuicatlán Valley, where one species (i.e., *S. lepidophylla*) has been documented across four municipalities (i.e., Coxcatlán, San José Miahuatlán, Tehuacán, and Zapotitlán), in the Puebla portion of this valley, which comprises a total of 31 municipalities (Riba and Lira, 1996). Recent records of *Selaginella* in Puebla include the presence of *S. sertata* Spring in Huehuetla (Mendoza-Ruiz and Ceja-Romero, 2020a) and the documentation of *S. polyptera* Valdespino in the municipality of Xicotepec de Juárez (Tzompa-Coatl et al., 2022).

Puebla shares over 85% of its plant species with Oaxaca, indicating significant overlap in their floristic composition (Rodríguez-Acosta et al., 2014). Based on a synthesis of previously published records from Puebla, 24 species of *Selaginella* have been documented for the state prior to this study (Mickel and Smith, 2004; Rodríguez-Acosta et al., 2014; Villaseñor, 2016; Tzompa-Coatl et al., 2022), a modest number compared to neighboring Oaxaca, which has around 53 species (Villaseñor, 2016). Given the environmental similarities between Puebla and the surrounding regions, it is likely that additional *Selaginella* species currently known from Oaxaca, Veracruz, and other neighboring states may also occur in Puebla. This suggests a potential for further discoveries in line with broader biogeographical patterns observed in Mexico.

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As further discoveries are expected, primarily through continued fieldwork in underexplored areas and the review of herbarium specimens, the number of recorded *Selaginella* taxa in Puebla is likely to increase. The primary objective of this study is to update the current knowledge of *Selaginella* diversity in Puebla by providing a comprehensive list of species, including newly documented records. The specific objectives are to: (1) calculate the Taxonomic Biodiversity Index (TBI; $\text{taxa}/\ln A$) for *Selaginella* in Puebla and compare it with neighboring states; (2) present a distribution map of the newly recorded species, along with notes on their habitats, geographic distribution, and diagnostic morphological features; and (3) develop an identification key for the *Selaginella* species currently known from Puebla.

Materials and Methods

Study area

The state of Puebla is located in central-eastern Mexico (Fig. 1A) and covers 1.7% of the national territory (34,306 km²) (Rodríguez-Acosta et al., 2014; INEGI, 2017). It borders the states of Hidalgo and Veracruz to the north, Veracruz and Oaxaca to the east, Morelos, State of Mexico, Tlaxcala,

and Hidalgo to the west, and Oaxaca and Guerrero to the south (CONABIO, 2011). The state is situated between the extreme geographical coordinates of 17°51'39.24" to 20°50'24.00"N and from 99°04'13.80" to 96°43'28.92"W (Fig. 1B).

Puebla encompasses seven biogeographical provinces: the Southern High Plateau (Zacatecano-Potosino), the Balsas Depression, the Trans-Mexican Volcanic Belt, the Gulf of Mexico, Oaxaca, and the Eastern and Southern Sierra Madre (CONABIO, 2011). The region features highly varied topography, with lowlands in the northeast, such as the municipalities Tenampulco and Tuzamapan (50 m), and a maximum elevation at Pico de Orizaba (5610 m) (Rodríguez-Acosta et al., 2014).

The state also displays a range of climates, predominantly temperate, followed by warm and semi-warm, with small portions of semi-arid, arid, semi-cold, and cold climates (CONABIO, 2011). According to Rzedowski's classification (Rzedowski, 2006), the state of Puebla includes major vegetation types such as mountain cloud forest, tropical evergreen forest, coniferous forest, *Quercus* forest, tropical deciduous forest, xeric scrub, grassland, and aquatic vegetation.

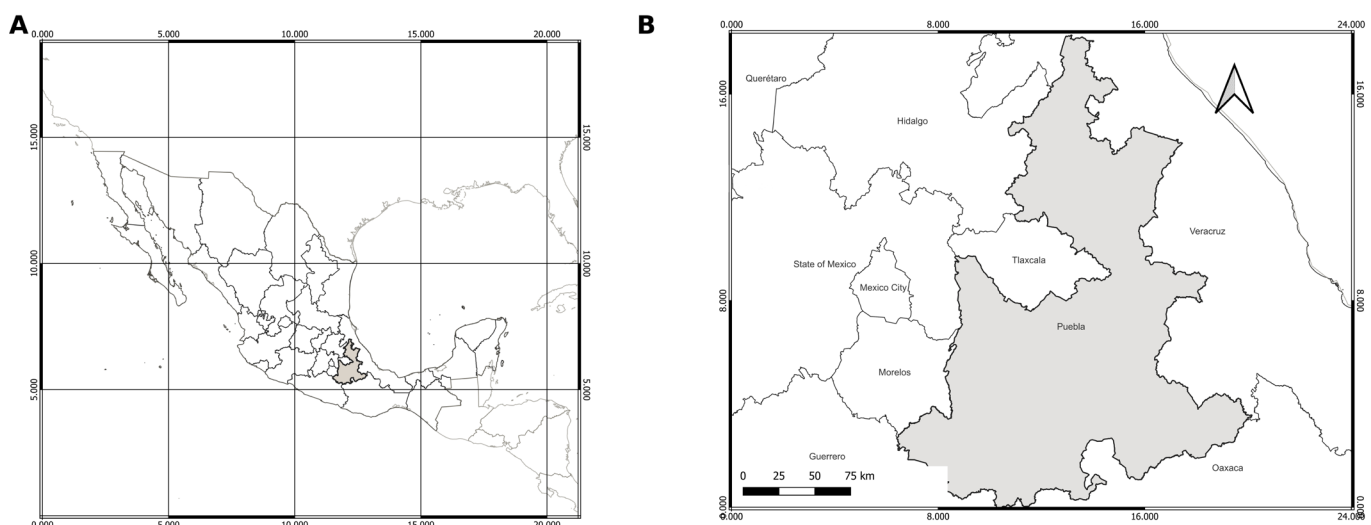


Figure 1: Geographic context of Puebla, Mexico. A. location of Puebla within Mexico (highlighted); B. Puebla and neighboring states in central-eastern Mexico (Puebla highlighted).



Data collection

This study relies on specimens deposited in the herbaria B, CAS, F, HUAP, K, MEXU, MICH, MO, NY, PMA, TEX, UC, and US (herbarium codes follow [Thiers, 2026](#)), as well as on data collected during fieldwork conducted in Puebla between 2014 and 2024, through 30 collecting trips to municipalities in the northern, central, and southeastern parts of the state, encompassing various vegetation types and habitats where ferns and lycophytes occur. During these surveys, specimens of ferns and lycophytes were collected, including all encountered *Selaginella* individuals considered suitable for documentation (i.e., mature individuals with well-developed vegetative characters and, when present, reproductive characters). Whole plants were collected, when possible, photographed *in situ*, and accompanied by field notes on habitat, substrate, elevation, and associated vegetation. Collected specimens were pressed, dried, and prepared as herbarium vouchers for subsequent identification and deposition in herbaria collections.

Additionally, relevant literature on the genus *Selaginella* in Mexico and Puebla was reviewed (i.e., [Alston, 1955](#); [Mickel and Smith, 2004](#); [Rodríguez-Acosta et al., 2014](#); [Villaseñor, 2016](#)), alongside the HUAP's herbarium *Selaginella* collection database and digitized images from PteridoPortal ([PteridoPortal, 2026](#)). In total, we examined 461 herbarium specimens (including material studied in person and on loan) and reviewed 241 digital records from PteridoPortal, for a total of 702 records analyzed. These sources were consulted to gather information on species occurrence in Puebla, habitat, vegetation type, distribution, and elevational range.

Descriptions, taxonomic and nomenclatural criteria

The terminology describing species morphology follows [Lellinger \(2002\)](#), [Mickel et al. \(2004\)](#), and [Valdespino et al. \(2024a; b\)](#). Although some authors have proposed splitting *Selaginella* into several genera ([Zhou and Zhang, 2023](#); [Zhou et al., 2025](#)), we treat *Selaginella* as the only genus within the family Selaginellaceae ([PPG I, 2016](#)), based on the rationale provided by [Valdespino et al. \(2024c\)](#), followed by [Velázquez-Montes and Martorell \(2025\)](#). Additionally, such split has not been widely accepted and diverges from the

consensus adopted by the Pteridophyte Phylogeny Group (PPG I) ([PPG I, 2016](#)). The subgeneric classification we follow is based on [Weststrand and Korall \(2016b\)](#). The nomenclature and species authors' citations follow The International Plant Names Index ([IPNI, 2026](#)).

Estimation of Taxonomic Biodiversity Index

To compare the richness of *Selaginella* in Puebla with that of neighboring states, we calculated the Taxonomic Biodiversity Index (TBI), defined as the number of taxa divided by the natural logarithm of the area in square kilometers ([Squeo et al., 1998](#)). This index has been used in previous pteridophyte studies (e.g., [Hernández-Álvarez et al., 2019](#); [Tzompa-Coatl et al., 2022](#)), though those studies differ in taxonomic focus, vegetation coverage, and spatial scale. Therefore, our TBI values are meant to serve as a standardized metric for comparing *Selaginella* diversity across states, rather than for direct numerical comparison with indices from broader or differently delimited floristic surveys.

The number of *Selaginella* species in the states of Mexico, Veracruz, Morelos, and Hidalgo was obtained from their respective state-level biodiversity studies ([Tejero-Díez, 2009](#); [Tejero-Díez et al., 2011](#); [Mendoza-Ruiz and Ceja-Romero, 2020b](#); [Villaseñor-Ríos et al., 2021](#)). For Oaxaca, a statewide biodiversity synthesis is available ([CONABIO and GEO, 2022](#)), but it does not include pteridophyte data; therefore, the number of *Selaginella* species for Oaxaca was taken from [Villaseñor \(2016\)](#). For Guerrero, data were compiled from the statewide floristic checklist ([Alvarado-Cárdenas et al., 2025](#)). Tlaxcala was excluded because the number of *Selaginella* species reported varies among authors, ranging from one to three ([Mickel et al., 2004](#); [Villaseñor, 2016](#)). State surface areas were obtained from INEGI publications ([1992](#); [2000](#); [2001](#); [2004](#); [2016](#); [2024a, b](#)).

