TAXONOMIC REVISION OF THE PETIOLATUM CLADE OF *ELAPHOGLOSSUM* SECT. *LEPIDOGLOSSA* (DRYOPTERIDACEAE)[1]

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Abstract

This paper provides a monograph of the petiolatum clade of *Elaphoglossum* Schott ex J. Sm. sect. *Lepidoglossa* Christ (Dryopteridaceae). This group has been recovered as monophyletic in several molecular phylogenetic analyses. Morphologically, the petiolatum clade is recognized by laminae with resinous dots and flat and/or stellate scales, rhizome scales with acute to filiform-tortuous apices, scales on the proximal portion of the petiole with dark apices, and perines broadly folded, sparsely echinulate with spines less than 1 µm high, or (in *E. petiolatum* (Sw.) Urb.) with sparse irregular microstructures. Eight species are recognized as a part of the clade, all of them distributed in the American tropics from Mexico to Panama, and one species in the Greater Antilles. Most of the species occur between 1000 and 2500 m elevation in tropical, temperate, and pine-oak forests. Presented here are an identification key, a full synonymy, detailed descriptions, a list of specimens examined, an index to collectors' names and collection numbers, images of the plants and their main structures, spore microphotographs, and distribution maps for all species. A new combination is made for *E. schmitzii* (Mett. ex Kuhn) Martínez-Bec. & A. Vasco, and lectotypes are designated for *Acrostichum intermedium* Fée, *E. muelleri* (E. Fourn.) C. Chr., *E. potosianum* Christ, *E. pringlei* (Davenp.) C. Chr., and *E. schmitzii*.

Resumen

Este artículo proporciona una monografía del clado petiolatum de *Elaphoglossum* Schott ex J. Sm. secc. *Lepidoglossa* Christ (Dryopteridaceae). Este grupo ha sido recuperado como monofilético en diferentes análisis filogenéticos moleculares. El clado petiolatum se reconoce morfológicamente por la presencia de puntos resinosos y escamas planas y/o estrelladas en las láminas foliares, escamas del rizoma con ápices agudos a filiforme-tortuosos, escamas de la porción proximal del pecíolo con ápices oscuros, y perinas con pliegues amplios y superficies escasamente equinuladas con espinas de menos de 1 µm de alto, o (en *E. petiolatum* (Sw.) Urb.) con microestructuras irregulares escasas. Dentro de este clado se reconocen ocho especies, todas distribuidas en los trópicos americanos desde México hasta Panamá, y una especie en las Antillas Mayores. La mayoría de las especies del clado se encuentra entre 1000 y 2500 m de elevación en bosques tropicales, templados, y de pino-encino. Se presenta una clave de identificación, una sinonimia completa, descripciones detalladas, una lista de especímenes examinados, un índice de los apellidos de los colectores y los números de colección, imágenes de las plantas y sus principales estructuras, microfotografías de esporas, y mapas de distribución para todas las especies. Se lleva a cabo una nueva combinación para *E.*

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schmitzii (Mett. ex Kuhn) Martínez-Bec. & A. Vasco y se designan lectotipos para *Acrostichum intermedium* Fée, *E. muelleri* (E. Fourn.) C. Chr., *E. potosianum* Christ, *E. pringlei* (Davenp.) C. Chr., y *E. schmitzii*.

Key words: Ferns, floristics, Mexico, morphology, nomenclature, resinous dots, taxonomy, tropics.

Elaphoglossum Schott ex J. Sm. (Dryopteridaceae) is a genus of tropical ferns with more than 600 accepted species out of the more than 1000 described (PPG I, 2016; Rouhan, 2020). The genus is distributed mainly in wet and cloud forests throughout the tropics, but it is most diverse in the American tropics, where approximately 75% of the species occur (Mickel & Atehortúa, 1980; Mickel, 1991; Moran et al., 2007; Rouhan, 2020).

Elaphoglossum is distinguished from other ferns by laminae that are almost always simple (six of the 600 species have divided laminae), dimorphic sterile and fertile leaves, free veins, and acrostichoid sori. While most species are epiphytes, there are also terrestrial, hemiepiphytic, and epipetric species (Mickel, 1995; Rouhan et al., 2008; Moran et al., 2010; Lagomarsino et al., 2012; Vasco et al., 2013; Rouhan, 2020; Zotz et al., 2021).

Phylogenetic molecular analyses have recovered *Elaphoglossum* as sister to *Mickelia* R. C. Moran, Labiak & Sundue. Both genera belong to the bolbitidoid clade (sensu Moran et al., 2010) in the Dryopteridaceae, one of the largest fern families in the world (Hasebe et al., 1995; Rouhan et al., 2004; Skog et al., 2004; Liu et al., 2007, 2016; Schuettpelz & Pryer, 2007; Vasco et al., 2009a; Moran et al., 2010; Lóriga et al., 2014; PPG I, 2016). Within *Elaphoglossum*, seven main clades, which have been ranked as sections, are currently recognized: (1) *Elaphoglossum* sect. *Amygdalifolia* (Christ) Mickel & Atehortúa, (2) *Elaphoglossum* sect. *Wrightiana* J. Lóriga, A. Vasco, L. Regalado, J. Heinrichs & R. C. Moran, (3) *Elaphoglossum* sect. *Elaphoglossum*, (4) *Elaphoglossum* sect. *Squamipedia* Mickel & Atehortúa, (5) *Elaphoglossum* sect. *Polytrichia* (Sodiro) Christ, (6) *Elaphoglossum* sect. *Setosa* (Christ) Mickel and Atehortúa, and (7) *Elaphoglossum* sect. *Lepidoglossa* Christ (Rouhan et al., 2004; Skog et al., 2004; Lóriga et al., 2014).

Elaphoglossum sect. *Lepidoglossa* is the most species-rich section, containing more than 200 species (Vasco, 2011). This section is characterized by laminae obviously scaly, rhizome and lamina scales typically flat (not subulate), and scale margins with unicellular, acicular, nonglandular marginal cells, herein called projections (Mickel & Atehortúa, 1980; Vasco et al., 2009b; Kessler et al., 2018).

Based on morphology, Mickel and Atehortúa (1980) recognized six subsections within *Elaphoglossum* sect. *Lepidoglossa*, differing mainly by the shape and density of the scales, the shape of the lamina apex, and the morphology of the spores. These subsections were called *Elaphoglossum* subsect. *Huacsaro* Mickel & Atehortúa, *Elaphoglossum* subsect. *Microlepidea* Christ, *Elaphoglossum* subsect. *Muscosa* Mickel & Atehortúa, *Elaphoglossum* subsect. *Petiolosa* Christ, *Elaphoglossum* subsect. *Pilosa* Christ, and *Elaphoglossum* subsect. *Polylepidea* Christ.

As a part of his floristic work on *Elaphoglossum* in Mexico, Mickel (2001) informally described a species group that he called "the *Elaphoglossum petiolatum* complex." In this complex, Mickel included about 11 species distributed throughout the tropics, characterized by resinous dots on the abaxial laminar surfaces, dark rhizome scales, and scales on the proximal portions of the petiole with dark apices (Table 1). Based on morphology, the 11 species described as part of the complex belong to *Elaphoglossum* subsect. *Pilosa*.

Elaphoglossum subsect. *Pilosa* was originally described by Christ (1899) and later circumscribed by Mickel and Atehortúa (1980). The species of *Elaphoglossum* subsect. *Pilosa* are characterized by short-creeping rhizomes; rhizome scales usually dark, entire, or with long projections; laminar scales stellate or with long projections; laminar resinous dots; and perines with broad folds. Mickel and Atehortúa (1980) suggested affinities of *Elaphoglossum* subsect. *Pilosa* with other subsections of *Elaphoglossum* sect. *Lepidoglossa*, such as *Elaphoglossum* subsect. *Microlepidea* and *Elaphoglossum* subsect. *Huacsaro*, mainly because of the presence of stellate laminar scales in the first and the presence of laminar resinous dots in the second.

Molecular phylogenetic analyses have shown that neither *Elaphoglossum* subsect. *Pilosa* nor the *E. petiolatum* complex is monophyletic, suggesting that the characters that define the subsection and the complex evolved multiple times during the evolutionary history of the genus (Rouhan et al., 2004; Vasco et al., 2009a; Lóriga et al., 2014). Particularly, the species of the complex were recovered into three different clades (Vasco et al., 2009a). One of these clades, the *E. ciliatum* clade, was monographed (Vasco et al., 2009b); another included many of the South American specimens previously identified as *E. petiolatum* (Sw.) Urb.; and the third, called the "Mexican-petiolatum clade," was found to include the Mexican endemic species considered to be part of the *E. petiolatum* complex (Vasco et al., 2009b). We are here renaming this last clade the "petiolatum clade" because our recent molecular phylogenetic analyses, based on plastid data, have shown that it is also distributed in Central America and the Greater Antilles (Martínez-Becerril & Vasco, in prep.), and be-

Table 1. Species belonging to the *Elaphoglossum petiolatum* (Sw.) Urb. complex sensu Mickel (2001) and their current known distribution. Species with an asterisk (*) are recovered as part of the petiolatum clade.

Species	Distribution
Elaphoglossum bifurcatum (Jacq.) Mickel	Saint Helena Island
E. blumeanum (Fée) J. Sm.	Bismarck Archipelago, Borneo, China, Indonesia, Malaysia, Philippines, Solomon Islands, Sumatra
E. dimorphum (Hook. & Grev.) T. Moore	Saint Helena Island
E. nervosum (Bory) Christ	Saint Helena Island
**E. petiolatum* (Sw.) Urb.	From Mexico to Panama and the Greater Antilles
**E. pringlei* (Davenp.) C. Chr.	Mexico
**E. rzedowskii* Mickel	Mexico
E. salicifolium (Willd. ex Kaulf.) Alston (= *E. lancifolium* (Desv.) C. V. Morton)	Bioko, Cameroon, Comoros, Congo, Gaba, Guinea, Liberia, Madagascar, Malawi, Mauritius Island, Mozambique, Réunion, Rwanda, Seychelles, Sierra Leone, Tanzania, Zambia, Zimbabwe
E. stelligerum (Wall. ex Baker) T. Moore ex Salomon	India
**E. trichomidiatum* Mickel (= *E. potosianum* Christ)	Mexico
E. yunnanense (Baker) C. Chr.	China, India, Malaysia, Vietnam

cause this clade includes sequences from an *E. petiolatum* specimen from Jamaica, the type locality of this species (Swartz, 1778; Proctor, 1985). This paper presents a taxonomic revision of the petiolatum clade.

Materials and Methods

This study is based on the examination of more than 2000 herbarium sheets representing about 809 gatherings deposited in 13 herbaria. Digital specimens from virtual herbaria and <https://pteridoportal.org> were also examined. The protologues and types of all the names in this group and their synonyms were checked, and all relevant literature was consulted (e.g., Proctor, 1985; Mickel, 1991; Mickel & Smith, 2004).

For the descriptions and key, the terminology of Lellinger (2002) and Tryon and Lugardon (1991) was used. Measurements, colors, and characteristics described are based on the herbarium specimens observed. Scales in the middle of rhizomes, petioles, and laminae were the ones measured and used in the descriptions and key. Plant measurements, including length and width of laminae and the proportion of the petiole, were taken from a representative sample of approximately 20 dried specimens per species that reflected the intraspecific morphological variation. Once selected, the largest leaf of each specimen was measured.

In the key and descriptions, the term "projection" describes the acicular marginal cells of the scales; small projections are less than half the scale width, while long projections are more than half the scale width. The term "microscale" describes small, hairlike, reduced scales found mainly on petioles and laminae; these same structures have been called trichomidia in previous treatments of *Elaphoglossum* (Mickel & Smith, 2004). In the petiolatum clade, microscales are often mixed with scales. If not indicated, leaf structures and scales described in the key and shown in the figures correspond to those of sterile leaves.

To make the distribution maps, all coordinates were converted from degrees to decimals; we estimated most coordinates using Google Earth (<https://www.google.com/earth/>) because this information was often not provided on specimen labels. Estimated coordinates for types are given in brackets. Distribution maps were made using the RStudio program version 4.3.1 (R Core Team, 2023) and the packages dplyr (Wickham et al., 2022), ggplot (Wickham, 2016), ggsaptial (Dunnington, 2023), raster (Hijmans, 2024a), rnaturalearth (Massicotte & South, 2024), sf (Pebesma, 2018), sp (Pebesma & Bivand, 2005), and terra (Hijmans, 2024b). To show the elevation intervals of the species, a box-and-whisker plot was produced in RStudio using the elevation of all collections recorded in meters.

Spore microphotographs and species plates were prepared from herbarium specimens for all species. Spores of 86 specimens from all species (at least three specimens per species) were examined and photographed following the methodology described by Moran et al. (2007) and detailed in Martínez-Becerril et al. (2021), using SEMs (Hitachi SU1510 at UNAM and Hitachi SU3600 at BRIT; Hitachi, Chiyoda City, Tokyo, Japan). The species plates were made using photographs taken with a camera coupled to a Leica M165C microscope (Leica, Wetzlar, Germany). Fieldwork was carried out in the Mexican states of Aguascalientes, Chihuahua, Jalisco, Puebla, and San Luis Potosí.

Table 2. Distribution of species of the petiolatum clade by country. Endemic species are in boldface. The number of taxa per locality appears in parentheses.

Country	Species
Costa Rica (1)	*Elaphoglossum petiolatum*
Cuba (1)	*E. petiolatum*
Dominican Republic (1)	*E. petiolatum*
El Salvador (2)	*E. muelleri*, *E. petiolatum*
Guatemala (4)	***E. auralolitae***, *E. muelleri*, *E. petiolatum*, *E. schiedei*
Honduras (2)	*E. muelleri*, *E. petiolatum*
Jamaica (1)	*E. petiolatum*
Mexico (7)	*E. muelleri*, *E. petiolatum*, ***E. potosianum***, ***E. pringlei***, ***E. rzedowskii***, *E. schiedei*, ***E. schmitzii***
Nicaragua (2)	*E. muelleri*, *E. petiolatum*
Panama (1)	*E. petiolatum*

Results

We recognize eight species within the petiolatum clade (Table 2), six of which (*E. petiolatum*, *E. potosianum* Christ, *E. pringlei* (Davenp.) C. Chr., *E. rzedowskii* Mickel, *E. schiedei* (Kunze) T. Moore, and *E. schmitzii* (Mett. ex Kuhn) Martínez-Bec. & A. Vasco) were included in our phylogenetic molecular analyses (Martínez-Becerril & Vasco, in prep.). Additionally, we consider two more, *E. auralolitae* Martínez-Bec. & A. Vasco and *E. muelleri* (E. Fourn.) C. Chr., as part of the clade based on sporophyte and spore morphology, as well as their distribution in Central America and Mexico. A new combination is made and five lectotypes are designated for species in the group or their synonyms. No infraspecific taxa are recognized. A list of collectors' names and their numbers for all examined specimens is given in Appendix 1.

There is not a unique morphological character that distinguishes the species of the petiolatum clade. The clade comprises small to medium-sized terrestrial, epipetric, or epiphytic ferns; usually less than 50 cm high, with short-creeping rhizomes with scales with acute to filiform apices; phyllopodia present, sometimes obscured by the rhizome scales; leaves with shiny, reddish- to yellowish-brown resinous dots (mostly on the abaxial surface of the lamina) often mixed with scales, the adaxial laminar scales with long projections; laminae narrowly elliptic to lanceolate with obtuse to acuminate apices, papyraceous to chartaceous; intersporangial scales not visible; and perines broadly folded, mainly with sparsely echinulate surfaces (with spines less than 1 μm high; Fig. 1).

In the species of the petiolatum clade, the resinous dots are found mainly on the abaxial laminar surfaces, mixed with scales or not; however, in some species of the clade, they can also occur on petioles or adaxial laminar surfaces. These dots have been interpreted as the bases of reduced scales that remain embedded in the epidermis of the laminae (Vasco et al., 2009b). Although present in all species belonging to the petiolatum clade, resinous dots are not unique to the clade, being found in other species of *Elaphoglossum* sect. *Lepidoglossa*, and thus they likely evolved independently multiple times during the evolutionary history of this section (Vasco et al., 2009a, 2009b).

Our SEM analyses show that the spores of all species (except *Elaphoglossum petiolatum*) in the petiolatum clade have perines with broad folds and sparsely echinulate surfaces, with spines less than 1 μm high (Martínez-Becerril et al., 2021; Fig. 1). *Elaphoglossum petiolatum* has broadly folded perines with sparsely irregular microstructures (Fig. 1D). The difference in spore ornamentation is a good character to differentiate *E. petiolatum* from the rest of the species in the clade; however, these differences can be distinguished only with the SEM. The perine character is included in the taxonomic key and descriptions, but it is not essential to key out species. In most cases, the key can be used with specimens lacking fertile leaves. The descriptions for each species do not repeat the characters that are constant for the clade.

The petiolatum clade is distributed from Mexico to Panama and in the Greater Antilles, mainly at elevations between 740 and 3050 m (Fig. 3). Seven of the eight species occur in Mexico, and four are endemic to that country (Fig. 2, Table 2). A list of species distribution that includes the specific states or departments in each country is given in Appendix 2. The petiolatum clade does not occur in South America or the Eastern Hemisphere; all species identified with names belonging to this clade in these regions need to be revised (see the notes under *Elaphoglossum petiolatum* for a detailed discussion).

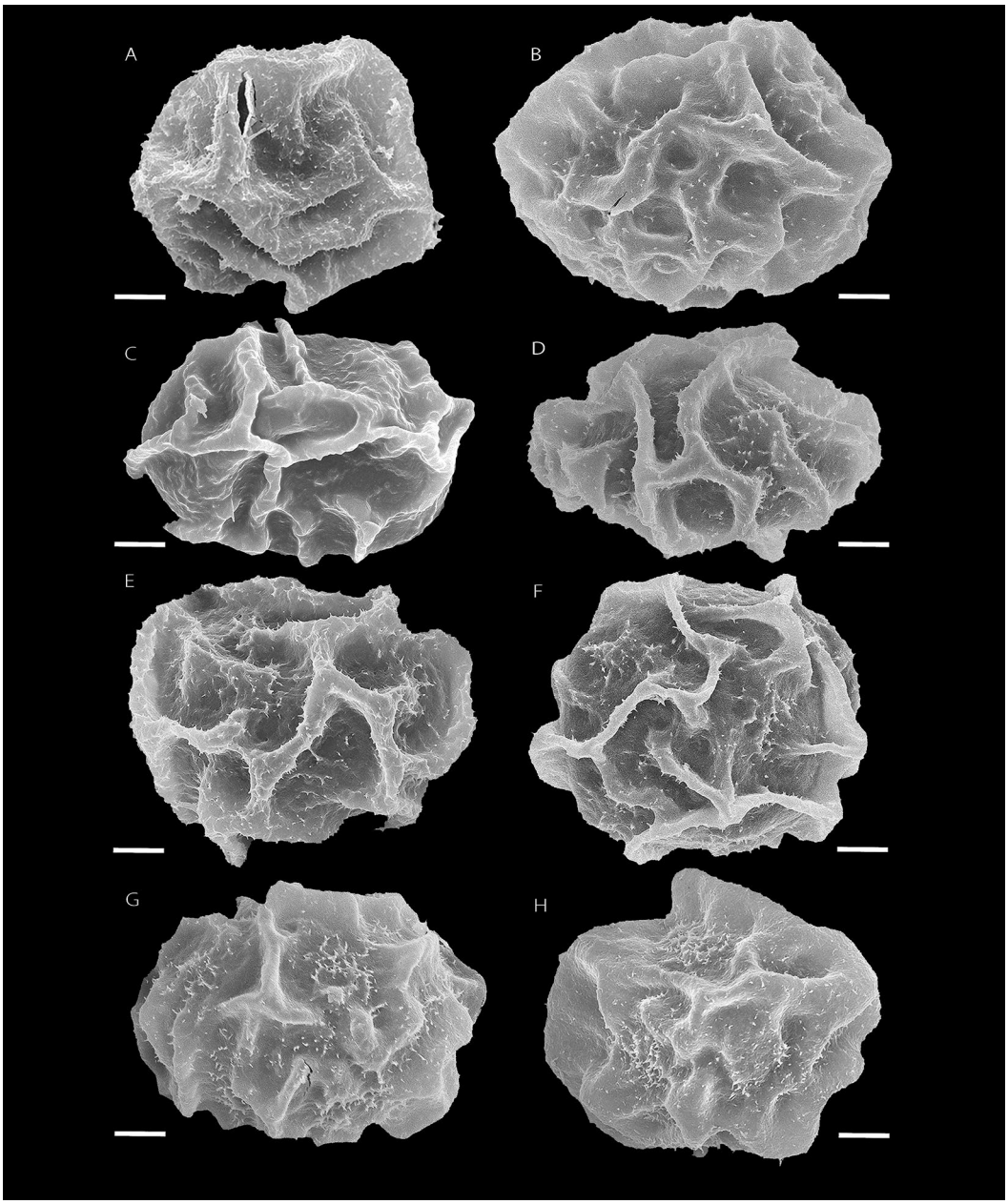

Figure 1. Spores of species of the petiolatum clade. —A. *Elaphoglossum auralolitae* Martínez-Bec. & A. Vasco from *Standley 58933* (F). —B. *Elaphoglossum muelleri* (E. Fourn.) C. Chr. from *Anderson 13211* (MEXU). —C. *Elaphoglossum petiolatum* (Sw.) Urb. from *Hellwig 440* (NY). —D. *Elaphoglossum potosianum* Christ from *Martínez-Becerril 399* (FEZA). —E. *Elaphoglossum pringlei* (Davenp.) C. Chr. from *Anderson 4778* (MEXU). —F. *Elaphoglossum rzedowskii* Mickel from *Martínez-Becerril 408* (FEZA). —G. *Elaphoglossum schiedei* (Kunze) T. Moore from *Gallardo Hernández 836* (MEXU). —H. *Elaphoglossum schmitzii* (Mett. ex Kuhn) Martínez-Bec. & A. Vasco from *McVaugh 23885* (MEXU). All scale bars = 10 µm.

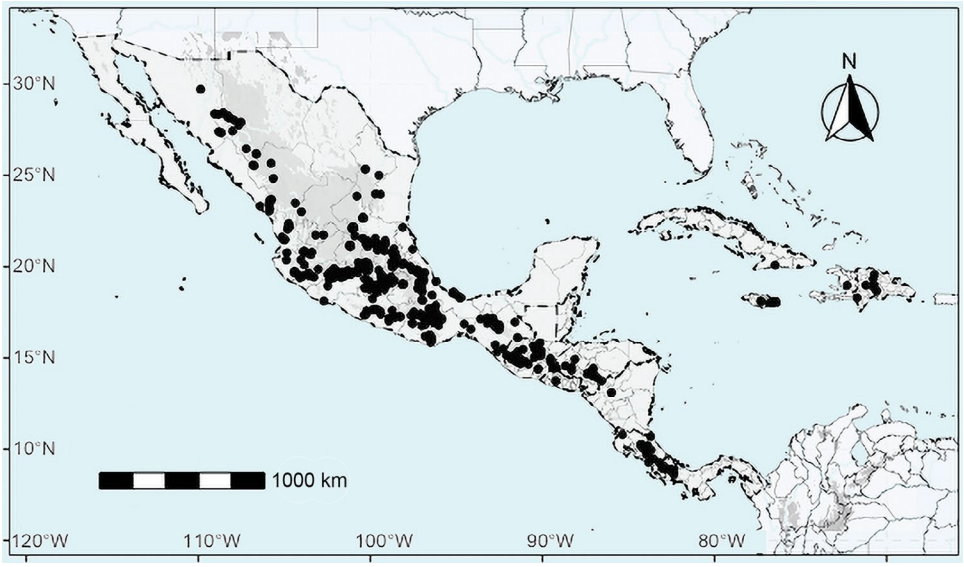

Figure 2. Distribution map of all species in the petiolatum clade.

Taxonomic Treatment

For the key and species descriptions, the scales measured were those in the middle of the rhizomes, petioles, and laminae. The term "projection" describes the acicular marginal cells of the scales; small projections are less than half the scale width, while long projections are more than half the scale width. For structures that are difficult to see, such as microscales, a stereoscope with at least ×40 magnification is necessary. If not indicated, leaf structures and scales correspond to those of the sterile leaves.

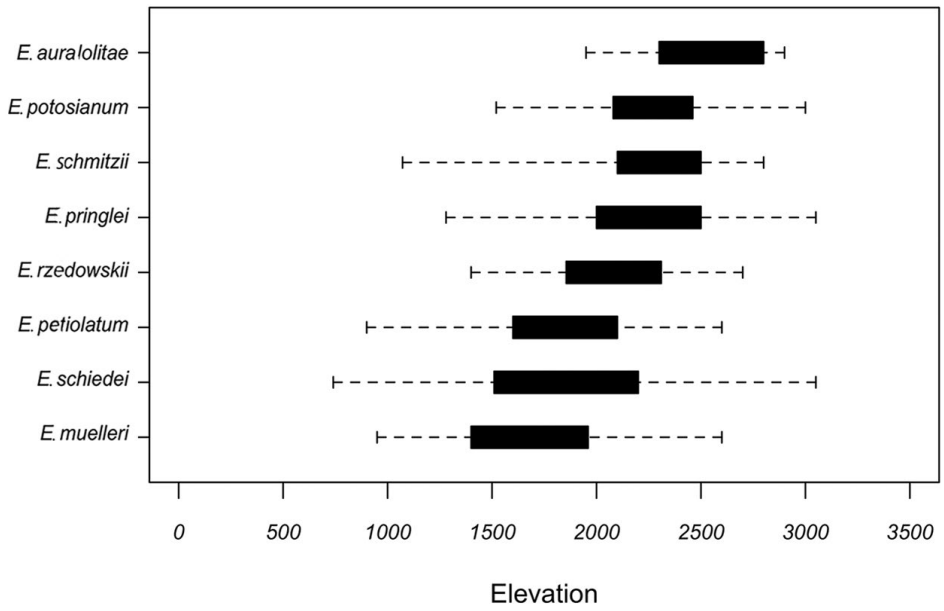

Figure 3. Box plot depicting elevational ranges of all species in the petiolatum clade.