Results

We recorded seven species of *Selaginella*, representing new state records for Puebla: *S. lineolata* Mickel & Beitel, *S. mickelii* Valdespino, *S. novoleonensis* Hieron, and *S. pulcherrima* Liebm. ex E.Fourn., *S. reflexa* Underw., *S. schizobasis* Baker, and *S. steyermarkii* Alston (Table 1; Fig. 2). Following the infrageneric classification proposed by



Table 1: *Selaginella* P.Beauv. species recorded in the state of Puebla, Mexico. Vegetation types: ABG=Alpine bunchgrass grassland; G=Grassland; MCF=Montane cloud forest; PF=*Pinus* forest; PF-QF=*Pinus-Quercus* forest; QF=*Quercus* forest; QF-PF=*Quercus-Pinus* forest; TDF=Tropical deciduous forest; TDF-QF=Tropical deciduous-*Quercus* forest; TEF=Tropical evergreen forest; TSF=Tropical sub deciduous forest; XS=Xeric scrub. Regions of Puebla: NW=Northwest; NE=Northeast; C=Central; SW=Southwest; SE=Southeast. ‡=Newly recorded species for the state; *=Species endemic to Mexico.

Taxa	Region	Altitude (m)	Vegetation	Specimens
1. <i>Selaginella apoda</i> (L.) C.Morren	NW	2139	MCF	A. B. Cerón-Carpio 2125 (HUAP), C. Pringle 10815 (LL, TEX)
2. <i>Selaginella delicatissima</i> Linden ex A.Braun	NW, NE	817-2192	MCF	L. Caamaño-Onofre 6362 (HUAP)
3. * <i>Selaginella extensa</i> Underw.	NW, NE	884-2201	MCF	L. Caamaño-Onofre 11131 (HUAP), A. J. Sharp 45375 (MEXU)
4. <i>Selaginella flexuosa</i> Spring	NW, NE, C	379-1486	MCF	A. B. Cerón-Carpio 1607 (HUAP)
5. <i>Selaginella hoffmannii</i> Hieron.	NW, NE	379-2450	MCF, TEF, TSF	A. B. Cerón-Carpio 1428 (HUAP), G. Cornejo Tenorio et al. 2725 (MEXU)
6. * <i>Selaginella landii</i> Greenm. & N.Pfeiff.	C	3658	ABG	Kenoyer 25 (US)
7. <i>Selaginella lepidophylla</i> (Hook. & Grev.) Spring	C, SW, SE	919-2208	QF, TDF, XS	A. B. Cerón-Carpio 1880 (HUAP), C. E. Smith et al. 3634 (MEXU)
8. ‡ <i>Selaginella lineolata</i> Mickel & Beitel	NE	1015	MCF	L. Caamaño-Onofre 6351 (HUAP)
9. <i>Selaginella martensii</i> Spring	NW, NE, C, SE	840-1725	MCF, TEF, PF	L. Caamaño-Onofre 6568 (HUAP), J. L. Contreras J. 4756 (MEXU)
10. ‡ <i>Selaginella mickelii</i> Valdespino	SE	91-425	TEF	L. Caamaño-Onofre 6623 (HUAP), A. B. Cerón-Carpio 2022 (HUAP, TEX)
11. * <i>Selaginella mixteca</i> Mickel & Beitel	NW, C-SE	1100-2148	MCF	J. Fermín-Escobar 1135 (HUAP)
12. * <i>Selaginella nothohybrida</i> Valdespino	SW	1227-1913	TDF-QF, XS	A. B. Cerón-Carpio et al. 2722 (HUAP), W. Boege 1924 (MEXU)
13. ‡ <i>Selaginella novoleonensis</i> Hieron.	SE	1900-2000	XS	C. A. Purpus 3155 (F-image, UC-image, MO-image).
14. <i>Selaginella pallescens</i> (C.Presl) Spring	NW, NE, C, SW, SE	568-2568	MCF, PF, QF, QF-PF, TDF, TEF, TSF, XS	A. B. Cerón-Carpio et al. 2710 (HUAP), P. Tenorio L. 15417 (MEXU)
15. * <i>Selaginella parishii</i> Underw.	C	2140	PF-QF	G. Arsène 7084 (MEXU)
16. <i>Selaginella peruviana</i> (Milde) Hieron.	C	2140	PF-QF	G. Arsène 7087 (MEXU), W. Boege 71 (MEXU)
17. <i>Selaginella pilifera</i> A.Braun	SW	1450	TDF	E. Guízar-Nolazco 1075 (MEXU)
18. <i>Selaginella polyptera</i> Valdespino	NW	138-1568	MCF, TEF	A. B. Cerón-Carpio 1737 (HUAP)
19. <i>Selaginella porphyrospora</i> A.Braun	NE, SE	1015-2288	MCF, QF	L. Caamaño-Onofre et al. 11597 (HUAP)
20. ‡ <i>Selaginella pulcherrima</i> Liebm. ex E.Fourn.	NE	750-1062	MCF, TSF	J. L. Contreras J. 6948 (HUAP, MEXU)
21. ‡ <i>Selaginella reflexa</i> Underw.	SW	1464	TDF-QF	L. Caamaño-Onofre et al. 1864 (HUAP)
22. <i>Selaginella rupicola</i> Underw.	SE	1900-2000	XS	C. A. Purpus 3156 (F, GH)
23. <i>Selaginella sartorii</i> Hieron.	NW, NE, C, SW, SE	1214-2566	MCF, PF, QF, XS	L. Caamaño-Onofre 7645 (HUAP)
24. * <i>Selaginella schiedeana</i> A.Braun	NW, NE	88-1200	MCF, TSF	A. B. Cerón-Carpio 2192 (HUAP)
25. ‡ <i>Selaginella schizobasis</i> Baker	NE, SE	91-425	TEF	A. B. Cerón-Carpio 1930 (HUAP), J. L. Contreras L. 7046 (MEXU)
26. <i>Selaginella sellowii</i> Hieron.	NW, C, SW	1940-2587	PF, PF-QF, QF-PF, XS	L. Caamaño-Onofre 9823 (HUAP), R. Riba et al. 406 (MEXU)
27. <i>Selaginella silvestris</i> Aspl.	NW, NE, C	809-2220	QF	L. Caamaño-Onofre 12060 (HUAP)
28. <i>Selaginella stellata</i> Spring	NW, NE, C, SE	106-1937	MCF, QF, TEF, TSF	A. B. Cerón-Carpio 2948 (HUAP), L. Scheinvar 615 (MEXU)

Table 1: Continuation.

Taxa	Region	Altitude (m)	Vegetation	Specimens
29. <i>Selaginella stenophylla</i> A.Braun	NW, NE	262-1949	MCF, TEF, TSF	A. B. Cerón-Carpio 2952 (HUAP), M. Cházaro B. 560 (MEXU)
30. ‡ <i>Selaginella steyermarkii</i> Alston	NE	1893	QF	L. Caamaño-Onofre 14543 (HUAP)
31. <i>Selaginella wrightii</i> Hieron.	SW	1161-2562	TDF, XS	L. Caamaño-Onofre et al. 9498 (HUAP), R. L. Hellwig et al. 1241 (MEXU)

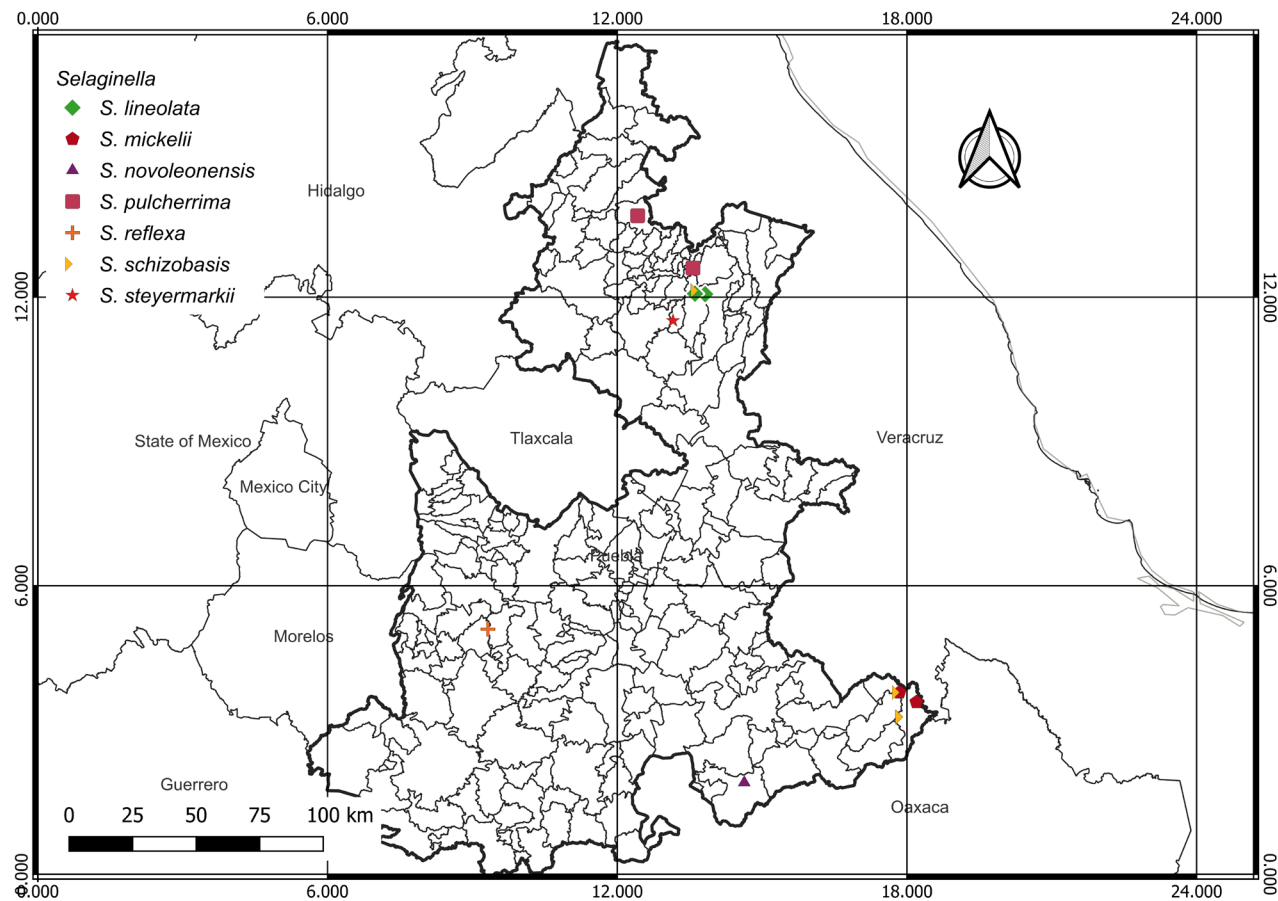


Figure 2: Geographic distribution of the seven *Selaginella* P.Beauv. species newly reported for Puebla, Mexico. Each symbol represents a collection record corresponding to the species listed in the legend.

Weststrand and Korall (2016b), these records comprise one isophyllous species in the subgenus *Rupestrae* Weststrand & Korall (i.e., *S. steyermarkii*), and six heterophyllous species: four in the subgenus *Stachygynandrum* (P.Beauv. ex Mirb.) Baker (i.e., *S. lineolata*, *S. mickelii*, *S. pulcherrima*, and *S. reflexa*), one in the subgenus *Gymnogynum*

(P.Beauv.) Weststrand & Korall (i.e., *S. schizobasis*), and one in the subgenus *Lepidophyllae* (Li Bing Zhang & X.M.Zhou) Weststrand & Korall (i.e., *S. novoleonensis*). With these additions, the number of *Selaginella* taxa documented for Puebla increases to 31 (Table 1). The greatest species richness occurs in montane cloud forests (16 species) and in

scrublands (8 species). Geographically, diversity is highest in the northeastern and northwestern regions of the state, particularly in the Sierra Nororiental and Sierra Norte, with 16 and 15 species, respectively.

Our calculations of the Taxonomic Biodiversity Index (TBI) showed that Puebla had a value of 3.0 taxa/lnA (Table 2), equal to that of Veracruz and nearly identical to Hidalgo (3.1 taxa/lnA). Although Guerrero also has 31 species of *Selaginella* (Alvarado-Cárdenas et al., 2025), its TBI is lower (2.8 taxa/lnA) because, when standardized by area (Taxa/lnA), richness per unit area is lower in a larger state. For comparison, Puebla's TBI represents approximately 65% of the value estimated for Oaxaca (4.6 taxa/lnA).

Table 2: Comparison of the *Selaginella* P.Beauv. Taxonomic Biodiversity Index (TBI) of the study area with that of neighboring states. The TBI of the state of Puebla is highlighted in bold.

States	Taxa	Area (km ²)	Taxonomic Biodiversity index
Oaxaca	53	93343	4.6
Hidalgo	31	20905.12	3.1
Veracruz	33	71826	3.0
Puebla	31	33995	3.0
Guerrero	31	63595.9	2.8
Estado de México	16	22333	1.6
Morelos	13	4878.9	1.5

Key to the *Selaginella* species in Puebla

- 1a. Plants isophyllous, leaves linear to linear-lanceolate, spirally arranged on the stems 2
- 1b. Plants heterophyllous, leaves of three types (lateral, median, axillary) in four rows on the stems 10
- 2a. Leaves dimorphic or slightly dimorphic (distinct dorsal and ventral leaves) 3
- 2b. Leaves monomorphic (all similar in shape and size) 6
- 3a. Upperside leaves acute or shortly aristate; underside leaves short- to long-acuminate 4
- 3b. Upper and lower leaves with long-aristate apices 5
- 4a. Upperside leaves with acute apices; underside leaves short-acuminate *S. parishii* Underw.
- 4b. Upperside leaves with shortly aristate apices; underside leaves long-acuminate *S. landii* Greenm. & N. Pfeiff.
- 5a. Underside leaves abruptly adnate; leaves apices 0.2-0.5 mm long *S. wrightii* Hieron.
- 5b. Underside leaves decurrent; leaves apices 0.6-1.0 mm long *S. peruviana* (Milde) Hieron.
- 6a. Stems erect to suberect; rhizophores restricted to their basal portion *S. rupicola* Underw.
- 6b. Stems creeping; rhizophores along the stem 7
- 7a. Leaf apices acuminate to short aristate; acumen 0.1-0.3 mm long *S. extensa* Underw.
- 7b. Leaf apices long-aristate; aristae 0.4-0.9 mm long 8
- 8a. Leaf bases decurrent *S. sellowii* Hieron.
- 8b. Leaf bases adnate 9
- 9a. Leaf bases hirsute with minute, stiff hairs; apices hyaline *S. steyermarkii* Alston
- 9b. Leaf bases pilose with long, curled hairs; apices whitish *S. sartorii* Hieron.
- 10a. Stems articulate 11
- 10b. Stems not articulate 13
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- 30b. Lateral leaves apices acute, axillary leaves oblong *S. schiedeana* A.Braun

Taxonomy

Lycopodiophyta

Lycopodiopsida

Selaginellales

Selaginellaceae

Selaginella P.Beauv., Mag. Encycl. 9(5): 478. 1804.

TYPE: *Selaginella spinosa* P.Beauv., nom. superfl.

$\equiv$ *Lycopodium selaginoides* L.

$\equiv$ *Selaginella selaginoides* (L.) P.Beauv. ex Schrank & Mart.

$\equiv$ *Selaginella spinulosa* A.Braun ex Döll, nom. superfl.

Monophyletic (Weststrand and Korall, 2016a), with the generic circumscription following Jermy (1990). It comprises approximately 700 species, although the actual number may be significantly higher. Six or seven subgenera are recognized, depending on the author (Zhou and Zhang, 2015; Weststrand and Korall, 2016b). The taxa listed here are reported for the first time from the state of Puebla. The specimen citation provided below corresponds to selected representative records.



Selaginella lineolata Mickel & Beitel, Mem. New York Bot. Gard. 46: 343. 1988.

TYPE: MEXICO. Oaxaca, dist. Putla, 24 km N of Putla, 1360 m, 11.X.1969, *J. T. Mickel 4014* (holotype: NY!; isotype: NY!).

Selaginella lineolata is characterized by its erect to suberect stems, flagelliform apices and branches; lateral leaves broadly ovate to oblong, with rounded to subcordate bases, acute apices, acroscopic margins long-ciliate to denticulate proximally and entire distally, basiscopic margins entire throughout, both margins hyaline, especially appreciable on the lower surface of the lateral leaves; median leaves broadly elliptic, biauriculate, the outer auricle larger than the inner one, with denticulate margins and long-aristate apices; axillary leaves similar to the lateral leaves but narrower; strobili dimorphic, with larger, greenish, spreading dorsal sporophylls and smaller, hyaline, ascending ventral sporophylls. *Selaginella lineolata* can be further identified by numerous elongate idioblasts on the leaf and sporophyll surfaces. Based on the subgeneric classification by [Weststrand and Korall \(2016b\)](#) and its morphological characteristics, this species is placed within the subgenus *Stachygynandrum*.

Distribution: Mexico (Colima, Guerrero, Hidalgo, Jalisco, State of Mexico, Nayarit, Oaxaca, Puebla, Querétaro, Sinaloa, Veracruz) and Guatemala.

Habitat: terrestrial or epipetric on wet slopes, limestone cliffs in cloud forests, oak-pine forests, and tropical evergreen forest, 1340-1375 m. In Puebla, all collections of this species are concentrated in the locality of San Juan Tahitic, within the municipality Zacapoaxtla in the Sierra Norte region.

Specimens examined: MEXICO. Puebla, municipality Zacapoaxtla, Cascada San Juan Tahitic, 1015 m, 19°57'42.37"N, 97°31'53.57"W, 19.XI.2014, *L. Caamaño and A. Coombes 6351* (HUAP); about 1 km SE of San Juan Tahitic, vicinity of waterfall just upstream from Puente

Tahitic, 1340 m, 19°55'35.04"N, 97°32'18.6"W, 18.VII.2015, *E. Schuettpelz 1638* (UC-image, US-image); between San Juan Tahitic and Xalacapan de Luque, vicinity of Puente Xilita, 1375 m, 19°55'45.37"N, 97°34'36.88"W, 18.VII.2015, *E. Schuettpelz et al. 1656* (US-image).

Taxonomic notes: in the PteridoPortal ([PteridoPortal, 2026](#)) database query, the collections *E. Schuettpelz 1638* (UC-image, US-image) and *E. Schuettpelz et al. 1656* (US-image) were identified as *Selaginella lineolata* by A.R. Smith in 2017, as noted on the specimens' annotation labels. Nevertheless, apparently this determinations were likely unknown to [Villaseñor \(2016\)](#), who did not include the species as occurring in Puebla. Upon reviewing the *L. Caamaño and A. Coombes 6351* (HUAP) collection, this species is confirmed to occur in Puebla.

Selaginella mickelii Valdespino, Brittonia 44: 316. 1992.

TYPE: MEXICO. Oaxaca, dist. Tuxtepec, 4-9 km S of Valle Nacional on Rte. 175, *J. T. Mickel 5871* (holotype: NY!; isotypes: MEXU!, MICH!, MO!, NY!, PMA!, UCI, US!).