Key to the Species of the Petiolatum Clade

1. Rhizome scales scattered, appressed, concolorous, oblanceolate, lustrous, sclerotic . . . . . 7. *E. schiedei* (Kunze) T. Moore
1′. Rhizome scales dense, spreading, bicolorous or concolorous, linear to lanceolate, dull or lustrous, not sclerotic.
2. Rhizome scales concolorous.
3. Microscales on abaxial laminar surface absent (use magnification).
4. Adaxial laminar scales absent or, if present, scattered to dense, not imbricate, the larger ones up to 1 mm, with occasional short or long projections and an attenuate apex; phyllopodia clearly visible; petiole scales scattered or dense mainly at the base; perines with sparse irregular surface microstructures . . . . . 3. *E. petiolatum* (Sw.) Urb.
4′. Adaxial laminar scales present, dense, usually imbricate, the larger ones up to 1.5. mm, with numerous long projections and a long-attenuate to filiform apex; phyllopodia usually obscured by rhizome scales; petiole scales dense throughout; perines with sparse echinulate surfaces . . . . . 1. *E. auralolitae* Martínez-Bec. & A. Vasco
3′. Microscales on abaxial laminar surface present (use magnification).
5. Abaxial laminar scales dense (only occasionally scattered), stellate or occasionally irregular; abaxial laminar microscales scattered (hard to see, even under a stereoscope); laminae narrowly elliptic . . . . . 2. *E. muelleri* (E. Fourn.) C. Chr.
5′. Abaxial laminar scales absent or scattered, irregular; abaxial laminar microscales dense (easy to see under a stereoscope); laminae linear-lanceolate to narrowly elliptic . . . . . 4. *E. potosianum* Christ
2′. Rhizome scales bicolorous.
6. Abaxial laminar scales present, dense, sometimes imbricate; phyllopodia usually obscured by rhizome scales; rhizome scales with acuminate to long-attenuate apex; laminae linear to elliptic. . . . . 6. *E. rzedowskii* Mickel
6′. Abaxial laminar scales absent or, if present, scattered to dense, never imbricate; phyllopodia clearly visible; rhizome scales with attenuate to filiform-tortuous apex (often broken); laminae narrowly elliptic or elliptic to lanceolate.
7. Laminae elliptic to lanceolate, the base decurrent; abaxial laminar scales present, substellate, irregular, or lanceolate; abaxial resinous dots absent or present . . . . . 5. *E. pringlei* (Davenp.) C. Chr.
7′. Laminae narrowly elliptic, the base cuneate; abaxial laminar scales absent or, if present, linear-lanceolate; abaxial resinous dots always present . . . . . 8. *E. schmitzii* (Mett. ex Kuhn) Martínez-Bec. & A. Vasco

1. Elaphoglossum auralolitae Martínez-Bec. & A. Vasco, Amer. Fern J. 113(2): 129. 2023. TYPE: Guatemala. San Marcos: San Pedro Sac. [Sacatepéquez], 2300 m, [14.95, –91.81], 19 Aug. 1992, *M. Véliz 92.2319* (holotype, MEXU [barcode] 903674!; isotype, BIGU [bc] 0030067!). Figures 1A, 4, 5.

Plants terrestrial. **Rhizomes** 3–3.5 mm wide, short-creeping; **rhizome scales** 2.5–4 mm, dense, spreading, linear-lanceolate to lanceolate, entire or with occasional short projections (shorter than width of scale), concolorous, dark reddish brown to dark brown, lustrous, base round, apex attenuate to filiform-tortuous. **Sterile leaves** 13.5–39.5(–45) cm, approximate; **phyllopodia** present, usually obscured by rhizome scales, 5–10 mm; **petioles** 5–15.5(–18) cm, 1/3–2/5 the length of sterile leaves; **larger petiole scales** to 3.5(–4) mm, dense, usually imbricate, spreading to appressed, linear-lanceolate to ovate, with occasional short projections, stramineous to brown, usually darker at apex, base round, apex attenuate to filiform-tortuous; **smaller petiole scales** to 0.3 mm (difficult to see), dense, appressed, irregular or lanceolate, with numerous long projections (as long as or longer than width of scale) or with occasional short projections, stramineous, base auriculate, apex attenuate, usually with a long projection close to apex; **laminae** 8.5–24(–27) × 1.2–2.4 cm, linear-elliptic to elliptic, chartaceous, base cuneate, apex acute to acuminate; **adaxial laminar scales** 0.5–1.4 mm, dense, usually imbricate, lanceolate, with numerous long projections, stramineous to whitish,

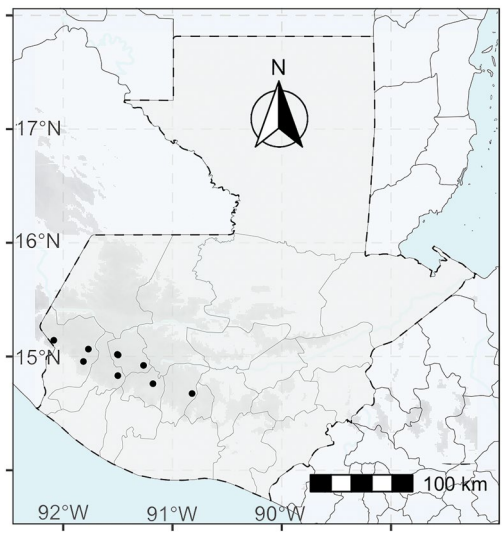

Figure 4. Distribution map of *Elaphoglossum auralolitae* Martínez-Bec. & A. Vasco.

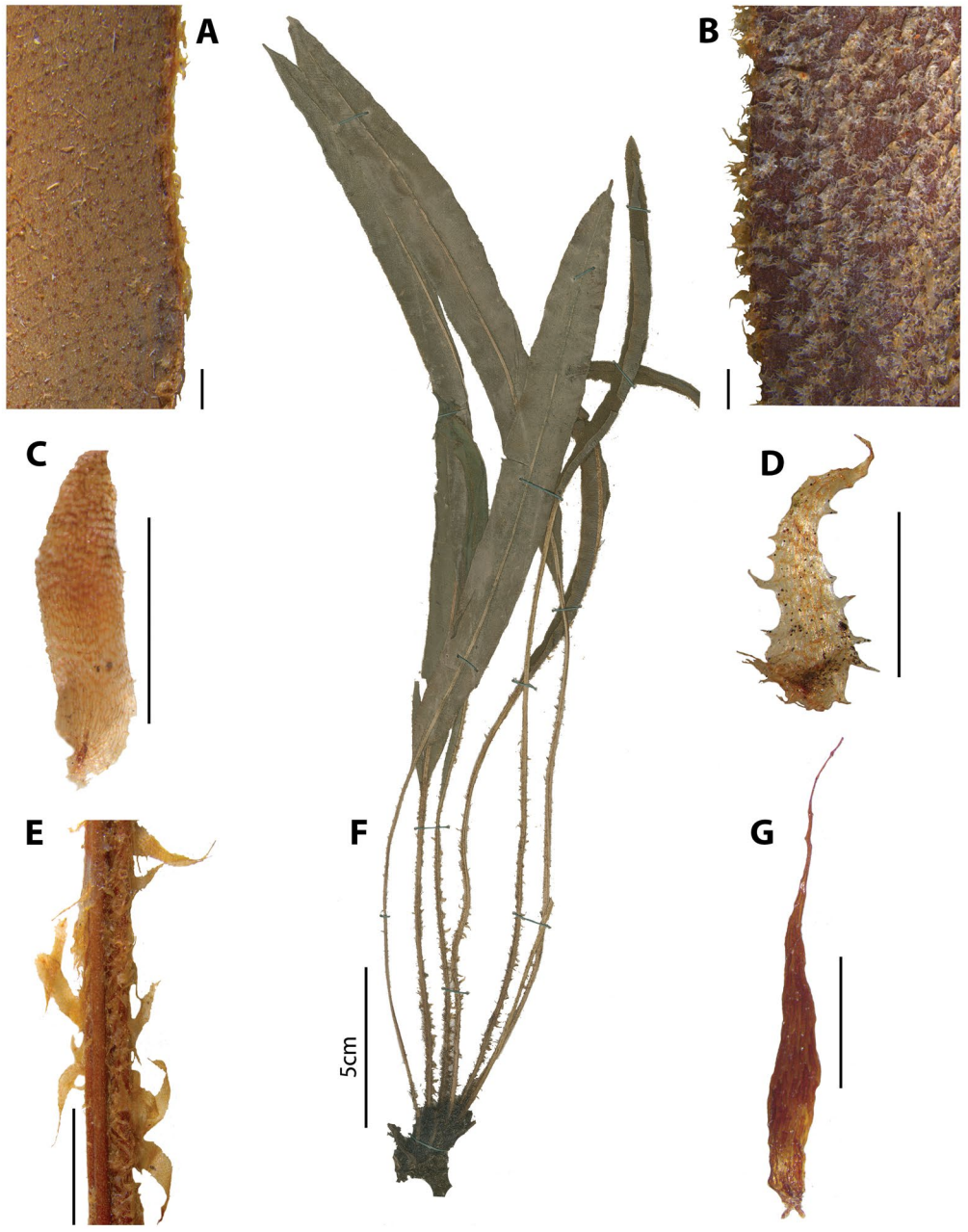

Figure 5. *Elaphoglossum auralolitae* Martínez-Bec. & A. Vasco. —A. Abaxial laminar surface. —B. Adaxial laminar surface. —C. Larger petiole scale with broken apex. —D. Abaxial costal scale. —E. Petiole detail. —F. Habit. —G. Rhizome scale. A–E, G, *Molina 30311* (MO); F, *Véliz 92.2319* (MEXU). All photos from sterile leaves. Scale bars = 1 mm, unless otherwise noted.

darker at point of attachment, base auriculate, apex long-attenuate to filiform, **adaxial resinous dots** absent; **abaxial laminar scales** to 0.5 mm, scattered to dense, not imbricate, irregular to lanceolate, when lanceolate, with numerous long projections, stramineous to light brown, base auriculate, apex attenuate; **abaxial resinous dots** present; **abaxial costal scales** 0.8–2(–3) mm, dense, usually imbricate, lanceolate with occasional short projections, stramineous, base round with long projections, apex long-attenuate to fili-

form; **marginal scales** 0.5–0.8(–1) mm, dense, not imbricate, lanceolate or irregular, when lanceolate, margin with numerous long projections, stramineous, base truncate with long projections, apex attenuate to filiform-tortuous. **Fertile leaves** similar to or sometimes longer than sterile leaves; **petioles** 1/3–3/5 the length of fertile leaves; **laminae** 14.1–22 × 0.9–1 cm, linear-elliptic to elliptic, base cuneate, apex acute, apiculate; **petiole scales** 2–3.1 mm, scattered to dense, not imbricate, deciduous, lanceolate to oblanceolate, with numerous long projections or with occasional short projections, stramineous, base round with long projections or truncate, apex long-attenuate to filiform; **adaxial laminar scales** 1–1.5 mm, dense, usually imbricate, lanceolate with numerous long projections, stramineous, base auriculate, apex long-attenuate to filiform; **abaxial costal scales** 0.5–1.5 mm, scattered to dense, not imbricate, deciduous, lanceolate to ovate-lanceolate or irregular, with numerous long projections, yellowish, base truncate with long projections, apex long-attenuate to filiform. **Perines** broadly folded, sparsely echinulate.

Habitat and distribution. *Elaphoglossum auralolitae* is endemic to southwestern Guatemala, at elevations of 1950–2900 m (Fig. 3). It is terrestrial and grows in cloud forests.

Phenology. Fertile specimens have been collected during December and January.

Etymology. This species is named in honor of Aura Lolita Chávez Ixcaquic (1972–), an indigenous activist from the K'iche' region and community in Guatemala.

Notes. *Elaphoglossum auralolitae* can be distinguished from all other species in the petiolatum clade by the longer and denser laminar scales, especially those of the sterile leaf abaxial costa, which can be up to 2(–3) mm (vs. up to 1.5 mm in the rest of the species, except *E. rzedowskii*, in which costal scales can be up to 2 mm; see comparison between these two species below); the larger scales of the sterile leaf adaxial surface, which can be up to 1.4 mm (vs. up to 1 mm); and the scales of the fertile leaf petiole, which are up to 3.1 mm (vs. up to 2.5 mm, except in *E. rzedowskii*, in which fertile petiole scales are in a few cases up to 3 mm). The fertile laminae of *E. auralolitae* are also the longest in the petiolatum clade, up to 22 cm (vs. up to 18[–20.5] cm in the rest of the species).

Elaphoglossum auralolitae most closely resembles *E. petiolatum* because of the presence of resinous dots on the laminar surface abaxially and the linear-lanceolate to lanceolate rhizome scales, which are dark reddish brown to dark brown with a filiform-tortuous apex. The two species can be distinguished by the perine ornamentation. *Elaphoglossum auralolitae* has sparsely echinulate perines (vs. perines with sparsely irregular microstructures in *E. petiolatum*). These two species also can be distinguished by the laminar scales of the sterile leaves (including those of the costa). *Elaphoglossum auralolitae* always has adaxial laminar scales, the larger ones up to 1.4 mm, dense, usually imbricate, with margins bearing numerous long projections, and apex long-attenuate to filiform (vs. adaxial laminar scales absent, or when present less than 1 mm, scattered to dense, not imbricate, with margins bearing only occasional short or long projections, and apex attenuate in *E. petiolatum*); and abaxial costal scales 0.8–2(–3) mm, dense, usually imbricate, and lanceolate (vs. 0.5–1.5 mm, scattered to dense, not imbricate, and lanceolate, substellate, or irregular in *E. petiolatum*).

These two species can be further distinguished by the scales of the petiole, adaxial lamina, and abaxial costa of the fertile leaves. The fertile leaf petiole scales of *Elaphoglossum auralolitae* are 2–3.1 mm, lanceolate to oblanceolate, with margins bearing numerous long projections or occasional short projections (vs. less than 1 mm, substellate or linear to linear-lanceolate, and when linear or linear-lanceolate with margins bearing occasional short projections in *E. petiolatum*). The fertile leaf adaxial laminar scales of *E. auralolitae* are 1–1.5 mm, dense, and usually imbricate (vs. less than 0.7 mm, scattered to dense, and not imbricate in *E. petiolatum*). Finally, the longest abaxial costal scales of fertile leaves of *E. auralolitae* are 1.5 mm with a long-attenuate to filiform apex (vs. 0.8 mm with an acuminate to attenuate apex).

The overlapping distributions of *Elaphoglossum auralolitae* and *E. petiolatum* and their morphological similarity could suggest possible hybridization events between these two species.

Elaphoglossum auralolitae can be confused with *E. rzedowskii* because both species have scaly leaves, but they differ in their rhizome scales and geographic distribution. *Elaphoglossum auralolitae* has concolorous, dark-reddish–brown to dark-brown, lustrous rhizome scales, and it is endemic to Guatemala (vs. rhizome scales bicolorous, stramineous to brown, darker at the point of attachment and toward the margins and apex, and dull in *E. rzedowskii*, which is endemic to Mexico).

Elaphoglossum auralolitae can be distinguished from *E. muelleri* because of the dark-reddish–brown to dark-brown rhizome scales and irregular to lanceolate abaxial laminar scales (vs. orange rhizome scales and stellate abaxial laminar scales in *E. muelleri*).

Outside the petiolatum clade, *Elaphoglossum auralolitae* can also be confused with *E. rufescens* (Liebm.) T. Moore, an endemic Mexican species, because both

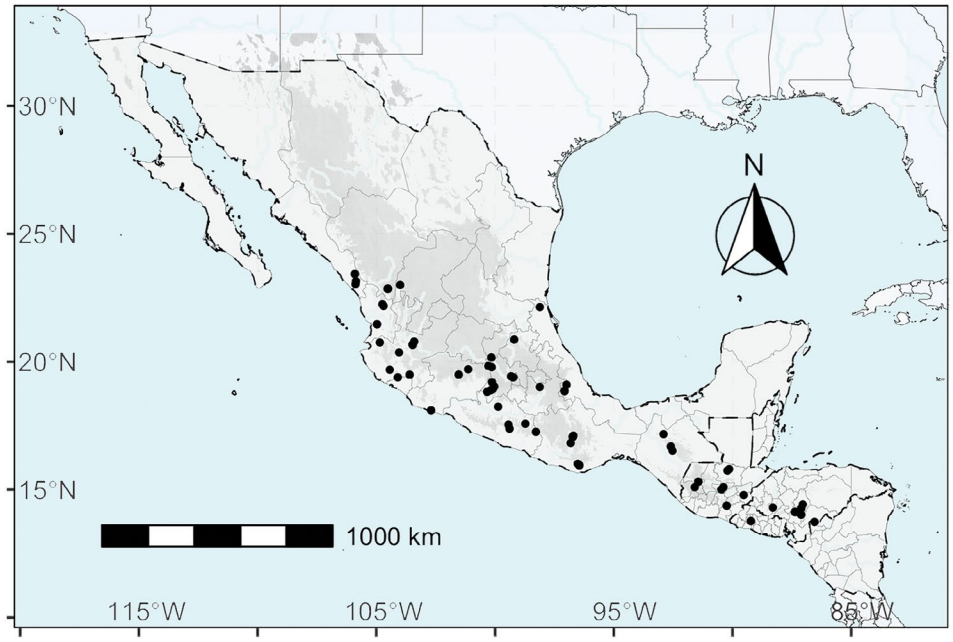

Figure 6. Distribution map of *Elaphoglossum muelleri* (E. Fourn.) C. Chr.

species have abundant scales on the laminae and costae (Mickel & Smith, 2004). However, *E. auralolitae* can be distinguished by the presence of resinous dots on the adaxial laminar surface (vs. no resinous dots in *E. rufescens*); petiole scales dense and usually imbricate (vs. scattered and not imbricate); adaxial laminar scales lanceolate, dense, and usually imbricate (vs. round to subdeltate, scattered, and not imbricate); and abaxial laminar scales irregular to lanceolate, stramineous to light brown (vs. narrow to deltate, orange) (Martínez-Becerril & Vasco, 2023).

Selected specimens examined. GUATEMALA. **Chimaltenango:** Mpio. Chimaltenango, 21 Dec. 1972, *Williams 41580* (F). **Escuintla:** Mpio. San Vicente Pacaya, Pacaya, 20 Aug. 1938, *Johnston 1346* (F). **Quetzaltenango:** Mpio. Quetzaltenango, Sierra Madre Mtns., about 4 km N of Olintepeque, 2600 m, 12 Dec. 1962, *Williams 22861* (F, TEX, US). **Quiché:** Mpio. Santo Tomás Chichicastenango, on moist forest bank of El Molino, 4 km from Chichicastenango, 2100 m, 14 Jan. 1974, *Molina 30311* (F, MO). **Sacatepéquez:** Mpio. Antigua Guatemala, cuesta de las cañadas, above Antigua, 1950 m, 6 Dec. 1938, *Standley 58933* (F). **San Marcos:** Mpio. Comitancillo, below Comitancillo & Santa Rosa jct., Sierra Madre Mtns., 2900 m, 2 Jan. 1965, *Williams 27065* (F, NY); Mpio. Sibinal, dry white clay slopes on ridge leading toward Volcán Tacaná, but on this side of Sibinal, vic. of Sibinal, 2500 m, 18 Feb. 1940, *Steyermark 35963* (F, US). **Sololá:** 2400 m, 22 Apr. 1974, *Copeland s.n.* (NY [bc] 03376687). **Totonicapán:** Mpio. Momostenango, ravine in cypress forest near Polagua, Sierra Madre Mtns., 20–25 km N of Cristóbal, 5 Dec. 1962, *Williams 22656* (F, TEX, US); *Williams 22688* (F, TEX, US).

2. Elaphoglossum muelleri (E. Fourn.) C. Chr., Index Filic. 311. 1905. *Acrostichum muelleri* E. Fourn., Mexic. Pl. 1: 68. 1872. TYPE: Mexico. Veracruz: Mpio. Orizaba Uluapa [1560 m], [18.86, –97.08], 1853, *F. Müller 41 quinter* (lectotype, designated here, P [bc] P00603618 image!). Figures 1B, 6, 7.

Acrostichum intermedium Fée, Mém. Foug. 8: 69. 1857, nom. illeg. hom., non *Elaphoglossum intermedium* Brack., 1854. TYPE: Mexico. Veracruz: prope Huatuzco, Cordova en terre (in protologue: sur la terre) [1370 m], [19.10, –96.99], July 1854, *W. Schaffner 22* (lectotype, designated here, RB [bc] 00543157 image!).

Elaphoglossum araneosum (D. C. Eaton) C. Chr., Index Filic. 303. 1905. *Acrostichum araneosum* D. C. Eaton, Proc. Amer. Acad. Arts 22: 461. 1887. TYPE: Mexico. Jalisco: Río Blanco: in wet shady spots in ravines [1530 m], [20.77, –103.39], Jun.–Oct. 1886 (in protologue: Aug. 1886), *E. Palmer 333* (lectotype, inadvertently designated by Mickel & Beitel [1988: 178], YU [bc] 000790 image!; isolectotypes, GH [bc] 00102874 image!, NY [bc] 00149579!, NY [bc] 00149581!, US [bc] 00067262!, US [bc] 01100828!).

Plants terrestrial or epipetric. **Rhizomes** 4–5(–10) mm wide, short-creeping; **rhizome scales** (2–)3–5 mm, dense, spreading, lanceolate, with occasional short projections (shorter than width of scale), concolorous, orange to light brown, darker at point of attachment, dull, base round, apex long-attenuate. **Sterile leaves** (7.5–)14–31(–40) cm, approximate; **phyllopodia** present, usually obscured by rhizome scales, ca. 5(–15)

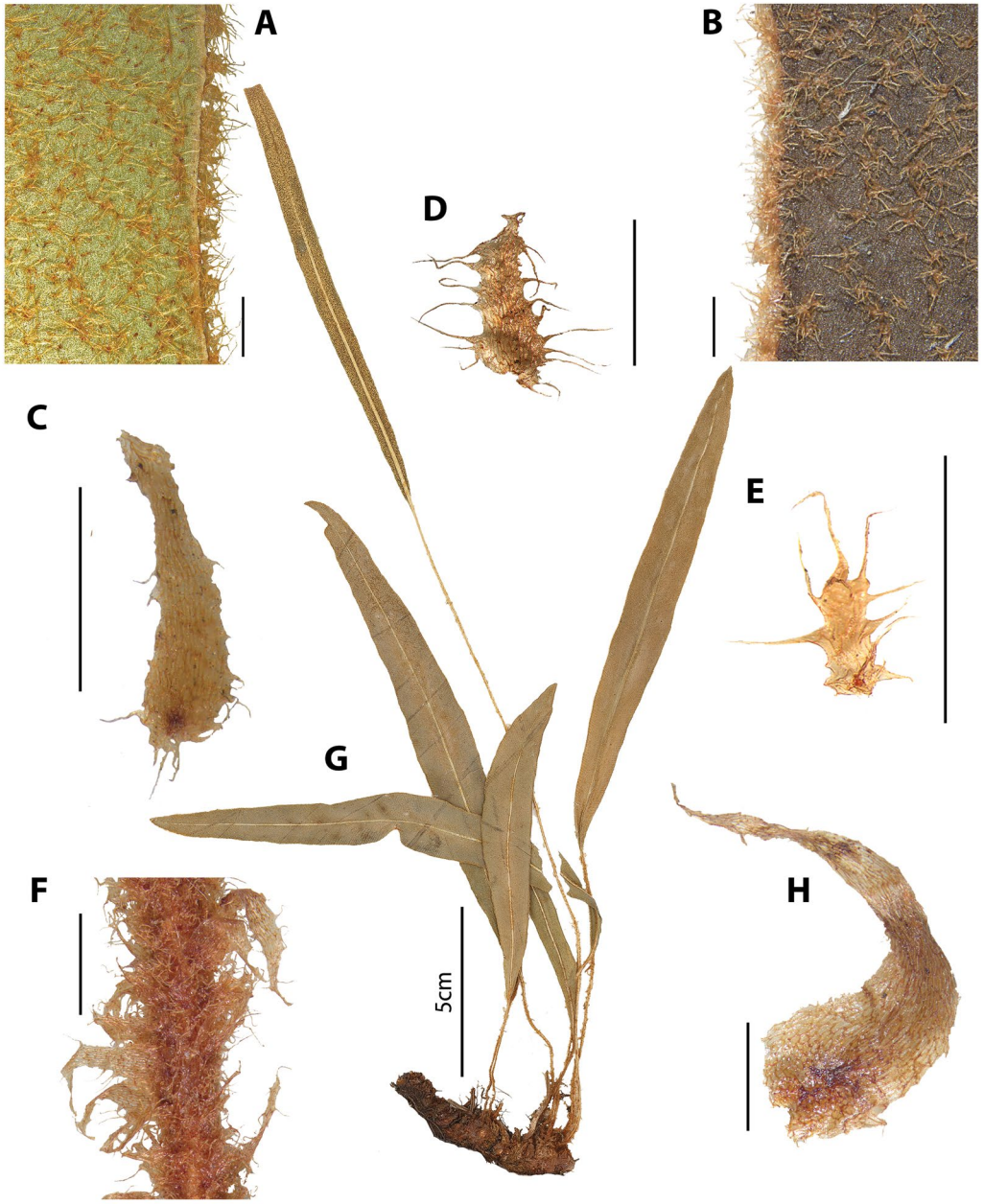

Figure 7. *Elaphoglossum muelleri* (E. Fourn.) C. Chr. —A. Abaxial laminar surface. —B. Adaxial laminar surface. —C. Smaller petiole scale with broken apex. —D. Abaxial costal scale. —E. Marginal scale. —F. Petiole detail. —G. Habit. —H. Rhizome scale. A, C–E, *Breedlove 17056* (NY); B, H, *Müller 41* (NY); F, *Pringle 2590* (NY); G, *Mickel 1164* (NY). All photos from sterile leaves. Scale bars = 1 mm, unless otherwise noted.

mm; **petioles** (2–)4–10.5(–15.5) cm, 1/5–1/3(–1/2) the length of sterile leaves; **larger petiole scales** to 4 mm, scattered to dense, not imbricate, spreading to appressed, linear-lanceolate to lanceolate, with numerous long projections (as long as or longer than width of scale), stramineous, base truncate, apex attenuate to filiform; **smaller petiole scales** to 1.5 mm, dense, not imbricate, mostly appressed, irregular, substellate, or lanceolate, when lanceolate, margin with occasional long projections, stramineous, base auriculate, apex

attenuate to filiform; **laminae** (3.5–)6–21 × (0.7–)1–2 cm; narrowly elliptic, papyraceous, base cuneate to decurrent, apex obtuse to acute, sometimes apiculate; **adaxial laminar scales** to 1 mm, dense, not imbricate, deciduous, linear-lanceolate, with numerous long projections, whitish to stramineous, darker at point of attachment, base auriculate, apex long-filiform; **adaxial resinous dots** absent; **abaxial laminar scales** mixed; microscales ca. 0.1 mm, 2- (to 3-)armed, reddish; scales to 0.7 mm, dense (only occasionally scattered), not imbricate, deciduous, stellate or occasionally irregular, whitish to stramineous; **abaxial resinous dots** usually present; **abaxial costal scales** 0.5–1 mm, dense, not imbricate, lanceolate with numerous long projections, stramineous, darker at point of attachment, base auriculate, apex acuminate to filiform; **marginal scales** (0.5)–1 mm, dense, usually imbricate, lanceolate to ovate-lanceolate, with numerous long projections, stramineous to yellowish, base truncate with long projections, apex long-attenuate to filiform, sometimes with a long projection close to apex. **Fertile leaves** longer than sterile leaves; **petioles** 1/2–2/3 the length of fertile leaves; **laminae** (5–)10–15.5(–18) × 0.7–0.9(–1.2) cm, linear-elliptic, papyraceous, base long-cuneate, apex round to acute, sometimes apiculate; **petiole scales** 0.5–2 mm, scattered to dense, not imbricate, linear-lanceolate to lanceolate, with numerous long projections, stramineous, base truncate, apex attenuate to filiform; **adaxial laminar scales** not seen; **abaxial costal scales** to 2 mm, scattered to dense, not imbricate, deciduous, linear-lanceolate, with numerous long projections, whitish to stramineous, darker at point of attachment, apex attenuate or filiform. **Perines** broadly folded, sparsely echinulate.