Selaginella mickelii is distinguished by its unique growth habit, characterized by erect stems with stolons and rhizophores confined to the basal portion of the stems and extending along the stolons; leaves heterophyllous throughout, coriaceous, with corrugate surfaces; lateral leaves on creeping stems appressed along the portion below the first branch, dimorphic on the erect portion above the first branch, ovate to broadly ovate, with rounded bases, long-ciliate margins proximally, denticulate margins distally, and acute apices; median leaves ovate, with oblique bases, margins slightly hyaline or greenish, long-ciliate proximally, the cilia reduced in size distally, and acuminate to short-aristate apices; axillary leaves similar to the lateral leaves, with cordiform bases and long-ciliate margins; strobili monomorphic, with ovate sporophylls and denticulate, hyaline margins. Given the subgeneric classification proposed by [Weststrand and Korall \(2016b\)](#) and its distinct morphological traits, this species is assigned to the subgenus *Stachygynandrum*.



Distribution: endemic to Mexico (Chiapas, Oaxaca, Puebla, Tabasco, and Veracruz).

Habitat: terrestrial and epipetric, on rocky slopes, in tropical evergreen forest, 91-425 m. *Selaginella mickelii* is known in Puebla from two collections in San Sebastián Tlacotepec. This municipality is located in the southeastern region of Puebla, near the border with Veracruz. It belongs to the Sierra Negra region. Collections of this species from Puebla are from lowland areas; however, specimens from Oaxaca have been collected at elevations above 2000 m.

Specimens examined: MEXICO. Puebla, municipality San Sebastián Tlacotepec, Río Matalapa - Puente de Tepetla, 123 m, 18°28'57.5"N, 96°51'42.8"W, 3.XII.2014, L. Caamaño 6623 (HUAP); Tepeyac, Puente Tepeyac, Río Tonto, 91 m, 18°28'57.5"N, 96°51'42.8"W, 12.XI.2014, A. Cerón-Carpio 2022 (HUAP, TEX).

Taxonomic notes: the specimen *E. B. Copeland 167* (MICH-image), collected in San Luis Potosí, was initially identified by Alston as *Selaginella schrammii* Hieron. ex Standl. The sheet also bears the annotation "*S. mickelii*" without attribution. *Selaginella schrammii* is a heterotypic synonym of *S. mollis* A.Braun, a species that has been confused with *S. mickelii* due to morphological similarity. A duplicate at UC is determined as *S. schiedeana*, and based on the specimen visible in the MICH image, *E. B. Copeland 167* is best referred to as *S. schiedeana*.

Selaginella novoleonensis Hieron., Nat. Pflanzenfam. (Engler & Prantl) I(4): 676. 1901.

TYPE: MEXICO. Nuevo León, Sierra de la Silla, near Monterrey, C. Pringle 2489 (holotype: B!; isotypes: ARIZ, CAS!, MEXU! (2 sheets), MSC, NY!, UC!, US!).

Selaginella novoleonensis is a rosette-forming species characterized by heteromorphic, coriaceous leaves with broadly hyaline margins; lateral leaves ovate-deltate to suborbicular, with rounded bases, margins short-ciliate proximally and otherwise denticulate, and cuspidate to short-aristate apices; median leaves ovate, with peltate to

subpeltate rounded bases covered with short cilia, broadly hyaline margins short-ciliate proximally, cuspidate to short-aristate apices, and a prominent midrib with readily visible stomata; axillary leaves similar to the lateral leaves but broadly ovate and exauriculate; strobili monomorphic, with ovate sporophylls and denticulate, hyaline margins. Given the subgeneric classification proposed by Weststrand and Korall (2016b) and its distinct morphological features, this species is assigned to the subgenus *Lepidophyllae*.

Distribution: endemic to Mexico (Baja California Sur, Chihuahua, Coahuila, México, Nuevo León, Oaxaca, Puebla, Sonora, and Tamaulipas).

Habitat: terrestrial or epipetric, dry scrublands, 1000-2554 m.

Specimen examined: MEXICO. Puebla, municipality Caltepec, collected in the vicinity of San Luis Tultitlanapa (San Luis Atolotitlán), near Oaxaca, 18°10'48"N, 97°27'00"W, VII.1908, C. A. Purpus 3155 (F-image, UC, MO-image).

Taxonomic notes: *Selaginella novoleonensis* is one of the Mexican *Selaginella* species known for forming rosettes. This characteristic has evolved multiple times within the genus and is found in the subgenus *Lepidophyllae* and some clades of *Stachygynandrum* (Weststrand and Korall, 2016a). Although Mickel et al. (2004) did not report this species in Puebla, nor did subsequent studies (Rodríguez-Acosta et al., 2014; Villasenor, 2016), a PteridoPortal (PteridoPortal, 2026) database query revealed the specimen C. A. Purpus 3155 (UC), identified by I.A. Valdespino in 2009, as *S. novoleonensis*. We concur with this identification and now report the presence of this species in the Tehuacán-Cuicatlán Valley area of Puebla. Other duplicates of C. A. Purpus 3155 are labeled as *S. lepidophylla* in some herbaria (NY, US); however, these labels likely reflect misidentifications, and we interpret the C. A. Purpus 3155 collection as *S. novoleonensis*. This species has recently been reported from Oaxaca (Villaseñor, 2016), although no specific specimens were cited. However, the specimens J. T. Mickel and R. L. Hellwig 4086 (NY, TEX, UC-image), J. T. Mickel and S. W. Leonard 4505 (NY-image, TEX, UC-image), and J.



T. Mickel and S. W. Leonard 4939 (NY, TEX, UC-image) from the municipalities Coixtlahuaca, Teotitlán de Flores Magón, and Tlacolula in Oaxaca, respectively, clearly represent *S. novoleonensis*. Notably, the specimen *J. T. Mickel and S. W. Leonard, 4505*, collected in the municipality Teotitlán de Flores Magón near the Puebla border and approximately 37 km from our new Puebla record, further supports the presence of *S. novoleonensis* in this region.

Selaginella pulcherrima Liebm. ex E.Fourn., Mexic. Pl. I: 147. 1872.

TYPE: MEXICO. Veracruz, near hacienda de Jovo, *F. M. Liebmann 2061* (lectotype: C (designated by [Alston, 1955](#): 239); isolectotypes: BM, K, NY!, US!).

Selaginella pulcherrima is characterized by its tall, erect, clustered stems with rhizomatous bases; leaves usually heterophyllous, although isophyllous leaves are spirally arranged on the stems below the first to third lateral branches, giving the plant a frondose appearance; lateral leaves ovate, with truncate bases often bearing short, stiff hairs, acroscopic margins long-ciliate proximally, basiscopic margins long-ciliate along the proximal $\frac{1}{3}$ and otherwise entire distally, and apices long-acuminate to aristate; median leaves ovate, with subcordate to oblique bases, the outer bases usually tufted with a few short, stiff hairs, margins short-ciliate proximally and denticulate distally, and apices acuminate to long-aristate; axillary leaves similar to the lateral leaves, with truncate, exauriculate bases, margins ciliate along the proximal half and otherwise denticulate distally; strobili quadrangular and monomorphic, with ovate sporophylls. Considering the distinctive morphological characteristics of *S. pulcherrima* and based on [Weststrand and Korall \(2016b\)](#) subgeneric classification, it is assigned to the subgenus *Stachygynandrum*.

Distribution: Mexico (Chiapas, Guerrero, Puebla, Oaxaca), Honduras, and Guatemala.

Habitat: terrestrial and occasionally epipetric, growing in shaded understory, along trails, open areas, in cloud forests and tropical sub-deciduous forests, 750-1062 m.

Specimens examined: MEXICO. Puebla, municipality Jonotla, Plan de Guadalupe, 1062 m, 20°01'15.5"N, 97°34'53.2"W, 26.VIII.2013, *A. Cerón-Carpio 1419* (HUAP). Municipality Jopala, 10 km al SE de Chicontla, por el camino a Jopala, 750 m, 20°12'50"N, 97°47'2"W, 27.I.1999, *J. L. Contreras 6948* (HUAP, MEXU).

Taxonomic notes: *Selaginella pulcherrima* belongs to the *Selaginella pallescens* (C.Presl) Spring complex, a taxonomically challenging group of species characterized by caespitose to rosette-forming stems, with adpressed, monomorphic leaves along the main axis below the 1st to 5th branches, which usually curl inward when dry ([Stolze, 1981](#)). This group can also be distinguished by its leaves, which have broadly hyaline and long-ciliate margins. Species delimitation within this group has varied among authors. Some authors subsumed many species into a broadly defined *S. pallescens* and a few other taxa ([Alston, 1955](#); [Stolze, 1981](#)).

On the other hand, [Mickel et al. \(2004\)](#) recognized *S. acutifolia* (Stolze) Valdespino, originally described as *S. pallescens* var. *acutifolia* Stolze, at the species rank. They also treated other taxa associated with the *S. pallescens* complex, including *S. harrisii* Underw. & Hieron., *S. microdendron* Baker, *S. nothohybrida*, *S. pallescens*, and *S. pulcherrima*, as distinct species, although the morphological limits among some of these taxa remain difficult to assess. Some species of this complex have been included in recent phylogenetic analyses. [Zhou et al. \(2015\)](#) and [Weststrand and Korall \(2016a\)](#) recovered a *Selaginella pallescens* clade with moderate to strong support, including taxa such as *S. harrisii*, *S. nothohybrida*, and *S. pulcherrima*. However, relationships within this complex remain poorly resolved, and accessions identified as *S. pallescens* do not consistently occupy the same phylogenetic position. Overall, species delimitation in the *S. pallescens* complex is challenging because diagnostic leaf macro- and micro-morphological characters are highly variable, and available phylogenetic analyses have not adequately resolved species boundaries or interspecific relationships within the complex, underscoring the need for broader sampling and integrative studies that combine genomic-scale data, detailed morphology, and phylogeographic analyses to test



monophyly and clarify species delimitations and relationships.