Habitat and distribution. *Elaphoglossum muelleri* grows in El Salvador, Guatemala, Honduras, Mexico, and northern Nicaragua, at elevations of (960–)1300–2600 m (Fig. 3). It is terrestrial or epipetric in tropical, temperate, and cloud forests. *Hernández 99* (MO), from Honduras, is the only specimen collected below 1000 m.

Elaphoglossum muelleri was reported by Mickel and Smith (2004) for the Mexican states of Guanajuato and San Luis Potosí, as well as for Costa Rica; we did not find collections of this species from these areas (see Appendix 2 for a list of places where we found it). The Mexican collections reported as *E. muelleri* by Mickel and Smith (2004)—*Ventura & López 7446* (IEB, MEXU) from Guanajuato and *Schaffner s.n.* (NY) from San Luis Potosí—were misidentified and correspond to *E. potosianum*.

Phenology. Fertile specimens have been collected from August to November.

Etymology. This species was named in honor of Fritz Müller [Johann Friedrich Theodor] (1822–1897), a German zoologist and botanist who also studied medicine and was appointed as a "traveling naturalist" by the Brazilian government. His collections are at B, G, K, and NY (TL-2).

Notes. *Elaphoglossum muelleri* can be distinguished from all other species in the petiolatum clade by having the longest rhizome scales (3–5 mm), scalier lamina margins (although the marginal scales are sometimes deciduous), and minute microscales on the abaxial laminar surface.

Elaphoglossum muelleri can be confused with *E. potosianum* because both have microscales on the abaxial laminar surface and tend to have orange to light-brown laminar scales (some specimens of *E. potosianum* can have dark-brown scales). These two species can be distinguished by rhizome scale length, abaxial laminar scales, and microscale length. In *E. muelleri* the rhizome scales are (2–)3–5 mm (vs. 2–3.5 mm in *E. potosianum*); the abaxial laminar scales are scattered to dense, not imbricate, deciduous, and stellate to irregular (vs. absent or scattered and irregular); and the microscales are ca. 0.1 mm and inconspicuous even with a stereomicroscope (vs. 0.2–0.3 mm and easy to see with a magnifying glass or stereomicroscope).

For the species description, we did not consider some collections that we identified as *Elaphoglossum muelleri* because they show small variations outside our typical concept for this species. For example, *Goldsmith 41* (F, MO, NY, US) from Colima (Mexico) has brown rather than the typical orange to light-brown rhizome scales; *Rzedowski 24310* (NY) from Estado de México (Mexico) does not have stellate scales on the abaxial laminar surface, and some leaves have just a few substellate scales; *Seiler 31* (F) from El Salvador has rhizome scales with long instead of short projections; *Martín 61* (MO) and *Berríos 97* (MO) from Honduras are smaller than the typical *E. muelleri*, and both specimens are sterile and thus probably not yet fully grown.

We chose P [bc] P00603618 as the lectotype because this is the single specimen we found where the collector and collection number (*Müller 41 quinter*), the locality (Orizaba, Uluapa), and the date (1853) on the label agree with those of the protologue. *Müller 41* [ex parte] NY [bc] 03231440 is not an isolectotype because it corresponds to *Elaphoglossum schiedei*, although it has the same collection date as the one stated in the protologue. We do not consider *Müller 41* [ex parte] NY [bc] 003231439 as a syntype because it has a different locality (Orizaba, aserradero de Santa Cruz) from the one in the protologue.

Mickel and Beitel (1988) cited *Schaffner 22* (P) as the type of *Acrostichum intermedium*. However, we did

not find this specimen among the material we examined, nor did Dr. Germinal Rouhan (curator of ferns at P, pers. comm.) find it at P. There is, however, a specimen of *Schaffner 22* at P ([bc] P00255156), and it belongs to *Kyllinga pumila* Michx. (Cyperaceae). Antoine Laurent Apollinaire Fée, the author of this species, deposited some of his types in STR (TL-2), but STR curators did not find a duplicate there either. The only specimen of *Schaffner 22* we were able to locate that corresponds to *A. intermedium* is at RB, and for that reason we chose this specimen as the lectotype. If in the future someone proves that there is only one specimen (*Schaffner 22* RB), this lectotypification can be superseded and the lectotype will be a holotype. Our choice now is to fix the application of the name in the sense in which we understand the species.

Selected specimens examined. EL SALVADOR. **San Salvador:** Mpio. San Salvador, Volcano San Salvador, on trail in crater, 1800 m, 12 June 1977, *Seiler 31* (F). GUATEMALA. **Baja Verapaz:** Mpio. Santa Cruz El Chol, Sierra de Chuacus, 6 km N of El Chol, 15 July 1970, *Harmon 3161* (MO); Mpio. Santa Rosa de Lima, N of Santa Rosa, 30 Mar. 1939, *Standley 69722* (F, US). **Chimaltenango:** Mpio. Chimaltenango, Km. 70 Molino de la Sierra, 21 Oct. 1973, *de Poll 1071* (F). **Chiquimula:** Mpio. Chiquimula, 31 Oct. 1939, *Steyermark 30919* (F). **Guatemala:** Mpio. San Raymundo, Chillani, 1500 m, 20 June 1921, *Rojas 60* (US [bc] 1564378). **Huehuetenango:** Mpio. Huehuetenango, betw. Democracia & canyon of Chamushú, 1300 m, 24 Aug. 1942, *Steyermark 51213* (F). **Quiché:** Mpio. Santo Tomás Chichicastenango, El Tesoro river, 3 km to Chichicastenango, 19 Sep. 1971, *Molina 26627* (F, MO). **Santa Rosa:** Mpio. Nueva Santa Rosa, El Chupadero, 1520 m, Aug. 1892, *Heyde 3149* (MO), *Heyde 4098B* (NY, US). HONDURAS. **Francisco Morazán:** Mpio. Distrito Central, Tegucigalpa, Ciudad Universitaria, campo abierto, 950 m, 1 Oct. 1981, *Hernández 99* (MO); Mpio. El Hatillo, 12 km al N de Tegucigalpa, 1400 m, 28 Aug. 1983, *Portillo 24* (MO); Mpio. San Matías, 20 km NO de Tegucigalpa, 1400 m, 25 Sep. 1983, *Martín 61* (MO). **Intibucá:** Mpio. Intibucá, 31 Jan. 1950, *Standley 25286* (F). MEXICO. **Chiapas:** Mpio. Pueblo Nuevo Solistahuacan, Linda Vista Biol. Station, 1580 m, Aug. 1967, *Gittins 4212* (NY); Mpio. Totolapa, 6–8 km W of Teopisca on the side of Cerro Chenek'ultik, 2150 m, 16 Aug. 1972, *Breedlove 27040* (MEXU, NY). **Ciudad de México:** Alcaldía Cuajimalpa, Santa Fé, 22 Aug. 1903, *Rose & Painter 6508* (NY, US). **Colima:** side of Jorge E side of Volcano Colima, 21 July 1905, *Goldsmith 41* (F, MO, NY, US). **Durango:** Mpio. El Mezquital, Cerro Blanco, cerca de Santa María de Ocotán, 17 Sep. 1986, *Mendía 154* (IEB). **Estado de México:** Mpio. Luvianos, 2–3 km al SW de Luvianos, 1900 m, 2 Sep. 1965, *Roe 1594* (BRIT, ENCB, US); Mpio. Malinalco, hacia Chalma Barranca, Sep. 1955, *Lyonnet 550900011* (MEXU); Mpio. Naucalpan, 2 km al SE de San Francisco Chimalpa, 2600 m, 3 Nov. 1967, *Rzedowski 24310* (ENCB, NY); Mpio. Temascaltepec, Vigas, 1080 m, *Hinton 1811* (NY, US); Mpio. Valle de Bravo, above Valle de Bravo, Mexico, June 1955, *Converse s.n.* (US [bc] 01564392). **Guerrero:** Mpio. Chilpancingo de los Bravo, 15 km al SE de Mazatlán, camino al cerro El Alquitrán, 2200 m, 4 Oct. 1989, *Fonseca 1667* (NY); Mpio. San Miguel Totolapan, Petlacala-Buenavista, 2275 m, 21 Nov. 1939, *Hinton 14882* (MO, NY, US); Mpio. Tlapa de Comonfort, 2.5 al NE de Chiepetepec, camino Chilapa–Tlapa, 1860 m, 7 Nov. 1983, *Lorea Hernández 2755* (ENCB, IEB, NY). **Hidalgo:** Mpio. Zimapan, from Encarnación to Mt. Cangandhó, 6 Aug. 1948, *Moore 4342* (MEXU). **Jalisco:** Mpio. Autlán de Navarro, along rd. betw. Autlán & Barra de Navidad (Méx. hwy. 80), 9–10 mi. S of Autlán, oak forests on mtn. slopes on either side of pass Puerto de los Mazos, 1450 m, 25 Sep. 1966, *Anderson 3740* (ENCB, MEXU, NY); Mpio. Ayutla, 49 km W of Ayutla on rd. to Talpa, 1850 m, 21–22 Sep. 1983, *Anderson 12744* (IEB, MEXU, NY); Mpio. Chapala, mtns. near Lake Chapala, 21 Nov. 1892, *s. coll.*, *s.n.* (F [bc] C0620887F); Mpio. Guadalajara, cool banks near Guadalajara, 24 Aug. 1893, *Pringle 5402* (BRIT, IEB, MEXU, VT, WTU). **Michoacán:** Mpio. Aquila, 12 Nov. 1909, *s. coll.*, *s.n.* (MEXU); Mpio. Morelia, Cerro San Miguel, près. Morelia, 2200 m, Nov. 1910, *Arsène s.n.* (P); Mpio. Coalcomán de Vázquez Pallares, 17 Nov. 1983, *Ramamoorthy 4660* (MEXU). **Nayarit:** Mpio. Del Nayar, 6 km al NW de La Mesa del Nayar, becha a Santa Teresa, 1900 m, 27 Sep. 1989, *Tenorio 16528* (MEXU); Mpio. Tepic, Cerro de San Juan, W of Tepic, 1000 m, 19 Sep. 1926, *Mexia 708* (F, NY, US). **Oaxaca:** Mpio. Coicoyán de las Flores, al N de Yuvi Ka'un 2 km al SW de Coicoyán, 2100 m, 17 Nov. 1988, *Avila 506* (MEXU); Mpio. Miahuatlán de Porfirio Díaz, along Hwy. 175 betw. Oaxaca & Pochutla, 77.8 mi. S of Miahuatlán, 20.3 mi. S of Suchixtepec, 9.9 mi. N of turnoff to Pluma Hidalgo, 1530 m, 29 Jan. 1979, *Croat 46092* (MO); Mpio. Oaxaca de Juárez, Cerro San Felipe, 1800 m, 9 Aug. 1962, *Mickel 1164* (ENCB, NY, TEX); Mpio. San Pedro Pochutla, 60 km by rd. N of Pochutla on rd. to Oaxaca (Hwy. 175), 1440 m, 17 Oct. 1983, *Anderson 13211* (IEB, MEXU, NY); Mpio. Villa Sola de Vega, 27–29 km S of Sola de Vega (Km. 105–107), 1798 m, 5 Aug. 1964, *Mickel 1662* (NY). **Puebla:** Mpio. Puebla, Barranca de Manzanilla, 2180 m, 12 Nov. 1909, *Hno. G. Nicolás* (F, MEXU, NY). **Querétaro:** Mpio. Amealco de Bonfil, Barranca de Amealco, 2200 m, 12 Aug. 1979, *Argüelles 1310* (MEXU). **Sinaloa:** Mpio. Badiraguato, Sierra de Surutato, 5 mi. NE of La Ciénega along rd. to Santa Rita, 2130 m, 5 Nov. 1969, *Breedlove 17056* (NY); Mpio. Concordia, Cerro de Sandía, NE de Pánuco, 30 Aug. 1935, *s. coll. 118* (MEXU [bc] 2000). **Veracruz:** Mpio. Orizaba, aserradero de Santa Cruz, 1853, *Müller 41* [ex parte] (NY). NICARAGUA. **Nueva Segovia:** Mpio. Dipilto, Santa María de los Pinos, 5 km al NE de Dipilto, 1200 m, 21 Sep. 1984, *Moreno 24747* (MO).

3. Elaphoglossum petiolatum (Sw.) Urb., Symb. Antill. 4: 61. 1903. *Acrostichum petiolatum* Sw., Prodr. 128. 1788. *Acrostichum viscosum* Sw., Syn. Fil. 10: 193. 1806, nom. superfl. *Elaphoglossum viscosum* (Sw.) J. Sm., J. Bot. (Hooker) 4: 148. 1842 [1841]. TYPE: Jamaica. 1778, *Swartz s.n.* (lectotype, inadvertently designated by Proctor [1985: 508], S-S-R-73 image!; isolectotypes, BM [bc] 000592488 image!, US [bc] 00067292 fragm. from lectotype). Figures 1C, 8, 9.

Plants terrestrial or epiphytic. **Rhizomes** 2–5 mm wide, short-creeping; **rhizome scales** 1.5–3.7(–5) mm, dense, spreading, linear to lanceolate, with occasional short projections (shorter than width of scale), concolorous, dark reddish brown to dark brown, dull, base truncate, apex filiform-tortuous, often broken. **Sterile leaves** (9.5–)10–36.5(–43.5) cm, approximate; **phyllopodia** present, clearly visible, 5–18 mm; **petioles**

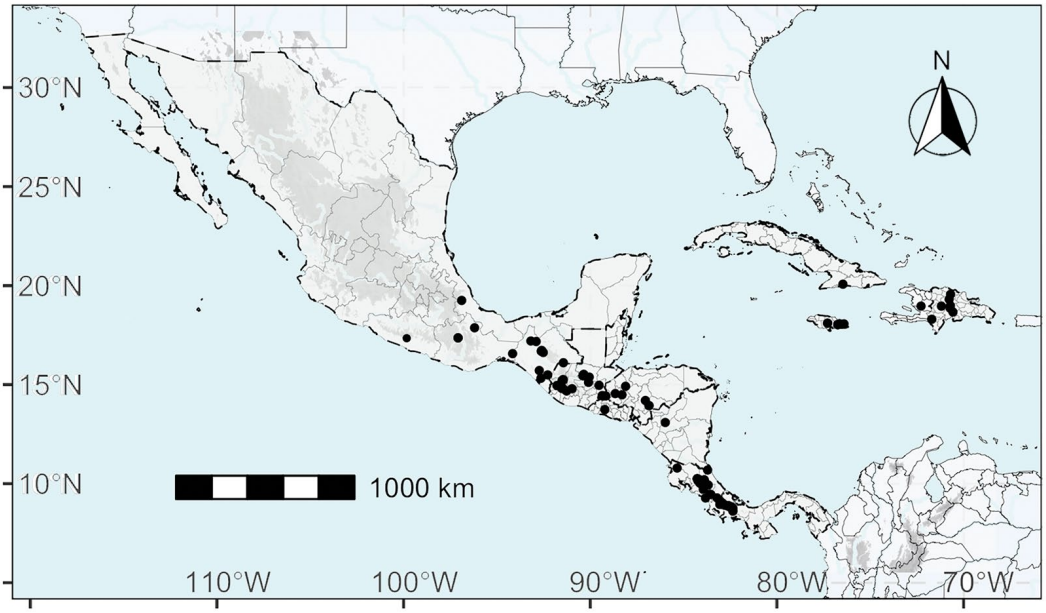

Figure 8. Distribution map of *Elaphoglossum petiolatum* (Sw.) Urb.

3–15 cm, (1/6–)1/4–1/3(–2/5) the length of sterile leaves; **larger petiole scales** to 3.5 mm, scattered, denser at base, not imbricate, spreading to appressed, linear to linear-lanceolate, entire or with occasional short projections, stramineous, sometimes darker at apex, base round, apex long-attenuate to filiform-tortuous, sometimes longer than scale body; **smaller petiole scales** to 1 mm, scattered to dense, usually imbricate, mostly appressed, irregular, substellate, or lanceolate, when lanceolate, margin with occasional short or long projections (as long as or longer than width of scale), stramineous, base round or auriculate, sometimes resinous at point of attachment, apex acuminate; **laminae** 6.5–30 × (0.6–)0.8–2(–2.3) cm, elliptic, chartaceous, base cuneate, apex acute to acuminate, usually apiculate; **adaxial laminar scales** absent, or when present to 1 mm, scattered to dense, not imbricate, lanceolate, with occasional short or long projections, whitish to yellowish, sometimes darker at point of attachment, base auriculate, apex attenuate; **adaxial resinous dots** sometimes present; **abaxial laminar scales** absent, or when present to 1 mm, scattered, lanceolate, with numerous long projections, yellowish, base truncate with long projections, apex attenuate to long-attenuate; **abaxial resinous dots** present; **abaxial costal scales** 0.5–1.5 mm, scattered to dense, not imbricate, lanceolate, substellate, or irregular, when lanceolate, margin with occasional short and/or long projections, stramineous, base, when lanceolate, truncate or auriculate, apex acuminate to attenuate; **marginal scales** absent, or when present to 0.8 mm, scattered to dense, not imbricate, irregular or lanceolate, when lanceolate, margin with numerous long projections and occasionally also with short projections, whitish to yellowish, base, when lanceolate, auriculate, apex long-attenuate, sometimes with a long projection close to apex. **Fertile leaves** slightly shorter to longer than sterile leaves; **petioles** (2/5–)3/5–1/2 the length of fertile leaves; **laminae** (8.5–)10–16.5(–20.5) × 0.6–1 cm, elliptic, chartaceous, base cuneate to decurrent, apex obtuse to acute; **petiole scales** to 1 mm, scattered to dense, not imbricate, linear to linear-lanceolate or substellate, when linear to linear-lanceolate, margin with occasional short projections, yellowish to light brown, darker toward apex, base round, apex long-attenuate to filiform-tortuous; **adaxial laminar scales** to 0.7 mm, scattered to dense, not imbricate, linear-lanceolate to lanceolate or substellate, when linear-lanceolate to lanceolate, margin with numerous long projections or with occasional short projections, whitish to light brown, base truncate, apex attenuate to long-attenuate; **abaxial costal scales** to 0.8 mm, scattered, linear to lanceolate or substellate, when linear or lanceolate, margin with occasional short projections, yellowish, base auriculate, apex acuminate to attenuate. **Perines** broadly folded with sparsely irregular microstructures.

Habitat and distribution. *Elaphoglossum petiolatum* grows in Costa Rica, Cuba, the Dominican Republic, El Salvador, Guatemala, Haiti, Honduras, Jamaica,

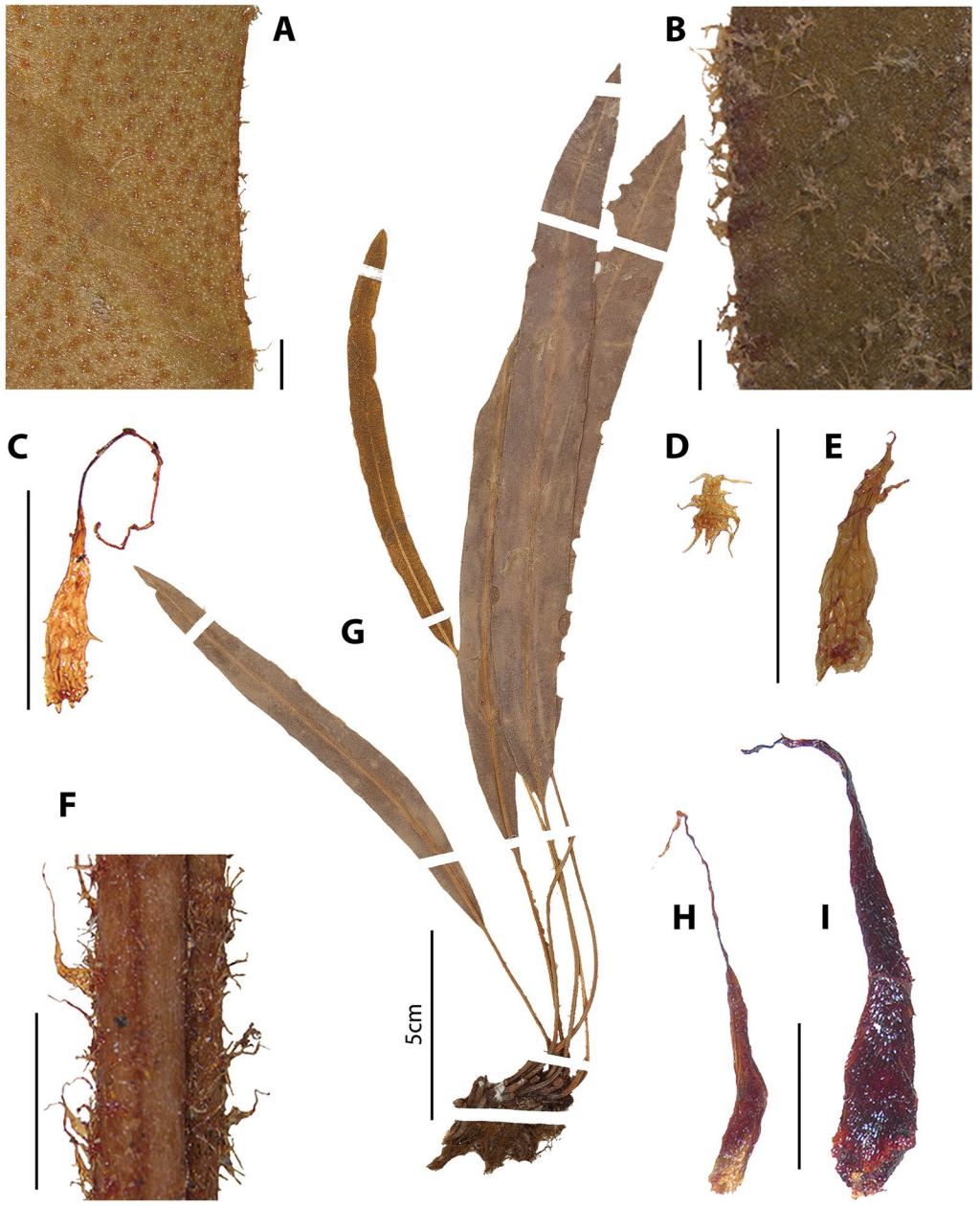

Figure 9. *Elaphoglossum petiolatum* (Sw.) Urb. —A. Abaxial laminar surface. —B. Adaxial laminar surface. —C. Larger petiole scale. —D. Marginal scale. —E. Abaxial costal scale. —F. Petiole detail. —G. Habit. —H, I. Rhizome scales. A, E, H, *Maxon 2648* (NY); B, G, *Clute 312* (NY); C, F, *Mickel 8447* (NY); D, *Evans 2702* (MO); I, *Moran 5646* (NY). All photos from sterile leaves. Scale bars = 1 mm, unless otherwise noted.

Mexico, Nicaragua, and western Panama, at elevations of (847–)900–2600 m (Fig. 3). It is terrestrial or epiphytic in tropical, temperate, and cloud forests.

Elaphoglossum petiolatum was reported to occur widely from Mexico to Venezuela (Mickel & Smith, 2004); however, we found that it is absent from South America and that most of the Mexican collections identified as this species correspond to other species of the petiolatum clade. In Mexico, *E. petiolatum* is restricted to Chiapas, Guerrero, Oaxaca, and Veracruz (Appendix 2).

We found only one collection of *Elaphoglossum pet-*

iolatum from Cuba: *Sánchez C. & Morejón R. s.n.* (HAJB). Most other reports of *E. petiolatum* from Cuba are based on misidentified specimens that correspond mostly to either *E. dussii* Underw. & Maxon or *E. palmeri* Underw. & Maxon (Lóriga, pers. comm.). See comparisons of both species with *E. petiolatum* in the notes section.

Phenology. Fertile specimens have been collected during the rainy season in Mexico and Central America, from July to October. There are three records from April, May, and June, respectively.

Etymology. The specific epithet apparently refers to the long and conspicuous petioles of the type.

Notes. *Elaphoglossum petiolatum* is the only species in the clade that can have a terrestrial or an epiphytic habit and that has broadly folded perines with sparsely irregular surface microstructures. All other species of the petiolatum clade are terrestrial or epipetric and have broadly folded perines with sparsely echinate surfaces (Fig. 1).

Another characteristic that helps distinguish *Elaphoglossum petiolatum* from the other species of the clade is that the resinous dots on the abaxial laminar surface can sometimes be nonshiny. These nonshiny dots are exclusive to *E. petiolatum* and are more common in specimens from Central America. They can be mixed or not with the more common shiny dots. In all other species of the petiolatum clade, the dots are exclusively shiny. The nonshiny resinous dots of *E. petiolatum* look dull in herbarium specimens and can easily be mistaken for peltate scales if not viewed under a stereoscope or light microscope. They tend to come off easily if touched with a needle, unlike shiny dots, which remain attached.

Within the petiolatum clade, *Elaphoglossum petiolatum* can be confused with *E. auralolitae*, *E. pringlei*, *E. schiedei*, and *E. schmitzii* mainly because of their overlapping distributions and the presence of shiny resinous dots on the abaxial laminar surface. The morphology of the rhizome scales, the presence or absence of resinous dots on the adaxial laminar surface, and the spore ornamentation can help distinguish them. Adaxial resinous dots are often present in *E. petiolatum* and *E. schmitzii* (vs. absent in all other species mentioned above), and the perines have sparsely irregular microstructures in *E. petiolatum* (vs. sparsely echinulate perines in all other species).

Some specimens of *Elaphoglossum petiolatum* from Guatemala have more scales than usual and are hard to distinguish from *E. auralolitae*. Examples include *Steyermark 47116* (F, US), *Standley 86178*, *85402* (F, US), *Kellerman 5592* (US), and *Williams 22175* (F, US). Nevertheless, the perines of the only fertile collection (*Williams 22175*, F) are not echinulate, agreeing with our concept of *E. petiolatum* (Martínez-Becerril et al., 2021). See *E. auralolitae* for a more detailed comparison with that species.

Elaphoglossum petiolatum can be further distinguished from *E. pringlei* by rhizome scales 1.5–3.7(–5) mm, concolorous, dark reddish brown to dark brown (vs. 1.4–2.5[–3.5] mm, bicolorous, light brown, and darker at the point of attachment).

Elaphoglossum petiolatum can be further distinguished from *E. schiedei* by its longer rhizome scales, 1.5–3.7(–5) mm, which are dense, spreading, linear to lanceolate, dull, and not sclerotic and have a filiform-tortuous apex (vs. rhizome scales 0.7–1.2[–1.5] mm, scattered, appressed, oblanceolate, reddish brown to dark brown, lustrous, sclerotic, with an acute to short-filiform apex); chartaceous lamina (vs. papyraceous); and lanceolate scales on the abaxial laminar surface (vs. stellate to irregular).

Elaphoglossum petiolatum can be further distinguished from *E. schmitzii* by its rhizome scales, which are concolorous, dark reddish brown to dark brown, with a filiform-tortuous apex (vs. bicolorous, light brown, darker only at the point of attachment and toward the apex, with an attenuate to filiform apex).

Specimens of *Elaphoglossum petiolatum* from the Antilles often have been confused with *E. dussii* and *E. palmeri*, which are part of the ciliatum clade (Vasco et al., 2009a, 2009b; Lóriga et al., 2014). *Elaphoglossum petiolatum* can be distinguished from *E. dussii* by its slender rhizome, 2–5 mm wide; rhizome scales 1.5–3.7 mm and dark reddish brown to dark brown; and phyllopodia clearly visible (vs. thicker rhizome, 5–8 mm wide; rhizome scales 3–6 mm and reddish brown; and phyllopodia usually hard to see because of dense rhizome scales).

Elaphoglossum petiolatum differs from *E. palmeri* by its dull rhizome scales, the absence of stellate laminar scales, and the presence of resinous dots (vs. lustrous rhizome scales, the presence of stellate laminar scales, and the absence of resinous dots) (Maxon, 1908; Lóriga et al., 2014).

Elaphoglossum petiolatum has the greatest intraspecific morphological variation of all species of the petiolatum clade. It varies in habit, leaf size, shape and color of rhizome scales, density of laminar scales, and density and type (shiny and nonshiny) of laminar resinous dots. For example, many collections from Guatemala have lighter or bicolorous rhizome scales with darker margins and apex, and their petioles, laminae, and costae tend to be scalier on the adaxial surface than the typical *E. petiolatum*. Those scaly specimens can be confused with *E. auralolitae* (see the species description for a comparison). Most of the Central American

specimens are epiphytes with ascending rhizomes and, in general, are smaller compared to the Mexican and Antillean representatives. Specimens from Jamaica and the Dominican Republic usually have shiny resinous dots on both laminar surfaces.

Mickel 9677 (NY) from Oaxaca has glabrescent rhizomes like *Elaphoglossum schiedei*; however, unlike *E. schiedei*, the few scales on the rhizomes and petioles have the typical filiform-tortuous apex characteristic of *E. petiolatum*. *Molina 26627* (MO) from Guatemala has larger, ovate costal scales up to 2 mm (vs. lanceolate, substellate, or irregular, 0.5–1.5 mm in typical *E. petiolatum*). *Seiler 698* (NY) from El Salvador has substellate and lanceolate scales with short projections on the abaxial laminar surface, in addition to the typical resinous dots present in *E. petiolatum*. *Standley 10011* (F) from Nicaragua has lighter rhizome scales that are unlike the typical dark reddish brown to dark brown of *E. petiolatum*. Despite these variations, we considered all the abovementioned specimens to be *E. petiolatum* because their other characteristics are typical for that species.

According to the morphological evidence from sporophytes and spores, and the molecular evidence found in our studies (Vasco et al., 2009a; Martínez-Becerril et al., 2021; Martínez-Becerril & Vasco, in prep.), *Elaphoglossum petiolatum* is restricted to Mexico (Chiapas, Guerrero, Oaxaca, and Veracruz), Central America (from Guatemala to Panama), and the Greater Antilles (Cuba, the Dominican Republic, Haiti, and Jamaica) (Appendix 2).

Historically, the name *Elaphoglossum petiolatum* has been erroneously applied to species from tropical America and the Eastern Hemisphere that have resinous dots on the abaxial laminar surface, dark rhizome scales, and scales of the proximal portions of the petiole with dark apices. Mickel (2001) proposed that the name *E. petiolatum* should apply only to specimens from tropical America, but we found that specimens from South America and the Eastern Hemisphere correspond to a different clade (Vasco et al., 2009a; Martínez-Becerril & Vasco, in prep.). Several names are available for specimens with the morphological characteristics mentioned above: for example, for South America, *E. ballivianii* Rosenst., *E. killipii* Mickel, *E. stenophyllum* (Sodiro) Diels, *E. viscidum* (Fée) Christ, and *E. yungense* de la Sota; for Southeast Asia, *E. yunnanense* (Baker) C. Chr.; for Africa, *E. lancifolium* (Desv.) C. V. Morton; and for India, *E. stelligerum* (Wall. ex Baker) T. Moore ex Salomon. Further morphological and taxonomic revisions focusing on the species of these areas are needed.

Elaphoglossum petiolatum can be distinguished from all the species mentioned above by the spores, which have perines with sparsely irregular microstructures (vs. perines with sparsely echinulate surfaces in all other species that we have studied); the laminae apices, which tend to be acute or acuminate in *E. petiolatum* (vs. attenuate to long-attenuate in all other species); and the adaxial laminar scales, which are usually absent in *E. petiolatum* or, if present, are scattered (vs. abundant and dense).

Morphological and phylogenetic analyses that include *Elaphoglossum petiolatum* show that the two varietal names described—*E. petiolatum* (Sw.) Urb. var. *dussii* (Underw. ex Maxon) Proctor and *E. petiolatum* var. *salicifolium* (Willd. ex Kaulf.) C. Chr.—are not part of the petiolatum clade (Rouhan et al., 2004; Vasco et al., 2009a, 2009b). *Elaphoglossum petiolatum* var. *dussii* (= *E. dussii*) was recovered and treated as part of the ciliatum clade (Vasco et al., 2009a, 2009b), and *E. petiolatum* var. *salicifolium* (= *E. lancifolium*) was not recovered as part of the petiolatum clade (Rouhan et al., 2004; Vasco et al., 2009a; Martínez-Becerril & Vasco, in prep.).

The name *Acrostichum viscosum* and its combination in *Elaphoglossum* are superfluous because, in its original description, Swartz (1806) cited the same type used for *A. petiolatum* in 1778.

Selected specimens examined. COSTA RICA. **Alajuela:** Cantón Poás, S of Volcán Poás on the rd. to San Pedro, 1500 m, 15 Aug. 1970, *Lellinger 1632* (CR, F, MO, US). **Cártago:** Cantón Turrilaba, 17 July 1965, *Lent 654* (F). **Guanacaste:** Cantón Liberia, P. N. Rincón de la Vieja, Cordillera Guanacaste, 1100 m, 18 Sep. 1994, *Taylor 236* (CR, MO). **Heredia:** Cantón Barva, end of rte. 113 where rd. crosses Río Patria about 100–200 m upstream, 2000 m, 27 June 1983, *Moran 3079* (CR, F, MO); cerro de Carizia, cordillère centrale, 1800 m, Sep. 1900, *Pittier 14065* (US); idem, *Pittier 14066* (NY, US [bc] 01564808). **Puntarenas:** Cantón Buenos Aires, P. N. La Amistad, cuenca Tiérrepa-Sierpe, estación Pittier, zona de acampar, 2300 m, 23 May 1996, *Moraga 513* (CR, MO, NY). **San José:** Cantón Desamparados, Cordillera de Talamanca, el Empalme, 2400 m, 2 Oct. 1994, *Rojas 1567* (CR, MO). CUBA. **Granma:** Mpio. Guisa, Punta de Lanza, subida y cima, 1400 m, 31 Jan. 2003, *Sánchez y Morejón s.n.* (HAJB [bc] 80606). DOMINICAN REPUBLIC. **La Vega:** Mpio. Constanza, Cordillera Central, en el lugar llamado Cruz de Cuaba, 9 km al E del cruce de la carretera Tireo arriba-Constanza, 1700 m, 24 Jan. 1986, *García 958* (NY). **Pedernales:** Sierra de Bahoruco, Sapotén (sitio abandonado de aserradero 15 años pasados), 5 km S del puesto militar de El Aguacate, en la carretera Internacional a Los Arroyos y Pedernales, 1500 m, 9 Sep. 1983, *Zanoni 27137* (NY). **Peravia:** Cordillera Central, arroyo La Nuez en la Loma de Los Chivos, una cabecera del Río Ocoa, 36.9 km N del Parque Central de San José de Ocoa, en la carretera a Constanza, 1800 m, 9 Sep. 1982, *Zanoni 23302* (JBSD, NY). **San Juan:** Cordillera Central, Parque Nacional Ramírez, en el arroyo del Río Prieto (un tributario del Río Yaque del Sur) próximo a la caseta del Parque Nacional, en el fondo del Valle Tetero, 1500 m, 23 June 1988, *Zanoni 41586* (JBSD, NY). **Santiago:** along Bao River, upper Bao Valley, headwaters of Bao River, 1700 m, 1 Oct. 1968, *Liogier 12877* (NY). EL SALVADOR. **Santa Ana:** Parque Nacional Monte Cristo, cordillera de Metapán, betw. Los Planes & main rd. to summit of mtn., 2250 m, 27 Jan. 1981, *Davidse 37303* (MEXU, MO). GUATEMALA. **Alta**

Verapaz: Sierra de Chama/Montana Yalijux, Finca Chelem-ha, Abstieg vom Grat ins Tal des Riachuelo Yalijux, ca. 15 km NE von Tucurú, 2300 m, 9 Sep. 1999, *Fôrther 10562* (US). **Baja Verapaz:** Mpio. Salamá, Chilasco, on Concepción rd., in high forest, 29 July 1971, *Contreras 10920* (MO, US). **Chimaltenango:** Mpio. Patzicía, Chichabac, 18 Aug 1933, *Skutch 546* (US). **Huehuetenango:** Mpio. Huehuetenango, mtns. along National Rte. 9 N, ca. 11 mi. S of Huehuetenango, 16 July 1960, *King 3391* (NY, US). **Quetzaltenango:** Mpio. San Carlos Sija, near Río Samalá, along rd. betw. Zunil & Cantel, 2300 m, 18 Jan. 1941, *Standley 83894* (F, US). **Sololá:** Mpio. San Pedro la Laguna, trail betw. slopes of Volcán Santa Clara & town to San Pedro, 2100 m, 6 June 1942, *Steyermark 47116* (F, US). **Zacapa:** Mpio. Copán, rd. from Chama Cobán [Copán], 1 Aug. 1920, *Johnson 548* (US); Mpio. Río Hondo, 4.5 mi. N of San Lorenzo, Sierra de las Minas, 2225 m, 15 July 1986, *Catling 7241* (F). HAITI. Massif de la Selle, Pétionville, Mt. Tranchant, 1750 m, 5 Aug. 1924, *Ekman 1326* (P); Massif du Nord, Port de Paix, Haut Piton [interpreted] 1000 m, 8 Aug. 1925, *Ekman 4611* (NY). HONDURAS. **El Paraíso:** forest of El Volcán Monserrat, 1700 m, 12 Aug. 1971, *Molina 26145* (F, NY). **Francisco Morazán:** Mpio. Cedros, Cordillera Opalaca, betw. Pela Naríz & Calaveras, rd. to La Esperanza, 2000 m, 3 Sep. 1968, *Molina 22621* (F, NY); Mpio. Distrito Central, San Juancito Mtns., E slopes of Peña Blanca, 2000 m, 22 Mar. 1951, *Morton 7316* (US). **Lempira:** Mpio. Gracias, Celaque National Park, trail from Camp 1 to Río Naranjal, 2000 m, 14 Nov. 1991, *Moran 5545* (MO, NY). **Ocotepeque:** Mpio. Ocotepeque, Bosque Montecristo [Trifinio], 2050 m, 6 Dec. 1978, *R. Seiler 774* (F, NY). **Santa Bárbara:** Mpio. Santa Bárbara, 7 km N of El Mochito, on the NE slopes of Mt. Santa Bárbara, 1880 m, 22 Nov. 1991, *Moran 5646* (MO, NY). JAMAICA. **Portland:** lower slopes of Blue Mtn. Peak, 1950 m, 16 Mar. 1920, *Maxon 1170* (F, NY, YU). **Saint Andrew:** New Haven Gap, 1700 m, 10 Feb. 1900, *Clute 312* (NY, US). **Saint Catherine:** *s. coll. 53* (NY). MEXICO. **Chiapas:** Mpio. Escuintla, Sierra Madre de Chiapas, along trail to E from high point on rd. betw. Finca Liquidambar & Nueva Colombia, 2500 m, 18 June 1985, *Luteyn 11586* (MEXU, NY); Mpio. Motozintla, along rd. betw. Motozintla de Mendoza an Siltepec 25.8 mi. N of Motozintla 9 mi. S of Siltepec, 1300 m, 11 Feb. 1979, *Croat 47404* (MO); Mpio. San Cristobal de las Casas, Mt. Pasitar, 3 Aug. 1937, *E. Matuda 1661* (MEXU). **Guerrero:** Mpio. Heliodoro Castillo, below Puerto El Gallo along rd. to Atoyac, 2255 m, 10 Oct. 1986, *Breedlove 65109* (NY). **Oaxaca:** Mpio. Ixtlán de Juárez, 2 km N of Natividad, on lower part of trail from San Pedro Nolasco to the Llano Verde, 2000 m, 4 Oct. 1969, *Mickel 3737* (NY); Mpio. Juchitán de Zaragoza, San Miguel Chimalapa, Cerro Baúl, filo S un poco al S de la cima, ca. 23 km en línea recta al N de San Pedro Tapanatepec, 1970 m, 18 July 1985, *Wendt 4971* (CHAPA, MEXU, MO, NY). **Veracruz:** Mpio. Zacualpan, Barranca de Tenampa Zacualpan, 2195 m, Nov. 1912, *C. A. Purpus 6190* (US). NICARAGUA. **Jinotega:** Mpio. Jinotega, 23 June 1947, *Standley 10011* (F). PANAMA. **Chiriquí:** Dtto. Boquete, Cerro Horqueta, 1650 m, 13 Aug. 1974, *Croat 26996* (MO, NY).

4. Elaphoglossum potosianum Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. 36: 119. 1899. TYPE: Mexico. San Luis Potosí: San Miguelito ("Migualito"), in montibus [1890 m], [22.17, –101.00], 1877, *W. Schaffner 77* (lectotype, designated here, P [bc] P00249860 image!; isolectotype, P [bc] P00249859 image!). Figures 1D, 10, 11.

Elaphoglossum trichomidiatum Mickel, Brittonia 53(4): 488. 2001 [2002]. TYPE: Mexico. San Luis Potosí: in the region of San Luis Potosí, 6000–8000 ft. [1828–2438 m],

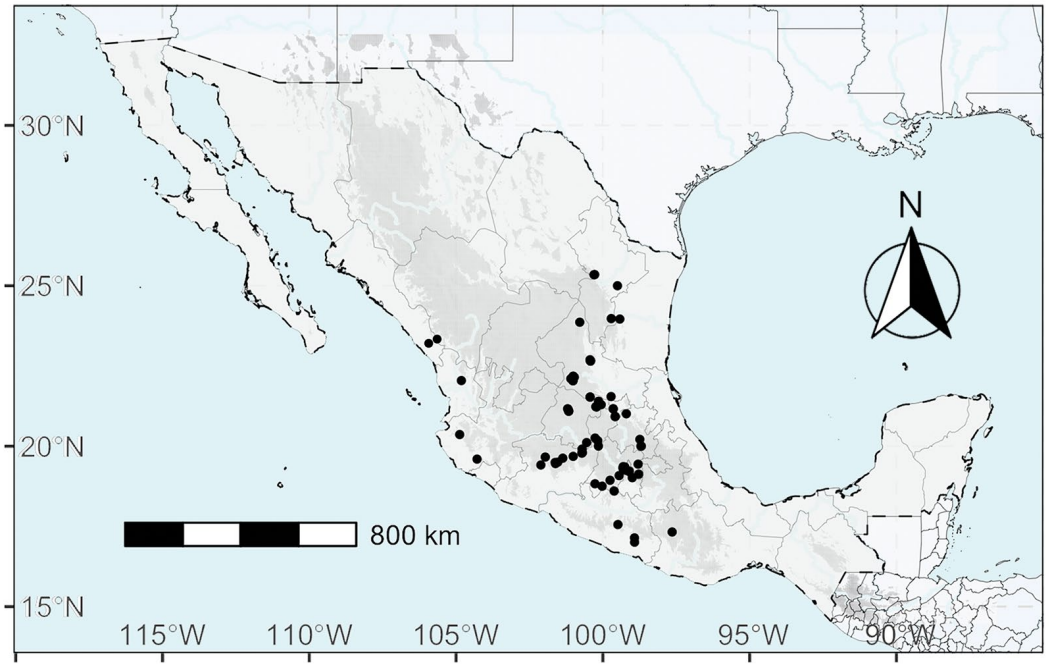

Figure 10. Distribution map of *Elaphoglossum potosianum* Christ.

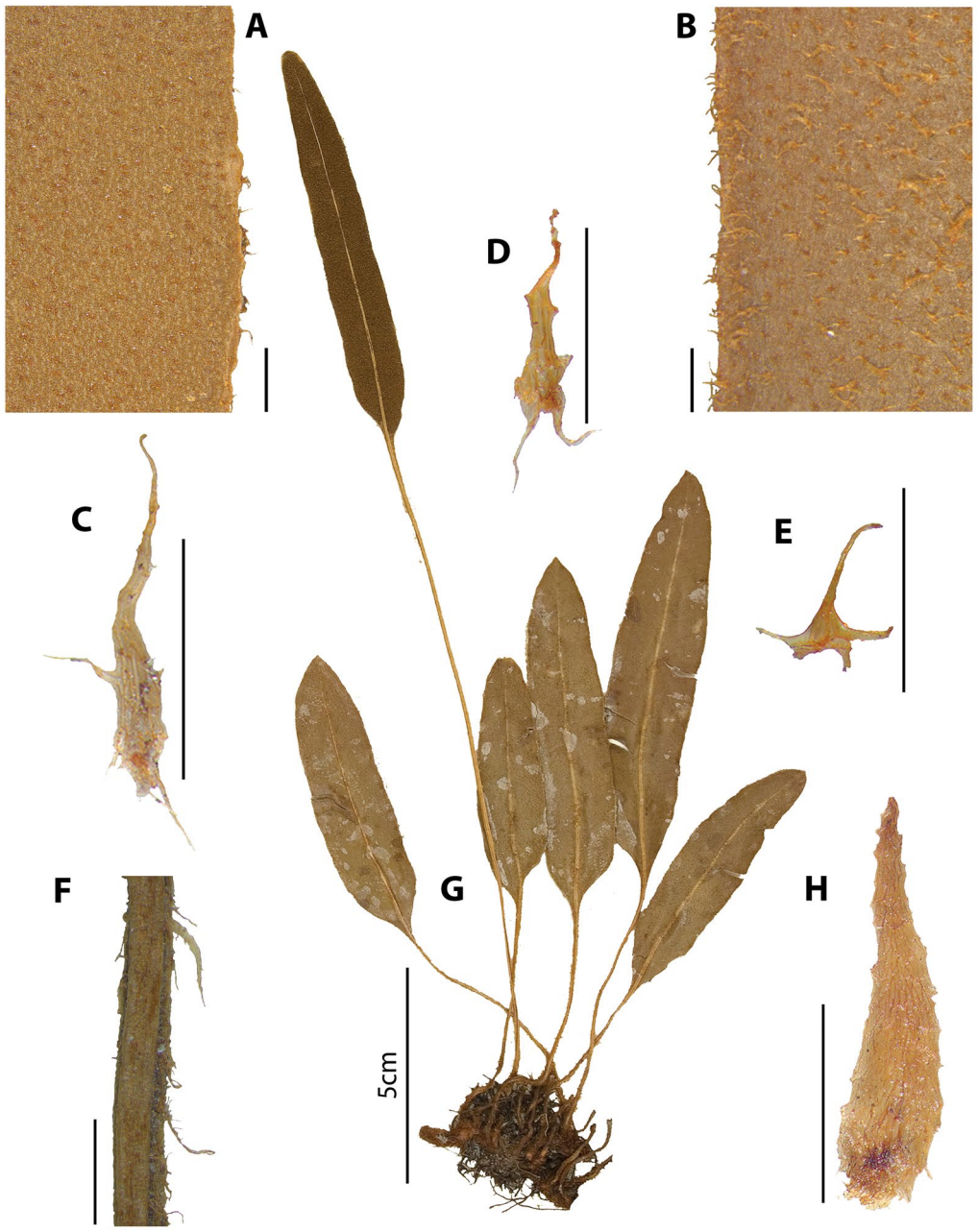

Figure 11. *Elaphoglossum potosianum* Christ. —A. Abaxial laminar surface. —B. Adaxial laminar surface. —C. Larger petiole scale. —D. Abaxial costal scale. —E. Marginal scale. —F. Petiole detail. —G. Habit. —H. Rhizome scale with broken apex. A–E, H, *Schaffner 92* (NY); F, *Schaffner 77* (P); G, *Parry & Palmer 1007* (VT). All photos from sterile leaves. Scale bars = 1 mm, unless otherwise noted.

[22.07, –100.99], [without day or month] 1878, *C. C. Parry & E. Palmer 1007* (holotype, NY [bc] 03231441!; isotypes, F [bc] C0620656F!, MO [bc] 1867264!, US [bc] 01564938!, VT [bc] UVMVT212789!).

Plants terrestrial. **Rhizomes** 2–4 mm wide, short-creeping; **rhizome scales** 2–3.5 mm, dense, spreading, linear-lanceolate, with occasional short projections (shorter than width of scale), concolorous, orange or light brown to dark brown, darker at point of attachment, dull, base truncate, apex attenuate to long-attenuate. **Sterile leaves** 12–26(–46) cm, approximate; **phyllopodia** present, sometimes obscured by petiole scales,

2–4(–40) mm; **petioles** 2–12(–29) cm, (1/5–)1/3–1/2 (–3/5) the length of sterile leaves; **larger petiole scales** to 3 mm, scattered to dense, not imbricate, spreading to appressed, linear-lanceolate to lanceolate, with occasional short projections and usually with occasional long projections (as long as or longer than width of scale) located mostly toward base, stramineous, sometimes darker at apex, base truncate, apex attenuate to filiform; **smaller petiole scales** to 1 mm, dense, not imbricate, mostly appressed, lanceolate, with occasional long projections, stramineous, base truncate, apex acute; **laminae** 7.5–23(–31.5) × 1.4–3.3(–4) cm, linear-lanceolate to narrowly elliptic, chartaceous, base cuneate, apex acute, sometimes apiculate; **adaxial laminar scales** to 1 mm, scattered to dense, not imbricate, deciduous, irregular, substellate or lanceolate, when lanceolate, margin with numerous long projections, stramineous, darker at point of attachment, base auriculate, apex acuminate; **adaxial resinous dots** absent; **abaxial laminar scales** mixed, microscales 0.2–0.3 mm, (2- to)3-armed, reddish, scales absent or when present to ca. 0.5 mm, scattered, irregular, with numerous long projections, stramineous, sometimes darker at point of attachment; **abaxial resinous dots** present; **abaxial costal scales** 1–1.2 mm, scattered to dense, not imbricate, lanceolate with occasional long projections, stramineous to yellowish, base truncate, apex acuminate; **marginal scales** to 0.5 mm, dense, not imbricate, lanceolate, with occasional long projections, stramineous, darker at point of attachment, base auriculate, apex long-acuminate. **Fertile leaves** longer than sterile leaves; **petioles** 3/5–2/3 the length of fertile leaves; **laminae** (8.2–)10–11.5 × 0.6–1 cm, linear, chartaceous, base attenuate to long-attenuate, apex obtuse to acute; **petiole scales** to 2.5 mm, scattered to dense, not imbricate, linear-lanceolate to lanceolate, with occasional long projections, stramineous, sometimes with darker apex, base round or truncate, apex attenuate or filiform; **adaxial laminar scales** lanceolate or substellate, when lanceolate, margin with numerous long projections, yellowish, apex acuminate to attenuate; **abaxial costal scales** to 1 mm, scattered to dense, not imbricate, lanceolate, with occasional long projections, stramineous, base auriculate, apex acute. **Perines** broadly folded, sparsely echinulate.