Selaginella reflexa Underw. Bull. Torrey Bot. Club. 21: 268. 1894.

TYPE: MEXICO. Jalisco, Barranca of Guadalajara (Guadalajara), *C. Pringle* 2635 (lectotype: NY! (designated by Mickel, 1992: 425); isoelectotypes: BM, MEXU!, NY!, UC!, US!).

Selaginella reflexa is characterized by creeping stems with rhizophores along their entire length, and by incurved lateral leaves appressed to the stems, giving the plants a narrow-cylindrical appearance; lateral leaves broadly ovate to orbicular, with semicordate to truncate bases, slightly hyaline margins, the acroscopic margins long-ciliate along the basal ½ and otherwise denticulate distally, basiscopic margins denticulate throughout, and apices obtuse or sometimes slightly mucronate; median leaves ovate, with cordate bases, hyaline margins, the inner margin long-ciliate proximally and denticulate distally, the outer margins long- to short-ciliate along the basal half and otherwise denticulate distally, and apices shortly aristate; axillary leaves oblong to narrowly oblong, with truncate bases, margins long-ciliate along the proximal half and otherwise denticulate distally, and obtuse apices. Given the subgeneric classification proposed by Weststrand and Korall (2016b) and its distinct morphological traits, this species is assigned to the subgenus *Stachygynandrum*.

Distribution: endemic to Mexico (Durango, Chiuhauhua, Guerrero, Hidalgo, Jalisco, Nuevo León, Puebla, Querétaro, San Luis Potosí).

Habitat: tropical deciduous forest and *Quercus* forests, 1464 m.

Specimen examined: MEXICO. Puebla, municipality Teopantlán, Cerro al E de Zoyatla, pasando el río, 1464 m, 18°45'9.5"N, 98°23'16"W, 22.XI.2012, *L. Caamaño* 1864 (HUAP).

Taxonomic notes: *Selaginella reflexa* is often confused with *S. carioi* Hieron., which was synonymized under the former by Alston (1955), Smith (1981), Stolze (1983), and Fraile et al. (1995). These two taxa are indeed morphologically similar. *Selaginella reflexa* is distinguished from *S. carioi* by its lateral and axillary leaf bases and the inner bases of the median leaves glabrous (vs. tufted with many (6-15) stiff and whitish cilia, broadly ovate (vs. oblong or oblong-ovate) lateral leaves, and the outer margins of the median leaves long-ciliate (vs. shortly ciliate to denticulate). For an additional discussion of these two species and related taxa, refer to Mickel et al. (2004). Finally, a search of PteridoPortal (PteridoPortal, 2026) database revealed three collections of *S. reflexa* from Guatemala: *R. L. Hellwig and G. P. Whitaker* 1397, 1408 (DUKE-images), and *P. Weatherwax* 189a (IND-image). However, we believe they are most likely *S. carioi*, suggesting that *S. reflexa* may be endemic to Mexico. In contrast, *S. carioi* has a broader distribution in Guatemala and Chiapas (Mexico).

Selaginella schizobasis Baker, J. Bot. 21: 333. 1883.

TYPE: MEXICO. Chiapas, *Giesbrecht* 605 (holotype: K!; isotype NY!).

= *Selaginella tuerckheimii* Hieron. ex Donn. Sm. Enum. Pl. Guatem. 6: 67. 1903.

TYPE: GUATEMALA. Alta Verapaz: Cubilquitz, 350 m, Jan 1901, *Tuerckheim* 8061 (US!; isotypes B!, NY!).

Selaginella schizobasis is characterized by its articulate, bistelic stems, broadly ovate lateral leaves, and peltate median leaves; lateral leaves broadly ovate, or ovate on secondary to tertiary branches, with biauriculate bases, the acroscopic auricle strongly overlapping the stem and denticulate, margins greenish and denticulate throughout, rarely short-ciliate along the proximal third, and apices broadly acute; median leaves ovate, peltate, with greenish margins denticulate throughout, and acuminate to short-aristate apices; axillary leaves oblong, with biauriculate bases, divergent and denticulate auricles,



margins denticulate throughout, and broadly acute apices; strobili monomorphic and quadrangular, except at the bases, which are globose due to the presence of a solitary megasporangium, mostly microsporangiate, with ovate sporophylls bearing greenish margins. Given the subgeneric classification proposed by Weststrand and Korall (2016b) and its distinct morphological traits, this species is assigned to the subgenus *Gymnogynum*.

Distribution: Mexico (Chiapas, Oaxaca, Puebla, Tabasco, and Veracruz), Guatemala, Belize, Honduras, Nicaragua, and Costa Rica.

Habitat: terrestrial in tropical evergreen forest, 90–425 m.

Specimens examined: MEXICO. Puebla, municipality San Sebastián Tlacotepec, en la cabecera municipal, Colonia Guadalupe, vereda, 425 m, 18°23'41.5"N, 96°51'6.6"W, 12.XI.2014, A. Cerón-Carpio 1930 (HUAP, TEX); 2 km de Tlacotepec rumbo a la cumbre, 452 m, 18°23'41.5"N, 96°51'6.6"W, 11.XII.2014, A. Cerón-Carpio 1993 (HUAP, TEX); Puente Tepeyac, Río Tonto, 91 m, 18°23'41.5"N, 96°51'6.6"W, 12.XI.2014, A. Cerón-Carpio 2036 (HUAP, TEX). Municipality Zacapoaxtla, 8 km por el camino Tahitic, 1500 m, 18°23'41.5"N, 96°51'6.6"W, 9.II.1999, J. L. Contreras 7046 (HUAP).

Taxonomic notes: *Selaginella schizobasis* belongs to the widely distributed Neotropical *Selaginella horizontalis* complex. This species is distinguished by its creeping stems with flagelliform apices and robust rhizophores that arise along the entire stem length. Its lateral leaves are broadly oblong, widest at mid-section, and the axillary leaves have divergent auricles. Leaf shape and auricle structure remain consistent across individuals, including those on the flagelliform apices. The identities of *S. schizobasis* and *S. sertata* have been debated in various taxonomic treatments across Mexico and Central America. Nevertheless, we treat these two taxa as separate species, as done by Alston (1955), Smith (1981), Stolze (1983), Mickel and Bitel (1988), and Mickel et al. (2004), who concur with this

assessment given their differences in geographic distribution and morphology.

Mickel et al. (2004) reported that *Selaginella schizobasis* is primarily distributed in eastern Mexico (Atlantic slope), while *S. sertata* is more common on the western side (Pacific slope). However, our recent examination of herbarium material indicates that *S. sertata* also occurs on the Caribbean slope, as evidenced by a specimen from the municipality Teapa in Tabasco (E. Matuda 37512, MEXU).

Moreover, available records of *S. schizobasis*, including J. T. Mickel and Pardue 6821 (MO, NY, TEX, UC); J. T. Mickel and L. Pardue 6856 (NY, UC); J. T. Mickel and L. Pardue 6865 (NY) and J. T. Mickel and R. L. Hellwig 4190 (NY) suggest that *S. schizobasis* and *S. sertata* may grow sympatrically in certain areas, particularly in the Isthmus of Tehuantepec. Both taxa are closely related and are often confused during identification, resulting in a significant number of specimens being misidentified. However, *S. schizobasis* exhibits a more stable, less variable macro-morphology than *S. sertata*. It differs from *S. sertata* by its broadly oblong lateral and axillary leaves (vs. oblanceolate to elliptic-lanceolate), median leaves with cuspidate apices (vs. long-acuminate), axillary leaves with divergent short-ciliate auricles (vs. auricles absent or, when present, incurved), and broadly acute apices on the lateral and axillary leaves (vs. acute).

Selaginella steyermarkii Alston, Ann. Mag. Nat. Hist., ser. 12, 7: 638. 1954.

TYPE: GUATEMALA. Huehuetenango, between San Sebastian H. and large penasco above town, *Steyermark 50501* (holotype: BM; isotype F!).

Selaginella steyermarkii is characterized by its prostrate stems, with rhizophores throughout; leaves monomorphic, with long-ciliate margins, adnate bases glabrous or puberulent, and green with reddish spots or entirely red when old, perhaps in response to environmental conditions; sporophylls with long-attenuate apices. As pointed out by Mickel et al. (2004), these characters help



distinguish *S. steyermarkii* from morphologically similar species.

Distribution: Mexico (Chiapas, Oaxaca and Puebla), Guatemala.

Habitat: *Quercus* forest, 1893 m.

Specimens examined: MEXICO. Puebla, municipality Xochiapulco, al N de Cruztatزالán, 1893 m, 19°50'7.6"N, 97°39'44.7"W, *L. Caamaño-Onofre 14543* (HUAP). Municipality Zacapoaxtla, just outside Apulco, 1550 m, ca. 19°55'12"N, 97°37'12"W, 22.VII.2015, *E. Schuettpelz et al. 1756* (US-image).

Taxonomic notes: this species is easily distinguished from other isophyllous species by its characteristic red spots or entirely red leaves. Although some populations of *Selaginella sartorii* Hieron., a morphologically similar species, may also exhibit reddish leaves, *S. steyermarkii* can be distinguished from the former by the length of the aristae on the leaves, which measures 0.5-0.8 mm (vs. 0.8-1.0 mm). Despite their strong morphological resemblance, *S. sartorii* and *S. steyermarkii* are not closely related phylogenetically. *Selaginella hansenii* Hieron., a taxon from central California, is the sister species of *S. steyermarkii*, whereas *S. sartorii* belongs to a more distantly related clade (Arrigo et al., 2013). Following the Weststrand and Korall (2016b) subgeneric classification, this species can be assigned to the subgenus *Rupestreae*.