Habitat and distribution. *Elaphoglossum potosianum* is endemic to Mexico, at elevations of (480–) 1500–2500(–3000) m (Fig. 3). It is terrestrial in temperate and pine-oak forests.

Aside from the state distributions reported by Mickel and Smith (2004), we report *Elaphoglossum potosianum* for the states of Durango, Estado de México, Guerrero, Jalisco, Michoacán, Nayarit, Oaxaca, and Querétaro (Appendix 2).

Phenology. Fertile specimens have been collected mainly from August to October, but there are a few collections from May, July, and December.

Etymology. The specific epithet *potosianum* refers to San Luis Potosí, the Mexican state where the holotype was collected.

Notes. *Elaphoglossum potosianum* can be distinguished from all other species of the petiolatum clade (except *E. muelleri*) by the presence of microscales mixed with scales and resinous dots on the abaxial laminar surface and by the presence of orange rhizome scales (some specimens of *E. potosianum* have dark-brown rhizome scales) (vs. absence of microscales on the abaxial laminar surface and stramineous, dark-brown, or dark-reddish–brown rhizome scales in all other species of the petiolatum clade). See *E. muelleri* for a comparison with that species.

Within *Elaphoglossum potosianum*, the density of laminar scales, microscales, and resinous dots is variable. Usually, microscales can be detected most easily by observing the specimen in profile.

According to the protologue of *Elaphoglossum potosianum*, a type specimen was at B, but we were not able to locate it there. Mickel and Smith (2004) cited the type at P, but we found two specimens of *Schaffner 77* at P. We chose P00249860 as the lectotype because it has a more complete label matching the protologue.

Selected specimens examined. MEXICO. **Ciudad de México:** Alcaldía Benito Juárez, Barrancas de Mixcoac, Sep. 1935, *Lyonnet 891* (MEXU, MO, US); Alcaldía Cuajimalpa, 2500 m, 11 Feb. 1951, *Matuda 20960* (MEXU, US); Alcaldía Magdalena Contreras, en cañada San Magdalena, 15 Oct. 1908, *Barnes 440* (F, US); Alcaldía Xochimilco, Santa Cecilia, 2550 m, 29 Jan. 1977, *Ventura 2545* (IEB). **Durango:** Mpio. Durango, about 29 mi. E of Santa Lucía on the rd. from Villa Unión to Durango, 2190 m, 28 Sep. 1953, *Reeder 2501* (US). **Estado de México:** Mpio. Amecameca, 1 km al N de San Antonio, 2500 m, 28 Sep. 1980, *F. Zerón 0A-1* (IEB); Mpio. Coatepec Harinas, Coatepec Harinas y Chiltepec, 2299 m, 17 June 2009, *Campos Salas 67* (MEXU); Mpio. Sultepec, a 23 km de Sultepec rumbo a Amatepec, 2300 m, 22 Feb. 1986, *Tejero-Díez 2311* (MEXU, NY); Mpio. Texcoco, 8 km al E Coatlinchán, 2600 m, 20 July 1967, *Rzedowski 24065* (ENCB, NY). **Guanajuato:** Mpio. Dolores Hidalgo, Km. 83 carretera Dolores Hidalgo–Guanajuato, 2400 m, 29 May 1992, *Carranza 4056* (HUMO, IEB, NY, OAX); Mpio. Jerécuaro, Puerto El Yesquero, 2600 m, 7 Nov. 1986, Díaz-Barriga 3317 (IEB); Mpio. Victoria, alrededores de San Agustín, 2400 m, 11 Sep. 1987, *Rzedowski 44767* (IEB). **Guerrero:** Mpio. Chilpancingo de los Bravo, al E de Omiltemi camino a La Bandera, 2400 m, 27 Aug. 1985, *Valdez 785* (NY); Mpio. Taxco, cerro El Huizteco, 4 km al N de Taxco, 2380 m, 27 Sep. 1988, *Lorea Hernández 4468* (IEB); Mpio. Leonardo Bravo, Chichihualco, 1 km al S de Tres Cruces, carr. Casas Verdes–Filo de Caballos, 2200 m, 23 Sep. 1980, *Lorea Hernández 851* (ENCB, MEXU). **Hidalgo:** Mpio. Jacala, 21 Oct. 1937, *Kenoyer 500* (F, MO); Mpio. Omitlán de Juárez, Sep. 1948,

Matuda 32531 (MEXU); Mpio. Zimapan, San Vicente, 2400 m, 8 Aug. 1946, *Fisher s.n.* (NY [bc] 03376692). **Jalisco:** Mpio. Talpa de Allende, Sierra de Cuale, SW of Talpa de Allende, SW of the prominent peak called Piedra Rajada, 2250 m, 19 Nov. 1952, *McVaugh 14247* (US). **Michoacán:** Mpio. Cherán, ladera NE del Cerro San Marcos, 2600 m, 15 Aug. 1987, *Zamudio 5464* (IEB, NY); Mpio. Nuevo Parangaricutiro, Cerro Capatzin, 2600 m, 4 Feb. 1996, *Medina García 3107* (IEB, MEXU); Mpio. Pátzcuaro, Cuanajo, Camino al Cerro del Frijol, 2400 m, 21 Aug. 1986, *J. M. Escobedo 1170* (ENCB, IEB, OAX); **Nayarit:** Mpio. Del Nayar, Km. 15–22 de la carretera San Pedro Ixcatán–Jesús María. 4 km antes de Santa Cruz de Guaymel, 480 m, 11 Oct. 2013, *Castro-Castro 3566* (IEB). **Nuevo León:** Mpio. General Zaragoza, Cerro El Viejo, 2200 m, 7 July 1992, *Hinton 22119* (MEXU, MO); Mpio. Pesquería, Dulces Nombres, just E of border into Tamaulipas, 1690 m, 19 July 1948, *Meyer 2806* (MO); Mpio. Santiago, La Camotera, El Tejocote, camino de Laguna de Sánchez–La Camotera, 1860 m, 19 Aug. 1986, *Rodríguez López 187* (MEXU). **Oaxaca:** Mpio. Heroica Ciudad de Tlaxiaco, 6 km NE of Tlaxiaco on Rte. 125, 50 km S of Panamerican Hwy., 2133 m, 25 Sep. 1972, *Mickel 6809* (NY). **Querétaro:** Mpio. Amealco de Bonfil, Cerro de Don Nica, Cañada del Venado, al E de San Pablo, 3000 m, 24 Nov. 1992, *Díaz-Barriga 7371* (ENCB, IEB, MEXU, NY); Mpio. Pinal de Amoles, 4 km al W de San Joaquín, 2450 m, 20 Oct. 1990, *Fernández 4696* (IEB, MEXU). **San Luis Potosí:** Mpio. Guadalcázar, aprox. a 3 km al E del Realejo, base del cerro Las Comadres, 2008 m, 9 Aug. 2018, *Martínez-Becerril 399* (BRIT, FEZA); Mpio. Rioverde, Las Mesas de San Isidro, Ejido Milpitas, 1760 m, 28 Mar. 1994, *Ballín 34* (MEXU). **Sinaloa:** rd. betw. Durango & Villa Unión, 57.7 mi. SW of El Salto Dgo. (5.1 mi. NE of El Paraíso), 2300 m, 29 Sep. 1953, *Ownbey 1962* (US). **Tamaulipas:** Mpio. Hidalgo, Galindo, 7 km al SE de Puerto Purificación, 6 June 1990, *González-Medrano 17496* (MEXU); San Agustín, Sep. 1875, *Schaffner 103* (MEXU).

5. Elaphoglossum pringlei (Davenp.) C. Chr., Index Filic. 313. 1905. *Acrostichum pringlei* Davenp., Bot. Gaz. 21(5): 253. 1896. TYPE: Mexico. Oaxaca: Sierra de San Felipe, 10,000 ft. [3048 m], [17.42, –96.46], 25 Sep. 1894, *C. G. Pringle 5605* (first-step lectotype, inadvertently designated by Mickel & Beitel [1988: 181], GH!; second-step lectotype, designated here, GH [bc] 00020353 image!; isolectotypes, F [bc] V0075926F!, GH [bc] 00102873 image!, GH [bc] 00102874 image!, K [bc] 000994450!, K [bc] 000994451 image!, P [bc] P00249935, US [bc] 01564931!, VT [bc] UVMVT001435 image!). Figures 1E, 12, 13.

Plants terrestrial. **Rhizomes** 2–2.5(– 4.5) mm wide, short-creeping; **rhizome scales** 1.4–2.5(–3.5) mm, dense, spreading, linear to lanceolate, with occasional short projections (shorter than width of scale), bicolorous, light brown becoming dark brown with age, darker at point of attachment, dull, base round, apex long-attenuate to filiform-tortuous, often broken. **Sterile leaves** 7–38 cm, approximate; **phyllopodia** present, clearly visible, 5–20(–30) mm; **petioles** (1.3–)3.5–13(–20) cm, (1/4–)3/8–3/7(–3/5) the length of sterile leaves; **larger petiole scales** to 2.5 mm, scattered to

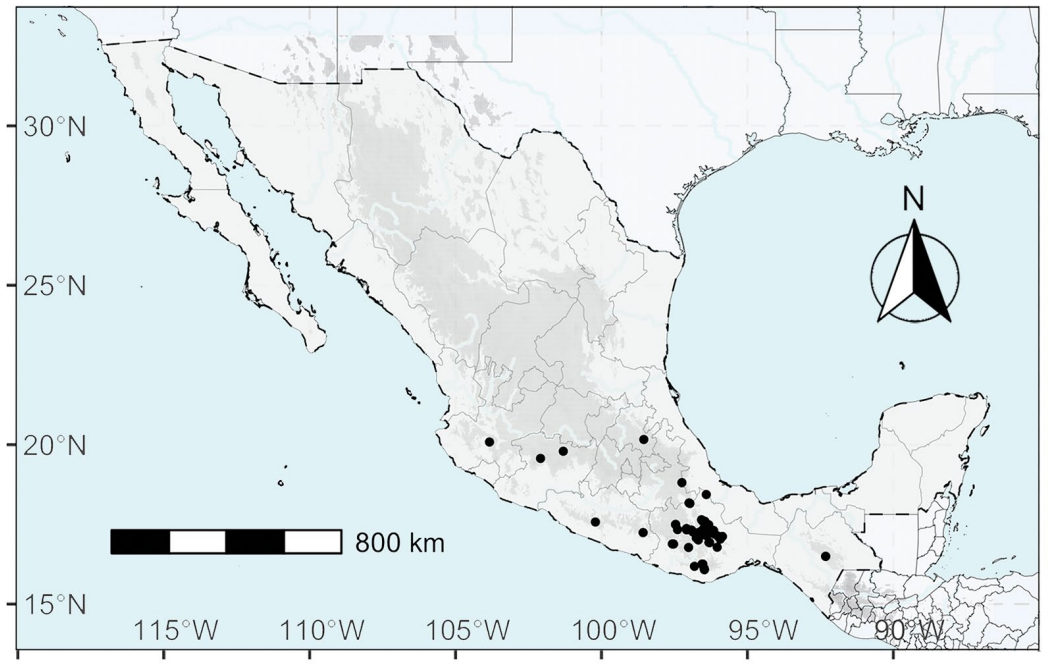

Figure 12. Distribution map of *Elaphoglossum pringlei* (Davenp.) C. Chr.

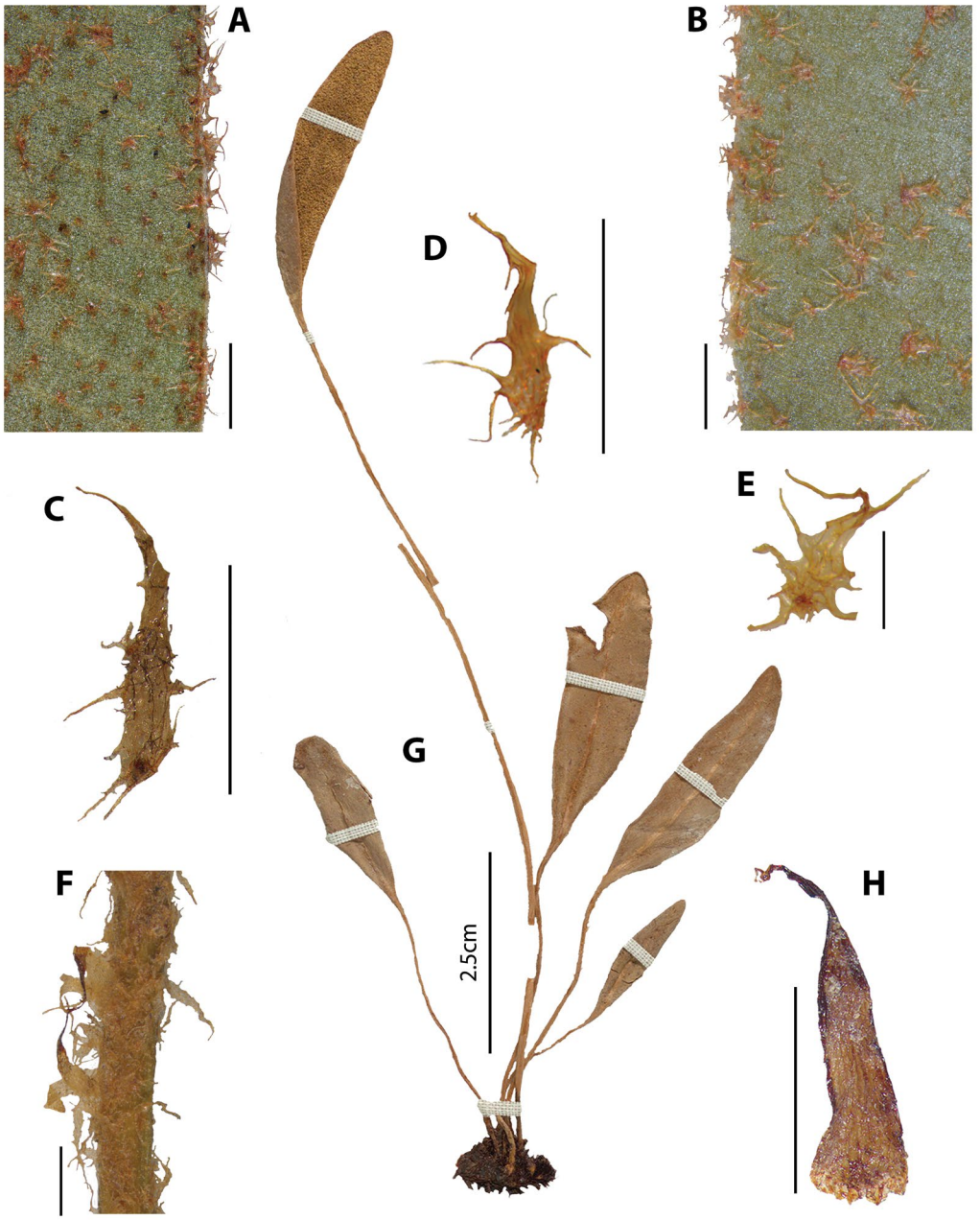

Figure 13. *Elaphoglossum pringlei* (Davenp.) C. Chr. —A. Abaxial laminar surface. —B. Adaxial laminar surface. —C. Larger petiole scale. —D. Abaxial costal scale. —E. Marginal scale. —F. Petiole detail. —G. Habit. —H. Rhizome scale. A–C, *Anderson 4778* (NY); D, E, G, *Pringle 5605* (US); F, H, *Mickel 3866* (NY). All photos from sterile leaves. Scale bars = 1 mm, unless otherwise noted.

dense, not imbricate, spreading to appressed, linear-lanceolate to lanceolate, with occasional short projections or with long projections (as long as or longer than width of scale), stramineous, sometimes darker at apex, base round or auriculate, apex acuminate to long-attenuate; **smaller petiole scales** to 1 mm, dense, not imbricate, deciduous, mostly appressed, irregular, substellate, or lanceolate, when lanceolate, margin with occasional short or long projections, stramineous, sometimes darker at apex, base round or auriculate, apex

acuminate to long-attenuate; **laminae** 4–22.5 × (0.5–) 1–2.5(–3) cm; elliptic to lanceolate, chartaceous, base decurrent, apex obtuse to acute, sometimes apiculate; **adaxial laminar scales** to 1 mm, dense or sometimes scattered, not imbricate, irregular, substellate, or lanceolate, whitish to yellowish, darker at point of attachment, when lanceolate, margin with numerous long projections, base auriculate, apex long-attenuate; **adaxial resinous dots** absent; **abaxial laminar scales** to 1 mm, dense, not imbricate, substellate, irregular, or lanceolate, when lanceolate, with numerous long projections, stramineous to yellowish, sometimes darker at point of attachment, base auriculate, apex long-attenuate to filiform; **abaxial resinous dots** present or absent; **abaxial costal scales** 0.5–1 mm, dense, not imbricate, lanceolate, substellate, or irregular, when lanceolate, margin with numerous long projections or with occasional short projections, stramineous, base, when lanceolate, auriculate, apex long-attenuate; **marginal scales** to 0.9 mm, dense, not imbricate, lanceolate, with numerous long projections, stramineous to yellowish, base truncate, apex long-attenuate, sometimes with a long projection close to apex. **Fertile leaves** longer than sterile leaves; **petioles** (2/3–)3/5–5/7 the length of fertile leaves; **laminae** 4–15.5 × 0.5–1.2 cm, elliptic to lanceolate, chartaceous, base long-cuneate, apex round to acute; **petiole scales** to 1 mm, scattered, linear-lanceolate to lanceolate or irregular, when linear to linear-lanceolate, margin with occasional short projections, stramineous, sometimes with darker margin, base round or auriculate, apex acuminate to long-attenuate; **adaxial laminar scales** lanceolate or substellate, when lanceolate, margin with numerous long projections, whitish to yellowish, apex attenuate to long-attenuate; **abaxial costal scales** to 1 mm, scattered, linear-lanceolate to lanceolate or irregular, when linear-lanceolate or lanceolate, with numerous long projections, stramineous to yellowish, base auriculate, apex acuminate to long-attenuate. **Perines** broadly folded, sparsely echinulate.

Habitat and distribution. *Elaphoglossum pringlei* is endemic to Mexico, at elevations of (1280–)1500–3050 m (Fig. 3). It is terrestrial in temperate and pine-oak forests.

Most collections of *Elaphoglossum pringlei* examined in this study, as well as those cited by Mickel and Smith (2004), are from Oaxaca; however, this species also occurs in Chiapas, Guerrero, Hidalgo, Jalisco, Michoacán, and Veracruz.

Phenology. Fertile specimens have been collected mainly from July to October, with a few in November and January.

Etymology. The specific epithet honors Cyrus Guernsey Pringle (1838–1911), an American botanist who collected in the Pacific Coast states of the United States, and in Mexico between 1880 and 1909. In 1902, Pringle funded the herbarium of the University of Vermont, which carries his name, the Pringle Herbarium (VT) (Nicholson, 2001; TL-2).

Notes. *Elaphoglossum pringlei* can be distinguished from all other species of the petiolatum clade by the elliptic to lanceolate laminae with substellate, irregular, or lanceolate scales. In addition, it is the only species in which abaxial resinous dots can be absent or present. *Elaphoglossum pringlei* also has the largest spores of any species in the petiolatum clade, suggesting it might be of polyploid origin as has been shown for other ferns with large spores (Wagner, 1974; Stebbins, 1985; Barrington et al., 1986, 2020; Farrar, 2006). The spores measure 40.4 µm in equatorial diameter and 31.6 µm in polar diameter, on average (vs. 31.2 µm and 28.5 µm, respectively, in the other species in the clade) (Martínez-Becerril et al., 2021).

Elaphoglossum pringlei is often misidentified as *E. petiolatum* because of its similar linear to lanceolate rhizome scales and its elliptic to lanceolate lamina shape. *Elaphoglossum pringlei* can be distinguished from *E. petiolatum* by its bicolorous, light-brown rhizome scales that become dark brown with age, with a darker point of attachment, and a long-attenuate apex ending in a thin hair (vs. rhizome scales concolorous, dark reddish brown to dark brown with a filiform to tortuous apex [very long but wider than a thin hair] in *E. petiolatum*); adaxial laminar surfaces without resinous dots (vs. resinous dots sometimes present); abaxial laminar surface resinous dots absent, or when present shiny (vs. abaxial laminar surface dots always present, shiny and/or nonshiny); and perines sparsely echinulate (vs. with sparsely irregular microstructures). Mickel and Smith (2004) suggested that one of the main differences between *E. pringlei* and *E. petiolatum* is that *E. pringlei* lacks resinous dots on the laminae and that the scales are substellate abaxially; however, we found that at least half the specimens of *E. pringlei* have resinous dots abaxially, and some specimens of *E. petiolatum* have substellate scales abaxially.

Elaphoglossum pringlei differs from *E. rzedowskii* by rhizome scales with a long-attenuate to filiform-tortuous, often broken apex (vs. rhizome scales with an acuminate to long-attenuate apex in *E. rzedowskii*); elliptic to lanceolate laminae with dense, not imbricate scales (vs. linear to elliptic laminae with dense, deciduous, sometimes imbricate scales); and the lack of resinous dots on the adaxial laminar surface (vs. the presence of resinous dots on the adaxial laminar surface). Average

spore size is also a good character to distinguish these species; in *E. pringlei* spores measure on average 40.4 µm in equatorial diameter and 31.6 µm in polar diameter (vs. 34.6 µm and 27.9 µm) (Martínez-Becerril et al., 2021). Mickel and Smith (2004) suggested that *E. pringlei* is related to *E. rzedowskii* and that these two could represent regional variations of the same species. We consider them two different species because of the morphological differences stated here.

The rhizome scales of *Elaphoglossum pringlei* have a gradient of shapes and colors, from linear to lanceolate and with different tones of brown, because they tend to darken with age. There is also variation in the density of laminar scales and resinous dots: some specimens have very scattered laminar scales, while others have dense laminar scales; and some specimens do not have any resinous dots on the laminae, while others have numerous resinous dots.

Mickel and Smith (2004) cited *Pringle 5605* (MEXU) as an isotype; however, we did not find this specimen among the material we examined.

Selected specimens examined. MEXICO. **Chiapas:** Mpio. San Cristobal de las Casas, dry, shaded bank near San Cristobal, 2 Jan. 1907, *Collins 137* (US). **Guerrero:** Mpio. General Heliodoro Castillo, Tlacotepec a 19.5 km al NE de Puerto del Gallo, camino Atoyac–Filo de Caballo, 2900 m, 23 Nov. 1983, *Martínez 5644* (MEXU); Mpio. Metlatónoc, 5 km antes de Zitlaltepec, viniendo de Huehuetepec, antes de Barranca Honda, 2100 m, 25 Nov. 2005, *Velázquez Montes 2480* (IEB). **Hidalgo:** Mpio. Huasca de Ocampo, 3 km al SSE de Huasca (camino a Zembo), 2200 m, 3 Dec. 1988, *Medina-Cota 3835* (IEB). **Jalisco:** in oak forest, rd. to Los Volcanes, 1960, *s. coll.*, *s.n.* (MEXU). **Michoacán:** Mpio. Malpaís, aprox. a 6 km al SW de Paracho, 2400 m, 7 Sep. 1990, *García 3261* (IEB); Mpio. Zinapécuaro, La Lomita, 1 km al NE de Jerécuaro, 2350 m, 20 Oct. 1988, *Jasso 366* (IEB). **Oaxaca:** Mpio. Comaltepec, Rte. 175 Oaxaca–Valle Nacional, ca. 3 km N of pass at summit of Cerro Pelón, along dirt rd. leading to "Las Cascadas de nubes," 2585 m, 16 Mar. 2015, *Testo 841* (NY, VT); Mpio. Ixtlán de Juárez, Rancho Vivero Teja, ca 5 km al NE de Ixtlán de Juárez, 2400 m, 5 Apr. 1981, *Lorence 3182* (ENCB, MEXU); Mpio. Juchitán de Zaragoza, San Miguel Chimalapa, Loma Larga, en la cabecera de la rama principal S del Río del Café al O de Cerro Guayabitos, ca. 40–45 km al N de San Pedro Tapanatepec, 1500 m, 11 Sep. 1985, *Maya 2143* (CHAPA, MEXU, NY); Mpio. Miahuatlán, San Pablo Coatlán, 8 km al SO de San Pablo Coatlán, carr. Miahuatlán–Piedra Larga, 1760 m, 11 Dec. 1987, *Torres-Colin 10761* (IEB, MEXU); Mpio. Oaxaca de Juárez, centro, Cerro de San Felipe del Agua, 1800 m, 9 Aug. 1985, *Saynes 761* (ENCB, MEXU, OAX); Mpio. San Pedro Pochutla, Oaxaca–Pochutla Rd., Km. 153 at Campamento Río Molino, 2280 m, 30 July 1973, *Mickel 1278* (NY); Mpio. Sola de Vega, 26–28 km W of Rte. 131 above Río Grutas (Río de Guevara, Río del Vado), above Santa María Lachixio, 2100 m, 9 Oct. 1969, *Mickel 3897* (NY); Mpio. San Pedro Yaneri, secondary rd. used to access La Cumbre, cascade referred to locally as "las cascadas," 2820 m, 29 Feb. 2012, *Sundue 3058* (VT); Mpio. San Pedro Yólox, a 1.5 km del Crucero San Pedro Yolox–San Martín Buenavista, 2557 m, 26 Mar. 2014, *Torres-Colin 17671* (NY); Mpio. Totontepec Villa de Morelos, trail from San Pedro Nolasco N to Llano Verde, 2190 m, 5 Oct. 1969, *Mickel 3773* (NY); Mpio. Villa de Etla, 49 km NW of Oaxaca on Rte. 190, 2280 m, 14 Sep. 1970, *Mickel 4478* (NY). **Veracruz:** Maltrata, 2195 m, July 1883, *Kerber 173a* (US).

6. Elaphoglossum rzedowskii Mickel, Brittonia 32: 337. 1980. TYPE: Mexico. Jalisco: Mpio. San Martín de Bolaños, Las Vidrieras, 10 km NW of El Platanar, 2450 m, [20.48, –103.07], 1 Sep. 1968, *J. Rzedowski 26161* (holotype, MICH [bc] 1287073 image!; isotype, NY [bc] 00149704!). Figures 1F, 14, 15.

Plants terrestrial or epipetric. **Rhizomes** 2.5–4 mm wide, short-creeping; **rhizome scales** (1–)1.5–2(–3) mm, dense, spreading, linear-lanceolate, with occasional short projections (shorter than width of scale), bicolorous, stramineous to brown, darker at point of attachment and toward margin and apex, dull, base round, apex acuminate to long-attenuate. **Sterile leaves** (8–)16–25 cm, approximate; **phyllopodia** present, usually obscured by rhizome scales, ca. 5 mm; **petioles** 3–6.5(–11.5) cm, 1/6–1/4(–1/2) the length of sterile leaves; **larger petiole scales** to 3 mm, dense, usually imbricate, spreading to appressed, linear-lanceolate to lanceolate, with occasional short projections, stramineous, sometimes darker toward apex, base truncate, apex attenuate to filiform; **smaller petiole scales** to 1 mm, dense, usually imbricate at petiole base, mostly appressed, irregular, substellate, or lanceolate, when lanceolate, margin with occasional long projections (as long as or longer than width of scale), stramineous, darker at point of attachment, base auriculate, apex acute; **laminae** 9.5–18.5 × (0.7–)1–1.5(–2) cm, linear to elliptic, chartaceous, base decurrent, apex acute to acuminate, sometimes apiculate; **adaxial laminar scales** to 1 mm, dense, not imbricate, deciduous, linear-lanceolate, with numerous long projections (as long as or longer than width of scale), stramineous, darker at point of attachment, base auriculate, apex long-filiform; **adaxial resinous dots** present, sometimes not visible because of dense laminar scales; **abaxial laminar scales** to 0.7 mm, dense, sometimes imbricate, lanceolate, with numerous long projections, stramineous, darker at point of attachment, base auriculate, apex long-filiform; **abaxial resinous dots** present, sometimes not visible because of dense laminar scales; **abaxial costal scales** 1–2 mm, dense, usually imbricate, linear-lanceolate with occasional short and/or long projections, stramineous, sometimes whitish, base auriculate, apex long-filiform; **marginal scales** to 1 mm, dense, usually imbricate, lanceolate, with numerous long projections, stramineous, base truncate with long projections, apex long-attenuate, sometimes

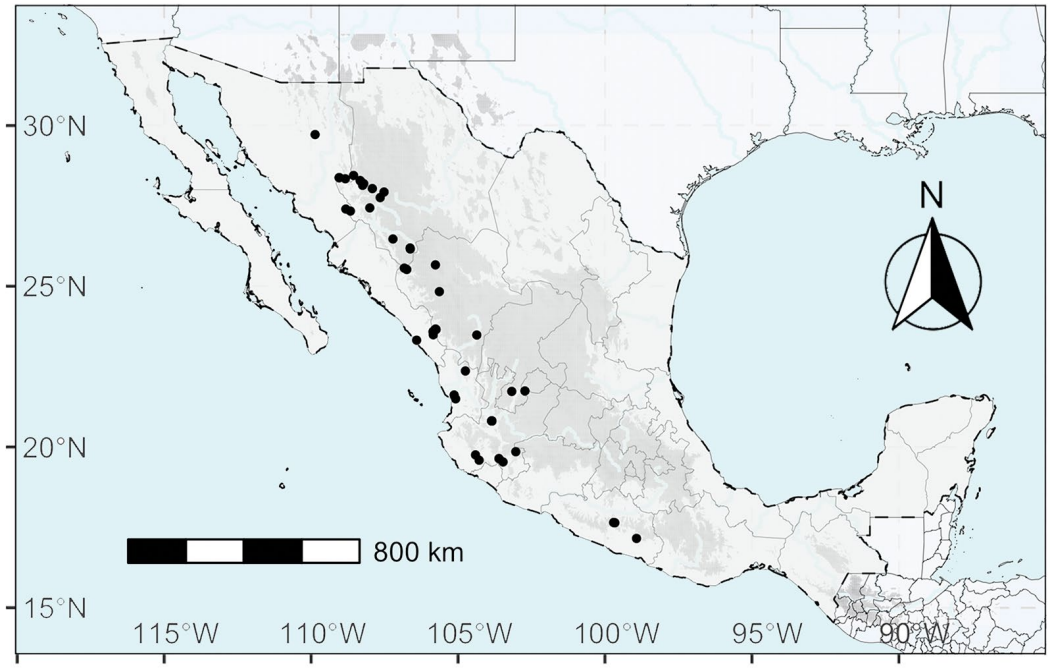

Figure 14. Distribution map of *Elaphoglossum rzedowskii* Mickel.

with a long projection close to apex. **Fertile leaves** similar to or slightly longer than sterile leaves; **petioles** 3/7–1/2 the length of fertile leaves; **laminae** 11–13.5 × 0.9–1.1 cm, linear-elliptic, chartaceous, base long-cuneate, sometimes unequal, apex acute to acuminate; **petiole scales** (1.5–)2.5(–3) mm, dense, usually imbricate, linear-lanceolate to lanceolate or irregular, when linear to linear-lanceolate, margin with occasional short or long projections, stramineous, sometimes with darker apex, base round or truncate, apex attenuate to filiform; **adaxial laminar scales** linear-lanceolate to lanceolate, when linear-lanceolate to lanceolate, margin with numerous long projections, yellowish, apex long-attenuate to filiform; **abaxial costal scales** to 2 mm, dense, usually imbricate, linear-lanceolate, with occasional short and/or long projections, stramineous, base auriculate, apex long-filiform. **Perines** broadly folded, sparsely echinulate.

Habitat and distribution. *Elaphoglossum rzedowskii* is endemic to western Mexico, at elevations of (800–) 1400–2700(–3050) m (Fig. 3). It is terrestrial or epipetric in temperate and pine-oak forests. *Gentry 18160* (NY) from Durango is the only collection made above 2700 m.

Elaphoglossum rzedowskii was reported by Mickel and Smith (2004) as occurring in the states of Guanajuato (*Rzedowski 45444*, IEB) and Michoacán (*Leavenworth 717*, NY), yet we did not find specimens belonging to this species in these states (Appendix 2). *Leavenworth 717* corresponds with *E. schmitzii*, and we were not able to locate *Rzedowski 45444*. Nevertheless, given its distribution (Appendix 2, Fig. 14), it is highly probable this species is present in both states.

Phenology. Compared to other species in the petiolatum clade, *Elaphoglossum rzedowskii* has the fewest collections, only a few of which are fertile. These were collected during August and September.

Etymology. The specific epithet honors Jerzy Rzedowski Rotter (1926–2023), a Polish-born naturalized citizen of Mexico, botanist, professor, and emeritus researcher who dedicated his career to studying Mexican plants (Anderson, 1996).

Notes. Among the species of the petiolatum clade, *Elaphoglossum rzedowskii* has the northernmost distribution, occurring as far north as the Mexican states of Chihuahua and Sonora. This species can be distinguished from all the other species in the petiolatum clade because its abaxial laminar scales can sometimes be so dense that they obscure not only the whole abaxial surface of the leaf, but also the resinous dots that are present. In most specimens, these resinous dots are easier to see on the adaxial surface. In general,

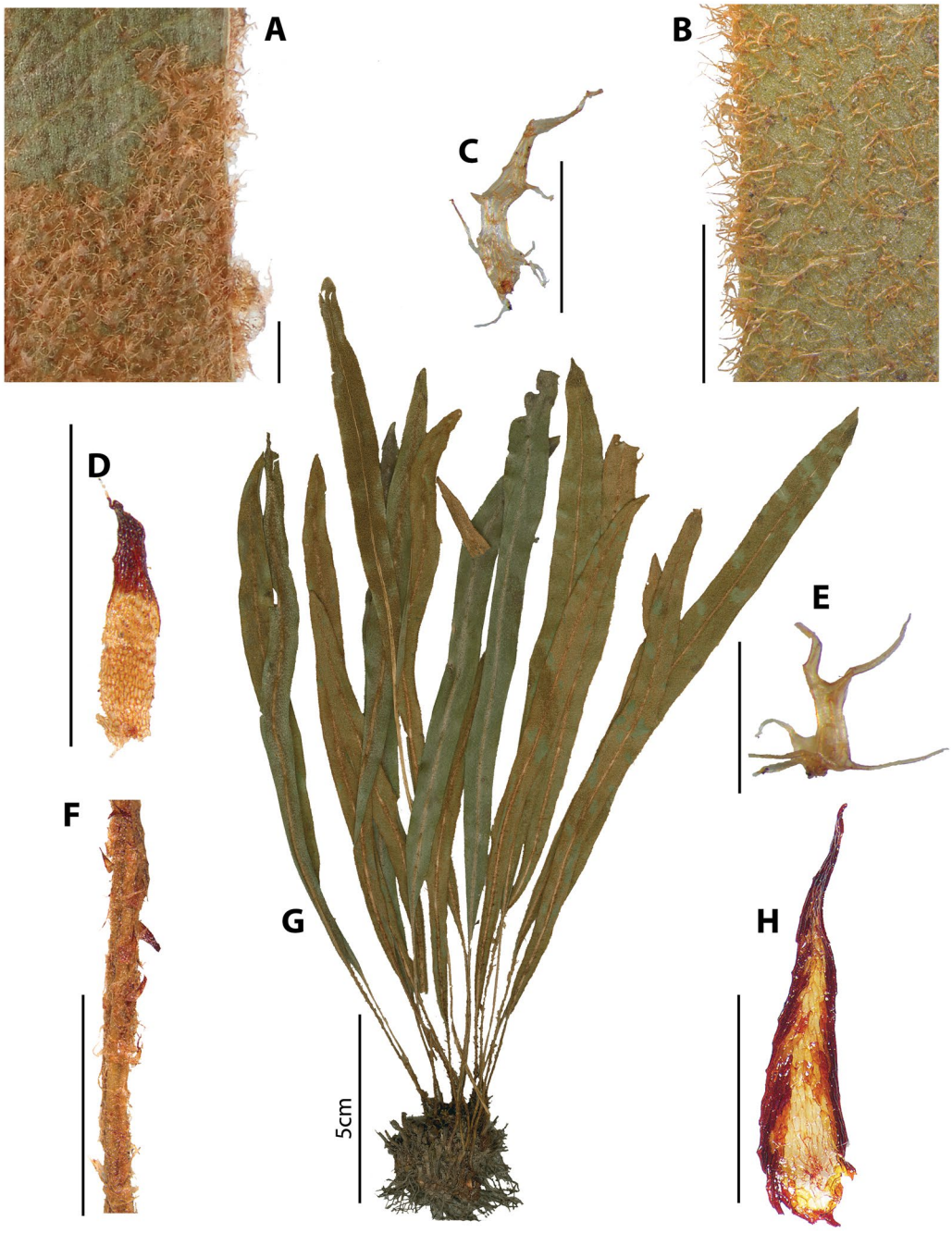

Figure 15. *Elaphoglossum rzedowskii* Mickel. —A. Abaxial laminar surface. —B. Adaxial laminar surface. —C. Abaxial costal scale. —D. Smaller petiole scale. —E. Marginal scale. —F. Petiole detail. —G. Habit. —H. Rhizome scale. A, D, F, G, *Rzedowski 26161* (NY); B, C, E, *Correll 22972* (MO); H, *Reina 96-183* (MO). All photos from sterile leaves. Scale bars = 1 mm, unless otherwise noted.

specimens from Durango and Guerrero have fewer laminar scales than the rest.

Elaphoglossum rzedowskii can be easily confused with *E. pringlei*. See *E. pringlei* for a comparison with this species.

Within *Elaphoglossum rzedowskii* we found variation in spore morphology. *Lorea 3148* (NY) from Guerrero, *Reveal & Atwood 3572* (NY) from Durango, and *Sanders 21191* (NY) from Sinaloa have perines with smooth surfaces instead of typical spines. These specimens are otherwise identical to *E. rzedowskii*, and here we are recognizing them as such.

The sheet that houses the holotype of *Elaphoglossum rzedowskii*, *Rzedowski 26161* (MICH), is mixed because two different plants are mounted. To differentiate the two plants, someone marked them directly on the sheet with the letters "a" and "b," and later they were assigned different barcodes: plant "a" MICH [bc] 1287073, and plant "b" MICH [bc]1259599. In the original description of this species, Mickel (1980) explained that the holotype of *E. rzedowskii* was plant "a," and that plant "b" corresponded to *E. gratum* (Fée) T. Moore. The current annotation labels on the specimen at MICH indicate that Mickel identified specimen "b" as *E. rzedowskii* in 1988. We believe that the initial determination by Mickel (1980) is correct: the holotype of *E. rzedowskii* is plant "a," and plant "b" corresponds to *E. gratum*.

Selected specimens examined. MEXICO. **Aguascalientes:** Mpio. Calvillo, El Hechadero, Barranca Obscura, Sierra de Laurel, 2320 m, 10 Aug. 1992, *Siqueiros 4106* (MEXU). **Chihuahua:** Mpio. Guachochi, ca. 3.5 mi. SE of Tónachic, 17 Mar. 1951, *McVaugh 11501* (MEXU, US); Mpio. Maguarachi, SW San Juanito, 22 Mar. 1957, *I. W. Knobloch 114* (MEXU, US); Mpio. Nabogame, 21 Mar. 1988, *J. E. Laferriére 1399* (MEXU, MO); Mpio. Ocampo, area de Cascada de Basaseachic at the confluence of Río Basaseachic & Río Durazno, ca. 2 mi. S of the village of Basaseachic, steep-sided canyon of Río Durazno, S of the parking area & campground, 2000 m, 17 Oct. 1986, *Nesom 5624* (MEXU); Mpio. Urique, Sierra Madre Occidental, steep slopes above Barranca Basihuare, 1815 m, *Peterson 17577* (IEB, US). **Durango:** Mpio. Gómez Palacio, San Ramón, 21 Apr. 1906, *Palmer 186* (F, IEB, MO, NY, US); Mpio. Lerdo, steep slopes at base of Espinazo del Diablo, 4 km NW of Los Angeles along the rd. betw. Mazatlán & Durango, 2500 m, 28 Oct. 1973, *Breedlove 35752* (MO); Mpio. Pueblo Nuevo, ca. 35 mi. SW of El Salto along rd. to Mazatlán, 3050 m, 13 Nov. 1959, *Gentry 18160* (NY, US); **Guerrero:** Mpio. Leonardo Bravo, Puerto Pichones, carretera Filo de Caballos–Chichihualco, aprox. 3 km al E de El Carrizal, 2450 m, 25 July 1981, *Lorea Hernández 1403* (ENCB, MEXU). **Jalisco:** Mpio. Autlán de Navarro, 30–35 km al SE de Autlán cerro El Muñeco, Sierra de Manantlán, 1900 m, 28 Sep. 1966, *Anderson 3784* (ENCB, MEXU, NY); Mpio. Tequila, camino a la cima del volcán Tequila, 2421 m, 11 Aug. 2018, *Martínez-Becerril 405* (BRIT, FEZA). **Nayarit:** Mpio. Del Nayar, along unused rd. from Mesa del Nayar to Santa Teresa, 1850 m, 12 Aug. 1980, *Breedlove 45511* (MEXU); Mpio. Tepic, al W de la Noria, 8.7 km sobre la desv. a El Cuarenteño, carr. Tepic–Miramar, 1700 m, 2 Oct. 1989, *González 797* (MEXU). **Sinaloa:** Mpio. Concordia, Sierra Madre Occidental off Hwy. 40 (Mazatlan–Durango Hwy.) at Rancho Liebre ca. 2 km W of El Palmito, trail from hwy. to large barranca ca. 2 km NW, 2160 m, 1 Sep. 1997, *Sanders 21170* (UCR); idem, *Sanders 21191* (MO, UCR). **Sonora:** Mpio. Pitiquio, El Aguajito, Barranca Honda, N slopes of Mesa del Campanero, 4.8 km W of Puerto de la Cruz on Mex. 16, 1640 m, 20 Feb. 1997, *Reina 96-183* (MO); idem, *Reina 97-183* (MEXU); Mpio. San Bernardo, Cerro Saguaribo, E de San Bernardo, 8 Aug. 1935, *Pennell 19656* (MEXU, US). **Zacatecas:** Mpio. Jalpa, 38 km al W de Jalpa, sobre la carretera a Tlaltenango, 30 km del entronque con la carretera Jalpa–Juchipila, 2250 m, 21 Oct. 1973, *Rzedowski 1006* (MICH).

7. Elaphoglossum schiedei (Kunze) T. Moore, Index Fil. 3: 14. 1857. *Acrostichum schiedei* Kunze, Analecta Pteridogr. 10. 1837. TYPE: Mexico. Veracruz: Mpio. Jalapa, ad ladera montimum prope El Molino de Pedreguera conf. [1430 m], [19.55, –96.93], June 1829, *W. Schiede s.n.* (lectotype, inadvertently designated by Mickel & Beitel [1988: 180], B [bc] 20-071835 image!; isolectotypes, BR [bc] 00000697192 image!, BR [bc] 00000697171 image!, HAL [bc] 0137800 image!, LE [bc] 00008871 image!, NY [bc] 00149705!, NY [bc] 00334944!, P [bc] P00603624 image!; probable isolectotype, MO-1867272!). Figures 1G, 16, 17.

Plants terrestrial. **Rhizomes** 2–10 mm wide, short-creeping; **rhizome scales** 0.7–1.2(–1.5) mm, scattered, appressed, oblanceolate, with occasional short projections (shorter than width of scale), concolorous, reddish brown to dark brown, sometimes lighter at point of attachment, sclerotic, lustrous, base round or truncate, apex acute to short-filiform. **Sterile leaves** 17–45.5 (–75) cm, approximate; **phyllopodia** present, clearly visible, 5–15(–19) mm; **petioles** 7–12(–18) cm, 1/3–3/5(–3/4) the length of sterile leaves; **larger petiole scales** to 2 mm, scattered to dense, not imbricate, spreading to appressed, linear-lanceolate to lanceolate, with occasional short projections, stramineous, sometimes reddish brown toward apex, base round or truncate, apex acuminate to filiform; **smaller petiole scales** to 1 mm, scattered to dense, not imbricate, mostly appressed, lanceolate, with short or long projections (as long as or longer than width of scale), stramineous, base truncate or round, apex attenuate; **laminae** 10–25(–57) × 1.5–2.8(–3.2) cm, elliptic, papyraceous, base acute, apex acute to acuminate; **adaxial laminar scales** to 1 mm, scattered to dense, not imbricate, deciduous, substellate or lanceolate, when lanceolate, margin with numerous long projections, whitish to yellowish, darker at point of attachment, base auriculate, apex attenuate; **adaxial resinous dots** absent; **abaxial laminar scales** absent, or when present to 0.7 mm, scattered to dense, not imbricate, stellate to irregular, yellowish, sometimes darker at point of attachment;

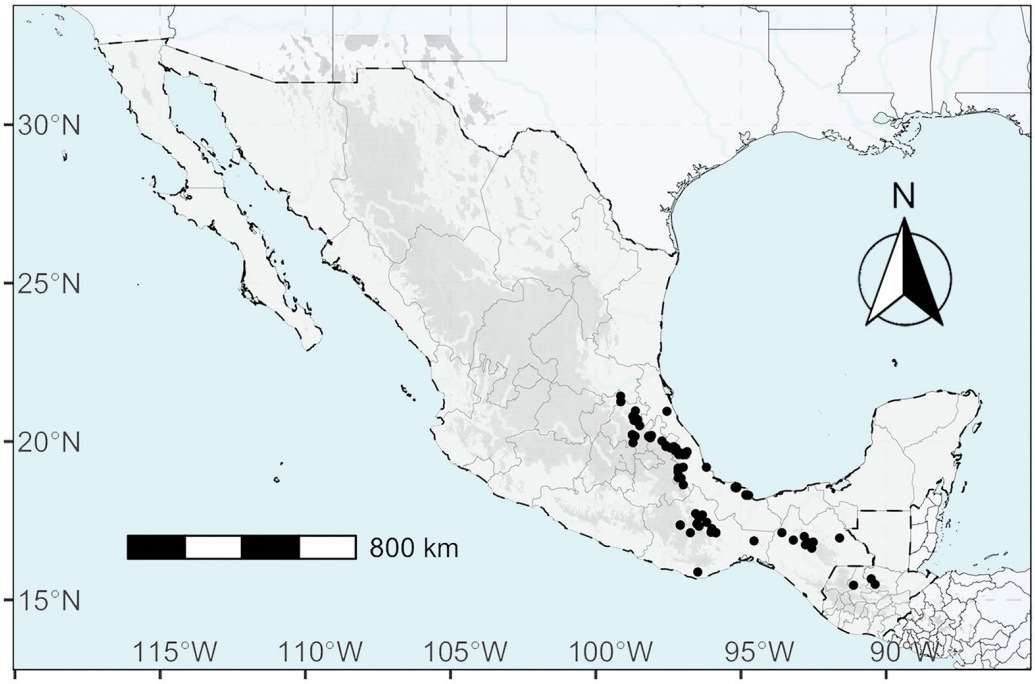

Figure 16. Distribution map of *Elaphoglossum schiedei* (Kunze) T. Moore.

abaxial resinous dots present; **abaxial costal scales** 0.5–1.2(–1.5) mm, scattered to dense, not imbricate, ovate to lanceolate with occasional short projections, stramineous to light brown, base truncate, apex acute to attenuate; **marginal scales** to 0.6 mm, scattered to dense, not imbricate, deciduous, linear-lanceolate or substellate, when linear-lanceolate, margin with numerous long projections, yellowish, base truncate, apex long-attenuate. **Fertile leaves** longer than sterile leaves; **petioles** 1/3–2/3(–3/4) the length of fertile leaves; **laminae** (7.5–)10–18 × (0.3–)0.7–1.3 cm, elliptic, papyraceous, base cuneate, apex obtuse to acute, sometimes apiculate; **petiole scales** to 2 mm, scattered to dense, not imbricate, lanceolate or substellate, when lanceolate, margin with short projections, stramineous to light brown, with darker apex, base round or truncate, apex acuminate or filiform; **adaxial laminar scales** to 0.5 mm, dense, not imbricate, lanceolate or substellate, when lanceolate, margin with numerous long projections or with occasional short projections, yellowish, base truncate, apex attenuate; **abaxial costal scales** to 0.7(–1.8) mm, scattered to dense, not imbricate, lanceolate to oblanceolate or substellate, when lanceolate or oblanceolate, with occasional long projections, yellowish, base auriculate, apex acute to short-filiform. **Perispores** broadly folded, sparsely echinulate.

Habitat and distribution. *Elaphoglossum schiedei* grows in western Guatemala and Mexico (eastern and southern), at elevations of (800–)1400–2700(–3050) m (Fig. 3). It is terrestrial in temperate and pine-oak forests.

Phenology. Fertile specimens have been collected mainly from June to November, with two each from January and March.

Etymology. The specific epithet honors Christian Julius Wilhelm Schiede (1798–1836), a German botanist, gardener, traveler, and plant collector, who arrived in Mexico in 1828 and spent the rest of his life exploring the states of Veracruz (Jalapa and Orizaba) and Morelos (Cuautla and Cuernavaca) (TL-2).

Notes. *Elaphoglossum schiedei* is the only species in the petiolatum clade with glabrescent rhizomes and sclerotic (hard), appressed rhizome scales. Furthermore, the rhizome scales are the smallest (0.7–1.2 mm) and the only ones in the clade that are wider than long. Sometimes the bases of the petioles and their scales densely cover the rhizomes, making it difficult to find the rhizome scales.