Discussion

Main findings and significance

Our survey raises Puebla's *Selaginella* checklist from 24 to 31 species by adding 7 previously unreported taxa (i.e., *S. lineolata*, *S. mickelii*, *S. novoleonensis*, *S. pulcherrima*, *S. reflexa*, *S. schizobasis*, and *S. steyermarkii*). The state of Puebla's Taxonomic Biodiversity Index for *Selaginella* (TBI=3.0 taxa/lnA) matches that of Veracruz and nearly equals that of Hidalgo (3.1 taxa/lnA). Although Guerrero also reports 31 *Selaginella* species (Alvarado-Cárdenas et al., 2025), its TBI is lower (2.8 taxa/lnA) because the

index standardizes richness by the natural logarithm of area.

Oaxaca has the highest *Selaginella* Taxonomic Biodiversity Index (TBI=4.6 taxa/lnA). This could be due to its wide elevational range, from Pacific lowlands to the crest of the Sierra Madre del Sur, which creates a mosaic of microhabitats, including some of the most extensive and well-conserved montane cloud forests in Mexico (CONABIO, 2011). This result aligns with the findings of Contreras-Medina et al. (2022), who demonstrated that Oaxaca harbors some of the highest fern and lycophyte richness and endemism in Mexico, particularly in the Sierra Norte region. Their analysis, based on beta-diversity-weighted endemism and fine-scale spatial data, supports the idea that Oaxaca's high *Selaginella* TBI is rooted in genuine biogeographic richness rather than sampling bias or taxonomic inflation.

By contrast, Puebla, Veracruz, and Hidalgo have TBI values around 3.0-3.1. Each contains sizable, contiguous tracts of cloud forest along the Sierra Madre Oriental, with comparable rainfall and humidity regimes (CONABIO, 2011) that favor a diverse *Selaginella* assemblage. Puebla's TBI 3.0 is noteworthy because it equals that of Veracruz, despite the latter being more than twice as large, and is only slightly below Hidalgo's TBI, positioning the Sierra Madre Oriental as a compact yet significant reservoir of *Selaginella* diversity. These relatively high *Selaginella* TBI values across central-eastern to southeastern Mexico (e.g., Oaxaca: 4.6; Puebla, Veracruz, and Hidalgo: ca. 3.0-3.1) are consistent with the region's topographic and ecological complexity and the substantial overlap in plant species composition documented among these states, and align with broader floristic relationships among these states.

Rodríguez-Acosta et al. (2014) demonstrated that Puebla shares strong floristic similarity with Oaxaca and other neighboring states based on vascular plant presence/absence data. This pattern supports the idea that *Selaginella* species richness in Puebla reflects not only the continuity of suitable habitats, particularly montane cloud forest, but also historical biogeographic connections among these regions that have facilitated the dispersal and persistence of species across environmentally connected areas. This pattern of floristic similarity is further reinforced by Puebla's



pronounced environmental heterogeneity, which supports a wide range of climates and vegetation types (Rodríguez-Acosta et al., 2014).

This is especially evident in the northern region and parts of the southeast, such as the Sierra Negra, where mountain cloud forest forms a relatively continuous strip that provides ideal conditions for lycophyte diversity. These results support prioritizing *in situ* conservation on the remaining cloud-forest fragments in Puebla. Nonetheless, the index assumes uniform sampling effort; municipal-level coverage in Puebla remains uneven, and additional surveys could increase both the number of species and the TBI. Lower TBI values in the State of Mexico and Morelos (1.5-1.6) likely reflect drier climates, extensive land-use conversion, and, in some cases, limited field access. In Guerrero, although 31 *Selaginella* species are reported (Alvarado-Cárdenas et al., 2025), difficult terrain and security concerns may still contribute to uneven collecting intensity across the state, potentially obscuring finer-scale patterns of diversity.

Our findings highlight the montane cloud forest of Puebla as one of the most species-rich habitats for *Selaginella*, with 16 taxa recorded (*S. apoda*, *S. delicatissima*, *S. extensa*, *S. flexuosa* Spring, *S. hoffmannii*, *S. lineolata*, *S. martensii* Spring, *S. mixteca* Mickel & Beitel, *S. pallescens*, *S. polyptera*, *S. porphyrospora*, *S. pulcherrima*, *S. sartorii*, *S. schiedeana*, *S. stellata*, and *S. stenophylla*). This is consistent with the environmental characteristics of these forests (mid-elevation, temperature, and high humidity), which are known to promote the diversity of ferns and lycophytes (Kluge et al., 2006; Carvajal-Hernández and Krömer, 2015).

Similarly, tropical evergreen forests (TEF) and *Quercus* forests (QF) also contribute significantly to *Selaginella* diversity in Puebla, jointly hosting 13 species (*S. hoffmannii*, *S. lepidophylla*, *S. martensii*, *S. mickelii*, *S. pallescens*, *S. polyptera*, *S. porphyrospora*, *S. sartorii*, *S. schizobasis*, *S. silvestris* Aspl., *S. stellata*, *S. stenophylla*, and *S. steyermarkii*). Although they differ in structure and seasonality, both vegetation types share key microclimatic features, including relatively stable humidity and moderate temperatures. Two species, *S. pallescens* and *S. stellata*, are shared between both forest types, reflecting their

ecological overlap. Tropical evergreen forests harbors eight species (*S. hoffmannii*, *S. martensii*, *S. mickelii*, *S. pallescens*, *S. polyptera*, *S. schizobasis*, *S. stellata*, and *S. stenophylla*), including species characteristic of humid, mid-elevation habitats. In comparison, QF supports seven species (*S. lepidophylla*, *S. pallescens*, *S. porphyrospora*, *S. sartorii*, *S. silvestris*, *S. stellata*, and *S. steyermarkii*), including some that extend into drier (e.g., *S. lepidophylla*) or more seasonal zones (*S. porphyrospora*). These findings emphasize the importance of both forest types in maintaining regional *Selaginella* richness, especially for hygrophilous species that thrive in less disturbed forest interiors.

Geographically, species richness is concentrated in the northeastern and northwestern parts of the state, particularly in the Sierra Nororiental and Sierra Norte, which together host over 20 *Selaginella* taxa. Of these, 11 species are shared between both regions, while 5 are unique to the northeast (*S. lineolata*, *S. porphyrospora*, *S. pulcherrima*, *S. schizobasis*, and *S. steyermarkii*) and four to the northwest (*S. apoda*, *S. mixteca*, *S. polyptera*, and *S. sellowii* Hieron. This pattern highlights both the ecological connectivity and the regional uniqueness of *Selaginella* assemblages in Puebla's cloud forests.

In contrast, less humid environments in the southern part of the state, especially seasonally dry tropical forests (TDF), tropical subdeciduous forests (TSF), and xerophytic scrublands (XS), also support a significant portion of the genus. These habitats represent the second most important group in terms of *Selaginella* species richness, collectively harboring 11 taxa (*S. hoffmannii*, *S. lepidophylla*, *S. nothohybrida*, *S. pallescens*, *S. rupicola* Underw., *S. sartorii*, *S. schiedeana*, *S. sellowii*, *S. stellata*, *S. stenophylla*, and *S. wrightii* Hieron.). Among these, four species are exclusive to TSF (*S. hoffmannii*, *S. schiedeana*, *S. stellata*, *S. stenophylla*), four are exclusive to XS (*S. nothohybrida*, *S. rupicola*, *S. sartorii*, *S. sellowii*), two are shared between TDF and XS (*S. lepidophylla*, *S. wrightii*), and one species (*S. pallescens*) occurs across all three habitats. These species are mostly isophyllous and rosette-forming, well suited to arid or seasonally dry conditions (Mickel et al., 2004). This highlights the ecological diversity of the genus and emphasizes the need to protect both humid and



xeric environments to preserve the full range of *Selaginella* in Puebla.

Context within previous floristic work

The most comprehensive treatment of *Selaginella* in Puebla to date was provided by Mickel et al. (2004), with subsequent checklists by Rodríguez-Acosta et al. (2014) and Villaseñor (2016) largely reiterating earlier records while perpetuating various omissions and misidentifications. Our revision resolves two recurrent issues in these floristic accounts.

Firstly, we document two previously unreported records for the state. For example, *S. lineolata* was correctly identified by A.R. Smith on herbarium specimens in 2017, yet its presence in Puebla was never formally published. Similarly, *S. novoleonensis* was reported from Oaxaca by Villaseñor (2016) without citing specimens, though multiple collections by J.T. Mickel and collaborators confirm its presence in the state. Our examination of the historical specimen C. A. Purpus 3155 (F, MO, UC), collected in the Tehuacán-Cuicatlán Valley, now formally establishes its presence in Puebla.

Second, our study revises recent misidentifications, including the specimen A. Mendoza R. et al. 2313 (UAMIZ-image) reported as *Selaginella sertata* from the municipality Huehuetla by Mendoza-Ruiz and Ceja-Romero (2020a). Upon careful examination of the specimen and available images, we determined that it is *S. stellata*. This correction removes *S. sertata* from the list of confirmed species in Puebla and underscores the importance of verifying identifications, particularly for taxa with overlapping morphological traits.

Ecological and biogeographic insights

Puebla harbors 31 species of *Selaginella*, representing 38.7% of the 80 species currently recognized in Mexico (Mickel et al., 2004). Its Taxonomic Biodiversity Index for *Selaginella* (TBI=3.0) matches that of Veracruz and is exceeded only by Oaxaca (TBI=4.6). Together, these values highlight Oaxaca as the primary center of *Selaginella* diversity nationally, while also underscoring a secondary concentration along the eastern Sierra Madre Oriental in Hidalgo, Puebla, and

Veracruz, where richness and TBI remain consistently high. This broader montane region collectively harbors nearly 70 distinct taxa, reflecting both high regional richness and strong floristic connectivity across mesic forest habitats. Despite its smaller size, the state of Puebla contributes a comparable number of species to Veracruz and supports a distinct set of geographically restricted taxa within the state (i.e., five known only from the northeastern region and four from the northwestern region). The high degree of species overlaps, approximately 52% of the *Selaginella* species recorded in Oaxaca, Veracruz, and Hidalgo, also occur in Puebla, further emphasizing the ecological continuity of cloud forests and transitional ecotones within this biogeographically cohesive region.

The seven taxa newly recorded for Puebla (*S. lineolata*, *S. reflexa*, *S. novoleonensis*, *S. pulcherrima*, *S. mickelii*, *S. schizobasis*, and *S. steyermarkii*) each expand the known national distribution of these species by adding a new state to their range. The case of *S. steyermarkii* is particularly significant. Originally described from Guatemala (departments Huehuetenango and Sololá) at elevations of 1900–2100 m, the species was first reported in Mexico by Tryon (1955) based on Matuda 1846 from Chiapas (US). Smith (1981) later confirmed its presence in the southern Sierra Madre of Chiapas, where it is considered uncommon, occurring between 1100–1600 m, particularly at the transition between the Central Depression and the Northern Highlands. Mickel et al. (2004) cited this information, maintaining the species' range as restricted to Guatemala and Chiapas. Although Villaseñor (2016) later listed the species for Oaxaca, no voucher was cited. We confirm its presence in Oaxaca based on a specimen collected and identified by A. Mendoza R. et al. 470 (MEXU) from 2080 m in the municipality San Mateo Peñasco. Our new record from Puebla further expands the known range of *S. steyermarkii* northward along the Sierra Madre Oriental, representing a considerable extension of its distribution in Mexico and underscoring the value of revisiting historical herbarium collections.

Furthermore, *S. novoleonensis* was previously known only from scattered localities in Baja California Sur, Sonora, Chihuahua, Coahuila, Nuevo León, Tamaulipas, State



of México, and Guerrero, where it is always found on dry, rocky slopes and limestone outcrops. Our new record from the xerophytic scrub of the Tehuacán Valley, Puebla, not only matches this ecological profile, but also fills an obvious geographic gap along the Sierra Madre Oriental. Instead of indicating undersampling, the Puebla record highlights the continuity of suitable arid habitats across central and northern Mexico and suggests that the species' range may be more continuous than previously suggested by its listed disjunct localities.

Among the species most frequently represented in herbarium collections and online databases, *S. pallescens* and *S. lepidophylla* stand out for their broad ecological tolerance, occurring from northern to southeastern Mexico (Fig. 3A-D). *Selaginella stellata* is likewise widespread, though its Mexican records are concentrated in central and southeastern regions (Fig. 3E,F) (Mickel et al., 2004; Villaseñor, 2016). Their prevalence in collections likely reflects both genuine ecological ubiquity and the ease with which their distinctive forms are detected in the field. The extensive distribution of *S. stellata* from Mexico to Panama may be facilitated by its capacity for vegetative propagation via stolons, a trait that promotes vegetative propagation, clonal spread, and the establishment of dense local populations (Guo et al., 2021; Farias et al., 2024). Coupled with a tolerance for diverse microhabitats, this reproductive strategy helps explain its presence throughout much of Mesoamerica.

By contrast, the rosette-forming *S. lepidophylla* and *S. pallescens* combine morphological and physiological traits, most notably desiccation tolerance and xylem features linked to hydraulic safety, that allow them to persist in seasonally dry environments (Pampurova and Van Dijck, 2014; Grego-Valencia et al., 2018). These features likely underpin their broad ecological amplitude and persistence across contrasting biogeographic regions. Notably, the morphologically variable *S. pallescens* is also reported from several other Neotropical countries, including Belize, Colombia, Costa Rica, Nicaragua, Panama, Suriname, and Venezuela, reinforcing its status as one of the most ecologically versatile members of the genus.

Selaginella porphyrospora is of particular conservation interest, as it is the only species of the genus currently listed under Mexico's endangered-species legislation NOM-059-SEMARNAT-2010 (SEMARNAT, 2019). Its confirmed presence in Puebla, as documented in this study, underlines the conservation value of the state's lycophyte flora and raises significant questions about the status and distribution of threatened taxa in the country. Despite its listing, *S. porphyrospora* is not a rare species in the field or in herbaria. It is frequently collected in Puebla and other states, especially along roadsides, on rocky slopes, and near stream habitats. This species has a broad Neotropical distribution, ranging from Mexico to northern South America (including Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, and Ecuador). Its success may be attributed to two efficient vegetative reproduction strategies: (1) flagelliform branch tips that produce gemmae capable of rooting upon contact with the substrate, and (2) stoloniferous creeping stems that enable rapid clonal spread. These features allow *S. porphyrospora* to colonize disturbed or marginal environments, including partially submerged rocks and seasonally wet slopes, and to form extensive, persistent populations.

The case of *S. porphyrospora* illustrates a potential mismatch between legal conservation status and ecological reality. Its widespread occurrence and adaptability suggest that its current endangered status may warrant reassessment, ideally supported by population-level studies that examine abundance, threats, and habitat trends. At the same time, the focus on this relatively common species may overshadow other, far more vulnerable species that remain unlisted. Puebla's *Selaginella* flora includes 8 of the 28 endemic species currently recognized in Mexico (28.6%), emphasizing its national importance for conservation efforts.

Among these, *S. mixteca* is particularly notable for its highly restricted range, occurring only in Puebla and Oaxaca. Species with more restricted distributions, particularly those endemic to threatened ecosystems like montane cloud forests, may face greater conservation concerns under current environmental pressures in Mexico. For instance, *S. orizabensis* Hieron. has been considered



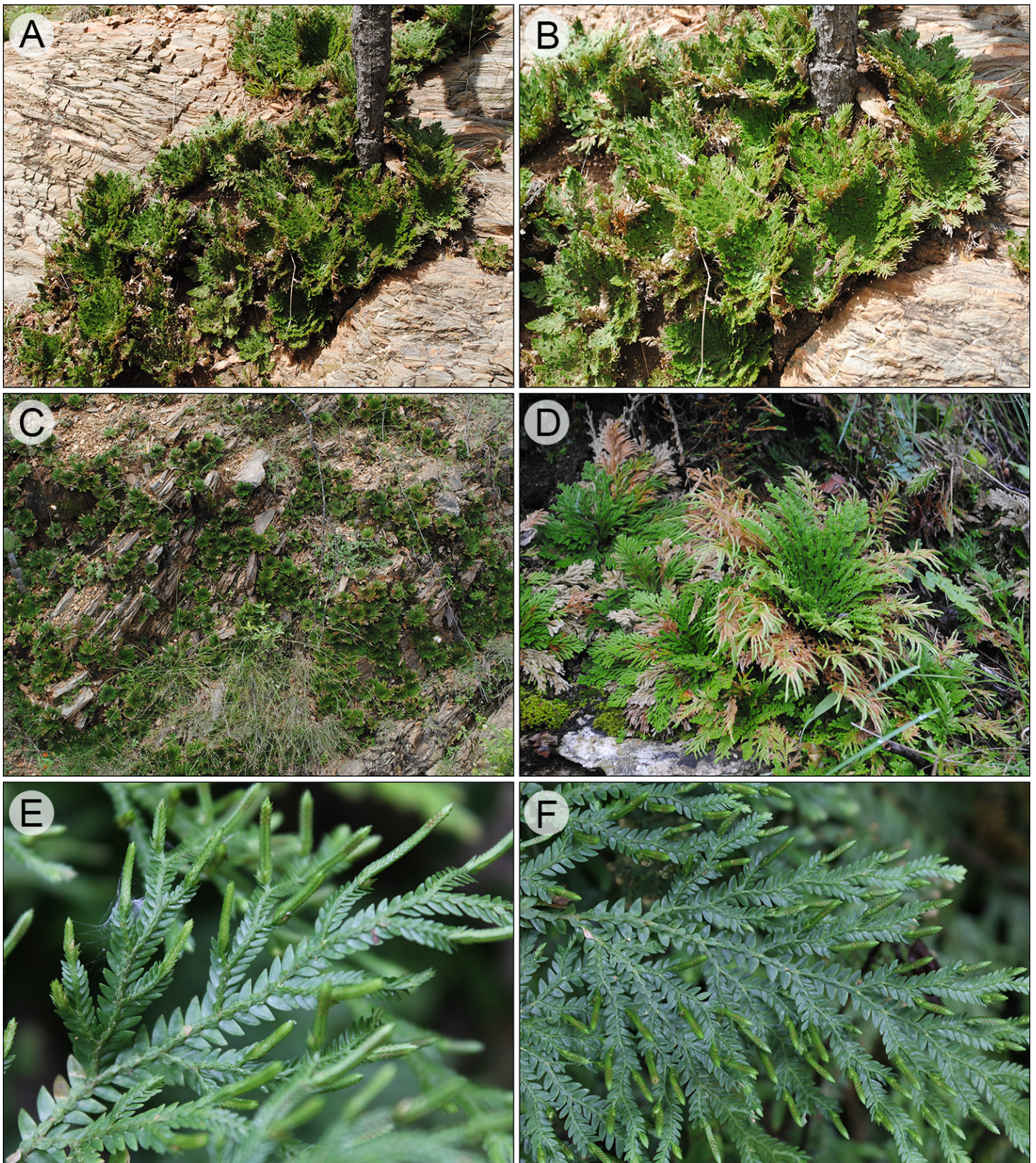


Figure 3: Field photographs of *Selaginella* P.Beauv. in Puebla, Mexico. A. population of *Selaginella lepidophylla* (Hook. & Grev.) Spring covering a rock on a hillside in Tepexi, Puebla; B. close-up of the same population; C. slope covered by *S. lepidophylla* and *S. pallescens* (C.Presl) Spring in the Sierra Mixteca; D. *S. lepidophylla* and *S. pallescens* growing sympatrically in the Sierra Mixteca, with *S. pallescens* on the right; E-F. upper branch surface of *Selaginella stellata* Spring in Cuetzalan del Progreso, Puebla. Photographs by Lucio Caamaño-Onofre (A-D) and C. López (E-F).

by some authors to be possibly extinct in nature, given the absence of collections for over 50 years (Tejero-Díez et al., 2011).