Elaphoglossum schiedei was considered a synonym of *E. petiolatum* (Proctor, 1985; Mickel & Beitel, 1988;

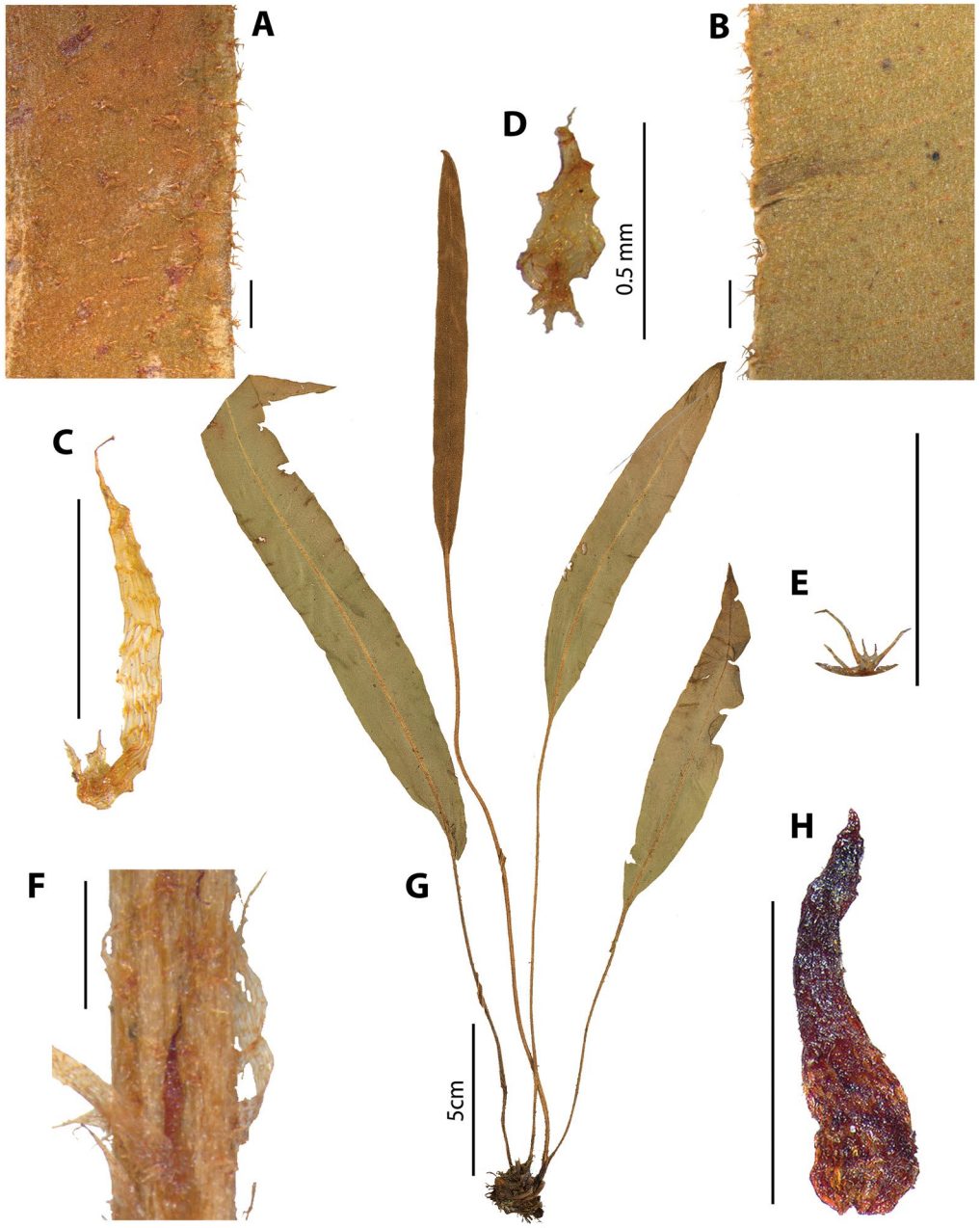

Figure 17. *Elaphoglossum schiedei* (Kunze) T. Moore. —A. Abaxial laminar surface. —B. Adaxial laminar surface. —C. Larger petiole scale. —D. Abaxial costal scale. —E. Marginal scale. —F. Petiole detail. —G. Habit. —H. Rhizome scale. A–F, *Castillo-Campos 19132* (CHAPA); G, *Pringle 13292* (VT); H, *Christ s.n.* (P). All photos from sterile leaves. Scale bars = 1 mm, unless otherwise noted.

Mickel & Smith, 2004); however, morphology supports its recognition as a different species. See *E. petiolatum* for a comparison with this species.

Mickel 4706, *4843*, and *4857* (all NY) from Oaxaca, Mexico, are unusual because they have rhizome scales longer than other specimens typical of the species (up to 1.5 mm), nonshiny resinous dots, and laminar scales substellate abaxially. These specimens otherwise agree with our concept of *Elaphoglossum schiedei* because they have glabrescent rhizomes, and the shape and color

of their rhizome scales are typical of this species. *Standley 92203* (F), from Guatemala, is atypical in presumably having been collected as an epiphyte.

We considered MO-1867272 as a probable isolectotype because it does not have collection data. However, the specimen corresponds to *Elaphoglossum schiedei*, and it could be a collection by Schiede.

Selected specimens examined. GUATEMALA. **Alta Verapaz:** Mpio. San Pedro Carchá, Chamá, 15 Oct. 1920, *H. Johnson 819* (US). **Quiché:** Mpio. Cobán, Chicoyou, 4 Aug. 1936, *Hatch 236* (BRIT, US); Mpio. Nebaj, Valley of Río de las Violetas, N of Nebaj, on mossy stump in oak forest, 1829 m, 25 June 1964, *Proctor 25126* (TEX, US). MEXICO. **Chiapas:** Mpio. Chamula, above San Juan Chamula, ca. 8 mi. from San Cristobal de las Casas, 2200 m, 9 July 1977, *Croat 40671* (MEXU, MO); Mpio. Ocozocuatla de Espinoza, 18–20 km al N de Ocozocuautla en el camino hacia Mal Paso, 800 m, 4 Nov. 1971, *Breedlove 21881* (MEXU, NY); Mpio. San Cristóbal de las Casas, 3 mi. N of San Cristóbal de las Casas on rd. up Cerro Zontehuitz, 2400 m, 27 July 1963, *Mickel 1214* (ENCB, MEXU, NY); Mpio. Zinacantán, along Mexican Hwy. 190 in Paraje Naven-chauk, 2200 m, 14 Nov. 1971, *Breedlove 22411 A* (CHAPA, MEXU, MO, NY, US). **Hidalgo:** Mpio. Mineral del Chico, Plan de Ayacahuite, 29 July 1952, *Sánchez Mejorada 756* (MEXU); Mpio. Omitlán de Juárez, El Carmen, Sep. 1950, *Sánchez Mejorada 407* (MEXU, US); Mpio. Tlalchinol, Km. 170–171 de la Carretera Federal 105, entre Tlalchinol y Tamazunchale, 1200 m, 4 Nov. 2000, *Rojas 5432* (ENCB, MEXU). **Oaxaca:** Mpio. Calpulálpan de Méndez, camino por el Bosque de La Cruz a la Y, 2150 m, 21 Mar. 2016, *Vasco 995* (BRIT, VT); Mpio. Ixtlán de Juárez, 58 km N of Ixtlán, 11 km N of the high point at Cerro Pelón, 2000 m, 27 Oct. 1969, *Mickel 4259* (NY); Mpio. Juchitán de Zaragoza, Santa María Chimalapa, Cerro del Venado, filo entre Río Blanco (O) y la rama E del Río Blanco, ca. 15.5 km en línea recta al ESE de Sta. María, cima del filo, 970 m, 21 Sep. 1986, *Wendt 5563* (CHAPA, NY); Mpio. San Pedro Nolasco, trail from San Pedro Nolasco N to the Llano Verde, 2190 m, 5 Oct. 1969, *Mickel 3840* (ENCB, MEXU, OAX, US); Mpio. Villa Alta, San Juan Petlalpa, trail from Yetzelalag toward Santa María Lovani, 1060 m, 2 Dec. 1971, *Hallberg 1497* (NY). **Puebla:** Mpio. Huachinango, salto de agua a 3 km al sur de Teziutlán, Aug. 1967, *Riba 333* (MEXU); Mpio. Zacapoaxtla, Atocpan, 1800 m, 24 June 1986, *Ventura 22088* (MO, NY); Mpio. Zapotitlán de Méndez, 2 km al NE de Zapotitlán, 800 m, 3 July 1987, *Campos Salas 499a* (MEXU). **Querétaro:** Mpio. Jalpan de Serra, Cañada Las Avispas, al SE de San Juan de los Durán, 1900 m, 3 Apr. 1991, *Díaz-Barriga 6558* (IEB, MEXU); Mpio. Landa de Matamoros, aprox. 7 km al NE de Acatitlán de Zaragoza, 1920 m, 12 July 1988, *Carranza 792* (IEB, MEXU, NY). **Veracruz:** Mpio. Acajete, along Mex. Hwy. 140 through extensive lava flow called "El Volcancillo," 26.5 km by rd. NW of Jalapa, 1.7 km W of La Joya, 2150 m, 19 July 1978, *Diggs 2120* (MEXU, NY); Mpio. Acatlán, 1650 m, 21 July 1973, *Ventura 8666* (CHAPA, IEB, MEXU); Mpio. Atzalán, cerca del panteón, 1600 m, 7 Nov. 1969, *Ventura 10* (ENCB, NY); Mpio. Banderilla, Chaltepec [Xaltepec], 1750 m, 12 Jan. 1970, *Ventura 356* (NY); Mpio. Coscomotepec, Pico Orizaba, ca. 2 km W of Tetelcingo, 2350 m, 26 June 1985, *Luteyn 11674* (MEXU, NY); Mpio. Jalacingo, Arroyo Cobre, 1850 m, 29 Sep. 1977, *Ventura 14525* (CHAPA, MEXU); Mpio. Jilotepec, ca. 1 km N of the main Jalapa–La Joya Rd., 2060 m, 29 July 1976, *Faden & Valdivia 76/47* (F, US); Mpio. Las Vigas de Ramírez, Km. 4 Toxtlacoaya–Perote, 2380 m, 23 Feb. 1999, *Castillo-Campos 19132* (IEB, MEXU); Mpio. Mecayapan, faldas del Volcán Santa Marta, Ejido Plan Agrario, 850 m, 28 Aug. 2006, *Krömer 2872* (MEXU, NY); Mpio. Orizaba, 1865, *Bourgeau 3065* (NY, US); aserradero de Santa Cruz, 1863 [interpreted], Müller 41 (NY [bc] 03231440); Mpio. Pajapan, cima del Volcán San Martín Pajapan, 1125 m, 2 Sep. 2006, *Krömer 2960* (MEXU); Mpio. Xalapa, pedregal near Las Vigas, 22 km NW of Xalapa in moist sunken pit in lava, 2250 m, 23 Dec. 1972, *Barrington 419* (MEXU, NY); Mpio. Zacualpan near Huatusco, Nov. 1906, *Purpus 2350* (F, MO, NY, UC, US); Mpio. Zongolica, Reserva Ecológica La Quinta, Amatitla, 1450 m, 4 Mar. 2008, *Krömer 3080* (MEXU).

8. Elaphoglossum schmitzii (Mett. ex Kuhn) Martínez-Bec. & A. Vasco, comb. nov. *Acrostichum schmitzii* Mett. ex Kuhn, Linnaea 36: 51. 1869. TYPE: Mexico, *W. Schaffner s.n.* (lectotype, designated here, ~~*W. G. Schaffner s.n.*~~, B [bc] 20-0071856 image!; isolectotypes, B [bc] 20 0071857 image!, B [bc] 20 0071858 image!). Figures 1H, 18, 19.

Plants terrestrial or epipetric. **Rhizomes** 1.5–3.5 mm wide, short-creeping; **rhizome scales** 2–4 mm, dense, spreading, linear to lanceolate, entire or with occasional short projections (shorter than width of scale), bicolorous, light brown becoming brown with age, darker at point of attachment and toward apex, dull, base round, apex attenuate to filiform. **Sterile leaves** (11–)14–34(–61) cm, approximate; **phyllopodia** present, clearly visible, 5–10 mm; **petioles** (3.5–)4–17.5 cm, (1/5–)1/4–1/2 the length of sterile leaves; **larger petiole scales** to 2.5 mm, scattered to dense, not imbricate, spreading, linear-lanceolate to lanceolate, with occasional short projections, stramineous, sometimes darker at apex, base round with long projections (longer than width of scale), apex long-attenuate to filiform; **smaller petiole scales** to 1 mm, scattered to dense, not imbricate, mostly appressed, substellate, stramineous; **laminae** (7.7–)11–25.5(–57) × 0.9–1.5(–2) cm; narrowly elliptic, papyraceous or chartaceous, base cuneate, apex acute to acuminate; **adaxial laminar scales** to 0.8 mm, dense, not imbricate, sometimes scattered, substellate, linear-lanceolate to lanceolate, when linear-lanceolate or lanceolate, margin with numerous long projections (as long as or longer than width of scale), stramineous, darker at point of attachment, base truncate with long projections, apex long-attenuate to filiform; **adaxial resinous dots** sometimes present; **abaxial laminar scales** absent, or when present to 1 mm, scattered to dense, not imbricate, linear-lanceolate, with numerous long projections, yellowish, sometimes darker at point of attachment, base truncate with long projections, apex long-attenuate; **abaxial resinous dots** present; **abaxial costal scales** 0.7(–1.5) mm, scattered, lanceolate with occasional short projections, stramineous, base truncate, apex acuminate to

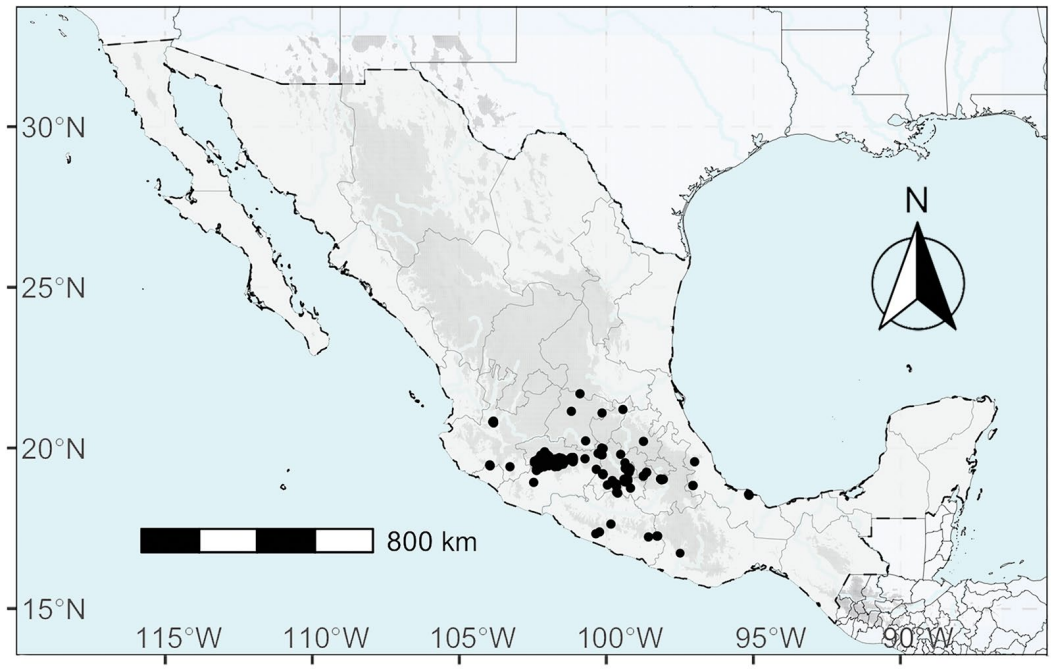

Figure 18. Distribution map of *Elaphoglossum schmitzii* (Mett. ex Kuhn) Martínez-Bec. & A. Vasco.

filiform; **marginal scales** 0.7(–1.2) mm, usually dense, not imbricate, deciduous, oblanceolate or substellate, when oblanceolate, margin with numerous long projections, yellowish, base round or truncate, apex attenuate. **Fertile leaves** longer than sterile leaves; **petioles** 1/2–2/3(–5/7) the length of fertile leaves; **laminae** (5.5–)9–15 × (0.5–)0.8–1.1 cm, narrowly elliptic, papyraceous or chartaceous, base cuneate to attenuate, apex obtuse to acute; **petiole scales** to 2.5 mm, dense, not imbricate, deciduous, linear-lanceolate to lanceolate or substellate, when linear to linear-lanceolate, margin with numerous long projections or with occasional short projections, stramineous, sometimes reddish brown toward apex, base round with long projections or truncate, apex long-attenuate to filiform; **adaxial laminar scales** to 0.7 mm, scattered to dense, not imbricate, lanceolate or substellate, when lanceolate, margin with numerous long projections, yellowish, base truncate with long projections, apex long-attenuate to filiform; **abaxial costal scales** to 1 mm, scattered to dense, not imbricate, deciduous, linear to lanceolate or stellate, when linear or lanceolate, with numerous long projections or with occasional short projections, yellowish, base truncate with long projections, apex attenuate. **Perines** broadly folded, sparsely echinulate.

Habitat and distribution. *Elaphoglossum schmitzii* is endemic to Mexico, at elevations of (609–)1015–2800 m (Fig. 3). It is terrestrial or epipetric in temperate and pine-oak forests. *Breedlove 18691* (NY) from Michoacán is the only collection that occurs at an elevation below 1015 m.

Phenology. Fertile specimens have been collected from July to November, and also one in April.

Etymology. The specific epithet honors Albert Schmitz (fl. 1870s), who collected in Mexico (Clifford & Bostock, 2007). We could not find any additional information about this collector.

Notes. *Elaphoglossum schmitzii* can be distinguished from all other species of the petiolatum clade because the margin of the lamina is thinner and lighter than the rest of the lamina. In contrast, the lamina margins of the other species of the clade have the same color and thickness.

Elaphoglossum schmitzii was considered a synonym of *E. petiolatum* (Proctor, 1985; Mickel & Beitel, 1988; Mickel & Smith, 2004); however, the two species can be distinguished by the size, color, and apex of the rhizome scales, and by the ornamentation of the spores. See *E. petiolatum* for a comparison with this species.

Elaphoglossum schmitzii also can be distinguished from *E. schiedei*, another species previously considered a synonym of *E. petiolatum* (Proctor, 1985; Mickel &

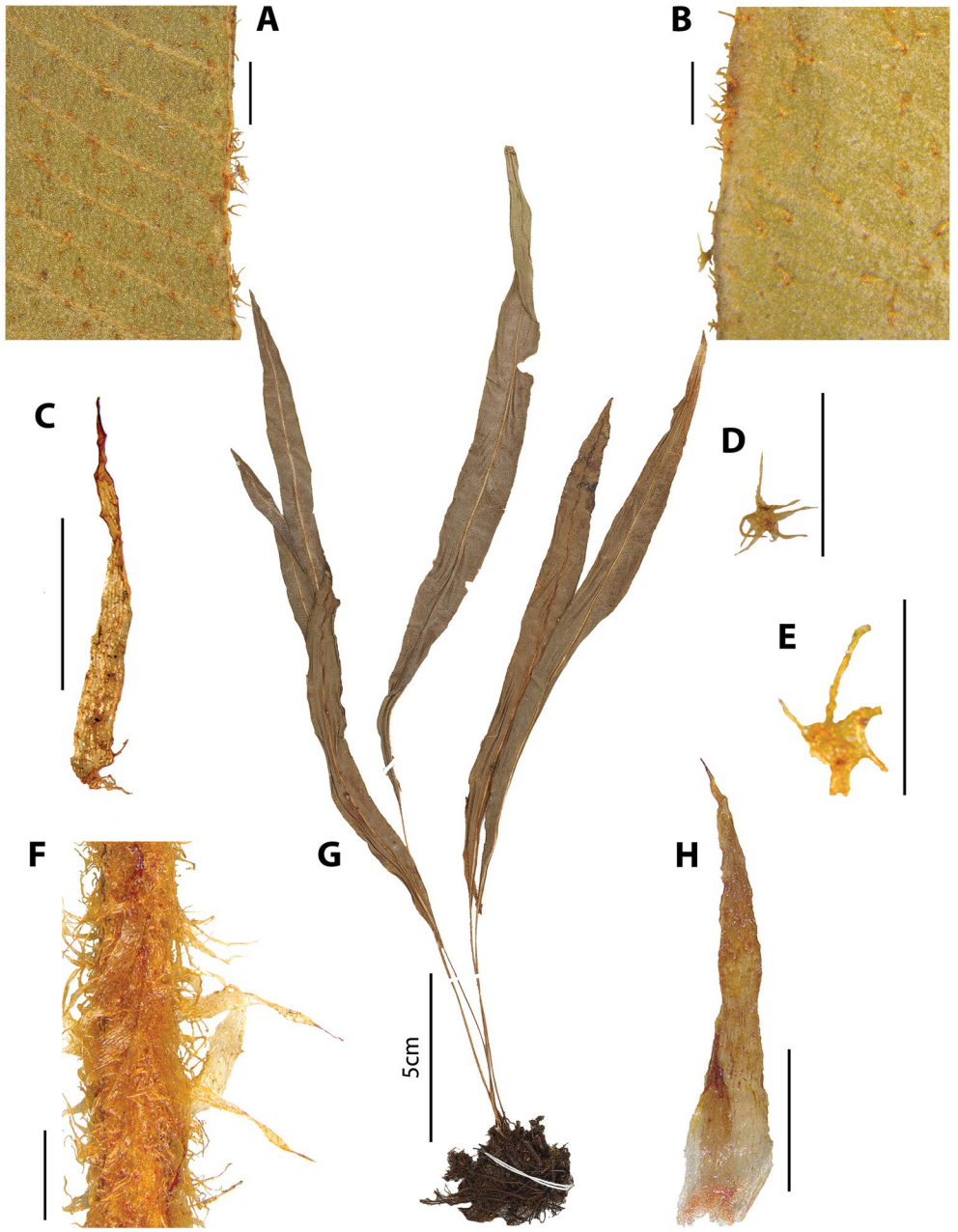

Figure 19. *Elaphoglossum schmitzii* (Mett. ex Kuhn) Martínez-Bec. & A. Vasco. —A. Abaxial laminar surface. —B. Adaxial laminar surface. —C. Larger petiole scale. —D. Abaxial costal scale. —E. Marginal scale. —F. Petiole detail. —G. Habit. —H. Rhizome scale. A, B, D, E, *García 3984* (IEB); C, F, *Rzedowski 45967* (IEB); G, *Burch 2751* (NY); H, *Arsène 8469* (P). All photos from sterile leaves. Scale bars = 1 mm, unless otherwise noted.

Beitel, 1988; Mickel & Smith, 2004), by rhizome scales 2–4 mm, dense, spreading, linear to lanceolate, bicolorous, light brown, not sclerotic, and dull (vs. rhizome scales 0.7–1.2[–1.5] mm, scattered, appressed, oblanceolate, concolorous, reddish brown to dark brown, sclerotic, and lustrous in *E. schiedei*).

Elaphoglossum schmitzii specimens present several variations. The density of resinous dots and of laminar and petiole scales varies greatly in *E. schmitzii*. Some specimens have leaves that are polystichously (radially) arranged, where some of the petioles seem to develop from the ventral side of the rhizome surrounding

them. In other specimens, the rhizome scales are concolorous (apices and margins both brown), instead of the typical bicolorous, light brown becoming brown with age. Some laminae have persistent bases of deciduous scales rather than resinous dots. These persistent bases fall off easily when touched with a dissecting needle. The nonshiny resinous dots of *E. petiolatum* do the same, but unlike the scales of *E. schmitzii*, which have round bases, the nonshiny resinous dots are flat.

Some other atypical specimens of *Elaphoglossum schmitzii* are the following: *Cochrine 12559* (NY) from Jalisco, a large specimen with leaves to 54 cm, laminae to 38 cm, and petioles to 16 cm; and *Rose 7256* (US) from Morelos, with the smallest sterile leaf recorded for this species, 4.4 cm, in contrast with most *E. schmitzii* specimens, which have fertile leaves 14–34 cm. These collections were not incorporated in the descriptions, but we still consider them to be *E. schmitzii* because they are otherwise typical—the scales of the rhizome, petiole, and lamina (including those of the margin) correspond to those described for this species.

In the original description of *Acrostichum schmitzii*, three syntypes are cited: *Karwinski s.n.*, *Schmitz 3* (ex parte), and *Schaffner s.n.* We were unable to find *Schmitz 3* (ex parte) or *Karwinski s.n.* However, we did find three syntypes of *Schaffner s.n.* at B and chose B [bc] 20 0071856 as the lectotype because it was annotated as *A. schmitzii* by Mettenius, the author of the species, and it is in good condition.

Schmitz s.n. B [bc] 20 0071855 is not a syntype because the location on its label differs from the one mentioned in the protologue. *Schmitz s.n.* NY [bc] 00149707, *Schmitz 56a* NY [bc] 00149706, and *Schaffner s.n.* P [bc] P00249994 are not syntypes either because their collection information differs from that stated in the protologue.