Other narrowly endemic species often overlooked in conservation policies may likewise be at high risk and deserve more urgent attention in future assessments. This concern is further supported by the fact that a significant proportion of the recently described Neotropical *Selaginella* species have been assigned threatened conservation statuses (Valdespino et al., 2024a,b), emphasizing the need to expand assessments beyond the more conspicuous or historically recognized taxa.

Compared with the ranges reported by Mickel and Smith (2004), our study documents upward or downward extensions in the elevational distributions of 15 *Selaginella* taxa in Puebla. For example, we recorded *S. delicatissima*, *S. extensa*, *S. lepidophylla*, *S. mixteca*, *S. nothohybrida*, *S. polyptera*, *S. schiedeana*, *S. stellata*, and *S. steyermarkii* at elevations lower than previously documented, with some extending their lower range limits to 298 m (Table 1). The previously reported elevational ranges for these species were: *S. delicatissima* (900–2500 m), *S. extensa* (700–2100 m), *S. lepidophylla* (100–2200 m), *S. mixteca* (1350–2100 m), *S. nothohybrida* (450–1800 m), *S. polyptera* (180–1750 m), *S. schiedeana* (0–1100 m), *S. stellata* (300–2200 m), and *S. steyermarkii* (960–1700 m).

Additionally, we observed significantly expanded upper limits for *S. hoffmannii* (previously 0–1950 m), *S. pulcherrima* (1200–2400 m), *S. sartorii* (1500–2350 m), *S. stenophylla* (150–1300 m), and *S. wrightii* (375–2000 m), with elevational ranges increased by 450 to 649 m in some cases. Notably, *S. sellowii* was reported by Mickel and Smith (2004) from a very narrow elevational range (1650–1700 m); in our dataset, all confidently identified vouchers of *S. sellowii* range from 1940 to 2587 m.

Although similar upper limits (1800–2250 m) were previously reported for Mexico by Madrigal and Bedolla (2021), our data represent the highest known elevation for the species to date. These elevational range extensions highlight the environmental breadth of *Selaginella* species in Puebla and suggest that earlier floristic treatments may have underestimated their distributions, particularly

in transitional or marginal habitats. This pattern likely reflects a combination of increased recent collecting, re-assessment of herbarium material, and broader access to digitized herbarium specimens through online repositories.

Taxonomic implications and future directions

Mexico remains understudied for *Selaginella*. Our results from Puebla, together with recent regional syntheses and updated records from other Mexican states (Madrigal and Bedolla, 2021; Velázquez-Montes and Martorell, 2025), underscore the continued incompleteness of current distributional knowledge and suggest that continued revisionary work and targeted collecting could raise the documented national total to more than 80 species.

Recent work has opened discussion about generic limits within Selaginellaceae (Zhou and Zhang, 2023; Zhou et al., 2025). Zhou et al. (2025), based on a global phylogeny with sampling across the Americas, adopt a more finely split classification recognizing multiple genera and subfamilies, including the proposal of *Mexiselaginella* Li Bing Zhang & X.M. Zhou as a putatively Mexican-endemic lineage. A particularly relevant example for Mexico concerns the placement of *S. rzedowskii* Lorea-Hern. In Zhou and Zhang (2023), *Lepidoselaginella* was characterized as a group of rosette-forming species with dorsal rhizophores, and *S. rzedowskii* was treated as a member of their genus *Selaginella* s.s. However, Valdespino et al. (2024c) argued that *Lepidoselaginella* Li Bing Zhang & X.M. Zhou, as defined by Zhou and Zhang (2023), does not fully conform to its stated diagnostic combination, because not all taxa allied to that group share a rosette habit. They emphasized that *S. lepidophylla*, *S. novoleonensis*, and *S. ribae* share a distinctive megaspore sculpture in which both proximal and distal faces are reticulate with high ridges and noted that *S. rzedowskii* matches these species in rhizophore position, leaf morphology, and megaspore sculpture despite having a creeping habit.

Valdespino et al. (2024c) further noted that, although Zhou and Zhang (2023) included *S. lepidophylla*, *S. novoleonensis*, and *S. ribae* in their molecular sampling, they did not sample *S. rzedowskii*. Consequently, its



placement within their genus *Selaginella* s.s. was inferred rather than directly tested. In this context, the transfer of *S. rzedowskii* to *Lepidoselaginella* by Zhou et al. (2025) directly engages the morphology-based critique of generic diagnoses and highlights how expanded sampling can shift inferred placements and, consequently, competing views on how many genera should be recognized in Selaginellaceae.

The uncertainty created by misidentifications, limited taxonomic knowledge, and the possible introduction of poorly documented taxa highlights important gaps in our understanding of *Selaginella* distributions in Mexico. The case of *Selaginella umbrosa* Lem. ex Hieron. is illustrative. It is known in Mexico based on two historical records from 1910: one from Tehuantepec, Oaxaca (Orcutt 2172, MO), and another, explicitly labeled as cultivated, from Veracruz (Orcutt 3172, US). Its status in Mexico remains unresolved and may reflect introduction rather than an overlooked native distribution. Misidentifications further compound this uncertainty: *E. Matuda* 3691 (MEXU) from Palenque, Chiapas, originally identified as *S. umbrosa*, is actually *S. mickelii*, and Romero 3444 (MEXU) from Yaxchilán, Chiapas, is confirmed as *S. hoffmannii*.

To enhance Mexico's standing at the forefront of lycophyte systematics, three tasks are paramount to be conducted: (1) a critical reassessment of taxonomically difficult groups such as the *S. pallescens* complex and others, where morphological plasticity has led to persistent misidentification; (2) targeted surveys in poorly sampled states (e.g., Aguascalientes, Tabasco, Tlaxcala) and underexplored habitats such as tropical evergreen forest and seasonally dry vegetation, which are likely to yield further novelties; and (3) integrated barcoding and morphological analyses to test species limits in morphologically complex groups, such as the *S. pallescens* complex, and to evaluate whether some entities merit recognition at species rank. In *Selaginella*, taxonomic confusion in species delimitation likely stems from long-standing misdeterminations, reflecting how outdated species concepts and inconsistent taxonomy have been perpetuated across floristic treatments and herbarium records.

More broadly, following the three points outlined above will not only advance understanding of Mexican *Selaginella* but also contribute to a better grasp of the genus globally. Taxonomic progress does not necessarily require further splitting based on insufficient and misleading evidence. Without solving the underlying challenge of accurate species identification, particularly in morphologically complex groups, any proliferation of names risks adding confusion rather than clarity. A stable, integrative approach grounded in both field and herbarium research remains essential to resolving the true diversity and relationships within *Selaginella*.

Notes on additional state records outside Puebla

In addition to the Puebla checklist, during herbarium work, we noted three new state records supported by revised identifications of MEXU material. *Selaginella nothohybrida* is newly recorded for Morelos from the municipality Miacatlán (L. Pacheco et al. 3445, MEXU), previously misidentified as *S. pallescens*. *Selaginella polyptera* is newly recorded for Querétaro from the neighboring municipalities Jalpan (B. Servín 847, MEXU) and Landa (H. Rubio 1509, MEXU), where it was initially identified as *S. harrisii*. Finally, *Selaginella sertata* is newly recorded for Tabasco from the municipality of Teapa (E. Matuda 37512, MEXU), based on a herbarium specimen previously overlooked in state-level treatments. These cases underscore the extent to which misidentifications can mask state-level diversity and reinforce the need for targeted revision in difficult species complexes.

Conclusions

Selaginella is well represented in Puebla, where our study raises the number of previously recorded species from 24 to 31, including 7 newly reported taxa. This brings Puebla's Taxonomic Biodiversity Index (TBI=3.0) to match that of Veracruz and nearly equal that of Hidalgo, highlighting its importance in the national context. As a standardized richness-based metric, the TBI provides a useful first-order tool for comparing *Selaginella* diversity among states, especially when taxonomic circumscription is consistent. However, because it is sensitive to uneven sampling and identification



effort, TBI contrasts should be interpreted cautiously and updated as inventories and determinations improve.

Species richness is especially concentrated in montane cloud, tropical evergreen, and *Quercus* forests, confirming these habitats as key reservoirs of lycophyte diversity. Seasonally dry tropical forests and xeric scrublands also support an important subset of species, underscoring the genus' ecological breadth. New elevational records and range extensions for multiple taxa emphasize the importance of continued fieldwork and herbarium revision.

Several widespread species, such as *S. lepidophylla* and *S. pallescens*, thrive across diverse environments, while narrowly endemic species like *S. mixteca* highlight the need for targeted conservation efforts. Our findings also reveal significant taxonomic issues, including misidentifications and underreported taxa, stressing the need for a reassessment of complex species groups.

Finally, Puebla's strong floristic connections with neighboring states, coupled with underexplored regions along its borders, suggest that further exploration may yield additional records. Strengthening inventories, clarifying species limits, and integrating morphological and molecular approaches are essential steps toward refining our understanding of *Selaginella* diversity in Mexico.

Author contributions

Conceptualization: CAL, ABCC; Data curation: CAL; Formal analysis: CAL, ABCC; Funding acquisition: CAL, ABCC, IAV; Investigation: CAL, ABCC, LCO; Methodology: CAL, ABCC; Project administration: CAL; Resources: CAL, ABCC; Supervision: CAL; Validation: CAL, IAV; Visualization: LCO, CAL; Writing – original draft: CAL, ABCC; Writing – review & editing: CAL, ABCC, LCO, IAV.

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Declaration of Artificial Intelligence Use

No generative AI tools were used to produce the scientific content, interpretations, or conclusions of this manuscript.

Data Accessibility Statement

The data supporting the findings of this study are available in SciELO Data and can be accessed at: <https://doi.org/10.48331/SCIELODATA.RKQ8TI>



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