Selected specimens examined. MEXICO. **Ciudad de México:** Alcaldía Alvaro Obregón, San Ángel, Oct. 1875, *Schaffner 94* (B, NY); Alcaldía Benito Juárez, Barrancas de Mixcoac, Dec. 1935, *Lyonnet 911* (IEB, MEXU, MO, NY, US); Alcaldía Cuajimalpa Barrancas près Santa Fe, 19 Aug. 1865, *Bourgeau 461* (US); Alcaldía Magdalena Contreras, 9 Aug. 1910, *Orcutt 3528* (F, MO). **Estado de México:** Mpio. Amecameca, Aug. 1855, *Schaffner 248b* (P); 1 km al NE de San Antonio, 2500 m, 29 Sep. 1968, *Rzedowski 26741* (ENCB, NY); Mpio. Chapa de Mota, cerro de las Animas, 2625 m, 24 Oct. 2009, *Trejo Díaz 227* (MEXU); Mpio. Coatepec Harinas, a 3 km de Coatepec Harinas rumbo a Cochisquila, 2050 m, 17 Jan. 1986, *Tejero-Díez 2272* (MEXU); Mpio. Huayanalco, 2700 m, 19 June 2009, *Campos Salas 121* (MEXU); Mpio. Huitzilac, Laguna Tonatihua, Zempoala, a 20 km al NNW del centro de Cuernavaca, 2750 m, 25 July 1989, *Tejero-Díez 3010a* (MEXU, NY); Mpio. Huixquilucan, cerca de Santiaguito, 2500 m, 9 Oct. 1974, *Rzedowski 32262* (IEB, MEXU); Mpio. Jilotzingo, Santa Ana Jilotzingo, 2 km al N de Espíritu Santo, 2250 m, 1 Jan. 1974, *Rzedowski 31628* (IEB); Mpio. Temascalcingo, a 1.53 km al W de San José de los Reyes, Ejido Pueblo Nuevo Solís, cerro Altamirano, 2714 m, 27 Aug. 2014, Álvarez 13618 (MO); Mpio. Valle de Bravo, 1800 m, 17 Sep. 1952, *Matuda 27228* (MEXU, US); Mpio. Villa Guerrero, Km. 54.5 a Villa Guerrero, 2160 m, 6 Sep. 1985, *Tejero-Díez 2148* (MEXU). **Guanajuato:** Mpio. Epitacio Huerta, terrenos próximos a El Tejocote, próximos a Polvillas, 2550 m, 29 Oct. 1990, *Rzedowski 50561* (IEB, NY); Mpio. Jerécuaro, Cañada de Matacrias, Sierra de los Agustinos, 2600 m, 30 Oct. 1987, *Díaz-Barriga 4415* (IEB, MEXU). **Guerrero:** Mpio. Atoyac de Alvarez, Km. 22 del camino Puerto El Gallo–Atoyac, 1700 m, 24 Aug. 1984, *Lorea Hernández 3176* (ENCB, IEB, NY); Mpio. Taxco, Parque Cerro el Huizteco, aproximadamente 4 km al N de Taxco, 2500 m, 1 Oct. 1984, *Lorea Hernández 3252* (ENCB, F); Mpio. Tetipac, 4 km al SE de Tetipac sobre carretera a Taxco, 2000 m, 4 Aug. 1968, *Rzedowski 26032* (NY). **Hidalgo:** Mpio. Zimapan, San Vicente, 2400 m, 8 Aug. 1946, *Fisher 46220* (BRIT, MO, US). **Jalisco:** Mpio. Autlán de Navarro, Sierra de Manantlán, upper W edge of Cerro Grande, a massive limestone plateau 18–50 km NW of Colima, 5.1 km by rd. (4 km airline distance) NNW of El Terreno, 37 km due NW of Colima, 2350 m, 8 June 1991, *Cochrane 12559* (NY); Mpio. Tecatitlán, Sierra del Halo, near a lumber rd. leaving the Colima Hwy. 7 mi. SSW of Tecatitlán & extending southeasterly toward San Isidro, 2000 m, 15 Aug. 1957, *McVaugh 16248* (MEXU, US); Mpio. Tequila, 10 km al sur de Tequila, cerro Tequila, 2400 m, 14 Sep. 1967, *McVaugh 23885* (MEXU); 2 km al W de El Terrero, 2300 m, 28 July 1992, *Santana 5843* (IEB, MEXU). **Michoacán:** Mpio. Charapan, Ojo de Agua, al S de Ocumicho, 2350 m, 23 Jan. 1990, *García 3111* (IEB, NY); Mpio. Cherán, ca. 3 km al WNW de Cherán, 15 Sep. 1992, *Carranza 4179* (IEB, MEXU); Mpio. Ciudad Hidalgo, 20 km al W de Ciudad Hidalgo, sobre la carretera a Morelia, 2250 m, 21 July 1964, *Rzedowski 18402* (NY, US); Mpio. Coalcomán de Vázquez Pallares, Barroloso, 2600 m, 22 Oct. 1939, *Hinton 15368* (MEXU, MO, NY, TEX, US); Mpio. Erongaríacuaro, camino a Zinziro, 2400 m, 22 Aug. 1991, *Escobedo 2072* (IEB, MEXU, NY); Mpio. Ichaqueo, Mexico Hwy. 15, 27 km W of Zacapu, betw. Zamora & Morelia, 2100 m, 27 Aug. 1981, *Yatskievych 81-376* (IND, MO, NY); Mpio. Los Reyes, 3 km al S de Los Reyes, 2750 m, 21 Oct. 1989, *Mejía 50* (ENCB, MEXU); Mpio. Morelia, parte alta del Pico Azul, cerca de San José de las Torres, 2550 m, 25 Nov. 1985, *Rzedowski 45967* (IEB, NY); Mpio. Nuevo Parangaricutiro, sparsely to densely vegetated slopes of lava flow (mal pais) E of San Juan Nuevo (ca. 8 km S of Uruapan), 1850 m, 11 Oct. 1961, *King 4768* (BRIT, MEXU, NY, US); Mpio. Quiroga, along Mexican Hwy. #15, 6.5 mi. NW of Quiroga, 609 m, 2 Nov. 1970, *Breedlove 18691* (NY); Mpio. Salvador Escalante, Agua Verde, 2100 m, 3 Aug. 1986, *Rzedowski 40217* (IEB); Mpio. Tangancícuaro, 11.8 km NW of Tanguancícuaro on rd. to Zacapu, 2100 m, 9 Oct. 1985, *Bartholomew 2830* (CHAPA, MEXU, MO, NY); Mpio. Uruapan, Pedregal al E de Capácuaro, 2400 m, 5 Aug. 1990, *García 3206* (IEB, MO); Mpio. Tancítaro, 2 mi. al S de Tancítaro, 1990 m, 18 Aug. 1940, *Leavenworth 717* (BRIT, F, MICH, MO, NY, US); Mpio. Zitácuaro, Aputzio, 2100 m, 11 Nov. 1938, *Hinton 13445* (ENCB, NY, P, US). **Morelos:** Mpio. Cuernavaca, Santa María Ahuacatitlán, 1800 m, *Sánchez Mejorada 200* (MEXU); Mpio. Huitzilac, Aug. 1930, *Lyonnet 591* (MEXU, NY, US); Mpio. Tepoztlán, shaded ledges, Sierra de Tepoztlán, 2286 m, 11 Sep. 1900, *Pringle 9118* (F). **Oaxaca:** Mpio. Coicoyán de las Flores, Localidad Yuvi Ka'un al SW de Coicoyán, 1 Aug. 1988, *De Avila 335* (MEXU, NY). **Puebla:** Hacienda Alamos rte. de Veracruz, 2170 m, 10 Oct. 1907, *Arsène 1871* (MEXU, US); Rte. de Vera Cruz, 10 Oct. 1907, *Arsène s.n.* (US [bc] 01564858). **Querétaro:** Mpio. Jalpan de Serra, 1–2 km al SW de Barriales, 1480 m, 30 July 1991, *Carranza 3337* (IEB). **Veracruz:** Mpio. Orizaba,

1866, *Bourgeau s.n* (US [bc] 1564835); Mpio. San Andrés Tuxtla, Ejido Barrio Lerdo, Faldas del Volcán San Martín Tuxtla, 1015 m, 12 Aug. 2005, *Krömer 2498* (MEXU).

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Appendix 1. List of collections studied. Numbers in parentheses refer to the species as treated in this revision. Accession (or barcode) numbers are given in brackets for specimens without a collection number. Numbers in bold correspond to type collections. 1. *Elaphoglossum auralolitae*, 2. *Elaphoglossum muelleri*, 3. *Elaphoglossum petiolatum*, 4. *Elaphoglossum potosianum*, 5. *Elaphoglossum pringlei*, 6. *Elaphoglossum rzedowskii*, 7. *Elaphoglossum schiedei*, 8. *Elaphoglossum schmitzii*.

Acebey 2392 (8); **Aguirre** 8 (3); **Alfaro** 706 (3); **Álvarez** 13618 (8); **Anderson** 3740 (2), 3784 (6), 4679 (5), 4778 (5), 12744 (2), 13211 (2); **Argüelles** 1310 (2), 2115 (4); **Arsène** 53 (8), 1871 (8), 5351 (2), 5713 (8), 8469 (8), 9041 (8), s.n. (P [bc] 01631289) (2), s.n. (US [bc] 01564858) (8).

Baez 658 (7); **Ballín** 34 (4); **Balls** 4758 (7); **Barkley** 7395 (8); **Barnes** 102 (7), 439 (4), 440 (4); **Barr** 62-763 (7); **Barringer** 3389 (3); **Barrington** 419 (7), 1732 (5); **Bartholomew** 2830 (8); **Bashor** 705 (6); **Beck** 1169A (8); **Berríos** 97 (2); **Blum** 2405 (3); **Bohs** 1756 (7); **Boom** 599 (7); **Bourgeau** 461 (8), 3065 (7), s.n. (NY [bc] 03354572) (8), s.n. (US [bc] 1564835) (8); **Breedlove** 11145 (3), 17056 (2), 18691 (8), 21881 (7), 22411A (7), 27040 (2), 27676 (7), 32506 (7), 35752 (6), 39271 (8), 45511 (6), 45676 (6), 51828 (7), 60611 (4), 64345 (8), 65109 (3); **Burch** 2751 (8); **Burguer** 6010 (3).

Caballero 215 (3); **Camou** 113 (6); **Campos** 860 (8); **Campos Salas** 56 (8), 67 (4), 67 (8), 121 (8), 128 (8), 130 (8), 499a (7); **Cano** 1 (8); **Carlson** 1389 (5), **Carranza** 792 (7), 3272 (4), 3337 (8), 3532 (4), 4056 (4), 4179 (8), 4368 (4), 5140 (4); **Castillo-Campos** 19132 (7); **Castro-Castro** 3566 (4); **Castañeda Robles** 1363 (8); **Catling** 7241 (3); **Caughlan** 337 (7); **Christenhuz** 3226 (3); **Clotter** 78 (2); **Clute** 312 (3); **Cochrane** 12559 (8); **Collins** 137 (5); **Conrad** 3081 (5); **Contreras** 10920 (3); **Converse** s.n. (US [bc] 2587710A) (2); **Conzatti** 4965 (2); **Copeland** s.n. (MEXU [bc] 1884) (5), s.n. (NY [bc] 3354539) (7), s.n. (NY [bc] 3376687) (1); **Cornejo Tenorio** 777 (8), 1401 (8), 1438 (4), 2119 (4); **Correll** 22972 (6), 28748 (7); **Croat** 26880 (3), 26958 (3), 26996 (3), 40671 (7), 40680 (7), 46005 (7), 46092 (2), 47404 (3); **Cruden** 1185 (5).

Davidse 28350 (3), 37303 (3); **De Avila** 335 (8), 506 (2); **De Poll** 1071 (2); **Díaz** 180 (3); **Díaz-Barriga** 1281 (8), 1470 (8), 3317 (4), 4415 (8), 4684 (4), 5107 (4), 6558 (7), 6643 (7), 6671 (4), 6722 (8), 7094a (4), 7185 (4), 7371 (4); **Diggs** 2120 (7), 2893 (7); **Dyer** 11 (4).

Edwards 849 (2); **Ekman** 1326 (3), 4611 (3); **Ernest** 2371 (5); **Escobedo** 1170 (4), 2072 (8); **Evans** 2702 (3).

Faden & Valdivia 76/47 (7); **Feddema** 2184 (2); **Fernández** 4696 (4); **Figueroa Brito** 299 (5); **Fishbein** 1800 (6), 1819 (6); **Fisher** 3791 (4), 46220 (8), s.n. (NY [bc] 03376692) (4); **Flores** 1462 (2); **Folsom** 4800 (3); **Fonseca** 1667 (2); **Fôrther** 10562 (3); **Fuentes** 541 (6).

Gallardo Hernández 836 (7); **García** 508 (3), 958 (3), 2770 (8), 2974 (8), 3111 (8), 3206 (8), 3261 (5), 3984 (8); **García-Mendoza** 606 (5), 9996a (5); **García Ruíz** 4551 (8), 4684 (8); **Gentry** 2127 (6), 18160 (6); **Gittins** 4189 (3), 4212 (2); **Goldsmith** 41 (2); **Gómez** 21470 (3); **González** 797 (6), 1163 (2); **González-Espinoza** 1596 (7); **González-Medrano** 17496 (4); **González Ortega** 5321 (6); **Grant** 92-01625 (3).

Hallberg 1497 (7), 1811 (5); **Harmon** 3161 (2); **Hatch** 236 (7); **Hellwig** 260 (5), 440 (3); **Hernández** 99 (2), 117 (5), 1461-a (7); **Hernández X.** 551 (4); **Herrera** 3523 (3); **Heyde** 226 (2), 3149 (2), 4098B (2); **Hinton** 1811 (2), 8241 (2), 13445 (8), 14882 (2), 15368 (8), 15613 (8), 22119 (4), 26824 (5), 26828 (5).

Iltis 1382 (4).

Jasso 366 (5), 538 (4); **Jiménez** 210 (3); **Johnson** 548 (3), 819 (7); **Johnston** 1346 (1); **Jones** 508 (6); **Juárez García** 514 (5).

Keil 9190 (7); **Kellerman** 5592 (3), 5944 (3); **Kenoyer** 500 (4); **Kerber** 173a (5); **King** 3391 (3), 4768 (8); **Knobloch** 114 (6), 682 (7), 2212 (5); **Kral** 25687 (6); **Krömer** 2041 (7), 2087 (7), 2247 (7), 2324 (7), 2374 (7), 2498 (8), 2872 (7), 2960 (7), 3080 (7), 3670 (7).

Labat 2516 (8); **Laferriére** 1399 (6); **Leavenworth** 567 (8), 717 (8), 1038 (8); **Lellinger** 660a (3), 950 (3), 1065 (3), 1085 (3), 1632 (3), 1693 (3), 1876 (3); **Lent** 654 (3); **Liebmann** s.n. (US [bc] 591293) (5); **Liogier** 12877 (3); **Little Jr.** 9924 (7), 9964 (3); **Lloyd** 4113 (3), 4134 (3); **López** 1514 (8); **Lorea Hernández** 851 (4), 1403 (6), 2099 (4), 2755 (2), 3148 (6), 3176 (8), 3252 (8), 4358 (6), 4468 (4); **Lorence** 3182 (5), 3630 (5); **Luteyn** 11586 (3), 11674 (7); **Lyonnet** 591 (8), 891 (4), 911 (8), 510900016a (8), 550900011 (2).

Manzanero 1010 (5); **Marcks** 758 (7), 1037 (5); **Martín** 61 (2), s.n. (MO [bc] 2101336) (6); **Martínez** 654 (8), 5644 (5), 18662 (7); **Martínez-Becerril** 399 (4), 405 (6), 406 (6), 407 (6), 408 (6); **Martínez-Cruz** 439 (4), 806 (4), 1186 (8); **Mass** 1517 (3); **Matuda** 1661 (3), 2584 (7), 18067 (3), 20960 (4), 27228 (8), 27734 (8), 32512 (7), 32531 (4), 32811 (2), s.n. (MEXU [bc] 442285) (8); **Maxon** 1170 (3), 2648 (3), 2668 (3), 5212 (3), 8496 (3); **Maya** 2143 (5); **Maysilles** 8427

(6); **McVaugh** 11501 (6), 13474 (8), 14247 (4), 16248 (8), 23885 (8); **Medina-Cota** 3835 (5); **Medina García** 1115 (8), 1952 (8), 2933 (8), 3107 (4); **Mejía** 50 (8); **Mendía** 154 (2); **Mendoza** 1764 (3); **Mexia** 708 (2), 1658 (2); **Meyer** 2806 (4); **Mickel** 776 (2), 801 (5), 822 (5), 855 (5), 896 (5), 1127 (5), 1164 (2), 1188 (5), 1214 (7), 1255 (5), 1278 (5), 1391 (5), 1662 (2), 2499 (3), 2675 (3), 3725 (5), 3737 (3), 3751 (5), 3773 (5), 3803 (7), 3833 (7), 3840 (7), 3866 (5), 3897 (5), 4051 (5), 4057 (5), 4166 (5), 4259 (7), 4391 (7), 4430 (5), 4463 (5), 4478 (5), 4514b (5), 4593 (5), 4605 (7), 4706 (7), 4843 (7), 4857 (7), 4858 (5), 4990 (5), 5017 (5), 5044 (5), 5057 (2), 5249 (5), 5329 (5), 5591 (7), 5615 (5), 6809 (4), 8447 (3), 9217 (3), 9677 (3); **Molina** 22326 (3), 22621 (3), 26145 (3), 26627 (2), 30311 (1); **Montgomery** 85-117 (3); **Moore** 58 (7), 5254 (2), 5323 (7), 5786 (7), 4342 (2); **Moraga** 513 (3); **Morales** 48 (2); **Moran** 2251 (3), 3079 (3), 3310 (3), 5545 (3), 5646 (3); **Moreno** 24747 (2); **Morton** 7316 (3); **Motte** 224 (8); **Müller** 41 (NY [bc] 03231439) (2), **41 (5 parte) (P [bc] P00603618) (2)**, 41 (ex parte) (41 (NY [bc] 03231440) (7); **Münch** 10 (3), s.n. (P [bc] 01405854) (7), s.n. (P [bc] 01405855) (7).

Navarro 16 (2); **Nee** 23537 (7), 32917 (7); **Nesom** 5095 (6), 5624 (6); **Neville Jones** 22578 (8); **Nicolás** s.n. (F [bc] C0620880F) (2); **Norris** 16720 (5).

Oliver 1004 (5); **Orcutt** 3528 (8), 3984 (7); **Ortega Ortiz** 0-510 (7); **Ozment** 53 (2).

Palmer 186 (6), **333 (2)**, 1008 (4); **Parry 1007 (4)**, 1008 (4); **Pennell** 19656 (6), 20094 (2); **Pérez** 88 (8), 231 (8); **Pérez Cálix** 783 (8); **Peterson** 17577 (6); **Pittier** 14065 (3), 14066 (3); **Portillo** 24 (2); **Pringle** 2590 (2), 5402 (2), **5605 (5)**, 9118 (8), 10837 (7), 11766 (2), 11767 (8), 13292 (7), 13703 (7), 15595 (7), s.n. (MEXU [bc] 1886) (4); **Proctor** 5297 (3), 25126 (7), s.n. (P [bc] 01566024) (3); **Purpus** 1589 (8), 1594 (8), 2350 (7), 6190 (3), s.n. (P [bc] 01624430) (7).

Ramamoorthy 4660 (2); **Ramos** 4805 (5); **Ramos Nava** 24 (7); **Rees** 375 (8); **Reina** 96-183 (6), 97-1381 (6), 97-183 (6); **Reveal** 3572 (6); **Riba** 02 (7), 287 (7), 333 (7), 335 (7), 336 (7), 754 (7), 6070 (7); **Rincón** 2711 (7); **Rivera** 1987 (5); **Rivera Reyes** 0921 (7); **Rodríguez López** 57 (4), 187 (4); **Roe** 1594 (2), 2011 (5); **Rojas** 60 (2); **Rojas A.** 1567 (3), 2900 (3), 2921 (3), 3282 (3), 5432 (7); **Rose & Painter** 6508 (2), 7256 (8); **Rovirosa** 851 (2); **Rzedowski** 18402 (8), 21009 (5), 24065 (4), 24310 (2), 26032 (8), **26161 (6)**, 26741 (8), 27339 (4), 31628 (8), 32262 (8), 40217 (8), 40487 (4), 44767 (4), 44913 (8), 45967 (8), 47827 (8), 50561 (8), 50966 (4), 51436 (8).

Saavedra 25 (3); **Sahagún-Godinez** s.n. (NY [bc] 3376699) (6); **Saiki** M-84 (6), M-183 (2); **Salazar** 5905 (4); **Salvatierra** 206 (4); **Sánchez & Morejón** s.n. (HAJB [bc] 80606) (3); **Sánchez García** 242 (8), 340 (8); **Sánchez Martínez** 2164 (7); **Sánchez Mejorada** 145 (7), 200 (8), 246 (8), 407 (7), 802 (8), 756 (7); **Sanders** 1592 (6), 21170 (6), 21191 (6), 22551 (6); **Sandoval** 72 (4); **Sandoval Gutiérrez** 287 (5); **Santana** 5843 (8), 6138 (2), 6298 (8); **Santos Martínez** 1724 (8); **Saynes** 100 (2), 761 (5); **Schaffner J. G. 22 (2)**, 92 (4), 93 (4), 94 (8), 95 (8), 103 (4); **Schaffner W. 77 (4)**, 248b (8), s.n. **(B [bc] B-20-0071856) (4)**, s.n. (MEXU [bc] 1189442) (8); **Schiede** s.n. **(B [bc] B-20-00071835) (7)**, s.n. (MO [bc] 1826639) (7); **Schmitz** s.n. **(B [bc] B-20-0071855) (8)**; **Schneé** s.n. (P [bc] 01464594) (3); **Seiler** 31 (2), 698 (3), 774 (3), 1029 (3); **Siqueiros** 474 (6), 4106 (6); **Skutch** 546 (3); **Smith** 311 (2); **Soto Nuñez** 5836 (8), 13808 (8), 13891 (8), 13988 (8); **Spellenberg** 12004 (6); **Standley** 10011 (3), 25286 (2), 58933 (1), 65835 (2), 69722 (2), 82292 (2), 82299 (3), 82490 (2), 83423 (1), 83894 (3), 85402 (1), 85535 (3), 86178 (1); **Stern** 1112 (3); **Stevenson** 528 (7); **Steyermark** 30919 (2), 35963 (1), 47116 (3), 50481 (2), 51213 (2); **Storer** 133 (7); **Suárez Soria** 66 (8), 95 (8); **Sundue** 102 (5), 3023 (5), 3035 (5), 3058 (5), 3086 (5), 3372 (5); **Swartz s.n. (S [bc] S-R-73) (3)**.

Taylor 236 (3), 332 (7); **Tejero-Díez** 2148 (8), 2228 (8), 2272 (8), 2311 (4), 2511 (8), 2551 (8), 2896 (8), 2914 (2), 2917 (4), 2992 (4), 3010a (8), 3110a, b (8); **Tenorio** 1373 (8), 16528 (2); **Testo** 841 (5); **Torres J.** 85 (2); **Torres L.** 529 (8); **Torres-Colin** 3514 (6), 3515 (6), 7088 (7), 10761 (5), 14657 (4), 15909 (4), 17671 (5); **Trejo Díaz** 227 (8).

Underwood 545 (3), 935 (3), 1673 (3), 3141 (3), 3214 (3).

Valdez 785 (4); **Valerio** 55 (3), 189 (3), A81 (3); **Van Devender** 97-152 (6); **Vasco** 890 (5), 928 (5), 995 (7); **Velasquez** 45 (2); **Velázquez Montes** 1861 (5), 2480 (5), 3650 (8); **Véliz 92.2319 (1)**; **Ventura** 10 (7), 31 (7), 356 (7), 2398 (4), 2545 (4), 7446 (4), 8666 (7), 9565 (4), 10111 (7), 14525 (7), 22088 (7); **Virlet d'Aoust** 2020 (4); **Von Türckheim** II1943 (3), II1945 (3), II2386 (3).

Webster 15879 (8); **Wendt** 4971 (3), 5563 (7); **Wiggins** 13195 (2); **Williams** 22061 (3), 22175 (3), 22656 (1), 22688 (1), 22861 (1), 27065 (1), 41580 (1).

Yatskievych 81-376 (8), 83-143 (5); **Young** 34 (7).

Zamudio 4569 (4), 5464 (4), 11782 (4); **Zanoni** 23302 (3), 27137 (3), 41586 (3), 42858 (3); **Zerón** 0A-1 (4).

Appendix 2. List of species distribution of the petiolatum clade detailing the specific states/departments in which they occur in each country.

1. *Elaphoglossum auralolitae* Martínez-Bec. & A. Vasco. GUATEMALA: Chimaltenango, Escuintla, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Totonicapán.
2. *Elaphoglossum muelleri* (E. Fourn.) C. Chr. EL SALVADOR: San Salvador. GUATEMALA: Baja Verapaz, Chimaltenango, Chiquimula, Guatemala, Huehuetenango, Quiché, Santa Rosa. HONDURAS: Francisco Morazán, Intibucá. MEXICO: Chiapas, Ciudad de México, Colima, Durango, Estado de México, Guerrero, Hidalgo, Jalisco, Michoacán, Nayarit, Oaxaca, Puebla, Querétaro, Sinaloa, Veracruz. NICARAGUA: Nueva Segovia.
3. *Elaphoglossum petiolatum* (Sw.) Urb. COSTA RICA: Alajuela, Cartago, Guanacaste, Heredia, Puntarenas, San José. CUBA: Granma. DOMINICAN REPUBLIC: La Vega, Pedernales, Peravia, San Juan, Santiago. EL SALVADOR: Santa Ana. GUATEMALA: Alta Verapaz, Baja Verapaz, Chimaltenango, Huehuetenango, Quetzaltenango, Sololá, Zacapa. HAITI: Artibonite, Ouest. HONDURAS: El Paraíso, Francisco Morazán, Lempira, Ocotepeque, Santa Bárbara. JAMAICA: Portland, Saint Andrew, Saint Catherine. MEXICO: Chiapas, Guerrero, Oaxaca, Veracruz. NICARAGUA: Jinotega. PANAMA: Chiriquí.
4. *Elaphoglossum potosianum* Christ. MEXICO: Ciudad de México, Durango, Estado de México, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacán, Nayarit, Nuevo León, Oaxaca, Querétaro, San Luis Potosí, Sinaloa, Tamaulipas.
5. *Elaphoglossum pringlei* (Davenp.) C. Chr. MEXICO: Chiapas, Guerrero, Hidalgo, Jalisco, Michoacán, Oaxaca, Veracruz.
6. *Elaphoglossum rzedowskii* Mickel. MEXICO: Aguascalientes, Chihuahua, Durango, Guerrero, Jalisco, Nayarit, Sinaloa, Sonora, Zacatecas.
7. *Elaphoglossum schiedei* (Kunze) T. Moore. GUATEMALA: Alta Verapaz, Quiché. MEXICO: Chiapas, Hidalgo, Oaxaca, Puebla, Querétaro, Veracruz.
8. *Elaphoglossum schmitzii* (Mett. ex Kuhn) Martínez-Bec. & A. Vasco. MEXICO: Ciudad de México, Estado de México, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Oaxaca, Puebla, Querétaro, Veracruz.